Variation in search and predatory attack strategies of shark mackerel *Grammatorcynus bicarinatus*

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I observed shark mackerel demonstrating multiple search and attack strategies. Strategies were categorized as three distinct types: (1) a linear search by single or groups of fish along reef features; (2) ambush from a stationary position on the seafloor; and (3) ambush from resting schools of co-occurring predators. Together these strategies were consistent with both information-sharing and producer-scrounger models of group foraging and indicate significant flexibility in individual fish foraging behaviour based on proximate conditions.

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Developing detailed information on variation in the search tactics and predation success of piscivorous fish is necessary for an improved understanding of spatial variability in predation rates and their role in structuring reef fish communities. However, there is little information in the literature on predation strategies, especially of highly mobile predators (but see Hobson, 1968; Parrish, 1993; Sancho, 2000). One such predator is the shark mackerel *Grammatorcynus bicarinatus* (Quoy & Gaimard, 1825). Shark mackerel are wide ranging piscivores distributed in the tropical waters of the western Pacific (Randall *et al.*, 1996).

I observed predation strategies of shark mackerel during daytime SCUBA dives conducted from 9-18 April 2003 at Ribbon Reef 10 (14°55'S 145°40'E) on the Great Barrier Reef. Search and attack strategies, target species of attacks, and associated piscivores were recorded both on underwater slates as well as directly on digital video tape for subsequent analysis. Shark mackerel (N = 24) were observed along the leeward side of the main ribbon reef and at adjacent features (i.e. carbonate mounds and pinnacles) across a depth-range of 3-20 m. Observations revealed this species used multiple search and attack strategies that were related to both landscape type and associated piscivorous predators. While there was variation in the timing and spatial extent of each predatory sequence, strategies were grouped into three distinct types: (1) a linear search by single or groups of fish along reef features; (2) ambush from a stationary position on the seafloor; and (3) ambush from resting schools of co-occurring predators. All shark mackerel were initially observed exhibiting simple generalized searches while swimming parallel to the sloping face of reefs. Behaviours switched from the

Corresponding author: P.J. Auster Email: peter.auster@uconn.edu simple search to more complex types of strategies when potential prey were isolated or in large groups (inferred based on directed stalking or attacks) and where local landscape conditions were amenable to such changes (e.g. presence of reef spurs, vertical reef faces and resting schools of piscivores).

Linear searches along the horizontal axis of reef features, the primary background behaviour for shark mackerel, were exhibited by individuals swimming singly or in groups (N = 10). Groups occurred with members swimming in a single line (i.e. with one individual in the lead), in parallel (i.e. with one individual closer to the reef face than the other), or as an aggregation swimming along the reef face. Red bass snapper (*Lutjanus bohar*) commonly followed shark mackerel short distances along the reef face (\sim 5 – 10 m), breaking off at discrete landscape features (e.g. tips of reef spurs, large crevices and other reef discontinuities). Shark mackerel occasionally would break from steady swimming and charge at potential prey. One group of five individuals broke formation and charged schools of fusiliers at the reef crest.

A second predation strategy involved a stealthy ambush from the seafloor (N = 3). Individuals that identified potential prey (i.e. based on eventual directed movements towards groups or individuals) ended their linear search strategy and began station keeping at a position hovering just above the seafloor using 'low frequency' movements of pectoral and caudal fins. Station keeping started at locations that were several metres off the down-current side of the distal end of reef spurs (i.e. at the edge of an area with a reduced current or eddy feature). Individuals rapidly shifted from their 'nominal' colour pattern (silver or blue-green upper side and back and silver lower side) to one with alternating vertical bars and stripes on the dorsal side of the body and spots on the ventral side (Figure 1A). On two occasions, 'high frequency' tail beats and pectoral fin movements were followed



Fig. 1. Shark mackerel station-keeping on seafloor after breaking off from linear search strategy. (A) Close view of colour and pattern shift with vertical bars and stripes on the dorsal side with spots on ventral side of the body; (B) stalking an acanthurid. Images are frame-grabs from video.

by a rapid charge upward and attack on schooling scissortail fusiliers (*Caesio caerulaurea*) that occurred in shallow water. Both attacks resulted in the successful capture of prey. Slow directed movement using 'low frequency' fin movements, after initial station-keeping behaviour and colour change, were used to stalk an individual surgeonfish for less than 30 seconds (Figure 1B). However, no attack resulted from this behaviour sequence and the mackerel then shifted back to nominal shading and continued a linear search along the reef face.

The third strategy involved ambush of prey from resting schools of co-occurring predators (N = 11). Shark mackerel joined resting schools of bigeye trevally (*Caranx sexfasciatus*) and used schools as cover to attack scissortail fusiliers along near vertical reef faces (Figure 2A). Generally only a single mackerel joined a resting school of bigeye trevally. However, up to eight mackerel had been observed at one time in a single resting school of bigeye trevally. Fusiliers (Caesionidae species) and other schooling fish (primarily Anthiinae species) generally did not react to resting schools and exhibited defensive and flight behaviours (coalescence of school or individual flight) only during attacks by single or multiple predators. Shark mackerel also broke away from resting schools of bigeye trevally to join proximate predatory attacks on fusiliers with bluefin trevally (*Caranx melampygus*). In one instance attacks included both bigeye and bluefin focused on the same schools of prey (Figure 2B, C). Unlike other species with coordinated attack strategies, shark mackerel attacked independently of the group of trevally and seemed to take advantage of coordinated movements of the co-occurring predators.

Other highly mobile piscivores have been shown to exhibit stationary ambush strategies. The 'ambush from the seafloor' strategy is similar to one described by Sancho (2000) for bluefin trevally at Johnston Atoll in the central Pacific. Bluefin trevally, that generally attack prey from midwater, rapidly adopted a pigmented colour pattern and ambushed prey from a sheltered position under corals. However, I found no published record of piscivores using resting schools as cover to ambush prey. This is a newly described strategy and future studies should assess if such behaviours are commonly used by other species.

The range of shark mackerel behaviours that involve other predators is consistent with multiple models focused on social or group foraging behaviours. Group foraging allows individuals to exploit prey discovered or otherwise made available by other group members. The behaviours described in this paper fit both information-sharing and producer-scrounger foraging models (Giraldeau & Beauchamp, 1999). For example, the behaviour of shark mackerel searching for prey as a



Fig. 2. Shark mackerel using resting school of fish to approach and attack prey. (A) Shark mackerel (centre) swimming with resting school of bigeye trevally; (B) shark mackerel and bigeye trevally manoeuvering to attack fusiliers from under the school; (C) shark mackerel breaks from association with resting school of bigeye trevally and joins bluefin trevally attacking a school of fusiliers; note resting school of bigeye trevally in the background. Images are frame-grabs from video.

group is consistent with conditions of the informationsharing model. This model assumes that individual fish independently search for prey while simultaneously searching for opportunities to join other fish in predatory attacks. Shark mackerel also exhibit behaviours consistent with the producer – scrounger model where individual fish exclusively either search for prey (i.e. producer) or search for opportunities to join others that have identified or are attacking prey. Shark mackerel joining groups of bluefin trevally when the latter have initiated attacks on prey is consistent with this model (i.e. bluefin trevally are the 'producers' and shark mackerel the 'scroungers' in this case). Red bass snapper can be classified as 'scrounger' while following shark mackerel in anticipation of an opportunity to obtain prey fragments or consume prey exposed by the 'producer'.

Additional studies that clarify common components of predation strategies, and understanding decision rules for their use may ultimately allow researchers to develop more refined observational and experimental approaches for quantifying predation rates across reef landscapes (e.g. Sandin & Pacala, 2005). Such information could improve visual foraging models by including factors related to interactions with conspecifics, co-occurring predators and landscape context.

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