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FACTORS INFLUENCING SPAWNING SITES OF TROPICAL FISH SPECIES

A REVIEW

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1. INTRODUCTION

This document has come about from a request by the Department of Conservation and Land Management – Marine Conservation Branch to review literature pertaining to spawning sites of site-attached tropical fish species. The purpose being to determine a "rule of thumb process" to identify potential fish spawning areas, which could be used in the marine reserve planning process, to locate or expand sanctuary zones within marine parks. Information obtained will be used as an input to the Pilbara marine reserve process and the Ningaloo marine park review. Potential spawning locations could be studied further to obtain scientific information on spawning or aggregation. Thus the questions we are attempting to answer are:

1) What factors determine where and when spawning occurs, whether as an aggregation or otherwise?
2) How can we identify these spawning sites *a priori*?

For decades local fishermen have been aware of, and exploited sites where fish aggregate to spawn. These sites occur in various reef regions depending on the species in question. Spawning may occur in pairs or groups, at regular sites, daily to annually, at various times of the day and at various phases of the moon and tide. It is this predictable behaviour that makes them vulnerable to overexploitation and in many areas aggregations have been fished so heavily they cease to exist (Colin 1992). Without careful management of aggregation sites we are in danger of continuing to reduce fish stocks at a critical phase in their life, i.e. when they are spawning.

Despite the number of papers in the literature there has been no consensus on how to identify spawning sites or spawning aggregation areas *a priori*. Indeed Colin (1978) stated that selection of spawning sites is a complex process with no single controlling factor. Fishers have usually come upon spawning sites by accident at some stage and historical information has then been passed on through generations. This local information has also been passed on to researchers who have then been able to study the areas and the habits of the fish species in question. Many more aggregation areas would surely have not yet been identified. A new organisation currently being established "The Society for the Conservation of Reef Fish Aggregations" (SCRFA) has set a goal to compile a comprehensive database of all known spawning aggregations (Domeier pers. comm.).

A common goal of marine reserves, and sanctuary zones in particular, is to provide protection for spawning stock and spawning aggregation areas but these goals are difficult to meet without knowledge and in-depth studies of the characteristics of such sites. But researchers are urging us to take stronger action to ensure these areas are identified and reserved. Johannes (1998) stated "Those who plan to establish or redefine a marine reserve in nearshore tropical waters should ensure that it is located, if possible so as to protect important spawning aggregations".

At this stage it is important to define some of the terms commonly used when studying or describing spawning behaviour and spawning site selection of fishes. Spawning is the simultaneous release of gametes (eggs and sperm) into the water column by fish. Eggs are fertilised in a cloud of sperm and the resultant fertilised eggs and larvae are often carried for a time by the current prior to settlement and recruitment to a particular area. Settlement may occur at distances far from a spawning site depending on the tidal and hydrodynamic conditions of the area. A spawning aggregation has been defined as "a group of conspecific (of the same species) fish gathered for the purposes of spawning, with fish densities or numbers significantly higher than those found in the area of aggregation during the non-reproductive period" (Domeier and Colin 1997). It should also be noted that spawning does not always occur in aggregations with pair spawning also common (Domeier and Colin 1997). In this report we are concerned with tropical fish species from many families including Acanthuridae, Caesionidae, Labridae, Lutjanidae, Mullidae, Scaridae and Serranidae. Unfortunately, no information could be found on Lethrinidae or Haemulidae. Appendix 1 details scientific and common names of all fish cited in this report.

Spawning sites and in particular spawning aggregation sites are likely to be subject to far greater fishing pressure in the future. In developing countries, the reliance on the fishing for a livelihood is growing with population and in more developed countries both recreational and commercial fishing pressures are likely to impact on aggregation areas. Constantly improved technology in the form of global positioning systems and echo sounding devices has enabled fishers to relocate aggregation sites with accuracy. A lucrative live fish trade is also growing in Asia with demands on Southeast Asian and Australian reefs to supply this market with species from the Serranidae which aggregate to spawn.

If we lose aggregations of these species and populations suffer on a regional scale there is a possibility of changes in reef structure. Trophic cascades have been well documented in the literature, citing examples of reefal scale changes as a consequence of losing keystone predators. A well-researched trophic cascade in Kenya has shown that the reduction of invertivorous fish through overfishing has lead to an increase in their prey, the urchin *Echinometra mathaei* (McClanahan and Muthiga 1988, McClanahan et al. 1996) and consequent changes in algal biomass. Anecdotal evidence from the Ningaloo region, in Western Australia suggests that overfishing of lethrinids and labrids has lead to an increase in abundance of the corallivorous gastropod *Drupella cornus* (Weaver 1998), however, this scenario has not yet been scientifically tested. Thus, by overexploiting spawning aggregation sites, we may be losing far more than the species that are being fished.

2. SPAWNING SITES

2.1 TOPOGRAPHIC COMPLEXITY

Topographic complexity may be the one of the main factors influencing the choice of spawning sites by fish. Sancho et al. (2000) recorded a significant correlation between the abundance of group spawning fishes and an index of topographic complexity, i.e. fish avoided areas of low topographic complexity. Beets and Friedlander (1998) also noted that spawning aggregations may be spatially correlated with habitat complexity. This may be due to the provision of shelter from predators that is afforded by reef crevices and ledges, increased larval dispersal from higher oceanic and tidal currents, and depth that allows the spawning fish to carry out there ritual of rushing to the surface as gametes are released. Each of these factors will be discussed in more detail.

There is an evident trend in the literature that many fish (including caesionids, chaetodontids, mullids, scarids, serranids and labrids) spawn in channel areas or deeper waters near promontories or other topographically complex features (Robertson 1983, Bell and Colin 1986, Johannes 1988, Sancho et al. 2000). This feature for spawning appears to be consistent for epinephelines of the family Serranidae (Colin 1992, Sadovy et al. 1994b, Aguilar-Perera and Aguilar-Davila 1996, Beets and Friedlander 1998) (see Appendix 2: Topographical features of spawning sites). Colin (1992) stated that all known aggregations of the Nassau grouper (*Epinephelus striatus*) occur at or near the continental shelf break and this is supported by Aguilar-Perera and Aguilar-Davila (1996) who observed aggregations of *E. striatus* on the continental shelf in the Mexican Caribbean. Colin et al. (1987) stated that aggregations of *Epinephelus guttatus* and *E. striatus* in the Western Atlantic were common at the ends of islands or on seaward projections. In a study of two aggregations of *E. striatus*, Colin (1992) noted that they aggregated near the shelf at one site, while they were near the dropoff into deeper water at another site. The greater number of fish observed at the deeper offshore site suggest this was preferred. Sadovy et al. (1994b) noted *E. guttatus* spawning sites were located in the vicinity of the edge of the insular platform, and may extend shoreward. Colin (1992) stated that it is difficult to identify any single factor which all known *E. striatus* aggregation sites have in common, except for their occurrence at or near the shelf break.

Other serranids exhibit similar site preferences with regard to deeper waters near fore-reef or defined promontories. Eklund et al. (2000) recorded spawning aggregations of *Mycteroperca bonaci* at 18-28m depth on the deep fore-reef slope. At 20m the fore-reef sloped steeply to sandplain at 28m with fossilised rock and coral reef which provided shelter for fish. Sadovy et al. (1994a) recorded a *Mycteroperca tigris* spawning site at a well defined promontory of deep reef 36-40m. *Plectropomus leopardus* spawning was observed in a steep walled channel, 10m wide which cut through the reef and opened into a lagoon sloping to a sandy bottom at 20-25m (Samoilys 1997). According to fishermen in the Solomon Islands most of the 30 passages that cut through the barrier reef to Morovo lagoon are aggregation sites for *Plectropomus areolatus* (Johannes 1988).

Beyond the more studied species that may be exploited by fishers, many other fish families group to spawn in topographically complex areas. In a study examining predation on spawning fishes, Sancho et al. (2000) noted 34 different species, that spawned in a 70m long channel that crosses the reef crest of an atoll, including Acanthuridae, Chaetodontidae, Labridae, Mullidae, Ostraciidae, Scaridae and Zanclidae. Other spawning events have been recorded on or near topographically complex features: the outer edge of reefs (*Acanthurus lineatus* and *A. nigrofuscus*) (Robertson 1983); reef edge over a vertical projection (*Thalassoma bifasciatum*) (Warner 1987, Warner 1995); spur reef that sloped from 5 to 35m (*Lutjanus jocu*) (Domeier and Colin 1997); reef abutting a sandy drop-off (*Lutjanus analis*) (Domeier et al. 1996); 24m reef pinnacle on the edge of a dropoff (*Scarus croicensis*) (Colin 1978); level reef adjacent to a deep channel (*Caesio teres*) (Bell and Colin 1986); over the extremities of underwater promontories on the outer reef slope (*Scarus gibbus*) (Johannes 1981); on the most seaward projection of a fringing reef that adjoined a sandy bottom at 20m (*Sparisoma rubrippine*) (Randall and Randall 1963); on the top of a coral reef pinnacle on the fore-reef (*Sparisoma iserti*) (Colin 1978) and the outer fore-reef of a promontory in 27-30m of water near the seaward end of a low relief coral shelf before the reef drops away to 50m (*Lutjanus jocu*) (Carter and Perrine 1994). In contrast to these studies Gladstone (1996) recorded aggregations of *Hipposcarus longiceps* with ripe gonads along a 1.5km stretch of inshore sand, however they were not observed spawning. Species discussed in this review and a brief description of the sites where they were observed spawning is provided in Appendix 2. As the review is focused on tropical species and aimed at marine reserve planning in Western Australia, the distribution of species noted within the Ningaloo-Dampier region is included.

It would appear from the literature that many fish select spawning sites based on some degree of topographic complexity and proximity to deeper areas near promontories or seaward projections. A clear understanding of the advantages of such spawning sites would aid researchers in locating them *a priori*, and provide an extremely useful tool for marine park planning. A logical reason for such spawning sites may be that larval dispersal is aided by higher currents that flow through these areas. Samoilys and Squire (1994) stated that currents were moderate to strong at a spawning aggregation of *P. leopardus*, but no measurements were made. Bell and Colin (1986) also noted that a site where a spawning aggregation of *C. teres*, occurred was strongly influenced by tidal currents. However, Gladstone (1996) recorded aggregations of *H. longiceps* in areas where larval dispersal would not be facilitated by currents or water movement, but did add that the tide was outgoing. Colin (1996) stated that there is little evidence supporting the hypotheses that spawning sites are selected to ensure rapid larval dispersal off reefs into offshore waters and suggested that other factors, such as sites being learned over time, and serving to coordinate spawning events, are possibly more important. These two latter studies focused on scarids and acanthurids. At a spawning aggregation of *E. striatus*, Colin (1992) released drogues with the gametes and showed that they either moved inshore or did not move far away from the shelf edge over several days. Aguilar-Perera and Aguilar-Davila (1996) commented that currents were slow when they observed a spawning aggregation of *E. striatus*. Samoilys (1997) measured current strength at two locations during spawning events of *P. leopardus*. Strong currents were associated with only 10% of recorded aggregation numbers at one site and 0% at the other, while over 70% were recorded in negligible to slight currents. It appears that a distinction needs to be made between oceanic currents and tidal currents. Fish that spawn in a channel between the reef and offshore areas will have the advantage that tidal currents will transport larvae further than in calm areas (Johannes 1988). Those aggregations in deeper areas where tidal influences are less may not find larvae being dispersed by currents.

The substrate type, forming topographically complex areas, may also be a factor in determining spawning sites. Aguilar-Perera and Aguilar-Davila (1996) noted that *E. striatus* aggregation sites were over low relief patchy hard corals (*Monastrea* sp and *Agaricia* sp.) with plexaurids (sea-fans) and gorgonians. Water depth was 6-20 m and the site was 200 m from a dropoff. *Mycteroperca tigris* spawning site was underlain with coral, predominantly *Monastrea anularis* (Sadovy et al. 1994a). Beets and Friedlander (1998) noted that a decline in coral development coincided with a decline in grouper numbers around a spawning site. In a study of lutjanid spawning sites (identified by fishermen) all sites included hard bottom and/or coral (Lindeman et al. 2000). Beets and Friedlander (1998) commented that spawning aggregation sites of *Epinephelus guttatus* may be spatially correlated with complex habitat, with spawning aggregations occurring over by dense scleractinian coral cover.

Sancho et al. (2000) used a topographic index (substrate rugosity index) to determine the spatial relief of a spawning site used by many species. Such an index may serve as a useful initial indicator of potential spawning sites in the absence of any confirmed sitings or observations by fishers.

In summary, spawning sites are generally located in areas of comparatively high topographic complexity, often at a well defined promontory in water greater than 5m deep and up to 120m. Sites are likely to be underlain by reef and coral communities but may be adjacent to sandy substrate. Strong currents do not appear to be favoured by spawning fishes.

2.2 WATER TEMPERATURE

It has been suggested that spawning of some serranids only occurs when water temperature reaches a certain threshold (Tucker et al. 1993, Samoilys 1997) and for *P. leopardus* this was noted to be 24°C. Other studies on the spawning characteristics of serranids have measured similar water temperatures at aggregation sites. *Mycteroperca tigris* was recorded spawning in 25°C (Sadovy et al. 1994a) and spawning periods of *E. striatus* occurred at temperatures of 25.0 - 25.5°C during gradually decreasing temperatures (Colin 1992). Carter and Perrine (1994) also recorded water temperature of 25.8° at a *Lutjanus jocu* spawning aggregation. Colin (1992) suggested that latitudinal shifts in spawning time appear to be related to water temperature.

2.3 TEMPORAL INFLUENCES

Lunar phase, tide and time of day may also strongly influence spawning events. Spawning occurred on or closely following the full moon for the serranids *E. striatus* (Colin 1992, Aguilar-Perera and Aguilar-Davila 1996), *E. guttatus* (Shapiro et al. 1993) and *M. tigris* (Sadovy et al. 1994a). Bell and Colin (1986) also recorded *Caesio teres* spawning from one day before to three days after the full moon and Gladstone (1996) observed *Hipposcarus longiceps* aggregations the first day after the full moon. Aggregations of *P. leopardus* were also recorded around 3 consecutive new moons (Samoilys 1997).

Perhaps the most consistent finding between studies is the occurrence of spawning events on an outgoing tide, in particular after the greatest high tide (or flood tide). Robertson (1983) recorded *Acanthurus nigrofuscus* spawning in areas with high tidal currents and observed that spawning activity was greatest after high tide and Bell and Colin (1986) noted spawning of *C. teres* commenced after high tide possibly to facilitate larval dispersal to outer reef areas. They concluded that the event was strongly influenced by tidal currents. Samoilys (1997) noted that between 67 and 81 % of counts for *P. leopardus* were recorded at the flood tide.

Many species appear to exhibit a crepuscular (at dusk) spawning pattern (Sadovy et al. 1994a, Samoilys 1997, Kiflawi et al. 1998), possibly to minimise predation on eggs and larvae (Sancho et al. 2000). Examples of this were noted by Colin (1992) with most *E. striatus* spawning occurring in the 10 minutes before sunset. Mass spawning of *Acanthurus nigrofuscus* was observed around sunset (Kiflawi et al. 1998) and *M. tigris* spawned within 1-2 minutes of sunset (Sadovy et al. 1994a). Samoilys (1997) observed aggregations of *P. leopardus* dispersing in the morning and re-establishing in the afternoon, presumably for a sunset spawning event. It is also possible that spawning occurs into the night, as some workers have cited difficulty in observing these dusk spawning events due to limited light. Sancho et al. (2000), whose study included fish from the families Acanthuridae, Chaetodontidae, Labridae, Mullidae and Scaridae noted an increase in the number of species spawning as the day progressed with maximum spawning between 1300 and 1900 hours and lowest between 1900 and 2000 hours (dusk). Spawning observations were predominantly scarids and acanthurids with *Chlorosus sordidus* and *Acanthurus nigroris* spawning between 1300 and 1700 hours (Sancho et al. 2000). Randall and Randall (1963) also noted the scarid *S. rubrippine* spawning in the afternoon and Gladstone (1996) recorded aggregations of *H. longiceps* between 0615 and 1000 hours.

Most studies on serranids in the Caribbean noted spawning events occurring in the period December to March (Colin 1992, Sadovy et al. 1994a, Eklund et al. 2000) while studies from the Great Barrier Reef have indicated spawning from August to December (Samoilys and Squire 1994, Samoilys 1997). Randall and Randall (1963) observed *S. rubrippine* spawning over a long season, possibly year round, and *H. longiceps* aggregations do not occur in the same months every year but differences were within a month, probably reflecting changes in lunar cycle (Gladstone 1996). The aggregations were recorded over a five year period in either March or April.

2.4 FISH MIGRATION

Some fish follow precise migration paths when travelling to and from spawning sites and this may leave them vulnerable to overexploitation. Fish build up as groups, progressing along these paths and knowledge of routes would enable exploitation by fishers. In such cases, restricting fishing in spawning sites alone may not be sufficient to ensure protection of spawning individuals. Warner (1995) noted *T. bifasciatum* migrate along specific pathways for more than 1.5 km to the spawning grounds on a daily basis and Mazeroll and Montgomery (1998) observed *A. nigrofuscus* followed the same routes on daily migration to feeding and spawning sites. Migrations appeared to be initiated by sunrise and sunset and the path was influenced by underwater landmarks. Zeller (1998) used ultrasonic telemetry to track the movements of *P. leopardus*. Fish moved between 220 and 5210m from home ranges to spawning aggregation sites. Males spent more time at aggregation sites and made more trips, increasing their vulnerability to overfishing. Tagging studies indicate *E. striatus* travel up to 240 km to a spawning site (Carter et al. 1994). Fulton et al. (1999) developed a simulation model based on biological and fisher information of *P. leopardus* to determine spawning season estimates of catch rates. They concluded that elevated catches resulted from a combination of fishers targeting aggregations and from catches of those fish that inhabited inaccessible locations before commencing migration to spawning sites.

2.5 RESIDENT AND TRANSIENT SPAWNING TYPES

Domeier and Colin (1997) have defined two spawning aggregation types, resident and transient. A resident aggregation type draws individuals from a localised area. The site can be reached through migration of a few hours. These aggregations occur regularly, often daily and may last only a few hours. These species feed low down the food chain and can consequently be sustained in large numbers (Domeier and Colin 1997). Families / species that would be classified as resident spawners are Acanthuridae (Robertson 1983, Colin and Clavijo 1988, Colin 1996, Mazeroll and Montgomery 1998), Scaridae (Randall and Randall 1963, Colin 1978) and *T. bifasciatum* (Labridae) (Warner 1995). These classifications are drawn from a limited number of species and further work is required to determine whether entire families fit within one spawning type. See Appendix 2 for a summary of resident and transient spawners.

A transient aggregation type draws individuals from a large area and migrations of days or weeks are needed to reach the site (Domeier and Colin 1997). These occur at a specific location only a few times of the year. Serranids such as *P. leopardus* (Samoilys 1997), *E. striatus* (Colin 1992) and *E. guttatus* (Sadovy et al. 1994b) fit this category. Transient aggregations last for only a few days (Colin 1992, Shapiro et al. 1993).

In the context of this review (Marine Park Planning in Western Australia) resident spawners (e.g. Acanthuridae, Scaridae) are less targeted by fishers (Sumner et al. 2000) possibly due to their lower palatability. Different methods are also required to catch them due to their herbivorous nature (i.e. nets or spears as opposed to lines). If their migrations are short, 100s of metres to maybe 2 kilometres, they may be afforded protection in sanctuary areas, assuming the sanctuary size exceeds the migratory extent of the fish species and provided spawning sites are first identified.

Areas used by transient spawners may be identified over time and these species may benefit from inclusion of their spawning grounds in the marine reserve planning process. As the majority of transient spawners use the same site each year (Colin and Clavijo 1988, Shapiro et al. 1993, Samoilys 1997, Zeller 1998), such sites can be set aside for partial or complete exclusion from fishing. However transient spawners are more difficult to protect due to longer migrations increasing their vulnerability to fishing (Fulton et al. 1999). Aggregations of transient spawners usually consist of the medium to large individuals (Sadovy et al. 1994b) (*E. striatus*) and many are sought after table fish (e.g. serranids).

As species that form transient aggregations (e.g. Serranidae) may come from great distances they may not be easily censused prior to any spawning event. *P. leopardus* and *Epinephelus tauvina* (Serranidae) have been noted in the Ningaloo region (Ayling and Ayling 1987, Sumner et al. 2000), however, the authors have not seen any of these in underwater visual census of over 20km^2 the reef spanning two years (1999-2000) (Westera et al. in prep). Other epinepheline serranids have been observed, including *E. fasciatus*, *E. rivulatus*, *E. bilobatus*, *E. lanceolatus* and *E. polyphekadion*. It is likely that these species and others aggregate in some areas of the 270 km long Ningaloo Reef. Their distribution extends to the north and it is also possible that such sites exist in other parts of the Pilbara region.

2.6 SITE FIDELITY

Resident and transient spawners commonly return to the same traditional spawning sites (Domeier and Colin 1997). The resident spawning scarid *Sparisoma rubripinne* was recorded spawning at the same location (within 20m) on two sampling occasions 11 years apart, in the Virgin Islands (Randall and Randall 1963, Colin 1996). Similarly, spawning aggregations of *Acanthurus bahanius* and *A. coerulus* were observed in the same location over a four year study period, and again four years after the study, to be massing in the thousands in the afternoon to spawn (Colin and Clavijo 1988). However, another aggregation of *A. coerulus* ceased to exist despite observations on the same dates, tides and lunar phases as previous years (Colin 1996). Another four year study between 1971 and 1975 recorded *Sparisoma iserti* (Scaridae) aggregations at a particular site. In 1988 the site was visited 12 days after a hurricane and *S. iserti* spawning activity was again observed (Kaufman 1983), however Gladstone (1996) recorded schools of *Hipposcarus longiceps* (Scaridae) spawning in different locations over a five day period.

Transient spawners have also been shown to exhibit high site fidelity. Samoilys (1997) noted that the serranid *P. leopardus* spawned at the same "primary" location each year. Other spawning sites were observed but the largest aggregations were in the same location. Zeller (1998) also recorded strong site fidelity for this species using ultrasonic telemetry to track their movements. *E. striatus* and *E. guttatus* have also been shown to aggregate in traditional locations (Colin et al. 1987, Shapiro et al. 1993).

3. SPAWNING BEHAVIOUR

3.1 COLOUR CHANGES

In order to identify suspected spawning sites, one may need to identify fish that are either gathering at an aggregation site or are in transit to a spawning aggregation. A number of the serranids go through colour changes during their courtship rituals. Colour changes for *E. striatus* usually fall into 4 categories (Colin 1992). These are: the normal pattern (during non-aggregating time); white belly (the abdominal area is white, this was observed early in the day among females, presumably ripe with eggs); bicolour (upper body to the midline is extremely dark and the belly is white, observed at the time of spawning); and a dark phase (dark grey to black with bars visible beneath the darkened colouration, possibly females ready to spawn). Fish were able to change colour in a few seconds. Aguilar-Perera and Aguilar-Davila (1996) also observed *E. striatus* colour changes at a spawning aggregation. Such patterns may be observed in other species and without in-depth species-specific knowledge, one could infer that any colour change justifies further investigation of proximity to a spawning site. Wicklund (1969) observed unusual colour patterns of fish in a spawning aggregation of *Lutjanus synagris*, but Carter and Perrine (1994) observed no such changes in aggregating *L. jocu*.

3.2 AGGREGATION SIZE

Aggregations of 37-75 $1000m^{-2}$ *P. leopardus* were recorded by Samoilys (1997), while *E. striatus* has been recorded in aggregations of 200-500 (Aguilar-Perera and Aguilar-Davila 1996), 2000-3000 (Colin 1992) and up to 100,000 (Smith 1972). Other species have been recorded in similarly high numbers with aggregations of over 10,000 *Thalassoma bifasciatus* which formed daily in a single area (Warner 1995) and 200-400 *Pseudopeneus maculatus* (Colin and Clavijo 1988). Other studies have recorded groups of 200 *Sparisoma rubripinne* as a spawning aggregation (Randall and Randall 1963). In the Ningaloo region, on west coast of Australia, scarids and acanthurids regularly gather in feeding schools of this size with no obvious evidence of spawning (Westera pers. ob.). These schools may require further investigation at likely spawning sites and times.

In any study of potential spawning sites, observation of unusually large groups (especially of solitary species) may justify investigation. Schools could be tracked over time by boat or snorkel, paying particular attention to times of the day when spawning of these families has been recorded elsewhere. Carter et al. (1994) observed schools of up to 500 *E. striatus* swimming along the shelf edge which were presumed to be in transit to an aggregation.

3.3 THE SPAWNING EVENT

Within an aggregation, fish may spawn in pairs or groups (Sancho et al. 2000). They also exhibit different spawning behaviour, even within the same species. Some rush toward the surface as spawn is released, while others "bob" at between 0.1 and 2 metres above the substrate. Mass spawning refers to the simultaneous spawning of the majority of a spawning aggregation (Kiflawi et al. 1998)

Carter and Perrine (1994) described a school of approximately 1400 *Lutjanus jocu* rushing from 50m to 10m depth. Between 10 and 5m depth they formed a "comet shaped cluster" at which point a mass spawning event took place with gametes being released into the water column. There are even observations of different species joining in a spawning aggregation including the rush to the surface with the school (Carter and Perrine 1994).

T. bifasciatum spawned in groups or pairs within an aggregation (Warner 1987). Shapiro et al. (1993) noted "clusters" of *E. guttatus* within an aggregation. Spearing showed that these consisted of either one male and two or three females, or all females. Colin (1992) also noted subgroups of *E. striatus* mating within an aggregation. Gamete release from these groups followed various types of movements through the water including vertical movement, vertical spirals, and rapid horizontal runs near the substratum.

Spawning fish also exhibit what has been referred to as a "spawning stupor", in which fish that are otherwise wary of divers become docile and complacent and are easily approached (Johannes et al. 1999). Such unusual behaviour may indicate a migration of fish in spawning condition or the location of a spawning site.

4. PREDATION ON SPAWNING FISH

4.1 NATURAL PREDATORS

Predation on spawning fish either through piscivory of the adult spawners or predation on gametes is common at spawning sites and may also be dependant on the spawning nature of the fish. Sancho et al. (2000) recorded significantly greater attacks on spawning fish that rushed to the surface than those that bobbed above a topographically complex substrate. Piscivorous predators included *Caranx melampygus* and *Aphareus furca* and the target prey were group spawning acanthurids and scarids. Attacks were observed during bobbing or rushing with no attacks on fish while feeding or migrating. Hixon and Beets (1993) commented that high habitat complexity with appropriate sized holes provides shelter from predators and may improve survival of spawning fish. Sancho et al. (2000) also suggested that fish are possibly more vulnerable to attack as they leave the refuges of more topographically complex substrates. The complacent nature of spawning fish (spawning stupor) may also increase their vulnerability to attack from predators.

Bell and Colin (1986) noted no predation of spawning fish despite many predators including carangids, lutjanids, sharks and serranids being present at a spawning site but predation on eggs was noted. Beets and Friedlander (1998) observed many predators at an *E. guttatus* spawning site, citing shark bites from buoys and the presence of *Lutjanus cyanopterus*, a large piscivore. Olsen and LaPlace (1979) observed sharks feeding on spawning fish.

4.2 EXPLOITATION BY FISHERS

As discussed, the fidelity of fish to spawning sites increases their vulnerability to overexploitation through fishing. Fishing on aggregations has occurred historically with some being depleted beyond recovery (Colin 1992, Sadovy and Ecklund 1999). Heavy fishing pressure in the Caribbean has lead to aggregations disappearing from their traditional sites (Sadovy 1995). *E. striatus* aggregations have been fished in Mexico since 1910 using hook and line, but more recently gill nets are being used (Aguilar-Perera and Aguilar-Davila 1996). Aguilar-Perera (1994) cited anecdotal evidence of fishermen tying a live female *E. striatus* to a line and retrieving it from the bottom to attract males to surface from within a spawning aggregation. They were then able to net males that follow the female to the surface.

Colin (1992) observed considerable change in abundance at one site over a one year period with nearly every individual being taken by fishermen in the second year and stated that of the known *E. striatus* aggregations in the Bahamas many have disappeared possibly due to overfishing. If an aggregation is fished below a certain level, a lack of numbers (of fish such as epinephelines) may result in a lack of spawning rather than a shift to another site (Colin 1996).

Aggregation sites have also been abandoned by fish for a number of years following the use of dynamite to stun fish (Colin 1992).

There is however, potential for restriction of fishing to aid the recovery of aggregations.. By 1980, at least two grouper (*E. striatus*) aggregations in the Virgin Islands were eliminated due to overfishing (Beets and Friedlander 1998) and overfishing of *E. guttatus* had lead to a reduction in mean length to 295mm. Seven years after a fishing closure, mean length (TL) had recovered to 395mm.

4.3 SEX RATIO

Zeller (1998) demonstrated that male *P. leopardus* spend more time at aggregation sites, making them more vulnerable to overexploitation than females. Beets and Friedlander (1998) recorded a female:male sex ratio of 15:1 that was attributed to overfishing. Following a fishing closure that ratio was reduced to 4:1. The sex ratio of epinephelines at other fished spawning aggregations has been shown to be skewed toward females. For *E. striatus*, Colin (1992) recorded a female:male sex ratio of 5:1 at one site and 3:1 at another, while Aguilar-Perera and Aguilar-Davila (1996) recorded a mean sex ratio of 1.4:1. It is possible that this is a result of overfishing.

5. SPAWNING SITES AND MARINE PARK PLANNING

The factors that influence the selection of spawning sites by fish are difficult to define, with no single factor has being identified (Colin 1996). However characterisation of habitat may provide important information for identification of potential spawning aggregation sites (Beets and Friedlander 1998). It is imperative that aggregation areas are investigated early in the marine reserve planning process. Eklund et al. (2000) documented an aggregation of black grouper (*M. microlepis*) in deep water less than 100m from an existing no take area and proposed enlarging the zone to encompass the slope-sand interface to 30m depth where the spawning took place. There is evidence of positive benefits of closing spawning aggregation areas to fishing. Ecklund et al. (2000) recorded recovery of *Epinephelus itjara* with a spawning aggregation of 10 individuals increasing to between 20 and 40 fish after a 10 year period. The Great Barrier Reef Marine Park Authority (GBRMPA) is also working to minimise target fishing of spawning aggregations through seasonal closures (Martin 2000).

A stepwise process should be employed to identify potential fish spawning sites in the marine reserve planning process. Firstly utilise local knowledge. Commercial and recreational fishers in the region may be inherently aware of spawning sites as may dive charter operators. Initial information from these people may be invaluable in narrowing down and characterising likely spawning areas. Any literature, whether scientific, commercial or anecdotal should be consulted. Biological or other scientific surveys that have been conducted may yield useful information on substrate topography. Many of the areas may have been subject to mining or oil leases and the companies that held these leases may have conducted surveys of the substrate using side scan sonar or similar. They may also have been required to conduct surveys or environmental reviews on their projects. Consultant reports may also be a source of information if the areas have been subject to any other development applications.

Remote sensing techniques would be required to determine reef regions that fit the criteria of potential fish spawning areas. As discussed these would include channel areas or well defined promontories with high topographic complexity that may be affected by tidal currents and are near to deeper waters. According to the literature sites would be greater than 5m deep, perhaps exceeding 100m but this will vary between species and region.

The topographic index (substrate rugosity index) of Sancho et al. (2000) may serve as a useful initial indicator of potential spawning sites when used in conjunction with overall topographic location i.e. channels, or promontories near deeper water. Measurement of rugosity and development of a topographic index at all known aggregation sites would enable comparison between regions and allow us to further define factors that influence spawning site location. Data collection for other coral reef ecological surveys could include a measurement of rugosity. The authors have conducted numerous underwater visual census and benthic video transects. Data on surface rugosity of each transect was also collected without much extra field effort. Rugosity was measured using the method of (Friedlander and Parrish 1998) with a depth gauge sensitive to 0.1 metre, at increments of 1 metre along the length of each transect and calculated as the straight line distance divided by the contour distance (McClanahan and Shafir, 1990; McClanahan, 1994). The resultant value can be compared between sites and regions. Sancho et al. (2000) measured rugosity by placing a fine link chain over the substrate along 2 x 1m axes within each of 50 (1x1m) quadrats. Depth has generally been measured in the papers reviewed and this should continue. Current should be more thoroughly measured (Colin 1992) where only estimations have been made and a distinction between tidal and oceanic currents is also important. The nature of the underlying substrate should be more thoroughly described, or measured if possible, to examine relationships between benthic structure and fish spawning events.

Suspected areas should be surveyed at times when the species in question are likely to spawn. This may difficult to ascertain where no records exist. Lunar phase and tide will have to be accounted for. Generally an outgoing spring (or flood) tide would be the most likely spawning time, lunar phase varies between species. Transient spawners, such as serranids appear to spawn in the period August to December in the Great Barrier Reef (*P. leopardus*) (Samoilys 1997) and December to March in the Caribbean (Colin 1992, Sadovy et al. 1994a, Eklund et al. 2000). Whereas resident spawners such as scarids and acanthurids are likely to spawn year round (Randall and Randall 1963, Gladstone 1996). Transient spawners are likely to spawn at sunset (Colin 1992, Sadovy et al. 1994a, Samoilys 1997) and residents during the day in either the morning (Gladstone 1996) or the afternoon (Sancho et al. 2000).

Once sites are located, further study should involve determining migration patterns. The simulation model of Fulton et al. (1999) showed that the greatest catch increases were produced by fish moving from inaccessible areas into fished locations and suggested that small scale closures around aggregation sites are insufficient to protect spawning *P. leopardus* and similar species. Zeller (1998) commented that male *P. leopardus* made a greater number of migrations to spawning sites which increased their vulnerability to overfishing. Small scale shifts in spawning aggregation sites may also leave them outside marine reserve boundaries. Tagging or ultrasonic telemetry studies and *in situ* observations would enable information on migration aggregation patterns to be built into any management objectives.

Once sites are identified and/or reserved it is important the aggregations are not targeted (eg for recreational diving tours) or disturbed in such a way that might reduce the success of spawning events. Ongoing monitoring would evaluate the effectiveness of fishing closures and must be conducted at the same season, lunar phase and daily time (Colin 1996).

A broad commonality between many of the aforementioned studies is the location of both resident and transient spawning aggregation sites in topographically complex areas that are in close proximity to deeper water. Spawning most often takes place on an outgoing spring tide where tidal currents may enhance dispersal of gametes and larvae. In the Ningaloo Marine Park much of the area of sanctuary zones lies within the outer reef (reef lagoon), in shallow < 4m deep water. Given the extent of Ningaloo reef (fringing 270 km of coast) it seems likely that aggregation sites would exist in these outer areas. As aggregation sites are generally located in deeper water near the outer edge of the reef it is also possible that they are not protected in the current sanctuary zones.

APPENDIX 1

Scientific and common names of fish cited in this report. Common names taken from (Allen 1997). - denotes no common name available.

SCIENTIFIC NAME	COMMON NAME	SCIENTIFIC NAME	COMMON NAME
ACANTHURIDAE		**MULLIDAE**	
Acanthurus lineatus	Blue-lined surgeonfish	*Parupeneus bifasciatus*	Doublebar goatfish
A. nigrofuscus	Dusky surgeonfish	*P. cyclostomus*	Yellow saddled goatfish
A. nigroris	-	*P. pleurostigma*	Sidespot goatfish
A. olivaceous	Orange-spot surgeonfish	*Pseudopeneus maculatus*	-
A. triostegus	Convict surgeonfish	**OSTRACIIDAE**	
Ctenochaetus striatus	Lined bristletooth	*Ostracion meleagris*	Spotted boxfish
Naso lituratus	Stripeface unicornfish	**SCARIDAE**	
Zebrasoma scopas	Blue lined tang	*Hipposcarus longiceps*	Longnosed parrotfish
AULOSTOMIDAE		*Scarus croicensis*	-
Aulostomus chinensis	Painted flutemouth	*S. gibbus*	-
CAESIONIDAE		*S. psittacus*	Palenose parrotfish
Caesio teres	Yellow and blueback fusilier	*S. rubroviolaceus*	Ember parrotfish
CHAETODONTIDAE		*S. sordidus*	Greenfinned parrotfish
C. trifasciatus	Redfin butterflyfish	*Sparisoma iserti*	Striped parrotfish
C. unimaculatus	Teardrop butterflyfish	*S. rubripinne*	Redtail parrotfish
LABRIDAE		**SERRANIDAE**	
Choerodon anchorago	Anchor tuskfish	*Epinephelus. bilobatus*	Frostback cod
Coris gaimard	Redfinned rainbowfish	*E. fasciatus*	Black tipped cod
Epibulus insidator	Slingjaw wrasse	*E. guttatus*	Red hind
Gomphosus varius	Clubnosed wrasse	*E. lanceolatus*	Queensland groper
Novaculichthys taeniourus	Carpet wrasse	*E. polyphekadion*	Small toothed cod
T. bifasciatum	Bluehead wrasse	*E. rivulatus*	Chinaman rockcod
T. lutescens	Green moon wrasse	*E. striatus*	Nassau grouper
LUTJANIDAE		*Plectropomus areolatus*	Polkadot cod
Lutjanus analis	-	*P. leopardus*	Coral trout
L. bohar	Red bass	*Mycteroperca microlepis*	Gag
L. cyanopterus	-	*M. phenax*	Scamp
L. gibbus	Paddletail	*M. tigris*	Tiger grouper
L. jocu	Dog snapper	**SIGANIDAE**	
Macolor niger	Black and white snapper	*Siganus canaliculatus*	-
		S. lineatus	Golden-lined rabbitfish
		ZANCLIDAE	
		Zanclus cornutus	Moorish idol

APPENDIX 2

Topographical features of spawning sites for fish species studied, and the nature of the aggregation. T = transient aggregating spawner, R = resident aggregating spawner, ? = presumed, - = unknown. Distribution details (Northwest Australia) from Allen (1997). Spawning type details from Domeier and Colin (1997)

SPECIES	SITE TYPE	SPAWNING TYPE	AUTHOR	DISTN NW-WA
ACANTHURIDAE				
A. lineatus	Outer edge of reef	R?	(Robertson 1983)	Y
A. nigrofuscus	Seaward extension of reef, or channels between lagoon and open ocean	R	(Robertson 1983)	Y
A. nigroris	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
A. olivaceous	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
A. triostegus	Seaward extension of reef, or channels between lagoon and open ocean	R	(Robertson 1983)	YY
Ctenochaetus striatus	Seaward extension of reef, or channels between lagoon and open ocean	R	(Robertson 1983)	Y
Naso lituratus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
Zebrasoma scopas	Pass of lagoon	R?	(Randall 1961)	Y
AULOSTOMIDAE				
Aulostomus chinensis	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
CAESIONIDAE				
Caesio teres	5-7m deep reef adjacent to a deep channel	-	(Bell and Colin 1986)	Y
CHAETODONTIDAE				
C. trifasciatus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
C. unimaculatus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
LABRIDAE				
Choerodon anchorago	Outer edge of the fringing reef	R	(Johannes 1981)	Y
Coris gaimard	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
Epibulus insidator	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
Gomphosus varius	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
Novaculichthys taeniourus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
Thalassoma bifasciatum	Downcurrent reef edge, over vertical projection; Seaward edge of submerged point in reef at a depth of 7.1m	R	(Warner 1987, Warner 1995)	N
T. lutescens	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
LUTJANIDAE				
Lutjanus analis	Reef abutting a sandy dropoff	T	(Domeier et al 1996)	N
L. bohar	Outer reef slope	-	(Johannes 1981)	Y
L. cyanopterus	Deep water 10 – 30m	T?	(Domeier and Colin 1997)	N
L. gibbus	Outer reef slope	-	(Johannes 1981)	Y
L. jocu	Spur reef that sloped from 5 to 35m deep	T	(Domeier and Colin 1997)	N
Macolor niger	Outer reefs	T	(Domeier and Colin 1997)	Y

SPECIES	SITE TYPE	SPAWNING MODE	AUTHOR	DISTN NW-WA
MULLIDAE				
Parupeneus bifasciatus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
P. cyclostomus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
P. pleurostigma	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
Pseudopeneus maculatus	Sandy bottom 21m, adjacent to coral reef	-	(Colin 1978)	N
OSTRACIIDAE				
Ostracion meleagris	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	N
SCARIDAE				
Hipposcarus longiceps	Very shallow partially enclosed bay	-	(Gladstone 1996)	Y
Scarus croicensis	24 m deep reef pinnacle, located on the edge of a dropoff	R	(Colin 1978)	N
S. gibbus	Over the extremities of underwater promontories on outer reef slope	-	(Johannes 1981)	N
S. psittacus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	YY
S. rubroviolaceus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y
S. sordidus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	YY
Sparisoma iserti	On the top of a coral pinnacle on the forereef	-	(Colin 1996)	N
S. rubripinne	Most seaward projection of fringing reef which ended in a sandy bottom at 20m depth	R	(Randall and Randall 1963)	N
SERRANIDAE				
Epinephelus guttatus	Structurally complex habitats, along the insular shelf edge	T	(Shapiro et al. 1993)	N
E. striatus	At or near the continental shelf break	T	(Colin 1992)	N
Mycteroperca microlepis	Deep water 50-120m on offshore reefs, incl. *Oculina* coral reefs on the shelf edge	T	(Gilmoure and Jones 1992)	N
M. phenax	Same general areas as *M. microlepis*	T	(Gilmoure and Jones 1992)	N
M. tigris	Coral reef 36-40m dominated by *Monastrea annularis*, within ~1km of insular shelf edge	T	(Sadovy et al. 1994a)	N
Plectropomus areolatus	passages that cut through the barrier reef	T	(Johannes 1988)	Y
P. leopardus	6m plateau with steep wall dropping seaward to gently sloping sandy substrate 17-25m	T	(Samoilys and Squire 1994)	Y
SIGANIDAE				
Siganus canaliculatus	Outer edge of fringing reefs	-	(Johannes 1981)	Y
S. lineatus	Sandy bottom at the outer reef slope	-	(Johannes 1981)	Y
ZANCLIDAE				
Zanclus cornutus	Channel 70m long, 28m wide, 4.5 m deep, crosses reef crest of the atoll	-	(Sancho et al. 2000)	Y

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