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ORIGINAL RESEARCH

Ecological redundancy between coral reef sharks and predatory teleosts

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Abstract Reef sharks may be ecologically redundant, such that other mesopredatory fishes compensate for their functions when they decline in number, preventing trophic cascades. Oral jaw gape, hereafter referred to as gape, determines maximum prey size in many piscivores and therefore affects the size structure of prey assemblages. Here, we examine whether gape and maximum prey size differ between five species of reef shark and 21 species of teleost (n = 754) using data collected from 38 reefs in the Indo-Pacific. Sharks displayed relatively small gape dimensions compared to most teleost species and, at smaller sizes, the giant trevally *Caranx ignobilis* and other teleosts may be able to consume larger prey than similar-sized sharks. However, ecological redundancy between reef sharks and teleosts appears to decline at larger sizes, such that the grey reef shark *Carcharhinus amblyrhynchos*, for example, may be capable of consuming larger prey than any other reef predator at its largest sizes, regardless of prey body shape. Moreover, sharks may be able to consume proportionally larger prey as they grow, in contrast to reef teleosts, which may largely be limited by their gapes to ever-smaller prey as a proportion of their body size. Our results also suggest that reef sharks may be unable to swallow whole prey that are > 36% of their length, consistent with gut-content studies. Conservation of reef ecological function may therefore depend not only on the protection of sharks but also particular size classes and key components of the mesopredatory guild.

Keywords Competition · Gape size · Lethal effects · Risk effects · Mesopredator · Overfishing

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Introduction

> When I came at last to know them… all these characteristics slipped away, and I saw them as they really are — indolent, awkward, chinless cowards.
> William Beebe, "The Arcturus Adventure" (1926)

The role of the apex predator, once a cornerstone of ecological theory, is increasingly disputed (Wallach et al. 2015). Recent studies suggest that supposedly strict "hypercarnivores" can play overlooked, non-apex roles within their ecosystems, with, for example, the great white shark *Carcharodon carcharias* now recognised as an important scavenger in marine ecosystems (Fallows et al. 2013) and the tiger shark *Galeocerdo cuvier* trophically inferior to reef sharks and tuna at some locations (Ferreira et al. 2017). Reef sharks have not been immune to reclassification and are now considered to be "mesopredators", mid-ranking carnivores that share prey and habitat with a diverse guild of other fish species (Frisch et al. 2016; Roff et al. 2016). Indeed, it has been argued that reef sharks may be ecologically redundant, such that their effect on the ecosystem via diet, feeding behaviour and habitat use is indistinguishable from that of other large mesopredators (Frisch et al. 2016). As a result, declines in shark abundance should, in theory, have no knock-on effects on the ecosystem, with competitors "compensating" for any lost functions (Frisch et al. 2016).

Yet there is also some evidence that elasmobranchs play distinct functional roles within their ecosystems (Ruocco and Lucifora 2016). Unplanned, large-scale, natural "experiments" (Barley and Meeuwig 2017) in which seasonal change, overfishing and/or tides alter the abundance of sharks suggest that declines in reef sharks can alter the diversity, abundance, biomass, diet, body condition (i.e. weight for a given length), morphology and growth of teleosts via a combination of "lethal" (killing) and "risk" (fear) effects (Madin et al. 2010; Ruppert et al. 2013; Rizzari et al. 2014; Barley et al. 2017a, b; Rasher et al. 2017; Hammerschlag et al. 2018). Indeed, a global analysis of tropical coral reefs and smaller-scale studies in New Caledonia, the British Indian Ocean Territory and French Polynesia have demonstrated that the vast majority of ecological functions, based on diet, size, home range and gregariousness, are characterised by low levels of redundancy, particularly among large and/or predatorial species (Guillemot et al. 2011; Mouillot et al. 2014; D'agata et al. 2016). Mouillot et al. (2014), for example, found that 38% of all functions on reefs in the central Indo-Pacific displayed no ecological redundancy (i.e. were supported by a single species), however there is evidence for higher redundancy in medium-sized invertebrate feeders (D'agata et al. 2016). Low ecological redundancy in coral reef fishes is consistent with theory suggesting that resource conflict (the "ghost of competition past"; Connell 1980) should drive diversification of habitat use, foraging patterns and/or morphology among competitors (Bonin et al. 2015).

Mouth size, or oral jaw gape, is one of the most important determinants of feeding behaviour in predatory teleosts (Detmer et al. 2018; Luiz et al. 2019). Mihalitsis and Bellwood (2019) concluded that variation in premaxilla-maxilla length, a proxy for oral jaw gape, may reflect the diversity of prey sizes and shapes available on coral reefs, and reported less variation in pelagic predators. Teleosts with larger gapes can consume larger, more energetically profitable prey, and display higher body condition values than smaller-mouthed but similar-sized conspecifics (Luiz et al. 2019). Moreover, the strong size structuring found in fish assemblages has been attributed primarily to gape limitation (Segura et al. 2015; Dunic and Baum 2017), such that the maximum prey size of most piscivores is determined by their gape (Hambright 1991; Scharf et al. 2000; Goatley and Bellwood 2009). Piscivores tend to consume whole prey head first (Reimchen 1991), with the prey's body depth typically aligned with the predator's oral gape width, such that the latter may determine the maximum size of prey (Werner 1974; Mihalitsis and Bellwood 2017).

There is some evidence for gape limitation in reef sharks. Although large, triangular and coarsely-serrated teeth allow some shark species to bite flesh from (i.e. kill) prey larger than their mouths (Frazzetta 1988; Lucifora et al. 2006), great white sharks lack such dentition until they reach large sizes (Tricas and McCosker 1984). Moreover, the smooth-edged teeth of the nurse shark *Ginglymostoma cirratum* and the sharpnose shark *Rhizoprionodon* spp appear to serve to grasp rather than slice prey (Matott et al. 2005; Marsili 2007; Meyers et al. 2008). Reef sharks such as the blacktip reef *Carcharhinus melanopterus* possess small, finely-serrated teeth (Randall and Helfman 1973; Naylor and Marcus 1994), and as such, may also have a limited capacity to mutilate prey. Moreover, even sharks that have the ability to evade gape limitation may still preferentially swallow prey whole, with, for example, the copper shark *Carcharhinus brachyurus* eating 97% of its pelagic teleost prey in this way (Lucifora et al. 2008).

Despite the ecological importance of gape limitation, few studies have measured gape in reef fishes (but see Goatley and Bellwood 2009; Dunic and Baum 2017; Mihalitsis and Bellwood 2017) and none have included sharks. Here, we examine whether twenty-six common predatory fish species on Indo-Pacific coral reefs, including five species of shark, display ecological redundancy with regard to gape. We estimate gape height and gape width as a proportion of body size ($GH_{\%}$ and $GW_{\%}$, respectively) in addition to maximum prey size, both as a proportion of predator length ($MPS_{\%}$) and in absolute terms (MPS_{cm}) based on three potential prey body shapes, deep-bodied, fusiform and elongate. We predict that if reef sharks are ecologically distinct members of the mesopredatory guild in terms of gape, their maximum prey size will be larger than that of any other teleost, both at their maximum and common lengths, in addition to within smaller size classes.

Methods

Fish sampling

In 2017 and 2018, 754 fishes from 26 species were non-lethally sampled using catch-and-release methods at three locations in Australia: the Great Barrier Reef Marine Park (32 reefs; April–June 2017/2018 and November–December 2017), the Torres Strait (3 reefs; November–December 2017) and the Kimberley region (3 reefs; July 2017) (Table 1). Fishes were non-lethally sampled due to the protected nature of the field sites and the inclusion of species of conservation concern, noting that non-destructive sampling is increasingly common in ecology (Minteer and Collins 2008; Barnett et al. 2010; Brook et al. 2015). Fishes were placed in a tank of freshly collected seawater and weighed using digital scales. Fork length (FL) and body depth at the anterior edge of the dorsal fin (BD) were measured to the nearest centimetre. In addition, gape height (GH; the maximum distance between the upper and lower oral jaws when the mouth was fully open) and gape width (GW; the distance between the left and right edges of the mouth when fully open) were measured (Wanzenböck 1995; Scharf et al. 2002; Schrandt et al. 2016).

Study species

The five species of shark included in the analysis, in order of decreasing maximum size, were the grey reef *Carcharhinus amblyrhynchos*, the Australian blacktip *Carcharhinus tilstoni*, the blacktip reef *C. melanopterus,* the milk *Rhizoprionodon acutus* and the whitecheek *Carcharhinus coatesi* shark. These species are common on Indo-Pacific reefs and consume reef-associated prey, although *C. amblyrhynchos*, *C. tilstoni* and *R. acutus* occasionally consume large amounts of prey from the pelagic zone adjacent to reefs (McCauley et al. 2012; Froese and Pauly 2019). *Galeocerdo cuvier* was not included in the study as this species is not gape-limited (Witzell 2017; Holland et al. 2019). As *C. coatesi* had a low sample size (n = 2), discussions of its results are qualitative. Twenty-one species of teleosts that potentially compete for prey with reef sharks were also sampled (Supp. Table S1). Maximum (MFL) and common (CFL) fork length values were sourced for all species (Table 2 and Supp. Table S2), noting that CFLs represent the most likely or ecologically "realistic" length of a species in the wild. Where CFLs were unavailable, they were estimated as 75% of the MFL, following Barley et al. (2017b). Where fork length values were unavailable, total or standard lengths were converted to FLs using conversion factors.

Data analysis

Absolute prey size

We assumed that the gape width of an individual predator was also the maximum body depth (BD) of a standard prey item. The fork length of a potential prey item was then calculated from its body depth using BD–FL conversion factors, with the result assumed to be the maximum prey size (MPS_{cm}) of each individual predator. We chose to convert BDs to FLs because size is an ecologically important trait that determines fecundity, speed, lifespan and feeding behaviour (Peters 1983). Prey FLs were calculated using the BD–FL relationships for three potential prey species with different body shapes: the fusiform Spanish flag snapper, *Lutjanus carponotatus* (*LC*), the elongate Marr's fusilier, *Pterocaesio marri* (*PM*), and the deep-bodied two-tone tang, *Zebrasoma scopas* (*ZS*). Unpublished data (Barley and Meeuwig) indicates that 34%

Table 1 Common names and sample sizes of 25 species of predatory fish included in the analysis, ordered in terms of increasing maximum fork length and originating from three locations in the Indo-Pacific: the Great Barrier Reef Marine Park (GBRMP), the Torres Strait and the Kimberley region

Species	Common name	*n* GBRMP	*n* Torres Strait	*n* Kimberley	*n* Total
Cephalopholis urodeta	Darkfin hind	8	0	0	8
Lutjanus carponotatus	Spanish flag snapper	51	8	20	79
Epinephelus quoyanus	Longfin grouper	10	0	0	10
Cephalopholis miniata	Coral hind	65	19	10	94
Carcharhinus coatesi	Whitecheek shark	0	0	2	0
Caranx papuensis	Brassy trevally	22	0	6	28
Lutjanus erythropterus	Crimson snapper	10	0	0	10
Lethrinus miniatus	Trumpet emperor	10	7	0	17
Lutjanus bohar	Twin-spot red snapper	59	3	0	62
Aprion virescens	Green jobfish	6	0	0	6
Plectropomus leopardus	Leopard coralgrouper	94	16	0	110
Plectorhinchus caeruleonothus	Blue bastard	29	0	0	29
Gnathanodon speciosus	Golden trevally	42	1	4	47
Scomberoides commersonnianus	Talang queenfish	8	0	8	16
Trachinotus blochii	Snubnose pompano	13	0	0	13
Grammatorcynus bicarinatus	Shark mackerel	9	2	0	11
Caranx melampygus	Bluefin trevally	6	0	1	7
Carangoides fulvoguttatus	Yellowspotted trevally	9	0	0	9
Plectropomus maculatus	Spotted coralgrouper	23	0	3	26
Rhizoprionodon acutus	Milk shark	0	0	10	10
Caranx ignobilis	Giant trevally	46	0	4	50
Carcharhinus melanopterus	Blacktip reef shark	27	0	8	35
Carcharhinus tilstoni	Australian blacktip shark	19	0	1	20
Carcharhinus amblyrhynchos	Grey reef shark	14	0	15	29
Thunnus albacares	Yellowfin tuna	7	0	0	7
Scomberomorus commerson	Narrow-barred Spanish mackerel	11	1	7	19
		598	57	99	754

of potential prey items on the studied reefs may be elongate while 66% may be non-elongate (i.e. either fusiform or deep-bodied).

The BD–FL relationship for *L. carponotatus* was derived from our data ($FL = 2.26 + 2.87 \times BD$; $n = 79$; $R^2 = 0.94$), while the relationships for the other two species were derived from the literature (Supp. Table S4). Following the above process, a hypothetical maximum prey size (MPS_{cm}) was generated for each individual of each species of predator. These values were then used to generate a mean MPS_{cm} value for each species. Intercept (B_0) and slope (B_1) values obtained from regression of MPS_{cm} against predator size were used to estimate MPS_{cm} at the MFL and CFL. Each species of predator was additionally grouped into size classes, ranging from 0–25 cm to 201–225 cm (in the case of MFL) and 0–25 to 151–175 cm (in the case of CFL), with 25 cm increments chosen because of the fine-scale differences between species in terms of MFL and CFL. The MPS_{cm} was then calculated for each species at the upper limit of each size class, assuming a fusiform prey body shape as this was considered to be representative of a typical prey item on the reef. To examine which predators were capable of consuming the largest prey, species were ranked in descending order of MPS_{cm} within each size class, an approach that was selected due to the nature of gape limitation,

Table 2 Mean maximum and common reported fork lengths (MFL and CFL, respectively) for 26 predator species, with values sourced from the literature (Supp. Table S2) and ranked in terms of increasing MFL. Also presented are gape height and gape width as a proportion of fork length ($GH_{\%}$ and $GW_{\%}$, respectively), mean maximum prey size as a proportion of predator size ($MPS_{\%}$) and absolute maximum prey size (MPS_{cm}) both at the MFL and the CFL

Species	MFL (SE)	CFL (SE)	$GW_{\%}$ (SE)	$GH_{\%}$ (SE)	Mean $MPS_{\%}$ (SE)			MPS_{cm} @ MFL (SE)			MPS_{cm} @ CFL (SE)		
					LC	*PM*	*ZS*	*LC*	*PM*	*ZS*	*LC*	*PM*	*ZS*
Cephalopholis urodeta	28	19.5 (1.5)	18.58 (0.74)	17.93 (0.36)	64.1 (2.04)	80.6 (3.19)	36.5 (1.37)	17.8 (0)	23.6 (0)	10.5 (0)	12.5 (0.93)	15.6 (1.41)	7.07 (0.61)
Lutjanus carponotatus	38.50	25.4 (3.5)	14.35 (0.17)	13.92 (0.12)	49.7 (0.45)	62.3 (0.75)	28.2 (0.32)	19.5 (0)	26.1 (0)	11.7 (0)	12.6 (1.83)	15.7 (2.78)	7.12 (1.2)
Epinephelus quoyanus	40	20 (10)	18.23 (0.74)	16.74 (0.78)	62.66 (2.85)	79.11 (3.22)	35.8 (1.48)	21.2 (0)	28.7 (0)	12.8 (0)	12.9 (4.2)	16.1 (6.3)	7.29 (2.73)
Cephalopholis miniata	47.5 (2.5)	35.7 (1.8)	16.96 (0.2)	16.76 (0.21)	58.5 (0.43)	73.3 (1.01)	33.1 (0.047)	24.1 (1.07)	32.9 (1.7)	15.1 (0.76)	19 (0.79)	24.9 (1.25)	11.5 (0.57)
Lutjanus erythropterus	70.8 (10.8)	45	13.66 (0.35)	12.17 (0.29)	43.19 (1)	59.29 (1.53)	26.31 (0.66)	31 (4.97)	43.7 (7.56)	19.2 (3.26)	19.1 (0)	25.7 (0)	11.4 (0)
Caranx papuensis	73.4 (4.5)	55	11.66 (0.36)	10.75 (0.25)	29.2 (1.24)	51.4 (1.55)	23.1 (0.69)	27.6 (1.58)	27.6 (1.59)	27.6 (1.59)	21.1 (0)	21.1 (0)	21.1 (0)
Aprion virescens	76.6 (15.1)	61.4 (12.3)	12.3 (0.22)	11.01 (0.39)	37.5 (1.76)	51.0 (2.48)	22.7 (1.09)	26.5 (3.67)	36.6 (5.54)	16.2 (2.41)	22.8 (2.98)	31.1 (4.5)	13.8 (1.96)
Trachinotus blochii	83.4 (26.6)	33.10	8.59 (0.26)	9.07 (0.46)	29.7 (0.89)	37.3 (1.15)	16.9 (0.51)	20.8 (5.17)	28 (7.83)	12.5 (3.4)	11 (0)	13.2 (0)	6.06 (0)
Lethrinus miniatus	83.80	37.20	9.75 (0.32)	13.04 (0.34)	35.3 (0.95)	42.3 (1.39)	19.4 (0.60)	26.7 (0)	37 (0)	16.4 (0)	12.8 (0)	15.9 (0)	7.22 (0)
Lutjanus bohar	85.40	66.6 (19.2)	14.09 (0.18)	13.86 (0.19)	46.6 (0.65)	60.6 (0.64)	27.0 (0.28)	35.9 (0)	50.9 (0)	22.4 (0)	28.7 (7.36)	40 (11.1)	17.7 (4.84)
Gnathanodon speciosus	99.7 (1.1)	75	11.1 (0.19)	10.5 (0.21)	36.8 (0.56)	48.0 (0.82)	21.5 (0.36)	32.9 (0.32)	46.5 (0.5)	20.5 (0.22)	25.5 (0)	35.2 (0)	15.6 (0)
Plectrorhinchus caeruleonothus	100	75	9.05 (0.21)	10.37 (0.33)	29.5 (0.56)	39.3 (0.91)	17.5 (0.39)	30.7 (0)	43.1 (0)	19 (0)	22.5 (0)	30.6 (0)	13.6 (0)
Scomberoides commersonnianus	104.70	90	10.31 (0.3)	10.63 (0.18)	33.5 (0.71)	44.8 (1.29)	20.0 (0.54)	37.1 (0)	52.7 (0)	23.2 (0)	31.5 (0)	44.3 (0)	19.6 (0)
Plectropomus leopardus	106.2 (10.9)	41.50	14.03 (0.15)	12.38 (0.097)	42.4 (0.43)	60.7 (0.67)	26.7 (0.29)	49.6 (5.18)	71.6 (7.84)	31.4 (3.4)	19 (0)	25.3 (0)	11.3 (0)
Rhizoprionodon acutus	113.7 (31.9)	77.5 (12.5)	10.01 (0.41)	7.58 (0.51)	33.01 (0.99)	43.4 (1.67)	19.45 (0.71)	44.4 (14.1)	64 (21.4)	28 (9.25)	28.4 (5.52)	39.7 (8.38)	17.5 (3.63)
Caranx melampygus	117	55.40	11.59 (0.36)	10.47 (0.27)	38.48 (1.16)	48.59 (1.41)	21.98 (0.62)	40.4 (0)	58.1 (0)	25.4 (0)	20.2 (0)	27.3 (0)	12.1 (0)
Carangoides fulvoguttatus	120	81.50	10.97 (0.5)	9.87 (0.34)	36.4 (1.52)	48.28 (1.95)	21.59 (0.88)	34.4 (0)	48.7 (0)	21.2 (0)	25.5 (0)	35.2 (0)	15.4 (0)
Plectropomus maculatus	120.6 (4.4)	64.1 (29.7)	15.35 (0.24)	13.81 (0.3)	49.7 (0.65)	66.6 (1.03)	29.7 (0.44)	58.4 (2.11)	85.1 (3.19)	37.3 (1.38)	31.4 (14.2)	44.1 (21.5)	19.5 (9.33)
Grammatorcynus bicarinatus	121 (9)	90.8 (6.7)	8.43 (0.27)	12.11 (0.4)	28.0 (0.80)	36.6 (1.18)	16.4 (0.51)	31.9 (2.23)	44.9 (3.38)	19.8 (1.47)	24.4 (1.67)	33.5 (2.54)	14.9 (1.1)
Caranx ignobilis	150.6 (4.3)	86.10	13.8 (0.23)	12.11 (0.25)	43.3 (0.64)	57.2 (1.95)	25.4 (0.84)	67.4 (1.97)	92.5 (2.76)	40.5 (1.2)	37.9 (0)	51.1 (0)	22.5 (0)
Carcharhinus melanopterus	155.6 (8.2)	110.9 (12)	11.9 (0.21)	10.9 (0.17)	36.3 (0.61)	51.4 (0.92)	22.7 (0.40)	55.5 (2.83)	80.5 (4.29)	35.3 (1.86)	40 (4.13)	57.1 (6.26)	25.1 (2.72)

Table 2 continued

Species	MFL (SE)	CFL (SE)	GW$_{\%}$ (SE)	GH$_{\%}$ (SE)	Mean MPS$_{\%}$ (SE)			MPS$_{cm}$ @ MFL (SE)			MPS$_{cm}$ @ CFL (SE)		
					LC	*PM*	*ZS*	*LC*	*PM*	*ZS*	*LC*	*PM*	*ZS*
Carcharhinus tilstoni	164.10	97.2 (25.9)	11.56 (0.22)	8.41 (0.38)	36.36 (0.6)	50.8 (1.00)	22.4 (0.43)	62.9 (0)	91.8 (0)	40.2 (0)	36 (10.4)	51.1 (15.8)	22.5 (6.85)
Carcharhinus amblyrhynchos	188 (27.6)	141 (22)	12.77 (0.27)	10.56 (0.46)	39.4 (0.75)	55.4 (1.16)	24.4 (0.50)	74.4 (11)	109.2 (16.6)	47.7 (7.2)	55.8 (8.73)	81 (13.2)	35.5 (5.74)
Scomberomorus commerson	196.5 (43.5)	99.6 (9.6)	7.99 (0.53)	10.97 (0.45)	25.6 (1.65)	34.6 (2.23)	15.4 (0.99)	36.6 (5.91)	52 (8.95)	22.9 (3.88)	23.4 (1.3)	32 (1.97)	14.2 (0.86)
Thunnus albacares	219.5 (19.5)	150	9.23 (0.12)	12.87 (0.21)	27.0 (1.24)	33.6 (2.68)	17.9 (0.23)	63.6 (5.57)	92.8 (8.43)	40.6 (3.66)	43.7 (0)	62.8 (0)	27.6 (0)

Standard errors (SE) are presented in parentheses where relevant. MPS values were estimated based on three potential prey species with differing body shapes: *L. carponotatus* (*LC*), *P. marri* (*PM*) and *Z. scopas* (*ZS*)

such that a teleost species must have an MPS value greater than or equal to that of a shark for it to act as a true ecological "substitute". Teleost species were classed as "close competitors" to sharks, rather than substitutes, if they displayed an MPS value within 10% of that of a larger shark species (i.e. if the MPS value of *C. amblyrhynchos* was 100 cm, competitor species must have MPS values ≥ 90 cm).

Percentage maximum prey size

We also calculated maximum prey size as a percentage of predator size (MPS$_{\%}$) for each individual predator, in addition to mean MPS$_{\%}$ (± SE) for each species. Mean MPS$_{\%}$ values for each species (as calculated for prey *LC*, *PM* and *ZS*) were then regressed against $\log_{10}$ transformed MFL and CFL values in order to explore whether larger-bodied species may have the capacity to consume smaller or larger prey relative to their own size compared with smaller-bodied species.

To explore the degree to which absolute and relative MPS, in addition to gape size, vary with predator size, (1) MPS$_{cm}$, (2) MPS$_{\%}$, (3) GH and (4) GW were regressed against predator size. For (1) and (2), regressions were conducted assuming three different prey body shapes, with the slope (B$_1$) indicating the rate of change in MPS (either in cm or as a proportion of predator length) with predator size. Slope values for each species from (2) were ranked in decreasing order to examine whether sharks outranked teleosts in terms of rate of change in MPS$_{\%}$ by size, and a two-sample *t* test assuming unequal variance was used to assess whether B$_1$ values differed significantly between sharks and teleosts. Finally, regressions (3) and (4) indicated rate of change in gape dimensions in relation to size for each species.

Species were also allocated trophic levels based on FishBase (Froese and Pauly 2019) and divided into four trophic groups following Barley et al. (2017a): 3.75–4.00; 4.01–4.25; 4.26–4.5; and 4.51–5.00. Mean MPS$_{cm}$ and MPS$_{\%}$ values (± SE) were also estimated by trophic group.

Prey body shape

In order to ascertain which prey body shapes were dominant at our study sites, we analysed abundance data (n = 33,573 teleosts from 53 families) collected via stereo-Baited Remote Underwater Video Systems from the Great Barrier Reef and Torres Strait, representing 87% of the sampled fishes in terms of their origin. We assigned each family a body shape category, either "non-elongate" (fusiform, deep-bodied, compressed, mixed) or "elongate" (Froese and Pauly 2019) and then calculated the percentage of the total fish abundance comprised by each family. We then summed the % abundance values by body shape category in order to ascertain what proportion of the total abundance was accounted for by "elongate" versus "non-elongate" fishes.

Results

Gape dimensions

For sharks, serranids and the majority of carangid species, GW usually exceeded GH regardless of individual body size (Fig. 1 and Supp. Fig. S1). Comparisons of slope values from regressions of GW and GH against predator size indicated that GW increased at a faster rate than GH in relation to length for all species except the narrow-barred Spanish mackerel *Scomberomorus commerson*, the yellowfin tuna *Thunnus albacares*, the green jobfish *Aprion virescens*, the trumpet emperor *Lethrinus miniatus*, the blue bastard *Plectorhinchus caeruleonothus*, the shark mackerel *Grammatorcynus bicarinatus* and *R. acutus* (Table 4). *Rhizoprionodon acutus* and *C. tilstoni* displayed the lowest $GH_{\%}$ values of all predators in the analysis (7.6% and 8.4%, respectively), with the remaining shark species also characterised by relatively low values (*C. amblyrhynchos*, 10.6%; *C. melanopterus*, 10.9%; Fig. 2a). For $GW_{\%}$ values see Fig. 2b and for sampled FL values see Supp. Table S1.

Maximum prey size (MPS_{cm})

MPS_{cm} values, both at MFL and CFL, were ranked in descending order (Fig. 3; Table 2). At its MFL of 188 cm, *C. amblyrhynchos* may be able to consume larger prey than any other species, with an MPS_{cm} value of 74.7 ± 11 cm (*LC*), 109.2 ± 16.6 cm (*PM*) and 47.7 ± 7.2 cm (*ZS*). A similar trend was identified at common fork lengths, with *C. amblyrhynchos* outranking all other species in terms of MPS_{cm} (CFL = 141 cm; MPS_{cm} = 55.8 ± 8.73 cm [*LC*], 81.0 ± 13.2 cm [*PM*] and 35.5 ± 5.74 cm [*ZS*]).

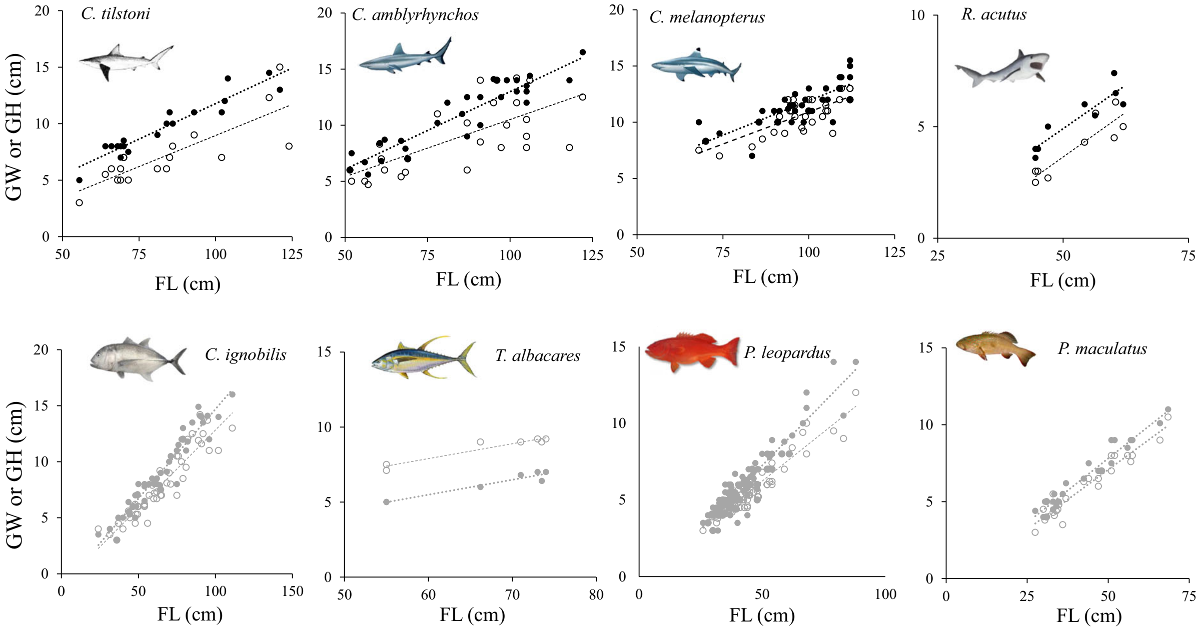

Fig. 1 Gape width (GW; filled circles; dotted line) and gape height (GH; empty circles; dashed line) plotted against fork length (FL) for four species of sharks (black) and four teleost competitors (grey), as identified by the analysis. See Table 4 for regression statistics and Supp Figure S1 for remaining species

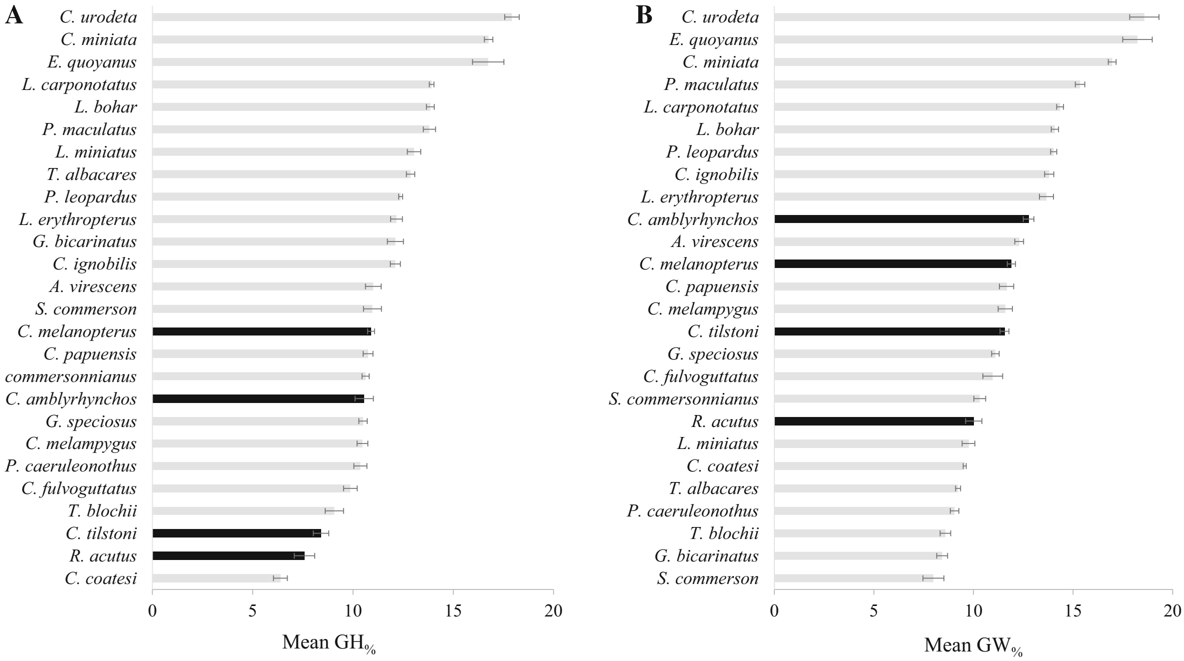

Fig. 2 Mean **A** gape height ($\text{GH}_{\%}$ ± SE) and **B** gape width ($\text{GW}_{\%}$ ± SE) as a proportion of fork length for 26 species of reef predator, with sharks indicated in black and teleosts in grey (Table 2)

The only teleost competitor to *C. amblyrhynchos* assuming a fusiform prey at MFLs was *C. ignobilis* (MFL = 150.6 cm; MPS_{cm} = 67.4 ± 1.97 cm [*LC*], 92.5 ± 2.76 cm [*PM*] and 40.5 ± 1.2 cm [*ZS*]), while for the other prey shapes, *C. amblyrhynchos* had no competitors (Table 3). *Carcharhinus tilstoni*, *C. melanopterus* and *R. acutus* each had a single competitor at their MFL, assuming a fusiform prey (the spotted coralgrouper *P. maculatus*, the leopard coralgrouper *P. leopardus* and the bluefin trevally *C. melampygus*, respectively). However, at common lengths, competitors were largely absent, with the exception of the brassy trevally *C. papuensis* (competitor to *C. tilstoni* [ZS]) and *P. maculatus* (competitor to *C. melanopterus* [LC]).

Size class analysis

Based on MFL values, *T. albacares* was the only predator species in the largest size class, 201–225 cm (MPS_{cm} = 65.1 cm; Fig. 4A[a]), yet still displayed a lower MPS than *C. amblyrhynchos* (MPS_{cm} = 79.2 cm), whose MFL limited it to size class 176–200 cm (Fig. 4A[b]). Within size class 176–200 cm, *C. amblyrhynchos* outranked the two other species, *T. albacares* (MPS_{cm} = 58.0 cm) and *S. commerson*, which may have an MPS_{cm} less than half that of a similar-sized *C. amblyrhynchos* (37.1 cm). In size classes 151–175 cm (Fig. 4A[c]) and 126–150 cm (Fig. 4A[d]), *C. amblyrhynchos*, *C. tilstoni* and *C. melanopterus* displayed the highest MPS_{cm} values, followed by *T. albacares* and *S. commerson*. Based on CFL, 126–150 cm (Fig. 4B[a]) was the largest size class and contained only two species, with *C. amblyrhynchos* (MPS_{cm} = 59.3 cm) outranking *T. albacares* (MPS_{cm} = 43.7 cm). In size class 101–125 cm (Fig. 4A[e]), under the MFL approach, 12 species were present and *P. maculatus* (MPS_{cm} = 60.6 cm) and *C. ignobilis* (MPS_{cm} = 55.7 cm) outranked the shark species. In contrast, size class 101–125 cm (Fig. 4B[b]) under CFL contained only two species: *C. amblyrhynchos* and *T. albacares.* In size class 76–100 cm (Supp. Fig. S2A) under MFL, 19 species were present and sharks were outranked by four teleosts (*P. maculatus, C. ignobilis, P. leopardus* and the twin-spot red snapper *L. bohar*) with, in contrast, this size class containing just 3 species of predator under CFL, of which two species were sharks (Fig. 4B[c]). In size class 51–75 cm (Supp. Fig. S2B) under MFL, 21 species were present

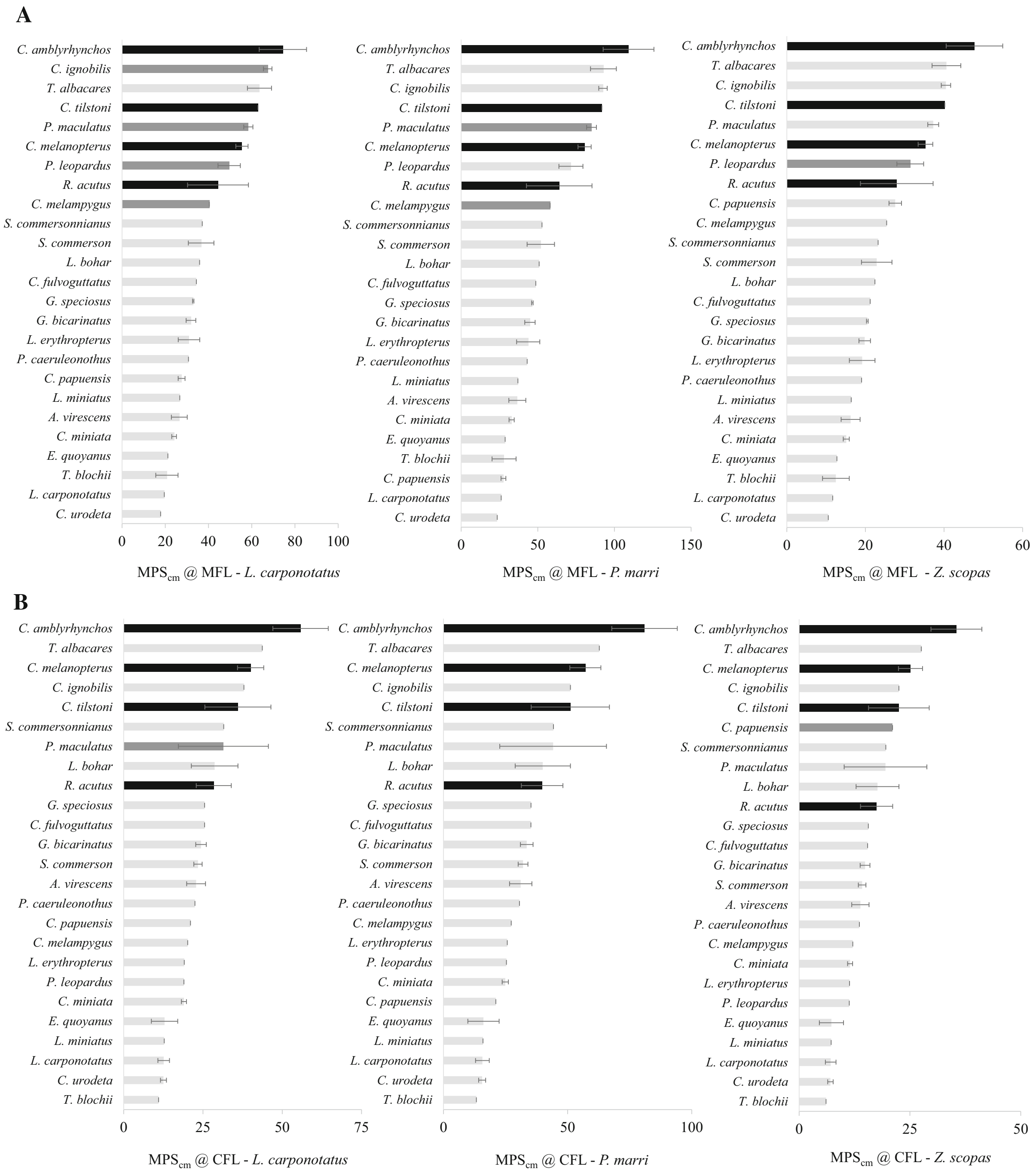

Fig. 3 Maximum prey sizes (MPS$_{cm}$ ± SE) for predators at their **A** maximum fork length (MFL) and **B** common fork length (CFL), ranked in descending order. MPS$_{cm}$ was estimated based on three potential prey species: *L. carponotatus*, *P. marri* and *Z. scopas*. Sharks are indicated in black, potential competitors (identified as having MPS$_{cm}$ values within 10% of that of a larger shark species) in dark grey and other teleosts in pale grey. See Table 2 for MPS$_{cm}$ values

Table 3 Teleost competitors to sharks in terms of maximum prey size (MPS_{cm}) at the maximum (MFL) and common (CFL) fork lengths. Competitors were identified based on whether their MPS value was within 10% of that of a larger shark, with the lower boundary of that range indicated in "MPS-10%". Where no teleost species met this criteria, "None" is indicated. While competitors were relatively common at MFLs, there were far few competitors at CFLs. See Fig. 3

	MFL						CFL					
	LC		PM		ZS		LC		PM		ZS	
	MPS-10%	Competitor	MPS-10%	Competitor	MPS-10%	Competitor	MPS-10%	Competitor	MPS-10%	Competitor	MPS-10%	Competitor
C. amblyrhynchos	66.96	*C. ignobilis*	98.28	None	42.93	None	50.22	None	72.9	None	31.95	None
C. tilstoni	56.61	*P. maculatus*	82.62	*P. maculatus*	36.18	*P. maculatus*	32.4	None	45.99	None	20.25	*C. papuensis*
C. melanopterus	49.95	*P. leopardus*	72.45	None	31.77	None	36	*P. maculatus*	51.39	None	22.59	None
R. acutus	39.96	*C. melampygus*	57.6	*C. melampygus*	25.2	None	25.56	None	35.73	None	15.75	None

and sharks were outranked by 5–6 species of teleost, while under CFL, sharks were outranked by *C. ignobilis* and represented four species among twelve (Fig. 4B[d]). Sharks were absent from the smallest predator size class, 0–25 cm, as young of these species are born at sizes greater than 30 cm (Supp. Figs. S2D, S3).

Relative maximum prey size ($MPS_{\%}$)

The darkfin hind *Cephalopholis urodeta,* the longfin grouper *Epinephelus quoyanus,* the coral hind *Cephalopholis miniata*, *L. carponotatus* and *P. maculatus* consistently displayed the highest $MPS_{\%}$ values (Table 2 and Fig. 5). The $MPS_{\%}$ value for *C. urodeta*, the highest-ranking species, ranged from 64.1% (*LC*) to 80.6% (*PM*) and 36.5% (*ZS*). Lutjanids were also characterised by relatively large $MPS_{\%}$ values with *L. bohar,* for example, displaying $MPS_{\%}$ values of 46.6% (*LC*), 60.6% (*PM*) and 27.0% (*ZS*). Shark species, in contrast, were characterised by low- to mid-ranking $MPS_{\%}$ values, ranging from 31.4–39.4% (*LC*) to 41.5–55.4% (*PM*) and 18.6–24.4% (*ZS*). Among the sharks, *C. amblyrhynchos* consistently displayed the highest $MPS_{\%}$ value, followed by *C. melanopterus, C. tilstoni, R. acutus* and *C. coatesi.* When *PM* was substituted for *LC*, $MPS_{\%}$ values increased on average by 33.5%, with sharks displaying some of the largest relative increases (+ 31.5–41.6%). In contrast, when *ZS* was substituted for *LC*, $MPS_{\%}$ values declined on average by 40%. Mean $MPS_{\%}$ values were highest for the second lowest trophic group (46.9%; 4–4.24), while the highest MPS_{cm} value (45.8 cm) was associated with the second highest trophic group, 4.25–4.49 (Supp. Fig. S4).

There was also a significant inverse relationship between mean $MPS_{\%}$ and both log MFL and log CFL, regardless of prey body shape, indicating that larger-bodied teleosts tend to have smaller maximum prey sizes as a proportion of their own length compared to smaller-bodied fishes (see Fig. 6 for *LC* and Supp. Fig. S5 for *PM* and *ZS*; see Supp. Table S3 for regression statistics). Mean $MPS_{\%}$ for *C. coatesi* was not included in the regression analysis but lay within the range of values observed for the other reef sharks.

The slope values (B_1) derived from linear regression of $MPS_{\%}$ against individual predator size differed significantly between sharks and teleosts when the prey was *L. carponotatus* (two-tailed *t*-test assuming

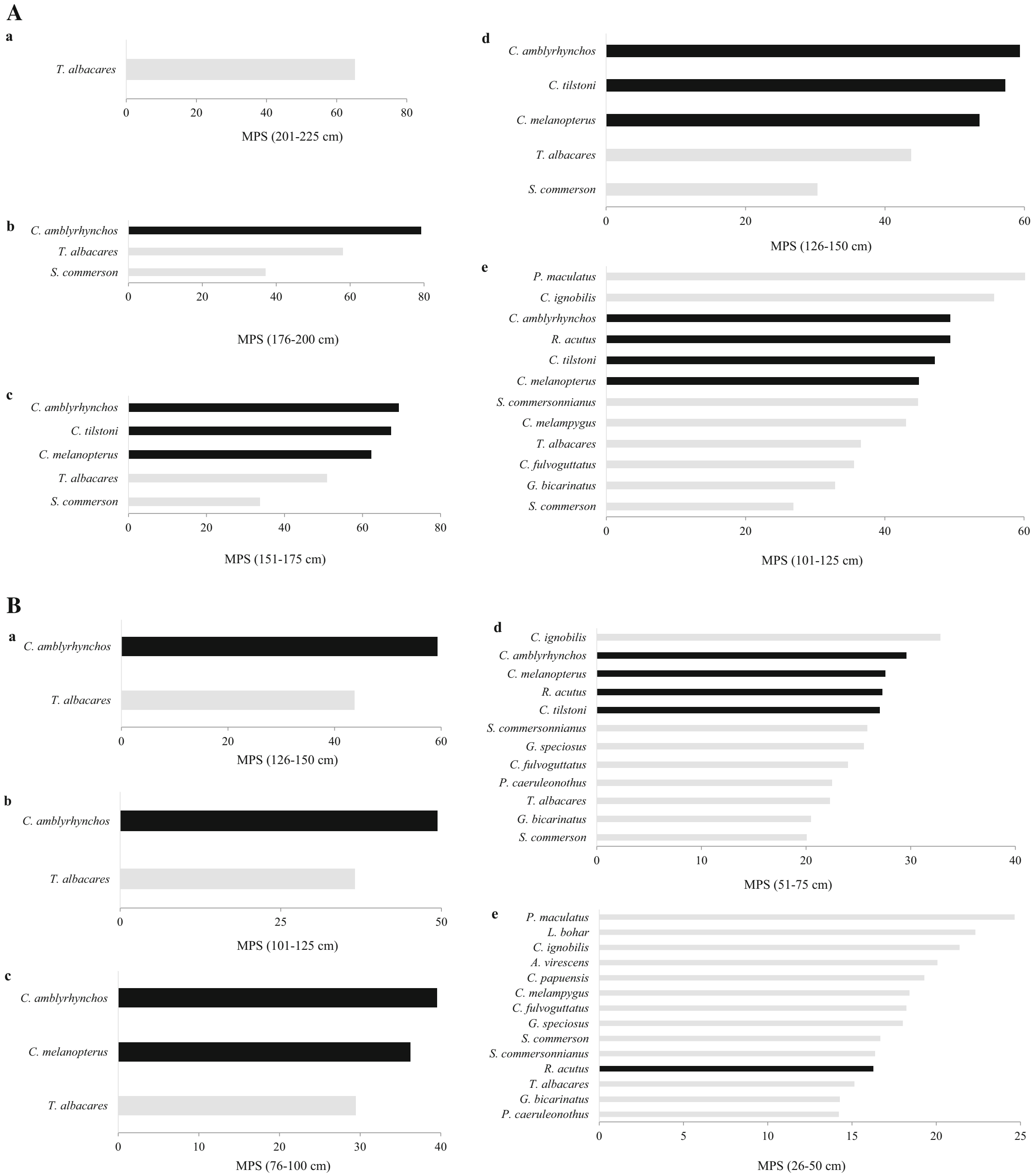

Fig. 4 Maximum prey size (MPS$_{cm}$) for a range of predator size classes, assuming either **A** maximum reported fork length (MFL) or **B** common reported fork length (CFL) as the largest size for each species. See Supp. Figs. 2 and 3 for smaller size classes and Table 2 for MPS values

unequal variance; 0.059 ± 0.013% vs − 0.14 ± 0.042%, n = 25, t = 2.66, $p = 0.016$) but not for *P. marri* (0.16 ± 0.046% vs 0.060 ± 0.098%, n = 25, t = 0.76, $p = 0.24$) or *Z. scopas* (0.062 ± 0.0080% vs − 0.0014 ± 0.015%, n = 25, t = 1.21, $p = 0.14$). The slope values for three shark

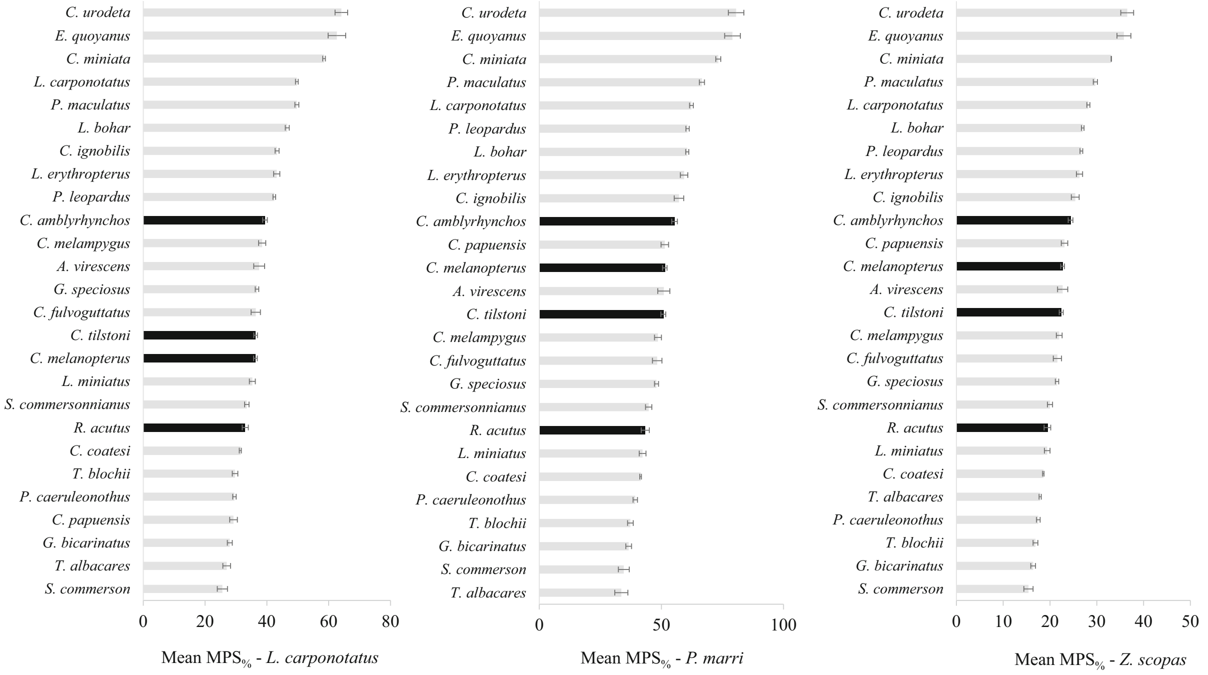

Fig. 5 Mean maximum prey size as a proportion of predator length (MPS$_{\%}$) for three potential prey species, *L. carponotatus*, *P. marri* and *Z. scopas*. See Table 2 for mean MPS$_{\%}$ values

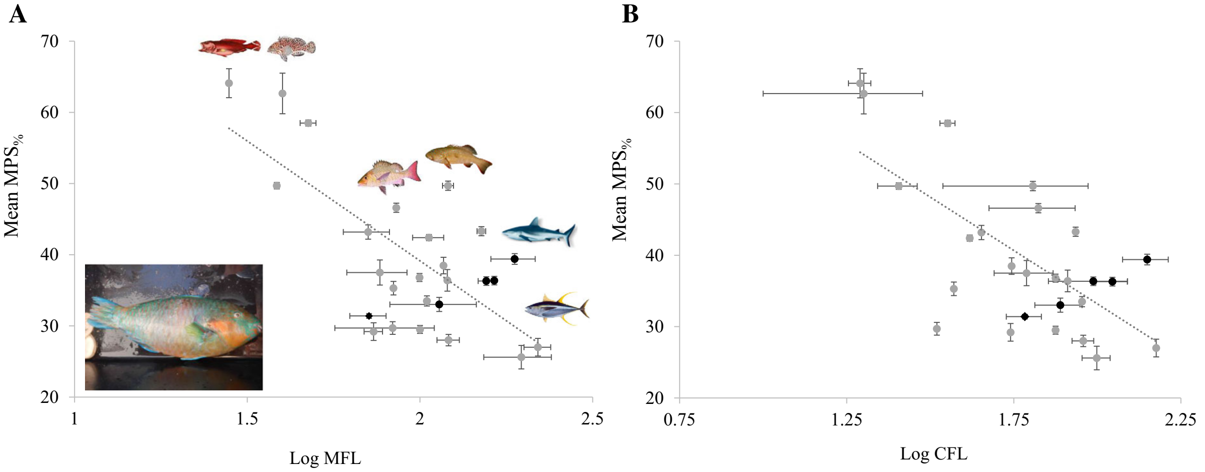

Fig. 6 Maximum prey size (MPS$_{\%}$ ± SE) plotted against log **A** maximum fork length (MFL) (MPS$_{\%}$ = − 33.7 × log MFL + 106.5, n = 25, R^2 = 0.51) and **B** common fork length (CFL) (MPS$_{\%}$ = − 29.9 × log CFL + 93.0, n = 25, R^2 = 0.46) for 26 species including sharks (black) and teleosts (grey). The analyses were conducted for three different prey species, however only that of *L. carponotatus* is presented here (see Supp. Fig. S5 for *P. marri* and *Z. scopas*). The whitecheek shark *C. coatesi* is indicated by a black diamond marker but was not included in the analysis due to low sample sizes (n = 2). Illustrations of representative species are, from left to right: darkfin hind *C. urodeta,* longfin grouper *E. quoyanus*, twin-spot red snapper *L. bohar*, spotted coralgrouper *P. maculatus*, grey reef shark *C. amblyrhynchos* and yellowfin tuna *T. albacares.* Also inset is a photo of a whole scarid prey removed from the mouth of a blacktip reef shark

Table 4 Statistics associated with three linear regressions: (1) gape height (GH) versus fork length (FL), (2) gape width (GW) versus FL and (3) $MPS_{\%}$ versus predator FL for three prey shapes, *L. carponotatus* (*LC*), *P. marri* (*PM*) and *Z. scopas* (*ZS*). Values for the intercept (B_0), slope (B_1) and the coefficient of variation (R^2) are presented for each regression

Species	GH versus FL			GW versus FL			$MPS_{\%}$ versus FL								
							LC			*PM*			*ZS*		
	B_0	B_1	R^2	B_0	B_1	R^2	B_0	B_1	R^2	B_0	B_1	R^2	B_0	B_1	R^2
Cephalopholis urodeta	− 0.74	0.21	0.85	− 0.65	0.22	0.52	63.35	0.04	0.00	61.47	0.91	0.04	29.84	0.32	0.03
Lutjanus carponotatus	− 0.37	0.15	0.87	− 1.10	0.19	0.84	46.83	0.11	0.01	43.80	0.68	0.19	21.50	0.25	0.14
Epinephelus quoyanus	1.00	0.12	0.92	0.81	0.15	0.93	76.49	− 0.55	0.56	90.00	− 0.43	0.27	41.40	− 0.22	0.34
Cephalopholis miniata	0.59	0.14	0.67	0.51	0.15	0.75	75.86	− 0.72	0.30	77.41	− 0.17	0.00	36.40	− 0.14	0.01
Caranx papuensis	0.29	0.11	0.84	− 0.48	0.13	0.84	47.80	− 0.17	0.13	51.68	0.00	0.00	24.33	− 0.03	0.01
Aprion virescens	− 2.31	0.15	0.93	1.71	0.09	0.99	52.82	− 0.25	0.27	68.30	− 0.28	0.17	30.73	− 0.13	0.19
Gnathanodon speciosus	0.36	0.10	0.67	0.27	0.11	0.76	41.97	− 0.11	0.08	48.62	− 0.01	0.02	22.48	− 0.02	0.01
Lethrinus miniatus	− 0.15	0.14	0.44	− 0.21	0.10	0.32	44.05	− 0.28	0.04	44.39	− 0.07	0.00	21.31	− 0.06	0.00
Carangoides fulvoguttatus	1.23	0.07	0.83	1.56	0.08	0.72	48.70	− 0.23	0.48	60.40	− 0.23	0.29	27.50	− 0.11	0.33
Lutjanus erythropterus	2.34	0.08	0.61	− 1.34	0.16	0.76	41.99	0.02	0.00	51.00	0.15	0.04	23.30	0.05	0.03
Lutjanus bohar	0.99	0.12	0.86	0.32	0.13	0.87	55.07	− 0.20	0.24	60.50	0.00	0.00	27.82	− 0.02	0.01
Trachinotus blochii	1.54	0.06	0.31	0.81	0.07	0.62	40.57	− 0.24	0.36	45.41	− 0.18	0.12	21.18	− 0.09	0.17
Scomberoides commersonnianus	0.20	0.10	0.92	− 1.69	0.13	0.93	29.47	0.07	0.13	32.48	0.20	0.36	15.21	0.08	0.31
Plectorhinchus caeruleonothus	− 2.64	0.15	0.76	− 1.58	0.12	0.81	25.90	0.05	0.05	27.45	0.18	0.21	13.00	0.07	0.17
Grammatorcynus bicarinatus	1.23	0.10	0.74	− 0.14	0.09	0.80	31.99	− 0.06	0.10	− 0.59	0.38	0.80	16.31	0.00	0.00
Caranx melampygus	0.43	0.09	0.98	− 0.10	0.11	0.95	42.82	− 0.11	0.34	48.00	0.02	0.00	22.40	− 0.01	0.01
Plectropomus leopardus	− 0.19	0.13	0.90	− 1.00	0.16	0.87	45.28	0.01	0.00	53.51	0.17	0.07	24.61	0.06	0.05
Rhizoprionodon acutus	− 4.37	0.16	0.81	− 2.91	0.16	0.83	21.21	0.22	0.26	18.70	0.47	0.40	9.32	0.19	0.37
Carcharhinus melanopterus	− 0.51	0.11	0.64	− 0.33	0.12	0.60	40.17	− 0.04	0.02	53.14	− 0.02	0.00	23.78	− 0.01	0.00
Plectropomus maculatus	− 0.69	0.16	0.92	− 0.54	0.17	0.95	51.13	− 0.03	0.01	61.09	0.13	0.08	28.02	0.04	0.04
Carcharhinus tilstoni	− 2.05	0.11	0.67	− 0.80	0.13	0.90	32.65	0.04	0.11	41.30	0.11	0.26	18.67	0.04	0.23
Caranx ignobilis	− 1.07	0.14	0.86	− 1.27	0.16	0.92	41.36	0.03	0.02	51.06	0.09	0.02	23.29	0.03	0.01
Scomberomorus commerson	1.97	0.09	0.52	3.00	0.04	0.33	44.39	− 0.21	0.47	57.14	− 0.25	0.37	25.73	− 0.11	0.39
Thunnus albacares	− 0.49	0.10	0.93	1.94	0.10	0.91	27.85	− 0.01	0.00	35.51	− 0.03	0.00	16.86	0.02	0.05
Carcharhinus amblyrhynchos	0.32	0.10	0.48	− 0.85	0.14	0.86	38.92	0.01	0.00	49.95	0.06	0.04	22.51	0.02	0.03

species (*C. amblyrhynchos*, *C. tilstoni* and *R. acutus*) were positive regardless of prey body shape (Table 4), suggesting that $MPS_{\%}$ increased with body size for the majority of sharks considered. In contrast, the majority of teleosts had negative slope values, at least for prey *LC* and *ZS*, suggesting that $MPS_{\%}$ decreases with body size, although there were exceptions such as *C. ignobilis* and *L. erythropterus.*

Discussion

Our results suggest that some ecological redundancy in terms of gape and maximum prey size exists between sharks and teleosts, particularly at smaller sizes. However, at larger sizes, sharks may be able to consume larger prey than any other teleost. *Carcharhinus amblyrhynchos* consistently outranked all other species in terms of maximum prey size, despite its relatively small gape, with $GH_{\%}$ and $GW_{\%}$ values of 10.9% and 12.8%, respectively. Indeed, at its maximum recorded size, *C. amblyrhynchos* was the only predator capable of consuming fusiform prey 67–74 cm in length or deep-bodied prey 41–48 cm long and *T. albacares* and *S. commerson*, despite attaining larger maximum lengths than *C. amblyrhynchos*, appear to be limited to smaller prey by their relatively small gapes. Teleosts with relatively large gape sizes as a proportion of their length, such as *C. ignobilis* and *P. maculatus*, also displayed lower maximum prey sizes (67.4 cm and 58.4 cm, respectively, assuming a fusiform prey) than *C. amblyrhynchos,* due to their relatively small maximum body sizes.

At common or more "ecologically realistic" sizes, our results suggest that ecological redundancy may decline still further among the largest reef predators in terms of gape. At common lengths, assuming a fusiform prey, *C. amblyrhynchos* is potentially the sole regulator of size structure in prey 44–56 cm in length. Notably, sharks had far fewer competitors when assessed at common rather than maximum sizes and, indeed, only *C. tilstoni* and *C. melanopterus* were identified as having competitors, assuming a deep-bodied and fusiform prey, respectively. Overall, these results suggest that fewer teleost species have the potential to act as "understudies" to large sharks when assessed at common rather than maximum reported sizes, such that the former may have limited capacity to compensate ecologically for the latter's effect on the size structure of reef assemblages.

Further evidence for limited ecological redundancy between large sharks and teleosts was provided by the size class analysis, particularly when species were compared based on common length. Sharks outranked teleosts in terms of maximum prey size in the top three size classes in which they featured, when assessed based on maximum reported lengths. *Carcharhinus amblyrhynchos, C. tilstoni* and *C. melanopterus* displayed the highest MPS_{cm} values in size classes 151–175 cm and 126–150 cm, such that sharks were the only species regulating prey 51–69 cm and 44–59 cm in length in each size class, respectively. Sharks also outranked teleosts in terms of MPS_{cm} in the top three size classes when the size class analysis was based on common lengths, however fewer teleost species were present in each size class, such that ecological redundancy was, effectively, reduced. For example, based on maximum lengths, sharks comprised three out of the five species in size class 126–150 cm and four out of 12 species in size class 101–125 cm, whereas when the analysis was based on common length, sharks comprised just one of two species in these size classes, and in both cases had an MPS that was ~ 35% higher than that of its closest competitor, *T. albacares.*

While our study suggests that *T. albacares, C. ignobilis*, *P. maculatus* and *P. leopardus* may, to some degree, compete with large-bodied reef sharks in terms of gape and maximum prey size, we note that some of these species diverge dramatically from sharks in behaviour and life history. *Carcharhinus amblyrhynchos* is found at depths up to four times greater than any teleost species included in this analysis and reaches an age almost twice that of most other species. It displays relatively high reef fidelity (White et al. 2017; but see Heupel et al. 2010) and consumes a mixture of reef-associated and pelagic prey (McCauley et al. 2012). In contrast, *T. albacares* is primarily a pelagic predator that undergoes migrations of 100 s to 1000 s of kilometres (Ely et al. 2005). Moreover, although we identified members of the genus *Plectropomus* as possible competitors to *C. tilstoni* and *C. melanopterus* in terms of gape, these teleosts are typically facultative structure users that rely on live branching corals as refugia (Wen et al. 2012; Kerry and Bellwood 2014). In contrast, many reef sharks actively avoid structure, preferring the open water column in high-energy fore-reef habitats (Roff et al. 2016). As such, many of the competitors identified here in terms of gape likely sculpt somewhat different landscapes of fear, across different habitats and depth scales, to reef sharks, limiting ecological redundancy in certain aspects.

Sharks were characterised by distinctively low gape height values as a proportion of body size, with two shark species displaying the lowest recorded $GH_{\%}$ values (7.6% and 10.9%). Teleost species, in contrast, attained $GH_{\%}$ values of up to 18%. Moreover, teleost species were characterised by a relatively broad range of $MPS_{\%}$ values (*LC*: 25.6–64.1%; *PM*: 33.6–80.6% and *ZS*: 15.4–36.5%) whereas all five species of shark may be constrained to consuming prey within a much narrower range of values (*LC*: 31.4–39.4%; *PM*: 41.5–55.4% and *ZS*: 18.6–24.4%). Given that the shark species in this study were characterised by a mean $MPS_{\%}$ of 36.6% for fusiform prey, with even lower values (22.2%) associated with deep-bodied prey, we note that our results are also consistent with gut contents studies suggesting that reef sharks do not consume prey greater than ~ 36% of their own length (Bethea et al. 2004; Baremore et al. 2009). Moreover, we observed a regurgitated Quoy's parrotfish *Scarus quoyi* and a shovelnose ray *Rhinobatidae* sp. inside the upper digestive tracts of *C. melanopterus*, with both specimens intact and characterised by body depths equal to or less than the gape width of the sampled shark and fork lengths 36–38% of that of the shark. These two records provide some independent evidence consistent with gape-limitation being the primary or "quotidian" mechanism determining upper prey size in reef sharks.

Our analysis also identified an inverse relationship between mean $MPS_{\%}$ and maximum and common size in teleosts. As such, the smallest fish species featured in the study, *C. urodeta*, appears to be able to consume the largest prey as a proportion of its body length whereas the largest species, *S. commerson*, was characterised by relatively low $MPS_{\%}$ values. In contrast, our results suggest that the opposite trend exists among shark species, with mean $MPS_{\%}$ increasing with maximum and common fork length and slope values (B_1) derived from linear regression of $MPS_{\%}$ against individual predator size differing significantly between sharks and teleosts for fusiform prey. We note that sharks and teleosts diverged approximately 400 million years ago, prior to major radiations in the teleost lineage (Wilga et al. 2007; Near et al. 2012). Moreover, teleosts are potentially descended from an inertial suction feeder whereas a "biting" ancestor may have given rise to sharks (Lauder 1985; Motta et al. 1997, 2002) and teleosts can closely regulate the speed and timing of their jaw muscles, whereas sharks have a relatively short jaw that increases bite force but reduces maximum vertical gape and upper jaw mobility (Motta et al. 1997, 2002).

The relationship between $MPS_{\%}$ and fork length points to another difference between teleosts and sharks. The majority of teleost species displayed negative slopes when $MPS_{\%}$ was regressed against individual fork length, a trend that may be adaptive, allowing individuals to feed most effectively, and therefore grow most rapidly, when they are smallest and the pool of potential predators is largest (Johansen et al. 2015). The negative relationship between $MPS_{\%}$ and length in teleosts may also reflect the "biomass pyramid" effect, as large-bodied prey are typically rarer than small prey (Trebilco et al. 2013). Moreover, while large meals are more profitable than smaller meals, their consumption may compromise swimming and other activities by diverting finite oxygen supplies towards digestion (Norin and Clark 2017). In contrast, the majority of shark species displayed the opposite trend, such that $MPS_{\%}$ values increased with individual body size, with a significant difference in slope values existing between sharks and teleosts for a fusiform prey. The physiology of sharks differs substantially from teleosts (Treberg and Speers-Roesch 2016) with the former characterised by, for instance, longer digestion times and greater inter-meal intervals (Wetherbee et al. 1990). Thus, sharks may arguably experience greater selective pressures than teleosts to be able to consume larger prey items.

Our analyses also provide evidence for ecological redundancy between small sharks and teleosts, consistent with recent studies such as Frisch et al. (2016) and Roff et al. (2016). For example, in size class 101–125 cm, *P. maculatus* and *C. ignobilis* outranked sharks, displaying MPS values of 60.6 cm and 55.7 cm, respectively, compared to the 49.4 cm MPS value displayed by *C. amblyrhynchos*, assuming maximum reported sizes. Indeed, our results suggest that *C. ignobilis* may be the most ecologically "analogous" competitor to reef sharks, due to its relatively low $MPS_{\%}$ value (43.3% for fusiform prey), large gape width relative to gape height and increasing

MPS$_{\%}$ values with body size. In addition, *C. ignobilis* reaches large sizes, consumes both teleosts and invertebrates via ram feeding and is relatively site-attached (Meyer et al. 2007). Moreover, *C. ignobilis* can not only kill sharks (McPherson et al. 2012) but has also been observed being escorted or "shadowed" by smaller sharks on the Great Barrier Reef (pers. comm. Richard Schumann), suggesting that it may display competitive superiority (i.e. "freedom" from risk effects) when the size ratio is favourable. *Plectropomus maculatus* may also act as an important competitor and/or ecological substitute for some reef sharks as it preys on small size classes within similar taxa such as the Apogonidae, Pomacanthidae and Clupeidae (Kingsford 1992) and is characterised by an unusually low suction index compared to other serranids, engaging instead, like sharks, in high-speed attacks on prey (Oufiero et al. 2012). Moreover, *P. maculatus* belongs to a genus that typically has a "designated" home range yet is also relatively mobile (Zeller 1997; Samoilys 1997), characteristics that are also displayed by many reef sharks (Papastamatiou et al. 2009; Roff et al. 2016). Lastly, *R. acutus* and its potential competitor, *C. melampygus*, both inhabit a mixture of pelagic and reef environments and display ram feeding (Froese and Pauly 2019).

Strong evidence for ecological redundancy in terms of gape between sharks and teleosts was also found in the smaller size classes. For example, the maximum prey size of *R. acutus* in the 26–50 cm size class (16.3 cm) was half that of a similar-sized *C. urodeta* (31.6 cm), and similar to that of a *C. urodeta* in the smallest size class (0–25 cm). Furthermore, sharks were outranked in terms of maximum prey size by more than five teleost species in size classes 51–75 cm and 76–100 cm, while some teleosts in size class 101–125 cm may have large enough gapes to consume newborn sharks (e.g. *P. maculatus*, with an MPS of 60.6 cm). Sharks and teleosts also displayed some ecological redundancy in terms of trends in gape width, such that, in the majority of predators, scombrids excluded, gape width typically exceeded gape height at a given length in addition to increasing more rapidly than gape height in relation to length, with 72% of species in the analysis displaying this trend.

A reasonable case can also be made for some ecological redundancy between shark species in terms of gape. Given that *C. amblyrhynchos* may be characterised by the largest maximum prey size of all reef predators at its largest sizes, it may therefore, in theory, be capable of compensating, at least in terms of gape, for any other species of shark. There was also substantial cohesion between shark species as they graduated through the size classes, with *C. amblyrhynchos*, *C. tilstoni* and *C. melanopterus* ranked consecutively in terms of MPS in several of the larger (> 100 cm) size classes. Indeed, our results suggest that *C. tilstoni* and *C. melanopterus* may display similar MPS$_{\%}$ values regardless of prey body shape (~ 36% for a fusiform prey) in addition to similar values of gape width as a proportion of length (11.6 ± 0.22% and 11.9 ± 0.21%, respectively). In theory, selective forces should drive competitors that overlap in one dimension to diverge in other dimensions (Connell 1980) and diversification of gape and other feeding apparatuses as a strategy to limit competition has been reported in a range of taxa (e.g. Kelly et al. 2016). In contrast, our analysis seems to be suggestive of two shark species overlapping in terms of gape and maximum prey size, despite potentially competing in other aspects.

Caveats

While our analyses focused on gape size, piscivores do not necessarily consume the largest prey possible and may instead feed preferentially on relatively small fishes (Bachiller and Irigoien 2013). Indeed, smaller prey are characterised by shorter handling times, reduced risk of injury and lower burst escape speeds than larger prey, plus their digestion is less likely to compromise competing energy-demanding processes (Ferry-Graham 2002; Scharf et al. 2003; Dörner et al. 2007; Norin and Clark 2017; Simkins and Belk 2017), although Scharf et al. (2003) concluded that prey manueverability may be more important a contributor to vulnerability than escape speed. Our results support this idea to some extent, as we found that predators in the trophic group 4.25–4.50 displayed higher MPS$_{\%}$ values than predators in the highest trophic group. Despite this caveat, there are also clear energetic advantages associated with attacking larger prey, thus gape limitation is still an ecologically important factor regulating prey choice (Goatley and Bellwood 2009; Norin and Clark 2017). Moreover, predators likely regulate prey behaviour in all vulnerable size classes via risk effects, regardless of what size of prey is typically consumed (Creel and Christianson 2008).

Another caveat is the possibility that we excluded some competitor species from the analysis, as coral reefs have high biodiversity relative to other ecosystems (Dunic and Baum 2017). However, we note that our study species were some of the most common representatives of the mesopredator guild at the study sites and that, even if some species were excluded, the results for each species are likely representative of other mesopredators with similar gapes and life history traits. Moreover, many teleosts have pharyngeal jaws that grasp prey within the oral cavity and may influence maximum prey size independently of the oral jaw gape (Mabuchi et al. 2007; Mehta and Wainwright 2007). However, we do not feel this was an influential factor in our study as there is good evidence that oral gape, rather than any internal gape dimensions, is the main determinant of maximum prey size in reef fishes due to the compressibility in food items (Mihalitsis and Bellwood 2017).

Conclusions

In 1926, William Beebe, a zoologist who was among the first to dive among reef sharks with the aid of a copper helmet, dismissed sharks as ecologically redundant. “Arousing no fear” in other fishes, sharks were inferior competitors to serranids, he concluded. “No shark was quicker, nor by a long way as effective in attack upon any fish… as these evil-mouthed fish,” Beebe commented. A century later, the ecological importance of sharks continues to be questioned. Reef sharks clearly overlap in prey type and habitat use with other reef mesopredators, guaranteeing a degree of ecological redundancy (Frisch et al. 2016; Roff et al. 2016). However, the differences in gape and maximum prey size reported in this study suggest that the largest reef sharks have the potential to have a singular effect on the size structure of reef food webs. Indeed, while *C. ignobilis* and *P. maculatus* emerge as potential ecological analogs to some shark species, our results do not support the hypothesis that a diverse array of mesopredatory teleosts exist on coral reefs that can compensate ecologically for reef sharks at their largest sizes, should the latter decline in abundance.

Our findings contribute new knowledge to conservation discussions regarding predators on coral reefs. Coral reefs and other ecosystems characterised by limited ecological redundancy are less resilient to disturbance (Bellwood et al. 2003; Hughes et al. 2005; Mouillot et al. 2014; D’agata et al. 2016). Moreover, fishing has caused substantial declines in sharks in the last century (Ward-Paige et al. 2010) and selectively removes larger, older individuals, causing mean sizes to decline (Anderson et al. 2008). As such, sharks may no longer attain the sizes that we identify here as necessary to exert a unique effect on the size structure of prey assemblages. For example, Barley et al. (2017b) found that the mean length of shark on reefs targeted by shark fishers in northwestern Australia was ~ 100 cm, yet at this size our study suggests that they would be outranked in terms of maximum prey size by five species of teleost. Moreover, shark fishing is typically accompanied by the removal of the few teleost species that could partially compensate for reef sharks, which may further lead to fisheries-induced selection in teleosts, whereby populations become dominated by rapidly-growing, early-maturing individuals (Clark et al. 2017). Protection of reef resilience may therefore rely not simply on the conservation of sharks with natural size distributions, but also their closest ecological analogs.

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