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The physical and biological processes driving fish aggregation behaviour.

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Statement of the use of generative AI

Generative AI technology was not used in the preparation of any part of this thesis.

General Abstract

It is common for coral reef fishes to aggregate on coral reefs for the purpose of spawning, and these aggregations are well known for their predictability in space and time. Ecologists have been fascinated for several decades on the how and why coral reef fishes form repeatable aggregations in space and time and the ecological importance of these aggregations to coral reef ecosystems. The objective of my study was to describe the oceanography at a fish aggregation site and patterns of aggregation for three species of larger reef fish. A particular strength of my study was the multiyear data base that identified persistent patterns of aggregation.

Here I evaluate how my findings align with published hypotheses concerning cues to aggregation (proximate cues) and the biological importance of aggregations in terms of adult fitness and survival of offspring (ultimate factors). My specific aims were to: (1) describe oceanographic patterns of a spawning aggregation site (Chapter 2); (2) describe the assemblages of fishes at the aggregation site in relation to environmental predictors (Chapter 3); (3) develop species specific models from a 13-year time series on abundance data of three functional groups of aggregating fish (Chapter 4); (4) describe the behaviour of three functional groups that form predictable aggregations in relation to size structure, growth characteristics, habitat use and hydrodynamics (Chapter 5).

The study focused on a small-scale reef pass tens to hundreds of meters wide, at Moore Reef in the northern section of the Great Barrier Reef Marine Park. The fine scale hydrodynamic study of the reef pass (Chapter 2) showed that water movement varied greatly at a scale of 10’s of meters and influenced the location of fish aggregation. The geomorphology and oceanography produced a distinct area of low water circulation adjacent the seaward opening of reef pass that favoured aggregation in coral reef fishes. The semi-diurnal tide with alternating flood and ebb tides allowed large movements of water to flow between the open ocean and coral lagoon. The tidal model demonstrated that current reversal and slack water occurred one to two hours in advance of high and low water. The highest current speeds were achieved at high and low water. Physically the small-scale reef pass had the dual capacity to concentrate oceanic plankton on flood tides, and ebb tides provided the suitable conditions for the immediate advection of reproductive material away from reef associated planktivores.

Evidence was provided that fish larvae would be retained near the natal reef and not dispersed to reefs further afield.

A key finding was the patterns of circulation in the reef pass were predictable, and they influenced the patterns of aggregation in coral reef fishes. I demonstrated that thirty-eight species of coral reef fish aggregate at Moore Reef pass. A multi-species comparison of fishes identified both seasonal and daily pattens of aggregation among 10 selected species from 5 trophic groups (Chapter 3). In all 10 species, the flood tide, or when water flowed from the ocean onshore towards the coral lagoon was the dominant factor influencing daily patterns of aggregation. The findings challenged paradigms on the timing and the biological purpose of aggregation. It was hypothesised that some coral reef fishes aggregated to forage while others aggregated for the primary purpose of spawning.

Chapter 4 presented the longest global data base of its type for three species of larger reef fish: *Plectorhinchus lineatus* (Haemulidae), *Acanthurus dussumieri* (Acanthuridae) and *Lutjanus bohar* (Lutjanidae). The major finding of this study was that timing of aggregation in all three species was persistent for 13 years. Furthermore, the timing of aggregation was unaltered by interannual fluctuations in seawater temperature and four major perturbations that included severe tropical cyclones and mass coral bleaching events. The persistent timing of aggregation allowed me to elucidate some robust individual species models that identified the proximal cues driving the continual patterns of aggregation. The cues or combination of cues varied between species. Both daylength and temperature combined were the dominant covariates explaining the continual aggregation in the austral spring months for the haemulid *Plectorhinchus lineatus*. In contrast, seawater temperature, independent of daylength was the dominant covariate for the acanthurid *Acanthurus dussumieri* forming predictably large aggregations in the coolest months of the year. In comparison, the daily aggregation of the piscivorous lutjanid, *Lutjanus bohar* at all times of the year was largely driven by flood tides. The persistent long-term patterns of aggregation correlated with two biological drivers, reproduction and foraging.

In a detailed behavioural study of the three species (Chapter 5), all fishes that aggregated were large adults and aggregation behaviour differed between species and reflected the ultimate factors of aggregation. The haemulid, *P. lineatus* formed highly dense seasonal aggregations for the primary purpose of reproduction. Spawning was cued by dusk and slack water, which occurred when small groups swam to deeper water away from the reef slope and the main aggregation. In contrast, the other seasonal aggregator, *A. dussumieri,* displayed both foraging and reproductive behaviour and was less concentrated and more dispersed throughout the fish aggregation site than observed for *P. lineatus*. Reproduction was the primary reason for this species to aggregate during the cooler months with spawning occurring in pairs at both dusk and dawn. A significant finding for both species was that fish were cued to spawn at slack water or low water movement, one to two hours prior high water. This provides further evidence that spawning during period of low water disturbance increases the probability of fertilisation. Due to the geomorphology and oceanography of the reef pass, the onset of the high water with maximum current flow would disperse the larvae away from the immediate reef environment towards a better feeding environment on the continental shelf. In contrast, the results showed the continual presence of the lutjanid, *L. bohar* was predominately linked with foraging on predicable resource pulses of small planktivores. The reef pass and the associated hydrodynamics also provided suitable spawning habitat for this known aggregator spawner.

In conclusion this comprehensive bio-physical study has contributed to a greater understanding of coral reef fish aggregations. Clear patterns of aggregation, and fish behaviour, were identified in space and time and there was some alignment by species of fish with current hypotheses of aggregation. Time of year, reef configuration and hydrodynamics were identified as compelling cues in fish aggregation formation. The biological importance of aggregation could be sensibly speculated from persistent patterns of aggregation and varied by species. The daily and seasonal hydrodynamic cycles produced clear patterns of aggregation for fishes to perform vital tasks such as feeding and reproduction. Furthermore, the study has outlined the importance of repeatable spawning aggregations in passes of small spatial scale. Aggregation sites created by geomorphology and predictable hydrodynamics produced predictable fish behaviour are critical to coral reef ecosystems by concentrating and connecting fishes. The predictable fish behaviour may also enhance coral reef energy budgets via trophic processes such as planktivory, piscivory, egg predation and coprophagy.

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Fisher EE, Choat JH, McCormick MI, Cappo M. (2018) Relative influence of environmental factors on the timing and occurrence of multi-species coral reef fish aggregations. PloS One 13:e0209234 DOI: 10.1371/journal.pone.0209234

Fisher EE, Choat JH, McCormick MI, Cappo M. (2018) Bio-physical features of a coral reef fish aggregation site. Australian Coral Reef Society Conference, Exmouth, Australia.

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Fisher EE, Whinney, JC, Marchant, RG (2019) Tidal jets and fish aggregations. Australian Coral Reef Society Conference, Tangalooma, Australia.

Fisher EE, Choat JH, Cappo M, Kingsford MJ (2022) What drives coral reef fish to aggregate? Australian Coral Reef Society Conference, Brisbane, Australia.

CHAPTER 1: General Introduction

A spectacular feature of the natural world is the ability of animals to form large temporary gatherings, or aggregations. In the terrestrial environment, animal aggregations are well known for many groups ranging from insects such as Monarch butterflies that reach densities of 10million per hectare while wintering in central Mexico (Calvert and Brower 1986) to large vertebrates such as wildebeest in the African savannahs (McNaughton 1976). Equally there are numerous examples in the marine environment including both invertebrate and vertebrate taxa. For example, the spider crab forms large aggregations in the shallow temperate Australian waters (Jenkins 2021) and the green sea turtle gathers in large numbers to mate and nest on Raine Island in the northern Great Barrier Reef (Limpus et al. 2003). Aggregations of animals can be conspecific or mixed and are often driven by the biological necessity to feed or mate and provide suitable conditions for survival of young. These temporary aggregations can make considerable contributions to local ecosystems through the creation of resource pulses transferred through complex food webs. For example, large foraging aggregations of Pacific herring and sand lance in the San Juan islands, USA, are preyed on by salmon, seals and mixed species sea birds (Zamon 2003). The underlying cues or proximate factors and the adaptive significance or ultimate causation of animal behaviour that has driven selection has intrigued biologists for centuries (Mayr 1961).

Animal aggregations occur in most marine ecosystems including coral reefs. A fish aggregation can be defined as temporary, predictable and repeatable gathering of large numbers of conspecifics in a particular space and time (Domeier and Colin 1997; Sadovy and Domeier 2005; Erisman et al. 2015). In recent decades, coral reef fish aggregations have gained increasing attention due to their spectacular nature and their heightened vulnerability to overfishing (Sadovy and Domeier 2005; SCRFA 2018; Biggs et al. 2021). Originally, attention was directed towards commercially important species from the families Serranidae and Lutjanidae and the impact of overfishing these aggregations on local ecosystems (Heyman et al. 2001; Sala et al. 2003; Nemeth 2005; Sadovy and Domeier 2005; Erisman et al. 2007; Russell et al. 2014). However, coral reef fishes represent a large diverse group of teleosts that vary greatly in body size, shape, trophic ecology and life history features (Munday and Jones 1998). Over 166 species from 20 families are known to form aggregations and this list includes both fish confirmed and suspected to form aggregations for reproductive purposes (Domeier 2012). Although, fish are known to aggregate for several other reasons including foraging, refuging and cleaning of which none are mutually exclusive. Therefore, the number of coral reef fish species forming aggregations is probably much higher (Russell et al. 2014).

Irrespective of why adult coral reef fishes form aggregations, wherever fishes aggregate, they are vulnerable to exploitation. Large temporary gatherings or aggregations of fishes at predictable times and places have been referenced as conservation bright spots to further protect ecosystem goods and services (Pittman and Heyman 2020). Predictable aggregations of coral reef fishes offer services that replenish and disperse fish populations (Johannes 1978; Domeier and Colin 1997), contribute to coral reef energy budgets (Mourier et al. 2016) and nutrient recycling (Archer et al. 2015; Shantz et al. 2015). Although a complex picture has emerged on the potential ecosystem dynamics of fish aggregations (Heyman and Kjerfve 2008; Nemeth 2009,2012) more empirical bio-physical studies on many aggregating species are required to gain a wider understanding of their contribution to ecosystem health.

1.1 Fish aggregation site geomorphology

Coral reef fishes are known to form aggregations within most coral reef systems in the Indo-Pacific and Western Atlantic (Domeier and Colin 1997; Claydon 2004; Sadovy de Mitcheson and Colin 2012; Russell et al. 2014). The geomorphological features of coral reefs, such as reef passes or channels along with promontories and outer reef slope drop-offs, have been categorised as key habitats for spawning aggregations of coral reef fishes (Colin and Bell 1991; Heyman et al. 2005; Sadovy de Mitcheson et al. 2008). In the Western Atlantic, a key characteristic of fish aggregation sites, is their location near sharp shelf edges and deeper water, typically where a downward slope (>20°) or abrupt change in depth or drop-off occurs (Kobara et al. 2013). Some distinctive multi-species fish aggregation sites also occur around promontories such as Gladden Spit in Belize, where there is a distinct turning point, or bend in the shelf edge, where the steep terrain protrudes prominently into deeper waters like a submerged headland (Heyman and Kjerfve 2008). In contrast, multi-species aggregations in the Indo-Pacific appear to be more associated with reef passes or channels (Claydon 2004).

Reef passes or passages can be defined as any channel within a reef that connects the open ocean with a confined water body or island, and they occur in all reef types including fringing, platform, barrier and atoll (Breckwoldt et al. 2022b). Reef passes vary in scale, with large-scale reef passes often a few kilometres wide that occur between reefs such as the Ribbon Reefs in the northern Great Barrier Reef (Hopley 1982) or within coral reef atolls like Enwetak in the northern Marshall Islands (Atkinson et al. 1981). Whereas, small-scale reef passes, 10's to hundreds of meters in width, which often occur within an individual coral reef. Both small- and large-scale reef passes have been identified as important fish spawning aggregation habitat (Johannes et al. 1999; Claydon 2004; Robbins and Renaud 2016). In New Caledonia both small- and large-scale passes are considered equal in terms of their ecological and cultural importance by local fisherman (Breckwoldt et al. 2022a).

Whether there are differences in terms of their biological importance between both scale passes requires further attention. Many fishes use both scale passes to form aggregations. For example, three large grouper species are known to form annual aggregations in both small- and large-scale reef passes in Palau, Micronesia and up to 56 other species from 13 families were observed forming spawning aggregations in all three reef passes (Johannes et al. 1999). Group spawning from similar species and families in the Palau study was also reported in a small-scale reef passes in Japan (Moyer 1989) and Johnston Atoll in the Central Pacific (Sancho et al. 2000b) and a large-scale reef pass at Enwetak Atoll (Colin and Bell 1991). The combined use of small- and large-scale reef passes by many fishes emphasises the need for further detailed physical and biological evidence on passes of all scales, to determine the ecological importance of these dynamic habitats. Further, this information would be valuable to future works designing marine protected areas within coral reefs.

1.2 Fish aggregation site oceanography

Multi-species fish aggregations sites, whether in the Western Atlantic or the Indo-Pacific have a key common feature, in that they occur at an abrupt interface between coral reef and open water. One possible selective criteria of these sites by many species, are that they offer variable and strong flow patterns which are advantageous to perform vital tasks such as foraging and spawning thus increasing individual fitness (Warner 1990; Choat 2012). In the Wider Caribbean, tidal currents are minimal, due to the mean tidal component amplitudes are

10.4 cm and local oceanography would be dominated by meteorological or ocean currents (Kjerfve 1981). The prevailing along shore currents when they interact with promontories or submerged sea capes produce predictable eddies and upwellings that concentrate nutrients and other particles such as fish eggs near the surface. The promontories that produced the most predictable current regimes have been utilised by many species to form spawning aggregations, such as Gladden Spit in Belize (Karnauskas et al. 2011). In contrast, the Indo-Pacific experience larger tidal amplitudes and currents (De Boer et al. 2000; Hamner et al. 2007). Tidal currents are amplified within reef passes, for example, Toyapakeh channel within Nusa Penida, Indonesia, experiences tidal currents up to 3.2m/s (Rachmat and Ilahude 2018). Current regimes in the Indo-Pacific can be complex, given interactions between abrupt topography, tides and oceanic currents which can impact plankton assemblages (Genin 2004) fish assemblages (Galbraith et al. 2021) and fish behaviour (Sancho et al. 2000b).

High currents can benefit fishes that form aggregations to forage and or reproduce. With coral reef fishes that form spawning aggregations, most of these fishes are pelagic spawners, in that they release eggs and sperm into the water column (Hamner and Largier 2012). It has been suggested that the grouper *Epinephelus ongus* selects spawning aggregation sites with the greatest current velocity in the Yonara Channel within Yaeyama Islands, Okinawa (Nanami et al. 2017). In reference to foraging, carnivorous fish families such as Carangidae and Lethrinidae were more prevalent in reef passes that experienced high currents (Sartori et al. 2021). In habitats, like reef passes, where tidal jets develop (Wolanski and Hamner 1988; Wolanski et al. 1988), can create predictable prey densities, which supports piscivorous feeding strongly coupled with tidal cycle (Zamon 2003). It is hypothesised that tidal currents create predictable changes in zooplankton distribution and abundance. Then planktivorous fishes aggregate in areas with increased plankton densities including spawn, which in turn these feeding aggregations attract piscivorous predators (Hamner and Wolanski 1988; Hamner et al. 1988; Zamon 2003; Genin 2004; Eggertsen et al. 2016). Reef passes appear to create a unique habitat where the interaction between geomorphology and oceanography is attractive to aggregating fishes for foraging and reproductive purposes.

Coral reef fishes living and performing foraging and reproductive tasks in areas of strong currents represents its own challenges. Grouper (Serranidae) and Snapper (Lutjanidae) species are the most widely reported coral reef fish families to form spawning aggregations (Russell et al. 2014; SCRFA 2018). Serranidae and Lutjanidae are generally compressed in form, meaning they could be unbalanced in fast current flow, compared to Carangidae with their fusiform body shape are more resistant swimmers in fast current flows (Eggertsen et al. 2016). For most fishes performing foraging or reproductive tasks in high energy environments, coral cover of either high or low complexity is an important parameter in regulating fishes distribution and behaviour (Eggertsen et al. 2016; Hall and Kingsford 2021; Russ et al. 2021; Sartori et al. 2021). Several studies have reported the potential importance of habitat complexity in fish aggregation sites (Carter et al. 1994; Johannes et al. 1999; Nemeth 2012; Nanami et al. 2017). Complex habitats not only provide refuge from high flow (Johansen et al. 2008) they also regulate predation (Eggertsen et al. 2016; Sartori et al. 2021), provide essential habitat to attract mates (Samoilys 1997; Johannes et al. 1999; Pet et al. 2005), and increase prey availability (Stewart and Jones 2001; Hall and Kingsford 2021). Current flow refuges for fishes either created by reef configuration or topographic complexity add another dynamic to fish aggregation sites in high energy environments. To disentangle the complexity of current regimes regulating fish aggregation behaviour, more fine scale or high-resolution data of hydrodynamic patterns at multi-species fish aggregation sites is required.

1.3 Proximate Cues

Coral reef fishes are known to form predictable aggregations in space and time for the purpose of spawning (Domeier and Colin 1997; Claydon 2004; Colin 2012). Given some studies of individual fish aggregation sites have persisted for more than a decade and that the longevity of most aggregating species is longer than 10 years (Biggs and Nemeth 2014; Rhodes et al. 2014; Ohta and Ebisawa 2017). For example, the grouper *Epinephelus ongus* with a life span of 20 years (Craig 2007), has formed annual spawning aggregations in Yonara channel, Okinawa, for a documented twenty years (Ohta and Ebisawa 2017). An acoustic telemetry study in Fakarava, French Polynesia demonstrated that individual *Epinephelus polyphekadion* are frequent annual visitors to the same fish aggregation site (Mourier et al. 2019). Individual fish site fidelity has frequently been shown for smaller reef fishes performing daily spawning aggregations. For example, the blue head wrasse *Thalossoma bifasciatum,* used the same spawning sites for generations in the San Blas Islands, Panama (Warner 1988). The fact that many fishes in all ocean basins form either daily or seasonal ephemeral aggregations with regular periodicity, asks what proximate cues drive such temporal fidelity.

Environmental factors such as daylength or photoperiod, water temperature, rainfall, trade winds (oceanic currents), lunar phase, ambient lighting (dusk and dawn), tidal phase including current speed and direction are recognised as important cues in timing fish aggregation behaviour (Colin and Clavijo 1988; Carter et al. 1994; Nemeth 2009; Colin 2012; Kobara et al. 2013). All these environmental factors are governed by the cyclic oscillation of the sun, moon and Earth. Accordingly, the periodicity of these oscillations ranges from hours to days to years. The timing of fish aggregations and the synchronisation of behaviour at specific locations often coincides with discrete environmental cycles. The influence of environmental cycles changes with location, in that temperature and photoperiod may be less of a driver to fish forming aggregations at low latitudes, compared to circannual changes in wind strength and rainfall (Claydon et al. 2014). Along with environmental cues, various biological cues such as presence of mates or intensity of courtship behaviour (Carter et al. 1994; Johannes et al. 1999) proximity to foraging grounds (Claydon et al. 2012) and production of specific sounds (Rowell et al. 2011) can also synchronise and perhaps fine tune spawning aggregation behaviour.

Proximate factors are extrinsic as well as intrinsic or physiological, and temperature is an important cue in the regulation of gametogenesis for many fishes (Lam 1983; Robertson 1991). For example, the appropriate temperature range for reproduction in Caribbean epinephelid groupers is between 25 and 27°C (Colin 1992; Asch and Erisman 2018; Gokturk et al. 2022). This narrow thermal tolerance can explain the geographical plasticity in spawning times for several groupers throughout the Caribbean (Nemeth et al. 2007b; Colin 2012). However, more than one environmental cycle ranging from hours to years are often responsible for synchronising behaviour. The grouper *Epinephelus merra* forming seasonal spawning aggregations in Okinawa provides an interesting case study of how several oscillating environmental cycles influence the various stages of gametogenesis. Water temperature increases in early Spring (April) which onsets vitellogenesis. The full moon initiates migration to spawning sites that cues final maturation of oocytes and ovulation. Spawning occurs at night for several nights after the full moon cued by spring ebb tide flows. Vitellogenesis is completed in a month and fish spawn more than once during the spawning season from April to July (Murata et al. 2021).

The regular periodicity of environmental and biological cues governs foraging and reproductive aggregative behaviour in coral reef fishes. Fishing or overexploitation of fish aggregations can interrupt this periodicity by reducing the number of fish, in that aggregations cease to form (Smith 1972; Johannes et al. 1999; Sadovy and Domeier 2005). Detrimental fishing practices such as dynamite or blast fishing often practiced through the coral triangle, not only removes adequate fish biomass, but it can also transform the habitat where it may be no longer suitable for fish to aggregate (Johannes et al. 1999; Pet et al. 2005). Severe tropical storms also can modify reef structures and lower reef complexity (De'ath et al. 2012; Cheal et al. 2017) and have the potential to disrupt coral reef fishes from forming periodical aggregations. Climate change through increasing frequency of bleaching events (Hughes et al. 2018c; Eakin et al. 2019) represents another perturbation that can potentially deliver poor outcomes for fish aggregations. Climate change may also modify fish aggregation phenology, given that most seasonal aggregators are cued by temperature and have a narrow thermal tolerance for reproduction (Asch and Erisman 2018; Gokturk et al. 2022). Although, little evidence exists if major perturbations disrupt temporal periodicity in aggregation of coral reef fishes perhaps because long term data sets are required. Furthermore, disruptions could result in immediate impacts or could lag in some responses.

1.4 Ultimate factors

Coral reef fishes display a diverse range of feeding and reproductive behaviour while forming ephemeral aggregations in space and time and this will influence the survival of different life history stages (Sala et al. 2003; Erisman et al. 2007; Heyman and Kjerfve 2008). Predictable short term foraging and reproductive behaviour appear critical in terms of generational survival and adaptive significance (Asch and Erisman 2018; Pittman and Heyman 2020). Short term foraging aggregations appear coupled with high prey densities cued by environmental factors. For example, during spring (northern hemisphere), the leopard grouper *Mycteroperca rosacea*, in the Gulf of California, Mexico forms daily foraging aggregations on resting schools of flat eye herring *Harengula thrissina* (Hobson 1965; Parrish 1992; Sala et al. 2003; Erisman et al. 2007). The foraging aggregations of *M. rosacea* are cued by the diel cycle with most of the feeding occurring around the crepuscular periods of dusk and dawn (Hobson 1965; Parrish 1992). Foraging aggregations on predictable prey ultimately improves adult fitness which may explain the high abundance of large males at the fish aggregation sites (Sala et al. 2003). Both foraging and spawning aggregations are known to overlap in the Gulf of California in space and time (Erisman et al. 2007), which ultimately improves the number and quality of progeny produced.

The adaptive significance or why many coral reef fishes spawn in aggregations has generated several substantial hypotheses (Table 1.1). All these hypotheses are not mutually exclusive to each other. For instance, the selfish herd and predator satiation hypotheses are similar in that dilution effect in that a trade-off is created between spawners and predators. Due to the predictability of spawning aggregations in times and places, predators of both adults and eggs are well known to congregate concurrently with spawning aggregations. For example, the aggregation of whale sharks *Rhincodon typus* that prey on eggs of two spawning lutjanid species in Belize (Heyman et al. 2001) or the grey reef shark *Carcharhinus amblyrhynchos* that prey on the adult grouper *Epinephelus polyphekadion* spawning aggregations in Tuamotu archipelago, French Polynesia (Mourier et al. 2016). The contrasting predator evasion and egg predation hypotheses involve spawning at times and places that would reduce predatory pressure on adults and eggs respectively. They contrast in that low light periods are a poor time for planktivores and ideal for piscivores or vice versa where the middle of the day is poor for piscivores and great for planktivores (Hobson 1965).

Table 1.1. Proposed hypotheses to explain adaptive significance of coral reef fishes spawning in aggregations.

Hypotheses	**Adaptive significance**	**Source**
Selfish herd	Predator dilution	(Hamilton 1971)
Predator satiation	Trade-off between spawners (adults and or eggs) and predators.	(Johannes 1978)
Predator evasion	Reduce predation on adults	(Shapiro et al. 1988)
Egg predation	Reduce predation on eggs	(Johannes 1978; Lobel 1978)
Larval dispersal	Dispersal of populations from natal reef	(Barlow 1981)
Larval retention	Retention of populations to natal reef	(Johannes 1978; Lobel 1978)
Pelagic survival	Larvae finding food in a patchy environment	(Doherty et al. 1985)
Synchronise behaviour	Higher probability of mate location and selection	(Lobel 1978; Colin and Clavijo 1988)

All coral reef fishes known to aggregate for spawning, produce a pelagic larval phase (Hamner and Largier 2012). Therefore, life for larvae in the open water is in broad contrast to reef attached adults. Many biological factors of reef fish larvae such as egg quality, length of planktonic and nektonic stage, food availability, swimming and sensory capabilities influences how the larvae interacts with the physical pelagic environment and its resultant fate (Leis and McCormick 2002). Models of survival, therefore, question whether spawning at predictable times and places benefit both adults and larval survivorship, or one over the other. One theory is that spawning events cued by environmental factors is only to synchronise activity of adults and not related to oceanographic conditions that increase larval survival (Colin and Clavijo 1988).

Alternatively, spawning at places in time with local or oceanic currents that immediately transports eggs offshore, may reduce predation by reef associated planktivores and possibly improve probability of larval survival (Johannes 1978; Lobel 1978). Once pelagic eggs and larvae have survived the ‘wall of mouths’ (Hamner et al. 1988), the secondary purpose of immediate offshore transport may be to aid larvae in finding food in open water (Doherty et al. 1985) or finding suitable settlement habitat either through dispersion from natal reef (Barlow 1981) or retention near natal reefs (Johannes 1978; Lobel 1978).

Opposing offshore transport theory is that several studies have observed that spawning occurred at slack water or minimal currents (Samoilys 1997; Nemeth et al. 2007b; Whaylen et al. 2007; Nanami et al. 2013). These studies concluded that that spawning in low velocity current may improve fertilisation, however dispersal would be lower. The studies also highlighted the requirement for more detailed information on local hydrodynamics to interpret the adaptive significance of aggregative spawning. Given the diverse array of foraging and reproductive behaviour shown by reef fishes there is likely to be more than one explanation for aggregative spawning.

1.5 Knowledge gaps

The study of coral reef fish aggregations has been extensive over the past few decades and critical, given the vulnerability of aggregating fishes to fishing and the need for conservation (Sadovoy de Mitcheson 2016; Heyman et al. 2019; Pittman and Heyman 2020). Yet, there are gaps on some of the key physical and biological factors and the interlinked ecological mechanisms that promote fish aggregation behaviour. Several studies have measured water currents in relation spawning behaviour and larval projection (Colin 1995; Sancho et al. 2000b; Colin 2010; Ezer et al. 2011; Sakaue et al. 2016). These studies have suggested the need for more fine scale oceanographic data. This gap is spatial as well as temporal, in that there is little information on flow patterns immediately adjacent the fish aggregation site, necessary to understand the impact of local geomorphology on hydrodynamic patterns. From a temporal sense, there is often gaps in fine-scale oceanographic information on fish aggregation sites inside and outside of known fish aggregation times. Such detailed temporal changes in flow, need to be coupled with other high scale resolution data on physical parameters such as wind (strength and direction), temperature and sea height to understand the physical drivers of local hydrodynamics. Detailed daily, seasonal and climatic oceanographic information of fish aggregation sites appears fundamental to understanding the biological story of fish aggregation behaviour.

The biological traits body size, trophic ecology and anatomy are considered important drivers in evolution of fish spawning aggregations (Choat 2012). However, there are knowledge gaps in the large reef fishes that form aggregations outside the commercially important families Serranidae and Lutjanidae. Although several significant studies have been conducted on fishes from ecological important families such as the Acanthuridae and Labridae, they were more often inclusive of small to intermediate size fishes (Sadovy de Mitcheson and Colin 2012). It is essential to investigate a range of large body coral reef fish species that display a variety of foraging and reproductive modes. This is important to determine the trophic and reproductive role of fish aggregation sites to the ecology of coral reefs. Such families for which there is little information include the Haemulidae.

Several environmental factors are acknowledged as proximate cues driving fish aggregation formation and longevity (Nemeth 2009; Colin 2012). There have been several long-term detailed studies investigating proximate cues for aggregating behaviour (Biggs and Nemeth 2014; Rhodes et al. 2014; Ohta and Ebisawa 2017). However, there are knowledge gaps or lack of detailed long-term high frequency data (daily) on aggregation patterns among years (Sadovoy de Mitcheson 2016) to interpret the specific role various environmental factors influence these patterns. This gap extends to our knowledge of how perturbations such as tropical cyclones and anthropogenic climate change influence coral reef fish aggregations and their behaviour. There is evidence that tropical cyclones do not disrupt spawning behaviour in some temperate fishes (Locascio and Mann 2005; Biggs et al. 2018) and such perturbations may even concentrate and retain larvae close to coastlines (Lobel and Robinson 1988). With respect to the timing of aggregations, more information is required during and the years following large perturbations such as Tropical Cyclones and marine heatwaves. A grasp of the proximate cues for individual species is required to infer the ultimate causation for displayed behaviour. Further, gaps exist in the detailed coupling of proximate cues and animal behaviour to determine the adaptive significance of aggregations for a range of coral reef fishes.

Coral reef fish aggregations have been studied in all ocean basins (Sadovy de Mitcheson and Colin 2012; SCRFA 2018), although on the Great Barrier Reef (GBR) studies have been limiting. In total, five studies have investigated fish aggregations in the GBR: with three studies devoted to the commercially important grouper species *Plectropomus leopardus* (Samoilys and Squire 1994; Samoilys 1997; Zeller 1998), one study on a large serranid

Epinephelus fuscoguttatus (Pears et al. 2007) and one study on the large parrotfish *Bolbometopon muricatum* (Gladstone 1986). Two of these studies, Gladstone (1986) and Samoilys (1997) occurred at large-scale and small-scale reef pass respectively. The study conducted at the small-scale reef pass at Elford reef in the northern section of the GBR indicated that the site was also used by multiple aggregating species (Samoilys 1997). Given the suspected importance of reef passes to fish aggregation ecology, I selected a known multi-species fish aggregation site that occurs near a small-scale reef pass in the northern section of the GBR for this study (Fisher et al. 2018).

1.6 Structure of the thesis

The broad objective of the thesis was to determine the behaviour of multiple species of reef fishes at a known aggregation site. My approach was to determine the cues that influence aggregation and inferences were made on the likely ultimate factors determining individual fitness, reproductive fitness and larval survivorship. My research program required data on the hydrodynamics of the site as well as distributional and behavioural data on the associated fishes.

Accordingly, the thesis had the following specific aims:

1. Describe oceanographic patterns of a spawning aggregation site (Chapter 2).
2. Describe the assemblages of fishes at the aggregation site in relation to environmental predictors (Chapter 3).
3. Develop species specific models from a 13-year time series on abundance data of three functional groups of aggregating fish (Chapter 4).
4. Describe the behaviour of three functional groups that formed predictable aggregations in relation to their size structure, distribution, position, time of day and hydrodynamics (Chapter 5).

Chapter Two examined the fine scale hydrodynamic patterns of fish aggregation site and small-scale reef pass. I used multiple several high sampling rate current meters to measure the temporal patterns of current flow relative to wind strength and direction, and the mixed semi-diurnal tide. The fine scale study showed that water movement varied greatly at a scale of 10’s of meters and influenced the location of the fish aggregation site. This chapter was critical to determine the distribution and behaviour of coral reef fish aggregations.

Chapter Three investigated the aggregation of 10 species of coral reef fishes from five trophic groups that formed regular aggregations. I used multivariate regression trees to examine temporal factors ranging from hours to years that influenced fish abundance, which produced a highly predictive model of community fish aggregation. The study identified daily and seasonal patterns of aggregation among the 10 selected species. This chapter highlighted the importance of reef configuration and hydrodynamics for large coral reef fishes forming aggregations on the Great Barrier Reef.

Chapter Four further examined the proximate cues in three large coral reef fish species that formed continual patterns of aggregation. This chapter presented a high frequency 13-year data base of aggregation for coral reef fishes. The patterns of aggregation in all three species were persistent over a decade. The timing of aggregations was unaltered by interannual fluctuations in seawater temperature and four major perturbations that included severe tropical cyclones and mass coral bleaching events. I used aggregated boosted regression trees to produce species specific models. Chapter Four demonstrated that the proximate cues behind aggregation varied among daily and seasonal aggregators.

Chapter Five explored fish behaviour to provide further insight into the cues of aggregation and infer ultimate factors influencing aggregation in three large coral reef fishes. This detailed behavioural study examined fishes aggregation behaviour relative to size structure, distribution, time of day and hydrodynamics. In conclusion I use the behavioural information to compare and contrast how the data align with existing models of fish aggregation.

CHAPTER 2: Fine-scale hydrodynamic patterns at a Great Barrier Reef fish aggregation site

2.1 Abstract

A high-resolution study of a small-scale reef pass hydrodynamics revealed that water volume and direction varied greatly from scales of 10's to 100's of meters and produced distinct patterns of water circulation with little seasonal variation. Tidal forcing was the principal driver influencing the hydrodynamics of the small-scale reef pass and fish aggregation site. The study was done at a pass located within Moore Reef, situated east of Cairns in the northern section of the Great Barrier Reef Marine Park. The restriction in tidal flow created by the reef pass, increased the current velocity which in turn increased the volume of water moving through the pass. Further, flows generated a tidal jet phenomenon in the pass that was driven by a semidiurnal tidal pattern and current reversal occurred one to two hours prior high and low water. Other evidence of a tidal jet phenomenon was the bifurcation of current towards the entrance of the seaward side, where the ambient water movement was slower, and this appeared favourable to the location of the multi-species fish aggregation site. The observed alternating current patterns resulted in the ingress of oceanics water on flooding tides both onto the reef and through the reef pass. In contrast, ebb tides flushed and directed Great Barrier Reef shelf and lagoonal reef waters of Moore Reef towards the open ocean.

There was little seasonal variation in these flow patterns, and wind had minor influence on tidal flows; evidence is provided of wind assisted events resulting in cold water intrusions from Ekman transport. The nature of flows and complex geomorphology suggested 'sticky water effects' that could concentrate oceanic nutrients, plankton and influence larval supply and retention in the near vicinity of a coral reef. This study was part of a larger study to link hydrodynamics of a fish aggregation site to fish aggregation behaviour. Furthermore, these findings highlight the potential biological importance of small-scale reef passes to fish aggregations, trophic dynamics, larval dispersal and connectivity among reefs.

Key Words: reef pass, tidal jets, bifurcation, temperature, fish aggregations, cold water intrusions, Ekman spiral

2.2 Introduction

Tropical coral reefs are highly diverse ecosystems that are surrounded by oligotrophic waters. The growth, metabolism and community structure of coral reefs are heavily influenced by the oceanic environment in which they live and hydrodynamic processes (Monismith 2007; Lowe and Falter 2015). How water circulation influences coral reefs, is a question of scale, time and the geomorphological nature of the coral reef system. An individual coral reef can be influenced by a variety of hydrodynamic processes operating on time scales from hours to years. At a larger scale, these can include oceanic currents occurring annually, seasonal wind driven currents and hourly tidal influences. Smaller scale hydrodynamic processes driven by upwelling, internal waves, eddy fields and tropical cyclones occurring at the shelf break also influence the flow patterns of an individual reef (Lowe and Falter 2015). Circulation patterns around an individual reef are combination of all these influences, further complicated by the interaction with the complex topography of the reef themselves and their proximity to other reefs (Kingsford et al. 1991; Wolanski and Spagnol 2000; Andutta et al. 2012). This in turn can influence the aggregation of plankton, the feeding activity of planktivores, fish aggregations and patterns of connectivity.

The Great Barrier Reef (GBR) is a large continental shelf system found in 10 - 60m depth of water comprising approximately 3000 individual coral reefs that vary in configuration and age, with the highest density of reefs occurring on the mid to outer continental shelf (Hopley 1982). The reefs, therefore, are nested together with other reefs on the continental shelf reef mosaic. A consistent topographical feature of individual coral reefs is the development of a reef front and crest on the windward face forming a barrier that encloses, or partially encloses a sheltered lagoonal environment. The South Equatorial Current and associated jets push oceanic water towards the shelf, then seasonal trade winds and astronomical tides on the continental shelf further mix these waters, the combination of these processes contribute to the regular flushing of the GBR (Andutta et al. 2013). Flow patterns within and around individual reefs are strongly influenced by wind driven currents and tides. Wind surface driven waves can also force oceanic water across reef flats and into reef lagoons (Atkinson et al. 1981; Monismith 2007; Falter et al. 2013). However, tides also contribute to the flushing of coral reef lagoons through the importation of oceanic water, rich in plankton and nutrients (Andrews et al. 1984; Wolanski and King 1990; Hamner et al. 2007). In addition, tidal flows combined with topographical controlled fronts have the capacity to aggregate plankton and fishes in short lived eddies and slicks (Alldredge and Hamner 1980; Hamner and Hauri 1981; Hamner et al. 1988; Kingsford 1990).

The influence of astronomical tides in modulating hydrodynamic and biological processes of coral reefs are often amplified through passes within coral reef mosaics and by individual coral reef configuration. When coral reefs are in close proximity, that is less than a few kilometers from each other, the tidal influence in these narrow passages produce a distinct suite of hydrodynamic features, that has been described in detail (Thomson and Wolanski 1984; Hamner and Wolanski 1988; Wolanski et al. 1988; Lambrechts et al. 2008). The restriction of water through these narrow passages results in an increase in current velocity, thus producing a pair of eddies on the down current side known as a mushroom jet, which can initiate upwelling. These tidal mushroom jets occur on both the flood and ebb tide through the ribbon reef passages and have been linked to the distribution of taxa. For example, banks of *Halimeda* algae on the leeward side of the Ribbon Reefs on the GBR (Wolanski and Hamner 1988; Wolanski et al. 1988) and the occurrence of the large pelagic fish Black Marlin forming regular spawning aggregations on the seaward side of the Ribbon reefs has been related to the hydrodynamics of these passages (Speare and Steinberg 2001; Domeier and Speare 2012).

Reef passes along with promontories and outer reef slope drop-offs have been categorised as key habitat for coral reef fish spawning aggregations (Colin and Bell 1991; Heyman et al. 2005; Sadovy de Mitcheson et al. 2008). Although, reef passes as fish aggregation sites may be limited to the Indo-Pacific (Kobara and Heyman 2007). A review of 108 geophysical characteristics of transient spawning fish aggregation sites examined in the Wider Caribbean revealed aggregations were associated with reef promontories, outer reef slopes or submerged capes (Kobara et al. 2013). In contrast, reef passes in many Indo-Pacific regions have been identified as important coral reef fish spawning aggregation sites (Johannes 1978; Robertson 1983; Johannes 1988; Moyer 1989; Colin and Bell 1991; Samoilys 1997; Craig 1998; Johannes et al. 1999; Sancho et al. 2000a; Hamilton 2005; Robinson et al. 2008; Robbins and Renaud 2016; Fisher et al. 2018). Reef passes can vary in scale from the passages between reefs or entrances to atolls that can be kilometers wide to the smaller narrow pass or channel within an individual reef that dissect the reef flat and can be 10’s to hundred meters in width. These small-scale passes act as conduits between sheltered lagoons and open oceans and can support multi-species fish aggregations of 100’s to 1000’s of fish (Fisher et al. 2018).

Research on the physical and biological processes of small-scale reef passes (meters to 10's of meters) compared to larger scale passes (hundreds of meters to kilometers) had been limiting. However, this work is critical to assess the viability of small-scale reef passes as an important driver of multi-species fish aggregation.

Coral reef fishes are well known to aggregate for reproductive purposes (Domeier and Colin 1997; Claydon 2004; Sadovy de Mitcheson and Colin 2012). Several environmental factors or proximate cues such as tides, lunar or solar have been suggested to synchronise fish aggregation behaviour at selected sites to increase mate selection, encounter rates and fertilization success (Colin and Clavijo 1988; Colin 1992). The focus on adult synchronicity to spawn in relation to circulation patterns to reduce predation on adults or egg to improve survivorship of the young, are as follows; predator satiation hypothesis or a tradeoff event where predators and spawners are satisfied (Johannes 1978), predator evasion hypothesis by spawning at sites and times with limited predators (Shapiro et al. 1988), egg predation hypothesis that spawners aggregate at sites and times to reduce gamete predation (Johannes 1978; Lobel 1978), egg dispersal hypothesis in that timing spawning with hydrodynamics to maximise dispersal to more suitable environments (Barlow 1981), larval retention hypothesis that spawning occurs in relation to hydrodynamic events that returns larvae to their natal reef (Johannes 1978; Lobel 1978), pelagic survival hypothesis by dispersal increases larvae chances to find resources in a patchy oceanic environment (Doherty et al. 1985). All these hypotheses are not exclusive of each other and nearly all make assumptions on the local hydrodynamics.

The presence of a pelagic larval phase in the life history of coral reef fish makes the study of spawning aggregations and subsequent connectivity patterns inherently bio-physical (Jones et al. 1999; Cowen et al. 2007). Previous studies both in the Indo-Pacific and Western Atlantic have quantified, and or modeled the hydrodynamics of fish aggregation sites in relation to spawning and predictable currents have supported a two-fold ecological advantage. Firstly the currents provide immediate advection of reproductive material away from the coral reef (Sancho et al. 2000b; Ezer et al. 2011; Sakaue et al. 2016) to ultimately reduce egg predation (Johannes 1978) and secondly the timing also coincides with oceanographic conditions that concentrate planktonic items and retain larvae close to coral reefs (Colin 1995; Ezer et al. 2011; Karnauskas et al. 2011; Donahue et al. 2015), and ultimately increasing survivorship and the likelihood of fish settling at or close to the natal reef (Johannes 1978; Lobel 1978).

The links between fish aggregations and hydrodynamics are more complex if aspects of the entire ecosystem are considered. Multi-species fish aggregation sites exhibit multiple trophic interactions and energy transfer within a predictable space and time (Nemeth 2012; Fisher et al. 2018) and provide nutrient subsidies that supplement coral reef energy budgets (Archer et al. 2015; Shantz et al. 2015). Fisher et al. (2018) proposed that the hydrodynamics of a reef pass on the GBR had a dual ecological purpose, in that it supported fish forming foraging aggregations based on flow patterns that concentrated plankton, planktivores and piscivores along with reversal flow patterns providing the necessary advection of gametes from spawning fish. Although some studies have outlined links between small-scale reef passes and the spawning of fish on ebb tide currents, these outflows were not exclusively tidal and predictable. This was due to wind and swell that could also influence flow patterns and inherently fish aggregation behaviour (Moyer 1989; Sancho et al. 2000b) Although such studies have outlined the importance of investigating site-specific hydrodynamics, their conclusions have often been based on limited sampling or the resolution of the fish aggregation site has been course in relation to the configuration of the reef pass.

The objective of this study was to evaluate the fine-scale water circulation patterns of a multi-species fish aggregation site within a mosaic of coral reefs on a diel and seasonal temporal scale. The fish aggregation site occurs on the seaward side adjacent to a reef pass within a patch reef on the northern GBR (Fisher et al. 2018). An array of current meters, a nephelometer to measure sea level height and a surface drifter were deployed during this study to address the following aims: 1) quantify diel and seasonal patterns of water circulation through this reef pass and fish aggregation site, 2) determine the influence of tide and wind on observed current and water temperature patterns, 3) discuss the hypothetical biological importance of small-scale reef pass hydrodynamics for coral reef fish forming aggregations.

2.3 Methods

2.3.1 Study site

The study site was approximately 55 km east of Cairns on the northwestern side of Moore Reef, situated on the outer margin of the continental shelf in the northern section of the Great Barrier Reef, Australia (Fig. 2.1A). Moore Reef has a crescent shape characterised by an extensive reef flat on the windward margins, with a well-developed reef front that partially encloses a lagoon dominated by isolated patch reefs (Fig. 2.1B). The reef pass dissects the reef flat and was ~330 m in length, 60 to 250 m in width and 14 to 22 m in depth with a north to south orientation. The reef front on the outer side of the pass and the leeward edge on the inner side of the pass both included spur and groove morphology. The inner and outer reef slopes terminated at ~ 20 m depth into a sand-rubble substratum dotted by isolated coral patches (Fig. 2.1C).

A fish aggregation can be defined as temporary, predictable and repeatable gathering of large numbers of conspecifics in a particular space and time (Domeier and Colin 1997; Sadovy and Domeier 2005; Erisman et al. 2015). The fish aggregation site (-16.845°, 146.23°) covers an area of ~3,500 m^2 and situated on the north-west aspect of the reef pass Fig. 2.1C). At this site, 40 species of reef fish from 12 families were known to aggregate, of which 10 species from 5 trophic groups were known to form predictable aggregations (Fisher et al. 2018). The Great Barrier Reef Marine Park Authority (GBRMPA) have classed Moore Reef as Marine National Park Zone or no take area and of high conservation value. Accordingly, fishes at the fish aggregation site were not affected by extraction. The research carried out in this study was conducted under GBRMPA research permit G12/35200.1.

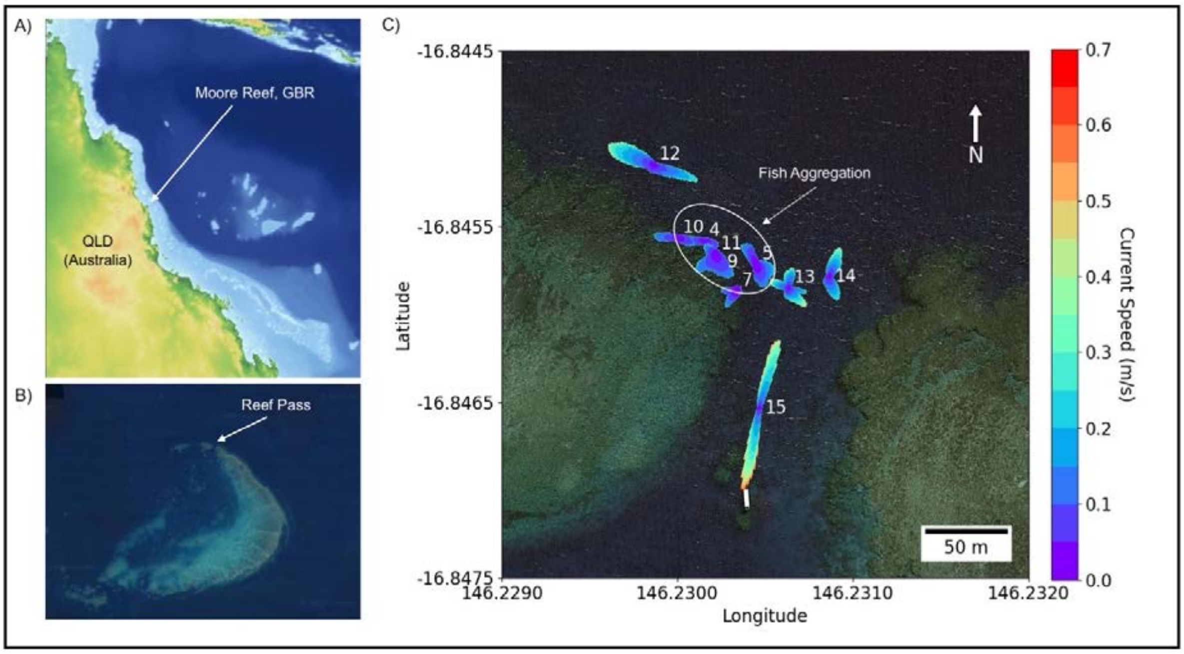


Fig 2.1. Moore Reef, small-scale reef pass hydrodynamics: A) The location of Moore Reef in the Great Barrier Reef, B) the investigated reef pass at the north-western aspect of Moore Reef and C) fine scale water movement within the study area illustrated by rose plots of all current speed (m sec-1) and direction values (one minute average) recorded between 15-Aug-2014 and 7-Dec-2015 from 10 Marotte HS. Each speed and direction bin of the rose plots indicated the direction the water was flowing. The white numerals represent each current meter station number, and current meter 11 was also the position of the Nephelometer (Table 2.1). The white oval outlines the outer perimeter of the fish aggregation area.

2.3.2 Instrumentation

An array of current meters, a nephelometer and a surface drifter were deployed during this study to quantify current patterns through the fish aggregation site and reef pass (outside fish aggregation site). Currents were measured with a *Marotte HS,* a drag-tilt current meter, this instrument was developed and manufactured by the Marine Geophysics laboratory at James Cook University. The instrument, consisted of a buoyant enclosure containing an electronic logger, which was then fixed to a stationary point. The buoyancy force causes the instrument to float directly upwards in the absence of current. Movement of the water exerts a drag force on the instrument, tilting it over until the buoyancy, drag and tether forces are balanced. The amount of tilt was proportional to the speed of the water (Marchant et al. 2014). The logger records the tilt angle using an accelerometer, and the tilt direction using a magnetometer. Both tilt and tilt angle were converted to current speed and direction in post-processing using a pre-defined tilt-to-speed calibration curve. The instrument also contained a temperature sensor (thermistor type with ± 0.2°C repeatability) that was fixed to the bottom of the logger (JCU and Marine-Geophysics-Laboratory 2017).

The current meters were fixed to star pickets 0.5 m above the substrate at selected locations, substrate types and depths through the fish aggregation site, and reef pass (Fig. 2.1C). The fixed current meters were positioned at several depths (Table 2.1) within and outside the fish aggregation site to counteract sampling bias and changes in water current speed and direction between surface and substrate. The loggers were set to record current speed and direction at one second intervals. The data were recorded on a micro-SD card and the instrument was powered by 2 AA batteries. The raw data was converted into current speed and direction and temperature with the *Marotte HS config program* (JCU and Marine-Geophysics-Laboratory 2017). Approximately every 3 months, the loggers were retrieved, cleaned downloaded and redeployed using SCUBA. Minimal biofouling was noted during all instrument deployment.

Table 2.1. The location (decimal degrees), depth, substrate type, duration of deployment, current speed range (m sec^{-1}) and temperature range (°C) for all *Marotte HS* current meters deployed.

Current Meter #	GPS (Decimal Degrees)	Depth (m)	Substrate Type	Deployment Duration	Current Speed Range (m/s)	Temperature Range (°C)
4	-16.845583 146.230150	8	Coral Rock	15/8/14 – 7/1215	0 – 0.31	22.83 – 30.6
5	-16.845717 146.230450	23	Sand/Rubble	4/11/14 – 7/12/15	0 – 0.45	22.65 – 29.85
7	-16.845867 146.230333	14	Rubble/Coral Rock	4/11/14 – 7/12/15	0 – 0.24	22.74 – 30.23
9	-16.845700 146.230250	11	Coral Rock	4/11/14 - 7/12/15	0 – 0.34	23.0 – 30.32
10	-16.845567 146.23000	8	Coral Rock	15/8/14 – 9/6/15	0 – 0.30	24.96 – 30.60
11	-16.845667 146.230217	9	Coral Rock	15/8/14 – 13/1/15	0 – 0.32	25.67 – 29.95
12	-16.845150 146.229867	12	Coral Rock	4/11/14 – 9/6/15	0 – 0.55	25.04 – 30.23
13	-16.845850 146.230633	21	Sand/Rubble	4/11/14 – 7/12/15	0 – 0.64	23.00 – 29.95
14	-16.845783 146.230867	20	Sand/Rubble	4/11/14 – 7/12/15	0 – 0.49	22.48 – 29.76
15	-16.846533 146.230467	6	Coral Rock	4/11/14 – 7/12/15	0 – 0.64	22.83 – 30.60

Tidal patterns at the study site were investigated with a nephelometer (optical backscatter turbidity logger) which incorporated a pressure sensor to measure sea level, a temperature sensor, and a pair of optical sensors to measure deposition and turbidity. The optical sensors measured light reflectance horizontally (turbidity) and vertically (deposition) via an optical fiber bundle to the outer surface of the instrument. These apertures were kept clean using a wiper applied every two hours. The wiper system allows deployment in tropical areas for long periods without biofouling (Ridd and Larcombe 1994). The instrument logged recordings every 10 minutes and was positioned on top of a coral head (-16.845667 °, 146.230217 °) at a depth of 9m (Current meter 11, Fig. 2.1C). To restrict movement and improve stability the instrument was fixed to a 32 kg steel frame. Deployment at the site was from 16-Apr-2013 to the 31-Aug-2013. The nephelometer was deployed and retrieved using SCUBA.

Moore Reef had no automated weather station to collect regular measurements of wind speed and directional data. The data used in this study to investigate the wind effect on recorded current patterns was collected from a neighboring reef called Arlington Reef. The automated weather station on Arlington Reef, ID 200879, height (10m), (-16.72°,146.11°) and lies ~18 km to the north-west of Moore Reef pass. The wind speed and directional data obtained for this study was recorded at 10-minute intervals between 21-Aug-2012 and 07-Dec-2015. Wind direction for this period was predominately from the southeast with occasional northerly winds in the summer months (see Appendix A Fig. A.1).

A surface drifter of opportunity was deployed to investigate the movement of water from the reef pass on one occasion. These instruments have previously been used in the GBR to illustrate complex flow patterns in low- and high-density reef matrices (Mantovanelli et al. 2012). The drifter used in this study was developed by Marine Geophysics laboratory at James Cook University (Marchant et al. 2015). The electronics of the instrument was housed in a PVC case attached to a surface float. A drogue set at a depth of 5m was attached to the surface float. The electronics of the device contained a non-differential GPS satellite messenger which recorded a position every 5minutes and transmitted the 6 recorded positions every 30 minutes via satellite. The drifter was released on the north side of Moore Reef pass on 17-Oct-13 and recovered 18-Oct-13. The electronic surface drifter data was plotted on a map and to illustrate movement of the instrument in relation to the reef pass from start to end time.

2.3.3 Data Analysis

A total of 3,962,311 observations of current speed and direction were collected from the 10 current meter stations between 15-Aug-2014 and 7-Dec-2015. These data were interpolated from a one second to a one-minute period with Gaussian smoothing kernel of sigma = 20 seconds to reduce noise and make the dataset more manageable in size. Rose plots were constructed to illustrate water movement at the study site. To convey the water movement more accurately, each speed and direction bin was scaled such that the displayed area was proportional to the volume of water moved.

The rose plots demonstrate total water moved around each current meter and to determine seasonal variation in flow patterns at a small spatial scale, two current meters were selected. Current meter 13 from the seaward entrance of the reef pass displayed multiple flow directions and this was compared to current meter 4 from the centre of the fish aggregation area and considered representative of that area (Fig. 2.1C). The data collected from both current meters 4 and 13 was partitioned into the 4 austral calendar seasons to produce individual rose plots displaying current direction for each season.

Tidal harmonics analysis was performed on the 10-minute interval sea level data to produce a tidal prediction of the Moore Reef site. The mean sea level was 10.72m and the analysis produced a model from 60 harmonic constituents to describe the tidal nature and the dominant constituents were also expressed as a form factor (Amin 1986). The observed sea level data was compared with predicted values to produce a residual and gauge the accuracy of the predictive tides.

The predicted tides were calculated for 7-Nov-14 to 10-Nov-14 from the harmonic analysis and used with the current meter data from each station to produce an animation of water movement at Moore Reef pass and the fish aggregation site. Rose plots for each current meter site were generated in the same manner as before but calculated over a rolling window of one hour of observations. A sequence of images was produced from 7-Nov-14 to illustrate water flow relative to various tidal stages. A cross correlation analysis was performed on the sea level and current data to determine the lag between both time series.

A key finding of the Fisher et al (2018) study was the flood tide was the dominant hydrodynamic feature influencing the timing of aggregation of 10 species of coral reef fish, from 5 trophic groups, independent if fish aggregated daily or seasonally. To illustrate this a grey ellipse symbolizes the presence of fish aggregations and absence was marked by no grey ellipse. The ellipse functions as a proxy of fish aggregation presence and not respective of fish richness and abundance. For more details on environmental cues driving fish aggregation assemblage at the Moore Reef site see Fisher et al (2018).

The predicted tides were also expressed in a time series along with observed seawater temperature, current speed and direction and wind speed direction from 4-Nov-14 to 7-Dec-15. The current speed and direction data were collected from current meter 15 (Fig. 2.1C) and converted to a vector in that each value has a magnitude and a direction along the direction of the passage. Positive values show current flowing to the north (ocean) and negative values show current flowing to the south (GBR Shelf). Wind direction was predominately from the south-east (Appendix A Fig. A.1) and the speed and direction data were also expresses as a vector rotated along the path of 135 degrees. In this case, positive values show wind blowing from the south-east and negative values show wind blowing from the north-west.

A p166 low pass filter was conducted on the current, wind, temperature and sea level time series which diminished high frequency features and revealed trends in the data. The linear relationship between the low pass filtered current as the response variable and low pass filtered wind the predictor variable was explored using a continuous time series in the data between 15-Jan-15 and 8-Jun-15. The time series data for both variables was found to be non-stationary using Kwiatkowski-Phillips-Schmidt-Shin (KPSS) test (Kwiatkowski et al. 1992) and also highly auto correlated. Time series regression techniques using auto regressive moving average models (ARMA) were fitted to both the low pass filtered current and wind time series. The order of the model for both time series was (p=0, d=1, q=5) where p was auto regressive component, d was first order differencing and q was the moving average component. A linear regression was then performed on the ARMA models where current was the response and wind the predictor variable.

Water temperature varied greatly in February compared to other months in this study. This month was selected to investigate correlations between low pass filtered variables of temperature, wind, current and sea level. The data of these time series was not distributed normally, and the nonparametric Spearman rank order method was used to measure the strength and direction of association between two variables. Partial correlation analysis using Spearman method was used to evaluate the strength of association between water temperature and the other three variables.

Analysis to produce the rose plots for all current meter stations, the supplemental animation and the p166 low pass filter of the entire time physical time series were performed using open source Python computing language (PythonSoftwareFoundation 2020). All other analyses were performed in R (RCoreTeam 2021) and used the open source libraries; circular (Agostinelli and Lund 2023), forecast (Hyndman et al. 2023), GGally (Schloerke et al. 2021), ggfortify (Horikoshi and Tang 2016), ggmap (Kahle and Wickham 2013), gtable (Wickham and Pedersen 2023), ppcor (Kim 2015), TideHarmonics (Stephenson 2016), tidyverse (Wickham et al. 2019), tseries (Trapletti and Hornik 2023), urca (Pfaff 2008) and xts (Ryan and Ulrich 2023).

2.4 Results

Water volume and direction through the reef pass varied greatly on scales from 10's to 100's meters, for 16 months of observations (Fig. 2.1C). Large volumes of water were consistently moved through the reef pass, compared to the fish aggregation area. Current speeds in the middle of the pass were up to three times greater than current speed recorded at the fish aggregation area. Current speeds within the fish aggregation area were consistent at all depths between 8 and 23 m (Table 2.1) and was generally less than 0.2 m sec^{-1} (Fig. 2.1C). Moving away from the fish aggregation site and further along the outer slope, current speed increased. Water movement through the reef pass was bidirectional with water flowing either northwards and out of the Moore Reef lagoon or flowing southwards and into the coral lagoon. In comparison to the fish aggregation area, water flow was low and mainly bidirectional with water either flowing towards the reef pass or away from it and running perpendicular to the outer reef slope (Fig. 2.1C).

There was little seasonal variation in the flow patterns described, with the exception for some fine scale variation near the seaward entrance of the reef pass. This area had a seasonal pattern, with current alternating in direction between north and south for Summer and Autumn, then switching to a north-westerly to a south-easterly flow in Winter and Spring (Fig. 2.2A). In comparison there was no seasonal variation in flow patterns from the fish aggregation area, with currents alternating in direction between the East and West (Fig. 2.2B).

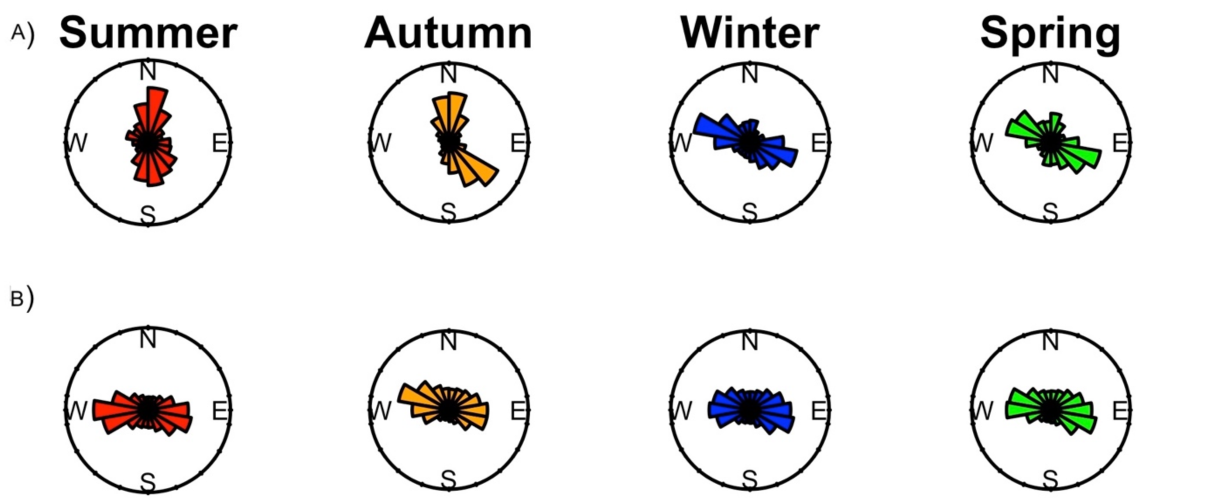


Fig. 2.2. Austral seasonal rose plots of current direction: A) current meter 13 from the seaward entrance of the reef pass and B) current meter 4 from the centre of fish aggregation area. Each speed and direction bin of the rose plots indicated the direction water was flowing to.

Moore Reef experienced a mixed semidiurnal tidal pattern, where there are generally two highs and two low periods within 24 hours and the tides are of mixed heights or asymmetrical. The main diurnal (K1, S1 and P1) and semidiurnal constituents (M2 and S2) produced from the tidal harmonics analysis of the reef pass sea level data (Table 2.2). These constituents were used to calculate the form factor (F) ~ 0. 73. The spring neap cycle was 14.7 days and the comparison between the observed data and fitted data illustrated tidal behaviour was regular and predictable (Fig. 2.3A) with difference between observed and predicted amplitude not exceeding 22 cm (Fig. 2.3B).

Table 2.2. The amplitude and phase of the 5 main constituents at Moore Reef.

Constituent	**Amplitude**	**Phase**
M2	0.512	261.4
K1	0.463	123.4
S2	0.321	209.4
S1	0.311	254.7
P1	0.193	102.4

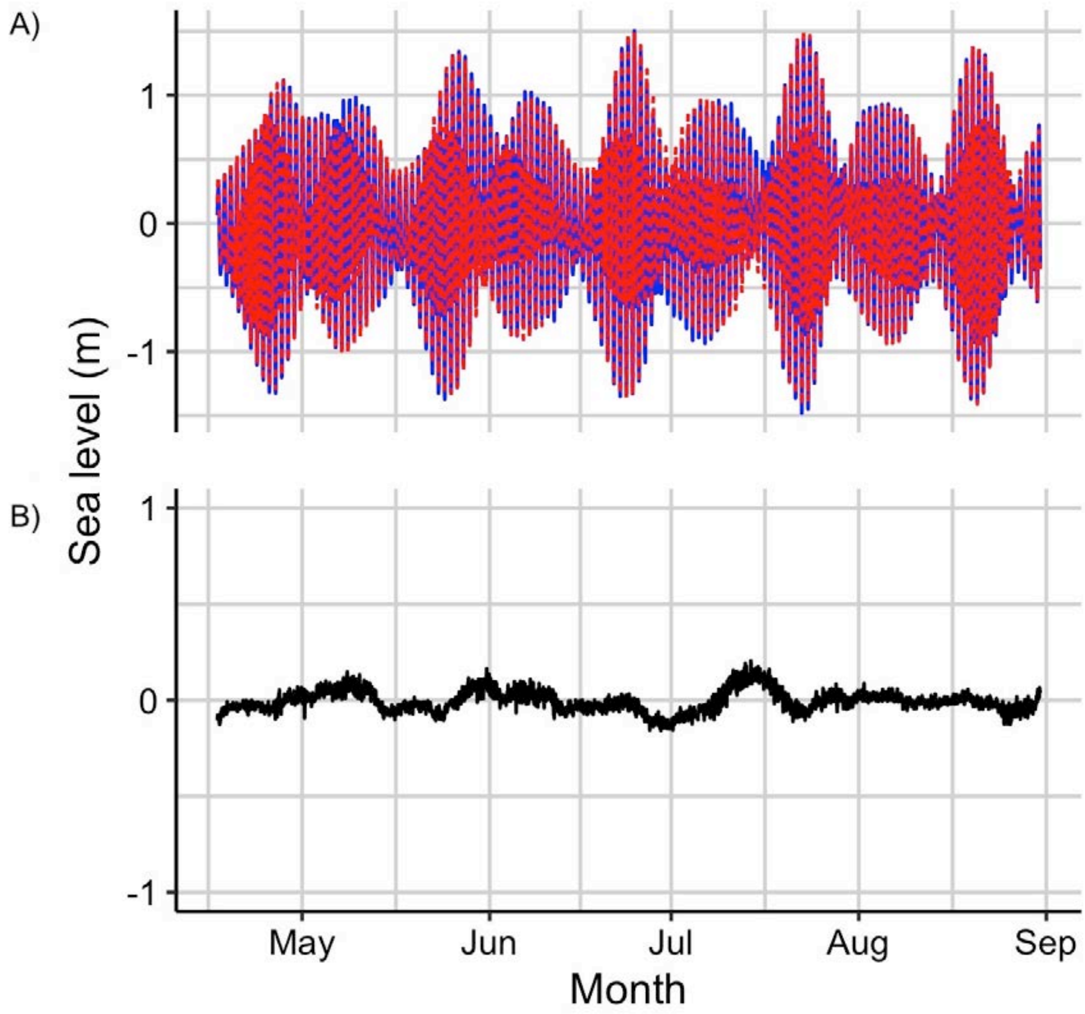


Fig. 2.3. Predicted versus observed tides at Moore Reef: A) The predicted tidal values (red dash line) at Moore Reef for April to September 2013 derived from tidal harmonic analysis using 60 harmonic constituents plotted with the actual sea-level observations (blue line) recorded by the nephelometer. B) The mean sea-level has been removed from both the observed and predicted sea level measurements. The black line shows the residual between the observed and predicted amplitude and indicated a high level of accuracy.

Astronomical tides were the principal driver of observed circulation patterns in the reef pass and fish aggregations site. (Fig. 2.4 and see animation Appendix A Video A.1). During one tidal cycle (7-Nov-14), the current speed at high water was > 0.4 m sec^{-1} in the middle of the pass and directed towards the north or away from Moore Reef. During this ebb phase currents at the fish aggregation site were < 0.1 m sec^{-1} and variable in direction (Fig. 2.4A). These current patterns persisted through the ebb tide phase (Fig. 2.4B), with the subsequent low water showing a reverse in flow patterns with water flowing from the open sea and through the reef pass and into the open lagoon. Fish aggregations were present at the fish aggregation site during this phase, which persisted through the flood tide phase (Fig. 2.4C & D) but absent during ebb tides as per Fisher et al (2018) (Fig 2.4A & B). Current speed at the fish aggregation site during flood tides was < 0.2 m sec^{-1}, although current direction varied between the cluster of current meters. The instruments detected a bifurcation of current direction, with current meters 5 and 7 flowing towards the pass and current meters 4 and 10 flowing the opposite direction. The current meters 9 and 11 situated near the middle of fish aggregation site were more variable in flow direction.

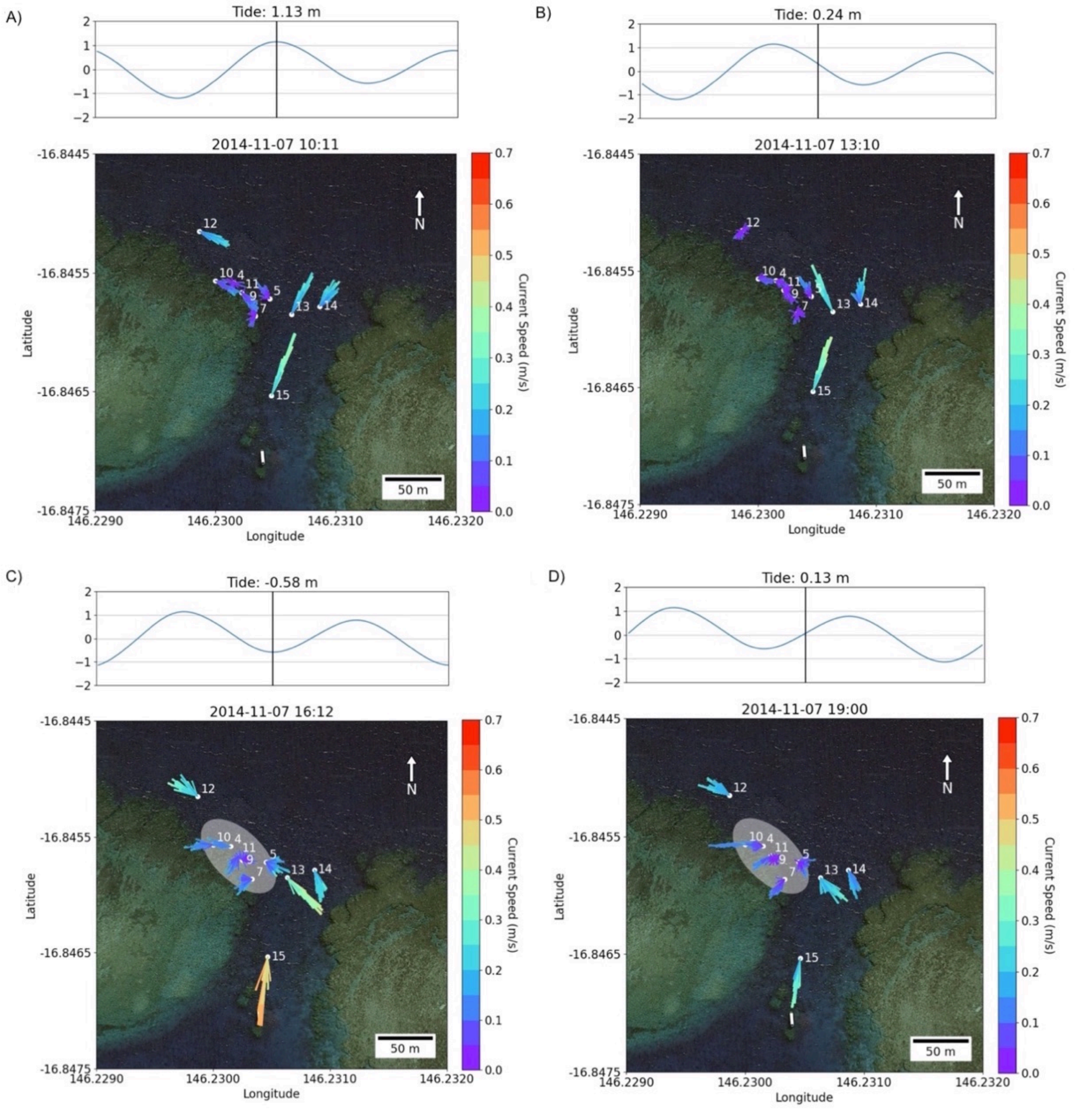


Fig. 2.4. Tidal currents at Moore Reef pass and fish aggregation site. A sequence of images from of the animation (Appendix A Video A.1) of all 10 current meters displaying current speed and directional changes in relation to the predicted tidal model for Moore Reef between 10:11 h and 17:00 h on the 7-Nov-2014 for four tidal stages; A) high water, B) ebb, C) low water and D) flood. The light grey ellipse illustrated fish aggregation presence, which only occurred during flooding tides as per Fisher et al (2018). Each speed and direction bin of the rose plots indicates the direction the water was flowing.

The maximum water velocities experienced in the reef pass occurred at high and low water and the relationship between current direction and tide was not synchronised, and current reversal occurred in advance to low or high water (see animation Appendix A Video A.1). The relationship between the two-time series improved with a negative lag of 1 to 2 hours (Fig. 2.5).

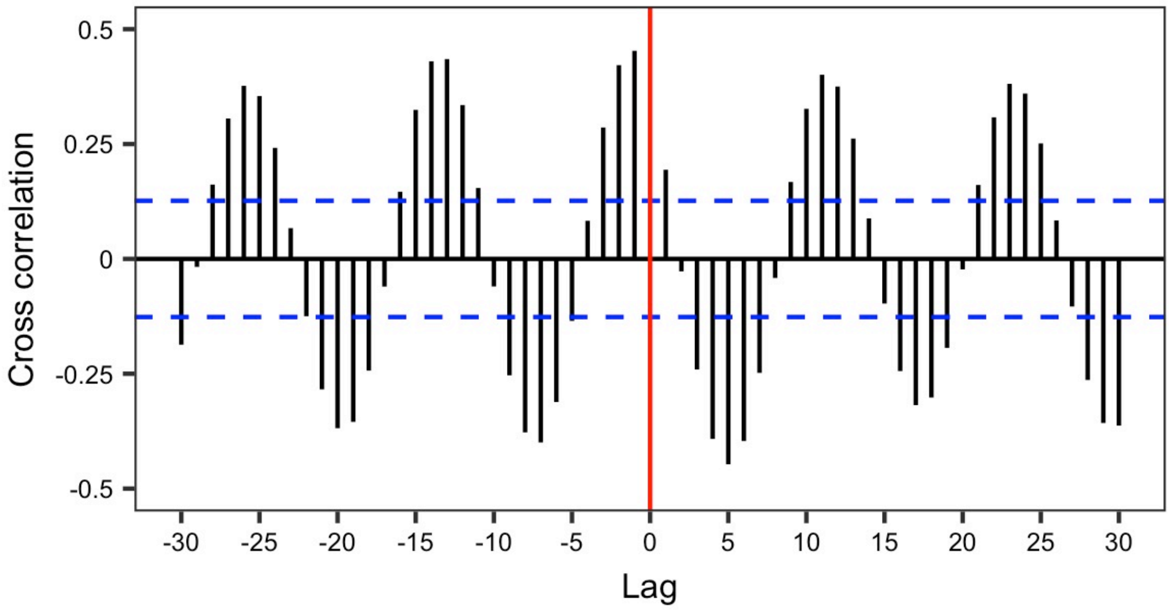


Fig. 2.5. Cross correlation plot of water current and sea level time series with the lag in hours and the vertical red line denote lag = 0.

Wind direction influenced current speed and direction and water temperature at the reef pass. The low pass filter carried out on the time series of temperature (Fig. 2.6A), wind speed (Fig. 2.6B), current speed (Fig. 2.6C) and sea level (Fig. 2.6D) revealed some interesting trends. Wind direction generally blew from the south-east, with 4 episodes of north-west winds greater than 8m sec^{-1} (Fig. 2.6B). Water currents exhibited a pattern consistent for mixed semi-diurnal tides (Fig. 2.6D), although a relationship existed between low pass filtered wind speed (Fig. 2.6B) and low pass filtered current speed (Fig. 2.6C) and the relationship appeared more evident during neap tides (Fig. 2.6D). A linear regression between low pass filtered current speed and low pass filtered wind speed was significant ($P < 0.05$, $F_{(1,3478)} = 542.9$, $R^2 = 0.135$). This weak relationship demonstrated that south-east winds assisted flood tidal currents, while north-west winds assisted ebb tidal currents, however the magnitude of these flows would be negligible < 0.05 m sec^{-1} (Fig. 2.7).

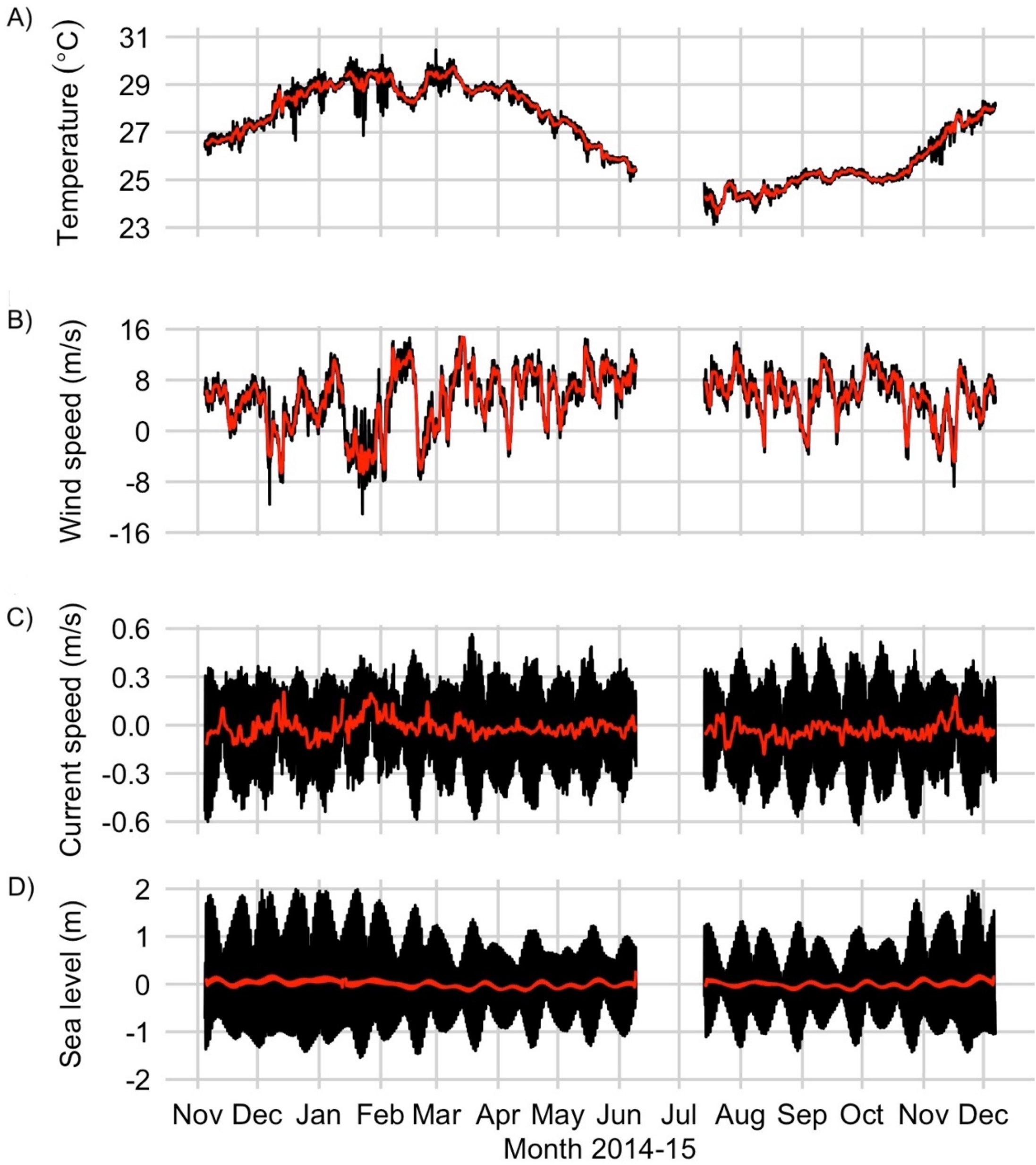


Fig. 2.6. Time series plots of environmental variables from 4-Nov-14 to 7-Dec-15; A) temperature in degrees Celsius, B) wind speed in meters per second with positive values showing wind that blew from the south-east and for negative values wind blew from north-west, C) current speed in meters per second with positive values showing current flowed to the north or towards the ocean and away from the reef and negative values for current that flowed south or into the coral lagoon and D) sea level in meters predicted from tidal harmonics analysis. The red line in all plots were produced from passing a p166 low pass filter through the hourly observations.

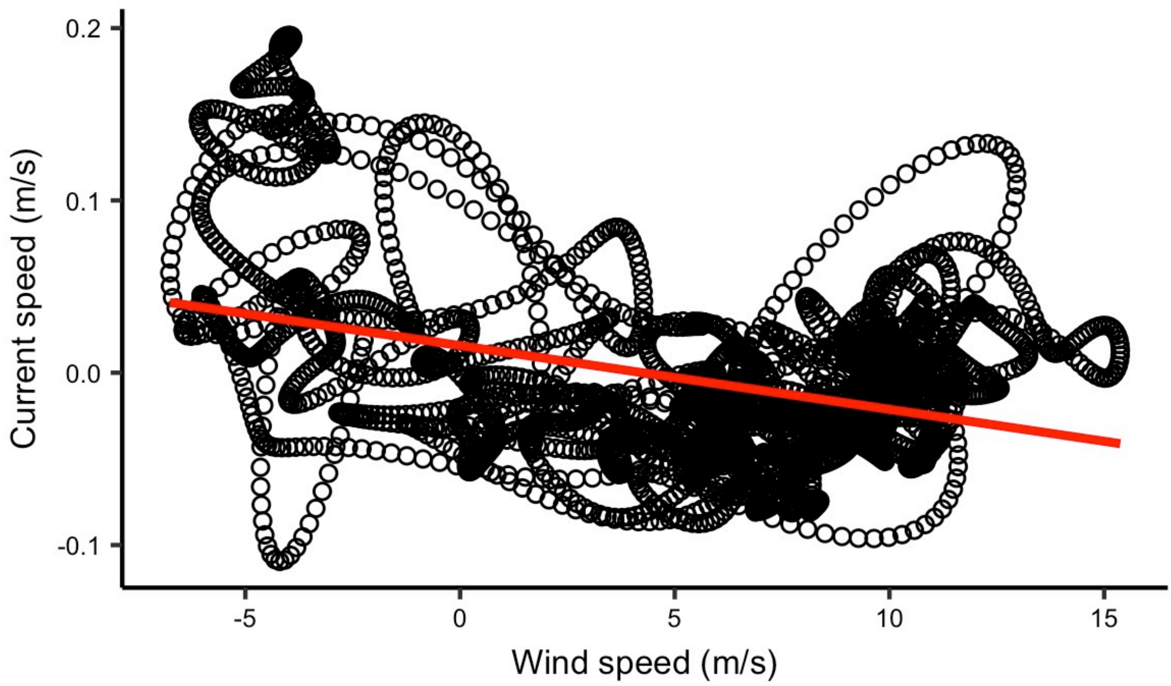


Fig. 2.7. The linear relationship between p166 low pass filter current speed and wind speed values in their dominant directions for 113 days between 15-Jan-15 and 8-Jun-15. Positive values for current speed, showed water flowed north through the reef pass and out to open sea and away from the coral lagoon. Positive values for wind speed represented wind direction from the south-east. The negative values for both variables illustrated flow patterns from the reciprocal direction in that current flowed south or from open ocean through the pass and into the coral lagoon and wind blew from the north-west. Speed for both variables represent hourly averages and was shown in meters per second.

Throughout the 12 months of study, sea water temperature in the reef pass ranged between 23 and 30 °C and the least amount of variation in temperature occurred during the spring months. In contrast, a greater variation in temperature occurred outside of spring and of considerable note was a 2 degree drop in temperature through mid-February (Fig. 2.6A). This drop coincided with a change in wind direction from the north-west to the south-east (Fig. 2.6B). Water temperature at the reef pass was cooler during early stages of a flooding tide after low water and more if the wind direction was from the south-east (Fig. 2.8). The correlation matrix showed that each pair of low pass filter variables had significant correlations with the highest correlation between temperature and sea level (Fig. 2.8). Partial correlation analysis confirmed the importance of sea level on temperature, with cooler water temperature associated with low water. Rho estimates between temperature with current and wind were close to 0 when sea level was included in the analyses. Although all correlations were significant between variable pairs while adding a third variable (Table 2.3).

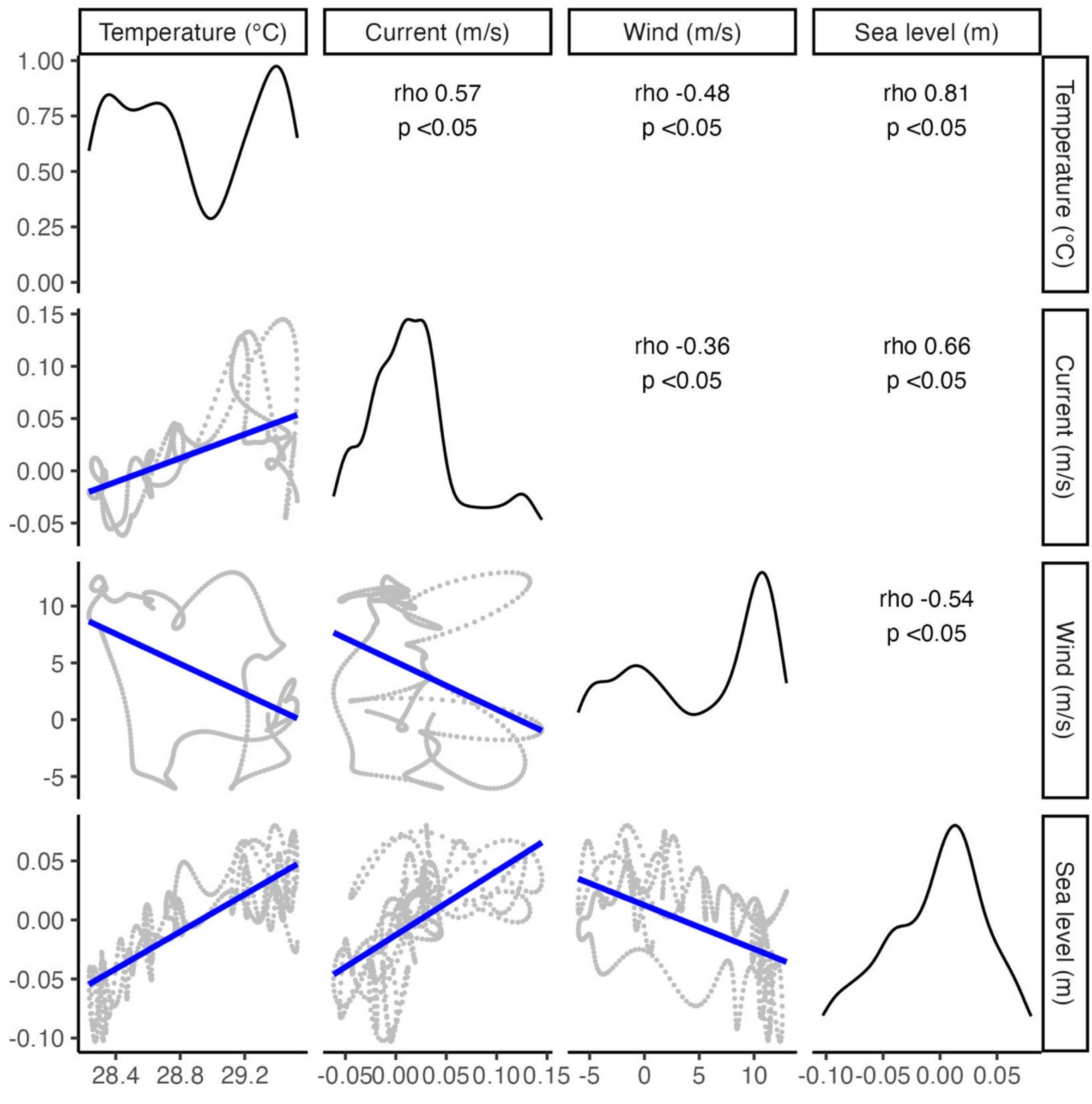


Fig. 2.8. Correlation matrix for the four low pass filtered variable pairs. The lower triangle of the matrix displays scatter plots between each variable pair fitted with regression line in blue. The diagonal plots show data distribution plots of each variable and the upper triangle of the

matrix display the rho estimate and p value for each spearman rank correlation analysis for each variable pair.

Table 2.3. Partial correlation analysis of low pass filter temperature and low pass filtered current, wind and sea level while adding a third variable. Rho estimate from spearman rank correlation method and P value are presented for each analysis (n=672).

Temperature versus	Third variable	Rho estimate	p value
Current	Sea level	0.07	<0.05
Current	Wind	0.48	<0.05
Wind	Current	-0.36	<0.05
Wind	Sea level	-0.08	<0.05
Sea level	Current	0.71	<0.05
Sea level	Wind	0.75	<0.05

The electronic surface drifter remained within a kilometer of the reef boundary during 17 hours of travel before being returned to the reef edge. The initial movement was rapid advection away from the reef when the instrument was released during the initial stage of a spring ebb tidal phase at the seaward entrance of the reef pass. The instrument then followed a track parallel to Moore Reef, tracking south-east first, then turned to travel north-west, almost along the same track. After several hours the instrument followed Moore Reef boundary, tracked south-west and then turned direction and travelled north-east along the same path before turning towards Moore reef and then became pinned on the reef crest and ceased to move, approximately 1km from the release point (Fig. 2.9).

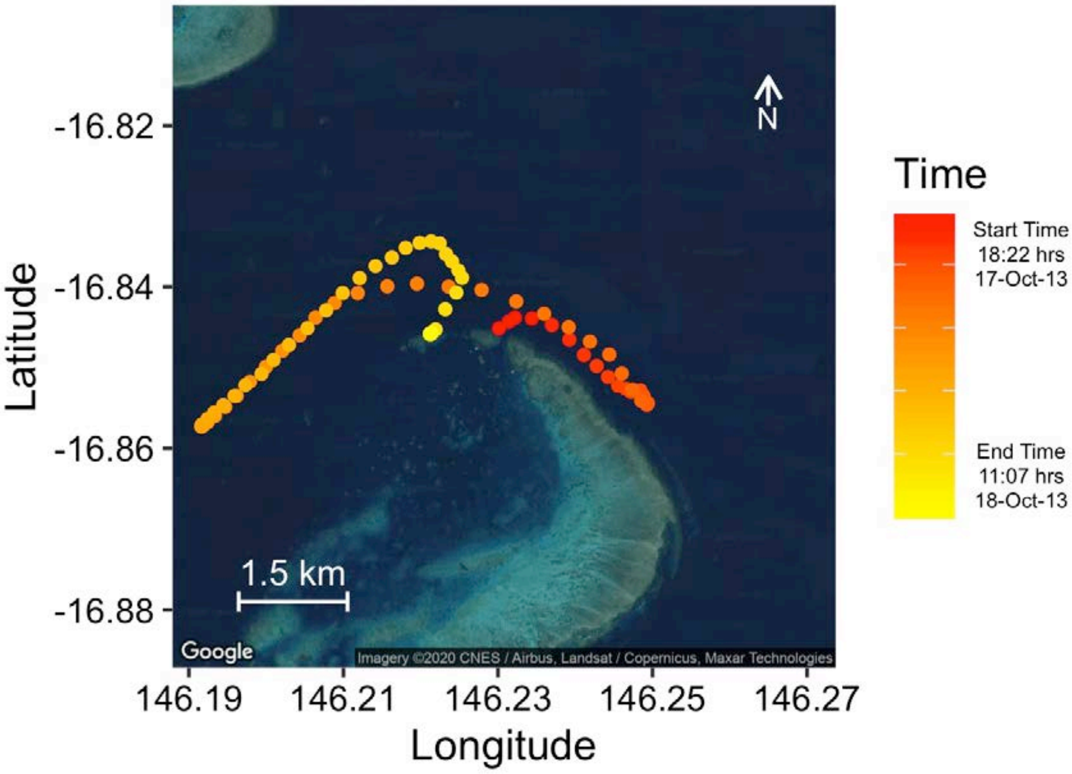


Fig. 2.9. The path of electronic surface drifter released at Moore Reef pass on the 17-Oct-13. The coloured dots progressing from red to yellow through the colour scale represent drifter location from start time to end time.

2.5 Discussion

This high-resolution study of a small-scale reef pass hydrodynamics revealed that water volume and direction varied greatly from scales of 10's to 100's of meters and produced distinct patterns of water circulation. There was some small-scale seasonal variation in flow which was likely driven by the dominate southeast trade winds in winter. Tidal forcing was the principal driver of the circulation patterns in the reef pass and fish aggregation site. The restriction in flow created by the reef pass produced an increase in current velocity which in turn increased the volume of water moving through the pass. The multi-species fish aggregation site occurred immediately adjacent the reef pass on the seaward side where there was little ambient water movement.

The results support that Moore Reef pass experiences tidal jet phenomenon (Wolanski et al. 1988) driven by a semidiurnal tidal pattern characteristic of this region of the GBR (Wolanski 1994). The observed alternating current patterns were orientated in that flooding tides ingressed oceanic water onto the reef and through the reef pass compared to ebb tides which flushed and directed lagoonal reef water onto the continental shelf. The maximum water velocities experienced in the reef pass occurred at high and low water because current reversal occurred in advance of low or high water. There was little seasonal variation in these flow patterns and specific wind directions had a negligible influence on tidal flows. This study provided evidence for other hydrodynamic features such as cold-water intrusions caused by Ekman transport from north-west winds that would have moved surface waters seaward and facilitated localised upwelling of cool water. This, combined with sticky water effects, would have caused the concentration of oceanic nutrients, plankton and larval supply in the near vicinity of a coral reef. Accordingly, tidal forcing on the reef pass has the physical capacity to concentrate and incorporate nutrient subsidies into coral reef systems and immediately disperse fish eggs. These fine scale physical processes can provide the right conditions for the formation of fish aggregations and related foraging behaviour, reproductive behaviour or both. Further, a knowledge of site-specific physical processes can be used to create a bio-physical understanding of fish aggregation sites.

The hydrodynamic features described in this study supports that small-scale reef passes produce tidal jets like larger scale reef passes found in other studies (Thomson and Wolanski 1984; Dumas et al. 2012; Delandmeter et al. 2017). Tidal jets can be summarised by the movement of large bodies of water through the middle of the pass produced by the narrow reef configuration, tidal currents, production of mushroom eddies on downstream side and bifurcation of currents on the upstream side (Wolanski et al. 1988; Lambrechts et al. 2008). Fishes responded to the physical oceanography of the study area. The fish aggregation site at Moore Reef pass occurred where there is little ambient water movement, despite its position directly adjacent the reef pass where water movement was significantly higher. During flood tides, the fish aggregation site experienced a bifurcation in current in that the current splits in the middle of the aggregation site, with some water flowing towards the pass and rest along the outer reef slope. Water moving in this area albeit slowly, has been advected from the seaward side and not lagoonal reef water.

The tidal jet features experienced at the pass are short-lived and governed by the predictable semi-diurnal tide cycle. Current strength varied according to the spring-neap tidal cycle, with spring tides producing higher current speeds in the pass. Moore Reef is located on the southern boundary and seaward edge of the northern GBR. The tidal harmonics analysis produced in this study was like other models used to describe tides in the central GBR. The top three constituents M2, K1 and S2 describe most of the tidal variation (Andrews and Bode 1988; King and Wolanski 1996). The alternating currents experienced in the reef pass correspond to changes in tidal amplitude with a 1 to 2 hour’s negative lag. The predictability of these currents was like a large-scale reef pass (1.2 km wide) in Enwetak atoll. At this location in the mid Pacific Ocean, maximum current speeds were 0.8 m/s, currents reversed with tide and slack water period was no more than a few minutes (Atkinson et al. 1981). There have been two studies that have examined the hydrodynamic patterns of small-scale reef passes in some detail (Moyer 1989; Sancho et al. 2000b) but both studies had limited oceanographic data and suggested that predicting currents from tides was difficult due to influences from wind driven waves and ocean swells. In contrast, the Moore Reef pass had predictable current flows.

Water movement through the Moore Reef pass was tidal driven and predictable, with wind having a negligible influence on tidal flows. In contrast to Moore Reef, other studies conducted at reef passes found wind to have a controlling influence on current direction. In French Polynesia, wind-driven currents were found to dampen or accentuate tidal jets produced by a reef pass and influence lagoon flushing times and oyster larvae retention

(Dumas et al. 2012). A similar non tidal finding of current circulation occurred in a reef pass (28m in width) at Johnston atoll. The study conducted a 55-day current meter record and discovered that 65.5% of the days showed bidirectional flow coupled with tides and 34.5% of the days displayed a unidirectional flow (Sancho et al. 2000b). In both these instances sudden and continual changes in flow direction influenced fish aggregation behaviour. Therefore, it would be expected the predictable flow patterns experienced at the Moore Reef pass would produce consistent patterns in fish aggregation behaviour.

This study provides evidence that tidal jets associated with a small-scale reef pass delivered cooler benthic water to Moore Reef. Water temperature at the reef pass was cooler during early stages of a flooding tide after low water and more if the wind direction was from the south-east. Upwelling's is another hydrodynamic feature often associated with tidal jets, although only documented from larger scale reef passes that occur close to the continental edge (Thomson and Wolanski 1984; Wolanski et al. 1988). In these events deep cold nutrient rich water from the continental slope were forced onto the continental shelf through narrow passages between reefs. Geographically, Moore Reef occurs ~ 15km inside from the continental shelf edge and the shelf to the east of this reef has an open reef matrix, however there was evidence of a summer cold water intrusion. In February of this study there was a 2 °C reduction in water temperature that following a large north-west blow and possibly high cloud cover (Leahy et al. 2013) that interrupted south-east trade winds. Cold water intrusions on to the seafloor in this area occur seasonally between October and March (Walther et al. 2013; Benthuysen et al. 2016). The Ekman spiral from northerly winds would also assist in the delivery of these cooler nutrient rich waters to Moore Reef.

Flooding currents have the capacity to introduce cooler plankton rich water, while the ebb current flows can flush the coral lagoon or export biological material (Hamner et al. 2007). Ebbing current flows from the reef pass were up to 0.6 m/s and similar in strength to other studies that quantified current speeds in reef passes (Atkinson et al. 1981; Sancho et al. 2000b). This immediate outflow could generate dispersal of reproductive material quite rapidly from the natal reef and Moore Reef has been identified as a source reef for coral (Hock et al. 2017). Accordingly, coral and fish eggs spawned at this reef, could seed other surrounding reefs and supports the egg dispersal hypothesis (Barlow 1981). The interesting finding in the lagrangian component of this study was that water did not disperse far from

Moore Reef and the semi-diurnal pattern retained water close to the reef. This was indicative of sticky water effects and reversing tides (Wolanski and Spagnol 2000; Andutta et al. 2012) and aligns with the larval retention hypothesis (Johannes 1978; Lobel 1978). A similar finding was found for Ulong Chanel in Palau, where drifters released during the ebb phase of the tidal jet only travelled 1-2km then travelled in direction of along reef edge current (Colin 2012). Even with low sticky water effects the retention rate for active swimming larvae can be as high as 20% and even 2% for non-swimming coral larvae (Wolanski and Kingsford 2014). In support of larval retention to Moore Reef, the lagoonal side of the Moore Reef Pass was found to concentrate crown-of-thorns starfish larvae, which transferred into high settlement rates (Uthicke et al. 2019).

The final aim of this study was to discuss the hypothetical biological importance of small-scale reef pass hydrodynamic patterns to the formation of coral reef fish aggregations. The current study demonstrated that the predictable hydrodynamics of the semi-diurnal tide has the potential to concentrate prey items for fish foraging aggregations (Hamner and Wolanski 1988; Hamner et al. 1988; Zamon 2003; Genin 2004; Eggertsen et al. 2016) and provide the immediate necessary advection of reproductive material for fish spawning aggregations (Johannes 1978; Lobel 1978; Choat 2012). At the fish aggregation site water movement was notably less compared to reef pass and further along outer reef slope. There are three possible physical processes that may influence concentration of prey items at the fish aggregation site as follows: bifurcation of tidal currents, upwelling and topographic complexity. Flood tides induce tidal jet associated upwelling and produce an area of slack water and bifurcation of currents at the aggregation site (Wolanski and Hamner 1988). The other plankton entrapment mechanism would be the topographic complexity and small scales eddies similar to the hydrodynamics of spur and groove morphology (Hamner et al. 1988). These three individual processes or a combination of, could readily concentrate prey items at the fish aggregation site daily.

Conversely, during ebb tides, there was evidence of eddy formation and limited current flow that may also concentrate plankton although plankton supplies during ebb tides are often low density due to high predation rates on flood tides (Hamner et al. 1988; Hamner et al. 2007). However, in terms or spawning aggregations this area would be suitable. However, fish spawning 10’s of meters toward the pass at slack water prior to high water would quickly have access to fast flowing water away from the reef due to the current reversal. Eggs would be quickly transported away from reef edge (Johannes 1978; Lobel 1978) and wall of mouths (Hamner et al. 1988) and onto the continental shelf. In contrast to other studies conducted around Pacific Islands (Moyer 1989; Sancho et al. 2000b) transport would be into the reef mosaic of the GBR and not out into the waters of the open ocean. The position of the fish aggregation site next to ebbing tidal jet provides the necessary mechanism for advection and considered a critical element in the evolution of spawning aggregations (Choat 2012).

This study was a high-resolution study at a small-scale reef pass only 10's of meters wide. In conclusion the physical oceanography of small-scale reef passes and adjacent near reef currents has important consequences for fish aggregation, trophic dynamics, larval dispersal and connectivity among reefs. The current study was a primary component to link fish aggregation behaviour to local hydrodynamics. However, these small-scale reef passes are common within coral reef habitats (Hopley 1982) and the biological significance of these areas has probably been underestimated.

CHAPTER 3: Relative influence of environmental factors on the timing and occurrence of multi-species coral reef fish aggregations

3.1 Abstract

Reef configuration and hydrodynamics were identified as the principle physical drivers behind coral reef fish aggregations on a mid-shelf patch reef in the northern section of the Great Barrier Reef (-16.845°, 146.23°). The study was carried out over a six-year period at a small reef pass on the oceanic margin of the northern Great Barrier Reef. Over this period (February 2006 – December 2012) tidal state, moon phase and surface seawater temperature were monitored. The timing of sampling was organised to assess variation in physical environment at daily, monthly, seasonal and annual time scales. Over these time scales, temporal patterns of occurrence of 10 species of coral reef fish from 5 families representing 5 defined trophic groups were monitored. The study incorporated 1,357 underwater visual census counts involving 402,370 fish and these estimates were collated with data on tidal state, water temperature, lunar and seasonal periodicity. Aggregated boosted regression trees analysed the univariate responses of fish abundance and species richness to the variation in the physical environment of the reef pass. Flood tides or when water flows from open water through the pass and into the Moore Reef lagoon had 2.3 times as many fish and 1.75 times as many species compared to counts made on ebb tides. Fish abundance was highest in late winter and spring months (Austral calendar), but notably when water temperatures were below the 6-year study mean of 27°C. Multivariate regression trees and Dufrêne-Legendre indicator predicted 4 out of 10 times the occurrence of all 10 species at any temporal scale ranging from hours to years. Flood tides were the principle driver underlying the occurrence of all 10 species regardless of their trophic classification and produced distinct seasonal assemblages, indicative of fishes aggregating to forage and reproduce.

3.2 Introduction

A typical feature of large reef fish behaviour is the formation of aggregations for the purposes of reproduction and feeding at characteristic sites in coral reef systems. These behaviours are frequently observed in reef passes, which provide abrupt transitions between productive shallow benthic reef habitats and open ocean ecosystems (Johannes 1978; Moyer 1989; Colin and Bell 1991; Sancho et al. 2000a; Mourier et al. 2016). Although tropical open oceanic environments are regarded as largely oligotrophic, they support large populations of macroplanktonic organisms including gelatinous zooplankters which make a substantial contribution to the flux of carbon and remineralization processes on adjacent reefs (Henschke et al. 2016). Oceanic waters adjacent to reefs are enhanced by hydrodynamic processes that induce upwelling of nutrient rich water (Andrews and Gentien 1982; Wolanski et al. 1988; Brinkman et al. 2002; Andutta et al. 2013). In addition to the transport and redistribution of potential food items for planktonic and nektonic feeding reef fishes, reef passes are also associated with current systems that may redistribute eggs and developing larvae of spawning reef fishes (Johannes 1978; Hamner et al. 2007; Choat 2012; Dumas et al. 2012). To date, much of the interest in reef fish-aggregations has focused on the significance of reproductive events and the role of the physical environment in determining the timing and intensity of spawning (Karnauskas et al. 2011; Donahue et al. 2015; Sakaue et al. 2016). Recent studies have noted the critical importance of environmental influences, especially temperature, on initiating reproductive activities and the need to monitor variation in the physical environment at locations that support aggregative behaviours (Asch and Erisman 2018).

There is extensive literature on the biological and environmental factors driving the formation of spawning aggregations (Sadovy de Mitcheson and Colin 2012). Also, the formation of aggregations to exploit food items that are concentrated in reef passes contemporaneously with spawning aggregations has been described (Colin 2012; Hartup et al. 2013; Mourier et al. 2016). However, foraging aggregations may develop from the environment created by the interaction of reef geomorphology and hydrodynamic forces, that concentrate plankton, nekton and nutrients in reef passes (Wolanski and Hamner 1988; Wolanski et al. 1988; Dumas et al. 2012). The importance of environmental variables in determining the timing of aggregations has been noted in recent studies, such as current direction, time of day (Sakaue et al. 2016) and temperature (Asch and Erisman 2018), with respect to spawning events. However, given the complexity of reef pass environments an understanding of the triggers for the formation of fish aggregations requires a more comprehensive knowledge of the temporal pattern of environmental variation in reef passes. Hydrodynamic processes operate on a variety of timescales. These range from daily tidal cycles to monthly lunar cycles in the strength of tidal flows, seasonal trends where the environment is modified by changing temperatures and prevailing winds, through to inter-annual variation reflecting episodic trends including El Niño-Southern-Oscillation (ENSO) events. For this reason, long-term environmental monitoring at aggregation sites is critical. Moreover, such data sets are necessary for modelling responses in fish aggregation dynamics to climate change (Damgaard and Weiner 2017).

The present study adapts a widely accepted definition for fish spawning aggregations (Domeier 2012) and defines fish aggregations as: a repeatable gathering of conspecific fish at a predictable time and space with a four-fold increase in density compared with non-aggregating times. However, in nature many fish aggregations sites are used by many species, and such aggregations include a variety of trophic groups and interactions. These include egg predators exploiting the products of spawning aggregations (Johannes 1978; Colin 2012; Fraser and McCormick 2014), and large aggregations of reef fish that represent prey for larger predators which also congregate at such sites (Sancho et al. 2000a; Mourier et al. 2016; Robbins and Renaud 2016). Finally, through defecation, reef-fish aggregations can subsidise nutrient inputs to reef ecosystems (Archer et al. 2015; Shantz et al. 2015) or directly augment food resources (Robertson 1982). Clearly, fishes can form aggregations for several reasons that are not necessarily mutually exclusive, including mate selection, spawning, and foraging.

The goal of the present study was to examine the extent to which key features of the hydrodynamic environment predicted the occurrence of 10 fish species from five distinct trophic groups at a fish aggregation site over a six-year period. The hydrodynamic features chosen for this study ranged in temporal scale from daily (tidal regimes) too seasonal (water temperature) through to inter-annual periodicities. Using multivariate hierarchical analysis, we examined the temporal changes in fish assemblages at a fish aggregation site and behavioural observations over time enabled predictions to be advanced regarding the drivers for aggregations at particular times. We predicted from research at other aggregation sites that: a) aggregation of fishes for the purpose of reproduction would have a seasonal signature, synchronised by lunar and tidal cues to take advantage of strong currents that advect gametes away from reef heterotrophs (Johannes 1978; Johannes et al. 1999; Colin 2012); b) tidal inputs of planktonic and smaller nekton may result in a consistent presence of planktivores and piscivorous fish predators (Hobson and Chess 1978; Hamner et al. 1988) and c) on short time scales reversals of the daily tidal cycle would be the most potent source of variation, with planktivores and their predators exploiting the incoming tidal flow, and reproductive aggregations and egg predators associated with the outgoing flow (Claydon 2004; Hamner et al. 2007). Because of the requirement of intensive sampling at limited locations, long-term studies involve a trade-off between temporal and spatial monitoring. While marine macroecology has benefitted from the analysis of spatially extensive data sites, inferences about processes are best evaluated by dynamic data collected over important temporal scales (Damgaard and Weiner 2017) and the latter was the focus for the current study. The long-term monitoring of this single location yielded a unique and detailed perspective of the significant temporal drivers of fish abundance at a tropical multi-species fish aggregation site at the scales of years, seasons, lunar phases and tides.

3.3 Methods

3.3.1 Study site

The study site (-16.845°, 146.23°), was situated approximately 55 km east of Cairns on the north-western side of Moore Reef, a mid-shelf patch reef located in the northern section of the Great Barrier Reef (GBR), Australia (Fig. 3.1A). Moore Reef has a crescent shape, characterised by an extensive reef flat on the windward margins, with a well-developed reef front that semi-encloses a lagoon dominated by isolated patch reefs (Fig. 3.1B). Several reef passages dissect the reef flat at the north-western corner of Moore Reef (Fig. 3.1C). The fish aggregation site (FA) was near a commercial tourism site that operates off a platform on the lagoon side of Moore Reef (~ 350 m direct line; Fig. 3.1C), which facilitated the means to perform underwater visual census counts (UVC) at the FA regularly. The Great Barrier Reef Marine Park Authority (GBRMPA) have classed Moore Reef as Marine National Park Zone. The commercial tourism company operates under GBRMPA permit G10/33331.1. The research carried out in this study was non-evasive but was conducted under GBRMPA research permit G12/35200.1. The UVC counts were conducted from February 2006 to November 2012. The larger reef passage is ~330 m in length, 60 to 250 m in width and 14 to 22 m in depth with a north to south orientation. This passage contained the FA, which was situated on the north-west aspect of the passage and covered an area of ~ 3,500 m^2 (Fig. 3.1C). Habitats within the FA included a reef crest and reef slope, mainly dominated by tabular and digitate hard corals. The reef fronts, on both the outer and inner side of the passage also included some groove and spur morphology and both slopes terminated at ~ 20 m depth into a sand-rubble substratum dotted by isolated coral patches (Fig 3.1B). On 3 February 2011, a large tropical cyclone (“Yasi”, Category 5 strength) destroyed 95% of the tabular corals at the FA.

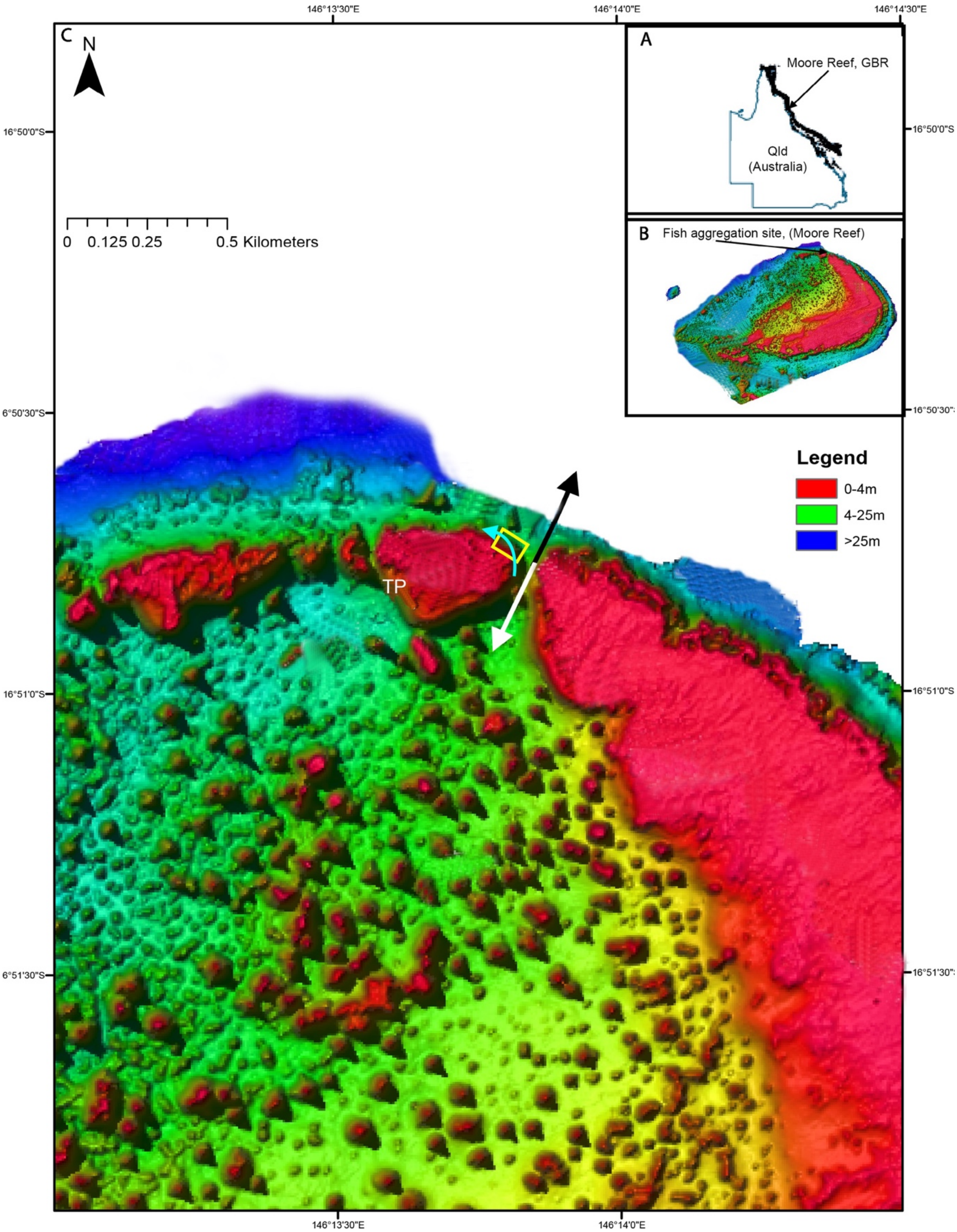


Fig 3.1. Site map of Moore Reef fish aggregation site: A) The location of Moore Reef in the Great Barrier Reef and B) the location of the fish aggregation site at Moore Reef with C) showing detailed bathymetry of reef scape at the Moore Reef fish aggregation site. The direction of flows through the passage are detailed by the white (flooding) and black (ebbing)

arrows. The letters (TP) refer to the location of a commercial tourism platform and the underwater visual census path is represented by the light blue arrow passing through the fish aggregation area (yellow box). The lidar (light imaging, detection and ranging) bathymetry data of Moore Reef was courtesy of Dr Robin Beaman, James Cook University.

3.3.2 Environmental variables

Outer reef fronts and passages experience changing environmental conditions on a daily and seasonal scale (Lowe and Falter 2015). The information on several environmental variables was collected between February 2006 and November 2012. These variables included tidal state, moon phase and surface seawater temperature (SST) (for data source information see Appendix B Table B.1). Two of the variables, water current direction and moon phase, require further explanation. The Moore Reef passage was similar to other reef passages such as the Ribbon Reefs in the northern GBR (Wolanski 1994) and the Marshall Islands in the central Pacific (Colin and Bell 1991), in that it experiences strong alternating currents generated by tides. At the study area, the flood tide causes water to flow onto the reef and lagoonwards, while the ebbing tide forces water to flow out through the passage to the Coral Sea (Fig. 3.1C). Moon phase has been represented as a fraction of luminosity, which is a quantitative way of describing the moon's phase (USNO 2023). The measurement ranges from zero to one. Zero described the new moon phase, while 1 described the full moon phase and the first and last quarters were represented by 0.5. First and last quarter can be distinguished by noting whether the fraction illuminated was increasing or decreasing. First quarter occurred when the fraction illuminated was increasing (moon waxing; in evening sky) and last quarter occurred when the fraction illuminated was decreasing (moon waning; in morning sky) (USNO 2023).

3.3.3 Species richness and abundance estimates

A pilot study was conducted at the study site from February 2005 to January 2006, during which time a species list of larger fish (>20 cm total length) that occur at the site was compiled (Appendix B Table B.2). A subset of 10 common species from 5 families was selected for this quantitatively descriptive study because they formed conspicuous aggregations compared to non-aggregating times and displayed a variety of foraging modes

(Table 3.1). These included pelagic predators (Carangidae), predators on reef-associated fishes (Lutjanidae), egg predators (*Macolor niger*) and planktivorous species (Acanthuridae) to represent fish exploiting food characteristics of the outer reef fronts. Species representing predators on benthic invertebrates (Lethrinidae, Haemulidae and some Carangidae) were selected to potentially represent fish exploiting the outflowing currents of a reef pass to reproduce.

Table 3.1. The 10 species of coral reef fish surveyed between February 2006 and November 2012 at the fish aggregation site, Moore Reef, classified into 5 broad trophic groups.

Trophic group	Family	Species	Reference source
Predators of small fish	Carangidae	*Caranx sexfasciatus*	(Hiatt and Strasburg 1960; Wright et al. 1986; Blaber et al. 1990; Farmer and Wilson 2011)
	Lutjanidae	*Lutjanus bohar*	(Farmer and Wilson 2011)
Predators of benthic invertebrates	Carangidae	*Trachinotus blochii*	(Lieske and Myers 2001)
	Haemulidae	*Plectorhinchus lineatus*	(Lieske and Myers 2001)
	Lethrinidae	*Lethrinus nebulosus*	(Carpenter and Allen 1989; Farmer and Wilson 2011)
	Lethrinidae	*Lethrinus olivaceus*	(Carpenter and Allen 1989) (also has consuming fish and cephalopods)
	Lethrinidae	*Monotaxis grandoculis*	(Hiatt and Strasburg 1960; Hobson 1974; Carpenter and Allen 1989)
Planktivores	Acanthuridae	*Naso annulatus*	(Choat et al. 2002)
Egg predators	Lutjanidae	*Macolor niger*	(Craig 1998; Colin 2012) (Appendix B Video B1)
Omnivores	Acanthuridae	*Acanthurus dussumieri*	Sand grazers (Barlow 1974), Detritivore (Choat et al. 2004), grazing herbivore (Basford et al. 2015), planktivore and faecal scavenger (Appendix B Table B.2 & Table B.2)

The abundance of the selected aggregating species was estimated 4 to 5 days a week for 6 years by the senior author. These UVC counts followed the same census path, starting at the mouth of the channel and moving north around the outer slope of the tourist pontoon reef (Fig. 3.1C). This survey was conducted daily between 1400 h and 1500 h while on snorkel. Although the sampling design was restrictive in its focus on fish abundance at different times of day. The high frequency study was designed to gather valuable information on the tidal, lunar and seasonal influence on fish aggregation presence. Notes were also taken during census on the trophic or reproductive behaviour of fish present (Appendix B Table B.2). Foraging behaviour was observed as the direct consumption of prey items, and with planktivores feeding behaviour was associated with the up and down movement in the water column. Courtship behaviour, such as specialised colour changes and chasing were identified from published examples (Robertson 1983; Thresher 1984; Sadovy de Mitcheson and Colin 2012).

3.3.4 Caesionidae abundance

Caesionidae represents a large component of outer slope reef fish communities on mid-shelf reefs in the GBR (Williams and Hatcher 1983). These fish are small, mobile, can form dense aggregations, feed on plankton and have been considered too difficult to count accurately in UVC studies (Hamner et al. 1988) and therefore were omitted from the original monitoring programme. Three of the five species of Caesionidae were known to form foraging aggregations at the fish aggregation site (Appendix B Table B.2). All three of these species were observed aggregating daily on flood and absent on ebb tidal flows (EEF unpublished data). To assess whether there were temporal changes in the abundance of these planktivores at the FA, a GoPro video camera was fixed to a star picket in 9m depth of water in approximately the centre of the FA. During October 2013 and February 2014, two days in each month were selected for videotaping. Preliminary data analysis indicated that the months October and February represented the highest and lowest abundance and species richness of aggregating fishes respectively. The two days in each month coincided with a flood and ebb tide phase, and on each day the camera recorded 4 hours of video footage. A 40-minute video from each four-hour video was selected that represented the middle of the tide phase. A random number generator was used to select 10 screen shots from each 40-minute video. The selected screen shots were used with the software Event Measure (SeaGIS

2022) to accurately count the abundance of caesionids present at up to 6m from the camera. The limited sampling design and technique was considered adequate to quantify the presence/absence of caesionids in relation to tidal phase. Given that these fish are ubiquitous on flood tides at the fish aggregation site and difficult to count visually, counting fish from screen shots was considered a more accurate representation of presence absence.

3.3.5 Statistical analyses

The data comprised 1,357 UVC counts at the FA between 1 February 2006 and 29 of November 2012. There were 402,370 individual fish from 10 species in this dataset. Date, month and moon phase were available for all counts, and SST was measured for all but 21 samples. We performed univariate and multivariate analyses on untransformed fish counts using two types of regression trees. Regression trees can be summarised in ways that give powerful ecological insight by representing complex information in a visual format that can be easily interpreted (De'ath 2002; Ouellette et al. 2012).

The univariate responses of species richness and raw fish counts of the 10 selected species were modelled using aggregated boosted regression trees (ABT) to summarise the relative influence of major predictors and to interpret interactions (De'ath 2007; Elith et al. 2008; Fabricius and De'ath 2008). The ABT models included the main effects and up to three-way interactions amongst the full suite of five explanatory covariates (tide, moon phase, month, decimal date, and SST), all predictors and up to third-order interactions. No monotonic constraints were applied to the functional form of selected individual predictors. Five methods were used to interpret and compare the models as per Fabricius and De'ath (2008). The best predictive models were determined by comparing the "prediction error" (PE) expressed as a percentage of models with varying levels of interactions.

Multivariate prediction and regression trees (MRT) were used to model the abundance of all 10 fish species in response to the most influential explanatory covariates identified in the univariate models. The overall fit of the model was the "relative error" (RE), or fraction of variance not explained by the tree (De'ath 2002). The RE over-estimates the performance of the tree when predicting for new data, so predictive accuracy was estimated from five-fold cross validation (the "cross-validated relative error"; CVRE). The most parsimonious models selected were the ones that simultaneously minimise RE and CVRE (De'ath 2002; Elith et al. 2008). The performance of the final model was assessed by comparing the best MRT with an unconstrained clustering of the same distance matrix with the same numbers of terminal nodes (clusters). If the unconstrained cluster analysis accounts for substantially more of the species variation than an MRT analysis, it was likely that additional, unmeasured covariates were responsible for the difference in explained species variation (De'ath 2002).

Each node of the tree can be defined by the multivariate mean of its samples, the predictors that define it, the number of samples that were grouped there, and by Dufrêne-Legendre species indicators (DLI). For a given species and a given tree node, the DLI was defined as the product of the mean species abundance occurring in the group divided by the sum of the mean abundances in all other groups ("specificity" A), times the proportion of sites within the group where the species occurs ("fidelity" B), multiplied by 100 (Dufrêne and Legendre 1997; De Cáceres and Legendre 2009; De Cáceres et al. 2010). Each species can be associated with the tree node (assemblage) where its maximum DLI value occurred. The index distinguishes between ubiquitous species that dominate many nodes in absolute abundance and species that occur consistently within single nodes but have a low abundance (De'ath 2002). Finally, the point-biserial correlation coefficient was used for determining the ecological preferences of species among the set of alternative tree nodes or node combinations. This was a generalisation of the Pearson's phi coefficient (De Cáceres et al. 2008). All analyses used the R open source libraries vegan, abt, mvpart, mvpartWRAP and indicspecies (Borcard et al. 2011).

3.4 Results

3.4.1 Abundance

Abundance patterns of the 10 species varied over the six-year sampling period, primarily in association with five environmental variables “tide”, “month”, “SST”, “date”, and “moon phase”. Partitioning of the five environmental variables demonstrated that tide was the dominant influence (64.8%), followed by month (19%) and SST (11%). Date, representative of among-year variation, and moon phase (frequently associated with reproductive periodicity), showed a minor influence (4% and 0.9%), respectively (Table 3.2 and Fig. 3.2A). Permutation tests showed the effects of dropping these minor influences had little effect on PE, but omitting tide caused a 1.5-fold increase in PE in relation to the full model (Table 3.2). Partial dependency (effects plots) showed that UVC counts made at the aggregation site on flood tides had 2.3 times as many fish as counts made on ebb tides (Fig. 3.2B).

Table 3.2. Relative influences (%) of environmental variables on total fish abundance and species richness (10 selected species) in underwater visual census counts at the Moore Reef fish aggregation site. The top row shows the prediction error (PE%) of the best aggregated boosted regression tree models. Subsequent rows show the results of permutation tests (n=1000 permutations) and the increase in PE% by dropping each variable, relative to the full model.

	Total Fish Abundance			Species Richness		
	Influence	**PE%**	**P**	**Influence**	**PE%**	**P**
abt full model		44.8			48.29	
Tide	64.82	150.7	<0.001	67.474	136.65	<0.0001
Month	18.92	27.50	<0.0001	11.098	12.69	<0.0001
Temperature °C	11.08	14.89	<0.0001	13.278	14.45	<0.0001
Decimal Date	4.23	4.01	<0.0001	6.96	6.81	<0.0001
Moon phase	0.94	0.50	<0.0001	1.1889	0.39	0.025

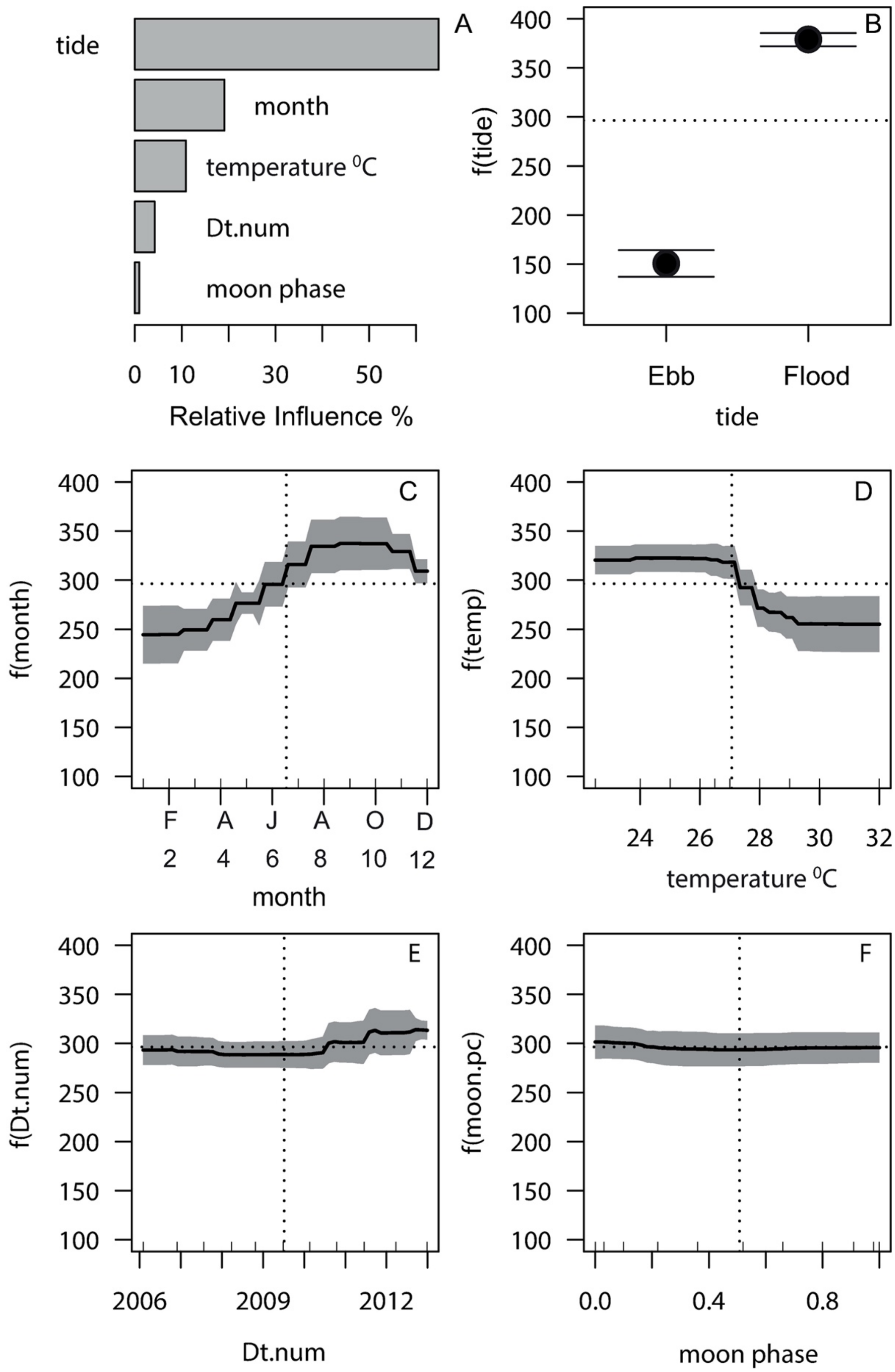


Fig. 3.2. Partial dependency plots for the univariate response of pooled fish abundance from the best aggregated boosted regression tree model: A) Relative influences of covariates on pooled fish abundance (10 selected species) in underwater visual census samples at Moore

Reef fish aggregation. Partial dependency plots of fish abundance on B) tidal direction, C) month, D) surface seawater temperature, E) decimal date (Dt.num) and F) moon phase, show the response of abundance as a function f () of each predictor, with the influence of all other predictors held to a constant. Shading around the response lines is 2 standard errors. Horizontal dotted lines show the mean fish abundance across all counts. Vertical dotted lines show the mean value for each predictor. Rugs on the x axes show the spread of sampling in ten-percentiles within the range of each predictor.

Fish abundance patterns of the 10 target species at the fish aggregation site were predictable. Models of main effects with 3-way interactions had a PE (44.8%) lower than that observed with models including 2-way interactions (47.6%), equating to an R^2 of 55.2% in explaining variance in total fish abundance. There was evidence of a recurring pattern of higher fish abundance in the second half of the year (the austral spring/summer) (Fig. 3.2C). This was heightened when SSTs were below the long-term mean (Fig. 3.2D), indicating the influence of among-year variation in temperature. There was a trend in increasing fish abundance post-mid 2011 (Fig. 3.2E), but lunar periodicity had no influence on fish abundance (Fig. 3.2F). Partial interaction plots showed that UVC samples from cooler seawater temperatures in the period August-November had higher than average fish abundance (Fig. 3.3A). Flooding tides had higher abundance than ebbing tides in all months, but that difference was greatest in the second half of the year (Fig. 3.3B).

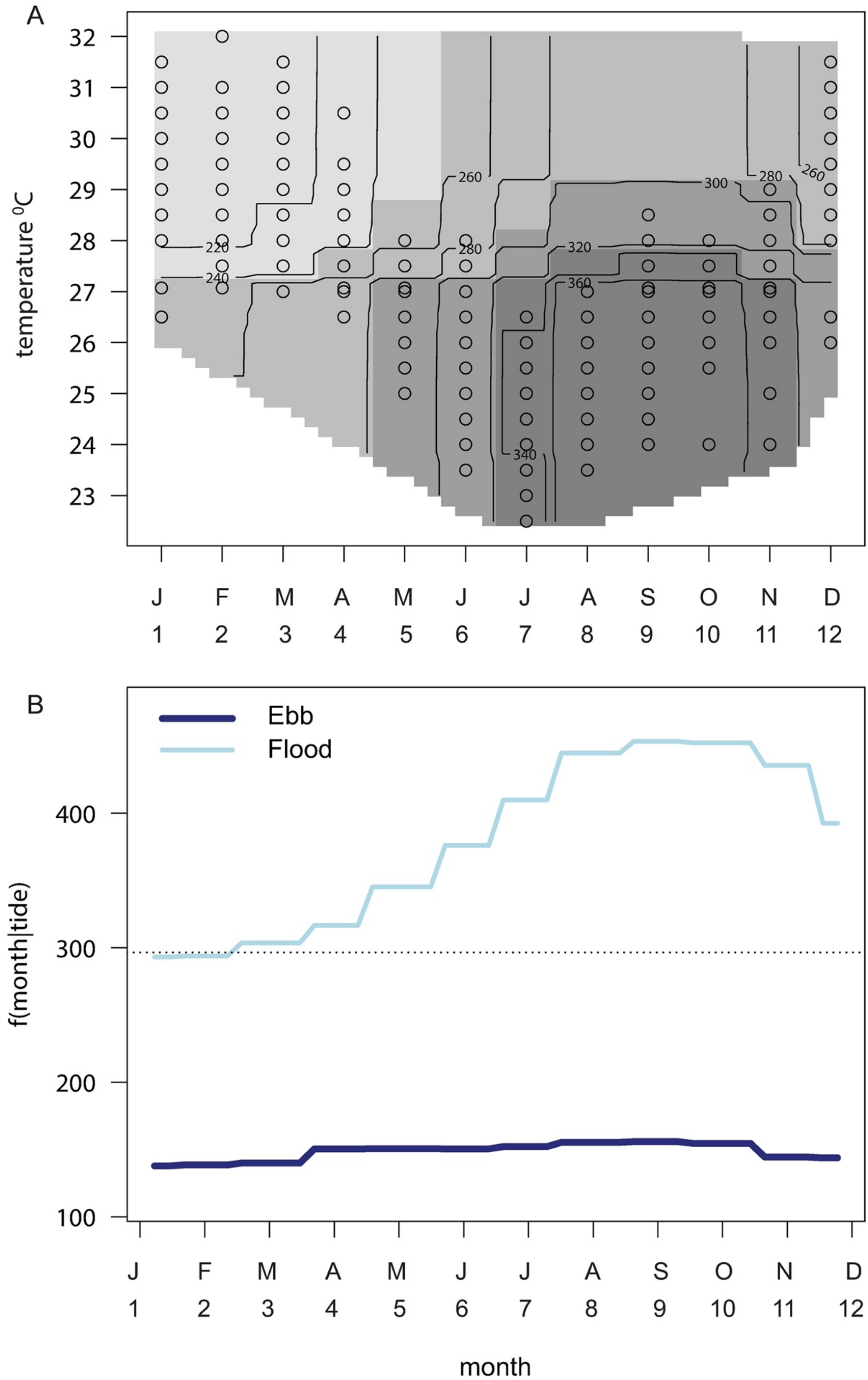


Fig. 3.3. Partial interaction plots from the best aggregated boosted regression tree model for pooled fish abundance (10 selected species): A) different seawater temperatures at different months and B) as a function f () of months given tidal direction. The contours of fish

abundance in A) show the spread of temperatures sampled in each month as ten-percentiles (open circles) and the increasing grey scale represents increasing fish abundance.

3.4.2 Species richness

The increase in total fish abundance at the fish aggregation site was driven by an increase in species richness. However, the species richness model of the 10 selected species was different to the abundance model in the order of dominant variables influencing the observed patterns. SST (13.3%), not month (11%), was the second dominant variable influencing the number of species at the fish aggregation site (Table 3.2 and Fig. 3.4A). Tide had the highest influence on species richness (67.5%), with decimal date (7%), and moon phase (1.2%) being the least influential (Table 3.2 and Fig. 3.4A). Partial dependency (effects plots) showed that UVC counts made at the aggregation site on flood tides had about 1.75 times as many species counts made on ebb tides (Fig. 3.4B). Species richness was higher in cooler months (Fig. 3.4C) and notably when temperatures were below the long-term mean (Fig. 3.4D). This was indicative of among-year variation in seasonal temperatures, and a yearly effect was noted in that species richness decreased under the mean from 2011 (Fig. 3.4E). Overall, lunar periodicity had no influence on species richness (Fig. 3.4F).

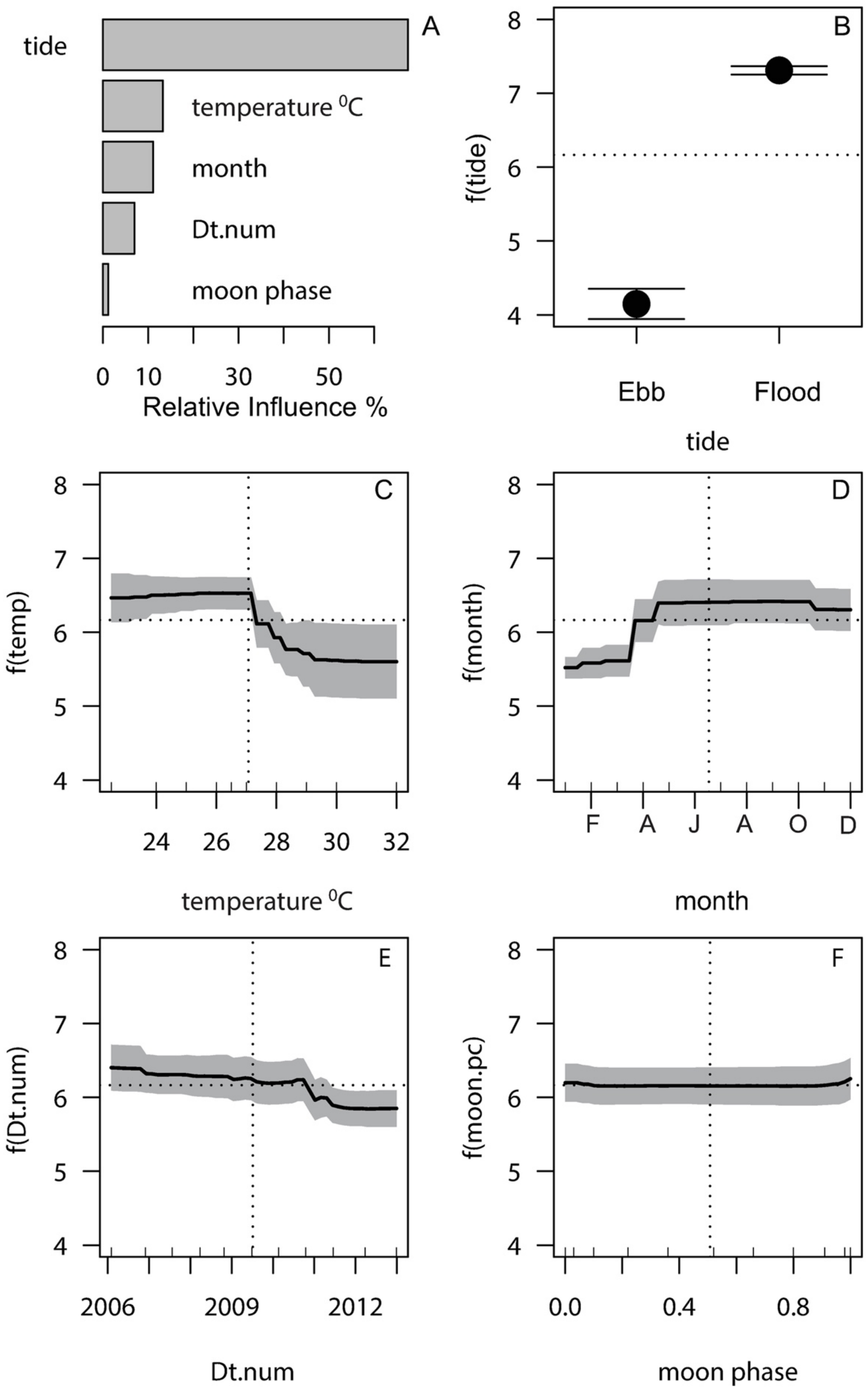


Fig. 3.4. Partial dependency plots for the univariate response of species richness from the best aggregated boosted regression tree model: A) Relative influences of covariates on

species richness in underwater visual census samples at Moore Reef fish aggregation site. Partial dependency plots of species richness (10 selected species) on B) tidal direction, C) surface seawater temperature, D) month, E) decimal date (Dt.num) and F) moon phase show the relationship of richness as a function f () of each predictor, with the influence of all other predictors held to a constant. Shading around the response lines are 2 standard errors. Horizontal dotted lines show the mean richness across all counts. Vertical dotted lines show the mean value for each predictor. Rugs on the x axes show the spread of sampling in ten-percentiles within the range of each predictor.

The best model, with 3-way interactions, had a relative PE of 48%, equating to an R^2 of 52% in explanation of the variance in species richness. Models of main effects (PE=55.7%) and 2-way interactions (PE=50.7%) had higher prediction errors. Permutation tests showed that the effects of dropping moon phase from the model had no significant effect on PE, but omitting tide caused a 1.3-fold increase in PE in relation to the full model (Table 3.2). The error in the model without tidal state was 1.14 times the overall variance in species richness. The interactions among the covariates of SST, month and tide were interpreted from partial interaction plots (Fig. 3.5). Species richness was higher than average with cooler SSTs in the period May-October (Fig. 3.5A), but higher richness on flooding tides in all months (Fig. 3.5B).

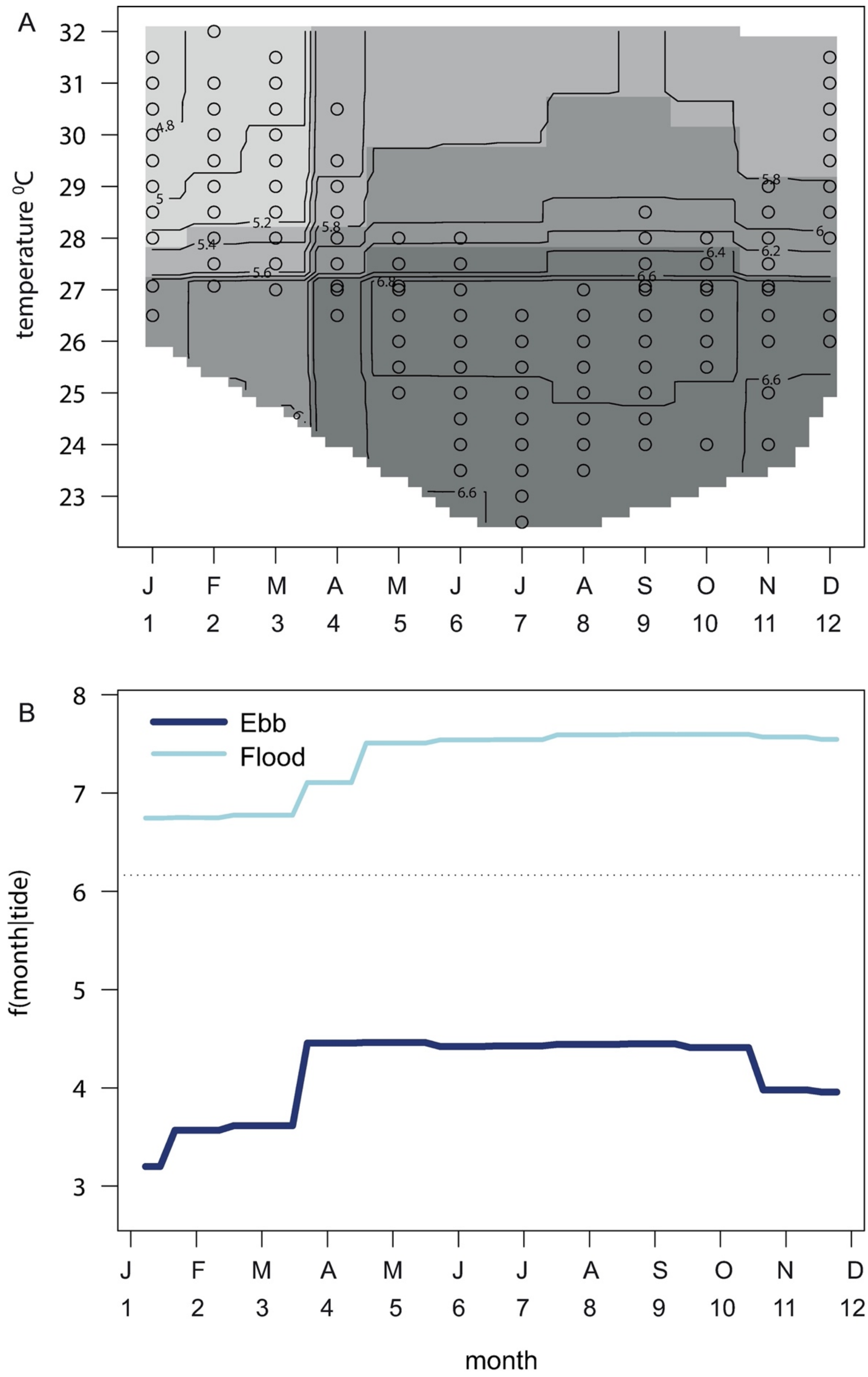


Fig. 3.5. Partial interaction plots from the best aggregated boosted regression tree model for species richness: A) different surface seawater temperatures at different months and B) as a function f () of months given tidal direction. The contour plot in A) shows the spread of

temperatures sampled in each month as ten-percentiles (open circles) and increasing grey scale with increasing species richness.

3.4.3 Assemblage structure

Analysis of the multi-species abundance data produced recognisable assemblages of reef fishes. These assemblages displayed fidelity and predictability with respect to the five environmental variables that were incorporated into MRT. The best performing MRT split the data into eight assemblages on tide, month and SST when moon phase was included (Fig. 3.6A). The substantial environmental influence on fish abundance patterns at the fish aggregation site was tide. Whether individual fish species occurred throughout the year or were seasonally represented, all 10 species, regardless of their trophic classification (Table 3.1), were more abundant on the flood side of the regression tree. The left-hand branches were the counts made on ebb tides, with low abundance of all species (Fig. 3.6A). The first split of the MRT explained a third of the tree variance, 14.4 % of the 41.2 % (Table 3.3).

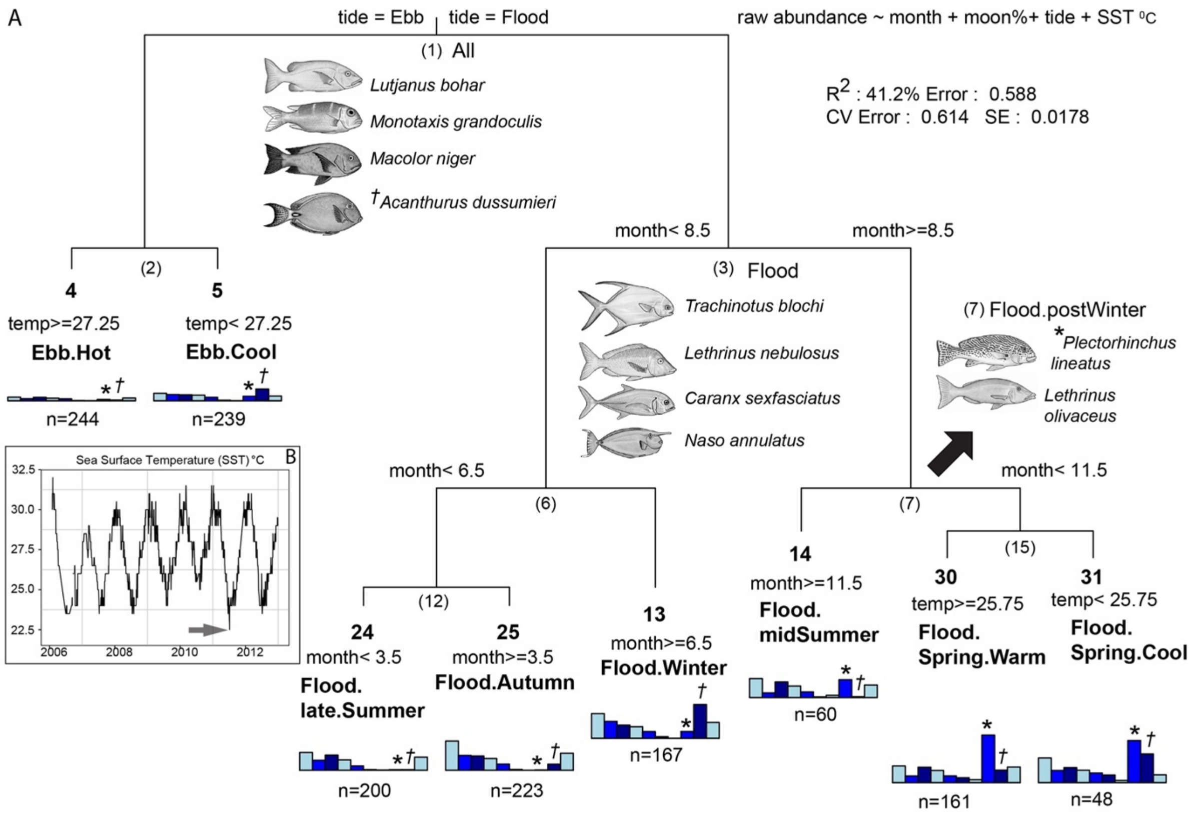


Fig. 3.6. Multivariate regression tree for 10 species of fish from Moore Reef fish aggregation site: A) The best tree structure from a multivariate regression tree analysis of the counts of 10 species predicted by month, surface seawater temperature, tidal direction, and moon phase. Histograms on the terminal nodes ("leaves") show the abundance of each species and the number of underwater visual census samples (n). The bars on the histograms, from left to right represent 1. *Trachinotus blochii*, 2. *Caranx sexfasciatus*, 3. *Lutjanus bohar*, 4. *Monotaxis grandoculis*, 5. *Macolor niger*, 6. *Lethrinus nebulosus*, 7. *Lethrinus olivaceus*, 8. *Plectorhinchus lineatus* (indicated by *), 9. *Acanthurus dussumieri* (indicated by †), 10. *Naso annulatus*. The node numbers are in boldface type for leaves and given in brackets for higher nodes. The DLI characterising the labelled nodes and leaves are an index of fidelity and specificity of a species to a node. B) annual variation in surface seawater temperature, with the arrow marking the lowest recorded temperature during the 6-year study period.

Table 3.3. Summary of the multivariate regression tree (Fig. 3.6). The overall amount of variation in species abundance in 1,357 underwater visual census samples (Species % variance), the species-specific variation explained by the MRT (Tree %variance), the node number and threshold values for the splits (Splits), and the individual and overall variation in species abundance explained by each split (Split % variance).

Splits	**1**	**2**	**3**	**6**	**12**	**7**	**15**	**Tree**	**Species**
Species	**(Tide=Ebb)**	**(Temp=27.25)**	**(Month=8.5)**	**(Month=6.5)**	**(Month=3.5)**	**(Month=11.5)**	**(Temp=25.75)**	**%variance**	**%variance**
Trachinotus blochii	4.8	0.09	0.29	0	0.72	0	0.12	6.04	16.2
Caranx sexfasciatus	1.01	0.11	0.43	0.12	0.13	0.03	0.06	1.87	6.79
Lutjanus bohar	1.65	0.04	0.01	0.01	0	0	0	1.72	3.71
Monotaxis grandoculis	0.93	0.06	0.01	0	0.01	0	0	1.01	2.25
Macolor niger	0.21	0.01	0.02	0.01	0.02	0.01	0.02	0.3	0.95
Lethrinus nebulosus	0.06	0	0.11	0	0	0.06	0.01	0.25	1.53
Lethrinus olivaceus	0.01	0	0.06	0	0	0	0	0.08	0.3
Plectorhinchus lineatus	2.53	0.06	13.82	0.25	0	1.99	0.06	18.71	28.78
Acanthurus dussumieri	0.67	0.77	0	5.78	0.16	0.58	0.51	8.47	15.97
Naso annulatus	2.48	0.02	0.03	0	0.09	0	0.12	2.75	23.52
Split % variance	14.35	1.17	14.79	6.19	1.14	2.66	0.9	41.2	100

The MRT model illustrated seasonal periodicities in fish abundance by producing distinct seasonal assemblages on the flood side of the tree categorised by month with the spring assemblage further divided into warm and cool, split at the threshold value of 25.7°C (Fig. 3.6A). Monthly temperature ranges varied (Fig. 3.3A and Fig. 3.5A), which was reflective of inter-annual variation in temperatures, with the lowest temperature recorded in 2011 and the highest in 2006 (Fig. 3.6B). Although no single species was an indicator for any leaf of the tree, all indicators occurred higher in the tree at combinations of nodes and branches (Fig. 3.6A and Table 3.4). This apparent discrepancy between the seasonality of abundance, but the lack of characteristic indicators for terminal seasonal leaves, may be due to the ambitious nature of the MRT. For example, *Acanthurus dussumieri* was a ubiquitous indicator at the root node, but this species showed clear peaks in abundance when seawater temperatures were cooler, on both the flood and ebb side of the tree (Fig. 3.6A). This was supported by the relatively high point biserial coefficient of association of 0.69 with tree leaves 13 (“Flood.Winter”) and 31 (“Flood.Spring.Cool”) (Table 3.5) and the lack of this species from the summer assemblages (Fig. 3.6A).

Table 3.4. The Dufrene-Legendre Indicator value for each of the 10 selected species at the Moore Reef fish aggregation site. The DLI is the product of “specificity” (A) and “fidelity” (B) and the nodes for which each species had a maximum in DLI are shown with probability values p.

Splits (Node)	**Species**	**A**	**B**	**DLI**	**p**
All (1)	*Lutjanus bohar*	0.97	0.92	0.89	0.001
All (1)	*Monotaxis grandoculis*	0.97	0.91	0.88	0.001
All (1)	*Macolor niger*	0.96	0.89	0.85	0.001
All (1)	*Acanthurus dussumieri*	0.98	0.85	0.83	0.001
Flood (3)	*Trachinotus blochii*	0.92	0.91	0.84	0.001
Flood (3)	*Lethrinus nebulosus*	0.96	0.85	0.81	0.001
Flood (3)	*Caranx sexfasciatus*	0.89	0.82	0.73	0.001
Flood (3)	*Naso annulatus*	0.92	0.6	0.55	0.001
Flood.post.Winter (7)	*Plectorhinchus lineatus*	0.89	0.93	0.83	0.001
Flood.post.Winter (7)	*Lethrinus olivaceus*	0.96	0.43	0.41	0.001

Each node and terminal leaf of the tree was defined by the predictors, the number of samples that were grouped there, and by DLI in Fig. 3.6A. Two species *Lethrinus olivaceus* and *Plectorhinchus lineatus*, both predators of benthic invertebrates, also showed predictable seasonal patterns of occurrence. Both *L. olivaceus* and *P. lineatus* had the highest DLI with the combination of leaves 14, 30 and 31 on the right hand branches in the MRT with node 7 ("Flood.post.Winter"). The "specificity" (A) of 0.96 for *L. olivaceus* at this node represented a 96% probability that any particular UVC count recording *L. olivaceus* would occur in this node. However, the "fidelity" of 0.43 showed that *L. olivaceus* occurred in only 43% of UVC samples in this node. In contrast, *P. lineatus* had both high specificity and a high fidelity (93% of samples in this node) (Table 3.4). The point-biserial coefficient of association between each species and nodes showed a relatively high association (0.73) between the abundance of *P. lineatus* and the node 15 "Flood.Spring" and leaves 30 and 31 of the MRT, regardless of differences in spring water temperatures (Table 3.5 and Fig. 3.6A).

Table 3.5. The point-biserial correlation coefficient of association (phi) between species and tree node.

Splits (Node)	Tree Leaves	Species	phi	p
Flood (3)	13+14+24+25+30+31	*Lutjanus bohar*	0.63	0.001
Flood (3)	13+14+24+25+30+31	*Monotaxis grandoculis*	0.60	0.001
Flood (3)	13+14+24+25+30+31	*Trachinotus blochii*	0.48	0.001
Flood (3)	13+14+25+30+31	*Macolor niger*	0.45	0.001
Flood (3)	13+14+24+25+30	*Naso annulatus*	0.26	0.001
Flood (3)	13+24+25+31	*Caranx sexfasciatus*	0.46	0.001
Flood (3)	14+30+31	*Lethrinus olivaceus*	0.45	0.001
Flood.Spring (15)	30+31	*Plectorhinchus lineatus*	0.73	0.001
Flood.Spring (15)	30+31	*Lethrinus nebulosus*	0.39	0.001
Flood (3)	13+31	*Acanthurus dussumieri*	0.69	0.001

The fish assemblages of all ten species on tidal or seasonal timescales were predictable. The MRT had a prediction error of 61% and a relative error of 58.8% equating to an explanation of 41.2% of the multivariate distance variation. This means that the model was able to predict 4 out of 10 times, the occurrence of all 10 species at any temporal scale, ranging from hours to years. A comparison of this MRT partitioning with an unconstrained clustering of the species for all tree sizes from 1 to 7 splits (8 leaves) showed a consistently lower performance of the MRT (by approximately 50%) in explaining variation in the assemblage structure. An unconstrained clustering with 8 groups had an error of 29.5%, nearly half of that for the MRT with 8 leaves (58.8%). This implied there were other environmental covariates, and perhaps some sampling biases, that had not been included as predictors in the MRT model. Although, there was not a close match between the species contributing most to the MRT and the overall variation in abundance. For example, *P. lineatus* comprised 28.8% of the variation in UVC counts and contributed nearly half (18.7%) of the distance variation explained by the MRT (R^2=41.2%), yet the same ratio for *N. annulatus* was 23.5%: 2.8%, which translates to explaining only 7% of the distance variation explained by the MRT (Table 3.3).

3.4.4 Caesionidae abundance

The small planktivorous caesionids were significantly more abundant at the fish aggregation site during the flood rather than ebb tides, regardless of the two months sampled (Fig. 3.7). No members of the Caesionidae family were recorded on ebb tides and both flood tide groups sampled produced outliers, indicating high abundance of caesionids during flood tide (Fig. 3.7).

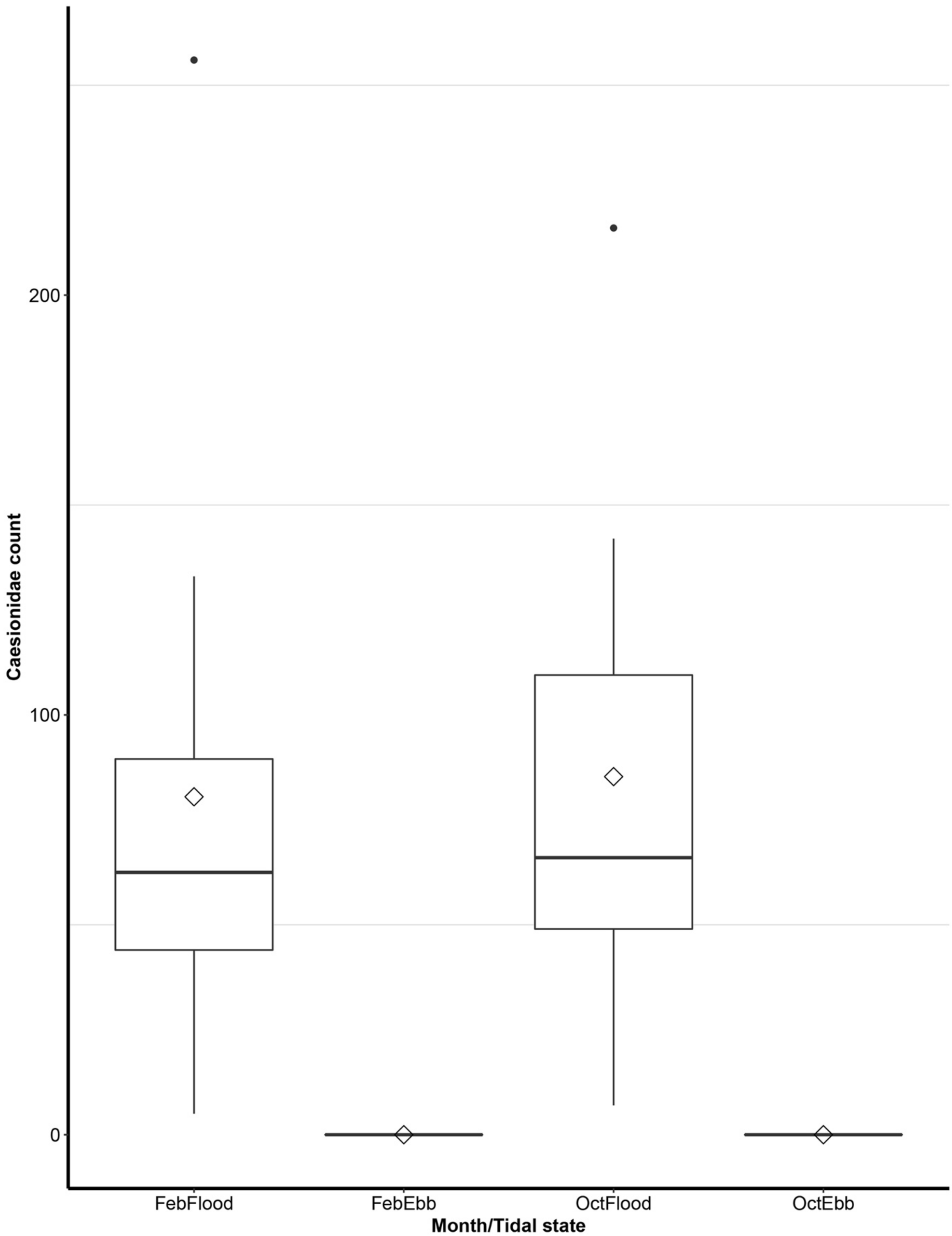


Fig. 3.7. Box plot of Caesionidae abundance on flood and ebb tides for the months of February (2013) and October (2014). The black line in box represents the median and whiskers indicate the variability outside the upper and lower quartiles. The diamond

represents the mean of the samples and the black circles at the end of boxplot represent outliers.

3.5 Discussion

This long-term monitoring study is one of the few studies to analyse the temporal periodicities of fish aggregations on time scales that range from hours to years. The structure of fish assemblages showed high levels of periodicity, with events strongly linked to the local hydrodynamics. The primary influence was the short-term semidiurnal tidal pattern characteristic of this region of the GBR (Wolanski 1994). Both ebb and flood tides were expected to influence the formation of reef fish aggregations. However, the analysis showed that the flooding tide was the dominant environmental factor associated with fish aggregating. Flood tides correlated substantially with several species forming foraging aggregations. Seasonal patterns in abundance and species richness of the selected species, not normally associated with outer reef habitats for foraging, may suggest a reproductive signature. Surprisingly, moon phase often associated with fish forming spawning aggregations (Johannes 1978; Johannes et al. 1999; Colin 2012) contributed very little to the overall structure of the fish assemblages. The results suggest a strong interaction between fish abundance and cooler SST reflective of seasonal preference of some aggregating species and inter-annual variation in total fish abundance of all 10 species. Species richness and abundance of all 10 species were highest throughout late winter and spring (Austral calendar). The study also suggests strong trophic links between aggregating functional groups, which included small planktivores with piscivores, and coprophagous fish with piscivores and invertivores.

Flood tides correlated substantially with the formation of fish aggregations at the site, wherein fish probably capitalise on the ingress of oceanic plankton with the incoming tide. Outer reef slopes vary in configuration due to the presence of grooves, spurs and passages and these morphological features can influence the oceanic forcing of water onto the hard reef (Wolanski 1994). Local topography, such as narrow passes between reefs, may entrain deep flowing water rich in zooplankton near the reef crest. Flood tides in a reef passage typically cause upwelling of water in front of the reef, which are then carried through the passage by tidal jets (Wolanski et al. 1988). The surface waters that enter the passage are drawn radially from a semi-circle of the ocean that was centered at the entrance of the passage and flow separation occurs at the two points on the upstream side of the passage (Wolanski and Hamner 1988). The FA occurs at one of these separation points (Fig. 3.1C), and water movement in this location on flood tides has been recorded to be slower compared to the passage, the other separation point and further along the outer reef slope (EEF, unpublished data). Like spur and groove morphology (Hamner et al. 1988), separation points may entrain planktonic material in the immediate area on flood tides for longer periods. The repeated occurrence of small and large planktivorous fish at the FA on flood tides provides some indirect evidence that there are regular periodicities in the importation of allochthonous plankton on flood tides.

In support of our predictions, the inputs of small plankton and nekton with flood tides supported the continual presence of planktivores and predators of small fish. The small planktivores from the family Caesionidae were more abundant at the FA on flood tides than ebb tides. Likewise, short-term temporal patterns in abundance were shown for the two predators of small fish, *Lutjanus bohar* and *Caranx sexfasciatus*. Both predators were consistent members of all flood assemblages and known to forage on small oceanic and reef associated fishes at the FA (Appendix B.2). The large planktivore *N. annulatus,* a consumer of larger planktonic items including gelatinous plankton (Choat et al. 2002), was also a consistent member of all flood assemblages at the FA. However, the analysis only explained 7% of the variation in the occurrence of *N. annulatus* in relation to the environmental covariates examined. This implies other variables that have not been accounted for, such as the unpredictable boom-bust cycles of gelatinous zooplankters (Henschke et al. 2016) and possibly other large-scale hydrodynamic processes (King and Wolanski 1996; Andutta et al. 2013), may influence the abundance of preferable planktonic prey for *N. annulatus*. Flood tides at the FA suggest coral reef fish potentially form foraging aggregations derived from oceanic resources.

The higher fish abundance and species richness of the 10 selected species in spring were a general feature of the six-year monitoring program and are suggestive of some species forming aggregations for reproductive purposes. The two species classed as predators of benthic invertebrates (*L. olivaceus* and *P. lineatus*) peaked in abundance during spring flood tides. Neither species was observed spawning on flood tides, although individuals of both species were observed to have swollen abdomens and appeared gravid (Appendix B.2), which has been considered as indirect evidence of imminent reproductive activity (Colin et al. 2003). The latter species occurred in consistently abundant during the spring each year of the monitoring period. There is indirect evidence that some members of the Haemulidae family form spawning aggregations in the west Indian Ocean (Samoilys et al. 2006) and the west Pacific Ocean (Johannes 1981). While there is a lack of published underwater information on the mating and spawning behaviour of any member of the Haemulidae, histological information from a western Atlantic Haemulid representative shows that, *Haemulon plumieri* collected from higher latitudes (> 17°) has a distinct spawning season (Farmer et al. 2017; Hoffmann et al. 2017).

The species *L. olivaceus* was also seasonal in appearance at the FA, with peaks in abundance during spring flood tides, suggestive that spawning may be the reason for their aggregation. Histological evidence from other studies indicates that some species of the lethrinids on the GBR have a distinct spawning season in the cooler periods of the year (Newman and Williams 2001; Williams et al. 2006; Currey et al. 2013), though details on mating systems of lethrinids on the GBR are lacking. In other locations, several species of the lethrinids are suggested to form spawning aggregations (Johannes 1981; Samoilys et al. 2006; Babcock et al. 2017), and histological evidence and acoustic telemetry suggested that *Lethrinus harak* made nightly spawning migrations coinciding with lunar and tidal cues in the Pacific Island of Guam (Taylor and Mills 2013). Nocturnal spawning has possible evolutionary advantages due to reduced egg predation (Johannes 1978). However, it is difficult to observe, possibly explaining why there is only one documented account of lethrinids aggregating to spawn (Hamilton 2005). Spawning at dusk or night has also been suggested for some members of the family Haemulidae from observations of oocyte development (Palazon-Fernandez 2007).

The indirect evidence of repeatable seasonal aggregations of *P. lineatus* and *L. olivaceus* at the FA are suggestive of fish forming spawning aggregations. Neither species normally forages on upper outer reef slopes (Lieske and Myers 2001), and observations made during the present study found that both aggregations contained fish with swollen abdomens (Appendix B.2). The question is why both species are more abundant on flood rather than ebb tides. We hypothesise the FA may act as a staging or courtship arena, increasing the probability of social interaction and mate selection (Nemeth 2012), and the tidal cue of flooding may synchronise these behaviours (Colin and Clavijo 1988). Lunar periodicity has been shown to synchronise spawning behaviour in some lethrinids (Hamilton 2005; Taylor and Mills 2013), although this was not a finding in the present study.

At the FA, SST was found to influence the abundance and species richness of fishes. Abundance and richness of the 10 selected species were highest when SST was below the long-term mean of 27°C. For abundance data, a yearly effect was detected with the highest abundance of all 10 species being recorded in the spring months of 2011 when the inter-annual SST was lowest for the monitoring period. The omnivore, *A. dussumieri,* showed species-specific thermal preferences and was highly abundant when water temperature was below 25.7°C. At this time, the species was seen to consume protein-rich faeces of piscivores and invertivores (Robertson 1982) (Appendix B.2 and B.4). The increase in abundance of *A. dussumieri* correlated with an increase in species richness of higher trophic groups and was suggestive of a tight interaction between aggregating species and fishes utilising resource pulses created by aggregating fishes. This study suggests coral reef fish aggregations could be influenced by large-scale meteorological events, such as El Niño, by producing warmer SST and as well as by anthropogenic climate change (Asch and Erisman 2018).

Tropical cyclones may also influence coral reef fish aggregations. At the FA, species richness showed an opposite trend to overall fish abundance with the lowest values recorded in 2011 and 2012. The trend in dropping richness may be associated with the high destruction of tabular corals at the fish aggregation site by the passage of the tropical cyclone “Yasi” in 2011. Tabular corals have been identified as important habitat for large mobile coral reef fish including the families Haemulidae, Lethrinidae and Lutjanidae and Acanthuridae (including *A. dussumieri* and *Naso sp.*) (Kerry and Bellwood 2015). The reduction in this important habitat type may have influenced the occurrence and abundance of 8 of the 10 species selected in this descriptive study.

3.6 Conclusions

Flood tides were the dominant environmental driver underlying the formation of aggregations by 10 large coral reef fishes on an outer slope adjacent to the seaward side of a passage of Moore Reef. The importance of flood tides to these aggregations emphasises the necessity to incorporate tide into the sampling design of monitoring studies to determine long-term changes in fish assemblages (Bijoux et al. 2013). The study found that some species aggregated at the site daily, and others were more seasonal in occurrence. The daily occurrence of small and large planktivores and piscivores were likely to be associated with fishes forming short-term foraging aggregations. In contrast, the seasonal presence of two species of benthic feeding invertivores appeared to be related to fishes forming spawning aggregations. Contrary to our predictions, flood tides were the dominant correlates of the possible trophic and reproductive aggregations. This comprehensive study, despite being limited to one site, does provide a detailed description of the temporal patterns of fish aggregations in relation to the physical environment and speculated the biological motive for trophically different species forming aggregations. To resolve this requires more specific information on their trophic and reproductive biology. Future work is planned in this area, but presently restricted by permits that allow large-scale collections. Research at more aggregation sites is also warranted to test the hypotheses that some fish from certain trophic groups aggregate to spawn and others to forage. Such research may also determine the generality of our finding that reef configuration and hydrodynamics are the most important physical drivers underlying coral reef fish forming aggregations.

Chapter 4: Temporal Periodicity of aggregation in three large coral reef fishes on the Great Barrier Reef

4.1 Abstract

Three large conspicuous coral reef fish species displayed a clear and consistent pattern of annual aggregation that persisted over the 13-year investigation. This high-resolution study recorded underwater visual census of fishes with concurrent information on several environmental variables to determine the proximate cues of aggregation for each species. The aggregation of the haemulid *Plectorhinchus lineatus* and the acanthurid *Acanthurus dussumieri* were strongly seasonal, while the lutjanid *Lutjanus bohar* was ubiquitous throughout the annual cycle. Aggregated boosted trees (ABTs) were used to resolve the proximate cues to fish forming and ceasing aggregation, with 70 to 80% efficiency. Photothermal cues, that was both surface seawater temperature (SST) and daylength ranked almost in equal importance for *P. lineatus*. However, there was strong evidence that SST, not daylength, was the primary cue for *A. dussumieri* aggregations. The flooding tidal phase of the semi-diurnal tidal cycle was the most important proximate cue within seasons for fish aggregations that formed and disbanded daily. For *L. bohar*, flood tides were the most important cue for daily aggregation formation. This long-term study also provided the opportunity to investigate how fish aggregation phenology was influenced by two tropical cyclones ("Hamish" & "Yasi") and two mass coral bleaching events (2016 & 2017); surprisingly these events did not disrupt the timing of aggregation, even years post perturbation. The detailed findings are highly relevant to understanding local changes in the distribution of fishes, aggregation periodicity and allow inferences to the ultimate causation of aggregation.

Key words. Fish aggregations, environmental cues, perturbation, phenology, proximate cues, ultimate factors.

4.2 Introduction

Reoccurring rhythms of feeding and reproductive behaviour in coral reef fish, plays a vital role in propagation and energy transfer through trophic interactions. For example, large aggregations of spawning coral reef fishes in French Polynesia sustains high densities of apex predators (Mourier et al. 2016; Robbins and Renaud 2016). Coral reef fishes are known to aggregate in all ocean basins at specific sites and times to forage, select mates, spawn and to be cleaned. (Domeier and Colin 1997; Claydon 2004; Sadovy de Mitcheson and Colin 2012). Coral reef fish aggregation sites are often used by many species that are diverse in their behaviour and trophic ecology (Sala et al. 2003; Heyman and Kjerfve 2008; Kobara et al. 2013), which provides insight into the proximate and ultimate causes of fish behaviour and evolutionary processes (Choat 2012; Wong and Buston 2013). Proximate factors are cues or underlying mechanisms leading to aggregation, while ultimate causes imply the reasons why or the adaptive significance for the displayed behaviour (Mayr 1961).

In this study fish aggregation can be defined as a temporary, predictable and repeatable gathering of large numbers of conspecifics in a particular space and time (Domeier and Colin 1997; Sadovy and Domeier 2005; Erisman et al. 2015) that aggregate to perform a specific vital task such as feeding or reproduction. Foraging aggregations may increase growth and related fitness from the ability to locate high concentrations of prey in a patchy environment (Alldredge and Hamner 1980; Hamner and Hauri 1981; Hamner et al. 1988; Kingsford 1990). In contrast, the ultimate factors for spawning aggregations can include, high probability of mate location and selection (Lobel 1978; Colin and Clavijo 1988), reduced predatory pressure on adults (Shapiro et al. 1988), eggs and larvae (Johannes 1978; Lobel 1978), heightened larval survival through finding resources (Doherty et al. 1985) and locating suitable settlement habitat, either through dispersion (Barlow 1981) or retention (Johannes 1978; Lobel 1978) from the natal reef.

Proximate factors or the underlying mechanisms behind the location and timing of fish aggregating, are extrinsic as well as intrinsic or physiological, with extrinsic factors relating to when and where fish aggregate (Robertson 1991). Large coral reef fish aggregations generally occur at the interface between coral reef and open water and can include habitats which vary in spatial scale, but include promontories, reef passes/narrow channels and outer slopes/drop-offs (Colin and Bell 1991; Heyman et al. 2005; Sadovy de Mitcheson et al.

2008). The timing of aggregations at these locations often coincides with discrete environmental cycles. Environmental cycles on coral reefs range in temporal scales from hours to years and can influence biological rhythms of migration and aggregation in both invertebrates and vertebrates (Nemeth 2009). Coral reefs occur in a broad band of 30° of latitude to the north and south of the equator and experience circannual cycles in daylength, temperature, rainfall, wind strength and direction (Kleypas et al. 1999). Oscillations in these environmental factors can cause distinct seasonal changes at an individual coral reef. Even close to the equator where changes in daylength and temperature are minimal, seasonal changes in trade winds, influences precipitation, which results in distinct wet and dry seasons. Within seasons, the movement of the sun and moon influence tidal patterns on a lunar, semi-lunar, diel and semi-diurnal rhythm (Amin 1986). Understanding the proximate factors underlying biological rhythms in animal behaviour, or phenology, has important consequences in the determination on how ecosystems function and related services respond to a changing environment (Helm and Stevenson 2014).

In addition to a frequently changing environment driven by oscillating environmental cycles operating over several temporal scales, coral reefs can experience significant perturbations events such as severe tropical cyclones and mass coral bleaching events. Tropical cyclones (TC) occur frequently within the Great Barrier Reef (GBR) and may provide beneficial services to coral reefs in the form of nutrients and temperature regulation (Andrews and Gentien 1982; Benthuysen et al. 2016), however the impacts to coral communities can be severe (De'ath et al. 2012; Cheal et al. 2017). Cyclone damage to live coral can range from coral fragmentation and dislodgment of colonies through to destroying large sections of live coral and even structural damage to reef framework. The extent of damage to coral reefs is dependent on the speed and intensity of the TC (Beeden et al. 2015). In severe cases over 90% of live coral cover can be lost (Gerlach et al. 2021).

Although TC frequency is unlikely to rise in the future, TC intensity is predicted to increase through anthropogenic climate change (Cheal et al. 2017). In comparison, mass coral bleaching events have been increasing in frequency and intensity since the 1980’s (Hughes et al. 2018c; Eakin et al. 2019). These significant perturbations can physically reduce live coral cover and coral diversity (Wilson et al. 2006; Hughes et al. 2018b), which can impact the biological structure of fish populations (Jones et al. 2004; Coker et al. 2013; Cheal et al. 2017; Pratchett et al. 2018). Although these studies provide insight into factors influencing ecosystem function, there is a dearth of information on how large disturbances influence the timing of biological rhythms such as fish aggregations.

Coral reef fish aggregations represent great proponents for phenological studies due to their predictability in space and time. Although, this predictable nature can be detrimental to specific fish populations from overfishing, it has also focused management actions to conserve these important biological rhythms (Claro and Lindeman 2003; Sala et al. 2003; Sadovy and Domeier 2005; Erisman et al. 2015). Recent thinking towards spawning aggregations has suggested a more holistic approach to adopt a suite of adaptive management strategies to preserve fish aggregations, sustain fisheries and ecosystem dynamics (Pittman and Heyman 2020). However, a more comprehensive approach towards all fish aggregation types and knowledge of environmental cues driving fish aggregation should be incorporated into fisheries and ecosystem management. No matter what reason fishes form aggregations, they are vulnerable to overfishing. As well as overexploitation, anthropogenic climate change has the potential to influence the spatial temporal dynamics of fish aggregations. For example, a modelling study has revealed that the Nassau grouper *Epinephelus striatus*, which has a narrow thermal tolerance when spawning, may change their aggregation phenology with rising seawater temperatures (Asch and Erisman 2018).

Investigating fish aggregation phenology requires high frequency monitoring, correlated with reoccurring environmental cycles ranging from hours to years. Although the importance of this has been emphasised to validate aggregation longevity (Colin 1996), few studies have managed to carry out this task for more than a decade (Biggs and Nemeth 2014; Rhodes et al. 2014; Ohta and Ebisawa 2017). These studies, focused on large commercial species from the families Epinephelidae and Lutjanidae and found quite a robust seasonal and lunar periodicity to form spawning aggregations. Given the potential importance of fish aggregations to coral reef ecosystems, either through replenishing fish populations (Domeier and Colin 1997; Erisman et al. 2019) or trophic interactions (Nemeth 2009; Archer et al. 2015; Shantz et al. 2015), it is essential to investigate a range of coral reef fish species that display a variety of foraging and reproductive modes.

A key question to the formation of all animal aggregations and phenological studies is what are the key environmental cues or proximate factors influencing their timing? An equally important question is, can a rapidly changing environment through increase perturbations influence aggregation phenology. The objective of this study was to investigate the timing of aggregation in three large coral reef fish species to determine the proximal cues responsible for aggregation. This study was conducted at a known multi-species coral reef fish aggregation site situated near a small-scale reef pass within the GBR (Fisher et al. 2018). The species selected for this study were *Acanthurus dussumieri* (Acanthuridae), *Plectorhinchus lineatus* (Haemulidae) and *Lutjanus bohar* (Lutjanidae). These species were selected because they differ in body shape, mouth morphology and diet. Underwater visual census of each species was conducted almost daily over a 13-year period at the known fish aggregation site. Fish abundance data was compared with several environmental variables operating over several temporal scales to determine proximate cues of aggregation for each species. During the study period several perturbation events such as tropical cyclones and the mass coral bleaching occurred at the study site. This opportunistically allowed comparison if significant perturbation evens influence the timing of aggregation at a multi-species fish aggregation site.

4.3 Methods

4.3.1 Study site

The study site was approximately 55 km east of Cairns on the north-western side of Moore Reef, situated on the outer margin of the continental shelf in the northern section of the Great Barrier Reef, Australia (Fig. 4.1A). Moore Reef has a crescent shape characterised by an extensive reef flat on the windward margins, with a well-developed reef front that partially encloses a lagoon dominated by isolated patch reefs (Fig. 4.1B). The fish aggregation site (-16.845°, 146.23°) covers an area of ~3,500 m^2 and situated on the north-west aspect of the reef pass and was near a commercial tourism site that operates off a platform on the lagoon side of Moore Reef (~ 350 m direct line; Fig 4.1C), which facilitated the means to perform underwater visual census (UVC = total counts) regularly. The reef pass dissects the reef flat and was ~330 m in length, 60 to 250 m in width and 14 to 22 m in depth with a north to south orientation. The reef front on the outer side of the pass and the leeward edge on the inner side of the pass both included spur and groove morphology. The inner and outer reef slopes terminated at ~ 20 m depth into a sand-rubble substratum dotted by isolated coral patches (Fig. 4.1C). The Great Barrier Reef Marine Park Authority (GBRMPA) have classed Moore Reef as Marine National Park Zone since 1981 with limited recreational fishing permitted (GBRMPA 1982), then in 2003 was converted to a no take area and of high conservation value (GBRMPA 2004). Accordingly, fishes at the fish aggregation site were not affected by extraction. The research carried out in this study was conducted under GBRMPA research permit G12/35200.1.

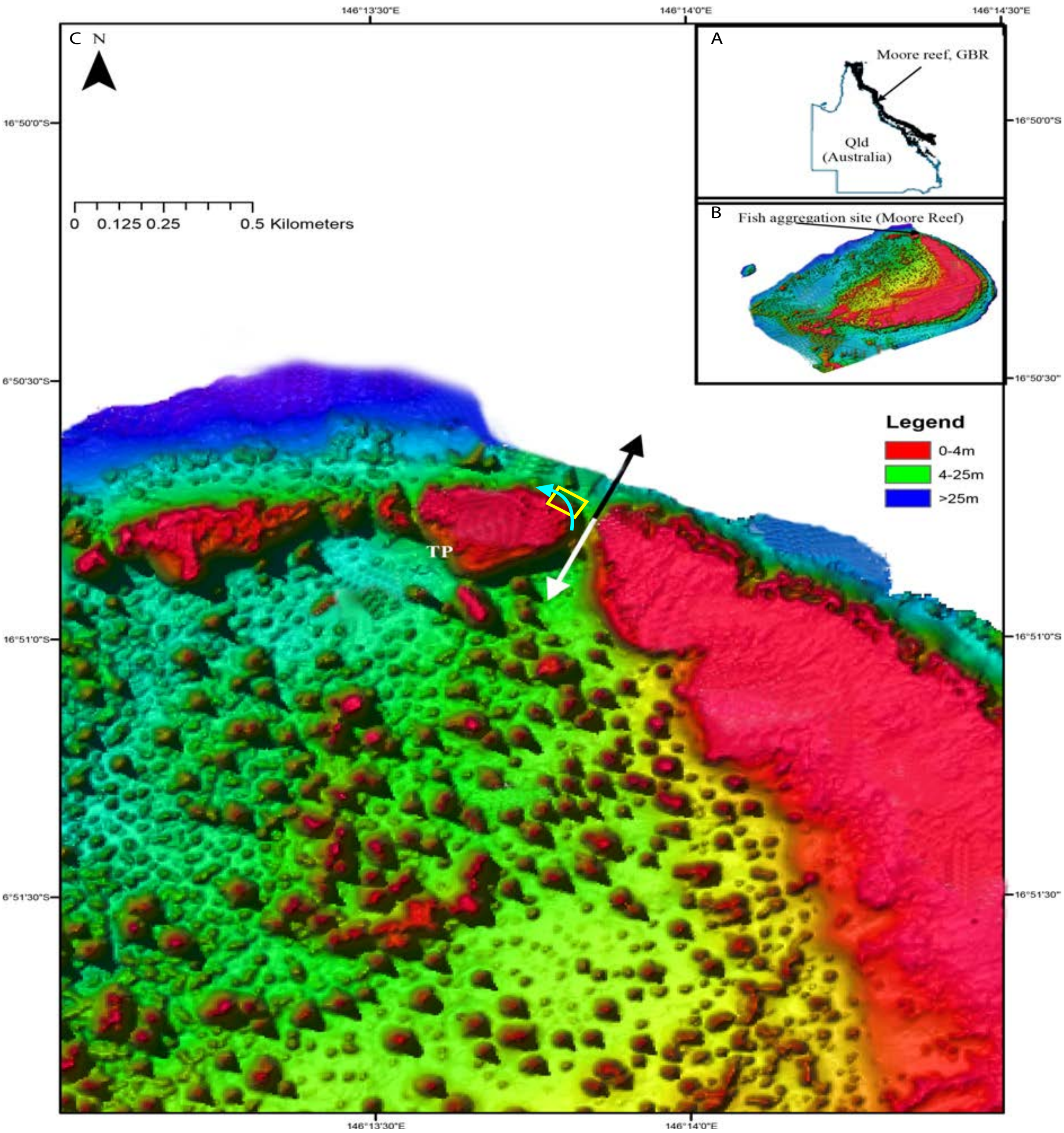


Fig 4.1. Site map of Moore Reef fish aggregation site: A) showing the location of Moore Reef in the Great Barrier Reef, B) the location of the fish aggregation site at Moore Reef and C) bathymetric map of reef scape at the Moore Reef fish aggregation site. The direction of flows through the passage are detailed by the white (flooding) and black (ebbing) arrows. The letters (TP) refer to the location of a commercial tourism platform. Underwater visual census path (light blue arrow) initiated in the pass behind the fish aggregation area (yellow box), then continued through this zone and along the outer slope. The lidar bathymetry data of

Moore Reef was courtesy of Dr Robin Beaman, James Cook University. This figure was published see (Fisher et al. 2018).

The study was conducted from February 2005 through to December 2017 and during this time the fish aggregation site experienced several disturbances. High intensity tropical cyclones (TC) “Hamish” and “Yasi” passed the study site in 2009 and 2011 respectively, which destroyed large coral sections, accumulated coral rubble and altered reef communities (De'ath et al. 2012; Cheal et al. 2017). At the study site TC “Hamish” produced slight coral damage, however TC “Yasi” destroyed 95% of tabulate corals on the reef front. Coral cover gradually increased in the years following the passing of TC “Yasi” due to settlement of *Acropora* tabulate corals (Ortiz et al. 2021). However, 90% of the corals at the fish aggregation site totally bleached white in both 2016 and 2017 mass bleaching events (Hughes et al. 2018a), although coral mortality was minimal (6%) at the fish aggregation site in these consecutive events. Trend data on reef health and coral cover at Moore Reef fish aggregation site has been reported regularly to the Great Barrier Reef Marine Park Authority’s, Eye on the Reef Integrated Monitoring system since 2007 (Beeden et al. 2014).

4.3.2 Underwater visual census of three large coral reef fishes

At the study site, 38 species of reef fish from 12 families were known to form regular aggregations (Fisher et al. 2018). The three species selected from three coral reef fish families were: *Plectorhinchus lineatus* (Haemulidae), *Lutjanus bohar* (Lutjanidae) and *Acanthurus dussumieri* (Acanthuridae). The species of pelagic spawners were selected for this quantitative study because they form conspicuous aggregations and display distinct foraging modes. The haemulid, *P. lineatus* predominately preys on benthic invertebrates in soft sediments of coral reefs (Lieske and Myers 2001). The lutjanid, *L. bohar* known to form spawning aggregations (Sadovy de Mitcheson and Colin 2012; Sakaue et al. 2016) represents a mesopredator that includes active piscivory and known to consume quite large prey relative to body size. Diet can include reef associated species from the families Acanthuridae and Scaridae, and mobile schooling species from the families Caesionidae and Pomacentridae (Wright et al. 1986; Farmer and Wilson 2011). The acanthurid *A. dussumieri* has an omnivorous diet with a variety of feeding modes that include sand grazer (Barlow 1974), detritivore (Choat et al. 2004; Cheal et al. 2012), grazing herbivore (Cheal et al. 2012;

Basford et al. 2015), planktivore and faecal scavenger (Fisher et al. 2018). The mating strategies and spawning behaviour of *A. dussumieri* and *P. lineatus* are relatively unknown.

The abundance of the three species was estimated four to five days per week for a 13-year period. The UVC followed the same census path of ~ 250m in length and 20m in width, starting inside the mouth of the channel, moving through the fish aggregation site and continuing along the outer slope of Moore Reef (Fig. 4.1C). Fish from each species was counted along the path via snorkel. The counter continuously traversed the path from the left to the right of the census path center and pausing to count fish in aggregations. The minimum abundance recorded for each fish species was zero if fishes absent from census path. This census path was conducted daily between 1400 hrs. and 1500 hrs. and provided good sunlight to survey deeper water depths most days to ~20 m. Poor water visibility can influence visual count estimates (McCormick and Choat 1987); therefore, two estimates of water visibility were collected in this study to include in the analysis of UVC results.

4.3.3 Environmental Variables

The environmental variables sampled in this study ranged in their cycles from hours to years and this information was collected between February 2005 and December 2017 (for data source information see Table 4.1). The combination of the sun and moon influenced regional tidal cycles. Moore Reef experiences a mixed semi-diurnal tide in that it generally has two high and two low waters of mixed height in 24-hour period, with tidal currents alternating between flood and ebb approximately every 6 hours (Chapter 2). At the study area, the flood tide causes water to flow onto the reef and lagoonwards, while the ebbing tide forces water to flow out through the reef pass and on to the continental shelf (Fig 4.1C). The moon passes around the earth approximately every 29.5 days and the moon phase has been represented as a decimal fraction of luminosity, which is a quantitative way of describing the moon's phase (USNO 2023). The measurement ranges from zero to one. Zero described the new moon phase, while 1 described the full moon phase and the first and last quarters were represented by 0.5. First and last quarter can be distinguished by noting whether the fraction illuminated was increasing or decreasing. First Quarter occurred when the fraction illuminated was increasing (Moon waxing; in evening sky) and Last Quarter occurred when the fraction illuminated was decreasing (Moon waning; in morning sky) (USNO 2023).

Sea surface temperature (SST), daylength, wind speed and direction and underwater visibility varied within and among years. During this 13-year study, SST varied seasonally between 22.5 – 32 °C and daylength at Cairns varied between 11.12 – 13.13 hours from the winter to summer solstice. Throughout the study, wind speed and direction were collected from three different sources (Table 4.1). The data collected from Moore Reef (ID 200846) was sporadic and supplemented with the data from the Arlington Reef weather station (ID 200879 from 2010. Prior the installation of Arlington Reef in 2010, regional reef wind information was collected from the automated weather station at Green Island (ID 31192). The two wind stations ran concurrently for 40 days and the data for each station was converted to 6 hourly averages to smooth out effect of physical separation. Then one speed was plotted against the other and a regression was carried out (Appendix C Fig. C.1). There was a significant relationship between the two data sets ($F_{1,167} = 6367$, $p < 0.05$). The equation relating wind speed at Arlington Reef (y) to Green Island (x) was $y = 0.5 + 0.87x$ and the equation explained approximately 97.4% of the variation. Wind values prior to 2010 were converted with this formula to supplement missing data from the Moore Reef station. The measurement of underwater visibility on coral reefs has often been used as a water quality indicator and has demonstrated seasonal rhythms (Macdonald et al. 2013). Two estimates were sampled in this study (Table 4.1) which includes a visual estimate conducted during UVC and discrete Secchi depth measurements.

Table 4.1. Describes the source of environmental conditions collated with the fish abundance data. The data was collected between 20 February 2005 to 29 December 2017, except the Secchi data which commenced 24 June 2007.

Environmental variable	Source	Units	Distance and direction of source from aggregation site
Tidal current (Describing the direction of water flowing through the passage)	Author	Flooding or Ebbing ~ 1400 hrs.	On site
Moon phase described as Lunar Luminosity (the fraction of the moon's visible disc illuminated by the sun every day between 1700 and 2100 hrs.)	United States Naval Observatory astronomical department http//aa.usno.many.mil/data/.	Values between 0 and 1 with 2 degrees of precision. Tables use Chamorro Standard Time (Guam, Pacific Ocean) Similar to AEST (UTC + 10:00)	
Sea surface temperature (SST)	Thermometer suspended ½ m below surface.	°C Readings taken ~ 1500 hrs.	350 m SSW
Daylength	United States Naval Observatory astronomical department http//aa.usno.many.mil/data/.	Duration of Daylight in hours with two degrees of precision	
Wind speed and direction	Cairns Bureau of Meteorology 1. Moore Reef 2. Green Island 3. Arlington Reef (- 16.72°,146.11°)	Speed in m s^{-1}, Direction between 0 – 360° Readings taken at 1400 hrs.	1. 450 m SSE 2. ~29 Km WNW 3. ~18 Km NW
Underwater Visibility	1. Secchi Disc 2. In water visual estimate	1. Readings taken ~ 1500 hrs. in meters (m) 2. Estimates in meters (m) ~1400 hours	1. 350 m SSW 2. On site

4.3.4 Statistical analyses

The data comprised of 2,377 UVC counts at the Moore Reef fish aggregation site between the 20-Feb-2005 and the 29-Dec-2017. There were 264,630 individual fish counted in the data set. The mean abundance data of sea surface temperatures (SST) and each coral reef fish species was used to display interannual trends over the 13-year period. Percentage deviations from the grand mean of SST and abundance of each species were used to illustrate interannual rate of change and show among year trend between SST and fish abundance.

To normalise the data, a square root transformation was performed on the fish abundance data for each species due to large number of zero counts. Date and data on tidal flow, moon phase, daylength, wind speed and direction were available for all counts and measurements of (SST) were available for all but 24 samples. Many values were missing for the two estimates of underwater visibility. There were 683 missing samples for Secchi disc measurements compared to 296 missing samples for visual estimates of underwater visibility. The Secchi disc measurements were excluded from analysis due to the higher number of missing values and there was a significant association between the two visibility estimates (Pearson's rank correlation, $r = 0.52$, $t = 24.7$, $p < 0.05$, $n = 1690$).

The univariate responses of fish abundance for the three selected species were modelled using aggregated boosted trees (ABTs) to summarise the relative influence of major predictors and to interpret interactions (De'ath 2007; Elith et al. 2008; Fabricius and De'ath 2008). The models included the main effects and up to three-way interactions amongst the full suite of explanatory covariates (decimal date, tide, moon phase, seawater temperature, daylength, wind and visibility), all predictors and up to third-order interactions. No monotonic constraints were applied to the functional form of selected individual predictors. Five methods were used to interpret and compare the models as per (Fabricius and De'ath 2008). The best predictive models were determined by comparing the "predictive error" (PE) expressed as a percentage, of models with varying levels of interactions. All analyses were performed in R (RCoreTeam 2021) and used the open source libraries; abt (De'ath 2017) and tidyverse (Wickham et al. 2019).

4.4 Results

All three species of coral reef fish demonstrated a clear and consistent pattern of annual aggregation over the 13-year study. The periodicity of aggregations was predictable and consistent (Fig. 4.2). Further, the timing of aggregation in each species were not disrupted by the perturbation events of TC “Hamish” and TC “Yasi” and the consecutive mass coral bleach events of 2016 and 2017. Sea Surface Temperature (SST) varied predictably according to seasonal cycle of high SST during summer and low SST during winter (Fig. 4.2A). Fishes displayed contrasting patterns of aggregation. The haemulid, *Plectorhinchus lineatus*, showed strong temporal periodicity to aggregate during the austral spring with peak abundances occurring during the month of October each year. This species was almost absent from the fish aggregation site at other times of the year (Fig. 4.2B). Similarly, *Acanthurus dussumieri* aggregated over a short period during the austral winter to early spring months and largely absent during other times of the year (Fig. 4.2C). In contrast, the piscivore *Lutjanus bohar* aggregated, with some minor fluctuations, at all times of the year (Fig. 4.2D).

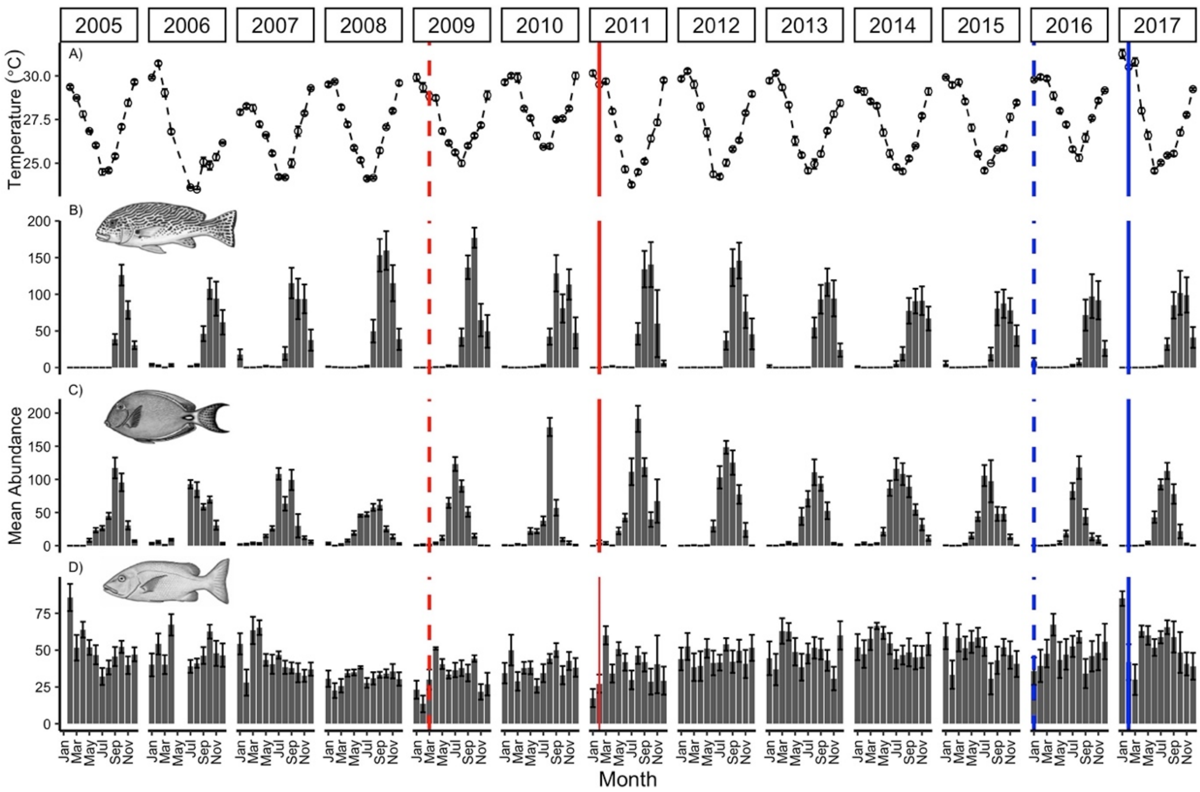


Fig. 4.2. Monthly plots of mean fish abundance from 2005 to 2013 at Moore Reef fish aggregation site: A) Mean Sea Surface Temperature, B) *Plectorhinchus lineatus,* C) *Acanthurus dussumieri* and D) *Lutjanus bohar*. All error bars are plus or minus one Standard Error, (n=2,377). Dashed red lines show the passing of tropical cyclone “Hamish” where the solid red lines showed the passing of tropical cyclone “Yasi”. The blue lines both dashed and solid represent the consecutive mass coral bleaching events in 2016 and 2017 respectively. No data on fish abundance was collected for the months in May and June 2006.

The amplitude of SST varied interannually over the study period (Fig 4.2A) and this variation did not affect the periodicity of aggregation of each coral reef fish species. There was some evidence that interannual variation in SST affected the mean abundance of *A. dussumieri* with this species being more abundant in cooler months (Fig. 4.2). The annual SST was 2% lower than annual average in 2006 and was 1.2% lower than the annual average in 2011 (Fig. 4.3A), which corresponded to the coolest annual winters. In contrast warmer winter mean SST were observed during the years 2010 and 2016 (Fig. 4.2A). The annual SST for 2010 was 3.1% higher and for 2016 was 3.7% higher than the annual average (Fig. 4.3A). Accordingly, the abundance of *A. dussumieri* was ~ 50% above the annual average for 2011 and ~ 40% lower than annual average in 2016 (Fig. 4.3B). *A. dussumieri* preference for cooler was also demonstrated in 2014, when SST was lower than the yearly average, this species was 25% more abundant than the yearly average. With *P. lineatus*, high fish abundance in 2006 and 2008 corresponded to lower annual SSTs, although in 2011 a cool year, fish abundance was below the annual average. In the warmer years from 2015, fish abundance declined below the annual average and the lowest annual abundance for *P. lineatus* occurred in 2016 when SST was highest (Fig. 4.3 B). The lutjanid, *L. bohar* showed no obvious trend with changes in interannual SST (Fig. 4.3 B).

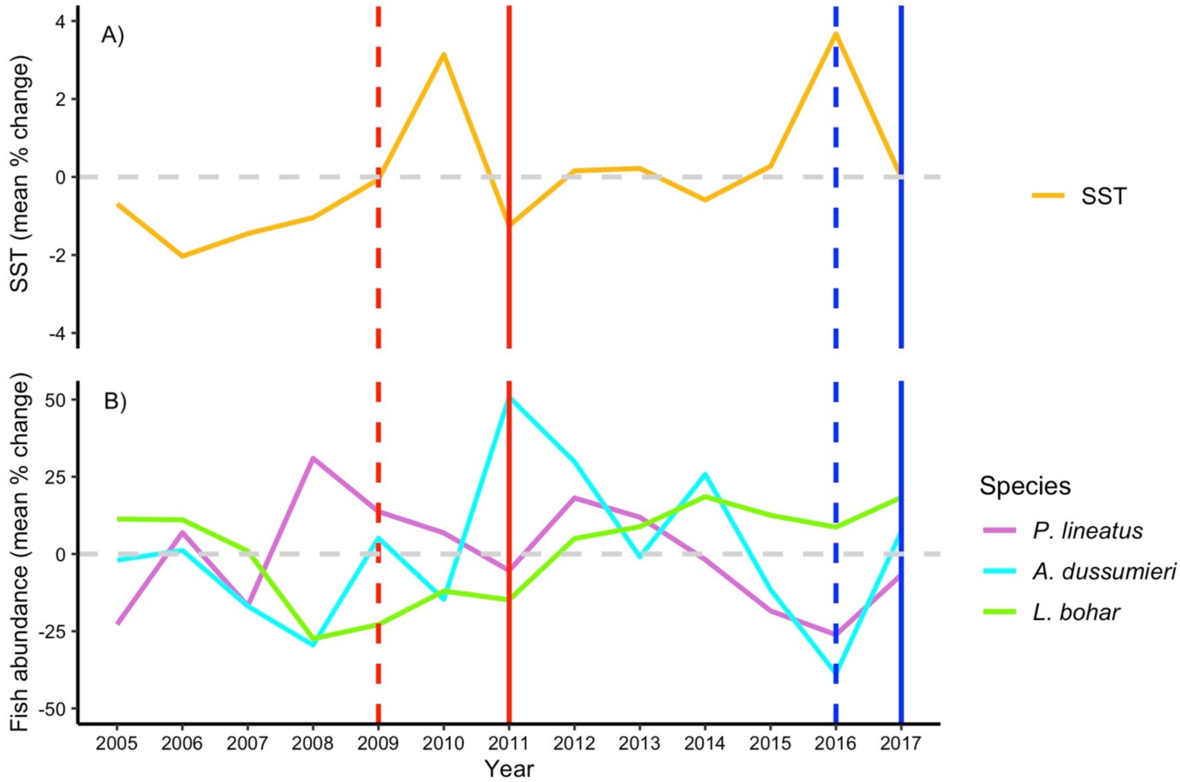


Fig. 4.3. Yearly percentage increase/decrease from overall mean: A) sea surface temperature (SST) and B) mean abundance for each fish species. Negative values represent a percentage decrease from overall SST and mean abundance of each species. Dashed red line show the passing of tropical cyclone "Hamish" where the solid red line showed the passing of tropical cyclone "Yasi". The blue lines both dashed and solid represent the consecutive mass coral bleaching events in 2016 and 2017 respectively.

The perturbation events of TC "Hamish" and TC "Yasi" and the consecutive mass coral bleach events did not disrupt the timing of aggregation for each coral reef fish species (Fig. 4.2B). The minor annual fluctuations in mean abundance of some species at the aggregation for each species did not appear relative to perturbation history (Fig. 4.3B).

Multiple environmental variables explained the timing of aggregation in the three selected coral reef fish species. Decimal date to describe interannual variation (Urquhart et al. 2023) was included in the best ABTs, for each species and had the second highest relative influence on the abundance of *L. bohar* and *A. dussumieri* (Fig. 4.4). The relative influence of predictors was different for each species. Surface seawater temperature (34.76%) followed closely by daylength (27.94%) were the dominant predictors for *P. lineatus* (Fig. 4.4A). The model of main effects with third order interactions had a PE (25.4%) equating to a R^2 of 74.6% in explaining variance in abundance for *P. lineatus* (Table 4.2). The other species with strong seasonality periodicity *A. dussumieri*, the dominant predictor was SST (59.98%) (Fig. 4.4B). The best model with third order interactions had a PE (21.4 %) equating to a R^2 of 78.6% in explaining variance in abundance for this species (Table 4.2). Within season for both species semi-diurnal tide cycle was an important predictor for synchronising daily aggregations (Fig. 4.4).

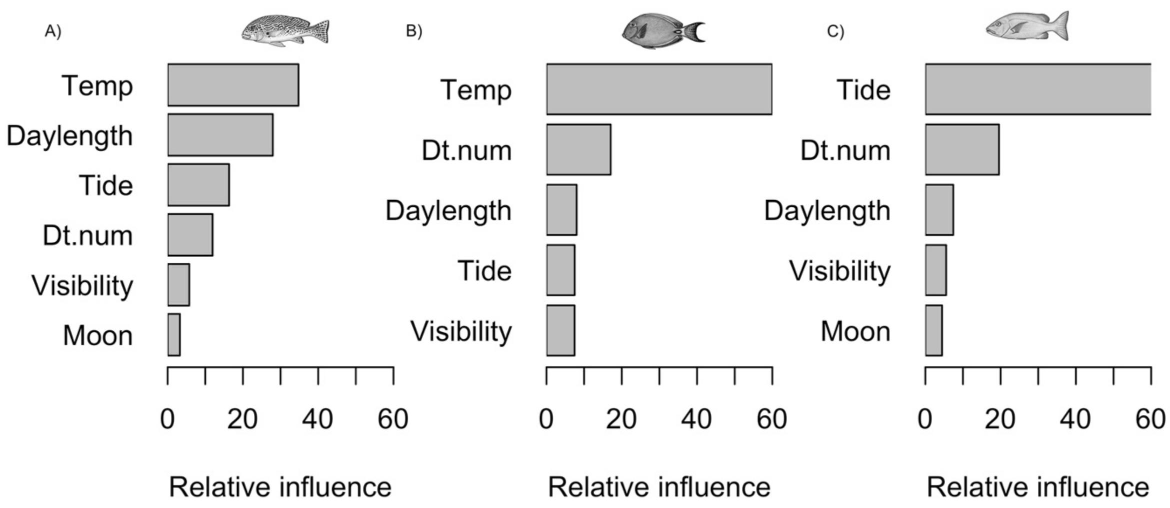


Fig. 4.4. Relative influence in percentage plots of aggregated boosted regression trees for reef fishes: A) *Plectorhinchus lineatus*, B) *Acanthurus dussumieri* and C) *Lutjanus bohar.* Dt.num represents the temporal predictor numerical date, that describes interannual variation.

Table 4.2. Summary of aggregated boosted tree analysis for the *Plectorhinchus lineatus*, *Acanthurus dussumieri* and *Lutjanus bohar*. The top row shows the prediction error (PE%) of the best aggregated boosted tree models and the subsequent rows show results of permutation tests (n=1000) and the increase in PE% by dropping each variable relative to the full model. Influence represents the relative influence (%) of each predictor and (NA) represents the predictor that was not included in the fish species best aggregated boosted tree models. The significance of the omission of predictors based on permutation test (P).

	Plectorhinchus lineatus			*Acanthurus dussumieri*			*Lutjanus bohar*		
	Influence	**PE%**	**P**	**Influence**	**PE%**	**P**	**Influence**	**PE%**	**P**
ABT full model		25.4			21.4			31.7	
Temperature	34.76	282.19	<0.05	59.98	397.95	<0.05	NA	NA	NA
Tide	16.33	136.45	<0.05	7.49	61.89	<0.05	63.02	366.88	<0.05
Daylength	27.94	424.78	<0.05	8.01	34.77	<0.05	7.43	13.1	<0.05
Decimal date	11.95	35.94	<0.05	17.07	67.98	<0.05	19.57	35.94	<0.05
Moon	3.26	8.85	<0.05	NA	NA	NA	4.46	5.58	<0.05
Visibility	5.75	28.73	<0.05	7.46	50.53	<0.05	5.53	13.84	<0.05

Tide (63.02%) was the dominant relative influence for *L. bohar* (Fig. 4.4C), which was at the aggregation site year-round, but only on flood tides. Surface seawater temperature had minimal variance and was not included as a predictor in the best ABTs and the model of main effects with third order interactions had a PE (31.7%) or an R^2 of 68.3% in explaining variance in *L. bohar* abundance (Table 4.2). Important to note that underwater visibility and the moon had a minor influence on the underwater visual census counts of each species in this study (Fig. 4.4). The next result section will examine the relative influence and interactions between predictors for the three study species in more detail.

4.4.1 Plectorhinchus lineatus

P. lineatus had a higher abundance at the Moore Reef fish aggregation site when seawater surface temperatures (SST) were cooler, the days longer and when tides were flooding in through the reef pass (Fig. 4.5). Permutation tests showed there were 8.2 times more fish present (Table 4.2) when counts were made when SST was below the mean of 27.2 °C and abundance decreased quickly when SST was >29 °C (Fig. 4.5A). Daylength also associated with reproductive periodicity (Wang et al. 2010) showed that there were 15.2 times more fish present (Table 4.2) when counts were made when daylength was greater than 12 hours per day (Fig. 4.5B). Hourly variation in abundance of *P. lineatus* at fish aggregation site was observed with 8.3 times more fish present when oscillating tidal cycles were flooding (Fig. 4.5C). That is when water was flowing through the reef pass from the open ocean and into the coral lagoon (Fig. 4.1). The partial dependency plots show that there were some notable peaks in abundance of this species before 2011 (Fig. 4.5D) and that higher visibility improved underwater visual census counts (Fig. 4.5E). Lunar cycles had a minor influence on predicting the abundance of *P. lineatus*, although there was a weak trend for fish abundance to be above the mean in the days leading up to the new moon compared to the full moon (Fig. 4.5F).

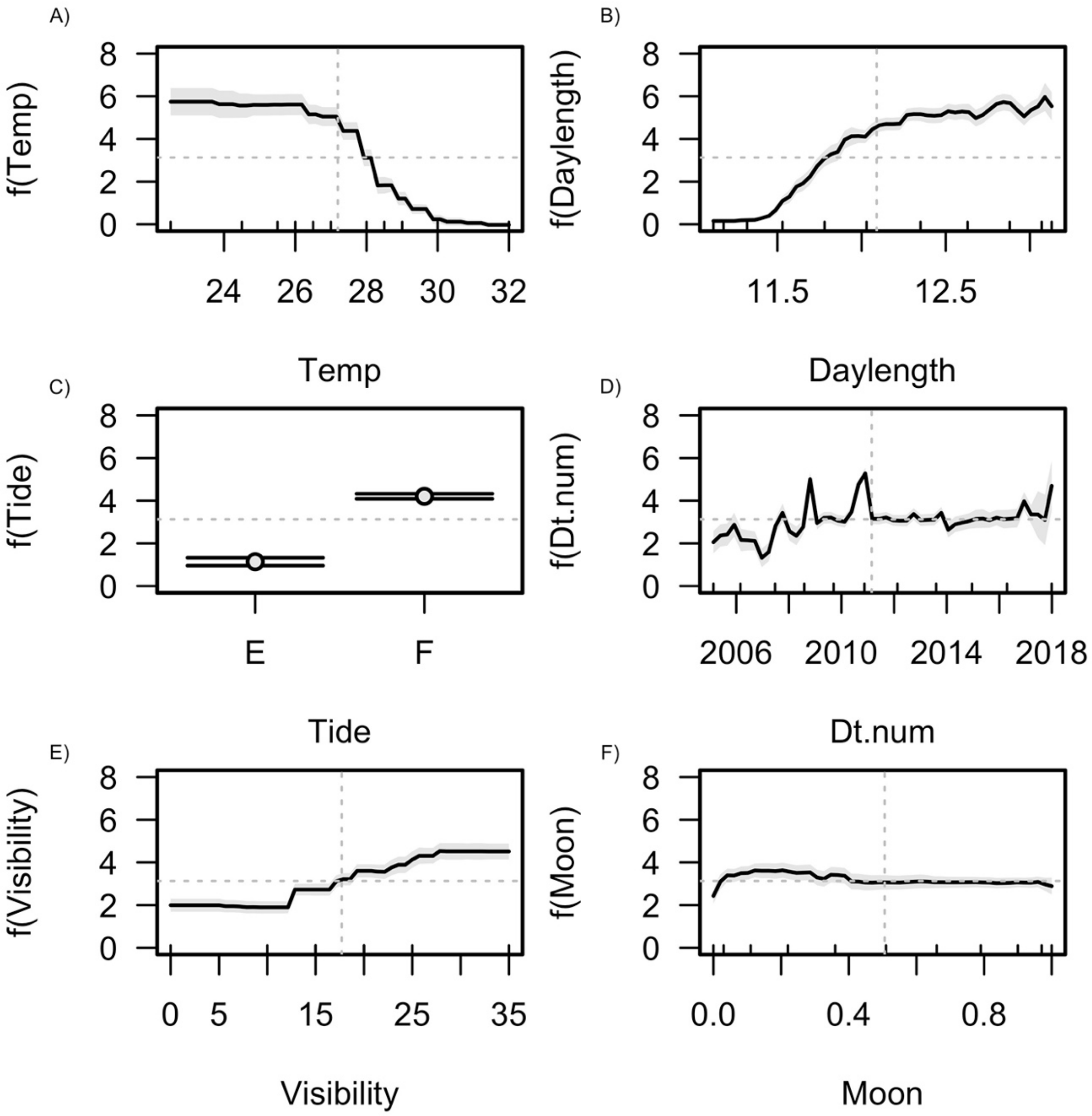


Fig. 4.5. Partial dependency plots for the response of *Plectorhinchus lineatus* abundance from the best aggregated boosted tree models against predictors: A) surface seawater temperature °C, B) daylength (hrs), C) tidal current, D) numerical date, E) visibility (m) and F) moon phase. Shading around the response lines is two standard errors. Horizontal lines show the mean relative abundance of *P. lineatus* and the vertical dotted lines show the mean value for each predictor.

The interaction of SST with the other environmental cycles best explains the predictive capabilities of the *P. lineatus* ABT model. The partial interaction plot between SST and the mixed semi-diurnal tidal cycle showed that fish abundance was always above the mean on flooding tides, even when SST was a degree above the annual average (Fig. 4.6A). More importantly the abundance of *P. lineatus* increased rapidly when daylight hours were greater than 11.5 hours and the cooler the SST the higher the response, which demonstrated the importance of the interaction between these two variables (Fig. 4.6B). The two annual cycles of SST and daylength contributed to almost 63% of the relative influence out of 6 covariates in predicting the occurrence of *P. lineatus* at the fish aggregation site (Table 4.2). There was a significant correlation between these two environmental rhythms (Spearman's rank correlation, rho=0.68, $p<0.05$, n=2353). However, the ABTs performed best when both these variables were included and there was a high interaction between SST on *P. lineatus* abundance (Table 4.3). The combination of increasing daylength in late winter or August with warming temperatures were the determining variables behind the persistent annual periodicity of *P. lineatus* (Fig. 4.2B) and this pattern showed little interannual variation (Fig. 4.6C).

Table 4.3. Spearman correlations of each predictor for *Plectorhinchus lineatus*, *Acanthurus dussumieri* and *Lutjanus bohar*. Numerical values highlighted in bold indicate a high association between predictors or predictor and species and (NA) represents the predictor that was not included in the fish species best aggregated boosted tree models.

	Moon	**Daylength**	**Tide**	**Visibility**	**Temp.**	**Dt.num**
Plectorhinchus lineatus	-0.001	0.200	0.302	0.302	-0.220	-0.007
Moon		0.013	-0.019	-0.008	0.018	-0.002
Daylength			-0.068	0.114	**-0.680**	0.005
Tide				0.034	-0.060	0.058
Visibility					-0.254	-0.302
Temp						0.069
Acanthurus dussumieri	NA	-0.486	0.271	0.394	**-0.724**	-0.034
Daylength	NA		-0.068	-0.114	**0.680**	0.005
Tide	NA			0.034	-0.060	0.058
Visibility	NA				-0.254	-0.302
Temp	NA					0.069
Lutjanus bohar	0.019	-0.015	**0.675**	-0.015	NA	0.149
Moon		0.013	-0.019	-0.008	NA	-0.002
Daylength			-0.068	-0.114	NA	0.005
Tide				0.034	NA	0.058
Visibility					NA	0.302

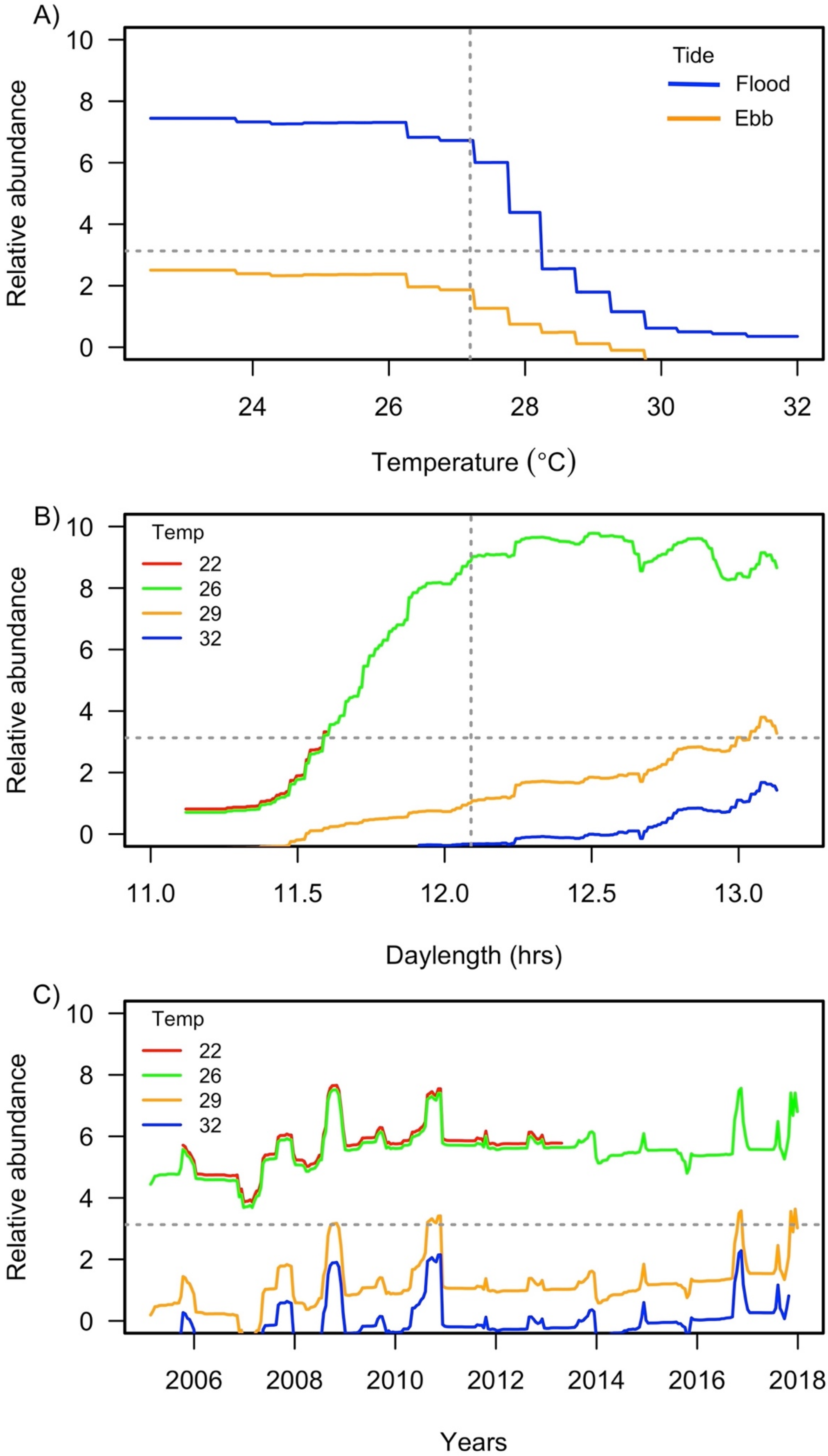

A)
Relative abundance
Tide
Flood
Ebb
Temperature (°C)
B)
Relative abundance
Temp
22
26
29
32
Daylength (hrs)
C)
Relative abundance
Temp
22
26
29
32
Years

Fig. 4.6. Partial interaction plots for the response *Plectorhinchus lineatus* abundance (sqrt(x)): A) as a function for surface seawater temperature °C (SST) given tidal direction, B) as a function for daylength to different surface seawater temperatures °C (SST) and C) as function numerical date to different SST's. Horizontal lines show the mean relative abundance of *P. lineatus* and the vertical dotted line shows the mean daylength in hours.

4.4.2 Acanthurus dussumieri

Surface seawater temperature was the dominant environmental predictor that influenced the occurrence of *A. dussumieri* at the Moore Reef fish aggregation site. Permutation tests show there were 6.6 times more fish (Table 4.2) when SST was below 26 °C (Fig. 4.7A). The reoccurring peaks in abundance each year (Fig. 4.7B) highlighted the preference for cooler SST associated with the austral winter months. Although shorter daylight hours are associated with the peak times in fish abundance, this predictor had minor influence (Fig. 4.7C). The short term semi-diurnal tidal cycle was also an important predictor (Table 4.2) and although there was a significant difference between tidal phases with more fish present during flooding tides, a proportion of fish remain at the fish aggregation site during ebb tides (Fig. 4.7D). Like the other two species in this study, visibility greater than 10 m improved UVC counts at the fish aggregation site (Fig. 4.7E).

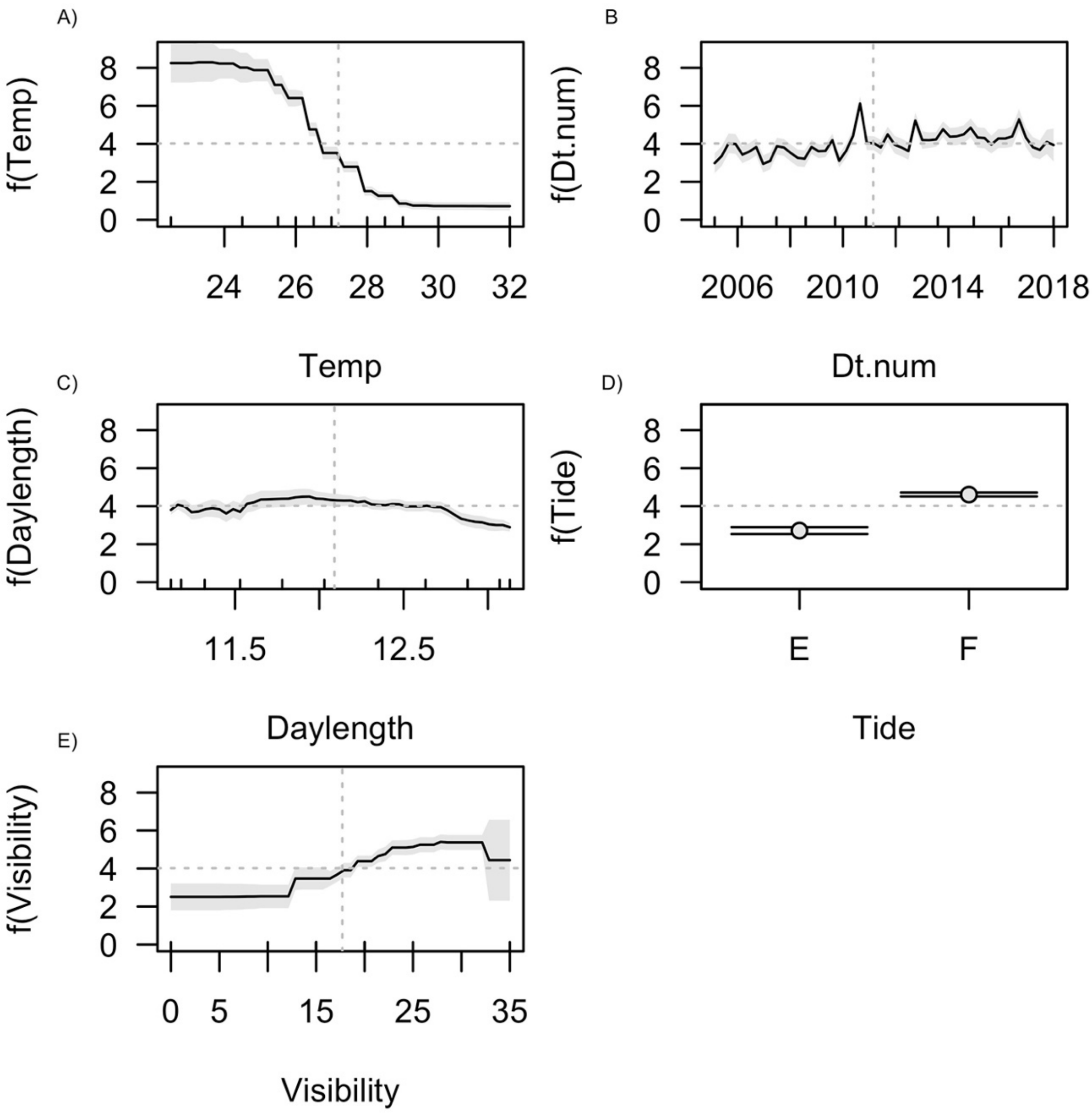


Fig. 4.7. Partial dependency plots for the response of *Acanthurus dussumieri* abundance from the best aggregated boosted tree models against predictors: A) surface seawater temperature, B) numerical date, C) daylength, D) tidal current and E) visibility. Shading around the response lines is two standard errors and the vertical dotted lines show the mean value for each predictor.

Cooler SST had the dominant influence on the occurrence of *A. dussumieri* (Table 4.2), and partial interaction plots were carried out to examine the interaction between SST with the hourly tidal cycle and then annual cycle of daylength. There were always more fish present when the tide was flooding compared to ebbing. During both stages of the short-term tidal cycle, relative fish abundance was above the mean when SST was < 26.5 °C (Fig. 4.8A). Maximum fish abundance was achieved when SST was coolest at 22 °C and the days relatively short. With increasing temperature and daylength, relative fish abundance was above the mean, if SST was at or below 26 °C. The abundance of *A. dussumieri* decreased rapidly once SST was above 26 °C, even during short days (Fig. 4.8B). Furthermore, this species preference for cooler SST's and the importance of SST as a cue was exemplified in the years that experienced cooler SSTs (Fig. 4.8C).

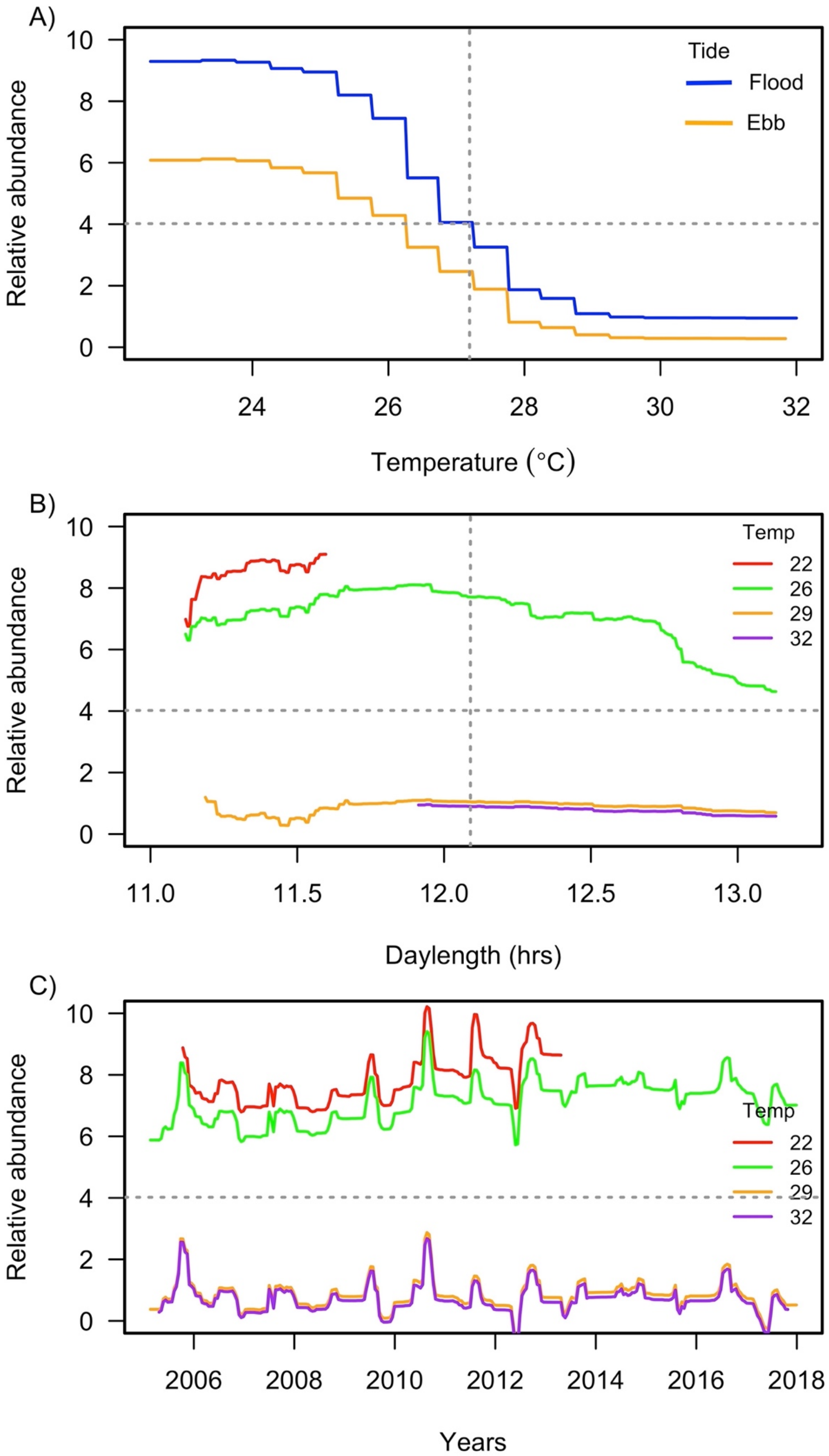

A)
Relative abundance
Temperature (°C)
Tide
Flood
Ebb
B)
Relative abundance
Daylength (hrs)
Temp
22
26
29
32
C)
Relative abundance
Years
Temp
22
26
29
32

Fig. 4.8. Partial interaction plots for the response *Acanthurus dussumieri* abundance (sqrt(x)): A) as a function for surface seawater temperature °C (SST) given tidal direction, B) as a function for daylength (hrs) to different SSTs and C) as a function of numerical date to different SSTs. Horizontal lines show the mean relative abundance of *A. dussumieri* in all plots and the vertical dotted line shows the mean SST for plot (A) and daylength for plot (B).

4.4.3 Lutjanus bohar

The mixed semi-diurnal tidal cycle was the dominant predictor out of a suite of five for *Lutjanus bohar* at the Moore Reef fish aggregation site. Permutation tests showed that there were 5.8 times more fish (Table 4.2) when counts were made on flood compared to ebb tides (Fig. 4.9A). The partial dependency plots showed variable fish abundance between years, with a trend in increasing abundance following 2011 (Fig. 4.9B). Daylength had no influences on changes of abundance as relatively high abundance was associated with short as well as long days (Fig. 4.9C). Lunar cycles had a negligible influence on predicting the occurrence of *L. bohar* (Fig. 4.9D). Underwater visual census counts of this mobile species improved when visibility was good, that is over 10 m (Fig. 4.9E). Permutation tests showed that visibility could have a 2.5-fold effect on UVC counts of *L. bohar* (Table 4.2). There was also a moderate degree of association between visibility and UVC counts made between years (Table 4.3). Nevertheless, this did not change the conclusion that fish were always present in high abundance on flood tides.

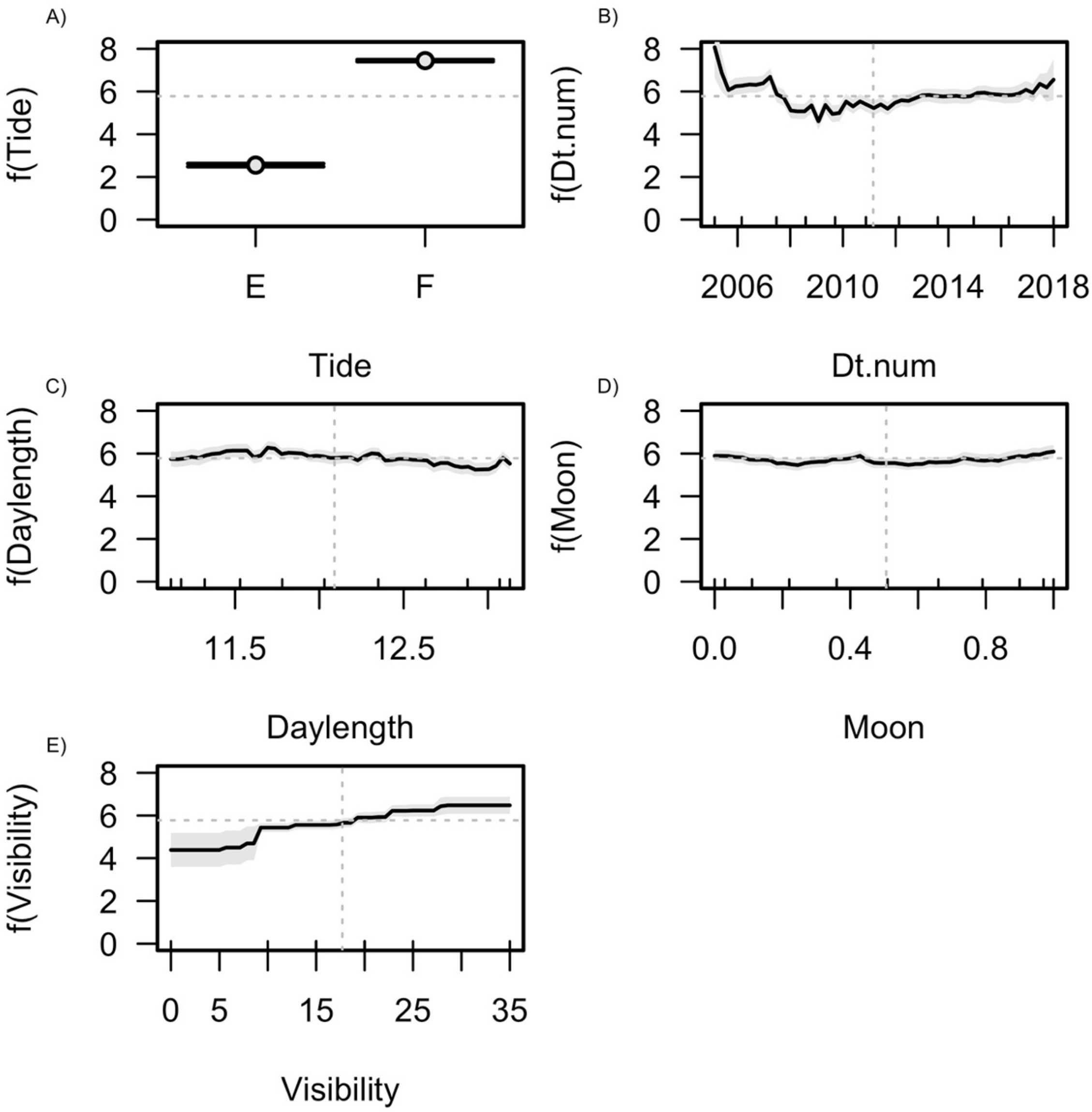


Fig. 4.9. Partial dependency plots for the response of *Lutjanus bohar* abundance from the best aggregated boosted tree models against predictors: A) tidal current, B) numerical date, C) daylength, D) moon phase and E) visibility. Shading around the response lines is two standard errors. Horizontal lines show the mean relative abundance of *L. bohar* and the vertical dotted lines show the mean value for each predictor.

4.5 Discussion

This study represents the highest resolution underwater visual census conducted on a multi-species fish aggregation site. The abundance of three large conspicuous coral reef species was collated and compared against a suite of proximate factors ranging in temporal cycles from hours to years. All three coral reef fish species displayed clear and consistent annual patterns of aggregation that persisted over the 13-year investigation. The annual patterns persisted, despite interannual fluctuations in surface seawater temperature (SST) and major perturbations such as mass coral bleaching and severe tropical cyclones (TC). The haemulid, *Plectorhinchus lineatus* and the acanthurid, *Acanthurus dussumieri* displayed strong seasonal cycles, while the lutjanid, *Lutjanus bohar* was ubiquitous throughout the annual cycle. The proximate cues predicting timing of aggregation were identified for the three coral reef fishes with high accuracy ranging between 70 to 80% efficiency. Although the timing of aggregation was consistent for each species, there were interannual and intermonthly fluctuations in mean abundance. The persistent patterns of aggregation in the selected fishes allowed inferences to be made on the adaptive significance of aggregation behaviour.

Two broad patterns of aggregation were identified among the three large fishes in this study. The haemulid, *P. lineatus* and the acanthurid *A. dussumieri* demonstrated regular seasonal periodicity, while the lutjanid *L. bohar* aggregated daily at the Moore Reef fish aggregation site. The seasonal cycles of the benthic invertivore *P. lineatus* and the omnivore *A. dussumieri,* corresponded to austral spring and austral winter seasons respectively. Although *A. dussumieri* aggregations often persisted through to mid-spring if SSTs were cool. Temporal sharing of aggregation sites by several species at discrete or overlapping seasons has been well documented for several other multi-species fish aggregation sites (Domeier and Colin 1997; Johannes et al. 1999; Claydon 2004; Heyman and Kjerfve 2008; Sadovy de Mitcheson and Colin 2012; Kobara et al. 2013; Sakaue et al. 2016). The Moore Reef fish aggregation site was used by fishes that aggregated seasonally and daily and the patterns could be explained by environmental cues.

The primary proximate cues triggering initiation and cessation of aggregation varied among fishes forming seasonal or daily aggregations and were also species specific. The two species that formed seasonal aggregations differed in the proximate cues initiating aggregation. Both

SST and daylength combined, cued *P. lineatus* aggregation in late austral winter/early spring months. A photothermal combination of SST and daylength were often responsible for synchronising reproductive activity in many temperate fish families (Wang et al. 2010). In tropical environments, seasonality is less marked than temperate. In the tropics the difference between summer and winter is approximately two hours where at 40 latitude the difference is approximately six hours. The importance of daylength in natural tropical environments as an entraining variable remains poorly understood (Pankhurst and Porter 2003). However, from my 13-year database I provided evidence for *P. lineatus* that both daylength and SST determined the aggregation of hundreds of fish; SST also modulated fish abundance and cessation of aggregation.

Daylength at the latitude of Moore Reef is less ambiguous in variation compared to SST and provided a consistent signal for initiation of *P. lineatus* aggregation in August each year. Some studies correlating environmental factors with fish aggregations have suggested the potential importance of photothermal cues in predicting aggregations. For example, decreasing photoperiod and water temperature cued the seasonal spawning aggregation of the serranid *Epinephelus striatus* in Belize (Carter et al. 1994) and *E. guttatus* aggregations in US Virgin Islands (Nemeth et al. 2007b). Whereas the spring equinox coupled with rising water temperature cued *Lutjanus cyanopterus* spawning aggregations at Gladden Spit, Belize (Heyman et al. 2005). These studies were not designed to empirically evaluate the importance of environmental variables on aggregation behaviour however they were extremely important in characterising fish aggregation behaviour. This current high-resolution study demonstrated the importance of photothermal cues in regulating and predicting the timing of aggregation in the tropical haemulid *P. lineatus*.

In contrast, SST was the primary proximate cue that determined the initiation and cessation of the seasonal *A. dussumieri* aggregation at Moore Reef. Each year of the study, SST modulated fish abundance and longevity of the aggregation. This was particularly evident in warmer years when cooler periods were constrained such as 2010. The influence of daylight hours in predicting fish aggregation was more likely related to the high correlation between SST and daylength. Water temperature plays a fundamental physical regulatory factor in all physiological stages of reproduction in fishes (Pankhurst and Porter 2003; Pankhurst and Munday 2011; Asch and Erisman 2018). Most fishes forming seasonal spawning aggregations demonstrate a thermal niche in which they reproduce, for example, the Nassau grouper *E. striatus* has a narrow thermal niche of 25-26.5 °C for reproduction (Nemeth 2009). The surgeon fish *A. dussumieri* represents one of the largest acanthurids and females are known to actively spawn in winter/spring in Hawaii (Pardee et al. 2022).

Although little information is known about *A. dussumieri* spawning behaviour. Many small to intermediate size (< 35 cm) acanthurids are known to form spawning aggregations (Robertson 1983; Colin and Clavijo 1988; Craig 1998; Mazeroll and Montgomery 1998; Claydon et al. 2012; Fisher et al. 2018), but spawning aggregations are only suspected in some larger acanthurids (Domeier 2012). The seasonal aggregations of hundreds of *A. dussumieri* at Moore Reef are determined by SST with a thermal range between 22-26°C. This had a significant effect on the number of fish aggregating and the period of aggregation. For example, in the years post 2014, the warmer winters produced smaller and shorter aggregations, which may constrain its aggregation behaviour in the future due to anthropogenic climate change (Asch and Erisman 2018).

The proximate factors daylength and or water temperature, are important in cuing seasonal reproductive activity in many fishes including aggregating fishes (Wang et al. 2010). Various other environmental factors such as lunar phase, tidal phase and time of day cue spawning behaviour within seasons (Colin 2012). Synchronising spawning with specific lunar phases has been well known for many large fishes such as epinephelids and lutjanids forming spawning aggregations (Johannes 1978; Colin 1992; Johannes et al. 1999; Heyman et al. 2005; Kadison et al. 2006; Sakaue et al. 2016; Murata et al. 2021). In this study, specific lunar phase was not an important cue for both *P. lineatus* and *A. dussumieri* in synchronising aggregations at the Moore Reef fish aggregation site. However, these results may be to the limited sampling design in that fish were only sampled during early afternoon. The focus of Chapter 5 was to further investigate fish aggregation behaviour during dusk and dawn in relation to tidal flow and lunar phase. Furthermore, poor water visibility also influenced the accuracy of results with fish counts higher on days when visibility was greater than 10m. Although, given the high frequency of counts and the mean visibility was 18m, this limitation had little influence on the overall conclusions.

A key finding was the importance of the flood stage of the semi-diurnal tidal cycle cued both *P. lineatus* and *A. dussumieri* to form and disperse daily, within their respective seasons. In contrast, the lutjanid *L. bohar* showed no seasonal or lunar pattern, only demonstrated a strong tidal pattern of aggregation cued by daily flood tides. The importance of tidal cycles synchronising spawning aggregations (Johannes 1978; Thresher 1984; Colin and Clavijo 1988; Claydon 2004; Nemeth 2009; Erisman et al. 2012; Fisher et al. 2018) and foraging aggregations (Wolanski and Hamner 1988; Zamon 2003; Genin 2004; Eggertsen et al. 2016) has been well documented in the literature. Semi-diurnal tidal rhythms at the Moore Reef pass produce predictable alternating current flows that are not influenced by season (Chapter 2). Flood tides were characterised when water flowed from the ocean, through the reef pass and into the coral lagoon of Moore Reef. On Ebb tides this pattern was reversed and water flowed out of the coral lagoon through the reef pass and onto the continental shelf. These flows have the capacity to import allochthonous plankton and export fish eggs (Hamner et al. 1988; Hamner et al. 2007; Morais and Bellwood 2019). Predictable oceanographic patterns are believed to be a selective feature for fishes forming spawning aggregations (Karnauskas et al. 2011; Choat 2012).

A significant finding was that large perturbation events such as severe TCs and mass coral bleaching events did not disrupt the timing of aggregation for all three species. This supports other studies that have found resilience in spawning aggregating fishes during intense episodic disturbances. The temperate estuarine species the spotted sea trout, *Cynoscion nebulosus* was found to spawn daily during and the days immediately after the passing of a severe hurricane in Texas (Biggs et al. 2018). The current study also provided evidence that the years post the passing of severe TC's did not disrupt timing of aggregation. Even after the passing of TC "Yasi" in 2011 at fish aggregation site, destroyed most tabulate corals and this drastic reduction in live coral habitat was characteristic for several reefs between Cairns and Townsville on the GBR (De'ath et al. 2012; Beeden et al. 2015). However, disruptive disturbance to coral habitat on the GBR are known to have little influence on the occurrence and abundance of large predatory fishes, including *L. bohar* (Emslie et al. 2017).

The robust patterns I found over a 13-year time series and strong inferences on the cues fishes used for aggregations, begs the question why? How would aggregation benefit the survival of adults and early life history. The seasonal occurrence of the haemulid *P. lineatus* and the acanthurid *A. dussumieri* cued by daylength and SST aligns with reproduction. The flooding tidal phase cued daily aggregations within season and aligns with several paradigms that include a focus on adults, such as the availability of mates and mate selection (Lobel 1978; Colin and Clavijo 1988) of reducing predation risk while spawning (Hamilton 1971;

Johannes 1978; Shapiro et al. 1988). In contrast, synchronicity may favour the survival of the young. Fishes known to synchronise their spawning behaviour with flood tides, most spawn at high water or change from flood to ebb when currents favour off reef transport (Colin and Clavijo 1988; Colin and Bell 1991; Sancho et al. 2000b; Nanami et al. 2013). If fishes at Moore Reef spawned at high water or when tidal flows changed direction, this would guarantee off reef transport of eggs (Chapter 2). Such spawning behaviour with predictable currents, favours paradigms that includes reduced predation on eggs (Johannes 1978; Lobel 1978), improved larval survivorship (Doherty et al. 1985), dispersal (Barlow 1981) or retention of pre-settlement fishes near the natal reef and into suitable nursery habitats (Johannes 1978; Lobel 1978). Local hydrodynamic data of Moore Reef fish aggregation site, support retention of larvae to Moore Reef over dispersal (Chapter 2). The results also questions do the persistent daily aggregations of the lutjanid *L. bohar* align with reproduction and or foraging on predictable prey coupled with flooding tides (Fisher et al. 2018). *L. bohar*, a known aggregative spawner (Sadovy de Mitcheson and Colin 2012) forms daily aggregations in Palau and spawns with lunar periodicity and changes in tidal flows (Sakaue et al. 2016). On the GBR, *L. bohar* has a prolonged spawning season (Marriott et al. 2007) and it seems plausible that both spawning and foraging may occur frequently at Moore Reef aggregation site by this mobile piscivore. Clearly there are potential benefits for group spawning, survival of larvae and a trophic advantage. The behaviour of fish, while aggregated, also provides insight to potential ultimate factors (Mayr 1961) and that is the focus of Chapter 5.

4.6 Conclusion

In summary, this study has provided one of the longest data sets on the activity of fishes at a known aggregation site. Contrasting patterns of aggregation were found among three species. Two species *P. lineatus* and *A. dussumieri* had strong periodicity in aggregation where they were only found at the site over a few months. In contrast, *L. bohar* was found at the aggregation site in large numbers at all times of the year. All three species were most abundant on the flood tide regardless of their seasonal periodicity. Predictive models for three species of fish were able to resolve with high accuracy the proximate cues entraining aggregation formation and provide understanding to phenology. Photothermal cue that is both SST and daylength ranked in importance for *P. lineatus*, but there was strong evidence that

SST not daylength was the primary cue for *A. dussumieri*. Perturbations that included cyclones and bleaching events did not affect the periodicity of aggregations. There was, however, some evidence that numbers at the site varied because of perturbations which may alter short-term variation in SST. For example, excessive cloud cover during Tropical Cyclones can cause SST to distinctly drop (Leahy et al. 2013) The findings of the study are highly relevant to understanding local changes in the distribution of fishes, spawning periodicity, expatriation and the retention of larvae and tropho-dynamics. Further research on aggregation behaviour at sites of small spatial scale, will provide a broader understanding of spatial and temporal variation in fish abundance and data that are relevant to fisheries management.

Chapter 5: Aggregation behaviour of three species of large coral reef fishes on the Great Barrier Reef

5.1 Abstract

Coral reef fishes aggregating in the Great Barrier Reef displayed distinct behavioural profiles at a multi-species fish aggregation site, that reflected the ultimate causes for fishes forming aggregations. This study utilised several non-invasive technologies for comparison among species to create a biophysical understanding of their aggregation behaviour. Behaviour was driven by reproduction in the haemulid *Plectorhinchus lineatus,* feeding in the snapper *Lutjanus bohar* and both feeding and reproduction in the large surgeon fish *Acanthurus dussumieri*. Prior to this study the reproductive behaviour of *P. lineatus* and *A. dussumieri* was unknown. Reproductive behaviour varied among species, with *P. lineatus* spawned in small groups of 6-10 individuals and *A. dussumieri* generally spawned in pairs. Of the hundreds of fishes continually aggregating adjacent this small-scale reef pass (60 m wide), most fishes were large adults. Although species distributions throughout the fish aggregation site overlapped, each species showed a distinct spatial profile and use of habitat to perform vital tasks. The haemulid *P. lineatus* formed highly dense aggregations, up to 180 fish per 10 m^2 in shallow water, whereas *A. dussumieri* and *L. bohar* were more broadly distributed throughout the water column with densities of 45 and 55 individuals per 10 m^2 respectively. Behaviours associated with feeding and reproduction were cued by time of day and weak tidal currents. Almost 75% of fishes aggregating displayed feeding or reproductive behaviour during slack water (0 - 0.1 m/s). This study provides empirical evidence of fish spawning with weak currents. Ultimately small-scale reef passes (~100 m wide), and associated oceanography support large coral reef fishes forming foraging and reproductive aggregations.

Key words: coral reef, fish aggregation, feeding, reproduction, reef pass, behaviour

5.2 Introduction

World-wide, many species of coral reef fish are known to gather in temporary aggregations at specific sites on coral reefs (Johannes 1981; Wolanski and Hamner 1988; Domeier and Colin 1997; Claydon 2004; Genin 2004; Sadovy de Mitcheson and Colin 2012; Claydon et al. 2014; Fisher et al. 2018; Galbraith et al. 2021). Physically, large coral reef fish aggregation sites are small spatial areas, often < 10,000 m^2 in area that occur adjacent to open water on outer reef fronts, promontories, reef passes, emergent reefs and submerged pinnacles (Wolanski and Hamner 1988; Genin 2004; Sadovy de Mitcheson et al. 2008; Choat 2012; Galbraith et al. 2021). The topography of these outer reef features is often exposed to variable hydrodynamics and have the capacity to import, temporarily concentrate or export biological material (Genin 2004; Hamner et al. 2007; Donahue et al. 2015). The combined physical processes of reef configuration and or hydrodynamics create favourable conditions for fish aggregations to feed and reproduce and consequently these areas are used by many reef fishes (Fisher et al. 2018). For example, 24 species of fish are known to aggregate at Gladden Spit in Belize to spawn and another 15 species of fish including sharks and rays that gather to forage on aggregators, or their eggs (Heyman and Kjerfve 2008). In turn, multi-species fish aggregation sites are biologically diverse and represent critical feeding and reproductive habitats to coral reefs (Heyman and Kjerfve 2008; Nemeth 2012). A fundamental aspect of determining the ecological importance of fish aggregation sites is to investigate the behaviour of aggregating species.

Coral reef fishes are known to form aggregations at predictable sites and times to perform vital tasks such as feeding, reproduction, resting and cleaning (Claydon 2004). Coral reef fish aggregation behaviour studies have mainly focused on fishes forming foraging aggregations (Parrish 1993; Genin 2004; Erisman et al. 2007) and spawning aggregations (Domeier and Colin 1997; Claydon 2004; Sadovy de Mitcheson and Colin 2012). Spawning in aggregations may increase reproductive output by increasing mate-encounter rates, facilitating mate choice and or improving fertilisation success (Molloy et al. 2012). Describing the how, when and where fish spawn in aggregations provides critical information on predator prey dynamics (Heyman et al. 2001; Mourier et al. 2016) and factors that may influence the fate of larvae (Heppell et al. 2008; Wolanski and Kingsford 2014). Within aggregations fish may spawn in pairs or in groups and sometimes the frequency of group spawns increases rapidly until the whole aggregation is spawning simultaneously (Robertson 1983; Myrberg et al. 1988;

Heyman et al. 2005). Pair spawning is characterised by spawning by a single male with a single female (Thresher 1984). In contrast, group spawning involves fish releasing gametes within groups containing several males and one or more females (Erisman et al. 2009). For example, the red snapper *Lutjanus bohar* often spawns in groups consisting of one female and several males (Sakaue et al. 2016).

With the frequency of these interactions increasing rapidly through a major event, predation on adults, egg predation, sperm competition and the volume of gametes per individual appear to be the selective forces driving pair versus group spawning behaviour within aggregations. Although there are no higher fertilisation benefits from spawning in groups compared to pair spawning (Petersen et al. 1992; Kiflawi et al. 1998), each mating strategy has its own cost and benefits. Spawning in pairs produces less gamete volume and a less visible egg cloud target for predators compared to group spawns (Robertson 1983). The risk of predation on pair spawning adults was also less compared to group spawning adults (Sancho et al. 2000a). However, it must also be considered that the predation risk on both eggs produced from multiple group spawns and spawning adults may be diluted due to the selfish herd hypothesis (Hamilton 1971). However, sperm competition or the conflict between two or more males to fertilize the eggs of females is often more intense in higher fish densities and fish of the same size (Erisman et al. 2009; Erisman and Hastings 2011). Sperm competition maybe a strong selective force to fish spawning in groups to improve reproductive fitness (Warner and Robertson 1978; Petersen et al. 1992; Warner 1997; Erisman et al. 2007; Molloy et al. 2012; Roff et al. 2017; Fitzpatrick 2020). Alternatively for some aggregative spawners, pair spawning may reduce the high metabolic costs associated with reproduction (Ginther et al. 2024).

For pelagic spawners, whether fish spawn in pairs or groups, the final act of spawning often involves a vertical rush upwards that culminates in the release of gametes at the apex, then followed by the rapid return of fish to the aggregation or substratum. This behaviour is commonly termed a spawning rush (Robertson and Warner 1978; Domeier and Colin 1997) and can occur close to the substrate, midwater or near the surface and is often species specific (Heyman and Kjerfve 2008). Where fish spawn in relation to substrate and water column appears dependent on body size and predatory pressure. Smaller bodied fish like several acanthurids are known to spawn only meters above the substrate in shallow water less than 10m meters (Robertson 1983; Myrberg et al. 1988; Craig 1998). In contrast, some larger body fish such as groupers and snappers tend to spawn in deeper water 10-30 m and up to 10's of meters in spawning rushes above the substrate (Samoilys and Squire 1994; Heyman et al. 2005). However, if the threat of predation is high, these rushes can be reduced to meters above the substrate for many larger fishes. For example, the marbled grouper *Epinephelus polyphekadion* restricted vertical rushes to less than 120 cm above substrate due to the high density and proximity of medium size sharks (Robbins and Renaud 2016).

Several other behaviours driven by proximal cues such as current flow, time of day and lunar phase may reduce predation risk to eggs, larvae and or adults and such cues can synchronise reproductive behaviour (Johannes 1978; Colin and Clavijo 1988). It has been suggested that aggregative spawners may time spawning when larger predators are less active such as the middle of the day or conversely at low light periods such as dawn and dusk when planktivores are less active (Shapiro et al. 1988). However, some large fishes time spawning at low light periods when larger planktivores such as the snapper *Macolor niger* target and consume egg clouds released by aggregative spawners (Colin 2012; Sadovy de Mitcheson and Colin 2012). Another factor influencing timing of spawning is coinciding gamete release with flows that immediately transport gametes away from outer reef environments (Johannes 1978) or the "wall of mouths" (Hamner et al. 1988) to open water is considered a strong evolutionary driver to when and where fish spawn (Choat 2012).

Predatory pressure on adults and or eggs and reproductive fitness appear as mechanisms driving aggregative spawning. However, trade-offs between spawning and predation on adults or eggs appear common in aggregative spawning of large fishes (Heyman et al. 2001; Heyman and Kjerfve 2008; Colin 2012; Mourier et al. 2016). The question is what mechanism drive aggregative foraging behaviour. In this study, foraging aggregations are defined as a repeatable gathering of conspecific fish in space and time for the primary purpose of feeding and are assigned a specific functional group classification such as piscivore, invertivore or coprophagous. It is well documented in the literature that large spawning aggregations of coral reef fish can attract predators that jointly aggregate to forage on temporary resource pulses, which is either the adults and or eggs (Craig 1998; Heyman et al. 2001; Heyman and Kjerfve 2008; Mourier et al. 2016; Robbins and Renaud 2016).

Local areas where currents interact with typography can concentrate prey items and initiate fish aggregations. For example, the repeatable gatherings of planktivores at specific locations on reefs such as spur and groove morphology of outer reef fronts (Hamner et al. 1988) and small-scale reef passes (Fisher et al. 2018) are gaining increasing attention due to their contribution to coral reef subsidies and productivity (Morais and Bellwood 2019; Morais et al. 2021). Like mixed species bird flocks that forage on predictable insect blooms (Sridhar et al. 2009) feeding aggregations of coral reef fish are often comprised of multiple species feeding on similar prey. For example, nine species of piscine predators were known to form diurnal feeding aggregations on several hundred thousand flat iron herring *Harengula thrissina* in the Sea of Cortez (Parrish 1992). One of the species was the leopard grouper *Mycteroperca rosacea*, known to form spawning and foraging aggregations at the same location (Sala et al. 2003; Erisman et al. 2007). Predictable high prey densities appear to be the dominant influence driving foraging aggregations although inter and intraspecific competition between predators of similar trophic ecology is probably ubiquitous at fish aggregation sites (Lester et al. 2021).

Given the dynamic nature of multi-species fish aggregation sites, foraging and reproductive behaviours are not mutually exclusive. For example, the lutjanid, *Lutjanus bohar* was observed feeding during spawning aggregative periods at the southern tip of Peleliu Island in Palau (Sakaue et al. 2016). Accordingly, site specific physical process such as geomorphology and hydrodynamic cycles influence fish aggregation behaviour. Seasonal, lunar, diel and tidal cycles are known proximal cues for many species of coral reef fishes to aggregate at precise times (Domeier and Colin 1997; Claydon 2004; Sadovy de Mitcheson and Colin 2012).

Previous work at a multi-species fish aggregation site on the Great Barrier Reef (GBR) demonstrated that three coral reef fish species displayed a clear and consistent pattern of annual aggregation that persisted over the 13-year investigation (Chapter 4). This suggested that there were two distinct phenomena occurring at this site, which governed seasonal and daily patterns of aggregation. The three species selected from three coral reef fish families were: *Plectorhinchus lineatus* (Haemulidae) a predator of benthic invertebrates (Lieske and Myers 2001), *Acanthurus dussumieri* (Acanthuridae) an omnivore (Barlow 1974; Choat et al. 2004; Cheal et al. 2012; Basford et al. 2015; Fisher et al. 2018) and *Lutjanus bohar* (Lutjanidae) a known aggregative spawner (Sadovy de Mitcheson and Colin 2012; Sakaue et al. 2016) and piscivore of small mobile reef associated fishes (Wright et al. 1986; Farmer and Wilson 2011). The three species represented excellent candidates to form a comparative study between fish behaviour and environmental cues. Quantitative information on the timing of aggregation behaviour either reproductive or trophic, relative to quantifiable current flows for many aggregating fish species remains relatively unknown.

This study was conducted on a multi-species fish aggregation site on the Great Barrier Reef (GBR) (Fisher et al. 2018) and investigated the aggregation behaviour of three selected coral reef fishes in this quantitative study. Previously there was a dearth of information and or data on the reproductive behaviour of *A. dussumieri* and *P. lineatus.* This study documents spawning behaviour in both species. The previous work that described high resolution aggregation patterns of these three species (Chapter 4) provided focus on when to study the behaviour of these fishes. Focus was directed to study fishes during dusk and dawn and lunar phases coinciding with slack water prior to current reversal at high water. Detailed observations were required to compliment broad descriptions of the timing and location of aggregations. Accordingly, to further investigate aggregation behaviour, this study focused on three components of their biology, which included defining: 1) temporal variation in the size structure of aggregating fish, 2) their depth-related positioning within the fish aggregation site and 3) characterise their behaviour in relation to variable current flows and lunar cycle.

5.3 Methods

5.3.1 Study Site

Moore Reef pass (Fig. 5.1A) is situated approximately 55km East of Cairns on the outer margin of the continental shelf in the northern section of the Great Barrier Reef (GBR) (Fisher et al. 2018). The reef pass dissects the reef flat and was ~330 m in length, 60 to 250 m in width and 14 to 22 m in depth with a north to south orientation. The reef front on the outer side of the pass and the leeward edge on the inner side of the pass both terminate at ~ 20 m depth into a sand-rubble substratum dotted by isolated coral patches. The fish aggregations site (-16.845°, 146.23°) covers an area of ~3,500 m^2 and situated on the north-west aspect of the reef pass (Fig. 5.1B). In 1981, the Great Barrier Reef Marine Park Authority (GBRMPA) have classed Moore Reef as Marine National Park Zone with limited recreational fishing permitted (GBRMPA 1982), then in 2003 it was listed as a no take area and of high conservation value (GBRMPA 2004). Accordingly, fishes at the fish aggregation site were not affected by extraction. The research carried out in this study was conducted under GBRMPA research permit G12/35200.1.

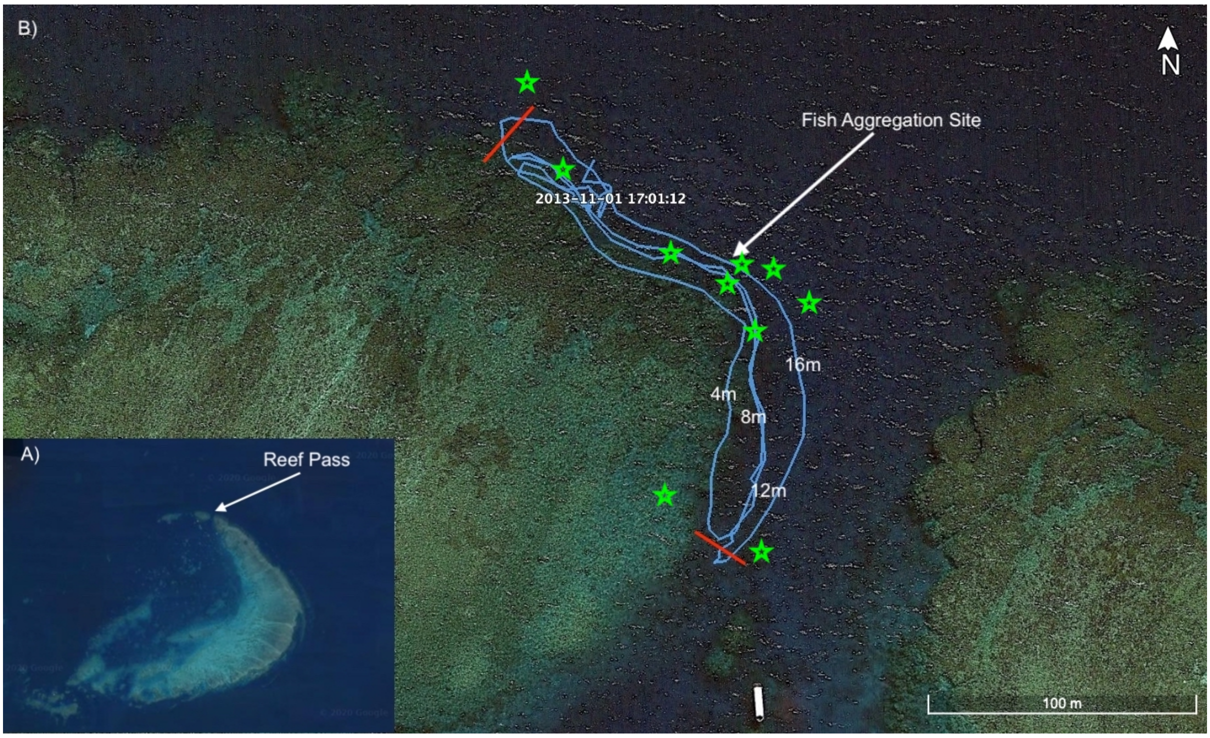


Fig. 5.1. Site map of Moore Reef pass and fish aggregation site; A) location of the reef pass within Moore Reef and B) the belt transect path conducted using the diver operated stereo-video system. The path on which fish were plotted was recorded from towing a handheld Garmin Global Positioning System Handset. The four paths represent four individual depth transects carried out at 16, 12, 8 and 4 meters. These paths initiated either along the outer reef slope or well inside the reef pass, marked by short red lines, then moved through the fish aggregation site. This path was recorded on 1-Nov-2013 and representative of all paths conducted through the sampling schedule. The green stars show the positions of the Marotte current meters used in this study.

5.3.2 Size structure and spatial positioning of aggregating fish

Diver operated stereo-video equipment was used to investigate the size structure of three large species of coral reef fish which were predictable in their occurrence at the Moore Reef fish aggregation site (Fisher et al. 2018). Stereo-video technology has been widely accepted as an accurate non-invasive method to survey the size structure of fish populations (Harvey et al. 2003; Taylor 2014; Rastoin-Laplane et al. 2020) and juvenile or small fishes less than 10cm (Castro-Fernández et al. 2022). Three individual stereo-video units were utilised over the length of this study. Each unit was comprised of two High-Definition Digital Cameras mounted in protective housings on an aluminium cross bar. A light emitting device was positioned at the centre of the cross bar and in-between the two cameras to synchronise the recorded frames and ensure there are no systematic errors from motion displacement (Shortis et al. 2009). Prior to use, the stereo-video units were calibrated using the CAL software (SeaGIS 2022).

The stereo-video was swum via SCUBA through the fish aggregation site along ~ 250 m transects (5 m wide) conducted at 16, 12, 8 and 4 m (Fig. 5.1B). The 16 and 8m transects initiated on the outer reef slope of Moore Reef, then moved through the fish aggregation site and terminated well inside the reef pass. This point was the start of the 12 and 4m transects, then moved north along the reef pass and through the fish aggregation site and terminated at the starting point of the 16 and 8m transects (Fig. 5.1B). The specific depth stratified transects followed the line or contour of the reef, which was considered the centre of the belt transect.

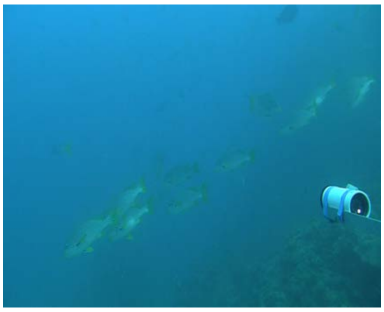
Spatial positions of individual fish were recorded from towing a handheld Garmin GPSMAP78 global positioning system (GPS) while conducting the specified depth transects for each sampling period. The GPS unit was mounted in a modified dive float with a waterproof PVC housing that kept the unit positioned vertically to ensure good connection with satellites. The unit was connected to the scuba diver with the stereo-video technology via a diver's reel to ensure the GPS was positioned directly above at depth (Nemeth et al. 2007a). The time on the GPS and video cameras were synchronised to allow accurate recording of fish positions along transects and positions of each fish were recorded in decimal degrees.

Time of day and variable current regimes have been identified as important cues for fish aggregation behaviour (Domeier and Colin 1997; Claydon 2004; Sadovy de Mitcheson and Colin 2012). Previous sampling had shown that the three selected species were abundant only on flooding tides and disperse from the fish aggregation site with the onset of ebbing tides (Chapter 4). Current reversal was observed when water moved out through the reef pass towards the open sea and away from the coral reef environment. This current regime was predictable and occurs 1-2 hours prior high water (Chapter 2). The coincidence of the last stages of the flood tide, slack water and then the initial stages of the ebb tide with sunset and sunrise meant that sampling was restricted to up to 4 days prior to new and full moons of the lunar cycle. Late afternoon refers to the hour immediately before sunset and early morning refers to the hour after sunrise. Sampling was conducted twice a month from September to December for both 2013 and 2014 during peak aggregation times. Outside the spring months additional sampling was conducted in April, July and August 2014 to provide information during non-peak aggregation times (Chapter 3).

5.3.3 Fish behaviour

The stereo-video transects allowed fish behaviour to be recorded along the sampling schedule, which was classified into specified categories for each species (Table 5.1). The haemulid, *Plectorhinchus lineatus* behaviour was categorised into three distinct behaviours which included: milling, travelling down and travelling up. Milling behaviour was described as the aggregation appeared stationary around a specific point in which many individuals that appeared gravid moved around or through the aggregation in a circular or random motion (Myrberg et al. 1988). Travelling down behaviour was associated with a small group (2-20 fish) that moved away from the stationary aggregation (milling), which continued to move down the outer reef slope and out to deeper water. This behaviour was associated with spawning. To clarify this behaviour, focal observations were taken on separate dives not dedicated to stereo-video transects. On several occasions it was observed that these fish moved away from the base of outer slope at ~ 18m deep, travelling quickly and chasing one individual out to deeper water (> 23 meters). This linear behaviour away from the wall, was often punctuated with pauses as individuals continued chasing each other in a circular motion. During these pauses, gravid fish were observed spawning, that was the release of white gamete clouds only meters off the substratum. Following this behaviour individuals often dispersed and returned to the slope and re-joined the main *P. lineatus* aggregation and this behaviour was recorded as travelling up (Table 5.1).

Table 5.1. Images showing classified behaviour for *Plectorhinchus lineatus*, *Acanthurus dussumieri* and *Lutjanus bohar* recorded during stereo-video transects.

Plectorhinchus lineatus	*Acanthurus dussumieri*	*Lutjanus bohar*
		
Milling	Active	Active
		
Travelling down	Courtship	
		
Travelling up		

The acanthurid, *Acanthurus dussumieri*, displayed two behaviours classed as active and courtship (Table 5.1). The active behaviour described individuals positioned out in open water away from the reef slope. These fish were either observed swimming slowly facing into the current and moving gently up and down, or fish were observed swimming closely behind larger fish. The fish being followed, represented several species of different trophic classification which included piscivores (Lutjanidae and Carangidae), predators of benthic invertebrates (Haemulidae and Lethrinidae) and planktivores (Acanthuridae and Caesionidae). The active behaviour was associated with foraging or searching for prey, either through planktivory or coprophagy (Fisher et al. 2018). Courtship behaviour was often associated with pairs and showed one individual developing a dark colouration on the head and chasing the other individual. These specialised colour changes and chasing behaviour are often associated with imminent spawning behaviour in coral reef fish (Robertson 1983; Thresher 1984; Sadovy de Mitcheson and Colin 2012).

The third species in this study, *Lutjanus bohar* only exhibited one behaviour which was categorised as active (Table 5.1). This behaviour was described as quite mobile aggregations, chasing prey (Caesionidae and spawning Acanthuridae), chasing each other and colouration changes more associated with feeding (Feitosa et al. 2012) than reproductive behaviour (Sakaue et al. 2016). Although *L. bohar* was always in aggregations spawning was not observed. The active behaviour described for both *A. dussumieri* and *P. lineatus* was associated with foraging. Although direct consumption of prey or faces was not always observed, the active behaviour was associated with searching for prey.

5.3.4 Water current speed and direction and lunar phase

Specific information on fine scale current speed and direction was collected from an array of current meters positioned along the stereo-video transect path (Fig. 5.1B), which ranged in depth between 4-23m (Table 5.2). Two versions of Marotte current meters were utilised in this study, firstly the Marotte, then followed by trials of the Marotte HS. The Marotte current meter consisted of a buoyant sphere with a HOBO logger inserted, that needed to be calibrated for direction. This instrument worked on the drag-tilt principle and recorded current speed and direction at one-minute intervals. These instruments were used during the sampling periods of 2013 and 2014. During September 2014, several prototype instruments of Marotte HS were trialed. These instruments worked on the same physical principle, however, were more refined in that they encased electronics had a built-in magnetometer and recorded current speed direction at one second intervals. The Marotte HS was powered by 2 x double A batteries and lasted several months, where the Marotte HOBO logger only had a capacity of 2 weeks. More detailed information on these instruments was provided in Chapter 3.

Table 5.2. The depth in meters, substrate type and position in decimal degrees of the 10 Marotte current meters positioned along stereo-video transect path.

Logger number	Depth (m)	Substrate Type	Position
1	5	Rubble/Coral Rock	-16.846283 146.230083
4	8	Coral Rock	-16.845583 146.230150
5	23	Sand/Rubble	-16.845717 146.230450
7	14	Rubble/Coral Rock	-16.845867 146.230333
9	11	Coral Rock	-16.845700 146.230250
10	8	Coral Rock	-16.845567 146.23000
11	9	Coral Rock	-16.845667 146.230217
12	12	Coral Rock	-16.845150 146.229867
13	21	Sand/Rubble	-16.845850 146.230633
15	6	Coral Rock	-16.846533 146.230467

Lunar phase for sampled days were represented as a decimal fraction of luminosity, which was a quantitative way of describing the moon's phase (USNO 2023). The measurement ranges from zero to one. Zero described the new moon phase, while 1 described the full moon phase. First and last quarters were represented by 0.5 and can be distinguished by noting whether the fraction illuminated was increasing or decreasing. First Quarter occurred when the fraction illuminated was increasing (Moon waxing; in evening sky) and Last

Quarter occurred when the fraction illuminated was decreasing (Moon waning; in morning sky) (USNO 2023).

5.3.5 Image and data analysis

Pairs of stereo-video frames were processed using EventMeasure Software (SeaGIS 2022) and each selected species inside each depth stratified transect area (~1,250m^2) was measured to the nearest mm (fork length) with a maximum root mean square error (RMS) of 20mm. In stereo-video surveys the RMS serves as an indicator for the reliability of measurement and fish were measured within 7m of the camera to ensure high accuracy (Harvey et al. 2010).

The data comprised 3,163 individual fish total length measurements from the three species during the sampling schedule of 2013 and 2014. The average precision of length measurements for each species was less than 10mm. Sampling periods were divided into A.M. (early morning) and P.M. (late afternoon) meridiem categories. The length data for each species was used to construct length frequency plots for both A.M and P.M sampling periods, with 1,947 fish sampled in the P.M., compared to 1,216 fish for the a.m. The Kolmogorov–Smirnov two-sample test was used to determine whether the distribution of fork length (50mm size classes) was the same across A.M. and P.M. samples for each species. Length frequency histograms for monthly samples were constructed to show fish size distribution over 2013 and 2014.

The spatial position (latitude and longitude in decimal degrees) and depth were recorded for each fish measured in this study along the stereo-video transects (Fig. 5.1). The fish aggregation site was divided into ~ 10 m^2 grid cells and the frequency of fish per grid cell were plotted for each species at the four specified transect depths.

A behavioural classification was also assigned to each fish measured along with its spatial position. This allowed the closest current meter station to be located and assign a current speed and direction value to the fish's behaviour. The current speed and direction data for each measurement was converted to a vector in that each value has a magnitude and a direction along the direction of the passage. Positive values show current flowing to the north or away from the reef and negative values show current flowing south or onto the reef. All analyses were performed in R (RCoreTeam 2021) and used the open-source libraries fishmethods (Gary 2022), ggmap (Kahle and Wickham 2013) and tidyverse (Wickham et al. 2019).

5.4 Results

5.4.1 Size Structure

All fishes aggregating at the Moore Reef fish aggregation site were large fish at lengths of 275mm or greater (Fig. 5.2). Differences in mean size between early morning (A.M.) and late afternoon (P.M.) were minimal (Fig. 5.2) and the Kolmogorov–Smirnov two-sample test found no significant difference in size frequency between early morning (A.M.) and late afternoon (P.M.) for each species (Table 5.3).

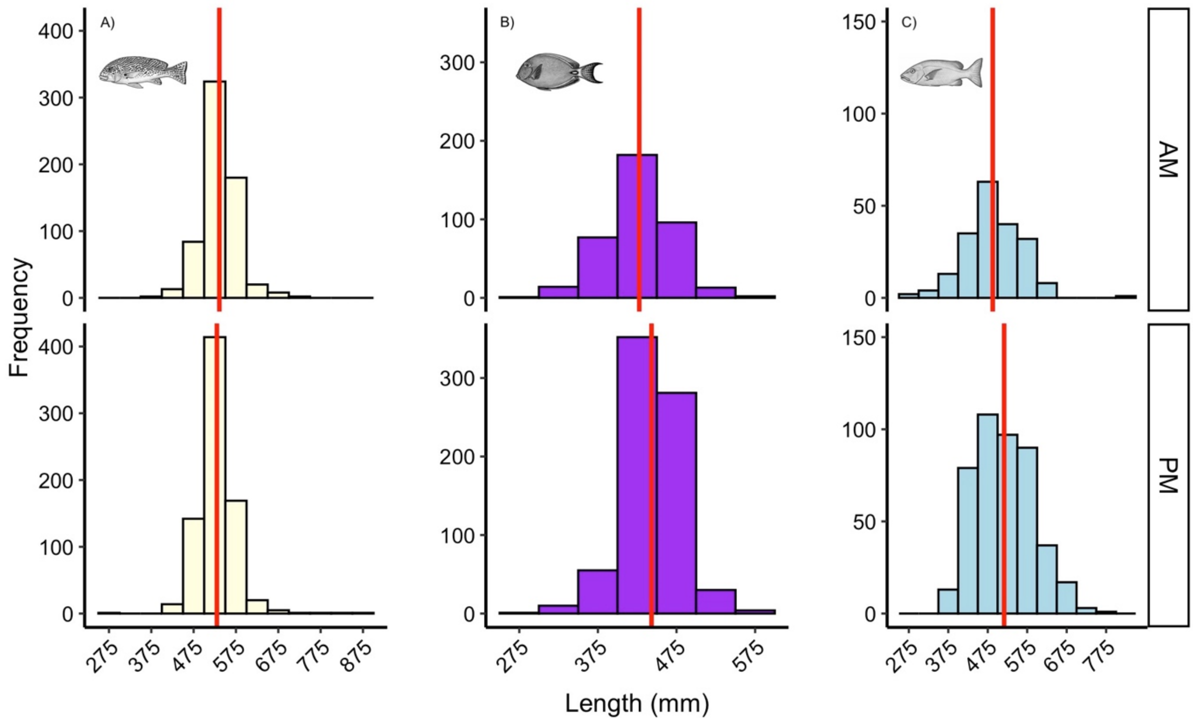


Fig. 5.2. Length frequency histograms for early morning (A.M.) and late afternoon (P.M.) sampling for fishes at the fish aggregation site; A) *Plectorhinchus lineatus*, B) *Acanthurus dussumieri* and C) *Lutjanus bohar*. Length measurements represent fork length (mm) and the bin width was 50mm. The mean size of each species for both early morning (A.M.) and late afternoon (P.M.) was illstrated by a vertical red line.

Table 5.3. Results of the Kolmogorov–Smirnov two-sample test for each species.

Statistics	***Plectorhinchus lineatus***	***Acanthurus dussumieri***	***Lutjanus bohar***
D	0.07	0.15	0.14
p	> 0.05	> 0.05	> 0.05
n	1,402	1,118	643

With *Plectorhinchus lineatus*, 77.5% of the aggregation ranged between 500 – 600 mm (Table 5.4). Overall fish ranged between the 293 and 873mm and fish less than 399 mm only comprised 0.2 % of the total sample. In contrast, larger fish (> 600 mm) represented 4.3% of the sample (Table 5.4). Large fish were also characteristic of the omnivore *Acanthurus dussumieri* aggregation, with 81.5% of the sample ranging between 400 and 500mm (Fig. 5.2B). Only 0.2% of fish sampled were less than 300 mm and the smallest fish recorded at the site was 269 mm. The largest *A. dussumieri* measured was 576 mm and fish greater than 500 mm made up 4.3% of the sample (Table 5.4). In comparison to the other two species, *Lutjanus bohar* was more broadly distributed in size (Fig. 5.2C) with 98.7% of the fish ranging between 350 to 700 mm (Table 5.4). The smallest fish measured was 254 mm and most small fish (250-349 mm) represented only 0.9% of the fish sampled (Table 5.4). The largest fish recorded was 827mm.

Table 5.4. Percentage length frequency table (fork length mm) for combined years of 2013 and 2014 for each species.

Size class (mm)	% *Plectorhinchus lineatus*	% *Acanthurus dussumieri*	% *Lutjanus bohar*
250 - 299	0.1	0.2	0.3
300 - 349	0	2.1	0.6
350 - 399	0.1	11.8	4.0
400 - 449	1.9	47.8	17.7
450 - 499	16.1	33.7	26.6
500 - 549	52.6	3.8	21.3
550 - 599	24.9	0.5	19.0
600 - 649	2.9		7.0
650 - 699	0.9		2.6
700 - 749	0.2		0.5
750 - 799	0.1		0.2
800 - 849	0.1		0.2
850 - 899	0.1		

The temporal fidelity of *P. lineatus* and *A. dussumieri* were reflected in the discrete monthly length frequency histograms over a 15-month period (Fig. 5.3). In both 2013 and 2014, *P. lineatus* was more frequent in occurrence from September to November or the spring months (Fig. 5.3A). Whereas *A. dussumieri* was more frequent in occurrence from July to October or winter to mid spring (Fig. 5.3B). Both species show a similar seasonal pattern with their dominant size classes (Table 5.3) occurring two months prior to their main seasonal aggregation. In *P. lineatus* the 500 to 550 mm size class occurred in July and for *A. dussumieri* the 400 to 450 mm size class occurred in April. These dominant size classes for both species persisted throughout the season and even in the final month of December. In contrast the daily representative *L. bohar,* was more broadly distributed across all size classes ranging between 350 to 700 mm for all months. Larger fish >700 mm only occurred in the spring and early summer months (Fig. 5.3C).

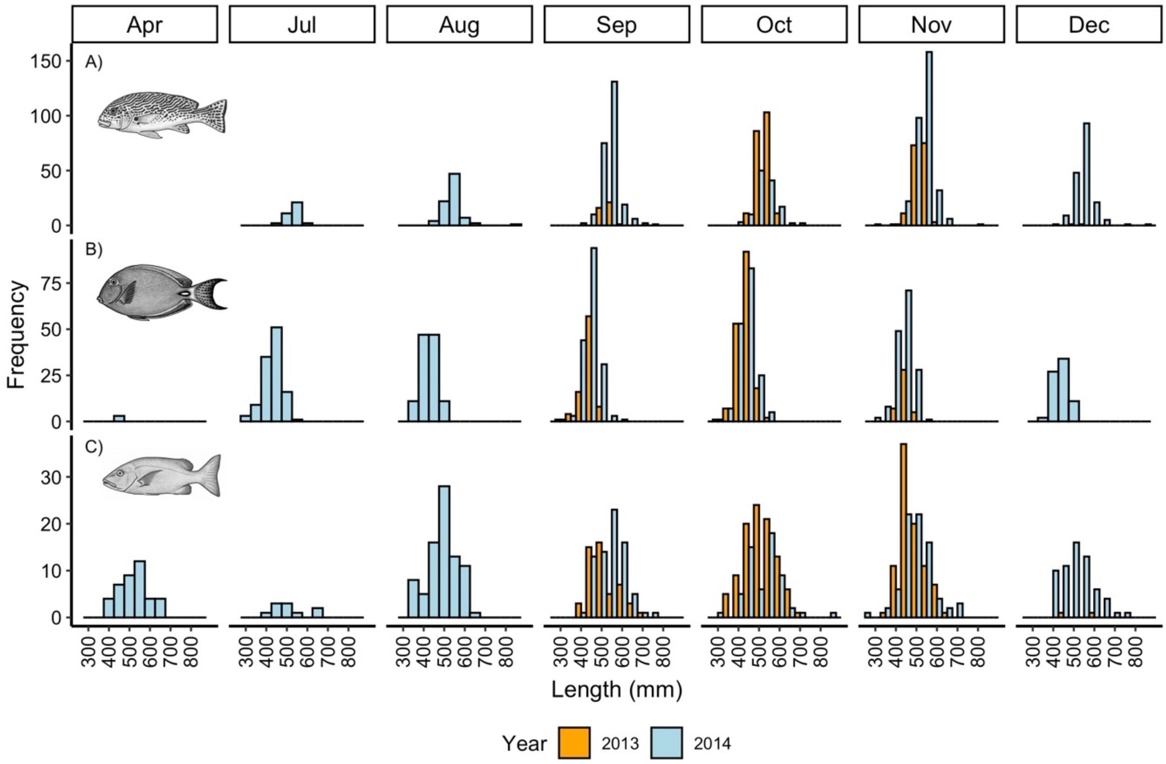


Fig. 5.3. Monthly length frequency histograms of fishes for the years 2013 (orange) and 2014 (light blue); A) *Plectorhinchus lineatus*, B) *Acanthurus dussumieri* and C) *Lutjanus bohar*. Length measurements represent fork length (mm) and the bin width was 50 mm (n=3,163).

5.4.2 Spatial location

All three coral reef fish species showed distinct depth and habitat preference within the fish aggregation site, which was influenced by time of day (see Figs. 5.4 & 5.5). All three species overlapped in their distribution, with the highest concentration of individuals supported on the front reef slope near the reef pass. The haemulid, *P. lineatus* had the highest densities with 180 fish per 10 m^2, with the highest concentrations occurring in shallow water (4 m). Whereas the other two species, *A. dussumieri* and *L. bohar* were more broadly distributed throughout the fish aggregation site with densities of 45 and 55 individuals per 10 m^2 respectively. Both species were evenly distributed from the outer reef slope to the reef pass and well inside the reef pass. In comparison to depth preference with *P. lineatus*, both other species were more represented at deeper depths, with *A. dussumieri* almost evenly distributed at all sampled depths. In contrast, *L. bohar* was more frequently encountered in shallower water (4 m) with 45.4% and 48% of the aggregation during both dawn and dusk respectively (Table 5.4).

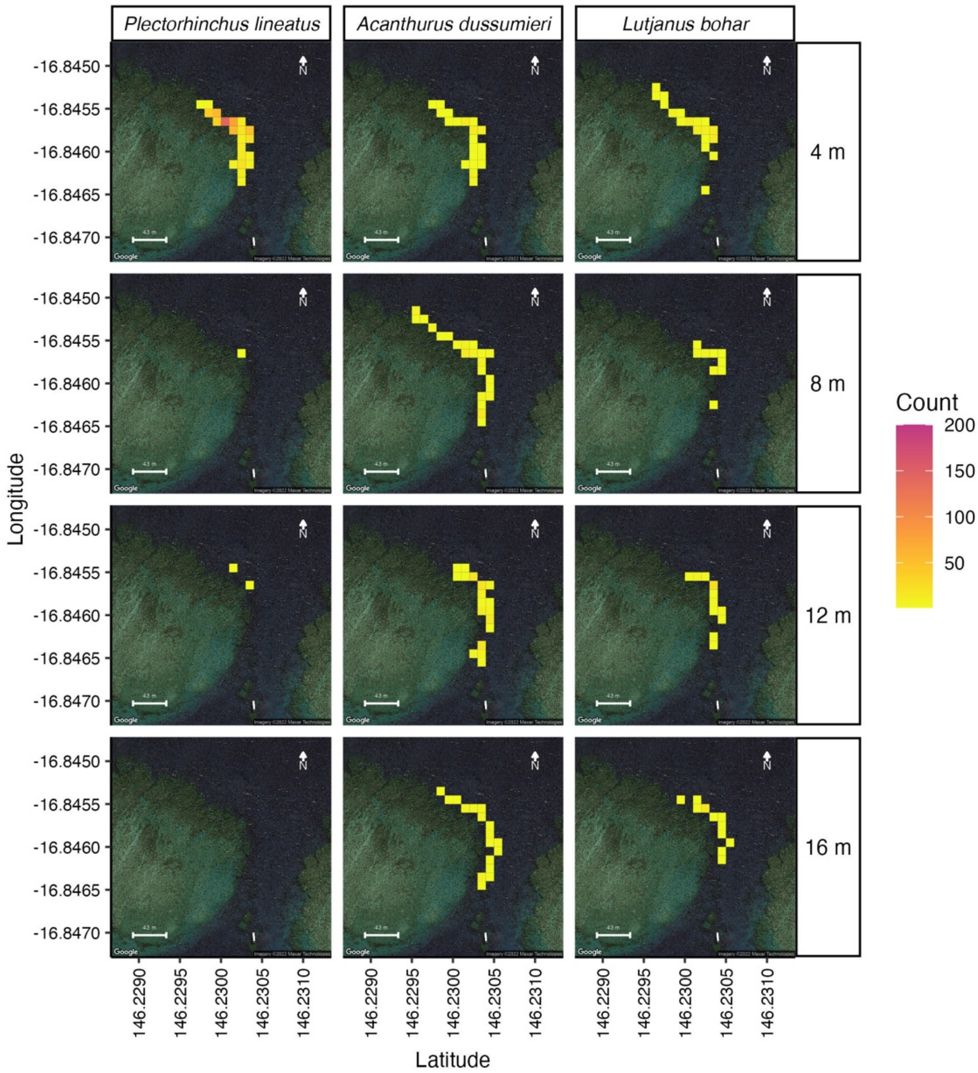


Fig. 5.4. Spatial distribution of each species faceted at depth for early morning periods (A.M.), n=1,216. Individual grid cells within the faceted plots represent (~10 m^2) and the darker the colouration the higher number of individuals per cell.

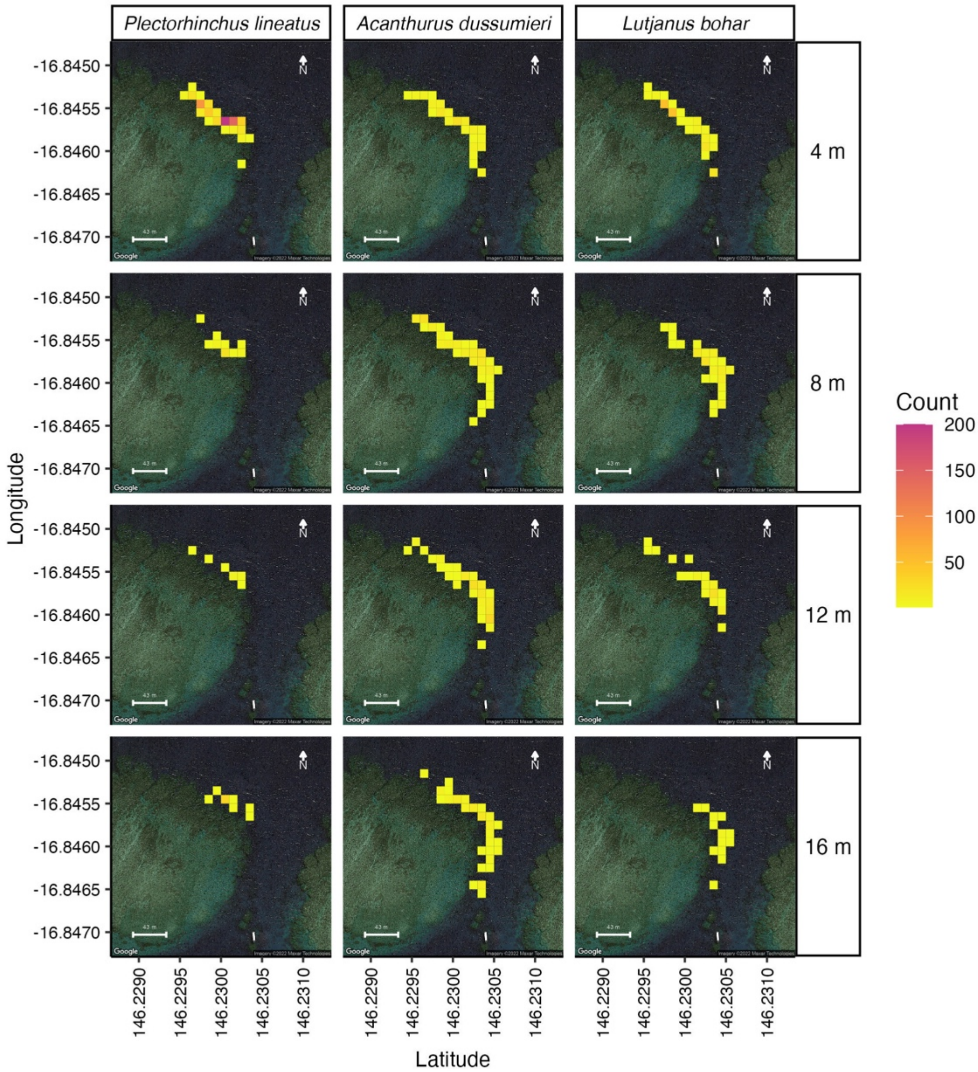


Fig. 5.5. Spatial distribution of each species faceted at depth (m) for late afternoon periods (P.M.), n=1,947. Individual grid cells within the faceted plots (~10 m^2) and the darker the colouration the higher number of individuals per grid cell.

Table 5.5. Percentage frequency table for each species at depth for both A.M. and P.M. periods.

	Plectorhinchus lineatus		***Acanthurus dussumieri***		***Lutjanus bohar***	
Depth (m)	% A.M.	% P.M.	% A.M.	% P.M.	% A.M.	% P.M.
4	99.5	86.7	21.5	23.1	48.0	45.4
8	0.2	5.9	27.8	29.7	10.6	28.5
12	0.3	1.9	35.1	27.0	25.2	19.1
16	0	5.5	15.6	20.2	16.2	7.0

Time of day had little influence on the distribution of *A. dussumieri* and *L. bohar* at the fish aggregation site, however this proximal cue influenced the distribution of the predator of invertebrates, *P. lineatus*. During early morning periods, 86.7% of the aggregation was at 4m with the remainder 13.3% distributed at deeper depths. In comparison almost all the *P. lineatus* aggregation (99.5%) was concentrated at 4 m during late afternoon periods (Table 5.5). Time of day also influenced where *P. lineatus* was distributed in the shallows (4 m), with fish during dawn also encountered well inside the reef pass (Fig. 5.4).

5.4.3 Behaviour

Fish aggregation behaviour varied among species, depth and time of day. The haemulid *P. lineatus* aggregation predominately exhibited milling behaviour at 4 m, where at deeper depths they were observed either travelling up or down the reef slope. This behaviour was associated with spawning and was only witnessed during late afternoon (Fig. 5.6A). Reproductive and foraging behaviour was also witnessed in the omnivorous acanthurid *A. dussumieri*. The courtship behaviour was observed in pairs of fish in both early morning and late afternoon periods and at all depths except for 12 m (Fig. 5.6B).

This surgeon fish *A. dussumieri* mainly exhibited active behaviour away from coral slope which was associated with foraging at all depths. The active behaviour in the piscivore *L. bohar* was also associated with foraging and was displayed during both early morning and late afternoon periods and at all depths. Although, this species was more frequently encountered in the shallows and like the other two species, more abundant at late afternoon compared to early morning (Fig. 5.6C).

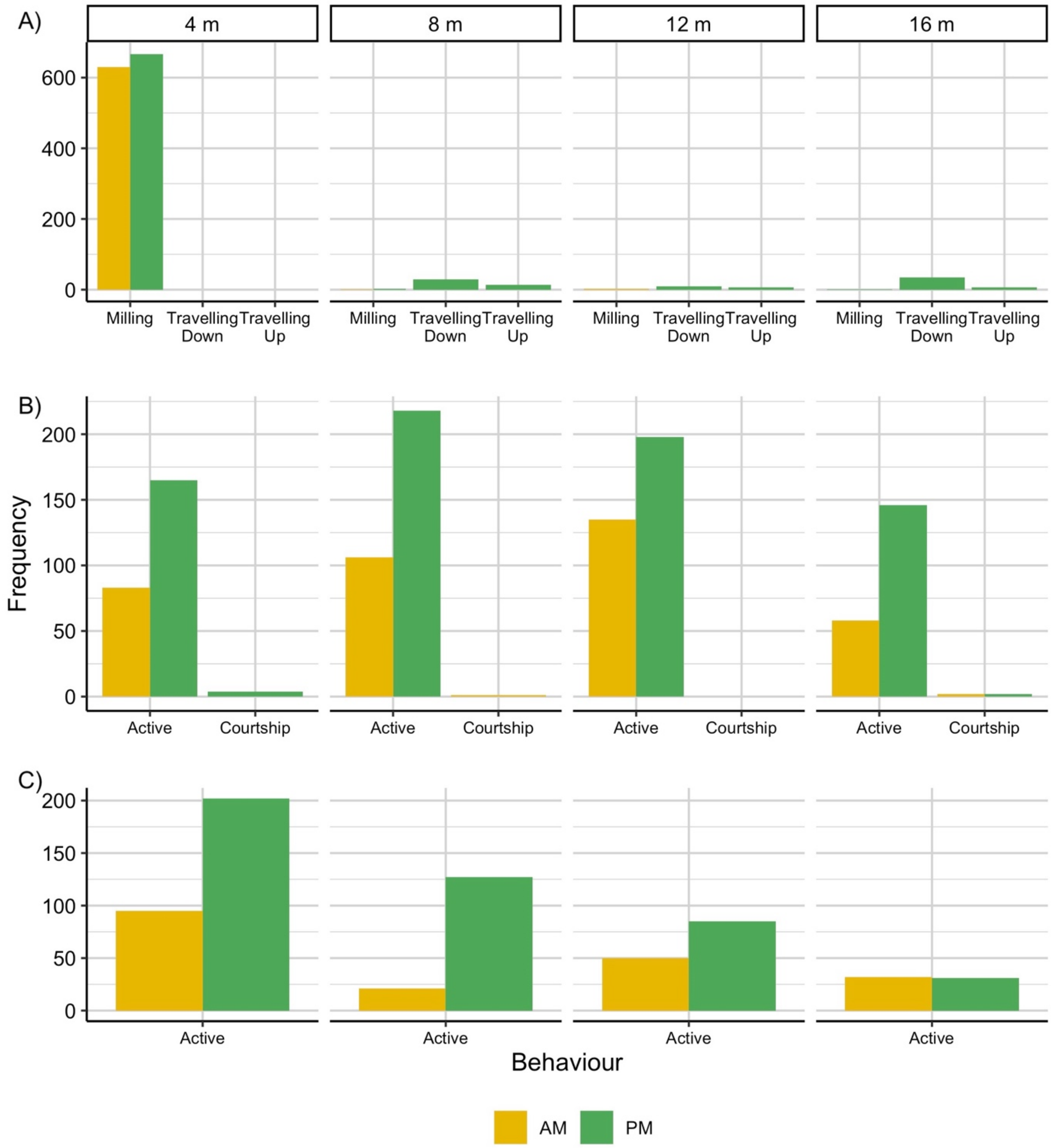


Fig. 5.6. Frequency behaviour histograms at each coral reef fish species at depth (m); A) *Plectorhinchus lineatus*, n=1,402, B) *Acanthurus dussumieri*, n= 1,118 and C) *Lutjanus bohar*, n=643 (C) for both A.M. (early morning) and P.M. (late afternoon).

Fish aggregation behaviour for each species appears was associated with low current speed of less < 0.2m/s (Fig. 5.7). The travelling down behaviour associated with spawning in *P. lineatus* was more frequent when the current flowed between 0.1 and 0.2 m/s. The direction of flow had little influence on this behaviour with 35.6 and 32.9 % travelling down the slope when the current flowed either away or towards the reef respectively (Table 5.6). This behaviour was particularly common on the days leading up to the full and new moon (Fig. 5.7A). Low or minimal current speeds also influenced foraging and reproductive behaviour of *A. dussumieri* (Fig. 5.7B) with 77% of the behaviour occurred when current flowed between 0 and 0.1 m/s, irrespective of direction of flow (Table 5.5). Likewise, the piscivore *L. bohar* was more active around the slack water mark (Fig. 5.7C) and 56% of fish favoured the current slightly flowing towards the reef at 0.1 m/s (Table 5.5). For all species lunar phase appeared to have little influence on behaviour (Fig. 5.7).

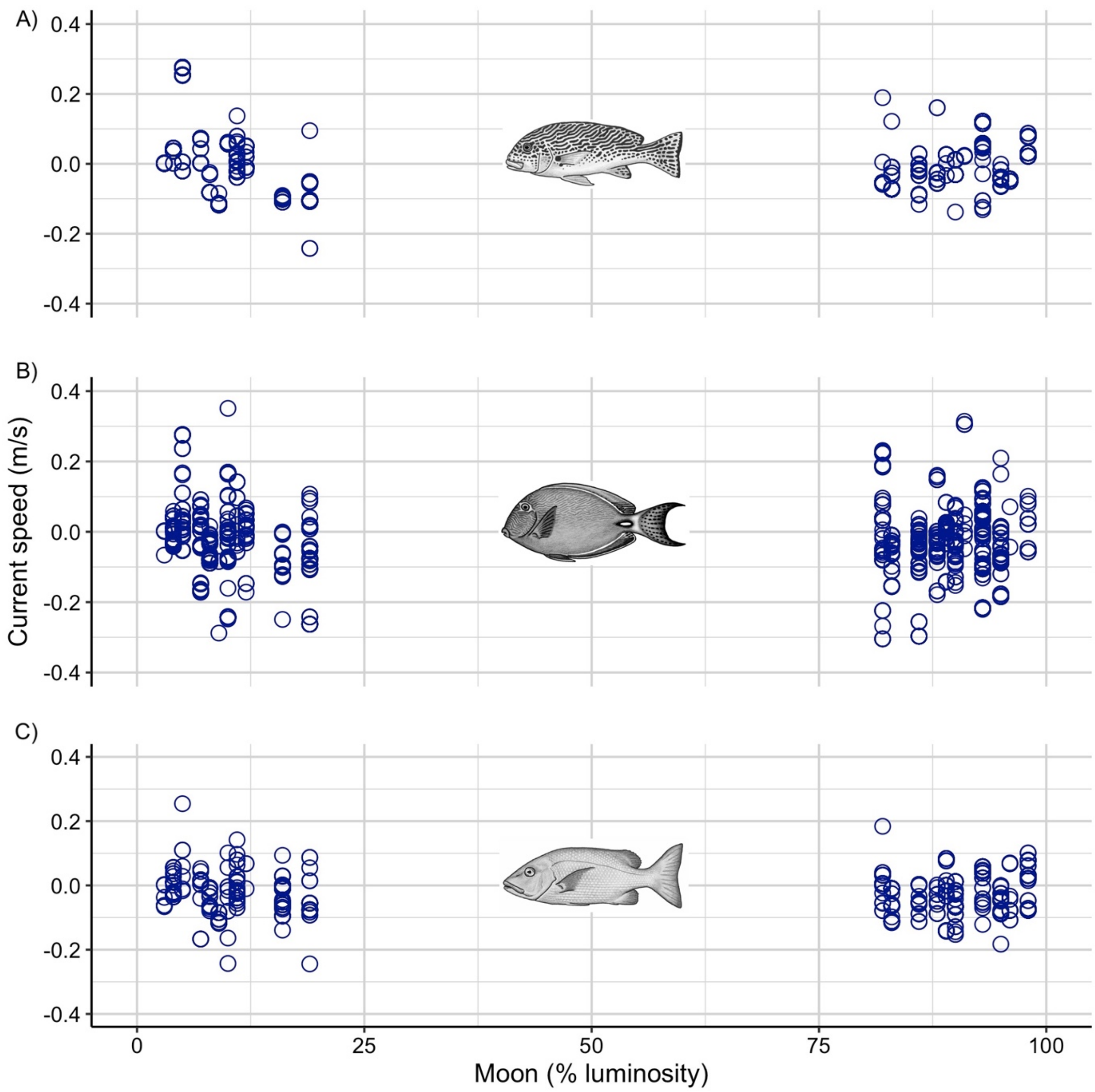


Fig. 5.7. Fish behaviour relative to lunar phase, current flow speed and direction. Each hollow circle represents spawning behaviour in A) *Plectorhinchus lineatus*, n=73, B) active and courtship behaviour in *Acanthurus dussumieri*, n=1,118 and C) active behaviour in *Lutjanus bohar*, n=643. On the x axis, lunar phase was represented as a percentage of lunar luminosity. Values ranging from 0-25 % are 1-5 days before new moon (0%) and 75-100% are 1-5 days before the full moon (100%). On the y axis, current speed (m/s) represented as a vector, in that each value attains a speed and direction. Positive values show water flowing away from reef and negative values show water flowing towards the reef.

Table 5.6. Percentage frequency table for each species behaviour relative to current speed and direction. Positive current bins values show water flowing away from reef and negative values show water flowing towards the reef.

Current bins (0.1m/s)	*% Plectorhinchus lineatus*	*% Acanthurus dussumieri*	*% Lutjanus bohar*
(-0.4, -0.3)	0	0.4	0
(-0.3, -0.2)	0	6.3	0.3
(-0.2, -0.1)	35.6	8.6	8.9
(-0.1, 0.0)	17.8	44.1	56.0
(0.0, 0.1)	13.7	32.9	31.6
(0.1, 0.2)	32.9	4.4	1.1
(0.2, 0.3)	0	2.0	0.2
(0.3, 0.4	0	0.4	0.0

5.5 Discussion

Coral reef fishes aggregating at Moore Reef in the Great Barrier Reef (GBR) displayed distinct behavioural profiles at a multi-species fish aggregation site, that reflected foraging and reproductive behaviour. This study utilised several non-invasive technologies to create a biophysical understanding of the proximal cues, lunar cycle, time of day, tidal currents (direction and speed) hypothesised to synchronise behaviour (Johannes 1978; Colin and Clavijo 1988). The research also allowed comparison among species. Of the hundreds and hundreds of fish continually aggregating adjacent this small-scale reef pass, most fishes were large adults which included the maximum known sizes (fork length) recorded for each species. There was some evidence in the timing of aggregation varied by size of the fish, especially in very large fish. Although species distribution throughout the fish aggregation site overlapped, each species showed a distinct spatial profile in fish density and use of habitat to perform vital tasks such as foraging and reproduction.

Prior to this study the spawning behaviour of the haemulid *Plectorhinchus lineatus* and the surgeonfish *Acanthurus dussumieri* were relatively unknown. There was minimal difference between full and new moon on reproductive and foraging behaviour, with time of day varying among species. An important finding was that 75% of fishes aggregating displayed reproductive and foraging behaviour during minimal tidal currents (0 – 0.1 m/s) prior and post slack water associated with high tide. Reproductive behaviour differed between *P. lineatus* and *A. dussumieri*, however both strategies were cued by low sunlight periods at slack water which ultimately would have reduced predation on eggs, increased fertilisation and improved chances of larval survival. The foraging behaviour in both *A. dussumieri* and the snapper *Lutjanus bohar* was cued by food availability in the presence of large predatory fishes and small planktivores, respectively (Fisher et al. 2018). This study supports that multi-species fish aggregation sites have clear multi-purpose ecological roles in providing goods and services for coral reef ecosystems (Heyman and Kjerfve 2008; Nemeth 2012).

The fish aggregation site was consistently used by large adult fishes during their temporal aggregations. The two seasonal occurring species *P. lineatus* and *A. dussumieri* were largely depicted by large size classes, that is greater than 500mm and 400 mm respectively. Very few small fish (0.2%) or fish less than 400mm (*P. lineatus*) or 300mm (*A. dussumieri)* were encountered at the fish aggregation site. Little published information exists on the size and age at maturity or any demographic information for *P. lineatus* (FishBase 2022) and the largest fish recorded in this study, exceeded previous maximum size by 107mm (Lieske and Myers 2001). An age-based study conducted on *A. dussumieri* in the northern GBR found from 43 individuals with a size range of 140-334 mm had a maximum age of 28 years and fish reached sexual maturity at 308 mm (Choat and Robertson 2002). In terms of habitat preference, juvenile *A. dussumieri* were more abundant in protected mid reef habitats (Mellin et al. 2007) and likewise for juvenile haemulids (Appeldoorn et al. 2009) than on more outer exposed outer reef habitats. Given the number of very small fish for both seasonal species, the Moore Reef fish site was rarely used by juvenile fish.

In contrast, the daily aggregating piscivore *L. bohar* was more broadly distributed across multiple size classes. On the GBR, female *L. bohar* mature at a larger size (428mm) compared to males (<300mm) (Marriott et al. 2007). Considering these combined size classes, potentially up to a fifth of the visiting fish were likely to be juveniles. This suggested that the fish aggregation site may have biological significance other than breeding to *L. bohar*. However, most fish were adults, with some large specimens recorded regularly. The largest fish recorded was 810 mm (F.L) and given that many large individuals greater than 700 mm were found to be between 70-79 years of age (Taylor et al. 2020). The large *L. bohar* in this study, represent some of the longest-lived tropical reef fish to consistently visit a fish aggregation site.

The high use of large fishes over time indicates the ecological complexity of the fish aggregation site had been maintained and provided the opportunity to investigate the aggregating behaviour of natural fish populations (Sadovoy de Mitcheson 2016; Pittman and Heyman 2020). The size structure of fishes did not differ between seasonal or diurnal cycles, however there were differences where fish occurred within the fish aggregation site. The haemulid *P. lineatus,* a nocturnal forager in soft sediments formed highly dense aggregations in shallow water on an outer reef slope for spawning. Several species of Haemulidae in the western Atlantic are known to form regular resting aggregations after nocturnal foraging in the adjacent seagrass beds and showed high fidelity for the same coral heads within a sheltered coral reef environment (Appeldoorn et al. 2009; Shantz et al. 2015). Post spawning, *P. lineatus* most likely continues foraging regimes in the soft sediments during the night and then forms the daily aggregations at the fish aggregation site cued by flood tide. No spawning behaviour was observed in the early morning aggregation cued by flood tide and suggestive that the behaviour was more likely aligned with resting.

This study provides the first documented account of haemulid aggregative spawning behaviour, that was cued by low light and slack water. Several haemulid species have been suggested to form seasonal spawning aggregations based on histological evidence at precise locations in similar high energy environments such as Gladden spit in Belize, although spawning had not been observed in this location (Heyman and Kjerfve 2008). During flooding tides, *P. lineatus* formed highly dense aggregations in shallow water on the outer reef slope, where individual fish move in a tight circular motion around each other. Gravid fish milling closely to one another may increase male-female interactions and trigger the final stages of ovulation. This was found in a small grouper species *Epinephelus merra*, a lunar synchronised spawner, where females receive pheromones from males that induce final oocyte maturation (Amagai et al. 2022). The dominant milling behaviour observed in *P. lineatus* was interrupted by small groups travelling down the outer reef slope and moving out to deeper water at dusk to spawn away from the reef near the substratum. This behaviour has been categorised as benthic shelf spawning and has been observed in other spawning aggregations such as the snapper *Lutjanus novemfasciatus* (Sala et al. 2003) and the hogfish *Lachnolaimus maximus* (Heyman and Kjerfve 2008). The strategy of spawning in multiple small groups away from the reef edge at low light conforms with reducing predatory pressure on eggs that ultimately increases the chance of larval survival (Johannes 1978; Lobel 1978).

In comparison, the surgeonfish *A. dussumieri* showed less use of precise locations and depth throughout the fish aggregation site. The habitat association was more linked to the open reef environment which may represent larger area to forage, and or more space to court in pairs. Frequently fish were observed displaying courtship behaviour in pairs throughout the fish aggregation site and this behaviour was associated with imminent spawning (Robertson 1983; Thresher 1984; Sadovy de Mitcheson and Colin 2012). This study provides the first description of the aggregating behaviour of this surgeonfish which was clearly different from what has been observed in non-aggregating fish. This species has a relatively low abundance with a broad distribution across most regions and cross shelf gradients of the GBR (Cheal et al. 2012). The non-aggregating behaviour was associated with daily resting patterns under large tabular corals and nocturnal foraging on algae/detritus on reef flats (Khan et al. 2017).

At the fish aggregation site, *A. dussumieri* regularly forms dense aggregations in the cooler periods of year to reproduce in pairs, with courtship cued by low light and slack water.

The final stages of reproduction in both seasonal aggregating species *A. dussumieri* and *P. lineatus,* timing gamete release with slack water. This was associated with the slack water approaching high water, prior a reversal in tidal current (Chapter 2). Imminent spawning behaviour for both study species was mainly observed during when current speeds were less than 0.1 m/s. Spawning during slack water is in direct contrast to the paradigm of spawning with fast currents that quickly transports eggs away from reef environment to reduce egg predation (Johannes 1978; Lobel 1978) and favour dispersal of populations (Barlow 1981). However, spawning at slack water in relatively calm or less turbulent conditions improves the chance of fertilisation (Petersen et al. 1992; Kiflawi et al. 1998). This study provides empirical evidence of timing spawning events when and where flow speeds are minimal. In contrast to other studies that correlated spawning in larger fishes with empirical oceanographic data; two snapper species (Lutjanidae) on a reef promontory in Palau were found to spawn frequently when current speeds were 0.28 m/s (Sakaue et al. 2016). Also, the large labrid, *Cheilinus undulatus* spawned when outflowing tidal currents were 0.17- 0.3 m/s (Colin 2010).

The process of fertilisation in most pelagic spawning reef fishes occurs within minutes (Bakker et al. 2006; Fitzpatrick 2020) and synchronising spawning with slack water at the Moore Reef pass would ensures immediate advection of fertilised eggs and newly formed progeny away from the coral reef environment and wall of mouths (Hamner et al. 1988). At this location, the current velocity increased to current speeds greater than 0.6 m/s, one to two hours after slack water (Chapter 2). The immediate advection of newly formed fish larvae further reduces predatory pressure and increase the chance of larval survival, independent of whether fish larvae are dispersed to other reefs or retained near the natal reef. Whether coral reef fishes spawn in pairs or in groups, the immediate advection of larvae away from the reef environment appears to be an important evolutionary driver for fish forming spawning aggregations (Choat 2012).

The snapper *L. bohar,* a known aggregative spawner (Colin 2012) was not observed spawning in this study. The persistent daily aggregations aligned with this species foraging on predictable aggregation of small planktivores coinciding with flood tides (Fisher et al.

2018). In Palau *L. bohar* form predictable aggregations where they forage which was 300m from their spawning ground (Sakaue et al. 2016). It appears plausible that other areas of the reef pass not sampled during this study may provide the appropriate spawning habitat. This species was also broadly distributed throughout the fish aggregation site which has the potential to increase their interaction with prey and provide direct energy through predictable resources to support reproductive growth.

Compensation or subsidising energy expenditure to capitalise on reproductive effort also appears to be a likely strategy for the omnivorous surgeon fish *A. dussumieri*. The dominant active behaviour observed in the omnivore *A. dussumieri* was associated with fish consuming the highly nutritious faeces from the families, Caesionidae, Carangidae, Lethrinidae and Lutjanidae (Bailey and Robertson 1982; Robertson 1982). The laterally compressed body plan combined with long intestine limits the room in the visceral cavity for gonads, thus limiting reproductive potential (Choat et al. 2004) To compensate energy at the spawning grounds and increase reproductive output, *A. dussumieri* frequently spawned in pairs and supplemented diets with additional protein through coprophagous foraging behaviour.

In conclusion, the multi-species aggregation allowed hundreds of adult fishes to aggregate at the same time which supported diverse reproductive and foraging behaviours. Similar proximal cues such as low light and slack water were used by fishes to time reproductive behaviour. Although, spawning behaviour differed among species the ultimate causes were likely a reduction in predatory pressure on adults and eggs, to improve larval survival through immediate advection of newly formed larvae onto the rich feeding grounds of the continental shelf (Gahan et al. 2023). Further the aggregation of two species had foraging benefits. The combined geomorphology and associated hydrodynamics of the reef pass created the important fish aggregation habitat for several fishes. Ultimately small-scale reef passes are a place where some species aggregate at certain times of the year, while they disperse at other times. In contrast, other taxa such as *L. bohar* aggregate at all times of year for feeding and likely spawning. Accordingly, reef passes need to be incorporated into understanding the dynamics of fish populations, their trophic interactions and requirements for spawning.

Chapter 6: General Discussion

This intensive bio-physical study of coral reef fishes at an aggregation site on the Great Barrier Reef (GBR) described patterns of aggregation, the proximate cues and made sensible speculation on ultimate causes of aggregation. Coral reef fish aggregations are well known for their predictability in space and time (Domeier and Colin 1997; Claydon 2004; Sadovy de Mitcheson and Colin 2012). It is this predictability that has fascinated ecologists and concerned fisheries biologists and managers for several decades (Sadovy de Mitcheson et al. 2008; Sadovoy de Mitcheson 2016; Erisman et al. 2019). When large adult fishes aggregate for any reason, they are vulnerable to exploitation and the removal of vast numbers of large fish can have catastrophic implications on fish populations. This was evident with the Nassau Grouper, *Epinephelus striatus* which were known to aggregate in the tens of thousands at various locations in the western Atlantic (Smith 1972) and have now been decimated to the point where aggregations no longer form, and the species has been classified as endangered in the ICUN (World Conservation Union) Red list (Sadovy de Mitcheson and Colin 2012). Ecologists have also been fascinated for several decades on the how and why coral reef fishes from repeatable aggregations in space and time, which led to the development of several hypotheses early to explain this phenomenon (Johannes 1978; Lobel 1978).

The objective of my study was to describe the oceanography at a fish aggregation site and patterns of aggregation for three species of larger reef fish: *Plectorhinchus lineatus* (Haemulidae), *Acanthurus dussumieri* (Acanthuridae) and *Lutjanus bohar* (Lutjanidae). A particular strength of my study was the multiyear data base that identified persistent patterns of aggregation. Multiple publications have proposed cues to aggregation (proximate factors) and the biological importance in terms of offspring (ultimate factors); *sensu* (Pearse and Giese 1974; Olive et al. 2000). My specific aims were as follows.

1. Describe oceanographic patterns of a spawning aggregation site (Chapter 2).
2. Describe the assemblages of fishes at the aggregation site in relation to environmental predictors (Chapter 3).
3. Develop species specific models from a 13-year time series on abundance data of three functional groups of aggregating fish (Chapter 4).
4. Describe the behaviour of three functional groups that form predictable aggregations in relation to size structure, growth characteristics, habitat use and hydrodynamics (Chapter 5).

I demonstrated that thirty-eight species of coral reef fish are known to aggregate at Moore Reef in a small-scale reef pass, northern Great Barrier Reef (Fisher et al. 2018). Small reef passes, often less than a couple hundred meters in width, and have been recognised as fish spawning aggregation habitat (Moyer 1989; Sancho et al. 2000b). Although most other studies have focused on larger scale reef passes (Colin and Bell 1991; Johannes et al. 1999; Robbins and Renaud 2016; Mourier et al. 2019). It has been hypothesised that the variable currents produced by wind and tides in all scale reef passes, provide the necessary advection away from reefs to increase the fate of egg survival by reducing predation risk from reef associated planktivores (Johannes 1978; Lobel 1978). The fine scale hydrodynamic study of the area showed the water movement varied greatly at a scale of 10’ s of meters. The semi-diurnal tide with alternating flood and ebb tides allowed large movements of water to flow between the open ocean and coral lagoon. Current speeds in the reef pass varied with tidal magnitude and the largest movements were recorded during the spring tides associated with the full and new moon phases. When water flowed strongly (> 0.6 m/s) on flood tides through the reef pass, a bifurcation point occurred adjacent the reef pass on the seaward side was created where water flowed less (< 0.3 m/s) (Chapter 2). Even on ebb tides with a reversal in flow, water movement was low in this area compared to the centre of the reef pass. The semi-diurnal tidal model for the reef pass showed that current reversal occurred one to two hours in advance of low or high water. Flood tide was characterised as water moving from the ocean or seaward side, through the reef pass and into the coral lagoon. The highest current speeds for either tidal phase was recorded at high and low water and slack water occurred one to two hours in advance of high or low water. The fish aggregation site was located near the bifurcation point where water moved the least near the reef pass.

The predictable pattens in flow produced by the semi-diurnal tide also produced predictable daily patterns in the timing of aggregation for 10 species of coral reef fish from five trophic groups. Flood tides were the dominant driver for all 10 species at the fish aggregation site and very few fish were encountered on ebb tidal phases. This behaviour does not align with the predictions of the egg predation hypothesis, in fact fish are aggregating to spawn when water was flowing onto the reef and not away from it. The timing of aggregation also violates the assumption of the egg dispersal hypothesis, where it is specified that spawning is timed to coincide with currents that disperse eggs further away from reefs (Barlow 1981). This in turn could increase the fate of larvae finding food in a patchy environment such as on the shelf of the Great Barrier Reef (Doherty et al. 1985), though are no published data on the distribution of planktonic food. However, some findings indicate that high densities of larval fish food (copepodites) are ubiquitously found mid-shelf on the GBR (Gahan et al. 2023).

Alternatively reef configuration and predictable hydrodynamics supported some fishes foraging on predictable resource pulses such as spawned eggs, patches of plankton and larval fish (Heyman et al. 2001; Sala et al. 2003; Zamon 2003; Genin 2004; Galbraith et al. 2021). The study showed that small planktivores only aggregate on flood tides along with larger piscivores and planktivores (Chapter 3). The flood tidal currents that created the bifurcation point and subsequent low current speeds at the fish aggregation site have the potential to concentrate oceanic nutrients and plankton. This entrapment mechanism was like the spur and groove morphology on outer reef environments that concentrates plankton and small planktivores (Hamner et al. 1988). The daily aggregations of planktivores and piscivores provides supporting evidence that reef pass produced predictable hydrodynamic patterns driving predicable daily fish aggregation patterns. Given that the ‘wall of mouths’ phenomenon on outer reefs are considered important proponents in the input of nutrients into coral reef environments (Hamner et al. 1988). Fish aggregation sites associated with small scale reef passes that concentrate resources, prey and predators have the potential to significantly contribute to coral reef energy budgets (Morais and Bellwood 2019; Morais et al. 2021) and should be investigated more widely.

A multi-species comparison of fishes identified both seasonal and daily pattens of aggregation among the ten selected species. Some fish species identified as predators of benthic invertebrates from the families Haemulidae and Lethrinidae along with a large omnivorous acanthurid showed distinct seasonal patterns. This 13-year study combined with high frequency monitoring of three species of fish demonstrated strong daily and seasonal patterns of aggregation that persisted among years. The major finding of this study was that timing of aggregation in all three species was remarkably persistent over the entire 13 years (Chapter 4). Furthermore, the timing of aggregation was unaltered by interannual fluctuations in seawater temperature and four major perturbations that included severe tropical cyclones "Hamish" and "Yasi" and the 2016 and 2017 mass coral bleaching events. The persistent timing of aggregation allowed me to elucidate some robust individual species models that identified the proximal cues driving the continual patterns of aggregation. The cues or combination of cues varied between species. Both daylength and temperature combined were the dominant covariates explaining the continual aggregation in the austral spring months for the haemulid *Plectorhinchus lineatus*. In contrast, seawater temperature, independent of daylength was the dominant covariate for the acanthurid *Acanthurus dussumieri* forming predictably large aggregations in the coolest months of the year. The daily aggregation of the piscivorous lutjanid, *Lutjanus bohar* at all times of the year was largely driven by flood tides. In contrast to the other two species, the persistent long-term patterns of aggregation correlated with two biological drivers, reproduction and foraging.

In the detailed study of three species (Chapter 5), all fishes that aggregated were large adults and aggregation behaviour differed between the three species and reflected the individual biology. The haemulid, *P. lineatus* formed highly dense aggregations between September and November each year on the shallow reef crest of the fish aggregation site. The behaviour showed this species aggregated to spawn, and spawning occurred in small groups down deep away from the reef slope close with the cues of dusk and slack water. The study provides the first detailed account of known spawning aggregation behaviour for tropical haemulids. In contrast, the other seasonal aggregator *A. dussumieri* displayed both foraging and reproductive behaviour and was less concentrated and more dispersed throughout the fish aggregation site than *P. lineatus*. Reproduction was the primary reason for this species to aggregate through the cooler months with spawning occurring in pairs at both dusk and dawn. The cues for spawning were low light at dusk and dawn and slack water. In comparison to piscivores, herbivores like surgeonfish have limited spatial capacity for large gonads (Choat et al. 2004) and daily energy must be divided between somatic and reproductive growth (Montgomery and Galzin 1993). To compensate energy budgets this species spawned in pairs and supplemented daily diet by the consumption of high protein rich faeces of carangids, lethrinids and lutjanids (Bailey and Robertson 1982; Robertson 1982). The shift in foraging behaviour from detritivore (Choat et al. 2004) to coprophagy coincided with the predictable resource pulses created by other aggregating species. The dual behaviour displayed by this species reinforces the array of factors influencing aggregation by fishes at chosen sites. Although the data showed the continual presence of the lutjanid, *L. bohar* was predominately linked with foraging on the predicable resource pulses of small planktivores. The reef pass and the associated hydrodynamics may also be suitable spawning ground for this known aggregator spawner (Colin 2012; Sakaue et al. 2016).

The robust patterns of aggregation in all three species reinforced the importance of timing of animal behaviour, either foraging or reproduction with the physical environment. This allowed speculation on the fate of adults, eggs and larvae of coral reef fishes at the aggregation site. A framework to evaluate hypotheses, proximate cues and ultimate factors concerning fish aggregation behaviour was created (Table 6.1). Multiple species from a range of trophic groups utilised the reef fish aggregation site at any one time. This supports the 'selfish herd' hypotheses in that the risk of predation to an individual is reduced (Hamilton 1971). The timing of aggregation was species specific and driven by clear multiple cues over a range of temporal scales from hours to years, which reinforced that environmental cues synchronised coral reef fishes aggregation behaviour (Lobel 1978; Colin and Clavijo 1988; Colin and Bell 1991), whether it was reproduction or foraging. In this study both seasonal aggregators coincided spawning with dusk and or dawn. Although, during these low light periods, the risk of egg predation by small planktivores was low (Hobson 1974; Hobson and Chess 1978). The risk of egg predation by large planktivores such as *Macolor niger* can be high (Colin 2012; Appendix B Video B1) and the risk of predation by larger piscivores would also be high (Shapiro et al. 1988; Robbins and Renaud 2016). The behaviour of spawning in pairs or small groups away from reef edge may also reduce predatory pressure on adults and eggs by being less conspicuous, compared to spawning in large groups. For example, in French Polynesia the large simultaneous spawning aggregation of the marbled grouper, *Epinephelus polyphekadion* attracts hundreds of the grey reef sharks, *Carcharhinus amblyrhynchos* (Mourier et al. 2016; Robbins and Renaud 2016). Large group spawning indicates a trade-off between predators and spawners, compared to predator avoidance or evasion behaviour of pair or small group spawning.

Table 6.1. Summary of proximate and ultimate factors that align with the patterns of aggregation documented in this study for three species of coral reef fishes.

Proximate factors	**Ultimate factors**		
	Plectorhinchus lineatus	***Acanthurus dussumieri***	***Lutjanus bohar***
Daylength	Synchronise spawning	No	No
Temperature	Synchronise spawning	Synchronise spawning	No
Lunar	No	No	No
Oceanic currents	No (Reduced connectivity for larvae)	No (Reduced connectivity for larvae)	No
Flood tidal currents	Predator evasion	Predator evasion and food availability (adults)	Food availability (adults)
Slack water	Increase fertilization	Increase fertilization	Food availability (adults)
Ebb tidal currents	Immediate egg dispersal and higher larval survival	Immediate egg dispersal and higher larval survival	No
Dusk (low light)	Reduced egg predation	Reduced egg predation	Food availability (adults)
Dawn (Low light)	No	Reduced egg predation	Food availability (adults)

Reduction in predatory pressure on adults and eggs appears to be a selective force driving aggregations (Choat 2012). However, a major finding in this study was that fish were spawning at slack or low water movement in the one to two hours prior to high water. Spawning during low water movement contradicts theory that fish aggregate to spawn in time with currents to ensure that eggs are dispersed quickly from the reef to avoid egg predation (Johannes 1978; Lobel 1978). The evidence provided suggests, that fish are timing spawning with periods of less water movement and low disturbance to increase fertilisation and within minutes subsequent larval development (Bakker et al. 2006; Fitzpatrick 2020). This reinforces the importance of timing and location. In the Caribbean, Lane Snapper, *Lutjanus synagris* time their spawning with oceanic features that increase larval fitness, survivorship and retention of larvae to the natal reef (Donahue et al. 2015). On the fish aggregation site within the Great Barrier Reef, physical location and timing spawning with predictable hydrodynamics provides the chance for increased larval fitness. The small-scale reef pass near the fish aggregation site produced tidal jet on high water. Releasing eggs near the edge of the reef pass prior to formation of tidal jet would quickly transport eggs and or newly formed larvae away from the reef environment and reduce the further risk of predation. Transporting eggs quickly onto the continental shelf combined with mechanisms that keep larvae in a good feeding environment aligns with the pelagic survival hypothesis (Doherty et al. 1985). Whether these mechanisms enhance larval survival requires quantitative information on surrounding plankton communities and continental shelf flow dynamics. Evidence provided in this study, supports that larvae would more likely be retained than dispersed further distances from the natal reef (Table 6.1) and minimise the loss of progeny from the mosaic of reefs.

Tides and a small-scale reef pass produced predictable patterns of water circulation in turn that produced predictable short- and long-term patterns of fish aggregation formation and behaviour in several large coral reef fish species. Small-scale reef passes have been identified as important reproductive grounds for smaller to intermediate coral reef fishes (Moyer 1989; Sancho et al. 2000b) and large-scale reef passes have been associated with larger coral reef fishes (Johannes et al. 1999; Hamilton 2005; Mourier et al. 2016; Mourier et al. 2019). This study further demonstrated the complexity and biological importance of small-scale reef passes and warrants the need for further investigative studies. On the Great Barrier Reef there is a dearth of information on known fish aggregation sites. A first approach would be quantifying the number of small-scale passes and ranking their likelihood as multi-species fish aggregation sites using modern mapping technology. Identifying and validating these sites would be useful in terms of resource management and protecting fish aggregations

(Erisman et al. 2015). Further studies are required to explore the role of these areas in connectivity and their role in supplementing coral reef energy budgets. The fine scale bio-physical model of the fish aggregation site produced in this study represents a known source of offspring and combined with eDNA technology could be used to investigate connectivity within and between reefs (Bylemans et al. 2016). Given that fish migrate to the fish aggregation site, tagging studies would generate invaluable information on intra- and inter-reef fish movements of fishes and their habitat use (Zeller 1998; Nemeth et al. 2007b). This information combined with isotopic studies could provide a holistic picture on energy transfer to and from a fish aggregation site and the changing distribution of fish biomass with time.

In conclusion this comprehensive bio-physical study has contributed to a greater understanding of coral reef fish aggregations. Clear patterns of aggregation, and fish behaviour, were identified in space and time and there was some alignment by species of fish with current hypotheses of aggregation. Time of year, reef configuration and hydrodynamics are the principal drivers in fish aggregation formation. The daily and seasonal hydrodynamic cycles produced clear patterns of aggregation for fishes to perform vital tasks such as feeding and reproduction. The longest global data base of its type was presented for three species of fish at the aggregation site. These patterns persisted over the 13-year study even with concurrent and major perturbations that included coral bleaching and severe cyclones. These patterns were detected in a small pass (tens to hundreds of meters wide) which and outlines the ecological importance of this type of geomorphology and related oceanography. The identification and ranking of cues for aggregation by species was robust due to the long time series of data I collected. The biological importance of aggregation could be inferred from patterns of aggregation and varied by species. Foraging aggregations clearly contribute to coral reef energy budgets through the importation of oceanic nutrients via planktivory and predation. Other trophic process such as egg predation, predation on adult fish that aggregate and coprophagy aid in nutrient recycling within reefs and these processes are probably underestimated in their contribution to reef trophodynamics. Moreover, fishes forming persistent spawning aggregations repeatably connect and replenish fish populations. This study demonstrated that fish aggregation sites have multiple ecological roles and fish aggregations are highly predictable, which means whenever fish are aggregating, they are vulnerable to fishing. In summary this high frequency long term study has showcased the predictable nature of coral reef fish aggregations, and that timing and location is everything to understanding the ecological aspects of multi-species coral reef fish aggregation sites.

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Appendix A

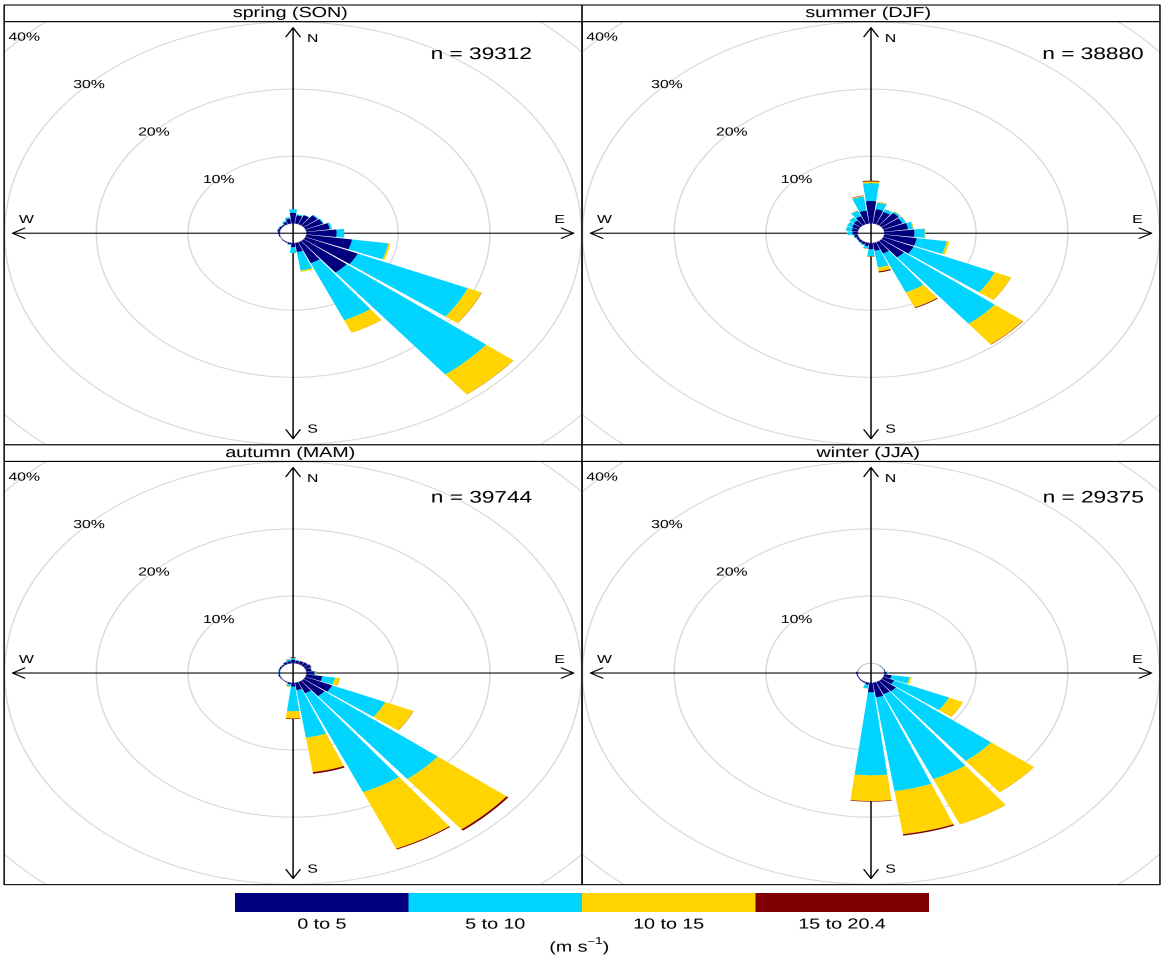
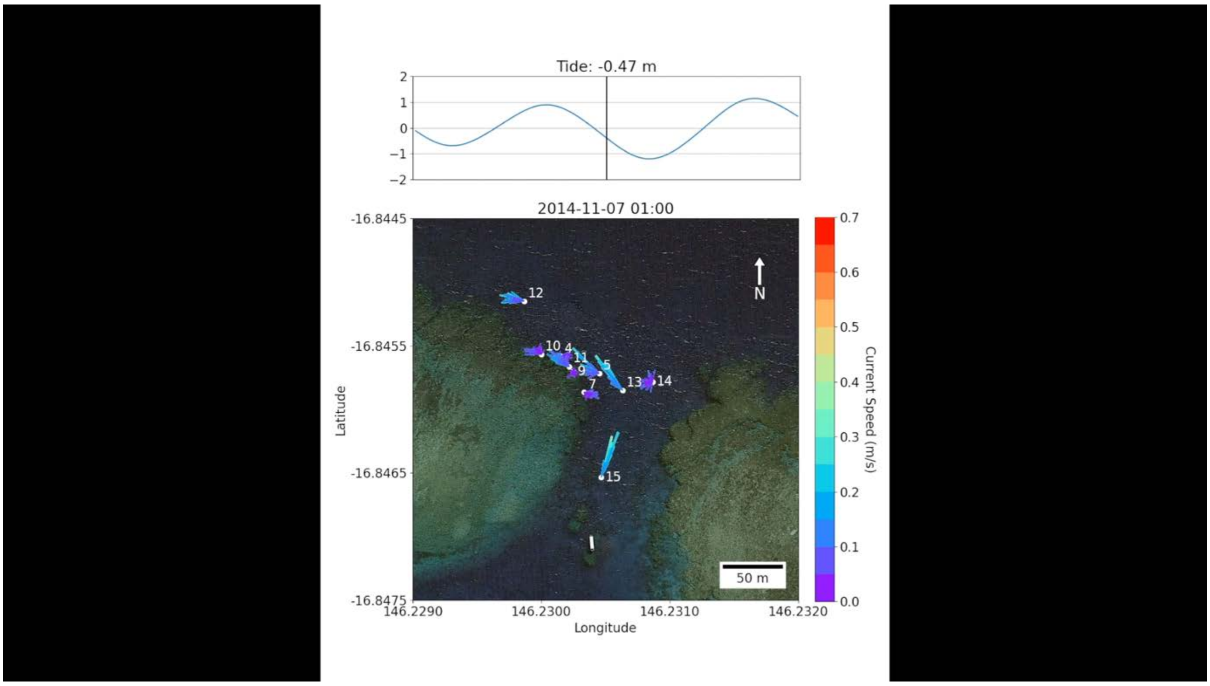


Fig. A.1. Seasonal rose plots (austral calendar) of the wind speed in m s-1 and directional data from Arlington Reef, between 20-Aug-2012 and 7-Dec-2015.

Video A.1. The animation displays current speed and directional changes for Moore Reef pass and fish aggregation site. Click here to see MP4. White numerals display current meters in relation to the predicted tidal model for Moore Reef on the 7-Nov-2014. The light grey ellipse illustrates fish aggregation presence.



Appendix B

Table B.1. Describes the source of environmental conditions collated with the fish composition and abundance data. The data was collected between 1 February 2006 to 29 November 2012, except the Secchi data which commenced 24 June 2007. Data collection for some variables marked with an * was collected sporadically and not continuous due to repository limitations.

Environmental variable	Source	Units	Distance and direction of source from aggregation site
Wind speed and direction	Cairns Bureau of Meteorology	Speed in m s^{-1}, Direction between 0 – 360° Readings taken at 1600 hrs	450 m SSE
Tidal Flow (Describing the direction of water flowing through the passage)	Senior Author	Flooding or Ebbing	On site
Moon phase described as Lunar Luminosity (the fraction of the moon's visible disc illuminated by the sun every day between 1700 and 2100 hrs)	United States Naval Observatory astronomical department http//aa.usno.many.mil/data/.	Values between 0 and 1 with 2 degrees of precision. Tables use Chamorro Standard Time (Guam, Pacific Ocean) Similar to AEST (UTC + 10:00)	
Surface temperature	Thermometer suspended ½ m below surface.	°C Readings taken ~ 1500 hrs	350 m SSW
Visibility	Secchi Disc	Readings taken ~ 1500 hrs in meters (m)	350 m SSW
Daily Global Solar Exposure (Total amount of solar energy falling onto a horizontal surface)	Cairns Bureau of Meteorology, Crc Environ Base Station (03125, Lat: 16 °.93 S Long: 145 °.77 E)	Recordings in m to one degree of precision. Reading taken ~ 1500 hrs in Megajoules m^{-2}	60 km West
Swell Height (significant wave height measured in meters, defined as the average of the highest one third of the wave heights in a 30-minute wave record)	Queensland Government Department of Environment and Heritage Protection Wave Rider Buoy (Lat: 16° 44.060' S Long: 145° 42.600' E, water depth 9m)	Recordings in (m) with two degrees of precision. The readings from the 1400 to 1430 hrs wave period were used.	60 km WNW

Table B.2. Species list of Moore Reef fish aggregation site. This list 110 fish (>20cm) from 21 families (in bold) and yes (Y) or no (N) whether these species form aggregations at the Moore reef fish aggregation site (with notes on foraging and reproductive behaviour of aggregating species or if unknown).

Species List	Aggregation	Behaviour
Acanthuridae		
Acanthurus dussumieri	Y	Foraging – coprophagy, plankton and hard substrate Reproductive –courtship (specialised colour patterns and chasing)
Acanthurus lineatus	Y	Reproductive – group spawning, egg predation by *Macolor niger*
Acanthurus mata	Y	Foraging - plankton
Acanthurus nigricans	N	
Acanthurus nigricauda	Y	Foraging - hard substrate
Acanthurus nigrofuscus	Y	Reproductive – group spawning, egg predation by *Macolor niger*
Acanthurus xanthopterus	Y	Reproductive - courtship (specialised colour patterns and chasing)
Ctenochaetus striatus	Y	Reproductive – group spawning, egg predation by *Macolor niger*
Zebrasoma veliferum	N	
Naso annulatus	Y	Foraging - plankton
Naso brachycentron	N	
Naso brevirostris	N	
Naso lituratus	Y	Unknown
Naso tuberosus	N	
Naso unicornis	Y	Unknown
Naso vlamingii	Y	Foraging - plankton
Balistidae		
Balistoides viridescens	Y	Reproductive - courtship and chasing

Odonus niger	N	
Caesionidae		
Caesio caerulaurea	Y	Foraging - plankton and fish eggs (labrid)
Caesio cuning	Y	Foraging - plankton and fish eggs (labrid)
Caesio lunaris	N	
Caesio teres	N	
Pterocaesio marri	Y	Foraging - plankton and fish eggs (labrid)
Carangidae		
Alectes ciliaris	N	
Carangoides ferdau	N	
Carangoides fulvoguttatus	Y	Unknown
Carangoides gymnostethus	N	
Caranx ignobilis	Y	Unknown
Caranx lugubris	N	
Caranx melampygus	N	
Caranx papuensis	N	
Caranx sexfasciatus	Y	Foraging – Clupeidae schools
Elagatis bipinnulata	N	
Megalaspis cordyla	N	
Scomberoides tol	N	
Trachinotus blochii	Y	Foraging - plankton (pteropods)
Chanidae		
Chanos chanos	Y	Unknown
Diodontidae		
Diodon hystrix	N	
Diodon liturosus	N	
Epinephlidae		
Cromileptes altivelis	N	
Epinephelus fuscoguttatus	N	

Epinephelus lanceolatus	N	
Epinephelus tukula	N	
Plectropomus areolatus	N	
Plectropomus laevis	N	
Plectropomus leopardus	N	
Ephippidae		
Platax pinnatus	N	
Platax teira	N	
Haemulidae		
Diagramma pictum	N	
Plectorhinchus chaetodonoides	N	
Plectorhinchus diagrammus	N	
Plectorhinchus gibbosus	N	
Plectorhinchus lineatus	Y	Reproductive – swollen abdomens and chasing
Plectorhinchus obscurum	N	
Kyphosidae		
Kyphosus cinerascens	Y	Unknown
Kyphosus vaigiensis	Y	Foraging – plankton (surface slicks)
Labridae		
Bodianus loxozonus	N	
Bolbometopon muricatum	Y	Foraging – day, hard substrate Reproductive - lek-based and pair spawning.
Cetoscarus bicolor	N	
Cheilinus undulatus	Y	Reproductive - lek-based and pair spawning
Chlorurus microrhinos	N	
Chlorurus bleekeri	N	
Hipposcarus longiceps	Y	Reproductive – initial phase male spawning in groups
Scarus altipinnus	Y	Foraging - hard substrate

Scarus dimidiatus	N	
Scarus frenatus	N	
Scarus ghobban	N	
Scarus oviceps	N	
Scarus rivulatus	Y	Foraging – hard substrate
Scarus ruibroviolaceus	N	
Scarus schlegeli	N	
Scarus sordidus	Y	Reproductive – pair spawning
Scarus spinus	N	
Lethrinidae		
Gymnocranius sp	N	
Lethrinus erythracanthus	N	
Lethrinus nebulosus	Y	Unknown
Lethrinus olivaceus	Y	Reproductive – swollen abdomen and chasing
Lethrinus xanthochilus	Y	Unknown
Monotaxis grandoculis	Y	Foraging – plankton (pteropods)
Lutjanidae		
Aprion virescens	N	
Lutjanus argentimaculatus	N	
Lutjanus bohar	Y	Foraging - caesionids, clupeids, juvenile *Scarus sordidus* schools and plankton (pteropods)
Lutjanus fulviflamma	N	
Lutjanus fulvus		
Lutjanus gibbus	Y	Unknown
Lutjanus rivulatus	N	
Lutjanus russelli	N	
Macolor macularis	N	
Macolor niger	Y	Foraging - plankton (including pteropods) and fish eggs (Acanthuridae)
Symphoricthys spilurus	Y	Unknown
Symphorus nematophorous	N	

Monocanthidae		
Aluterus scriptus	N	
Ostraciidae		
Ostracion cubicus	N	
Pomocanthidae		
Pomocanthus semicirculatus	N	
Pomocanthus sextriatus	N	
Pomocanthus xanthometopon	N	
Scombridae		
Euthynnus affinis	N	
Grammatorcynus bicarinatus	N	
Scomberomorus commerson	N	
Thunnus obesus	N	
Thunnus tonggol	N	
Siganidae		
Siganus corallinus	N	
Siganus doliatus	N	
Siganus vulpinus	N	
Sphyraenidae		
Sphyraena barracuda	N	
Sphyraena jello	Y	Unknown
Sphyraena putnamiae	Y	Unknown
Tetradontidae		
Arothron caeruleapunctatus	N	
Arothron mappa	N	
Zanclidae		
Zanculus cornutus	Y	Unknown

Video B.1. Egg predation by *Macolor niger* on *Acanthurus lineatus* group spawning aggregations. Click here to see MP4.

Video B.2. Faecal scavenging by *Acanthurus dussumieri* from predators of benthic invertebrates. Click here to see MP4.

Appendix C

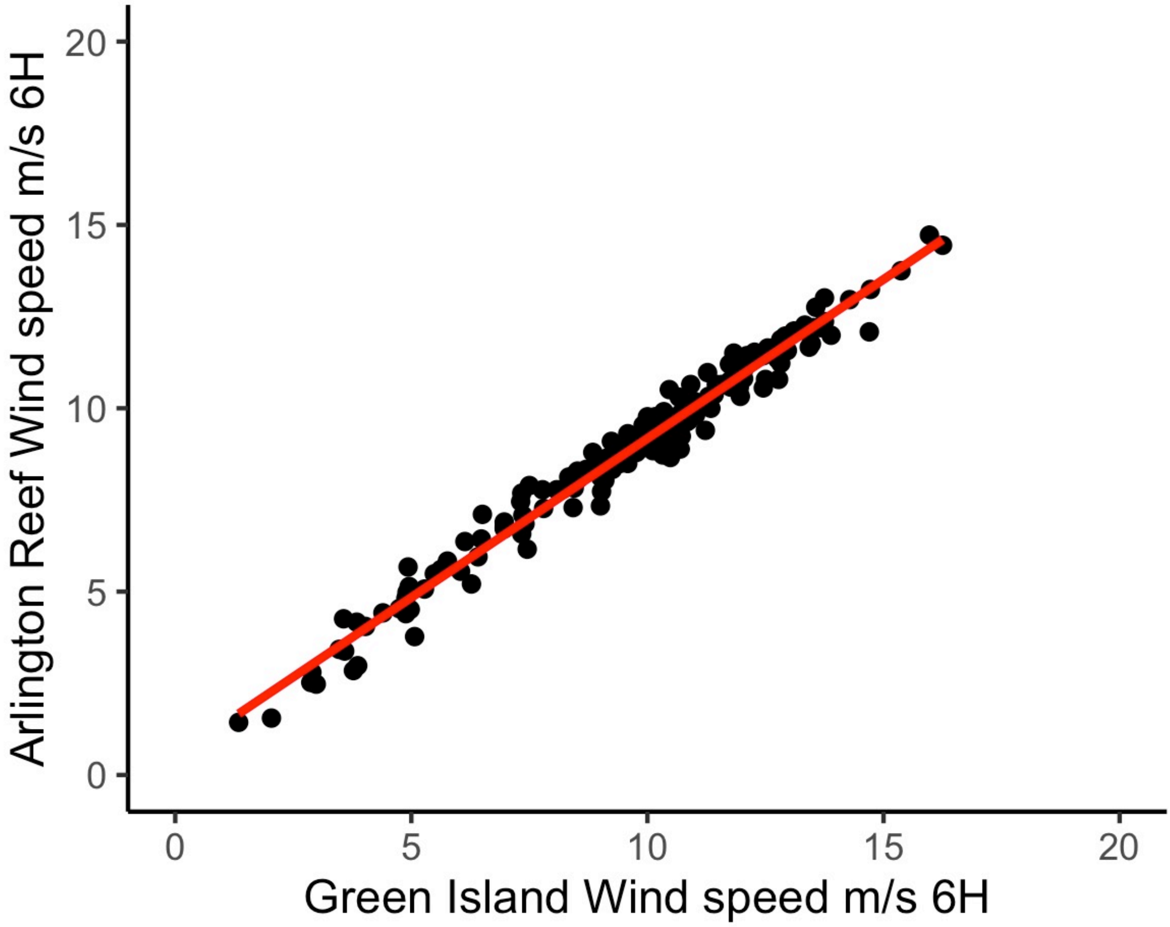


Fig. C.1. The linear relationship between Arlington Reef and Green Island wind stations. Wind speed measured in meters per second was converted to 6 hourly averages.