Oceanographic drivers of circulation, thermodynamics and connectivity within a wave- and tide driven coral reef atoll

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This thesis is presented for the degree of Doctor of Philosophy at The University of Western Australia

Oceans Graduate School
ARC Centre of Excellence for Coral Reef Studies
Australian Institute of Marine Science
2022
Thesis declaration

I, Camille Mathilde Grimaldi, certify that:

This thesis has been substantially accomplished during enrolment in this degree. This thesis does not contain material which has been submitted for the award of any other degree or diploma in my name, in any university or other tertiary institution. In the future, no part of this thesis will be used in a submission in my name, for any other degree or diploma in any university or other tertiary institution without the prior approval of The University of Western Australia and where applicable, any partner institution responsible for the joint-award of this degree.

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This research was supported by an Australian Government International Research Training Program (RTP) scholarship, an Australian Government International Research Training Program (RTP) fee offset scholarship, an Australian Institute of Marine Science Top-Up scholarship and the Robson and Robertson Award.

Technical assistance in field and laboratory work was kindly provided by Carlin Bowyer, Kim Brooks, in addition to the Captain and crew of the R/V Solander.

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Abstract

Understanding the natural variability of reef systems and identifying environmental conditions that promote coral reef resilience and recovery is pivotal to advance our ability to conserve and manage reefs. As a result, it is essential to characterize the oceanographic processes that underpin the circulation and shape a range of key ecologically relevant processes. Waves and tides act as the two primary forcing mechanisms driving the hydrodynamics of coral reefs worldwide. Although wave- and tide-driven flows are individually well understood, there remain considerable gaps in our understanding of how their interactions control the circulation, flushing and residence times of coral reefs. This thesis uses both in situ observations and numerical simulations to investigate how oceanographic and atmospheric processes, specifically wave- and tide-driven flows, control the circulation, temperature variability, and connectivity at Mermaid Reef—a coral reef atoll located on the edge of Australia’s North West Shelf.

In Chapter 2, an 11-month study of the hydrodynamic conditions across Mermaid Reef revealed that the atoll is regularly exposed to a range of waves and tidal conditions. Using a validated wave-flow numerical model, we show that wave- and tide-driven processes continuously interact to non-linearly drive the reef’s circulation through several mechanisms. These include wave-current interactions and tidal water level modulation of wave-driven flows. The atoll morphology, particularly the higher elevation of the western reef flat, was found to be a key factor controlling the relative importance of waves and tides. Wave-driven processes dominated for tidal ranges smaller than required to expose the shallower western reef flat; in contrast, tidal processes dominated for larger tidal ranges, when the exposed western reef flat temporarily acted as a physical barrier to incoming and outgoing flows. The residual (tide-averaged) circulation was consistently directed eastward across the atoll. While Mermaid Reef can, on-average, be classified as a tide-dominated reef, the incident wave energy and spring-neap tidal range variability can also allow wave processes to drive the reef circulation.

Temperature is one of the key environmental variables controlling coral health and survival. Along with atmospheric conditions, the hydrodynamic drivers of water flow contribute to shape temperature variability on coral reefs. In Chapter 3, the analysis
of 11 months of in situ temperature measurements and atmospheric conditions revealed the relative importance of different drivers of temperature variability across key reef zones (reef flat, lagoon, fore-reef) of Mermaid Reef. Over diurnal timescales, temperature variability across the reef flat and lagoon zones was driven by the interactions between net diurnal air-sea heat exchange and mean depth of the site. As a result, we show that local deviations in mean daily temperature of lagoon and reef flat waters from offshore remotely sensed sea surface temperature values could be predicted as a function of the net air-sea heat exchange and mean depth. Advection of heat seemed to play an important role in the temperature variability observed on the fore-reef, which experienced some of the largest temperature anomalies over rapid timescales (10 min). Such temperature anomalies are most likely driven by large amplitude internal waves, prominent on Australia’s North West Shelf. Identifying the oceanic and atmospheric drivers of temperature variability (and thermal stress) occurring across reef-scales (<1 km) is critical for Mermaid Reef and coral reefs globally, to determine the triggers and patterns of coral bleaching events as well as their longer-term responses to climate change.

Larval connectivity is central to coral reef resilience and recovery from disturbance, particularly in isolated reef systems such as Mermaid Reef. In Chapter 4, the advection of water by wave- and tide-driven flows is shown to play a major role in transporting and controlling the amount of time coral larvae spend in the reef system before being transported to the open ocean. By applying a wave-flow hydrodynamic model coupled with Lagrangian particle tracking and biological properties of coral larvae, a mean transport eastward across the atoll is apparent and is driven by a combination of wave- and tide-driven flows. The oscillatory movement generated by tides reduced net export of particles from the reef, whereas the continuous and unidirectional flow generated by waves increased net export to the open ocean. Over the ~40 years of coral spawning events considered, little variability in hydrodynamic conditions was observed. However, the occasional influence of tropical cyclones caused large deviations from the typical dispersal pathways during spawning events, resulting in rare connectivity pathways within the reef system.

Overall, this thesis advances our understanding of the key role that hydrodynamic processes play in driving the circulation, temperature variability and connectivity at Mermaid Reef atoll. These findings are relevant for a number of reef systems worldwide exposed to both tides and waves, and provide a baseline for future
studies examining other key ecologically relevant processes (e.g., nutrient dynamics, carbonate chemistry variability).
Acknowledgments

I acknowledge that this thesis was written on the land of the Whadjuk people (Perth) of the Noongar nation (South-west of Western Australia), the traditional custodians of this country and its waters. I pay my respects to the Elders past and present, and to emerging leaders.

First and foremost, I would like to thank my supervisors: Ryan Lowe, Jessica Benthuysen, Rebecca Green and Michael Cuttler for their continued guidance and endless supply of fascinating ideas to explore over the last couple of years. I learned an immense amount from each and every one of you and I cannot express how grateful I am for your time and patience. You have shaped me as a scientist, and I am looking forward to working with you in the future. Carlin Bowyer, thank you for being an incredible mentor, for trusting me and teaching me everything there is to know about fieldwork.

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Finally, to my 11-year-old self and all the young girls dreaming about being an oceanographer or pursuing a career in science, technology, engineering or maths, you can do anything you put your mind to!

Camille
Authorship declaration

This thesis contains work that is currently in review for publication. Details regarding the stage, co-authors and author contributions of these manuscripts are detailed below.

Details of the work:


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C.G., R.L., J.B. and R.G. conceived and planned the numerical experiments. C.G., R.G., J.R. and H.K. carried out the numerical experiments. C.G., R.L., J.B., and R.G. contributed to the interpretation of the results. C.G. wrote the manuscript with input from all authors.

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C.G., collected, analysed, and interpreted the data and it with input from R.L., J.B., M.C., and R.G. C.G. wrote the manuscript with input from all authors.

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# Contents

Thesis declaration .................................................................................. i  
Abstract................................................................................................... ii  
Acknowledgments .................................................................................. v  
Authorship declaration .......................................................................... vii  
Contents .................................................................................................. x  
List of figures .......................................................................................... xiv  
List of tables ............................................................................................ xxii  
List of Abbreviations ............................................................................ xxiii  

1. Introduction ......................................................................................... 1  
   1.1. Background ..................................................................................... 1  
   1.2. Hydrodynamic processes on coral reefs ........................................... 2  
   1.3. Mermaid Reef .................................................................................. 4  
   1.4. Research questions ......................................................................... 5  
   1.5. Thesis structure .............................................................................. 7  

2. Wave- and tide-driven flow dynamics within a coral reef atoll off northwestern Australia ..................................................................................... 9  
   2.1. Abstract .......................................................................................... 9  
   2.2. Introduction .................................................................................... 10  
   2.3. Methods .......................................................................................... 13  
      2.3.1. Site description .......................................................................... 13  
      2.3.2. Field observations ..................................................................... 15  
      2.3.3. Numerical modelling ................................................................. 17  
   2.4. Results ........................................................................................... 21  
      2.4.1. Observations ............................................................................ 21  

2.4.2. Hindcast model validation ................................................................. 26
2.4.3. Isolating wave and tidal contributions to atoll circulation ........... 28
2.5. Discussion and Conclusions ................................................................. 40
  2.5.1. Tide-driven circulation on asymmetrical atoll reefs .................. 41
  2.5.2. Mechanisms responsible for wave and tide-driven circulation .... 42
  2.5.3. Relative importance of hydrodynamic forcing ............................ 43
  2.5.4. Conclusions ............................................................................... 44
2.6. Acknowledgements ............................................................................ 45
2.7. Supporting information for Chapter 2 .................................................. 46

3. Drivers of temperature variability within a coral reef atoll off northwestern Australia .......................................................... 53

3.1. Abstract ............................................................................................ 53
3.2. Introduction ....................................................................................... 54
3.3. Methods ............................................................................................ 55
  3.3.1. Study site and sampling design .................................................. 55
  3.3.2. Estimates of heat exchange ........................................................ 58
  3.3.3. Data analysis .............................................................................. 59
  3.3.4. Satellite sea surface temperature (SST) ..................................... 59
3.4. Results .............................................................................................. 60
  3.4.1. Oceanic and atmospheric conditions ........................................ 60
  3.4.2. Water temperature variability ..................................................... 61
  3.4.3. Drivers and key mechanisms of temperature variability .......... 65
  3.4.4. Differences between reef and offshore water temperatures ...... 69
3.5. Discussion .......................................................................................... 71
  3.5.1. Distinct temperature across a coral reef atoll ............................ 71
  3.5.2. Significance for thermal stress experienced by coral reef communities .................................................. 73
3.6. Conclusions ...................................................................................... 74
4. Hydrodynamic drivers of fine-scale connectivity within a coral reef atoll off northwestern Australia

4.1. Abstract

4.2. Introduction

4.3. Study site

4.4. Methods

4.4.1. Biophysical model

4.4.2. Meteorological and oceanographic conditions

4.4.3. Analysis of the transport network

4.5. Results

4.5.1. Meteorological and oceanographic conditions during coral spawning events

4.5.2. Circulation patterns during typical hydrodynamic conditions

4.5.3. Relative importance of hydrodynamic forcing

4.5.4. Influence of tropical cyclones on connectivity patterns

4.6. Discussion

4.6.1. Coral reef connectivity at Mermaid Reef

4.6.2. Retention and export: hydrodynamic and geomorphic controls

4.6.3. Influence of fine-scale reef hydrodynamic processes on regional connectivity predictions

4.6.4. Implications for inter-reef connectivity at the Rowley Shoals

4.7. Conclusions

4.8. Acknowledgements

4.9. Supporting information for Chapter 3

4.9.1. Coral communities’ observations

4.9.2. Spatial habitat modelling

4.9.3. Biophysical model sensitivity to time of release
4.9.4. Regional currents and wind conditions during coral spawning ..... 102
4.9.5. Biophysical model sensitivity to wind ............................................. 102
4.9.6. Biophysical model sensitivity to regional currents ....................... 103
4.9.7. Circulation throughout a tidal cycle .............................................. 105
4.9.8. Supplementary tables ..................................................................... 106

5. General discussion .................................................................................. 109

5.1. Thesis overview and summary of main findings ................................ 109
5.1.1. A wave and tide-dominated atoll reef ......................................... 109
5.1.2. Temperature variability across reef environments .................... 110
5.1.3. Fine-scale coral reef connectivity .................................................. 112
5.2. Broader implications ........................................................................... 113
5.3. Concluding remarks and recommendations for future research ........ 115

References .................................................................................................. 119
List of figures

Figure 1-1. LANDSAT image of (a) the North West Shelf (NWS) of Australia, showing the Rowley Shoals and Mermaid reef (indicated by the red square), Scott Reef and Ashmore Reef. Inset map shows Australia’s North West Shelf and (b) shows Mermaid Reef.................................................................5

Figure 1-2. Conceptual overview of the thesis and chapter overview. Coral reefs are exposed to a wide range of hydrodynamic processes including to surface waves, tides, regional currents and internal waves. Surface waves and tides and the reef morphology control the circulation and flushing inside of the atoll (Chapter 2). By doing so, they also control the thermal variability and connectivity inside the reef (Chapter 3 and 4). However, those processes are also influenced by hydrodynamics occurring outside of the reef including but not limited to the propagation of internal waves or regional currents. Schematics not to scale..........................................................6

Figure 2-1: (a) Schematic diagram of a circular coral reef atoll with a fore-reef slope, reef flat, lagoon and channel; (b) conceptual model of wave-driven flow; tide-driven flow for (c) flood tide and (d) ebb tide for a symmetrical atoll reef (i.e., similar topographic elevation on both sides of the atoll). MSL = mean sea level; \( q_{wave} \) = wave-driven flow rate; \( \eta_{setup} \) = wave setup; \( q_{tide} \) = tide-driven flow rate; HHT: highest high tide; LLT= lowest low tide; W= West; E=East.........................................................11

Figure 2-2: (a) Site location and bathymetry (relative to MSL) of Mermaid Reef. Brown colours represent the reef flat (depths 2 m above to 2 m below MSL). White lines denote the cross sections used to calculate flow in/out of the atoll using the numerical model (see section 2.3.3). (b) The three atolls comprising the Rowley Shoals: Imperieuse, Clerke and Mermaid Reef. Tidal current ellipses (based on the dominant \( M_2 \) tide) are superimposed, as derived from the TPXO8.0 global tidal solution. The inset map shows the Rowley Shoals’ location (red dot) on Australia’s North West Shelf and (c) bathymetry cross section from the west to the east of the atoll (A to B on Figure 2-2a)..................................................................................................................14

Figure 2-3: (a) Percent occurrence of significant wave height and tidal range over the study period (26/11/2017 to 14/10/2018) at the fore-reef site (S1). Oceanographic conditions during a three-month period (1/12/2017 to 1/03/2018): (b) water level relative to mean sea level, (c) significant wave height (\( H_s \)) and peak period (\( T_p \)), (d)
incoming wave direction ($\theta_{\text{wave}}$) at the fore-reef site (S1) and (e) wind speed and incoming direction ($\theta_{\text{wind}}$) at the Bureau of Meteorology weather station (ID: 200713).

Figure 2-4: (a) Cross section of the western reef flat of Mermaid Reef with S1, S8 and S9, (b) time series of offshore significant wave height ($H_s$) at S1 and S8 (fore-reef) and S9 (reef flat) focusing on a sample two-month period (05/12/17 – 05/02/18), (c) significant wave height as a function of the water depth at S9 and (d) time series comparing 33 h low-pass filtered offshore significant wave height at S1 with wave setup ($\eta_{\text{setup}}$) over the reef flat at S9.

Figure 2-5: (a) Water level (relative to MSL) at the fore-reef (S1) and lagoon (S2) sites and (b) illustrative photo of Mermaid Reef’s reef flat (south of the channel, taken from the ocean side out to the lagoon), which becomes exposed when offshore water level falls below the reef flat elevation.

Figure 2-6: (a) Depth-averaged current velocities, with arrows representing the time-averaged current vectors and ellipses indicating the standard deviation of the current variability from a principal component analysis over a three-month period (1/12/2017 to 1/03/2018). The total current velocities are plotted in black and the subtidal current (33 h low-pass filtered) in red. Note the difference in scale of current velocities between the solid lines for the reef flat and lagoon sites (S2 and S4) and the dotted lines for the channel site (S3) given the much larger velocities in the channel. Subtidal velocities are plotted as a function of significant wave height and tidal velocities as a function of the water level at (c) S4, (d) S2 and (e) S3. Note that a 2-hour lag was applied to the field observations of tidal velocities to account for the effect of tidal truncation (see Section 2.3.1.4).

Figure 2-7: Hindcast numerical simulations (in black) compared against the field observations (in red) showing a one-month period that includes spring tides, neap tides, low and high wave energy. (a, d and g) Water levels (m) (b, e and h) streamwise tidal velocity (m/s) and (c, f and i) streamwise subtidal velocity (m/s) at S4 (reef flat), S2 (lagoon) and S3 (channel). Positive (negative) streamwise velocity indicates water coming into (out of) the atoll.

Figure 2-8: Wave-only scenarios. The time- and spatially-averaged discharge, $q_i$, for the $i$th cross section in/out of the atoll for significant wave height ($H_s$) (a) $H_s = 1$ m and (b) $H_s = 3$ m (at mean sea level). Blue (red) arrows indicate inflow (outflow) and are plotted on the $z = -2$ m contour. Note that the dotted arrow represents the
discharge through the channel, which was scaled 10 times smaller than for the other cross sections (represented by solid arrows). (c) The $q_{west}$ (cross section 1 to 8) as a function of $H_s$. The dotted and solid red line represent the minimum and maximum, and mean $H_s$ over the 11-month dataset, respectively. .............................................................. 29

Figure 2-9: Tide-only scenarios. The spatially and time-averaged flow rate, $q_i$, over the $M_2$ period (12.42 h), for the $i^{th}$ cross section, in/out of the atoll for tidal range (a) TR = 1 m and (b) TR = 3 m. Blue (red) arrows indicate inflow (outflow) and are plotted on the $z = -2$ m contour. Note that the dashed arrow represents the discharge through the channel, which is scaled 100 times smaller than for the other cross sections (represented by solid arrows). (c) Western reef flat flow rate, $q_{west}$, as a function of tidal range. The black dashed and solid lines represent $q_{west}$ with and without taking into account the $M_2$ phase difference across the NWS. The red dotted and solid lines represent the minimum, maximum and mean tidal range over the 11-month dataset respectively; (d) and (e) Hovmöller diagrams of the spatially-averaged flow rate, $q_i$, as a function of time. Note that the channel (cross section 14) displays values an order of magnitude greater than the rest of the cross sections ($\pm 2.8$ and $\pm 11.4$ m$^2$/s respectively for TR = 1 and 3 m). The dashed grey line represents the water level threshold at which the western reef flat becomes exposed ($\eta \sim -0.7$ m relative to MSL). .......................................................... 31

Figure 2-10: Tide-only simulation for a spring tidal range of 3 m. (a) Water levels with dashed black line represent the threshold at which the western reef flat becomes exposed ($\eta \sim -0.7$ m relative to MSL) and (b) atoll cross section with light blue shaded area represents the water level for given times after high tide. (c) Current velocity vectors for given times after high tide. See Supporting information Figure S 2-4 for the neap tidal range of 1 m. .................................................................................................................. 33

Figure 2-11: (a) $q_{west}$ as a function of tidal range (TR) and significant wave height ($H_s$) for the combined waves and tides scenarios, (b) $q_{west}$ as a function of tidal range and significant wave height for the linear superposition of the tide-only and wave-only scenarios and (c) percent difference between (a) and (b) normalised by (b). ........ 34

Figure 2-12: Hydrodynamic regimes for the western reef flat’s time-integrated flow rate, $q_{west}$, for wave, tide and combined waves and tides scenarios. Symbols represent scenarios forced with TR = 0.5, 1, 1.5, 2, 3 and 4 m. Dashed grey lines represent the values associated with the same TR and varying $H_s$. Colours represent scenarios forced with $H_s = 0.5, 1, 1.5, 2$ and 2.5 m. .......................................................... 36
Figure 2-13: Flow $q_{west}$ averaged along the western reef flat, as a function of both significant wave height ($H_s$) (right y-axis) and water level (left y-axis) for tidal range (TR) of (a) 1 m and (b) 3 m. The solid grey line represents the ocean water levels for hours after low tide and the dashed grey line represent the threshold at which the western reef flat becomes exposed ($\eta \sim 0.7$ m relative to MSL). .......................................................... 37

Figure 2-14: Flow rate across the western reef flat over a tidal cycle for a combined tide and wave driven flow ($q_{\text{combined}}$, red line), pure wave driven flow at different static water levels ($q_{\text{Wave}}$, black line), and the linear addition of a pure tide and pure wave driven flow at mean sea level ($q_{\text{Tide}} + q_{\text{Wave},0}$, blue line) for constant $H_s$ of (a) 0.5 m and (b) 2 m. ........................................................................................................... 38

Figure 2-15: (a) Volumetric flow rate $Q$ ($m^3/s$) as a function of tidal range (TR (m)) and (b) significant wave height ($H_s$ (m)) for $Q_{\text{channel}}$ (cross section 14), $Q_{\text{eastern reef flat}}$ (cross section 9 to 13 and 15 to 16), and $Q_{\text{east total}}$ (cross section 9 to 16). .................................................................................................................. 40

Figure 2-16: Conceptual model of tide-driven flow of (a) flood and (b) ebb tide for an asymmetrical (western reef flat higher in elevation than eastern reef flat) atoll reef where the tidal range is greater than two times the reef flat elevation. The flow through the channel is represented on the plan view diagrams. MSL = Mean sea level; $q_{\text{tide}}$ = tide-driven flow; HHT = highest high tide; LLT = lowest low tide; W = West; E = East; $h_{\text{west}}$ = western reef flat elevation. ................................................................................................. 42

Figure 3-1: Bathymetry (depths relative to mean sea level; MSL) and instrument locations at Mermaid Reef. Brown colours represent the reef flat (depths 2 m above to 2 m below MSL). Inset map shows Mermaid Reef’s location (red dot) on Australia’s North West Shelf (red box). ........................................................................................................... 57

Figure 3-2: Met-ocean conditions at Mermaid Reef from 1/12/2017 to 1/10/2018 (local time, UTC+8). (a) Water levels ($\eta$) measured at S1; (b) wave height ($H_s$) and mean period ($T_{\text{m01}}$) measured at S1; both (c) wind velocity 10 m above the surface and (d) net ($Q_n$), sensible ($Q_S$), latent ($Q_L$), longwave ($Q_{\text{LW}}$) and shortwave ($Q_{\text{SW}}$) radiation fluxes were extracted from ERA5 and averaged over Mermaid Reef. ........ 61

Figure 3-3: Temperature variability over several timescales across the reef zones of Mermaid Reef (local time, UTC+8). (a) Seasonal temperature variability (low pass filtered, half power of 33 hours), (b) sub-diurnal (low pass filtered, half power of 33 hours) temperature variability and (c) hourly temperature variability across the reef
zones of Mermaid Reef. The bold line and shading represent the mean and standard deviation across all sites of a reef zone.

Figure 3-4: Power spectral density of temperature as a function of frequency (cycles per day) from the in situ temperature at the (a) reef flat, (c) lagoon and (e) deep fore-reef from 26/11/2017 to 1/10/2018. Power spectral density of temperature was not computed at the shallow fore-reef site as the data was only available for ~3 months out of the ~11-month experiment. Diurnal ($S_1$) and semi-diurnal ($M_2$) frequencies are indicated by the dashed grey lines. Daily change in temperature since midnight ($ΔT$) as a function of the hours of the day (over 24 hours) at the (b) reef flat, (d) lagoon, (f) deep fore-reef sites. The bold line and shading represent the mean and standard deviation across all sites of a reef zone, and (g) shows the mean depth as a function of the mean daily temperature range ($ΔT_d$) across the key reef zones.

Figure 3-5: (a) Significant wave height ($H_s$) and direction ($θ_{wave}$) measured at the fore-reef site (S1) and (b) temperature changes during the passage of Tropical Cyclone Marcus, from 20/03/2018 to 25/03/2018 (local time, UTC+8) across key reef zones.

Figure 3-6: Rate of temperature change at the (a) reef flat and (b) lagoon zones calculated from the in situ temperature time series (solid line) and calculated using Eq. (3.2) based on the air-sea heat flux term (dashed line). The bold line and shading represent the mean and standard deviation across all sites of a reef zone.

Figure 3-7: (a) Temperature at reef flat and lagoon site (black and grey line, respectively) (28/11/2017 to 23/12/2017); (b) Hour of day when low tide (from water level measured at S1) and peak solar irradiance (estimated from the maximum daily $Q_N$) occurred. Grey shading represents night-time (6 pm to 6 am the following day, local time, UTC+8); (c) Boxplot of the mean daily temperature range ($ΔT_d$) on the reef flat as a function of the lag between peak solar and low tide in hour ($ΔHr$) from 26/11/2017 to 1/10/2018. On each boxplot, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers, and the outliers are plotted individually using the ‘+’ marker symbol.

Figure 3-8: Cold water pulses across the western reef flat. Temperature variability across the western reef flat at S1 (deep fore-reef), S8 (shallow fore-reef), S9 and S4
(reef flat) at a 10-min interval. Grey shading represents night-time (6 pm to 6 am the following day, local time, UTC+8).

Figure 3-9: (a) Time series of the remotely sensed SST for the reef flat, lagoon and offshore waters. (b) Differences in night-time SST between the reef flat, lagoon and offshore ($\Delta T_{\text{SST}}$). The dashed line indicates zero difference in temperature. (c and d) indicate the daily average difference in temperature between reef and offshore waters versus the ratio of daily average air-sea heat flux term ($qNgh\rho cp$, Eq. 3.2) for the period from 26/11/17 to 01/10/18 at the reef flat and lagoon sites, respectively. The grey lines represent the best-fit linear regression for each fitted regression.

Figure 3-10: (a) and (b) show time series (26/11/17 to 20/09/18) of daily mean SST$_{\text{offshore}}$ from the MUR satellite data and modelled ($T_{\text{modelled}}$) and observed ($T_{\text{reef}}$) daily night-time mean temperatures at the reef flat and lagoon zones, respectively.

Figure 4-1: (a) Bathymetry (depths relative to mean sea level; MSL) of Mermaid Reef. Brown colours represent the reef flat (depths 2 m above to 2 m below MSL). Hydrodynamic regions across Mermaid Reef are represented by the dotted black boxes. The reef flat (RF) regions were defined between +/- 2 m and the lagoon (L) regions were defined inside the reef flat. Inset map shows Mermaid Reef’s location on Australia’s North West Shelf. (b) Probability of presence of Acropora spp. derived from the benthic habitat model using the combination of tow-camera footage, laser airborne depth surveys, statistical modelling approach and from quantified percentage cover of Acropora spp. (referred to as long term monitoring or LTM); see Supplemental Information for data collection and benthic habitat model methods.

Figure 4-2. Hydrodynamic conditions during periods of coral spawning at Mermaid Reef (1980 to 2020): (a, b and c) tidal water levels with dashed blue line representing the threshold between neap and spring tide, (d, e and f) wave height ($H_i$)and (g, h and i) wave directions ($\theta_{\text{wave}}$). Periods include the primary mass spawning in March (a, d and g) without tropical cyclones (TCs) present and influenced by tropical cyclones (b, e and h), and the secondary mass-spawning in October (spring) (c, f and i). Plain black lines represent the mean, and red shading represents the standard deviation over the time period. Grey lines represent each individual year, and black dashed and dotted lines represent TC Vivienne and TC Fay, respectively.

Figure 4-3. Residual (time-averaged) flow patterns during the spawning period for typical conditions (excluding cyclone years). Depth-averaged velocity magnitude
(colours) and unit velocity vectors during typical spawning conditions, time-averaged over (a) the 10-day simulation, (b) neap tides and (c) spring tides (see Figure 4-2a). No winds or regional currents were included in these simulations yet had little influence on the flows within the atoll (see Figure S 4-5 and Figure S 4-6). All residual flows were plotted as unit vector arrows using the curvvec function in Matlab (Stevens et al. 2021).

Figure 4-4: Connectivity at Mermaid Reef. (a) Encounter Probability Distribution (EPD) after 10 days, (b) average connectivity matrix after 10 days of larval dispersal and (c) spatial connectivity of larvae among sites, where the line thickness reflects the strength of the connectivity.

Figure 4-5: Comparison between wave-only and tide-only simulations. (a) Atoll retention rate associated with different study cases tide-only and wave-only simulations based on typical (non-TC) conditions. Time- and depth-averaged residual flow velocities for (b) wave-only conditions, with $H_s = 1$ m and $\theta_{\text{wave}} = 220^\circ$N, (c) tide-only conditions for neap, and (d) tide-only conditions for spring tides.

Figure 4-6: Influence of Tropical Cyclone Vivienne (1996) and Tropical Cyclone Fay (2004) on hydrodynamic conditions and connectivity. (a) Atoll retention rate for typical spawning conditions and TC Vivienne and TC Fay over the dispersal period. (b, c) The time-average velocities over the 10 days of dispersal. (d, e) The difference in EPD ($\Delta$ EPD) of larvae between each TC and values calculated for typical spawning conditions. Red (blue) colours indicate smaller EPD than in the typical spawning conditions case (Figure 4-4a).

Figure 4-7: Encounter Probability Distribution (EPD) after 10 days for Acropora spp. coral cover (Figure 4-1b). Larvae were released from the eastern side of the atoll (i.e., red polygon).

Figure 4-8: March 2011 autumn mass spawning larvae tracking simulation using (a) the 2D coupled wave-flow hydrodynamic model with BRAN 2020 surface velocity currents and using (b) Parcels forced with the BRAN 2020 surface velocity currents. Larval mortality was not incorporated here. Mermaid, Clerke and Imperieuse are the northern-most to southern-most reefs, respectively, and are represented by their 2 m depth contour.

Figure 5-1: Tide-dominated atolls (~10% of the reef’s worldwide) based on Lowe and Falter 2015 and Green, 2018. The atolls are colour coded as a function of (a) the maximum wave height ($H_s$, extracted from Centre for Australian Weather and Climate...
Research (CAWCR)) and (b) the % of time during which $H_s > 2 \text{ m}$ over 41 years (1980-2020).

Figure 5-2: LANDSAT-8 and various aerial images of (a, b) Mermaid, (c, d) Clerke and (e, f) Imperieuse. Photo credit: (a, c and e) LANDSAT; (b) wanderlust Kimberley; (d) Department of Biodiversity, Conservation and Attractions (DBCA); (f) Sharyn Hickey.
List of tables

Table 2-1: Instrument deployment information (26/11/2017 - 14/10/2018).............. 15
Table 2-2: Hydrodynamic parameters used within the series of idealized scenarios. $H_s =$ significant wave height, $T_p =$ peak period and $TR =$ tidal range................................. 21
Table 2-3: Statistical parameters (Skill and RMSE) to assess the validity of the numerical simulations for water level (m) and current velocities (m/s) at S2, S3 and S4 for the three-month simulation period (1/12/2017 to 1/03/2018). ........................................ 27
Table 3-1: Instrument deployment information.......................................................... 57
## List of Abbreviations

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Meaning or description</th>
</tr>
</thead>
<tbody>
<tr>
<td>2DH</td>
<td>Depth-averaged</td>
</tr>
<tr>
<td>ADCP</td>
<td>Acoustic Doppler Current Profiler</td>
</tr>
<tr>
<td>AIMS</td>
<td>Australian Institute of Marine Science</td>
</tr>
<tr>
<td>BRAN</td>
<td>Bluelink ReANalysis 2020</td>
</tr>
<tr>
<td>CAWCR</td>
<td>Centre for Australian Weather and Climate Research</td>
</tr>
<tr>
<td>C&lt;sub&gt;D&lt;/sub&gt;</td>
<td>Drag coefficient</td>
</tr>
<tr>
<td>c&lt;sub&gt;p&lt;/sub&gt;</td>
<td>Specific heat of water</td>
</tr>
<tr>
<td>DBCA</td>
<td>Department of Biodiversity, Conservation and Attractions</td>
</tr>
<tr>
<td>D&lt;sub&gt;p&lt;/sub&gt;</td>
<td>Peak wave direction</td>
</tr>
<tr>
<td>ECMWF</td>
<td>European Center for Medium-Range Weather Forecasts</td>
</tr>
<tr>
<td>EPD</td>
<td>Encounter Probability Distribution</td>
</tr>
<tr>
<td>GHRSSST</td>
<td>Group for High Resolution Sea Surface Temperature</td>
</tr>
<tr>
<td>h</td>
<td>Still-water depth</td>
</tr>
<tr>
<td>H&lt;sub&gt;0&lt;/sub&gt;</td>
<td>Offshore (deep water) wave height</td>
</tr>
<tr>
<td>h&lt;sub&gt;o&lt;/sub&gt;</td>
<td>Offshore still-water depth</td>
</tr>
<tr>
<td>HHT</td>
<td>Highest high tide</td>
</tr>
<tr>
<td>H&lt;sub&gt;s&lt;/sub&gt;</td>
<td>Significant wave height</td>
</tr>
<tr>
<td>H&lt;sub&gt;r&lt;/sub&gt;</td>
<td>Threshold wave height below which the wave-driven circulation is negligible</td>
</tr>
<tr>
<td>h&lt;sub&gt;west&lt;/sub&gt;</td>
<td>Mean depth of the western reef flat</td>
</tr>
<tr>
<td>JPL</td>
<td>Jet Propulsion Laboratory</td>
</tr>
<tr>
<td>K&lt;sub&gt;1&lt;/sub&gt;</td>
<td>Lunar diurnal tidal constituent</td>
</tr>
<tr>
<td>LADS</td>
<td>Laser Airborne Depth Sounder</td>
</tr>
<tr>
<td>LLT</td>
<td>Lowest Low tide</td>
</tr>
<tr>
<td>LTM</td>
<td>Long-term monitoring</td>
</tr>
<tr>
<td>m&lt;sub&gt;0&lt;/sub&gt;</td>
<td>Zeroth moment of wave energy between 2 and 30 sec</td>
</tr>
<tr>
<td>M&lt;sub&gt;2&lt;/sub&gt;</td>
<td>Principal lunar semidiurnal tidal constituent</td>
</tr>
<tr>
<td>MSL</td>
<td>Meal Sea Level</td>
</tr>
<tr>
<td>Abbreviation</td>
<td>Definition</td>
</tr>
<tr>
<td>--------------</td>
<td>------------</td>
</tr>
<tr>
<td>MTR</td>
<td>Mean Tidal range</td>
</tr>
<tr>
<td>MUR</td>
<td>Multi-scale Ultra-high Resolution</td>
</tr>
<tr>
<td>N(t)</td>
<td>Number of particles (N) within the domain at time t</td>
</tr>
<tr>
<td>N_0</td>
<td>Number of particles in the domain at the initial release time t_0</td>
</tr>
<tr>
<td>N_2</td>
<td>Larger lunar elliptic semidiurnal tidal constituent</td>
</tr>
<tr>
<td>NWS</td>
<td>North West Shelf</td>
</tr>
<tr>
<td>O_1</td>
<td>Lunar diurnal tidal constituent</td>
</tr>
<tr>
<td>P</td>
<td>Pressure</td>
</tr>
<tr>
<td>P_0</td>
<td>Offshore (deep water) pressure</td>
</tr>
<tr>
<td>P_1</td>
<td>Solar diurnal tidal constituent</td>
</tr>
<tr>
<td>p-value</td>
<td>Probability of obtaining test results at least as extreme as the results observed</td>
</tr>
<tr>
<td>Q_{tide}</td>
<td>Residual flow associated with tides</td>
</tr>
<tr>
<td>Q_{wave}</td>
<td>Residual flow associated with waves</td>
</tr>
<tr>
<td>Q_1</td>
<td>Larger lunar elliptic diurnal tidal constituent</td>
</tr>
<tr>
<td>Q_L</td>
<td>Latent heat flux</td>
</tr>
<tr>
<td>Q_{Lw}</td>
<td>Longwave radiation flux</td>
</tr>
<tr>
<td>Q_N</td>
<td>Net heat flux</td>
</tr>
<tr>
<td>Q_r</td>
<td>Cross-reef discharge</td>
</tr>
<tr>
<td>Q_S</td>
<td>Sensible heat flux</td>
</tr>
<tr>
<td>Q_{Sw}</td>
<td>Shortwave radiation flux</td>
</tr>
<tr>
<td>R(t)</td>
<td>Retention rate at a time t</td>
</tr>
<tr>
<td>R</td>
<td>Correlation coefficient</td>
</tr>
<tr>
<td>\rho</td>
<td>Water density</td>
</tr>
<tr>
<td>RMSE</td>
<td>Root Mean Square Error</td>
</tr>
<tr>
<td>S(f)</td>
<td>One-dimensional surface elevation spectra</td>
</tr>
<tr>
<td>S_2</td>
<td>Principal solar semidiurnal tidal constituent</td>
</tr>
<tr>
<td>SST</td>
<td>Sea Surface Temperature</td>
</tr>
<tr>
<td>T</td>
<td>Temperature</td>
</tr>
<tr>
<td>TC</td>
<td>Tropical cyclone</td>
</tr>
<tr>
<td>T_{m01}</td>
<td>Mean wave period</td>
</tr>
<tr>
<td>T_p</td>
<td>Peak wave period</td>
</tr>
<tr>
<td>Symbol</td>
<td>Definition</td>
</tr>
<tr>
<td>--------</td>
<td>------------</td>
</tr>
<tr>
<td>TR</td>
<td>Tidal Range</td>
</tr>
<tr>
<td>u</td>
<td>Depth averaged velocity</td>
</tr>
<tr>
<td>U&lt;sub&gt;10&lt;/sub&gt;</td>
<td>Eastward components of wind velocity at 10 m</td>
</tr>
<tr>
<td>UTC</td>
<td>Coordinated Universal Time</td>
</tr>
<tr>
<td>V&lt;sub&gt;10&lt;/sub&gt;</td>
<td>Northward components of wind velocity at 10 m</td>
</tr>
<tr>
<td>WA</td>
<td>Western Australia</td>
</tr>
<tr>
<td>WS</td>
<td>Willmott skill</td>
</tr>
<tr>
<td>X&lt;sub&gt;model&lt;/sub&gt;</td>
<td>Model simulation variable X</td>
</tr>
<tr>
<td>X&lt;sub&gt;obs&lt;/sub&gt;</td>
<td>Field observations variable X</td>
</tr>
<tr>
<td>γ</td>
<td>Wave breaker index</td>
</tr>
<tr>
<td>ΔH&lt;sub&gt;r&lt;/sub&gt;</td>
<td>Phasing of low tidal water level and maximum solar heating in hours</td>
</tr>
<tr>
<td>ΔT&lt;sub&gt;d&lt;/sub&gt;</td>
<td>Daily temperature range</td>
</tr>
<tr>
<td>ΔT&lt;sub&gt;SST&lt;/sub&gt;</td>
<td>Difference between reef temperature and offshore SST temperature</td>
</tr>
<tr>
<td>θ&lt;sub&gt;wave&lt;/sub&gt;</td>
<td>Wave direction</td>
</tr>
<tr>
<td>θ&lt;sub&gt;wind&lt;/sub&gt;</td>
<td>Wind direction</td>
</tr>
<tr>
<td>θ&lt;sub&gt;sp&lt;/sub&gt;</td>
<td>Directional wave spreading</td>
</tr>
</tbody>
</table>
1. Introduction

1.1. Background

Anthropogenic activities and associated environmental changes (e.g., ocean warming, ocean acidification, eutrophication) are major threats to coral reefs. In recent decades, coral reef ecosystems have suffered unprecedented loss of habitat-forming hard corals (Bruno et al. 2009; De’ath et al. 2012; Gardner et al. 2003; Gilmour et al. 2019a; Hughes et al. 2017) and most warm-water coral reefs are projected to rapidly decline by 2040–2050 (Hoegh-Guldberg et al. 2017). This severe degradation of reef ecosystems will cause loss in biodiversity, food and revenue sources for reef-dependent populations (Hoegh-Guldberg et al. 2007; Costanza et al. 2014). While climate action is critical to ensure a future for coral reefs, understanding the natural variability of these ecosystems and identifying environmental conditions that promote coral reef resilience and recovery could advance our ability to conserve and manage reefs at local scales while global threats to coral reefs are being addressed (Goergen et al. 2020).

Hydrodynamic flows play a primary role in regulating the environmental conditions of coral reefs. Such flows directly control the transport and retention of water and organisms in reef systems before being exported to the open ocean. By doing so, they fundamentally influence local environmental conditions such as water temperature (Zhang et al. 2013), nutrients (Falter et al. 2004) and oxygen (Gruber et al. 2017) and can either promote or impede coral reef resilience. For instance, shallow reef flats can become isolated from offshore waters during low tide and experience limited circulation. The resulting stagnant pools of water (i.e., water with long residence times) can increase the likelihood of temperature extremes and potentially enhance thermal stress (Lowe et al. 2016). Conversely, the reef’s outer slopes can be exposed to internal tidal bores (generated by tidal forcing in stratified environments, Wang et al. 2007; Leichter et al. 2012; Green et al. 2019b; Reid et al. 2020). They typically
transport cooler water from below the thermocline over short timescales (i.e., minutes to hours), providing potential relief from temperature extremes (Storlazzi et al. 2020; Wyatt et al. 2020).

In addition to influencing environmental conditions on coral reefs, hydrodynamic flows play an essential role in the reef’s population dynamics and recovery from disturbances through the direct transport and dispersal of marine organisms (Pineda 1999; Cowen and Sponaugle 2009). Most scleractinian corals are broadcast spawners and release gametes directly into the water column where fertilization occurs (Babcock and Heyward 1986). Given their limited swimming abilities, the larvae are highly dependent upon hydrodynamic flows for dispersal. The dispersal through hydrodynamic flows is particularly important in the face of recurrent disturbances (e.g., marine heat waves), as successful recruitment is one of the main ways that reefs can recover naturally from disturbances (Gilmour et al. 2013).

1.2. Hydrodynamic processes on coral reefs

Hydrodynamic processes vary over a wide range of temporal and spatial scale on coral reefs (Monismith 2007; Lowe and Falter 2015). Over large spatial scales (e.g., 10s of kilometres and larger), circulation is often shaped by large-scale regional current systems, tides, buoyancy differences and the Coriolis effect (Monismith 2007). Over finer spatial scales (or reef-scales; e.g., 100s of metres), tides and waves are generally the primary drivers of lagoon circulation and flushing (Callaghan et al. 2006; Monismith 2007; Hearn 2011; Lowe and Falter 2015). Wind stresses often only play a secondary role; however, wind forcing can be important or even dominant in the circulation of deeper and more sheltered lagoons, especially at sites with weak wave and tidal forcing (Atkinson et al. 1981; Lowe et al. 2009a; Dumas et al. 2012). Similarly, within some reefs, buoyancy-driven flows can be important when thermal gradients (e.g., between deep and shallow regions; Herdman et al. 2015) or salinity gradients (e.g., due to evaporation or river discharge) occur.

On wave-driven reef systems, wave forces (radiation stress gradients) generated by breaking wind waves increase the mean water level in the surf zone through wave setup, establishing pressure gradients that drive flow across reef flats and towards back reef or lagoon where present, and eventually back to the ocean through channels in the reef (Munk and Sargent 1954; Young 1989; Symonds et al. 1995; Gourlay 1996; Hench et al. 2008; Lowe et al. 2009a). In contrast, on tide-driven reefs,
tidal water level variations create sea level gradients between the reef and offshore, which drive flow cyclically in and out of a reef through the ebb and flood tide (Dumas et al. 2012; Lowe et al. 2015; Green et al. 2018; Gruber et al. 2019).

A simple metric for classifying reefs based on exposure to waves and tides is the ratio of the mean tidal range (MTR) to annual mean wave height (Hₜ), defined by Lowe & Falter (2015). “Wave-dominated” reefs are defined as experiencing MTR / Hₜ <1 and “tide-dominated” reefs are defined as experiencing MTR / Hₜ >1. Based on this definition, wave-dominated and tide-dominated reefs are estimated to account for approximately 2/3 and 1/3 of reefs worldwide, respectively (Lowe & Falter, 2015). While often dominated by one primary hydrodynamic mechanism, reefs are almost always exposed to a combination of interacting hydrodynamic forces. For example, reefs with moderate-to-large tidal ranges can be frequently exposed to high energy wave conditions generated by storm events either locally or from remote sources of large swell (e.g., Cheriton et al. 2016; Gilmour et al. 2019a; Puotinen et al. 2020).

Overall, the relative importance of these physical forces often depends on a combination of the local wave conditions, tidal range, and properties of the reef morphology (e.g., reef depth, width and fore-reef slope).

Atolls represent a geologic endmember for reefs and are a common feature throughout the world’s tropical oceans, where ~30% of the reef systems have been classified as “atolls” (~1490 reef systems include ~439 atoll reefs; Goldberg 2016). Atoll geomorphology includes ring-shaped reef flats encircling a lagoon that is connected to the surrounding ocean through one or multiple channels. Globally, there is a dominance of atolls with relatively small tidal ranges (i.e., wave-dominated), particularly in the Pacific Ocean; but about ~10% of the world’s atolls—mainly off northwestern Australia, the Coral Triangle (western Pacific Ocean) and eastern Africa—are tide-dominated (Green 2018). Yet, tide-dominated atolls can also be sporadically or regularly exposed to large swells or tropical cyclones, which could significantly modify the overall atoll circulation and flushing mechanisms. Atolls experiencing both large waves and tides remain poorly studied, and thus how those interactions shape different flushing regimes and key ecologically relevant processes have received little attention in the literature.
1.3. Mermaid Reef

The North West Shelf (NWS) of Australia extends from the North-West Cape in the south to the Timor Sea in the North (Figure 1-1a). Tidal dynamics are dominated by the semi-diurnal principal lunar ($M_2$) and solar ($S_2$) components and experience some of the largest tides around Australia, with coastal mean spring tides ranging from 11 m in the inshore region to approximately 4 m on the continental shelf (Holloway 1983). The NWS also experiences a low to moderate wave energy climate (annual mean $H_s < 2$ m) with a wave direction predominantly from the southwest forced by oceanic swells (annual mean $\theta_{\text{wave}} \sim 240^\circ$) (Drost et al. 2017).

The Rowley Shoals is a reef system located on the edge of the outer continental shelf of the NWS (Figure 1-1a), composed of three coral reef atolls (Mermaid Reef, Imperieuse Reef and Clerke Reef). The reef system is located ~300 km from the closest centre of urbanisation (i.e., Broome) and ~400 km from the closest neighbouring reef system (i.e., Scott Reef). The surrounding waters are on average 500 m deep, descending to more than 2000 m off the edge of the continental shelf. Mermaid Reef, the northernmost atoll of the Rowley Shoals, is the study location for this thesis (Figure 1-1b). Mermaid Reef (14.9 x 7 km; covering ~87.5 km$^2$) has a near-continuous reef flat that encloses a central lagoon (50 km$^2$ and ~20 m-deep). An 8 m-deep, 250 m-wide channel is located on the northeast side and is the primary opening to the open ocean. Most of the atoll is submerged at mean sea level (MSL), except for a small (up to ~400 m in diameter) sandy island located on the northeast side of the atoll that is ~2.1 m above mean sea level. The western reef flat varies in width from 1600 to 2500 m with depths ranging from 0.7 to 2.0 m. The eastern reef flat is much narrower, varying in width from 500 to 700 m, with depths ranging from 1.2 to 5 m. Hence, the western and eastern reef flats of the atoll differ in elevation up to a few meters (on average ~1.5 m).

The first morphological and hydrodynamic observations of Mermaid Reef were provided by Fairbridge (1950) and since then numerous studies have worked toward characterising its biological characteristics (e.g., Long and Holmes 2009; Bryce et al. 2018; Gilmour et al. 2019a). Of particular relevance is a long-term coral monitoring program established in 1996 by the Australian Institute of Marine (AIMS). Since the mid-1990s, the Rowley Shoals have maintained a high and stable coral cover and have not experienced a major coral bleaching event, contrary to most coral reefs in Western Australia and around the world (Gilmour et al. 2019a; Darling et al. 2019).
However, minor bleaching was documented in 2005, 2016 and 2020 (Rosser and Gilmour 2007; Gilmour et al. 2019b; Gilmour et al. 2021). Connectivity between the three atolls and within the reef slope and lagoons were investigated using genetic analyses, which showed periodic dispersal and connectivity among and within the three reefs (Underwood 2009; Thomas et al. 2019). However, such processes have been investigated separately from the reef hydrodynamics, as the physical environment of the Rowley Shoals remains relatively unstudied.

![Figure 1-1. LANDSAT image of (a) the North West Shelf (NWS) of Australia, showing the Rowley Shoals and Mermaid reef (indicated by the red square), Scott Reef and Ashmore Reef. Inset map shows Australia’s North West Shelf and (b) shows Mermaid Reef.](image)

1.4. Research questions

Although the individual effects of both wave- and tide-driven flows on coral reef atolls are relatively well understood, there remain considerable gaps in our understanding of how they interact to control the circulation, flushing and residence time on coral reef atolls. As a result, a comprehensive understanding of how such mechanisms shape key ecologically relevant processes such as temperature variability and larvae dispersal (Figure 1-2) is still lacking. The aim of this research is to specifically address the following questions:

- Chapter 2: How do reef-scale hydrodynamic processes, specifically waves and tides, independently and jointly shape the circulation and flushing of Mermaid Reef? How can we quantify the relative importance of each forcing and what is the role of the reef morphology?
• Chapter 3: How do hydrodynamic and atmospheric processes, including surface waves, tides, internal waves and solar radiation interact to shape the spatio-temporal temperature variability within Mermaid Reef? How are different reef zones (e.g., lagoon, reef flat, fore-reef) within the same reef system influenced by different oceanic and atmospheric drivers?

• Chapter 4: How do reef-scale hydrodynamic processes, specifically waves and tides, and their temporal variability over long time scales (~40 years) shape the fine-scale connectivity of Mermaid Reef? What are the main dispersal pathways within and around Mermaid Reef? How can the temporal variability of reef-scale hydrodynamic processes give way to new dispersal pathways and what happens if such processes are not considered in the characterisation of coral reef connectivity?

Figure 1-2. Conceptual overview of the thesis and chapter overview. Coral reefs are exposed to a wide range of hydrodynamic processes including to surface waves, tides, regional currents and internal waves. Surface waves and tides and the reef morphology control the circulation and flushing inside of the atoll (Chapter 2). By doing so, they also control the thermal variability and connectivity inside the reef (Chapter 3 and 4). However, those processes are also influenced by hydrodynamics occurring outside of the reef including but not limited to the propagation of internal waves or regional currents. Schematics not to scale.
1.5. Thesis structure

This thesis is, in accordance with postgraduate and research scholarships regulation 31(1) of the University of Western Australia, presented as a series of scientific manuscripts that resulted from the study. The five chapters of the thesis consist of an introductory account of the research (Chapter 1), followed by three chapters representing the core body of research (Chapters 2-4), and a final chapter synthesizing the main findings and conclusions of the thesis (Chapter 5). Some repetition of introductory and methodological material of Chapters 2-4 was necessary to ensure they stand as individual publishable units.

In Chapter 2 (‘Wave- and tide-driven flow dynamics within a coral reef atoll off northwestern Australia’), field measurements of water levels, wave conditions, and currents were combined with a numerical ocean circulation model to investigate the relative importance of waves and tides in driving the circulation and flushing at Mermaid Reef. This chapter extends our understanding of changing drivers (i.e., dominance of waves or tides) of reef flushing and characterises the role of atoll morphology in shaping their relative importance.

In Chapter 3 (‘Drivers of temperature variability within a coral reef atoll off northwestern Australia’), field measurements of water temperature across Mermaid reef were used to investigate the role of atmospheric and oceanographic processes across the various reef zones including the fore-reef, reef flat, and lagoon. These findings extend our understanding of the broad temporal and spatial spectrum of temperature variability and associated drivers across a single reef environment.

In Chapter 4 (‘Hydrodynamic drivers of fine-scale connectivity within a coral reef atoll off northwestern Australia’), the validated model presented in Chapter 2 was used to investigate the reef-scale hydrodynamic drivers of connectivity of the dominant coral genus Acropora spp. during ~40 years of mass spawning at Mermaid Reef. We highlight the effect of tropical cyclones on connectivity pathways through the modification of local reef hydrodynamics. These findings extend our understanding of how critical reef-scale hydrodynamic processes are for accurately estimating connectivity and specifically illustrates the consequences when those processes are overlooked.

The final chapter (Chapter 5) presents a general discussion of the thesis and concluding remarks. This chapter draws together the main findings of the thesis and
discusses the implications of this research in a broader context and outline some future research questions.
2. Wave- and tide-driven flow dynamics within a coral reef atoll off northwestern Australia

This work is published in the *Journal of Geophysical Research: Oceans*.

2.1. Abstract

Waves and tides are often the two primary forcing mechanisms responsible for driving hydrodynamic processes within coral reefs worldwide. Although wave- and tide-driven flows are individually well understood, there remain considerable gaps in our understanding of how their interactions control the circulation, and consequently how they shape a range of ecological processes. During eleven months of hydrodynamic measurements across Mermaid Reef, a coral reef atoll off northwestern Australia, the atoll was regularly exposed to a range of wave and tidal conditions. Using a validated wave-flow numerical model, we showed that wave- and tide-driven processes interacted to drive the reef’s circulation through several mechanisms including wave-current interactions and tidal water level modulation of wave-driven flows. The atoll morphology, particularly the higher elevation of the western reef flat, was found to be a key factor controlling the relative importance of waves and tides. Wave-driven processes dominated for tidal ranges smaller than required to expose the shallower western reef flat. In contrast, tidal processes dominated for larger tidal ranges, when the western reef flat temporarily acted as a physical barrier to incoming and outgoing flows. The residual (tide-averaged) circulation was consistently directed eastward across the atoll. Over time scales of several months to years, Mermaid Reef can be classified as a tide-dominated reef. However, due to the incident wave energy and spring-neap tidal range variability, the relative importance of the dominant hydrodynamic drivers can vary on time scales of hours to days allowing
wave processes to dominate the reef circulation.

2.2. Introduction

The circulation of water within reef systems and water exchange with the surrounding ocean regulates reef environmental conditions (e.g., temperature variability) and the transport of material within and between reefs (e.g., coral larvae, nutrients and sediment; Lugo-Fernández et al. 2001; Storlazzi et al. 2004; Falter et al. 2004; Gruber et al. 2019). Reef circulation is generally driven by a combination of oceanic and atmospheric processes including waves; tides; wind; buoyancy; and regional-scale ocean circulation (Monismith 2007; Lowe and Falter 2015), with the relative importance of each mechanism varying by the conditions at a site and scale of the flows considered (Monismith 2007). At the coastal or island scale (e.g., scales of 10s of kilometres and larger), circulation is often shaped by large-scale regional current systems, tides, buoyancy differences and the Coriolis effect (Monismith, 2007). At the reef scale (e.g., scales of 100s of meters), tides and waves are generally the primary drivers of lagoon circulation and flushing (Callaghan et al. 2006; Monismith 2007; Hearn 2011; Lowe and Falter 2015), with wind stresses often playing only a secondary role; however, wind forcing can be important or even dominant in the circulation of deeper and more sheltered lagoons, especially at sites with weak wave and tidal forcing (Atkinson et al. 1981; Lowe et al. 2009a; Dumas et al. 2012). Similarly, within some reefs, buoyancy-driven flows can be important when thermal gradients (e.g., between deep and shallow regions; Herdman et al. 2015) or salinity gradients (e.g., due to evaporation or river discharge) occur.

For wave-driven reefs, wave forces (radiation stress gradients) generated by breaking waves increase the mean water level (wave setup) in the surf zone, establishing pressure gradients that drive flow across reef flats and into a lagoon, with water eventually returning back to the ocean through channels in the reef (Figure 2-1a and b) (Munk and Sargent 1954; Young 1989; Symonds et al. 1995; Gourlay 1996; Lowe et al. 2009a). For tide-driven reefs, tides create sea level gradients between the reef and offshore that drive oscillatory flows in and out of a reef over a tidal cycle (Figure 2-1a, c and d) (Dumas et al. 2012; Lowe et al. 2015; Green et al. 2018; Gruber et al. 2019). The relative importance of these physical forces often depends on a combination of the local wave conditions, tidal range, and properties of the reef morphology (e.g., reef depth, width and fore-reef slope).
While there is no strict definition of when wave forcing versus tidal forcing will be most important, one simple metric for classifying reefs based on exposure to waves and tides is the ratio of the mean tidal range \( (MTR) \) to annual mean wave height \( (H_s) \): i.e., ‘wave-dominated’ reefs where \( MTR / H_s < 1 \) and ‘tide-dominated’ reefs where \( MTR / H_s > 1 \) (Lowe & Falter, 2015). Based on this definition, wave-dominated and tide-dominated reefs were estimated to account for approximately 2/3 and 1/3 of reefs worldwide, respectively (Lowe & Falter, 2015). However, while often dominated by one hydrodynamic forcing, reefs are almost always exposed to a combination of interacting hydrodynamic forces.

On reef systems exposed to both wave- and tide-driven flows, several mechanisms drive the interaction between waves and tides. Tidal variations in the water depth over reefs modify how waves break as the wave setup generation is governed by the rate of wave attenuation in the surf zone and the local water depth. For given incident wave condition, setup is generally enhanced at shallower tidal depths; however, the effect of bottom stresses can also be enhanced in shallower water columns, restricting wave-driven flows (Symonds et al. 1995; Hearn 1999; Jago et al. 2007; Gourlay 2011;
Wegner 2013; Buckley et al. 2015). How these momentum balances between wave setup (pressure gradients) and bottom stresses respond to depth variations governs the response of wave-driven mean flows across the reef to tidal variations. In addition, as waves transform and break on reefs, the associated wave-current interactions result from the transformation of the wave-driven currents owing to background tidal currents. Tide-driven currents can then appear as enhanced (reduced), if the wave-driven current is oriented in the same (opposite) direction (Gourlay, 2011). For example, during falling phases of the tide, tide-driven currents can occasionally be blocked by wave-driven currents when significant wave heights are sufficiently large, resulting in continuous inflow throughout the tidal cycle (Gourlay and Hacker, 2008a; Gourlay and Hacker, 2008b).

In this study, we investigate the hydrodynamic processes driving the circulation at Mermaid Reef, a coral reef atoll (annular reef enclosing a central lagoon) that is part of the Rowley Shoals, located on Australia’s North West Shelf (NWS) (Figure 2-2). At Mermaid Reef, $\text{MTR} / H_s \sim 0.6$ is smaller than 1, and thus could be classified as a tide-dominated reef. However, by using a combination of field observations and numerical modelling, we show that Mermaid Reef is regularly exposed to high wave energy events and a variety of tidal ranges over a spring neap cycle, making it an ideal site to test how these forcing mechanisms govern atoll circulation. Specifically, we investigate how the atoll morphology and the relative roles of hydrodynamic drivers (i.e., waves and tides) control the atoll circulation and identify the key mechanisms through which waves and tides interact. The study is organised as follows: a description of the study site, experimental and wave-flow numerical model design and analysis are presented in section 2.3. Results are presented in section 2.4, where we first describe the field observations collected between 26/11/2017 and 14/10/2018 (section 2.4.1), followed by a description of the hindcast numerical simulations (Section 2.4.2). Finally, we test a series of idealized hydrodynamic conditions at Mermaid Reef to isolate the specific processes driving the circulation under distinct representative forcing conditions (Section 2.4.3). In Section 2.4, we discuss the results and provide a new conceptual framework for tide-driven circulation on atoll reefs with asymmetrical reef flats and summarize how the tide and wave-driven processes and the atoll morphology shape the hydrodynamic regimes and reef circulation.
2.3. Methods

2.3.1. Site description

Mermaid Reef is one of three coral reef atolls that make up the Rowley Shoals, located on the edge of Australia’s NWS. The NWS experiences a low to moderate wave energy climate ($H_s \sim 1 - 2$ m), with a wave direction predominantly from the southwest forced by oceanic swell (~240 °N) (Drost et al. 2017). The NWS also experiences some of the largest tides around Australia, with coastal mean spring tides ranging from 11 m in the inshore region to approximately 4 m further out on the continental shelf. The tidal ellipses (Figure 2-2b, derived from the TPXO8.0 global tide solution; Egbert & Erofeeva, 2002), shown for the dominant semi-diurnal $M_2$ constituent on the NWS, are orientated in a southeast-northwest direction, with the tidal range (related to the major axis of the current ellipses) increasing towards the southeast as the depth decreases over the continental shelf.

Bathymetry for the atoll was obtained from a 25 m resolution bathymetric dataset collected using Laser Airborne Depth Sounder and provided by the Australian Navy (Hydrographic Service RAN). The bathymetric measurements were collected relative to the lowest astronomical tide and were converted to mean sea level (MSL; relative to the Australian Height Datum) using the correction coefficients provided by the Australian Hydrographic Office (+ 2.1 m), and hence mean sea level was set to zero elevation ($\eta = 0$). Each depth reported throughout this study is referenced relative to MSL. Mermaid Reef (14.9 × 7 km; covering ~87.5 km$^2$) has a near-continuous reef flat that encloses a central lagoon (50 km$^2$ and ~20 m-deep). An 8 m-deep, 250 m-wide channel is located on the northeast side and is the primary opening to the open ocean (Figure 2-2a). The majority of the atoll is submerged at MSL, except for a small (up to ~400 m in diameter) sandy island located on the northeast side of the atoll that is ~2.1 m above MSL. The western reef flat varies in width from 1600 to 2500 m with depths ranging from 0.7 to 2.0 m. The eastern reef flat is much narrower, varying in width from 500 to 700 m, with depths ranging from 1.2 to 5 m. Hence, the western and eastern reef flats of the atoll differ in elevation by up to a few meters (on average ~1.5 m) (Figure 2-2c). The surrounding waters are on average 500 m deep and fall to more than 2000 m off the edge of the continental shelf.
Figure 2-2: (a) Site location and bathymetry (relative to MSL) of Mermaid Reef. Brown colours represent the reef flat (depths 2 m above to 2 m below MSL). White lines denote the cross sections used to calculate flow in/out of the atoll using the numerical model (see section 2.3.3). (b) The three atolls comprising the Rowley Shoals: Imperieuse, Clerke and Mermaid Reef. Tidal current ellipses (based on the dominant M2 tide) are superimposed, as derived from the TPXO8.0 global tidal solution. The inset map shows the Rowley Shoals’ location (red dot) on Australia’s North West Shelf and (c) bathymetry cross section from the west to the east of the atoll (A to B on Figure 2-2a).
2.3.2. Field observations

2.3.2.1. Data collection

During an eleven-month field study (26/11/2017 - 14/10/2018), an array of hydrodynamic instruments was deployed across Mermaid Reef to measure velocity profiles and pressure (Table 2-1). Wind speed and direction were measured every 6 hours at the Bureau of Meteorology weather station (ID: 200713, -17.52° N, 118.95°E, located at Imperieuse Reef, about ~85 km southwest of Mermaid Reef; Figure 2-2b).

Table 2-1: Instrument deployment information (26/11/2017 - 14/10/2018)

<table>
<thead>
<tr>
<th>Site</th>
<th>Instrument</th>
<th>Depth (MSL, m)</th>
<th>Sampling information</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1 (Fore-reef)</td>
<td>NORTEK 1 MHz AWAC</td>
<td>13.4</td>
<td><strong>Currents:</strong> Profile interval = 15 min; Bin size * bin number = 1 m * 20</td>
</tr>
</tbody>
</table>
|            | RDI 600 kHz Acoustic Doppler Current Profiler (ADCP) | 11.4           | Waves: 2048 samples at 2 Hz every hour  
|            | **Currents:** Profile interval = 5 min Bin size * bin number = 0.5 m * 39 |
| S2 (Lagoon)| NORTEK 2 MHz Aquadopp Profiler (ADP) | 7.2            | **Currents:** Profile interval = 5 min Bin size * bin number: 0.2 m * 35         |
| S3 (Channel)| NORTEK 2 MHz ADP HR                  | 2.7            | **Currents:** Profile interval = 1 sec Bin size * bin number = 0.07 m * 11     |
| S4 (Reef flat)| NORTEK 2 MHz ADP HR                 |                | **Pressure:** Sampling interval = 1 Hz                                      |
| S6 (fore-reef), S7, S8, S9, S11 (reef flat) and S10 (lagoon)| RBR Solo3D |                | NA                                                                                 |

2.3.2.2. Data analysis

2.3.2.2.1. Water levels and wave setup

Following the approach described by Lowe et al. (2009a), the burst-averaged pressure (P) data can be decomposed into contributions from atmospheric pressure (P\text{atm}), a reference still-water depth (h) (e.g., relative to mean sea level), and the water level associated with tides (\eta\text{tide}) and wave setup (\eta\text{setup}). By assuming that wave setup is negligible at the fore-reef site (S1, used as the reference water level), the
difference in pressure ($\Delta P$) between the pressure $P$ at an arbitrary site and the pressure $P_0$ at the reference site S1 is:

$$\Delta P = P - P_0 = \eta_{\text{setup}} + h - h_0$$

(2.1)

A low pass filter was then applied to $\Delta P$ to obtain the subtidal variability (PL66 filter, Alessi et al. 1985). Estimating the wave setup from $\Delta P$ requires knowing the still water level difference between the pair of sites ($h-h_0$). As the instrument elevations were not surveyed, we inferred this water level difference by assuming wave setup varied linearly with offshore significant wave height $H_s$ at S1 according to:

$$\eta_{\text{setup}} = aH_s - b$$

(2.2)

Eq. (2.1) can then be re-written as:

$$\Delta P = aH_s - c \quad \text{with} \quad c = b - h + h_0$$

(2.3)

In Eq. (2.3), the coefficient $c$ was obtained from a linear least square regression of $\Delta P$ versus $H_s$. The coefficient $b$ was obtained from the depth-averaged current measurements on the reef flat (S4) by evaluating the threshold wave height ($H_r$) below which the wave-driven circulation is negligible, that is where $H_0 = H_r$, and $\eta_{\text{setup}}$ on the reef is zero such that $b = aH_r$, where $b = 0.31$.

Finally, the water level associated with tides ($\eta_{\text{tide}}$), was obtained by removing local atmospheric pressure variations and assuming a mean seawater density of 1025 kg/m$^3$. To implement a common vertical reference datum, we assumed that the water level was uniform at all sensor locations at high tide and determined the mean depth offset of each instrument. Next, we adjusted each instrument so that $\eta = 0$ m corresponded to the mean sea level measured outside the atoll at S1 during the study period (Lowe et al. 2015). The tidal range ($TR$) was then defined as the height difference between high tide and low tide for each tidal cycle.

2.3.2.2.2. Waves

Directional wave spectra were computed using the Maximum Likelihood Method on water elevations from Acoustic Surface Tracking (Thomson and Emery 2014) from the AWAC deployed on the fore-reef (S1). For all shallower wave sites with pressure sensors, one-dimensional surface elevation spectra $S(f)$ were derived from the pressure time series using linear wave theory and used to calculate significant wave heights as $H_s = 4(m_0)^{1/2}$, where $m_0$ is the zeroth moment of wave energy between 2 and 30 sec.
2.3.2.2.3. **Current velocities**

Current velocities, wave spectra and water level data were quality controlled to remove outliers and time-averaged onto a uniform 10-min time interval. The velocity was averaged over all vertical bins to produce time series of depth-averaged current velocities. Depth-averaged current velocities were then separated into subtidal and tidal components. The subtidal component was determined by applying a low-pass filter using the PL66 filter with a half-period of 33 h (Alessi et al. 1985). The tidal component was obtained by subtracting the subtidal time series from the original time series, thus containing any flow variability with timescales shorter than 33 h. A principal component analysis (PCA) was then applied to each component to rotate the velocities into streamwise (major axis) and cross-stream (minor axis) velocities (Table 2-1).

2.3.3. **Numerical modelling**

A numerical coupled wave-flow model based on Delft3D Flexible Mesh (FM) was developed for Mermaid Reef (Section 2.3.3.1) and compared to field data (Section 2.3.3.2) to initially the accuracy of the model to simulate the range of hydrodynamic conditions measured during the field experiment. The validated model was then applied with idealized forcing to isolate the role of waves and tides in the atoll flow and was used to investigate how the two processes interact (Section 2.3.3.3).

2.3.3.1. **Delft3D Flexible Mesh combined wave-flow model**

A coupled version of Delft3D FM suite flow and wave modules was used to simulate the hydrodynamics of Mermaid Reef for a period of 3 months (1/12/2017 - 1/03/2018), encompassing spring and neap tidal ranges and a range of wave conditions. The Delft3D FM suite has been successfully applied to simulate the hydrodynamics of reefs (e.g., Green et al. 2018; Baird et al. 2020) and other complex coastal systems including estuarine environments (Thanh et al. 2017).

The flow module, D-Flow FM (http://content.oss.deltares.nl/delft3d/manuals), solves the unsteady shallow water equations derived from the three-dimensional Navier-Stokes equations for incompressible free surface flow using unstructured meshes (as a combination of quadrilaterals and triangles). The model domain covered a 45 × 40 km region and was designed with a combination of rectangular and triangular cells progressively varying from 500 m resolution in the deep (offshore) region to 30 m resolution inside the reef, allowing for an efficient, yet accurate,
representation of the fine scale bathymetry features and computation of its hydrodynamics using a reduced number of computational cells. This numerical model was run in 2DH mode (horizontal depth-averaged) and provided the necessary resolution to resolve fine-scale flows, whilst still being able to simulate the larger-scale tidal circulation around the atoll and its interactions with the atoll system. The influence of the Earth’s rotation was accounted for through a Coriolis parameter $f$, based on a constant latitude (-17.1°N). The four model boundaries were forced every 10 km with the eight primary tidal constituents ($M_2$, $S_2$, $N_2$, $K_2$, $K_1$, $O_1$, $P_1$, $Q_1$) derived from the TPXO8.0 global tide solution (1/30° resolution, Egbert & Erofeeva, 2002). The water levels measured on the fore-reef (S1) showed good agreement with the water levels derived from the TPXO8.0 global tide solution (Supporting information in Section 2.7; Figure S 2-1b, R ~0.97; p-value <0.01). Bed stresses ($\tau_b$) were parameterised using a quadratic drag law $\tau_b = \rho C_D |\vec{u}|\vec{u}$, where $C_D$ is a depth variable drag coefficient calculated using a Manning formulation $C_D = g n^2/h^{1/3}$, $h$ is the water depth, $g$ is the gravitational acceleration and $n$ is the Manning coefficient (Roelvink & Reniers, 2012). For water depths ranging from 0.5 m to 20 m across the atoll, a Manning coefficient of 0.06 yields to $C_D$ values ranging from 0.013 to 0.021, which is well within the range of $C_D$ values reported for numerical and field investigations of reef environments (Kraines et al. 1999; Lowe et al. 2009b; van Dongeren et al. 2013; Quataert et al. 2015; Cuttler et al. 2018; Rogers et al. 2018).

The wave module, D-Waves (http://content.oss.deltares.nl/delft3d/manuals/), is based on the third-generation SWAN (Simulating WAves Nearshore, Booij et al. 1999) model, which computes wave propagation, wave generation by wind, nonlinear wave-wave interactions and dissipation. D-Waves presently does not allow the use of unstructured grids but was implemented on triple nested grids which covered the reef flat contours around the atoll (curvilinear grid, cross-reef resolution of 20 m and along-reef resolution of 50 m), small domain around Mermaid Reef (18 × 10 km rectangular grid, 125 m resolution) and finally a larger domain around Mermaid Reef (55 × 55 km rectangular grid, 500 m resolution) (see supporting information Figure S 2-2a, b, c and d). The four boundaries of the domain were forced every 10 km with spatially and time-varying wave and wind conditions. Hourly significant wave height $H_s$, peak period $T_p$, direction $D_p$, directional spreading $\theta_{sp}$, wind speed and direction, derived from the Centre for Australian Weather and Climate Research (CAWCR) Wave Hindcast, an ocean wave hindcast updated monthly from 1979 to present (Durrant et
al. 2019), which uses WaveWatch III. The wave parameters were used to specify a parametric directional wave spectrum, assuming a JONSWAP temporal distribution with a default peak enhancement factor value of 3.3. Wave-wave interactions and energy dissipation due to white capping, breaking (with a constant breaker index, \( \gamma \), of 0.73), and bottom friction (based on Madsen et al. (1989) eddy-viscosity model with a friction coefficient of 0.1 m), were included. Other model parameters were used in default values as described in the manual. The significant wave height and peak period measured on the fore-reef (S1) showed good agreement with the output from CAWCR Wave Hindcast (see supporting information Figure S 2-1a, c and d; \( R \sim 0.94; p\)-value <0.01 and \( R \sim 0.67; p\)-value <0.01, respectively).

Bathymetry for both the flow and wave modules was based on a combination of the 25 m resolution gridded bathymetry of the Rowley Shoals atolls, referenced to MSL and a 250 m resolution Australian Bathymetry and Topography Grid produced by Geoscience Australia compiling different bathymetric datasets (Whiteway 2009). Both datasets were interpolated by Delaunay triangulation to the flexible mesh grid for D-Flow FM and to the regular mesh grids for D-Waves. The two-way coupling between D-Flow FM and D-Waves was performed using a communication file with an hourly data transfer between the two modules. The dissipation-based wave forces computed by D-Waves was applied as forcing terms in the flow momentum equations. The flow bed shear stress increases nonlinearly by wave orbital velocity contributions using the formulation of Fredsøe (1984). Water depths and velocity fields calculated by D-Flow FM are passed on by D-Waves to SWAN when updating the wave fields.

2.3.3.2. Model performance metrics

To assess the accuracy of the model performance in simulating the range of hydrodynamic conditions measured during the field experiment, time series of water level and current velocity were extracted from the numerical simulations at the location of the field measurements and compared to the field measurements. The model simulation variables (\( X_{\text{model}} \)) were quantitatively compared to field observations (\( X_{\text{obs}} \)) by computing the root-mean-squared error (RMSE, Eq. 2.4) and the Willmott skill score (\( \text{Skill} \), Willmott et al. 1985), Eq. 2.5):
\[
RMSE = \sqrt{\frac{1}{N} \sum_{i=1}^{i=N} (X_{obs} - X_{model})^2} 
\]

\[
Skill = 1 - \frac{\Sigma(X_{model} - X_{obs})^2}{\Sigma(|X_{model} - X_{obs}| + |X_{obs} - X_{obs}|)^2} 
\]

where the overbar indicates time averaging of these values over a specified time period. A Skill of 1 indicates perfect agreement between the observations and the model predictions, whereas a value of 0 indicates no agreement.

2.3.3.3. Idealized simulations

To isolate the effect of tidal and wave forcing and understand how they interact to determine the atoll circulation, the validated model was used to conduct a series of idealized simulations with a range of forcing conditions that occur at the site. ‘Wave-only’ scenarios were first tested (Section 2.4.3.1) using significant wave heights ranging from 0 to 3 m with a constant peak wave period of 10 s, constant peak wave direction of 270°N (eastward), which represents the average direction of incident waves at the site (see Section 2.4.1), and constant mean sea level. ‘Tide-only’ scenarios were tested (Section 2.4.3.2) with waves turned off in the model and tidal ranges ranging from 0.5 to 4 m, generated by the tidal amplitude and phase difference observed across the domain for the \( M_2 \) component. Finally, ‘combined waves and tides’ scenarios were tested by combining the ‘wave-only’ and ‘tide-only’ scenarios (Table 2-2) where the module coupling was applied. The idealized simulations captured the range of hydrodynamic conditions experienced at the atoll (Figure 2-3a). Each forcing condition was held constant within each scenario and the model was run for 49.6 h (four tidal cycles). The first 24.8 h (two tidal cycles) were discarded to remove model “spin-up” effects with the remaining 24.8 h retained for analysis due to the hydrodynamics having reached a quasi-steady state (not shown).

The flow entering and exiting the atoll was quantified using the model output of volumetric flow rates \( Q_i \) (in \( \text{m}^3/\text{s} \), for the \( i^{th} \) cross section defined along the reef flat around the atoll as shown in Figure 2-1a). We use a convention where positive (negative) flow rates indicate flux entering (exiting) the atoll lagoon. The overbar indicates the time-averaged flow rate, \( \bar{Q}_i \), i.e., the residual flow rate over a complete tidal cycle (12.4 h, data outputted every 10 min). Finally, we define the cross section-
averaged discharge as the volumetric flow rate \( Q_i \) or \( \bar{Q}_i \) respectively) divided by the length of the \( i \)th cross section \( L_i \) in m:

\[
\langle q_i \rangle = \frac{Q_i}{L_i} \quad \text{or} \quad \langle \bar{q}_i \rangle = \frac{\bar{Q}_i}{L_i}
\]  

(2.6)

We define cross section 1 to 8 as “west” and 9 to 16 as “east”, as the average discharge along the western and eastern sections of the atoll, respectively:

\[
\langle q_{\text{west}} \rangle = \frac{\sum_{i=1}^{8} Q_i}{\sum_{i=1}^{8} L_i} \quad \text{and} \quad \langle q_{\text{east}} \rangle = \frac{\sum_{i=9}^{16} Q_i}{\sum_{i=9}^{16} L_i}.
\]  

(2.7)

Table 2-3: Hydrodynamic parameters used within the series of idealized scenarios. \( H_s \) = significant wave height, \( T_p \) = peak period and \( TR \) = tidal range.

<table>
<thead>
<tr>
<th>Hydrodynamic forcing</th>
<th>( H_s ) (m)</th>
<th>( T_p ) (s)</th>
<th>( TR ) (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wave-only (i.e., no tides)</td>
<td>0.5, 1, 1.5, 2, 2.5, 3</td>
<td>10</td>
<td>-</td>
</tr>
<tr>
<td>Tide-only (i.e., no waves)</td>
<td>-</td>
<td>-</td>
<td>0.5, 1, 1.5, 2, 3, 4</td>
</tr>
<tr>
<td>Combined waves and tides</td>
<td>0.5, 1, 1.5, 2, 2.5, 3</td>
<td>10</td>
<td>0.5, 1, 1.5, 2, 3, 4</td>
</tr>
</tbody>
</table>

### 2.4. Results

#### 2.4.1. Observations

**2.4.1.1. Offshore forcing conditions**

The full deployment (26/11/2017 - 14/10/2018) captured 24 spring-neap tidal cycles and a wide range of wave conditions (Figure 2-3a). At S1, the tidal range averaged 2.4 m (mean neap TR of 0.9 m; mean spring TR of 3.9 m, Figure 2-3b) and the significant wave height averaged 0.9 m (varying from 0.3 to 3.2 m; Figure 2-3b). The incident waves measured at S1 had a mean wave period \( T_p \) averaging \( \sim 11 \) s (varying between 2 and 14 s; Figure 2-3c) and a mean wave direction averaging \( \sim 270^\circ \text{N} \) (i.e., coming from the west, varying from 55 to 350°N; Figure 2-3d). The wind speed averaged around \( \sim 30 \) km/h with a direction predominantly from the southwest (mean direction = 200°N, Figure 2-3e).

**2.4.1.2. Wave conditions and wave setup**

Over a cross-reef transect on the western side of the atoll (Figure 2-4a), both fore-reef sites (S1 and S8) experienced comparable wave heights, varying approximately weekly due to the cyclic arrival of swell events (Figure 2-4b). Wave heights on the reef
flat were strongly dependent on tidal depth variations (Figure 2-4c). When $H_s$ reached ~3 m offshore, wave setup reached values as high as ~0.12 m on the reef flat (S9; Figure 2-4d) and ~0.09 m in the lagoon (S10, not shown). There was a strong correlation between $\eta_{setup}$ and $H_s$ ($R = 0.91$, $p$-value <0.01) over the eleven-month period (a two-month sample period is shown in Figure 2-4d), indicating that the wave setup increased proportionally to the incident offshore wave height.

Figure 2-3: (a) Percent occurrence of significant wave height and tidal range over the study period (26/11/2017 to 14/10/2018) at the fore-reef site (S1). Oceanographic conditions during a three-month period (1/12/2017 to 1/03/2018): (b) water level relative to mean sea level, (c) significant wave height ($H_s$) and peak period ($T_p$), (d) incoming wave direction ($\theta_{wave}$) at the fore-reef site (S1) and (e) wind speed and incoming direction ($\theta_{wind}$) at the Bureau of Meteorology weather station (ID: 200713).

2.4.1.3. Tidal water level variability

In the lagoon (S2), the tidal range averaged 2.0 m (mean neap $TR = 0.7$ m and mean spring $TR = 3.5$ m; Figure 2-5a) over the eleven-month period. The average duration of the falling tide was consistently ~1.2 hours longer than the average duration of the rising tide, whereas equivalent values for fore-reef sites were split evenly over the dominant ~12.4-hr semi-diurnal ($M_2$) tidal cycles. As a result, low tide
water levels inside the lagoon were typically 0.1 - 0.2 m and 0.3 - 0.6 m higher than on the fore-reef during neap and spring tide, respectively (Figure 2-5a). This pattern is indicative of ‘tidal truncation’ by topographic constriction with the fore-reef water levels falling well below the reef flat elevation during low tides, causing the reef flat to become exposed (Figure 2-5b) and restricting water exchanges with the open-ocean (Lowe et al. 2015). At these times, the flow in or out of the lagoon can only happen through the channel and where the reef flat is submerged, until the tidal water levels are high enough to submerge the reef flat again.

Figure 2-4: (a) Cross section of the western reef flat of Mermaid Reef with S1, S8 and S9. (b) time series of offshore significant wave height ($H_s$) at S1 and S8 (fore-reef) and S9 (reef flat) focusing on a sample two-month period (05/12/17 – 05/02/18). (c) significant wave height as a function of the water depth at S9 and (d) time series comparing 33 h low-pass filtered offshore significant wave height at S1 with wave setup ($\eta_{\text{setup}}$) over the reef flat at S9.
Figure 2-5: (a) Water level (relative to MSL) at the fore-reef (S1) and lagoon (S2) sites and (b) illustrative photo of Mermaid Reef’s reef flat (south of the channel, taken from the ocean side out to the lagoon), which becomes exposed when offshore water level falls below the reef flat elevation.

2.4.1.4. Reef-lagoon circulation

The time-averaged circulation pattern (arrows in Figure 2-6a) observed between 1/12/2017 - 1/03/2018 revealed a mean eastward flow across the reef flat (S4) and through the lagoon (S2) and channel (S3). On the reef flat and in the lagoon, most of the current variance (ellipses in Figure 2-6a) can be explained by the variability occurring at subtidal frequencies (red arrow and ellipses, Figure 2-6a). In the channel, most of the current variance is dominated by flows occurring at tidal frequencies (i.e., the intra-tidal variability is represented by the largest area between the ellipses).

An indication of the importance of the two forcing mechanisms (i.e., waves and tides) was quantified by computing correlation coefficients (R) with significance (p-values) relating each forcing mechanism to the local depth-averaged currents (Figure 2-6b-d). Due to the effect of ‘tidal truncation’ (section 2.4.1.3), the water levels inside the atoll often lagged up to 2 hours behind the water levels in the open-ocean, particularly at low tide. Hence, a 2-hour lag was applied to the tidal velocities for the correlation analysis. On the reef flat (S4), subtidal current velocities were positively correlated with $H_s$ ($R = 0.76; p$-value $<0.01$), while tidal velocities and water levels were negatively correlated ($R = -0.36; p = 0.57$). In the lagoon (S2), subtidal current velocities were positively correlated with $H_s$ ($R = 0.32; p$-value $<0.01$), and the tidal currents velocities were positively correlated with the water levels ($R = 0.51; p$-value $<0.01$). In the channel (S3), subtidal current velocities were positively correlated with $H_s$ ($R = 0.34$;
and the tidal currents velocities were positively correlated with the water levels ($R = 0.55; p\text{-value} < 0.01$). These results indicate that both waves and tides contribute substantially to driving the flow variability at the three sites; however, additional drivers (e.g., wind and buoyancy) may also contribute to some of the observed flow variability.

Figure 2-6: (a) Depth-averaged current velocities, with arrows representing the time-averaged current vectors and ellipses indicating the standard deviation of the current variability from a principal component analysis over a three-month period (1/12/2017 to 1/03/2018). The total current velocities are plotted in black and the subtidal current (33 h low-
pass filtered) in red. Note the difference in scale of current velocities between the solid lines for the reef flat and lagoon sites (S2 and S4) and the dotted lines for the channel site (S3) given the much larger velocities in the channel. Subtidal velocities are plotted as a function of significant wave height and tidal velocities as a function of the water level at (c) S4, (d) S2 and (e) S3. Note that a 2-hour lag was applied to the field observations of tidal velocities to account for the effect of tidal truncation (see Section 2.3.1.4).

2.4.2. Hindcast model validation

The wave model provided a reasonably accurate prediction of the observed wave heights ($H_s$) at S1, S6, S7 and S11 (see supporting information Table S 2-1 and Figure S 2-3a, b, c and d; Skill: 0.51-0.89, RMSE = 0.29-0.55 m). Numerical predictions of water level variations and tidal and subtidal contributions to the current velocities were accurately reproduced at most sites (Figure 7, Table 3). In the lagoon (S2), the subtidal component of the flow had a relatively low Skill (~0.4) which could be due to the fact that the subtidal flows in the lagoon are comparatively very weak due to the depth of the lagoon. On the western reef flat (S4), the model reproduced the subtidal current variability driven by waves (Skill ~0.8), although it under predicted the flow during large flow conditions (26/01/18 – 4/02/18). The discrepancies between the subtidal velocities in the in situ observations and numerical simulations at the reef flat could be due to several reasons. First, the instrument at S4 was located on the back reef, in an area where there is considerably more spatial variability in the bathymetry relative to seaward locations on the reef flat, as the depths transition to the deeper lagoon (not shown). In addition, given that much of the subtidal flow over the reef flat and into the lagoon returns out through the channel, the channel site provides a more representative measure of the integrated flow through the atoll, with the magnitude of the channel flow agreeing much better with the observations. As mass is conserved within the atoll, this further suggests that the flow recorded at the reef flat site S4 may not be representative of flow over the broader reef flat. Finally, the discrepancies could also be due to sources of error within the model itself, e.g., due to inaccuracies in bottom stress parametrisation, too coarse bathymetry resolution (25 m), or discrepancies with the offshore wave boundary conditions.
Figure 2-7: Hindcast numerical simulations (in black) compared against the field observations (in red) showing a one-month period that includes spring tides, neap tides, low and high wave energy. (a, d and g) Water levels (m) (b, e and h) streamwise tidal velocity (m/s) and (c, f and i) streamwise subtidal velocity (m/s) at S4 (reef flat), S2 (lagoon) and S3 (channel). Positive (negative) streamwise velocity indicates water coming into (out of) the atoll.

Table 2-3: Statistical parameters (Skill and RMSE) to assess the validity of the numerical simulations for water level (m) and current velocities (m/s) at S2, S3 and S4 for the three-month simulation period (1/12/2017 to 1/03/2018).

<table>
<thead>
<tr>
<th>Site</th>
<th>Willmott Skill Score (Skill)</th>
<th>Root Mean Square Error (RMSE)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Water level</td>
<td>Current velocities</td>
</tr>
<tr>
<td></td>
<td>Tidal</td>
<td>Subtidal</td>
</tr>
<tr>
<td>S2 (lagoon)</td>
<td>0.98</td>
<td>0.90</td>
</tr>
<tr>
<td>S3 (channel)</td>
<td>0.99</td>
<td>0.94</td>
</tr>
<tr>
<td>S4 (reef flat)</td>
<td>0.99</td>
<td>0.68</td>
</tr>
</tbody>
</table>

The tidal and subtidal velocity time series at the three sites (Figure 2-7) provided a good indication of the relative importance of the wave and tidal forcing. When the incident wave height was small ($H_i < 1$ m; Figure 2-3c), the tidal currents were greater than the subtidal currents at all sites. In contrast, when the incident wave height was
greater \((H_s > 1 \text{ m}; \text{Figure 2-3c})\), both tidal and subtidal currents were similar in the lagoon \((-0.2 \text{ m/s), whereas the subtidal currents were smaller in the channel (up to 2 m/s for tidal currents and 0.6 m/s for subtidal currents) but greater on the reef flat (up to 0.2 m/s for tidal currents and 0.4 m/s for subtidal currents). Since both tides and waves contributed during these times, we conducted a set of idealised experiments to isolate each hydrodynamic forcing and determine their relative contribution to the total circulation.

### 2.4.3. Isolating wave and tidal contributions to atoll circulation

To isolate the effect of tidal and wave forcing and understand how they interact to determine the atoll circulation, the validated model was used to conduct a series of idealized simulations with a range of forcing conditions that occur at the site. We first investigate the wave-driven circulation (Section 2.4.3.1) and tide-driven circulation mechanisms separately (Section 2.4.3.2), then investigate how the interactions between the two mechanisms modify the atoll circulation (Section 2.4.3.3).

#### 2.4.3.1. Wave-only circulation

In the first set of simulations, waves are the only forcing mechanism considered, using the average direction and peak period of incident waves at the site (constant eastward wave direction of 270°N and peak period of 10 sec). For both mean \((H_s = 1 \text{ m})\) and maximum \((H_s = 3 \text{ m})\) wave conditions at Mermaid Reef, the waves break on the western reef flat, establishing a pressure gradient and driving an inflow of water across the western reef flat (Figure 2-8a and b, cross section 1 to 8) and outflow of water through eastern reef flat and channel (Figure 2-8a and b, cross section 9 to 16).
Figure 2-8: Wave-only scenarios. The time- and spatially-averaged discharge, \( \langle q_i \rangle \), for the \( i \)th cross section in/out of the atoll for significant wave height \( H_s \) (a) \( H_s = 1 \) m and (b) \( H_s = 3 \) m (at mean sea level). Blue (red) arrows indicate inflow (outflow) and are plotted on the \( z = -2 \) m contour. Note that the dotted arrow represents the discharge through the channel, which was scaled 10 times smaller than for the other cross sections (represented by solid arrows). (c) The \( \langle q_{\text{west}} \rangle \) (cross section 1 to 8) as a function of \( H_s \). The dotted and solid red line represent the minimum and maximum, and mean \( H_s \) over the 11-month dataset, respectively.

Over the full range of \( H_s \), the magnitude of mean volumetric flow rate \( \langle q_{\text{west}} \rangle \) increases slightly less than linearly with increasing \( H_s \) (Figure 2-8c). The time and spatially averaged discharge for each of the cross sections around the atoll \( \langle q_i \rangle \) indicates constant and relatively small instantaneous flow rates (~\( \pm 0.1 \) m\(^2\)/s for \( H_s = 1 \) m and ~\( \pm 0.4 \) m\(^2\)/s for \( H_s = 3 \) m). The discharge at cross section 14 (channel) displays values an order of magnitude greater than the rest of the cross sections (~0.5 and -2.5 m\(^2\)/s respectively for \( H_s = 1 \) and 3 m, respectively).

2.4.3.2. Tide-only circulation

2.4.3.2.1. Tidal water level variations

In this set of simulations, tides are the only forcing mechanism considered, using tidal ranges varying between 0.5 and 4 m generated by the tidal amplitude and phase difference observed across the domain for the \( M_2 \) component.

For a neap tidal range (\( TR = 1 \) m, Figure 2-9a), the net residual flow is ~0 m\(^2\)/s at all cross sections, indicating that local inflows balance outflows when averaged over a
tidal cycle. For a spring tidal range ($TR = 4$ m, Figure 2-9b), the net residual flow is an order of magnitude greater than for neap tidal range and directed eastward, with inflow across the western reef flat and outflow through the opposite side of the atoll, primarily through the channel. The average discharge across the western reef flat ($\bar{q}_{west}$), increases approximately linearly with increasing tidal range when the tidal range is greater than $\sim 1$ m (Figure 2-9c). The net residual flow in the spring tide-only and wave-only scenarios were spatially similar, with water entering the lagoon over the western reef flat cross sections and exiting out the eastern side of the atoll. However, for the wave-only scenarios, the residual net flows were generally one to two orders of magnitude larger than for the tide-only scenarios through the reef flat cross sections but were similar through the channel.

For each atoll cross section, the Hovmöller diagram of ($q_i$) throughout a tidal cycle (Figure 2-9d and e) indicates greater instantaneous flows ($\sim 0.5$ to $0.5$ m$^2$/s and -2 to 2 m$^2$/s for $TR = 1$ and 3 m, respectively), compared to the wave-only scenarios. For all cross sections, ($q_i$) indicates consistent inflows (positive ($q_i$), blue values) into the lagoon during rising tide (from $\sim 0.5$ to $\sim 6.5$ hours after low tide) and outflows (negative ($q_i$), red values), during falling tide (from $\sim 6.5$ to $\sim 12.4$ hours after low tide). The magnitude of these tidal flows is generally higher on the eastern side of the atoll (cross sections 12 to 15) due to the eastern reef flat’s lower elevation. For $TR = 1$ m, there is continuous inflow and outflow through all cross sections and at all times, as the entire reef flat remains submerged during the entire tidal cycle (see supporting information Figure S 2-4). However, for $TR = 3$ m, the flow is prevented from entering or exiting the lagoon through the western side of the atoll ($\bar{q}_{west} \sim 0$ m$^2$/s) when the offshore water levels are below $h_{west}$ (dashed grey line, Figure 2-9e).
Figure 2-9: Tide-only scenarios. The spatially and time-averaged flow rate, $\langle q_i \rangle$, over the $M_2$ period (12.42 h), for the $i$th cross section, in/out of the atoll for tidal range (a) $TR = 1$ m and (b) $TR = 3$ m. Blue (red) arrows indicate inflow (outflow) and are plotted on the $z = -2$ m contour. Note that the dashed arrow represents the discharge through the channel, which is scaled 100 times smaller than for the other cross sections (represented by solid arrows). (c) Western reef flat flow rate, $\langle q_{west} \rangle$, as a function of tidal range. The black dashed and solid lines represent $\langle q_{west} \rangle$ with and without taking into account the $M_2$ phase difference across the NWS. The red dotted and solid lines represent the minimum, maximum and mean tidal range over the 11-month dataset respectively; (d) and (e) Hovmöller diagrams of the spatially-averaged flow rate, $\langle q_i \rangle$, as a function of time. Note that the channel (cross section 14) displays values an order of magnitude greater than the rest of the cross sections ($\pm 2.8$ and $\pm 11.4$ m$^2$/s respectively for $TR = 1$ and $3$ m). The dashed grey line represents the water level threshold at which the western reef flat becomes exposed ($\eta \sim -0.7$ m relative to MSL).
2.4.3.2.2. **Tidal water levels and atoll morphology**

To investigate the influence of the reef morphology's asymmetry on the flow and how it affects the residual circulation in the atoll, we examine the tidal water level variations across a west-east transect (Figure 2-10a) and the velocity vector fields along the entire atoll (Figure 2-10b) over a tidal cycle with a 3 m (spring) tidal range. At high tide ($t = 0$ h), the water levels inside and outside of the lagoon are equal. As the tide starts to fall ($t = 3$ h), the water levels fall faster outside the lagoon than inside the lagoon. The water levels remain slightly higher inside the lagoon due to frictional resistance that impedes flow out of the lagoon. The flow is directed towards the outside of the lagoon over the entire reef perimeter. As the water levels approach low tide, the western reef flat becomes exposed when the water level drops below $h_{west}$ and acts as a physical barrier to incoming and outgoing water. At low tide, both the western and eastern reef flat are exposed, leaving the channel as the only connection to the ocean. The water level is then higher inside the lagoon than offshore, and the flow is directed eastwards over the entire reef perimeter. As the tide begins to flood ($t = 7$ h), the water level rises faster outside the atoll than inside the lagoon as the western reef flat is still exposed, and the flow on the eastern side of the atoll reverses direction. When the ocean water level re-submerges the western reef flat (from $t = 8$ h to 11 h, not shown), the flow is directed into the lagoon over the entire reef perimeter. With higher water level outside the atoll, an inward-directed pressure gradient exists until high tide as water levels due to the lag of water level in the lagoon.
Figure 2-10: Tide-only simulation for a spring tidal range of 3 m. (a) Water levels with dashed black line represent the threshold at which the western reef flat becomes exposed ($\eta \sim 0.7$ m relative to MSL) and (b) atoll cross section with light blue shaded area represents the water level for given times after high tide. (c) Current velocity vectors for given times after high tide. See Supporting information Figure S 2-4 for the neap tidal range of 1 m.

2.4.3.3. Combined wave and tidal forcing

Finally, we consider the combined wave and tide-driven circulation using the same range of conditions presented in the wave-only and tide-only scenarios (i.e., TR
= 0 to 4 m and $H_s = 0$ to 3 m). A comparison of differences between the combined wave and tide scenarios, with the sum of the wave-only and tide-only scenarios, indicates the extent to which wave and tidal hydrodynamics interact to modify the circulation of the atoll. For the case of combined wave and tidal forcing (Figure 2-11a), the flow along the western reef flat, $\langle \bar{q}_{\text{west}} \rangle$, is reduced compared to the linear sum of the discharges driven by adding the corresponding wave-only and tide-only results (Figure 2-11b). When comparing the percentage flow reduction (Figure 2-11c), a greater reduction is indicated by the dark blue values. Across the parameter space, the greatest reduction (by typically 30 to 60%) occurs for small wave heights, i.e., when $H_s = 0.5$ to 1 m. The flow is typically reduced by ~20% for $H_s > 1$ m. Overall, for the combined wave and tidal forcing case, the inflow along the western reef flat increases for increasing $H_s$ at a constant tidal range. However, the inflow does not monotonically increase with increasing tidal range for constant $H_s$.

Figure 2-11: (a) $\langle \bar{q}_{\text{west}} \rangle$ as a function of tidal range (TR) and significant wave height ($H_s$) for the combined waves and tides scenarios, (b) $\langle \bar{q}_{\text{west}} \rangle$ as a function of tidal range and significant wave height for the linear superposition of the tide-only and wave-only scenarios and (c) percent difference between (a) and (b) normalised by (b).
To quantify the relative importance of each forcing mechanism and the extent to which they interact non-linearly, we define the following non-dimensional parameters (Eq. 2.8 and 2.9) based on the western reef flat’s time-averaged (residual) flow, \( \bar{q}_{west} \), for the different forcing scenarios (Figure 2-12):

\[
X = \frac{\langle \bar{q}_{west} \rangle \text{ (wave)}}{\langle \bar{q}_{west} \rangle \text{ (wave)} + \langle \bar{q}_{west} \rangle \text{ (tide)}}
\]

(2.8)

and

\[
Y = \frac{\langle \bar{q}_{west} \rangle \text{ (combined)}}{\langle \bar{q}_{west} \rangle \text{ (wave)} + \langle \bar{q}_{west} \rangle \text{ (tide)}}
\]

(2.9)

Here \( X \) characterises the relative strength of the net wave-driven flow component assuming the wave and tidal forcing act independently; i.e., \( X \) ranges from 0 when the tide-driven flow dominates to 1 when the wave-driven flow dominates. \( Y \) represents how closely the net flow from the combined wave and tide scenarios follows the linear superposition of the wave and tide conditions acting independently. Therefore, tides and waves interact linearly when \( Y = 1 \), with nonlinear interactions being stronger when \( Y \) values increasingly deviate away from 1. In addition, the case \( X = 1 \) and \( Y = 1 \) represents the wave-only scenarios given that \( \langle \bar{q}_{west} \rangle \text{ (tide)} = 0 \), and \( X = 0 \) and \( Y = 1 \) represents the tide-only scenarios given that \( \langle \bar{q}_{west} \rangle \text{ (wave)} = 0 \).

For \( TR < 1.5 \text{ m} \), \( \langle \bar{q}_{west} \rangle \) for the combined wave and tide scenarios approximately follow the \( X = 1 \) vertical line, thus reflecting the dominance of the wave processes in driving the net residual circulation for small tidal ranges. For increasing tidal ranges and decreasing wave heights, \( Y \) values decrease, indicating that increasing nonlinear interactions reduce the combined net flow (Figure 2-12), consistent with Figure 2-11c. For \( TR > 1.5 \text{ m} \), \( X \) values decrease as the tidal range increases, thus reflecting the increasing relative importance of the tidal processes to the net residual circulation. The \( Y \) values also increase with increasing \( H_s \), which suggests wave and tidal contributions act more linearly to drive the flow.
Figure 2-12: Hydrodynamic regimes for the western reef flat's time-integrated flow rate, $\langle \dot{q}_{\text{west}} \rangle$, for wave, tide and combined waves and tides scenarios. Symbols represent scenarios forced with $TR = 0.5, 1, 1.5, 2, 3$ and $4$ m. Dashed grey lines represent the values associated with the same $TR$ and varying $H_s$. Colours represent scenarios forced with $H_s = 0.5, 1, 1.5, 2$ and $2.5$ m.

Figure 2-12 revealed that the residual flow within the atoll was reduced when forced by a combination of waves and tides compared to a linear superposition of pure wave and pure tidal flows. Figure 2-13 illustrates how the significant wave height modifies the duration and strength of the flow along the western reef flat, $\langle \dot{q}_{\text{west}} \rangle$, for $TR = 1$ m (Figure 2-13a) and $TR = 4$ m (Figure 2-13b) over a range of different $H_s$. For a neap tidal cycle ($TR = 1$ m; Figure 2-13a), all wave heights result in an eastward flow over the western reef flat. As $H_s$ increases, the inflow (positive $\langle \dot{q}_{\text{west}} \rangle$, blue values) also increases, lasting for up to 7 hours for $H_s = 3$ m compared to 5 hours for $H_s = 0.5$ m. For a spring tidal cycle ($TR = 4$ m; Figure 2-13b), both the inflow and outflow are blocked when the western reef flat is exposed (i.e., when the water level is $< -0.7$ m MSL from 0 to 2.2 h and 10 to 12.4 h after low tide). As $H_s$ increases, the inflow lasts up to 3 hours.
longer for $H_s = 3$ m compared to $H_s = 0.5$ m. In contrast, as $H_s$ decreases the outflow lasts for up to 3 hours longer, with no outflow for $H_s = 3$ m in contrast to $H_s = 0.5$ m.

Figure 2-13: Flow $(q_{west})$ averaged along the western reef flat, as a function of both significant wave height ($H_s$) (right y-axis) and water level (left y-axis) for tidal range (TR) of (a) 1 m and (b) 3 m. The solid grey line represents the ocean water levels for hours after low tide and the dashed grey line represent the threshold at which the western reef flat becomes exposed ($\eta \sim 0.7$ m relative to MSL).

When tidal flows are superimposed on a wave-driven mean flow, intra-tidal current variability can be due to a combination of tidal advection forced by tidal pressure gradients (i.e., as in the tide-only scenario) as well as how tidal water level variations modulate wave-driven flows. The latter effect can be described heuristically by considering how tidal depth changes can alter the cross-reef momentum balances responsible for the wave-driven flows over a tidal cycle. On the reef flat seaward of the surf zone, where it is assumed that wave setup gradients across the reef are balanced by bottom stresses, the cross-reef discharge ($q_r$) is governed by (Hearn 1999; Lowe et al. 2009a):

$$q_r \approx \left( -\frac{\partial \eta_{setup}}{\partial x} \frac{gh_r^3}{C_D} \right)^{\frac{1}{2}} \tag{2.10}$$

where a quadratic drag formulation is assumed, $\partial \eta_{setup}/\partial x$ is the cross-reef setup gradient, $h_r$ is the reef flat depth, and $C_D$ is a bottom drag coefficient. Thus, for a given setup gradient across the reef and a fixed $C_D$, the discharge $q_r$ should increase as the depth over the reef flat increases. However, an increase in the water depth over the reef will also reduce wave setup gradients across the reef, given that the maximum setup generated on a reef $(\eta_{setup,r})$ tends to scale as $\eta_{setup,r} \sim H_0 - \gamma h_r$ (Tait 1972),
where $H_0$ is the offshore (deep water) wave height and $\gamma h_r$ is a depth-limited breaking wave height over the reef flat given an empirical breaking parameter $\gamma$. This reduction in the setup gradient in Eq. (2.10) with increasing water depth can thus reduce the response of the $q_r$ to tidal depth increases.

To further investigate the mechanisms responsible for these nonlinear wave and tidal flow interactions, two final numerical experiments were conducted with constant wave forcing only (e.g., wave-only, $H_s = 0.5$ and 2 m) for several static ocean water levels ($\eta = -2, -1, -0.5, 0, 0.5, 1, 1.5, 2$ m), spanning the spring tidal range. Results of $\langle q_{\text{west}} \rangle$ for different static water level scenarios (Figure 2-14a and b), denoted $q_{\text{wave}}$ (black lines), thus represent how different water levels affect wave-driven flows in the absence of tidal advection. We can evaluate how the instantaneous combined wave and tidal flow timeseries (denoted $q_{\text{Combined}}$) compares against the timeseries of the linear addition of the tide-only and wave-only flow at mean sea level ($\eta = 0$) (denoted $q_{\text{tide}} + q_{\text{wave},0}$) over a tidal cycle (Figure 2-14).

![Figure 2-14](image_url)

*Figure 2-14: Flow rate across the western reef flat over a tidal cycle for a combined tide and wave driven flow ($q_{\text{Combined}}$, red line), pure wave driven flow at different static water levels ($q_{\text{wave}}$, black line), and the linear addition of a pure tide and pure wave driven flow at mean sea level ($q_{\text{tide}} + q_{\text{wave},0}$, blue line) for constant $H_s$ of (a) 0.5 m and (b) 2 m.*

For both wave conditions ($H_s = 0.5$ and 2 m), the wave-driven flow becomes shutoff ($q_{\text{wave}} \sim 0$ m$^2$/s) (black lines, Figure 2-14) for low water levels ($\eta \sim \sim 0.7$ m) when the western reef flat is exposed and increases as the water level increases above this threshold. The wave-driven contributions to flows through the atoll are thus enhanced with elevated water depths over the reef at high stages of the tide. Based on Eq. (2.10), this indicates that any reduction in setup generation at greater depths is less
important than the enhanced contribution to the discharge by the deeper water column (i.e., $h^3$ term) over the full range of depths at the site. For the smaller significant wave heights ($H_s = 0.5$ m; Figure 2-14a), both $q_{\text{combined}}$ (red line) and $q_{\text{tide}} + q_{\text{wave,0}}$ (blue line) tend to closely follow each other, except for a period totalling ~4 hour during low water levels ($\eta <\sim 0.7$ m, when the western reef flat is exposed). During this time, $q_{\text{combined}}$ effectively shuts off whereas flow continues for $q_{\text{tide}} + q_{\text{wave,0}}$. This indicates that for the combined case, at low tide, the wave-driven flow shuts down for a substantial portion of the tidal cycle due to flow blockage by the western reef flat, thereby explaining the reduction of the residual flows for the combined forcing scenarios.

Similarly, for the larger significant wave heights ($H_s = 2$ m; Figure 2-14b), there is a similar discrepancy between $q_{\text{combined}}$ (red line) and $q_{\text{tide}} + q_{\text{wave,0}}$ (blue line) when the western reef flat becomes exposed at low tide ($\eta <\sim 0.7$ m). However, unlike for the $H_s = 0.5$ m case, for this larger wave condition, the $q_{\text{combined}}$ becomes elevated over $q_{\text{tide}} + q_{\text{wave,0}}$ at high stages of the tide. This enhancement occurs because the wave driven flow ($q_{\text{wave}}$, black line) increases at greater water depths over the reef flat. These two counteracting processes driven by the influence of tidal depths on the wave driven flows thus appears to be the reason why the strength of nonlinear interactions between the wave and tidal flows decrease as wave heights increase (i.e., as $Y$ increases towards 1 in Figure 2-12).

2.4.3.4. Flow along the eastern side of the atoll: channel versus reef flat contributions

The focus on prior sections was on the average discharge along the western reef flat, $\langle q_{\text{west}} \rangle$, which contributes consistent inflow to the general atoll circulation and is higher in elevation compared to the rest of the atoll reef flat. By mass conservation, when averaged over a tidal cycle, the total flow across the western side of the atoll (where there is net inflow) must balance the total flow across the eastern side (where there is net outflow), which was confirmed through an assessment of the mass balances (not shown). However, in contrast to the western side, flow on the eastern side of the atoll is much more spatially variable. For example, the outflow through the channel was found to be up to two orders of magnitude greater than the discharges across the rest of the eastern reef flat (Figure 2-9).

In Figure 2-15, we show the volumetric flow rate through the channel ($\bar{Q}_{\text{channel}}$, cross section 14), the eastern reef flat ($\bar{Q}_{\text{eastern reef flat}}$, cross section 9 to 13 and 15 to 16)
and through the entire eastern side of the atoll (\( \bar{Q}_{\text{east total}} \), cross section 9 to 16) as a function of both TR and \( H_s \). In the tide-only scenarios (Figure 2-15a), the channel outflow (black line) increases as TR increases. However, the flow across the eastern reef flat (red line), contributes continuous inflow, with the strength increasing as TR increases, thus contributing to reduce the total outflow across the eastern side of the atoll (blue line). In the wave-only scenarios (Figure 2-15b), both the channel and the reef flat contribute continuous and increasing outflow as \( H_s \) increases. The channel contributes smaller volumetric compared with the other parts of the eastern reef flat and most of the flow across the eastern side of the atoll exits through the reef flat.

![Figure 2-15: (a) Volumetric flow rate \( \bar{Q} \) (m³/s) as a function of tidal range (TR (m)) and (b) significant wave height (\( H_s \) (m)) for \( \bar{Q}_{\text{channel}} \) (cross section 14); \( \bar{Q}_{\text{eastern reef flat}} \) (cross section 9 to 13 and 15 to 16), and \( \bar{Q}_{\text{east total}} \) (cross section 9 to 16).](image)

### 2.5. Discussion and Conclusions

Using a combination of field observations and numerical simulations, our study provides new insight into the complex hydrodynamic processes that govern interactions between wave- and tide-driven flows within a coral reef atoll. First, we summarize the mechanisms associated with tide-driven circulation by defining a conceptual model for coral reef atoll with a topographic asymmetry where the tidal range is greater than two times the reef flat elevation. We then summarize the mechanisms responsible for the combined wave and tide-driven circulation and
discuss various ways of investigating the relative importance of waves and tides in driving the atoll flushing.

2.5.1. Tide-driven circulation on asymmetrical atoll reefs

The importance of tides on coral reefs circulation is well-recognized (King and Wolanski 1996; Kench 1998; Dumas et al. 2012; Lowe et al. 2015; Green et al. 2018). On micro-tidal reef environments (TR < 2 m), the ocean water level is usually greater than the reef flat elevation, even at low tide (Atkinson et al. 1981; Tartinville et al. 1997; Kench 1998; Tartinville and Rancher 2000; Kench and McLean 2004; Callaghan et al. 2006; Dumas et al. 2012; Figure 2-1c and d). We show that when tidal ranges are smaller than \(2h_{\text{west}}\) (i.e., \(\approx 1.4 \text{ m},\) representing neap tide) at Mermaid Reef, the circulation resembles the one of a micro-tidal reef. During these conditions, the western and eastern sides of the reef flat remain submerged throughout the entire tidal cycle and the flow rate into the lagoon mainly relies on the pressure gradient created by the difference in water level between the ocean and lagoon water levels. The water inflow at flood tide is then locally balanced by outgoing flows at ebb tide.

However, Mermaid Reef also regularly experiences tidal ranges exceeding \(2h_{\text{west}}\) (i.e., \(\approx 1.4 \text{ m},\) representing spring tide), causing the reef flat to become exposed for part of the tidal cycle at low tidal water levels. During this period, with the reef flat fully exposed, the inflow and outflow can only occur through the channel. In addition, due to the asymmetry reef flat bathymetry, as the tide rises, water levels outside of the reef first submerge the eastern reef flat, while the western reef flat is still exposed (Figure 2-16). This creates an additional residual outflow across the eastern reef flat, independent of the channel (note that in Supplementary Information Figure S2-5, we demonstrate this with a case forced by the same conditions but with the channel removed from the atoll bathymetry). Interestingly, as the tidal range increases to its largest values (e.g., TR = 4 m), the time during which only the western reef flat is exposed (and the eastern reef flat is still submerged) becomes smaller compared to the duration when both reef flats are exposed. In this case, most of the residual flow across the atoll can be attributed to the channel. As the tide rises and water levels outside of the reef become greater than \(h_{\text{west}}\), both the inflow and outflow can then occur across the entire atoll. Overall, when considering the integrated flow over entire tidal cycle, the timing and patterns of the reef flat exposure led to substantial eastward residual flow across the reef that would not be expected to occur on micro-tidal atolls with symmetrical bathymetry (Figure 2-1c and d).
Figure 2-16: Conceptual model of tide-driven flow of (a) flood and (b) ebb tide for an asymmetrical (western reef flat higher in elevation than eastern reef flat) atoll reef where the tidal range is greater than two times the reef flat elevation. The flow through the channel is represented on the plan view diagrams. MSL = Mean sea level; $q_{\text{tide}}$ = tide-driven flow; HHT = highest high tide; LLT = lowest low tide; $W$ = West; $E$ = East; $h_{\text{west}}$ = western reef flat elevation.

2.5.2. Mechanisms responsible for wave and tide-driven circulation

As demonstrated here and observed on various reefs worldwide, meso-tidal reef environments can also be periodically exposed to high wave conditions (e.g., Cheriton et al. 2016; Costa et al. 2017; Rogers et al. 2017; Green et al. 2019b). Here, we show that waves and tides interact through three main mechanisms to drive the circulation at Mermaid Reef. First, wave-driven flows can interact with tide-driven flows to modify the strength and duration of the combined reef inflows and outflows (Figure 2-13). For both small (neap) and large (spring) tidal ranges, we observed a total reversal of the flow on the western side of the atoll, resulting in no or very short period of outflow on the western side of the atoll. Similar complete reversal of the flow, with continuous inflow throughout the tidal cycle, was previously documented on reefs experiencing relatively large tides ($TR >2 \text{ m}$) when waves were sufficiently large ($H_s >1.5 \text{ m}$) (e.g., Heron Reef in the southern Great Barrier Reef, Gourlay & Hacker 2008 a and b). Second, when the water level drops below the reef flat elevation during low tide, a barrier is created to both wave and tide-driven flow into the lagoon (Figure 2-14; Costa et al. 2017; Rogers et al. 2017). Finally, a reduction in wave setup generation can occur in greater water depths (i.e., high water levels), which was found to be less important than the enhanced contribution to the discharge by the deeper water column.

Finally, we show that those mechanisms, particularly the first and second mechanisms described, played a key role in driving the for the circulation at Mermaid
Reef. For small wave conditions ($H_s = 0.5$ m), the flow blockage by the western reef flat occurring at low tide is mainly responsible for the observed differences between combined wave and tide scenarios and the simple linear addition of ‘tide-only’ and ‘wave-only’ scenarios. For larger wave conditions ($H_s = 2$ m), the flow blockage by the western reef flat appears to be largely compensated by the enhanced wave-driven contribution to the discharge at high stages of the tide. As a result, for small $H_s$ ($H_s < 0.5$ m), the inflow into the lagoon is reduced by up to 60% for $TR > 1.5$ m (e.g., neap tide) and up to 30% for $TR < 1.5$ m (e.g., spring tide) if nonlinear interactions are not accounted for (e.g., by the flows driven by pure tides and pure waves added linearly). Over the 11-month experiment, Mermaid Reef experienced $0.5 > H_s > 1$ m for 88% of the time (Figure 2-3a), implying that tides will generally play a substantial role in reducing the strength of the wave-driven flows.

### 2.5.3. Relative importance of hydrodynamic forcing

While the metric for classifying reefs based on exposure to waves and tides ($MTR/H_s$, Lowe & Falter, 2015) provides a useful indication of which forcing mechanisms (i.e., wave versus tide) are potentially important at a site, the hydrodynamic conditions at most reefs can vary substantially over time scales of several hours to months (e.g., spring-neap tidal cycles; changing waves conditions due to storm event). Based on the $MTR/H_s$ definition, Mermaid Reef ($MTR/H_s = 0.6$) can be classified as a marginally tide-dominated reef; however, we showed that over the range of conditions both tides and waves can, at times, be the dominant driver of the atoll’s circulation. This distinction was only made possible by the long-term hydrodynamic measurements collected at high temporal and spatial resolution during the study. Studies on the order of a couple of weeks might therefore not capture the full extent of experienced oceanographic conditions, processes, and interactions occurring on coral reef systems, and might miss the short periods during which the dominant hydrodynamic forcing change.

Reef geometry has also been widely used as an indicator of the relative importance of the main hydrodynamic drivers. Atolls with numerous or large passages (“open-reefs”) have been described as generally flushed by tidal circulation, whereas atolls that have almost continuous reef flat around their lagoon (“closed-reefs”) have been described as more likely to be flushed through wave action over the top of the reef flat (Callaghan et al. 2006). Based on that “geometric” definition alone, Mermaid Reef could be classified as a closed reef, as it displays an almost continuous reef flat.
surrounding a lagoon, and as a result, would be flushed through wave action. However, we show that Mermaid Reef’s circulation mainly results from the interaction between wave and tide-driven flows and that the dominance of wave versus tide can vary significantly over several days. As pointed out by Lindhart et al. (2021), classification of reefs as “open” or “closed” based on geometry is an insufficient predictor of reef hydrodynamics as a reef might transition from one driver to another depending on wave and tidal conditions.

We found that the threshold controlling the relative dominance of wave or tide-driven processes at Mermaid Reef is the higher reef flat elevation of the windward (western) side, which is usually due to greater carbonate reef deposition to withstand high wave energy (Kench et al. 2008; Kench 2012). As a result, if the tidal range is sufficiently large to expose the western reef flat, i.e., >2hwest (equivalent to one-half of the tidal range), tide-driven processes dominate. On the contrary, for tidal ranges smaller than 2hwest, wave-driven processes dominate. Over the 11-month experiment, Mermaid Reef experienced a TR >2hwest (i.e., 1.4 m) for 79% of the time and TR <2hwest (i.e., 1.4 m) for the remaining 21% of the time. Therefore, Mermaid Reef transitions through ‘tide-dominated’ and ‘wave-dominated’ periods over short time scale (hours to days) but its circulation mainly results from persistent interactions between the two hydrodynamic forcing and the reef morphology.

2.5.4. Conclusions

Atoll reefs display a wide variety of size and shapes and are often exposed to continuously changing and interacting hydrodynamic processes. An in-depth characterization of these parameters is therefore essential to better understand the circulation patterns and flushing of coral reef atolls. Using 11 months of hydrodynamic measurements spanning Mermaid Reef, we show that the atoll is regularly exposed to a range of waves and large (meso-) tidal ranges. As a results, wave- and tide-driven processes continuously interact to drive the reef circulation through several mechanisms including wave-current interactions and tidal water level modulation of wave-driven flows. Such mechanisms interact nonlinearly to drive the circulation, as the residual flow resulting from the combined wave and tide forced circulation was reduced compared to the linear sum of the flow driven by adding the corresponding wave-only and tide-only flows. For small wave conditions, the inflow into the lagoon is reduced by up to 60% during spring tide and by up to 30% during neap tide.
We show that the threshold controlling the relative dominance of wave or tide-driven processes at Mermaid Reef is the higher reef flat elevation of the windward (western) side. Therefore, as the tidal range varies from spring to neap tidal cycles, Mermaid Reef transitions through ‘tide-dominated’ and ‘wave-dominated’ periods but its circulation mainly results from persistent interactions between the two hydrodynamic forcing and the reef morphology. Over the 11-month experiment, tide-driven processes dominated for 79% of the time and wave-driven processes dominated for the remaining 21% of the time.

Overall, we showed that the time-averaged flow rate had a consistent eastward direction across the atoll for most hydrodynamic forcing combinations (i.e., tide-only, wave-only and combined waves and tides), which likely influences a range of biological, geological and chemical processes occurring on the reef (e.g., reef water quality, temperature variability, and material transport between different parts of a reef). The effect of these complex physical processes on lagoon thermodynamics and connectivity variability will be investigated in future studies.

2.6. Acknowledgements

This dataset was collected during multiple research cruises (from November 2017 to October 2018) as part of the North West Shoals to Shore research program led by the Australian Institute of Marine Science (AIMS) and supported by Santos as part of the company’s commitment to better understand Western Australia’s marine environment. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. We thank the captain and crew of the R/V Solander, and the scientific participants, in particular Carlin Bowyer from the University of Western Australia and Kim Brooks from AIMS for their collective support with fieldwork. We are grateful to Ap van Dongeren and the Delft3D FM support team at Deltares for technical advice and initial assistance with the model development. Funding was provided by the ARC Centre of Excellence for Coral Reef Studies, the Australian Institute of Marine Science, Australian Government Research Training Program (RTP) Scholarship and the Robson and Robertson award to C. G. This work was supported by resources provided by the Pawsey Supercomputing Centre with funding from the Australian Government and the Government of Western Australia. We also thank an anonymous reviewer for providing feedback that helped improve the manuscript. We acknowledge the availability of the CAWCR wave hindcast (All
2.7. Supporting information for Chapter 2

Figure S 2-1. Comparison between in situ measurements at S1 with global tide model TPXO8.0 and global wave model from the Centre for Australian Weather and Climate Research (CAWCR). (a) Significant wave height (Hs), (b) water level, (c) mean wave direction (θwave) and (d) peak period (Tp) for 3-months (1/12/2017 to 1/03/2018).
Figure S2-2. Details of the (a, c) unstructured and (b, d) structured grids used in the coupled flow-wave numerical model. The grey line represents the -2 m bathymetric contour.
Figure S 2-3. Hindcast numerical simulations of significant wave heights against in situ observation over a 1-month period at (a) S1 (western fore-reef), (b) S6 (eastern fore-reef), (c) S7 (southwestern fore-reef), and (d) S11 (northwestern fore-reef).

Table S 2-1: Statistical parameters (RMSE and Skill) to assess the validity of the numerical simulations for Hs (m) at S1, S6, S7 and S11 for 3-months (1/12/2017 to 1/03/2018).

<table>
<thead>
<tr>
<th>Site</th>
<th>Skill</th>
<th>RMSE (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>S1 (western fore-reef)</td>
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</tr>
<tr>
<td>S6 (eastern reef slope)</td>
<td>0.87</td>
<td>0.39</td>
</tr>
<tr>
<td>S7 (south-eastern reef slope)</td>
<td>0.51</td>
<td>0.29</td>
</tr>
<tr>
<td>S11 (north-eastern reef slope)</td>
<td>0.71</td>
<td>0.55</td>
</tr>
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Figure S 2-4. Tide-only simulation for a neap tidal range of 1 m. (a) atoll cross section with light blue shaded area represents the water level for given times after high tide. Dashed black line denotes the mean sea level. (b) Current velocity vectors for given times after high tide.
Figure S2-5. (a) Mermaid Reef with the bathymetry modified to remove the channel (region denoted by the red box) by replacing the channel bathymetry to match the surrounding reef flat elevation; (b) spatially and time-averaged flow rate, \( \langle \bar{q}_i \rangle \), over the \( M_2 \) period (12.42 h), for the \( i^{th} \) cross section, in/out of the atoll for a tidal range \( TR = 4 \text{ m} \).
Table S 2-2. Cross section number, length and depth.

<table>
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<th>Cross section number</th>
<th>Length (m)</th>
<th>Depth (m)</th>
<th>Width (m)</th>
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Table S 2-3. Flow rates (integrated over time and cross section length) through the western eastern side over a full tidal cycle (12.4 hours) for all the considered significant wave heights and tidal ranges in idealized numerical simulations.

<table>
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<tr>
<th>Scenario</th>
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<tr>
<td>46</td>
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3. Drivers of temperature variability within a coral reef atoll off northwestern Australia

3.1. Abstract

Quantifying the drivers of ocean temperature variability occurring across reef-scales (<1 km) is critical to determine patterns of thermal stress and bleaching of corals within reef systems. In this study, an 11-month record of in situ temperatures and hydrodynamics within a coral reef atoll located off northwestern Australia was used to assess how mechanisms responsible for temperature variability varied spatially across different reef zones (i.e., fore-reef, reef flat and lagoon). Temperature variability in each reef zone was characterised by prominent peaks of variability occurring at seasonal, diurnal, and semi-diurnal frequencies, with most of the variability generating temperature differences between reef zones occurring at diurnal and higher frequencies. Over such frequencies, the temperature variability across the reef flat and lagoon zones was mainly driven by the interactions between net diurnal atmospheric heating, and mean depth of the site. We also show that temperatures on the reef can present large deviations from offshore water temperatures, and that such differences are largely driven by the net air-sea heat exchange and mean depth over the reef. On the fore-reef zone, high frequency temperature fluctuations (timescales of minutes) were driven by cold water intrusions likely generated by internal waves, which are prominent on Australia’s North West Shelf. Similar spatial and temporal temperature variability likely occurs across reef systems worldwide. Identifying the drivers of natural temperature variability across reef system is critical to
understand how reefs will acclimate and adapt to changing temperature conditions in the future.

3.2. Introduction

With elevated ocean temperatures being the primary cause of mass coral bleaching (Hughes et al. 2018), climate-induced marine heatwaves increasingly threaten coral reefs. Over large spatial scales (hundreds of kilometres), regional ocean warming events (e.g., marine heatwaves) can cause widespread bleaching (Hughes et al. 2018). However, temperature variability can also occur over much smaller spatial scales (tens to hundreds of meters; Gorospe and Karl 2011; Pineda et al. 2013; Zhang et al. 2013), resulting in highly heterogeneous bleaching patterns within individual reef systems (Penin et al. 2007; Grimsditch et al. 2010; Green et al. 2019b). For that reason, accurate quantification of temperatures and drivers of reef-scale temperature variability are critical, not only to help target management efforts and conserve reefs (Hoegh-Guldberg et al. 2007; Hughes et al. 2017), but also to help understand how systems will acclimate and adapt to changing temperature conditions (e.g., Lowe et al. 2016).

Temperature variability within reefs is broadly driven by a combination of local atmospheric conditions and oceanic processes. Atmospheric conditions such as solar radiation, air temperature, cloud cover and wind speed alter air–sea heat fluxes that locally warm or cool reef waters (McCabe et al. 2010; McGowan et al. 2010; MacKellar et al. 2013; Zhang et al. 2013). Advection of heat by ocean hydrodynamic processes such as tides (McCabe et al. 2010; Lowe et al. 2016), internal waves (Leichter et al. 2005; Storlazzi et al. 2020; Wyatt et al. 2020), and wave-driven flows (Davis et al. 2011; Falter et al. 2014), can also interact with reef bathymetry to determine water residence times, that in turns regulate reef heat budgets (MacKellar et al. 2013; Zhang et al. 2013; Lowe and Falter 2015). For example, a shallow reef flat with long water residence times will be more efficiently warmed or cooled compared to a rapidly flushed lagoon with short water residence time. As a result, and depending on the combination of local atmospheric fluxes and advective forcing variability, significant temperature (and in turn coral bleaching) variability has been observed at reef scales (Leichter et al. 2005; McCabe et al. 2010; Davis et al. 2011).

In order to characterise temperature variability occurring at the reef-scale (<1 km), previous studies have tended to focus on specific reef zones (e.g., lagoon, reef flat;
Ouillon et al. 2005; Andréfouët et al. 2006; Dumas et al. 2012; Reid et al. 2020) or the role of specific hydrodynamic drivers, (e.g. internal waves; Leichter et al. 2005; Reid et al. 2019; Storlazzi et al. 2020; Davis et al. 2020 and tides McCabe et al. 2010; Lowe et al. 2016). Yet, few studies have investigated the variability in atmospheric and oceanic drivers within a reef system, or characterised the resulting distinct temperature regimes occurring at the reef-scale (Leichter et al. 2006; Rogers et al. 2017b). Such studies are especially relevant as remotely sensed sea surface temperature (SST) data, which are an invaluable tool for monitoring global oceans’ temperatures, does not resolve the fine-scale temporal and spatial variability (order of 1000s of meters and days for most products) of temperatures within reefs.

In this study, we use an ~11-month temperature record across a coral reef atoll to identify the dominant drivers of temperature variability within key reef zones (reef flat, fore-reef, and lagoon) of a coral reef atoll. We first describe the oceanic and atmospheric conditions observed during the experiment and discuss the relative importance of such drivers across multiple temporal and spatial scales across reef zones. We then investigate temperature differences between the reef and offshore waters and show that the deviations are mainly driven by a combination of net atmospheric heat fluxes and local mean water depths. Finally, we discuss the significance of our findings in the context of coral reef communities worldwide. Our results advance our understanding of fine-scale temperature variability within coral reef and highlight the existence of distinct temperature regimes within key reef zones.

### 3.3. Methods

#### 3.3.1. Study site and sampling design

Mermaid Reef is a coral reef atoll that is part of the Rowley Shoals, located on Australia’s North West Shelf (NWS). The atoll rises from 500 m depth, with a steep fore-reef slope and reef flat enclosing a large lagoon (50 km², 20 m-deep), with a single channel (8 m-deep, 250 m-wide) on the northeast side that serves as the only continuous opening to the open-ocean. The NWS experiences some of the largest tides around Australia, with coastal mean spring tides ranging from 11 m in the inshore region to approximatively 4 m further out on the continental shelf (Holloway 1983). Large amplitude internal tides have been observed across the NWS (Gong, 2021). These often occur due to a combination of steeply sloping bathymetry, strong tidal forcing, and a stratified water column. The NWS is also exposed to a low to moderate
wave climate (annual mean $H_s < 2$ m) with a southwest wave direction ($\sim 240 \, ^\circ$N) resulting from sporadic large wave height conditions forced by oceanic swell and episodic tropical cyclones (Drost et al. 2017). As a result, Mermaid Reef is regularly exposed to a range of wave conditions (0 to 3 m significant wave height) and large (meso-) tides (1 to 4 m tidal range) (Chapter 2).

Over ~11 months (26/11/2017 – 14/10/2018), an array of 14 temperature loggers (HOBO U22 Pro-v2, ± 0.2°C accuracy) sampling at 10-min interval were deployed on top of lead weights (sampling ~0.1 m above the bed) within different reef zones (i.e., reef flat, lagoon, and fore-reef) of Mermaid Reef (Figure 3-1, Table 3-1). The water depths of these sites varied from 1 to 14 m (mean sea level, MSL). In addition, a thermistor chain (vertical array of temperature loggers attached to a float at the surface) was deployed in the northern centre of the lagoon (S5) with 7 loggers deployed every 2 meters from the bottom (14 m depth, MSL) to the surface. Two additional temperature loggers were deployed on the eastern and western shallow fore-reef for a ~3-month duration (26/11/2017 – 14/03/2018; S6 and S8; Figure 3-1). The loggers were checked for consistency in a room-temperature water bath for 5-day periods both before and after the deployments, ensuring all read within 0.1°C of each other, for temperatures varying between 17 and 28°C. Temperature records using calibrated loggers (VEMCO Minilog-II-T, ± 0.1°C accuracy) were also available at two long-term monitoring sites (RS1 and M12) for the duration of the field experiment (AIMS, 2021). Finally, wave parameters (significant wave height $H_s$ and mean period $T_{m01}$) and pressure were measured at S1 (fore-reef slope; 13.4 m depth) using a 1 MHz Nortek AWAC acoustic wave and current profiler. Pressure was also measured using RBR Solo3D instruments continuously recording pressure at 1 Hz at locations on the reef flat (S4, S6, S8) and inside the lagoon (S2) (Figure 3-1; Table 3-1).
Figure 3-1: Bathymetry (depths relative to mean sea level; MSL) and instrument locations at Mermaid Reef. Brown colours represent the reef flat (depths 2 m above to 2 m below MSL). Inset map shows Mermaid Reef’s location (red dot) on Australia’s North West Shelf (red box).

Table 3-1: Instrument deployment information.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Reef zones</th>
<th>Sites</th>
<th>Location of measurements; depth (m, MSL)</th>
<th>Deployment dates; sampling interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>Deep fore-reef</td>
<td>S1</td>
<td>Bottom; 13.4 m.</td>
<td>26/11/2017 – 14/10/2018; 10 min</td>
</tr>
<tr>
<td>Temperature</td>
<td>Reef flat</td>
<td>S4, S7, S9, S19, S21, S23</td>
<td>Bottom; 2.7, 2.4, 2.1, 1.2, 1 m, respectively.</td>
<td>26/11/2017 – 14/10/2018; 10 min</td>
</tr>
<tr>
<td>Temperature</td>
<td>Shallow fore-reef</td>
<td>S8, S6 and RS1</td>
<td>Bottom; 6.5, 7, 6 m, respectively.</td>
<td>26/11/2017 – 14/03/2018; 10 min</td>
</tr>
<tr>
<td>Temperature</td>
<td>Lagoon</td>
<td>S2, S17, S18, S20, S22, M12</td>
<td>Bottom; 12, 3.2, 7.5, 9, 6 m, respectively.</td>
<td>26/11/2017 – 14/10/2018; 10 min</td>
</tr>
<tr>
<td>Temperature</td>
<td>Lagoon</td>
<td>S5</td>
<td>Water-column; 14 m with measurements every 2 m.</td>
<td>26/11/2017 – 14/10/2018; 10 min</td>
</tr>
<tr>
<td>Wave conditions</td>
<td>Deep fore-reef</td>
<td>S1</td>
<td>Bottom; 13.4 m</td>
<td>26/11/2017 – 14/10/2018; 2048 samples at 2 Hz every hour</td>
</tr>
<tr>
<td>Pressure</td>
<td>Lagoon and reef flat</td>
<td>S2 and S4</td>
<td>Bottom; 11.4 and 2.7 m, respectively</td>
<td>26/11/2017 – 14/10/2018; 1 Hz</td>
</tr>
<tr>
<td>Pressure</td>
<td>Deep and shallow fore-reef</td>
<td>S1, S6 and S8</td>
<td>Bottom; 13.4, 6 and 6 m</td>
<td>26/11/2017 – 14/10/2018; 1 Hz</td>
</tr>
</tbody>
</table>
3.3.2. Estimates of heat exchange

Hourly atmospheric data were obtained from the fifth generation atmospheric reanalysis of the global climate the European Center for Medium-Range Weather Forecasts (ECMWF) ERA5 dataset (Hersbach et al. 2020; 2021) available from January 1979 to present. Data were extracted at the available 0.25° resolution for Mermaid Reef (119.45 to 119.75°E; -17.25 to -16.85°N) and included latent heat flux ($Q_L$), sensible heat flux ($Q_S$), longwave radiation flux ($Q_{LW}$), shortwave radiation flux ($Q_{SW}$), and the eastward and northward components of the wind velocity at 10 m above the surface ($U_{10}$ and $V_{10}$, respectively). The net heat flux across the air–sea interface ($Q_N$) is the sum of the shortwave radiation flux, net longwave radiation flux, sensible heat flux, and latent heat flux:

$$Q_N = Q_{SW} + Q_{LW} + Q_S + Q_L$$

(3.1)

where $Q_N > 0$ denotes a net heat flux into the water column.

The net air-sea heat flux and advection of heat play a role in regulating rates of ocean temperature changes, especially in shallow waters. For the case where a flow is aligned in a dominant stream-wise ($x$) direction, horizontal diffusion is comparatively negligible relative to advection, and there is no heat flux from the sea floor, the depth-averaged temperature ($T$) is governed by the 1D heat budget equation (e.g., Herdman et al. 2015):

$$\frac{dT}{dt} = \frac{Q_N}{\rho \ c_p h} - u \frac{dT}{dx}$$

(3.2)

The first term in Eq. (3.2) represents the depth averaged temperature time rate of change (°C s$^{-1}$); the second term represents a net air-sea heat flux term, where $\rho$ is the seawater density, $c_p$ is the specific heat of water, and $h$ is the water depth; and the third term represents a heat advection term, where $u$ is the depth-averaged stream-wise velocity. In the present study, we apply Eq. (3.2) to estimate the role of local net-air sea heat exchange versus advection to temperature variability specifically within the reef flat and lagoon zones where flows are steered into consistent directions by the reef bathymetry. While we could assess the role of advection would require high-resolution horizontal temperature gradient information, which was not available.
3.3.3. Data analysis

The pressure measurements were converted to water levels ($\eta$) by removing local atmospheric pressure variations and assuming a mean seawater density of $1025 \text{ kg m}^{-3}$. To implement a common vertical reference datum, we assumed that the water level was uniform at all sensor locations at high tide and determined the mean depth offset of each instrument throughout the experiment. Next, we adjusted each instrument so that $\eta = 0 \text{ m}$ corresponded to the mean sea level. Directional wave spectra were computed using the Maximum Likelihood Method on water elevations from Acoustic Surface Tracking (Thomson and Emery 2014) from the AWAC deployed on the deep fore-reef (S1).

Each site was assigned to a reef zone based on their location on the atoll and depth range (Table 3-1), and the results from the analyses are reported as the mean and standard deviation between the sites composing each reef zone. The seasonal and sub-diurnal variability of the temperature across the reef was evaluated by applying a low pass filter (half-period of 33 h; using a PL66 filter, Alessi et al. 1985) to the temperature measurements. The magnitude of temperature changes across a 24-hour day (midnight to midnight) were quantified using a daily temperature range ($\Delta T_d$), calculated as the difference between maximum and minimum temperatures for each day at each site. A power spectra analysis was performed at all sites across the 11-month dataset using Welch’s averaged periodogram method on detrended temperatures (i.e., mean for the duration of the experiment removed).

3.3.4. Satellite sea surface temperature (SST)

A number of studies have shown that the in situ temperatures of reefs waters can deviate significantly from the temperature of offshore waters (Leichter et al. 2006; Castillo and Lima 2010; Pineda et al. 2013; Falter et al. 2014). We investigated such deviations by using remotely sensed SST measurements, as continuous measurements of offshore temperatures (e.g., from moorings) were not available at Mermaid Reef. Daily SST measurements were then extracted from the Group for High Resolution Sea Surface Temperature (GHRST) Level 4 sea surface temperature analysis on a global $0.01^\circ$ grid produced as a near-real-time dataset (one day latency) at the National Aeronautics and Space Administration Jet Propulsion Laboratory (JPL). The product used here (GHRST Level 4 Multi-scale Ultra-high Resolution (MUR) Global Foundation Sea Surface Temperature Analysis v4.1, JPL MUR MEaSUREs Project. 2015; Chin et al.
is a version 4 analysis based upon night-time GHRSSST L2P skin and subskin SST observations from several instruments. Daily SST was extracted at locations both on the reef (i.e., reef flat site S4 and lagoon site S5) and offshore from Mermaid Reef (~10 km to the West). The night-time daily SST product was first compared to in situ night-time temperature measurements and used to characterize the contribution of air-sea fluxes to the difference in temperature observed between offshore and reef waters during the duration of the field experiment (November 2017 to October 2018).

3.4. Results

3.4.1. Oceanic and atmospheric conditions

The full instrument deployment captured 24 spring-neap tidal cycles, with an average tidal range of 2.4 m at S1 (mean neap tidal range of 0.9 m and a mean spring tidal range of 3.9 m, Figure 3-2a) and a wide range of incident wave conditions, with an average $H_s$ of 0.9 m (varying from 0.3 to 3.2 m) (Figure 3-2b). The incident waves measured at S1 had a mean wave period ($T_{m01}$) (Figure 3-2b) varying between 2 and 14 s (averaging ~11 s) and a mean wave direction varying from 55 to 350°N, averaging ~270°N (i.e., coming from the west, not shown). The wind speed averaged 5.3 m s$^{-1}$ with a direction predominantly from the southwest (Figure 3-2c, mean direction = 200°N, not shown).

Over the 11-month study period, there was net heating (positive $Q_N$) in the austral spring–summer period from December 2017 through April 2018 and net cooling (negative $Q_N$) in the austral autumn–winter period from May through August 2018 (Figure 3-2d). The air–sea heat flux variability was predominantly driven by variations in the positive solar energy input ($Q_{SW}$) and heat loss due to evaporation ($Q_L$). Net longwave ($Q_{LW}$), sensible ($Q_S$), and latent ($Q_L$) heat fluxes exhibited an 11-month average (i.e., over the experiment duration) of -85, -7, and -157 W m$^{-2}$, respectively, with the latent heat flux acting as the dominant heat loss term (Figure 3-2d). Latent radiation was the largest contributor to the variance in $Q_N$ from May through September.
Figure 3-2: Met-ocean conditions at Mermaid Reef from 1/12/2017 to 1/10/2018 (local time, UTC+8). (a) Water levels ($\eta$) measured at S1; (b) wave height ($H_s$) and mean period ($T_{m01}$) measured at S1; both (c) wind velocity 10 m above the surface and (d) net ($Q_N$), sensible ($Q_s$), latent ($Q_L$), longwave ($Q_{LW}$) and shortwave ($Q_{SW}$) radiation fluxes were extracted from ERA5 and averaged over Mermaid Reef.

3.4.2. Water temperature variability

Water temperature across Mermaid Reef varied both temporally and between the reef zones. The temperature variability reveals a seasonal cycle, with monthly low-pass-filtered temperatures ranging between 22.8 to 31.3°C. While there is a broad consistency in this seasonal temperature variability across all reef zones, fore-reef temperatures were consistently colder throughout the year, while lagoon temperatures were consistently warmer throughout the year (Figure 3-2a). Consistent with the seasonal variations in net air-sea heat ($Q_N$, Figure 3-2c), temperatures were warmest from November through April, with the maximum monthly mean occurring in
April (30.6 ± 0.4°C; monthly mean ± standard deviation) at all reef zones. A sudden and sharp decrease in temperature (30 to 27°C in 10 days) occurred in May, likely driven by a strong winter storm (Figure 3-2c) followed by temperatures gradually decreasing until September, with a minimum occurring in August (24.6 ± 0.6°C monthly mean). At frequencies higher than 33 hours (i.e., representative of sub-diurnal variability), temperatures went through regular increases over several weeks followed by sharp decreases (up to ~2°C) over short periods of time (i.e., one week; Figure 3-3b). Most of the variability between reef zones occurred at diurnal and higher frequencies (Figure 3-3c).

The patterns revealed from the spectral analysis of the temperature timeseries (Figure 3-4) highlight the contribution of several frequencies to the total temperature variance. While there is greater energy at lower frequencies (>33 hours, i.e., reflecting the seasonal variability and other sources of sub-diurnal variability such as occasional storms; Figure 3-2b-c), substantial peaks in energy were also observed at diurnal (24-h period) and semi-diurnal (main tidal component $M_2$ frequency: 12.4-h period) frequencies. At such frequencies, the shallow reef flat zone experienced large mean daily temperature ranges (mean and maximum daily range 2.1 and 7.1°C, respectively; Figure 3-4b) compared to the deeper lagoon sites (mean and maximum daily range ~ 0.5°C and 1.6°C, respectively; Figure 3-4d). The fore-reef site, even though deeper (~14 m), also experienced large mean daily temperature ranges (mean and maximum daily range ~1.3 and 5.6°C, respectively; Figure 3-4f), linked to a clear series of drops in temperature followed by a subsequent return to pre-event conditions (Figure 3-3c). Across all reef zones, the highest temperatures occurred between 12 pm and 6 pm, and the lowest temperatures occurred between dusk and mid-morning local time (Figure 3-4).
Figure 3-3: Temperature variability over several timescales across the reef zones of Mermaid Reef (local time, UTC+8). (a) Seasonal temperature variability (low pass filtered, half power of 33 hours), (b) sub-diurnal (low pass filtered, half power of 33 hours) temperature variability and (c) hourly temperature variability across the reef zones of Mermaid Reef. The bold line and shading represent the mean and standard deviation across all sites of a reef zone.
Figure 3-4: Power spectral density of temperature as a function of frequency (cycles per day) from the in situ temperature at the (a) reef flat, (c) lagoon and (e) deep fore-reef from 26/11/2017 to 1/10/2018. Power spectral density of temperature was not computed at the shallow fore-reef site as the data was only available for ~3 months out of the ~11-month experiment. Diurnal (S1) and semi-diurnal (M2) frequencies are indicated by the dashed grey lines. Daily change in temperature since midnight (ΔT) as a function of the hours of the day (over 24 hours) at the (b) reef flat, (d) lagoon, (f) deep fore-reef sites. The bold line and shading represent the mean and standard deviation across all sites of a reef zone, and (g) shows the mean depth as a function of the mean daily temperature range (ΔT_d) across the key reef zones.
3.4.3. Drivers and key mechanisms of temperature variability

3.4.3.1. Seasonal and sub-diurnal temperature variability

The seasonal temperature variability was reasonably well-correlated with the seasonal air-sea heat fluxes variations across all reef zones (Figure 3-5a; $R \sim 0.43$ to $0.55$; $p$-values $< 0.01$). At sub-diurnal frequencies, the temperature was correlated with wave height ($R \sim 0.31$ to $0.45$; $p$-values $< 0.01$) and wind speed ($R \sim 0.32$ to $0.43$; $p$-values $< 0.01$) across all reef zones. In addition, a tropical cyclone (Tropical Cyclone Marcus, category 5) developed $\sim 250$ km away from the reef during the study period (14 - 27 March 2018), leading to an increase in $H_s$ of $\sim 2$ m (Figure 3-5a). During that time, a decrease in mean temperatures and higher frequency variability was observed across all reef zones compared to pre-cyclone temperatures (Figure 3-5b).

Figure 3-5: (a) Significant wave height ($H_s$) and direction ($\theta_{\text{wave}}$) measured at the fore-reef site (S1) and (b) temperature changes during the passage of Tropical Cyclone Marcus, from 20/03/2018 to 25/03/2018 (local time, UTC+8) across key reef zones.
3.4.3.2. Diurnal and semi-diurnal temperature variability

On the reef flat and the lagoon, the temperature variability was strongly influenced by mechanisms acting at diurnal and semi-diurnal frequencies. As hypothesised in section 3.2.2, we show that such variability results from the net air-sea heat fluxes and heat advection (Eq. 3.2). Here, we specifically assess the contribution of the air-sea heat flux term to the observed diurnal temperature variability across both the reef flat and lagoon zones, as the advection term in the heat budget equation could not be accurately estimated.

Across both reef zones, the rate of temperature change indicated good agreement with the air-sea heat flux term, especially at the lagoon site ($R= 0.7$ and $0.8$; $p$-values $<0.001$, for the reef flat and lagoon respectively; Figure 3-6). However, the phase lags observed on the reef flat and the large deviations occurring at timescales higher than the diurnal frequencies, indicate the importance of other drivers, e.g., advection of heat. At the lagoon sites, the diurnal variability was most pronounced compared to the bottom measurements (not shown). However, from the mooring at S2, the lagoon temperatures were generally well-mixed throughout the water column (bottom and surface temperatures root mean square error (RMSE) $= 0.27^\circ C$, $R = 0.98$, $p$-value $<0.01$), with no clear seasonal trend in the thermal stratification (not shown).

Figure 3-6: Rate of temperature change at the (a) reef flat and (b) lagoon zones calculated from the in situ temperature time series (solid line) and calculated using Eq. (3.2) based on the air-sea heat flux term (dashed line). The bold line and shading represent the mean and standard deviation across all sites of a reef zone.
The daily temperature variability on the reef flat zone (Figure 3-7a) was partly controlled by the phasing of low tidal levels and maximum surface heat fluxes (Figure 3-7b). The maximum solar heating was estimated from the maximum daily $Q_N$ and occurred around midday each day, while the time of the offshore low tide gradually shifted relative to maximum surface heat fluxes over the study period because of the 12.42-hour period of the dominant $M_2$ tide (Figure 3-7b). The maximum diurnal temperature fluctuations at the reef flat sites therefore occurred when low tide and solar peak were in phase (small $\Delta Hr$; Figure 3-7c) and both processes were reasonably correlated with daily temperature variation ($R = 0.55$, $p$-value <0.01). This mechanism was not evident in the lagoon (not shown), which displayed some of the smallest diurnal variability ($\sim 0.5 \pm 0.1 ^\circ C$; Figure 3-7a grey line) over the 11-month study across all reef zones, as the lagoon was deeper than the reef flat at all sites.

![Figure 3-7](image)

**Figure 3-7:** (a) Temperature at reef flat and lagoon site (black and grey line, respectively) (28/11/2017 to 23/12/2017); (b) Hour of day when low tide (from water level measured at S1) and peak solar irradiance (estimated from the maximum daily $Q_N$) occurred. Grey shading represents night-time (6 pm to 6 am the following day, local time, UTC+8); (c) Boxplot of the mean daily temperature range ($\Delta T_d$) on the reef flat as a function of the lag between peak solar and low tide in hour ($\Delta Hr$) from 26/11/2017 to 1/10/2018. On each boxplot, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers, and the outliers are plotted individually using the ‘+’ marker symbol.
3.4.3.3. Hourly and higher frequency temperature variability

The fore-reef site (S1) experienced variability at semi-diurnal and higher frequencies, where rapid temperature fluctuations occurred as series of drops in temperature followed by a subsequent return to pre-event conditions (Figure 3-8). Through the 11-month temperature hourly time series, we identified ~290 events on the fore-reef where rapid temperature drops (over hourly timescales) led to a decrease of at least 1°C in the in situ temperature measurements at the fore-reef site (not related to night-time cooling). The cold-water pulses averaged 0.5°C in magnitude over typical time periods of approximately hours and occurred ~2 times per day on average. These fluctuations resulted in cooler mean daily temperatures (28.0°C) and larger mean daily ranges (2.2°C) at the fore-reef site compared to the rest of the atoll. Such cold-water pulses also occasionally influenced the temperature of shallower fore-reef and reef flat sites (S8 and S9, S4, respectively; Figure 3-8), where temperature drops were intermittently observed. At the eastern reef slope sites, similar rapid temperature drops were observed (not shown).

Figure 3-8: Cold water pulses across the western reef flat. Temperature variability across the western reef flat at S1 (deep fore-reef), S8 (shallow fore-reef), S9 and S4 (reef flat) at a 10-min interval. Grey shading represents night-time (6 pm to 6 am the following day, local time, UTC+8).
3.4.4. Differences between reef and offshore water temperatures

We have demonstrated that temperature variability varies widely between the different reef zones of Mermaid Reef. Here, we show that the reef’s water temperatures can also deviate significantly from the temperature of offshore waters ($\Delta T_{SST} = T_{reef} - SST_{offshore}$) throughout the year, reaching up to $\sim 2.6^\circ C$ lower at the reef flat zone in May 2018 (Figure 3-9a and b). As demonstrated in section 3.4.3.2, the air-sea heat flux term in Eq. (3.2) plays a key role in modulating the reef’s temperature variability at diurnal timescales across the reef flat and lagoon sites. We therefore investigate to which extent the net air-sea fluxes drive the differences between reef and offshore waters’ temperatures by relating those differences ($\Delta T_{SST}$) to the net daily heat flux across the air–sea boundary and mean water level following:

$$\Delta T_{SST} = a \left( \frac{Q_N}{hpc_p} \right) + b$$  \hspace{1cm} (3.3)

where $a$ and $b$ are the best-fit slope and y-intercept computed from a linear regression of $\Delta T_{SST}$ and the air-sea heat flux term $\left( \frac{Q_N}{hpc_p}, \text{Eq. 3.2} \right)$ at each reef zone (Figure 3-9a and b). Linear correlations between both parameters were significant at both the reef flat and lagoon reef zones ($R= 0.76$ and $0.41$ and $p$-values $<0.01$, respectively; Figure 3-9c and d). By doing so, we can then model daily average temperatures at each reef zone ($T_{modelled}$) by empirically correcting the $SST_{offshore}$ data with $\Delta T_{SST}$ calculated from Eq. (3.3) according to Eq. (3.4):

$$T_{modelled} = SST_{offshore} + \Delta T_{SST}$$  \hspace{1cm} (3.4)

The comparison between daily corrected $SST_{offshore}$ ($T_{modelled}$) based on the net air-sea heat flux contribution showed good agreement with $T_{reef}$ observations ($RMSE= 0.37$ and $0.31^\circ C$ for the reef flat and lagoon zones respectively; Figure 3-10a and b), confirming the role of the air-sea fluxes as a main driver of temperature differences between the reef and offshore waters. In addition, despite the simplicity of the predictive model given by Eq. (3.3), accounting for the local atmospheric heat fluxes alone helps to substantially improve predictions of in situ temperatures from knowledge of offshore sea temperatures surrounding reefs.
Figure 3-9: (a) Time series of the remotely sensed SST for the reef flat, lagoon and offshore waters. (b) Differences in night-time SST between the reef flat, lagoon and offshore (ΔT_{SST}). The dashed line indicates zero difference in temperature. (c and d) indicate the daily average difference in temperature between reef and offshore waters versus the ratio of daily average air-sea heat flux term ($\frac{Q_N}{\rho c_p}$, Eq. 3.2) for the period from 26/11/17 to 01/10/18 at the reef flat and lagoon sites, respectively. The grey lines represent the best-fit linear regression for each fitted regression.
3.5. Discussion

The analysis of an 11-month time series of temperature measurements along with oceanic and atmospheric conditions has provided insight into the drivers of temperature variability within different zones of Mermaid Reef. We summarize the distinct temperature regimes encountered across the reef zones and discuss the implications for coral reef communities.

3.5.1. Distinct temperature across a coral reef atoll

Over sub-diurnal timescales (on the order of days to weeks), Mermaid Reef was regularly exposed to westerly wave and wind climate. In addition to regular sources of swell, tropical cyclones are particularly frequent on Australia’s NWS and episodically influence Mermaid reef’s hydrodynamic conditions (Drost et al. 2017; Chapter 4). During these events, the associated large wave energy and cloud-cover-
driven reduction in solar radiation had a cooling effect on both the mean reef water temperatures and their higher frequency variability (Figure 3-5b; Chiang et al. 2011; Carrigan and Puotinen 2014; Green et al. 2019b).

Most of the temperature variability between reef zones occurred at diurnal and higher frequencies, where distinct forcing mechanisms impacted the reef zones. The reef flat sites, characterised by shallow waters prone to rapid heating, displayed large variability in diurnal temperatures contrary to the deeper lagoon sites. Similar to other reefs with strong tidal forcing, diurnal temperature variability for both the reef flat and lagoon zones was dominantly shaped by the interaction of tidal water levels and solar radiation (McCabe et al. 2010; Lowe et al. 2016).

While the role of the local net-air sea heat exchange on rates of temperature change was evaluated in this study, assessing the role of advection requires high-resolution horizontal temperature gradient information, which was not available during the study period. Nonetheless, the advection of heat undoubtedly played an essential role in driving the temperature variability at Mermaid Reef. For example, deeper reef zones such as the fore-reef experienced some of the largest temperature anomalies over rapid timescales (order minutes), most likely due to large amplitude internal waves, which have been observed both across Australia’s NWS and on other surrounding coral reef atolls (Scott Reef, located ~400 km from the Rowley Shoals; Green et al. 2019b). Such rapid temperature decreases (of several degrees), driven by internal waves, have been observed on numerous fore-reefs among corals reefs worldwide (Leichter et al. 1996; Sevadjian et al. 2012; Comfort et al. 2019; Lee et al. 2020; Wyatt et al. 2020), with temperature fluctuations occurring at time scales down to order minutes. Within Mermaid Reef, these cold-water pulses could occasionally propagate up and across the reef flat (Figure 3-8), as previously observed in other reef systems (Reid et al. 2019). Additional temperature measurements throughout the water column are however required to determine the exact mechanisms and conditions favourable for such transport to happen across the steep reef slope bathymetry (Reid et al. 2019).

Finally, we find that temperatures across the reef zones presented large deviations from offshore water temperatures (up to 2.6°C lower), highlighting the value of in situ temperature measurements on coral reefs as remotely sensed sea surface temperature techniques currently do not widely resolve the fine-scale temporal and spatial variability (order of 100s of meters and minutes to hours) of temperatures within
reefs. Given that obtaining in situ temperature measurements can be logistically-challenging and cost and time-prohibitive—especially in remote areas like Mermaid Reef, developing predictions of on-reef temperature from SST measurements (e.g., downscaling prediction methods) is vital. Here we show that an accurate reconstruction of reef temperatures at the reef flat and lagoon sites can be obtained by simply correcting $\text{SST}_{\text{offshore}}$ by an air-sea heat flux term. Similar approaches have been used on wave-driven reefs where the temperature variability was driven by offshore wave and atmospheric data, provided by global climate models (Falter et al. 2014).

3.5.2. Significance for thermal stress experienced by coral reef communities

Temperature variability plays a crucial role in coral reef ecology and understanding the full range of temperature variability to which specific reef zones are normally exposed to is critical to determining thermal stress, coral bleaching thresholds and longer-term response of reef communities to global warming. Even though the low frequency temperature variability did not vary substantially from one reef zone to the other, higher frequency temperature variability resulted in distinct temperature regimes and potential heating across the considered reef zones. Temperature fluctuations occurring on diurnal or tidal variations expose shallow corals to potentially stressful temperatures, which could occur over periods short enough to avoid coral mortality but long enough to help adaptation (Oliver and Palumbi 2011; Palumbi et al. 2014; Safaie et al. 2018; DeCarlo et al. 2019). Therefore, coral reef organisms from such thermally variable environments have been hypothesized to show greater resilience to future marine heatwaves (e.g., reef flat; Rivest et al. 2017) and be more resistant to anomalous temperatures and bleaching than corals in areas, where temperatures are more stable (e.g., lagoon; Barshis et al. 2013; Thomas et al. 2018). In addition, drops in temperatures observed on the fore-reef sites related to internal waves reduce overall mean temperatures and are increasingly recognized as providing temperature refugia for coral reefs (Storlazzi et al. 2020; Wyatt et al. 2020).

The various thermal environments described here are consistent with the bleaching response observed following the 2016 marine heatwave in Western Australia (Benthuyisen et al. 2018). Indeed, little to no bleaching ($\leq 10\%$) was recorded at fore-reef sites (exposed to cold water pulses) compared to the lagoon sites (exposed to little diurnal temperature variability), where moderate bleaching (30%) was recorded (Gilmour et al. 2019b). Bleaching patterns result from a combination of environmental
factors (e.g., light intensity, water flow, depth, nutrient availability; Safaie et al. 2018; DeCarlo et al. 2020) and biological factors (e.g., species-specific responses, genotype; Burgess et al. 2007; Thomas et al. 2018). However, the insights into fine-scale temperature variability provided here could help improve our understanding of past bleaching variability and constrain predictions of future bleaching patterns at Mermaid Reef and other reefs worldwide.

3.6. Conclusions

Our detailed 11-month record of in situ temperature across Mermaid Reef provided insight into the distinct temperature variability encountered across the various reef zones, including reef flat, lagoon and fore-reef sites. Such reef zones displayed different mean depths and degree of exposure to the main oceanic and atmospheric drivers of temperature variability. Most of the temperature differences between reef zones occurred on diurnal and higher frequency timescales. At such frequencies, temperature variability in reef flat and lagoon zones were driven by a combination of net diurnal atmospheric heating and mean depth. As a result, we showed that local deviations in the mean daily temperature of in situ temperature of reef waters from offshore remotely sensed sea surface temperature values were a linear function of the combined effect of net atmospheric heating and water level. On the fore-reef zone, especially at the deeper site, temperature variability was driven by cold water intrusions likely generated by internal waves that are prominent on Australia’s North West Shelf. Overall, these results highlighted the importance of quantifying the drivers of temperature variability across reef systems as they shape distinct temperature regimes, and result in variable thermal stress across a single reef system.

3.7. Acknowledgements

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4. Hydrodynamic drivers of fine-scale connectivity within a coral reef atoll off northwestern Australia

This work is under review in *Limnology and Oceanography*.

4.1. Abstract

An accurate representation of physical and biological processes is crucial to resolve larval dispersal pathways and characterise connectivity of coral reef ecosystems. We investigate how hydrodynamic forcings drive larval retention rates during the bi-annual mass coral spawning of the coral genus *Acropora* within a coral reef atoll (Mermaid Reef), located off northwestern Australia. By analysing hydrodynamic conditions during 41 years of historical spring and autumn coral spawning events, we identify ‘typical’ and ‘extreme’ hydrodynamic forcing conditions. Numerical simulations using a validated coupled wave-flow hydrodynamic model forced with typical hydrodynamic conditions during coral spawning along with Lagrangian particle tracking, revealed a mean transport of larvae eastward across the atoll, driven by a combination of wave-driven mean flows and tidal residual currents. The oscillatory (non-residual) component of the flow generated by tides reduced the net export of particles from the reef, whereas both the residual tidal flow and unidirectional flow generated by waves increased the net export from the reef. Importantly, however, numerical simulations forced with ‘extreme’ hydrodynamic conditions generated by episodic tropical cyclone conditions (11 out of 41 years) show that large deviations from the typical eastward
flow can occur during autumn spawning events, generating different connectivity pathways within the reef system. Considering the substantial time larvae can be retained within reef systems, we demonstrate the need to consider these fine-scale hydrodynamic processes within regional connectivity predictions, which is generally not considered yet critical to understand the capacity of reefs to recover following disturbances.

4.2. Introduction

Coral reefs are among the most impacted marine ecosystems by human activities (Halpern et al. 2008), including due to the growing threat of climate change (Hoegh-Guldberg et al. 2017). Understanding coral larvae transport, both within and between reef systems, is crucial for assessing the capacity of individual reefs to act as sources and sinks of larvae and help target efforts to enhance their recovery from disturbances (e.g., Treml et al. 2007; Magris et al. 2014).

Hydrodynamic flows determine the transport of coral larvae and other reef organisms that have a planktonic larval stage with limited swimming ability (Cowen and Sponaugle 2009). From gamete release to recruitment, planktonic larvae are dispersed by circulation patterns over a range of spatial scales. Over large spatial scales (10s to 1000s of kilometres), hydrodynamic flow features such as upwelling, mesoscale eddies, and coastal currents can influence dispersal patterns that govern connectivity between reef systems once larvae escape their natal reef (Foster et al. 2012; Rairden et al. 2017; Lequeux et al. 2018; Pata and Yñiguez 2019). Over finer spatial scales (10s to 1000s of metres), reef-scale hydrodynamic processes such as tidally- and wave-driven flows and bathymetric features such as channels and lagoons regulate dispersal and connectivity patterns within reef systems (Tartinville et al. 1997; Monismith 2007; Dumas et al. 2012; Lowe and Falter 2015; Rogers et al. 2017).

Numerical ocean circulation models can provide valuable insight into coral connectivity by simulating the hydrodynamic processes that govern how material is transported over a range of spatial and temporal scales. However, most studies to date have used relatively coarse spatial and temporal scales to infer connectivity (e.g., kilometre scale and daily hydrodynamic forcing; Treml et al. 2007; Romero-Torres et al. 2018; Lequeux et al. 2018), which cannot resolve reef-scale hydrodynamic processes. As a result, such studies may give an inaccurate estimate of larvae released within a reef that are available for transport in deeper oceanic waters.
surrounding reefs; and more broadly, inaccurate estimates of the connectivity within and between reef systems. To date, only few studies have used the fine spatial resolution necessary to resolve reef-scale hydrodynamic processes (Storlazzi et al. 2018b; Taninaka et al. 2019; Frys et al. 2020).

In addition, the transient nature of ocean flows, from hourly to decadal timescales, can also strongly influence connectivity and larval sources or sinks over time (Treml et al. 2015). For example, tropical cyclone activity can generate extreme and atypical flows that are thought to cause rare dispersal events, linking reef systems that are not typically connected (Radford et al. 2014; Edmunds et al. 2018). Similarly, tropical cyclone activity could modify the reef-scale hydrodynamics and create new dispersal pathways within a reef system. Yet, most studies overlook the temporal variability in hydrodynamic conditions and connectivity patterns by focusing on a limited number of spawning seasons or events (e.g., Storlazzi et al. 2017; Frys et al. 2020).

In this study, we provide an in-depth investigation of the relative influence and temporal variability (both long- and short-term) of the hydrodynamic drivers of fine-scale reef connectivity on dispersal patterns within an atoll reef system. We focus specifically on the spawning times and larval characteristics of the coral genus Acropora and start by identifying ‘typical’ (representative) and ‘extreme’ (tropical cyclone) climatic and oceanographic conditions during 41 years of historical bimannual mass spawning events (1980-2020). We then use a validated, numerical hydrodynamic model forced both ‘typical’ and ‘extreme’ hydrodynamic conditions, with Lagrangian particle tracking to simulate the transport pathways of coral larvae. Finally, we discuss the importance of properly accounting for the reef-scale hydrodynamic processes when assessing connectivity, as transport distances can be greatly overestimated when ignoring the significant time larvae can be retained within a reef relative to their overall competency period.

4.3. Study site

Mermaid Reef (14.9 × 7 km; covering ~87.5 km²) is the northernmost of three reef atolls at the Rowley Shoals (comprising Mermaid, Clerke and Imperieuse Reef) located on Australia’s NWS (Figure 4-1a). The atoll rises from 500 m depth, with a steep fore-reef slope and reef flat enclosing a large lagoon (50 km²) that is approximately 20 m-deep, with a single channel (8 m-deep, 250 m-wide) as the only continuous

78
opening to the open-ocean on the northeast side. Mermaid Reef is exposed to a combination of waves and large (meso-) tides and regularly experiences flow regimes dominated by waves and/or tides depending on the surrounding oceanographic conditions. The residual circulation within the atoll is controlled by how waves and tides interact with the reef morphology, which result in an eastward residual transport across the atoll (Chapter 2).

Across the reef system, hard corals (Figure S 4-1, quantified in complementary studies see Supplemental Information) are present in parts of the lagoon (small lagoonal bommie habitats), reef-flat, reef-crest and particularly on the outer eastern reef-slope. Of the total hard coral cover, Acropora spp. cover reaches up to 60% in parts of the atoll (Figure 4-1b). Given the dominance of Acropora spp. relative to the total coral cover, we focus on its spawning time and larval characteristics to investigate the larval dispersal and connectivity across Mermaid Reef.

![Figure 4-1:](image)

Figure 4-1: (a) Bathymetry (depths relative to mean sea level; MSL) of Mermaid Reef. Brown colours represent the reef flat (depths 2 m above to 2 m below MSL). Hydrodynamic regions across Mermaid Reef are represented by the dotted black boxes. The reef flat (RF) regions were defined between +/- 2 m and the lagoon (L) regions were defined inside the reef flat. Inset map shows Mermaid Reef’s location on Australia’s North West Shelf. (b) Probability of presence of Acropora spp. derived from the benthic habitat model using the combination of tow-camera footage, laser airborne depth surveys, statistical modelling approach and from quantified percentage cover of Acropora spp. (referred to as long term monitoring or LTM); see Supplemental Information for data collection and benthic habitat model methods.
4.4. Methods

4.4.1. Biophysical model

A coupled wave-flow hydrodynamic model (Delft3D Flexible Mesh), covering a 45 x 40 km region (119.5 to 119.8 °E; -16.9 to -17.3 °N) at a resolution ranging from 30 to 500 m, was previously developed and validated for a 3 month-period (1/12/2017 and 1/03/2018) at Mermaid Reef (refer to Chapter 2 for details). The coupled model is composed of a flow module (D-Flow FM, which solves the unsteady shallow water equations derived from the three-dimensional Navier-Stokes equations for incompressible free surface flow), and a wave module (D-Waves, based on the Simulating WAves Nearshore or SWAN wave model, which computes random, short-crested wind-generated waves and associated wave-averaged flows; Booij et al. 1999). The two modules were used both independently and iteratively coupled together (with hourly data transfer between the two modules) to investigate the relative importance and interactions between tide- and wave-driven flows on larvae dispersal. The model boundaries were forced with tidal constituents derived from the TPXO8.0 global tide solution (1/30° resolution; Egbert & Erofeeva, 2002) and hourly spatially and time-varying wave conditions derived from the Centre for Australian Weather and Climate Research (CAWCR) Wave Hindcast, which uses WaveWatch III (Smith et al. 2021). The model showed good agreement with time series of observed water level, significant wave height and current velocity measured across key locations of Mermaid Reef (Grimaldi et al. 2022). The model was run in 2DH mode (horizontal, depth-averaged), which is a reasonable assumption given the homogeneity of the current velocities throughout the shallow water column of Mermaid Reef’s lagoon. The upper (i.e., surface to 6-m depth) and lower (i.e., 6-m depth to bottom 12-m depth) water column velocity estimated from an Acoustic Doppler Current Profiler deployed for 3 months (25/11/2017 – 11/03/2018) in the lagoon (in 12-m depth; S2 in Grimaldi et al. 2022) displayed a root mean square deviation = 0.01 m/s. However, more pronounced vertical flow structures are likely to occur in deeper waters surrounding the atoll, which would be more important to resolve when simulating larval dispersal outside of the atoll.

In this study, the hydrodynamic model was forced using tidal and wave parameters observed during both ‘typical’ and ‘extreme’ hydrodynamic conditions occurring over 41 years of spawning events (spanning 1980-2020) detailed further
below. Regional currents and winds displayed small velocities during ‘typical’ spawning conditions and were found to have little impact on the atoll circulation for these ‘typical’ conditions (see below and Supplemental Information) and were therefore not included. However, regional currents and winds displayed much larger velocities during the years affected by tropical cyclone activity and were then included. In these cases, the four model boundaries were forced every 10 km with daily wind and regional surface current velocities, extracted from the Bluelink ReANalysis (BRAN) 2020 (denoted BRAN 2020), an ocean reanalysis that combines ocean observations with a near-global, 10-km resolution (eddy-resolving) ocean model available from 1993 to 2019 (Chamberlain et al. 2021).

The Lagrangian transport of particles (i.e., larvae; Eq. 4.1) was then simulated using the depth-averaged velocity fields computed by the model (for the eastward transport component) as:

$$x_i^{n+1} = x_i^n + (u)\Delta t$$

(4.1)

The eastward (x-direction) position of the $i^{th}$ particle at time step $n+1$ ($x_i^{n+1}$), was calculated from its previous position ($x_i^n$), the eastward velocity component ($u$) and the model time step ($\Delta t$, i.e., 10 min). An analogous expression was used for the northward (y-direction) position at time step $n+1$ ($y_i^{n+1}$), calculated from its previous position ($y_i^n$), the northward velocity component ($v$) and the model time step ($\Delta t$). We assumed that the transport of particles was dominated by the contribution of advection, with no diffusion scheme (i.e., based on a random-walk method) included. A measure of the potential contribution of advective to diffusive transport can be assessed based on evaluating a Peclet number ($Pe = uL/K_h$). Considering $u$=0.1 m/s (a typical weakest flow velocity in the lagoon), $L$~60 m (the typical scale of the model resolution on the atoll), and assuming a typical horizontal dispersion coefficient of order $D_h$~1 m$^2$/s in reefs (Jones et al. 2008; Lowe et al. 2009b), $Pe=10 >>1$ such that transport is expected to be dominated by advection. This is consistent with a other reef connectivity studies using particle tracking that have indicated advective transport is dominant over diffusive transport based on model sensitivity analyses (e.g., Lowe et al. 2009; Xu et al. 2016; Mayorga-Adame et al. 2017). Within the particle tracking scheme, the modelled flow velocities were used to advect particles by numerical integration of the flow vectors output between each time steps (i.e., every hour). A total of $\sim$9000 particles, each representing a patch of coral larvae, were released every 100 m equally spaced over the entire atoll, including the reef flat and
in the lagoon (Figure S 4-2) after 13 hours of model “spin-up” (i.e., \( t=13 \) hours). While in reality there are vast numbers of larvae released during spawning event, the particles represent a patch of larvae that are in close proximity and which would be transported with the same local flow conditions. Each particle was then tracked over time and updated hourly until the end of the simulation. The sensitivity of the model results to the time of release over the different stages of the tidal cycle was assessed but found to have little impact on the resulting atoll retention rates (Figure S 4-3).

Biologically specific processes that influence the distribution of larvae viable for potential settlement, including spawning time, larval competency periods, and mortality were also incorporated. Spawning time generally occurs around the third quarter of the moon (i.e., 9 days after full moon) on neap tides and \(~1\) hour after sunset for both austral autumn and spring mass coral spawning on the NWS (Table S 4-1, Gilmour et al. 2016). After coral spawning, the resulting larvae were treated as sufficiently developed for settlement after \(~3\) days and for up to 10 days after coral spawning (Gilmour et al. 2009; Heyward and Radford 2019), which we define as the larval competency period. Natural rates of mortality for coral larvae in their planktonic stage are not precisely known, however, based on data from larval experiments and \textit{in situ} observed decreases in abundances of larvae following spawning (Heyward et al. 2002; Nishikawa et al. 2003; Gilmour et al. 2009; Connolly and Baird 2010), we estimate mortality rates of 40% each day. As a result, 40% of the larvae were randomly removed from the total number of larvae each day.

4.4.2. Meteorological and oceanographic conditions

Oceanographic conditions during bi-annual coral spawning were investigated by analysing historical tidal water levels, waves, regional currents, and wind conditions at Mermaid Reef from 1980 to 2020 using global hindcast models described earlier to determine the ‘typical’ (representative) and ‘extreme’ (tropical cyclone) hydrodynamic conditions during spawning events. ‘Extreme’ hydrodynamic conditions were defined when a tropical cyclone coincided with a spawning event. Tropical cyclones were identified using the Bureau of Meteorology tropical cyclone database (http://www.bom.gov.au/cyclone/tropical-cyclone-knowledge-centre/databases), with tropical cyclones resulting in \( H_s > 2 \) m surrounding Mermaid Reef \((119.55^\circ E; -17.1^\circ N)\) retained for ‘extreme’ conditions simulations.
4.4.3. Analysis of the transport network

4.4.3.1. Encounter probability distribution

An “encounter probability distribution” (EPD) was defined as the probability of a coral larvae patch to encounter a specific part of the reef in time, regardless of where the larvae are sourced from. This definition is analogous to the approach reported in van Sebille et al. (2018), used to describe particle pathways. For the purpose of the analysis, we consider a 45 × 40 km regular grid covering the model domain, with a spatial resolution of 100 × 100 m. The probability for a coral larvae patch to encounter a grid cell was obtained by cumulatively summing up the number of particles occupying each grid cell at each time step (i.e., hourly) over the whole duration of the competency period (i.e., from day 3 to 10 after release) and dividing each grid cell count by the total number of recorded particles across the domain at the end of the competency period (i.e., 10 days after release). The encounter probability distribution was not normalized by the cell surface area as we consider a regular grid. The values are presented as percentages; for example, a value of 3% means that of larvae released throughout the entire reef, there is a 3% probability for the larvae to pass through a given location during the competency period and could represent a potential settlement site (depending on favourable substrate, depth and light regime, for example).

4.4.3.2. Retention rate and travelled distances

A “retention rate” (R) was defined as the percentage of particles retained within the atoll over time, i.e.,

\[ R(t) = \frac{N(t)}{N_0} \times 100\% \quad (4.2) \]

where \( R(t) \) represents the percentage of retained particles based on the number of particles (\( N \)) within the atoll at time \( t \) (i.e., all sub-regions in Figure 4-1a) and the number of particles (\( N_0 \)) in the domain at the initial release time \( t_0 \).

To determine the distance travelled by the larvae, we used both the “relative distance” travelled, defined as the distance between the release location and location after 10 days of dispersal, and the “cumulative distance”, defined by cumulatively integrating the particle movements (i.e., independent of direction) hourly between release time and 10 days of dispersal.
4.4.3.3. Connectivity strength

To determine the sources and sinks of larvae transported to different areas across Mermaid Reef, we divided the release zone into four sub-regions spanning the reef flat and six sub-regions spanning the lagoon (Figure 4-1a). The connectivity strength \( C_{ab} \) was calculated as the proportion of the total number of particles released in a source \( a \) that reaches a sink \( b \) after the dispersal duration (i.e., 10 days). Connectivity matrices were computed to illustrate the connectivity strength between selected sub-regions as sources (rows) and sinks (columns).

4.5. Results

4.5.1. Meteorological and oceanographic conditions during coral spawning events

Over the 41-year period (1980-2020), the austral spring (March) and autumn (October) mass spawning events at Mermaid Reef typically occurred near neap tide, transitioning to spring tidal range (TR) over the course of a 10-day larvae competency period (Figure 4-2a, b and c). Tidal water level variations over the larvae competency period were similar for both spring and autumn spawning (mean ± standard deviation, TR = 2.6 ± 0.3 m and 2.5 ± 0.3 m, respectively; minimum neap TR of 0.1 and 0.2 m, respectively; maximum spring TR of 4.4 and 4.3 m, respectively), and were used to represent the ‘typical’ water level conditions during spawning.

The wave climate was episodically affected by tropical cyclones (TC) in the region, especially during the autumn spawning season. To investigate differences between cyclone and non-cyclone years, we first considered years during which no tropical cyclone activity coincided with autumn spawning (30 out of 41 years), where significant wave height values ranged from 0.6 to 2 m (\( H_s = 1 \text{ m} ± 0.3 \text{ m} \)), with a mean wave period (\( T_p \)) of ~13 sec and direction (\( \theta_{\text{wave}} \)) from the southwest (~213 ºN) (Figure 4-2d and g). There were no years when TCs coincided with spring spawning, and \( H_s \) ranged from 0.7 to 3.2 m (\( H_s = 1.3 ± 0.3 \text{ m} \)), with a mean period of ~11 sec and direction from the southwest (~223 ºN) (Figure 4-2e and h). In the absence of tropical cyclone activity, wave conditions for both spawning seasons were similar, so we considered waves with \( H_s = 1 \text{ m} \); \( \theta_{\text{wave}} = 220 \text{ ºN} \) to represent typical wave conditions during spawning.

The 11 years during which tropical cyclones influenced local hydrodynamics at Mermaid Reef during austral autumn spawning (Table S 4-1) were considered...
separately. Tropical cyclones caused peak $H_s$ ranging from 2 to 5 m ($H_s = 2.9 \pm 0.5$ m, Figure 4-2e) and affected local wave conditions on the reef for up to 6 days (grey lines in Figure 4-2e). The average peak wave periods and directions were far more variable than during spawning periods without TC activity (Figure 4-2h).

Over the 27 years available from BRAN 2020 (1993 to 2019), wind velocities displayed different patterns during the austral spring and autumn spawning conditions. In March (austral autumn), wind velocities ranged from 0.9 to 6.7 m/s (1.6 m/s on average) and were mainly directed towards the north (Figure S 4-4a). In October (austral spring), wind velocities ranged from 1.7 to 5.9 m/s (3.5 m/s on average) and were mainly directed towards the north-east (Figure S 4-4b). In March,
regional currents (derived from BRAN 2020) usually ranged from 0 to 0.3 m/s and were directed southward to southwestward (Figure S 4-4c). In October, the regional currents displayed speeds of up to ~ 0.1 m/s and were directed northward to northeastward (Figure S 4-4d). The effect of winds and regional currents on reef hydrodynamics (i.e., within the atoll) was assessed by using numerical simulations both with and without mean wind and regional surface currents forcing included during both spring and autumn spawning; both were found to have little impact on the local reef hydrodynamics (Figure S 4-5 and Figure S 4-6). However, these regional currents determine the speed and direction of currents surrounding the atoll and are therefore important for driving dispersal and larval connectivity among other atolls at the Rowley Shoals (see section 4.6).

4.5.2. Circulation patterns during typical hydrodynamic conditions

The typical hydrodynamic conditions during both spawning periods were used to force the biophysical model of larval dispersal (i.e., no TC activity, neap tidal range, $H_s=1$ m, $\theta_{\text{wave}}=220$ °N). The time-averaged circulation patterns (Figure 4-3a) revealed a general north-eastward flow across the reef, with flow entering the reef through the western reef flat and exiting the reef through the north-eastern reef flat. Residual current speeds were similar on both the eastern and western reef flats (0.1 m/s), slowest in the lagoon (0.02 m/s), and fastest in the channel (up to 0.2 m/s). During neap tides (Figure 4-3b), there was a general eastward residual flow across the atoll, entering over the western reef flat and exiting over the eastern reef flat and channel. During spring tides (Figure 4-3c), the residual flow entered over the western and southern reef flat, flowing north-east in the lagoon, before exiting over the reef flat and through the channel.

Through 10 days of dispersal, the larvae cohort travelled eastward, with few remaining on the western edge of the reef flat and most dispersing to just outside of the atoll to reside on the eastern reef slope. The maximum encounter probability distribution was $E_{\text{PD}} = 0.05\%$ on the eastern reef slope and $E_{\text{PD}} = 0.02\%$ in the lagoon (Figure 4-4a). Larvae released on the western reef flat travelled a relative distance of ~4000 m on average after 10 days. The larvae released in the lagoon travelled a relative distance of ~500 m on average after 10 days (min. ~250 m, max. ~860 m, sub-region L4 and L2 respectively); those released on the eastern reef flat travelled an average of ~190 m before leaving the atoll reef. Overall, the connectivity was strongest between the western to eastern part of the reef (Figure 4-4b and c) due to
the dominant residual mean circulation patterns (Figure 4-4). The western and southern sides of the reef flat were more strongly connected to the lagoon, and the western part of the lagoon (sub-regions L1, L2 and L3) were most strongly connected to the east (L4, L5, and L6), which is then connected to the east of Mermaid Reef (outside of the reef, i.e., offshore).

![Diagram](image)

**Figure 4-3.** Residual (time-averaged) flow patterns during the spawning period for typical conditions (excluding cyclone years). Depth-averaged velocity magnitude (colours) and unit velocity vectors during typical spawning conditions, time-averaged over (a) the 10-day simulation, (b) neap tides and (c) spring tides (see Figure 4-2a). No winds or regional currents were included in these simulations yet had little influence on the flows within the atoll (see Figure S 4-5 and Figure S 4-6). All residual flows were plotted as unit vector arrows using the curvvec function in Matlab (Stevens et al. 2021).

### 4.5.3. Relative importance of hydrodynamic forcing

We investigated the influence of tidal versus wave forcing on the connectivity by isolating the effects wave and tidal forcing in the simulations. With “Wave-only” conditions, there was a general eastward flow across the reef, entering the reef over
the western reef flat, and exiting the reef over the eastern reef flat and through the channel (Figure 4-5b). On average, relative and cumulative dispersal distances associated with wave-driven flows after 10 days were similar (~4650 and 5200 m respectively, after 10 days), with the retention rate steadily decreasing to ~0 % (Figure 4-5a).

![Figure 4-4: Connectivity at Mermaid Reef. (a) Encounter Probability Distribution (EPD) after 10 days, (b) average connectivity matrix after 10 days of larval dispersal and (c) spatial connectivity of larvae among sites, where the line thickness reflects the strength of the connectivity.](image)

As the tide rose and fell, the oscillatory (unsteady) movement of the tide forced water in and out of the lagoon, with a portion of particles exiting the atoll during the ebb phase of the tidal cycle getting advected back into the atoll during the flood phase of the tidal cycle. As a result, the net distances travelled from the point of release were usually small (~1650 m on average), in contrast to the much larger cumulative distances travelled (~17700 m on average) after 10 days. The retention rate associated with tide-only reached ~20% after 10 days (Figure 4-5<a>). In this case, however, retention rates did not decrease steadily but oscillated with rising and falling
Comparing the retention rates of the tide-only with the combined wave and tide condition, we observed larger differences during the first 5 days of the simulation (i.e., neap and transitioning to spring tides), during which the retention rate was higher for the tide-only simulation (up to ~20% higher). After 5 days, the retention rate for the tide-only simulation became larger than for the combined wave and tide condition. This transition suggests that the role of waves was more prominent during the neap tide period than during spring tides.

Figure 4-5: Comparison between wave-only and tide-only simulations. (a) Atoll retention rate associated with different study cases tide-only and wave-only simulations based on typical (non-TC) conditions. Time- and depth-averaged residual flow velocities for (b) wave-only conditions, with $H_s = 1$ m and $\theta_{wave} = 220^\circ$N, (c) tide-only conditions for neap, and (d) tide-only conditions for spring tides.

4.5.4. Influence of tropical cyclones on connectivity patterns

Mermaid Reef experienced TC activity during the austral autumn mass spawning in 11 out of the 41 years considered. All cyclones altered the typical hydrodynamic
conditions and displayed a range of wave heights, directions, regional current velocities, timings, durations, and cyclone trajectories (Figure 4-2e and h; Table S 4-2). We investigated the effects of two specific cyclones (TC Vivienne and TC Fay) on larval dispersal and connectivity pathways. These two specific cyclones captured both the largest average $H_s$ (maximum $H_s = 4$ and 4.4 m respectively; Figure 4-2e), and $T_p$ (maximum $T_p = 19$ and 12 sec respectively; period not shown), over the 11 years considered, as well as different $\theta_{wave}$ compared to typical conditions (mean $\theta_{wave} \sim 94$ and 119 °N respectively). In addition, TC Vivienne and Fay occurred at different times of the competency period and thus interacted with both neap and spring tide. TC Vivienne caused a residual north-east flow in the lagoon (Figure 4-6b) and the accumulation of larvae on the western reef slope (Figure 4-6d), rather than the eastern reef slope and in the middle of the lagoon that occurred during typical conditions. TC Fay caused a residual northward flow and the accumulation of larvae in the western lagoon and northern parts of the reef (Figure 4-6c), causing a high proportion to be carried off the reef to the North (Figure 4-6e).

Figure 4-6: Influence of Tropical Cyclone Vivienne (1996) and Tropical Cyclone Fay (2004) on hydrodynamic conditions and connectivity. (a) Atoll retention rate for typical spawning conditions and TC Vivienne and TC Fay over the dispersal period. (b, c) The time-average velocities over the 10 days of dispersal. (d, e) The difference in EPD ($\Delta$ EPD) of larvae between each TC and values calculated for typical spawning conditions. Red (blue) colours indicate smaller EPD than in the typical spawning conditions case (Figure 4-4a).
In addition to altering the typical patterns of larval dispersal and connectivity within the reef, the cyclones also both increased and decreased the overall retention rates, ranging between 0% and 12% over the 10-day dispersal period, with all events resulting in a 0% retention rate after 10 days (Figure 4-6a). Differences in the retention rate between the cyclones depended on their proximity to Mermaid Reef and timing during the tidal cycle. For example, TC Vivienne occurred within 1 day of spawning, reducing retention rates, and increasing dispersal for much of the competency period.

4.6. Discussion

4.6.1. Coral reef connectivity at Mermaid Reef

Under typical conditions, our results highlighted relatively constant hydrodynamic conditions during both the primary coral spawning period in March and the secondary period in October. We observed a dominant eastward flow across the atoll leading to a high probability of larvae accumulating on the eastern half of the reef, before being transported outside of the atoll. This pattern thus predicted there would be a typical larval supply from the western slope and reef flat, to the eastern part of the lagoon and the adjacent reef-flat and reef-slope.

However, these typical hydrodynamic conditions changed dramatically when tropical cyclones passed in the vicinity of the reef system, producing large waves coming from varying directions and large winds and surface regional currents. As a result of changing hydrodynamic conditions, the strength of source and sink regions varied greatly and caused large deviations from the general eastward flow. For instance, we observed a dominant westward flow across the atoll leading to a high probability of larvae accumulating on the western side of the reef. TC conditions could therefore be the only way to provide dispersal pathways to the western side of the reef. By considering both fine-scale hydrodynamic processes and sufficiently long-term hydrodynamic variability, we showed that incorporating different spatial and temporal scales is critical for understanding both the mean hydrodynamic conditions as well as extreme event conditions.

Hard corals, and particularly different coral taxa (Figure S 4-1), are not uniformly distributed across a reef. Simulating larval release across all shallow water habitats on a reef (e.g., Storlazzi et al. 2017; Frys et al. 2020) does not reflect variation in habitat suitability and the distribution of different coral taxa, and therefore, realistic patterns
of connectivity among populations. To investigate dispersal of the dominant Acropora species, additional typical simulations were run with release from eastern reef lagoon and slope, where their cover was highest (Figure 4-1 and Figure 4-7 red polygon). During the typical conditions, very few of the Acropora spp. larvae were retained on the reef, with most travelling eastward and off-reef, but remaining within a few hundred metres of the reef slope for 10 days (Figure 4-7).

4.6.2. Retention and export: hydrodynamic and geomorphic controls

Reef-scale hydrodynamic processes and morphology affected export and retention mechanisms (Leichter et al. 2013; Storlazzi et al. 2018) and played a fundamental role in the dispersal of coral reef larvae. The oscillatory movement of the tide, that varied over ebb and flood phases, tended to reduce export from the reef and generate recirculation cells that can recirculate existing water back onto the reef (Winter et al. 2020). Waves, however, tended to increase export from the reef, due to the persistent forces created by waves breaking on the western reef flat that drive the wave-driven flow patterns. Subsequently, retention rates varied by up to 40% within the first two days (Figure 4-5a), depending on the strength of the tidal forcing during neap to spring phases and wave forcing. Such findings are particularly relevant in the
context of wave- and tide-dominated reefs (accounting for about two-third and one-third of reefs worldwide respectively, Lowe and Falter, 2015), as the results indicate that tide-dominated reefs would likely experience higher retention rates compared to wave-dominated reefs. In the case of combined waves and tides (e.g., characteristic of typical spawning conditions at Mermaid Reef), the relative importance of the dominant forcing varied as a function of the tidal range and significant wave height (Kraines et al. 1999; Andréfouët et al. 2001; Callaghan et al. 2006). Similar to what has previously been described at Mermaid Reef, for small wave conditions ($H_s \sim 1$ m), wave-driven processes dominate atoll flushing during small tidal ranges (i.e., neap tides), and tide-driven processes dominate during large tidal ranges (i.e., spring tidal ranges) (Chapter 2).

Atolls such as Mermaid Reef are characterised by shallow reef flats that partially or completely surround a deeper lagoon and can be connected to the open ocean through narrow channels. Geomorphologic features such as reef flats can act as a physical barrier to flow and dispersal of material. For many atolls worldwide, at least part of the reef flat is completely closed to water exchange for part of the tidal cycle, and thus promote water and material retention in the lagoon (e.g., Callaghan et al. 2006; Dumas et al. 2012) compared to potentially more open systems such as fringing reefs. In the case of reef systems with large tidal ranges such as Mermaid Reef, reef flats can also become exposed for part of the tidal cycle and prevent exchange between the lagoon and the open ocean (Lowe et al. 2015; Green et al. 2018; Chapter 2). The complex morphology of atoll reefs also results in large bathymetric variations, causing gradients in flow velocities over relatively short spatial scales (i.e., of order 10s to 100s of metres). For instance, reef flats display higher topographic elevation and roughness, which contribute to current attenuation through several mechanisms (e.g., wave breaking, bottom friction; Lowe et al. 2005; Hench and Rosman, 2013) and results in smaller lagoon current velocities, leading to higher retention rates and smaller dispersal distances. Although hydrodynamic forcing controls the temporal variability in current speeds at a given location, the result indicates that the overall reef geomorphology has an even greater control on flow velocities and retention rates (Leichter et al. 2013; Storlazzi et al. 2018; Reid et al. 2020).
4.6.3. Influence of fine-scale reef hydrodynamic processes on regional connectivity predictions

To further highlight the implications of over-looking reef-scale processes (i.e., fine-scale hydrodynamic processes and bathymetry), as well assuming that coral larvae are immediately available to be transported off-reef by regional currents, we performed two additional simulations. We simulated the dispersal and connectivity patterns during a typical spawning year (i.e., March 2011) at Mermaid Reef using: (1) our fine-scale coupled wave-flow model forced with daily surface currents from BRAN 2020, and (2) the Lagrangian with daily surface currents from BRAN 2020 only. Using both approaches, we simulated the advective transport of ~9000 particles (Figure 4-8). The fine-scale hydrodynamic model had a much higher local retention and smaller dispersal distances, with most of the larvae remaining on the atoll or in close proximity, travelling a maximum of 10 km in the north-west direction (Figure 4-8a). Conversely, the regional-scale model only properly representing the flow conditions that would occur outside the atoll had much larger dispersal distances, with larvae travelling up to 150 km to the south-west in 10 days (Figure 4-8b). Overall, these results suggest that it is often critical to properly resolve these fine-scale reef hydrodynamic processes, or at least parameterise them, within biophysical models of larval connectivity, to improve management of coral reefs over local and regional scales.

Figure 4-8: March 2011 autumn mass spawning larvae tracking simulation using (a) the 2D coupled wave-flow hydrodynamic model with BRAN 2020 surface velocity currents and using (b) Parcels forced with the BRAN 2020 surface velocity currents. Larval mortality was not incorporated here. Mermaid, Clerke and Imperieuse are the northern-most to southern-most reefs, respectively, and are represented by their 2 m depth contour.
4.6.4. Implications for inter-reef connectivity at the Rowley Shoals

Within several hundred meters of Mermaid Reef, the bathymetry descends rapidly to ~500 m depth. Consequently, if larvae remain off-reef, the likelihood of their dispersing from Mermaid Reef to the other atolls at the Rowley Shoals (Clerke and Imperieuse Reef located ~30 km and ~85 km to the southwest respectively) is influenced by the speed and direction of regional currents. Over the course of the 23 years, the regional currents surrounding Mermaid Reef could occasionally reach up to 0.5 m/s during tropical cyclone conditions (not shown). Under a scenario when some larvae are able to rapidly be transported off-reef (e.g., from the eastern edge), they could potentially be carried over ~100 km if such currents were sustained for ~3 days. Previous studies have also hypothesised about the role of TCs on the inter-reef connectivity of the NWS, suggesting that tropical cyclones increased the potential for wide-scale dispersal, with larvae covering considerable distances (100 km or more) away from parental reef populations (Radford et al. 2014). Large dispersal distances ranging from 28 to 132 km over the course of 10 days were also evident from the release of three drifters offshore from Mermaid Reef at different times of the year over three years (2003–2006, Gilmour et al. 2009). Considering such dispersal distances, ecological connectivity may be spatially extended as unusually large numbers of larvae can be exported between the three atolls of the Rowley Shoals depending on the strength and direction of the oceanographic currents. Other features such as recirculation eddies around reefs and islands, on the other hand, strongly increase local retention, possible re-circulation on the reef and hence reduce larger-scale particle dispersal (King and Wolanski 1996; Burgess et al. 2007; Figueiredo et al. 2013; Limer et al. 2020).

In addition to regional current speeds, whether larvae carried off-reef can recruit successfully to neighbouring atolls also depends on their upper competency period, their rates of survival prior to settlement, entrapment by another atoll’s local hydrodynamics and transport to a suitable habitat. Periodic dispersal and connectivity among the three atolls of the Rowley Shoals is evident in genetic analyses of Acropora spp. (Underwood 2009; Thomas et al. 2019). However, genetic analyses reflect dispersal events over many generations and can be shaped by the occasional migrants that disperse over long distances. Without data on coral species distributions across a reef; their reproductive output; times of spawning; and larval ecology coupled with fine- and regional-scale hydrodynamics in biophysical models, we
cannot accurately quantify larval connectivity within reef systems. Yet, most of these data are not available for most of the world’s coral reefs. Based on the available data for the Rowley Shoals, we conclude that the dispersal of spawning corals among atolls occurs periodically and in sufficient numbers to aid recovery following severe disturbances over decades, but that most recruits are generated from within the natal reef.

4.7. Conclusions

At Mermaid Reef, both waves and tides interact to shape the circulation of the coral reef atoll. In this study, we provide insight into how fine-scale reef hydrodynamic processes control the retention and export of larvae and therefore play a key role in shaping dispersal and connectivity patterns during the Acropora spp. bi-annual mass coral spawning. During typical hydrodynamic conditions, spawning occurs during neap tides (and transitions to spring tides over the 10-day competency period), with wave conditions generally consistent between events (averaging $H_s \sim 1\, \text{m}$, $\theta_{\text{wave}} \sim 220^\circ\text{N}$). The ebb and flood phases of the tides and the wave-driven flows on the western reef flat both contribute to create dispersal pathways from the western to the eastern side of the atoll. Such conditions provide relatively consistent sources and sinks of larvae over the years. Extreme hydrodynamic conditions associated with tropical cyclones introduce larger variability in the wave climate (both in $H_s$, $T_p$, $\theta_{\text{wave}}$), and create rare and unique dispersal pathways that physically connect parts of the reef that are not typically connected. The individual contribution of waves and tides is distinct as the oscillatory movement generated by the ebb and flood of tides tends to reduce the net export of modelled larvae from the reef, whereas the continuous and unidirectional force created by waves breaking tends to increase the net export from the reef. These results emphasise that overlooking these key fine-scale reef hydrodynamic processes may greatly overestimate larval transport distances, with larvae instead spending a substantial portion of their competency period retained by hydrodynamic processes within the reef. We emphasize the need for such temporal and spatial scale to be included when inferring patterns of larval connectivity within and among coral reef systems, which will be increasingly important for coral recovery and adaptation under climate change.
4.8. Acknowledgements

We are grateful to Michelle Jeuken and the Delft3D FM support team at Deltares for technical advice and initial assistance with the model development. Funding was provided by the ARC Centre of Excellence for Coral Reef Studies, the Australian Institute of Marine Science, Australian Government Research Training Program (RTP) Scholarship, and the Robson and Robertson award to C. G. This work was supported by resources provided by the Pawsey Supercomputing Centre with funding from the Australian Government and the Government of Western Australia. We acknowledge the availability of the CAWCR wave hindcast (All Rights (including copyright) Bureau of Meteorology, CSIRO 2019). We thank Mark Case and Matt Birt for assisting in the processing of the BRUVS and single point surveys data.

4.9. Supporting information for Chapter 3

4.9.1. Coral communities’ observations

Coral cover across the reef was quantified using a range of methods in complementary studies (long-term monitoring sites, tow-camera system, snorkeler visual surveys at single point and on Baited Remote Underwater Video). The total cover of benthic groups and coral genera was first quantified at long-term monitoring (LTM) sites at reef-slope (6 m lowest astronomical tide, LAT), -crest (2 m), -flat (0 m) and lagoon (1 – 7 m) sites between 2013 and 2018 by laying along permanent transects at every metre (Figure S 4-1) (Gilmour et al. 2022). The percentage cover of benthic groups and hard coral genera in habitats were also quantified using a tow-camera system during surveys in in March 2018 and October 2019 (Cresswell et al. 2021). In addition, the percentage cover of benthic groups and hard corals at sites and habitats was estimated from visual surveys at single point by a snorkeler and by an observer documenting fish abundances on Baited Remote Underwater Video Stations (BRUVS) (Birt et al. 2021).

4.9.2. Spatial habitat modelling

4.9.2.1. Input bathymetry datasets sampling design

Bathymetry data for the Rowley Shoals was derived from two existing Laser Airborne Depth Sounder (LADS) datasets, from the Royal Australian Navy for depths down to 45 m. Depth models were used at a pixel resolution of 6 m for all modelling. The sampling design using Generalized Random-Tessellation Stratified (GRTS) Survey
Design (Stevens and Olsen 2004) applied to unsupervised prior classes depth and rugosity (depth range using meter pixel). This provided a habitat-stratified, spatially weighted sampling design covering the area of interest (see https://science.nature.nps.gov/im/datamgmt/statistics/r/advanced/grts.cfm). Once points were selected, they became the initial starting point for slow/towed video transects covering approximately 500 meters running down slope perpendicular to the shallow reef crest or edge. LTM transects were also surveyed using slowed video and this data was incorporated into modelling. These data types have been shown statistically to provide comparable representation of major coral groups transects surveys (Cresswell et al. 2021).

4.9.2.2. Tow-video and tow-camera systems

The AIMS tow-system was used to quantify percentage cover of benthic organisms at monitoring sites. The system comprises a forward-facing video camera with lights and a live video feed to a vessel-based image classification system together with a downward-facing high resolution still camera and strobe system programmed to take sequential still images at fixed time intervals of ten seconds. The towed platform was deployed over the stern of the vessel, maintained within a metre of the seabed, and towed at 1-2 knots (1.5 nominal) until a minimum distance of 0.5 km was covered in a continuous line transect (or the whole LTM transect). On the vessel, a computer-based towed video program managed collation of position, depth, and operator-derived habitat classification data, which was captured in real-time as an operator interpreted the live video feed. This was then archived for subsequent spatial analysis. The AIMS LTM Reef Cloud classification system was used to assign benthic categories both for real-time video and for still images, which includes substrata types (e.g. sand) dominant benthic groups (e.g. algae, sponges, soft corals) and hard corals divided among family, genera and/or growth forms (e.g. branching Acropora spp., genera of hard corals).

4.9.2.3. Data analysis

4.9.2.3.1. Preparation of secondary datasets from LADS laser airborne survey data

A variety of secondary (textural) datasets which may correlate with seafloor properties were developed from the bathymetry using terrain analysis techniques. These techniques were applied to elevation data, quantifying the relationships
among elevation values in small neighbourhoods to reveal textural differences. Using a gridded elevation (or bathymetry) dataset, calculations are run on a small number of cells surrounding each pixel.

In this case, all neighbourhood calculations (such as the mean, mode, or slope) are run on the central cell plus the eight surrounding cells, and the value assigned to the central cell in the output, thus creating a derivative dataset. Analysis was completed using the “focalstatistic” function in the ESRI python ArcPy library (ESRI 2009).

4.9.2.3.2. Spatial modelling

To infer spatial distributions of marine biota and abiotic substrate, we characterised environmental relationships in detail using the combination of towed video footage; LADS airborne layers surveys and a statistical modelling approach. Towed video provides data on benthic diversity and cover, while bathymetry and textural datasets provide information on environmental characteristics and give full coverage of the field area. To model the relationship between physical and biological parameters, we implemented the “randomForest” assembler model method (Breiman 2001, 2002). randomForest can fit both linear and complex non-linear models very efficiently without being prone to overfitting. These models have high accuracy compared to other comparable methods and provide outcomes, which are ecologically interpretable. A detailed description of the application of assembler models with ecological data is outlined in Elith et al. 2006, 2011, Elith and Leathwick 2009 and in the R library “Dismo”. Generation of input features for modelling was done using a cluster analysis using Partitioning Around Medoids (PAM) analysis (Reynolds et al. 2006) to provided inputs into randomForest modelling.

The towed video benthic analysis models were evaluated using a subset of the video observations reserved prior to modelling (~33% of the full dataset was selected via Variogram so has to be spatially independent from the training data). The model accuracy was assessed by predicting the values against this blind validation dataset using a confusion matrix using in conjunction with total accuracy and Kappa statistics. Kappa was calculated with model maximum likelihood. Models with Kappa > 0.8 have high predictive power, values between 0.7 and 0.8 are acceptable, and models with Kappa of <0.5 have no power of discrimination. For each site, raster models were produced presenting the most class maximum likelihood-based habitat class for each pixel.
Figure S 4-1. Hard coral cover probability of presence derived from a benthic habitat model and observed Hard coral cover, see supplementary text for data collection and benthic habitat model methods. BRUVS refers to Baited Remote Underwater Video Stations.

Figure S 4-2. Virtual larvae release location across Mermaid Reef plotted over the reef flat bathymetric contours (depths 2 m above to 2 m below MSL).
4.9.3. Biophysical model sensitivity to time of release

In our simulations, virtual larvae are released at one point in time only, for computational power and storage optimization. In reality, spawning lasts between a few days and a week and therefore larvae are released continuously throughout multiple phases of the tidal cycle and during multiple tidal ranges. If we consider the typical conditions presented earlier, we conducted four distinct simulations where virtual larvae were released on four different phases of the tide: 0°, 90°, 180°, and 270° corresponding to peak high, ebbing, peak low, and flooding. For the four different release events (i.e., high tide, low tide, mid-rising tide and mid-falling tide), the largest difference in the retention rates was ~10%. After 10 days, the strongest retention rates (i.e., ~22%) were observed for a release during falling tide and the weakest retention rates (i.e., ~12%) were observed for a release during rising tide. As mentioned, retention rates associated with tides vary on the order of 10% in a couple of hours. Given that the variation of retention rate was in the range of hourly retention rate variation, we can assume that there was no detectable effect of variations in tidal stage of virtual larvae release (Figure S 4-3). Networks of moving water masses are spatially and temporally variable, and their effects on the movement of virtual larvae will therefore depend on when and where the virtual larvae first enter the environment. Other studies have also found that model results are not very sensitive to the precise timing of spawning and its duration (Lowe et al. 2009a; Frys et al. 2020).

![Figure S 4-3 Retention rate associated with release at different stages of the tidal cycle. Mortality rates are not included.](image)

Mortality rates are not included.
4.9.4. Regional currents and wind conditions during coral spawning

Figure S4-4. Mean wind (a and b) and regional current (c and d) velocities and directions for the austral autumn (a and c) and (b and d) spring spawning periods averaged over 1993 to 2020.

4.9.5. Biophysical model sensitivity to wind

Here, we show the results between three simulations, the first one forced with the typical hydrodynamic conditions described in section 4.3.2 without wind forcing at the model boundary conditions (Figure S 4-5a). Two other sets of simulation were forced combining with the typical hydrodynamic conditions as well as the wind conditions observed during both the austral autumn and spring spawning events conditions (Figure S 4-5b and c). Figure S 4-5b and c represent the time-averaged circulation over the 10 days simulations, while Figure S 4-5d and e show the difference between the cases with and without wind forcing at the model boundaries. The changes in current speeds on the atoll associated with regional current forcing at the model boundaries are small (< 0.03 m/s) and can therefore be omitted in our study.
Figure S 4-5: 10-day time averaged wind velocities associated with (a) no wind, mean wind conditions for (b) March and (c) October. (d) and (e) are the difference between the (a) and (b) and (a) and (c) respectively.

4.9.6. Biophysical model sensitivity to regional currents

Here, we show the results between three simulations, the first one forced with the typical hydrodynamic conditions described in section 4.1 without regional currents forcing at the model boundary conditions (Figure S 4-6a). Two other sets of simulations were forced combining with the typical hydrodynamic conditions as well as the mean regional current conditions observed during both the austral autumn and spring spawning events conditions (Figure S 4-6b and c). Figure S 4-6b and c represent the time averaged circulation over the 10 days simulations, while Figure S 4-6d and e show the difference between the cases with and without regional current forcing at the model boundaries. The changes in current speeds on the atoll associated with regional current forcing at the model boundaries are small (< 0.01 m/s) and can therefore be omitted in our study. However, such regional currents are crucial to consider as soon as the virtual larvae leaves the atoll reef.
Figure S 4-6. 10-day time averaged current velocities associated with (a) no regional current velocity forcing, mean regional current conditions for (b) March and (c) October. (d) and (e) are the difference between the (a) and (b) and (a) and (c) respectively.
**4.9.7. Circulation throughout a tidal cycle**

Figure S 4-7. Tide-only conditions. Time averaged velocities and streamlines over (a, b, c) neap tides conditions and (d, e, f) spring tides-conditions for rising tide (a and d), falling tide (b and e) and averaged over a tidal cycle (c and f).

Figure S 4-8. Typical hydrodynamic conditions during spawning. Time averaged velocities and streamlines over (a, b, c) neap tides conditions and (d, e, f) spring tides-conditions for rising tide (a and d), falling tide (b and e) and averaged over a tidal cycle (c and f).
### 4.9.8. Supplementary tables

*Table S 4-1. 1980 to 2020 austral autumn and spring mass spawning at Mermaid Reef, WA*

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Table S 4.2. Tropical cyclones additional information

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5. General discussion

5.1. Thesis overview and summary of main findings

Understanding the natural variability of reefs systems and identifying environmental conditions that promote coral reef resilience and recovery is pivotal to advance our ability to conserve and manage reefs. For that reason, multi-disciplinary studies of physical processes driving ecological dynamics across reef systems are especially relevant. This thesis investigated how oceanographic and atmospheric processes, specifically wave- and tide-driven flows, control the circulation (Chapter 2) and key ecologically relevant processes such as temperature variability (Chapter 3) and reef connectivity (Chapter 4) at Mermaid Reef, a coral reef atoll located on the edge of the Australia’s North West Shelf.

5.1.1. A wave and tide-dominated atoll reef

In Chapter 2, 11 months of hydrodynamic measurements across Mermaid Reef revealed that the atoll is regularly exposed to a range of wave conditions and tidal ranges. As a result, wave- and tide-driven processes continuously interact to drive the reef’s circulation through several mechanisms including: first, wave-current interactions, where wave- and tide-driven flows interact to modify the strength and duration of reef inflows and outflows; second tidal water level modulation of wave-driven flows, where the water level drop below the reef flat elevation at low tide, and acts as a barrier to both wave and tide-driven flow into the lagoon; and finally wave setup generation reduction in greater water depths (i.e., high water levels), which was however found to be less important than the enhanced contribution to the discharge by the deeper water column.

Those mechanisms, particularly the first and second interact nonlinearly to drive the circulation at Mermaid Reef, as the residual flow was reduced compared to the linear sum of the flow driven (i.e., adding wave-only and tide-only flows). For small wave conditions, the flow blockage by the western reef flat occurring at low tide is mainly responsible for the differences observed between the combined wave and
tide scenarios, and the simple linear addition of tide-only and wave-only scenarios. For larger wave conditions, the flow blockage by the western reef flat appears to be largely compensated by the enhanced wave-driven contribution to the discharge at high stages of the tide. As a result, for small wave conditions, the inflow into the lagoon was reduced by up to 60% for TR > 1.5 m (e.g., spring tide) and by up to 30% for TR < 1.5 m (e.g., neap tide) compared to if nonlinear interactions were not accounted for (e.g., by the flows driven by pure tides and pure waves added linearly). Over the 11-month experiment, Mermaid Reef experienced 0.5 >Hs >1 m for 88% of the time, implying that tides will generally played a substantial role in reducing the strength of the wave-driven flows.

Finally, while the metric for classifying reefs based on exposure to waves and tides (MTR/Hs, Lowe & Falter, 2015), or simple geometrical observations of reefs (Callaghan et al. 2006) can provide an indication of which the dominant forcing mechanisms (i.e., wave versus tide) at a site, the hydrodynamic conditions can vary substantially over time scales of several hours to days on most reefs. At Mermaid Reef, we find that the threshold controlling the relative dominance of wave or tide-driven processes at Mermaid Reef is the higher reef flat elevation of the windward (western) side. Tide-driven processes dominate if the tidal range is sufficiently large to expose the western reef flat, i.e., >2hwest (equivalent to one-half of the tidal range) and wave-driven processes dominate for tidal ranges smaller than 2hwest. Over the 11-month experiment, Mermaid Reef experienced a TR >2hwest (i.e., 1.4 m) for 79% of the time and TR <2hwest (i.e., 1.4 m) for the remaining 21% of the time. Therefore, Mermaid Reef transitions through ‘tide-dominated’ and ‘wave-dominated’ periods over short timescales (hours to days), albeit its circulation mainly results from persistent interactions between the two hydrodynamic forcing and the reef morphology.

Overall, this research provides new insights into the complex hydrodynamic processes that govern interactions between wave- and tide-driven flows within a coral reef atoll. These findings are both relevant to Mermaid Reef and other reef environments worldwide, whose circulation is driven by the interaction between wave- and tide driven flows (e.g., Monismith et al. 2013; Cheriton et al. 2016; Costa et al. 2017; Rogers et al. 2017; Green et al. 2019b; Section 5.2).

5.1.2. Temperature variability across reef environments

In Chapter 3, 11 months of temperature measurements spanning Mermaid Reef revealed that the advection of water temperature (e.g., wave and tide-driven flows),
local atmospheric heat exchange processes (e.g., solar heating cycles), and the topographic complexity of reefs (e.g., depth variability) were key drivers of reef temperature variability across Mermaid Reef. As a result, distinct thermal environments and variability were observed across the key reef zones (lagoon, reef flat and fore-reef zones).

Most of the temperature variability between reef zones occurred at diurnal and higher frequencies, where distinct forcing mechanisms impacted the reef zones. Similar to other reefs with strong tidal forcing, diurnal temperature variability for both the reef flat and lagoon zones was shaped by the interaction of tidal water levels and local net air-sea heat exchange (McCabe et al. 2010; Lowe et al. 2016). Indeed, the role of local net air-sea heat exchange was evident at reef flat sites, characterised by shallow waters prone to rapid heating, which displayed large diurnal temperature variability. The effect of local net air-sea heat exchange was also evident in the lagoon sites, which displayed smaller diurnal temperature variability due to the greater depth observed through the lagoon.

While quantifying heat advection required high-resolution horizontal temperature gradient information—which was not available during the study period—it likely played an important role in driving the temperature variability at Mermaid Reef. For example, fore-reef zones experienced some of the largest temperature anomalies over rapid timescales (order hours), most likely due to internal waves, which typically transport cooler water from below the thermocline. Internal waves and associated rapid temperature decreases (of several degrees) have been observed both across Australia’s NWS and on numerous fore-reefs among corals reefs worldwide (Leichter et al. 1996; Sevadjian et al. 2012; Green et al. 2019a; Comfort et al. 2019; Wyatt et al. 2020).

Finally, temperatures across the reef zones presented large deviations from offshore water temperatures (up to 2.6°C lower). This finding highlighted the value of in situ temperature measurements on coral reefs, as remotely sensed sea surface temperature techniques observations currently do not resolve the fine-scale temporal and spatial temperature variability (order of 100s of meters and minutes to hours) within reefs. Given that in situ temperature measurements can be both cost- and time-prohibitive (especially for remote areas like Mermaid Reef), there is a critical need to link large-scale temperature pattern detectable via remote sensing (e.g., downscaling prediction methods) to reef-scale temperature. For example, the simple
approach presented in Section 3.4.4 allowed an accurate reconstruction of reef temperatures at the reef flat and lagoon sites by simply correcting $SST_{\text{offshore}}$ by an air-sea heat flux term. Similar approaches have been used on wave-driven reefs where the temperature variability was driven by offshore wave and atmospheric data (Falter et al. 2014).

Overall, this study provided new insights into the complex drivers of ocean temperature variability occurring across reef-scales (<1 km) at Mermaid Reef, with potential applicability to other reef environments worldwide which present similar degrees of complexity (e.g., depth variation) and exposure to various oceanographic and atmospheric drivers. Developing such information is critical to determine patterns of thermal stress and bleaching of corals within reef systems and will be especially relevant to assess the longer-term responses of reefs to climate change.

5.1.3. Fine-scale coral reef connectivity

Finally, in Chapter 4, we showed the importance of reef-scale hydrodynamic drivers, especially wave- and tide-driven flows, in the transport of coral larvae through the advection of water across the atoll. We found that the flow generated by tides displayed much greater instantaneous velocities, but the associated oscillatory (non-residual) component reduced the net export of particles from the reef. On the contrary, the flow generated by waves displayed smaller instantaneous velocities, but its unidirectionality increased the net export from the reef. Understanding the net circulation occurring on reefs is not only relevant to coral larvae but to a number of other marine organisms and material find across reef systems (e.g., sediment, plastic). Such findings are particularly relevant in the context of wave- and tide-dominated reefs (accounting for about 2/3 and 1/3 of reefs worldwide respectively, Lowe and Falter, 2015), as the results indicate that tide-dominated reefs would likely experience higher retention rates compared to wave-dominated atoll reefs.

By investigating the long-term variability of such hydrodynamic conditions (i.e., waves and tides; over ~40 years), we found relatively consistent conditions during the bi-annual spawning events of Acropora spp., with a start on neap tides and continuous small eastward wave conditions. As demonstrated in Chapter 2, during typical conditions, wave-driven flows dominated the atoll residual circulation. As the tidal range transitioned to spring tidal range over the course of the larvae competency period (~10 days), tide-driven flows dominated the atoll residual circulation. During typical conditions, transport of larvae across the atoll occurred
eastward. Importantly however, the occasional influence of tropical cyclones during spawning events significantly modified wave heights, direction, and regional current conditions. By doing so, the typical circulation patterns within the reef varied substantially, providing coral larvae with new dispersal pathways (e.g., westward).

Overall, this work shows that fine-scale hydrodynamic processes contribute to retain larvae (and likely other marine organisms or material) for substantial amounts of time within Mermaid Reef—and potentially other reef system worldwide. Therefore, such fine-scale hydrodynamic processes and their long-term temporal variability need to be considered within regional connectivity predictions to understand the capacity of reefs to recover following disturbances through successful recruitment.

5.2. Broader implications

This thesis highlights the importance of reef-scale hydrodynamic processes—particularly tides and waves—in driving the circulation, temperature variability, and reef connectivity within a coral reef atoll. The results presented here are relevant for other reefs worldwide where circulation is shaped by the interaction between wave- and tide-driven flows. That includes wave-dominated reef environments experiencing small tidal ranges (~2/3 of the world’s reefs; Monismith et al. 2013; Koweek et al. 2015; Cheriton et al. 2016; Rogers et al. 2017); but particularly tide-dominated reef environments occasionally experiencing large wave conditions (~1/3 of the world’s reefs; Costa et al. 2017; Green et al. 2018). Of these two, tide-dominated reefs exposed to large wave conditions have received little attention in the literature, particularly in the case of atolls.

Tide-dominated atolls account for about ~10% of the world’s atolls, being mainly located off northwestern Australia, in the Coral Triangle and off eastern Africa (Green et al. 2018) (Figure 5-1). A 41-year analysis of wave conditions (1980-2020, extracted from Centre for Australian Weather and Climate Research) shows that many tide-dominated atolls worldwide can be exposed to hydrodynamic conditions such as the ones encountered throughout this thesis. For example, many of these atolls experience large $H_s$ ($H_s > 2$ m; Figure 5-1a), with some rare extreme events leading to $H_s$ reaching up to 15 m (Figure 5-1b). To our knowledge, the only previous investigation of the hydrodynamic circulation on an atoll reef exposed to both large tidal ranges and wave conditions was conducted on Rocos Atoll, located East of Brazil (Costa et al. 2017). Aligning with the findings of this thesis, the tidal water levels oscillation with
respect Rocas Atoll reef flat elevation (and morphology more broadly), also played a central role in controlling atoll circulation. Tidal water levels played a fundamental role in water exchange, not only through the pressure gradients created by sea level differences but also through a threshold for hindering or allowing a wave pumping mechanism.

![Figure 5-1: Tide-dominated atolls (~10% of the reef’s worldwide) based on Lowe and Falter 2015 and Green, 2018. The atolls are colour coded as a function of (a) the maximum wave height ($H_s$, extracted from Centre for Australian Weather and Climate Research (CAWCR)) and (b) the % of time during which $H_s > 2$ m over 41 years (1980-2020).](image)

Among the northwestern Australian reefs (i.e., Rowley Shoals, Scott and Ashmore Reef), Scott Reef’s hydrodynamic circulation has also been investigated (Green et al. 2018). Even though characterised as tide-dominated, Scott Reef experienced large $H_s$ for about ~10 % over the 1980-2020 period (Figure 5-1a), which could partly or fully modify the atoll’s typical circulation patterns. A longer hydrodynamic study of Scott Reef could provide us with larger range of hydrodynamic conditions and allow us to examine the effect of interacting waves and tides on the atoll’s circulation.

This further highlight the value of long-term measurements such as provided in this thesis, where ~11 months of hydrodynamic measurements (e.g., waves, currents, water levels) collected at Mermaid Reef captured a wide range of hydrodynamic conditions including large swell, several neap and spring tidal cycles, and tropical
cyclones which could have been missed if the deployment time frame was any shorter. Long term hydrodynamic studies of wave and tide-driven atolls, if any, remain sparse worldwide, especially in the East African atoll reefs, which appear to experience $H_s > 2$ m for up to 45% of the time spanning 1980 to 2020. Yet, to our knowledge, no hydrodynamic studies have been conducted on these reefs.

In this thesis, we show that a better understanding of the interactions between wave and tide-driven processes provided a key understanding of the circulation and flushing of Mermaid Reef, which underpin several key ecologically relevant processes such as temperature variability and reef connectivity. A knowledge of the physical processes and how they shape the reef’s circulation is essential to understand ecological processes occurring within reef systems and help target management efforts for conservation, especially as many of these reefs have been highlighted as conservation priorities due to their potential to replenish other degraded coral reefs and having limited thermal stress exposure (Beyer et al. 2018).

5.3. Concluding remarks and recommendations for future research

The work presented here provides insight on how a range of physical and atmospheric drivers occurring across various temporal and spatial scales shape the circulation, temperature variability, and coral larvae connectivity across coral reef atolls, using Mermaid Reef as a case study. This research advances our overall understanding of the oceanography of coral reef atolls and raises a number of interesting questions for future research.

A first potential extension of this work would be to conduct a similar hydrodynamic study at the two other coral reef atolls of the Rowley Shoals (Imperieuse and Clerke Reef). Mermaid, Clerke and Imperieuse Reef each represent different stages of atoll formation (Berry and Marsh 1986), with Imperieuse Reef being the most recently formed atoll, and Mermaid Reef the oldest formed reef. As a result, the three atolls have different geomorphological and bathymetric features. For instance, Mermaid Reef has one relatively large channel (250-m wide and 8-m deep), Clerke Reef has three smaller-sized channels, while Imperieuse Reef has only one channel (Figure 5-2). Similarly, Mermaid Reef has one large and relatively deep lagoon, while Clerke Reef and Imperieuse Reef have two and three smaller lagoons, respectively.

As discussed in Chapter 2, atoll bathymetry plays a crucial role in determining the flushing patterns and the relative dominance of tides and waves in atoll circulation.
The differences in bathymetry observed between these three atolls would therefore lead to different circulation and flushing patterns. Resolving the flushing mechanisms on the two other atolls would then provide us with further insight of how the wave and tide-driven flow are modulated by the atoll morphology and would inform as to what the circulation of Mermaid Reef resembled in earlier atoll development stages.

Figure 5-2: LANDSAT-8 and various aerial images of (a, b) Mermaid, (c, d) Clerke and (e, f) Imperieuse. Photo credit: (a, c and e) LANDSAT; (b) wanderlust Kimberley; (d) Department of Biodiversity, Conservation and Attractions (DBCA); (f) Sharyn Hickey.

Temperature variability shapes important ecological processes on reef systems. Yet, monitoring in situ temperature can be both costly and time-consuming, particularly in remote coral reefs such as the ones of the Rowley Shoals. Here, we developed a simple model to predict in situ temperatures based on SST, offering a potentially powerful tool to better understand coral heat stress in shallow waters of
remote or poorly monitored areas. As a result, one of the key priorities includes further improvements of simple models to predict the reef temperature based on available remotely sensed SST.

The accurate assessment of the advection of heat through wave and tide-driven flows would also provide valuable insight and could be achieved through additional numerical modelling and field observations of the flow. Additional high frequency in situ temperature measurements through the water column across both the western, eastern fore-reefs could help confirm the mechanisms responsible for the cold-water pulses observed on the western deeper fore-reef. The transfer of such cold-water pulses across the fore-reef and reef flat on coral reef systems could be given further consideration through additional temperature measurements throughout the water column to determine the exact mechanisms and favourable conditions for such transport to happen across the steep reef slope bathymetry. Finally, the use of numerical models could also allow the simulation of hypothetical scenarios to investigated and uncover the cooling mechanisms occurring during marine heatwaves. Potential thermal ‘refugia’ location across Mermaid Reef could then be identified.

Coral reef connectivity is key for coral reef recovery especially for isolated reef systems, which rely heavily on local populations for re-population after disturbances. In this thesis, we modelled larval dispersal of the dominant coral genus (Acropora spp.) based on over 40 years of hydrodynamic conditions. Future work could incorporate additional coral larvae traits including vertical location in the water column or larval swimming patterns for example. Additional work would also ideally incorporate a coupling with a large-scale hydrodynamic model resolving regional scale processes (e.g., meso-scale eddies and regional currents) to better understand the fate of coral reef larvae when they leave the natal reef. For instance, extending the model domain to the three coral reef atolls of the Rowley Shoals could provide insights on the re-circulation of larvae onto reefs and on the connectivity between reef systems. This could then be further extended to the NWS and include Scott Reef and Ashmore Reef, as genetic analyses suggest inter-reef connectivity (Underwood 2009).

Overall, characterizing the hydrodynamic processes underpinning the circulation within Mermaid Reef has laid a strong foundation to better understand its ecology. As these processes control the retention or export of water and its properties, as well as other material (e.g., heat, nutrients, larvae, plastic) occurring inside the atoll, the study
presented here provides a framework to study a range of additional biological, chemical and geological processes (e.g., nutrient dynamics, carbonate chemistry variability) occurring at Mermaid Reef and their possible local or regional resilience to future environmental changes.
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119


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