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Aggregation and spawning of the humphead wrasse *Cheilinus undulatus* (Pisces: Labridae): general aspects of spawning behaviour

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The humphead wrasse *Cheilinus undulatus* formed resident spawning aggregations daily after high tide at specific locations along the seaward edge of the Palau barrier reef. The location and extent of one aggregation site remained consistent for 6 years with no physical features distinguishing it from adjacent areas. Spawning was documented most months and probably occurred year round with possible seasonal and lunar variation. Spawning males arrived first at the site, followed by females and potentially small primary males. The aggregation female to male sex ratio was estimated to be between 6:1 and 10:1. A maximum of 15 males and 100–150 females were observed at the site. A male courtship posture with the anal fin pointed, the caudal fin folded down and the dorsal fin folded against the body was maintained while swimming a few metres off the bottom in view of females. When ready to spawn females rose up as the posturing male passed and the pair released gametes in a relatively sedate fashion near the surface along the shelf break. No attempted predation on spawning adults was seen. Egg predation after spawning was uncommon. On days with early to mid-day high tides the spawning period started 2.0–2.5 h after high tide when the speed of lagoon–ocean tidal currents peaked and lasted *c.* 1 h. On days with later afternoon high tides, spawning occurred sooner after high tide and before current speeds peaked. Other fishes with planktonic eggs spawned at the site as pairs or small groups in a rough succession after high tide with *C. undulatus*, the last species to spawn.

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Key words: currents; migration; spawning aggregation.

INTRODUCTION

The humphead wrasse *Cheilinus undulatus* Rüppel is the world's largest labrid and one of the largest bony fishes occurring on coral reefs. Also known as Maori wrasse and Napoleon fish and in Palauan as *Maml*, the species occurs from the Red Sea across the tropical Indo-west Pacific Ocean to the Marshall, Line, Cook and Tuamotu Islands. In recent decades increasing fishing pressure, often for the live reef-fish trade (LRFT), resulted in placement on the CITES Appendix 2 of threatened species, limiting international trade to sustainable levels (Sadovy *et al.*, 2003), as well as on the IUCN Red List as endangered.

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Cheilinus undulatus is still moderately abundant in the Republic of Palau and at present fully protected (no fishing, possession or sale allowed). A spawning aggregation was located in April 2001 using information about where large numbers had been seen from a knowledgeable dive guide. Additional aggregations were subsequently located.

Little firm information has been published regarding the aggregation and spawning of *C. undulatus*. For Palau, Johannes (1981) reported that 'Palauans are uncertain as to when *mamel* (sic *maml*) spawn and no one I talked to had ever knowingly witnessed the spawning act'. At Layang Layang Atoll in the South China Sea 300 km north-west of the coast of Sabah, Malaysia, a single spawning aggregation of *C. undulatus* was observed, with the fish migrating to the western end of this small atoll to spawn on a regular basis *c.* 2 h after high tide (S. G. Oakley, pers. obs.). Aggregation and spawning have been documented in a few areas of the Great Barrier Reef, Queensland, Australia, with video recordings of the spawning and social behaviour (J. H. Choat & R. Fitzpatrick, pers. comm.). Chateau & Wantiez (2007) acoustically tagged a 45 cm total length (L_T) *C. undulatus* (almost certainly female) which may have left their study site to potentially migrate to an aggregation area. They indicated, based on observations of others, the aggregation season of *C. undulatus* in New Caledonia to run from December to March and April and for aggregations to occur on the 'outer barrier reef near passages'. There are unconfirmed reports of aggregation by *C. undulatus* (Sluka, 2000; R. E. Johannes & L. Squire, unpubl. data; J. Pet & A. H. Muljadi, unpubl. data), which have been accepted and repeated (Russell, 2001; Claydon, 2004) without confirmation. None would qualify, even using indirect criteria, as verified spawning aggregations by the criteria of the Society for the Conservation of Reef Fish Aggregations (www.scrfa.org).

Choat *et al.* (2006) reported protogyny while Sadovy *et al.* (2003) indicated that both primary and secondary males occur. Females reach sexual maturity at *c.* 5 years of age and 35–50 cm L_T (Sadovy *et al.*, 2003). Choat *et al.* (2006) indicated that sex change from female to male occurs at *c.* 9 years of age. Males continue to grow rapidly while the growth rate of fish remaining female slows compared to males. Males reach a maximum L_T of *c.* 150 cm and age of *c.* 25 years, although the largest seen by Choat *et al.* (2006) was 140 cm. Females reach *c.* 100 cm L_T and an age of 30 years, although such large and old individuals are likely to be a relatively small part of the female population. These fish are diurnally active, sheltering (sleeping) at night in crevices in the reef within a normal home range that may differ from spawning aggregation sites (Sadovy *et al.*, 2003).

Slamet & Hutapea (2005) reported the species to have a spherical egg 620–670 μm in diameter with newly hatched larvae 1.6–1.7 mm L_T with a mouth gape of 133 μm and a transition to juveniles after an *c.* 25 day larval life. It is not presently amenable to aquaculture, having proven difficult to rear in large numbers, and has slow early growth with 6 month-old juveniles only 5–6 cm L_T .

This study was undertaken to understand interactions and to promote the sustainable management of this vulnerable species. The present paper describes the seasonal, lunar and daily periods of aggregation and spawning by *C. undulatus* largely at a single study site and includes general information on environmental conditions associated with reproduction.

MATERIALS AND METHODS

STUDY AREA

This work was undertaken in the Republic of Palau, the westernmost group in the Caroline Island chain [Fig. 1(a)] over a total of 6 years. The study site [Fig. 1(b)–(d)], locally known as Siaes Reef, was visited regularly during the first 2 years of the study in an attempt to discern the seasonal, lunar and daily patterns to aggregation and spawning. Summer weather conditions of strong westerly (monsoon) winds often made it difficult to visit outer reef areas of the western barrier reef due to large waves; hence, access for prolonged periods was often not possible. On most survey days, the sequence of objectives was to: (1) verify that aggregation was occurring; (2) verify that spawning was occurring; (3) estimate the numbers of males and females present at the site; (4) determine their distribution throughout the site and (5) examine whether the aggregation was within, or extended beyond, previously known limits along the reef. Additional tasks at other times included photographing behaviour, collecting eggs after spawning and measuring currents at sites within the aggregation area.

During the last 4 years, effort was focused on other aspects of the ecology of the fish, and observations largely limited to filling in gaps in the documentation of seasonal and lunar occurrence of aggregation and spawning, plus on occasion a census of the prime study aggregation and determination of its distributional limits. In April 2007, a final census and distribution survey was conducted to examine whether noticeable change had occurred in either variable since 2001.

SITE MAPPING

The site was mapped using logging global positioning system (GPS) receivers (www.garmin.com) and aerial photographs. The entire outer profile of the study reef was transited by a snorkeller while towing a GPS receiver in a waterproof housing logging positions every 5 s. The resultant track was later downloaded and the profile matched to that present in vertical aerial photos, providing a detailed geo-referenced image of the study site [Fig. 1(c)]. The geo-referencing of this image was verified by subsequently determining the positions of identifiable features in the photographs and comparing actual positions with those determined from the image.

CENSUS TECHNIQUES

Regular attempts to fully census the population were made at the site; however, several factors made obtaining accurate fish abundance data difficult. Usually, multiple transects were swum a short distance out from the reef drop off, in order to see both onto the shallow fore reef and also down the reef slope, by snorkelling or scuba diving. Surveys were swum continuously from one end of the aggregation area to the other, a distance of 250 m of reef front, counting fish as they were seen. Surveys continued at least another 50 m beyond either end of the known aggregation areas to make certain no fish were present. The fish were shy and wary of humans, keeping a minimum distance of 6–8 m minimum from observers, normally making it impossible to discern or photograph the individual identifying markings on the head and body. Fish near the shelf break usually moved in the same direction ahead of a person swimming along the shelf edge. Effectively, the fish were driven ahead of the observer. Presumed females, based on size and colouration, were often so numerous that it was usually impossible to keep track of individuals during the census. More reliable counts were obtained for males as they were less numerous, larger and tended to stay further above the bottom. On some occasions the number of males present was uncertain as males could swim out of sight ahead of the observer and a few might have been double counted. For such surveys an absolute lowest number (no double counting) was determined. Survey swims of the entire aggregation area were made at the site at times other than aggregation periods to document population levels during times outside of aggregation.

A second technique was used to get additional aggregation numbers. Starting from one end of the aggregation area, a scuba diver would swim on the outer slope at 20–25 m depth

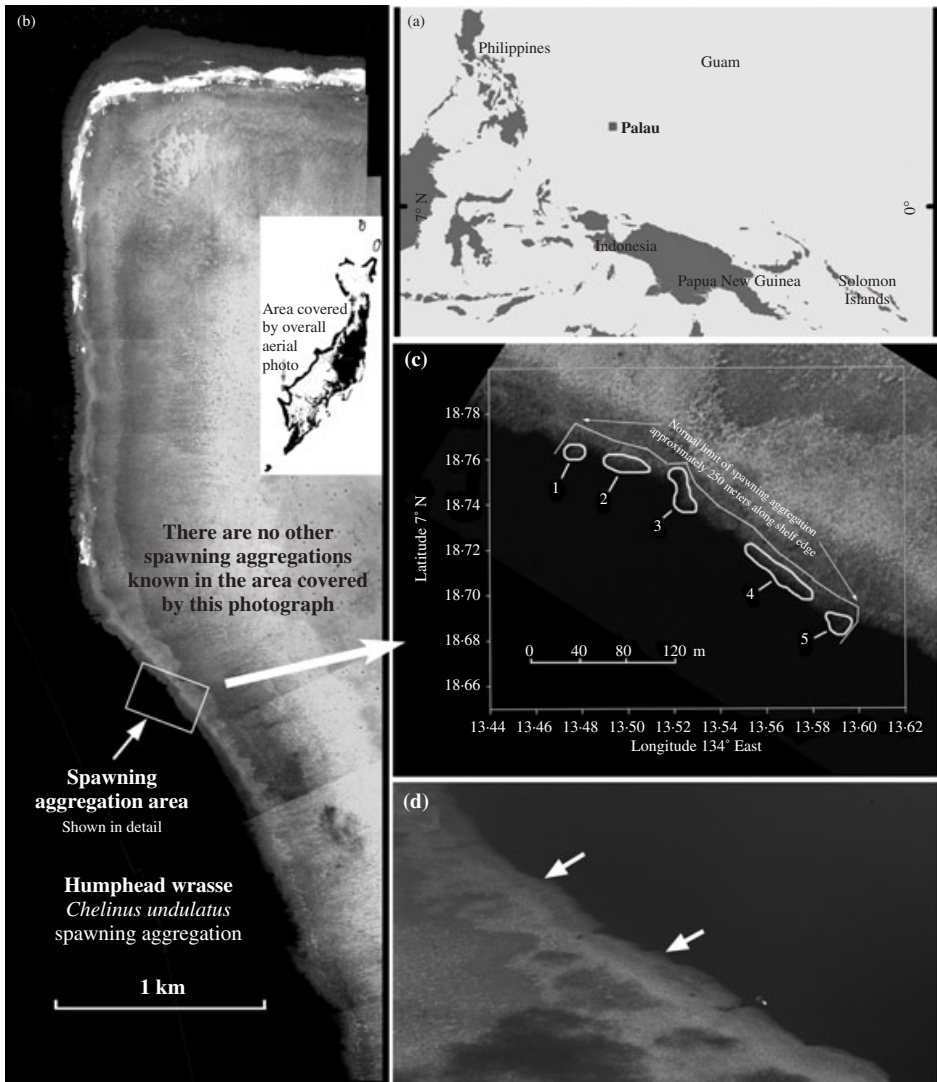


FIG. 1. Location and configuration of a *Cheilinus undulatus* spawning aggregation site in Palau. (a) Location of Palau in the western Pacific. (b) Section of the western barrier reef of Palau indicated on insert, where the spawning aggregation occurs. (c) Spawning aggregation site covering *c.* 250 m of shelf edge reef, with aggregation cluster sites indicated by the numbered areas. (d) Oblique aerial view of the site looking south with the aggregation area indicated between the arrows, showing how the site is typical of the wider western barrier reef.

below the roughly 10 m-deep drop off. At intervals the diver would rise up to do a quick count of fish seen from a position out beyond the drop off without approaching the fish or driving them along the reef. The diver would then return to depth and move along the reef to a new point to rise and survey fish. Using this successive pop-up technique, all of the aggregation area could be surveyed and provided data on the numbers in the aggregation comparable with the survey swims. Due to their numbers, definitive surveys of females at the

site were not done; however, estimates of number of presumed females were made based on the techniques described.

PHOTOGRAPHIC AND VIDEO DOCUMENTATION

Aggregation and spawning were documented using an underwater video camera (Sony DV-1000; www.sony.net) and digital still cameras (Nikon D-100; www.nikon.com). The still camera allowed rapid sequences of spawning behaviour to be photographed, however, the images provide almost no information on true colour of fish due to use of available light for rapid photo sequences.

CURRENT AND TEMPERATURE MEASUREMENTS

Currents across the reef were driven by the semi-diurnal tides of Palau, with two highs and two lows on most days. Current speed was measured using two General Oceanics flowmeters (www.generaloceanics.com) with low speed rotors installed above the sites. Meters were suspended on a line from the bottom using a small float (Colin *et al.*, 2003), so they were 0.75–1.0 m below the surface and close to the depth range where the fish were spawning. The meters were manually read at regular intervals, generally every 10–15 min, and numbers of revolutions recorded on underwater slates. Current direction was determined by the orientation of the flowmeters, which face into the current, using an underwater compass. Temperature was measured by recording thermography.

FISH LENGTH DATA

No specimens were collected for this study. Whereas lengths are indicated in the results section, these were L_T estimated visually underwater and are assumed to have an accuracy within ± 10 –15% of the actual value.

LOCATIONS OF ADDITIONAL AGGREGATIONS

GPS-tracked survey swims looking for additional aggregation sites were made using diver propulsion vehicles or towing a diver behind a boat along other reef edge areas. Such surveys were done only after first verifying the occurrence of aggregation at the primary site, since early in the study knowledge of aggregation timing was limited. While this reduced the amount of time that could be spent searching for additional aggregations, it was necessary to increase the likelihood-spawning aggregations that would be encountered if they were occurring elsewhere. In this manner a few other aggregations were located. There are no particular features, such as reef promontories or channels, identified as indicative of *C. undulatus* aggregations to aid the search.

RESULTS

THE LOCATION OF PRIMARY AND ADDITIONAL AGGREGATION SITES

The first aggregation located, selected for intensive study, was a typical outer barrier reef margin (Siaes Reef) on the nearly 150 km-long western barrier reef of Palau. The aggregation area included *c.* 250 m of barrier reef edge (Fig. 1) and went inshore from the reef depth break no more than 10–20 m. It did not have any obvious features distinguishing it from adjacent similar barrier reef. Its outer edge was steep (30–60° slope) with abundant coral. During periods when aggregation and spawning were not occurring (*e.g.* low tide), the site had at most a few *C. undulatus*

with no resident males normally present. Compared with the up to 150 individuals present during spawning, the population difference easily exceeds the nominal three-fold plus minimum threshold of increase in numbers for an aggregation (Domeier & Colin, 1997).

The nearest *C. undulatus* aggregation to the primary study area occurred to the south 2.7 km away. To the north of the primary site, no additional aggregations were found along 5 km of reef surveyed [Fig. 1(b)]. Several other additional aggregation sites were located and include both reef edge areas similar to the primary site and some areas with reef projections where spawning occurred. In all locations, timing of spawning retained the same relationship with high tide as that at the primary site. No aggregation sites have been located in the inner lagoon areas of Palau, although such may exist as mature fish are occasionally found in areas far distant (*e.g.* tens of km across open lagoon bottoms) from the shelf edge reefs where all other aggregations are known.

AGGREGATION, COURTSHIP AND SPAWNING BEHAVIOUR

The oceanographic conditions at the aggregation site and along all areas of the western barrier reef varied with the stage of the tide. On rising tides [Fig. (2a)] water present on the ocean side of the barrier reef, usually slightly cooler (28.5–30.0° C) and usually clearer than lagoon water, passed across the shallow barrier reef into the lagoon. On falling tides [Fig. 2(b)], the current reversed from lagoon to ocean bringing warmer (0.5° C more than oceanic water) and usually more turbid lagoon water across the shallow reef to the ocean side. This water appeared less dense than the ocean water and flowed out from the shallow reef as a distinct layer *c.* 3–4 m thick. *C. undulatus* released its eggs into this out-flowing lagoon water.

Fish occurred and spawned throughout the aggregation area, but there were five areas where males and females tended to cluster during aggregation [Fig. 1(c)]. There could be one to several males in a cluster with many more females. Normally fish tended to stay within a single cluster area during spawning, but moved freely between areas if disturbed by a diver. At times fish were continuous between two cluster sites, but then broke apart into the separate clusters a few minutes later. When surveying, the fish would often move ahead of the observer into a new cluster area, then stop when they encountered other *C. undulatus* and would remain there for some time. Within each cluster one male appeared to have a dominant role. Smaller males tended to remain near by and within sight, but not closer than 6–9 m away, as a number of females were also found in such areas.

The longest time between first and last spawning observed on 1 day was 87 min, while the mean \pm s.d. spawning period for days, when the entire sequence was believed to have been documented, was 46 ± 15 min ($n = 24$). These should be considered minimum data, as spawning could still have been occurring in areas outside of the observer's presence. Given the short period for spawning, and a large number of females relative to males, competition for females may be reduced by clustering. Although more dominant males obtain more spawning, smaller males had the opportunity to spawn with a few females which otherwise would be waiting many minutes to spawn with the dominant males.

Males adopted a very distinctive posture with the anal fin folded to a point, the caudal fin folded down so that its margins were overlapping (scissored) and slightly

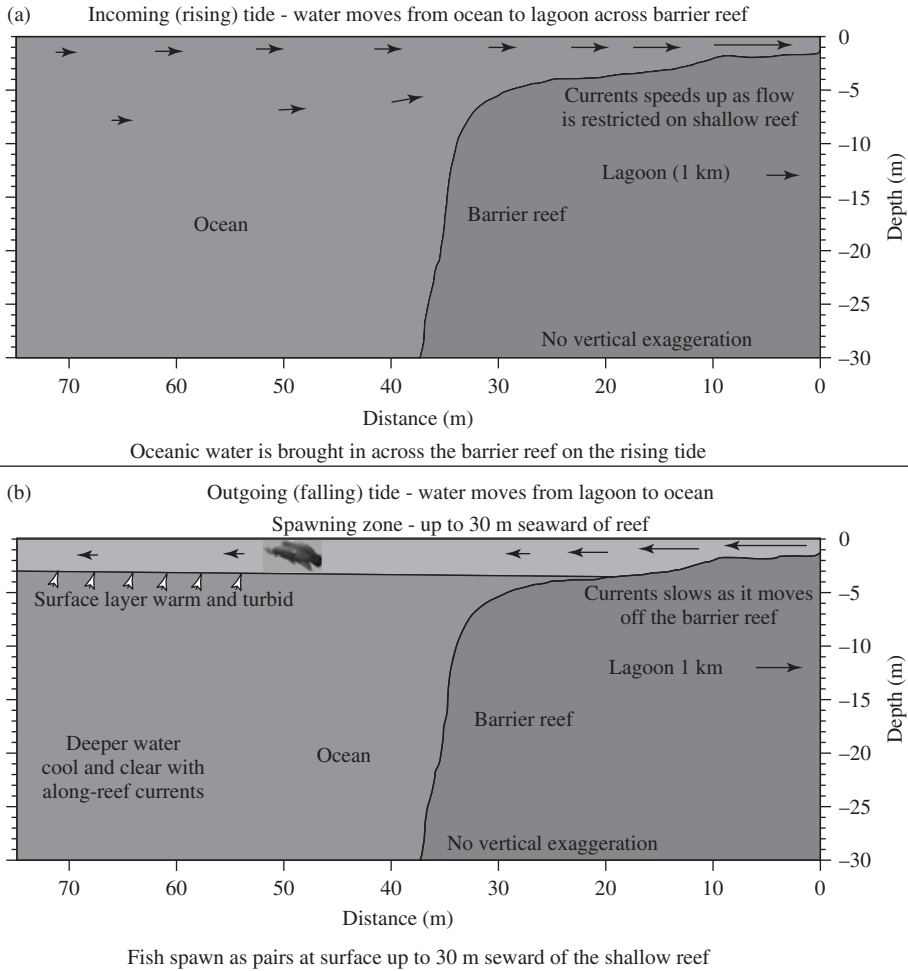


FIG. 2. General view of tidal currents at the aggregation site of *Cheilinus undulatus*, on the western barrier reef of Palau. (a) On rising tides oceanic water moves from the ocean across the barrier reef into the lagoon gaining speed as it is driven across the shallow reef. (b) On falling tides water moves from the lagoon to ocean across the barrier reef which is normally warmer and lower salinity than ocean water. Tidal currents cause this lagoon water moves out from the reef as a sheet 2–3 m thick which floats on top of denser ocean water. It is in this lagoon water moving off the reef that *C. undulatus* spawns, moving off the reef as much as 30 m from the drop-off edge.

cocked upward, and the dorsal fin folded against the body (Fig. 3). Their cheeks became bluish in colour and head markings less distinct. Holding this posture the male swam a few metres off the bottom in the water column (but not near the surface) using pectoral sculling in a display which was plainly visible to females. They did not engage in types of courting movements known from other labrids, such as looping (Colin & Bell, 1991). At times the males came close to the reef, but once spawning started, they tended to stay high above the reef with the females rising to join them.



FIG. 3. Large (*c.* 1.2 m total length) male *Cheilinus undulatus* in courting posture with dorsal fin folded, caudal fin scissored and anal fin dropped and pointed. The fish swims in the water column maintaining this posture by sculling of the pectoral fins. The markings on the head are faint and the cheeks acquire a bluish tinge.

In the aggregation area, several males would be swimming in this manner spread out over a wide area. The largest males swam higher in the water column, and indeed if a smaller male approached too closely to a posturing large male, the larger fish would usually move aggressively towards the smaller. The latter generally responded by dropping its courting posture and swimming away from the larger fish. This was usually the end of the aggressive activity between males; the smaller males remained nearby while the larger male returned to posturing above the reef.

Surveys *c.* 10 min apart (*i.e.* the amount of time it took to swim from one end of the aggregation area to the other) at the start of aggregation indicated that the fish numbers increased greatly during successive survey swims at the aggregation site. Males were generally seen to arrive first and were found deeper along the drop off or farther out in the water column some distance off the reef. They were not seen to actively court when first observed, but started adopting their characteristic courting posture and patrolling slightly later. Females and potentially small primary males appeared later, moving over the reef front near the bottom, occasionally in groups of several individuals (Fig. 4). The number of fish within view of a stationary video camera pointed out to sea (Fig. 5) at one of the aggregation focal points documented the rapid appearance of fish for spawning. As many as 25 females were in view of the camera at one time, and generally at least 10–15 were present during the early period of aggregation. About 35 min after first appearance of females, their numbers started decreasing so that by *c.* 45 min after the start of aggregation they were down to <10 individuals (and generally fewer) as spawning came to a halt for the day.

When aggregated at the study site, the ratio of females to males was estimated between 6:1 and 10:1. These numbers were obtained from survey counts made on the first survey through the aggregation area once substantial numbers of fish were present, but the before the continued presence of an observer disturbed the fish. Due to the general wariness of the fish described previously, the numbers are subject to some errors. On several occasions, a maximum of 15 males were observed on

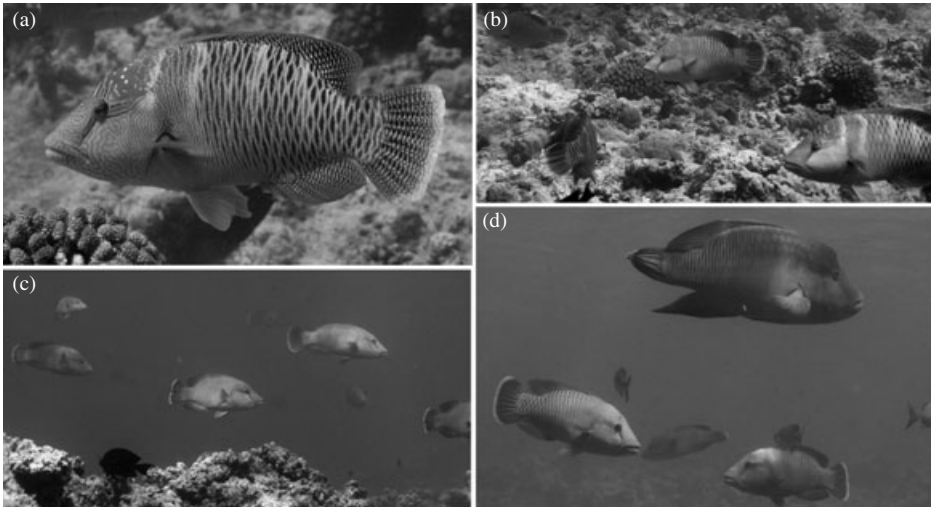


FIG. 4. Prespawning activity of *Cheilinus undulatus* on the western barrier reef of Palau. (a) Typical female *c.* 45 cm total length stationed just above the reef before the start of spawning. The unique markings on the head of each fish are clearly visible. (b) Females grouping on the shallow reef before spawning with four females visible in the photograph. (c) Females stationing themselves up in the water column at the drop off ready to spawn with males. (d) Females along drop off with male in courtship posture above them. The females rise up sequentially to spawn with a male such as this individual.

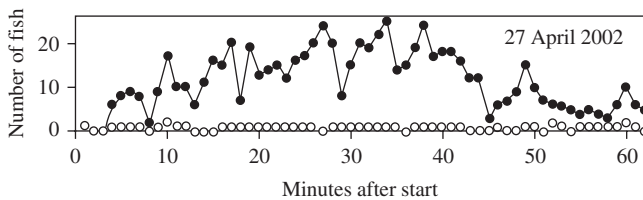


FIG. 5. Numbers of *Cheilinus undulatus* at a spawning aggregation site on the western barrier reef of Palau visible to a stationary video camera located in the centre of aggregation cluster site 2 [Fig. 1(c)] and pointed towards the open ocean. Numbers are the maximum number of individuals of each sex (●, females; ○, males) visible at once during a 1 min period. The graph covers the initiation of aggregation and the spawning period through to the time fish were nearly finished with spawning for the day.

complete surveys through the aggregation site. At times, even on immediately successive counts (*i.e.* the observer turned at the end of the aggregation and repeated the survey in the opposite direction), fewer males were seen. The highest estimates of the number of females, which are less certain than for male numbers, were 100–150 and is used to estimate the general 6:1–10:1 sex ratio.

When ready to spawn, females rose up in the water column as the posturing male passed nearby (Figs 4 and 6). There might be several females potentially ready to spawn, all stationed in the water at various distances above the bottom. The male, if ready to spawn, swam towards the waiting female which then rose higher in the water coming very close to the surface. She joined the male in gamete release during a relatively sedate movement. In a typical spawning rush (Fig. 6), the fish swam in

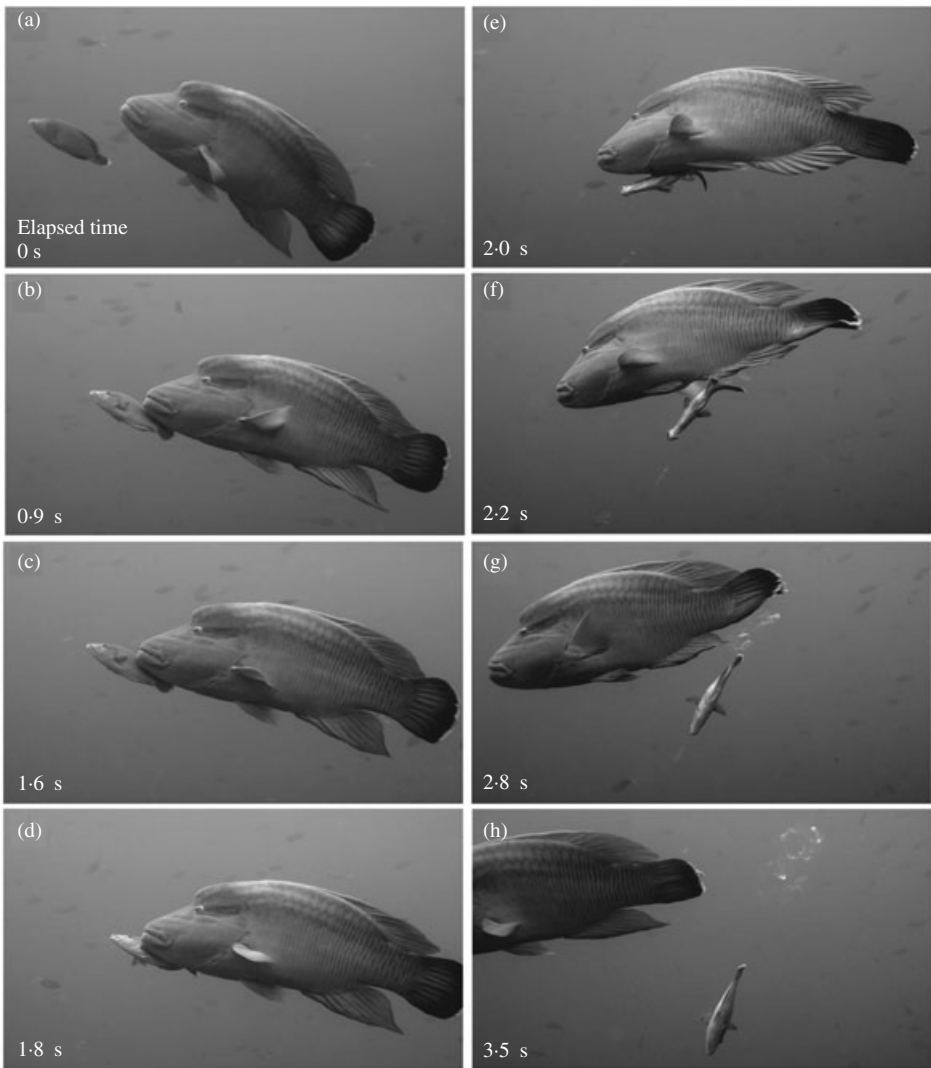


FIG. 6. Spawning sequence of *Cheilinus undulatus* on the western barrier reef of Palau. The elapsed time of the sequence is shown on individual panels. (a) The male (larger fish) rises to meet a female which has ascended into the water column to spawn. When preparing to spawn, the male drops the courting posture and spreads the caudal, anal and dorsal fins to their normal extension. (b) The male touches lower jaw to posterior half of female to initiate the spawning movements. (c) The two fish remain in contact for a short period. (d) The male moves forward while the female remains stationary and rotates slightly. (e) The male bends slightly while continuing to move forward, the female sliding along his belly. It is likely that the male is releasing sperm at this point. The female opens the mouth and bends laterally. (f) The male moves past the female as she dives away from him. The wisps of the eggs released can be seen beneath the anal fin of the male. (g) The female moves towards the bottom while the male continues forward leaving the gamete cloud behind them. (h) The gamete cloud is left behind as the fish move away, the male forward towards another waiting female and the female towards the shelter of the bottom. The gamete cloud is not vigorously mixed by the actions of the fish and dissipates over several seconds without any turbulent mixing as occurs in other reef fishes. Total elapsed time for the spawning was 3.5 s.

a slight arc above the bottom. The male swam past the waiting female, apparently releasing sperm after she had expelled a flow of concentrated eggs (Figs 6 and 7), and then the pair moved apart. There was no postspawning display by the male, such as is seen in some other labrids (Colin, 1983; Colin & Bell, 1991). The male remained in the water column and often quickly spawned again with another waiting female. In all cases where a female was followed after the egg release, she swam directly back to the bottom, then started swimming away from the aggregation area. No multiple spawning by females was seen. Although none were followed for more than a few minutes, it was clear that after spawning females were not remaining in the water column or close to the spawning area. The numbers of females present gradually decreased as the daily spawning period progressed until none were left. A few males persisted in the aggregation area after spawning had stopped, but they ceased to posture or display themselves in the water column.

Gamete release usually occurred along the shelf break, and in many cases the pair swam both upward and away from the shelf break into more open water before spawning. At times the pair was lost to sight of an observer stationed at the reef edge; a distance of at least 20–30 m from the nearest shelter. There were some sharks present at the study area, including grey reef sharks *Carcharhinus amblyrhynchos* (Bleeker) and smaller white tip reef sharks *Triaenodon obesus* (Rüppell), but no instances of attempted predation on spawning adults were observed, despite this apparent exposure.

Egg predation after spawning was not common. On a few occasions, *Naso vlamingii* (Valenciennes), a planktivorous surgeonfish common high above the reef, rushed to the site of egg release within 2–3 s and ingested the concentrated mass of eggs [such as is shown in Fig. 7(c)] before the eggs had significantly dispersed. This egg predation was a simple ingestion of the egg mass, rather than picking individual eggs (typical of *Caesio* spp.) or a filtering of eggs from the water [typical of *Rastrelliger kanagurta* (Cuvier)].

Based on relative size in photographs, the female in Figs 6 and 7 was estimated to be 35–40 cm L_T , about one-third or slightly less of the L_T of the male, estimated at 120 cm. The upper size limit for aggregation fish seen to spawn as females was close to 70–90 cm estimated L_T which may overlap that of small males. It was difficult to distinguish between the two sexes in this size range. The abdomens of females did not look swollen before spawning (Fig. 4), so provided no indication of their sex or state of readiness. It was found in the field, however, that any fish with evidence of a bump on the profile of the head would spawn as a male.

During gamete release, it appears that the female exuded a dense stream of eggs [Fig. 7(a)] as the male moves forward, his vent passing by the area [Fig. 7(b)] where the eggs were in the water, but still in a dense mass. As he passed, the female broke away from him angling towards the bottom leaving a small cloud of eggs with sperm behind her [Fig. 7(c)]. The cloud of gametes was not highly turbulent, as is seen in some other fishes, but was slightly swirling, tending to mix the gametes after release. Eggs collected during the present study from open water were nearly spherical, 660–670 μm in diameter; clear with no pigment and a single oil droplet of 140 μm in diameter. Slamet & Hutapea (2005) indicated an egg diameter of 620–670 μm .

The earliest spawning observed was at 0915 hours after a high tide at 0713 hours with sunrise at *c.* 0600 hours. No attempts were made to observe spawning earlier

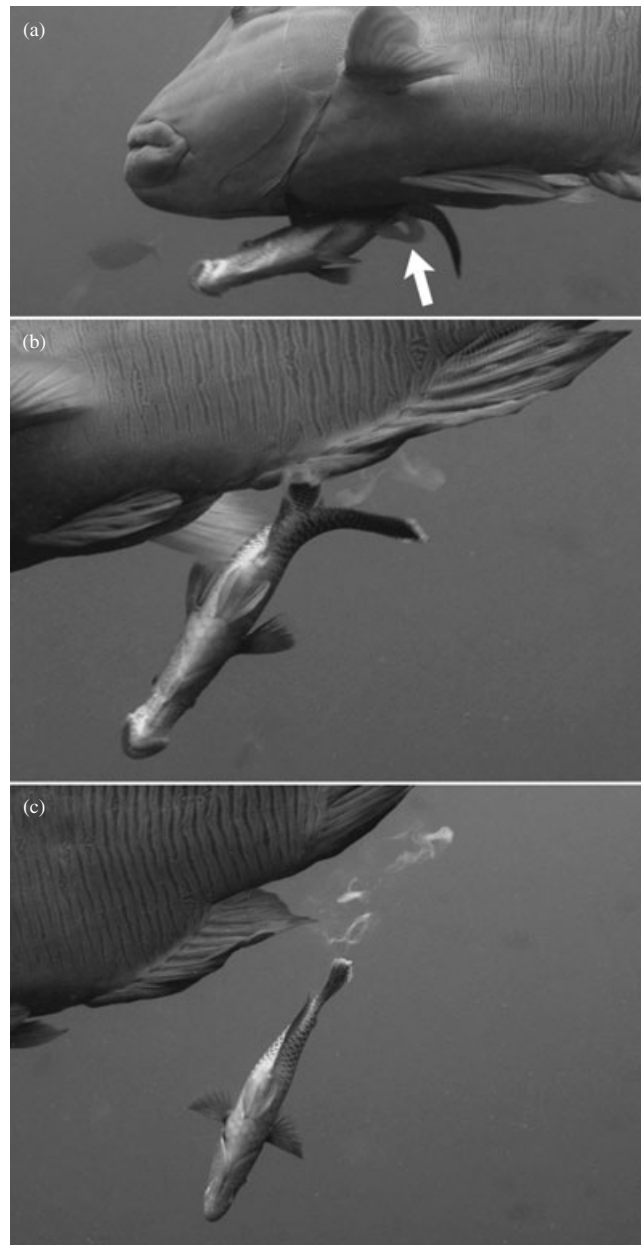


FIG. 7. Details of spawning sequence of *Cheilinus undulatus* shown in Fig. 5. (a) The female releases a dense stream of eggs (\Rightarrow) far ahead of the vent area of the male as the male passes above her. She bends laterally and the mouth is flared open, perhaps indicating a general condition of muscular contraction to assist in extruding the eggs. There is no visible sperm release from the male. (b) The male vent area, presumably exuding sperm, passes over the area of the eggs released by the female *c.* 0.2 s earlier. The female continues to bend laterally and starts to dive away from the male. (c) The gamete cloud left by the pair is dense, but not mixing turbulently. It dissipates to become nearly invisible within 5–10 s.

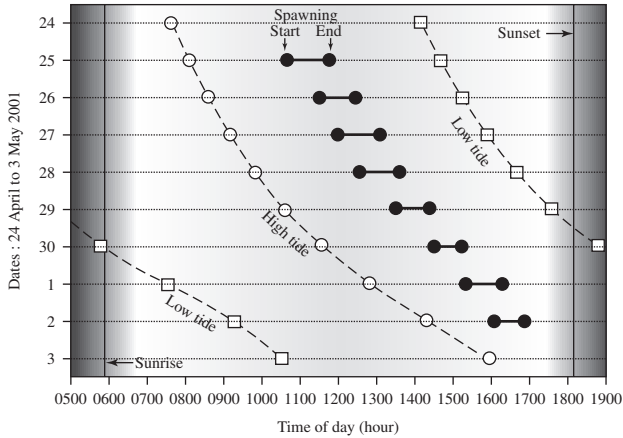


FIG. 8. The aggregation and spawning of *Cheilinus undulatus* on the western barrier reef of Palau on eight successive days (24 April to 3 May 2001) occurred 2.0–2.5 h after high tides on days when high tide was during the morning to early afternoon. As the time of high tide became closer to sunset, the time between high tide and spawning became reduced to c. 1.5 h (2 May), presumably to allow the fish time to return to their home ranges for the night.

in the morning, so it was uncertain how early the species might spawn. The latest spawning were observed at c. 1700 hours (Figs 8 and 9), just over an hour before sunset.

When high tide was mid-day, spawning occurred during periods of strongest current off the reef [Fig. 9(a), (b)]. The current regime during falling tide periods varied day to day with tidal amplitude and winds; hence, some differences existed in the current speed pattern over the falling tide. The highest current speeds recorded in the aggregation area were c. 30 cm s^{-1} . On some days [29 April 2001, Fig. 9(b)], the current speed was nearly consistent at $17\text{--}24 \text{ cm s}^{-1}$ for at least 2 h around mid-tide. Tidally dominated currents were found only in the upper layer of water, and at depths below 3–4 m beyond the shelf break, a gentle ($0\text{--}10 \text{ cm s}^{-1}$) along reef flow predominated. As the time of spawning approached sunset, the fish begin spawning soon after high tide (Fig. 8), even before the current had reached its maximum speed off the shallow reef [Fig. 9(d)].

SEASONALITY AND LUNAR PERIODICITY

Palau normally has two distinct seasons, winter and spring with north-east trade winds and summer with periods of westerly monsoonal winds. Intermediate periods are mixed, with occasional periods of calms or light winds. During trade wind periods, the study area was usually protected from large lagoon waves by the barrier reef and was most accessible. Strong westerly winds made the study site inaccessible, producing waves of 1–1.5 m, and interrupted efforts to make a daily series of aggregation observations. Oceanic swells also produced heavy surf at the site, even without wind. When typhoons passed to the north of Palau between Guam and Yap a few times a year, the resultant swell reached the westerly barrier reef a few days later, making it inaccessible.

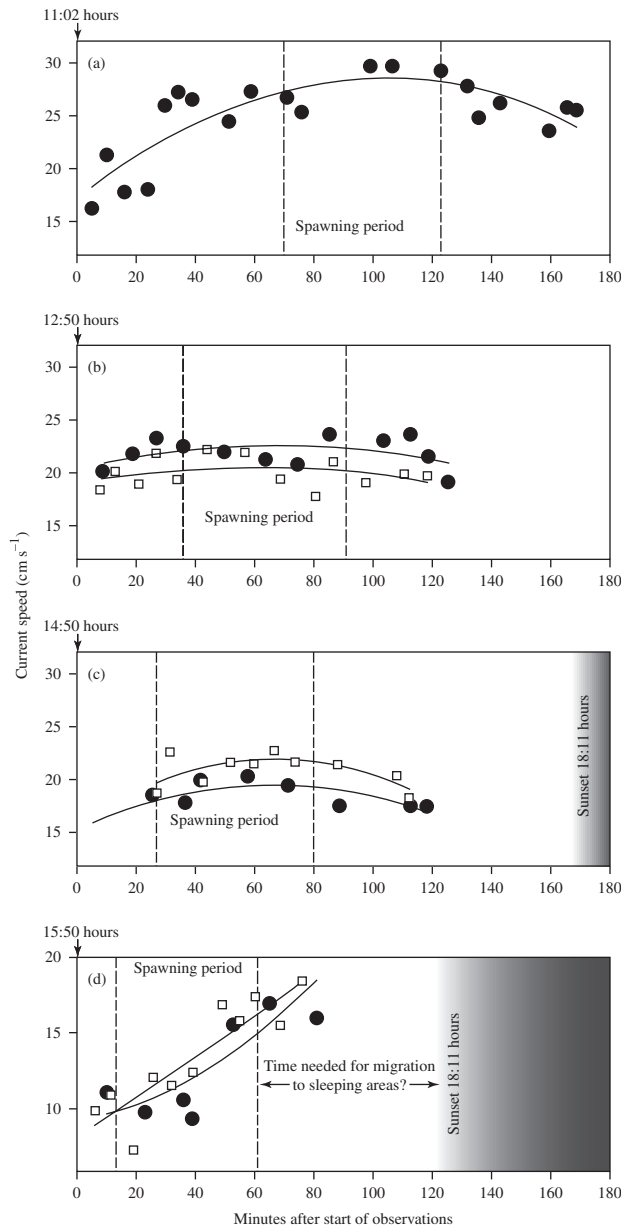


FIG. 9. The relationship between spawning occurrence of *Cheilinus undulatus* at Siaes Reef, Palau and tidal currents across the barrier reef on 4 days included in Fig. 8: (a) 27 April, (b) 29 April, (c) 1 May and (d) 2 May 2001. Current data are from one (●) or two (□) flowmeters moored above the bottom at the spawning site. Curves show a regression for each flowmeter to give general impression of current regimes on each day (which vary with tidal amplitude and weather conditions). (a)–(c) On days with morning to early afternoon high tides, *C. undulatus* spawned on the mid-tide when currents were strongest from the lagoon to the ocean. (d) As the time of maximal current speed approaches sunset, the fish spawned earlier as the tidal currents were still increasing, rather than at their maximum values. See Fig. 8 for times of high and low tides on particular days.

Data indicate that aggregation and spawning probably occurred year round, although there might be some lunar and seasonal differences in the level of activity. Aggregation and spawning had been observed in all months except January and October. It was not possible to visit the site during those 2 months. January spawning had been observed elsewhere in Palau (M. Etpison, pers. comm.); hence, it is probable that the species aggregated and spawned year round.

Aggregation and spawning were also seen in the period after high tide during most lunar phases over several months, including days with spring and neap tides. Most positive observations were made from a few days before to up to 8 days after the new moon, but spawning was also seen on some days around the full moon. It was not possible, however, to do a continuous series of daily observations of aggregation and spawning uninterrupted over the course of an entire lunar month, so there were still some lunar phases for which few data were available concerning presence and levels of aggregation and spawning. Attempts to make aggregation and spawning observations were also complicated by the effects of weather on the exact timing of tides. Strong winds changed the time of high tide, as evidenced by current direction, up to a few hours, and given that the fish appeared to be responding to tidal currents in initiating aggregation and spawning, their timing might have changed considerably due to weather and be missed by the observer.

During a period of settled weather, the daily aggregation and spawning period shifted with the time of high and low tides (Fig. 8). Generally aggregation and spawning began *c.* 2.0–2.5 h after high tide and occurred for a period of just over 1 h midway between high and low tides. As the time of high tide approached sunset, the time between high tide and spawning was reduced to ≤ 1 h.

During summer periods, the direction of westerly winds were often counter to the current coming off the shallow reef, so that the surface where the fish are spawning was moderately choppy with short steep waves 20–50 cm high. This did not seem to disturb the fish or cause them to spawn deeper. On a few days when the site was visited during higher westerly seas of 1–1.5 m, the fish were still spawning, not disturbed by turbulent conditions with breaking waves on the shallow reef.

The location of the primary study aggregation remained consistent for >6 years from April 2001 to April 2007. During that time the location and exact area of the aggregation, the general numbers, cluster locations and behaviour of fish did not change. Given the length of the reproductive life of individual fish, up to *c.* 25 years for females and 16 years for males (Choat *et al.*, 2006), individual fish have probably been part of this aggregation for the duration of this study and the consistency of the location was not surprising in that regard.

OTHER SPECIES SPAWNING AT THE SITE

Many other reef fishes producing planktonic eggs spawned at the study reef as pairs or small groups. These included: the scarids [*Cetoscarus bicolor* (Rüppell), *Chlorurus sordidus* Forsskål, *Scarus globiceps* Valenciennes, *Scarus niger* Forsskål, *Scarus prasinathos* Valenciennes, *Scarus spinus* Kner]; the labrids (*Anampses caeruleopunctatus* Ruppell, *Epibulus insidiator* (Pallas), *Gomphosis varius* Lacépède, *Halichoeres hortulanus* (Lacépède), *Halichoeres marginatus* Rüppell, *Hemigymnus melapterus* (Bloch), *Labroides dimidiatus* (Valenciennes), *Thalassoma amblycephalum* (Bleeker)]; the acanthurids [*Ctenochaetus striatus* (Quoy & Gaimard), *Acanthurus*

nigrofuscus (Forsskål), *Acanthurus olivaceus* Bloch & Schneider, *Zebrasoma scopas* (Cuvier), *Zebrasoma velliferum* (Bloch)]; and two others, *Ostracion meleagris* Shaw and *Zanclus cornutus* (L.). There was a rough succession of species spawning at the aggregation site. This has also been documented in more detail elsewhere in Palau where all these species, but not *C. undulatus* aggregations, occur. Some species started courtship, followed by spawning, shortly after high tide as the current first started to move off the reef, while others did not initiate such behaviour for ≥ 1 h. By the time *C. undulatus* spawning commenced, ≥ 2 h or after high tide, nearly all other species had finished or were in the final stages of their spawning. At the conclusion of spawning by *C. undulatus*, no other species was still seen courting or spawning, all having ceased their activity some time before; thus, *C. undulatus* was the last species in the daily sequence to finish spawning.

DISCUSSION

Apart from spawning aggregations *C. undulatus* is generally solitary, although occasionally several females may occur together (Sadovy *et al.*, 2003). Males are seldom found in the company of other males and when two males meet other than at spawn aggregations, mild aggressive encounters often occurred (pers. obs). In Palau the species forms resident spawning aggregations (Domeier & Colin, 1997) daily at specific locations along the barrier reef in the hours after high tide and this pattern appears the same in the few other locations (Layang Layang Atoll, Malaysia, and the Great Barrier Reef, Australia) where spawning has been documented (S. G. Oakley & J. H. Choat, pers. comm.). In Palau, aggregation may occur year round, particularly as water temperature has only minor variation (1.5° C) during the year (Colin, 2010). While there may be some variation in levels of spawning activity during different lunar phases (*i.e.* this has not been fully documented and remains uncertain), spawning occurrence is documented for most of the lunar month.

Understanding the reproductive strategy of *C. undulatus* is critical to effective measures to conserve the species. This study clearly shows, despite its large size, *C. undulatus* has reproductive behaviour similar to many other labrid fishes and cannot simply be lumped with other large fishes, such as groupers, into a strategy for protecting spawning aggregations. Indo-west Pacific groupers for which spawning aggregations are known, typified by the trio of *Epinephelus fuscoguttatus* (Forsskål), *Epinephelus polyphkadion* (Bleeker) and *Plectropomus areolatus* (Rüppell) (Johannes *et al.*, 1999; Rhodes & Sadovy, 2002), have transient aggregations (Domeier & Colin, 1997) around the new moon for several months of the year. In other families (Lutjanidae) transient aggregations may occur around the full moon, often with strong seasonal components. There may be ≥ 50 resident aggregations of *C. undulatus* along the outer barrier reef of Palau. Its aggregations are much more numerous than the above grouper aggregations and represent a very different character to aggregation and spawning than the large transient aggregation species.

It is hoped that the present paper will clearly identify what is a spawning aggregation and the spawning behaviour in *C. undulatus*, given the past confusion in the available literature. Similar aggregation and spawning on the northern Great Barrier Reef have been observed (J. H. Choat, pers. obs.), with some possible differences in social structure potentially related to differences in numbers of fish present and

oceanographic conditions compared to Palau. The physical features of their observations are in agreement with the present work.

Despite its large size, prominence in reef environments and importance in Palauan culture, there was evidently no recorded traditional ecological knowledge (TEK) of either spawning or aggregation of the fish in Palau as based on interviews of fishers (Johannes, 1981; Y. Sadovy, pers. comm.). While TEK is important and useful, it is not necessarily inclusive even in an area like Palau which has had many knowledgeable informants, and has its limits with regard to management efforts.

The previous reports of *C. undulatus* spawning aggregations indicate why carefully documented and verified information on spawning aggregations is needed to guide management efforts. R. E. Johannes & L. Squire (unpubl. data) reported *C. undulatus* on the Great Barrier Reef to aggregate in groups of 200–300 fish from November to February. They noted no colour or behaviour differences among fish enabling divers to distinguish between males and females and were not seen exhibiting courtship behaviour or spawning. They suggested the fish spawn at night. It is uncertain what these observations represent, yet they have been widely cited. J. Pet & A. H. Muljadi (unpubl. data) reported spawning aggregations at Komodo Island National Park in Indonesia without any spawning observations and intermittent data on fish occurrence. They reported *C. undulatus* to have a peak spawning season of September to December and to be 'a new moon spawner, based on the increase frequency of spawning signs during this moon phase'. This conclusion, however, may be a result of nothing more than the timing of their observational dives which would not have included early morning, mid-day and late afternoon courtship and spawning. Some of the spawning signs indicated may have little to do with reproduction. Sluka (2000) implied that spawning aggregations occur in *C. undulatus* in the Maldives without any data, repeating the belief of R. E. Johannes & L. Squire (unpubl. data) that *C. undulatus* aggregates to spawn 'in large numbers at sites that appear to be similar to sites where grouper aggregate'.

Despite sensitivities about revealing the positions of newly located spawning aggregation sites (Society for the Conservation of Reef Fish Aggregations; www.scrfa.org), detailed information was provided to describe the relationship of the physical aspects of the site to the biology of aggregation and spawning. The occurrence of aggregation and spawning at the primary aggregation site is now widely known in Palau, making confidentially irrelevant. *Cheilinus undulatus* is now fully protected in Palauan waters reducing potential effects of fishers on populations from such detailed information; no capture is allowed and there is thought to be only minor poaching. Finally, after many decades of regular spear fishing in Palau, *C. undulatus* is wary of humans in the water, except at a few popular dive sites, and usually cannot be closely approached during the day, even when aggregated.

All the known aggregation sites of *C. undulatus* in the main Palau group occur on the outer barrier reef, although fringing reef, channel and inshore reef aggregation sites may also occur. There do not appear to be any easily distinguished characteristics of aggregation sites, although both general reef face and projecting areas may have aggregations. At Helen Reef, an atoll in the south-west islands of the Republic of Palau, in September 2008 *C. undulatus* was seen to aggregate and spawn within the single large tidal channel between ocean and lagoon. Such non-specificity of aggregation sites is also found in many other large reef fishes (Colin, in press).

It seems probable then that the primary study site draws its aggregation population from at least 2–3 km distance, mostly from along the outer barrier reef. Without any cross-reef channels within several km, any fish coming from inside the barrier reef would have to cross the shallow reef to reach the aggregation site. This is possible on high tides before spawning, but after spawning the tide is near its daily low with the barrier very shallow or aerially exposed. It seems likely that mature *C. undulatus* would be unable or reluctant to return to home range sites by swimming across the increasingly shallow reef. Some outer-reef aggregation sites may draw their participants only from the fore-reef area either side of the aggregation. Other barrier-reef aggregation areas, near cross-reef channels, may draw part of their participants from more inshore areas. In some barrier-reef channels in Palau, large *C. undulatus* are common and sometimes appear to be migrating through the channels. Some aggregations may occur in channels, although none is presently known with certainty from the main Palau group, as such has been seen at Helen Reef.

The species is relatively long lived and spawning populations do not develop quickly. The length of aggregating and spawning females in Palau is not precisely known as no fish were collected. Sadovy *et al.* (2003) reported females to reach sexual maturity at *c.* 35–50 cm L_T , which would be roughly 5 years old (Choat *et al.*, 2006) and males do not mature for several more years. At least a decade would be required for a heavily exploited population to begin recovery from fishing pressure once protection is provided. At present, efforts are underway to rescind the protection of *C. undulatus* on Palau's reefs, allowing a probable 2–3 month fishing season, despite protection for only a few years and a lack of monitoring of population status.

The social system of spawning is lek-like, with fish clustering in specific areas of the aggregation site, but also able to move the short distances, at most 50 m, between sites. Given the flexibility of fish to apparently move between clusters, the social structure within a cluster was believed to be temporary and variable. There was no strong male–male aggression, as no direct contact, biting or close encounters were seen. There did appear to be a definite dominance hierarchy, as smaller fish at a cluster site immediately retreated if approached by a larger male when aggregation was occurring. Smaller males were believed to achieve some spawning, as many females appeared ready to spawn nearly simultaneously, but dominant males were not able to spawn immediately with all of them.

Once initiated, spawning generally occurs for <1 h. There was an indication on days when more males were seen in the aggregation area, the spawning period observed was longer, however, this needs to be better quantified to confirm or refute. Males generally spawn numerous times in rapid succession during the aggregation, but it is probable that females spawn only once a day since no multiple spawning by females were seen and they leave the area quickly after spawning. The egg size of *C. undulatus* is typical of many smaller wrasses and consistent with other data that indicate no clear correlation of egg size with adult size (Colin & Bell, 1991).

At least 21 species of other fishes with planktonic eggs spawn in the aggregation area after high tide. Most spawning occurs before the start of *C. undulatus* spawning, and all other species observed had ceased their spawning some time before the conclusion of spawning by *C. undulatus*.

Spawning occurs in a variety of wind and sea conditions. Westerly monsoonal winds during summer months have not been observed to interrupt spawning; however, the effect such strong winds and large waves on the shallow reef has on the transport of eggs is unknown. It is probable that they may be carried across the reef into the lagoon by wave pumping.

The spawning of *C. undulatus* in Palau was characterized by no observed predation attempts on spawning adults, low levels of egg predation and spawning at times which promote the movement of eggs short distances away from the barrier reef. While some sharks capable of attacking mature *C. undulatus* were in the area, few other piscivorous reef fishes are capable of taking even a moderate-sized *C. undulatus*. Despite this, *C. undulatus* are still wary during courtship and spawning. Decades of spear fishing (now illegal in Palau) are believed to have made the species shy of humans, although at tourist dive sites some large males, which are regularly hand-fed, have lost this inhibition. Successful attacks by piscivores on spawning reef fishes are generally rare, on the order of one per 1000 spawns, although when they occur they are often highlighted in reports. Colin (in press) has recently reviewed this subject.

The only instances of egg predation were the immediate ingestion of the egg mass by *N. vlamingii*, a zooplanktivore living in the water column high above reefs. The distance above and seaward from the reef where *C. undulatus* spawns is further and higher than any other reef fishes spawning in the area. This puts its eggs beyond the reach of virtually all benthic-based egg predators; hence, the low levels of egg predation observed are not surprising.

Spawning at the mid-stage of falling tides is conducive to short distance offshore transport of eggs released into lagoon water crossing the barrier reef. The entrainment of eggs and larvae into oceanic currents systems is much less certain. The lagoon water moving across the barrier reef, into which eggs are released, advects only a few 100 m away from the reef, then generally stops moving further away from the reef. It then moves along the reef in response to general along reef currents (Hamner *et al.*, 2007). If there are strong winds blowing on or off the reef, they may push the water towards or further away from the reef. During relatively calm conditions, the lagoon plume crossing the reef remains a distinct surface layer in near reef water, but if rough, it quickly becomes mixed with more oceanic water and an entirely different fate for eggs and larvae may ensue. In some cases eggs released on falling tides may be brought back to the barrier reef or even into the lagoon on the next rising tide (Hamner *et al.*, 2007).

Many spawning aggregations, both resident and transient, are known to persist at the exact same location for decades (Colin, 1996; Domeier & Colin, 1997). There have been many suggestions put forward as to why aggregations persist, and while the present paper is not intended to review the subject, the study does provide information for an additional species. There seems to be nothing distinctive, compared to nearby reef edge areas, about the aggregation sites or the current regimes in these areas.

Despite increasing interest in the subject and its importance in fishery management, fish-spawning aggregations in the Indo-west Pacific Ocean have received surprisingly little attention. The present paper is the first documentation of resident-spawning aggregations of a large reef fish in the region, and is particularly timely since the species is considered 'threatened'. In most respects, the reproductive behaviour of *C. undulatus* is similar to other labrids and is quite distinct from large reef fishes in some other families, such as the Serranidae, which are usually cited as models

for management efforts and conservation planning (Johannes *et al.*, 1999). The 6 year time frame during which the aggregation location has remained consistent is in agreement with most lengthy observations for other species (Colin, 1996, in press). In addition, the behaviour associated with aggregation and spawning maintains similar patterns over a wide geographic range, and it is hoped that the present effort will simplify efforts to document spawning in the species throughout its geographic range.

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