



# Fisheries Centre Research Reports

*2009 Volume 17 Number 2*

---

Modelling the trophic role of  
marine mammals in tropical  
areas: data requirements,  
uncertainty, and validation

# Modelling the trophic role of marine mammals in tropical areas: data requirements, uncertainty, and validation

by

Lyne Morissette, Jenny Lynn Melgo, Kristin Kaschner and Leah Gerber

*Fisheries Centre Research Reports 17(2)*  
*120 pages © published 2009 by*

*The Fisheries Centre,*  
*University of British Columbia*

*2202 Main Mall*  
*Vancouver, B.C., Canada, V6T 1Z4*

*ISSN 1198-6727*

Fisheries Centre Research Reports 17(2)  
2009

MODELLING THE TROPHIC ROLE OF MARINE MAMMALS IN TROPICAL AREAS: DATA  
REQUIREMENTS, UNCERTAINTY, AND VALIDATION

by  
Lyne Morissette, Jenny Lynn Melgo, Kristin Kaschner and Leah Gerber

CONTENTS

	Page
DIRECTOR'S FOREWORD .....	1
ABSTRACT .....	2
GENERAL INTRODUCTION .....	3
An Ecosystem Approach to the ' <i>whales eat fish</i> ' Issue.....	3
References .....	4
FOOD WEB MODEL AND DATA FOR STUDYING THE INTERACTIONS BETWEEN MARINE MAMMALS AND FISHERIES IN THE NORTHWEST AFRICAN ECOSYSTEM .....	6
Abstract.....	6
Introduction .....	6
Materials and methods .....	7
Study area .....	7
Harvesting on the ecosystem.....	8
Whaling.....	8
Fishery.....	8
Model description .....	13
Groups 1 - 10. Marine mammals.....	16
11. Seabirds.....	27
12. Large pelagics.....	27
13. Mesopelagic predators.....	28
14. Bathydemersal predators .....	28
15. Sharks .....	29
16. Rays.....	29
17. Coastal tunas .....	30
18. Coastal demersals .....	30
19. Clupeids.....	31
20. Other coastal pelagics .....	32
21. Cephalopods.....	32
22. Crustaceans.....	33
23. Benthos .....	33
24. Benthic producers .....	34
25. Zooplankton.....	34
26. Phytoplankton .....	34
27. Detritus.....	34
Balancing the model.....	35
Time series data .....	40
Biomass .....	40
Effort .....	43
Uncertainty analyses.....	44
Sensitivity analysis .....	45
'Ecoranger' analysis .....	45

Fitting the model to time series data.....	46
Simulating the removal of great whales in the ecosystem .....	46
Discussion .....	46
A new dataset built for Northwest Africa.....	46
Strengths and weaknesses of these modelling efforts .....	47
Acknowledgements .....	47
References .....	47
FOOD WEB MODEL AND DATA FOR STUDYING THE INTERACTIONS BETWEEN MARINE MAMMALS AND FISHERIES IN THE CARIBBEAN ECOSYSTEM.....	53
Abstract .....	53
Introduction .....	53
Materials and methods .....	55
Study area .....	55
Model description .....	56
Resource exploitation of the ecosystem .....	61
Balanced ecosystem model for the Caribbean region .....	70
Groups 1 - 10. Marine mammals .....	70
11. Seabirds .....	79
12. Seaturtles.....	80
13. Large tunas and billfishes .....	81
14. Small tunas.....	81
15. Dolphinfish.....	82
16. Flyingfish.....	83
17. Other offshore predators .....	83
18. Pelagic sharks .....	84
19. Coastal and demersal sharks and rays .....	85
20. Scombrids .....	85
21. Small and schooling pelagics .....	86
22. Reef fishes.....	87
23. Coastal predators .....	88
24. Cephalopods .....	88
25. Crustaceans and benthos .....	89
26. Zooplankton .....	89
27. Benthic producers .....	90
28. Phytoplankton .....	90
29. Detritus .....	90
Balancing the model .....	91
Time series data .....	98
Fishing effort.....	105
Uncertainty analyses.....	107
Sensitivity analysis .....	107
'Ecoranger' analysis.....	108
Fitting the model to time series data.....	108
Discussion .....	109
Strengths and weaknesses of the model.....	110
Acknowledgements .....	111
References .....	111
APPENDICES .....	117



*A Research Report from the Fisheries Centre at UBC*  
120 pages © Fisheries Centre, University of British Columbia, 2009

FISHERIES CENTRE RESEARCH REPORTS ARE ABSTRACTED IN THE FAO AQUATIC SCIENCES AND FISHERIES ABSTRACTS (ASFA)

ISSN 1198-6727

## DIRECTOR'S FOREWORD

---

This document demonstrates the importance of making the best use of local data while addressing critical issues in marine ecology and fisheries management. So far only few attempts have been made to describe the foodwebs in data-scarce areas of the world such as Northwest Africa or the Caribbean. However, whenever such attempts have been made, one realizes that hidden treasures do exist in such cases. Moreover, when data is integrated into a foodweb model, we gain a lot of knowledge by examining that whole ecosystem and determining where more data and research are needed, which can be very fulfilling.

Indeed, once we have a complete description of the whole food web, not only can we learn about the dynamics of the system and the ecology of each species included in it, but we can also discover indirect effects that the complexity of these systems holds. These indirect effects are only seen when examining the whole ecosystem structure, and can lead to counter-intuitive impacts on some trophic groups by others. In the case of marine mammals and their interaction with fish and fisheries, these effects can become very important conservation matters.

Marine mammals are part of ecosystem complexity, and often, they are not considered in models built for fisheries management. By applying an *Ecopath with Ecosim* approach, this report demonstrates that these animals can be incorporated in marine ecosystem models, and that their role in structuring the ecosystem is important. Thus, assessing their impact on the ecosystem or their interactions with fisheries requires a holistic overview of the ecosystem complexity, not only an assessment of predator-prey issues involving two or three species.

The 'whales eat fish' issue is a major point of discussion internationally, and more importantly in tropical countries who are highly depending on marine resources and where fisheries have encountered severe declines over the last decades. When addressing a very socio-politically complex issue such as the interactions between marine mammals and fisheries, it is crucial to make the best use of the data available in tropical countries and to integrate that into an ecosystem approach. A key contribution of this report is that it represents the most updated database on the biology and ecology of all marine organisms in two tropical ecosystems: the Caribbean and Northwest Africa. This was not only collected through an in-depth literature review, but also validated by many local experts in both areas during workshops held in Bridgetown, Barbados, and Dakar, Senegal.

Once again, the current report demonstrates how one of the key areas of research at our Centre can be used to provide insights into fisheries that would otherwise not be studied at the ecosystem level because of the usual excuse of "no data".

Rashid Sumaila  
May 12, 2009

## ABSTRACT

---

This Fisheries Centre Research Report includes two papers that describe whole-ecosystem models of two tropical breeding areas for baleen whales: Northwest Africa and the Caribbean. A mass-balance model, sources of data, and derivations of model parameters are detailed for each region. Exploration of the different sources of uncertainty and their effects on the modelling outcomes are also provided. Analyses based on these models examine the potential competition between whales and fisheries for marine resources.

## GENERAL INTRODUCTION

---

### AN ECOSYSTEM APPROACH TO THE ‘WHALES EAT FISH’ ISSUE<sup>a</sup>

Lyne Morissette

*Arizona State University,*

*Institut des Sciences de la mer de Rimouski*

&

*Fisheries Centre, The University of British Columbia*

*2202 Main Mall, Vancouver BC V6T 1Z4, Canada*

*Email: lyne.morissette@globetrotter.net*

Whales are large animals that are often seen as important predators in the world's oceans. Recently, some studies have even suggested that whales could be the cause of declined fish populations and that consequently they should be culled (Anonymous 2001a, Komatsu and Misaki 2003; also documented in Struck 2001; Jackson 2007; Holt 2007). For example, Tamura (2003) proposed that the total annual prey consumption by cetaceans in the world was three to six times the amount taken in marine fisheries. The idea of whaling is then propagated as a solution to increase food supply available for fisheries (Anonymous 2001a). This is often proposed that whales are responsible for the worldwide decline of fisheries resources (Komatsu and Misaki 2003) and that an eventual surplus of biomass (the 249-436 million tons of fish consumed by whales) could be directly available for human consumption if the abundance of cetaceans was to be reduced (Anonymus 2001b).

Living marine organisms have evolved together in an intricate web of feeding relationships structured on a template of these complex ocean habitats. However, fisheries are now depleted, and the abundance of marine organisms (including whales) has decreased drastically over the past century. Although these food webs are robust in the face of extreme seasonal change and have persisted in the face of long-term fluctuations over the years, tropical ecosystems are especially delicate in the face of human influences, especially commercial fishing, whaling, and pollution. These ecosystems are now severely suffering from a major crisis resulting from depleted fish stocks (Palomares and Pauly 2004; Fanning *et al.* 2007).

While trying to gain an understanding of what could explain the collapse in their fisheries, many national research agencies of both Northwest African and Caribbean countries have been working at collecting data on the different species or links or these food webs. At the same time, some foreign agencies explain the crisis by proposing that whales are consuming fish and that this is why there is nothing left to catch in tropical areas. By doing so, they try to end the moratorium on commercial whaling at the International Whaling Commission (IWC) and resume the hunt of the so-far-protected whales. While many local managers and government members consider this to be a credible argument, most scientists assert that whales are not having much of an impact in these tropical breeding areas. In reality, it is now well-documented that overfishing is happening on a global scale (Jackson *et al.* 2001; Pauly *et al.* 2002; Baum *et al.* 2003; Myers and Worm 2003), and there is no scientific evidence for the existence of large-scale competition between marine mammals and fisheries (Kaschner 2004; Morissette 2007). Last but not least, given the importance of indirect effects in ecosystems, the true consequences of culling are unpredictable (Paine *et al.* 1998; Scheffer *et al.* 2001; Corkeron 2009). Nonetheless, ‘whales eat fish’ has become a very controversial issue and now comes back to the table year after year during IWC meetings (Gerber *et al.* 2009). Meanwhile, the public profile of “whales don’t eat fish”, promoted by many NGOs such as Lenfest Ocean Program, IFAW, WWF and Greenpeace, has never been higher.

---

<sup>a</sup> Cite as: Morissette, L. (2009) An ecosystem approach to the ‘whales eat fish’ issue. In: Morissette, L., Melgo, J.L., Kaschner, K. and Gerber, L.R. (eds.) Modelling the trophic role of marine mammals in tropical areas: data requirements, uncertainty, and validation. Fisheries Centre Research Reports 17(2). Fisheries Centre, University of British Columbia, Vancouver, Canada, pp. 3-5.

It is now clear that ocean ecosystems throughout the world have experienced a dramatic shift in structure as a result of extensive fishing activities and the removal of top predators (see Estes *et al.* 2007). In order to address issues on the interactions between marine mammals and fisheries (such as the 'whales eat fish' issue), an ecosystem approach is essential, as there are a large number of indirect and direct interactions through which these two groups might influence each other (Bax 1998; Morissette *et al.* 2006). When these complex trophic interactions are taken into account, it has been shown in a number of cases that culling of marine mammals would not necessarily lead to recovery of fish stocks, nor otherwise benefit the commercial fishery (Punt and Butterworth 1995; Plagányi and Butterworth 2002; Morissette 2007; Gerber *et al.* 2009). Beneficial predations effects, e.g., marine mammals and other high-level predators increasing fisheries catches by feeding on other species that could be competing with the fleets, is more and more documented (Punt and Butterworth 1995, Walters and Kitchell 2001; Morissette). Only by considering all possible direct and indirect trophic linkages can the effect on current fisheries yields of the partial or complete removal of large whales be reliably assessed.

Here, we examine the scientific evidence for the assertion that commercial fisheries are negatively impacted by whales. We use the *Ecopath with Ecosim (EwE)* approach, a quantitative whole-ecosystem model that tracks trophic flows in the food web from plankton, through pelagic and benthic fishes, all the way to marine mammals. *EwE* is one of several ecosystem modelling approaches that are widely used in understanding the interactions between marine mammals and fisheries (Morissette 2007). That approach is important because it represents a rational way of quantifying the trade-offs between sustainable exploitation of natural marine resources and conservation of charismatic fauna (Pitcher, 2005). The models also have the advantageous possibility of being tuned (or validated) to conventional stock assessment data or surveyed biomass estimates. The project focuses on two regions where the "whales eat fish" assertion has become a political and management issue: Northwest Africa and the Caribbean.

We employ a precautionary approach to understanding management scenarios regarding the reduction of the abundance of great whales in Northwest Africa. While there is great uncertainty in many model parameters, we suggest that rather than engaging in discussions about the interactions between whales and fish in the absence of data, models can be developed with the best assumptions available and refined as more data become available (Hammill and Stenson 2007; Currie 2007). Models may also be used to consider the range of possible scenarios for a wide range of uncertainty about parameters. Addressing uncertainty is critical to providing useful management advice for the 'whales eat fish' issue, but presents a difficult challenge to whole-ecosystem modeling. Data on the biology, life-cycle, and exploitation of marine organisms that need to be captured in whole ecosystem simulations are often lacking for tropical ecosystems. Consequently, an in-depth uncertainty analysis has to be performed in both models to examine the extent to which our analyses are influenced by data quality and uncertainty.

This report also documents two workshops, held in Dakar, Senegal on 15-17 May 2008 and in Bridgetown, Barbados on 25-27 September 2008 and through which the 'whales eat fish' and data availability issues were explored. Thus, this report documents the updated models following these workshops, where African and Caribbean researchers worked with our team on refining our models' structure and data.

The present report is freely available at the website of the Fisheries Centre of the University of British Columbia. ( [www.fisheries.ubc.ca/publications/reports/fcrr.php](http://www.fisheries.ubc.ca/publications/reports/fcrr.php) ).

## REFERENCES

- Anonymous 2001a. What can we do for the coming food crisis in the 21st century? Institute of Cetacean Research. 4pp.  
 Anonymous. 2001b. Increasing competition between fisheries and whales. Japan's whale research in the Western North Pacific (JARPA II). Fisheries Agency.  
 Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, J. and Doherty, P.A.. 2003. Collapse and conservation on shark populations in the Northwest Atlantic. *Science* 299: 389-392.  
 Bax, N.J. 1998. The significance and prediction of predation in marine fisheries. *ICES Journal of Marine Sciences* 55: 997-1030.  
 Corkeron, P. 2009. Marine mammals' influence on ecosystem processes affecting fisheries in the Barents Sea is trivial. *Biology Letters* 1098/rsbl.2008.0628  
 Currie, D. 2007. Whales, Sustainability and International Environmental Governance. *Review of European Community & International Environmental Law* 16: 45-57  
 Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M. and Brownell Jr., R.L. 2007. Whales, whaling, and ocean ecosystems. University of California Press, 418 p.



- Fanning, L., Mahon, R. McConney, P., Angulo, J., Burrows, F., Chakalall, B., Gil, D., Haughton, M., Heileman, S., Martínez, Ostine, L., Oviedo, A., Parsons, S., Phillips T., Arroya, C.S., Simmons, B., and C. Toro. A large marine ecosystem governance framework. *Marine Policy* 31: 434-443.
- Gerber, L., Morissette, L., Kaschner, K., and Pauly, D. 2009. Should whales be culled to increase fishery yield? *Science* 323: 880-881.
- Hammill, M.O. and Stenson, G.B. 2007. Application of the precautionary approach and conservation reference points to management of Atlantic seals. *ICES Journal of Marine Science* 64: 702-706.
- Holt, S.J. 2007. Whaling: Will the Phoenix rise again? *Marine Pollution Bulletin* 54: 1081-1086
- Jackson, J. B. C., M.X. Kirby, W. H. Berger, K.A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Ponder, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629-638.
- Jackson, J.B.C. 2007. When ecological pyramids were upside down. pp. 23-37 *In* Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M. and Brownell Jr., R.S. (Eds.) *Whales, Whaling, and Ocean Ecosystems*. University of California Press, Berkeley and Los Angeles, California.
- Kaschner, K. 2004. Modelling and mapping of resource overlap between marine mammals and fisheries on a global scale. Ph.D., University of British Columbia.
- Katona, S. and Whitehead, H. 1988. Are cetaceans ecologically important? *Oceanography and Marine Biology Annual Reviews* 26: 553-568.
- Komatsu, M. and Misaki, S. 2003. Whales and the Japanese: how we have come to live in harmony with the bounty of the sea. The Institute of Cetacean Research, Tokyo, 170 pp.
- Morissette, L. 2007. Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence. PhD thesis, Zoology, University of British Columbia, Vancouver BC, Canada.
- Myers, R. A. and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280-283.
- Paine, R.T., Tegner, M.J., and Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535-545.
- Palomares, M.L.D. and Pauly, D. (Eds.) 2004. *West African marine ecosystems: models and fisheries impacts*. Fisheries Centre Research Reports 12(7).
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R. and Zeller, D. 2002. Towards sustainability in world fisheries. *Nature* 418: 689-695.
- Pitcher, T.J. (2005) Simulating Antarctic ecosystems and fisheries: weapons of mass construction. In: Palomares, M.L.D., Plagányi, E.E. and D.S. Butterworth. 2002. Competition with fisheries. pp 268-273 *In* Perrin, W.F., Würsig, B., and Thewissen, H.G.M. (Eds.) *Encyclopedia of Marine Mammals*. Academic Press, San Diego.
- Pruvost, P., Pitcher, T.J., Pauly, D. (eds.) *Modeling Antarctic marine ecosystems*.
- Punt, A.E. and Butterworth, D.S. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals *Arctocephalus pusillus pusillus* and the Cape hakes *Merluccius capensis* and *M. paradoxus*. *South African Journal of Marine Science* 16: 255-285.
- Scheffer, M., S. Carpenter, J. A., Foley, C. Folke, and Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591-596.
- Springer, A.M., Estes, J.A., van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M., Forney, K.A., and Pfister, B. 2003. Sequential megafaunal collapse in the North Pacific Ocean; an ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences* 100: 12 223-12 228.
- Struck, D. 2001. Japan blames whales for lower fish catch. *International Herald Tribune* (July 28-29).
- Tamura, T. 2003. Regional assessments of prey consumption and competition by marine cetaceans in the world. In *Responsible Fisheries in the Marine Ecosystem*. pp. 143-170 *In* Sinclair, M. and Valdimarsson, G. (Eds.). *Responsible Fisheries in the Marine Ecosystem*, Fishery Industries Division, CAB International: FAO, Rome (Italy) and Wallingford (United Kingdom).
- Walters, C. and J.F. Kitchell. 2001. Cultivation/Depensation Effects on Juvenile Survival and Recruitment: Implications for the Theory of Fishing. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 39-50.

# FOOD WEB MODEL AND DATA FOR STUDYING THE INTERACTIONS BETWEEN MARINE MAMMALS AND FISHERIES IN THE NORTHWEST AFRICAN ECOSYSTEM<sup>a</sup>

---

Lyne Morissette<sup>1,2,3</sup>, Jenny Lynn Melgo<sup>1</sup>, Kristin Kaschner<sup>4</sup>, Leah Gerber<sup>1</sup>, Idrissa Lamine Bamy<sup>5</sup>,

<sup>1</sup>Arizona State University, School of Life Sciences,  
P.O. Box 874501, Tempe, AZ 85287-4501, USA

<sup>2</sup>Institut des sciences de la mer de Rimouski,  
310, Allée des Ursulines, C.P. 3300, Rimouski, QC, G5L 3A1, CANADA

<sup>3</sup>Fisheries Centre, The University of British Columbia  
2202 Main Mall, Vancouver BC V6T 1Z4, CANADA

<sup>4</sup>Albert-Ludwigs-University, Institute of Biology I (Zoology)  
Evolutionary Biology & Ecology Lab, Freiburg, GERMANY

<sup>5</sup>Centre National des Sciences Halieutiques de Boussoura,  
BP-3738 Boussoura, Conakry, GUINEA

[Lyne.Morissette@globetrotter.net](mailto:Lyne.Morissette@globetrotter.net)  
[Jennylynn.Melgo@asu.edu](mailto:Jennylynn.Melgo@asu.edu)  
[Kristin.Kaschner@biologie.uni-freiburg.de](mailto:Kristin.Kaschner@biologie.uni-freiburg.de)  
[Leah.Gerber@asu.edu](mailto:Leah.Gerber@asu.edu)  
[ibamy@caramail.com](mailto:ibamy@caramail.com)

## ABSTRACT

This report describes the data and methodology used to construct a model for Northwest Africa during the late 1980s. The model for Northwest Africa includes the Large Marine Ecosystem (LME) of the Canary Current, which is located on the eastern part of the Atlantic Ocean, and bounded by the coasts of Morocco, Mauritania, Senegal, Guinea-Bissau, the Canary Islands (Spain), Gambia, Cape Verde and Western Sahara. The model was developed to examine the trophic interactions between marine mammals and fisheries and uses simulations to examine the potential impact of a reduction in the abundance of great whales on fishery yield. The model includes 10 marine mammals groups and 17 additional groups comprised of fish, seabirds, invertebrates, and plankton. Both local and foreign fleets are also included in the model.

## INTRODUCTION

A mass-balanced model of the Northwest coast of Africa was constructed using *EwE* (Christensen and Walters 2004). It took as a starting point an *Ecopath* model developed by Samb and Mendy (2004), as well as six other *Ecopath* models developed in the context of “Fisheries Information and Analysis System”

---

<sup>a</sup> Cite as: Morissette, L., Melgo, J.L., Kaschner, K., Gerber, L., and Bamy, I.L. (2009) Food web model and data for studying the interactions between marine mammals and fisheries in the Northwest African ecosystem. In: Morissette, L., Melgo, J.L., Kaschner, K. and Gerber, L.R. (eds.) Modelling the trophic role of marine mammals in tropical areas: data requirements, uncertainty, and validation. Fisheries Centre Research Reports 17(2). Fisheries Centre, University of British Columbia, Vancouver, Canada, pp. 6-47.

(SIAP), after two workshops in Dakar (February and August 2001), which were attended by scientists from the six countries represented by the models: Cape Verde, Gambia, Guinea, Guinea-Bissau, Mauritania, and Senegal. We used the Senegambian ecosystem model (Samb and Mendy 2004) as a starting point, and included relevant information about marine mammals and other important trophic group for the greater Northwest Africa region.

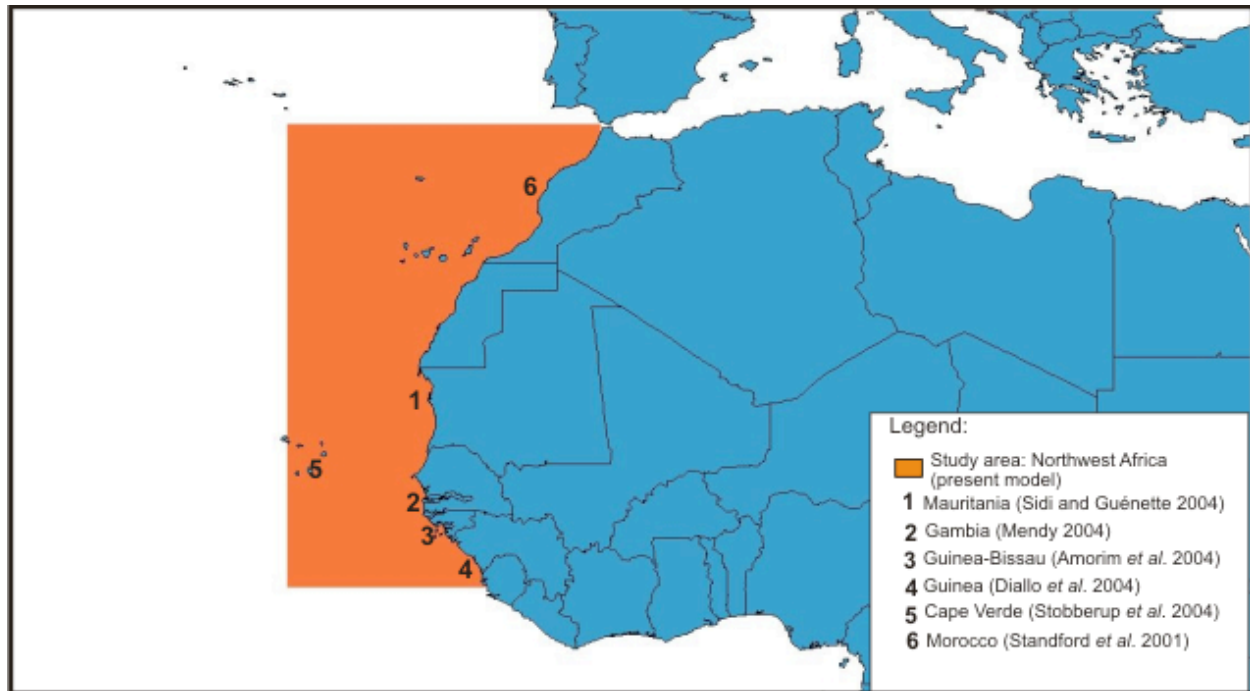
This report describes the data sources used for constructing the *Ecopath with Ecosim* model of Northwest Africa, and the uncertainty analyses performed on input and output data. The aim of this report is to present our preliminary results to the participants of the “Whale and fish interactions: are great whales a threat to fisheries?” workshop in Dakar, Senegal on 8-9 May, 2008. Preliminary results of the research are still being refined and will be presented at the meeting. We hope to receive expert advice and feedback on our research methodology, data and preliminary results during the discussions held at the workshop. We also hope to confirm that we are not missing key data that should be included in our model. The model will be continuously updated as more data are collected. Ultimately, our model may be used as a basis to evaluate the trophic role of great whales in the ecosystem of Northwest Africa.

## MATERIALS AND METHODS

### STUDY AREA

Our study area is located off the coast of Northwest Africa, bounded by Morocco, Mauritania, Senegal, Guinea-Bissau, the Canary Islands (Spain), Gambia, Cape Verde and Western Sahara (Figure 1). This area defined by the United States National Oceanic and Atmospheric Administration (NOAA) as the Canary Current large marine ecosystem (LME), and is included in the Food and Agriculture Organization's (FAO's) Eastern Central Atlantic (Major Fishing Area 34), mainly covering subdivision 34.1 (Northern coastal), and part of subdivision 34.2 (Northern oceanic). The specific area of this model covers latitudes from 8.5 N to 35.97 N, and longitudes from 30 W to 6.5 W, for a total area of 3,561,029 km<sup>2</sup> (Figure 1). Our study area includes the continental shelf as well as the deeper area.

The Northwest coast of Africa is characterized by the presence of the Canary Current, which flows along the African coast from north to south between 30°N and 10°N and offshore to 20°W (Fedoseev 1970). As a consequence, one major characteristic of this ecosystem is that it shows a major upwelling and other seasonal nutrient enrichments. Climate is the primary force driving the dynamics of this ecosystem, with intensive fishing as the secondary driving force (Bas 1993).



**Figure 1.** Map of the study area; the coast of Northwest Africa.

## HARVESTING ON THE ECOSYSTEM

### Whaling

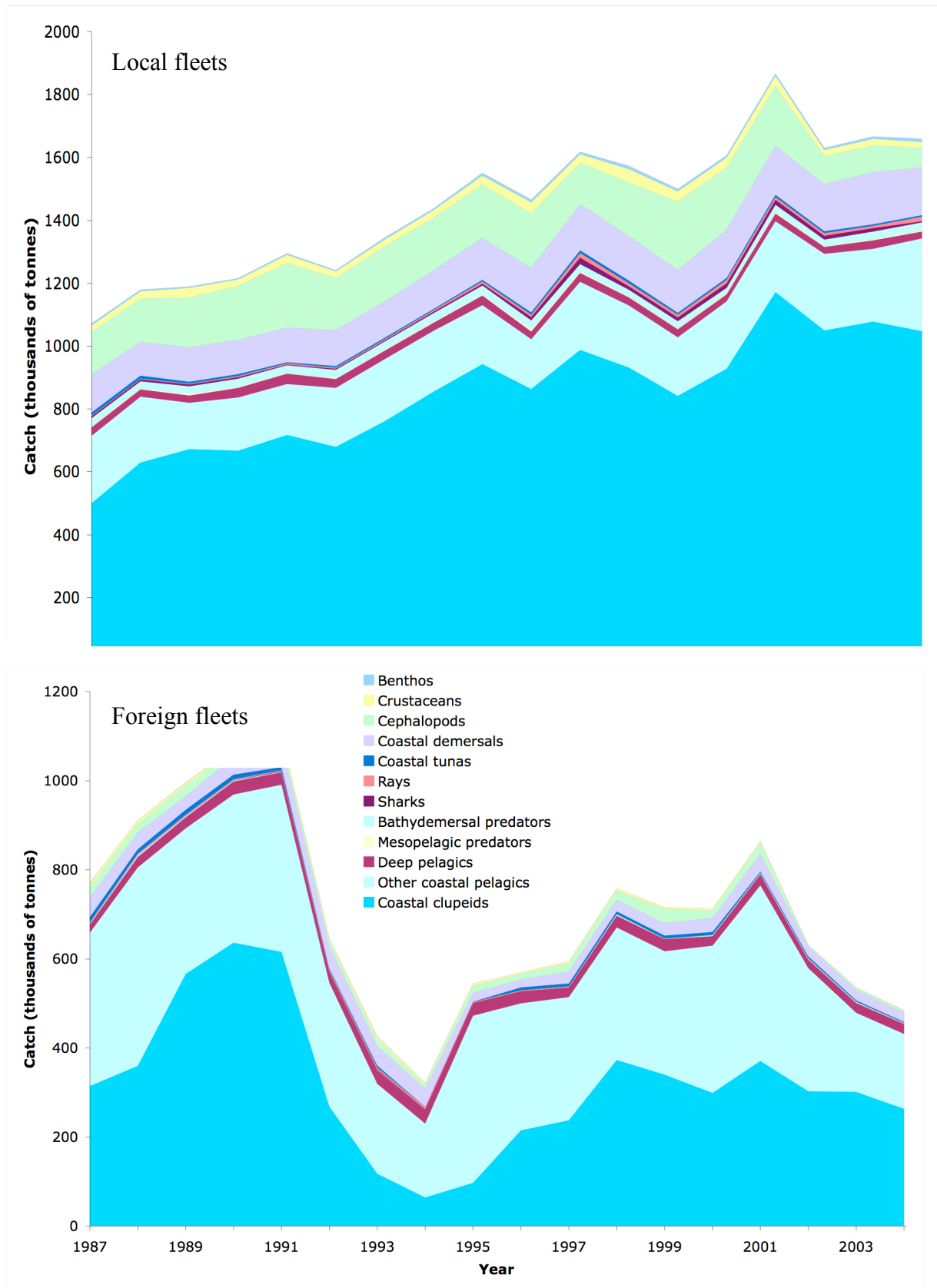
Whaling is known to occur in Northwest African waters (Reeves 2002), but to our knowledge no official data on actual harvests are available. The only record available documents aboriginal subsistence whaling in Equatorial Guinea, where Indigenous Africans principally target humpback whales (and mainly calves). No estimate is available on the annual take, but Aguilar (1985) guessed that it was approximately three humpback whales annually. These whales are assumed to be part of a Southern Hemisphere population of humpback whales (Reeves 2002).

### Fishery

The area of Northwest Africa is generally thought to be overexploited for most coastal demersal species (Samb and Mendy 2004). As a result, fishing effort is often reported for species such as sardinellas, for which acoustic survey shows a relatively stable abundance. However, Samb and Mendy (2004) mention that this shift from fishing coastal demersal species to a situation where sardinellas are very important in the catch should be better addressed since sardinellas have an important role in maintaining the structure of the food web.

The Northwest African ecosystem supports both local and foreign fleets, representing an average of 2,153,091 tonnes of fish caught annually in the system. From 1987 to 2004, local fleets generally caught the majority of this biomass, but the proportion of local fleets vs. foreign fleets varied from a minimum of 53.1% of catches taken by local fleets in 1990 to a maximum of 81.7% of the catches in 1994 (Figure 2).

Demersal fisheries have increased substantially over the last few decades (Gascuel et al. 2007), but it seems that few studies can describe catches and fishing effort adequately, and that FAO data are not reliable for the area (Gascuel et al. 2007).



**Figure 2.** Local and foreign catches off the coast of Northwest Africa from 1987-2004. Source: *Sea Around Us* Project database, [www.searoundus.org](http://www.searoundus.org)

We synthesized available information about the catch composition for the period 1987-2004 by species, year, and country for local and foreign fleets fishing off the coast of Morocco, Mauritania, Senegal, Guinea-Bissau, Canary Islands, Gambia, Cape Verde, and Western Sahara (Tables 1 and 2). We relied on estimates of unreported catch and by-catch of industrial fisheries and the database of fisheries catch developed by the *Sea Around Us Project* (SAUP) at the University of British Columbia ([www.seaaroundus.org](http://www.seaaroundus.org)).

Fisheries catch taken in all three study areas were obtained from the *Sea Around Us* database (Sea Around Us, 2008). A global database on marine fisheries and ecosystems. World Wide Web site [www.seaaroundus.org](http://www.seaaroundus.org). Fisheries Centre, University British Columbia, Vancouver (British Columbia, Canada). [Visited February 2008]). Time series of annual total catches taken between 1987 and 2004 were specified by the respective countries fishing in the area and by the taxa that were taken. We assigned taxa to the appropriate functional group of each *Ecopath* model using available information about life history, ecology and habitat preferences of the taxa. Catches were then divided into local and foreign fisheries. Local fisheries were defined as all countries bordering on our study area, disregarding of whether or not catches were taken within each country's own EEZ waters or in neighboring waters. All other fishing countries were defined as foreign fleets (Figure 2). We used our database to reconstruct the catch composition for the period 1987-2004.

**Table 1.** Time series of local fleets' catches by trophic group in the Ecopath model for Northwest Africa (in '1000 tonnes).

	10	11	12	13	14	15	16	17	18	19	20	21	
	Large pelagics	Mesopelagic predators	Bathy-demersal predators	Sharks	Rays	Coastal tunas	Coastal demersals	Clupeids	Other coastal pelagics	Cephalo-pods	Crustaceans	Benthos	Total
1987	26.915	5.388	24.568	6.017	1.774	10.672	120.415	500.891	213.504	134.650	20.709	6.845	<b>1072.348</b>
1988	23.375	3.734	21.582	6.521	2.427	9.162	107.468	629.245	210.107	136.912	23.308	4.702	<b>1178.544</b>
1989	23.735	3.972	24.713	6.037	2.208	6.745	109.722	672.237	147.371	158.504	30.032	3.401	<b>1188.676</b>
1990	30.165	4.622	24.757	5.454	3.807	6.166	109.685	667.183	169.282	169.978	20.981	3.453	<b>1215.534</b>
1991	32.851	2.534	24.264	3.217	3.370	3.613	109.248	717.077	161.821	206.445	24.976	4.914	<b>1294.329</b>
1992	27.097	2.544	27.128	3.471	4.001	3.972	115.562	679.073	188.770	165.040	20.254	4.595	<b>1241.507</b>
1993	27.447	3.775	25.942	3.215	4.134	3.801	115.915	761.000	196.992	174.518	22.201	5.249	<b>1344.189</b>
1994	25.501	3.272	27.374	4.211	5.477	3.553	123.068	854.852	194.105	166.253	24.227	5.745	<b>1437.637</b>
1995	30.396	3.507	28.191	5.936	6.794	5.145	132.434	942.914	187.792	171.359	27.164	8.681	<b>1550.315</b>
1996	24.826	7.201	28.259	10.190	7.115	7.404	141.367	863.837	157.882	173.034	35.566	8.366	<b>1465.047</b>
1997	28.102	4.159	23.436	21.334	13.816	8.647	147.355	987.874	216.845	131.279	27.518	6.743	<b>1617.110</b>
1998	25.795	4.560	19.726	11.751	9.815	8.320	140.712	931.278	197.237	171.030	42.228	10.613	<b>1573.065</b>
1999	25.745	4.472	21.831	12.194	8.540	5.336	136.188	841.400	186.154	217.558	32.879	7.465	<b>1499.761</b>
2000	22.495	4.246	16.535	14.592	10.278	6.836	152.896	927.665	214.420	199.105	29.896	7.165	<b>1606.129</b>
2001	25.208	4.149	23.614	15.614	9.234	6.820	156.339	1171.271	225.264	189.168	31.663	7.841	<b>1866.186</b>
2002	21.883	3.893	19.642	12.537	7.749	6.291	150.478	1050.218	243.100	88.259	19.687	6.330	<b>1630.067</b>
2003	26.922	3.701	24.948	10.870	6.629	5.244	165.718	1078.499	230.319	85.690	20.898	6.215	<b>1665.654</b>
2004	21.440	3.747	25.759	4.318	13.930	4.607	152.834	1047.249	294.973	62.420	17.416	10.185	<b>1658.877</b>

**Table 2.** Time series of foreign fleets' catches by trophic group in the Ecopath model for Northwest Africa (in '1000 tonnes).

	10	11	12	13	14	15	16	17	18	19	20	21	
Year	Large pelagics	Mesopelagic predators	Bathydemersal predators	Sharks	Rays	Coastal tunas	Coastal demersals	Clupeids	Other coastal pelagics	Cephalopods	Crustaceans	Benthos	Total
1987	18.133	0.000	3.537	0.860	1.688	10.972	44.027	314.194	344.466	23.178	8.488	0.426	<b>769.969</b>
1988	23.423	0.000	4.339	0.919	2.416	9.774	37.594	359.614	445.571	19.852	6.710	0.140	<b>910.352</b>
1989	24.700	0.000	3.028	0.862	2.077	10.973	30.130	565.703	327.247	24.036	5.943	0.325	<b>995.025</b>
1990	29.010	0.000	2.071	0.903	2.208	10.022	41.111	635.854	333.376	13.816	5.261	0.029	<b>1073.660</b>
1991	27.706	0.000	1.465	1.212	2.365	6.323	52.960	615.550	375.413	14.854	5.275	0.000	<b>1103.124</b>
1992	23.680	0.000	0.783	1.796	3.810	1.941	50.265	268.615	277.797	11.726	4.730	0.000	<b>645.142</b>
1993	30.062	0.000	0.064	1.491	4.674	4.117	44.020	117.591	202.228	14.379	6.365	0.667	<b>425.658</b>
1994	29.583	0.000	0.259	1.408	4.840	0.569	41.305	64.681	165.995	8.650	4.089	0.000	<b>321.378</b>
1995	27.854	0.001	0.464	0.139	2.664	0.490	20.222	96.962	375.167	15.962	4.197	0.040	<b>544.160</b>
1996	26.786	0.001	0.149	0.104	1.840	6.720	17.739	214.901	285.468	11.998	3.219	0.000	<b>568.925</b>
1997	22.050	0.000	0.647	0.037	0.963	7.052	27.036	237.487	276.764	17.916	3.969	0.010	<b>593.931</b>
1998	26.707	0.000	2.863	0.072	0.310	6.194	26.508	373.057	297.179	20.290	4.173	0.009	<b>757.360</b>
1999	26.917	0.000	0.898	0.080	0.433	6.872	27.587	340.364	277.016	32.015	3.861	0.005	<b>716.048</b>
2000	21.277	0.000	1.863	0.105	0.732	6.392	31.781	299.077	330.533	17.193	3.322	0.003	<b>712.278</b>
2001	25.377	0.000	1.555	0.427	0.683	3.177	39.891	370.917	393.755	23.882	3.851	0.003	<b>863.518</b>
2002	19.030	0.000	2.311	0.338	0.507	4.217	20.634	302.658	276.657	3.262	1.089	0.000	<b>630.702</b>
2003	21.486	0.000	2.001	0.433	0.625	2.753	23.338	301.637	177.633	4.339	1.198	0.000	<b>535.443</b>
2004	23.157	0.000	1.109	0.016	0.582	2.463	20.238	263.034	168.238	4.295	0.865	0.000	<b>483.996</b>



## MODEL DESCRIPTION

The ecosystem model for Northwest Africa was modified based on a model for the Senegambian ecosystem in the 1990s (Samb and Mendy 2004). The Senegambian ecosystem model was used because it was representative of a typical ecosystem in Northwest Africa, and could thus be extrapolated to represent our larger study area. This was not the case, for example, for the Mauritanian EEZ model (Sidi and Guénette 2004), which represents an upwelling ecosystem, with more particular characteristics (D. Gascuel pers. comm.). Originally including 18 trophic groups, the model was modified to include a better representation of the different marine mammals species, and also commercially important fish groups for the Northwest African region. In order to construct comparable models for other focal areas where we are studying the interaction between marine mammals and fisheries (e.g. Caribbean and South Pacific), biomass was aggregated into distinct functional feeding groups. These groups were defined based on the similarities in food habits, habitats, and biological variables (Essington 2006). The model for Northwest Africa presented here consists of 27 trophic groups: 10 marine mammal groups, one seabirds group, 9 fish groups, cephalopods, large crustaceans, 2 benthos groups, zooplankton, phytoplankton, and detritus (Table 3).

For most trophic groups, we used adult diet data, as most of the biomass estimates available were only for the spawning stock or adult biomass.

Cetacean groups were included in this ecosystem model at a high taxonomic resolution because of the aim of our study. It is important to note though, that feeding patterns of the baleen whales in particular are such, that very little of their annual food consumption (if any) is taken in Northwest African waters. The tropical, warmer waters covered by our three study areas represent, in fact, breeding areas for baleen whales, in which these species are known to mainly fast (Brodie 1975; Sergeant 1977; Brown and Lockyer 1984; Corkeron and Connor 1999; Perry *et al.* 1999; Clapham 2002; Jann *et al.* 2003). Indeed, blue, fin, sei and humpback whales spend their feeding season in the colder waters of north Atlantic in the Atlantic part of Northern Hemisphere or in the Antarctic waters in the Southern Hemisphere. Lockyer (1981) showed that most baleen whales feed considerably less in their breeding grounds than they would in feeding areas. She proposed that the average amounts consumed off breeding areas probably amount to about 10% or less of that in the feeding ground. This reduced consumption rate of 10% was then applied to many other ecosystems by different authors (Brown and Lockyer 1984; Mohammed 2003).

In our model, we treated these migratory species as part of the ‘system’ all the time in terms of some calculated impacts like fishing, whaling, and general trophic interactions. To account for the fact that most feeding activity occurs outside the system, we set a high diet proportion as ‘Import’ in the *Ecopath* diet consumption matrix (Christensen *et al.* 2005).

**Table 3.** List of trophic groups and species included in the *Ecopath* model for Northwest Africa. Species **in bold** represent to key species for each trophic group.

<b>Ecopath group</b>	<b>Species</b>
1. Minke whales	<i>Balaenoptera acutorostrata</i>
2. Fin whales	<i>Balaenoptera physalus</i>
3. Humpback whales	<i>Megaptera novaeangliae</i>
4. Bryde's whales	<i>Balaenoptera brydei</i>
5. Sei whales	<i>Balaenoptera borealis</i>
6. Blue whales	<i>Balaenoptera musculus</i>
7. Sperm whales	<i>Physeter macrocephalus</i>
8. Killer whales	<i>Orcinus orca</i>
9. Beaked whales	<i>Mesoplodon densirostris</i> , <i>M. europaeus</i> , <i>Ziphius cavirostris</i>
10. Small cetaceans	<i>Delphinus delphis</i> , <i>Feresa attenuate</i> , <i>Globicephala macrorhynchus</i> , <i>Grampus griseus</i> , <i>Kogia breviceps</i> , <i>Kogia simus</i> , <i>Lagenodelphis hosei</i> , <i>Peponocephala electra</i> , <i>Pseudorca crassidens</i> , <i>Sousa teuszii</i> , <i>Stenella attenuate</i> , <i>Stenella clymene</i> , <i>Stenella coeruleoalba</i> , <i>Stenella frontalis</i> , <i>Stenella longirostris</i> , <i>Steno bredanensis</i> , <i>Tursiops truncatus</i>
11. Seabirds	<i>Actitis hypoleucos</i> , <i>Calidris ferruginea</i> , <i>Calonectris diomedea</i> , <i>Ceryle rudis</i> , <i>Chlidonias niger</i> , <i>Halcyon malimbica</i> , <i>Limosa lapponica</i> , <i>Numenius phaeopus</i> , <i>Oceanites oceanicus</i> , <i>Pagrodama nivea</i> , <i>Pelecanus rufescens</i> , <i>Phalacrocorax africanus</i> , <i>Phoenicopiterus ruber</i> , <i>Pluvialis squatarola</i> , <i>Sterna caspia</i> , <i>Sterna hirundo</i>
12. Large pelagics	<i>Acanthocybium solandri</i> , <i>Brama brama</i> , <i>Centrolophidae</i> , <i>Coryphaena hippurus</i> , <i>Cubiceps gracilis</i> , <i>Istiophoridae</i> , <i>Istiophorus albicans</i> , <i>Istiophorus platypterus</i> , <b><i>Katsuwonus pelamis</i></b> , <i>Makaira nigricans</i> , <i>Ranzania laevis</i> , <i>Ruvettus pretiosus</i> , <i>Schedophilus medusophagus</i> , <i>Tetrapturus albidus</i> , <i>Tetrapturus pfluegeri</i> , <i>Thunnus alalunga</i> , <b><i>Thunnus albacares</i></b> , <b><i>Thunnus obesus</i></b> , <i>Thunnus thynnus</i> , <i>Xiphias gladius</i>
13. Mesopelagics predators	<b><i>Aphanopus carbo</i></b> , <i>Astronesthes niger</i> , <i>Atherina presbyter</i> , <i>Benthosema glaciale</i> , <i>Borostomias elucens</i> , <i>Chauliodus danae</i> , <i>Diplospinus multistriatus</i> , <i>Evermannella balbo</i> , <i>Lampris guttatus</i> , <i>Lepidocybium flavobrunneum</i> , <i>Leptostomias gladiator</i> , <i>Maurollicus muelleri</i> , <i>Micromesistius poutassou</i> , <b><i>Micromesistius poutassou</i></b> , <i>Mora moro</i> , <i>Moridae</i> , <i>Myctophum asperum</i> , <i>Myctophum nitidulum</i> , <i>Myctophum punctatum</i> , <i>Nealotus tripes</i> , <i>Photonektes margarita</i> , <i>Polyacanthonotus challengerii</i> , <i>Rhadinesthes decimus</i> , <i>Sternoptyx diaphana</i> , <i>Stomias boa boa</i> , <i>Stomiidae</i> , <i>Trachichthyidae</i> , <i>Trachyrincus scabrus</i> , <i>Vinciguerrria nimbaria</i> , <i>Xenodermichthys copei</i>
14. Bathydemersal predators	<i>Beryx</i> sp., <i>Beryx decadactylus</i> , <i>Caelorinchus caelorhincus</i> , <i>Caelorhincus</i> , <i>Caproidae</i> , <i>Chimaera monstrosa</i> , <i>Coryphaenoides rupestris</i> , <i>Coryphaenoides zaniophorus</i> , <i>Gadiformes</i> , <i>Gempylidae</i> , <i>Helicolenus dactylopterus dactylopterus</i> , <i>Lophiidae</i> , <b><i>Lophius budegassa</i></b> , <i>Lophius piscatorius</i> , <i>Lophius vaillanti</i> , <i>Lotidae</i> , <i>Merlucciidae</i> , <b><i>Merluccius merluccius</i></b> , <i>Merluccius polli</i> , <b><i>Merluccius senegalensis</i></b> , <i>Muraena helena</i> , <i>Nezumia aequalis</i> , <i>Nezumia sclerorhynchus</i> , <i>Phycidae</i> , <i>Phycis blennoides</i> , <i>Phycis phycis</i> , <i>Polyprion americanus</i> , <i>Pristis pectinata</i> , <i>Spectrunculus grandis</i> , <i>Synaphobranchus kaupii</i>
15. Sharks	<i>Alopias</i> sp., <i>Alopias superciliosus</i> , <i>Alopias vulpinus</i> , <i>Alopiidae</i> , <i>Carcharhinidae</i> , <i>Carcharhinus falciformis</i> , <b><i>Carcharhinus limbatus</i></b> , <i>Carcharhinus longimanus</i> , <i>Carcharhinus obscurus</i> , <i>Carcharhinus plumbeus</i> , <i>Centrolophidae</i> , <i>Centrophorus granulosus</i> , <i>Centroscyllium fabricii</i> , <i>Centrophorus squamosus</i> , <i>Centrophorus uyato</i> , <i>Centroscymnus coelolepis</i> , <i>Centroscymnus cryptacanthus</i> , <i>Centroscymnus crepidater</i> , <i>Cetorhinus maximus</i> , <i>Dalatias licha</i> , <i>Deania calcea</i> , <i>Elasmobranchii</i> , <i>Etmopteridae</i> , <i>Etmopterus princeps</i> , <i>Etmopterus pusillus</i> , <i>Galeorhinus galeus</i> , <i>Galeus melastomus</i> , <i>Galeus polli</i> , <i>Ginglymostoma cirratum</i> , <i>Hexanchus griseus</i> , <i>Isurus</i> sp., <i>Isurus oxyrinchus</i> , <i>Lamna nasus</i> , <i>Lamnidae</i> , <i>Mustelus asterias</i> , <i>Mustelus mustelus</i> , <i>Prionace glauca</i> , <i>Pristidae</i> , <i>Rhizoprionodon acutus</i> , <i>Scyliorhinidae</i> , <i>Scyliorhinus canicula</i> , <i>Scyliorhinus stellaris</i> , <i>Sphyrna lewini</i> , <i>Sphyrna zygaena</i> , <i>Sphyrnidae</i> , <i>Squalidae</i> , <i>Squalus acanthias</i> , <i>Squalus blainville</i> , <i>Squalus megalops</i> , <i>Squatina squatina</i> , <i>Squatinae</i> , <i>Triakidae</i>

16. Rays	Dasyatidae, <i>Dasyatis margarita</i> , <i>Dasyatis pastinaca</i> , <i>Dipturus batis</i> , <i>Dipturus oxyrinchus</i> , <i>Gymnura altavela</i> , <i>Leucoraja naevus</i> , Myliobatidae, <i>Myliobatis aquila</i> , <b><i>Raja clavata</i></b> , <i>Raja miraletus</i> , <i>Raja montagui</i> , <i>Raja straeleni</i> , Rajidae, Rajiformes, Rhinobatidae, <i>Rhinobatos cemiculus</i> , <b><i>Rhinobatos rhinobatos</i></b> , <i>Rhinoptera bonasus</i> , <i>Rhinoptera marginata</i> , Torpedinidae, <i>Torpedo</i> sp.
17. Costal tunas	<i>Auxis rochei</i> , <i>Auxis thazard</i> , <b><i>Euthynnus alletteratus</i></b> , <i>Oreynopsis unicolor</i> , <b><i>Sarda sarda</i></b> , <b><i>Scomberomorus tritor</i></b>
18. Coastal demersals	Acanthuridae, <i>Albula vulpes</i> , Ammodytidae, <i>Anthias anthias</i> , <i>Aphia minuta</i> , <i>Apogon imberbis</i> , Apogonidae, <i>Argentina sphyraena</i> , <i>Argyrosomus regius</i> , <i>Ariomma bondi</i> , <b><i>Ariidae</i></b> , <i>Ariomma melanum</i> , <i>Arius heudelotii</i> , <i>Arnoglossus laterna</i> , <i>Aulopus cadenati</i> , Balistidae, <i>Boops boops</i> , <i>Bothidae</i> , <i>Bothus podas</i> , <i>Brachydeuterus auritus</i> , <i>Brotula barbata</i> , <i>Campogramma glaycos</i> , <i>Capros aper</i> , <i>Cepola macrophthalmus</i> , <i>Chaetodon hoeferi</i> , <i>Charis charis</i> , <i>Chelidonichthys obscurus</i> , <i>Chlorophthalmus agassizi</i> , <i>Conger conger</i> , Congridae, <i>Ctenolabrus rupestris</i> , Cynoglossidae, <i>Cynoglossus senegalensis</i> , <i>Dentex angolensis</i> , <i>Dentex canariensis</i> , <i>Dentex dentex</i> , <i>Dentex gibbosus</i> , <i>Dentex macrophthalmus</i> , <i>Dentex maroccanus</i> , <i>Dicentrarchus</i> sp., <i>Dicentrarchus labrax</i> , <i>Dicologlossa cuneata</i> , <i>Diplodus bellottii</i> , <i>Diplodus cervinus cervinus</i> , <i>Diplodus sargus cadenati</i> , <i>Diplodus vulgaris</i> , <i>Drepane africana</i> , Echeneidae, Emmelichthyidae, <i>Epinephelus marginatus</i> , <i>Epinephelus aeneus</i> , <i>Epinephelus goreensis</i> , <i>Eucinostomus melanopterus</i> , <i>Fistularia tabacaria</i> , <i>Gaidropsarus</i> sp., <i>Galeoides</i> sp., <i>Galeoides decadactylus</i> , <i>Gerres nigri</i> , <i>Gobius niger</i> , <i>Gobius paganellus</i> , Haemulidae, <i>Halobatrachus didactylus</i> , Labridae, <i>Lepidorhombus</i> sp., <i>Lepidotrigla cadmani</i> , <i>Lepidotrigla dieuzeidei</i> , <i>Lethrinus atlanticus</i> , <i>Lithognathus mormyrus</i> , <i>Liza aurata</i> , <i>Liza dumerili</i> , <i>Liza falcipinnis</i> , <i>Liza grandisquamis</i> , <i>Liza ramado</i> , <i>Lutjanus</i> sp., <i>Lutjanus goreensis</i> , <i>Macroramphosus scolopax</i> , <i>Molva</i> sp., <i>Microchirus</i> sp., <i>Microchirus boscanion</i> , <i>Microchirus variegates</i> , <i>Monochirus hispidus</i> , Mugilidae, <i>Mugil capurrii</i> , <i>Mugil cephalus</i> , Mullidae, <i>Mullus barbatus</i> , <i>Mullus</i> sp., <i>Mullus surmuletus</i> , Muraenidae, <i>Mycteroperca rubra</i> , <i>Oblada melanura</i> , <i>Plectorhinchus macrolepis</i> , <i>Pagrus</i> sp., <i>Pagrus pagrus</i> , <i>Pagrus caeruleostictus</i> , <i>Pagellus</i> sp., <i>Pagellus bellottii</i> , <i>Pagellus acarne</i> , <i>Pagellus bogaraveo</i> , <i>Pagellus erythrinus</i> , <i>Pegusa lascaris</i> , <i>Pentanemus quinquarius</i> , <i>Platichthys flesus</i> , <i>Plectorhinchus macrolepis</i> , <i>Plectorhinchus mediterraneus</i> , Pleuronectidae, Pleuronectiformes, <i>Pleuronectes platessus</i> , Polynemidae, Pomacentridae, <i>Polydactylus quadrifilis</i> , <i>Pontinus kuhlii</i> , <i>Pomadasys jubelini</i> , <i>Pomadasys incisus</i> , <i>Pomadasys perotaei</i> , <i>Pomadasys rogerii</i> , <i>Pseudolithus typus</i> , <i>Pseudolithus senegalensis</i> , <i>Pseudolithus elongatus</i> , <i>Pseudolithus senegallus</i> , <i>Pseudupeneus prayensis</i> , <i>Pteroscion peli</i> , <i>Pseudupeneus prayensis</i> , <i>Rachycentron canadum</i> , <i>Sarpa salpa</i> , <i>Saurida brasiliensis</i> , Scaridae, <b><i>Sciaenidae</i></b> , <i>Sciaena umbra</i> , <i>Schedophilus pamarco</i> , Scophthalmidae, <i>Scophthalmus rhombus</i> , Serranidae, <i>Selene dorsalis</i> , Scorpaenidae, <i>Scorpaena maderensis</i> , <i>Scorpaena notata</i> , <i>Syacium guineensis</i> , Soleidae, <i>Solea senegalensis</i> , <i>Solea solea</i> , <b><i>Sparidae</i></b> , <i>Sparus auratus</i> , <i>Sparus caeruleostictus</i> , <i>Spondyliostoma cantharus</i> , <i>Stephanolepis hispidus</i> , <i>Stromateus fiatola</i> , <i>Symphodus mediterraneus</i> , <i>Symphodus melops</i> , <i>Synagrops microlepis</i> , <i>Synaptura lusitanica</i> , <i>Trachinus draco</i> , <i>Trachinocephalus myops</i> , Triglidae, Tetraodontidae, <i>Trisopterus minutus</i> , <i>Trisopterus luscus</i> , <i>Umbrina cirrosa</i> , <i>Umbrina canariensis</i> , <i>Zeus faber</i> , <i>Zenopsis conchifer</i>
19. Clupeids	<i>Alosa alosa</i> , Clupeidae, Clupeiformes, <i>Engraulis encrasicolus</i> , <b><i>Ethmalosa fimbriata</i></b> , <i>Ilisha africana</i> , <i>Sardina pilchardus</i> , <i>Sardinella</i> sp., <b><i>Sardinella aurita</i></b> , <b><i>Sardinella maderensis</i></b> , <i>Sprattus sprattus</i>
20. Other coastal pelagics	<i>Alectis alexandrinus</i> , <i>Aphanopus intermedius</i> , Belonidae, Carangidae, <i>Caranx</i> sp., <i>Caranx hippos</i> , <b><i>Caranx rhonchus</i></b> , <i>Caranx senegallus</i> , <i>Cheilopogon heterurus</i> , <i>Chloroscombrus chrysurus</i> , <i>Decapterus</i> sp., <i>Decapterus punctatus</i> , <i>Dicentrarchus punctatus</i> , <i>Elops lacerta</i> , Exocoetidae, <i>Exocoetus obtusirostris</i> , Hemiramphidae, <i>Hemiramphus</i> sp., <i>Lepidopus caudatus</i> , <i>Lichia amia</i> , <i>Pomatomus saltatrix</i> , <i>Promethichthys pomethus</i> , <i>Regalecus glesne</i> , <i>Scomber</i> sp., <b><i>Scomber japonicus</i></b> , <i>Scomber scombrus</i> , <i>Scomberesox saurus saurus</i> , <i>Scomberomorus</i> sp., Scombridae, <i>Seriola</i> sp., <i>Sphyraena</i> sp., <i>Sphyraena barracuda</i> , <i>Spicara</i> sp., <i>Trachinotus</i> sp., <i>Trachinotus ovatus</i> , <i>Trachurus</i> sp., <i>Trachurus mediterraneus</i> , <i>Trachurus picturatus</i> , <i>Trachurus trachurus</i> , <b><i>Trachurus trecae</i></b> , Trichiuridae, <i>Trichiurus lepturus</i> , <i>Tylosurus acus</i>
21. Cephalopods	<i>Alloteuthis subulata</i> , Cephalopoda, <i>Illex coindetii</i> , Loliginidae, <i>Loligo</i> sp., <b><i>Loligo vulgaris</i></b> , Octopodidae, <b><i>Octopus vulgaris</i></b> , Ommastrephidae, <i>Sepia bertheloti</i> , <i>Sepia elobyana</i> , <i>Sepia officinalis</i> , <i>Sepia orbignyana</i> , Sepiidae, Teuthida, <i>Todarodes sagittatus</i>

---

22. Crustaceans	Aristeidae, <i>Aristeus antennatus</i> , <i>Aristeus varidens</i> , <b>Brachyura</b> , <i>Calappa rubroguttata</i> , <i>Cancer pagurus</i> , <i>Carcinus maenas</i> , <i>Crangon</i> sp., <i>Crangon crangon</i> , Crangonidae, <i>Geryon</i> sp., <i>Geryon maritae</i> , <i>Homarus gammarus</i> , Leucosiidae, <i>Maja squinado</i> , Metapenaeus, Munidae, Natantian decapods, <i>Necora puber</i> , <i>Nephrops norvegicus</i> , Paguridae, Palaemonidae, <i>Palinurus</i> sp., <i>Palinurus elephas</i> , <i>Palinurus mauritanicus</i> , <i>Panulirus regius</i> , <i>Panulirus</i> sp., <i>Parapenaeopsis</i> sp., <i>Parapenaeopsis atlantica</i> , <b>Parapanaeus longirostris</b> , Penaeidae, <b>Penaeus</b> sp., <b>Penaeus kerathurus</b> , <b>Penaeus notialis</b> , <i>Pleoticus robustus</i> , <i>Plesionika heterocarpus</i> , <i>Plesiopenaeus edwardsianus</i> , Portunidae, Scyllaridae,
23. Benthos	Anthozoa, <i>Arca</i> sp., Arcidae, Bivalvia, Cardiidae, <i>Cardium edule</i> , <i>Chama crenulata</i> , Conidae, <i>Crassostrea</i> sp., <i>Crepidula porcellana</i> , <i>Cymbium</i> sp, Donacidae, <i>Donax</i> sp., Epizoanthidae, Gastropoda, Glycymerididae, Haliotidae, <i>Haliotis tuberculata</i> , <i>Modiolus</i> sp., <i>Murex</i> sp., Muricidae, Mytilidae, Naticidae, <i>Ostrea edulis</i> , <i>Patella</i> sp., <i>Pecten maximus</i> , Pectinidae, Porifera, <i>Pyura dura</i> , <i>Ruditapes decussates</i> , <i>Solen</i> sp., Solenidae, <i>Tapes</i> sp., <i>Thais haemastoma</i> , Veneridae, <i>Venus rosalina</i> , <i>Venus verrucosa</i> , Volutidae
24. Benthic producers	Algae, benthic bacteria
25. Zooplankton	Copepoda, Hydrozoa, Scyphozoa, fish larvae, eggs
26. Phytoplankton	
27. Detritus	

---

### Groups 1 - 10. Marine mammals

Ten groups of marine mammals were added to the original model for the purpose of our study. We considered species of commercial interest individually and aggregated remaining species to facilitate model simulations. Given the lack of local, long-term dedicated surveys to provide reliable cetacean abundance estimates, density estimates had to be derived from a global database (Kaschner 2004). However, comparison with other densities from surveys conducted in similar habitats are ground-truthing these estimates (Table 4). Similarly, most estimates about diet for marine mammals came from other areas. The lack of studies on the diet of marine mammals off the coast of Northwest Africa is mainly explained by the fact that these stocks of whales are not known to feed in this area (Brodie 1975; Sergeant 1977; Lockyer 1981; Brown and Lockyer 1984; Corkeron and Connor 1999; Perry *et al.* 1999, Clapham 2002; Jann *et al.* 2003). When data were lacking for diet for marine mammals in Northwest Africa, we relied on diet information from feeding areas. This approach has been employed in other ecosystem models (Bundy *et al.* 2000; Okey 2001; Guénette and Christensen 2005; Morissette 2007). Nonetheless, our results should be interpreted with caution given the uncertainty in our diet parameters. To address this issue, we performed different model scenarios by changing diet composition to increase the proportion of commercially important fish in order to examine the extent to which our diet assumptions might change the outcomes of our models.

**Table 4.** Comparison of predicted cetacean densities in Northwest African waters based on global model developed by Kaschner et al (2006) and Kaschner (2004) and observed densities in similar habitats (subtropical & tropical waters). A = aerial surveys, S = ship based surveys. Density estimates that are corrected for animals missed on the track-line are indicated in the G(o) corrected column. All other observed estimates might represent underestimations. Bold observed density values represent lowest and highest observed estimates, respectively for each species.

Common Name	Estimated density [animals / 1000 km <sup>2</sup> ]	Observed density [animals / 1000 km <sup>2</sup> ]	CV	G(o) corrected	Geographic area	Survey years	Survey type	Source
Blue whale	0.03	<b>0.07</b>	0.24	no	Eastern Tropical Pacific	1986-1990	S	Wade and Gerrodette 1993
Blue whale	0.03	1.10	0.33	yes	NE Pacific, Baja California	1993	S	Calambokidis and Barlow 2004
Blue whale	0.03	0.00	0.00	yes	NE Pacific, west coast US	1996	S	Calambokidis and Barlow 2004
Blue whale	0.03	3.11	0.28	yes	NE Pacific, west coast US	1996	S	Barlow 2003a
Blue whale	0.03	0.95	0.44	yes	NE Pacific, west coast US	2001	S	Barlow 2003a
Blue whale	0.03	0.11	0.99	yes	NE Pacific, California inshore	1991-1992	A	Forney et al. 1995
Blue whale	0.03	3.27	0.24	yes	NE Pacific, west coast US	1991-1993	S	Barlow 2003a
Blue whale	0.03	1.26	0.27	yes	NE Pacific, California offshore	1991-1996	S	Calambokidis and Barlow 2004
Blue whale	0.03	<b>4.96</b>	0.13	yes	NE Pacific, California inshore	1991-1996	S	Calambokidis and Barlow 2004
Blue whale	0.03	0.76	0.50	no	SW Indian Ocean, Madagascar plateau (southern block)	1996	S	Best et al. 2003
Blue whale	0.03	0.82	0.65	no	SW Indian Ocean, Madagascar plateau (northern block)	1996	S	Best et al. 2003
Bryde's whale	0.49	0.11	0.61	no	NW Atlantic, northern Gulf of Mexico (SEFSC)	1996-2001	S	Mullin and Fulling 2004
Bryde's whale	0.49	<b>0.67</b>	0.20	no	Eastern Tropical Pacific	1986-1990	S	Wade and Gerrodette 1993
Bryde's whale	0.49	<b>0.67</b>	0.21	no	Eastern Tropical Pacific	1998	S	Gerrodette and Forcada 2002
Bryde's whale	0.49	0.50	0.24	no	Eastern Tropical Pacific	1999	S	Gerrodette and Forcada 2002
Bryde's whale	0.49	0.48	0.20	no	Eastern Tropical Pacific	2000	S	Gerrodette and Forcada 2002
Bryde's whale	0.49	0.19	0.45	yes	NE Pacific, Hawaii waters	2002	S	Barlow 2006
Bryde's whale	0.49	0.06	0.53	yes	NE Pacific, west coast US	1991-1993	S	Barlow 2003a
Bryde's whale	0.49	0.02	1.01	yes	NE Pacific, west coast US	1991-1993	S	Barlow 2003a
Bryde's whale	0.49	0.05	1.07	no	NW Atlantic, northern Gulf of Mexico (Oceanic Surveys)	1996-1997	S	Davis et al. 2000
Bryde's whale	0.49	0.43	1.05	no	NW Atlantic, northern Gulf of Mexico (GulfCet I EPA survey)	1996-1997	S	Davis et al. 2000

**Table 4** (cont.)

Common Name	Estimated density [animals / 1000 km <sup>2</sup> ]	Observed density [animals / 1000 km <sup>2</sup> ]	CV	G(o) corrected	Geographic area	Survey years	Survey type	Source
Fin whale	0.22	0.00	0.00	yes	NOAA 91-96 California inshore	1991	A	Forney et al. 1995
Fin whale	0.22	<b>16.09</b>	0.22	no	NW Mediterranean	1992	S	Forcada et al. 1995
Fin whale	0.22	1.97	0.35	yes	NE Pacific, west coast US	1991-1993	S	Barlow 2003a
Fin whale	0.22	3.18	0.34	yes	NE Pacific, west coast US	1996	S	Barlow 2003a
Fin whale	0.22	3.92	0.56	yes	NE Pacific, west coast US	2001	S	Barlow 2003a
Fin whale	0.22	<b>0.07</b>	0.72	yes	NE Pacific, Hawaiiin waters	2002	S	Barlow 2003b
Fin whale	0.22	0.19	1.01	yes	NE Pacific, California inshore	1991-1992	A	Forney et al. 1995
Fin whale	0.22	0.07	1.15	no	NW Atlantic, US east coast, south of Maryland	1998	S	Mullin and Fulling 2003
Fin whale	0.22	1.85	0.48	no	NW Atlantic, Virginia Capes	2002	S	Garrison et al. 2003
Humpback whale	0.10	1.22	0.41	yes	NE Pacific, California inshore	1991-1992	A	Forney et al. 1995
Humpback whale	0.10	3.50	0.21	yes	NE Pacific, California inshore	1991-1996	S	Calambokidis and Barlow 2004
Humpback whale	0.10	<b>0.03</b>	0.37	yes	NE Pacific, California offshore	1991-1996	S	Calambokidis and Barlow 2004
Humpback whale	0.10	1.46	0.42	yes	NE Pacific, California waters	1991	A	Forney and Barlow 1993
Humpback whale	0.10	0.00	0.00	yes	NE Pacific, Baja California	1993	S	Calambokidis and Barlow 2004
Humpback whale	0.10	0.66	0.41	yes	NE Pacific, west coast US	1991-1993	S	Barlow 2003a
Humpback whale	0.10	0.14	0.72	yes	NE Pacific, west coast US	1996	S	Calambokidis and Barlow 2004
Humpback whale	0.10	1.81	0.44	yes	NE Pacific, west coast US	1996	S	Barlow 2003a
Humpback whale	0.10	0.89	0.49	yes	NE Pacific, west coast US	2001	S	Barlow 2003a
Humpback whale	0.10	7.44	0.48	no	SE Atlantic, Gabon waters (northern strata)	2002	A	Rosenbaum et al. 2004
Humpback whale	0.10	24.34	0.31	no	SE Atlantic, Gabon waters (southern strata)	2002	A	Rosenbaum et al. 2004
Humpback whale	0.10	46.49	0.47	no	SW Indian Ocean, Madagascar (eastern block)	1994	S	Best et al. 1996
Humpback whale	0.10	<b>112.32</b>	0.27	no	SW Indian Ocean, Madagascar (southern block)	1994	S	Best et al. 1996
Humpback whale	0.10	67.47	0.15	no	SW Indian Ocean, Mozambique	2003	S	Findlay et al. 1994

**Table4** (cont.)

Common Name	Estimated density [animals / 1000 km <sup>2</sup> ]	Observed density [animals / 1000 km <sup>2</sup> ]	CV	G(o) corrected	Geographic area	Survey years	Survey type	Source
Minke whale	1.28	0.42	0.68	yes	NE Pacific, California waters	1991	A	Forney and Barlow 1993
Minke whale	1.28	0.28	0.62	yes	NE Pacific, California inshore	1991-1992	A	Forney et al. 1995
Minke whale	1.28	0.27	0.44	yes	NE Pacific, west coast US	1991-1993	S	Barlow 2003a
Minke whale	1.28	<b>0.93</b>	0.51	yes	NE Pacific, west coast US	1996	S	Barlow 2003a
Minke whale	1.28	0.86	0.77	yes	NE Pacific, west coast US	2001	S	Barlow 2003a
Minke whale	1.28	<b>0.03</b>	1.29	no	NW Atlantic, US east coast, south of Maryland	1998	S	Mullin and Fulling 2003
Sei whale	0.10	0.06	0.53	yes	NE Pacific, west coast US	1991	S	Barlow 2003a
Sei whale	0.10	0.05	0.79	yes	NE Pacific, west coast US	1991	S	Barlow 2003a
Sei whale	0.10	0.10	0.73	yes	NE Pacific, west coast US	1996	S	Barlow 2003a
Sei whale	0.10	<b>0.03</b>	1.01	yes	NE Pacific, west coast US	2001	S	Barlow 2003a
Sei whale	0.10	0.03	1.06	yes	NE Pacific, Hawaiiin waters	2002	S	Barlow 2003b
Killer whale	0.11	0.44	0.37	no	Eastern Tropical Pacific	1986-1990	S	Wade and Gerrodette 1993
Killer whale	0.11	0.31	0.76	yes	NE Pacific, California waters	1991	A	Forney and Barlow 1993
Killer whale	0.11	0.25	0.69	yes	NE Pacific, California inshore	1991-1992	A	Forney et al. 1995
Killer whale	0.11	0.55	0.50	yes	NE Pacific, west coast US	1991-1993	S	Barlow 2003a
Killer whale	0.11	0.74	0.61	yes	NE Pacific, west coast US	1996	S	Barlow 2003a
Killer whale	0.11	0.58	0.73	yes	NE Pacific, west coast US	2001	S	Barlow 2003a
Killer whale	0.11	<b>0.14</b>	0.98	yes	NE Pacific, Hawaiiin waters	2002	S	Barlow 2006
Killer whale	0.11	0.69	0.42	no	NW Atlantic, northern Gulf of Mexico (Oceanic Surveys)	1991-1994	S	Hansen et al. 1995
Killer whale	0.11	<b>0.79</b>	0.48	no	NW Atlantic, northern Gulf of Mexico (GulfCet I survey)	1991-1994	S	Davis and Fargion 1996
Killer whale	0.11	0.17	1.01	no	NW Atlantic, northern Gulf of Mexico (Oceanic Surveys)	1996-1997	S	Davis et al. 2000
Killer whale	0.11	0.37	0.49	no	NW Atlantic, northern Gulf of Mexico (SEFSC)	1996-2001	S	Mullin and Fulling 2004

**Table 4** (cont.)

Common Name	Estimated density [animals / 1000 km <sup>2</sup> ]	Observed density [animals / 1000 km <sup>2</sup> ]	CV	G(o) corrected	Geographic area	Survey years	Survey type	Source
Sperm whale	1.09	1.33	0.22	yes	Eastern Tropical Pacific	1986-1990	A & S	Wade and Gerrodette 1993
Sperm whale	1.09	0.92	0.38	no	Eastern Tropical Pacific	1998	S	Gerrodette and Forcada 2002
Sperm whale	1.09	1.24	0.60	no	Eastern Tropical Pacific	1999	S	Gerrodette and Forcada 2002
Sperm whale	1.09	<b>0.19</b>	0.73	no	Eastern Tropical Pacific	2000	S	Gerrodette and Forcada 2002
Sperm whale	1.09	3.36	0.81	yes	Northeastern Tropical Pacific	1997	S	Barlow and Taylor 2005
Sperm whale	1.09	<b>4.10</b>	0.36	no	Northeastern Tropical Pacific	1997-2000	S	Barlow and Taylor 2005
Sperm whale	1.09	0.20	1.07	yes	NE Pacific, California waters	1991	A	Forney and Barlow 1993
Sperm whale	1.09	3.42	0.99	yes	NE Pacific, California inshore	1991-1992	A	Forney et al. 1995
Sperm whale	1.09	1.41	0.40	yes	NE Pacific, west coast US	1991-1993	S	Barlow 2003a
Sperm whale	1.09	0.47	0.56	yes	NE Pacific, west coast US	1996	S	Barlow 2003a
Sperm whale	1.09	1.90	0.59	yes	NE Pacific, west coast US	2001	S	Barlow 2003a
Sperm whale	1.09	0.90	0.13	yes	NE Pacific, Hawaii waters	1993-1998	A	Mobley et al. 2000
Sperm whale	1.09	2.79	0.81	yes	NE Pacific, Hawaii waters	2002	S	Barlow 2006
Sperm whale	1.09	2.06	0.51	no	NW Atlantic, US east coast, south of Maryland	1998	S	Mullin and Fulling 2003
Sperm whale	1.09	1.14	0.85	no	NW Atlantic, Virginia Capes	2002	S	Garrison et al. 2003
Sperm whale	1.09	2.31	0.31	yes	NW Atlantic, northern Gulf of Mexico (SEFSC)	1991-1994	S	Hansen et al. 1995
Sperm whale	1.09	1.31	0.31	no	NW Atlantic, northern Gulf of Mexico (Oceanic Surveys)	1991-1994	S	Hansen et al. 1995
Sperm whale	1.09	1.74	0.30	no	NW Atlantic, northern Gulf of Mexico (GulfCet I survey)	1991-1994	S	Davis and Fargion 1996
Sperm whale	1.09	0.96	0.45	no	NW Atlantic, northern Gulf of Mexico (Oceanic Surveys)	1996-1997	S	Davis et al. 2000
Sperm whale	1.09	1.62	0.56	no	NW Atlantic, northern Gulf of Mexico (GulfCet I survey)	1996-1997	S	Davis et al. 2000
Sperm whale	1.09	0.85	0.57	no	NW Atlantic, northern Gulf of Mexico (GulfCet I EPA survey)	1996-1997	S	Davis et al. 2000
Sperm whale	1.09	3.80	0.23	no	NW Atlantic, northern Gulf of Mexico (SEFSC)	1996-2001	S	Mullin and Fulling 2004



## 1. Minke whales

Minke whales (*Balaenoptera acutorostrata*) are the most abundant species of whales in our study area. According to quantitative estimations by Kaschner (2004), there is an average abundance of 4574 whales off the coast of Northwest Africa annually, translating to a density of 1.28 individuals per 1000 km<sup>2</sup> and representing a total biomass of 30,050 tonnes, or an annual biomass density of 0.00844 t\*km<sup>-2</sup>. The predicted density (individuals per 1000 km<sup>2</sup>) was in the same range as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 4).

The annual mortality of minke whales was estimated by Evans (1998) to be around 0.09 – 0.10. We assumed this stayed constant over the study period, and also that following Allen (1971), this mortality equals the production to biomass ratio (P/B) needed for model's construction. This was similar to the P/B values specifically used for Minke whales in another *Ecopath* model (Guénette *et al.* 2006). A P/B value of 0.099 yr<sup>-1</sup> was used here.

Unfortunately, there are few quantitative descriptions of diet for cetaceans in general, and Minke whales are no exception. Since no study has been conducted on minke whale diet in Northwest African countries, we used a set of six papers published in the literature about the diet of Minke whales in the North Atlantic (Table 5). The average diet was used as an input in our *Ecopath* model, while minimum and maximum values were used as ranges for calibration.

**Table 5.** Available information on the diet composition of minke whales in the North Atlantic. The average diet was used in the *Ecopath* model for Northwest Africa.

Prey groups ( <i>Ecopath</i> )	Northeast Atlantic (Nørdoy and Blix, 1992)	Northeast Atlantic (Haug <i>et al.</i> 1996)	North Sea (Olsen and Holst 2001)	Norway (Lydersen <i>et al.</i> 1991)	Norwegian waters (Haug <i>et al.</i> 1995)	Norwegian waters (Olsen and Holst 2001)	Norwegian waters (Smout and Lindstrom 2007)	Eastern Norway (Sivertsen 2006)	Avg. diet
14. Bathydemersal predators	0.053	0.232		0.003	0.078			0.067	<b>0.054</b>
18. Coastal demersals	0.025	0.134	0.896	0.081	0.132				<b>0.159</b>
19. Clupeids	0.501	0.358	0.011	0.916	0.382	1.000	0.039	0.303	<b>0.439</b>
20. Coastal pelagics		0.031	0.093		0.326		0.222	0.153	<b>0.103</b>
25. Zooplankton	0.421	0.245			0.082		0.739	0.477	<b>0.245</b>
<b>Total</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>

## 2. Fin whales

Fin whales (*Balaenoptera physalus*) are another important species of baleen whales in the area. Kaschner (2004) estimated their abundance to 780 individuals in the area of Northwest Africa, translating to a density of 0.22 individuals per 1000 km<sup>2</sup>, representing a total biomass of 43,372 tonnes, or an annual biomass density of 0.012 t\*km<sup>-2</sup>. The predicted density (individuals per 1000 km<sup>2</sup>) was similar in terms of magnitude as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 4).

The generally accepted natural mortality rate for adult fin whales ranges from 0.04 to 0.06 (Clark 1982; de la Mare 1985; Perry *et al.* 1999). Total mortality was assumed to be a bit higher, but no information was available about that. Consequently, we used a P/B value of 0.099 yr<sup>-1</sup>, following Heymans' (2005) estimate for the same species in the Aleutian Islands and the Gulf of Alaska.

No information was available on the diet of fin whales in Northwest Africa, so we used the study by Sigurjónsson and Víkingsson (1997) on the feeding of fin whales in Icelandic waters (Table 6). Fin whales were mostly feeding on zooplankton, but fish remains were also found in their stomach.

**Table 6.** Diet composition of fin whales used for *Ecopath* model Northwest Africa.

<b>Prey groups (<i>Ecopath</i>)</b>	<b>Diet (Sigurjónsson and Víkingsson 1997)</b>
18. Coastal demersals	0.002
20. Coastal pelagics	0.014
25. Zooplankton	0.984
<b>Total</b>	<b>1.000</b>

### 3. Humpback whales

Humpback whales (*Megaptera novaeangliae*) also occur in the waters of Northwest Africa. Quantitative estimations by Kaschner (2004) showed that there is an average abundance of 354 whales in our study area annually, representing a density of 0.10 individuals per 1000 km<sup>2</sup>, for a total biomass of 10,770 tonnes, or an annual biomass density of 0.0030 t\*km<sup>-2</sup>. The predicted density (individuals per 1000 km<sup>2</sup>) was similar in terms of magnitude to the range of observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 4).

Following Heymans (2005), we used a P/B ratio of 0.099 yr<sup>-1</sup> for humpback whales. This value was used in the Aleutian Islands and the Gulf of Alaska for the same species, and in absence of any other information on total mortality of humpback whales, we assumed that this ratio was similar in Northwest Africa.

The only information available on the diet of humpback whales in Atlantic waters came from Mitchel (1973). However, since this study only listed proportions of “krill” and “fish” as prey in the diet, we used a more recent study by Witteveen *et al.* (2006) to distribute “fish” prey into more precise categories. Consequently, the diet of humpback whales used in the Northwest Africa model was mainly composed of zooplankton, coastal pelagic, and coastal demersal fish (Table 7).

**Table 7.** Diet composition of humpback whales used for *Ecopath* model Northwest Africa.

<b>Prey groups (<i>Ecopath</i>)</b>	<b>Diet (Sigurjónsson and Víkingsson 1997, after Mitchel 1973)</b>
14. Bathydemersal predators	0.086
18. Coastal demersals	0.171
19. Clupeids	0.086
20. Coastal pelagics	0.275
25. Zooplankton	0.400
<b>Total</b>	<b>1.000</b>

### 4. Bryde's whales

The distribution of Bryde's whale, *Balaenoptera brydei*, in Northwest Africa is scarcely documented. However, there were reported sightings of this species in the waters of Morocco and in the Caribbean by Kato (2002). From the quantitative estimates of Kaschner (2004), the annual abundance of this species in the region is approximately 1,731 individuals or a density of 0.49 individuals per 1000 km<sup>2</sup>, with a total biomass of 27, 961 tonnes or a biomass density of 0.00785 t\*km<sup>-2</sup>. Predicted and observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats were similar in terms of magnitude (Table 4).

In the absence of mortality value or P/B ratio of this species in the region, an average P/B ratio of 0.099 yr<sup>-1</sup> for baleen whales in Aleutian Islands, Alaska (Guénette *et al.*, 1996) was used in the present model.

The dietary information for the Bryde's whale is lacking in the region. Thus, we used diet information of this species from Best (2001) in South Africa. It was documented that Bryde's whale feed mainly on

zooplankton (60.3%), other coastal pelagics (28.8%), mesopelagic predators (5.0%), clupeids (3.2%) and bathydemersal predators (2.7%) (Table 8).

**Table 8.** Diet composition of Bryde's whales used for *Ecopath* model Northwest Africa.

Prey groups ( <i>Ecopath</i> )	Diet (Best 2001)
13. Mesopelagic predators	0.050
14. Bathydemersal predators	0.027
19. Clupeids	0.032
20. Coastal pelagics	0.288
25. Zooplankton	0.603
<b>Total</b>	<b>1.000</b>

## 5. Sei whales

Sei whales, *Balaenoptera borealis*, are known to inhabit the waters of Northwest Africa during their breeding season (Klinowska 1991). Population of this species in the region had been reduced because of commercial whaling in the early 1950s (Klinowska 1991; Horwood 2002). Based on the recent quantitative estimate of sei whales in Northwest Africa by Kaschner (2004), their annual total abundance is approximately 339 individuals, translating to a density of 0.10 individuals per 1000 km<sup>2</sup>, and a biomass of 5,697 tonnes or a biomass density of 0.0016 t\*km<sup>-2</sup>. The predicted densities (individuals per 1000 km<sup>2</sup>) were similar in terms of magnitude as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 4).

Minke whales (*Balaenoptera acutorostrata*) are the most abundant species of whales in our study area. According to quantitative estimations by Kaschner (2004), there is an average abundance of 4574 whales off the coast of Northwest Africa annually, translating to a density of 1.28 individuals per 1000 km<sup>2</sup> and representing a total biomass of 30,050 tonnes, or an annual biomass density of 0.00844 t\*km<sup>-2</sup>.

The P/B ratio of 0.020 yr<sup>-1</sup> used for sei whales in the present model for Northwest Africa was obtained from the Alaska Gyre ecosystem model (Pauly *et al.* 1996).

There is no existing dietary information of sei whales in the region. Hence, we used the diet information of this species from the North Atlantic (Sigurjónsson and Víkingsson 1997; Mitchell 1974). The dietary contents of sei whales were mainly composed of zooplankton (98.0%) and a few species of fish (Table 9).

**Table 9.** Diet composition of sei whales used for *Ecopath* model Northwest Africa.

Prey groups ( <i>Ecopath</i> )	Diet (Sigurjónsson and Víkingsson 1997)
14. Bathydemersal predators	0.007
18. Coastal demersals	0.007
20. Coastal pelagics	0.007
25. Zooplankton	0.980
<b>Total</b>	<b>1.000</b>

## 6. Blue whales

The species of baleen whales included in this group is the blue whale (*Balaenoptera musculus*). This group inhabits the Cape Verde Islands during breeding seasons. According to Kaschner's estimates (2004), this group represents a total abundance of 96 individuals annually, or 0.03 individuals per 1000 km<sup>2</sup>, representing a biomass 9,831 tonnes, or a biomass density 0.00276 t\*km<sup>-2</sup> in the region. The predicted density (individuals per 1000 km<sup>2</sup>) was similar in terms of magnitude as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats and showed in Table 4.

The P/B ratio of 0.04 yr<sup>-1</sup> used for the baleen whale in the present model is the average value taken from many *Ecopath* models of this group (Guénette and Christensen 2005; Okey 2004; Pauly *et al.* 1996). This value ranges from 0.01 to 0.05 yr<sup>-1</sup>, depending on the source and baleen whales species included in these models.

In absence of dietary information of baleen whale species (blue whale) in Northwest Africa, we incorporated diet results of blue whales from Icelandic waters (Sigurjónsson and Víkingsson 1997). Blue whales consume mainly zooplankton (Sigurjónsson and Víkingsson 1997) (Table 10). This was also mentioned by several experts (e.g. Hjort and Ruud 1929; Klinowska 1991; Sears 2002; Hewitt and Lipsky 2002) that describe the ecology and distribution of blue whales.

**Table 10.** Available information on the diet composition of blue whales used for *Ecopath* model in the Northwest African ecosystem.

Prey groups ( <i>Ecopath</i> )	Diet (Sigurjónsson and Víkingsson 1997)
25. Zooplankton	1.000
<b>Total</b>	<b>1.000</b>

## 7. Sperm whales

Sperm whale (*Physeter macrocephalus*) abundance was calculated by Kaschner (2004) to be around 3878 whales off the coast of Northwest Africa annually, representing a density of 1.09 individuals per 1000 km<sup>2</sup>, for a total biomass of 71,865 tonnes, or an annual biomass density of 0.020 t\*km<sup>-2</sup>. This estimated density (in individuals per 1000 km<sup>2</sup>) is similar in terms of magnitude as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 4).

The annual mortality of sperm whales was estimated by Perry *et al.* (1999) to be around 0.05. In the absence of any other information, we assumed this to be equivalent to the P/B for that species (following Allen 1971). Thus, the P/B value of our model was 0.05 yr<sup>-1</sup>.

Most publications on sperm whales diet indicate that they feed primarily on cephalopods (Kawakami 1980; Clarke *et al.* 1993; González *et al.* 1994; Roberts 2003). However, a study by Best (1999) also includes fish prey in the diet. In any case, no information was available specifically for the Northwest Africa region, and we thus used an average diet based on all information available in North Atlantic waters (Table 11). The average diet was used as an input in our *Ecopath* model, while minimum and maximum values were used as ranges for calibration.

**Table 11.** Available information on the diet composition of sperm whales in the North Atlantic. The average diet was used in the *Ecopath* model for Northwest Africa.

Prey groups ( <i>Ecopath</i> )	West coast of South Africa (Best 1999)	Vigo, Spain (Kawakami 1980)	Madera, Spain (Kawakami 1980)	Azores (Clarke <i>et al.</i> 1993)	South Crête, Greece (Roberts 2003)	Northwest Spanish Atlantic coast (González <i>et al.</i> 1994)	Avg. diet
12. Large pelagics	0.014						<b>0.002</b>
13. Mesopelagic predators	0.014						<b>0.002</b>
14. Bathydemersal predators	0.014						<b>0.002</b>
21. Cephalopods	0.876	1.000	1.000	1.000	1.000	1.000	<b>0.979</b>
22. Crustaceans	0.041						<b>0.007</b>
23. Benthos	0.041						<b>0.007</b>
<b>Total</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>

## 8. Killer whales

Killer whales (*Orcinus orca*) are the top predators in the Northwest African ecosystem, occupying the highest trophic level of the food web. Kaschner (2004) estimated their abundance as 409 individuals in

the area of Northwest Africa annually, based on a estimated density of 0.11 individuals per 1000 km<sup>2</sup>, for a total biomass of 933 tonnes, or an annual biomass density of 0.00026 t\*km<sup>-2</sup>. Predicted density (individuals per 1000 km<sup>2</sup>) was similar in terms of magnitude as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 4).

The P/B value we used for the model was taken from Sidi and Guénette (2004) who calculated a ratio of 0.02 yr<sup>-1</sup> based on a calculation by Trites and Heise (1996).

Diet composition of this group was also based on Sidi and Guénette (2004) for Mauritania (after a study by Paul *et al.* 1998), who estimated that killer whales mainly feed on dolphins, coastal demersals, and cephalopods (Table 12).

**Table 12.** Diet composition of killer whales used for *Ecopath* model Northwest Africa.

Prey groups ( <i>Ecopath</i> )	Diet (Sidi and Guénette 2004)
10. Dolphins	0.384
12. Large pelagics	0.010
14. Bathydemersal predators	0.010
18. Coastal demersals	0.379
19. Clupeids	0.048
20. Coastal pelagics	0.038
21. Cephalopods	0.131
<b>Total</b>	<b>1.000</b>

## 9. Beaked whales

Three species of beaked whales were included in that group: Cuvier's beaked whale (*Ziphius cavirostris*), Blainville's beaked whale (*Mesoplodon densirostris*), and Gervais' beaked whale (*M. europaeus*). Kaschner (2004) estimated a total annual abundance of 693 beaked whales, representing a biomass 446 tonnes, or a biomass density 0.0001 t\*km<sup>-2</sup>.

The P/B ratio was taken from Heymans (2005) who used a value of 0.036 for beaked whales species in their model of the Aleutian Islands.

Information on the diet of beaked whales species were available for all three species included in our model. Here again, the diet was calculated as a weighted average of these three diets, based on the fact that Cuvier's beaked whales consume 66% of the food in our study area, while Blainville's beaked whales consume 24%, and Gervais' beaked whales consume 10% (Kaschner 2004). The resulting diet composition is mainly made up of cephalopods and bathydemersal predators (Table 13). Here again, the average diet was used as an input in our *Ecopath* model, while minimum and maximum values were used as ranges for calibration.

**Table 13.** Available information on the diet composition of beaked whales in the North Atlantic. A weighted average diet (based on the % of food consumption by each species) was used in the *Ecopath* model for Northwest Africa.

Prey groups ( <i>Ecopath</i> )	Cuvier's beaked whale Canary Islands (Santos <i>et al.</i> 2007)	Blainville's beaked whale Canary Islands (Santos <i>et al.</i> 2007)	Gervais' beaked whales Canary Islands (Santos <i>et al.</i> 2007)	Weighted average diet
13. Mesopelagic predators		0.002	0.291	<b>0.029</b>
14. Bathydemersal predators		0.847		<b>0.207</b>
21. Cephalopods	1.000	0.152	0.710	<b>0.763</b>
<b>Total</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>	<b>1.000</b>

### 10. Small cetaceans

A total of 17 species of dolphins and other small toothed whales are included in that group (Table 3). Most species are currently observed in the Northwest Africa area, but some are rarely observed or only in stranding events (Sidi and Guénette 2004). The database compiled by Kaschner (2004) allowed us to estimate a total annual abundance of 180,735 individuals, for a total biomass of 19,921 tonnes, or a density of 0.0055 yr<sup>-1</sup>.

The original model by Samb and Mendy (2004) included a specific trophic group for dolphins, so we used the P/B value initially presented there for our model. Consequently, the value of 0.0047 yr<sup>-1</sup> is used in this broader model and assumed to represent all species of small toothed cetaceans and dolphins of the Northwest African area.

Diet information about dolphins was also taken directly from the initial model by Samb and Mendy (2004). The diet was based on Northridge (1984) and mainly composed of coastal fish as well as zooplankton (Table 14).

**Table 14.** Diet composition of dolphins used for *Ecopath* model Northwest Africa.

<b>Prey groups (<i>Ecopath</i>)</b>	<b>Diet (Samb and Mendy 2004)</b>
18. Coastal demersals	0.080
19. Clupeids	0.291
20. Coastal pelagics	0.098
21. Cephalopods	0.193
25. Zooplankton	0.339
<b>Total</b>	<b>1.000</b>

### Food consumption by marine mammals

Kaschner (2004) developed a basic food consumption model based on Trites *et al.* (1997). This model was used to generate the biomasses and consumption (Q/B) values needed for each *Ecopath* group. Annual food consumption was calculated as:

$$Q_i = 365 * \sum_s N_{i,s} W_{i,s} R_{i,s}$$

where the annual food consumption  $Q$  of species  $i$  was assumed to be 365 times the daily food consumption. Daily food consumption is calculated based on the number of individuals  $N$  of the sex  $s$  of a species  $i$ , and a weight-specific daily ration  $R$  consumed by an individual with a species- and sex-specific mean body mass.

Abundances and sex ratios were taken directly from the Kaschner (2004) database. Mean species and sex-specific body mass was taken from Trites and Pauly (1998). For all cetaceans, except baleen whales, we used the empirical model developed by Innes *et al.* (1987) to estimate food consumption of cetaceans that was later modified by Trites *et al.* (1997) to account for the difference between consumption for growth and for maintenance and then applied to all marine mammal species. Food intake of specific species per day was calculated using:

$$R_{i,s} = 0.1 * W_{i,s}^{0.8}$$

where  $R$  is the daily food intake of an individual of sex  $s$  belonging to species  $i$  and  $W$  is the mean body weight of that individual, in kilograms.

For all baleen whales daily food ration was estimated based on a model by Armstrong and Siegfried (1991) for food consumption of minke whales in the Antarctic. These authors suggested a modification to the

empirical model of Innes *et al.* (1986) equation for baleen whales to account for larger body sizes and seasonal variation in food intake. This approach was later used to estimate food consumption of whales around Iceland (Sigurjónsson and Víkingsson 1997) and represents one of the methods used by Tamura (2003) to estimate global food intake of cetaceans. This feeding rate is calculated as:

$$R_{i,s} = 0.42 * W_{i,s}^{0.67}$$

Annual food consumption for each species of marine mammals was then divided by the biomass estimates, in order to get the final consumption to biomass (Q/B) ratios used in the *Ecopath* model (Table 15).

**Table 15.** Consumption estimates for each marine mammal group of the *Ecopath* model of Northwest Africa.

<i>Ecopath</i> groups	Annual food consumption (tonnes*km <sup>-2</sup> )	Annual biomass (tonnes*km <sup>-2</sup> )	Q/B
1. Minke whales	0.071	0.00844	8.4212
2. Fin whales	0.051	0.01220	4.1608
3. Humpback whales	0.014	0.00302	5.0781
4. Bryde's whales	0.049	0.00785	6.2600
5. Sei whales	0.010	0.00160	6.1776
6. Blue whales	0.009	0.00276	3.3978
7. Sperm whales	0.102	0.02020	5.0251
8. Killer whales	0.002	0.00026	7.7634
9. Beaked whales	0.001	0.00013	9.9234
10. Dolphins	0.306	0.00559	13.7390
<b>Average</b>	<b>0.045</b>	<b>-</b>	<b>6.995</b>

## 11. Seabirds

Seabirds of Northwest Africa are migrating species and are mostly present in the study area from November until March (Samb and Mendy 2004). Very little information is available for seabirds species in that area, and input values in the original model came from southern Benguela (Crawford *et al.*, 1991). The input values for that group are thus a total biomass of 0.118 t\*km<sup>-2</sup>, a P/B of 0.12 year<sup>-1</sup>, and a Q/B of 118 year<sup>-1</sup>. Diet composition was mainly composed of zooplankton, pelagic fish, and other small fish (Jarre-Teichmann *et al.* 1998).

## 12. Large pelagics

This group is mainly composed of large tunas that are important target of “surface” fisheries, and bycatch by longlines. The most important species of this group are yellowfin (*Thunnus albacares*), skipjack (*Katsuwonus pelamis*), and bigeye (*Thunnus obesus*) tunas. These species are large and migrating species that are mainly caught by a global fishery that happens outside Northwest African countries' EEZ.

Samb and Mendy (2004) estimated a biomass density of 2.54 t\*km<sup>-2</sup> for the Senegambian ecosystem. This value was assumed to represent our study area of Northwest Africa. The biomass value for large pelagic species could range from 0.427 to 5.346 t\*km<sup>-2</sup> in other models for the Northwest African region. Thus, this represents an intermediate value.

The average annual catch of large pelagic fish in the 1990s was 0.0078 t\*km<sup>-2</sup> for local fleets, and 0.0075 t\*km<sup>-2</sup> for foreign fleets, for an average total catch of 0.0153 t\*km<sup>-2</sup> for the 1990s in Northwest Africa.

Natural mortality for tropical tunas was estimated to range between 0.6 to 0.8 yr<sup>-1</sup> (Samb and Mendy 2004). Total mortality (Z) of yellowfin tuna was estimated to 1.6 yr<sup>-1</sup> (ICCAT 1999a,b), following Allen (1971). This represents a higher value compared to other P/B values used for large pelagics in similar

*Ecopath* models in Northwest Africa, which range from 0.300 yr<sup>-1</sup> (Diallo *et al.* 2004) to 1.908 yr<sup>-1</sup> (Stanford *et al.* 2001). An average value of 1.016 yr<sup>-1</sup> was used here.

Q/B ratio of large pelagic species range from 3.560 yr<sup>-1</sup> (Sidi and Guénette 2004 for Mauritania) to 34.490 yr<sup>-1</sup> (Stobberup *et al.* 2004 for Cape Verde) in Northwest Africa. For the present model, we used an average Q/B of 11.698 yr<sup>-1</sup>.

Diet information was taken from Cayré *et al.* (1988) who estimated that large pelagic tunas feed mainly on fish, crustaceans, and molluscs.

### 13. Mesopelagic predators

This group was not originally included in the Senegambian *Ecopath* model of Samb and Mendy (2004), but was added because fisheries data indicate that mesopelagic predators are commercially important in the study area. The key species of that group for Northwest Africa are blue whiting (*Micromesistius poutassou*) and black scabbardfish (*Aphanopus carbo*).

The biomass of mesopelagic predators was taken from similar species group of the Guinea-Bissau model (Amorim *et al.* 2004) and was set to 0.735 t\*km<sup>-2</sup>yr<sup>-1</sup>.

The P/B ratios used in different *Ecopath* models of the Northwest Africa area were ranging from 3.990 yr<sup>-1</sup> in Mauritania (Sidi and Guénette 2004) to 5.105 yr<sup>-1</sup> in Morocco (Stanford *et al.* 2001). An average value of 4.362 yr<sup>-1</sup> was used for the present model.

The Q/B ratios available for Northwest Africa were ranging from 4.440 yr<sup>-1</sup> in Mauritania (Sidi and Guénette 2004) to 37.506 yr<sup>-1</sup> in Morocco (Stanford *et al.* 2001). An average value of 31.609 yr<sup>-1</sup> was used for the model covering the greater area of Northwest Africa.

The diet of mesopelagic predators also comes from the Guinea-Bissau model and is assumed to be representative of the larger ecosystem of Northwest Africa. According to Amorim *et al.* (2004), mesopelagic predators mainly fed on large pelagic fish, clupeids, and cephalopods.

### 14. Bathydemersal predators

Here again, the bathydemersal predators group was not initially included in the Senegambian *Ecopath* model of Samb and Mendy (2004) because this model was only covering the continental shelf, and most of the bathydemersal predators are found in deeper waters. Since our study area covers deeper waters, we added a trophic group to cover these species. The key species of that group for Northwest Africa are Senegalese hake (*Merluccius senegalensis*), European hake (*Merluccius merluccius*) and Black-bellied angler (*Lophius budegassa*).

The biomass of bathydemersal predators was taken from a similar species group of the Cape Verde model (Stobberup *et al.* 2004) and was set to 0.255 t\*km<sup>-2</sup>yr<sup>-1</sup>. Over the whole study area, this value could range from 0.255 to 0.729 t\*km<sup>-2</sup>yr<sup>-1</sup>.

The P/B ratios used in different *Ecopath* models of the Northwest Africa area were ranging from 0.384 yr<sup>-1</sup> (Stobberup *et al.* 2004) to 2.710 yr<sup>-1</sup> (Sidi and Guénette 2004). The lowest value of 0.384 yr<sup>-1</sup>, taken from the Cape Verde model (Stobberup *et al.* 2004), was assumed to represent the Northwest Africa region, since it was calculated for the same trophic group (bathydemersals) in both models.

The Q/B ratio used in this model also comes from the Cape Verde model (Stobberup *et al.* 2004) and was set to 3.844 yr<sup>-1</sup>. This was the lowest value of the range of Q/B for Northwest Africa models. Maximum Q/B observed in the area was 17.43 yr<sup>-1</sup> in Mauritania (Sidi and Guénette 2004).



The diet of bathydemersal predators also comes from the Cape Verde model and is assumed to be representative of the larger ecosystem of Northwest Africa. According to Stobberup *et al.* (2004), bathydemersal predators mainly feed on large crustaceans, coastal demersal fish, zooplankton, and benthos.

## 15. Sharks

Most shark species of the area belong to the Carcharhinidae family. The key species of that group is the blue shark, *Prionace glauca*. Species belonging to the Squalidae family (dogfish sharks) as well as mustelus (smooth-hounds) species are also important. Surveys by the *Centre de Recherche Océanographique de Dakar-Thiaroye* (CRODT) evaluated the biomass to be around 5,600 tonnes for the Senegambian area, equivalent to a biomass density of  $0.290 \text{ t*km}^{-2}$ . According to mission reports from Norwegian vessel Fultjort Nansen and their 2007 survey for the Northwest African area (unpublished data), this biomass decreased to 3470 tonnes in FAO area 34 (or approximately  $0.126 \text{ t*km}^{-2}$ ). The biomass value could vary from 0.144 (Sidi and Guénette 2004) to 0.729 (Stanford *et al.* 2001) in our study area.

The average annual catches were estimated by SAUP to  $0.0011 \text{ t*km}^{-2}$  for local fleets and  $0.0004 \text{ t*km}^{-2}$  for foreign fleets for the 1990s period, for a total catch of  $0.0015 \text{ t*km}^{-2}\text{yr}^{-1}$  for sharks. These values represent a fishing mortality of  $0.0074 \text{ yr}^{-1}$  over the study area.

The biology of sharks remains generally unknown in the study area. P/B (or total mortality) was estimated from growth parameters of *Carcharhinus limbatus* presented in Bransletter (1987). The author estimated the  $L_{\infty}$  to be 176 cm FL (or 210 cm TL), and a K of  $0.27 \text{ yr}^{-1}$ . Using the equation of Pauly (1980), these growth parameters and an average temperature of  $22^{\circ}\text{C}$ , a natural mortality of  $0.28 \text{ yr}^{-1}$  was estimated by Samb and Mendy (2004). This natural mortality added to fishing mortality give a Z or P/B of  $0.905 \text{ yr}^{-1}$  which was used in the model. This value could vary from  $0.300 \text{ yr}^{-1}$  (Diallo *et al.* 2004) to  $1.338 \text{ yr}^{-1}$  (Stanford *et al.* 2001) in other published models of our study area.

The Q/B of sharks in Northwest Africa could range from  $3.000 \text{ yr}^{-1}$  (Mendy 2004) up to  $11.477 \text{ yr}^{-1}$  (Stanford *et al.* 2001) for sharks. An average value of  $7.497 \text{ yr}^{-1}$  was used here and assumed to represent the entire area of Northwest Africa.

Diet of sharks was based on Samb and Mendy (2004), and was mainly composed of zooplankton and coastal clupeid fish.

## 16. Rays

Rays were grouped separately from sharks because of their particular ecology. Indeed, since these species live on the bottom of the ocean, their feeding behaviour is different than that of sharks. The key species of this group is the common guitarfish (*Rhinobatos rhinobatos*). For the 1990s, Samb and Mendy (2004) estimated an average annual biomass of  $0.112 \text{ t*km}^{-2}$ , which is what we used in the model. However, in 2007, this biomass increased to 4340 tonnes (or approximately  $0.157 \text{ t*km}^{-2}$ ) in the area, according to the mission reports from Norwegian vessel Fultjort Nansen survey off the coast of Northwest Africa in 2007 (I.L. Bamy, Centre National des Sciences Halieutiques de Boussoura, unpublished data).

Catch data came from the Sea Around Us database (R. Watson, Sea Around Us Project, personal communication), and resulted in a total of  $0.0018 \text{ t*km}^{-2}\text{yr}^{-1}$  of rays caught in the 1990s for our study area. This catch was almost equally divided between local fleets ( $0.0010 \text{ t*km}^{-2}\text{yr}^{-1}$ ) and foreign fleets ( $0.0008 \text{ t*km}^{-2}\text{yr}^{-1}$ ).

Based on what was available for the common guitarfish, Samb and Mendy (2004) estimated a P/B of  $1.000 \text{ year}^{-1}$  based on maximal length of 100 cm (after Schneider 1990) and an average temperature of  $22^{\circ}\text{C}$ , using Pauly's (1980) equation to estimate natural mortality. Total mortality (Z) was then obtained

by adding fishing mortality to the natural mortality. This value was assumed to equal the production rate, based on Allen (1971). The range of possible P/B used in other models of the Northwest Africa region was from 0.423 yr<sup>-1</sup> (Stobberup *et al.* 2004) to 1.000 yr<sup>-1</sup> (Samb and Mendy 2004). A median of 0.755 yr<sup>-1</sup> was used here as a starting point.

Q/B was averaged from similar models (De la Cruz-Aguero 1993, Opitz 1993, Paula e Silva *et al.* 1993) and set to 6.000 year<sup>-1</sup>. This value can range from 3.912 yr<sup>-1</sup> in Guinea-Bissau (Amorim *et al.* 2004) to 6.3 yr<sup>-1</sup> in Mauritania (Sidi and Guénette 2004) for similar *Ecopath* models.

Diet composition was mainly composed of benthos, but also includes a small proportion of coastal demersal species.

## 17. Coastal tunas

This group includes a dozen species, of which the most important are little tunny (*Euthynnus alletteratus*), Atlantic bonito (*Sarda sarda*), West African Spanish mackerel (*Scomberomorus tritor*), and Frigate tuna (*Auxis thazard*). These species are present all year round in the Northwest African waters, and are predominantly fished by artisanal fisheries.

The biomass of coastal tunas was taken directly from the estimate of Samb and Mendy (2004) for the Senegambian ecosystem and was set to 2.89 t\*km<sup>-2</sup>yr<sup>-1</sup>.

The average annual catches were estimated by SAUP to 0.0013 t\*km<sup>-2</sup> for local fleets and 0.0017 t\*km<sup>-2</sup> for foreign fleets for the 1990s period, for a total catch of 0.0030 t\*km<sup>-2</sup>yr<sup>-1</sup> for coastal tunas.

Growth parameters have been estimated for the little tunny by Pauly (1978, 1979), Diouf (1980), and Pauly and Munro (1984). Samb and Mendy (2004) used these parameters to estimate the mortality of this group, based on Pauly's (1980) equation. The M was calculated to 0.34 yr<sup>-1</sup> based on growth parameters and water temperature of 22°C. Assuming that fishing mortality was equal to their exploitation rate of 0.5 yr<sup>-1</sup>, a Z value of 0.800 was estimated for coastal tunas in the area. This value was assumed to represent the average coastal tunas in the ecosystem and was then used as an input in the Northwest African model. Other P/B values in Northwest African models could range from 0.642 yr<sup>-1</sup> (Stanford *et al.* 2001) to 0.987 yr<sup>-1</sup> (Stobberup *et al.* 2004).

The Q/B ratio used in this model also comes directly from the Senegambian model (Samb and Mendy 2004) and was set to 9.500 yr<sup>-1</sup>. This was close to the highest value of the range of Q/B for Northwest Africa models (with a maximum Q/B of 9.872 yr<sup>-1</sup> in Cape Verde [Stobberup *et al.* 2004]). Minimum Q/B observed in the area was 3.774 yr<sup>-1</sup> in Morocco (Stanford *et al.* 2001).

Diet of coastal tunas was based on Samb and Mendy (2004), who cite a study by Postel (1955) describing the diet of coastal tunas to be mainly composed of small coastal pelagics, crustaceans, and cephalopods.

## 18. Coastal demersals

demersal species differ a lot depending on the habitat type and depth. They include a wide range of species that are subject to an important level of exploitation (Samb and Mendy 2004). Two types of coastal demersals are included in that group. Fish living on soft sediments in warmer estuarine waters with high productivity belong to the sciaenidae (*Pseudotolithus* spp.), polynemidae (*Galeoides* spp.), carangidae (*Scyris* spp.) and cynoglossidae (*Cynoglossus* spp.) families. Other fish live on diverse sediment types, varying from rocks to mud, and from depths from 30 to 100 meters, in colder waters. The latter species belong to the sparidae (*Dentex* spp.), serranidae (*Epinephelus* spp.), sparidae (*Pagellus* spp. and *Sparus* spp.) and mullidae (*Pseudupaeneus* spp.) families.

The coastal demersal fish are highly exploited in the Northwest African area. Consequently, our data collection allowed us to realize that most information available on fisheries or biomass surveys are for these species. According to Samb and Mendy (2004), most of the region's coastal demersal species are overexploited. Based on a synthesis of eight trawl surveys in the senegambian area (Caverivière and Thiam 1992), the exploitable biomass declined substantially from 1986 to 1991, going from 173,000 to 81,000 tonnes.

The biomass of coastal demersal fish in the Senegambian waters was estimated to  $4.696 \text{ t*km}^{-2}$  by Samb and Mendy (2004). Assuming this density represents the whole Northwest African region, this value is in the lower range of possible biomass used in other *Ecopath* models published in the same area, ranging from  $2.634 \text{ t*km}^{-2}$  (Sidi and Guénette 2004) to  $27.267 \text{ t*km}^{-2}$  (Stanford *et al.* 2001). The biomass of this species is also known to be decreasing. According to a survey of the Norwegian vessel Fultjort Nansen off the coast of Northwest Africa in 2007 (Mission reports, I.L. Bamy, Centre National des Sciences Halieutiques de Boussoura, unpublished data), the biomass of the major demersal groups in Northwest Africa was 49,860 tonnes (or  $1,765 \text{ t*km}^{-2}$ ).

The P/B ratio used in our model was calculated from an estimation of natural mortality of  $0.4 \text{ yr}^{-1}$  (Franqueville 1983) for red Pandora (*Pagellus bellottii*). Using that M, Samb and Mendy (2004) estimated a natural mortality (M) of  $0.5 \text{ yr}^{-1}$ , based on Pauly (1980) equation and with a  $L_{\infty}$  of 37 cm (LT) and a K of  $0.24 \text{ yr}^{-1}$ , for an average temperature of  $22^{\circ}\text{C}$ . When this M is added to a calculated fishing mortality of  $0.7 \text{ yr}^{-1}$  (Samb and Mendy 2004), this results in a P/B of  $1.200 \text{ yr}^{-1}$ . This represents the lowest value of the range of possible values found for Northwest Africa models. The highest part of the range was  $13.940 \text{ yr}^{-1}$  in Guinea (Diallo *et al.* 2004).

The Q/B ratio used in this model comes from an estimate by Samb and Mendy (2004) using an equation from Palomares and Pauly (1998), resulting in a value of  $6.000 \text{ yr}^{-1}$ . This represents the lowest value from the range of possible Q/B for coastal demersal species in Northwest Africa. The highest Q/B value found for this species group was  $57.279 \text{ yr}^{-1}$  in Guinea-Bissau (Amorim *et al.* 2004). An extreme Q/B value of  $107.636 \text{ yr}^{-1}$  (Stobberup *et al.* 2004) was not considered in the range.

The diet of coastal demersal fish is as diverse as the species composing that group. The main prey of this group include crustaceans, zooplankton, pelagic fish, cephalopods, benthos, and detritus (Fischer *et al.* 1981, Franqueville 1983, Sidibé 2003). According to Samb and Mendy (2004), coastal demersal fish feed mainly on benthic producers and plankton.

## 19. Clupeids

Clupeids represent with other coastal pelagics the most important marine resource in terms of landings in the area. Depending on the years, coastal pelagics could reach 70% of declared catches in the Senegambian area (Samb 1997). The most important clupeid species of the area are round and madeiran sardinellas (*Sardinella aurita* and *Sardinella maderensis*, respectively), which are considered as the key species for the clupeids group. Bonga shad (*Ethmalosa fimbriata*) is also an important species of coastal and estuarine zones of our study area.

The biomass of sardinellas in the area results from the N/O Dr Fridtjof Nansen survey that performed acoustic survey campaigns each November from 1995 to 1999 in the EEZ of Senegal and Gambia (Saetersdal *et al.* 1995; Toresen 1996, 1997, 1998; Toresen and Kolding 1999; Samb and Pauly 2000). Average biomass for the round sardinella was 237,000 tonnes, and it was 373,000 tonnes for the madeiran sardinella. In the 2007 survey, the biomass of these species was 248,000 and 328,000 tonnes, respectively (Mission reports, I.L. Bamy, Centre National des Sciences Halieutiques de Boussoura, unpublished data). Using the 1990s biomass, we ended up with a total annual biomass density of  $22.130 \text{ t*km}^{-2}$  for Northwest Africa.

Catch data were collected from the SAUP database and represent an average of  $0.1931 \text{ t*km}^{-2}$  for local fleets and  $0.1423 \text{ t*km}^{-2}$  for foreign fleets, totaling an average  $0.3354 \text{ t*km}^{-2}$  of clupeids caught annually in the area in the 1990s.

Natural mortality for sardinellas was estimated by many authors in the area, notably Camarena-Luhrs (1986), Samb (1988), and Fréon (1988). Samb and Mendy (2004) used a natural mortality of  $0.96 \text{ yr}^{-1}$  for round sardinella and  $0.5 \text{ yr}^{-1}$  for madeiran sardinella. Added to fishing mortality, the authors ended up with a P/B of  $1.54 \text{ yr}^{-1}$  for round sardinella and  $0.72 \text{ yr}^{-1}$  for madeiran sardinella. Since this group was aggregated in the present model, a weighted average P/B of  $1.33 \text{ yr}^{-1}$  was used here. In other published models from the same study area, this value could range from  $1.100 \text{ yr}^{-1}$  (Stanford *et al.* 2001) to  $3.100 \text{ yr}^{-1}$  (Diallo *et al.* 2004).

The Q/B ratio for sardinellas was also averaged from Samb and Mendy (2004), and represents  $16.347 \text{ yr}^{-1}$ . The authors used Q/B ratios of  $20.200 \text{ yr}^{-1}$  and  $13.900 \text{ yr}^{-1}$  for round sardinella and madeiran sardinella, respectively. In other models published for our study area, these values could range from  $9.000 \text{ yr}^{-1}$  in Gambia (Mendy 2004) to  $28.389 \text{ yr}^{-1}$  in Guinea-Bissau (Amorim *et al.* 2004).

Diet of sardinellas was mainly composed of zooplankton and phytoplankton (Nieland 1982; Medina-Gaertner 1985).

## 20. Other coastal pelagics

The key species of that group are ray-finned fish species such as the chub mackerel (*Scomber japonicus*), horse mackerels (*Trachurus* spp.), and largehead hairtail (*Trichiurus lepturus*). Samb and Mendy (2004) mention that for the Senegambian area, the commercially important species in terms of catches are the cunene horse mackerel (*Trachurus trecae*) and the false scad (*Decapterus rhonchus*). Other coastal pelagic species are also caught, including bigeye grunt (*Brachydeuterus auritus*), Atlantic bumper (*Chloroscombrus chrysurus*), and sompat grunt (*Pomadasys jubelini*).

An average biomass of  $13.116 \text{ t*km}^{-2}$  was used by Samb and Mendy (2004), based on the survey of the N/O *Dr Fridtjof Nansen* during the early 2000s. The total biomass was estimated to be around 362,000 tonnes for carangidae and other coastal pelagic species in the Senegambian area. In 2007, this biomass was down to 224,000 for FAO area 34 (Mission reports, I.L. Bamy, Centre National des Sciences Halieutiques de Boussoura, unpublished data). The density estimated by Samb and Mendy (2004) in the Senegambian area was assumed to be representative of our study area in the late 1980s.

The average total catch of coastal pelagic species in the 1990s was estimated to reach 502,153 tonnes per year, for a density of  $0.1410 \text{ t*km}^{-2}$  in our study area. From this amount,  $0.0924 \text{ t*km}^{-2}$  were caught by foreign fleets, and  $0.0487 \text{ t*km}^{-2}$  by local fleets.

Samb and Mendy (2004) used a total mortality (equal to P/B) of  $1.100 \text{ yr}^{-1}$ , based on a natural mortality of  $0.5 \text{ yr}^{-1}$  for cunene horse mackerel, estimated by Maxim (1995). This P/B was an intermediate value and was assumed to be representative of the whole Northwest African area, which could range from  $0.600 \text{ yr}^{-1}$  (Mendy 2004) to  $4.380 \text{ yr}^{-1}$  (Sidi and Guénette 2004), according to other published *Ecopath* models in the area.

The consumption rate of coastal pelagic species used in our model was  $10.635 \text{ yr}^{-1}$ , based on Samb and Mendy (2004). However, this could range from  $4.440 \text{ yr}^{-1}$  (Amorim *et al.* 2004) to  $41.050 \text{ yr}^{-1}$  (Sidi and Guénette 2004) from other models published in the study area.

Diet of this trophic grouping was mainly composed of zooplankton, and also included some phytoplankton (Samb and Mendy 2004).

## 21. Cephalopods

Cephalopods are important species for fisheries in Northwest Africa, especially in Morocco and Mauritania (Samb and Mendy 2004). Octopus (*Octopus* spp.) and cuttlefish (*Sepia* spp.) are the dominant species of cephalopods caught in the study area, but other species such as European common

squid (*Alloteuthis subulata*), short-finned squid (*Illex coindetii*), European squid (*Loligo vulgaris*), European flying squid (*Todarodes sagittatus*) are also included in this group.

Depending on the years we see important fluctuations in the biomass of squids in the study area. The average biomass in the Senegambian area was estimated to 30,000 tonnes for the 1990s. This resulted in a biomass density of  $1.087 \text{ t*km}^{-2}$ , assumed to be representative of the whole study area. However, in 2007, a survey by the Norwegian vessel Fultjort Nansen off the coast of Northwest Africa (Mission reports, I.L. Bamy, Centre National des Sciences Halieutiques de Boussoura, unpublished data), estimated the biomass to be down to 3,630 tonnes (approximately  $0.131 \text{ t*km}^{-2}$ ) for FAO area 34 (Northwest Africa).

As mentioned by many authors, cephalopods are an important commercial species for all Northwest African countries. Total catches in our study area averaged 193,953 tonnes per year in the 1990s, representing a density of  $0.0545 \text{ t*km}^{-2}$ .

The P/B of cephalopods is relatively unknown. In the study area, this value could range from  $1.900 \text{ yr}^{-1}$  (Samb and Mendy 2004) to  $4.700 \text{ yr}^{-1}$  (Diallo *et al.* 2004). An average value of  $3.300 \text{ yr}^{-1}$  was used to represent our study area.

Similarly little information was available for the Q/B of cephalopods in Northwest Africa. Other published *Ecopath* models used values ranging from  $11.700 \text{ yr}^{-1}$  in Senegambian and Moroccan ecosystems (Samb and Mendy 2004; Stanford *et al.* 2001) to  $23.400 \text{ yr}^{-1}$  (Sidi and Guénette 2004). An average of  $16.735 \text{ yr}^{-1}$ , based on three models of Northwest Africa (Samb and Mendy 2004; Amorim *et al.* 2004; Stanford *et al.* 2001; Sidi and Guénette 2004), was used in our model.

Diet of cephalopods was mainly composed of zooplankton, macrobenthos, and also included some fish species (Samb and Mendy 2004, after Diata *et al.* 2001).

## 22. Crustaceans

This group was not originally included in the model of Samb and Mendy (2004), but was added because an important fishery occurs on shrimp (*Parapenaeus longirostris* and *Penaeus* spp.). Biomass was obtained from similar crustacean species of the Cape Verde model (Stobberup *et al.* 2004), and was set to  $13.048 \text{ t*km}^{-2}\text{yr}^{-1}$ .

Based on the SAUP database, we used an average total catch of 27,159 tonnes of crustaceans per year in the 1990s for Northwest Africa. This represents a density of  $0.0076 \text{ t*km}^{-2}$  for our model. Crustaceans are mainly caught by local fleets ( $0.0062 \text{ t*km}^{-2}$ ), but also by foreign fleets ( $0.0014 \text{ t*km}^{-2}$ ).

P/B ratio could range from  $2.500 \text{ yr}^{-1}$  (Diallo *et al.* 2004) to  $15.190 \text{ yr}^{-1}$  (Amorim *et al.* 2004). The average P/B ratio available among four models in the whole Northwest Africa area was  $6.443 \text{ yr}^{-1}$ . This was used as the input value in our model.

Q/B ratios are ranging from  $10.000 \text{ yr}^{-1}$  (Stobberup *et al.* 2004) to  $54.840 \text{ yr}^{-1}$  (Amorim *et al.* 2004) in different models available from Northwest Africa. An average value of  $31.963 \text{ yr}^{-1}$  based on five models of the same area, was used as an input here.

The diet of large crustaceans also comes from Cape Verde and is assumed to be representative of the larger ecosystem of Northwest Africa. According to Stobberup *et al.* (2004), crustaceans mainly feed on benthos and detritus.

## 23. Benthos

Macrobenthos is an important source of food for demersal fish, but knowledge about this group is very limited (Samb and Mendy 2004). In the original model, this group was divided between macrobenthos

and meiobenthos, and the different parameters were based on a model from Jarre-Teichmann (1998). In the present model, macro and meiobenthos are grouped, and the different input data are aggregated and weighted by their biomass. Total biomass density for benthos was estimated to  $112.600 \text{ t*km}^{-2}$ .

The P/B could range from  $1.687 \text{ yr}^{-1}$  (Samb and Mendy 2004) to  $7.000 \text{ yr}^{-1}$  (Sidi and Guénette 2004). An extreme value of  $108.300 \text{ yr}^{-1}$  (Amorim *et al.* 2004) was not included in the range here. An average value of  $4.33 \text{ yr}^{-1}$  was used in our model.

The range of possible Q/B values provided from other models in Northwest Africa was from  $13.481 \text{ yr}^{-1}$  (Samb and Mendy 2004) to  $48.670$  (Sidi and Guénette 2004). Here again, an extreme value of  $243.100 \text{ yr}^{-1}$  (Amorim *et al.* 2004) was not included in the average. In the present model, we used an average value of  $32.730 \text{ yr}^{-1}$ , based on three models from Northwest Africa.

Based on information on macrobenthos and meiobenthos groups in the model by Samb and Mendy (2004), our aggregated 'Benthos' group was assumed to have an average diet mainly composed of detritus (84%), but also benthic producers and other benthic species (11%).

## 24. Benthic producers

Since data about benthic production is very sparse, the original model of Samb and Mendy (2004) obtained information on benthic production from another ecosystem model (southern Benguela, by Jarre-Teichmann *et al.* 1998). We decided to leave that group unmodified, and thus used a biomass value of  $10.500 \text{ t*km}^{-2}$  and a P/B value of  $15.000 \text{ yr}^{-1}$  for the current model.

## 25. Zooplankton

Research on secondary production, mostly done in waters surrounding Cape-Verde, suggest a strong relationship between the abundance of zooplankton and the strength of the upwelling. In this area, copepods compose the major part of the biomass, which totals  $20.636 \text{ t*km}^{-2}$  (based on Touré 1983). Based on Samb and Mendy (2004), we used a P/B of  $58.356 \text{ yr}^{-1}$  and a Q/B of  $274.805 \text{ yr}^{-1}$ . The latter value may seem high, but in fact, it falls within the range of what is usually seen in the literature for zooplankton's consumption. Other published *Ecopath* models of the northwestern African region present P/B values ranging from  $28.000 \text{ yr}^{-1}$  in Mauritania (Sidi and Guénette 2004) to  $78.356 \text{ yr}^{-1}$  in Guinea (Diallo *et al.* 2004), and Q/B values ranging from  $106.330 \text{ yr}^{-1}$  in Mauritania (Sidi and Guénette 2004) to  $280.000 \text{ yr}^{-1}$  in Cape Verde (Stobberup *et al.* 2004).

## 26. Phytoplankton

Primary production was calculated by Samb and Mendy (2004) as an average of different estimates. Primary production can be very important in the Northwest African area because it's highly influenced by the upwelling that makes the area very rich in oxygen and have a high productivity (Voiturier and Herbland 1982). In the area, the maximum production is observed at the surface, where maximal values of  $70$  to  $80 \text{ mg*m}^{-2}$  has been recorded (Voiturier and Herbland 1982). We used an average biomass value of  $82.000 \text{ t*km}^{-2}$  and a P/B of  $138.189 \text{ yr}^{-1}$ , based on Samb and Mendy (2004).

## 27. Detritus

Information is very sparse about the biomass of detritus on the coast of Northwest Africa. As a result, an arbitrary total biomass of  $10 \text{ t*km}^{-2}$  was initially used by Samb and Mendy (2004). The lack of information on detritus is very common for other *Ecopath* models. Most of the time, a very generalized value is

assumed (Morissette *et al.* 2003; Morissette 2005). Detritus is assumed to include benthic and pelagic detritus that fall on the bottom of the ocean, as well as benthic bacteria involved in the microbial loop (Morissette *et al.* 2003).

## BALANCING THE MODEL

The unbalanced model for Northwest Africa is shown in Table 16. In order to obtain a balanced solution, different levels of verification have been made. First, it was important to make sure that gross efficiency (GE), which is the ratio of production to consumption (P/Q) was always within the 0.1 – 0.3 range. According to Christensen and Pauly (1992), GE ranges between 10 and 30%, with the exception of top predators, e.g., marine mammals and seabirds, which can have lower GE (between 0.1 and 1%), and small, fast growing fish larvae or nauplii or bacteria, which can have higher GE (between 25% and 50%) (Christensen and Pauly 1992).

**Table 16.** Input data for the *Ecopath* model of Northwest Africa. Unbalanced values are shown in bold.

<i>Ecopath</i> group	Biomass (t*km <sup>-2</sup> )	P/B (year <sup>-1</sup> )	Q/B (year <sup>-1</sup> )	EE	GE
1. Minke whales	0.00844	0.0990	8.4212	0.0000	0.0118
2. Fin whales	0.0122	0.0990	4.1608	0.0000	0.0238
3. Humpback whales	0.00302	0.0990	5.0781	0.0000	0.0195
4. Brydes whales	0.00785	0.0990	6.2600	0.0000	0.0158
5. Sei whales	0.00160	0.0200	6.1776	0.0000	0.0032
6. Sperm whales	0.0202	0.0500	5.0251	0.0000	0.0100
7. Killer whales	0.000262	0.0200	7.7634	0.0000	0.0026
8. Baleen whales	0.00276	0.0400	3.3978	0.0000	0.0118
9. Beaked whales	0.000125	0.0360	9.9234	0.0000	0.0036
10. Dolphins	0.00559	0.0470	13.7390	<b>2.9729</b>	0.0034
11. Seabirds	0.1180	0.1200	118.0000	0.0000	0.0010
12. Large pelagics	2.5400	1.0160	11.6980	0.9474	0.0869
13. Mesopelagic predators	0.7350	4.3620	31.6090	0.1170	0.1380
14. Bathydeersal predators	0.2550	0.3840	3.8440	<b>7.6971</b>	0.0999
15. Sharks	0.2900	0.9050	7.4970	0.0106	0.1207
16. Rays	0.1120	0.7550	6.0000	0.0216	0.1258
17. Coastal tunas	2.8900	0.8000	9.5000	0.0026	0.0842
18. Coastal demersal	4.6960	1.2000	6.0000	0.3142	0.2000
19. Clupeids	22.1300	1.3300	16.3466	<b>1.3062</b>	0.0814
20. Other coastal pelagics	13.1160	1.1000	10.6350	0.9500	0.1034
21. Cephalopods	1.0870	3.3000	16.7350	<b>2.3499</b>	0.1972
22. Crustaceans	13.0480	6.4430	31.9630	0.0053	0.2016
23. Benthos	112.6000	4.3340	32.7300	0.6620	0.1324
24. Benthic producers	10.5000	107.3600	-	0.2634	-
25. Zooplankton	20.6360	58.3560	274.8050	0.4015	0.2124
26. Phytoplankton	82.0140	138.1890	-	0.5109	-
27. Detritus	10.0000	-	-	0.3672	-

The modifications to the original model needed to reach a balanced solution are listed below:

1. The biomass for dolphins originally came from an estimate by Northridge (1984), and had a higher value ( $0.039 \text{ t*km}^{-2}$ ). In our modified version of the model, biomass was calculated from K. Kaschner's database, and had a value of  $0.0059 \text{ t*km}^{-2}$ . However, because dolphins are also an important prey of killer whales in this ecosystem, the lower biomass of dolphins created an imbalance (too much predation for the available biomass and production), and an ecotrophic efficiency (EE) higher than 1. To reach a balanced solution, an intermediate value of  $0.02225 \text{ t*km}^{-2}$  (the average of the minimal and maximal value) was used for dolphins.
2. The group representing large pelagics was not balanced in our model. Consequently, we used the highest possible P/B and Q/B values for this group, equivalent to  $1.908 \text{ yr}^{-1}$  and  $11.60 \text{ yr}^{-1}$ , respectively. This resulted in a balanced solution and allowed us to keep our initial biomass of  $2.54 \text{ t*km}^{-2}$ .
3. Bathydemersal predators is a group that was added to the Senegalo-Gambian ecosystem to represent an important fishery for the coast of Northwest Africa. Since this group was not in the initial model from Samb and Mendy (2004), we first assumed that the biomass of bathydemersal predators would be the same in terms of density ( $0.255 \text{ t*km}^{-2}$ ) than what is presented for Cape Verde by Stobberup *et al.* (2004). However, this seems to be inadequate to reach a balance solution, so we let the model estimate the biomass needed to be at equilibrium with the rest of the foodweb (using a EE of 0.95). Consequently, we used the highest P/B value available in our range (2.71, from Sidi and Guénette 2004), and let the model estimate the Q/B using the assumption that P/Q ratio is 30% (Christensen and Pauly 1992). The estimated biomass for bathydemersal predators is  $0.2928 \text{ t*km}^{-2}$  and the Q/B is  $9.033 \text{ yr}^{-1}$ , which are still within the range of possible values for similar species living on the coast of Northwest Africa.
4. Clupeids were clearly overestimated in our model, even if their EE was close to balance in our model, with a value of 1.28. In order to reach a balanced solution, we reduced the proportion of clupeids in the predators' diet, used a maximal P/B value of  $3.100 \text{ yr}^{-1}$  from the *Ecopath* model of Guinea (Diallo *et al.* 2004). This was sufficient to balance the model.
5. In our unbalanced model, there were not enough 'other coastal pelagic' fish to reach a balanced solution. We thus used an average P/B value of  $2.61 \text{ yr}^{-1}$  and this was sufficient to reach a balanced scenario.
6. Many species feed on cephalopods in our ecosystem, and consequently the input parameters used as a starting point were not sufficient to cope with the consumption by all predators of these species in our model. Thus, we used a maximum P/B of  $4.700 \text{ yr}^{-1}$  from the Guinean model (Diallo *et al.* 2004). We also used a biomass of  $2.4092 \text{ t*km}^{-2}$  to be consistent with the available time series of biomass for this species in the area. This biomass represents an intermediate within the range of possible values computed for all models for Northwest Africa (ranging from  $1.038 \text{ t*km}^{-2}$  in Mauritania [Sidi and Guénette 2004] to  $4.507 \text{ t*km}^{-2}$  in Guinea-Bissau [Amorim *et al.* 2004]), and is assumed to be representative of the area.
7. Benthic producers had a low P/B of  $15 \text{ yr}^{-1}$  in our ecosystem, and this created an imbalance in the initial parameterization of our model. However, we know that the P/B of benthic producers is higher in other models such as Guinea-Bissau (Amorim *et al.* 2004) where they used a P/B of  $199 \text{ yr}^{-1}$ , and could even reach  $213 \text{ yr}^{-1}$  in Cape Verde (Stobberup *et al.* 2004). We thus increased the production rate of benthic producers to an intermediate value of  $107.362 \text{ yr}^{-1}$ . This produced a balanced solution for that group.
8. All these adjustments created an imbalance on other coastal pelagics (EE = 1.352), so we used an average P/B of  $2.612 \text{ yr}^{-1}$  (within the range of possible values for Northwest Africa) to reach a balanced solution for that group.
9. Finally, coastal tunas had a GE lower than 10%, so we used the highest possible P/B ( $0.820 \text{ yr}^{-1}$  from Sidi and Guénette 2004), combined with the lowest possible Q/B ( $3.774 \text{ yr}^{-1}$  from Stanford *et al.* 2001) to re-balance the model. The resulting GE was 22% which is within the range of what Christensen and Pauly (1992) suggested.



The final balanced model for Northwest Africa is given in Table 17. A diet matrix showing the proportion of each prey in all predators' diets is provided in Table 18.

**Table 17.** Balanced *Ecopath* model of Northwest Africa. Estimated parameters are shown in **bold**.

<i>Ecopath</i> group	Trophic level	Biomass (t*km <sup>-2</sup> )	P/B (year <sup>-1</sup> )	Q/B (year <sup>-1</sup> )	EE	GE
1. Minke whales	<b>3.54</b>	0.00844	0.0990	8.4212	<b>0.0000</b>	<b>0.0118</b>
2. Fin whales	<b>3.01</b>	0.0122	0.0990	4.1608	<b>0.0000</b>	<b>0.0238</b>
3. Humpback whales	<b>3.44</b>	0.00302	0.0990	5.0781	<b>0.0000</b>	<b>0.0195</b>
4. Brydes whales	<b>3.39</b>	0.00785	0.0990	6.2600	<b>0.0000</b>	<b>0.0158</b>
5. Sei whales	<b>3.02</b>	0.00160	0.0200	6.1776	<b>0.0000</b>	<b>0.0032</b>
6. Sperm whales	<b>4.12</b>	0.0202	0.0500	5.0251	<b>0.0000</b>	<b>0.0100</b>
7. Killer whales	<b>3.94</b>	0.000262	0.0200	7.7634	<b>0.0000</b>	<b>0.0026</b>
8. Baleen whales	<b>3.00</b>	0.00276	0.0400	3.3978	<b>0.0000</b>	<b>0.0118</b>
9. Beaked whales	<b>4.21</b>	0.000125	0.0360	9.9234	<b>0.0000</b>	<b>0.0036</b>
10. Dolphins	<b>3.54</b>	0.0225	0.0470	13.7390	<b>0.7386</b>	<b>0.0034</b>
11. Seabirds	<b>3.78</b>	0.1180	0.1200	118.0000	<b>0.0000</b>	<b>0.0010</b>
12. Large pelagics	<b>3.31</b>	2.5400	1.9080	11.6980	<b>0.5045</b>	<b>0.1631</b>
13. Mesopelagic predators	<b>3.95</b>	0.7350	4.3620	31.6090	<b>0.1170</b>	<b>0.1380</b>
14. Bathydeersal predators	<b>3.40</b>	<b>0.2928</b>	2.7100	<b>9.0333</b>	0.9500	0.3000
15. Sharks	<b>3.43</b>	0.2900	1.3380	7.4970	<b>0.0116</b>	<b>0.1785</b>
16. Rays	<b>2.65</b>	0.1120	1.0000	6.0000	<b>0.0318</b>	<b>0.1667</b>
17. Coastal tunas	<b>3.35</b>	2.8900	0.8200	3.7740	<b>0.0026</b>	<b>0.2173</b>
18. Coastal demersal	<b>2.28</b>	4.6960	13.9400	<b>46.4667</b>	<b>0.0492</b>	0.3000
19. Clupeids	<b>2.77</b>	22.1300	3.1000	16.3466	<b>0.5217</b>	<b>0.1896</b>
20. Other coastal pelagics	<b>2.80</b>	13.1160	2.6120	10.6350	<b>0.4112</b>	<b>0.2456</b>
21. Cephalopods	<b>3.13</b>	2.4092	4.7000	16.7350	<b>0.7445</b>	<b>0.2808</b>
22. Crustaceans	<b>2.67</b>	13.0480	6.4430	31.9630	<b>0.0140</b>	<b>0.2016</b>
23. Benthos	<b>2.02</b>	112.6000	4.3340	32.7300	<b>0.7222</b>	<b>0.1324</b>
24. Benthic producers	<b>1.00</b>	10.5000	107.3600	-	<b>0.3266</b>	-
25. Zooplankton	<b>2.00</b>	20.6360	58.3560	274.8050	<b>0.4266</b>	<b>0.2124</b>
26. Phytoplankton	<b>1.00</b>	82.0140	138.1890	-	<b>0.5151</b>	-
27. Detritus	<b>1.00</b>	10.0000	-	-	<b>0.3695</b>	-

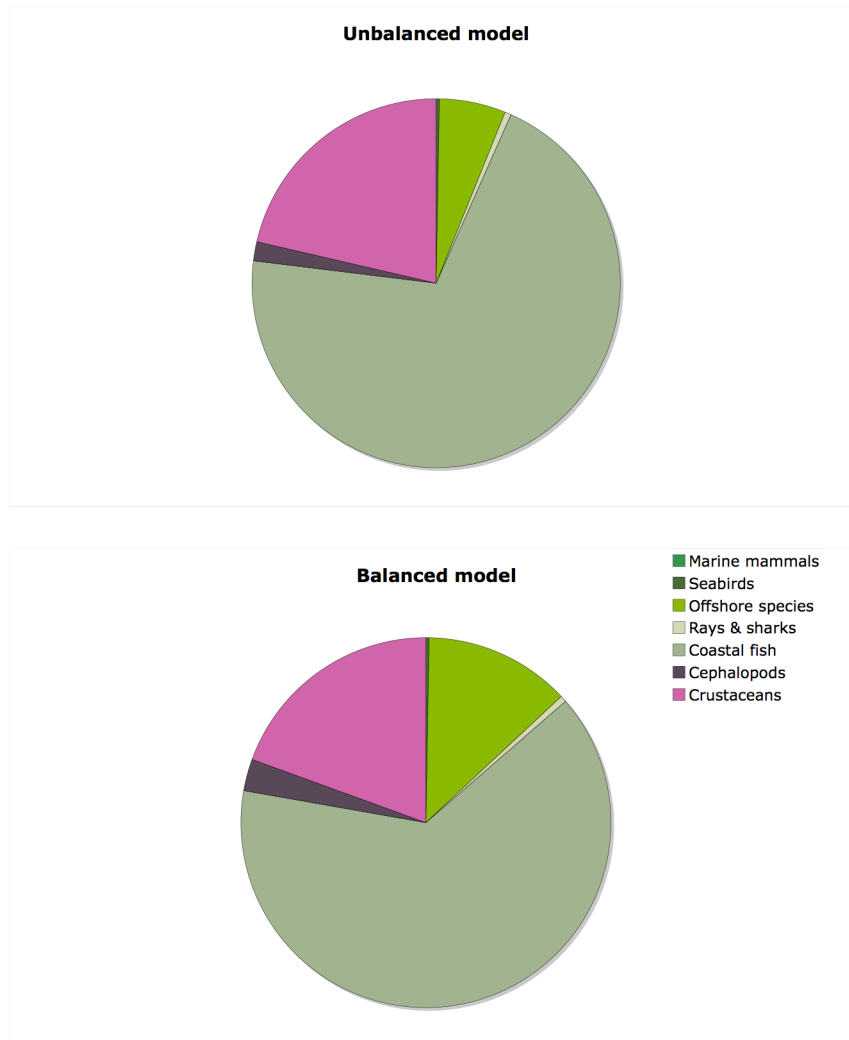
**Table 18.** Diet matrix for the *Ecopath* model of Northwest Africa.

[illegible]

**Table 18 (cont.).** Diet matrix for the *Ecopath* model of Northwest Africa.

[illegible]

The changes in the general trophic structure from the unbalanced model to balanced models are presented below. For both scenarios the system is dominated by coastal fish (coastal tunas, clupeids, and other coastal pelagics), and the 'offshore species' group is the one that changed the most in terms of biomass. This is due to the increase of biomass of two offshore species groups that were initially unbalanced: large pelagics and bathydemersal predators, for which we let the model estimate the biomass needed to cope for all the mortalities, using an ecotrophic efficiency of 95%. In both cases, the biomass of these groups almost doubled, but was still within the range of possible values for similar species in other models of Northwest Africa.



**Figure 4.** Comparison of the biomass structure (not including benthic invertebrates & plankton) of the unbalanced vs balanced Ecopath models.

## TIME SERIES DATA

### *Biomass*

Few time series data on biomass were available for Northwest African waters. Martial Laurens (2005) published his PhD thesis on stock assessments of marine resources of western Africa. In his thesis, time series of biomass of different coastal demersal fish are presented. However, all the species covered by his

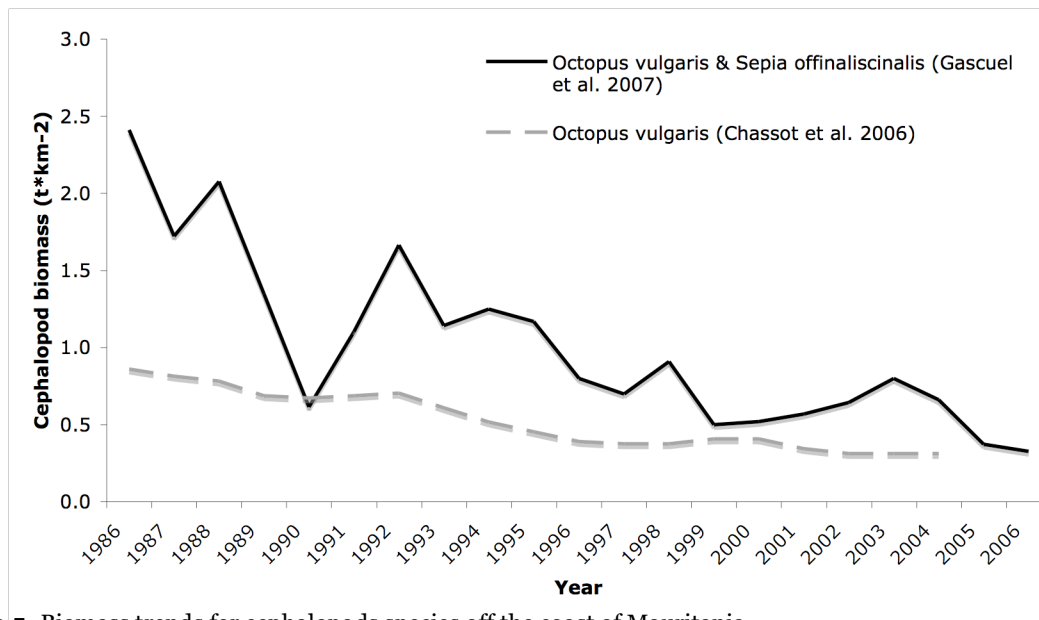
analysis fall into our ‘coastal demersals’ trophic group: white grouper (*Epinephelus aeneus*), red Pandora (*Pagellus bellottii*), bluespotted seabream (*Pagrus caeruleostictus*), West African goatfish (*Pseudupeneus prayensis*), and lesser African threadfin (*Galeoides decadactylus*). We summarized these data into an aggregated time series representing coastal demersals (Table 19).

Gascuel *et al.* (2007) estimated the biomass of 24 different demersal taxa, selected for their importance in the survey catches and/or the fishery in Mauritania. This was presented as year-to-year fluctuations from 1982 to 2006. Different *Ecopath* trophic groups were covered by this study: bathydemersal predators (*Merluccius* sp.), sharks (*Mustelus mustelus*), Rays (*Raja miraletus*, *R. straeleni*), and cephalopods (*Octopus vulgaris*, *Sepia officinalis*). The resulting time series, in density ( $t \cdot km^{-2}$ ), is presented in table 19.

A report of the FAO (2002) presents the outcomes of the Working Group on the Assessment of Small Pelagic Fish off Northwest Africa, after their workshop in Banjul, Republic of the Gambia, 5-12 April 2002. In that document, indices of biomass were calculated for *Sardinella aurita* and *S. maderensis* from acoustic surveys of the R/V by Dr. Fridtjof Nansen. The surveyed area covered the coastal shelf and immediately adjacent waters and ranges from Safi, in Morocco, to Ghana (from about 32°N to 5°N) a distance of some 2,500 nmi. This is similar to what our study area covers. After converting the biomass of these acoustic surveys into densities ( $t \cdot km^{-2}$ ), we ended up with time series for our “clupeid” group for the *Ecopath* model (Table 19).

Another report by the International Commission for the Conservation of Atlantic Tunas (ICCAT 1999c) estimated the biomass trends for skipjack tuna (*Katsuwonus pelamis*), which is one of the key species of our “large pelagics” group for the model. As an alternative to the traditional production models used by the Standing Committee on Research and Statistics (SCRS), a new model was presented by Dr. Maury during an inter-session stock assessment session of Atlantic skipjack in Funchal, Madeira, 28 June to 2 July 1999. This original non-equilibrium production model was developed for skipjack stocks, and although various runs of this experimental production model were made, only the results from a total Atlantic stock model were presented and discussed. It was considered that the results obtained from this model are probably dominated by the eastern Atlantic fisheries, which are consistent with our study area of Northwest Africa. The resulting time series of biomass densities for the large pelagics are presented in table 19.

Additionally, a report by Chassot *et al.* (2006) presented a global dynamic model developed in a Bayesian context to evaluate the stock of common octopus (*Octopus vulgaris*) in Mauritania from 1971 to 2005. Biomasses estimated by the model include uncertainty linked to natural variability, and error in observation to give a realistic representation of the dynamics of common octopus stocks in the area. According to these data, the biomass declined by more than 80% between 1971 and 2005. Since the study by Gascuel *et al.* (2007) presented more cephalopods species, and because the trend of declining biomass is similar in both studies (see Figure 5), we decided not to use the time series of Chassot *et al.* (2006) a priori. However, these data were considered as alternative values for model validation.



**Figure 5.** Biomass trends for cephalopods species off the coast of Mauritania.

Finally, Gascuel and Laurans (2003) published a stock status report for 11 stocks of Guinea, Senegal and Cape Verde. A working group met at Mindelo in October 2001 for the '*Système d'information et d'analyse des pêches*' (SIAP) project, and focused on two categories of analysis: stock assessment using the global approach, and estimation of time series of abundance with general linear models. The pink lobster (*Palinurus charlestoni*) stock of Cape Verde was one of the species presented in that report, and is a key species in our "crustaceans" group for the *Ecopath* model. The resulting time series of biomass density are presented in Table 19.

**Table 19.** Time series of biomass for different trophic groups of our *Ecopath* model of Northwest Africa.

	10	12	13	14	16	17	19	20
Year	Large pelagics (t*km <sup>-2</sup> )	Bathy-demersal predators (t*km <sup>-2</sup> )	Sharks (t*km <sup>-2</sup> )	Rays (t*km <sup>-2</sup> )	Coastal demersals (t*km <sup>-2</sup> )	Clupeids (t*km <sup>-2</sup> )	Cephalopods (t*km <sup>-2</sup> )	Crustaceans (t*km <sup>-2</sup> )
1986	0.0066	0.0910	0.6143	0.4567			2.4092	0.0022
1987	0.0068	0.0548	0.3103	0.4330	2.7609		1.7203	0.0026
1988	0.0068	0.0374	0.1114	0.7788	2.4289		2.0763	0.0016
1989	0.0067	0.0318	0.2590	0.6085	2.4811		1.3455	0.0017
1990	0.0068	0.0262	0.4066	0.4382	2.7366		0.6146	0.0011
1991	0.0068	0.0817	0.3367	0.5338	2.6307		1.0995	0.0004
1992	0.0062	0.0901	0.2102	0.8500	2.5328		1.6619	0.0007
1993	0.0065	0.0568	0.1833	0.1719	2.2504		1.1425	0.0006
1994	0.0061	0.0638	0.1693	0.1201	2.0164		1.2481	0.0006
1995	0.0056	0.0514	0.1843	0.1588	1.8904	2.8000	1.1685	0.0004
1996	0.0056	0.0750	0.2723	0.1558	1.7628	2.5190	0.7975	0.0005
1997	0.0034	0.0431	0.0954	0.1394	1.7329	1.4595	0.6968	0.0006
1998	0.0019	0.0646	0.0759	0.1112	1.5284	1.4595	0.9087	
1999	0.0034	0.0240	0.1963	0.1450	0.5353	2.8973	0.4978	
2000		0.1082	0.1449	0.1223		2.1514	0.5194	
2001		0.0836	0.1963	0.1614		2.5730	0.5689	
2002		0.1455	0.1395	0.0924			0.6433	
2003		0.0615	0.2464	0.0959			0.7969	
2004		0.0754	0.0868	0.0804			0.6611	
2005		0.0669	0.1257	0.0610			0.3718	
2006		0.0195	0.3119	0.0092			0.3269	

## Effort

For clupeids and other coastal pelagics (groups 19 and 20 in our model), we used a report from the FAO *Working Group on the Assessment of Small Pelagic Fish off Northwest Africa* (FAO 2003). This report provides an exhaustive analysis and trends in the basic data (landings, catch, effort, length distribution and age distribution) collected by each country, for sardine, sardinellas, horse mackerels and mackerel. The assessment of the stocks was based on a variety of methods, including analysis of long-term trends in fishery data (landings, effort, CPUE, etc.).

Fernandez *et al.* (2005) monitored and analyzed the catches that were landed from the Spanish deepwater trawl fishery for black hake off Mauritania. This is a highly specialized fishery, with two species of black hake (*Merluccius senegalensis* and *M. polli*) constituting between 77–99% of total landings, which have annually averaged 9 300 tons over the past two decades. Landings data from the fishery off Mauritania were collected between 1984 and 2001, by fishing expedition and vessel. The captains' log was useful for analyzing the fishing effort by fishing expedition as measured in fishing days. This information was available for the period 1992 – 2001, and is assumed to represent the effort on bathydemersal predators (group #14) in Ecosim. To have a complete time series of effort, we completed it with catch/biomass values for 1986 – 1991.

Effort data was available for ten different species of tuna from the Standing Committee on Research and Statistics (SCRS) of the International Commission for the Conservation of Atlantic Tunas (ICCAT – <http://www.iccat.int/t2ce.asp>). In Northwest Africa, tuna fisheries continue to occupy an important place in the fishing sector, in particular, at the socioeconomic level, due to the important volume of investments made, the large number of direct and indirect employment generated, and the diversity of the fishing

methods, including artisanal fisheries, small boats, and industrial activities (ICCAT 2006). Countries from our study area that were covered by this database are Cape Verde, Ivory Coast, Ghana, Guinea, Morocco. The fishing effort on all tuna species provided a time series from 1986 to 1999 over the study area.

The catch and effort time series for sardina in the different fleets and zones of Northwest Africa were available from FAO CECAF Scientific Committee (2002). When all zones considered, the fishing effort on sardine show a decline since the early 1990s, then an increase from 1997 to 2000. This report also mentions that the effort has been declining since the early 1980s. Consequently, we completed our time series to cover 1986-2001 with a  $F=C/B$ .

For all other groups where we didn't have fishing mortalities or effort time series available, the biomass and catch time series described above were used to estimate fishing mortality ( $C/B$ ) for the years that biomass estimates were available, and projected for the years that they were not. When no complete time series of biomass data were available, we forced the model to fit the catch time series. This technique has been used in other *Ecosim* models when data was unavailable (see Heymans 2005 for an example).

**Table 19.** Time series of effort (standardized values based on days at sea data) for different trophic groups of our *Ecopath* model of Northwest Africa.

	12	14	15	16	18	19	21	22
Year	Deep pelagics (t*km <sup>-2</sup> )	Bathy-demersal predators (t*km <sup>-2</sup> )	Sharks (t*km <sup>-2</sup> )	Rays (t*km <sup>-2</sup> )	Coastal demersals (t*km <sup>-2</sup> )	Clupeids (t*km <sup>-2</sup> )	Cephalopods (t*km <sup>-2</sup> )	Crustaceans (t*km <sup>-2</sup> )
1986	1.0000	1.0000	1.0000	1.0000				1.0000
1987	1.0000	0.7868	1.0000	1.0000	1.0000			1.0000
1988	0.8819	1.0479	2.9096	0.9768	0.9919			1.0594
1989	0.8523	1.4457	1.2169	0.8870	0.9192			1.3051
1990	0.8361	1.6170	0.7086	2.2608	0.8864	1.0000	1.0000	1.4911
1991	0.7101	0.5380	0.5991	1.9476	1.0408	0.9926	1.0301	1.7772
1992	0.7913	0.5248	1.1402	1.5703	1.0453	0.8331	0.9612	1.3629
1993	0.7088	0.9000	1.1459	7.2792	1.0570	0.8662	0.9014	1.6574
1994	0.6439	0.8667	1.3779	13.1076	1.1969	0.9834	1.0475	1.8317
1995	0.8889	0.8500	1.3249	9.7551	1.1714	1.0793	1.1863	2.1599
1996	0.7435	0.6833	1.5928	10.2987	1.3728	0.8935	1.0571	2.5034
1997	1.5253	0.6333	7.6822	20.6519	1.4956	0.6578	1.2995	2.0445
1998	2.5972	0.4500	5.2338	18.5378	1.7000	0.8982	0.9706	2.6327
1999	1.3069	0.4000	2.3347	12.9123	4.6958	1.0193	1.0506	3.2340
2000	1.3069	0.4833	3.2508	16.6169	2.1598	1.4191	1.3185	2.8202
2001	1.3069	0.6833	2.7467	11.7156	2.3240	0.9675	0.8262	3.2831
2002	1.3069	0.1937	3.9135	16.0606	2.5566	5.8382	1.1528	1.5637
2003	1.3069	0.5977	1.7999	14.4493	2.6934	6.1333	1.1528	1.4884
2004	1.3069	0.4951	5.8154	15.0962	2.9124	6.5126	1.1528	1.2261
2005	1.3069	0.3961	11.5865	18.9650	3.1108	6.8288	1.1528	1.1965
2006	1.3069	0.2690	12.6787	19.9667	3.3069	7.1871	1.1528	1.1491

## UNCERTAINTY ANALYSES

Given the high level of uncertainty in data, parameterization and model structure (Plagányi and Butterworth 2004; Plaganyi 2007; Essington 2007), we conducted several levels of uncertainty analyses. Effort was focussed on appropriate data collection to assist in shedding light as to the most appropriate choice of model form to represent feeding behaviour. Three levels of uncertainty analyses were performed here. First, a simple sensitivity routine included in *Ecopath* was used to explore the effects of uncertainty



on the model results. A second uncertainty analysis was performed using *Ecoranger*, a resampling routine based on input probability distributions. Finally, the robustness of our models' structure was tested with *Ecosim* by comparing predicted biomasses with time series of observed data.

### *Sensitivity analysis*

A sensitivity routine is included in *Ecopath* to allow users to explore the effects of uncertainty on the model results. The method is quite simple, and consists of plotting relative output changes against relative changes in the inputs. The routine varies all basic input parameters (biomass [B], production to biomass ratio [P/B], consumption to biomass ratio [Q/B], ecotrophic efficiency [EE]) in steps from -50% to +50% for each trophic group of the model, and then checks what effect each of these steps has for each of the input parameters on all of the "missing" basic parameters for each group in the system (Christensen *et al.* 2000). The output is then given as the proportion of the difference between the estimated and original parameter to the original parameter, and converted to a percentage (Christensen *et al.* 2000). This method only re-estimates the parameters for which no data was available, and that were left to be estimated by the model, using the mass-balance constraints.

We conducted a sensitivity analysis for biomass, P/B, Q/B and EE input parameters. Our results suggest that the sensitivity of these estimated parameters to a change in input values is relatively low (Appendix 1). A 50% change in any of the input parameters of any trophic group generated an overall response of about 35% in the estimated parameters of other groups. Most of the changes in biomass would have a greater effect on the EE of other trophic groups (a 50% change in biomass generates an average 20% change in the EE of other trophic groups). In average, a 50% change in input biomass of any trophic group generated a response of 30% in the estimated parameters of other groups.

For P/B ratio, a change in input values is more likely to affect EE parameters (with an average 50% of change after a 50% change in P/B). Overall, a 50% change in the P/B inputs of any group would generate a response of less than 48% in the estimated parameters of other groups.

Similarly, for Q/B input values, a 50% change of this value for any group would generate a response of less than 25% in the estimated parameters of other trophic groups. The highest impact of a 50% change in Q/B is seen in estimating EE (with an average response of 28% difference).

Finally, a change in EE input values generated an average 38% change in the estimated parameters. The most important effect of such change was seen on estimated biomass parameters, with an average 40% change after the EE is modified by  $\pm 50\%$ .

Overall, our sensitivity analysis suggests that potential errors in model results are approximately linearly related to potential error in model parameters, etc. This result is consistent with those of Essington (2007). This underscores the importance of enhancing the quality of data included in our model.

### *'Ecoranger' analysis*

To account for the inherent uncertainty of input parameters, a resampling routine called *Ecoranger* is included in the *EwE* software and accepts input probability distributions for the biomasses, consumption and production rates, ecotrophic efficiencies, catch rates, and diet compositions. *Ecoranger* then draws random input variables using the range of possible values for each parameter, and the resulting model is then evaluated (based on least sum of squared residuals and physiological and mass-balance constraints) (Christensen *et al.* 2005).

Starting with the initial model and these setups, 10,000 models were run by *Ecoranger*, until 200 model runs passed the selection criteria, and the best fitting model for the coast of Northwest Africa was used for further analysis.

### *Fitting the model to time series data*

The *Ecosim* model behaviour is based on a ‘foraging arena’ theory (Walters and Martell, 2004), which assumes that predator and prey behaviours cause partitioning of prey populations, which are either available or unavailable to predators. There is continuous change between these two stages for any given potential prey, whether it is hiding from predation in some refuge, or it is out to feed. This availability of prey to predators is called ‘vulnerability’ in *Ecosim*. Mackinson *et al.* (2003) demonstrated the importance of setting the vulnerabilities to fit model predictions to time-series data, as *Ecosim* predictions are very sensitive to this parameter. Using default values for  $v$  has strong implications for assumptions about species abundance relative to their carrying capacity (V. Christensen, Fisheries Centre, UBC, personal communication). Basically, it assumes that each group can at most increase the predation mortality they impose on their prey with a factor of 2.0 (the default  $v$  value). A lower value implies a donor driven density-dependant interaction. On the other hand, a higher value involves a predator driven density-independent interaction, in which predation mortality is proportional to the product of prey and predator abundance (i.e., Lotka-Volterra). This implies a high flux rate for prey species in and out of vulnerable biomass pools (Ainsworth 2006). Vulnerabilities were thus adjusted based on the specific ecology of each species or trophic groups (if their behaviour, niche, or diet make them more or less vulnerable to predators).

Using the few time series of biomass available for the trophic groups in our model, we compared *Ecosim*’s projections with observed data, and adjusted  $v$ ’s and other input parameters (within their range of uncertainty) until we obtained a model configuration that allowed us to reproduce as much as possible the trends in biomass.

Using credible models that can reproduce observed historical response to disturbances such as fishing is a useful approach to validating our model in light of the highly uncertain data included in the model. Fitting time series data to model predictions therefore enhances our confidence about the possible impact of removing marine mammals in the ecosystem (Morissette 2007).

### *Simulating the removal of great whales in the ecosystem*

A hunting pattern was chosen which generated an important increase in the mortality on the marine mammals, in order to drive their populations close to extinction. Vasconcellos *et al.* (1997) showed that for fish species, a 5-fold increase in anthropogenic predation leads to serious depletion in a group. Also, such an extreme scenario is routinely applied to many fish populations and often associated with stock collapse (Patterson, 1992). For marine mammals, Morissette (2007) proposed that the same kind of increase in anthropogenic mortality is needed to simulate a crash in marine mammal biomass. Thus, we employed a similar approach for our analysis. A 100 years simulation was performed, and the biomass trends before and after the removal of whales were compared.

## DISCUSSION

### *A new dataset built for Northwest Africa*

All the data collected and presented in this report were used to build an *Ecopath* model assessing the interactions between marine mammals and fisheries in Northwest African waters. Data presented here represent the updated version of an initial dataset presented to local experts during a workshop held in Dakar, Sénégal, in May 2008 (“*Whale and Fish interactions: Are great whales a threat to fisheries*”, see [http://www.lenfestocean.org/whales\\_fisheries.html](http://www.lenfestocean.org/whales_fisheries.html)).

The initial model presented in Dakar was

Additional data that became available after this workshop were included in the model, and thus greatly improved the predictive ability of our model simulations. We received a great amount of feedback from local experts, fisherman, and stakeholders about our model development and methodology. We also identified additional data on biomass, diet, and fishing effort for many species included in the model. As a consequence, we think that we increased our accuracy to represent key ecological processes in Northwest African waters.

### *Strengths and weaknesses of these modelling efforts*

The synthesis of available ecosystem information is allowing to have a whole-system view using parameters that are basic to understanding populations and the ecosystem (Okey and Pauly 1999). However, models are not a perfect representation of the reality. The uncertainties remaining in the understanding of the ecosystem structure and function may occur for different reasons. In some case, it is just because no data exist on the key species. In other cases, aggregation of species within one ecological box is inappropriate. Finally unknown mechanisms can also occur in the ecosystem (Morissette *et al.* 2003). For example, in *Ecopath* models, the only mechanism used to represent interactions between species is direct consumption. It ignores the fact that consumers often do more than skim production off their prey; consumers can shift diet composition to species with lower productivity and alter the P/B ratio of the group (Ruesink 1998), or have behaviours that indirectly affect other species in the system.

The structure of the model provides an overall view of the ecosystem and reveals the uncertainties that could be examined in future studies. Consequently, one of the most important questions that can be asked of *Ecopath* models is: in which portion of the food web are the dynamics most uncertain? (Ruesink 1998). In our case, addressing the uncertainties linked to cetaceans and commercially important fish species was very important. On the other hand, a common problem in ecosystem modelling is that less information is available for the lower trophic levels (Moreau *et al.* 1993; Walline *et al.* 1993; Lin *et al.* 1999). These recurrent gaps generally force modellers to rely heavily on the literature and arbitrary assumptions to construct the models (Moreau *et al.* 1993), and the Northwest African region was no exception to that. This emphasizes the need for an increased research effort into the biomass, production, consumption, and diet of the various species of the ecosystem, not only the larger fish.

Finally, in order to have reliable prediction from the model's simulations, it is very important to have local time series data on biomass, catch, and fishing effort. Unfortunately, such time series are very scarce in the Northwest African region. Even if our different uncertainty analyses suggested that our major findings are unlikely to change if we change data inputs, local research efforts aiming to fill the gaps in our knowledge of data would be useful. In that sense, that report represents a great tool to identify these gaps.

### ACKNOWLEDGEMENTS

Authors would like to thank all the participants to the Dakar workshop for providing inputs and comments on the methods and data used for the construction of this model. Special thanks are also given to Martial Laurans, Didier Gascuel, and Jean-Claude Brêthes for providing data and support for constructing this preliminary version of the model.

### REFERENCES

- Aguilar A. and Borrell, A. 2007. Open-boat whaling on the straits of Gibraltar ground and adjacent waters. *Marine Mammal Science* 23: 322-342
- Ainsworth, C.H. 2006. Strategic marine ecosystem restoration in Northern British Columbia. PhD thesis, University of British Columbia, Canada.
- Allen, K.R. 1971. Relation between production and biomass. *Journal of Fisheries Research Board of Canada* 28: 1573-1581.
- Amorim, P., Duarte, G., Guerra, M. Morato, T., and Stobberup, K.A. 2004. Preliminary Ecopath model of the Guinea-Bissau continental shelf ecosystem (NW Africa), pp. 95-112. *In* Palomares, M.L.D., and Pauly, D. (eds.) *West African marine ecosystems: models and fisheries impacts*. Fisheries Centre Research Reports 12(7).
- Armstrong, A.J., Siegfried, W.R. 1991. Consumption of Antarctic krill by minke whales. *Antarctic Science* 3(1): 13-8.

- Barlow, J. 2003a. Preliminary estimates of the abundance of cetaceans along the U.S. west coast: 1991-2001. Administrative Report, Admin. Rept. LJ-03-03. Southwest Fisheries Science Center (SWFSC), National Marine Fisheries Service, (NMFS), National Oceanic and Atmospheric Administration (NOAA), La Jolla, CA, USA.
- Barlow, J. 2003b. Cetacean abundance in Hawaiian waters during summer/fall 2002. Administration report, Admin. Rept. LJ-03-13. Southwest Fisheries Science Center (SWFSC), National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), La Jolla, CA, USA.
- Barlow, J. 2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. *Marine Mammal Science*, 22: 446-464.
- Barlow, J. and Taylor, B.L. 2005. Estimates of sperm whale abundance in the northeastern temperate Pacific from a combined acoustic and visual survey. *Marine Mammal Science*, 21: 429-445.
- Bas, C. 1993. Long-term Variability in the Food Chains, Biomass Yields, and Oceanography of the Canary Current Ecosystem. pp. 94-103 *In* Sherman, K., Alesander, D.G., Gold, B.D. (Eds.), *Large Marine Ecosystems: Stress, Mitigation, and Sustainability*. American Association for the Advancement of Science, Washington DC.
- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, J. and Doherty, P.A. 2003. Collapse and conservation on shark populations in the Northwest Atlantic. *Science* 299: 389-392.
- Bax, N.J. 1998. The significance and prediction of predation in marine fisheries. *ICES Journal of Marine Sciences* 55: 997-1030.
- Best, P.B. 1999. Food and feeding of sperm whales *Physeter macrocephalus* of the west coast of South Africa. *South African Journal of Marine Science* 21: 393-413.
- Best, P.B. 2001. Distribution and population separation of Bryde's whale *Balaenoptera edeni* off southern Africa. *Marine Ecology Progress Series* 220: 277-289.
- Best, P.B., Sekiguchi, K., Rakotonirina, B., and Rossouw, A. 1996. The distribution and abundance of humpback whales off southern Madagascar, August-September 1994. Reports of the International Whaling Commission, 46: 323.
- Best, P.B., Rademeyer, R.A., Burton, C., Ljungblad, D.K., Sekiguchi, H., Shimada, D., Thiele, D., Reeb, D., and Butterworth, D.S. 2003. The abundance of blue whales on the Madagascar Plateau, December 1996. *Journal of Cetacean Research and Management* 5: 253-260.
- Bransletter, S. 1987. Age and growth validation of newborn sharks in laboratory aquaria with comments on the life story of the Atlantic sharpnose shark. *Copeia* 2: 291-299.
- Brodie, P.F. 1975. Cetacean energetics, an overview of intraspecific size variation. *Ecology* 56: 152-161.
- Brown, S.G. and Lockyer, C.H. 1984. Whales. pp. 717-781 *In* Laws, R.M. (Ed.) *Antarctic ecology* Vol. 2. Academic Press, London.
- Bucke, D. 1989. Histology. pp. 69-97 *In* Austin, B., Austin, D.A. (Eds.), *Methods for the Microbiological Examination of Fish and Shellfish*. Wiley, New York.
- Bundy, A., Lilly, G., and Shelton, P. 2000. A mass balance model of the Newfoundland-Labrador shelf. *Canadian Technical Report of Fisheries and Aquatic Sciences* 2310.
- Calambokidis, J. and Barlow, J. 2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. *Marine Mammal Science* 20: 63-85.
- Camarena Luhrs, T. 1986. Les principales espèces de poissons pélagiques côtiers au Sénégal : biologie et évaluation des ressources. Thèse de Doctorat, Université de Bretagne Occidentale, France. 187 p.
- Caverivière, A. and Thiam, M. 1992. Indices d'abondances et niveaux d'exploitation des espèces démersales du plateau continental Sénégalais. Estimations à partir des résultats des campagnes de chalutage stratifié (1986-1991). CRODT. Document Scientifique n°132.
- Cayré P., Kothias, J.M., Stretta M., and Diouf, T. 1988. La biologie des thonidés de l'Atlantique tropical Est, pp. 157-264 *In* A. Fonteneau, A. and Marcille, J. (Eds.) *Ressources, pêche et biologie des thonidés tropicaux de l'Atlantique tropicale* Centre Est. FAO. Document Technique des Pêches No. 292.
- Chassot E., Balguerías E., Guitton J., Jouffre D., Tfeil B. and Gascuel D. 2006. Diagnostic de l'état du stock de poulpe (*Octopus vulgaris*) mauritanien. Synthèse et nouvelles évaluations par approche globale. Rapport de la sous commission Poulpe, groupe d'évaluation des stocks démersaux, IMROP, Nouadhibou 11-16 janvier 2006.
- Christensen, V. and Pauly, D. 1992. The ECOPATH II – software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61: 169-185.
- Christensen, V. and Walters, C.J. 2004. *Ecopath with Ecosim*: methods, capabilities and limitations. *Ecological Modelling* 172: 109-139.
- Christensen, V., Walters, C.J., and Pauly, D. 2000. *Ecopath with Ecosim*: a User's Guide. October 2000 Edition, Fisheries Centre, University of British Columbia, Vancouver, B.C. and ICLARM, Penang, Malaysia.
- Christensen, V., Walters, C.J. and Pauly, D. 2005. *Ecopath with Ecosim*: a User's Guide. Fisheries Centre, University of British Columbia, Vancouver. November 2005 edition, 154 p.
- Clark, W.G. 1982. Historical rates of recruitment to Southern Hemisphere fin whale stocks. Report of the International Whaling Commission 32:305-324.
- Clarke, M.R., Martins, H.R. and Pascoe, P. 1993. The diet of sperm whale (*Physeter macrocephalus* Linnaeus 1758) off the Azores. *Philosophical Transactions of the Royal Society of London (Series B)* 339: 67-82.
- Corkeron, P.J. and Connor, R.C. 1999. Why do baleen whales migrate? *Marine Mammal Science* 15: 1228-1245.
- Crawford, R.J.M., P.G. Ryan and Williams, A.J. 1991. Seabird consumption and production in the Benguela and Western Agulhas ecosystems. *South African Journal of Marine Science* 11: 357-375.
- Currie, P. 2007. Whales, Sustainability and International Environmental Governance. Review of European Community & International Environmental Law 16: 45-57.
- Davis, R.W. and Fargion, G.S. 1996. Distribution and Abundance of Marine Mammals in North-Central and Western Gulf of Mexico: Final Report. Volume II: Technical Report. Technical Report, OCS Study MMS 96-0027. US Department of the Interior, Minerals Management Service.
- Davis, R.W., Evans, W.E., and Wursig, B. 2000. Cetaceans, Sea Turtles and Seabirds in the Northern Gulf of Mexico: Distribution, Abundance and Habitat Associations. Volume II: Technical Report. Technical Report, OCS Study MMS 2000-003 - USGS/BRD/CR-1999-0005. Texas A&M University at Galveston and the National Marine Fisheries Service.
- De la Cruz-Aguero, G. 1993. A preliminary model of Mandinga lagoon, Veracruz, Mexico, pp. 193-196. *In* Christensen, V. and Pauly, D. (Eds.) *Trophic models of aquatic ecosystems*. ICLARM Conference Proceedings 26.
- De la Mare, W.K. 1985. On the estimation of mortality rates from whale age data, with particular reference to minke whales (*Balaenoptera acutorostrata*) in the Southern Hemisphere. Report of the International Whaling Commission 35: 239-250.

- Diallo, I., Cissé, I., and Bah, A. 2004. Modèle trophique du système côtier du plateau continental Guinéen, pp. 113-123. In Palomares, M.L.D. and Pauly, D. (Eds.) West African marine ecosystems: models and fisheries impacts. Fisheries Centre Research Reports 12(7).
- Diatta, Y., Ba, F.L., and Capape, C. 2001. Rôle trophique du poulpe commun, *Octopus vulgaris*, chez les élasmobranches de la côte du Sénégal (Atlantique oriental tropical); comparaison avec les espèces des côtes Tunisiennes (Méditerranée centrale). Acta Adriat. 42 (1): 77-88.
- Diouf, T. 1980. Pêche et biologie de trois scombridae exploités au Sénégal: *Euthynnus alletteratus*, *Sarda sarda* et *Scomberomorus tritor*. Thèse de Doctorat 3ème cycle, Université de Bretagne Occidentale, France. 159 p.
- Essington, T.E., 2006. Pelagic Ecosystem Response to a Century of Commercial Fishing and Whaling. pp. 38-49 In Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M., and Brownell Jr R.L. (Eds.) Whales, Whaling, and Ocean Ecosystems. University of California Press, Berkeley CA.
- Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M. and Brownell Jr., R.L. 2007. Whales, whaling, and ocean ecosystems. University of California Press, 418 p.
- Evans, P.G.H. 1998. Biology of cetaceans of the north-east Atlantic (in relation to seismic energy). Proceedings of the Seismic and Marine Mammals Workshop, London, 23-25 June 1998 (Eds.) Mark L Tasker and Caroline Weir.
- FAO, 2002. Report of the FAO Working Group on the Assessment of Small Pelagic Fish off Northwest Africa - Banjul, Republic of the Gambia, 5-12 April 2002. FAO Fisheries Report No. 686.
- FAO. 2003. Report of the FAO Working Group on the Assessment of Small Pelagic Fish off Northwest Africa - Agadir, Morocco, 31 March-10 April 2003. FAO Fisheries Report No. 723.
- FAO CECAF Scientific Committee. 2002. Status of stocks and resources - Sardine - Northwest of Africa, 2002. FIRMS Reports. FAO - Rome. Updated Mar 20 2006. Available via FIRMS-Web from: <http://firms.fao.org/firms/resource/10086> [Accessed May 23 2008].
- Fedoseev, A., 1970. Geostrophic circulation of surface waters on the shelf of north-west Africa. Rapp. P.-V. Reun. Cons. Int. Explor. Mer., 159, 32-37.
- Fernández, L., Salmerón, F. and Ramos, A. 2005. Change in Elasmobranchs and Other Incidental Species in the Spanish Deepwater Black Hake Trawl Fishery off Mauritania (1992–2001). *J. Northw. Atl. Fish. Sci.*, **35**: 325-331.
- Findlay, K.P., Best, P.B., Peddemors, V.M., and Gove, D. 1994. The distribution and abundance of humpback whales on their southern and central Mozambique winter grounds. Reports of the International Whaling Commission 44: 311-320.
- Fischer, W., G. Bianchi and Scott, W.B. 1981. Fiches FAO d'identification des espèces pour les besoins de la pêche. Atlantique centre-est ; zones de pêches 34, 47 (en partie). Canada Fonds de dépôts. Ottawa, Ministère des Pêcheries et Océans, en accord avec la FAO, Vols. 1-7.
- Forney, K.A. and Barlow, J. 1993. Preliminary winter abundance estimates for cetaceans along the California coast based on a 1991 aerial survey. Reports of the International Whaling Commission, 407-415.
- Forney, K.A., Barlow, J., and Carretta, J.V. 1995. The abundance of cetaceans in California waters: Part II. Aerial surveys in winter and spring of 1991 and 1992. US National Marine Fisheries Service Fishery Bulletin, 93, 15-26.
- Forcada, J., Notarbartolo, D.S.G., and Fabbri, F. 1995. Abundance of fin whales and striped dolphins summering in the Corso-Ligurian Basin. *Mammalia* 59: 127-140.
- Franqueville, C. 1983. Biologie et dynamique de population des daurades (*Pagellus bellottii*, Steindacher, 1982) le long des côtes Sénégalaises. Thèse Doc. D'Etat. Université d'Aix-Marseille II. 276 p.
- Fréon, P. 1988. Réponses et adaptation des stocks de clupéidés d'Afrique de l'Ouest à la variabilité du milieu ; analyse et réflexion à partir de l'exemple du Sénégal. Études et thèses, ORSTOM, Paris.
- Garrison, L.P., Swartz, S., Martinez, A., Burks, C., and Stamates, J. 2003. A marine mammal assessment survey of the Southeast US Continental Shelf: February - April 2002. NOAA Technical Memorandum, NMFS-SEFSC-492. U.S. Department of Commerce.
- Gascuel D. and Laurans, M. 2003. Évaluation des stocks par l'approche globale et évolutions d'abondance. Synthèse du groupe de travail "Analyses mono-spécifiques" de Mindelo (octobre 2001). pp. 35-40 In Gascuel D., Barry M., Laurans M., and Sidibé A. 2003. Évaluations des stocks démersaux en Afrique du Nord-Ouest, travaux du groupe "Analyses mono-spécifiques" du projet SIAP. COPACE / PACE, 03/65, Rome FAO.
- Gascuel, D. Labrosse, P., Meissa, B. Taleb Sidi, M.O. and Guénette, S. 2007. Decline of demersal resources in North-West Africa: an analysis of Mauritania trawl-survey data over the past 25 years. *African Journal of Marine Science* 29(3): 331-345.
- Gerrodette, T. and Forcada, J. 2002. Estimates of abundance of western/southern spotted, whitebelly spinner, striped and common dolphins, and pilot, sperm and Bryde's whales in the Eastern Tropical Pacific Ocean. Administrative Report, Admin. Rept. LJ-02-20. Southwest Fisheries Science Center (SWFSC), National Marine Fisheries Service, (NMFS), National Oceanic and Atmospheric Administration (NOAA), La Jolla, California.
- Gonzalez, A.F., Lopez, A., Guerra, A., Barreiro, A. 1994. Diets of marine mammals on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. *Fisheries Research* 21: 179-191
- Guénette, S. and Christensen, V. 2005. Food web models and data for studying fisheries and environmental impacts in Eastern Pacific ecosystems. *Fisheries Centre Research Reports* 13(1).
- Guénette, S., Heymans, S.J.J., Christensen, V., and Trites, A.W. 2006. Ecosystem models show combined effects of fishing, predation, competition, and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 2495-2517.
- Hammill, M.O. and Stenson, G.B. 2007. Application of the precautionary approach and conservation reference points to management of Atlantic seals. *ICES Journal of Marine Science* 64: 702-706.
- Hansen, L.J., Mullin, K.D., and Roden, C.L. 1995. Estimates of cetacean abundance in the northern Gulf of Mexico from vessel surveys. Contribution No. MIA-94/95-25. SEFSC, Miami Laboratory, Miami, USA.
- Haug, T., Gjøsæter, H., Lindstrøm, U. and Nilssen, K.T. 1995. Diet and food availability for Northeast Atlantic minke whales (*Balaenoptera acutorostrata*), during the summer of 1992. *ICES Journal of Marine Science* 52: 77-86.
- Haug, T., Lindstrøm, U., Nilssen, K.T., Røttingen, I. and Skaug, H.J. 1996. Diet and food availability for Northeast Atlantic minke whales, *Balaenoptera acutorostrata*. Report of the International Whaling Commission 46: 371-82.
- Heymans, J.J. 2005. Ecosystem model of the Eastern Aleutians and the Gulf of Alaska in 1963. pp 83-105 In Guénette, S. and Christensen, V. (Eds.). Food web models and data for studying fisheries and environmental impacts on Eastern Pacific ecosystems. *Fisheries Centre Research Reports* 13(1).
- Holt, S.J. 2007. Whaling: Will the Phoenix rise again? *Marine Pollution Bulletin* 54: 1081-1086

- ICCAT. 1999a. Rapport de la période biennale 1998-1999. 1ère partie (1998)-Vol. 1. Version Française. Madrid, Espagne.
- ICCAT. 1999b. Rapport de la période biennale 1998-1999. 1ère partie (1998)-Vol. 2. Version Française. Madrid, Espagne.
- ICCAT. 1999c. Report of the ICCAT SCRS skipjack stock assessment session, Funchal, Madeira, Portugal, 28 June to 2 July 1999, ICCAT Report SCRS/99/21, 52 pp.
- ICCAT. 2006. Report on the Standing Committee on Research and Statistics (SCRS), Madrid, Spain, October 2 to 6, 2006. 195 pp.
- Innes S., Lavigne, D.M., Eagle, W.M., Kovacs, K.M. 1986. Estimating feeding rates of marine mammals from heart mass to body mass ratios. *Marine Mammal Science* 2: 227-229.
- Jackson, J.B.C. 2007. When ecological pyramids were upside down. pp. 23-37 *In* Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M. and Brownell Jr., R.S. (Eds.) *Whales, Whaling, and Ocean Ecosystems*. University of California Press, Berkeley and Los Angeles, California.
- Jackson, J. B. C., M.X. Kirby, W. H. Berger, K.A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pondolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629-638.
- Jarre-Teichmann, A. 1998. The potential role of mass balance models for the management of upwelling ecosystems. *Ecological Applications/Supplement* 8(1): 93-103.
- Jarre-Teichmann, A., Shannon, L.J., Moloney C.L. and Wickens, P.A. 1998. Comparing trophic flows in the Southern Benguela to those in other upwelling ecosystems. *South African Journal of Marine Science* 19: 391-414.
- Kaschner, K. 2004. Modelling and mapping of resource overlap between marine mammals and fisheries on a global scale. Ph.D., University of British Columbia.
- Katona, S. and Whitehead, H. 1988. Are cetaceans ecologically important? *Oceanography and Marine Biology Annual Reviews* 26: 553-568.
- Kawakami, T. 1980. A review of sperm whale food. *Scientific Report of the Whales Research Institute Tokyo* 32: 199-218.
- Klinowska, M. 1991. Dolphins, porpoises, and whales of the world: the IUCN red data book. IUCN - The World Conservation Union, Gland, Switzerland.
- Laurans, M. 2005. Évaluation des ressources halieutiques en Afrique de l'ouest : dynamique des populations et variabilité écologique. Thèse de Doctorat Halieutique, Ensa-Rennes. Organisme d'accueil : Pôle Halieutique Agrocampus Rennes.
- Lockyer, C. 1981. Growth and energy budgets of large baleen whales from the southern hemisphere. p. 379-488. *In* FAO Fisheries Series 5 ; Mammals in the Sea.
- Lydersen, C., Weslawski, J.M., and Oritsland, N.A. 1991. Stomach content analysis of minke whales *Balaenoptera acutorostrata* from the Lofoten and Vesteralen areas, Norway. *Holarctic Ecology*, 14, 219-222.
- Mackinson, S., Blanchard, J.L., Pinnegar, J.K., and Scott, R. 2003. Consequences of alternative functional response formulations in models exploring whale-fishery interactions. *Marine Mammal Science* 19: 661-681.
- Maxim, C. 1995. Horse mackerel and false scad stock assessment and catch projections, CECAF Division 34.1.3 and 34.3.1. *Sci. Mar.* 59(3-4): 611-627.
- Medina-Gaertner, M. 1985. Étude du zooplancton côtier de la Baie de Dakar et de son utilisation par les poissons comme source de nourriture. Thèse, Université de Bretagne Occidentale. 141 p.
- Mitchell, E. 1973. Draft report on humpback whales taken under specific scientific permit by eastern Canadian land stations, 1969-1971. Report of the International Whaling Commission, 23: 138-154.
- Mobley, J.R.J., Spitz, S.S., Forney, K.A., Grotefendt, R.A., and Forestall, P.H. 2000. Distribution and abundance of odontocete species in Hawaiian waters: Preliminary results of 1993-98 aerial surveys, Administration Report LJ-00-14C. Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, California, USA.
- Mohammed, E. 2003. A generic marine ecosystem model for the Southeastern Caribbean in the late 1990s: application to Grenada and the Grenadines. pp. 191-225 *In* Zeller, D., Booth, S., Mohammed, E., and Pauly, D. (Eds.) *From Mexico to Brazil: Central Atlantic fisheries catch trends and ecosystem models*. Fisheries Centre Research Reports 11(6).
- Morissette, L. 2005. Addressing uncertainty in ecosystem modelling. Pages 127-142 *In* Levner, E, Linkov, I. and Proth, J.M. (eds.). *Strategic management of marine ecosystems*. NATO Science Series: IV: Earth and environmental sciences, Volume 50. Springer-Verlag, Heidelberg, Germany.
- Morissette, L. 2007. Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence. PhD thesis, Zoology, University of British Columbia, Vancouver BC, Canada.
- Morissette, L., Despatie, S.-P., Savenkoff, C Hammill, M.O., Bourdages, H. and Chabot, D. 2003. Data gathering and input parameters to construct ecosystem models for the northern Gulf of St. Lawrence (mid-1980s). *Canadian Technical Report of Fisheries and Aquatic Sciences*. 2497: vi+94 p.
- Mullin, K.D. and Fulling, G.L. 2003. Abundance of cetaceans in the southern U.S. Atlantic ocean during summer 1998. *Fishery Bulletin* 101: 603-613.
- Mullin, K.D. and Fulling, G.L. 2004. Abundance of cetaceans in the oceanic northern Gulf of Mexico, 1996-2001. *Marine Mammal Science* 20: 787-807.
- Myers, R. A. and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423: 280-283.
- Nieland, H. 1982. The food of *Sardinella aurita* (Val.) and *Sardinella eba* (Val.) off the coast of Senegal. *Rapp. P.-V. Réunion. J. Cons. int. Explor. Mer* 180: 369-373.
- Nordøy, E.S. and Blix, A.S. 1992. Diet of minke whales in the northeastern Atlantic. Report of the International Whaling Commission 43: 393-399.
- Northridge, S.P. 1984. World review of interactions between marine mammals and fisheries. FAO Fisheries Technical Paper, No.251. 197 p.
- Okey, T.A. 2001. A 'straw-man' Ecopath model of the Middle Atlantic Bight continental shelf, United States. pp. 151-166 *In* Guénette, S., Christensen, V., and D. Pauly (eds.). *Fisheries impacts on North Atlantic ecosystems: Models and analyses*. Fisheries Centre Research Reports 9(4).
- Okey, T.A. 2004. Shifted community states in four marine ecosystems: some potential mechanisms. Ph.D. Thesis, Zoology, University of British Columbia, Vancouver, BC, Canada.
- Okey, T. A. and Pauly, D. 1999. A trophic mass-balance model of Alaska's Prince William Sound ecosystem, for the post-spill period 1994-1996. *Fisheries Centre Research Report* 7, 155pp
- Olsen, E. and Holst, J. C. 2001. A note on common minke whale (*Balaenoptera acutorostrata*) diets in the Norwegian Sea and the North Sea. *Journal of Cetacean Research and Management*, 3: 179-183.

- Opitz, S. 1993. A quantitative model of the trophic interactions in a Caribbean coral reef ecosystem, p. 259-268. *In* Christensen, V. and Pauly, D. (Eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26.
- Paine, R.T., Tegner, M.J., and Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535-545.
- Palomares, M.L.D. and Pauly, D. 1998. Predicting the food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine and Freshwater Research* 49(5): 447-453.
- Paula e Silva, R. de, R., M.I. Sousa and A. M. Caramelo. 1993. The Maputo Bay ecosystem (Mozambique), pp. 214-223 *In* Christensen, V and Pauly, D. (Eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26. ICLARM, Manila, Philippines.
- Pauly, D. 1978. A preliminary compilation of fish length growth parameters. *Ber. Inst. Meereskd. Christian-Albrechts-Univ. Kiel* (55):1-200.
- Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. *Ber. Inst. Meereskd. Christian-Albrechts Univ. Kiel* 63. 156 p.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. int. Explor. Mer* 39(2): 175-192.
- Pauly, D. and Munro, J. 1984. Once more on growth comparison in fish and invertebrates. *Fishbyte* 2(1):21.
- Pauly, D., Christensen, V. and Haggan, N. (Eds.). 1996. Mass-balance model of Alaska Gyre. Fisheries Centre Research Reports 4(1).
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R. and Zeller, D. 2002. Towards sustainability in world fisheries. *Nature* 418: 689-695.
- Perry, S.L., DeMaster, D.P., and Silber, G.K. 1999. The great whales: History and status of six species listed as endangered under the U.S. Endangered Species Act of 1973. *Marine Fisheries Review*, 61(1): 1-74.
- Plagányi, É.E. 2007. Models for an ecosystem approach to fisheries. FAO fisheries technical paper 477. 126 p.
- Plagányi, E.E. and D.S. Butterworth. 2002. Competition with fisheries. pp 268-273 *In* Perrin, W.F., Würsig, B., and Thewissen, H.G.M. (Eds.) *Encyclopedia of Marine Mammals*. Academic Press, San Diego.
- Plagányi, É.E. and D.S. Butterworth. 2004. A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. *African Journal of Marine Sciences* 26 : 261-287.
- Postel, E. 1955. Résumé des connaissances acquises sur les Clupéidés de l'Ouest Africain. *Rapp. J. Cons. int. Explor. Mer* 137: 14-17.
- Punt, A.E. and Butterworth, D.S. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals *Arctocephalus pusillus pusillus* and the Cape hakes *Merluccius capensis* and *M. paradoxus*. *South African Journal of Marine Science* 16: 255-285.
- Roberts, S.M. 2003. Examination of the stomach contents from a Mediterranean sperm whale found south of Crete, Greece. *Journal of the Marine Biological Association of the United Kingdom* 83:667-670.
- Rosenbaum, H.C., Strindberg, S., and Ersts, P.J. 2004. Initial estimates of abundance and distribution of humpback whales on their wintering grounds in the coastal waters of Gabon (southeastern Atlantic Ocean, Area B) based on aerial surveys. (SC/56/SH2). *In* International Whaling Commission - Scientific Committee Meeting, pp. 9. (unpublished), Sorrento, Italy.
- Ruesink, J. L. 1998. Ecosystem models as caricatures: the case of Prince William Sound. Pp. 87-89 *In* Okay, T.A. and Pauly, D. (Eds.) Trophic mass-balance model of Alaska's Prince William Sound ecosystem for the post-spill period 1994-1996. Fisheries Centre Research Report 7.
- Saetersdal, G., Ofstad, A., Nore, A., Olsen, S., and Moore G.K.F. 1995. Survey of the pelagic fish resources off North West Africa. Senegal-Gambia. 7-16 November 1995. NORAD/FAO/UNDP GLO 82/001. 16 p
- Samb, B. 1988. Seasonal growth, mortality, recruitment pattern of *Sardinella maderensis* off Senegal, pp. 257-271 *In* Venema, S.C., Christensen, J.M., and Pauly, D. (Eds.) Contributions to tropical fisheries biology. FAO/DANIDA Follow-up Training Course on Fish Stock Assessment in the Tropics, Denmark 1986, Philippines, 1987. FAO Fisheries Report n° 389. Rome.
- Samb, B. 1997. Synthèse des évaluations récentes sur l'état des stocks de sardinelles, chinchards et maquereaux dans la zone nord COPACE. Document COPACE/FAO. 11th Session du COPACE/FAO sur l'Evaluation des Stocks. 24 au 26 Septembre 1997, Accra, Ghana.
- Samb, B. and Mendy, A.N. 2004. Dynamique du réseau trophique de l'écosystème Sénégalais en 1990, pp. 57-70 *In* Palomares, M.L.D. and Pauly, D. (Eds) West African marine ecosystems: models and fisheries impacts. Fisheries Centre Research Reports 12(7). Fisheries Centre, UBC, Vancouver.
- Samb, B. and Pauly, D. 2000. On 'variability' as a sampling artifact: the case of *Sardinella* in north-western Africa. *Fish and Fisheries* 1: 206-210.
- Santos, M.B., Martin, V., Arbelo, M., Fernandez, A. and Pierce, G.J. 2007. Insights into the diet of beaked whales from the atypical mass stranding in the Canary Islands in September 2002. *Journal of Mar. Ass. U.K.* 87: 243-251.
- Scheffer, M., S. Carpenter, J. A., Foley, C. Folke, and Walker, B. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591-596.
- Schneider, W. 1990. FAO species identification sheets for fishery purposes. Field guide to the commercial marine resources of the Gulf of Guinea. Prepared and published with the support of the FAO Regional Office for Africa. FAO, Rome. 26 p.
- Sergeant, D.E. 1977. Stocks of fin whales *Balaenoptera physalus* in the North Atlantic Ocean. Report of the International Whaling Commission 27: 460-473.
- Sidi, M.T. and Guénette, S. 2004. Modèle trophique de la ZEE mauritanienne: comparaison de deux périodes (1987 et 1998). pp 12-38 *In* Palomares, M.L.D. and Pauly, D. (Eds.) West African marine ecosystems : models and fisheries impacts. Fisheries Centre Research Reports 12(7).
- Sidibé, A. 2003. Les ressources halieutiques démersales côtières de la guinée ; exploitation, biologie et dynamique des principales espèces de la communauté à Sciaenidés. Ph.D. Thesis, Ecole Nationale Supérieure Agronomique de Rennes, France.
- Sigurjónsson, J. and Víkingsson, G.A. 1997. Seasonal abundance of and estimated food consumption by cetaceans in Icelandic and adjacent waters. *Journal of Northwest Atlantic Fishery Science*, 22: 271-287.
- Sivertsen K. 2006. Overgrazing of kelp beds along the coast of Norway. *Journal of Applied Phycology*. 18. 599-610.
- Sivertsen, S.P., Pedersen, T., Lindstrøm, U.L.F. and Haug, T. 2006. Prey partitioning between cod (*Gadus morhua*) and minke whale (*Balaenoptera acutorostrata*) in the Barents Sea. *Marine Biology Research*, 2(2): 89-99.
- Smout, S. and Lindstrom, U. 2007. Multispecies functional response of the minke whale *Balaenoptera acutorostrata* based on small-scale foraging studies. *Marine Ecology Progress Series* 341: 277-291.
- Springer, A.M., Estes, J.A., van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M., Forney, K.A., and Pfister, B. 2003. Sequential megafaunal collapse in the North Pacific Ocean; an ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences* 100: 12 223-12 228.
- Stanford, R., Lunn, K., and Guénette, S. 2001. A preliminary ecosystem model for the Atlantic coast of Morocco in the mid-1980s. pp

- 314-344 In Guénette, S., Christensen, V., and Pauly, D (Eds.). Fisheries impacts on North Atlantic Ecosystems: models and analyses. Fisheries Centre Research Reports 9(4).
- Stewart, D.A., Agnew, D., Boyd, R., Briggs, R., and Toland, P. 1993. The derivation of changes in Nephrops per unit effort values for the Northern Ireland fishing fleet. Fisheries Research 17, 273-292.
- Stobberup, K.A., Ramos, V.D.M., and Coelho, M.L. 2004. Ecopath model of the Cape Verde coastal ecosystem, pp. 39-56 In Palomares, M.L.D. and Pauly, D. (Eds.) West African marine ecosystems: models and fisheries impacts. Fisheries Centre Research Reports 12(7). Fisheries Centre, UBC, Vancouver.
- Struck, D. 2001. Japan blames whales for lower fish catch. International Herald Tribune (July 28-29).
- Tamura, T. 2003. Regional assessments of prey consumption and competition by marine cetaceans in the world. In Responsible Fisheries in the Marine Ecosystem. pp. 143-170 In Sinclair, M. and Valdimarsson, G. (Eds). Responsible Fisheries in the Marine Ecosystem, Fishery Industries Division, CAB International: FAO, Rome (Italy) and Wallingford (United Kingdom).
- Toresen, R. 1996. Survey of the pelagic fish resources off North West Africa. Part 3 Senegal-Gambia. 1-9 November 1996. NORAD/FAO/UNDP GLO 92/013. 13 p.
- Toresen, R. 1997. Survey of the pelagic fish resources off North West Africa. Cruise report N° 11/97. 4 - 12 November 1997. Part I Senegal-Gambia. NORAD/FAO/UNDP GLO 92/013. 14 p.
- Toresen, R. 1998. Survey of the pelagic fish resources off North West Africa. Cruise report N° 11/98. 30 October - 9 November 1998. Part I Senegal-Gambia. NORAD/FAO/UNDP. 14 p.
- Toresen, R. and Kolding, J. 1999. Survey of the pelagic fish resources off North West Africa. Cruise report N° 11/98. 30 October - 9 November 1999. Part I Senegal-Gambia. NORAD/FAO/UNDP. 31 p.
- Touré, D. 1983. Contribution à l'étude de l'upwelling de la baie de Gorée (Dakar Sénégal) et de ses conséquences sur le développement de la biomasse phytoplanctonique. Doc. Sci. CRODT n° 93.
- Trites, A.W. 2002. Predator-prey relationships. pp 994-997 In Perrin, W.F., Wursig, B., and H.G.M. Thewissen (eds.). Encyclopedia of Marine Mammals. Academic Press, San Diego.
- Trites, A.W. and Pauly, D. 1998. Estimating mean body masses of marine mammals from maximum body lengths. Canadian Journal of Zoology 76: 886-896.
- Trites, A.W. and Heise, K. 1996. Marine Mammals: Southern BC Shelf Model, pp. 51-55. In: D. Pauly, V. Christensen and N. Haggan (eds.) Mass balance models of the north-eastern Pacific ecosystems. Fisheries Centre Research Reports 4(1), University of British Columbia, Vancouver.
- Vasconcellos, V., Mackinson, S., Sloman, K., and Pauly, D. 1997. The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecological Modelling 100: 125-143.
- Voituriez, B. and Herbland, A.. 1982. Comparaison des systèmes productifs de l'Atlantique Tropical Est : dômes thermiques, upwellings côtiers et upwellings équatorial. Rapp. P.-V. Réun. CIEM, 180: 114-30.
- Wade, P.R. and Gerrodette, T. 1993. Estimates of cetacean abundance and distribution in the Eastern Tropical Pacific. Reports of the International Whaling Commission 43: 477-493.
- Walters, C. and Martell, S. 2004. Fisheries ecology and management. Princeton University Press, Princeton, New Jersey.
- Witteveen, B.H., Foy, R.J. and Wynne, K.M. 2006. The effect of predation (current and historical) by humpback whales (*Megaptera novaeangliae*) on fish abundance near Kodiak Island, Alaska. Fish. Bull. 104 : 10-20.



## FOOD WEB MODEL AND DATA FOR STUDYING THE INTERACTIONS BETWEEN MARINE MAMMALS AND FISHERIES IN THE CARIBBEAN ECOSYSTEM<sup>a</sup>

---

Jenny Lynn Melgo<sup>1</sup>, Lyne Morissette<sup>1,2,3</sup>, Kristin Kaschner<sup>4</sup> and Leah R. Gerber<sup>1</sup>

<sup>1</sup>*Arizona State University, School of Life Sciences,  
P.O. Box 874501, Tempe, AZ 85287-4501, USA*

<sup>2</sup>*Institut des sciences de la mer de Rimouski,  
310, Allée des Ursulines, C.P. 3300, Rimouski, QC, G5L 3A1, CANADA*

<sup>3</sup>*Fisheries Centre, The University of British Columbia  
2202 Main Mall, Vancouver BC V6T 1Z4, CANADA*

<sup>4</sup>*Albert-Ludwigs-University, Institute of Biology I (Zoology)  
Evolutionary Biology and Ecology Lab, Freiburg, GERMANY*

[Lyne.Morissette@globetrotter.net](mailto:Lyne.Morissette@globetrotter.net)  
[Jennylynn.Melgo@asu.edu](mailto:Jennylynn.Melgo@asu.edu)  
[Kristin.Kaschner@biologie.uni-freiburg.de](mailto:Kristin.Kaschner@biologie.uni-freiburg.de)  
[Leah.Gerber@asu.edu](mailto:Leah.Gerber@asu.edu)

### ABSTRACT

A mass balanced ecosystem model was constructed to examine the trophic interaction between whales and fisheries in the Caribbean ecosystem. This model includes data from the ecosystem models of the Lesser Antilles, Bahia Ascencion Mexican Caribbean, Southern Mexican Caribbean, Grenada and the Grenadines, Colombian Caribbean Sea, Caribbean coral reef ecosystem, Costa Rica, Eastern Tropical Pacific and Central Atlantic. Our model includes twenty nine trophic groups for the Caribbean ecosystem model, comprising 10 marine mammal groups, one seabird group, one sea turtle group, eleven fish groups, one cephalopod group, one crustaceans and benthos group, one benthic producers group, one zooplankton, one phytoplankton and one detritus group. Time series catches of some cetaceans and all fish and non-fish groups in 1987's to 2005's are also included in the model. Data quality, uncertainty, *Ecoranger* and simulation analysis for the removal of great whales and fisheries in the ecosystem are included in this report.

### INTRODUCTION

A food web is defined as the complex trophic links between organisms (prey-predator) living in an ecosystem. The prey-predator relationships in food webs are typically arranged in oriented graphs with hierarchical or layered structures that show energy pathways and matter transfer within the ecosystem (Paine *et al.* 1998; Pimm 2002). The structure and functions of food webs are

---

<sup>a</sup> Cite as: Melgo, J.L., Morissette, L., Kaschner, K., and Gerber, L. (2009) Food web model and data for studying the interactions between marine mammals and fisheries in the Caribbean ecosystem. *In*: Morissette, L., Melgo, J.L., Kaschner, K. and Gerber, L.R. (eds.) Modelling the trophic role of marine mammals in tropical areas: data requirements, uncertainty, and validation. Fisheries Centre Research Reports XX(X). Fisheries Centre, University of British Columbia, Vancouver, Canada, pp. 48-107.

important to many ecologists and biologists in understanding the role of certain species and the ecosystem, predator-prey interactions on how directly or indirectly they influence each other in the ecosystem and the possible competition among species in the area (Trites *et al.* 1997; Bax 1998; Pauly *et al.* 1998a; Constable and Gales 2002; Morissette *et al.* 2006). For example, in the context of marine mammals and fisheries, Estes *et al.* (2007) assert that the ocean ecosystems throughout the world have experienced a dramatic shift in structure as a result of the removal of top predators and extensive fishing activities. Moreover, when complex trophic interactions are taken into consideration, it has been shown that culling of marine mammals would not lead necessarily to the recovery of fish stocks (Punt and Butterworth 1995; Plagányi and Butterworth 2002; Morissette 2007). The application of food web models to these questions and the generated results may allow ecologists, managers and even policy makers to identify which species or communities might be vulnerable to disturbance and would need immediate attention.

Currently, little is known about the interaction of marine mammals and fisheries in the Caribbean ecosystem. The Lesser Antilles pelagic ecosystem model by Mohammed *et al.* (2007b) investigated the interaction of marine mammals and fisheries in the area. However, their study focuses on marine mammal species that reside almost throughout the year in the waters surrounding the Lesser Antilles, while the present study also includes all of the numerous migratory, large and small marine mammal species occurring in the entire Caribbean ecosystem. There are also other ecosystem models constructed in different areas of the Caribbean Sea and the Gulf of Mexico (Opitz 1996; Wolff *et al.* 1998; Duarte and Garcia 2002; Mohammed 2003a; Alvarez-Hernández 2003; Vidal and Basurto 2003). These studies focus, however, on the continental shelf, coral reef or coastal and large pelagic components of the ecosystem addressing questions related to the trophic interaction of reef fishes and/or interactions among large pelagic fisheries and some top predators.

At least 31 species of marine mammals (6 baleen whales, 24 toothed whales, 1 sirenian) are known to occur in the Caribbean Sea (UNEP 2002). While many of the smaller odontocete species (e.g. dolphins) inhabit this region year-round, most of the larger mysticetes (e.g. humpback whales) migrate to the Caribbean Sea for calving and breeding (Klinowska 1991; Debrot *et al.* 1998; Reeves *et al.* 2001; UNEP 2002; Swartz *et al.* 2003). It has been proposed that some or all of these higher vertebrate species compete with other marine organisms or fisheries for the available food resources (Mohammed *et al.* 2007b). For example, Tamura (2003) have estimated that marine mammals around the world annually consume 250-440 million tonnes of fish, and thus consume three to six times the amount taken annually by marine fisheries. However, other scientists have shown that there is currently no real scientific evidence for existing large-scale competition between marine mammals and fisheries (Kaschner 2004; Morissette 2007). In addition, there is mounting evidence and a robust documentation of overfishing on a global scale including the Caribbean (Jackson *et al.* 2001; Pauly *et al.* 2002; Baum *et al.* 2003; Myers and Worm 2003; Mahon and McConney 2004), which by itself could easily explain the observed depletion of the fish stocks in this area.

In this study, we examined the scientific evidence for the trophic interaction between marine mammals and fisheries (distinguishing between foreign and local fleets); using the local data obtained from several published literatures and reports studied in the adjacent areas of the Caribbean ecosystem supplemented with additional details about marine mammal abundances, diets and food consumption. Our approach was to develop a mass-balanced ecosystem model using the *Ecopath and Ecosim (EwE)* program (Christensen and Walters 2004). We used the *EwE* program because it is one of several ecosystem modelling approaches that is widely used in understanding the interactions between marine mammals and fisheries (Morissette 2007). This model allowed us to characterize the structure and functionality of the ecosystem in terms of biomass, mortalities, consumption rates, food habits, general ecosystem indicators and fisheries.

## MATERIALS AND METHODS

### Study area

Our study area was located in the southeastern edge of the Caribbean Sea. It was part of a Large Marine Caribbean Ecosystem including the Dominican Republic at its northern point and extending to Trinidad and Tobago at its southern point. The Caribbean islands covered by our model included Anguilla, Antigua and Barbuda, Barbados, British Virgin Islands, Dominica, Dominican Republic, Grenada and the Grenadines, Guadeloupe, Martinique, Montserrat, Puerto Rico, St Kitts and Nevis, St Lucia, St Vincent, and Trinidad and Tobago, and the US Virgin Island. Generally, the topography of these islands was characterized by steep drop-off with wide pelagic environment, but in some areas (e.g. Virgin Islands, Puerto Rico), we can also observed deep basins and shallow wide areas of coral reefs and seagrass beds (Opitz 1996; UNEP 2002; Martin *et al.* 2005). The nominal EEZ's (within a distance of 200 n. mi. out from its coast) of the Caribbean islands defined the boundary of our study areas, from 10 N to 19 N latitudes and 71.75 W to 56 W longitudes, with a total area of approximately 2 million km<sup>2</sup> (Figure 1).



**Figure 1.** Map of study area: The Caribbean region. The numbers shown in the map were the study sites of eight adjacent South or Central American tropical models which provided data for the confidence interval inputs of each input parameter in our model. Legends: model study area (green shaded polygon); Bahia Ascension [1] (Vidal and Basurto 2003); Southern Mexican Caribbean[2] (Alvarez-Hernández 2003); Grenada and the Grenadines[3] (Mohammed 2003); Colombian Caribbean Sea[4] (Duarte and Garcia 2002); Costa Rica[5] (Wolff *et al.* 1998); Caribbean coral reef[6] (Opitz 1996); Central Atlantic[7] (Vasconcellos and Watson 2004) and Eastern Tropical Pacific[8] (Olson and Watters 2003).

The pelagic marine environment of the Caribbean Sea is influenced by the North Equatorial currents that pass through between the Lesser Antilles arc (Johns *et al.* 2002). This water mass inflow is considerably nutrient-poor water which is important for coralline formation in the region (Richards and Bohnsack 1990). The Caribbean Sea is considered to be an ecosystem with low productivity ( $<150 \text{ gCm}^{-2}\text{yr}^{-1}$ ) based on SeaWiFS global primary productivity estimates (Richards and Bohnsack 1990). However, there is considerable spatial and temporal heterogeneity in productivity in some areas (e.g. seagrass beds, mangroves areas, local upwelling, riverine flows) in the region (Heileman 2007). The complex dynamics of these high productive coastal areas and offshore waters contributes and support the Caribbean regions valuable marine ecological and biological diversity (Heileman 2007). Because of its location and unique marine environment, the fishing and tourism industry is an economically important source of income for locals in the region (Opitz 1996; Bacci 1998; CANARI 1999).

## MODEL DESCRIPTION

The list of trophic groups described in this report is shown in Table 1. This includes whale species, fish species, cephalopods species, crustaceans, planktons, benthic producers and detritus.

**Table 1.** List of trophic groups and species included in the Ecopath model for Caribbean. Species in **bold** represent the key species for each of the trophic group based on its importance in biomass and in fisheries in the area.

Ecopath group	Species
1. Minke whales	<i>Balaenoptera acutorostrata</i>
2. Fin whales	<i>Balaenoptera physalus</i>
3. Humpback whales	<i>Megaptera novaeangliae</i>
4. Bryde's whales	<i>Balaenoptera brydei</i>
5. Sei whales	<i>Balaenoptera borealis</i>
6. Blue whales	<i>Balaenoptera musculus</i>
7. Sperm whales	<i>Physeter macrocephalus</i> , <i>Kogia breviceps</i> , <i>Kogia simus</i>
8. Killer whales	<i>Feresa attenuata</i> , <i>Orcinus orca</i> , <i>Pseudorca crassidens</i>
9. Beaked whales	<i>Mesoplodon densirostris</i> , <i>Mesoplodon europaeus</i> , <i>Ziphius cavirostris</i>
10. Small cetaceans	<i>Delphinus capensis</i> , <i>Delphinus delphis</i> , <i>Globicephala macrorhynchus</i> , <i>Grampus griseus</i> , <i>Lagenodelphis hosei</i> , <i>Sousa teuszii</i> , <i>Stenella attenuata</i> , <i>Stenella clymene</i> , <i>Stenella coeruleoalba</i> , <i>Stenella frontalis</i> , <i>Stenella longirostris</i> , <i>Steno bredanensis</i> , <i>Tursiops truncatus</i>
11. Seabirds	<i>Actitis hypoleucos</i> , <i>Ajaia ajaja</i> , <i>Calidris ferruginea</i> , <i>Calonectris diomedea</i> , <i>Ceryle rudis</i> , <i>Chlidonias niger</i> , <i>Halcyon malimbica</i> , <i>Limosa lapponica</i> , <i>Numenius phaeopus</i> , <i>Oceanites oceanicus</i> , <i>Pagrodama nivea</i> , <i>Pelecanus rufescens</i> , <i>Phalacrocorax africanus</i> , <i>Phoenicopterus ruber</i> , <i>Pluvialis squatarola</i> , <i>Sterna caspia</i> , <i>Sterna hirundo</i>
12. Seaturtles	<i>Caretta caretta</i> , <i>Chelonia mydas</i> , <i>Eretmochelys imbricata</i> , <b><i>Dermochelys coriacea</i></b>
13. Large tunas and billfishes	<b>Istiophoridae</b> , <i>Istiophorus albicans</i> , <b><i>Makaira nigricans</i></b> , <i>Parexocoetus brachypterus</i> , <b><i>Tetrapturus albidus</i></b> , <i>Tetrapturus pfluegeri</i> , <b><i>Thunnus alalunga</i></b> , <b><i>Thunnus albacares</i></b> , <i>Thunnus obesus</i> , <i>Thunnus thynnus</i> , <b><i>Xiphias gladius</i></b>
14. Small tunas	<b><i>Auxis</i> sp.</b> , <b><i>Euthynnus alletteratus</i></b> , <b><i>Katsuwonus pelamis</i></b> , <b><i>Sarda sarda</i></b> , <b><i>Thunnus atlanticus</i></b>
15. Dolphinfish	<b><i>Coryphaena hippurus</i></b> , <b>Coryphaenidae</b>
16. Flyingfish	<b><i>Hirundichthys affinis</i></b> , <b><i>Cheilopogon cyanopterus</i></b> , <i>Cypselurus cyanopterus</i> , <b><i>Parexocoetus brachypterus</i></b> , <i>Exocoetidae</i>

**Table 1.** (cont.)

17. Other offshore predators	<b>Alepocephalidae</b> , <i>Argyropelecus olfersi</i> , <i>Bathylagus nigrubenys</i> , <i>Cyclothone</i> sp., <b>Gonostomatidae</b> , <i>Gonostoma bathyphilum</i> , <i>Lampris guttatus</i> , <i>Lampanyctus macdonaldi</i> , <i>Lobotes surinamensis</i> , <i>Melanocetus</i> sp., <b>Moridae</b> , <b>Myctophidae</b> , <i>Pomatomus saltator</i> , <i>Ruvettus pretiosus</i> , <i>Scopelogadus beanie</i> , <i>Sternoptyx diaphana</i>
18. Pelagic sharks	<i>Carcharhinidae</i> , <i>Carcharhinus acronotus</i> , <b><i>Carcharhinus brevipinna</i></b> , <i>Carcharhinus falciformis</i> , <i>Carcharhinus leucas</i> , <i>Carcharhinus limbatus</i> , <b><i>Carcharhinus longimanus</i></b> , <i>Carcharhinus perezi</i> , <i>Elasmobranchii</i> , <b><i>Galeocerdo cuvier</i></b> , <i>Lamnidae</i> , <b><i>Lamna nasus</i></b> , <b><i>Prionace glauca</i></b> , <i>Isurus oxyrinchus</i> , <b><i>Isurus paucus</i></b> , <i>Sphyrna lewini</i> , <i>Urolophidae</i>
19. Coastal sharks and rays	<i>Aetobatus narinari</i> , <i>Dasyatidae</i> , <b><i>Dasyatis americana</i></b> , <b><i>Ginglymostoma cirratum</i></b> , <i>Mustelus</i> sp., <i>Myliobatidae</i> , <i>Negaprion brevirostris</i> , <i>Raja</i> sp., <i>Rajiformes</i> , rays, <i>Rhizoprionodon terraenovae</i> , small/juvenile sharks, <i>Squalidae</i>
20. Scombrids	<b><i>Acanthocybium solandri</i></b> , <b><i>Scomberomorus brasiliensis</i></b> , <b><i>Scomberomorus cavalla</i></b> , <i>Scomberomorus maculatus</i> , <i>Scomberomorus regalis</i> , <i>Scomberomorus</i> sp., <i>Scombridae</i>
21. Small and schooling pelagics	<i>Ablennes hians</i> , <i>Alectis ciliaris</i> , <i>Anchoa hepsetus</i> , <i>Anchoa lucida</i> , <i>Anchoa lyolepis</i> , <i>Belonidae</i> , <i>Carangoides ruber</i> , <i>Caranx crysos</i> , <i>Caranx latus</i> , <i>Caranx lugubris</i> , <i>Cetengraulis edentulous</i> , <i>Cetengraulis edentulous</i> , <i>Clupeidae</i> , <i>Clupeiformes</i> , <b><i>Chloroscombrus chrysurus</i></b> , <b><i>Decapterus macarellus</i></b> , <b><i>Decapterus punctatus</i></b> , <b><i>Decapterus</i> sp.</b> , <b><i>Dorosoma petenense</i></b> , <i>Elagatis bipinnulata</i> , <i>Elops saurus</i> , <i>Engraulidae</i> , <i>Etrumeus teres</i> , <b><i>Harengula clupeola</i></b> , <b><i>Harengula humeralis</i></b> , <b><i>Harengula</i> sp.</b> , <i>Hyperoglyphe bythites</i> , <i>Hypoatherina harringtonensis</i> , <i>Jenkinsia lamprotaenia</i> , <i>Lepidocybium flavobrunneum</i> , <i>Neoopisthopterus tropicus</i> , <i>Oligoplites saurus</i> , <i>Opisthonema oglinum</i> , <i>Peprius alepidotus</i> , <i>Peprius</i> sp., <i>Platybelone argalus</i> , <b><i>Sardinella aurita</i></b> , <b><i>Sardinella brasiliensis</i></b> , <b><i>Selar crumenophthalmus</i></b> , <i>Selene brevoortii</i> , <i>Selene orstedii</i> , <i>Selene peruviana</i> , <i>Selene setapinnis</i> , <i>Sphyræna barracuda</i> , <i>Sphyræna</i> sp., <i>Stromateidae</i> , <i>Strongylura timucu</i> , <i>Trichiuridae</i> , <i>Trichiurus lepturus</i> , <i>Tylosurus acus</i> , <i>Tylosurus crocodilus</i>

**Table 1.** (cont.)

22. Reef fishes

*Abudefduf saxatilis*, *Abudefduf taurus*, *Acanthostracion polygonius*,  
*Acanthostracion quadricornis*, *Acanthuridae*, *Acanthurus bahianus*,  
*Acanthurus chirurgus*, *Acanthurus coeruleus*, *Albula vulpes*, *Alphestes afer*,  
*Aluterus schoepfii*, *Aluterus scripta*, *Anisotremus surinamensis*, *Anisotremus*  
*virginicus*, *Antennarius striatus*, *Apogon maculatus*, *Aulostomus maculatus*,  
*Balistes capricornis*, *Balistes vetula*, *Balistidae*, *Bodianus rufus*, *Bothus lunatus*,  
*Bothus ocellatus*, *Brotula barbata*, *Calamus bajonado*, *Calamus calamus*,  
*Calamus pennatula*, *Cantherhines macrocerus*, *Cantherhines pullus*,  
*Canthidermis sufflamen*, *Canthigaster rostrata*, *Centropomus undecimalis*,  
*Centropyge argi*, *Cephalopholis cruentata*, *Cephalopholis fulva*,  
*Chaetodipterus faber*, *Chaetodon aculeatus*, *Chaetodon capistratus*, *Chaetodon*  
*ocellatus*, *Chaetodon sedentarius*, *Chaetodon striatus*, *Chilomycterus*  
*antennatus*, *Chilomycterus antillarum*, *Chromis cyanea*, *Chromis multilineata*,  
*Clepticus parrae*, *Coryphopterus glaucofraenum*, *Dactylopterus volitans*,  
*Diodon holocanthus*, *Diodon hystrix*, *Diplectrum formosum*, *Diplodus*  
*argenteus* *caudimacula*, *Echidna catenata*, *Enchelycore nigricans*,  
*Entomacrodus nigricans*, *Ephippidae*, *Epinephelus adscensionis*, *Epinephelus*  
*itajara*, *Epinephelus morio*, *Epinephelus nigritus*, *Epinephelus niveatus*,  
*Epinephelus striatus*, *Equetus lanceolatus*, *Equetus punctatus*, *Eucinostomus*  
*argenteus*, *Eugerres plumieri*, *Fistularia tabacaria*, *Gerreidae*, *Gerres cinereus*,  
*Gnatholepis thompsoni*, *Gobiosoma evelynae*, *Gobiosoma horsti*, *Grama*  
*loreto*, *Grama melacara*, *Gymnothorax funebris*, *Gymnothorax miliaris*,  
*Gymnothorax vicinus*, **Haemulidae**, *Haemulon album*, *Haemulon*  
*aurolineatum*, *Haemulon carbonarium*, *Haemulon chrysargyreum*, *Haemulon*  
*flavolineatum*, *Haemulon macrostomum*, *Haemulon melanurum*, *Haemulon*  
*parra*, *Haemulon plumieri*, *Haemulon sciurus*, *Halichoeres bivittatus*,  
*Halichoeres garnoti*, *Halichoeres maculipinna*, *Halichoeres poeyi*, *Halichoeres*  
*radiatus*, *Hemiramphus brasiliensis*, *Holacanthus ciliaris*, *Holacanthus*  
*tricolor*, *Hypoplectrus aberrans*, *Hypoplectrus chlorurus*, *Hypoplectrus*  
*nigricans*, *Hyporhamphus unifasciatus*, *Joturus pichardi*, **Kyphosus incisor**,  
**Kyphosus sectatrix**, *Labridae*, *Labrisomus guppyi*, *Labrisomus nuchipinnis*,  
*Lachnolaimus maximus*, *Lactophrys bicaudalis*, *Lactophrys triqueter*,  
*Lopholatilus chamaeleonticeps*, *Malacanthidae*, *Malacanthus plumieri*,  
*Melichthys niger*, *Menticirrhus littoralis*, *Micropogonias furnieri*,  
*Micropogonias undulates*, *Microspathodon chrysurus*, *Monacanthidae*,  
*Monacanthus ciliatus*, *Monacanthus tuckeri*, *Mullidae*, *Mycteroperca bonaci*,  
*Mycteroperca rubra*, *Mycteroperca tigris*, *Mycteroperca venenosa*, *Myrichthys*  
*breviceps*, *Myrichthys ocellatus*, *Myripristis jacobus*, *Neoniphon marianus*,  
*Odontoscion dentex*, *Ogcocephalus nasutus*, *Ophidiidae*, *Ophioblennius*  
*atlanticus*, *Opistognathus aurifrons*, *Opistognathus macrognathus*,  
*Opistognathus maxillosus*, *Opistognathus whitehursti*, *Ostraciidae*,  
*Parablennius marmoreus*, *Paralichthyidae*, *Paralichthys* sp., *Paranthias*  
*furcifer*, *Pareques acuminatus*, *Phaeoptyx conklini*, *Plectrypops retrospinis*,  
*Pogonias cromis*, *Polynemidae*, *Pomacanthidae*, *Pomacanthus arcuatus*,  
*Pomacanthus paru*, *Pomacentridae*, *Priacanthus arenatus*, *Pseudupeneus*  
*maculatus*, *Rypticus saponaceus*, *Scaridae*, *Scartella cristata*, *Scarus*  
*coelestinus*, *Scarus coeruleus*, *Scarus guacamaia*, *Scarus iserti*, *Scarus*  
*taeniopterus*, *Scarus vetula*, *Scorpaenodes caribbaeus*, *Serranidae*, *Serranus*  
*tabacarius*, *Serranus tortugarum*, *Sparisoma aurofrenatum*, *Sparisoma*  
*chrysopterum*, *Sparisoma radians*, *Sparisoma rubripinne*, *Sparisoma viride*,  
*Sphoeroides spengler*, *Stegastes fuscus*, *Stegastes leucostictus*, *Stegastes*  
*planifrons*, *Stegastes variabilis*, *Stephanolepis setifer*, *Symphurus chabanaudi*,  
*Tetraodontidae*, *Thalassoma bifasciatum*, *Xanthichthys ringens*, *Xyrichtys*  
*novacula*, *Xyrichtys splendens*

**Table 1.** (cont.)

23. Coastal predators	<i>Achirus klunzingeri</i> , <b><i>Alectis ciliaris</i></b> , <i>Archosargus probatocephalus</i> , <b><i>Belonidae</i></b> , <b><i>Caranx hippos</i></b> , <b><i>Caranx</i> sp.</b> , <i>Cynoponticus coniceps</i> , <i>Cynoscion</i> sp., <i>Heteropriacanthus cruentatus</i> , <i>Holocentridae</i> , <i>Holocentrus coruscus</i> , <b><i>Elegatis bipinnulata</i></b> , <b><i>Lutjanidae</i></b> , <b><i>Lutjanus analis</i></b> , <b><i>Lutjanus apodus</i></b> , <b><i>Lutjanus cyanopterus</i></b> , <b><i>Lutjanus griseus</i></b> , <b><i>Lutjanus jocu</i></b> , <b><i>Lutjanus mahogoni</i></b> , <b><i>Lutjanus purpureus</i></b> , <b><i>Lutjanus synagris</i></b> , <i>Megalops atlanticus</i> , <i>Mugil cephalus</i> , <i>Mugil curema</i> , <i>Mugil liza</i> , <i>Mugilidae</i> , <i>Mulloidichthys martinicus</i> , <i>Myrichthys breviceps</i> , <i>Myrichthys ocellatus</i> , <i>Myripristis jacobus</i> , <i>Ocyurus chrysurus</i> , <b><i>Oligoplites</i> sp.</b> , <i>Ophichthus ophis</i> , <i>Pempheris poeyi</i> , <i>Peprilus medius</i> , <i>Peprilus snyderi</i> , <i>Pomadasys corvinaeformis</i> , <i>Pomadasys crocro</i> , <i>Rachycentron canadum</i> , <i>Rhomboplites aurorubens</i> , <i>Sargocentron vexillarium</i> , <i>Sciaenidae</i> , <i>Scorpaena grandicornis</i> , <i>Scorpaena inermis</i> , <b><i>Seriola dumerili</i></b> , <b><i>Seriola rivoliana</i></b> , <b><i>Seriola</i> sp.</b> , <i>Syacium latifrons</i> , <i>Syacium ovale</i> , <i>Synodus foetens</i> , <i>Synodus intermedius</i> , <i>Trachinotus carolinus</i> , <i>Trachinotus falcatus</i> , <i>Trachinotus goodie</i> , <i>Trachinotus paitensis</i>
24. Cephalopods	<i>Alloteuthis subulata</i> , <i>Loliginidae</i> , <i>Loligo pealeii</i> , <b><i>Loligo</i> sp.</b> , <i>Loligo vulgaris</i> , <i>Lolliguncula panamensis</i> , <i>Octopodidae</i> , <b><i>Octopus vulgaris</i></b> , <i>Ommastrephidae</i> , <i>Sepia bertheloti</i> , <i>Sepia elobyana</i> , <i>Sepia officinalis</i> , <i>Sepia orbignyana</i> , <i>Sepiidae</i> , <i>Thysanoteuthis rhombus</i> , <i>Todarodes sagittatus</i>
25. Crustaceans and benthos	<i>Aristeidae</i> , <i>Arca</i> sp., <i>Arcidae</i> , <i>Aristeus antennatus</i> , <i>Aristeus varidens</i> , <i>Bivalvia</i> , <i>Brachyura</i> , <i>Busycon</i> sp., <i>Calappa rubroguttata</i> , <i>Callinectes sapidus</i> , <i>Cancer pagurus</i> , <i>Carcinus maenas</i> , <i>Cardiidae</i> , <i>Cardium edule</i> , <i>Chama crenulata</i> , <i>Chitonidae</i> , <i>Conidae</i> , <i>Crangon crangon</i> , <i>Crangonidae</i> , <i>Crassostrea rhizophorae</i> , <b><i>Crassostrea virginica</i></b> , <i>Crepidula porcellana</i> , <i>Crustacea</i> , <i>Diadema</i> sp., <i>Donacidae</i> , <i>Echinoderms</i> , <i>Gastropoda</i> , <i>Geryon maritae</i> , <i>Geryon quinquedens</i> , <i>Haliotis tuberculata</i> , <i>Homarus gammarus</i> , <i>Leucosiidae</i> , <i>Maja squinado</i> , <i>Menippe mercenaria</i> , <i>Miscellaneous marine mollusks</i> , <i>Muricidae</i> , <i>Mytilidae</i> , <i>Naticidae</i> , <i>Necora puber</i> , <i>Nephrops norvegicus</i> , <i>Paguridae</i> , <i>Palaemonidae</i> , <i>Palinurus elephas</i> , <i>Palinurus mauritanicus</i> , <b><i>Panulirus argus</i></b> , <i>Panulirus regius</i> , <i>Panulirus</i> sp., <i>Parapanaeus longirostris</i> , <i>Parapanaeopsis atlantica</i> , <i>Pecten maximus</i> , <i>Pectinidae</i> , <i>Penaeidae</i> , <i>Penaeus kerathurus</i> , <i>Penaeus brasiliensis</i> , <i>Penaeus notialis</i> , <b><i>Penaeus</i> sp.</b> , <i>Perna perna</i> , <i>Pleoticus robustus</i> , <i>Plesionika heterocarpus</i> , <i>Plesiopenaeus edwardsianus</i> , <i>Porifera</i> , <i>Portunidae</i> , <i>Portunus</i> sp., <i>Pyura dura</i> , <i>Ruditapes decussates</i> , <i>Scyllaridae</i> , <i>Solenidae</i> , <b><i>Strombus</i> sp.</b> , <i>Veneridae</i> , <i>Venus rosalina</i> , <i>Venus verrucosa</i> , <i>Volutidae</i> , <i>Xiphopenaeus kroyeri</i>
26. Benthic producers	Algae, benthic autotrophs
27. Zooplankton	<i>Chaetognatha</i> , <i>Copepoda</i> , <i>Euphausiacea</i> , <i>Hydrozoa</i> , <i>Hyperidae</i> , <i>Mysidacea</i> , <i>Scyphozoa</i> , <i>ichthyoplankton</i> , <i>macroplankton</i> , <i>meroplankton</i> , <i>planktonic decapods</i> , <i>larvae</i> , and <i>eggs</i>
28. Phytoplankton	
29. Detritus	

The initial mass-balanced ecosystem model for the Caribbean used herein was originally based on the trophic model of the Lesser Antilles pelagic ecosystem (LAPE) by Mohammed *et al.* (2007b). There were 31 trophic groups in the initial model, consisting of four marine mammal functional groups, one seabird group, two seaturtle groups, eighteen fish groups, two squid groups, two zooplankton groups, one phytoplankton group and one detritus group. In order to address our goal to examine the trophic interaction between fisheries and whales in the entire Caribbean ecosystem, we modified the structure of this model. In particular, we aggregated some similar non-marine mammal trophic groups based on habitat, feeding category and biological variables (Essington 2006), but retained some important fish species (e.g. dolphinfish, flyingfish) based on local expert suggestions received during the regional workshop held in Barbados on September 2008. We also added an additional 7 cetacean trophic groups to the existing marine mammal groups (e.g. Bryde's whales, killer whales and deep-diving cetaceans) in the initial model. The modified structure of this model provided a better representation of great whales and of commercially important fish groups in the context of the 'whales eat fish' issue. These changes reduced the number of trophic groups of the present model from 31 to 29, consisting of 10 marine

mammal groups, one seabirds group, one seaturtles group, eleven fish groups, one cephalopods group, one crustaceans and benthos group, one benthic producers group, one zooplankton group, one phytoplankton group, and one detritus group (Table 1).

Published literature documenting other Caribbean ecosystem models from the surrounding areas was used to establish confidence intervals inputs for calibration of biomass, P/B, Q/B and diet matrix. Such models were available for Caribbean coral reef (Opitz 1996), Colombian Caribbean Sea (Duarte and Garcia 2002), Southeastern Caribbean (Mohammed 2003a), Southeastern Mexican Caribbean (Alvarez-Hernández, 2003), Bahia Ascencion Mexican Caribbean (Vidal and Basurto 2003), and the coast of Costa Rica (Wolff *et al.* 1998). In addition, we also considered two models that were not from the Caribbean area, but represented typical pelagic, tuna-dominated ecosystems: the Central Atlantic (Vasconcellos and Watson 2004) and the Eastern tropical Pacific (Olson and Watters 2003) models. These areas were included in the present analysis because they have similar offshore migratory pelagics species as of the Caribbean ecosystem (Mohammed *et al.* 2007b). In order to maintain the same trophic groups from those eight *Ecopath* ecosystem models for adjacent Caribbean areas, we matched their existing trophic groups and corresponding species to the structure of our model. There were some species belonging to the trophic groups in the other *Ecopath* models that were different from our trophic groups' species lists. This was resolved by taking the key species of the trophic groups for each ecosystem models and aggregating them according to the structure of our established trophic groups of the present Caribbean model.

Diet information of the trophic groups represented the adult diet only, since most of the biomass estimates available were only for the spawning or adult biomass. In general, we incorporated the trophic diet data from Heileman *et al.* (2007) and Opitz (1996).

Cetacean biomass and abundance inputs for all marine mammal groups included in our model were provided by Kristin Kaschner based on a global database of marine mammal occurrence and densities (Kaschner 2004) since there were currently no reliable abundance estimates for the majority of cetaceans from dedicated surveys conducted in the area. Cetacean abundances within the study area were estimated based on global abundance estimates that were converted into densities per 0.5 degree latitude by 0.5 degree longitude cells falling within the range of predicted occurrence for each species and weighted by the relative suitability of the habitat of each cell for a given species (Kaschner *et al.* 2006).

The data provided by Kaschner was updated and validated wherever possible using abundance estimates obtained during dedicated cetacean surveys conducted in other areas associated with similar types of subtropical habitat. Marine mammal mortality rate data were extracted from several published references (e.g. Trites and Heise 1996; Perry *et al.* 1999). Marine mammal quantitative diet information in the Caribbean was generally scarce, in particular for baleen whales which generally come to breed or calve in these waters. These migratory whales generally are not known to feed in breeding areas, but rather consume most of their food during their sojourn in their subpolar or polar feeding grounds of the North Atlantic (Klinowska 1991; Clapham 2002; Jann *et al.* 2003). Lockyer (1981) estimated that consumption in breeding areas is approximately 10% of feeding rates in feeding ground. Several subsequent studies (e.g. Brown and Lockyer 1984; Horwood 1990) support this estimate. This was taken into account and applied by Mohammed (2003a) in the Grenadines' ecosystem model and by Morissette *et al.* (submitted) in Northwest African ecosystem.

Published and unpublished sources for cetacean quantitative dietary information were retrieved using several search engines (e.g. ASFA, Google scholar, Web of Science, ScienceDirect) as well as an extensive Endnote library database for marine mammals provided by Kristin Kaschner (Albert-Ludwigs-University, Freiburg, Germany, personal communication) and further updated by our team. In spite of an exhaustive literature search, very little quantitative dietary information on cetaceans in the region was found. Cetaceans, especially great whales feeding habits or diet studies are less important in the breeding areas because, as noted above, this is not where they



feed (Klinowska 1991; Perrin *et al.* 2002). In cases like these, we incorporated cetacean quantitative diet information from similar ecosystems where data were available.

For methodological reasons, all cetacean biomass and food consumption estimates represented an annual averages, thus indirectly assuming that species remain year-round in the study area as part of the 'system' in terms of calculated impacts (e.g. fishing, whaling and general trophic interactions). However, we represented the feeding ecology for most of the baleen whales (i.e. minke whales, humpback whales, fin whales, sei whales blue whales) more realistically by setting a high *Ecopath* diet proportion as 'import' in the *Ecopath* diet consumption matrix (Christensen *et al.* 2005) thus assuming that the majority of the food consumption occurred outside our study area. Hence, food intake of the above-mentioned baleen whales for each prey group in the Caribbean was reduced to 10%, while the remaining 90% of the intake were considered to be taken outside of our study. Bryde's whales were exempted from this, since the species is known to occur in Caribbean areas yearround (Mohammed *et al.* 2007b). Finally, our balanced trophic model, the Caribbean ecosystem, was reviewed and validated by local experts of the Caribbean region during the "*whales eat fish*" workshop held in Barbados on 23-25 September 2008, facilitated by the project with the assistance of the Lenfest Ocean Program ([http://www.lenfestocean.org/whales\\_fisheries.html](http://www.lenfestocean.org/whales_fisheries.html)).

## Resource exploitation of the ecosystem

### Whaling

Whaling was initiated in the Caribbean in the late 1800's, specifically occurring in the islands of Bequia St. Vincent, the Grenadines and St. Lucia (Mahon 1993; Quimby 2000; Reeves 2002, Mohammed *et al.* 2007a). An approximate harvest of two to three humpback whales per season is documented for St. Vincent and the Grenadines under an "aboriginal" clause of the International Whaling Commission's 1986 moratorium on commercial whaling (Hawley 1999; Goetz *et al.* 1999; Quimby 2000; Reeves 2002). Aboriginal subsistence whaling has been ongoing because it represents a valuable source of protein, and therefore whaling is considered to be an integral part of traditional practices (Hawley 1999; Quimby 2000; Perrin *et al.* 2002; Reeves 2002). Thus far, whales and smaller odontocetes are still harvested in some parts of the region for subsistence of indigenous peoples and for scientific research (Quimby 2000; Reeves 2002). Mohammed *et al.* (2007a), who recently documented catches of cetaceans in the region, states that about 140 dolphins, 13 pilot whales (*Globicephala macrorhynchus*) and one false killer whale (*Pseudorca crassidens*) have been caught annually in St. Lucia from 2000's to 2005's. The same study also documented catches of killer whales (5.63 tonnes/year) and shallow-diving small cetaceans (0.51 tonnes/year) from period of 2000's to 2005's in St. Vincent and the Grenadines. The most common small cetacean species harvested in some eastern Caribbean countries are bottlenose dolphins (*Tursiops truncatus*), spotted dolphins (*Stenella frontalis*), spinner dolphins (*S. longirostris*), and striped dolphins (*S. coeruleoalba*) (Rambally 1999; Mohammed *et al.* 2007a). Additionally, many small cetacean species in the Caribbean are incidentally captured in fishing gear (Mohammed *et al.* 2007a).

Although there are some on-going whaling activities in the region (Quimby 2000; Reeves 2002, Mohammed *et al.* 2007a), there was no official timeseries landings found for the marine mammals catches except for killer whales and small cetaceans species. So far, only the pelagic fisheries report of Mohammed *et al.* (2007a) documented annual catches for killer whales and small cetacean species in Lesser Antilles countries for the period of 2001 to 2005.

### Fishery

Local communities in the Caribbean region are highly dependent on the marine environment for their livelihood (Jeffrey 2000; Mahon and McConney 2004; Heileman 2007; Mohammed *et al.*

2007a). Employment and the income of locals in the region are generated in the fisheries sector mainly through commercial fisheries, recreational fishing and tourism (Opitz 1996; Mohammed *et al.* 2007a). Artisanal fishing (small-scale fishing) in some areas in the Caribbean is important as well, however, since near-shore resources have become depleted, fishing activities continues to expand in the open-ocean, exploiting offshore resources in the adjacent waters of the Caribbean (Mahon and McConney 2004; CLME 2007; Heileman 2007; Mohammed *et al.* 2007a). For instance, Mahon (1996) reported that fishery for large pelagics in Grenada has grown since the early 1980's from 45 to 110 small long-liners fishing one-day trips and seven short-stay longliners. In St Lucia, 45 new vessels were introduced into the large pelagics fishery between 1989 and 1992, and 82 vessels were introduced in Barbados fisheries between 1979 and 1989 (Mahon 1996; Mohammed *et al.* 2007a).

The fisheries in the Caribbean ecosystem include a diverse array of resources (Mahon 1999; Mahon and McConney 2004). The most important fisheries in the region are targeting flyingfish, dolphinfish, yellowfin tuna, albacore tuna, billfishes, swordfish, sailfish, skipjack tuna, wahoo, snappers, jacks, weakfish, reef fishes, lobsters, shrimps and conch shells (Opitz 1996; Mahon 1999; Restrepo *et al.* 2003; Mahon and McConney 2004; CLME 2007; Heileman 2007; Mohammed *et al.* 2007a). Different species of sharks (list some examples here) are also caught in the region, although most sharks are taken as bycatch (Mohammed *et al.* 2007a). In the southeast Caribbean (e.g. Lesser Antilles countries), fishing trips focus mainly on large pelagic fishes and flyingfish species (Mahon 1999; Mohammed *et al.* 2007a). For other Caribbean countries with extensive coastal shelves (e.g. Puerto Rico, the Virgin Islands), fishing is primarily targeting coastal species (reef fishes, demersal fishes crustaceans, coastal pelagics) and large pelagic fishes when they are available within the inshore areas (Mahon 1999; Mohammed *et al.* 2007a). The most common fishing gear used includes gillnets, trolling, longline, beach seines, purse seines, hooks and dredges (Opitz 1996; Cummings and Matos-Caraballo 2007; Mohammed *et al.* 2007a). In addition, large pelagics are targeted using smaller and larger vessels employing gillnets, troll nets and long-lines (Mahon and McConney 2004; Mohammed *et al.* 2007a).

The timeseries catch data (1987-2005) used in the developed model of the Caribbean ecosystem were obtained both from the report of *Lesser Antilles Pelagic Ecosystem* (LAPE) project (Mohammed *et al.* 2007a) and from the *Sea Around Us* database (unpublished database supplemented by Reg Watson of the *Sea Around Us* Project and [www.seaaroundus.org](http://www.seaaroundus.org)) (Tables 2-4). The LAPE fisheries report contained reported 2001-2005 landings within the Lesser Antilles countries' EEZ (Antigua and Barbuda, Barbados, Dominica, Grenada and the Grenadines, Guadeloupe, Martinique, St Kitts and Nevis, St Lucia, St Vincent, and Trinidad and Tobago) compiled from a number of different sources. In order to cover our entire study area, which encompassed but did not exactly match the LAPE project area, and to make the best use of data on timeseries of catches in the area for model analysis, we included catches from the *Sea Around Us Project* (SAUP) covering the earlier period of 1987-2004 (unpublished database supplemented by Reg Watson of the *Sea Around Us* Project and [www.seaaroundus.org](http://www.seaaroundus.org)). The latter also includes catches of foreign fleets fishing in the EEZs of Caribbean nations starting from 1987 to 2004. It should be noted that SAUP catch data for specific areas is derived using a complex set of databases to attribute specific catches reported to FAO back to their geographic origin (Watson *et al.* 2004). Local fleets were defined as all fisheries operated by countries encompassed by our study area, regardless of whether or not catches were taken within each country's own EEZ waters or neighboring waters. All other fishing countries were defined as foreign fleets. Local fleets included fisheries from Anguilla, Antigua and Barbuda, Barbados, British Virgin Islands, Dominica, Dominican Republic, Grenada and the Grenadines, Guadeloupe, Martinique, Montserrat, Puerto Rico, St Kitts and Nevis, St Lucia, St Vincent, and Trinidad and Tobago, and US Virgin Island. The foreign fleets fishing the region were primarily from USA and Puerto Rico, while only a very small percentage of catches in the area were made by fleets from Venezuela, Netherlands Antilles and Colombia. The comparison of both databases showed that the small and schooling pelagic group were harvested the most by both local (SAUP and LAPE databases) and foreign fleets (SAUP).

In order to combine fisheries catch data sets from LAPE and SAUP, we calculated the catch densities for each trophic group in the model. For example, local catches from 1987 to 2000 for each trophic group were taken from SAUP. These catches were then divided by the total Caribbean area defined for SAUP database extraction (7778039.50 km<sup>2</sup>). Local catches for the 2001-2005 periods were obtained from both LAPE database (for countries of the Lesser Antilles) and SAUP database for all remaining countries (local in our study area but not covered by LAPE). We divided their catch data for each trophic group by its total areas i.e. catches from *Sea Around Us Project* were divided by 7778039.50 km<sup>2</sup> and catches from LAPE fisheries report were divided by 610,000.00 km<sup>2</sup>. These catch densities were then summed by year and trophic groups resulting the total local catches for the 2001-2005 periods in our study area. Catch densities of foreign fleets were only available from the SAUP database, thus, we used these data sets for the period of 1987 to 2004 and calculated the catch densities for trophic groups accordingly.

Generally, local fleets (~ 87%) contributed largely to the overall catches in the Caribbean in comparison to the foreign fleets (~13%). The majority of these catches were comprised of the small and schooling pelagics, averaging 0.032 t\*yr\*km<sup>-2</sup> for local fleets, and 0.002 t\*yr\*km<sup>-2</sup> for foreign fleets in the Caribbean (Tables 5 and 6). According to Heileman-Manickchand (1992), huge quantities of small schooling pelagics (e.g. sardines, herrings) are caught in the region for bait in commercial and recreational fishing in the area, and some are utilized for canned and smoked products. Catches of crustaceans and benthos, scombrids, reef fishes, coastal predators and small tunas were also important in terms of tonnage for local fleets of the Caribbean region (Table 5), while for foreign fleets; these species were moderately important landings (Table 6). The local catches for cetaceans and seaturtles were low in the region (Table 5), and not recorded for foreign fleets (Table 6).

Fisheries catch trends of all trophic groups caught by local fleets in the area fluctuated considerably between 1987's to 2005's (Figure 2). The fluctuation hit its peak around 2003. After that peak, catch densities fell to a record low in 2005 (Figure 2). In contrast, the catch density trends for foreign fleets showed distinct fluctuation with two peaks around 1994 and 1997. They also had two major low points on 1996 and 1999. In the subsequent years catches of both local and foreign fisheries have decreased substantially.

**Table 2.** Local fleets' catches (tonnes) by trophic group in the Caribbean region. Catch data were derived from *Sea Around Us Project* supplemented by input provided by Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org).

	13	14	15	16	17	18	19	20	21	22	23	24	25
Year	Large tunas and billfishes	Small tunas	Dolphin-fish	Flying-fish	Other offshore predators	Pelagic sharks	Coastal sharks and rays	Scombrids	Small and schooling pelagics	Reef fishes	Coastal predators	Cephalopods	Crustaceans and benthos
1987	585.04	778.60	656.33	91.57	0.02	90.97	285.32	3435.73	17499.41	4696.55	2038.29	68.63	3097.91
1988	657.03	803.20	657.96	121.37	0.02	58.19	217.48	4014.71	11902.86	3580.05	2072.09	72.16	4239.27
1989	601.64	1218.37	749.14	28.04	0.03	55.74	256.94	4130.20	13886.08	4050.54	2368.14	88.70	7044.68
1990	691.44	1431.29	832.50	33.31	0.03	52.63	219.38	4092.50	13251.95	3828.67	2370.38	77.05	6946.97
1991	831.68	1311.43	873.63	85.53	0.03	80.24	265.54	3578.67	14443.72	4273.78	2181.19	81.06	7203.85
1992	859.04	1145.20	905.11	157.46	0.03	76.55	158.12	4318.24	12120.32	2982.40	2452.37	98.03	5921.84
1993	1022.77	1093.26	901.28	140.44	0.04	81.21	121.63	4148.43	11957.31	3453.40	2314.77	43.35	5894.89
1994	1015.47	1300.84	1160.77	83.87	0.05	69.03	155.78	3583.23	11058.42	5854.14	3412.48	37.57	7988.82
1995	967.07	1530.66	1089.53	99.56	0.05	73.54	198.93	4548.46	11509.30	5706.56	2822.23	61.26	5927.83
1996	890.67	1220.98	1238.78	133.23	0.06	57.72	167.25	4725.64	12455.30	2448.73	3121.59	69.48	4321.04
1997	724.62	1114.64	1248.20	77.73	0.06	60.59	204.10	4127.40	13776.04	3449.33	3054.46	54.53	5102.19
1998	548.37	1175.56	1001.51	182.08	0.04	65.77	174.86	3465.81	12163.74	1551.59	2329.85	141.44	6571.06
1999	423.74	867.24	1291.39	115.00	0.04	72.61	241.34	2741.91	13984.83	2246.66	1699.98	76.91	5471.79
2000	964.50	937.74	1305.87	143.41	0.03	61.77	220.42	3187.50	14159.13	2245.15	2611.97	176.97	7943.62
2001	323.16	344.26	141.55			4.33	92.28	504.20	4622.35	1989.00	2010.32	112.95	4653.39
2002	343.57	423.28	339.45			2.35	12.26	642.22	2466.69	2743.37	2679.67	141.83	6467.29
2003	803.17	426.06	119.81			1.94	89.93	629.27	6556.28	2541.70	3744.34	137.91	4680.39
2004	333.62	95.13	134.02				39.64	600.96	4893.51	1804.28	2388.27	89.67	4442.54

**Table 3.** Local fleets' catches (tonnes) by trophic group in Lesser Antilles. Catch data were derived from *LAPE* fisheries report by Mohammed *et al.* (2007a) .

	7	10	12	13	14	15	16	18	19	20	21	22	23	24
	Killer whales	Small ceta- ceans	Sea turtles	Large tunas and billfishes	Small tunas	Dolphin -fish	Flying- fish	Pelagic sharks	Coastal sharks and rays	Scom- brids	Small and schooling pelagics	Reef fishes	Coastal predators	Cepha- lopods
Year														
2001	7.87	13.54	7.00	1965.04	2752.12	2457.15	2085.67	102.77	893.90	3750.73	7688.02	226.44	417.01	5.00
2002	7.63	10.54	12.44	1553.25	3705.20	2396.07	1842.93	72.66	1210.22	3885.24	7475.29	232.08	529.36	3.00
2003	6.37	11.19	13.19	1955.43	2871.73	2082.34	2021.02	116.14	810.71	2973.89	7325.05	243.31	363.13	
2004	4.73	9.38	11.32	1805.02	2878.99	2173.95	1210.70	107.38	990.90	2935.74	7205.89	271.16	347.59	
2005	3.14	8.42	33.87	2189.97	2738.80	1875.68	1192.85	80.42	460.19	3399.43	6660.05	188.53	407.78	

**Table 4.** Foreign fleets' catches (tonnes) by trophic group in the Caribbean region. Catch data were derived from *Sea Around Us Project* supplemented by input provided by Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org).

Year	13 Large tunas and billfishes	14 Small tunas	15 Dolphin- fish	17 Other offshore predators	18 Pelagic sharks	19 Coastal sharks and rays	20 Scom- brids	21 Small and schooling pelagics	22 Reef fishes	23 Coastal predators	24 Cepha- lopods	25 Crustaceans and benthos
1987	456.29	23.48	7.52	140.74	7.85	90.21	607.06	2131.93	528.26	942.73	14.76	815.26
1988	400.86	34.73	13.38	135.00	23.57	177.54	616.97	2292.80	739.60	1096.68	10.47	876.53
1989	317.18	26.67	26.25	104.00	30.03	225.50	560.26	2300.13	903.05	1109.74	1.41	825.25
1990	165.53	33.47	30.50	118.35	26.77	188.53	571.57	2747.85	804.29	995.45	1.48	855.70
1991	158.59	39.51	40.14	111.94	21.54	144.48	579.12	2069.55	794.24	1020.75	16.63	1072.12
1992	308.97	71.63	21.49	92.81	32.04	159.15	601.10	1967.13	682.04	902.55	1.81	815.23
1993	135.48	53.91	21.07	86.59	29.47	123.31	740.98	2402.84	875.26	1173.11	298.09	2062.55
1994	116.88	34.38	26.33	131.65	52.35	535.05	700.53	1983.81	1130.24	3157.13	8.30	1337.35
1995	357.93	21.60	41.62	41.54	40.36	116.24	614.77	1928.09	723.24	891.40	12.92	1352.32
1996	97.90	18.35	31.39	10.24	13.36	46.59	186.35	1156.23	594.69	644.37	0.53	1115.07
1997	184.98	44.66	32.41	30.81	35.67	114.98	723.37	2411.06	576.01	862.41	9.02	1191.82
1998	114.96	36.83	13.68	31.74	39.05	115.26	690.34	1590.97	635.49	792.81	17.24	999.40
1999	95.88	27.81	23.57	21.92	25.37	69.39	441.22	504.63	157.47	509.66	7.87	896.25
2000	117.41	28.98	21.15	20.52	115.38	61.68	663.11	1163.59	742.75	757.01	4.71	820.54
2001	52.65	34.87	17.46	20.11	107.29	56.36	674.99	900.27	724.96	778.43	9.50	621.19
2002	64.21	38.47	16.52	17.87	37.14	74.95	640.93	1314.33	750.15	751.36	14.65	692.70
2003	66.44	55.77	16.18	17.60	43.36	81.49	720.55	995.19	755.43	817.45	9.98	1376.03
2004	64.89	20.17	16.14	32.49	64.27	192.47	787.79	919.15	680.26	772.56	3.04	709.48

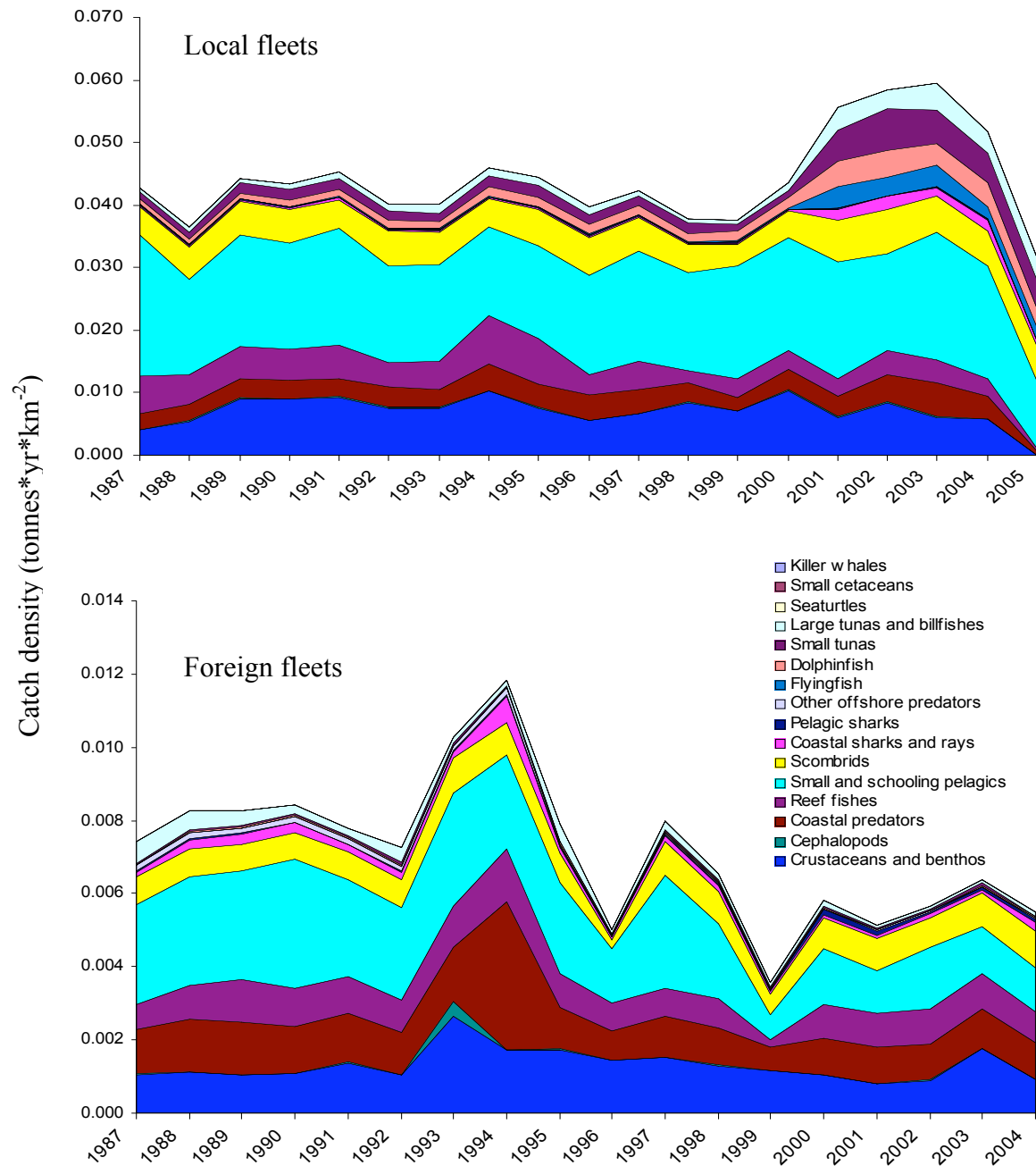
**Table 5.** Local fleets' catch densities (tonnes\*yr\*km<sup>-2</sup>) of each trophic group in the Caribbean. Data were derived from *Sea Around Us Project* (supplemented by input provided by Reg Watson of SAUP and [www.seararoundus.org](http://www.seararoundus.org)) and LAPE fisheries report (Mohammed *et al.* 2007a)

	7	10	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Year	Killer whales	Small cetaceans	Sea turtles	Large tunas and billfishes	Small tunas	Dolphin-fish	Flying-fish	Other offsh. predators	Pelagic sharks	Coastal sharks and rays	Scombrids	Small and school. pelagics	Reef fishes	Coastal pred.	Cephalopods	Crustaceans and benthos
1987				7.519E-04	1.001E-03	8.436E-04	1.177E-04	2.320E-08	1.169E-04	3.667E-04	4.416E-03	2.249E-02	6.036E-03	2.620E-03	8.821E-05	3.982E-03
1988				8.445E-04	1.032E-03	8.457E-04	1.560E-04	2.812E-08	7.480E-05	2.795E-04	5.160E-03	1.530E-02	4.601E-03	2.663E-03	9.275E-05	5.449E-03
1989				7.733E-04	1.566E-03	9.629E-04	3.605E-05	3.232E-08	7.164E-05	3.302E-04	5.308E-03	1.785E-02	5.206E-03	3.044E-03	1.140E-04	9.054E-03
1990				8.887E-04	1.840E-03	1.070E-03	4.282E-05	3.562E-08	6.764E-05	2.820E-04	5.260E-03	1.703E-02	4.921E-03	3.047E-03	9.903E-05	8.929E-03
1991				1.069E-03	1.686E-03	1.123E-03	1.099E-04	4.011E-08	1.031E-04	3.413E-04	4.600E-03	1.856E-02	5.493E-03	2.803E-03	1.042E-04	9.259E-03
1992				1.104E-03	1.472E-03	1.163E-03	2.024E-04	4.442E-08	9.839E-05	2.032E-04	5.550E-03	1.558E-02	3.833E-03	3.152E-03	1.260E-04	7.611E-03
1993				1.315E-03	1.405E-03	1.158E-03	1.805E-04	4.672E-08	1.044E-04	1.563E-04	5.332E-03	1.537E-02	4.439E-03	2.975E-03	5.572E-05	7.577E-03
1994				1.305E-03	1.672E-03	1.492E-03	1.078E-04	6.273E-08	8.872E-05	2.002E-04	4.605E-03	1.421E-02	7.524E-03	4.386E-03	4.828E-05	1.027E-02
1995				1.243E-03	1.967E-03	1.400E-03	1.280E-04	7.004E-08	9.452E-05	2.557E-04	5.846E-03	1.479E-02	7.335E-03	3.627E-03	7.874E-05	7.619E-03
1996				1.145E-03	1.569E-03	1.592E-03	1.712E-04	7.514E-08	7.419E-05	2.150E-04	6.074E-03	1.601E-02	3.147E-03	4.012E-03	8.930E-05	5.554E-03
1997				9.313E-04	1.433E-03	1.604E-03	9.990E-05	7.190E-08	7.788E-05	2.623E-04	5.305E-03	1.771E-02	4.433E-03	3.926E-03	7.009E-05	6.558E-03
1998				7.048E-04	1.511E-03	1.287E-03	2.340E-04	5.428E-08	8.453E-05	2.247E-04	4.455E-03	1.563E-02	1.994E-03	2.995E-03	1.818E-04	8.446E-03
1999				5.446E-04	1.115E-03	1.660E-03	1.478E-04	4.896E-08	9.332E-05	3.102E-04	3.524E-03	1.797E-02	2.888E-03	2.185E-03	9.885E-05	7.033E-03
2000				1.240E-03	1.205E-03	1.678E-03	1.843E-04	4.487E-08	7.939E-05	2.833E-04	4.097E-03	1.820E-02	2.886E-03	3.357E-03	2.275E-04	1.021E-02
2001	1.290E-05	2.219E-05	1.148E-05	3.637E-03	4.954E-03	4.210E-03	3.419E-03		1.740E-04	1.584E-03	6.797E-03	1.854E-02	2.928E-03	3.267E-03	1.534E-04	5.981E-03
2002	1.252E-05	1.728E-05	2.039E-05	2.988E-03	6.618E-03	4.364E-03	3.021E-03		1.221E-04	2.000E-03	7.195E-03	1.542E-02	3.906E-03	4.312E-03	1.872E-04	8.312E-03
2003	1.043E-05	1.834E-05	2.162E-05	4.238E-03	5.255E-03	3.568E-03	3.313E-03		1.929E-04	1.445E-03	5.684E-03	2.043E-02	3.666E-03	5.408E-03	1.772E-04	6.016E-03
2004	7.761E-06	1.537E-05	1.855E-05	3.388E-03	4.842E-03	3.736E-03	1.985E-03		1.760E-04	1.675E-03	5.585E-03	1.810E-02	2.764E-03	3.639E-03	1.153E-04	5.710E-03
2005	5.141E-06	1.380E-05	5.553E-05	3.590E-03	4.490E-03	3.075E-03	1.955E-03		1.318E-04	7.544E-04	5.573E-03	1.092E-02	3.091E-04	6.685E-04		

**Table 6.** Foreign fleets' catch densities (tonnes\*yr\*km<sup>-2</sup>) of each trophic group in the Caribbean. Data were derived from *Sea Around Us* supplemented by input provided from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org).

	13	14	15	17	18	19	20	21	22	23	24	25
Year	Large tunas and billfishes	Small tunas	Dolphin-fish	Other offshore predators	Pelagic sharks	Coastal sharks and rays	Scombrids	Small and schooling pelagics	Reef fishes	Coastal predators	Cephalopods	Crustaceans and benthos
1987	0.000586	0.000030	0.000010	0.000181	0.00001	0.00012	0.00078	0.00274	0.000679	0.001212	1.89732E-05	0.00104784
1988	0.000515	0.000045	0.000017	0.000174	0.00003	0.00023	0.000793	0.002947	0.000951	0.00141	1.34629E-05	0.00112659
1989	0.000408	0.000034	0.000034	0.000134	0.00004	0.00029	0.00072	0.002956	0.001161	0.001426	1.81754E-06	0.00106068
1990	0.000213	0.000043	0.000039	0.000152	0.00003	0.00024	0.000735	0.003532	0.001034	0.001279	1.90863E-06	0.00109982
1991	0.000204	0.000051	0.000052	0.000144	0.00003	0.00019	0.000744	0.00266	0.001021	0.001312	2.13798E-05	0.00137798
1992	0.000397	0.000092	0.000028	0.000119	0.00004	0.00020	0.000773	0.002528	0.000877	0.00116	2.33207E-06	0.00104781
1993	0.000174	0.000069	0.000027	0.000111	0.00004	0.00016	0.000952	0.003088	0.001125	0.001508	0.000383128	0.00265096
1994	0.00015	0.000044	0.000034	0.000169	0.00007	0.00069	0.0009	0.00255	0.001453	0.004058	1.0674E-05	0.00171887
1995	0.00046	0.000028	0.000053	5.34E-05	0.00005	0.00015	0.00079	0.002478	0.00093	0.001146	1.66035E-05	0.00173811
1996	0.000126	0.000024	0.000040	1.32E-05	0.00002	0.00006	0.00024	0.001486	0.000764	0.000828	6.83352E-07	0.00143318
1997	0.000238	0.000057	0.000042	3.96E-05	0.00005	0.00015	0.00093	0.003099	0.00074	0.001108	1.15883E-05	0.00153183
1998	0.000148	0.000047	0.000018	4.08E-05	0.00005	0.00015	0.000887	0.002045	0.000817	0.001019	2.21631E-05	0.00128451
1999	0.000123	0.000036	0.000030	2.82E-05	0.00003	0.00009	0.000567	0.000649	0.000202	0.000655	1.01135E-05	0.00115193
2000	0.000151	0.000037	0.000027	2.64E-05	0.00015	0.00008	0.000852	0.001496	0.000955	0.000973	6.04873E-06	0.00105463
2001	6.77E-05	0.000045	0.000022	2.58E-05	0.00014	0.00007	0.000868	0.001157	0.000932	0.001001	1.22057E-05	0.0007984
2002	8.25E-05	0.000049	0.000021	2.3E-05	0.00005	0.00010	0.000824	0.001689	0.000964	0.000966	1.88268E-05	0.00089032
2003	8.54E-05	0.000072	0.000021	2.26E-05	0.00006	0.00010	0.000926	0.001279	0.000971	0.001051	1.2821E-05	0.00176859
2004	8.34E-05	0.000026	0.000021	4.18E-05	0.00008	0.00025	0.001013	0.001181	0.000874	0.000993	3.91262E-06	0.00091188





**Figure 2.** Trophic groups catch densities for local fleets (1987-2005) and foreign fleets (1987-2004) in the Caribbean region. Data derived from SAUP (supplemented by data provided by Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)) and LAPE fisheries report (Mohammed *et al.* 2007a)

## BALANCED ECOSYSTEM MODEL FOR THE CARIBBEAN REGION

### *Groups 1 - 10. Marine mammals*

Ten groups of marine mammals were added to the original model for our study. Given the lack of local, long-term dedicated surveys to provide reliable cetacean abundance estimates, density estimates had to be derived from a global database (Kaschner 2004). However, comparison with other densities from surveys conducted in similar habitats are ground-truthing these estimates (Table 7). These biomasses, P/B and diet are described below for each group, followed by a section on how we calculated food consumption (Q/B) for these ten groups. As mentioned above, no official timeseries records of annual catches for marine mammals, excluding killer whales and small cetacean species, were found in the region.

**Table 7:** Comparison of predicted cetacean densities in Caribbean waters based on global model developed by Kaschner et al (2006) and Kaschner (2004) and observed minimum and maximum densities in similar habitats (subtropical & tropical waters). A = aerial surveys, S = ship based surveys. Density estimates that are corrected for animals missed on the track-line are indicated in the G(o) corrected column. All other observed estimates might represent underestimations.

Common Name	Estimated density [animals / 1000 km <sup>2</sup> ]	Observed density [animals / 1000 km <sup>2</sup> ]	CV	G(o) corrected	Geographic area	Survey years	Survey type	Source
Blue whale	0.02	0.07	0.24	no	Eastern Tropical Pacific	1986-1990	S	Wade and Gerrodette 1993
Blue whale	0.02	4.96	0.13	yes	NE Pacific, California inshore	1991-1996	S	Calambokidis and Barlow 2004
Bryde's whale	0.28	0.67	0.20	no	Eastern Tropical Pacific	1986-1990	S	Wade and Gerrodette 1993
Bryde's whale	0.28	0.04	0.85	no	NW Atlantic, northern Gulf of Mexico (GulfCet I survey)	1991-1994	S	Davis and Fargion 1996
Fin whale	0.22	1.85	0.48	no	NW Atlantic, Virginia Capes	2002	S	Garrison et al. 2003
Fin whale	0.22	0.07	0.72	yes	NE Pacific, Hawaiiin waters	2002	S	Barlow 2003a
Humpback whale	6.50	0.03	0.37	yes	NE Pacific, California offshore	1991-1996	S	Calambokidis and Barlow 2004
Humpback whale	6.50	112.32	0.27	no	SW Indian Ocean, Madagascar (southern block)	1994	S	Best et al. 1996
Minke whale	0.73	0.93	0.51	yes	NE Pacific, west coast US	1996	S	Barlow 2003b
Minke whale	0.73	0.03	1.29	no	NW Atlantic, US east coast, south of Maryland	1998	S	Mullin and Fulling 2003
Sei whale	0.05	0.10	0.73	yes	NE Pacific, west coast US	1996	S	Barlow 2003b
Sei whale	0.05	0.03	1.01	yes	NE Pacific, west coast US	2001	S	Barlow 2003b
Killer whale	0.06	0.14	0.98	yes	NE Pacific, Hawaiiin waters	2002	S	Barlow 2006
Killer whale	0.06	0.79	0.48	no	NW Atlantic, northern Gulf of Mexico (GulfCet I survey)	1991-1994	S	Davis and Fargion, 1996
Sperm whale	1.03	0.85	0.57	no	NW Atlantic, northern Gulf of Mexico (GulfCet I EPA survey)	1996-1997	S	Davis et al. 2000
Sperm whale	1.03	3.80	0.23	no	NW Atlantic, northern Gulf of Mexico (SEFSC)	1996-2001	S	Mullin and Fulling 2004

## 1. Minke whales

Although this represents probably the southern most extent of this species distributional range, minke whales are seasonally found in the northwestern Caribbean during the breeding period (Klinowska 1991; Perrin *et al.* 2002). Their annual abundance in the region was estimated to be 1,352 individuals, translating to a density of 0.73 individuals per 1000 km<sup>2</sup> and representing a total annual biomass of 8,882 tonnes, or biomass density of 0.0045 t\*km<sup>-2</sup> annually based on a global model of cetacean densities developed by Kaschner (2004). The predicted densities (individuals per 1000 km<sup>2</sup>) were within the range of observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 7).

The reported general annual mortality of minke whales ranges from 0.09 to 0.10 yr<sup>-1</sup> in Northeast Atlantic (Evans 1998). We assumed that this mortality rate of minke whales would also apply in the Caribbean region. Since the annual mortality rate is equal to the production to biomass (P/B) ratio (Allen 1971), an annual mortality rate of 0.099 yr<sup>-1</sup> was used as the P/B input for minke whales in the present model. This value was also used for minke whales in Alaska (Guénette *et al.* 2006) and in Northwest African model (Morissette *et al.* submitted)

There was no appropriate quantitative diet information available for minke whales in the Caribbean region. Hence, we used the available data for this species from North Atlantic (Table 8). Minke whale diet information from the different published studies was redistributed to match our pre-defined trophic groups. These were then weighted, based on the proportion of prey wet weight over the overall prey weights in whale's stomach. Most of the minke whales' diet (49.0%) was composed of small and schooling pelagics followed by zooplankton (25.9%), coastal predators (12.1%), other offshores pelagics (9.8%) and scombrids (3.2%) (Table 7).

**Table 8.** Available information on the diet composition of minke whales in the Caribbean. The average diet was used in the *Ecopath* model for the Caribbean ecosystem.

Source	Areas	17 Other offshore predators	20 Scombrids	21 Small and schooling pelagics	23 Coastal predators	26 Zooplank- ton	Total
Lydersen <i>et al.</i> 1991	Norway	0.084		0.916			1.000
Nørdoy and Blix 1992	Northeastern Atlantic	0.078		0.501		0.421	1.000
Haug <i>et al.</i> 1995	Norwegian waters	0.126		0.708	0.084	0.082	1.000
Haug <i>et al.</i> 1996	Northeast Atlantic	0.343		0.388	0.026	0.244	1.000
Olsen and Holst 2001	North Sea	0.029	0.093	0.011	0.867		1.000
	Norwegian Sea			1.000			1.000
Sivertsen <i>et al.</i> 2006	Barent Sea	0.090		0.433		0.477	1.000
Smout and Lindstrom 2007	Norwegian Sea			0.261		0.739	1.000
	Bear Island	0.096		0.504		0.400	1.000
	North Sea	0.087	0.317		0.597		1.000
Windsland <i>et al.</i> 2007	Norwegian Sea	0.036		0.916		0.049	1.000
	Southern Barent Sea	0.247		0.713	0.004	0.036	1.000
	Spitsbergen	0.062		0.016		0.922	1.000
<b>Average Minke whale diet</b>		<b>0.098</b>	<b>0.032</b>	<b>0.490</b>	<b>0.121</b>	<b>0.259</b>	<b>1.000</b>

## 2. Fin whales

Fin whales, breeding in the Caribbean ecosystem are typically migrants from the North Atlantic (Klinowska 1991; Perrin *et al.* 2002), although, like the minke whales, this species is probably only found rarely as far south as our study area. During the recent cetaceans sighting survey by NOAA Gordon Gunter, one fin whale was sighted in the Lesser Antilles waters (Mohammed *et al.* 2007b).

According to the quantitative estimates by Kaschner (2004), approximately 139 fin whales occur annually in the Caribbean, representing a density of 0.22 individuals per 1000 km<sup>2</sup> and an annual biomass of 7742 tonnes or average annual biomass density of 0.0062 t\*km<sup>-2</sup>. The predicted density (individuals per 1000 km<sup>2</sup>) was in the same range as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 7).

Here again, we used the total annual mortality rate as the P/B input in the model, following Allen (1971). Different studies reported the natural mortality rates ranging from 0.4 yr<sup>-1</sup> to 0.5 yr<sup>-1</sup> for adult fin whales (Clarke 1982; de la Mare 1985; Perry *et al.* 1999). Perry *et al.* (1999) stated that this rate may be higher if immature whales of both sexes were included. On the other hand, Heymans (2005) used P/B ratio of 0.099 yr<sup>-1</sup> for fin whales in Aleutian Islands and in the Gulf of Alaska. We used this value in the present model and assumed it to be constant as well in the Caribbean. The same P/B ratio value for fin whales was used as well by Morissette *et al.* (submitted) in Northwest Africa model.

In the absence of diet information for fin whales in the Caribbean, we used diet information for this species that was available from Icelandic waters Sigurjónsson and Víkingsson (1997). Based on that, it was thus assumed that fin whales eat 98.4% zooplankton, 1.4% coastal pelagics and 0.2% coastal predators (Table 9). Note that a small proportion of 'mixture remains' identified by Sigurjónsson and Víkingsson (1997) were not included herein because this represents unknown prey type.

**Table 9.** Diet composition of fin whales used for *Ecopath* modelling in the Caribbean ecosystem.

Source	Areas	21 Small schooling pelagics	23 and Coastal predators	26 Zooplankton	Total
Sigurjónsson and Víkingsson 1997	Icelandic adjacent waters	0.014	0.002	0.984	1.000

### 3. Humpback whales

Known breeding areas of the north Atlantic humpback whale population include a number of areas in and around the Lesser Antilles, Dominican Republic, Puerto Rico, the Virgin Islands and the South Grenadines (Katona and Beard 1990; Klinowska 1991; Debrot *et al.* 1998; Perry *et al.* 1999; Reeves *et al.* 2001; Romero *et al.* 2001; Swartz *et al.* 2003). This whale species calves in the Caribbean ecosystem from January to May (Debrot *et al.* 1998; Reeves *et al.* 2001; Romero *et al.* 2001; Swartz *et al.* 2003). All individuals from the total North Atlantic population of this species [about 10,750 whales estimated by Stevick *et al.* (2003), translating to 6.50 individuals per 1000 km<sup>2</sup>, and representing 326,888 tonnes in biomass] are thought to migrate to the Caribbean for breeding at some stage during the winter. However, since the species occurrence in the area is restricted to about five months (Reeves *et al.* 2001), we calculated annual biomass density proportionally, thus obtaining an estimate of 0.0696 t\*km<sup>-2</sup>. The latter value was used in the present model as the overall annual biomass density of humpback whales in the Caribbean ecosystem, and is similar to the range of observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 7).

Similar to other baleen whale species, P/B ratio of 0.099 used by Heymans (2005) in Aleutian Islands and in the Gulf of Alaska was used for humpback whale in our model. This value was assumed to be similar in the Caribbean region as well.

Romero *et al.* (2001) stated that humpback whales do not feed in the Caribbean region, and no diet information of this species could be found for the region. We, therefore, used two available quantitative diet studies providing diet information in wet weight available for humpback whales: one by Witteveen *et al.* (2006) in Kodiak, Alaska, and the other one by Mitchell (1973) in Canadian waters which was then used by Sigurjónsson and Víkingsson (1997) in Icelandic waters. We incorporated the "fish" and "krill" ratio of 60:40 from Mitchell (1973) obtained in the Canadian waters to quantify the trophic groups used in the present model that were based on the more recent and detailed humpback fish prey list found in Witteveen *et al.* (2006). Thus, the diet of humpback whales in the Caribbean model was assumed to be 40.0% zooplankton, 34.3% small and schooling pelagics, 8.6% other offshore pelagics and 1.7% coastal predators (Table 10).

**Table 10.** Diet composition of humpback whales used for *Ecopath* model in the Caribbean.

Source	Areas	17 Other offshore predators	21 Small and schooling pelagics	23 Coastal predators	26 Zooplankton	Total
Sigurjónsson Vikingsson 1997	and Icelandic and adjacent waters	0.086	0.343	0.171	0.400	1.000

#### 4. Bryde's whales

Bryde's whales are the only species of baleen whales known to occur year-round in the Caribbean region, particularly in the southeastern Caribbean (Klinowska 1991; Debrot *et al.* 1998; Romero *et al.* 2001). Bryde's whales are usually found off Venezuela, and often associated with schools of *Sardinella anchovia* (Romero *et al.* 2001). The annual abundance of this species in our study area was estimated to be 524 whales representing a density of 0.28 individuals per 1000 km<sup>2</sup> and a total biomass 8,463 tonnes or an annual biomass density of 0.0043 t\*km<sup>-2</sup> based on the global density estimates by Kaschner (2004). Predicted and observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats were similar in terms of magnitude (Table 7).

In general, P/B ratios for baleen whales used in the *Ecopath* models in other ecosystems ranged from 0.02 yr<sup>-1</sup> to 0.099 yr<sup>-1</sup> (Pauly *et al.* 1996; Trites and Heise 1996; Zeller and Freire 2001; Okey *et al.* 2004; Guénette *et al.* 2006). Since there was no P/B ratio available, specifically for Bryde's whales; hence, we took an average value of 0.05 yr<sup>-1</sup> based on all reported other baleen whales P/B ranges. We used the latter value in the present model representing Bryde's whales in the Caribbean ecosystem.

Bryde's whale diet information was taken from the Gulf of California, Mexico (Tershy 1992) and Lesser Antilles pelagic ecosystem (Heileman *et al.* 2007). This species primarily feeds on small and schooling pelagics (53.6.5%), zooplankton (24.5%) and other offshores pelagics (14.9%). They also feed occasionally on scombrids fishes (7.0%) (Tershy 1992; Heileman *et al.* 2007) (Table 11).

**Table 11.** Available information on Bryde's whales' diet composition used in the *Ecopath* model for the Caribbean ecosystem.

Source	Areas	17 Other offshore predators	20 Scombrids	21 Small schooling pelagics	26 Zooplankton	Total
Tershy 1992	Gulf of California, Mexico			0.886	0.114	1.000
Heileman <i>et al.</i> 2007	Lesser Antilles	0.297	0.141	0.187	0.375	1.000
<b>Average Bryde's whale diet</b>		<b>0.149</b>	<b>0.070</b>	<b>0.536</b>	<b>0.245</b>	<b>1.000</b>

#### 5. Sei whales

The sei whales are known to regularly occur around Caribbean islands area during its breeding period (Klinowska 1991; Perrin 2002). We used an annual abundance estimate of 99 whales occurring in the region, representing a density of 0.05 individuals per 1000 km<sup>2</sup> for a total biomass of 1,667 tonnes or an annual biomass density of 0.0009 t\*km<sup>-2</sup> (Kaschner 2004). The predicted densities (individuals per 1000 km<sup>2</sup>) were similar in terms of magnitude as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 7).

The P/B for sei whales in the Caribbean ecosystem was assumed to be similar to what was used for this species in the Alaska Gyre ecosystem (Pauly *et al.* 1996), which was 0.0200 yr<sup>-1</sup>.

In the absence of any diet information for sei whale in the Caribbean region, we incorporated the sei whale diet information from Sigurjónsson and Vikingsson (1997) in Icelandic waters. Sei whales' diet

was composed of zooplankton (98.0%), other offshore predators (0.67%), small and schooling pelagics (0.67%) and coastal predators (0.67%) (Table 12).

**Table 12.** Available information on the dietary composition of sei whale used in the *Ecopath* model for the Caribbean.

Source	Areas	17 Other offshore predators	21 Small and schooling pelagic	23 Coastal predators	26 Zooplankton	Total
Sigurjónsson and Víkingsson 1997	Icelandic and adjacent waters	0.0067	0.0067	0.0067	0.980	1.000

## 6. Blue whales

Similar to the other large whales, the blue whales, *Balaenoptera musculus*, are also found in the Caribbean during the breeding period (Klinowska 1991). Based on the estimated global densities provided by Kaschner (2004), the annual abundance of blue whales in the study area was approximately 47 whales representing a density of 0.02 individuals per 1000 km<sup>2</sup> for a total biomass 4,852 tonnes and an annual biomass density of 0.0025 t\* km<sup>-2</sup>. The predicted density (individuals per 1000 km<sup>2</sup>) was similar in terms of magnitude as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats and showed in Table 7.

We used an average P/B value of 0.06 yr<sup>-1</sup> for baleen whales in the Caribbean, based on that of several baleen whales groups from other *Ecopath* models (Pauly *et al.* 1996; Okey *et al.* 2004; Guénette *et al.* 2006). This P/B ratio was also used for the same species in Northwest Africa (Morissette *et al.* submitted).

Quantitative diet information for blue whales was lacking in the Caribbean region. Thus, we used the information used by Sigurjónsson and Víkingsson (1997) in Icelandic waters to calculate the diet of baleen whales. The blue whales in North Atlantic mainly consumed zooplankton (i.e. krill) (Table 13). This finding was affirmed by several experts (e.g. Hjort and Ruud 1929; Klinowska 1991; Christensen *et al.* 1992; Tershy 1992; Pauly *et al.* 1998b; Hewitt and Lipsky 2002; Sears 2002) that have described blue whales ecology and distribution.

**Table 13.** Available information on the dietary composition of blue whale used in the *Ecopath* model for the Caribbean.

Source	Areas	26 Zooplankton	Total
Sigurjónsson and Víkingsson 1997	Icelandic and adjacent waters	1.000	1.000

## 7. Sperm whales

Based on life history similarities, we combined the following three species into a single trophic group: *Kogia breviceps* (pygmy sperm whales), *Kogia simus* (dwarf sperm whales) and *Physeter macrocephalus* (sperm whales). These species are frequent in the Caribbean ecosystem from October to March (Debrot *et al.* 1998; Mohammed *et al.* 2007b) and rarely present during the summer months (Northridge 1984). The sperm whales are distributed in the deeper basins of the Caribbean Sea and the Gulf of Mexico (Klinowska 1991; Perry *et al.* 1999). Their annual abundance in the Caribbean was 2,154 whales, for a density of 1.03 individuals per 1000 km<sup>2</sup>, and an annual biomass of 36,904 tonnes or an annual biomass density of 0.0188 t\*km<sup>-2</sup> (Kaschner 2004). This estimated density (in individuals per 1000 km<sup>2</sup>) is similar in terms of magnitude as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 7).

The annual total mortality rate for sperm whales species in the Caribbean region was 0.05 yr<sup>-1</sup> (Perry *et al.* 1999) and was used as the P/B inputs in the present model after Allen (1971). This value falls within the reported mortality rates for different sexes and life stages of sperm whales in the similar ecosystems ranging from 0.05 yr<sup>-1</sup> to 0.09 yr<sup>-1</sup> (Evans 1998; Perry *et al.* 1999).

In the Caribbean region and surrounding areas, sperm whales were documented to feed primarily on cephalopods species (99.6%); and rarely on crustaceans and benthos (0.4%) and other offshore pelagics (<0.01%) (Table 14). These diet values were weighted based on the estimated consumption of each species of sperm whales.

**Table 14.** Available information on the diet composition of sperm whales used in the *Ecopath* model for the Caribbean ecosystem.

Source	Whale species	Areas	17 Other offshore predators	24 Cephalopods	25 Crustaceans and benthos	Total
dos Santos and Haimovici 2001	<i>Kogia breviceps</i>	Southern Brazil Galicia (NW)		1.000		1.000
Santos <i>et al.</i> 2006	<i>Kogia breviceps</i>	Spain)	0.0003	0.999	0.00008	1.000
Santos <i>et al.</i> 2006	<i>Kogia breviceps</i>	France		0.833	0.167	1.000
Santos <i>et al.</i> 2006	<i>Kogia breviceps</i>	Scotland (UK)		1.000		1.000
Kawakami 1980	<i>Physeter macrocephalus</i>	Peru		1.000		1.000
Kawakami 1980	<i>Physeter macrocephalus</i>	Chile		1.000		1.000
Clarke <i>et al.</i> 1980	<i>Physeter macrocephalus</i>	Brazil Patagonia,		1.000		1.000
Pascoe <i>et al.</i> 1990	<i>Physeter macrocephalus</i>	Argentina		1.000		1.000
Smith and Whitehead 2000	<i>Physeter macrocephalus</i>	Galapagos, Ecuador		1.000		1.000
Hickmott 2005	<i>Physeter macrocephalus</i>	Northern Bahamas		0.977	0.023	1.000
<b>Weighted average diet for Sperm whales</b>			<b>&lt;0.0001</b>	<b>0.996</b>	<b>0.004</b>	<b>1.000</b>

## 8. Killer whales

The species *Feresa attenuata* (pygmy killer whale), *Orcinus orca* (killer whales) and *Pseudorca crassidens* (false killer whale) were combined into single killer whales group. All three species occur throughout the Gulf of Mexico and around the Lesser Antilles (Klinowska 1991; Mohammed *et al.* 2007b). Debrot *et al.* (1998) reported that killer whale species occur almost throughout the year in the southeastern Caribbean. The combined annual abundance of all three species in this group in the Caribbean region was estimated to be 1,076 individuals (or 0.06 individuals per 1000 km<sup>2</sup>) with a total annual biomass of 574 tonnes or an annual biomass density of 0.0003 t\*km<sup>-2</sup> based on the quantitative estimates by Kaschner (2004). The annual catch density of killer whale species in the region was 0.00001 t\*km<sup>-2</sup> (Mohammed *et al.* 2007a). Predicted density (individuals per 1000 km<sup>2</sup>) was similar in terms of magnitude as observed densities reported from dedicated marine mammals surveys conducted in other areas with similar habitats (Table 7).

The P/B ratio input we used for killer whales was 0.02 yr<sup>-1</sup>, the same value that was used by Trites and Heise (1996), Sidi and Guénette (2004); and Mohammed *et al.* (2007b) for killer whales in other *Ecopath* models.

Diet information for killer whales diet information was obtained from the Strait of Magellan, Tierra Del Fuego (Alonso *et al.* 1999), Icelandic waters (Sigurjónsson and Víkingsson 1997) and Lesser Antilles pelagic waters (Heileman *et al.* 2007). The diet composition of killer whales consisted of 36.5% cephalopods, 26.4% small and schooling pelagics, 15.0% small cetaceans, 14.6% other offshore pelagics and 7.5% zooplankton. These diet proportions were adjusted based on the estimated consumption of each killer whale species (Table 15).



**Table 15.** Diet composition of killer whales used for the *Ecopath* model in the Caribbean ecosystem.

Source	Whale species	Areas	10 Small cetaceans	17 Other offshore predators	21 Small and schooling pelagics	24 Cephalo- pods	26 Zooplan- kton	Total
Alonso <i>et al.</i> 1999	<i>Pseudorca crassidens</i>	Tierra Fuego (Chile)		0.249		0.751		1.000
Sigurjónsson and Víkingsson 1997	<i>Orcinus orca</i>	Icelandic waters			1.000			1.000
Heileman <i>et al.</i> 2007	<i>Orcinus orca</i> , <i>Feresa attenuata</i>	Lesser Antilles	0.300	0.15	0.100	0.300	0.150	1.000
<b>Weighted average diet for Killer whales</b>			<b>0.15</b>	<b>0.146</b>	<b>0.264</b>	<b>0.365</b>	<b>0.075</b>	<b>1.000</b>

### 9. Beaked whales

Three species of beaked whales were included in this group: Blainville's (*Mesoplodon densirostris*), Gervais' (*Mesoplodon europaeus*) and Cuvier's (*Ziphius cavirostris*) beaked whales. Beaked whale species are known to occur widely throughout the Caribbean ecosystem in spring and summer months (Debrot *et al.* 1998). The total annual abundance in the Caribbean ecosystem was estimated to be 264 beaked whales amounting a total annual biomass of 168 tonnes or an average annual biomass density of  $0.00013 \text{ t} \cdot \text{km}^{-2}$  (Kaschner 2004).

The P/B ratio of  $0.036 \text{ yr}^{-1}$  was used in the present model, based on what was used by Guénette *et al.* (2006) in Alaskan ecosystem.

Diet information of beaked whale species were obtained from whales strandings in Curacao (Debrot and Barros 1992), western Mediterranean (Blanco and Raga 2000), Northwest Spain and Scotland (Santos *et al.* 2001), Northern Bahamas (Hickmott 2005) and Canary Island (Santos *et al.* 2007). All prey items of beaked whales taken from different sources were weighted based on the estimated consumption of each species of beaked whales. These weighted prey items of beaked whales' species were averaged, and then summed to represent the prey items of our three beaked whale's species. As a result, we found that beaked whales in the Caribbean fed mostly on cephalopods (68.7%) followed by other offshores pelagics (17.8%), crustaceans and benthos (8.9%) and zooplankton (4.6%) (Table 16).

**Table 16.** Available information on the diet composition of beaked whales: Cuvier's beaked whales, Blainvilles beaked whales and Gervais beaked whales, in the Caribbean region. A weighted average diet (based on the percentage of food consumption by each species) was used in the *Ecopath* model for the Caribbean ecosystem.

Source	Whale species	Areas	17 Other offshore predators	24 Cephalopods	25 Crustaceans and benthos	26 Zooplankton	Total
Hickmott 2005	<i>Mesoplodon densirostris</i>	Northern Bahamas	0.500	0.500			1.000
Santos <i>et al.</i> 2007	<i>Mesoplodon densirostris</i>	Canary Island	0.848	0.152			1.000
Debrot and Barros 1992	<i>Mesoplodon europaeus</i>	Curacao	0.124	0.433		0.443	1.000
Blanco and Raga 2000	<i>Ziphius cavirostris</i>	Western Mediterranean		1.000			1.000
Santos <i>et al.</i> 2001	<i>Ziphius cavirostris</i>	Northwest Spain		1.000			1.000
Santos <i>et al.</i> 2001	<i>Ziphius cavirostris</i>	North (Scotland) Uist		1.000			1.000
Hickmott 2005	<i>Ziphius cavirostris</i>	Northern Bahamas		0.316	0.684		1.000
Santos <i>et al.</i> 2007	<i>Ziphius cavirostris</i>	Canary Island		0.9999	0.00014		1.000
<b>Weighted average diet for Beaked whales</b>			<b>0.178</b>	<b>0.687</b>	<b>0.089</b>	<b>0.046</b>	<b>1.000</b>

### 10. Small cetaceans

A total of 13 species of small cetaceans were included and aggregated into one group in our model (Table 1). These were *Delphinus capensis*, *Delphinus delphis*, *Globicephala macrorhynchus*, *Grampus griseus*, *Lagenodelphis hosei*, *Sousa teuszii*, *Stenella attenuata*, *S. clymene*, *S. coeruleoalba*, *S. frontalis*, *S. longirostris*, *Steno bredanensis* and *Tursiops truncatus*. Some of these species migrate seasonally into the waters of the Caribbean ecosystem, but many can be found in the area throughout the year (Debrot *et al.* 1998; Mohammed *et al.* 2007b). Their combined annual average abundance was estimated to be 115,963 individuals amounting to a total annual biomass of 10,467 tonnes and an average annual biomass density of 0.0053 t\*km<sup>-2</sup> based on the quantitative estimates by Kaschner (2004). The small cetacean species are caught rarely for fisheries in the region with an annual catch density of 0.00002 t\*km<sup>-2</sup> (Mohammed *et al.* 2007a)

The production to biomass ratio of small cetaceans in the Caribbean ecosystem is 0.03 yr<sup>-1</sup> (Mohammed 2003a). This value was incorporated in the present model and was assumed to be representative of small cetaceans P/B ratio for the entire Caribbean ecosystem.

Diet information for small cetaceans was derived from the results of Lesser Antilles pelagic ecosystem (Heileman *et al.* 2007). Diet inputs in the latter study were originally obtained from the marine mammal's diet composition study by Pauly *et al.* (1998b) (Table 17). Heileman *et al.* (2007) weighted these diet compositions by small cetaceans biomass sighted during their Lesser Antilles cetacean survey. In the same study, an import value in small cetacean's diet was assumed, suggesting that this group feed outside the Lesser Antilles system. However, in our model, we assumed that small cetaceans feed within the Caribbean region and thus, its diet import value from Heileman's *et al.* (2007) was redistributed equally to the prey trophic groups of small cetaceans. As a result, small cetaceans diets were composed of 58.73% cephalopods, 37.04% other offshore predators, 4.22% small and schooling pelagics and 0.01% small cetaceans.

**Table 17.** Available information on the diet composition of small cetaceans in the Caribbean region. A weighted average diet (based on the percentage of food consumption by each species) was used in the *Ecopath* model for the Caribbean ecosystem.

Source	Areas	17 Small cetaceans	22 Other offshore pelagics	25 Small schooling and pelagics	26 Cephalopods	Total
Heileman <i>et al.</i> 2007	Lesser Antilles	0.0001	0.3704	0.0422	0.5873	1.000

### Food consumption by marine mammals

Kaschner (2004) developed a basic food consumption model based on Trites *et al.* (1997). This model was used to generate the biomass and consumption (Q/B) values needed for each *Ecopath* group. Annual food consumption was calculated as:

$$Q_i = 365 * \sum_s N_{i,s} R_{i,s}$$

where  $Q$  of species  $i$  was assumed to be 365 times the daily food consumption. Daily food consumption was calculated based on the number of individual  $N$  of sex  $s$  of a species  $i$ , and a weight-specific daily ration  $R$  calculated based on the mean individual body mass  $W$  of sex  $s$  belonging to species  $i$ , consumed by each individual of species  $i$  and sex  $s$ .

Abundances and sex ratios were taken directly from the Kaschner (2004) database. Mean species and sex-specific body mass was taken from Trites and Pauly (1998). For all cetaceans, except baleen whales, we used the empirical model developed by Innes *et al.* (1987) to estimate food consumption of cetaceans that was later modified by Trites *et al.* (1997) to account for the difference between consumption for growth and for maintenance and then applied to all marine mammal species. Food intake of specific species per day was calculated using:

$$R_{i,s} = 0.1 * W_{i,s}^{0.8}$$

where  $R$  is the daily food intake of an individual of sex  $s$  belonging to species  $i$  and  $W$  is the mean body weight of that individual, in kilograms.

For all baleen whales daily food ration was estimated based on a model by Armstrong and Siegfried (1991) for food consumption of minke whales in the Antarctic. These authors suggested a modification to the empirical model of Innes *et al.* (1986) equation for baleen whales to account for larger body sizes and seasonal variation in food intake. This approach was later used to estimate food consumption of whales around Iceland (Sigurjónsson and Víkingsson 1997) and represents one of the methods used by Tamura (2003) to estimate global food intake of cetaceans. This feeding rate is calculated as:

$$R_{i,s} = 0.42 * W_{i,s}^{0.67}$$

Annual food consumption for each species of marine mammals was then divided by the biomass estimates, in order to get the final consumption to biomass (Q/B) ratios used in the *Ecopath* model (Table 18).

**Table 18.** Consumption estimates for each marine mammal groups of the *Ecopath* model of the Caribbean.

Ecopath groups	Annual food consumption (tonnes*km <sup>-2</sup> )	Annual biomass (tonnes*km <sup>-2</sup> )	Q/B
Minke whales	0.0381	0.0045	8.421
Fin whales	0.0257	0.0062	4.161
Humpback whales	0.8470	0.1667	5.081
Bryde's whales	0.0270	0.0043	6.260
Sei whales	0.0053	0.0009	6.178
Blue whales	0.0084	0.0025	3.398
Sperm whales	0.0947	0.0188	5.030
Killer whales	0.0028	0.0003	9.468
Beaked whales	0.0013	0.0001	9.933
Small cetaceans	0.0769	0.0053	14.404

## 11. Seabirds

Twenty one species of seabirds were included in this model and pooled into one group (Table 1). Most of these seabirds' species are commonly found nesting in the Bahama archipelago, Greater and Lesser Antilles and Trinidad and Tobago (Mohammed *et al.* 2007b). Seabirds population in the West Indies occur in relatively low density and are often found in offshore rock or inaccessible cliffs (Schreiber and Lee 2000; Mohammed *et al.* 2007b). Most of their habitats or nesting areas have been converted into coastal developments (Mohammed *et al.* 2007b). Only few information of the population status of seabirds in the Caribbean exist (Mohammed *et al.* 2007b). Hence, the seabird species considered in our model are restricted to species that has trophic impact on the pelagic fish species, following the Lesser Antilles pelagic ecosystem model (Mohammed *et al.* 2007b).

The annual biomass density of 0.0002 t\*km<sup>-2</sup> seabirds in Lesser Antilles pelagic ecosystem model by Mohammed *et al.* (2007b) was based on the product of the number of nesting pairs in the West Indies (Schreiber and Lee 2000) and individual weights of seabirds (Vasconcellos and Watson 2004; Mackinson *et al.* 2005; Priddel *et al.* 2005). The latter value was then incorporated in the present model and assumed to be representative for the Caribbean ecosystem.

The seabirds P/B ratio of 0.13 yr<sup>-1</sup> used in the present model for Caribbean ecosystem was obtained from the Lesser Antilles pelagic ecosystem model (Mohammed *et al.* 2007b). This was assumed to be

similar P/B ratio for all seabird species in the entire Caribbean ecosystem. Likewise, Q/B estimate of the similar species for seabirds used in the Caribbean ecosystem model was taken from Lesser Antilles pelagic ecosystem model (Mohammed *et al.* 2007b). This Q/B value was  $73.690 \text{ yr}^{-1}$  and assumed to be representative in the entire Caribbean ecosystem.

The diet information for seabirds in the present model was obtained from Opitz (1996). The diet of seabirds is composed of other offshore predators, reef fishes, coastal predators, crustaceans and benthos and zooplankton (Opitz 1996).

## 12. Seaturtles

In the present model, the seaturtles group included were green seaturtle (*Chelonia mydas*), hawksbill seaturtle (*Eretmochelys imbricate*), leatherback turtle (*Dermochelys coriacea*), and loggerhead seaturtle (*Caretta caretta*). The leatherback and hawksbill turtles are critically endangered species, and the green turtle is considered to be a threatened species (Grazette *et al.* 2007). These species are nesting in the Caribbean, from Costa Rica to Colombia, from French Guiana to Surinam, along the central Brazilian coast, Guyana, Trinidad, the Dominican Republic, Virgin Islands, Puerto Rico and along the western coast of Mexico to Panama (Grazette *et al.* 2007; Read *et al.* 2007). The seaturtles population in the Caribbean ecosystem are threatened from coastal and upland developments, introduction of domestic and nonindigenous animals, boating (both commercial and recreational), incidental capture in fisheries and illegal harvest of adults and eggs (Bell *et al.* 2007; Mohammed *et al.* 2007b). Their aggregated annual biomass in the Lesser Antilles pelagic ecosystem was estimated to  $0.001 \text{ t*km}^{-2}$  (Mohammed *et al.* 2007b). Other published *Ecopath* models used annual biomass of the similar species for seaturtles ranging from  $0.0026 \text{ t*km}^{-2}$  in Eastern Tropical Pacific ecosystem (Olson and Watters 2003) to  $0.070 \text{ t*km}^{-2}$  in Southern Mexican Caribbean (Alvarez-Hernández 2003). Here, we used mid-range annual biomass value of  $0.037 \text{ t*km}^{-2}$  (based on eight ecosystem models) for the present model and assumed to be representative for the Caribbean ecosystem.

Seaturtles are traditionally harvested in the Caribbean ecosystem (Bell *et al.* 2007; Grazette *et al.* 2007; Mohammed *et al.* 2007b). These animals are a valuable fishery resource for meat (Finlay 1984), shells sold in local and formerly on international market (Eckert and Eckert 1990). Their eggs are also considered a traditional delicacy in some areas in the Caribbean (Grazette *et al.* 2007). Seaturtles are caught with harpoons, spearguns and sometimes nets (Grazette *et al.* 2007; Mohammed *et al.* 2007b). The annual average catch density of seaturtles for local fleets in the Caribbean was  $0.00003 \text{ t*km}^{-2}$  (Mohammed *et al.* 2007b). There was no information about foreign fleets' catches of this group in the area. Of all seaturtle species included herein, it is the leatherback turtle that are commonly caught in region (Mohammed *et al.* 2007a).

The P/B ratio of  $0.15 \text{ yr}^{-1}$  for seaturtles, used in the Lesser Antilles pelagic ecosystem was originally derived from Opitz (1996) for the Caribbean coral reefs ecosystem. In the other published models for the Caribbean areas, this parameter ranged from  $0.15 \text{ yr}^{-1}$  in Eastern Tropical Pacific (Olson and Watters 2003) to  $1.52 \text{ yr}^{-1}$  in Southern Mexican ecosystem Caribbean (Alvarez-Hernández 2003). Based on the eight published ecosystem model, we used mid-range value of  $0.835 \text{ yr}^{-1}$  in the present model representing the seaturtle P/B ratio for the entire Caribbean ecosystem.

The Q/B value of the similar species for seaturtles used in the Lesser Antilles pelagic ecosystem was  $3.500 \text{ yr}^{-1}$  (Mohammed *et al.* 2007b). This value was originally obtained from the Caribbean coral reef ecosystem model by Opitz (1996). Additionally, the latter value was the minimum range of the Q/B values in the other study areas of the Caribbean that ranged from  $3.500 \text{ yr}^{-1}$  in Eastern Tropical Pacific (Olson and Watters 2003) to  $3.570 \text{ yr}^{-1}$  in the Caribbean coast of Southern Mexican ecosystem (Alvarez-Hernández 2003). In the present model, we used mid-range Q/B value of  $3.535 \text{ yr}^{-1}$  (based on eight published ecosystem models) representing the Caribbean ecosystem.

Seaturtle diet information inputs in the present model were obtained from Opitz (1996). According to Opitz (1996), seaturtle prey on small and schooling pelagics, reef fishes and benthic producers.

### 13. Large tunas and billfishes

In the initial model, of albacore (*Thunnus alalunga*), bigeye tuna (*T. obesus*), yellowfin tuna (*T. albacares*), swordfish (*Xiphias gladius*) and billfishes (*Istiophorus* sp. *Tetrapturus albidus*,) were treated as separate trophic groups (Mohammed *et al.* 2007b). However, in the present model, these trophic groups were aggregated into one group as large tunas and billfishes. Likewise, their *Ecopath* parameter values were aggregated as well. The large tuna and billfish species are commercially important fish species migrating along Caribbean, Western Atlantic and Eastern Pacific (Mohammed *et al.* 2007b). The keystone species of this group were albacore tuna, bigeye tuna, yellowfin tuna, swordfish and billfishes. Their annual biomass around the Lesser Antilles pelagic ecosystem ranged from 0.0006 t\*km<sup>2</sup> to 0.0120 t\*km<sup>2</sup> and was 0.0272 t\*km<sup>2</sup> after aggregating process (Mohammed *et al.* 2007b). The latter value was incorporated in the present model and assumed to be representative in the Caribbean ecosystem.

The large tunas and billfishes are overfished in the area (Mohammed *et al.* 2007a). The annual average catch density for local fleets was 0.00467 t\*km<sup>-2</sup> and was 0.0002 t\*km<sup>-2</sup> for foreign fleets (Mohammed *et al.* 2007a; *Sea Around Us database* unpublished data from Reg Watson and www.seaaroundus.org). This group is usually exploited by locals during fishing trips using boats and canoes with outboard engines (Mahon 1990; Mohammed *et al.* 2007a; Mohammed *et al.* 2007b). Some have larger inboard powered launches with ice containers (Mahon 1990). The yellowfin tuna is the most important and targeted large pelagic species in the Caribbean Sea and in the Atlantic Ocean (Marcano *et al.* 2004; Mohammed *et al.* 2007a; Mohammed *et al.* 2007b). The key landing sites for billfishes are in Barbados, Grenada, St. Lucia and St. Vincent, and the Grenadines (Mahon *et al.* 1994a). In addition, Restrepo *et al.* (2003) and Marcano *et al.* (2004) suggested that large tuna's species are highly targeted by recreational or artisanal fisheries, and some are bycatch of tuna longline operations.

The P/B ratios of large tunas and billfishes group in the initial model were derived from the information on the natural and fishing mortalities of the similar species used in ICCAT (2004) stock assessments and from Pauly (1980). This P/B estimates ranged from 0.37 yr<sup>-1</sup> to 2.0 yr<sup>-1</sup> in the Lesser Antilles pelagic ecosystem, and was 1.25 yr<sup>-1</sup> after aggregation (Mohammed *et al.* 2007b). The latter value was then used in the present model representing the P/B ratio for large tunas and billfishes in the entire Caribbean ecosystem.

The aggregated Q/B value of 15.530 yr<sup>-1</sup> for the similar species of large tunas and billfishes from the Lesser Antilles pelagic ecosystem model was used in the present model representing the Caribbean ecosystem. This Q/B value in Lesser Antilles pelagic ecosystem could range from 4.596 yr<sup>-1</sup> to 17.590 yr<sup>-1</sup> (Mohammed *et al.* 2007b).

Large tunas and billfishes group preys mostly on large tunas (juveniles), small tunas, dolphinfish, other offshore predators, flyingfish, scombrids, small and schooling pelagics, coastal predators, cephalopods and zooplankton (Heileman *et al.* 2007).

### 14. Small tunas

The small tunas group was mainly composed of Atlantic skipjack tuna (*Katsuwonus pelamis*), blackfin tuna (*Thunnus atlanticus*), bullet tunas (*Auxis* sp.), Atlantic bonito (*Sarda sarda*) and little tunny (*Euthynnus alletteratus*). Originally, in the initial model, this group was separated into two trophic groups; the skipjack tuna and other offshore predators group. In the present model, these two trophic groups were aggregated into one group as small tunas, in order to reduce the complexity of the model. In general, there is limited information on the stock structure and abundance of small tuna species except for Atlantic skipjack tuna (Mohammed *et al.* 2007b). This species is found in the Caribbean, off Brazil, in the Gulf of Mexico, and in the Gulf of Guinea for their spawning season during summer months (Fonteneau and Marcille 1993). The skipjack tuna occurring in the Caribbean region is considered part of the western Atlantic stock (Mohammed *et al.* 2007b). Since skipjack tuna is an important species for the small tuna trophic group in the area, we decided to use the *Ecopath* parameter values of this species obtained from Mohammed *et al.* (2007b) as inputs for the present model. These inputs were assumed to be representative in the Caribbean ecosystem.

The annual biomass, P/B and Q/B estimates used in the present model for the Caribbean ecosystem were  $0.0119 \text{ t*km}^{-2}$ ,  $1.96 \text{ yr}^{-1}$  and  $19.610 \text{ yr}^{-1}$ , respectively.

The annual average catch density of small tunas for local and foreign fleets in the Caribbean was  $0.00678 \text{ t*km}^{-2}$  and  $0.00005 \text{ t*km}^{-2}$ , respectively (Mohammed *et al.* 2007a; *Sea Around Us database* unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)). This group is targeted for both recreational and artisanal fishing in some areas in the Caribbean (Restrepo *et al.* 2003).

According to Heileman *et al.* (2007), small tunas mainly feed on small tuna species, small and schooling pelagics and cephalopods. This species rarely feed on dolphinfish, flyingfish, coastal predators, scombrids and zooplankton.

## 15. Dolphinfish

The common dolphinfish, *Corypahena hippurus*, and the pompano dolphinfish, *C. equiselis* compose the dolphinfish group in our model. This group was retained herein as a separate group because of its significant importance to both commercial and recreational fisheries for large pelagic fishes in the Western Central Atlantic as well as in the Caribbean ecosystem (Mahon 1996; Mahon 1999; Oxenford 1999; Parker *et al.* 2001; Mohammed *et al.* 2007b). Dolphinfish species are migratory fish species that occur mostly in Southeastern US, Bermuda, Lesser Antilles areas and in north coast of Brazil (Oxenford and Hunte 1986; Mahon 1999; Mahon and Oxenford 1999; Die 2004). According to the genetic study of this group by Die (2004), the dolphinfish stock in the Caribbean belongs to a single stock in the Western Central Atlantic.

The annual biomass of this group was obtained from the Lesser Antilles pelagic ecosystem model developed by Mohammed *et al.* (2007b). Dolphinfish annual biomass was  $0.0278 \text{ t*km}^{-2}$  and assumed to be representative for the Caribbean ecosystem.

The status of dolphinfish stock in the Caribbean is highly uncertain (Mohammed *et al.* 2007a). Some experts (e.g. Prager 2000; Die 2004) suggest that the stock is not overfished, while others (e.g. Parker *et al.* 2001) show that the dolphinfish stock is under intense overfishing. According to Mahon (1999), distant water fleets fishing in the Caribbean areas do not report any dolphinfish landings, in particular recreational fisheries and bycatch in large-scale commercial fisheries, resulting to an unclear decline status of this resource in the area. Based on the timeseries catch densities results of this group from Mohammed *et al.* (2007a) and *Sea Around Us database* (unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)), it showed that the annual average catch density of dolphinfish in the region was  $0.00512 \text{ t*km}^{-2}$  and  $0.00003 \text{ t*km}^{-2}$  for local and foreign fleets, respectively. Similar to the large tunas and billfishes group, the dolphinfish stocks are widely exploited in the region as well (Mahon 1990; Mahon and Oxenford 1999). They are caught by a wide range of fisheries: artisanal, small-scale commercial, large scale-commercial and recreational (Mahon 1999; Mohammed *et al.* 2007a).

The P/B ratio of  $4.72 \text{ yr}^{-1}$  of dolphinfish used in the present model for Caribbean ecosystem was obtained from Mohammed *et al.* (2007b) for the Lesser Antilles pelagic ecosystem model. This value was the mid-range value used in the Lesser Antilles based from the reported total mortality rates (equivalent to P/B ratio) in the same study area, ranged from  $3.53 \text{ yr}^{-1}$  to  $8.67 \text{ yr}^{-1}$  (see Oxenford 1985; Murray 1985; Bentivoglio 1988; Parker *et al.* 2001).

The dolphinfish Q/B input in Lesser Antilles was  $20.000 \text{ yr}^{-1}$  (Mohammed *et al.* 2007b). The latter value was directly used in the present model and assumed to be representative in the entire Caribbean ecosystem.

Generally dolphinfish are piscivorous, eating a wide variety of fish species including large tunas and billfishes, small tunas, other offshore predators, flyingfish, scombrids and coastal predators (e.g. jacks) (Oxenford and Hunte 1999; Heileman *et al.* 2007). They also prey on cephalopods, crustaceans and benthos and zooplankton (Heileman *et al.* 2007).

## 16. Flyingfish

Flyingfish species are an important component of pelagic fisheries in the Southeastern Caribbean (Mahon 1990; Mohammed *et al.* 2007a). Specifically, the fourwing flyingfish, *Hirundichthys affinis*, contributes 95% of the fishery catches in the Lesser Antilles (Mahon 1989; Mohammed *et al.* 2007b). Other most common flyingfish species in the Southeastern Caribbean are margined flyingfish (*Cheilopogon cyanopterus*) and sailfin flyingfish (*Parexocoetus brachypterus*) (Mahon 1989). Because of the high importance of these three flying fishes, they were considered as the representative for the flyingfish group for the Caribbean ecosystem model.

The biomass of flyingfish in Mohammed's *et al.* (2007b) model for the Lesser Antilles pelagic ecosystem was derived from population surveys of the species in the area conducted by Oxenford *et al.* (1995). As a result, the annual biomass of flyingfish group in the area was  $0.2080 \text{ t*km}^{-2}$  (Mohammed *et al.* 2007b). This value was also incorporated in present model and assumed to be representative in the Caribbean ecosystem.

The annual average catch density of this group for local fleets in the Caribbean was  $0.00288 \text{ t*km}^{-2}$  (Mohammed *et al.* 2007a). There was no catches of flyingfish in the foreign fleets. The most targeted flyingfish species was fourwing flyingfish, *H. affinis* that contributed almost 95% of the landings in the Lesser Antilles (Mohammed *et al.* 2007b). Additionally, flyingfish were mainly caught by trolling boat with dipnets in St. Vincent and the Grenadines and by outboard fleets using gillnets in Grenada (Mohammed *et al.* 2007a).

The P/B ratio of  $4.0 \text{ yr}^{-1}$  for flyingfish group used in the present model for the Caribbean ecosystem was obtained from the Lesser Antilles pelagic ecosystem model developed by Mohammed *et al.* (2007b). Additionally, the used P/B value from Lesser Antilles was derived total mortalities values and overall catches percentages of the keystone species of the group: fourwing flyingfish, margined flyingfish and sailfin flyingfish (Mohammed *et al.* 2007b). Likewise, the Q/B estimate of this group was obtained Lesser Antilles pelagic ecosystem model. The value was  $24.760 \text{ yr}^{-1}$  (Mohammed *et al.* 2007b).

The flyingfish species found in the region feed mainly on small and schooling pelagics and zooplankton (Heileman *et al.* 2007).

## 17. Other offshore predators

The "other offshore predators": group was described as fish species that was found in mesopelagic all the way to the deep layers of the ocean. Originally, the offshore predator in the initial model was composed of small tuna species and oceanic triggerfish. However, since we established a separate trophic group for small tunas, we decided to aggregate oceanic triggerfish and small to large mesopelagic fish from LAPE model into a group for "other offshore predators". Other fish species belonging to this group were Alepocephalidae, Gonostomatidae, Macrouridae, Moridae and Myctophidae (Table 1). The annual biomass of the similar species of this group in Lesser Antilles ranged from  $8.7240 \text{ t*km}^{-2}$  to  $10.8330 \text{ t*km}^{-2}$  (Mohammed *et al.* 2007b). This estimate was derived from hydroacoustic and pelagic trawl surveys in Lesser Antilles pelagic ecosystem by Melvin *et al.* (2007). The ranges of annual biomass of other offshore predators in other ecosystem models in adjacent Caribbean ranged from  $0.0006 \text{ t*km}^{-2}$  to  $3.2540 \text{ t*km}^{-2}$ , which were both used in Central Atlantic ecosystem (Vasconcellos and Watson 2004). In the present model, we used an annual biomass of the similar species for other offshore predators of  $1.627 \text{ t*km}^{-2}$  and assumed to be representative in the Caribbean ecosystem. The latter value was a mid-range estimate of the similar species used in the other published ecosystem models in the adjacent Caribbean areas.

The annual catch density of the similar species for other offshore predators group for local fleets was as little as  $0.0000005 \text{ t*km}^{-2}$  (SAUP unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)). The annual catch of this group for foreign fleets was  $0.00008 \text{ t*km}^{-2}$  (Mohammed *et al.* 2007a; SAUP unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)). This group is caught on the same fishing trips with dolphinfish, flyingfish, and large tunas and billfishes (Mahon 1990).

The P/B ratio, ranged from  $0.355 \text{ yr}^{-1}$  to  $3.76 \text{ yr}^{-1}$ , for other offshore group in Lesser Antilles was based on the mean habitat temperature ( $15^{\circ}\text{C}$ ) and growth parameters from FishBase ([www.fishbase.org](http://www.fishbase.org); Mohammed *et al.* 2007b). This P/B estimates were then calculated using the empirical equation after Pauly (1980). In other *Ecopath* models in adjacent Caribbean ecosystem, the P/B ratio of the similar species for other offshore predators ranged from  $0.15 \text{ yr}^{-1}$  to  $3.757 \text{ yr}^{-1}$  in Central Atlantic (Vasconcellos and Watson 2004). We used herein mid-range P/B estimate of  $1.863 \text{ yr}^{-1}$  (based on eight ecosystem models) and assumed to be representative for the Caribbean ecosystem.

The Q/B value of other offshore predators in Lesser Antilles was  $3.550 \text{ yr}^{-1}$  to  $15.000 \text{ yr}^{-1}$  (Mohammed *et al.* 2007b). This was calculated based on the mean habitat temperature and on asymptotic weight and aspect ratios from Fishbase ([www.fishbase.org](http://www.fishbase.org)) using the the empirical equation after Pauly (1980) (Mohammed *et al.* 2007b). The other Q/B estimates of the similar species for other offshore predators in adjacent Caribbean ranged from  $0.290 \text{ yr}^{-1}$  to  $18.250 \text{ yr}^{-1}$  in Central Atlantic (Vasconcellos and Watson 2004). In the present model, a mid-range value of  $9.270 \text{ yr}^{-1}$  was used representing the entire Caribbean ecosystem.

According to Heileman *et al.* (2007), the other offshore predators feed mainly on benthic producers.

### 18. Pelagic sharks

Various sharks' species were included in this group (Table 1). The most important species of the group were the blue shark (*Prionace glauca*), longfin mako (*Isurus paucus*), oceanic whitetip (*Carcharhinus longimanus*), porbeagle (*Lamna nasus*), shortfin mako (*I. oxyrinchus*), spinner shark (*C. brevipinna*) and tiger shark (*Galeocerdo cuvier*). The pelagic sharks are distributed throughout the Atlantic Ocean (Mahon 1990). The annual biomass of this group used in the present model for the Caribbean ecosystem was  $0.0116 \text{ t*km}^{-2}$ . The latter value was derived from the annual biomass of the same group in the Lesser Antilles pelagic ecosystem model by Mohammed *et al.* (2007b). The estimate further represents an intermediate value of the possible annual biomass ranges of the similar species for pelagic sharks from other ecosystem models in adjacent areas of the Caribbean, ranging from  $0.0004 \text{ t*km}^{-2}$  in Eastern Tropical Pacific (Olson and Watters 2003) to  $0.0300 \text{ t*km}^{-2}$  in Bahia Ascension, Mexican Caribbean (Vidal and Basurto 2003).

The timeseries catch density for pelagic sharks in the Caribbean ecosystem were taken from the Lesser Antilles national fisheries report (Mohammed *et al.* 2007a) and from *Sea Around Us Database* (unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)). The average annual catch density for pelagic sharks was  $0.00025 \text{ t*km}^{-2}$  for local fleets and as low as  $0.00005 \text{ t*km}^{-2}$  for foreign fleets (Mohammed *et al.* 2007a; *Sea Around Us Database* unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)). Pelagic shark species species were taken as bycatch and some are targeted in commercial fisheries using bottom gillnet and long line at certain times of the year (Chan and Shing 1999; Mohammed *et al.* 2007a).

The P/B ratios used for pelagic sharks in the Caribbean ecosystem model was  $0.4 \text{ yr}^{-1}$ . This value was obtained from the same group in the Lesser Antilles pelagic ecosystem model (Mohammed *et al.* 2007b).

Likewise, Q/B value of  $10.000 \text{ yr}^{-1}$  for the same group in the Lesser Antilles pelagic ecosystem model (Mohammed *et al.* 2007b) was incorporated in the present model. This was assumed to be representative for the entire Caribbean ecosystem.

Pelagic sharks largely feed on small cetaceans, seaturtles, large tunas and billfishes, small tunas, dolphinfish, other offshore pelagics, pelagic sharks, scombrids, small and schooling pelagics, reef fishes, coastal predators, cephalopods, zooplankton and detritus (Opitz 1996; Heileman *et al.* 2007).



## 19. Coastal and demersal sharks and rays

The coastal sharks and rays included herein are shown in Table 1. The important species of the group were nurse sharks (*Ginglymostoma cirratum*), rays (Myliobatidae) and southern stingray (*Dasyatis americana*). The coastal sharks and rays group was not included in the initial model since their interest focussed mainly on the pelagic ecosystem in Lesser Antilles. In the present model, we cover all areas in the Caribbean including the coastal habitats of marine organisms in the region. Hence, we decided to add the group of sharks and rays inhabiting the coastal zone in the Caribbean ecosystem. Coastal sharks are occasionally present in the region, while rays are fairly common in the coral reefs (Opitz 1996).

The annual biomass of the similar species for coastal and demersal sharks and rays in the adjacent Caribbean ecosystem ranged from 0.0002 t\*km<sup>-2</sup> in Eastern Tropical Pacific (Olson and Watters 2003) to 0.4000 t\*km<sup>-2</sup> in Southern Mexican Caribbean (Alvarez-Hernández 2003). Here, a mid-range annual biomass estimate of 0.2000 t\*km<sup>-2</sup> was used in the present model and assumed to be representative in the entire Caribbean ecosystem.

The coastal and demersal sharks and rays are harvested in region (Mahon 1990; Opitz 1996). Some of the species of this group are incidentally caught in trap or handline fisheries on the island shelves (Mahon 1990). The most common shark species caught in the latter gear are nurse sharks (*G. cirratum*) (Mahon 1990). Based from the LAPE national fisheries (Mohammed *et al.* 2007a) and *Sea Around Us database* (unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)), the annual average catch density of this group for local fleets and foreign fleets were 0.000177 t\*km<sup>-2</sup> and 0.00018 t\*km<sup>-2</sup>, respectively.

The P/B estimates of the similar species for this group in the adjacent Caribbean could range from 0.112 yr<sup>-1</sup> in Central Atlantic (Vasconcellos and Watson 2004) to 0.6 yr<sup>-1</sup> in Southeastern Caribbean (Mohammed 2003a). In the present model, a P/B estimate of 0.356 yr<sup>-1</sup> was used representing the Caribbean ecosystem. This value was mid-range P/B estimate of the similar species used in eight ecosystem models in the adjacent Caribbean ecosystem.

The coastal sharks and rays Q/B estimates in the Caribbean areas ranged from 1.800 yr<sup>-1</sup> in Central Atlantic (Vasconcellos and Watson 2004) to 9.160 yr<sup>-1</sup> in Eastern Tropical Pacific (Olson and Watters 2003). Here, a mid-range value of 5.480 yr<sup>-1</sup> was used in the present model and assumed to be representative in the Caribbean ecosystem.

Sharks and rays largely feed on variety of preys such as seaturtles, small tunas, dolphinfish, coastal and demersal sharks and rays, small and schooling pelagics, scombrids, coastal predators, reef fishes, cephalopods, crustaceans and benthos, and benthic producers (Opitz 1996; Heileman *et al.* 2007).

## 20. Scombrids

In the initial model, scombrids species such as wahoo and other mackerels were grouped separately. However, we decided to aggregate all the scombrids species in order to reduce the complexity of the present model for the Caribbean ecosystem. The important species of the scombrids group were cero (*Scomberomorus regalis*), king mackerel (*S. cavalla*), Spanish mackerel (*S. brasiliensis*) and wahoo (*Acanthocybium solandri*). These species are migratory and occupy US coastal waters of the South Atlantic and the Gulf of Mexico (Mahon and McConney 2004). Their annual biomass in the Lesser Antilles areas ranged from 0.0010 t\*km<sup>-2</sup> to 0.0650 t\*km<sup>-2</sup>, and was 0.0660 t\*km<sup>-2</sup> after aggregation (Mohammed *et al.* 2007b). These biomass estimates were based on the ratio of catches inside the Lesser Antilles pelagic ecosystem and the total catch (Mohammed *et al.* 2007b). The aggregated annual biomass (0.0660 t\*km<sup>-2</sup>) of this group from LAPE model was used directly in the present model for the Caribbean ecosystem.

The scombrids species are commercially important component in the Caribbean fisheries (Mahon 1990; Opitz 1996; Oxenford *et al.* 2003; Mohammed *et al.* 2007ab). These fish species are also targeted for recreational fishing in the area (Mohammed *et al.* 2007b). The average annual catch density of scombrids in the area was 0.01129 t\*km<sup>-2</sup> for local fleets and 0.00079 t\*km<sup>-2</sup> for foreign fleets (*Sea*

*Around Us database* unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)). The most harvested scombrids in the Caribbean ecosystem are king mackerel, Spanish mackerel and wahoo (Mahon 1990; Mohammed *et al.* 2007a).

The P/B ratio used in the present model for the Caribbean ecosystem was  $1.09 \text{ yr}^{-1}$ . This value was obtained from the P/B ratio of mackerel/scombrids group in the Lesser Antilles pelagic ecosystem (Mohammed *et al.* 2007b).

The Q/B value of  $10.310 \text{ yr}^{-1}$  incorporated in the present model was derived from the Q/B estimate of the mackerel group in the Lesser Antilles pelagic ecosystem (Mohammed *et al.* 2007b). This value seemed to be the mid-range of the possible Q/B estimates of the similar species for scombrids in the other ecosystem models in adjacent areas in the Caribbean, ranging from  $9.150 \text{ yr}^{-1}$  in Caribbean coral reefs ecosystem model (Opitz 1996) to  $11.400 \text{ yr}^{-1}$  in Eastern Tropical Pacific model (Olson and Watters 2003).

Diet information of scombrids was obtained from Heileman *et al.* (2007). From their study, it showed that scombrids preyed mainly on flyingfish, coastal predators, cephalopods and zooplankton, and occasionally feed on small tunas, scombrids, and small and schooling pelagics.

## 21. Small and schooling pelagics

In this model, the small coastal pelagics and small offshore pelagic fish trophic groups from Mohammed *et al.* (2007b) version were pooled into 'small and schooling pelagics' because of their similarities in ecological importance in the study area, and also to have a simplified model structure for the Caribbean ecosystem model. This group represents various species of small and schooling pelagic included in the model: anchovies, halfbeaks, herrings, scads and small jacks (Table 1). The key species of this group were anchovies (*Anchoa* sp.), Atlantic bumper (*Chloroscombrus chrysurus*), bigeye scad (*Selar crumenophthalmus*), herring (*Harengula* sp.), sardine (*Sardinella* sp.), scad (*Decapterus* sp.), and threadfin shad (*Dorosoma petenense*).

The aggregated annual biomass of small and schooling pelagics in Mohammed *et al.* (2007b) model for the Lesser Antilles pelagic ecosystem was  $0.2440 \text{ t*km}^{-2}$  to  $7.3940 \text{ t*km}^{-2}$  and was  $10.1970 \text{ t*km}^{-2}$  after aggregating process (Mohammed *et al.* 2007b). Other ecosystem models in adjacent areas of the Caribbean used annual biomass values that ranged from  $0.1500 \text{ t*km}^{-2}$  in Bahia Ascencion, Mexican Caribbean (Vidal and Basurto 2003) to  $33.0000 \text{ t*km}^{-2}$  in Southeastern Caribbean (Mohammed 2003a). In the present model, we used an intermediate or mid-range annual biomass value of  $16.575 \text{ t*km}^{-2}$  for the similar species of small and schooling pelagic in the Caribbean ecosystem.

The average annual catch density for local and foreign fleets of small and schooling pelagics was  $0.03478 \text{ t*km}^{-2}$  and  $0.0022 \text{ t*km}^{-2}$ , respectively (Mohammed *et al.* 2007a; *Sea Around Us database* unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)). The small and schooling pelagics are usually caught by longline fleets in the region (Mohammed *et al.* 2007a). In addition, catches of most of these species are used for live bait fishing for commercial and recreational fisheries in the region (Heileman-Manickchand 1992).

The P/B ratio for small and schooling pelagics groups in the Lesser Antilles pelagic ecosystem model ranged from  $3.5 \text{ yr}^{-1}$  to  $3.6 \text{ yr}^{-1}$ , and was  $3.245 \text{ yr}^{-1}$  after the group aggregations (Mohammed *et al.* 2007b). Other models for adjacent areas of the Caribbean P/B used values from  $0.38 \text{ yr}^{-1}$  in the Caribbean coral reef ecosystem model (Opitz 1996) to  $5.5 \text{ yr}^{-1}$  in Costa Rica (Wolff *et al.* 1998). Thus, we used herein an intermediate or mid-range P/B ratio of  $2.94 \text{ yr}^{-1}$  and assumed to be representative for the Caribbean ecosystem.

The small and schooling pelagics Q/B values in the Lesser Antilles pelagics ecosystem was  $14.640 \text{ yr}^{-1}$  after aggregation process (Mohammed *et al.* 2007b). The Q/B estimates for similar species in other Caribbean ecosystems models could vary from  $3.900 \text{ yr}^{-1}$  to  $43.400 \text{ yr}^{-1}$  in Caribbean coral reefs ecosystem (Opitz 1996). Here, a mid-range Q/B estimate of  $23.650 \text{ yr}^{-1}$  was used for small and schooling pelagics in our model.

Diet information for small and schooling pelagics was obtained from Heileman *et al.* (2007). Therein, it was documented that small and schooling pelagics feed mostly on small and schooling pelagics, reef fishes, crustaceans and benthos, and zooplankton.

## 22. Reef fishes

The reef fish trophic group in the initial model was pooled with the coastal predators group. However, because of the importance of reef fishes in some areas (e.g. Virgin Islands, Puerto Rico) in the Caribbean (see Opitz 1996), we decided to make “reef fishes” separate in the present model. The reef fish resources are a major source of fish and fishery products to the domestic food market in many Caribbean islands (Jeffrey 2000). Many reef fish species are included herein (Table 1). The key species of this group were species belonging to Bermuda chab (*Kyphosus sectatrix*), grouper (*Epinephelus* sp.), Haemulidae, queen parrotfish (*Scarus vetula*) and rainbow parrot fish (*Scarus guacamaia*). These species inhabits not only the coral reef areas but are also found along the seagrass beds, and its juveniles are often in the mangrove areas (Opitz 1996). According to Mahon (1990), the reef fishes in the region are considered to be overexploited with possible exemption of a few islands with large shelves.

The annual biomass of the similar species for reef fish group in other *Ecopath* models in the adjacent areas in the Caribbean ranged from 0.007 t\*km<sup>-2</sup> in Southeastern Caribbean (Mohammed 2003a) to 46.688 t\*km<sup>-2</sup> in Caribbean coral reef ecosystem (Opitz 1996). The extremely high range of annual biomass (99.000 t\*km<sup>-2</sup>) of the similar species in the Southern Mexican Caribbean was not used to factor the mid-range annual biomass value for the reef fishes group. Consequently, we used annual biomass estimate of 0.654 t\*km<sup>-2</sup> for reef fishes group, representing the Caribbean ecosystem. The latter value was a mid-range estimate of the available annual biomass values of the similar species derived from the eight ecosystem models in the adjacent Caribbean areas.

The timeseries catch density of reef fish group from 1987 to 2005 were taken from Lesser Antilles fisheries report (Mohammed *et al.* 2007a) and in *Sea Around Us* database (unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)). Its annual average catch for both local and foreign fleets in the Caribbean was 0.00792 t\*km<sup>-2</sup> and 0.00091 t\*km<sup>-2</sup>, respectively. Reef fish species in the Caribbean region are highly targeted for artisanal or inshore fishery operations (Nemeth 2005) and some are used for baits or harvested for aquarium trade (Opitz 1996). Reef fish species belonging to Haemulidae, Holocentridae, Monacanthidae, Mullidae, Muraenidae, and Serranidae are frequently caught in the area (Gobert 2000). These species are caught mostly using traps and handlines (Munro 1983; Recksiek *et al.* 1991; Mahon 1990; Gobert 2000). Most of the reef fishes in some areas in the Caribbean (e.g. Martinique, Guadeloupe, Puerto Rico) are overfished and heavily exploited (Opitz 1996; Gobert 2000; Jeffrey 2000)

The P/B ratios for reef fish groups in the other *Ecopath* ecosystem models in adjacent areas of the Caribbean ranged from 0.37 yr<sup>-1</sup> to 3.14 yr<sup>-1</sup>. These values minimum and maximum P/B ranges were both originate from the Caribbean coral reefs ecosystem model (Opitz 1996). In the present model, mid-range P/B estimate of 1.755 yr<sup>-1</sup> was used, representing the Caribbean ecosystem.

In the other study areas of the Caribbean, the Q/B used values of the similar species for reef fishes ranged from 2.300 yr<sup>-1</sup> to 39.700 yr<sup>-1</sup>. These ranges were both originate from the Caribbean coral reef ecosystem (Opitz 1996). Here, a mid-range Q/B estimate of 21.000 yr<sup>-1</sup> for reef fishes group, based on eight Caribbean models, was used in the present model representing the Caribbean ecosystem.

The diet of the reef fishes group was mainly composed of reef fishes, small and schooling pelagics, cephalopods, crustaceans and benthos, zooplankton, benthic producers and phytoplankton (Opitz 1996).

### 23. Coastal predators

The key species of coastal predators group were amberfish (*Seriola* sp.), common snook (*Centropomus undecimalis*), jacks (*Caranx* sp.), leatherjacks (*Oligoplites* sp.), needle fish (Belonidae), pompanos (*Alectis ciliaris*, *Trachinotus* sp.), rainbow runner (*Elegatis bipinnulata*) and snapper (*Lutjanus* sp.). Their annual biomass used in the present model for the Caribbean ecosystem was  $1.260 \text{ t*km}^{-2}$ . This value was directly derived from the same group in the Lesser Antilles pelagic ecosystem model (Mohammed *et al.* 2007b).

The average annual catch density for local and foreign fleets of coastal predators in the region was  $0.00735 \text{ t*km}^{-2}$  and  $0.00128 \text{ t*km}^{-2}$ , respectively (Mohammed *et al.* 2007a; *Sea Around Us database* unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)). The snappers and jacks are widely harvested coastal predators species in the Caribbean region (Mohammed *et al.* 2007a).

The P/B ratio input for coastal predators in present model for the Caribbean ecosystem model was  $0.72 \text{ yr}^{-1}$ . This value was obtained from the same group in the Lesser Antilles pelagic ecosystem model (Mohammed *et al.* 2007b).

Likewise, Q/B input value of  $7.220 \text{ yr}^{-1}$  in the present model was obtained from the Lesser Antilles pelagic ecosystem model (Mohammed *et al.* 2007b). The latter value was assumed to be representative for coastal predators in the entire Caribbean ecosystem.

The diet contents of coastal predators are composed of coastal predator species, reef fishes, small and schooling pelagics, cephalopods, crustaceans and benthos, zooplankton and benthic producers (Opitz 1996).

### 24. Cephalopods

The large and small squid groups in the Lesser Antilles pelagic ecosystem model were pooled together as one cephalopods group in the present model for the Caribbean ecosystem. Likewise, input *Ecopath* parameter values on these groups were aggregated. The most important cephalopod species were leatherback, *Loligo* sp. and *Octopus vulgaris*. Their annual biomass in the Lesser Antilles pelagic ecosystem ranged from  $0.177 \text{ t*km}^{-2}$  to  $1.157 \text{ t*km}^{-2}$  (Mohammed *et al.* 2007b). After aggregating the small and large squid groups into one group, the resulting annual biomass was  $1.334 \text{ t*km}^{-2}$ . This estimate was close to the maximum range of cephalopod's annual biomass in the other *Ecopath* models in the Caribbean areas, which ranged from  $0.0051 \text{ t*km}^{-2}$  in Central Atlantic (Vasconcellos and Watson 2004) to  $10.0 \text{ t*km}^{-2}$  in Southern Mexican Caribbean (Alvarez-Hernández 2003). In the present model, we used mid-range annual biomass of  $5.000 \text{ t*km}^{-2}$  of the similar species (based on the eight ecosystem models in the Caribbean areas) and assumed to be representative in the Caribbean ecosystem.

Its annual average catch density in the region was  $0.00027 \text{ t*km}^{-2}$  for local fleets and  $0.00003 \text{ t*km}^{-2}$  for foreign fleets (Mohammed *et al.* 2007a; *Sea Around Us database* unpublished data from Reg Watson and [www.seaaroundus.org](http://www.seaaroundus.org)).

The P/B ratio of cephalopods in the Lesser Antilles pelagic ecosystem model ranged from  $4.6 \text{ yr}^{-1}$  to  $5.5 \text{ yr}^{-1}$  (Mohammed *et al.* 2007b), and was then  $5.05 \text{ yr}^{-1}$  after the aggregation process. The other estimates of P/B ratios documented in adjacent areas in the Caribbean ranged from  $1.15 \text{ yr}^{-1}$  Central Atlantic (Vasconcellos and Watson 2004) to  $8.3 \text{ yr}^{-1}$  in Costa Rica (Wolff *et al.* 1998). A mid-range P/B ratio of  $4.725 \text{ yr}^{-1}$  was used in the present model based on the eight Caribbean ecosystem models. This value was assumed to be representative for the cephalopods in the entire Caribbean ecosystem.

The Q/B values, ranging from  $15.860 \text{ yr}^{-1}$  to  $18.330 \text{ yr}^{-1}$ , estimated by Mohammed *et al.* (2007b) were based on the gross food conversion efficiency (P/Q) of the species. While, cephalopods Q/B used values in other *Ecopath* ecosystem models in adjacent areas in the Caribbean ranged from  $2.300 \text{ yr}^{-1}$  to  $36.500 \text{ yr}^{-1}$ . These ranges were both came from the Central Atlantic ecosystem model (Vasconcellos and Watson 2004). Here, a mid-range Q/B estimate of  $19.400 \text{ yr}^{-1}$  from the similar species was used in the present models representing the Caribbean ecosystem.

Cephalopods dietary contents are composed of small and schooling pelagics, reef fishes, cephalopods, crustaceans and benthos, benthic producers and zooplankton (Opitz 1996).

## 25. Crustaceans and benthos

There was no crustaceans and benthos group in the initial model. We included a trophic group for crustaceans and benthos in the present model because of its importance to the Caribbean fishery. The crustaceans and benthos species included in the present model are shown in Table 1. The most important species of this group were conch (*Strombus* sp.), crabs, shrimps (*Penaeus* sp.), oyster (*Crassostrea virginica*) and spiny lobster (*Panulirus argus*). The annual biomass of the similar species for this group ranged from 0.050 t\*km<sup>-2</sup> in Bahia Ascencion, Mexican Caribbean (Vidal and Basurto 2003) and in Colombian Caribbean Sea (Duarte and Garcia 2002) to 23.935 t\*km<sup>-2</sup> in Southeastern Caribbean (Mohammed 2003a). The extremely high range of annual biomass (842.000 t\*km<sup>-2</sup>) of the similar species in the Southern Mexican Caribbean was not used to factor the mid-range value of annual biomass for the crustaceans and benthos group. Consequently, the mid-range value for the similar species of crustaceans and benthos annual biomass used in the present model was 11.993 t\*km<sup>-2</sup>, representing the Caribbean ecosystem.

Based on the information from *Sea Around Us database* (unpublished data from Reg Watson and www.seaaroundus.org), the average annual catch density of crustaceans and benthos species was 0.01419 t\*km<sup>-2</sup> and 0.00132 t\*km<sup>-2</sup> for local and foreign fleets, respectively. The most commercially important crustacean fisheries in the Caribbean region are spiny lobsters and conch (Mahon 1990; Opitz 1996). There were no catches data reported of this group from LAPE national fisheries report.

The P/B estimates of this group ranged from 0.31 yr<sup>-1</sup> in Caribbean coral reef ecosystem (Opitz 1996) to 30.0 yr<sup>-1</sup> in Costa Rica (Wolff *et al.* 1998). Here, we used mid-range P/B estimate of 15.155 yr<sup>-1</sup>, based on the eight Caribbean ecosystem models, for the crustaceans and benthos group. The latter value was assumed to be representative in the Caribbean ecosystem.

Other published models in adjacent areas of the Caribbean used Q/B values of similar species ranging from 2.370 yr<sup>-1</sup> in Southern Mexican Caribbean (Alvarez-Hernández 2003) to 150.000 yr<sup>-1</sup> in Costa Rica (Wolff *et al.* 1998). In the present model, a mid-range Q/B estimate of 76.185 yr<sup>-1</sup> was used (based on the eight Caribbean ecosystem models) representing the whole of the Caribbean ecosystem.

Crustaceans and benthos diet information was obtained from Opitz (1996). According to this study, crustaceans and benthos diet contents are composed of reef fishes, cephalopods, crustaceans and benthos, benthic producers, zooplankton, phytoplankton and detritus.

## 26. Zooplankton

Chaetognatha, Copepoda, Euphausiacea, Hydrozoa, Hyperiididae, Mysidacea, Scyphozoa, ichthyoplankton, macroplankton, meroplankton, planktonic decapods, larvae, and fish eggs comprised the zooplankton group. The zooplankton annual biomass in the Lesser Antilles was obtained from the results of hydroacoustic and pelagic trawl surveys by Melvin *et al.* (2007) conducted under the LAPE project. The annual biomass of large zooplankton in the area was estimated to be 9.636 t\*km<sup>-2</sup> while small zooplankton was estimated to amount to 40.000 t\*km<sup>-2</sup> (Mohammed *et al.* 2007b). Summing these estimates, a total biomass density for zooplankton of 49.636 t\*km<sup>-2</sup> was obtained. We incorporated the latter value in the present model and assumed to be representative in the Caribbean ecosystem.

The P/B ratio estimates, ranging from 8.7 yr<sup>-1</sup> to 17.3 yr<sup>-1</sup>, for zooplankton in Lesser Antilles pelagic ecosystem were initially derived from the Caribbean coral reef ecosystem model (Mohammed *et al.* 2007b). This P/B range was aggregated resulting to 12.9 yr<sup>-1</sup>, and was incorporated in the present model representing the Caribbean ecosystem.

The Q/B estimate of zooplankton in Mohammed *et al.* (2007b) for Lesser Antilles pelagic ecosystem ranged from 29.000 yr<sup>-1</sup> to 57.700 yr<sup>-1</sup> and was 43.350 yr<sup>-1</sup> after aggregation process. The latter value was used in the present model and assumed to be representative for zooplankton in the Caribbean ecosystem.

Diet information of zooplankton group was obtained from Heileman *et al.* (2007). In their study, they stated that this group feed on crustaceans and benthos (juveniles), zooplankton, benthic producers, phytoplankton and detritus.

## 27. Benthic producers

Benthic producers were composed of benthic autotrophs, marine algae species, and symbiotic algae. There is no benthic producers group in the initial model. However, we added herein the trophic group for benthic producers because it is an ecologically important component in the Caribbean ecosystem.

The annual biomass of this group ranged from 0.500 t\*km<sup>-2</sup> in Costa Rica (Wolff *et al.* 1998) to 27.871 t\*km<sup>-2</sup> in Southeastern Caribbean (Mohammed 2003a). The extremely high range of annual biomass (1641.0 t\*km<sup>-2</sup>) of the similar group in the Southern Mexican Caribbean was excluded from the average annual biomass value for the crustaceans and benthos group. Consequently, the mid-range value for benthic producers annual biomass of 14.186 t\*km<sup>-2</sup> was used in the present model representing the Caribbean ecosystem

An intermediate or mid-range P/B value of 71.75 yr<sup>-1</sup> for benthic producer group was used in the present model for the Caribbean ecosystem. This value was derived from the eight models in the adjacent areas in the Caribbean that ranged from 13.25 yr<sup>-1</sup> in Southern Mexican Caribbean (Alvarez-Hernández 2003) to 280.0 yr<sup>-1</sup> in Coral reef ecosystem (Opitz 1996).

## 28. Phytoplankton

The phytoplankton input parameters in the Lesser Antilles pelagic ecosystem model by Mohammed *et al.* (2007b) were taken from primary production study by LAPE project and the production/biomass of phytoplankton by Forget (2007). The annual biomass and P/B ratio of phytoplankton used in the present model were 32.0 t\*km<sup>-2</sup> and 42.8 yr<sup>-1</sup>, respectively. These values were derived from the Lesser Antilles pelagic ecosystem developed by Mohammed *et al.* (2007b), and assumed to be representative in the Caribbean ecosystem.

## 29. Detritus

Particulate organic materials (POM) and dissolved organic materials (DOM) along the water column or in the bottom of the ocean constituted the detritus group in the model. The detritus annual biomass was estimated from Pauly *et al.* (1993) empirical equation on detritus biomass as function of primary production and euphotic depth by Rajendra *et al.* (1991) and from primary production results by Forget (2007). Mohammed *et al.* (2007b) estimated that the annual biomass for detritus was 15.075 t\*km<sup>-2</sup> in the Lesser Antilles pelagic ecosystem. This value is extremely low compared to the other annual biomass range of detritus in the Caribbean areas that range from 13.000 t\*km<sup>-2</sup> in Bahia Ascencion, Mexican Caribbean (Vidal and Basurto 2003) to 600 t\*km<sup>-2</sup> in Southern Mexican Caribbean (Alvarez-Hernández 2003). We used an intermediate or mid-range annual biomass estimate of 306.500 t\*km<sup>-2</sup> (based on eight ecosystem models) for detritus group in the present model representing the Caribbean ecosystem.

## BALANCING THE MODEL

The unbalanced model for the Caribbean is shown in Table 19. In order to obtain a balanced solution, two major levels of verification have been made. First, the ecotrophic efficiency (EE) terms were examined to evaluate the balance among our trophic groups and within the whole system. If a particular group was ‘unbalanced’ (with an EE higher than 1.00), this indicated that biomass or P/B values for the groups were underestimated, or that the Q/B was overestimated. Secondly, it was important to make sure that gross efficiency (GE), which is the ratio of production to consumption (P/Q), was always within the 0.1 – 0.3 range. According to Christensen and Pauly (1992), GE should range from 10% to 30%, with exception of top predators, e.g., marine mammals and seabirds, which can have lower GE (between 0.1 and 1%). Small, fast growing fish larvae or nauplii or bacteria are also exempted because they can have higher GE (between 25 and 50%) (Christensen and Pauly 1992).

**Table 19.** Input data for the Ecopath model of the Caribbean. Unbalanced values are shown in **bold**.

	Ecopath group	Trophic level	B (t*km <sup>-2</sup> )	P/B (year <sup>-1</sup> )	Q/B (year <sup>-1</sup> )	EE
1	Minke whales	3.98	0.005	0.099	8.421	0.000
2	Fin whales	3.26	0.006	0.099	4.161	0.000
3	Humpback whales	3.84	0.070	0.099	5.081	0.000
4	Brydes whales	3.92	0.004	0.050	6.260	0.000
5	Sei whales	3.26	0.001	0.020	6.178	0.000
6	Blue whales	3.25	0.002	0.060	3.398	0.000
7	Sperm whales	4.45	0.019	0.050	5.030	0.000
8	Killer whales	4.19	0.0003	0.020	9.468	<b>1.724</b>
9	Beaked whales	4.05	0.0001	0.036	9.933	0.000
10	Small cetaceans	3.93	0.005	0.030	14.404	<b>3.350</b>
11	Seabirds	3.55	0.0002	0.130	73.690	0.000
12	Seaturtles	4.31	0.037	0.835	3.535	0.464
13	Large tunas and billfishes	4.34	0.027	1.250	15.530	0.555
14	Small tunas	4.08	0.012	1.960	19.610	<b>8.965</b>
15	Dolphinfish	4.52	0.028	4.720	20.000	0.763
16	Flyingfish	3.33	0.208	4.000	24.760	0.534
17	Other offshore predators	2.06	1.627	1.863	9.270	0.057
18	Pelagic sharks	4.52	0.012	0.400	10.000	0.265
19	Coastal and demersal sharks and rays	3.98	0.200	0.356	5.480	0.181
20	Scombrids	4.31	0.066	1.090	10.310	0.483
21	Small and schooling pelagics	3.29	16.575	2.940	23.650	0.400
22	Reef fishes	3.15	0.654	1.755	21.000	<b>10.004</b>
23	Coastal predators	3.74	1.260	0.720	7.220	<b>1.979</b>
24	Cephalopods	3.45	5.000	4.725	19.400	0.188
25	Crustaceans and benthos	2.38	11.993	15.155	76.185	<b>3.800</b>
26	Zooplankton	2.25	49.636	12.900	43.350	0.669
27	Benthic producers	1.00	14.186	71.750	-	0.222
28	Phytoplankton	1.00	32.000	42.800	-	0.962
28	Detritus	1	306.500	-	-	0.688

In the Ecopath approach, estimates of the different parameters (Biomass, P/B, Q/B or diet composition) for all groups of the foodweb can be adjusted to bring the groups and the model into balance. Since there were multiple connections among groups, a change in the estimate for a trophic group may in turn have changed the degree of balance of other groups that connected with it. While these adjustments could be seen as a “trial and error” (or haphazard) process, the systematic method we used here [based on methodology developed by Morissette *et al.* (in press) and Savenkoff *et al.* (2007)]

all allowed to make the changes within a range of possible values based on similar species and foodwebs in the Caribbean area. Doing so, we avoided the arbitrary parameter adjustments that may lead to unnecessary erosion of model realism (Okey 1999). Modifications to the original model needed to reach a balanced solution are listed below:

1. The EE for small cetaceans was higher than 1.000, indicating that there was not enough biomass in the model to account for all sources of mortality on this group. Given the unavoidable degree of uncertainty associated with density estimates derived from the global model used by Kaschner (2004) to provide small cetacean density estimates, we considered a substantial increase of small cetacean biomass density justifiable and likely to still fall within the bounds of uncertainty. To the new estimate was the same as the one used by Vidal and Basurto (2003) in Bahia Ascension, Mexican Caribbean, where similar species of dolphins reach a biomass of  $0.040 \text{ t*km}^{-2}$ .
2. Killer whales were an important group of marine mammals in the Caribbean ecosystem, and were also exploited by whaling. In the initial model, their EE was higher than 1.000. This means that their biomass was too low, or biomass of their prey was insufficiently low. Since they partially feed on small cetaceans (which was also unbalanced, see below), their EE was set to 0.950 to determine which biomass would be needed to support the level of exploitation of this group. However, this was done only after having incorporated the above increase the biomass for the small cetaceans group and thus having creating more food for the killer whales. The resulting killer whale biomass ( $0.000526 \text{ t*km}^{-2}$ ) was acceptable and within the range of possible values provided by Kaschner's (2004) database.
3. There was also an EE higher than 1.000 for small tunas. To compensate for that, we first decreased the proportion of small tunas in the diet of large tunas, based on the proportion of the key-species of small tuna (skipjack tuna) in the diet of the key-species of large tunas (yellowfin tuna). The diet of small tunas on small tunas (cannibalism) was also decreased to a minimal proportion of 0.010. The main predator of small tunas in our system was coastal and demersal sharks and rays. The proportion of small tunas in the diet of this group was also reduced, assuming that the coastal and demersal sharks and rays group features, a more coastal diet for our study area, compared to the more pelagic environment used by small tunas. The new proportion of small tunas in the coastal and demersal sharks and rays group was adjusted by increasing the proportions of small and schooling pelagics and other offshore predators in the diet. The biomass, P/B and Q/B of coastal and demersal sharks and rays were also decreased to minimal values (within the range of possible values for surrounding areas) of  $0.040 \text{ t*km}^{-2}$  (Duarte and Garcia 2002),  $0.112$  and  $1.800 \text{ yr}^{-1}$  (Vasconcellos and Watson 2004), respectively. Finally, in order to get a balanced solution for the small tunas group, we used maximal values of  $2.500$  and  $25.000 \text{ yr}^{-1}$  for small tunas' P/B and Q/B, respectively, based on the range of possible values for similar and neighboring ecosystem models. These inputs were the same as the values used by Olson and Watters (2003) in eastern tropical Pacific ecosystem. Biomass was also adjusted using an EE of 0.950. The resulting B ( $0.0145 \text{ t*km}^{-2}$ ) was part of the range of possible values, and similar to what was seen in southeastern Caribbean ecosystem (Mohammed 2003a) and Lesser Antilles pelagic ecosystem (Mohammed *et al.* 2007b).
4. The EE of reef fishes was also higher than 1.000. In order to compensate for that, we used an EE of 0.950 and let *Ecopath* calculate the biomass required to reach a balanced scenario. The resulting value ( $24.272 \text{ t*km}^{-2}$ ) was within the range of possible values, and about half the value used by Opitz (1996) for Caribbean coral reefs.
5. The EE for coastal predators was higher than 1.000, indicating that there was not enough biomass in the model to account for all sources of mortality on this group. The main problem here was a very high cannibalism. Thus, we allowed a proportion of 0.010 instead of 0.140 for cannibalism. The remaining proportion was redistributed between small and schooling pelagics, and crustaceans and benthos, the two main preys of coastal predators.
6. For crustaceans and benthos, cannibalism also seemed overestimated and unrealistic. This was due to aggregation of distinct species in the original model that were now part of the same group. Consequently, we reduced the cannibalism of crustaceans and benthos from 0.238 to



0.050, and increased the proportion of detritus in the diet (the main prey) to compensate for that change. Finally, we increased the P/B to 20.0 yr<sup>-1</sup> (close to the maximal value from Wolff *et al.* [1998] in Costa Rica), and used EE=0.95 to let Ecopath calculate a biomass (51.201 t\*km<sup>-2</sup>, which was in the range of possible values for this group in the area), to finally reach a balanced solution for crustaceans and benthos group.

7. The changes on crustaceans and benthos created slight imbalance in benthic producers and phytoplankton. Thus, we used an EE of 0.6 for both groups to get a new biomasses of 23.157 t\*km<sup>-2</sup> (Mohammed 2003a) and 79.081 t\*km<sup>-2</sup>, for benthic producers and phytoplankton groups, respectively. The new biomass estimate of the latter group was off from the possible values, 0.426 t\*km<sup>-2</sup> (Olson and Watters 2003) to 47.0 t\*km<sup>-2</sup> (Alvarez-Hernández 2003), found in similar ecosystem models. However, this was not considered to have huge variation compared to what used by Opitz (1996) for phytoplankton annual biomass in the Caribbean coral reef ecosystem, which was 1300 t\*km<sup>-2</sup>. The latter value was considered as an outlier for our ranges.
8. Changed the diet of zooplankton on detritus from 0.2 to 0.15 (re-distributing the 0.05 to phytoplankton) to balance for detritus.
9. Higher biomass of crustaceans and benthos also created an imbalance of detritus. Consequently, we slightly reduced the proportion of this group (crustaceans and benthos) in the diet of predators (reef fish and crustaceans and benthos) to create less predation, and thus a smaller biomass calculated with the EE of 0.95. The final biomass of crustaceans and benthos is 61.755 t\*km<sup>-2</sup> (this was still within the range of possible values from adjacent ecosystems) using an EE of 0.95. The new biomass estimate used for crustaceans and benthos group falls a bit outside the range of the possible values, 0.050 t\*km<sup>-2</sup> (Vidal and Basurto 2003) to 23.935 t\*km<sup>-2</sup> (Mohammed 2003a), found in similar ecosystem models. However, this new crustaceans and benthos biomass estimate was not considered to have huge variation compared to what was used in the southern Mexican Caribbean ecosystem model (842 t\*km<sup>-2</sup>) by Alvarez-Hernández (2003), which was considered as an outlier for our ranges.

The final balanced model for the Caribbean region is given in Table 20. A diet matrix showing the proportion of each prey in all predators' diets is provided in Table 21.

**Table 20.** Balanced version of the *Ecopath* model of the Caribbean. Estimated parameters are shown in **bold**.

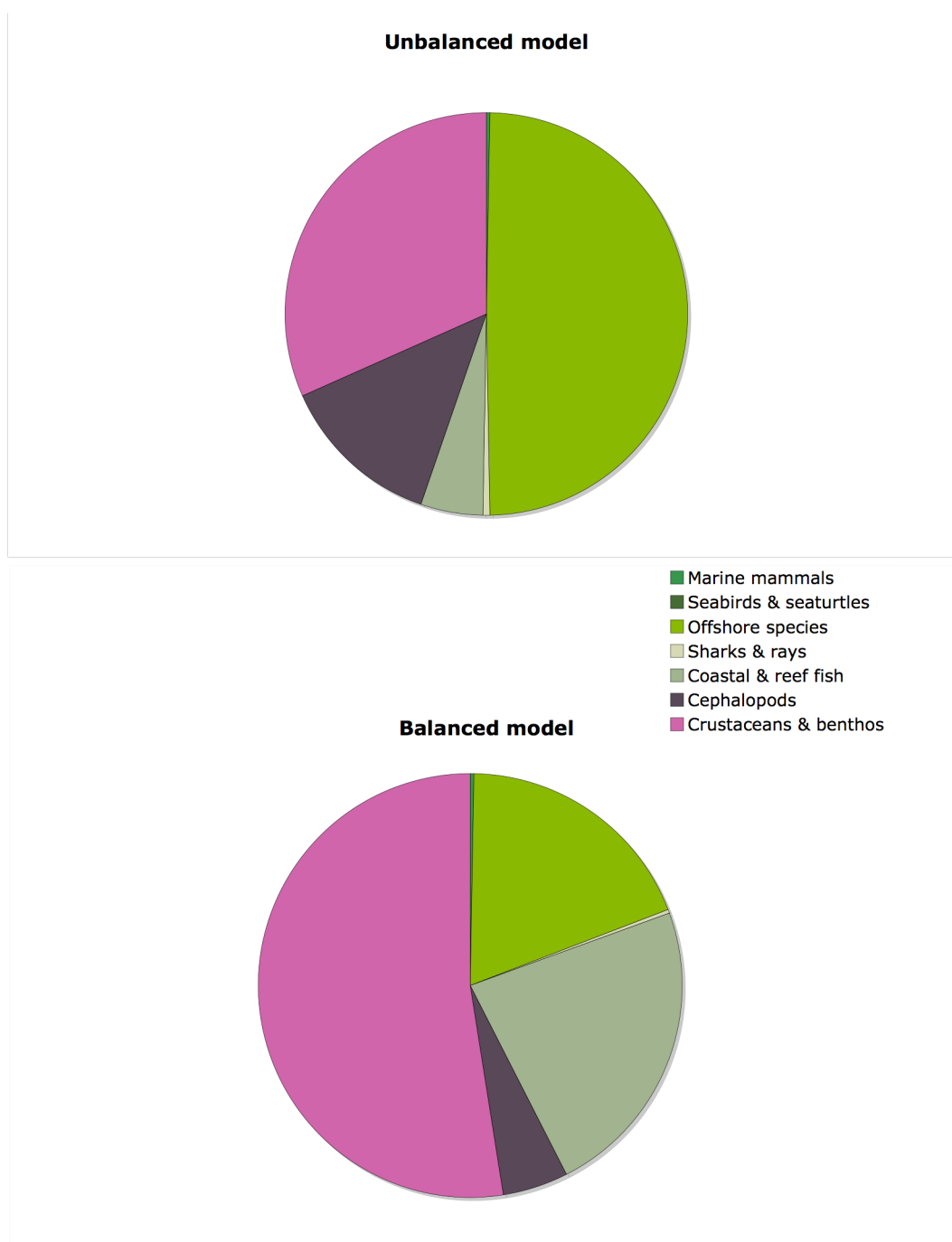
	<b>Ecopath group</b>	<b>Trophic level</b>	<b>B (t*km<sup>-2</sup>)</b>	<b>P/B (year<sup>-1</sup>)</b>	<b>Q/B (year<sup>-1</sup>)</b>	<b>EE</b>
1	Minke whales	3.890	0.005	0.099	8.421	<b>0.000</b>
2	Fin whales	3.220	0.006	0.099	4.161	<b>0.000</b>
3	Humpback whales	3.740	0.070	0.099	5.081	<b>0.000</b>
4	Brydes whales	3.860	0.004	0.050	6.260	<b>0.000</b>
5	Sei whales	3.220	0.001	0.020	6.178	<b>0.000</b>
6	Blue whales	3.200	0.002	0.060	3.398	<b>0.000</b>
7	Sperm whales	4.240	0.019	0.050	5.030	<b>0.000</b>
8	Killer whales	4.070	<b>0.0005</b>	0.020	9.468	0.950
9	Beaked whales	3.880	0.000	0.036	9.933	<b>0.000</b>
10	Small cetaceans	3.800	0.040	0.030	14.404	<b>0.784</b>
11	Seabirds	3.370	0.0002	0.130	73.690	<b>0.000</b>
12	Seaturtles	4.060	0.037	0.835	3.535	<b>0.298</b>
13	Large tunas and billfishes	3.980	0.027	1.250	15.530	<b>0.642</b>
14	Small tunas	3.600	<b>0.014</b>	2.500	25.000	0.950
15	Dolphinfish	4.440	0.028	4.720	20.000	<b>0.741</b>
16	Flyingfish	3.290	0.208	4.000	24.760	<b>0.543</b>
17	Other offshore predators	2.050	1.627	1.954	9.270	<b>0.169</b>
18	Pelagic sharks	4.280	0.012	0.400	10.000	<b>0.265</b>
19	Coastal and demersal sharks and rays	3.740	0.040	0.112	1.800	<b>0.596</b>
20	Scombrids	4.090	0.066	1.090	10.310	<b>0.346</b>
21	Small and schooling pelagics	3.220	16.575	2.940	23.650	<b>0.528</b>
22	Reef fishes	2.950	<b>21.233</b>	1.755	21.000	0.950
23	Coastal predators	3.410	1.260	0.720	7.220	<b>0.675</b>
24	Cephalopods	3.250	5.000	4.725	19.400	<b>0.526</b>
25	Crustaceans and benthos	2.100	<b>51.201</b>	20.000	76.185	0.950
26	Zooplankton	2.200	49.636	12.900	43.350	<b>0.847</b>
27	Benthic producers	1.000	14.186	71.750	-	<b>0.950</b>
28	Phytoplankton	1.000	32.000	100.000	-	<b>0.950</b>
29	Detritus	1	306.5	-	-	<b>0.903</b>

**Table 21.** Diet matrix for the *Ecopath* model of the Caribbean

[illegible]

**Table 21 (cont.).** Diet matrix for the Ecopath model of the Caribbean.

[illegible]



**Figure 3.** Comparison of the biomass structure (excluding benthic producers and plankton) of the unbalanced vs. balanced *Ecopath* models

The changes in the general trophic structure from the unbalanced to balanced models are presented in Figure 3. In both models, the system was dominated by benthic species and crustaceans, but coastal predators and reef fishes were also important. The group that changed the most as a result of balancing the model, in terms of biomass, was the ‘crustaceans and benthos’ group. This group tripled in terms of biomass density in the balanced scenario, but it was still within the range of possible values for similar species in other models of the Caribbean islands.

## TIME SERIES DATA

### CPUEs

The timeseries catch per unit effort (CPUE) data for all marine species in the Caribbean region were obtained from published papers and reports during a thorough search of aquatic sciences and fisheries abstracts (ASFA), google scholar, web of science and fish and fisheries worldwide online databases. In the Caribbean region, we found a total of 14 sources for fish and shellfishes timeseries CPUE information (Table 22). This included CPUE data sets starting from 1960's to 2006's, however, there were time lags with each source for different species (Table 22). The CPUE timeseries data were available to albacore, bigeye tuna, yellowfin tuna, atlantic white and blue marlins, billfishes, dolphinfish, flyingfish, wahoo, sharks, grouper, miscellaneous reef fishes, snapper, Caribbean queen conch and spiny lobster. These species were assigned and aggregated to our established trophic groups with a total of eight trophic groups: large tunas and billfishes, dolphinfish, flyingfish, pelagic sharks, scombrids, coastal predators, reef fishes, and crustaceans and benthos group (Table 22). However, the CPUE information of all trophic groups was not easily compared across studies due to the difference in sampling gears or efforts used in estimating the catch per unit effort (e.g. tonnes per trip, tonnes per hooks, tonnes per dives, tonnes per line fisher). Hence, we noted the different CPUEs units used of each species in the different literatures by aggregating similar species CPUE's units (Tables 23-26).

The catch per unit effort (CPUE) for mutton snapper line and pot fisheries in Puerto Rico was described by Cummings (2007). This study covered the updated and recent CPUE information for mutton snapper (*Lutjanus analis*) in Puerto Rico. It contains CPUE data from 1989 to 2006 for line fishery and for the pot (trap) fishery of mutton snapper. Cummings (2007) also described the procedures used to update the mutton snapper Puerto Rico CPUE indices. The mutton snapper was categorized in our model as belonging to the "coastal predator" trophic group (Table 22). Consequently, its CPUE data were assigned to the other coastal predators, and aggregated with other sources describing species of that group that have similar CPUE units as tonnes per trips (Table 24).

The stock assessment of the Caribbean queen conch (*Strombus gigas*) by Southeast Data, Assessment, and Review (SEDAR 2007) reported CPUE's information for queen conch from the period of 1981 - 2005 in St. Croix and 1989 - 2005 in Puerto Rico. This species was part of the trophic group "crustaceans and benthos" in our model. The CPUE unit of this group was tonnes per trips (Tables 22 and 23). According to the results of SEDAR (2007), queen conch stocks and CPUEs are declining. Furthermore, this species is an important commercial invertebrate in the region, which is currently being exploited by many conch gatherers in the coastal areas (Boulon and Clavijo 1986; Mahon 1987; Opitz 1996; SEDAR 2007). The primary fishing ground of queen conch in the Caribbean is the U.S. Virgin Islands and its adjacent areas (Opitz 1996).

Four-year fishery monitoring of the tiger grouper (*Mycteroperca tigris*) spawning aggregation in Puerto Rico was investigated by Matos-Caraballo *et al.* (2006) (Table 22). They reported the decline of tiger grouper's CPUE from 1996 to 1998 (Table 26). We summarized these data into an aggregated timeseries representing reef fishes with CPUE units being 'tonnes per boat per day'.

The blue shark (*Prionace glauca*) caught by Venezuelan pelagic longline fishery was assessed by Arocha *et al.* (2005). Their main focus of the study was the length composition of blue shark from the Venezuelan pelagic longline fishery for the period of 1994 – 2003 (Table 22). According to Arocha *et al.* (2005), harvest of blue sharks during the first quarter off Guyana and Suriname increase progressively towards Trinidad and further in the Caribbean during the second and third quarter. Fishers move further towards the Caribbean areas and concentrate their harvest in area during the fourth quarter of the year. The blue shark species was categorized in our report as pelagic sharks. We aggregated its CPUE information under 'pelagic sharks' with CPUE units being 'numbers of species per 1000 hooks' (Table 26).

Esquivel-Valle (2005) constructed standardized indices of spiny lobster abundance using the data from NOAA Fisheries Trip Interview Program (TIP) in Puerto Rico. The available CPUE data for spiny lobsters in the area covered a longer time period from 1983 to 2003. According to Esquivel-Valle (2005) the fishery for spiny lobster in the area operates year round. Their study also noted the irregular sampling of the

catches that may underrepresent the total landings. The spiny lobster CPUE's was aggregated as crustaceans and benthos group with CPUE units as 'tonnes per trip' (Tables 21 and 22).

Nemeth (2005) investigated the population characteristics of a recovering U.S. Virgin Islands red hind (*Epinephelus guttatus*) spawning aggregation. The study presented five years of red hind CPUE, wherein a fluctuation in the population trend of the species was observed. Together with the other reef-associated fishes mentioned above, the timeseries data of this species were summarized and aggregated representing the reef fish group with CPUE units as 'tonnes per trap' (Tables 21 and 25).

Saul *et al.* (2005) conducted a preliminary analysis and standardized catch per unit effort indices for yellowtail snapper (*Ocyurus chrysurus*) fishery resulting independent data from 1988 to 2001 in Puerto Rico (Table 22). Their nominal hook and line CPUE for snappers, which categorized as 'coastal predators' herein, increased in the early 1990's, and remained stable from 1993 to 2001 (Table 26). This species was aggregated representing coastal predators group with CPUE unit as 'tonnes per hook and line'.

Early stock assessment of SEDAR (2005b) dealt with the spiny lobster (*Panulirus argus*) CPUE data for the 1974-2003 period and yellowtail snapper (*Ocyurus chrysurus*) for 1984-2003 (Table 22). In this report, they documented a declining catch rates or CPUE's of spiny lobster and yellowtail snapper in the area. In our analysis, the spiny lobster and snapper were categorized as crustaceans and benthos and coastal predators, respectively. The CPUEs units used by SEDAR (2005b) were 'tonnes per trip' (Table 23) for spiny lobsters and 'tonnes per linefisher' (Table 26) for yellowsnapper.

The Caribbean red snapper (*Lutjanus purpureus*) and yellowedge grouper (*Epinephelus flavolimbatus*) biomass assessment of the 1981-2000 periods was done by Mendoza and Larez (2004) (Table 22). The authors showed decreasing CPUEs trends for red snapper and yellow grouper in the Caribbean because of the overexploitation by handliner and longliner operations in the region. They also concluded that red snapper is more exploited than yellow grouper, and they inferred that this is because the differences in habitat depth between species and the greater efficiency of handliners targeting the red snapper (Mendoza and Larez 2004). These species were grouped and aggregated as coastal predators for snapper and reef fishes for yellowedge grouper with CPUE units being 'tonnes per lines per day' (Table 24).

The study of Marciano *et al.* (2002) provides CPUE (tonnes per 100hooks) information for the small longline tuna fishery from eastern Venezuela during the period of 1986 to 2000 (Table 22). This information included catch and efforts for tunas, wahoo, billfishes and sharks in the Caribbean and Atlantic subareas. CPUE data of these species were assigned as large tuna and billfishes, scombrids and pelagic shark in our model (Table 25). Marciano *et al.* (2002) reported decreasing trends of average annual CPUE's for most species in the Caribbean. Among all the species, yellowfin tuna was the most important species contributing higher percentages of the total catches in the Caribbean and Atlantic (Marciano *et al.* 2001).

Parker (2002) proposed a preliminary analysis for flyingfish fishery of Barbados. Their study recorded total landings, catch rates and fishing efforts from 1985 – 2001 (Table 22). Based on their results, CPUEs of flyingfish in the area was fluctuating over time. Flyingfish CPUE unit was 'tonnes per trip' (Table 23).

Exploitation trends for demersal reef fishes in Grenada were studied by Jeffrey (2000). The species included in this study were snappers, groupers and miscellenaous reef fishes (i.e. snook, squirrelfishes, parrotfishes, tilefishes, surgeonfishes, grunts, goatfishes and porgies). CPUE data for snapper species were grouped with coastal predators, and groupers and miscellenaous reef fishes were aggregated to the reef fishes group with CPUE units as 'tonnes per trip' (Tables 22 and 23). Their study revealed that reef fishery resources in the area are declining, as well as monthly catch per unit effort for groupers and snappers declined with increasing fishing intensity during the study period, suggesting overfishing (Jeffrey 2000).

Finally, Mahon and Oxenford (1999) dealt with the precautionary assessment and management of dolphinfish in the Caribbean. Their study contained CPUE information for dolphinfish around the Caribbean waters. Mahon and Oxenford (1999) stated that the continuation of the high amount of catches of the dolphinfish in the area could lead to stock depletion. The dolphinfish CPUE units used in their study were 'tonnes per trip' and 'fish per 100 trips' (Tables 23 and 26). These catch rates were incorporated into our model analysis.

**Table 22.** The different sources of trophic group CPUE information available for the Caribbean region.

Source	Species studied	Ecopath Group	Year covered	Countries	CPUE's unit
Cummings 2007	Mutton Snapper	Coastal predators	1989-2006	Puerto Rico	tonnes/trip
SEDAR 2007	Caribbean queen conch	Crustaceans and Benthos	1989-2005	Puerto Rico	tonnes/trip
SEDAR 2007	Caribbean queen conch	Crustaceans and Benthos	1981-2005	St.Croix	tonnes/trip
Esquivel-Valle 2005	Spiny lobster	Crustaceans and Benthos	1984-2003	Puerto Rico	tonnes/trip
SEDAR 2005a	Spiny lobster	Benthos	1974-2003	Virgin Islands	tonnes/trip
Parker 2002	Flyingfish	Flyingfish	1985-2001	Barbados	tonnes/trip
Jeffrey 2000	Snapper	Coastal predators	1986-1993	Grenada	tonnes/trip
Jeffrey 2000	Grouper	Reef fishes	1986-1993	Grenada	tonnes/trip
Jeffrey 2000	Miscellaneous reef fishes	Reef fishes	1986-1993	Grenada	tonnes/trip
Mahon and Oxenford 1999	Dolphinfish	Dolphinfish	1961-1989	Barbados	tonnes/trip
Mahon and Oxenford 1999	Dolphinfish	Dolphinfish	1982-1989	Grenada	tonnes/trip
Mahon and Oxenford 1999	Dolphinfish	Dolphinfish	1978-1989	Puerto Rico	tonnes/trip
Mahon and Oxenford 1999	Dolphinfish	Dolphinfish	1985-1989	St. Lucia	tonnes/trip
Mendoza and Larez 2004	Southern red snapper	Coastal predators	1981-1999	Southeastern Caribbean	tonnes/lines/day
Mendoza and Larez 2004	Yellow grouper	Reef fishes	1981-1999	Southeastern Caribbean	tonnes/lines/day
Marcano <i>et al.</i> 2002	Yellowfin tuna	Large tunas and billfishes	1986-1999	Caribbean Sea	tonnes/100hooks
Marcano <i>et al.</i> 2002	Albacora	Large tunas and billfishes	1986-2000	Caribbean Sea	tonnes/100hooks
Marcano <i>et al.</i> 2002	Big eye tuna	Large tunas and billfishes	1986-2000	Caribbean Sea	tonnes/100hooks
Marcano <i>et al.</i> 2002	Billfishes	Large tunas and billfishes	1986-2000	Caribbean Sea	tonnes/100hooks
Marcano <i>et al.</i> 2002	Shark	Pelagic sharks	1986-2000	Caribbean Sea	tonnes/100hooks
Marcano <i>et al.</i> 2002	Wahoo	Scombrids	1986-2000	Caribbean Sea	tonnes/100hooks
Matos-Caraballo <i>et al.</i> 2006	Tiger grouper	Reef fishes	1995-1998	Puerto Rico	tonnes/boat-day
Arocha <i>et al.</i> 2005	Blue shark	Pelagic sharks	1994-2003	Trinidad, Caribbean	numbers/1000 hooks
Nemeth 2005	Red hind	Reef fishes	1997-2003	US Virgin Islands	tonnes/traps and line
Saul <i>et al.</i> 2005	Yellow snapper	Coastal predators	1988-2001	Puerto Rico	tonnes/hook
SEDAR 2005b	Yellow snapper	Coastal predators	1984-2003	St.Thomas/St.John	tonnes/linesfisher
Mahon and Oxenford 1999	Dolphinfish	Dolphinfish	1978-1989	St. Vincent	Fish/100trips



**Table 23.** Catch per unit effort (tonnes/trip) by trophic groups in the Caribbean region. Data were derived from Cummings 2007; SEDAR 2007; Esquivel-Valle 2005; SEDAR 2005b; Parker 2002; Jeffrey 2000, and Mahon and Oxenford 1999.

<b>Year</b>	<b>15 Dolphinfish</b>	<b>16 Flyingfish</b>	<b>22 Reef fishes</b>	<b>23 Coastal predators</b>	<b>25 Crustaceans and Benthos</b>
1961	0.010260				
1962	0.009470				
1963	0.005130				
1964	0.016970				
1965	0.010260				
1966	0.009470				
1967	0.010660				
1968	0.017760				
1969	0.030400				
1970	0.026050				
1971	0.051824				
1972	0.040452				
1973	0.024984				
1974	0.031294				
1975	0.052224				
1976	0.045281				
1977	0.047401				
1978	0.058390				
1979	0.044860				
1980	0.072170				
1981	0.037900				61.688562
1982	0.037675				51.709530
1983	0.047546				24.796385
1984	0.023632				34.782628
1985	0.117004	0.062647			40.226885
1986	0.093794	0.037059	0.113646	0.016322	20.877702
1987	0.075233	0.039706	0.098343	0.028582	32.968786
1988	0.111068	0.058235	0.078968	0.016539	31.152399
1989	0.111908	0.060882	0.026949	0.011829	14.407557
1990		0.027353	0.036907	0.012872	10.324577
1991		0.039706	0.037512	0.012667	104.310557
1992		0.043235	0.009872	0.011142	59.970940
1993		0.031765	0.027032	0.014099	43.399383
1994				0.001424	40.072024
1995			0.043000	0.001546	54.474754
1996		0.015882	0.058000	0.001502	52.358285
1997		0.023824	0.050400	0.001386	47.631743
1998		0.020294	0.028950	0.001598	51.640306
1999		0.036176		0.002219	44.195341
2000		0.044118		0.002037	43.778594
2001		0.033529		0.001944	48.845334
2002				0.001918	47.066394
2003				0.003095	49.712851
2004				0.002076	62.746928
2005				0.001633	68.946033
2006				0.001476	

**Table 24.** Catch per unit effort (tonnes/lines\*day) by trophic groups in the Caribbean region. Data derived from Mendoza and Larez 2004.

<b>Year</b>	<b>22 Reef fishes</b>	<b>23 Coastal predators</b>
1981	0.000205	0.01012
1982	0.00018	0.0105
1983	0.000162	0.011413
1984	0.000148	0.00563
1985	0.000143	0.004641
1986	0.000158	0.003957
1987	0.000298	0.007685
1988	0.000157	0.004793
1989	0.000159	
1990	0.000159	0.011261
1991	0.000099	
1992	0.00013	0.007457
1993	0.000059	0.004793
1994	0.000034	0.003348
1995	0.000088	0.002815
1996	0.000098	0.004489
1997	0.000102	0.001902
1998	0.00011	0.002663
1999		0.002283
2000	0.000049	

**Table 25.** Catch per unit effort (tonnes/100 hooks) by trophic groups in the Caribbean region. Data were derived from Marciano *et al.* 2002.

<b>Year</b>	<b>13 Large tunas and billfishes</b>	<b>18 Pelagic sharks</b>	<b>20 Scombrids</b>
1973			
1974			
1975			
1976			
1977			
1978			
1979			
1980			
1981			
1982			
1983			
1984			
1985			
1986	0.000430	0.000032	
1987	0.000486	0.000045	
1988	0.000355	0.000025	
1989	0.000401	0.000026	0.000005
1990	0.000324	0.000028	0.000026
1991	0.000720	0.000019	0.000020
1992	0.000688	0.000070	0.000005
1993	0.000654	0.000068	0.000008
1994	0.000675	0.000064	0.000080
1995	0.000529	0.000053	0.000026
1996	0.000433	0.000046	0.000040
1997	0.000233	0.000074	0.000018
1998	0.000474	0.000011	0.000002
1999	0.000657	0.000068	0.000004
2000	0.000561	0.000062	0.000003
2001			
2002			

**Table 26.** Catch per unit effort of trophic groups that has single data sets for CPUE units: Fish/100 trips, numbers/1000hooks, tonnes/traps, tonnes/day/boat, tonnes/lines fisher and tonnes/hook and line. Data derived from Matos-Caraballo *et al.* 2006; Arocha *et al.* 2005; Nemeth 2005; Saul *et al.* 2005 and SEDAR 2005a.

Year	15 Dolphinfish Fish/100trips	18 Pelagic sharks numbers/1000 hooks	22 Reef fishes tonnes/traps	22 Reef fishes tonnes/day/boat	23 Coastal predators tonnes/lines fisher	23 Coastal predators tonnes/hook and line
1960						
1961						
1962						
1963						
1964						
1965						
1966						
1967						
1968						
1969						
1970						
1971						
1972						
1973						
1974						
1975						
1976						
1977						
1978	31.107000					
1979	33.960000					
1980	23.389000					
1981	20.705000					
1982	29.933000					
1983					0.424290	
1984	16.510000				0.350663	
1985	32.114000				0.386697	
1986	31.950000				0.192831	
1987	16.170000				0.189783	
1988	31.610000				0.212644	0.000004
1989	30.100000				0.343982	0.000005
1990					0.288760	0.000003
1991					0.401008	0.000010
1992					0.341976	0.000045
1993					0.420043	0.000017
1994		3.880000			0.400830	0.000030
1995		2.290000		0.043000	0.633578	0.000026
1996		1.410000		0.058000	0.742939	0.000029
1997		3.010000		0.050400	0.674515	0.000028
1998		4.850000		0.028950	0.622669	0.000000
1999		4.250000			0.460215	0.000021
2000		2.870000	0.001576		0.571602	0.000025
2001		4.670000	0.001591		0.704565	0.000014
2002		2.620000	0.004453		0.652160	
2003		0.800000	0.001102		0.658344	
2004			0.007319			

## FISHING EFFORT

Fishing effort of single species is the preferred type of data to use as time series to drive changes in biomass for the dynamic simulations in Ecosim (Christensen *et al.* 2005). Unfortunately, there was only little information available for timeseries fishing effort for single species in the region (Table 27). The timeseries fishing effort data we found on single species were: yellowtail snapper in St. Thomas/St. John (SEDAR 2005a) and Puerto Rico (Saul *et al.* 2005), spiny lobsters in Puerto Rico (Esquivel-Valle 2005) and flyingfish in Tobago (Potts *et al.* 2002). We did not incorporate timeseries fishing effort information from multiple species since it was hard to segregate information of their combined fishing efforts data. Timeseries effort data for multiple species in the region were available in several sources (e.g. Mahon *et al.* 1994b; Mohammed 2003b; Zeller *et al.* 2003). Fishing effort timeseries data from single species were used in our simulation analysis.

Similar to the CPUE information, the timeseries fishing effort data for all stocks have different fishing effort units. Hence, we categorized the fishing effort by our trophic groups as well as by effort units. Consequently, we have fishing effort series for three trophic groups with number per trip: large tunas and billfishes, flyingfish and crustaceans and benthos (Table 28), one group with number per line fishers and number per hook and line: coastal predators (Table 29), and one group with number per dives and number per traps: crustaceans and benthos (Table 29).

**Table 27.** The different sources of timeseries fishing effort for the Caribbean region

Source	Species studied	Trophic groups	Fishing Effort Units	Country
Potts <i>et al.</i> 2002	Flyingfish	Flyingfish	no. of trips	Tobago
Mahon <i>et al.</i> 1994a	Pelagic fishes	Large pelagic tunas and billfishes	no. of trips	Gouyave Grenada
Mahon <i>et al.</i> 1994a	Pelagic fishes	Large pelagic tunas and billfishes	no. of trips	Melville Grenada
Esquivel-Valle 2005	Spiny lobsters	Crustaceans and benthos	no. of trips	Puerto Rico
Esquivel-Valle 2005	Spiny lobsters	Crustaceans and benthos	no. of dive	Puerto Rico
Esquivel-Valle 2005	Spiny lobsters	Crustaceans and benthos	no. of fish traps	Puerto Rico
Esquivel-Valle 2005	Spiny lobsters	Crustaceans and benthos	no. of lobster traps	Puerto Rico
Saul <i>et al.</i> 2005	Yellow snapper	Coastal predators	no. of hook&line	Puerto Rico
SEDAR 2005a	Yellow snapper	Coastal predators	no. line fishers	St. Thomas/St John

**Table 28.** Fishing effort as ‘number of trips’, for three trophic groups. Data derived from Potts (2002) and Mahon *et al.* (1994b).

Year	13 Large pelagic tuna and billfishes	16 Flyingfish	25 Crustaceans and benthos
1981	327		
1982	314		
1983	301		
1984	287		144
1985	346		66
1986	387		52
1987	397	1340	82
1988	300	1371	8
1989	299	1644	126
1990	233	1192	124
1991			181
1992		1192	183
1993		1605	146
1994		990	63
1995		1091	133
1996			112
1997		686	61
1998		319	116
1999			151
2000			124
2001			157
2002			104
2003			135

**Table 29.** Fishing efforts: ‘no. of line fishers’, ‘no. of hook & line’, ‘no. of dives’, ‘no. of lobster trap’, for two trophic groups. Data derived from Esquivel-Valle (2005); Saul *et al.* (2005) and SEDAR (2005a).

Year	23		25		
	Coastal predators		Crustaceans and benthos		
	no. line fishers	no. of hook and line	no. of dive	no. of fish traps	no. of lobster traps
1983	25				
1984	25			144	
1985	25		1	65	
1986	25		3	49	
1987	25		20	58	4
1988	25	127.8	0	8	
1989	20	680	79	32	
1990	28	81	110	8	
1991	28	97.2	130	31	7
1992	28	40.5	138	25	4
1993	28	81	118	16	4
1994	28	72.27	41	20	1
1995	25	102.99	119	13	
1996	20	60.3	88	17	
1997	20	15	45	13	3
1998	20	0	92	10	9
1999	30	43.59	114	25	5
2000	30	45	104	11	5
2001	30	29.49	136	13	5
2002	30		84	14	1
2003	30		108	17	

## UNCERTAINTY ANALYSES

Given the high level of uncertainty in data, parameterization and model structure (Plagányi and Butterworth 2004; Essington 2006; Plagányi *et al.* 2007), we conducted several levels of uncertainty analyses. Our efforts focused on facilitating data collection that would shed light on the most appropriate choice of model form with which to represent feeding behaviour. Three levels of uncertainty analyses were performed here. First, a sensitivity routine included in *Ecopath* was used to explore the effects of uncertainty of inputs values on the model's outputs. A second uncertainty analysis was performed using *Ecoranger*, a resampling routine based on input probability distributions. Finally, the robustness of our models' structure was tested with *Ecosim* by comparing predicted biomasses with time series of observed data.

### Sensitivity analysis

A sensitivity routine was included in *Ecopath* to allow users to explore the effects of uncertainty on the model results. The method was quite simple, and consisted of plotting relative output changes against relative changes in the inputs. The routine varies all basic input parameters (biomass [B], production to biomass ratio [P/B], consumption to biomass ratio [Q/B], ecotrophic efficiency [EE]) in steps from -50.0% to +50.0% for each trophic group of the model, and then checks what effect each of these steps has for each of the input parameters on all of the “missing” basic parameters for each group in the system (Christensen *et al.* 2005). The output is then given as the proportion of the difference between the estimated and original parameter to the original parameter, and converted to a percentage (Christensen *et al.* 2005). This method only re-estimates the parameters for which no data were available, and that were left to be estimated by the model, using the mass-balance constraints.

We conducted a sensitivity analysis for biomass, P/B, Q/B and EE input parameters. Our results suggested that the sensitivity of these estimated parameters to a change in input values was relatively low (Appendix 1). A 50.0% change in any of the input parameters of any trophic group generated an overall response of

about 39% in the estimated parameters of other groups. All the changes in inputs parameters produced by the sensitivity analysis routine had their effect on the EE of other trophic groups.

The most impacted factor in our model seems to be the EE. For biomass inputs, a change would affect all and any parameter with an average 24.7% of change, and EE would change by about 26.0% after a change of 50% in any biomass input. For the P/B ratio, a 50.0% change of any group would generate an average response of 73.6% of any parameter, and a response of 63.5% in the estimated EE of other groups. Similarly, for Q/B input values, a 50.0% change of this value for any group would generate an overall response of 21.7% on any parameter, and an average 19.8% change in the estimated EE of other trophic groups.

Overall, our sensitivity analysis suggested that potential errors in model results were approximately linearly related to potential error in model parameters, etc. This result was consistent with those of Essington (2006). This underscores the importance of enhancing the quality of data included in our model.

### *‘Ecoranger’ analysis*

To account for the inherent uncertainty of input parameters, a resampling routine called *Ecoranger* was included in the *EwE* software and accepted input probability distributions for the biomasses, consumption and production rates, ecotrophic efficiencies, catch rates, and diet compositions. *Ecoranger* then draws random input variables using the range of possible values for each parameter, and the resulting model was then evaluated (based on least sum of squared residuals and comparison with independent data and physiological and mass-balance constraints) (Christensen *et al.* 2005).

Starting with the initial model and these setups, 10,000 models were run by *Ecoranger*, until 200 model runs passed the selection criteria, and the best fitting model for the Caribbean islands was used for further analysis.

### *Fitting the model to time series data*

The *Ecosim* model behaviour is based on a ‘foraging arena’ theory (Walters and Kitchell 2004), which assumed that predator and prey behaviors cause partitioning of prey populations, which were either available or unavailable to predators. There was continuous change between these two stages for any given potential prey, whether it was hiding from predation in some refuge, or it was out to feed. This availability of prey to predators was called ‘vulnerability’ in *Ecosim*. Mackinson *et al.* (2003) demonstrated the importance of setting the vulnerabilities to fit model predictions to time-series data, as *Ecosim* predictions are very sensitive to this parameter. Using default values for  $v$  has strong implications for assumptions about species abundance relative to their carrying capacity (V. Christensen, Fisheries Centre, UBC, personal communication). Basically, it assumed that each group can at most increase the predation mortality they imposed on their prey with a factor of 2.0 (the default  $v$  value). A lower value implies a donor driven density-dependent interaction. On the other hand, a higher value involved a predator driven density-independent interaction, in which predation mortality was proportional to the product of prey and predator abundance (i.e., Lotka-Volterra). This implies a high flux rate for prey species in and out of vulnerable biomass pools (Ainsworth 2006). Vulnerabilities were thus adjusted based on the specific ecology of each species or trophic groups (if their behaviour, niche, or diet make them more or less vulnerable to predators).

Using the few time series of biomass available for the trophic groups in our model, we compared *Ecosim*’s projections with observed data, and adjusted  $v$ ’s and other input parameters (within their range of uncertainty) until we obtained a model configuration that allowed us to reproduce as much as possible the trends in biomass.

Using credible models that can reproduce observed historical response to disturbances such as fishing was a useful approach to validating our model in light of the highly uncertain data included in the model. Fitting time series data to model predictions therefore enhances our confidence about the possible impact of removing marine mammals in the ecosystem (Morissette 2007).



## DISCUSSION

The present sets of data were used to construct our model for analyzing the trophic interaction of marine mammals and fisheries in the Caribbean ecosystem. This model was revised after the validation made by the local experts on fisheries, species ecology and biology, and in ecosystem modelling in the Caribbean during a workshop held in Barbados (“Whales and Fish interactions: Are great whales a threat to fisheries”, see [http://www.lenfestoceano.org/whales\\_fisheries.html](http://www.lenfestoceano.org/whales_fisheries.html)) in September 2008. Suggestions made by local experts included the addition of more important commercial fish groups (e.g. billfishes, dolphinfish, flyingfish, pelagic sharks) in our model and better incorporation of local fisheries data from the region (i.e. LAPE national report). These suggestions were followed and we revised our initial model to its actual form.

### *Uncertainty in the input data*

Several sources of uncertainty influenced the modelling results presented in this report. The most reliable published fisheries catch estimates for commercial fish and non-fishes species in the Caribbean were from *Lesser Antilles Pelagic Ecosystem* (LAPE) fisheries report and *Sea Around Us Project* (SAUP). The LAPE database contained recent catches of the Lesser Antilles countries that were obtained from local fisheries departments for the 2001-2005 periods. On the other hand, the *Sea Around Us database* contained longer time series catch estimates (starting in the 1950s; we used data for the 1987-2004 period) for fish and shellfish groups in the region. However, recent work on catch data is not included in the SAUP database (E. Mohammed, Fisheries Division, Government of Trinidad and Tobago, personal communication). Due to the expected discrepancies between the two data sets, catch estimates of Lesser Antilles countries from LAPE and SAUP databases were compared. This analysis showed that catches in both databases were relatively similar in terms of the total catches for all local countries combined. They only differ in minute decimal places of their total catches. However, if we considered catch data for individual countries, high discrepancies were observed. These differences could be due to the way catches of species were re-allocated to their geographic origin for each country by the SAUP database *versus* the reported landings in the LAPE database. In addition to this uncertainty in the databases, catch estimates could involve underestimated catches due to unreported landings from recreational fleets and small-scale fisheries (Mahon and Oxenford 1999, Mohammed *et al.* 2007a) and in species identification of the catch.

The catch per unit effort (CPUE) estimates extracted from literatures (e.g. Marcano *et al.* 2002; Parker *et al.* 2002; Restrepo *et al.* 2003; Arocha *et al.* 2005; Esquivel-Valle 2005; Cummings 2007) were generally based on fleets and landings. Such processes could cause variation and uncertainty in the data because the main objective in real time fishing was to gather as much fish as possible with no regards to species or type; and the used of advance fishing gear and equipment that enable the fishermen to find the most abundant fishing sites, could results to higher catch rates (CPUE). In addition, the scarcity of information for catch rates of single species could be explained by the fact that most fisheries or fishermen follow a generalistic harvesting strategy i.e. fleets harvesting demersal species can fish for large pelagics while on route to their destination (Mahon and Oxenford 1999).

The Ecopath parameter estimates (B, P/B, Q/B) of similar species across local studies can vary. Additionally, some of these local studies based their Ecopath parameter values on the same source that we included in our model, for example P/B value for seaturtles used by Olson and Watters 2003, and Mohammed *et al.* 2007b was derived from similar species of seaturtles from Opitz 1996. Hence, in order to avoid over-representation of some inputs when averaging all values from other models, we used the mid-range (rather than mean) estimates of annual biomass, P/B and Q/B for some trophic groups in the present model. However, it is important to note that the input parameters for most of the trophic groups of our model are based on field surveys, stomach contents analysis and stock assessments in the area. While these estimates from local studies of our trophic groups were relatively reliable, uncertainty still occurs. An example of such uncertainty was the selectivity variations that were linked to field sampling for species abundance. This variation is not usually quantified (Mohammed *et al.* 2007b). In addition, the mortality rates (and thus their P/B) of large pelagic species (e.g. yellowfin tuna, albacore, billfishes, wahoo) depend on the quality of the available catch data from regional stock assessment (Mohammed *et al.* 2007b). This stock assessment information includes areas outside the Caribbean ecosystem (Mohammed *et al.* 2007b) which, therefore, could overestimate the fishing mortality of fish species due to migration out of the study area. Fishing mortality could be underestimated as well, i.e. under reporting catches (particularly for dolphinfish), small sized fish species utilized as baits, or discards (Mahon and Oxenford 1999; Mohammed *et al.* 2007b). As for marine mammal biomass, the updated global biomass

densities estimates of Kaschner (2004) are so far the most reliable source. The latter developed a model to capture pattern of species occurrence and densities even for areas that have not been covered by marine mammal surveys or for species that are extremely difficult to observe in the wild. Whenever possible, we validated estimates derived from the global, model were validated using abundance estimates from dedicated surveys conducted in similar habitats (Morissette *et al.* submitted). These standardized abundance estimates of marine mammals are continuously updated with recent published population studies up and compiled in a global marine mammal database by Kaschner (2004).

The diet information is important for investigating the interaction of predator-prey relationship (Morissette 2005). By having quantitative diet estimates of cetaceans, fish groups and non-fish groups, we can determined their dynamics with other compartments of the ecosystem, whether cetaceans were competing with fisheries or eat other species that were less important for fishing. In the Caribbean region, the quantitative information on diet composition for cetacean was limited. The only available cetacean diet information reported for our study area specifically was for the Bryde's whales (Tershy 1992; Heileman *et al.* 2007), sperm whales (Kawakami 1980; Clarke *et al.* 1980; Pascoe *et al.* 1990; Smith and Whitehead 2000; dos Santos and Haimovici 2001; Hickmott 2005), killer whales (Alonso *et al.* 1999; Heileman *et al.* 2007), and beaked whales (Debrot and Barros 1992; Hickmott 2005). The majority of stomach contents analyses available were obtained from whale stranding samples. This will introduce biases, however, since samples may not be representative for the actual diet of the whole population. Cetacean diet composition varies over time as well as locations; and thus, what they eat is certainly not a function of what food items are present in the area in the certain quantities and proportions (Lavigne 1996; Holt 2006). We were, however, unable to find diet information for minke whales, fin whales, humpback whales, sei whales and blue whales in the Caribbean areas. According to Mohammed *et al.* (2007b), most of these large whales are migrating species that seasonally occur in the Caribbean areas, and hence, less studied and observed in the region. Nevertheless, we incorporated the best available quantitative diet information for cetaceans in the area and from the similar ecosystem providing its general diet compositions and the amount of energy contributed by each prey to cetaceans' diet. With the available literature on the diet and biology of cetaceans (e.g. Pauly *et al.* 1998b; Perrin *et al.* 2002), and general knowledge on the biology and ecology of whales, the prey species for cetacean diets were aggregated according to our trophic groups in our model.

### *Strengths and weaknesses of the model*

Significant effort was devoted to review all the existing *Ecopath* models available for the region and any available stock assessment studies on commercial fish species. Our model covered the Caribbean region and included many important marine mammal species as well as important commercial fish and non-fish group, in particular fish species harvested by humans (e.g. tuna, billfishes, flyingfish, scombrids, reef fishes) in the Caribbean ecosystem. To address uncertainty, we conducted a sensitivity and *Ecoranger* analyses on our data input. In this context, the inclusion of data sets from the existing *Ecopath* models in adjacent Caribbean areas for confidence interval limits of our input data provided ranges of *Ecopath* parameters values of our trophic groups important in the Caribbean ecosystem. This is an important step in the way we used and analysed *Ecopath* models, and have been done only few times so far (Morissette 2005; Morissette *et al.* submitted; Savenkoff *et al.* 2007; Bundy *et al.* in press) The inclusion of SAUP data also allowed us to conduct Ecosim analysis and validation over a longer time period, from 1987 to 2005. With this analysis, our model becomes a useful and reliable tool for policy makers in implementing management scenarios appropriate with the available resources. These efforts made our model more advantageous compared to the rest of *Ecopath* models in the adjacent Caribbean areas.

On the other hand, the lack of local timeseries biomass of marine mammals and other trophic groups, scarcity of timeseries CPUE data, fishing efforts and diet information of cetaceans in the region are serious caveats, although the uncertainty analysis indicated that our major findings are unlikely to change with improved or updated data. Nevertheless, regional research efforts aiming to fill the gaps in data would be useful. Such data would be essential to further test more realistic scenarios between the interaction of marine mammals and fisheries in the Caribbean ecosystem. Further research on marine mammals abundance, catches and diets, as well as fisheries catches in the area would enhance the quality and precision of the model.

## ACKNOWLEDGEMENTS

The authors were thankful for the support of Lenfest Ocean Program and for all the participants of the Caribbean workshop in Barbados. Their inputs and comments on the methods and data used for the construction of this model were priceless. Special thanks were also given to Paul Fanning, Robin Mahon, Elizabeth Mohammed and Silvia Opitz for their constructive insights and support in constructing this preliminary version of the model, and to Margaret Columbe and Allison Hoynes-O'Connor for editing the manuscript. Reg Watson and Dirk Zeller were acknowledged for their willingness and assistance in clarifying the Caribbean fisheries data.

## REFERENCES

- Ainsworth, C.H. 2006. Strategic marine ecosystem restoration in Northern British Columbia. University of British Columbia, Canada.
- Allen, K. 1971. Relation between production and biomass. *Fish. Res. Board Can.* **28**:1573–1581.
- Alonso, M.K., Pedraza, S.N., Schiavini, A.C.M., Goodall, R.N.P., and Crespo, E.A. 1999. Stomach contents of false killer whales (*Pseudorca crassidens*) stranded on the coasts of the Strait of Magellan, Tierra del Fuego. *Mar. Mamm. Sci.* **15**:712–724.
- Alvarez-Hernández, J. H. 2003. Trophic model of a fringing coral reef in the southern Mexican Caribbean [modelo trófico para un arrecife de coral de tipo borde-barrera en el sur del caribe mexicano]. pp 227–335. In D. Zeller, Booth, S., Mohammed, E., and Pauly, D., (Eds). From Mexico to Brazil: Central Atlantic fisheries catch trends and ecosystem models. *Fish. Centre Res. Rep.* 11(6):227–335. The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Arocha, F.T., R., Silva, J., and Marciano, L. 2005. Blue shark (*Prionace glauca*) length composition from the Venezuelan pelagic longline fleet in the northwestern Atlantic: period 1994–2003. *Int. Comm. Conserv. Atl. Tunas, Collect. Vol. Sci. Pap.* **53**:942–950.
- Armstrong, A. J. and W. R. Siegfried. 1991. Consumption of Antarctic krill by minke whales. *Antarctic Science* **3**:13–18.
- Bacci, M.E. 1998. Marine protected areas in the Eastern Caribbean. Caribbean Natural Resources Institute (CANARI) Technical Report 251. Caracas, Venezuela.
- Barlow, J. 2003a. Cetacean abundance in Hawaiian waters during summer/fall 2002. Administration report, Admin. Rept. LJ-03-13. Southwest Fisheries Science Center (SWFSC), National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), La Jolla, CA, USA.
- Barlow, J. 2003b. Preliminary estimates of the abundance of cetaceans along the U.S. west coast: 1991–2001. Administrative Report, Admin. Rept. LJ-03-03. Southwest Fisheries Science Center (SWFSC), National Marine Fisheries Service, (NMFS), National Oceanic and Atmospheric Administration (NOAA), La Jolla, CA, USA.
- Barlow, J. 2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. *Marine Mammal Science*, **22**: 446–464.
- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., and Doherty, P.A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**:389–392.
- Bax, N. J. 1998. The significance and prediction of predation in marine fisheries. *ICES J. Mar. Sci.* **55**:997–1030.
- Bell, C.D., Solomon, J.L., Blumenthal, J.M., Austin, T.J., Ebanks-Petrie, G., Broderick, A.C., and Godley, B.J. 2007. Monitoring and conservation of critically reduced marine turtle nesting populations: lessons from the Cayman Islands. *Anim. Conserv.* **10**:39–47.
- Bentivoglio, A.A. 1988. Investigations into the growth, maturity, mortality rates and occurrence of the dolphin (*Coryphaena hippurus*, Linnaeus) in the Gulf of Mexico. University College of North Wales, Bangor, UK. Master Thesis. pp 37.
- Best, P.B., Sekiguchi, K., Rakotonirina, B., and Rossouw, A. 1996. The distribution and abundance of humpback whales off southern Madagascar, August–September 1994. Reports of the International Whaling Commission, **46**: 323.
- Blanco, C. and Raga, J.A. 2000. Cephalopod prey of two *Ziphius cavirostris* (Cetacea) stranded on the western Mediterranean coast. *J. Mar. Biol. Assoc. U.K.* **80**:381–382.
- Boulon, R.H.J. and Clavijo, I.E. 1986. Utilization of the Virgin Islands biosphere reserve by artisanal fishermen. Virgin Islands Biosphere Reserve Research Report Virgin Islands Resource Management Cooperative, Virgin Islands National Park. pp 36.
- Brown, S.G. and Lockyer, C.H. 1984. Whales. pp 717–781. In R. M. Laws, (Ed). *Antarctic Ecology*. Academic Press, London, UK.
- Bundy, A., Heymans, S.J.J., Morissette, L., and Savenkoff, C. in press. Seals, cod and forage fish: a comparative exploration of variations in the theme of stock collapse and ecosystem change in Northwest Atlantic ecosystems. *Prog. Oceanogr.*
- Calambokidis, J. and Barlow, J. 2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. *Marine Mammal Science* **20**: 63–85.
- CANARI. 1999. Community-base tourism in the Caribbean. Caribbean Natural Resources Institute. pp 22.
- Chan, C. and Shing, A. 1999. Shark fisheries in the Caribbean: the status of their management including issues of concern in Trinidad and Tobago, Guyana and Dominica. In R. Shotton, (Ed). Case studies of the management of elasmobranch fisheries. Part 1. Food and Agriculture Organization of the United Nations, Rome, Italy. pp 479
- Christensen, I., Haug, T., and Øien, N. 1992. A review of feeding and reproduction in large baleen whales (Mysticeti) and sperm whales *Physeter macrocephalus* in Norwegian and adjacent waters. *Fauna Norv. Ser. A* **13**:39–48.
- Christensen, V. and Pauly, D. 1992. Ecopath II - a software for balancing steady-state models and calculating network characteristics. *Ecol. Model.* **61**:169–185.
- Christensen, V. and Walters, C.J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.* **172**:109–139.
- Christensen, V., Walters, C.J., and Pauly, D. 2005. Ecopath with Ecosim: a user's guide. Fisheries Centre, University of British Columbia, Vancouver, Canada and International Center for Living Aquatic Resources Management, Penang, Malaysia. pp 131
- Clapham, P.J. 2002. Humpback whale - *Megaptera novaeangliae*. pp 589–592. In W.F. Perrin, Würsig, B., and Thewissen, J.G.M., (Eds). *Encyclopedia of Marine Mammals*. Academic Press, San Diego, CA.
- Clarke, M.R., MacLeod, N., Castello, H.P., and Pinedo, M.C. 1980. Cephalopod remains from the stomach of a sperm whale stranded at Rio Grande do Sul in Brazil. *Mar. Biol.* **59**:235–239.

- Clarke, W.G. 1982. Historical rates of recruitment to Southern Hemisphere fin whale stocks. *Rep. Int. Whal. Commn* **32**:305-324.
- CLME. 2007. Caribbean Large Marine Ecosystem (CLME) Project. Available online at <http://cavehill.uwi.edu/cermes/clmeInfo.html>, accessed on November 18, 2008.
- Constable, A. and Gales, N. 2002. Evaluating the strength of interactions between predators and prey species in food webs: an Index of Predator Influence (IPI) on controlling available production of prey. Paper presented during the Intersessional Workshop on Modelling Cetacean-Fishery Interactions, La Jolla.
- Cummings, N. 2007. Updated commercial catch per unit of effort indices for mutton snapper line and pot fisheries in Puerto Rico, 1983-2006, SEDAR14 AWO1. SEDAR-14 Assessment Workshop Report 1.
- Cummings, N. and Matos-Caraballo, D. 2007. Information on commercial removals of the mutton snapper, *Lutjanus analis*, in Puerto Rico from 1983 through 2005 and trends in nominal catch per unit effort, SEDAR14-DW-7. SEDAR-14 Data Workshop Report 4.
- Davis, R.W. and Fargion, G.S. 1996. Distribution and Abundance of Marine Mammals in North-Central and Western Gulf of Mexico: Final Report. Volume II: Technical Report. Technical Report, OCS Study MMS 96-0027. US Department of the Interior, Minerals Management Service.
- Davis, R.W., Evans, W.E., and Wursig, B. 2000. Cetaceans, Sea Turtles and Seabirds in the Northern Gulf of Mexico: Distribution, Abundance and Habitat Associations. Volume II: Technical Report. Technical Report, OCS Study MMS 2000-003 - USGS/BRD/CR-1999-0005. Texas A&M University at Galveston and the National Marine Fisheries Service.
- de la Mare, W. K. 1985. On the estimation of mortality rates from whale age data, with particular reference to minke whales (*Balaenoptera acutorostrata*) in the Southern Hemisphere. *Rep. Int. Whal. Commn.* **35**:239-250.
- Debrot, A. and Barros, N.B. 1992. Notes on a Gervais' beaked whale *Mesoplodon europaeus* and a dwarf sperm whale *Kogia simus* stranded in Curacao, Netherlands Antilles. *Mar. Mamm. Sci.* **8**:172-178.
- Debrot, A.O., de Meyer, J.A., and Dezentje, P.J.E. 1998. Additional records and a review of the cetacean fauna of the Leeward Dutch Antilles. *J. Sci.* **34**:204-210.
- Die, D. 2004. Status and assessment of large pelagic resources. In R. Mahon, and McConney, P.A., (Eds). Management of large pelagic fisheries in CARICOM countries. *FAO Fish. Tech. Pap.*, Rome.
- dos Santos, R. A. and Haimovici, M. 2001. Cephalopods in the diet of marine mammals stranded or incidentally caught along southeastern and southern Brazil (21-34degreeS). *Fish. Res. (Amsterdam)* **52**:99-112.
- Duarte, L.O. and Garcia, C.B. 2002. Testing responses of a tropical shelf ecosystem to fisheries management strategies: a small-scale fishery from the Columbian Caribbean Sea. *Fish. Centre Res. Rep.* 10:142-149. The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Eckert, K.L. and Eckert, S.A. 1990. Leatherback Sea Turtles in Grenada, West Indies: A Survey of Nesting Beaches and Socioeconomic Status. Report to the Foundation for Field Research and Fisheries Department, Ministry of Agriculture, Lands, Forestry and Fisheries, St George's, Grenada.
- Esquivel-Valle, M. 2005. Standardized catch rates of spiny lobsters (*Panulirus argus*) estimated from the Puerto Rico commercial trip interview program (1980-2003) in SEDAR. In SEDAR 8 Stock Assessment Report. Caribbean Spiny Lobsters and Yellowtail Snapper. Southeast Fisheries Science Center, NOAA, Charleston, SC.
- Essington, T.E. 2006. Pelagic Ecosystem Response to a Century of Commercial Fishing and Whaling. pp 38-49. In J.A. Estes, DeMaster, D.P., Doak, D.F., Williams, T.M., and L., R.L., Brownell Jr. (Eds). Whales, Whaling, and Ocean Ecosystems. University of California Press, Berkeley, California, USA.
- Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M., and Brownell Jr., R.L. 2007. Whales, whaling, and ocean ecosystem. University of California Press.
- Evans, P.G.H. 1998. Biology of cetaceans of the north-east Atlantic (in relation to seismic energy) in M. L. Tasker, and Weir, C., editors, London. pp 418
- Finlay, J. 1984. National report for Grenada. pp 184-196. In P.R. Bacon, Berry, F., Bjørndal, K., Hirth, H., Ogren, L., and Weber, M., (Eds). Proceedings of the Western Atlantic Turtle Symposium. University of Miami Press, Miami, USA., San Jose, Costa Rica.
- FishBase. Available at world wide web <http://www.fishbase.org/>, accessed on May 2, 2008.
- Fonteneau, A. and Marcille, J. 1993. Resources, fishing and biology of the tropical tunas of the Eastern Central Atlantic. FAO, Rome.
- Forget, M.H. 2007. Scientific basis for ecosystem-based management in the Lesser Antilles including interactions with marine mammals and other top predators: phytoplankton community and primary production in the Caribbean waters: the biological oceanography component of the LAPE project. FI/GCP/RLA/140/JPN. FAO Technical Document Barbados.
- Garrison, L.P., Swartz, S., Martinez, A., Burks, C., and Stamates, J. 2003. A marine mammal assessment survey of the Southeast US Continental Shelf: February - April 2002. NOAA Technical Memorandum, NMFS-SEFSC-492. U.S. Department of Commerce.
- Gobert, B. 2000. Comparative assessment of multispecies reef fish resources in the Lesser Antilles. *Fish. Res.* **44**:247-260.
- Goetz, S.J., Prince, S.D., Goward, S.N., Thawley, M.M., and Small, J. 1999. Satellite remote sensing of primary production: an improved production efficiency modeling approach. *Ecol. Model.* **122**:239-255.
- Grazette, S., Horrocks, J.A., Phillip, P.E., and Isaac, C.J. 2007. An assessment of the marine turtle fishery in Grenada, West Indies. *Oryx* **41**:330-336.
- Guénette, S., Heymans, S.J.J., Christensen, V., and Trites, A.W. 2006. Food web models and data for studying fisheries and environmental impacts in Eastern Pacific ecosystems. *Can. J. Fish. Aquat. Sci.* **63**:2495-2517.
- Haug, T., Gjosaeter, H., Lindstrøm, U., and Nilssen, K. T. 1995. Diet and food availability for Northeast Atlantic minke whales (*Balaenoptera acutorostrata*), during the summer of 1992. *ICES J. Mar. Sci.* **52**:77-86.
- Haug, T., Lindstrøm, U., Nilssen, K.T., Røttingen, I., and Skaug, H.J. 1996. Diet and food availability for northeast atlantic minke whales, *Balaenoptera acutorostrata*. *Rep. Int. Whal. Commn.* **46**:371-382.
- Hawley, C. 1999. A Caribbean whaler speaks up for tradition despite activists' outcry. The Chicago Tribune, May 25, 1999.
- Heileman-Manickchand, S.C. 1992. A preliminary survey of clupeoid fishes in Trinidad, West Indies, and their use in live bait fishing. *Proc. Gulf Caribb. Fish.* **41**:403-415.
- Heileman, S. 2007. Thematic report for the insular Caribbean sug-region. Caribbean Large Marine Ecosystem (CLME) Project. University of the West Indies, Barbados. pp 63.
- Heileman, S., Mohammed, E., and Fanning, P. 2007. Scientific basis for ecosystem-based management in the Lesser Antilles including interactions with marine mammals and other top predators: derivation of diet compositions in the Lesser Antilles Pelagic Ecosystem. FAO, Barbados. pp vii+77

- Hewitt, R.P. and Lipsky, J.D. 2002. Krill. pp 676-684. In Perrin, W.F. Würsig, B., and Thewissen, J.G.M., (Eds). Encyclopedia of Marine Mammals. Academic Press, San Diego, CA.
- Heymans, S.J.J. 2005. Ecosystem model of the eastern Aleutian and central Gulf of Alaska in 1963. pp 80-105. In S. Guénette, and Christensen, V., (Eds). Food web models and data for studying fisheries and environmental impacts on Eastern Pacific ecosystems. *Fish. Centre Res. Rep.* 13(1):80-105. The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Hickmott, L.S. 2005. Diving behaviour and foraging ecology of blainville's and cuvier's beaked whales in the northern Bahamas. Department of Marine and Fisheries Biology. University of Aberdeen, Scotland, U.K. Master thesis. pp ii+102
- Hjort, J. and Ruud, J.T. 1929. Whaling and fishing in the North Atlantic. *Rapp. P.-v. Reun. Cons. perm. int. Explor. Mer.* **56**:1-123.
- Holt, S.J. 2006. Whales competing? an analysis of the claim that some whales eat so much that they threaten fisheries and the survival of other whales. Paciano, Italy. pp 86,
- Horwood, J. 1990. Biology and exploitation of the minke whale. CRC Press, Boca Raton, FL, USA.
- ICCAT. 2004. Atlantic yellowfin tuna stock assessment session. *Col. Vol. Sci. Pap.* **56**:443-527.
- Innes, S.D., Lavigne, M., Earle, W.M., and Kovacs, K.M. 1987. Feeding rates of seals and whales. *J. Anim. Ecol.* **56**:115-130.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C. B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., and Warner, R.R. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**:629-637.
- Jann, B., Allen, J., Carrillo, M., Hanquet, S., Katona, S.K., Martin, A.R., Reeves, R.R., Seton, R., Stevick, P.T., and Wenzel, F.W. 2003. Migration of a humpback whale (*Megaptera novaeangliae*) between the Cape Verde Islands and Iceland. *J. Cetacean Res. Manage.* **5**:125-129.
- Jeffrey, C. F. G. 2000. Annual, coastal and seasonal variation in Grenadian demersal fisheries (1986 -1993) and implications for management. *Bull. Mar. Sci.* **66**:305-319.
- Johns, W.E., Townsend, T.L., Fratantoni, D.M., and Wilson, W.D. 2002. On the Atlantic inflow to the Caribbean Sea. *Deep-Sea Res. (I Oceanogr. Res. Pap.)* **49**:211-243.
- Kaschner, K. 2004. Modelling and mapping of resource overlap between marine mammals and fisheries on a global scale. MMRU, Fisheries Centre, Department of Zoology. University of British Columbia, Vancouver, Canada. PhD Thesis. pp 184
- Kaschner, K., Watson, R., Trites, A. W., and Pauly, D. 2006. Mapping worldwide distributions of marine mammals using a Relative Environmental Suitability (RES) model. *Mar. Ecol. Prog. Ser.* **316**:285-310.
- Katona, S. K. and Beard, J. A. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Rep. Int. Whaling Comm.* **12**:295-305.
- Kawakami, T. 1980. A review of sperm whale food. *Sci. Rep. Whales Res. Inst. (Tokyo)* **32**:199-218.
- Klinowska, M. 1991. Dolphins, porpoises, and whales of the world: the IUCN red data book. IUCN - The World Conservation Union, Gland, Switzerland.
- Lavigne, D.M. 1996. Ecological interactions between marine mammals, commercial fisheries and their prey: unravelling the tangled web. In W. A. Montecchi, (Ed). Studies of high latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems. Canadian Wildlife Service Occasional Paper Ottawa.
- Lenfest Ocean Program. Available at World Wide Web <http://www.lenfestocean.org/>, accessed on September 30, 2008.
- Lockyer, C. 1981. Growth and energy budgets of large baleen whales from the southern hemisphere. Mammals in the Seas: General Papers and Large Cetaceans. FAO Fisheries Series 5:379-487. Rome.
- Lydersen, C., Weslawski, J.M., and Oritsland, N.A. 1991. Stomach content analysis of minke whales *Balaenoptera acutorostrata* from the Lofoten and Vesterålen areas, Norway. *Holarctic Ecol.* **14**:219-222.
- Mackinson, S., Blanchard, J. L., Pinnegar, J. K., and Scott, R. 2003. Consequences of alternative functional response formations in models exploring whale-fishery interactions. *Mar. Mammal Sci.* **19**:661-681.
- Mackinson, S., Okey, T.A., Vasconcellos, M., Vidal-Hernandez, L., and Mahmodi, B. 2005. An ecosystem model of west Florida shelf for use in fisheries management and ecological Research. A report prepared for the Florida Marine Research Institute, St Petersburg, Florida.
- Mahon, R. 1989. Developing a management strategy for the flyingfish fishery of the Eastern Caribbean. *Proc. Gulf Caribb. Fish. Instit.* **39**:389-402.
- Mahon, R. 1990. Fishery management options for Lesser Antilles countries. FAO Fisheries Technical Paper. FAO, Rome. pp 126
- Mahon, R. 1993. Lesser Antilles. Marine fishery resources of the Antilles. *FAO Fish. Tech. Pap.* **326**:5-98.
- Mahon, R. 1996. Fisheries and research for tunas and tuna-like species in the Western Central Atlantic. *FAO Fish. Tech. Pap.* **357**:62.
- Mahon, R. 1999. Dolphinfish fisheries in the Caribbean region. *Sci. Mar.* **63**:411-420.
- Mahon, R. and McConney, P.A. 2004. Management of large pelagic fisheries in CARICOM countries. FAO, Rome.
- Mahon, R. and Oxenford, H.A. 1999. Precautionary assessment and management of dolphinfish in the Caribbean. *Sci. Mar.* **63**:429-438.
- Mahon, R., Rennie, J., Ryan, R., and Singh-Renton, S. 1994a. Billfish catch and effort data from Barbados, Grenada, St. Lucia and St. Vincent and the Grenadines. *Col. Vol. Sci. Pap. ICCAT* **41**:431-441.
- Mahon, R., Singh-Renton, S., Jennings-Clarke, S., Rennie, J., Ryan, R., and Willoughby, S. 1994b. Yellowfin tuna catch and effort data from Barbados, Grenada, St. Lucia and St. Vincent and the Grenadines. *Col. Vol. Sci. Pap. ICCAT* **42**:199-203.
- Marcano, J.S., Lárez, A., and Gutiérrez, X. 2002. Pesquería de tunidos por pequeños palangreros en el mar caribe y el océano atlántico durante el período 1986-2000. *Bol. Inst. Oceanogr. Venezuela, Univ. Oriente* **41**:73-82.
- Marcano, J.S., Lárez, A., Gutierrez, X., Alio, J. J., Salazar, H., and Marquez, M. 2004. Incidental catch of billfish and other species by Venezuelan longline vessels in the Caribbean Sea and western Atlantic Ocean: period 1986-2000. *Cienc. Mar.* **30**:201-217.
- Marcano, L.A., Alió, J.J., Arocha, F., and Gutiérrez, X. 2001. Tendencia actual de la pesquería artesanal de peces de pico en La Costa Central de Venezuela. período 1988-1999 SCRS/20002074. *Col. Vol. Sci. Pap. ICCAT* **53**:281-290.
- Martin, C.S., Jeffers, J., and Godley, B.J. 2005. The status of marine turtles in Montserrat (Eastern Caribbean). *Anim. Biodivers. Conserv.* **28**:159-168.
- Matos-Caraballo, D., Posada, J.M., and Luckhurst, B. 2006. Fishery-depended evaluation of a spawning aggregation of tiger grouper (*Mycteroperca tigris*) at Vieques Island, Puerto Rico. *Bull. Mar. Sci.* **79**:1-16.
- Melvin, G., Fanning, P., O'Donnell, C., Dahl, M., Edwards, L., Gardner, R., Simon, H., and Theophille, D. 2007. Scientific basis for ecosystem-based management in the Lesser Antilles including interactions with marine mammals and other top predators: acoustic biomass estimates of pelagic forage species in the offshore waters of the Lesser Antilles. FAO, Barbados.
- Mendoza, J.J. and Lárez, A. 2004. A biomass dynamics assessment of the southeastern Caribbean snapper-grouper fishery. *Fish. Res.* **66**:129-144.



- Mitchell, E. D. 1973. Draft report on humpback whales taken under special scientific permit by eastern Canadian land stations. *Rep. Int. Whal. Commn.* **32**:161-169.
- Mohammed, E. 2003a. Part II: ecosystem models - A generic marine ecosystem model for the southeastern Caribbean in the late 1990s: application to Grenada and the Grenadines. *Fish. Centre Res. Rep.* 11(6):191-225. The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Mohammed, E. 2003b. Reconstructing fisheries catches and fishing effort for the southeastern Caribbean (1940-2001): general methodology. pp 11-20. In D. Zeller, Booth, S., Mohammed, E., and Pauly, D., (Eds). From Mexico to Brazil: Central Atlantic fisheries catch trends and ecosystem models. *Fish. Centre Res. Rep.* 9. The Fisheries Centre, University of British Columbia, Vancouver, Canada.
- Mohammed, E., Fanning, P., Parker, C., Theophille, D., Martin, L., Punnett, S., Wilkins, R., Rambally, J., Philip, P., Isaac, C., Philmore, J., and Barrett, A. 2007a. Scientific basis for ecosystem-based management in the Lesser Antilles including interactions with marine mammals and other top predators: estimated catch, price and value for national fleet sectors from pelagic fisheries in the Lesser Antilles, Rome, Italy.
- Mohammed, E., Vasconcellos, M., Mackinson, S., Fanning, P., Heileman, S., and Carocci, F. 2007b. Scientific basis for ecosystem-based management in the Lesser Antilles including interactions with marine mammals and other top predators: A trophic model of the Lesser Antilles Pelagic Ecosystem. FAO, Barbados.
- Morissette, L. 2005. Addressing uncertainty in marine ecosystems modelling. pp127-142. In E., Levner, I., Linkov and Proth, J.M. (Eds). NATO Science Series IV: Earth and Environmental Sciences/NATO Science Series IV: Earth and Environmental Sciences. Springer Netherlands.
- Morissette, L., Hammill, M.O., and Savenkoff, C. 2006. The trophic role of marine mammals in the Northern Gulf of St. Lawrence. *Mar. Mamm. Sci.* **22**:74-103.
- Morissette, L. 2007. Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence. Zoology. University of British Columbia, Vancouver, BC, Canada. PhD thesis.
- Morissette, L., Kaschner, K., and Gerber, L. submitted. Do whales deplete fisheries in Northwest African waters? *Ecol. Appl.*
- Morissette, L., Savenkoff, C., Castonguay, M., Swain, D., Chabot, D., Hammill, M.O., and Hanson, J.M. in press. Contrasting changes between the northern and southern Gulf of St. Lawrence ecosystems associated with the collapse of groundfish stocks. *Deep Sea Res. II.*
- Mullin, K.D. and Fulling, G.L. 2003. Abundance of cetaceans in the southern U.S. Atlantic ocean during summer 1998. *Fishery Bulletin* 101: 603-613.
- Mullin, K.D. and Fulling, G.L. 2004. Abundance of cetaceans in the oceanic northern Gulf of Mexico, 1996-2001. *Marine Mammal Science* 20: 787-807.
- Munro, J.L. 1983. Caribbean coral reef fishery resources. *ICLARM Stud. Rev.* 7:276
- Murray, P.A. 1985. Growth and mortality in the dolphin-fish, *Coryphaena hippurus*, caught off Saint Lucia. *W.I. FAO Fish. Rep.* **327**:147-151.
- Myers, R.A. and Worm, B. 2003. Rapid world-wide depletion of predatory fish communities. *Nature* **423**:280-283.
- Nemeth, R. 2005. Population characteristics of a recovering US Virgin Islands red hind spawning aggregation following protection. *Mar. Ecol. Prog. Ser.* **286**:81-97.
- Nørdoy, E.S. and Blix, A.S. 1992. Diet of minke whales in the northeastern Atlantic. *Rep. Int. Whaling Comm.* 42:393-398.
- Northridge, S.P. 1984. World review of interactions between marine mammals and fisheries. FAO - Food and Agricultural Organisation of the United Nations, Rome. pp 190
- Okey, T.A. 1999. Constructing and balancing the PWS model. pp 68-72. In T.A. Okey, and Pauly, D., (Eds). Trophic mass-balance model of Alaska's Prince William Sound ecosystem, for the post-spill period 1994-1996. *Fish. Centre Res. Rep.* 7(4). The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Okey, T.A., Banks, S., Born, A.R., Bustamante, R.H., Calvopina, M., Edgar, G.J., Espinoza, E., Farina, J.M., Garske, L.E., Reck, G.K., Salazar, S., Shepherd, S., Toral-Granda, V., and Wallem, P. 2004. A trophic model of a Galapagos subtidal rocky reef for evaluating fisheries and conservation strategies. *Ecol. Model.* **172**:383-401.
- Olsen, E. and Holst, J.C. 2001. A note on common minke whale (*Balaenoptera acutorostrata*) diets in the Norwegian Sea and the North Sea. *J. Cetacean Res. Manage.* **3**:179-183.
- Olson, R. and Watters, G. 2003. A model of the pelagic ecosystem in the eastern tropical Pacific Ocean *Bull. I-ATCC* **22** (3):135-152.
- Opitz, S. 1996. Trophic interactions in Caribbean coral reefs. International Center for Living Aquatic Resources Management Technical Report, Makati City, Philippines. PhD thesis pp xiv + 341pp.
- Oxenford, H.A. 1985. Biology of the Dolphin *Coryphaena hippurus* and its implications for the Barbadian Fishery. The University of the West Indies, Cave Hill Campus, Barbados. PhD thesis. pp 366.
- Oxenford, H.A. 1999. Biology of the dolphinfish (*Coryphaena hippurus*) in the western central Atlantic: a review. *Sci. Mar.* **63**:277-301.
- Oxenford, H.A. and Hunte, W. 1986. A preliminary investigation of the stock structure of the dolphin, *Coryphaena hippurus*, in the Western Central Atlantic. *Fish. Bull.* **84**:451-460.
- Oxenford, H.A. and Hunte, W. 1999. Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the eastern Caribbean. *Sci. Mar.* **63**:303-315.
- Oxenford, H. A., Mahon, R., and Hunt, H. 1995. Distribution and relative abundance of flyingfish (Exocoetidae) in the eastern Caribbean. I. Adults. *Mar Ecol Prog Ser.* **117**:11-23.
- Oxenford, H. A., Murray, P. A., and Luckhurst, B. 2003. The biology of wahoo (*Acanthocybium solandri*) in the Western Central Atlantic. *Proc. Gulf Caribb. Fish. Inst.* **15**:33-49.
- Paine, R.T., Tegner, M.J., and Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* **1**:535-545.
- Parker, C., Singh-Renton, S., Hackett, A., and Lauckner, F.B. 2001. Assessment of dolphinfish (*Coryphaena hippurus*) fishery using Eastern Caribbean data. *CARICOM Fishery Report* **9**:41-53.
- Parker, C. 2002. Preliminary analysis of the flyingfish fishery of Barbados and interim recommendations. pp 156. In FAO/Western Central Atlantic Fishery Commission. Report of the Second Meeting of the WECAFC Ad Hoc Flyingfish Working Group of the Eastern Caribbean. Bridgetown, Barbados, 8-12 January 2001. FAO Fisheries Report, Rome, FAO.
- Pascoe, P. L., Mickiewicz, M. C., and Castello, H.P. 1990. Cephalopod remains from the stomach of a sperm whale stranded off Patagonia. *Mar. Biol.* **104**:1-4.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons.* **39**:175-193.

- Pauly, D., Soriano-Bartz, M.L., and Palomares, M.L.D. 1993. Improved construction, parametrization and interpretation of steady-state ecosystem models. pp 1-13. In V. Christensen, and Pauly, D., (Eds). Trophic models of aquatic ecosystems. ICLARM Conference Proceedings.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. J. 1998a. Fishing down marine food webs. *Science* **279**:860-863.
- Pauly, D., Trites, A.W., Capuli, E., and Christensen, V. 1998b. Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci.* **55**:467-481.
- Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U. R., Walters, C. J., Watson, R., and Zeller, D. 2002. Towards sustainability in world fisheries. *Nature* **418**:689-695.
- Pauly, D., Christensen, V., and Haggan, N. 1996. Mass-balance model of Alaska Gyre. *Fish. Centre Res. Rep.* 4(1). The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Perrin, W. F., Würsig, B., and Thewissen, J.G.M. 2002. Encyclopedia of marine mammals. Academic Press, San Diego, CA. pp 1414
- Perry, S.L., DeMaster, D.P., and Silber, G.K. 1999. The great whales: history and status of six species listed as endangered under the U.S. Endangered Species Act of 1973. *Mar. Fish. Rev.* **61**:1-74.
- Pimm, S. L. 2002. Food Webs. University of Chicago Press.
- Plagányi, É.E. and Butterworth, D.S. 2002. Competition with fisheries. pp 268-273. In W.F. Perrin, Würsig, B., and Thewissen, J.G.M., (Eds). Encyclopedia of Marine Mammals. Academic Press, San Diego, CA.
- Plagányi, É.E. and Butterworth, D.S. 2004. A critical look at the potential of ECOPATH with ECOSIM to assist in practical fisheries management. *Afr. J. Mar. Sci.* **26**:261-287.
- Plagányi, É.E., Rademeyer, R.A., Butterworth, D.S., Cunningham, C.L., and Johnston, S.J. 2007. Making management procedures operational - innovations implemented in South Africa. *ICES J. Mar. Sci.* **64**:626-632.
- Potts, A.C., Thomas, A.D., and Nichols, E. 2002. An economic and social assessment of the flyingfish (pelagic) fishery of Trinidad and Tobago. FAO/Western Central Atlantic Fishery Commission. Report of the second meeting of the WECAFC Ad Hoc Flyingfish Working Group of the Eastern Caribbean. FAO Fisheries Report Bridgetown, Barbados.
- Prager, M.H. 2000. Exploratory assessment of dolphinfish, *Coryphaena hippurus*, based on US landings from the Atlantic Ocean and Gulf of Mexico. Laboratory Document, NMFS, NOAA, Beaufort, NC. pp 18.
- Priddel, D., Hutton, I., Olsen, S., and Wheeler, R. 2005. Breeding biology of masked boobies (*Sula dactylatra tasmani*) on Lord Howe Island, Australia. *Emu*. **105**:105-113.
- Punt, A.E. and Butterworth, D.S. 1995. The effects of future consumption by Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals *Arctocephalus pusillus pusillus* and the Cape hake *Merluccius capensis* and *Merluccius paradoxus*. *S. Afr. J. Mar. Sci.* **16**:255-285.
- Quimby, S. 2000. Whaling. *Caribbean Currents* 8(2):1-8.
- Rambally, J. 1999. Whaling in St Lucia: a dying tradition? Department of Fisheries, Ministry of Agriculture, Forestry, Fisheries and the Environment, St Lucia.
- Rajendra, M.D.K., Khan, A.A., Knight, D., O'Reilly, O., Chang Yen, I., Wagh, A.B. and Desai, B.N. 1991. Some aspects of nutrient chemistry of the Caribbean Sea. *Caribb. Mar. Stud.* **2**:81-86.
- Read, A.J., Halpin, P.N., Crowder, L.B., Best, B.D., and Fujioka, E. 2007. OBIS-SEAMAP: mapping marine mammals, birds and turtles.
- Recksiak, C.W., Appeldoorn, R.S., and Turingan, R.G. 1991. Studies of fish traps as stock assessment devices on a shallow reef in south-western Puerto Rico. *Fish. Res.* **10**:177-197.
- Reeves, R. R. 2002. The origins and character of 'aboriginal subsistence' whaling: a global review. *Mammal Rev.* **32**:71-106.
- Reeves, R.R., Swartz, S.L., Wetmore, S.E., and Clapham, P.J. 2001. Historical occurrence and distribution of humpback whales in the eastern and southern Caribbean Sea, based on data from American whaling logbooks. *J. Cetacean Res. Manage.* **3**:117-129.
- Restrepo, V., Prince, E.D., Scott, G.P., and Uozumi, Y. 2003. ICCAT stock assessments of Atlantic billfish. *Mar. Freshwater Res.* **54**:361-367.
- Richards, W.J. and Bohnsack, J.A. 1990. The Caribbean Sea: a large marine ecosystem in crisis. pp 44-53. In Sherman, K., Alexander, L.M., and Gold, B.D., (Eds). Large Marine Ecosystems: Stress, Mitigation, and Sustainability. American Association for the Advancement of Science, Washington, D.C.
- Romero, A., Agudo, A. I., Green, S. M., and Notarbartolo-di-Sciara, G. 2001. Cetaceans of Venezuela: Their Distribution and Conservation Status. NMFS. pp 60
- Santos, M.B., Martin, V., Arbelo, M., Fernández, A., and Pierce, G.J. 2007. Insights into the diet of beaked whales from the atypical mass stranding in the Canary Islands in September 2002. *J. Mar. Biol. Assoc. U. K.* **87**:243-251.
- Santos, M. B., Pierce, G. J., Herman, J., López, A., Guerra, A., Mente, E., and Clark, M. R. 2001. Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): a review with new information on the diet of this species. *J. Mar. Biol. Assoc. U. K.* **81**:687-694.
- Santos, M.B., Pierce, G.J., Lopez, A., Reid, R.J., Ridoux, V., and Mente, E. 2006. Pygmy sperm whales *Kogia breviceps* in the northeast Atlantic: New information on stomach contents and strandings. *Mar. Mamm. Sci.* **22**:600-616.
- Saul, S., Diaz, G., and Rosario, A. 2005. Preliminary analysis and standardized catch per unit effort indices for yellowtail snapper fishery independent data in Puerto Rico in SEDAR, editor. SEDAR 8 Stock Assessment Report. Caribbean Spiny Lobsters and Yellowtail Snapper. Southeast Fisheries Science Center, NOAA, Charleston, SC.
- Savenkoff, C., Swain, D.P., Hanson, J.M., Castonguay, M., Hammill, M.O., Bourdages, H., Morissette, L., and Chabot, D. 2007. Effects of fishing and predation in a heavily exploited ecosystem: comparing pre- and post-groundfish collapse periods in the southern Gulf of St. Lawrence (Canada). *Ecol. Model.* **204**:115-128.
- Schreiber, E.A. and Lee, D.S. 2000. West Indian seabirds: a disappearing natural resources. In E.A. Schreiber, and Lee, D. S., (Eds). Status and Conservation of West Indian Seabirds. Society of Caribbean Ornithology, Special Publication, Ruston, Louisiana.
- Sears, R. and Harriet, H. 2002. Blue Whale - *Balaenoptera musculus*. pp 112-122. In W.F. Perrin, Würsig, B., and Thewissen, H.G.M., (Eds). Encyclopedia of Marine Mammals. Academic Press, San Diego, CA.
- Sea Around Us Project (SAUP). Available at World Wide Web <http://www.seaaroundus.org/>, accessed on August 15, 2008.
- SEDAR. 2005a. SEDAR 8 Stock assessment report I: Caribbean yellowtail snapper, Charleston, SC.
- SEDAR. 2005b. SEDAR 8 Stock assessment report II: Caribbean spiny lobster, Charleston, SC.
- SEDAR. 2007. Caribbean queen conch. SEDAR 14 stock assessment report 3. Southeast Fisheries Science Center and the South Atlantic Fishery Management Council, North Charleston, SC.

- Sidi, M.T. and Guénette, S. 2004. Modèle trophique de la ZEE mauritanienne: comparaison de deux périodes (1987 et 1998). pp 12-38. In M.L.D. Palomares, and Pauly, D., (Eds). West African marine ecosystems: models and fisheries impacts. *Fish. Centre Res. Rep.* 12(7). The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Sivertsen, S.P., Pedersen, T., Lindstrom, U.L.F., and Haug, T. 2006. Prey partitioning between cod (*Gadus morhua*) and minke whale (*Balaenoptera acutorostrata*) in the Barents Sea. *Mar. Biol. Res.* 2:89-99.
- Smith, S. C. and Whitehead, H. 2000. The diet of Galapagos sperm whales *Physeter macrocephalus* as indicated by fecal sample analysis. *Mar. Mamm. Sci.* 16:315-325.
- Smout, S. and Lindstrom, U. 2007. Multispecies functional response of the minke whale *Balaenoptera acutorostrata* based on small-scale foraging studies. *Mar. Ecol. Prog. Ser.* 341:277-291.
- Swartz, S.L., Cole, T., McDonald, M.A., Hildebrand, J.A., Oleson, E.M., Martinez, A., Clapham, P. J., Barlow, J., and Jones, M. L. 2003. Acoustic and visual survey of humpback whale (*Megaptera novaeangliae*) distribution in the eastern and southeastern Caribbean Sea. *Caribb. J. Sci.* 39:195-208.
- Tamura, T. 2003. Regional assessment of prey consumption and competition by marine cetaceans in the world. Pp 143-170. In M. Sinclair, and Valdimarsson, G., (Eds). Responsible Fisheries in Marine Ecosystems. Food and Agricultural Organisation of the United Nations and CABI Publishing, Wallingford, UK.
- Tershy, B. R. 1992. Body size, diet, habitat use, and social behavior of *Balaenoptera* whales in the Gulf of California. *J. Mammal.* 73:477-486.
- Trites, A. and Heise, K. 1996. Marine Mammals. pp 25-30. In D. Pauly, Christensen, V., and Haggan, N., editors. Mass-balance models of North-eastern Pacific ecosystems. *Fish. Centre Res. Rep.* 4(1). The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Trites, A.W., Christensen, V., and Pauly, D. 1997. Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. *J. Northwest. Atl. Fish. Sci.* 22:173-187.
- Trites, A.W. and Pauly, D. 1998. Estimating mean body masses of marine mammals from maximum body lengths. *Can. J. Zool.* 76:886-896.
- UNEP. 2002. Activities of the Caribbean Environment Programme (CEP) of UNEP on the conservation of marine mammals in the wider Caribbean, Monaco.
- Vasconcellos, M. and Watson, R. 2004. Mass balance of Atlantic oceanic systems. pp 171-214. In M. L. D. Palomares, and Pauly, D., (Eds). West African marine ecosystems: models and fisheries impacts. *Fish. Centre Res. Rep.* 12(7). The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Vidal, L. and Basurto, M. 2003. A preliminary trophic model of Bahía de la Ascensión, Quintana Roo, Mexico [modelo trófico preliminar de Bahía Ascención, Quintana Roo, México]. *Fish. Centre Res. Rep.* 11:255-264.
- Wade, P.R. and Gerrodette, T. 1993. Estimates of cetacean abundance and distribution in the Eastern Tropical Pacific. Reports of the International Whaling Commission 43: 477-493.
- Walters, C. and Kitchell, J.F. 2004. Fisheries ecology and management. Princeton University Press, Princeton, New Jersey.
- Watson, R., Kitchingman, A., Gelchu, A., and Pauly, D. 2004. Mapping global fisheries: sharpening our focus. *Fish Fish.* 5:168-177.
- Windsland, K., Lindstrom, U., Nilssen, K.T., and Haug, T. 2007. Relative abundance and size composition of prey in the common minke whale diet in selected areas of the northeastern Atlantic during 2000-04. *J. Cetacean Res. Manage.* 9:167-178.
- Witteveen, B.H., Foy, R.J., and Wynne, K.M. 2006. The effect of predation (current and historical) by humpback whales (*Megaptera novaeangliae*) on fish abundance near Kodiak Island, Alaska. *Fish. Bull.* 104:10-20.
- Wolff, M., Koch, V., Chavarria, J.B. and Vargas, J.A. 1998. A trophic flow model of the Golfo de Nicoya, Costa Rica. *Rev. Biol. Mar. Tropical* 46:63-79.
- Zeller, D., Booth, S., Mohammed, E., and Pauly, D. 2003. From Mexico to Brazil: Central Atlantic Fisheries Catch Trends and Ecosystem Models. *Fish. Centre Res. Rep.* 11(6). The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.
- Zeller, D. and Freire, K. 2001. A north-east Atlantic marine ecosystem model for the Faroe Islands (ICES Area VB): input data. *Fish. Centre Res. Rep.* 9:207-212. The Fisheries Centre, University of British Columbia, Vancouver, B.C., Canada.



## APPENDICES

**Appendix 1.** Results of the sensitivity analysis for the Northwest African model. Input and estimated parameter numbers correspond to *Ecopath* groups.

Input parameter			Estimated parameter	Change in input parameters										
				-50%	-40%	-30%	-20%	-10%	0%	10%	20%	30%	40%	50%
5	B	8	EE	-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
5	Q/B	8	EE	-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
8	B	8	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
8	P/B	8	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
9	B	17	B	-0.154	-0.123	-0.092	-0.062	-0.031	0	0.031	0.062	0.092	0.123	0.154
9	B	18	B	-0.188	-0.150	-0.113	-0.075	-0.038	0	0.038	0.075	0.113	0.150	0.188
9	B	23	EE	-0.146	-0.117	-0.087	-0.058	-0.029	0	0.029	0.058	0.087	0.117	0.146
9	Q/B	17	B	-0.154	-0.123	-0.092	-0.062	-0.031	0	0.031	0.062	0.092	0.123	0.154
9	Q/B	18	B	-0.188	-0.150	-0.113	-0.075	-0.038	0	0.038	0.075	0.113	0.150	0.188
9	Q/B	23	EE	-0.146	-0.117	-0.087	-0.058	-0.029	0	0.029	0.058	0.087	0.117	0.146
10	P/B	10	B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
10	P/B	17	B	0.062	0.041	0.026	0.015	0.007	0	-0.006	-0.010	-0.014	-0.018	-0.021
10	P/B	18	B	0.140	0.093	0.060	0.035	0.016	0	-0.013	-0.023	-0.032	-0.040	-0.047
10	P/B	19	B	0.242	0.161	0.104	0.060	0.027	0	-0.022	-0.040	-0.056	-0.069	-0.081
10	P/B	23	EE	0.091	0.061	0.039	0.023	0.010	0	-0.008	-0.015	-0.021	-0.026	-0.030
10	Q/B	18	B	-0.070	-0.056	-0.042	-0.028	-0.014	0	0.014	0.028	0.042	0.056	0.070
10	Q/B	19	B	-0.121	-0.097	-0.073	-0.048	-0.024	0	0.024	0.048	0.073	0.097	0.121
10	Q/B	23	EE	-0.046	-0.037	-0.027	-0.018	-0.009	0	0.009	0.018	0.027	0.037	0.046
10	EE	10	B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
10	EE	17	B	0.062	0.041	0.026	0.015	0.007	0	-0.006	-0.010	-0.014	-0.018	-0.021
10	EE	18	B	0.140	0.093	0.060	0.035	0.016	0	-0.013	-0.023	-0.032	-0.040	-0.047
10	EE	19	B	0.242	0.161	0.104	0.060	0.027	0	-0.022	-0.040	-0.056	-0.069	-0.081
10	EE	23	EE	0.091	0.061	0.039	0.023	0.010	0	-0.008	-0.015	-0.021	-0.026	-0.030
11	B	10	B	-0.259	-0.208	-0.156	-0.104	-0.052	0	0.052	0.104	0.156	0.208	0.259
11	B	12	B	-0.496	-0.397	-0.297	-0.198	-0.099	0	0.099	0.198	0.297	0.397	0.496
11	B	16	B	-0.056	-0.045	-0.034	-0.023	-0.011	0	0.011	0.022	0.034	0.045	0.056
11	B	17	B	-0.037	-0.030	-0.022	-0.015	-0.007	0	0.007	0.015	0.022	0.030	0.037
11	B	18	B	-0.044	-0.035	-0.026	-0.017	-0.009	0	0.009	0.017	0.026	0.035	0.044
11	B	19	B	-0.185	-0.148	-0.111	-0.074	-0.037	0	0.037	0.074	0.111	0.148	0.185
11	B	20	EE	-0.496	-0.397	-0.297	-0.198	-0.099	0	0.099	0.198	0.297	0.397	0.496
11	B	23	EE	-0.042	-0.034	-0.025	-0.017	-0.008	0	0.008	0.017	0.025	0.034	0.042
11	P/B	11	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
11	Q/B	10	B	-0.259	-0.208	-0.156	-0.104	-0.052	0	0.052	0.104	0.156	0.208	0.259
11	Q/B	11	EE	-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
11	Q/B	12	B	-0.496	-0.397	-0.297	-0.198	-0.099	0	0.099	0.198	0.297	0.397	0.496
11	Q/B	16	B	-0.056	-0.045	-0.034	-0.023	-0.011	0	0.011	0.022	0.034	0.045	0.056
11	Q/B	17	B	-0.037	-0.030	-0.022	-0.015	-0.007	0	0.007	0.015	0.022	0.030	0.037
11	Q/B	18	B	-0.044	-0.035	-0.026	-0.017	-0.009	0	0.009	0.017	0.026	0.035	0.044
11	Q/B	19	B	-0.185	-0.148	-0.111	-0.074	-0.037	0	0.037	0.074	0.111	0.148	0.185
11	Q/B	20	EE	-0.496	-0.397	-0.297	-0.198	-0.099	0	0.099	0.198	0.297	0.397	0.496
11	Q/B	23	EE	-0.042	-0.034	-0.025	-0.017	-0.008	0	0.008	0.017	0.025	0.034	0.042
12	P/B	12	B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
12	P/B	16	B	0.060	0.040	0.026	0.015	0.007	0	-0.005	-0.010	-0.014	-0.017	-0.020
12	P/B	20	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
12	Q/B	20	EE	-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
12	EE	12	B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
12	EE	16	B	0.060	0.040	0.026	0.015	0.007	0	-0.005	-0.010	-0.014	-0.017	-0.020
12	EE	20	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
13	B	13	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
13	P/B	13	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
14	B	14	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
14	P/B	14	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
15	B	15	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
15	B	17	B	-0.147	-0.118	-0.088	-0.059	-0.029	0	0.029	0.059	0.088	0.118	0.147
15	B	18	B	-0.123	-0.099	-0.074	-0.049	-0.025	0	0.025	0.049	0.074	0.099	0.123
15	B	19	B	-0.164	-0.131	-0.098	-0.066	-0.033	0	0.033	0.066	0.098	0.131	0.164
15	B	23	EE	-0.147	-0.117	-0.088	-0.059	-0.029	0	0.029	0.059	0.088	0.117	0.147
15	P/B	15	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
15	Q/B	17	B	-0.147	-0.118	-0.088	-0.059	-0.029	0	0.029	0.059	0.088	0.118	0.147
15	Q/B	18	B	-0.123	-0.099	-0.074	-0.049	-0.025	0	0.025	0.049	0.074	0.099	0.123
15	Q/B	19	B	-0.164	-0.131	-0.098	-0.066	-0.033	0	0.033	0.066	0.098	0.131	0.164

15	Q/B	23	EE	-0.147	-0.117	-0.088	-0.059	-0.029	0	0.029	0.059	0.088	0.117	0.147
16	P/B	16	B	1.005	0.669	0.430	0.251	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.334
16	EE	16	B	1.005	0.669	0.430	0.251	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.334
17	P/B	17	B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
17	P/B	23	EE	0.672	0.448	0.288	0.168	0.075	0	-0.061	-0.112	-0.155	-0.192	-0.224
17	Q/B	23	EE	-0.336	-0.269	-0.202	-0.134	-0.067	0	0.067	0.134	0.202	0.269	0.336
17	EE	17	B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
17	EE	23	EE	0.672	0.448	0.288	0.168	0.075	0	-0.061	-0.112	-0.155	-0.192	-0.224
18	P/B	18	B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
18	P/B	23	EE	0.224	0.150	0.096	0.056	0.025	0	-0.020	-0.037	-0.052	-0.064	-0.075
18	Q/B	23	EE	-0.112	-0.090	-0.067	-0.045	-0.022	0	0.022	0.045	0.067	0.090	0.112
18	EE	18	B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
18	EE	23	EE	0.224	0.150	0.096	0.056	0.025	0	-0.020	-0.037	-0.052	-0.064	-0.075
19	P/B	16	B	0.123	0.082	0.052	0.031	0.014	0	-0.011	-0.020	-0.028	-0.035	-0.041
19	P/B	18	B	0.058	0.039	0.025	0.014	0.006	0	-0.005	-0.010	-0.013	-0.016	-0.019
19	P/B	19	B	1.005	0.669	0.430	0.251	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.334
19	P/B	23	EE	0.060	0.040	0.026	0.015	0.007	0	-0.005	-0.010	-0.014	-0.017	-0.020
19	Q/B	16	B	-0.061	-0.049	-0.037	-0.024	-0.012	0	0.012	0.024	0.037	0.049	0.061
19	EE	16	B	0.123	0.082	0.052	0.031	0.014	0	-0.011	-0.020	-0.028	-0.035	-0.041
19	EE	18	B	0.058	0.039	0.025	0.014	0.006	0	-0.005	-0.010	-0.013	-0.016	-0.019
19	EE	19	B	1.005	0.669	0.430	0.251	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.334
19	EE	23	EE	0.060	0.040	0.026	0.015	0.007	0	-0.005	-0.010	-0.014	-0.017	-0.020
20	B	20	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
20	B	21	B	-0.458	-0.367	-0.275	-0.183	-0.092	0	0.092	0.183	0.275	0.367	0.458
20	P/B	20	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
20	Q/B	21	B	-0.458	-0.367	-0.275	-0.183	-0.092	0	0.092	0.183	0.275	0.367	0.458
21	P/B	21	B	1.786	1.053	0.625	0.345	0.147	0	-0.114	-0.204	-0.278	-0.339	-0.391
21	Q/B	21	B	-0.124	-0.101	-0.078	-0.053	-0.027	0	0.029	0.060	0.092	0.127	0.164
21	EE	21	B	1.786	1.053	0.625	0.345	0.147	0	-0.114	-0.204	-0.278	-0.339	-0.391
23	B	23	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
23	B	24	Q/B	-0.490	-0.392	-0.294	-0.196	-0.098	0	0.098	0.196	0.294	0.392	0.490
23	P/B	23	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
23	Q/B	24	Q/B	-0.490	-0.392	-0.294	-0.196	-0.098	0	0.098	0.196	0.294	0.392	0.490
24	B	24	Q/B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
24	P/B	24	Q/B	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333

**Appendix 2.** Results of the sensitivity analysis. Input and estimated parameter numbers correspond to *Ecopath* groups.

				Change in input parameters										
Input parameter	Estimated parameter			-50%	-40%	-30%	-20%	-10%	0%	10%	20%	30%	40%	50%
1 B	14 EE			-0.071	-0.057	-0.043	-0.029	-0.014	0	0.014	0.029	0.043	0.057	0.071
1 Q/B	14 EE			-0.071	-0.057	-0.043	-0.029	-0.014	0	0.014	0.029	0.043	0.057	0.071
3 B	14 EE			-	-0.048	-0.036	-0.024	-0.012	0	0.012	0.024	0.036	0.048	0.060
3 Q/B	14 EE			0.060										
				-	-0.048	-0.036	-0.024	-0.012	0	0.012	0.024	0.036	0.048	0.060
4 B	14 EE			0.060										
4 Q/B	14 EE			-0.325	-0.260	-0.195	-0.130	-0.065	0	0.065	0.130	0.195	0.260	0.325
4 Q/B	14 EE			-0.325	-0.260	-0.195	-0.130	-0.065	0	0.065	0.130	0.195	0.260	0.325
7 B	10 EE			-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
7 Q/B	10 EE			-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
10 B	10 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
10 B	13 EE			-0.193	-0.154	-0.116	-0.077	-0.039	0	0.039	0.077	0.116	0.154	0.193
10 P/B	10 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
10 Q/B	13 EE			-0.193	-0.154	-0.116	-0.077	-0.039	0	0.039	0.077	0.116	0.154	0.193
11 B	11 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
11 B	16 EE			-0.153	-0.122	-0.092	-0.061	-0.031	0	0.031	0.061	0.092	0.122	0.153
11 P/B	11 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
11 Q/B	16 EE			-0.153	-0.122	-0.092	-0.061	-0.031	0	0.031	0.061	0.092	0.122	0.153
12 B	12 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
12 P/B	12 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
13 B	13 EE			0.413	0.275	0.177	0.103	0.046	0	-	-0.069	-0.095	-0.118	-0.138
13 B	17 EE			-0.039	-0.031	-0.023	-0.016	-	0	0.008	0.016	0.023	0.031	0.039
								0.008						
13 P/B	13 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
13 Q/B	13 EE			-0.294	-0.235	-0.176	-0.117	-0.059	0	0.059	0.117	0.176	0.235	0.294
13 Q/B	17 EE			-0.039	-0.031	-0.023	-0.016	-	0	0.008	0.016	0.023	0.031	0.039
14 B	14 EE													
				1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
14 B	23 EE			-0.081	-0.064	-0.048	-0.032	-0.016	0	0.016	0.032	0.048	0.064	0.081
14 P/B	14 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
14 Q/B	23 EE			-0.081	-0.064	-0.048	-0.032	-0.016	0	0.016	0.032	0.048	0.064	0.081
15 B	11 EE			-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
15 B	12 EE			-0.115	-0.092	-0.069	-0.046	-0.023	0	0.023	0.046	0.069	0.092	0.115
15 B	15 EE			0.233	0.155	0.100	0.058	0.026	0	-0.021	-0.039	-0.054	-0.066	-0.078
15 B	16 EE			-0.099	-0.079	-0.059	-0.040	-0.020	0	0.020	0.040	0.059	0.079	0.099
15 P/B	15 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
15 Q/B	11 EE			-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
15 Q/B	12 EE			-0.115	-0.092	-0.069	-0.046	-0.023	0	0.023	0.046	0.069	0.092	0.115
15 Q/B	15 EE			-0.384	-0.307	-0.230	-0.154	-0.077	0	0.077	0.154	0.230	0.307	0.384
15 Q/B	16 EE			-0.099	-0.079	-0.059	-0.040	-0.020	0	0.020	0.040	0.059	0.079	0.099
16 B	16 EE			0.573	0.382	0.245	0.143	0.064	0	-0.052	-0.095	-0.132	-0.164	-0.191
16 B	19 EE			-0.035	-0.028	-0.021	-0.014	-0.007	0	0.007	0.014	0.021	0.028	0.035
16 P/B	16 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
16 Q/B	16 EE			-0.214	-0.171	-0.128	-0.086	-0.043	0	0.043	0.086	0.128	0.171	0.214
16 Q/B	19 EE			-0.035	-0.028	-0.021	-0.014	-0.007	0	0.007	0.014	0.021	0.028	0.035
17 B	17 EE			0.793	0.528	0.340	0.198	0.088	0	-0.072	-0.132	-0.183	-0.226	-0.264
17 P/B	17 EE			1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
17 Q/B	17 EE			-0.104	-0.083	-0.062	-0.042	-0.021	0	0.021	0.042	0.062	0.083	0.104
18 P/B	12 EE			2.488	1.230	0.667	0.349	0.143	0	-0.106	-0.187	-0.251	-0.303	-0.346
18 P/B	15 EE			0.684	0.338	0.183	0.096	0.039	0	-0.029	-0.051	-0.069	-	-0.095
18 P/B	16 EE													
				0.177	0.087	0.047	0.025	0.010	0	-	-0.013	-0.018	-0.022	-0.025
18 P/B	17 EE													
				0.606	0.300	0.163	0.085	0.035	0	-0.026	-0.046	-0.061	-0.074	-
18 P/B	19 EE													
				2.461	1.216	0.660	0.345	0.142	0	-0.105	-0.185	-0.248	-	-0.343
18 P/B	22 EE													
18 P/B	23 EE			1.352	0.669	0.363	0.189	0.078	0	-0.057	-0.102	-0.136	-0.165	-0.188
18 Q/B	12 EE			-0.484	-0.404	-0.316	-0.221	-0.116	0	0.128	0.271	0.431	0.611	0.817
18 Q/B	15 EE			-0.133	-0.111	-0.087	-0.061	-0.032	0	0.035	0.074	0.118	0.168	0.225
18 Q/B	16 EE			-0.034	-0.029	-0.022	-0.016	-	0	0.009	0.019	0.031	0.043	0.058
18 Q/B	17 EE													
				-0.118	-0.098	-0.077	-0.054	-0.028	0	0.031	0.066	0.105	0.149	0.199
18 Q/B	19 EE			-0.479	-0.399	-0.313	-0.218	-0.114	0	0.127	0.268	0.426	0.605	0.808
18 Q/B	22 EE			-0.151	-0.126	-0.099	-0.069	-0.036	0	0.040	0.085	0.135	0.191	0.255

18	Q/B	23	EE	-0.263	-0.220	-0.172	-0.120	-0.063	0	0.070	0.147	0.234	0.332	0.444
19	B	19	EE	0.886	0.591	0.380	0.222	0.098	0	-0.081	-0.148	-0.204	-0.253	-0.295
19	P/B	19	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
19	Q/B	19	EE	-0.057	-0.046	-0.034	-0.023	-0.011	0	0.011	0.023	0.034	0.046	0.057
20	B	17	EE	-0.085	-0.068	-0.051	-0.034	-0.017	0	0.017	0.034	0.051	0.068	0.085
20	Q/B	17	EE	-0.085	-0.068	-0.051	-0.034	-0.017	0	0.017	0.034	0.051	0.068	0.085
21	P/B	21	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
21	Q/B	21	EE	-0.500	-0.400	-0.300	-0.200	-0.100	0	0.100	0.200	0.300	0.400	0.500
22	B	17	EE	-0.126	-0.101	-0.075	-0.050	-0.025	0	0.025	0.050	0.075	0.101	0.126
22	B	19	EE	-0.048	-0.039	-0.029	-0.019	-0.010	0	0.010	0.019	0.029	0.039	0.048
22	B	22	EE	0.884	0.589	0.379	0.221	0.098	0	-	-0.147	-0.204	-0.253	-0.295
										0.080				
22	B	23	EE	-0.082	-0.066	-0.049	-0.033	-0.016	0	0.016	0.033	0.049	0.066	0.082
22	P/B	22	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
22	Q/B	17	EE	-0.126	-0.101	-0.075	-0.050	-0.025	0	0.025	0.050	0.075	0.101	0.126
22	Q/B	19	EE	-0.048	-0.039	-0.029	-0.019	-0.010	0	0.010	0.019	0.029	0.039	0.048
22	Q/B	22	EE	-0.058	-0.047	-0.035	-0.023	-0.012	0	0.012	0.023	0.035	0.047	0.058
22	Q/B	23	EE	-0.082	-0.066	-0.049	-0.033	-0.016	0	0.016	0.033	0.049	0.066	0.082
23	B	12	EE	-0.292	-0.234	-0.175	-0.117	-0.059	0	0.059	0.117	0.175	0.234	0.292
23	B	15	EE	-	-0.064	-0.048	-0.032	-0.016	0	0.016	0.032	0.048	0.064	0.080
										0.080				
23	B	17	EE	-0.071	-0.057	-0.043	-0.029	-0.014	0	0.014	0.029	0.043	0.057	0.071
23	B	19	EE	-0.289	-0.231	-0.174	-0.116	-0.058	0	0.058	0.116	0.174	0.231	0.289
23	B	22	EE	-0.369	-0.295	-0.221	-0.147	-0.074	0	0.074	0.147	0.221	0.295	0.369
23	B	23	EE	0.552	0.368	0.237	0.138	0.061	0	-0.050	-0.092	-0.127	-0.158	-0.184
23	P/B	23	EE	1.000	0.667	0.429	0.250	0.111	0	-0.091	-0.167	-0.231	-0.286	-0.333
23	Q/B	12	EE	-0.292	-0.234	-0.175	-0.117	-0.059	0	0.059	0.117	0.175	0.234	0.292
23	Q/B	15	EE	-	-0.064	-0.048	-0.032	-0.016	0	0.016	0.032	0.048	0.064	0.080
										0.080				
23	Q/B	17	EE	-0.071	-0.057	-0.043	-0.029	-0.014	0	0.014	0.029	0.043	0.057	0.071
23	Q/B	19	EE	-0.289	-0.231	-0.174	-0.116	-0.058	0	0.058	0.116	0.174	0.231	0.289
23	Q/B	22	EE	-0.369	-0.295	-0.221	-0.147	-0.074	0	0.074	0.147	0.221	0.295	0.369
23	Q/B	23	EE	-0.224	-0.179	-0.134	-	-0.045	0	0.045	0.090	0.134	0.179	0.224
										0.090				

---