

Contents

Acknowledgements	ii
Abstract	iii
Résumé	iv
1 Introduction	3
1.1 Marine plankton	3
1.2 What are mixoplankton?	6
1.2.1 Mixoplankton functional types and role in marine ecosystems	6
1.3 Cryptophytes: the <i>Teleaulax/Plagioselmis/Geminigera</i> clade	10
1.4 The ciliate <i>Mesodinium</i>	12
1.5 The dinoflagellate <i>Dinophysis</i>	16
1.6 The cryptophyte- <i>Mesodinium-Dinophysis</i> complex	21
1.7 Modelling biological processes	23
1.8 Research aim	25
2 Material and Methods	28
2.1 System dynamics modelling approach	28
2.2 Sensitivity Analyses	29
2.2.1 Steady State Sensitivity Analysis	30
2.2.2 Dynamic Sensitivity Analysis	30
2.3 Tuning	31
2.4 Validation	31
2.5 Experimental methods	32
2.5.1 Experimental set-up	32
2.5.2 Cell numbers and biovolume	33
2.5.3 Chl <i>a</i>	34
2.5.4 Inorganic carbon uptake - ¹⁴ C incorporation	34
2.5.5 Dissolved inorganic carbon (DIC)	35
2.5.6 Cellular organic carbon, nitrogen & phosphorous (C, N, P)	36
2.5.7 Dissolved inorganic nitrogen and phosphorous	37

3	Niche separation between different functional types of mixoplankton: results from NPZ - style N - based model simulations	38
3.1	Introduction	40
3.2	Methods	41
3.2.1	protoZ variant	44
3.2.2	protP, Alg1 and Alg2 variants	45
3.2.3	CM variant	46
3.2.4	GNCM variant	46
3.2.5	SNCM variant	47
3.2.6	Simulations	48
3.3	Results	48
3.3.1	Results Sensitivity analyses	48
3.3.2	Functional dependence	49
3.3.3	Dynamic simulations	50
3.3.4	protoZ	50
3.3.5	GNCM	54
3.3.6	SNCM	54
3.3.7	CM	55
3.3.8	protP	55
3.3.9	General results	56
3.3.10	Physiological features	57
3.4	Discussion	57
3.4.1	Model overview	57
3.4.2	Ecological and biogeochemical implications	62
3.4.3	Niche separation between protist types	64
3.4.4	protoZ and protP	64
3.4.5	GNCM and SNCM	65
3.4.6	CM	67
3.4.7	Further model development	68
4	Acquired phototrophy and its implications for bloom dynamics of the cryptophyte-<i>Mesodinium-Dinophysis</i>-complex	69
4.1	Introduction	70
4.2	Methods	72
4.2.1	Mixoplankton food web of the model	73
4.2.2	Model modifications from Anschütz and Flynn (2020)	75
4.2.3	Sub-model additions to the model by Anschütz and Flynn (2020)	75
4.2.4	Model parametrisation	76
4.2.5	Dynamic Sensitivity Analysis	81
4.2.6	Simulations, caveats and general settings	82
4.3	Results	82

4.3.1	Dynamic Sensitivity Analysis	82
4.3.2	Biotic interactions	84
4.3.3	Abiotic interactions	89
4.4	Discussion	93
4.4.1	Eutrophication	95
4.4.2	Predator-prey ratio	96
4.4.3	Irradiance	96
4.4.4	Temperature	97
4.4.5	Mixed layer depth	98
4.4.6	Current input and advection	98
4.5	Conclusion	99
5	Growth and stoichiometry of <i>T. amphioxeia</i> in phosphorous limiting conditions – a combined experimental-modelling approach	101
5.1	Introduction	102
5.2	Methods	104
5.2.1	Cultures and culture conditions	104
5.2.2	Experiment	104
5.2.2.1	Cell numbers and biovolume	104
5.2.2.2	Bacterial cell numbers	105
5.2.2.3	Inorganic carbon uptake - ¹⁴ C incorporation	105
5.2.2.4	Dissolved inorganic carbon (DIC)	105
5.2.2.5	Dissolved inorganic nitrogen and phosphorous	106
5.2.2.6	Cellular organic carbon, nitrogen & phosphorous (C, N, P)	106
5.2.2.7	Chl <i>a</i>	106
5.2.3	Model	106
5.2.3.1	Model description	106
5.2.3.2	Configuration of the "Perfect Beast" model as <i>T. amphioxeia</i>	109
5.2.3.3	Tuning the model to the experimental data	111
5.2.3.4	Dynamic Sensitivity Analysis of the "Perfect Beast" model configured as <i>T. amphioxeia</i>	114
5.2.3.5	Effect of phosphorus stored in bacteria on growth and biomass yield of <i>T. amphioxeia</i>	114
5.3	Results	115
5.3.1	Effect of bacteria as prey on nutrient levels and <i>T. amphioxeia</i> biomass	115
5.3.2	Dynamic Sensitivity Analysis	117
5.3.3	Model fit to biomass data	117
5.3.4	Model fit to external nutrients and internal stoichiometry	120
5.3.5	Chlorophyll to carbon ratio and photosynthesis	120

5.3.6	Potential contribution of bacterivory to growth in <i>T. amphioxeia</i> . . .	123
5.4	Discussion	125
5.5	Conclusion	127
6	Global discussion	129
6.1	Introduction	129
6.2	Niche separation of mixoplankton functional types (chapter 3)	130
6.3	Implications of nutrient and prey availability for the mixoplankton types in the TMD complex (chapter 4)	132
6.4	The first variable stoichiometric model of the CM <i>T. amphioxeia</i> tuned to experimental data (chapter 5)	134
6.5	Perceptions of the modelling process	136
6.6	Limitations of study	137
6.6.1	Future study of mixoplankton	139
6.7	What next?	140
6.7.1	Possible implications of mixoplankton for environmental management	142
	Bibliography	145
A	Supplementary Material for N-based TMD-model - model equations	164
B	Supplementary Material for the CNP <i>Teleaulax</i> model - model equations	206

List of Figures

1.1	Schematic of the plankton size spectrum	3
1.2	Schematic of a general foodweb	4
1.3	Schematics of dichotomic plankton paradigm vs mixoplankton paradigm	6
1.4	Schematic of protist functional types by Flynn et al. 2019	8
1.5	Comparison of food web models by Flynn et al. (2019)	10
1.6	Illustrations of species of <i>Teleaulax</i>	11
1.7	Species that prey on <i>T. amphioxeia</i>	13
1.8	Schematic of <i>Mesodinium</i> and pictures of <i>Mesodinium</i> spp. containing kleptochloroplasts	14
1.9	Schematic of <i>Dinophysis</i> and pictures of different species of <i>Dinophysis</i>	16
1.10	Schematic of the mixoplankton food chain of the <i>Teleaulax-Mesodinium-Dinophysis</i> complex	22
2.1	Forrester diagram of a conceptual model	29
2.2	Experiment set-up of the <i>T. amphioxeia</i> experiment	33
2.3	Schematic of Coulter counter measurement	34
2.4	Schematic of Chl <i>a</i> measurement	34
2.5	Schematic of inorganic carbon uptake - ¹⁴ C incorporation	35
2.6	Schematic of DIC measurement	36
2.7	Schematic of analysis of organic carbon, nitrogen and phosphorous (CNP) and DIN and DIP	37
3.1	Schematic representations of the five protist functional type configurations	43
3.2	Schematic of the main NPZ- style model and its state variables	43
3.3	3D-mesh plots showing the relationship between growth rate (μ ; day ⁻¹) and sources of energy supplied as light	51
3.4	3D-mesh plots providing niche comparisons between pairs of protist variants	52
3.5	niche comparisons between protP and the other protist configurations	53
3.6	Changes in biomass and nutrient concentrations in simulated systems of different nutrient loading	58
3.7	Daily averaged (of light and dark) biomass specific growth rates	59
3.8	General NPZ-model: Daily averaged rates of inorganic nitrogen uptake by the phototrophic protist variants	60
3.9	General NPZ-model: Variation in the NCM prey ingestion index	61

4.1	TMD model: schematic of the main model and its state variables	74
4.2	Results from the DSA	83
4.3	TMD-model: changes in biomass and nutrient concentrations at different nutrient loadings	86
4.4	Comparison of the N-based TMD model with a grazer for <i>Dinophysis</i> . . .	87
4.5	TMD-model: changes in biomass and nutrient concentrations at different organism inoculum	88
4.6	TMD-model: changes in biomass and nutrient concentrations at different irradiances	90
4.7	TMD-model: changes in biomass and nutrient concentrations at different temperatures	91
4.8	TMD-model: changes in biomass and nutrient concentrations at different MLDs	92
4.9	Global distribution of <i>Teleaulax</i> sp., <i>Mesodinium</i> sp. and of mixoplankton <i>Dinophysis</i> species	94
5.1	Conceptual model of the "Perfect Beast" model (Flynn and Mitra, 2009) . .	108
5.2	Schematic of the food web in Mitra et al. (2014)	108
5.3	Food web schematic of configured <i>T. amphioxeia</i> model	110
5.4	Analysis on bacterial phosphorous impact: results	116
5.5	DSA: results	117
5.6	Fit of the "Perfect Beast" model to experimental data of <i>T. amphioxeia</i> biomass	119
5.7	Fit of the "Perfect Beast" model to experimental data of <i>T. amphioxeia</i> stoichiometry	121
5.8	Fit of the "Perfect Beast" model to experimental data of photosynthesis by <i>T. amphioxeia</i>	122
5.9	Comparison of model fit of experimental data of <i>T. amphioxeia</i> with and without prey	124
6.1	Bottom-up benefits of mixoplankton research to coastal management . . .	132

List of Tables

3.1	Definition of mixoplankton types, with examples of species	42
3.2	Functionality of the protist model in each variant setting	42
4.1	Published models on <i>Dinophysis</i> and <i>Mesodinium</i>	71
4.2	Literature values for the configuration of the organisms in the TMD model .	77
4.3	DSA: varied abiotic parameters	79
4.4	List of physiological values of different species of <i>Dinophysis</i>	80
4.5	DSA: varied values	81
4.6	Tested assumptions for dynamic sensitivity analysis	81
5.1	Configuration of the "Perfect Beast" model to experiment conditions and organism	110
5.2	Initial nutrient concentrations and inoculum of the experiment	112
5.3	Tuned physiological constants of the "Perfect Beast" model (Flynn and Mittra, 2009) configured as <i>T. amphioxeia</i>	113
5.4	DSA: tested constants	114
5.5	DSA: tested conditions	114
A.1	Complete equations of the TMD model	165
B.1	Complete equations of the "Perfect Beast" model configured as <i>T. amphioxeia</i> 207	