

Foraging mode of the grey reef shark, *Carcharhinus amblyrhynchos*, under two different scenarios

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Abstract Knowledge of an animal's predatory interactions provides insight into its ecological role. Until now, investigation of reef shark predation has relied on artificial stimuli to facilitate feeding events, with few sightings of natural predation events. Here we document two different foraging modes of the grey reef shark, *Carcharhinus amblyrhynchos* (f. Carcharhinidae), recorded without the influence of baits or burley. The first mode saw an aggregation of sharks targeting a morning mass spawning event of marbled grouper (f. Serranidae). We observed 120 separate grouper spawns over a 104-min period. Detailed analysis of 52 spawns showed an average of five groupers and 2.7 sharks involved in each spawn, with sharks usually on site within 1.29 s of spawn initiation. The success rate of investigating sharks was relatively low (8.1 %), and conspecific competition, rather than cooperative behaviour, was repeatedly observed among sharks. The second foraging mode documented was the nocturnal predation of individual fishes in the same reef pass 2 weeks later. Here, 128 separate fish pursuits were observed, with fusiliers (f. Caesionidae) comprising 88 % of targeted individuals. Multiple sharks usually investigated each fish, with over 300 interaction events recorded. Over 100 bite attempts

were observed, and again the rate of predation was low, with fish taken in only 5.3 % of investigations (16 % of attempted bites). Our findings show that grey reef sharks naturally prey on species across a range of trophic levels, employing foraging techniques optimised for prey species and circumstance. Although a high-order mesopredator, the low rates of predation success observed suggest that grey reef sharks may have limited direct impact on lower-trophic-order species; however, this remains to be verified.

Keywords Prey selection · Feeding · Kinematics · Predation · Carcharhinid · Diet

Introduction

Reef sharks (f. Carcharhinidae) are medium-sized sharks, ubiquitously distributed across the tropical Indo-Pacific. The three species most commonly sighted on Indo-Pacific coral reefs are the grey reef shark, *Carcharhinus amblyrhynchos*; the blacktip reef shark, *C. melanopterus*; and the whitetip reef shark, *Triaenodon obesus* (Robbins 2006; DeMartini et al. 2008; Rizzari et al. 2014a). These species are found across all reef habitats, with *C. amblyrhynchos* and *T. obesus* predominantly found at resource-rich areas of high current, such as reef edges and drop-offs (Robbins 2006; Rizzari et al. 2014a). All three species of reef shark are born at a size comparable to the adults of many reef teleost predators (Robbins 2006; Chin et al. 2013), potentially offering each species a wide variety of prey choices from birth. However, observations of natural reef shark predations are rare due to their relative scarcity compared to teleost fauna, even on relatively undisturbed reef systems (Sandin et al. 2008; Rizzari et al. 2015).

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Reef shark predatory behaviours were first investigated in the 1960s, when a variety of bait, burley and acoustic attractants were used to evaluate the sensory cues of wild animals (Hobson 1963; Tester 1963). These studies found that *C. amblyrhynchos* was the most aggressive species towards potential prey items placed mid-water, preying on all bait types offered (Hobson 1963). *Carcharhinus amblyrhynchos* also appeared to be the species most sensitive to olfactory cues, responding vigorously to scents in the water (Hobson 1963; Tester 1963). These experiments provided valuable information on reef sharks' stimulus responses and demonstrated the variety of senses that reef sharks use to detect potential prey items. The studies also highlighted the potential dominance of *C. amblyrhynchos* over other reef shark species, especially for prey items located above the substrate. However, they could not examine natural predation events.

Natural reef shark predation events have since been surmised through stomach content analysis of captured individuals (Randall 1977; Salini et al. 1992; Papastamatiou et al. 2006). Reef sharks appear to have a predominantly piscivorous diet, with smaller proportions of cephalopods, muraenids, crustaceans and molluscs (Randall 1977; Salini et al. 1992; Wetherbee et al. 1997). Similar to other sharks and tropical fish predators (McElroy et al. 2006; Papastamatiou et al. 2006; Hernaman et al. 2009), species such as *C. amblyrhynchos* appear to be somewhat opportunistic with their diet, preferentially targeting more abundant prey types (Salini et al. 1992; Brewer et al. 1995). On coral reefs, identifiable prey species include larger teleosts from the families Acanthuridae, Monacanthidae and Labridae, together with smaller species such as those from the families Holocentridae and Pomacentridae (Papastamatiou et al. 2006).

Dietary analyses suggest that carcharhinid sharks occupy a high trophic niche (Cortés 1999), with many considered to be mesopredators which are occasionally preyed on by larger shark species (e.g., Mourier et al. 2013). Non-lethal analysis of reef shark stable isotopes supports the high trophic classification of reef sharks, with *C. amblyrhynchos* occupying highest trophic position of the three commonly sighted reef shark species (Speed et al. 2012). The trophic position of *C. amblyrhynchos* increases with body size, suggesting an ontogenetic shift towards larger prey items as *C. amblyrhynchos* grows; however, continued high levels of $\delta^{13}\text{C}$ across all body sizes also suggest that the species retains some reliance on lower-trophic-order species (Speed et al. 2012).

As *C. amblyrhynchos* is often the most abundant reef shark recorded in high-energy coral reef habitats (Robbins 2006; Graham et al. 2010; Rizzari et al. 2014a), this species has a high potential to exert a regulatory role in coral reef trophodynamics. However, the extent to which reef sharks

exert top-down control on coral reefs is unclear as natural shark predation rates have not been quantified. As reef sharks are heavily impacted by anthropological disturbances such as fishing (Friedlander and DeMartini 2002; Robbins et al. 2006; DeMartini et al. 2008), determining the potential role of reef sharks on coral reefs is an important consideration for coral reef management. An important step in this process is to investigate the range of species that reef sharks target and successfully prey on in the wild.

In this study, we document two different foraging modes of *C. amblyrhynchos* and quantify the success rates of each mode. Importantly, no burley or baits were employed; diver presence and sometimes artificial lighting were the only non-natural stimuli. This allowed us to investigate *C. amblyrhynchos* prey selection and foraging behaviours under essentially natural conditions.

Materials and methods

Location

Sampling took place at Fakarava Atoll, in the French Polynesian Tuamotu group (16°31.137'S; 145°27.660'W). This rectangular atoll encompasses an area of approximately 1110 km², with 16 km² of low-lying land. The population comprises fewer than 900 people, living predominantly in the north-eastern village of Rotoava. The southern end of the atoll has a deep (~35 m) pass, with the channel width ranging from ~350 m at the mouth to ~120 m at its narrowest point. The shark interactions observed in this study took place at the mouth of or within this southern pass.

Sampling

Data were extracted from underwater video footage taken during the June 2013 filming of a Khaled bin Sultan Living Oceans Foundation documentary, *Sharks of the Coral Canyon*. A professional film crew was employed to document the once-per-year winter spawning of the marbled grouper *Epinephelus polyphekadion*. The spawning event took place at the mouth of the pass, at ~35 m depth during the incoming morning tide, and was recorded by up to six cameras from its beginning until completion. Camera operators remained loosely together, but attempted to capture different sections of the spawning event. Cameras used included a RED EPIC, Sony EX, Canon 5D MkII and a Panasonic GH2. Additional recordings were captured by the lead author using a Sony Action Cam and GoPro Hero2 HD video camera and were analysed in conjunction with the professional footage.

Nocturnal *C. amblyrhynchos* fish predation events were recorded ~300 m inside the southern Fakarava reef pass 2 weeks after the spawning event. Divers entered the water at 2220 hrs and began filming soon after. Interactions took place immediately above the benthos and were illuminated using underwater filming lights. No baits, visual or olfactory attractants were used to entice or excite the sharks, and the divers remained in the same approximate area throughout the dive.

Analysis

Footage of both components was collated and manually analysed on shore by the lead author, using either AVS video editor or RED player. Analyses were separated into the daytime *E. polyphekadion* spawning and the nocturnal predations 2 weeks later.

Grouper spawning

The number of *E. polyphekadion* spawns, time of spawning events, number of fish involved in each spawn, number of sharks entering the spawn cloud and fate of the fish were determined in all footage. The spawning rushes of *E. polyphekadion* typically took around 2 s to complete and were deemed to begin when one or more of the fish involved first reached a vertical orientation. Sharks were seen to rush into the spawning site or swim through the spawn cloud up to ~5 s after spawn initiation. Footage was therefore analysed for shark abundance at 1, 2, 3 and 5 s after each spawn initiation.

To account for individual spawns possibly being captured by multiple cameras, we first identified a number of clearly distinguishable events captured by multiple cameras. These events were used to synchronise the timestamps of the different cameras, allowing us to convert each camera's timestamp to a single reference time. Using this reference time, we then identified spawns which had been recorded within 10 s of each other. These spawns were then reviewed simultaneously on two computer monitors to determine whether they were different spawning events or different views of the same spawning event. If the footage was of a single event, the best footage was retained for full analysis and the other removed from the dataset. Regression analyses were conducted in MS Excel, with variables $\ln(x + 1)$ transformed when required to reduce variance.

Nocturnal predations

Nocturnal footage of shark interactions was analysed for the number of shark interactions with fishes, the type of fish involved, number of bite attempts at pursued fishes and the number of successful shark predations. An interaction was defined as a change in direction by a shark to actively

approach a fish, continued pursuit of a fish following an unsuccessful predation attempt or re-engaging in pursuit of a fish at a later time. As fishes could not always be reliably identified to species due to distance from the camera, silt from sharks' swimming and shadows cast from obstacles or sharks, data were analysed at the family level. As multiple cameras were used to capture the footage, timestamps were re-synchronised and duplicate footage removed as above.

Results

Grouper spawning

The *E. polyphekadion* spawning event was estimated to involve as many as 10,000 individual fish (Y. Sadovy de Mitcheson, pers. comm.) (Fig. 1a). Visual estimates on descent and during the dive placed the area in which spawning occurred at approximately 10,000 m² (100 m × 100 m), of which we estimate we captured 25–30 % during filming. Five species of shark were sighted at the mass spawning event: the grey reef shark, *C. amblyrhynchos*; silvertip shark, *C. albimarginatus*; blackfin shark, *C. limbatus*; lemon shark, *Negaprion acutidens*; and

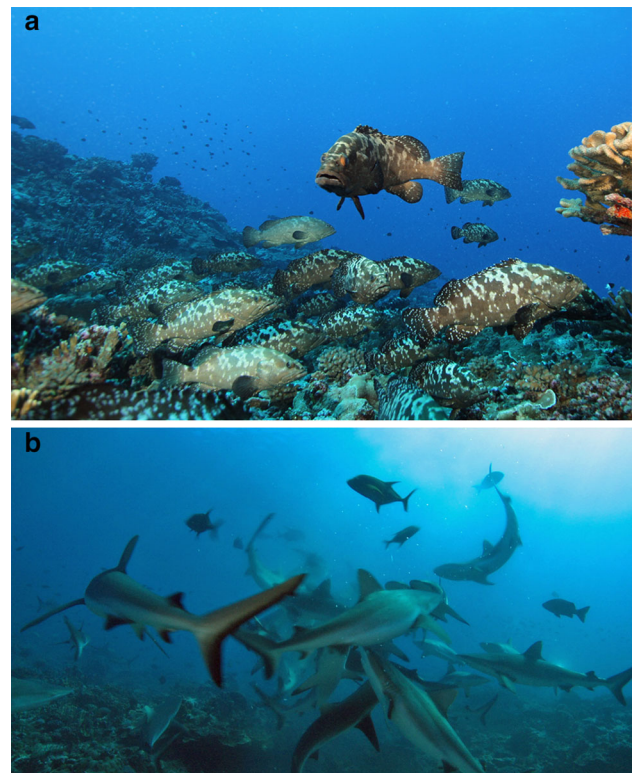


Fig. 1 **a** *Epinephelus polyphekadion* gathering for a mass spawning event; **b** *Carcharhinus amblyrhynchos* fighting over a captured *E. polyphekadion*. Shining specks are scales being dislodged as the fish is torn apart

the whitetip reef shark, *T. obesus*. Diver estimates of the total numbers of sharks seen during filming were collected post-dive, with the overall consensus being 146 ± 24 (mean \pm SE) individuals sighted during the spawning event. *Carcharhinus amblyrhynchos* was estimated to represent 88 % of the sharks present and was the only species observed directly interacting with *E. polyphkadion*.

The *E. polyphkadion* spawning event took place over 104 min, during which almost 3 h of usable footage was taken across the six cameras. We identified 120 separate spawns, averaging one spawn every 52 s. There were 52 spawns appropriately positioned in camera frame to allow detailed analysis of grouper and shark numbers. Of these, an average of 5.02 ± 0.30 *E. polyphkadion* were involved in each spawn; however, not every individual was observed to release gametes. Spawns typically took less than 1 s from initiation to gamete release, with fish estimated to travel 40–120 cm above the substrate to reach the point of release.

Each of the 52 spawns was analysed for 5 s following its initiation. Sharks were observed to rush to the immediate area once a spawn was initiated, in an apparent attempt to capture prey through speed. A total of 115 *C. amblyrhynchos* attended 83 % of spawns, averaging 2.67 ± 0.28 sharks per spawn. We found 19 % of sharks arrived in the first second, 29 % in the second second and a further 26 % in the third second. New sharks continued to investigate subsequently, but by that time all *E. polyphkadion* had invariably returned to the substrate. The fastest time for a *C. amblyrhynchos* to arrive at a spawn was 0.16 s after initiation, and the average time for sharks to arrive was 1.29 ± 0.11 s.

Successful predation events were easily identified, even from a distance. Successful sharks would be forced up into the water column, fighting conspecifics for their catch (Fig. 1b). Assuming a comparable rate of shark attendance at spawns not analysed in detail, *C. amblyrhynchos* were successful at 8.1 % of attended spawns. Events of the spawn remained remarkably consistent; the only significant correlation found was between the time taken for sharks to first arrive and the number of *E. polyphkadion* involved in the spawn (Table 1). This positive relationship may indicate that spawns involving greater numbers of *E. polyphkadion* were not more obvious to nearby *C. amblyrhynchos* or that larger groups of groupers spawned only when sharks were further away. Sharks were not more abundant at spawns with larger numbers of groupers, suggesting that sharks did not linger around pockets of higher grouper densities waiting for spawns to occur.

The rate of grouper spawns decreased over time, although this relationship was non-significant (Table 1). Instead, groupers appeared to synchronise the end of the

mass spawning event. Sharks maintained their interest throughout the spawning event, even though their predation efficiency did not improve as the event unfolded (Table 1). Although many surgeonfish (Acanthuridae) and fusiliers (Caesionidae) were present higher in the water column apparently eating spawn, no predation attempts on these fishes were seen.

Nocturnal predations

Over 1 h 13 min of footage was recorded, of which 50 min was suitable for analysis. Both *C. amblyrhynchos* and *T. obesus* were observed in the area, although only *C. amblyrhynchos* interacted with fishes within our view. Unlike the rapid rushes witnessed towards the grouper spawns, in nocturnal predation events sharks pursued fishes in a slow, controlled manner which usually allowed them within an estimated 20 cm of the fish before attempting predation. Predation attempts then consisted of rapid sideways snap of the head (Fig. 2; Electronic Supplementary Material).

We observed 128 occasions when fish were pursued by *C. amblyrhynchos* (Fig. 3). We could not uniquely identify individual fishes, so some pursuits may have involved previously sighted individuals. In 88 % of cases, the targeted fish was a fusilier, although acanthurids, chaetodontids, epinephelids, fistularids, lutjanids and scarine labrids were also opportunistically targeted (Fig. 3). Benthic fishes were only pursued if they left the substratum after being spooked by nearby sharks. Interestingly, sharks did not pursue every fish, swimming within a body length of visibly obvious fusiliers 36 times without interaction and ignoring other nearby species a total of 22 times.

Each pursued fish was investigated by up to five different sharks while on camera, with a mean of 1.41 ± 0.06 sharks involved in each pursuit. Over 300 separate *C. amblyrhynchos* investigations of fishes were identified, at 2.42 ± 0.15 shark interactions per fish. Shark investigations resulted in a bite attempt 34 % of times, and these involved 54 % of pursued fish. Successful predation took place in 16 % of bite attempts, although this only equated to 5.3 % of total shark interactions. Two predations occurred behind projecting substrate, preventing positive identification of prey species. Of the remaining predations, fusiliers were prey in 93 % of occasions, and a *Naso brevirostris* (f. Acanthuridae) was taken on the other occasion (Fig. 3). Attempts by conspecifics to take prey from successful individuals were again observed, although these were not common because successful sharks were usually distant from potential competitors.

Table 1 Regression analysis of *Carcharhinus amblyrhynchos* predations on an *Epinephelus polyphkadion* mass spawning event

Independent variable	Regression variable	MS	F	P
Time elapsed since spawning began	Shark abundance (1 s)	0.740	2.059 _{1,50}	0.158
	Shark abundance (2 s)	0.027	0.032 _{1,50}	0.859
	Shark abundance (3 s)	0.775	0.407 _{1,50}	0.527
	Shark abundance (5 s)	0.192	0.541 _{1,50}	0.466
	First shark arrival time	0.116	1.229 _{1,40}	0.274
	Successful predations	0.004	0.044 _{1,71}	0.835
	Grouper abundance spawn ⁻¹	0.262	2.424 _{1,48}	0.126
	Grouper spawns min ⁻¹	3.523	3.451 _{1,97}	0.066
Number of groupers	Shark abundance (1 s)	1.048	2.935 _{1,48}	0.093
	Shark abundance (2 s)	1.282	1.482 _{1,48}	0.229
	Shark abundance (3 s)	4.399	2.357 _{1,48}	0.131
	Shark abundance (5 s)	0.034	0.094 _{1,47}	0.761
	First shark arrival time	0.798	10.396 _{1,40}	0.003 ^a

^a Indicates significant result

Discussion

This study is the first documentation of natural foraging modes employed by the grey reef shark, *C. amblyrhynchos*. This species was the most active shark we observed, being responsible for all recorded predation events even in the presence of numerous other shark species. We documented two different foraging modes of *C. amblyrhynchos* in the absence of baits or burley attractants: opportunistic predation on a daytime mass spawning aggregation of *E. polyphkadion* and nocturnal hunting of individual fishes in the same reef pass 2 weeks later. Both scenarios required very different foraging modes to be employed by *C. amblyrhynchos*.

The annual *E. polyphkadion* spawning event represents a brief opportunity for sharks to hunt predatory teleosts preoccupied with spawning. This opportunistic behaviour is similar to that seen in other reef shark species such as *C. melanopterus*, which may target large aggregations of striated surgeonfish, *Ctenochaetus striatus*, similarly involved with spawning (Weideli et al. 2015). In our study, the medium-sized *E. polyphkadion* appeared to have limited agility, and sharks took advantage of this by rushing at the spawning fish following spawn initiation. In this situation, burst speed rather than finesse was the predation technique employed. This behaviour is in direct contrast to the nocturnal predations observed in the same reef pass 2 weeks later. Smaller fusiliers are highly manoeuvrable and can dart rapidly over short distances. As such, sharks used a slow, controlled approach to these fish which minimised the distance between the shark and the fish before predation was attempted. This method limited the fish's agility advantage and resulted in a more effective predation mode per attempted bite at the fish. The sideways

snap of the shark's head was also quicker than its linear acceleration over the same distance (pers. obs.), maximising the shark's striking speed once proximal to the prey.

These two foraging modes show that *C. amblyrhynchos* employs attack behaviours suited to both prey type and circumstance. In both situations, *C. amblyrhynchos* also predominantly targeted the most common fish species observed in the immediate area. This finding corroborates previous studies of stomach content analyses, which also found numerically dominant fishes taken in higher proportions by *C. amblyrhynchos* (Salini et al. 1992; Brewer et al. 1995). With the ability to change its foraging behaviour to suit local circumstances, *C. amblyrhynchos* appears to act more as an opportunistic generalist, rather than a specialist with respect to fish species and predation tactics.

The nocturnal feeding behaviours continued as sharks and prey fish entered and exited the area illuminated with our lights. Although our lights may have assisted *C. amblyrhynchos* in the detection and capture of individual fishes, it is unlikely that the sharks evolved this foraging technique over the short duration divers were illuminating the area. The presence of divers did not seem to excite the sharks, and previous research has demonstrated that underwater cameras appear to have little effect on wild shark behaviours (Robbins et al. 2011, 2013). It is therefore most likely that the behaviours observed here represent a natural foraging mode of these sharks which would also occur outside of artificially lit situations. Employing previously refined feeding strategies together with knowledge of the local habitat can increase predation success while minimising energetic costs (Goldman and Anderson 1999). Taking recognised food resources can also reduce the risks associated with tackling novel prey (Thomas et al. 2010).

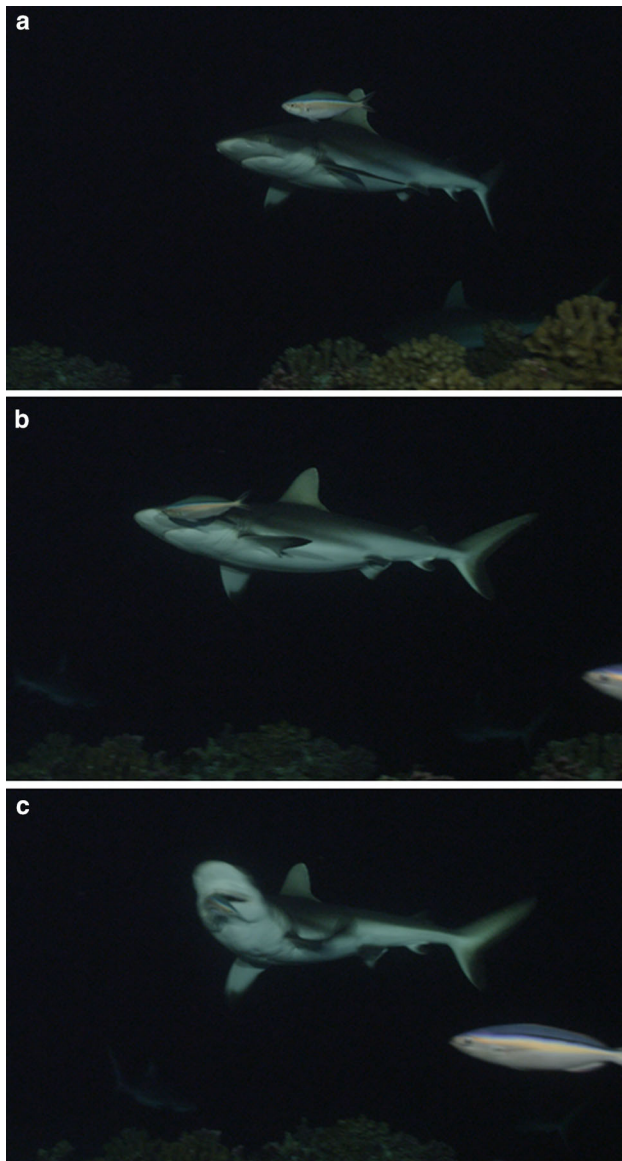


Fig. 2 Nocturnal predation of a fusilier by a *Carcharhinus amblyrhynchus*. **a**, **b** the shark's controlled approach to the fish before, **c** a rapid sideways head snap

In this respect, attempts by sharks to take prey from successful conspecifics further reduce the risk of damage from struggling prey, as the prey has already been subdued or incapacitated.

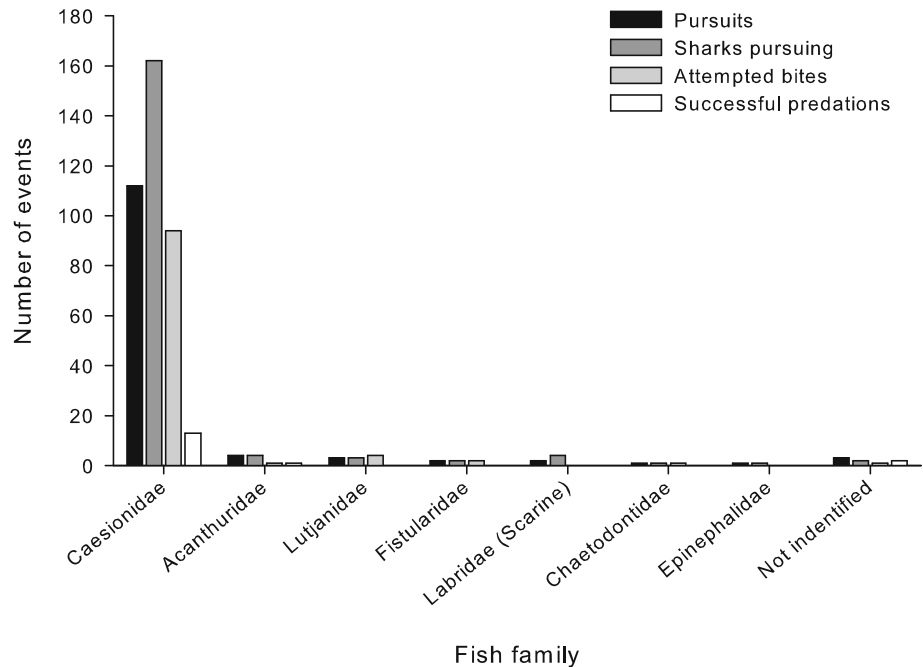
Previous research has suggested that densities of 1.0–2.6 *C. amblyrhynchus* ha^{-1} are indicative of healthy coral reefs (Robbins et al. 2006). However, we observed much higher densities at both the *E. polyphkadion* mass spawning event and in the weeks after the grouper aggregation had dispersed. Environmental factors such as reef habitat, exposure and temperature can all affect local reef shark abundances (Economakis and Lobel 1998; Robbins 2006; Barnett et al. 2012; Chin et al. 2012), as can fishing and

other anthropological pressures (Nadon et al. 2012; Friedlander et al. 2014). The high shark densities we observed at the South Fakarava reef pass are likely a combination of both the area's geographical isolation limiting detrimental human impacts and the consistently high current flows which are common in reef passes in the region (Dumas et al. 2012). High current flows allow *C. amblyrhynchus* to conserve energy throughout the day by eliminating the need to swim continuously. They also aid sharks in processes such as parasite removal, which requires high currents to allow sharks to maintain their position above cleaner fish stations (O'Shea et al. 2010; Wheeler et al. 2013). High current flows also increase planktonic delivery onto the reef, enhancing local coral and larger reef fish production (Frisch et al. 2014).

The high shark abundances seen in our study markedly increased our chances of witnessing multiple types of shark foraging behaviour. Documentation of similar wild feeding events is rare, most likely due to the lower chance of their observation in areas with more typical reef shark densities. Nevertheless, similar reef shark foraging modes are likely to occur on coral reefs in other regions, especially as such non-cooperative behaviours would be aided by lower conspecific densities. We note that further, undocumented foraging modes also exist in this species. For example, during non-filming dives, we also observed *C. amblyrhynchus* individuals twice attempting to dislodge suspected prey items from the reef matrix during daylight hours. Moreover, we also observed *C. amblyrhynchus* trailing schools of *Decapterus* spp. as they moved across the reef flat at dusk, and footage obtained from the same location the previous year revealed multiple *C. amblyrhynchus* preying on a moving school of *Decapterus* spp. at night. Quantifying the interactions of additional foraging modes would provide a useful addition to the data presented here.

Our findings show that reef sharks such as *C. amblyrhynchus* naturally prey on multiple prey species from multiple trophic levels. They also show that the species employs foraging modes best suited to the local situation. However, the rate of predation success was surprisingly low in both situations documented here. Reef sharks have been hypothesised to exert only low levels of direct top-down control on other species (Rizzari et al. 2015), accounting for the dichotomy of high shark abundance without noticeably diminished fish abundance found on some healthy Pacific coral reefs (Stevenson et al. 2007; Friedlander et al. 2014). Our observation of low predation success appears to support this paradigm; however, further evidence is required to substantiate the hypothesis. Reef sharks may, however, have indirect, non-consumptive effects on the behaviour of potential prey species (Madin et al. 2010; Rizzari et al. 2014b), exerting greater influence

Fig. 3 Number of documented nocturnal fish predation events by prey family. Prey family could not be identified in two pursuits due to distance and obstacles between the fish and the cameras. *Black bars* show pursuits of fish, *dark grey bars* show numbers of sharks pursuing fishes, *light grey bars* show attempted bites, *white bars* show successful predations



than that observed within this study. With *C. amblyrhynchos* capable of comprising almost half the biomass of higher-order predators on coral reefs (Friedlander et al. 2014), continued investigation into reef shark interactions would provide valuable insights into coral reef trophodynamics and help determine the extent to which mesopredators such as reef sharks influence lower-trophic-order species.

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