

FACTORS INFLUENCING FISH DIETS IN REEF FOOD WEBS

by

Germán Andrés Soler
BSc and MMarSc

Quantitative Marine Sciences,
Institute for Marine and Antarctic Studies (IMAS)

Submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy in Quantitative Marine Science

April 2016
University of Tasmania



STATEMENTS AND DECLARATIONS

1.1.1.1 Declaration of Originality

This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis, and to the best of my knowledge and belief no material previously published or written by another person except where due acknowledgement is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

1.1.1.2 Authority of Access

This thesis may be made available for loan and limited copying and communication in accordance with the Copyright Act 1968.

1.1.1.3 Statement regarding published work contained in thesis

The publishers of the papers comprising Chapters 2,3,4 and 5 hold the copyright for that content, and access to the material should be sought from the journal. The remaining non published content of the thesis may be made available for loan and limited copying and communication in accordance with the Copyright Act 1968.

1.1.1.4 Statement of Ethical Conduct

The research associated with this thesis did not required ethical approval on behalf of the University of Tasmania.

Signed

German A. Soler

Date

1.1.1.5 Statement of Co-Authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

- German A. Soler, Institute for Marine and Antarctic Studies, UTAS
- Professor Graham J. Edgar, Institute for Marine and Antarctic Studies, UTAS
- Dr. Russell J. Thomson, Institute for Marine and Antarctic Studies, UTAS
- Dr. Rick D. Stuart-Smith, Institute for Marine and Antarctic Studies, UTAS
- Dr. Anthony D.M. Smith, CSIRO Oceans and Atmosphere, GPO Box 1538, Hobart, TAS, 7001, Australia.
- Dr. Stuart Kininmonth, Institute for Marine and Antarctic Studies, UTAS; Stockholm Resilience Centre, Stockholm University, Kräftriket 2B, SE-106 91 Stockholm, Sweden
- Dr. Stuart J. Campbell, Wildlife Conservation Society, Indonesia Marine Program, Jl. Burangrang No. 18, Bogor Jawa Barat 16151, Indonesia Geography
- Dr. Terence P. Dawson, School of the Environment, University of Dundee, Perth Rd, Dundee, DD1 4HN, UK
- Dr. Neville S. Barrett, Institute for Marine and Antarctic Studies, UTAS
- Dr. Anthony T.F. Bernard, South African Environmental Observation Network, Elwandle Node, 18 Somerset Street, Grahamstown, South Africa: Zoology and Entomology Department, Rhodes University, Box 94, Grahamstown, South Africa
- Dr. David E. Galván, Centro Nacional Patagónico – CONICET Blvd Brown 2915 (9120) - Puerto Madryn - Chubut – Argentina
- Dr. Trevor J. Willis, School of Biological Sciences, Institute of Marine Sciences, University of Portsmouth, Ferry Road, Portsmouth P04 9LY, UK
- Dr. Timothy J. Alexander, Department of Fish Ecology and Evolution, Centre of Ecology, Evolution and Biogeochemistry, EAWAG Swiss Federal Institute of Aquatic Science and Technology, Seestrasse 79, CH-6047 Kastanienbaum, Switzerland; Division of Aquatic

Ecology and Evolution, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse
6, CH-3012 Bern, Switzerland

1.1.1.6 Papers included in this thesis and authors' roles:

Paper 1, Reef fishes at all trophic levels respond positively to effective marine protected areas

Reproduced in chapter 2: is published in PLOS One

German A. Soler, Graham J. Edgar, Russell J. Thomson, Stuart Kininmonth, Stuart J. Campbell, Terence P. Dawson, Neville S. Barrett, Anthony T.F. Bernard, David E. Galván, Trevor J. Willis, Timothy J. Alexander, & Rick D. Stuart-Smith (2015). Reef fishes at all trophic levels respond positively to effective marine protected areas. PLOS One

Authors' contribution: GAS, GJE and RDS-S conceived the project; GAS, GJE, RJT, SK, RDS-S drafted the paper with substantial input from SJC, TPD, NSB, ATFB, TJW and TJA; GAS, RJT, SK and DEG analysed data and prepared figures. Data presented in this work were provided by the Reef Life Survey Foundation.

Paper 2, Contributions of body size, habitat and taxonomy to predictions of temperate Australian fish diets

Reproduced in chapter 3: is published at Marine Ecology Progress Series.

German A. Soler¹, Russell J. Thomson¹, Rick D. Stuart-Smith¹, Anthony D.M. Smith², Graham J. Edgar (2016). Contributions of body size, habitat and taxonomy to predictions of temperate Australian fish diets. MEPS. DOI 10.3354/meps11584

Authors' contribution: GJE and GAS conceived the project; GAS, drafted the paper with substantial input from RJT, GJE, RJT, RDS-S and ADMS; GAS and RJT developed the diet predictive model and prepared figures.

Paper 3, Predicting the diet of coastal fishes at a continental scale based on taxonomy and body size

Reproduced in chapter 4: has been published at Journal of Experimental Marine Biology and Ecology.

Soler GA, Edgar GJ, Stuart-Smith RD, Smith ADM, Thomson RJ (2016). Predicting the diet of coastal fishes at a continental scale based on taxonomy and body size. Journal of Experimental Marine Biology and Ecology, 10.1016/j.jembe.2016.03.017

Authors' contribution: GAS developed and drafted the paper with the original idea provided by GJE; GJE collected the data; RJT, GAS and GJE analysed data and developed the predictive diet model; all authors contributed substantially to the writing of the manuscript.

Paper 4, Moving beyond trophic groups: evaluating fishing-induced changes to temperate reef food webs

Reproduced in chapter 5. This paper is in review at Ecological Applications.

Soler GA, Edgar GJ, Stuart-Smith RD, Smith ADM, Thomson RJ (*in review*). Moving beyond trophic groups: evaluating fishing-induced changes to temperate reef food webs.

Authors contribution: GAS developed and drafted the paper with the original idea provided by GJE; GJE, RDS-S and GAS collected the data; GAS, RJT and GJE analysed data; all authors contributed substantially to the writing of the manuscript.

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Signed:

German A. Soler

PhD Candidate

Institute for Marine and Antarctic Studies – Fisheries and Coasts Centre

University of Tasmania

Signed:

Professor Graham J. Edgar

Primary Supervisor

Institute for Marine and Antarctic Studies – Fisheries and Coasts Centre

University of Tasmania

Signed:

Prof. Craig Johnson

Head, Ecology & Biodiversity Centre

Institute for Marine and Antarctic Studies

University of Tasmania

Prof Chris Carter
Acting Executive Director

ACKNOWLEDGEMENTS

Foremost I would like to express my sincere gratitude to my supervisors Professor Graham Edgar, Dr. Russell Thomson, Dr. Rick Stuart-Smith and Dr. Anthony Smith for their complete support through this work. I would also like to thank other fellow Ph.D students and staff at IMAS for their support in the different steps of this thesis. I would like to especially thank Dr. Kilian Stehfest and Dr. Klaas Hartmann for support in R coding. I would like to thank Justin Hulls for designing the maps of the study area, and Dr. Simon Wotherspoon and Dr. Andre Punt for their input and comments in developing the diet predictive model for Chapters 3 to 5. Other important contributors were the many divers associated to the Reef Life Survey Foundation who collected information used in this thesis. Many thanks to the different park officers and colleagues who assisted the collection of RLS information by providing permits and assistance in the field, as well as several marine institutions around the world for hosting these survey trips. I also want to extend a special recognition to my wife, Carolina Garcia Imhof, to my parents German Soler and Myriam Alarcon, my brother Juan Gabriel Soler and all my friends and family for their unconditional support not only through this work but through my life.

GENERAL ABSTRACT

The effects of environmental and anthropogenic factors on fish community structure are typically assessed by compartmentalizing fish species into functional groups. In many cases species are placed in specific trophic groups (e.g. higher carnivores, benthic carnivores, planktivores and herbivores) independent of their size. This assumes that species and individuals within species have similar roles within each trophic group, regardless of the stage of ontogenetic development. This simplistic approach contradicts Hutchinson's well-known paradigm, which suggests that each species possesses a unique role (niche) within the environment it inhabits.

The studies presented in this thesis investigate the effects of no-take marine protected areas (MPAs) as well as other factors on fish community structure using this traditional approach (i.e. functional trophic group) and, alternatively, by using diet predictions generated from size- and taxon-based quantitative models. Prey predictions for individual fish have been summed to estimate total fish community consumption, providing a new tool for analysis of trophic pathways in ecological studies. These diet predictions represent an innovative approach for analysing the fish community as a continuum based on the estimated diets of fishes.

The removal of large predators from a fish community theoretically should cause a trophic release, allowing the next lower trophic group to increase in size. As part of the work presented in this thesis, I test this assumption by investigating fish community structure using a global dataset with over 1,800 sites, including both no-take MPAs and open-access fishing sites. The trophic release theory predicts that lower trophic groups of smaller size will have lower biomass in MPAs relative to fished sites. As expected, larger (>30cm) fish for all four trophic groups had significantly higher biomasses in MPAs, but, in contrast to expectations, none of the small (<7.5cm) fish groups showed a significant decrease in biomass in MPAs. These results suggest that fishing affects the biomass of all fish trophic groups

and size classes, and that this effect is stronger than trophic release through the near absence of larger predator fishes.

A predictive dietary model was developed using a comprehensive data set for predator fish and their prey for Western Port, Australia. The predictive dietary model used *k*-nearest neighbour procedures to predict prey type, and linear models to predict prey size for fish classified at species level, size and location. We obtained reasonable predictions for prey type (mean percent overlap between predicted and actual prey types =77%) and prey size (r^2 between predicted and observed prey size =93%) when the taxonomic identity of the fish and its size were included in the model. Contrary previous expectation, the most important predictor for prey type was the size of the fish, while the most important predictor for prey size was fish' taxonomic identity. Little loss of accuracy was detected when only family rather than species identity was used in the model.

This predictive dietary model, developed for a single location, was applied to widely dispersed locations with differing species composition across southern Australia. At this wider geographical scale the model was robust enough to predict with moderate accuracy prey type (accuracy=67%) and prey size (r^2 = 56%) using training data from Western Port. Predictions for prey type (accuracy=73%) and mean prey size (r^2 =89%) substantially improved when data from all southern Australian sites rather than just Western Port were used to 'train' the model. Exclusion of site, habitat, ecoregion or province as factors resulted in little loss in accuracy. Accuracy of continental-scale predictions declined very little when family instead of species was used in the model. Application of our models in situations where family identity and size of the consumer fish are known provides a mechanism for broad-scale testing of influential ecological hypotheses dealing with community-level consumption and trophic structuring. These dietary predictions are appropriate for addressing key questions about the ecology of marine systems and human impacts and management interventions, as well as the effects of environmental variables.

In an application of the dietary model, I assessed the effect of no-take MPA protection on fish community consumption for a set of 376 reef sites surveyed using underwater visual census methods in temperate Australia. I found that consumption was higher and prey was larger in MPAs relative to

open access sites. This agreed with the coarse trophic group analysis. However, the diet predictive model approach showed that certain diet types were consumed in greater abundances than indicated by the trophic group approach. This finding has important ecological consequences. Our predictive diet model also estimates higher daily consumption of prey of larger size by bigger and more abundant fishes in MPAs, in relation to fished sites. I concluded that more complex ecological pathways appear to operate within no-take MPAs. Fish assemblages in no-take protected areas with sufficient surveillance and enforcement appear to include more habitat-modifying species, and higher numbers of fish species, than in fished locations, thereby contributing to complex ecological processes with possible implications in the habitat structure of the ecosystems.

TABLE OF CONTENTS

STATEMENTS AND DECLARATIONS.....	ii
ACKNOWLEDGEMENTS.....	x
GENERAL ABSTRACT.....	xi
TABLE OF CONTENTS.....	xiv
LIST OF FIGURES.....	xvi
LIST OF TABLES.....	xxv
Chapter 1 GENERAL INTRODUCTION AND THESIS STRUCTURE	29
Chapter 2 REEF FISHES AT ALL TROPHIC LEVELS RESPOND POSITIVELY TO EFFECTIVE MARINE PROTECTED AREAS	35
2.1 Abstract	36
2.2 Keywords	36
2.3 Introduction.....	36
2.4 Materials and Methods	39
2.4.1 Statistical analysis.....	41
2.5 Results	45
2.6 Discussion	47
2.6.1 Higher biomass in all trophic groups.....	48
2.6.2 Other drivers of reef fish trophic structure	51
2.7 Acknowledgments	52
2.8 Supporting Information	54
Chapter 3 THE CONTRIBUTIONS OF BODY SIZE, HABITAT AND TAXONOMY TO PREDICTIONS OF TEMPERATE AUSTRALIAN FISH DIETS.....	61
3.1 Abstract	62
3.2 Keywords	62
3.3 Introduction.....	62
3.4 Materials and Methods	65
3.5 Results	71
3.6 Discussion	79
3.7 Acknowledgments	83
3.8 Supplementary material.....	84

Chapter 4	PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE	92
4.1	Abstract	93
4.2	Keywords.....	94
4.3	Introduction	94
4.4	Methodology	96
4.5	Results	100
4.6	Discussion	109
4.7	Acknowledgments	114
4.8	Supplementary material.....	114
Chapter 5	MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS.....	118
5.1	Abstract	119
5.2	Keywords.....	119
5.3	Introduction	119
5.4	Methodology	121
5.5	Results	127
5.6	Discussion	132
5.7	Acknowledgments	136
5.8	Supplementary material.....	138
Chapter 6	GENERAL DISCUSSION AND CONCLUSIONS	142
6.1	Synthesis of research findings	142
6.2	Conclusions	146
REFERENCES		149

LIST OF FIGURES

Figure 1.1 Thesis outline.....	31
Figure 2.1. Global map showing sites investigated. The density of fill color applied to each marine ecoregion (Spalding et al. 2007) relates to the number of sites surveyed within it.	40
Figure 2.2. Percentage difference in biomass (\pm 95% confidence intervals) for covariates investigated. Percentage difference in biomass per 1°C change in mean sea surface temperature (A), 1°C change in the annual range in sea surface temperature (B), 1 Einstein/m ² /day change in annual mean photosynthetically-active radiation (C), and a single unit increase in the index of local population density (D) for each of the four trophic groups. Ratios were obtained from the β coefficients and transformed into % increment in biomass, by $100 * (\exp(\beta) - 1)$. Asterisks denote statistically significant difference ($p < 0.05$).	43
Figure 2.3. Percentage difference in biomass of different trophic groups in protected areas relative to open-access zones. Log ratios of biomass ($\log(\text{biomassMPA}/\text{biomassOPEN})$) between effective and less effective MPAs relative to open-access zones, for each trophic group (\pm 95% confidence intervals). Ratios were obtained from the coefficient for Protection, β_5 , in equation 1 and transformed into percentage increments in biomass, by $100 * (\exp(\beta_5) - 1)$. Asterisks denote a statistically significant difference ($p < 0.05$). The model also adjusted for SST mean, SST range, PAR-mean and human population.	46

Figure 2.4. Percentage difference in biomass of the different trophic groups size categories in temperate and tropical areas. Log ratios of fish biomass ($\log(\text{biomassMPA}/\text{biomassOPEN})$) between trophic and body size groups in effective MPAs in temperate (A) and tropical (B) regions, relative to open access zones ($\pm 95\%$ confidence intervals). Small fishes <7.5 cm; medium fishes from 7.5 to 30 cm; large fishes >30 cm. Ratios were obtained from the coefficient for Protection, β_5 , and transformed into percentage increments in biomass, by $100 * (\exp(\beta_5) - 1)$. Asterisks denote a statistically significant difference ($p < 0.05$). The model also adjusted for SST mean, SST range, PAR-mean and human population.47

Figure 2.5. (S1 Fig) Percentage difference in biomass ($\pm 95\%$ confidence intervals) for relief index. Percentage difference in biomass for 1 unit increase in the relief index (range 1-4) for each of the four trophic groups. The ratios were obtained from the coefficient for Relief, β_5 , from the LMM equation (S1 Appendix) and transformed into percentage increments in biomass, by $100 * (\exp(\beta_5) - 1)$. Asterisks denote a statistically significant difference ($p < 0.05$).59

Figure 2.6. (S2 Fig) Percentage difference in biomass ($\pm 95\%$ confidence intervals) of the different trophic groups in protected areas relative to open-access zones when accounting for, and not accounting for, the relief index. Log ratios of biomass ($\log(\text{biomassMPA}/\text{biomassOPEN})$) with relief index and without relief index included in the LMMs. The difference in biomass in effective MPAs were relative to open-access zones, for each trophic group ($\pm 95\%$ confidence intervals). Ratios were obtained from the coefficient for Protection, β_6 , from the LMM equation (S1 Appendix) and transformed into

percentage increments in biomass, by $100 * (\exp(\beta_6) - 1)$. Asterisks denote a statistically significant difference ($p < 0.05$). The LMM model also adjusted for SST mean, SST range, PAR-mean and human population.	60
Figure 3.1 Western Port, showing locations of sampling sites.	66
Figure 3.2 Predictors used in the ‘Consume’ 2-step model, and how they combined to produce the output matrix with prey type, prey type percentages and mean prey size for a consumer fish.	68
Figure 3.3 Scatterplots relating \log_e predicted and observed mean prey size (mm) using a linear model with all predictors (species, genus, family, wet weight (WW), prey type, site, habitat and month; weighted correlation): (A) All fish included, $R^2 = 0.90$ (79 species); (B) Subset of 12 individuals per species ($R^2 = 0.93 \pm 0.01$, 42 species, where \pm indicates the variation in R^2 generated by different sets of individuals randomly selected to represent each species). The green line outlines the upper prediction interval and red line the lower prediction interval (95%). The blue line is the locally weighted scatterplot smoothing curve (LOWESS).	73
Figure 3.4 Scatterplots relating \log_e of wet weight (WW) of consumer fish (g) and \log_e of observed mean prey size in mm; (A) all fish included, $R^2 = 0.54$; (B) Subset of 12 individuals per species ranging in size, $R^2 = 0.68 (\pm 0.01)$; (C) All fish included but without <i>Aldrichetta forsteri</i> , $R^2 = 0.71$. The blue lines are the locally weighted scatterplot smoothing curves (LOWESS).	76
Figure 3.5 Scatterplot relating predicted and observed square root of the standard deviation (SD) of mean prey size for fishes in Western Port. $R^2 = 0.36$. The blue line is the locally weighted scatterplot smoothing curves (LOWESS).	77

Figure 3.6 Scatterplot relating observed standard deviation of the \log_e prey size and the \log_e of the wet weight (WW) of consumer fish. $R^2=0.02$. Red line is the 90% quantile regression. The blue line is the locally weighted scatterplot smoothing curves (LOWESS).	78
Figure 3.7 Boxplots, showing the relationship between the \log_e wet weight (WW) of the consumer fish and the observed prey types. Prey abbreviations are: a=algae, oe=other epifauna, ce=crustacean epifauna, ci=crustaceans infauna, s=sponges, me=mollusc epifauna, pi=polychaetes infauna, pe=polychaetes epifauna, f=fish, and mi=mollusc infauna. The mid-line is the median and box limits are 25 th and 75 th percentiles. The whiskers are 1.5 times the inter-quartile range or the maximum or minimum value, whichever is closer to the median. The points are outliers.	79
Figure 4.1 Locations sampled in southern Australia.	97
Figure 4.2 Predicted prey type percentages in relation to \log_e wet weight (WW) of the consumer fish. Predictions were based on all predictors other than taxonomic information for the consumer fish. Prey types: algae (a), sponges (s), epifaunal polychaetes (pe), infaunal polychaetes (pi), other epifauna (oe), infaunal mollusc (mi), epifaunal mollusc (me), fish (f), infaunal crustaceans (ci) and epifaunal crustaceans (ce).	103
Figure 4.3 Scatterplot relating predicted and observed \log_e mean prey size for southern Australia including Western Port ($r^2=0.89$). The solid black line is the locally-weighted scatterplot smoothing curve (LOWESS). The dash black lines outline the upper prediction interval and the lower prediction interval (95%); both lines were estimated using LOWESS.	105

Figure 4.4 Scatterplot relating predicted and observed \log_e mean prey size for all consumer fish in the southern Australia locations (Western Port excluded) using training data from Western Port ($r^2=0.56$). The solid black line is the locally-weighted scatterplot smoothing curve (LOWESS). 106

Figure 4.5 Scatterplot relating \log_e of observed (grey squares) and predicted (darker grey crosses) mean prey size in mm (\log_e) against \log_e wet weight (WW) of the consumer fish in g (\log_e) for all locations investigated in southern Australia, including Western Port. The model used a random sample of 12 individuals per species with a wide range of size. The dashed black line ($r^2=0.65$) is the observed mean prey size locally-weighted scatterplot smoothing curve (LOWESS). The black solid LOWESS line relates predicted mean prey size ($r^2=0.94$) to the size of the consumer fish (WW), with habitat, location and ecoregion included in models but no taxonomic information. 107

Figure 4.6 Scatterplot relating predicted standard deviation of the \log_e mean prey size (mm) and the \log_e of the wet weight (WW) of the consumer fish (g) for all locations investigated in southern Australia using all predictors ($r^2=0.03$). LOWESS curve is shown in solid black. 109

Figure 5.1 Reef Life Survey (RLS) sites investigated in South Australia, Victoria and Tasmania. 122

Figure 5.2 (A) Percentage difference in prey types consumed ($\pm 95\%$ confidence intervals) by the fish community at sites in protected areas relative to fished zones. Log ratios of daily prey consumption in no-take MPAs relative to fished zones ($\log(C_{\text{preyMPA}}/C_{\text{preyOPEN}})$) were obtained for each prey type from the coefficient for Protection, β_5 . (B) Percentage difference for a

single unit increase in the index of local human population density obtained for each prey type from the coefficient for PopIndex, β_4 . Ratios were obtained from the coefficients for POPindex, β_4 and Protection, β_5 , and transformed into percentage difference in biomass using the relation $100 * (\exp(\beta_{4,5})$ from Equation 1 on this manuscript. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero. Prey types: algae (*a*), sponges (*s*), epifaunal polychaetes (*pe*), infaunal polychaetes (*pi*), infaunal molluscs (*mi*), epifaunal molluscs (*me*), fishes (*f*), planktonic fish larvae (*fp*), infaunal crustaceans (*ci*), epifaunal crustaceans (*ce*), planktonic crustaceans (*cp*), other epifauna (*oe*), other infauna (*oi*)..... 128

Figure 5.3 (A) Percentage difference in daily consumption of different size classes for all prey types consumed by the fish community in protected areas (no-take MPAs) relative to fished zones ($\pm 95\%$ confidence intervals). (B) Percentage difference for a single unit increase in the index of local human population density obtained for each prey size bin from the coefficient for PopIndex, β_4 . Ratios were obtained from the coefficients for POPindex, β_4 and Protection, β_5 , and transformed into percentage difference in biomass using the relation $100 * (\exp(\beta_{4,5})$ from Equation 1 on this manuscript. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero..... 129

Figure 5.4 (A) Percentage difference in biomass for different trophic groups and size categories due to the level of protection at sites surveyed in Tasmania, Victoria and South Australia ($\pm 95\%$ confidence intervals). (B) Percentage difference for single unit increase in the population density index ($\pm 95\%$

confidence intervals) for each of four major trophic groups and size classes in the surveyed sites. Ratios were obtained from the coefficients for POPindex, β_4 and Protection, β_5 , and transformed into percentage difference in biomass using the relation $100 * (\exp(\beta_{4 \text{ or } 5}) - 1)$, Equation 1 of Soler et al. (2015). The model adjusted for SST mean, SST range, PAR-mean and human population. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars extended above or below zero..... 130

Figure 5.5 (Fig. S1) (A) Percentage difference in daily consumption of different size classes for all prey types consumed by the fish community in protected areas relative to fished zones ($\pm 95\%$ confidence intervals). (B) Percentage difference for a single unit increase in the index of local human population density obtained for each prey size bin from the coefficient for PopIndex, β_4 . Ratios were obtained from the coefficients for POPindex, β_4 and Protection, β_5 , and transformed into percentage difference in biomass using the relation $100 * (\exp(\beta_{4,5}) - 1)$ from Equation 1 on this manuscript. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero. This graph fuses the prey sizes smaller than 0.5 mm in one group and in a second size class prey types larger than 11 mm. 138

Figure 5.6 (Fig. S2) Percentage difference in biomass ($\pm 95\%$ confidence intervals) for covariates investigated. Percentage difference in biomass per 1°C change in mean sea surface temperature (A), 1°C change in the annual range in sea surface temperature (B), and 1 Einstein/ m^2/day change in annual mean photosynthetically active radiation (C), for each of the prey size classes.

Ratios were obtained from the β coefficients from Equation 1 of this paper and transformed into % increment in biomass, by $100 * (\exp(\beta) - 1)$. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero. This graph fuses the prey sizes smaller than 0.5 mm in one group and in a second size class prey types larger than 11 mm. 139

Figure 5.7 (Fig. S3) Percentage difference in biomass (\pm 95% confidence intervals) for covariates investigated. Percentage difference in biomass per 1°C change in mean sea surface temperature (A), 1°C change in the annual range in sea surface temperature (B), and 1 Einstein/m²/day change in annual mean photosynthetically active radiation (C) for each of the prey types. Ratios were obtained from the β coefficients from Equation 1 of this paper and transformed into % increment in biomass, by $100 * (\exp(\beta) - 1)$. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero. Prey types: algae (a), sponges (s), epifaunal polychaetes (pe), infaunal polychaetes (pi), infaunal molluscs (mi), epifaunal molluscs (me), fishes (f), planktonic fish larvae (fp), infaunal crustaceans (ci), epifaunal crustaceans (ce), planktonic crustaceans (cp), other epifauna (oe), other infauna (oi). 140

Figure 5.8 (Fig. 4S) Percentage difference in biomass (\pm 95% confidence intervals) for covariates investigated. Percentage difference in biomass per 1°C change in mean sea surface temperature (A), 1°C change in the annual range in sea surface temperature (B), and 1 Einstein/m²/day change in annual mean photosynthetically active radiation (C) for each of the prey size classes.

Ratios were obtained from the β coefficients from Equation 1 of this paper
and transformed into % increment in biomass, by $100 * (\exp(\beta) - 1)$ 141

LIST OF TABLES

Table 2.1. (S1 Table). Marine Protected Areas (MPAs) level of effectiveness and number of sites. Some MAPs had sites that differed in level of effectiveness.	54
Table 2.2. (S2 Table). Covariates used as predictors in linear mixed models. PAR-mean, Nitrate, Phosphate, Silicate, Chlomean, SST range and SST mean were obtained from Bio-ORACLE (Tyberghein et al. 2012). Pop index was calculated using the quadratic kernel function described by (Silverman 1986).	57
Table 3.1 Percentage correct between predicted and observed prey type for the full data set and for a random subset of 12 individuals per species with a wide range of sizes for Western Port. Also shown is the percentage correct of the predicted prey for all predictors and the subsequent loss in accuracy when removing factors from model. WW= log _e wet weight of consumer fish. These predictions of prey type were based on step one of the <i>Consume</i> model using the <i>k</i> -nearest neighbour algorithm.	72
Table 3.2 Correlation between observed and predicted mean prey size for the full data set and for a random subset of 12 individuals per species with a wide range of sizes for Western Port. Also shown are the correlations for all the predictors available and the subsequent loss in accuracy when removing some of them. Weighting of the correlation was based on the predicted percentages of prey type. WW= log _e wet weight of consumer fish. The difference in the	

prediction intervals indicates the fit with the different combinations of predictors.....	74
Table 3.3 Correlation between the predicted and the observed standard deviations of the predicted mean prey size for Western Port. Also shown are the correlations for all the predictors available and the subsequent loss in accuracy when removing some of them. The weighting of the correlation was based on the predicted percentages of prey type. WW= log _e wet weight of consumer fish.	77
Table 3.4 (Table 1S Supplement 4) Prey type percentage of proportions correct and mean number of fish used in the model for different cut-offs for the whole dataset. Proportions correct were estimated as the overlap between the predicted and observed data for each prey type.....	84
Table 3.5 (Table 2S Supplement 4) Percentage correct of the prey type for a random selection of individuals per species. Shown are the number of species and number of fish used in the model to estimate the percentage of the prey type correct. The percentage correct was estimated as the overlap between the percentage of each prey type and the observed prey. The optimum number of fish per species was 12 with an average of 77% correct predicted prey types.	85
Table 3.6 (Table 3S Supplement 4) ANOVA results for the predictors for mean prey size for the full dataset. Asterisks denote statistically significant differences (***) = p<0.001). WW= log _e wet weight of consumer fish.	86
Table 3.7 (Table 4S Supplement 4) ANOVA results for the predictors for mean prey size for the subset of 12 individuals per species. Asterisks denote statistically	

significant differences (**=p<0.01; *** = p<0.001). WW= log_e wet weight of consumer fish.....87

Table 3.8 (Table 5S Supplement 4) Number of fish surveyed with gut contents in Western Port. Average wet weight (WW) in grams, maximum WW and minimum WW are shown for each species. The average percentage consumed of each prey type by each fish species is shown. Prey abbreviations are: a=algae, oe=other epifauna, ce=crustacean epifauna, ci=crustaceans infauna, s=sponges, me=mollusc epifauna, pi=polychaetes infauna, pe=polychaetes epifauna, f=fish, and mi=mollusc infauna.....88

Table 4.1 Accuracy (%) for predicted prey type of fishes at all sampled locations in southern Australia, including Western Port (WW= log_e wet weight of consumer fish). 101

Table 4.2 Accuracy (%) for predicted prey type of fishes in southern Australian locations except Western Port, using model trained only with Western Port data (WW= log_e wet weight of consumer fish). 102

Table 4.3 Correlations between observed and predicted mean prey size of fishes in southern Australia including Western Port, and change in accuracy when predictors removed (WW= log_e wet weight of consumer fish). 103

Table 4.4 Correlations between observed and predicted mean prey size of fishes in southern Australia (Western Port excluded), using only Western Port dataset for model training, and change in accuracy when predictors removed (WW= log_e wet weight of consumer fish)..... 105

Table 4.5 Correlation between the predicted and the observed standard deviations in dietary items for all of southern Australia, Western Port included (WW= log _e wet weight of consumer fish).	107
Table 4.6 (Table 1S) Number of fish sampled at each site included in this study. Also shown are the sites for each ecoregion and province (Spalding et al. 2007).	114
Table 4.7 (Table 2S) ANOVA results for the predictors for mean prey size for 12 individuals per species with a wide range of size for all sites included. Asterisks denote statistically significant differences (***) = p<0.001). WW= log wet weight of consumer fish.....	117
Table 5.1 Sources of diet information and number of fish included in the model as prediction data set. Level of information was based on the type on information available. Prey type was expressed as percentage of diet.....	127
Table 5.2 Comparison of community consumption estimates from <i>Consume</i> with those derived from trophic group model, with results expressed as percent ratio increase for no-take MPAs/fished areas and for one unit increase in the population index. Means of the biomass change of trophic groups and total means were calculated as the geometric mean of the ratios and converted to percentage change. <i>N.S.</i> = no significant difference. <i>S</i> = Small; <i>M</i> =Medium; <i>L</i> =Large.	131

Chapter 1

GENERAL INTRODUCTION AND THESIS STRUCTURE

Marine protected areas (MPAs) as no-take zones, amongst other uses, offer a set of experimental sites where field observations of the effect of anthropogenic impact can be assessed. Effective MPAs also offer a reference of near pristine ecosystems for contrast with places with high human impact (Willis & Millar 2005). As part of this thesis I wanted to test a widely predicted ecological consequence of fishing; that trophic reorganization occurs as a result of reduced top-down control of large fishes populations depressed by fishing. Based on this prediction, large carnivore species that are excessively targeted by fishers should increase in abundance and size in no-take MPAs. The increment of large predatory fishes population would increase predation pressure, cascading through the food web and variably affecting smaller fish (Sala et al. 1998, Steneck 1998, Graham et al. 2003, Micheli et al. 2004).

Community ecology traditional approach considers species as the central unit within an ecosystem, with similar roles amongst individuals. Nevertheless, the diet of most species suffers profound changes through their ontogenetic development, and body size and prey size can both increase several orders of magnitude (Cushing 1975, Rudolf & Rasmussen 2013). Species role in the ecosystem through their life history should be regarded as flexible, changing with body size, and thus providing a fundamental reason to develop size-based analyses of food webs (Dickie et al. 1987, Jennings & Warr 2003, Blanchard et al. 2011, Zhang et al. 2014).

In this thesis, I first analyse fish community structure with an empirical global dataset. Fish community structure was investigated using the trophic group (i.e. dividing the fish into higher carnivores, benthic carnivores, planktivores and herbivores) approach, evaluating how anthropogenic and environmental factors affected the fish biomass distribution within each fish assembly associated with a given site. However, I also wanted to assess the trophic group perspective using a novel approach by classifying the fish assemblages using diet predictions based on taxonomy and size of the predator fish. To do so, in my second data chapter, I developed a predictive diet model using a comprehensive dataset for fish and fish diet from Western Port, Australia. These diet predictions can be aggregated to estimate community level consumption. In my third data chapter, I expanded the predictive diet model to a continental scale and tested the accuracy of the predictions using a different dataset for training the model. Finally, using the predictive diet model I estimated the prey size, prey type and fish daily consumption for 376 reef sites surveyed by divers in southeastern Australia (Tasmania, Victoria and South Australia). Additionally, I tested how MPAs as no-take zones and different environmental and anthropogenic factors affected daily consumption by fishes for each prey type and size. I compared these results on daily fish consumption with the more traditional approach of assessing the fish community based on trophic group categorisation. The predictive diet model adds a new method to the trophic ecology toolbox, offering a novel perspective on food web studies.

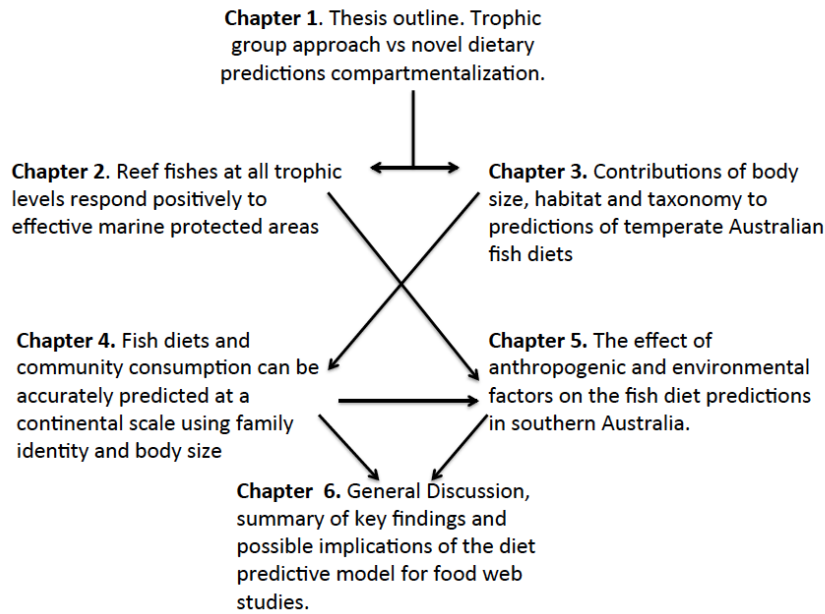


Figure 1.1 Thesis outline

All chapters were led, analysed and written by myself, with support from supervisors. All four analytical chapters have been submitted to journals with supervisors as secondary co-authors. In Chapter 2 I explored aspects of fish community structure suggested by Lotka-Volterra theory, which predicts that an increase in the abundance of predators will, over time, reduce the density of their prey. In the marine environment, recovery of fishery-targeted predators has been shown to affect invertebrate grazers in many different environments, leading in some cases to trophic cascades that alter habitat structure. In Chapter 2 I also assess whether the reinstatement of predator densities in effective no-take MPAs leads to reduction in fish species at lower trophic levels. I contrast this prediction with the possibility that fishers capture fishes at all trophic levels, with overall negative impact on abundances of small fishes, herbivores and invertivores, in addition to the large higher carnivores that have greatest commercial value.

I addressed this issue through analysis of the Reef Life Survey (RLS – www.reeflifesurvey.org) dataset, which is based on consistent field methods (Edgar &

Stuart-Smith 2014) applied across a global span of nearly 2,000 sites. This unprecedented survey effort under high quality and systematic methodology was achieved through joint efforts of professional biologists and citizen scientists. The latter were trained and tested to scientific standards prior to incorporation of their data into the main dataset. Data collected by trained volunteers has previously been tested against data produced by trained research scientists, with non-significant differences found; <1% of total spatial variation (Edgar & Stuart-Smith 2009).

The linkages between chapters 2, 3, 4 and 5 come into view when the anthropogenic and environmental effects found to affect the fish community structure, based on the trophic group analysis, in Chapter 2 are assessed from the fish community diet predictions perspective in Chapter 5. Hence the different apparent direction of chapter 2 when compared with chapters 3 and 4 is resolved when prey consumption of the fish community is evaluated in chapter 5 using methods developed in chapters 3 and 4, and outcomes compared with results of chapter 2.

In Chapter 3 and its associated paper, I provide a novel approach to food webs by developing models that predict the size and composition of dietary items consumed by individual fishes, and assess the accuracy of these models. The role of species in an ecosystem is best viewed as dynamic, changing with body size through the different life stages of an individual. Models that consider size of the predator fish as well as its prey can shed new light on food-web interactions and functions of a given fish community. In Chapter 3 I describe the full range of trophic interactions between the fish and their prey at Western Port, Australia, using a dataset on fish and fish diet contents collected by my supervisor (Edgar & Shaw 1995a, b). I estimate the diet of fishes using a dietary model based on *k*-nearest neighbour techniques to predict prey type, and linear models to predict prey size. The importance of these predictions is that they can then be aggregated at the

community level to provide general estimates of ecosystem-level fish consumption and food web transfers involving fishes. This aspect is further explored in Chapter 5.

The modelling approach outlined in Chapter 3 provides the foundation for a major advance in food web analysis, with individual animals as the basis of calculations rather than trophic categories. Studies that predict and give insight to trophic pathways represent important tools for ecology (Edgar & Shaw 1995c).

In Chapter 4 I scale up the predictive diet model developed in Western Port using a continental-scale dataset on fish size-distribution and prey composition compiled by my supervisor (Edgar & Shaw 1995c). For this Chapter I used the information collected by Edgar and Shaw (1995a, b, c) for shallow environments in southern Australia; extending over 3,000 km from Rottnest Island in Western Australia to Jervis Bay in New South Wales.

The relevance of these continental-scale predictions is that dietary data often do not exist at this scale, or at least not for the majority of species present in a fish community. Dietary predictions for individual animals, representative of fish across a community, will allow more accurate models of community consumption and food webs with which to answer key questions about the ecology of marine systems and human impacts and management interventions, as well as the effects of environmental variables. However, testing ecological predictions at a larger spatial scale is scientifically challenging due to spatial and temporal variation in the natural environment as well as logistical constraints (Peters 1991, Edgar & Shaw 1995c). The scaling up of the model was an essential step to predict the diet of fishes for the Reef Life Survey sites in southeastern Australia described in Chapter 5.

In Chapter 5 I scaled up the predictive dietary model further to estimate the prey type, prey size and daily prey consumptions for the fish communities present at 376 reef sites in southeastern Australia (Tasmania, Victoria and South Australia). At present, the

diversity of fishes of different body sizes at any location makes it next to impossible to integrate data from all the individuals present into community level patterns to assess the impact of fishing as well as other threats to food web processes.

One of the advantages of estimating prey consumption based on fish taxonomy and size is that each species does not have to be placed in a unique trophic compartment (e.g. benthic carnivores) but instead can be distributed in a continuum based on the prey type and prey size consumed. This approach differs from models such as Ecopath, Ecospace and Ecosim (Polovina 1984, Pauly et al. 2000b) since it does not require allocation of species to pre-conceived functional groups, which in many cases do not account for ontogenetic changes of species through their life history. A few trophic models have considered predatory fish size (i.e. biomass, gape size), with the assumption that size is the most important factor in the ecological system (Shin & Cury 2001, Brown & Gillooly 2003, West & Brown 2005, Fulton et al. 2011). Additionally, the dissimilarities in the diets of fish of the same species at different sizes have been pointed out by previous authors (Cushing 1975, Edgar & Shaw 1995b, Jennings et al. 2002b). The estimates for community prey consumption developed in Chapters 3 through 5 present a novel approach in ecology to assess material and energy fluxes through the food web as well as a useful tool to assess the environmental and anthropogenic factors affecting fish assemblages.

Chapter 2

REEF FISHES AT ALL TROPHIC LEVELS RESPOND POSITIVELY TO EFFECTIVE MARINE PROTECTED AREAS

Preface:

This work has been published in a refereed journal and is presented below in identical form. The citation for the original publication is:

Soler GA, Edgar GJ, Thomson RJ, Kininmonth S, Campbell SJ, Dawson TP, Barrett NS, Bernard ATF, Galvan DE, Willis TJ, Alexander TJA, Stuart-Smith RD (2015) Reef fishes at all trophic levels respond positively to effective marine protected areas. Plos One, e0140270.

2.1 Abstract

Marine Protected Areas (MPAs) offer a unique opportunity to test the assumption that fishing pressure affects some trophic groups more than others. Removal of larger predators through fishing is often suggested to have positive flow-on effects for some lower trophic groups, in which case protection from fishing should result in suppression of lower trophic groups as predator populations recover. We tested this by assessing differences in the trophic structure of reef fish communities associated with 79 MPAs and open-access sites worldwide, using a standardised quantitative dataset on reef fish community structure. The biomass of all major trophic groups (higher carnivores, benthic carnivores, planktivores and herbivores) was significantly greater (by 40% - 200%) in effective no-take MPAs relative to fished open-access areas. This effect was most pronounced for individuals in large size classes, but with no size class of any trophic group showing signs of depressed biomass in MPAs, as predicted from higher predator abundance. Thus, greater biomass in effective MPAs implies that exploitation on shallow rocky and coral reefs negatively affects biomass of all fish trophic groups and size classes. These direct effects of fishing on trophic structure appear stronger than any top down effects on lower trophic levels that would be imposed by intact predator populations. We propose that exploitation affects fish assemblages at all trophic levels, and that local ecosystem function is generally modified by fishing.

2.2 Keywords

Trophic cascades, marine reserves, effects of fishing, predator-prey relationships

2.3 Introduction

Marine protected area (MPA) networks represent an experimental set of ecological

plots with reduced human extraction pressure. As such, MPAs provide an ideal focus for improved understanding of broad-scale effects of protection through comparison of differences in fished and protected areas (Walters & Holling 1990). Effective MPAs also provide a reference benchmark as undisturbed ecosystems for comparison with sites with high human impact (Willis & Millar 2005). Nevertheless, many MPAs do not appear to be effectively achieving conservation goals (Jones 2002, Kingsland 2002, Ban et al. 2012, Edgar et al. 2014).

One widely predicted ecological consequence of fishing, which can be tested using MPAs, is that trophic reorganization occurs as a result of decreased top-down control from exploited populations of large fishes. According to this prediction, large predatory species that are disproportionately targeted by fishers should benefit more from MPAs than other groups, with effects of increased predation pressure cascading through the food web and variably affecting non-predatory species (Sala et al. 1998, Steneck 1998, Graham et al. 2003, Micheli et al. 2004).

An example where an MPA was used to examine fish community restructuring comes from northeastern New Zealand, where protection was found to reduce the density of some small cryptic fish species within reserves with higher abundance of predators relative to nearby open-access areas (Willis & Anderson 2003). Likewise, most prey species of the fishery-targeted coral trout (*Plectropomus* spp.) were less abundant in studied no-take zones in the Great Barrier Reef Marine Park that had high coral trout biomass (Graham et al. 2003). Reduced abundance and biomass of fish prey species within MPAs were also noted in a global meta-analysis (Micheli et al. 2004), indicative of possible indirect effects of competition or predation. On the other hand, a lack of prey abundance may limit predator growth (Hollowed et al. 2000) and abundance (Stewart & Jones 2001) demonstrating a bottom up effect on community structure. We hypothesized that a general control of top-down processes by fishing would result in a comparatively

low biomass of smaller size classes of lower trophic groups within effective MPAs, in which carnivore biomass was known to be high relative to fished areas.

While predatory fishes are most heavily exploited, fishers can also target species in lower trophic groups such as herbivores, which may lead to reduced grazing of macroalgae with negative effects on live coral cover (Edwards et al. 2014). In the Caribbean, for example, the abundance of large parrotfishes increased in MPAs, which resulted in a doubling of grazing pressure on macroalgae, a major competitor of coral (Mumby et al. 2006). Such examples highlight the complex trophic changes that can follow MPA establishment, and the potential importance of fish size as well as trophic level when assessing trophic responses to fishing and protection. Other factors, independent from direct trophic cascades, can also play a role in shaping the fish community trophic structure (Kellner et al. 2010); spatial variability in recruitment, competition, isolation and oceanographic conditions can all contribute to the variation in biomass of the different trophic groups (Jennings & Polunin 1997, Edgar et al. 2014).

We use a global-scale dataset obtained with consistent survey methodology to test the generality of divergence in food webs in MPAs in relation to open-access sites as an indication of the impacts of fishing on trophic structure. We address the following specific questions:

(1) Do different levels of MPA protection differentially affect the biomass of the four major fish trophic groups (higher carnivores, benthic carnivores, planktivores and herbivores)?

(2) Do patterns in fish biomass partitioning among trophic groups across the global MPA network support the trends in trophic restructuring observed in some individual MPAs? Specifically, is there a general trend for reduced biomass of non-target species in effective MPAs where predator biomass is greater?

2.4 Materials and Methods

Marine ecological survey data were collected worldwide through the Reef Life Survey program (RLS: www.reeflifesurvey.org) from September 2006 until November 2012 (see Edgar and Stuart-Smith (2014) for details). The following authorities gave permission for field studies: Australia Department of Environment, Costa Rica Sistema Nacional de Areas de Conservacion, Galapagos National Parks Service, NSW Department of Primary Industries, New Zealand Department of Conservation, Panama Autoridad Nacional del Ambiente, Parks Victoria, Parques Nacionales Naturales de Colombia, Rottnest Island Authority, South Australia Department of Environment Water and Natural Resources, Tasmania Parks and Wildlife Service, United States Fish and Wildlife Service, United States National Park Service, Western Australia Department of Parks and Wildlife. Data covered 1,844 rocky and coral reef sites in 11 realms and 74 ecoregions (Spalding et al. 2007) (Fig. 2.1). The level of protection from fishing of each site was classed as no-take (no fishing allowed), restricted fishing (some form of fishery restrictions in place), or open-access. The ecological effectiveness of MPAs also depends on compliance with regulations and time since declaration (Edgar et al. 2014). Here we considered no-take zones to be effective if they exhibited a medium to high level of enforcement and had been established for at least five years prior to the fish survey (S1 Table). MPAs at which limited fishing was allowed, where enforcement of regulations was poor, and/or less than five years had elapsed since creation were considered less effective. Sites were assessed for effective protection using information on zoning in management plans, patrolling capacity, and infractions observed while in the field undertaking surveys, as described in Edgar et al. (2014). Open-access sites lay outside MPAs, or inside MPAs in zones with no restrictions on fishing other than national

REEF FISHES AT ALL TROPHIC LEVELS RESPOND POSITIVELY TO EFFECTIVE MARINE PROTECTED AREAS

regulations (e.g. no explosives). A total of 79 MPAs were investigated, including some with multiple zones of differing effectiveness. A total of 405 sites within 50 MPAs were classified as effective no-take areas, 509 sites within 54 MPA were classified as low effectiveness, and 930 sites were open-access.

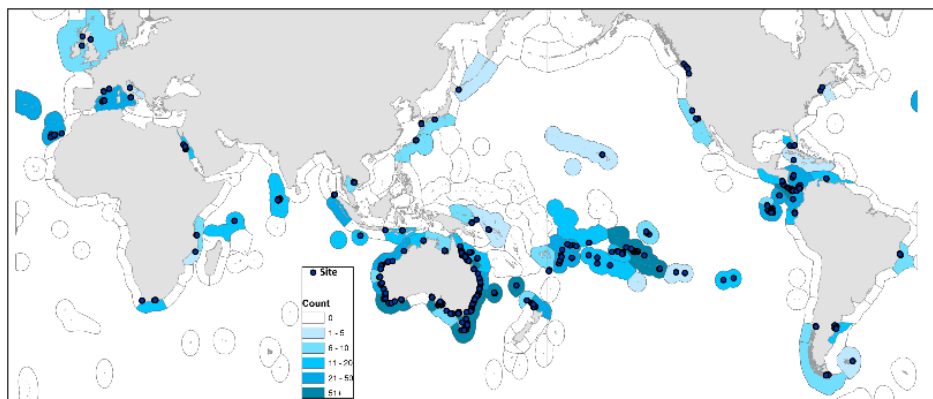


Figure 2.1. Global map showing sites investigated. The density of fill color applied to each marine ecoregion (Spalding et al. 2007) relates to the number of sites surveyed within it.

Fish species, abundance and size classes were surveyed using methods described in Edgar and Stuart-Smith (2014). In summary, divers laid a 50 m transect line and surveyed fishes within duplicate 5 m strips either side of the line (total area surveyed = 500 m²). All fish species present in each survey were identified, and their abundances and sizes estimated. Fish lengths were allocated into 2.5 cm bins to 15 cm, 5 cm bins between 15 and 40 cm, and to 12.5 cm bins for fish larger than 50 cm. Fish biomass was estimated using the abundance and sizes of fishes on transects and species-specific length-weight relationships provided in Fishbase. When length-weight relationships were unknown for a species, values were taken from a similarly-shaped relative. Fish surveys under the RLS program were conducted by both professional scientists and trained volunteer divers. Prior assessment of data quality showed no significant difference between these two

groups (Edgar & Stuart-Smith 2009). Training of volunteer divers and data quality control processes are outlined in Edgar and Stuart-Smith (2014).

For data analyses, fishes were divided into four major trophic groups: higher carnivores, benthic carnivores, planktivores and herbivores, based on dietary information obtained from Fishbase (www.fishbase.org). If insufficient information was available for a particular species, the closest relative was used as a proxy. Higher carnivores were those fishes with diets primarily composed of other fishes, decapods and cephalopods. Benthic carnivores fed predominantly on invertebrate fauna, most commonly peracarid crustaceans, molluscs, polychaetes, sponges or corals. Herbivorous species included all fishes for which algal food sources formed a major part of the diet. This group included detritivorous and omnivorous species, as well as scraping and excavating parrotfishes. It thereby covered a diverse range of more specialized trophic groups and functional roles (Bellwood et al. 2006).

Regardless of trophic level, larger fishes are less likely to be negatively affected through predation by large carnivores. Thus, trophic groups were also sub-categorized into three size classes: small (<7.5 cm), medium (7.5 – 30 cm) and large (>30 cm), depending on the observed size of fishes during the surveys.

2.4.1 Statistical analysis

Linear Mixed Models (LMMs) were applied using all sites within an ecoregion to compare the effect of protection, adjusting for five important environmental and anthropogenic covariates. These covariates represented factors found to influence the spatial patterns of biomass in prior analyses (Stuart-Smith et al. 2013, Edgar et al. 2014). Environmental data, including annual mean sea surface temperature (SST), SST range and photosynthetically-active radiation (PAR-mean), were extracted from Bio-Oracle (Tyberghein et al. 2012) (S2 Table). PAR-mean was calculated by averaging daily PAR

for each month and then across the year (Tyberghein et al. 2012). A human population index (Pop index) was calculated by fitting a smoothly tapered surface to each settlement point created with the glp00g gridded world population density dataset (<http://sedac.ciesin.columbia.edu/data/collection/gpw-v3/sets/browse>). The quadratic Kernel function was applied, as described in Silverman (1986). Populations were screened to only include populations with density greater than 1000 people per 0.04° cell. The values did not directly represent the population values since they were both modelled (quadratic) and smoothed. However, these values provide a comparative index of population density/pressure.

Of ten environmental and anthropogenic covariates examined (S2 Table), SST mean, SST range, PAR-mean and the population index had the greatest influences on the biomass of the four trophic groups (Fig. 2.2). Consequently, analyses of MPA effects first accounted for these four factors, plus the random effects of site nested hierarchically within ecoregion (Spalding et al. 2007), which in turn was nested within realm.

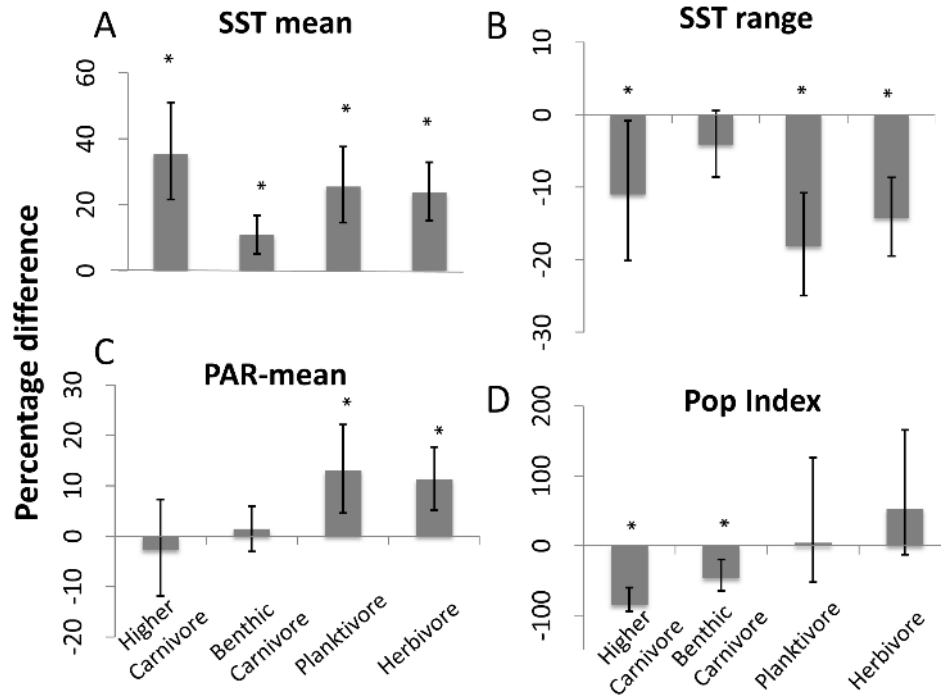


Figure 2.2. Percentage difference in biomass (\pm 95% confidence intervals) for covariates investigated. Percentage difference in biomass per 1°C change in mean sea surface temperature (A), 1°C change in the annual range in sea surface temperature (B), 1 Einstein/m²/day change in annual mean photosynthetically-active radiation (C), and a single unit increase in the index of local population density (D) for each of the four trophic groups. Ratios were obtained from the β coefficients and transformed into % increment in biomass, by $100 \cdot (\exp(\beta) - 1)$. Asterisks denote statistically significant difference ($p < 0.05$).

The effect of MPA protection on the different trophic groups was assessed using LMMs, with MPA protection introduced after the influences of other variables (SST mean, SST range, PAR, Pop index) were considered in models. This allows us to test the influence of protection while considering other factors, which affected the observed biomass of the different trophic groups. This same model was also applied to test for differences in biomass of the size classes of different trophic groups:

$$y_{rei} = \mu + \beta_1 \text{SSTmean}_i + \beta_2 \text{SSTrange}_i + \beta_3 \text{PARmean}_i + \beta_4 \text{POPindex}_i \\ + \beta_5 \text{Protection}_i + \delta_r + \gamma_{re} + \varepsilon_{rei}$$

(Equation 1)

where $y_{rei} = \log(\text{total biomass of fishes} + 100, \text{ in g})$ at the i th site, given the effects of SST mean, SST range, PAR-mean and human population, conducted in the Ecoregion e and Realm r ; μ = overall mean; $\beta_{1,2,3,4,5}$ = effect of SST mean (1), SST range (2), PAR mean (3) and Pop index (4) and Protection (5) on the mean; δ_r = effect of the r th realm; γ_{re} = effect of the e th ecoregion within the r th realm (both realm and ecoregion are random effects); ε_{rei} = residual error. Due to the absence of some trophic groups in some sites surveyed, we added a constant (= 100) to all raw fish biomass $[\ln(y+100)]$. Given that biomass was scaled in grams, the addition of 100 g to the transect was chosen as a reasonable ecological value for the step between no biomass and minimum observed biomass (Ortiz et al. 2000). A 4th root transformation of biomass was also tested, and provided similar outcomes as the log transformation. Results from the log transformation are presented here so that the effect size can be presented as % difference in biomass.

Effects of the two effectiveness categories of MPAs relative to open-access areas were estimated within LMMs by estimating the log ratios of biomass ($\log(\text{biomassMPA}/\text{biomassOPEN})$). These were obtained from the coefficient for Protection, β_5 and were transformed into % increment in biomass, by $100 * (\exp(\beta_5) - 1)$. P-values generated were based on the Wald statistic. Likelihood ratio tests (LRT) were also applied; nevertheless, due to the very large sample size, conclusions were the same as with the LMMs, so LRT results are not additionally presented here.

Numerous ecoregions did not have sites within both MPAs and open-access areas. Consequently, additional LMMs were constructed with a subset that included the reduced set of 35 ecoregions that contained representatives of two zone types (protected areas vs open-access zones). Similar results were found with this subset of the data compared with

the results obtained using the whole data set; therefore, results presented were based on the complete data set.

All statistical analyses were performed in R-Studio using the package nlme (R-Core-Team 2014). The map was also created using R (R-Core-Team 2014).

2.5 Results

The population index was used as a proxy for human pressure, and had a significant negative effect on biomass of higher and benthic carnivores (Fig. 2.2). The three environmental covariates, SST mean, SST range and PAR-mean, also had significant effects on fish biomass. However, only SST mean was significant for all four trophic groups (Fig. 2.2). PAR-mean had a significant positive effect for biomass of planktivores and herbivores. SST range had a significant negative effect on biomass of higher carnivores, planktivores and herbivores (Fig. 2.2).

Protection from fishing clearly affected reef fish community structure. All trophic groups possessed significantly higher biomass in effective MPAs compared to open-access areas (Fig. 2.3). The biomass of higher carnivores, herbivores and planktivores were also significantly higher in less effective MPAs compared to open-access areas (Fig. 2.3), and differences between effective MPAs and less effective MPAs were only non-significant for planktivores.

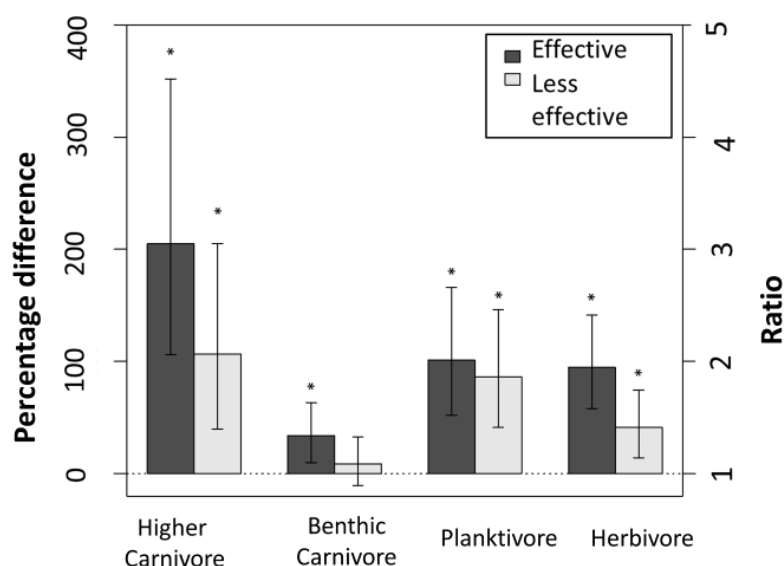


Figure 2.3. Percentage difference in biomass of different trophic groups in protected areas relative to open-access zones. Log ratios of biomass ($\log(\text{biomassMPA}/\text{biomassOPEN})$) between effective and less effective MPAs relative to open-access zones, for each trophic group (\pm 95% confidence intervals). Ratios were obtained from the coefficient for Protection, β_5 , in equation 1 and transformed into percentage increments in biomass, by $100 \cdot (\exp(\beta_5) - 1)$. Asterisks denote a statistically significant difference ($p < 0.05$). The model also adjusted for SST mean, SST range, PAR-mean and human population.

Differences in fish biomass between effective MPAs and open-access areas were remarkably consistent for different fish size classes and trophic groups between tropical and temperate realms (Fig. 2.4). Biomass of large fishes (maximum length >30 cm) was significantly higher than in open-access areas for all four trophic groups, in both tropical and temperate zones. Biomass of medium-sized fishes (7.5 - 30 cm) in effective MPAs was also higher for most of the trophic groups in the tropics and temperate regions, with the exception of medium-sized benthic carnivores in temperate zones and medium-sized herbivores in the tropics. For the small size classes (<7.5 cm), planktivores were recorded in significant higher biomass in effective MPAs in the tropics. Small higher carnivores and planktivores exhibited significant higher biomass in effective temperate MPAs (Fig.

2.4). Although some groups exhibited similar biomass across MPAs and open-access areas, no size classes of any trophic group had significantly lower biomass in effective MPAs relative to open access areas.

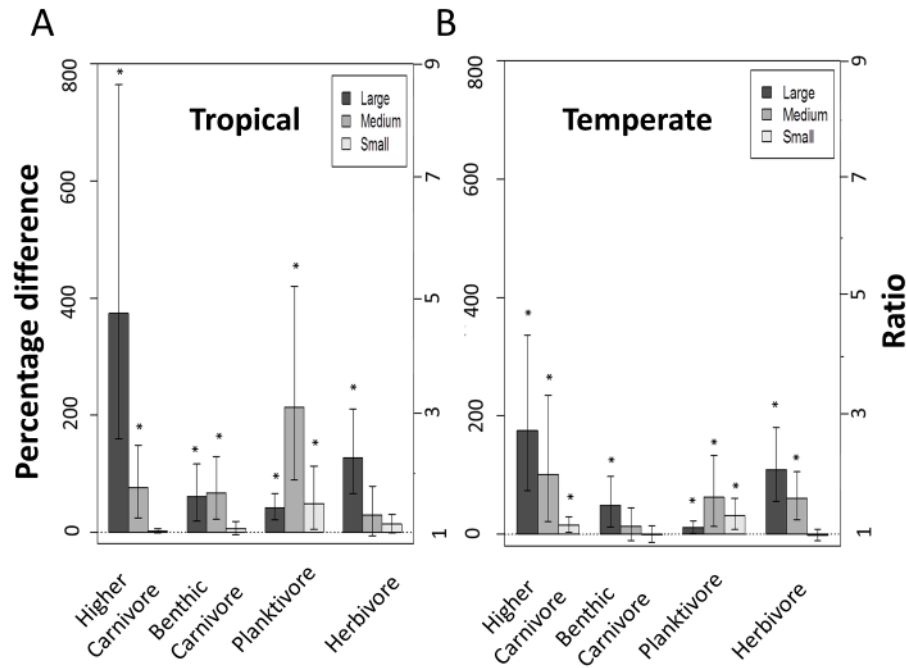


Figure 2.4. Percentage difference in biomass of the different trophic groups size categories in temperate and tropical areas. Log ratios of fish biomass ($\log(\text{biomassMPA}/\text{biomassOPEN})$) between trophic and body size groups in effective MPAs in temperate (A) and tropical (B) regions, relative to open access zones ($\pm 95\%$ confidence intervals). Small fishes <7.5 cm; medium fishes from 7.5 to 30 cm; large fishes >30 cm. Ratios were obtained from the coefficient for Protection, β_5 , and transformed into percentage increments in biomass, by $100 \cdot (\exp(\beta_5) - 1)$. Asterisks denote a statistically significant difference ($p < 0.05$). The model also adjusted for SST mean, SST range, PAR-mean and human population.

2.6 Discussion

Our results show clear differences in fish community structure due to protection from fishing in effective MPAs (i.e. no-take, with medium to high enforcement and over

5 years old). Higher biomass of large predatory species was particularly marked, while the biomass of all other trophic groups was either greater or equal in effective MPAs compared with open-access sites. Thus, none of the trophic or size groups had negative biomass ratios in MPAs compared with open-access sites that would indicate patterns for top-down control of the fish community in the presence of greater biomass of predatory fishes. This result was consistent even when considering only the MPAs identified as most effective and having the five attributes of protection outlined in Edgar et al. (2014) and known to have elevated biomass of the major groups of predatory and exploited species. This does not imply that cascading trophic interactions have not occurred in effective MPAs, as our study did not look at individual species, but rather at the scale of whole trophic size groups. However it does present two clear, novel outcomes with respect to general MPA effects: (1) that protection from fishing appears to favor all trophic groups, some much more than might be expected (e.g. medium-sized planktivores); and (2) that regardless of whether cascading trophic interactions occur within MPAs, the disparity in the biomass ratios between MPAs and open access sites for the different size-classes of trophic groups implies a trophic re-organisation that is likely to have substantial consequences for ecological functions.

2.6.1 Higher biomass in all trophic groups

Our findings are also in accordance with previous studies (Halpern 2003, Micheli et al. 2004) that show higher fish biomass in effective MPAs (Pauly et al. 2000a). As predicted, the greatest difference involved large higher carnivores. However, none of the trophic groups showed lower biomass in MPAs in relation to open-access sites, implying that impacts of exploitation across marine food webs may often be underestimated.

Preferential targeting of large herbivorous species has been well documented in many tropical regions (Mumby et al. 2006, Edwards et al. 2014), and is opposite to the

effect of the fishing down the food web (Pauly et al. 2000a). We suggest that while large-scale commercial fisheries, which operate in deep and pelagic offshore waters, may often first remove higher trophic level species, exploitation of reef species from shallow, coastal waters, including artisanal fisheries and recreational anglers, is less trophically-selective. If correct, then caution is needed when applying the widely used Marine Trophic Index (Pauly & Watson 2005) as an indicator for fishing impacts in shallow reef habitats. A highly consistent response among larger size classes of all trophic groups supports hypotheses that fishing impacts are more size-based than focused on particular trophic groups.

Despite the apparently greater importance of size than trophic group, differences of biomass between effective MPAs and open-access sites were unequal across trophic groups. The biomass difference was greatest for large higher and benthic carnivores in general, with a more pronounced difference in effective MPAs. The simplest explanation is that fishing has had the greatest impact on these groups outside effective MPAs. This is supported by a significantly lower biomass of carnivorous fishes in locations with highest human population density (Fig. 2.2). Nevertheless, at least two other mechanisms associated with protection could also potentially lead to this result: (1) biomass recovery may be faster for large carnivorous fishes, and (2) predation pressure by large higher carnivores and benthic carnivores may limit potential increases in biomass of other groups, rather than reducing their biomass.

The first of these two alternative explanations is plausible, given that individual growth is generally rapid in piscivorous fishes, and that many of the effective MPAs studied were still young relative to the time required for growth of individual fishes. Only 40% of effective MPAs investigated were more than 10 years old, and thus much of the recorded differences in biomass is likely to be associated with direct recovery of fished

species (Edgar et al. 2009, Babcock et al. 2010).

A short time frame also supports the second alternative explanation, in that predator biomass is still likely increasing and may not yet have reached the point where prey biomass suppression is evident. Furthermore, top down control may never manifest if the impact of fishing on smaller sizes and/or lower trophic groups is greater than predation pressure from large predatory fishes alone. Thus, in some cases the top-down pressure from humans may be of much greater magnitude than that exerted by predatory fishes in completely unexploited communities.

Our results likely represent a combination of the two potential mechanisms described above, with additional complexity added by recruitment, competition, oceanographic conditions, isolation, predation from higher vertebrates and invertebrates, and habitat structure. With respect to habitat structure, we conducted additional analyses using a subset of sites (482) for which we had data on the structure of the reef, scored using an index of vertical relief (S1 Appendix). Higher relief index values were associated with elevated biomass of higher carnivores, benthic carnivores and planktivores (S1 Fig.), confirming the importance of structural complexity in supporting greater fish biomass in general (Rogers et al. 2014). After accounting for complexity in this subset of sites, the effect of protection remained consistent with those from analysis of the full dataset (S2 Fig.). Thus, both protection and relief have significant effects on the biomass of fish independently, but our conclusions relating to MPA effects are unlikely confounded by habitat complexity.

Another potential source of bias is that faster moving fish are typically oversampled in underwater visual censuses (Ward-Paige et al. 2010). This should not affect conclusions if the bias is systematic between fished and unfished locations, but if

behavioural patterns change in MPAs, with attraction to divers, then the magnitude of difference between fished and unfished locations for large carnivores will be overstated.

When differences in fish biomass between MPAs and open-access sites across the various size and trophic groups are considered together, our data suggest that protected reef fish communities probably function quite differently to those in fished locations. As shown in Fig. 2.4, larger carnivorous fishes are present in proportionally greater biomass in effective MPAs compared to open-access sites, and this is likely to have important ecological implications. For example, a substantial shift to larger herbivores may increase resilience in coral reef locations (Hughes et al. 2007), while recovery of large predators in a temperate MPA has been hypothesized to contribute to ecosystem resistance to tropicalisation (Bates et al. 2014).

2.6.2 Other drivers of reef fish trophic structure

SST mean was positively related to the biomass of the four trophic groups, which aligns with the latitudinal gradient in total fish biomass (Gaston 2000, Hillebrand 2004). Furthermore, SST range was negatively related to the biomass of three of the trophic groups. High variation in SST throughout the year is typical of high latitudes and sheltered embayments (Edgar & Shaw 1995a, c). Interestingly, benthic carnivores were least affected by extreme seasonality, possibly reflecting greater stability in food sources in such areas, or possibly more varied generalist behavioral and feeding strategies within this very broad group of fishes. Biomass of planktivores and herbivores showed a significant positive relationship with PAR-mean, as would be expected based on increased productivity of benthic algal and phytoplankton-driven food sources (Kelble et al. 2005).

A trend for decreasing fish biomass with increasing human population density is an

increasingly common finding of broad-scale studies (Jennings & Polunin 1997, Barrett et al. 2007, Babcock et al. 2010, Mora et al. 2011, Edgar et al. 2014). Our results expand on prior results by suggesting a greater negative impact on carnivorous species than herbivores or planktivores when examined at the global level. This result, and the substantial variability in the effect of human population density on herbivorous and planktivorous species, likely reflects stronger regional inconsistencies in exploitation of these two groups, as well as patchy impacts associated with habitat degradation near population centers. Other factors that potentially contributed to observed results, but were not considered in this study, include the possible increase in other predators such as seals (Kelaher et al. 2015) and lobsters (Babcock et al. 2010) in effective MPAs.

In conclusion, effective MPAs provide protection for multiple components of food webs, not just larger carnivorous fishes. General trends of top-down control by larger predator fish on smaller fish were less pronounced in our global analysis than prior reports for particular species at some individual MPAs. Elevated biomass of particular trophic and size groups will inevitably result in variability of local ecological processes. Human impacts on reef fish community structure were inferred to be stronger than top-down control by the larger predatory species when considered at the global scale; however, more time is needed for fish communities within the global MPA network to re-organize to the point where indirect trophic effects of fishing are strongly defined.

2.7 Acknowledgments

We thank the many Reef Life Survey (RLS) divers who collected the data. We are grateful to the many park officers and colleagues who assisted the study by providing permits and assisting with field activities, and to numerous marine institutions worldwide for hosting survey trips. We also thank Carolina Garcia Imhof for support and revision of

REEF FISHES AT ALL TROPHIC LEVELS RESPOND POSITIVELY TO EFFECTIVE
MARINE PROTECTED AREAS

this manuscript.

2.8 Supporting Information

Table 2.1. (S1 Table). Marine Protected Areas (MPAs) level of effectiveness and number of sites. Some MAPs had sites that differed in level of effectiveness.

Name MPA	Effective	Less effective	No. of sites
APA Ponta da Baleia-Abrolhos	6	4	10
Baie Ternay	2		2
Batemans Marine Park	6	50	56
Beacon Island Reef Observation Area	1	2	3
Beware Reef Marine Sanctuary	8	2	10
Bonaire		14	14
Bronte-Coogee Aquatic Reserve		3	3
Bushrangers Bay Aquatic Reserve	1		1
Cabbage Tree Bay Aquatic Reserve	3	1	4
Caletas		3	3
Camaronal		3	3
Cape Banks Aquatic Reserve		2	2
Cape Byron Marine Park		3	3
Cape Howe Marine National Park	4	5	9
Cape Rodney Okakari Point Marine Reserve	4		4
Channel Islands National Marine Sanctuary	6	7	13
Cocos National Park	23		23
Coiba National Park	26	22	48
Coral Patches Reef Observation Area	2		2
Coringa-Herald Nature Reserve		10	10
Fiordo Comau Marine and Coastal Protected Area		4	4
Florida Keys National Marine Sanctuary	12	5	17
Fly Point-Halifax Park	4	3	7
Galapagos Marine Reserve	42	27	69
Golfo de Chiriqui Marine National Park		4	4
Governor Island Marine Nature Reserve	1	4	5
Great Barrier Reef MP	43	28	71
Hanauma Bay Marine Life Conservation District	2		2
Illa del Toro		1	1
Isla de Taboga e Isla de Uraba Wildlife Refuge		3	3

REEF FISHES AT ALL TROPHIC LEVELS RESPOND POSITIVELY TO EFFECTIVE

MARINE PROTECTED AREAS

Name MPA	Effective	Less effective	No. of sites
Jawbone Marine Sanctuary		2	2
Jervis Bay	15	39	54
Jurien Bay	2	4	6
Kawasan Wisata		17	17
La Reserve Naturelle Marine de Cerbere Banyuls	4	6	10
La Restinga-Mar de las Calmas MPA	3		3
Las Perlas Marine Special Management Zone		25	25
Leo Island Reef Observation Area	1		1
Levante de Mallorca Cala Ratjada		1	1
Lord Howe Island Marine Park	26	25	51
Machalilla		13	13
Malpelo Flora and Fauna Sanctuary	11		11
Maria Island Marine Reserve	4		4
Marmion Marine Park	1	3	4
Mnazi Bay-Ruvuma Estuary Marine Park		1	1
Motu Motiro Hiva		8	8
Mushi Mas Mingili Thila	1		1
Ninepin Point Nature Marine Reserve		2	2
Ningaloo Marine Park	13	22	35
North Sydney Harbour Aquatic Reserve		14	14
Pangaimotu Reef MPA	1		1
Panglima Laut		4	4
Point Cooke Marine Sanctuary		1	1
Point Lobos State Marine Reserve		1	1
Poor Knights Island Marine Reserve	16		16
Port Davey Marine Reserve	3		3
Port Noarlunga Reef	1		1
Port Phillip Heads Marine National Park	22	10	32
Port Stephens Great Lake Marine Park	3	41	44
Regno di Nettuno		8	8
Rickett's Point Marine Sanctuary	2		2
Rottnest Island	3	20	23
Seaflower Area Marina Protegida		15	15
Sesoko Scientific Research Area	1		1
Shiprock Aquatic Reserve	1		1
Shiraiwazaki Marine Park	1		1
Solitary Islands Marine Park	16	6	22
St. Abbs and Eyemouth Voluntary Marine Reserve		6	6
Strangford Lough Marine Nature Reserve		5	5

REEF FISHES AT ALL TROPHIC LEVELS RESPOND POSITIVELY TO EFFECTIVE

MARINE PROTECTED AREAS

Name MPA	Effective	Less effective	No. of sites
Sund Rock Marine Preserve	1		1
Table Mountain National Park	4	2	6
Tawharanui Marine Reserve	3		3
Tinderbox Marine Reserve	5	2	7
Tsitsikamma National Park	3		3
Tulamben	3		3
Ushibuka Marine Park	1		1
Wadi El Gemal - Hamata Reserve		5	5

Table 2.2. (S2 Table). Covariates used as predictors in linear mixed models. PAR-mean, Nitrate, Phosphate, Silicate, Chlomean, SST range and SST mean were obtained from Bio-ORACLE (Tyberghein et al. 2012). Pop index was calculated using the quadratic kernel function described by (Silverman 1986).

Code	Variable	Units	Scale	Range
Pop index	Index of population pressure	index	4.6 km	0 - 1
PAR-mean	Photosynthetically-available radiation	Einstein /m ² /day	9.2 km	26.3 - 50.9
SST mean	mean sea surface temperature	°C	9.2 km	5.35 - 31.09
SST range	Range of sea surface temperature	°C	9.2 km	0.96 - 17.93
Nitrate	Mean nitrate	umol/l	9.2 km	0.14 - 15.31
Phosphate	Mean phosphate	umol/l	9.2 km	0.02 - 2.26
Silicate	Mean silicate	umol/l	9.2 km	0.31 - 37.9
Chlomean	Mean chlorophyll A	mg/m ³	9.2 km	0.02 - 15.99
Latitude	Site latitude	decimal degrees	0.0001°	-55.1 - 78.5
Longitude	Site longitude	decimal degrees	0.0001°	-179 - 175

S1 Appendix

Assessment of potential confounding of MPA effects by variation in habitat complexity

A relief index, a proxy for habitat complexity, was included as an extra covariate for the subset of 482 sites for which this information was available. The relief index was based on the size of boulders, crevices and general variation in reef height within the area surveyed. The relief index ranged from one to four, and was subjectively scored for the 482 sites by two of the authors during fish surveys. A score of one was given when the substrate was relatively flat (<0.5 m elevation), with few hiding places suitable for fishes, while a score of four indicated high complexity in the structure (i.e. large boulders and deep crevices) varying by >2 m in vertical height. The sites with relief information were located both in MPAs (239 sites) and open-access sites (243).

In our main analyses, the effect of MPA protection on the different trophic groups was assessed using Linear Mixed Models (LMMs), with MPA protection introduced after the influences of other variables (SST mean, SST range, PAR, Population index) were considered in the models. To test for the effect of complexity on our MPA effects, and therefore whether our major conclusions could be confounded by unaccounted for effects of complexity, we included relief as a fifth factor in LMMs for the subset of 482 sites. The model used is explained below:

$$y_{rei} = \mu + \beta_1 \text{SSTmean}_i + \beta_2 \text{SSTrange}_i + \beta_3 \text{PARmean}_i + \beta_4 \text{POPindex}_i + \beta_5 \text{Relief}_i + \beta_6 \text{Protection}_i + \delta_r + \gamma_{re} + \varepsilon_{rei}$$

where y_{rei} = log (biomass of fish + 100) at the i th site, given the effects of SST mean, SST range, PAR-mean, human population and Relief, conducted in the Ecoregion e and Realm r ; μ = overall mean; $\beta_{1,2,3,4,5,6}$ = effect of SST mean (1), SST range (2), PAR

mean (3) and Pop index (4), Relief (5) and Protection (6) ; δ_r = effect of the r th realm; γ_{re} = effect of the e th ecoregion within the r th realm (both realm and ecoregion are random effects); ε_{rei} = residual error.

The relief index had a positive effect on biomass of higher carnivores, benthic carnivores and planktivores at the subset of 482 sites (S1 Fig.). The difference in biomass due to the increase of one unit of relief (range from 1-4) was obtained from the coefficient for Relief, β_5 , from the LMMs and transformed into % increment in biomass, by $100 * (\exp(\beta_5) - 1)$.

Thus, both relief and protection were independently related to higher biomass of all trophic groups. The magnitudes of the effect of protection were similar after adjusting for relief, with the effect of protection remaining positive for all trophic groups (S2 Fig.).

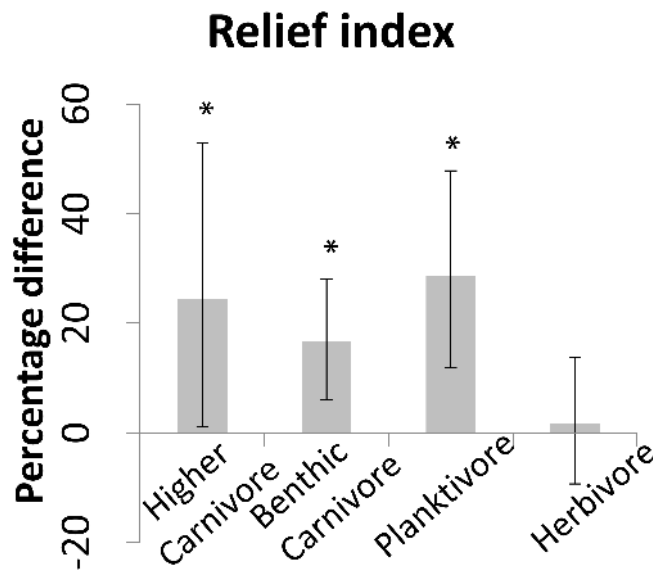


Figure 2.5. (S1 Fig) Percentage difference in biomass (\pm 95% confidence intervals) for relief index. Percentage difference in biomass for 1 unit increase in the relief index (range 1-4) for each of the four trophic groups. The ratios were obtained from the coefficient for Relief, β_5 , from the LMM equation (S1 Appendix) and transformed into percentage increments in biomass, by $100 * (\exp(\beta_5) - 1)$. Asterisks denote a statistically significant difference ($p < 0.05$).

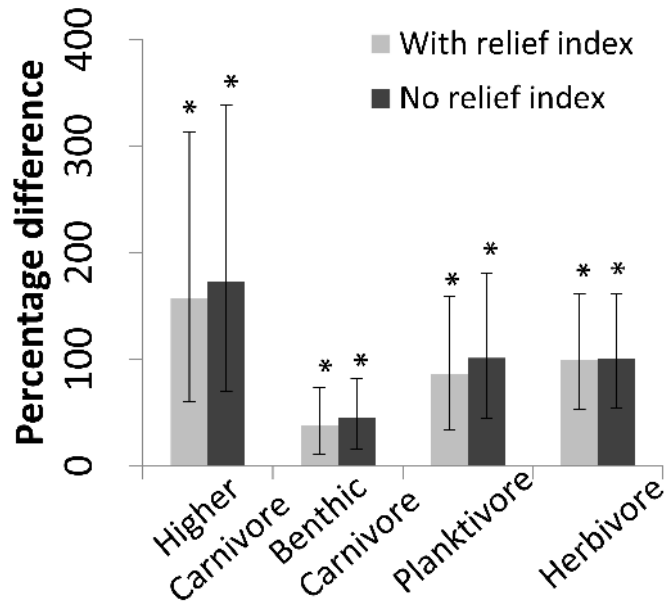


Figure 2.6. (S2 Fig) Percentage difference in biomass (\pm 95% confidence intervals) of the different trophic groups in protected areas relative to open-access zones when accounting for, and not accounting for, the relief index. Log ratios of biomass ($\log(\text{biomassMPA}/\text{biomassOPEN})$) with relief index and without relief index included in the LMMs. The difference in biomass in effective MPAs were relative to open-access zones, for each trophic group (\pm 95% confidence intervals). Ratios were obtained from the coefficient for Protection, β_6 , from the LMM equation (S1 Appendix) and transformed into percentage increments in biomass, by $100 \cdot (\exp(\beta_6) - 1)$. Asterisks denote a statistically significant difference ($p < 0.05$). The LMM model also adjusted for SST mean, SST range, PAR-mean and human population.

Chapter 3

CONTRIBUTIONS OF BODY SIZE, HABITAT AND TAXONOMY TO PREDICTIONS OF TEMPERATE AUSTRALIAN FISH DIETS

Preface:

This work has been published in a refereed journal and is presented below in identical form. The citation for the original publication is:

Soler GA, Thomson RJ, Stuart-Smith RD, Smith T, Edgar GJ, (2016) Contributions of body size, habitat and taxonomy to predictions of temperate Australian fish diets. Mar Ecol Prog Ser. DOI 10.3354/meps11584

In Chapter 3 we develop a predictive diet model to estimate prey type and prey size of fish in Western Port, Australia. Chapter 3 does not link directly with Chapter 2 but progresses into Chapter 4, where the diet predictive model is tested at a larger geographical scale. This diet predictive model developed in Chapter 3 and 4 is then used to estimate the diet of the fish communities in the Reef Life Survey sites of Tasmania, Victoria and South Australia. In Chapter 5 we analysed the effect of no-take MPAs as well as other anthropogenic and environmental variables on the diet predictions of the fish communities, including their ecological implications.

3.1 Abstract

Using k-nearest neighbour procedures to predict prey type and linear models to predict mean prey size, we developed a 2-step dietary model based on the stomach contents of fish of known species, size and location from Western Port, Victoria (Australia). The model, nicknamed 'Consume', was used to assess the relative extent to which fish diet varied with body size, species identity, season, and location. Both prey type (mean overlap between predicted and actual prey types = 77%) and mean prey size (r^2 between predicted and observed mean prey size = 93%) were predicted with reasonable accuracy when species identity and length of consumer fish were known. The most important predictor for prey type was the size of the individual consumer, while the most important predictor for mean prey size was the consumer's taxonomic identity. Predictors were individually removed from both k-nearest neighbour and linear models to assess their relative contributions to the model. Little loss of accuracy (1%) was evident when family rather than species identity was used for both prey type and mean prey size. Environmental information associated with the time and location of fish sampling (habitat, site and season) contributed only marginally to predictions of prey type. Use of the Consume model will allow for an improved understanding of community-level trophic pathways through the integration of prey type and size predictions for consumer fishes.

3.2 Keywords

Predator-prey relations, Diet prediction, Australia, *Consume* model, Tropho-dynamics, Allometry

3.3 Introduction

Studies that predict and give insight to trophic pathways represent important tools for ecology (Edgar & Shaw 1995c). Furthermore, studies that consider size of consumers as well as their prey can offer new understanding of food-web structure and function, as well as

providing new approaches in the integration of community and ecology with energetic and metabolic theory (Brown et al. 2004, Belgrano 2005, Trebilco et al. 2013). Using a comprehensive dataset for consumers and their prey from Western Port, Australia (Edgar & Shaw 1995b), we present a new predictive diet model based on the combination of k -nearest neighbour procedures to predict prey type and a linear model to predict the size of the prey. The k nearest neighbour (kNN) algorithm is an instance-based learning classification technique that classifies new cases using a similarity measures between the new case and a training data set. Here, the new cases are fish, and the similarity measure is calculated from the predictor variables. The kNN method has the advantage over previous methods for predicting fish diet, in that it is non-parametric, relatively simple and thus makes fewer assumptions about the data.

The classical approach in community ecology considers species as the central unit within an ecosystem, with similar roles amongst individuals. Nevertheless, individuals of many species experience profound changes in their diet through their life histories, and their body size and that of their prey can both increase several orders of magnitude (Cushing 1975, Rudolf & Rasmussen 2013). Moreover, per-unit-biomass consumption rates and population density decrease with animal size. Hence, higher metabolic rates and higher per-biomass consumption rates are typical of small individuals (Rudolf & Rasmussen 2013).

The trophic role of species in aquatic ecosystems should therefore be regarded as flexible, changing with body size, a fundamental reason to develop size-based analyses of food webs (Dickie et al. 1987, Jennings & Warr 2003, Blanchard et al. 2011, Zhang et al. 2014). Furthermore, studies from the North Sea and the Western Arabian Sea found that while body size was only a weak predictor of trophic position within species, there was a strong community-scale relationship between trophic position and body size (Jennings et al. 2001, Al-Habsi et al. 2008). Amongst the few studies with predictive models for diets of fishes, Link (2004) developed a Rank Proportion Algorithm (RPA) model that predicted prey preference from first principles of predation. Link's model also used ambient prey

Taxonomy and size in diet predictions

concentrations, prey selectivity, consumption rates, predator biomass and prey biomass to predict diet composition. This RPA model ranked each component of the interaction between predator and prey as an individual event. Using the RPA, the preferences of a particular prey type were assessed for a given predator (Link 2004). Furthermore, by partly using the RPA model, a subsequent study (Pinnegar et al. 2014) predicted the effect of an invasive species in a Corsican inshore food-web using predicted diets as input to the modelling framework, Ecopath.

Another approach to modelling diet consumption used prey concentration (as a proxy of encounter rate) and prey size to predict the diet of planktivorous bluegill (Werner & Hall 1974, O'Brien et al. 1976). Wright and O'Brien (1984) studied feeding selectivity of planktivorous white crappie by assuming that the predation process could be subdivided into different steps—prey location, pursuit, attack and retention. Each of these steps was assigned a probability, and the predicted consumed prey was calculated as the sum of the individual probabilities. Other studies assessed predator-prey size/mass ratios (Hahm & Langton 1984, Scharf et al. 2000), with prey abundance and prey type as important factors in determining optimum foraging patterns. A recent study investigated morphological and behavioural traits of prey that make individuals more vulnerable to predation by lionfish (Green & Côté 2014). Based on these traits, the authors predicted which prey was more susceptible to predation. They cross-validated their results based on in situ observation and stomach content of captured lionfish, obtaining a high correlation. Stable isotope analyses have also been used to predict predator-prey ratios and trophic transfer efficiencies (Jennings et al. 2002b).

Early quantitative studies in Western Port, Victoria, on dietary pathways linking benthic invertebrate to fish communities focused on seagrass and unvegetated habitats (Edgar & Shaw 1995c, b, a). The fish community predominantly consisted of small sized (<10 g) animals, and was significantly more abundant and productive in seagrass habitats compared with unvegetated habitats. Crustacean production was highly correlated with fish production, and crustaceans greater than 1 mm were the most important dietary component (Edgar &

Taxonomy and size in diet predictions

Shaw 1995b). On average, prey length was 7.5% of consumer fish length. Furthermore, major ontogenetic changes in diet were evident in Western Port, with diets of adult and juvenile fish of the same species differing as much as between different species.

The present study uses the Western Port dataset, consisting of individual items counted and measured from fish stomach contents (Edgar & Shaw 1995c, b, a), to address the following specific questions:

- Through application of *k*-nearest neighbours theory, how accurately can the prey types of a fish of known species and size be predicted?
- What is the loss in accuracy, using the *k*-nearest neighbours model, in prey type prediction if identity to species-level is unknown (e.g. only genus or family are known) or if size information for the consumer fish is lacking?
- Can the mean size of each prey type consumed by a fish of known size and species be estimated accurately using a linear model?
- What is the loss in accuracy in the linear model for mean prey size predictions without complete taxonomic or size information?
- Can the accuracy of the *k*-nearest neighbour predictions for prey type and the linear model predictions for mean prey size be improved by including environmental factors such as site, habitat and season?

3.4 Materials and Methods

This study is based on data described by Edgar and Shaw (1995a, b, c) from Western Port, Victoria, southeastern Australia. The 2,974 individual fishes used in this study were collected using seine and gill nets from three different habitat types (seagrass, unvegetated intertidal flats, unvegetated channel) at five locations (Fig. 3.1). Of the five locations sampled, three (Peck Point, Rhyll and Tooradin) contained all three habitat types. Rhyll Spit was composed of two habitat types (seagrass, unvegetated intertidal flats) and Loelia Shoal one habitat (unvegetated channel). The term ‘site’ refers to the six locations studied.

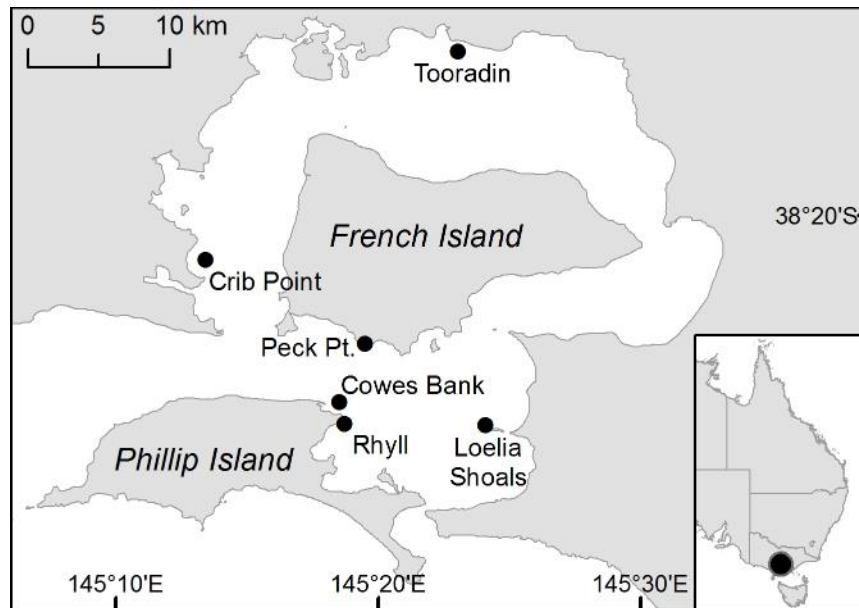


Figure 3.1 Western Port, showing locations of sampling sites.

Fish caught at these sites using gill and seine nets were identified to species, weighed, and their length to caudal fork measured. Calculations used to estimate fish densities (m^{-2}) are described by Edgar and Shaw (1995a). Individual prey in stomachs of captured fishes were identified and body lengths measured using a microscope graticle or Vernier calipers, and binned into 19 different log size-classes ranging from 0.125 mm to 64 mm (Edgar & Shaw 1995b). A percentage of total gut contents was allocated in the case of algae, sponges, bryozoans, ascidians and hydroids, or in the case of prey that were unidentifiable because of advanced states of digestion. The percentage of these prey items was estimated as a proportion of the biomass of prey in the stomach of a fish (for details refer Edgar and Shaw (1995b)). Prey items were grouped by taxon into eleven major prey types (algae, sponges, crustaceans epifauna, crustaceans infauna, mollusc epifauna, mollusc infauna, polychaetes epifauna, polychaetes infauna, others epifauna, others infauna and fish). Using this information, a matrix was constructed showing environmental information (habitat, site and month), taxonomic information (family, genus and species), morphometric information (length and wet weight of fish) and prey information (prey items, prey taxon and prey type).

Taxonomy and size in diet predictions

The *Consume* model was constructed in two steps in R (R-Core-Team 2014) (Supplement 1, 2 and 3), with results combined in an output matrix, which shows the prey type, prey type percentage, and mean prey size predictions within each prey type for each fish individual (Fig. 3.2). The first model step used the premise of the k-nearest neighbours algorithm (Barber 2011, Conway & White 2012) to predict the prey type in percentages for each particular fish. The second step of the model used linear models to predict the size of the prey for each particular prey type consumed by a fish. The training dataset used for this algorithm is described by Edgar and Shaw (1995b). As predictors for the prey type of a particular fish and size of its prey, we used the environmental, taxonomic, morphometric and prey information. We used the same predictors for prey size as for prey type and included the estimates of prey type as another predictor. We opted for this approach because it brought together information associated with prey type, established with input from a dietary database, into the predictions of prey size. Furthermore, prey type proved to be an important predictor for the prey size model as observed from the variation explained in the sum of squares calculations. We were unable to develop a model that simultaneously estimated prey type, prey type percentage, and prey size; however the two-step approach avoided undue model complexity and achieved good results in comparisons between predicted and observed values.

Taxonomy and size in diet predictions

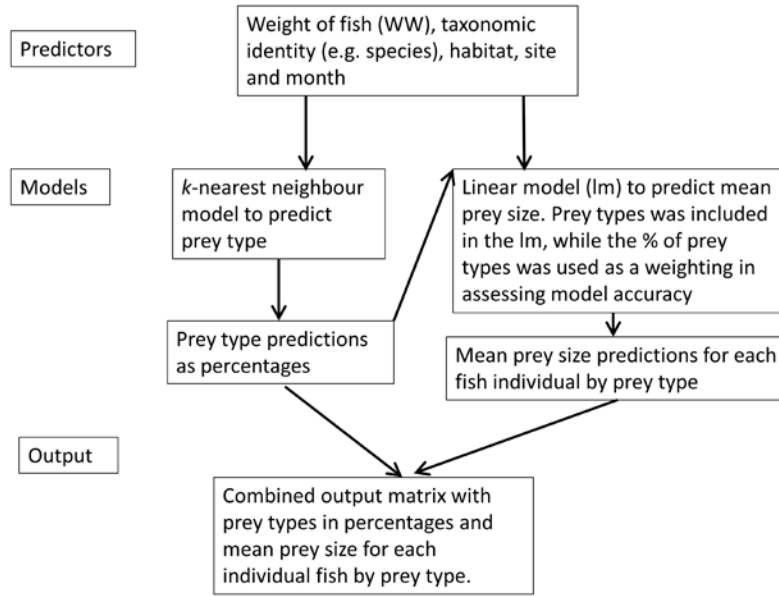


Figure 3.2 Predictors used in the ‘Consume’ 2-step model, and how they combined to produce the output matrix with prey type, prey type percentages and mean prey size for a consumer fish.

The algorithm for the first step of the *Consume* model used a combination of the importance or weighting of the predictors as well as an optimum number of neighbouring fish, k . Neighbouring fish, k , refers to the most similar fish in size and taxonomy used as a predictor. The optimum weighting of the predictors and k were chosen using a leave-one-out cross validation technique. This was done by predicting the prey type of each fish based on the rest of the data set for various weights and values of k . The weights that gave the greatest accuracy of the predictions were subsequently used.

Nearest neighbours were chosen based on pairs of fish with the smallest dissimilarity, where dissimilarity was calculated as the weighted sum of the absolute difference between the values of predictors for each pair of fish;

$$D_{ij} = \sum_{k=1}^{n_p} w_k \text{ abs}(\beta_{ik} - \beta_{jk})$$

(Equation 1)

and D_{ij} is the a dissimilarity between fish i and fish j , $i \neq j$ and $k=1, \dots, n_p$ with n_p being the total number of predictor variables; w_k is the given weight or importance of predictor k ;

Taxonomy and size in diet predictions

$\text{abs}(\beta_{ik} - \beta_{jk})$ is the absolute difference between fish i and fish j , for predictor variable k . When the predictor variable is a factor, this is equal to zero if the predictors are the same, or one otherwise. Wet weight of the consumer fish was \log_e transformed before calculating the absolute difference.

A number of dissimilarity cut-offs were trialled through several runs of the model, with the accuracy of predictions used to determine the most appropriate cut-off. Decreasing the cut-off to a maximum dissimilarity between individuals of 0.01 maximised model accuracy (75.8%). This reduced the number of individuals used to predict prey type to an average of 1.1 (Table 1S Supplement 4). If all dissimilarities exceeded the cut-off, the individual with the minimum dissimilarity was used to predict prey type.

Computing the overlap in the percentage between the predicted and the observed values assessed the accuracy of the model for prey type predictions. For example if a fish was predicted to have a diet content of 20% crustacean epifauna and 80% mollusc epifauna and the observed data was 10% crustacean epifauna, 10% algae, 70% mollusc epifauna and 10% mollusc infauna, then the model was estimated to have an accuracy of 80%. In this case the overlap in the proportion that was correct was 80% (10% crustaceans epifauna + 70% mollusc epifauna). In computing the accuracy of the model, the predicted diet content of the fish was never based on a model that included the fish in question (i.e. $i \neq j$ in equation 1).

The algorithm for the second step of the *Consume* model, to predict the size of the diet consumed by each fish, was based on a linear model as described below.

$$y_i = \mu + \beta_1 \text{Species}_i + \beta_2 \text{WW}_i + \beta_3 \text{Prey type}_i + \beta_4 \text{Habitat}_i + \beta_5 \text{Site}_i + \beta_6 \text{Month}_i + \varepsilon_i$$

(Equation 2)

where y_i = the natural log of the mean prey size prediction for the i th fish, given the effects of Species, Wet weight (WW), Prey type, Habitat, Site and Month; μ = overall mean; ε_i = residual error. A natural log transformation made the data more normally distributed. The

Taxonomy and size in diet predictions

mean prey size within each prey type for a specific fish was predicted using these factors. We also tested a linear mixed effect model with random nested effects of Family/Genus/Species. However, the results of the linear model and the linear mixed effects model were almost the same in predicting mean prey size. We chose the linear model because it allowed us to more easily test the decrease in accuracy when removing each of the predictors one at a time. We tried different combinations of omitted predictors to assess their individual effect on the accuracy of the linear model. We measured the accuracy of the linear model as the square of the Pearson's weighted correlation between the predicted values and the observed ones, without including information for the fish that the model was predicting for (leave one out cross validation). The weighting of the correlation was based on the predicted percentages of prey type.

We also developed a third model to predict the standard deviation of the mean prey size. The importance of this measure is to better understand the circumstances that affect whether individual fish focus on prey within a narrow size band, or are largely unselective, capturing prey in a variety of sizes. This third model used the same predictors used for the mean prey size predictions and included the mean prey size estimates as another predictor. We used a generalized linear model, described below, to predict the standard deviation.

$$y_i = \mu + \beta_1 \text{Species}_i + \beta_2 \text{WW}_i + \beta_3 \text{Prey type}_i + \beta_4 \text{Habitat}_i + \beta_5 \text{Site}_i + \beta_6 \text{Month}_i \\ + \beta_7 \text{Mean Prey size}_i + \varepsilon_i$$

(Equation 3)

where y_i = square root of the standard deviation of the predictions of the \log_e mean prey size for the i th fish. $\beta_{1,2,3,4,5,6}$ were the same predictors as described above for mean prey size predictions. β_7 was the mean prey size prediction used in the model. This way our model predicted the standard deviation of the predicted mean prey size with the idea to test if these predictions were comparable to the standard deviations of the observed prey size. We used the square root transformation to make the data more normally distributed. A similar process used on the second model was followed for the third model; we tested the effect on the

weighted correlation between the observed standard deviation and the predicted standard deviation by removing the different predictors.

In order to standardize the contribution of different species for the prediction of the model, we examined two aspects of data selection. First, to account for the differences in the number of individuals per species, we used a random sample of 12 individuals per species with a wide range of sizes. The sampling was achieved with a random number selector based on each individual fish, which were beforehand numbered. Species were also dropped if the inter-quartile range of the \log_e of the wet weight was < 0.25 . Thirty-seven out of the 79 species for the full dataset were dropped using this criterion. Basically this excluded species with only a narrow size range sampled, and included species with a wide range in sizes. Furthermore, this also excluded species that had less than 12 individual fish sampled. Trials indicated that the greatest accuracy achieved was when 12 individuals per species was used, giving the most accurate predictions for prey type and mean prey size. Second, we tested whether different numbers of fish per species greatly affected prey type predictions, and found that changes were negligible when at least 5 fish were considered (Table 2S Supplement 4).

3.5 Results

The k -nearest neighbour model algorithm predicted the prey types of fishes with an average accuracy of 76% when using the whole dataset (Table 3.1). We standardized the contribution of each species by randomly selecting only 12 individuals per species with a wide range of sizes. By doing this we only used 42 species with a total of 504 fish from the original data that comprised 79 species and 2,974 fish (Table 2S Supplement 4). With this subset of the dataset our prey type predictions increased marginally to $77 \pm 1\%$. The variation in the results was due to the fact that the algorithms randomly chose a different set of 12 fish per species in each run of the model.

Taxonomy and size in diet predictions

Table 3.1 Percentage correct between predicted and observed prey type for the full data set and for a random subset of 12 individuals per species with a wide range of sizes for Western Port. Also shown is the percentage correct of the predicted prey for all predictors and the subsequent loss in accuracy when removing factors from model. WW= \log_e wet weight of consumer fish. These predictions of prey type were based on step one of the *Consume* model using the *k*-nearest neighbour algorithm.

Predictors		% correct with all fish included	% correct with subset of 12 animals per species
With all predictors	Species, WW, habitat, site, month	76	77
Without species	Genus, WW, habitat, site, month	76	77
Without species and genus	Family, WW, habitat, site, month	75	76
Without species, genus and family	WW, habitat, site, month	70	74
Without WW	Species, habitat, site, month	62	61
Without habitat	Species, WW, site, month	74	76
Without site	Species, WW, habitat, month	75	76
Without month	Species, WW, habitat, site	74	76
Without habitat, site, month	Species, WW	72	75
Without all predictors but site	Site	23	18
Without all predictors but habitat	Habitat	23	18

We assessed the loss in accuracy in the prey type predictions by step-wise removal of the predictors from the model (Table 3.1). By doing this we determined that the most important predictor for prey type was wet weight (WW) of the consumer fish. By removing this predictor, the model lost over 16% of its accuracy. The taxonomic predictors proved to be of small relative importance with a loss in accuracy of 3%. The least important predictors were habitat, site and month, which decreased the accuracy of the model by 1% when removed. If all predictors were removed, other than site or habitat, then the accuracy of the model dropped to 18%.

Taxonomy and size in diet predictions

The accuracy of the linear model for the estimation of the size of the prey, measured as the square of the weighted correlation between the predicted and observed mean prey size, was $R^2=0.90$ (Fig. 3.3A) when using all the predictors and all fish from the dataset. With the subset of 12 individuals per species this weighted correlation increased to $R^2=0.93\pm0.01$ (Fig. 3.3B). This model used the prey type prediction from step one of the model as part of the predictors and used for the weighting of the correlation the predictions for prey type. The most important predictors were taxonomic group, size of the consumer fish and prey type (Table 3S and 4S Supplement 4).

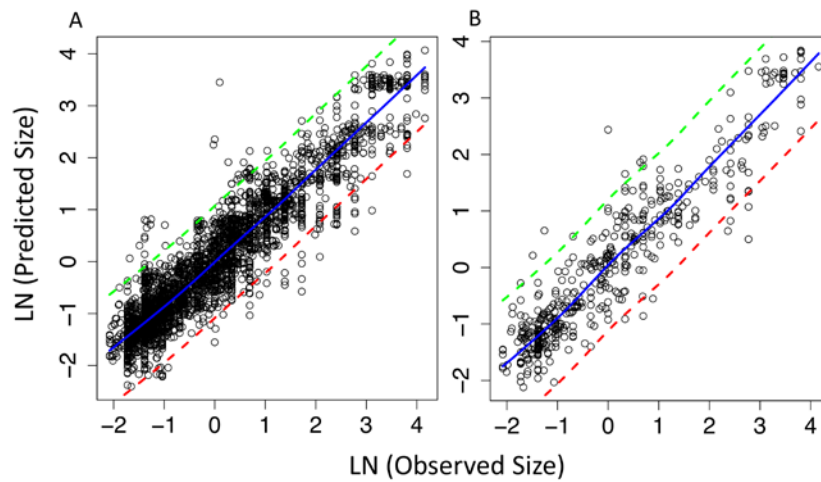


Figure 3.3 Scatterplots relating \log_e predicted and observed mean prey size (mm) using a linear model with all predictors (species, genus, family, wet weight (WW), prey type, site, habitat and month; weighted correlation): (A) All fish included, $R^2 = 0.90$ (79 species); (B) Subset of 12 individuals per species ($R^2 = 0.93 \pm 0.01$, 42 species, where \pm indicates the variation in R^2 generated by different sets of individuals randomly selected to represent each species). The green line outlines the upper prediction interval and red line the lower prediction interval (95%). The blue line is the locally weighted scatterplot smoothing curve (LOWESS).

Removing the species and genus information of the consumer had little effect on the accuracy of the model, provided that the family designation was retained along with the other predictors ($R^2=0.92\pm0.01$; Table 3.2). Consumer taxonomic information proved to be the most important predictor in mean prey size prediction (Table 3.2). In order to determine the relative importance of each factor, we removed the different predictors one at the time and estimated the loss in accuracy of the model (Table 3.2). When wet weight was excluded, the

Taxonomy and size in diet predictions

correlation dropped to $R^2=0.86$ (Table 3.2). Consequently, the loss in accuracy when wet weight was not used was around 0.07. When the taxonomic information was removed and all other predictors included, the correlation dropped to $R^2=0.80$. This corresponded to a loss in accuracy for mean prey size predictions of 0.13 when not using the taxonomic information. When using the whole dataset, the loss in accuracy when not using taxonomic information was 0.16. This result indicates the importance of taxonomic information as the most important predictor of mean prey size. On the other hand, the loss in accuracy was extremely small (<0.005) when habitat, site or month were removed (Table 3.2). Moreover, when these three predictors were all removed from the model, the accuracy was affected by only 0.01 (Table 3.2).

Table 3.2 Correlation between observed and predicted mean prey size for the full data set and for a random subset of 12 individuals per species with a wide range of sizes for Western Port. Also shown are the correlations for all the predictors available and the subsequent loss in accuracy when removing some of them. Weighting of the correlation was based on the predicted percentages of prey type. WW= log_e wet weight of consumer fish. The difference in the prediction intervals indicates the fit with the different combinations of predictors.

Predictors		R^2 with all fish included	R^2 with subset of 12 ind. per sp.	Mean difference between upper and lower prediction Interval
With all predictors	Species, WW, prey type, habitat, site, month	0.9	0.93	2.02
Without species	Genus, WW, prey type, habitat, site, month	0.9	0.93	2.01
Without species and genus	Family, WW, prey type, habitat, site, month	0.89	0.92	2.09
Without species, genus and family	WW, prey type, habitat, site, month	0.74	0.8	2.83
Without WW	Species, prey type, habitat, site, month	0.85	0.86	2.59
Without habitat	Species, WW, prey type, site, month	0.9	0.93	2.22
Without site	Species, WW, prey type, habitat, month	0.9	0.93	2.25

Predictors		R^2 with all fish included	R^2 with subset of 12 ind. per sp.	Mean difference between upper and lower prediction Interval
Without month	Species, WW, prey type, habitat, site	0.9	0.93	2.2
Without habitat, site, month	Species, WW, prey type	0.89	0.93	2.28
Without prey type	Species, WW, habitat, site, month	0.89	0.92	2.31
Without all predictors but site	Site	0.11	0.1	5.52
Without all predictors but habitat	Habitat	0.06	0.05	5.61

We also tested if some species affected our predictions more than others. The diet of the most abundant species, the yellow-eye mullet (*Aldrichetta forsteri*) had previously been found to consist of anomalously small mean prey size (Edgar & Shaw 1995b). By including the yellow-eyed mullet in the model, the weighted correlation between WW of the consumer fish and the observed prey size was $R^2=0.54$ for all fish species, $R^2 = 0.68 \pm 0.01$ for the subset of 12 individuals per species (Fig. 3.4A and 3.4B). The weighted correlation without the yellow eye mullet was $R^2=0.71$ (all data included) and $R^2=0.70\pm0.01$ (for the subset of 12 individuals per species) (Fig. 3.4C). Most of the yellow-eye mullet measured around 270 mm (approximate exponential of 5.6), which is where the largest variation of prey size was observed (Fig. 3.4A). Other species could potentially also contribute substantially to the variation on prey size but were not tested independently.

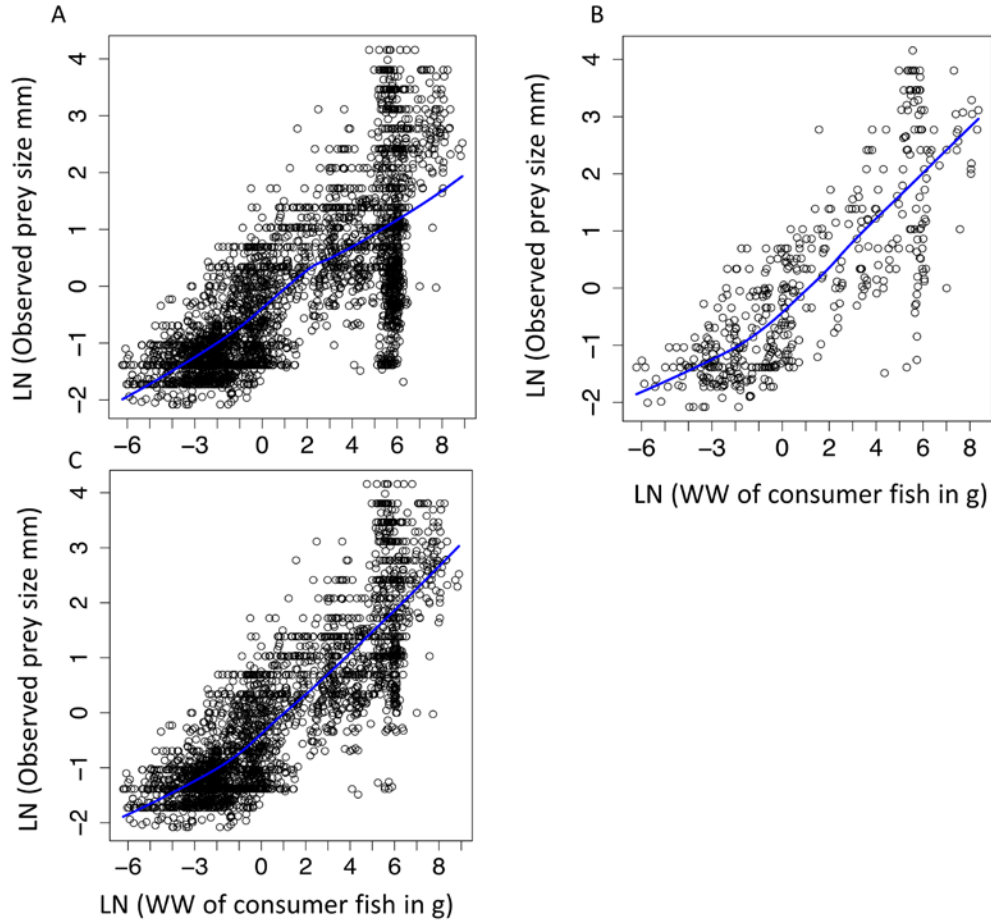


Figure 3.4 Scatterplots relating \log_e of wet weight (WW) of consumer fish (g) and \log_e of observed mean prey size in mm; (A) all fish included, $R^2=0.54$; (B) Subset of 12 individuals per species ranging in size, $R^2=0.68 (\pm 0.01)$; (C) All fish included but without *Aldrichetta forsteri*, $R^2=0.71$. The blue lines are the locally weighted scatterplot smoothing curves (LOWESS).

We estimated the standard deviation of the predicted mean prey size using a third model that used predicted mean prey size as well as all other predictors. We found a significant correlation between the predicted and the observed standard deviation ($R^2=0.36$) (Fig. 3.5). As observed for the correlation between predicted and observed mean prey size, removing predictors indicated that the most important predictor was taxonomic information (Table 3.3). Furthermore, regression of the 90% quantile between the \log_e of the wet weight of the consumer fish and the \log_e of the standard deviation of the observed prey size had a positive trend (slope=1.24, 95% CI=(0.04, 2.13)), suggesting that the diet of bigger fish had a wider size range (Fig. 3.6).

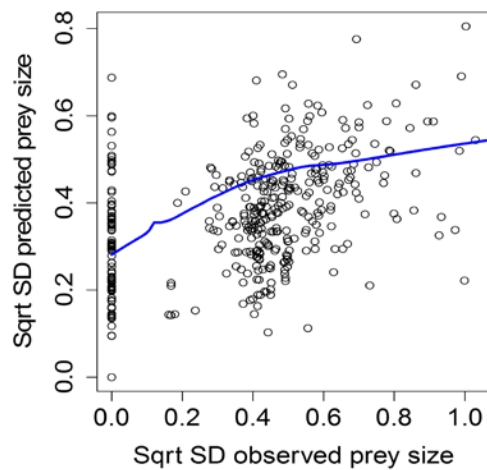


Figure 3.5 Scatterplot relating predicted and observed square root of the standard deviation (SD) of mean prey size for fishes in Western Port. $R^2=0.36$. The blue line is the locally weighted scatterplot smoothing curves (LOWESS).

Table 3.3 Correlation between the predicted and the observed standard deviations of the predicted mean prey size for Western Port. Also shown are the correlations for all the predictors available and the subsequent loss in accuracy when removing some of them. The weighting of the correlation was based on the predicted percentages of prey type. WW= \log_e wet weight of consumer fish.

Predictors		R^2 with subset of 12 animals per species
With all predictors	Species, WW, prey type, mean prey size, habitat, site, month	0.36
Without species	Genus, WW, prey type, mean prey size, habitat, site, month	0.32
Without species and genus	Family, WW, prey type, mean prey size, habitat, site, month	0.3
Without species, genus and family	WW, prey type, habitat, mean prey size, site, month	0.19
Without WW	Species, prey type, mean prey size, habitat, site, month	0.34
Without habitat	Species, WW, prey type, mean prey size, site, month	0.34

	Predictors	R ² with subset of 12 animals per species
Without site	Species, WW, prey type, mean prey size, habitat, month	0.32
Without month	Species, WW, prey type, mean prey size, habitat, site	0.33
Without habitat, site, month	Species, WW, prey type, mean prey size	0.3
Without prey type	Species, WW, mean prey size, habitat, site, month	0.29
Without mean prey size	Species, WW, prey type, habitat, site, month	0.34
Without all predictors but site	Site	0.01
Without all predictors but habitat	Habitat	0.03

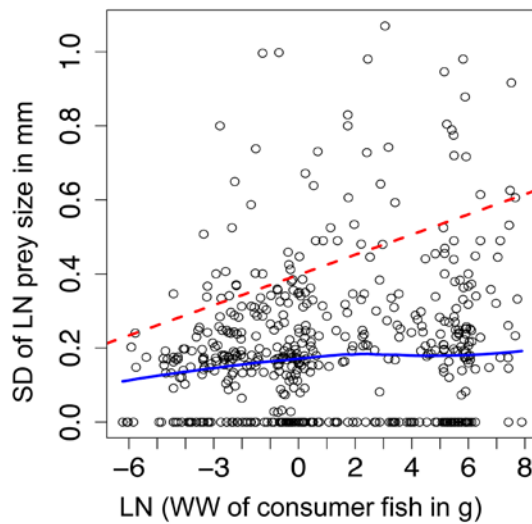


Figure 3.6 Scatterplot relating observed standard deviation of the \log_e prey size and the \log_e of the wet weight (WW) of consumer fish. $R^2=0.02$. Red line is the 90% quantile regression. The blue line is the locally weighted scatterplot smoothing curves (LOWESS).

We plotted the relation between the observed prey types and the \log_e wet weight of the consumer fish and found that certain prey types were significantly related with the size of the fish (Fig. 3.7).

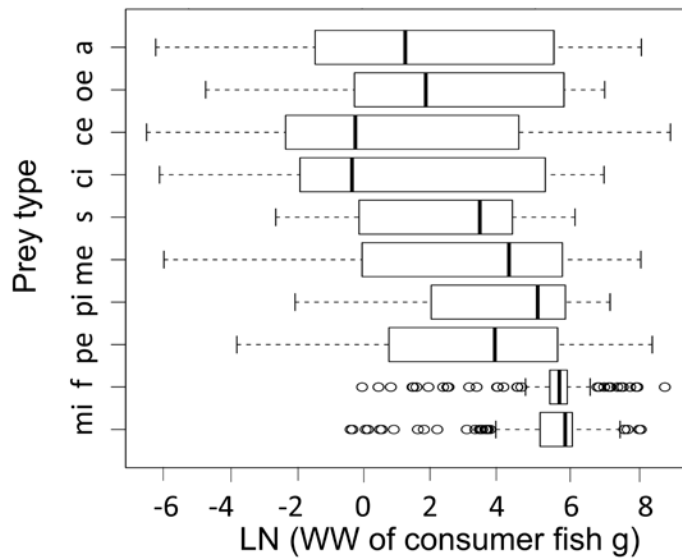


Figure 3.7 Boxplots, showing the relationship between the log_e wet weight (WW) of the consumer fish and the observed prey types. Prey abbreviations are: a=algae, oe=other epifauna, ce=crustacean epifauna, ci=crustaceans infauna, s=sponges, me=mollusc epifauna, pi=polychaetes infauna, pe=polychaetes epifauna, f=fish, and mi=mollusc infauna. The mid-line is the median and box limits are 25th and 75th percentiles. The whiskers are 1.5 times the inter-quartile range or the maximum or minimum value, whichever is closer to the median. The points are outliers.

3.6 Discussion

This paper quantitatively assesses the importance of body size and taxonomic identity in predicting fish diet composition. We found that for diet estimates, family identity was nearly as important as species identity, and identity was approximately equivalent to body size. Thus, both body size and taxonomic information are required to adequately predict the diet of a fish. Moreover, species identity is more important than body size in predicting the size of each prey type consumed, whereas consumer size is more important than species identity in determining which prey categories are consumed. These results are the inverse of expectations (i.e. consumer size is the best predictor of prey size, and fish species identity is the best predictor of prey type). If this finding is found to be general, it could have important implications for the development and application of size-based models used to assess the impacts of fishing on community structure and function (Shin & Cury 2001, 2004, Hall et al. 2006, Andersen & Pedersen 2010).

Taxonomy and size in diet predictions

The majority of marine trophic models use taxonomic identity of the fish and functional groups to draw their conclusions (Polovina 1984, Pauly et al. 2000b), regardless that species change their ecological roles by eating different prey of progressively larger size at different stages of their ontogenetic development (Cushing 1975, Maury et al. 2007a, Maury et al. 2007b, Rudolf & Rasmussen 2013). Only a few studies have considered body size as the most important factor in the ecological system (Shin & Cury 2001, Brown & Gillooly 2003, West & Brown 2005). Our two-step model integrates both the taxonomic identity of a fish as well as its size to achieve accurate predictions of diet consumptions. The predictive diet model developed for the fish community of Western Port should theoretically be applicable to other locations, providing that the necessary information of the consumer fishes and their prey is available to input. Further research is underway to test such extension.

Our *Consume* model predicted the percentages of different prey types with reasonable accuracy, as well as the size of dietary items consumed for a particular fish of known species and size within Western Port, Victoria. The loss in accuracy was also assessed for both prey type and mean prey size predictions if lacking taxonomic, size or environmental data. The most important predictor was wet weight of the consumer fish for prey type predictions.

The fact that consumer size was the most important predictor for the prey type is likely related to ontogenetic changes of the different species consuming different diets at different stages in their life, which implies changing ecological roles within their habitat (Cushing 1975, Dickie et al. 1987, Jennings & Warr 2003, Rudolf & Rasmussen 2013). Certain prey types are also of larger size and only available to larger fish, such as the situation when fish prey on other fish. The relationships found between prey type and size of the fish (Fig. 3.7), explain why predicted prey types were more accurately predicted when using the size of the fish than with taxonomic or other predictors. It is interesting that mollusc infauna (*mi*) were consumed mainly (but not exclusively) by elephant sharks (*Callorhynchus mili*) of relatively large size with specialized mouth pieces which help them dig these molluscs from the sediment (Table 5S). Changes in prey type related to size have also been documented in a

Taxonomy and size in diet predictions

general review of the literature (Werner & Gilliam 1984). Our results show that this trend relates not only to individual species but also at the level of the whole fish community in Western Port.

The most important predictor for mean prey size was information on species, genus or family of the consumer fish. Fish size was second in importance as a predictor after the taxonomic information, but also predicted the size of the prey with reasonable accuracy. Nevertheless, we expected size of the consumer fish to be the most important predictor for both prey type and prey size based on previous work in southern Australia (Edgar & Shaw 1995c) as well as other studies highlighting the importance of size for prey predictions (Cushing 1975, Rudolf & Rasmussen 2013). However, Edgar and Shaw (1995b) also pointed out in their study in Western Port that the relationship between size of the consumer and its prey was consistent for most species encountered other than the yellow-eyed mullet (*Aldrichetta forsteri*), which consumed prey considerably smaller than predicted for its size. The importance of taxonomic information as a factor in the model is largely explained by the variation in prey size shown by certain species outside size predictions, as was the case for yellow-eyed mullet.

In order to balance the contribution of each species to overall predictions, the model randomly selected only 12 individuals per species with a wide range in sizes. This was necessary because some species, most notably *A. forsteri*, contributed a disproportionately large number of individuals to the total sample ($n = 325$ for *A. forsteri*), biasing results. The loss in accuracy for mean prey size predictions for the balanced contribution diminished from 16% to 13% when the model used the subset of 12 individuals per species. Previous studies have also found that the distribution of predator size - prey size was also related to species identity and had an asymmetric distribution (Scharf et al. 2000). They also indicate that the larger piscivorous fishes continue to consume prey of small size as well as including larger prey items in their diet, and that the slope in the relation between the fish and the maximum

Taxonomy and size in diet predictions

prey sizes showed a significant variation between species, adding support to the importance of taxonomic information for prey size predictions.

The importance of the taxonomic information in predicting mean prey size is also explained by inter-specific variation in maximum body size. For example, a greater range of body sizes is possible for the larger fish species, and hence the potential for ontogenetic diet shifts will be greater than for small species that quickly reach maximum size. Furthermore, some prey types will not be available to small fish species. A relationship between prey type and mean size of prey suggests this was the case within the dataset, and that maximum body size of fishes likely contributed to the importance of taxonomic identity to prey size predictions.

The standard deviation of the mean prey size confirms the assumption that larger fish consumed a wider size range of prey. Furthermore, the estimated standard deviations could also be used to feed into community level studies, to generate predictive probability distributions that describe likelihood of prey of a particular size being consumed. The sequential removal of predictors shows that taxonomic information is the most important estimator for prey size breadth.

Little loss of information occurred when family rather than species identity was used. Thus, predictions for a fish species lacking detailed dietary information may have much the same accuracy as prediction for a fish species belonging to the same family for which this information is available. This has important positive implications for community level analyses where many species have not been previously studied.

In conclusion, the *Consume* model presented in this manuscript allows accurate prediction of the type and mean size of prey, and prey size distribution for consumer fish of known identity and size. Rather than trophically subdividing fishes using categorical divisions based on species (e.g. higher carnivores, benthic carnivores, herbivores and planktivores), the models will allow more rigorous compartmentalization of prey consumption by describing diets at an individual fish level, including for fish species that exhibit large ontogenetic

changes in diet. Through aggregation of data on total prey consumption for whole assemblages of individual fish at sites, this new approach should open new pathways in trophic ecology.

3.7 Acknowledgments

This study was supported by the Australian Research Council, a postgraduate scholarship from TGRS (to G.A.S.), and the Marine Biodiversity Hub, a collaborative partnership funded under the Australian Government's National Environmental Research Program. We would like to thank Craig Shaw for assistance in field sampling, Justin Hulls for designing the map of the study area (using ArcGIS), and Dr. Kilian Stehfest in supporting the development of the model. We would also like to thank Dr. Simon Wotherspoon and Dr. Andre Punt for their input and comments in developing the diet predictive model.

3.8 Supplementary material

Supplements 1, 2 and 3 are attached to the thesis as separate files. Supplements 1 and 2 are R scripts. Supplement 3 is a large ‘.csv’ file . These files will appear online once Paper 2 of this thesis is published.

Table 3.4 (Table 1S Supplement 4) Prey type percentage of proportions correct and mean number of fish used in the model for different cut-offs for the whole dataset. Proportions correct were estimated as the overlap between the predicted and observed data for each prey type.

Cut-off	Mean proportion correct	Mean number of fish
0.01	75.8	1.1
0.02	75.3	1.3
0.03	74.6	1.5
0.04	74.0	1.8
0.05	73.7	2.0
0.1	71.8	3.2
0.2	48.9	14.6
0.3	28.8	46.9
0.4	24.1	107.8
0.5	22.9	199.4
0.6	22.4	311.0
0.7	22.3	414.2
0.8	22.2	508.5
0.9	22.2	596.3
1	22.3	680.2

Taxonomy and size in diet predictions

Table 3.5 (Table 2S Supplement 4) Percentage correct of the prey type for a random selection of individuals per species. Shown are the number of species and number of fish used in the model to estimate the percentage of the prey type correct. The percentage correct was estimated as the overlap between the percentage of each prey type and the observed prey. The optimum number of fish per species was 12 with an average of 77% correct predicted prey types.

No. of fish per species	No. of species	No. of fish	% correct
2	62	124	69
5	51	255	76
10	43	430	76
12	42	504	77
15	41	615	76
20	37	740	75
All animals	79	2974	75

Table 3.6 (Table 3S Supplement 4) ANOVA results for the predictors for mean prey size for the full dataset. Asterisks denote statistically significant differences (*** = $p < 0.001$). WW = \log_e wet weight of consumer fish.

	Df	Sum Sq	Mean Sq	F value		Pr(>F)	
Species	78	6154.3	78.9	266	<	2.20E-16	***
WW	1	544.7	544.7	1837	<	2.20E-16	***
Prey type	9	327.8	36.42	123	<	2.20E-16	***
Habitat	2	0.6	0.32	1.09		0.34	
Site	5	20.8	4.16	14	<	1.28E-13	***
Month	3	33.1	11.02	37	<	2.20E-16	***
Residuals	4195	1243.9	0.3				

Table 3.7 (Table 4S Supplement 4) ANOVA results for the predictors for mean prey size for the subset of 12 individuals per species. Asterisks denote statistically significant differences (**= $p < 0.01$; *** = $p < 0.001$). WW= \log_e wet weight of consumer fish.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Species	41	1159.6	28.3	121.9	< 2.2E-16	***
WW	1	138	138	594.6	< 2.2E-16	***
Prey type	8	53.9	6.7	29	< 2.E-16	***
Habitat	2	0.2	0.1	0.4	0.66	
Site	5	4.9	1	4.3	<0.001	***
Month	3	3.5	1.1	5	0.002	**
Residuals	644	149.5	0.2			

Table 3.8 (Table 5S Supplement 4) Number of fish surveyed with gut contents in Western Port. Average wet weight (WW) in grams, maximum WW and minimum WW are shown for each species. The average percentage consumed of each prey type by each fish species is shown. Prey abbreviations are: a=algae, oe=other epifauna, ce=crustacean epifauna, ci=crustaceans infauna, s=sponges, me=mollusc epifauna, pi=polychaetes infauna, pe=polychaetes epifauna, f=fish, and mi=mollusc infauna.

Family	Species	Number of fish	Average WW	Max. WW	Min. WW	a	ce	ci	f	me	mi	oe	oi	s	pe	pi
Apogonidae	<i>Siphamia cephalotes</i>	27	0.83	1.72	0.002	0	99	0	0	1	0	0	0	0	0	0
	<i>Vincentia conspersa</i>	8	1.9	10.85	0.33	0	98	0	0	0	0	0	0	0	2	0
Arripidae	<i>Arripis trutta</i>	43	283.11	416	18.68	2	2	0	94	1	0	0	0	0	0	0
	<i>Arripis truttaceus</i>	51	284.17	423.8	87.7	0	0	0	94	6	0	0	0	0	0	0
Atherinidae	<i>Atherinasoma microstoma</i>	3	0.35	0.95	0.04	0	100	0	0	0	0	0	0	0	0	0
	<i>Atherinid</i> sp.	36	0.02	0.13	0.002	0	96	0	0	4	0	0	0	0	0	0
	<i>Kestratherina brevirostris</i>	24	1.04	2.4	0.42	0	93	0	0	0	0	3	0	0	4	0
	<i>Kestratherina esox</i>	22	1.38	5.58	0.25	0	100	0	0	0	0	0	0	0	0	0
Callorhynchidae	<i>Callorhynchus milii</i>	62	647.47	3100	36.7	0	10	3	0	5	75	0	0	0	6	0
Carangidae	<i>Pseudocaranx georgianus</i>	67	222.59	601	17.57	2	71	2	0	1	1	0	0	0	22	0
	<i>Trachurus declivis</i>	2	349.5	360	339	0	0	0	100	0	0	0	0	0	0	0
Cheilodactylidae	<i>Dactylophora nigricans</i>	2	148.7	158.8	138.6	0	3	0	0	0	0	0	0	0	48	50
Clinidae	<i>Cristiceps australis</i>	22	5.77	49.2	0.05	0	67	0	32	1	0	0	0	0	0	0
	<i>Heteroclinus adelaidei</i>	16	4.18	7.9	0.03	0	88	0	2	1	0	0	0	0	10	0
	<i>Heteroclinus forsteri</i>	3	0.75	1.08	0.36	0	96	0	0	0	0	0	0	0	4	0
	<i>Heteroclinus perspicillata</i>	133	2.81	24.8	0.014	3	75	0	0	1	0	0	0	0	17	3
Clupeidae	<i>Hyperlophus vittatus</i>	59	0.5	4.5	0.006	0	95	0	0	5	0	0	0	0	0	0
	<i>Sardinops neopilchardus</i>	19	1.04	2.3	0.22	0	98	0	0	2	0	0	0	0	0	0
Diodontidae	<i>Diodon nichthemerus</i>	58	174.05	841.7	0.007	1	75	0	0	5	13	2	0	0	4	0

CONTRIBUTIONS OF BODY SIZE, HABITAT AND TAXONOMY TO PREDICTIONS OF TEMPERATE AUSTRALIAN FISH DIETS

Family	Species	Number of fish	Average WW	Max. WW	Min. WW	a	ce	ci	f	me	mi	oe	oi	s	pe	pi
Engraulidae	<i>Engraulis australis</i>	20	0.89	5.19	0.01	0	84	0	0	15	0	0	0	0	0	0
Enoplosidae	<i>Enoplosus armatus</i>	3	0.27	0.44	0.18	0	100	0	0	0	0	0	0	0	0	0
Gempylidae	<i>Thyrsites atun</i>	3	471.47	797.3	116.2	0	0	0	67	33	0	0	0	0	0	0
Gobiesocidae	<i>Parvicrepis sp.1</i>	20	0.06	0.21	0.007	0	86	5	0	1	0	8	0	0	0	0
Gobiidae	<i>Arenigobius bifrenatus</i>	69	0.31	3.33	0.002	29	60	6	0	2	0	0	1	0	2	0
	<i>Arenigobius frenatus</i>	159	0.82	8.1	0.003	35	44	7	0	2	1	0	1	0	9	2
	<i>Callogobius depressus</i>	1	1.94	1.94	1.94	0	0	0	0	0	0	0	0	0	100	0
	<i>Favonigobius lateralis</i>	17	0.81	1.5	0.012	17	54	6	0	7	0	0	0	0	16	0
	<i>Favonigobius tamarensis</i>	124	0.27	1.78	0.003	7	79	4	0	2	0	0	0	0	7	2
	<i>Gobiopterus semivestitus</i>	14	0.04	0.09	0.003	0	94	6	0	0	0	0	0	0	0	0
	<i>Nesogobius hindsbyi</i>	3	0.23	0.34	0.14	0	67	33	0	0	0	0	0	0	0	0
	<i>Nesogobius maccullochi</i>	9	0.46	1.54	0.03	0	56	23	0	9	0	0	0	0	12	0
	<i>Nesogobius pulchellus</i>	22	0.61	1.83	0.012	0	70	6	0	14	0	0	0	0	5	5
	<i>Pseudogobius olorum</i>	85	0.15	0.37	0.003	60	36	3	0	1	0	0	0	0	0	0
	<i>Tasmanogobius lasti</i>	7	0.02	0.03	0.012	0	75	25	0	0	0	0	0	0	0	0
Hemiramphidae	<i>Hyporhamphus melanochir</i>	25	12	76.43	0.44	41	15	0	0	0	0	40	0	0	4	0
Monacanthidae	<i>Acanthaluteres spilomelanurus</i>	52	0.67	4.31	0.06	55	22	5	0	8	0	0	0	9	1	0
	<i>Brachaluteres jacksonianus</i>	11	0.31	1.58	0.04	0	65	1	0	22	0	0	0	0	11	0
	<i>Eubalichthys gunnii</i>	2	3.35	4.82	1.88	1	16	0	0	73	0	0	0	8	2	0
	<i>Meuschenia freycineti</i>	52	64.11	406	0.02	18	11	1	0	39	0	2	0	21	7	0
	<i>Scobinichthys granulatus</i>	2	4.63	8.39	0.88	35	65	0	0	0	0	0	0	0	0	0
Moridae	<i>Pseudophycis bachus</i>	64	233.49	873.4	123.3	0	60	13	20	5	0	0	0	0	1	0
Mugilidae	<i>Aldrichetta forsteri</i>	325	281.07	640	0.013	49	24	3	0	17	3	0	0	0	2	1

CONTRIBUTIONS OF BODY SIZE, HABITAT AND TAXONOMY TO PREDICTIONS OF TEMPERATE AUSTRALIAN FISH DIETS

Family	Species	Number of fish	Average WW	Max. WW	Min. WW	a	ce	ci	f	me	mi	oe	oi	s	pe	pi
Myliobatidae	<i>Myliobatis australis</i>	2	3465	4310	2620	0	90	0	0	0	0	0	10	0	0	0
Odacidae	<i>Haletta semifaciata</i>	30	78.12	294.3	1.63	1	35	0	3	47	2	0	0	0	8	4
Ophichthidae	<i>Muraenichthys breviceps</i>	6	18.24	35.16	8.2	6	51	9	24	0	0	0	0	0	10	0
Ophidiidae	<i>Genypterus tigerinus</i>	2	280.45	322.3	238.6	0	78	0	22	0	0	0	0	0	0	0
Ostraciidae	<i>Aracana ornata</i>	1	15.96	15.96	15.96	0	52	0	0	0	0	0	0	0	48	0
Parascylliidae	<i>Parascyllium ferrugineum</i>	4	675.55	1018.1	512.8	0	0	0	0	21	0	0	0	0	46	33
Pegasidae	<i>Acanthopegasus lancifer</i>	1	0.65	0.65	0.65	0	79	21	0	0	0	0	0	0	0	0
Pentacerotidae	<i>Pentaceropsis recurvirostris</i>	1	1093	1093	1093	0	0	0	0	0	0	100	0	0	0	0
Platycephalidae	<i>Platycephalus bassensis</i>	71	179.96	2274	0.11	1	68	1	19	7	0	0	0	0	4	0
	<i>Platycephalus laevigatus</i>	93	525.07	1850	0.03	1	61	0	35	3	0	0	0	0	0	1
Pleuronectidae	<i>Ammotretis rostratus</i>	8	12.6	34.03	0.88	0	72	5	0	0	0	0	0	0	23	0
	<i>Rhombosolea tapirina</i>	33	110.8	470.5	0.003	0	56	4	4	2	7	0	0	0	19	8
Pomatomidae	<i>Pomatomus saltator</i>	19	276.85	404	208.85	0	0	0	95	5	0	0	0	0	0	0
Rajidae	<i>Raja lemprieri</i>	2	373.2	542.3	204.1	0	86	11	0	3	0	0	0	0	0	0
Rhinobatidae	<i>Trygonorrhina guaneri</i>	3	4741.68	7300	103.7	0	83	0	0	0	0	0	0	0	16	0
Scorpaenidae	<i>Neosebastes scorpaenoides</i>	3	5.73	12.5	2.07	0	37	0	0	14	0	0	0	0	49	0
Scyliorhinidae	<i>Juncrus vincenti</i>	1	406	406	406	0	20	0	0	80	0	0	0	0	0	0
Sillaginidae	<i>Sillaginodes punctatus</i>	52	40.31	310.6	0.007	6	70	6	0	0	0	0	0	0	17	2
	<i>Sillago bassensis</i>	1	84.6	84.6	84.6	0	0	0	0	93	0	0	0	0	7	0
Sphyracidae	<i>Sphyracna novaehollandiae</i>	2	1252	1288	1216	0	0	0	100	0	0	0	0	0	0	0
Syngnathidae	<i>Hippocampus abdominalis</i>	1	0.19	0.19	0.19	0	100	0	0	0	0	0	0	0	0	0
	<i>Mitotichthys semistriatus</i>	87	0.56	2.65	0.07	0	99	1	0	0	0	0	0	0	0	0
	<i>Stigmatopora argus</i>	61	0.32	1.03	0.01	0	98	0	0	2	0	0	0	0	0	0
	<i>Stigmatopora nigra</i>	194	0.14	1.55	0.002	0	100	0	0	0	0	0	0	0	0	0

CONTRIBUTIONS OF BODY SIZE, HABITAT AND TAXONOMY TO PREDICTIONS OF TEMPERATE AUSTRALIAN FISH DIETS

Family	Species	Number of fish	Average WW	Max. WW	Min. WW	a	ce	ci	f	me	mi	oe	oi	s	pe	pi
Tetraodontidae	<i>Stipecampus cristatus</i>	1	3.49	3.49	3.49	5	0	27	0	0	0	0	0	0	68	0
	<i>Urocampus carinirostris</i>	143	0.16	1.17	0.005	1	92	6	0	1	0	0	0	0	0	0
	<i>Vanacampus phillipi</i>	102	0.37	1.25	0.005	0	95	2	0	0	0	0	0	0	3	0
	<i>Contusus brevicaudus</i>	8	147.57	508.4	1.63	0	39	0	0	13	48	0	0	0	0	0
	<i>Contusus richiei</i>	1	0.02	0.02	0.02	0	100	0	0	0	0	0	0	0	0	0
	<i>Tetractenos glaber</i>	134	25.96	66.5	1.95	2	71	2	0	7	4	0	0	1	9	3
Tetrarogidae	<i>Gymnapistes marmoratus</i>	57	18.09	54.3	0.008	0	85	2	1	1	0	0	0	0	11	0
Triakidae	<i>Galeorhinus australis</i>	8	311.93	426.2	224.1	0	0	0	81	19	0	0	0	0	0	0
Urolophidae	<i>Mustelus antarcticus</i>	81	1841.61	6200	186.4	1	88	0	3	0	0	0	0	0	4	4
	<i>Urolophus cruciatis</i>	8	97.88	308.3	45.1	0	45	2	0	0	0	0	4	0	48	1
	<i>Urolophus paucimaculatus</i>	5	153.44	398.6	23.7	0	54	5	0	19	0	0	0	0	22	0
	<i>Urolophus viridis</i>	2	20.8	27.7	13.9	0	82	15	0	0	0	0	0	0	3	0

Chapter 4

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

Preface:

This has been published in a refereed journal and is presented below. The citation for the original publication is:

Soler GA, Edgar GJ, Stuart-Smith RD, Smith ADM, Thomson RJ (2016) Predicting the diet of coastal fishes at a continental scale based on taxonomy and body size. *Journal of Experimental Marine Biology and Ecology*, 480, 1-7.

In Chapter 4 we expand the geographical scope to test the accuracy of the predictive diet model developed in Chapter 3 at a continental scale. This predictive diet model is subsequently used in Chapter 5 to estimate the diet consumption of fish in the Reef Life Survey sites in Tasmania, Victoria and South Australia.

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

4.1 Abstract

Predicting diet of animals in ecological communities is necessary for a better understanding of trophic links and piecing together food webs to inform ecosystem-based management. A dietary model, *Consume*, was recently developed to predict detailed dietary information for fishes on the basis of fish identity and size. This model was field-tested over a continental scale, predicting community-level consumption for other temperate marine fish communities that differed in species composition and size structure. Using local stomach contents data to field-test predictions, accurate performance of the model was found across 14 locations around southern Australia. Prey type and mean prey size were predicted for fishes at new locations with high accuracy (mean percentage overlap between predicted and actual prey types = 73 %; r^2 between predicted and observed mean prey size = 89%) when trained with stomach contents data from subsets of sampled fishes at all locations. Model accuracy dropped, but was still respectable, when using training data only from one location (prey type accuracy = 67 %; mean prey size r^2 = 56 %). Prey type was more accurately predicted on the basis of consumer body size than species identity, while consumer family identity and size were needed for accurate prediction of mean prey size. The most important factors were evaluated by leaving out predictors (species, genus and family identity; size of consumer; habitat, location, ecoregion and biogeographic province). Exclusion of geographical location information resulted in little loss in accuracy. Our results highlight the need for consideration of consumer body size in trophic models, rather than binning species into functional groups solely on the basis of taxonomy. Application of *Consume* to situations where no dietary information exists, but at least fish family identity and size structure are known, will provide a novel mechanism for

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

testing important ecological hypotheses and assessing trophic consequences of anthropogenically-induced changes in community structure.

4.2 Keywords

Temperate Australia; Trophic model; Community consumption; Mean prey size; Seagrass

4.3 Introduction

Predation is an important process determining the structure of marine communities (Russ 1980), with critical information on the nature and magnitude of this captured in the diet of predators in the system (Edgar & Shaw 1995c, b). Fish represent major predators in shallow marine systems, and the ability to predict the diet of fishes at a given location should allow improved understanding of the ecological dynamics of the community (Edgar & Shaw 1995c).. Making predictions is often necessary because dietary data do not typically exist, at least not for the majority of species present in a fish community. Dietary predictions for individual animals will allow more accurate models of community consumption and food webs with which to answer key questions about the ecology of marine systems in relation to human impacts and management interventions, in the context of the effects of environmental variables. Nevertheless, the challenge with testing ecological predictions at large spatial scales is considerable due to logistical constraints and the great spatial variability in the natural environment (Peters 1991, Edgar & Shaw 1995c). Community-level calculations are useful, such as when assessing impacts of fishing and other threats on food web processes. At present, because of data deficiencies associated with the range of fishes of different body sizes at any single location, few attempts have been made to identify community-level patterns

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

of consumption by integration of data for individual fishes, let alone dietary studies of fish communities that extend across multiple locations.

A predictive diet model, *Consume*, was developed using dietary data from shallow water marine fishes sampled in Western Port, Victoria (Soler et al. 2016b). That study found that: (a) prey type and mean prey size were accurately predicted for consumer fish of known species and size (77% accurate for prey type and 93% for mean prey size, where prey type accuracy was calculated as the mean percentage overlap between predicted and actual prey types, and mean prey size accuracy as the correlation (r^2) between predicted and observed mean prey size); (b) when only the family of the consumer, rather than the species identity, was included, the loss in accuracy of the models was small (~1%); (c) the most important predictor for prey type was the size of the consumer; and (d) the most important predictor for mean prey size was the taxonomic identity of the consumer.

In this study, the accuracy of the *Consume* model was tested across a larger spatial and taxonomic domain in order to determine the generality and broader utility of this novel means to quantify food web links in the absence of detailed dietary information. The fish stomach content dataset described by Edgar and Shaw (1995a,b) was used for model training and field-testing, and encompassed 14 locations in southern Australia, plus five locations in Western Port, Victoria (Fig. 4.1). These locations extend over 3,000 km of coast and six marine ecoregions of the world and two provinces (Spalding et al. 2007).

The most important predictors of fish diet were tested to determine if they could be generalized over large spatial scales, or whether important location-specific factors and local community composition result in idiosyncratic patterns of prey consumption which may prohibit accurate larger-scale size-based food web modelling. To examine this, the loss in accuracy was tested when predicting fish diet for the 14 locations in

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

southern Australia using models trained only on the Western Port dataset, and therefore naïve to locally-collected dietary data, in comparison to model accuracy when trained with local data from a subset of sampled fishes. Finally, the loss in accuracy was estimated for prey type and mean prey size predictions when information on taxonomy, consumer fish size or locality (habitat, location, province and/or ecoregion) is lacking.

4.4 Methodology

A total of 4,336 fishes were sampled using seine and gill nets from 19 shallow marine locations in southern Australia, extending from Rottnest Island in Western Australia to Jervis Bay in New South Wales, including five in Western Port, Victoria (Fig. 4.1, Table 1S; Edgar and Shaw, 1995c). For each location, fish were caught, measured, weighed, and the stomach contents studied using consistent methods (see Edgar and Shaw (1995c)). Stomach contents were identified to the lowest taxonomic level possible, measured using a microscope graticle or Vernier callipers, and binned into 19 log-scale size-classes ranging from 0.125 mm to 64 mm (Edgar & Shaw 1995b).

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

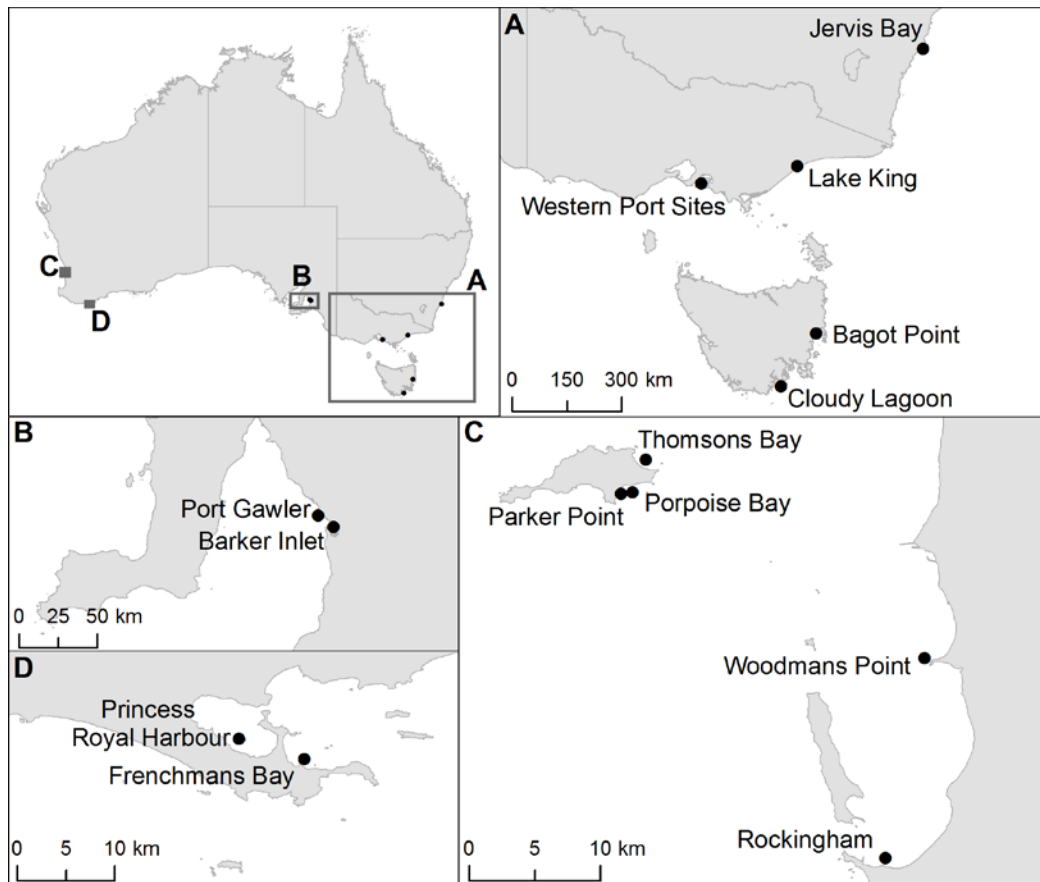


Figure 4.1 Locations sampled in southern Australia.

For dietary predictions, the *Consume* model developed in R–Studio ([R-Core-Team 2014](#)) in a previous study (Soler et al. 2016b) was used. *Consume* has two steps, the first step involved predicting the percentage of different prey types for each individual fish. For the second step, the mean prey size was predicted for a given prey type of an individual fish. The prediction of prey type percentage for a given fish was made using a set of fish with known diets, that are most similar to the given fish. This method is akin to a k -nearest neighbour procedure (Barber 2011, Conway & White 2012). The prediction of mean prey size (step 2) was made using linear regression models, where the assumptions of normality were met by applying a log transformation to the mean prey size. The importance of predictors was evaluated via cross validation for both steps of the *Consume* model.

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

In order to estimate the effect of location in the diet predictions, province and ecoregion (Spalding et al. 2007) were included in the *Consume* model. The Western Port and southern Australia dataset was used to predict the prey type and mean prey size for fish at all locations. To measure the accuracy of the prey type predictions, the overlap in percentages of different dietary items between predicted and observed values was calculated, as described by Soler et al. (2016b). The correlation (r^2) between predicted and observed mean prey size was used as a measure of accuracy of the model (Soler et al. 2016b). Different combinations of predictors were omitted to assess their effects on the accuracy of the model.

The accuracy of mean prey size predictions was tested as the weighted correlation (r^2) between the predicted mean prey size and the observed mean prey size. The weighting of the correlation was based on the diet percentage predictions. This means that each of the predicted prey types was not given equal weight, but rather the calculation weighted by the proportion of each of the predicted prey types. If a weighted correlation had not been used and, for example, the model predicted 1% prey type A and 99% prey type B but size was not predicted well for prey type A, this would have resulted in a low correlation despite the fact that prey type A was rare. Little difference between the weighted correlation and the non-weighted correlation was found, suggesting that the mean prey size was predicted with reasonable consistency across the different prey types. To graph the relationship between the predicted and the observed mean prey size, the locally-weighted smoothing LOWESS line was used. The LOWESS line allows for a curvilinear relationship whereas the regression forces the curve to be linear.

For computing the accuracy of models, predictions were based on a training dataset that excluded data from the consumer fish whose diets were being predicted (Soler et al. 2016b). In order to assess if the model based on a localised dataset was able to predict

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

across larger scales, the Western Port data was used to inform predictions of prey type and mean prey size for fishes across the 14 other locations. Results were validated using information on observed fish diets from these locations.

To avoid a few species with large sample sizes biasing predictions, the same algorithm as used in Soler et al. (2016b) to randomly select 12 individual fish was applied, encompassing a wide range of sizes, to represent each species, location and habitat. Initial trials indicated that 12 individuals per species gave the maximum accuracy for prey type and mean prey size predictions (Soler et al. 2016b). Different subsets of 12 individuals per species were used as predictors for fish diet in different runs of the model, and variability associated with selection of subsets was assessed.

The model used for predictions of mean prey size was (Soler et al. 2016b):

$$y_i = \mu + \beta_1 \text{Species}_i + \beta_2 \text{WW}_i + \beta_3 \text{Prey type}_i + \beta_4 \text{Habitat}_i \\ + \beta_5 \text{Location}_i + \beta_6 \text{province}_i + \beta_7 \text{ecoregion}_i + \varepsilon_i$$

(Equation 1)

where y_i = the log_e mean prey size prediction for the i th consumer fish, given the effects of Species, Wet weight (WW), Prey type, Habitat, Location, province and ecoregion; μ = overall mean; ε_i = residual error.

When predicting for the southern Australian locations using only Western Port data, the model prediction progressed sequentially from species to genus to family, and finally to wet weight, whenever the exact match was not found. This allowed the model to generate predictions for consumer fish that lacked information on that species, genus or family in the Western Port dataset. Furthermore, when predicting for southern Australian locations using the Western Port dataset, the habitat, location, ecoregion or province were not included in the models. Habitat was excluded because southern

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

Australian locations included an additional habitat (*Posidonia*) that was not present in Western Port. Moreover, both ecoregion and province comprised extra levels not present in Western Port.

From preliminary analyses, Soler et al. (2016b), identified that the most important predictors were taxonomy, size of the consumer fish (wet weight) and prey type. Hence, the model used for predicting the diet of fish for the southern Australian locations using the Western Port data was as follows (using notation as in Equation 1):

$$y_i = \mu + \beta_1 \text{Species}_i + \beta_2 \text{WW}_i + \beta_3 \text{Prey type}_i + \varepsilon_i$$

(Equation 2)

Prey types were categorised into similar trophic and functional groups as applied in the initial Western Port model (Soler et al. 2016b) with eleven prey types in total: algae, sponges, epifaunal crustaceans, infaunal crustaceans, epifaunal molluscs, infaunal molluscs, epifaunal polychaetes, infaunal polychaetes, other epifauna, other infauna, and fishes (as prey).

In order to assess breadth in mean prey size within diets, the standard deviation of mean prey size in guts was predicted for the 14 locations in southern Australia using the Western Port dataset, and the same model described by Soler et al. (2016b). This model also included a progression mechanism from species to genus to family and finally to wet weight whenever the exact taxonomic match was not found, as described above for mean prey size predictions.

4.5 Results

When using the *Consume* model (Soler et al. 2016b) to predict the diet of fish at a continental scale, prey type was predicted with an accuracy of $73 \pm 1\%$, where $\pm 1\%$ indicates the variation associated with different sets of 12 individual fish per species

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

randomly selected in each run of the model. These predictions were based on the complete dataset including Western Port and other southern Australian locations. The accuracy in prey type predictions for southern Australia (Western Port excluded), only dropped marginally, to $67 \pm 1\%$, when only Western Port data were used to train the model (and when all predictors were used).

The loss in the accuracy in the prey type predictions when predictors were sequentially dropped is presented for all locations in Table 4.1, and with Western Port locations excluded in Table 4.2. In both cases, the most important predictor for prey type was the wet weight of the consumer fish, while taxonomic identity contributed little. When the weight of the consumer fish was removed from the model, the accuracy dropped to $62 \pm 1\%$ (11% loss in accuracy) for the complete dataset and to $40 \pm 1\%$ (27% loss in accuracy) using only Western Port data to train the model. The loss in accuracy when taxonomic information was excluded was $\leq 3\%$ (Tables 1 and 2).

Table 4.1 Accuracy (%) for predicted prey type of fishes at all sampled locations in southern Australia, including Western Port (WW= log_e wet weight of consumer fish).

	Predictors	Accuracy (%) with all locations included
With all predictors	Species, WW, habitat, location, province, ecoregion	73
Without species	Genus, WW, habitat, location, province, ecoregion	73
Without species and genus	Family, WW, habitat, location, province, ecoregion	73
Without species, genus and family	WW, habitat, location, province, ecoregion	70
Without WW	Species, habitat, location, province, ecoregion	62
Without habitat	Species, WW, location, province, ecoregion	73
Without location	Species, WW, habitat, province, ecoregion	72

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

Predictors		Accuracy (%) with all locations included
Without ecoregion	Species, WW, habitat, province	71
Without province	Species, WW, habitat	71
Without all predictors but species and WW	Species, WW	71
Without all predictors but location	Location	24
Without all predictors but province	Province	20

Table 4.2 Accuracy (%) for predicted prey type of fishes in southern Australian locations except Western Port, using model trained only with Western Port data (WW= log_e wet weight of consumer fish).

	Predictors	Accuracy (%)
With all predictors	Species, WW	67
Without species	Genus, WW	67
Without species and genus	Family, WW	67
Without species, genus and family	WW	66
Without WW	Species	40

When the predicted prey type percentages were related to the natural log of the wet weight of the consumer fish, the most common prey types were found to change with consumer size (Fig. 4.2). For this figure (Fig. 4.2), the predicted prey type was estimated without the taxonomic information. The prey types that changed the most with consumer size were crustacean epifauna (ce), small fish (f), and mollusc infauna (mi). In the small size classes, crustacean epifauna (ce) was the preferred prey, dropping with increasing size of the consumer. Small fish (f) prey type increased with increases in the wet weight of the consumer, whereas mollusc infauna (mi) was a relatively

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

important prey type for the larger fishes (Fig. 4.2). Algae (a) also became a relatively important food item for the middle-sized fishes.

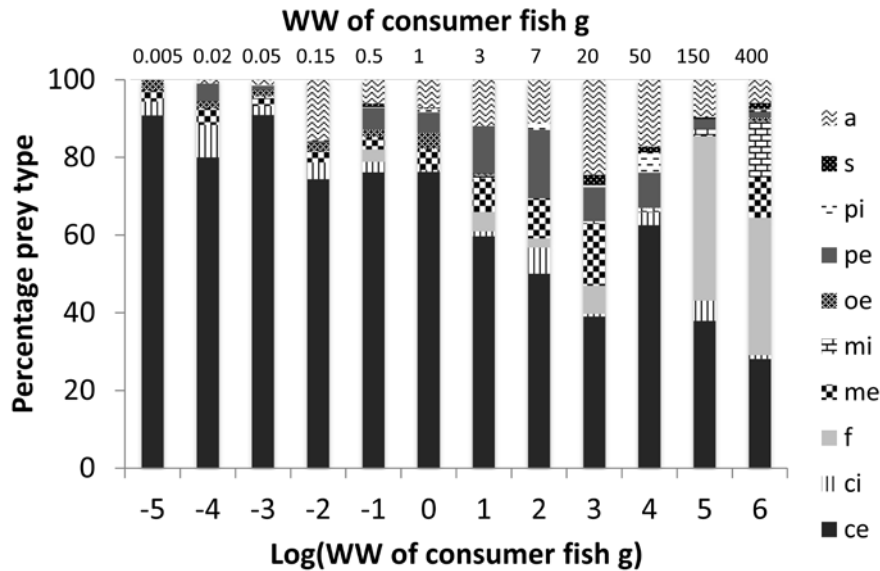


Figure 4.2 Predicted prey type percentages in relation to loge wet weight (WW) of the consumer fish. Predictions were based on all predictors other than taxonomic information for the consumer fish. Prey types: algae (a), sponges (s), epifaunal polychaetes (pe), infaunal polychaetes (pi), other epifauna (oe), infaunal mollusc (mi), epifaunal mollusc (me), fish (f), infaunal crustaceans (ci) and epifaunal crustaceans (ce).

The correlation (r^2) between observed and predicted mean prey size (Table 4.3; Fig. 4.3) for the complete dataset was high ($r^2 = 0.89 \pm 0.01$). Most of the predictors included had a significant contribution in the calculations (Table 2S). Predictions for the mean prey size (Table 4.4; Fig. 4.4) in southern Australia using only training data from Western Port were lower, but still respectable ($r^2 = 0.56 \pm 0.01$).

Table 4.3 Correlations between observed and predicted mean prey size of fishes in southern Australia including Western Port, and change in accuracy when predictors removed (WW= loge wet weight of consumer fish).

Predictors	r^2
------------	-------

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

	Predictors	r²
With all predictors	Species, WW, prey type, habitat, location, province, ecoregion	0.89
Without species	Genus, WW, prey type habitat, location, province, ecoregion	0.89
Without species and genus	Family, WW, prey type habitat, location, province, ecoregion	0.87
Without species, genus and family	WW, prey type, habitat, location, province, ecoregion	0.79
Without WW	Species, prey type, habitat, location, province, ecoregion	0.81
Without habitat	Species, WW, prey type, location, province, ecoregion	0.87
Without location	Species, WW, prey type, habitat, province, ecoregion	0.89
Without ecoregion	Species, WW, prey type, habitat, province	0.88
Without province	Species, WW, prey type, habitat	0.88
Without prey type	Species, WW, habitat, location, province, ecoregion	0.86
Without all predictors but species, WW and prey type	Species, WW, prey type	0.87
Without all predictors but species, WW and prey type	Species, WW	0.87
Without species, genus, family and WW	Prey type, habitat, location, province, ecoregion	0.42
Without species, genus, family, WW and prey type	Habitat, location, province, ecoregion	0.23
Without all predictors but location	Location	0.22
Without all predictors but province	Province	0.03

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

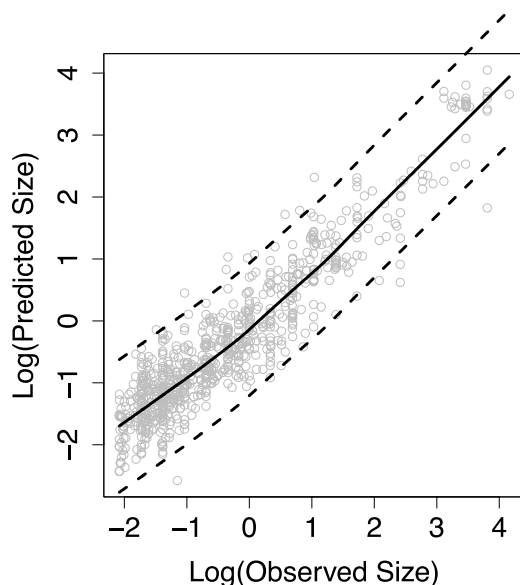


Figure 4.3 Scatterplot relating predicted and observed \log_e mean prey size for southern Australia including Western Port ($r^2=0.89$). The solid black line is the locally-weighted scatterplot smoothing curve (LOWESS). The dash black lines outline the upper prediction interval and the lower prediction interval (95%); both lines were estimated using LOWESS.

Table 4.4 Correlations between observed and predicted mean prey size of fishes in southern Australia (Western Port excluded), using only Western Port dataset for model training, and change in accuracy when predictors removed (WW= \log_e wet weight of consumer fish).

Predictors		r^2
With all predictors	Species, WW, prey type	0.56
Without species	Genus, WW, prey type	0.55
Without species and genus	Family, WW, prey type	0.55
Without species, genus and family	WW, prey type	0.39
Without WW	Species, prey type	0.42
Without all predictors but prey type	Prey type	0.11

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

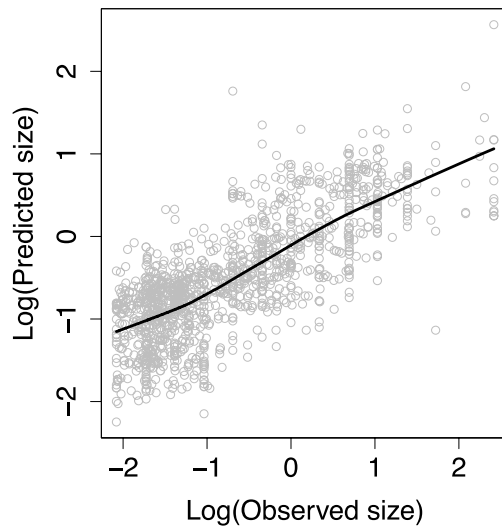


Figure 4.4 Scatterplot relating predicted and observed \log_e mean prey size for all consumer fish in the southern Australia locations (Western Port excluded) using training data from Western Port ($r^2=0.56$). The solid black line is the locally-weighted scatterplot smoothing curve (LOWESS).

The most important predictor for the mean prey size was the taxonomic information to at least family level; nevertheless, this was only marginally more important than the weight of the consumer fish, both for the whole dataset and when using only Western Port data as the training dataset (Tables 3 and 4). Furthermore, a high correlation was evident between the wet weight of the consumer fish and observed mean prey size consumed (Fig. 4.5; $r^2 = 0.65$ for full dataset). The correlation between the predicted mean prey size, using all predictors except taxonomic information, and the weight of the consumer fish, was high (Fig. 4.5; $r^2 = 0.94$). The loss in accuracy of predictions on mean prey size and prey type was small when geographical factors (location, ecoregion and province) were removed from the model (Table 4.1 and 3).

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

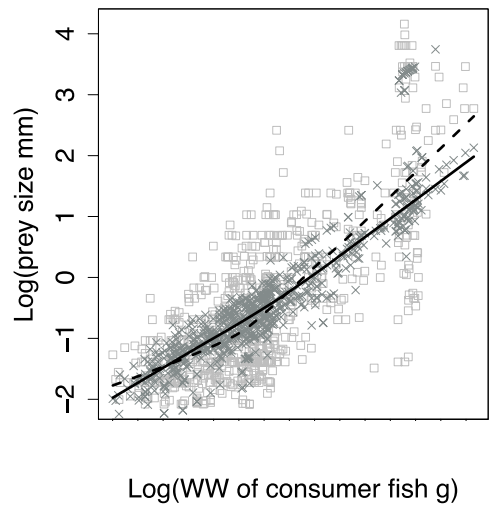


Figure 4.5 Scatterplot relating \log_e of observed (grey squares) and predicted (darker grey crosses) mean prey size in mm (\log_e) against \log_e wet weight (WW) of the consumer fish in g (\log_e) for all locations investigated in southern Australia, including Western Port. The model used a random sample of 12 individuals per species with a wide range of size. The dashed black line ($r^2=0.65$) is the observed mean prey size locally-weighted scatterplot smoothing curve (LOWESS). The black solid LOWESS line relates predicted mean prey size ($r^2=0.94$) to the size of the consumer fish (WW), with habitat, location and ecoregion included in models but no taxonomic information.

The correlation between the standard deviation of the natural log of the predicted mean prey size and the wet weight of the consumer fish shows only a slight positive relation ($r^2 = 0.03$) (Fig. 6). The loss in accuracy between the predicted and the observed standard deviation (SD) of the natural log of mean prey size indicates that taxonomic information is the most important predictor for SD of the prey (Table 4.5; Fig. 6).

Table 4.5 Correlation between the predicted and the observed standard deviations in dietary items for all of southern Australia, Western Port included (WW= \log_e wet weight of consumer fish).

	Predictors	r^2
With all predictors	Species, WW, prey type, mean prey size, habitat, location, ecoregion	0.28

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

Without species	Genus, WW, prey type, mean prey size, habitat, location, ecoregion	0.27
Without species and genus	Family, WW, prey type, mean prey size, habitat, location, ecoregion	0.25
Without species, genus and family	WW, prey type, habitat, mean prey size, location, ecoregion	0.13
Without WW	Species, prey type, mean prey size, habitat, location, ecoregion	0.25
Without habitat	Species, WW, prey type, mean prey size, location, ecoregion	0.26
Without location	Species, WW, prey type, mean prey size, habitat, ecoregion	0.26
Without ecoregion	Species, WW, prey type, mean prey size, habitat, location	0.25
Without habitat, location, ecoregion	Species, WW, prey type, mean prey size	0.24
Without prey type	Species, WW, mean prey size, habitat, location, ecoregion	0.23
Without mean prey size	Species, WW, prey type, habitat, location, ecoregion	0.28
Without all predictors but location	Location	0.05
Without all predictors but habitat	Habitat	0.02

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

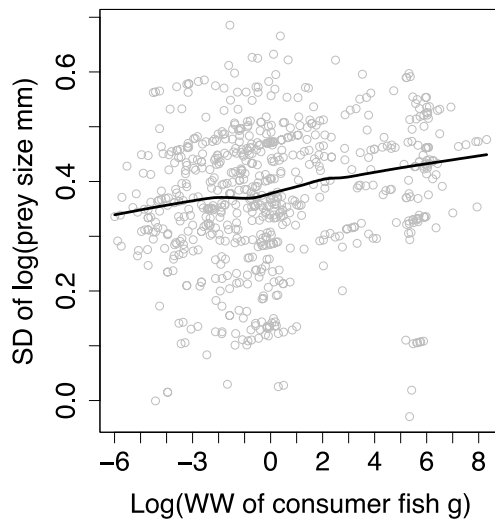


Figure 4.6 Scatterplot relating predicted standard deviation of the \log_e mean prey size (mm) and the \log_e of the wet weight (WW) of the consumer fish (g) for all locations investigated in southern Australia using all predictors ($r^2=0.03$). LOWESS curve is shown in solid black.

4.6 Discussion

Diet predictions for fishes based on taxonomy and size provide opportunities to better understand the ecological dynamics of fish communities. A problem with many mechanistically-scaled models is that predictions cannot be tested – predictions are needed because empirical field data are lacking (Rastetter et al. 2003). The present study is unusual in that it includes assessments of the accuracy of predictions for prey type and mean prey size on the basis of observed dietary data. By demonstrating the accuracy of the model in circumstances where little or no dietary data are included, we have shown the utility of this tool for ecological studies in other locations containing different sets of species and for which no dietary data currently exists.

Diet prediction accuracy using the *Consume* model for prey type and mean prey size declined when predictions for southern Australian locations were made only on the basis of dietary data from Western Port; nevertheless, the correlation between predicted

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

and observed values remained relatively high. Furthermore, the initial findings for Western Port were corroborated regarding the importance of taxonomy and size of the consumer fish to accurately predict its diet. Size of the consumer fish was by far the most important predictor for prey type at the larger geographical scale. While the initial findings from Western Port were also validated, showing that taxonomic identity was the most important predictor for prey size, the influence of consumer size was of near equal importance. In both prey type and prey size predictions, taxonomy and body size together achieved the best predictions.

Body size is the most important predictor for prey type, presumably because of the magnitude of changes in the diets of fishes through different life-history stages (Soler et al. 2016b). Individuals of different size within a species must therefore play different functional roles within marine ecosystems. Other authors have previously recognised the importance of ontogenetic changes in prey size, as well as variations in the trophic level. For example, Cushing (1975) found that the prey size of herring (*Clupea harengus*) ranged up to 4 orders of magnitude through different life history stages. Body size also relates to the quantity of resources exploited (Werner & Gilliam 1984), and has been suggested as a good measure of trophic energy flow within the fish community, relating the size of the fish and its prey (Dickie et al. 1987). The length of food chains is affected by predator-prey mass ratios, highlighting the importance of body size in ecological studies (Jennings & Warr 2003).

The importance of ontogenetic dietary shifts is also well-known from other taxa and ecosystems, including aquatic instar development in freshwater insects like dragonflies, and further illustrates the variety of ways in which ontogenetic changes can affect community structure (Rudolf & Rasmussen 2013). Thresholds are often evident, where certain prey types only become available when an animal reaches a particular size. This has been particularly noted for carnivorous marine fishes (Kulbicki et al. 2005). In the

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

associated Western Port study (Soler et al. 2016b), it was found that profound changes in the predicted prey category were directly related to the wet weight of the consumer fish, although in that case, it was due to a shift in feeding strategy with growth in body size, as diet categories were inclusive of the full range of potential prey size.

As highlighted by other authors (Maury et al. 2007a, Maury et al. 2007b), the majority of trophic models in marine ecosystems categorise the system using species and functional groups, with the underlying assumption that individuals within these groups are similar (Polovina 1984, Pauly et al. 2000b). By contrast, a few models have considered animal size (e.g. biomass), with the assumption that size is the most important factor driving the strength of interactions in the ecological system (Shin & Cury 2001, Brown & Gillooly 2003, West & Brown 2005, Fulton et al. 2011). These models reasonably assume that most predators are larger than their prey, determining that the predator-prey relations are mostly based on the size of the predator (Scharf et al. 2000, Jennings et al. 2001, Jennings et al. 2002a). Furthermore, Jennings et al. (2001) showed that while body size was only a weak predictor of trophic position within species, there was a strong community-scale relationship between trophic position and body size in the North Sea. The *Consume* model indicates that body size, rather than taxonomy, is the most important predictor of which prey types are being consumed by shallow water marine fishes. This predictive diet model should therefore enable improved assessments of the trophic compartments occupied by individuals of a species through its lifespan.

Although taxonomic identity (at the species, genus or family level) was not as important as size when predicting the type of food consumed by fish, it was critical for predicting the size of prey consumed. This was identified in the original Western Port study, and was here confirmed at a continental scale. Previous studies have reached a similar conclusion: that taxonomic identity was related to prey size and that, within

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

species, prey size was related with the size of the predatory fish (Juanes 1994, Mittelbach & Persson 1998, Scharf et al. 2000, Andersen & Beyer 2006, Law et al. 2012, Soler et al. 2016b). In the current study, the size of the consumer fish (i.e. wet weight) was also a good predictor for prey size. The correlation between the predicted mean prey size (with no taxonomic information) and wet weight of the consumer fish was higher than the correlation between the observed mean prey size and wet weight (Fig. 4.5). A possible explanation for why the observed size correlation is lower is that the empirical field data are affected by a range of other factors not considered in the models, which add noise to the relationship.

The standard deviation of sizes of items in stomach contents was better predicted by taxonomic information than body size. This indicates that certain species are feeding from a larger prey size array than members of other species of similar size; species with relatively small mouths, such as mullet (*Mugilidae*), were found to consume a smaller range of prey sizes than those with larger mouths. In a study conducted in the northeast US where the diet of 18 fish species was considered, the maximum and minimum prey size, as well as the breadth of prey size, were also found to be principally related to the taxonomic identity of the predatory fish (Scharf et al. 2000).

Another important result from this study was that the loss in accuracy of the predictions was small when using the family of the consumer fish as the taxonomic identity, instead of the species. This has important implications for generality of the results, suggesting that prey type and size can be accurately predicted for other previously unassessed members of the families included to train the model. Any available information from published studies on diets of other species in the family would add further to the accuracy of predicted diets for unstudied species. Clearly, diets of species are constrained by morphological rigidity at the family level – most families are visibly recognisable because of similar sets of particular morphological

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

characteristics. The results suggest there is an equivalent degree of rigidity in diet amongst species. Exceptions clearly exist, however, particularly amongst very large families such as wrasses and gobies, where great morphological diversity occurs. A study of New Caledonian marine fishes reported significant intra-family variation in diets (in Lethrinidae), as well as prey consumption similarities within other families (Kulbicki et al. 2005).

Geographical location was found to contribute only marginally to diet predictions for both prey type and prey size - consumer fishes of a particular family and body size had similar diets regardless of location. Considering the patchiness in the availability of each particular food type across the marine domain, a number of possible mechanisms could contribute to this result. It is possible that local representatives of each family associate with particular sets of conditions or microhabitats that contain similar mixes of potential prey types, regardless of location. Diet type categories used in this study were relatively broad, and are more likely to occur across multiple regions than had prey type been more finely partitioned, but they will still occur in varying proportions at different locations. It may also be that fishes selectively remove particular prey items, regardless of density in the seascape, and such selectivity has an element of consistency within families. While further work is needed to determine this, the results of this study most likely reflect a combination of these and other mechanisms.

In conclusion, the *Consume* model generated accurate predictions of prey type and prey size for consumer fishes at a continental scale. The model was sufficiently robust to predict across a geographical domain using training data from a single location, although accuracy substantially improved, particularly for prey size, when broader-scale training data were utilised. The most essential predictors for the diet estimates were the size of the consumer fish followed by family identity, albeit these elements contributed differently when predicting prey type versus prey size. Community-level estimates

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED ON TAXONOMY AND BODY SIZE

using this dietary model, where diet predictions based on body size and family identity are aggregated for all individuals at a location, should provide a novel perspective to food web studies, and can capitalise on more readily available community-structure data.

4.7 Acknowledgments

This study was supported by the Australian Research Council (LP100200122), a Tasmania Graduate Research Scholarship (to G.A.S.), and the Marine Biodiversity Hub, a collaborative partnership funded under the Australian Government's National Environmental Science Programme. We would like to thank Justin Hulls for designing the map (using ArcGIS) and Dr Kilian Stehfest for supporting the development of the model. We would also like to thank Dr Simon Wotherspoon and Dr Andre Punt for their input and comments in developing the predictive diet model. The authors have no conflict of interest to declare.

4.8 Supplementary material

Table 4.6 (Table 1S) Number of fish sampled at each site included in this study. Also shown are the sites for each ecoregion and province (Spalding et al. 2007).

Province	Ecoregion	Location	Site	Habitat	No. of fish
Southeast Australasian Shelf	Bassian	Bagot	Bagot Point	Shallow unvegetated	43
				<i>Zostera</i>	80
		Bruny Island	Cloudy Lagoon	Shallow unvegetated	66
				<i>Zostera</i>	61
	Cape Howe	Jervis Bay	Jervis Bay	<i>Posidonia</i>	81
				Shallow unvegetated	55
				<i>Zostera</i>	89

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

Province	Ecoregion	Location	Site	Habitat	No. of fish
		Lake King	Lake King	Shallow unvegetated	26
				<i>Zostera</i>	65
	Western Bassian	Adelaide	Barker Inlet	Shallow unvegetated	19
				<i>Zostera</i>	89
			Port Gawler	Posidonia	77
				<i>Zostera</i>	43
		Western Port	Crib Point	Shallow unvegetated	73
				<i>Zostera</i>	59
			French Island	Deep unvegetated	214
				Shallow unvegetated	320
				<i>Zostera</i>	743
				Deep unvegetated	73
			Rhyll	Deep unvegetated	92
				Shallow unvegetated	310
				<i>Zostera</i>	523
				Deep unvegetated	71
			Tooradin	Shallow unvegetated	228
				<i>Zostera</i>	268
Southwest Australian Shelf	Leeuwin	King George Sound	Frenchmans Bay	<i>Posidonia</i>	36
			Princess Royal Harbour	<i>Posidonia</i>	168
				Shallow unvegetated	21
			Rockingham	<i>Posidonia</i>	104

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

Province	Ecoregion	Location	Site	Habitat	No. of fish
				Shallow unvegetated	47
		Rottnest	Natural jetty Rottnest	Shallow unvegetated	5
			Parker Point	Shallow unvegetated	45
			Porpoise Bay	<i>Posidonia</i>	34
			Thompsons Bay	<i>Posidonia</i>	24
		Woodmans	Woodmans Point	<i>Posidonia</i>	79
				Shallow unvegetated	5
					4336

PREDICTING THE DIET OF COASTAL FISHES AT A CONTINENTAL SCALE BASED
ON TAXONOMY AND BODY SIZE

Table 4.7 (Table 2S) ANOVA results for the predictors for mean prey size for 12 individuals per species with a wide range of size for all sites included. Asterisks denote statistically significant differences (***) = $p < 0.001$. WW= log wet weight of consumer fish.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Species	62	1597.5	25.8	90.1	< 2.2E-16	***
WW	1	151.2	151.2	528.5	< 2.2E-16	***
Prey type	9	102.5	11.4	39.8	< 2.2E-16	***
Habitat	5	3.1	0.6	2.1	0.06	
Site	18	15.7	0.9	3.1	0	***
Residuals	1048	299.8	0.3			

Chapter 5

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

Preface:

This paper is in review at Ecological Applications

Soler GA, Edgar GJ, Stuart-Smith RD, Smith ADM, Thomson RJ (*in review*)

Moving beyond trophic groups: evaluating fishing-induced changes to temperate reef food webs. Ecological Applications

In Chapter 5 we used the predictive diet model developed in Chapter 3 and 4 to estimate the diet consumptions of the fish assemblages in sites visually surveyed in Tasmania, Victoria and South Australia. In this Chapter we test the effect of protection from fishing as well as other variables on the estimates of diet consumptions of the fish community. Furthermore, in this Chapter we also draw a parallel with the trophic group analysis presented in Chapter 2.

5.1 Abstract

Exploitation of fish resources has far-reaching but inadequately assessed implications in marine food webs. Exploration of such effects is typically undertaken using trophic models that rely on partially subjective categorisation of species into trophic groups, and that mostly overlook the substantial contribution of ontogenetic dietary variation within fish species and community size structure. Here we apply a recently-developed diet model that predicts diet for individual fish to then estimate community-level fish consumption across 376 southern Australian sites. These data allow evaluation of the impacts of fishing and human population density as top down pressures on shallow reef communities. In addition to a 79% increase in total consumption by fishes in southern Australian no-take MPAs, we identify unexpectedly high consumption of algae and sessile invertebrates, results not apparent when species are pre-allocated to trophic groups. Individual size-structured modelling potentially fills important knowledge gaps in understanding human impacts on marine food webs.

5.2 Keywords

Predictive diet model, marine reserve, southern Australia fish diets, SCUBA dive fish surveys

5.3 Introduction

Environmental and human influences on marine food webs are typically assessed through trophic models that quantify, or in qualitative models link, connections between trophic groups. These models are invariably highly simplified, typically requiring considerable subjectivity in decisions on the number of trophic compartments and

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

arrangements within which the multitude of species that occur in marine habitats are grouped (Polovina 1984, Pauly et al. 2000b). Species are assumed to act similarly within compartments, regardless that this assumption contradicts Hutchinson's well known niche paradigm, in which each species inhabits a unique niche (Hutchinson 1978). The validity of trophic models clearly rests on the realism of assumptions and the appropriateness of theory that underlies modelled relationships. Whether the simplifications necessary to develop modelled relationships matter depends on the purposes to which the model is put. Yet biases associated with trophic categorisations are generally unknown, and in many cases unknowable, other than when field observations of manipulated communities can be undertaken to validate predictions.

The ecological role of aquatic species is highly flexible through their life history (Cushing 1975, Edgar & Shaw 1995b, Jennings et al. 2002b, Rudolf & Rasmussen 2013), with body size an important determinant of the location of individuals within the food web (Dickie et al. 1987, Jennings & Warr 2003, Blanchard et al. 2011, Zhang et al. 2014). In particular, similarly-sized taxa from vastly different phylogenetic lineages may share greater similarity in diet than juveniles and adults of the same species (Soler et al. 2016b). Thus, an ideal model would include body size and allow species to change ecological roles as they grow, with progression through prey types and sizes (Shin & Cury 2001, Brown & Gillooly 2003, West & Brown 2005, Fulton et al. 2011). A recent advance in this area has been the development of the model *Consume*, which predicts the diet of individual fishes with high accuracy on the basis of body size and taxonomic identity: (Soler et al. 2016a, Soler et al. 2016b).

Here we apply the *Consume* model to an extensive dataset of fish community structure (including species and size distributions) from Reef Life Survey (RLS; (Edgar & Stuart-Smith 2014) field surveys at sites spanning four marine ecoregions (Spalding et al. 2007). We estimate community-level consumption at each site, and use those

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

predictions to test hypotheses associated with key environmental and anthropogenic drivers of fish community structure. Specifically, we address the questions:

(1) How do fishing and other human disturbances indirectly affect lower trophic levels of temperate reef ecosystems?

(2) How do ecological outcomes derived from predictions of community consumption using *Consume* differ from those inferred using models with traditional trophic groups?

For (1), we assess how fishing and proximity to human population centres influences mean prey size, prey type, and total consumption of rocky reef fish assemblages, after accounting for environmental influences. This analysis uses no-take marine protected areas (MPAs) as a broad-scale experimental framework for understanding consequences of removal of fishes by fishing pressure. For (2), we compare results from (1) with model output using the same reef fish community data, but with fishes categorised into four commonly used reef fish trophic groups (higher carnivores, benthic carnivores, herbivores and planktivores).

We hypothesise that reduced total fish biomass in locations that are fished or in close proximity to human population centres will result not only in reduced overall community consumption, but notable differences in the types and sizes of prey consumed, due to depressed abundance of large individuals and higher trophic level fishes (Halpern 2003, Edgar et al. 2014).

5.4 Methodology

We used *Consume* to predict prey consumption for fish assemblages surveyed by visual census methods at 376 shallow rocky reef sites in Tasmania, Victoria and South Australia (Fig. 5.1).

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES
TO TEMPERATE REEF FOOD WEBS



Figure 5.1 Reef Life Survey (RLS) sites investigated in South Australia, Victoria and Tasmania.

Data on fish community structure included species-level abundance and size structure for all fishes sighted along 50 x 5 m belt transects by divers in the Reef Life Survey program (RLS; (Edgar & Stuart-Smith 2014). Detailed fish survey methods are described by Edgar and Stuart-Smith (2014). RLS sites for this study were located in shallow reef habitats between 1 and 23 m depth, with mean depth of 7.5 m.

Consume possesses two components, the first using premises of k -nearest neighbours (Barber 2011, Conway & White 2012) to predict percentages of different prey categories for each individual fish observed in the RLS data. The second step applies linear models to predict the mean size of prey for each fish. The results of the two models are then combined in an output matrix of percentages by prey type and mean prey size for each individual fish. Full details of the models and their predictive ability are provided in Soler et al. (2016b) and Soler et al. (2016a).

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

For this study, *Consume* was trained using detailed dietary information from 137 fish species collected across southern Australia (Edgar & Shaw 1995b, c), as well as publically-available information for an additional 2,230 species through Fishbase (www.fishbase.org) and other published and unpublished sources (Table 5.1). Dietary information was only utilized from published sources when the size of individual fish, species identity, and percentage of different prey types were provided. A total of 134 of the 252 fish species present in the RLS data used for this study were matched with the diet content data collected across southern Australia by Edgar and Shaw (1995c) at the species-, genus- or family level. For the species not present in that dataset, the component of *Consume* that predicts prey type (Soler et al. 2016a, Soler et al. 2016b) used 109 species from Fishbase and other publically-available data. Only 11 species present in the RLS field survey data did not have a match to dietary information at family-level or better (following the sequential process described in Soler et al. (2016a)), and thus prey type for these was estimated based only on wet weight of the consumer fish. When diet information at the species-level was lacking, and genus- or family-level dietary information applied, the loss of accuracy was minimal, as assessed and demonstrated in prior studies (Soler et al. 2016a, Soler et al. 2016b).

Prey types were classed within 13 categories (algae (*a*), ‘sponges’ (*s*), epifaunal polychaetes (*pe*), infaunal polychaetes (*pi*), infaunal molluscs (*mi*), epifaunal molluscs (*me*), fishes (*f*), planktonic fish larvae (*fp*), infaunal crustaceans (*ci*), epifaunal crustaceans (*ce*), planktonic crustaceans (*cp*), other epifauna (*oe*), other infauna (*oi*)). The category ‘sponges’ included sponges, ascidians and hydroids, while ‘algae’ included some seagrass, and ‘planktonic fish larvae’ also included fish eggs.

Daily prey consumption per fish was calculated by combining the model output of the percentage of each prey type and daily consumption rates (in proportion to fish weight). We used species-specific values for the latter whenever the daily consumption for a particular species was available, and 3.1% of body weight per day as a standard for

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

species for which consumption rates were unknown (following Robertson (1984) and Robertson and White (1986); and applied in Edgar and Shaw (1995b)). These calculations provided a predicted daily consumption for each fish recorded on RLS surveys for each prey type. Total community consumption was calculated as the sum of values for all individuals at a site.

By binning the predicted mean prey size following the sieve size categorization described in Edgar and Shaw (1995b), we estimated the prey consumed for each fish community by prey type for each size bin. A total of 19 size bins were considered: 0.125, 0.178, 0.25, 0.355, 0.5, 0.71, 1, 1.4, 2, 2.8, 4, 5.6, 8, 11.2, 16, 22.5, 32, 45 and 64 mm. Because model accuracy was affected by long tails of the prey size distribution, we also undertook an analysis that combined all size classes smaller than 0.5 mm (<0.5) and all size classes larger than 11.2 mm (>11.2). Outputs of this analysis matched findings with the finer scale bins, and are presented as supplementary material (Figs. S1, S2).

The effects of fishing and general human impacts on predicted community consumption were assessed using Linear Mixed Models (LMMs), with effect of protection from fishing (no-take MPAs) introduced after the influences of other anthropogenic and environmental variables (SST mean, SST range, PAR, Pop index – human population index) were considered. Environmental data, including annual mean sea surface temperature (SST), SST range, and photosynthetically-active radiation (PAR-mean) were extracted from Bio-Oracle (Tyberghein et al. 2012), as described in more detail in Soler et al. (2015). The human population index (Pop index) was calculated using a quadratic Kernel function (Silverman 1986) to a smoothly tapered surface for each of the human population centres (Soler et al. 2015). These covariates were chosen as they were shown to influence the distribution of fish composition and biomass at regional scales in prior analyses (Stuart-Smith et al. 2013, Edgar et al. 2014, Soler et al. 2015).

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

For analysis of MPA effects, the level of protection for a given site was classed as no-take or fished. Sites were considered no-take based on their level of governance, effectiveness, and time since declaration (Edgar et al. 2014). Open-access sites lay outside MPAs or inside MPAs that allowed fishing or had negligible enforcement (Edgar et al. 2014).

LMMs allowed the influence of protection to be examined while considering other factors (environmental and anthropogenic) plus the random effect of ecoregion (Spalding et al. 2007), using the following equation:

$$y_{pei} = \mu + \beta_1 \text{SSTmean}_i + \beta_2 \text{SSTrange}_i + \beta_3 \text{PARmean}_i + \beta_4 \text{POPindex}_i + \beta_5 \text{Protection} + \gamma_e + \varepsilon_{ei}$$

(Equation 1)

where y_{pei} = \log_e prey consumed (in g) at the i th site, given the effects of SST mean, SST range, PAR-mean and human population; μ = overall mean; γ_e = effect of the e th ecoregion (random effect); ε_{ei} = residual error. Due to the absence of some prey consumed at some of the prey sizes in some of the predictions, we added a constant (= 0.05) to all of the predictions [$\ln(y+0.05)$]. Given the prey consumption predictions were scaled in grams, the addition of 0.05 grams to the predictions was chosen as a reasonable ecological value for the step between no prediction and minimum daily predicted prey consumed (Ortiz et al. 2000). A 4th root transformation of the predictions for daily prey consumption was also applied, providing the same conclusions as log transformation with 0.05 g constant added. Results from the log transformation are presented here so that the effect of the different covariates can be shown as percentage (%) difference in predicted daily prey consumed.

Ecological inferences based on *Consume* predictions were compared with conclusions arising from more classical trophic group analysis. Four trophic groups that are commonly applied to reef fishes were used: higher carnivores, benthic carnivores,

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

planktivores and herbivores, based on dietary information obtained from Fishbase (www.fishbase.org) and previous studies with the same dataset (Stuart-Smith et al. 2013, Edgar et al. 2014, Soler et al. 2015). A more detailed list of prey types for each trophic group is described in Soler et al. (2015). Trophic groups were further categorized into three size classes: small (<7.5 cm), medium (7.5 – 30 cm) and large (>30 cm), based on the total length of fishes observed during the surveys. LMMs were then applied to the 376 sites to assess the effects of protection (no-take MPAs vs fished sites) and other environmental and anthropogenic variables on the biomass of fishes in the 12 trophic group by size class categories. The same environmental and anthropogenic variables were investigated as with *Consume* output, and effect sizes calculated in terms of % difference in relative biomass for the same set of sites.

Community consumption differences in no-take MPAs compared with fished sites were assumed to be proportional to relative biomass differences, partitioned between the twelve trophic groups by size class categories. Even though the ratios for prey types and trophic groups come from different calculations and their magnitudes differed, they show a high correlation. For planktivores and herbivores, total % biomass differences of the three size classes were estimated as the geometric mean of the ratios and transformed to percentage difference of the increase in consumption of plankton and algae, respectively. Consumption of fishes (*f*) as prey was predicted as the geometric mean of the ratios of medium and large higher carnivores, as small individuals are likely not feeding on fishes. The geometric mean estimates were transformed into percentage increase of medium and large higher carnivores. Consumption of benthic invertebrates was predicted from the geometric mean of the ratios of small higher carnivores and all sizes of benthic carnivores; this geometric mean estimate was then transformed to a percentage difference. A similar process for human population effect was followed assuming that consumption differences were proportional to biomass differences for the twelve trophic groups by size categories.

5.5 Results

Prey type, mean prey size and daily prey consumption were estimated for 44,024 individuals observed in 376 sites across Tasmania, South Australia and Victoria. 1,160 species out of a total of 1,650 species recorded in the RLS data did not possess dietary information at that taxonomic level. Estimates of mean prey size based on species-level matches (plus wet weight) were possible in 14,089 cases (32%), genus-level matches in 6,662 cases (15%), family only-level matches in 14,946 cases (34%), while wet weight only was used to generate diet predictions in 8,327 cases (19%). These numbers imply poorer predictions of prey size than prey type (Table 5.1), with prey type predictions from family-level or better matches in 42,270 cases (96%), and predictions based only on wet weight of the consumer fish in 1,754 cases (4%).

Table 5.1 Sources of diet information and number of fish included in the model as prediction data set. Level of information was based on the type of information available. Prey type was expressed as percentage of diet.

Region	Reference	# of fish	# of species	Level of information
Southern Australia	(Edgar & Shaw 1995a, b)	4336	137	Prey type; prey size
Tasmania, Australia	Soler and Edgar (<i>unpublished</i>)	11	4	Prey type; prey size
Eastern Island	DiSalvo et al. (2007)	77	37	Prey type; some prey size information
Madagascar	Harmelin-Vivien (1979)	110	110	Prey type; some prey size information
West Indies	Randall (1967)	163	125	Prey type; some prey size information
Marshall Islands	Hiatt and Strasburg (1960)	75	70	Prey type
Hawaii	Hobson (1974)	82	77	Prey type
Global	Fishbase	3845	1586	Prey type

Community-level predictions of type and size of prey consumed were influenced by a number of anthropogenic and environmental factors (Figs. S3, S4). For each 1°C rise in annual mean SST, daily consumption by the fish community of most prey types

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

increased, especially crustacean infauna and sponges. Temperature fluctuation through the year (temperature range) had a negative effect on community consumption of most prey types, with algae (*a*), mollusc epifauna (*me*), other epifauna (*oe*) and sponges (*s*) most affected (Fig. S3). PAR-mean, a metric of light available for primary production, had a positive influence on consumption of crustacean infauna (*ci*).

After accounting for these environmental drivers of fish community structure, and therefore total consumption, greater biomass of fishes in all trophic groups within no-take MPAs resulted in significantly higher predicted community daily consumption of most prey types compared with fished sites outside of no-take MPAs (Fig. 5.2A). Consumption of algae (*a*), small fishes (*f*) and sponges (*s*) differed most between fish assemblages inside no-take MPAs relative to fished sites (222%, 310% and 305% positive difference, respectively). Human population density had little effect on daily consumption of most prey types; nevertheless, algae (*a*), mollusc infauna (*mi*) and polychaete (*pi*) infauna were positively affected by increasing human population density, and crustacean infauna (*ci*) was negatively affected (Fig. 5.2B; Table 5.2).

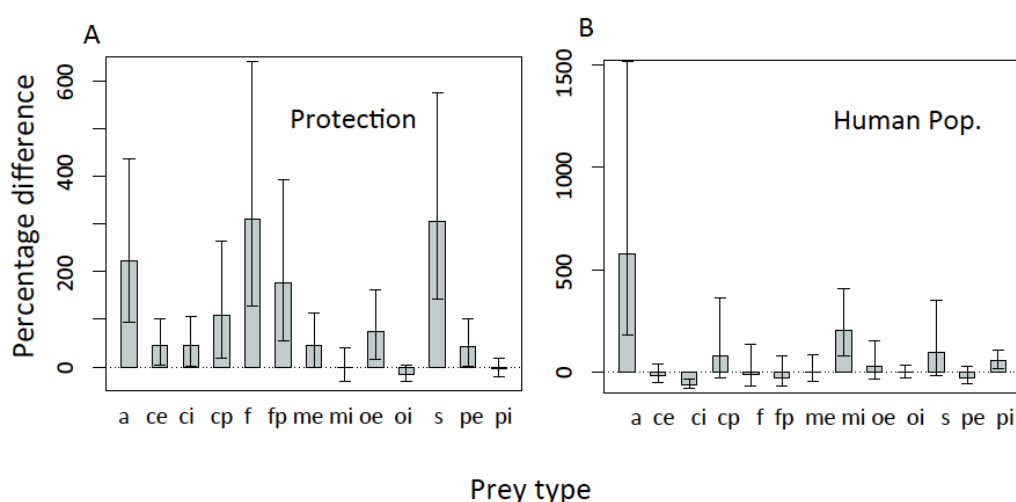


Figure 5.2 (A) Percentage difference in prey types consumed (\pm 95% confidence intervals) by the fish community at sites in protected areas relative to fished zones. Log ratios of daily prey

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

consumption in no-take MPAs relative to fished zones ($\log(C_{\text{preyMPA}}/C_{\text{preyOPEN}})$) were obtained for each prey type from the coefficient for Protection, β_5 . (B) Percentage difference for a single unit increase in the index of local human population density obtained for each prey type from the coefficient for PopIndex, β_4 . Ratios were obtained from the coefficients for POPindex, β_4 and Protection, β_5 , and transformed into percentage difference in biomass using the relation $100 * (\exp(\beta_{4,5}))$ from Equation 1 on this manuscript. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero. Prey types: algae (*a*), sponges (*s*), epifaunal polychaetes (*pe*), infaunal polychaetes (*pi*), infaunal molluscs (*mi*), epifaunal molluscs (*me*), fishes (*f*), planktonic fish larvae (*fp*), infaunal crustaceans (*ci*), epifaunal crustaceans (*ce*), planktonic crustaceans (*cp*), other epifauna (*oe*), other infauna (*oi*).

Most prey size classes greater than 1.4 mm were consumed in greater quantities by fish assemblages protected in no-take MPAs relative to fished areas (Fig. 5.3A). Larger prey consumed inside no-take MPAs reflected recovery of populations of larger fish species, and larger average sizes of fishes at protected sites. Prey size predictions were not significantly different between locations of high and low human population density; except for the 1.4 and 2 mm size classes (Fig. 5.3B).

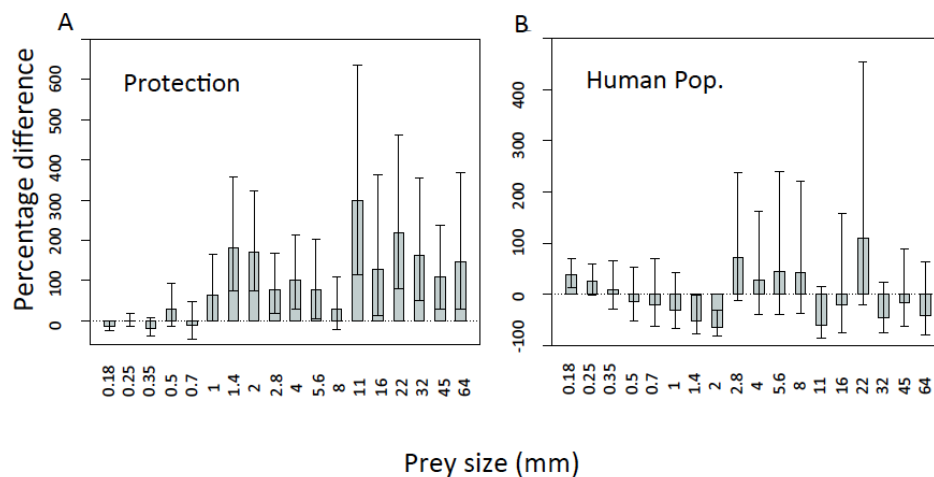


Figure 5.3 (A) Percentage difference in daily consumption of different size classes for all prey types consumed by the fish community in protected areas (no-take MPAs) relative to fished zones ($\pm 95\%$ confidence intervals). (B) Percentage difference for a single unit increase in the index of local human population density obtained for each prey size bin from the coefficient for PopIndex,

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

β_4 . Ratios were obtained from the coefficients for POPindex, β_4 and Protection, β_5 , and transformed into percentage difference in biomass using the relation $100 \cdot (\exp(\beta_{4,5}) - 1)$ from Equation 1 on this manuscript. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero.

Large and medium size classes of the four trophic groups had significantly greater biomass inside no-take MPAs relative to fished sites (Fig. 5.4A). Based on this trophic group analysis the consumption increase of fishes and large invertebrates was on average 116% and algae 62% higher in MPAs (Table 5.2). The small class of higher carnivores, medium and large classes of benthic carnivores as well as medium and large classes of planktivores also had greater biomass in no-take MPAs, with corresponding implications for consumption of mobile invertebrates, small fishes and plankton. An increase in small invertebrate consumption was identified for the small higher carnivores and benthic carnivores combined. These results contrast those from the predictions from *Consume*, with the most notable differences in the proportional magnitude of increased consumption of sponges (*Consume* predictions are substantially greater; Table 5.2). The correlation of the geometric means of the ratios between prey types and trophic groups due to the effect of protection was high and significant ($r^2 = 0.83$).

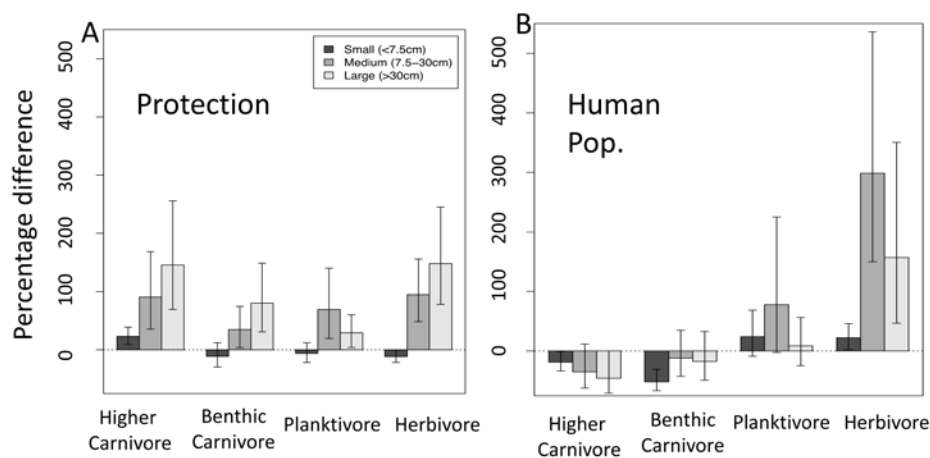


Figure 5.4 (A) Percentage difference in biomass for different trophic groups and size categories due to the level of protection at sites surveyed in Tasmania, Victoria and South

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

Australia ($\pm 95\%$ confidence intervals). (B) Percentage difference for single unit increase in the population density index ($\pm 95\%$ confidence intervals) for each of four major trophic groups and size classes in the surveyed sites. Ratios were obtained from the coefficients for POPindex, β_4 and Protection, β_5 , and transformed into percentage difference in biomass using the relation $100 * (\exp(\beta_{4 \text{ or } 5}) - 1)$, Equation 1 of Soler et al. (2015). The model adjusted for SST mean, SST range, PAR-mean and human population. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars extended above or below zero.

The human population index (Pop index) had a varied effect on the biomass of the different trophic groups (Fig. 5.4B). In general, mean biomasses of higher carnivores and benthic carnivore were both negatively influenced by higher population densities, whereas herbivore biomass tended to be greater. Not many differences were significant, however, resulting in relatively small magnitude of differences in prey consumption estimates, similar to those predicted by *Consume*, but notably overlooking increased consumption of molluscan infauna and polychaete infauna (Table 5.2). The correlation of the geometric means of the ratios between prey types and trophic groups due to the effect of population index was high and significant ($r^2 = 0.85$).

Table 5.2 Comparison of community consumption estimates from *Consume* with those derived from trophic group model, with results expressed as percent ratio increase for no-take MPAs/fished areas and for one unit increase in the population index. Means of the biomass change of trophic groups and total means were calculated as the geometric mean of the ratios and converted to percentage change. *N.S.* = no significant difference. S = Small; M=Medium; L=Large.

Trophic group	Prey category	Trophic group estimates for no-take MPAs	<i>Consume</i> estimates for no-take MPAs	Trophic group estimates per unit increase in pop index	<i>Consume</i> estimates per unit increase in pop index
Herbivores	algae	62	222	132	577
Higher carnivores L + M	fishes	116	310	-41	-13 (<i>N.S.</i>)
Benthic	sponges	28	305	-27	94 (<i>N.S.</i>)

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES
TO TEMPERATE REEF FOOD WEBS

Trophic group	Prey category	Trophic group estimates for no-take MPAs	Consume estimates for no-take MPAs	Trophic group estimates per unit increase in pop index	Consume estimates per unit increase in pop index
carnivores S+M+L & Higher carnivores S	epifaunal crustaceans		45		18 (N.S.)
	epifaunal molluscs		45		-1 (N.S.)
	epifaunal polychaetes		44		-27(N.S.)
	other epifauna		73		30 (N.S.)
	infaunal crustaceans		45		-62
	infaunal molluscs		1 (N.S.)		202
	infaunal polychaetes		1 (N.S.)		57
	other infauna		1 (N.S.)		-1 (N.S.)
Planktivores S+M+L	planktonic fish larvae	27	176	34	-27 (N.S.)
	planktonic crustaceans		108		79 (N.S.)
Total mean		48	79	34	26

5.6 Discussion

Comparison of outputs of the trophic group analysis with those from the *Consume* model indicated that simplification of trophic structure using the former did not provide misleading conclusions when assessing ecological implications of fishing down marine food webs; however, some important trends were undetected. In particular, these included a failure to detect increased consumption of sponges in protected communities, and increased consumption of infaunal soft sediment prey types by fishes near human population centres.

Sponges were presumably included amongst items consumed by ‘benthic carnivores’, but are functionally very different to crabs or urchins, which are also included within this dietary group. In the trophic group analysis, the category ‘benthic carnivores’ includes most predators of sponges based on diet information from Fishbase

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

(www.fishbase.org), but some sponge predators could also be classed as herbivores or in other trophic categories, depending on the dietary mix and ontogenetic stage. Diet predictions of daily consumption at the species level indicate that sponges were consumed by different fish species of different sizes for the four trophic groups. Thus, a disadvantage of the trophic group analysis is that model outputs are based on compartmentalisation into pre-conceived trophic groups, whereas the predictive diet model provides finer taxonomic and size-related resolution.

The *Consume* model provided new insights into fishing-induced changes to food webs. Of particular interest was much higher consumption of sessile biota such as algae and sponges in no-take MPAs when the whole fish assemblage is considered, which is quite different to expectations under the paradigm that fishing primarily removes larger fish, many of them top predators.

Reduction of sessile biota represents a key mechanism through which fishes can directly shape their habitat, with changes to habitat-formers expected to ramify further through food webs. Macroalgal stands represent a key habitat for invertebrates and fishes on temperate rocky reefs through increased habitat complexity. Greater benthic invertebrate and fish populations are also generally associated with vegetated habitats (Ling 2008). Thus, greater numbers of fish in no-take MPAs have the potential to alter the habitat complexity of macrophyte- and sponge-dominated systems by direct consumption of the sessile biota or by predation of macro-invertebrates. Such effects are likely to persist through the long term through a balance of regulatory mechanisms between primary producers, grazers and predators (Christie et al. 2009).

Overall increased consumption by the fish community as a result of recovering biomass in no-take MPAs, as predicted through both modelling approaches, has important implications with respect to energy flow through the system. Community consumption was greater and mean prey size was larger in no-take MPAs relative to

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

fished sites, due to a direct consequence of increased abundance of large fishes in no-take MPAs (Halpern 2003, Edgar et al. 2014). Depression of the fish community through exploitation has clearly altered energy pathways involving invertebrates. Lower prey consumption at fished sites may mean that a substantial proportion of the benthic invertebrate productivity does not get eaten by the fish community, but rather is consumed by other invertebrates or suffers other sources of mortality. If this were the case, then higher abundances of benthic invertebrates should be present at fished sites compared to no-take MPA sites (Langlois et al. 2005, 2006). No-take MPAs either have higher invertebrate production to support the overall higher fish consumption rates, a disproportionately greater influence of fishes on lower trophic levels, or food is not limiting. Assessing between these alternatives requires direct assessment of whether production of infaunal and epifaunal communities is higher, lower or equivalent inside no-take MPAs relative to outside.

Infaunal polychaetes have long been associated with locations that are heavily urbanised. For example, as human population density increases in nearby catchments, macrobenthic assemblages in Tasmanian estuaries undergo a pronounced shift from crustaceans to infaunal molluscs and polychaetes, a consequence of silt runoff transforming sedimentary habitats from sand to mud (Edgar & Barrett 2000). Our model detected increased foraging rates on infaunal molluscs (*mi*) and polychaetes (*pi*) by the whole fish community with increasing human population densities, despite no information of prey availability being incorporated. Our predictions were driven by the composition and size distribution of fish species present, rather than spatial patterns in pollution-tolerant infauna. This suggests concomitant changes in fish community structure in polluted locations that match known pollution impacts on infaunal invertebrate Edgar and Barrett (2000).

Greater fish biomass inside no-take MPAs in south-eastern Australia was observed in most trophic groups, but the opposite pattern was evident for small herbivores. This

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

result contrasts with results of a global study based on a much expanded RLS dataset, where no reduction in small herbivores was evident (Soler et al. 2015). Top-down control by larger carnivores preying on small herbivores inside no-take MPAs may be responsible, as inferred to occur elsewhere (Graham et al. 2003, Willis & Anderson 2003, Micheli et al. 2004). We suggest that in places where fishing pressure is highest both large and small fish are taken with subsequent reduction in their numbers. Therefore we propose that not only large fish numbers increase in no-take MPAs but small fish populations also recover from fishing pressure. However, in Australia, subsistence fishing does not occur and small fishes are not directly reduced in numbers at fished sites, so have little potential to recover when protected in no-take MPAs. Rather, numbers decline as populations of their predators increase. Notably, all size classes for herbivores showed a significant increase in biomass near human population centres, a likely response to organic enrichment in temperate Australian seas where recreational anglers do not generally target herbivores.

Model accuracy of the predictive diet model was potentially affected by several sources of error and bias. Error introduced by non-species level matches was considered negligible for estimates of prey type, given that lack of any taxonomic information in a prior southern Australian study only decreased accuracy from 67% to 66% (Soler et al. 2016a), where accuracy was defined as the mean percentage of overlap between predicted prey types and those recorded in stomach contents. However, mean prey size accuracy, defined as the correlation (r^2) between predicted and observed mean prey size, declined from 0.56 to 0.39 when no taxonomic information was available, indicating the introduction of statistical noise into our estimates of prey size. Regardless, the extremely strong correlation observed between the wet weight of the fish and the predicted mean prey size ($r^2=0.94$) for the southern Australian study (Soler et al. 2016a) indicates that estimates of prey size based solely on the size of the fish should be accurate.

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

Summation of prey predicted to be consumed by individuals across the community added additional error. Daily consumption estimates relied on a single constant for feeding rate derived from the studies of Robertson (1984) and Robertson and White (1986) for small fish in shallow temperate Australian environments. While many of the species present in our dataset were shared with the earlier studies at the species, genus or family level, some fishes were of larger body size while others were from different families. Daily consumption estimates expressed as a percentage of body mass can vary from species to species, food processing modes and are also affected by temperature and prey type digestibility and nutritional value (Palomares & Pauly 1998, Mendes et al. 2015). Furthermore, food consumption per unit weight of fish is generally greater for immature individuals of the same species compared with mature animals (Trites 2003), and for animals of relatively small body size (Rudolf & Rasmussen 2013). Regardless, data analysed here comprise means for thousands of individuals, consequently error associated with calculations should partly average out across the dataset and be consistent in relative comparisons, and so not greatly affect the general trends identified.

In summary, estimates of prey consumption generated by *Consume* provide more nuanced descriptions of material and energy fluxes through the food web than have been generated by models reliant on coarse trophic groups, and here have allowed the identification of additional trophic pathways altered through the selective human exploitation of particular species and size classes of fishes. Through consumption of habitat-forming algae and sponges, fishes potentially play a more important role in influencing habitat complexity of rocky reef systems than previously recognised.

5.7 Acknowledgments

This study was supported by the Australian Research Council, a Tasmania Graduate Research Scholarship (to G.A.S.), and the Marine Biodiversity Hub, a collaborative partnership supported through the Australian Government's National Environmental

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

Science Programme. We also thank Justin Hulls for designing the map of the study area (using ArcGIS) and Dr. Kilian Stehfest for supporting the development of the *Consume* model. Additionally, we thank Dr. Stuart Kininmonth for providing estimates of human population across the study area. Input and comments by Dr. Simon Wotherspoon and Dr. Andre Punt when developing the predictive diet model were much appreciated.

5.8 Supplementary material

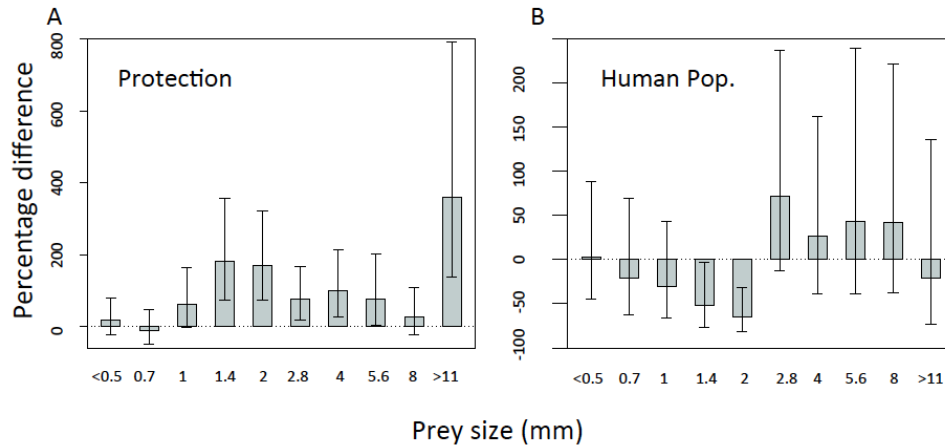


Figure 5.5 (Fig. S1) (A) Percentage difference in daily consumption of different size classes for all prey types consumed by the fish community in protected areas relative to fished zones (\pm 95% confidence intervals). (B) Percentage difference for a single unit increase in the index of local human population density obtained for each prey size bin from the coefficient for PopIndex, β_4 . Ratios were obtained from the coefficients for POPindex, β_4 and Protection, β_5 , and transformed into percentage difference in biomass using the relation $100 \cdot (\exp(\beta_{4,5}))$ from Equation 1 on this manuscript. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero. This graph fuses the prey sizes smaller than 0.5 mm in one group and in a second size class prey types larger than 11 mm.

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

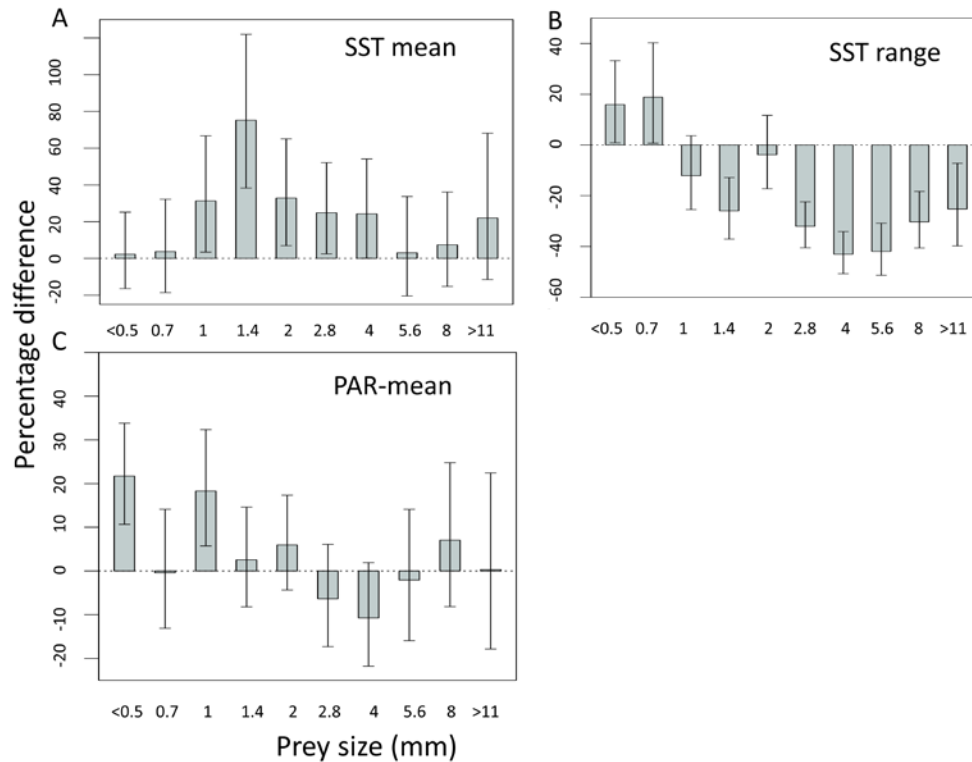


Figure 5.6 (Fig. S2) Percentage difference in biomass (\pm 95% confidence intervals) for covariates investigated. Percentage difference in biomass per 1°C change in mean sea surface temperature (A), 1°C change in the annual range in sea surface temperature (B), and 1 Einstein/m²/day change in annual mean photosynthetically active radiation (C), for each of the prey size classes. Ratios were obtained from the β coefficients from Equation 1 of this paper and transformed into % increment in biomass, by $100 \cdot (\exp(\beta) - 1)$. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero. This graph fuses the prey sizes smaller than 0.5 mm in one group and in a second size class prey types larger than 11 mm.

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

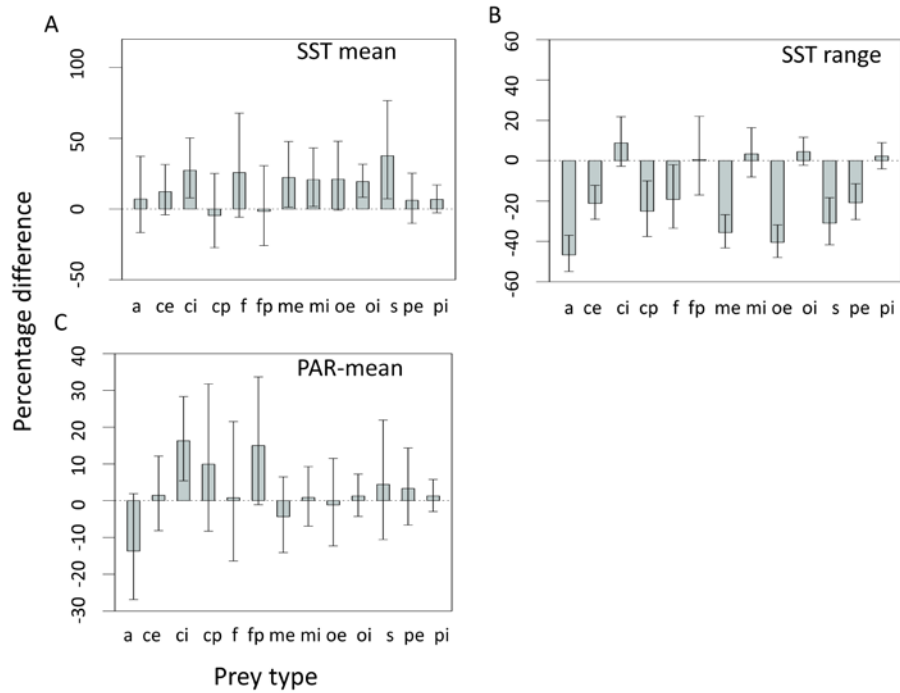


Figure 5.7 (Fig. S3) Percentage difference in biomass (\pm 95% confidence intervals) for covariates investigated. Percentage difference in biomass per 1°C change in mean sea surface temperature (A), 1°C change in the annual range in sea surface temperature (B), and 1 Einstein/m2/day change in annual mean photosynthetically active radiation (C) for each of the prey types. Ratios were obtained from the β coefficients from Equation 1 of this paper and transformed into % increment in biomass, by $100 * (\exp(\beta) - 1)$. Significant differences ($p < 0.05$) were evident when the maximum and minimum values of the confidence interval bars did not overlap zero. Prey types: algae (a), sponges (s), epifaunal polychaetes (pe), infaunal polychaetes (pi), infaunal molluscs (mi), epifaunal molluscs (me), fishes (f), planktonic fish larvae (fp), infaunal crustaceans (ci), epifaunal crustaceans (ce), planktonic crustaceans (cp), other epifauna (oe), other infauna (oi).

MOVING BEYOND TROPHIC GROUPS: EVALUATING FISHING-INDUCED CHANGES TO TEMPERATE REEF FOOD WEBS

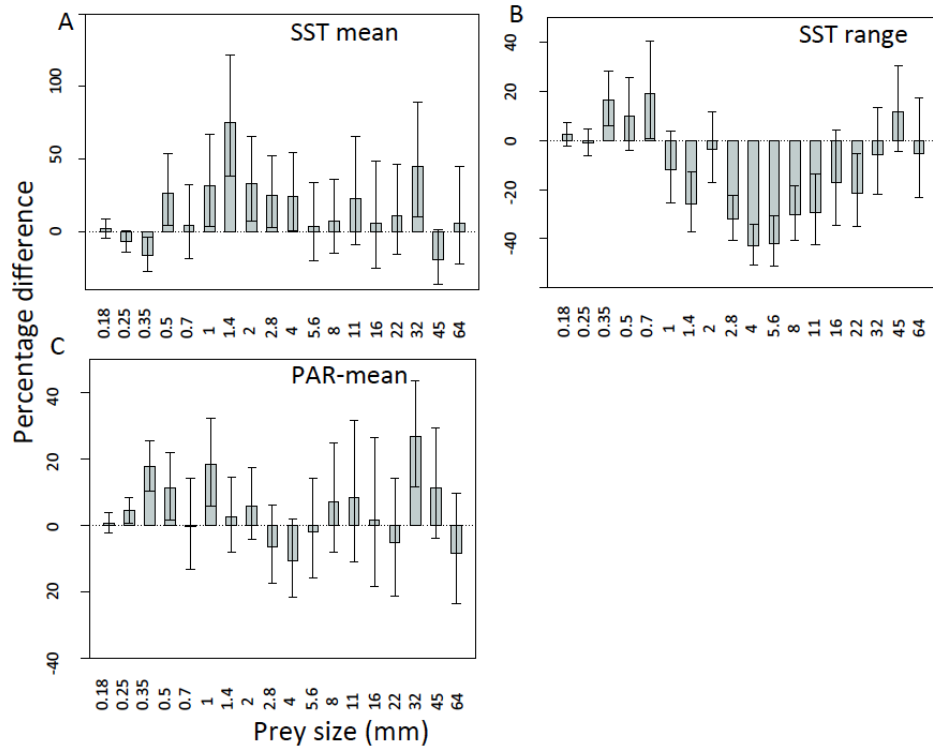


Figure 5.8 (Fig. 4S) Percentage difference in biomass (± 95% confidence intervals) for covariates investigated. Percentage difference in biomass per 1°C change in mean sea surface temperature (A), 1°C change in the annual range in sea surface temperature (B), and 1 Einstein/m²/day change in annual mean photosynthetically active radiation (C) for each of the prey size classes. Ratios were obtained from the β coefficients from Equation 1 of this paper and transformed into % increment in biomass, by $100 \cdot (\exp(\beta) - 1)$.

Chapter 6

GENERAL DISCUSSION AND CONCLUSIONS

This thesis presented different approaches for evaluating how no-take MPAs, human population density, and environmental factors alter fish community structure. As a first approach, fish community structure was analysed from the more traditional perspective of partitioning species into categorical trophic groups, before assessing the effect of protection on these. Nevertheless, I hypothesised that important information is lost in such categorisation at the species level, so I developed new methods for predicting diets of individuals that could be aggregated together to provide community level estimates of consumption, and then validated the resulting models over larger scales. I applied these to broad-scale observational data on fish assemblages across southeastern Australia. This revealed unexpected effects of predator consumption within no-take MPAs, such as much greater ingestion of sponges and other sessile invertebrates than anticipated, and which could not be easily predicted from the coarse categorisation of species into trophic groups. These results also indicate that trophic studies should generally put at least as much emphasis on the size distribution of fishes as is presently placed on taxonomic aspects.

6.1 Synthesis of research findings

The results for Chapter 2 and its associated paper showed clear differences in fish community structure due to protection from fishing in effective MPAs (i.e. no-take, with medium to high enforcement and over 5 years old) and were in accordance with previous studies (Pauly et al. 2000a, Halpern 2003, Micheli et al. 2004, Edgar et al. 2014). Higher

GENERAL DISCUSSION AND CONCLUSIONS

biomass of large predatory species was particularly marked, while the biomass of all other trophic groups was either greater or equal in effective MPAs compared with fished sites. Thus, none of the trophic or size groups had negative biomass ratios in no-take MPAs compared with fished sites that would indicate patterns for top-down control of any particular trophic group within the fish community in the presence of greater biomass of predatory fishes, as found for certain species in other studies (Graham et al. 2003, Willis & Anderson 2003, Micheli et al. 2004). That none of the trophic or size groups showed negative biomass ratios in no-take MPAs in relation to fished sites leads to the novel conclusion that the impact of fishing acts as a stronger top-down force that may over-ride important ecological processes in fish assemblages; probably due to fishers retaining less desirable species once high value species have been locally depleted. Trophic differences in fish assemblages within no-take MPAs at a global scale were found to be driven more by fishing effort than indirect effects resulting from top-down predation. Thus, results from Chapter 2 suggest that fishing pressure depresses not only the biomass of large carnivorous fishes but also has a general negative effect across all trophic groups regardless of size class when assessed at the global scale.

Chapters 2, 3, 4 and 5 link together when the anthropogenic and environmental effects found to affect fish community structure in Chapter 2 are assessed from the fish community diet predictions perspective in Chapter 5 using methods developed in Chapters 3 and 4.

Chapter 3 assessed the importance of the taxonomy and size of the fish for predicting the diet of predatory fishes. Using a comprehensive data set for predator fish as well as the prey consumed, I assessed the accuracy of a predictive diet model that estimates prey type and prey size of predator fish.

In Chapter 3 I evaluated how important is body size and taxonomic identity of a fish for predicting their diet. I found that for diet estimates, family identity is nearly as

GENERAL DISCUSSION AND CONCLUSIONS

important as species identity, and identity is about equivalent to body size, so both body size and identity are needed to properly predict the diet of a fish. Moreover, species identity was more important than body size in predicting prey size, whereas predator size was more important than species identity in determining which prey categories were consumed. The importance of body size as the best predictor for prey type was likely related to ontogenetic changes with fish species consuming different prey types at different times in their life (Cushing 1975, Dickie et al. 1987, Jennings & Warr 2003). Changes in prey type related to size have also been documented in a general literature review (Werner & Gilliam 1984). The importance of the taxonomic information in predicting prey size was partly explained by certain species possessing either large or small body size. In a broad geographical study from the northeast US continental shelf the taxonomic identity of a fish was directly related with the size of its prey as well as the breadth of prey sizes consumed (Scharf et al. 2000). In my study I also found that taxonomic information determines the breadth of prey sizes.

In Chapter 4 and its associated paper I expanded the geographical scale of the study to include 14 other sites in southern Australia, from Jervis Bay in New South Wales to Rottnest Island in Western Australia. Chapter 4 was a necessary step in the geographical scaling of the predictive diet model presented in Chapter 3. This analysis stands by itself with novel results and conclusions, and leads to Chapter 5 where the predictive diet model was used for estimates of fish community prey consumption. In Chapter 4 I found that geographical location only had a marginal effect on the diet estimates both for prey type and prey size; predatory fishes of a particular family and body size had similar diets regardless of location. An important result from the continental study was that the loss in accuracy of the predictions was small when using the family of the predatory fish instead of the species as taxonomic input to the model, which was robust enough to predict across continental-scale geographical domain using training data from a single location.

GENERAL DISCUSSION AND CONCLUSIONS

The most essential predictors for the diet estimates were the size of the predatory fish followed by taxonomic identity, albeit these elements contributed differently when predicting prey type versus prey size. The predictive diet model developed in Chapter 3 and Chapter 4 can estimate with reasonable accuracy the prey type and prey size using training data from a different location. The relevance of this finding is that dietary data does not exist for many ecosystems, or at least not for the majority of species present in a fish community. The predictive diet model allows predictions for all species at a community-level, with diet predictions based on body size and family identity aggregated for all individuals at a site. These predictions will allow more accurate models of community consumption and food webs with which to answer key questions about the ecology of marine systems, and human impacts and management interventions, as well as the effects of environmental variables on trophic pathways.

Chapter 5 presented a novel approach to predictions of prey consumption of reef fish based on the predictive diet model. Prey predictions for individual fishes were added together to estimate total fish community consumption presenting a new tool to analyse trophic pathways for ecological studies. An important parameter for trophic models is an estimate of consumption by a given population of fish in an ecosystem (Polovina 1984, Christensen & Pauly 1992).

Instead of categorizing the fish into pre-conceived trophic groups, I used the daily diet consumptions to assess the effects on the fish community of protection from fishing, proximity to human population centres, as well as environmental factors. I found that prey size was larger and that prey daily consumption was higher in no-take MPAs in relation to fished sites. I also found that the trophic group analysis did not necessarily match the findings at the prey daily consumptions level. One example of this was the estimates of sponges as an important prey item, with threefold higher consumption inside MPAs in relation to fished sites. The trophic group analysis did not find a significant

GENERAL DISCUSSION AND CONCLUSIONS

increase in the biomass of benthic carnivores, the trophic group that sponge feeders are categorized within, in no-take MPAs in relation to fished sites in southern Australia. These differences likely result from finer categorizations of prey types possible when applying the predictive diet model, also that multiple trophic groups, not just benthic carnivores, consume sponges at different stages of ontogenetic development. In the predictive diet model, sponges were found to be consumed by different fish species of different sizes within all four trophic groups. This result suggests that, while the trophic group analysis requires compartmentalization into pre-ordained trophic groups, the predictive diet model allows the data to determine this categorisation for itself. I propose that more complex changes in ecological pathways than previously assumed, based solely on trophic group analysis, are at play in no-take MPAs relative to fished areas, and that at least in some instances can be detected based on prey consumptions estimates. Greater consumption of prey should result in faster recycling of energy and biomass, and lead to more complex ecological pathways. The direct and indirect pressures that fish as predators exert on their prey can potentially alter the habitat complexity of the ecosystem.

6.2 Conclusions

Throughout this thesis I provide further support for no-take MPAs structuring fish assemblages. Effective MPAs with high levels of protection allow fish assemblages to establish greater biomass of larger fishes, more closely resembling pristine natural trophic systems. Human impacts on reef fish community structure are inferred to be stronger than top-down control by the larger predatory species, when considered at the global scale.

However, I wanted to see how valid was the trophic group approach under an alternative analytical perspective. To do so I developed a predictive diet model to estimate the fish community prey consumption. The predictive diet model was first developed for Western Port Bay, Victoria, and later scaled up to encompass temperate

GENERAL DISCUSSION AND CONCLUSIONS

Australia. Finally, I predicted the diet consumptions for fish surveyed underwater under the Reef Life Survey (www.reeflifesurvey.org) methodology and assess the effect of protection as well as other factors on these predictions.

The most essential predictors of fish diet are the size of the predatory fish and taxonomic identity, albeit these elements contributed differently when predicting prey type versus prey size. I found that the predictive diet model generated predictions with reasonable accuracy when estimating the prey type and prey size consumed at the continental scale of temperate Australia. Furthermore, the model was robust enough to predict across a geographical domain using training data from a single location. Little loss in accuracy occurred when only taxonomic information at the family level was used both for prey type and prey size. Geographical factors (Province and Ecoregion) only marginally improved predictions. Thus, the diet of predatory fish of a given family and size can be predicted with reasonable accuracy using training data from a different geographical location. By generating information on the accuracy of our model, we increase the utility of this tool for predicting prey type and mean prey size in ecological studies where the diet of the individual fish in a community is unknown.

I found fishes in no-take MPAs to consume larger prey on average, and have higher total daily prey consumption, than in open-access areas. I propose that higher daily consumption of prey of larger size by larger and more abundant fish in no-take MPAs in relation to open-access sites could be playing a key factor in the ecosystem, allowing faster recycling of energy. Furthermore, I suggest that the influence of human activities could have more complex consequences in the fish assemblages and their interactions with the sessile biota than previously suspected. Fishing pressure has the potential of altering fish biomass, which in turn would have a direct effect on the interactions between the fish species at different size-classes. The removal of key species at different size-

GENERAL DISCUSSION AND CONCLUSIONS

classes could also have important ramifications by altering their predation potential on other fish as well as on other taxa including sessile biota and macro-invertebrates.

Disparities were evident between no-take MPA effects identified using predictive diet models and analyses based on trophic groups. These dissimilarities are partly related to finer discrimination of prey types using the predictive diet model, which not only takes into account the species of the fish but also its size. The pre-conceived allocation of species to trophic groups based on the average of the species does not take into account the ontogenetic changes, with the consequence that biases may arise in the ecological role assigned to species at a given size. Estimates for prey consumption using predictive diet models are suggested to provide more accurate approximations of material and energy fluxes through the food web, and can be used to estimate the biomass of different size-classes of invertebrates and small fish consumed daily in a given fish community. These biomass estimates allow more accurate models of community consumption, which can be applied in investigations addressing key questions about the ecology of marine systems, including the contribution of human impacts and management intervention to changing patterns of biodiversity, as well as influences of particular environmental variables.

REFERENCES

- Al-Habsi S, Sweeting C, Polunin N, Graham N (2008) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ elucidation of size structured food webs in a Western Arabian Sea demersal trawl assemblage. *Mar Ecol Prog Ser* 353:55-63
- Andersen KH, Beyer J (2006) Asymptotic size determines species abundance in the marine size spectrum. *Am Nat* 168:54-61
- Andersen KH, Pedersen M (2010) Damped trophic cascades driven by fishing in model marine ecosystems. *Proceedings of the Royal Society B: Biological Sciences* 277:795-802
- Babcock RC, Shears NT, Alcala A, Barrett NS, Edgar GJ, Lafferty KD, McClanahan TR, Russ GR (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc Natl Acad Sci U S A* 107:18251-18255
- Ban NC, Cinner JE, Adams VM, Mills M, Almany GR, Ban SS, McCook LJ, White A (2012) Recasting shortfalls of marine protected areas as opportunities through adaptive management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22:262-271
- Barber D (2011) *Bayesian Reasoning and Machine Learning*. Cambridge University Press, Cambridge
- Barrett NS, Edgar GJ, Buxton CD, Haddon M (2007) Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. *J Exp Mar Biol Ecol* 345:141-157

REFERENCES

- Bates AE, Barrett NS, Stuart-Smith RD, Holbrook NJ, Thompson PA, Edgar GJ (2014) Resilience and signatures of tropicalization in protected reef fish communities. *Nat Clim Change* 4:62-67
- Belgrano A (2005) *Aquatic food webs: an ecosystem approach*. Oxford University Press, USA
- Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping Functional Group Drives Coral-Reef Recovery. *Curr Biol* 16:2434-2439
- Blanchard JL, Law R, Castle MD, Jennings S (2011) Coupled energy pathways and the resilience of size-structured food webs. *Theoretical ecology* 4:289-300
- Brown JH, Gillooly JF (2003) Ecological food webs: high-quality data facilitate theoretical unification. *Proceedings of the National Academy of Sciences* 100:1467-1468
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Towards a metabolic theory of ecology. *Ecology* 85:1771-1789
- Christensen V, Pauly D (1992) ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol Model* 61:169-185
- Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. *Mar Ecol Prog Ser* 396:221-233
- Conway D, White J (2012) *Machine Learning for Hackers*. O'Reilly Media, Inc., Sebastopol, CA
- Cushing DH (1975) *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge
- Dickie LM, Kerr SR, Boudreau PR (1987) Size-dependent processes underlying regularities in ecosystem structure. *Ecol Monogr* 57:233-250
- Edgar GJ, Barrett NS (2000) Effects of catchment activities on macrofaunal assemblages in Tasmanian estuaries. *Estuarine, Coastal and Shelf Science* 50:639-654

REFERENCES

- Edgar GJ, Barrett NS, Stuart-Smith RD (2009) Exploited reefs protected from fishing transform over decades into conservation features otherwise absent from seascapes. *Ecol Appl* 19:1967–1974
- Edgar GJ, Shaw C (1995a) The production and trophic ecology of shallow-water fish assemblages in southern Australia. I. Species richness, size-structure and production of fishes in Western Port, Victoria. *J Exp Mar Biol Ecol* 194:53-81
- Edgar GJ, Shaw C (1995b) The production and trophic ecology of shallow-water fish assemblages in southern Australia. II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. *J Exp Mar Biol Ecol* 194:83-106
- Edgar GJ, Shaw C (1995c) The production and trophic ecology of shallow-water fish assemblages in southern Australia. III. General relationships between sediments, seagrasses, invertebrates and fishes. *J Exp Mar Biol Ecol* 194:107-131
- Edgar GJ, Stuart-Smith RD (2009) Ecological effects of marine protected areas on rocky reef communities: a continental-scale analysis. *Mar Ecol Prog Ser* 388:51-62
- Edgar GJ, Stuart-Smith RD (2014) Systematic global assessment of reef fish communities by the Reef Life Survey program. *Sci Dat* 1
- Edgar GJ, Stuart-Smith RD, Willis TJ, Kininmonth S, Baker SC, Banks S, Barrett NS, Becerro MA, Bernard AT, Berkhout J, Buxton CD, Campbell SJ, Cooper AT, Davey M, Edgar SC, Forsterra G, Galvan DE, Irigoyen AJ, Kushner DJ, Moura R, Parnell PE, Shears NT, Soler G, Strain EM, Thomson RJ (2014) Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506:216-220
- Edwards CB, Friedlander A, Green A, Hardt M, Sala E, Sweatman H, Williams I, Zgliczynski B, Sandin S, Smith J (2014) Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proceedings of the Royal Society B: Biological Sciences* 281:20131835

REFERENCES

- Fulton EA, Link JS, Kaplan IC, Savina-Rolland M, Johnson P, Ainsworth C, Horne P, Gorton R, Gamble RJ, Smith ADM, Smith DC (2011) Lessons in modelling and management of marine ecosystems: the Atlantis experience. *Fish and Fisheries* 12:171-188
- Gaston KJ (2000) Global patterns in biodiversity. *Nature* 405:220-227
- Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environ Conserv* 30:200-208
- Green SJ, Côté IM (2014) Trait- based diet selection: Prey behaviour and morphology predict vulnerability to predation in reef fish communities. *J Anim Ecol* 83:1451-1460
- Hahn W, Langton R (1984) Prey selection based on predator/prey weight ratios for some northwest Atlantic fish. *Mar Ecol Prog Ser*
- Hall SJ, Collie JS, Duplisea DE, Jennings S, Bravington M, Link J (2006) A length-based multispecies model for evaluating community responses to fishing. *Can J Fish Aquat Sci* 63:1344-1359
- Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? *Ecol Appl* 13 (Suppl):117–137
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *Am Nat* 163:192-211
- Hollowed AB, Bax N, Beamish R, Collie J, Fogarty M, Livingston P, Pope J, Rice JC (2000) Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? *ICES J Mar Sci* 57:707-719
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17:360-365

REFERENCES

- Hutchinson GE (1978) An introduction to population ecology. Yale Univ. Press, New Haven
- Jennings S, Pinnegar JK, Polunin NV, Boon TW (2001) Weak cross- species relationships between body size and trophic level belie powerful size- based trophic structuring in fish communities. *J Anim Ecol* 70:934-944
- Jennings S, Pinnegar JK, Polunin NV, Warr KJ (2002a) Linking size-based and trophic analyses of benthic community structure. *Mar Ecol Prog Ser* 226:77-85
- Jennings S, Polunin NVC (1997) Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs* 16:71-82
- Jennings S, Warr KJ (2003) Smaller predator-prey body size ratios in longer food chains. *Proceedings of the Royal Society of London Series B: Biological Sciences* 270:1413-1417
- Jennings S, Warr KJ, Mackinson S (2002b) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. *Mar Ecol Prog Ser* 240:11-20
- Jones PJ (2002) Marine protected area strategies: issues, divergences and the search for middle ground. *Rev Fish Biol Fish* 11:197-216
- Juanes F (1994) What determines prey size selectivity in piscivorous fishes? In: Stouder D, Fresh K, Feller R (eds) *Theory and application in fish feeding ecology*. University of South Carolina Press, Columbia
- Kelaher BP, Tan M, Figueira WF, Gillanders BM, Connell SD, Goldsworthy SD, Hardy N, Coleman MA (2015) Fur seal activity moderates the effects of an Australian marine sanctuary on temperate reef fish. *Biol Conserv* 182:205-214
- Kelble CR, Ortner PB, Hitchcock GL, Boyer JN (2005) Attenuation of photosynthetically available radiation (PAR) in Florida Bay: Potential for light limitation of primary producers. *Estuaries* 28:560-571

REFERENCES

- Kellner JB, Litvin SY, Hastings A, Micheli F, Mumby PJ (2010) Disentangling trophic interactions inside a Caribbean marine reserve. *Ecol Appl* 20:1979-1992
- Kingsland SE (2002) Creating a science of nature reserve design: perspectives from history. *Environmental Modeling & Assessment* 7:61-69
- Kulbicki M, Bozec Y-M, Labrosse P, Letourneur Y, Mou-Tham G, Wantiez L (2005) Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. *Aquat Living Resour* 18:231-250
- Langlois TJ, Anderson MJ, Babcock RC (2005) Reef-associated predators influence adjacent soft-sediment communities. *Ecology* 86:1508-1519
- Langlois TJ, Anderson MJ, Babcock RC (2006) Inconsistent effects of reefs on different size classes of macrofauna in adjacent sand habitats. *J Exp Mar Biol Ecol* 334:269-282
- Law R, Plank MJ, Kolding J (2012) On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES J Mar Sci* 69:602-614
- Ling SD (2008) Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia* 156:883-894
- Link JS (2004) A general model of selectivity for fish feeding: a rank proportion algorithm. *Trans Am Fish Soc* 133:655-673
- Maury O, Faugeras B, Shin Y-J, Poggiale J-C, Ari TB, Marsac F (2007a) Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 1: the model. *Progress in Oceanography* 74:479-499
- Maury O, Shin Y-J, Faugeras B, Ari TB, Marsac F (2007b) Modeling environmental effects on the size-structured energy flow through marine ecosystems. Part 2: simulations. *Progress in Oceanography* 74:500-514
- Mendes TC, Cordeiro CAM, Ferreira CEL (2015) An experimental evaluation of macroalgal consumption and selectivity by nominally herbivorous fishes on subtropical rocky reefs. *J Exp Mar Biol Ecol* 471:146-152

REFERENCES

- Micheli F, Halpern BS, Botsford LW, Warner RR (2004) Trajectories and correlates of community change in no-take marine reserves. *Ecol Appl* 14:1709-1723
- Mittelbach GG, Persson L (1998) The ontogeny of piscivory and its ecological consequences. *Can J Fish Aquat Sci* 55:1454-1465
- Mora C, Aburto-Oropeza O, Ayotte PM, Banks S, Bauman AG, Beger M, Bessudo S, Bocos AA, Bonilla HR, Booth DJ, Brokovich E, Brooks A, Chabanet P, Cinner J, Cortés J, Cruz-Motta JJ, DeMartini E, Edgar GJ, Feary DA, Ferse SC, Friedlander A, Gaston KJ, Gough C, Graham NA, Green A, Guzman H, Hardt M, Kulbicki M, Letourneur Y, Loreau M, Loya Y, Magaña AC, Martinez C, Mascareñas-Osorio I, Morove T, Nadon M-O, Nakamura Y, Paredes G, Pérez AL, Polunin N, Pratchett MS, Rivera F, Sala E, Sandin S, Soler G, Stuart-Smith R, Tessier E, Tittensor DP, Tupper M, Usseglio P, Vigliola L, Wantiez L, Williams I, Wilson SK, Zapata FA (2011) Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biol* 9:e1000606
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades and the process of grazing on coral reefs. *Science* 311:98-101
- O'Brien WJ, Slade NA, Vinyard GL (1976) Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). *Ecology* 57:1304-1310
- Ortiz M, Legault C, Ehrhardt N (2000) An alternative method for estimating bycatch from the US shrimp trawl fishery in the Gulf of Mexico, 1972-1995. *Fish Bull* 98:583-599
- Palomares MLD, Pauly D (1998) Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Mar Freshw Res* 49:447-453

REFERENCES

- Pauly D, Christensen V, Froese R, Palomares ML (2000a) Fishing down aquatic food webs: Industrial fishing over the past half-century has noticeably depleted the topmost links in aquatic food chains. *Am Sci* 88:46-51
- Pauly D, Christensen V, Walters C (2000b) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science [ICES J Mar Sci]* 57:697-706
- Pauly D, Watson R (2005) Background and interpretation of the 'Marine Trophic Index' as a measure of biodiversity. *Phil Trans R Soc B* 360:415-423
- Peters RH (1991) *A Critique for Ecology*. Cambridge University Press, Cambridge, U.K
- Pinnegar JK, Tomczak MT, Link JS (2014) How to determine the likely indirect food-web consequences of a newly introduced non-native species: A worked example. *Ecol Model* 272:379-387
- Polovina JJ (1984) Model of a coral reef ecosystem. *Coral Reefs* 3:1-11
- R-Core-Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Rastetter EB, Aber JD, Peters DP, Ojima DS, Burke IC (2003) Using mechanistic models to scale ecological processes across space and time. *Bioscience* 53:68-76
- Robertson AI (1984) Trophic interactions between the fish fauna and macrobenthos of an eelgrass community in Western Port, Victoria. *Aquat Bot* 18:135-153
- Robertson CH, White RWG (1986) Feeding patterns of *Nesogobius* sp., *Gymnapistes marmoratus*, *Neodax balteatus* and *Acanthaluteres spilomelanurus* from a Tasmanian seagrass meadow. *Aust J Mar Freshw Res* 37:481-489
- Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. *Curr Biol* 24:1000-1005

REFERENCES

- Rudolf VH, Rasmussen NL (2013) Ontogenetic functional diversity: Size structure of a keystone predator drives functioning of a complex ecosystem. *Ecology* 94:1046-1056
- Russ GR (1980) Effects of predation by fishes, competition, and structural complexity of the substratum on the establishment of a marine epifaunal community. *J Exp Mar Biol Ecol* 42:55-69
- Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing, trophic cascades, and the structure of algal assemblages: Evaluation of an old but untested paradigm. *Oikos* 82:425-439
- Scharf FS, Juanes F, Rountree RA (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar Ecol Prog Ser* 208:229-248
- Shin Y-J, Cury P (2001) Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. *Aquat Living Resour* 14:65-80
- Shin Y-J, Cury P (2004) Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Can J Fish Aquat Sci* 61:414-431
- Silverman B (1986) Density estimation for statistics and data analysis. Chapman and Hall, New York
- Soler GA, Edgar GJ, Stuart-Smith RD, Smith ADM, Thomson RJ (2016a) Predicting the diet of coastal fishes at a continental scale based on taxonomy and body size *J Exp Mar Biol Ecol* 480:1-7
- Soler GA, Edgar GJ, Thomson RJ, Kininmonth S, Campbell SJ, Dawson TP, Barrett NS, Bernard ATF, Galvan DE, Willis TJ, T.J. A, Stuart-Smith RD (2015) Reef fishes at all trophic levels respond positively to effective marine protected areas. *Plos One*

REFERENCES

- Soler GA, Thomson RJ, Stuart-Smith RD, Smith ADM, Edgar GJ (2016b) Contributions of body size, habitat and taxonomy to predictions of temperate Australian fish diets. *Mar Ecol Prog Ser* 545:239-249
- Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, McManus KD, Molnar J, Recchia CA, Robertson J (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57:573-583
- Steneck RS (1998) Human influences on coastal ecosystems: does overfishing create trophic cascades? *Trends Ecol Evol* 13:429-430
- Stewart BD, Jones GP (2001) Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey-fish mortality. *Mar Biol* 138:383-397
- Stuart-Smith RD, Bates AE, Lefcheck JS, Duffy JE, Baker SC, Thomson RJ, Stuart-Smith JF, Hill NA, Kininmonth SJ, Airoidi L (2013) Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature* 501:539-542
- Trebilco R, Baum JK, Salomon AK, Dulvy NK (2013) Ecosystem ecology: size-based constraints on the pyramids of life. *Trends Ecol Evol* 28:423-431
- Trites AW (2003) 8 Food Webs in the Ocean: Who Eats Whom and How Much? Responsible fisheries in the marine ecosystem:125
- Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Glob Ecol Biogeogr* 21:272-281
- Walters CJ, Holling CS (1990) Large-scale management experiments and learning by doing. *Ecology* 71:2060-2068
- Ward-Paige C, Flemming JM, Lotze HK (2010) Overestimating fish counts by non-instantaneous visual censuses: consequences for population and community descriptions. *Plos One* 5:e11722

REFERENCES

- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annu Rev Ecol Syst* 15:393-425
- Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042-1052
- West GB, Brown JH (2005) The origin of allometric scaling laws in biology from genomes to ecosystems: towards a quantitative unifying theory of biological structure and organization. *J Exp Biol* 208:1575-1592
- Willis TJ, Anderson MJ (2003) Structure of cryptic reef fish assemblages: relationships with habitat characteristics and predator density. *Mar Ecol Prog Ser* 257:209-221
- Willis TJ, Millar RB (2005) Using marine reserves to estimate fishing mortality. *Ecol Lett* 8:47-52
- Wright DI, O'Brien WJ (1984) The development and field test of a tactical model of the planktivorous feeding of white crappie (*Pomoxis annularis*). *Ecol Monogr*:65-98
- Zhang L, Hartvig M, Knudsen K, Andersen KH (2014) Size-based predictions of food web patterns. *Theoretical ecology* 7:23-33