MODELLING THE EFFECT OF NUTRIENT SUPPLY, TEMPERATURE AND LIGHT INTENSITY ON CNIDARIAN-ALGAE SYMBIOSIS

MALIN GUSTAFSSON

February 2014

A THESIS SUBMITTED IN FULFILMENT OF THE REQUIERMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN SCIENCE

DEPARTMENT OF ENVIRONMENTAL SCIENCE,

PLANT FUNCTIONAL BIOLOGY AND CLIMATE CHANGE CLUSTER

UNIVERSITY OF TECHNOLOGY, SYDNEY

i. CERTIFICATE OF ORIGINAL AUTHORSHIP

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

Production Note: Signature removed prior to publication.

07/08/2013

Malin Gustafsson

i. Acknoledgments

Foremost, I would like to thank my supervisors Professor Peter Ralph and Dr. Mark Baird for their continuous support over the past years. It has been a challenging but rewarding experience, which would not have been possible without their assistance. Thank you Peter for all the encouragement and for being an endless source of ideas. I would also like to extend a special thanks to Mark Baird for spending hours and hours on Skype discussing the project, he has been an invaluable source of knowledge and support throughout my candidature.

Furthermore, I would like to thank Mathieu Pernice and Mathieu Mongin for their collaboration and contribution towards this project. Additionally, I would like to extend my appreciation to Ross Hill, David Suggett and Kay Bishof for supplying experimental data to this project.

I would also like to thank all my colleges at UTS whom have come with ideas and suggestions to aid the progress of this project. I would particularly like to thank John Moore for helping out with the administration, and Verena Schrameyer for bringing me along to Heron Island.

During my candidature I have spent time at CSIRO in Hobart and would like to thank Richard Matear everyone else there that have taken an interest in my project, and taking time to discuss and give valuable feedback, particularly during the model development phase.

I also thank the Australian Research Council (DP110105200) and the University of Technology, Sydney for providing funds for the University of Technology, Sydney President's scholarship and the International Postgraduate Research Scholarship. Last but not least, I would like to thank my family and friends for their support and understanding throughout my candidature, particularly my parents, my sister and Martin for listening and discussing all aspects of my project. It is a privilege to have you all in my life. Here I would also like to extend a warm thank you to Noni, Puj, Ginny, Miriam, James and Mark for taking me into their homes and making me feel like family. I will miss my visits to Sydney and to Hobart.

ii. PUBLICATIONS

PEER REVIEWED JOURNAL ARTICLES ARISING DIRECTLY FROM THIS THESIS

Chapter 2:

Gustafsson, M. S. M., M. E. Baird, and P. J. Ralph. 2013. The interchangeability of autotrophic and heterotrophic nitrogen sources in Scleractinian coral symbiotic relationships: A numerical study. Ecological Modelling **250**: 183-194.

Chapter 3:

Gustafsson, M. S. M., M. E. Baird, and P. J. Ralph. (in press). Modeling photoinhibition and bleaching in Scleractinian coral as a function of light, temperature and heterotrophy. Limnology and Oceanography.

iii. TABLE OF CONTENT

i.	ACK	NOLEDGMENTS	
ii.	PUB	LICATIONS	5
iii.	TA	BLE OF CONTENT	6
iv.	LIS	ST OF FIGURES	
v.	LIST	OF TABLES	
vi.	AE	BREVIATIONS	21
vii.	AE	STRACT	23
1	. Ge	neral Introduction	27
	1.1	Coral physiology	29
	1.2	Heterotrophy vs. Autotrophy	31
	1.3	Photosynthesis, Photoinhibition and Bleaching	32
	1.4	Ocean acidification and coral calcification	35
	1.5	Corals in their environment	37
	1.6	Modelling biological systems	
	1.7	Scope of thesis	41
2	. Th	e interchangeability of autotrophic and heterotrophic nitro	gen sources in
S	clerac	tinian coral symbiotic relationships: a numerical study	45
	2.1	Introduction	45
	2.2	Methods	48
	2.2	.1 Model structure	48
	2.2	.2 Model parametertisation	51

	2.2	.1	Numerical experimental design	58
	2.2	.2	Sensitivity analysis	58
2	.3	Res	ults	59
	2.3	.1	Variation in nitrogen source and irradiance	59
	2.3	.2	Nitrogen and carbon budgets at steady-state	62
	2.3	.3	Sensitivity to parameter values	64
2	.4	Dise	cussion	67
2	.5	Sun	nmary	71
3. of l	Mo ight,	delli tem	ng photoinhibition and bleaching in Scleractinian coral as a func perature and heterotrophy	tion:73
3	.1	Intr	oduction	73
3	.2	Met	thods	79
	3.2	.1	Model structure	80
	3.2	.2	Electron transport	83
	3.2	.3	Photon absorption and the xanthophyll cycle	85
	3.2	.1	Reduction and re-oxidation of RCII	87
	3.2	.2	Reactive oxygen production	90
	3.2	.1	Photosystem Repair	90
	3.2	.2	Rubisco activity	91
	3.2	.3	Antioxidant activity	92
	3.2	.4	Bleaching	92
	3.2	.5	Model evaluation	93
	3.2	.6	Feeding simulations	96
3	.3	Res	ults	98
	3.3	.1	Feeding simulations	100

3.4	Dise	cussion	. 102
3	3.4.1	H ₂ O ₂ production	. 104
3	3.4.2	Degree Heating Days	. 106
3	3.4.3	Future work	. 111
4. U	Jptake	and translocation of carbon and nitrogen between a Cnidarian	host
and a	utotroj	phic symbionts	. 114
4.1	Intr	oduction	. 114
4.2	Met	hods	. 117
4	1.2.1	Anemone symbiosis	. 117
4	1.2.2	Aiptasia experiment	. 118
4	1.2.3	Carbon content and uptake rate	. 119
4	ł.2.1	Anemone model	. 120
4	1.2.2	Symbiont nitrogen reserves	. 121
4	1.2.3	Inorganic carbon and nitrogen uptake	. 121
4	ł.2.1	Translocation of photosynthates	. 122
4	1.2.2	Model evaluation and validation	. 124
4.3	Res	ults	. 126
4	4.3.1	Coral C uptake and translocation	. 130
4.4	Dise	cussion	. 132
5. A Austr	Applicat calia	tion of a model of coral symbiosis at a reef scale: Heron Isl	land, . 136
5.1	Intr	oduction	. 136
5.2	Met	hods	. 139
5	5.2.1	Study site	. 139
5	5.2.2	Model framework	. 141
5	5.2.3	Water column chemistry model	. 142

	5.2.	2.4 Ecological model	
	5.2.	2.5 Model setup	152
5.	3	Results	153
	5.3.	3.1 Water column nutrients	155
	5.3.	3.2 Age tracer and water nutrient content	
	5.3.	3.3 Coral biomass	164
	5.3.	3.4 Coral nutrient uptake and release	
	5.3.	3.5 Water column change in pH	172
5.	4	Discussion	
	5.4.	4.1 Comparison with process-based field observations	178
	5.4.	4.2 Analysis of model assumptions	179
6.	Gen	eneral Discussion	
6.	1	Structuring the model	183
6.	2	Ecosystem scale modelling	
6.	3	Model application and use	187
6.	4	Future directions and research	188
7.	Sup	pplementary Material	190
7.	1	Isotopic incubation	190
7.	2	Tissue preparation for TEM and NanoSIMS analyses	190
7.	3	TEM analyses	191
7.	4	NanoSIMS analyses	
8.	Refe	eferences	

iv. LIST OF FIGURES

Figure 1.2: A) Diagram of photosynthetic electron flow. B) Temperature dependent inactivation of Rubisco blocks the ETC resulting in accumulation of electron. C) Sites of ROS production and reactions (C).

Figure 1.1: Schematic of coral body plan, with a coral polyp to the left and the organization of coral tissue to the right.

Figure 2.1: Schematic of coral tissue organization. A) General drawing of a coral polyp. B) Coral tissue layers and organization of zooxanthellae within the gastrodermal cells. C) Flux of organic and inorganic nitrogen between the coral host and the zooxanthellae symbiont.

Figure 2.2: Schematic of coral nitrogen (A) and carbon (B) model. Boxes represent state variables and arrows fluxes. Blues and green boxes indicate that the pool belongs to the host and symbiont respectively. The numbers inside the brackets indicate the corresponding equation in Table 1 and 2.

Figure 2.3: Steady state values of model state variables as a function of irradiance, ranging between 0-1000 μ mol photon m⁻² s⁻¹ (0, 1, 10, 25, 35, 50, 75, 100, 200, 300, 400, 600, 800, 1000 μ mol photon m⁻² s⁻¹), and four N-scenarios; combinations of

two DIN uptake rates (V_{DIN}^H : 0.5 and 5 µg N cm⁻² d⁻¹) and two feeding rates (Z_N : 0.5 and 5 µg N cm⁻² d⁻¹). Panel A and B show the C_F^H and C_R^H respectively. Panel C and D show C_F^S and C_R^S for the entire symbiont population (*S*). Panels E and F show C_F^S and C_R^S for one symbiont cell. Panels G and H show the chlorophyll concentration for the symbiont population and for an individual symbiont cell respectively. Note that the scale on the y-axis differ between panels.

Figure 2.4: Average daily coral N fluxes at steady state and a light level of 1000 μ mol photon m⁻² s⁻¹ for the four nutrent cases: A) high Z_N + high V_{DIN}^H B) high Z_N + low V_{DIN}^H C) low Z_N + high V_{DIN}^H D) low Z_N + low V_{DIN}^H . Blue and green boxes represent host and symbiont state variables respectively. The size of the boxes indicates the size of the individual N state variables, with the numerical value given in μ g N cm⁻². The arrows show the direction of the fluxes and the thickness of the arrow and numerical value in μ g N cm⁻² d⁻¹ quantifying the magnitude of the flux.

Figure 2.5: Average daily coral C fluxes at steady state and a light level of 1000 μ mol photon m⁻² s⁻¹ for the four nutrient cases: A) high Z_N + high V_{DIN}^H B) high Z_N + low V_{DIN}^H C) low Z_N + high V_{DIN}^H D) low Z_N + low V_{DIN}^H . Blue and green boxes represent host and symbiont state variables respectively. The size of the boxes indicates the size of the individual C state variables, with the numerical value given in μ g C cm⁻². The arrows show the direction of the fluxes and the thickness of the arrow and numerical value in μ g C cm⁻² d⁻¹ quantifying the magnitude of the flux.

Figure 2.6: Percentage of change in host (C_F^H) and symbiont population biomass $(C_F^S S)$ between the four nutrient cases; high feeding rate on prey (Z_N) + high DIN diffusion rate (V_{DIN}^H) , high Z_N + low V_{DIN}^H , low Z_N + high V_{DIN}^H , low Z_N + low V_{DIN}^H .

The arrows indicate the direction of comparison, and the number the percentage decreases (negative numbers) or increase (positive numbers) in the state variable.

Figure 3.1: Schematic of photoinhibition model, boxes indicate state variables and arrows are fluxes. ΔRO_f is not considered a state variable, as we assume that it will immediately react with symbiont tissues at the site of formation, hence inhibit the photosystem. The numbers in the brackets correspond to the equation number in Table 3.3. The dashed arrow and box refereeing to ROS in the host are not included in the model.

Figure 3.2: Model fitted to data from Hill et al. (2012). Solid lines represented the 25°C model run over a 2 day period. Dashed line is the model run at 31°C. Filled markers indicate the experimental data for the 25°C treatment and open markers the 31°C treatment with ±standard deviation (SD). (A) is diurnal light oscillation. (B) F_v : F_m data with corresponding Q_a : Q_t in the model. (C) Photochemistry Y(II) corresponding in model was Q_{ox} : Q_t . (D) Y(NPQ) corresponding in the model D_t : ($D_t + D_d +$ ChI). (E) Y(NO) calculated using the assumption Y(II)+Y(NPQ)+Y(NO)=1.

Figure 3.3: F_{v} : F_{m} at (A) 10:30 h and (B) 05:30 h for the modeled and Borell and Bischof (2008) experimental data during the ten day feeding experiment. Closed and open markers show the measured F_{v} : F_{m} for fed and unfed coral, respectively. Black and grey lines indicate the modeled F_{v} : F_{m} (Q_{a} : Q_{t}) for fed and unfed coral, respectively.

Figure 3.4: Symbiont population size after two days acclimation under non-stress and non-feeding conditions (Reference) and after 10 days of elevated temperature for fed and starved corals. Light grey bar shows the measurements ±standard error (SE) from Borell and Bischof (2008).

Figure 3.5: Concentration of reactive oxygen species per symbiont cell (RO_S) and H₂O₂ measurements (mean ±SE) from two *Symbiodinium* clades (A1 and B1) in culture, from Suggett et al. (2008). (A) 100 μ mol photon m⁻² s⁻¹ treatment. (B) 1000 μ mol photon m⁻² s⁻¹ treatment.

Figure 3.6: Percentage of chlorophyll concentration remaining per coral unit surface area as a function of heat stress and heterotrophic feeding over time. Vertical dashed lines indicate 100 DHD. (A) 90 day simulation at T_{mean} (28°C) for corals feeding heterotrophically at a range of rates. (B) 2°C above T_{mean} . (C) 3°C above T_{mean} . (D) 4°C above T_{mean} . (D) Legend gives line shading for heterotrophic the feeding rates.

Figure 3.7: (A) Concentration of ROS (RO_S) and (B) reserves (C_R^S) in the symbiont for T_{mean} , +2°C, +3°C and +4°C heating over 90 days and a heterotrophic feeding rate of 100 μ g N cm⁻² d⁻¹.

Figure 4.1: Schematic over C fluxes between the environment, host and the symbiont. Symbols and abbreviations are explained in Table 4.1 and 4.2.

Figure 4.2: Accumulation rate of C in the symbiont (A) and host tissues (B). The model values correspond to the lines and are the sum of the change in the functional and the reserve pools. The circles shows the measured ¹³C accumulation rate at four hours for the 200 μ mol photon m⁻² s⁻¹ light treatment (closed circle) and 50 μ mol photon m⁻² s⁻¹ light treatment (open circle) ± 1 SD.

Figure 4.3: Modelled carbon budget diagram for the sea anemone *Aiptasia pulchella*, rates are given in μ g C mg⁻¹ h⁻¹, and percentages of internal fluxes to the total photosynthates rate in brackets. Light intensity of 200 (A) and 50 µmol photon m⁻² s⁻¹ (B). Dashed arrow marked mC corresponds to the carbon the host acquired from dead symbiont that died due to natural mortality.

Figure 4.4: Modelled carbon budget diagram for the coral, rates are given in μ g C cm⁻² h⁻¹.

Figure 5.1: Location of Heron Reef, Wistari Reef and One Tree Reef on the Great Barrier Reef (A). Heron Reef with the three different coral zones (B): Black= bommies, dark gray = crest, light gray = slope.

Figure 5.2: Red line represents the surface elevation, dashed the water velocity and the solid black line the intensity at 420 nm for two sites on the reef: Coral slope (top panel) and bommies (bottom panel). The red boxes show the two selected periods: $7-8^{\text{th}}$ ($P_{\text{velocity}}^{\text{high}}$) and $18-19^{\text{th}}$ ($P_{\text{velocity}}^{\text{low}}$).

Figure 5.3: Tidal height for P_{velocity}^{high} and P_{velocity}^{low}. Letters indicate the output points and the black and white bars represent night and day, respectively. The x-axis shows the date and local time of day.

Figure 5.4: PON at the surface of the water column for P_{velocity}^{high} in unit mg N m⁻³. The title of each panel states the time point letter as well as the date and time of day. Arrows represent the current direction and strength. The black contour marks the rim of the reefs.

Figure 5.5: PON at the surface of the water column for P^{low}_{velocity} in unit mg N m⁻³. The title of each panel states the time point letter as well as the date and time of day. Arrows represent the current direction and strength. The black contour marks the rim of the reefs.

Figure 5.6: DIN at the surface of the water column for P_{velocity}^{high}, unit mg N m⁻³. The title of each panel states the time point letter as well as the date and time of day. Arrows represent the current direction and strength. The black contour marks the rim of the reefs.

Figure 5.7: DIN at the surface of the water column for P_{velocity}, unit mg N m-3. The title of each panel states the time point letter as well as the date and time of day. Arrows represent the current direction and strength. The black contour marks the rim of the reefs.

Figure 5.8: Vertical profiles of PON, DIN, Age and water velocity from three sites on the reef (lagoon, bommies and reef slope). The top row of panels represents the values from

P^{high}_{velocity} and the bottom row P^{low}_{velocity}.

Figure 5.9: Age of water at the surface over the reef for $P_{velocity'}^{high}$ unit hours.

Figure 5.10: Age of water at the surface over the reef for P^{low}_{velocity}, unit hours.

Figure 5.11: Mean biomass of coral host and symbiont population for $P_{velocity}^{high}$ (I and III) column) and $P_{velocity}^{low}$ (II and IV) in mg N m⁻². The star in IV shows the location of the point evaluated in Figure 5.12.

Figure 5.12: Simulated change in coral biomass, PON concentration, DIN concentration, tidal height and water velocity for one point at the bommies during the month of January, the location of the point is shown in Figure (5.11 IV). The rectangles show two periods of coral growth, one "enhanced" and one "reduced".

Figure 5.13: Uptake rate of inorganic nitrogen by corals (mg N m⁻² d⁻¹).

Figure 5.14: Mass transfer rate coefficient (m d⁻¹) over the corals for output point with DIN uptake for both periods.

Figure 5.15: Uptake rate of organic nitrogen by corals through heterotrophic feeding (mg N m⁻² d⁻¹). Note that the letter representing each panel corresponds to the time point identification in Figure 5.3.

Figure 5.16: Potential uptake rate of organic nitrogen by corals through heterotrophic feeding (mg N m⁻² d⁻¹). Note that the letter representing each panel corresponds to the time point identification in Figure 5.3.

Figure 5.17: Surface water pH during P_{velocity}.

Figure 5.18: Surface water pH during P_{velocity}.

Figure 5.19: Profile of DIN uptake by the coral community, and change DIN concentration, pH and water age at the surface of the water column, as well as water velocity directly over the substrate. A) red line shows the location of the profile over Heron Reef. Water velocity, pH, water age, DIN concentration in the water column, DIN uptake over the coral population and coral host N biomass along the transect for $P_{velocity}^{high}$ (B), and $P_{velocity}^{low}$ (C). The arrow in indicate the direction of the current. At the bottom of the panels showing biomass different colour bars indicate different parts of the reef; black=reef slope, gray=reef crest and dashed=bommies.

v. LIST OF TABLES

Table 2.1: Model equation for symbiont. Each rate or state calculation is given anumber which corresponds to a number in figure 2.

Table 2.2: Model equations for coral host: Each rate or state calculation is given anumber which corresponds to a number in figure 1.

Table 2.3: Model parameters

Table 2.4: Sensitivity of model parameters under two of the nutrient scenarios; high Z_N + low V_{DIN}^H , low Z_N + high V_{DIN}^H . Each model parameter was changed +/-10% separately and the power to which the model state variables changed due to the change in one parameter is seen here. The red colors indicate positive changes in the state variable when increasing the parameter and vice verse for the blue colors. Color intensity indicates strength of the response. Parameters with a power law exponent of less than 0.3 (-0.3<p<0.3) were excluded.

Table 3.1: Assumptions made when deriving the model.

Table 3.2: New state variable equations for the photoinhibition model. The number in brackets refers to the equation numbers used in the text.

Table 3.3: State variable equations from the GBR13 model, where Eqs. 9-12 include the alterations made for this model. Equation numbers are given in brackets, and equation numbers following GBR13 indicate which equation it refers to in Gustafsson et al. (2013).

Table 3.4: Photoinhibition model equations, the number in brackets refers to the equation numbers used in the text.

Table 3.5: Description and value of model parameters.

Table 3.6: Equations from Gustafsson et al. (2013) (GBR13) relevant to this photoinhibition model. The numbers in brackets refers to the equation numbers in GBR13.

Table 3.7: Parameters from Gustafsson et al. (2013) (GBR13) relevant to this photoinhibition model.

Table 8: Definition of state variables and initial conditions for *Pocillopora damicornis* and *Stylophora pistillata*. The initial values for the symbiont population size and pigment pools for *P. damicornis* were derived from Hill et al. (2012) whereas the initial total values of the RCII pools were estimated from Suggett et al. (2008) and divided into the three pools so that initial F_v : F_m and Y(II) values

corresponded with those in Hill et al. (2012). For *S. pistillata* the initial values were derived by spinning up the model for 2 days using a smaller symbiont cell size.

Table 4.1: Model equations

Table 4.2: Model parameters, variables and rates used in the anemone model and the coral model. Bracketed values represented the parameters different in the coral-model.

Table 4.3: Initial conditions for Tremblay et al. (2012).

Table 4.4: Experimental dataset: Uptake rate of ¹³C by different tissues, and total C content of the host and the symbiont (average of three samples). The light levels were HL: 200 μ mol photon m⁻² s⁻¹ and LL: 50 μ mol photon m⁻² s⁻¹ (Pernice pers. comm.).

Table 5.1: Ecology state variables

Table 5.2: Model equations associated with corals

Table 5.3: Model parameters.

vi. ABBREVIATIONS

APX	Ascorbate peroxidises
С	Carbon
ССМ	Carbon Concentrating Mechanism
Chl	Chlorophyll
CSIRO	Commonwealth Scientific and Industrial Research Organisation
DIC	Dissolved Inorganic Carbon
DIN	Dissolved Inorganic Nitrogen
DOM	Dissolved Organic Matter
ETC	Electron Transport Chain
e-	Electron
e ⁻ Fv/Fm	Electron Maximum quantum yield of photosystem II
e ⁻ Fv/Fm IPCC	Electron Maximum quantum yield of photosystem II Intergovernmental Panel of Climate Change
e ⁻ Fv/Fm IPCC H ₂ O ₂	Electron Maximum quantum yield of photosystem II Intergovernmental Panel of Climate Change Hydrogen peroxide
e ⁻ Fv/Fm IPCC H ₂ O ₂ MTL	Electron Maximum quantum yield of photosystem II Intergovernmental Panel of Climate Change Hydrogen peroxide Mass Transfer Limited
e ⁻ Fv/Fm IPCC H ₂ O ₂ MTL N	Electron Maximum quantum yield of photosystem II Intergovernmental Panel of Climate Change Hydrogen peroxide Mass Transfer Limited Nitrogen
e ⁻ Fv/Fm IPCC H ₂ O ₂ MTL N	Electron Maximum quantum yield of photosystem II Intergovernmental Panel of Climate Change Hydrogen peroxide Mass Transfer Limited Nitrogen National Oceanic and Atmospheric Administration
e ⁻ Fv/Fm IPCC H ₂ O ₂ MTL N NOAA NPQ	Electron Maximum quantum yield of photosystem II Intergovernmental Panel of Climate Change Hydrogen peroxide Mass Transfer Limited Nitrogen National Oceanic and Atmospheric Administration Non-photochemical quenching

- ¹O₂* Singlet oxygen
- OEC Oxygen Evolution Complex
- POC Particulate Organic Carbon
- POM Particulate Organic Matter
- PON Particulate Organic Nitrogen
- ROS Reactive Oxygen Species
- PQ Plastoquinone
- PSII Photosystem II
- PSI Photosystem I
- SHOC Spares Hydrodynamic Ocean Code
- SOD Superoxide dismutase
- SST Sea Surface Temperature

vii. ABSTRACT

Understanding the symbiotic association between a coral host and their algae symbiont is essential if we are to be able to simulate and predict how expected changes in ocean sea surface temperatures and other environmental conditions associated with climate change may influence coral reefs in the future. In this thesis a mechanistic coral-algae symbiosis model is proposed, a model which captures the interaction between a heterotrophic host and an autotrophic symbiont with varying sources of nutrients, and various temperature and light intensities. This modelling effort includes mathematical representations of important physiological processes, such as growth, respiration, photosynthesis, calcification, translocation of photosynthates, mortality and mucus production, as well as photoinhibition, ROS production and bleaching. Validating the model using experimental data, showed the model capable of capturing the nutrient dynamics between the environment, the cnidarian host and the symbiotic algae, photoinhibition and bleaching as a function of elevated temperature and light, as well as the mitigating effects heterotrophic feeding may have during elevated thermal stress.

The basic coral symbiosis model, first developed, considered the nutrient dynamics of the symbiosis. The coral acquires nitrogen (N) through two processes, uptake of dissolved inorganic nitrogen (V_{DIN}^H) and heterotrophic feeding (Z_N). Numerical experiments were used to highlight the importance of these different sources of N for coral survival and growth. The model outputs showed the importance of the algae symbionts to the coral host as a source of both N and C when the feeding rate was limited. In contrast, with no light or low light, conditions under which the symbiont population dies, the host was able to survive if Z_N was sufficient to sustain its metabolic requirements. Translocation and recycling of nutrient were shown to be two of the most important features of this model, emphasizing why it is essential to resolve host and symbiont in a coral model.

During the second phase of this thesis a photoinhibition and bleaching model was added to the basic symbiosis model. The resulting modelled rate of bleaching depended on temperature, light intensity and the potential for heterotrophic feeding. The validation showed that the model was capable of capturing both the diurnal change in the state of the photosystem, as well as changes in the symbiont population and the coral host caused by different temperature, light and feeding treatments. Elevated temperatures and light led to a degradation of the photosystem and the expulsion of symbiont cells. If the coral fed heterotrophically, this degradation of the photosynthetic apparatus due to temperature and light stress was reduced, but still a clear decrease in Fv/Fm and cell numbers was observed when the coral was exposed to elevated temperature.

During the first two phases of this modelling effort it was noted that translocation and the uptake of inorganic nutrients needed more consideration. These processes were redefined using experimental (nanoSIMS) data of uptake and translocation in the symbiotic sea anemone *Aiptasia pulchella*. The new definitions proposed that the uptake of DIN and DIC from the environment were symbiont driven and directly associated with photosynthetic activity. The new translocation definition has two components including a representation of the "host release factor" as well as a release of excess photosynthates. This exercise also allowed us to show that the model worked well for a symbiotic association other than the corals.

The final part of this project was to incorporate the coral symbiosis model into a reef scale fully coupled hydrodynamic biogeochemical model of Heron Island Reef. Due to the high complexity of the model a simplified version of the basic symbiosis model was included. Even so the month long model runs showed how the coral influenced the nutrient dynamics over the reef and how changes in water column properties, water velocity and bottom friction influenced coral uptake of nutrients.

The model developed in this thesis highlights that the interchangeability of N sources, and the ability to exchange and recycle nutrients in the host-symbiont system, is the key to coral survival in nutrient poor environments. The photoinhibition model showed that heterotrophic feeding can mitigate the effect of

temperature and light stress as it enhances repair rates and tissue synthesis. The model is also applicable to other host-symbiont associations (such as the sea anemone) and it can be decoupled and used for the animal or the algae part separately. This model is a good tool to explore host-symbiont interactions, however there is always room for improvement and further development.