Blue Water Spawning by Moorish Idols and Orangespine Surgeonfish in Palau: Is it a "Suicide Mission"?

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Abstract

Spawning aggregations of the moorish idol (MI) and orangespine surgeonfish (OSS) were found on the western barrier reef of Palau. MI aggregated around the first quarter moon from Dec. to Mar., with largest groups in Jan. and Feb. Fish arrived near the sites in the morning, grouped together and moved up and down the reef face up in late morning attracting the attention of predators. At mid-day they ascend from the reef out into open water away from the reef. Gray reef sharks follow them and attack at the surface in a feeding frenzy. A high percentage of the ascending adults are eaten and few return safely to the reef. OSS aggregated in the same months, but on the last quarter moon with fewer observations being made. The observation of both fishes ascending high above and moving away from the reef to spawn is unusual and is termed "blue water spawning" with only a few similar examples known. Previously the importance of reef sharks in influencing reef fish spawning behavior has been reported as non-existent to "moderate" (a few spawning fish taken by sharks). This example of many individuals being taken by predators represents an extreme only reported previously for a grouper aggregation. The occurrence of sharks at the site during aggregation and spawning is indicative of a close relationship with reef fishes. The apparent high rate of predation on spawning MI and OSS may be specific to these study sites and it is likely individual fishes are generally iteropareous.

Zusammenfassung

Am westlichen Barriereriff Palaus konnte an Halfterfischen (HF) Zanclus cornutus und an Kuhkopf-Doktorfischen (KD) Naso lituratus gruppenweises Ablaichen beobachtet werden. HF versammelten sich etwa zur Zeit des ersten Mondviertels von Dezember bis März, mit den größten Gruppierungen im Januar und Februar. Die Fische kamen am Morgen zu den Laichplätzen, schlossen sich zu Gruppen zusammen und bewegten sich über der Rifffläche auf und ab und zogen dabei die Aufmerksamkeit von Beutegreifern auf sich. Um die Mittagszeit steigen sie vom Riff auf und begeben sich ins freie Wasser jenseits vom Riff. Graue Riffhaie folgen ihnen, greifen sie an der Oberfläche an und verzehren viele von ihnen in einem Fressrausch. Ein hoher Prozentsatz der aufsteigenden erwachsenen HF wird von den Haien gefressen, nur wenige können in die sichere Zone des Riffs zurückkehren. KD versammeln sich in denselben Monaten, aber in der Zeit des letzten Mondviertels – wobei es hierüber weniger Berichte gibt. Die Beobachtungen bei beiden Fischarten, dass sie weit nach oben steigen und sich zum Ablaichen vom Riff entfernen, gelten als ungewöhnlich; das Verhalten wird als „Blauwasserlaichablage" bezeichnet, und es gibt wenige weitere Beispiele. Bisher hatte man die Bedeutung von Riffhaien als Einfluss auf das Laichverhalten von Rifffischen als bedeutungslos bis „mäßig" eingestuft (nur wenige laichende Fische würden von Haien gefressen, hieß es bisher). Das Beispiel der HF und KD, bei denen sehr viele Individuen von Beutegreifern gefressen werden, ist als Extrem zu werten, das man bisher nur von Zackenbarsch-Gruppen kennt. Das Auftreten von Haien an den Laichplätzen während der Gruppenbildung und Laichablage lässt auf eine enge Beziehung zu den Rifffischen schließen. Die offensichtlich hohe Erfolgsquote beim Erbeuten von HF und KD mag eine Besonderheit dieser erforschten Laichplätze sein, und es ist wahrscheinlich, dass die einzelnen Fische sich grundsätzlich iteropar verhalten, also Verluste durch erneutes Ablaichen ausgleichen können.

Résumé

Les concentrations de frai de l'idole maure (MI) et orangespine poisson chirurgien (OSS) ont été trouvés sur la barrière de corail de l'ouest de Palau. Regroupés autour de la MI Premier quartier de lune à partir de Décembre à Mars, avec des groupes plus importants en Janvier et Février. Les poissons sont arrivée en proximité des sites le matin, regroupés et déplacé vers le haut et vers le bas le récif de face dans la fin de matinée attire l'attention des prédateurs. À la mi-journée ils montent du récif out simplement dans l'eau loin du récif. Les requins gris de récif de les suivre et d'attaque à la surface dans une frénésie d'alimentation. Un pourcentage élevé de l'ordre croissant adultes sont mangés et peu de retourner en toute sécurité dans le récif. OSS regroupés dans le même mois, mais le dernier quartier de lune avec moins d'observations effectuées. L'observation des les deux poissons ascendant au-dessus et en s'écartant de la reef pour frayer est inhabituelle et est appelé "l'eau bleue" de frai avec seulement quelques exemples similaires connues. Auparavant, l'importance des requins de récif à influencer le comportement de frai des poissons de récif a été rapporté comme inexistant à "modérée" (un peu de la fraie des poissons pris par les requins). Cet exemple d'un grand nombre de personnes prises par les prédateurs représente un extrême seulement rapportés précédemment pour une agrégation de mérous. L'apparition de requins sur le site au cours de l'agrégation et la reproduction est l'indice d'une relation étroite avec poissons de récif. L'apparente taux élevé de prédation sur les frayères MI et de l'OSS peuvent être spécifiques à ces sites d'étude et il est probable que les poissons sont en général iteropareous.

Sommario

Presso la barriera corallina occidentale di Palau sono state osservate aggregazioni di idoli moreschi (MI) e di pesci unicorno arancione (OSS) legate alla fase della deposizione delle uova. Gli MI si sono riuniti intorno al primo quarto di luna da dicembre a marzo, con gruppi più numerosi a gennaio e febbraio. I pesci sono arrivati vicino ai siti al mattino, si sono raggruppati e mossi su e giù per la barriera a tarda mattinata attirando l'attenzione dei predatori. A metà giornata sono risaliti dalla scogliera e si sono portati in acque aperte lontano dalla barriera corallina. Gli squali grigi della scogliera li hanno seguiti e attaccati in preda a una frenesia alimentare. Un'alta percentuale di adulti è stata mangiata e pochi sono ritornati sani e salvi nella barriera corallina. Gli OSS si sono ammassati negli stessi mesi, ma nell'ultimo quarto di luna si sono fatte meno osservazioni. L'osservazione di entrambi i pesci che risalgono la colonna d'acqua e si allontanano dalla scogliera per deporre le uova è insolita e viene definita "deposizione in acque blu" con solo pochi esempi simili noti. Precedentemente l'importanza degli squali di barriera nell'influenzare il comportamento di deposizione dei pesci nella barriera corallina è stata segnalata come inesistente o "moderata" (pochi pesci riproduttori catturati dagli squali). Questo esempio di molti individui presi dai predatori rappresenta un caso estremo segnalato in precedenza solo per un'aggregazione di cernie. La presenza di squali nel sito durante l'aggregazione e la deposizione delle uova è indicativo di una stretta relazione con i pesci della barriera corallina. L'apparente alto tasso di predazione su MI e OSS durante la deposizione delle uova può essere specifico per questi siti di studio ed è probabile che questi pesci siano specie iteropare.

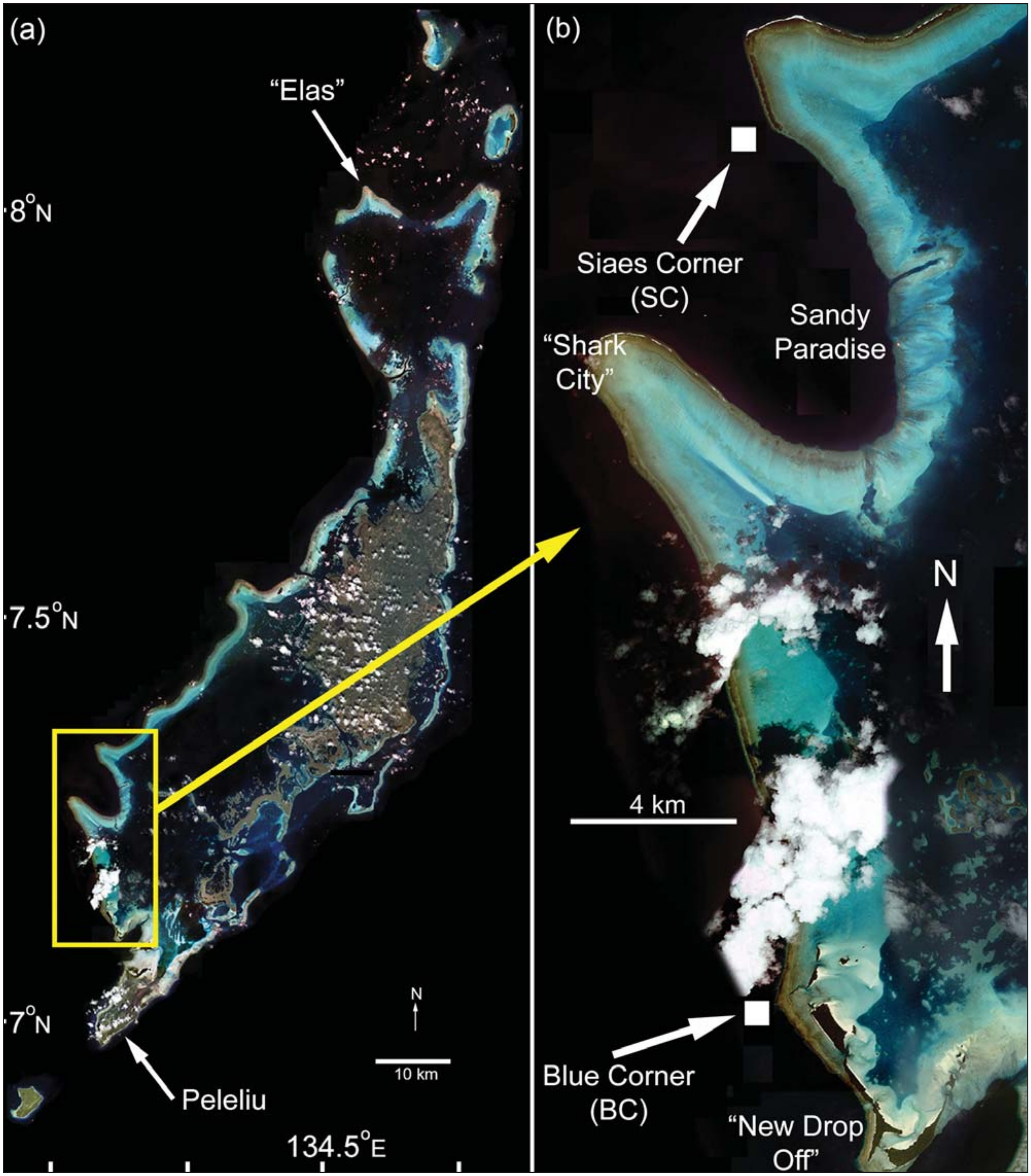
INTRODUCTION

The reproduction of reef fishes forming spawning aggregations has become better known in the last few decades (Sadovy de Mitcheson and Colin 2012) but basic information is still lacking for many species that aggregate or are likely to do so, limiting the understanding of relationships of spawning behavior, interspecific relationships and environmental conditions. In many areas aggregations have been heavily fished, often to ecological extinction (they no longer form). Palau in the western tropical Pacific is an exception, retaining numerous spawning aggregations, making it an ideal location for their study. It also has fishermen and tourist dive guides who are observant and often discover new knowledge about fish reproductive behavior adding to traditional knowledge known for decades, if not centuries (Johannes 1981, Sadovy 2007). Many such reports are now validated scientifically by in situ observations with information on aggregating fish species also included in a number of popular books and publications, such as Colin (2009) and Etpison (2009, 2014).

Most reef fishes with planktonic eggs, both male-female pairs and group spawners with 3 or more fish, remain within sight of shelter when spawning and release their gametes within 5-10 m of structures to which they can quickly retreat for shelter from predators. They engage in a rapid vertical or angled movement away from the bottom, the "spawning rush", with eggs and sperm released at the peak and fishes quickly returning to near the bottom. This behavior is generally believed to reduce egg predation from benthic-based planktivores (eggs released high above the reef) (Nemeth 2012) and predation on the spawners by piscivores (Molloy et al. 2012).

The aggregation and spawning of two reef fishes, moorish idol, Zanclus cornutus (Linnaeus, 1758) (hereafter referred to as "MI") and the orangespine surgeonfish, Naso lituratus (Bloch & Schneider, 1801) (hereafter referred to as "OSS"), violate this generality by swimming high above and far away from the reef to release their gametes, even with a high predation risk from sharks. Our information predominantly concerns MI, but includes some comparative data on OSS, which use the same spawning sites on a different lunar schedule. We term this reproductive strategy "blue water spawning" in which the spawning fishes range 50-100 meters away from the shelter of the reef, often to the surface, to spawn. While doing this, the adults may suffer high predation rates from sharks. The large numbers of sharks which gather, then focus their attention on the spawning fish, begs the question of whether sharks gather to specifically target the spawning aggregations and also why these fish put themselves at such risk of predation?.

The MI is an iconic fish found throughout the Indo-Pacific tropics. Colin et al. (2012: 513, 515) reported a few instances of pair and aggregation spawning in Palau from December through March with peaks in January and February. The schooling



Figs 1a-b. (**a**) Landsat 7 images of the main Palau Island group with area shown in right panel indicated. (**b**) Detailed area of western barrier reef with locations mentioned in text indicated.

of adults preparatory to spawning on outer reef slopes has been known since the 1990s (Etpison 1994, 2009) while in 2009 the ascent of large numbers from the reef in mid-day was first seen (Etpison 2014). Elsewhere a few pair spawns were reported at Johnston (Sancho et al. 2000) and Enewetak Atolls (Colin & Bell 1991) but none for group spawning. The maximum life span is not known but they are reported to live up to several years in aquaria. There is no external way to distinguish sexes.

The OSS is common and distinctive on outer reef slopes often seen some distance above the bottom. Johannes (1981) indicated Palau fishermen reported aggregation, but provided no specific information. OSS occur in large schools, recognized as possible spawning aggregations, off the Palau barrier reef from December to March, often in the company of other acanthurids (Etpison 2004, 2009). These schools were subject to attack by groups of gray reef sharks, Carcharhinus amblyrhynchos, hereafter referred to as “GRS” (Colin 2012). Taylor et al. (2014) reported a life span maximum of 14 years in Guam while sexual maturation occurred at 15 and 18 cm fork length for male/female OSS.

MATERIALS AND METHODS

Most observations were made at two locations on the outer slope of the western barrier reef; “Blue Corner” (hereafter referred to as “BC”, 7°08.08’N; 134°13.25’E) and “Siaes Corner” (hereafter referred to as “SC”, 7°18.85’N; 134°13.22’E) (Fig. 1); sites that are visited daily by many divers. Our observations on occurrence and behavior were centered on six aggregation periods: 1) Jan 2009, 2) Dec 2009-Feb 2010, 3) Dec 2011-Jan 2012, 4) Jan 2015, 5) Jan 2016 and 6) Dec 2016-Jan 2017. Additional observations made on an irregular basis at a series of other outer reef areas; Peleliu, New Drop-off, Shark City, Sandy Paradise and Elas (Fig. 1b). Vertical and oblique aerial photographs of the sites were used to plot the areas of fish presence and their movements (Fig. 2). Underwater photographs from these sites were used to identify and map underwater locations relative to the aerial images. GPS surveys of areas established latitude/longitude positions of features on the reef and helped to quantify the geography of the fish movements.

Observations were made while SCUBA diving or snorkeling. Initially observation dives were made at all seasons, lunar phases and time of day by many observers regarding presence/absence of fishes. Over several years the times during which groups of a hundred to several thousand fish (termed a “running school”) move together one direction along the reef face, then turn in near unison at the ends of their swim pattern and move in the opposite direction, occurred were narrowed down and associated with particular seasons and lunar phases. Behavior was documented using diver operated digital still and video cameras with the numbers of fishes participating in the aggregation and ascending to spawn counted from photographs. After groups of fishes left the reef to spawn due to the speed of their swimming, divers could no longer follow, and we used boats to track the fishes from the surface. At those times documentation was limited to GoPro cameras held over the side of the boat on poles to record the activity.

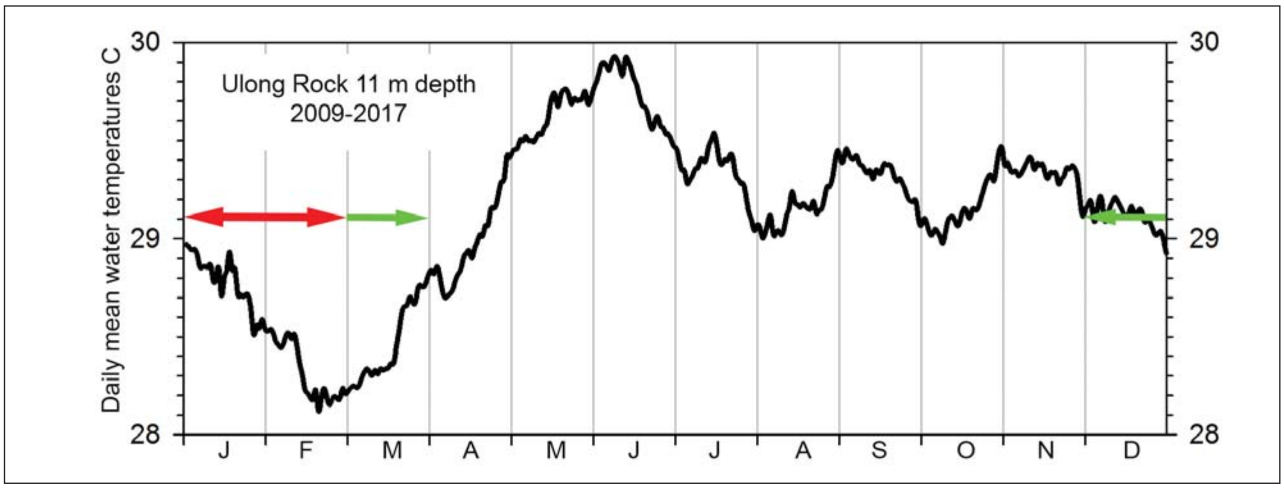


Fig. 2a-b. (**a**) Physiography of the aggregation/spawning at Siaes Corner (SC) reef. (**b**) Physiography of aggregation/ spawning site to Blue Corner (BC) reef.

RESULTS

A. Geography and currents (or tides) of the aggregation sites. Palau has a semi-diurnal tide with spring amplitudes up to 2.3 m on full and new moons around sunrise and sunset. The first and last quarter ("half") moons have neap tides with high tides occurring at mid-day with amplitude around 0.7-1.2 m. Water temperatures (Fig. 3) range annually between about 28° and 30°C while aggregation occurs during decreasing temperature from late December (about 29°C) to March (around the annual low of 28°C).

The western barrier reef of Palau is typically 1.0-1.5 km wide between lagoon and ocean (Fig. 1) with alternating cross reef (lagoon-ocean) currents driven by the tides. Our primary study sites, while part of the barrier reef, are different from typical areas. BC has a distinct promontory and a much wider reef flat

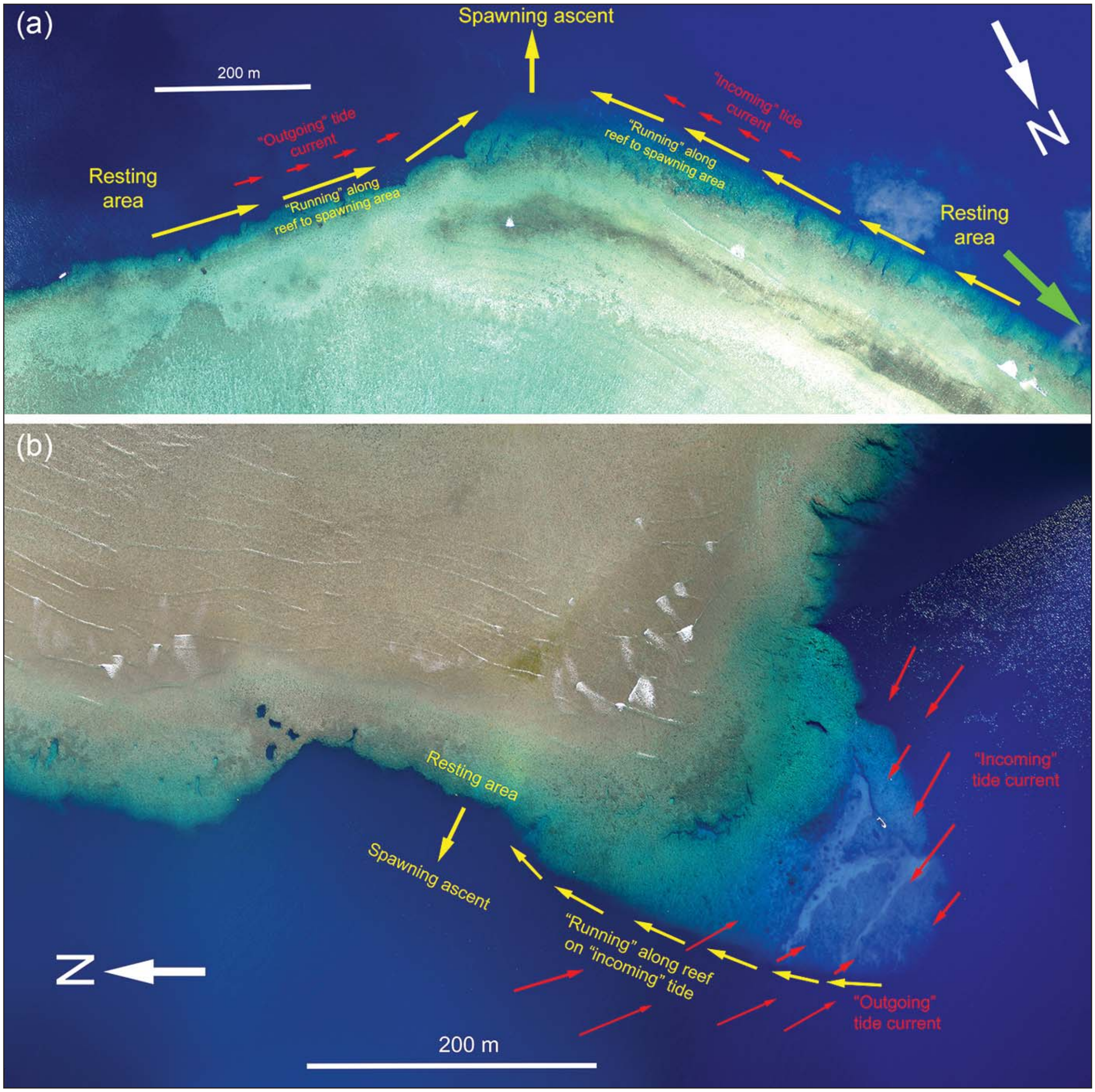


Fig. 3. Annual daily mean temperature profile for Ulong Rock 11 m depth, near study sites, averaged for the years 2009-2016 and the first half of 2017. Green arrows indicate full seasonal aggregation and spawning period while red arrow indicates the peak period.

with islands on it somewhat restricting the lagoon-ocean flow. Currents in such areas tend to be dominated by along reef oceanic flows which often diverge at the promontories. SC has a projection of reef, less prominent than BC, a similarly wide reef flat (but without islands), and along reef currents which diverge (Fig. 1b). There are still some tidally-influenced currents at both sites, the patterns of which have been characterized from diver observations over many years (Etpison 2009, 2016) as "incoming" (rising) and "outgoing" (ebbing). The currents at these sites need further quantification.

The two sites on the western barrier reef are 32 km apart along the reef edge (20 km straight line distance) (Fig. 1). During winter, when the aggregations occur, Palau normally has northeast trade winds of 10-15 knots and the sites are protected from NE winds and waves in the lee of the reef. During the summer, the non-spawning season for these species, the western reefs often have strong south to southwesterly monsoon winds, which produce rough conditions with high surf on the reef.

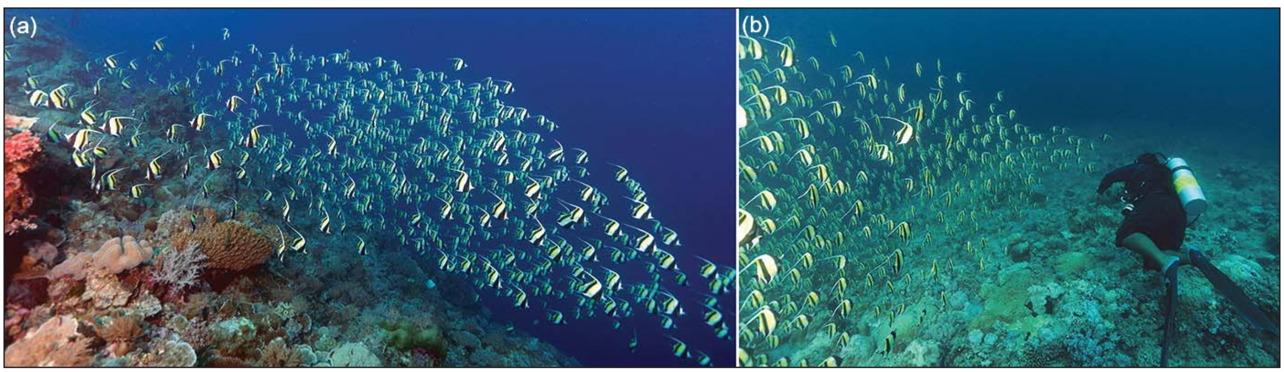
The distinct promontory at BC gradually slopes at its outer end becoming steep to vertical faces around its perimeter starting at 5 to 30 m depth. A discrete area (termed the "resting area") about 300 m north of the promontory end and only about 60-70 m in length is utilized by MIs during rising tides as a gathering place prior to animals moving up and away to spawn (Fig. 2). Fish seen migrating to this site from the south come around the promontory of BC from distances of at least 1 km. It is uncertain whether fish also migrate to the site from the north so overall the catchment area for this aggregation is uncertain. When ready to spawn, the fish will rise from the middle of this area, angle away from the reef and move towards the surface. They are subsequently driven further offshore by the sharks which follow their ascent.

At SC the MI were observed to migrate to the site from both the north and south. This area has two distinct "resting areas" while the location where the fish ascend to spawn lies between them, 100 and 450 m away. The reef corner where ascent occurs has a distinct transition with its southern wall, vertical from depths of 20 m to 50 m, transitioning to a slope leading downward to depths of about 60 m, then becoming near vertical. In roughly the hour prior to spawning sharks gather in large numbers along the vertical wall at the ascent area.

B. Moorish idols. Numbers and behavior in aggregations. From the late 1990s to 2005, the MI aggregations observed every year by dive guides at BC were estimated to be 5,000-10,000 fish. During 2009-2012 the numbers aggregating were estimated visually at BC appeared to decrease while the numbers at SC increased. During 2015-2017 the largest groups, estimated at 1,000-3,000 individuals, were seen at SC while only a few hundred fish were seen aggregating at BC each season. These numbers must be considered only as rough estimates obtained from observations without any means to accurately quantify the numbers of individuals.

Stages of aggregation and spawning. There are several sequential stages and events involved with the aggregation and spawning. These will be detailed in sequence.

Schooling and aggregation along the reef – Occurrence of aggregations, aggregation size and numbers. Starting in 2009 aggregations were seen at BC and SC for roughly 6 days around the first quarter moon; a period of neap tides with high wa-

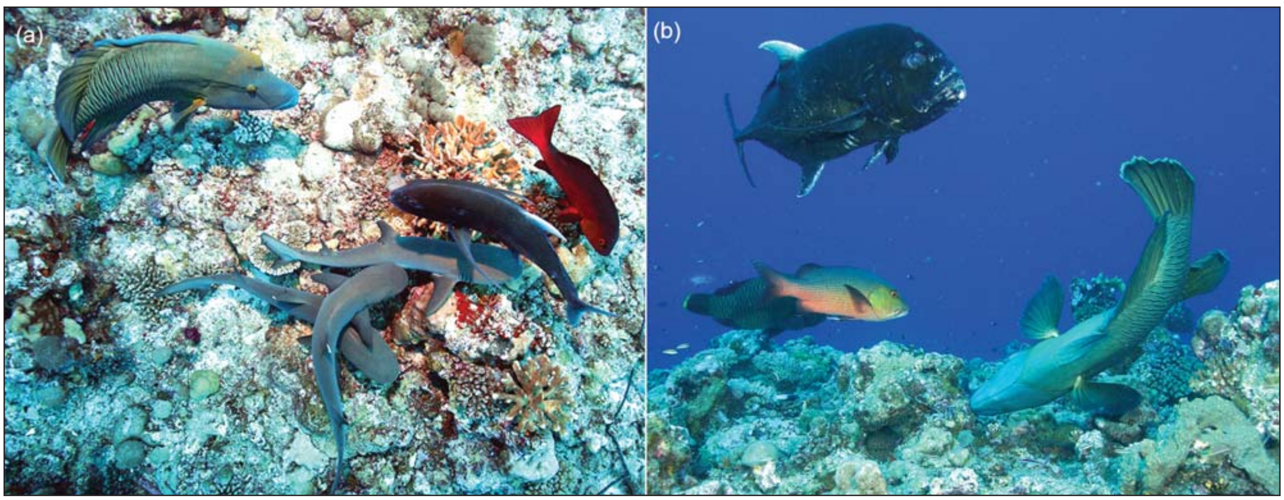


Figs 4a-b. (**a**) Aggregation of MIs "running" along reef at BC, 7 Jan 2017, 11:18 AM one day after first quarter moon. The photo has an approximately 668 fish based counts of individuals visible in photo. (**b**) A portion of an aggregation is seen "running" along the reef (with diver for scale) on 15 Jan 2016, 12:40 PM, two days before first quarter moon. Photos copyright M. T. Etpison.

ter occurring at mid-day. Spawning ascents with the most fish were generally seen from two days before to the day after the first quarter moon. The aggregation appears at the site during the morning on the rising tide, moving up and down the reef ("running") as a tight school at 20 to 35 m depth, fish turning in synchrony with some distance between individuals. Groups varied in size with a minimum of 100-200 individuals up to multiple hundreds. For example, one photos (Fig. 4) has approximately 668 individuals visible in it.

The school moving up and down the reef was often trailed by large numbers of grey reef sharks, *Carcharhinus amblyrhynchus* (subsequently referred to as GRS). Other predators such as small white tip reef sharks *(Triaenodon obsesus),* giant trevally *(Caranx ignobilis),* brown-marbled grouper *(Epinephelus fuscoguttatus),* twin-spot snapper *(Lutjanus bohar),* humphead wrasse *(Cheilinus undulatus)* and moray eels *(Gymnothorax javanicus)* wait on the reef and work as multi-species hunting packs. As the tide rose towards high water, these predators attempted to separate individuals or small groups of MIs from the school (Fig. 5a) by rushing the group from a distance. The individual MIs are fairly safe when in the larger school on the reef, as the school itself is not attacked, but if an individual is separated, several predators immediately dive towards it and, if not eaten immediately, force it to take shelter in crevices or beneath rocks or coral heads (Fig. 5b). Once a fish is cornered under shelter, the predators chaotically try to push each other aside to get closer. The white tip reef sharks and giant trevally jam themselves under the rocks trying to get to the fish, often sustaining visible scraps and scratches as a result. Humphead wrasses, groupers and twin-spot snappers, relying more on their eyesight and speed, wait for others to flush out the hiding fish and then pursue it. The moray eels are often able to maneuver into locations where the fish is sheltering and, if not quickly eaten by the eel, the MI will subsequently flee the shelter. Once again in the open, the waiting predators then attack and often succeed in capturing it.

The ascent of MI towards the surface and away from the reef. While swimming and then milling along the reef no behavior by MI interpreted as courtship was seen. However, near the time of high tide the movement of the group up and down the reef ceases, the fish moving towards the ascent location after the tide switches to outgoing and ascending somewhat as a group (Fig. 6). The GRS remain close by, often to the side and slightly above of the group. About one half to one hour after high tide the MI start the ascent and spawning soon follows. They start by initiating partial ascents in which the fish rise as a group for several meters, but then turn back towards the reef. We interpret this as a "false start" to the ascent; a type of behavior seen in many other reef fishes prior to the actual spawning ascent and gamete release (Sadovy de Mitcheson and Colin 2012). Numerous GRS continue to shadow their movements and then return to near the bottom when the MI do.



Figs 5a-b. (**a**) Three small white tip reef sharks, a giant trevally, a twin spot snapper and a large male humphead wrasse attempting to prey upon a MI which has taken shelter under a small coral head. Photo taken January 2016 (**b**) Predators going after MI under coral head. Two moray eels are beneath the coral head with only their sides visible through small openings in the reef. Photo taken December 2014. Photos copyright M. T. Etpison.

Groups of fish ascending, as counted from photos with clearly distinguishable individuals, numbered 290, 311, 360 and 544 (Figs 7 and 8), while others where individuals could not be readily counted had apparently similar numbers. Groups approaching 1,000 fish rise towards the surface for spawning. The aggregation often splits up when preparing to ascend and not all individuals ascend at the same time. In early years we believed the grey reef sharks were actively herding groups forcing them to move away from the reef, however, since 2009 we have repeatedly observed MI schools move off the reef and ascend by themselves, at times with no sharks nearby. The column of fish leaving the reef remains cohesive with the individual fish staying a few body lengths apart and turning in synchrony. When splitting into several smaller schools during ascent, the subgroups often move in different directions. The GRSs do not make obvious moves to force the fish to ascend, but rather seem to anticipate when and where this will take place. Once clear of the reef the ascending column of fish forms an elongate mass or ball (Fig. 7). The GRS take up position at the lower end of the group (Fig. 8), not impeding their rise, but remaining close beneath the MI potentially discouraging their return to the reef. In essence, the ascent now is irreversible and the fish are committed to continuing the ascent to its conclusion. As the group of MI and sharks ascend from the reef, they immediately get caught in whatever currents are moving along the reef face. These, combined with the now falling tide bringing water from the lagoon across the reef to the ocean, tend to push the groups even further away from the reef.

Fig. 6. Gray reef sharks holding station above an aggregation of MIs shortly before they ascended off the reef to spawn. 15 Jan 2016. Photo copyright M. T. Etpison.

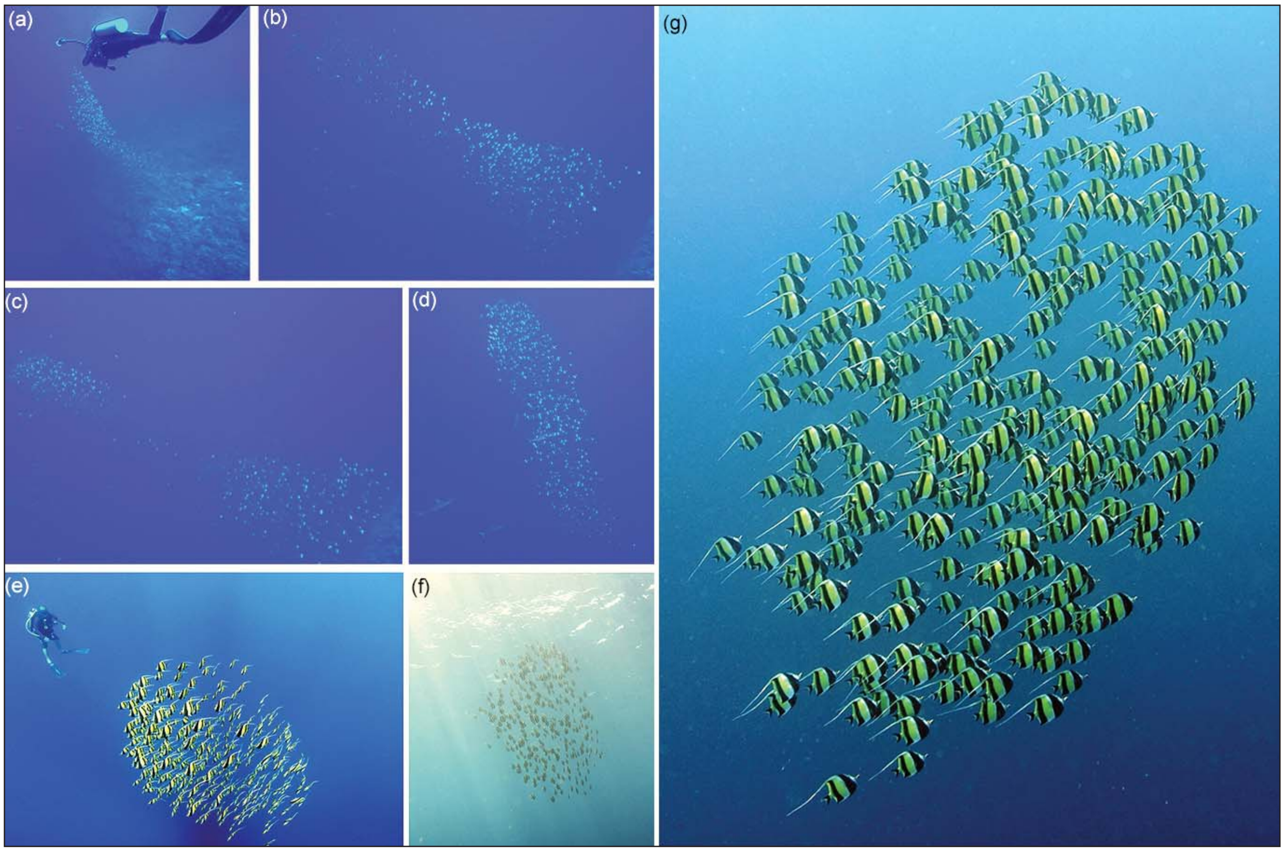
Spawning Behavior in Blue Water and Shark Presence/Predation. The actual spawning of ascending groups was seldom observed, although Colin et al. (2012) did see one instance of mass spawning at the conclusion of the ascent. Given the behavior of the fish swimming upward away from the reef, we make the assumption, in those instances seen, that their intention was to spawn in very shallow water, as seen previously. The presence of sharks following the ascending groups complicated observations. In January 2015 we followed several groups of fish up from the reef out into open water, but lost sight of them and the sharks. At short time later, while we were hovering about 6 m below the surface in mid-water with no fish around, a small school of MIs came to us out of open water, then milled about apparently trying to hide amongst the diving observers. No sharks were present at that time and a few minutes later the school suddenly darted away towards the surface and out of sight. Spawning by them was not observed. Due to the potential danger to diving observers from sharks when the MIs reach the surface and presumably spawn, divers would return to the boat and then motor outward to areas where the thrashing of the sharks attacking the MIs was readily apparent on the surface.

In January 2015, 2016 and 2017 we observed and took photos/video of the spawning movements of the MI at the two sites. At SC in January 2016 over 100 grey reef sharks (numbers determined from photographs) gathered in the spawning area. In January 2017 the GRS numbered over 200 at their peak. During morning incoming tides as the aggregation formed on the fore reef, fifty or more GRS were seen trailing the MI aggregation; swimming in an unhurried manner, but occasionally diving at and attacking the schools. When the MI school gathered to ascend from the reef, the sharks became extremely agitated and aggressive, following the MI school in a tight cluster. We had seen close to 100 GRS daily along the reef for several days, but when the MI ascended off the reef, they were joined by an additional 100 GRS (numbers determined from photographs), which had evidently been present in open water off the reef just beyond the limits of visibility (about 30 m).

The MIs split into several groups once they had risen away from the reef. One group was seen to return directly back to the reef while all others swam directly away from the reef and up towards the surface (Fig. 8). Unable to keep up with the idols and sharks on scuba, observers returned to the boat. A short time later the boat arrived at an offshore location where five schools of MI being attacked by packs of GRS were observed on the surface a hundred meters or more away from each other (Fig. 9). Several small silvertip sharks *(Carcharhinus albimarginatus)* were also filmed trailing the grey reef sharks. Our boat had to move at 10 knots speed just to keep up with movements of the frenzied fishes on the surface. GoPro cameras on poles, held over the side of the boat while it motored along, were immediately and repeatedly attacked by GRS; one camera housing was crushed by a shark bite while another was badly scratched after several sharks bit it. At this time the sharks were in a full feeding frenzy and would certainly have attacked anything in the water or moving on the surface.

After several minutes the chaotic feeding frenzy, during which many of the MIs were eaten, it ceased, the remaining MI formed schooling groups observed to have up to 20 individuals which swimming together at the surface in open water. The sharks continued to chase the remaining fish at the surface, ending up, based on GPS positions, three km from the nearest reef (Fig. 10). Numbers of GRS were shadowing small groups of actively swimming MI at the surface but once the MI numbers were reduced and dispersed by the predation, those individual MI left appeared to be more effective in eluding the sharks. However, the sharks were seen to slowly pick off the exhausted MI, which had nowhere to hide or shelter, one by one. MI also tried to station themselves under our boat, which was moving along at several knots. The presence of the boat trailing the MI and sharks may well have affected their interactions, but by the time our boat-based observations were broken off, there were only a few MI left on the surface. Our observers returned to the reef and dove again, and during subsequent observations, no MI were seen returning directly to the reef.

Post spawning behavior. On some occasions when observers remained on the reef after the spawning ascent started and MI disappeared offshore, remnants of the schools of MIs were observed returning



Figs 7a-g. Variation in size and shape of ascending groups of MI at BC and SC. (**a-d**) General groups ascending from the reef, numbers not specified. Ascending groups of (**e**) approximately 290 fish, (**f**) 311 fish, (**g**) approximately 392 fish. A numbers based on counts of individuals from photos. Photos copyright M. T. Etpison.

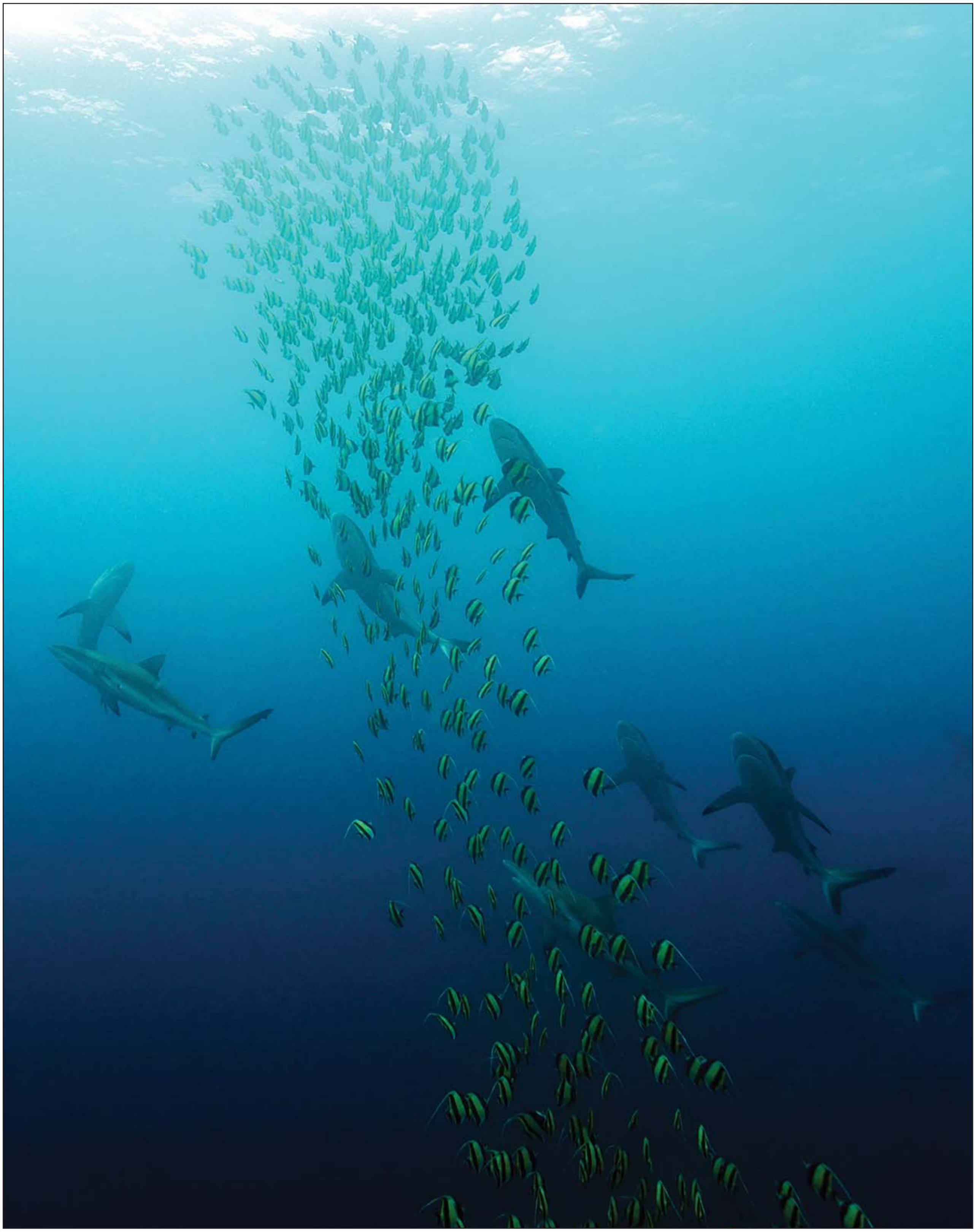


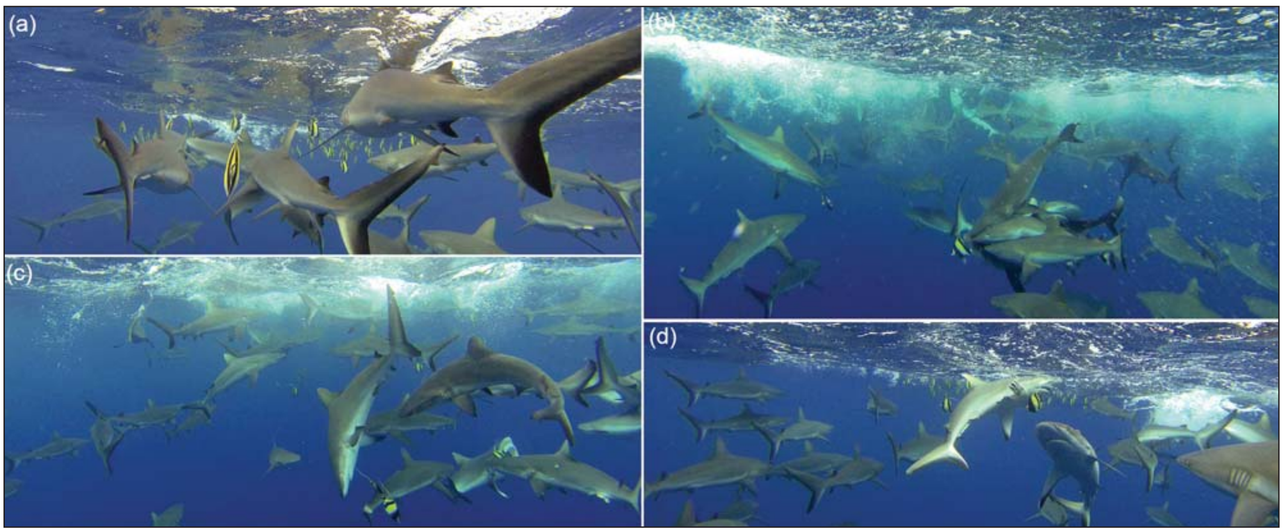
Fig. 8. Ascending aggregation of MIs (approximately 544 fish visible in photo) being shadowed by gray reef sharks, as they move towards the surface, Jan 2015. Photo copyright M. T. Etpison.

to the reef from open water after their ascent. It is unknown if those returning fish had successfully spawned or aborted their run out into open water prior to spawning. Almost immediately they dispersed and started feeding on the shallow reef slopes during the remainder of the outgoing tide, mixing with other individuals which may not have been ready to spawn. The sharks and other predators appeared uninterested in pursuing them.

The morning after MI spawning, if within the multi-day spawning window, the process usually repeated, but over days of a given lunar month spawning period, the schools and numbers of fish visibly diminished each day. What had been several thousand fish seen during the first month/days of aggregation diminished to a few hundred. Similarly, in the days following MI spawning, most sharks dispersed and were not seen at the sites in such numbers, suggesting the GRSs were gathered specifically to target the spawning. While the attrition levels of the aggregating/spawning populations are difficult to quantify, we have observed when spawning and shark predation are high during December/January, the fish often do not aggregate and spawn in February/March, perhaps a critical mass needed to spawn is no longer present. Other years if aggregation/spawning does not start until January, it will continue into March.

C. Orange spine surgeonfish: Aggregation and spawning. Although we have much less information, OSS use the same aggregation sites (BC, SC) with the same seasonal pattern, December to March, with a peak in January or February; the same as MI. They have a different lunar timing, aggregating and spawning on the last quarter moon (approaching the new moon) instead of the first quarter moon. OSS have been seen to use an additional location, called "New Drop Off" (approximately 7°6.15'N; 134°14.29'E), not known as a spawning site for MI. They are more challenging than MI for divers to observe as they move more rapidly along the reef, their groups are less compact and higher up in the water column (Fig. 11), making it difficult to follow them for any period of time. Randall (2001) confirmed that those *N. lituratus* with caudal fin extensions represent mature males, while mature females lack these. Examining several photographs of orange spine surgeonfish "running" along the reef during times of aggregation indicates, based on caudal fin extensions, the presence of considerably more females than males

D. Additional Species of Surgeonfishes using sites. The bignose unicornfish, Naso vlamengii, has been seen to aggregate at BC and SC on days from first quarter to full moon in October and November, spawning high in the water column and are also pursued by GRS. Their aggregations are difficult for divers to observe as they usually swim quickly and at a distance away from the reef in strong currents. At BC the blackstreak surgeonfish, Acanthurus nigricauda, (Etpison 2004, 2009) has also been observed to join together in large mixed aggregating schools to spawn in the summer months, pursued by GRS and other reef predators. We are still gathering more information on the exact dates and timing on these unusual mixed spawning aggregations.



Figs 9a-d. Attacks by gray reef sharks on MIs commence once the small fish are at or near the surface, and the sharks drive the now vulnerable MIs out to sea away from the reef. Photos copyright M. T. Etpison.

DISCUSSION

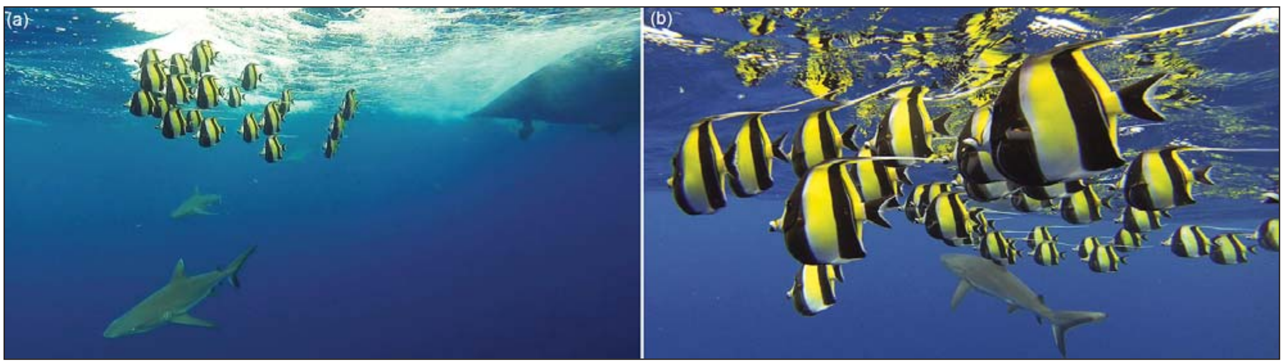
Only a few sites on Palau's western barrier reef are known to have MI and OSS spawning aggregations. These are tourist dive sites, visited nearly every day, and if large numbers of sharks and spawning fishes are present this would be noted. This offers some confidence that the presently known aggregations, seen during specific limited periods, are not occurring at other times. We have many fewer observations of OSS than MI, due to the difficulties mentioned in working with the former species. We aim to rectify this discrepancy in the future and also include more species occurring in these areas.

MI and OSS are common on outer reefs to 60 m depth but few reliable quantitative data on fish density are available. Qualitatively the numbers occurring within spawning schools could likely be drawn from a relatively small catchment area with migration distances less than a few km. It is reasonable to assume with over 300 km of barrier and outer fringing reefs many more aggregation/spawning sites for these fishes exist in Palau. Many areas are seldom visited by divers, but using known times of aggregation, additional areas can be examined to discover additional aggregations, expanding knowledge of reproduction for management purposes.

The use of same sites and seasons by MI and OSS for spawning, but on opposite phases of the quarter moon (MI first quarter, OSS last quarter), means they do not directly compete for reef space for either spawning preliminaries or ascent/spawning. Their larvae would also not be entrained into the same water masses, reducing competition for early life history food resources. Both have their spawning during lunar periods of neap tides with midday high tides. Neap periods have smaller tidal currents on and off the reef, generated by lagoon-ocean water level differences. Where the shallowest portion of barrier reef is narrow (about 200 m width), tidal currents cross the reef cleanly, moving between lagoon and ocean or vice versa (Colin 2009, Fig. 2.17). The present aggregation areas are not as simple, with a much broader shelf between lagoon and ocean, as well as projections producing eddies as along reef currents pass by them. There is need for a detailed study of the currents associated with these sites to better understand the relationship of currents to spawning.

In their spawning behavior MI and OSS ascend and move away from the reef sufficiently far before releasing eggs and sperm at locations where, even with 30+ m water visibility, the reef is no longer visible. Only a few fishes with similar strategies are known in Palau. The large bumphead parrotfish, *Bolbometopon muricatum,* aggregates on the new moon and rises above and moves far away from the reef to spawn at morning high tide (based on 45 days pers. obs.) and no predation attempts by sharks (and seldom the presence of any sharks) were seen. This was also noted by Roff et al. (2017) based on one day's observations. The large twin-spot snapper, *Lutjanus bohar,* aggregates in the thousands every month before the full moon at some reef promontories (Sakaue et al. 2016, pers. obs.) and moves high in the water and far off the reef to spawn early in the morning. Bull sharks *(Carcharhinus leucas)* and oceanic blacktip sharks *(Carcharhinus limbatus)* occur with them and normally a few attacks during spawning, often successful, occur every day.

It is very surprising that a relatively small fish like the MI would ascend so far above and away from the reef to spawn. Among comparably-sized deep bodied reef fishes, such as butterflyfishes and angelfishes, for which there are spawning observa-



Figs 10a-b. (**a**) After the initial feeding frenzy, small groups of MI form at the surface trying to avoid shark predation. (**b**) Remnant group of MI at surface in blue water with GRS in background, photo taken from boat using GoPro camera on pole. Photos copyright M. T. Etpison.

tions, they are not known to do so. It is possible some of the species in these families which normally station themselves high above the reef (such as members of the chaetodonid genus *Hemitaurichthys)* might have behavior similar to MI, but their spawning is unknown.

It is clear that at our study sites many MI ascending from the reef to spawn are eaten by sharks during the process. There are two stages to the predation event, an initial feeding frenzy lasting several minutes followed by a period of slow attrition of the remaining MI found schooling at the surface. During this time, currents carry the groups along or away from the reef. Qualitatively only a small number of fish are seen returning to the reef after ascending, perhaps only 10% of individuals return to the same reef area. The remainder are presumed eaten by sharks or when far off the reef in open water drifting to end up far away from the reef area where they ascended, their possible return to the reef not noted and fate unknown. Subsequent days during the spawning period had decreasing numbers of MI each day, potentially due to predation, but this could also be attributed the normally tapering numbers of fish within most aggregations after a peak day (Sadovy de Mitcheson and Colin 2012).

The success rate for spawning (releasing all or a major proportion of gametes) prior to predation is unknown. The undisturbed spawning seen in prior years (Colin et al. 2012) indicates the gamete release is similar to that known for other reef fishes. The process of releasing gametes took a short time (minutes?) and was not a single massive release. When a spawning group is attacked, it is likely only a portion of the fish will be ingested prior to releasing gametes, and it is also likely that as some are eaten, a portion of their gonadal products may be dispersed into the water as the body of the fish is ripped apart.

Given our present state of knowledge, we surmise that spawning by MI at the sites examined has a high likelihood of death for the spawning adults. In that sense, this activity might be considered "suicidal" for the individual fish, but spawning is a behavior for which there is a high incentive to undertake. Swimming en masse up and away from the shelter of the reef to spawn is unusual, particu-

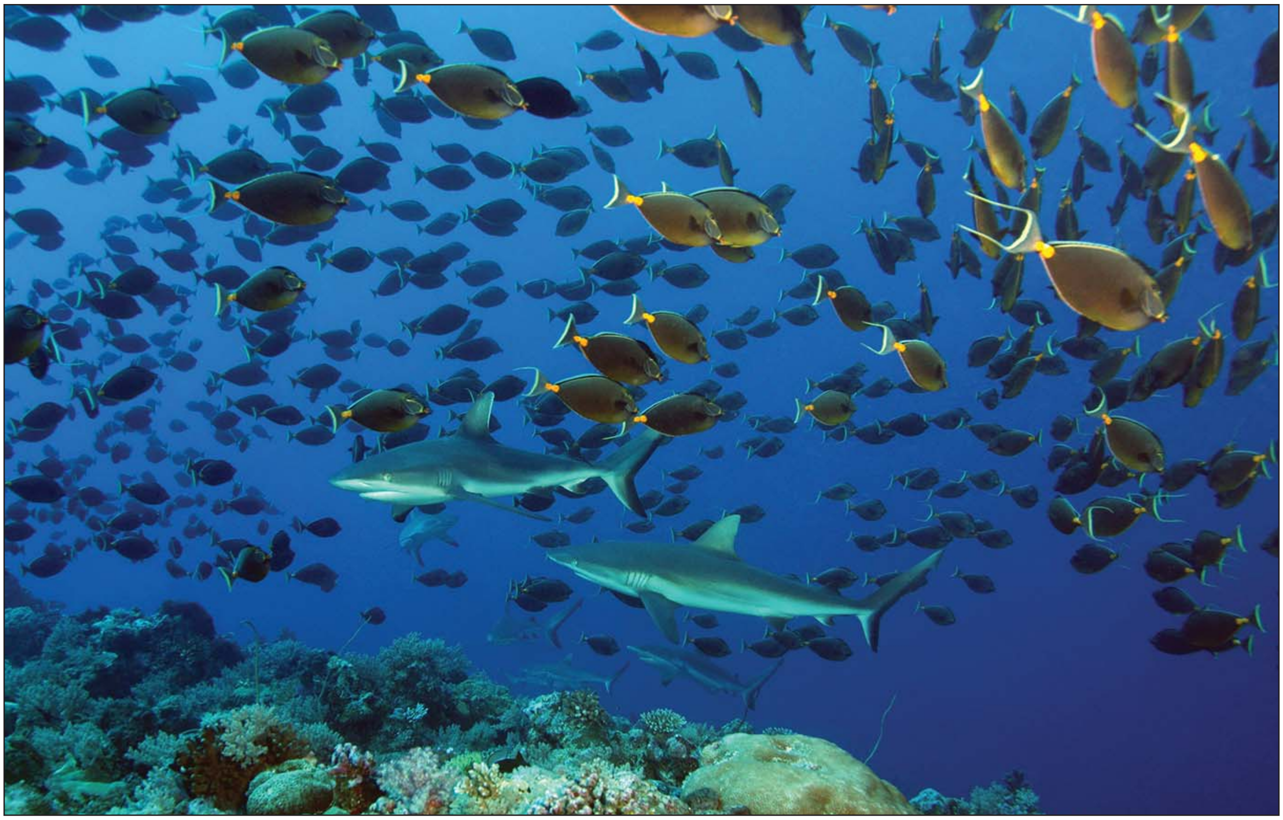


Fig. 11. Spawning aggregation of OSS, *Naso lituratus*, at BC with gray reef sharks visible on the reef and within the overall aggregation, 18 Jan 2009, day of last quarter. There are at least 377 OSS (313 females, 64 males as identified by the males having visible caudal fin extensions). Photo copyright M. T. Etpison.

larly for a small species vulnerable to predation. Prior to the spawning ascent, a few individuals may be taken by predators, but only when individuals are separated from the larger group and attacked from multiple directions by several predators. While ascending MI are not typically attacked and only when they are near the surface do attacks commence, initially as a very chaotic feeding frenzy in which the sharks rush the schools of MI from all sides, contorting themselves and biting wildly. Despite this activity, video footage indicates the sharks have a hard time ingesting the small fish, since their mouths are on their ventral surface, the prey is small and they are not biting chunks out of a large prey. Even amid the thrashing and confusion of the frenzy, individual MI can be seen successfully evading predation for some time. Over minutes, however, individuals make mistakes and are taken, normal predation avoidance tactics are no longer effective, and the numbers of prey fish decrease. Each remaining fish receives increasing attention from multiple sharks and the MI become exhausted by the sheer numbers of sharks chasing them.

At some point, after the initial frenzy has subsided, the remaining MI form small groups which swim together aimlessly in open ocean some distance away from the nearest reef and, based on video filmed from boats, can swim without being constantly attacked by sharks. GRS continue to trail them. staging infrequent attacks, but the small numbers of fish left appeared to enjoy a modest degree of protection from further attacks. It might be argued this was due to the inability of the sharks to capture them except in a chaotic feeding frenzy type situation. Potentially the MI might follow sound back to the nearest reef, as they are far beyond visual range.

Palauan fishermen had a traditional term, *Plutek,* for rare occasions when they have observed packs of extremely aggressive sharks swimming fast in tight formation outside the reef (Johannes 1981: 142) and their response would be to immediately get out of the water. In January 2015 we surfaced in open water about 100 m out from the reef after losing sight of the MI schools and the pursuing sharks. While waiting on the surface for our boat to pick us up, packs of grey reef sharks (Fig. 12) came under us out of the blue, swimming spread out like a carpet in formation back to the reef after finishing their open water predation; a perfect example of *plutek.*

Why these fish do not spawn closer to the substrate, like many other reef fishes, is unknown. The "running" schools are followed and attacked by predators prior to their ascent, it is possible fish would face the same risk of predation even if spawning occurred closer to the reef. While rising further off the bottom may enhance the chances of their eggs surviving, this question needs further consideration as we cannot yet identify any compelling reason why the fishes ascend so high in the water column to spawn.

Is the high predation rate on spawning adults part of the life history trajectory for these fishes? While there are certainly instances of semelparous (one time spawning followed by death) life histories among fishes (salmon being a prime example), it

Fig. 12. Probable *Plutek* group of sharks returning to the reef after venturing offshore in pursuit of MI. Photo copyright M. T. Etpison.

seems likely MI and OSS (like nearly all other reef fishes) rely on an iteroparous (spawning multiple times) life history and the high predation risk at our sites is a product of the unusually large numbers of predators often present at the spawning areas.

The large numbers of sharks present at the sites before spawning, as well as the movement of the fishes away from the protection of the reef, is remarkable. There are examples, such as Mourier et al. (2016) in which spawning is anticipated by predators to prey on adult fishes, and many others where egg predators are stationed at locations to quickly feed on released eggs (Sadovy de Mitcheson and Colin 2012). The attacks on the fishes, particularly MI, at the surface is a true feeding frenzy, something seen in Palau only in association with pelagic “bait balls”, not with reef fishes (Etpison 2016). Diving observers have wisely chosen to exit the water and observe the behavior from the safety of a boat.

The numbers of GRS seen at BC and SC grow significantly during the late winter/early spring and are roughly correlated with the presence of the aggregating fishes, as well as many other species reproducing around the same time. Tourism dive operators constantly assess their abundance, so although the numbers are qualitative, we believe they are realistic. Vianna et al. (2012) pointed out the depths inhabited by GRS varied with water temperatures, seasons and time of day, adding some complication to visual assessment of shark abundance. Based on present knowledge, they may have also underestimated the maximum numbers of GRS populations based on acoustic tagging and visual observations, reporting there were about 100 GRS at the five sites they investigated, present efforts have documented via photographs up to 200 GRS at just SC when the MI were preparing to spawn.

Other outer reef areas in Palau, based on numbers of GRS seen via time-lapse cameras and Baited Remote Underwater Video (S. Lindfield, pers. comm.), have much smaller shark populations. Why do BC and SC have so many GRS? The two sites are focal points for spawning and the lunar sequencing of aggregations (first and last quarter) for MI and OSS, as well as full and new moon for other species, extends the periods of high fish abundance over the entire lunar month, increasing the potential benefits to GRS from remaining in the areas during winter months.

The level of shark predation on aggregating fishes seems to vary across locations and species. Based on collective observations and information known at the time, Colin (2012) suggested that the risks of shark predation were relatively minor in aggregation spawning events and did not remove large numbers nor influence behavior of spawning fishes. That generality has been upset by the present observations and those of Mourier et al. (2016) requiring that this assumption of limited influence by predators on spawning behavior be reexamined. Our study sites (BC and SC) may be extremes in the continuum of predation risk and unusual in the context of the present day due to the high numbers of sharks normally present, but they also may represent more the natural populations of sharks and spawning of fishes without fishing pressure by humans having removed large predators.

Given that the large numbers of sharks seen during the spawning periods are not always present, what is the benefit to the GRS from the effort involved in targeting of the aggregations? Individual MI are not a large food items for a shark. Sixteen individuals 95-125 mm standard length weighed 47 to 100 g, averaging 65 g (Colin et al. 2012). The biomass of 500 ascending fish would consequently be only 30-35 kg, yet these fish might be targeted by 100 or more GRS. Predation on OSS and other surgeonfishes would produce a food content on the order of 200-400 g per fish, so there would be a higher return per fish, but perhaps still not a particularly large return on effort. During mid-day, though, when MI and OSS spawning occurs there may be few other opportunities for predation (based on the rarity of divers seeing predation events at those times) and the MI and OSS may represent the easiest species to target as a small, but reliable, food source.

The spawning by MI in the face of a high predation risk might suggest the spawning fish are in a “spawning stupor” as proposed by Johannes (1981) in which fish in their intent to spawn become so oblivious to predation dangers that they continue to follow through with their spawning no matter the predation around them. There is no evidence for these two species exhibiting a spawning stupor as the individuals are fully aware and MI exhibit predator avoidance by rapid, agile movements when attacked making them surprisingly difficult for predators to capture. Colin (2012) argued the evidence for the existence of a “stupor” was based on misinterpreted observations and that although the predation risks may be high, spawning fishes are extremely aware of their surroundings and the presence of predators.

Each year over the successive monthly spawning cycles, the schools of MI, initially numbering up to thousands of individuals, are seen to diminish to near zero. The little information we have on growth rates and life spans of MI comes from fish maintained in aquaria, but does indicate a multi-year life span with moderate growth rate, so fish observed spawning are at least a few years old. An important focus of future research will be to document the population sizes more accurately before and after the spawning season, as well as the attrition over that time. Why there are such large numbers of sharks found at BC and SC is not understood. Whether the promontory areas attract and retain large numbers of fishes is uncertain, but that type of geomorphology is often associated with high fish populations. Throughout most the world's reefs numbers of both predators and their prey fishes have been greatly reduced through overfishing. The remarkable behavior documented here illustrates how little is known about the life histories of many common reef fishes.

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