Key Ecological Processes in Kimberley Benthic Communities: Recruitment and Herbivory

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WAMSI Kimberley Marine Research Program

Final Report

Project 1.1.2

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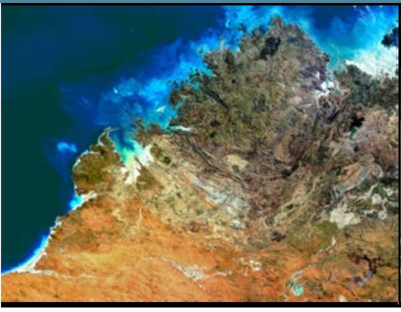

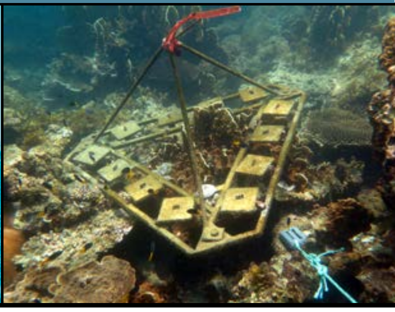

WAMSI Kimberley Marine Research Program

Initiated with the support of the State Government as part of the Kimberley Science and Conservation Strategy, the Kimberley Marine Research Program is co-invested by the WAMSI partners to provide regional understanding and baseline knowledge about the Kimberley marine environment. The program has been created in response to the extraordinary, unspoilt wilderness value of the Kimberley and increasing pressure for development in this region. The purpose is to provide science based information to support decision making in relation to the Kimberley marine park network, other conservation activities and future development proposals.

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Front cover images (L-R)

Image 1: Satellite image of the Kimberley coastline (Image: Landgate)

Image 2: Bite marks on seagrass from the herbivorous golden-lined rabbitfish *Siganus lineatus* (Image: Mat Vanderklift)

Image 3:Humpback whale breaching (Image: Pam Osborn)

Image 4:Coral recruitment tiles on metal frame deployed at Hal's Pool, one of five locations in Cygnet Bay and the Sunday Island group (Image: AIMS)

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Structure of Report: This final report for WAMSI 1.1.2 *Ecological processes in Kimberley benthic communities: recruitment and herbivory* is structured and presented as three independent chapters for the following subprojects; a) Fish recruitment, b) Coral recruitment and c) Herbivory.

Metadata link for AIMS fish and coral recruitment subprojects:

http://data.aims.gov.au/metadataviewer/faces/view.xhtml?uuid=05f33378-b7df-433f-8019-16e9c7eb8620

http://catalogue.aodn.org.au/geonetwork/srv/eng/metadata.show?uuid=05f33378-b7df-433f-8019-16e9c7eb8620

Metadata link for CSIRO herbivory subproject:

http://www.marlin.csiro.au/geonetwork/srv/eng/search#!8d910bf0-2f4e-4fc2-8a6e-f0447ed2d996

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Contents

1 Executive Summary

Replenishment and herbivory fundamentally underlie the ongoing health of coastal marine ecosystems. Regular recruitment is essential for sustaining populations of fish and invertebrates, whilst herbivory transfers energy from primary consumers to higher trophic levels and inhibits overgrowth of reefs by fleshy macroalgae. This project aimed to better understand these ecological processes in the Kimberley region by quantifying when, where and how coral and fish replenishment takes place and who is responsible for the bulk of grazing on primary production (seagrass and algae) in coastal marine areas. Recruitment studies focused on hard corals, as they provide habitat for millions of species but their long-term persistence is threatened by climate change, and teleost fish, which are of ecological, cultural and commercial value. Herbivory studies focused on fish and turtles, which are prominent feeders of seagrass and algae in the tropics and are culturally significant to indigenous people throughout the Kimberley.

Our studies were around Cygnet Bay and the Sunday Island group which experiences tidal fluctuations of up 12m and is typical of the West of the Kimberley. The area is remote, although small local communities and industry (e.g. pearling) are present and are reliant on the ecosystem services provided by the ocean, emphasizing the value of understanding key processes in the area. An Indigenous Protected Area was declared in 2013 and management of the IPA by the Bardi Jawi Rangers is outlined in the Bardi Jawi Healthy Country Management Plan.

This report is divided into three stand-alone sub-projects: fish recruitment, coral recruitment and herbivory. The major findings from each of these sub-projects are outlined below.

1.1 Fish recruitment:

Our research remit was to develop techniques suitable to quantify juvenile fish recruitment in the challenging macro tidal conditions of the Kimberley (how); provide baseline levels of abundance and diversity of juvenile fish across a range of representative Kimberley marine habitats (how many), identify the seasonal timing of fish recruitment (when); identify important juvenile fish nursery grounds or habitats (where) and provide advice on relevant sites as a basis for any future monitoring. In collaboration with the Bardi Jawi Rangers and the Kimberley Marine Research Station, this research was focused in the Cygnet Bay and the Sunday Island group at the mouth of King Sound in the West Kimberley. In total, a series of eight fish recruitment field trips were completed from March 2015 - March 2016.

Our initial pilot study (March 2015) compared seven separate fish recruitment sampling techniques across six locations which together encompassed four different habitats; inter-tidal pools, seagrass, mangrove and coral reefs. The comparative analyses considered sampling effort, ability to accurately quantify juvenile fish diversity and abundance across a range of habitats, precision and safety. Unbaited stereo remote underwater video (stereo-RUVs) came out as a clear winner among techniques. During this pilot study, it also became clear that tidal current strength and habitat type were critically important variables structuring fish recruitment patterns. To address this, we restricted core sampling to neap tides or 1.5 hours either side of spring high and low tides and added in algal meadows as a fifth habitat.

In total, we recorded 125 species of adult and juvenile fish during surveys. Eleven (9%) of these were observed only as juveniles, 43 (33%) as both juveniles and adults, and 74 (60%) as only adults. Among species, 88% of all recorded juveniles were represented by the top 12 species. Interestingly, many of these are considered as highly valued species to the Bardi Jawi community (e.g. Mangrove jack, Golden-lined rabbitfish, Spanish flag) because of their dietary and/or cultural significance.

Among habitats, mangroves, seagrass and algal habitats were all represented by juvenile fishes from 18-20 species, intertidal pools by 13 and coral reefs by 35 species with only 6% of the species pool observed in all five habitats. A closer look at the distribution of species among habitats revealed very distinct partitioning of nursery grounds. Our analyses showed that mangroves and seagrass areas were critical nursery habitats for many important species and that many of these species exclusively recruited to these habitats. In comparison, the other three habitats shared a common species pool indicating that any future sampling should concentrate on mangrove, seagrass and, given their increased diversity, coral reef habitats to provide comprehensive coverage of fish recruitment.

Seasonally, fish recruitment was strongest in the wet season (March / April) for most species although there were exceptions. Interestingly, some of the species considered most important to the local indigenous community are species that we identified as having strong year round recruitment providing scientific support for documented traditional Bardi Jawi fishing knowledge and management practices.

Our sampling program provides a blueprint for future monitoring of fish recruitment in the challenging Kimberley marine environment. Here we have established best-practice sampling techniques and provided locations of appropriate monitoring sites for quantifying juvenile fish recruitment across a range of representative habitats to form the basis for future long-term monitoring in the Western Kimberley.

1.2 Coral recruitment

Corals are an essential element of reef ecosystems, providing a structural framework for reef growth, as well as a habitat and food source for many other organisms. For benthic organisms like corals, sexual reproduction and the pelagic larval stage provides an opportunity for genetic mixing of populations and recovery from disturbances. In the inshore Western Kimberley, at Cygnet Bay and the Sunday Island group, reproductive and recruitment patterns for corals have not been previously studied. We modified existing, standardised methods of surveying coral larval supply, by attaching coral settlement plates to frames that enabled their deployment and retrieval from the surface, rather than by SCUBA divers. These frames were specifically designed to withstand the strong currents of the macro-tidal Kimberley environment.

Monthly sampling at 5 locations for a 13 month period allowed us to discern temporal patterns in coral recruitment and identify likely periods of mass spawning. However, extreme water temperatures that persisted through summer and autumn culminated in a coral bleaching event that peaked in March-April, affecting between 30-60% of the community. The bleaching coincided with the predicted mass-spawning period, and reduced rates of recruitment for all corals, particularly for spawning corals. Given the duration and severity of the temperature anomalies, the quantified rates of recruitment are unlikely to reflect those during years without such stress. Nonetheless, the recruitment of *Acropora* peaked in March-April 2016 and to a lesser extent in September-October, at the same time as mass- and multi-specific spawning events were documented on oceanic reefs in the Kimberley and Pilbara to the south. Recruits from the family Pocilloporidae (comprising both brooders and broadcast spawners) and genus *Isopora* were more abundant in the summer months. Additionally, we provide the first definitive evidence of reproductive output and recruitment by corals in family Poritidae over many months throughout the year, supporting anecdotal evidence from reproductive studies at oceanic reefs in the region.

The number and composition of coral recruits differed considerably among the study locations, reinforcing the spatial heterogeneity evident in most studies of biological communities in the Kimberley. Fine-scale spatial heterogeneity also varied as expected among coral groups, with evidence of recruitment variation in brooding corals over distances of less than a few hundred metres, compared with tens of kilometres for groups of spawning corals, which corresponded to genetic evidence from WAMSI Project 1.1.3. Continuation of sampling in future years, applying the methods developed here, would allow a further assessment of spatial and temporal variation in recruitment of corals at inshore Kimberley reefs, and presumably track the recovery of communities to background levels of recruitment following the bleaching disturbance.

1.3 Herbivory

The main aim of this research was to understand the relative importance of direct consumption of seagrass as a proportion of total seagrass production in the Kimberley, to identify the key herbivores, and to understand the relative importance of different primary producers to their diet. Although primary producers occupy a wide variety of habitats, the primary focus of this study were the seagrass meadows of Tallon Island (Jalan) and Sunday Island (Iwany) located in the Bardi Jawi Indigenous Protected Area. The research used and extended research conducted as part of WAMSI Kimberley Marine Research Program (KMRP) project 2.2.4 (Benthic primary productivity).

We measured higher rates of grazing on seagrass than anywhere else studied in the world — in some locations during some surveys, rates of consumption were more than ten times that of growth. This was particularly pronounced for the seagrass *Thalassia hemprichii* (otherwise known as turtlegrass), for which average consumption was higher than average growth. *Thalassia* is one of the most abundant seagrasses in the terraced lagoons that are characteristic of the Kimberley, and the apparent contradiction of high abundance and high consumption is probably reconciled by a combination of fast growth rates and patchy grazing; indeed rates of consumption of *Thalassia* varied by two orders of magnitude. It is plausible (even likely), that the measured rates of consumption are higher than the long-term averages, which would explain how seagrass can exist and grow in a place with such high rates of herbivory.

In contrast, consumption of the seagrass *Enhalus acoroides* was on average lower than growth. An inference from this finding is that much of its production is probably not consumed by herbivores. We did not set out to study the fate of seagrass production, but it is likely that much leaf biomass for *E. acoroides* is ultimately exported from the meadows as detritus.

There were several species of herbivores that were abundant in the seagrass meadows, but the golden-lined rabbitfish, *Siganus lineatus,* was ubiquitous and abundant in all Remote Underwater Video (RUV) deployments. Stable isotope and gut-content analyses confirmed that the diet of *S. lineatus* is primarily comprised of seagrass, especially *Thalassia*. *S. lineatus* is a highly valued seasonal food source for the Bardi Jawi people, who call them *barrbal*.

Another potentially significant herbivore is the green turtle, *Chelonia mydas*. Green turtles were seen during RUV deployments, but not in great abundance. However, boat-based transects during the rising tide found that they were abundant over the seagrass beds of Jalan and Iwany. Stable isotope and gut-content analyses showed that Green Turtles consumed a range of plant foods, but brown algae and the seagrass *Thalassia* were particularly prominent in their diet. There was some, albeit equivocal, evidence that different individuals might have preference for brown algae or seagrass. Satellite tags showed that individual turtles frequently tended to spend their time in places with abundant seagrass.

2 Implications for management

2.1 Fish recruitment

The key considerations and recommendations from this research for natural resource managers and other potential end-users are:

- Conservation policy and planning should recognize that all marine habitats provide a unique contribution to the overall pool and diversity of the Kimberley’s fish fauna by providing fish nurseries and therefore warrant some level of protection.
- Sampling in the Kimberley usually requires additional resources, development, refinement and testing of established and innovative techniques to ensure they work in this remote and challenging environment.
- Juvenile fish diversity in the Cygnet bay and Sunday Island group was surprisingly low considering its proximity to the equator and global centre of fish diversity. More research into how challenging macro-tidal systems affect patterns of juvenile fish recruitment is needed.
- This project provides quantitative scientific evidence that traditional management practices are well founded.

- Future monitoring should concentrate sampling in the wet season (March / April) within mangrove, seagrass and coral reef habitats in order to get the strongest and most comprehensive assessment of juvenile fish recruitment.
- Fish recruitment underlies replenishment of populations; however rates of recruitment vary spatially and temporally and comprehensive monitoring of fish recruitment will be expensive, especially in remote locations like the Kimberley. Monitoring of adult fish numbers, which are less variable, may be an easier way to assess the health of the Kimberly's fish fauna and should therefore take priority over recruitment surveys. When monitoring of fish recruitment is possible it should focus on species under the greatest anthropogenic pressure and those that perform key ecological roles.

2.2 Coral recruitment

The key considerations and recommendations from this research for natural resource managers and other potential end-users are:

- Corals are important habitat-forming organisms in the inshore Kimberley, and they rely on movement of larvae to maintain populations and recover from disturbance. Understanding coral reproduction & recruitment promotes a greater understanding of which populations are potentially vulnerable to disturbance.
- A protocol was developed for quantifying coral recruitment using frames deployed and retrieved from a small vessel, without requiring SCUBA diving or long periods in the water, to accommodate the hazardous conditions in the Kimberley.
- The recruitment frames were retrieved, tiles changed, and then re-deployed, by the Bardi Jawi Rangers during most months throughout the year. The tiles were also processed and preserved for later analysis by the Bardi Jawi Rangers.
- Coral spawning was detected in March-April and, to a lesser extent, October-November, at similar times to other reefs in the region. However, the occurrence of a coral bleaching event during the primary time of spawning meant that results could not be considered as typical (recruit numbers may be higher in the absence of coral bleaching).
- A large proportion of the coral recruits were from brooding species, with recruitment occurring in many months of the year. For some family groups containing brooding corals, higher recruit numbers were recorded during the summer months. In other family groups, recruitment occurred in many months throughout the year.
- Differences among locations (10s of km apart) were considerable, with variation in both the number and families of coral recruits. For some coral groups, differences at smaller spatial scales (100s of metres) were also important.
- Additional sampling in future years would provide information on recruitment in a more typical year for comparison. Sampling should encompass several locations and a nested sampling design to further examine spatial variability in recruitment patterns.
- To provide useful information on larval supply from coral recruitment studies, it is critical to know the reproductive mode of recruiting corals, the times of spawning and planulation, and to standardise the periods over which tiles are weathered prior to recruitment and are retrieved afterwards.

2.3 Herbivory

The key considerations and recommendations from this research for natural resource managers and other potential end-users are:

- The research reinforces the importance of marine plants, especially seagrasses, to the diet of Kimberley marine fauna. We have shown that seagrass consumption is high, and is a major component of the diet of several herbivores. The herbivores are important to the Bardi Jawi (both golden-lined rabbitfish (*S. lineatus*) and green turtles as a seasonal food cultural resource) and likely to other saltwater communities of the Kimberley. Management plans for areas that contain seagrass beds or stands of macroalgae should consider these as Key Performance Indicators;
- Given the important ecological role that seagrass consumers play, monitoring abundances of these taxa is desirable. The imperative for monitoring the abundance of Green Turtles is also supported by their status as a protected species and their high value in monitoring and management of the indigenous Healthy Country Plans for the region;
- Some work is still needed to develop methods for monitoring that can be adopted and applied uniformly by indigenous ranger groups for Healthy Country Plan monitoring, preferably one consistent with current state-of-the-art methods used for monitoring of marine protected areas;
- The importance of seagrasses to large vertebrate herbivores can be easily monitored through simple tethering experiments which can be useful to assess the resilience of the seagrass and its grazers; and
- Studies of the movement of green turtles might help identify seagrass beds and other important primary producer habitats.

3 Key residual knowledge gaps

3.1 Fish recruitment

This project is the first to provide baseline information on fish recruitment processes in the Kimberley using surveys of post-recruitment juvenile fish. However, a number of knowledge gaps remain including:

- **Spatial area:** While the project provides a solid baseline of knowledge on fish recruitment processes in the Cygnet Bay and Sunday Island group at the entrance to King Sound, results should not be extrapolated outside this area. An expansion of surveys using the same technique would be needed to properly characterise the Kimberley.
- **Duration of study:** Recruitment of all marine organisms is inherently variable from year to year and what variables drive these patterns under what conditions remains a hotly debated topic. Further, 2015/16 recorded unprecedented high-water temperatures in NW Australia suggesting that reproduction and recruitment activities may have been severely affected. Surveys over decadal time periods would be needed, coupled with oceanographic studies over local and regional scales before a detailed understanding of this process could be made possible.
- **Habitat heterogeneity:** The nature of the Kimberley benthos in the survey area is a mixture of inter-blended habitat types. While the importance of discrete nursery habitats is beginning to be understood, the significance of habitat mosaics to fish recruitment processes and their value as nursery grounds remains largely unknown.
- **Macro tidal systems:** Fish diversity was surprisingly and unexpectedly low considering the range of nursery habitats available and the survey area's proximity to the equator and global centre of fish biodiversity. Further, of the 134 species recorded in our surveys, less than half were recorded in their juvenile forms suggesting that macro tidal conditions may well provide unassailable challenges to many fish species, particularly small juveniles. Further targeted research into the ecological strategies used by fishes to overcome these barriers is needed to better understand fish recruitment processes in challenging conditions.

3.2 Coral recruitment

This project provides baseline information on coral recruitment processes in the Kimberley using surveys of coral recruits settling on artificial substrate (settlement plates). A number of knowledge gaps remain, including:

- **Temporal variability:** As this study took place in an atypical year (when an unprecedented coral bleaching event occurred), sampling in additional years would be necessary to gain a more detailed understanding of seasonal variation in recruitment processes.
- **Spatial variability:** The variation among locations in this study highlighted the potential diversity present within Kimberley coral reefs. Due to these high levels of spatial variability, the findings documented here may not be directly applicable to reefs in the wider Kimberley region.
- **Post-recruitment survival:** Survival from settlement into the juvenile and adult life stages was not part of the scope of this project, but is a key element of the maintenance of coral communities. Long-term monitoring programs can provide further insight into coral growth and survival, which shape the coral reef community.
- **Larval movements:** Understanding the sources of larvae and their patterns of movement before settlement remains relatively unknown. Understanding patterns of larval movement could help predict areas of high and low recruitment.
- **Reproductive modes:** The mode of reproduction (spawner, brooder) remains unknown for some common Kimberley corals. In particular, some species of massive *Porites* were previously assumed to be spawning corals, although brooders have since been reported. It is not known whether the extended period of *Porites* recruitment was due to protracted spawning and/or recruitment of brooded larvae.

3.3 Herbivory

This project has significantly increased our understanding of the importance of herbivory as a process in the Kimberley, and the relative importance of different primary producers as food for herbivores. It has also highlighted a number of knowledge gaps. Key among those gaps are:

- **Abundance of herbivores:** we have limited information about the true abundance of key herbivores such as the golden-lined rabbitfish and green turtles. Green turtles are listed threatened species that are also important food and cultural resources for indigenous communities in the Kimberley, and there is a need to understand their patterns of abundance and distribution;
- **Movement:** we were able to conduct relatively limited studies of the movement of green turtles, but these showed that individuals range widely over relatively short time periods, in contrast to other parts of Australia. Many individuals moved between regions covered by different Healthy Country Plans, implying a hitherto under-appreciated level of connectivity. This remains poorly understood;
- **Wider understanding:** We were only able to focus on herbivory in one type of habitat (seagrass meadows), and the diet of two key herbivores (golden-lined rabbitfish and green turtle). The importance of herbivory in other habitats (e.g. reef), and by other key herbivores (e.g. surgeonfish, dugongs) remains unstudied in the Kimberley; and
- **Deeper meadows:** as highlighted in the WAMSI KMRP project 2.2.4 (Benthic primary productivity), our understanding of ecological processes in deep meadows is poor. These meadows are potentially more important for dugong and there is a need to understand niche resource partitioning among Kimberley herbivores.

4 Management questions

This project directly addresses the following questions outlined in the Kimberley Marine Research Program Science Plan in addition to questions raised by the managers and planners.

Key Question	**Informed Response**
1. What are current baseline levels of fish and coral recruitment and how do these compare to other areas of Australia?	An informed response needs to be prefaced with the fact that sampling was partially conducted during unprecedented high-water temperatures which have been found to have both positive and negative effects on the strength of coral and fish recruitment. Thus, while data was collected on both fish and coral recruitment, 2015/16 was an anomaly period making it difficult to categorise this data as baseline without further evidence of interannual variation. **Fish Recruitment:** For fish, baselines are not comparable to other areas of Australia because this program was the first to use Remote Underwater Video as a method to quantify juvenile reef fishes. The method uses MaxN, which is the maximum number of individuals from each species seen within a single frame, making comparisons with direct counts (the method commonly used elsewhere in Australia) impossible. **Coral Recruitment:** For corals, recruitment is not directly comparable with other areas of Australia due to the occurrence of coral bleaching during the primary period of predicted mass spawning (March-April). However, there were recruits from spawning corals (*Acropora)* detected primarily during this time, and again in low numbers in Oct-Nov, which suggests that the timing of mass spawning, under normal conditions, would be similar to that documented at other Western Australian reefs (for spawning corals: major spawning event in March-April, smaller spawning event in October-November).
2. What are current baseline levels of herbivory, and how do these compare to other areas of Australia?	Current levels of herbivory on seagrass appear to be among the highest in the world. Estimates of consumption of *Thalassia* were higher than those of *Enhalus*, and were comparable to (albeit higher than) estimates from tropical seagrasses in Indonesia. The estimates are, on average, higher than those recorded elsewhere in Australia.
3. What's the spatial and methodological framework for managers to do this work in the future (how do we collect data on these processes over the long term)?	This project was concentrated in the Cygnet Bay and Sunday Island group of the west Kimberley only. Rollout to the rest of the Kimberley would best be approached utilizing local indigenous knowledge in areas of interest, areas of perceived importance or those under imminent threat. For regional patterns of recruitment of fishes and corals, studies over large geographic areas would need to be conducted in synchrony by multiple teams at multiple geographic locations. It is unlikely that this is feasible and we recommend local-scale sampling using the methods developed here. The macro-tidal conditions found in the Kimberley provided an opportunity to develop and refine new methods and techniques which are robust enough to deal with the challenging hydrological conditions of the Kimberley (e.g. tidal currents, turbidity, exposure). This included; **1) Fish Recruitment:** Unbaited remote underwater video frames using stereo cameras to accurately determine size of individuals. This coupled with sampling on neap tides or 1-2 hours either side of spring highs and lows to enhance underwater visibility for camera work. **2) Coral Recruitment:** We designed, developed, tested and constructed frames on which coral recruitment tiles were mounted. This allowed the frames to be deployed and retrieved from the surface, without the need for SCUBA diving, which is logistically difficult in remote areas. The frames were able to withstand strong currents without movement or vibration (which may affect settlement processes). Use of the frames also assisted in re-locating the coral tiles when visibility was poor (common at two of the five locations). **3) Coral Recruitment:** In future, ideal methodologies would combine the methods used during this sampling program, with other complementary surveys (coral long-term monitoring program, reproductive surveys, genetic analyses). This would build on the understanding of larval supply which we gained from this project, by expanding knowledge of the abundance of various coral genera at each location, and gain further understanding of patterns of larval movement, identifying 'sources' and 'sinks' of coral larvae, and post-settlement survival rates of corals. The implementation of a coral long-term monitoring program in particular would improve our understanding of the response of the unique coral reefs in the inshore Kimberley to global threats to coral reefs, such as coral bleaching.

	4) Herbivory: Measurements were done in seagrass meadows of the raised lagoons on Sunday and Tallon Islands, using methods proven to be effective elsewhere. Different species of seagrasses are likely to be present in other habitats (e.g. deeper water), and in more turbid regions of the Kimberley. In addition, the study of diet focused on species of particular importance in the study area. Green turtles are likely to be just as important in other parts of the Kimberley, but their diet might vary depending on the resources available. Other species of fish will be more or less important in other habitats (e.g. parrotfish and surgeonfish are likely to be more important on reef habitats). While information on diets of other species and places will be valuable (and can be collected using the methods outlined here), greater emphasis in the short-term should probably be placed on developing robust monitoring for seagrasses. Knowledge of green turtle abundance remains a critical knowledge gap. Together these developments and refinements provide a blueprint of how to survey and monitor recruitment and herbivory in the Kimberley marine environment, the equipment needed and steps to take for their accurate assessment and quantification.
4. What are the important months for spawning and recruitment?	**Fish Recruitment:** Seasonal sampling of fish recruits in mangrove, seagrass, algal, coral reef and inter-tidal pool habitats identified the wet season (March/April) was providing the strongest signal of fish recruitment for both abundance and diversity although there were exceptions (see report Figure 8). In addition, bi-monthly sampling of fish recruits in coral reef habitats identified that seven of the top ten species would be best surveyed between the December and April period. **Coral Recruitment:** Coral recruitment occurred throughout the calendar year, although overall recruit numbers were highest in November 2015, followed by September and October 2016. The coral families Pocilloporidae and Poritidae (the most common recruits) were present in all months of the year. For both of these families, this could be due to a combination of brooding species releasing larvae monthly, and spawning corals releasing gametes in many months (both families contain both spawning and brooding species). We saw a small peak in abundance of *Acropora* recruits in March-April, and again in smaller numbers in October at some locations, although numbers of these recruits were likely reduced by the stress associated with coral bleaching observed during March-May at the study locations (coral bleaching is documented to reduce reproductive output both during and after bleaching events).
5. What habitats support which species and what do we need to do to support the important species of the Kimberley?	Fish nursery habitats differed in their fish recruitment support roles with each of the five habitats supporting a different assemblage of species. Species assemblages were most different in mangrove and seagrass habitats with coral reefs, algal and intertidal pools having a stronger potential to act as surrogates for each other under a more restricted program. Mangroves strongly and almost exclusively provided a nursery habitat for juvenile Mangrove jack (*Lutjanus argentimaculatus* - Maarran) and Moses perch (*Lutjanus russelli*), seagrass beds the important herbivorous Golden-lined rabbitfish (*Siganus lineatus* – Barrbal) with the remaining three habitats supporting a more diverse and mixed assemblage. Safeguarding the health and diversity of all five Kimberley habitat types is the best way to ensure ongoing replenishment of fish stocks at the local level.
NEW QUESTIONS POSED BY MANAGERS ON 28TH FEBRUARY 2017	
What works and what doesn't when it comes to quantifying these ecological processes?	**WORKS** **1) Fish Recruitment:** Working in with relevant indigenous marine rangers to understand and share local geographical, oceanographic and ecological knowledge is critical to underpin this research and/or monitoring. **2) Fish Recruitment:** Deploying any underwater video technique either during neap tides or 1-2 hours either side of spring high and low tides is essential to minimise turbulence and ensure best visibility. **3) Fish Recruitment:** Underwater camera rigs recording fish recruits do not need to be baited as this will likely attract predators. Accessing standard bait items such as pilchards can also be logistically difficult in remote areas of the Kimberley. Juvenile fishes tend to be sedentary so unbaited rigs provide good estimates of abundance and diversity within camera field of view. **4) Coral Recruitment:** The use of frames (allowing coral recruitment tiles to be raised and lowered from the sea bed without divers) was very successful and provided monthly data indicating when coral recruitment was taking place. **5) Coral Recruitment:** The local management of monthly sampling by the Bardi Jawi Rangers was vital to the success of the coral recruitment project. Retrieving the frames was often delayed due to poor weather

	conditions affecting both sea state and visibility. Without the input of local groups, the project would have consumed vastly greater resources (both cost and time) with much fewer results. **6) Coral Recruitment:** Maximising the available working time by utilizing the most suitable tidal windows was critical. Again, without the extensive local knowledge brought by the involvement of the Bardi Jawi Rangers, this would have been difficult to impossible. **7) Herbivory:** Simple tethering methods, in conjunction with studies of seagrass growth, were effective. Caging experiments would provide additional value to support the inferences. **DOESN'T WORK** **1) Fish Recruitment:** Divers underwater for census work; still camera, box trawls and patch reef aggregation devices for quantifying fish recruitment. **2) Fish Recruitment:** Trying to stratify sampling regime by specific habitat because the benthic community tends to be a diverse mosaic of inter-mixed habitats. Exceptions are seagrass and mangrove habitats which tend to be more homogenous and able to be stratified. **3) Coral Recruitment:** The timing of deployment and retrieval of tiles in relation to the predicted times of spawning is critical (e.g. tile changeovers on a particular day). If tiles are not deployed at the appropriate times the approach does not work- data are not comparable among months, years and/or other studies. **4) Coral Recruitment:** Incorporating additional measures quantifying the coral communities at each location, and in the broader region, in more detail would assist in interpreting coral recruitment data and understanding the relationships between larval supply, recruitment and the survival of corals into adulthood. **5) Coral Recruitment:** As recruit numbers were relatively low, we suggest that future surveys consider incorporating additional replication at the tile level, in order to capture sufficient numbers of recruits for analysis (although to some extent, the low numbers were likely a reflection of stress associated with increased water temperatures and coral bleaching). **6) Herbivory:** Placement of cameras near areas of mangrove yielded poor video that could not be analysed. In addition, attempts to trap herbivorous fish largely did not work.
Where to from here, relevant questions?	**1)** Did unprecedentedly high water temperatures in 2015/16 impact coral and fish recruitment numbers? **2)** Are the patterns observed in the Cygnet Bay and Sunday Island group indicative of those of the rest of the Kimberley region **3)** How can the measures of fish recruitment with RUVs be modified so they can be compared to data from other locations? **4)** Is the low diversity found in the juvenile fish fauna a consequence of the challenging hydrological conditions of Cygnet Bay and Sunday Island group and the challenges it poses to small larval fishes or representative of the Kimberley region in general? **5)** How stable are fish nursery grounds given they are living habitats which also respond to global pressures personified by climate change in the marine environment? **6)** Are the low numbers of coral recruits at some locations, and in some coral groups, persistent, or variable among years? **7)** Can a combined approach utilizing additional techniques (reproductive sampling, genetic analysis, coral monitoring program) provide more detailed, species- or genera-level information regarding which corals reproduce at which time, and on the movement of larvae throughout the study area? **8)** Knowledge of the abundance of green turtles is a critical knowledge gap. The ubiquity of green turtles as KPIs throughout the Kimberley, in marine parks plans and Healthy Country plans, all highlight the need for this knowledge.
Restrictions in what the information will provide to management.	Recruitment of corals and fish is inherently stochastic in nature requiring multi-year studies to detect significant changes or detrimental effects. Once detected, determination of whether it is a larval supply (i.e. regional) or juvenile survivorship (i.e. local-scale) issue then needs addressing. This is a decade-long exercise. All results herein must also be interpreted with some caution given sampling was conducted during a period where protracted water

	temperatures were the highest experienced (as evidenced by the local indigenous communities comments that they had no history of corals bleaching). **Fish Recruitment:** What this project has clearly identified for fish recruitment is which habitats provide fish nursery areas to which species; the range and importance of habitat type to this process, ways in which to conduct accurate surveys and the best timing to conduct these. **Coral Recruitment:** What this project has clearly identified for coral recruitment, is the large variation among locations and months for most groups of coral recruits. The information is also limited to key coral groups, so more detailed information regarding individual coral species and/or genera requires the addition of complementary approaches. **Herbivory:** What this project has clearly identified for herbivory is that consumption of seagrass is very high (especially of *Thalassia*), and that seagrass in turn comprises a very important part of the diet of rabbit fish and green turtles, which are culturally important for the Bardi Jawi people. The activities of the herbivores likely shape the seagrass ecosystem.

5 Report Structure

The full report for WAMSI project 1.1.2 is structured as an executive summary, three individual sub-project reports that focus on different marine organisms.

The following sub-reports are included as separate documents:

1.1.2a	Key Ecological Processes in Kimberley Benthic Communities: Fish Recruitment
1.1.2b	Key Ecological Processes in Kimberley Benthic Processes: Coral Recruitment
1.1.2c	Key Ecological Processes in Kimberley Benthic Processes: Herbivory

6 Key communication activities

Students supported

Camilla Piggott commenced a PhD in November 2014 as part of the fish recruitment component of the project. Camilla is based at AIMS / OI with her PhD candidature administered through the School of Plant Biology at the University of Western Australia. The nominal title of her PhD is "Fish replenishment processes in the Kimberley region of NW Australia". She is expected to submit her thesis in August 2018.

Lisa DeWever (M. Sc., European Institute for Marine Studies, France), Lucie Chovrelat (M. Sc., European Institute for Marine Studies, France), Emy Guilbault (M. Sc., Montpellier SupaGro, France) all satisfied part of the requirements of their degrees through specific projects that added value to the work presented here, including the rabbitfish stomach contents, and seagrass tethering.

Journal publications

Proceedings/Technical Reports

Kendrick GA, Fraser MW, Cayabyab N, Vanderklift M (submitted) Seagrasses of the Kimberley. Natural World of the Kimberley Proceedings. Kimberley Society Seminar 16th October 2016, The University of Western Australia, Crawley

Submitted manuscripts

As above

Presentations

Depczynski M (2017) Parks and Wildlife Lunch n Learn Series (28th February 2017) Presentation on Key Ecological Processes in Kimberley Benthic Communities – Fish recruitment

Depczynski M (2016) Presentation to Kimberley Marine Research Station. April 2017.

Gilmour J (2017) Parks and Wildlife Lunch n Learn Series (28th February 2017) Presentation on Key Ecological Processes in Kimberley Benthic Communities – Coral recruitment

Vanderklift M (2015) Presentation to One Arm Point school

Vanderklift M (2016) The ecology of green turtles in Bardi Jawi sea country. 3rd Australian Sea Turtle Symposium, Darwin, 22-24th August 2016.

Vanderklift M (2016) Presentation to Kimberley Marine Research Station. April 2014.

Vanderklift (2017) Parks and Wildlife Lunch n Learn Series (28th February 2017) Presentation on Key Ecological Processes in Kimberley Benthic Communities - Herbivory

Regular presentations of project results to Bardi Jawi rangers during each survey by all sub-project leaders.

Other communications achievements

Class and field activities with One Arm Point Remote Community School.

Key methods for uptake (ie advisory committee, working group, website compendium of best practice.)

KISSP Presentation mid 2016.

KSN 1.1.2 Summary Document (Feb 2017) – Key Ecological Processes in Kimberley Benthic Communities https://indd.adobe.com/view/64e01346-0848-4800-9a1c-1424014b6e44

KSN 1.1.2 KMRP Meeting with Node Leader and KMRP Advisory Group to discuss management needs and application (28 February 2017)

Other

KMRS Newsletter (October 2014) *"No diet restriction for the rabbitfish"*

Science Network WA (May 2015) *"What's eating you? Solving the seagrass mystery."* http://www.sciencewa.net.au/topics/aboriginal-science-a-knowledge/item/3536-what-s-eating-you-solving-the-seagrass-mystery

WAMSI Article (August 2015) *"Schools out on tropical fish nurseries in the Kimberley"* http://www.wamsi.org.au/news/school%E2%80%99s-out-tropical-fish-nurseries-kimberley

KMRS Newsletter (October 2015) *"Juvenile fish recruitment dynamics"& "Coral communities"*

KMRS Newsletter (February/March 2016) *"Juvenile fish recruitment dynamics"*

KMRS Newsletter (April/May 2016) *"Tagging turtles"*

KMRS Newsletter (April/May 2016) *"Juvenile fish recruitment"*

KMRS Newsletter (April/May 2016) *"Tagging turtles"*

KMRS Newsletter (June/July 2016) *"Milly's return – Juvenile fish recruitment"*

WAMSI Article (November 2016) *"Field trip finds turtle and fish food abundant in Bardi Jawi country"* http://www.wamsi.org.au/news/field-trip-finds-turtle-and-fish-food-abundant-bardi-jawi-country

CSIRO ECOS Blog Article (December 2016) A field trip to Bardi Jawi country: turtles and fish and seaweed, oh my! https://blog.csiro.au/a-field-trip-bardi-jawi-country-turtles-fish-food-and-fun/

DPaW Kimberley Tide Article (December 2016) Field trip to Bardi Jawi country

KMRP WAMSI 1.1.2 Summary: Key ecological processes in the Kimberley: recruitment and herbivory

western australian
marine science institution

Key Ecological Processes in Kimberley Benthic Communities: Fish Recruitment

Martial Depczynski M[1,2,7], Katherine Cure[1,2,7], Zac Egdar[3,7], Kevin George[3,7], Tom Holmes[2,4,7], Azton Howard[3,7], Phillip McCarthy[3,7], Glenn Moore[5,7], Daniel Oades[3,7], Camilla Piggott[2,7], Mike Travers[2,6,7], Shaun Wilson[2,4,7]

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WAMSI Kimberley Marine Research Program

Final Report

Subproject 1.1.2a

April 2017

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Department of Primary Industries and Regional Development

THE UNIVERSITY OF WESTERN AUSTRALIA

WAMSI Kimberley Marine Research Program

Initiated with the support of the State Government as part of the Kimberley Science and Conservation Strategy, the Kimberley Marine Research Program is co-invested by the WAMSI partners to provide regional understanding and baseline knowledge about the Kimberley marine environment. The program has been created in response to the extraordinary, unspoilt wilderness value of the Kimberley and increasing pressure for development in this region. The purpose is to provide science based information to support decision making in relation to the Kimberley marine park network, other conservation activities and future development proposals.

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Front cover images (L-R)

Image 1: Satellite image of the Kimberley coastline (Image: Landgate)

Image 2: Bite marks on seagrass from the herbivorous golden-lined rabbitfish *Siganus lineatus* (Image: Matt Vanderklift)

Image 3: Humpback whale breaching (Image: Pam Osborn)

Image 4: Juvenile mangrove jack *Lutjanus argentimaculatus* (maarrarn) (Image: CSIRO)

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Structure of Report: This final report for WAMSI 1.1.2 *Ecological processes in Kimberley benthic communities: recruitment and herbivory* is structured and presented as three independent chapters for the following subprojects; a) Fish recruitment, b) Coral recruitment and c) Herbivory.

Metadata link for AIMS fish and coral recruitment sub-projects:

http://data.aims.gov.au/metadataviewer/faces/view.xhtml?uuid=05f33378-b7df-433f-8019-16e9c7eb8620

http://catalogue.aodn.org.au/geonetwork/srv/eng/metadata.show?uuid=05f33378-b7df-433f-8019-16e9c7eb8620

Metadata link for CSIRO herbivory sub-project: -
http://www.marlin.csiro.au/geonetwork/srv/eng/search#!8d910bf0-2f4e-4fc2-8a6e-f0447ed2d996
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Author Contributions

MD, TH, MG, CP, MT & SW designed the field techniques and sampling programs; MD, KC, TH, MG, CP, MT & SW conducted the fieldwork; KC, SW, CP & MD conducted data analyses; KC and two independent contractors conducted video analyses (Todd Bond, Matt Birt, The University of Western Australia). MD & KC wrote the report.

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Kimberley Traditional Owner agreement: This research was enabled by the Bardi Jawi Traditional Owners through their advice, participation and consent to access their traditional lands.

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Collection permits/ethics approval: Fish recruitment: Department of Fisheries Western Australian Exemption number 2709. Department of Parks and Wildlife Permit number SF 010199 & SF010529: **Coral recruitment:** Department of Fisheries Western Australian Exemption number 2709. Department of Parks and Wildlife Permit number SF010529 and 01-00034-1: **Herbivory:** All flora and fauna collections were performed under permits issued by the Department of Parks and Wildlife (DPaW) in accordance with the Wildlife Conservation Act 1960 (Fauna licence SF010795 and flora license SW01557 issued to MV), and by the Department of Fisheries in accordance with the Fish Resources Management Act 1994 (Exemption 2463).

Contents

Executive summary

Fish recruitment, the process of juvenile fish moving into adult populations, is a fundamental determinant of population size. It is often measured as the local abundance of juvenile fish, although there are often some locations, habitats or times of year where recruitment of fish is higher than others. Consequently, knowing when and where recruitment is highest identifies ecologically important times and locations which can inform conservation and fisheries management. As measures of recruitment are also dependent on the technique employed it is imperative that location and taxa appropriate methods are developed to acquire relevant recruitment information.

Our research remit was to develop techniques suitable to quantifying juvenile fish recruitment in the challenging macro tidal conditions of the Kimberley (how); provide baseline levels of abundance and diversity across a range of representative Kimberley marine habitats (how many), identify the seasonal timing of fish recruitment (when); identify important juvenile fish nursery grounds or habitats (where) and provide advice on relevant sites as a basis for any future monitoring. In collaboration with the Bardi Jawi Rangers and the Kimberley Marine Research Station, this research was focused in the Cygnet Bay and Sunday Island group at the mouth of King Sound in the Western Kimberley. In total, a series of eight fish recruitment field trips were completed from March 2015 - March 2016.

Our initial pilot study (March 2015) compared seven separate fish recruitment sampling techniques across six locations which together encompassed four different habitats; inter-tidal pools, seagrass, mangrove and coral reefs. Following analyses that considered sampling effort, ability to accurately quantify juvenile fish diversity and abundance across a range of habitats, precision and safety, unbaited stereo remote underwater video (stereo-RUVs) was shown to be the most appropriate technique. This method is well suited to monitoring in the Kimberley, however, it is not commonly employed to measure fish recruitment, making it difficult to make comparison with other studies. During this pilot study, it also became clear that tidal current strength and habitat type were critically important variables structuring fish recruitment patterns. To address this, we restricted core sampling to neap tides or 1.5 hours either side of spring high and low tides and added in algal meadows as a fifth habitat.

In total, we recorded 125 species of adult and juvenile fish during surveys. Eleven (9%) of these were observed only as juveniles, 43 (33%) as both juveniles and adults, and 74 (60%) only as adults. Among species, 88% of all recorded juveniles were represented by the top 12 species. Interestingly, many of these are considered as highly valued species to the Bardi Jawi community (e.g. Mangrove jack, Golden-lined rabbitfish, Spanish flag) because of their dietary and/or cultural significance.

Among habitats, mangroves, seagrass and algal habitats were all represented by juvenile fishes from 18-20 species, intertidal pools by 13 and coral reefs by 35 species with only 6% of the species pool observed in all five habitats. A closer look at the distribution of species among habitats revealed very distinct partitioning of nursery grounds. Our analyses showed that mangroves and seagrass areas were critical nursery habitats for many important species and that many of these species exclusively recruited to these habitats. In comparison, the other three habitats shared a common species pool indicating that any future sampling should concentrate on mangrove, seagrass and, given their increased diversity, coral reef habitats to provide comprehensive coverage of fish recruitment. Our findings therefore support the need for representative protection of all these habitats to ensure conservation of the full cohort of fish biodiversity.

Seasonally, fish recruitment was strongest in the wet season (March / April) for most species although there were exceptions. Interestingly, some of the species considered most important to the local indigenous community are species that we identified as having strong year round recruitment providing scientific support for documented traditional Bardi Jawi fishing knowledge and management practices.

Our sampling program provides a blueprint for future monitoring of fish recruitment in the challenging Kimberley marine environment. Here we have established best-practice sampling techniques, provide locations of appropriate monitoring sites for quantifying juvenile fish recruitment across a range of representative habitats to form the basis for future long-term monitoring in the southern Kimberley region. Regular monitoring enables

assessments of how recruitment influences adult populations relative to other anthropogenic pressures (e.g. fishing, climate change). As such recruitment surveys should be conducted in conjunction with monitoring of ecologically, recreationally, commercial and culturally significant adult fish, which are typically the focus and priority of monitoring programs.

1 Introduction

Fish population replenishment typically occurs via recruitment of larvae from offshore pelagic into shallow-water environments where they settle and grow into juveniles (Cowen et al. 2007). The supply of new recruits is inconsistent and varies enormously between years, seasons, locations and habitats for various reasons (Doherty & Williams 1988, Doherty 1991). Among other factors, the number of mature adults and their reproductive output, oceanographic currents, sea temperature, pelagic food supply and behavioural aspects of larval fishes all contribute to variation in the rates of supply of new recruits (Russell et al. 1977, Robertson et al. 1999). Additionally, once newly-recruited fishes settle into shallow water environments, the rates of juvenile survivorship also vary greatly due to ecological factors linked to resource availability (*e.g.* food and habitat) and predation rates (Jones 1991, Trip et al. 2014). The net outcome of all these processes determines the future of adult fish populations (Hixon et al. 2012, Wilson et al. 2016). Therefore, understanding the spatial and temporal patterns of fish recruitment processes is crucial for assessing the future of fish populations and developing local management and conservation strategies.

The Kimberley region is rich in biodiversity (Wilson 2013) and remains one of the least explored and pristine marine ecosystems on the planet (Halpern et al. 2008), although the region is under increasing stress from climate change (Halpern et al. 2015). Like most ecological processes, fish recruitment in the Kimberley is poorly described or understood (DEWHA 2007) although patterns of shelf and offshore fish larval distribution have been investigated (Holliday D, 2011). Compounding this lack of information, the environment of the Kimberley region is complex and unique. Daily tidal ranges of up to 12 m, a labyrinth of islands that funnel and accelerate multi-directional water flow, significant seasonal freshwater input and complex bathymetry (Wilson 2013, Lowe et al. 2016) bring together complex conditions for larval/juvenile fishes whether they be transiting from a pelagic to a benthic environment, or have already metamorphosed and settled to shallow coastal waters. These complex conditions are likely to both help and hinder fish recruitment processes to nearshore areas. For example, strong tidal flows affect larval transport into shallow water environments depending on the timing and alignment of recruits with moon and daily tidal cycles (Stephens et al. 2006). Strong tidal currents and associated reef circulation may also bring more planktonic food to growing recruits but at the same time make waters turbid, possibly reducing foraging success and overall survivorship (De Robertis et al. 2003).

Research over the past two decades has shown that self-recruitment back to natal habitats is an important feature in tropical marine fishes making up anywhere between 15-89% of recruitment numbers (Jones et al. 1999, 2005, Swearer et al. 1999). Since this finding, attention has focused on how larval fishes are able to navigate back to their parent's birthplace. This body of work has shown astonishing evidence of very sophisticated behaviour (*e.g.* position in water column to facilitate directional travel, strong and sustained swimming ability) and sensory faculties (sight, smell, sound) that help explain this phenomenon (Fisher et al. 2000, Leis et al. 2003, Paris & Cowen 2004, Simpson et al. 2005, Dixson et al. 2008). But how well do these faculties and features operate under the extreme hydrological conditions of the Kimberley? Recent genetic evidence in two fish species (the benthic egg layer damselfish *Pomacentrus milleri* and the open-water spawning snapper *Lutjanus carponotatus* using single nucleotide polymorphism markers) suggests demographically independent populations exist between the Kimberley and neighbouring Pilbara Regions (Berry et al. 2016). This and other studies in the region indicate that, unlike the Pilbara region of Western Australia, genetic exchange within the Kimberley region itself as well as among offshore shoals can be surprisingly limited (in the order of hundreds of kilometres) in a number of taxonomic groups including fish (Underwood et al. 2012). This suggests that the extreme hydrological conditions in the Kimberley can promote genetic retention rather than widespread dispersal of fish larvae, and that local adult fish stocks may have a comparatively large influence on the patterns of recruitment strength within localised areas of the Kimberley. High rates of self-recruitment may therefore be a strong feature in this region, making the assessment of local recruitment processes and their variation particularly relevant for understanding and managing local fish populations.

Indigenous Australians have been managing their own aquatic resources for millennia (Yunupingu & Muller 2009, Noble et al. 2016). The Kimberley coastline not only plays a significant role in the daily lives of indigenous people by providing natural resources, but is also deeply embedded in their social, cultural and spiritual values. There are many examples of traditional codes of best practice governing conservation measures such as seasonal restrictions on marine resource extraction, off-limit areas and limits to catch sizes (Ross & Pickering 2002). These conservation measures are based on knowledge, which is collectively termed "indigenous knowledge", and based on "traditional ecological knowledge" that has been honed over historical time periods through trial and error (Gadgil et al. 1993). However, modern day coastal Australia including the Kimberley is facing growing pressures from many new sources. Increased commercial, recreational and indigenous fishing, coastal development, tourism and industry are all potential threats to finfish. In addition, forces such as climate change which affects sea temperatures, food and habitat resource supply and quality, freshwater regimes and incidences of damaging disturbances such as storms and cyclones are also increasing and relevant to modern management (Wu et al. 2012, Cai et al. 2015). Faced by unprecedented pressures on marine resources, there is a shared realisation by indigenous and non-indigenous managers alike that the integration of traditional knowledge systems and western science provides a potent way in which to better understand our coastline ecosystems in order to meet and respond to these new challenges. Providing baselines for fish recruitment across space and time in the Kimberley is therefore timely and an important step towards providing a rigorous way to measure any future effects of chronic or acute anthropogenic and non-anthropogenic pressures on local fish populations.

The benefits of understanding fish recruitment processes include providing an indication of future demographic trends (*e.g.* Wilson et al., 2016), identifying nurseries of importance (*e.g.* Dorenbosch et al., 2006; Evans et al., 2014), assessing the general and continued health and well-being of fish fauna within an ecosystem, understanding the potential for recovery following an acute disturbance, and providing a way to identify and understand the mechanisms responsible for recruitment processes into particular areas (Sale 1980, Wilson et al. 2006, Halford & Caley 2009). Understanding fish recruitment is therefore very relevant to the spatial management of fish stocks for indigenous and government agencies tasked with conservation planning and policy.

Here, we document the spatial and seasonal patterns of fish recruitment in the Cygnet Bay Sunday Island area of the Western Kimberley during a 12 month period, with an aim to;

1) Develop cost-effective techniques suitable to the Kimberley marine region that, wherever possible, allow direct comparisons with other data-sets in Western Australia
2) Provide baseline quantitative information on levels of fish recruitment across a gradient of commonly available Kimberley habitats
3) Identify seasonal trends in fish recruitment for selected important species
4) Provide an overview of the relative importance of representative habitats to fish recruitment processes
5) Identify possible biodiversity hotspots and population strongholds for juvenile fishes
6) Establish monitoring sites to form the basis for a future long-term monitoring program

Before fish recruitment could be properly surveyed, an in-depth investigation to develop an appropriate sampling technique for the Kimberley was completed, given the extreme hydrodynamic conditions of the region, which make traditional diver-based methods of quantifying fish recruitment unfeasible (see Depczynski et al. 2015). New remote methods to suit Kimberley conditions had to be developed, tested, refined and compared to each other in order to provide the best alternative to traditional diver-based methods. In addition to the challenging hydrology, the Kimberley benthos is typically composed of a mosaic of overlapping habitats rather than categorically homogenous environments (Wilson 2013). Given that many fish species either have a preference for or even exclusively recruit and grow up in specific nursery habitats (Dorenbosch et al. 2006, Wilson et al. 2010), it was necessary that the method chosen could adequately deal not only with extreme hydrological conditions but also sample all types and combinations of habitats. Ultimately, the method chosen was a replicated set of remote underwater stereo-video stations (RUVs) that could be safely deployed in all coastal habitats identified and were able to adequately capture differences in the community structure of fish recruits. The method used twin cameras allowing accurate size measurements (Cappo et al. 2003, 2006), which were required to delineate recruits from adults based on size cut-off points for adult *vs*. juvenile life stages. Stereo-RUVs proved to be the best technique for assessing spatiotemporal variation in fish recruitment patterns in the Kimberley. A full and detailed analysis of technique comparisons can be found in Depczynski et al. (2015) and is summarised in the next section.

2 Materials and Methods

As described above, a pilot study aimed at developing, testing and refining cost-effective techniques suitable to quantifying juvenile fishes in the testing Kimberley conditions was undertaken during the wet season in April 2015 (see Depczynski et al. 2015). In summary, seven techniques: remote underwater stereo-video systems (RUVs), rotenone, box trawls, drop cameras, and underwater visual census (transect, stationary and block), were thoroughly trialed at six locations which together encompassed four contrasting habitats; intertidal rockpools, seagrass, mangrove and coral reefs. A further two techniques were explored, but deemed unsuitable before the field trial stage. Although no single technique was able to comprehensively capture the full diversity of the Kimberley juvenile fish assemblage within any habitat, stereo-RUVs was the most consistent technique across habitats (Depczynski et al. 2015). RUVs were also the only technique that could be used successfully in all four habitats importantly allowing among-habitat comparisons to be made. In fact, RUVs were the only method to successfully record juvenile fishes in mangroves. Additionally, they provide a permanent record, are safe to use (do not require divers), repeatable, easily deployed and reasonably time efficient in providing precise estimates of abundance and acceptable levels of diversity when compared to all other techniques trialed. Finally, stereo-video techniques have previously proved successful for sampling small fishes (<300 mm total length; Davis et al. 1997, Norcross & Mueter 1999, Cappo et al. 2006, Santana-Garcon et al. 2014). Precision estimates indicated that five replicate RUV units were sufficient to ensure robust quantification of juvenile fishes for each location *x* habitat combination providing an efficient and consistent method to address the aims outlined above.

2.1 Study location

This study was conducted in shallow nearshore habitats in the Cygnet Bay and Sunday Island areas in the western Kimberley, northwest Australia (approx. 16.5°S, 123°E, see Appendix 1 for specific site details) (Figure 1). The Sunday Island group forms a string of islands at the tip of the Dampier Peninsula that extends to the east across the opening of King Sound. The area is rich in biodiversity, with high levels of endemism and a mosaic of habitat types including intertidal rockpools, mangroves, seagrass and algal beds, and well developed coral reef systems (Fox & Beckley 2005, Thorburn et al. 2007, Jones et al. 2015).

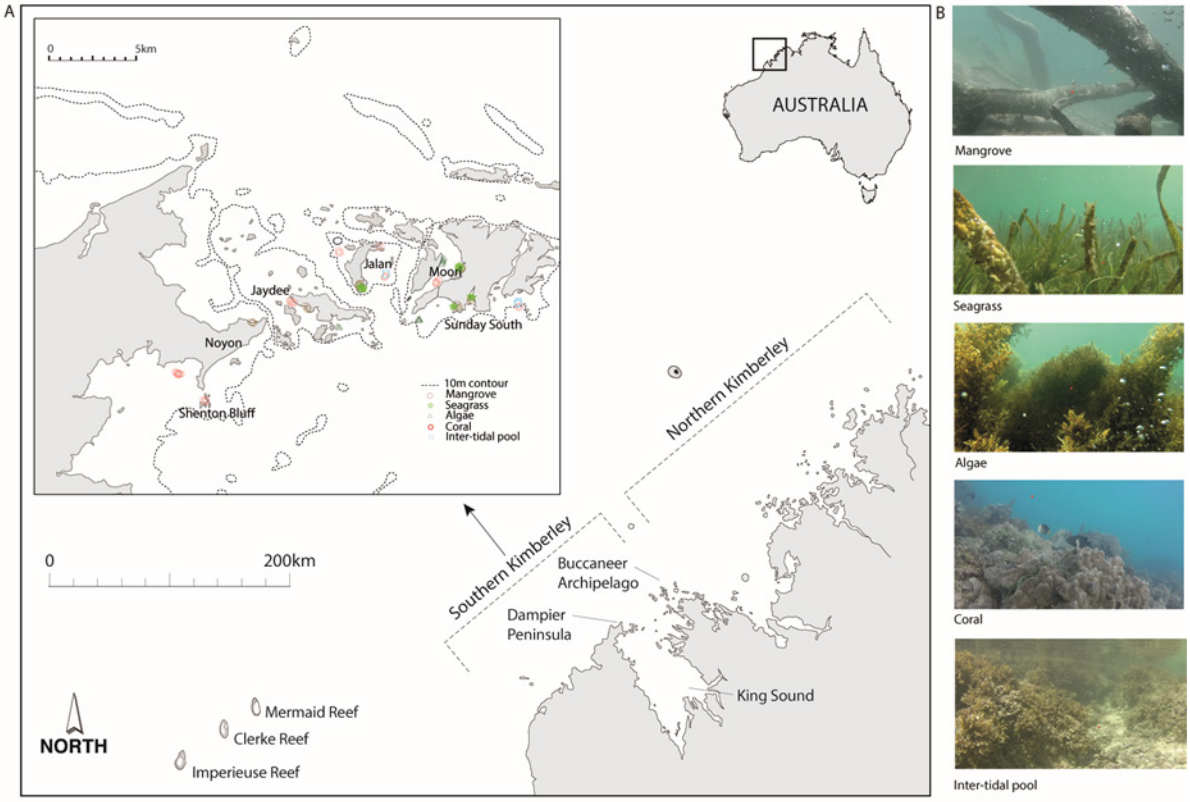

Figure 1. Map of the six study locations in the Cygnet Bay and Sunday Island areas of the western Kimberley region in northwest Australia (Jaydee= Jackson Island, Jalan= Tallon Island) (a). Stereo-RUV deployments were conducted during wet (March-April 2016) and dry (October 2015) seasons in five different nearshore habitats (mangroves, seagrass beds, macroalgal beds, submerged coral reefs, and inter-tidal rockpools, b), and bi-monthly at coral reefs. Each location by habitat combination was treated as a site, and stereo-RUVs replicated randomly at each site through time. For sampling details see Tables 1 and 2.

The diverse coastal and marine communities of the western Kimberley region are strongly influenced by the unique oceanography of the area. Tidal ranges of up to 12 m occur on spring tides twice a day, creating tidal currents of up to 10 knots (Purcell 2002, Lowe et al. 2015), with the biggest tides occurring towards the end of the rainy season from March to April (Ruprecht & Rogers 1998). During these extreme tidal fluxes coastal ecosystems may be completely exposed to air for up to four hours, resulting in daily sea temperature fluctuations of up to 7^{o}C in very shallow or intertidal areas, to which local organisms such as corals have become adapted (Purcell 2002, Richards et al. 2015, Schoepf et al. 2015). On coral reef habitats in particular, tidal fluxes create large intertidal reef terraces that alternate between periods of complete submersion and exposure, and create a series of intertidal rockpools of differing size (Purcell 2002, Schoepf et al. 2015).

2.2 Sampling design and methods

To evaluate spatial trends, seasonal trends, and habitat preferences in patterns of fish recruitment, two separate studies were conducted using stereo-RUV deployments replicated at six locations. In the first study, seasonal trends across all five habitats were assessed during wet (March-April) and dry (October) seasons (Figure 1, Table 1). The second study was aimed at further exploring temporal patterns in fish recruitment on a bi-monthly basis over a 12-month period (Oct 2015 – Aug 2016) in subtidal coral reef habitats only (Table 2), which were taken as a higher-resolution proxy for temporal patterns in all other habitats. All drops were made in water depths between 0.4 and 6.9 m. To minimise the effects of extreme tidal currents, drops were either timed to coincide with neap tides or restricted to one hour either side of peak high and low spring tides to facilitate identifications by minimizing turbidity while sampling. All habitats within each location were separated by at least one kilometre with the exception of mangrove and seagrass beds, which were usually found adjacent to each other.

Stereo-RUV deployments were all unbaited because of the potential biases of bait attracting predators of juvenile fishes and therefore limiting their appearance in the field of view (Harvey et al. 2007). Stereo-RUV units consisted of two GoPro Hero 3+ video cameras in waterproof housings mounted on a custom made base bar made of light aluminium frame (SeaGIS Pty. Ltd; www.seagis.com.au, Figure 2). Each system was optimised for sampling of smaller bodied fishes with video cameras mounted 0.4 m apart on the base bar, and converged inwardly at a 6° angle, resulting in an optimised field of view with stereo-coverage from 0.5 m in front of the cameras outwards to 3 m. Stereo-RUV units were calibrated in a pool prior to deployment in the field using a standard calibration cube (www.seagis.com.au).

Five stereo-RUVs separated by a distance of 50 m were deployed consecutively during daylight hours from a small vessel (10 m) at each location x habitat combination (*i.e.* site) and left to record for 20 minutes. We chose 20-min deployments as optimal based on a combination of video analysis/field efficiency and pilot study data calculations based on species and abundance accumulation curves, which identified maximum species diversity and relative abundance of juvenile fishes was adequately captured within this period (C Piggott unpublished data). We also judged 50 m spacings of replicate units to be sufficiently well spaced on the basis of the restricted home ranges of most juvenile fishes. The same sampling design was followed on subsequent surveys (seasonal and bi-monthly) at each of the sites surveyed, with specific RUV deployment locations selected at random within each site.

Table 1. Summary of stereo-RUV deployments during the wet (March-April 2016) and dry (October 2015) seasons at five habitats (mangrove, seagrass, algae, coral and inter-tidal rockpools), across six locations in the Sunday Islands, western Kimberley. A total of 151 stereo-RUVs were deployed in the region, across 17 sites (location x habitat combination).

	Mangrove		**Seagrass**		**Algae**		**Coral**		**Inter-tidal pools**	
Location	***wet***	***dry***	***wet***	***dry***	***wet***	***dry***	***wet***	***dry***	***wet***	***dry***
ShentonBluff	0	0	0	0	0	0	5	5	0	0
Noyon	5	0	0	0	0	0	5	4	0	0
Jaydee	5	4	0	0	5	3	5	5	0	0
Jalan	4	5	5	5	0	0	0	0	5	0
Moori	4	3	5	4	5	5	4	5	0	0
SundayIsland	5	5	4	4	4	5	0	0	8	6
Total	*23*	*17*	*14*	*13*	*14*	*13*	*19*	*19*	*13*	*6*

Table 2. Summary of bi-monthly stereo-RUV deployments at subtidal coral reef habitat across five locations in the Sunday Islands, western Kimberley. A total of 107 stereo-RUVs were deployed at coral reef habitat during the 12 month period. *Note that location and site are equivalent for this dataset, given that only coral reef habitat was surveyed.

Location	**Oct15**	**Dec15**	**Feb16**	**Mar/Apr16**	**May16**	**Jul/Aug16**
Noyon	4	5	0	5	4	5
Jaydee	5	5	4	5	4	0
Jalan	0	5	3	4	3	5
Moori	5	4	4	4	5	4
SundayIsland	0	0	5	5	0	5
Total	*14*	*19*	*16*	*23*	*16*	*19*

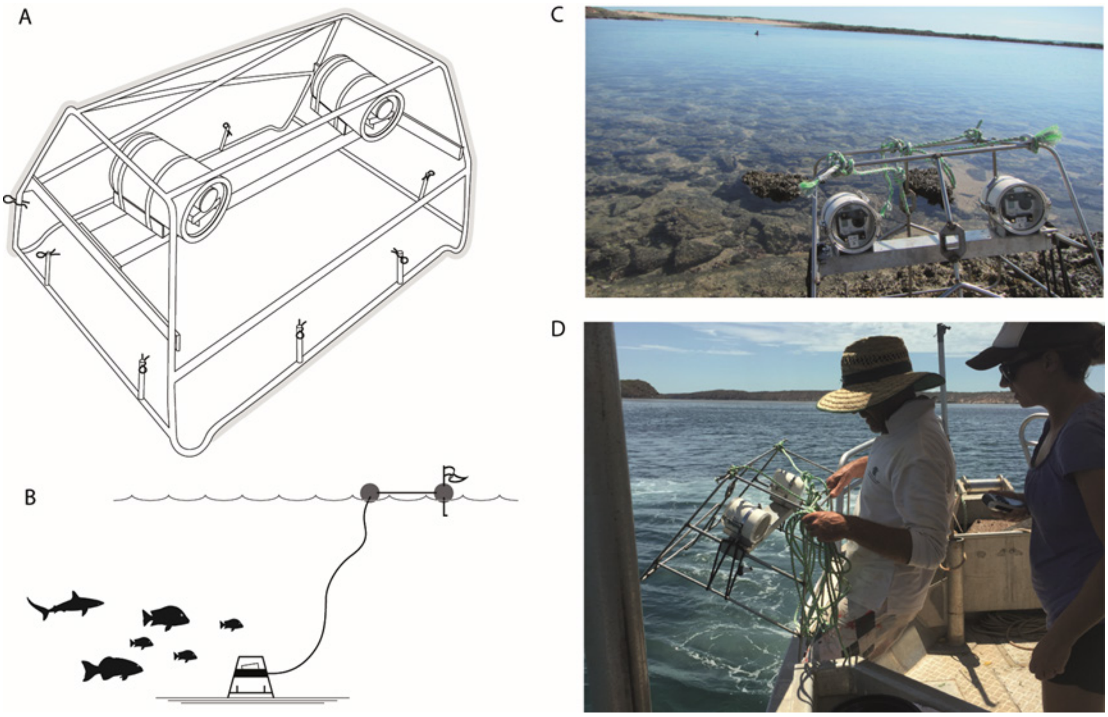

Figure 2. Diagram showing the design (a), functioning (b) and deployment of stereo-RUV units at an inter-tidal rockpool (c) and from a small vessel (d) in the western Kimberley.

2.3 Image analyses

2.3.1 Fish assemblages

Video footage was analysed using the software EventMeasure™ (SeaGIS Pty. Ltd), following calibrations using the software CAL (SeaGIS Pty. Ltd) (Harvey & Shortis 1998). All fish recorded within 3 m of the cameras were identified to the lowest taxonomic level possible, measured (to the nearest 0.1 mm) and categorised as juvenile or adult (see criteria below). All planktonic schooling fishes from the families Caesionidae (fusiliers) and Clupeidae (sprats/anchovies) were excluded from the analyses because of their lack of site fidelity to distinct habitats and potential to bias fish recruitment patterns. To avoid repeat counts of individual fish re-entering the field of view, a conservative measurement of relative abundance (MaxN) was recorded. MaxN is defined as the maximum number of individuals of the same species appearing in a single paused frame (Priede et al. 1994). MaxN was recorded separately for adult and juvenile fishes, resulting in two separate MaxN 'by life-cycle stage' measurements per species.

Individuals were classified as juvenile based on colouration and body size (L_{33}, <33% of maximum adult total length) (Nagelkerken & van der Velde 2002, Dorenbosch et al. 2005). Information on maximum adult total length (L_{max}) for each species was obtained preferentially from published literature (Allen & Swainston 1988, Allen et al. 2003) or FishBase (www.fishbase.org) in circumstances where no published literature existed. For individuals that could not be reliably identified to species, the average L_{max} of the three most likely species was used to calculate L_{33}. Juvenile fish lengths (Total length [L_T]) were taken at the corresponding MaxN 'by life-cycle stage' frame, to avoid making repeated measurements of the same individuals. In order to get a better side view of each individual for measurement purposes, if required, video frames were advanced from the time of MaxN, making sure individual fish were followed through the sequence. Where a measurement of an individual fish was not possible (*e.g.* bent position, present in only one camera, bad visibility etc.), it was conservatively classified as an adult and discounted from the juvenile data set. All video analyses were performed by three experienced observers (KC, TB, MB) under the same set of strict guidelines. Cross-checking of a subset of videos between observers was then conducted in order to guarantee consistency for both MaxN and species identification.

2.3.2 Habitat variables

Habitat type for each stereo-RUV deployment was initially classified into five categories: mangrove, seagrass, algae, coral and inter-tidal rockpools, based on the general habitat targeted during each RUV deployment. Initial exploration of RUV videos indicated that these habitat categories were often a mosaic of overlapping habitats. For this reason we estimated more detailed habitat composition measures for each stereo-RUV, so that we were able to define patterns of fish recruitment (abundance and species composition) based on continuous, rather than categorical habitat data. This provided a more robust and realistic picture of the benthic habitat in the Kimberley. Continuous habitat data (% cover) were estimated following the rapid annotation methods described in McLean et al. (2016) and using the software TransectMeasure™ (SeaGIS Pty. Ltd). Benthic composition for each stereo-RUV deployment was quantified along a 5 x 4 grid overlaid onto a high definition habitat image obtained from each RUV deployment. The dominant habitat type at each of these grid rectangles was classified according to seven broad benthic categories: hard corals, consolidated substrates, macroalgae, mangroves, seagrasses, sponges and unconsolidated sediments, following the CATAMI classification scheme (Althaus et al. 2013). An ‘open water’ category was included for rectangles where no biota was present.

2.4 Data analyses

Two juvenile fish datasets were generated for statistical interrogation following video analyses; a wet *vs.* dry season analysis targeting fish recruitment patterns across all five habitat types; and a bi-monthly analysis for the coral reef habitat only (see Tables 1 & 2). We used univariate generalised additive mixed models (GAMMs) to investigate patterns of abundance and multivariate distance-based linear models (DistLMs) to examine changes in community composition for each data set. In all models, habitat was treated as a continuous variable (% cover or proportion), season and sampling period (for bi-monthly surveys) as factors, and site (*i.e.* each location x habitat combination) as a random effect. Habitat variables were transformed (log10(x + 1) or square root) where necessary to downplay outlying values and better represent relationships with juvenile fish abundance and species composition.

For both univariate and multivariate models, variable importance metrics were calculated for each predictor variable based on weighted Akaike’s information criterion values corrected for finite sample sizes (wAICc) (Burnham & Anderson 2002). Variable importance metrics assisted model interpretation and allowed identification of the most important predictors of the relative abundance of juvenile fishes and their species composition. Each variable importance value was calculated as the average Akaike weight of all subsets of models containing that variable, scaled between 0 and 1 and multiplied by the R^2 value of the best fitted model.

2.4.1 Patterns of abundance

GAMMs were fitted to univariate data on total juvenile fish abundance (MaxN per replicate) with package ‘mgcv’ in R version 3.3.1 (R Development Core Team 2014). GAMMs were chosen due to their capacity to deal with non-linear relationships between dependent and continuous predictor variables (Austin 2007), and their inclusiveness of random effects that account for correlation between observations on the same sampling unit (*e.g.* RUV deployments within site). GAMMs with all possible variable subsets were fitted to untransformed juvenile fish relative abundance data, and the appropriate distribution used for model analyses (*i.e.* Gaussian distribution with log-link function for seasonal data, and Poisson for bi-monthly data). Models containing variables with a correlation >0.40 were excluded from the full subset of models to eliminate strong collinearity. Model selection was based on AICc, which was used to compare models and select the most parsimonious one (*i.e.* fewer number of predictors and within two AICc units of the model with the lowest AICc value).

2.4.2 *Patterns of species composition, temporal recruitment of selected species and species diversity*

For multivariate data on species composition, we used DistLMs (Legendre & Anderson 1999) to better understand spatiotemporal patterns in the juvenile fish assemblage. A Bray-Curtis dissimilarity matrix was calculated for square root transformed data on fish abundance at the species level (MaxN per species per replicate), and DistLMs fitted using a full subsets approach excluding models with correlated variables (>0.40). Model selection procedures to choose the most parsimonious model were based on a multivariate analogue of the AICc in a manner equivalent to that described for GAMMs above (see Anderson et al. 2008). Analyses used the PERMANOVA+ add-on package for PRIMER v.6 (Anderson et al. 2008). Distance-based redundancy analysis (dbRDA; Legendre & Anderson 1999), a form of ordination, was then used to visualise the chosen model with vectors overlaid for individual fish species, habitat variables (% cover) and factors (season or sampling period); only vectors with Pearson correlations >0.25 with the dbRDA axes were included.

For a more in-depth exploration of temporal recruitment patterns in the most abundant juvenile fish species in the Kimberley region, we constructed basic summary plots of average juvenile fish abundance (MaxN ± SE) pooled across habitats during each season, and at coral-reef habitat during each sampling period. In addition, we used fish length data (L_T) on the most abundant juvenile species, to produce length-frequency distributions pooled at either the season or sampling period level, taking all length measurements irrespective of habitat surveyed. Bin-widths for length-frequency distributions were selected according to the maximum juvenile length for each species (L_{33}, <33% of maximum adult total length). Finally, we constructed species accumulation curves to examine species diversity at the five general habitat types surveyed (mangroves, seagrasses, algae, corals and inter-tidal rockpools), and during wet *vs.* dry seasons. These curves allowed us to compare the number of species present at each habitat type, while taking into account dissimilarities in sampling effort between habitats, and were fitted using the 'vegan' package in R version 3.3.1 (R Development Core Team 2014).

3 Results

3.1 General abundance and species diversity patterns

We identified 125 fish species from 22 families. Eleven (9%) of these species were observed only as juveniles, 43 (33%) as both juveniles and adults, and 73 (60%) only as adults (Appendix 2). Of the species for which juveniles were observed, detected abundance was mostly low, with 88% of the abundance represented by only 12 species (*Choerodon cyanodus*, *Scarus JHC sp3*, *S. ghobban*, *Lutjanus carponotatus*, *Gerres oyena*, *Scaevius milii*, *Dischistodus darwiniensis*, *Siganus lineatus*, *S. doliatus*, *Lethrinus laticaudis*. *Acanthurus grammoptilus* and *Plectropomus maculatus*), and 39% of total abundance represented solely by *Choerodon cyanodus* (igoolan). These species were the main drivers of recruitment patterns in the study area.

Overall, detected juvenile species diversity was similar among mangrove, seagrass and algae habitats (18-20 spp. in total) and lowest in the inter-tidal rockpools (13 spp.), with the coral reef habitat supporting the highest number of species (35 spp.) (Appendix 3). Only three juvenile fish species (6% of juvenile species pool) were observed in all five habitats (Appendix 3), indicating a high degree of habitat specificity among the Kimberley juvenile fish community. RUV surveys captured recruitment for at least seven of the species that are most important to the local Bardi Jawi community as a food resource (*Lutjanus carponotatus* (joorloo), *L. argentimaculatus* (maarrarn), *L. russellii* (ilnilirr), *Siganus lineatus* (barrbal), *S. doliatus*, *Choerodon cyanodus* (igoolan) and *C. schoenleinii*) (Figure 3)). Overall, recruitment was much stronger during the wet (March/April) than in the dry (October) season for all five habitats with among-habitat comparisons indicating that the lowest abundances were found in the mangroves (Figure 3).

3.2 Seasonal patterns in abundance, species diversity and assemblage structure

Our results show strong seasonal and habitat-gradient patterns in fish recruitment strength (Figure 4). Spatiotemporal variation in the total abundance of juvenile fishes was best explained by a model using a combination of mangrove presence (% cover) and season, with this model accounting for 36% of variation in the data (Figure 4a, Table 3). Total juvenile fish abundance was lowest in mangroves (Figure 4b) but showed similar values at the other four habitats surveyed: seagrass, algae, coral and inter-tidal rockpools. At all habitats, the abundance of juvenile fishes was significantly higher during the wet season (Figure 4c).

Multivariate analyses revealed that fish assemblages differed between the habitats surveyed (Figure 5a, Appendix 3). Sites clustered into three distinct groups depending on the habitat targeted: (1) mangrove, (2) seagrass, and (3) a combined group consisting of algae, coral and inter-tidal rockpools, which all had a more similar species composition (Figure 5a). The model that best accounted for the spatiotemporal variation in juvenile fish assemblages included the amount (% cover or proportion) of mangrove, seagrass and unconsolidated sediments, combined with season, which together accounted for 24% of the variation in our data set (Figure 5b, Table 3). Twelve species were significantly correlated with the dBRDA axes (>0.25) and were primarily responsible for driving separation between habitats. The snappers *Lutjanus argentimaculatus* (maarrarn) and *L. russellii* (ilnilirr) associated strongly with mangrove habitats, *Gerres oyena*, *Siganus lineatus* (barrbal) and *Scaevius milii* with seagrass, and *Pomacanthus sexstriatus* (gorno), *Acanthurus grammoptilus* (gambarl), *Choerodon schoenleinii* (baramba), *C. cyanodus* (igoolan), *Dischistodus darwiniensis* (doodany), *Lutjanus carponotatus* (joorloo) and *Lethrinus laticaudis* (madalngoorr) with the mixed cluster of coral, algae and inter-tidal pools (Figures 3 and 5a). There was also a seasonal signal in the suite of species that recruited in the wet and dry seasons respectively (Figure 5a, Appendix 4). Species such as *Scaevius milii* and *Siganus lineatus* recruited strongly during the wet season whilst *Pomacanthus sexstriatus*, *Acanthurus grammoptilus* and *Choerodon schoenleinii* recruited in higher numbers during the dry season (Figure 5a).

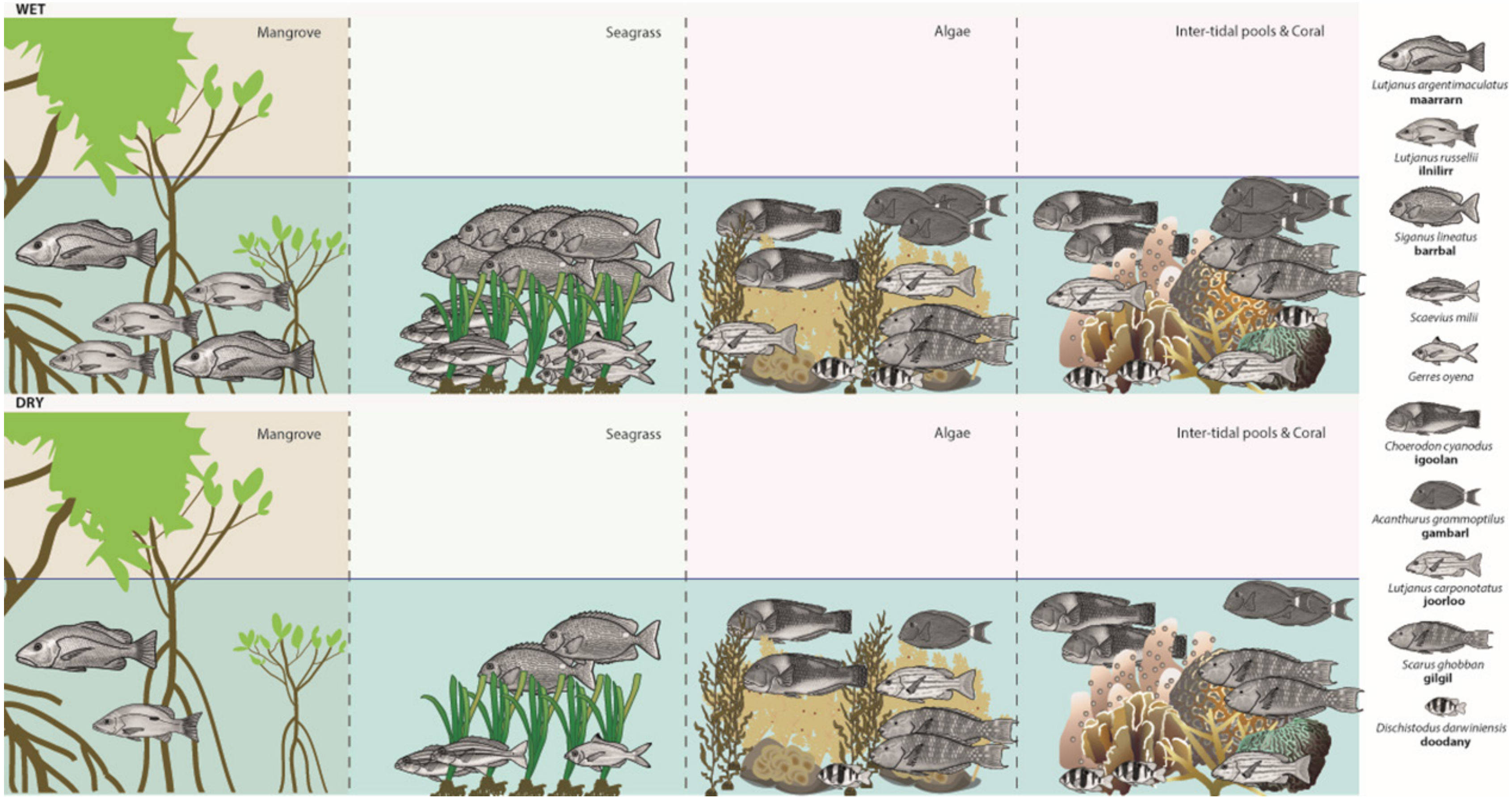

Figure 3. Graphical representation summarizing our findings from juvenile fish RUV surveys during the wet (top panel) and dry (bottom panel) seasons across five habitat types (mangrove, seagrass, algae, coral and inter-tidal rockpools; separated by dashed lines). Habitats portrayed from left to right follow a typical Kimberley habitat profile from inter-tidal mangroves to adjacent seagrass meadows and algal fields to elevated inter-tidal rockpools and submerged coral reefs. Colour shades in the background of each habitat represent groupings based on observed statistical differences in fish assemblage structure among habitats (brown - mangroves, green - seagrass, and pink - algae, coral and inter-tidal rockpools). Each fish diagram represents a different juvenile species; key to right shows scientific and Bardi Jawi names. Only the ten most abundant species distinguishing between fish assemblages at the habitat level are presented. The number of fish in each panel is equivalent to the average number of juvenile fishes per RUV replicate (*e.g.* MaxN = 5 in mangrove habitat during the wet season).

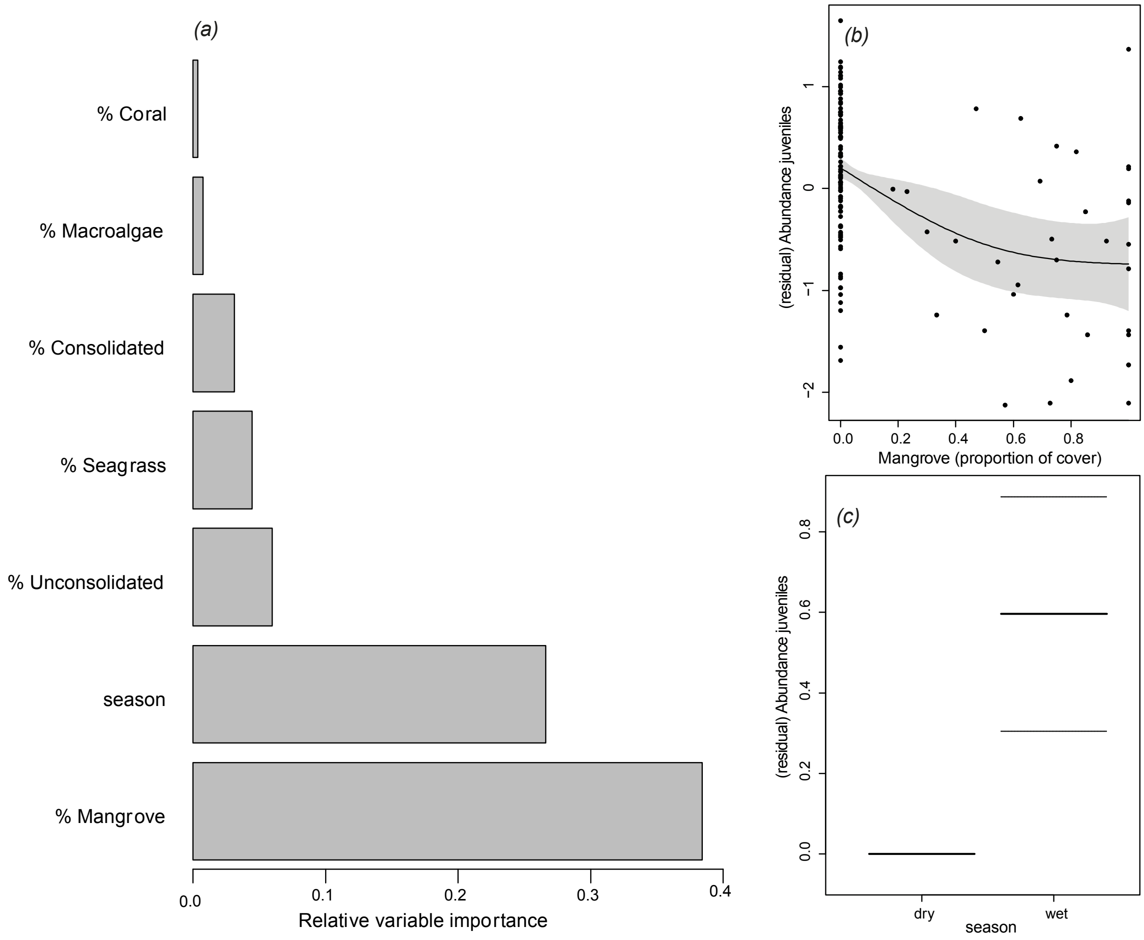

Figure 4. Graphical representation of the most parsimonious generalised additive mixed model (GAMM) for explaining variation in total abundance of juvenile fishes according to habitat (% or proportion of cover) and season surveyed; (a) shows relative variable importance for all explanatory variables used in the full subset of fitted GAMMs; (b and c) show residual abundance of total juvenile fishes in response to their most important explanatory variables: mangrove cover and season, identified via the most parsimonious GAMM (see Table 3 for model selection). Solid black lines represent model fit (estimated smoothing curve for continuous variables), and shading (b) or dotted lines (c) represent ± 2*SE of the model fit estimate.*Note there is no SE associated with the dry season in (c), because this was taken as the reference level for factor season by the model.

Table 3. Best univariate (GAMMs; *a*) and multivariate (DistLMs, *b*) models, selected from the full subset of fitted models for predicting total abundance of juvenile fishes in the southern Kimberley region. The most parsimonious model (in **bold**) had the lowest Akaike Information Criterion value corrected for finite sample sizes (AICc), and fewest variables. In (*a*) the five best GAMMs are presented and in (*b*) all DistLMs within 2 AICc units of each other.

Dependent variable	Explanatory Variables	edf	R^2	AICc
Juvenile MaxN seasonal data five habitats (# fish per RUV)				
(a) GAMMs	**Mangrove, season**	**12.65**	**0.364**	**357.469**
	Mangrove, unconsolidated, season	13.82	0.376	359.700
	Consolidated, mangrove, season	10.47	0.335	361.058
	Mangrove, seagrass, season	6.62	0.258	361.576
	Season	7.59	0.250	362.879
(b) DistLMs	Mangrove, seagrass, coral, unconsolidated, season		0.253	1057.000
	Macroalgae, mangrove, seagrass, unconsolidated, season		0.252	1057.100
	Mangrove, seagrass, unconsolidated, season		**0.239**	**1057.600**
	Macroalgae, mangrove, seagrass, coral, season		0.246	1058.300
	Consolidated, macroalgae, mangrove, seagrass, coral, season		0.257	1058.400
	Macroalgae, mangrove, seagrass, coral, unconsolidated, season		0.255	1058.700
	Consolidated, mangrove, seagrass, coral, unconsolidated, season		0.255	1058.800
	Consolidated, macroalgae, mangrove, unconsolidated, season		0.255	1058.900
	Consolidated, macroalgae, mangrove, coral, unconsolidated, season		0.254	1058.900

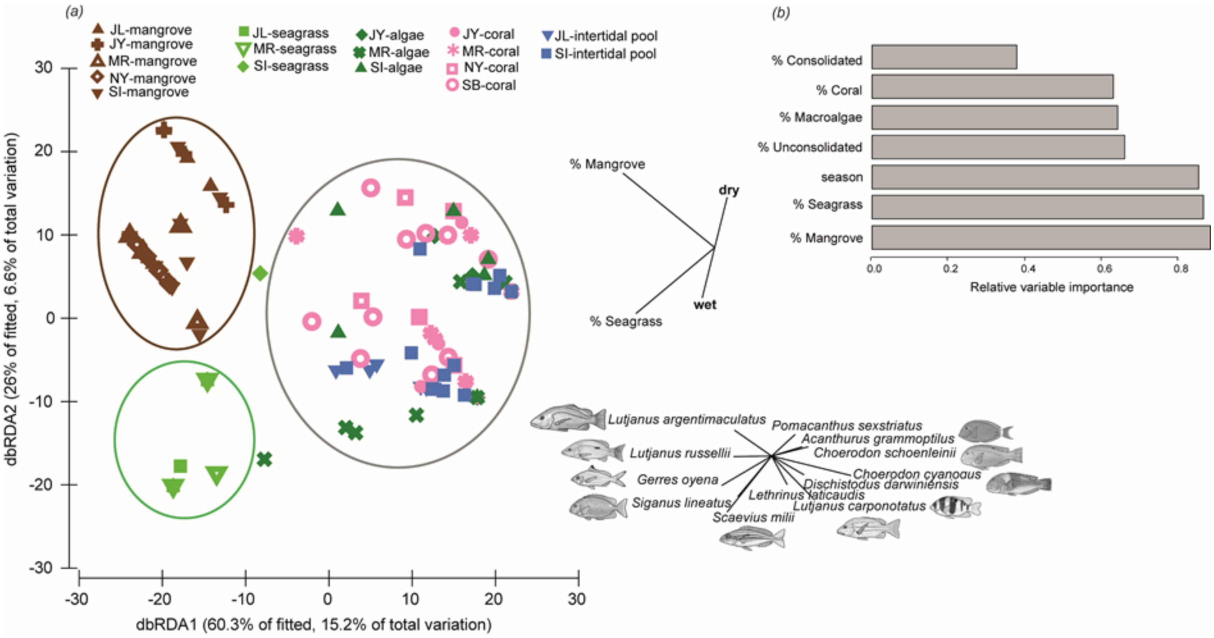

Figure 5. Distance based redundancy analyses (dBRDA) showing spatiotemporal variation in juvenile species assemblages (bottom right vectors) and significant variables explaining this variation (top right vectors) (a). Data are MaxN per RUV replicate plotted at the site level and represented by symbols and colours as shown in the legend according to habitat targeted (brown - mangrove, light green - seagrass, dark green - algae, pink - coral and blue - inter-tidal rockpools). Circles depict the three major clusters visually identified, and have no statistical significance. Relative variable importance values for all explanatory variables in the full subset of fitted distance-based linear models (DistLMs) are shown in (b); for model selection see Table 4.

3.3 Bi-monthly patterns in juvenile fish abundance and species diversity - coral reef habitat

Percentage coral cover, sampling period and % consolidated substrate cover provided the best combination of variables to explain variation in recruit abundances with 45% of total variance explained (Figure 6a, Table 4). Juvenile fish abundance was fairly constant across low to medium levels of coral cover (0 to 60%) but increased slightly from 60-80% cover before plateauing (Figure 6b). Overall, highest recruitment was seen from December to April with the highest peak in December, and weakest recruitment was observed during July to October with the lowest in July/August (Figure 6c). The influence of consolidated substrate cover (*i.e.* boulders, rock, bedrock), showed fish abundance peaked at intermediate levels of cover (Figure 6d).

Juvenile fish assemblages differed markedly between peak dry season (October) and all other bi-monthly surveys (Figure 7a, Appendix 5). This separation was mostly driven by the higher abundances of the wrasse *Choerodon schoenleinii*, coral trout *Plectropomus* spp. and angelfish *Pomacanthus sexstriatus* during peak dry season (October). Outside of October, bi-monthly surveys revealed the persistence of a more uniform juvenile fish assemblage although there were finer-scale differences observed here which also appear to relate to wet (December-March/April samples) and dry (May-July/August) survey periods. Unsurprisingly, our modelling identified period as the main influential variable (11% of variation) driving patterns in assemblage structure among bi-monthly surveys (Figure 7b, Table 4). However, coral habitats in the Kimberley are often a mix of coral and algae and both % macroalgae and coral cover were quite influential in influencing assemblage structure (Figure 7b).

In general, there was a high degree of concordance between our bi-monthly survey results and those exhibited among all habitats in our seasonal surveys suggesting that a reduced sampling design covering the end of the wet and dry seasons (*i.e.* March-April and October) provided a good representation of the spatiotemporal variation in the juvenile fish assemblages of the southern Kimberley region.

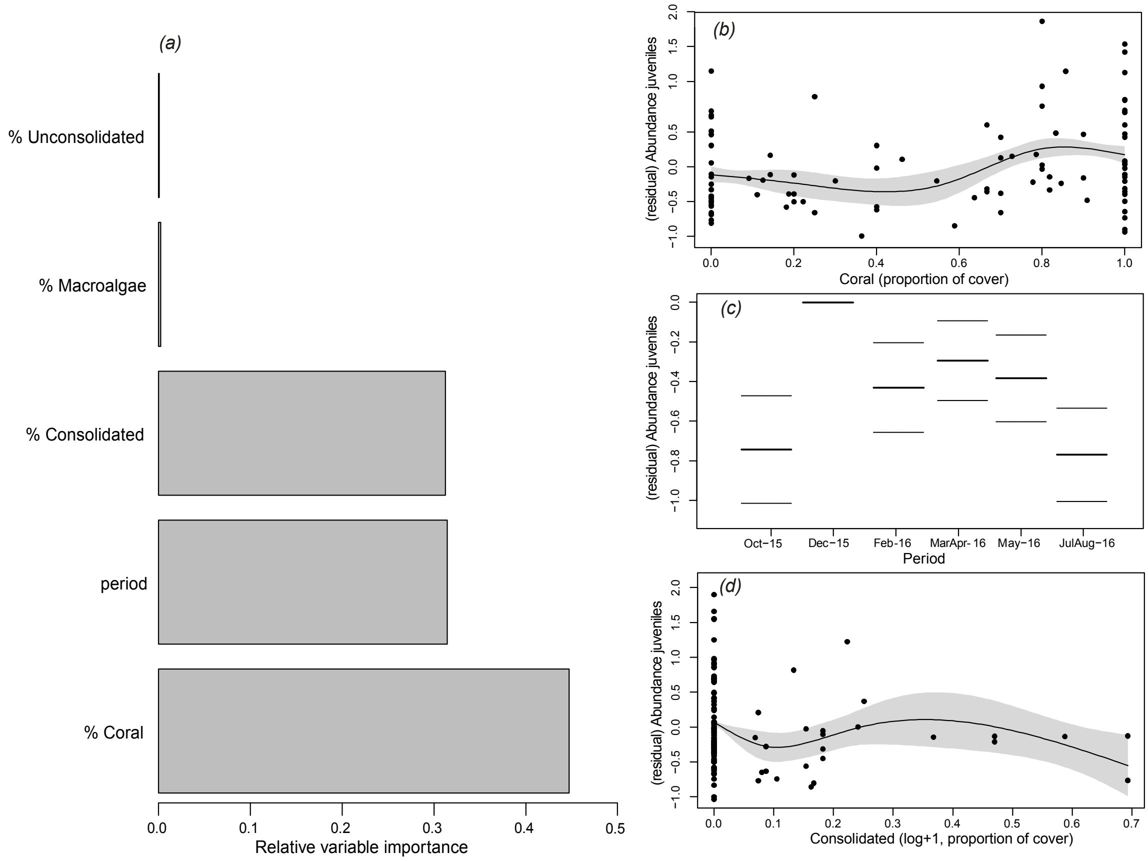

Figure 6. Graphical representation of the most parsimonious generalised additive mixed model (GAMM) for explaining variation in total abundance of juvenile fishes according to habitat (% or proportion of cover) and sampling period; (a) shows relative variable importance for all explanatory variables used in the full subset of fitted GAMMs; (b), (c) and (d) show residual abundance of total juvenile fishes in response to their most important explanatory variables presented in order of importance (see Table 3 for model selection criteria). Solid black lines represent model fit (estimated smoothing curve for continuous variables), and shading (b and d) or dotted lines (c) represent ± 2*SE of the model fit estimate. *Note there is no SE associated with the December period in (c), because this was taken as the reference level for factor period by the model.

Table 4. Output from the best univariate (GAMMs; *a*) and multivariate (DistLMs, *b*) models, selected from the full subset of fitted models for predicting total abundance of juvenile fishes in coral reefs in the southern Kimberley region in response to habitat and sampling period. In (*a*) the five best GAMMs are presented and in (*b*) all DistLMs within 2 AICc units of each other. The final models selected were the ones with the lowest Akaike Information Criterion value corrected for finite sample sizes (AICc), and with the fewest variables (most parsimonious; in bold).

Dependent variable	Explanatory Variables	edf	R^2	AICc
Juvenile MaxN bi-monthly data coral habitat (# fish per RUV)				
(a) GAMMs	**Consolidated, coral, period**	**16.42**	**0.447**	**746.784**
	Coral, period	13.23	0.410	757.378
	Consolidated, macroalgae, period	15.69	0.425	757.429
	Coral, unconsolidated, period	14.20	0.412	759.284
	Consolidated, unconsolidated, period	13.57	0.396	766.243
(b) DistLMs	Macroalgae, period		0.145	746.900
	Coral, period		0.138	747.800
	Macroalgae, unconsolidated, period		0.155	748.140
	Macroalgae		0.037	748.400
	Period		**0.113**	**748.570**
	Consolidated, algae, period		0.151	748.600
	Consolidated, coral, period		0.150	748.700
	Macroalgae, coral, period		0.150	748.720
	Coral, unconsolidated, period		0.149	748.890

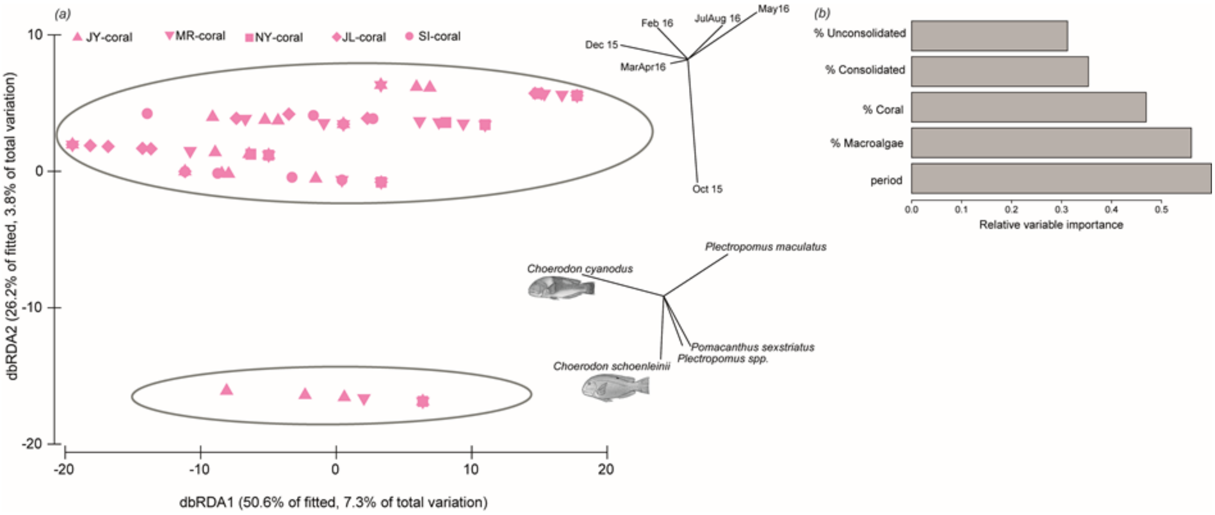

Figure 7. Distance based redundancy analyses (dBRDA) showing variation in juvenile species assemblages (bottom right vectors) in coral reef habitat according to sampling period (top right vectors) (a). Data are MaxN per RUV replicate plotted at the site level and represented by symbols in the legend. Relative variable importance values for all explanatory variables in the full subset of fitted distance-based linear models (DistLMs) are shown in (b); for model selection see Table 4. Circles depict the two major clusters visually identified, and have no statistical significance.

3.4 Abundance and size-structure patterns of the ten most abundant juvenile fish species

Species-specific abundances between wet and dry seasons in the ten most abundant species show that recruitment strength is typically higher in the wet season (Figure 8a). Higher wet season recruitment was more pronounced in some species, such as *Gerres oyena*, *Siganus lineatus* (both seagrass associated), and *Scarus ghobban* (coral-algae associated) (Figures 5 and 8a). In contrast, species such as *Choerodon cyanodus* and *Lutjanus carponotatus* show considerably less differences between wet and dry seasons indicating the potential for year-round recruitment (Figure 8a). A more detailed analysis of species-specific abundance patterns across bi-monthly surveys (coral habitat only) generally agreed with these seasonal patterns. Seven of the top ten most abundant species showed higher recruitment during wet season months (December to April, Figure 8b to f, and k). In stark contrast, three species (*Dischistodus darwiniensis*, *Choerodon schoenleinii*, *Plectropomus maculatus* (biindarral) and *Chaetodon aureofasciatus* (roola)) recruited in higher numbers during the dry season months (Figure 8g to j).

Length-frequency distributions highlighted the seasonal and bi-monthly differences in juvenile fish abundance patterns, and allowed us to assess recruitment more directly by looking at patterns in the smaller juvenile size classes for four species with a good representation of length measurements (Figure 9). A clear recruitment pulse was identified for *Choerodon cyanodus* (igoolan) during March and April (end of the wet season), although some level of recruitment was present throughout the year (Figure 9a). *Lutjanus carponotatus* (joorloo) showed the strongest evidence of recruitment during October (end of the dry season) although a second, weaker recruitment pulse was observed during March and April (Figure 9b). Both *Scarus* species showed evidence of recruitment throughout the year with no clear recruitment pulses detected (Figure 9c and d).

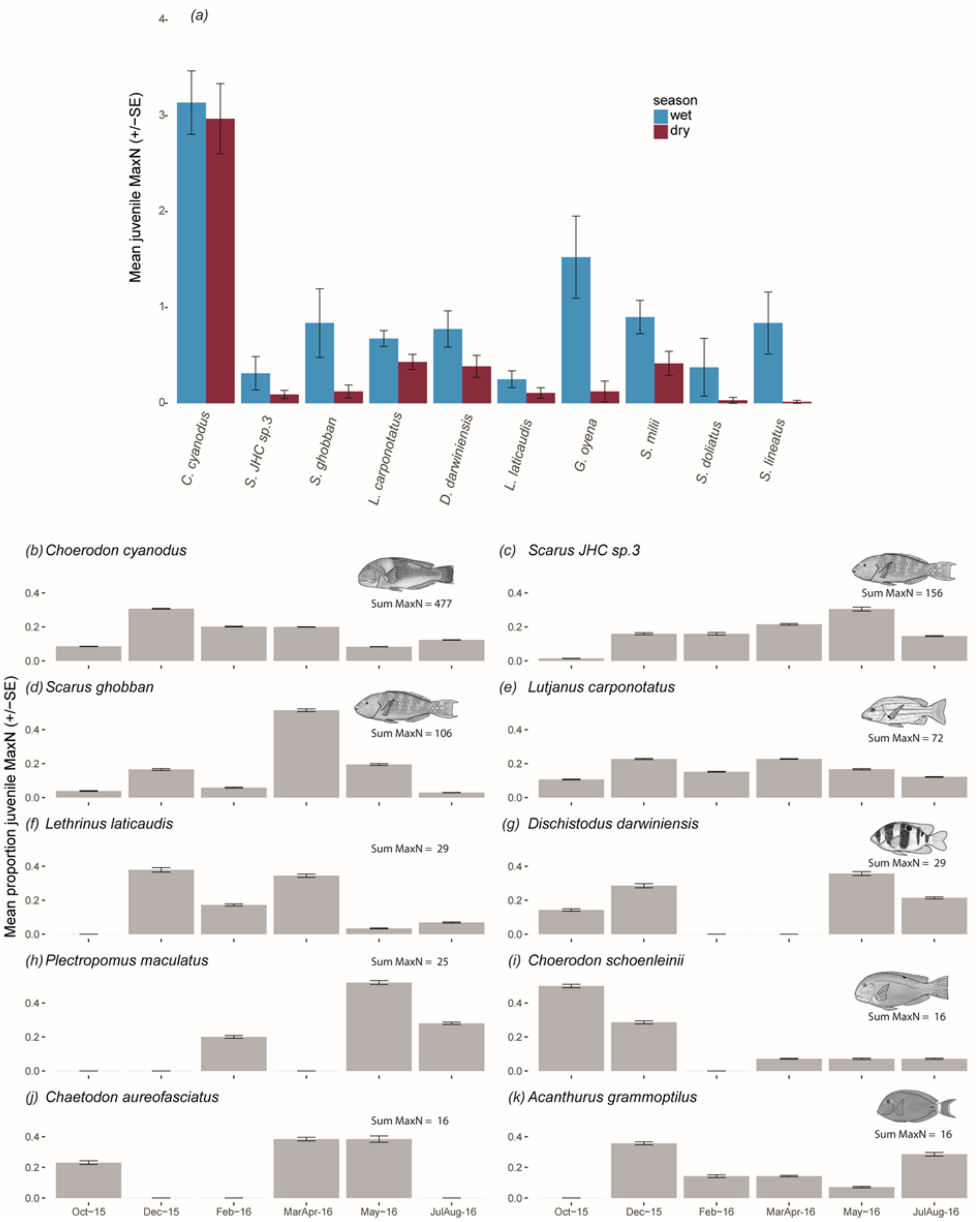

Figure 8. Average juvenile abundance (MaxN ±SE) for the ten most abundant fish species in all habitats surveyed across wet and dry seasons (a), and proportion of total abundance per sampling period for the ten most abundant species found in coral reef habitat (b to k). Fish images are included for species that were the most important in discriminating juvenile fish assemblage structure across habitats sampled (see Figures 6 and 7). Sum MaxN represents the total number of fish identified in coral reef RUVs across the six time periods surveyed.

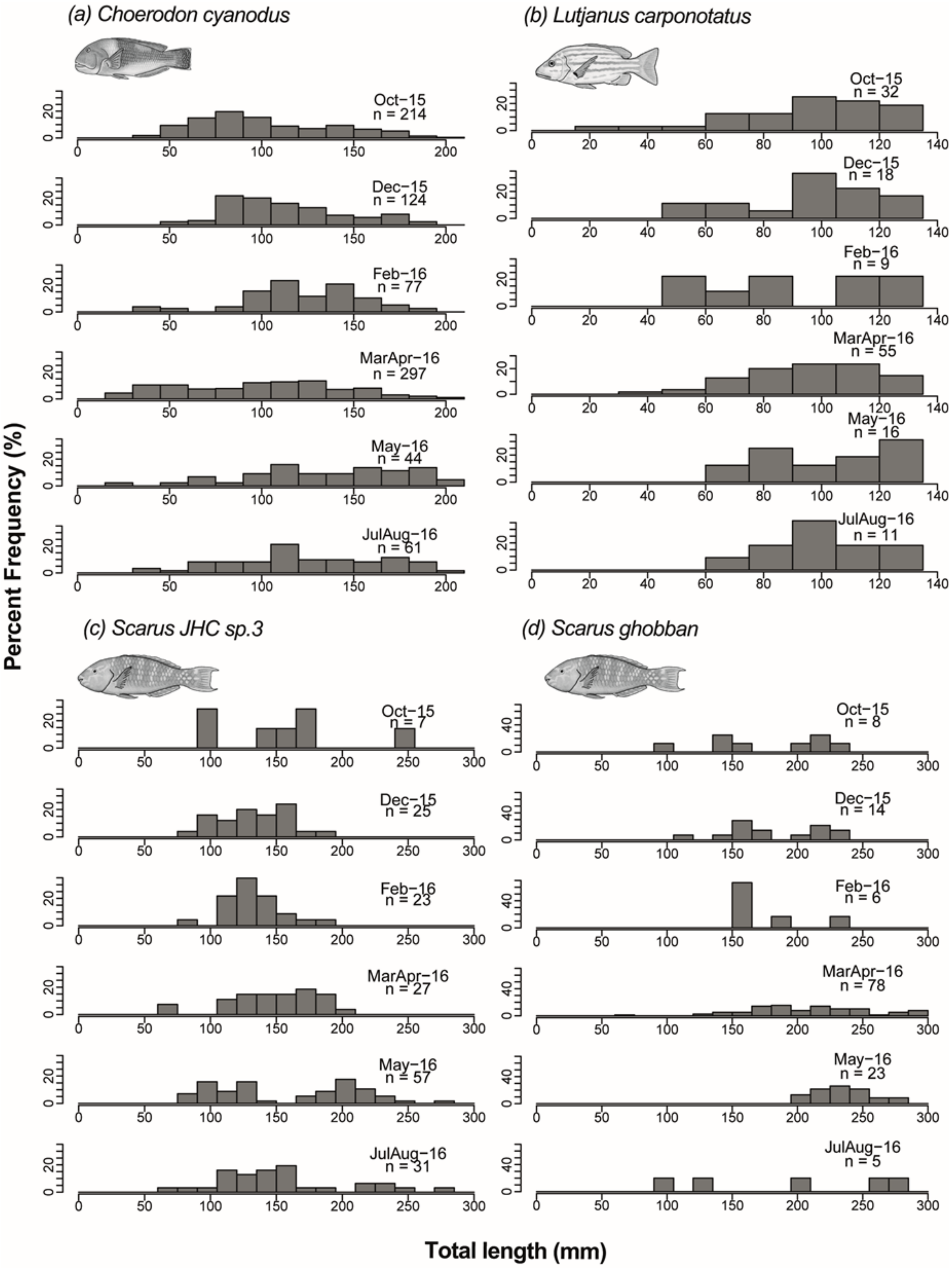

Figure 9. Length-frequency distributions according to the six bi-monthly periods surveyed for four species for which length data were best represented throughout the year (a-d); shown are percent frequencies according to selected bins based on maximum juvenile total length (L_T); n = sample size. Note the different scales along the *Y*-axis for *Scarus ghobban.* Length-frequency data represent length measurements gathered at all habitats surveyed; note that Dec-15, Feb-16, May-16 and JulAug-16 contain only coral reef data.

3.5 Species accumulation curves and sampling effort

The accumulation of species with increasing sampling effort (no. of RUVs) showed no asymptote at any level of sampling suggesting that some latent diversity remains in all habitats (Figure 10). Among habitats, sampling effort produced fairly similar numbers of species (Figure 10a, Appendix 3). Coral habitats recorded the highest species diversity followed by seagrass habitats (Figure 10a, Appendix 3). Similarly, species accumulation curves between wet and dry seasons showed no real marked point at which it was obvious that replication is sufficient to encompass >90% of overall diversity (Figure 10b). Sampling effort produced similar numbers of species between seasons, with slightly higher number of species recorded during the wet season (Figure 10b, Appendix 4).

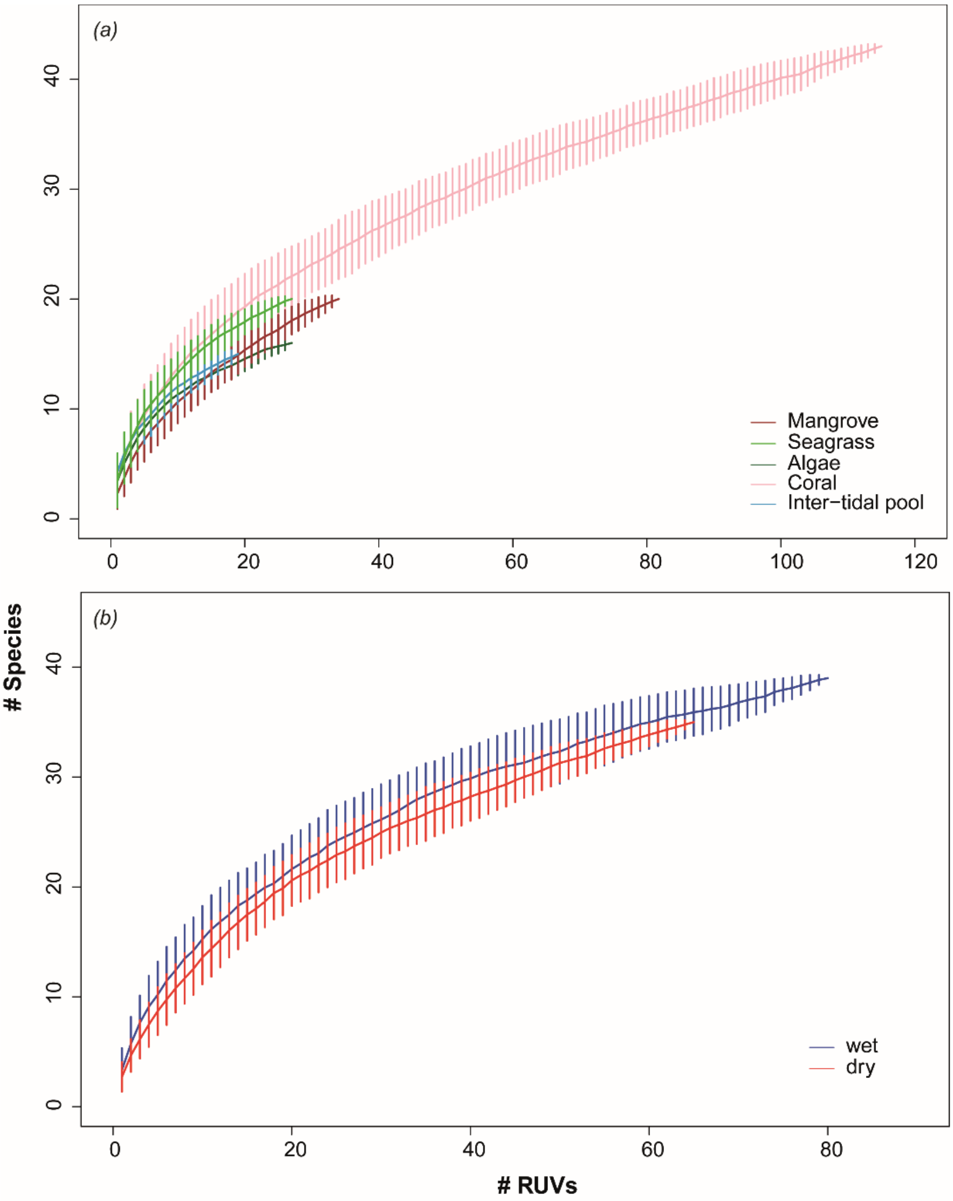

Figure 10. Species accumulation curves showing the number of unique species identified according to the number of RUV samples obtained at each of the five main habitats sampled (mangrove, seagrass, algae, coral and inter-tidal rockpools; a), and wet *vs.* dry seasons (b).

4 Discussion and Conclusions

This study has documented the spatial and temporal patterns of fish recruitment in the Cygnet Bay and Sunday Island group and addressed several key objectives:

1. *Develop cost-effective techniques suitable to the Kimberley marine region that, wherever possible, allow direct comparisons with other data-sets in Western Australia*

We identified and developed stereo remote underwater video systems (stereo-RUVs) to optimally survey and monitor fish recruitment at the different shallow water habitats identified in the western Kimberley. Specific camera requirements and design for sampling small fish recruits with this baitless stereo-video method are described in methods section 2.2. Stereo-RUVs were suitable for deployment at all habitats safely (without divers), were repeatable, provided a permanent record, and could be easily deployed in a reasonable timeframe. Our trials further indicated that stereo-RUVs were efficient in providing precise estimates of abundance and acceptable levels of diversity, when compared to the eight other techniques trialed (*i.e.* rotenone, box trawls, drop cameras, underwater visual census (transect, stationary and block), patch reefs and pearling panels; see Depczynski et al. 2015). A potential downside of the method is the post processing time needed for video analyses after initial data collection, but this time can be reduced considerably by focusing on the most abundant and representative species recruiting to the region (see objective 2 below). We recommend this focused approach to video analyses for future recruitment monitoring in the Kimberley via stereo-RUVs.

It is important to note that the deployment of RUVs requires reasonably clear waters and is highly dependent on tides in the Kimberley region. This study was conducted in a relatively clear region of the western Kimberley, after careful consideration of the local tidal regimes. Extension of these sampling methods to areas further east in the Kimberley which are typically turbid, will require previous evaluation of local conditions to determine feasibility. This will be crucial for direct comparisons between similar datasets for the region, given that the estimates for abundance from stereo-video techniques are based on the conservative measure of MaxN. Therefore, comparison with recruitment estimates from other methods may not be appropriate.

2. *Provide baseline quantitative information on levels of fish recruitment across a gradient of commonly available Kimberley habitats*

Remote underwater video was moderately successful in revealing fish recruitment in the study area, with recruits detected in more than 40% of all species recorded in the RUVs, allowing us to gather baseline quantitative information of recruitment at five different shallow water habitats: mangroves, seagrass, algae, coral reefs and inter-tidal rockpools. However, detected abundance of recruits was very low for most species, with 88% of total juvenile abundance contributed by only 12 species, and 39% of total juvenile abundance represented by a single species - *Choerodon cyanodus* (igoolan). Note that many of these 12 species are those of greatest importance to the Bardi Jawi community in terms of diet and cultural significance (see results section 3.1). The reasons for this generally low detected diversity and abundance are not known, but a combination of variables may be responsible including environmental, seasonal, biological/behavioural and methodological. For example, strong tidal fluxes in the region, together with high input of sediments and low salinity may affect larval connectivity and survival (Holliday et al. 2011). The Sunday Strait, directly to the east of the Sunday Island Group, has been found to be a potentially important barrier to larval dispersal, at least in some species (Berry et al. 2016). In addition, although deemed to be the most versatile and safest monitoring method across all habitats in the area (Depczynski et al. 2015), the capacity for RUVs to detect fish recruits is limited by factors such as water visibility and the cryptic nature of many juvenile fishes, including those that bury under soft sediments (*e.g.* wrasse Choat & Bellwood 1998). Therefore, recruits might be difficult to detect, especially in weed or mangrove habitats (Wilson et al. 2010, Evans et al. 2014) or recruit to deeper areas offshore. Finally, during 2016 water temperatures were extremely high with the hottest sea surface temperate anomalies on record, resulting in widespread coral bleaching in northern Australia (Bureau of Meteorology 2017); this is likely to have impacted fish recruitment and survival (*e.g.* Pankhurst & Munday 2011), potentially leading to underestimates of typical recruit abundance in Cygnet Bay and the Sunday Island group. Furthermore, interannual variability in recruitment is typically very high (Doherty 1991, Sampey et al. 2004, Trip et al. 2014). For these reasons, future monitoring to examine recruitment processes in more detail, assess interannual variability and responses to local environmental drivers, is suggested.

3. *Examine seasonal trends in fish recruitment for selected important species*

Recruitment was strongest during the wet season across all habitats and for nearly all species, although there is evidence for some level of recruitment during both seasons for at least some species (*e.g. Choerodon cyanodus*). Warm water temperatures are known to promote gonad development, larval growth and survival (Takahashi et al. 2012) and where seasonal differences in light and temperature are pronounced (*e.g.* subtropical and temperate seas) fish typically recruit during the summer months (Wilson et al. 2010, Cure et al. 2015). Although seasonal differences in sea temperature in the Kimberley are generally small (~2 ^{0}C, Ivey et al. 2016), these might still promote greater recruitment and survival during the warmer water months of the wet season (November to April). In addition, higher freshwater input during the wet season could increase the quantity of planktonic food available for fish recruits to feed on (De Robertis et al. 2003).

Unsurprisingly, our results also suggest that season is unlikely to be an exclusive driver of patterns in recruitment. Models that incorporate both season and habitat provided the strongest predictor of recruitment. This is expected because, among other things, habitats change from season to season (see point 4 below), and also because the influence of seasonal patterns are more evident in some habitats than others. Species-specific patterns also need to be taken into consideration, with some species apparently recruiting in only one season and/or a single habitat.

Our results appear to correlate strongly with traditional fishing knowledge and management. Some of the species considered most important to the Bardi Jawi community (e.g. *Acanthurus grammoptilis*, *Choerodon cyanodus*, *Lutjanus carponotatus*) are species that we have identified as having year round recruitment. These species are the mainstay of Bardi Jawi fishing and the community recognises that they can harvest year round without adversely affecting stocks (Smith 1997). There are exceptions. Some species of cultural significance to the Bardi Jawi community recruit most strongly in the wet season. For example, one of the most sought after species, *Siganus lineatus* (barrbal), is mostly targeted when they are 'fat' during the dry season (Smith 1997). This is during reproductive quiescence, when the fish accumulate fat stores in preparation for the next spawning season and are expected to hold higher levels of nutrients. While fish with more fat are more desirable, discussions with members of the Bardi Jawi community (see acknowledgements) demonstrate that this is also a deliberate method of avoiding the spawning season and conserving local fish stocks (see Rouja et al. 2003).

4. *Determine the relative importance of representative habitats to fish recruitment processes*

We identified aspects of both habitats and locations that promote juvenile fish diversity in the Kimberley region. The presence of a variety of coastal habitats in close proximity to each other creates a mosaic of recruitment habitats, food resources and environmental conditions, which allow species with different ecological requirements to successfully settle into the region. Furthermore, the presence of areas with high coral cover clearly promotes a greater abundance and species richness of juvenile fishes, as well as intermediate levels of consolidated substrates such as bedrock and boulders.

Different habitats clearly provide for different fish recruitment patterns, both in terms of species composition and abundance. Although some habitats tend to have higher abundance and diversity of fish recruits, there are differences in the type of fish that recruit to these habitats. For example, although mangroves and seagrass beds have lower diversity than coral reefs, some of the species important for local Bardi Jawi and recreational fisheries appear to recruit exclusively to just one of these habitats (*e.g. Lutjanus argentimaculatus* (maarrarn) to mangrove, and *Siganus lineatus* (barrbal) to seagrass beds). Therefore, conservation planning needs to recognize that all these habitats contribute to the overall pool and diversity of the Kimberley's fish fauna, are potential nurseries and warrant some level of protection, particularly to ensure sustainability of local fisheries resources.

However, the similarity in species assemblages and total juvenile abundance between algae, coral and intertidal rockpool habitats, suggests that these habitats can be united as one sampling unit of coral-macroalgal reef. This united sampling unit is complex because it represents a spatial mosaic of dominant benthic cover as well as a seasonally temporal continuum of algal cover associated to growth and senescence life history patterns. This united habitat would be ideal for monitoring recruitment strength because several of the most abundant and fishery-important species in the region are best represented here (*e.g. Choerodon cyanodus* (igoolan)*, Lutjanus carponotatus* (joorloo)).

5. Assess possible biodiversity hotspots and population strongholds for juvenile fishes

We were able to identify which aspects of locations and habitats promote species diversity, but weren't able to determine particular locations which could be considered a biodiversity hotspot. One of the reasons behind this is that sampling limitations didn't allow us to survey all habitats evenly at all locations, and therefore a comparison of diversity and abundance patterns according to locations was not appropriate. Nonetheless, our findings suggest that season and habitat differences are the most important indicators of juvenile fish diversity and abundance and that some level of protection of nursery grounds from different habitat types particularly during the wet season, would be ideal for the conservation of biodiversity and juvenile fish populations at the location level. Our analyses indicate that these factors (habitat and season), are more important than just location as determinants of juvenile recruitment patterns.

6. Implications for future monitoring studies

We have established initial monitoring sites for juvenile fish recruitment in representative habitats to form the basis for future long-term monitoring in the southern Kimberley region, and provided baseline data including species important for local and artisanal fisheries. Ideally, greater replication and complete replicate blocks would allow a better comparison between locations and habitats (see Table 1). However, sampling in the Kimberley is challenging due to strong tides and low visibility and deployment and retrieval of equipment is often limited to small windows of time, or delayed for extended periods.

Comparison of the seasonal and bi-monthly RUV datasets indicated that sampling during the end of the wet (March-April) and dry seasons (October) was appropriate for capturing temporal variation in recruitment. However, any future monitoring of fish recruitment should be concentrated during the wet season when abundances are at their maximum across nearshore habitats in the Kimberley region.

The spatial and temporal variability of the united sampling unit of 'coral-macroalgal reef' necessitates treating this as a continuous variable rather than a categorical one. The implication of this is that a stereo-RUV unit can effectively be dropped anywhere in this habitat at any time with no *a priori* expectation of the dominant habitat type because it can be quantified from the video *a posteriori*. This simplifies future monitoring in this particular habitat mosaic and requires less expertise or habitat appraisal by the team deploying the RUVs.

Remote underwater video (RUV) was the most appropriate for the region, as determined by a pilot study (Depczynski et al. 2015). However, accurate identifications are the basis of most biological and ecological studies and this is not always possibly with remote video techniques, particularly where individuals are small in size (*e.g.* juveniles), closely related species are visually very similar and visibility is low. While every care was taken to correctly identify individuals in the present study, the relatively high number of ambiguous identifications (*e.g.* to sp. or spp.; Appendix 2) demonstrates the limitation of this method. In saying that, the twelve species responsible for driving separation between habitats, as determined by the dBRDA analysis, are all generally easy to identify from video and confidence in our identifications of these species is high. Future video-based fish recruitment monitoring in the region should focus on these important and identifiable species to streamline efforts.

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Key Ecological Processes in Kimberley Benthic Communities: Coral Recruitment

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WAMSI Kimberley Marine Research Program

Final Report

Subproject 1.1.2b

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WAMSI Kimberley Marine Research Program

Initiated with the support of the State Government as part of the Kimberley Science and Conservation Strategy, the Kimberley Marine Research Program is co-invested by the WAMSI partners to provide regional understanding and baseline knowledge about the Kimberley marine environment. The program has been created in response to the extraordinary, unspoilt wilderness value of the Kimberley and increasing pressure for development in this region. The purpose is to provide science based information to support decision making in relation to the Kimberley marine park network, other conservation activities and future development proposals.

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Front cover images (L-R)

Image 1: Satellite image of the Kimberley coastline (Image: Landgate)

Image 2: Isopora coral recruit on terracotta settlement plate (Image: AIMS)

Image 3: Humpback whale breaching (Image: Pam Osborn)

Image 4: Coral recruitment tiles on metal frame deployed at Hal’s Pool, one of five locations in Cygnet Bay and the Sunday Island group (Image: AIMS)

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Metadata link for CSIRO herbivory sub-project: -
http://www.marlin.csiro.au/geonetwork/srv/eng/search#!8d910bf0-2f4e-4fc2-8a6e-f0447ed2d996
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Contents

Executive Summary

Corals are an essential element of reef ecosystems, providing a structural framework for reef growth, habitat and food source for many other organisms. For benthic organisms like corals, sexual reproduction and the associated pelagic larval stage provides an opportunity for genetic mixing of populations and recovery from disturbances. In the inshore Kimberley, at Cygnet Bay and the Sunday Island group, reproductive and recruitment patterns for corals have not been previously studied. We modified existing, standardised methods of surveying coral larval supply, by attaching coral settlement plates to frames that enabled their deployment and retrieval from the surface, rather than by SCUBA divers. These frames were specifically designed to withstand the strong currents of the macro-tidal Kimberley environment.

A protocol of monthly sampling at 5 locations for a 13 month period was designed to discern temporal patterns in coral spawning and recruitment, identifying likely periods of mass spawning and background brooding. However, extreme water temperatures that persisted through summer and autumn culminated in a coral bleaching event that peaked in March-April, affecting between 30-60% of the community. The bleaching coincided with the predicted mass-spawning period, and reduced rates of recruitment for all corals, particularly for spawning corals. Given the duration and severity of the temperature anomaly, the quantified rates of recruitment are unlikely to reflect those during years without such stress. Nonetheless, the recruitment of *Acropora* peaked in March-April 2016 and to a lesser extent in September-October, at the same time as mass- and multi-specific spawning events documented on oceanic reefs in the Kimberley and in the Pilbara reefs to the south. Recruits from the family Pocilloporidae (comprising both brooders and spawners) and genus *Isopora* were more abundant in the summer months. Additionally, we provide the first definitive evidence of reproductive output and recruitment by corals in family Poritidae, which potentially include both brooding and spawning species, over many months throughout the year, supporting anecdotal evidence from reproductive studies at oceanic reefs in the region.

The number and composition of coral recruits differed considerably among the study locations, reinforcing the spatial heterogeneity evident in most studies of biological communities in the Kimberley. Fine-scale spatial heterogeneity also varied as expected among coral groups, with evidence of recruitment variation in brooding corals over distances of less than a few hundred metres, compared with tens of kilometres for groups of spawning corals. Continuation of sampling in future years would allow a further assessment of spatial and temporal variation in recruitment of corals at inshore Kimberley reefs, and presumably track the recovery of communities to background levels of recruitment following the bleaching disturbance.

Finally, during 2016 water temperatures were extremely high with the hottest sea surface temperate anomalies on record, resulting in widespread coral bleaching in northern Australia (Bureau of Meteorology 2017); this is likely to have impacted fish recruitment and survival (*e.g.* Pankhurst & Munday 2011), potentially leading to underestimates of typical recruit abundance in the Sunday Islands. Furthermore, interannual variability in recruitment is typically very high (Doherty 1991, Sampey et al. 2004, Trip et al. 2014). For these reasons, future monitoring examining recruitment processes in more detail, assess interannual variability and responses to local environmental drivers, is suggested.

1 Introduction

Corals are a critical component of reef ecosystems, providing a structural framework for reef growth, as well as creating habitats and acting as a food source for many species (Knowlton et al. 2010). Reefs of the inshore Kimberley, Western Australia, inhabit a unique environment, but have not been well studied and processes related to the coral life cycle are little known (Wilson 2013).

The movement of pelagic larvae and their subsequent settlement onto the reef ("recruitment") is an important aspect of the life cycle of corals and other benthic organisms (Harrison & Wallace 1990). For these otherwise sessile organisms, which spend the remainder of their life attached to the reef, larval movement allows the offspring of coral colonies to spread into new habitats, or re-colonize areas where adult corals have been lost or damaged. Larval movement can also allow genetic mixing among populations, although the extent to which this occurs is highly variable (Underwood 2009).

Corals reproduce both sexually, by releasing gametes and/or larvae, and asexually, where fragments of the parent colony that are broken off grow to become new colonies (Harrison & Wallace 1990). In most cases, sexual reproduction is the dominant mode of reproduction among corals, and can be further divided into "spawners" (those which release unfertilized gametes into the water column) and "brooders" (where sperm is released, but eggs are fertilized inside the parent colony, and released as larvae) (Harrison 2011). For spawning corals, larvae routinely travel greater distances (up to 10s of km), than the larvae released by brooding corals, which are competent to settle shortly after being released (less than a few kilometres) (e.g. Berry (2016) and Underwood (2009)). The majority of corals reproduce by spawning, which often occurs during mass- or multi-specific spawning events, with many coral colonies from many species releasing sperm and eggs at the same time (Baird et al. 2009). In other off shore Kimberley reefs (e.g. Scott Reef, Rowley Shoals, Ashmore Reef) the main mass-spawning of the year occurs in autumn, with a smaller multi-specific spawning event in spring (Gilmour et al. 2009, Rosser 2013, Gilmour et al. 2016a, Gilmour et al. 2016b).

For coral communities, a regular influx of larval recruits is a key process for sustaining and renewing populations. Levels of recruitment influence both community structure and recovery times after a disturbance event (e.g. severe bleaching, disease, cyclone, pollution spill); as well as providing an indication of the reproductive health of the overall system (Bak & Meesters 1998). Recent efforts to understand recruitment processes have provided evidence that coral populations are often genetically localized and largely self-seeded at relatively small (<10s km) spatial scales (e.g. Berry et al. (2016), and Underwood (2009)), highlighting the crucial importance of local management. However, spatial patterns of larval supply and recruitment in corals vary considerably, due to the differing reproductive modes and larval duration among coral groups, the variation in large- and small-scale hydrodynamic conditions among sites, and differences in weather conditions throughout the period of larval dispersal. It is therefore important to investigate patterns of larval supply and recruitment at a range of nested scales.

The Kimberley region of Western Australia is diverse, extensive and unique, with coral reefs in the Kimberley facing a range of extreme conditions (Wilson 2013, Richards et al. 2015). In the inshore reefs, large tides drive strong, localized currents, which may act as a barrier to movement of larvae (Wilson 2013, Berry et al. 2016), contributing to the formation of extremely patchy habitat distributions. Large fluctuations in water temperatures, high turbidity and periodic exposure to cyclones are also likely to influence coral communities in this region (Richards et al. 2015, Schoepf et al. 2015). Despite extreme environmental conditions, diverse assemblages of corals have been documented in this region (Richards et al. 2015).

In addition to the typically extreme environmental conditions experienced by corals in the inshore Kimberley, high sea water temperatures in 2016, associated with El Nino conditions, resulted in the occurrence of coral bleaching in the Indian and Pacific Oceans, including extensive bleaching at some reefs in north-western Australia. Bleaching commenced in late March 2016 and continued through April, concurrent with the predicted mass spawning time for corals. Impacts were as expected, based on the NOAA temperature predictions and the history of severe bleaching during extreme El Nino conditions in 1998. In Western Australia, the offshore and inshore reefs of the Kimberley region were affected. Variation in bleaching among the reefs was similar to that in 1998, but in 2016 the inshore reefs of the Kimberley bleached. At Cygnet Bay and the Sunday Island group, estimates of bleaching ranged from 19-40% (S. Wilson, unpubl. data).

Coral bleaching, as well as causing whole- and partial-colony mortality, can also affect the growth and reproduction of coral colonies at the time of bleaching (Baird & Marshall 2002, Ward et al. 2002, Negri et al. 2007). Post-bleaching, coral mortality may result in large reductions in recruit numbers for extended periods (several years) while surviving colonies regrow. At Scott Reef, an isolated offshore reef in the Kimberley region, extremely low recruitment was documented after the 1998 bleaching, with larval supply reduced by 94% for 6 years post-bleaching (Gilmour et al. 2013).

There are no studies of coral recruitment and very few data on coral reproduction for assemblages in the inshore Kimberley region (Gilmour et al. 2016a). Inferences of coral reproduction in the region are largely based on reproductive surveys during one or two years at a small group of islands within the Bonaparte Archipelago. The main season of spawning on inshore Kimberley reefs is probably during autumn (beginning of the dry season), but with a second multi-specific spawning also occurring during spring (beginning of the wet season) at a similar time to the oceanic reefs in the region. Of the species of *Acropora* sampled in spring (n = 35) and autumn (n = 16), 42% were inferred to spawn in spring and 87% in autumn. Of the 60 common non-*Acropora* species, there was evidence of only 5% spawning in spring and 7% in autumn (Gilmour et al. 2016a). Key knowledge gaps include an understanding of the timing of spawning and planulation for inshore Kimberley reefs, and the proportion of corals that brood or spawn.

Provided they are designed correctly, studies of coral recruitment can provide valuable insights into patterns of reproduction and larval supply. In turn, these data make a valuable contribution to management strategies, by providing a basis for understanding of future demographic trends and the spatial patterns of local and regional adult community structures. In the Kimberley region, pre-bleaching coral recruitment patterns are unknown; however, our monthly surveys throughout the period of bleaching provide a baseline from which to assess increases in post-bleaching recruitment and their relationship to the distribution and abundance of adult colonies. At the same inshore Kimberley reefs studied in several complementary WAMSI projects, at locations around Cygnet Bay and the Sunday Island group, we quantified rates of larval supply and recruitment to determine the main periods of reproductive output for spawning and brooding corals, and to identify any obvious sinks of coral recruitment among the reefs. Our spatially-nested design allowed us to examine the spatial scales over which recruitment processes vary. Quantifying levels of coral recruitment, and their spatial and temporal variation, provides an indication of the current health of coral communities in Cygnet Bay and the Sunday Island group.

2 Materials and Methods

2.1 Coral recruitment

2.1.1 Approach

We used coral settlement plates ("tiles") to assess coral recruitment in the Cygnet Bay area and Sunday Island group, (e.g. Mundy (2000), Heyward et al. (2010), and Gilmour et al. (2013)). Settlement plates are pre-conditioned terracotta tiles (110 mm x 110 mm x 10 mm), which provide a standard-sized unit of artificial substrate for coral spat to settle on. Settlement plates were deployed for two months. One month is required for the tiles to become covered with a fouling community of natural biofilms and coralline algae that induces settlement in coral larvae (Morse et al. 1988, Heyward & Negri 1999, Harrington et al. 2004, Webster et al. 2004). The second month is required for settling larvae to excrete a calcium carbonate skeleton of sufficient size to be identifiable after tiles are retrieved and bleached. The experimental substrata and the schedule of deployment and retrieval are critical to obtain reasonable estimates of coral recruitment that are also comparable to other studies. By the time the settlement plates were retrieved, the coral spat were of a size that can be counted, and certain taxonomic groups identified, as in numerous previous surveys of coral recruitment in Western Australia.

In this study, we modified existing methods to suit the macro-tidal Kimberley environment, by placing tiles on a frame rather than attaching directly to the reef. Apart from the use of a frame, the methodology was the same so the data were comparable to most other studies of coral recruitment, particularly in Western Australia (e.g. Gilmour et al. (2013)). A previous study has compared recruit density between settlement plates attached directly to the substrate and to metal frames, and found that there was no difference between the two methods (Mundy 2000).

We designed, developed and tested steel frames which could be lowered from the surface, not requiring SCUBA diving, and could withstand the strong currents present at Kimberley reefs (see Figure 1). SCUBA diving was avoided due to the logistical difficulties of working underwater in this region (e.g. large tides and strong currents), the increased exposure to hazards associated with in-water work (exposure to Irukandji jellyfish, crocodiles), and to allow monthly tile changeovers to be conducted by the Bardi Jawi Rangers. The design allowed the frame to be hooked at the apex with a grappling hook, and pulled to the surface for existing settlement plates to be removed and replaced with new plates. The coral settlement plates were fixed to the frames using a threaded bolt and wingnut with a small plastic spacer underneath, to provide cushioning from impacts associated with raising and lowering the frames to and from the seabed, as well as preventing any movement or vibration resulting from the high current flows in the area which can interrupt settlement. Field testing of the frames was completed in March 2015, with the conclusion that the frames were suitable in high-current areas, and could be deployed and retrieved from the work vessel in use.

2.1.1 Study locations and habitats

Coral settlement plates were deployed on frames at five locations across Cygnet Bay and the Sunday Island group in October 2015 (see Figure 1). Locations chosen were subtidal, coral-dominated areas, which varied in coral cover, diversity and exposure to currents (Table 1). Of the 5 locations where frames were deployed, both Jalan and Jorrol experience very strong currents, with a steady flow even during neap tides. Jalan also had the highest overall coral cover and the greatest diversity in coral morphology (morphologies present included massive, tabulate, foliose corals); while Jorrol had the lowest overall coral cover of any location. Hal’s Pool experienced moderate currents with little protection, and relatively low coral cover. Catamaran Bay was the most sheltered with minimal current, and coral diversity and abundance were second-highest of the locations (after Jalan). Shenton Bluff was protected from the incoming tide by a rocky outcrop, but experienced strong currents on the outgoing tide. Shenton Bluff also had relatively high coral cover (third highest, after Jalan and Catamaran Bay) but low diversity – corals present were primarily branching (staghorn) *Acropora* (95% of coral present) forming large patches. Catamaran Bay and Shenton Bluff both experienced high levels of sedimentation during the study period.

Habitat comparisons were made for each of the locations using images captured from remote underwater video (RUV) footage. Footage was recorded at five sites in the area around the recruitment tile locations, every eight weeks during the survey period, tide permitting. Habitat images were analyzed using visual estimates of dominant habitat type in a gridded image in Transect Measure (SeaGIS). Habitats were characterized by visually estimating the dominance of broad categories (hard coral, macroalgae) and morphology-based categories within each of the broad categories (for hard corals: branching, erect fine branching, erect coarse branching, columnar, encrusting, foliose/plate, massive, blue corals). Corals were also categorized as live or bleached. Bleached corals included those recently bleached and those with new filamentous algal growth on the bleached structure.

Additionally, surveys of coral bleaching were carried out in late March 2016. Areas of 2 m radius were examined at five locations (Shenton Pool, Shenton Bluff, Jorrol, Catamaran Bay and Jackson Island), three of which coincided with locations where coral recruitment tiles were placed (Shenton Bluff, Jorrol, and Catamaran Bay). Within the survey area, all coral colonies were identified to genus level and recorded as healthy, pale or bleached (Appendix 6, S. Wilson, unpubl. data). At each location, between two and 13 areas (each 2 m radius) were examined, depending on time constraints.

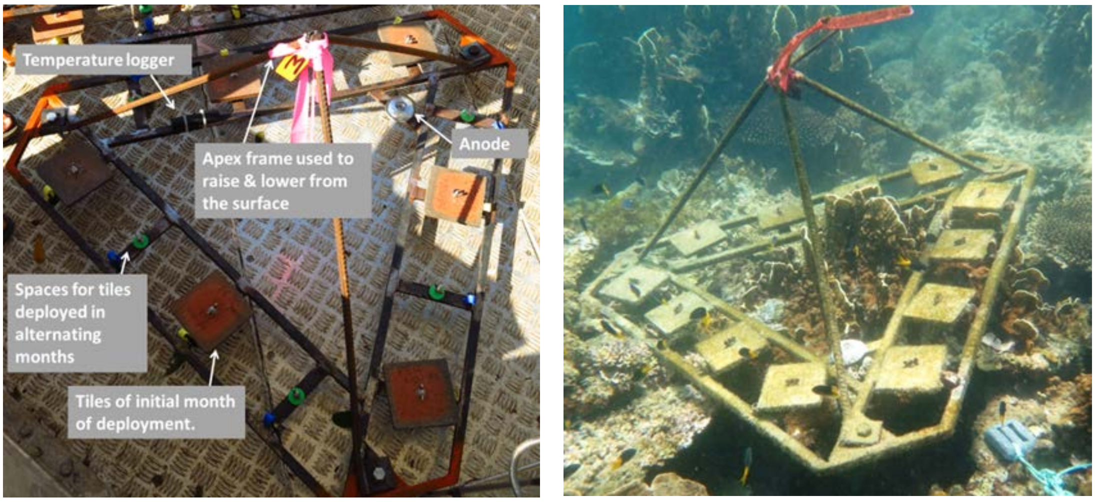

Figure 1. Coral settlement plates on metal frame ready for deployment (left); and deployed at Jalan, one of five locations in Cygnet Bay and the Sunday Island group. Settlement plates on frame have been deployed for one and two months, and are covered with turfing algae and biofilms, making the tiles suitable for coral settlement.

Table 1. Qualitative ranks of study locations based on site-wide observations coral cover, coral diversity (morphological types; e.g. massive, branching, tabulate), and exposure to current (Philip McCarthy and Camilla Piggott, pers comm).

Ranking	Coral cover	Coral diversity	Exposure to current
1 (highest)	Jalan	Jalan	Jalan
2	Catamaran Bay	Catamaran Bay	Jorrol
3	Shenton Bluff	Hals Pool	Hals Pool
4	Hals Pool	Jorrol	Shenton Bluff
5 (lowest)	Jorrol	Shenton Bluff	Catamaran Bay

2.1.2 *Experimental design*

The same experimental design was employed as in other coral recruitment studies by AIMS at WA reefs, making recruitment data following mass-spawning events comparable among studies. At each of the five study locations, three frames were deployed 50 m apart, each frame containing 12 tiles. Six tiles were retrieved and replaced each month with a staggered deployment pattern to allow a two month deployment period for each tile set and to ensure that tiles were always available with a suitable fouling community to induce larval settlement. This spatially nested design allowed us to examine differences in recruitment among various spatial scales, to examine the timing of coral settlement throughout the year, to capture predicted mass spawning periods and to record likely recruitment of brooded larvae over several months through the year. Dates of tile deployment and retrieval can be found in Table 2.

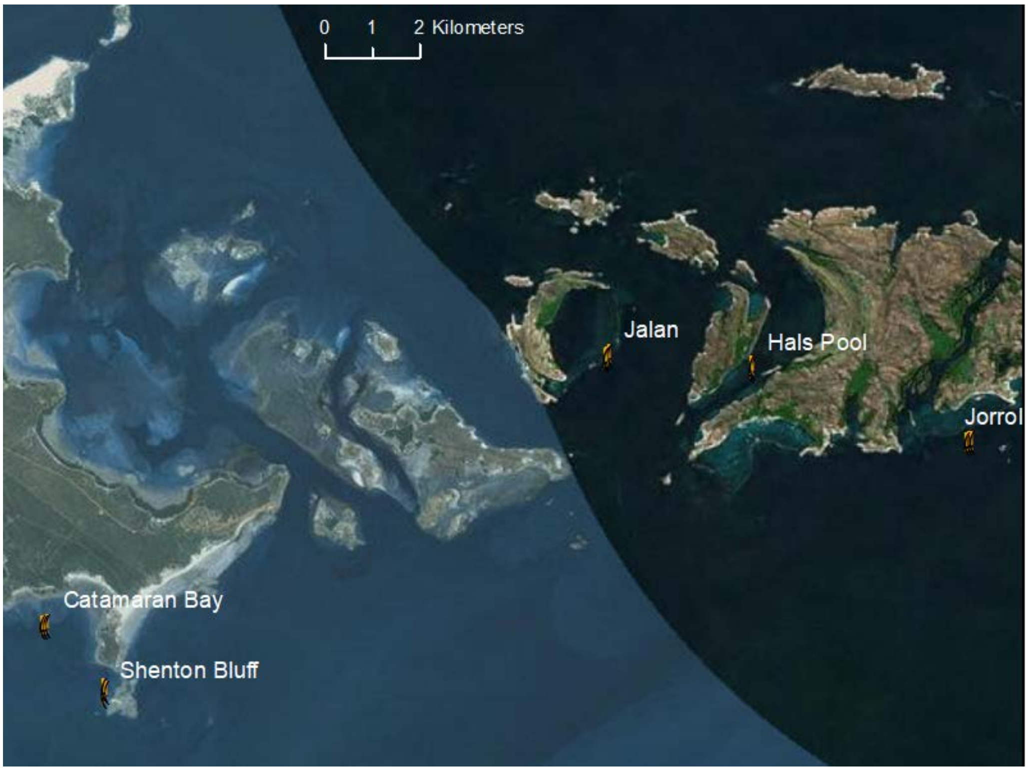

Figure 2. The locations of the coral frames in five coral-dominated areas in Cygnet Bay and the Sunday Island group. At each location, there are three frames each containing six tiles per month.

Table 2. Schedule of tile deployment and retrieval over the survey period (October 2015-October 2016). Scheduled deployment dates are 7-9 nights after full moon, to coincide with neap tides (conditions are most workable) and predicted coral spawning times.

Scheduled deployment dates (7-9 nights after full moon)	Deploying tiles labelled	Removing tiles labelled
5-7 Oct 2015	Month 01	-
3-5 Nov 2015	Month 02	-
3-5 Dec 2015	Month 03	Month 01
2-4 Jan 2016	Month 04	Month 02
1-3 Feb 2016	Month 05	Month 03
2-4 Mar 2016	Month 06	Month 04
31 Mar - 2 Apr 2016	Month 07	Month 05
30 Apr - 2 May 2016	Month 08	Month 06
29-31 May 2016	Month 09	Month 07
28-30 Jun 2016	Month 10	Month 08
27-29 Jul 2016	Month 11	Month 09
25-27 Aug 2016	Month 12	Month 10
23-25 Sep 2016	Month 13	Month 11
23-25 Oct 2016	-	Month 12
21-23 Nov 2016	-	Month 13

After being in place for two months, the tiles were removed from the frame and replaced with new tiles. The retrieved tiles were placed onto a metal rod, with foam spacers between each tile to prevent damage to any coral recruits. Rigid plastic squares at the ends of each rod (larger than the settlement plates) further protected the settlement plates from damage during preservation, storage and transport. The settlement plates were placed in seawater until preservation, when they were transferred to a chlorine solution which removed the coral tissue, leaving the coral skeletons behind. The tiles were then air-dried and packed for transport. Monthly tile deployments, collections and tile preservation were conducted by the Bardi Jawi Rangers. Later, the settlement plates were examined under a dissecting microscope and the coral skeletons counted and identified to the highest taxonomic resolution possible.

2.1.3 Sample processing and identification of coral recruits

Recruits on tiles were identified and grouped into those which could be reliably identified at this stage of development: *Acropora*, *Isopora*, Pocilloporidae, Poritidae and Other (AIMS 20??, Babcock et al. (2003)). Example photographs of the coral groups can be found in Figure 3; further examples can be found in Appendix 7. Of these, the genus *Acropora* are spawning corals, and the genus *Isopora* are brooding corals (Baird et al. 2009, Harrison 2011, Gilmour et al. 2016a). The members of the genus *Porites* (within the family Poritidae) that are known to occur in the inshore Kimberley are spawning corals (Veron 2000, Baird et al. 2009, Richards et al. 2014, Richards et al. 2015, Madin et al. 2016). Spawning also occurs in the genus *Pocillopora* of the family Pocilloporidae, but other genera of the same family (*Stylophora, Seriatopora*) are brooding corals (Baird et al. 2009, Harrison 2011, Gilmour et al. 2016a). Brooding and spawning species of the families Pocilloporidae or Poritidae could not be distinguished at this stage of growth (AIMS, (Babcock et al. 2003). The 'Other' group includes corals from all other families, which are likely to be mainly spawning corals, given that the majority of corals reproduce by spawning.

2.1.4 Data analyses

Variation in the abundance and composition of recruits among sites, locations and months, was explored through multivariate analyses of transformed (square root) data in the software PRIMER (Clarke & Warwick 2001). Data were averaged to explore the degree of variation in recruitment within and among locations, and among months throughout the year. A Bray-Curtis dissimilarity matrix was produced for each set of transformed and averaged data, and illustrated with a non-metric Multi-Dimensional Scaling (MDS) plot. A 5% metric weighting was applied to the non-metric analyses of variation in recruitment throughout the year to account for the relatively small differences among some months (e.g. winter) compared to others (e.g. April), and the tendency for groups to collapse on top of each other in multi-dimensional space. Vectors were overlayed on each plot to highlight the coral groups that best distinguished the patterns of recruitment in space or time.

To determine importance of various factors, i.e. month of the year and location, data was analysed in R (version 3.2.3, R Core Team (2015)), using a complete-subsets modelling approach where a complete model set was constructed and fitted using the appropriate statistical methods and subsequently compared using Akaike Information Criterion (AICc), AICc weight values (ωi) and R^2 (Burnham & Anderson 2002). Models were fitted using the GAM function in the mgcv package (Wood 2006), with the number of coral recruits modelled as a Tweedie distribution. We used GAMs rather than linear mixed models to allow for potential non-linear relationships between the response variable and the various continuous environmental predictors. Smoothing terms were fit with a cubic spline (Wood 2006), with the "k" argument limited to 5 (to reduce over-fitting and ensure ecologically interpretable monotonic relationships). Assumptions were evaluated using residual plots and found to be adequately met. Following standard convention, the simplest model within 2 AICc values of the model with the lowest AICc was considered the optimal model (Burnham & Anderson 2002). A null model consisting of only an intercept and the random factors was also included in the model set, to test if any of the included factors were indeed useful predictors. The relative importance of each variable (variable importance) was determined by summing the ωi values for all models containing the variable, with higher summed values representing increased importance of that predictor to the response variable (Burnham & Anderson 2002).

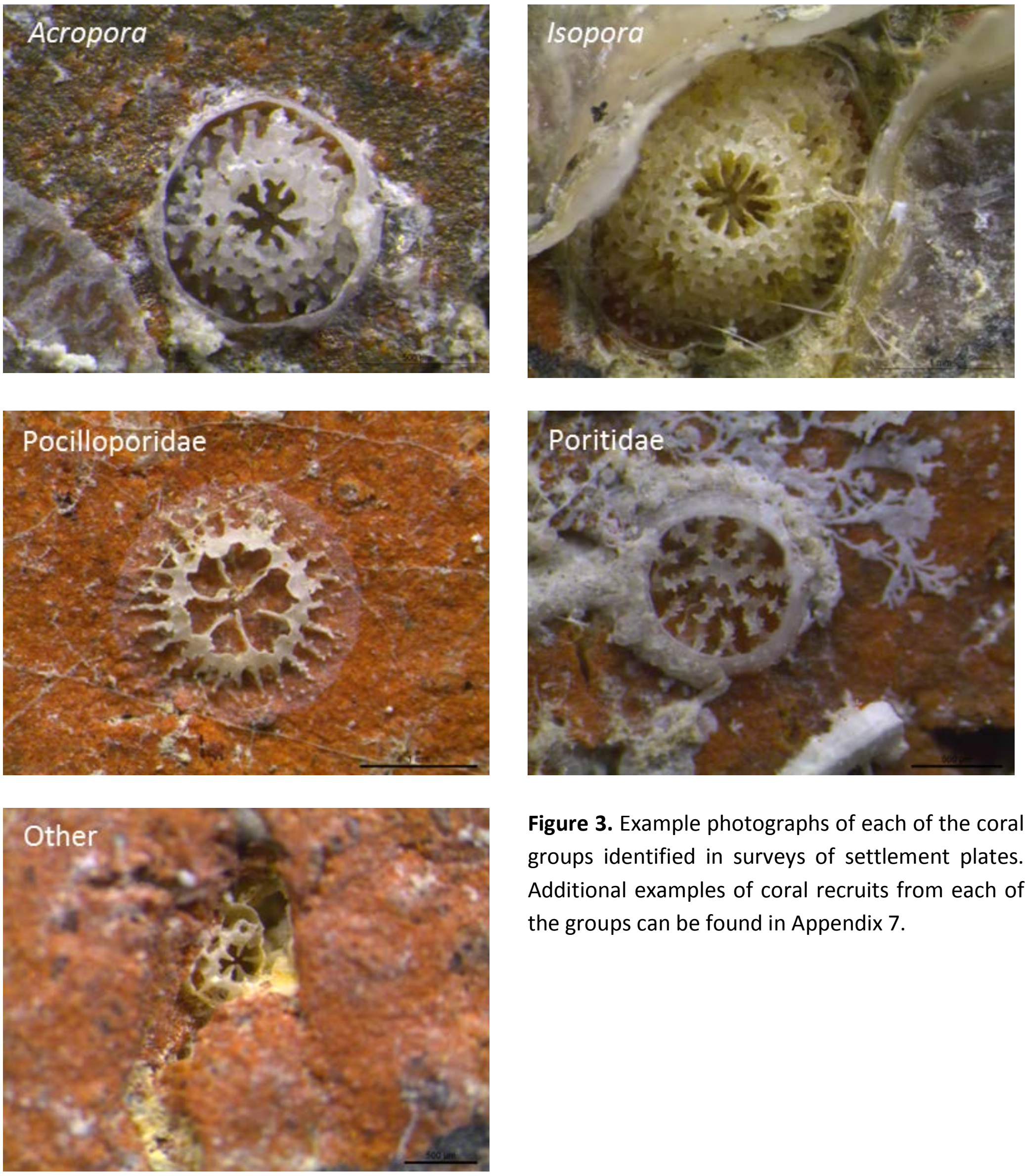

Figure 3. Example photographs of each of the coral groups identified in surveys of settlement plates. Additional examples of coral recruits from each of the groups can be found in Appendix 7.

3 Results

3.1 Coral recruitment

3.1.1 Summary of results

The number and diversity of coral recruits varied in both space and time (Figure 4). There was evidence of *Acropora* spawning at the same time (March-April) as the mass-spawning on most other Western Australian reefs, and at the same time (October-November) as the multi-specific spawning that occurs on the oceanic reefs of the Kimberley and at Pilbara reefs (Figure 4). Poritidae and particularly Pocilloporidae recruits were the most abundant and were present throughout the year, despite *Acropora* and *Isopora* being the most abundant adult genera (Figure 4, Z. Richards, pers. comm.). However, the *Acropora* and *Isopora* are also among the most susceptible coral genera to bleaching, and their rates of reproductive output and recruitment were likely reduced by the temperature anomalies through summer and autumn (2016), that led to the bleaching of between 30-60% of the coral in the region.

For all five coral groups both month and location (10s km apart) consistently made important contributions to the observed variation in recruitment for all coral groups, but the relative importance of temporal variation (month) and small-scale (site within location; 50-100m) variation reflected their different reproductive modes (Table 3); temporal variation was more important for the spawning corals that recruit during discrete periods than for the brooding corals that recruit over several months, while variation among sites was more important for the brooding corals that have more localized dispersal and recruitment than the spawning corals. The results of this study are consistent with the general patterns of reproduction and recruitment observed at the oceanic reefs of the Kimberley and the Pilbara reefs to the south, while also providing the first definitive evidence of reproduction and recruitment of *Porites* over several months throughout the year.

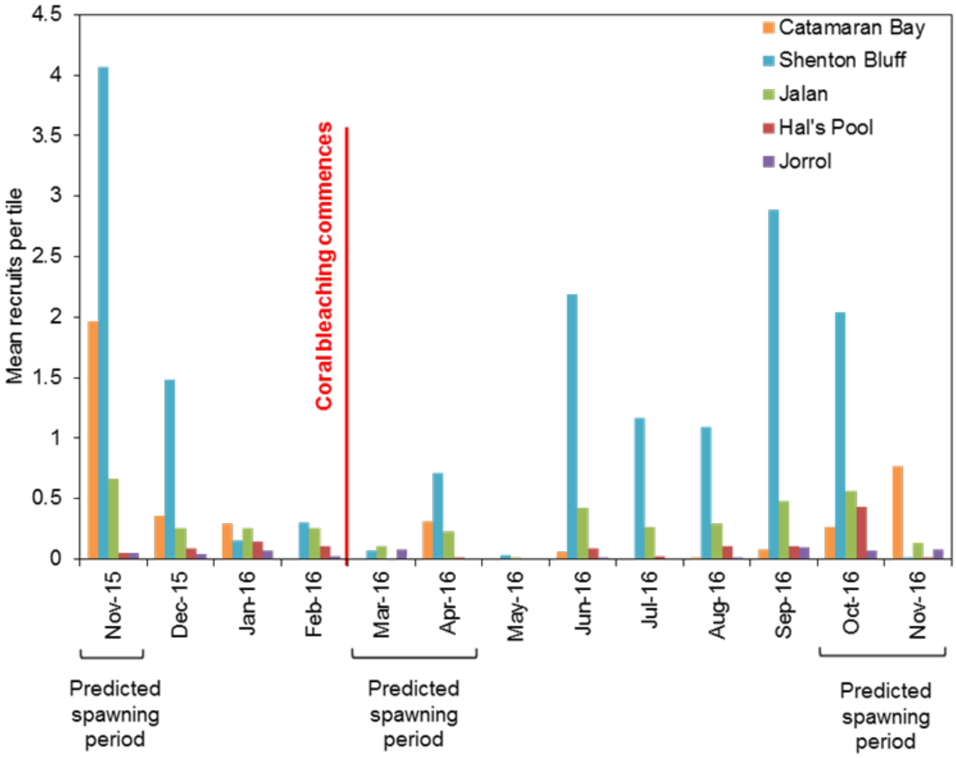

Figure 4. Mean coral recruits at each location over the months surveyed (all coral groups included). Time of coral bleaching event and predicted spawning times are indicated. Note Catamaran Bay tiles were not successfully retrieved in Feb-16 and Mar-16.

3.1.2 Temporal variation in coral recruitment

Recruitment at the inshore western Kimberley reefs displayed similar seasonal variation to that observed at other north-west reefs, but was also affected by severe temperature anomalies through summer and autumn in 2016 (Figure 5). Coral community surveys in late March quantified bleaching at locations surveyed for coral recruitment, ranging from 19% at Jorrol to 40% at Shenton Bluff (Figure 5). Bleaching was reported for all the families identified as recruits: Pocilloporidae (*Pocillopora*, *Seriatopora*, *Stylophora*), Poritidae (*Porites*, *Goniopora*), Acroporidae (*Acropora*, *Montipora*) and Others (Fig 6). The exception was the *Isopora*, which were not present in the surveys quantifying bleaching, but this genus is typically among the most susceptible to temperature induced bleaching. The bleaching of coral communities was also evident in the broad habitat surveys through March (25%) to May (43%, Figure 5). The temperature stress, coupled with typically low recruitment during winter months, resulted in the lowest rates of recruitment occurring during May, with comparably little variation among the other winter months (Figure 4, 8).

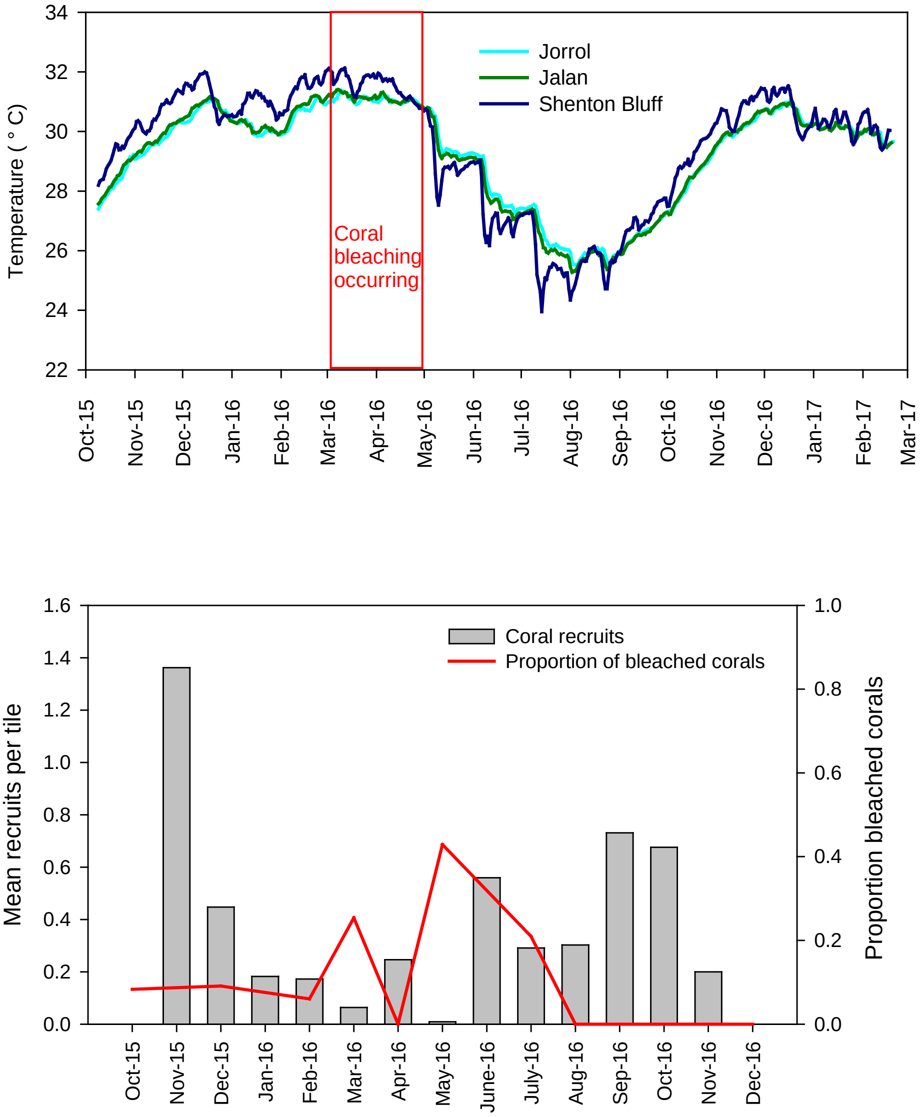

Figure 5. Average daily temperature data from loggers deployed alongside coral settlement tiles at Jalan, Jorrol and Shenton Bluff (top panel); and (bottom panel) variation in mean recruits over the survey period (for all locations and family groups), overlaid with observations of bleaching (proportion of bleached corals) from the habitat comparison. Note: In April 2016, bleaching observations were from 1 location only (Jalan).

Figure 6. Example images of bleached corals from bleaching surveys conducted in late March 2016, at 5 locations around Cygnet Bay and the Sunday Island group. Several different coral genera and families can be seen, bleached, in the images.

The low abundance of *Acropora* recruits overall (n = 57) may reflect the effects of temperature stress, given the bulk of their reproductive output probably coincided with the timing of the mass-bleaching in March and April (Figure 4, 5). However, the relative peaks in recruitment for the spawning *Acropora* occurred during March, April, and October, during the predicted period of mass- and multi-specific spawning, respectively (Figure 7, 9). At one location (Jalan), *Acropora* recruits were seen in February, in addition to March, April and October (Figure 7, 9). The peak in recruitment of spawning *Acropora* in autumn clearly differentiated the March-April period from other months through the year (Figure 9). The absence of *Acropora* recruits in November 2015 (Figure 7, 9), coupled with the high number of other recruits during that month, and the signal of spring spawning even after the bleaching on 2016, suggest that the *Acropora* may have participated in a multi-specific spawning in October, prior to the commencement of this study (Figure 7). Full-subsets modelling of factors influencing recruitment revealed the best fitting model for this group included an additive effect of month of the year and location, with this model having a higher model weight and lower AICc than other models (Table 3, Figure 9). The impact of location did appear limited as the model with only month had an AICc within 2 (Table 3). Month appears to be highly important to *Acropora* colonies.

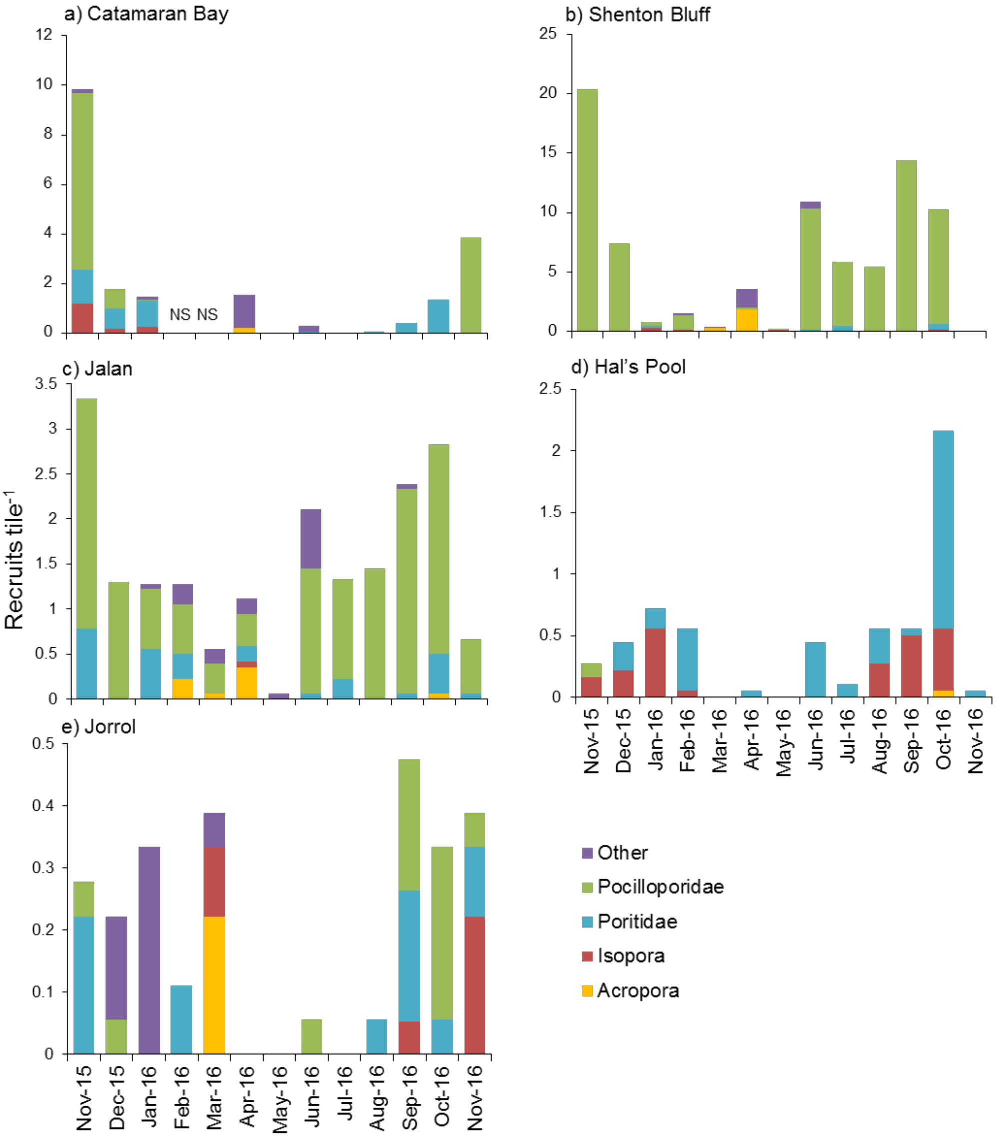

Figure 7. Mean coral recruits of the groups *Acropora*, *Isopora*, Pocilloporidae and Poritidae at each location. Note differing scales on the vertical axes. NS = Not surveyed; Catamaran Bay tiles were not successfully retrieved in 2 months (March and April 2016).

Apart from the *Acropora,* the Poritidae were the other family containing spawning corals, but their recruitment occurred consistently over many months of the year, rather than peaking during autumn and/or spring (Figure 7, 9). The Poritidae were the second most abundant (n = 240) group of recruits, after the Pocilloporidae, which also recruited over most months throughout the year and were by far the most abundant (n = 1833). The Pocilloporidae, which probably include both spawning (*Pocillopora*), and brooding (*Seriatopora, Stylophora*) species, had distinct peaks in recruitment during the summer months, as did the *Isopora,* which are exclusively brooding corals and recruited in relatively low abundance (n = 91). Recruitment of *Isopora* was generally low and variable, and appeared to vary across all locations. The highest number of *Isopora* recruits were observed at Hal's Pool (Fig 7, 9).

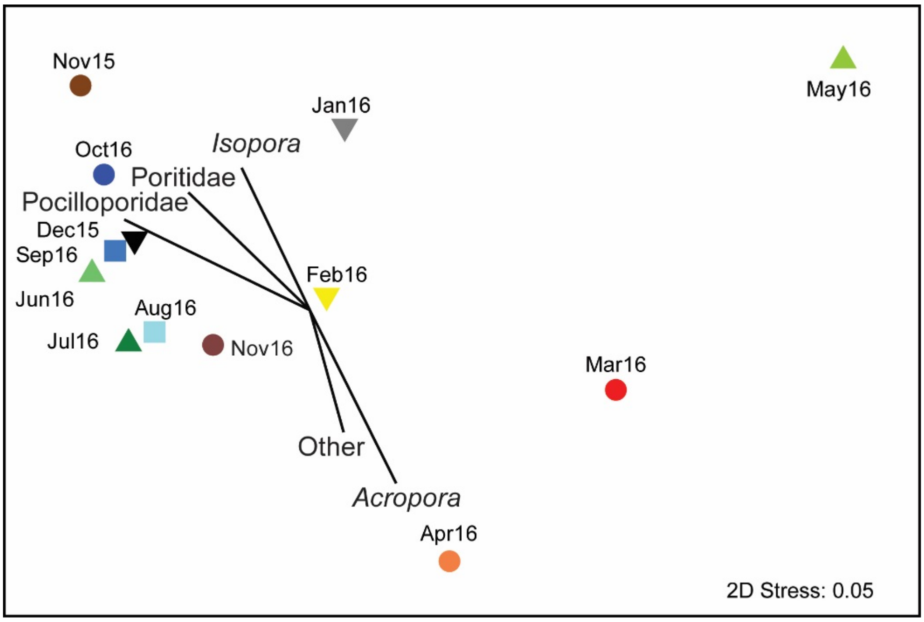

Figure 8. Multivariate plot of variation in the abundance and diversity of coral recruits among months throughout the year. Vectors highlight coral groups that distinguish the variation among months.

When conducting full-subsets analysis of factors influencing recruitment for Poritidae, it was apparent that recruitment was best described by an additive effect of month and location (Figure 9, Table 3). The model best describing recruitment of Pocilloporidae was a complex interaction between month of the year and location, along with additive impacts of location and site (Table 3, Figure 9). Recruitment of *Isopora* colonies was best described by an interaction between month and location, while site is included in the next best model (Figure 9, Table 3).

Based on relative explanatory values of the fixed predictors, month appeared to be the most important factor across all family groups (Figure 10). The number of Pocilloporidae recruits was most well explained by the model fits, and from this location had the largest impact on recruitment, followed by site and then month (Figure 10). For Poritidae, site had the largest impact on recruitment, followed by month and location (Figure 10). Corals grouped as "Other" were most impacted by month, followed by site and then location (Figure 10). *Acropora* recruitment was most impacted by month, followed by location and there was very limited impact of site. Lastly, *Isopora* recruitment was equally impacted by month, location and site, which all had limited impact (Figure 10).

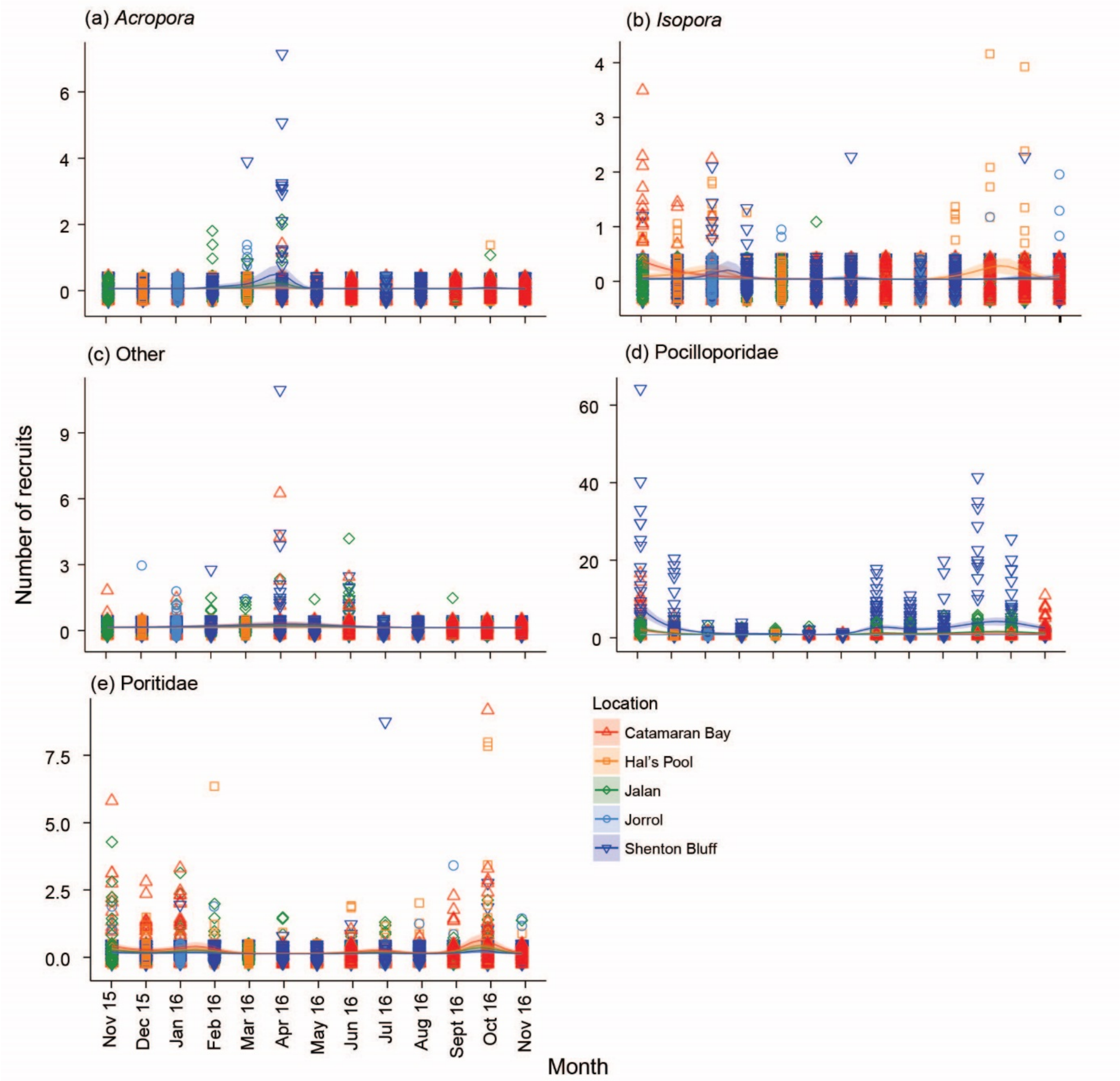

Figure 9. Number of settled recruits of (a) *Acropora*, (b) *Isopora*, (c) Other, (d) Pocilloporidae and, (e) Poritidae during each month at the 5 locations. Raw data (triangles) is presented with modelled relationships (lines) and 95% confidence intervals (ribbons).

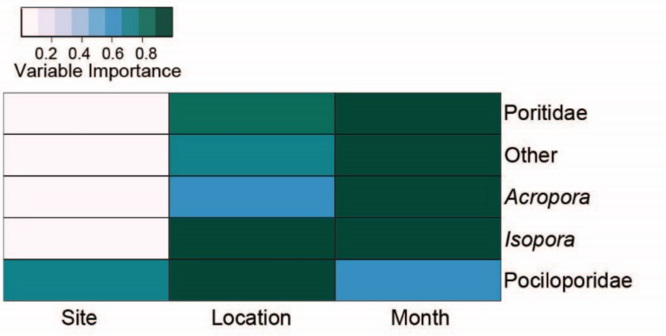

Figure 10. Variable importance of each of the fixed factors included in the models, including Month, Location and Site, with darker colours indicating increased importance of that variable.

Table 3. Top model fits (generalised additive model) for the number of settled recruits for each of the fixed factors, location and month of settlement. Shown are the fitted model, number of parameters (*n*), Akaike information criterion (AICc), δ AICc, model weights, and R^2 values. The model with the fewest parameters within 2 AICc is considered the most parsimonious, and therefore the best model.

Coral group	Model	*n*	AICc	δ AICc	AICc weight	R^2
Acropora	Month + Location	13	3409.31	0	0.64	0.01
	Month	9	3410.70	1.4	0.32	0.01
	Month x Location	19	3415.97	6.7	0.02	0.00
Isopora	Month x Location	23	3382.47	0	0.91	0.02
	Month + Site	27	3400.15	17.7	0.00	0.02
	Month + Location	13	3433.24	50.8	0.00	0.01
Other	Month + Location	11	3464.54	0	0.39	0.01
	Month	7	3467.14	2.6	0.10	0.01
	Month x Location	15	3467.55	3.0	0.08	0.01
Pocilloporidae	Month x Location + Location + Site	44	4972.63	0	0.35	0.23
	Month x Location + Site	44	4972.96	0.3	0.29	0.22
	Month x Location + Location	29	4973.21	0.6	0.26	0.21
Poritidae	Month + Location	15	3644.47	0	0.87	0.01
	Month x Location	21	3648.50	4.0	0.11	0.02
	Month x Location + Location	27	3653.48	9.0	0.01	0.02

3.1.3 Spatial variation in coral recruitment

Coral recruitment varied considerably among the five locations surveyed, and among the coral groups identified. Differences were apparent in both the numbers and families of recruits present on the tiles (Figure 7, 11). Variation among locations (10s km apart) was considerable, while there was comparatively little variation among sites (50-100 m apart, Figure 12). Variation among sites reflected variations in the local conditions (exposure, current speed) at each location, and the reproductive modes of the dominant recruits.

The five study locations differed considerably in the abundance and composition of recruits. Of all the locations, Jorrol had the lowest coral cover, the lowest proportion of hard corals (44%) and second lowest diversity of coral forms (Table 1). Coral recruitment was most unique at Jorrol (Figure 11, 12), having a very low abundance (n = 48), but relatively high diversity and proportional representation of coral groups: Pocilloporidae (27%), Poritidae (29%), Other (21%), *Isopora* (15%) and *Acropora* (8%). Hal's Pool was also distinguished by a low total abundance (n = 107) of coral recruits, but the sites had moderate cover (ranked 4th) and diversity (ranked 3rd) of corals, which composed 65% of the community. Recruitment at Hal's Pool was distinguished by a relatively high proportion of Poritidae (59%) and particularly *Isopora* (38%), and a very low proportion of *Acropora* (1%) and Pocilloporidae (2%).

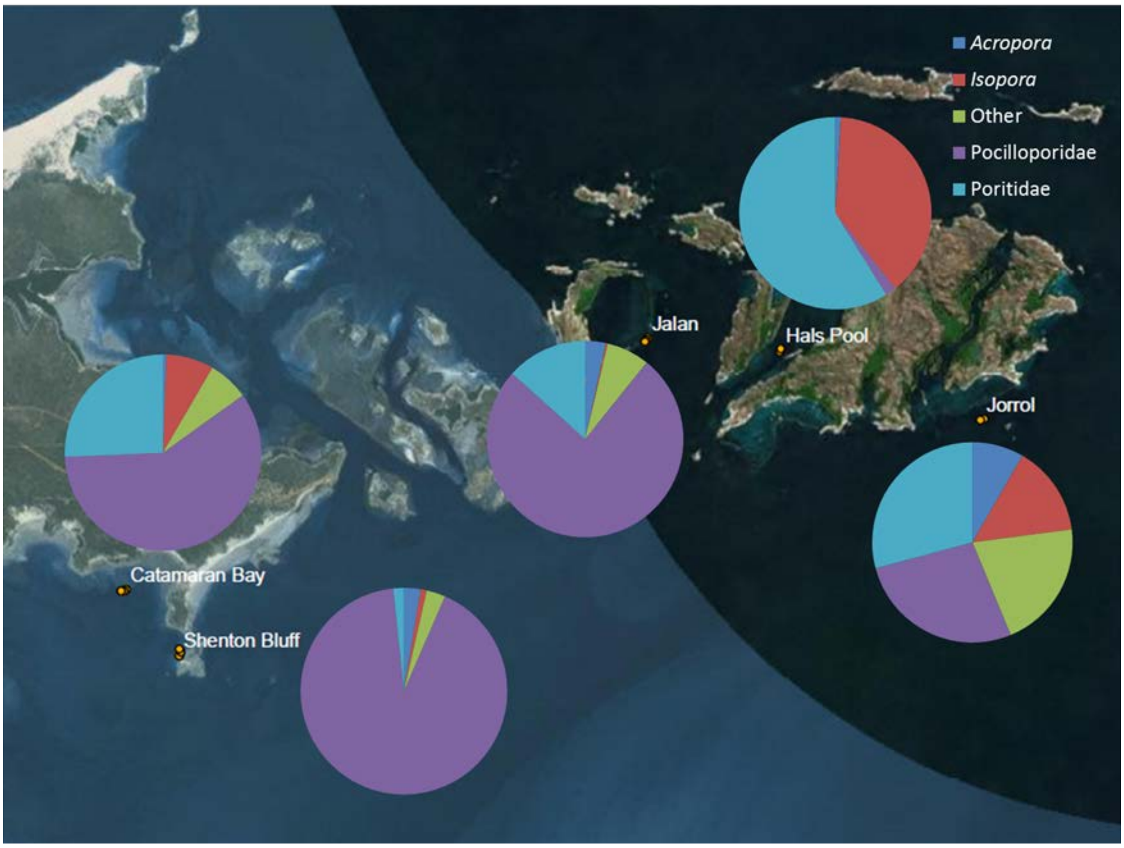

Figure 11. Overall composition of recruits at each location, from November 2015 - November 2016.

The remaining locations had large differences in the total number of recruits, but a similar composition of recruits that was dominated by the Pocilloporidae and with a mix of other coral groups (Figure 10). Shenton Bluff recorded the highest total number of recruits (n = 1458) of all locations, of which the majority were Pocilloporidae (92%). Shenton Bluff also had high coral cover, with a community that was dominated by hard corals (98%). However, the community had relatively low diversity because most of the corals were branching *Acropora*. Despite their dominance, only 2% of the recruits at Shenton Bluff were *Acropora*, and the remaining coral groups (*Isopora*, Poritidae, Other) were also in low abundance (<3%).

Catamaran Bay had a high total number of recruits (n = 358), and the sites had a high cover and diversity of hard corals that dominated (93%) the community. The Pocilloporidae were the most common (58%) group of coral recruits, with the Poritidae (26%) and particularly the *Isopora*, Other and *Acropora* recruits in low or very low abundance (<8%). Jalan also had a high total number of recruits (n = 352), and a high cover and diversity of corals (Table 1); although the abundance of macroalgae at the location in December 2015 and August 2016 resulted in corals composing only 55% the community throughout the year. The Pocilloporidae were again the most common (76%) group of coral recruits, with the Poritidae (13%) and other groups (<7%) in low abundance

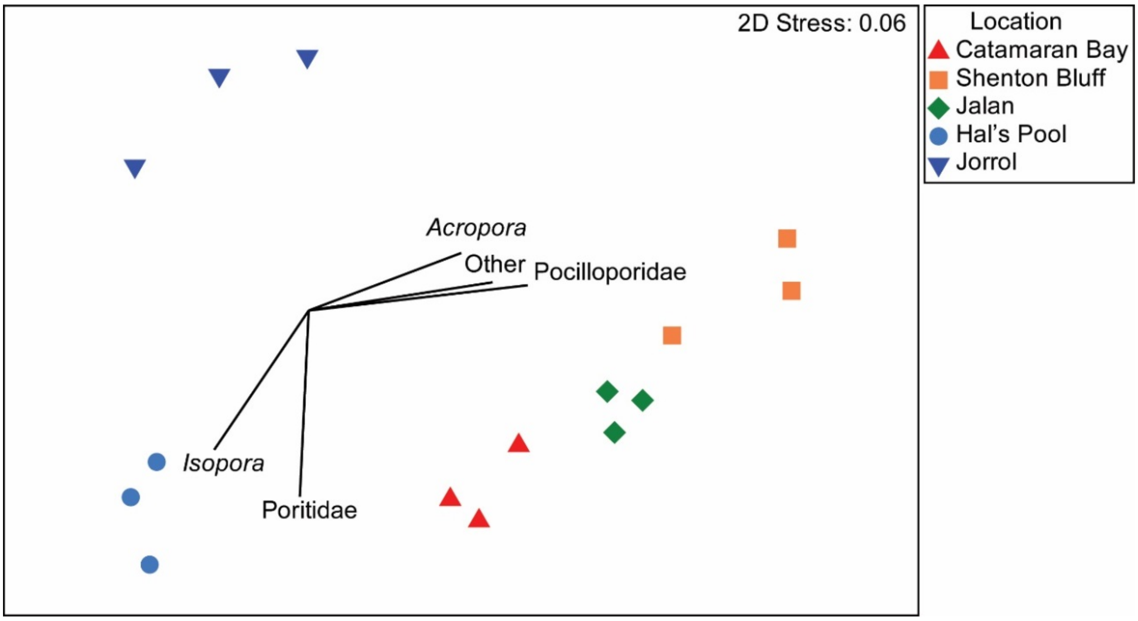

Figure 12. Multivariate plot of variation in the abundance and diversity of coral recruits among locations, and sites (within locations). Vectors highlight coral groups that distinguish the variation among locations and sites.

4 Discussion and Conclusions

Unusually high temperatures in early 2016 resulted in an unprecedented coral bleaching event in the Cygnet Bay area and Sunday Islands group (Fig 5, 6). At our study locations, estimates of bleaching ranged from 19-40% in late March, with higher overall proportions of bleaching recorded later in May (43%, Fig 6). The months March and May were associated with very low total recruit numbers, which coincided with the highest proportion of bleached corals. Recruit numbers in the months following the bleaching were not obviously reduced in comparison to pre-bleaching, possibly because temperature stress through summer had already stressed corals and reduced their reproductive output prior to the mass bleaching. Around half the corals had not bleached and continued to produce recruits over the following months. Whether recruitment rates in the months before and after the mass-bleaching were lower than in the absence of temperature stress remains unknown. Temperature stress and coral bleaching has been shown to reduce reproductive output in corals for up to two years (Michalek-Wagner & Willis 2001) and above (Baird & Marshall 2002). Therefore, it is important to interpret these results in the context of this study occurring during an exceptional year. To establish an understanding of the typical recruitment patterns of the region, sampling during multiple additional years would be necessary, as inter-annual variation in coral recruitment is common (Harriott & Banks 1995, Dunstan & Johnson 1998).

Recruits settling on tiles were most commonly from the family Pocilloporidae, followed by Poritidae. Adults from these families were recorded at all locations surveyed (S. Wilson, unpubl. data), however they were not the most common adult genera (*Acropora* and *Isopora* were observed to be the most common adult genera, Z. Richards, pers. comm.). However, the *Acropora* and *Isopora* are also among the most susceptible to temperature stress and coral bleaching. The extreme temperatures that persisted through summer and autumn most likely caused prolonged stress, injury and mortality to the *Acropora* and *Isopora*, reducing their reproductive output and recruitment for much of the study period.

Acropora recruits (produced by spawning) were present at the times of predicted spawning, in March-April and October-November, although we did not detect a large pulse of *Acropora* recruits, as would be expected from a mass, multi-specific spawning event. As the time of predicted spawning occurred after coral bleaching conditions began, the reproductive output of *Acropora* (and other corals) during this year may have been abnormally low due to temperature stress. However, *Acropora* recruits were present only in these months, plus in February at one location (Fig 7), providing evidence that spawning events do occur at the same times of year as other Western Australian reefs. The absence of *Acropora* recruits in November 2015 suggests that the *Acropora* may have spawned in the previous month, before the beginning of the surveys. Repeating the surveys in additional years would assist with determining whether our observed results were within the normal range, or reduced due to temperature stress.

March and April were clearly differentiated from other months, with *Acropora* numbers driving the difference (Fig 8). Modelling also showed that Month was the most important factor affecting numbers of *Acropora* recruits (Table 3, Fig 9), reflecting the prevalence of synchronous spawning within this coral genus. This suggests that in other years (when coral bleaching does not occur), spawning would likely occur primarily in March-April, and secondarily in October-November. Corals in the 'Other' group were also most abundant in April (Fig 9), and were likely predominantly spawning corals, given that the majority of corals do reproduce by spawning. This aligns with the mass spawning events documented in other Kimberley reefs (Gilmour et al. 2009, Heyward et al. 2010). Further reproductive sampling would be necessary to determine the species and proportion of colonies which participate in either spawning event; we are unable to determine this from our results given that recruits cannot be identified to species level.

The month of May was the most different from other months (Fig 8), with virtually no recruits of any type recorded during this month (Fig 4, 9). This coincided with an increased proportion of bleached corals (quantified by habitat comparison, Fig 5). It is likely that the decreased numbers of recruits in May were a result of temperature stress associated with coral bleaching. Additionally, winter months (June, July, August) were grouped together (Fig 8). There was a trend towards lower recruit numbers during winter in some of the coral groups (Pocilloporidae, *Isopora*), although other groups reproduced during winter. On other WA reefs, there is little evidence of reproductive output and spawning through winter months (Gilmour et al. 2016a).

Pocilloporidae reproduced mainly during the summer months (Fig 7, 9), over several months. The model best describing recruitment of Pocilloporidae was a complex interaction between month of the year and location, along with additive impacts of location and site (Table 3, Fig 9). This pattern of reproduction is similar to that expected for brooding corals, with recruitment affected by local population structure at smaller scales than for brooders, although the family Pocilloporidae contains both brooding (genera *Seriatopora* and *Stylophora*) and spawning corals (genus *Pocillopora*), which could not be separated reliably at this stage of development. All three of these genera were recorded in at least one of the study locations (S. Wilson, unpubl. data), so further reproductive sampling would be required to determine whether the recruitment patterns represent brooding corals releasing larvae monthly, spawning occurring in multiple months, or a combination of brooders and spawners reproducing at different times throughout the year.

Recruits from the family Poritidae were present throughout the year, including during winter (Fig 7, 9). This was reflected by the increased importance of location, compared to *Acropora*, in the best model (Fig 9, 10). Previously, spawning in the *Porites* has only been documented over the summer months in Australia (Kojis & Quinn 1981, Harriott 1983, Stoddart et al. 2012). *Porites* corals are known to spawn in early December in Dampier (Stoddart et al. 2012). However, additional spawning at another time was possible, as colonies were not sampled throughout the year (September-December only), although nearly all Porites colonies (92%) sampled did have mature oocytes prior to the December spawning (Stoddart et al. 2012). Studies on the Great Barrier Reef have also recorded *Porites* spawning in December (Harriott 1983), and in another case spawning occurred over several months during summer (November-April, Kojis and Quinn (1981)). Conversely, our data suggests corals from the family Poritidae reproduce throughout the year in the Cygnet Bay and the Sunday Island group. However, we are not able to differentiate between recruits produced by spawning over multiple months, and those produced from brooded larvae, as recruits could only be identified to the family level.

Most corals in the family Poritidae reproduce by spawning, but there are exceptions which brood larvae (Madin et al. 2016). Of the Poritidae, two species known to be brooding corals, *Porites murrayensis* and *P. stephensoni* (Madin et al. 2016) have recently been identified in the inshore Kimberley (Z. Richards, pers. comm.). This suggests that brooding corals within the family Poritidae may exist around Cygnet Bay and the Sunday Island group, and some of the recruits documented in this study may be a result of brooded larvae. Our results, where recruits from the family Poritidae were found during months when spawning has not been documented, suggest that brooding larvae could be an important means of reproduction in this coral family. Further reproductive sampling would be required to confirm the relative importance of each reproductive mode (brooding larvae vs spawning gametes) within the Poritidae in the inshore Kimberley region.

Isopora recruit numbers were low and variable (Fig 7, 9). Recruits were mainly present in the summer months, and were most common at Hal's Pool (Fig 7, 9). Recruitment of *Isopora* colonies was best described by an interaction between month and location, while site is included in the next best model (Fig 9, Table 3). This is consistent with the classification of *Isopora* as a brooding coral (Fig 9). The factors location, month and site explained only low, but equal, amounts of variance in the model (Fig 10). As a brooding coral, *Isopora* recruits generally travel a relatively short distance (<500m) from the parent colony, which has been recently confirmed in the inshore Kimberley (Berry et al. 2016). For brooding corals like the *Isopora*, variation at smaller spatial scales is often expected to be more important than for spawning corals, as seen in our results, although the amounts of variance explained by the model were low.

In conclusion, these results demonstrate the variation in larval supply among months, coral groups and at various spatial scales (from 10s of kilometres to 50-100 metres). Assessing coral recruitment with extended monthly sampling over more than a year-long period confirmed predicted patterns of recruitment for spawning corals (March-April and, to a lesser extent, October-November spawning periods, as for other Western Australian reefs), and revealed that coral recruits from some groups were settling during more months than expected (Poritidae during the winter months). Temperature stress associated with a coral bleaching event during the year likely affected the numbers of recruits occurring in some months, particularly during the predicted spawning period in March-April, and also in May, so sampling in additional years would likely yield different results.

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Key Ecological Processes in Kimberley Benthic Communities: Herbivory

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WAMSI Kimberley Marine Research Program

Final Report

Subproject 1.1.2c

October 2017

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WAMSI Kimberley Marine Research Program

Initiated with the support of the State Government as part of the Kimberley Science and Conservation Strategy, the Kimberley Marine Research Program is co-invested by the WAMSI partners to provide regional understanding and baseline knowledge about the Kimberley marine environment. The program has been created in response to the extraordinary, unspoilt wilderness value of the Kimberley and increasing pressure for development in this region. The purpose is to provide science based information to support decision making in relation to the Kimberley marine park network, other conservation activities and future development proposals.

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Front cover images (L-R)

Image 1: Satellite image of the Kimberley coastline (Image: Landgate)

Image 2: Bite marks on seagrass from the herbivorous golden-lined rabbitfish *Siganus lineatus* (Image: Matt Vanderklift)

Image 3: Humpback whale breaching (Image: Pam Osborn)

Image 4: Bardi Jawi Ranger measuring seagrass growth (Image: Mat Vanderklift)

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Structure of Report: This final report for WAMSI 1.1.2 *Ecological processes in Kimberley benthic communities: recruitment and herbivory* is structured and presented as three independent chapters for the following subprojects; a) Fish recruitment, b) Coral recruitment, and c) Herbivory.

Metadata link for AIMS fish and coral recruitment sub-projects:
http://data.aims.gov.au/metadataviewer/faces/view.xhtml?uuid=05f33378-b7df-433f-8019-16e9c7eb8620
http://catalogue.aodn.org.au/geonetwork/srv/eng/metadata.show?uuid=05f33378-b7df-433f-8019-16e9c7eb8620

Metadata link for CSIRO herbivory sub-project: -
http://marlin.csiro.au/geonetwork/srv/eng/search#!8d910bf0-2f4e-4fc2-8a6e-f0447ed2d996

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Contents

Executive Summary

The main aim of this research was to understand the relative importance of direct consumption of seagrass as a proportion of total seagrass production in the Kimberley, to identify the main species of herbivores, and to understand the relative importance of different primary producers to the diet of selected key species of herbivores. Although primary producers occupy a wide variety of habitats, the primary focus of this study was the seagrass meadows of Tallon Island (Jalan) and Sunday Island (Iwany) located in the Bardi Jawi Indigenous Protected Area. The research used data collected, and extended research conducted, as part of WAMSI Kimberley Marine Research Program (KMRP) Project 2.2.4 (Benthic primary productivity).

We measured higher rates of grazing on seagrass than anywhere else in the world — in some places during some surveys the rates of consumption were more than ten times the rates of growth. This was particularly pronounced for the seagrass *Thalassia hemprichii* (otherwise known as turtlegrass), for which average consumption across the study was higher than growth. *Thalassia* is one of the most abundant seagrasses in the terraced lagoons that are characteristic of the Kimberley, and the apparent contradiction of high abundance and high consumption is probably reconciled by a combination of fast growth rates and patchy grazing; indeed rates of consumption of *Thalassia* varied by two orders of magnitude among sites and surveys.

In contrast, consumption of the seagrass *Enhalus acoroides* was on average lower than growth. An inference from this finding is that much of its production is probably not consumed by herbivores. We did not set out to study the fate of seagrass production, but it is likely that much leaf biomass is ultimately exported from the meadows as detritus.

There were several species of herbivores that were abundant in the seagrass meadows, but the golden-lined rabbitfish *Siganus lineatus* was ubiquitous and abundant in all Remote Underwater Video (RUV) deployments. Stable isotope and gut-content analyses confirmed that the diet of *S. lineatus* is primarily comprised of seagrass, especially *Thalassia*. *S. lineatus* is a highly valued food source for the Bardi Jawi people, who call them *barrbal*.

Another potentially significant herbivore is the green turtle *Chelonia mydas*. Green turtles were seen during RUV deployments, but were not abundant. However, boat-based observations during the rising tide found that they were abundant in some areas. Stable isotope and gut-content analyses showed that *C. mydas* consumed a variety of plants, but brown algae and the seagrass *Thalassia* were particularly prominent in their diet. There was some, albeit equivocal, evidence that different individuals might have preference for either brown algae or seagrass. Satellite tags showed that they frequently tended to spend their time in places with abundant seagrass.

1 Introduction

Herbivory is a key ecological process that sustains and underpins food webs, and can regulate the biomass of primary producers in an ecosystem. It has long been hypothesized that rates of herbivory are greatest in the tropics, although strong evidence to support this is limited. Nevertheless, one of the ecosystems in which rates of herbivory are typically high is tropical corals reefs (Poore et al. 2012; Hyndes et al. 2016). Tropical seagrasses might also once have hosted particularly high rates of herbivory, but in many parts of the world populations of large herbivores have been reduced, and so herbivory on tropical seagrasses may be lower than it once was (Heck and Valentine 2006). Contemporary rates of herbivory on seagrasses are not typically high (Poore et al. 2012).

Parts of the Kimberley host extensive stands of seagrasses and macroalgae, and research has recently revealed that their rates of productivity are exceptionally high (Kendrick et al. 2017). In addition, compared to many other tropical regions, the Kimberley has experienced relatively low rates of harvest of marine fauna, raising the possibility that rates of herbivory might be higher than those found elsewhere. Indeed, initial research within the WAMSI Kimberley Marine Research Program (KMRP) indicated that consumption of seagrass, although patchy, was generally quite high, especially on the seagrass *Thalassia hemprichii* (Kendrick et al. 2017). However, the identity of the main herbivores, and the importance of seagrasses, macroalgae and other potential food sources to their diet were not resolved by that study.

A key initial step in understanding herbivory is to identify the main species of herbivores, and characterise their diet. This study aimed to provide initial information addressing these knowledge gaps. Because resources were limited, most effort was focused on addressing the knowledge gaps for the seagrass-dominated ecosystems within the region.

2 Materials and Methods

The research on herbivory was focused on the islands and coast of the Bardi Jawi Indigenous Protected Area (IPA), encompassing Jalan (Tallon Island) and Iwany (Sunday Island), where there are two sampling locations (Laanyi and Ngaloon) in the West Kimberley of Western Australia (16.4°S, 123.2°E). We conducted four surveys from October 2014 to April 2016 (Figure 1).

At these locations the following measurements or collections were made (not all measurements were made during each survey):

1. Remote underwater video to identify the species of herbivores present, with particular focus on the species present in seagrass habitats.
2. Rates of herbivory on seagrass. These data are presented in the report for WAMSI KMRP Project 2.2.4, here the focus is on assessing rates of herbivory as a proportion of primary production;
3. Collections of golden-lined rabbitfish (*Siganus lineatus*) for stomach content and stable isotope analyses;
4. Blood samples from green turtles (*Chelonia mydas*) for stable isotope analyses; and
5. Satellite telemetry of green turtles to test whether individuals spent a large proportion of time in seagrass habitat.

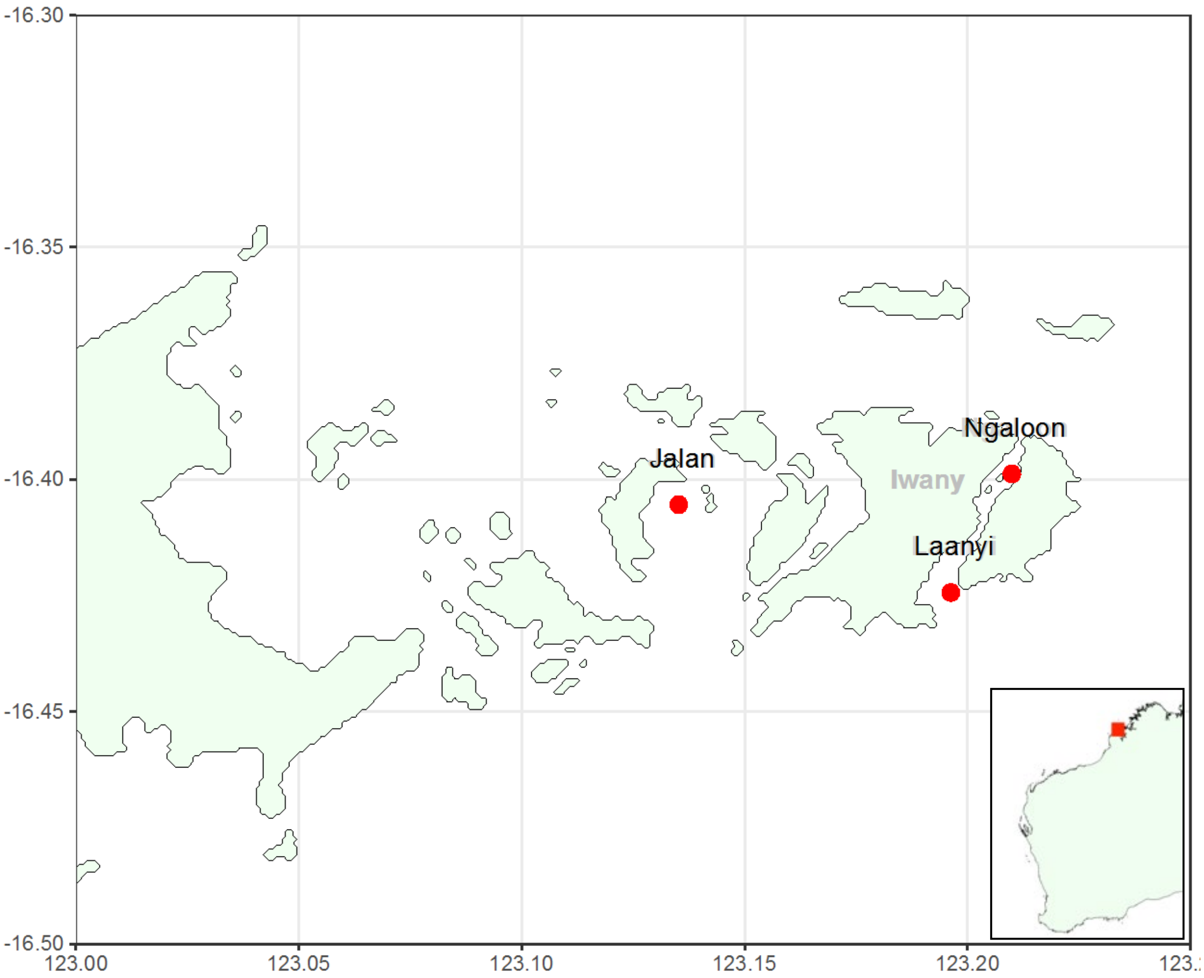

Figure 1: Locations where herbivory measurements and rabbitfish collections were made during this study. The locations Ngaloon and Laanyi are on Sunday Island (iwany, noted in grey font).

2.1 Remote Underwater Video (RUV)

Data from stereo-RUV deployments described earlier in Section 2.2 (Sampling design and methods) were used to identify the main consumers of seagrass or macroalgae present in each of the five main Kimberley habitats (macroalgal beds, coral reefs, mangrove, intertidal rockpools and seagrass meadows). Briefly, five stereo-RUV units (comprising two GoPro Hero 3+ video cameras in waterproof housings mounted on a custom-made aluminium base bar) were deployed in each habitat during daylight hours. Each unit was separated by a distance of 50 m and left to record for 20 minutes. Note that while data used in section 2 was for juvenile fishes only, data presented here includes all fishes recorded by stereo-RUVs regardless of their life stage (i.e. juveniles and adults).

Species were identified by three experienced observers using expert knowledge aided by published fish guides wherever necessary. The relative abundance was then calculated as the MaxN of these species in each habitat (i.e. the maximum number of individuals per species seen in a single video frame) and averaged across all deployments. Herbivorous pomacentrids (damselfishes) were not included because they do not typically consume large erect algae or seagrass.

Additional RUV deployments were done in seagrass meadows at Jalan and Ngaloon during April 2015 (two of the sites included in measurements of rates of herbivory) to quantify variation in the composition and relative abundance of potential herbivores, as well as quantify bite rates by fish. These deployments used different systems than those described above for estimating abundance of herbivorous fishes, and comprised single GoPro Hero 4 Silver cameras in waterproof housings. On each of three days, ten units were deployed in meadows of each of the two main species of seagrass, *Thalassia hemprichii* and *Enhalus acoroides*. Each camera filmed for 3-4 hours during each deployment. Cameras were placed on steel camera frames; each held two cameras facing in opposite directions. Individual frames were separated by at least 25 m. In the laboratory, 34 minutes from each camera during each deployment were analysed using EventMeasure software (SeaGIS Pty Ltd). The observer recorded the MaxN for each fish species, as well as the total number of bites on the seagrass canopy made by each species of fish. The mean MaxN for each species was calculated for each camera.

2.2 Rates of herbivory

Net rates of herbivory (as a percentage of growth) were calculated from data collected during the companion WAMSI KMRP Project 2.2.4 (Kendrick et al. 2017). Rates of growth of the seagrasses *Thalassia hemprichii* and *Enhalus acoroides* were calculated as mm^2 per shoot per day from surveys in which growth was measured using a standard hole-punch method described in Kendrick et al. 2017. Rates of consumption were calculated as mm^2 per shoot per day from tethering experiments. Rates of consumption of *T. hemprichii* and *E. acoroides* were measured through simple tethering experiments. Shoots of each species were collected, the leaves were cut with scissors at the base above the leaf sheath, and leaves were separated and placed between two sheets of acrylic glass (the top sheet clear and the bottom sheet white), then photographed. Intact (ungrazed and uneroded leaves) were preferred; partially grazed or eroded leaves were discarded. If no intact leaves could be found, they were trimmed with scissors. Leaves were then rebundled and attached to a short piece of sisal rope with clothes pegs. Three shoots from a single species were attached to each piece of rope, which was then placed in a meadow of the matching species (i.e. *Thalassia* was placed in *Thalassia* meadows, *Enhalus* was placed in *Enhalus* meadows). The pieces of rope were firmly secured by inserting tent pegs through each end of the rope into the substrate. After approximately 24 h leaves were collected and photographed. This process was repeated on two separate days during three different surveys (October 2014, April 2015, November 2015) at three different sites: Jalan (Tallon Island: 16.405°S, 123.135°E), Laanyi (16.424°S, 123.196°E) and Ngaloon (16.398°S, 123.209°E) (both on Sunday Island). Fifteen shoots of each species were deployed on each day (n = 270 shoots per species).

Net herbivory was calculated as consumption/growth × 100. Standard errors were calculated from the appropriate methods for error propagation for multiplication.

2.3 Rabbitfish collections

Golden-lined rabbitfish (*S. lineatus*) were collected by spear in October 2014 and April 2015. Ten individuals were collected from Jalan, Laanyi and Ngaloon in each survey (n=60). Individuals were weighed (wet weight, in grams) and measured (total length, in mm), and a small piece of dorsal muscle excised by scalpel for stable isotope analysis. The stomach was removed from individuals taken in October 2014 (n=30). Samples were frozen (-20°C) and transported to the CSIRO Floreat laboratories (Perth, Western Australia).

2.4 Green turtles

Green turtles (*C. mydas*) were captured during two surveys: April 2015 (n=32) and April 2016 (n=30). Turtles were captured using the "rodeo" method, in which individuals are captured in the water by an experienced person jumping from a boat. After capture, each individual turtle was weighed and measured (curved carapace length, in mm). Blood was extracted from a vein in the neck using a 22G x 1.5 inch needle, and immediately frozen (-20°C) and transported to the CSIRO Floreat laboratories (Perth, Western Australia) for stable isotope analyses (described below).

Stomachs of five individual green turtles were donated by Bardi Jawi hunters in early 2016 for stomach content analyses.

2.5 Stomach content analyses

After thawing, the stomachs of rabbitfish (*S. lineatus*) were separated from the rest of the digestive tracts and rinsed with distilled water. The entire stomach was used. For green turtles (*C. mydas*) a randomly-selected subsample of approximately 50 ml was taken from each stomach, because the total amount of material was too great. For both rabbitfish and turtles, the stomach contents were spread in a 13 cm diameter glass dish with filtered water set over a sheet with 60 randomly-positioned dots. Stomach contents were viewed through a magnifying lamp and food items covering each dot recorded to the highest taxonomic level.

Permutational multivariate analysis of variance (PERMANOVA) was used to test whether there were differences in the composition of stomach contents of *S. lineatus* among sites. The stomach content data contained numerous zeros, so tests were based on Bray-Curtis dissimilarities calculated using untransformed data. Analyses were conducted using the vegan package in R.

2.6 Stable isotope analyses

Data for potential diet sources (seagrasses, macroalgae, mangroves) were collected as part of a companion study (WAMSI KMRP Project 2.2.4), and the methods for collection of those data are described in Kendrick et al. 2017. Briefly, seagrass leaves, macroalgae thalli and mangrove leaves were collected by hand, frozen (-20°C) and transported to the CSIRO Floreat laboratories, where they were later thawed, cleaned, dried in an oven at 60°C, and ground into a fine powder using a mixer mill (Retsch MM200, Dusseldorf, Germany). Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) were measured at the West Australian Biogeochemistry Centre and are expressed in ‰ using conventional delta (δ) notation δX (‰) = $[(R_{sample} / R_{standard})-1] \times 1000$; where X is ^{13}C or ^{15}N, and R is the $^{15}N/^{14}N$ (nitrogen) or $^{13}C/^{12}C$ (carbon) ratio in the sample and standards (Vienna PDB equivalent for carbon and the IAEA international standard of atmospheric N_2 for nitrogen).

Rabbitfish muscle tissue was thawed, cleaned, dried in an oven at 60°C, and ground into a fine powder using a mixer mill (Retsch MM200, Dusseldorf, Germany). Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) were measured at the West Australian Biogeochemistry Centre using a continuous-flow system consisting of a Delta V Plus mass spectrometer connected with a Thermo Flush elemental analyser. Stable nitrogen and carbon isotope compositions are reported in the standard *δ*-notation (e.g. Skrzypek 2013) after multi-point normalization of raw isotope data to isotope international reference scale (VPDB for carbon and atmospheric N_2 for nitrogen) using international standards provided by International Atomic Energy Agency ($\delta^{13}C$ - NBS22, USGS24, NBS19, LSVEC; $\delta^{15}N$ - N1, N2, USGS32) and laboratory standards (Skrzypek 2013). The uncertainty associated with stable isotope analyses (one standard deviation) was not more than 0.10‰.

Mixed-effects ANOVA was used to test if patterns in $\delta^{13}C$ and $\delta^{15}N$ of *S. lineatus* muscle varied among sites (three levels, random) or surveys (two levels, fixed). ANOVA was also used to test whether $\delta^{13}C$ and $\delta^{15}N$ of *C. mydas* blood varied among years.

Overall patterns of $\delta^{13}C$ and $\delta^{15}N$ among species were visualized through biplots.

Further analyses were performed using a Bayesian Isotope Mixing Model with prior information on the dietary proportions gained from the gut content analyses. Analyses were done using the SIAR (Stable Isotope Analysis with R) package (Parnell et al. 2010). $\delta^{13}C$ and $\delta^{15}N$ of seagrass and macroalgae were taken using the data collected in the companion study (WAMSI KMRP Project 2.2.4), and the isotopic signatures for diazotrophic cyanobacteria were taken from the literature (Capper et al. 2006). Mixing models were run with carbon and nitrogen enrichment factors of 0.7 ± 0.42 ‰ and 3.35 ± 2.33 ‰ respectively.

For turtles, the main seagrass observed in stomachs was *Thalassia hemprichii*, so this was the only seagrass species retained in models. A variety of macroalgae were observed, but most had very similar

$\delta^{13}C$ and $\delta^{15}N$ and so a single group of macroalgae was modeled. *Turbinaria* typically had lower $\delta^{13}C$, but were not included in models because they were very infrequent in turtle stomachs (<1%). There was evidence of a bimodal distribution in turtle $\delta^{13}C$, so separate models were run for turtles that yielded red blood cell $\delta^{13}C$ greater and less than -14‰.

2.7 Movement of green turtles

Ten green turtles were tagged with satellite tags: four in April 2015, and six in April 2016. SPLASH10-F-296A and SPLASH10-F-296C Wildlife Computer Argos transmitter with Fastloc® GPS, temperature and depth recorders were used. Tags were programmed to transmit 254 times per day with position estimates having priority over depth and temperature.

Satellite tags were attached to the first two vertebral scutes immediately posterior to the nuchal scute using a two-part epoxy resin (Sika AnchorFix®-3+, Sika Australia Pty Ltd). Prior to attachment, a paint scraper was used to remove any flaking scute material. This was followed by gently sanding the area with wet and dry sandpaper. The area was then wiped with 100% ethanol and allowed to dry before attaching the tag. Once the epoxy resin had set, the tag was coated with antifoul paint (International Ultra high strength hard antifouling paint) and allowed to dry overnight. Tagged animals were released close to their capture site either on the same day, or the day after, capture.

The satellite fixes were plotted to enable visual estimation of long distance movements and home range estimates (50 and 95% kernel utilization distribution: KUD) were calculated using the adhabitateHR package in R.

KUDs were calculated for all satellite-tagged turtles using raw (unfiltered) GPS data (Fastloc). These data were downloaded from the Wildlife Computers Portal. To reduce the influence of position accuracy on KUD estimates, only Fastloc data were used in the analysis. Argos locations typically have an accuracy of several hundred metres to several kilometres (Hays et al. 2001; Teo et al. 2004; Witt et al. 2010). The accuracy of Fastloc-GPS locations is significantly better with positions calculated using 4 satellites within 724 m of true position and when 6 or more satellites detect the tag, accuracy is within 70 m of the true location in 95 % of calculations (Dujon et al. 2014).

The KUD is a probability density function that quantifies an individual’s relative use of space (Kernohan et al. 2001). It depicts the probability of an animal occurring at a location within its home range as a function of relocation points (data obtained from satellite tag detections) (White and Garrot 1990).

The 50 and 95% KUD’s were plotted on maps of modelled seagrass distribution produced from spectral classification of Landsat imagery taken in September 2014 as part of a companion project (WAMSI KMRP Project 1.2.5). Seagrass coverage was modelled using a Bayesian likelihood model using spectral classification of Landsat imagery taken in 2014 (see Bayliss and Wilcox 2016). This seagrass map has a significant uncertain spectral class of “possible seagrass” throughout that requires extensive field validation; hence our ability to classify the importance of seagrass is preliminary. Field-based observations of seagrass suggest that while the modelled seagrass distribution accurately reflects large seagrass beds, the ability to incorporate sparse seagrass and seagrass in deep water is limited. Furthermore, green turtle diet is not restricted to seagrass with animals also feeding on a variety of benthic algae.

3 Results

3.1 Remote Underwater Video (RUV)

The main species of herbivorous fish (Appendix 2) varied among habitats (Figure 2). In coral- and algae-dominated habitats, the highest MaxN were yielded by the surgeonfish *Acanthurus grammoptilus*, while in seagrass meadows the highest MaxN were yielded by the golden-lined rabbitfish *Siganus lineatus*. MaxN of all herbivorous species tended to be low in mangrove and rockpool habitats.

The results from the comparisons among habitats were broadly reflected in the comparison of two of the seagrass-dominated sites used for the measurements of herbivory during April 2015 (Figure 3, note that the numbers differ from Figure 2 because the locations were different). The golden-lined rabbitfish *S. lineatus* was abundant at both sites; the surgeonfish *A. grammoptilus* was abundant only at Ngaloon. Observations of potential bite rates recorded from the same set of videos revealed idiosyncratic patterns that varied between the two sites, and between meadows of the two most dominant species of seagrasses (*T. hemprichii* and *E. acoroides*) (Figure 4). *A. grammoptilus* was recorded frequently biting at *Thalassia* at Ngaloon, while *S. lineatus* was recorded most frequently biting at *Enhalus* at Jalan. The damselfish *Dischistodus darwiniensis* was frequently recorded biting at *Thalassia* at Jalan. Note that observations of bites do not necessarily allow inference of herbivory on seagrass, because individuals could be selectively biting at epiphytic algae growing on the seagrass blades.

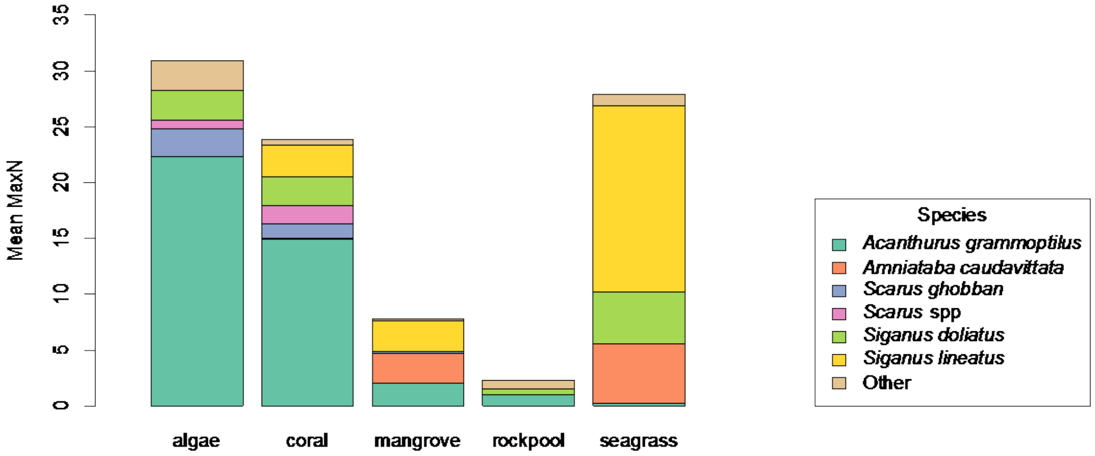

Figure 2: Mean MaxN of the most abundant species of herbivorous fish observed in five distinct habitats in the Bardi Jawi IPA. The "Other" category includes the pooled means of all other observed species of herbivores: pooling MaxN in this way does not have any ecological meaning, but is shown simply to illustrate patterns.

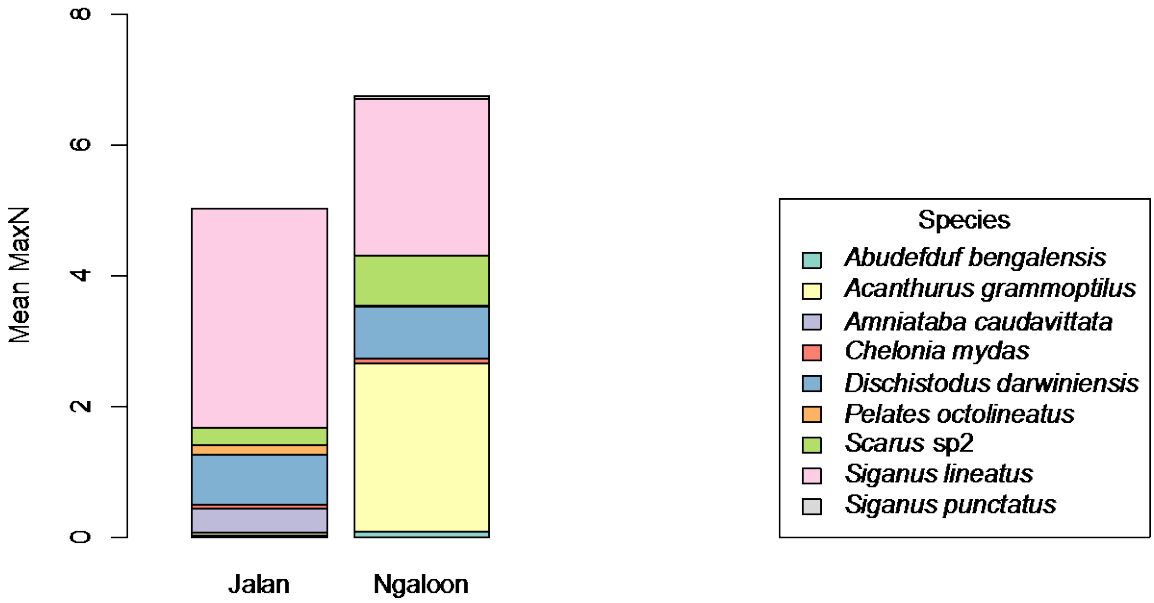

Figure 3: Mean MaxN of the most abundant species of herbivorous fish (plus the green sea turtle *Chelonia mydas*) observed in two of the seagrass meadows in the Bardi Jawi IPA. Data were obtained from RUV deployments during April 2015.

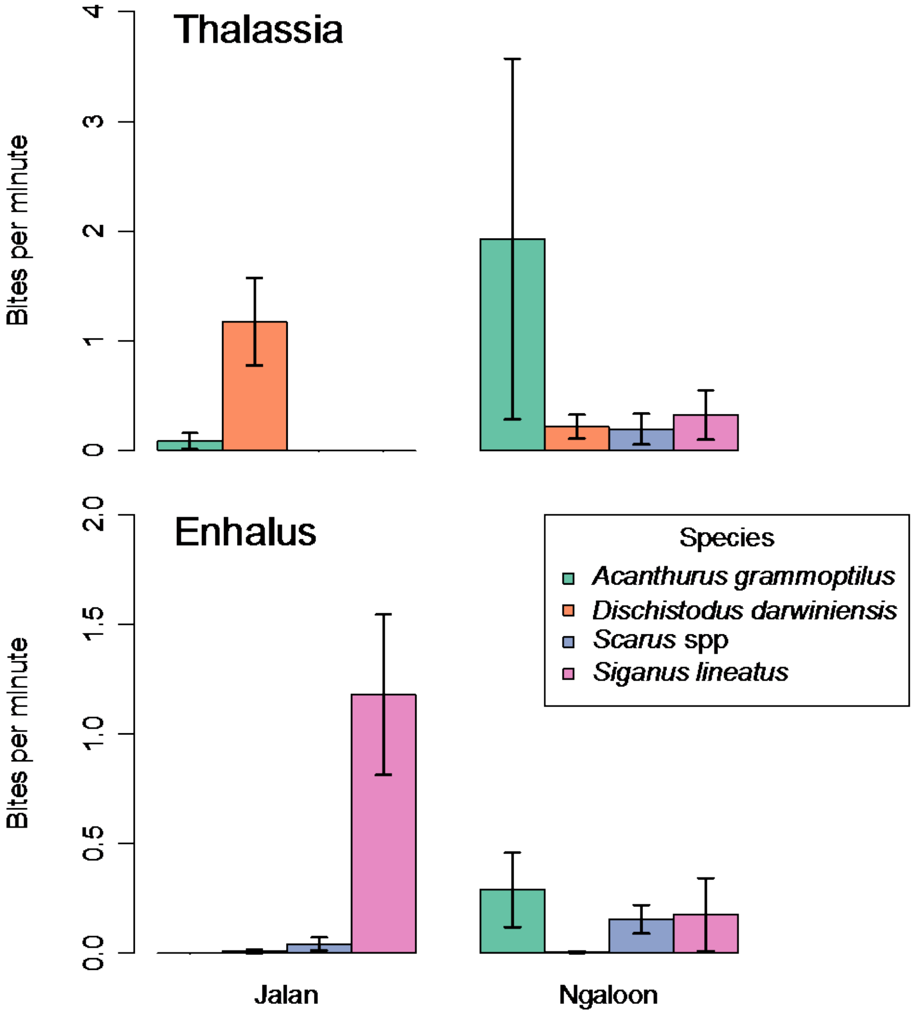

Figure 4: Mean bites per minute (±SE) of herbivorous fish recorded from RUV deployments at two sites (Jalan, Ngaloon) in April 2015 (n=24 at Jalan, n=32 at Ngaloon).

3.2 Rates of herbivory

Net rates of herbivory (as a proportion of daily production) were highly variable, ranging from 38-1433% for *Thalassia* and 0-572% for *Enhalus* (Figure 5). The mean net consumption of *Thalassia* was 401%, and the mean net consumption of *Enhalus* was 166%, indicating that on average rates of consumption exceeded growth.

Thalassia was consumed during each deployment at each location, and on five deployments the rates of consumption exceeded the rates of growth (55% of deployments). Rates of consumption were an order of magnitude higher than rates of growth (>1000%) at Ngaloon during two deployments. *Enhalus* was not consumed at all during four deployments, and was consumed at rates exceeding those of growth on four deployments.

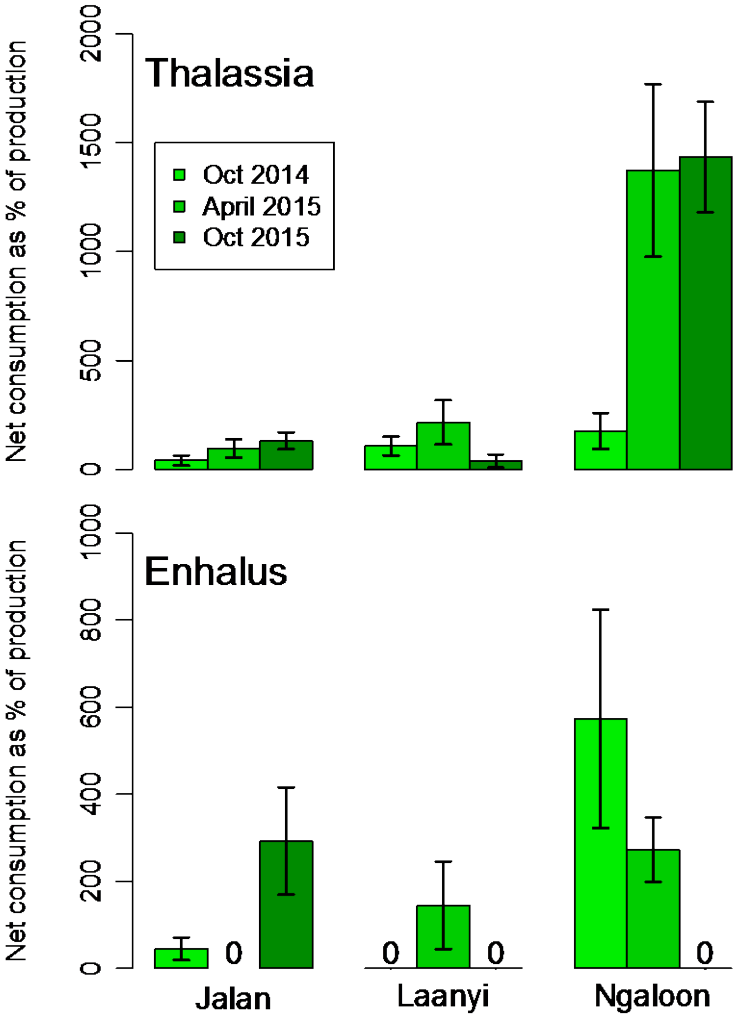

Figure 5: Net rates of herbivory (±SE) as a percentage of daily growth for *Thalassia* and *Enhalus* at three sites during three surveys. 0 indicates that there was no consumption of seagrass recorded on tethered seagrass during that deployment.

3.3 Diet of green turtles

Of the five individual green turtles (*C. mydas*) for which stomach contents were quantified, three were dominated by the seagrass *T. hemprichii* (80-100%: Figure 6). The stomach of the other two individuals contained exclusively macroalgae of various kinds. No animal matter was recorded in the stomach of any of the five individuals.

$\delta^{13}C$ and $\delta^{15}N$ of *C. mydas* blood did not differ between 2015 and 2016 (P>0.2 in each case), so data for all subsequent analyses were pooled. $\delta^{13}C$ spanned a wide range (-20.61‰ to -7.97‰), but the range in $\delta^{15}N$ was smaller (4.24‰ to 8.93‰) (Figure 7). $\delta^{13}C$ exhibited a bimodal distribution, with a breakpoint around -14‰. Separate mixing models were performed for two groups of turtles: those with blood $\delta^{13}C$ greater than -14‰, and those with blood $\delta^{13}C$ less than -14‰. Results from the two analyses were slightly different, but seagrass was indicated to be likely the main diet source for both groups. 95% confidence intervals for macroalgae were 0-56% for individuals with $\delta^{13}C$ less than -14‰, and 1-40% for individuals with $\delta^{13}C$ greater than -14‰. 95% confidence intervals for seagrass were 44-100% for individuals with $\delta^{13}C$ less than -14‰, and 60-99% for individuals with $\delta^{13}C$ greater than -14‰ (Figure 8).

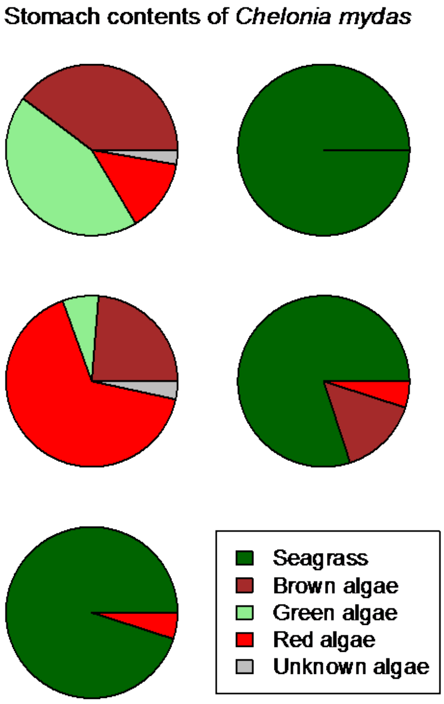

Figure 6: Stomach contents of five individual *C. mydas* captured by Bardi Jawi hunters. Each pie chart shows the stomach contents of a single individual.

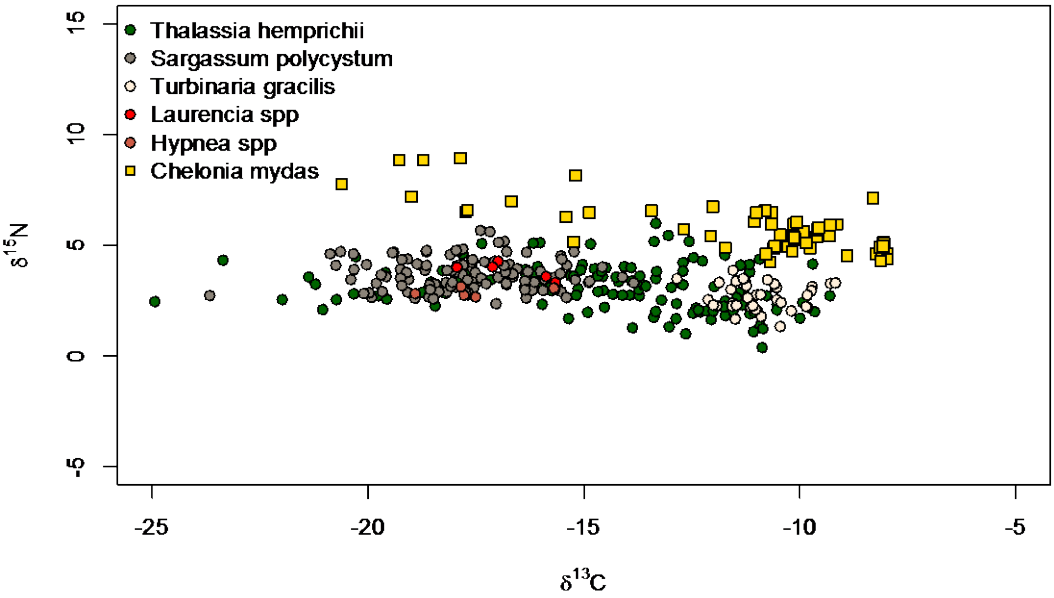

Figure 7: Individual measurements of $\delta^{13}C$ and $\delta^{15}N$ of *C. mydas* blood and benthic primary producers likely to be consumed by *C. mydas.* All data were collected from within the Bardi Jawi IPA.

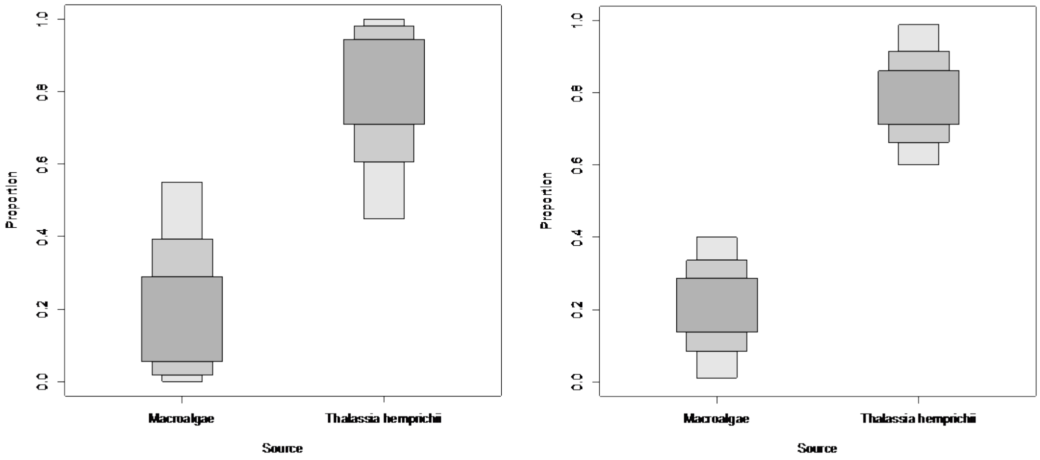

Figure 8: Boxplots showing likely proportions of macroalgae and seagrass (*T. hemprichii*) consumed by *C. mydas*. Individuals were separated into two groups based on δ^{13}C of blood, those with δ^{13}C below -14‰ (left, n=42) and above -14‰ (right, n=12) as described in the text. Plots show the 50%, 75%, and 95% probabilities for each potential food source.

3.4 Diet of the golden-lined rabbitfish

The stomach contents of golden-lined rabbitfish *S. lineatus* varied significantly among sites (F = 3.07, p = 0.026). At all sites seagrass (primarily *T. hemprichii*) comprised the bulk of the stomach contents (Table 1, Figure 9). At Jalan a large proportion of bluegreen algae was also found in the stomachs, while at Laanyi and Ngaloon proportionally more red algae was observed.

The δ^{15}N, but not δ^{13}C, of *S. lineatus* muscle varied significantly among sites (Table 2). δ^{15}N was lower in April 2015 (7.15‰ ± 0.19) than October 2014 (8.24‰ ± 0.13), but the difference was not statistically significant (Table 2). Subsequent analyses considered *S. lineatus* collected at different sites separately. δ^{13}C of *S. lineatus* spanned a narrower range than that of *C. mydas* (-18.89‰ to -9.22‰), and the range in δ^{15}N was relatively low (5.41‰ to 9.20‰) (Figure 10).

Mixing models indicated that the diet of *S. lineatus* at all sites was likely dominated by seagrass (Figure 11), and the ranges of plausible contributions at all sites were similar (5-95% percentiles: 60-89% at Jalan, 55-90% at Ngaloon, 58-90% at Laanyi). Macroalgae was the likely next most consumed at all sites, while the likely contributions of cyanobacteria were relatively low.

Table 1: The relative abundance (as %) of foods observed in the stomachs of *Siganus lineatus*. Data are mean relative abundance (out of a maximum possible value of 60 dots), ± standard errors, n=10 in each case.

Site	Seagrass	Mangrove root	Red algae	Brown algae	Green algae	Bluegreen algae	Other
Jalan	39.6 ± 6.4	0.3 ± 0.2	3.2± 2.6	0.2 ± 0.2	0.8 ± 6.8	15.4 ± 6.8	0.5 ± 0.5
Laanyi	39.9 ± 4.2	0.0	14.1 ± 3.5	0.2 ± 0.2	0.0	5.8 ± 3.9	0.0
Ngaloon	48.5 ± 2.1	0.0	10.1 ± 2.3	0.2 ± 0.2	0.0	0.0	1.2 ± 1.0

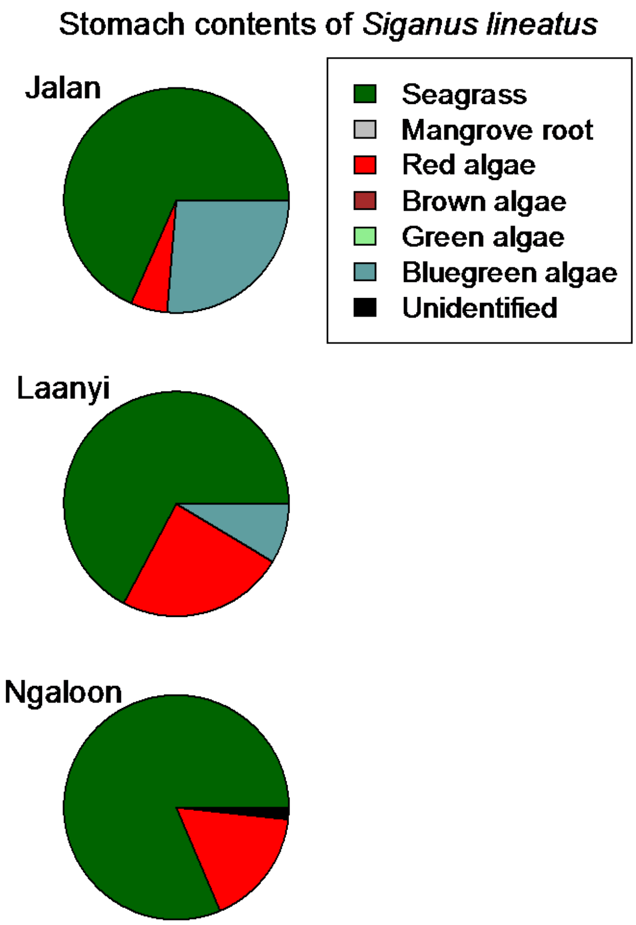

Figure 9: Stomach contents of *S. lineatus*. Each pie chart shows the mean values for each site (10 individuals per site).

Table 2: Results of analyses of variances testing for patterns in the stable isotope compositions ($\delta^{13}C$ and $\delta^{15}N$) of dorsal muscle of the rabbitfish *S. lineatus*.

	$\delta^{13}C$ [‰ VPDB]						$\delta^{15}N$ [‰ AIR]				
Source	**df**	**SS**	**MS**	**F**	**p**		**df**	**SS**	**MS**	**F**	**p**
Location [L]	2	4.55	2.27	0.71	0.493		2	6.06	3.03	4.77	**0.012**
Survey year/season?? [S]	1	1.70	1.70	5.15	0.162		1	17.00	16.99	13.33	0.070
L × S	2	0.33	0.16	0.05	0.949		2	2.55	1.27	2.01	0.143
Residual	53	168.13	3.17				53	33.65	0.63		

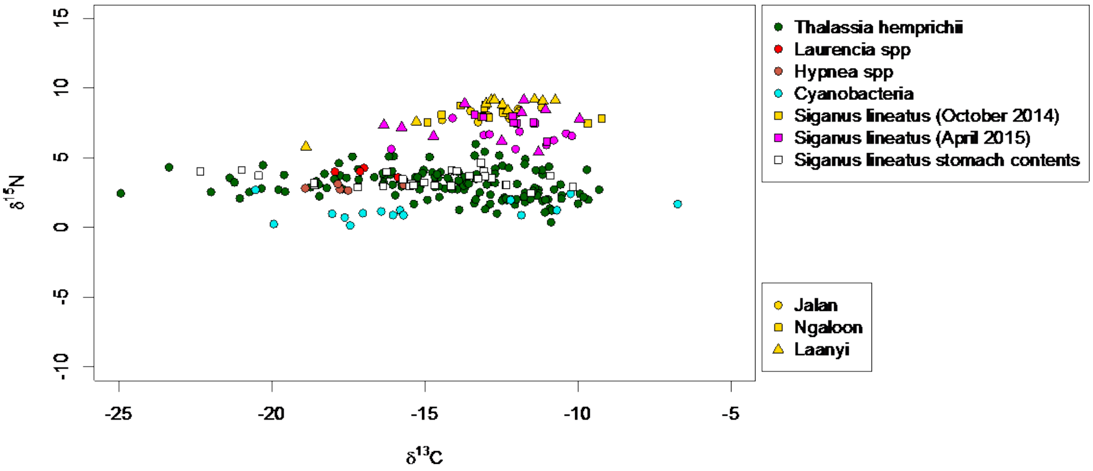

Figure 10: Individual measurements of $\delta^{13}C$ and $\delta^{15}N$ of *S. lineatus* muscle tissue and benthic primary producers (shown as different colours) likely to be consumed by *S. lineatus. S. lineatus* collected from different sites are denoted by different symbols. All data were collected from within the Bardi Jawi IPA.

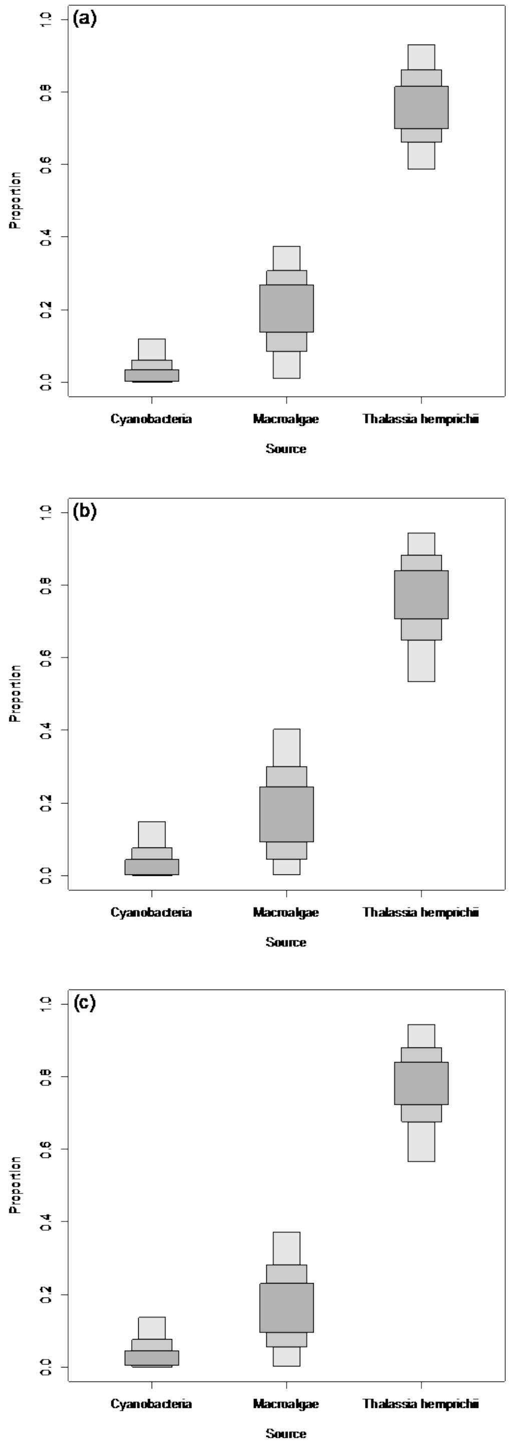

Figure 11: Likely proportions of cyanobacteria, macroalgae and seagrass (*Thalassia hemprichii*) in the diet of *Siganus lineatus* collected from (top) Jalan, (middle) Ngaloon, and (bottom) Laanyi. Plots show the 50%, 75%, and 95% probabilities for each potential food source.

3.5 Movement of satellite-tagged green turtles *Chelonia mydas*

Satellite tags were attached to 10 green turtles of varying size (62 – 92 cm curved carapace length), sex and maturity (Table 3). There was no obvious pattern in home range size related to size or sex. Core home range estimates (50% KUD) ranged from as little as 1.95 km^2 to 5,780 km^2. Large home range estimates of animals that moved long distances along the shore either west or east are less informative and likely to be an overestimate of total area used.

Table 3: Details of 10 individual green turtles *C. mydas* tagged with Argos transmitters. CCL = curved carapace length (cm); CW = curved carapace width (cm); A = adult, SA = sub adults, J = juvenile

Date tagged	Tag ID	Duration of tag detections (days)	CCL (cm)	Mass (kg)	Sex	Age class	Name	50 % KUD (km²)	95 % KUD (km²)	Total Fastloc detections
20/04/2016	53245	130	62.7	26.4	I	J	Brianna	122.35	1427.24	90
21/04/2016	53283	113	70.9	38	F	SA	Princess	91.92	423.16	36
21/04/2016	53284	176	74.0	45.8	F	SA	Willamena	5780.78	57728.14	566
21/04/2016	53285	164	88.6	71	M	A	Monsta	425.53	2089.49	425
14/04/2015	131863	151	62.9	27.7	I	SA	Ambol	1.95	8.48	664
22/04/2016	131864	187	92.4	84.8	F	A	Kimberly	61.01	279.61	533
16/04/2015	131867	186	77.3	103	I	SA	Savannah	2.79	18.67	291
15/04/2015	131870	86	79.7	101	F	A	Iwanj	270.31	2558.65	221
15/04/2015	139289	163	84.3	91	F	A	Jarmina	2371.85	14349.04	170
22/04/2015	153515	198	86.0	67.1	F	A	Phillomena	6.00	40.88	47

The movements of 10 satellite-tagged green turtles spanned more than 600 km (Figure 12 [top]). Three individuals left the region shortly after tagging: one moved into Talbot Bay, one to the vicinity of James Price Point, and the third moved into the Pilbara near Port Hedland. The remaining 7 individuals spent most of their time around One Arm Point and nearby islands and shoals (Figure 12 [bottom]). For animals that undertook large-scale movements, of those monitored for more than two months, all animals had at least one month where core home range (50 % KUD) was less than 5 km^2 (Table 4).

Table 4: Monthly 50% KUD (km^2) for ten green turtles tagged with satellite tags.

Tag_ID	Year	April	May	June	July	August	September	October
53246	2016	36.53	5.79	967.49	2.46			
53283	2016	40.30	121.90					
53284	2016	6146.69	9492.99	0.00	1.48	11.80	4.43	1378062.78
53286	2016	107.72	1.94	1.72	33.42	1.37	1.05	
131863	2015	0.44	0.35	9.09	1.39	1.10	0.49	
131864	2016	26.27	282.15	6.78	3.39	1.69	2.54	2.54
131867	2015	17.06	0.99	1.25	1.96	0.85	2.41	0.99
131870	2015	2712.21	3.51	0.79	1.23			
139289	2015	3.42	2502.09	4.53	2.10	2.65	2.87	
153515	2015	16.64	2.70					

Of the seven individuals that remained close to where they were tagged (Figure 13), some — but not all — showed evidence of overlap with areas where seagrass was present (or was likely to be present) based on our own observations of seagrass beds as well Landsat imagery. The proximity of large areas of high benthic algae cover to seagrass beds combined with a lack of detailed habitat maps to delineate between the two food resources (seagrass and algae) makes interpreting turtle movement in relation to habitat type difficult. For the majority of turtles that were resident within the Bardi Jawi IPA (six of seven) there was a high degree of overlap between satellite locations (Tag ID 131867, 131863, 153515, 53283, 53285 and 13864) and seagrass presence suggesting that for these individuals, seagrass might be an important part of the diet. For the individuals where satellite locations and KUD estimates didn't overlap with seagrass, it is likely that either estimates of seagrass distribution are inaccurate, animals were feeding predominantly feeding on algae or that GPS locations did not accurately reflect the animals foraging area.

Of the turtles that moved away from where they were captured, only Tag ID 131870 moved into an area where we have data on seagrass presence. Fastloc detections from this animal did not overlap with seagrass distribution in this area of Talbot Bay, however dugong (*Dugong dugon*) were observed feeding on *Halophila* spp. by one of the authors (Richard Pillans) in the areas with the highest density of Fastloc detections.

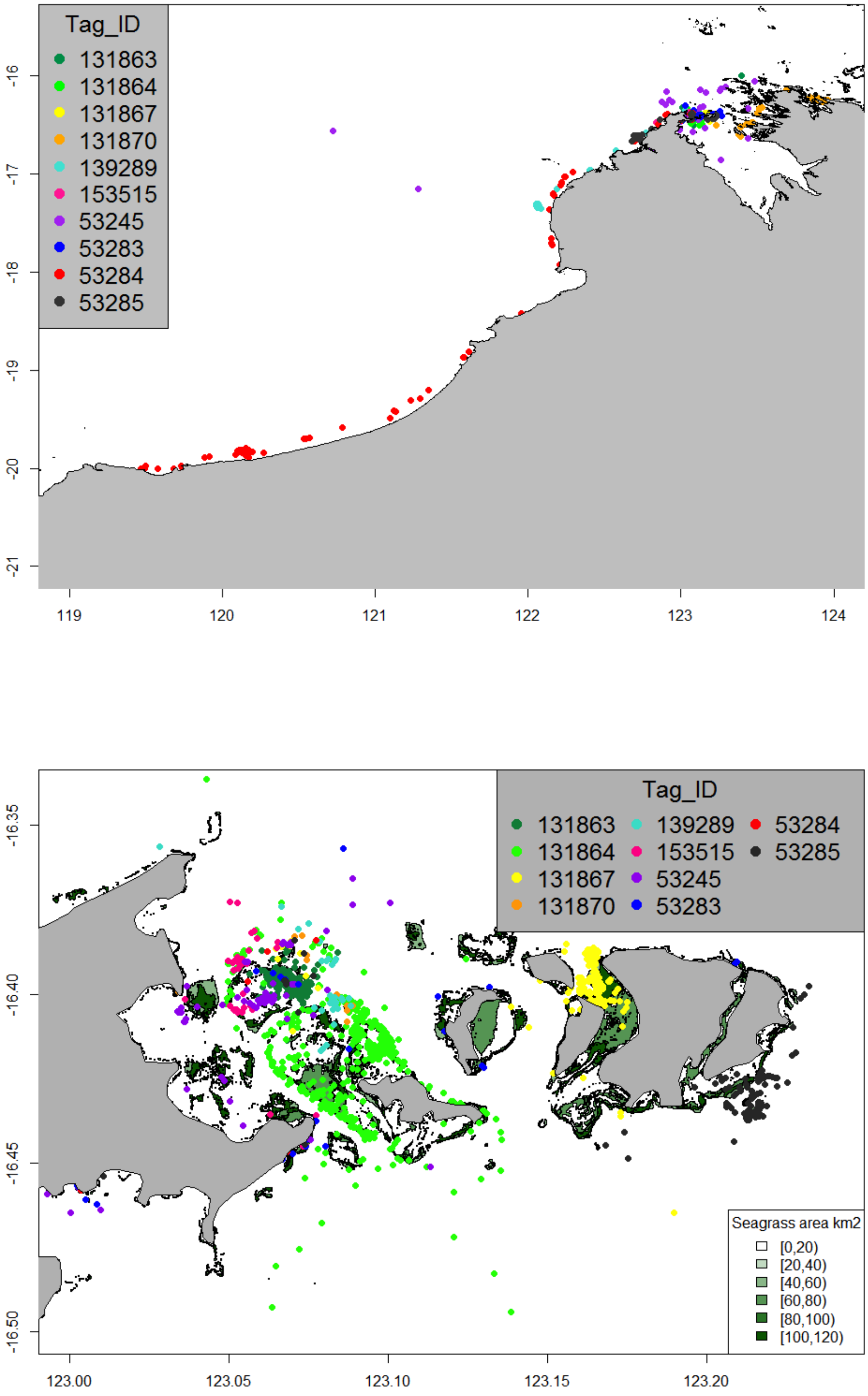

Figure 12: Fastloc GPS position estimates for each of the 10 green turtles, showing: (top) the entire geographical extent encompassed by movements, and (bottom) Fastloc GPS positions within the Bardi Jawi IPA. The green shading reflects the total area of seagrass polygons with darker shading representing larger polygons (areas of seagrass).

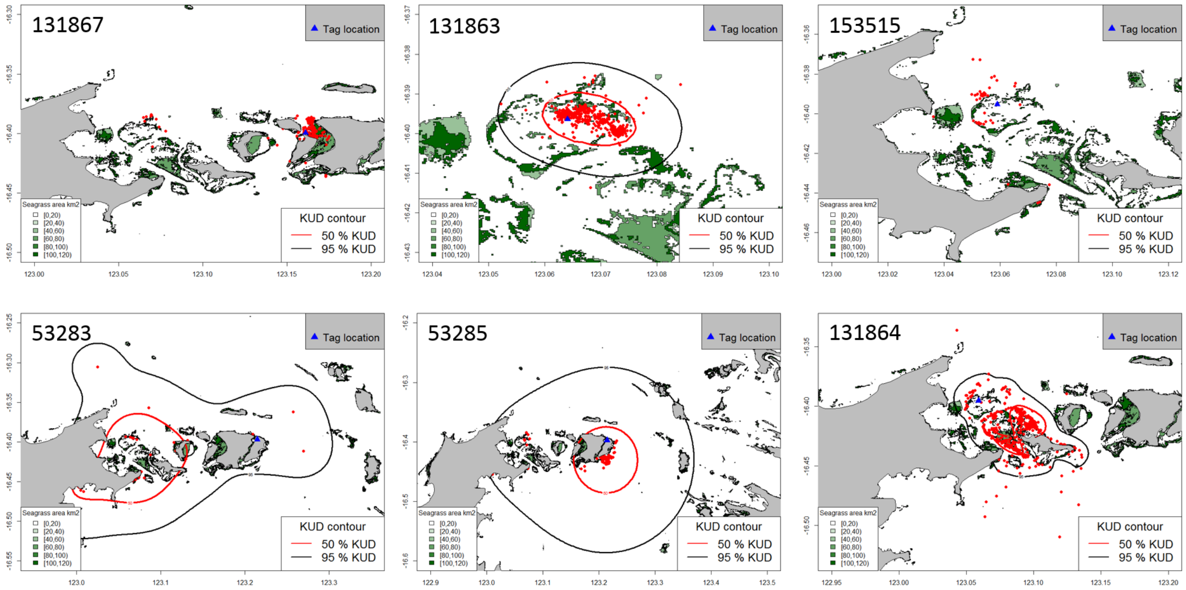

Figure 13: Fastloc GPS position and 50 and 95 % KUD estimates for 6 individual green turtles that remained in the area around One Arm Point and adjacent islands. The tag location is represented with a blue triangle and the satellite detection locations are represented by red circles. The green shading reflects the total area of seagrass polygons with darker shading representing larger polygons (areas of seagrass).

4 Discussion and Conclusions

4.1 Identity and composition of herbivores

The composition and relative abundance of species of nominally herbivorous fish varied among habitats. In habitats dominated by large brown algae or coral, the most abundant herbivorous fish was the surgeonfish *Acanthurus grammoptilus*, while in seagrass-dominated habitats the golden-lined rabbitfish *Siganus lineatus* was the most abundant species. Parrotfish (*Scarus ghobban* and *Scarus JHC* sp.3) were also present in algae- and coral-dominated habitats, and the barred rabbitfish *Siganus doliatus* was also present, but these species were less abundant.

Within these broad trends, some variation was evident between the seagrass meadows we focused on for detailed studies of herbivory. *S. lineatus* was abundant at Jalan and Ngaloon, but *A. grammoptilus* was also abundant at Ngaloon. Four species of herbivorous fishes were observed making biting movements in seagrass meadows at these sites, but patterns were inconsistent, with the damselfish *Dischistodus darwiniensis* yielding high bite rates in *Thalassia* meadows in Jalan, *A. grammoptilus* in *Thalassia* meadows in Ngaloon, and *S. lineatus* in *Enhalus* meadows at Jalan. Note that these observations do not necessarily reflect herbivory, because individuals could be biting at epiphytes on the seagrass, or even fauna inhabiting the meadows.

Green turtles *Chelonia mydas* were observed on RUV at both sites, but were not observed grazing.

The patterns observed are broadly consistent with the composition of fish faunas observed in other tropical ecosystems, particularly Indo-Pacific ecosystems dominated by *Thalassia* and *Enhalus*. Siganids (rabbitfish) are typically among the most common herbivores, and can be among the most abundant of all fish (Blaber et al. 1992; Gullstrom et al. 2002). Scarids (parrotfish) can also be abundant (Gullstrom et al. 2008), particularly in Caribbean seagrass meadows (Valentine et al. 2007). Few studies have found that acanthurids (surgeonfish) are abundant in seagrass meadows. Our observations of *A. grammoptilus* at Ngaloon might be due to the close proximity of algae-dominated habitat nearby.

4.2 Rates of herbivory

The rates of consumption of seagrass we measured were among the highest recorded anywhere in the world (Heck and Valentine 2006). Using simple tethering experiments, we estimate that consumption rates frequently exceed growth rates, indicating that most seagrass production likely enters grazing pathways. Rates were patchy, but in *Thalassia* meadows were on average 401% (median 131%) of daily production, and were sometimes up to 1433%. In *Enhalus* meadows, the rates of consumption were on average 166% (median 76%) of daily production, and up to 572%. Unsworth et al. (2007) recorded similar rates of grazing in Sulawesi, but the pattern was reversed — they recorded higher rates of grazing on *Enhalus* (average 787% of daily production) than on *Thalassia* (average 64% of daily production). In the study by Unsworth et al. (2007) scarids were identified as the likely major herbivore. Kirsch et al. (2002), in a study conducted in the Caribbean, also found that rates of consumption at times exceeded rates of production, and again identified scarids as the most likely herbivores.

The observations of rates of grazing that exceed rates of production appear incongruent with the existing dense seagrass meadows. However, we observed that grazing rates were not uniformly high, and even in *Thalassia* meadows there were times and places for which production exceeded consumption. It is likely that the patchiness in activities of herbivores compensates for the episodic high grazing.

4.3 Diet of key herbivores

Given the bite rates observed on RUV in our study, it is unlikely that scarids are significant herbivores in the Kimberley seagrass meadows we studied, unlike the findings of other studies (Kirsch et al. 2002, Unsworth et al. 2007). Based on the observations of the Bardi Jawi rangers, we focused on the golden-lined rabbitfish *S. lineatus* as a likely herbivore — this was subsequently supported by the RUV observations. In addition, given the observed high abundances of green turtles *C. mydas* at our sites during the incoming tide, we also focused on their diet.

Two lines of evidence support inferences about diet: direct observations of stomach contents, and stable isotope mixing models. For *S. lineatus*, both lines of evidence yielded very similar results. Stomachs of individuals tended to have large proportions of seagrass, and this was consistent at all three sites and during both surveys. On average, more than two-thirds of the stomach contents (by volume) was comprised of seagrass — mostly this appeared to be *Thalassia*. Stable isotope mixing models supported this for all sites, with the 95% probability intervals for the proportion of seagrass consumed being 60-92% at Jalan, 53-94% at Ngaloon, and 56-94% at Laanyi.

The diet of *S. lineatus* on the Great Barrier Reef is more typically comprised of macroalgae, with little seagrass recorded (Fox et al. 2009, Hoey et al. 2013). However, this might simply be due to the habitats in which these studies were conducted — there do not appear to be published studies of the diet of *S. lineatus* in seagrass-dominated ecosystems. Other siganids are known to consume seagrass.

Results for green turtles were more complex. The number of stomachs obtained was low (n=5), because of the ethical restrictions involved in sacrificing turtles for diet analysis and the consequent need to rely on samples donated by hunters. Of the five stomachs examined, three were dominated by seagrass (*Thalassia*); one of these contained only seagrass while two had small amounts of macroalgae. The other two stomachs contained a mixture of different macroalgae.

Patterns in stable isotopes also indicated the possibility that diet varied among individuals, because there was a wide range in the $\delta^{13}C$ of blood. Separate mixing models were performed for two groups of turtles: those with blood $\delta^{13}C$ greater than -14‰, and those with blood $\delta^{13}C$ less than -14‰: seagrass was likely the main diet source for both groups with 95% confidence intervals of the contribution of seagrass to diet being 45-100% for individuals with $\delta^{13}C$ less than -14‰, and 60-99% for individuals with $\delta^{13}C$ greater than -14‰.

The findings for the diet of green turtles are broadly consistent with those of other studies, which have found that they are generally herbivorous and can consume a range of seagrasses and macroalgae (Brand-Gardner et al. 1999; Andre et al. 2006). It is possible that within this population-level generality, there is some individual-level specialization, with at least some individuals consuming very specific diets over a long period (Vander

Zanden et al. 2013). Our stable isotope data is consistent with this hypothesis, but because stable isotope composition of blood reflects relatively short-term diet (days to weeks), it is not conclusive.

4.4 Movement of green turtles

Satellite tagging of green turtles revealed that, while some individuals remained close to where they were captured, others undertook large-scale movements both to the east and west of One Arm Point. Since tagging occurred outside nesting season, these movements are likely to be associated with movements to alternative foraging grounds. Movements of non-nesting turtles up to several hundred kilometers have been documented on the east coast of Australia (Babcock et al. 2015) where animals moved north and south of Gladstone Harbour and established relatively confined home ranges between long distance movements. A similar pattern was observed in the turtles that moved away from One Arm Point with animals moving up to 670 km away before establishing a 50% KUD of less than 12 km^2 that persisted for months. For all turtles, the average 50% KUD in months where they didn't undertake linear movements > 30 km was 3.1 ± 3.5 km^2 which is comparable to other studies on green turtles around the world where 50% KUDs have been found to be between 0.18–4.04 km^2 (Mendonca 1983; Brill et al. 1996; Renaud et al. 1994; Whiting and Miller 1998; Seminoff et al. 2002; Makowski et al. 2006; MacDonald et al. 2012).

Such long-range movements away from a foraging area by animals that are not partaking in courtship or breeding activities are uncommon (Balazs 1980; Limpus et al. 1994; C Limpus pers. comm. March 2015). While it is common for animals to move tens of kilometres between foraging areas (Whiting and Miller 1998) and even between reefs (Gredzens et al. 2014), the scale of movement demonstrated by three of the satellite tagged turtles at One Arm Point has not been previously documented for green turtles on the west coast of Australia. Despite Babcock et al. (2015) demonstrating long distance movement of three satellite tagged non-nesting adult turtles, overall, long-range movements in Queensland are also uncommon with recapture data from Queensland turtle tagging program (tens of thousands of individuals) as well as satellite tracks from more than 60 green turtles tagged along the Queensland coast, only demonstrated one similar case of large-scale movement where a resident adult female turtle, tagged in Moreton Bay, moved to Mon Repos (~320 km by water) and then between Mon Repos and Platypus Bay (~70 km by water) (C Limpus pers. comm.). Gredzens et al. (2014) reported the movement of a "transient" adult female turtle in Torres Strait, however, this individual moved at a much smaller linear scale (approximately 40 km between reefs) than the turtles in the current study.

Given the large tidal range in the Kimberley (up to 11 m) there is likely to be a considerable tidal influence on movement of green turtles. Tidally influenced movement patterns have been found in green turtles tagged with acoustic tags in Gladstone Harbour (Babcock et al. 2015). Data from Gladstone revealed that turtles moved into shallow intertidal seagrass beds with the flood tide and then back into the subtidal channels as water depth over the seagrass became too low. Babcock et al (2015) also demonstrated that while acoustic tags revealed tidal movement, in animals tagged with both acoustic and satellite tags, satellite detections (which only provide far fewer detections per day) did not provide enough detections to adequately demonstrate tidal movement patterns. For green turtles tagged in the current project, the average number of Fastloc detections per day was 7.3 ± 4.9 (± standard deviation), which was similar to the average number of daily detections of satellite tagged turtles in Gladstone Harbour (6.1 ± 4.7) suggesting that our ability to interpret tidal movement will be limited by the amount of available data.

Almost all the resident green turtles displayed a high degree of spatial overlap with predicted seagrass presence which is consistent with dietary analysis of turtles in this study. For all animals there were more satellite detections on the periphery of modelled seagrass beds. The ability of carapace mounted satellite tags to obtain Fastloc GPS position estimates is influenced by a range of factors including animal behaviour (e.g. surfacing angle, surface time, level of disturbance), wind strength and direction as well as swell and atmospheric conditions. Babcock et al. (2015) demonstrated that in green turtles tagged with both satellite and acoustic tags, satellite detections resulted in KUDs on the edge of seagrass beds with more overlap of the subtidal channel and bare sand. Acoustic detections from the same individuals revealed repeated use of shallow intertidal seagrass beds with KUDs centered on seagrass beds. Therefore, the relatively few detections of tagged turtles directly over seagrass beds is potentially due to behavioural differences while animals are feeding on seagrass, incorrect seagrass distribution maps, or animals feeding on a variety of benthic algal resources. The evidence of high contribution of seagrass to green turtle from both stomach content and stable isotope analysis suggests that the most plausible reason is a combination of fewer detections while animals were feeding over seagrass beds and an inability of the seagrass distribution model to incorporate all seagrass. Visual observations of seagrass suggest the hyperspectral imagery and associated model align with areas of high seagrass density, however in deeper areas or areas with sparse coverage of species such as *Halophila* spp. the model is not a good reflection of likely seagrass presence.

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