

**Sea turtle conservation and ecosystem-based management with a focus
on green turtles (*Chelonia mydas*) and seagrass beds**

by

COLETTE CATHERINE CHANTAL WABNITZ

B.Sc. (Biology and Environmental Sciences), McGill University, 1998

M.Sc. (Tropical Coastal Management), University of Newcastle-Upon-Tyne, 2000

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES
(Geography)

THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

April 2010

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Abstract

The design of effective species management and recovery plans for sea turtle populations requires targets that are informed by an understanding of knowledge gained at the level of individuals/populations in the context of the wider goal of protecting an ecosystem's structural and functional attributes. In this thesis I present the first detailed investigation of the multiple levels at which sea turtles, particularly green turtles (*Chelonia mydas*), interact with ecosystems.

I begin by developing a framework for an age-structured population-level assessment of food consumption for hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), and green turtles. This entailed construction of species-specific growth models for the western Atlantic, and subsequent integration of results with morphometric, survival, abundance, and food conversion efficiency to derive consumption estimates.

At the ecosystem level, I developed models for the Caribbean and Hawai'i, where green turtles are present at very low abundances and reaching carrying capacity, respectively. In the Caribbean, results showed that green turtle grazing of seagrass substantially altered habitat complexity, reducing the refuge role of seagrass to reef fish and invertebrates, and leading to potentially dramatic changes in species biomass and composition. In Hawai'i, by feeding on algae, green turtles were found to contribute to the resilience of reefs in the face of disturbance, a functional role that needs to be explicitly included in future studies of reef dynamics. Taken together, these findings highlight the need to consider trophic and indirect interactions in the evaluation of sea turtles' role within ecosystems.

Accurate and reliable estimates of foraging habitat extent are essential to inform realistic and sustainable turtle recovery targets, particularly given the current degraded state of coastal ecosystems. Using Landsat satellite imagery, I present a novel mapping approach for seagrass habitats at large scales. Such regional initiatives are also urgently needed if the international community is to meet aims to conserve 10 – 30 % of specific habitats. A comparison between reef extent, determined using remote sensing and existing data, showed that discrepancies ranged from + 1,316 % to - 64 %, underlining our limited ability to ascertain progress towards adopted global marine conservation targets based on current data.

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Acknowledgements

There are many to whom I am indebted for their assistance, advice, and moral support in the completion of my doctoral work. I offer my sincerest gratitude to all who have made this effort possible. First and foremost, I wish to extend a most sincere thank you to all members of my committee, Dr Daniel Pauly, Dr Brian Klinkenberg, Dr Karen Bjorndal, Dr Alan Bolten, Dr Villy Christensen, and Dr Jackie Alder, for their support, and encouragement. 'Merci' also for affording me great independence in research, providing me with the freedom and opportunity to explore my potential during my time at UBC (in particular through the pursuit of a wide variety of contract opportunities), and for your responsiveness and the extra time and effort you put in at the 11th hour so I could squeeze in the extra chapter and still deliver.

Sections of this thesis were conducted as part of the *Sea Around Us Project*, a scientific cooperation between UBC and the Pew Environment Group. Funding towards completion of my studies was also provided by a tuition (and partial tuition) waiver UBC scholarship, a Mia Tegner Grant, and two research fellowships: one provided by the US National Marine Fisheries Service (Grant # WC 133F04 SE1183), the other by the Disney Wildlife Conservation Fund (Grant # UF-04-01) to Dr Karen Bjorndal, Dr. Alan Bolten and myself. Support was further provided by: the Institut de Recherche pour le Développement (IRD) through Dr. Serge Andréfouët; the University of South Florida (USF) through Dr. Serge Andréfouët and Dr. Frank Müller-Karger and the University of Florida, through Dr. Alan Bolten and Dr. Karen Bjorndal, during my stay as a visiting scientist at both institutions; a variety of contract opportunities I took on while completing my dissertation; and in times of need the gracious support of my family, Savas, and Danaé.

I extend deep gratitude to my main research advisor, Dr Daniel Pauly. Thank you for your guidance, patience, support, and dedication, for always forcing me to go beyond the horizon, think outside of the box, and find insights by looking at old datasets in entirely new ways! You always will be a source of inspiration, ideas, wisdom, and good company. I am also indebted to my co-supervisors Dr Karen Bjorndal and Dr Alan Bolten. Thank you for your commitment, pragmatism, dedication, keen eye for detail, and the inherent trust you laid in my abilities - not an easy task given that I was so far away (physically!). For his enthusiasm, understanding, and unwavering support, I would also like to offer a deep thank you to my fourth co-supervisor, Dr Brian Klinkenberg. Tusind tak skal du have for al din hjælp Dr Villy Christensen - and for welcoming me so warmly always...

and letting me walk out of your office ‘not blue’!. Thanks are also due to Dr Jackie Alder for agreeing to serve on my committee and for your continued assistance and support throughout my time at UBC.

Un vraiment grand grand merci à Serge Andréfouët, for taking me under your wing and being an incredible mentor. I thank you for always making time for me, for the patience and guidance you have offered me along the way, for inspiring me, for always having faith in me, and thinking about me when opportunities for collaboration arose. It has been a privilege, and I am richer for having had the opportunity to work with you.

Along the way I have also had the incredible fortune to receive the much appreciated support from what is now a very long list of people.

Chapter 2 - I would like to thank: E. Harrison and B. Krueger, for the provision of unpublished biometric data for nesting green turtles at Tortuguero, Costa Rica, and foraging hawksbill turtles in Barbados respectively; J. Blumenthal, for sharing raw published data on hawksbill and green sea turtles in the Cayman islands(Blumenthal *et al.* 2009a, Blumenthal *et al.* submitted); A. Harewood for providing nesting information for hawksbill turtles in Barbados; P. Eliazar for assistance in tracking down a number of references; M. Etienne and R. Ahrens for statistical advice; D. Varkey for her patience and assistance with coding in R; and T.T. Jones for discussions concerning certain methodological aspects of this chapter. B. Hunt is acknowledged for stimulating discussions and constructive comments on earlier drafts.

Chapter 3 - I would like to thank M. Coll for advice and guidance in the development of this chapter. I also wish to acknowledge P. Mumby for insightful discussions about seagrass beds and reef ecosystems. B. Hunt is acknowledged for constructive comments on earlier drafts.

Chapter 4 - Thanks are due to J. Polovina for his help in getting this project off the ground. R. Most and the National Park Service are acknowledged for facilitating many aspects of my work and valuable input throughout the study. M. Rice and students of the Hawai‘i Preparatory Academy (Kamuela, Hawai‘i) are acknowledged for their help in collecting information on green turtles. E. Brown, T. Clark, M. Deagle, H. Jessop, R. Hoover, M. Landry, L. Marrack, M. Weijerman, K. Uyehara, S. Waddington, and T. Wurth are acknowledged for assistance during the development of the model and/or provision of often unpublished data. I wish to thank C. Payri, J. Smith, C. Squair, and T. Sauvage for all questions related to algae; F. Parrish for discussions pertaining to model

development and valuable feedback on earlier drafts; and M. Bailey for drawing up such wonderful illustrations of species representative of functional groups; M. Coll for valuable feedback on analyses; and B. Hunt for assistance on all zooplankton and phytoplankton aspects of the model and constructive comments on earlier drafts.

Chapter 5 and 6 - I acknowledge the support provided by the NASA Data Buy Program led by F. Policelli and T. Frisbie who funded the acquisition of the IKONOS images between 2000 and 2002. The Millennium Coral Reef Mapping Project was funded by NASA grants NAG5-10908 to SA and grant CARBON-0000-0257 to J. Robinson. The NASA/Interdisciplinary Program grant NNG04GO90G to S. Anfréouët and F. Müller-Karger provided additional support. Field data in Panama were collected thanks to H. Guzmán and J. Akl. C. Kranenburg at USF helped with all aspects of Landsat data management. Thanks are due to N. Davis and S. Morgan for constructive comments on earlier drafts.

I don't think anyone can truly understand what a PhD thesis "does to you" unless you go through that very process. It is at once the most frustrating and self-deconstructing experience, yet all the while also representing the most remarkable and enlightening learning challenge (and test of endurance). If I traveled this path standing tall at the end of it, it is for I have been blessed, truly, with remarkable colleagues, peers, and the most amazing group of friends. I would particularly like to thank R. Ahrens, S. Guénette, M. Palomares and D. Zeller as well as C. Payri, for valuable input, suggestions at various times during my dissertation and most importantly for your support in the process! Janice and Ann - thank you for what you do! Thank you also to my fellow FC students and friends, current and past, I won't list names, you know who you are :o) - for listening to my woes and rejoicing when celebrating was in order. A warm ☺ to ISTS folks.

My beautiful friends - my world quite truly would not be the same without you! You have helped me considerably throughout this venture, both logistically and emotionally, in your own ways. Your encouragement and boundless faith over the years have helped keep me together and on track. Thank you to all of you who stood by my side through thick and thin, when my patience was fading. For seeing me through the fog, for always reaching out and knowing how to touch me and make me smile, even when I was withdrawn, and for letting me lean on you. Know that I feel blessed for having you in my life, and never have, nor will, take your friendship for granted: Heather (for being so strong and tolerating my close company for 3 years ... and some interesting parking practices!); Frederic (still there after all those years :o)); Nick W (for noodles, raw egg

drinks, and doing the incredible task of reading my intro and conclusions! an out of space sized thank you :o)); Sian (for helping to put me back together when I fell apart once); Joanna (yay for being on my team); Emma; Leigh (for all those moments); Joe; Wilf (for all those favours, and particularly your patience and understanding these last few months!) Michael J (we will have that bottle of wine!); Suzanne; Michelle and the “Brady” bunch; Sonia B (te adoro pecesito); Chiara and Pablito; Zaz, Michelle, Isabel and Rebs - for keeping me in your hearts and thoughts during all these (sometimes withdrawn) years and for your warm welcomes and manic schedule rearrangements so that I could stay with you and/or see you whenever I came for a flying visit through the UK. TTodd - for showing me how it is done, helping a sister out and teaching me what really makes turtles go. Looking forward to that rum in Hawai‘i! Peter M. - for having such faith in me, always thinking of me and counting me in, and granting me opportunities others could only dream of. Barry - for the hugs, redirecting your flights via Vancouver all these years for an annual visit, for the laughs and those shared tough moments, and for restocking my rum cabinet! Divya - for your time, your patience, essential advice, for checking in on me, and always being there for me. You are a wonderful friend to me. Boris - for your enthusiasm, making the time for me, your kind words, and most importantly your warmth and support. Savas - for getting me into this mess to start with ;o), for your incredible generosity, and for keeping me in your heart the way you do. Marta - for your unwavering support, level-headedness, ecopath advice, and treasured friendship. Dr. Lou - for always thinking of me, for giving me what I needed most whenever I needed it most. Walking, at times running, down much of this road with you has been truly special; for your friendship and for all that we share BEAMS** and love. Kate - for always checking up on me, for being such a source of strength and guidance, and truly leading by example. You are a true star and I admire you a great deal! John P – for being the most wonderful you, defining what true friendships are, making me smile and sending beams of support, love and for understanding me the way you do. Danaé - ma sœursister, pour ta tendresse, ta patience, ta présence, ta confiance, tes pom-pom balls, et pour avoir toujours été à l’écoute et gardé ma main dans la tienne tout au long de cette course parfois éperdue. Neil - for your love, compassion and encouragement, for having shared such an important part of this journey and listened and held my hand, and for allowing us both to learn all that was needed in the spaces in between. Mike M. - for willing me on and to be STRONG :o), for sending strength and positivity, always, and for your continuous support despite the distance *HUG*! Julie - ma belle, quel plaisir de t’avoir rencontréemerci, merci merci pour avoir été à l’écoute, pour tes coups de pouces surtout dans la dernière ligne droite, pour m’avoir fait rire, et su me remettre d’aplomb quand les émotions prenaient le dessus parfois ;o) Karen - for your enthusiasm and courage,

remembering the important moments, and for volunteering to proof read my thesis, even though you were traveling to Oz and jetlagged. May the future see our collaboration plots come to fruition!

I cannot end without thanking my family, on whose constant encouragement and never-ending love I have relied throughout my studies. Despite the distance you have always stood by my side, supported me in any - and all - the ways you could, and pushed me when I thought I couldn't anymore. Pama in particular, thank you for the enormous amount of faith you've always had in me, for teaching me to never give up, strive for the best, and for believing in my dreams, even when at times they seemed far fetched, rather quirky, and unreal! Mon cici et poussin, pour avoir toujours été présents toutes ces années, malgré la distance et le tumulte quotidien de vos vies respectives. I feel blessed to have you as siblings and may we always look after ourselves and each other.

...and Brian... I would not have seen the light at the end of this very long and at times dark tunnel if it wasn't for you - thank you for your love and encouragement; for being there for me in my most doubtful hours, and pulling me through by showing me again how to walk one step at a time; for your patience and forcing me to slow down sometimes; for keeping me true to myself, helping me reconnect with my core and find my inner strength, and reminding me to see the forest for the trees; for letting me lean on you as hard as I have; for reading drafts after drafts after drafts after drafts after drafts; for your advice and unwavering patience. Your insights, focus, brilliance, discipline, support, faith in what is, and love have been, and will continue to be, an inspiration. I love you. Let the thesis-free life begin and the good times roll! :o)

Dedication

For Chantal and Hans-Werner Wabnitz

Co-authorship statement

With the exception of Chapters 1 and 7, all chapters have been prepared as stand-alone, peer-reviewed publications. Chapters 4 to 6 are either published or in review at refereed journals, while Chapters 2 and 3 are in preparation for submission. I am the senior author on all papers and assume primary responsibility for design, implementation, analysis, and writing of all co-authored chapters. Any errors or omissions are my own. Details of co-authorship contributions are detailed below.

Chapter 2: My co-author Dr. Daniel Pauly developed the original vision for this chapter. I embraced the opportunity to transform these ideas into reality and developed a much more complex methodology than originally envisaged. I expanded on the original idea, developed and carried out all analyses, and drafted the text. Dr. Daniel Pauly directed my thoughts at critical phases of methodological and analytical progress, which went through multiple redevelopments. Dr. Karen Bjorndal provided data, methodological guidance, and contributed to the idea of this chapter through stimulating discussions and comments on drafts of the manuscript. Dr. Andrew Cooper provided guidance on statistical aspects of the analyses and comments on drafts of the manuscript.

Chapter 3: My co-authors Dr. Karen Bjorndal and Dr. Alan Bolten had the original idea of using Ecopath with Ecosim to investigate the role of green turtles in Caribbean seagrass beds. I transformed this idea into testable hypotheses given the limitations of available data. I compiled all data for the manuscript, carried out model development and analyses, and drafted the text. Dr. Marta Coll was of guidance in model development and analysis. Dr. Villy Christensen and Dr. Daniel Pauly provided edits, comments, and suggestions on drafts of the paper.

Chapter 4: This chapter's idea was put forward by researchers at the National Marine Fisheries Service in Hawai'i, who saw it as an interesting comparison to Chapter 3. I expanded upon it, collected all information for the manuscript, carried out all data management, model development and analyses, and drafted the text. George Balazs and Stacy Hargrove provided green turtle data for the model, stimulating discussions, as well as edits and comments on multiple drafts of the manuscript. Sallie Beavers provided access to data, facilitated contacts to researchers in Hawai'i and made constructive edits and comments to drafts of the paper. Dr. Villy Christensen contributed helpful suggestions during model development. Dr. Daniel Pauly, Dr. Karen Bjorndal, and Dr. Alan Bolten provided guidance on multiple stages of the work, and edits to several iterations of the paper.

Chapter 5: The original idea and its conceptualization for this paper are mine. I carried out all data management and analyses (with the exception of the image analysis for the Bahamas, which was performed by my co-author Damaris Torres-Pulliza), and drafted the text. Dr. Serge Andréfouët provided guidance on all aspects related to image processing and analysis and granted me access to the Millennium Coral Reef database. He also contributed suggestions to the interpretation of results and edits to drafts of the manuscript. Dr. Phil Kramer provided high resolution imagery and ground truth data. Dr. Frank Müller Karger indirectly financially supported this part of my research by hosting me for several months as a visiting scientist at the University of South Florida, granted me access to the NASA image database, and provided edits to the text.

Chapter 6: As with chapter 5 the idea and its conceptualization for this paper are mine. I analyzed all data and drafted the text. My co-author Dr. Serge Andréfouët provided guidance on, and the data required for the analyses, contributed to sections of the text, and offered constructive feedback on numerous iterations of the paper. Dr. Frank Müller Karger indirectly provided funding to support my research by hosting me for several months as a visiting scientist at the University of South

Florida, granted me access to the NASA image database, and made suggestions on an earlier draft of the manuscript.

1. Introduction

"We have lived by the assumption that what was good for us would be good for the world. We have been wrong. We must change our lives so that it will be possible to live by the contrary assumption that what is good for the world will be good for us. And that requires that we make the effort to know the world and to learn what is good for it. We must learn to cooperate in its processes, and to yield to its limits"

- Wendell Berry

1.1 Rationale

Sea turtles can have major impacts on the structure and function of the ecosystems that they inhabit and their ecological role at historical abundances has been described as essential to the maintenance of healthy marine ecosystems (Jackson 1997, Jackson 2001, Bjorndal 2003, McClenachan *et al.* 2006). The detailed investigation of the multiple levels at which sea turtles interact with ecosystems constitutes an important and first step towards determining the abundance at which sea turtles fulfil their ecological roles. Such a comprehensive analysis has never been undertaken for any sea turtle population and is essential for the design of effective future species management and recovery plans.

Sea turtle populations have suffered severe declines primarily as a result of overexploitation (Parsons 1962, Hirth 1997). In the Caribbean for example, estimates of historical green turtle (*Chelonia mydas*) abundance suggest that the present population represents only approximately 3 – 7 % of the abundance levels prior to European arrival (Jackson *et al.* 2001a, Moran and Bjorndal 2005, McClenachan *et al.* 2006). To date, these pre-settlement estimates of sea turtle populations have been considered the most appropriate baselines against which to assess current population status.

However, such 'baseline population levels' may not serve as appropriate recovery targets given the present degraded state of marine habitats and altered food web structures (Bjorndal and Bolten 2003, Pandolfi *et al.* 2003, Marsh *et al.* 2005). For example, documented accounts of permanent loss of seagrass beds (Waycott *et al.* 2009), the main foraging habitat of green turtles in the western Atlantic (Bjorndal 1980), mean that fewer individuals may now be supported by these ecosystems.

Quantitative models, such as those developed using the software Ecopath with Ecosim (EwE) (Christensen and Walters 2004), are useful tools that can help clarify the changes in ecological interactions and ecosystem dynamics that would result from recovering numbers of sea turtles.

Given the degraded state of coastal ecosystems, an accurate and reliable estimate of current seagrass extent (in the case of Caribbean green turtles for example) is needed to adequately inform the development and implementation of successful recovery targets. Such estimates would also provide the baseline data necessary to respond to calls by the international policy-making community to conserve at least 10 % of the world's marine habitats (CBD 2006). In the absence of comprehensive spatial data this goal remains elusive. Remote sensing is the only practical and most cost-effective means of making large scale synoptic assessments of coastal resources (Mumby *et al.* 1999, Andréfouët *et al.* 2000). Surprisingly, despite 30 years of tropical coastal habitat remote sensing, seagrass extent has never been mapped at large scales, although such maps are needed to assist in targeted species recovery plans, and more generally, inform transboundary coastal ecosystem-based management initiatives, including the development of comprehensive networks of Marine Protected Areas (MPAs) (Wood *et al.* 2008).

1.2 Context

Sea turtles are remarkable creatures. They hatch on land, scurry over the sand at night into the sea, and on entering the water will swim vigorously and continuously for 24 hours (the “swimming frenzy”) (Salmon and Wyneken 1987, Wyneken and Salmon 1992), so as to be carried out, away from the coast (neritic zone) (Bolten 2003a) and the hungry mouths of predators (Gyuris 1994). In the western Atlantic, once offshore, they join up with major current systems (gyres) (Carr and Meylan 1980, Witham 1991), drift and swim while feeding on organisms within large seaweed rafts and other flotsam (Carr 1986a, Bolten 2003b). With the exception of Atlantic loggerhead turtles (*Caretta caretta*) we know relatively little about this oceanic phase of sea turtles’ life history (Witham 1980, Carr 1987, Zug and Glor 1998, Bolten 2003b, Reich *et al.* 2007). For hard shelled species (i.e., with the exception of the leatherback) in the Atlantic, after having spent from a few years to a decade out at sea, the small turtles return close to shore, presumably when the benefit of conditions in the neritic zone outweigh those of staying in the oceanic environment for longer (Snover 2008). They then spend decades at neritic foraging grounds until they reach maturity, at which point they undertake the often long migration back to their natal beaches, and if a female, crawl onto the sand and deposit several clutches of eggs, to start the cycle anew (Musick and Limpus 1997).

Humans have a long-standing fascination for sea turtles and they have figured prominently in the mythology of many cultures (Frazier 2003)... and in their diet (Wing and Wing 2001). Harvesting of sea turtles for the trade of their meat, oil, shells, and eggs has reduced populations that once numbered in the millions to the brink of extinction (Meylan 1999, Jackson *et al.* 2001a). Hawksbill turtles were particularly sought after for their richly patterned scutes, also referred to as tortoiseshell or bekko, and considered a precious material for millennia (Meylan 1999). Known for the delicacy of their meat, Caribbean peoples may have used green turtles for thousands of years without overexploiting the resource, but indigenous subsistence use was outpaced by the intensive capture of

sea turtles that began following the arrival of Columbus (Carr 1986b). Sea turtles could easily be caught while nesting, or harpooned on their foraging grounds. Most importantly sea turtles could be kept alive with a daily dousing of saltwater until needed (Nietschmann 1979), ensuring the provision of fresh meat on the long sailing journeys during the period of exploration, expansion, and settlement of the New World (Parsons 1962). While many countries now have regulations in place to limit this trade, or have banned it altogether, an increasing demand for subsistence and local markets, particularly of green and hawksbill turtles, and a suite of other threats contribute to the continued decline of a number of sea turtle populations. With a few notable exceptions (Bjorndal *et al.* 1999, Balazs and Chaloupka 2004a, Chaloupka *et al.* 2008), many populations are considered depleted or declining (e.g., Meylan 1999, Witherington *et al.* 2009). Besides directed take, sources of mortality include high volumes of incidental capture in fishing gear, debris ingestion, disease, and the widespread loss or degradation of coastal habitats (Eckert 1995). As a result of their marked reduction, sea turtles are classified as Endangered or Critically Endangered by IUCN (World Conservation Union) (IUCN 2009) and listed under the Endangered Species Act in the United States as either threatened or endangered.

In response to the dramatic declines, scientists and conservation practitioners throughout the world have accelerated their attempts to aid in the recovery of sea turtle populations. Current conservation practices include the protection of eggs and females on nesting beaches; reduced or no lighting on nesting beaches, chiefly to avoid the disorientation of hatchlings going to sea (Bjorndal *et al.* 1999); and the implementation of a number of measures to reduce bycatch of sea turtles in a variety of fisheries, such as spatial or temporal no-fishing closures (Lewison *et al.* 2003), turtle excluder devices (TEDs) in trawl fisheries (Crouse *et al.* 1987), and changes in hook design and bait type in pelagic longlines (Watson *et al.* 2005, Cox *et al.* 2007).

From lessons learned in fisheries management, we now know that initiatives focused on single species, with little consideration for the ecosystem in which the species occurs, are to be avoided (Pauly *et al.* 1998, Trites *et al.* 1998). Animals or populations do not occur in isolation, but depend on the environment in which they live, and successful long-term recovery of endangered species can only be achieved if conservation efforts consider the wider goal of protecting an ecosystem's structural (e.g., diversity) and functional (e.g., resilience) attributes. The explicit consideration of the ecosystem in developing management strategies for the recovery of protected species was recognised and embraced in the recommendations for a new, coordinated and comprehensive National U.S. Ocean Policy (U.S. Commission on Ocean Policy 2004), and re-emphasised at a National Oceanic and Atmospheric Administration (NOAA) protected-species stock-assessment implementation plan workshop (Merrick *et al.* 2007). Planning for the successful recovery of a species therefore, needs to include looking at how changes in a focal species (e.g., increased abundance) affect the complex interaction networks it is involved in at the scale of natural communities (Menge 1995) (i.e., ecosystem-based management).

1.2.1 Ecosystem-based management

From the above, it is clear that the development of successful national and international sea turtle management regimes require detailed knowledge of species biology and population dynamics in order to promote population stabilization and species recovery. Yet these regimes need to be anchored in a solid understanding of the ecological roles sea turtles play in the ecosystems of which they are a part (Jones *et al.* 2004). To that end, a holistic approach is required whereby knowledge gained (i) at the level of individuals, including vital rates such as fecundity, mortality, and growth can be combined with information at the population level and (ii) further integrated at the ecosystem scale.

(i) Individual

Individual growth rates are an important factor in setting the age structure and other demographics of a population, and understanding such biological processes has important implications for devising successful population management strategies. A number of studies have derived growth estimates based on mark-recapture programmes of wild animals (e.g., Boulon 1994, Bjorndal *et al.* 1995, Bresette and Gorham 2001, Balazs and Chaloupka 2004b) and skeletochronology on stranded animals (e.g., Zug and Glor 1998, Snover and Hohn 2004, Zug *et al.* 2006). To date, a meta-analysis of existing data has not been conducted. Such an analysis would provide a means to smooth out local variability and the data shortcomings of individual studies, and produce parameter estimates that are broadly applicable at the regional scale. By combining data from feeding experiments with mortality schedules and a generalised growth model, one can then derive food consumption estimates of an individual over its life cycle, which, together with an approximation of population size, can be scaled to an entire population (Pauly 1986, Palomares and Pauly 1989).

(ii) Ecosystem

Once the ‘mechanics’ of growth, mortality, and food consumption have been understood at the scale of an individual and current populations, this understanding needs to be placed into an ecosystem context. Given the drastic reduction in population numbers of sea turtles, their importance, and likely impact, at historic abundance levels is difficult to imagine (and oft forgotten). Thus, to answer the question:

“Are sea turtle species central to and essential for healthy ecosystem processes or are they relict species whose passing would have little effect on ecosystem function?” (Bjorndal 1999)

knowledge of their ecology needs to be integrated into the trophic matrix of the system within which they are found. Important aspects of their ecology to consider are their (a) direct impact as consumers, including their dietary preferences and food consumption rates; and (b) indirect impact resulting from foraging behaviour (e.g., changes to the structure of their foraging habitat and associated behavioural changes in other species). In the case of green turtles in the western Atlantic for example, which feed almost exclusively on turtlegrass (*Thalassia testudinum*) and crop blades down to 2 - 4 cm from the sediment layer (Bjorndal 1980), such indirect impacts include the potential reduction in the refuge capacity of seagrass beds for a variety of juvenile fish (Jackson *et al.* 2001a, Adams *et al.* 2006). Overall, prior to the work presented in this thesis, the integrative study of such ecosystem-level interactions has remained relatively poorly explored (but see Bjorndal (2003)).

1.2.2 Role of sea turtles and ecosystem models as support tools

A very useful way to investigate biological interactions in natural communities is to develop ecosystem models. The primary role of models in ecosystem science is to permit controlled exploration of a complex reality and to help elucidate patterns and processes that are not apparent from empirical data alone, thereby guiding research and management efforts. Within pre-defined temporal and spatial resolutions, an ecosystem model must be able to describe the changes in a system based on the selected components that make up the system and generalities of how a system functions, including quantitative estimates of biomasses, flows, trophic and non-trophic interactions (see previous section) and functional dynamic relations. Such models should ideally contribute to a greater understanding of how the system behaves and the driving forces and interactions of the system, as well as allow a prediction in terms of future states of the system.

Probably the fore-runner in its field and the most widely used of such models is the Ecopath with Ecosim (EWE) family of mass balance ecosystem models (Christensen and Pauly 1992, Walters *et al.*

1997, Plaganyi 2007). Following the original work by Polovina (1984), EwE is a unique suite of ecological modelling software in that, unlike most traditional ecological models, it allows the user not only to present an analysis on model parameters and structure at time t (Ecopath) (Christensen and Pauly 1993), but also incorporates a time dynamic aspect of ecological systems (i.e., attempts to predict ecosystem structure and function at time $t+1$ (Ecosim)) (Walters *et al.* 1997). As such, EwE allows the integration of a wide variety of information and enables the user to make predictions over a wide range of possible states of nature (Walters and Martell 2004). Moreover, it has the unique advantage, over probably most other modelling methods, of explicitly incorporating indirect non-trophic effects such as mediation (Walters and Martell 2004, Christensen 2008). Such non-trophic effects have often been overlooked and/or ignored, yet are fundamental to fully understanding changes in marine food webs (Heithaus *et al.* 2008).

Following protection, a number of sea turtle populations have started to recover (Garduño-Andrade *et al.* 1999, Beggs *et al.* 2007) and some populations are reported as close to ‘full’ recovery (Chaloupka *et al.* 2008). Application of EwE then represents a useful and unique heuristic means to investigate the potential wider ecological changes brought about by an increase in turtle abundance, as well as to describe the importance of these animals within their ecosystem. While ecosystem models are unlikely to reach the stage where they can quantitatively and accurately predict all ecosystem dynamics, they may be useful for identifying robust management strategies and exposing trade-offs. Results can also help to identify current gaps in understanding and help to focus research programmes (Walters and Holling 1990).

1.2.3 Sea turtle habitat - large scale mapping using remote sensing

Once a better understanding of the role of sea turtles within an ecosystem context has been obtained, the provision of reliable information on the extent of their foraging habitat is an important next step

towards determining sustainable recovery goals. This is particularly true given that anthropogenic impacts have led to significant reductions in the area and health of sea turtle foraging grounds (e.g., seagrass (Orth *et al.* 2006, Short *et al.* 2006, Waycott *et al.* 2009)), further highlighting that historical population estimates of sea turtles may be inappropriate recovery goals.

With a few exceptions, current available habitat data suffer from poor spatial representation and low spatial resolution. Given the geopolitical transboundary nature of sea turtle migrations, it appears sensible to develop habitat information at large, eco-regional scales (Lourie and Vincent 2004). Satellite remote sensing provides a tool to develop a reliable, methodologically consistent database of habitat extent over large regions, in a cost effective, objective, and timely fashion (Mumby *et al.* 1999, Balmford *et al.* 2005). But mapping at such a large scale will require overcoming a number of methodological challenges, including the heterogeneity of habitats and the lack of field data to be able to validate many of the products. The results of such an initiative, moreover, can provide the sea turtle community with important data from which to develop meaningful recovery targets and conservation plans (including, for example, representative MPA networks) (Gibson and Smith 1999). The products should also provide researchers and managers with a useful and much needed baseline to monitor changes registered in coastal habitats over time.

1.3 Objectives

The research I present in this thesis is framed in the context of two main objectives. The first is to develop a better understanding of the ecological role of sea turtles in neritic habitats, focusing on green turtles as a case study. The second is to develop a reliable methodology for the consistent large scale mapping of neritic foraging habitats using remote sensing, and looking at seagrass beds in the

wider Caribbean region as a focal study. The ultimate goal of these two objectives is to inform sustainable and ecologically meaningful recovery targets for sea turtles.

1.4 Thesis outline

In total there are seven chapters in this thesis, consisting of five research chapters, a general introductory chapter (this, Chapter 1) and concluding chapter. The first three research chapters relate to the first objective, to develop a better understanding of the role of (green) turtles in their neritic foraging environments. In Chapter 2, I summarise relevant ecological information for three species of sea turtles (hawksbill, loggerhead, and green turtles) at the scale of the western Atlantic. The first step includes developing broadly applicable length-mass relationships and a meta-analysis of available growth data. I then integrate these with mortality schedules over the different life stages of the species to present age-structured biomass estimates for the entire population. I finally combine these data with estimates of food conversion efficiency to determine food consumption for each age class. In Chapter 3, using the Ecopath with Ecosim software, I investigate the changes likely to accrue to a seagrass ecosystem through an increase in green turtle biomass. I particularly focus on the likely impacts brought about by the increased grazing activity of a large number of green turtles, and thus concomitant decline in habitat complexity at the ecosystem level (i.e., reduction in refuge capacity of seagrass for small fish and invertebrates). In Chapter 4, I present a detailed Ecopath model to investigate the role of green turtles at a Hawaiian foraging ground, where ancillary data suggest that green turtles are at carrying capacity. In Chapters 5 and 6, I address objective 2. In Chapter 5, I present maps for a number of seagrass areas in the Caribbean region and the methodology I developed to be able to (a) classify remote sensing images consistently over large scales, and (b) assess image accuracy based on a suite of data sets and types. In Chapter 6, I evaluate the accuracy of existing large scale habitat information and highlight the importance of developing

reliable databases at such scales to inform both species recovery plans and marine conservation initiatives more broadly. Finally, in Chapter 7, I provide a synthesis of the findings presented in this thesis, comment on strengths and weaknesses of the research, and discuss potential applications of the research findings, as well as future research directions.

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2. Population dynamics and food consumption of hawksbill

(*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), and green (*Chelonia mydas*) sea turtles in the western Atlantic¹

2.1 Introduction

Hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), and green turtles (*Chelonia mydas*) are three of the six extant sea turtle species found in the Atlantic Ocean. Their populations have been overexploited for centuries (Bräutigam and Eckert 2006) and continue to be threatened throughout their range due to directed take, disease, incidental capture by fishers, destruction of critical nesting and foraging habitat, pollution, and climate change (e.g., Eckert 1995, Lutcavage *et al.* 1997, Meylan 1999, Mortimer *et al.* 2000, Lewison *et al.* 2004). Consequently, hawksbill turtles are classified by the

¹ A version of this chapter will be submitted for publication. Wabnitz, C.C.C., Cooper, A., Bjorndal, K., and Pauly, D. Population dynamics and food consumption of hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), and green (*Chelonia mydas*) sea turtles in the western Atlantic.

World Conservation Union (IUCN) as Critically Endangered and loggerhead and green turtles are both listed as Endangered (IUCN 2009).

Sea turtles can have major impacts on the structure and function of the ecosystems that they inhabit (Bjorndal and Jackson 2003). Given their current depleted abundances, sea turtles' role as predators and grazers are likely substantially below historic levels. Conservation actions that facilitate increases in turtle abundance, therefore, have significant implications for trophic food webs.

Hawksbill turtles are considered to be the largest spongivores on coral reefs (Meylan 1990, van Dam and Diez 1996). Notably, they selectively feed on *Chondrilla nucula* (León and Bjorndal 2002), a species recorded as an aggressive competitor in the struggle for space between sponges and corals on reefs (Vicente 1978, Suchanek *et al.* 1983, Hill 1998). By breaking into the tough exterior of sponges, hawksbill turtles also facilitate feeding on the internal tissue by other spongivores, such as fish (Meylan 1988, Blumenthal *et al.* 2009a). At natural abundance levels hawksbill turtles may therefore play a key role in maintaining the structure and dynamics, and thus resilience, of coral reef ecosystems. Green turtles are an herbivorous species whose diet, in the Caribbean region, consists primarily of the seagrass species *Thalassia testudinum* (Bjorndal 1980). Green turtle grazing has been shown to result in the compensatory growth of seagrass (Moran and Bjorndal 2005), to significantly increase seagrass blades' energy and nitrogen content (Moran and Bjorndal 2007), and to increase the speed of nutrient recycling by reducing the decomposition times of *Thalassia testudinum* blades (Thayer *et al.* 1984). At pre-exploitation levels the intense grazing of several million green turtles would have led to a large scale reduction in the complexity of seagrass beds (Jackson 1997, Bjorndal and Bolten 2003, Bjorndal and Jackson 2003), in all likelihood affecting the densities of associated fauna and the nature of predator-prey relationships (Thayer *et al.* 1984, Chapter 3). The longer blades, and associated longer nutrient cycling times, that characterise today's systems have been postulated to, at least partly, facilitate the development and spread of seagrass die offs due to disease (Jackson 2001).

As governments, researchers, and conservation advocates plan for effective management and conservation solutions to recover sea turtle populations, there is pressing need to understand the ecological role of sea turtles in order to quantify their current and future impacts on ecosystems.

Two critical aspects of sea turtle life history are required in order to do so:

- (i) Growth rates - Sea turtles are characterised by slow growth rates, late maturity, and high longevity (Chaloupka and Musick 1997). Their life histories are complex, comprising at least an oceanic and neritic (coastal) stage (Bolten 2003a), and spanning entire ocean basins and several decades (Musick and Limpus 1997). Individual turtles' growth rates may be influenced by a variety of factors, including age/body size, sex, and source rookery (Bjorndal *et al.* 2000a); food quality and quantity (Diez and van Dam 2002, Kubis *et al.* 2009); competitors (Bjorndal *et al.* 2000a); predators; and ambient temperature (Kamezaki 2003). However, it remains unclear how the physiological and environmental variables highlighted above act, either singly or in concert, to influence the growth of sea turtles.
- (ii) Food consumption - Upon emergence, hatchlings enter the Atlantic and remain in the oceanic environment until, at a range of sizes, depending on species and location, they recruit to the neritic zone. Little is known about the oceanic phase. But oceanic juveniles of all three of the species considered here are thought to be largely carnivorous, feeding primarily on epipelagic prey such as cnidaria, ctenophores, and salps (Booth and Peters 1972, Bjorndal 1997, Witherington and Witherington 2002, Bolten 2003b, Frick *et al.* 2009). The transition to the neritic environment is associated with a dietary shift, which differs appreciably among species. Hawksbill turtles in the western Atlantic preferentially consume sponges (Acevedo *et al.* 1984, Meylan 1988, van Dam and Diez 1997, Blumenthal *et al.* 2009a) and are fairly selective in their choice of prey species (Meylan 1988, León and Bjorndal 2002), despite also foraging on other benthic invertebrates (Carr and Stancyk 1975, Den Hartog 1980, Pemberton *et al.* 2000, Blumenthal *et al.* 2009a). Loggerhead turtles consume a variety of slow moving or sessile hard

shelled, benthic invertebrates with diets varying among geographic areas and seasons (Lutcavage and Musick 1985, Dodd 1988, Seney and Musick 2007). Green turtles are largely herbivorous, feeding, in the Caribbean, predominantly on the seagrass *Thalassia testudinum* and/or algae (Bjorndal 1980, Bjorndal 1982) - although some populations are known to consume small to considerable quantities of animal matter, particularly jellyfish, salps, sponges, and invertebrates (Bjorndal 1980).

With quantitative data on growth rates, diet, and food consumption rates, it is possible to model the population dynamics and trophic impact of turtles within an ecosystem. This will not only enhance our understanding of their ecological roles, but also facilitate the development of management scenarios. Simulation of populations' response and their trophic impact to such initiatives will be informative prior to the implementation of conservation strategies in the field.

At the level of individual populations, sea turtles may show great variability in growth rates (e.g., Balazs 1982, Kubis *et al.*, 2009) and food consumption. The continued study of growth patterns at local scales (e.g., of individual foraging aggregations) will undoubtedly be valuable in teasing apart some of the factors thought to impact sea turtle life-history trajectories. However, in many instances, the conclusions drawn from small scale studies are marred by their small sample sizes, short recapture intervals, and limited size range of animals encountered at a given site. Moreover, sea turtles' migratory behaviour means that a single individual may be subject to variations in growth rates and food consumption associated with regionally different conditions. A synthesis of existing data for sea turtles in the western Atlantic (Figure 2.1) presents a means to smooth out regional variability and the data shortcomings of individual studies, and produce parameter estimates that are broadly applicable to the region. Given the encouraging outlook from a number of rookeries following protection from human pressures (e.g., Garduño-Andrade *et al.* 1999, Richardson *et al.* 2006, Beggs *et al.* 2007, Chaloupka *et al.* 2008), a meta-analysis of growth rate and food consumption

is necessary to answer key questions such as: what are the likely impacts of increased sea turtle abundances; what is the carrying capacity of today's ecosystems; and how do these numbers compare with historical population estimates? Such an understanding would also improve our ability to predict how environmental changes are likely to affect sea turtle populations and assist in the development of multilateral agreements and regional conservation strategies.

Here, I have undertaken a meta-analysis of the key facets of sea turtle life history required for deriving regional estimates of sea turtle biomass and food consumption. At the scale of the western Atlantic, using data compiled from a comprehensive review of the literature for hawksbill, loggerhead, and green turtles, this study presents: (i) length-mass relationships based on data sampled throughout the species' size ranges; (ii) estimates of K (the curvature parameter of the von Bertalanffy growth function (VBGF)) based on estimates of asymptotic size and several sets of published growth rate data; (iii) estimates of population biomass based on the results of (i) and (ii), as well as published information on life history parameters (e.g., size at recruitment and sexual maturity, survival); (iv) consumption/biomass estimates (Q/B), that were derived by calculating conversion efficiencies for each of the three species, combining these values with growth rate information, and integrating these over the modelled populations' age/size distribution to obtain total population food consumption. The latter calculations build on efforts by Bjorndal and Jackson (2003) and McClenachan *et al.* (2006), who present consumption estimates for historical abundances of adult Caribbean green and hawksbill turtles.

The method presented is intended as an example of how one might approach the question of how much sea turtle populations consume, to gain greater understanding of species' impact on ecosystems as predators/grazers. The study's objective was also to highlight some of the current knowledge gaps in order to help guide future research and improve upon the estimates presented here.

2.2 Materials and methods

2.2.1 Length-mass relationships

The relationship between total length (L) and mass (W), for most animals, is generally represented by the equation:

$$W = a \cdot L^b \quad (1)$$

whose parameters (a, b) are estimated by the antilog of the intercept, and the slope, respectively, of a regression of the log(W) against log(L). The value of (b) is generally close to 3.

Sea turtles can be measured in a number of ways, thus often requiring standardisation before datasets can be compared. Straight carapace length (SCL) and curved carapace length (CCL) are the most commonly used measurements. Although variations exist in how these can be taken (e.g., there are three possible straight-line carapace lengths: maximum, notch-to-tip, and minimum (Pritchard *et al.* 1983, Bolten 1999)), most authors do not detail the specific technique used in measuring individuals beyond CCL or SCL. For all analyses, discrepancies were assumed to be minimal. CCL data were converted to SCL, based on published linear regressions of paired CCL and SCL data for the species in question (see equations listed in Table 2.1). Length-mass data pairs from different studies were compiled to cover the widest possible range of sizes to make the parameters of length-mass relationships as representative of all developmental stages (i.e., juveniles, subadults, and adults) as possible (Safran 1992). Data were fitted to the log of length and mass. In the case of hawksbill turtles, the samples were weighted by the mass of individuals, because the large sample size of juveniles would have otherwise biased the results.

2.2.2 Growth rates

I created a database of growth increments derived from mark-recapture studies on animals caught in the wild, or assessed using skeletochronology on stranded wild individuals. Published growth rates were often expressed as the difference between two sizes over the time passed and reported as the arithmetic mean of a given number of individuals within 10 cm-class size bins. In order to make all published data comparable, where growth measurements were given for individual animals, the arithmetic mean of these measurements for the same 10-cm size bins was calculated. Zero growth values and negative growth increments were included in the analysis. However, in a few instances, published 10-cm binned growth rates were derived from measurements that did not include zero and/or negative increments. Discrepancies in growth rates between SCL and CCL were assumed to be minimal (Bjorndal and Bolten 1989).

Short recapture time intervals are less reliable in estimating growth due to measurement errors (Chaloupka and Musick 1997); although individual studies often report no significant difference in results when short intervals are excluded from the analysis (e.g., Collazo *et al.* 1992). When findings were detailed enough to allow it, only measurements obtained from recapture intervals > 6 months (if possible > 12 months) were included.

For the purpose of this study, growth was assumed to follow a von Bertalanffy growth function (VBGF) (von Bertalanffy 1938), with growth rates declining linearly with length, reaching zero at asymptotic length, and which typically has the form:

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \quad (2)$$

where L_t is the length at age t , L_∞ the asymptotic length or the mean size an animal would reach if it were to grow indefinitely, K a growth coefficient of dimension time^{-1} and t_0 is a theoretical age at which $L = 0$. In this form, emphasis is placed on t_0 , which can only be estimated when data regarding absolute age(s) are available (i.e., captive specimens or for species that can be aged reliably in the wild). Sea turtles recruit to the neritic environment after an unknown time as oceanic juveniles, and therefore age is rarely known. Equation (2) can be rewritten as (von Bertalanffy 1960):

$$L_t = L_\infty - (L_\infty - L_0) \cdot e^{-Kt} \quad (3)$$

where L_0 is the size of hatchlings as they emerge from the nest (which replaces t_0) and the other parameters being as defined in equation (2) (see below for estimates of L_∞). The assumption here is that growth from hatching onwards follows the VBGF, which is unlikely. It is more probable that hatchling growth is initially exponential before assuming a VBGF growth pattern. When related to biomass estimates this limitation is easily compensated for by the fact that overall mass attributed to these size classes is small compared to the remainder of the population.

Three estimates of asymptotic length (L_∞) were derived for each species: (i) the mean size of nesting females in the western Atlantic, $L_{\infty(\text{min})}$, as sea turtles have near zero growth rates after first nesting (Frazer and Ehrhart 1985) and therefore ' L_∞ ' can be seen to represent mean population nesting length; (ii) the mean size of nesting females / 0.9, $L_{\infty(\text{mid})}$, as some authors consider asymptotic size to be slightly above adult mean size, with older adults distributed normally about the mean (Frazer *et al.* 1990); and (iii) the size of the largest nesting female recorded in the region, $L_{\infty(\text{max})}$. These values were compared to the intercept of the weighted regression line derived from measured growth rate increments at $y = 0$ ($L_{\infty\text{RL}}$) to ensure that they fell within the confidence interval generated around $L_{\infty\text{RL}}$, and were therefore reasonable given data.

To account for unequal sample sizes, all data were analysed using weighted general least squares linear regression models. Weights were set equal to the sample size, as standard errors were often unavailable. As datasets did not meet the assumptions of homogeneous variance about the regression line, an additional exponential term was used to correct for heteroskedasticity in the data. For each species, three K (growth curvature) parameters were derived, by ‘forcing’ the weighted regression line through each of the three calculated L_{∞} estimates. Age-at-length for all three species was then obtained through equation (3).

2.2.3 Population biomass estimates and life cycle

Mass-at-age was determined using equation (3) and the species-specific length-mass relationships as defined in equation (1).

Individual species’ life cycles were split into four phases: yearlings, oceanic juveniles, neritic juveniles, and adults (Bolten 2003a). Mortality is usually modelled as:

$$N_t = N_r \cdot e^{-Z(t-t_r)} \quad (4)$$

where N_t and N_r are number of individuals of a given population at times t and t_r respectively, with t_r representing the age at recruitment into a given life phase, and where Z is the total instantaneous mortality rate applicable over each life phase. Size at hatching, size at which juveniles recruit from the oceanic into the neritic environment, and size at maturity (Table 2.2), as well as accepted ranges of survival rates from one phase to the next were all derived from the published or gray literature.

The size of individuals at transition between phases was held constant, based on literature estimates, and variation in age at transition was therefore a function of growth curves derived in this study.

Population estimation is complicated by the fact that females of all three sea turtle species nest several times within a breeding season, typically nest in non-annual breeding intervals that may vary in length, and may be reproductively active for decades (Miller 1997). I derived a range of annual number of hatchlings entering the population, based on published (i) number of annual nesters (Appendix 1 - 3), in so far as possible, averaged over a number of years to minimise bias in estimated rookery size caused by interannual variability in breeding numbers (Miller 1997, Broderick *et al.* 2003, Heppell *et al.* 2003a); (ii) mean number of total eggs laid per female (i.e., eggs per clutch (Appendix 4) x number of clutches); and (iii) mean emergence success (Appendix 5). Based on the range of hatchling number estimates, and assuming a stable population, I ran 1,000,000 Monte Carlo simulations to determine individual species' age-structured abundance distribution. All solutions for which the total calculated number of adults fell within estimates of total adult population size were retained (3 - 16 % for all runs). Total adult population estimates were derived from published data on the number of nesters, mean remigration interval, and assuming a 1:1 sex ratio (see Appendix 1 - 3). Finally, each species' age-structured population biomass distribution was calculated by multiplying the resulting matrix of number of individuals-at-age by the corresponding estimate of mass for each of the three estimates of K.

2.2.4 Food conversion and estimates of food consumption

Pauly (1986) proposed the following model to estimate the consumption to biomass ratio Q/B:

$$\frac{Q}{B} = \frac{\int_{t_r}^{t_{\max}} \frac{(dw/dt) \cdot N_t}{CE_t} dt}{\int_{t_r}^{t_{\max}} W_t \cdot N_t \cdot dt} \quad (5)$$

where N_t is the number of individuals at age t , W_t their mean individual mass, CE_t their food conversion efficiency, t_r the age at which individuals recruit into the population (or life phase), and t_{\max} the maximum age in the population (or life stage) (Palomares and Pauly 1998). Key assumptions to this equation are (i) a stable age distribution, and (ii) that individuals in this population grow according to the VBGF.

Food conversion efficiency (CE), most often derived from feeding experiments, is defined as the ratio of an individual animal's mass gain to food ingested (F) over a given time interval (Ivlev 1945):

$$CE = \frac{(dW_t/dt)}{F} \quad (6)$$

As shown in Pauly (1986), CE can also be related to mass by:

$$CE = 1 - \left(\frac{W_t}{W_\infty} \right)^\beta \quad (7)$$

where β is an exponent estimated as the slope of the linear regression

$$-\log(1 - CE) = \beta \log W_\infty - \beta \log W \quad (8)$$

An advantage of equation (7) over equation (6) is that CE approaches 0 as W_t approaches W_∞ . The model implies that $CE = 1$ when $W = 0$, irrespective of the values of β and W_∞ .

CE was determined using data from published feeding experiments conducted on animals in the western Atlantic region that reported intake and mass gain of captive individuals concurrently

(Stickney *et al.* 1973, Kaufmann 1975, Buitrago 1987, Swingle *et al.* 1993, Gutiérrez Montero and Cabrera Peña 1995). Food conversion efficiencies derived from data presented in Gutiérrez Montero and Cabrera Peña (1995) did not appear realistic, and were excluded from further analysis, as they did not decline with increasing age and were much higher than any other published values, in one instance even exceeding 100 %. For all studies considered, temperature ranged between 25° C and 29° C. All animals were chiefly fed different species of fish, up to three times daily. Data from studies where diets consisted of, or included, dried pellets were excluded from analysis due to uncertainty associated with pellet composition and reliable conversion rates between wet and dry mass. For each species, three general least square regression models were computed based on equation (8) ‘forcing’ the regression line through individual W_{∞} values ($W_{\infty(\min)}$, $W_{\infty(\text{mid})}$, and $W_{\infty(\max)}$ corresponding to individual species’ L_{∞} values). Data for loggerhead turtles from Swingle *et al.* (1994) showed significantly higher conversion efficiency rates than data from other included studies. This effect is the result of ingesting a nutritionally balanced diet (i.e., much lower intake of artificial diets are required, compared to fish, to produce a gram of mass gain) (Bjorndal 2003). Based on current available information, we do not know the extent to which a turtle can ingest a nutritionally ‘optimal’ diet in the wild, and therefore, whether intake rates on balanced or unbalanced diets are better estimates for wild populations. To allow more direct comparison among the three species, a multiple regression analysis was conducted including a dummy variable for data from Swingle *et al.* (1994). Thus, the final regression line was drawn using the entire dataset, but removing the ‘artificial diet effect’.

The rate of food consumption as a function of age (F_t) can be determined by rearranging equation (6):

$$F_t = \frac{(dW_t/dt)}{CE_t} \quad (9)$$

where CE_t is an individual’s conversion efficiency as a function of age.

Validation of food consumption models

To validate the food consumption models, metabolic rates (MRs) obtained from data used in this study were compared with published values for green and loggerhead sea turtles within their typical temperature range, and derived from respirometry and doubly labelled water studies. See the review by Wallace and Jones (2008) for a discussion of methods used to measure, infer, or model MRs, and their Table 2 for a summary of reported MRs used for validation purposes. The energy that an animal derives from its food is either used or stored (e.g., for somatic growth, or as adipose tissue respectively) (Nagy 1989, Speakman 1997, Sherwood 2005). The fate of ingested food energy (C) can be expressed by the following equation (Nagy 1989, Speakman 1997):

$$C = P + R + S + D + M_e + U \quad (10)$$

where P = production (i.e., somatic and reproductive growth), R = respiration (i.e., metabolic rate (MR)), S = storage (e.g., glycogen) (these terms are often listed together simply as P), D = defecation, M_e = methane gas produced in the alimentary tract, and U = excretion (i.e., nitrogenous waste). The combined efficiency of P , S , R , and U (net absorbed energy) is known as assimilation efficiency (AE). Based on data for growth and food intake (F_t) as gross energy intake, conversion rates ($1 - CE$), and assimilation efficiency (AE), equation (10) can also be rewritten as (Jones 2009):

$$MR = F_t \cdot (1 - CE) \cdot AE \quad (11)$$

Digestive efficiencies (relative percent of ingested energy that is absorbed across the gut wall (Kitchell and Windell 1972)) can be assumed to range between 60.5 % (mean weighted by the number of turtles) for *Thalassia testudinum* organic matter in *Chelonia mydas* (Bjorndal 1985) and

upwards of 85 % for most reptiles feeding on animal tissue (Zimmerman and Tracy 1989). As all captive animals were fed a carnivorous diet, assimilation efficiency was conservatively estimated at 80 % (where AE is digestive efficiency minus the absorbed energy that is lost through excretion of nitrogenous waste (Kitchell and Windell 1972)).

All intake rates from the published literature (in g) were converted into Watts ($\text{Joules}\cdot\text{s}^{-1}$) based on the diet composition detailed in the references used (see previous section), and energy contents provided for corresponding food items in Sidwell (1981). Obtained MR values were then transformed into mass-specific rates by dividing them by the midpoint of two consecutive weight measurements.

In the case of green turtles, the combined size-dependent intake levels (g dry mass (DM) *T. testudinum*) listed in Bjorndal (1980) and Williams (1988) were also converted into MRs so as to allow comparison to those derived above. Bjorndal (1980) calculated intake rates based on indigestible lignin ratio and daily faeces production, while Williams (1988) based her estimates on observed individuals' daily bite counts and bite size. For MR calculations the different-sized turtles reported in the studies were assumed to represent only one growing individual. The length of time between individual mass measurements was estimated from green turtle-specific growth rate and length-mass relationship modelled in this study (see sections 2.2.1 and 2.2.2). *Thalassia testudinum* energy content was set at $14,000 \text{ KJ}\cdot\text{kg}^{-1} \text{ DM}$ (Bjorndal 1990) and DM to wet mass (WM) ratio at 0.144 (Patriquin 1973). Mass-specific MR calculations were then performed as described above.

Unfortunately, to my knowledge, no directly measured MRs for hawksbill turtles are available to compare with rates estimated here from dietary intake values.

Population estimate of food consumption

The overall (all life stages) food consumption for each species' western Atlantic population was computed, as a function of age, for estimates of 'low K', 'K', and 'high K' based on (i) individual species' mass gain as a function of age, (ii) estimates of CE as predicted from equation (7), and (iii) the size of the population as a function of age (see section 2.2.3 above). Consumption/biomass ratios (Q/B) (year^{-1}) were computed for each species by dividing the total population's intake by the population's biomass according to equation (5). Food consumption estimates and Q/B ratios were also derived for each species' neritic portion of the population only (neritic juveniles and adults).

All statistical analyses were performed in R (R Foundation for Statistical Computing, version 2.10.1).

2.3 Results

2.3.1 Length-mass relationships

The meta-analysis resulted in the length-mass relationships shown in Figure 2.2 Figure 2.4. Data available for both green and hawksbill turtles had a bimodal size distribution: the vast majority of individuals were between 20 and 70 cm carapace length, with few individuals sampled in the 70 to 90 cm range, and a second grouping at > 90 cm carapace length. Hawksbill turtles were the smallest of all turtles, while green turtles registered the largest length and mass. Excluding hatchlings, carapace lengths ranged from 22.5 to 98.9 cm for hawksbill turtles, 41.1 to 104.8 cm for loggerhead turtles, and 26.8 to 121.9 cm for green turtles. Individuals' mass ranged from 0.9 to 86.3 kg for hawksbill turtles, 10.0 to 154.0 kg for loggerhead turtles, and 2.4 to 224.0 kg for green turtles.

2.3.2 Growth rates

A total of 138 mean growth rate estimates were obtained from the literature (47 for hawksbill turtles, 50 for loggerhead turtles, and 41 for green turtles), summarized per 10-cm size class bins. Each 10-cm published mean growth rate value was itself based on measurements recorded from a number of animals. Sample sizes used to obtain these means varied between 1 and 168 sea turtles. Overall, the sample sizes for mean calculations were highest for hawksbill and green turtles (Figure 2.5), with the greatest number of growth rate values recorded between 20 and 60 cm. Sample sizes were small for > 60 cm size classes. With a few exceptions, loggerhead turtle sample sizes were < 10 individuals (Figure 2.5, centre panel), with similar number of samples per 10-cm size class bins.

Median growth rate values for each size class are presented in Figure 2.6. Mean growth rates for individual 10-cm size class bins ranged from negligible ($0.29 \text{ cm}\cdot\text{year}^{-1}$ for hawksbill turtles, $0.1 \text{ cm}\cdot\text{year}^{-1}$ for loggerhead turtles, and $1.18 \text{ cm}\cdot\text{year}^{-1}$ for green turtles), to $\geq 9 \text{ cm}\cdot\text{year}^{-1}$. Juvenile loggerhead turtles (45-cm size class) caught in Union Creek, Bahamas grew the fastest ($15.7 \text{ cm}\cdot\text{year}^{-1}$, Figure 2.7, centre panel; and Figure 2.9) (Bjorndal and Bolten 1988a).

Variation in growth rates was evident both within and among species for any given 10-cm size class bin (Figures 2.8 - 2.10), with the greatest variation observed for the smallest size classes. In some cases individual population trajectories showed increased growth with increasing size (Figure 2.7). However, the overwhelming population trend for all three species was one of declining growth with increasing size, and this was well captured using a linear model (Figures 2.8 - 2.10). This linear trend was strongest for hawksbill turtles (Figures 2.6 and 2.8). Interestingly, both loggerhead and green turtles had a tendency to register a small increase in growth rate upon recruiting to neritic environments, though this 'hump' did not deviate appreciably from the linear model (Figure 2.6).

For hawksbill turtles, $L_{\infty RL}$ was 94.4 cm (CI = ± 48.5 cm) (Figure 2.8). Thus, estimates of 86 cm, 95 cm, and 114 cm for $L_{\infty(min)}$, $L_{\infty(mid)}$, and $L_{\infty(max)}$ respectively, fell within the confidence intervals generated by the weighted linear regression. Results were similar for loggerhead turtles, with $L_{\infty RL} = 112.1$ cm (CI = ± 79.8 cm), and $L_{\infty(min)} = 92.0$ cm, $L_{\infty(mid)} = 102$ cm, and $L_{\infty(max)} = 115$ cm (Figure 2.9), and for green turtles, with $L_{\infty RL} = 123$ cm (CI = ± 118.2 cm), and $L_{\infty(min)} = 106$ cm, $L_{\infty(mid)} = 117$ cm, and $L_{\infty(max)} = 134$ cm (Figure 2.10). For graphical purposes only, small, medium and large sample sizes, as indicated in Figures 2.8 - 2.10, corresponded to < 10 , > 10 to < 30 , and > 30 for hawksbill and loggerhead turtles, and < 15 , > 15 to < 40 , and > 40 for green turtles respectively.

Species-specific K estimates derived from weighted linear regression forced through each of the three L_{∞} estimates are presented in Table 2.2. K values ranged from 0.0359 year⁻¹ for green turtles, to 0.0955 year⁻¹ for loggerhead turtles.

2.3.3 Population biomass estimates and life cycle

A summary of the life history parameters for each of the three turtle species in this study is presented in Figures 2.11 - 2.13. An estimated mean of 2,020,000 hawksbill, 5,337,000 loggerhead, and 10,178,000 green turtle hatchlings enter the western Atlantic each year. Survival rates for each life history stage were based on published estimates, and ranged between a minimum of 0.475 for yearlings and a maximum of 0.920 for adult loggerhead turtles (Figures 2.11 - 2.13).

Based on data presented in the literature, size at recruitment to the neritic environment was set at 20 cm, 45 cm, and 25 cm for hawksbill, loggerhead, and green turtles respectively, while size at maturity was set at 75 cm, 87 cm, and 92 cm (Table 2.2). Dependent on estimates of K, hawksbill turtles were found to recruit to the neritic environment at between 3 and 4 years of age, and become sexually mature between the ages of 22 and 24 years (Figure 2.11). Loggerhead turtles recruited to

the neritic environment at between 7 and 9 years of age, and reached sexual maturity between 25 and 30 years of age (Figure 2.12), while green turtles were 4 to 5 years old and 31 to 36 years old at neritic recruitment and sexual maturity respectively (Figure 2.13).

Total biomass estimates for hawksbill, loggerhead, and green turtle populations in the western Atlantic are presented in Table 2.3 and Figure 2.14. Not surprisingly, based on the annual number of nesters in the region, green turtles had the greatest, and hawksbill turtles the lowest, overall biomass. Figure 2.14 clearly highlights that for each species, the neritic juvenile stage encompassed the greatest proportion of total population biomass, while adults only represented a small fraction (Table 2.3).

2.3.4 Food conversion and estimates of food consumption

Based on feeding regimens from captive studies, β values (see equations (7) and (8)) ranged between a low of 0.0286 for green turtles and a high of 0.0430 for hawksbill turtles (Table 2.4). At the individual species level, close congruence was found among β values derived using $L_{\infty(\min)}$, $L_{\infty(\text{mid})}$, and $L_{\infty(\max)}$.

Out of all species, the forced regression line derived for hawksbill turtles fitted the available data best (Figure 2.15, top left panel). As outlined in the materials and methods section, datasets for loggerhead turtles kept at the Virginia Marine Science Museum and Columbus Zoo, USA (Swingle *et al.* 1993) showed higher conversion efficiencies than other published estimates (Figure 2.15, top right panel). This is a result of animals being fed nutritionally balanced diets, compared to ‘fish muscle’ in all other studies. A multiple regression that included a dummy variable (‘artificial diet’ = 1, ‘fish muscle’ = 0) allowed the use of the whole dataset while excluding the ‘artificial diet factor’. Very limited data from the Atlantic (Georgia (USA) and Colombia) were available to calculate

conversion efficiencies for green turtles (Figure 2.15, bottom panel). Although the regression was drawn using these data only, data from the Pacific coast of Mexico are also presented to illustrate that calculated estimates approximated the empirically derived rates, inclusive of larger sizes.

Mass-specific metabolic rates (MRs) calculated from data used to derive the food consumption model showed relatively good congruence with resting and field MR measurements using doubly labelled water and respirometry (Figure 2.16). Note that in the case of green turtles, previously published values and data converted from direct food consumption estimates from wild animals provide independent validation of estimates that were derived in this study from captive data.

Age-structured food consumption estimates at the scale of the entire western Atlantic for hawksbill, loggerhead, and green turtle populations are shown in Figure 2.17 (all life stages). Integrating under the curves in Figure 2.17 for the neritic life stages only, total consumption by neritic juveniles and adults amounted to between 21,700 and 43,800 tonnes, 242,000 and 715,000 tonnes, and 720,000 and 1,400,000 tonnes for hawksbill, loggerhead, and green turtles respectively. Q/B estimates for the neritic life stages only of each species, ranged between 2.14 (low K) for green turtles and 3.86 (high K) for loggerhead turtles (Table 2.5).

2.4 Discussion

A relatively large number of empirical studies, of growth trends in particular, on hawksbill, loggerhead, and green turtles have been carried out in the western Atlantic. The application of meta-analytical methods allowed the combination of such studies, conducted at different localities and of varying samples sizes, and to generate a suite of models that are generally applicable to the western Atlantic region. The identification of such commonalities is of critical importance in the

development of large scale conservation and management strategies for highly migratory and shared resources such as sea turtles.

2.4.1 Length-mass relationships

Combining datasets of length and mass for hawksbill, loggerhead, and green turtles provided a robust relationship throughout the individual species' size ranges. A number of published regressions to date, for logistical reasons, have focused on separate foraging (e.g., Bjorndal and Bolten 1988b, e.g., van Dam and Diez 1996) and nesting aggregations (e.g., Beggs *et al.* 2007, CCC unpublished), and thus tend to include only a subsample of a species' size-spectrum at the regional scale.

Monitoring of the body mass to carapace length relationships for local aggregations is important, and can give insights into changes in turtle condition factor for example, while further contributing to our knowledge of sea turtles as a whole. Conversely, relationships representative of the size-spectra of hawksbill, loggerhead, and green turtles at the scale of the western Atlantic provide a means to generate biomass estimates for data-poor locations, constitute a basis for comparison with other ocean basins, and are a necessary step in the calculation of population consumption estimates as presented below. Results from the meta-analysis revealed that there are only few length/mass measurements for hawksbill and green turtles in the 65 to 85 cm size range. Future initiatives should, therefore, target this size range, as well as oceanic phase individuals for which, with the exception of loggerhead turtles, measurements are rare.

2.4.2 Growth rates

For all three species, considerable overlap was found in growth rates among individual aggregations in the western Atlantic (Figure 2.6). The growth model presented depends on two key assumptions: (i) that growth trajectories can be fitted according to the 'simplest' growth model, the VBGF, and (ii)

that reasonable estimates of L_{∞} are available. A wide range of studies with records of nesting female sizes provided the latter. Concerns over the application of the VBGF have been discussed (Chaloupka and Musick 1997, Day and Taylor 1997, Heppell *et al.* 2003a). However, combined at the regional level, regression of growth rates at age for all three species did not substantially deviate from the assumption of an overall monotonic declining growth curve with increasing carapace length (Figures 2.8 - 2.10). Such a pattern, therefore, suggests that the VBGF provides reasonable estimates of growth rates and size classes. Moreover, even in instances where growth patterns seemed to not entirely conform to the VBGF, with some aggregations of loggerhead and green turtles registering peak growth rates a few years following neritic recruitment (Figure 2.7), the extent of deviation will not result in substantial different estimates of population level intakes (one of this study's key objectives). It is unclear whether the increased growth rates shortly following settlement may represent a continuation from the pelagic stages or a surge in growth following neritic settlement (Heppell *et al.*, 2003a). In a recent study, Bjorndal and Bolten (2010) hypothesize that such dome-shaped patterns at small size classes in the Atlantic may be associated with delayed growth during the transition from oceanic to neritic diets. The authors further suggest that this 'limited nutrition' transition period could be followed by a time of compensatory growth.

In the context of results presented here, departure of individual data points from the overall relationship is expected. Efforts should focus on increasing sample sizes at small (especially for loggerhead turtles) and large size classes (all species), as some apparent trajectories may in part be an artefact of sample size (Figure 2.5). Although continued data sampling at the local scale and further analysis of the source and significance of this variation are important, so are analyses presenting a summary of current results and overarching patterns. As growth data accumulate for all stages of sea turtle species these will provide useful updates to models presented here.

2.4.3 Age at maturity

Measuring age at maturity directly in wild sea turtles is difficult given the geographic scope and long time spans that any such effort would involve (but see Limpus (2009) for notching of hatchlings). Models based on the assembly of growth rate data, therefore, represent a valuable approach to determine age for any given size. Part of the difficulty in generating such estimates for sea turtles is that, currently, limited or no data are available on the growth and/or duration of the epipelagic phase of western Atlantic green turtles (Zug and Glor 1998, Reich *et al.* 2007) and hawksbill turtles, respectively. Estimates of age at maturity thus assume that (i) pelagic growth follows the same pattern as indicated by neritic growth measurements, a pattern that seems warranted for loggerhead turtles in the Atlantic (Parham and Zug 1997, Bjorndal *et al.* 2001) (Figure 2.7 and Figure 2.9); and (ii) growth rates are negligible post maturation. It is reasonable to assume that a similar pattern holds in the Atlantic, and data for loggerhead turtles nesting at Melbourne Beach, Florida (Bjorndal *et al.* 1983), and hawksbill turtles at Tortuguero, Costa Rica (Bjorndal *et al.* 1985), support the latter.

Hawksbill turtle (*Eretmochelys imbricata*)

Results indicated that a hawksbill turtle spends on average between 18 and 21 years at neritic foraging grounds, prior to becoming sexually mature (Figure 2.11). This range is in line with the age at maturity estimate of 25 years adopted by Meylan and Donnelly (1999). Individual studies found hawksbill turtles to take 9.4 years to grow from 45.0 to 77.7 cm (at which size the turtle nested) (Bjorndal and Bolten 2010), < 14.7 years between neritic recruitment in Puerto Rico at 23.0 cm and average breeding size (Diez and van Dam 2002), and 16.5 years to grow from 21.3 to 78.8 cm, the minimum adult female size at Buck Island, USVI (Boulon 1994). For comparative purposes, age at maturity for Australian hawksbill turtles is thought to range between 20 and 50 years (Chaloupka and Limpus 1997, Limpus and Chaloupka 1997, Chaloupka *et al.* 2004).

Loggerhead turtle (*Caretta caretta*)

Assuming ca. 42.4 to 59.5 cm SCL (converted from 46.0 to 64.0 cm CCL) as the range during which most loggerhead turtles leave the oceanic habitat, Bjorndal *et al.* (2000b) and Bjorndal *et al.* (2003a) estimated the duration of the oceanic stage for North Atlantic loggerhead turtles to last between 6.5 and 11.5 years. This range corroborates the estimates of 7 to 9 years provided by the model presented here - based on the assumption that loggerhead turtles recruited to neritic habitats at a size of 45 cm SCL, and a growth model that accounted for three separate estimates of L_{∞} . The range of values presented for the neritic stage (16 - 23 years) also agrees with estimates derived by Braun-McNeil *et al.* (2008) (24 year long neritic stage). Similarly, the herein modelled age at maturity estimates (25 - 30 years) (Figure 2.12) are in line with results from earlier studies, which placed age at maturity between 12 and 30 years (Frazer and Ehrhart 1985, Zug *et al.* 1986, Klinger and Musick 1995), and estimated that it would take approximately 26.5 years for a loggerhead to grow to a size of ~81 cm SCL (converted from CCL) (Bjorndal *et al.* 2001). A more conservative age at maturity estimate (34 years) was chosen for a stage-based demographic model, presented in the recently completed recovery plan for the northwest Atlantic population of the loggerhead sea turtle (2009). The model assumed a total of 7 years in the oceanic stage, based on data presented in Bjorndal *et al.* (2000b).

Green turtle (*Chelonia mydas*)

Of the species considered, green turtles took the longest to reach sexual maturity (31 - 36 years, Figure 2.13); a finding that is consistent with their slow growth rates. The long neritic juvenile stage (26 - 32 years) of green turtles is probably due to their herbivorous diet in post-pelagic habitats (Heppell *et al.* 2003a) and associated lower food assimilation efficiency (~ 60 %, whereas energy digestibility coefficients of 80 % are expected for higher quality diets). Estimates derived herein are

in line with results from earlier studies suggesting that green turtles would require 6 (Zug and Glor 1998) to 17 years (Bjorndal and Bolten 1988b, 1995, Bjorndal *et al.* 2000a) to grow from ~ 30 to 75 cm SCL, and reach mean nesting size between 18 and 36 years of age (Mendonca 1981, Frazer and Ehrhart 1985, Frazer and Ladner 1986). Similarly, Bjorndal *et al.* (2000a) noted that it takes ~ 30 years for green turtles at Union Creek, Bahamas, to grow from 30 to 82 cm SCL. For comparative purposes, in Hawai'i, pelagic juveniles only recruit to neritic foraging grounds at a size of ca. 35 cm SCL and are thought to reach maturity between 35 and 50 years of age (Balazs and Chaloupka 2004). This range is consistent with age at maturity estimates derived for several foraging-ground populations comprising the southern Great Barrier Reef green turtle genetic stock (Limpus and Chaloupka 1997, Chaloupka *et al.* 2004). In contrast, green turtles in Bahía de los Angeles, central Gulf of California, are expected to attain maturity after 9 to 21 years (recruiting to neritic habitats at ~ 20 cm SCL (Seminoff *et al.* 2002)).

For all three species considered, it is encouraging to see that, by and large, estimates of time spent at neritic foraging grounds prior to sexual maturity derived from individual datasets, irrespective of the means with which these were analysed, corroborated each other.

2.4.4 Population biomass estimates and life cycle

Biomass estimates for western Atlantic sea turtle populations were derived by combining disparate datasets on length-mass relationships, growth, and mortality. Of these three aspects of sea turtle's life history, mortality, particularly for pelagic and neritic size-classes, remains one of the most data poor (Heppell *et al.* 2003b). This is unsurprising given the long time series required and inherent difficulties in estimating survival from field data (Bjorndal *et al.* 2003b). The majority of published estimates tend to fall into one of two categories. First, survival probabilities often reflect apparent survival (e.g., Campbell and Lagueux 2005) rather than true survival, due to mortality estimates

confounding mortality and permanent emigration (Frazer 1987, Heppell *et al.* 1996, Bjørndal *et al.* 2003c). Second, published data tend to represent inferred values rather than empirical estimates (e.g., NMFS 2001, Heppell *et al.* 2003b). The advantage to the approach presented here lies in the use of survival probability distributions to represent and incorporate some of the natural variability and uncertainty in these estimates. However, as longer time series and more data become available these should be used to revise and update the distributions presented. The synthesis of information conducted in this study has also underscored the need to address a number of existing information deficiencies, including the need for additional demographic information on annual reproductive output (e.g., hatching/emergence success and clutch frequency).

Each species' model assumed equal adult sex ratio, as encountered for example in loggerheads at northern foraging ground aggregations (NMFS 2001). It is important to note however, that some authors have reported an apparent female dominance (e.g., immature loggerhead turtles along the southern Atlantic coast of the USA (Wibbels *et al.* 1991, Shoop *et al.* 1998, Braun-McNeil *et al.* 2009) and hawksbill aggregations in the Caribbean (León and Diez 1999, Geis *et al.* 2003)), while others have noted a slightly male-biased sex ratio (e.g., foraging hawksbill turtles at Mona Island, Puerto Rico (Diez and Dam 2003)). Based on current available evidence, a primary sex ratio of 1 : 1, therefore, remains a reasonable assumption.

2.4.5 Food consumption

The food consumption model presented is the first to have been derived for any hard-shelled species of sea turtle over the course of its life history. Combined data, once standardised between the difference sources, were shown to behave coherently across gradients. For example, conversion efficiency values declined with increasing size and the resulting slopes, β , were generally consistent, despite the different species under study and variation in feed provided.

Comparison of MRs calculated from data used in this study with published MRs, and those converted from intake levels measured in the field (for green turtles), provided independent validation of the food consumption model. The meta-analysis demonstrated remarkable consistency in MR estimates, given the temporal, spatial, and dietary range of studies utilised. The agreement between datasets was particularly surprising in the case of green turtles, where data comparison included green turtles fed carnivorous diets and green turtles feeding on their natural seagrass diet.

The estimated total consumption for neritic hawksbill turtles (i.e., neritic juveniles and adults), ranging between 21,700 and 43,800 tonnes·year⁻¹, was determined using data from captive turtles that were fed fish. These estimates were converted to a corresponding biomass of sponge that hawksbill turtles would consume in the wild. For illustrative purposes, I will use the sponges *Chondrilla nucula* and *Geodia neptunia* because their energy content has been studied (Bjorndal 1990, Meylan 1990), and both are selectively preyed upon by hawksbill turtles (Meylan 1988, León and Bjorndal 2002, Blumenthal *et al.* 2009a). From data presented in Buitrago (1987) and Kaufmann (1975), and from fish composition data in Sidwell (1981), the energy content of the average feed was estimated to average 4,530 kJ·kg⁻¹. Assuming a DM to WM ratio of 0.17 (Rützler 1978, Trautman *et al.* 2000), the mean annual intake for the neritic portion of the hawksbill population was estimated at between 36,400 and 153,000 tonnes sponge WM·year⁻¹ (Table 2.6). This would correspond to a Q/B estimate of 3.6 - 9.5. Based on a rough estimate of annual digestible energy intake of 11,000 kJ·kg⁻¹, energy digestibility coefficients between 43 and 90 % and the energy content of *C. nucula*, Bjorndal and Jackson (2003) estimated that hawksbill turtles consume on average 0.77 - 1.61 kg sponge DM·kg⁻¹ turtle·year⁻¹. Using *Geodia neptunia* energy content published in Meylan (1990) neritic hawksbill turtles would have to consume slightly more to fulfil their energetic requirements (1.60 - 3.35 kg sponge DM·kg⁻¹ turtle·year⁻¹). Based on neritic hawksbill biomass estimates derived in this study (9,960 tonnes - 16,000 tonnes) (Table 2.3), the resulting consumption levels amount to

between 45,000 tonnes and 315,000 tonnes of sponge WM·year⁻¹ (Table 2.6). The discrepancy in estimates partly reflects differences in applied energy digestibility coefficients: 43 % in the study by Bjorndal and Jackson (2003), which the authors highlight is likely to be too low because hawksbill turtles feed primarily on sponges; and 80 % in estimates derived in this study, which may well be too high given the refractive nature of much of the sponge organic matter.

Food consumption calculations for the neritic life stages of an age-structured green turtle population, based on data from captive studies, yielded estimates of between 719,000 and 1,400,000 tonnes of fish·year⁻¹. Assuming a digestible energy content of 14,000 kJ·kg⁻¹ *Thalassia* DM, this is equivalent to 2,140,000 - 4,160,000 tonnes *Thalassia* WM·year⁻¹ (Table 2.6). This corresponds to Q/B estimates ranging between 6.2 and 7.5. Previous studies found green turtles to consume, on average, 0.74 to 1.77 kg DM·kg⁻¹ turtle·year⁻¹ (Bjorndal 1980, Bjorndal 1982, Williams 1988). Extrapolating to the modelled neritic green turtle population biomass estimates (i.e., 345,000 and 557,000 tonnes (Table 2.3)) yields total consumption estimates ranging between 1,770,000 and 6,840,000 tonnes *Thalassia* WM·year⁻¹ (based on a DM to WM ratio of 0.144 (Patriquin 1973)) (Table 2.6). Overall, the derived consumption values compare favourably with modelled estimates.

Food consumption estimates derived for an age-structured population represent an important contribution towards our understanding of sea turtles' roles within their ecosystems. The approach described here directly builds, while at the same time considerably expands, on studies by Bjorndal and Jackson (2003) and McClenachan *et al.* (2006), in which the authors present intake estimates for the adult portion of Caribbean hawksbill and green turtle populations. Nevertheless, the results described in this study are still necessarily rough as they are based on the small available intake/growth trials of small captive turtles on unnatural diets - some of which are nutritionally balanced and others not. As such, these calculations also illustrate the need, over a range of size

classes, for well-designed feeding trials with appropriate diets, and studies attempting to estimate intake rates of wild animals.

2.4.6 Conclusions

This study provides an important step in furthering the evaluation of the impact sea turtles have on their ecosystems and, therefore, in improving our understanding of how these may change as a result of recovering populations of sea turtles. The estimates put forward represent an attempt at describing in quantitative terms the impact sea turtles have at their neritic foraging grounds, integrating data on growth, variable mortality schedules, and food consumption estimates for individual species' life phases. Estimates presented here should be further validated and updated through initiatives aimed at determining the level of prey selectivity that loggerhead turtles, for example, exhibit in the wild (Bjorndal and Jackson 2003), and accurate intake levels of all species for different sizes at different sites in the wild.

A solid understanding of the role of sea turtles within their ecosystems will also improve our ability to predict how anthropogenic impacts, for example, will affect populations, and therefore our capacity to make more informed management decisions (Bjorndal 2003). In the context of the severely degraded state and accelerated loss of most coastal ecosystems (Gardner *et al.* 2003, Pandolfi *et al.* 2003, Hughes *et al.* 2009, Waycott *et al.* 2009), such knowledge would help elucidate the carrying capacity achievable by recovering populations of sea turtles (Chaloupka *et al.* 2008, Wabnitz *et al.* 2008).

Table 2.1 - Empirical equations used to convert curved carapace length (CCL - cm) into straight carapace length (SCL - cm) measurements for hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), and green turtles (*Chelonia mydas*).

Species	Equation	R ²	Reference
<i>Eretmochelys imbricata</i>	$SCL = 0.939 * CCL - 0.154$	n.a.	CITES (2002)
<i>Caretta caretta</i>	$SCL = 0.948 * CCL - 1.442$	0.97	Teas (1993)

Table 2.2 - Life history parameters extracted from the published literature for all three species of sea turtle considered here. K values were not derived from the literature, but were estimated through weighted general least squares linear regression models of growth data (see methods). High K, K, and low K estimates were derived based on $L_{\infty(\min)}$, $L_{\infty(\text{mid})}$, and $L_{\infty(\max)}$ respectively.

Species	Hatchling (cm)	Neritic recruitment (cm)	Sexual maturity (cm)	$L_{\infty(\min)}$ ⁱ (cm)	$L_{\infty(\text{mid})}$ ⁱ (cm)	$L_{\infty(\max)}$ ⁱ (cm)	High K	K	Low K
<i>Eretmochelys imbricata</i>	4.2 ⁱⁱ	20 ⁱⁱⁱ	75 ^{iv}	86	95	114	0.0824	0.0671	0.0467
<i>Caretta caretta</i>	4.5 ^v	45 ^{vi}	87 ^{vii}	92	102	115	0.0955	0.0749	0.0543
<i>Chelonia mydas</i>	5.0 ^{viii}	25 ^{ix}	92 ^x	106	117	134	0.0555	0.0457	0.0359

ⁱ See text

ⁱⁱ Witzell (1983); van Buskirk *et al.* (1994); Barry Kruger (pers. comm.)

ⁱⁱⁱ Carr (1987); Boulon (1994); van Dam and Diez (1998); León and Diez (1999); Diez and van Dam (2002); Meylan (1999); Blumenthal *et al.* (2009a)

^{iv} “most nesting hawksbill turtles are at least 75 cm in carapace length” (CITES 2002); in Cuba, 50 % mature by 76 - 80 cm SCL and 100 % by 80 cm SCL (Moncada Gavilán *et al.* 1999); in Puerto Rico hawksbill turtles are assumed to mature at a mean size between 70 and 75 cm SCL (van Dam 1997)

^v Dodd (1988); van Buskirk and Crowder (1994); Snover *et al.* (2007);

^{vi} Bjorndal *et al.* (2000b) - converted from a CCL of 49 cm using $CCL = 1.388 + 1.053 SCL_{nt}$

^{vii} Crouse *et al.* (1987)

^{viii} Hirth (1997); van Buskirk and Crowder (1994)

^{ix} Bjorndal *et al.* (2000a), Bagley *et al.* (2008)

^x Derived from a visual inspection of the histogram in Carr and Goodman (1970)

Table 2.3 - Total number of individuals in the western Atlantic (all life stages), percentage of adults, and overall population biomass (all life stages) for hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), and green turtles (*Chelonia mydas*). Results presented are individual means for three separate values of K (in this case, the slope of the weighted regression line forced through the individual asymptotic sizes (L_{∞})); values in brackets represent the 2.5 % and 97.5 % quantiles.

<i>Eretmochelys imbricata</i>	Low K	K	High K
Total number of individuals in population	5,460,000 [2,760,000 - 8,520,000]	5,610,000 [2,950,000 - 8,600,000]	5,790,000 [3,080,000 - 8,820,000]
% adults in population	0.46 [0.24 - 0.87]	0.44 [0.24 - 0.82]	0.43 [0.23 - 0.77]
Total biomass of population (tonnes)	11,000 [6,700 - 16,100]	14,000 [8,610 - 20,300]	16,800 [10,200 - 24,400]
Biomass of neritic stages only (tonnes) (neritic juveniles and adults)	9,960 [6,200 - 14,400]	13,400 [8,280 - 19,200]	16,000 [9,770 - 23,100]
<i>Caretta caretta</i>			
Total number of individuals in population	20,700,000 [14,400,000 - 27,900,000]	20,300,000 [14,300,000 - 27,100,000]	22,200,000 [15,700,000 - 29,600,000]
% adults in population	0.59 [0.39 - 0.86]	0.60 [0.41 - 0.87]	0.54 [0.37 - 0.79]
Total biomass of population (tonnes)	144,000 [98,900 - 199,000]	166,000 [116,000 - 225,000]	242,000 [168,000 - 330,000]
Biomass of neritic stages only (tonnes) (neritic juveniles and adults)	97,600 [69,000 - 132,000]	129,000 [91,000 - 173,000]	197,000 [137,000 - 266,000]
<i>Chelonia mydas</i>			
Total number of individuals in population	47,100,000 [29,500,000 - 67,300,000]	49,500,000 [31,400,000 - 70,000,000]	53,200,000 [34,300,000 - 75,100,000]
% adults in population	0.47 [0.29 - 0.75]	0.44 [0.28 - 0.70]	0.41 [0.26 - 0.64]
Total biomass of population (tonnes)	357,000 [255,000 - 477,000]	439,000 [316,000 - 583,000]	566,000 [406,400 - 753,200]
Biomass of neritic stages only (tonnes) (neritic juveniles and adults)	345,000 [248,000 - 459,000]	439,000 [316,000 - 583,000]	557,000 [400,000 - 740,000]

Table 2.4 - Slope (β estimates) of $-\log(1-CE)$ [conversion efficiency] vs. $\log(W)$ [mass] plots for hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), and green turtles (*Chelonia mydas*) and given three estimates of asymptotic mass ($\log(W_{\infty})$). $W_{\infty(\min)}$ is associated with an estimate of 'high K', whereas $W_{\infty(\max)}$ corresponds to values derived for 'low K'.

<i>Eretmochelys imbricata</i>	<i>Caretta caretta</i>	<i>Chelonia mydas</i>
$W_{\infty \min} = 59.39 \text{ kg}$	$W_{\infty \min} = 96.23 \text{ kg}$	$W_{\infty \min} = 152.60 \text{ kg}$
$y = -0.043x + 0.2052$	$y = -0.0315x + 0.1607$	$y = -0.0314x + 0.163$
$W_{\infty} = 77.34 \text{ kg}$	$W_{\infty} = 126.85 \text{ kg}$	$W_{\infty} = 204.83 \text{ kg}$
$y = -0.0402x + 0.1968$	$y = -0.0328x + 0.1634$	$y = -0.0302x + 0.1604$
$W_{\infty \max} = 125.42 \text{ kg}$	$W_{\infty \max} = 174.91 \text{ kg}$	$W_{\infty \max} = 306.92 \text{ kg}$
$y = -0.036x + 0.183$	$y = -0.0301x + 0.1579$	$y = -0.0286x + 0.1571$

Table 2.5 - Consumption to biomass ratios for hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), and green turtle (*Chelonia mydas*) populations (all life stages) in the western Atlantic. Standard deviations are presented in parentheses. Values presented in [square brackets] are for the neritic portion of the population only.

Species	Q/B		
	Low K	K	High K
<i>Eretmochelys imbricata</i>	2.30 (±0.07) [2.17 (±0.05)]	2.60 (±0.05) [2.53 (±0.05)]	2.80 (±0.05) [2.73 (±0.04)]
<i>Caretta caretta</i>	2.78 (±0.04) [2.48 (±0.02)]	3.22 (±0.04) [2.98 (±0.02)]	3.86 (±0.04) [3.63 (±0.02)]
<i>Chelonia mydas</i>	2.14 (±0.03) [2.08 (±0.03)]	2.34 (±0.03) [2.31 (±0.03)]	2.54 (±0.03) [2.51 (±0.02)]

Table 2.6 - Estimates of food consumption for an age-structured population of hawksbill (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) (neritic life phases only). Modelled estimates represent this study's model outputs whereas the second set of values for each species represents estimates of food consumption based on published intake rates kg⁻¹ turtle. Estimates are presented as dry mass (DM) and wet mass (WM) assuming a DM : WM ratio of 0.17 for sponge (Rützler 1978, Trautman *et al.* 2000) and 0.144 for seagrass (Patriquin 1973).

Food consumption for all neritic life stages					
Eretmochelys imbricata					
		Low	High		References and comments
Modelled <i>(extrapolated from results obtained based on a fish diet)</i>		21,700	43,800	tonnes year ⁻¹	
C. nucula	(DM)	6,180	12,500	tonnes year ⁻¹	Assuming 80 % digestibility
	(WM)	36,400	73,300	tonnes year ⁻¹	
G neptuni	(DM)	12,900	25,900	tonnes year ⁻¹	Assuming 80 % digestibility
	(WM)	75,700	153,000	tonnes year ⁻¹	
From published intake rates					
C. nucula	(DM)	0.77	1.61	kg kg ⁻¹ turtle year ⁻¹	Bjorndal and Jackson (2003); Assuming 43 – 90 % digestibility
	(DM)	7,660	25,700	tonnes year ⁻¹	
	(WM)	45,000	151,000	tonnes year ⁻¹	
G neptuni	(DM)	1.60	3.35	kg DM kg ⁻¹ turtle year ⁻¹	Bjorndal and Jackson (2003); Meylan (1990) Assuming 43 – 90 % digestibility
	(DM)	15,900	53,510	tonnes year ⁻¹	
	(WM)	93,800	315,000	tonnes year ⁻¹	
Chelonia mydas					
Modelled <i>(extrapolated from results obtained based on a fish diet)</i>		719,000	1,400,000	tonnes year ⁻¹	
Thalassia testudinum	(DM)	308,000	599,000	tonnes year ⁻¹	Assuming 60.5 % digestibility based on Bjorndal (1985)
	(WM)	2,140,000	4,160,000	tonnes year ⁻¹	
From published intake rates					
		0.74	1.77	kg DM kg ⁻¹ turtle year ⁻¹	Bjorndal (1980) ; Bjorndal (1982); Williams (1988)
	(DM)	255,000	985,000	tonnes year ⁻¹	
	(WM)	1,770,000	6,840,000	tonnes year ⁻¹	



Figure 2.1 - Western Atlantic region. Map modified from www.reefbase.org

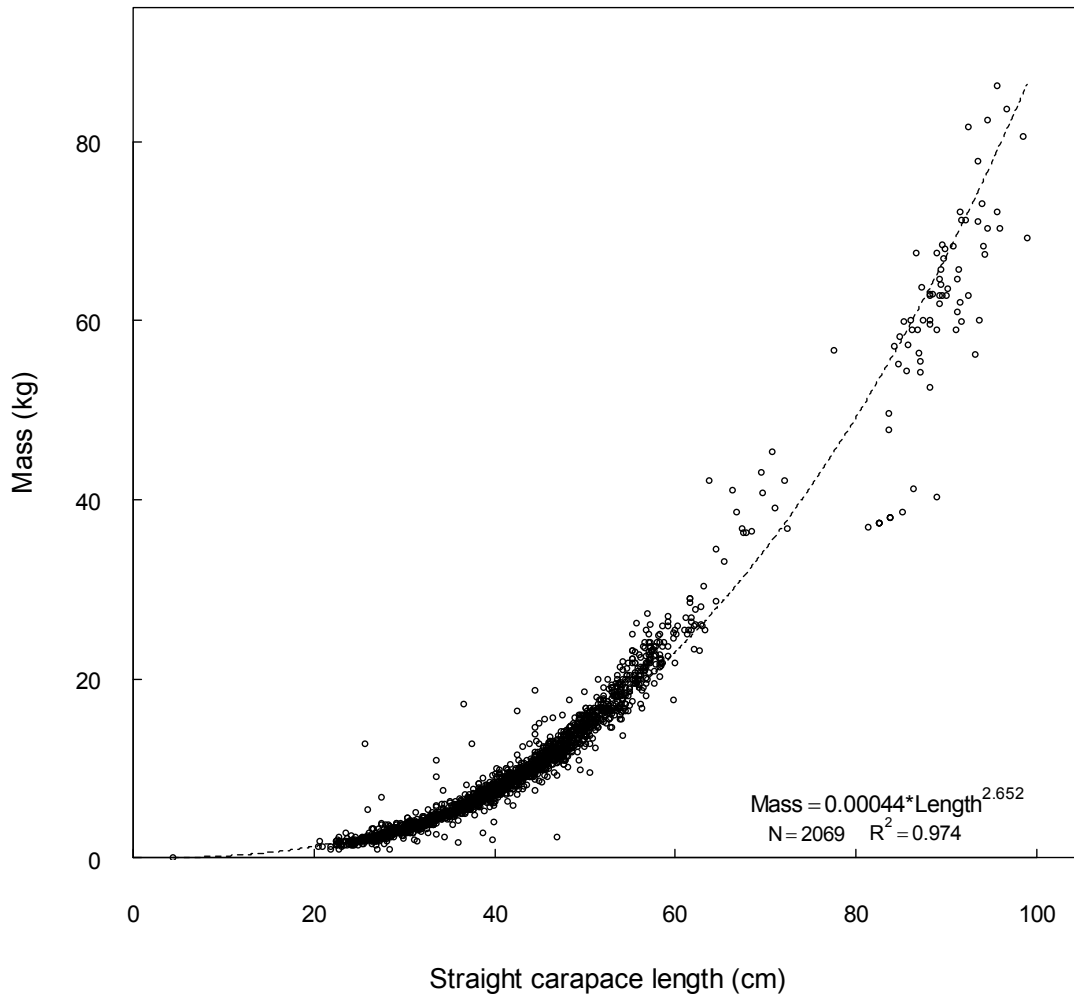


Figure 2.2 - Length-mass relationship for western Atlantic hawksbill (*Eretmochelys imbricata*) turtles. Data are from Barbados (Beggs *et al.* 2007, Krueger unpublished), the Bahamas (Bjorndal and Bolten unpublished), the Cayman Islands (Blumenthal *et al.* 2009a, Blumenthal *et al.* 2009b), Honduras (Dunbar *et al.* 2008), Puerto Rico (USA) (van Dam and Diez 1996), and Suriname (Pritchard 1969).

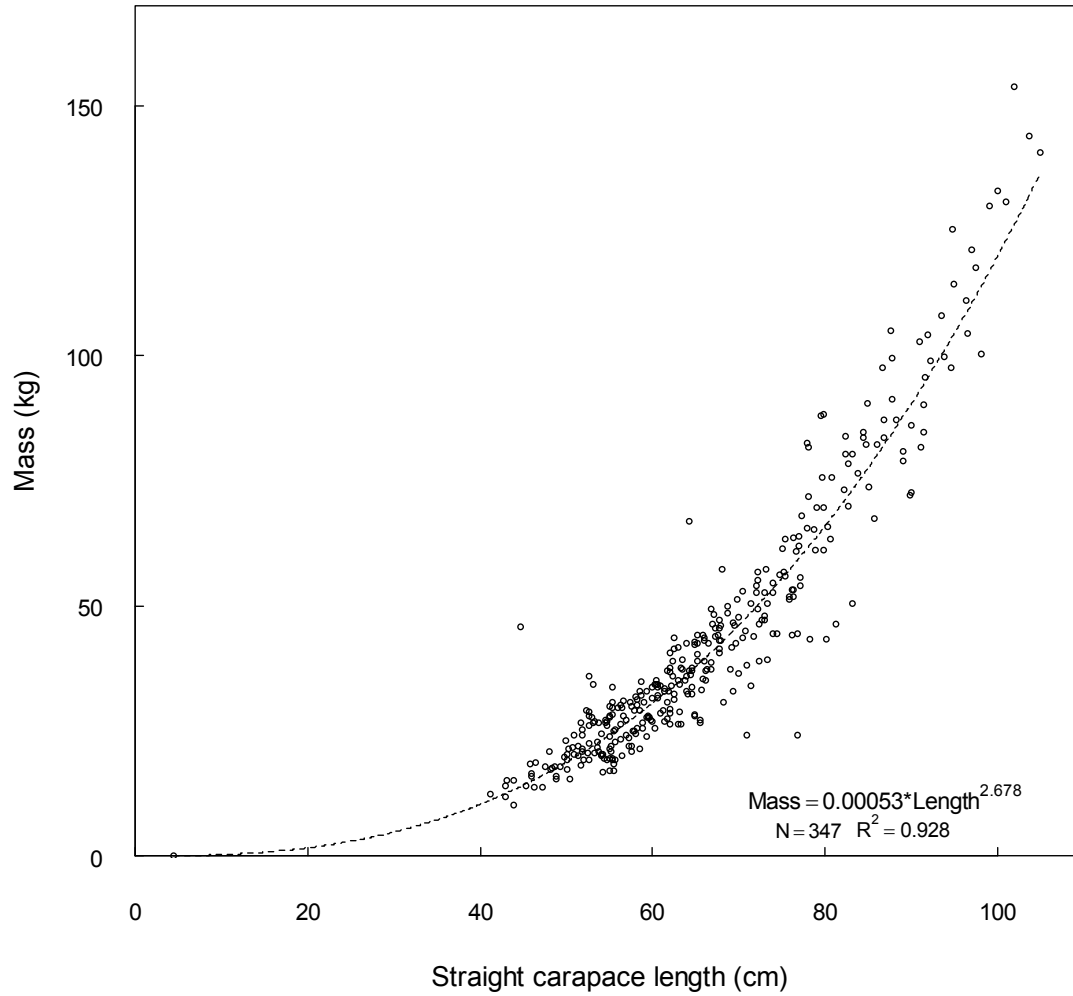


Figure 2.3 - Length-mass relationship for western Atlantic loggerhead (*Caretta caretta*) turtles. Data are from the Chesapeake (VA), USA (Byles 1988, Coles 1999); Florida, USA (Barichivich *et al.* 1997, Campbell and Sulak 1997); and Delaware Bay (NC), USA (Eggers *et al.* 1992).

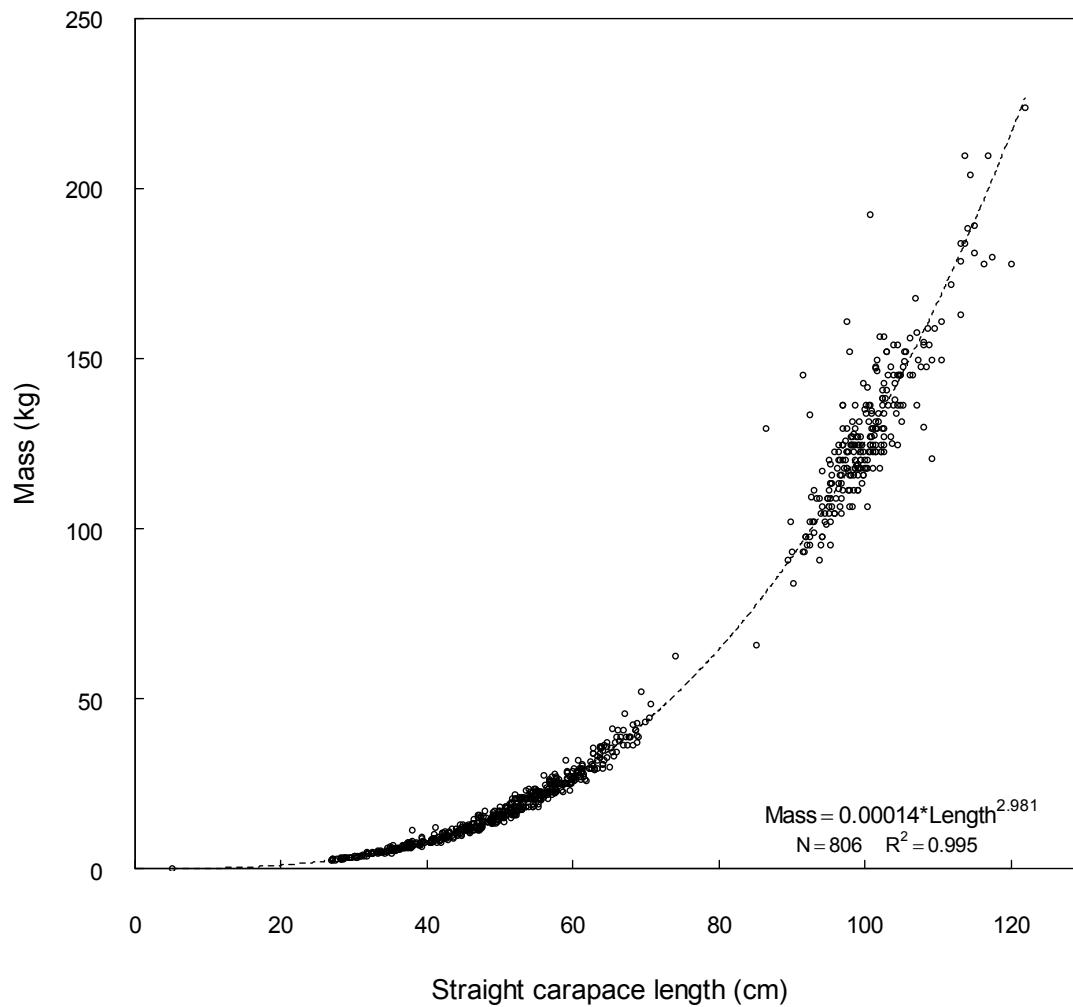


Figure 2.4 - Length-mass relationship for western Atlantic green (*Chelonia mydas*) turtles. Data are from the Cayman Islands (Blumenthal *et al.* submitted); Florida (USA) (Carr and Caldwell 1956, Barichivich *et al.* 1997, Campbell and Sulak 1997, Gilbert 2005); Suriname (Pritchard 1969); Tortuguero, Costa Rica (CCC unpublished); and Great Inagua, Bahamas (Bjorndal and Bolten 1988b).

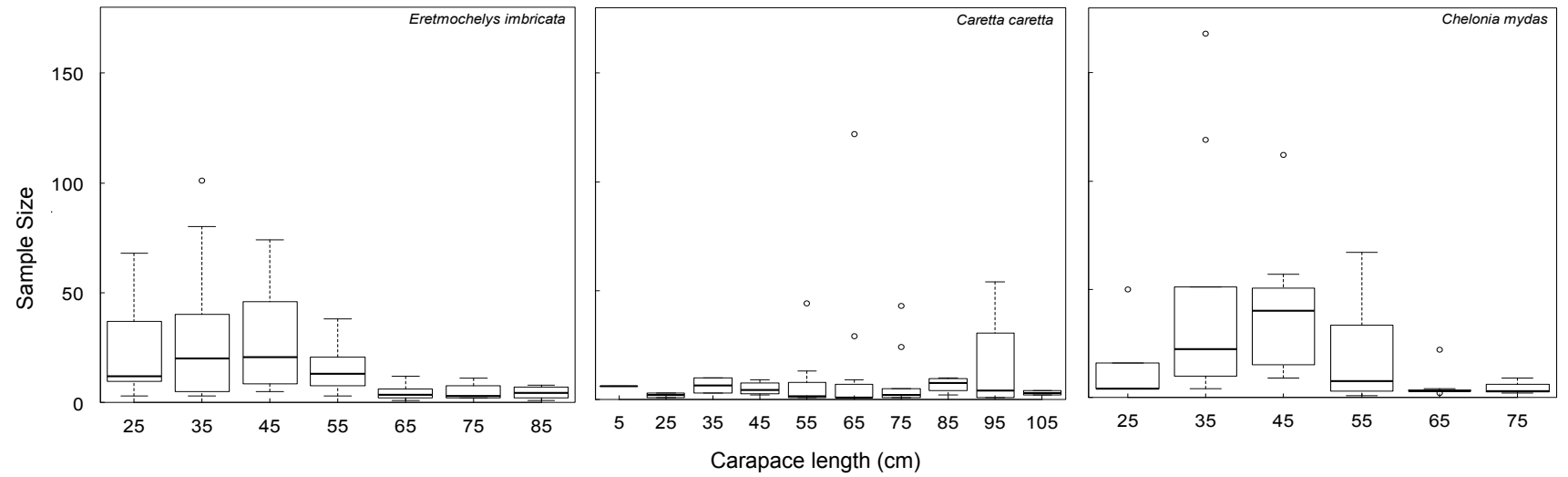


Figure 2.5 - Median sample size (indicated by the horizontal black line in the middle of individual boxes) for growth rate measurements per 10-cm size class for hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), and green turtles (*Chelonia mydas*) (left to right panel) in the western Atlantic. Open circles represent mild outliers. Note that the x-axis scale differs among species.

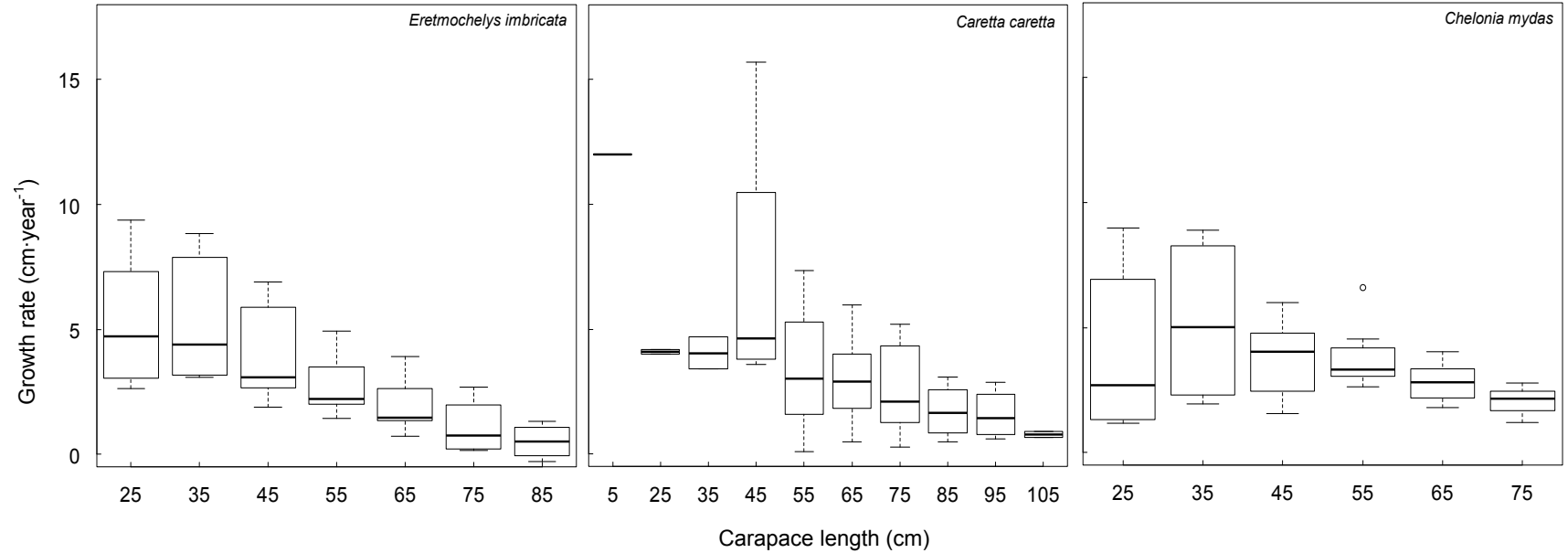


Figure 2.6 - Median growth rates in carapace length (cm·yr⁻¹) according to 10-cm size bins for hawksbill (left panel), loggerhead (centre panel), and green turtles in the western Atlantic. Median values are indicated by the horizontal black line in the middle of individual boxes; open circles represent mild outliers. Note that the x-axis scale differs among species.

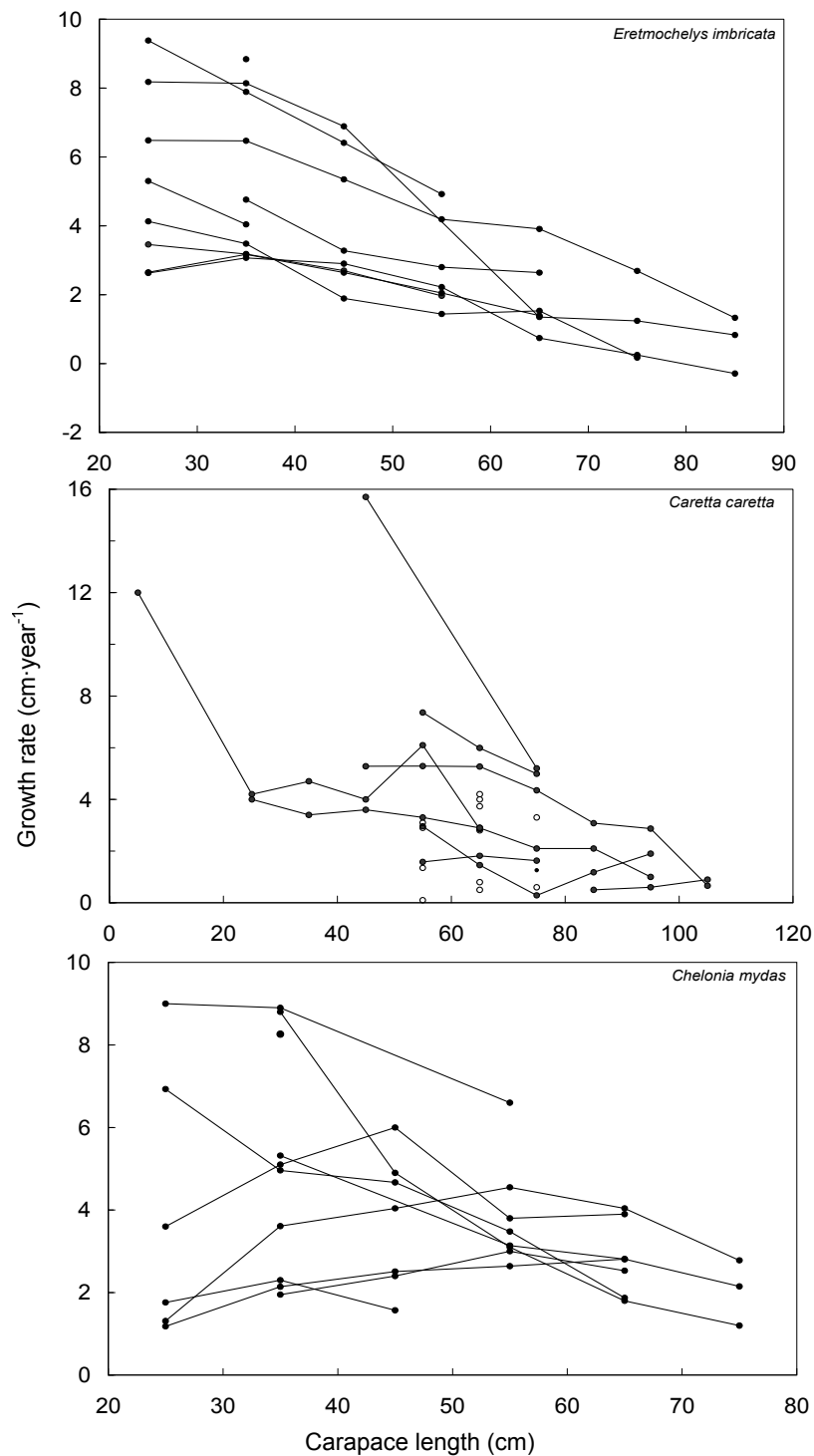


Figure 2.7 - Relationship of growth rate (cm·yr⁻¹) to carapace length for hawksbill (top panel), loggerhead (centre panel), and green turtles (bottom panel) at different sites in the western Atlantic. Lines connect mean values of 10-cm carapace length increments. Data points plotted as open circles were not linked as information to this end was lacking. Note that the x-axis scale differs among species.

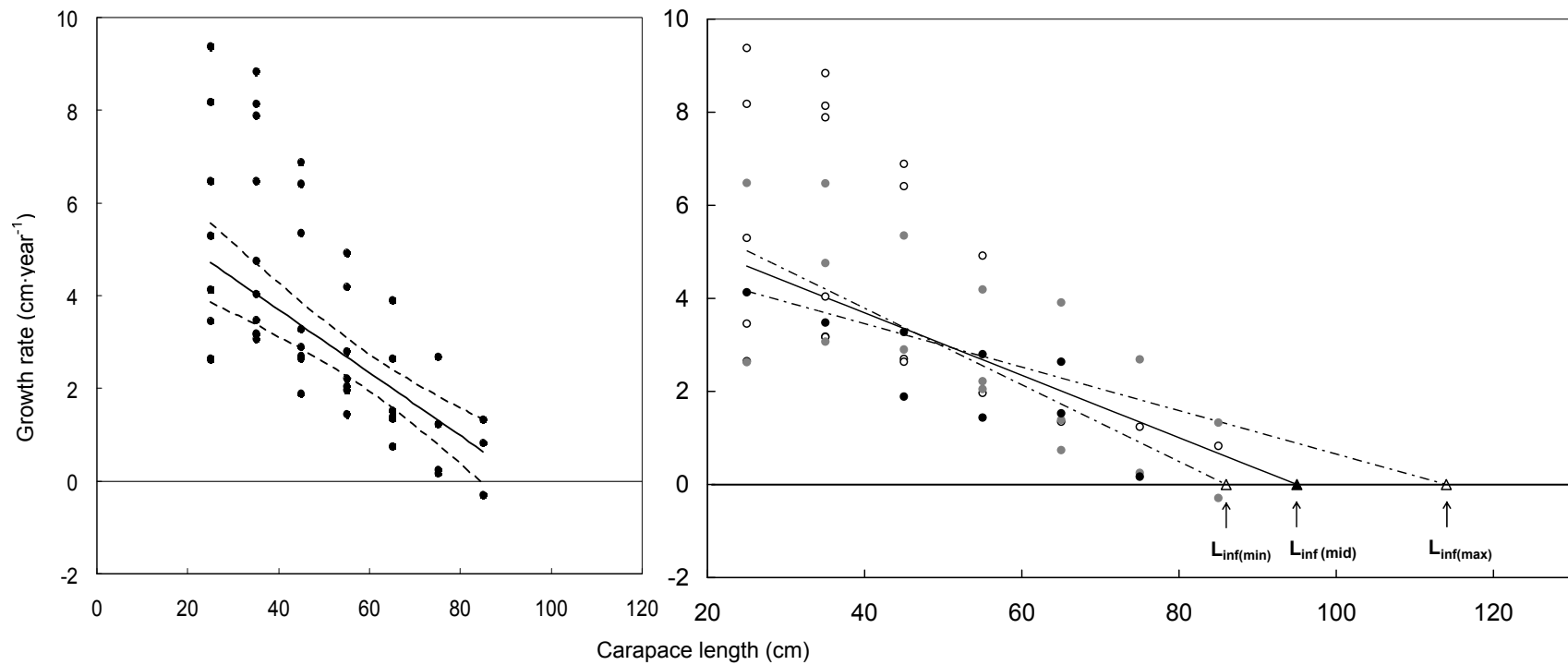


Figure 2.8 - Hawksbill turtle (*Eretmochelys imbricata*) growth rate (cm carapace length) for 10-cm size bins. Left panel: The black and dashed lines represent the weighted linear regression and the 95 % confidence intervals respectively. Right panel: Growth rate regression lines forced through $L_{\infty\min} = 86$ cm, $L_{\infty\text{(mid)}} = 95$ cm, and $L_{\infty\max} = 114$ cm. Open circles, grey circles, and solid circles represent data with small, medium, and large sample sizes respectively (see text for definition of sample sizes). Data are from Cabo Rojo, muelle oeste, playa oeste and Lanza Zo, in the Dominican Republic (León and Diez 1999 in CITES 2002); Dolce Legas, Isla Pinos (CITES 2002), and one other site (Manolis *et al.* 2006) in Cuba; Mona cliff wall, Mona reef, and Monito cliff wall, in Puerto Rico (Diez and van Dam 2002); West coast bank reef in Barbados (Krueger unpublished data) (Krueger pers. comm. in CITES 2002); and the U.S. Virgin islands (Boulon 1994).

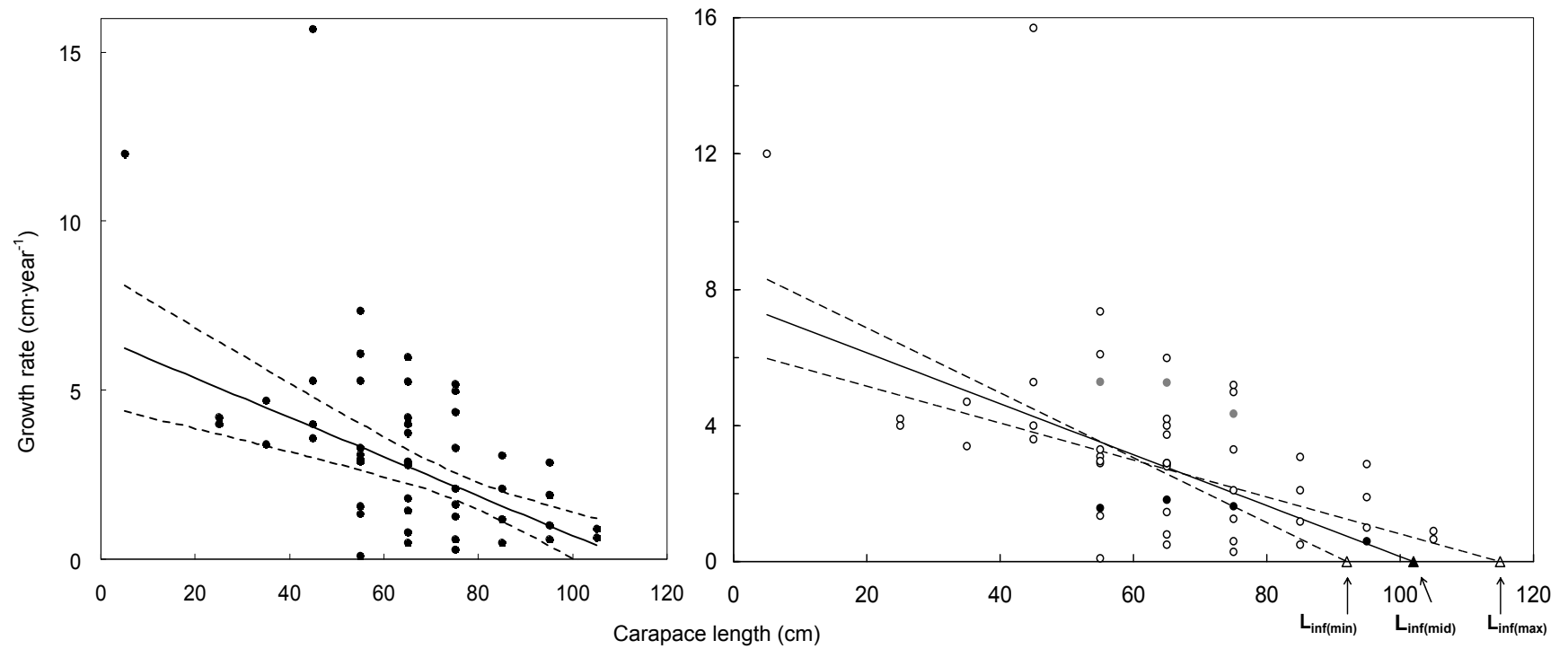


Figure 2.9 - Loggerhead turtle (*Caretta caretta*) growth rate (cm carapace length) for 10-cm size bins. Left panel: The black and dashed lines represent the weighted linear regression and the 95 % confidence intervals respectively. Right panel: Growth rate regression lines forced through $L_{\infty(\min)} = 92$ cm, $L_{\infty(\text{mid})} = 106$ cm, and $L_{\infty(\max)} = 115$ cm. Open circles, grey circles, and solid circles represent data with small, medium, and large sample sizes respectively (see text for definition of sample sizes). Data are from the Azores (Bjorndal *et al.* 2000b); Great Inagua, Bahamas (Bjorndal and Bolten 1988a); Chesapeake Bay (VA), USA (Klinger and Musick 1995); Mosquito lagoon (FL), USA (Mendonca 1981); Cape Canaveral (FL), USA (Eckert and Martins 1989); Cumberland island (GA), USA (Parham and Zug (1997) as in Bjorndal *et al.*(2003)); Melbourne Beach (FL), USA (Bjorndal *et al.* (1983) in Bjorndal *et al.* (2003)); and Core and Pamlico Sounds (NC), USA (Snover *et al.* 2007, Braun-McNeil *et al.* 2008).

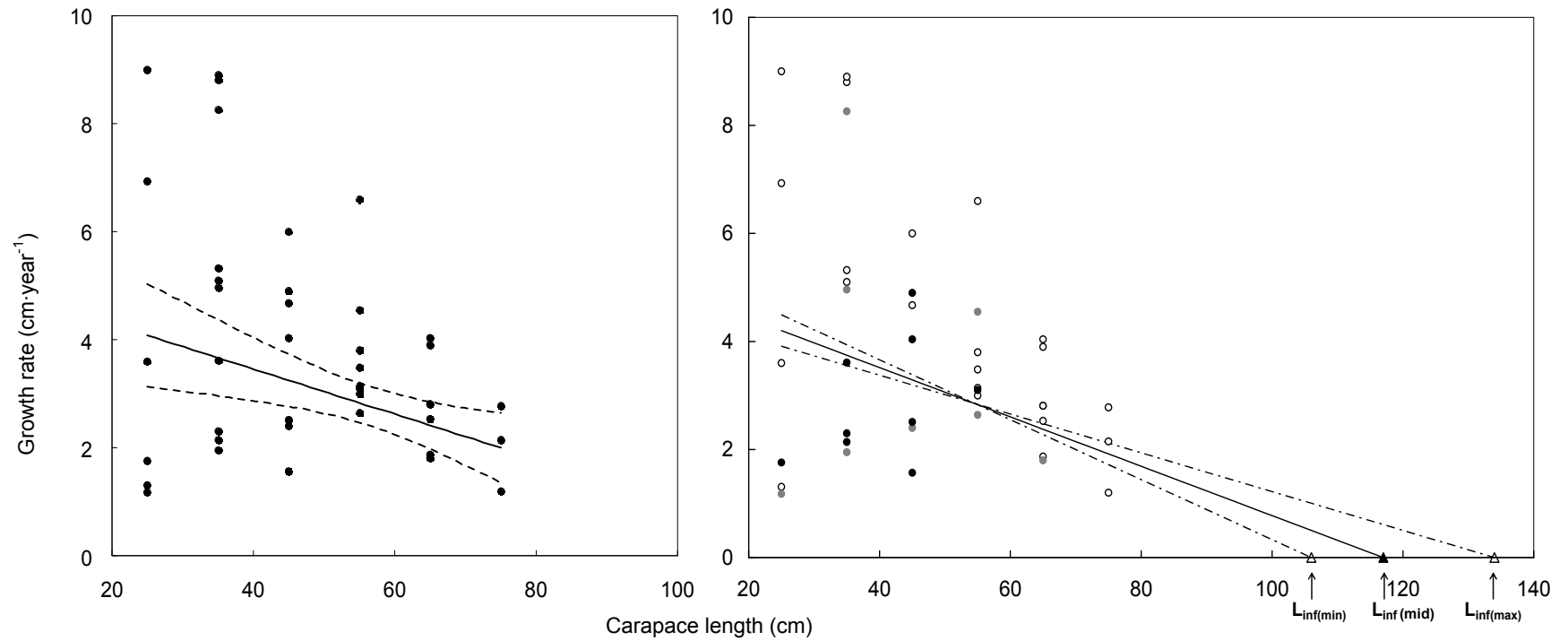


Figure 2.10 - Green turtle (*Chelonia mydas*) growth rate (cm carapace length) for 10-cm size bins. Left panel: The black and dashed lines represent the weighted linear regression and the 95 % confidence intervals respectively. Right panel: Growth rate regression lines forced through $L_{\infty\min} = 106$ cm, $L_{\infty(\text{mid})} = 117$ cm, and $L_{\infty\max} = 134$ cm. Open circles, grey circles, and solid circles represent data with small, medium, and large sample sizes respectively (see text for definition of sample sizes). Data are from the Cayman Islands (Blumenthal *et al.* submitted); Culebra, Puerto Rico (Collazo *et al.* 1992); Great Inagua, Bahamas (Bjorndal and Bolten 1988b); Indian River Lagoon (FL), USA (Zug and Glor 1998); Mansfield Channel (TX), USA (Shaver 1994); Mosquito Lagoon (FL), USA (Mendonca 1981); St Lucie county (FL), USA (Bresette and Gorham 2001); Trident Submarine Basin, Indian River Lagoon, Sebastian Inlet and St Lucie (FL), USA (Kubis *et al.* 2009); and the U.S. Virgin Islands (Bjorndal and Bolten 1988b, Boulon and Frazer 1990).

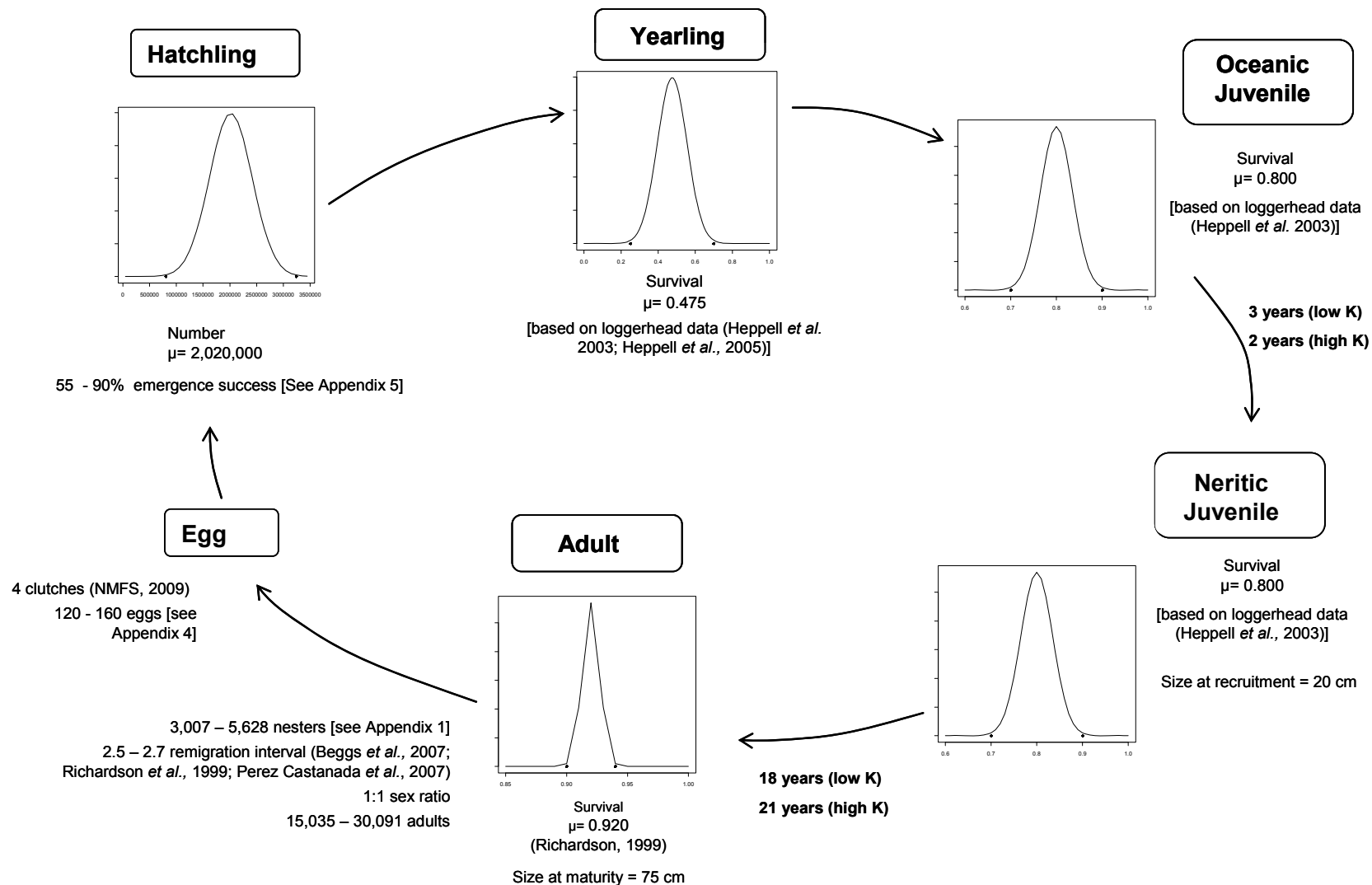


Figure 2.11 - Generalised life history diagram for western Atlantic hawksbill turtles (*Eretmochelys imbricata*). Number of years by arrows represents the time range hawksbill turtles are thought to spend as oceanic and neritic juveniles respectively, according to model calculations. All measurements are in SCL (cm).

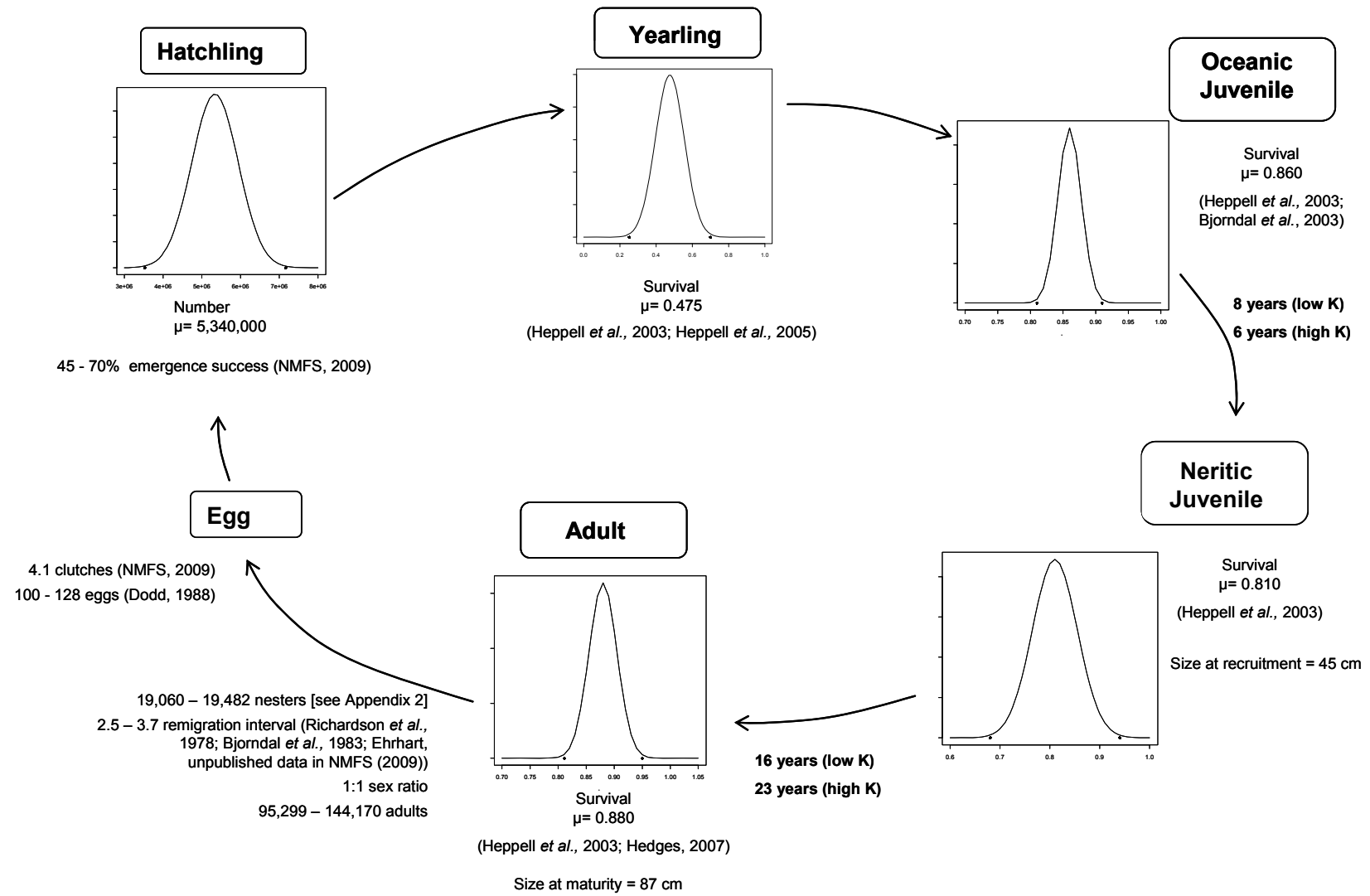


Figure 2.12 - Generalised life history diagram for western Atlantic loggerhead (*Caretta caretta*) turtles. Number of years by arrows represents the time range loggerhead turtles are thought to spend as oceanic and neritic juveniles respectively, according to model calculations. All measurements are in SCL (cm).

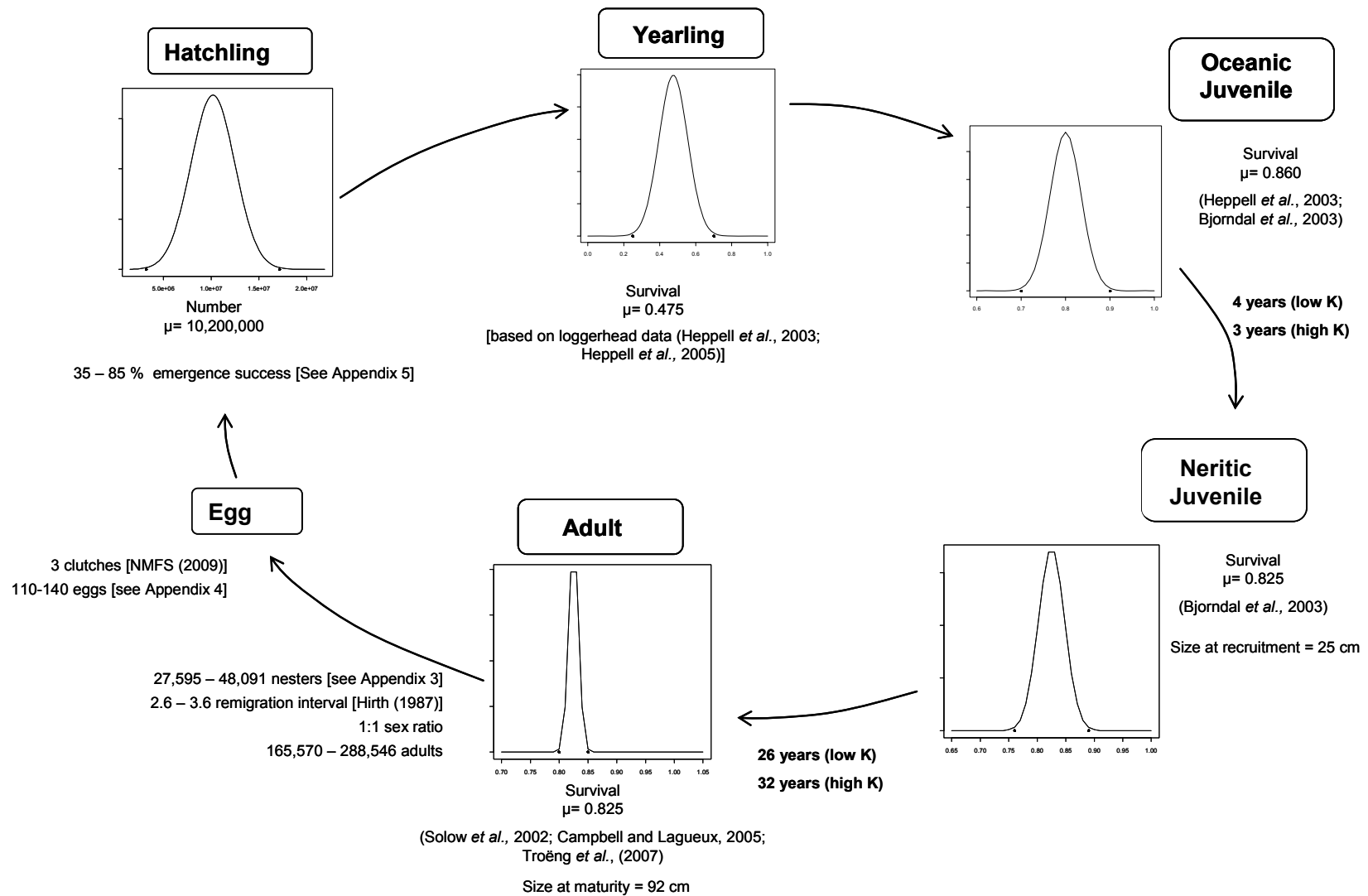


Figure 2.13 - Generalised life history diagram for western Atlantic green turtles (*Chelonia mydas*). Number of years by arrows represents the time range green turtles are thought to spend as oceanic and neritic juveniles respectively, according to model calculations. All measurements are in SCL (cm).

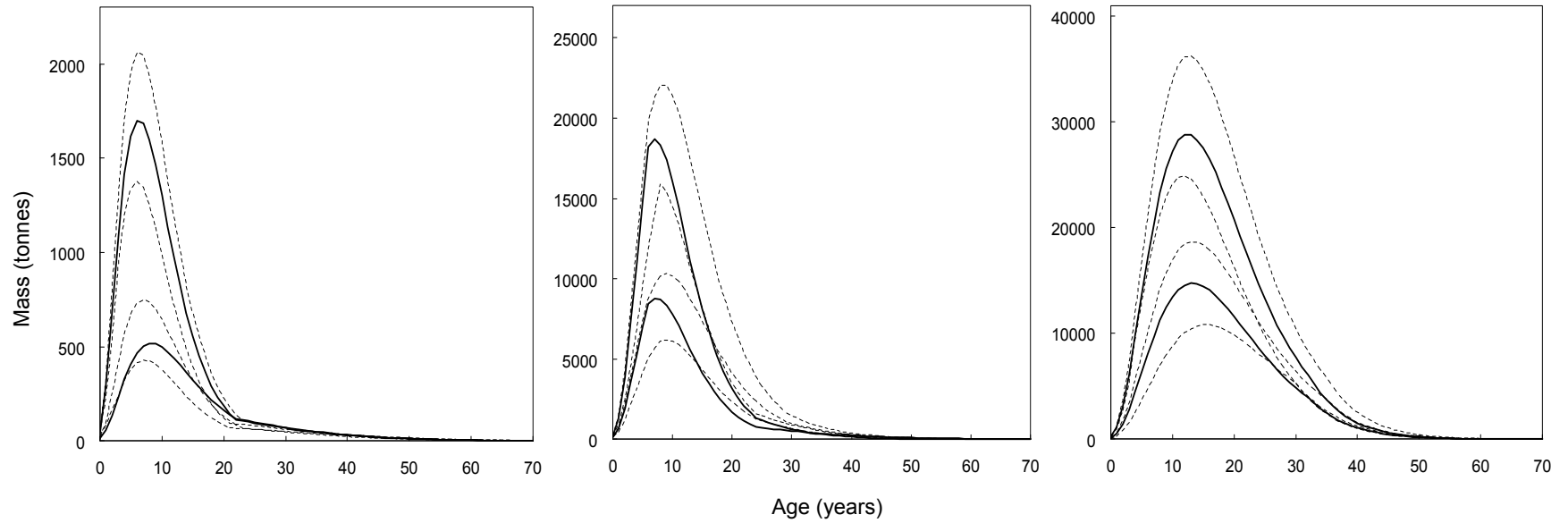


Figure 2.14 - Age-structured population biomass distribution for hawksbill (left), loggerhead (centre), and green turtles in the western Atlantic based on survivorship (Figures 10 - 12) and assuming a von Bertalanffy length/age model and a stable age distribution. The solid lines represent results for the upper and lower quantiles of model runs for life history parameters associated with $L_{\infty(\text{mid})}$. The lower and upper sets of dashed lines represent results for the upper and lower quantiles of model runs using life history parameters associated with $L_{\infty(\text{min})}$ and $L_{\infty(\text{max})}$ respectively. Note that the y-axis scale differs among species.

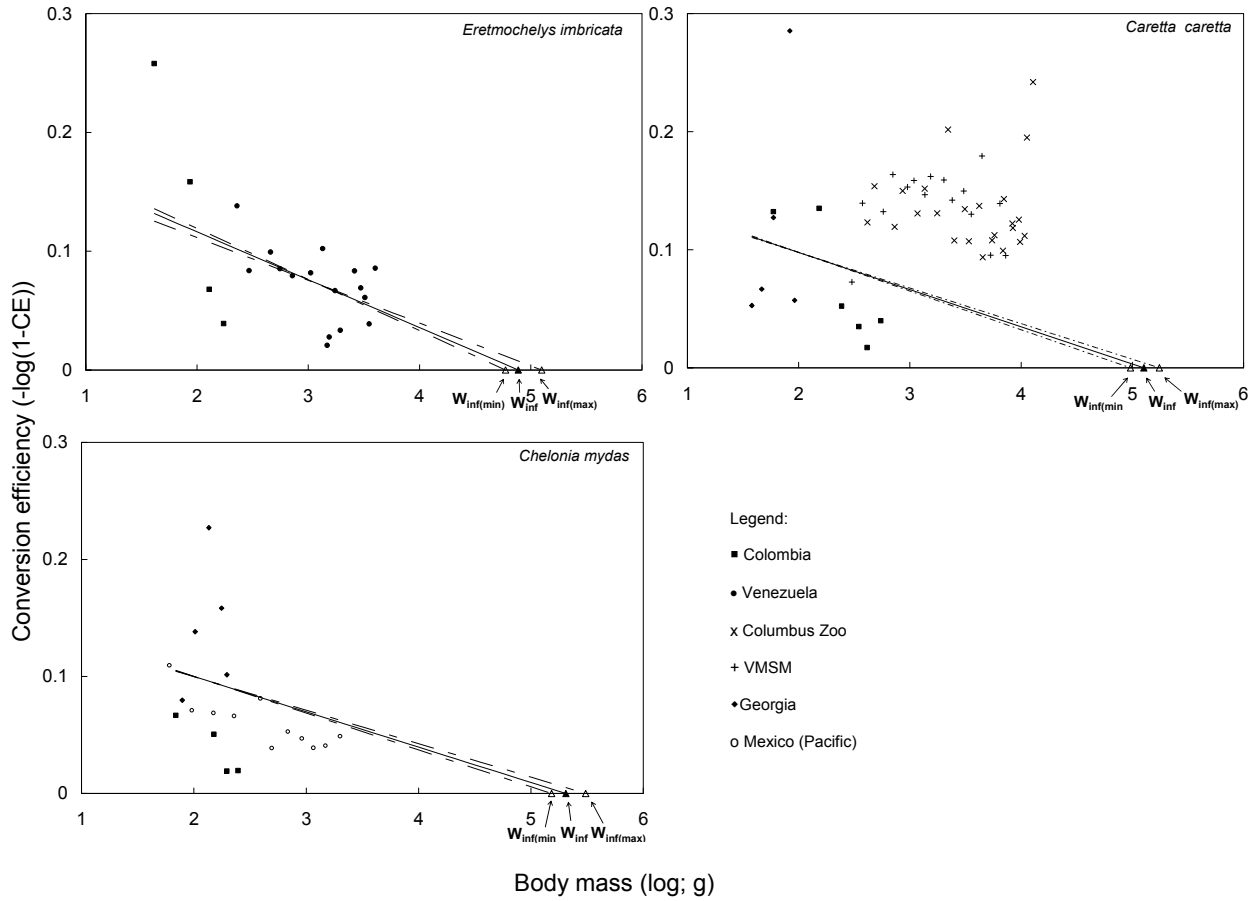


Figure 2.15 - Log - log plot of food conversion efficiency 'CE' for hawksbill (top left panel), loggerhead (top right panel), and green turtles (bottom panel), showing the fitted curve through $W_{\infty(min)}$, $W_{\infty(mid)}$, and $W_{\infty(max)}$. Data for hawksbill turtles are from Colombia (Kaufmann 1975) and Venezuela (Buitrago 1987); for loggerhead turtles from Colombia (Kaufmann 1975), two zoological facilities (Swingle *et al.* 1993) and Georgia, USA (Stickney *et al.* 1973); and green turtles from Colombia (Kaufmann 1975), and Georgia, USA (Stickney *et al.* 1973). Although not included in calculations of the regression line for green turtles, extra data points for the Pacific coast of Mexico (Godínez-Domínguez *et al.* 1993) (open circles) are shown here to illustrate the decline in 'CE' with increasing body size. For loggerhead turtles, inclusion of a dummy variable to account for 'artificial diet' versus 'fish diet' differences, allowed us to draw the regression line based on the entire dataset while removing the 'artificial diet' factor from relevant datapoints (see text for a more detailed explanation).

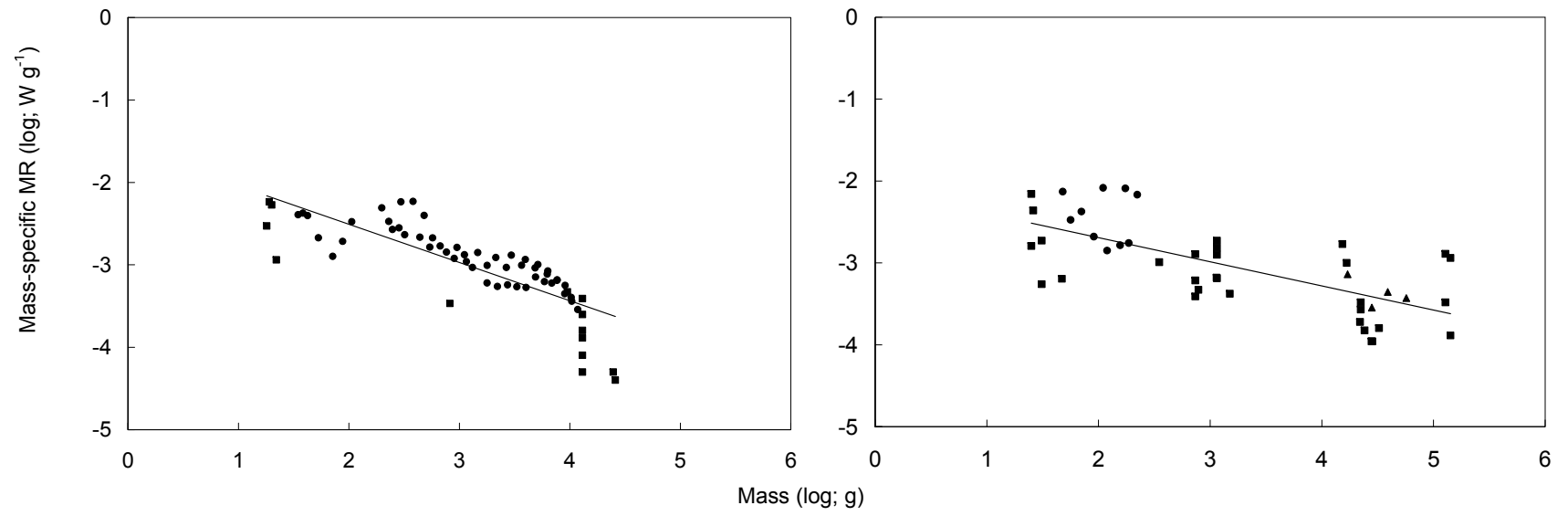


Figure 2.16 - Mass-specific metabolic rates (MR) (log; W g⁻¹) for loggerhead (left panel) and green turtles determined from feeding experiment data used in this study (●) plotted with MRs of values compiled in Wallace and Jones (2008) (■). Data converted from field consumption estimates for green turtles are represented as (▲).

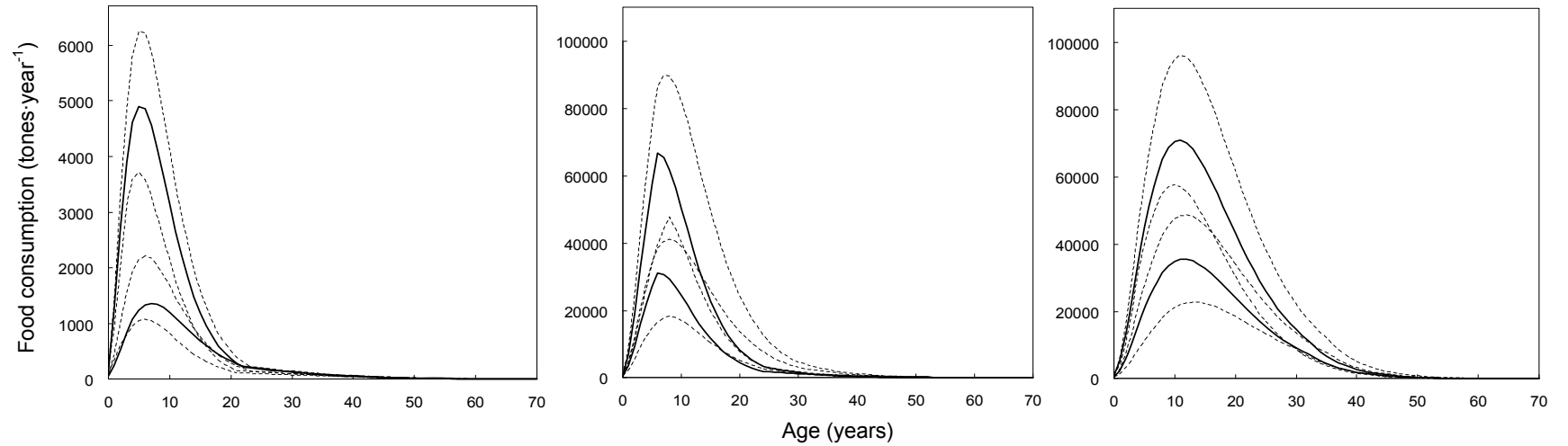


Figure 2.17 - Age-structured food consumption estimates (tonnes·year⁻¹) for the western Atlantic hawksbill (top panel), loggerhead, (middle panel), and green sea turtle populations. The full lines represent results for the upper and lower quantiles of model runs for life history parameters associated with $L_{\infty(\text{mid})}$. The lower and upper sets of dashed lines represent results for the upper and lower quantiles of model runs using life history parameters associated with $L_{\infty(\text{min})}$ and $L_{\infty(\text{max})}$ respectively. Note that the y-axis scale differs among species.

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3. Restoration of *Chelonia mydas* in the Caribbean: Ecosystem changes resulting from a reduction in seagrass habitat complexity ²

3.1 Introduction

Sea turtles have suffered substantial reduction in numbers throughout the Caribbean (Parsons 1962, NMFS 1993, Seminoff 2004, Bräutigam and Eckert 2006, NMFS 2007a, 2007b). Overharvesting, in addition to threats resulting from disease, incidental capture by fishers, and destruction of critical nesting and foraging habitat, has resulted in a decline of over 90 % of many stocks compared with historic levels (Jackson *et al.* 2001). Over the last few decades, conservation and management programmes have been implemented throughout the region to help reverse these severe declines.

² A version of this chapter will be submitted for publication. Wabnitz, C.C.C., Coll, M., Bjorndal, K., Bolten, A., Christensen, V. and Pauly, D. Restoration of *Chelonia mydas* in the Caribbean: Ecosystem changes resulting from a reduction in seagrass habitat complexity.

The green turtle (*Chelonia mydas*) nesting populations at Tortuguero (Costa Rica) (Bjorndal *et al.* 1999) and Florida (USA) (Chaloupka *et al.* 2008), for example, have responded to protection efforts and are now demonstrating increases in population size.

In the Caribbean, green turtles feed mainly on turtle grass *Thalassia testudinum* (Bjorndal 1980) and together with manatees are considered the largest seagrass herbivore in the region. Green turtles remove a large proportion of seagrass standing stock by cropping blades 2 - 4 cm above the base without disturbing the underground rhizome system (Lanyon *et al.* 1989, Brand-Gardner *et al.* 1999). Individuals commonly show a high degree of fidelity to feeding sites by repeatedly returning to the same grazing plots (Bjorndal 1980, Ogden 1980). At comparatively high turtle densities, these individual grazing plots may merge into one single-cropped seagrass bed (Williams 1988).

Green turtles have had the strongest ecological and evolutionary impacts on seagrass since the extinction of the diverse dugongid fauna before the Pleistocene (Domning 2001). Before human exploitation, green turtles may have been as important in determining seagrass productivity as terrestrial herbivores were in grasslands (McNaughton 1979, Pandolfi *et al.* 2003). Hence, it seems valid to ask what ecosystem-wide changes are likely to be observed as a result of the relatively consistent population increases exhibited by Caribbean green turtles. In the context of ecosystem-based management, this means that actions taken to help green turtle populations recover need to consider aspects of this species' population biology, as well as its interactions with other species in the ecosystem, at all stages of its life history. Therefore, seagrass, which constitutes the main habitat at foraging grounds for green turtles in the Caribbean, need to be explicitly considered in any species management and recovery plan.

Seagrass beds can form dense meadows in the coastal zone. They can typically be found in close proximity to coral reefs and/or mangroves, and represent important 'nursery' (Beck *et al.* 2001, Adams *et al.* 2006) and foraging grounds for a variety of organisms from reef habitats (Hemminga

and Duarte 2000). While many herbivorous fish shelter on reefs at night, they usually are found foraging in adjacent seagrass habitats during the day (see review by Valentine and Duffy (2006)). Conversely, many reef-associated carnivores (e.g., grunts (Haemulidae) and snappers (Lutjanidae)) will venture to feed in vegetated habitats at night (Ogden 1980, Baelde 1990, Burke 1995, Cox *et al.* 1997, Kopp *et al.* 2007, Luo *et al.* 2009), and many seagrass-associated fish and invertebrates figure prominently in the diets of reef predators (Randall 1967, Heck and Weinstein 1989). As essential 'nursery' areas for the juvenile stages of many species, often of commercial importance (Nagelkerken *et al.* 2000a, Beck *et al.* 2003, Heck *et al.* 2003, Mumby *et al.* 2004, Dahlgren *et al.* 2006), seagrass directly or indirectly support fisheries (Gillanders 2006). This nursery function is understood to be the provision of a habitat where juveniles have greater survival and growth rates than on nearby unvegetated substrate (Adams *et al.* 2006). It is assumed that such benefits are primarily the result of high food abundance (Cocheret de la Moriniere *et al.* 2003a, Cocheret de la Moriniere *et al.* 2003b), low predation pressure resulting from the high structural complexity of the habitat at fine scales (Parrish 1989, Heck and Orth 2006, Verweij *et al.* 2006), and increased space availability for settlement recruits (Shulman and Ogden 1987). All of these observations strongly point towards a reliance of reef fish on seagrass-based production (Nagelkerken *et al.* 2000a, Nagelkerken *et al.* 2001).

As major grazers of seagrass, it is likely that a recovery of green turtle populations will have a significant impact on the present structure of seagrass beds. Specifically, a shift from today's ungrazed pastures, characterised by long fronds, to grazed pastures with very short blades can be expected. Changes are not only expected to be structural. Sustained grazing by green turtles has already been shown to lead to compensatory growth by seagrass (Moran and Bjorndal 2005), and increases in the nutritional quality of the blades (Moran and Bjorndal 2007). However, our knowledge of the community-wide changes that sustained high-level green turtle grazing would have on seagrass community dynamics are less clear.

In this study I sought to assess the theoretical impacts that an increasing green turtle biomass would have on a typical Caribbean seagrass/reef/mangrove ecosystem, as commonly found in the coastal landscape of the U.S. Virgin Islands (USVI) and Puerto Rico (Figure 3.1). This was done through the use of a model implemented in Ecopath with Ecosim (EwE) (Christensen and Walters 2004). Our model realisation considered the three ecosystems together as important exchanges typically occur between them (Nagelkerken *et al.* 2000a, Mumby *et al.* 2004).

Available evidence seems to indicate that decreasing habitat complexity will provide decreasing refuge to prey species by interfering with predator success (e.g., Gotceitas and Colgan 1989, Lipcius *et al.* 1998, Heck and Orth 2006, Horinouchi 2007). Repeated and increased grazing by recovering green turtle populations will lead to a dramatic reduction in the canopy height of seagrass. This loss of structural complexity (i.e., loss of refuge) is likely to be associated with significant changes in direct and indirect trophic interactions within coastal ecosystems. Therefore, under the overall scenario of increased turtle abundance, I contrasted model outputs resulting from the implementation of three alternative functions describing changes to prey vulnerability with an increasing loss of habitat complexity:

1. A 'step' function - Based on experimental studies with *Zostera marina*, amphipods as prey, and pinfish and grass shrimp as predators, Nelson (1979) found that predation rate may not be a simple linear function of seagrass density. Instead, a threshold seagrass density might be required before any significant reduction in predator foraging efficiency is observed. In other words, predator effectiveness increases with decreasing seagrass complexity according to a step function (see Figure 3.2, dotted line);
2. A 'dome' function - Results from experiments conducted with bluegills and a variety of invertebrates led Crowder and Cooper (1982) to propose that a predator's foraging efficiency is maximized at intermediate levels of habitat complexity, and low at both high and low macrophyte biomass (see Figure 3.2, dashed line);

3. A flat line - Contrary to previous experiments that were conducted with constant numbers of prey and predators at differing densities of seagrass, Mattila *et al.* (2008) and Canion and Heck (2009) increased predators and prey with increasing seagrass density, thereby mimicking what is observed in nature. Results from outdoor tank and field (mesocosms) experiments showed that seagrass provides significantly more shelter than unvegetated substrate, but that no significant differences occur in predator success among seagrass densities (Mattila *et al.* 2008, Canion and Heck 2009). In other words, similar refuge levels can be expected from grazed and ungrazed beds (Figure 3.2, solid line).

The model presented here was derived from species-level data. However, in discussing outputs from simulation runs for each of the three scenarios, I sought to highlight overarching tendencies and patterns rather than arrive at specific numerical conclusions of declines or increases in given species groups. Key data gaps, brought to light by my analysis, are also outlined. I recommend that these be considered as critical research priorities to add a quantitative basis to our understanding of the role of green turtles in reducing habitat complexity in seagrass meadows.

3.2 Materials and methods

3.2.1 Study area

The model developed for this study represents an average annual mid-1990s situation in the coastal waters, from the water's edge to a depth of approximately 50 - 75 m, around the U.S. Virgin Islands (USVI) and Puerto Rico (Figure 3.1). This area is meant to be representative of a Caribbean region coastal system. The area below 75 m was not included as the model focused on system dynamics in seagrass beds/coral reefs. Analyses of the products of a recent mapping effort reveal that Puerto Rico harbours a total 1,599 km² of coastal habitats (3 % of which are unconsolidated sediment, 45 %

submerged vegetation, 5 % mangroves, and 47 % coral reef and colonized hardbottom), while the USVI coastal habitats cover 487 km² (5 % of which are unconsolidated sediment, 33 % submerged vegetation, and 62 % coral reef and hard bottom) (Kendall *et al.* 2001).

3.2.2 Modelling approach: Ecopath with Ecosim (EwE)

The foundation of the Ecopath with Ecosim (EwE) suite is a trophic mass balance model (Polovina 1984, Christensen and Pauly 1992) that creates a static snapshot of the resources in an ecosystem and their interactions, represented by trophically linked biomass ‘pools’ (Christensen and Pauly 1992). The biomass pools, hereafter referred to as functional groups, consist of a single species, single size/age group of a given species, or species groups representing ecological guilds (sharing similar trophic behaviour, habitats, and other ecological traits). These may be further split into ontogenetic (juvenile/adult) groups that can then be linked in Ecosim (see stanzas below).

Ecopath operates under two main assumptions. The first is that biological production (P) of each functional group (i) in the ecosystem equals the sum of mortality due to fisheries (Y_i) and predators (j) (B_j·M_{2ij}), net migration (E_i), biomass accumulation (BA_i), and other unexplained mortality (P_i·(1-EE_i)) where EE is the ecotrophic efficiency:

$$P_i = \sum_j B_j \cdot M_{2ij} + Y_i + E_i + BA_i + P_i \cdot (1 - EE_i) \quad (1)$$

Equation (1) can be re-expressed as:

$$B_i \cdot \left(\frac{P}{B} \right)_i = \sum_j B_j \cdot \left(\frac{Q}{B} \right)_j \cdot DC_{ij} + Y_i + E_i + BA_i + B_i \cdot \left(\frac{P}{B} \right)_i \cdot (1 - EE_i) \quad (2)$$

where (P/B)_i indicates the production of (i) per unit of biomass and is equivalent to total mortality, or Z, under steady-state conditions (Allen 1971); (Q/B)_i is the consumption of (i) per unit of

biomass; and DC_{ij} indicates the proportion of (i) that is in the diet of predator (j) in terms of volume or weight units. EwE parameterises the model by describing a system of linear equations for all the functional groups of the model, where for each equation three of the basic parameters: B_i , $(P/B)_i$, $(Q/B)_i$, or EE_i have to be known for each group (i). The principle behind this modelling approach is that, on an annual basis, biomass and energy in an ecosystem and each of its components are conserved (Walters *et al.* 1997, Walters and Martell 2004a). The second assumption is that consumption within a group equals the sum of production, respiration, and unassimilated foods. Flows are expressed in $t \cdot km^{-2} \cdot year^{-1}$ wet weight organic matter for flows, and biomasses in $t \cdot km^{-2}$. The Ecopath model was considered balanced when realistic estimates of the missing parameters were calculated ($EE < 1$) (Christensen *et al.* 2005).

Ecosim, the time-dynamic module of the software, was then used to investigate the impact that an increase in turtle biomass would have on the ecosystem. Using a system of time-dependent differential equations, biomass fluxes amongst functional groups are calculated as a function of time by accounting for changes in predation, consumption, and emigration rates, as well as fishing (Christensen and Pauly 2004). For each group, biomass growth rate is expressed as:

$$\frac{dB_i}{dt} = \left(\frac{P}{Q} \right)_i \cdot \sum Q_{ji} - \sum Q_{ij} + I_i - (M_i + F_i + e_i) \cdot B_i \quad (3)$$

where $(P/Q)_i$ is the gross efficiency; M_i is the natural non-predation mortality rate; F_i is the fishing mortality rate; e_i is the emigration rate; I_i is the immigration rate; and B_i is the biomass of the functional group (i). Calculations of consumption rates Q_{ij} are based on “foraging arena” theory, where the biomass of prey (i) is divided into vulnerable and non-vulnerable pools to predation (Walters and Kitchell 2001, Walters and Martell 2004b). Low vulnerability rates to predators imply donor-driven (prey is limiting), density-dependent interactions. High rates, on the other hand, indicate predator-driven interactions where (a) the behaviour of both prey and predator have weaker

effects on limiting predation rates; (b) predation mortality is proportional to the product of prey and predator abundance; and (c) the predator's initial biomass is low compared to its carrying capacity (Christensen *et al.* 2005). Vulnerability of seagrass to turtles was set high (i.e., turtles are far from carrying capacity). This appears to be a reasonable assumption, given that the current green turtle population in the Caribbean represents 3 - 7 % of pre-exploitation levels (Jackson *et al.* 2001) and that green turtles show specific physiological adaptations to a seagrass diet (Bjorndal 1980).

For species with complex life histories, individual life history stages can be incorporated into Ecosim through 'stanzas'. This approach was used to model the juvenile and adult stages of snappers, grunts, parrotfish (Scaridae), and surgeonfish (Acanthuridae) (see below for rationale behind this choice of species). The stanzas are linked to each other and usually the adults are set as the leading group. $(P/B)_i$ and diet composition were provided for both juvenile and adult groups, while B_i and $(Q/B)_i$ were introduced for the leading stanza group only (Christensen *et al.* 2005).

For more detailed methods as well as model capabilities and limitations refer to Christensen *et al.* (2005), and Christensen and Walters (2004) and Coll *et al.* (2009) respectively.

3.2.3 Functional groups and model parameters

Based in part on a species list drawn up by Delgado (2004), data were obtained for 282 species of fish known to occur in the area. These were then aggregated into 14 functional groups (for a total of 29 functional groups including non-fish groups and detritus) chiefly according to their feeding type and predators. An additional important consideration was the degree to which species are known to utilise seagrass as a nursery habitat during the juvenile portion of their life history, and/or whether they are often found foraging in seagrass beds (e.g., Randall 1963, Carr and Adams 1973, Kikuchi

and Peres 1977, Ogden and Zieman 1977, Robblee and Zieman 1984, Nagelkerken *et al.* 2000a, Nagelkerken *et al.* 2000b). For example, grunts, like many reef fish in the Caribbean exhibit ontogenetic shifts in habitat utilisation (Lindeman *et al.* 2000), and seagrass beds have been identified as particularly important for their juvenile stages (Ogden and Zieman 1977, McFarland *et al.* 1985, Shulman 1985a, Adams and Ebersole 2002, Cocheret de la Moriniere *et al.* 2002). Adult grunts also often associate with coral reefs during the day, but migrate to forage primarily on benthic invertebrates in seagrass beds at night (Ogden 1980, Gaut and Munro 1983, Hammerschlag and Serafy 2009). Based on a review of the available literature, local variations notwithstanding, the most dominant species recorded as having juveniles using seagrass beds as refuge and adults foraging in seagrass included: snappers, grunts, surgeonfish, and parrotfish (Robblee and Zieman 1984, Nagelkerken *et al.* 2000a, Mateo and Tobias 2001, Layman and Silliman 2002, Chittaro *et al.* 2005, Aguilar-Perea and Appeldoorn 2007, Dorenbosch *et al.* 2007, Mateo and Tobias 2008). I therefore included multi-stanzas (i.e., separate juvenile and adult groups) for these trophic guilds. As these species also are known to substantially contribute to the local recreational and commercial fisheries (Hawkins and Roberts 2004), I maintained them as separate groups. Species that do not depend on seagrass beds during their juvenile stages, but nonetheless will regularly forage in this habitat were aggregated based on feeding preferences primarily (e.g., herbivores, piscivores, Mobile Invertebrate Feeders [MIF], and, for purposes of identification, they are listed separately from other species through the use of the prefix 'SG').

Species composition and biomass, and the extent to which individual habitats are likely to serve as 'nurseries', have been found to vary depending on the landscape configuration of these habitats (Baelde 1990, Bouchon-Navaro *et al.* 2004, Mateo and Tobias 2004, Mateo and Tobias 2007, Grober-Dunsmore *et al.* 2008, Nagelkerken *et al.* 2008). Therefore, in the context of model configuration, I assumed a landscape arrangement similar to that found in a number of coastal bays of Puerto Rico and the USVI, whereby shallow seagrass beds are located adjacent to reefs with

mangroves lining the shoreline. In other words, reefs would be located in relative close proximity to seagrass and mangrove habitats, and not separated by deep channels.

Data required to parameterize the model (B, P/B, Q/B, and diet) were informed by a model developed by Opitz (1996). Complementary data, specifically for fish groups, were obtained from the published literature for the USVI and Puerto Rico preferentially, and other regions of the Caribbean where necessary. Natural mortality (M) parameters were chiefly derived according to Pauly (1980). Catches and fishing mortality estimates were informed by data in Hawkins and Roberts (2004), Dunn *et al.* (2009), Rothenberger *et al.* (2008), and García-Sais *et al.* (2005). The food intake by a group during a certain period of time (here a year) divided by its biomass (Q/B), was estimated based on Palomares and Pauly (1989, 1998) for fish species, and adapted from Moran and Bjorndal (2005) and Bjorndal and Jackson (2003) for green turtles. For seagrass, biomass and P/B values were adjusted giving special attention to results in Gacia (1999) and Zieman *et al.* (1984), and Moran and Bjorndal (2005) and Bjorndal and Jackson (2003), respectively. Limited data were available for biomass estimates of ‘invertebrates’ on reef and in seagrass beds. Given that the majority of non-herbivorous reef fish consume and/or selectively feed on invertebrate prey (Randall 1967, Ogden 1980), I felt it reasonable to assume that predation mortality ‘used’ the largest proportion of invertebrate production in the system. Therefore, the biomass of all three invertebrate functional groups (Reef invertebrates, SG_small invertebrates, and SG_invertebrates) included in the model were based on demand and estimated by setting $EE = 0.95$. Once the model was balanced, the obtained biomasses were then transferred as input variables. B, P/B, and Q/B parameters for the remaining groups were informed from previously published models for the region including Opitz (1996), Manickchand-Heileman *et al.* (1998), Okey (2004), and Arias-González (1998). Diet information was compiled from the published literature (e.g., Randall 1967, Ogden 1976, Brook 1977, Ogden and Zieman 1977, Hay 1981, Tribble 1981, Zieman *et al.* 1984, Lewis and Wainwright 1985, Shulman 1985b, Sweatman and Robertson 1994, McGlathery 1995, McAfee and Morgan

1996, Kirsch *et al.* 2002, Layman and Silliman 2002, Cocheret de la Moriniere *et al.* 2003a, Cocheret de la Moriniere *et al.* 2003b) as well as FishBase (www.fishbase.org).

For all input data, parameters were set for each of the fish species in the model. Upon aggregation, each species contribution to the overall functional group value was weighted according to the individual species' biomass contribution.

From the results of an Ecopath model, several indices can be generated that provide information about the overall structure and functioning of the ecosystem in the study area (Christensen 1995). Therefore, a few of the overall statistics of the system are presented (Christensen and Walters 2004).

3.2.4 Dynamic simulations

I compared results from the implementation of three published models (see introduction for details), that describe the response of predator foraging efficiency to changes in habitat complexity. These models predict : (a) an increase in predator foraging efficiency with declining seagrass biomass according to a step function (Nelson 1979) (Figure 3.2, dotted line); (b) highest prey vulnerability to predators at intermediate levels of complexity (Crowder and Cooper 1982) (Figure 3.2, dashed line); and (c) no change in predator foraging efficiency with changing habitat complexity (Canion and Heck 2009) (Figure 3.2, solid line). Such non-trophic effects, whereby the biomass of a particular group affects the vulnerability of (i) prey to a given predator (j), can be captured in Ecosim through so-called 'mediation' functions. The three functions (see Figure 3.2) were then applied separately to all groups that benefit from the sheltering capacity of seagrass (i.e., our four juvenile fish groups and two seagrass invertebrate guilds). In applying mediation functions 1 and 2 in Ecosim, effects of changes in prey vulnerabilities are weighted so as to increase (or decrease) to all their predators as the biomass of seagrass declines due to the greater abundance of green turtles. Findings on coral

reefs in Hawai'i (Hixon and Beets 1993) support the assumption that predators may non-selectively reduce all prey populations in proportion to their initial relative abundances (Hixon 1991).

In Ecosim, predator-prey interactions are each attributed a vulnerability term. This vulnerability parameter shows the maximum increase in predation mortality a given predator can cause on a given prey (see 'Modelling approach: Ecopath with Ecosim' section for details). Typically, models are calibrated in Ecosim using time series 'reference' data (e.g., relative and absolute biomass data of different species over a particular historical period), so that, where possible, model simulations match observed trends. This calibration is usually done by adjustment of the 'vulnerability' parameters (Walters *et al.* 1997, Walters *et al.* 2000). In the absence of time series data and other information that would justify adjusting vulnerabilities upwards or downwards, these were left at the default value; with the exception of the vulnerability term of seagrass to green turtles. The latter was set high based on evidence that green turtles have had the strongest ecological and evolutionary impacts on seagrass (Domning 2001) and their biomass is currently far from carrying capacity.

The starting seagrass biomass, with the lowest turtle grazing impact, was deemed representative of the maximum seagrass biomass attainable in the system (see grey block arrow, Figure 3.2). I initially ran the model to check start and end biomasses. This was done to ensure that the simulations spanned the range of seagrass biomass required to represent the full range of habitat complexity under the mediation 1 model.

Epiphyte biomass was assumed to decline steeply and linearly with declining seagrass biomass, as continuous grazing of seagrass blades by green turtles would not give epiphytic microalgae a chance to attach to seagrass fronds. This was implemented in Ecosim through another mediation function, whereby a decline in seagrass biomass was linked to a significant decline in the P/B of epiphytes.

The default value of maximum relative P/B for seagrass was raised from two to three, based on the comparison of mass-specific growth measurements recorded over the course of a 16-month seagrass clipping experiment (Moran and Bjorndal 2005).

To mimic an increase in turtle biomass two approaches were used:

1. Starting with an estimated current biomass of green turtles, it was then “forced” to increase at a constant rate through loading of increasing turtle biomass time series data in Ecosim;
2. I assumed a higher than observed starting biomass of green turtles, but with an intense fishery on the species that effectively kept starting biomass orders of magnitude below estimated carrying capacity levels (157 - 374.8 tonnes·km⁻² (Moran and Bjorndal 2005)). Simulations were then run by removing the fishery and describing ecosystem changes as green turtle biomass increased.

The advantage of scenario (2) over (1) is that an increase in green turtle biomass over time is calculated by Ecosim in light of entered input parameters for the group.

3.3 Results and discussion

3.3.1 Ecopath model of the Caribbean ecosystem

Input and output parameters of the balanced model representing a Caribbean ecosystem are shown in Table 3.1. The diet composition matrix of the balanced model is presented in Table 3.2.

Ecotrophic efficiencies (EE), respiration/assimilation ratios (R/A), production/respiration ratios (P/R), and net food conversion efficiencies were within the expected range for all functional groups (Christensen *et al.* 2005).

The total biomass (including detritus) encompassed within our model was approximately 994 g wet mass·m⁻² (Table 3.3). Primary producers were the most important group, comprising 46 % of the total biomass, followed by invertebrates, which accounted for 32 % of total biomass. Fish only made up 5.5 % of total biomass, 82 % of which was represented by species that utilise the seagrass for forage and/or as refuge habitat. At current biomass levels, green turtles accounted for only a very small proportion of total biomass (< 1 %). Fish groups that do not venture much on to the seagrass were dominated by zooplanktivores and herbivores, while surgeonfish and snappers dominated the 'seagrass' (SG) trophic guilds.

Results show that a large component of the highest trophic levels' production was being removed by fisheries rather than predators. This finding is not surprising given the history of exploitation of marine resources, particularly of higher level trophic groups, within the region (Wing and Wing 2001), and the conspicuous absence of large predatory fish. This in turn also explains the relatively low EE values obtained for some of the herbivorous groups (e.g., parrotfish and surgeonfish), and the generally large biomass registered by low trophic level groups relative to higher trophic level groups in the system. Mean trophic level of the catch was 3.2 and accounted only for 26.2 % of the primary production in the system (PPR %).

Results of the model further indicated that functional groups were mainly organised within four trophic levels (TL), with the highest TLs corresponding to the two piscivorous groups (TL 3.7 and 3.6, respectively), followed by snappers, grunts, and invertebrate feeders (Table 3.1). The lowest groups, by definition, were the primary producers and detritus groups (TL = 1).

3.3.2 Ecosystem wide changes as a result of an increase in green turtle biomass

Mediation 1

Nelson (1979) proposed a step function (Figure 3.2, dotted line) to represent the inverse relationship he observed between prey vulnerability and seagrass biomass (analogous to complexity). Applying this function through Mediation 1, an increase in turtle biomass resulted in a dramatic decline in the biomass of seagrass, 'SG_seagrass invertebrates', seagrass MIF, and seagrass piscivores (Figure 3.3). Parrotfish were among the most affected groups, as a decline in seagrass biomass represented a decline in a significant source of forage, but also reduced the survivorship of juveniles that successfully recruit to adulthood. Adult snappers underwent dramatic declines as a result of (a) increased predation by seagrass piscivores that had lost a large component of their diet, including seagrass herbivores and juvenile fish (the latter group being negatively affected by a loss in seagrass); and (b) a decline in their own prey, mostly juvenile fish. As a result of the decline in predators, snapper juveniles first registered an increase in biomass, but with a further reduction in seagrass and concomitant increase in their own vulnerability, subsequently suffered a dramatic decline in biomass. The adults' biomass decline due to lack of forage was therefore further exacerbated by only few juveniles making successful ontogenetic migrations to adulthood. However, a decline in snappers was associated with an increase in the biomass of grunts. Snappers were an important predator on grunt juveniles, due to their high initial biomass relative to other piscivorous groups. That release from predation, together with a relatively stable biomass of their main food source, small seagrass invertebrates, allowed for strong grunt recruitment to adulthood. The fact that adults themselves fed on small seagrass invertebrates, and were thus able to compensate for the decline in other diet items, further contributed to the observed overall increase in grunt biomass. Surgeonfish benefited from a similar increase in their biomass due to the release from predation by snappers and the fact that algae biomass, one of their main forage sources, increased, in part as a result of the decline in parrotfish.

Mediation 2

Experiments conducted with bluegills and a variety of invertebrates led Crowder and Cooper (1982) to propose a model whereby a predator's foraging efficiency is maximised at intermediate levels of habitat complexity (Figure 3.2, dashed line). The effect of Mediation 2 under conditions of increasing turtle biomass was clearly divided into two phases. Until halfway through the simulations, corresponding to the peak in prey vulnerability, results were similar to those obtained under Mediation 1 (see above). The biomass of seagrass piscivores, particularly snappers, declined following the trend of a number of its diet components, including juvenile fish and parrotfish. The decline in seagrass piscivores and snapper biomass released grunts from predation, enabling their biomass to increase. Seagrass invertebrates and other groups to which the mediation function was applied to, also declined, a trend paralleled by the key predators of these groups. However, as turtle grazing reduced seagrass biomass beyond intermediate habitat complexity levels, prey vulnerability began to decrease. In response, surgeonfish juvenile (and later adult) and seagrass invertebrate biomass began to increase, a trend that was mirrored, with a slight delay, by their predators such as seagrass invertebrate feeders (Figure 3.4). Juvenile fish and parrotfish were similarly affected. As a consequence, seagrass piscivores began to recover, introducing a downward trend in grunt biomass from their peak abundance at intermediate levels of habitat complexity.

Mediation 3

The third mediation function was based on findings by Mattila *et al.* (2008) and Canion and Heck (2009) (Figure 3.2, solid line) that showed prey vulnerability to be independent of seagrass biomass. Increasing turtle biomass, while implementing Mediation 3, was therefore expected to primarily have an impact on species that are heavily dependent on seagrass for forage. This was indeed

matched by model simulations. Mediation 3 resulted in the decline of parrotfish, the only trophic guild composed of species (especially *Sparisoma radians*) with a large seagrass diet component (Figure 3.5). I assumed for both juveniles and adults to consume large quantities of seagrass and more minor quantities of algae, thus the trajectory of both groups mirrored that of declining seagrass quite closely.

Overall, our findings demonstrate that if allowed to recover to the range of carrying capacity biomasses that have been estimated from field-based seagrass productivity and green turtle food consumption studies (157 - 374.8 tonnes·km⁻²) (Moran and Bjorndal 2005), reef ecosystems would look different to what we see today. Results for all three mediations were observed whether turtle biomass was increased by ‘releasing’ turtles from predation, or whether biomass was ‘forced’ to increase over time (results not shown). The only difference was that vulnerabilities of seagrass to turtles had to be set much higher for the latter scenario. In the case of the “biomass forcing scenario”, green turtle biomass at the start of simulations was much lower, and thus much further removed from carrying capacity. Given the underlying Ecosim equations, the increase in turtle biomass over time is accompanied by a concomitant decline in Q/B. This results in simulations having no effect (i.e., no seagrass biomass decline with increasing turtle biomass), and is obviously aberrant. To compensate for this, the vulnerability of seagrass to turtles had to be set very high. This finding confirms that at current abundance levels, green turtles are functionally extinct. Once vulnerabilities were adjusted, however, the results were comparable to those obtained when initialising the model with a higher turtle biomass, subsequently removing the turtle fishery, and allowing green turtle populations to recover. As highlighted previously, the benefit to this approach is that it allows Ecosim to compute the rate at which turtle biomass should be recovering based on the parameters entered in the model (rather than forcing an incremental yearly biomass increase through time series data).

As emphasised in the introduction, model outputs are meant to highlight overarching patterns for each of the three scenarios, rather than represent specific numerical conclusions of declines or increases in given species groups. Of note however, is that the magnitude of predicted biomass trajectories in Ecosim is sensitive to the vulnerability parameter value. Future efforts should therefore target collection of data and design of experiments that can help set more realistic vulnerability parameters, and thus help lend more confidence to the magnitude of the biomass declines/increases. It is likely for example that functional groups seen to ‘collapse’ should have lower vulnerability parameters.

3.3.3 Insights offered by the modelling exercise

Diet composition - behavioural and dietary adaptive flexibility

Our findings indicate that based on currently available evidence and understanding of reef life cycle ecology, increased turtle grazing will result in direct and indirect changes in seagrass ecosystems. It is important to note that the observed changes are, to a large degree, influenced by the diet matrix of the starting Ecopath model (although, the diet composition can and does change in Ecosim as a function of the relative abundance of various groups within the system). It is clear from the dietary data available in the literature that our knowledge of species diets has yet to capture the full extent of their spatial and temporal variability (plasticity). Moreover, given the importance of seagrass invertebrate guilds in the diet of a number of especially juvenile, but also adult reef fish, more research is urgently needed to characterise these communities. Moreover, targeted surveys should be conducted to clarify what aspects of seagrass beds are most important in determining species composition and densities, and how these are likely to change under a scenario of increased turtle grazing.

Limited observations of juvenile parrotfish foraging behaviour from the Atlantic indicate that they are mostly herbivorous (Overholtzer and Motta 1999, 2000). However, stomach content analysis and other evidence from Australia show that juvenile parrotfish are either carnivorous or omnivorous (Bellwood 1988, Chen 2002). Therefore, more research is needed to resolve to what degree juvenile parrotfish in particular selectively feed on algae and/or seagrass (or possibly small invertebrates), and to what extent both juveniles and adults may switch to consuming a significantly larger proportion of algae than seagrass in the absence of their preferred diet item (which may also point towards more time spent on the reef to forage on algae for example). Fish are thought to exhibit adaptive flexibility in diet composition (Dill 1983, Gerking 1994) suggesting that such a response in foraging behaviour appears reasonable. Interestingly, however, correlative field studies have found a significant positive relationship between leaf nitrogen content and grazing by parrotfish, indicating preferential feeding on leaves rich in nitrogen (e.g., Goecker *et al.* 2005). Given that turtles have been shown to improve the nutritional content of their food by regular re-cropping of the same plots (Moran and Bjorndal 2005), it is likely that herbivorous fish will in turn, up to a point, preferentially feed on these turtle-grazed leaves. Further research is needed to elucidate this, and should include comparative studies between herbivore consumption rates of *T. testudinum* in ungrazed conditions and seagrass that has been continuously cropped by turtles. Such experiments should also include replicates under different vulnerability to predation scenarios.

The increase in grunt biomass under Mediation 1 and 2 was partly linked to a release from predation by declining snappers. Gut content data available for snappers often only indicate “small/juvenile” fish/fish in analysis results (Cocheret de la Moriniere *et al.* 2003a, Nagelkerken *et al.* 2006). It is therefore standard practice to allocate diet proportions to predators based on prey ratios. In light of our results, future studies should strive to determine (a) whether predators exhibit prey selectivity, or just feed in relative proportion to available prey items (this also influences a prey’s vulnerability to specific predators); (b) design field experiments to record potential changes in the diet composition

of these predators under scenarios of declining habitat complexity and thus prey availability; and (c) determine to what extent adults and juveniles may forage more heavily within habitats that previously may have represented peripheral foraging habitats (e.g., mangrove and/or reef). Cautiously extrapolating from results demonstrating that linkages between coastal ecosystems may be dependent on the spatial arrangement of habitats within the seascape (Nagelkerken *et al.* 2008), such a hypothesis could well be corroborated.

Habitat complexity and fish behaviour

Results from the studies conducted on reefs where fish had limited access to seagrass nursery habitats show that some species may demonstrate behavioural plasticity in the habitats used by their juveniles. Dorenbosch *et al.* (2004), for example, demonstrated that when seagrass abundance was low, the juveniles of six out of 17 species known to use bays with seagrass and mangroves as nurseries were also observed on the reef. It is suggested that these species are able to use the reef as an alternative nursery and do not depend strictly on bays with seagrass beds and mangroves. For other, less 'adaptable' species, reefs with limited connectivity to specific nursery habitats resulted in significantly lower biomass of adults on the reef, when compared to sites that had greater availability of these nursery habitats (Dorenbosch *et al.* 2006, Mumby 2006, Grober-Dunsmore *et al.* 2007). For some species, behavioural plasticity in nursery habitat selection is further supported by the observation that juveniles may be obligate users of seagrass beds at one site, use additional habitats at another site (Nagelkerken *et al.* 2001, Adams and Ebersole 2002), or vary their habitat use inter-annually (Adams *et al.* 2006). This inherent variability indicates that caution is necessary when extrapolating findings from one location to another. Adams *et al.* (2006) have highlighted the general lack of baseline data on juvenile habitat use in tropical coastal systems, underscoring their overall poorly understood function as nursery sites. These data gaps make it difficult to reliably estimate the large scale impact of turtle grazing on the nursery function of seagrass beds.

Aside from increasing juvenile vulnerability to predation, competition and other interspecific interactions may significantly influence their abundance, and be affected by a reduced canopy height. However, given their demonstrated behavioural plasticity, juvenile fish may show an adaptive response to increased predation risk (and/or increased competition, and/or lowered food availability) and move to a different habitat (Mumby 2006). For example, it is not unreasonable to suggest that in the presence of large numbers of turtles, and thus closely cropped seagrass blades, species known to transition between mangrove and seagrass (e.g., bluestriped grunt (*Haemulon sciurus*) (Mumby *et al.* 2004, Faunce and Serafy 2007)) prior to their ontogenetic migration onto the reefs, may remain in the mangrove habitat during the entire portion of their early life cycle. Mangrove roots are typically considered key habitats, because they afford many species shelter from predators and support a diverse assemblage of epiphytic algae and invertebrates, providing an array of potential food sources for both predators and grazers (Farnsworth and Aaron 1996, Verweij *et al.* 2006). Our ability to predict the response of fish species to increased turtle grazing would be greatly improved if we had a better understanding of how the nursery function of different habitats was affected by their accessibility, availability, and relative structure. These therefore represent key areas for future research.

The prey 'refuge' concept is also likely to be dependent on the prey's behaviour, the predator's foraging strategy (Coen *et al.* 1981, Horinouchi 2007), the number of prey species of a given predator (Toscano *et al.* 2010), and the interaction of both predator and prey with the structure of the seagrass bed. Ambush predators, for example, utilise dense seagrass as camouflage, and may be more strongly affected than search and pursuit predators by the loss of habitat structure (Flynn and Ritz 2001). Changes in predator avoidance behaviour by prey in response to less structurally complex habitat may potentially be more important than physical interference of the habitat with predators while foraging (Main 1987).

Green turtles have been shown to introduce complexity within a seagrass bed through the maintenance of grazing plots (i.e., regular re-grazing of the same areas (Bjorndal 1980, Ogden *et al.* 1980)). At the landscape level, the patchwork-like pattern of grazed and ungrazed blades is likely to impact predator-prey spatial dynamics significantly. This type of heterogeneity is expected to be particularly important for juvenile fish that may prefer the open spaces for feeding, but are simultaneously in close proximity to effective protection from predators (Kerfoot and Sih 1987). Therefore, these edges or 'ecotones' may facilitate foraging, leading to a higher proportion of predators and fewer prey species than homogenous areas (Heck and Orth 1980, Irlandi 1994). One could hypothesise that intermediate turtle densities would create the most heterogeneous seagrass habitat and thus potentially sustain the greatest diversity (and/or abundance) of species. Moreover, juvenile fish densities in seagrass beds, although high relative to 'reef' habitats for example, are typically low overall (Christian 2003). Such a patchwork may lead to similar total abundance, but greater densities of juveniles within 'better' refuge patches. This in turn may increase, or alter, the outcome of potential competitive interactions between prey species and have unpredictable reciprocal effects on shared predators, given more limited refuge space.

Clearly, the behavioural response of different species to habitat structure may have a significant bearing on model outputs. The dramatic decline in snappers together with a visible increase in grunts resulting from Mediation 1 and 2 is an example of a relationship that may be substantially altered by behavioural adaptations. Although both trajectories can be explained from the changes accruing to the different groups based on prey availability and changes in vulnerability to predation, it is highly unlikely that structural changes brought about by turtle grazing would lead to the collapse of any one species. Future studies should, therefore, emphasise aspects that may guide the calibration of predator/prey vulnerability parameters. Field observations of grunts indicate that they react most strongly to spatial changes in habitat availability (P. Mumby, University of Exeter, pers. comm.), making their increase in biomass as a result of predation release surprising. This result

further underscores the need to more accurately quantify diet compositions and demonstrates the power of simulating changes in predator efficiency as a result of changes in habitat complexity at the ecosystem scale. It also highlights the need to conduct field experiments to accurately quantify response functions at the species level (Heck and Orth 1980, Bell and Westoby 1986) and in the presence of multiple predators (Toscano *et al.* 2010). This is further emphasized by the work of Young and Young (1978), who found that the variations in responses to seagrass blade clipping over a one year period did not consistently correspond to taxonomic groupings or feeding type, but instead resulted in species-specific changes.

3.3.4 Conclusions

The model presented in this study, and simulated predator-prey interactions, highlight the potential changes that may be brought about by the recovery of a species whose grazing activity strongly alters habitat structure at the ecosystem level. Specifically, our results demonstrate that these changes are more complex than suggested by simple predator-prey experiments conducted under different seagrass densities. Small-scale studies performed in controlled conditions, and with a limited set of predator and prey species, are valuable to our understanding of how habitat complexity may mediate such interactions. However, under natural conditions, trophic pathways are governed by complex multi-species interactions. This is particularly true for species with ontogenetic migrations that will face different predators and feed upon different prey in different habitats. Ecological models help translate predictions made at experimental scales and consider changes that arise from trophic and non-trophic interactions (i.e., mediated through changes in habitat complexity) at the level of the ecosystem. They further highlight existing gaps in our current understanding of ecosystem processes and the need for field studies that mimic natural conditions. Field experiments in the form of green turtle exclosures, or experiments that mimic turtle grazing in dense seagrass beds, are required to add an empirical basis to some of the ecosystem-wide considerations highlighted in this

study (e.g., to what degree are given species associated with seagrass and/or to what degree do they exhibit adaptive flexibility to seagrass habitat use compared to mangrove/reef habitat).

The importance of seagrass, mangrove, and reef habitats as nursery areas and/or foraging grounds through the life history of single fish species (Nagelkerken *et al.* 2002, Christensen *et al.* 2003) highlights the need for a more holistic approach to conservation strategies (Sagarin and Crowder 2009). For example, the dramatic decline in mangrove extent worldwide (Valiela *et al.* 2001), including in the Caribbean, where local extinction of species that rely almost exclusively on mangrove habitats as juveniles has occurred (Mumby *et al.* 2004), needs to be considered in the context of the potential increased importance of mangroves with a decline in seagrass biomass due to recovering green turtle populations. While the design of Marine Protected Areas (MPA), one of a suite of oft advocated potential management tools (Agardy 1994, Allison *et al.* 1998, Jones 2001), involves numerous considerations (Carr *et al.* 2003), this study suggests that coral reef areas selected for conservation should focus on encompassing functionally linked essential habitat patches within the protected landscape. Model results further highlight the need for conservation measures that target sea turtle population recovery to consider ecosystem-level processes, and to develop such recovery initiatives within an ecosystem-based management framework.

Table 3.1 - Trophic parameters for all functional groups of the balanced Caribbean reef model. Outputs are presented in *italics*. B = biomass; TL = Trophic level; P/B = Productivity biomass ratio; Q/B = consumption rate; EE = Ecotrophic efficiency; P/Q = Production to consumption ratio or gross efficiency; P/R = Production to respiration ratio. MIF = Mobile Invertebrate Feeders; SIF = Sessile Invertebrate Feeders; SG = prefix for species known to forage in seagrass beds

	Group name	TL	B	P/B	Q/B	EE	P/Q
1	Piscivores	<i>3.59</i>	1.640	0.458	4.500	<i>0.556</i>	<i>0.102</i>
2	SG_Piscivores	<i>3.67</i>	3.470	0.320	4.760	<i>0.461</i>	<i>0.067</i>
3	MIF	<i>3.13</i>	1.860	0.640	6.590	<i>0.602</i>	<i>0.097</i>
4	SIF	<i>2.92</i>	0.700	0.800	7.200	<i>0.684</i>	<i>0.111</i>
5	Zooplanktivores	<i>3.02</i>	2.500	1.590	13.400	<i>0.599</i>	<i>0.119</i>
6	Herbivores	<i>2.08</i>	2.900	1.940	35.010	<i>0.693</i>	<i>0.055</i>
7	Green turtles	<i>2.00</i>	0.020	0.150	10.420	<i>0.114</i>	<i>0.014</i>
8	SG_MIF	<i>3.31</i>	2.600	0.690	5.050	<i>0.696</i>	<i>0.137</i>
9	SG_Other	<i>3.11</i>	1.980	2.400	14.020	<i>0.691</i>	<i>0.171</i>
10	SG_Herbivores	<i>2.01</i>	2.700	0.480	17.490	<i>0.811</i>	<i>0.027</i>
11	Lutjanidae (adults)	<i>3.39</i>	9.517	0.710	5.740	<i>0.946</i>	<i>0.124</i>
12	Lutjanidae (juveniles)	<i>3.07</i>	1.325	0.700	13.591	<i>0.955</i>	<i>0.052</i>
13	Haemulidae (adults)	<i>3.26</i>	6.490	0.850	7.870	<i>0.893</i>	<i>0.108</i>
14	Haemulidae (juveniles)	<i>3.07</i>	0.167	1.300	28.975	<i>0.926</i>	<i>0.045</i>
15	Scaridae (adults)	<i>2.01</i>	5.175	1.410	43.200	<i>0.633</i>	<i>0.033</i>
16	Scaridae (juveniles)	<i>2.01</i>	1.239	1.580	85.258	<i>0.925</i>	<i>0.019</i>
17	Acanthuridae (adults)	<i>2.01</i>	9.651	0.580	27.040	<i>0.559</i>	<i>0.021</i>
18	Acanthuridae (juveniles)	<i>2.22</i>	0.066	1.200	142.112	<i>0.915</i>	<i>0.008</i>
19	SG_smallInvertebrates	<i>2.07</i>	<i>39.980</i>	7.010	125.000	0.950	<i>0.056</i>
20	SG_Invertebrates	<i>2.44</i>	<i>27.943</i>	3.700	18.000	0.950	<i>0.206</i>
21	Reef Invertebrates	<i>2.13</i>	<i>24.854</i>	2.800	15.000	0.950	<i>0.187</i>
22	Urchins	<i>2.00</i>	100.000	1.100	3.700	<i>0.088</i>	<i>0.297</i>
23	Seagrass	<i>1.00</i>	221.470	10.950	-	<i>0.103</i>	-
24	Algae	<i>1.00</i>	195.974	15.000	-	<i>0.443</i>	-
25	Epiphytes	<i>1.00</i>	37.553	25.000	-	<i>0.276</i>	-
26	Zooplankton	<i>2.01</i>	32.000	45.000	95.000	<i>0.417</i>	<i>0.474</i>
27	Phytoplankton	<i>1.00</i>	25.000	120.000	-	<i>0.760</i>	-
28	Corals/sponges	<i>1.92</i>	121.000	1.100	6.000	<i>0.182</i>	<i>0.183</i>
29	Detritus	<i>1.00</i>	100.000	-	-	<i>0.566</i>	-

Table 3.2 - Diet composition matrix for the functional groups in the balanced model for the Caribbean. Shaded cells indicate diet proportion <0.0009.

		Predator										
Prey		1	2	3	4	5	6	7	8	9	10	11
1	Piscivores	0.001	-	-	-	-	-	-	-	-	-	-
2	SG Piscivores	0.020		-	-	-	-	-	-	-	-	-
3	MIF	0.030	0.019	-	-	-	-	-	-	-	-	-
4	SIF	0.030	0.010	-	-	-	-	-	-	-	-	-
5	Zooplanktivores	0.101	0.099	-	-	-	-	-	-	-	-	-
6	Herbivores	0.200	0.140	0.009	-	-	-	-	-	-	-	-
7	Green turtles				-	-	-	-	-	-	-	-
8	SG MIF	0.010	0.050	0.005	-	-	-	-	-		-	-
9	SG Other	0.051	0.110	0.005	-	-	-	-		-	-	0.015
10	SG Herbivores	0.007	0.020	0.005	-	-	-	-	-	0.007	-	0.005
11	Lutjanidae	0.114	0.090	0.005	-	-	-	-	-	0.007	-	-
12	Lutjanidae (juv)	0.015	0.044		-	-	-	-			-	-
13	Haemulidae	0.070	0.120	0.005	-	-	-	-	-	0.007	-	0.016
14	Haemulidae (juv)	0.008	0.003		-	-	-	-			-	0.002
15	Scaridae	0.219	0.107	0.005	-	-	-	-	-	0.009	-	0.012
16	Scaridae (juv)	0.010	0.042		-	-	-	-			-	0.019
17	Acanthuridae	0.030	0.120	0.005	-	-	-	-	-	0.00100	-	0.007
18	Acanthuridae (juv)	0.001	0.001		-	-	-	-			-	
19	SG smallInvertebrates	-	-	-	-	-	-	-	0.007	0.015	0.005	
20	SG Invertebrates	0.001	0.024	0.010	-	0.001	-	-	0.789	0.261	-	0.744
21	REEF Invertebrates	0.017		0.880	0.048	0.200	0.001	-	0.063	0.100	-	0.100
22	Urchins	0.015		0.040	-	-	-	-	0.100	-	-	0.015
23	Seagrass	-	-	-	-	-	0.005	0.920	0.030		0.220	
24	Algae	-	-	0.010	0.005	0.010	0.608	0.030		0.037	0.610	
25	Epiphytes	-	-	-	-		0.005	-	-	-	0.155	0.001
26	Zooplankton	-	-	-	0.001	0.739	0.001	-	-	0.480	-	0.009
27	Phytoplankton	-	-	-	-	-	-	-	-	-	-	-
28	Corals sponges	-	-	0.015	0.946	0.050	0.090	-	0.00100	0.074	-	-
29	Detritus	-	-	0.001			0.290	0.050	0.009		0.010	0.005
30	Import	0.050	-	-	-	-	-	-	-	-	-	0.050

Table 3.2. - cont.

Prey/Predator		Predator												
		12	13	14	15	16	17	18	19	20	21	22	26	27
1	Piscivores	-	-	-	-	-	-	-	-	-	-	-	-	-
2	SG Piscivores	-	-	-	-	-	-	-	-	-	-	-	-	-
3	MIF	-	-	-	-	-	-	-	-	-	-	-	-	-
4	SIF	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Zooplanktivores	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Herbivores	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Green turtles	-	-	-	-	-	-	-	-	-	-	-	-	-
8	SG_MIF	-	-	-	-	-	-	-	-	-	-	-	-	-
9	SG Other	-	-	-	-	-	-	-	-	-	-	-	-	-
10	SG Herbivores	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Lutjanidae	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Lutjanidae (juv)	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Haemulidae	-	-	-	-	-	-	-	-	-	-	-	-	-
14	Haemulidae (juv)	-	-	-	-	-	-	-	-	-	-	-	-	-
15	Scaridae	-	-	-	-	-	-	-	-	-	-	-	-	-
16	Scaridae (juv)	-	-	-	-	-	-	-	-	-	-	-	-	-
17	Acanthuridae	-	-	-	-	-	-	-	-	-	-	-	-	-
18	Acanthuridae (juv)	-	-	-	-	-	-	-	-	-	-	-	-	-
19	SG smallInvertebrates	0.979	0.400	0.979	-	0.010	0.010	0.200	0.008	0.350	0.001	-	-	0.001
20	SG Invertebrates	0.010	0.563	0.010	-	-	-	-	-	0.020	0.001	-	-	-
21	REEF Invertebrates	-	0.010	-	-	-	-	-	-	0.010	0.090	-	-	-
22	Urchins	-	-	-	-	-	-	-	-	0.010	0.005	-	-	-
23	Seagrass	-	-	-	0.700	0.200	0.048	0.001	-	0.001	0.008	0.120	-	-
24	Algae	0.001	0.010	0.001	0.080	0.530	0.761	0.380	0.120	0.010	0.231	0.660	-	-
25	Epiphytes		-		0.120	0.249	0.171	0.404	0.001	0.200	-	0.120	-	-
26	Zooplankton	0.010	0.007	0.010	-	-	-	0.005	0.062	0.010	0.010	-	0.006	0.309
27	Phytoplankton	-	-	-	-	-	-	-	0.010	-	-	-	0.650	0.350
28	Corals sponges	-	-	-	0.009	0.001	-	-	-	0.001	0.010	-	-	-
29	Detritus	-	0.010	-	0.091	0.010	0.010	0.010	0.799	0.388	0.644	0.100	0.344	0.34
30	Import	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 3.3 - Ecological indicators of the Caribbean model as pertaining to community energetics, community structure, and cycling of nutrients. The 'cycling index' is the fraction of an ecosystem's throughput that is recycled and is expressed here as percentage.

Parameter	Value	Unit
Sum of all consumption	11,002	t/km ² /year
Sum of all exports	4,473	t/km ² /year
Sum of all respiratory flows	4,833	t/km ² /year
Sum of all flows into detritus	10,279	t/km ² /year
Total system throughput	30,587	t/km ² /year
Calculated total net primary production	9,303	t/km ² /year
Total primary production/total respiration	1.93	
Total primary production/total biomass	10.6	
Total biomass/total throughput	0.029	
Total biomass (excluding detritus)	880	t/km ²
Mean trophic level of the catch	3.21	
Mean transfer efficiency	8.9%	
Network flow indices		
Finn's cycling index	13.62	% of total throughput
System Omnivory Index	0.091	



Figure 3.1 - Puerto Rico and the US Virgin Islands. The dashed line represents the approximate delineation between the US Virgin Islands and the British Virgin Islands. Map modified from <http://reefgis.reefbase.org>

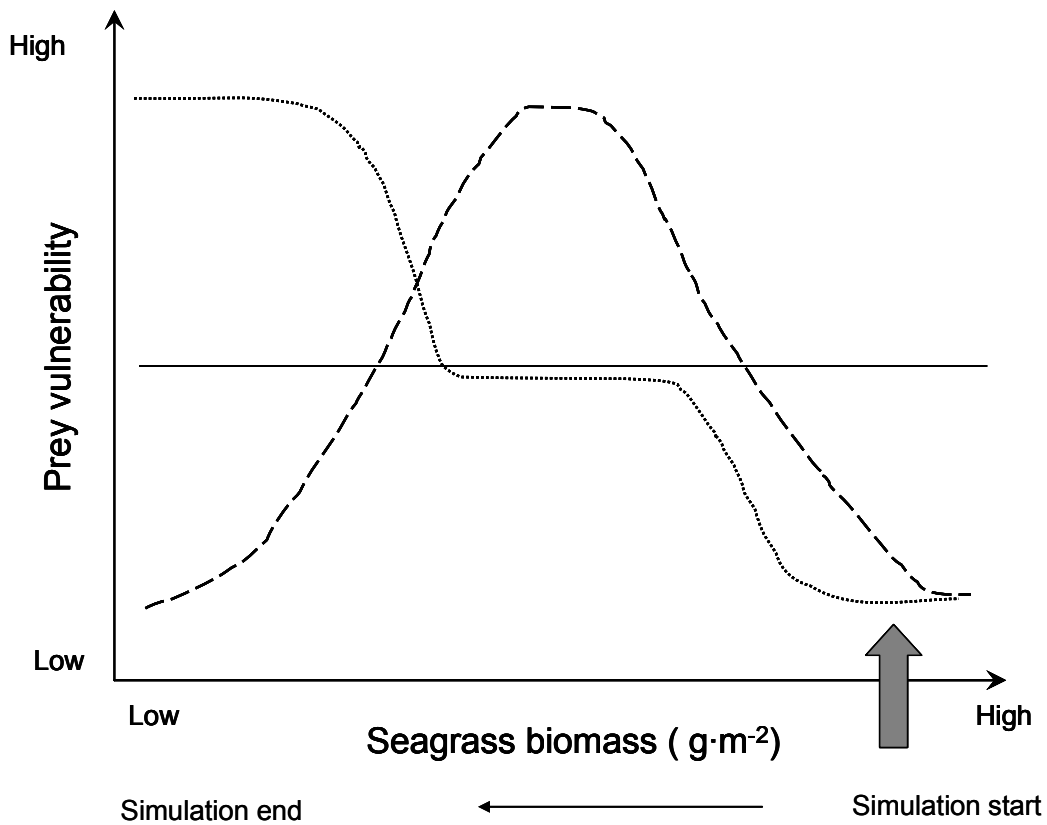


Figure 3.2 - Potential relationship between seagrass biomass (i.e., refuge capacity) with increasing green turtle abundance and vulnerability of prey to predators (modified after Canion and Heck (2009) and implemented in Ecopath as mediation scenarios). Mediation 1 = dotted line; mediation 2 = dashed line; mediation 3 = solid line.

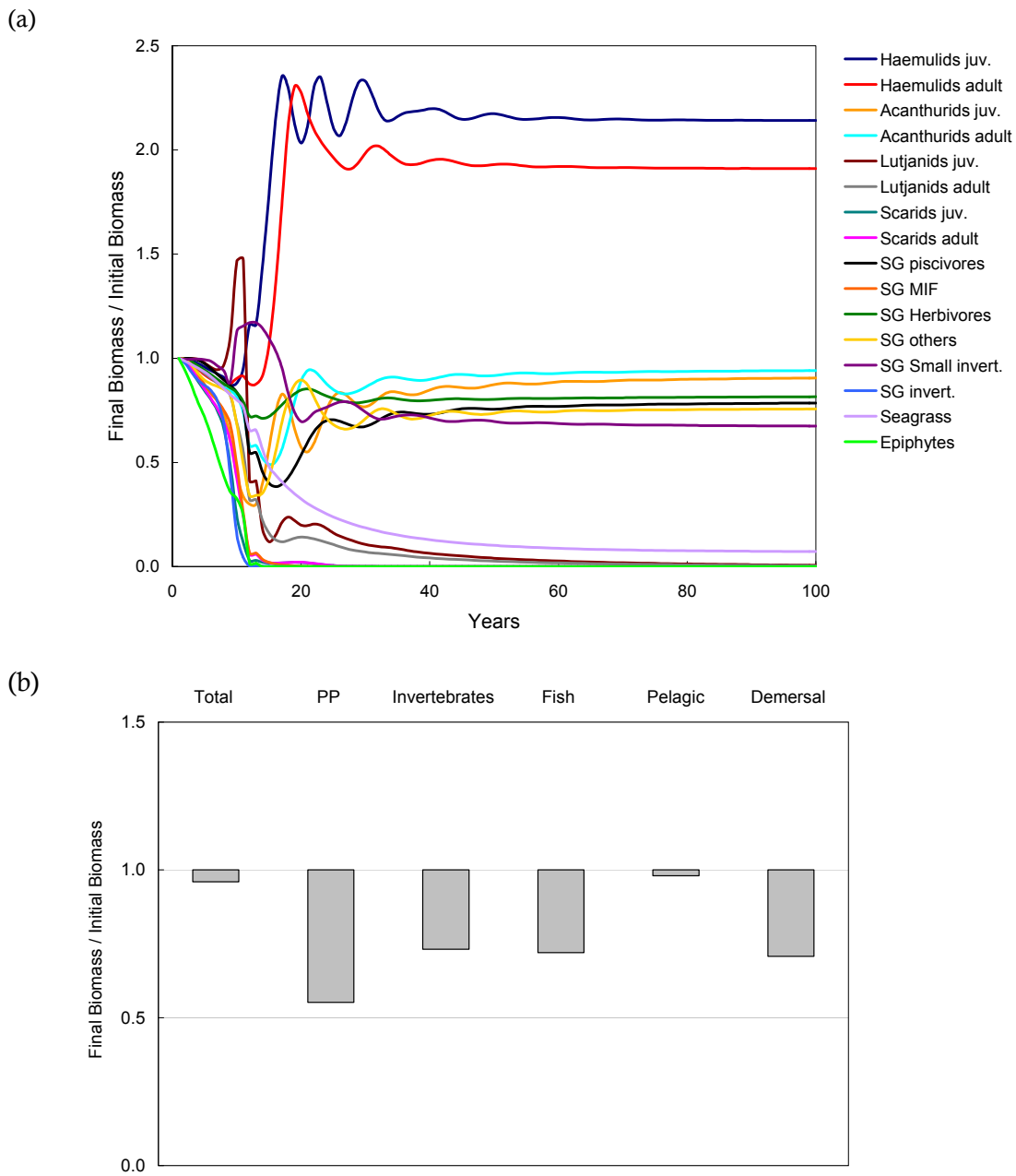


Figure 3.3 – (a) Biomass trajectories (final relative to initial biomasses) of selected trophic guilds under a simulated increase in turtle biomass implemented concomitantly with mediation 1. Illustrated in panel (b), for the same time frame, is the ratio of all final relative to initial biomasses grouped by primary producers (PP), invertebrates, fish, and all pelagic versus demersal/benthic trophic guilds. SG = prefix for species known to forage in seagrass beds

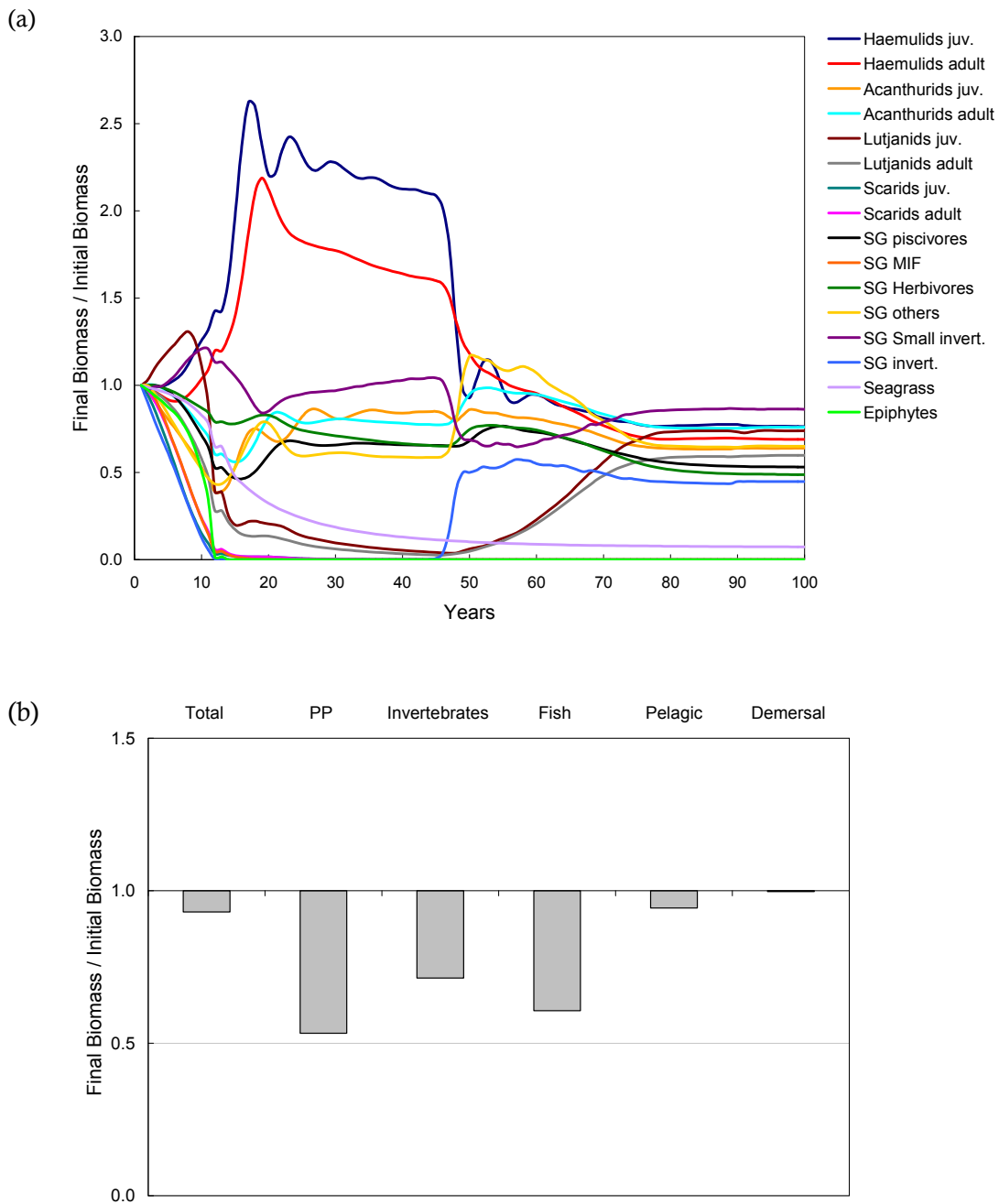


Figure 3.4 – (a) Biomass trajectories (final relative to initial biomasses) of selected trophic guilds under a simulated increase in turtle biomass implemented concomitantly with mediation 2. Illustrated in panel (b), for the same time frame, is the ratio of all final relative to initial biomasses grouped by primary producers (PP), invertebrates, fish, and all pelagic versus demersal/benthic trophic guilds. SG = prefix for species known to forage in seagrass beds

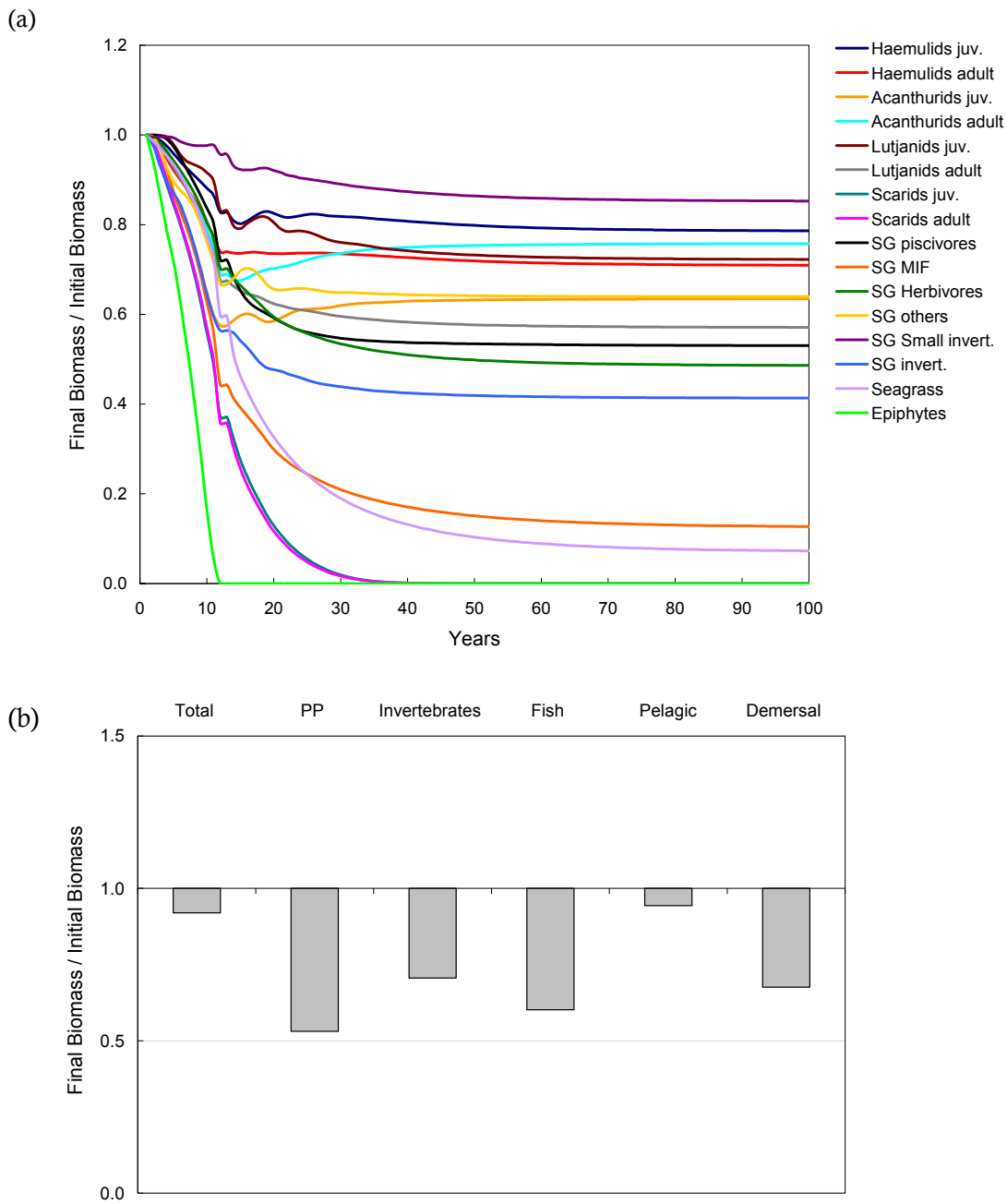


Figure 3.5 – (a) Biomass trajectories (final relative to initial biomasses) of selected trophic guilds under a simulated increase in turtle biomass implemented concomitantly with mediation 3. Illustrated in panel (b), for the same time frame, is the ratio of all final relative to initial biomasses grouped by primary producers (PP), invertebrates, fish, and all pelagic versus demersal/benthic trophic guilds. SG = prefix for species known to forage in seagrass beds

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4. Carrying capacity of green sea turtles (*Chelonia mydas*) at Kaloko-Honokōhau, Hawai‘i, and their role in reef resilience³

4.1 Introduction

Grazing by macroherbivores is one of the major processes structuring benthic coral reef communities. Studies highlighting the role of herbivores in promoting reef resilience and recovery to coral-dominated states, where disturbance has led to increased algal biomass (e.g., Bellwood *et al.* 2004), have focused almost exclusively on fish and sea urchins (Hay 1984a, Carreiro-Silva and McClanahan 2001, Mumby *et al.* 2006a, Paddack *et al.* 2006, Albert *et al.* 2008). Numerous Caribbean reefs have transitioned from coral to algal-dominated states (Gardner *et al.* 2003) following either a dramatic reduction in fish stocks that limited the distribution, abundance, and

³ A version of this chapter has been accepted for publication. Wabnitz, C.C.C., Balazs, G., Beavers, S., Bjorndal, K.A., Bolten, A.B., Christensen, V., Hargrove, S. and Pauly, D. Carrying capacity of green sea turtles (*Chelonia mydas*) at Kaloko-Honokōhau, Hawai‘i, and their role in reef resilience. *Marine Ecology Progress Series* (in press)

production of algae (Ogden and Lobel 1978, Hay 1981, Lewis 1986), and/or the region-wide loss to disease of an important echinoid herbivore (*Diadema antillarum*) in systems that had previously seen a shift from fish-dominated to echinoid-dominated herbivory (Lessios 1988, Mumby *et al.* 2006b). At some locations, increased anthropogenic nutrient loading has further increased the abundance of primary producers (Burkepile and Hay 2006, Littler and Littler 2007).

Few studies have focused on the role of green sea turtles (*Chelonia mydas*) in maintaining coral reef resilience. This is understandable in the Caribbean where green turtles mostly forage on seagrass (Bjorndal 1980, Mortimer 1981, Thayer *et al.* 1984) and thus, predominantly, have an indirect impact on the trophodynamics of reef systems (Valentine *et al.* 2002, Heck and Valentine 2006). In Hawai'i, although the majority of reefs are not as severely impacted as those throughout the Caribbean region (Brainard *et al.* 2002, Waddell and Clarke 2008), several locations have shown increasing signs of stress as a result of mounting anthropogenic pressures on the coastal zone through development and runoff, tourism and recreation activities, and overfishing (Grigg 1994, Hunter and Evans 1995, Friedlander *et al.* 2008, Williams *et al.* 2008). Unlike in the Caribbean region, Hawaiian green turtles feed primarily on algal species that commonly occur on the reef (McCutcheon *et al.* 2003, McDermid *et al.* 2007, Arthur and Balazs 2008, Russell and Balazs 2009) and may therefore play a direct role in maintaining the resilience of coral ecosystems. The fact that green turtles feed on non-native algae, *Acanthophora* spp. and *Hypnea* spp. (Doty 1961, Russell 1992, Russell and Balazs 1994, Arthur and Balazs 2008, Russell and Balazs 2009) further highlights their contribution to the promotion of reef resilience.

Since turtle harvesting ended in the late 1970s (Witzell 1994), an approximately linear increase in abundance of nesting females has occurred at French Frigate Shoals (Balazs and Chaloupka 2004a, 2006), which accounts for > 90 % of all nesting within the Hawaiian Archipelago (Balazs 1980). This increase in abundance is interpreted as a recovery trend, because the Hawaiian nesting

population has been continuously monitored using dependable methodology for several decades (Balazs and Chaloupka 2004a, Chaloupka *et al.* 2008). Population trends at a number of foraging grounds that also have been subject to long-term monitoring seem to mirror this trajectory (Chaloupka and Balazs 2007).

An understanding of the role of turtles as grazers on reefs requires a process-oriented approach that assesses, preferably quantitatively, the relative contributions of all herbivore functional groups (i.e., fish, sea urchins and green turtles). Such an approach is currently lacking, though it may provide significant insights into the need for, and consequences of, improved turtle conservation and management.

Ecological modelling has developed ways to describe mathematically the complexity and nonlinear behavior of ecological systems. Ecopath with Ecosim (EwE) is a freely available, widely used, software for describing the structure of ecosystems and their food webs. It was recently named as one of the 10 major scientific breakthroughs in the 200-year history of the National Oceanic and Atmospheric Administration (see <http://celebrating200years.noaa.gov/breakthroughs/welcome.html>). Rather than providing outputs at the population level of biological organization, typical of many models, the EwE approach provides outputs at the ecosystem level, reflecting food-web linkages, energy cycling, and changes in biomass of each species group defined in the model (Christensen 2008). Although determining carrying capacity of a system has been highlighted as one of the uses of this software, few studies have investigated this aspect through the use of EwE (e.g., Christensen and Pauly (1998)).

I developed an Ecopath trophic model to investigate the role that green turtles play in the coral reef ecosystem of Kaloko-Honokōhau National Historical Park (hereafter referred to as Kaloko).

Located on the west coast of Hawai'i Island (the 'Big Island') (Figure 4.1), the park is characterised

by a healthy and relatively diverse coral habitat with little evidence of non-native species of macroalgae or diseased coral (Gibbs *et al.* 2007). Kaloko supports a low fish biomass yet high fish diversity (Parrish *et al.* 1990, Beets *et al.* 2006). The park also has a resident foraging population of immature green turtles that has been the subject of a mark-recapture study by the U.S. National Marine Fisheries Service (NMFS) and the U.S. National Park Service (NPS) since 1999. Three lines of evidence suggest that this foraging population has reached carrying capacity: (i) the significant increase in green turtle abundance within the archipelago over the last 10-20 years has been associated with a significant decrease in somatic growth rates (Balazs and Chaloupka 2004b), probably the result of density dependence (Bjorndal *et al.* 2000); (ii) field measurements of body volume and mass as an index of body condition show that turtles at foraging locations near Kaloko have lower body condition indices than green turtles at other sites in Hawai'i (Kubis *et al.* 2008); and (iii) recent necropsy reports cite emaciation as a probable contributor in the death of a number of green turtles found stranded at foraging locations along the west coast of the Big Island (Work 2007, 2008a, 2008b).

The trophic model will also provide a 'baseline' of ecosystem state for Kaloko prior to major developments projected for areas around the park. Concern has been expressed over the future health of Kaloko's coastal resources given proposed plans for development of lands adjacent to the south boundary of the park, including a 300 % expansion of a small-boat harbor, and construction of hotels, condominiums, and a light industrial park (Gibbs *et al.* 2007). Expected impacts include a reduction in groundwater flow, an important feature at Kaloko, with a concomitant increase in groundwater loads of sediment, nutrient, and chemical pollutants (Oki *et al.* 1999, Paytan *et al.* 2006, Johnson *et al.* 2008).

The goals of this study were, therefore, threefold:

1. to develop an ecosystem model of the marine portion of the park, synthesizing available data and describing the ecological structure and ecosystem processes of the reef system at Kaloko;
2. to ascertain whether Kaloko green turtles are at carrying capacity, by determining whether grazing by green turtles and other reef herbivores matches overall algal production;
3. to provide the management community with a tool that can simulate effects of increased urban development in the Kaloko area, as well as compare the outcomes of a range of potential management scenarios.

4.2 Material and methods

4.2.1 Study area

Kaloko-Honokōhau National Historical Park was established in 1978 and spans 5.17 km², of which 2.48 km² is marine (Gibbs *et al.* 2007). The park is bordered to the south by the Honokōhau Small-Boat Harbor, and large scale industrial/commercial developments are located to the east (Figure 4.1). The terrestrial portion includes more than 180 anchialine (brackish) pools, two large ponds and wetlands modified for fish production by early Hawaiians, and a fish trap (Kaloko, 'Aimakapā and 'Ai'ōpio respectively; Figure 4.1). The coastal waters and reefs of Kaloko are within the West Hawai'i Fisheries Management Area and are currently managed by the State of Hawai'i. The legislated park boundary extends offshore for about 1,000 m at the widest point and to maximum depths of ca. 70 m (Parrish *et al.* 1990). Beyond this boundary the seabed drops off to depths > 180 m. Approximately 73 % of the marine section of the park is composed of hardbottom substrate. The remaining 27 % comprises unconsolidated sediment and artificial/historical features. Most of the hardbottom area has 10 % to < 50 % coral cover, and ~ 12 % has 50 % to 100 % coral cover (Gibbs *et al.* 2007). Benthic habitats are considered relatively healthy, with no signs of diseased corals or

non-native algal species (Marrack *et al.* 2009, Weijerman *et al.* 2009). Low sedimentation rates and the presence of relatively high coral cover in protected locations suggest that currently, the reef habitat in Kaloko is primarily controlled by natural wave-induced stresses (DeVerse 2006).

4.2.2 Modelling approach

For model development, I used the Ecopath and Ecosim approach (EwE) (Christensen and Walters 2004, Christensen *et al.* 2005, <http://www.ecopath.org>). The Ecopath component of any EwE model provides a quantitative representation of an ecosystem for a defined time period as a snapshot of the resources in an ecosystem and their interactions, represented by trophically linked mass-balanced biomass ‘pools’ (Polovina 1984, Christensen and Pauly 1992). The biomass pools, hereafter referred to as functional groups, consist of a single species, or species groups representing ecological guilds. The idea behind the mass-balance approach is that “at any time within the system, and within the elements of that system, the amounts of matter that flow in must balance the amount that goes out, plus the change in biomass” (Pauly and Christensen 2002 p. 215). Ecopath, therefore, operates under two main assumptions:

- (a) That biological production within a functional group equals the sum of mortalities, i.e., on an annual basis, biomass and energy in an ecosystem are conserved (Walters *et al.* 1997, Walters and Martell 2004). This relationship can be expressed as follows:

$$B_i \cdot (P/B)_i = \sum_{j=1} B_j \cdot (Q/B)_j \cdot DC_{ij} + Y_i + E_i + BA_i + B_i(P/B)_i \cdot (1 - EE_i) \quad (1)$$

where B_i and B_j are biomasses of prey (i) and predator (j) respectively; $(P/B)_i$ is the production to biomass ratio, equivalent to total mortality (Z) under most circumstances (Allen 1971); $(Q/B)_j$ is the food consumption per unit biomass of (j); DC_{ij} is the fraction of prey (i) in the average diet of predator (j); Y_i is the total fishery catch rate of group (i); E_i is

the net migration rate (emigration - immigration); BA_i is the biomass accumulation rate of group (i); and EE_i is the ecotrophic efficiency, defined as the fraction of production that is consumed within the system or is removed by fishers.

- (b) That consumption within a group equals the sum of production, respiration, and unassimilated foods. This relationship can be expressed as follows:

$$B \cdot (Q/B) = B \cdot (P/B) + (1 - GS) \cdot Q - (1 - TM) \cdot P + B(Q/B) \cdot GS \quad (2)$$

where GS is the proportion of food unassimilated and TM is the trophic mode expressing the degree of heterotrophy of groups represented within the system - with 0 representing autotrophs, 1 heterotrophs, and intermediate values facultative consumers.

Ecopath then uses a set of algorithms to solve simultaneously n linear equations of the form in equation 1, where n is the number of functional groups. For each functional group, three of the basic parameters: B_i , $(P/B)_i$, $(Q/B)_i$ or EE_i must be known, in addition to the fisheries yield (Y_i), and the diet composition. Units of the model are expressed in $t \cdot km^{-2} \cdot year^{-1}$ wet weight organic matter for flows, and $t \cdot km^{-2}$ wet weight for biomasses. P/B and Q/B have the dimension $year^{-1}$. For a review of Ecopath with Ecosim's capabilities and limitations see Christensen and Walters (2004) and Plaganyi (2004, 2007).

To balance the model, changes were first made to the diet matrix, as diet compositions represent only snapshots of the feeding habits of individual species and are likely to be relatively variable based on location and time periods of data collection. The model required only minor adjustments and was considered balanced when: (a) the balanced model produced realistic ecotrophic efficiencies ($EE < 1$); and (b) values of the production to consumption ratio (P/Q) for functional groups ranged between 0.05 and 0.35, with the exception of groups with fast growth rates (higher ratios), and top predators with lower values (Christensen *et al.* 2005).

4.2.3 Model parameters and functional groups

The model represented an annual average situation of ecosystem conditions in the marine portion of Kaloko-Honokōhau National Historical Park in 2005. I defined a total of 26 groups spanning the main trophic components of the ecosystem (including detritus) (Table 4.1, Figure 4.2). Eight groups were made up of fish, and represented the aggregation, based on ecological and biological similarities (e.g., diet, size, habitat, mortality), of 106 fish species recorded during underwater visual census studies (Beets *et al.* 2006) (see Appendix 6).

Biomass estimates for individual species were based on values from field studies, local expert opinion or from the literature. For species with data reported only from selected habitats, biomass values were extrapolated to the entire park by calculating an area-weighted biomass for each species relative to the proportion that each benthic habitat category covered within park waters (the latter based on Gibbs *et al.* 2007). For instances where P/B was equal to only natural mortality, estimates were taken directly from the literature or derived using the empirical formula of Pauly (1980). For exploited species, fishing mortality values were based on Friedlander and Parrish (1997) (see Fisheries section below). Where possible, the consumption of each group was obtained through field studies; otherwise consumption was estimated from empirical equations such as those available in Fishbase (www.fishbase.org) for all finfish. The diet matrix was constructed using data from field studies in Hawai'i, preferentially the Kona Coast. Where no such data were available, the matrix was complemented with data obtained from the literature for the same species in similar ecosystems. Details of data sources and estimation methods for all parameters can be found in Appendix 7.

Fisheries

Kaloko's waters were designated as a Fish Replenishment Area (FRA) on December 31, 1999, effectively banning collection of fish for the aquarium trade in park waters, in response to declines of species targeted by collectors (Tissot *et al.* 2004). Biomass of targeted species may have responded to the closure, and because fishing pressure for ornamentals has been removed, P/B was set to natural mortality (M) for all formerly collected species (E. Brown, U.S. National Park Service, pers. comm.).

The park is a popular location for subsistence fishing and shoreline gathering, traditional activities that are permitted as long as they are consistent with state law and park mandates (i.e., with legal fishing gear for personal consumption) (DeVerse 2006). Harvesting is done primarily from shore using several methods, such as throw nets, spear, and pole fishing. Gill, or 'lay' netting, a serious threat to marine resources, including marine mammals and sea turtles, was restricted within park waters in August 2005 to locally constructed, handmade nets of natural fibres. The state of Hawai'i does not have recreational and subsistence permitting or reporting requirements (Friedlander and Parrish 1997), despite surveys in the late 1980s that indicated that 19 - 35 % of residents fish (Smith 1993), and recent studies concluding that these fisheries dominate the catch of coral reef species (Zeller *et al.* 2005, Williams *et al.* 2008). Although several studies conducted throughout the Hawaiian Archipelago have assessed the importance of fishing impacts on coral reef fish assemblages (e.g., Tissot *et al.* 2004, Williams *et al.* 2008, Tissot *et al.* 2009, DAR unpublished data, in Weijerman *et al.* 2009), few data exist to quantify fishing mortality along the western shores of the Big Island. In the absence of catch or effort data specific to Kaloko, I assumed catch data/standing stock proportions in the park to be comparable to those in Hanalei Bay, Kauai (Friedlander and Parrish 1997), adjusting values to reflect species known to be targeted at Kaloko. As no data are available on macroinvertebrates in Kaloko (with the exception of sea urchins), nor information

regarding whether fishing occurs on those groups in the park, no catch was allocated to the benthic invertebrate group.

I divided existing fisheries into two 'fleets', one targeting 'sharks and jacks' specifically, and a recreational/subsistence fishery representing fishers operating mainly from shore using pole, spear, and line, and targeting small reef fish. I calculated the ratio of catch to standing stock for fish families targeted by fishers from Friedlander and Parrish (1997) and doubled them, given that fishing pressure is likely to be higher now than it was in 1997 (DAR unpublished data 2006 in Weijerman *et al.* 2009). I then applied these indices to fish families harvested in Kaloko (E. Brown, U.S. National Park Service, unpublished data 2008). For species groups targeted in Kaloko, but for which data were not available from the Friedlander and Parrish (1997) study, I applied the same value as for fish families in the same functional group. Fishing mortality for individual species/functional groups was calculated using $F = \text{catch} / \text{biomass}$.

Model analysis, indices, and uncertainty around input data

I quantified total trophic flows within the ecosystem in terms of consumption, production, respiration, exports and imports, and flow to detritus ($\text{t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$). I then used ecological indices as obtained through Ecological Network Analysis (ENA) to evaluate the food web (Wulff *et al.* 1989, Christensen and Pauly 1993). ENA is a modelling technique used for understanding the structure and flow of material between components of an ecosystem (Ulanowicz 1997). As integrated in Ecopath, ENA allows for the calculation of ecosystem macro descriptors that quantify trophic structure, organic matter recycling, and ecosystem size and organization. These descriptors include total system Throughput (T), Ascendency (A), development Capacity (C), and the Relative Overhead (O/C). Throughput describes the size of a system and represents a measure of its metabolism (Christensen and Pauly 1993). Ascendency integrates both size and organization of a

given system (Christensen 1995). The development Capacity quantifies the upper limit to Ascendency while the system's Overhead (O) is complementary to the Ascendency and measures the level of 'redundancy' of particular links (Heymans 2003). The O/C ratio was proposed by Heymans (2003) as an index of the resilience of the system (i.e., an index of the system's ability to withstand disturbance (Ulanowicz 1997)). ENA further allows the derivation of Transfer Efficiencies (TE), summarizing the proportion of consumption that is passed up a food web. The TE is the ratio between the production of a given trophic level and the preceding trophic level (Pauly and Christensen 1995). Finally, I ran the Mixed Trophic Impact (MTI) analysis (Ulanowicz and Puccia 1990), which allows the theoretical quantification of direct and indirect interactions among functional groups within the food network. In other words, this analysis provides a first-order quantification of the beneficial and negative impacts of one group on another.

Any ecosystem model realization requires acknowledging the large amount of data required in its development, and the difficulty in quantifying the flows between the food web's individual functional groups. Group dynamics can be verified by fitting model data to actual population trends over time. Such time series data do not exist for Kaloko. Given the primary goal of determining whether green turtles are at carrying capacity in Kaloko, I focused on sources of uncertainties associated with estimates of green turtle biomass, P/B, and Q/B; the proportion of sea urchins' diet that was derived from turf growing on the nearshore lava bench ($turf_{LB}$ - green turtles' primary forage base); and variability associated with $turf_{LB}$ biomass and P/B. To address these uncertainties, probability distributions for all input parameters were entered through the 'pedigree' (Funtowicz and Ravetz 1990) function of Ecopath (Pauly *et al.* 2000). Using a Monte Carlo resampling routine, the 'Ecoranger' module of Ecopath subsequently draws random input variables from within the confidence intervals defined for each parameter type in the pedigree tables and uses these as prior probability distributions for all input data. This approach leads to a large number of model realizations that are evaluated for their conformity to user-defined criteria as well as physiological

and mass-balance constraints. The results include probability distributions for the estimated parameters along with distributions of parameters in the accepted model realizations. This routine can be run for the model overall, as pedigrees are associated with all input parameters. However, I focused on uncertainty associated with input parameters that would affect the objective of estimating carrying capacity of green turtles.

4.3 Results

Trophic parameters and the diet matrix for the 26 groups of the final balanced Ecopath model for Kaloko are presented in Table 4.1 and Table 4.2 respectively. Trophic flows between all functional groups are depicted in Figure 4.2. Sea urchins (*Tripneustes gratilla*, *Echinometra mathaei*, *Heterocentrotus mammilatus*, and *Echinothrix* spp.) accounted for the largest proportion of total living biomass in the system (40 %) (Figure 4.3). Green turtles and reef fish groups, including ‘sharks and jacks’, only represented 0.2 % and 5.5 % of total biomass respectively (Figure 4.3). Reef fish groups were dominated by herbivorous and species characterised as Mobile Invertebrate Feeders (‘MIF’). Not surprisingly, consumption by sea urchins had the biggest impact (45 %) on available resources at Kaloko; whereas fish accounted for 14.4 % and green turtles for 0.2 % of total consumption. Total fisheries catches represented < 1 % of the total fish biomass (Table 4.1). ‘Sharks and jacks’ were caught in large quantity compared with their relatively low biomass in the assemblage. Mean trophic level of the catch was 2.59 (Table 4.3).

Ecotrophic efficiency (EE) values (the proportion of a functional group’s production used within the system) were lowest for some of the highest trophic levels (e.g., ‘spinner dolphins’, ‘monk seals’, and ‘sea birds’), as well as for ‘crown-of-thorns starfish’, ‘hawksbill turtles’, ‘green turtles’, ‘sea urchins’, and ‘corals’ (Table 4.1). For the higher trophic level groups, this valuation is based on these species

deriving a significant proportion of their food from outside park waters. They were included chiefly to ensure that the model was representative of the system at Kaloko (i.e., to acknowledge that these species occur in the park, and may at some point in the future suffer from indirect effects of park development, even if they do not feed exclusively or primarily in park waters). For the five other groups, the low EE values are a result of low predation and fishing pressure being exerted on these species. Fish groups, overall, also had relatively low EE values, with higher values registered by those species pools that were subject to higher fishing mortality. This valuation suggests that the system generates a reasonable amount of surplus secondary production. Indeed, the largest component of the mortality coefficients within the system was due to predation mortalities, with the exception of 'sharks and jacks' for which the fishing mortality rate was greater than predation mortality. In contrast, most of the production by the macro- and turf algal groups, 'zooplankton', 'benthic invertebrates', and 'phytoplankton' was accounted for through consumption by other trophic groups within the model ($EE > 90 \%$). In other words, sea urchins, herbivorous fish, and green turtles maintained all algae at Kaloko in a cropped state. Reef building corals, octocorals, benthic invertebrates, and zooplanktivorous fish were the main predators of zooplankton, while zooplankton consumed most of the phytoplankton production in the system. Benthic invertebrates were preyed on mostly by MIF reef fish and species within the benthic invertebrate group itself.

Throughput (total flows) values for each functional group highlighted the importance of turf algae, zooplankton, and phytoplankton, as well as sea urchins in system structure. The high EEs attained for all algal groups indicated that the system was at carrying capacity with respect to grazing, including for green turtles. The primary producers' high EEs were also reflected in the low production/respiration ratio of 1.12 for the system overall (Table 4.3).

Focusing on mega- and macro-herbivores in the system only, the MTI routine highlighted the resource competition both within and between sea urchins, herbivorous fish, and green turtles

(Figure 4.4). Sea urchins were responsible for the largest between-group effect, impacting negatively on both fish and green turtles, and overall had the largest impact on algal and detrital resources. Given green turtles' feeding preference on turf_{LB} , they were the group most impacted by changes in turf_{LB} (Figure 4.4).

When accounting for the uncertainty around parameters affecting consumption of turf_{LB} , EE values of turf_{LB} in successfully balanced model-runs ranged between 0.416 and 0.998.

The mean transfer efficiency in the ecosystem as a whole was 4.6 %, with 4.5 % for flows originating from primary producers and 4.7 % from the detritus. This low efficiency was due to consumption dominating total system throughput for the lower trophic levels, whereas respiration and flow to detritus dominated the higher trophic levels in the model (Figure 4.5). This result is to be expected in a system with low biomass at the highest trophic levels. Some upper trophic level species, such as trevally (also locally known as 'ulua' or 'jacks'), are highly vagile. As a consequence, although not being heavily fished for in park waters, their abundance may still be depressed because of high fishing pressure along the remainder of the Kona Coast. Ascendancy was 31.5 % of capacity and relative overhead 68.5 % (Table 4.3), 46 % of which were attributable to internal flows, indicating that the system contains a number of 'redundant' trophic linkages. These observations are consistent with a system exhibiting relatively high resilience to perturbation with respect to energy flows, or a high system stability *sensu* Odum (1971).

Net primary productivity was $3,895 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ and was accompanied by a high flow to the detritus pool (Table 4.3). Turf algae (including turf_{LB}) and phytoplankton accounted for 57 % and 24 % of total production in the system, or 65 % and 27 % of total primary production. Sea urchins (38 %) were the major contributor to the detrital pool, followed by zooplankton (28 %), while the combined fish groups (mainly herbivores) contributed 11 % of all flows to the detritus. The ratio between

primary production and respiration (PP/R) of Kaloko indicates that the system was at a low developmental stage, *sensu* Odum (1969, 1971). This finding was corroborated by the low Finn's cycling index, showing that only a small fraction of the throughput (including detritus) was recycled (6 %) (Table 4.3). The proportion of flows originating from the detritus was 0.27 %.

The overall pedigree (i.e., 'quality') index of the model (0.539) was high in comparison to 50 other models for which pedigree values ranged between 0.164 and 0.676 (Morissette 2007).

4.4 Discussion

4.4.1 Description of the Kaloko-Honokōhau system

Quantitative descriptions of the flux of matter and energy can provide significant insights into the fundamental structure of ecosystems. The Kaloko system is dominated by primary production (PP), 27 % of which is contributed by phytoplankton and 65 % by algal turfs, which is slightly lower than other published estimates for primary producers in tropical systems (e.g., Wanders 1976, Adey and Steneck 1985, Adey and Goertemiller 1987). The trophic networks at Kaloko were dominated by grazing, with herbivores accounting for 43 % of all living biomass within the system (Figure 4.3), of which 93 % were sea urchins. This dominance of grazing behaviour was further highlighted by the high EEs achieved for the main PP functional groups. Results from rapid assessment surveys throughout the state confirm that herbivorous fish, and sea urchins in particular, are commonly found on reefs in Hawai'i (Rodgers *et al.* 2004). In contrast, relatively low EEs of higher trophic level functional groups indicate that the foraging activities of herbivores are not limited by predation pressure, as demonstrated by the analysis of total system throughput (Figure 4.5). Indeed, few predators commonly occur in the park, and fewer still have been observed feeding in the park. Therefore, as highlighted by the model's average transfer efficiency of 4.6 %, which is lower than the

mean of 10 % obtained for various other ecosystems (Christensen and Pauly 1993), only a small proportion of production is being transferred up the food chain. Comparison between two sets of underwater visual census data (E. Brown and NPS, unpublished data 2007) showed a fivefold increase in piscivore biomass between 2005 and 2007. This inter annual difference may have been a result of real differences between the two datasets, possibly reflecting the restrictions on gillnetting in park waters implemented in August 2005. Differences in species biomass and composition may also reflect either variability in survey accuracy for species displaying vagile (e.g., *Caranx melampygus*) or cryptic behaviour (e.g., *Gymnothorax flavimarginatus*, *Gymnothorax meleagris*, *Cephalopholis argus*), or seasonal changes (Friedlander and Parrish 1998, Vitousek *et al.* 2009), as the 2005 and 2007 datasets were collected in April and October, respectively. Future surveys should, therefore, focus on good intra annual coverage to represent seasonal variation.

Phytoplankton and zooplankton had some of the highest EEs. The waters around Hawai'i are generally oligotrophic (Bienfang *et al.* 2009) and, consequently, low biomass of phytoplankton and zooplankton groups is to be expected. Reef environments along the west coast of the Big Island are close to the deep slope of the Pacific and subject to strong wave action and currents along the shore (Presto *et al.* 2007). Therefore, I assumed that zooplanktivores on the reef derive a substantial portion of their diet from open-ocean plankton. I further assumed that ocean plankton also contributes to the energy intake of benthic invertebrates and other functional groups that feed on plankton. Experiments should be conducted to ascertain the proportion of ocean plankton that contributes to the diet of reef organisms at Kaloko or other similar systems in Hawai'i.

At $42.54 \text{ t}\cdot\text{km}^{-2}$, the model's benthic invertebrate biomass was similar to estimates provided for models in Raja Ampat, Indonesia ($51.68 \text{ t}\cdot\text{km}^{-2}$) (Ainsworth *et al.*, 2007), and the Great Barrier Reef, Australia ($61.41 \text{ t}\cdot\text{km}^{-2}$) (Tudman, 2001), but substantially lower than estimates for Moorea, French Polynesia (barrier reefs = $198.26 \text{ t}\cdot\text{km}^{-2}$ and fringing reefs = $322.8 \text{ t}\cdot\text{km}^{-2}$) (Arias-González 1994,

Arias-González *et al.* 1997). Few studies have investigated the composition of benthic invertebrates on reefs, yet they are an important prey for a variety reef fish (e.g., Hobson 1974) and can represent an important fishery (Friedlander and Parrish 1997). Given that benthic invertebrates accounted for 6 % of total system biomass, species composition and their relative contribution to total group biomass of the benthic invertebrate community of Kaloko should be determined.

Sea urchin densities at Kaloko (~ 5 individual per m^{-2} for *E. mathaei* and < 1 individual per m^{-2} for all other species) were comparable to sea urchin densities recorded on reefs throughout the State of Hawai'i (Rodgers *et al.* 2004), and similar to, or lower than, those reported from other reef locations (e.g., 5 to 6.8 individuals per m^{-2} (chiefly *E. mathaei* and *T. gratilla*) at La Réunion (Naim *et al.* 1997) and 2 to 4 individuals per m^{-2} (*Echinometra*) in Fiji (Appana and Vuki 2006)). Current sea urchin densities at Kaloko are also comparable to those recorded in the 1970s (Ebert 1971). These similarities suggest that high sea urchin densities are natural and not a release from predation pressure due to increased fishing pressure in the last 30 years, as noted at a number of locations along the coast of Kenya (Muthiga and McClanahan 1987, McClanahan 1998).

4.4.2 Turtles at carrying capacity

Green turtles are at carrying capacity at Kaloko based on (a) their biomass estimates and consumption rates; (b) estimates of turf algae biomass growing on the lava bench (turf_{LB}) as well as the primary production rates of these algae; and (c) the high degree to which sea urchins feed on the green turtles' main food resource. Balanced model outputs under Ecoranger, taking into account the uncertainty surrounding these input parameters, showed that the EE of turf_{LB} could range between 0.416 and 0.998. Specifically, it reflects the wide range in published biomass and mass-specific productivity rates for turf algae. For example, biomass estimates were found to vary between 230 $\text{g}\cdot\text{m}^{-2}$ (T. Sauvage, pers. comm. 2008) and 600 $\text{g}\cdot\text{m}^{-2}$ (Smith *et al.* 2001) in Hawai'i alone, 78 $\text{g}\cdot\text{m}^{-2}$ in

the Solomon Islands (Albert *et al.* 2008), and 850 g·m⁻² in the Caribbean (Bruggemann *et al.* 1994). Even greater ranges in productivity have been recorded for the different algal groups that constitute ‘turf’, particularly in relation to depth and seasonal cycles (Payri 2000). An evaluation of algal turf productivity and consumption rates by green turtles at Kaloko would help refine the estimates presented here.

Results from the MTI analysis highlighted the strong competition for the same resource between sea urchins, fish, and green turtles. Grazing pressure exerted by herbivorous fish does not occur uniformly on a reef. Grazing may be reduced in places where reef structure affords little refuge from predation (Lewis 1986). However, this may not be a significant factor at Kaloko where overall predation pressure is limited due to the low abundance of piscivores. Foraging efficiency may also be reduced on shallower portions of the reef because of high wave intensity. It was, therefore, assumed that fish at Kaloko chiefly grazed on reef turf algae rather than turf_{LB} specifically (Table 4.2).

Recent evidence from the South Pacific demonstrates that few of the fish species previously classified as ‘herbivores’ are indeed exclusively herbivorous (Choat *et al.* 2002, Cvitanovic *et al.* 2007). Many appear to predominantly feed on detritus, only incidentally removing turf from the reef in the process (Crossman *et al.* 2001, 2005). Data on the extent of algae removed, but not consumed, are needed to correct the current assumption that all algal material removed by fish was ingested. MTI results reflected resource competition between turtles and fish primarily for macroalgae, which appeared ‘magnified’ as macroalgae biomass overall in the park is low. As sea urchins occur in the shallows (M. Weijerman, pers. comm. 2008, L. Marrack, U.S. National Park Service, pers. comm. 2008), probably emerging at night to feed (Mills *et al.* 2000, Vaitilingon *et al.* 2003), a small proportion of turf_{LB} was included in the echinoids’ diet matrix (Table 4.2). Quantification in the field of this overlap and the extent to which relative densities among the three herbivore groups may

change with time would help refine carrying capacity estimates for green turtles. Clarification of the extent to which sea urchins feed on turf_{LB} also has implications for their role in maintaining low algal biomass levels in the face of increased nutrient input associated with urban development activities around the park (see below).

Observations of Kaloko turtles appearing unusually ‘skinny’ (Kubis *et al.* 2008) and exhibiting low growth rates (Balazs and Chaloupka 2004b), compared to turtles at certain other Hawaiian foraging grounds, support input parameters within the range used in my model (Table 4.1). A key difference among individual foraging sites that may help explain variations in observed growth rates is that green turtles at Kaloko forage on turf, the dominant algal group on the central west coast of Hawai‘i, whereas other foraging grounds throughout the Hawaiian Archipelago have macroalgae available as forage. Recent observations have indicated a behavioural shift in the turtles’ foraging patterns. Fewer turtles are utilizing the shallow reef area in the summer months than they did up to about 2006 (S. B., unpublished data 2009). More interactions with humans as a result of recent increases in visitor use may be partly responsible for greater movement of green turtles than previously observed (S. B., unpublished data 2009). Greater turtle movement possibly away from Kaloko further strengthens the case for carrying capacity having been reached at the park because of limited available forage.

Turf algae growing on the lava bench close to shore and intertidal area were included in the model as a separate functional group, as resident turtles at Kaloko have been seen to concentrate their foraging to this portion of the park. Such focused foraging behaviour may occur for three reasons:

- (i) By focusing their feeding activities on shallow portions of the reef, individual turtles exert less effort foraging as the lava bench supports a highly productive algal mat that can grow unrestricted by space competition with live coral. If turtles were to forage on deeper sections of the reef, for a similar intake of algae, animals would have to roam over wider areas and pick

algae from in and around coral heads, resulting in greater energy expenditure. Results, corroborated by local observations of turf algae throughout the park being closely cropped (F. Parrish, NOAA, pers. comm. 2008), indicate that the system is also close to carrying capacity for overall turf algae, thus making foraging by green turtles in deeper reef sections even less energy efficient. ‘True’ carrying capacity of turf algae on the reef may actually be realized at lower EE values, because turf algae laden with sediment does not allow for much of the algae to be available to grazers.

- (ii) Green turtles may prefer to forage on the lava bench because of the protection afforded by the shallows against predation by tiger sharks. Sharks are regularly sighted at Kaloko (DLNR 2001, Thompson 2005), and a log of necropsies performed on turtles at Kaloko indicate that shark attacks were responsible for the death of 4 turtles since 1992 (obviously attacks that resulted in the complete ingestion of turtles by sharks cannot be monitored) (G. B., unpublished data 2009). Thus, the distribution of turtles, and the algae they consume, may be affected by differential vulnerability of turtles to shark predation in different habitats (Heithaus *et al.* 2002, 2006). From a predation perspective, nutritionally profitable microhabitats at Kaloko also appear to be low risk.
- (iii) The repeatedly grazed turf_{LB} may be more palatable to green turtles than algae growing on deeper sections of the reef. The area where turtles aggregate to feed is located close to ‘Ai’ōpio fishtrap, an area of considerable groundwater discharge (Johnson *et al.* 2008). As groundwater is the only conduit for nutrients into the coastal zone, the nutritional content of algae in this specific location may be significantly different from algae on the remainder of the reef.

4.4.3 Potential threats and impacts on natural resources as a result of urban development

On many coral reefs located near human population centres, benthic community composition has shifted from coral-dominated to macroalgae-dominated (Hughes 1994, Hunter and Evans 1995,

McClanahan and Mangi 2001). These shifts, often termed ‘phase shifts’ (Done 1992), have been attributed to increased anthropogenic nutrient input (e.g., Lapointe 1997) and to reductions in the abundance of herbivores (e.g., Hay 1984b). Studies investigating changes in grazing intensity at sites that have undergone phase shifts, such as Kāne‘ohe Bay, Hawai‘i, have focused primarily on the role of herbivorous fish, and to a lesser extent mesoherbivores (Cheroske *et al.* 2000) and sea urchins (Hunter and Evans 1995, Stimson *et al.* 2001, Smith *et al.* 2008). As results clearly demonstrate, future studies need to explicitly consider green turtles because of their important role as herbivores. Their consumption of non-native algae, including *G. salicornia* (Russell and Balazs 2009), abundant at a number of locations across Hawai‘i, including Kāne‘ohe Bay, further highlights their role in promoting resilience.

Ongoing and planned urban development activities and associated population growth around Kaloko will likely have significant and diverse impacts on the condition of the nearby reefs. Expected impacts include, but are not restricted to: (a) a reduction in groundwater discharge quality (i.e., increased nutrient loading) that could lead to increased macroalgal growth and subsequently a deterioration in the health of corals (e.g., Fabricius 2005, Smith and Smith 2006) particularly if combined with a reduction in the urchin population; and (b) an increase in fishing pressure and a resulting decrease in the herbivore fish population, which could lead to an increase in the abundance of macroalgae on the reef (Stimson *et al.* 2001, Williams *et al.* 2007). Based on this study’s findings, some key points emerge that should be taken into account if dynamic simulations of various ‘impact scenarios’ are run in the future.

Increased nutrient input and increased fishing pressure may lead to an increase in the proportion of macroalgal cover at Kaloko and potential forage for resident herbivores. In 2008, the NPS initiated a long-term, marine water quality monitoring program (quarterly sampling) that includes optical chlorophyll sampling. Additionally, plans are underway through a partnership between the NPS and

the U.S. Geological Survey to use stable isotope tracers to identify sources of nutrient inputs to park groundwater. The NPS, in partnership with the University of Hawai'i, Hilo, recently also initiated a pilot fisheries harvest monitoring program to identify and quantify fishing pressure within the park; this should be a long-term initiative. Nutrient and fisheries' catch time series in conjunction with regular monitoring of algal cover within the different habitats at Kaloko, and the herein developed Ecopath model, may help to determine the impacts of such changes at the ecosystem level. Based on model findings, I would expect the following responses to two scenarios:

(i) *increased nutrient delivery to the reef system without changes in fishing pressure*

Under conditions of nutrient enrichment and intense herbivory, algal productivity may be high while biomass remains low (Hatcher and Larkum 1983). Our results demonstrate that current rates of herbivory by sea urchins, fish, and turtles maintain all algal groups closely cropped and may therefore be able to consume increases in algal production. This grazing disturbance, in turn, limits the establishment of macroalgae (Lewis 1986, Williams *et al.* 2001, Paddock *et al.* 2006), thereby implying that the current system is relatively resilient to change (as indicated by Kaloko's O/C ratio). Indeed, it is the synergy of these three herbivorous groups that makes Kaloko an interesting case study. The 'redundancy' in herbivory at Kaloko stands in contrast to areas of the Caribbean, where sea urchin biomass remains low 20 years after the region-wide loss of the key echinoid herbivore to disease (Mumby *et al.* 2006b) and where, high fishing pressure may have limited the ability of herbivorous fish to maintain a high proportion of reef area free of macroalgae. Some evidence suggests that even robust herbivorous fish populations may be capable of maintaining only 50 % to 65 % of the substratum in a cropped state (Williams *et al.* 2001). Although herbivorous fish may be capable of increasing their grazing rates and/or population sizes in response to higher algal production, evidence for this in the published literature is limited (McClanahan *et al.* 1999, Williams *et al.* 2001, Garpe *et al.* 2006). Moreover, herbivorous fish, with the exception of *Naso* spp. (Choat *et al.* 2002), all prefer turf algae over other algal resources, and frequently avoid macroalgae (Bellwood

and Choat 1990, Bruggemann *et al.* 1994). Turtles and sea urchins, however, commonly feed on macroalgae, thus highlighting their respective roles in upholding reef resilience (Nystrom 2006).

(ii) *increased nutrient delivery to the reef system with increase in fishing pressure*

Herbivorous fish and sea urchins both play different and complementary roles in maintaining low algal cover on reefs in the face of disturbance (e.g., Morrison 1988). Under a scenario of increased fishing pressure, model parameterization indicates that sea urchin abundance may increase as a direct response to more abundant forage on the reef and reduced predation pressure due to harvesting of the urchins' predators. Sea urchins, when abundant, can have a considerable impact on benthic ecology. Healthy populations of sea urchins have been associated with reductions in macroalgal cover and increased coral recruitment (Edmunds and Carpenter 2001, Carpenter and Edmunds 2006). Typically, sea urchins will consume a greater diversity of algae than herbivorous fish and, as such, they will be more effective than the latter at controlling algal growth in the event of increased nutrient levels. Alternatively, as some species of echinoids can remove a large amount of calcium carbonate (CaCO_3) while foraging (Hutchings 1986, Carreiro-Silva and McClanahan 2001), an overabundance of sea urchins can lead to rapid erosion of the reef framework (McClanahan and Kurtis 1991, Bak 1994, Mapstone *et al.* 2007). For example, *Echinothrix diadema* and *Echinometra mathaei* typically erode 20 % of the calcium carbonate accreted (Carreiro-Silva and McClanahan 2001). However, the relative contributions of grazing and bioerosion are species-dependent. The predominant browsing by *Tripneustes gratilla* predominantly suggests that this species would have less impact on the reef framework (Mills *et al.* 2000).

Currently, sea urchin densities are greatest in the shallows, while reef fish dominate grazing processes at depth. Higher fishing pressure may reduce fish grazing intensity on deeper reef sections. In response to reduced predation and increased forage availability, sea urchins could increase in abundance at greater depths. Similarly, green turtles may also displace some of their foraging

activities to deeper reef areas to take advantage of increased algal biomass (i.e., profitable, high-risk microhabitat *sensu* Heithaus). Increases in algal biomass would further be exacerbated if mixing carries nutrients to those deeper sections of the reef.

4.4.4 Conclusions

The model presented allowed an evaluation of the trophic linkages and flows on a Hawaiian reef. This study is unique in its detailed analysis of herbivory levels and focus on the role of herbivores to determine whether a given functional group, in this instance green turtles, is at carrying capacity. Integration of additional quantitative field data on biomass, distribution, consumption rates, and diet selection of the three herbivore groups would clarify the proportion and type of algae consumed by sea urchins and green turtles versus herbivorous fish on a Hawaiian reef and further elucidate their respective roles in, and contribution to, reef resilience (Nystrom and Folke 2001, Bellwood *et al.* 2004).

Table 4.1 - Trophic parameters for all functional groups of the balanced Kaloko-Honokōhau National Historical Park (Kaloko) model. Outputs from the balanced model are presented in italics. B = biomass; TL= Trophic level; P/B= Productivity biomass ratio; Q/B = consumption rate; EE= Ecotrophic efficiency; P/Q Production to consumption ratio or gross efficiency; P/R= Production to respiration ratio. MIF = Mobile Invertebrate Feeders; SIF = Sessile Invertebrate Feeders; Zoo = Zooplanktivorous fish; CCA = Crustose Coralline Algae

		TL	B	P/B	Q/B	EE	P/Q	P/R	Catches
Group name			(t/km ²)	(/year)	(/year)				(t/km ² /year)
1	Spinner dolphins	3.21	2.740	0.151	11.519	0.007	0.013	0.017	
2	Monk seals	3.89	0.179	0.121	11.508	0.033	0.011	0.013	
3	Sea birds	3.17	0.002	0.127	76.515	0.012	0.002	0.002	
4	Rays	3.15	4.233	0.200	3.100	0.002	0.065	0.065	
5	Sharks and jacks	3.53	0.070	1.058	5.100	0.453	0.207	0.35	0.030
6	Hawksbill sea turtles	3.18	0.054	0.100	3.500	0.066	0.029	0.029	
7	Green sea turtles	2.00	1.591	0.109	6.764	0.039	0.016	0.021	
8	Reef fish - piscivores	3.39	1.730	0.615	6.121	0.527	0.100	0.144	0.003
9	Reef fish - herbivores	2.02	20.335	1.400	27.149	0.205	0.052	0.069	0.162
10	Reef fish - corallivores	2.60	0.542	2.100	12.918	0.547	0.163	0.255	
11	Reef fish - detritivores	2.00	2.260	1.900	32.272	0.282	0.059	0.079	0.018
12	Reef fish - MIF	3.13	9.761	0.950	8.108	0.394	0.117	0.172	0.130
13	Reef fish - SIF	2.84	0.544	1.700	9.581	0.224	0.177	0.285	
14	Reef fish - Zoo	2.85	3.046	1.450	13.378	0.585	0.108	0.157	0.004
15	Urchins	2.00	280.000	0.484	8.547	0.056	0.057	0.076	
16	Crown-of-thorns	2.59	0.117	0.411	9.000	0.007	0.046	0.061	
17	Benthic InvtS	2.18	42.538	2.910	15.250	0.950	0.191	0.313	
18	Corals	1.58	130.000	0.140	2.100	0.594	0.067	0.075	
19	Octocoral	2.07	2.900	0.200	4.630	0.484	0.043	0.054	
20	Macroalgae	1.00	22.691	9.824	-	0.925	-	-	
21	CCA	1.00	37.818	1.770	-	0.358	-	-	
22	Turf algae	1.00	128.780	19.000	-	0.942	-	-	
23	Turf algae_java bench	1.00	3.065	25.000	-	0.921	-	-	
24	Zooplankton	2.02	1.240	219.000	949.000	0.979	0.231	0.625	
25	Phytoplankton	1.00	3.290	325.458	-	0.984	-	-	
26	Detritus	1.00	100.000	-	-	0.694	-	-	

Table 4.2 - Diet composition matrix for the functional groups in the balanced model for Kaloko. Shaded cells indicate diet proportion < 0.001

Prey	Predator								
	1	2	3	4	5	6	7	8	9
1 Spinner dolphins	-	-	-	-	0.008	-	-	-	-
2 Monk seals	-	-	-	-	0.002	-	-	-	-
3 Sea birds	-	-	-	-		-	-	-	-
4 Rays	-	-	-	-		-	-	-	-
5 Sharks and jacks	-	-	-	-	0.010	-	-	-	-
6 Hawksbill sea turtles	-	-	-	-	0.001	-	-	-	-
7 Green sea turtles	-	-	-	-	0.019	-	-	-	-
8 Reef fish - piscivores	-	0.200	-	-	0.110	-	-	0.010	-
9 Reef fish - herbivores	-	0.050	-	-	0.206	-	-	0.400	-
10 Reef fish - corallivores	-	-	-	-	0.040	-	-	0.050	-
11 Reef fish - detritivores	-	-	-	-	0.085	-	-	0.100	-
12 Reef fish - MIF	-	0.080	-	-	0.120	-	-	0.200	-
13 Reef fish - SIF	-	-	-	-	0.062	-	-	0.010	-
14 Reef fish - Zoo	0.010	-	0.010	-	0.051	-	-	0.100	-
15 Urchins	-	-	-	-	0.010	-	-	-	-
16 Crown-of-thorns	-	-	-	-	0.001	-	-	-	-
17 Benthic Invertebrates	0.190	0.107	0.578	-	0.070	0.894	-	0.129	0.004
18 Corals	-	-	-	-	-	0.001	-	-	0.001
19 Octocoral	-	-	-	-	-	-	-	-	-
20 Macroalgae	-	-	-	-	-	-	0.001	-	0.050
21 Crustose Coralline Algae (CCA)	-	-	-	-	-	-	-	-	-
22 Turf algae	-	-	0.010	-	-	-	-	-	0.782
23 Turf algae_java bench	-	-	-	-	-	-	0.998	-	-
24 Zooplankton	-	-	0.001	0.010	0.050	0.005	0.001		0.013
25 Phytoplankton	-	-	0.001	-	-	-	-	-	-
26 Detritus	-	-	0.001	-	0.005	-	-	-	0.150
27 Import	0.800	0.563	0.399	0.990	0.150	0.100	-	-	-

Table 4.2 - cont.

		Predator											
		10	11	12	13	14	15	16	17	18	19	24	
Prey													
1	Spinner dolphins	-	-	-	-	-	-	-	-	-	-	-	
2	Monk seals	-	-	-	-	-	-	-	-	-	-	-	
3	Sea birds	-	-	-	-	-	-	-	-	-	-	-	
4	Rays	-	-	-	-	-	-	-	-	-	-	-	
5	Sharks and jacks	-	-	-	-	-	-	-	-	-	-	-	
6	Hawksbill sea turtles	-	-	-	-	-	-	-	-	-	-	-	
7	Green sea turtles	-	-	-	-	-	-	-	-	-	-	-	
8	Reef fish - piscivores	-	-	-	-	-	-	-			-	-	
9	Reef fish - herbivores	-	-	0.010	-	-	-	-			-	-	
10	Reef fish - corallivores	-	-	0.001	-	-	-	-			-	-	
11	Reef fish - detritivores	-	-		-	-	-	-			-	-	
12	Reef fish - MIF	-	-	0.010	-	0.010	-	-			-	-	
13	Reef fish - SIF	-	-	0.001	-		-	-			-	-	
14	Reef fish - Zoo	-	-	0.010	-	0.009	-	-			-	-	
15	Urchins	-	-	0.085	0.032	-	-	-			-	-	
16	Crown-of-thorns	-	-	-	-	-	-	-	-		-	-	
17	Benthic Invertebrates	0.074	-	0.814	0.420	0.100	-	-	0.046		-	-	
18	Corals	0.865	-	0.005	0.450	-		0.961			-	-	
19	Octocoral	-	-	-	0.025	-	-	0.038			-	-	
20	Macroalgae	-	-	0.001	0.001	0.001	0.070	-	0.017		-	-	
21	Crustose Coralline Algae (CCA)	-	-	-	-	-	0.010	0.001	-		-	-	
22	Turf algae	0.050	0.300	0.032	0.050	0.050	0.745	-	0.098		-	-	
23	Turf algae_ Java bench	-	-	-	-	-	0.025	-	-		-	-	
24	Zooplankton	0.011	-	0.030	0.023	0.316	-	-	0.120	0.500	0.350	0.020	
25	Phytoplankton	-	0.005	-	-	0.050	-	-	0.120	0.100	0.380	0.800	
26	Detritus	-	0.695	0.001		0.014	0.150	-	0.598	0.330	0.250	0.175	
27	Import	-	-	-	-	0.450	-	-	-	0.070	0.020	0.005	

Table 4.3 - Summary of outputs from the Ecological Network Analysis

Parameter	Value	Unit
Sum of all consumption	5,332.03	t/km ² /year
Sum of all exports	520.07	t/km ² /year
Sum of all respiratory flows	3,477.31	t/km ² /year
Sum of all flows into detritus	1,700.15	t/km ² /year
Total system throughput	11,030.00	t/km ² /year
Calculated total net primary production	3,895.09	t/km ² /year
Total primary production/total respiration	1.12	
Total biomass (excluding detritus)	699.53	t/km ²
Total catches	0.35	t/km ² /year
Mean trophic level of the catch	2.59	
Throughput cycled (excluding detritus)	54.52	t/km ² /year
Finn's cycling index	6.13	% of total throughput
Ascendency	31.50	%
Relative overhead (O/C)	68.50	%

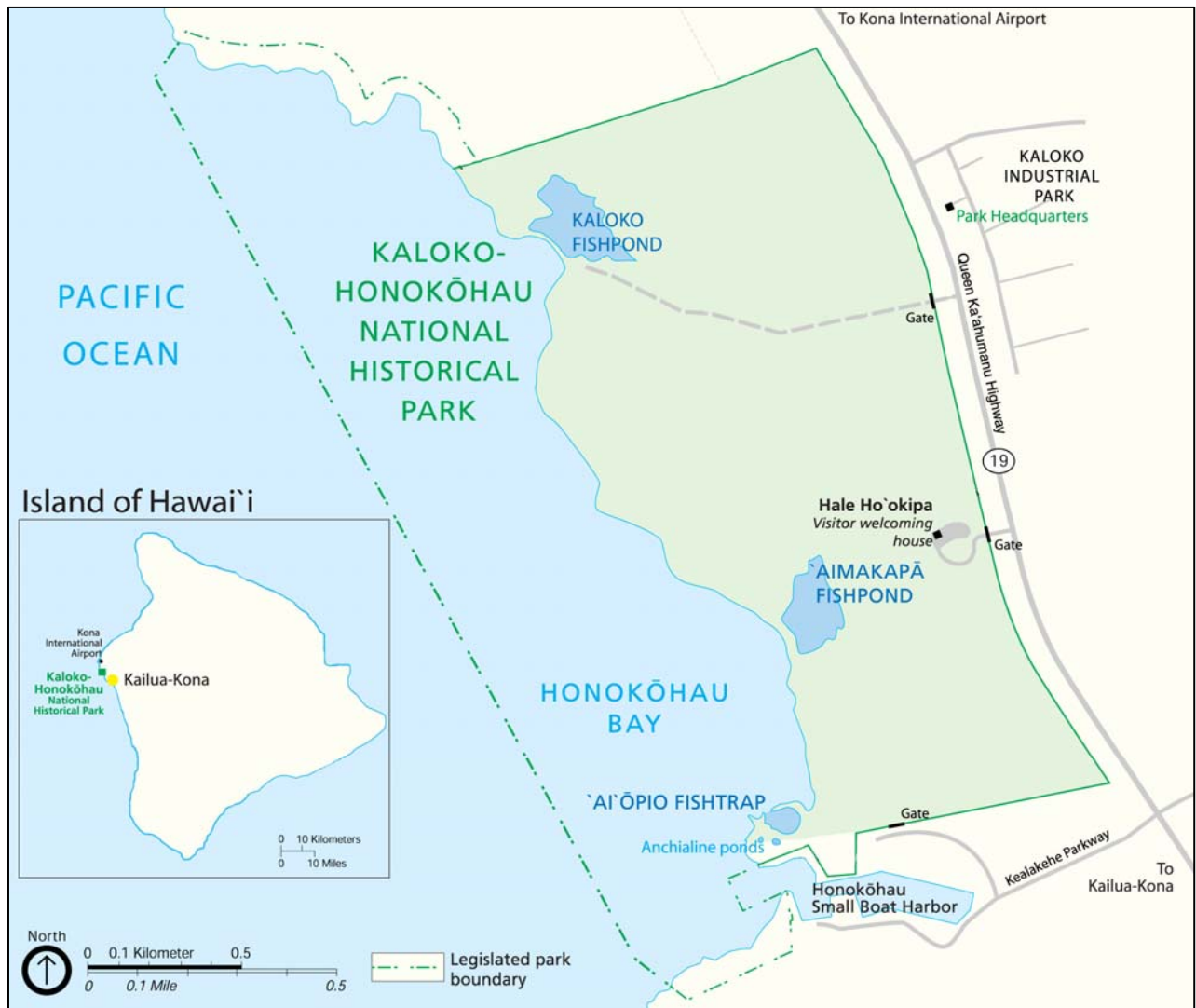


Figure 4.1 - Map of Kaloko-Honokōhau National Historical Park (Kaloko) (modified from www.nps.gov with permission from S. Beavers).

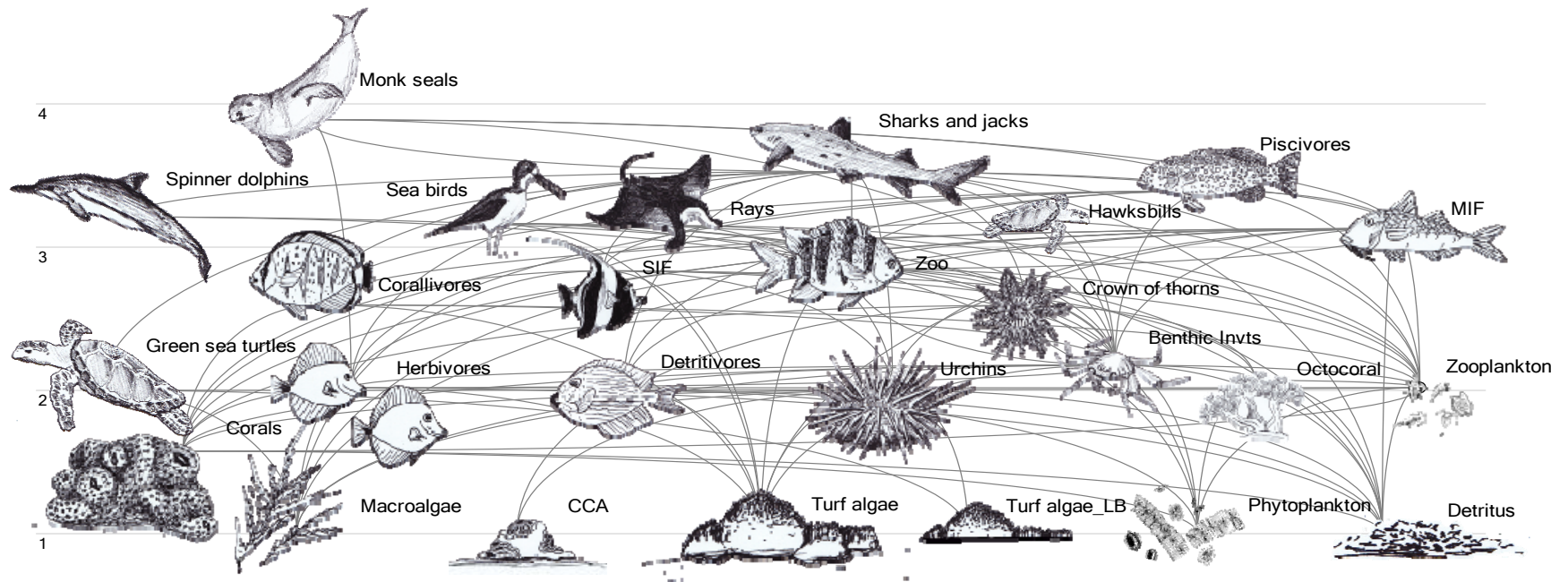


Figure 4.2 - Graphical representation of trophic flows within the Kaloko reef ecosystem. Each functional group is identified here by an illustration (© M. Bailey); where relevant, an image of a species representative of its guild is depicted. Images are not drawn to scale or proportional to the group's biomass. The light grey horizontal lines and associated numbers represent trophic levels; lines connecting individual functional groups represent trophic links. Zoo = Zooplanktivorous fish; MIF = Mobile Invertebrate Feeding fish; SIF = Sessile Invertebrate Feeding fish; Turf_{LB} = turf growing on the lava bench area; CCA = Crustose Coralline Algae; Benthic Invts = Benthic invertebrates.

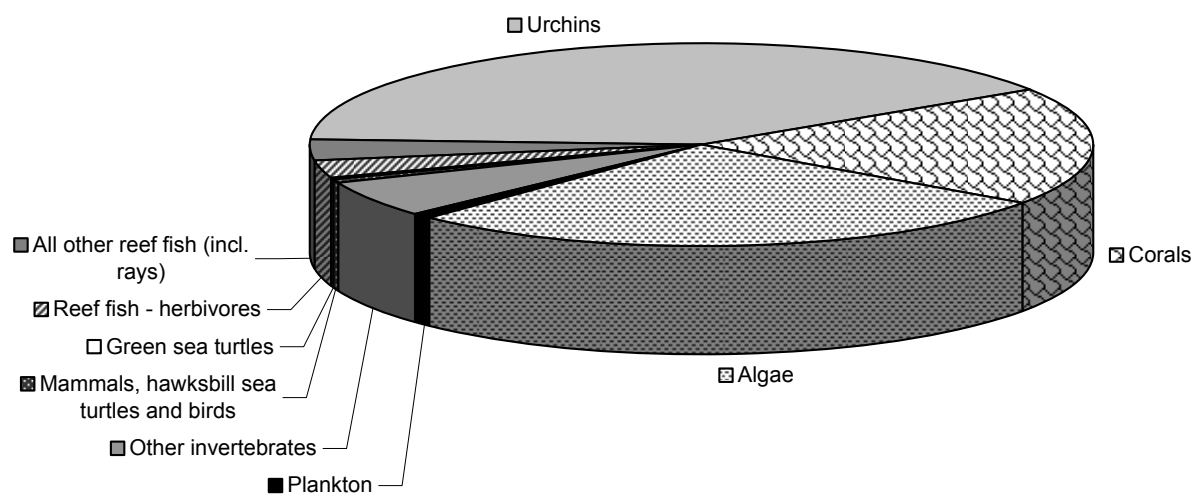


Figure 4.3 - Proportions (%), in terms of biomass ($t \cdot km^{-2}$) of aggregated functional groups at Kaloko.

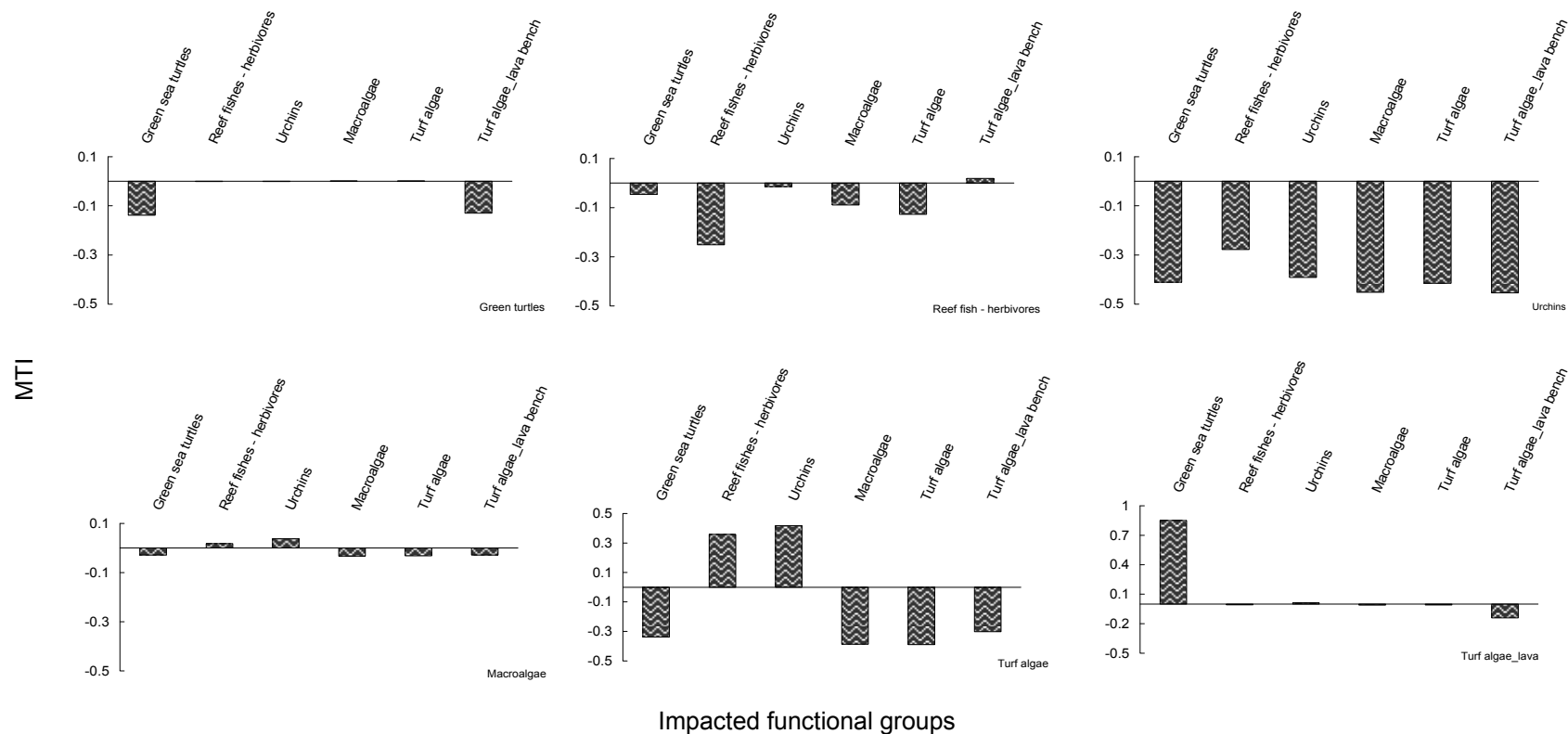


Figure 4.4 - Mixed trophic impact analysis for herbivores at Kaloko. Impacts of increases in the biomass of a particular group (impacting) on another (impacted), resulting in an increase in the latter's biomass, are recorded as a positive on the y-axis. Impacts resulting in a decline of the impacted group are recorded as a negative value. Group names along the upper x-axis represent the impacted groups. The impacting group is indicated on the lower right of individual graphs.

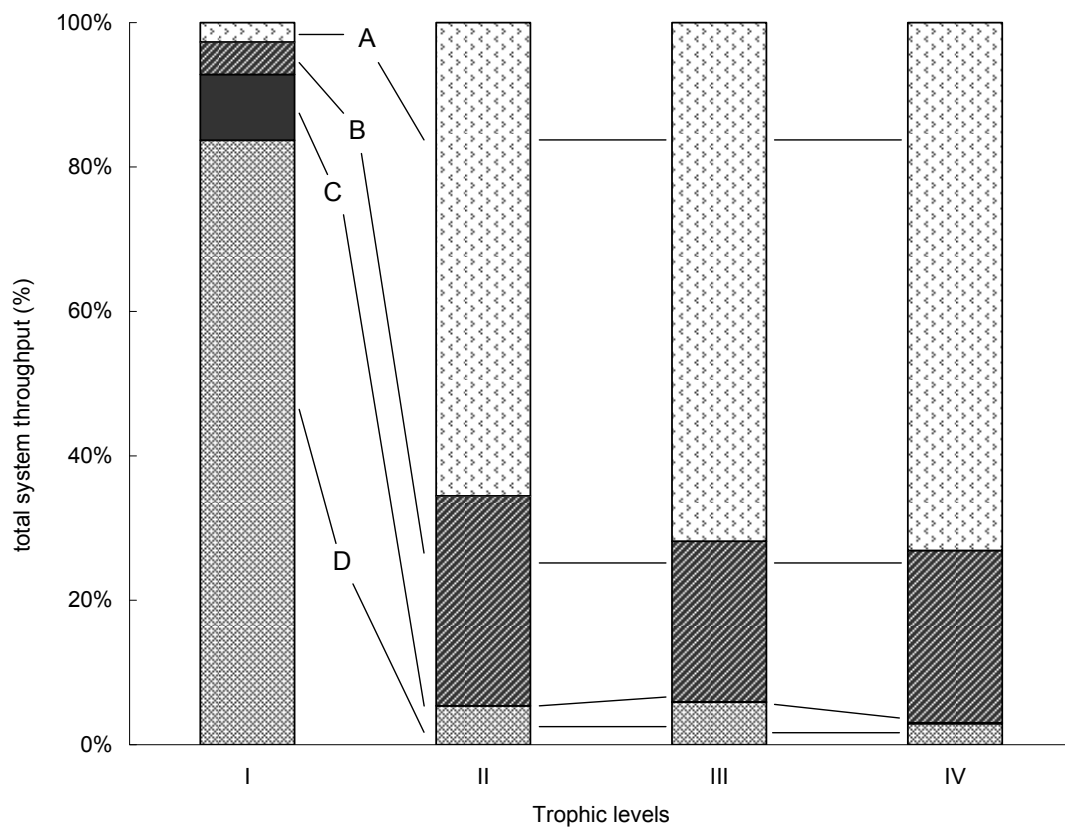


Figure 4.5 - Fate of total system throughput (A = Respiration, B = Flow to detritus, C = Export, D = Consumption by predator) in percentage-per-integer trophic level.

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5. Regional-scale seagrass habitat mapping in the wider Caribbean using Landsat sensors: Applications to conservation and ecology⁴

5.1 Introduction

Seagrass are submerged flowering plants (angiosperms) that can form dense beds in shallow subtidal, mostly clear and sheltered, soft-bottomed marine and estuarine environments (Phillips and Menez 1988). These ‘seagrass meadows’ are important tropical, temperate, and subarctic coastal habitats (Hemminga and Duarte 2000, den Hartog and Kuo 2006), covering the equivalent of approximately 0.05 - 0.15 % of the surface area of the oceans globally (Spalding *et al.* 2003). By providing substratum for epiphytic algae, shelter for invertebrates and fish, and foraging areas for a variety of

⁴ A version of this chapter has been published. Wabnitz C.C.C., Andréfouët S., Torres-Pulliza D., Müller-Karger F.E., and Kramer P.A. (2008) Regional-scale seagrass habitat mapping in the wider Caribbean region using Landsat sensors: Applications to conservation and ecology *Remote Sensing of Environment* 112: 3455-67

organisms, they significantly contribute to the biodiversity of coastal waters (Williams and Heck 2001, Duffy 2006). The combined productivity of seagrass and epiphytic algae rank them among the most productive systems on Earth (Duarte and Cebrián 1996, Duarte and Chiscano 1999). These meadows also serve as critical breeding and nursery grounds for juvenile stages of many economically and ecologically important species (Beck *et al.* 2003, Heck *et al.* 2003, Dahlgren *et al.* 2006, Gillanders 2006).

Established in coastal zones, seagrass beds are inherently dynamic systems prone to natural physical disturbance, particularly in temperate regions (Fonseca *et al.* 2002). However, changes or losses in abundance, species composition, structure, and extent have commonly resulted from activities such as eutrophication, overfishing, and habitat alteration or destruction (Short and Wyllie-Echeverria 1996, Duarte 2002). Until recently, relatively little attention had been paid to the impacts of human activities on seagrass food webs (Jackson 2001, Duarte 2002), with most studies focusing on how physical disturbance alters the structure and function of the seagrass habitats themselves (Duarte 2002). The presence of green turtles (*Chelonia mydas*) may have had substantial ecological and evolutionary effects: increasing the productivity of seagrass in the same way as grazers in terrestrial grasslands (McNaughton 1979, Pandolfi *et al.* 2003, Moran and Bjorndal 2005, 2007). Changes in temperature, nutrient levels, and salinity, as well as a 93 - 97 % reduction in the Caribbean green turtle population compared to its size prior to human contact (Jackson *et al.* 2001), have been implicated in die-offs of seagrass throughout the region (Robblee *et al.* 1991, Jackson 1997, Fourqurean and Robblee 1999). Overall, anthropogenic impacts have contributed to seagrass now ranking among the most threatened of marine habitats (Green and Short 2003, Lotze *et al.* 2006, Orth *et al.* 2006).

Given ongoing coastal zone development around the globe, it is imperative to design and implement effective ways to protect coastal resources. Specifically, at the Fifth World Parks Congress (WPC) in

2003, the recommendation was made to develop extensive networks of Marine Protected Areas (MPAs) that “include strictly protected areas [amounting] to at least 20 - 30 % of each habitat” by 2012. However, exact predictions of the potential status of seagrass in the future and best ways to protect them are hampered - chiefly by the absence of consistent and reliable information concerning the present extent of this habitat. Similarly, current carrying capacity estimates of green turtles for the Caribbean (16 - 586 million) are based on only a very rough idea of seagrass extent thought to be available for foraging (Jackson *et al.* 2001).

A literature review conducted for this study suggests that there are many site specific studies and records of seagrass bed extent and distribution for the wider Caribbean Region (WCR). However, with few exceptions (e.g., Puerto Rico and the U.S. Virgin Islands), relevant documents are difficult to access and rarely, or poorly, document mapping methods or accuracies. Digital maps in GIS formats are often unavailable, or their use restricted. The only existing database generating a global overview was developed by the United Nations Environment Program-World Conservation Monitoring Centre (UNEP-WCMC) in 2003. The resulting “*World Atlas of Seagrasses*” was the first synthesis of the distribution and status of seagrass habitat at that scale (Green and Short 2003). However, direct habitat maps (i.e., chiefly derived from remotely sensed data), which provide the most accurate data on habitat distribution, were only available for a very limited subset of the world. The majority of geographic information thus falls into two main categories: (i) interpolation of expert knowledge and observations; and (ii) point-based samples, which are useful in providing information regarding species presence, but give no information as to actual seagrass extent (Spalding *et al.* 2003). As a result, the worldwide UNEP-WCMC database, including the Caribbean section, suffers from substantial inaccuracy (vast commission or omission errors (i.e., including a seagrass pixel in a non-seagrass area and vice versa)), poor spatial representation, and limited spatial resolution.

Satellite remote sensing provides a tool to develop a reliable, methodologically consistent database of seagrass extent over large regions, in a cost-effective, objective, and timely fashion (Mumby *et al.* 1999, Krause-Jensen *et al.* 2004, Balmford *et al.* 2005). Habitat mapping on the scale of a region poses new environmental and methodological challenges rarely addressed in tropical initiatives to date (but see the Millennium Coral Reef Mapping Project (Andréfouët and Guzmán 2005, Andréfouët *et al.* 2006)). First, the diversity of environments (estuaries, cross-shelf areas, banks, atolls, and narrow continental reef terraces), the heterogeneity of habitats, and the vast extent of the targeted region imply that expertise and field data are seldom available with comparable quality, and often cannot be acquired due to their prohibitive costs. Second, high-resolution regional mapping requires hundreds of Landsat images to achieve complete cloud-free coverage. Working with such a large dataset presents substantial calibration problems in marine environments, and complicates or even prevents the use of standard analytical and statistical image processing approaches (Andréfouët *et al.* 2001, Thome 2001, Teillet *et al.* 2006).

This paper reports on the approach used to map seagrass beds using consistent methods, throughout the WCR, given the constraints associated with working at large spatial scales. First, I provide results obtained for well-documented sites throughout the region, where cross-comparison with ancillary data allowed for direct or indirect measures of accuracy. Second, I outline the implications of my findings for mapping seagrass beds in a cost effective fashion throughout the WCR. Finally, I discuss the relevance of the products presented and results for: (a) generally advancing future biodiversity research, conservation, and management in the region, and (b) specifically re-assessing carrying capacity estimates for green turtles.

5.2 Data and methods

5.2.1 Landsat data and Millennium Coral Reef Mapping Project (MCRMP)

The archive of Landsat 7 Enhanced Thematic Mapper Plus (ETM+) images compiled by the MCRMP (Andréfouët *et al.* 2006) constituted the main data set used for seagrass mapping in this study. Most images in the database were acquired between 2000 and 2002. One to six images were available for each Landsat scene (path-row) intersecting coastlines. Where clouds were persistent, several Landsat Thematic Mapper 5 (TM) images, acquired mainly in the early 1990s, were also available (and often used). Images were all re-sampled to UTM WGS 84 projection, at 30-m spatial resolution. Only the first four bands were considered for the work presented here (blue, green, red, and near infra-red).

For each image path-row, MCRMP created polygons that characterise and delineate coral reef geomorphology according to a typology that is globally relevant (for more detailed information regarding the methodology applied see Andréfouët *et al.* (2006)). Individual Millennium classes are easily associated with a given set of environmental attributes (zonation, depth, hydrodynamic exposure), which favor the development of some habitats (e.g., seagrass), but not others. Although linkages between ‘geomorphology’ and ‘habitats’ have not been exhaustively quantified to date, preliminary analysis for several Caribbean sites where detailed habitat maps have been produced confirm that Millennium polygons can be used for *a priori* contextual editing (see Section 5.2.3 Image processing). By doing so, areas of the image unlikely to contain seagrasses are excluded, avoiding misclassification in subsequent analyses.

5.2.2 Study areas

Table 5.1 lists the 19 focal areas of the WCR considered in this study (see also Figure 5.1). These sites were chosen based on the availability of independent information to: (a) compare obtained accuracies with published values and qualitatively contrast available thematic maps with products from this study; or (b) assess the accuracy of seagrass extent estimates derived from Landsat data using IKONOS imagery and/or field data points. The sites represent various levels of geomorphological complexity typical of the region.

5.2.3 Image processing

For each site within a Landsat image, polygons were constructed that encompassed one, several, or all MCRMP classes with any likelihood of containing seagrass (see Figure 5.2 and Figure 5.3). For instance, one is unlikely to find seagrass within the deeper classes and on several exposed ‘reef’ areas (i.e., forereefs). The degree to which MCRMP classes were merged depended on the geomorphological complexity of the site.

A priori contextual editing has been reported by Andréfouët *et al.* (2003) and Andréfouët and Guzmán (2005) as a relatively simple and efficient way to enhance classification richness and improve accuracy of results. The method consists in applying a contextual decision rule throughout the image to sets of habitats which have similar spectra, but different yet predictable physical environments (Groom *et al.* 1996). By removing beforehand image areas that may create spectral confusion for the classes of interest, the classification process is much more accurate (Andréfouët *et al.* 2003). Given the scale of the area covered, this straight forward and reliable approach was favored here over the use of water column correction techniques, or the construction of depth-invariant indices. However, I am well aware of the benefits of the latter methodology (Andréfouët *et*

al. 2003), and in the few cases where polygons include a large number of habitats and significant depth range (e.g., wide cross-shelf areas), my assumption may not hold. In such instances, low map accuracies indicate Caribbean coastal configurations where bathymetric corrections would be required. Elsewhere, to quantify the validity of my assumption, I compared my results with those obtained from independent studies that corrected for the effects of the water column and published accuracy values.

For very large continuous areas spanning several Landsat scenes (e.g., Bahamas, Belize), images were inter-calibrated and normalized prior to classification (Figure 5.2). For this, digital counts (DN) were transformed into at-sensor reflectance using the gain/bias coefficients available for each image. A dark pixel correction scheme was then applied to remove part of the atmospheric effect. Specifically, subsequent to Rayleigh correction (Zhang *et al.* 1999), a deep-water reflectance value (average value of pixels sampled in ‘deep water’ in the short-wave infra-red band) was subtracted from pixels in all other bands, assuming a white aerosol signal (Zhang *et al.* 1999, Hu *et al.* 2001). Finally, using one arbitrary reference image, the next Landsat scene in the composition was adjusted using an empirical line calibration approach, based on training areas that have not changed between the different images (i.e., according to shapes of dense seagrass and sand patches, cf. Andréfouët *et al.* (2001)). This was possible since all Landsat scenes overlap neighboring scenes and I assumed stable conditions between the acquisitions of images (less than two years). All images were joined in a mosaic, which was expanded one image at a time. For all images, where necessary, clouds and shadows were masked out prior to classification.

Image classification training regions (e.g., sand, coral, and seagrass of different densities) were mostly selected by visual-interpretation, due to the lack of extensive field data for the majority of polygons. Generally, three to five classes were generated, but no more than eight, depending on intra-polygon spectral variability. Standard supervised classification, using ENVI ®’s Maximum

Likelihood classifier, was conducted for each image to produce a habitat map. Individual seagrass classes were subsequently merged to a maximum of three categories according to the density of the submerged vegetation: (i) dense (70 - 100 % cover); (ii) medium-dense (30 - 70 %); and (iii) sparse (<30 %). These closely correspond to categories derived for seagrass cover in other studies within the region (e.g., Mumby and Harborne 1999). All other habitat classes were merged into a generic 'other' class.

The study aimed to map overall seagrass presence/absence and density of cover throughout the region, without reference to particular seagrass species. However, turtle grass (*Thalassia testudinum* Banks ex König) is considered to be the most common species off the coast of Florida and throughout the Caribbean. *Halodule wrightii* Kütz. and *Syringodium filiforme* Aschers. are the other two species typically encountered, albeit at lower densities; and they are generally considered to be pioneer species (Gallegos *et al.* 1994).

5.2.4 Accuracy assessment

The accuracy of classified images is generally assessed using a set of geo-referenced field data (Lillesand *et al.* 2004). However, ground-truth data that are adequately documented, of comparable quality, and that uniformly cover all areas of interest, present a substantial challenge for large scale mapping efforts. Such information is not uniformly available for seagrass beds throughout the WCR. Therefore, several strategies were adopted as proxies (Figure 5.2):

- (i) Data were gleaned from non peer-reviewed literature (e.g., consultancy reports, newspaper articles, electronic information, and government reports). The database developed from this information contains references of disparate quality and level of detail. Only a handful of these references provided detailed thematic maps or geographic coordinates of point observations associated with specific habitat classes. Only information gathered for Roatán Island

(Honduras) was considered of sufficient quality to enable accuracy assessment of our product (Porcher *et al.* 2001a, 2001b).

- (ii) Maps were extracted from peer-reviewed articles. Documented areas with published thematic maps allowing for qualitative comparisons with our products included Roatán (Maeder *et al.* 2002), Los Roques (Schweizer *et al.* 2005), Lee Stocking Island (Armstrong 1993, Call *et al.* 2003, Louchard *et al.* 2003), Martinique and Guadeloupe (Chauvaud 1997, Chauvaud *et al.* 1998, 2001), Glovers Atoll (Andréfouët *et al.* 2003), Alacranes (Bello-Pineda *et al.* 2005), Vieques Island (Hernández-Cruz *et al.* 2006, Shapiro and Rohmann 2006), Puerto Rico (Shapiro and Rohmann 2005), and Columbia (Díaz *et al.* 2003, Díaz and Gómez-López 2003). For these, accuracy values were generally reported. Although a number of other peer-review articles report on their seagrass mapping efforts in the Caribbean, the absence of available habitat maps precluded direct qualitative comparisons (e.g., Luczkovich *et al.* 1993, Mumby *et al.* 1998, Mumby and Edwards 2002, Garza-Perez *et al.* 2004).
- (iii) *in situ* data from mapping projects undertaken by the National Oceanic and Atmospheric Administration (NOAA) for coastal waters under US jurisdiction (NCCOS 2001) were downloaded from NOAA's website. Under this initiative, habitat maps were created by visual interpretation of aerial photos. *In situ* data for Puerto Rico and the US Virgin Islands were available as: (a) 'ground-truth' points (large data set, geographically widespread for training); and (b) accuracy assessment data points (estimated at only two locations within the project area). The accuracy of our seagrass products was assessed using the larger 'ground-truth' dataset.
- (iv) Habitat survey points collected by S. Andréfouët and P. Kramer between 2001 and 2003 were collated into a single database (see Table 5.2). The dataset, providing seagrass presence/absence observations, spans San Blas (Panama), Los Roques (Venezuela), and Lee Stocking and Andros Islands (Bahamas).

- (v) 'Virtual ground truthing' points were derived from high spatial resolution IKONOS imagery (Figure 5.4). High resolution images, such as aerial photographs, allow enhanced visual-interpretation of many benthic features, including seagrass beds (cf. NOAA's approach). Although confusion with other submerged aquatic vegetation types remains possible, this method allows the practitioner to locate points (or polygons) within specific habitat types effectively and with a high level of confidence - even at depth. IKONOS images, collected between 2000 and 2003, were obtained from the National Aeronautics and Space Administration (NASA) Data Buy program archive. Several of these images had already been processed for habitat mapping purposes, with the resulting products and analyses published (e.g., Mumby and Edwards 2002, Andréfouët *et al.* 2003). To my knowledge, the use of other scenes is reported here for the first time.
- (vi) *in situ* points collected by contributors to the study by Andréfouët *et al.* (2003) were collated into a separate dataset and augmented for this study by visual-interpretation (Figure 5.4). Sites processed included: Boca Paila, Majahual, and Akumal (Mexico); Andros and Lee Stocking Island (Bahamas) (Figure 5.5); Roatán (Honduras); Glovers Atoll, Lighthouse Atoll, lagoonal patch reefs and two sites off the barrier reef (Belize).

In general, the time lag between the acquisition of ground observations, Landsat images, and IKONOS images ranged between a few months and a year. It was therefore assumed that, for the most part, the delineation of seagrass bed extent would not have dramatically changed during that timeframe.

The accuracy of habitat maps produced here was determined from confusion matrices elaborated using data obtained under (iii), (iv), (v), and (vi) above. Such a matrix allows for the calculation of specific accuracy measures including the overall accuracy and user's and producer's accuracies (Congalton 1991). Overall accuracy is computed by dividing the total number of correctly classified

pixels by the total number of pixels in the matrix (Congalton 1991). The 'producer's accuracy' refers to the probability of a reference pixel being correctly classified (i.e., measures the error of omission); whereas the 'user's accuracy' indicates the probability that a pixel classified on the map represents that category on the ground (i.e., measures the error of commission) (Congalton and Green 1999). An estimate of the Kappa coefficient, which quantifies the improvement of the classified map over a random class assignment, is also provided (Congalton and Green 1999, Foody 2002).

Locations used for the accuracy assessment spanned the entire WCR and included a large variety of habitat types, depth ranges, and water conditions inherent to the region. Therefore, these estimates were assumed to be representative of accuracies derived for thematic maps produced for the remainder of the Caribbean (ongoing project). NOAA outlined a similar approach to assess the accuracy of their Caribbean products (NCCOS 2001). However, for seagrass beds located in turbid estuaries and large coastal lagoons (e.g., Mexico and Venezuela) this assumption is unlikely to be verified and accuracy assessment of products derived for these areas will require the development of alternative strategies. Such sites were not included in this analysis.

5.3 Results

Confusion matrices derived when using three seagrass classes of variable densities plus one 'other' (all non-seagrass areas) class, showed significant confusion between individual seagrass classes, resulting in low overall accuracy. However, as a whole, 'seagrass' was correctly classified. Consequently, the 'medium' and 'sparse' seagrass classes were merged to form a single 'medium-sparse' class (< 70 % cover) (see discussion for details). Associated ground-truth points were also merged for corresponding accuracy assessments. The 'dense' class (> 70 % cover) was left

unchanged. This improved accuracy, with overall values ranging between 46 % and 77 % (see Table 5.2).

Kappa values were found to vary widely between sites, spanning from 0.00 for a site west of La Parguera, Puerto Rico, to 0.64 for Los Roques, Venezuela (see Table 5.2). Overall accuracy averaged 68 %. Lowest overall accuracies were obtained for the classification of a site west of La Parguera, Puerto Rico (45 %). Highest accuracies were recorded for Akumal, Mexico (87 %) and San Blas, Panama (85 %). Given the local topographic complexity and patterns, thematic maps encompassed only one seagrass class for these two sites. Highest overall accuracy for sites with two distinct seagrass classes was registered at Los Roques, Venezuela (77 %). The ‘other’ class showed high producer accuracies, except for Puerto Rico. At all sites, most misclassifications still occurred between the two seagrass classes and some seagrass pixels that classified as “other”. My products can therefore be considered as conservative seagrass distribution maps (i.e., not overestimating seagrass areas) since very few “other” pixels were classified as seagrass (with the exception of Puerto Rico).

Figure 5.5 and Figure 5.6 show examples of thematic maps produced for two classes of seagrass, and one ‘other’ class for the Bahamas, Los Roques (Venezuela), and Alacranes (Mexico). Seagrass extent at each site is reported in Table 5.3. For comparative purposes, Figure 5.5 also includes current data available for seagrass extent in the Bahamas from UNEP-WCMC. Figure 5.6 includes sites for which qualitative comparisons were drawn with previously published seagrass maps. At these two sites and for areas of Martinique, Guadeloupe, and Roátan (not shown here) the two sets of products showed high consistency in distribution and extent of seagrass meadows.

As existing maps for Alacranes and Los Roques had also been derived from Landsat images, further analysis was undertaken for these two sites. At Alacranes, seagrass beds were predominantly found along the eastern rim of the bank. Minor discrepancies included seagrass beds mapped along the north part of the outer slope and areas within reef passes. Seagrass distribution and extent for my product at Los Roques closely matched those provided by Schweizer *et al.* (2005). Main differences included thinner seagrass margins in my product along the mangrove-lined northern and southeastern portions of the central atoll. While visual comparisons do not constitute quantitative accuracy assessments *per se*, the close agreement between my maps and those produced (a) with significant quantities of ground-truthed data, and (b) using depth correction techniques, provides confidence in the methodology developed for the purposes of this study.

5.4 Discussion

5.4.1 Remote sensing considerations

Accuracies reported here span a broad range of values (46 - 88 %; Table 5.2), but they are comparable to those from previous Landsat-based seagrass mapping efforts. Despite the diverse datasets used to assess the accuracy of thematic maps, values do not reveal any positive or negative bias towards a 'groundtruthing' source. For example, two of the three poorest overall accuracies recorded (Majahual, Mexico, and Belize patch reef), and the best overall accuracy (Akumal, Mexico), were evaluated based on IKONOS image interpretation. For the two areas with highest accuracies, San Blas and Akumal, different sources were used in the assessment: *in situ* and IKONOS respectively.

Overall accuracies achieved in this study are well within the range of values reported in previous studies within the Caribbean, including results obtained using water column correction techniques

(e.g., Schweizer *et al.* 2005 for Los Roques). For most areas, the use of Millennium polygons to guide *a priori* contextual editing emerged as a useful approach to limit misclassifications in the absence of a formal water column correction step. However, the site west of La Parguera (Puerto Rico) stands out as a clear exception. This location is a wide cross-shelf area with a gentle slope from the shore down to a depth of 40 m, and is characterised by a variety of different habitats that are spectrally similar (deep diffuse seagrass, shallow dense seagrass, gorgonian plains, coral escarpment, and hard substrate covered with varying densities of algae). Yet, this mosaic of habitats is included in one single Millennium polygon labelled as ‘shelf slope’. In such instances, the practitioner is therefore faced with the usual challenges of benthic habitat mapping. Application of water column correction as an image pre-processing step to these sites is expected to yield improved accuracies. As a note, the very high accuracy reported by NOAA for Puerto Rico (100 % for submerged vegetation) is for the area of La Parguera itself (NCCOS 2001), characterised by much shallower seas and several distinct Millennium classes which facilitate classification.

Given the scale of the work presented here, it is necessary to put into perspective the different groundtruth data sets employed and the maps produced in previous studies. Although all authors mapped ‘dense’, ‘medium-dense’, and ‘sparse’ seagrass beds according to some comparable threshold of seagrass density, a closer look at individual studies reveals variations in definitions:

- NOAA has a fairly detailed scheme, with 5 seagrass classes, that needed to be interpreted and simplified into three classes of seagrass density (NCCOS 2001);
- *in situ* data for Lee Stocking Island and Andros were semi-quantitative, using an index of cover on a scale from 0 to 5 during the surveys (Andréfouët *et al.* 2003);
- *in situ* data for San Blas made use of a continuous measure of seagrass cover along boat tracks (Andréfouët, unpublished data). The data set thus needed to be broken down by Landsat pixels, resulting in only one class of seagrass density, as variations in cover were very patchy and tended to occur within one Landsat pixel;

- data generated through visual-interpretation of IKONOS imagery, even when trained using well-know sites, may not always generate consistent density categories between sites. Consistency is difficult to maintain because of the variability in sediments and seagrass beds themselves, which may produce different signatures for similar benthic cover and densities. Variations such as leaves colonized by epibionts or calcareous growth, beds temporarily just below or even above the water surface at low tide, and dark background sediments, may all lower the spectral contrast of seagrass blades (Fyfe 2003), complicating the interpretation of densities. Similar challenges apply to categorizing *in situ* data despite measurable field experience (e.g., Lee Stocking Island, Andros, Glovers).

As algae can easily be mistaken for seagrass on Landsat images due to their highly similar spectral signatures (Green *et al.* 2000, Schweizer *et al.* 2005), a brief discussion of how I dealt with the issue follows. All ground-truth data that reported *dominance* (> 70 %) of algae were included in the ‘other’ class. Seagrass beds with varying levels of algae density were included in the appropriate corresponding seagrass class. Although very few ‘other’ pixels were classified as seagrass, seagrass pixels had a tendency to be inappropriately classified as ‘other’. In some instances, availability of several images acquired at different dates for individual Landsat scenes, recorded significant changes in the extent of submerged vegetation over short time periods (Figure 5.7). Since tropical seagrass beds are typically stable over the temporal scale of years, even in the advent of severe storms (but see also Fourqurean and Rutten 2004 and Byron and Heck 2006), these variations are most likely caused by ephemeral changes in algal biomass, and/or cyanobacterial blooms. Accounting for this factor during validation of final products allowed for large errors potentially associated with overestimating the extent of dense seagrass beds to be avoided. In some instances, such as across the shallow Bahama Banks, this type of image comparison constituted a critical aspect of the mapping effort.

High values registered for producer and user accuracies of the 'other' class indicate that the thematic maps do not overestimate seagrass extent. Moreover, confusion between individual seagrass classes explained most of the low accuracy. This is confirmed by the high accuracy results obtained in San Blas and Akumal where only one seagrass class was mapped. In these two focal areas, seagrass beds were primarily located on back reefs and terraces, and were typically small in size. Given the spatial resolution of Landsat images (30 m pixels), it was not possible to confidently discriminate between seagrass patches of different densities and, thus, only one seagrass class was mapped.

Uncertainty in pixel classification (e.g., differentiating between fuzzy 'medium' or 'sparse' classes given slight differences in class definitions) led me to collate the initial three-class seagrass typology into a two-class seagrass scheme. Although this approach may not be entirely satisfactory for all applications, given the constraints and goals of this study, the methodology adopted is a valuable first attempt at obtaining realistic figures of seagrass extent and distribution across the WCR.

Areas with dense seagrass cover are frequently patchy and narrow. These were generally correctly captured in shape and extent in classified images. Yet ground-truth points for dense seagrass often fell just onto the patch's edge, or just outside the area classified as dense, leading to an incorrect classification assessment for that class. Misregistration of Landsat images, and/or ground-truth points, may partly explain this observation. Landsat image specifications may have up to 250 m geolocation errors (up to 7 pixels) (NASA 2007). My field experience further demonstrates that common errors are due to being off by one to two pixels (30 - 60 m); a distance still large enough to miss small targets defined on IKONOS images or *in situ*. It is usually possible, following personal data collection, to manually correct either images or GPS points to ensure their proper overlap. Here, such adjustments were impossible as data were collected from widely different sources. The problem was less common for medium and sparse seagrass beds, which generally cover wider areas. Areas of very low cover (< 5 %), which includes sandy areas, were generally classified as 'other'.

Since one of my principle mapping objective was to re-estimate green turtle carrying capacity for the Caribbean, accurate mapping of low density seagrass beds was not of primary importance. Optimal turtle foraging grounds tend to consist of dense seagrass beds. I therefore assumed that accurate mapping of dense and medium-dense seagrass beds was an essential first step towards establishing turtle (and other) conservation targets.

Based on these observations, I suggest that thematic maps are both more useful and more valid for spatial analysis than the results of confusion matrices alone may indicate. Consistently higher values could have been achieved had images with high spectral and/or spatial resolution been used to map seagrass extent (Mumby and Edwards 2002, Andréfouët *et al.* 2003, Hochberg and Atkinson 2003). However, data availability and costs justify the use of Landsat images here. As of 2007, IKONOS and Quickbird licensed data cost 15 - 20 US\$ per km² depending on products, availability in archives, or needs for tasking an acquisition. In comparison, an archived copyright-free Landsat 7 image costs 600 US\$, corresponding to a cost of ~ 0.02 US\$ per km². Therefore, although enhancement in accuracies and resolution may be substantial using IKONOS, Quickbird, or hyperspectral data - to date, given acquisition costs - none of these solutions present realistic approaches for large scale mapping efforts.

5.4.2 Implications for conservation

While I recognize that my mapping efforts have limitations, results obtained to date are encouraging given the scale of the achievement, the rapid production of maps applying a consistent and uniform methodology, and the objectives to (a) regionally assist with management and conservation planning targets in a cost effective fashion; and (b) regionally re-assess carrying capacity estimates for green turtles.

Turtles and many fish species may move over large spatial scales and across different environments over the course of their life histories. Providing Caribbean-wide habitat information therefore significantly improves our ability to manage and conserve the goods and services provided by seagrass beds at biologically relevant scales (Olson and Dinerstein 2002, Stevens 2002). Indeed, it has been suggested that effective mapping for successful conservation should be carried out at transboundary (i.e., ecoregional) scale (Beck and Odaya 2001, Lourie and Vincent 2004), with a strong emphasis on methodological consistency. The products may also provide researchers and managers with a useful and much needed (Creed *et al.* 2003) baseline to monitor changes registered in seagrass ecosystems over time due to mounting human pressures on coastal ecosystems (Burke and Maidens 2004), and to develop spatially explicit models of impacts due to disturbances (e.g., Kelly *et al.* 2001). Even for management at a national level, the maps developed through this research can form the basis of efforts targeted at capturing important landscape patterns that may have significant management implications at a more local scale (Fonseca *et al.* 2002, Bell *et al.* 2006).

The average accuracy of 68 % across all sites does not adequately reflect the utility of organizing disaggregated spatial data into consolidated map products. Ultimately, which product is more environmentally relevant (i.e., higher classification accuracy but smaller spatial extent versus lower classification accuracy but larger spatial extent) will depend on the conservation task at hand. In the case of green turtle conservation for instance, deriving a more reliable estimate of seagrass extent represents a critical first step in re-assessing a regional estimate of carrying capacity. This in turn can inform the goals set for population recoveries. In doing so it is noteworthy that the theoretical number of green turtles that could be sustained by present seagrasses might not be consistent with turtle numbers that would assure optimal long-term seagrass productivity. This is clearly demonstrated in the diverse estimates of turtle carrying capacity for the WCR, derived from varying levels of seagrass productivity: from 586 million turtles for highly productive seagrass beds to 39 million in stressed meadows (Bjorndal *et al.* 2000).

5.4.3 Conclusion and perspectives

Recognizing the urgency in establishing enhanced GIS data sets on the spatial distribution of habitats for large scale ecological and conservation applications, this study assessed the feasibility of using Landsat sensors to map seagrass beds effectively and subsequently apply consistent methods throughout the WCR. I processed a total of 40 Landsat 7 (ETM+) images covering regionally representative sites with contrasted sizes, structure, geomorphology, and seagrass bed extent. The results reported here are encouraging for the completion of a WCR-wide map of seagrass habitat using Landsat images, MCMRP coral reef products, and further IKONOS imagery. Such an effort is currently in progress, and builds on the discussion developed here. This is, to my knowledge, the largest such effort worldwide.

Accuracies obtained at individual sites are in agreement with local studies previously published using different methods. Comparison of the regional results also point to where some of the traditional image processing challenges in shallow coastal environments will be the most acute: wide cross shelf areas, such as those around Puerto Rico. Similar environments in the Bahamas, Cuba, and Florida, will require image depth-correction if useful accuracies are to be achieved.

Next steps include the processing of all remaining available images for the region and compiling the results into a GIS layer to facilitate use by the conservation and scientific community. In parallel, further map validation based on local expertise and high resolution images will help to highlight weaknesses and strengths of my products. There are mounting threats facing coastal areas (Burke and Maidens 2004), and significant gaps in existing habitat databases. Therefore, availability of consistent regional seagrass habitat maps for the WCR will assist governments and their partners in developing successful conservation plans. Furthermore, the design employed in this study should

also be useful in other tropical regions where reliable habitat data are critically needed for integrated coastal management purposes.

Table 5.1 - List of sites for which thematic seagrass habitat maps were derived in this paper. Available ancillary data and references on previous remote sensing and habitat mapping work at these same sites are also presented. Where applicable, the type of data used to assess accuracy of my products is indicated.

Focal area	Landsat Path-Row	Accuracy assessment data	IKONOS data	References
Bahamas	13-41, 14-41, 14-42, 13-42, 12-42, 15-43, 14-43, 13-43, 12-43, 11-43, 15-44, 14-44, 13-44, 12-44, 11-44, 10-44, 12-45, 11-45, 10-45, 9-45	IKONOS & in situ	Lee Stocking Island Andros Island. (AUTEC)	Armstrong (1993); Andréfouët <i>et al.</i> (2003); Call <i>et al.</i> (2003), and Louchard <i>et al.</i> (2003)
Belize	19-48, 18-48, 19-49, 18-49	IKONOS	Lighthouse Atoll Glovers Atoll Barrier Reef section Patch Reef section	Andréfouët <i>et al.</i> (2003)
Mexico (Yucatán coast)	20-45, 19-45, 18-45, 19-46, 18-46, 19-47, 18-47	IKONOS	Akumal Boca Paila Mahahual	Andréfouët <i>et al.</i> (2003); Garza-Perez <i>et al.</i> (2004)
Roatán (Honduras)	17-49	IKONOS	Roatán	Maeder <i>et al.</i> (2002)
St Croix (US Virgin Island)	4-48	NOAA		NOAA (2001)
Puerto Rico (south coast)	5-48	NOAA		NOAA (2001)
San Blas offshore banks and islands (Panama)	11-53	in situ		Andréfouët and Guzmán (2005)
Los Roques (Venezuela)	4-52	in situ		Schweizer <i>et al.</i> (2005)
Alacranes Bank (Mexico)	20-45	N/A (published value: 77 %)		Bello-Pineda <i>et al.</i> (2005)
Guadeloupe	1-49	N/A (published value: 95.7 %)		Chauvaud <i>et al.</i> (2001)
Bay du Robert (Martinique)	1-50	N/A (published value: 94 %)		Chauvaud <i>et al.</i> (1998)
Providence Island (Colombia)	14-51	N/A		Díaz <i>et al.</i> (2003)
San Andrés (Colombia)	14-51	N/A		Díaz <i>et al.</i> (2003)

Table 5.2 - Accuracy achieved for two seagrass classes (* with the exception of San Blas and Akumal) and one generic 'other' class using the following data for the assessment: IKONOS imagery, direct ground-truth data collected in situ, and NOAA ground-truth data. n is the total number of points used for each site.

Focal area	Source	n	Accuracy		Dense seagrass (> 70 %)		Medium/Sparse Seagrass (< 70 %)		Other	
			Overall	Kappa	Producer (%)	User (%)	Producer (%)	User (%)	Producer (%)	User (%)
			Accuracy (%)	coefficient						
Lee Stocking Island	IKONOS & <i>in situ</i>	170	71.8	0.48	15.4	50.0	74.0	72.5	86.2	72.3
East Andros	IKONOS & <i>in situ</i>	502	63.3	0.19	41.5	32.3	23.3	50.0	74.1	77.3
Roatán	IKONOS	296	71.3	0.54	65.1	50.0	55.4	64.8	82.7	86.7
Lighthouse Atoll	IKONOS	181	69.1	0.53	25.0	76.5	86.2	53.8	87.3	87.3
Glovers Atoll	IKONOS	120	71.7	0.51	75.0	32.2	31.7	68.5	95.5	87.7
Belize patch reefs	IKONOS	76	64.5	0.05	N/A	N/A	0.0	0.0	96.1	66.2
Belize barrier reef	IKONOS	102	55.9	0.34	33.3	29.6	42.9	85.7	86.1	57.4
Mahahual	IKONOS	54	55.6	0.18	21.8	83.3	0.0	0.0	100	52.1
Boca Paila	IKONOS	87	72.4	0.52	52.4	55.0	57.2	42.1	84.6	91.7
Akumal*	IKONOS	57	87.7	0.46	N/A	N/A	57.1	50.0	92.0	93.9
St Croix	NOAA	294	63.9	0.24	46.8	47.8	24.1	12.3	72.9	83.2
La Parguera	NOAA	81	45.7	0.0	59.4	47.8	100.0	8.3	32.6	60.9
San Blas*	<i>in situ</i>	293	85.3	0.57	66.2	67.2	N/A	N/A	90.8	90.4
Los Roques	<i>in situ</i>	279	77.1	0.64	90.5	79.2	49.4	88.9	86.8	71.2

Table 5.3 - Estimated seagrass surface areas (in km²) at each study site, with the exception of Puerto-Rico due to low accuracy achieved for the product.

Site	Seagrass (km ²)
Bahamas	65,436
Belize	2,092
Mexico (Yucatán coast)	1,319
Roatán (Honduras)	64
St Croix (US Virgin Island)	62
San Blas offshore banks and islands (Panama)	11
Los Roques (Venezuela)	150
Alacranes Bank (Mexico)	58
Guadeloupe Island (France)	179
Providence Island (Colombia)	2.6
San Andrés (Colombia)	17



Figure 5.1 - Map of the Caribbean region and geographic location of sites processed for this study. Belize PR = Belize Patch Reef, Belize BR = Belize Barrier Reef (background map from www.reefbase.org). The lower panel shows data (both points and polygons) currently available on seagrass distribution for the region as displayed in “World Atlas of Seagrasses” (Green and Short 2003) and as taken here from the interactive IMAPS system (<http://storp.unep-wcmc.org>). Inset: Global location of region.

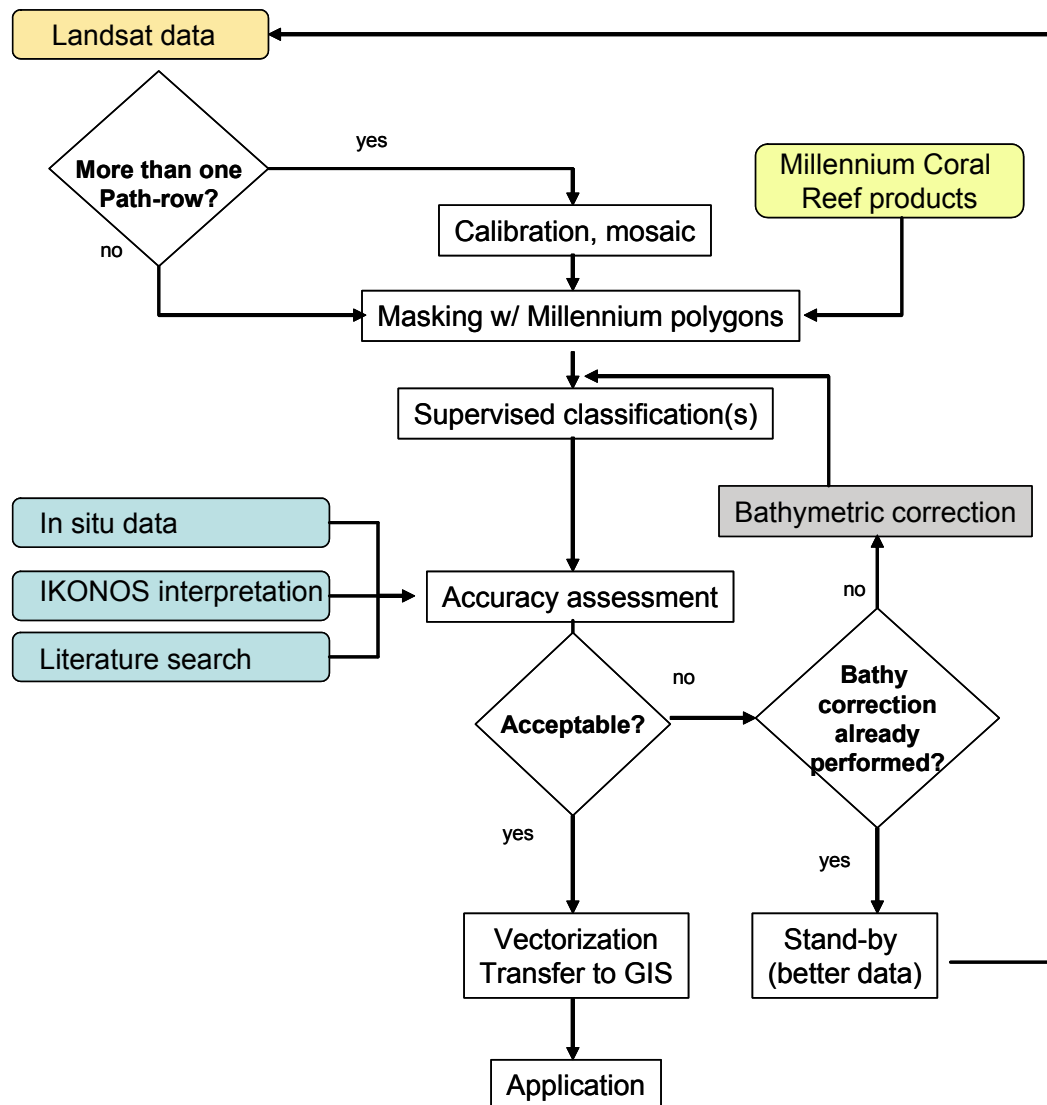


Figure 5.2 - Flow chart of data processing steps involved in mapping seagrasses at the large scale of the Caribbean Region (WCR). 'Path-Row' > 1 = is more than one path-row covering the study site? Rounded boxes = objects; square boxes = processing steps; diamond shaped boxes = highlight specific tests or conditions that need to be fulfilled. Bathymetric correction is highlighted in grey as it was not utilised here, but is recommended for sites where depth presents a confounding factor (e.g., site west of La Parguera, Puerto Rico).

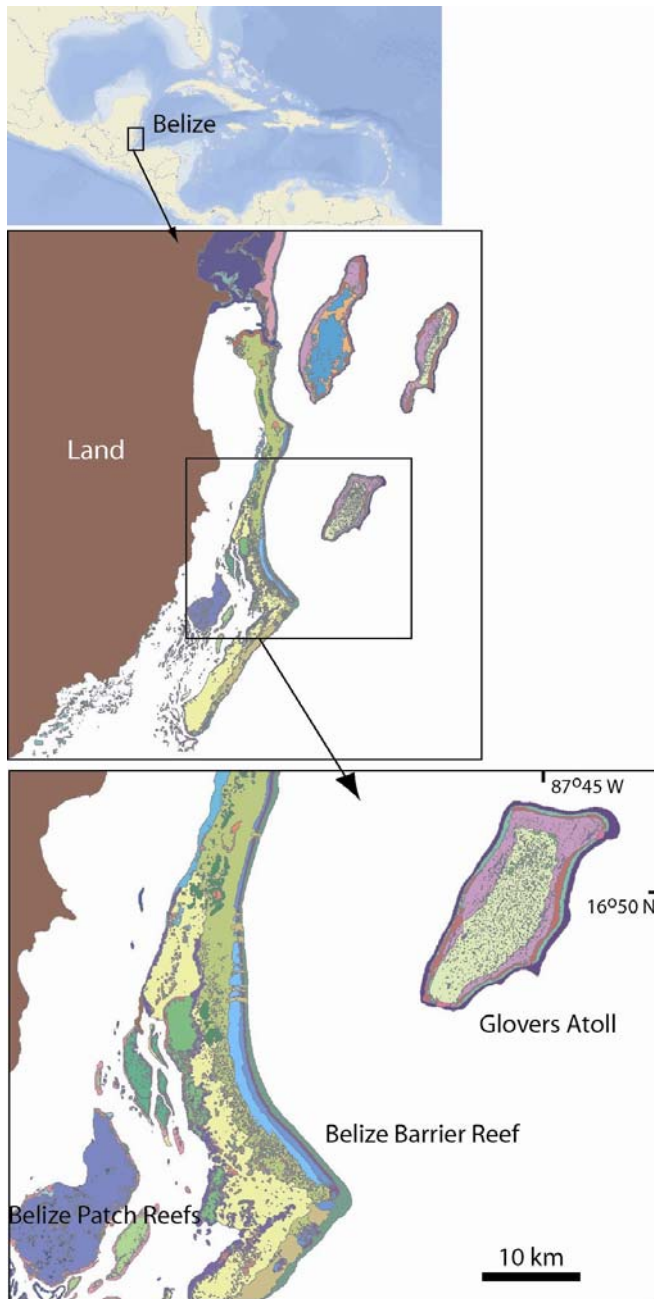


Figure 5.3 - Examples of Millennium polygons for the Belizean focal area. Detailed geomorphological classes provided by the Millennium Coral Reef Mapping Project allow for *a priori* contextual editing prior to spectral supervised classification. The figure aims to highlight the complexity and details of the structures and products provided. This area includes close to 100 classes; thus for the purposes of readability and simplicity, no thematic legend has been provided.

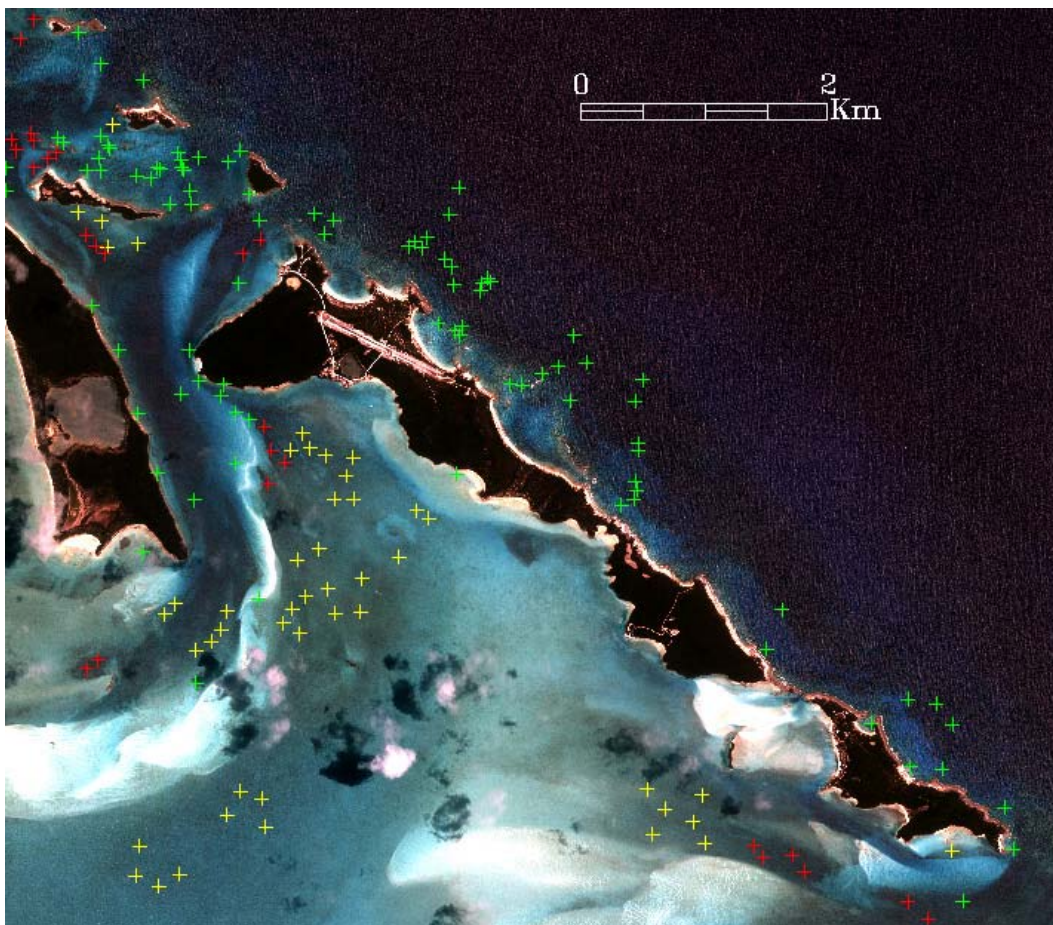


Figure 5.4 - Accuracy assessment points selected for Lee Stocking Island (Exuma, Bahamas) using an IKONOS image and augmented with in situ observations. Red: dense seagrass, yellow: medium-sparse seagrass, green: 'other'.

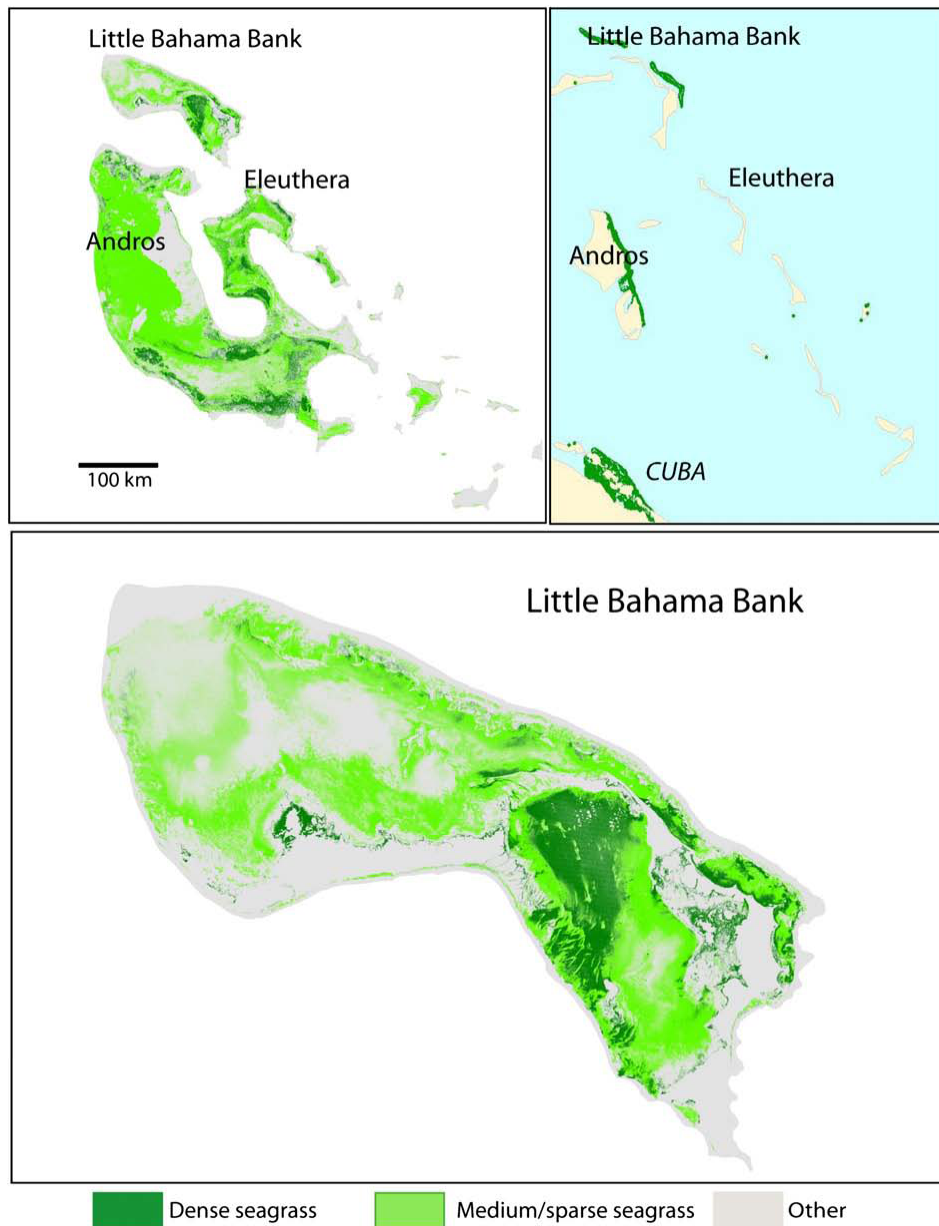


Figure 5.5 - Thematic map for all of the Bahamas and for the Little Bahama Bank with two seagrass classes (green) and a single 'other' class (white). Here, the 'other' class includes areas that were removed by *a priori* contextual editing for the actual seagrass mapping effort as well as processed areas classified as 'non-seagrass'. The upper right panel shows the current seagrass product available from UNEP-WCMC, displayed with the interactive IMAPS service (<http://storp.unep-wcmc.org>). It is included here for comparative purposes and highlights commission and omission errors in the existing seagrass coverage for the Bahamas.

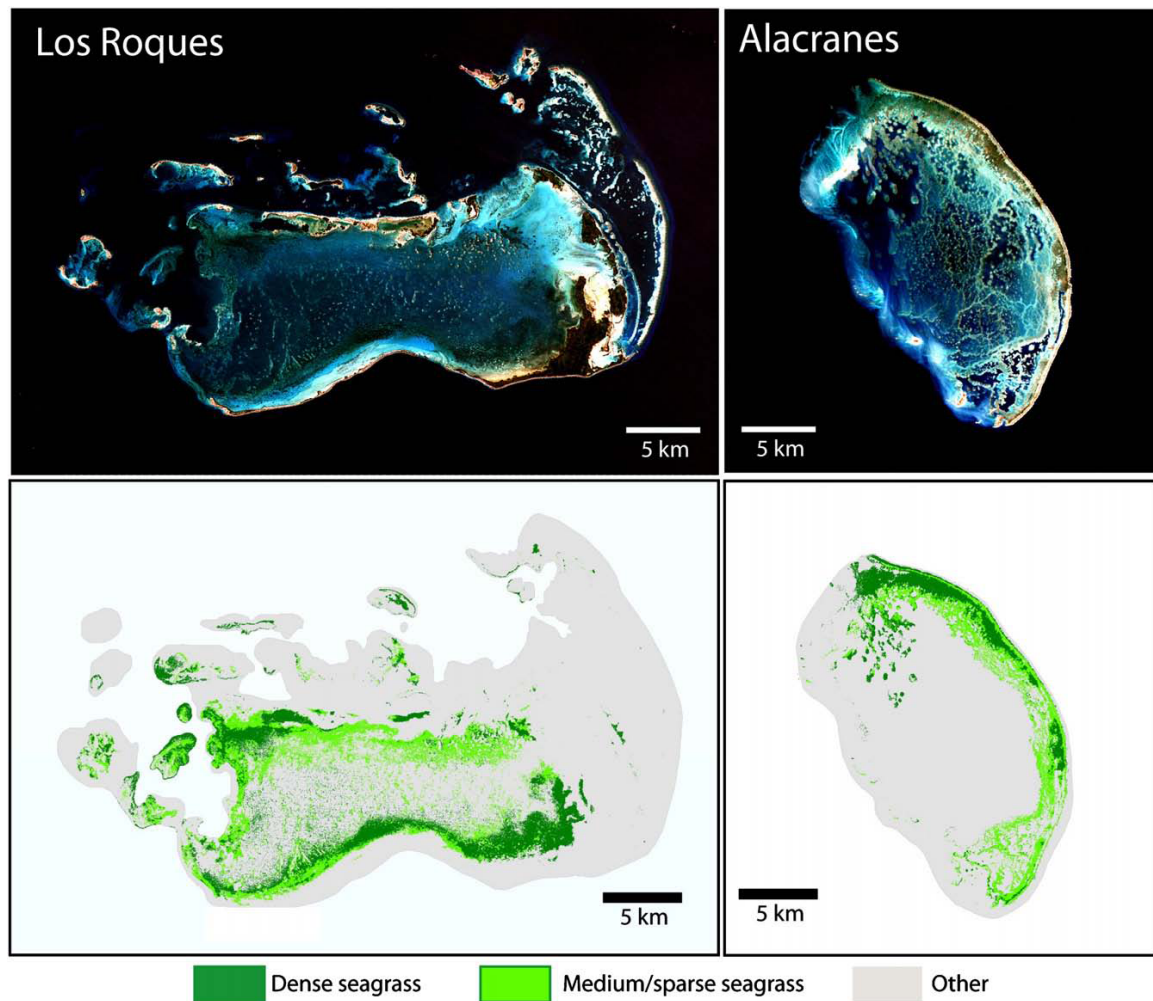


Figure 5.6 - Examples of habitat maps displaying two seagrass classes and a single 'other' class that can be compared with previous published peer-reviewed studies: Los Roques (to use in comparison with Schweizer *et al.* 2005), and Alacranes (to be compared to Bello-Pineda *et al.* 2005).

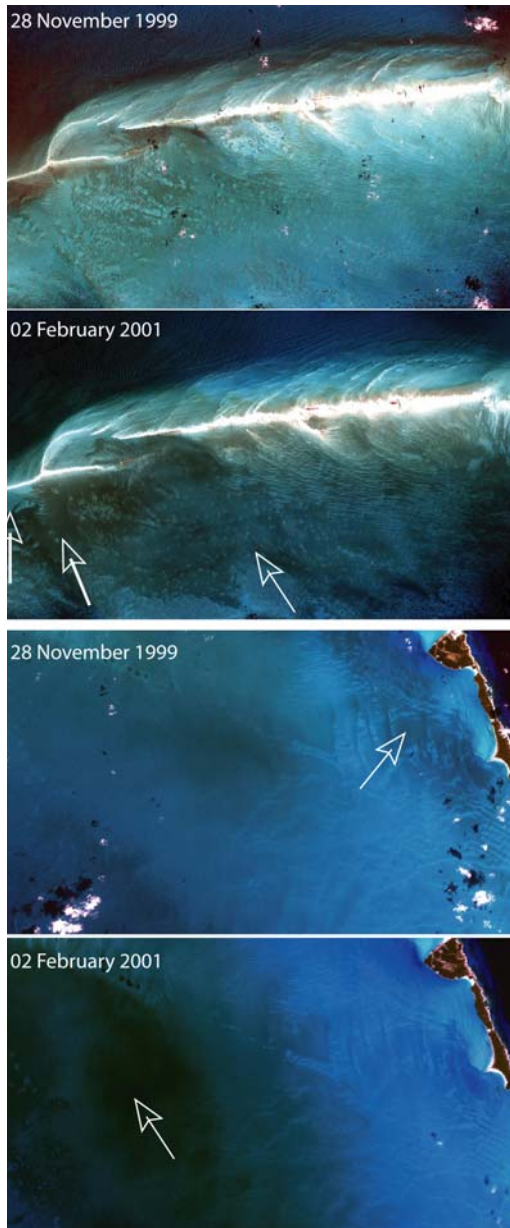


Figure 5.7 - Examples of temporal variation in vegetation cover, probably due to algal blooms, in two pairs of Landsat images taken less than 14 months apart (path-row 12-53, Bahamas). In the top pair, extensive darker areas appear on the bottom image. Note also (arrow most left) that dark areas have shifted to bright areas in the same period of time. In the second image pair, patches of dark water and darker bottoms appear on the bottom image (left arrow). Over the same time period (right arrow), vegetation has decreased on hard-bottom areas. These rapid changes from dark to bright and vice-versa are not typical of dense or medium-dense seagrass beds and are most likely to be associated with changes in algal cover.

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6. Measuring progress toward global marine conservation targets⁵

6.1 Introduction

In an effort to halt and reverse the worldwide destruction and overexploitation of marine resources, the international community (i.e., governments, NGOs, international organizations, and research institutions) has agreed to ambitious biodiversity conservation goals. For marine systems, three global protection initiatives have been outlined in the past decade. The 2002 World Summit on Sustainable Development (WSSD), in its Plan of Implementation, pledged to establish a network of marine protected areas (MPAs), representative of a variety of habitats around the world by 2012. The following year, members of the 2003 fifth World Parks Congress (WPC), adopted a recommendation to “[g]reatly increase the marine and coastal area managed in marine protected areas by 2012”, further specifying that “these networks should include strictly protected areas that amount to at least 20-30 % of each habitat”. In 2006, a target to effectively conserve 10 % of each of

⁵ A version of this chapter has been published. Wabnitz C.C.C., Andréfouët S., Müller-Karger F.E. (2009) Measuring progress toward global marine targets *Frontiers in Ecology and the Environment* doi: 10.1890/080109

the world's ecological regions, specifically including coastal and marine realms, by 2010 was adopted at the Eighth Ordinary Conference of the Parties to the Convention on Biological Diversity (CBD). For marine systems, emphasis has been placed on vulnerable tropical marine and coastal habitats such as coral reefs, mangroves, and seagrass.

Two assumptions are implicit in these habitat targets. First, the protection of representative tropical habitats will conserve biodiversity at species and population levels (Ferrier *et al.* 2002). Although there are few explicit tests of this assumption, protecting representative habitats does seem to be a feasible compromise between 'perfect' biodiversity information and the current capacity for data collection (Pressey 2004). Second, for the establishment of MPA networks, it is assumed that quantitative and standardized estimates of the surface area and representativity of individual ecosystems at country and regional scales exist. Such standardized metrics are presently lacking (Green *et al.* 2005), and existing datasets tend to be confounded by errors of both omission and commission - the former occur when a user excludes an area from the category to which it belongs; errors of commissions occur when the user includes an area in an incorrect category.

6.1.1 Need for accurate baselines on tropical marine habitat areas

All three initiatives listed above concede that severe gaps exist in our knowledge of the area of selected tropical ecosystems. However, the quality of data currently used to define the area of habitats for inclusion in MPA networks is often considerably poorer than acknowledged.

Representative results from a global comparison between reef sections mapped using remote sensing under the Millennium Coral Reef Mapping Project (MCRMP) (Andréfouët *et al.* 2006) and published estimates of reef area that are currently in use, show substantial discrepancies.

6.2 Data and methods

Based on the complete array of reef structures that can be identified from a global set of Landsat satellite images (<http://seawifs.gsfc.nasa.gov/cgi/landsat.pl>), the MCRMP developed a reef typology applicable at a global scale. This led to the definition of 800 individual reef classes that can be mapped accurately and consistently worldwide (for more detailed information on the development of the classification scheme and the principles followed see Andréfouët *et al.* (2006)). Evidently, no single reef is mapped using all 800 classes; it is the global diversity of detectable reef units with satellite imagery that reaches this number. The number of classes for any given reef varies between 1 (e.g., a fringing slope around a new oceanic volcanic island) and several tens (e.g., < 30 for a complex Maldivian atoll or > 40 for a large barrier reef system in New Caledonia). The actual mapping process then relied on image segmentation and photo-interpretation techniques to delineate individual image segments into meaningful homogeneous sections and label them appropriately. This procedure allows a customized, hierarchical description of any coral reef worldwide for any chosen application. In other words, initiatives with a fisheries' focus may wish to include large back-reef sedimentary zones as part of their coral reef definition, while applications looking at carbonate production, for instance, may wish to only include zones with a high probability of high hard coral and coralline cover (e.g., forereefs, reef crests, and reef flats). Given the methodology developed, MCRMP GIS products allow for such customized estimates to be calculated at regional scales according to a consistent 'reef labeling' system.

6.3 Results and discussion

Estimates of total reef areas for countries or regions presented here (Table 6.1) were obtained by merging only the highly-productive sections such as reef flats, forereefs, and lagoons with dense construction (Klumpp and McKinnon 1989). Previously published reef area data (used here in Table

6.1 for comparative purposes) were estimated by relevant authors from a variety of sources, sampled at different spatial resolutions. Underestimations reach 1,316 % (for Palau) and overestimations are on average 50 % (Table 6.1). For the Maldives, comparison of MCRMP values with previously published reef area estimates (Naseer and Hatcher 2004), also derived from Landsat imagery, seem to indicate an overestimate of 37 %. However, once MCRMP classes were merged in accordance with Naseer and Hatcher's (2004) reef classification scheme (i.e., including sandy back reef flat sections), total reef area was found to be comparable: 4,092 km² and 4,285 km² respectively; highlighting the importance of using a consistent 'reef' definition even when using similar data sources.

Reef area estimates for Myanmar (see Table 6.1) are presented to draw attention to challenges associated with habitat mapping in turbid waters. Myanmar's coastal waters are characterised by heavy suspended particulate loads; for the most part a direct result of the large sedimentary discharge from the Ayeyarwady River (Irrawady River). Sediment laden waters reflect more sunlight, rendering the coastal zone 'opaque' to optical satellite sensors. As a consequence, small and shallow reefs that may exist even in turbid waters may not be visible on Landsat imagery. Although the MCRMP value suggests that reef area previously had been overestimated, this figure should be considered as a conservative estimate (Table 6.1). However, in the case of Myanmar, we believe that earlier values were nevertheless overestimated given the spatial distribution of reefs evident from previously available maps (Spalding *et al.* 2001).

Thus, overall, discrepancies highlighted in Table 6.1 are primarily due to:

- 1 *Differences in spatial resolution, environmental quality of the data, and mapping methodology.*

MCRMP's dataset was developed from satellite imagery with a 30 m resolution. Most previously published reef estimates listed in Table 6.1 were derived from navigational charts and topographic map series re-sampled at a 1 km scale (Spalding *et al.* 2001). In most

instances, this coarse spatial resolution will lead to an overestimation of reef area, as most reefs (especially fringing reefs) are unlikely to attain such width. Improving the spatial resolution of data used (i.e., from navigational charts to Landsat imagery) will tend to reduce the calculated reef area. For example, in the case of the Maldives, image analysis by the MCRMP and Naseer and Hatcher (2004) led to reef estimates of approximately 4,000 km², whereas calculations based on 1km re-sampled data provided a value of 8,920 km² (Spalding *et al.* 2001). However, depending on the spatial configuration of reefs, increasing the spatial resolution of the source data may in some instances lead to new estimates actually being *greater* than previous figures. In the case of Palau, reef area mapped using Landsat imagery was 1,316 % larger than previously estimated. Using images with finer spatial resolution allowed for small reef structures, invisible at coarse resolution, to be detected. Trends may also in part be influenced by image quality, where a poor high resolution image may ultimately be less useful than mapping based on an excellent lower resolution image.

- 2 *The lack of a consistent and systematic definition of 'coral reef' driving the inclusion (or exclusion) of information held in currently utilised databases.* As pointed out above in the case of the Maldives, differences in the definition of what constitutes a 'reef' led to discrepancies in estimates of reef area. This in itself does not constitute a problem if the data used for mapping purposes can consistently handle changes in reef definitions, i.e., systematically include or exclude given sections depending on the chosen definition.

The wide scale application of remote sensing would also considerably improve mapped distributions of (a) seagrass and mangrove habitats, for which existing inventories suffer from similar problems of inaccuracy (Spalding *et al.* 2003); as well as (b) saltmarshes, for which reliable inventories are currently not available, barring a few studies at the local and regional scale (e.g., Isacch *et al.* 2006). To our knowledge, there are no current efforts to systematically map these systems globally, based

on consistent remote sensing methods and habitat typology (but see Chapter 5 for results from a mapping exercise conducted for seagrasses at the scale of the Caribbean Region).

Given the magnitude of estimated discrepancies between datasets in the case of coral reefs and the lack of a baseline for most other marine habitats, it is clearly challenging to realistically evaluate action towards global targets seeking to conserve at least 10 % of tropical coastal habitats (e.g., Wells *et al.* 2007). Current estimates of loss rate average a minimum of 1 - 2 % year⁻¹ for salt marsh (Lotze *et al.* 2006), 2 - 5 % year⁻¹ for seagrass (Orth *et al.* 2006) and 2 - 4 % year⁻¹ for mangrove ecosystems (Valiela *et al.* 2001). Although declines in the distribution and area of coastal habitats have been identified as an important indicator of environmental change, the utility of such trend metrics may be futile if accurate baselines against which to assess the magnitude of losses are lacking. Large scale mapping based on remote sensing and consistent habitat classifications would make it possible to revise and to estimate more accurately regional/global loss rates of salt marshes, seagrass, and mangrove ecosystems in particular.

6.3.1 Need for functional information derived from habitat inventories

Effective MPAs will require the protection of not only taxonomic biodiversity but also the functional processes of ecosystems. For example, connectivity between reefs and other marine habitats is an important feature listed under the CBD framework, and needs to be incorporated into MPA networks design. As such, the mapped resolution of habitats, as well as their shape and spacing has important implications for managing connectivity between reefs. Data generated by the MCRMP show that many small coral reef areas are entirely missing from current regional resource maps (Figure 6.1), with considerable implications for the efficient design of 'connected' MPA networks.

6.3.2 The way forward: Using remote sensing to establish accurate baselines

Although the benefits of remote sensing for biodiversity conservation purposes have been recognized for well over a decade (e.g., Roughgarden *et al.* 1991) and repeatedly emphasized since then, its wide scale application to the coastal realm remains limited. Remote sensing offers the potential to meaningfully inform conservation planning by for example: (a) collecting data at a scale that cannot be realized using traditional methods; and (b) allowing for map classification schemes to be developed in a manner that is consistent, systematic, repeatable, and spatially exhaustive.

Consistency and comparability of habitat datasets, in terms of information quality and quantity, are essential for any future assessment of large scale conservation priorities for biodiversity protection and reserve efficacy. The applicability of remote sensing to the development of reliable, accurate, and relatively detailed large scale coastal habitat maps makes it an invaluable tool for effectively realizing 10 - 30 % habitat protection targets.

A number of obstacles presently challenge the international community's capacity and willingness to map biodiversity via remote sensing. First, donor agencies most often invest in novel approaches to biodiversity conservation, and/or visible campaign actions, rather than in the generation of large scale baseline habitat databases. Second, there is a common misconception that reliable coastal ecosystem inventories are readily available, which has greatly impaired the funding of large scale, high resolution mapping programs (but see MCRMP initiated by the U.S. National Aeronautics and Space Administration (NASA)). Third, although many small scale habitat mapping programs are being conducted around the world to inform the designation of conservation areas at a national level, the majority of these lack systematic labeling, protocols, and standards that would enable their integration into consistent regional databases (Mumby and Harborne 1999) - fundamental to achieving successful conservation planning at these larger scales. Fourth, exhaustive and detailed mapping efforts conducted at the scale of $< 5,000 \text{ km}^2$ (e.g., NCCOS 2005) may have given the

impression that such programs, if conducted at the global scale, would be prohibitively expensive. Effective biodiversity conservation need not require such costly programs. For example, the 2005 rezoning of the Great Barrier Reef Marine Park was largely based on thematically simple, but spatially accurate, maps derived from satellite imagery acquired in the 1980s (Jupp *et al.* 1985). The current state of technology and know-how should allow a low cost strategy to globally achieve what the Australian government created for the Great Barrier Reef.

6.3.3 Conclusion

Globally consistent measures of habitats' areas are essential to meaningful assessments of how we are faring with respect to international conservation targets for 2010 - 2012, and for the large scale application of predictions and recommendations currently being generated from innovative biodiversity and conservation research. The concept is simple and essential, and the current lack of momentum towards this task is both surprising and unfortunate (but see call for action in the form of the Group on Earth Observations Biodiversity Observation Network initiative (2008)). Standardized global habitat mapping using remote sensing is a cost-effective and high resolution solution that should be the conservation community's top priority if we are serious about commitments expressed at the 2002 WSSD. Although I strongly agree with Roberts *et al.* (2003) that "it is a poor strategy to postpone the creation of reserves on the grounds that we are still ignorant of scientific subtleties", the problems identified and detailed here are not subtleties. They represent basic knowledge required for the effective implementation of MPAs and our ability to ascertain global progress towards international conservation targets.

Table 6.1 - Representative comparison of coral reef areas as estimated by the Millennium Coral Reef Mapping Project (MCRMP) based on remote sensing (Landsat ETM+) with previously published estimates from Spalding *et al.* (2001), Naseer and Hatcher (2004), and NCCOS (2005). Spalding *et al.* (2001) based their estimates on Nautical Chart Digitization, while Naseer and Hatcher (2004) and NCCOS (2005) also used remote sensing, but followed a different reef classification scheme from the MCRMP (see main text). ‘% difference’ values were calculated as follows $((\text{MCRMP} - \text{previous figure}) / \text{previous figure}) * 100$; (+) in the column indicate countries for which MCRMP derived reef area is greater than previous estimates, i.e., latter were underestimates, whereas (-) indicate countries for which previous figures represent overestimates of reef area.

Countries	MCRMP (km ²)	Previous figure (km ²)	% difference	Site Specifics and Conservation planning
Bahamas and Turks and Caicos	6,213	3,880 ¹	(+) 60	On-going MPA network design and implementation; & reef connectivity study.
Belize	893	1,330 ¹	(-) 33	Includes fringing, patch, barrier reefs, and atolls. Numerous conservation activities, currently probably the most studied Caribbean site.
French Polynesia	2,140	6,000 ¹	(-) 64	Here 4 archipelagos (Tuamotu, Austral, Society (incl. Tahiti), and Gambier); atolls with Biosphere Reserve status.
Maldives	2,697	4,285 ²	(-) 37	Largest reef and lagoon system in the Central Indian Ocean.
Micronesia	3,172	5,440 ¹	(-) 42	Focus of the Micronesia Challenge, which targets protection of 30% of coastal waters.
Myanmar	577	1,870 ¹	(-) 69	Extensive island archipelagoes and fringing reef systems; turbid waters limit RS performances
New Caledonia	4,537	5,980 ¹	(-) 24	Includes the Chesterfield-Bellona reef system. New Caledonia reefs UNESCO World Heritage Site since July 2008.
Guam and Commonwealth of the Northern Mariana Islands	284	263 ³	(+) 8	Pacific Ocean reefs recently mapped by NOAA with 4m resolution IKONOS imagery. Areas comparable to MCRMP based on 30m Landsat data
Palau	708	<50 ¹	(+) 1,316	One of longest barrier reefs in the Pacific Ocean and one of the highest diversity of reef geomorphological units for a single oceanic island.
Papua-New-Guinea (Milne Bay)	3,009	8,110 ¹	(-) 63	Focus of numerous conservation planning activities.

¹Spalding *et al.* (2001); ² Naseer and Hatcher (2004); ³ NCCOS (2005)

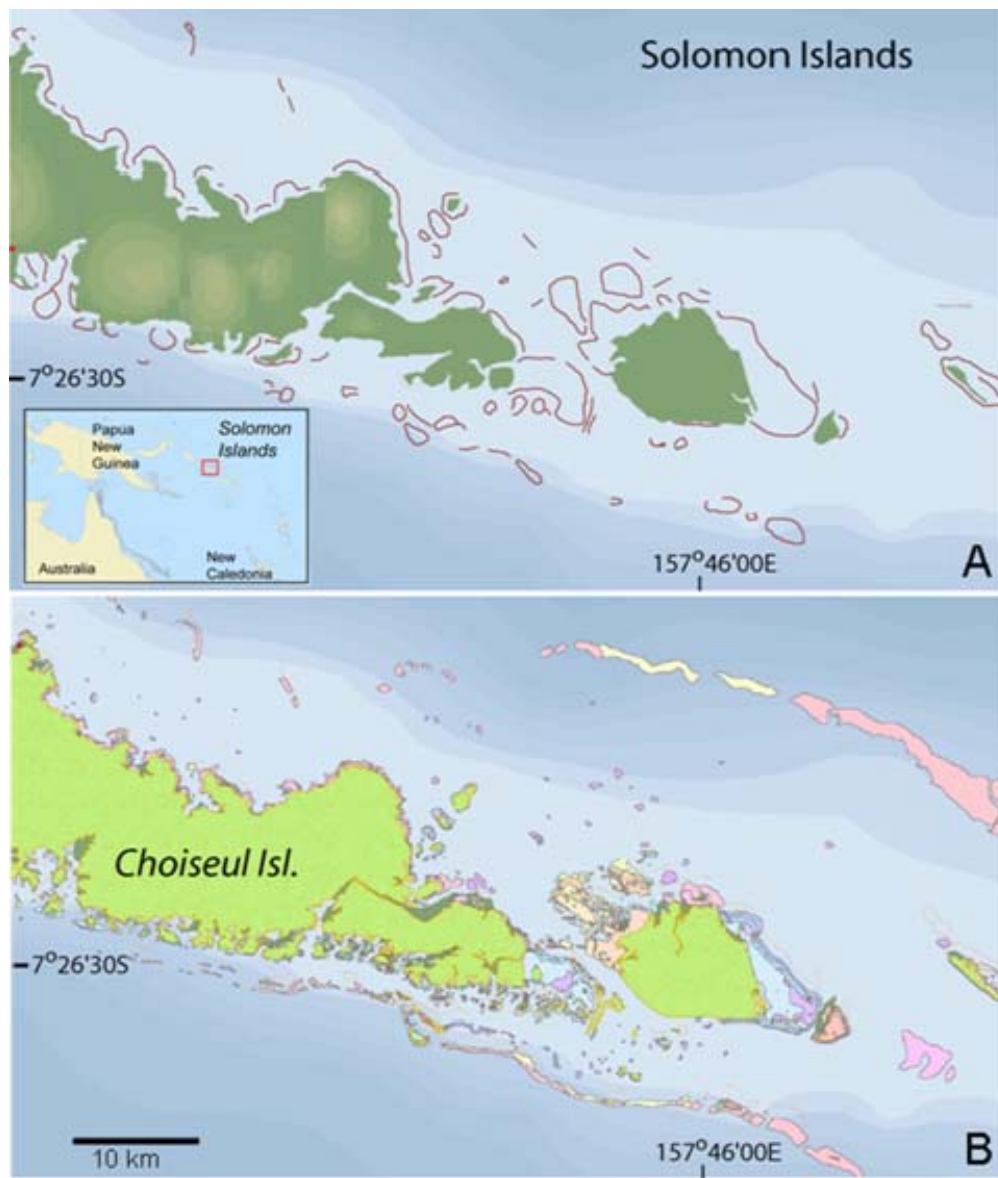


Figure 6.1 - Reef habitat connectivity. **A:** UNEP-WCMC reef layers displayed with the online Reefbase GIS system (www.reefbase.org) for part of the Solomon Islands (see inset map for Solomon Islands location - also from reefbase). Coral reefs (light orange lines) were digitized from nautical charts, and reef areas were estimated from 1-km buffers around these lines (Spalding *et al.* 2001). **B:** MCRMP coral reef polygons. Different colors depict different reefal and non-reefal categories. Small reefs are adequately resolved, providing a markedly different perception of reef density and potential habitat connectivity from that given by the top panel.

6.4 References

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7. Conclusions

Sea turtles are considered important consumers in coastal habitats, and at historical abundances had a significant impact on their forage resource (Jackson 1997, Bjorndal 2003, Bjorndal and Jackson 2003). As highlighted in Chapter 1, most current sea turtle populations have been overharvested, some to the brink of extinction (Parsons 1962, Meylan 1999, Pandolfi *et al.* 2003, Bell *et al.* 2007), and overall remain shadows of past abundances (McClenachan *et al.* 2006). These declines have triggered significant conservation initiatives (e.g., Pritchard 1980, Marcovaldi and dei Marcovaldi 1999, Troëng and Rankin 2005, Gilman *et al.* 2006) and the implementation of regulations (e.g., Aridjis 1990, Crowder *et al.* 1995, Gilman *et al.* 2007) to assist in their recovery. To that end a goal or target, that initiatives can aim towards, is typically necessary. Although historical abundance levels are vivid reminders of the drastic impacts humans have had on our marine environment, they do not necessarily represent the most appropriate recovery targets. Anthropogenic activities have not only adversely impacted sea turtles themselves, they have also led to profound changes in the health of coastal habitats (Burke and Maidens 2004, Lotze *et al.* 2006, Orth *et al.* 2006). It is therefore questionable whether today's ecosystems are even able to sustain sea turtles at historical abundance levels. Instead, there have been calls for recovery targets to be based on abundance levels at which sea turtles fulfil their ecological role (Bjorndal and Bolten 2003). This approach has been adopted by, among others, the Marine Turtle Specialist Group (Marine Turtle Specialist Group 1995).

An understanding of what sea turtles' ecological roles are should take into account both their ecosystem requirements and their ecosystem impacts through their foraging activity. Although critical to establishing realistic recovery targets, to date, only limited efforts have been expanded to identify what these roles may be (but see Bjorndal 2003, Bjorndal and Jackson 2003). In this thesis I sought to address this question through a multilevel stepwise approach, building knowledge first at

the level of the individual, followed by the population, ecosystem (focusing particularly on green turtles), and habitat (especially seagrass).

Specifically, in Chapter 2, I conducted a novel meta-analysis that has contributed to the knowledge and understanding of population dynamics and food consumption of hawksbill, loggerhead, and green turtles in the western Atlantic. In Chapters 3 and 4, I provided the first detailed models to have explicitly integrated sea turtles in an ecosystem context, highlighting their role as (a) consumers of algae on coral reefs, and thus playing a critical role in maintaining reef resilience (Chapter 4); and (b) ecosystem ‘engineers’ (*sensu* Jones *et al.* (1994)), through the important changes brought about by their grazing on the refuge capacity of seagrass, particularly for juvenile fish and invertebrates, and thus trophic linkages among reef/mangrove/seagrass ecosystems (Chapter 3). Recognising the importance of habitat conservation (Gray 1997, Noss *et al.* 1997), for healthy coastal ecosystems in general and for turtle conservation in particular, in Chapter 5, I presented a new approach to mapping habitats at the large scale, focussing on seagrass, while in Chapter 6, I highlighted the pressing need for the design and implementation of such large scale mapping efforts to meet conservation targets agreed to by the international community.

In combination, the chapters of my thesis represent a significant advancement in our understanding of the ecological role of sea turtles, and provide key tools to help facilitate continued research and implement conservation and management actions. A concluding summary of the findings presented in this thesis, their limitations, as well as suggestions for future work, is provided below.

In Chapter 2, I present a framework with which to conduct sea turtle population level assessments of food consumption. As a first step, I developed a model for the growth of hawksbill, loggerhead, and green turtles that is regionally applicable at the scale of the western Atlantic. Integrating these data with length-weight estimates, survival estimates for individual life stages, overall current population abundance estimates, and food conversion efficiency estimates, allowed me to then present total

biomass and total food consumption for age-structured populations of each species at the scale of the western Atlantic. This chapter's work directly builds, and expands upon, efforts by Bjorndal (2003), Bjorndal and Jackson (2003), and McClenachan *et al.* (2006), who present preliminary estimates of adult food consumption to highlight the impact historical sea turtle populations must have had on their food resources and ecosystem processes. The novelty of my approach is that calculations were based on current estimates of abundance and were derived for an age-structured population. In other words, I provided estimates of food consumption that integrated population demographics and were ecologically realistic in extant ecosystems.

A key assumption of the growth model that I developed was that the von Bertalanffy growth function (VBGF) is a valid model to describe sea turtle growth. Growth may be defined in quantitative terms in many ways (Hilborn and Walters 1992), but the von Bertalanffy model is typically recognized as having the most straightforward and widespread application. My meta-analysis showed that, at the scale of the western Atlantic, the available growth data did not deviate significantly from the VBGF and that it was therefore valid to accept the 'simplest model' as a working hypothesis. As such, my efforts are a valuable and insightful first step towards developing a broadly applicable model for demographically-integrated population-level food consumption by sea turtles. It is important to note, however, that although the data fit the VBGF, this does not necessarily mean that turtles actually grow according to the VBGF. As more data become available, the model should continue to be updated, and it may be that future efforts demonstrate that a different model is more appropriate (e.g., Chaloupka and Musick 1997).

The growth model was developed using 10-cm size class data, as these size increments have been the standard means of publishing growth measurements in the sea turtle literature. I believe that my statistical approach to account for differences in sample size provided a robust means of overcoming these coarse grained data and presenting valid overarching patterns. It would be interesting, however, to invite researchers from the region to pool their original growth measurements and

conduct the same meta-analysis using raw data. One would then be able to investigate whether the resulting overarching growth pattern from analysis of fine-grain data significantly differs from the one presented in my thesis, quantitatively ascertain to what extent local growth trajectories deviate from the overall trend, and more closely investigate what some of the underlying dynamics responsible for these differences may be; if indeed there are any.

The synthesis of a number of datasets on the ecology of hawksbill, loggerhead, and green turtle populations, has also underscored the need to address a number of existing information deficiencies (Seminoff 2004). For example, there is a clear need for additional demographic information on annual reproductive output (e.g., hatching/emergence success and clutch frequency). Moreover, although it is assumed that growth rates become negligible once sea turtles have reached sexual maturity, data collection from nesting adults at a number of sites would be valuable towards quantitative confirmation of this. Given the number of existing beach monitoring programs, much of this information already exists, but a comprehensive synthesis has not been published. The compilation, standardization, and analysis of these data would provide a valuable and powerful resource. Such an initiative could be spear-headed through a workshop that would bring together regionally active biologists and managers, such as those within the Wider Caribbean Sea Turtle Network (WIDECAST). My findings also clearly underscore the need for expansion of existing monitoring work at foraging areas to collect growth rate measurements, particularly for loggerhead and green turtles. Such understanding would significantly strengthen the basis from which to develop meaningful and successful management initiatives for sea turtle recovery.

Sea turtles do not exist in isolation, but form an integral part of the natural environment. Thus, once the basic features of growth, mortality, and food consumption have been understood at the scale of the individual and current populations, this understanding needs to be placed into an ecosystem context. In attempting to understand dynamics at the ecosystem level, community models are one of the most valuable tools available to permit controlled exploration of a complex reality and to help

elucidate patterns and processes that are not apparent from empirical data alone. However, the application of such models often has tended to emphasise 'direct effects', where changes in the abundance of a species resulted from its trophic interaction with another species. Specifically, such models have typically focused on the effect of changes (reductions) in large predator abundance on their prey (Paine 2006), not least because these have been some of the most pervasive and visible of human impacts on marine resources (Pauly *et al.* 1998). However, another potential cause of variation in community structure is 'indirect' effects, where a species indirectly alters the abundance of another species to which it does not have a direct trophic link (Wootton 1994, Wilbur 1997, Abrams 2007, Agrawal *et al.* 2007). The importance of habitat structure in mediating direct and indirect interactions among multiple predators and prey has been highlighted (Janssen *et al.* 2007, Grabowski *et al.* 2008), but its explicit application in ecosystem models has been lagging behind implicit acknowledgment of its significance. To date only a few examples have clearly incorporated the mediating role that habitat complexity plays in structuring dynamics at the level of an ecosystem (e.g., Fulton and Smith 2004, Espinosa *et al.* 2009). Ecopath with Ecosim (EwE; the modelling software used in this thesis), presents the unique advantage, over most other modelling methods, of being able to explicitly incorporate such indirect non-trophic effects (Walters and Martell 2004, Christensen 2008).

The work I present in Chapter 3 is the first attempt to explicitly investigate, through the use of an ecosystem model, the potential changes that may result from the recovery of a species whose grazing activity strongly alters habitat structure at the ecosystem level. My results demonstrated that by integrating trophic and non-trophic interactions (called 'mediation' functions in EwE) at the ecosystem scale, and thus considering multiple predator-prey interactions in addition to the refuge capacity of a primary producer, simulated ecosystem responses are more complex than suggested by simple predator-prey experiments. The results also underscored the importance of inter-habitat exchanges and how the recovery of a megaherbivore may potentially affect these linkages and/or the role of individual habitats as nursery areas for a variety of species, including commercially important

fish. These findings demonstrate that the recovery plans for sea turtle populations need to be more detailed than merely aiming for a target of species' abundances. Using green turtles as an example, they should explicitly acknowledge the role that green turtles play in structuring seagrass beds, and highlight the need to (a) gain greater understanding of what the implications this role may have for the 'functioning' of seagrass beds today and into the future, and (b) perhaps help redefine at what levels green turtle populations may be considered to have made a full recovery.

To the extent that models represent a valuable quantitative tool for increasing our understanding of environmental interactions, they also allow us to identify critical gaps in our current knowledge of how an ecosystem functions. To better parameterise the model I developed in Chapter 3 and allow for its use in the development of future management scenarios, research is needed on the degree to which a reduction in the canopy of seagrass influences the density, diversity, and abundance of fish (i.e., nursery function of seagrass beds). Moreover, local and regional comparisons are needed to investigate the degree to which specific species may increase use of mangrove and/or reef habitat given structurally simpler seagrass beds. To this end, experiments could be conducted using turtle exclosures/enclosures, as well as regional comparisons of sites that are known to have 'healthy' foraging populations of green turtles (e.g., sites in the Bahamas and U.S. Virgin islands).

The recovery of green turtles in the Caribbean, and their impact on seagrass, is a unique opportunity to investigate the role a megaherbivore plays in the functioning and dynamics of coastal ecosystems via changes in habitat complexity. However, primarily due to their current extremely low abundances, even their direct impact as consumers at the scale of ecosystems has been relatively poorly studied to date. Hawai'i therefore represents a unique setting to investigate the role of green turtles as consumers (Chapter 4), although, unlike in the Caribbean, in the eastern Pacific green turtles chiefly feed on algae (Bjorndal 1997). A turtle fishing ban implemented in the late 1970s (Witzell 1994) has resulted in a dramatic increase of the number of green turtles at foraging areas, with several lines of evidence suggesting that aggregations are reaching carrying capacity (Balazs

and Chaloupka 2004a, 2004b). Model results demonstrated that the combined grazing pressure of the different herbivorous groups (i.e., reef fish, sea urchins, and green turtles) in the Hawaiian ecosystem modelled (Kaloko Honokōhau National Historical Park) matched total algal production. Numerous studies have highlighted the role that large herbivores, typically parrotfish, play in maintaining reef resilience (e.g., Mumby *et al.* 2006, Hughes *et al.* 2007a, 2007b). The results presented here underscore that at healthy abundance levels, green turtles play a critical role as consumers, maintaining low algal cover and thus the resilience of reefs in the face of disturbance. The fact that green turtles feed on non-native algae, including macroalgae (Russell 1992, Arthur and Balazs 2008, Russell and Balazs 2009), further strengthens their contribution to the promotion of reef resilience, as herbivorous fish often show a preference for filamentous algae, limiting the ability of macroalgae-dominated reefs to revert to coral dominated states (Ledlie *et al.* 2007). It is therefore important that green turtles be explicitly included in studies of ecosystem dynamics on reefs.

The Hawai'i model also provided a functional tool for Kaloko managers to make informed decisions about natural resource management in the light of coastal urban expansion plans, while incorporating an ecological perspective. By integrating known information from a wide variety of sources and helping to organise and track information that would not be possible otherwise, the model also highlighted future research foci. These included the collection of more detailed consumption and diet information for some of the grazers, their spatial distribution on the reef and nutrient input time series data. Such data will increase the model's ability to produce realistic projections, particularly in light of ongoing development, and the desire by park managers to use the model to highlight future management opportunities as well as trade-offs.

The models produced in Chapter 3 and 4 have served to highlight the significant ecological role that green turtles play in structuring coastal ecosystems. This role is centred on their capacity as herbivores. Similar studies need to be conducted for other turtle species, whose different diets imply very different ecological roles and interactions. The data presented in Chapter 2, and the knowledge

gained through the development of the ecosystem models for Chapter 3 and 4, provide clear and tangible frameworks that can be used to facilitate the development of similar models for hawksbill and loggerhead turtles. By feeding chiefly on sponges - often superior aggressive competitors of corals (Vicente 1978, Suchanek *et al.* 1983, Hill 1998) - hawksbill turtles may play a key role in maintaining the structure, dynamics, and thus resilience of coral reef ecosystems - at least when they are present at natural abundance levels. Loggerhead turtles consume a wide range of mostly slow moving or sessile hard shelled invertebrates (Dodd 1988). As loggerhead turtles prey on commercially important species (Bjorndal 2003), loggerhead predation may be affected by changes in prey availability due to fishing activities, especially shrimp trawling, or other anthropogenic impacts, such as dredging (Youngkin 2001). In Chesapeake Bay, an important foraging ground for juvenile and adult loggerhead turtles, stomach content analyses over a 20-year period showed a significant dietary shift from horseshoe crab (Lutcavage and Musick 1985) to blue crab, to mainly finfish (menhaden and croaker) as a result of horseshoe and blue crab depletions (Seney and Musick 2007). This suggests that turtles are foraging in greater numbers in or around fishing gears and on discarded bycatch (Seney and Musick 2007). Development of an ecosystem model for loggerhead turtles of the type presented here for green turtles would allow researchers and managers to (a) gain a deeper understanding of the role of loggerhead turtles as consumers in the system, (b) calculate the degree of overlap between loggerhead consumption and fisheries, (c) investigate the impact of fisheries on loggerhead turtles via bycatch and discards, and (d) visually depict the impact of different policy scenarios and assist in the formulation of management strategies that conserve sea turtles, but may also present sustainable options for the industry.

Ultimately, as is implicit throughout this thesis, the successful recovery of sea turtles is highly dependent on the conservation of the habitats on which they depend. Overharvesting and habitat destruction together represent the greatest threats to biodiversity and therefore the loss of ecosystem function and a reduction in the provision of ecosystem services (Sala and Knowlton 2006). Clearly, without healthy habitats, management schemes directed at particular species are doomed to failure

(Lovejoy 1996). Coral reefs and seagrass beds are some of the most threatened coastal ecosystems worldwide (Hughes 1994, Pandolfi *et al.* 2003, Orth *et al.* 2006, Waycott *et al.* 2009). Successful conservation of coastal, particularly foraging, habitats (Eckert and Abreu-Grobois 2001) is therefore critical to the conservation of sea turtles. Indeed, much of the findings in this thesis highlight the close connection between achieving sustainable long-term sea turtle recovery and management, and the conservation of critical coastal habitats, including reef and seagrass.

Marine protected areas (MPAs) form an integral part of ecosystem-based management (Sumaila *et al.* 2000), because they have the potential to maintain and restore ecosystems, biodiversity and ecological processes; buffer against natural and anthropogenic uncertainty; and promote integrated management of marine resources (Gerber *et al.* 2003, Lubchenco *et al.* 2003, Roberts *et al.* 2003).

Recently, the World Commission on Protected Areas highlighted the need to ensure

access to and application of the best available information on species, especially those that are threatened (and listed on the IUCN Red List of Threatened Species TM), in particular in relation to ecosystem functioning. Such information is critical not only for enhancing the case for establishing MPAs, but also for ensuring their optimal design, monitoring their progress and for informing and feeding into the adaptive management process. (Sadovy *et al.* 2007)

The data presented in Chapters 2 to 4 provide what I feel is a valuable contribution to attaining that goal.

In addition, international calls for the increased implementation of MPAs have highlighted the need for their inclusion of at least 10 – 30 % of each habitat (WPC 2003, CBD 2006). However, with a few exceptions, currently available habitat data suffer from poor spatial representation and low spatial resolution. The current lack of appropriate baseline data for marine habitats has limited the implementation of ‘representative’ networks of marine protected areas, and represents a hindrance to the attainment of the above- mentioned recently- adopted global- conservation targets. In Chapter

5, I present a simple and cost effective methodology to map coastal habitats at large scales, focusing on seagrass as a case study. In the context of sea turtle conservation in particular, such mapping efforts are critical to species conservation in an ecosystem context. A robust database, detailing habitat extent, obtained in a methodologically consistent manner as outlined in Chapter 5, would also ensure that countries party to the Convention on Biological Diversity, and thus with a mandate to attain the targets outlined above, have a chance at meeting them.

This latter point is further emphasized in Chapter 6, where discrepancies between existing published estimates of reef area (often based on bathymetric data) and those I derived from remote sensing data ranged from + 1,316 % to - 64 %. Currently available estimates of the global extent of most coastal marine habitats are based on data that are clearly too poorly resolved to be useful in evaluating progress towards the 2012 targets. Large scale initiatives using the methodology described in Chapter 5 should therefore be undertaken to derive accurate inventories of coastal habitats. These would also provide a reliable baseline against which to assess the impact of anthropogenic activities, especially climate change, as well as measure the success of targeted conservation initiatives. The provision of such data will further facilitate place prioritization studies that utilise habitats (such as seagrass and/or reef) as surrogates for biodiversity, because our knowledge of global biodiversity is incomplete and more detailed data cannot typically be obtained in the timeframe within which landscape- or seascape-altering decisions are made (Margules and Pressey 2000, Mumby *et al.* 2008, Dalleau *et al.* 2010).

In view of the migratory and transboundary nature of sea turtles (Musick and Limpus 1997, Plotkin 2003), the large scale nature of required conservation activities cannot be overemphasised. However, for such management initiatives to be successful and sustainable at the ecosystem level, results presented in this thesis highlight the need to (a) quantify the dependence of species on habitat resources, and related direct trophic effects between species; (b) identify the role that key species play in structuring habitats, and resulting indirect impacts on other ecosystem components; and (c)

accurately determine the extent of these habitats. Such a holistic approach to management is integral to ecosystem-based management (Crowder *et al.* 2008). The research presented here therefore not only contributes to the available literature underscoring the value of such an approach, but also presents a tangible example as well as a framework for how to implement critical aspects of such an approach, using endangered species as an example. My findings further highlight that, in the context of ecosystem-based management, networks of no-take MPAs that protect important foraging habitats (e.g., reefs and seagrass) and the life stages that have been determined as most responsive to enabling population recovery (Crouse *et al.* 1987), constitute an important step towards long-term conservation of sea turtles.

7.1 References

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Appendices

Appendix 1 - Total estimate of adult hawksbill turtles based on numbers of annual nesting females. Unless otherwise indicated, data as in NMFS (2007).

Country/Location	Annual number of nesting females		References and notes
	Min	Max	
Antigua (Jumby Bay)	52	52	
Antigua/Barbuda	50	75	
Bahamas	100	333	
Barbados	483	483	
Bonaire	3	19	
Cayman Islands	1	2	Aiken <i>et al.</i> (2001); Bell <i>et al.</i> (2007)
Cuba	400	833	
Dominican Republic	50	407	
Trois Ilets and Folle Anse, Guadeloupe	35	94	
Martinique	50	100	
Jamaica	200	275	
Grenada	6	37	
Puerto Rico (Culebra, Caja de Muertos, Humacao)	51	85	
Mona island, Puerto Rico	199	333	van Dam and Diez (2008)
St Kitts	6	37	
Trinidad and Tobago	150	150	
BVI	4	6	McGowan <i>et al.</i> (2008)
Buck island reef, USVI	56	56	
USVI	30	222	
Belize	8	56	
Isla Fuerte, Colombia	19	93	
Tortuguero, Costa Rica	10	10	
Cahuita, Costa Rica	6	37	
Bay islands, Honduras	10	10	
Mexico	534	891	
El Cocal, Nicaragua	15	25	
Pearl Cays, Nicaragua	30	52	
Panama	27	45	
Chiriqui beach, Panama	84	150	
Venezuela	32	53	
Brazil	306	607	
Total number of annual nesting females	3,007	5,628	
Total number of females	7,518	15,196	Based on lowest [2.5 years] and highest [2.7 years] remigration interval
Total number of adults	15,035	30,091	Based on 1:1 sex ratio

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Appendix 2 - Estimate of total number of adult loggerhead turtles based on numbers of annual nesting females. Where appropriate, we converted total number of nests to annual number of nesters using an average clutch size per female of 4.1.

Annual Number of nesting females			
Country/Location	Min	Max	References and notes
Cay Sal Bank, Bahamas	122	146	Addison and Morford (1996); Addison (1998)
Brazil	1,180	1,180	Marcovaldi and Chaloupka (2007); Marcovaldi and Laurent (1996)
Cuba	250	300	Moncada-Gavilán in Ehrhart <i>et al.</i> (2003)
Southeastern US and Gulf of Mexico			
Northern	1,272	1,272	NMFS (2009)
South Florida	15,735	15,735	NMFS (2009)
Dry Tortugas	60	60	NMFS (2009)
Florida panhandle	221	221	NMFS (2009)
Yucatán, Mexico	220	569	Zurita <i>et al.</i> (2003)
<hr/>			
TOTAL number of annual nesting females	19,060	19,483	
<hr/>			
Total number of females	47,649	72,089	Based on lowest [2.5 years] and highest [3.7] remigration interval
<hr/>			
Total number of adults	95,299	144,177	Based on 1:1 sex ratio

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Appendix 3 - Total estimate of adult green turtles based on numbers of annual nesting females. Data as in NMFS (2007)

Country/location	Annual Number of nesting females		Notes
	Min	Max	
Florida, USA	5,055	5,055	
Cuyo and Holbox, Mexico	1,500	1,500	
Tortuguero, Costa Rica	17,402	37,290	
Aves island, Venezuela	335	443	
Galibi Reserve, Suriname	1,803	1,803	
Ilha de Trindade, Brazil	1,500	2,000	
Total number of annual nesting females	27,595	48,091	
Total number of females	82,785	144,273	Based on 3 year remigration interval
Total number of adults	165,570	288,546	Based on 1:1 sex ratio

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Appendix 4 - Clutch size for hawksbill, loggerhead, and green turtles

Species	Location	Clutch size	SD	Sample size	Reference
<i>Eretmochelys imbricata</i>					
	Bahia, Brazil	136	-	1,335	Marcovaldi <i>et al.</i> (1999)
	Celestun, Mexico	140	9.0	1,474	Perez-Castaneda <i>et al.</i> (2007)
	El Cuyo, Mexico	145	5.0	2,894	Perez Castaneda <i>et al.</i> (2007)
	Isla Holbox, Mexico	142	7.0	2,176	Perez Castaneda <i>et al.</i> (2007)
	Tortuguero, Costa Rica	158		93	Bjorndal (1985)
	Cayman islands	154	9.0	4	Aiken <i>et al.</i> (2001)
	Barbados	127	30.3	32	Horrocks and Scott (1991)
	Barbados	135	-	113	van Buskirk and Crowder (1994)
	Barbados	152	27.5	-	A. Harewood pers. comm.
	Pearl cays, Nicaragua	150	41.9	94	Lageux <i>et al.</i> (2006)
	Cuba	135	-	512	Moncada Gavilán <i>et al.</i> (1999)
	Antigua	155	-	93	Richardson <i>et al.</i> 1999 (1999)
	Shell beach, Guyana	158	-	7	Pritchard (1969)
	Suriname	146	-	13	Schulz (1975)
	Mona Island, Puerto Rico	148	-	30	van Buskirk and Crowder (1994)
	Grenada	119	-	36	Goodwin (1980; 1981) in Witzell (1983)
	Buck island, USVI	148	-	308	Diez <i>et al.</i> (1996)
	USVI	149	23.9	45	Hillis (1990)
	Guadeloupe	137	26	86	Kamel <i>et al.</i> (2009)
<i>Caretta caretta</i>	Overall	100-128	-		van Buskirk and Crowder (1994); NMFS (2009)
<i>Chelonia mydas</i>					
	Jupiter beach, Florida	118	-	163	Rusenko and Wood (1996)
	Bigi Santi, Suriname	138	-	566	van Buskirk and Crowder (1994)
	Melbourne Beach, Florida	135	-	229	van Buskirk and Crowder (1994)
	Quinatana Roo, Mexico	116	-	33	van Buskirk and Crowder (1994)
	El Cuyo, Mexico	113	-	19	van Buskirk and Crowder (1994)
	Shell beach, Guyana	122	-	6	Pritchard (1969)
	Tortuguero	113	23	2519	Bjorndal and Carr (1989)

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Appendix 5 - Emergence success data for hawksbill, loggerhead, and green turtles

Species	Location	Emergence success (%)	SD	Sample size	Reference
<i>Eretmochelys imbricata</i>					
	Grenada	62.2		22	Goodwin (1980,1981) in Witzell (1983)
	Guadeloupe	81.9		86	Kamel <i>et al.</i> (2009)
	Barbados	75.5		32	Horrocks and Scott (1991)
	Barbados	84.2	26.0	-	Olson 1985 in Witzell (1983)
	Barbados	51.9	43.7	-	A. Harewood (pers. comm. undeveloped beaches)
	Puerto Rico	67.1			A. Harewood (pers. comm. developed beaches)
	Virgin Islands	60.2		61	Small 1982 (all nests) in Bjorndal (1985)
	Tortuguero, Costa Rica	58.3		11	Bjorndal (1985)
	Celestun, Mexico	85.0		1,218	Perez Castaneda <i>et al.</i> (2007)
	El Cuyo, Mexico	82.0		2,268	Perez Castaneda <i>et al.</i> (2007)
	Isla Holbox, Mexico	88.0		1,805	Perez Castaneda <i>et al.</i> (2007)
	Antigua	72.6		102	McIntosh <i>et al.</i> (2003)
	Mona Island, Puerto Rico	73.9		-	Diez <i>et al.</i> (1996)
	Nicaragua	68.0		164	Lagueux <i>et al.</i> (2006)
<i>Caretta caretta</i>	Overall	45 - 70			NMFS (2009)
<i>Chelonia mydas</i>	Jupiter beach, Florida	86.9		163	Rusenko and Wood (1996)
	Cape San Blas, Florida	33.5		54	Lamont and Carthy (2007)
	Cape San Blas, Florida	54.1		80	Lamont and Carthy (2007)
	Cape San Blas, Florida	41.5		62	Lamont and Carthy (2007)
	Tortuguero, Costa Rica	54.0		-	Carr and Hirth (1962)
	Suriname	85.0		-	Schulz (1975)

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Appendix 6 - Species included under each reef fish functional group (based on 2005 underwater visual census surveys (Beets *et al.* 2006))

Functional Group	2005 survey data
Coralivores	<i>Arothron meleagris</i> <i>Cantherhines dumerillii</i> <i>Chaetodon multicinctus</i> <i>Chaetodon ornatissimus</i> <i>Chaetodon quadrimaculatus</i> <i>Plectroglyphidodon johnstonianus</i>
Detritivores	<i>Ctenochaetus hawaiiensis</i> <i>Ctenochaetus strigosus</i>
Herbivores	<i>Abudefduf sordidus</i> <i>Acanthurus blochii</i> <i>Acanthurus dussumieri</i> <i>Acanthurus leucopareius</i> <i>Acanthurus nigrofuscus</i> <i>Acanthurus nigroris</i> <i>Acanthurus olivaceus</i> <i>Acanthurus triostegus</i> <i>Calotomus carolinus</i> <i>Canthigaster jactator</i> <i>Cantherhines sandwichiensis</i> <i>Centropyge fisheri</i> <i>Centropyge potteri</i> <i>Chlorurus sordidus</i> <i>Cirripectes vanderbilti</i> <i>Melichthys niger</i> <i>Melichthys vidua</i> <i>Naso lituratus</i> <i>Naso unicornis</i> <i>Scarus psittacus</i> <i>Scarus rubroviolaceus</i> <i>Stegastes fasciolatus</i> <i>Zebrasoma flavescens</i> <i>Zebrasoma veliferum</i>
Mobile Invertebrate Feeders	<i>Bodianus bilunulatus</i> <i>Coris gaimard</i> <i>Coris venusta</i> <i>Diodon hystrix</i> <i>Echidna nebulosa</i>

Functional Group	2005 survey data
Mobile Invertebrate Feeders (cont.)	<i>Forcipiger longirostris</i> <i>Gomphosus varius</i> <i>Halichoeres ornatissimus</i> <i>Lutjanus kasmira</i> <i>Malacanthus brevirostris</i> <i>Macropharyngodon geoffroy</i> <i>Monotaxis grandoculis</i> <i>Mulloidichthys flavolineatus</i> <i>Paracirrhites arcatus</i> <i>Parupeneus bifasciatus</i> <i>Parupeneus multifasciatus</i> <i>Parupeneus pleurostigma</i> <i>Plectroglyphidodon imparipennis</i> <i>Pseudojuloides cerasinus</i> <i>Pseudocheilinus evanidus</i> <i>Pseudocheilinus octotaenia</i> <i>Pseudocheilinus tetrataenia</i> <i>Rhinecanthus aculeatus</i> <i>Rhinecanthus rectangulus</i> <i>Sebastapistes connota</i> <i>Stethojulis balteata</i> <i>Sufflamen bursa</i> <i>Sufflamen fraenatus</i> <i>Thalassoma duperrey</i> <i>Thalassoma trilobatum</i> <i>Xyrichtys aneitensis</i>
Piscivores	<i>Aphareus furca</i> <i>Aulostomus chinensis</i> <i>Cephalopholis argus</i> <i>Fistularia commersonii</i> <i>Gymnothorax flavimarginatus</i> <i>Labroides phthiophagus</i> <i>Oxycheilinus unifasciatus</i> <i>Parupeneus cyclostomus</i> <i>Paracirrhites forsteri</i> <i>Plagiotremus ewaensis</i> <i>Plagiotremus goslinei</i>
Sessile Invertebrate Feeders	<i>Chaetodon auriga</i> <i>Chaetodon lineolatus</i> <i>Chaetodon lunula</i> <i>Forcipiger flavissimus</i> <i>Ostracion meleagris</i> <i>Zanclus cornutus</i>

Functional Group	2005 survey data
Zooplanktivores	<i>Abudefduf abdominalis</i>
	<i>Abudefduf vaigiensis</i>
	<i>Acanthurus thompsoni</i>
	<i>Chromis agilis</i>
	<i>Chromis hanui</i>
	<i>Chaetodon miliaris</i>
	<i>Chromis vanderbilti</i>
	<i>Chromis verater</i>
	<i>Dascyllus albisella</i>
	<i>Heniochus diphreutes</i>
	<i>Hemitaurichthys thompsoni</i>
	<i>Myripristis berndti</i>
	<i>Myripristis kuntee</i>
	<i>Naso hexacanthus</i>
	<i>Xanthichthys auromarginatus</i>

Appendix 7 - Input data, references, and relevant observations by functional group for the Kaloko Honokōhau National Historical Park ecopath model. Whenever several species were included as part of a trophic guild, overall values were weighted according to individual species' biomass contribution within their respective groups. For species/groups that only typically occur in a given habitat, their biomass was area-weighted relative to the proportion of each benthic habitat category within park waters. The listed references indicate studies on which our calculations were based to derive input values for Ecopath.

Functional group	Value	References	Comments
<i>1. Spinner dolphins</i>			
B	2.74 t·km ⁻²	Norris <i>et al.</i> (1994)	Nine hundred and sixty animals are considered to regularly frequent the shore of the Big Island. We assumed for only a fraction of this number (100 dolphins) to be considered resident within Kaloko and feed there regularly. Average mass = 68 kg.
P/B	0.151 year ⁻¹	Barlow and Boveng (1991)	Assumed P/B to be equal to M and an average longevity of 20 years (NOAA 2003, 2005a).
Q/B	11.52 year ⁻¹	Average of three methods	
Method 1	15.70 year ⁻¹	See comments	Estimate based on a daily ration $R = 0.1 \cdot W^{0.8}$, as modified from Innes <i>et al.</i> (1987) in Trites and Heise (1996), where W is body weight in kg and R the daily ration in kg·day ⁻¹ . Hunt <i>et al.</i> (2000) describe energy requirements using the equation $E = a \cdot W^{0.75}$ where E is the energy requirement per day (kcal·day ⁻¹), W the mean body weight (kg) and a is a coefficient varying with the group of mammals (a = 320 for otariids, 200 for phocids, 192 for mysticetes, 317 for odontocetes, and 320 for sea otters).
Method 2	12.2 year ⁻¹	Hunter (2005)	Coefficient estimate was changed from 0.75 to 0.714
Method 3	6.66 year ⁻¹	Benoit-Bird (2004)	Based on assumption that daily maintenance energy needs of a spinner dolphin range between 2,430 kcal and 4,050 kcal, with an estimate of 3,520 kcal for an average adult.
Diet		Norris and Dohl (1980); Norris (1994); Perrin and Gilpatrick (1994); Würsig (1994); Perrin (1998); Benoit-Bird and Au (2003).	Small mesopelagics; bottom dwelling, and small numbers of surface dwelling species; as well as crustaceans. As species is expected to also feed outside of park waters, a substantial proportion of its diet was assumed to be 'imports'.
<i>2. Monk seals</i>			
B	0.179 t·km ⁻²	Baker and Jahonos (2004); T. Wurth (Pacific Islands Fisheries Science Center, pers. comm., 2007)	Assumed for 2 out of the minimum 52 individuals recorded during a 2001 aerial survey in the Hawaiian Islands (Baker and Johanos 2004) to be using and feeding in park waters. Although seals regularly haul out in the park, most of them cannot be assumed to utilise the parks' near shore resources as foraging habitat (i.e., have the resources contribute to their diet). Average mass = 187.5 kg (NOAA 2005b, NMFS 2006).

Functional group	Value	References	Comments
2. Monk seals			
P/B	0.121 year ⁻¹	Barlow and Boveng (1991)	Assumed P/B to be equal to M and a longevity estimate of 25 years (NOAA 2005b, 2006, NMFS 2007).
Q/B	11.51 year ⁻¹	See comments	As detailed above for spinner dolphins and two estimates of average caloric prey content calculated from data presented in Goodman-Lowe <i>et al.</i> (1999a) and Goodman-Lowe <i>et al.</i> (1999b).
Method 1	10.27 year ⁻¹		
Method 2	12.82 year ⁻¹		
Diet		Goodman-Lowe (1998); Longenecker <i>et al.</i> (2006)	Typical prey species include marine eels (Congridae, Muraenidae, and Ophichthidae) and various reef fish such as wrasse (Labridae), squirrelfish and soldierfish (Holocentridae), as well as triggerfish (Balistidae), followed by cephalopods and crustaceans. As species are expected to also feed outside of park waters, a proportion of its diet was assumed to be 'imports'.
3. Birds			
B	0.0024 t·km ⁻²	S. Waddington (Cyanotech, pers. comm. 2007) and K. Uyehara (pers. comm. 2008)	Model included Hawaiian stilt, sanderling (<i>Calidris alba</i>), ruddy turnstone (<i>Arenaria interpres</i>), wandering tattler (<i>Heteroscelus incanus</i>), Pacific golden-plover (<i>Pluvialis fulva</i>), and black-crowned night-heron (<i>Nycticorax nycticorax hoactli</i>) as these species are known to use the rocky intertidal beach areas for feeding, especially during low tides (Morin 1994). Portion of park available to forage = 0.1 km ² (S. Waddington, pers. comm. 2007). Individual species' weight data were extracted from a number of sources (e.g., Anonymous 1996a, Anonymous 1996b, Reed <i>et al.</i> 1998, Nettleship 2000, Gill <i>et al.</i> 2002, MacWhirter <i>et al.</i> 2002).
P/B	0.127 year ⁻¹	Reed <i>et al.</i> (1998); Nettleship (2000); Gill <i>et al.</i> (2002)	Computed from survivorship data.
Q/B	76.515 year ⁻¹	Nilsson and Nilsson (1976 in Wada (1996))	
Diet		See comments	Hawaiian stilts are opportunistic feeders that eat a variety of invertebrates and vertebrates available in shallow water and mudflats, such as polychaete worms, small crabs, aquatic insects, and small fish (Mitchell <i>et al.</i> 2005). Sanderlings' diet are known to markedly change between seasons, consisting almost exclusively of insects during the breeding season, and small crabs, isopods, insects, amphipods, polychaetes, and small mollusks in winter (Perez Hurtado <i>et al.</i> 1997, Tsipoura and Burger 1999, Petracci 2002, Anonymous 2005b, Nuka <i>et al.</i> 2005). Pacific golden plovers feed primarily on terrestrial insects, but are also known to forage in the intertidal areas and opportunistically prey on aquatic invertebrates (Kato <i>et al.</i> 2000, Anonymous 2005b). Outside of the breeding season, ruddy turnstones are known to prey on crustaceans, mollusks, polychaetes, and small fish (Tsipoura and Burger 1999, Nettleship 2000, Anonymous 2005c). The diet of wandering tattlers varies with season and in winter tends to consist of invertebrates such as marine worms, aquatic insects, mollusks, crustaceans, and small fish (Gill <i>et al.</i> 2002, Anonymous 2005d). The black-crowned night heron is an

Functional group	Value	References	Comments
			opportunistic feeder, whose diet consists mainly of fish, though it will occasionally feed on other items such as earthworms, aquatic and terrestrial insects (Wolford and Boag 1971). It has also been observed to feed on crayfish, mussels, squid, amphibians, lizards, snakes, and plant material (Davis 1993). As species are expected to also feed outside of park waters, a proportion of their diet was assumed to be 'imports'.
4. Rays			
B	4.233 t·km ⁻²	T. Clark (unpublished data, University of Hawai'i, 2009)	Includes the spotted eagle ray (<i>Aetobatus narinari</i>) and the manta ray (<i>Manta birostris</i>)
P/B	0.2 year ⁻¹	Z = M where M = empirical equation from Pauly (1980)	
Q/B	3.1 year ⁻¹	Fishbase; Olson and Watters (2003)	
Diet		Fishbase; T. Clark (unpublished data, University of Hawai'i, 2009)	Manta rays: Zooplankton; Spotted eagle rays: mostly benthic invertebrates. As species are expected to also feed outside of park waters, a proportion of their diet was assumed to be 'imports'.
5. Sharks and jacks			
B	0.07 t·km ⁻²	Parrish <i>et al.</i> (1990); Friedlander and DeMartini (2002)	Includes tiger sharks (<i>Galeocerdo cuvier</i>) (DLNR 2001, Thompson 2005, Meyers <i>et al.</i> 2009) and whitetip reef sharks (<i>Triaenodon obesus</i>), as well as other top predators such as bluefin trevally (<i>Caranx melampygus</i>), bigeye trevally (<i>Caranx sexfasciatus</i>), mackerel scad (<i>Decapterus macarellus</i>), golden trevally, (<i>Gnathanodon speciosus</i>), doublespotted queenfish (<i>Scomberoides lysan</i>), bigeye scad (<i>Selar crumenophthalmus</i>) and greater amberjack (<i>Seriola dumerili</i>) (http://www.nps.gov/kaho/).
P/B	1.058 year ⁻¹	Z = F + M where M = empirical equation from Pauly (1980); F based on Friedlander and Parrish (1997)	
Q/B	5.1 year ⁻¹	Fishbase	
Diet		Fishbase; Lowe (1996)	Predates on all groups with the exception of coral and algal groups and phytoplankton.
6. Hawksbill sea turtles			
B	0.054 t·km ⁻²	S. B. (unpublished data, 2009)	Hawksbill turtles are seen at specific sites within Kaloko on a regular basis (S.B., unpublished data, 2009). Although a number of them just travel through, hawksbill turtles have been filmed feeding and attempting to mate in park waters. Assumed for three hawksbill turtles to be 'resident' at Kaloko. Each turtle was assumed to weigh about 45 kg.

Functional group	Value	References	Comments
6. Hawksbill sea turtles			
P/B	0.109 year ⁻¹	Crouse <i>et al.</i> (1999)	Hawksbill turtles primarily feed on sponges and benthic invertebrates (Bjorndal 1997). In Hawai'i sponges are not abundant, and limited information gained through necropsies and visual observations indicate that hawksbill turtles appear to feed on sea cucumbers (S. B., pers. comm., 2009), fireworms (C. King, pers. comm., 2009), and red algae (G. B., NOAA National Marine Fisheries Service's (NMFS) Marine Turtle Research Program, unpublished data, 2009). As species is expected to also feed outside of park waters, a small proportion of its diet was assumed to be 'imports'.
Q/B	3.5 year ⁻¹	Best estimate	
Diet		See comments	
7. Green sea turtles			
B	1.591 t·km ⁻²	G. B. (unpublished data, 2008); S. B. (NPS unpublished data, 2008)	Of the 196 turtles associated with Kaloko, 143-161 show high site fidelity and can thus be considered Kaloko 'resident'. Average weight of green turtles captured in 2005 was 27.6 kg (NOAA NMFS Marine Turtle Research Program and the National Park Service (NPS), unpublished data, 2008).
P/B	0.109 year ⁻¹	Bjorndal <i>et al.</i> (2003)	Based on an average body weight intake of 1.8 % per day (recalculated from Brand <i>et al.</i> (1999) using length weight relationship as published in Arthur <i>et al.</i> (2006), as the original study was conducted in Australia; note, however, that both studies were conducted in seagrass environments).
Q/B	6.764 year ⁻¹	Brand <i>et al.</i> (1999)	
Diet		G. B. (unpublished data, 2008); NPS (unpublished data, 2009)	Turf algae and macroalgae, with turf _{LB} constituting the primary dietary component of green turtles within park waters based on green turtles seen to focus foraging activities on the lava bench.
8 - 14. Reef fish			
B			Fish biomass values were based on data for colonised hardbottom (CHB) and uncolonised hardbottom (UCH) only and extrapolated to the entire park using the proportion each benthic habitat category covers within park waters following Gibbs <i>et al.</i> (2007). Fish species were grouped according to the same functional groups used by Beets <i>et al.</i> (2006): corallivores, detritivores, herbivores, mobile invertebrate feeders (MIF), piscivores, sessile invertebrate feeders (SIF), and zooplanktivores (Zoo). See Appendix B for species list.
Piscivores	1.73 t·km ⁻²	Beets <i>et al.</i> (2006)	
Herbivores	20.34 t·km ⁻²		
Corallivores	0.54 t·km ⁻²		
Detritvores	2.26 t·km ⁻²		
MIF	9.76 t·km ⁻²		
SIF	0.54 t·km ⁻²		
Zooplanktivores	3.05 t·km ⁻²		

Functional group	Value	References	Comments
<i>8 - 14. Reef fish</i>			
P/B			
Piscivores	0.62 year ⁻¹	Z = F + M where M = empirical equation from	
Herbivores	1.40 year ⁻¹	Pauly (1980); F based on Friedlander and	
Corallivores	2.10 year ⁻¹	Parrish (1997)	
Detritivores	1.90 year ⁻¹		
MIF	0.95 year ⁻¹		
SIF	1.70 year ⁻¹		
Zooplanktivores	1.45 year ⁻¹		
Q/B			
Piscivores	6.12 year ⁻¹	Fishbase	
Herbivores	27.15 year ⁻¹		
Corallivores	12.92 year ⁻¹		
Detritivores	32.27 year ⁻¹		
MIF	8.11 year ⁻¹		
SIF	9.58 year ⁻¹		
Zooplanktivores	13.38 year ⁻¹		
Diet		(Hobson 1974); Fishbase; Bruggemann <i>et al.</i> (1994, 1998, 2001, 2006)	See diet table for diet composition of individual groups.
<i>15. Urchins</i>			
B	280 t·km ⁻²	Dotan (1990); McClanahan (1991); Rahman (2001); Rahman (2004); Muthiga (2005); Marrack <i>et al.</i> (2009) ; Weijerman <i>et al.</i> (2009).	The most frequently encountered urchins during surveys were <i>Echinometra mathaei</i> , <i>Echinothrix</i> spp. (i.e., <i>Echinothrix diadema</i> and <i>Echinothrix calamaris</i>), <i>Heterocentrotus mammilatus</i> and <i>Tripneustes gratilla</i> . Test size for <i>Echinothrix</i> spp., <i>T. gratilla</i> , <i>E. mathaei</i> , and <i>H. mammilatus</i> were recorded on the reef by local researchers (M. Weijerman, U.S. National Park Service, pers. comm., 2008; H. Jessop, University of Hawai'i, pers. comm., 2008) and converted to biomass based on published test size-weight relationships (Dotan 1990, McClanahan and Kurtis 1991, Rahman <i>et al.</i> 2001, 2004, Muthiga and Jaccarini 2005). We assumed for urchins to occur chiefly on colonized substrate with at least 10 % coral cover (M. Weijerman, pers. comm., 2008) and in reduced numbers at depth (F. Parrish, NOAA, National Marine Fisheries Service, Pacific Islands Fisheries Science Center, pers. comm., 2008).

Functional group	Value	References	Comments
<i>15. Urchins</i>			
P/B	0.484 year ⁻¹	Brey (2001)	
Q/B	8.547 year ⁻¹	See comments	Q/B rates for <i>T. gratilla</i> were derived based on feeding experiments conducted: (i) on <i>T. gratilla</i> and using averages for three species of algae employed in trials (M. Deagle, University of Hawai'i, pers. comm., 2007) (14.72 year ⁻¹); and (ii) on <i>T. gratilla</i> and <i>Echinothrix</i> sp. using <i>Gracilaria</i> only (H. Jessop, pers. comm., 2007) (13.9 year ⁻¹)., Q/B for <i>E. mathaei</i> was set at 4.44 year ⁻¹ based on data for Kenya from Carreiro-Silva and McClanahan (2001) and McClanahan and Kurtis (1991). For <i>Echinothrix</i> sp. the Q/B was set at 7.86 year ⁻¹ , the average between values reported by Carreiro-Silva and McClanahan (2001) and those obtained from feeding trials by H. Jessop (pers. comm., 2007). <i>H. mammilatus</i> was assigned the same Q/B rate as <i>Echinothrix</i> sp.
Diet		See comments	Observations at Kane'ohe Bay, Oahu, Hawai'i, by Stimson <i>et al.</i> (2007) show that <i>T. gratilla</i> 's diet composition typically reflects the algal distribution found on the reef, with individuals observed feeding on a variety of macroscopic algae, coralline algae, endolithic algae, and turfs. In Hawai'i, <i>E. calamaris</i> has been observed feeding on coralline algae, filamentous algae, brown algae (Castro, 1971 in 1982). <i>Echinothrix diadema</i> is known to forage on algae and encrusting organisms (Mortensen, 1940 in 1982). <i>Heterocentrotus mammilatus</i> has been seen to gnaw algae from bare substrate or the coral surface (Mortensen, 1943b and Dart, 1972 in de Ridder and Lawrence 1982) and consume crustose coralline algae (CCA) (Regis and Thomassin 1983). <i>E. mathaei</i> is a generalized herbivore, feeding on a variety of macrophytes (McClanahan <i>et al.</i> 2001), and preferentially on turf growing on the surface of dead coral or pavement, which explains why calcium carbonate sediments are usually the largest fraction of the gut content of <i>Echinometra</i> (Odum and Odum 1955, Black <i>et al.</i> 1984, McClanahan and Kurtis 1991, Mills <i>et al.</i> 2000).
<i>16. Crown of thorns</i>			
B	0.117 t km ⁻²	Marrack <i>et al.</i> (2009); Weijerman <i>et al.</i> (2009)	We assumed that (i) an individual weighs on average 466 g (Branham <i>et al.</i> 1971) and (ii) <i>A. planci</i> only occurs in areas with > 50 % coral cover.
P/B	0.411 year ⁻¹	Brey (2001)	Maximum age was set to eight years (Zann <i>et al.</i> 1990) and maximum weight was derived from Branham <i>et al.</i> (1971).
Q/B	9 year ⁻¹	Moran (1990), Keesing and Lucas (1992), Reyes-Bonilla and Caldero-Aguilera (1999), Scandol (1999)	Estimates ranged between 5.969 year ⁻¹ and 12.065 year ⁻¹ .
Diet		Birkeland and Lucas (1990)	Hermatypic scleractinian corals.

Functional group	Value	References	Comments
17. Benthic			
<i>Invertebrates</i>			
B	Estimated by Ecopath (EE = 0.95)	Parrish <i>et al.</i> (1990)	Only qualitative data available. Species include: white-spotted cucumber (<i>Actinopyga mauritiana</i>), snapping shrimp (<i>Alpheus crassimanus</i>), helmet urchin (<i>Colobocentrotus atratus</i>), lightfoot crab (<i>Grapsus tenuicrustatus</i>), sea cucumbers (<i>Holothuria</i> sp.), black purse shell (<i>Isognomon californicum</i>), black nerite (<i>Nerita picea</i>) (freshwater, brackish), banded coral shrimp (<i>Stenopus hispidus</i>), and the cushion star (<i>Culcita novaeguineae</i>). Although not surveyed, it seems reasonable to assume that polychaetes would constitute a significant proportion of the benthic invertebrate functional group.
P/B	2.910 year ⁻¹	Tudman (2001)	
Q/B	15.250 year ⁻¹	Tudman (2001)	
Diet		Brey (2001)	Zooplankton, phytoplankton, and detritus. A small portion of their diet was assumed to be 'imports' to reflect contribution of zooplankton from outside park waters.
18. Corals			
B	130 t·km ⁻²	Gibbs <i>et al.</i> (2007); Marrack <i>et al.</i> (2009); Weijerman <i>et al.</i> (2009)	We assumed that 0.5 km ² of Kaloko was covered with 100% coral and used estimations of Odum and Odum (1955) for biomass of heterotrophic tissue (polyps) and zooxanthellae (average of 0.021 g and 0.0038 g dry weight·cm ⁻² of coral skeleton). Values published in Atkinson and Grigg (1984) were used for dry to wet weight conversions.
P/B	0.14 year ⁻¹	Babcock (1991); Chadwick-Furman <i>et al.</i> (2000)	Based on 3 species of corals with relatively similar life characteristics to <i>Porites</i> spp., the dominant genus at Kaloko.
Q/B	2.1 year ⁻¹	Johannes and Tepley (1974); Palardy <i>et al.</i> (2008)	We assumed here for autotrophically acquired carbon to contribute about 60% of animal respiration (Johannes and Tepley 1974). Reduced original estimate (5.84 year ⁻¹) based on the proportion of energy the species derive from heterotrophic feeding and evidence of patchy distribution of zooplankton over reefs (Palardy <i>et al.</i> 2006).
Diet		Rosenfeld <i>et al.</i> (1999); Ribes <i>et al.</i> (2003a); Palardy <i>et al.</i> (2008);	Zooplankton, followed by detritus and phytoplankton. A small portion of their diet was assumed to be 'imports' to reflect contribution of zooplankton from outside park waters.
19. Octocorals			
B	2.9 t·km ⁻²	Beets <i>et al.</i> (2006); Marrack <i>et al.</i> (2009)	<i>Sarcothelia edmonsoni</i> .
P/B	0.2 year ⁻¹	Goffredo and Lasker (2008)	Despite benefiting from the photosynthetic products of its endosymbionts, <i>S. edmonsoni</i> may derive a significant proportion of its carbon through suspension feeding of particulate and dissolved organic matter from the surrounding environment (Fabricius <i>et al.</i> 1995, 1998). We therefore assumed heterotrophically acquired carbon to contribute about 80 % of animal respiration.

Functional group	Value	References	Comments
Q/B	4.63 year ⁻¹	Sorokin (1991); Ribes <i>et al.</i> (2003b)	Reduced from 9.25 year ⁻¹ based on the proportion of energy the species derives from heterotrophic feeding and evidence of patchy distribution of zooplankton over reefs (Palardy <i>et al.</i> , 2006).
Diet		Coma <i>et al.</i> (1994); Ribes <i>et al.</i> (1998); Ribes <i>et al.</i> (1999); Orejas <i>et al.</i> (2003); Ribes <i>et al.</i> (2003b); Rossi <i>et al.</i> (2004); Tsounis <i>et al.</i> (2006); Picciano and Ferrier-Pages (2007)	Zooplankton, phytoplankton, and detritus. A small portion of their diet was assumed to be 'imports' to reflect contribution of zooplankton from outside park waters.
20. Macroalgae			
B	22.691 t·km ⁻²	Smith <i>et al.</i> (2001); Beets <i>et al.</i> (2006); T. Sauvage (unpublished data, 2008); Marrack <i>et al.</i> (2009); Weijerman <i>et al.</i> (2009)	Estimates based on cover (0.62 % (Beets <i>et al.</i> 2006, Marrack <i>et al.</i> 2009, Weijerman <i>et al.</i> 2009)) and data published by Smith <i>et al.</i> (2001) and those kindly provided by T. Sauvage from experiments conducted in 2003 and 2004 in Waikiki (unpublished data, 2008).
P/B	9.824 year ⁻¹	Payri (2000)	
21. CCA			
B	37.818 t·km ⁻²	Smith <i>et al.</i> (2001); Beets <i>et al.</i> (2006); T. Sauvage (unpublished data, 2008); Marrack <i>et al.</i> (2009); Weijerman <i>et al.</i> (2009)	Estimates based on cover (10.46 % (Beets <i>et al.</i> 2006, Marrack <i>et al.</i> 2009, Weijerman <i>et al.</i> 2009)) and data published by Smith <i>et al.</i> (2001).
P/B	1.777 year ⁻¹	Payri (2000)	Conversion rates between gC, dry mass (DM) and wet weight (WW) were taken from Atkinson and Grigg (1984).
22. Turf algae			
B	128.78 t·km ⁻²	Smith <i>et al.</i> (2001); Beets <i>et al.</i> (2006); T. Sauvage (unpublished data, 2008); Marrack <i>et al.</i> (2009); Weijerman <i>et al.</i> (2009)	Include 20 different algal genera (McDermid <i>et al.</i> , 2007). Estimates based on cover (33.13 % (Marrack <i>et al.</i> 2009, Weijerman <i>et al.</i> 2009)) and data published by Smith <i>et al.</i> (2001) and those kindly provided by T. Sauvage from experiments conducted in 2003 and 2004 in Waikiki (unpublished data, 2008).
P/B	19 year ⁻¹	Payri (2000)	Conversion rates between gC, dry mass (DM) and wet weight (WW) were taken from Atkinson and Grigg (1984).
23. Turf algae_ava bench			
B	3.065 t·km ⁻²		Restricted to the shallow lava bench and intertidal area in Honokōhau Bay, (0.026 km ²) (based on Gibbs <i>et al.</i> (2007)). Assumed 65 % cover (T. Sauvage, University of Hawai'i, pers. comm., 2008).
P/B	25 year ⁻¹	Klumpp and McKinnon (1992), Arias-González (1994); Payri (2000); Bozec <i>et al.</i> (2004)	Higher than turf algae on the rest of the reef as shallow dense turf is known to register higher productivity rates than deeper reef turf (T. Sauvage, University of Hawai'i, pers. comm., 2008). Conversion rates between gC, dry mass (DM) and wet weight (WW) were taken from Atkinson and Grigg (1984).

Functional group	Value	References	Comments
<i>24. Zooplankton</i>			
B	1.24 t·km ⁻²	Bienfang (1980, 1983)	Zooplankton biomass (g WW) for the entire park area was derived by integrating the average tow biomass (Bienfang 1980, Bienfang 1983) over an average water column depth weighted by the surface area of each of 12 habitats, as listed in Gibbs <i>et al.</i> (2007).
P/B	219 year ⁻¹	Calbet <i>et al.</i> (2000)	Zooplankton samples were dominated by copepods (see Table 2 in Hoover and Gold (2005)).
Q/B	949 year ⁻¹	Bienfang (1980, 1983); Calbet <i>et al.</i> (2000);	Zooplankton samples were dominated by copepods (see Table 2 in Hoover and Gold (2005)).
Diet		Bienfang (1980, 1983); Roman (2001)	We assumed zooplankton species at Kaloko to be mostly herbivorous but included a fraction of their diet as detritus and zooplankton. Assumed for a small portion of zooplankton's diet to come from outside park waters (i.e., included as imports).
<i>25. Phytoplankton</i>			
B	3.295 t·km ⁻²	Bienfang and Johnson (1980)	We used the average value of measurements made in 1980 at 1.5 m and 5 m depth at the oceanic station 150 m outside of the Honokōhau Harbor. Phytoplankton biomass for the entire park was calculated using the same protocol as for zooplankton. In line with values observed in 1994-1996 and 2000 at coastal sites in the park 100 m to 200 m offshore of Kaloko and 'Aimakapa ponds (Brock and Kam (1997), Marine Consultants (2000) in Hoover and Gold (2005)).
P/B	325.458 year ⁻¹	Bienfang and Johnson (1980)	Used average C: Chl ratio of 90 based on values in Charpy and Blanchot (1998), Barbosa (2001), Yahel (1998), and Taylor (1997).
<i>26. Detritus</i>			
B	100 t·km ⁻²		Default value in Ecopath.

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