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Trophic ecology of large predatory reef fishes: energy pathways, trophic level, and implications for fisheries in a changing climate

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Abstract Large predatory fishes are disproportionately targeted by reef fisheries, but little is known about their trophic ecology, which inhibits understanding of community dynamics and the potential effects of climate change. In this study, stable isotope analyses were used to infer trophic ecology of a guild of large predatory fishes that are targeted by fisheries on the Great Barrier Reef, Australia. Each of four focal predators (*Plectropomus leopardus*, *Plectropomus maculatus*, *Lethrinus miniatus* and *Lutjanus carponotatus*) was found to have a distinct isotopic signature in terms of $\delta^{13}C$ and $\delta^{15}N$. A two-source mixing model (benthic reef-based versus pelagic) indicated that *P. leopardus* and *L. miniatus* derive the majority (72 and 62 %, respectively) of their production from planktonic sources, while *P. maculatus* and *L. carponotatus* derive the majority (89 and 74 %, respectively) of their production from benthic reef-based sources. This indicates that planktonic production is important for sustaining key species in reef fisheries and highlights the need for a whole-ecosystem approach to fisheries management. Unexpectedly, there was little isotopic niche overlap between three of four focal predators, suggesting that inter-specific competition for prey may be low or absent. δ^{15}Nitrogen indicated that the closely related *P. leopardus* and *P. maculatus* are apex predators (trophic level > 4), while $\delta^{13}C$ indicated that each species has a different diet and degree of trophic specialisation. In view of these divergent trophic ecologies, each of the four focal predators (and the associated fisheries) are anticipated to be differentially affected by climate-induced disturbances. Thus, the results presented herein provide a useful starting point for precautionary management of exploited predator populations in a changing climate.

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Introduction

Trophic interactions can have profound influences on demography, habitat structure and fishery yields (Myers et al. 2007; Estes et al. 2011) and thus are a cornerstone of community ecology and a fundamental consideration for ecosystem-based management. Food webs provide a useful framework to understand trophic interactions because they depict important trophic properties such as diet, source of primary production (e.g. algae, phytoplankton, coral) and trophic level (TL), which is a continuous measure of the number of energy transfers from producer to consumer (herbivore TL = 2, predator TL = 3–5). Sound knowledge of trophic interactions is imperative for defining species' roles within ecological communities (Ginzberg and Arditi 2012), assessing the implications of harvesting key functional groups such as apex predators (Heithaus et al. 2008), and evaluating the sustainability of multispecies fisheries (Pauly and Watson 2005). Despite these important applications, the trophic ecology of many exploited fishes remains

poorly understood, which inhibits awareness of community dynamics and limits capacity for ecosystem-based management.

Marine apex predators are large fishes and sharks that occupy the top level of food webs (TL > 4). They often have disproportionate influences on ecosystem properties via 'top-down' control of prey abundance and behaviour (Heithaus et al. 2008; McCauley et al. 2010). In some cases, altering the density of apex predators invokes community-wide trophic cascades that involve multiple intervening trophic levels. In the north-west Atlantic, for example, over-fishing of large sharks caused the 'release' of cownose ray, which led to increased predation on scallops and, ultimately, collapse of a scallop fishery (Myers et al. 2007). Depletion of apex predators can therefore have far-reaching, detrimental consequences that threaten the supply of fisheries resources and the human livelihoods that depend on them.

Due to the intensifying worldwide decline of coral reefs (Hughes 1994; Bruno and Selig 2007; De'Ath et al. 2013), there is an urgent need to improve management of local and regional anthropogenic pressures such as fishing in order to strengthen reef resilience and to offset the effects of increasing global pressures such as climate change (Hughes et al. 2010). The contribution of large predatory fishes to maintenance of reef resilience is unclear (Heithaus et al. 2008; Nystrom et al. 2008), but is potentially very important. Recently, it was demonstrated that protected reefs (which have higher density of large predatory fishes than do fished reefs) suffer fewer outbreaks of coral-eating starfish and coral disease (Sweatman 2008; Raymundo et al. 2009). Thus, a better understanding of large predatory fishes and their ecological functions is imperative for guiding management actions that aim to preserve or enhance ecosystem resilience.

Reef fisheries tend to remove a disproportionate quantity of large predators relative to other trophic groups (Dalzell 1996; Bellwood et al. 2004). As a result, fishing has severely reduced the densities of large predators such as groupers (Epinephelidae), emperors (Lethrinidae) and snappers (Lutjanidae) in many parts of the world (Huntsman et al. 1999; Sadovy 2005). Little is known about the trophic ecology of these fishes, which makes it difficult to understand the dynamics of reef communities and to predict the broader ecological consequences of reef fishing. Hence, the objective of this study was to define, using stable isotope analysis, the trophic ecology of a guild of dominant predatory fishes (groupers, emperors, snappers) that are targeted by reef fisheries. In particular, we sought to (1) estimate the contributions of pelagic versus reef-based sources of primary production that support targeted predatory fishes, (2) estimate TL of targeted predatory fishes and thus identify potential 'apex' predators (TL > 4) and

(3) define the trophic niche of targeted predatory fishes and thus evaluate the potential for dietary overlap (Vaudo and Heithaus 2011). Integration of this information will provide insights into the dependency (or lack thereof) of reef fisheries on reef-based primary producers (e.g. coral and macroalgae), which are forecast to undergo radical demographic changes in the near future due to global warming and ocean acidification (Hoegh-Guldberg et al. 2007).

Australia's Great Barrier Reef (GBR) supports an extensive line-fishery involving up to 369 licensed commercial motherships and up to 80,000 registered recreational vessels (Lunow and Holmes 2011; Taylor et al. 2012). Although >100 species are harvested, most of the catch is comprised of leopard coral trout, *Plectropomus leopardus* (~50 %); bar-cheek coral trout, *Plectropomus maculatus* (~10 %); red-throat emperor, *Lethrinus miniatus* (~15 %); and stripey snapper, *Lutjanus carponotatus* (~10 %) (Frisch et al. 2008; Welch et al. 2008). These four species are dominant predators, both at the GBR and at many other reefs in the Indo-Pacific region (Williams and Hatcher 1983; Blaber et al. 1990; Newman et al. 1997; Watson et al. 2009). At some locations, coral trouts are the largest conspicuous predators, thereby prompting some authors to assume they are apex predators (Goeden 1982; Huntsman et al. 1999). Although limited information is available regarding the diets of coral trouts and other targeted species, nothing is known about the ultimate source of primary production (reef or pelagic), and it is yet to be demonstrated whether coral trouts are indeed apex predators (TL > 4). For these reasons, *P. leopardus*, *P. maculatus*, *L. miniatus* and *L. carponotatus* constitute the foci of the present study (i.e. the focal predators). Due to the broad geographic distributions of these species, our results will serve as a useful model to explore the trophic ecology of predatory fish communities on coral reefs throughout the Indo-Pacific region and elsewhere.

Materials and methods

Method selection

The classical approach to trophic ecology has been stomach content analysis, but this method provides only a snapshot of an individual's diet over a short time period and is biased by a range of factors such as differential rates of digestion (Baker et al. 2013). To provide a more comprehensive and long-term view of trophic ecology, scientists are increasingly utilising stable isotope analysis, which is based on the concept that stable isotopes such as ^{15}N and ^{13}C pass from producers to consumers through food webs such that the isotopic signature of consumers relates to that of their prey (Fry 2006). Relative abundance of ^{13}C to ^{12}C

(δ^{13}C) changes little from prey to predator, whereas relative abundance of ^{15}N to ^{14}N (δ^{15}N) increases by 3–4 ‰ per TL (Sweeting et al. 2007a, b). Thus, δ^{13}C is considered to represent the ultimate source of primary production in a food web, and δ^{15}N provides an index of TL relative to that of another organism, such as a producer (TL = 1), herbivore (TL = 2) or herbivore predator (TL = 3). The combined measurement of δ^{13}C and δ^{15}N in tissue samples of key species thus provides an integrated food web perspective of diet, TL and source of primary production. For these reasons, we inferred trophic ecology of focal species on the basis of δ^{15}N and δ^{13}C.

Study site and sample collection

The study was conducted in April 2012 at Northwest Island (23°18′S, 152°43′E), which is a coral atoll in the southern section of the GBR (for a map of the study area, see Frisch 2007). Adjacent to the island is a central sandy lagoon (~2,000 ha) that is surrounded by a well-developed coral reef, beyond which the seafloor is flat and sandy. The reef is ~90 km from the mainland coast, so terrestrial nutrient and sediment input are low, except for rare pulses during major flood events on the mainland (Devlin and Brodie 2005). Although Northwest Island is a popular fishing destination, the fish and coral communities are largely intact, with little evidence of major disturbances (such as coral bleaching and *Acanthaster* outbreaks) during recent decades (authors' pers. obs.). This suggests that trophic interactions and energy pathways at the study site are suitably representative of a functional coral reef. For a detailed description of the structure and diversity of fish and coral communities on mid-shelf reefs of the GBR, see Done (1982), Williams and Hatcher (1983) and Newman et al. (1997).

Plectropomus leopardus, *P. maculatus* and *L. carponotatus* typically inhabit shallow (1–20 m) reef areas with high coral cover and topographic complexity (Connell and Kingsford 1998; Kingsford 2009), whereas *L. miniatus* has a broader habitat distribution that extends to low-relief shoals (5–40 m) (Cappo et al. 2007). In most parts of the GBR, *P. leopardus* and *P. maculatus* do not co-exist (Williams and Hatcher 1983; Frisch and van Herwerden 2006), presumably due to strong niche-based competition. Northwest Island therefore provides unique opportunity to investigate trophic mechanisms that facilitate coexistence of these apparently ecologically equivalent species. The diet of *P. leopardus* has been well defined and is dominated by pomacentrids, labrids, scarids and caesionids (Kingsford 1992; St John 1999; St. John et al. 2001), but only limited data exist for *L. carponotatus* (Connell 1998) and *L. miniatus* (Walker 1978; Kulbicki et al. 2005), and no data exist for *P. maculatus*. On the basis of the available dietary information, we selected a broad spectrum of potential prey and primary producers from both pelagic and reef habitats (Table 1). Each trophic group was comprised of a single species, except where logistical constraints rendered it necessary to collect multiple species. Herbivores were divided into scrapers and grazers, the former being parrotfish (*Scarus rivulatus*), which feed on turf algae (Choat 1991) and the latter being a combination of unicornfish (*Naso unicornis*) and rabbitfish (*Siganus doliatus*), which feed on macroalgae and (to a lesser extent) turf algae (Mantyka and Bellwood 2007; Hoey and Bellwood 2009). Surface phytoplankton was used to characterise the base of pelagic food webs, whereas coral, algae and microphytobenthos (MPB) were used to characterise the base of reef-associated food webs. Pelagic planktivores and pelagic predators were collected at the outer edge of the coral reef. All other organisms were collected on the forereef (sensu Hopley 2008). Sample sizes and body sizes are listed in Table 1. Although ontogenetic diet shifts occur in many reef fishes including *P. leopardus* (St John 1999, Greenwood et al. 2010), we deliberately targeted large individuals of focal predators to ensure that our results were relevant to reef fisheries.

Approximately 1 cm^3 of white muscle tissue was collected from the anterior dorsal region of fish or the chelae of crustaceans, and care was taken to ensure that shell, bone and connective tissue was excluded from the sample. White muscle was selected for analysis due to its low lipid content and low variance in both δ^{13}C and δ^{15}N relative to other tissue types (Pinnegar and Polunin 1999). Plankton was collected using a 63 µm net that was towed horizontally at the surface (5 min at ~30 m min^{-1}) in calm weather during high tide, thereby minimising contamination with suspended sediment and organic matter. Plankton was filtered consecutively with 500-, 250- and 63-µm sieves to separate large (250–500 µm) and small (63–250 µm) fractions, which were subsequently defined as zooplankton and phytoplankton, respectively (Abrantes and Sheaves 2009). Microphytobenthos mats were collected from the surface of sandy substrate using a spatula, taking care to minimise contamination with sediment. Each sample was placed in a capped plastic bottle with ~500 ml of seawater and shaken vigorously to suspend MPB, which were subsequently collected using a 63-µm sieve. Coral and algae samples consisted of pieces or fragments (2–5 cm in length) that were collected from different colonies or thalli (respectively) using a wire cutter or forceps. All samples were stored frozen (−20 °C) until further analysis.

Laboratory processing and isotope analyses

Coral tissue was removed from its carbonate skeleton using a jet of water from a waterpik (Waterpik, Fort Collins, USA). Microphytobenthos samples were resuspended

Table 1 Putative functional groups and sample metrics of focal predators, representative prey and primary producers that were collected at Northwest Island, Australia

Taxa	Putative trophic group	Abbreviation	Known prey of…	Sampling method	No. of samples	Mean body size $\pm$ SE (mm L_t)	Range of body sizes (mm L_t)
Plectropomus leopardus	Large predator	Pleo	–	Spearfishing	10	509 $\pm$ 25	410–645
Plectropomus maculatus	Large predator	Pmac	–	Spearfishing	10	501 $\pm$ 14	440–580
Lethrinus miniatus	Large predator	Lmin	–	Angling	10	418 $\pm$ 06	395–450
Lutjanus carponotatus	Large predator	Lcar	–	Spearfishing	10	326 $\pm$ 03	310–345
Scombridae (mostly *Scomberomorus commerson*) and Carangidae	Large pelagic predator	PPr	–	Angling	9	800 $\pm$ 102	478–1030
Labridae (*Thalassoma lunare*)	Small demersal predator	SDP	*P. leopardus*	Spearfishing	10	164 $\pm$ 11	103–210
Chaetodontidae (*Chaetodon rainfordi, Chaetodon baronessa*)	Coralivore	Crv	–	Spearfishing	10	92 $\pm$ 4	82–108
Caesionidae (*Pterocaesio marri, Caesio cuning*)	Pelagic planktivore	PPl	*P. leopardus*	Spearfishing	10	206 $\pm$ 20	105–310
Pomacentridae (*Acanthochromis polyacanthus, Pomacentrus moluccensis*)	Demersal planktivore	DPl	*P. leopardus*	Spearfishing	10	78 $\pm$ 7	60–110
Crustacea (portunid and xanthid crabs)	Omnivore	Omn	*L. miniatus*	By hand	10	49 $\pm$ 4[b]	37–84[b]
Scaridae (*Scarus rivulatus*)	Herbivore (turf scraper)	HSc	*P. leopardus*	Spearfishing	10	304 $\pm$ 5	274–328
Siganidae (*Siganus doliatus*) and Acanthuridae (*Naso unicornis*)	Herbivore (macroalgal grazer)	HGr	–	Spearfishing	9	256 $\pm$ 4	135–460
Zooplankton	Pelagic herbivore	Zoo	Planktivores	Tow net	4[a]	–	0.25–0.50[c]
Phytoplankton	Pelagic producer	Phy	Zooplankton	Tow net	3[a]	–	0.063–0.25[c]
Microphytobenthos	Producer	MPB	–	Spatula	3[a]	–	–
Coral (*Acropora* spp.)	Producer	Cor	Coralivores and herbivores (scrapers)	By hand	8[a]	–	–
Macroalgae (*Sargassum, Caulerpa*)	Producer	Mac	Herbivores (grazers)	By hand	10	–	–
Turf algae	Producer	Trf	Herbivores (scrapers)	By hand	4[a]	–	–

Diets of large predators are based on stomach content analyses, as per St John (1999), Walker (1978) and Connell (1998). Diets of other groups are reported by Cole et al. (2008) and Choat (1991)

[a] Each sample consisted of many individuals

[b] Carapace width

[c] Presumed range of body sizes based on mesh size of plankton net

in deionised water and centrifuged (5 min at 3,000 g) to remove sediment. Sediment and debris were removed from all other samples by thorough rinsing in deionised water. All samples were subsequently oven-dried (60 °C for 48 h) and grounded to a fine powder using a mortar and pestle. A small subsample of non-fish samples was tested for presence of carbonates by adding three drops of 1 M hydrochloric acid. If effervescence was visible, acid was slowly added to half of the remaining sample until effervescence ceased, followed by oven-drying. For acid-treated samples (i.e. phytoplankton and turf algae), $\delta^{13}C$ was measured in the acid-treated subsample and $\delta^{15}N$ was measured in the untreated subsample (Pinnegar and Polunin 1999).

Samples were weighed to the nearest 0.001 g, and isotope content was measured using a continuous-flow isotope ratio mass spectrometer (Delta V Plus, Thermo Finnigan, Sydney, Australia) coupled to an elemental analyser (ECS 410, Costech Analytical Technologies, Valencia, USA) at the Advanced Analytical Centre, James Cook University, Australia. Results are expressed as parts per thousand (‰)

deviation from Peedee belemnite (vPDB) and atmospheric nitrogen standards for $\delta^{13}C$ and $\delta^{15}N$, respectively (Pinnegar and Polunin 1999). Experimental precision (standard deviation of replicates of internal standard) was 0.1 ‰ for $\delta^{13}C$ and 0.2 ‰ for $\delta^{15}N$.

Lipids are depleted in ^{13}C relative to proteins, so excessive lipid content in animal tissues may bias stable isotope analysis (Post et al. 2007). However, white muscle of fish is typically low in lipid content (Pinnegar and Polunin 1999), so lipid removal was deemed unnecessary. Nonetheless, if the C:N ratio (an indicator of lipid content) of a fish sample exceeded 3.5, then normalisation of $\delta^{13}C$ was achieved using the method of Post et al. (2007): adjusted $\delta^{13}C$ = measured $\delta^{13}C$—3.32 + 0.99 × C:N ratio.

The range of C:N ratios was 3.0–4.2 for *P. leopardus*, 3.0–3.8 for *P. maculatus*, 3.0–3.7 for *L. miniatus* and 3.0–3.3 for *L. carponotatus*, suggesting that lipid content was uniformly low and unlikely to generate marked variation in $\delta^{13}C$ between groups. The resulting corrections to $\delta^{13}C$ were 0.84, 0.44 and 0.34 ‰ or less for *P. leopardus*, *P. maculatus* and *L. miniatus,* respectively, which were approximately an order of magnitude smaller than differences in $\delta^{13}C$ between focal predators (on the order of 3–5 ‰, see below), suggesting that normalisation for lipid content would have little influence on overall results. Nonetheless, it is acknowledged that lipid correction models may be species specific and may produce biased estimates of $\delta^{13}C$ in some circumstances (Mintenbeck et al. 2008; Fagan et al. 2011). Therefore, we present both corrected and uncorrected data in the 'Results' section. Normalisation was not required for marine primary producers because they do not store large quantities of lipid.

Data analyses

To estimate the contributions of pelagic versus reef-based sources of primary production that support focal predators, we used a two-source mixing model with the most ^{13}C-depleted *Scomberomorus commerson* (Spanish mackerel) and the least ^{13}C-depleted *P. maculatus* as end members. The former is a well-known pelagic piscivore that predominantly eats pelagic fishes such as engraulids and clupeids (Blaber et al. 1990; Farmer and Wilson 2011). The latter is a coral reef specialist whose distribution is strongly linked to live coral cover (Evans et al. 2010; Frisch et al. 2012). Notwithstanding this, *P. maculatus* was selected retrospectively as an end member because of its enriched $\delta^{13}C$ signature relative to all other focal predators. Similarity of $\delta^{13}C$ signatures between large predators and potential food sources was considered to indicate consumption of the respective source by the predator (Hussey et al. 2011; McCauley et al. 2012).

To estimate TL on the basis of $\delta^{15}N$, it was first necessary to define any systematic covariation between $\delta^{13}C$ and $\delta^{15}N$ among trophic groups (Abrantes and Sheaves 2010). To do this, trophic groups were aggregated into three broad trophic positions: primary producers, intermediate consumers and large predators. Due to uncertainty in the TL of some groups (e.g. omnivores and corallivores), all trophic groups other than primary producers and large predators were categorised as intermediate consumers. The significance and consistency of relationships between $\delta^{15}N$, $\delta^{13}C$ and trophic position were evaluated by analysis of covariance (ANCOVA), with mean $\delta^{15}N$ as the dependent variable, trophic position as the fixed factor and $\delta^{13}C$ as the covariate. Within each trophic position, the significance and consistency of relationship between $\delta^{15}N$ and $\delta^{13}C$ were evaluated by separate least-squares regression analyses, with $\delta^{15}N$ as the dependent variable and $\delta^{13}C$ as the independent variable (Abrantes and Sheaves 2010).

Trophic level (TL) of focal predators was estimated using the equation

$$TL = \lambda + \left(\delta^{15}N_{predator} - \delta^{15}N_{base} \right) / \Delta_n,$$

where λ is the TL of the base group, $\delta^{15}N_{predator}$ and $\delta^{15}N_{base}$ are the direct estimates of mean $\delta^{15}N$ in each focal predator and base group, respectively, and Δ_n is the enrichment of $\delta^{15}N$ per trophic level (Estrada et al. 2003). The latter was assumed to 3.2 ‰ based on mean fractionation of $\delta^{15}N$ in white muscle tissue of fish (Sweeting et al. 2007a). To acknowledge uncertainty in $\delta^{15}N_{base}$, we estimated TL of focal predators using several different base groups: primary producers (pooled macroalgae and turf algae), herbivores (pooled scrapers and grazers), a small demersal predator (*Thalassoma lunare*) and a large pelagic predator (*Scomberomorus commerson*). Coral and phytoplankton were excluded from estimation of primary producer $\delta^{15}N_{base}$ because the former is not strictly an autotroph and the latter may be contaminated with zooplankton. Base trophic levels (λ) of primary producers and herbivores were assumed to be 1 and 2, respectively, and λ of *T. lunare* (3.65) and *S. commerson* (4.47) were derived from the literature (Farmer and Wilson 2011). Due to differences in $\delta^{13}C$ between focal predators and base groups, values of $\delta^{15}N_{predator}$ were adjusted using the regression formula derived from the linear relationship between $\delta^{15}N$ and $\delta^{13}C$ of large predators (see below). To calculate mean TL, each estimate of TL was weighted according to λ (rounded down to the nearest integer), because uncertainty increases with each trophic step due to potential error in diet-tissue fractionation of $\delta^{15}N$ (Sweeting et al. 2007a).

Isotope data were plotted in $\delta^{13}C$–$\delta^{15}N$ space ('isotopic niche space') to enable computation of isotopic metrics. Total area occupied by each species is a proxy for the

isotopic trophic diversity within that species and was calculated as the area of the convex hull that encompasses all individuals (Vaudo and Heithaus 2011). Total area was then used to calculate the percentage of each hull that was non-overlapping (unique) and the proportion of individuals in unique space. Convex hull area and overlap were calculated manually by dividing the hull into multiple triangles and then determining the constituent areas via Heron's formula:

$$A = 0.25\sqrt{(4a^2b^2 - (a^2 + b^2 - c^2)^2)}$$

where a, b and c are the lengths of the three sides. The degree of hull overlap was considered to be indicative of the degree of niche overlap and the potential for trophic competition. To identify isotopically distinct groups, cluster analysis was applied to mean $\delta^{13}C$ and $\delta^{15}N$ of each trophic group (Ward's minimum variance method based on squared Euclidean distances).

Isotopic signatures ($\delta^{15}N$ and $\delta^{13}C$) of focal predators were compared using separate one-way analysis of variance (ANOVA) followed by Tukey's HSD test to identify significantly different groups. For each ANOVA, the relevant assumptions were checked using probability plots (for normality) and Levene's test (for homogeneity of variance). In cases where nonparametric data could not be stabilised by transformation, group medians were compared using Kruskal–Wallis (K–W) tests. All statistical analyses were performed using SPSS computer software (SPSS, Chicago, USA), and a significant difference was considered to exist if $p < 0.05$. All data in the text and figures are presented as the arithmetic mean ± one standard error (SE), unless otherwise stated.

Results

Forty-nine large predators, 73 intermediate consumers and 28 primary producers were analysed for $\delta^{13}C$ and $\delta^{15}N$. Trophic groups were broadly distributed throughout $\delta^{13}C$–$\delta^{15}N$ space (Fig. 1), indicating a broad range of TLs and potential food sources. Mean $\delta^{13}C$ ranged from -9.43 ± 0.92 ‰ in coral to -21.67 ± 0.09 ‰ in phytoplankton, and mean $\delta^{15}N$ ranged from 2.48 ± 0.20 ‰ in turf algae to 11.67 ± 0.18 ‰ in *S. commerson*. There were significant differences in the distribution of $\delta^{13}C$ among primary producers (Kruskal–Wallis test, $H_4 = 16.16$, $p = 0.003$) and intermediate consumers (Kruskal–Wallis test, $H_7 = 54.65$, $p < 0.001$), which makes it possible to infer major trophic pathways and origins of primary production. In general, organisms that were known to participate in pelagic food webs (e.g. phytoplankton and *S. commerson*) were well separated in bivariate space from organisms that were known to participate in reef-based food webs (e.g. coral and corallivores) (Fig. 1). Cluster
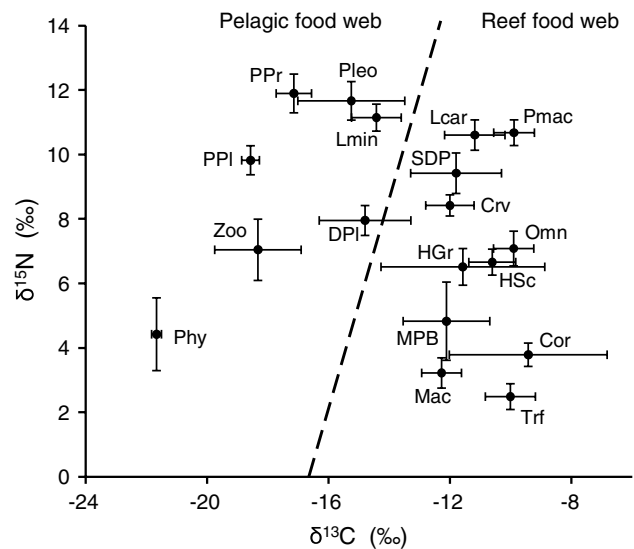

Fig. 1 $\delta^{13}C$ and $\delta^{15}N$ signatures of large predators, potential prey and ultimate sources of primary production. Data points are group means, and *error bars* are standard deviations. Abbreviations are defined in Table 1. *Dashed line* depicts the hypothesised division between pelagic and reef-based food webs (slope of line is 3.2/1.5 due to differential fractionation of $\delta^{15}N$ and $\delta^{13}C$; Sweeting et al. 2007a, b)

analysis identified two major trophic groupings (reef and pelagic) and two minor trophic groupings (consumer and producer), based on the distribution of 'known' trophic groups (Fig. 2). *Plectropomus leopardus* and *L. minatus* were grouped with pelagic consumers, and *P. maculatus* and *L. carponotatus* were grouped with reef-based consumers.

Among focal predators, mean $\delta^{13}C$ was most depleted in *P. leopardus* and least depleted in *P. maculatus* (Fig. 3). Differences in $\delta^{13}C$ between focal species were statistically significant (ANOVA, $F_{3,36} = 50.33$, $p < 0.001$), suggesting consumption of different food sources. According to the mixing model, *P. leopardus* and *L. miniatus* derive the majority of their food sources from pelagic food webs, which are driven by primary producers such as phytoplankton. In contrast, *P. maculatus* and *L. carponotatus* derive the majority of their food sources from reef-based food webs, which are driven by benthic primary producers such as coral and algae (Table 2).

There was a negative trend in the relationship between $\delta^{13}C$ and $\delta^{15}N$ across the three broad trophic positions (Fig. 4). ANCOVA indicated that this trend was not significant ($F_{1,14} = 3.78$, $p = 0.072$), but there was a significant positive effect of trophic position on $\delta^{15}N$ ($F_{2,14} = 76.10$, $p < 0.001$). In all cases, primary producers had the lowest mean $\delta^{15}N$ and large predators had the highest mean $\delta^{15}N$ (Fig. 4). In contrast to the ANCOVA results, the negative relationship between $\delta^{13}C$ and $\delta^{15}N$ in large predatory fishes was significant (Linear regression, $r^2 = 0.91$,

Fig. 2 Bivariate cluster analysis of $\delta^{13}C$ (an indicator of food source) and $\delta^{15}N$ (an indicator of trophic level) in large predatory fishes, potential prey and primary producers that were collected at Northwest Island. Two major clusters (reef and pelagic food webs) and two minor clusters (producers and consumers) are apparent
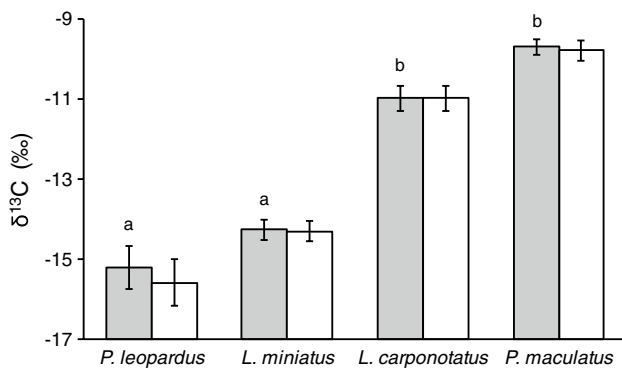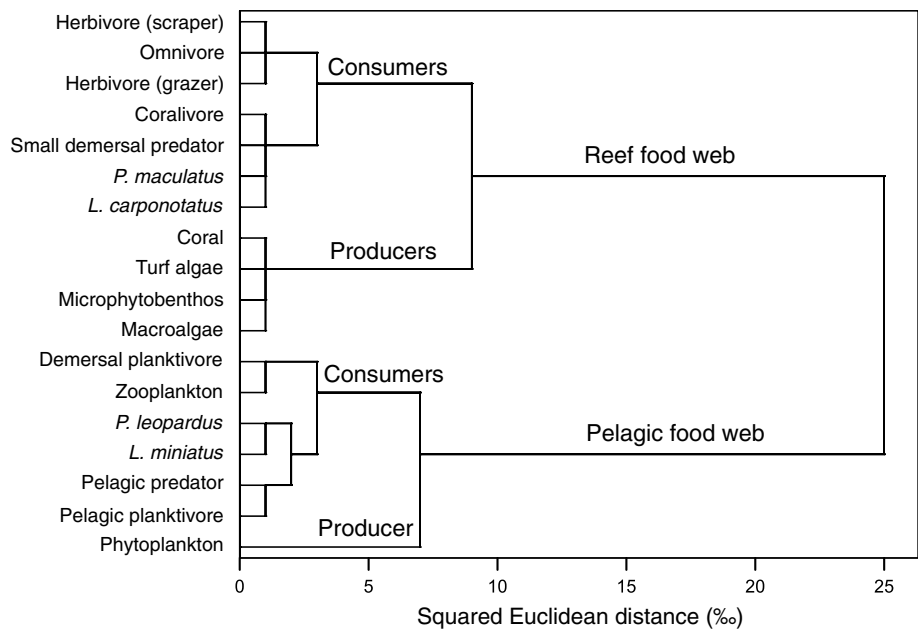

Fig. 3 Comparison of lipid-corrected $\delta^{13}C$ (an indicator of food source) among large predatory fishes (*grey bars*). Uncorrected data (*white bars*) are also shown to demonstrate that lipid correction had little influence on overall results. Data are presented as mean ± standard error of ten samples per species. Lipid-corrected groups with the *same letter* are not significantly different

$F_{1,3} = 30.21$, $p = 0.012$), which was well described by the regression equation:

$$\delta^{15}N_{predator} = -0.185 \times \delta^{13}C + 8.69$$

However, there was no significant relationship between $\delta^{13}C$ and $\delta^{15}N$ for intermediate consumers (Linear regression, $r^2 = 0.15$, $F_{1,6} = 1.03$, $p = 0.35$) or primary producers (Linear regression, $r^2 = 0.23$, $F_{1,3} = 0.91$, $p = 0.41$; Fig. 4).

With regard to focal predators, mean $\delta^{15}N$ (an indicator of TL) was highest in *P. leopardus* and lowest in *P. maculatus* and *L. carponotatus* (Fig. 5), and differences between species were statistically significant (ANOVA, $F_{3,36} = 10.61$, $p < 0.001$). However, when $\delta^{15}N_{predator}$ was corrected for the negative relationship with $\delta^{13}C$ to allow a more meaningful comparison of $\delta^{15}N$ among predators that feed on different carbon sources (using the above regression equation), differences in TL between species were

Table 2 Summary of isotopic metrics for large predatory fishes

Focal predator	Pelagic source (%) (mean ± SE)	Reef source (%) (mean ± SE)	Total area	Unique area (%)	Individuals in unique area (%)
Plectropomus leopardus	72.1 ± 6.1	27.9 ± 6.1	8.53	64.79	50
Plectropomus maculatus	10.7 ± 2.3	89.3 ± 2.3	1.99	100	100
Lethrinus miniatus	62.6 ± 2.8	37.4 ± 2.8	4.48	36.84	70
Lutjanus carponotatus	25.5 ± 3.4	74.5 ± 3.4	2.30	92.38	90

End members for the two-source mixing model were the most ^{13}C-depleted *Scomberomorus commerson* (a pelagic specialist) and the least ^{13}C-depleted *Plectropomus maculatus* (a putative coral reef specialist). Isotopic niche space was inferred from the total area of the convex hull that encompassed all individuals (see Fig. 6)
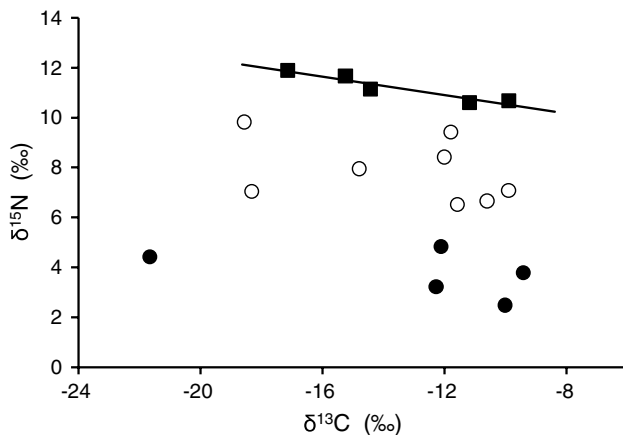
Fig. 4 Relationship between $\delta^{13}C$ and $\delta^{15}N$ for large predators (*filled square*), intermediate consumers (*open circle*) and primary producers (*filled circle*). Intermediate consumers include all trophic groups other than primary producers and large predators (see Table 1). Each *data point* represents the mean of a single trophic group, and the *line* represents best-fit based on regression analysis (see text for regression equation). The large predators are (from left to right) *Scomberomorus commerson*, *Plectropomus leopardus*, *Lethrinus miniatus*, *Lutjanus carponotatus* and *Plectropomus maculatus*
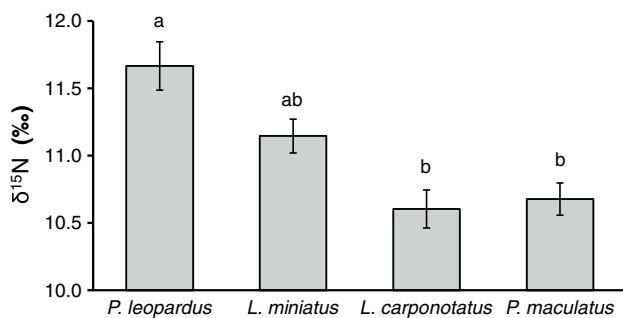

Fig. 5 Comparison of raw $\delta^{15}N$ (an indicator of trophic level) among large predatory fishes. Data are presented as mean ± standard error of ten samples per species. Groups with the same *letter* are not significantly different

small (Table 3). Depending on the base group, TL was estimated to be ~3.5–4.5 for *P. leopardus* and *P. maculatus*, and 3.4–4.4 for *L. miniatus* and *L. carponotatus*. Weighted means generated TL's that were slightly above 4 for *P. leopardus* and *P. maculatus*, and slightly below 4 for *L. miniatus* and *L. carponotatus* (Table 3).

Trophic niche space of large predatory fishes ranged from 1.99 U^2 for *L. carponotatus* to 8.53 U^2 for *P. leopardus* (Table 2). Percentage of unique space was highest (100 %) for *P. maculatus* and lowest (36.84 %) for *L. miniatus*. There was a high degree of overlap (a proxy for trophic competition) between *P. leopardus* and *L. miniatus*, but there was no overlap between *P. maculatus* and any other focal species (Fig. 6).

Discussion

Each of four focal predators (*P. leopardus*, *P. maculatus*, *L. miniatus* and *L. carponotatus*) was found to have a distinct isotopic signature in terms of $\delta^{13}C$ and $\delta^{15}N$, from which we inferred sources of primary production, TL and trophic niche space. Previously, these four focal predators were explicitly or implicitly assumed to be ecologically equivalent in terms of trophic function (Williams and Hatcher 1983; Graham et al. 2003; Frisch et al. 2012). However, results from the present study indicate that at least some of the focal predators utilise resources from different food webs and occupy different isotopic niches, which have implications for the function of reef communities and for ecosystem-based management of reef fisheries.

Inter-group comparisons of $\delta^{13}C$ (an indicator of food source) suggest that each focal predator is partly or wholly supported by different sources of primary production (Figs. 1, 3). Assuming that diet-tissue fractionation of $\delta^{13}C$ is small (≤ 1.5 ‰; Sweeting et al. 2007b), *P. leopardus* and *L. miniatus* appear to derive the majority (72 and 62 %, respectively) of their production from planktonic sources, while *P. maculatus* and *L. carponotatus* appear to derive the majority (89 and 74 %, respectively) of their production from benthic reef-based sources (Table 2). These contrasting results are supported by the differential $\delta^{13}C$ values of fishes such as *S. commerson* (large pelagic predator) and *Chaetodon* spp. (coralivore), which are known to participate predominantly (or exclusively) in pelagic and reef food webs, respectively (Figs. 1, 2). Surprisingly, previous studies of gut contents indicate that a substantial proportion of prey items ingested by *P. leopardus* and the majority of prey items ingested by *L. miniatus* are from reef-based food webs (Walker 1978; Kingsford 1992; St John 1999; St. John et al. 2001). For example, pomacentrid, labrid and scarid fishes are commonly found in the guts of *P. leopardus* (Kingsford 1992; St. John et al. 2001). Given the $\delta^{13}C$ signatures of *P. leopardus* in the present study (Fig. 1), it is possible that *P. leopardus* mainly eat planktivorous species of pomacentrids and labrids, rather than benthic-feeding species of these taxa. It is also possible that previous studies of *P. leopardus* underestimated the importance of pelagic prey such as clupeids and engraulids, which are small, soft-skinned and thus rapidly digested (relative to coral reef prey). Differential digestion is a fundamental problem with gut content analyses (Baker et al. 2013) and highlights the utility of stable isotope analyses as a complimentary method for investigation of trophic ecology.

The ultimate sources of carbon for reef fish productivity are typically assumed to be benthic microalgae, macroalgae and the symbiotic microalgae (zooxanthellae) of corals (Harrison and Booth 2007). Phytoplankton is seldom considered to contribute to reef fish production (Polunin 1996).

Table 3 Trophic level (TL) of focal predators relative to the TL of different base groups, inferred using corrected $\delta^{15}N$

Base group	*Plectropomus leopardus*	*Plectropomus maculatus*	*Lethrinus miniatus*	*Lutjanus carponotatus*
Primary producer ($\lambda = 1$)	3.50	3.50	3.38	3.40
Herbivore ($\lambda = 2$)	3.35	3.35	3.23	3.25
Small demersal predator ($\lambda = 3.65$)[a]	4.19	4.19	4.07	4.09
Large pelagic predator ($\lambda = 4.47$)[a]	4.54	4.54	4.43	4.44
Weighted mean TL ($\pm$ SE)	4.09 $\pm$ 0.28	4.09 $\pm$ 0.28	3.98 $\pm$ 0.28	3.99 $\pm$ 0.28

Mean $\delta^{15}N$ of primary producers (macroalgae, turf algae) and herbivores (scrapers, grazers) was calculated by pooling across groups. A base trophic level (λ) of 1 and 2 was assumed for primary producers and herbivores, respectively. Fractionation of $\delta^{15}N$ was assumed to be 3.2 ‰ per TL (Sweeting et al. 2007a)

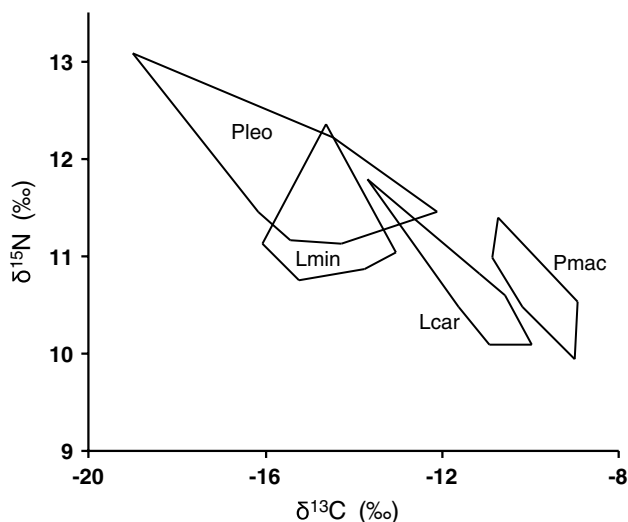[a] Base trophic level (λ) was derived from the literature (Farmer and Wilson 2011)

Fig. 6 Isotopic niche space of large predatory fishes. Each *polygon* represents the convex hull that encompasses all $\delta^{13}C$ and $\delta^{15}N$ values of individuals in a species. Abbreviations are defined in Table 1, and area parameters are listed in Table 2

However, results from the present study suggest that *P. leopardus* and *L. miniatus*, which are among the largest and most abundant predators on many Indo-West Pacific coral reefs, are predominantly sustained by planktonic production. This result reconciles two important but often overlooked observations: i.e. planktivores comprise 43–70 % of total fish biomass on forereefs of the GBR (Williams and Hatcher 1983) and that large inputs of phytoplankton production are necessary to balance ecosystem (Ecopath) models of coral reefs (Polovina 1984; Bozec et al. 2004). Thus, benthos such as corals and algae must not always be considered as the dominant source of carbon that supports reef fisheries. It is also apparent that *P. leopardus* and *L. miniatus* facilitate ecosystem connectivity by energetically coupling resource pools in adjacent habitats, to the extent that conservation of coastal pelagic ecosystems may be critically important for sustaining reef-based fishery yields.

An integrated or ecosystem-based approach to management of reef fisheries is therefore warranted.

Due to the effects of global warming and ocean acidification, coral reefs are forecast to undergo radical demographic changes in the near future, including reductions in the abundance of corals and coral-dependent fishes such as chaetodontids, gobiids and apogonids (Hoegh-Guldberg et al. 2007; Pratchett et al. 2008). Since many of these fishes are prey for important fishery species such as *P. leopardus* (St. John et al. 2001), a primary concern for the GBR's line-fishery is a decline in yield due to reductions in availability of prey to predators. In contrast to coral reefs, the GBR's coastal pelagic habitats and associated fisheries are predicted to be less affected by future climate change (Kingsford and Welch 2007), and phytoplankton productivity is predicted to increase in the GBR region (Fulton 2011). In view of these contrasting predictions for reef and pelagic ecosystems, we propose two additional predictions, based on the results of the present study. Firstly, *P. leopardus* and *L. miniatus* may be less affected by future climate change than *P. maculatus* and *L. carponotatus*, because the former two species are less reliant on reef-based food webs than are the latter two species. Secondly, the commercial sector of the GBR line-fishery may be less vulnerable to future climate change than the recreational sector, because the former mainly harvests *P. leopardus* and *L. miniatus* while the latter mainly harvests *P. maculatus* and *L. carponotatus* (Lunow and Holmes 2011; Taylor et al. 2012). It should be noted that these predictions are only preliminary, but they are presented here to provide a basis on which to guide further research and precautionary management.

Mean $\delta^{15}N$ (an indicator of TL) was variable among focal predators (Fig. 5) and was used to quantify TL relative to one of four base groups. For all focal predators, estimates of TL were lower when the base group was a producer ($\lambda = 1$) or primary consumer ($\lambda = 2$), relative to when the base group was a secondary consumer (small demersal predator, $\lambda = 3.65$; large pelagic predator, $\lambda = 4.47$) (Table 3). This trend was presumably due

to over-estimation of $\delta^{15}N$ diet-tissue fractionation (Sweeting et al. 2007a) and/or over-estimation of $\lambda_{secondary\ consumer}$, which was derived via stomach content analysis (Farmer and Wilson 2011). Regardless of its source or magnitude, error was unlikely to drive the observed differences in species-specific TL, because any bias in fractionation value or λ was (by default) applied equitably across all focal species. Thus, we are confident that differences in estimated TL between focal predators reflect actual differences in TL between species.

Weighted mean TLs were slightly above 4 for *P. leopardus* and *P. maculatus*, and slightly below 4 for *L. miniatus* and *L. carponotatus* (Table 3). Surprisingly, the estimated TLs of *P. leopardus* and *P. maculatus* were similar to those of reef sharks, which have a mean TL of 4.1 (Cortes 1999). According to convention, *P. leopardus* and *P. maculatus* (and reef sharks) qualify as apex predators, since their estimated TLs were >4. This result confirms previous assumptions that *Plectropomus* are apex predators (Goeden 1982; Huntsman et al. 1999). Quantification of TL is a useful exercise because it provides an indication of a species' functional role in a food web and, more broadly, provides an indication of fishery sustainability (Pauly and Watson 2005). In particular, it is now widely accepted that apex predator fisheries are often unsustainable because *K*-selection renders apex predators vulnerable to over-exploitation (Huntsman et al. 1999; Heithaus et al. 2008). It is also increasingly apparent that apex predators have disproportionate effects on community structure (McCauley et al. 2010; Estes et al. 2011). Together, these concepts provide sound justification for precautionary management of *Plectropomus* populations on the GBR and elsewhere.

Bivariate isotope data indicate little or no overlap of isotopic niche space between the focal predators, except for *P. leopardus* and *L. miniatus* (Fig. 6, Table 2). The lack of isotopic overlap suggests that the relevant species have mutually exclusive diets and that inter-specific competition for prey may be low or absent. This is perhaps a crucial feature that enables a high diversity of large predators to co-exist in a single habitat. With regard to *P. leopardus* and *L. miniatus*, isotopic overlap is probably the result of consuming different prey species that share a similar TL and source of production, rather than the result of consuming the same prey species, because *P. leopardus* and *L. miniatus* have substantially different mouth morphologies, feeding behaviours and activity patterns (authors' pers. obs.).

Total area of isotopic niche space was substantially larger for *P. leopardus* and *L. miniatus* relative to *P. maculatus* and *L. carponotatus* (Fig. 6, Table 2), indicating that populations of the former two species are more generalist (less specialist) in their diet than are populations of the latter two species. If the degree of dietary specialisation is an indicator of vulnerability to change, then *P. leopardus* and *L. miniatus* may be more resilient than *P. maculatus* and *L. carponotatus* to climate-related disturbances such as coral bleaching, which is predicted to reduce the abundances of important prey species (Pratchett et al. 2008). If so, climate-related disturbances may have less impact on the commercial sector of the GBR line-fishery than on the recreational sector. However, these hypotheses must be interpreted with caution because the size and shape of each species' isotopic niche space may change with increasing sample size.

The interpretations and predictions presented thus far are dependent on two key assumptions. Firstly, it was assumed that the reef-based and pelagic sources of production that we represented with end members in the mixing model were the key sources of production supporting the focal predators, i.e. these predators primarily rely on some combination of reef and pelagic production, and not on additional or alternate sources such as deep-water inter-reef food webs. Although the selected end members almost certainly do not represent the complete isotopic signature of these habitats and food webs, concordance between the isotopic signatures of end members, relevant intermediate consumers, and producers (Fig. 1) suggests that the selected end members do indeed serve as suitably accurate isotopic proxies for reef and pelagic systems. Secondly, it was assumed that diet-tissue fractionation of $\delta^{15}N$ was 3.2 ‰. While this value is currently the best estimate available for fish tissue (Sweeting et al. 2007a), the actual fractionation values for the focal species in the present study have not been determined, which generates a degree of uncertainty in our estimates of TL. It is noteworthy, however, that the difference between pooled mean $\delta^{15}N$ of large predators and intermediate consumers was 3.0 ‰ (Fig. 4). This suggests that (1) the assumed fractionation value (3.2 ‰) is a reasonable approximation of diet-tissue fractionation in the predator species studied here, and (2) our estimates of TL are sufficiently representative.

Two limitations of this study are the relatively small sample size ($n = 10$ per species) and the absence of spatial or temporal replication, which limits generality of the results. However, this is the first data of its kind from the GBR, so it provides useful first approximations of the relevant parameters and thus creates a suitable foundation for future research and precautionary management. This is important given that managers of high diversity fisheries, such as the GBR line-fishery, often operate in a data-limited environment. In view of the moderate intra-specific variation that was identified here (Fig. 1), we recommend that future studies aim for a minimum sample size of 20 per species. Similarly, it is recommended that future studies replicate across a range of spatial and temporal scales to test the generality of our results.

In summary, four dominant predator species at Northwest Island were found to have distinct isotopic signatures, from which we inferred key parameters of trophic ecology. In particular, it appears that *P. leopardus* and *L. miniatus* derive much of their production from pelagic sources rather than reef-based sources, which indicates the importance of planktonic production for sustaining reef fisheries and highlights the need for a whole-of-ecosystem approach to fisheries management. In addition, it appears that the closely related *P. leopardus* and *P. maculatus* are apex predators (TL > 4) and each has a different diet and degree of trophic specialisation. Should further research confirm that the divergent trophic ecologies described here are consistent across space and time, then each of the four focal predators are anticipated to be differentially affected by future climate change, with cascading socio-economic consequences for recreational and commercial reef fisheries. The results presented herein provide a useful starting point for precautionary management of exploited predator populations.

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