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TECHNICAL DOCUMENT No. 2

FAO/GOVERNMENT COOPERATIVE PROGRAMME

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

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

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A TROPHIC MODEL OF THE LESSER ANTILLES PELAGIC ECOSYSTEM

Report prepared for the

Lesser Antilles Pelagic Ecosystem Project

(GCP/RLA/140/JPN)

By

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

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ABSTRACT

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, by Elizabeth Mohammed[1]; Marcelo Vasconcellos[2]; Steve Mackinson[3]; Paul Fanning[2]; Sherry Heileman[4]; Fabio Carocci[2]. FAO, Barbados, 2008. xiii + 168 pp. 14 Tables and 61 Figures. FI:GCP/RLA/140/JPN. Technical Document No. 2

An Ecopath with Ecosim model describing the pelagic ecosystem of the waters surrounding the Lesser Antilles islands in the eastern Caribbean was constructed. It incorporates data derived from published sources as well as unpublished databases and data collection activities conducted by the FAO project "Scientific basis for ecosystem-based management in the Lesser Antilles including interactions with marine mammals and other top predators". Although the model provides a reasonable and useful representation of the Lesser Antilles pelagic ecosystem, there remain many uncertainties in both the model inputs and the model structure. Future research to address these is highly recommended.

Surveys of cetaceans and forage biomass were included in the project as well as diet studies to elucidate ecosystem structure. The model includes 29 consumer functional groups as well as primary producers and detritus, for a total of 31 functional groups. The migratory nature of many of the key pelagic species included in the model required innovative approaches to partitioning information pertinent to the study area from other parts of the stock range. The model imputs for each group are described in the report. The ecosystem statistics derived from the Ecopath model are consistent with an 'open' ecosystem and fisheries targeting primarily high trophic level predators.

Several policy issues identified in consultations with regional stakeholders were examined using Ecosim. One important finding is that, subject to important uncertainties and caveats, the current and planned increases in longline fishing effort directed at large pelagics may have important impacts on bait species and ecologically dependent predators (e.g. dolphinfish). Food security could become an issue for those fishers currently dependent on the coastal pelagic fisheries for food and livelihood. Further examination of this issue is needed before policy decisions are taken.

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The Ecosystem Modelling Working Group, which met five times during the development of this model, provided invaluable information and insight into the specifics of each islands' fish stocks and fisheries. It was also an important forum for identification, development and interpretation of the issues affecting the pelagic fisheries of the Lesser Antilles.

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GLOSSARY

Balanced or balancing: model balancing is the procedure that evaluates and adjusts parameters of an Ecopath model to achieve accordance with mass-balance assumptions and ecological constrains.

Cannibalism: in addition to the conventional definition of cannibalism, i.e. intra-specific predation, there is cannibalism within a mass-balance model using functional groups in cases where one species within the group feeds on another species within the same group.

Ecopath: model component of EwE that is used to construct a static mass-balanced assessment of the resources in an ecosystem and their interactions, represented by trophically linked biomass 'pools'.

Ecosim: model component of EwE that provides dynamic simulation capabilities at the ecosystem level, with key initial parameters inherited from the base Ecopath model.

Ecospace: model component of EwE that provides spatial simulation capabilities at the ecosystem level, with key initial parameters inherited from the base Ecopath model and from Ecosim.

Ecopath with Ecosim (or EwE) - a modelling system implementing a mass-balance model of tropho-dynamics frequently applied to aquatic systems and fisheries systems in particular (see www.ecopath.org for further description, the software and documentation)

Functional group: - a life-stage, species or group of species which plays an ecologically distinct role and is ecologically homogeneous i.e. similar prey field and predator field

Lesser Antilles Pelagic Ecosystem, LAPE: - the study area defined as approximating the combined Exclusive Economic Zones of the countries in the Lesser Antilles chain inclusive of St. Kitts in the north to Trinidad in the south.

Trophic level: dimensionless index that indicates the position that an organism occupies in a food chain.

Tropho-dynamic: description of the flows of energy (or proxies such as biomass or carbon) through a foodweb (an ecosystem) by predation, exploitation and physiological processes.

INTRODUCTION

BACKGROUND TO THE LESSER ANTILLES PELAGIC ECOSYSTEM PROJECT

General

The LAPE Project was designed to introduce the concept of the Ecosystem Approach to Fisheries (EAF) in the Lesser Antilles and broader eastern Caribbean region. In the Project Document establishing the project the purpose was to initiate implementation of this approach through discussions and consultations with stakeholders, to identify critical issues in fisheries management and to acquire ecological, economic and other fishery related information to facilitate use of ecosystem and geographic information system models for exploration of fishery management options.

The process of creating an ecosystem model is a complex one. Information is required on the species and species groups making up the ecosystem and a wide array of biological, economic and fisheries processes affecting them. In addition to the data needs, model construction also demands a substantial amount of expert judgement as well as the use of conventional assumptions and rules of thumb. The LAPE project adopted a working group approach to the process with a series of five meetings held over the last two years. This working group reviewed model inputs and assumptions, provided data from national data sets and wasa venue for the exchange of ideas and concerns about the model being developed. The results of the working groups' deliberations have been incorporated in the ecosystem model reported in this document.

Ecosystem approach to fisheries (EAF)

An ecosystem approach to fisheries *strives to balance diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries* (FAO, 2003). Principles of this approach have been included in a number of international agreements and conference documents dating back to the 1972 World Conference on Human Development, including the 1982 United Nations Law of the Sea Convention, the 1992 United Nations Conference on Environment and Development and associated Agenda 21, the 1992 Convention on Biological Diversity, the 1995 United Nations Fish Stocks Agreement, the 1995 FAO Code of Conduct for Responsible Fisheries, the 2001 Reykjavik Declaration and the 2002 World Summit on Sustainable Development (WSSD). At the WSSD participating countries committed to encouraging the application of an ecosystem approach towards addressing cross-sectoral linkages related to oceans, seas, islands and coastal areas by 2010 (Cicin-Sain *et al*., 2002). The development and facilitation of diverse approaches and tools such as the ecosystem approach, elimination of

destructive fishing practices, networks of marine protected areas, time/area closures for nursery grounds, proper coastal land use, watershed planning and integration of marine and coastal area management into key sectors were other commitments aimed at maintaining biodiversity and ecosystem functions with a target date of 2012.

Utility of ecosystem modeling in EAF

Ecosystem modeling using Ecopath with Ecosim (EwE) is an holistic approach to fisheries assessment which incorporates many of the elements of the EAF approach. Since the trophic linkages among all species in the ecosystem are considered, impacts of fishing on both the target and non-target species can be examined. Further, ecological modeling is an heuristic tool which brings to decision makers new information about the roles and functions of organisms within the ecosystem, as well as general ecosystem characteristics to better select an appropriate management strategy. The approach also highlights areas of uncertainty and critical data gaps to direct scientific research and has the capability to examine the impacts of fishing on diverse societal objectives (social, economic and ecological) in arriving at suitable management policy options, as well as highlighting the tradeoffs associated with multi-criteria management objectives.

PURPOSE OF MODEL CONSTRUCTION

The use of Ecopath with Ecosim was proposed to examine management policy options for pelagic fisheries in the LAPE (FAO, 2004a). Following a series of stakeholder consultations to identify and prioritize management issues (Grant, 2007) four areas of concern were highlighted based on the perceived level of importance, the number of countries impacted and the practicality for examination using the LAPE model constructed in EWE. These areas of concern are, in decreasing order of priority:

(a) Bait fishery: Can the required increase in catches of the small pelagic and flyingfish (bait) fisheries be sustained to meet the demands of an expanding large pelagic fishery?

(b) Trophic linkage between flyingfish and dolphinfish: What would be the likely impacts of increasing effort in the flyingfish fishery on the biomass, catch and value of large pelagic fisheries, in particular dolphinfish? What would be the impact of increasing effort of fisheries targeting dolphinfish on the biomass, catch and value of the flyingfish fishery? Is there a potential for increasing flyingfish catches in the region? What are the likely impacts on the availability of other species to fisheries in the region? Would there be any benefits to a reduction of effort on the flyingfish fishery?

(c) Cetaceans: It was noted that the populations of marine mammals in the region have been increasing due to reduced incidental capture in fishing gear. As a result cetaceans are likely to compete with other species in the ecosystem

for the same prey, or to compete with fisheries for the available resources. What would be impact of increasing population of marine mammals on the available resources for fisheries? What would be the impact of a developing fishery for marine mammals on catches of fish species?

(d) Climate change: It is predicted that global warming will result in increased run-off from major rivers and hence primary productivity in the region. What would be the likely impact of increasing productivity on the biomass of fish available to fisheries in the region?

The model structure and functional groups have been included to address policy exploration of these issues explicitly. As well, ecologically sensitive species caught in association with pelagic fisheries e.g., marine turtles and seabirds, have been included in the model structure to facilitate associated policy exploration in future.

STUDY AREA AND RATIONALE FOR SELECTION OF MODEL BOUNDARY

The trophic model represents the entire pelagic ecosystem of the LAPE, defined to be the nominal EEZs (within either equidistant or 200 n. mi. lines, whichever is lesser) of all the islands from Antigua and Barbuda and St. Kitts/Nevis in the north to Trinidad in the south, excluding the Gulf of Paria (Figure 1). The total area of the ecosystem thus defined is of 610 000 km^2. The geographical boundaries, though not ecologically meaningful since the region is an open system, represent the area of ocean space for which the countries of the LAPE have responsibility for management of the associated marine living resources. It was felt that to include an area outside of this region would render the implementation of appropriate management policies impractical by the countries of the LAPE region only. Since little data exists for the species within the LAPE area however, a 200 nautical mile buffer zone around the EEZs of the respective countries was defined, for which data would be accepted to make inferences about the functional groups in the LAPE.

FISHERIES IN THE LAPE

The fisheries sector makes an important contribution to the economy of the Lesser Antilles Islands, and most of the countries making up the island grouping are traditional fish eaters. Employment and income are generated in the fisheries sector mainly through commercial fisheries, recreational fishing and tourism. However, many of the fisheries of these countries are artisanal in nature and may represent the only possible source of income for the fishers, reinforcing the importance of the sector to food security.

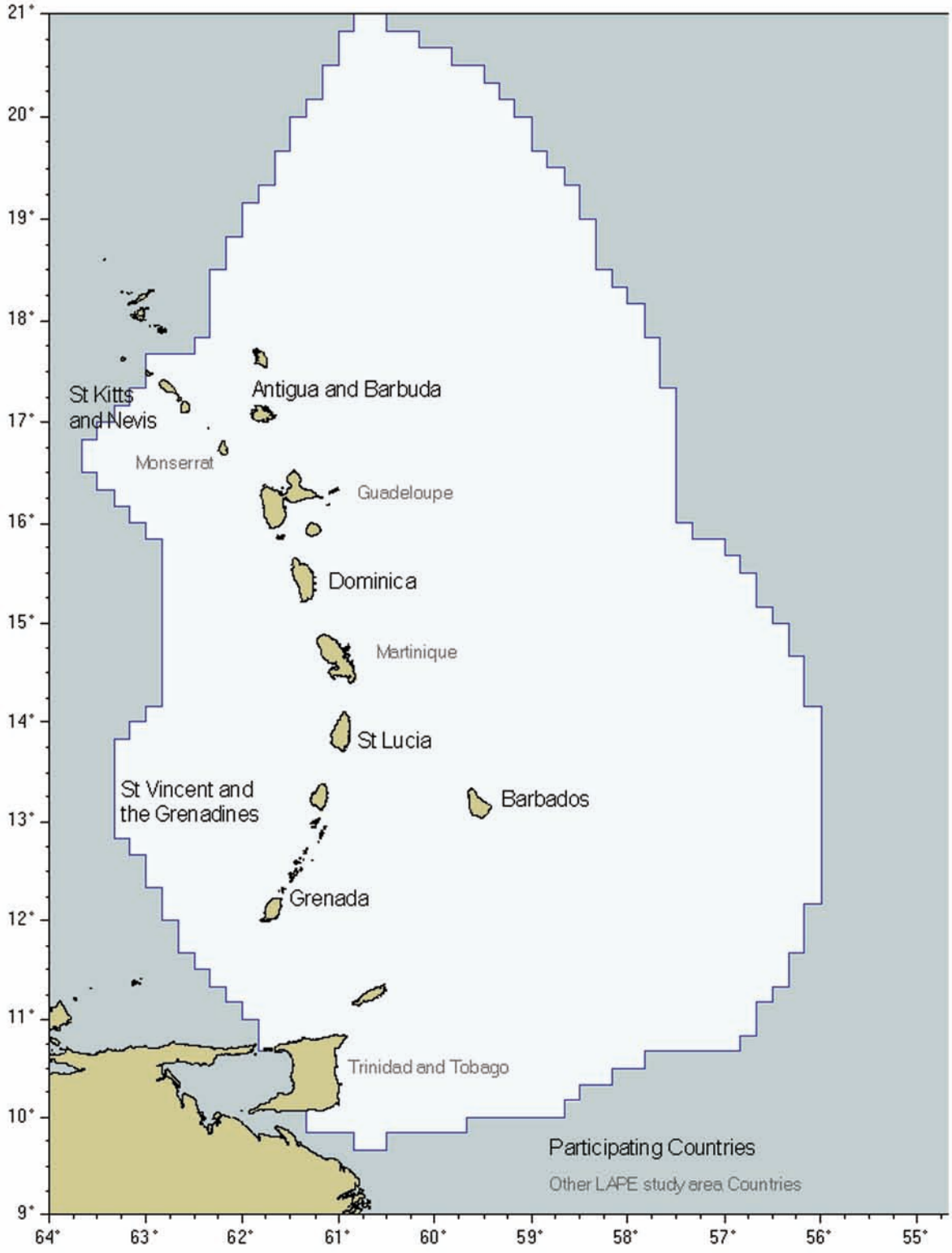

Figure 1Area of the Lesser Antilles Pelagic Ecosystem model.

As a result of the heavy dependence by the countries of the region on fish, most coastal resources are overexploited or fully exploited (especially those of higher commercial value), while the demand for fish (including tourism and recreation) continues to grow. In response to this, there has been growing interest, from both fishers and the governments, in the pelagic resources of the waters adjacent to their coasts. As examples, in Grenada a fishery for large pelagics has grown since starting in the early 1980s to 110 small long-liners

fishing 1-day trips and seven short-stay longliners (Mahon, 1996). In St Lucia, 45 new vessels were introduced into the fishery between 1989 and 1992, with heavy emphasis on fishing for large pelagics, while in Barbados, 82 vessels with ice holds and able to stay at sea for 7 - 14 days were introduced to the fleet between 1979 and 1989 and the country is committed to further expansion if economically viable (Mahon, 1996).

The resources in the pelagic ecosystem of the Lesser Antilles sub-region which support important fisheries include a number of large pelagic species, including oceanic and highly migratory stocks, such as yellowfin tuna, skipjack tuna, swordfish, billfish and others, and more localized large pelagics such as wahoo, blackfin tuna and mackerel species *Scomberomorus* spp. Sharks are also landed frequently in the region, although most are taken as bycatch in fisheries targeting other species. The three most common species of shark are the smalleye smooth-hound shark, the Brazilian sharpnose shark, and the Caribbean sharpnose shark (Chan A Shing, 1999). Within the WECAFC region, landings of sharks have escalated spectacularly since 1950 and, with some fluctuation, apparently are continuing to do so. Landings peaked at nearly 37 000 t in 1994 but have fallen back to approximately 31 000t in 1996 and 1997.

There are also important fisheries for flyingfish *Hirundichthys affinis* and the common dolphinfish *Coryphaena hippurus*. The four-winged flyingfish supports locally important fisheries in some of the Lesser Antilles islands, including Barbados, Grenada and Tobago. Landings of this species peaked at nearly 6 000 t in 1988, but more typically fluctuate between 1 000 and 2 500 t, as they have done throughout the 1990s. The common dolphinfish is also important to the small island states. Landings of common dolphinfish in the WECAFC region doubled from 2 014 t in 1984 to 4 297 t in 1997.

Mahon (1993) stated that some whaling is carried out from the islands of St Vincent and the Grenadines and from St Lucia, with the primary target species being blackfish (pilot whale) *Globicephala macrorhynchus*. He reported that an average of 224 animals per year were landed by St Vincent between 1962 and 1974, but does not give more recent statistics. He did not give any landings figures for St Lucia. No landings of marine mammals are recorded on Fishstat for the period 1984 to 1998 inclusive. He also reported that 10 other species of whale are taken by St Vincent, including false killer whale *Pseudorca crassidens*, small sperm whales *Physeter catodon*, pygmy killer whale *Feresa attenuata* and the dwarf sperm whale *Kogia simus*. Rambally (1999) reviewed the history of cetacean fisheries and gave recent catch statistics of small cetaceans, and national progress reports from some eastern Caribbean countries indicated that bottlenose dolphins (*Tursiops trancatus*), spotted dolphins (*Stenella frontalis*), spinner dolphins (*S. longirostris*), striped dolphins (*S. coeruleoalba*), Fraser's dolphins (*Lagenodelphis hosei*) and common dolphins (*Delphinus delphis*) have been harvested. Three nations reported catching humpback whales and black fish.

All of these, and many other stocks less important to fisheries, inhabit the pelagic zone of the Caribbean Sea and many of them will be linked through biological interactions, such as predation and competition, as well as through technological interactions such as being taken by the same fishing gear. Through these interactions, fishing activities that influence the abundance of any one of the stocks are likely to influence at least some of the others. These direct and indirect influences should be taken into account when management strategies are developed and implemented for any of the fisheries.

Complicating the issue further, none of the stocks mentioned above or other Caribbean pelagic stocks are likely to be confined to the EEZs of the Lesser Antilles islands. Some of these stocks will be distributed widely throughout the Caribbean Sea while others are distributed over the Atlantic Ocean. They are therefore likely to inhabit the Lesser Antilles EEZs for only a part of the time. The dynamics of their movements is, at best, only poorly understood. Nevertheless, most of these stocks will be shared, highly migratory, or straddling and therefore fall under the requirements of the UN Fish Stocks Agreement, which requires some form of international cooperation in their management.

The pelagic resources of the Lesser Antilles States therefore exhibit three characteristics which, together, require that urgent and comprehensive attention be given to identifying and describing their dynamics and inter-relationships. These are: the fisheries targeting them are expanding; the stocks show widespread distribution throughout the sub-region and beyond; and there are significant biological and technological interactions between them. This project aims to consider all three features and to develop a management plan that takes them into account and ensures that any fisheries, or other uses, to which they are subjected are conducted in a sustainable and responsible fashion. It also aims to assist in the development of research and management capacity to provide the participating countries with the skills to continue such ecosystem assessment for responsible management beyond the life of this project.

INCORPORATING MIGRATORY SPECIES IN THE LAPE MODEL

One of the challenges in construction of the LAPE model was the representation of the trophic dynamics of highly migratory and straddling species and the associated impacts of fishing in the time simulation component of Ecopath (Ecosim). The LAPE is an "open ecosystem" in that many important species spend only part of their time in the LAPE and are affected by fisheries and other sources of mortality both inside and outside the LAPE. They move freely between the two areas and while in the LAPE they feed on species with distribution ranges that are limited to the LAPE or Western Central Atlantic Area. For example, the distribution ranges of large tunas and billfishes extend beyond the LAPE region and some are as extensive as the entire Atlantic Ocean. Estimated catches outside the LAPE account for between 30% (wahoo) and 99% (for each of yellowfin, skipjack, albacore and bigeye tuna) total catch of

individual species (Mohammed *et al*., 2007). In fact, only between 0.37% (swordfish) and 9.78% (white marlin) of the overall biomass of the associated stocks in the Atlantic Ocean is estimated to occur in the LAPE area (Appendix 1).

Four options were considered for representation of migratory species in the LAPE model: the diet import method (Christensen *et al*., 2004; Vasconcellos *et al*., 2004); the two-compartment method or model expansion approach (Christensen *et al*., 2004; Vasconcellos *et al*., 2004); the F-scaled method (suggested by Carl Walters) and the balanced migration method (suggested by Villy Christensen). The details of associated testing are documented in FAO (2007, Field Document No. 6. Appendix 4). The F-scaled method was selected for use in the LAPE model. This method involves partitioning the total estimated fishing mortality (F) for the respective species to represent the F realized both inside and outside the LAPE, based on the relative catches in the two regions. The approach implies similar catchability of the two fleets, although given the vast differences in fleet characteristics (inside LAPE fleets are mainly artisanal while outside LAPE fleets are industrial) it is highly unlikely that this is in fact the situation. Using the equation Biomass = Catch/Fishing Mortality (at equilibrium), along with estimates of biomass and fishing mortality in the two regions, a new, "re-scaled" catch is computed. This approach appears to represent the dynamics of the species as in a closed system where the growth and consumption of predators are dependent on food availability and predation inside the LAPE. Given that the majority of the biomass of these species resides outside the LAPE, it is expected that the outside LAPE fishery would have considerably greater impacts on these species than the inside LAPE fishery. This is correctly modeled using the F-scaled approach. As well, use of the LAPE model is not recommended for management policy exploration associated with these species. A model that more accurately considers the distribution ranges of these species e.g., the Central Atlantic model after Vasconcellos and Watson (2004) is more appropriate for this purpose.

MODEL PARAMETERIZATION

The LAPE model is constructed to represent an average year between 2001 and 2005 using the Ecopath with Ecosim (Version 5.1) software . An average habitat temperature of 28 ^{o}C was used, after Opitz (1996). This estimate was consistent with the results of the LAPE Project ecosystem survey.

There are 31 functional groups in the LAPE area. The functional groups and the species included in each are listed in Appendix 2. The grouping of marine mammals is based on their distribution (vertical and horizontal) and diet composition. One previous version of the model (Vasconcellos *et al*., 2004) characterized three groups based on species detectability from the LAPE Large Scale Survey (FAO, 2007) and trophic role: Baleen whales, Deep-diving whales and Shallow-diving small cetaceans. However, to avoid within group

cannibalism the Deep-diving whale group was further subdivided so as to explicitly represent killer whales.

The current model is based on two previous models, a preliminary model of the EEZs of countries in the southeastern Caribbean (Mohammed, 2003) and a preliminary trophic model of the LAPE region (Vasconcellos *et al*., 2004) as well as new information (diet composition and biomass estimates of some species, primary production, fisheries catches) generated by the Project or in the published literature. There is however, a general lack of information, specific to the LAPE region, for most functional groups. It was therefore necessary to use parameters from other models of pelagic ecosystems or ecosystems with similar species in the LAPE model parameterization. These models were of the central Atlantic Ocean (Vasconcellos and Watson, 2004), west Florida shelf (Mackinson *et al*., 2005), central Pacific Ocean (Cox *et al*., 2002), coral reef system of the US Virgin Islands (Opitz, 1996). A summary of the LAPE model input parameters is given in Appendix 3.

Biomass

Biomass estimates of large, migratory pelagic finfish were taken from stock assessments conducted by the International Commission for the Conservation of Atlantic Tunas (ICCAT) or estimated, assuming equilibrium stock conditions, as the ratio of catch and fishing mortality (B = C/F). A spatial analysis of cumulated catches between 2000 and 2004 (ICCAT Task I Database) was used to estimate the proportion of time that migratory species spent inside the LAPE region, using the methodology suggested by Die *et al*. (2005), (Appendix 1). This estimate was used as a proxy for the total stock biomass occurring within the LAPE area over a given year and used to estimate biomass in the LAPE area. However, since the local fleets do not fully explore their entire EEZ catch data from both inside the LAPE as well as the buffer zone was used to generate a more realistic estimate of the proportion of overall biomass inside the LAPE. Cetacean sighting surveys and an ecosystem survey (utilizing acoustic and pelagic trawl sampling techniques) provided data from which the biomass of marine mammals, mesopelagic fish (small and large), squids (small and large), small pelagics and zooplankton (small and large) were estimated (Melvin *et al*., 2007). There were no estimates of biomass for several small tuna and mackerel species. In the model balancing a high number of functional groups, without specified biomasses, results in positive feedback loops. To avoid this problem an estimate of fishing mortality was assumed based on the fishing mortality computed from regional assessments (CFU, 2002; CRFM, 2005 and 2006) for similar species caught in the same fishery, and biomass was estimated as the ratio of catch and fishing mortality for these species/groups, assuming that the stocks are at equilibrium. The biomass inside the LAPE was computed as the product of the proportion inside the LAPE and buffer zone (F. Carocci, pers. com.) and total biomass. Some species are caught both inside and outside the LAPE, but are not represented in the ICCAT Task I database to facilitate spatial analysis to estimate the index as abundance, hence the ratio of catches inside

LAPE and total catches (from national databases and ICCAT CATDIS database) was used as a proxy for biomass inside LAPE. Biomass of phytoplankton was calculated as the product of primary production and the production: biomass ratio of phytoplankton, both parameters estimated by the LAPE Project (Forget, 2007). Biomass of detritus was estimated using the following relationship (Pauly *et al*., 1993):

$$Log_{10}D = -2.41 + 0.954\ Log_{10}PP + 0.863\ Log_{10}E \quad (1)$$

Where 'D' is detritus biomass in gCm^{-2}, 'PP' is primary production in $gCm^{-2}year^{-1}$ and 'E' is the euphotic depth in metres.

Production:Biomass-

P/B is is equivalent to the instantaneous rate of total mortality (Z) which can be estimated from catch curve analysis. Total mortality in some instances is estimated as the sum of fishing mortality and natural mortality, with natural mortality estimated using the empirical equation after Pauly (1980):

$$M = K^{0.65} \cdot L_{\infty}^{-0.279} \cdot Tc^{0.463} \quad (2)$$

where 'M' is the natural mortality ($year^{-1}$); 'K' is the curvature parameter of the von Bertalanffy growth function ($year^{-1}$); 'L_{∞}' is the symptotic length (total length, cm) and 'Tc' is the mean habitat (water) temperature (28 ^{o}C after Opitz, 1996).

Total instantaneous mortality can also be calculated from mean length, assuming steady recruitment, from the following equation (Beverton and Holt, 1956):

$$Z = K\ (L\infty - L_{avg})/(\ L\infty - L') \quad (3)$$

where $L\infty$ is the asymptotic length (total length, cm); L_{avg} is the mean length in the population, estimated from L' and upwards; L' is the mean length at entry into the fishery, assuming knife-edge selection.

Consumption : Biomass

Q/B is the consumption: biomass ratio. It is estimated using one of two empirical equations. Either (Palomares and Pauly, 1989):

$$Q/B = 3.06\ W_{\infty}^{-0.2018}\ Tc^{0.6121}\ Ar^{0.5156}\ 3.53^{Hd} \quad (4)$$

where 'Q/B' is the annual food consumption/biomass ratio, 'W_{∞}' is the asymptotic weight, H*d* is the food type (0 for carnivores and 1 for herbivores and detritivores), 'Tc' is the mean habitat temperature (28 ^{o}C after Opitz, 1996 for the LAPE area) and 'Ar' is the aspect ratio of the caudal fin.

or (Pauly *et al*., 1990):

$$Q/B = 10^{6.36}\ 0.0313^{\ Tk}\ W_{\infty}^{\ 0.168}\ 1.38^{\ Pf}\ 1.89^{\ Hd} \quad (5)$$

where 'Q/B' is the annual food consumption/biomass ratio, T*k* is an expression for mean annual habitat temperature (T*k* = 1000/(T°C + 273.1) after Regier *et al*. (1990), P*f* is 1 for apex predators and/or zooplankton feeders and 0 for other feeding types, W∞ and H*d* are as described in equation (4).

The length-weight relationship is used to convert asymptotic length to the corresponding weight: $W_\infty = aL_\infty^b$, where 'W' is the weight (g), 'L' is the length (cm) and 'a' and 'b' are the intercept and slope of the relationship between length and weight.

Diet

Diet composition was obtained from a review of existing literature, FishBase (www.fishbase.org) as well as recent diet studies conducted under the LAPE Project (Heileman *et al*., 2007). Diets for each species were first weighted based on the number of samples examined and the group diet composition was weighted based on the relative consumption of the respective species. In the absence of information on biomass, a systematic approach was followed for the second weighting (functional group) of diet composition, beginning with the assumption of no difference in relative consumption among the species in multi-species functional groups. When estimates of biomass and Q/B were available, diet composition was weighted by relative consumption. In the absence of biomass data, it was assumed that catches were representative of biomass in the system and diets were weighted accordingly. The sources and modifications to diet data to estimate the diet composition matrix for input to the LAPE ecosystem model are described in detail in Heileman *et al*. (2007) and input data summarized in Appendix 4. Since the model focuses on trophic linkages in the pelagic ecosystem, reef and demersal species components of the diet were treated as imports. As well, since the small pelagic group was split into two components, small offshore pelagics and small coastal pelagics, the associated diet contribution to predators was estimated by splitting the initial contribution of small pelagics based on the relative biomass of both groups obtained from acoustic and trawl surveys conducted in the LAPE ecosystem survey. Additionally the entire initial contribution of small pelagics to the diet of other offshore predators was attributed to small offshore pelagics and the entire initial contribution of small pelagics to the diet of coastal predators was attributed to small coastal pelagics. The contribution to the diet of swordfish was attributed only to small coastal pelagics.

Catch and unit price

Catches by Lesser Antilles countries, as well as Barbados and Trinidad and Tobago, were assumed to be taken inside the LAPE area whereas catches by other countries were assumed to be taken outside the LAPE area. Catch data were obtained from three main sources: Fisheries Departments of countries in the LAPE region, the International Commission for the Conservation of Atlantic Tunas (ICCAT) Task I Database (accessed June 04, 2007) and the Food and Agriculture Organization (FAO) FISHSTAT Plus Database (accessed June 12,

2007). Adjustments to the data are described in Mohammed *et al*. (2007). The fleet types after Mahon and McConney (2004) was used as the basis for description of fleets in the region, with modifications to facilitate examination of four policy issues identified above. Catches of non-participating countries in the LAPE project which are located within the LAPE area (Martinique and Guadeloupe) are also accounted for in the model. An "outside LAPE" catch is also incorporated to account for exploitation of migratory fish species by countries not located in the LAPE area. Given the catch reporting systems in the countries of the LAPE and the systems for estimating total catches from recorded or sampled data, the catch estimates in the LAPE region are considered underestimates. Data limitations are described in Mohammed *et al*. (2007). Catches of finfish species which are not fully distributed within the LAPE region have been re-scaled to incorporate the impacts of exploitation outside the LAPE region as the trophic model considers only the component of total biomass inside the LAPE region. The actual catches are given in Mohammed *et al*. (2007) and re-scaled catches in Appendix 5. Details of ex-vessel prices for species in the LAPE model are presented in Mohammed *et al*. (2007) and the average unit price by functional group is presented in Appendix 6.

FUNCTIONAL GROUPS

1. SEABIRDS

Background

The majority of seabirds in the West Indies (Bahama archipelago, Greater and Lesser Antilles and Trinidad and Tobago) now exist at a relatively low density (Schrieber and Lee, 2000). Most colonies are also currently restricted to offshore rocks and Cays as well as inaccessible cliffs, having been displaced by coastal development on mainlands. They feed at sea, some distance away from their breeding sites, and produce only one slow-growing chick per year. This low reproductive output makes it difficult for populations to recover from disturbance. There is currently little knowledge about the status of seabirds in the Caribbean. In the early 1980s van Halewyn and Norton (1984) and Sprunt (1984) wrote on the status of seabirds in the Caribbean, however, more indepth inventories have shown that population numbers were overestimated at the time and that in fact, there have been declines in a number of nesting pairs. Of the 21 species of seabirds nesting in the West Indies, more than half of these are small populations with conservation status of concern currently.

Little information exists on population numbers and diet composition. As a result the species represented in the LAPE model are restricted to those which exert a trophic impact on the pelagic fish species, in particular small pelagics targeted by fisheries for consumption or use as bait.

Although seabirds traverse expansive areas in some cases they rarely move between islands (Schrieber and Lee, 2000). In the LAPE model migration is not considered for seabirds. It is assumed that the species considered are mainly tropical and confined to the general study area.

The seabird functional group comprises twenty-one species of seabirds which nest in the West Indies (Schreiber and Lee, 1999). These species are: the Black-capped Petrel (*P. hasitata*), Brown Pelican (*Pelecanus occidentalis*), Cayenne Tern (*Sterna s. eurygnatha*), Common Tern (*Sterna hirundo*), Gull-billed Tern (*Sterna nilotica*), Royal Tern (*Sterna maxima*), Least Tern (*Sterna antillarum)*, Sandwich Tern (*Sterna sandvicensis*), Roseate Tern (*Sterna dougallii*), Bridled Tern (*Sterna anaethetus*), Sooty Tern (*Sterna fuscata*), Laughing Gulls (*Larus atricilla*), Black Noddy (*Anous tenuirostris*), Brown Noddy (*Anous stolidus*), Masked Booby (*Sula dactylatra*), Brown Booby (*Sula leucogaster*), Red-footed Booby (*Sula sula*), Red-billed Tropicbird (*Phaeton lepturus*), White-tailed Tropicbird (*Phaeton aethereus*), Audubon's Shearwater (*Puffinus lherminieri*) and Magnificent Frigatebird (*Fregata magnificens*).

Biomass

Biomass was estimated as the product of population numbers, derived from information on the range of number of nesting pairs in the West Indies after Schreiber and Lee (1999), and individual weight from Vasconcellos and Watson (2004); Mackinson *et al*. (2005); and Priddel *et al*. (2005). The midpoint number of pairs was used. Biomass was estimated at 4×10^{-5} t·km^{-2} for the West Indies (Bahama archipelago, Greater and Lesser Antilles and Trinidad and Tobago) as described in Schrieber and Lee (2000) and an estimate of 2×10^{-5} t·km^{-2} was assumed for the LAPE.

Production:Biomass

Estimates of P/B were taken from Vasconcellos and Watson (2004) for the associated species and weighted by biomass. The weighted P/B for the group was 0.13 year^{-1}.

Consumption:Biomass

Estimates of Q/B were taken from Vasconcellos and Watson (2004) and weighted by biomass. The weighted Q/B for the group was 73.69 year^{-1}.

Diet

See Heileman *et al*. (2007).

Catch

There are no reports of catches of seabirds in the LAPE region between 2001 and 2005.

2. BALEEN WHALES

Background

This group is comprised of the Bryde's whale, *Balaenoptera edeni,* and the humpback whale *Megaptera novaeangliae.* Bryde's whale, *Balenoptera edeni*, has a worldwide distribution in tropical to temperate waters, and is usually found below 35° latitude in both hemispheres (IWC). It has an offshore migration path with some limited north-south seasonal movements. In the North Pacific the species distribution is limited to the 15° C isotherm (Northridge, 1984). By the mid-1980s Northridge (1984) acknowledged the limited information available about the stock structure and population numbers of Bryde's whale. There are currently no comprehensive estimates of population numbers in the North Atlantic. Trites *et al*. (1997) reported an estimate for the world's population of Bryde's at 112,000 (this number is based on reviews made during the 1980s and early 1990s). According to the authors 86% of this total is in the Pacific. Therefore the maximum possible number in the Atlantic is of 15,680 animals. The estimate of population size in the northern Gulf of Mexico, provisionally considered a stock unit by the U.S., is of 40 animals (NOAA, 2003a).

A review made by Ivashin (1980) indicated the existence of many local populations of Bryde's throughout the world. In this review the author suggested the existence of a western population in the southwest of the North Atlantic, including the waters of the Caribbean Sea, Gulf of Mexico and off the southeast coast of the United States. Northridge (1984) also considered the possibility of a resident population in the Western Central Atlantic, given the restricted migration range of the species. Bryde's whale is the most common mysticete off Venezuela, and often associated with schools of *Sardinella anchovia* (Romero *et al*., 2001). Past sightings records in the area suggest the existence of a resident population that, according to the authors, arrives in the area in late spring and early summer, remains feeding in the area for several months and migrate to equatorial waters in winter time, when only a few individuals remain in the area.

Distinct stocks of humpback whales, *Megaptera novaeangliae*, are recognized in the North Atlantic, separated based on the fidelity of animals to feeding grounds in higher latitudes (NOAA, 2003b). Humpback whales feed during spring, summer and fall over a range which encompasses the eastern coast of the United States (including the Gulf of Maine), the Gulf of St. Lawrence, Newfoundland/Labrador, and western Greenland, and also in areas off Iceland and northern Norway, including off Bear Island and Jan Mayen (NOAA, 2003b). The estimated stock size reported by IWC for the Western North Atlantic is 11,570 animals. Practically all North Atlantic stocks use the Caribbean as mating and calving areas during the winter months. The majority of the whales are found in the waters of the Dominican Republic, with lower densities in the Lesser Antilles (NOAA, 2003b). As the species does not feed in the LAPE area it was excluded from the model.

Biomass

The cetacean sighting surveys recorded eight sightings comprising four humpback whales and five Bryde's whales. Biomass of Bryde's whale was estimated as the product of the number of animals estimated, and the mean individual weight after Trites and Pauly (1998). The estimate, 2.51 x 10^{-2} t·km^{-2} should, however, be put within wide confidence bounds considering the CV of 42% of the Large Scale Survey density estimates (FAO, 2007).

Production:Biomass

A range of P/B ratios for Baleen whales have been reported in the literature: 0.02 year^{-1} (Trites and Heise, 1996; Trites *et al*., 1999); 0.05 year^{-1} (O'Key and Pauly, 1999; Zeller and Freire, 2002); 0.1 year^{-1} (Bundy *et al*., 2000). NOAA (2003a) estimated a maximum net productivity rate of 4% for baleen whales, which could be translated into a P/B ratio of 0.04 year^{-1}. A P/B ratio of 0.04 year^{-1} was provisionally adopted, however, the range from 0.02 to 0.1 year^{-1} as possible alternatives was considered during model balancing.

Consumption:Biomass

Several estimates of Q/B ratios are reported in the literature: 14.6 year^{-1} (Trites and Heise, 1996), 10.95 year^{-1} (O' Key and Pauly, 1998); 11.79 year^{-1} (Bundy *et al*., 2000); 11.38 year^{-1} (Trites *et al*., 1999); 12.26 year^{-1} (Zeller and Freire, 2002). The annual Q/B estimated based on mean weight of Bryde's whales and the predicted daily ration from Innes *et al*. (1987) and Trites *et al*. (1997) is 5.2 year^{-1}. As noted by Mohammed (2003), this estimate is probably too low for baleen whales, considering that all other available estimates are at least twice as high. In the model an average Q/B of 12.19 year^{-1} was provisionally adopted, however, the range from 5.2 to 14.6 year^{-1} as possible alternative values was considered during model balancing.

Diet

See Heileman *et al*. (2007).

Catch

Man-induced mortality of Bryde's whales was considered insignificant for the northern Gulf of Mexico stock (NOAA, 2003a). No catches of baleen whales were reported in the LAPE region between 2001 and 2005.

3. DEEP-DIVING WHALES

Background

The IWC recognizes one single stock of sperm whale, *Physeter catodon,* in the North Atlantic (NOAA, 2002a). There are no available estimates of biomass for the whole stock. Northridge (1984) reports a total population size in the Atlantic of 22,000 animals and suggests that a figure in the order of thousands animals visit the Western Central Atlantic and the Caribbean seasonally. Sperm whales seem to be more frequent in the Caribbean from October to March and present in scarcer numbers during the summer months (Northridge, 1984). According

to IWC only adult males sperm whales move into latitudes higher than 45° in both hemispheres to feed, although seasonal movements from higher to lower latitudes between summer and winter do occur in some segments of populations.

The Gervais beaked whale *Mesoplodon europaeus* has a distribution confined to the warm temperate and tropical waters of the Northwest Atlantic, being centered on the Antillean region (Northridge, 1984). Most records are from the east and Gulf coasts of North America, but there are also many sighting records in the Caribbean islands (Jefferson *et al*., 1993). There are three other species of *Mesoplodon* spp. common in the Northwest Atlantic and northern Gulf of Mexico that are likely to be confused with *M. europaeus*: *M mirus*, M. *densirostris* and *M. bidens* (NOAA, 1995; 2003c). However, considering the geographic limits of distribution of the species, *M. europaeus* is the one most likely to be sighted in the Lesser Antilles area (Jefferson *et al*., 1993).

Biomass

Sperm whale abundance in the Atlantic coast of USA and Canada and in the northern Gulf of Mexico was estimated at 4,702 and 1,349, respectively (NOAA, 2002a; 2003d). In the model the sum of these abundance values (6,051) was considered a minimum estimate of the size of the North Atlantic population that visits the LAPE area. The biomass (1.837×10^{-1} t ·km^{-2}) was estimated as the product of number of animals and mean individual weight (18,519 kg) after Trites and Pauly (1998).

NOAA (1995 and 2005) report estimates of stock size of Gervais beaked whale in the Western North Atlantic and in the Northern Gulf of Mexico of 612 and 106 animals, respectively. As there is no basis to differentiate stocks in the North Atlantic, these numbers should be considered area specific minimum abundance estimates – the diving behavior of the species is likely to cause an underestimation of population abundance by surveys. The sum of the biomass estimates for sperm whales and Gervais beaked whale (718 animals) was considered a minimum estimate of the size of the population that visits the LAPE. The biomass (4.6×10^{-4} t ·km^{-2}) was estimated as the product of number of animals and mean individual weight (393 kg) after Trites and Pauly (1998).

The total biomass of Deep-diving whale stocks that visit the LAPE (0.184 t ·km^{-2}) was calculated as the sum of the biomass of sperm whale and Gervais' beaked whale stocks. The cetacean sighting surveys of the LAPE project recorded nine sightings of deep-diving whales comprising four sperm whales and eleven beaked whales. The biomass, calculated as the product of the number of animals estimated from the survey and mean individual weight from Trites and Pauly (1998), was 1.45×10^{-2} t ·km^{-2}, representing approximately 8% of the total biomass estimated here for the North Atlantic.

Production:Biomass

The maximum net reproductive rate of both Gervais beaked whale and sperm whale was considered 0.04 year^{-1} (NOAA, 2003 c and d). Trites and Heise (1996)

used a P/B of 0.02 year^{-1} for toothed whales. This estimate would probably be more realistic for the large sperm whales. In the model a P/B of 0.04 year^{-1} was used.

Consumption:Biomass

Q/B was estimated using a modified version of the daily ration equation proposed by Innes *et al*. (1986) cited in Trites *et al*. (1997). The equation calculates daily ration based on the species mean weight. For sperm whales the estimated Q/B is 5.11 year^{-1} and for Gervais beaked whale Q/B was estimated at 11.05 year^{-1}. A weighted average of 5.44 year^{-1} was used in the model for the group.

Diet

See Heileman *et al*. (2007).

Catch

The total fishery-related mortality and serious injuries of sperm whales and Gervai's beaked whales in the Gulf of Mexico stock and western North Atlantic are considered insignificant, being probably less than 10% of the rate of potential biological removal (NOAA 2003 c and d). No catches were reported in the LAPE region between 2001 and 2005.

4. KILLER WHALES

This group comprises the killer whale (*Orcinus orca*), the false killer whale (*Pseudorca crassidens*) and the pygmy killer whale (*Feresa attenuate*). The false killer whale has a wide distribution in tropical and temperate waters, feeding on fish and cephalopods but has also been known to attack other small cetaceans.

Biomass

The LAPE cetacean sighting surveys (both large and small scale) recorded six sightings of killer whales, comprising eight true killer whales (*Orcinus orca*) and sixteen false killer whales (*Pseudorca crassidens*). The number of animals sighted is too few to derive an estimate of abundance. It was assumed, based on the area covered in the surveys and the relative quantities of marine mammals sighted, that killer whale density was about one third of that of deep-diving whales. Biomass was estimated as the product of number of animals and mean individual weight from Trites and Pauly (1998). The estimated killer whale biomass in the LAPE was 1.58 x 10^{-3} t·km^{-2}.

Production:Biomass

A P/B ratio of 0.02 (Trites and Heise, 1996) was used.

Consumption:Biomass

Several estimates of Q/B are available for killer whales in the literature: 12.1 and 14 year^{-1} (Trites and Heise, 1996); 6.04 and 8.67 year^{-1} (Okey, 2002); 7.4 year^{-1} (Martell *et al*., 2002). An average estimate of 9.64 year^{-1} was used. However,

the range of possible alternatives (7.4 to 14 year^{-1}) was considered during model balancing.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 5.95 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

5. SHALLOW-DIVING SMALL CETACEANS

Background

This group includes ten species of shallow-diving small cetaceans which were most frequently observed during the cetacean sighting surveys. Information about the distribution and feeding habits of these species is documented in Northridge (1984) and Jefferson *et al*. (1993). The short-finned pilot whale, *Globicephala macrorhynchus,* and the melon-headed whale, *Peponocephala electra*, have a worldwide distribution in warm temperate and tropical waters, feeding both on fish and squids. The Atlantic spotted dolphin, *Stenella frontalis*, is restricted to the Atlantic Ocean, ranging from southern Brazil to New England in west Atlantic. The species feed on variety of fish and squids. Bottle nose dolphin, *Tursiops truncatus*, is found primarily in coastal and inshore areas of tropical and temperate waters. In some areas the species has a limited migratory behavior, while in others they can perform longer range migrations. Bottle nose dolphins can be considered opportunistic feeders, but with a preference to demersal coastal fishes. The short-snouted spinner dolphin, *Stenella clymene* is found only in the subtropical and tropical Atlantic, feeding on small fish, including myctophids, and also squids. The pantropical spotted dolphin, *Stenella attenuata*, habits oceanic tropical waters of all oceans, feeding largely on epipelagic fish and squid. The striped dolphin, *Stenella coeruleoalba* is generally restricted to oceanic waters in tropical and temperate regions, with diet consisting primarily of small, mid-water squid and fish, especially lanternfish. Finally, the Fraser's dolphin, *Lagenodelphis hosei* is an oceanic species with a pantropical distribution, feeding on mid-water fish, squid and crustaceans. The rough-toothed dolphin, *Steno bredanensis*, is tropical and subtropical in distribution. Although the species generally inhabits deep oceanic waters, it has been known to occur in shallow coastal waters in some areas e.g., off the coast Brazil and in the Lesser Antilles where it is caught. The species feeds on cephalopods and fish, including dolphinfish. It is suggested that the rough-toothed dolphin may be adapted to become a specialist feeder on dolphinfish (http://seamap.env.duke.edu/species/tsn/180417).

In general there is no available information about the stock structure and estimates of the population size of these species. In the U.S. the species are provisionally separated into two stocks for management purposes, one for the northern Gulf of Mexico and one for the east coast of North America. Estimates

of stock sizes are provided in NOAA's stock assessment report webpage http://www.nmfs.noaa.gov/pr/sars. Considering that many of these species do not perform large migrations, in the model it was assumed the existence of resident stocks in the LAPE area. Nonetheless the existence of stocks associated with each of the islands and also the hypothesis of interactions with the stocks of northern Gulf of Mexico and Atlantic coast of North America should not be disregarded.

Biomass

The LAPE cetacean sighting surveys recorded 25 sightings of shallow-diving small cetaceans, comprising 25 short-finned pilot whales, 127 melon-headed whales, 15 bottlenose dolphins, five short-snouted spinner dolphins, 245 pantropical-spotted dolphins (five unidentified dolphins assumed to be this species), 35 Atlantic spotted dolphins, one Fraser's dolphin, and five unidentified marine mammals. The mean density of shallow-diving small cetaceans estimated from the results of the surveys was 1,000 animals per 10^3n.m^2 (FAO, 2007). The product of mean density and mean individual weight (after Trites and Pauly, 1998), gave a biomass estimate of 0.0336 t·km^{-2} in the LAPE area. The wide confidence interval of this density estimate (CV of 89%) was taken into account in model balancing.

Production:Biomass

The available P/B estimates for dolphins, taken from other models, vary between 0.02 and 0.1 year^{-1} (Browder, 1993; Bundy *et al.*, 2000; Buchary *et al.*, 2002; Fulton and Smith, 2002). In the present version of the model a P/B of 0.05 year^{-1} (slightly higher than the one used for larger whales) was used, but the range of values provided in the literature was considered as possible alternative values during model balancing.

Consumption:Biomass

The Q/B ratios for dolphins taken from other models vary between 9.8 and 41.01 year^{-1}(Browder, 1993; Bundy *et al.*, 2000; Buchary *et al.*, 2002; Fulton and Smith, 2002). In the model, the weighted average Q/B (13.50 year^{-1}) of individual species, calculated using the daily ration formula of Innes (Trites *et al.*, 1997), was used. However, the range of values provided in the literature was considered as possible alternative values during model balancing.

Diet

See Heileman *et al.* (2007).

Catch

An average annual catch of 16.77 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al.*, 2007).

6. SWORDFISH

Background

Three stocks of swordfish are currently recognized, in the Mediterranean, north and south Atlantic (ICCAT, 2003a). The north Atlantic stock of swordfish was considered overfished for many years, but since 1997 the stock has been showing some improvement owing to a sequence of strong recruitment and reduced catches (ICCAT, 2003a).

Biomass

The total biomass of the North Atlantic stock was estimated at 70,564 tonnes (ICCAT, 2006a) or 1.157×10^{-1} t·km^{-2}. The biomass in the LAPE area was estimated at 8.98×10^{-4} t·km^{-2}.

Production:Biomass

The most recent stock assessment information indicates that the biomass is at 99% of B_{msy} and that the fishing mortality rate is 0.86 times the F_{msy} (ICCAT, 2006a). Current fishing mortality rate estimated based on surplus production model is 0.172 year^{-1} (r = 0.49 and F_{cur}/F_{msy} = 0.86; ICCAT, 2006a). Fishing mortality, estimated by VPA, varies from 0.28 to 0.55 year^{-1} for ages 1 to 5 (ICCAT, 2003a). In the model a fishing mortality rate of 0.172 year^{-1} and a natural mortality rate of 0.2 year^{-1} (currently adopted by ICCAT) were used. The P/B was therefore estimated as the sum of fishing and natural mortality, 0.372 year^{-1}.

Consumption:Biomass

Estimates of the Q/B ratio for swordfish vary between 2.93 and 5 year^{-1} (FishBase; Brown *et al*., 1991; Cox *et al*., 2002). In the model the Q/B of the species was estimated at 5.31 year^{-1} using the empirical equation after Palomares and Pauly (1989), growth, length-weight parameters, aspect ratio and food type from FishBase (www.fishbase.org; Froese and Pauly, 2000) and assuming an environmental temperature of 28 ^{o}C.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 182 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

7. OTHER BILLFISHES

This is an aggregate group comprising Atlantic blue marlin (*Makaira nigricans*), Atlantic white marlin (*Tetrapturus albidus*), Atlantic sailfish (*Istiophorus platypterus*), Longbill spearfish (*Tetrapturus pfluegeri*) and black marlin (*Makaira indica*). Sailfish is divided between west and east Atlantic stocks (ICCAT, 2001a). A single Atlantic stock is assumed for both blue and white marlins respectively (ICCAT, 2001b; 2003b). The longbill spearfish and black marlin are

the least known species among the billfishes. Longbill spearfish has been only recently reported as a new species (Fonteneau and Marcille, 1993). The stock structure of both these species is unknown (Mahon, 1996; ICCAT, 2001 a and b). The status of the west Atlantic stock of sailfish and of the stock of spearfish are currently unknown (ICCAT, 2001a). ICCAT (2001a) acknowledges that early decreases in the biomass of sailfish may have brought the stock to levels that may be producing sustainable catches.

Biomass

Blue and white marlins are considered overfished (ICCAT, 2006b). Biomass of blue marlin is approximately 43% of Bmsy and current fishing mortality is about two times higher than Fmsy. White marlin biomass is 47% of Bmsy and the current fishing mortality is 0.98 times Fmsy. Estimates of biomass of blue and white marlins reported by ICCAT (2006b) were used in the model, 11,228 tonnes and 6,355 tonnes respectively. Estimates of biomass of sailfish (1.07 x 10^{-2} t km^{-2}), black marlin (3.9 x 10^{-4} t $\cdot km^{-2}$) and spearfish (8.5 x 10^{-4} t $\cdot km^{-2}$) were calculated as the ratio of catch and fishing mortality (F). A fishing mortality of 0.2 $year^{-1}$, as proposed by Brown *et al*. (1991) for the model of the Gulf of Mexico was assumed for sailfish and spearfish and a fishing mortality of half that of blue marlin was assumed for black marlin. The overall biomass of the group (4.64 x 10^{-2} t $\cdot km^{-2}$) was estimated as the sum of the individual species biomass. Biomass in the LAPE area was estimated at 5.5 x 10^{-3} t $\cdot km^{-2}$.

Production:Biomass

Estimates of fishing mortality of blue and white marlin reported by ICCAT (2006b) were 0.16 $year^{-1}$ and 0.44 $year^{-1}$, respectively. Natural mortality rates are in the range of 0.15 to 0.30 $year^{-1}$ for blue marlin and 0.1 to 0.2 $year^{-1}$ for white marlin (ICCAT, 2001 a and b). Mid-range values were used in the present model. Natural mortality rate of sailfish and spearfish (combined data) is in the range from 0.2 to 0.3 $year^{-1}$ (ICCAT, 2001a) and a fishing mortality rate 0.2 $year^{-1}$ was assumed (Brown *et al*., 1991). The fishing mortality of black marlin was assumed half that of the blue marlin and the natural mortality was assumed the same. The P/B for each species was estimated as the sum of F and M. The group P/B was estimated as the weighted average (0.42 $year^{-1}$).

Consumption:Biomass

The Q/B ratio for blue and black marlin was set to 4 $year^{-1}$, and to 5 $year^{-1}$ for the other billfishes (Cox *et al*., 2002). The group Q/B (4.59 $year^{-1}$) was estimated as the weighted average across all species.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 453 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

8. YELLOWFIN TUNA, *THUNNUS ALBACARES*

Background

The species is found worldwide in tropical and subtropical waters. A single Atlantic stock is hypothesized (ICCAT, 2004a). Adults usually occur above the thermocline, while juveniles are found in schools at the surface mixing with skipjack and bigeye tunas. Large and adult fish are found in deeper waters and also extend their range into higher latitudes than smaller fish (ICCAT, 2004a).

Biomass

The stock biomass was estimated as the ratio between catches and fishing mortality, assuming that the stock is currently at equilibrium. Fisheries catches inside and outside the LAPE were obtained as described in Mohammed *et al*. (2007) using data submitted by Fisheries Departments of participating countries in the LAPE Project and the ICCAT Task I Database. The average annual catch between 2001 and 2005 was 1 226 tonnes. Fishing mortality is estimated to be close to an F_{msy} of 0.72 year^{-1} (ICCAT, 2004a). The resulting total biomass estimate was 178 815 tonnes or 3.204 x 10^{-1} t·km^{-2}. Estimated biomass in the LAPE area was 1.24 x 10^{-2} t·km^{-2}.

Production:Biomass

Natural mortality rates between 0.8 year^{-1} (ages 0 and 1) and 0.6 year^{-1} (ages 2+) are normally used in stock assessments (ICCAT, 2004a). Hampton (2000) estimated M between 0.44 and 0.69 year^{-1} for midsized yellowfin tuna in the Pacific. The F_{msy} is estimated at 0.72 and F_{2001}/F_{msy} is in the range of 0.73 and 1.10 (ICCAT, 2004a). Using the midpoint estimate of F_{2001}/F_{msy} and F_{msy} the fishing mortality was estimated at 0.6588 year^{-1}. A natural mortality of 0.7 year^{-1} was assumed and P/B estimated at 1.3588 year^{-1}.

Consumption:Biomass

Menard *et al*. (2000) estimated the daily rations of yellowfin tuna smaller than 90 cm and larger than 90 cm at 6.12% and 2.59%, respectively. That corresponds to a Q/B ratio for the species between 9.2 year^{-1} and 21.7 year^{-1}. Cox *et al*. (2002) applied Q/B of 14 year^{-1} and 17.6 year^{-1} for large and small yellowfin tuna for the model of the Central Pacific ocean. In the present model Q/B was set to 15.53 year^{-1} to represent an expected average metabolic rate during the life span of the species.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 1 254 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

9. ATLANTIC SKIPJACK, *KATSUWONUS PELAMIS*

Background

Skipjack tuna occurring in the LAPE is considered part of the western Atlantic stock. A gregarious species, found in schools in tropical and subtropical waters of the three oceans, the species is predominant under FADs where it is caught in association with juvenile yellowfin tuna, bigeye tuna and other species of the epipelagic fauna (ICCAT, 1999). Skipjacks spawn in equatorial waters throughout the year, and in subtropical waters from spring to early fall. Most spawning takes place during summer months in the Caribbean, off Brazil, in the Gulf of Mexico, and in the Gulf of Guinea (Fonteneau and Marcille, 1993). Abundance indices from the Brazilian baitboat fishery and the Venezuelan purse seine fishery had indicated a stable stock status in western Atlantic during the 1990s (ICCAT, 1999). However, the many changes in the skipjack fishery since then, particularly associated with the use of FADs and westward expansion of the fishery on the eastern Atlantic stock, have increased the catchability, and therefore the proportion of both stocks (east and west Atlantic) that is exploited. It is also suggested that the use of FADs has altered the behaviour of schools and movement of the species, and may also negatively impact growth (ICCAT, 1999). Recently the stock was considered moderately to fully exploited (FAO, 2005), however, no estimates of fishing mortality are available. Catch per unit of effort (CPUE) in the Brazilian baitboat fishery has remained stable while CPUE in the Venezuelan purse seine fishery has decreased in recent years. Current fishing mortality rates are expected to be at or around F_{msy}.

Biomass

In the Pacific, where stocks are also considered moderately exploited, F was estimated between 0.3 and 0.5 $year^{-1}$ for fish between 40 and 70 cm, which comprise the bulk of the exploited size range (Hampton, 2000). The mid-point, 0.4 $year^{-1}$, was assumed for the LAPE. Biomass (68 876 tonnes or 1.129×10^{-1} $t \cdot km^{-2}$) was estimated as the ratio between F and catch (annual average of 27 550 tonnes between 2001 and 2005), assuming that the stock is under equilibrium conditions. The LAPE biomass was estimated at 1.19×10^{-2} $t \cdot km^{-2}$. Fisheries catches inside and outside the LAPE were obtained as described in Mohammed *et al*., (2007) using data submitted by Fisheries Departments of participating countries in the LAPE Project and the ICCAT Task I Database.

Production:Biomass

The average M for fish between 40 and 70 cm was 1.9 $year^{-1}$ (Hampton, 2000). However, M for skipjack was estimated at 0.94 $year^{-1}$ using Pauly (1980) empirical equation. In the present model a mid-range value for M was adopted (M= 1.4 $year^{-1}$). P/B was therefore estimated as the sum of F and M, 1.8 $year^{-1}$.

Consumption:Biomass

The daily ration of skipjack tuna in the equatorial Atlantic was estimated at 5.51% (Menard *et al*. 2000), corresponding to a Q/B of 19.61 $year^{-1}$. This value is

consistent with the Q/B of 20 year^{-1} used by Cox *et al*. (2002) for skipjacks in the Central Pacific.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 250 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

10. ALBACORE, THUNNUS ALALUNGA

Background

Albacore is a temperate species widely distributed throughout the Atlantic Ocean and Mediterranean Sea (Fonteneau and Marcille, 1993). Albacore occurring in the LAPE was considered part of the north Atlantic stock. Until the age of maturity (5 years) albacore is mainly found in surface waters, where they are targeted by surface gears. Some adult albacore are also caught using surface gears but, as a result of their deeper distribution, they are mainly caught using longlines (Fonteneau and Marcille, 1993).

Biomass

The northern Atlantic stock is considered overfished as B = 0.7 B_{msy} and F = 1.1 F_{msy} (ICCAT, 2004b; FAO, 2005). No absolute F values are reported by ICCAT for the northern stock. The natural mortality rate was estimated at 0.28 year^{-1} using Pauly's (1980) empirical equation while ICCAT (2004) uses an M of 0.3 year^{-1}. The latter estimate was used in the LAPE model and it was assumed that fishing mortality was equal to natural mortality. Assuming that the stock is under equilibrium conditions, total biomass was estimated at 88 328 tonnes (0.15 t·km^{-2}) using the ratio of total catch (annual average of 26 445 tonnes between 2001 and 2005) and F (0.3 year^{-1}). Biomass in the LAPE area was estimated at 9.7 x 10^{-3} t·km^{-2}.

Production:Biomass

The P/B was estimated as the sum of F and M, 0.6 year^{-1}.

Consumption:Biomass

Cox *et al*. (2002) estimated Q/B ratios between 7.3 and 9.6 year^{-1} for large and small albacore in the Central Pacific. A Q/B of 6 year^{-1} was estimated using empirical equations and population parameters available in FishBase (www.fishbase.org; Froese and Pauly, 2000). In the present model Q/B was set to a mid-range value, i.e., 7.8 year^{-1}.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 60 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

11. BIGEYE TUNA, *THUNNUS OBESUS*

Background

The geographical distribution of bigeye tuna is very wide and covers almost the entire Atlantic Ocean between 50° N and 45° S (Fonteneau and Marcille, 1993). A single wide stock in the Atlantic is currently accepted by ICCAT. Adult bigeye dwells in deeper water than other tuna species and performs extensive vertical movements. Young fish form schools mostly mixed with other tunas such as yellowfin and skipjack tunas. Spawning takes place in tropical waters and after spawning fish tend to migrate into temperate waters. (Fonteneau and Marcille, 1993).

Biomass

The most recent assessment suggested that the stock is currently not overfished and showing signs of improvement (ASPIC model; ICCAT, 2005a). The current biomass was estimated at 1.068 times B_{msy}, (B_{msy} = 222 200 tonnes) and F is 0.461 times F_{msy} (F_{msy} = 0.729), (ICCAT, 2005a). The biomass estimate from the ASPIC model (237 310 tonnes or 3.89×10^{-1} t·km^{-2}) was used. Biomass in the LAPE was estimated at 1.68×10^{-3} t·km^{-2}.

Production:Biomass

Fishing mortality was estimated at 0.34 year^{-1} based on results of the ASPIC model (ICCAT, 2005a). Natural mortality rate was estimated at 0.29 year^{-1} based on Pauly (1980). However, ICCAT uses an M of 0.8 year^{-1} for the juveniles and 0.4 year^{-1} for adult bigeye. Hampton (2000) estimated that M varies between 0.15 and 0.9 year^{-1} for bigeye larger than 40 cm. In this model M was set to 0.4 year^{-1}. P/B was therefore estimated as the sum of F and M, 0.74 year^{-1}.

Consumption:Biomass

The daily ration of bigeye in the equatorial Atlantic was estimated at 4.82% (Menard *et al*., 2000), which corresponds to a Q/B of 17.59 year^{-1}.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 29 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

12. BLACKFIN TUNA, *THUNNUS ATLANTICUS*

Background

There is generally very limited information about the stock structure and abundance of this species. However, the species is an important component of fisheries in the LAPE.

Biomass

Biomass was estimated as the ratio of total catch and fishing mortality. Annual average catch was estimated at 2 752 tonnes (Mohammed *et al*., 2007). It was assumed that fishing mortality was the same as that estimated for wahoo (1.1 $year^{-1}$) since the species is captured in the same fishery as subjected to the same fishing intensity. It is recognized that catchability is a key component to estimation of F, and that some countries target blackfin tuna in beach seines (which is not used to target wahoo). However, it is difficult to assess the impact of the beach seine fishery on F in the absence of data. Assuming that the stock is under equilibrium conditions, biomass was estimated at 2 501 tonnes (4.1×10^{-3} $t \cdot km^{-2}$) using the ratio of total catch and F (1.1 $year^{-1}$). Since the species is not explicitly represented in the ICCAT Task I Database the proportion of biomass inside and outside the LAPE was estimated as the ratio of the annual average catch between 2001 and 2005 in the respective areas. Biomass inside the LAPE was estimated at 2.1×10^{-3} $t \cdot km^{-2}$.

Production:Biomass

The P/B ratio (1.85 $year^{-1}$) was estimated as the sum of F and M, F assumed 1.1 $year^{-1}$ and M estimated at 0.75 $year^{-1}$ using the empirical equation after Pauly (1980) and growth parameters from FishBase (www.fishbase.org; Froese and Pauly, 2000).

Consumption:Biomass

The Q/B ratio was estimated at 9.89 $year^{-1}$ using the empirical equation after Palomares and Pauly (1989), with growth parameters, aspect ratio and food type from FishBase (www.fishbase.org; Froese and Pauly, 2000).

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 1 415 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

13. OTHER OFFSHORE PREDATORS

Background

This is an aggregate functional group comprising other small tunas (Atlantic bonito, *Sarda sarda*, frigate and bullet tunas, *Auxis* spp., and little tunny, *Euthynnus alletteratus*) as well as two species of triggerfish (spotted ocean

triggerfish, *Canthidermis maculatus*; ocean triggerfish, *Canthidermis sufflamen*) observed in offshore waters during the LAPE ecosystem survey. In general, there is very limited information about the stock structure and abundance of these species.

Biomass

Biomass was estimated as the ratio of catch and fishing mortality, assuming that the stocks are at equilibrium. A fishing mortality of 1.1 year^{-1}, as estimated for wahoo (Murray and Sarvay, 1987 and Murray and Joseph, 1996), was assumed as the associated species are caught in the same fishery and subject to the same fishing intensity. Since the species are not explicitly recorded in the ICCAT Task I Database the proportion of biomass inside the LAPE was assumed to be the ratio of catches inside the LAPE area and total catch. Biomass inside the LAPE was estimated at 2.3 x 10^{-3} t·km^{-2}.

Production:Biomass

An average natural mortality rate of 0.85 year^{-1} was estimated using reported growth parameters in FishBase (www.fishbase.org; Froese and Pauly, 2000) and the empirical relationships after Pauly (1980). Since growth parameters were not available for *Canthidermis* spp. to facilitate estimation of natural mortality using the equation after Pauly (1980) the mean estimate of natural mortality for small tunas was assumed for the species. The P/B was estimated as the sum of natural mortality and the assumed fishing mortality. The weighted P/B for the group was 1.87 year^{-1}.

Consumption:Biomass

The Q/B was estimated using growth parameters, aspect ratio and food type from FishBase (www.fishbase.org; Froese and Pauly, 2000) in the empirical equation after Palomares and Pauly (1989). In the absence of growth parameters for *Canthidermis maculatus* the average Q/B of small tunas was assumed. The estimated weighted Q/B for the group was 7.44 year^{-1}.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 1 577 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

14. MACKERELS

Background

This is an aggregate group composed of Serra Spanish mackerel, *Scomberomorous brasiliensis*, king mackerel, *S. cavalla*, Spanish mackerel, *S. maculatus* and cero mackerel, *S. regalis*. Serra Spanish mackerel is found in Western Atlantic along the Caribbean and Atlantic coasts of Central and South America from Belize to southern Brazil. King mackerel is found from Gulf of

Maine to Brazil and throughout the Gulf of Mexico and Caribbean Sea. Spanish mackerel occurs throughout the Gulf of Mexico and west coast of the US. Cero mackerel occurs from Massachusetts to Brazil, and is particularly abundant in the Bahamas and West Indies (Collette and Nauen, 1983). All of them are known to perform long distance seasonal migrations between spawning and wintering areas. For king and Spanish mackerels two migratory stocks are recognized: one in the waters of the western Atlantic from Massachusetts to Brazil and the other in the Gulf of Mexico (Die, 2004).

Biomass

According to assessments conducted by NOAA the status of the Atlantic migratory groups of king and Spanish mackerel and the Gulf migratory group of Spanish mackerel are within acceptable biological limits, i.e., there is no overfishing occurring and the stocks are not overfished (Die, 2004). By contrast the Gulf of Mexico migratory stock of king mackerel is suffering overfishing and is being overfished (Die, 2004). Assessments conducted on the portion of the stocks of Serra Spanish mackerel and king mackerel in the eastern Caribbean suggest that these may be heavily fished (Martin and Nowlis, 2005; Martin and Hoggarth, 2006), however the authors have recommended caution in interpretation of the assessment results due to uncertainties in growth parameters and catch data. Biomass of this group was estimated as the ratio of overall catch and fishing mortality (see below). Since the species are not explicitly recorded in the ICCAT Task I Database the proportion of biomass inside the LAPE was assumed to be the ratio of catches inside the LAPE area and total catch. Biomass inside the LAPE was estimated at 7.8×10^{-3} t·km^{-2}.

Production:Biomass

The mean fishing mortality of age 2+ fish in the Gulf of Mexico king mackerel stock between 2001 and 2002 was estimated at 0.176 year^{-1} (Ortiz, 2004). Martin and Hogarth (2006) however, estimated the 2004 fishing mortality at between 1.48 and 1.99 year^{-1} assuming a southern Caribbean stock. The mid-point, 1.735 year^{-1}, was used in the LAPE model. The stock of Serra Spanish mackerel off Trinidad and Tobago is heavily fished. Estimated F_{msy} is between 0.198 and 0.2038 year^{-1} and F_{2002}/F_{msy} is between 0.7614 and 1.167 (Martin and Nowlis, 2004). The fishing mortality (0.1937 year^{-1}) corresponding to the mid-point estimate of F_{2002}/F_{msy} and F_{msy} was used. It is noted however, that in the late 1980s average total mortality rate of Serra Spanish mackerel off Trinidad & Tobago was estimated at 1.04 year^{-1} (Sturm *et al*., 1987 and Julien-Flus, 1988). Fishing mortality of the other mackerel species was not known and the mean fishing mortality estimated for the Serra Spanish mackerel and king mackerel was assumed as these species are all caught in the same fishery and are subject to similar fishing intensity. Natural mortality of the king mackerel was estimated at 0.55 year^{-1}, (Martin and Hoggarth, 2006). Natural mortality of other species was estimated using growth parameters from FishBase (www.fishbase.org; Froese and Pauly, 2000) and the empirical equation after Pauly (1980). The P/B was estimated as the sum of fishing and natural mortality, the weighted group estimate being 1.09 year^{-1}.

Consumption:Biomass

The Q/B was estimated using growth and length-weight parameters as well as food type from FishBase along with the aspect ratios in Opitz (1996) in the empirical equation of Palomares and Pauly (1989). The weighted estimate of Q/B for the group was 10.31 $year^{-1}$.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 2 881 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

15. WAHOO, *ACANTHOCYBIUM SOLANDRI*

Background

Wahoo is an oceanic species with a circum-tropical distribution, occurring in tropical and subtropical waters of the Atlantic, Pacific and Indian Oceans (Collette and Nauen, 1983). In the western central Atlantic region the species is distributed between the northeast coast of Brazil in the south and Rhode Island in the north (Oxenford *et al*., 2003 citing Robins and Ray, 1986 and Goodyear, 1999). Although there is little knowledge of movement or migration of the species it is generally agreed that the species moves seasonally, venturing into cooler waters within the summer months and migrating within and beyond the EEZs of countries in the western central Atlantic region (Oxenford *et al*., 2003). Genetic studies suggest that a single stock exists in the western central Atlantic (Oxenford *et al*., 2003 citing Collymore, 2000) with the stock boundary possibly extending beyond the region (Oxenford *et al*., 2003 citing Constantine, 2002).

The species is particularly important in the Caribbean, being targeted by both commercial and recreational fisheries. As well the species is targeted by commercial and recreational fisheries in the northern Gulf of Mexico, the Atlantic from Florida straits to North Carolina and Bermuda and off South America (Oxenford *et al*., 2003). Anchored fish aggregating devices (FADs) are used in the fisheries operating off Martinique and Guadeloupe.

Biomass

Biomass was estimated as the ratio of catch and fishing mortality, assuming that the stock is at equilibrium. Since the species is not explicitly recorded in the ICCAT Task I Database the proportion of biomass inside the LAPE was assumed to be the ratio of catches inside the LAPE area and total catch. Biomass inside the LAPE was estimated at 7.43×10^{-4} t·km^{-2}.

Production:Biomass

Murray and Sarvay (1987) and Murray and Joseph (1996) estimated M at approximately 0.54 $year^{-1}$ and F at 1.1 $year^{-1}$. George *et al*. (2000) estimated M at 0.63 $year^{-1}$ and F at 3.98 $year^{-1}$, concluding that stock in the eastern Caribbean is

under heavy overfishing. However, as noted by Die (2004), the latter estimate of F is likely to be overestimated because the authors assumed a separate stock in the Eastern Caribbean and did not account for migration out of the system. As a result, the mortality values reported by Murray and Sarvay (1987) and Murray and Joseph (1996) were used to estimate a P/B of 1.64 $year^{-1}$. The wide variation in estimated mortality parameters (natural mortality between 38 and 44% and fishing mortality between 46 and 83%) from these studies should be noted (Oxenford *et al*., 2003).

Consumption:Biomass

The Q/B was estimated using growth parameters from Murray and Nichols (1990), length-weight parameters from George *et al*. (2000) along with the aspect ratio from FishBase (www.fishbase.org; Froese and Pauly, 2000) in the empirical equation of Palomares and Pauly (1989). The estimated Q/B was 31.81 $year^{-1}$. The wide range in growth parameter estimates (asymptotic length between 141 cm TL and 221 cm FL, curvature parameter (k) between 0.152 and 3.93) cited in Oxenford *et al*. (2003) is noted.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 499 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

16. DOLPHINFISH

Background

This is an aggregate group comprising the common dolphinfish, *Coryphaena hippurus* and the pompano dolphinfish, *Coryphaena equiselis*. The common dolphinfish is found worldwide in tropical and subtropical seas (Palko *et al*., 1982). In the western Atlantic, they are distributed within the 20°C summer isotherm or from Cape Cod to southern Brazil (Collette, 1978). Oxenford and Hunte (1986) showed that differences in the seasonality of catch data, mean size landed, growth, and maturity supported the hypothesis that at least two stocks of dolphinfish occur in the Caribbean Sea: a northeast and southeast stock. The migration circuit of the northeast stock incorporates the northern Caribbean islands, the southeastern US and Bermuda, while the migratory circuit of the southeastern stock includes the southeastern Caribbean islands and the north coast of Brazil. Although this hypothesis has been refuted by recent genetic studies that showed that dolphinfish belong to a single stock in the Western Central Atlantic (Die, 2004), the migratory path proposed by Oxenford and Hunte (1986) is useful to characterize the feeding time of dolphinfish in the LAPE. The status of the stock is highly uncertain. Some studies suggest that it is not overfished (Prager, 2000; Die, 2004) while others (Parker *et al*., 2001) show that the stock is under intense overfishing.

Biomass

Biomass for the group was estimated as the ratio of catch and fishing mortality, assuming that the stock is at equilibrium. However, there are no estimates of catch and fishing mortality of *C. equiselis*. *Coryphaena hippurus* is the main species in the catch. The fishing mortality for the species was taken from Oxenford (1999). Since *Coryphaena* spp. is not explicitly recorded in the ICCAT Task I Database the proportion of biomass inside the LAPE was assumed to be the ratio of catches inside the LAPE area and total catch. Biomass inside the LAPE was estimated at 1.2×10^{-3} t·km^{-2}.

Production:Biomass

Reported longevity of *Coryphaena hippurus* in western central Atlantic varies from 1 year to 4 years (Oxenford, 1999). All studies reported by the author suggest very low survivorship after the first year. Total mortality rates reported in the same study varied from 3.53 to 8.67 year^{-1} (3.9 year^{-1} in Oxenford (1985), 3.53 year^{-1} in Murray (1985), 8.2 – 8.7 year^{-1} in Bentivoglio (1988) and 5.98 year^{-1} in Parker *et al*. (2000)). A mid-range value of 4.72 year^{-1} was used, this being consistent with the P/B of 5 year^{-1} estimated for dolphinfish in the Central Pacific (Kitchell *et al*., 1999). Since no estimates of mortality or catch are available for *C. equiselis* the estimate derived for *C. hippurus* was assumed representative of the group.

Consumption:Biomass

The estimated Q/B of 20 year^{-1}, after Kitchell *et al*. (1999), was used as representative of the group.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 2 200 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

17. SHARKS

Background

This is an aggregate group representing oceanic shark species such as blue shark (*Prionace glauca*), porbeagle (*Lamna nasus*), longfin mako (*Isurus paucus*), shortfin mako (*Isurus oxyrinchus*), threshers (*Alopias vulpinus* and *Alopias superciliosus*), bluntnose sixgill (*Hexanchus griseus*), oceanic whitetip (*Carcharhinus longimanus*), tiger shark (*Galeocerdo cuvier*), blacktip shark (*Carcharhinus limbatus*), silky shark (*Carcharhinus falciformis*), sandbar shark (*Carcharhinus plumbeus*), spinner shark (*Carcharhinus brevipinna*) and the hammerhead sharks (*Sphyrna* spp.). Two coastal species are also represented smalltail shark (*Carcharhinus porosus*) and Caribbean sharpnose shark (*Rhizoprionodon porosus*).

Most species of oceanic sharks may also be found on the shelf and shallow coastal areas during feeding and reproduction. There is growing evidence of multiple stocks in the Atlantic for some species (ICCAT, 2001c). Tagging studies have showed, for instance, that blue sharks on the north Atlantic constitute a single stock, and that there are two distinct stocks of porbeagles in the eastern and western regions of both North and South Atlantic (ICCAT, 2001c). Pelagic sharks are caught in several gears in the Atlantic Ocean, Gulf of Mexico and Caribbean, including longlines, gillnets, handlines, rod and reel, trawls, trolls and harpoons (ICCAT, 2005b). However, they are mostly caught as bycatch in pelagic longline fisheries targeting swordfish and tunas. There are also recreational fisheries in the United States, Canada, EC-United Kingdom and EC-Ireland. Buencuerpo *et al*. (1998) showed that five species of large sharks seem to dominate the bycatch in swordfish longline fisheries in the northeast Atlantic: *Isurus oxyrinchus*, *Prionace glauca*, *Alopias superciliosus*, *Alopias vulpinus* and *Sphyrna zygaena*. Likewise, the blue shark is one the most frequent species in the shark bycatches from Venezuelan tuna and swordfish fisheries and comprised more than 90% of total shark by-catch in the Japanese tuna longline fishery operating between 40 and 60º N (ICCAT, 2001c; ICCAT, 2005b). The rate of discards of some species may be high. NMFS (2002) estimated that 75% of the discarded sharks in U.S. fisheries are blue sharks. It was found that the by-catch rate of sharks in tropical waters is higher than that from temperate waters (ICCAT, 2005b).

Length frequency data as well as the presence of small sharks suggest that the area between 30 and 40 º N may be nursery grounds for blue sharks, and it is hypothesized that females migrate north after birth and at maturity migrate south while males migrate south after birth and even further south at maturity (ICCAT, 2005b). Juvenile makos are also found in the area between 30 and 40 º N.

The population dynamics of the species in the group are poorly known as there have been few attempts at detailed stock assessments in the Atlantic (ICCAT, 2001). In 2004 assessments were conducted on the blue shark and shortfin mako shark, based on the separate North Atlantic, South Atlantic and Mediterranean stock hypothesis (ICCAT, 2005b). The results suggested that current levels of fishing mortality are sustainable for blue sharks (current biomass greater than biomass at MSY) but not for shortfin mako sharks. However, due to limitations in the quality and quantity of information the results were considered preliminary.

Biomass

Biomass was estimated by the model assuming an ecotrophic efficiency of 0.99. The high EE value is justified by the high fishing pressure on the species of the group.

Production:Biomass

Natural mortality rates between 0.1497 and 0.43 year^{-1} were estimated based on (Pauly, 1980). Mohammed (2003) estimated a P/B of 0.255 year^{-1} for pelagic

sharks in the preliminary model of the LAPE and Cox *et al*. (2002) estimated P/B ratios for blue and other large sharks at 0.32 and 0.39 year^{-1}, respectively. Assessment of the North Atlantic stock of blue shark (catchfree model) estimated current fishing mortality at between 0.0187 and 0.0198 year^{-1} (average = 0.0193 year^{-1}) and natural mortality at 0.15 year^{-1} (ICCAT, 2005b). The corresponding P/B is 0.17 year^{-1}. Similarly, assessment of the North Atlantic stock of shortfin mako estimated fishing mortality at between 0.0392 and 0.068 year^{-1} (average = 0.0507 year^{-1}) and natural mortality at between 0.180 and 0.19 year^{-1} (average = 0.1844 year^{-1}). The corresponding P/B is 0.24 year^{-1}. The P/B weighted by the relative catches of the two species, 0.18 year^{-1}, was considered representative of the group.

Consumption:Biomass

Q/B ratios were estimated at about 10 year^{-1} for large pelagic sharks (Stillwell and Kohler, 1992), 3.7 year^{-1} for pelagic sharks in the preliminary model of LAPE (Mohammed, 2003,) and between 2.5 and 3.5 year^{-1} for large sharks of the tropical Pacific (Cox *et al*., 2002). The former estimate was adopted in the present model since it is closer to values reported for other large piscivores sharks in other tropical systems (e.g. 7 year^{-1} for *Negaprion brevirostris* (Cortes, 1997); 10.5 year^{-1} for Large oceanic piscivores (Mackinson *et al*., 2005).

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 970 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

18. FLYINGFISH

Background

Most background information about flyingfish resources of the Lesser Antilles were obtained from Mahon (1992) and Oxenford *et al*. (1993). Three species are common in the southeastern Caribbean, *Hirundichthys affinis*, *Parexocoetus brachypterus* and *Cheilopogon cyanopterus*), but the fourwing flyingfish, *H. affinis*, is considered the most important component of the pelagic fisheries in the southeastern Caribbean (Mahon, 1989). The fourwing flyingfish is believed to contribute to 95% of the catches in the Lesser Antilles. The species was therefore considered representative of the functional group in the model.

There is no information on whether *H. affinis* in the eastern Caribbean comprises one large stock or several local ones. Mahon (1992) noted that the similarity between interannual patterns in catch rates in Barbados and Martinique suggest a single stock but could also result from local stocks responding to environmental factors operating on a regional scale. Tagging studies indicated that there are considerable movements of the species between the countries in the Eastern Caribbean, which suggest that the minimum

appropriate management unit for *H. affinis* should be the combined EEZs of the eastern Caribbean countries (Oxenford *et al*., 1993).

There are two spawning peaks, in February/March and from May to August. There is indication of post-spawning mortality. Fish grow to about 20 cm during the first year and the maximum observed size of about 30 cm suggests that the species does not live past 18 months. Oxenford *et al*. (1993) showed that the species attain sexual maturity with 7-8 months and have a 1 year life span.

Biomass

Biomass (8×10^{-4} t·km^{-2}) was estimated as the ratio of catch (1 671 tonnes) and fishing mortality (3.3 year^{-1} after Samlalsingh and Pandohee, 1992a), assuming that the stock is at equilibrium. However, this estimate seemed too low, given the commercial importance of the species in the catch. Biomass was therefore estimated using survey data reported by Oxenford *et al*. (1995). The total number of fish counted, of the three species, was extrapolated to population number in the surveyed area assuming that 10% of *H. affinis*, 20% of *P. brachypterus* and *C. cyanopterus* took to flight during the passage of the survey vessel. This assumption is reasonable since *H. affinis* exists at greater depths compared to the other two species. The area surveyed was computed as the product of the total distance surveyed and a band width of 20 metres (10 metres surveyed on either side of the vessel, Mahon pers. comm.). The population number was converted to the corresponding weight, assuming that all fish were at maximum length (30.5 cm TL for *H. affinis* from Samlalsingh and Pandohee, 1992a; 20 cm TL for *P. brachypterus* and 40 cm TL for *C. cyanopterus* from FishBase (www.fishbase.org; Froese and Pauly, 2000), and using the length weight parameters from Samlalsingh and Pandohee (1992b) as representative of the group. The estimated biomass of *H. affinis*, *P. brachypterus* and *C. cyanopterus* was 1.12×10^{-3} t·km^{-2}, 2.11×10^{-4} t·km^{-2} and 3.3×10^{-5} t·km^{-2} respectively. The total group biomass was 1.37×10^{-3} t·km^{-2}. This biomass estimate still seems low for the group and therefore a wide confidence interval (± 50 - 80 %) was used in model balancing.

Production:Biomass

Total mortality of *H. affinis* was estimated at 5.8 year^{-1} for the four-winged flyingfish off Tobago (Samlalsingh and Pandohee, 1992a). A negligible fishing mortality (0.01 year^{-1}) was assumed for the other two species, while natural mortality was computed using growth parameters from FishBase (www.fishbase.org; Froese and Pauly, 2000) and the empirical equation of Pauly (1980). The estimated P/B for *P. brachypterus* and *C. cyanopterus* was 4.01 year^{-1} and 1.65 year^{-1} respectively. The weighted P/B, assuming that *H. affinis* contributes 95%, *P. brachypterus* 2.5% and *C. Cyanopterus* 2.5% to the overall catch, was estimated at 5.65 year^{-1}. This is quite likely an over-estimate however, representing a combination of both mortality and migration.

Consumption:Biomass

The Q/B of the four-winged flyingfish was estimated using the mean growth parameters published in Samlalsingh and Pandohee (1992) and Oxenford *et al*. (1993) with length-weight parameters from Oxenford *et al*. (1993) and an aspect ratio from FishBase (www.fishbase.org; Froese and Pauly, 2000) in the empirical equation of Palomares and Pauly (1989). The estimated Q/B was 24.51 year^{-1}. The Q/B for the other two species was estimated using growth parameters, aspect ratios and length-weight parameters from FishBase (www.fishbase.org; Froese and Pauly, 2000) in the empirical equation of Palomares and Pauly (1989). The estimated Q/B for *P. brachyperus* and *C. cyanopterus* was 37.48 year^{-1} and 21.53 year^{-1} respectively. The weighted group Q/B (24.76 year^{-1}) was computed assuming the same contributions to overall catch above.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 1 671 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

19. COASTAL PREDATORS

Background

The group represents small-medium size, epipelagic and reef-associated species which feed on pelagic species in the coastal areas. The group includes several species of needlefish (Belonidae), barracudas (Sphyraenidae), jacks (Carangidae: *Caranx* spp.), pompanos (Carangidae: *Alectis ciliaris* and *Trachinotus* spp.), rainbow runner (Carangidae: *Elegatis bipinnulata*), leatherjacks (Carangidae: *Oligoplites* spp.), amberfish (Carangidae: *Seriola* spp.), common snook (Centropomidae: *Centropomus undecimalis*), yellowtail snapper (Lutjjanidae: *Ocyurus chrysurus*), tripletails (Lobotidae) and Bermuda sea chub (*Kyphosus sectatrix*).

Biomass

The biomass was left for estimation by the model assuming an ecotrophic efficiency of 0.95, after Christensen *et al*. (2000).

Production:Biomass

The P/B ratio (0.72 year^{-1}) was estimated based on the calculated Q/B, and assuming a P/Q ratio of 0.1 (P/Q = P/B divided by Q/B).

Consumption:Biomass

The Q/B was estimated using aspect ratios, growth parameters and length-weight parameters from FishBase (www.fishbase.org; Froese and Pauly, 2000) in the empirical equation after Palomares and Pauly (1989), as indicated in Garcia and Duarte (2002). It was assumed that the stocks are at equilibrium and

therefore catches are representative of biomass. The group average, weighted by catch, was estimated at 7.22 year^{-1}.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 589 tonnes was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

20. SMALL OFFSHORE PELAGICS AND 21. SMALL COASTAL PELAGICS

Background

This small offshore pelagic group was included in the model following analysis of the hydroacoustic and pelagic trawl surveys which indicated high concentrations of juveniles of large pelagic species as well as reef species in offshore waters, beyond the shelf area (Melvin *et al*., 2007). These individuals are assumed to perform the same ecological role as small coastal pelagics. The separation of small offshore pelagics and small coastal pelagics as distinct groups was necessary to facilitate policy exploration associated with the beach seine fisheries which target small pelagics in coastal areas. The small coastal pelagics group represents small coastal pelagic species occurring on the shelf areas of the LAPE, including small jacks, scads, robins, halfbeaks and anchovies. The associated species include *Chloroscombrus chrysurus*, *Decapterus* spp., *Selar crumenophthalmus*, *Dorosoma petenense*, *Harengula* spp., *Sardinella* spp, *Anchoa* spp., *Opisthonema oglinum*, *Pellona harroweri*, *Jenkinsia lamprotaenia*, *Hemicaranx amblyrhynchus*, *Hemiramphus* spp., *Hyporhamphus unifasciatus*, *Peprilus paru* and *Sygnathus pelagicus*.

Biomass

The biomass of these two groups was estimated from results of hydro-acoustic and pelagic trawl surveys conducted under the LAPE Project. Biomass of small offshore pelagics was estimated at 7.394 t·km^{-2} and biomass of small coastal pelagics was estimated at 12.2 t·km^{-2}. The estimate for the small coastal pelagic group is applicable to the shelf area which occupies about 2% of the total LAPE area (Melvin *et al*., 2007).

Production:Biomass

The P/B of both groups (each 2.15 year^{-1}) was estimated using the Q/B ratio estimated below and an assumed P/Q ratio 0.147, based on the mean of similar species in other models (Arreguín-Sanchez *et al*., 1993 a and b; Mendoza, 1993; Vega-Cendejas *et al*., 1993; Opitz, 1996; Manickchand-Heileman *et al*., 1998 a and b).

Consumption:Biomass

The Q/B was estimated using aspect ratios, growth parameters and length-weight parameters from FishBase (www.fishbase.org; Froese and Pauly, 2000) in

the empirical equation after Palomares and Pauly (1989), as indicated in Garcia and Duarte (2002). It was assumed that the stocks are at equilibrium and therefore catches are representative of biomass. The group average, weighted by catch, was estimated at 14.64 $year^{-1}$.

Diet

See Heileman *et al*. (2007). The diet of small offshore pelagics was assumed the same as small coastal pelagics. Predation on the small offshore and small coastal pelagic groups was pro-rated based on the relative biomass of these groups. Additional adjustments included refinement of the diet composition of other offshore predators to include only small offshore pelagics and the diet of coastal predators to include only small coastal pelagics for the initial component of the diet representing small pelagics.

Catch

An average annual catch of 3 537 tonnes of small coastal pelagics was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

22. SMALL MESOPELAGIC FISH

Background

Mesopelagic fish are the species that perform large vertical migrations, spending the day in the mesopelagic zone (200 to 1000 m) and rising to the upper 200 meters of the ocean during the night. The most common species are in the families Myctophidae and Gonostomatidae. Information on the ecology, growth, distribution and biomass of small mesopelagic fish was obtained mainly from Gøjsaeter and Kawaguchi (1980) who reported the main species in the Caribbean Sea and the Lesser Antillean region to include *Ceratoscopelus warmingi*, *Notolychnus valdiviae*, *Diaphus dumerili*, *Lepidophanes guentheri* and *Lampanyctus nobilis*.

Biomass

The biomass of mesopelagic fish in the area is considered to be low (Gøjsaeter and Kawaguchi, 1980). The authors reported an average biomass of 0.12 $t \cdot km^{-2}$ for the Caribbean and Lesser Antilles. They considered, however, that the biomass was underestimated. The biomass of small mesopelagic fish, 19.36 $t \cdot km^{-2}$ was estimated from results of hydroacoustic and pelagic trawl surveys (Melvin *et al*., 2007) conducted under the LAPE Project.

Production:Biomass

The longevity of small mesopelagic species can vary from 1 to 5 years, with P/B ratios varying from 0.56 to 5 $year^{-1}$ (Mann, 1984). A P/B ratio of 3.76 $year^{-1}$ was used in the LAPE model based on the balanced central Atlantic model of Vasconcellos and Watson (2004). The authors however, had used an initial estimate of 0.987 $year^{-1}$ after Childress *et al*. (1980) and Gorelova (1986).

Consumption:Biomass

A Q/B ratio of 18.25 $year^{-1}$ was used in the model based on Vasconcellos and Watson (2004) after Childress *et al*. (1980) and Gorelova (1986).

Diet

See Heileman *et al*. (2007).

23. LARGE MESOPELAGIC FISH

Background

Due to their larger size and differences in life history, the mesopelagic fish *Gempylus serpens* and *Alepisaurus ferox* were grouped into a large mesopelagic fish group. Both species feed actively on mesopelagic fauna and perform marked diel migrations between the surface and 1000 m (Post, 1984).

Biomass

The biomass of large mesopelagic fish, 10.83 $t \cdot km^{-2}$ was estimated from results of hydroacoustic and pelagic trawl surveys (Melvin *et al*., 2007) conducted under the LAPE Project.

Production:Biomass

A P/B ratio of 0.15 $year^{-1}$ was estimated based on a mean habitat temperature of 15°C (to account for vertical migration) using growth parameters from FishBase (www.fishbase.org; Froese and Pauly, 2000) in the empirical equation after Pauly (1980).

Consumption:Biomass

A Q/B ratio of 3.55 $year^{-1}$ was estimated based on a mean habitat temperature of 15°C (to account for vertical migration), and on asymptotic weight and aspect ratios taken from FishBase (www.fishbase.org; Froese and Pauly, 2000), using the empirical equation after Palomares and Pauly (1989).

Diet

See Heileman *et al*. (2007).

24. LEATHERBACK TURTLES AND 25. OTHER TURTLES

Background

Although turtles have little trophic linkage within the pelagic realm it was agreed at the first meeting of the Ecosystem Modelling Working Group that functional groups representing marine turtles would be included in the LAPE model to incorporate international concern about the by-catch of turtles in fishing gear. However, the documentation of marine turtle catches is inadequate in the LAPE area and this issue was not highlighted as a priority in the stakeholder consultations to identify EAF management issues in the region (Grant, 2007)). Lee Lum (2003) estimated that more than 3,000 leatherback turtles were caught in 2000, based on interviews of 126 fishers in Trinidad.

Some turtles are released (between 66 and 91 percent live releases) but some also die from drowning or are slaughtered to avoid damage to fishing nets.

Adult leatherback turtles (*Dermochelys coriacea*) are highly migratory and are more pelagic in their activities compared to all other species of sea turtles. The species is almost entirely pelagic, entering coastal waters infrequently except during the breeding season and nesting mainly in the tropics (Read *et al*., 2007 - OBIS-SEAMAP at http://seamap.env.duke.edu/species/tsn/173843; accessed October 04, 2007). Nesting colonies have been identified in the Caribbean, from Costa Rica to Colombia, from French Guiana to Surinam, along the central Brazilian coast, Guyana, Trinidad, the Dominican Republic, St Croix and along the western coast of Mexico to Panama. Little is known about the pelagic distribution of post-hatchling or juvenile leatherbacks. The species is considered endangered throughout its global distribution range. Declines in the number of nesting females have been reported in the West Indies (Bacon, 1970, Eckert, 1989). Nesting off the coasts of the United States and wider Caribbean occurs mainly between March and July.

Other turtles represented in the LAPE model include the hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*) and green turtle (*Chelonia mydas mydas*). The hawksbill turtle is distributed worldwide, in tropical oceans. The US National Marine Fisheries Service has designated Mona Island in Puerto Rico as critical habitat for the species (Read *et al*., 2007 - OBIS-SEAMAP at http://seamap.env.duke.edu/species/tsn/173836; accessed October 04, 2007). Loggerhead turtles, though distributed throughout global sub-tropical and temperate waters, are mainly found on continental shelves and in estuaries. A large aggregation of nests has been recorded on the Caribbean coast of Mexico and along the Atlantic coast of Florida and along the coast to North Carolina (Read *et al*., 2007 - OBIS-SEAMAP at http://seamap.env.duke.edu/species/tsn/173830; accessed October 04, 2007). The olive ridley is tropical in distribution, although the species is thought to occur rarely in the Caribbean (Read *et al*., 2007 - OBIS-SEAMAP at http://seamap.env.duke.edu/species/tsn/1738440; accessed October 04, 2007). Green turtles are found circumglobally in tropical and subtropical waters, with juveniles occurring in the pelagic convergence zones (Read *et al*., 2007 - OBIS-SEAMAP at http://seamap.env.duke.edu/species/tsn/173833; accessed October 04, 2007). Within the wider Caribbean the species nests on the east coast of Florida, the U.S. Virgin Islands, Puerto Rico and Aves Island.

Biomass

The biomass of leatherback and other turtles was left to be estimated by the model, assuming an ecotrophic efficiency of 0.99 (consistent with their threatened or endangered status under the IUCN Redlist).

Production:Biomass

A P/B of 0.15 year^{-1} was assumed based on the model for the US Virgin Island reef (Opitz, 1993).

Consumption:Biomass

A Q/B of 3.50 year^{-1} was assumed based on the model for the US Virgin Island reef (Opitz, 1993).

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 3.42 tonnes of leatherback turtles and 21.3 tonnes of other turtles was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

26. SMALL SQUIDS AND 27. LARGE SQUIDS

Background

Squids were split in two functional groups: small and large squids. The representation of two groups is supported by differences in feeding habits, since smaller/juvenile squids feed preferentially on zooplankton and macrocrustaceans while larger/adult squids feed mainly on fish (Nixon, 1987). Cannibalism is common for both small and large squids (Nixon, 1987). Also, as suggested by Pauly *et al*. (1998), the split between small and large squids would separate families such as Gonatidae (maximum length < 50 cm), Onychoteithidae and Architeuthidae (maximum length > 50 cm), the latter two important food sources of toothed whales. According to Arnold (1979) almost all oegopsid families (Ommastrephidae, Onychoteuthidae, Gonatidae, Architeuthidae and Enoploteuthidae) occur in oceanic waters and occupy epipelagic, mesopelagic and bathypelagic zones. Some species are adapted to live in the surface waters (e.g. *Onychia* spp. and *Cranchia* spp), while other spend their entire life at depths greater than 500 m (Clarke, 1996).

The pelagic cephalopod assemblage in the epi-mesopelagic zone (0-1000 m) of the Eastern Gulf of Mexico has been shown to be very diverse (47 species were identified), with a biomass estimated between 10.1 and 42.0 kg.km^{-2} (Passarela and Hopkins, 1991). The most abundant species were from the families Enoploteuthidae and Cranchiidae. Most of the species sampled in this area showed a diel vertical migration pattern occurring in the upper 200 m at night and staying 100 and 400 m during the day (Passarela and Hopkins, 1991). The same vertical migratory behaviour is also reported for ommastrephid squids (Dawe and Stephen, 1988).

Biomass

Biomass assessment of oceanic species is normally hampered by their difficult sampling and complicated life cycles and distribution patterns (Clarke, 1987; Piatkowski *et al*., 2001). The few available estimates of oceanic squid abundance were made indirectly, based on the estimated consumption by top predators, such as sperm whales, seals and birds. Clarke (1987) estimated, for instance, that the amount of squids consumed by top predators in the Antarctic Sea at *ca*.

35 million tonnes per year. Using the same rationale on a global scale, the author estimated that biomass of squids required to sustain the world population of sperm whales annually is about 100 million tonnes. Similar studies in the North Atlantic estimated that over 2.4 million tonnes of cephalopods are consumed by sperm whales (Santos *et al*., 2001) and *ca*. 103 000 tonnes are consumed by seabirds in the Eastern North Atlantic (Furness, 1994).

Biomass of small squids (1.51×10^{-2} t·km^{-2}) and large squids (1.771×10^{-1} t·km^{-2}) in the LAPE area was estimated from results of hydroacoustic and pelagic trawl surveys (Melvin *et al*., 2007) conducted under the LAPE Project. However, these figures are considered underestimates due to difficulties in retaining these species in the trawl nets.

Production:Biomass

Most squids have a fast growth and short life cycles, dying after spawning normally when they are between 1 and 3 years old (Arnold, 1979). Species of small (*I. illecebrosus* and *Todarodes* sp.) and large (*Dosidicus gigas)* squids have an estimated life span of 1 year (Mangold, 1987; Arguelles *et al*., 2002). Assuming that 99% of squids in a population die after 1 year, with an exponential decrease in numbers, the natural mortality rate is estimated at 4.6 year^{-1}. This value was therefore accepted as an estimate of the P/B ratio for both small and large squids. In the preliminary model of the LAPE, Mohammed (2003) used a P/B ratio of 2.34 year^{-1} from Optiz (1996). This value was considered a minimum reference point during model balancing.

Consumption:Biomass

The daily feeding rate of pelagic cephalopods was estimated between 3.5 and 10% (O'Dor and Wells, 1987) and the gross food conversion efficiency (P/Q) at 29% (Amaratunga, 1983; O'Dor and Wells, 1987). The high food conversion efficiency of cephalopods is in part explained by the ability most species have of avoiding metabolic waste by not ingesting, for instance, the hard crustacean exoskeleton (Boucher-Rodoni *et al*., 1987) and also by a highly efficient (up to 70%) incorporation of food into the body tissues (Nixon, 1987). The Q/B of small and large squids was estimated at 15.86 year^{-1}, based on the P/Q ratio reported above.

Diet

See Heileman *et al*. (2007).

Catch

An average annual catch of 4 tonnes of large squid was estimated in the LAPE area between 2001 and 2005 (Mohammed *et al*., 2007).

28. SMALL ZOOPLANKTON AND 29. LARGE ZOOPLANKTON

Background

To represent differences in size, two zooplankton functional groups were defined: small and large zooplankton. Small zooplankton includes organisms of the micro-mesoplankton, of sizes up to 3 and 4 cm. Large zooplankton includes organisms of the macroplankton, of sizes larger than 3 to 4 cm, consisting mainly of decapods, large euphasiids, mysids and gelatinous plankton.

Biomass

Biomass of small zooplankton (3.9×10^{-3} t·km^{-2}) and large zooplankton (4.2×10^{-3} t·km^{-2}) in the LAPE area was estimated from results of hydroacoustic and pelagic trawl surveys (Melvin *et al*., 2007) conducted under the LAPE Project. However, these figures are considered underestimates due to difficulties retaining these species in the trawl nets.

Production:Biomass

Longhurst and Pauly (1987) reported turnover rates of mesozooplankton in the tropical Atlantic of between 0.15 and 0.62 day^{-1}. Assuming a turnover rate of 0.15 day^{-1} as representative for small zooplankton, the P/B ratio for the group was estimated at 54.75 year^{-1}. Lower P/B ratios are expected for large zooplankton. In the LAPE model a P/B ratio of 40 year^{-1}, for zooplankton groups in the US Virgin Islands reef model (Opitz, 1996), was provisionally adopted.

Consumption:Biomass

Q/B ratios were estimated based on the P/Q ratio of 0.24 after Optiz (1996). Therefore Q/B was estimated at 228.13 year^{-1} for small zooplankton and at 166.67 year^{-1} for large zooplankton.

Diet

See Heileman *et al*. (2007).

30. PHYTOPLANKTON

Background

Several estimates of primary production are available for the Caribbean region. In the late 1960s Beers *et al.* (1968) estimated primary production between 0.19 and 0.62 gCm^{-2}day^{-1}, with an annual average of 139 gCm^{-2} off Barbados. Stevens (1971) estimated a lower primary production, 105 gCm^{-2}, in the tropical western Atlantic Ocean, near Barbados. Houde (1977) estimated even lower primary production in the central Caribbean Sea and Gulf of Mexico (50 gCm^{-2}year^{-1}), while Longhurst (1995) estimated primary production 190 gCm^{-2}year^{-1} in the Caribbean Province. High estimates of primary production were derived using data from the *Sea Around Us Project* (SAUP) at the Fisheries Centre of the University of British Columbia for the area from St Lucia in the north to Trinidad and Tobago as documented in an earlier version of the LAPE model

(Mohammed, 2003). The associated estimates for the southeastern Caribbean ranged between 174 $gCm^{-2}year^{-1}$ off Saint Lucia and 356 $gCm^{-2}year^{-1}$ off Trinidad and Tobago, and were considerably lower than estimates for the coastal areas of the Guianas, where upwellings contribute to a production of 699 $gCm^{-2}year^{-1}$ (Longhurst, 1995).

Biomass

Within the LAPE area water samples were taken during the LAPE Ecosystem survey to facilitate estimation of primary production and the production/biomass of phytoplankton (Forget, 2007). The results of the study showed lower chlorophyll concentrations in the component of the LAPE north of 16° N compared to the south. The annual cycle suggested stable chlorophyll concentration with some blooming events in the southern region attributed to outflow of the major South American rivers (Forget, 2007). Biomass of phytoplankton was estimated as the product of primary production and the P/B. Primary production was estimated using two approaches, subregional and nearest neighbour. Based on the regional approach, primary production ranged between 239.28 and 378.91 $mgCm^{-2}d^{-1}$ (average 975.59 $t \cdot km^{-2}year^{-1}$ ww, using the conversion factor of 9gww/gC). The nearest neighbour approach produced slightly lower estimates of between 202.87 and 358.68 $mgCm^{-2}d^{-1}$ (average 892.16 $t \cdot km^{-2}year^{-1}$ ww). Two estimates of P/B were derived, the first (43.5 $year^{-1}$) associated with portioning the LAPE into three regions (coastal, north and south of 16° N) and the second (42.1 $year^{-1}$) associated with weighting by area. The corresponding biomass, computed using the primary production from both approaches outlined above and the two estimates of P/B, ranged between 20.5 and 23.13 $t \cdot km^{-2}$. The average biomass, 21.82 $t \cdot km^{-2}$, was used in the LAPE model.

Production:Biomass

An average P/B of 42.8 $year^{-1}$ after Forget (2007) was used.

31. DETRITUS

Biomass

Detritus biomass was estimated using the equation proposed by Pauly *et al*. (1993) with the two estimates of primary production using the subregional (108.39 $gCm^{-2}year^{-1}$) and nearest neighbour (99.13 $gCm^{-2}year^{-1}$) approaches after Forget (2007) and a euphotic depth of 85 m from Rajendra *et al*. (1991). The associated detritus biomass was 15.72 and 14.43 $t \cdot km^{-2}$ respectively. The average biomass, 15.075 $t \cdot km^{-2}$, was used in the LAPE model.

MODEL BALANCING

The process of balancing a trophic model in Ecopath involves the solving of simultaneous linear equations describing production, consumption, fishery removals, other mortality, net migration and biomass accumulation for all

groups in the system to satisfy the two Ecopath master equations after Christensen *et al.* (2000).

Master Equation I:

Production = catches + predation mortality + biomass accumulation + net migration + other mortality

$$P_i = Y_i + B_i * M2_i + E_i + BA_i + P_i * (1 - EE_i) \quad (6)$$

where P_i is the total production rate of (i), Y_i is the total fishery catch rate of (i), $M2_i$ is the total predation rate for group (i), B_i is the biomass of the group, E_i is the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate for (i), while $P_i * (1 - EE_i)$ is the other mortality rate for (i). Equation I is re-expressed, explicitly, to incorporate the Ecopath input parameters as follows:

$$B_i * (P/B)_i = Y_i + \sum B_j * (Q/B)_j * DC_{ji} + E_i + BA_i + (P/B)_i * B_i * (1 - EE_i) \quad (7)$$

Where B_i is prey biomass; $(P/B)_i$ is the production:biomass ratio; EE is ecotrophic efficiency or the proportion of production utilized in the system; Y_i is the total fishery catch rate; B_j is the predator biomass; $(Q/B)_j$ is the consumption:biomass ratio of the predator; DC_{ji} is the proportion of the prey i in the diet of the predator j; $\sum B_j \cdot (Q/B)_j \cdot DC_{ji}$ across all predators (j) represents the total consumption or predation mortality; E_i is the net migration rate of i; BA_i is the biomass accumulation rate for i; $(P/B)_i \cdot B_i \cdot (1 - EE_i)$ is the other mortality rate of i.

Master Equation II:

Consumption = Production + Respiration + Unassimilated food

$$Q = P + R + U \quad (8)$$

Imbalance in the first master equation is reflected as an estimated ecotrophic efficiency greater than one, indicating that more production of a particular group is being utilized in the system than is produced. To achieve mass balance either the biomass, consumption or diet component of the predator must be reduced and/or catches must be reduced or the biomass and/or production/biomass of the prey must be increased (Equation 7). Alternatively the P/B of the predator may be increased to increase its food conversion efficiency. Imbalance in the second master equation is reflected as a negative respiration, usually requiring an increase in consumption or reduction in production of the group of the group if unassimilated food is correctly represented.

An attempt at the automated mass balancing (Kavanagh *et al.*, 2004) failed to converge to a solution even when up to five times the confidence intervals associated with data pedigrees were specified. This suggested that the input parameters required severe changes to achieve mass balance. As a result the model balancing was performed manually.

The manual process of balancing the LAPE model was guided by the estimates of ecotrophic efficiency generated by EWE, the pedigree of input data (Table 1.) and the range of P/B and Q/B estimates from ecosystem models of the central Atlantic (Vasconcellos and Watson, 2004), Florida shelf (Mackinson *et al.*, 2005), central Pacific (Cox *et al.*, 2002), USVI reef (Opitz, 1996). Highest confidence was placed in biomass estimates generated by the cetacean and ecosystem surveys of the LAPE Project, in particular, those for marine mammals, mesopelagics and phytoplankton. As a result, these groups initially served as anchor points. Among the input parameters, there was lowest confidence in the biomass and diet inputs. Many biomass estimates were derived assuming that the respective stocks were at equilibrium and using the equation B = C/F. However, in conventional stock assessment the Baranov equation, with inputs of total mortality, fishing mortality and catch estimates a biomass much greater than that estimated as C/F. Both a bottom-up (given high confidence in PP and P/B associated with phytoplankton) and top-down (given the need to ensure that the estimated primary production is sufficient to meet the consumption demands of top predators) approach was used in balancing the LAPE model.

Table 1 Data Pedigree for the LAPE model (Note: adjusted based on changes during balancing; initial biomass estimates for coastal predators, small mesopelagic fish, small squids, small zooplankton and large zooplankton from LAPE Ecosystem Survey were re-estimated).

	Functional Group	Biomass	P/B	Q/B	DC	Catch
1	Seabirds	± 50 - 80	± 50	± 50	± 80	
2	Baleen whales	± 40	± 50	± 50	± 80	
3	Deep-diving whales	± 40	± 50	± 50	± 80	
4	Killer whales	± 40	± 50	± 50	± 80	± 80
5	Shallow-diving small cetaceans	± 40	± 50	± 50	± 80	± 80
6	Swordfish	± 50 - 80	± 50	± 50	± 50	± 50
7	Other Billfishes	Estimated	± 50	± 80	± 50	± 50
8	Yellowfin tuna	Estimated	± 50	± 80	± 50	± 50
9	Skipjack	± 50 - 80	± 50	± 50	± 50	± 50
10	Albacore	± 50 - 80	± 50	± 50	± 50	± 50
11	Bigeye	± 50 - 80	± 50	± 50	± 50	± 50
12	Blackfin tuna	Estimated	± 50	± 50	± 50	± 50
13	Other offshore predators	± 50 - 80	± 50	± 50	± 50	± 50
14	Mackerels	± 50 - 80	± 50	± 50	± 50	± 50
15	Wahoo	Estimated	± 50	± 50	± 50	± 50
16	Dolphinfish	± 50 - 80	± 50	± 50	± 50	± 50
17	Pelagic sharks	Estimated	± 50	± 50	± 50	± 50
18	Flyingfish	Estimated	± 90	± 50	± 50	± 50
19	Coastal predators	Estimated	± 50	± 50	± 50	± 50
20	Small offshore pelagics	± 40	± 50	± 50	± 50	
21	Small coastal pelagics	± 40	± 50	± 50	± 50	± 50
22	Small Mesopelagic fish	Estimated	± 50	± 50	± 50	
23	Large Mesopelagic fish	± 40	± 50	± 50	± 50	
24	Leatherback turtles	Estimated	± 80	± 80	± 80	± 80
25	Other turtles	Estimated	± 80	± 80	± 80	± 80
26	Small squid	Estimated	± 50	± 50	± 50	

Functional Group		Biomass	P/B	Q/B	DC	Catch
27	Large squid	± 50 - 80	± 50	± 50	± 50	± 50
28	Small Zooplankton	Estimated	± 50	± 50	± 50	
29	Large Zooplankton	Estimated	± 50	± 50	± 50	
30	Phytoplankton	± 40	± 10			
31	Detritus	± 40				

A first attempt in balancing the LAPE model required a reduction in cannibalism of the pelagic shark group to 20% of used production, as the specified diet composition suggested that cannibalism exceeded predation mortality. It is noted however, that the biomass of the top predator pelagic shark group is subjected only to catches and cannibalism i.e. there is almost no predation by other groups, in the LAPE model.

Ecotrophic efficiencies exceeding one were estimated for most groups, except killer whales, shallow-diving cetaceans, yellowfin, albacore, small mesopelagics and large squids.

The high EE of phytoplankton, indicating about three times the production was utilized in the system, prompted a review of input parameters of the major consumer, small zooplankton. The Q/B of small zooplankton was reduced from 228 $year^{-1}$ to 57.7 $year^{-1}$ as suggested by Vasconcellos and Watson (2004) and for consistency a similar change was made for large zooplankton (Q/B reduced from 166.67 $year^{-1}$ to 29 $year^{-1}$). To maintain the required P/Q, the P/B of small and large zooplankton was replaced by estimates of Vasconcellos and Watson (2004). It was also necessary to decrease cannibalism, increase the proportion of detritus and decrease the proportion of phytoplankton in the diet of small zooplankton.

To meet the consumption requirements of predators, it was necessary to increase the biomass of the following prey groups: swordfish, other billfishes, blackfin tuna, other offshore predators, mackerels, dolphinfish, flyingfish, small squids, small zooplankton, large zooplankton and phytoplankton. These biomass increases varied between 0.5 (phytoplankton) and almost 13,000 (small zooplankton) times the original biomass. Biomass of yellowfin, bigeye tuna, and small mesopelagic fish were reduced slightly (maximum change of 0.5 initial biomass input) to relieve predation pressure on associated prey.

Biomass of pelagic sharks, leatherback and other turtles was estimated assuming an EE of 0.99 because of high exploitation of these groups. Final biomass of billfishes, yellowfin tuna, blackfin tuna, wahoo, coastal predators, small mesopelagics and small squids, were estimated assuming an EE of 0.95 as suggested by Christensen *et al*. (2000).

Small squids were removed from the diet of small mesopelagics and the diet import increased. The proportion of small mesopelagics in the diet of large mesopelagics was increased for consistency with results of stable isotope analyses (MacNeil, 2007). The proportion of diet import of small mesopelagics

was increased for the same reason. It is noted here that the specified biomass of small mesopelagics includes juveniles of large mesopelagics, as both groups perform similar ecological roles in the system. The high EE of large mesopelagics was due to high predation by small squids. However, since this predation is on juveniles, this component of the diet was re-allocated to small mesopelagics. Large mesopelagics were included in the diet of large squids and the proportion of small mesopelagics was reduced.

The proportion of the diet of killer whales attributed to shallow-diving cetaceans was reduced considerably (from 30% to 1.4%) in order to reduce the EE of the latter.

The initial diet composition did not include predation on leatherbacks. A small proportion was attributed to diet of pelagic sharks (consistent with input for other turtles). A very small component of the diet of killer whales was attributed to pelagic sharks (0.001), to represent feeding on juvenile sharks.

To more accurately represent the trophic linkage between dolphinfish and flyingfish, the diet composition after Oxenford and Hunte (1999) was used instead of an aggregation of information from studies off Brazil, Malaysia, North Carolina and Gulf of Mexico. The diet of flyingfish was also adjusted from 100% small zooplankton to include small proportions of small coastal and offshore pelagics as well as a diet import (crustaceans not included in model structure). The inclusion of finfish in the diet of flyingfish is consistent with the study by Gillett and Ianelli (1991) for *Hirundichthys affinis*. This adjustment was also necessary to maintain consistency with results of the stable isotope study (MacNeil, 2007).

The first review of the model (Mackinson, pers com) recommended that the biomass and mortality estimates of flyingfish be re-examined. The low EE (0.083) estimated for the group, with 92% of total mortality attributed to other mortality (not explained by the model), was likely due to biomass estimates that are too high or mortality estimates that are too low. Initially, the biomass estimate derived from Oxenford *et al*. (1995) was considered too low (0.0014 $t \cdot km^2$) and was increased manually to meet the consumption demands of predators. Subsequent changes in diet composition of predators however, resulted in considerably lower predation mortality on flyingfish, than expected. The flyingfish biomass was therefore left for estimation by Ecopath, assuming an EE of 0.95.

The high predation rates on dolphinfish (due mainly to cannibalism) and wahoo (due to mackerel predation) in comparison to that for small pelagics was questioned. The high predation of mackerel on wahoo was due to redistribution of unidentified scombrids in the diet of mackerels. The associated proportion of mackerel diet attributed to wahoo was reduced, but this did not completely resolve the problem of high predation due to feeding by both dolphinfish and skipjack on wahoo. The contribution of wahoo to the diet of these two species was reduced. Further, the low EE of mackerels (0.38) seemed inconsistent with

stock assessments conducted in the region (Martin and Nowlis, 2006; Martin and Die, 2007), this is possibly due to overestimation of biomass. As a result the biomass estimate was reduced to achieve an EE > 0.5. The dolphin cannibalism problem was not resolved. Diet studies conducted in Brazil, the Gulf of Mexico and the Caribbean all show high levels of cannibalism for the group (Satoh *et al*., 2004; Junior, 2000; Manooch *et al*., 1983; Oxenford and Hunte, 1998). It is therefore recommended that future versions of the LAPE model split the dolphinfish functional group into juvenile and adult components to address the problem.

The first model review also highlighted the problem of cannibalism, which accounted for the largest source of mortality, in small and large squids as well as small zooplankton. The cannibalism of small zooplankton was comparable in magnitude to consumption by large zooplankton. As well, it was noted that small squid did not feature in the diet of large squid (such a trophic linkage is expected given that predation is associated with relative size of predator and prey) while cannibalism in small squids was extremely high. The cannibalism in the small and large squid groups was reduced (cannibalism reduced to 0.5% of diet composition in each case) and a higher contribution of small squid was attributed to the diet of large squid (small squid accounting for 22% of diet of large squid). As well, based on consideration of relative size of predator and prey, the component of the diet of small squid attributed to other offshore predators and mackerels was reduced to zero and small squid diet composition normalized to one. Cannibalism in the small zooplankton was reduced but resulted in an EE > 1 for phytoplankton. This was due mainly to the high biomass of small zooplankton, increased considerably from the estimated 0.0039 $t \cdot km^{-2}$ based on results of the LAPE Ecosystem Survey to 50 $t \cdot km^{-2}$, to meet the high demands of predation (due mainly to cannibalism). It is noted that there was however, low confidence in the biomass estimate for the group from the LAPE Ecosystem Survey. The biomass of zooplankton was therefore reduced in small increments until phytoplankton EE < 1 was achieved.

Another observation from the first model review was the relatively high consumption of small zooplankton compared to the large zooplankton group (850:16). Following the diet composition changes mentioned above for small zooplankton the consumption of small zooplankton was much reduced, resulting in a lower relative consumption of small zooplankton compared to large zooplankton (460:13). The low EE of large zooplankton (0.217) was questioned however, it is noted that this was comparable to the estimate derived for a similar group in the central Atlantic (Vasconcellos and Watson, 2004). Mackinson (2007) also commented on the high fraction of total mortality due to fishing associated with killer whales. As top predators there was initially no predation on this group and the fishing mortality was based on the catch data submitted by participating countries in the LAPE Project. As a result, no changes were made to the killer whale group.

DATA CONSISTENCY

Biological constraints facilitate the checking of input data consistency. For example, the gross food conversion efficiency (P/Q) normally ranges between 0.05 and 0.3 (Christensen *et al.*, 2000). This constraint was met for most groups with the exception of marine mammals and seabirds. Diet composition attributed to species at higher trophic levels was constrained so that this did not exceed 10% and cannibalism was constrained so that it did not exceed 2% of the diet composition of the respective group.

FINE-TUNING MODEL INPUT PARAMETERS AFTER BALANCING

After balancing the model, and prior to the first review, the P/B and Q/B parameters were fine-tuned to achieve the required P/Q. P/B of 0.54 for pelagic sharks was reduced to 0.4. The P/B of large mesopelagics was changed from 0.15 $year^{-1}$ (Vasconcellos and Watson, 2004) to 0.35 $year^{-1}$ to reduce the associated EE of the group to <1 and to improve the estimate of P/Q.

BALANCED MODEL PARAMETERS

Parameters of the mass balanced LAPE model, after changes resulting from the first model review, are given in Table 2 (B; P/B; Q/B; EE) and Table 3 (diet composition). Adjustments made to functional group biomass (Figure 2) were large in some cases. Reductions in biomass to achieve mass balance ranged between 4% (albacore) and 55% (small mesopelagic fish) while increases in biomass of some groups ranged between 0.001% (large mesopelagic fish) and over 200 000% (large zooplankton). Greatest increases in biomass are noted for other offshore predators, mackerels, flyingfish, small squids, small zooplankton and large zooplankton. Biomass estimates for small offshore pelagics, small coastal pelagics, large mesopelagic fish and large squid, derived from the LAPE Ecosystem Survey, were retained during model balancing. However, similar estimates for coastal predators, small mesopelagic fish, small squids, small zooplankton and large zooplankton were changed, the biomass for non-zooplankton groups estimated assuming an EE of 0.95. In all cases, except for small mesopelagics, the new biomass estimate was higher than that estimated by the Ecosystem Survey. Changes in the P/B and Q/B were within 150% of original input estimates (Figure 3). Increases in P/B > 50% are noted for bigeye tuna, pelagic sharks, small offshore pelagics, small coastal pelagics and large mesopelagic fish, while declines in P/B > 50% are noted for small and large zooplankton. The greatest decreases in Q/B are noted for small and large zooplankton.

Changes in the original diet input to achieve mass balance are presented in Table 4. Minute quantities of small offshore pelagics and small coastal pelagics were included in the diet of flyingfish to increase the group trophic level, based on results of the LAPE stable isotope studies (MacNeil, 2007). A small proportion of the diet of killer whales was attributed to pelagic sharks to represent consumption of juvenile shark by killer whales. Other additions to the diet composition included a small amount of leatherback turtles to the diet of

pelagic sharks and small coastal pelagics to the diet of large mesopelagic fish. The greatest change was an increase of 156 times the initial input of import in the diet of small mesopelagic fish and an increase of 101 times the initial input of small mesopelagics in the diet of large mesopelagics. Large mesopelagic fish was eliminated from the diet of mackerels, as was the proportion of small squid in the diet of small mesopelagic fish, and the proportion of other offshore predators, mackerels and large mesopelagic fish in the diet of small squids.

The estimated ecotrophic efficiency of marine mammals (except shallow-diving cetaceans) is low, reflecting little utilization in the system, particularly of baleen and deep-diving whales. The high EE of swordfish (0.911) is consistent with estimates of stock status by ICCAT, while the EE of small offshore pelagics seems low if the group is an important food source for large pelagic species.

Table 2 Input and mass-balanced parameter values for functional groups in the LAPE Ecopath model. Caption notation as given in text. Estimated EE bold and italicized.

Functional Group		Trophic level	Habitat Area	Biomass in habitat area ($t.km^2$)	Biomass ($t \cdot km^{-2}$)		P/B ($year^{-1}$)		Q/B ($year^{-1}$)		EE	P/Q	UF
					Input	Balanced	Input	Balanced	Input	Balanced			
1	Seabirds	4.49	1.00	0.0002	0.0002	0.0002	0.1333	0.1300	73.6944	73.6900	***0.4470***	0.0020	0.2
2	Baleen whales	4.30	1.00	0.0251	0.0251	0.0251	0.0400	0.0400	12.1900	12.1900	***0.0000***	0.0030	0.2
3	Deep-diving whales	5.13	1.00	0.0145	0.0145	0.0145	0.0400	0.0400	5.4372	5.4400	***0.0000***	0.0070	0.2
4	Killer whales	4.75	1.00	0.0016	0.0016	0.0016	0.0200	0.0200	9.6400	9.6400	***0.3220***	0.0020	0.2
5	Shallow-diving small cetaceans	4.76	1.00	0.0336	0.0336	0.0336	0.0500	0.0500	13.4981	13.5000	***0.7960***	0.0040	0.2
6	Swordfish	4.71	1.00	0.0070	0.0009	0.0070	0.3720	0.3700	5.3069	5.3100	***0.9110***	0.0700	0.2
7	Other Billfishes	4.37	1.00	0.0099	0.0055	0.0099	0.4180	0.4600	4.5962	4.6000	0.9500	0.1000	0.2
8	Yellowfin tuna	4.86	1.00	0.0059	0.0124	0.0059	1.3588	2.0000	15.5300	15.5300	0.9500	0.1290	0.2
9	Skipjack	4.85	1.00	0.0119	0.0119	0.0119	1.8000	1.9600	19.6100	19.6100	***0.6950***	0.1000	0.2
10	Albacore	4.58	1.00	0.0097	0.0097	0.0097	0.6000	0.7800	7.8000	7.8000	***0.8880***	0.1000	0.2
11	Bigeye	4.50	1.00	0.0017	0.0017	0.0017	0.7400	1.7590	17.5900	17.5900	***0.7690***	0.1000	0.2
12	Blackfin tuna	4.20	1.00	0.0052	0.0021	0.0052	1.8519	1.8500	9.8865	9.8900	0.9500	0.1870	0.2
13	Other offshore predators	4.57	1.00	0.2900	0.0024	0.2900	1.8732	1.8700	7.4368	7.4400	***0.1850***	0.2510	0.2
14	Mackerels	4.27	1.00	0.0650	0.0078	0.0650	1.0918	1.0900	10.3077	10.3100	***0.6420***	0.1060	0.2
15	Wahoo	4.81	1.00	0.0010	0.0007	0.0010	1.6400	2.5000	31.8127	31.8100	0.9500	0.0790	0.2
16	Dolphinfish	4.44	1.00	0.0278	0.0012	0.0278	4.7200	4.7200	20.0000	20.0000	***0.9590***	0.2360	0.2
17	Pelagic sharks	4.76	1.00	0.0116		0.0116	0.1770	0.4000	10.0000	10.0000	0.9900	0.0400	0.2
18	Flyingfish	3.03	1.00	0.2080	0.0014	0.2080	5.6515	4.0000	24.7581	24.7600	0.9500	0.1620	0.2
19	Coastal predators	3.60	1.00	1.2570		1.2570	0.7223	0.7200	7.2234	7.2200	0.9500	0.1000	0.2
20	Small offshore pelagics	2.96	1.00	7.3940	7.3938	7.3938	2.1524	3.6000	14.6424	14.6400	***0.3320***	0.2460	0.2
21	Small coastal pelagics	2.96	0.02	12.2000	0.2440	0.2440	2.1524	3.5000	14.6424	14.6400	***0.9570***	0.2390	0.2
22	Small Mesopelagic fish	3.05	1.00	8.7240	19.3590	8.7240	3.7570	3.7600	18.2500	15.0000	0.9500	0.2510	0.2
23	Large Mesopelagic fish	4.02	1.00	10.8330	10.8328	10.8328	0.1500	0.3550	3.5500	3.5500	***0.1770***	0.1000	0.2
24	Leatherback turtles	3.99	1.00	0.0006		0.0006	0.1500	0.1500	3.5000	3.5000	0.9900	0.0430	0.2
25	Other turtles	3.50	0.02	0.0383		0.0008	0.1500	0.1500	3.5000	3.5000	0.9900	0.0430	0.2
26	Small squid	3.86	1.00	1.1570	0.0151	1.1570	4.6000	5.5000	15.8621	18.3300	0.9500	0.3000	0.2
27	Large squid	4.40	1.00	0.1770	0.1771	0.1771	4.6000	4.6000	15.8621	15.8600	***0.3590***	0.2900	0.2
28	Small Zooplankton	2.00	1.00	40.0000	0.0039	40.0000	54.7500	17.3000	228.1250	57.7000	***0.6660***	0.3000	0.4
29	Large Zooplankton	3.01	1.00	9.6360	0.0042	9.6360	40.0000	8.7000	166.6667	29.0000	***0.1520***	0.3000	0.4
30	Phytoplankton	1.00	1.00	32.0000	21.8254	32.0000	42.8000	42.8000			***0.8420***	-	
31	Detritus	1.00	1.00	15.0750	15.0750	15.0750					***0.7190***	-	

Table 3 Diet composition of predators in the mass-balanced LAPE Ecopath model

Group	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Seabirds															
2	Baleen whales															
3	Deep-diving whales															
4	Killer whales															
5	Shallow-diving				0.0140	0.0001										
6	Swordfish															
7	Billfishes									0.0020			0.0070			
8	Yellowfin						0.0020	0.0030		0.0100		0.0100				
9	Skipjack						0.0020	0.0440	0.0840	0.0050		0.0100				
10	Albacore						0.0020	0.0030	0.0100	0.0100		0.0100				
11	Bigeye						0.0020	0.0070	0.0009	0.0050						
12	Blackfin tuna						0.0020	0.0030	0.0100	0.0100		0.0100			0.0020	
13	Other offshore		0.0770				0.0020	0.0900	0.1540	0.1280		0.0100			0.0100	0.2030
14	Mackerels		0.0770				0.0270	0.0030	0.0100	0.0100		0.0100			0.0010	0.0004
15	Wahoo						0.0020	0.0030	0.0010	0.0010		0.0100			0.0002	0.0030
16	Dolphinfish						0.0020	0.0120	0.0050	0.0010		0.0220				
17	Pelagic sharks				0.0010											
18	Flyingfish	0.0750					0.0030	0.0180	0.0130	0.0360		0.2010	0.0730		0.0480	0.0350
19	Coastal predators	0.0120					0.1100	0.0230	0.0790	0.0590	0.0008	0.0020	0.2830	0.0001	0.3490	0.0210
20	Small offshore pelagics	0.2080	0.0960	0.0010	0.0660	0.1510		0.6440	0.1440	0.0040	0.2130	0.2090	0.1290	0.0670	0.0690	0.1920
21	Small coastal pelagics	0.0580	0.0270	0.0003	0.0180	0.0420	0.1230	0.0210	0.0050	0.0001	0.0070	0.0070	0.0040		0.0200	0.0060
22	Small mesopelagics		0.1550	0.0080	0.2250	0.1090	0.0360	0.0001	0.0130	0.1130	0.0690	0.0870				0.0009
23	Large mesopelagics			0.0120	0.2250	0.1090	0.1240	0.0530	0.1210	0.2160	0.3760	0.3160	0.0390			0.1870
24	Leatherback turtle															
25	Other turtles															
26	Small squids	0.4900		0.0080	0.2630	0.3220	0.3940	0.0490	0.1540	0.1150	0.0710	0.0180	0.1220	0.7400	0.1450	0.1580
27	Large squids			0.0500	0.1880	0.2630	0.0230	0.0002	0.0030		0.0080					0.0030
28	Small zooplankton	0.0050							0.0020	0.0010			0.1620	0.1100	0.1350	0.0030
29	Large zooplankton	0.0050	0.3100				0.0180	0.0003	0.0630	0.0250	0.0240	0.0290			0.0380	
30	Phytoplankton															
31	Detritus															
	Import	0.147	0.258	0.921		0.003	0.126	0.024	0.128	0.247	0.23	0.04	0.18	0.083	0.183	0.189
	Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 3. Diet composition of predators in the mass-balanced LAPE Ecopath model (continued).

Group	Prey \ Predator	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	Seabirds		0.0001												
2	Baleen whales														
3	Deep-diving whales														
4	Killer whales														
5	Shallow-diving cetaceans		0.0090												
6	Swordfish		0.0190												
7	Billfishes	0.0020	0.0100												
8	Yellowfin		0.0009												
9	Skipjack	0.0005	0.0004												
10	Albacore		0.0004												
11	Bigeye		0.0004												
12	Blackfin tuna	0.0030	0.0004												
13	Other offshore predators	0.0080	0.0010		0.0002				0.0002						
14	Mackerels	0.0060	0.0200		0.0004										
15	Wahoo	0.0010	0.0004												
16	Dolphinfish	0.2160	0.0003												
17	Pelagic sharks		0.0150												
18	Flyingfish	0.4310	0.0001		0.0120				0.0060				0.0550		
19	Coastal predators	0.1510	0.2350		0.0060				0.0060			0.0010	0.0550		
20	Small offshore pelagics	0.0080	0.0250	0.0210				0.0410	0.0560						0.0030
21	Small coastal pelagics	0.0003	0.0008	0.0003	0.0790			0.0001	0.0001						0.0001
22	Small mesopelagics	0.0007	0.0050		0.0020			0.0050	0.5760			0.3570	0.2220		
23	Large mesopelagics	0.0020	0.0740						0.0050				0.1100		
24	Leatherback turtle		0.0007												
25	Other turtles		0.0007												
26	Small squids	0.0520	0.1780		0.0200				0.0820			0.0050	0.2220		
27	Large squids								0.0040				0.0040		
28	Small zooplankton	0.0190		0.7550	0.0780	0.5570	0.5580	0.7690	0.0980	0.0200	0.0500	0.1620		0.0030	0.9970
29	Large zooplankton	0.0360	0.0007		0.0030	0.0010	0.0010		0.0620	0.9800	0.0500	0.4460	0.2220		
30	Phytoplankton					0.0250	0.0240							0.4980	
31	Detritus		0.0040		0.0020	0.0020	0.0020							0.4980	
	Import	0.063	0.398	0.224	0.797	0.415	0.415	0.185	0.104		0.9	0.028	0.11		
	Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

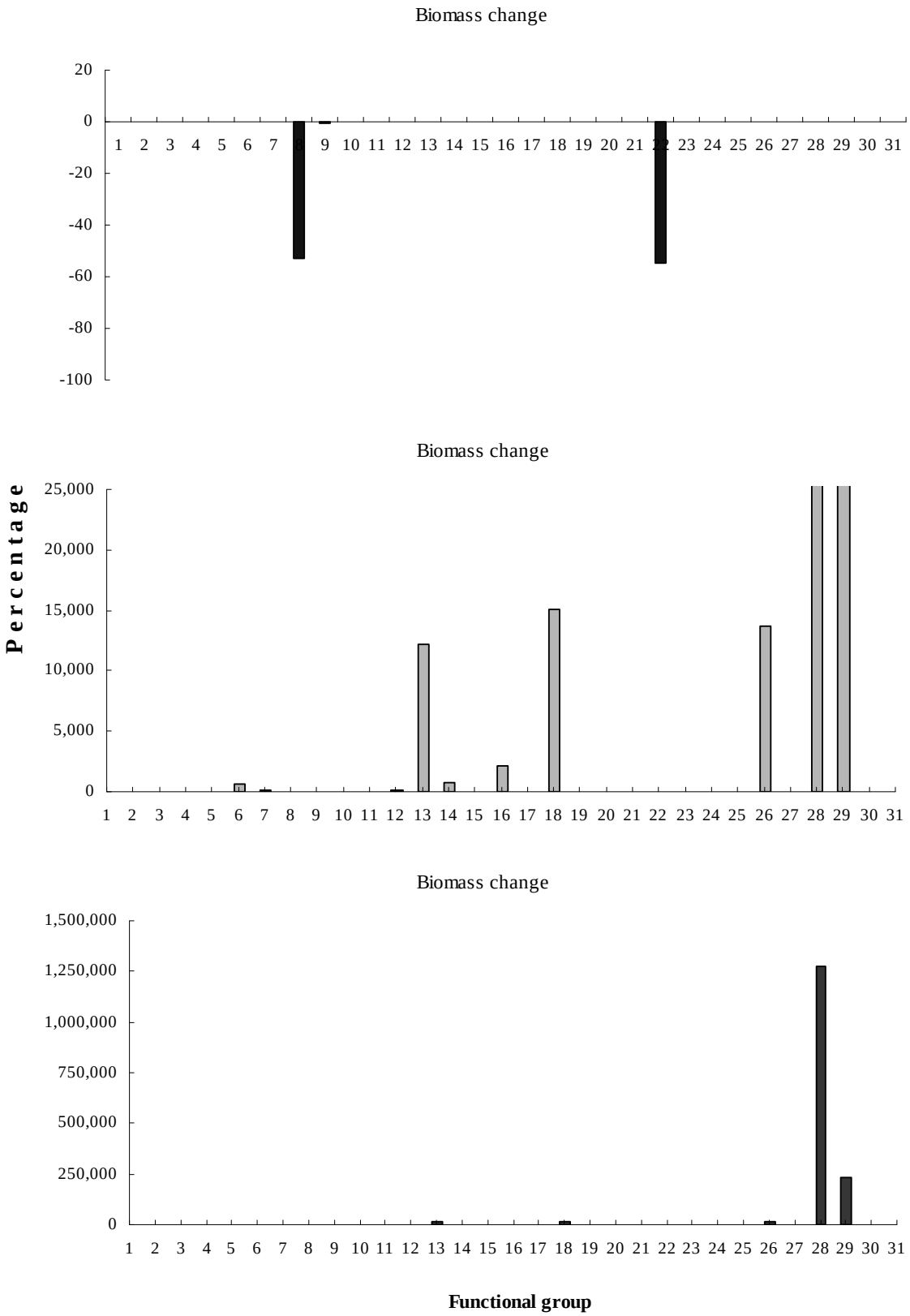

Figure 2 Percentage change in biomass of functional groups (numbers correspond to Table 2) to achieve a mass-balanced LAPE model. Percent reductions (upper panel), percent increases (middle panel) and absolute biomass change (lower panel)

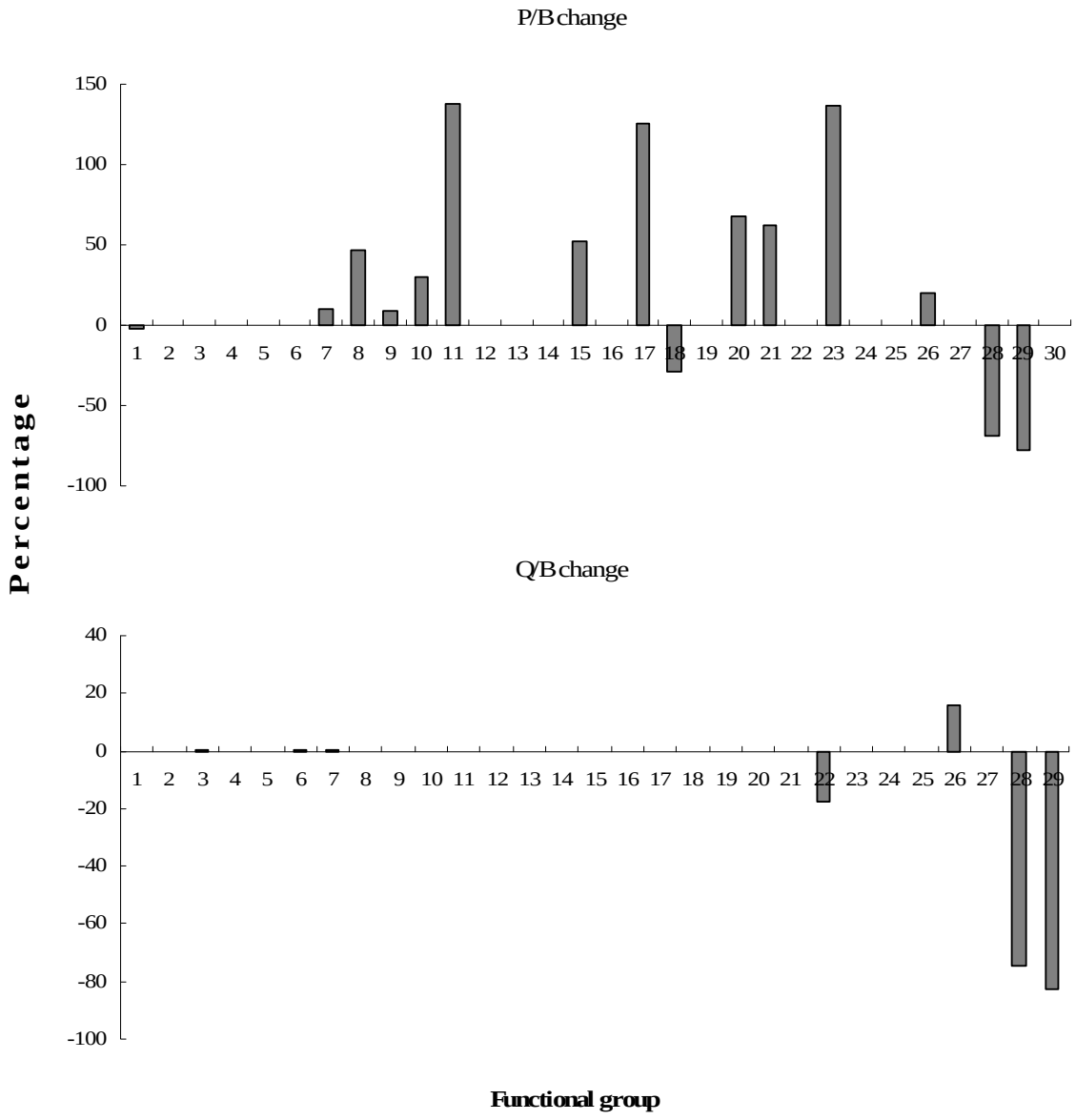

Figure 3 Percentage change in P/B (upper panel) and Q/B (lower panel) of functional groups to achieve a mass-balanced LAPE model. Functional group numbers correspond to Table 2.

Table 4. Changes in input diet composition, relative to input values, to achieve mass balance (change = [new input – initial input]/initial input). 'NEW' in cell indicates diet component added in balancing, grey cells indicate large changes (> 50 times) and black cells indicate diet component removed during balancing.

Group	Functional Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Seabirds															
2	Baleen whales															
3	Deep-diving whales															
4	Killer whales															
5	Shallow-diving small cetaceans				-0.95	0.10										
6	Swordfish															
7	Other Billfishes									0.16			0.80			
8	Yellowfin tuna						0.27	-0.57		0.25		-0.16				
9	Skipjack						0.27	-0.61	-0.10	-0.46		-0.16				
10	Albacore						0.27	-0.57	-0.10	0.25		-0.16				
11	Bigeye						0.27	-0.62	-0.92	-0.45						
12	Blackfin tuna						0.27	-0.57	-0.10	0.25		-0.16			2.31	
13	Other offshore predators		0.03				0.21	-0.61	-0.08	0.27		-0.16			8.88	-0.29
14	Mackerels		0.03				0.00	-0.57	-0.10	0.25		-0.16			-0.49	0.07
15	Wahoo						0.27	-0.57	-0.91	-0.88		-0.16			-0.67	6.80
16	Dolphinfish						0.33	-0.63	-0.24	0.25		-0.18				
17	Pelagic sharks				NEW											
18	Flyingfish	-0.09					-0.05	-0.62	-0.09	0.28		-0.20	0.76		8.09	0.06
19	Coastal predators	-0.10					0.00	-0.62	-0.08	0.27	-0.32	-0.28	0.78	0.16	8.71	0.08
20	Small offshore pelagics	0.16	-0.34	-0.48	-0.32	-0.33		3.87	2.05	-0.98	27.40	7.44	-0.74	0.25	-0.92	0.25
21	Small coastal pelagics	8.77	4.63	4.38	4.63	4.66	0.00	3.81	2.21	-0.98		7.56	-0.76		-0.31	0.18
22	Small Mesopelagic (forage) fish		0.03	0.00	0.50	0.05	0.01	-0.65	-0.06	0.26	-0.22	-0.20				-0.24
23	Large Mesopelagic (forage) fish			0.00	0.50	0.05	0.00	-0.61	-0.09	0.27	-0.21	-0.20	0.75			0.08
24	Leatherback turtles															
25	Other turtles															
26	Small squid	-0.10		0.00	0.50	0.05	0.00	-0.61	-0.08	0.27	-0.21	-0.20	0.79	-0.01	8.48	0.08
27	Large squid			0.00	0.50	0.05	0.00	-0.63	0.08		-0.22					0.08
28	Small Zooplankton	-0.13							-0.03	0.29			0.78	-0.01	8.44	0.10
29	Large Zooplankton	-0.19	0.03				0.03	-0.61	-0.07	0.27	-0.21	-0.19			7.97	
30	Phytoplankton															
31	Detritus															
	Imports	-0.10	0.03	0.00		0.11	0.00	-0.61	-0.09	0.27	-0.22	-0.20	0.79	-0.01	8.80	0.08

Table 4. Changes in input diet composition (continued).

Group	Functional Group	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	Seabirds		-0.98												
2	Baleen whales														
3	Deep-diving whales														
4	Killer whales														
5	Shallow-diving small cetaceans		-0.04												
6	Swordfish		0.14												
7	Other Billfishes	-0.83	-0.33												
8	Yellowfin tuna		0.06												
9	Skipjack	-0.29	0.01												
10	Albacore		0.05												
11	Bigeye		-0.02												
12	Blackfin tuna	-0.71	0.05												
13	Other offshore predators	-0.30	-0.07		0.70				0.09			-1.00			
14	Mackerels	-0.42	0.13		0.70							-1.00			
15	Wahoo	-0.91	0.05												
16	Dolphinfish	0.02	0.26												
17	Pelagic sharks		-0.66												
18	Flyingfish	1.16	0.53		0.82				-0.97				-0.34		
19	Coastal predators	-0.33	0.09		-0.91				-0.52			-0.88	-0.34		
20	Small offshore pelagics	-0.89	-0.47	NEW					9.03						
21	Small coastal pelagics	-0.89	-0.47	NEW	-0.80				NEW						
22	Small Mesopelagic (forage) fish	-0.53	0.12		1.10			-0.48	**101.06**			0.25	0.33		
23	Large Mesopelagic (forage) fish	-0.29	0.12						-0.99			-1.00			
24	Leatherback turtles		NEW												
25	Other turtles		0.16												
26	Small squid	-0.33	0.09		0.83			-1.00	-0.16			-0.96	0.33		
27	Large squid								-0.20				-0.98		
28	Small Zooplankton	-0.35		-0.25	0.81	0.00	0.00	-0.22	-0.09	0.00	0.00	0.15		-0.97	0.00
29	Large Zooplankton	0.25	0.17		0.50	-0.13	-0.13		-0.11	0.00	0.00	0.15	0.33		
30	Phytoplankton					0.05	0.00							-0.38	
31	Detritus		-0.10		0.55	0.27	0.27							3.98	
	Imports	-0.33	0.05		0.67	0.00	0.00	**156.42**	-0.37		0.00	0.17	-0.34		

Trophic Levels

Trophic levels (TL) of the balanced LAPE model ranged between 1.00 for phytoplankton and detritus to 5.13 for deep-diving whales. The relative TL derived for shallow-diving small cetaceans and killer whales suggest that some adjustments to the diet of these groups is necessary as it is expected that the highly predaceous killer whales would occupy a similar or somewhat higher TL than the shallow-diving small cetacean group. The high TL of large mesopelagics is due to the variety of fish as well as large squid in the diet. Large squids consume finfish (including mesopelagics) as well as squid and large zooplankton, all of relatively high TL. The high TL of large zooplankton is due to the inclusion of a small proportion of finfish in the diet. The unusually high TL of leatherback turtles is due to the consumption of large zooplankton (jellyfish). The balanced trophic model suggests that on average the fisheries operate as a predator of trophic level 4.15. Trophic levels associated with catches of the respective fleets are: beach seine 3.39; decked, inboard (troll, longline, gillnets) 3.35; longliners 4.43; open, outboard (troll, longine, gillnets) 4.22; marine mammal (SVG) 4.17; marine mammal (STL) 4.40; open, outboard (other) 3.55; recreational 4.57 and outside LAPE 4.62.

Further refinement of model diet composition inputs based on results of stable isotope studies (MacNeil, 2007) would improve the relative trophic level representation of groups in the system.

Utilization and flows of energy

Total system throughput is 5 966 $t \cdot km^{-2} year^{-1}$, comprising 48.8% flows to consumption, 26.8% flows to detritus, 16.8% flows to respiration and 7.5% to exports. Total primary production, 1,370 $t \cdot km^{-2} year^{-1}$ is due to phytoplankton only.

The flows in biomass associated with flyingfish, small coastal pelagics, dolpinfish, shallow-diving small cetaceans and killer whales are shown in Figure 4 to Figure 13. These figures also demonstrate the trophic level of associated predators, prey and the trophic level equivalent of the take of the associated fleets. The major prey linkage of flyingfish is with small zooplankton, while major predatory linkages are with dolphinfish, large mesopelagics, large squids and coastal predators (thick red lines). Flyingfish are taken mainly by decked inboard boats using troll, longlines or gillnets (thick green line) with the Barbados iceboat fleet being the only contributor. However, the fleet linkages do not accurately predict the flow to fisheries since catches from Tobago, where flyingfish is a major contributor to annual catch, are not incorporated in the model. Small coastal pelagics show the strongest prey linkage with small zooplankton (thick blue line) and the strongest predatory linkage (thick red line) with coastal predators, while the beach seine fleet takes the major portion of the catch (thick green line). Dolphinfish prey comprise

mainly flyingfish and coastal predators, while the majority of the catch is taken by the inside LAPE, open-outboard (troll, longline, gillnets) fleet and the outside LAPE fleet. The decked, inboard (troll, longline and gillnet) fleet in the LAPE also takes appreciable quantities of dolphinfish, though to a lesser extent in comparison to the open outboard (inside LAPE) and outside LAPE fleets. The largest predatory linkages of shallow-diving small cetaceans are with killer whales and pelagic sharks, while the largest prey linkages are with squids (small and large), small offshore pelagics as well as small mesopelagics, though to a lesser extent. The greatest take of shallow-diving small cetaceans is by the marine mammal fleet of St Lucia. Killer whales exhibit the greatest linkage with mesopealgics and squids, their main prey. Although there may be very small predation by sharks on killer whales (not represented in the graph because of the very small magnitude), no other groups feed on killer whales. The St Vincent marine mammal fleet captures the greatest quantity of killer whales compared to other regional fleets.

The transfer efficiencies between successive discrete trophic levels is estimated as the ratio between the sum of the exports and the flow transferred from one trophic level to the next, and the throughput on the trophic level Table 5). The efficiency of detritus is not defined as this is a non-living group. The mean transfer efficiency from TL II to IV for the LAPE is 13.6% (geometric mean). The transfer efficiency is typically estimated at 10% (Christensen and Pauly, 1993a).

Table 5 Transfer efficiency in the LAPE.

Source \ Trophic Level	**I**	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**	**IX**	**X**	**XI**	**XII**
Producer		19.90	10.40	12.20	5.70	6.10	10.30	18.90				
Detritus		20.00	10.40	12.20	5.70	6.10	10.30	18.90				
All flows		19.90	10.40	12.20	5.70	6.10	10.30	18.90	21.80	22.50	22.60	
Proportion of total flow originating from detritus:										0.52		
Transfer efficiencies (calc. as geometric mean for TL II-IV)												
From primary producers:										13.6%		
From detritus:										13.6%		
Total:										13.6%		

The throughput that is recycled in the LAPE amounts to 8.11 t·km^{-2}·year^{-1} (excluding detritus) or 1 711 t·km^{-2}·year^{-1} (including detritus). This suggests high recycling of detritus. Finn's cycling index, which represents the fraction of an ecosystem's throughput that is recycled (Christensen *et al*., 2000), is 28.67% for the LAPE. This index is considered an indicator of system maturity, resilience and stability. The 'predatory cycling index' which excludes cycles involving detritus is 0.29%. The path length is the average number of groups that an inflow or outflow passes through. It is estimated as the total system throughput divided by the the sum of all exports and respiration. The mean path length in the LAPE is estimated at 4.1, while the straight-through path length is estimated at 2.74 (without detritus) or 2.93 (with detritus).

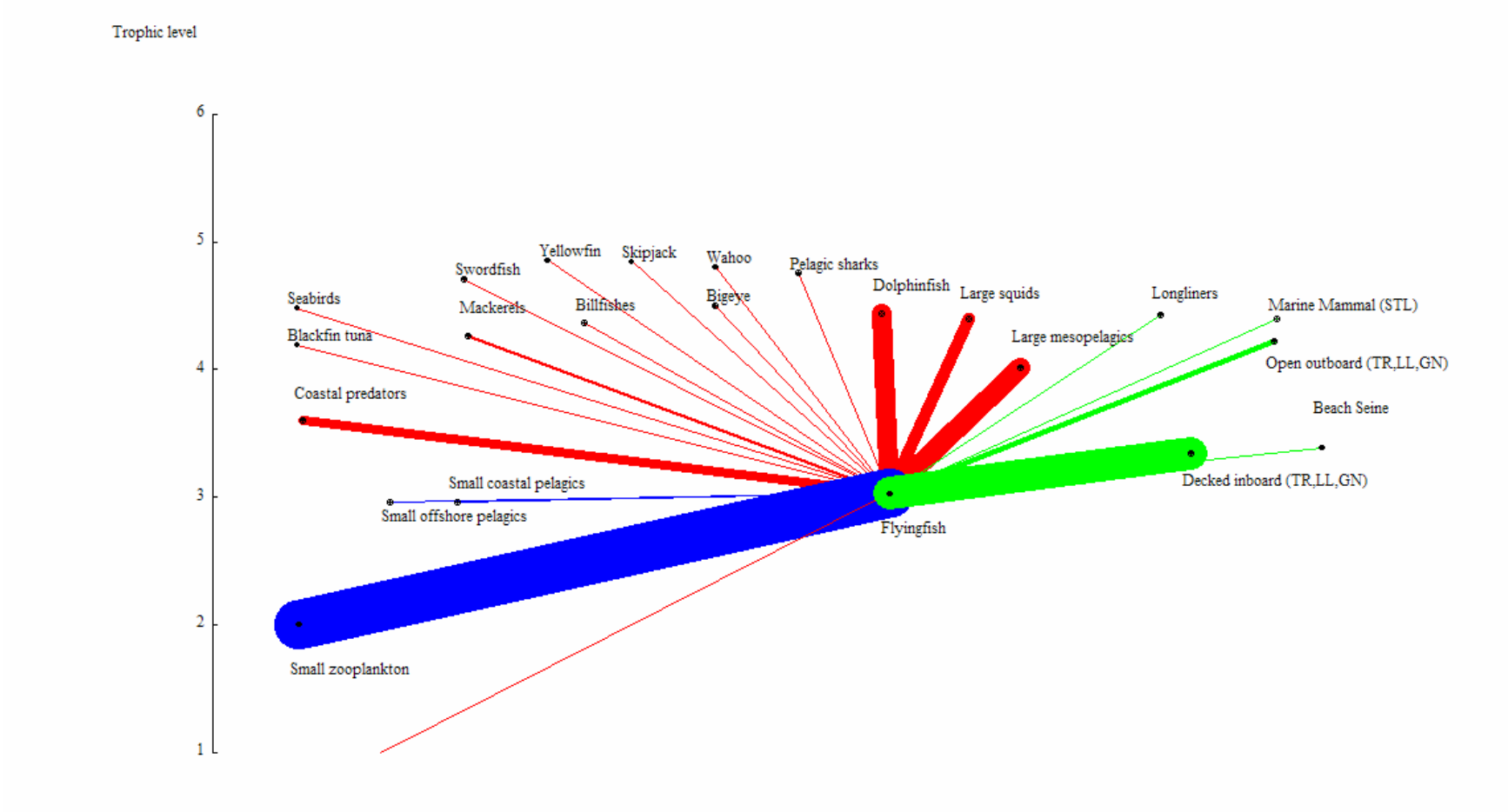

Figure 4 Biomass flows to and from flyingfish. The thickness of the lines denotes the magnitude of flow. Red lines are linkages to predators, blue lines are linkages to prey and green lines are linkages to fisheries. NOTE: the length of the lines is of no ecological significance, merely for graphical clarity.

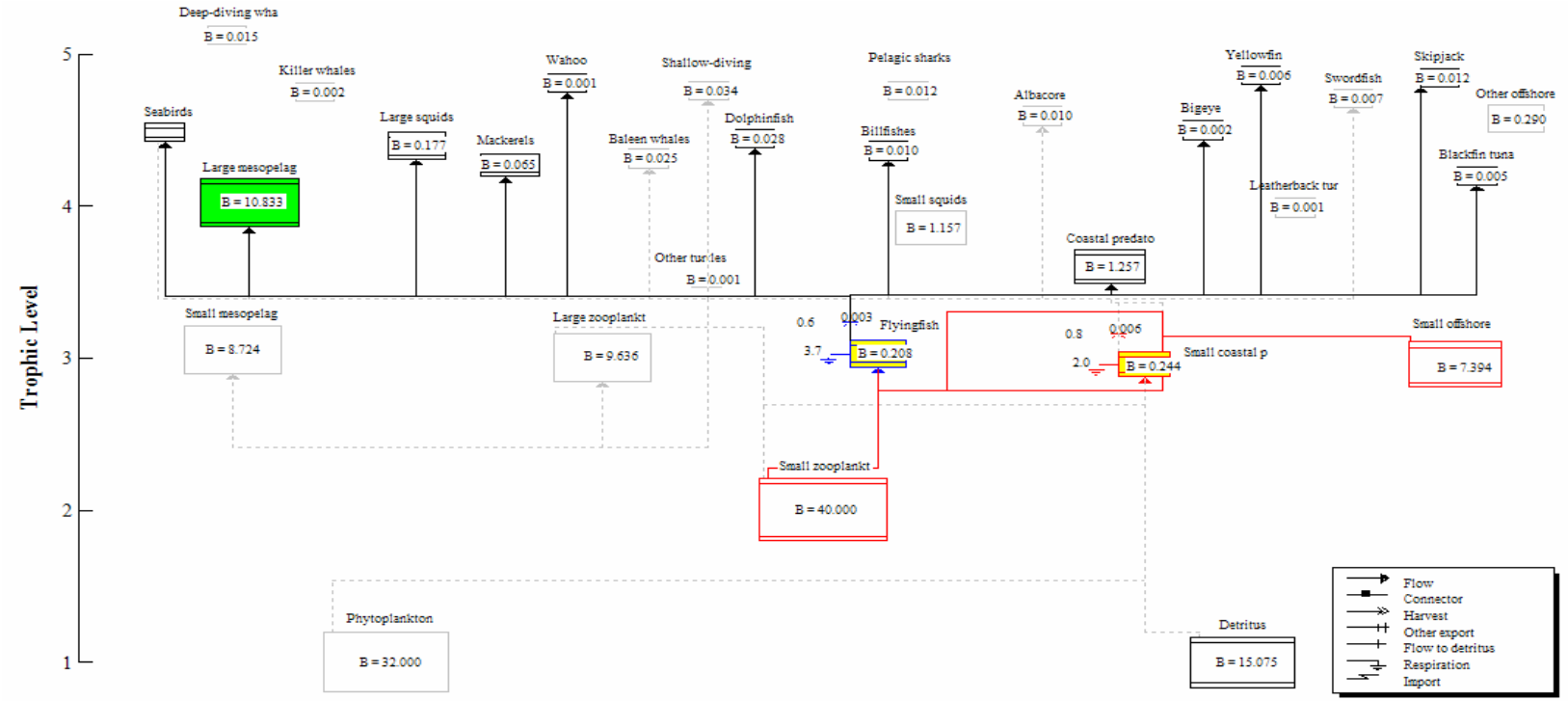

Figure 5 Trophic linkages of flyingfish, black lines indicate predation on the group, red lines consumption by the group.

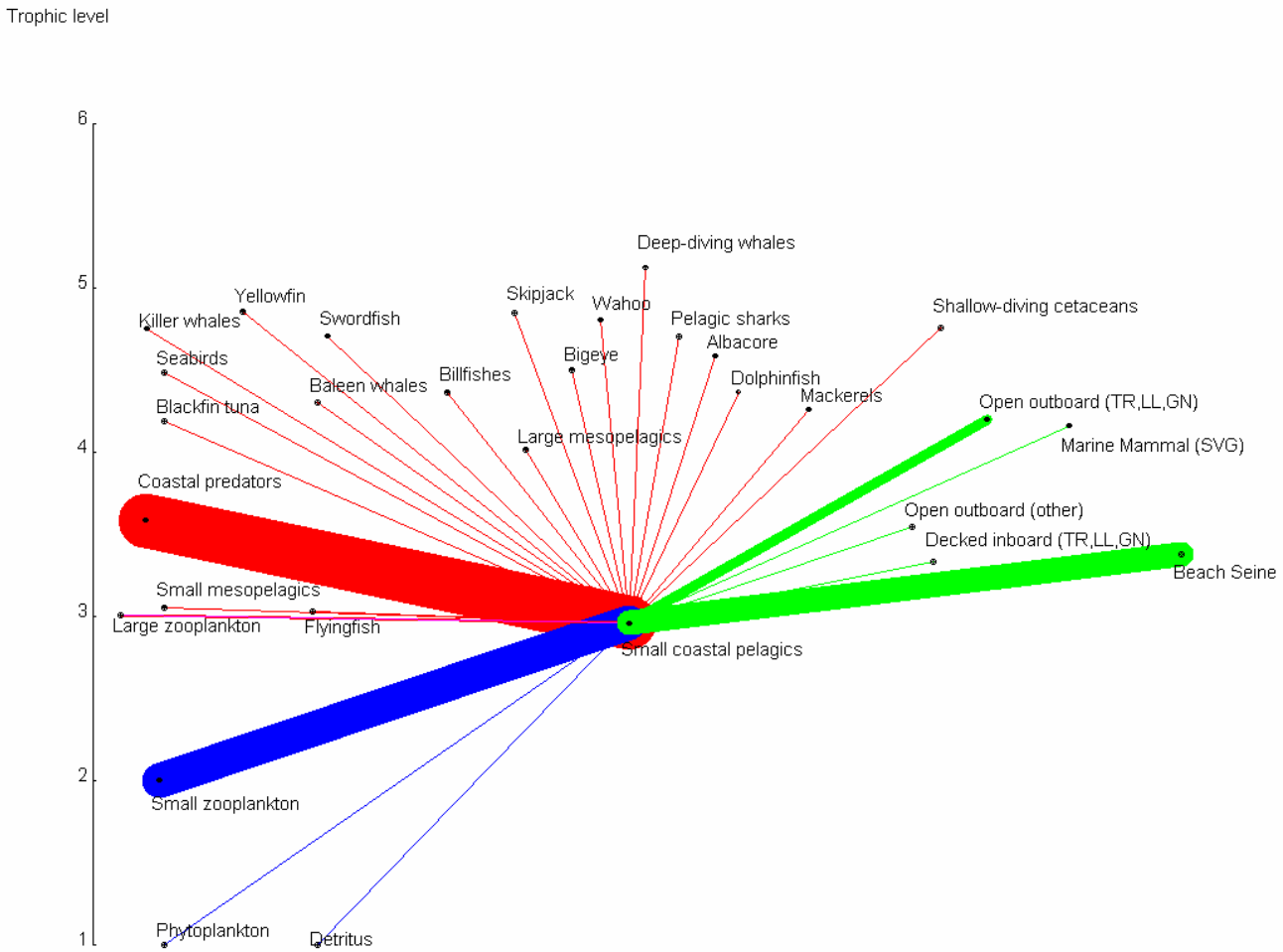

Figure 6 Biomass flows to and from small coastal pelagics. The thickness of the lines denotes the magnitude of flow. Red lines are linkages to predators, blue lines are linkages to prey and green lines are linkages to fisheries. NOTE: the length of the lines is of no ecological significance, merely for graphical clarity.

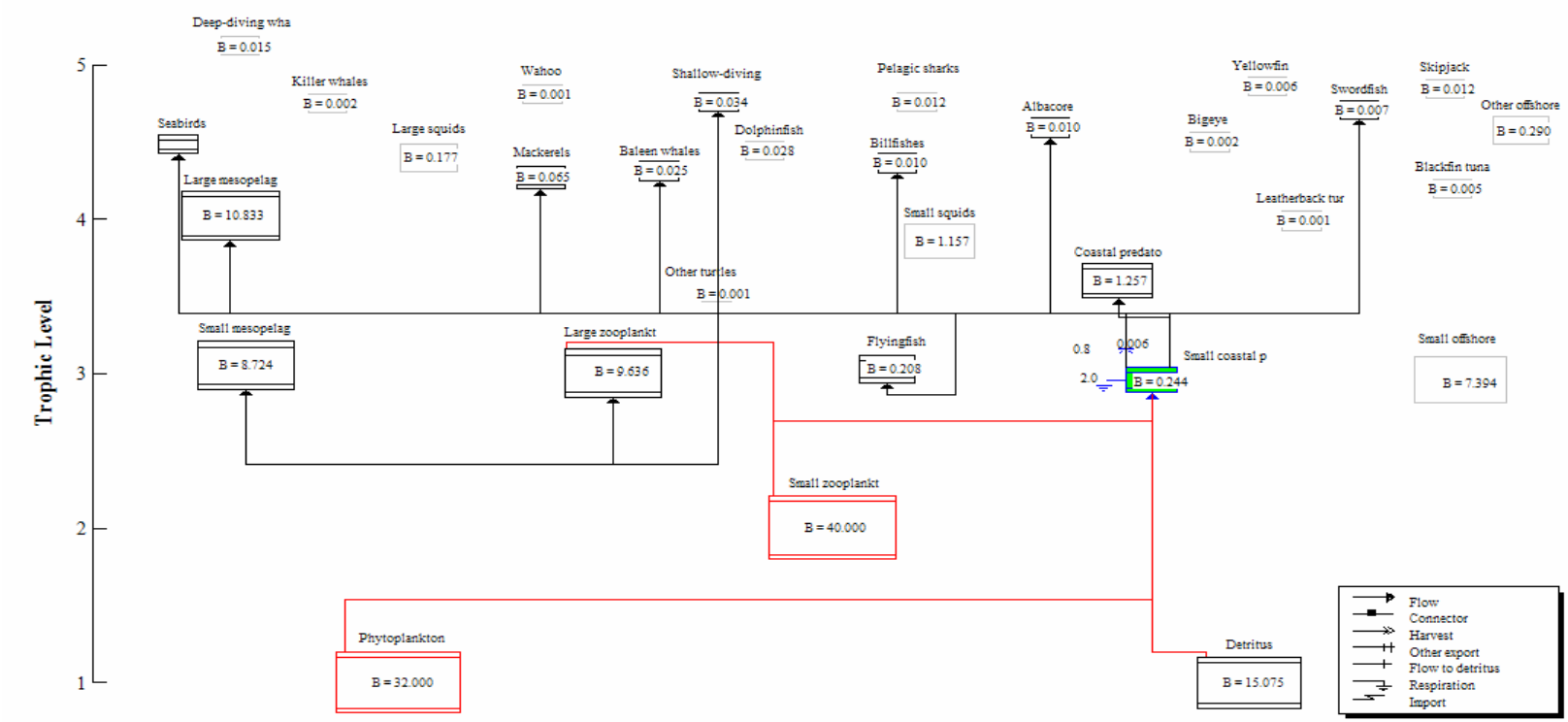

Figure 7 Trophic linkages of small coastal pelagics, black lines indicate predation on the group, red lines consumption by the group.

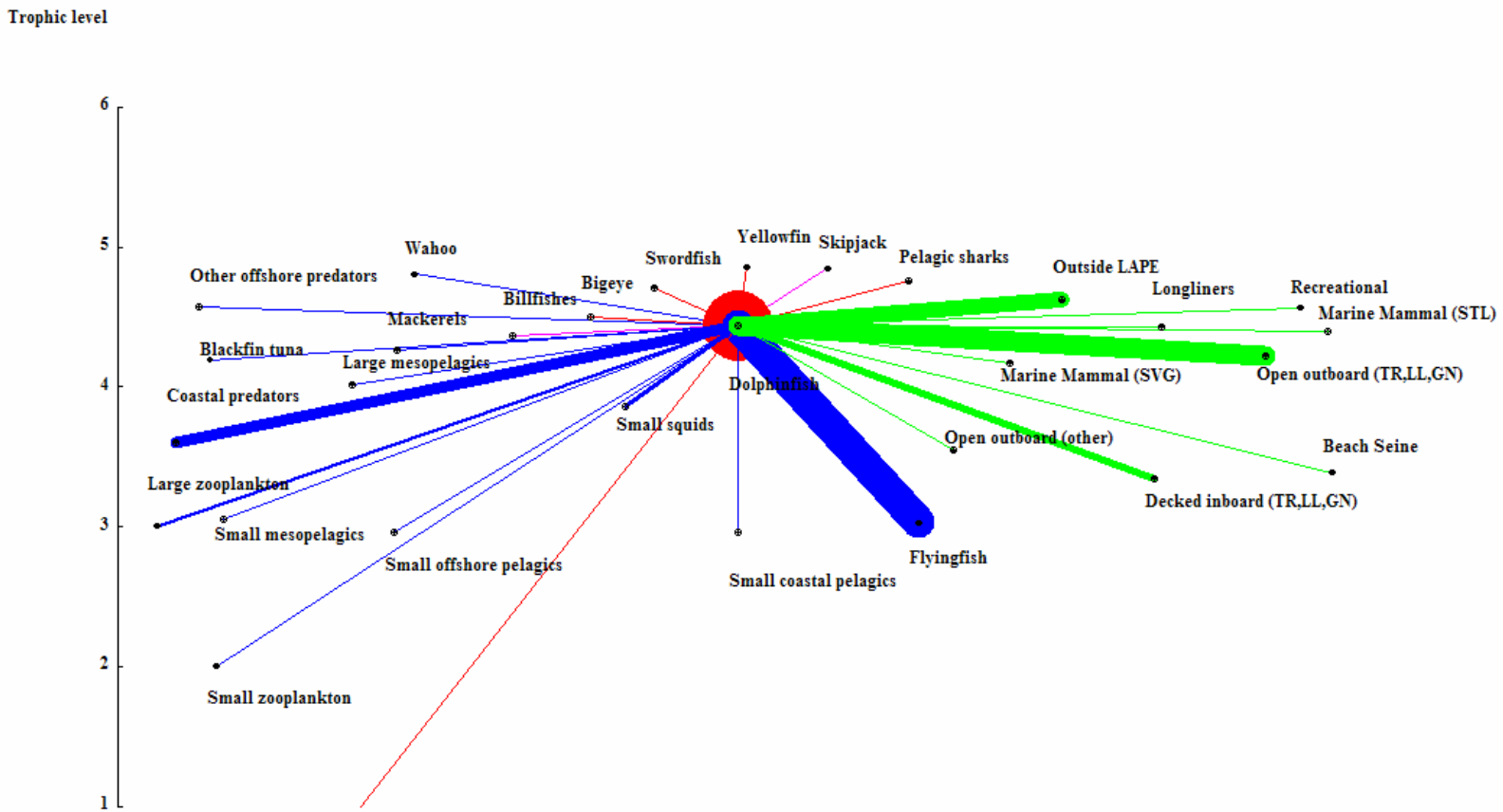

Figure 8 Biomass flows to and from dolphinfish. The thickness of the lines denotes the magnitude of flow. Red lines are linkages to predators, blue lines are linkages to prey and green lines are linkages to fisheries. The large red (predation) circle indicates cannibalism. NOTE: the length of the lines is of no ecological significance, merely for graphical clarity.

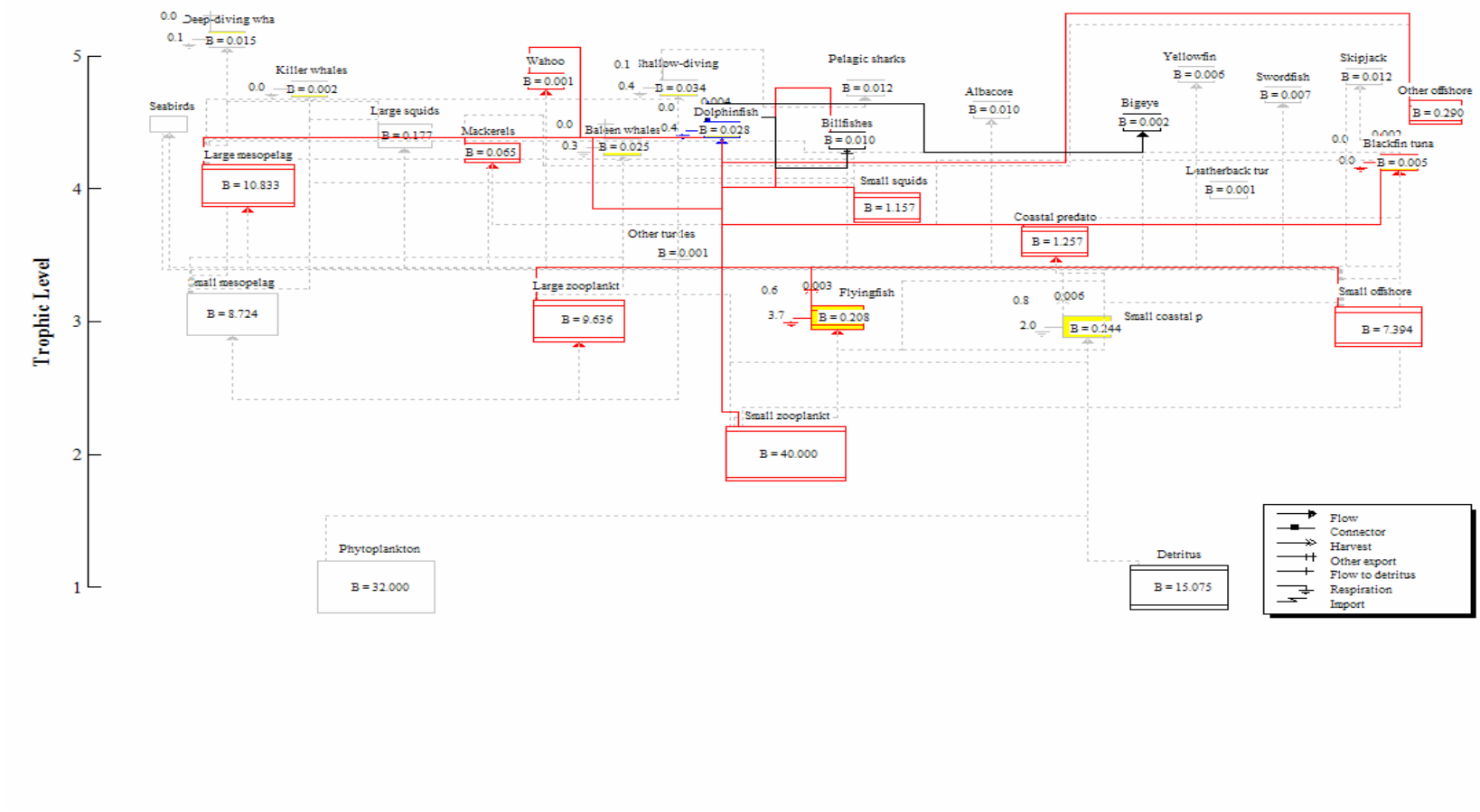

Figure 9 Trophic linkages of dolphinfish, black lines indicate predation on the group, red lines consumption by the group.

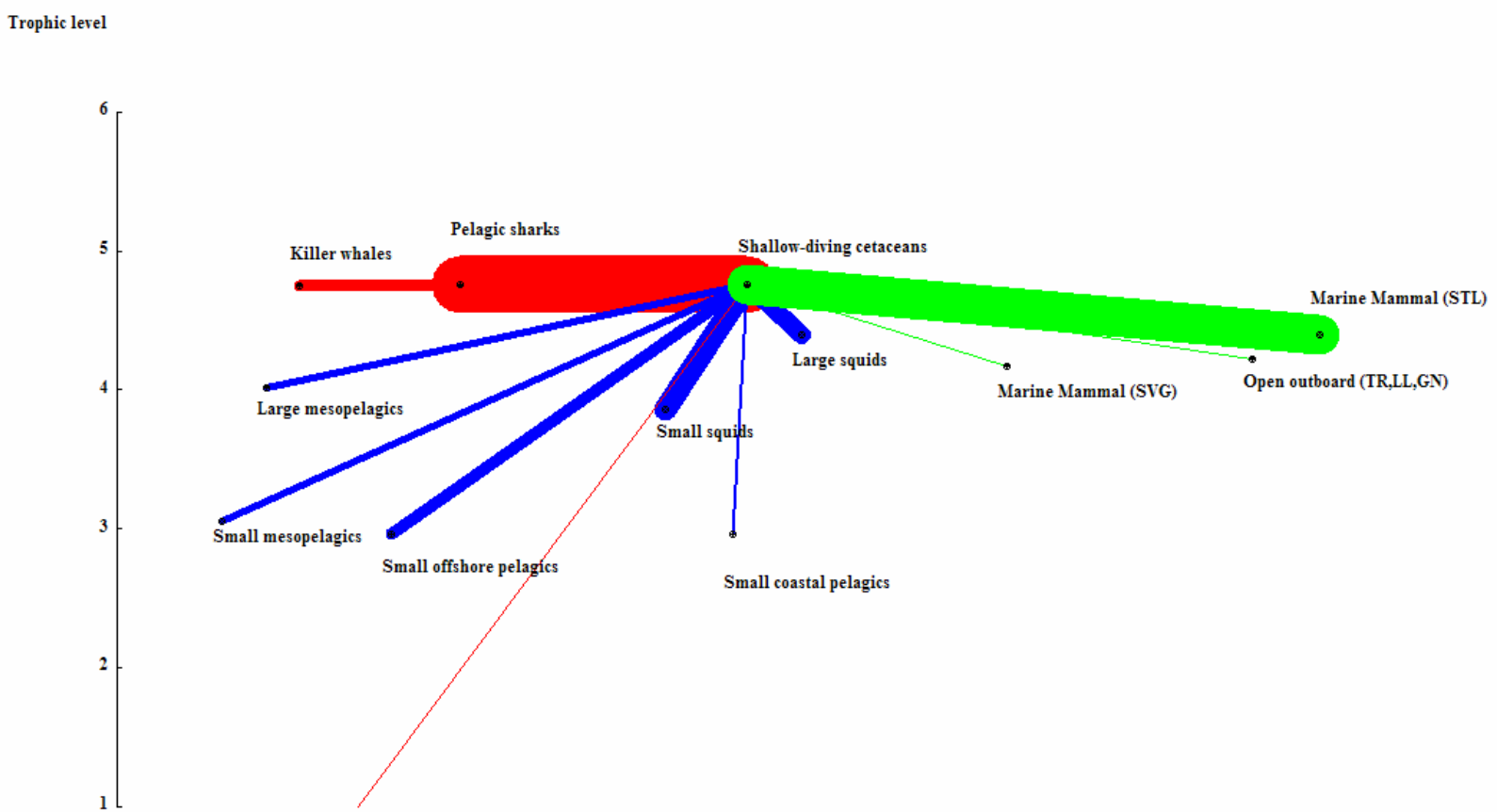

Figure 10 Biomass flows to and from shallow-diving cetaceans. The thickness of the lines denotes the magnitude of flow. Red lines are linkages to predators, blue lines are linkages to prey and green lines are linkages to fisheries. NOTE: the length of the lines is of no ecological significance, merely for graphical clarity.

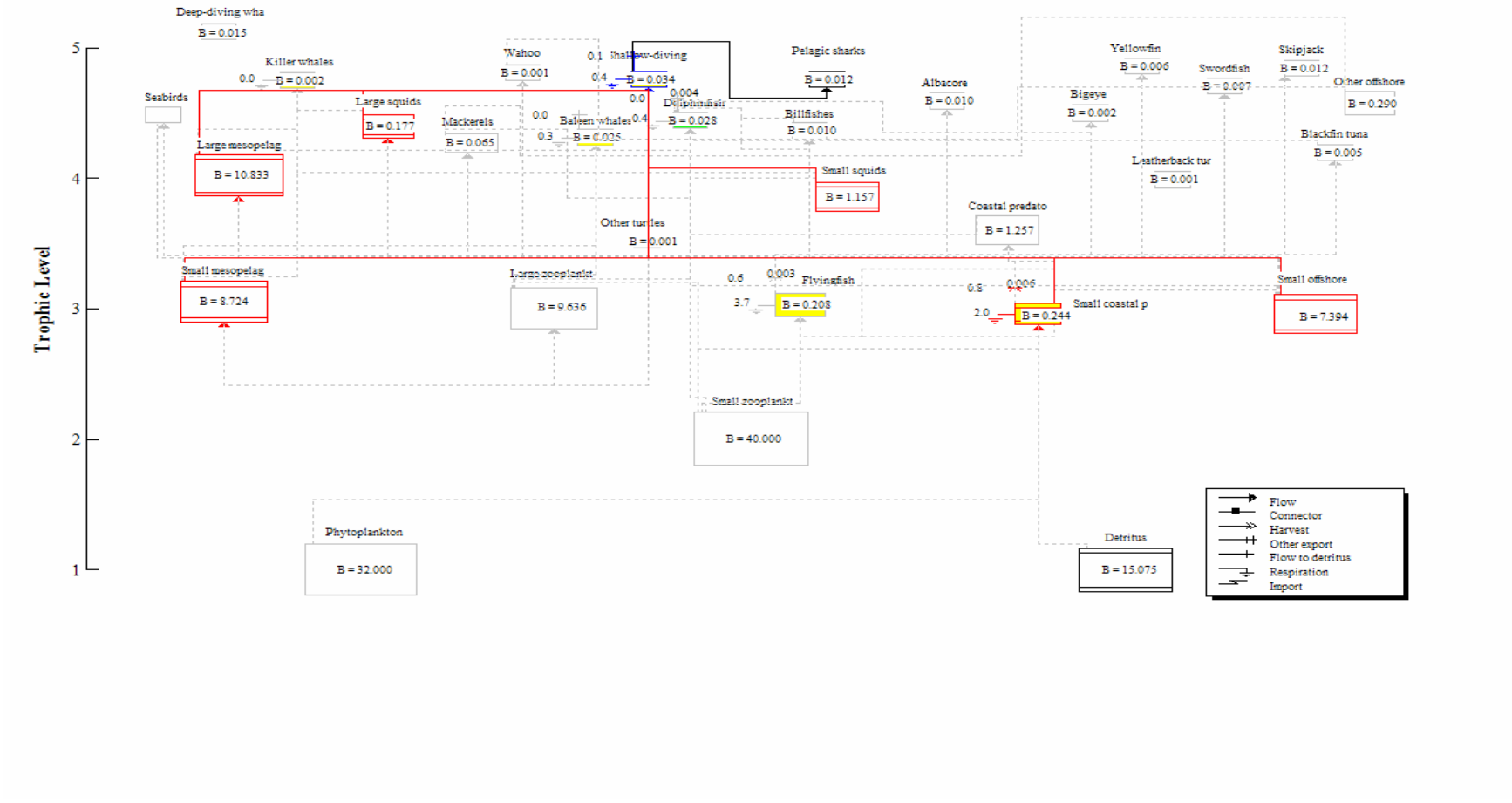

Figure 11 Trophic linkages of shallow-diving cetaceans, black lines indicate predation on the group, red lines consumption by the group.

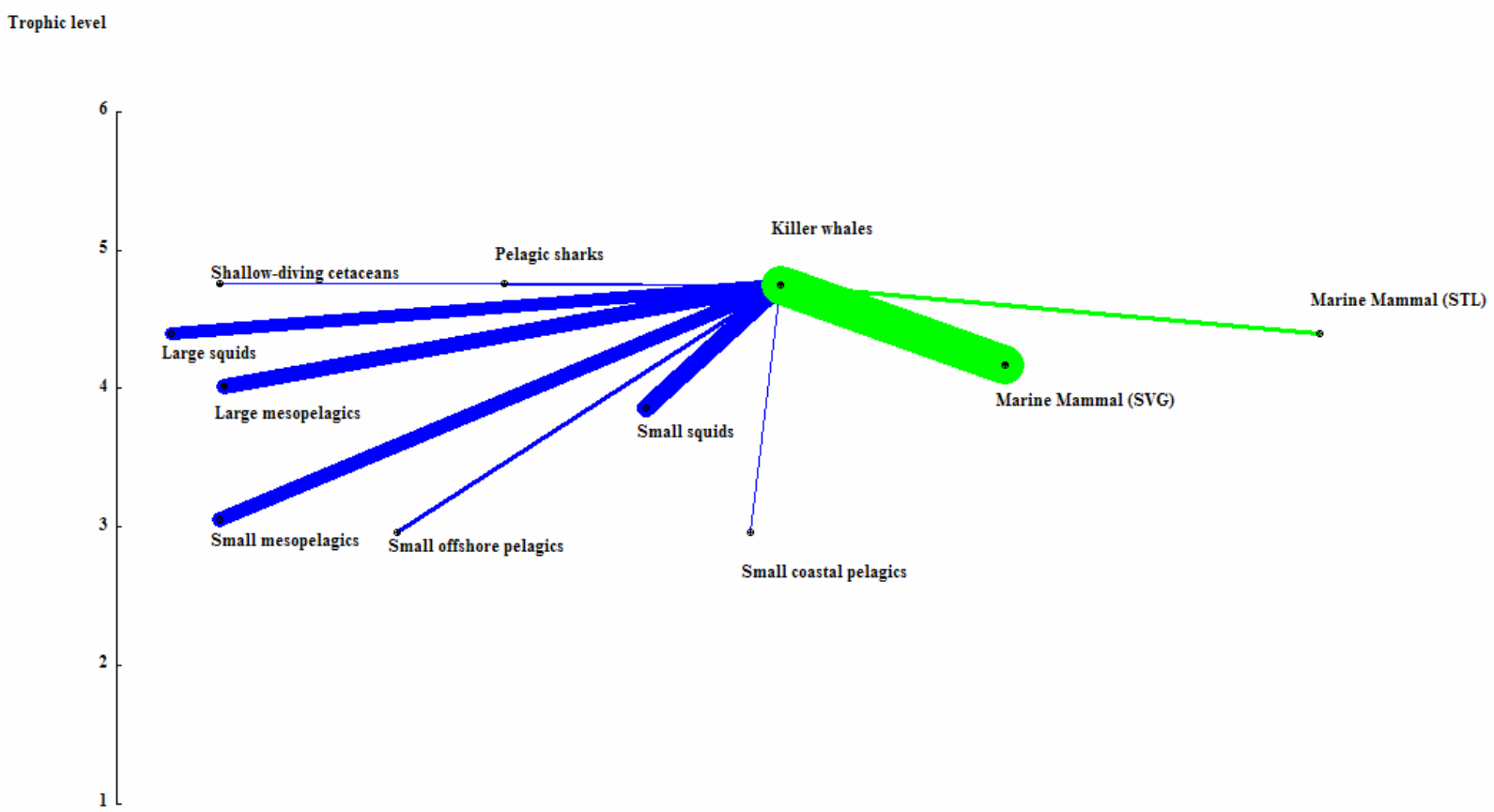

Figure 12 Biomass flows to and from killer whales. The thickness of the lines denotes the magnitude of flow. Red lines are linkages to predators, blue lines are linkages to prey and green lines are linkages to fisheries. NOTE: the length of the lines is of no ecological significance, merely for graphical clarity.

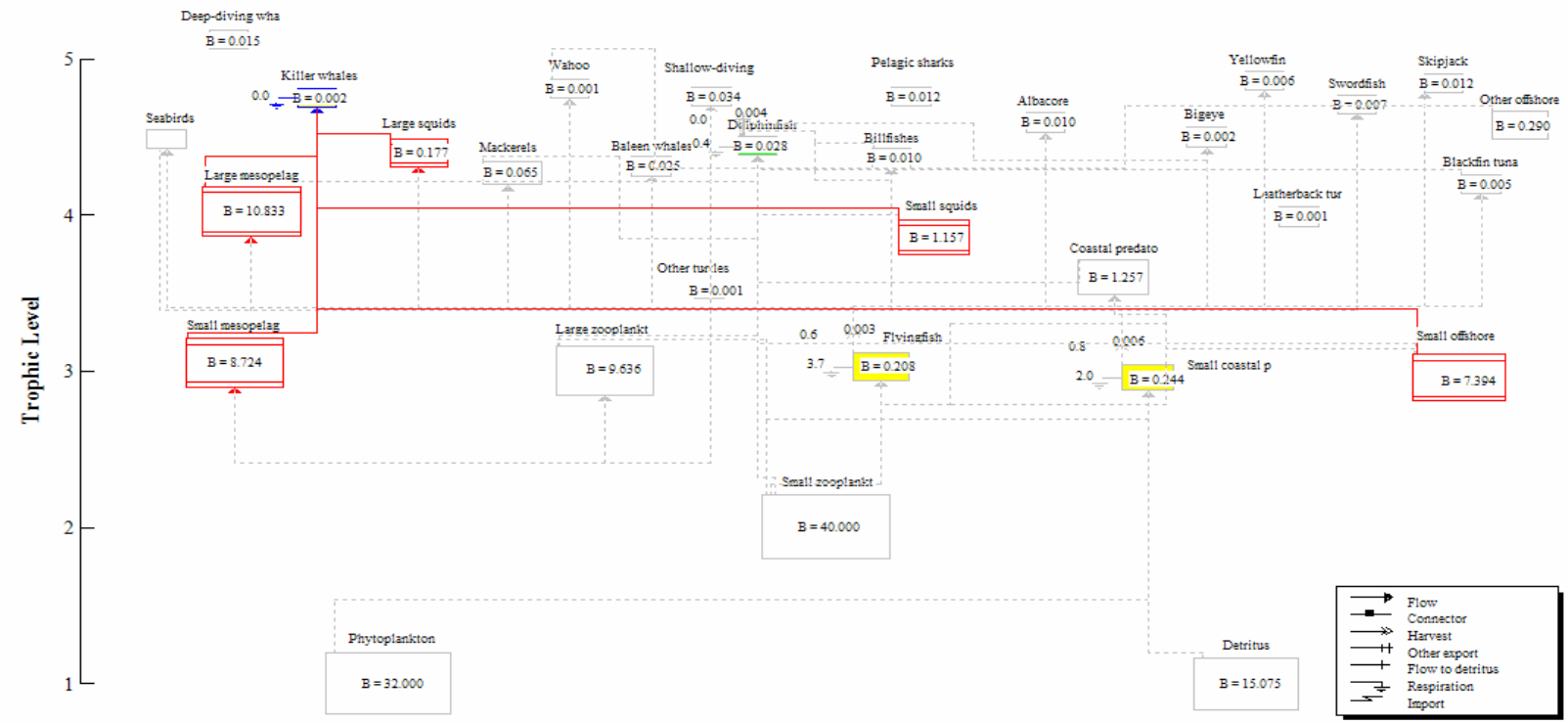

Figure 13 Trophic linkages of killer whales, black lines indicate predation on the group, red lines consumption by the group.

Key Indices

The key indices generated by Ecopath enable review of the model consistency through examination of specific indicators, namely the Respiration/Assimilation, Production/Respiration and Respiration/Biomass ratios (Table 6). Estimates of these ratios should be consistent with relative production and respiration rates associated with varying trophic levels in the system.

Table 6 Key indices generated for the LAPE model (R- respiration, A- assimilation, P- production, B-biomass).

Functional Group	Trophic level	R $t.km^{-2}.year^{-1}$	A $t.km^{-2}.year^{-1}$	R/A	P/R	R/B $year^{-1}$
Seabirds	4.49	0.012	0.012	0.998	0.002	58.822
Baleen whales	4.30	0.244	0.245	0.996	0.004	9.712
Deep-diving whales	5.13	0.063	0.063	0.991	0.009	4.312
Killer whales	4.75	0.012	0.012	0.997	0.003	7.692
Shallow-diving	4.76	0.361	0.363	0.995	0.005	10.75
Swordfish	4.71	0.027	0.03	0.913	0.095	3.878
Billfishes	4.37	0.032	0.036	0.875	0.143	3.22
Yellowfin	4.86	0.061	0.073	0.839	0.192	10.424
Skipjack	4.85	0.164	0.187	0.875	0.143	13.728
Albacore	4.58	0.053	0.061	0.875	0.143	5.46
Bigeye	4.50	0.021	0.024	0.875	0.143	12.313
Blackfin tuna	4.20	0.032	0.041	0.766	0.305	6.062
Other offshore	4.57	1.184	1.726	0.686	0.458	4.082
Mackerels	4.27	0.465	0.536	0.868	0.152	7.158
Wahoo	4.81	0.024	0.026	0.902	0.109	22.948
Dolphinfish	4.44	0.314	0.445	0.705	0.418	11.28
Pelagic sharks	4.76	0.088	0.093	0.95	0.053	7.6
Flyingfish	3.03	3.292	4.125	0.798	0.253	15.808
Coastal predators	3.60	6.357	7.263	0.875	0.142	5.056
Small offshore	2.96	59.98	86.599	0.693	0.444	8.112
Small coastal	2.96	2.004	2.858	0.701	0.426	8.212
Small mesopelagics	3.05	71.886	104.689	0.687	0.456	8.24
Large mesopelagics	4.02	26.92	30.766	0.875	0.143	2.485
Leatherback turtle	3.99	0.002	0.002	0.946	0.057	2.65
Other turtles	3.50	0.002	0.002	0.946	0.057	2.65
Small squids	3.86	10.607	16.973	0.625	0.6	9.164
Large squids	4.40	1.432	2.247	0.637	0.569	8.088
Small zooplankton	2.00	692.8	1384.8	0.5	0.999	17.32
Large zooplankton	3.01	83.833	167.666	0.5	1	8.7
Phytoplankton	1.00	0	-	-	-	-
Detritus	1.00	0	-	-	-	-

The ratio of respiration to assimilation is usually close to one for top predators due to their relatively low production, and of a lower, but positive value, for organisms at lower trophic levels (Christensen *et al.*, 2000). In the LAPE model

the Respiration/Assimilation constraint (R/A cannot exceed 1) has been met by all functional groups. However, it must be noted that the constraint was initially violated for several groups: seabirds, baleen whales, deep-diving whales, killer whales, other billfishes, albacore, bigeye, other offshore predators, mackerels, pelagic sharks, coastal predators and turtles (leatherbacks and other turtles). Closer examination however, revealed that this was due to a software problem rather than a real inconsistency in model parameters.

The ratio of respiration to production expresses the fate of unassimilated food (Christensen et al., 2000). Since a greater proportion of assimilated food goes to respiration than production in top predators and a greater proportion of assimilated food goes to production rather than respiration in low TL organisms it is expected that the Production/Respiration ratio would be higher for low TL organisms compared to high TL organisms. Exceptions occur in cases of low TL organisms of slow turnover rates such as marine turtles as well as high TL organisms with high turnover rates such as dolphinfish (Figure 14). Production/Respiration is constrained to estimates of one or less. This constraint has been met for all functional groups within the LAPE.

The Respiration/Biomass (R/B) ratios, indicative of the activity levels or turnover rates, are high for some fish groups (Figure 15). Mackinson (2006) suggested estimates of 1 to 10 $year^{-1}$ for fish groups and higher estimates for faster turnover organisms such as zooplankton. In the LAPE model R/B was greater than 10 $year^{-1}$ for yellowfin tuna, skipjack, bigeye, wahoo, dolphinfish and flyingfish. It appears however, that given the fast growth rates of dolphinfish and flyingfish that the associated estimates may be realistic for these groups. However, further review is necessary to confirm whether or not this is so and to identify realistic estimates for the other groups.

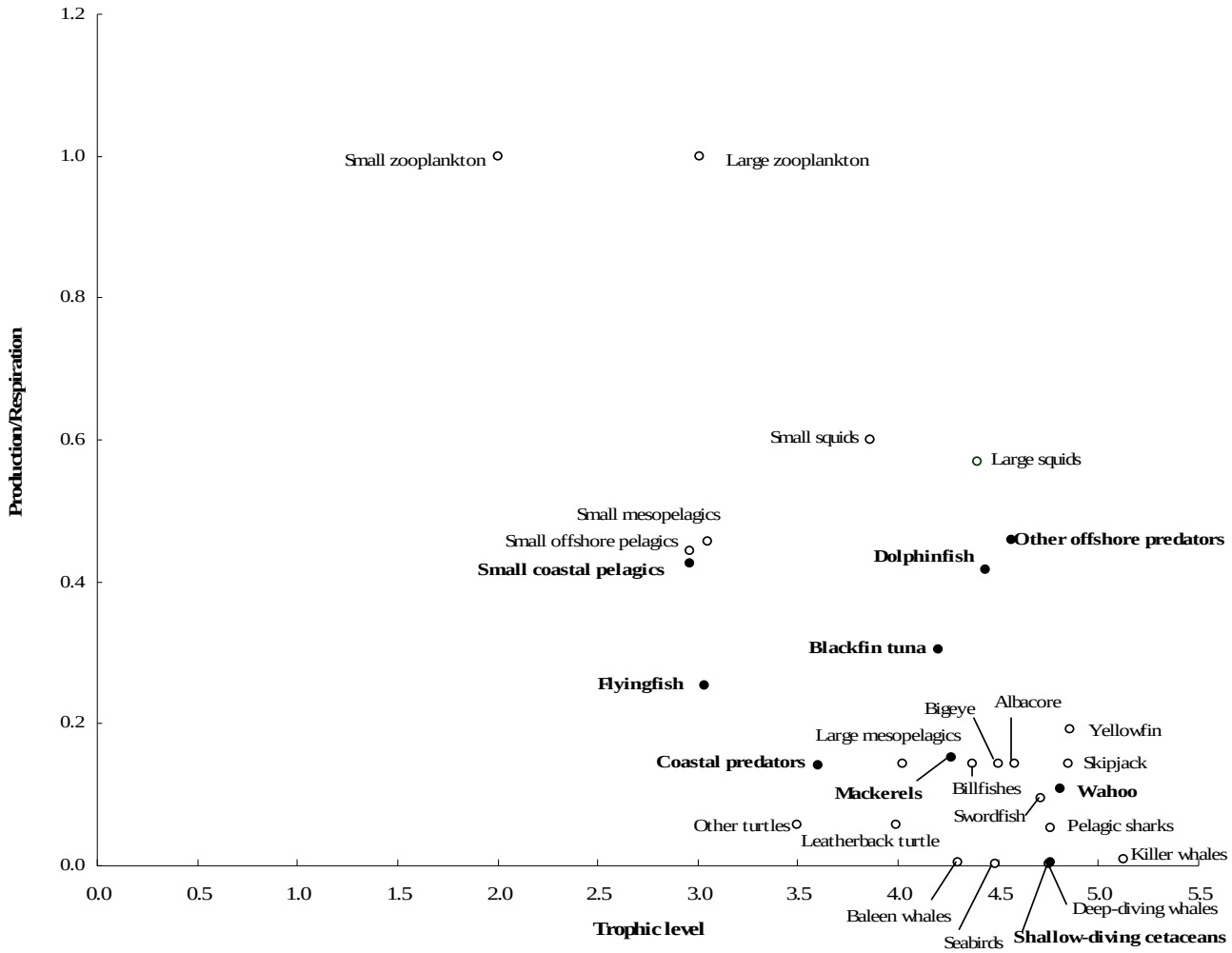

Figure 14 Relationship between trophic level and corresponding production/respiration ratios for functional groups in the LAPE model.

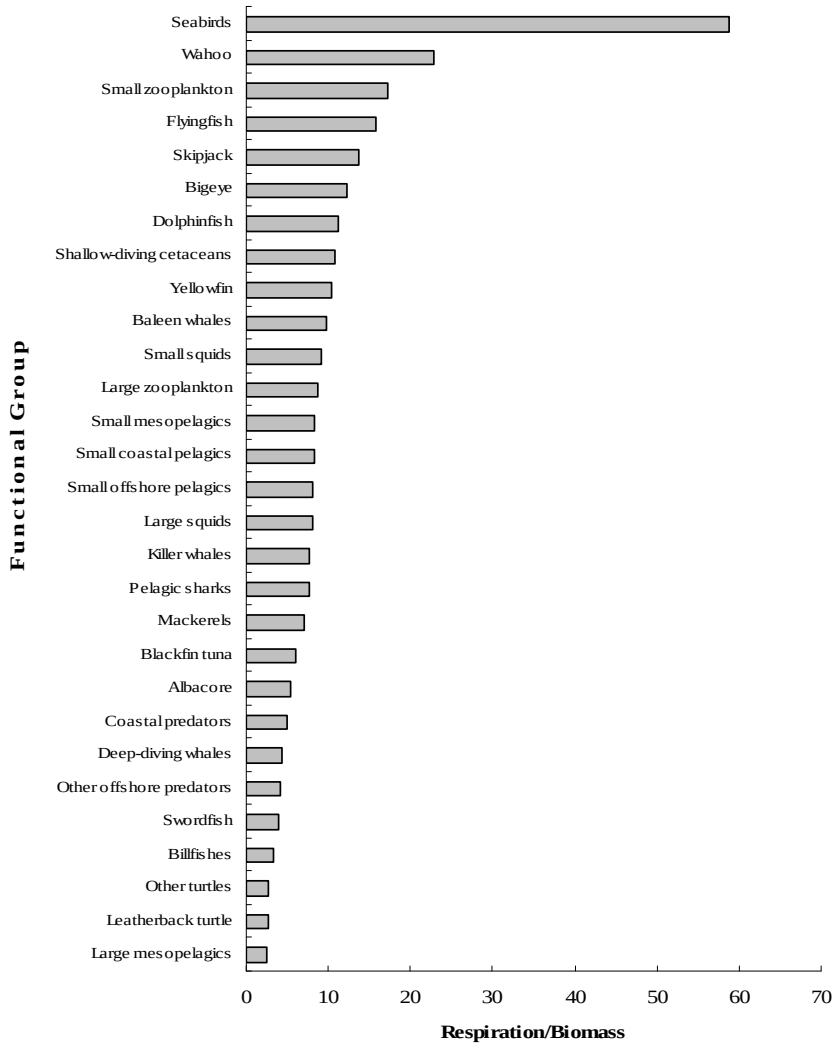

Figure 15 Respiration/Biomass of functional groups in the LAPE model

Mortality and Consumption

Total mortality represents the sum of fishing mortality, predation mortality and other mortality (death due to old age and disease). Generally, predation mortality accounted for 69.9% of total mortality, while other mortality accounted for 26.2% and fishing mortality a mere 3.8% across all represented groups in the LAPE area (Table 7).

Table 7 Mortality of functional groups in the LAPE model.

Functional group	Total Mortality P/B = Z	Fishing Mortality	Predation Mortality	Other Mortality	F as % of P/B	Predation Mortality as % of P/B	Other Mortality as % of P/B
Seabirds	0.130	0.000	0.058	0.072	0.000	44.615	55.385
Baleen whales	0.040	0.000	0.000	0.040	0.000	0.000	100.000
Deep-diving whales	0.040	0.000	0.000	0.040	0.000	0.000	100.000
Killer whales	0.020	0.006	0.000	0.014	30.000	0.000	70.000
Shallow-diving cetaceans	0.050	0.001	0.039	0.010	2.000	78.000	20.000
Swordfish	0.370	0.022	0.315	0.033	5.946	85.135	8.919

Functional group	Total Mortality P/B = Z	Fishing Mortality	Predation Mortality	Other Mortality	F as % of P/B	Predation Mortality as % of P/B	Other Mortality as % of P/B
Billfishes	0.460	0.123	0.314	0.023	26.739	68.261	5.000
Yellowfin	2.000	1.396	0.504	0.100	69.800	25.200	5.000
Skipjack	1.960	0.400	0.962	0.598	20.408	49.082	30.510
Albacore	0.780	0.300	0.393	0.087	38.462	50.385	11.154
Bigeye	1.759	0.340	1.014	0.406	19.329	57.646	23.081
Blackfin tuna	1.850	0.446	1.311	0.092	24.108	70.865	4.973
Other offshore predators	1.870	0.009	0.337	1.525	0.481	18.021	81.551
Mackerels	1.090	0.115	0.584	0.391	10.550	53.578	35.872
Wahoo	2.500	0.786	1.589	0.125	31.440	63.560	5.000
Dolphinfish	4.720	0.130	4.394	0.196	2.754	93.093	4.153
Pelagic sharks	0.400	0.245	0.151	0.004	61.250	37.750	1.000
Flyingfish	4.000	0.013	3.787	0.200	0.325	94.675	5.000
Coastal predators	0.720	0.010	0.674	0.036	1.389	93.611	5.000
Small offshore pelagics	3.600	0.000	1.197	2.403	0.000	33.250	66.750
Small coastal pelagics	3.500	0.024	3.324	0.152	0.686	94.971	4.343
Small mesopelagics	3.760	0.000	3.572	0.188	0.000	95.000	5.000
Large mesopelagics	0.355	0.000	0.063	0.292	0.000	17.746	82.254
Leatherback turtle	0.150	0.010	0.139	0.001	6.667	92.667	0.667
Other turtles	0.150	0.046	0.103	0.001	30.667	68.667	0.667
Small squids	5.500	0.000	5.225	0.275	0.000	95.000	5.000
Large squids	4.600	0.000	1.653	2.947	0.000	35.935	64.065
Small zooplankton	17.300	0.000	11.515	5.785	0.000	66.561	33.439
Large zooplankton	8.700	0.000	1.326	7.374	0.000	15.241	84.759
Phytoplankton	42.800	0.000	36.041	6.759	0.000	84.208	15.792
TOTAL	115.174	4.422	80.584	30.169	3.839	69.967	26.194

When only exploited groups are considered, fishing mortality accounted for 15.6% of total mortality, while predation and other mortality accounted for 70.3% and 15.7% respectively. The dominance of predation mortality in the system is also evident in examination of mortality parameters for non-highly migratory species which are of regional commercial importance (Figure 16). However, fishing mortality is comparatively greater for some groups, e.g., wahoo, blackfin tuna, mackerels, dolphinfish when compared to fishing mortality on small coastal pelagics, flyingfish, shallow-diving cetaceans, coastal predators and other offshore predators.

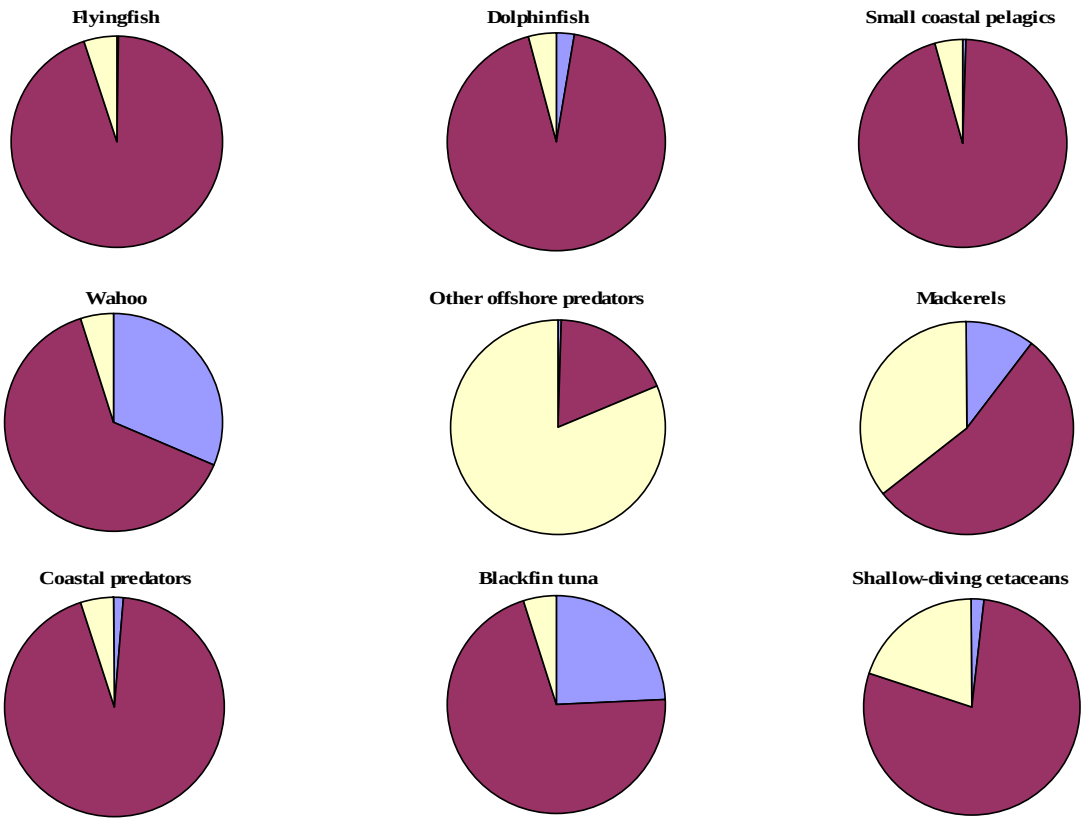

Figure 16 Mortality of selected species in the LAPE model (fishing mortality is blue, predation mortality is magenta and other mortality is yellow).

Predation mortality (Figure 17, Table 8) and associated consumption (Table 9, Figure 18) show that the highest predation mortality on small coastal pelagics is exerted by coastal predators, while dolphinfish exert greatest predation mortality on flyingfish. Cannibalism appears high in dolphinfish and is responsible for the greatest contribution to total predation mortality on the species. Pelagic sharks, top predators, are responsible for the highest predation mortality on shallow-diving cetaceans. Regional pelagic species experience high predation mortality due to consumption of skipjacks on blackfin tuna, dolphinfish on wahoo, dolphinfish and large mesopelagics on flyingfish and coastal predators on small coastal pelagics. Interestingly, baleen whales appear to exert the greatest predation mortality on mackerels. The contribution of mackerels to the diet is based on assumptions taken to assign fish groups in the LAPE ecosystem to generalized diet estimates by Pauly *et al*. (1997).

The level of cannibalism on dolphinfish requires confirmation because of the potential impacts on the adult stock. In the current version of the model this cannibalism results in the third highest predation mortality being attributed to dolphinfish, just below that for small squids and small zooplankton. Similarly the diet of baleen whales should be adjusted to more closely represent that in the Caribbean region, although there is currently little associated information.

Competition

Ecopath outputs which demonstrate the complexity of feeding interactions in the ecosystem include the predator and prey overlap in diets (varying between 0 and 1, demonstrates the likely consequences of changes in biomass of one group on the others), the omnivory index (a measure of the variation in trophic levels of the prey of a consumer), the electivity index (indicating the predator's prey preference ranging between -1 and 1; where -1 represents total avoidance of prey, 0 represents the consumption of prey in proportion to its abundance in the system and 1 represents absolute preference for a particular prey) and the mixed trophic impact (representing how increases in biomass of one group may affect the other).

There is considerable overlap (> 50% shared) in the prey items taken by flyingfish and small coastal pelagics (Table 10), although flyingfish also shows a high overlap in prey items taken by small offshore pelagics, small mesopelagics and large zooplankton. Due to cannibalism in dolphinfish, no other group shows any appreciable overlap in prey with this group. Marine mammals demonstrate prey overlap with several groups in the system e.g., baleen whales show > 50% overlap in diet with leatherback turtles and squids (small and large) while the more predatory marine mammals such as killer whales and shallow-diving small cetaceans demonstrate a high degree of overlap with several finfish groups (swordfish, yellowfin, skipjack, albacore, bigeye, other offshore predators, wahoo, large mesopelagics) as well as squid. Similar predators take flyingfish, coastal predators and small coastal pelagics (level of sharing > 50%), Predator overlap (Table 11) indicates that shallow-diving small cetaceans share the same predators with swordfish, billfish, pelagic sharks, leatherback and other turtles.

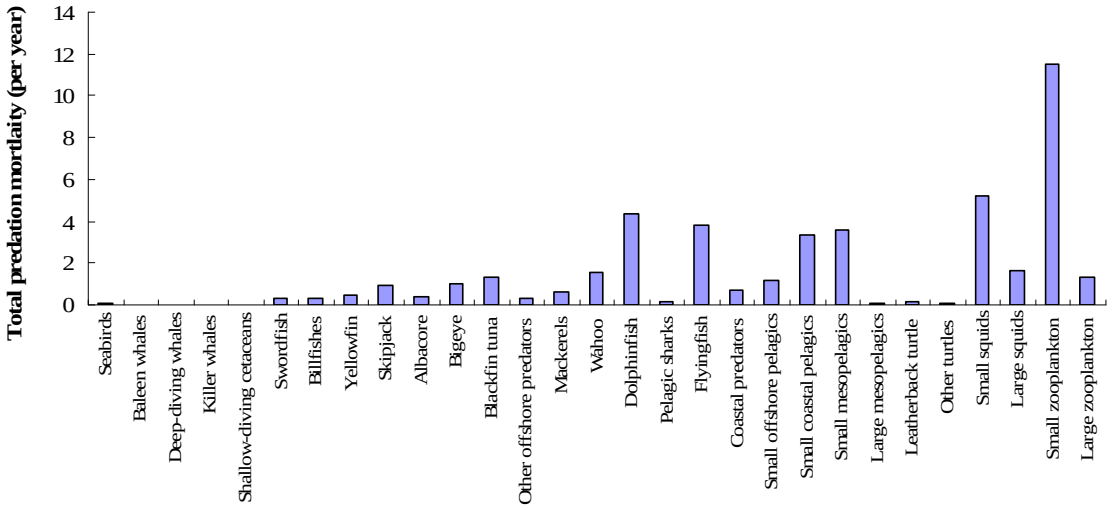

Figure 17 Total predation mortality on functional groups in the LAPE.

Table 8 Predation mortality in the LAPE Ecopath model.

Functional Group		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Seabirds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Deep-diving whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Shallow-diving cetaceans	-	-	-	0.006	0.001	-	-	-	-	-	-	-	-	-	-
6	Swordfish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Billfishes	-	-	-	-	-	-	-	-	0.048	-	-	0.037	-	-	-
8	Yellowfin	-	-	-	-	-	0.013	0.023	-	0.401	-	0.05	-	-	-	-
9	Skipjack	-	-	-	-	-	0.006	0.167	0.64	0.098	-	0.025	-	-	-	-
10	Albacore	-	-	-	-	-	0.008	0.014	0.094	0.242	-	0.03	-	-	-	-
11	Bigeye	-	-	-	-	-	0.044	0.19	0.049	0.7	-	-	-	-	-	-
12	Blackfin tuna	-	-	-	-	-	0.014	0.026	0.175	**0.451**	-	0.057	-	-	0.258	-
13	Other offshore predators	-	0.082	-	-	-	0	0.014	0.048	0.104	-	0.001	-	-	0.023	0.023
14	Mackerels	-	**0.365**	-	-	-	0.015	0.002	0.014	0.036	-	0.005	-	-	0.01	0
15	Wahoo	-	-	-	-	-	0.071	0.131	0.087	0.226	-	**0.283**	-	-	0.129	0.095
16	Dolphinfish	-	-	-	-	-	0.003	0.02	0.016	0.008	-	0.023	-	-	-	-
17	Pelagic sharks	-	-	-	0.001	-	-	-	-	-	-	-	-	-	-	-
18	Flyingfish	0.005	-	-	-	-	0.001	0.004	0.006	0.041	-	0.028	0.018	-	0.154	0.006
19	Coastal predators	0	-	-	-	-	0.003	0.001	0.006	0.011	0	0	0.012	0	0.186	0.001
20	Small offshore pelagics	0	0.004	0	0	0.009	-	0.004	0.002	0	0.002	0.001	0.001	0.02	0.006	0.001
21	Small coastal pelagics	0.003	0.034	0	0.001	0.078	0.019	0.004	0.002	0	0.002	0.001	0.001	-	0.055	0.001
22	Small mesopelagics	-	0.005	0	0	0.006	0	0	0	0.003	0.001	0	-	-	-	0
23	Large mesopelagics	-	-	0	0	0.005	0	0	0.001	0.005	0.003	0.001	0	-	-	0.001
24	Leatherback turtle	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	Other turtles	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	Small squids	0.006	-	0.001	0.003	0.126	0.013	0.002	0.012	0.023	0.005	0	0.005	1.379	0.084	0.005
27	Large squids	-	-	0.022	0.016	0.675	0.005	0	0.002	-	0.003	-	-	-	-	0.001
28	Small zooplankton	0	-	-	-	-	-	-	0	0	-	-	0	0.006	0.002	0
29	Large zooplankton	0	0.01	-	-	-	0	0	0.001	0.001	0	0	-	-	0.003	-
30	Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 8. Predation mortality in the LAPE (continued)

Functional Group		15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	Seabirds	-	-	0.058	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Deep-diving whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Shallow-diving cetaceans	-	-	**0.031**	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Swordfish	-	-	0.315	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Billfishes	-	0.113	0.118	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Yellowfin	-	-	0.017	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Skipjack	-	0.022	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Albacore	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Bigeye	-	-	0.03	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Blackfin tuna	-	0.321	0.01	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Other offshore predators	0.023	0.015	0	-	0.006	-	-	-	0.02	-	-	-	-	-	-	-
14	Mackerels	0	0.051	0.036	-	0.05	-	-	-	-	-	-	-	-	-	-	-
15	Wahoo	0.095	**0.519**	0.048	-	-	-	-	-	-	-	-	-	-	-	-	-
16	Dolphinfish	-	**4.323**	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-
17	Pelagic sharks	-	-	0.15	-	-	-	-	-	-	-	-	-	-	-	-	-
18	Flyingfish	0.006	**1.151**	0	-	**0.523**	-	-	-	**1.11**	-	-	-	**0.74**	-	-	-
19	Coastal predators	0.001	0.067	0.022	-	0.043	-	-	-	0.184	-	-	0.017	0.122	-	-	-
20	Small offshore pelagics	0.001	0.001	0	0.015	-	-	-	0.726	0.292	-	-	-	-	-	0.113	-
21	Small coastal pelagics	0.001	0.001	0	0.006	**2.941**	-	-	0.05	0.016	-	-	-	-	-	**0.11**	-
22	Small mesopelagics	0	0	0	-	0.002	-	-	0.075	2.539	-	-	0.868	0.072	-	-	-
23	Large mesopelagics	0.001	0	0.001	-	-	-	-	-	0.018	-	-	-	0.029	-	-	-
24	Leatherback turtle	-	-	0.139	-	-	-	-	-	-	-	-	-	-	-	-	-
25	Other turtles	-	-	0.103	-	-	-	-	-	-	-	-	-	-	-	-	-
26	Small squids	0.005	0.025	0.018	-	0.157	-	-	-	2.729	-	-	0.092	0.539	-	-	-
27	Large squids	0.001	-	-	-	-	-	-	-	0.87	-	-	-	0.059	-	-	-
28	Small zooplankton	0	0	-	0.097	0.018	1.507	0.05	2.516	0.094	0	0	0.086	-	0.173	6.964	-
29	Large zooplankton	-	0.002	0	-	0.003	0.011	0	-	0.248	0	0	0.983	0.065	-	-	-
30	Phytoplankton	-	-	-	-	-	0.085	0.003	-	-	-	-	-	-	35.95	-	-

Table 9 Consumption by functional groups in the LAPE

	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	Seabirds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Deep-diving whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Shallow-diving cetaceans	-	-	-	0.000	0.000	-	-	-	-	-	-	-	-	-	-	-
6	Swordfish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Billfishes	-	-	-	-	-	-	-	-	0.000	-	-	0.000	-	-	-	0.001
8	Yellowfin	-	-	-	-	-	0.000	0.000	-	0.002	-	0.000	-	-	-	-	-
9	Skipjack	-	-	-	-	-	0.000	0.002	0.008	0.001	-	0.000	-	-	-	-	0.000
10	Albacore	-	-	-	-	-	0.000	0.000	0.001	0.002	-	0.000	-	-	-	-	-
11	Bigeye	-	-	-	-	-	0.000	0.000	0.000	0.001	-	-	-	-	-	-	-
12	Blackfin tuna	-	-	-	-	-	0.000	0.000	0.001	**0.002**	-	0.000	-	-	0.001	-	**0.002**
13	Other offshore predators	-	0.024	-	-	-	0.000	0.004	0.014	0.030	-	0.000	-	-	0.007	0.007	0.004
14	Mackerels	-	**0.024**	-	-	-	0.001	0.000	0.001	0.002	-	0.000	-	-	0.001	0.000	0.003
15	**Wahoo**	-	-	-	-	-	0.000	0.000	0.000	0.000	-	0.000	-	-	0.000	0.000	0.001
16	Dolphinfish	-	-	-	-	-	0.000	0.001	0.000	0.000	-	0.001	-	-	-	-	**0.120**
17	Pelagic sharks	-	-	-	0.000	-	-	-	-	-	-	-	-	-	-	-	-
18	Flyingfish	0.001	-	-	-	-	0.000	0.001	0.001	0.008	-	0.006	0.004	-	0.032	0.001	**0.240**
19	Coastal predators	0.000	-	-	-	-	0.004	0.001	0.007	0.014	0.000	0.000	0.015	0.000	0.234	0.001	0.084
20	Small offshore pelagics	0.003	0.029	0.000	0.001	0.069	-	0.029	0.013	0.001	0.016	0.006	0.007	0.145	0.046	0.006	0.004
21	Small coastal pelagics	0.001	0.008	0.000	0.000	0.019	0.005	0.001	0.000	0.000	0.001	0.000	0.000	-	0.013	0.000	0.000
22	Small mesopelagics	-	0.047	0.001	0.003	0.050	0.001	0.000	0.001	0.027	0.005	0.003	-	-	-	0.000	0.000
23	Large mesopelagics	-	-	0.001	0.003	0.050	0.005	0.002	0.011	0.051	0.028	0.009	0.002	-	-	0.006	0.001
24	Leatherback turtle	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	Other turtles	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	Small squids	0.007	-	0.001	0.004	0.146	0.015	0.002	0.014	0.027	0.005	0.001	0.006	1.596	0.097	0.005	0.029
27	Large squids	-	-	0.004	0.003	0.119	0.001	0.000	0.000	-	0.001	-	-	-	-	0.000	-
28	Small zooplankton	0.000	-	-	-	-	-	-	0.000	0.000	-	-	0.008	0.237	0.090	0.000	0.011
29	Large zooplankton	0.000	0.095	-	-	-	0.001	0.000	0.006	0.006	0.002	0.001	-	-	0.025	-	0.020
30	Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31	Detritus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Import	0.002	0.079	0.073	-	0.001	0.005	0.001	0.012	0.058	0.017	0.001	0.009	0.179	0.123	0.006	0.035
	Sum	0.015	0.306	0.079	0.015	0.454	0.037	0.045	0.091	0.234	0.076	0.029	0.051	2.158	0.670	0.033	0.556

Table 9. Consumption of functional groups in the LAPE (continued).

	Prey \ Predator	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	T
1	Seabirds	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0**
2	Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.047	**0**
3	Deep-diving whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.002	**0**
4	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0**
5	Shallow-diving cetaceans	-	**0.00**	-	-	-	-	-	-	-	-	-	-	-	-	-	0.091	**0**
6	Swordfish	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.008	**0**
7	Billfishes	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.000	**0**
8	Yellowfin	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.019	**0**
9	Skipjack	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.054	**0**
10	Albacore	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.001	**0**
11	Bigeye	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.001	**0**
12	Blackfin tuna	**0.00**	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.011	**0**
13	Other offshore predators	0.00	0.00	-	0.00	-	-	-	0.006	-	-	-	-	-	-	-	0.049	**0**
14	Mackerels	0.00	0.00	-	0.00	-	-	-	-	-	-	-	-	-	-	-	0.000	**0**
15	**Wahoo**	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.007	**0**
16	Dolphinfish	**0.12**	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.016	**0**
17	Pelagic sharks	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	0.011	**0**
18	Flyingfish	**0.24**	0.00	-	**0.10**	-	-	-	**0.231**	-	-	-	**0.15**	-	-	-	0.622	**0**
19	Coastal predators	0.08	0.02	-	0.05	-	-	-	0.231	-	-	0.021	0.15	-	-	-	0.094	**0**
20	Small offshore pelagics	0.00	0.00	0.10	-	-	-	5.365	2.157	-	-	-	-	-	0.838	-	-	**8**
21	Small coastal pelagics	0.00	0.00	0.00	**0.71**	-	-	0.012	0.004	-	-	-	-	-	0.027	-	0.751	**0**
22	Small mesopelagics	0.00	0.00	-	0.01	-	-	0.654	22.15	-	-	7.576	0.62	-	-	-	27.812	**3**
23	Large mesopelagics	0.00	0.00	-	-	-	-	-	0.193	-	-	-	0.30	-	-	-	10.857	**0**
24	Leatherback turtle	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0**
25	Other turtles	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**0**
26	Small squids	0.02	0.02	-	0.18	-	-	-	3.159	-	-	0.106	0.62	-	-	-	4.561	**6**
27	Large squids	-	-	-	-	-	-	-	0.154	-	-	-	0.01	-	-	-	1.084	**0**
28	Small zooplankton	0.01	-	3.89	0.70	60.294	1.99	100.62	3.775	0.00	0.00	3.447	-	6.931	278.57	-	1154.61	**4**
29	Large zooplankton	0.02	0.00	-	0.02	0.108	0.00	-	2.389	0.00	0.00	9.469	0.62	-	-	-	182.832	**1**
30	Phytoplankton	-	-	-	-	2.706	0.08	-	-	-	-	-	-	1150.53	-	-	216.273	**1**
31	Detritus	-	0.00	-	0.01	0.216	0.00	-	-	-	-	-	-	1150.53	-	-	-	**1**
	Import	0.03	0.04	1.15	7.23	44.923	1.48	24.207	4.007	-	0.00	0.596	0.30	-	-	-	0.000	**8**
	Sum	0.55	0.11	5.15	9.07	108.24	3.57	130.86	38.45	0.00	0.00	21.21	2.80	2308.00	279.44	0.00	1599.81	**2**

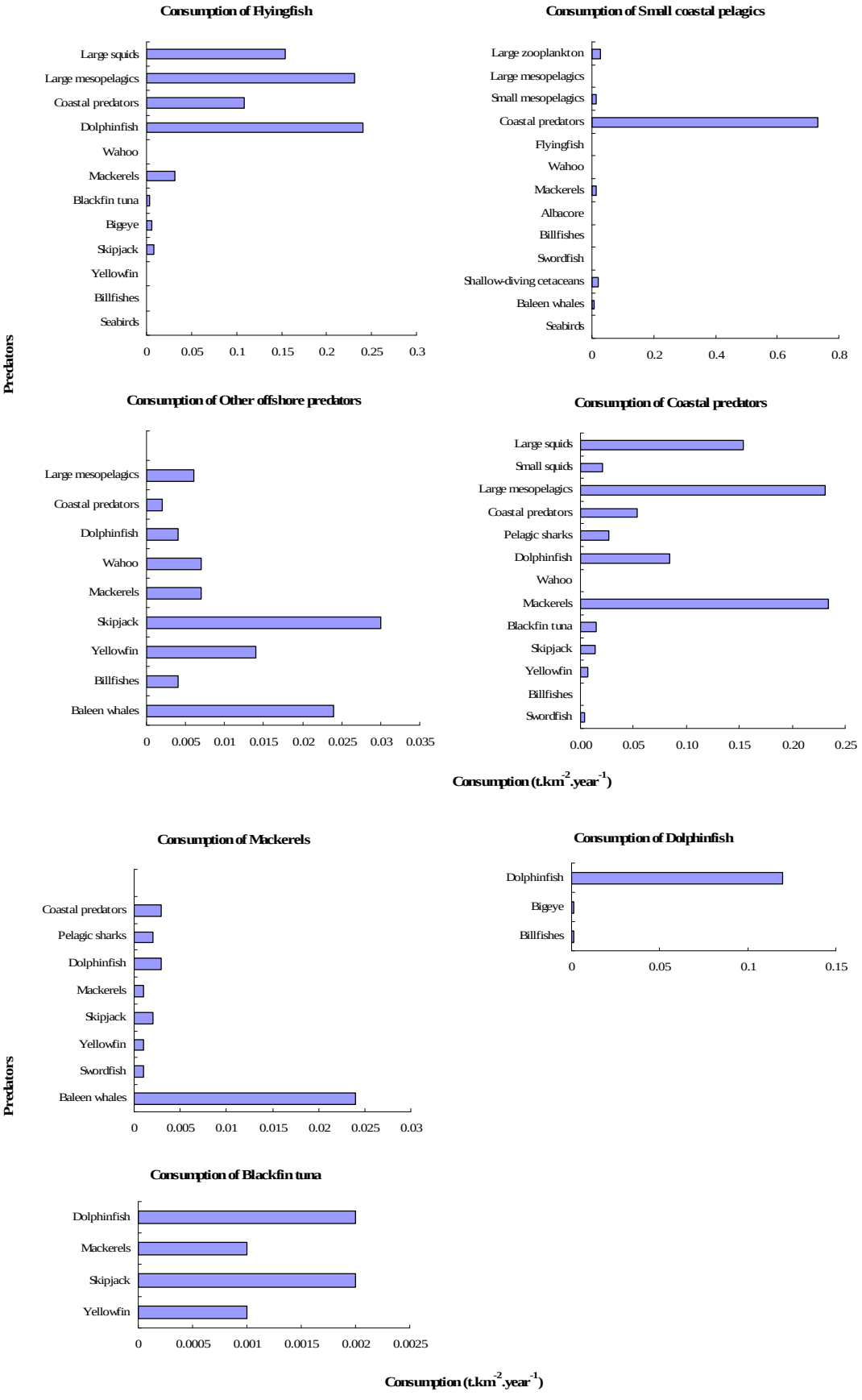

Figure 18 Consumption (t·km^{-2}year^{-1}) of selected functional groups in the LAPE.

Table 10 Prey overlap index in the LAPE Ecopath model. Overlap of more than 50% in bold.

Group	Group name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Seabirds	**1.000**	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Baleen whales	0.107	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Deep-diving whales	0.028	0.019	1.000	-	-	-	-	-	-	-	-	-	-	-	-
4	Killer whales	**0.570**	0.237	0.151	1.000	-	-	-	-	-	-	-	-	-	-	-
5	Shallow-diving cetaceans	**0.746**	0.179	0.161	**0.898**	1.000	-	-	-	-	-	-	-	-	-	-
6	Swordfish	**0.818**	0.097	0.060	**0.710**	**0.737**	1.000	-	-	-	-	-	-	-	-	-
7	Billfishes	0.445	0.243	0.008	0.211	0.367	0.100	1.000	-	-	-	-	-	-	-	-
8	Yellowfin	**0.547**	0.396	0.060	**0.518**	**0.539**	**0.579**	0.474	1.000	-	-	-	-	-	-	-
9	Skipjack	0.310	0.307	0.092	**0.681**	0.462	**0.563**	0.128	**0.751**	1.000	-	-	-	-	-	-
10	Albacore	0.326	0.229	0.062	**0.660**	**0.506**	0.395	**0.512**	**0.600**	**0.672**	1.000	-	-	-	-	-
11	Bigeye	0.280	0.264	0.049	**0.541**	0.393	0.264	**0.505**	**0.540**	**0.627**	**0.876**	1.000	-	-	-	-
12	Blackfin tuna	0.442	0.087	0.021	0.278	0.345	0.491	0.344	**0.534**	0.352	0.299	0.335	1.000	-	-	-
13	Other offshore predators	**0.880**	0.018	0.021	**0.513**	**0.633**	**0.763**	0.159	0.371	0.256	0.176	0.072	0.330	1.000	-	-
14	Mackerels	0.406	0.133	0.014	0.224	0.292	**0.523**	0.205	0.478	0.314	0.143	0.159	**0.958**	0.344	1.000	-
15	Wahoo	**0.559**	0.245	0.054	**0.555**	**0.562**	**0.523**	**0.563**	**0.897**	**0.746**	**0.727**	**0.668**	0.425	0.370	0.308	1.000
16	Dolphinfish	0.223	0.066	0.003	0.063	0.076	0.175	0.065	0.177	0.186	0.032	0.425	0.421	0.100	0.401	0.153
17	Pelagic sharks	0.493	0.043	0.049	0.435	0.442	**0.719**	0.131	**0.605**	**0.542**	0.318	0.229	**0.790**	0.405	**0.833**	0.444
18	Flyingfish	0.020	0.006	0.000	0.004	0.008	0.000	0.027	0.013	0.003	0.012	0.011	0.350	0.149	0.280	0.018
19	Coastal predators	0.087	0.024	0.035	0.058	0.068	0.126	0.010	0.104	0.090	0.018	0.034	0.302	0.086	0.255	0.063
20	Small offshore pelagics	0.010	0.001	-	-	-	0.000	0.000	0.006	0.003	0.000	0.000	0.396	0.140	0.314	0.007
21	Small coastal pelagics	0.010	0.001	-	-	-	0.000	0.000	0.006	0.003	0.000	0.000	0.396	0.140	0.314	0.007
22	Small mesopelagics	0.029	0.042	0.002	0.048	0.035	0.007	0.051	0.025	0.027	0.035	0.038	0.363	0.150	0.288	0.029
23	Large mesopelagics	0.163	0.466	0.038	**0.616**	0.374	0.234	0.111	0.190	0.427	0.323	0.335	0.156	0.159	0.130	0.163
24	Leatherback turtle	0.009	**0.550**	-	-	-	0.030	0.000	0.115	0.047	0.041	0.049	0.006	0.003	0.071	0.000
25	Other turtles	0.004	0.211	-	-	-	0.009	0.000	0.061	0.027	0.012	0.015	0.108	0.019	0.100	0.002
26	Small squids	0.203	**0.794**	0.023	0.405	0.279	0.260	0.016	0.240	0.306	0.162	0.170	0.173	0.236	0.224	0.089
27	Large squids	0.380	**0.523**	0.194	**0.798**	**0.689**	**0.594**	0.065	**0.535**	**0.711**	**0.507**	**0.514**	0.375	0.313	0.385	0.428
28	Small zooplankton	0.002	-	-	-	-	-	-	0.001	0.000	-	-	0.058	0.022	0.046	0.001
29	Large zooplankton	0.009	0.001	0.000	0.000	0.001	0.000	0.003	0.004	0.002	0.001	0.001	0.285	0.141	0.232	0.006

Table 10. Prey overlap index in the LAPE Ecopath model. (continued).

Group	Group name	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	Seabirds	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Deep-diving whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Shallow-diving cetaceans	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Swordfish	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Billfishes	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Yellowfin	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Skipjack	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Albacore	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Bigeye	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Blackfin tuna	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Other offshore predators	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	Mackerels	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	Wahoo	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	Dolphinfish	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-
17	Pelagic sharks	0.259	1.000	-	-	-	-	-	-	-	-	-	-	-	-
18	Flyingfish	0.035	0.002	1.000	-	-	-	-	-	-	-	-	-	-	-
19	Coastal predators	0.088	0.175	0.214	1.000	-	-	-	-	-	-	-	-	-	-
20	Small offshore pelagics	0.037	0.000	**0.954**	0.286	1.000	-	-	-	-	-	-	-	-	-
21	Small coastal pelagics	0.037	0.000	**0.955**	0.286	1.000	1.000	-	-	-	-	-	-	-	-
22	Small mesopelagics	0.036	0.004	**0.994**	0.222	**0.960**	**0.960**	1.000	-	-	-	-	-	-	-
23	Large mesopelagics	0.043	0.120	0.158	0.065	0.163	0.163	0.248	1.000	-	-	-	-	-	-
24	Leatherback turtle	0.059	0.001	0.020	0.009	0.019	0.019	0.019	0.092	1.000	-	-	-	-	-
25	Other turtles	0.021	0.001	0.131	**0.644**	0.177	0.177	0.136	0.047	0.104	1.000	-	-	-	-
26	Small squids	0.085	0.117	0.252	0.107	0.268	0.268	0.307	**0.711**	0.625	0.182	1.000	-	-	-
27	Large squids	0.293	**0.518**	-	0.103	0.001	0.001	0.030	0.506	0.261	0.122	**0.587**	1.000	-	-
28	Small zooplankton	0.006	0.007	0.153	0.043	0.187	0.186	0.153	0.025	0.003	0.024	0.041	-	1.000	-
29	Large zooplankton	0.030	0.000	**0.962**	0.163	**0.851**	**0.852**	**0.946**	0.139	0.020	0.100	0.223	-	0.142	1.000

Table 11 Predator overlap index in the LAPE Ecopath model

Group	Group name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Seabirds	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Deep-diving whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Shallow-diving cetaceans	**0.959**	-	-	-	1.000	-	-	-	-	-	-	-	-	-	-
6	Swordfish	**1.000**	-	-	-	**0.959**	1.000	-	-	-	-	-	-	-	-	-
7	Billfishes	**0.534**	-	-	-	**0.577**	**0.534**	1.000	-	-	-	-	-	-	-	-
8	Yellowfin	0.042	-	-	-	0.042	0.042	0.263	1.000	-	-	-	-	-	-	-
9	Skipjack	0.005	-	-	-	0.006	0.005	0.103	0.321	1.000	-	-	-	-	-	-
10	Albacore	0.018	-	-	-	0.019	0.018	0.247	**0.917**	**0.634**	1.000	-	-	-	-	-
11	Bigeye	0.039	-	-	-	0.040	0.039	0.264	**0.960**	0.428	**0.923**	1.000	-	-	-	-
12	Blackfin tuna	0.005	-	-	-	0.005	0.005	0.181	0.255	0.183	0.279	0.257	1.000	-	-	-
13	Other offshore predators	0.001	-	-	-	0.001	0.001	0.120	0.277	0.246	0.339	0.304	**0.529**	1.000	-	-
14	Mackerels	0.021	-	-	-	0.023	0.021	0.044	0.025	0.018	0.027	0.026	**0.822**	**0.675**	1.000	-
15	Wahoo	0.005	-	-	-	0.005	0.005	0.282	0.239	0.180	0.265	0.243	**0.983**	**0.533**	**0.795**	1.000
16	Dolphinfish	0.000	-	-	-	0.000	0.000	**0.517**	0.003	0.034	0.004	0.003	0.170	0.038	0.031	0.313
17	Pelagic sharks	**1.000**	-	-	-	**0.963**	**1.000**	**0.537**	0.042	0.006	0.018	0.039	0.005	0.001	0.021	0.005
18	Flyingfish	0.000	-	-	-	0.000	0.000	0.258	0.013	0.019	0.014	0.013	0.387	0.280	0.388	0.446
19	Coastal predators	0.015	-	-	-	0.015	0.015	0.050	0.009	0.008	0.010	0.009	**0.857**	0.469	**0.836**	**0.828**
20	Small offshore pelagics	0.000	-	-	-	0.001	0.000	0.001	0.000	0.003	0.001	0.001	0.036	0.035	0.033	0.034
21	Small coastal pelagics	0.000	-	-	-	0.002	0.000	0.000	0.000	0.001	0.001	0.001	0.014	0.061	0.125	0.013
22	Small mesopelagics	0.000	-	-	-	0.000	0.000	0.000	0.001	0.000	0.001	0.001	0.000	0.234	0.183	0.000
23	Large mesopelagics	0.003	-	-	-	0.004	0.003	0.007	0.018	0.009	0.018	0.017	0.005	0.060	0.001	0.005
24	Leatherback turtle	**1.000**	-	-	-	**0.959**	**1.000**	**0.534**	0.042	0.005	0.018	0.039	0.005	0.001	0.021	0.005
25	Other turtles	**1.000**	-	-	-	**0.959**	**1.000**	**0.534**	0.042	0.005	0.018	0.039	0.005	0.001	0.021	0.005
26	Small squids	0.003	-	-	-	0.005	0.003	0.008	0.005	0.004	0.005	0.005	0.104	0.447	0.431	0.101
27	Large squids	-	-	-	-	0.013	-	-	0.000	0.001	0.000	0.000	0.000	0.020	0.000	0.000
28	Small zooplankton	-	-	-	-	-	-	0.000	0.000	0.000	0.000	0.000	0.001	0.007	0.007	0.001
29	Large zooplankton	0.000	-	-	-	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.010	0.364	0.391	0.010
30	Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 11. Predator overlap index in the LAPE Ecopath model (continued).

Group	Group name	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	Seabirds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Baleen whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Deep-diving whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Killer whales	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Shallow-diving	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Swordfish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Billfishes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Yellowfin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Skipjack	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	Albacore	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Bigeye	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Blackfin tuna	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Other offshore predators	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	Mackerels	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	Wahoo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	Dolphinfish	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	Pelagic sharks	0.000	1.000	-	-	-	-	-	-	-	-	-	-	-	-	-
18	Flyingfish	0.311	0.000	1.000	-	-	-	-	-	-	-	-	-	-	-	-
19	Coastal predators	0.045	0.015	**0.667**	1.000	-	-	-	-	-	-	-	-	-	-	-
20	Small offshore pelagics	0.001	0.000	0.106	0.070	1.000	-	-	-	-	-	-	-	-	-	-
21	Small coastal pelagics	0.000	0.000	**0.547**	0.380	0.036	1.000	-	-	-	-	-	-	-	-	-
22	Small mesopelagics	0.000	0.000	0.296	0.119	**0.651**	0.021	1.000	-	-	-	-	-	-	-	-
23	Large mesopelagics	0.000	0.003	0.372	0.148	0.252	0.007	**0.706**	1.000	-	-	-	-	-	-	-
24	Leatherback turtle	0.000	**1.000**	0.000	0.015	0.000	0.000	0.000	0.003	1.000	-	-	-	-	-	-
25	Other turtles	0.000	**1.000**	0.000	0.015	0.000	0.000	0.000	0.003	**1.000**	1.000	-	-	-	-	-
26	Small squids	0.004	0.003	0.343	0.241	0.138	0.103	**0.735**	0.474	0.003	0.003	1.000	-	-	-	-
27	Large squids	0.000	0.000	0.417	0.156	0.091	0.011	0.272	0.460	-	-	0.245	1.000	-	-	-
28	Small zooplankton	0.000	-	0.007	0.005	0.376	0.042	0.171	0.007	-	-	0.015	0.003	1.000	-	-
29	Large zooplankton	0.001	0.000	0.063	0.056	0.038	0.007	**0.514**	0.149	0.000	0.000	**0.763**	0.072	0.014	1.000	-
30	Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	**0.565**	0.000	1.000

The electivity index (Table 12) shows seabirds, blackfin tuna, mackerels, wahoo, dolphinfish, coastal predators, large mesopelagics and large squid all having a high preference (electivity index > 0.5) for flyingfish. Predators showing high preference for small coastal pelagics include seabirds, baleean whales, shallow-diving small cetaceans, swordfish, albacore and coastal predators. Bigeye tuna show a high preference for dolphinfish and cannibalism plays an important role in dolphinfish diet. Apart from killer whales which show a high preference for shallow-diving small cetaceans, no other group in the LAPE shows a high preference for marine mammals in their diet. Generally however, marine mammals (except for baleen whales) prefer large squids. Apart from cannibalism dolphinfish show a high preference for flyingfish while flyingfish prefer small zooplankton and small offshore pelagics and small coastal pelagics prefer small zooplankton.

The omnivory index (Figure 19) shows pelagic sharks as having the greatest variation (across trophic levels) in the diet while groups such as leatherback turtles, small mesopelagics, small squids and flyingfish are more specialized, feeding across a small range of trophic levels. The mixed trophic impact (Figure 20) depicts how an increase in biomass in one group is likely to impact the biomass of others. Flyingfish are positively impacted (i.e. increase in biomass) by increasing biomass of small zooplankton (their main prey), but are negatively impacted by increasing biomass of large zooplankton. The impact of increasing dolphinfish on flyingfish abundance is negative but too small to be shown on the graph. Small coastal pelagics are severely negatively impacted by coastal predators (as expected since these are their main predators) and positively impacted by small zooplankton. Marine mammals are little impacted by commercial fish groups (the magnitude being too small to depict on the graph). The only negative impact of marine mammals is associated specifically with increasing abundance of baleen whales on the biomass of mackerels, although baleen whales also have a positive impact on blackfin tuna and coastal predators. It is interesting to note that most positive impacts on commercial groups are due to increasing biomass of small offshore pelagics, mesopelagics, squids and zooplankton.

Table 12 Electivity index of functional groups in the LAPE Ecopath model

Group	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Seabirds															
2	Baleen whales															
3	Deep-diving whales															
4	Killer whales															
5	Shallow-diving cetaceans				0.797	-0.899										
6	Swordfish															
7	Billfishes									-0.267			0.962			
8	Yellowfin						0.536	0.215		0.721		0.793				
9	Skipjack						0.212	0.885	0.953	0.504		0.575				
10	Albacore						0.314	-0.044	0.478	0.549		0.649				
11	Bigeye						0.882	0.905	0.166	0.854						
12	Blackfin tuna						0.329	-0.028	0.491	0.561		0.659			0.806	
13	Other offshore predators		0.915				-0.886	-0.042	0.162	0.152		-0.760			0.089	0.969
14	Mackerels		0.856				-0.264	-0.959	-0.885	-0.865		-0.826			0.235	-0.941
15	Wahoo						0.463	0.125	0.606	0.666		0.748			0.867	0.309
16	Dolphinfish						-0.218	0.128	-0.371	-0.807		0.554				
17	Pelagic sharks				0.232											
18	Flyingfish	0.858					-0.856	-0.734	-0.824	-0.525		0.434	0.771		0.697	0.548
19	Coastal predators	-0.786					-0.613	-0.968	-0.908	-0.918	-0.937	-0.996	0.362	-0.996	0.518	-0.738
20	Small offshore pelagics	0.097	-0.219	-0.972	-0.741	-0.499		-0.597	-0.907	-0.997	0.703	-0.799	-0.327	-0.138	-0.521	-0.129
21	Small coastal pelagics	0.871	0.732	-0.747	0.124	0.509	0.677	-0.601	-0.902	-0.997	0.702	-0.796	-0.355		-0.567	-0.156
22	Small mesopelagics		-0.262	-0.880	-0.552	-0.761	-0.953	-1.000	-0.995	-0.950	-0.047	-0.949				-0.996
23	Large mesopelagics			-0.793	-0.484	-0.719	-0.817	-0.972	-0.946	-0.889	0.756	-0.793	-0.813			-0.325
24	Leatherback turtle															
25	Other turtles															
26	Small squids	0.871		-0.424	0.384	0.465	0.277	-0.873	-0.686	-0.719	0.752	-0.934	0.281	0.998	0.430	0.408
27	Large squids			0.998	0.954	0.984	0.083	-0.994	-0.918		0.820					-0.334
28	Small zooplankton	-0.991							-1.000	-1.000			-0.830	-0.694	-0.834	-0.997
29	Large zooplankton	-0.955	0.242				-0.968	-1.000	-0.968	-0.985	-0.406	-0.977			-0.767	

Table 12. Electivity index of functional groups in the LAPE Ecopath model (continued).

Group	Prey \ Predator	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	Seabirds		0.298												
2	Baleen whales														
3	Deep-diving whales														
4	Killer whales														
5	Shallow-diving cetaceans		-0.020												
6	Swordfish		0.865												
7	Billfishes	-0.287	0.576												
8	Yellowfin		-0.306												
9	Skipjack	-0.797	-0.777												
10	Albacore		-0.732												
11	Bigeye		-0.041												
12	Blackfin tuna	-0.030	-0.724												
13	Other offshore predators	-0.853	-0.976		-0.746				-0.814			-0.090			
14	Mackerels	-0.920	-0.711		-0.660							-0.266			
15	Wahoo	0.456	-0.645												
16	Dolphinfish	0.976	-0.921												
17	Pelagic sharks		0.682												
18	Flyingfish	0.608	-0.998		0.844				0.620				0.741		
19	Coastal predators	-0.807	-0.663		0.111				-0.520			-0.890	-0.364		
20	Small offshore pelagics	-0.994	-0.977	0.678				0.770	0.220						-0.251
21	Small coastal pelagics	-0.994	-0.977	0.346	0.952			-0.397	-0.845						-0.266
22	Small mesopelagics	-1.000	-0.997		-0.934			0.774	0.849			0.747	-0.549		
23	Large mesopelagics	-0.999	-0.954						0.199				-0.480		
24	Leatherback turtle		0.657												
25	Other turtles		0.549												
26	Small squids	-0.866	-0.537		0.415				0.825			0.914	0.316		
27	Large squids								0.701				0.973		
28	Small zooplankton	-0.998		0.982	-0.463	0.994	0.994	0.952	-0.439	-0.789	0.705	-0.190		0.155	0.997
29	Large zooplankton	-0.979	-1.000		-0.871	-0.589	-0.589		0.141	1.000	0.987	0.866	-0.434		

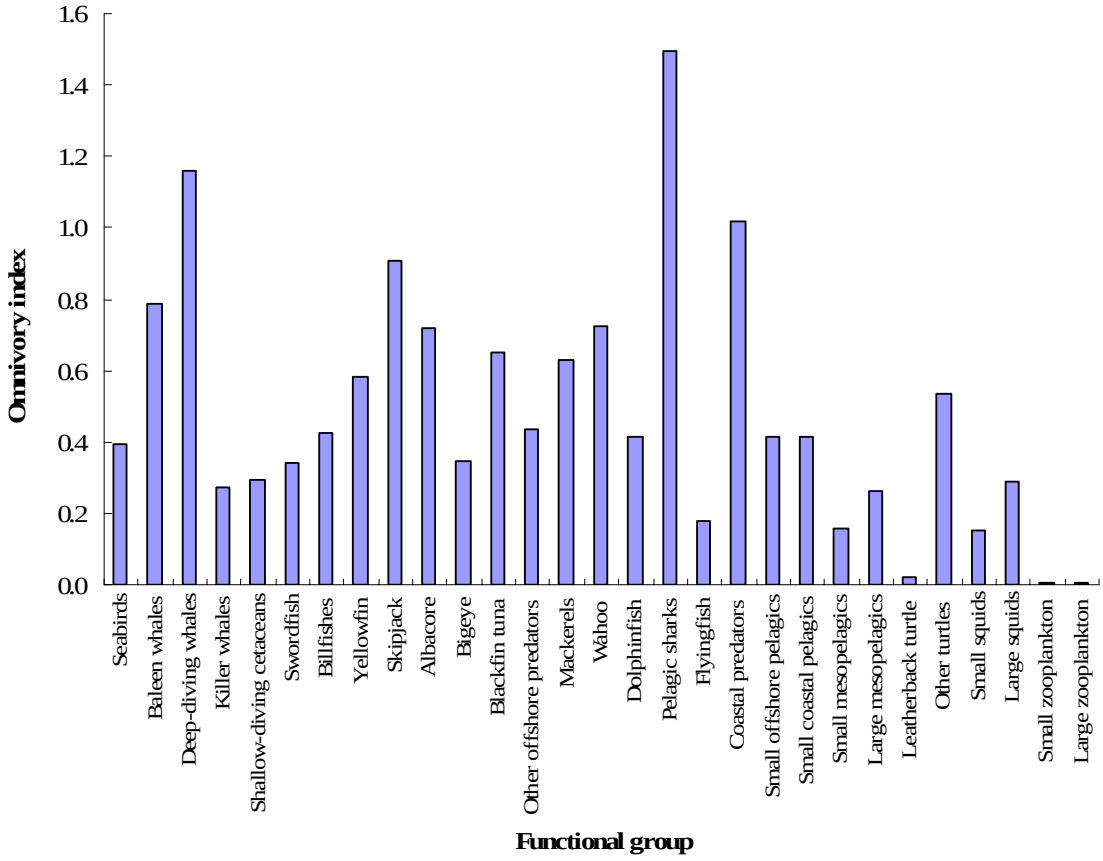

Figure 19 Omnivory index for functional groups in the LAPE Ecopath model.

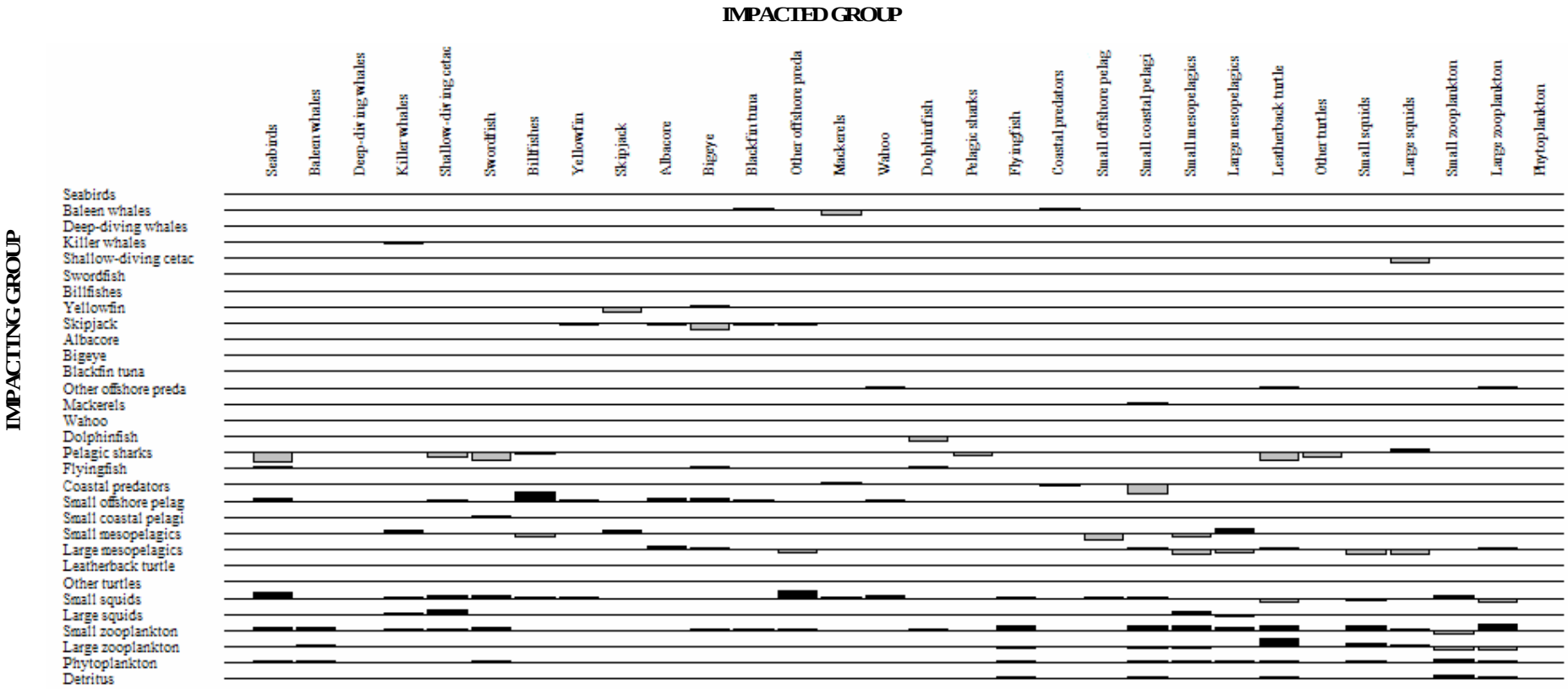

Figure 20 Mixed trophic impact of functional groups in the LAPE (black bars indicate a positive impact of increasing species abundance on the y-axis and grey bars indicate a negative impact). The impacts are percentage changes which are relative and therefore com parable between groups.

MODEL SENSITIVITY

Ecopath produces a test of sensitivity of estimated or missing basic parameters in the model to variation in input parameters (± 50%). Input parameters are each varied separately and the output is given as the difference between the new estimated parameter (Pn) and original parameter (Po) represented as a fraction of the original parameter ((Pn – Po)/Po).

In the LAPE model the sensitivity of estimates of small coastal pelagic (SCP) biomass and flyingfish (FF) biomass to changes in input parameters was investigated. Small coastal pelagic biomass is sensitive to changes in input biomass of mackerels, large mesopelagic fish, large squid and dolphinfish (Figure 21 top), however, there is greatest sensitivity to changes in dolphinfish biomass. Changes in the Q/B of mackerels, large mesopelagic fish, large squid, dolphinfish and coastal predators impact on the estimates of small coastal pelagic biomass (Figure 21 middle). Greatest sensitivity is shown for changes in Q/B of coastal predators, this group exerting highest consumption on SCP, while mackerels and large mesopelagics also show high impact on SCP biomass, though to a lesser in comparison to coastal predators. As well, changes in P/B of coastal predators also show high impact on SCP biomass (Figure 21 bottom), this understandably so given the high predation pressure exerted by coastal predators on SCP.

Flyingfish biomass is sensitive to changes in biomass of mackerels, large mesopelagic fish, large squid and dolphinfish (Figure 22 top). Greatest sensitivity to changes in dolphinfish and large mesopelagic biomass is observed. As well, FF biomass is sensitive to changes in Q/B of mackerels, large mesopelagic fish, large squid, dolphinfish and coastal predators (Figure 22 middle). However, changes in mackerel, large mesopelagic fish and dolphinfish Q/B exert the greatest impacts. Like SCP, biomass of FF is highly sensitive to changes in P/B of coastal predators (Figure 22 bottom).

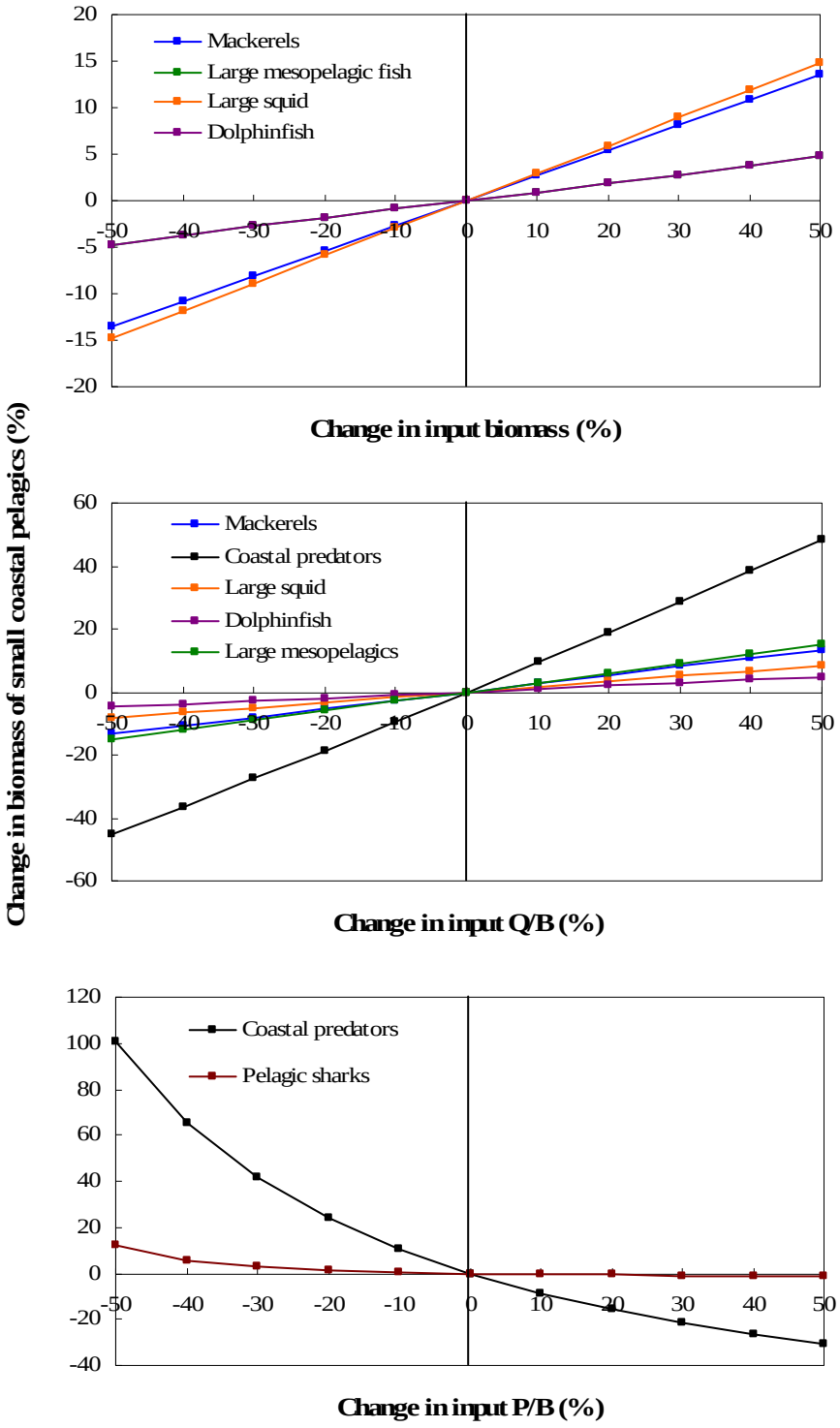

Figure 21 Sensitivity of small coastal pelagic biomass to changes in Ecopath input parameters.

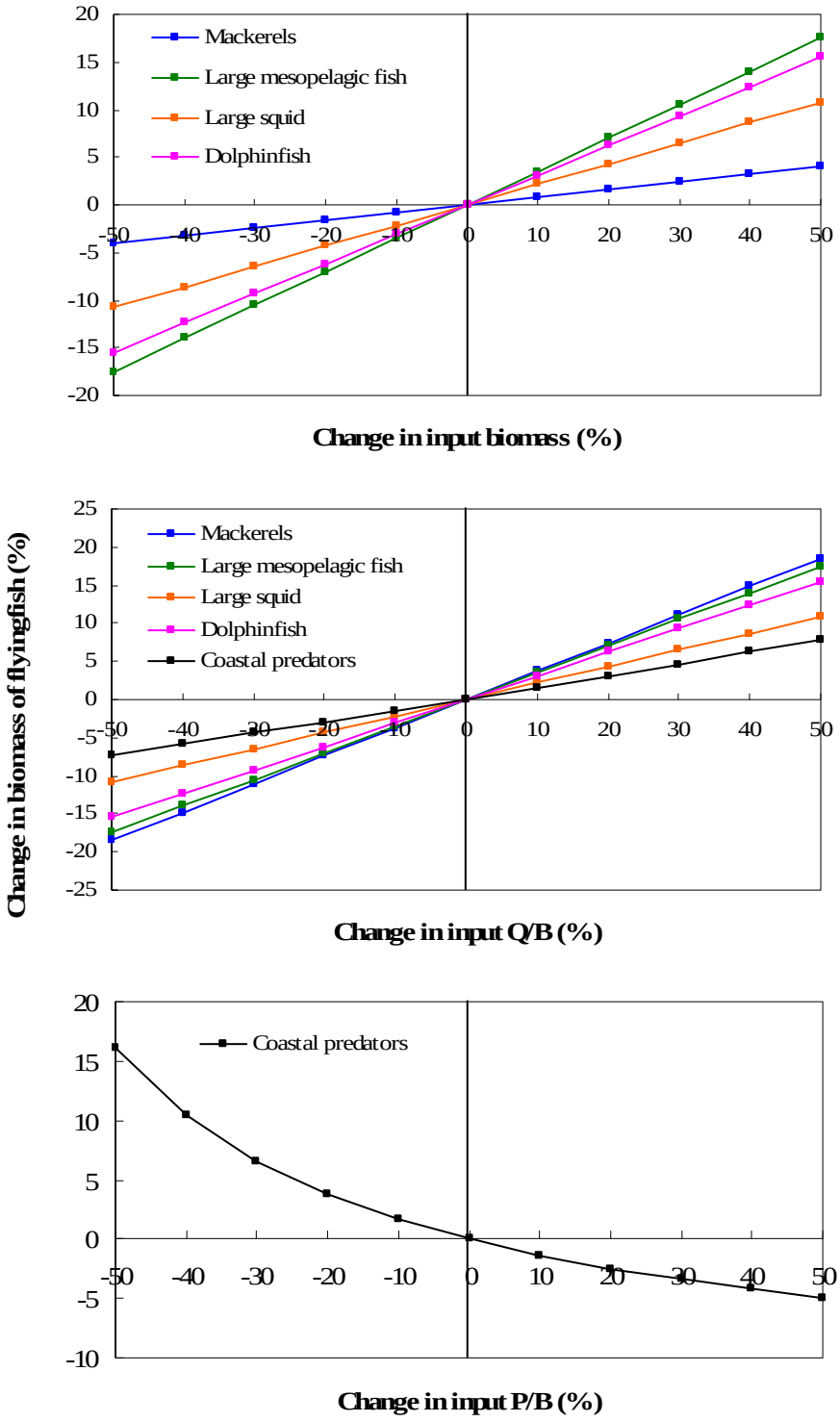

Figure 22 Sensitivity of flyingfish biomass to changes in Ecopath input parameters.

ECORANGER

The current balanced version of the LAPE model is but one of many possible representations of the flows in the system which adheres to physiological and thermodynamic constraints. The Ecoranger module allows consideration of the uncertainty in Ecopath input parameters (a statistical-based approach) in arriving at a suitable mass-balanced model (Christensen *et al*., 2000). A range of values for all basic input parameters is specified and the user selects the appropriate frequency distribution for each parameter type. Input variables are selected at random from the specified frequency distribution and the resulting model is evaluated based on a user-specified criteria (e.g., least sum of squared residuals) as well as physiological and mass-balance constraints. The process is repeated in a Monte-Carlo approach and the best fitting model is selected based on a least square criterion. The module outputs include a histogram with the range of parameter distributions for each group considered plausible according to the specified criteria.

The Ecoranger module is usually executed with the initial Ecopath input parameters and specified ranges. In this instance however, the mass-balanced LAPE model is used simply to demonstrate the utility of the Ecoranger module. A maximum of 10 000 runs was specified and the pedigree input used to define the input parameter range. A normal distribution was assumed for biomass, P/B and Q/B inputs and a uniform distribution for EE and diet compositions. The sampling/resampling component of the module was selected. Histograms specifying the range of plausible input parameters for small coastal pelagics and flyingfish are presented in Figure 23 and Figure 24 respectively. Plausible biomass estimates range between 0.195 and 0.294 $t \cdot km^{-2}$, while P/B ranges between 2.8 and 4.2 $year^{-1}$ and Q/B ranges between 11.7 and 17.6 $year^{-1}$ for small coastal pelagics. The resulting EE ranges between 0.102 and 0.927. The red line in each panel represents the initial input estimate. Similarly, plausible biomass estimates for flyingfish range between 0.1 and 0.217 $t \cdot km^{-2}$, while P/B ranges between 3.2 and 4.8 $year^{-1}$ and Q/B ranges between 19.8 and 29.7 $year^{-1}$. The resulting EE ranges between 0.878 and 0.967.

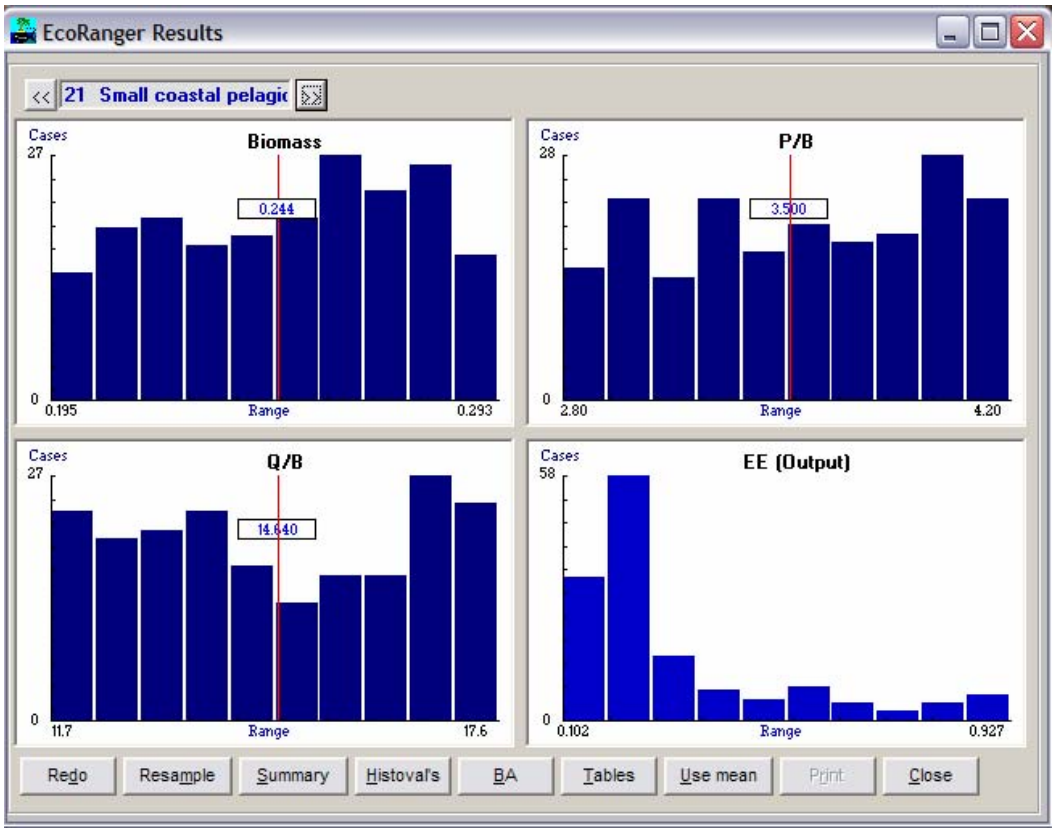

Figure 23 Paremeter distributions for small coastal pelagics in all accepted Ecoranger runs. (Red line depicts the baseline or current balanced model estimate)

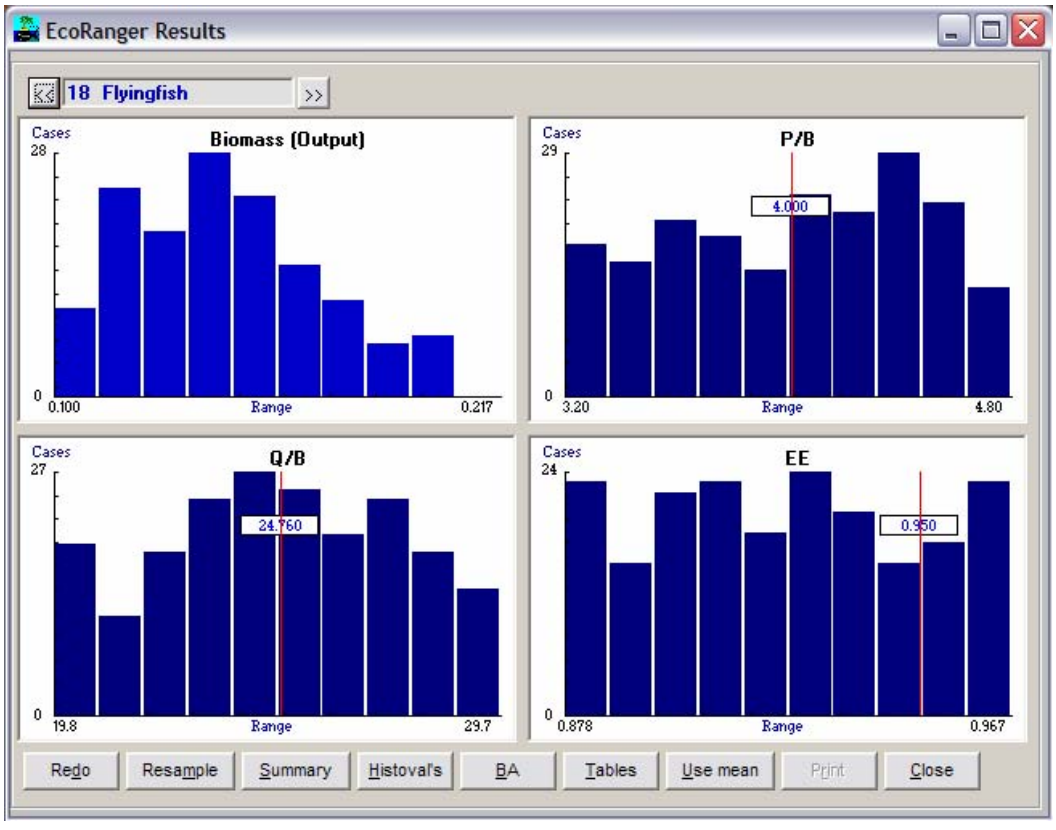

Figure 24 Paremeter distributions for flyingfish in all accepted Ecoranger runs. (Red line depicts the baseline or current balanced model estimate)

COMPARISON OF THE LAPE WITH THE CENTRAL ATLANTIC SYSTEM

A comparison of Ecopath output parameters (system statistics) for the LAPE with that of the central Atlantic in the 1990s (Vasconcellos and Watson, 2004) is given in Table 13. As expected, the flows within the LAPE are smaller than those in the central Atlantic. This difference in due to the fact that many of the large, highly migratory species are not confined to the LAPE. Mean trophic level of the LAPE catch is smaller than that for the Central Atlantic (4.15 compared to 4.26) primarily because catches of top predatory fish within the LAPE are considerably lower than those for the central Atlantic. The extremely low gross efficiency (the ratio of catch to net primary production) in both cases is characteristic of fisheries targeting top predators. High ratios are characteristic of fisheries which target functional groups that are low in the food web, such as upwelling systems, while high ratios either represent under exploited fish stocks or fisheries targeting apex predators (Christensen and Pauly, 1993b). A weighted average of 0.0002 is estimated for most fisheries of the world (Mackinson *et al*., 2005).

The ratios of primary production to respiration (PP/R) and primary production to biomass (PP/B) reflect the maturity and development of an ecosystem (Odum, 1971). During the developmental stages of an ecosystem PP/R is usually greater than one, but approaches one in mature systems and is less than one in systems subject to organic pollution (Mackinson *et al*., 2005). Mature systems show a low PP/B due to the accumulation of biomass over time.

Table 13 Comparison of system statistics between the LAPE model and the Central Atlantic model of Vasconcellos and Watson (2004).

Parameter	LAPE	Central Atlantic	Units
Sum of all consumption	2911.813	6339.418	t/km²/year
Sum of all exports	449.094	99.1829	t/km²/year
Sum of all respiratory flows	1005.073	2965.062	t/km²/year
Sum of all flows into detritus	1599.814	2907.314	t/km²/year
Total system throughput	5966	12311	t/km²/year
Sum of all production	2221	5069	t/km²/year
Mean trophic level of the catch	4.15	4.26	
Gross efficiency (catch/net p.p.)	0.000042	0.000003	
Calculated total net primary production	1369.6	2964.245	t/km²/year
Total primary production/total respiration	1.363	0.9997	
Net system production	364.527	-0.8171	t/km²/year
Total primary production/total biomass	12.212	18.8159	
Total biomass/total throughput	0.019	0.0128	
Total biomass (excluding detritus)	112.154	157.5398	t/km²
Total catches	0.058	0.0098	t/km²/year
Connectance Index	0.293	0.1702	
System Omnivory Index	0.413	0.244	

ECOSIM PARAMETERIZATION

Ecosim facilitates dynamic simulation, at the ecosystem level, of the impacts of changing fishing mortality and to a lesser extent, changing environmental conditions, on the biomass, yield and associated value of functional groups defined in the system. It uses the initial base parameters from the Ecopath model (Christensen *et al*., 2000). The impacts of fishing (mortality) and predation on the biomass of the respective groups in the ecosystem is expressed using a system of differential equations:

$$dB_i/dt = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i) B_i$$

Where the left side gives the growth rate of group i in terms of its biomass, gi is growth efficiency, F_i is fishing mortality rate, e_i is emigration rate, I_i is immigration rate, and the C_{ij} are consumption rates of type i biomass by type j organisms. The C_{ij} are calculated by assuming that

a) the B_i are divided into vulnerable and invulnerable components (Walters *et al*., 1997), and it is the transfer rate (v_{ij}) between these two components (adjustable by the user) which determines if control is top-down (i.e., Lotka-Volterra), bottom-up (i.e., donor-driven), or intermediate (see below);

b) in case of split pools (juveniles vs. adults of the same species), account is kept of the numbers that recruits from the juvenile to the adult stages (using the Deriso-Schnute delay-difference model, which allow the inclusion of stock-recruitment relationships (not discussed here) as part of the Ecosim outputs.

These assumptions lead to the rate equation:

$$C_{ij} = (v_{ij} a_{ij} B_i B_j)/(v_{ij} + v'_{ij} + a_{ij} B_j)$$

Where

C_{ij} is the trophic flow between prey (i) and predator (j) pools

B_i and B_j are the prey and predator biomasses respectively

a_{ij} is the rate of effective search for prey I by predator j and

v_{ij} and v'_{ij} are prey vulnerability parameters, default setting of $v_{ij} = v'_{ij}$

Flow control

Ecosim predictions are most sensitive to the flow control parameter (vulnerability, 'v'). The parameter expresses the exchange rate between vulnerable and non-vulnerable states of prey (Christensen *et al*., 2000). Three independent methods are available in EWE for estimation of vulnerability parameters: searching for vulnerability parameters using a given exploitation rate to enable movement from one model state to another model state, each state representing a different time period; seeking the evolutionary optimum between spending more time feeding and therefore growing at a faster rate with the tradeoff of a higher mortality risk and fitting model predictions to time

series data as a means of identifying vulnerability parameters associated with the best goodness of fit measure At this time it is not possible to explore these options for estimating vulnerability for groups in the LAPE and therefore policy exploration is conducted for a range of flow control parameters.

Time series fitting

Similar to single species stock assessment Ecosim also relies on the fitting of predicted trends to observed time series data by varying input parameters (total mortality, vulnerability, feeding time adjustment rates) as a means of validation. The inclusion of time series data in Ecopath with Ecosim facilitates the use of the software for examining policy options for ecosystem-based management of fisheries (Christensen *et al*., 2000). Fishing effort or fishing mortality is the driving factor for this process and a statistical measure of goodness of fit is generated. This process is intended to demonstrate the ability of the model to replicate known historical trends and in so doing increases confidence in the use of the model for policy exploration.

Currently the LAPE model has not yet been validated since the time period over which it applies is quite recent (average between 2001 and 2005). There exists however, information on biomass of large, highly migratory species from ICCAT assessments as well as estimates of catch per unit of effort estimates for dolphinfish (Oxenford and Hunte, 1986: 1961-1982); the four-winged flyingfish (Parker *et al*., 2001: 1960 – 2001) and wahoo (Parker *et al*., 2005: 1994 – 2003) which, if updated annually, could be used to validate the model in future. As a result of non-validation of the LAPE model, the reader is cautioned with respect to interpretation of results from policy exploration conducted on the model in its current state. Policy exploration demonstrated in this document, is intended to demonstrate the potential utility of Ecopath with Ecosim by highlighting a few of the range of possible applications.

In the absence of time series fitting the general approach was to evaluate the model behaviour when the system is made to deviate from the Ecopath equilibrium state, as was done with the model of the West Florida Shelf (Mackinson *et al*., 2005). By adding behaviour to predator and prey, related to feeding time adjustments and vulnerability, four common causes of model instability can be eliminated: (1) predator-prey cycles and related multi-trophic level patterns; (2) system simplification (loss of biomass pools due to competition/predation effects); (3) stock-recruitment instabilities (cyclic or erratic changes in recruitment and stock size for split pool groups); (4) numerical 'chatter' in time solutions (mainly in Ecospace), (Christensen *et al*., 2000).

In the LAPE model the first two sources of instability are applicable. These were addressed in policy exploration by presentation of outcomes for a range of vulnerability settings. Although vulnerability of each prey group to each of its specific predators could be individually set, in the analyses presented in this report the changes were applied homogeneously (i.e. equally across all groups). The feeding time adjustment rate of seabirds and marine mammals was set at

0.5 (the default); at 0.1 for top predators (as these are subject to low predation risks and are therefore less likely to adjust feeding time); at 1.0 for flyingfish, coastal predators, small offshore pelagics, small coastal pelagics, mesopelagics, turtles and squids as these are major prey groups i.e. subject to high predation risks, requiring fast responses in feeding time when food availability changes; at 0 for zooplankton groups as these demonstrate no control in behaviour, their distribution being subject to the prevailing ocean currents and eddies.

Model sensitivity

Analysis of model instability is based on the suggestions of Christensen *et al* (2000).

A small disturbance in fishing effort

A small change was made in fishing effort of combined gears and the system response was evaluated. Responses varied depending on the input estimate of flow control (vulnerability). Bottom-up control (v = 1) resulted in the least disturbance, with the system returning to its original state in the shortest time; within 5 years (Figure 25). Mixed control (v = 2) resulted in slightly greater disturbance than the previous scenario with the system returning to its original state in 10 years (Figure 26). Greatest instability was observed with top-down control (v = 4), the system did not return to its original state and bigeye tuna were the first to go extinct (Figure 27).

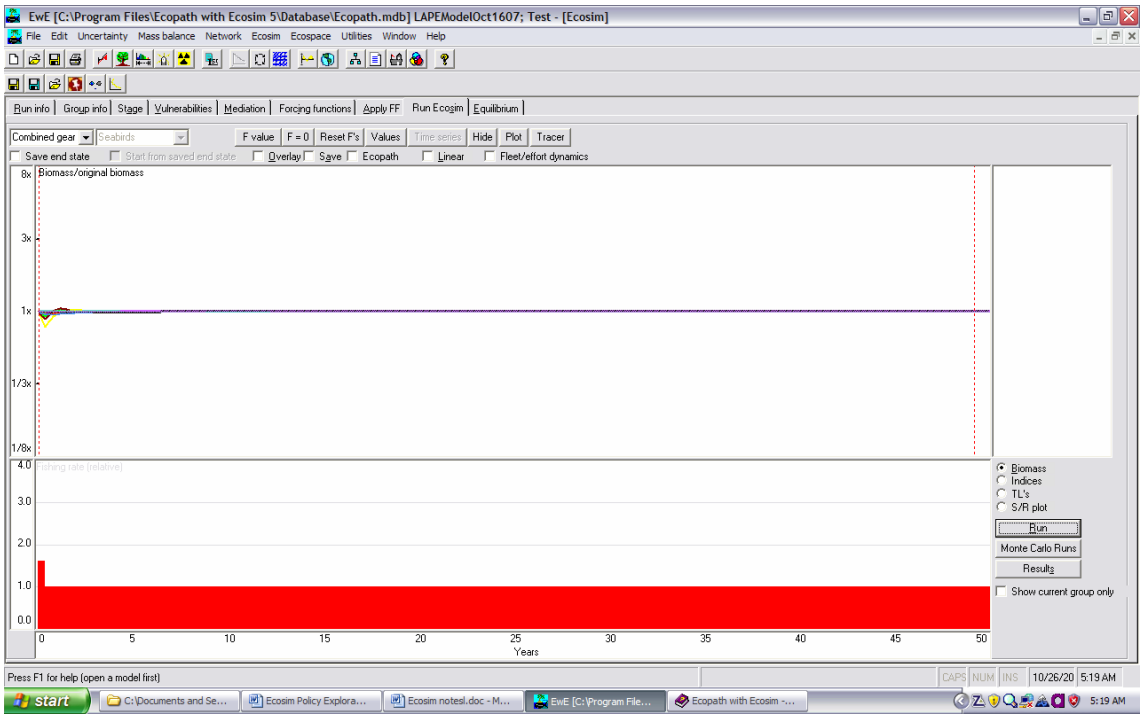

Figure 25 Small disturbance in fishing rate of the combined fleet at v = 1 (bottom-up control).

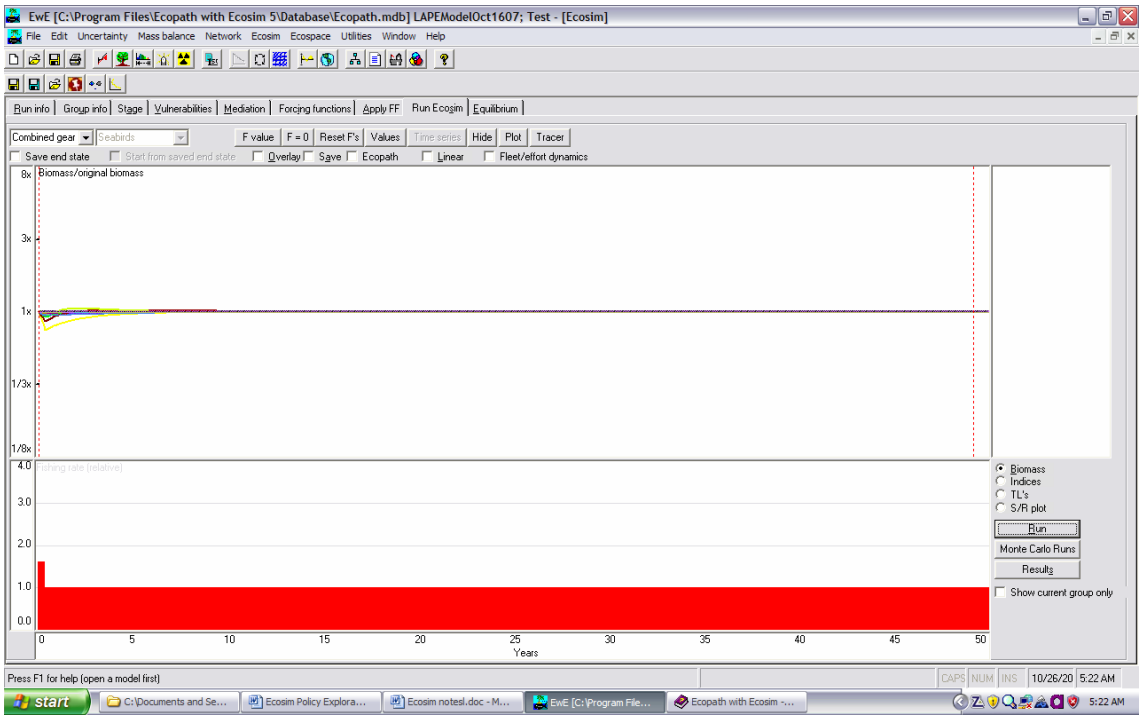

Figure 26 Small disturbance in fishing rate of the combined fleet at v = 2 (mixed control)

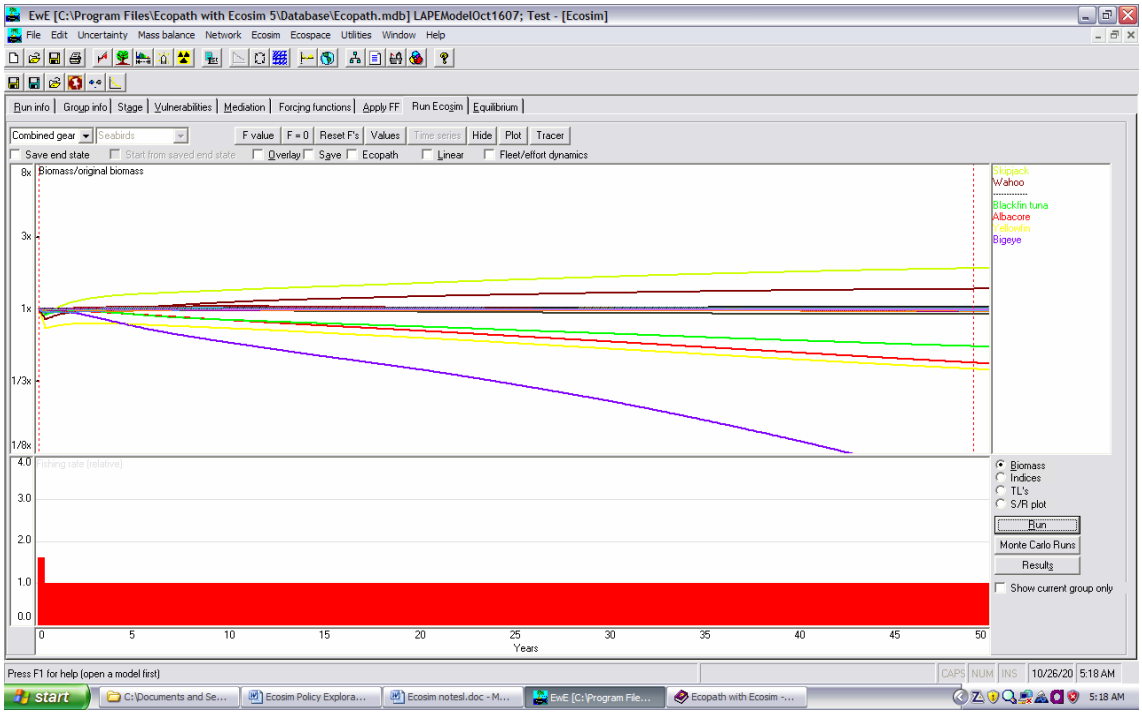

Figure 27 Small disturbance in fishing rate of the combined fleet at v = 4 (top-down control)

Fishery closure

Closure of all fisheries between the 5th and 15th year resulted in increases in the biomass of yellowfin tuna and pelagic sharks at v = 1 (Figure 28). These species are subject to high fishing mortality in the LAPE (1.395 and 0.245 year^{-1}

respectively), although F of wahoo, blackfin tuna and bigeye tuna exceed that of pelagic sharks. Under the assumption of mixed trophic control the biomass of yellowfin increases substantially, (Figure 29), while top-down control resulted in system instability (Figure 30).

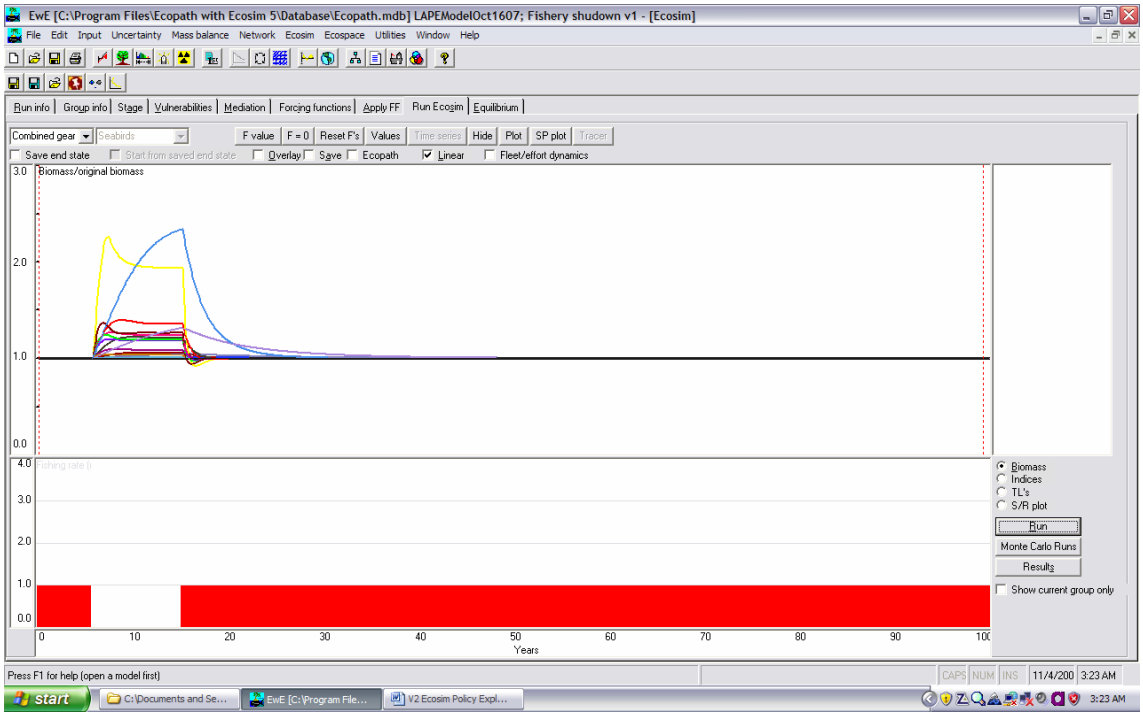

Figure 28 Closure of fishery (combined gear) with responses for v = 1 (yellow line: yellowfin; blue line: pelagic sharks; red line; albacore).

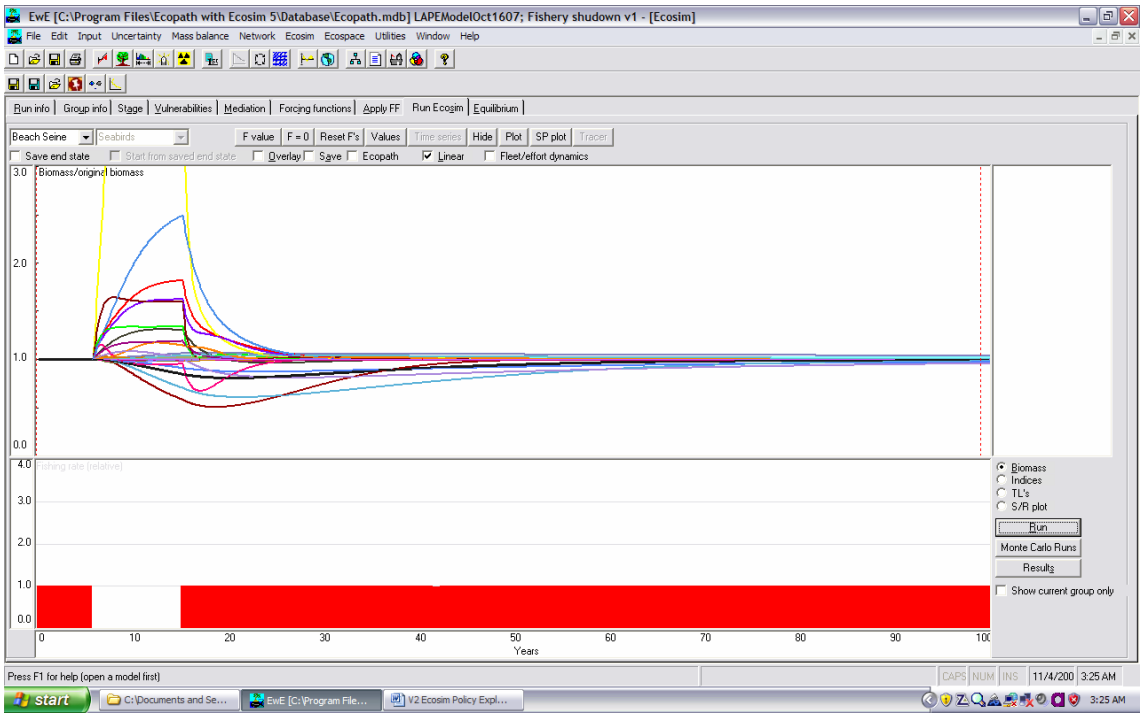

Figure 29 Closure of fishery (combined gear) with responses for v = 2 (yellow line: yellowfin; blue line: pelagic sharks; red line; albacore).

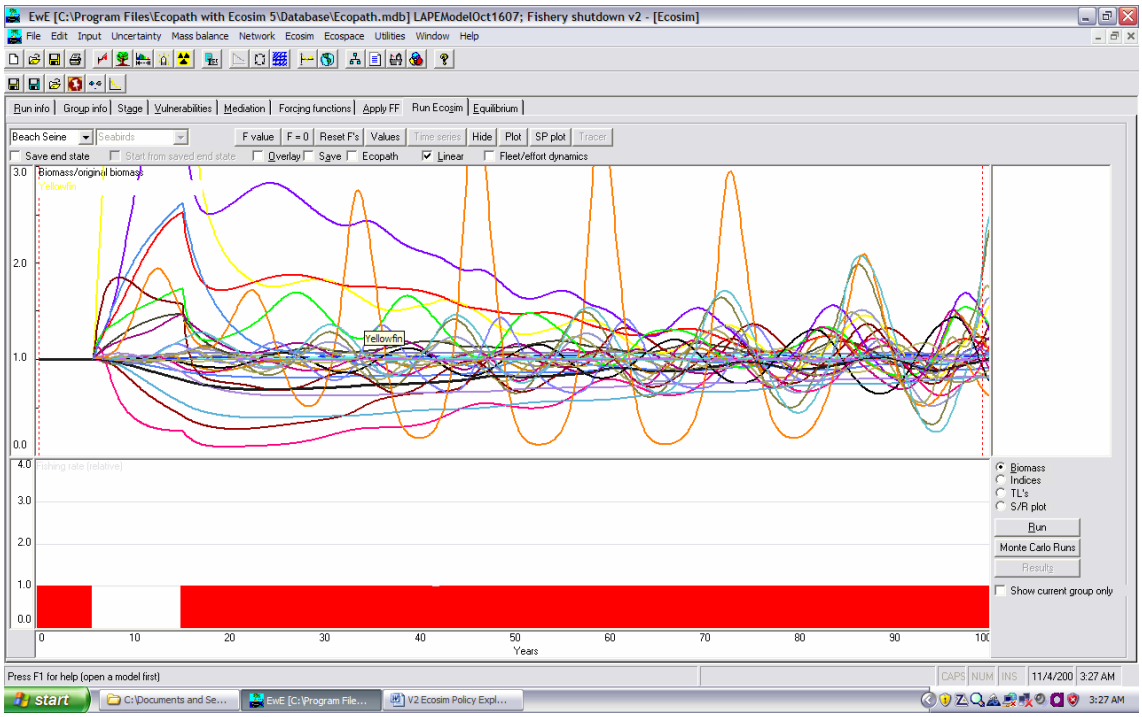

Figure 30 Closure of fishery (combined gear) with responses for v = 3.

A complete closure of all fisheries (combined gear) from year 1 at bottom-up control (v = 1) resulted in increases in biomass of yellowfin tuna and pelagic sharks i.e. groups subject to high fishing mortality previously (Figure 31). At mixed control (v = 2) the biomass of pelagic sharks, albacore and bigeye increase substantially, however there is also an explosion in yellowfin biomass (Figure 32). At top-down control, biomass explosions are observed for both yellowfin and bigeye, while biomass of swordfish and leatherback are considerably reduced and several groups, including small coastal pelagics exhibit Lotka-Volterra-like predator-prey cycles (Figure 33).

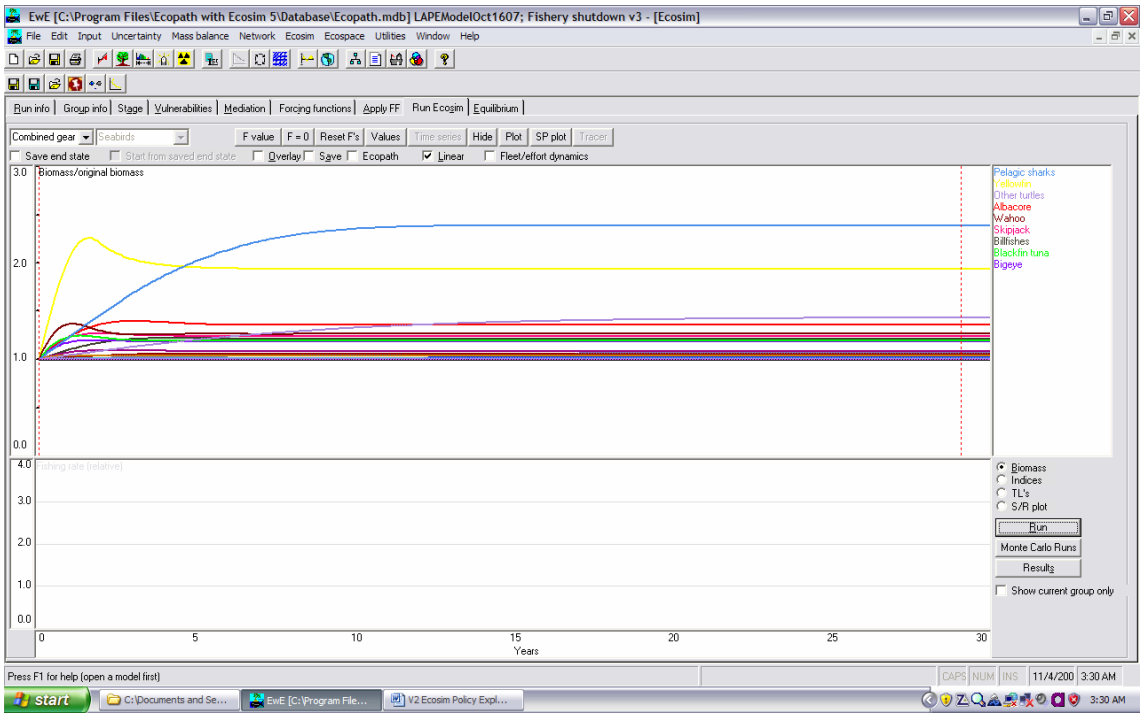

Figure 31 Complete fishery closure (combined gears) with v = 1.

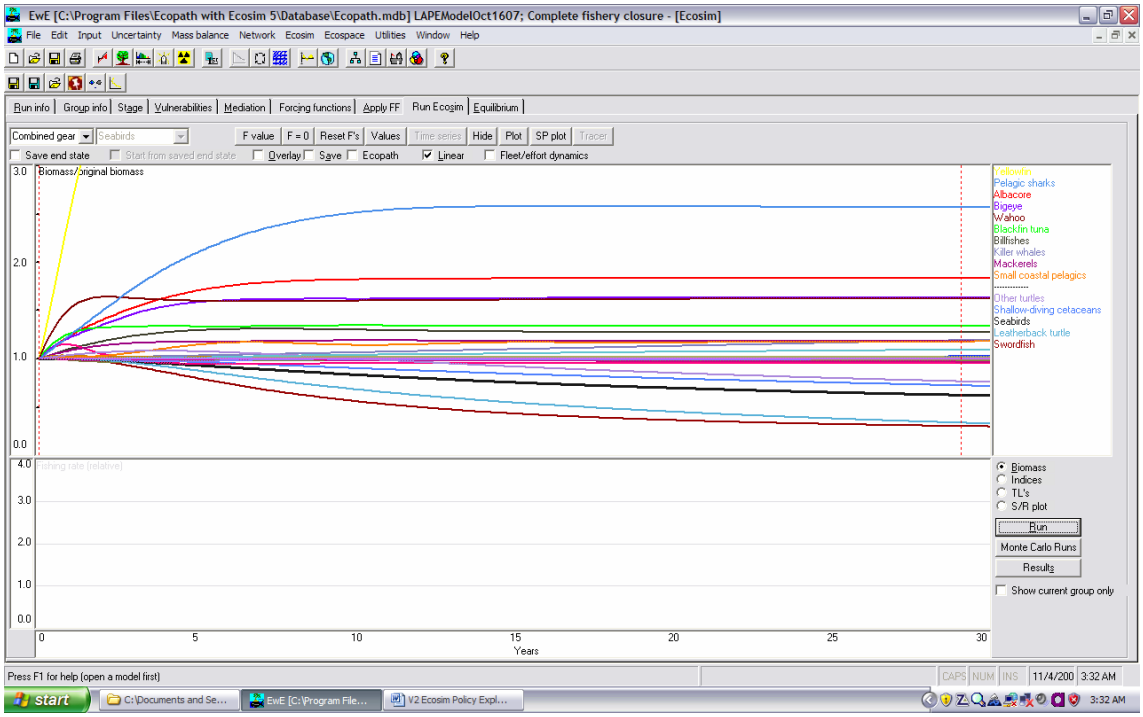

Figure 32 Complete fishery closure (combined gears) with v = 2.

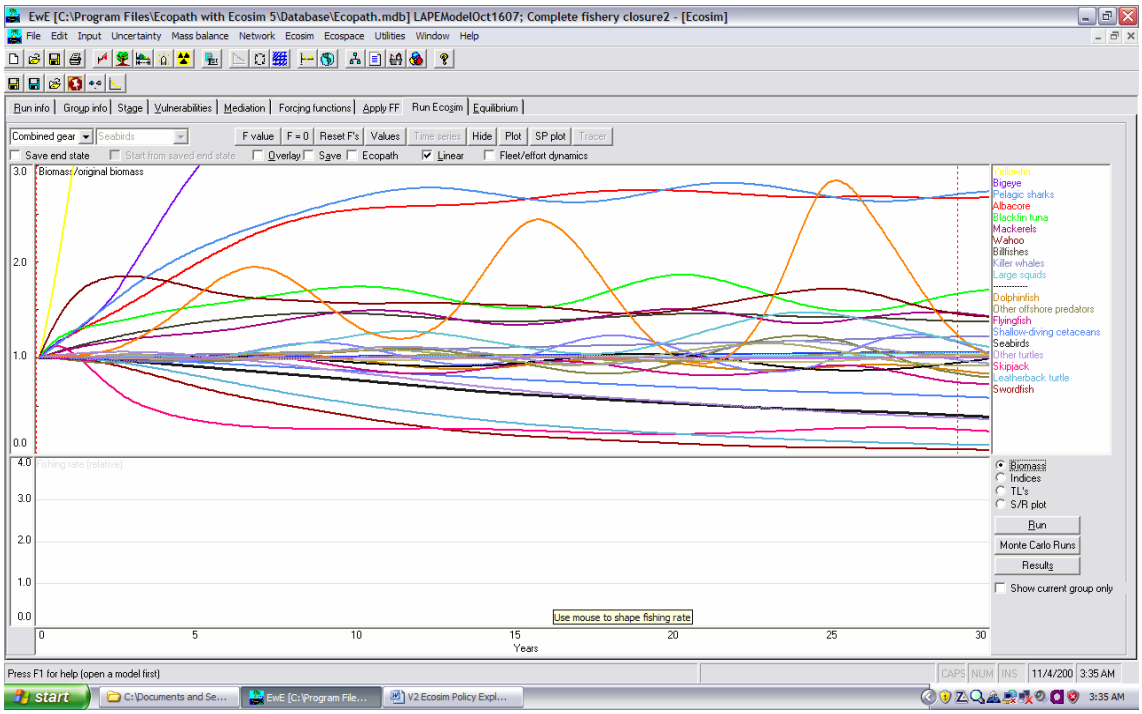

Figure 33 Complete fishery closure (combined gears) with v = 3.

Scenario 1.Impact of increasing catches of small coastal pelagics

Although this scenario was intended to examine the impacts of increasing catches of both small coastal pelagics and flyingfish (caught as bait) on the populations of other species in the system it was not possible to investigate the flyingfish component as there are no records on associated bait catches. As a result, this scenario examined the impacts of increased fishing rate on small coastal pelagics on the biomass, catch and value of associated species. The base fishing mortality of small coastal pelagics was 0.024 year^{-1}; predation mortality was 3.324 year^{-1} and other mortality 0.152 year^{-1}. There is greatest prey overlap (i.e. competition) of small coastal pelagics with flyingfish, blackfin tuna, mackerels and coastal predators. The group shares predators with flyingfish, mackerels, large mesopelagics and coastal predators.

Considerable increases in fishing rates (up to 10 times the base value) were necessary to effect an appreciable change in the biomass of small coastal pelagics (Figure 34). However, in general, marine turtles seem most adversely affected, at smaller increases in fishing rate.

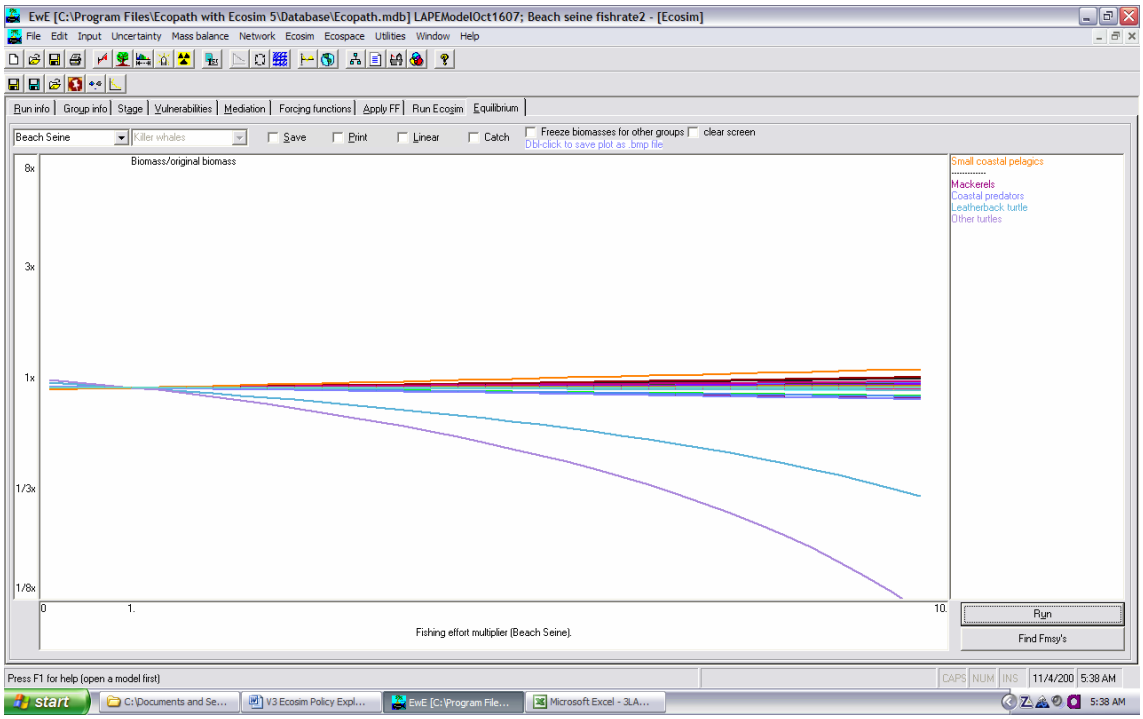

Figure 34 Equilibrium analysis; changes in beach seine effort; v = 2.

At four times the base fishing rate and v = 1, biomass of other turtles showed a decline (Figure 35). Both turtle groups were negatively impacted and small coastal pelagics (orange line) were positively impacted at v = 2 (Figure 36). A repeat of the analysis with v = 3 resulted in a dominance of the Lotka-Volterra phenomenon (Figure 37).

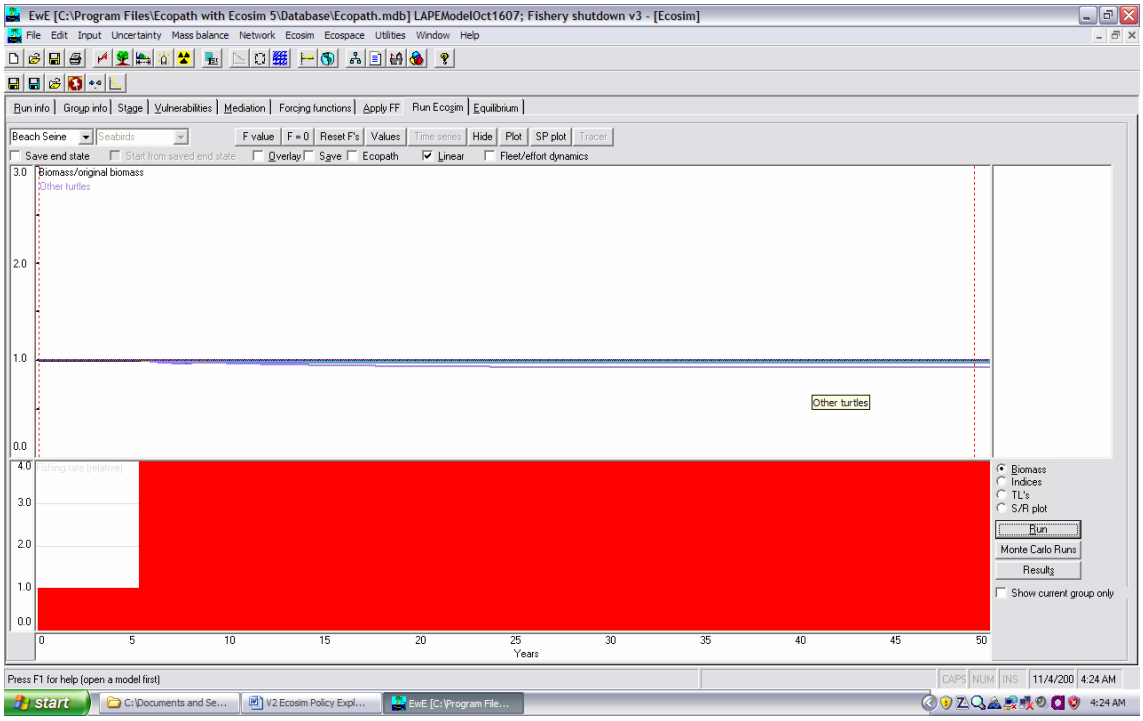

Figure 35 Fishing rate x4 base rate for beach seine fleets at v = 1.

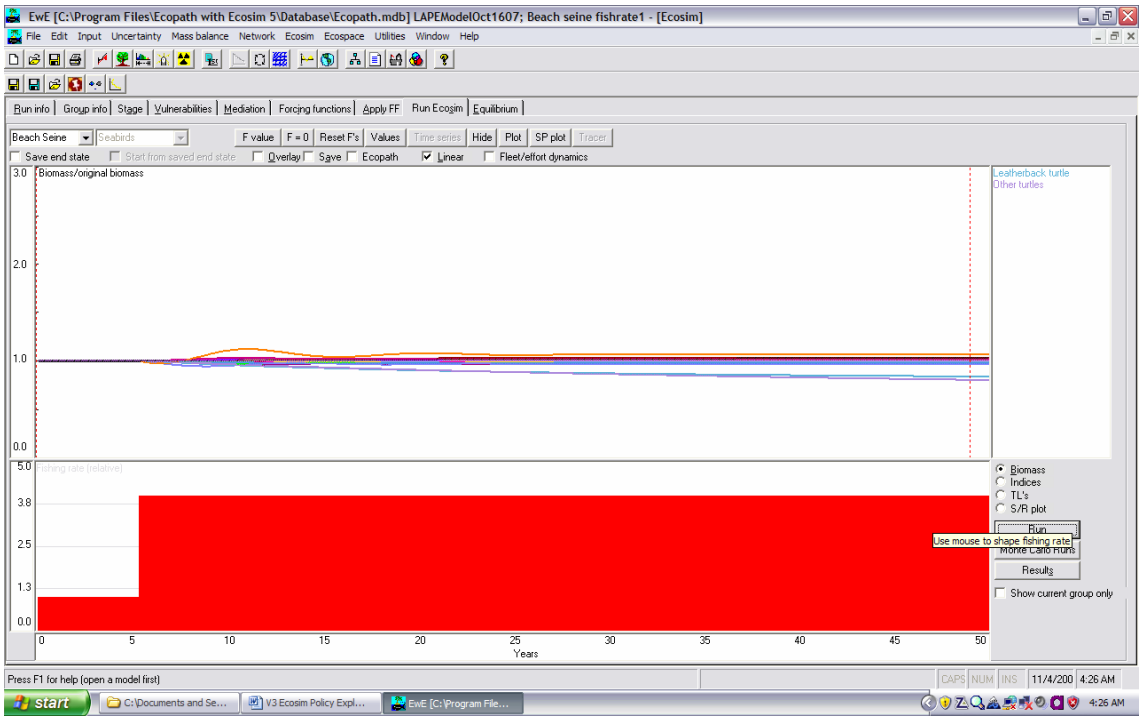

Figure 36 Fishing rate x4 base rate for beach seine fleets at v = 2.

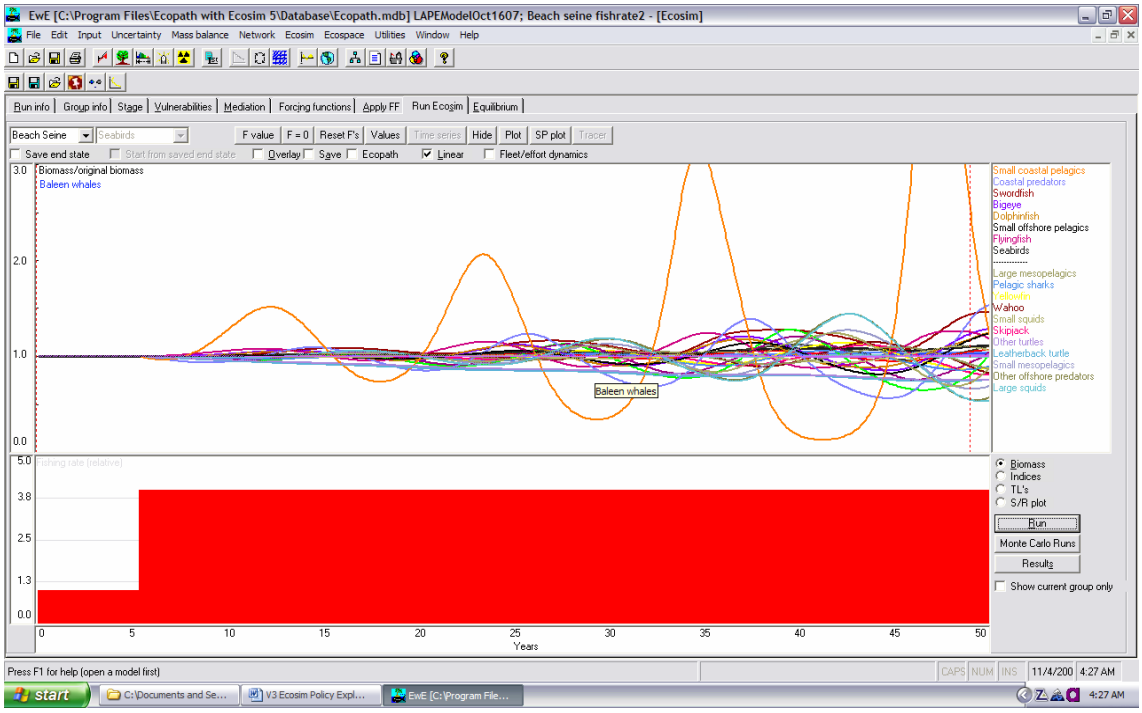

Figure 37 Fishing rate x4 base rate for beach seine fleets at v = 3.

A comparison of the long-term (50 years) and short-term (5 years) consequences of increases in fishing rate (4x) (Figure 38) shows considerable increases in biomass, catch and value of small coastal pelagics over the long term, the increased biomass due mainly to capture of the major predator of small coastal pelagics (coastal predators). Generally, short-term catches, biomass and value are greater than the long-term estimates for major prey species.

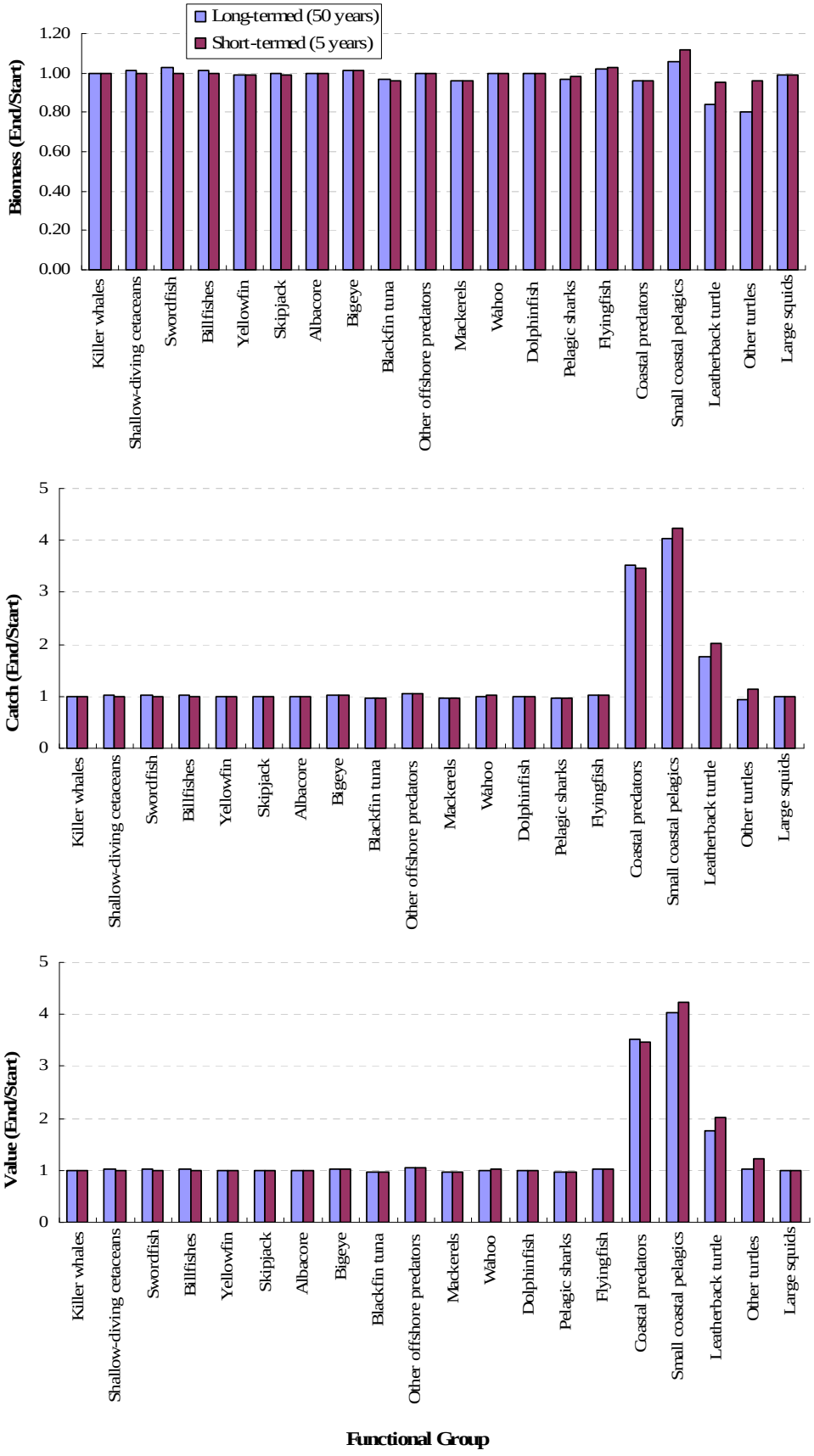

Figure 38 Scenario 1 – Impacts of 4x increase in fishing mortality due to beach seines on biomass, catch and value; v = 2.

Equilibrium analyses show that increasing fishing mortality on small coastal pelagics results in a biomass decline of coastal predators (Figure 39) at v =1, however at higher v = 2 a comparatively smaller increase in fishing mortality causes a crash in the small coastal pelagic resource (Figure 40).

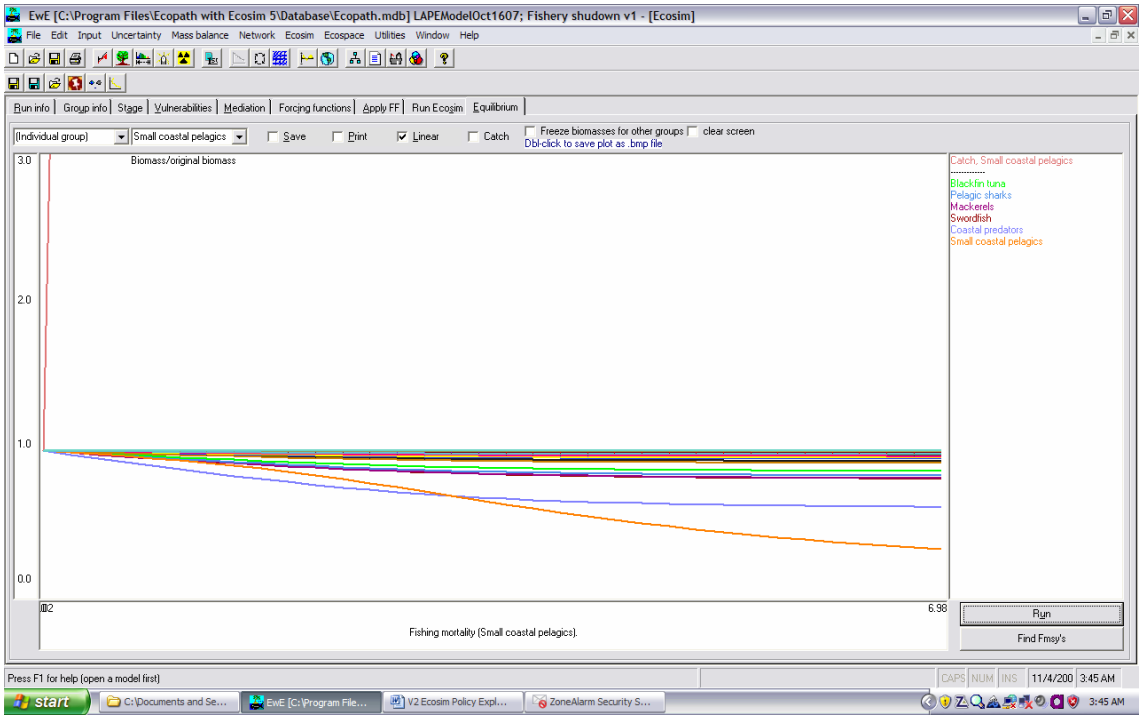

Figure 39 Scenario 1 Equilibrium analysis for small coastal pelagics at v = 1.

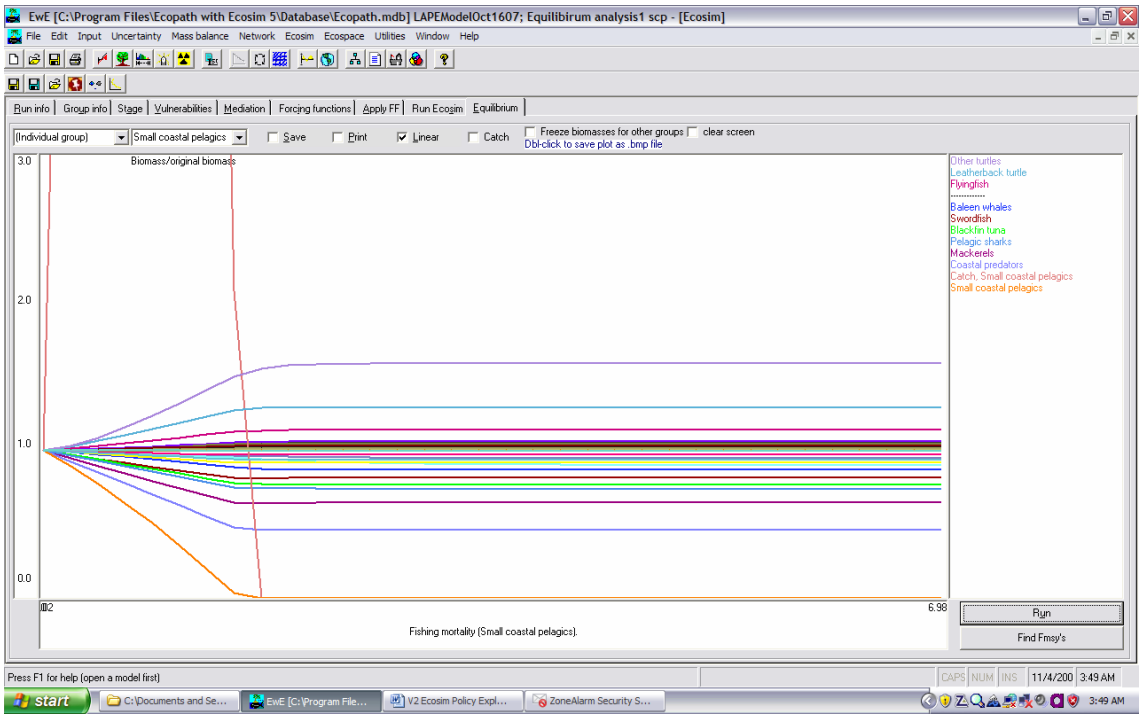

Figure 40 Scenario 1 Equilibrium analysis for small coastal pelagics at v = 2.

Scenario 2: Impact of increasing fishing on flyingfish on the biomass, catch and value of large pelagic species, in particular, dolphinfish

The base fishing mortality of flyingfish was 0.013 $year^{-1}$; predation mortality was 3.787 $year^{-1}$ and other mortality 0.2 $year^{-1}$. There is greatest prey overlap of flyingfish with blackfin tuna, and mackerels and other offshore predators. The group shares predators with dolphinfish (cannibalism), wahoo and blackfin tuna.

The fishing mortality of flyingfish is very low in the current LAPE model (0.013 $year^{-1}$; compared to 3.3 $year^{-1}$ estimated by Samlalsingh and Pandohee, 1992a, although the latter estimate is likely too high due to a combination of both fishing and migration). It is noted that a considerable portion of the catch i.e., that taken by fleets from Tobago, as well as the quantity of flyingfish utilized as bait in several countries, is not incorporated in the LAPE model. To explore the associated impact of fishing it was assumed that the open, outboard (troll, longline and gillnet) boats combined (Tobago fleets and bait component) take the same flyingfish catch per unit area as the decked, inboard (troll, longline, gillnet) fleet (0.00228 $t \cdot km^{-2}$). The catch of the open-outboard (troll, longline, gillnet) fleet was adjusted to maintain the original species composition, with the new estimate of flyingfish catch. It was necessary to rebalance the model as the resulting estimates of EE were greater than one for several species: seabirds; shallow-diving cetaceans; swordfish; dolphinfish and small coastal pelagics. Except for dolphinfish and small coastal pelagics, all that was necessary to rebalance the model was to reduce the proportion of the repective species in the diet of pelagic sharks. Cannibalism was reduced in dolphinfish and the proportion of the diet of coastal predators attributed to small coastal pelagics was reduced. The new estimates of flyingfish biomass was changed only slightly, 0.219 $t \cdot km^{-2}$ compared to 0.208 $t \cdot km^{-2}$ (assuming EE = 0.95) and the fishing mortality was increased to 0.021 $year^{-1}$. The feeding time adjustments mentioned previously were maintained and fishing impacts were examined with vulnerability estimates ranging between 2 and 4.

Considerable impacts are experienced with little increase in fishing mortality associated with the open, outboard (troll, longline, gillnet) fleet at v = 1 (Figure 41). Biomass of leatherback turtles, dolphinfish, mackerels, wahoo, blackfin tuna, pelagic sharks and pelagic turtles decline, but the greatest impacts are experienced by the latter four groups. The same simulation at v = 2 results in several groups including wahoo, blackfin tuna, pelagic sharks, mackerels and small coastal pelagics going extinct (Figure 42), suggesting that either adjustment of Ecosim input parameters is required or that the system exhibits bottom-up control. In contrast, considerable increase in fishing mortality (relative to the base estimate) associated with the open, decked, inboard (troll, longline, gillnet) is required to promote noticeable change in biomass at v = 1 (Figure 43). This is due mainly to the fewer functional groups caught by this fleet. Wahoo is most impacted at v = 2, because of the higher initial fishing mortality on the group compared to dolphinfish and flyingfish (Figure 44).

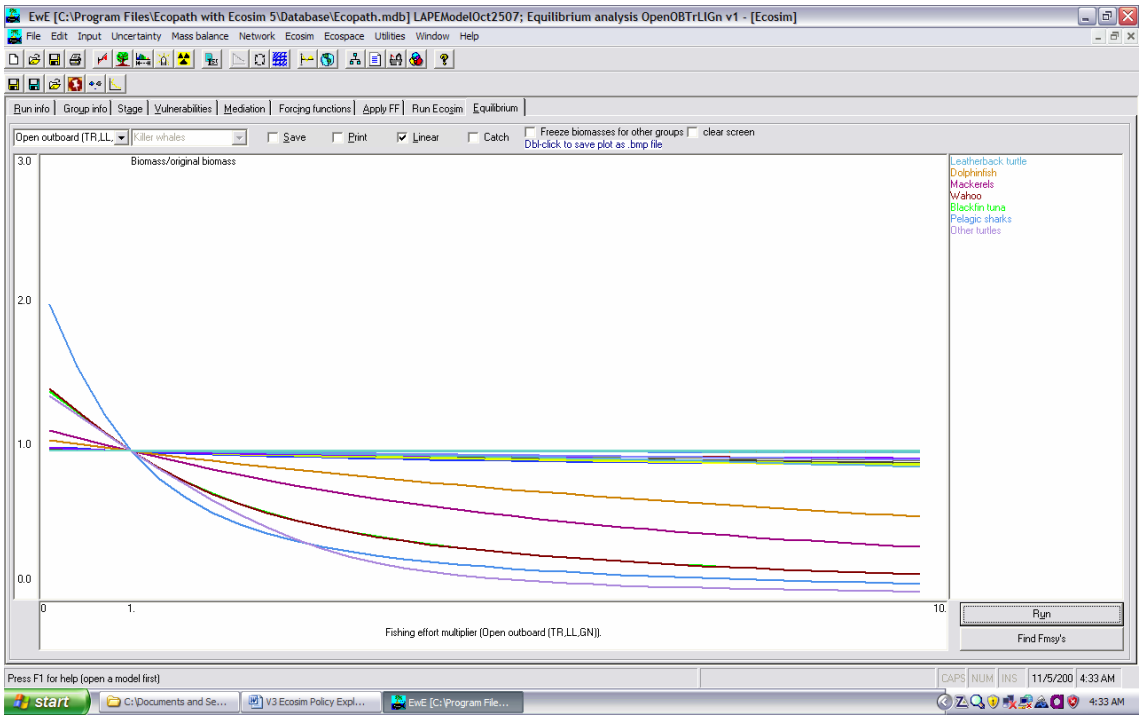

Figure 41 Equilibrium analysis for the open, outboard (troll, longline, gillnet) fleet at v = 1.

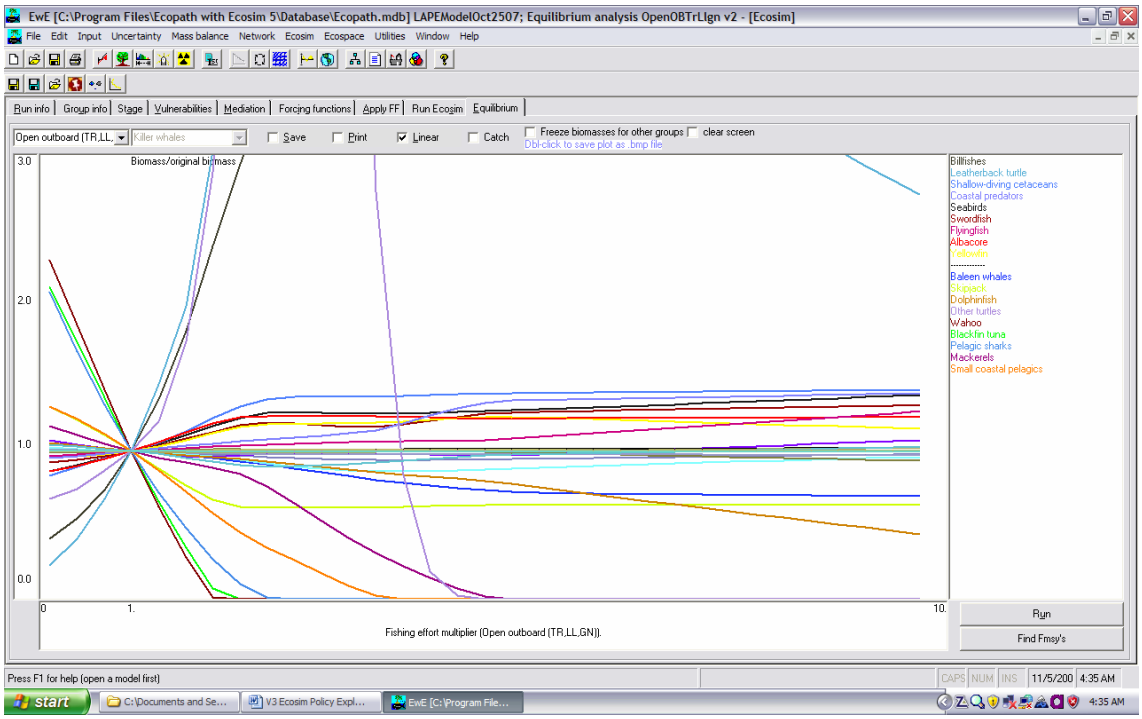

Figure 42 Equilibrium analysis for the open, outboard (troll, longline, gillnet) fleet at v = 2.

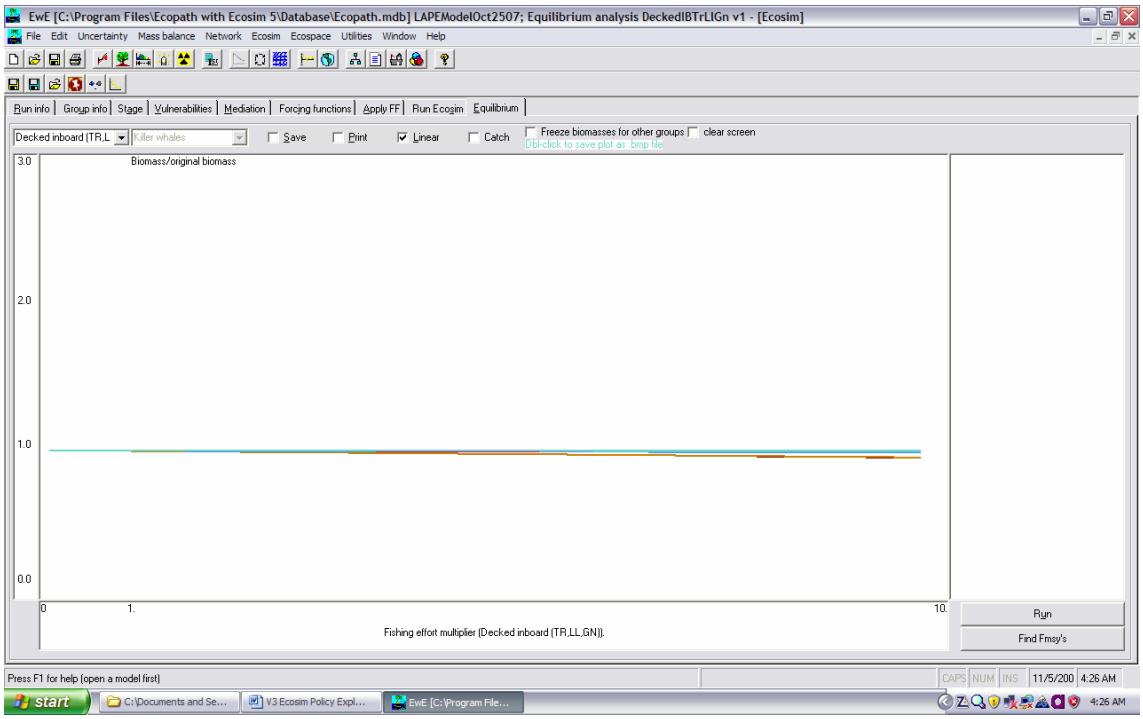

Figure 43 Equilibrium analysis for the decked, inboard (troll, longline, gillnet) fleet at v = 1.

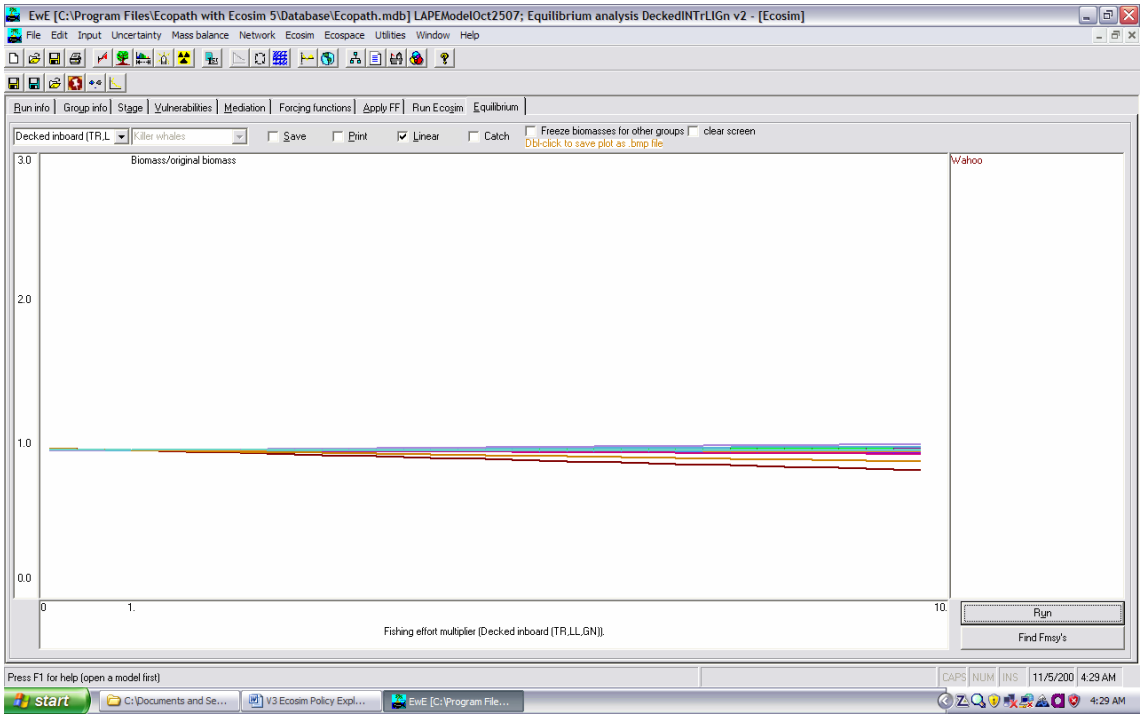

Figure 44 Equilibrium analysis for the decked, inboard (troll, longline, gillnet) fleet at v =2.

Equilibrium analyses of the individual groups, at varying vulnerability (flyingfish in Figure 45 and Figure 46; dolphinfish in Figure 47 and Figure 48), show that increased fishing mortality on flyingfish has a negative impact on dolphinfish biomass (at v = 1), moreso than the initial impacts on flyingfish

itself, while increased fishing mortality on dolphinfish appears to have either very little impact (at v = 1) or a positive impact on flyingfish biomass, due to predation release (at v = 2). At v = 2, increasing flyingfish fishing mortality to almost twice the base estimate results in a complete loss of the group.

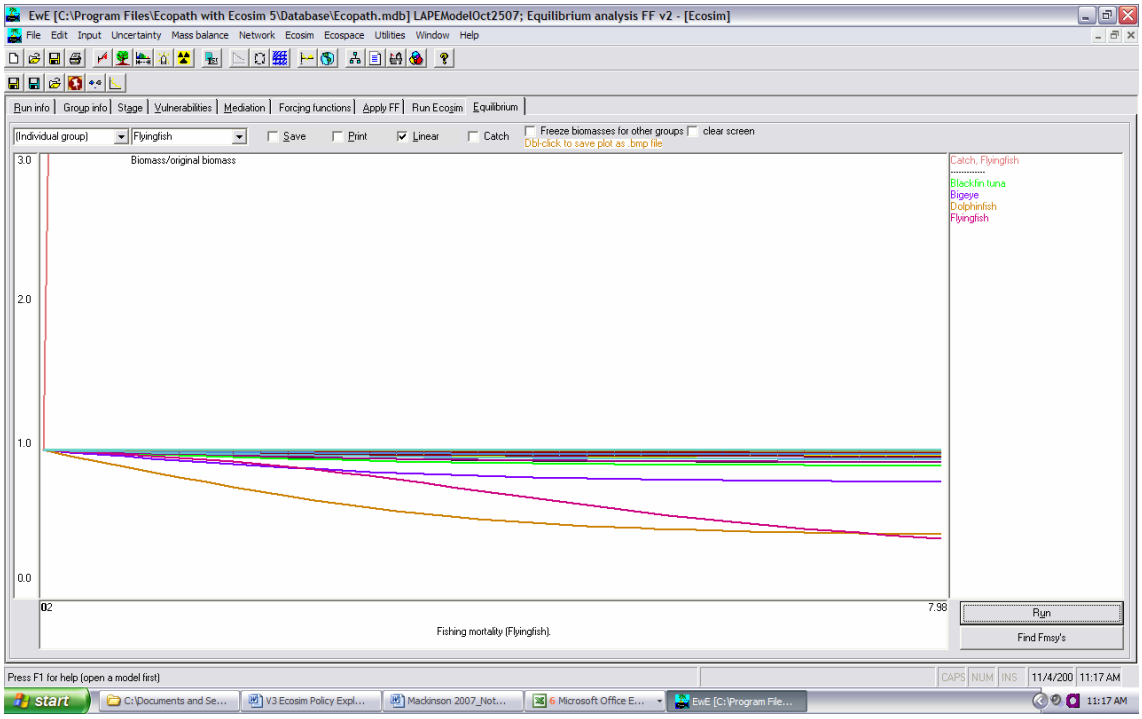

Figure 45 Equilibrium analysis of flyingfish at v = 1.

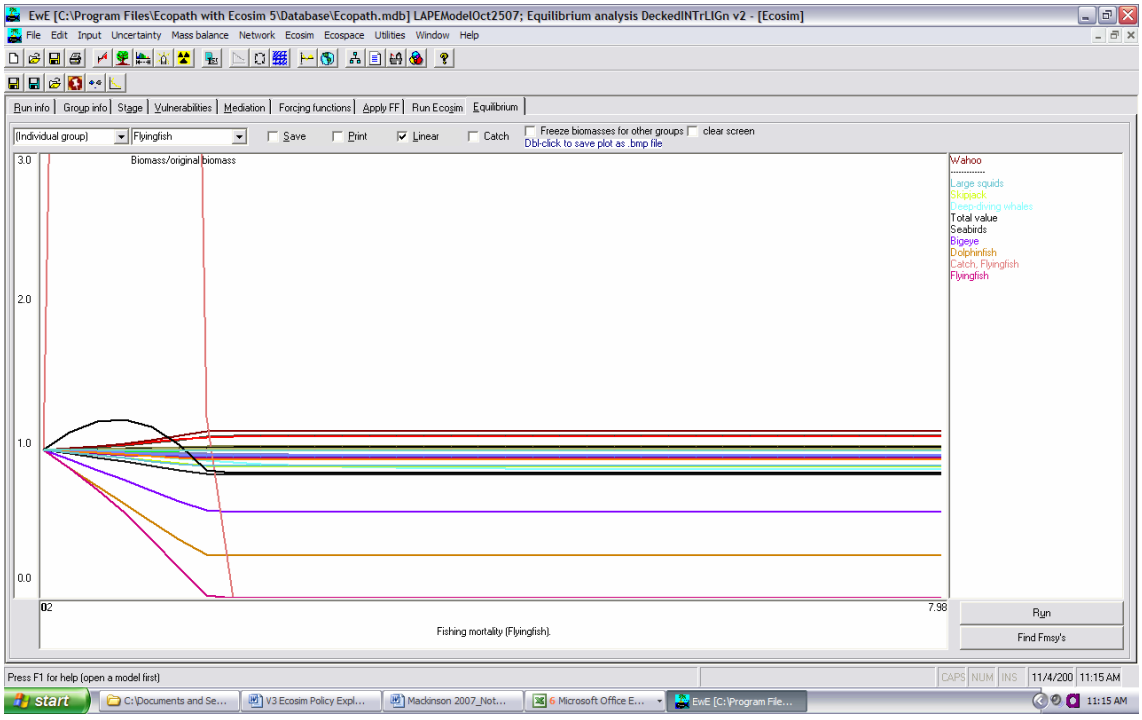

Figure 46 Equilibrium analysis of flyingfish at v = 2.

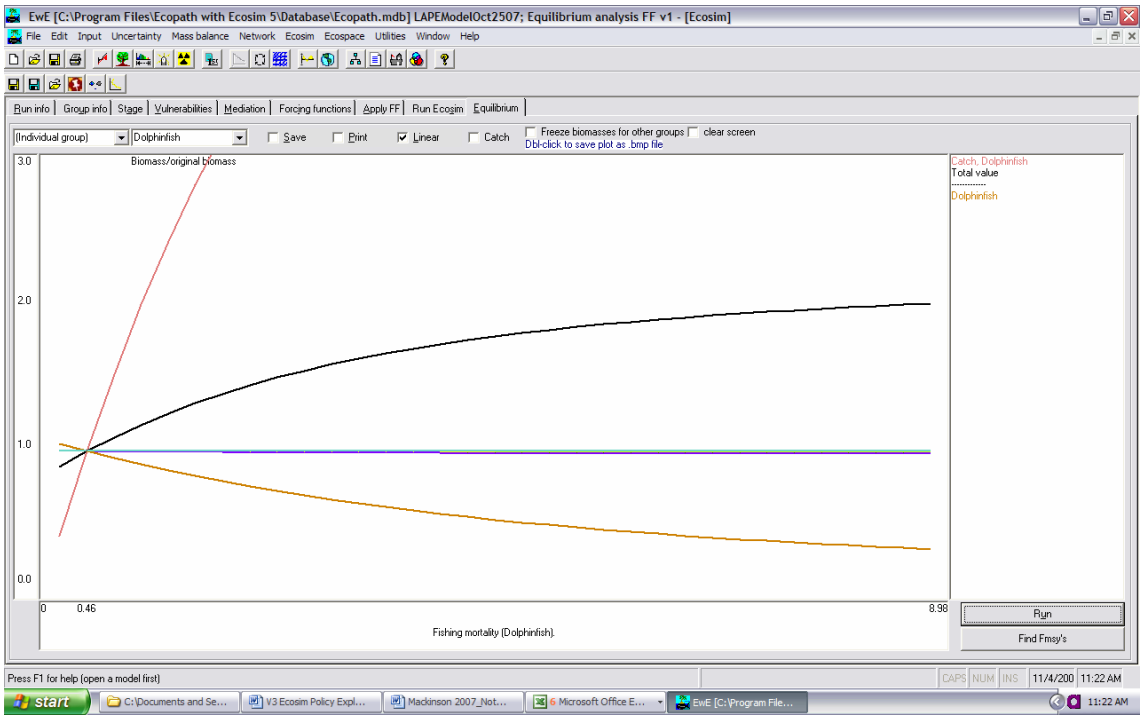

Figure 47 Equilibrium analysis of dolphinfish at v = 1.

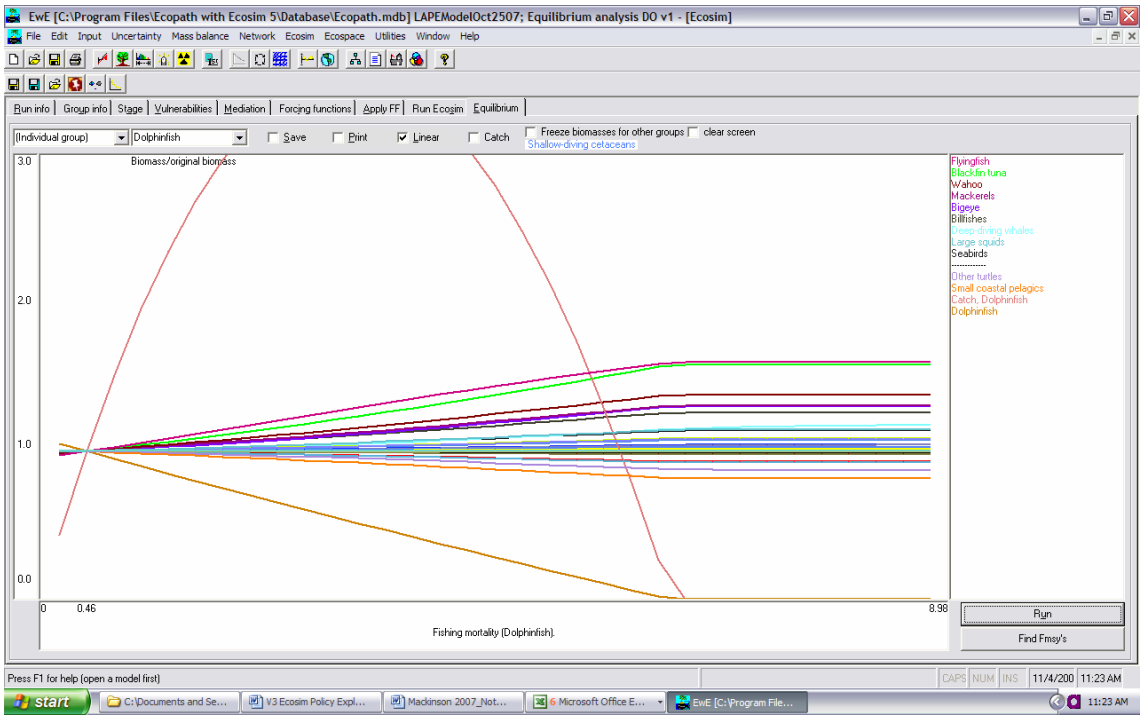

Figure 48 Equilibrium analysis of dolphinfish at v = 2.

When the fishing mortality of flyingfish is increased from the baseline to 1.0 at year 5, and sustained at this level for an additional 15 years, dolphinfish, as a key predator of flyingfish, is negatively impacted (Figure 49). When dolphinfish is subject to a similar pattern in fishing mortality the increases in flyingfish biomass are modest (Figure 50). A combined increase in fishing mortality of the two groups is detrimental to dolphinfish (Figure 51). The inequality in responses to increased fishing on flyingfish and dolphinfish suggests that prey

availability is a stronger control in the dolphinfish – flyingfish dynamics, than predator control.

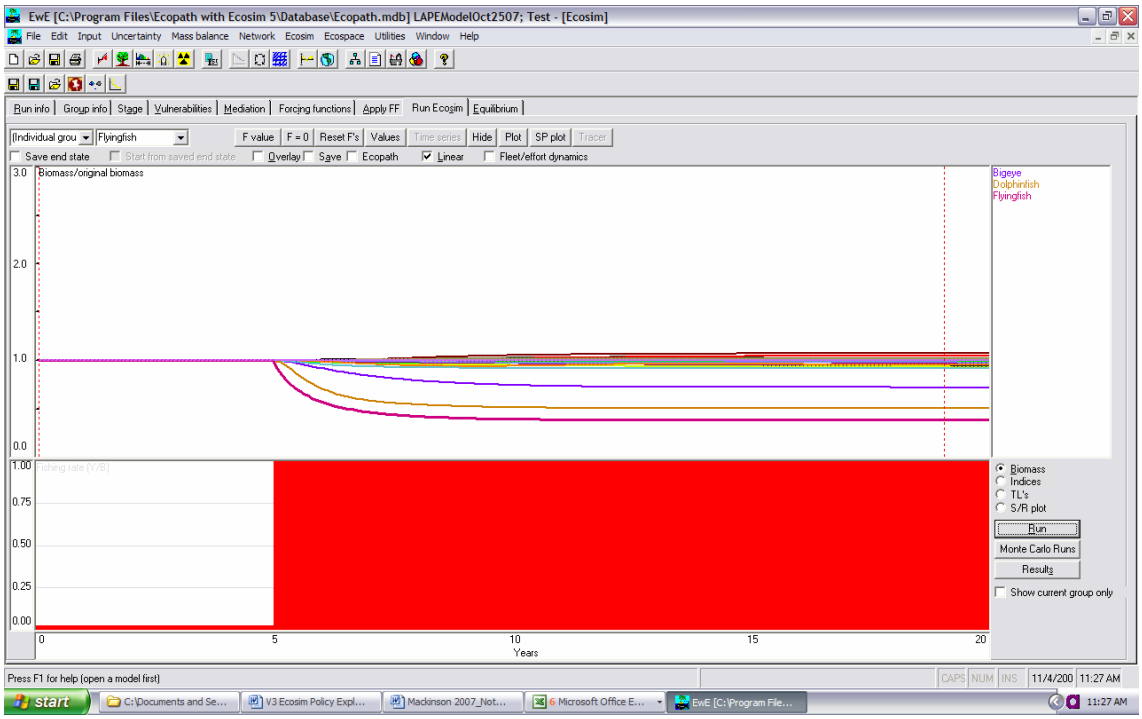

Figure 49 Increased fishing rate on flyingfish at v = 2.

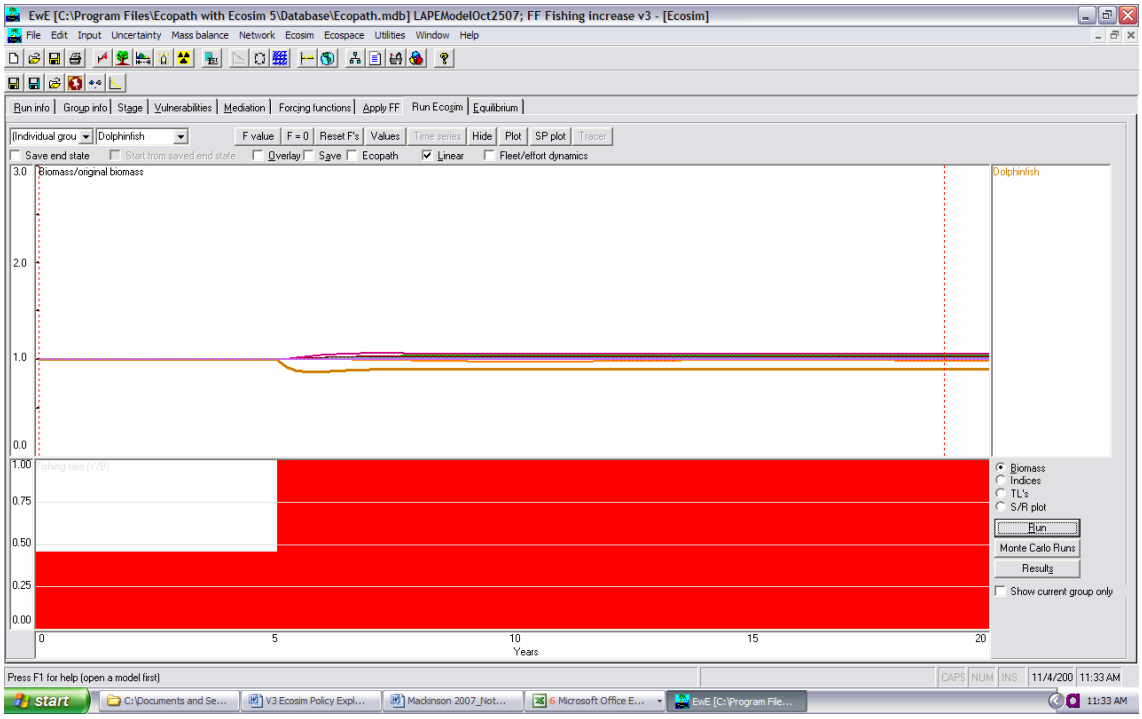

Figure 50 Increased fishing rate on dolphinfish at v = 2.

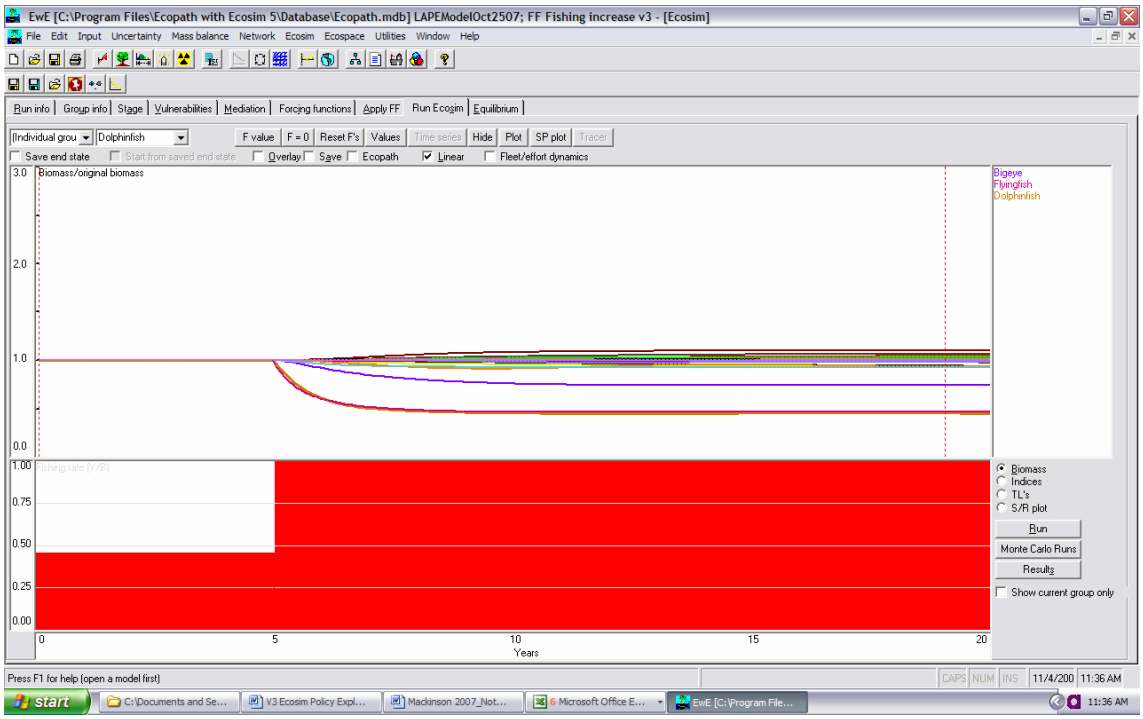

Figure 51 Increased fishing rate on dolphinfish and flyingfish combined at v = 2.

The corresponding changes in group catch (Figure 52), biomass (Figure 53) and individual fleet catches (Figure 54) associated with the increases in fishing mortality described above support the observation that dolphinfish abundance is highly dependent on prey (flyingfish) availability. The decked, inboard (troll, longline, gillnet) fleet is most impacted by the changes in flyingfish fishing mortality. This is because the fleet is fairly specialized, compared to others, with flyingfish comprising the majority of the catch.

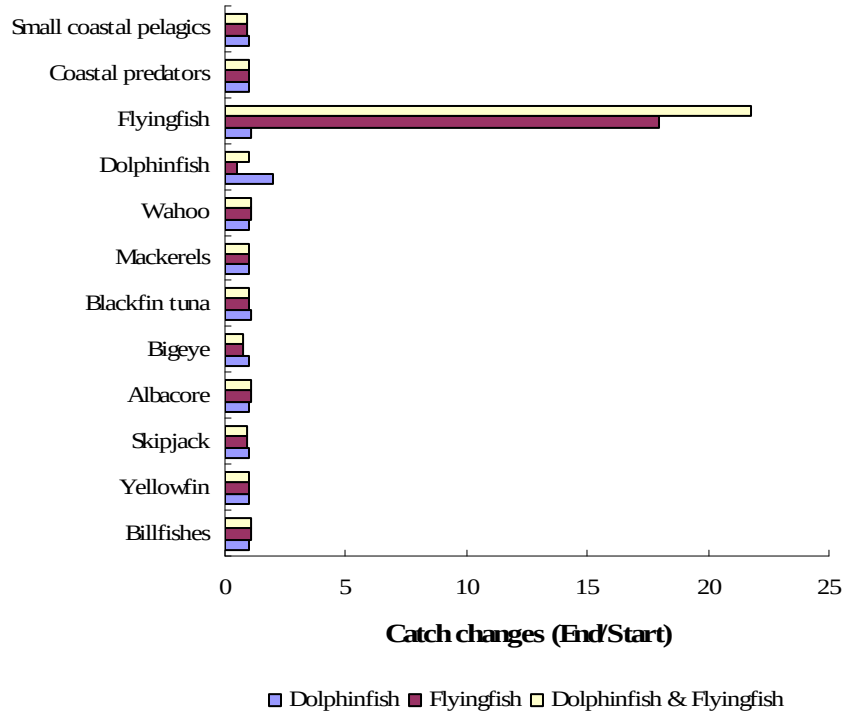

Figure 52 Changes in catches resulting from increased fishing mortality on dolphinfish and flyingfish independently and combined. Fishing mortality increased from base estimate to 1.0 year^{-1} at v = 2. Change is represented after a 20 year period.

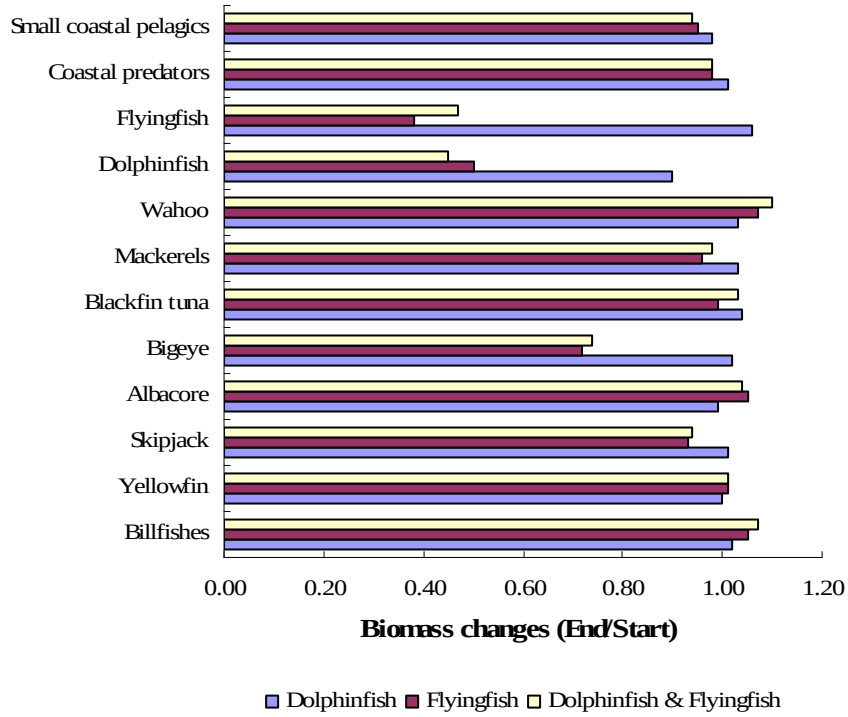

Figure 53 Changes in biomass resulting from increased fishing mortality on dolphinfish and flyingfish independently and combined. Fishing mortality increased from base estimate to 1.0 year^{-1} at v = 2. Change is represented after a 20 year period.

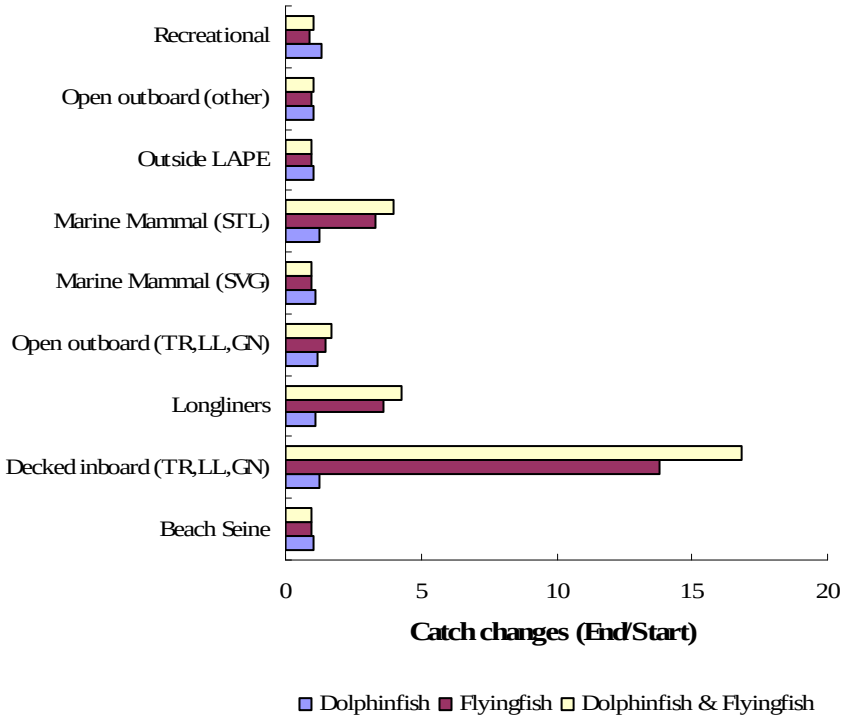

Figure 54 Changes in by fleet resulting from increased fishing mortality on dolphinfish and flyingfish independently and combined. Fishing mortality increased from base estimate to 1.0 year^{-1} at v = 2. Change is represented after a 20 year period.

Estimates of F_{msy} from a surplus production model range between 0.739 and 1.218 year^{-1} for flyingfish (Figure 55) and between 2.61 and 2.88 year^{-1} for dolphinfish (Figure 56).

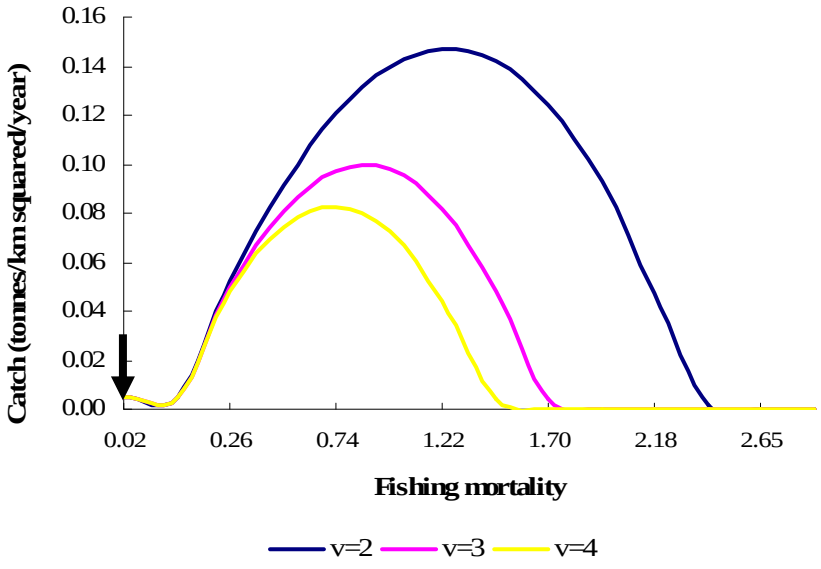

Figure 55 Predicted equilibrium catch for flyingfish at different fishing mortality rates and vulnerability settings. Baseline fishing mortality indicated by arrow.

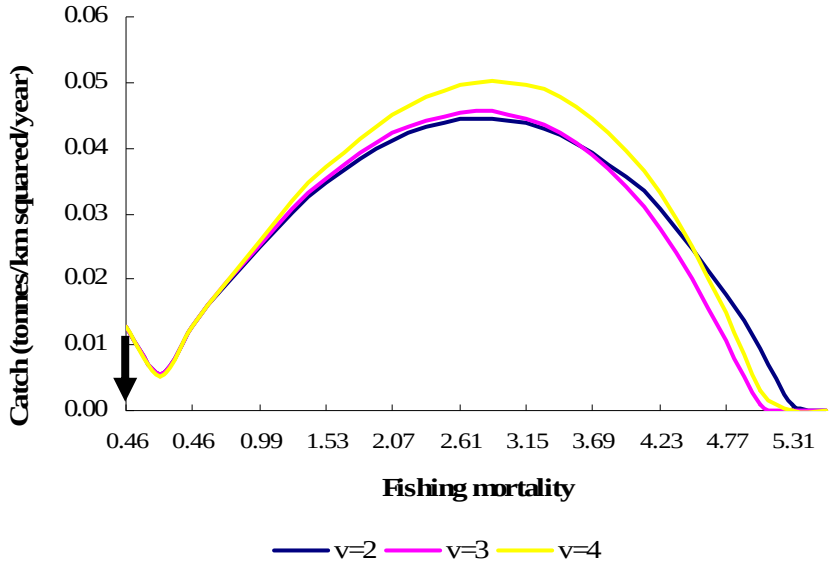

Figure 56 Predicted equilibrium catch for dolphinfish at different fishing mortality rates and vulnerability settings. Baseline fishing mortality indicated by arrow.

Scenario 3: Impact of increasing marine mammal population on the available resources for fisheries and the impact of a developing fishery for marine mammals on catches of fish species.

This scenario was not tested due to time constraints. However, some guidelines are provided for testing this scenario in future. Increasing population (biomass) of marine mammal biomass could be represented in the model in two ways: (1) introduction of a small accumulation of marine mammal biomass or (2) use of the force biomass option, with fitting of time series data on marine mammal biomass based on some hypothesis as to the rate of increase. Although a decrease in fishing mortality would also cause an increase in marine mammal biomass, this increase would be limited to exploited groups (killer whales and shallow-diving cetaceans) and is therefore not recommended if the impact of increasing biomass of all marine mammal groups (exploited and non-exploited) is to be examined. A dynamic simulation with the increase in marine mammal biomass could be run and the impacts on the biomass of other functional groups in the system examined. The impact of increased fishing on marine mammals could be investigated by simply increasing fishing mortality on the exploited groups and using a forced biomass decline for unexploited groups.

It should be noted that the impacted groups in any Ecosim scenario are dictated by the linkages specified in the diet composition. The LAPE Project included diet studies on marine mammals however the results were sparse and were expressed in terms of prey numbers rather than weight. Direct inclusion of these results in the input diet composition was thus not attempted. The more general information from Pauly *et al*. (1997) was used. As a result there are no area-specific data in the estimated diet composition for marine mammals.

In addition to increasing the number of marine mammal diet samples, there is a need for improved information on the size (weight) composition of the prey groups. A reference collection of fish otoliths and squid beaks from fully identified specimens of forage species, with relevant morphometric data (length, weight, length/weight relationships, etc) is required. As well as assisting with species identification of otolith and squid beak remains the morphometric relationships enable estimation of prey length and prey weight.

Scenario 4: Impact of increasing productivity on the biomass of fish available to fisheries in the region.

This scenario was not tested due to time constraints. The planned approach to model a potential impact of global climate change hypothesized an increase in run-off from major South American rivers. This would be expected to drive increased primary productivity in the region, applied in the model to the production rate of phytoplankton using a forcing function. This scenario would have wide-ranging bottom-up effects which would be interesting to examine the cascading effects through the LAPE. As well, the relative impacts in the northern and southern LAPE regions could be investigated (using a model to represent each region) as studies have confirmed relatively higher productivity in the southern LAPE region compared to the north (Forget, 2007).

Scenario: Skipjack-Yellowfin interaction.

An unexpected trophic interaction emerged in the Ecosim model between yellowfin tuna and skipjack tuna. It is a consequence of yellowfin feeding on skipjack, while skipjack in turn feed on yellowfin juveniles. In a specific scenario, fishing is doubled for 10 years (years 5 to 15 in Figure 57). Both yellowfin (yellow bottom line) and bigeye tuna (purple bottom line) are hit hard and take a long time to recover. On the other hand, skipjack (bright pink, top line), after a brief dip initially, increases to a new plateau during the 10 years of increased fishing, presumably because of predation release from reduced yellowfin tuna abundance. Skipjack is able to increase abundance again when fishing effort returns to the baseline level because of the decrease in fishing pressure while yellowfin takes a long time to recover. It appears that this an element of depensation; predation by skipjack is retarding the recovery of yellowfin from its' low biomass. Skipjack thus holds down its own key predator. When fishing mortality is doubled on skipjack alone (Figure 58), yellowfin biomass (yellow line in top panel) increases because of the reduced predation, even though skipjack (bright pink line in bottom panel) are key prey item of yellowfin. There is no delay effect in the recovery though. When the fishery returns to the baseline level, the skipjack biomass immediately begins to recover.

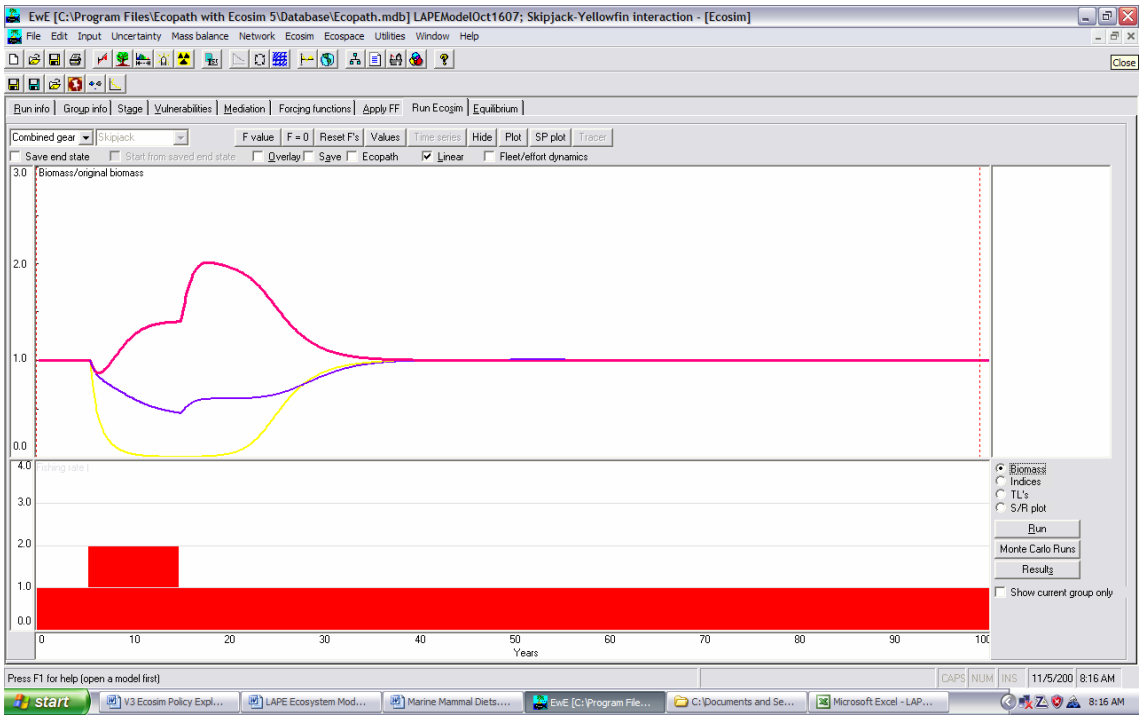

Figure 57 Increased fishing (twice the base rate) of combined gears at v = 2. Yellow line represents yellowfin tuna; purple line represents bigeye tuna and bright pink line represents skipjack tuna.

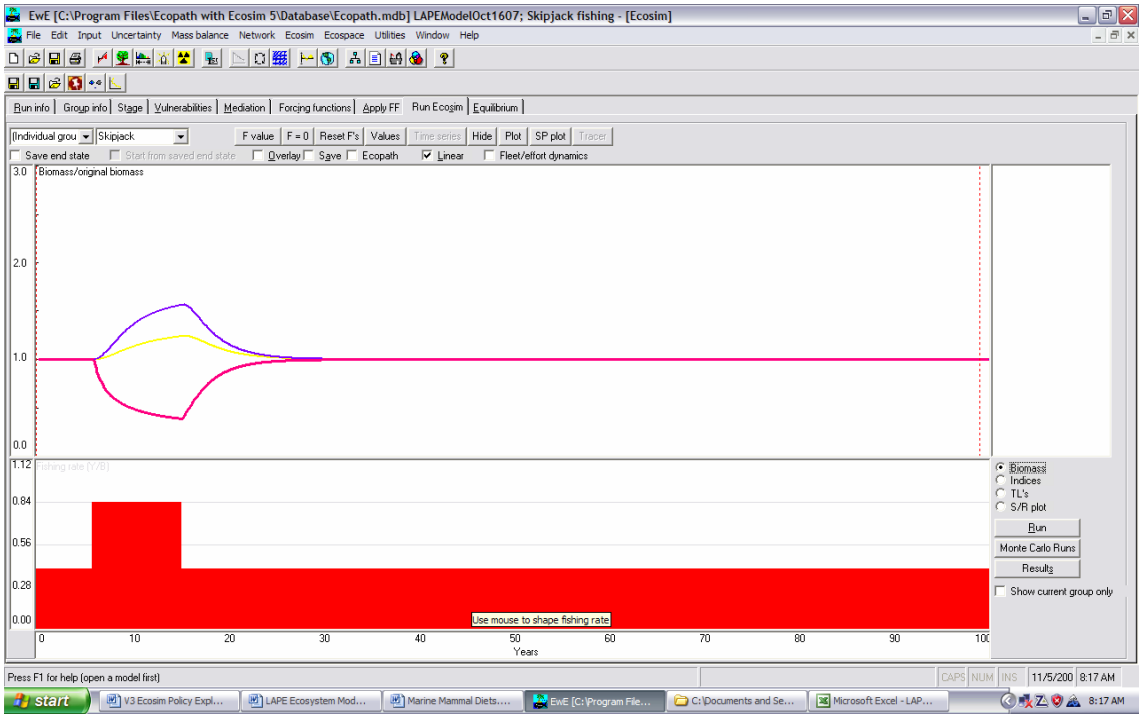

Figure 58 Increased fishing (twice the base rate) of skipjack tuna at v = 2. Yellow line represents yellowfin tuna; purple line represents bigeye tuna and bright pink line represents skipjack tuna.

CONCLUSIONS

The EwE framework, though limited in some respects, is used globally and accounts for the vast majority of fisheries ecosystem models. The LAPE model reported herein has incorporated most of the existing data resources although there is room to improve the quality of model parameterization (e.g. by incorporating more or better data, by further analysis of the output statistics of the balanced model, and by comparison with other relevant models). Particular issues of data quality and availability are discussed below. Bearing in mind both general and specific caveats, the existing model is a reasonably well-developed representation of the study area. The limitations and uncertainties that remain mean that the model is best suited for qualitative assessment of interactions and scenarios. At this stage of development the direction and importance of model responses should be given careful consideration in policy analysis but not so the specific quantitative values.

A clear example of the need to understand ecological linkages is apparent from some of the results available so far. The two management issue scenarios evaluated in some detail in this report were originally identified as two distinct issues; the interaction between bait fisheries and large pelagic longline fisheries was a separate issue from the question of flyingfish-dolphinfish interaction. However, the fact that flyingfish are an alternative bait source for longliners and flyingfish are a critical forage species for dolphinfish means that these two issues turn out to be strongly linked ecologically. Many of the LAPE regional countries are looking to increase their activity in large pelagics fisheries and it appears now that this has the potential for important negative impacts on dolphinfish production as an unintended consequence.

Model limitations

Christensen *et al.* (2000) discuss in detail the capabilities, limitations and major pitfalls of the Ecopath with Ecosim approach in general. The authors give guidelines for avoiding or addressing major pitfalls, all of which should be carefully considered in further development of the LAPE model.

One of the important uncertainties in EwE models is associated with the 'vulnerability' parameters i.e. the parameters which quantify the flow of biomass between predator and prey groups. EwE model simulations are highly sensitive to the choice of these values as they affect the stability of the model, the estimates of system productivity and resilience, and the reliability of predictions associated with the ecosystem impacts of fishing. One useful means of estimating vulnerabilities is fitting of model simulations to relevant time series of fisheries or ecological data. This requires starting with a model of some point in the past, from which the simulated time series can be predicted for comparison to observed data. As the LAPE model is a current time model (2000-2005 base period) there no data yet available for time series comparison.

By identifying appropriate data series now and ensuring that national data collection systems capture the required information there is an opportunity to ensure that time series fitting will be possible over the next five to ten years, leading to improved confidence in model results.

The ability to provide an economic analysis, on a fleet by fleet basis, depends on a significant expansion of the socio-economic information in the current model. The inclusion of economic data (detailed price and costs data, employment data) will allow detailed and realistic modelling of the economic impacts of policy choices.

The current LAPE model is structured to explore management policy at the regional level i.e. within the Lesser Antilles. The stock distribution of several large pelagic groups (e.g. large tunas and billfish) extends far outside the LAPE area. As a result, significant portions of the biomass (>75%) and the majority of biological and technological interactions occur outside the model area. These wide-ranging species are the focus of international management measures through ICCAT and, in these cases, it is strongly cautioned that the LAPE model is not an appropriate tool for management policy exploration.

Model uncertainties

In addition to the limitations inherent in modelling the complexity of ecosystems and the constraints of the software being used, it is important that the uncertainties in model inputs be included in any interpretation of model results. Data uncertainties in the LAPE model were characterized by first documenting the range of input estimates for similar groups in other models and by assigning data pedigrees to the various inputs based on the information source and its specificity to the system being modelled. Because of the wide range of data types needed to construct a trophic model (biomass, catch, diet composition, and a range of physiological parameters) most model studies, including this one, are likely to 'adopt' at least some information from other localities or related species. The pedigree values assigned to parameter estimates are intended to reflect how closely the adopted information is expected to represent the LAPE area.

Diet composition information is an area for which locally-derived data are most valuable. Diet information drawn from the study area will reflect the prey field available there. A given predator can and will feed on different prey in other stock areas or other parts of an overlapping range. An apparent example in this case is the dolphinfish. A study from the LAPE area indicates a very high proportion of flyingfish in the diet while studies from other areas reported far less flyingfish. Although the LAPE project conducted diet studies on selected species within the region, the diet composition information is still dominated by published literature, most of which is drawn from other areas. Additional diet studies could target some key areas of uncertainty including dolphinfish, cetaceans and flyingfish. For a number of larger predators, information on

changes in diet as a result of growth would allow separation of these groups into juvenile and adult functional groups.

With few exceptions, catch data must be locally-derived. For several groups in the LAPE model e.g. flyingfish, small coastal pelagics and marine mammals, the catch estimates are almost certainly underestimates. Improving the quality and completeness of the catch data, both in volume and species composition, is an immediate means of improving the quality of the EwE model and is within the scope of the national fisheries agencies.

Few estimates of biomass are available for functional groups in the LAPE and there were uncertainties with most of those that were available. In some cases published biomass estimates, e.g. flyingfish from Oxenford *et al*. (1995), were found to be incompatible with the modelled consumption by associated predators. The LAPE project had conducted surveys to estimate biomass of selected groups in the region, however, statistical confidence levels associated with these results varied and in some cases were quite low. Also, survey estimates may be biased by selectivity variations but these were not quantified. A common practice, when biomass estimates are not available, is to estimate biomass from catch and fishing mortality estimates. However, in cases where catch or F estimates are biased this practice can result in large errors.

Fishing mortality estimates are available for several species in the LAPE region. However, the quality of these estimates also depends on the quality of available catch data. In addition, regional assessments of species distributed beyond the Lesser Antilles can over-estimate fishing mortality due to migration out of the area. Finally, uncertainties and the potential for over-estimating fishing mortality are increased for functional groups that aggregate species which are ecologically similar but subject to differing rates of fishing mortality. This can arise as estimates of fishing mortality tend to be more available for heavily exploited species and are often not available for lightly exploited species within a functional group.

Studies aimed at reducing the uncertainties outlined above can considerably improve the quality of the LAPE model and add to the ecological knowledge of the region.

Guidelines for use of the LAPE model

The ultimate use of ecosystem models is to assist policy makers in decision making by providing information on the likely impacts and potential unforeseen consequences of management actions. The LAPE model is currently structured to enable examination of management policy options associated with fisheries at the LAPE regional scale.

Although highly migratory species are represented in the LAPE model it is recommended that the model not be used to examine management policy options specific to these groups as the technical and biological interactions occurring throughout their range are not well represented in the model. Use of

the central Atlantic model (Vasconcellos and Watson, 2004) is a recommended alternative for management policy exploration for these species or functional groups.

The LAPE model provides a framework for critical analysis which can be used to assess the compatibility of new and existing information for the region. It can also be used as tool to develop hypotheses about the biological and technical interactions within the LAPE and to identify research needs for understanding these interactions and their relevance to management.

The current LAPE model is one of a number of possible representations of the biomass flows within the system. Additional research will make it possible to refine the model and in so doing increase the reliability of its predictions. The current model provides a template which researchers are encouraged to critically examine, both the structure and the associated inputs, and to modify to address new issues as they emerge. The model should be considered complementary to single-species assessments, for example through assessing the validity of single-species parameter estimates in the multi-species context or, in turn, contributing improved parameter estimates for inclusion in single species models.

Recommended modifications to the LAPE model

1. Split top predator groups (including dolphinfish) into adult and juvenile components to more realistically model dynamics (e.g. stock-recruitment). This modification requires that catch, diet, predation and biomass estimates be split accordingly;
2. Improve group-specific vulnerability parameter estimates (see Christensen *et al*., 2000) and feeding time adjustment rates through discussions with species experts, to better model the associated ecological dynamics;
3. Use Ecoranger and other techniques (e.g. sensitivity analyses) to evaluate the adequacy and robustness of the existing model and its resulting predictions, as well as the range of parameters for alternative balanced models.
4. Use results from stable isotope analyses (MacNeil, 2007), which indicate relative trophic levels, to guide the adjustment of diet composition in model balancing;
5. Specify the bait fisheries as separate fleets (both small coastal pelagics and flyingfish) to better examine the associated ecosystem and fishery-related impacts in Ecosim;
6. Address the remaining diet oddities outlined in Appendix 7;
7. Incorporate socio-economic data to allow analysis of multi-criteria objectives in management policy exploration. Some socioeconomic data are available (Appendix 8 and Ferreira, 2002) but the data set is incomplete.

Research to enhance policy exploration of management issues.

Issue: Bait fisheries

8. Improve estimates of the quantities and species composition of catches in beach seine fisheries and to track the quantities for food sales and bait use;
9. Improve estimates of the catches of flyingfish and to track the quantities for food sales and bait use.

Issue: Flyingfish-dolphinfish linkage

10. Conduct dolphinfish diet study to ascertain the regional importance of cannibalism and flyingfish;
11. Conduct studies to improve estimates of flyingfish biomass and fishing mortality (single species assessments, surveys, size and age composition analysis);
12. Conduct studies to improve estimates of dolphinfish biomass and fishing mortality (single species assessments, surveys, size and age composition analysis);
13. Improve estimates of catches of the respective species from all fisheries involved.
14. Conduct diet studies on large mesopelagics to ascertain their role as competitors with dolphinfish for flyingfish;
15. Conduct studies to ascertain dolphinfish and flyingfish stock structure and regional distribution;

Issue: Interactions between marine mammals and fisheries

16. Conduct further diet composition studies to identify and quantify by functional group, the finfish and other prey in the diet of marine mammals of interest.

Key lessons for construction of trophic models

The management issues that are to be explored by the model should be identified as early as possible, preferably prior to model construction. This ensures that the model structure includes all the relevant groups and that field research addresses the key input parameters for those groups.

Allowing too much of the available time to be utilized in model construction (structure, data inputs) and balancing should be avoided. Construction of ecosystem models of this complexity is an on-going process; there always remain deficiencies and opportunities for refinement. The equally important step of analyzing the model outputs can thus be delayed or overlooked. As a result, the opportunities to learn more about the ecosystem dynamics of the area, to identify research priorities for reducing model uncertainties, and to apply the results to management policy questions are reduced.

The Ecosystem Modelling Working Group of the LAPE project was a key contributor to the process of model construction. Although this group

comprised mainly fisheries experts, such a group in future should include experts in ecology and biology, ecosystem modelling, fisheries assessment and management, and socio-economic analysis in an iterative process of model construction and critical review of model outputs.

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APPENDIX 1 ESTIMATION OF AN ABUNDANCE INDEX AND RELATED QUANTITIES FOR MAIN TUNA AND BILLFISHES SPECIES IN THE LAPE

Modeling highly migratory species in EwE requires as one of the input parameters the proportion of the time each species spend feeding outside the boundaries of the ecosystem. In the absence of more precise information about species migratory dynamics, we used as a proxy to the time feeding outside the ecosystem an estimate of the proportion of the stock biomass outside the LAPE and its adjacent areas (buffer zone).

To estimate this proportion we first calculated a spatially explicit abundance index using the ICCAT database of catches by species, gear, year and quarters at 5° of latitude by 5° of longitude resolution. Data were available for the following species: Albacore, *Thunnus alalunga* (ALB); Bigeye tuna, *Thunnus obesus* (BET); Atlantic blue marlin, *Makaira nigricans* (BUM); Sailfish, *Istiophorus albicans* (SAI); Skipjack tuna, *Katsuwonus pelamis* (SKJ); Swordfish, *Xiphias gladius* (SWO); Yellowfin tuna, *Thunnus albacares* (YFT); and Atlantic white marlin, *Tetrapturus albidus* (WHM).

The assumption here is that an index of abundance can be estimated from the cumulative catches of a certain period from a given area, as suggested by Die (2004). In the present study we used the last five years of available catch data (2000-2004) because it was shown to a period of relative stability in the spatial distribution of catches of the above mentioned species.

Three spatial units were defined (Figure A1- 1) the LAPE study area (Inside), a buffer zone of 200 nautical miles around the LAPE study area (Buffer), and the remaining areas of the Atlantic occupied by the stock of each species (Outside). ICCAT defines the official management unit boundaries for each stock, with latitude and longitude coordinates.

To estimate the Index of abundance for each spatial unit we used the formula described in Die (2004):

$$I_{i,u} = \sum_g \left(\frac{P_{u,g}}{H_g} I_{i,g} \right)$$

where

$I_{i,u}$ is the Index of abundance of species *i* in spatial unit *u*

$P_{u,}$g is the surface of each spatial unit inside each 5x5 cell *g*

H_g is the actual surface of each 5x5 cell *g*

$I_{i,}$g is the cumulative catch (tonnes) of species *i* in each 5x5 cell *g*

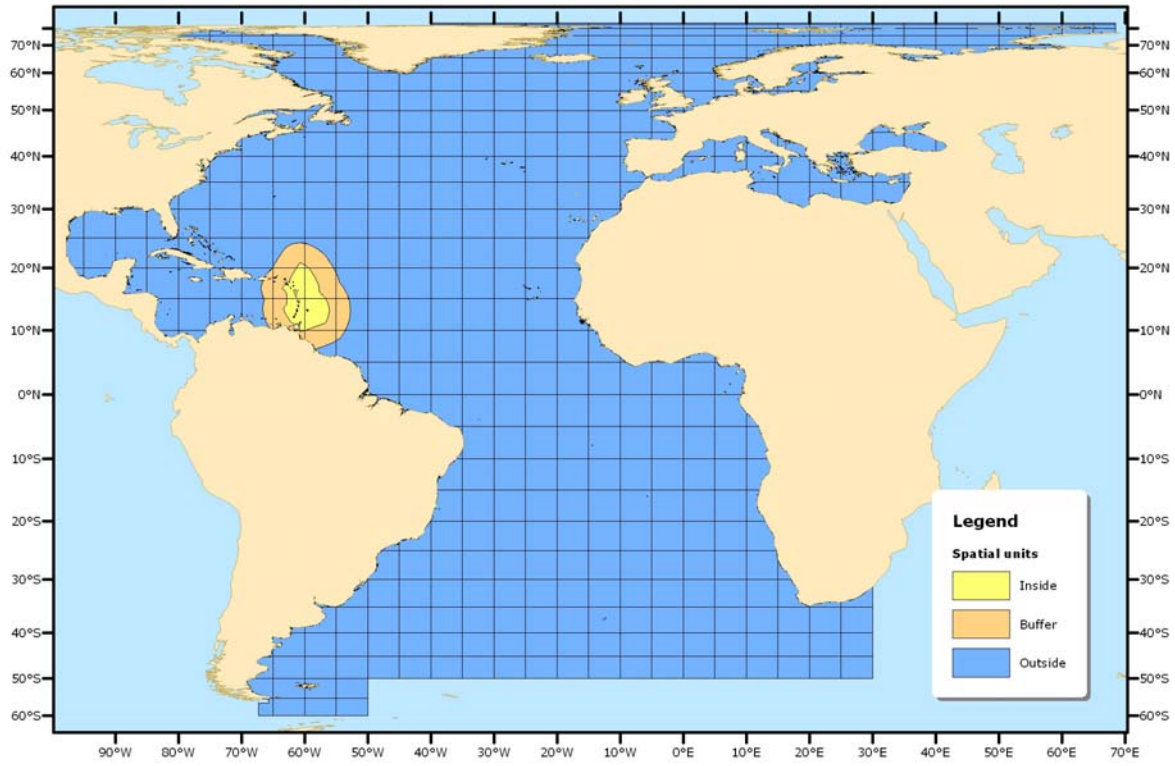

Figure A1- 1 Spatial units for biomass estimates

Using GIS geoprocessing capacity, three layers representing the spatial units were overlaid in order to obtain the surface ratio of each spatial unit inside each 5x5 cell.

Cumulative catches of stocks have been allocated to each spatial unit proportionally to the surface, as described above. Assuming the proportionality between the abundance index and the species biomass we also calculated the percentage of the biomass of the species inside each spatial unit. The results are shown in Table A1- 1, Figure A1- 2 and Figure A1- 3.

Table A1- 1 Abundance Index and biomass proportions by LAPE spatial units and by species.

	Abundance index (tonnes)			Biomass percentages		
Species	Inside	Buffer	Outside	Inside	Buffer	Outside
Blue marlin	245.21	293.93	13,329.66	1.77	2.12	96.11
White Marlin	241.36	366.58	3,670.25	5.64	8.57	85.79
Swordfish	794.22	893.49	215,738.80	0.37	0.41	99.22
Sailfish	815.23	1,147.25	6,373.22	9.78	13.76	76.46
Bigeye tuna	357.90	1,471.95	423,216.57	0.08	0.35	99.57
Albacore	4,637.61	10,356.98	208,809.85	2.07	4.63	93.30
Skipjack tuna	2,367.05	14,371.40	141,491.08	1.50	9.08	89.42
Yellowfin	4,899.08	20,756.80	636,800.31	0.74	3.13	96.13

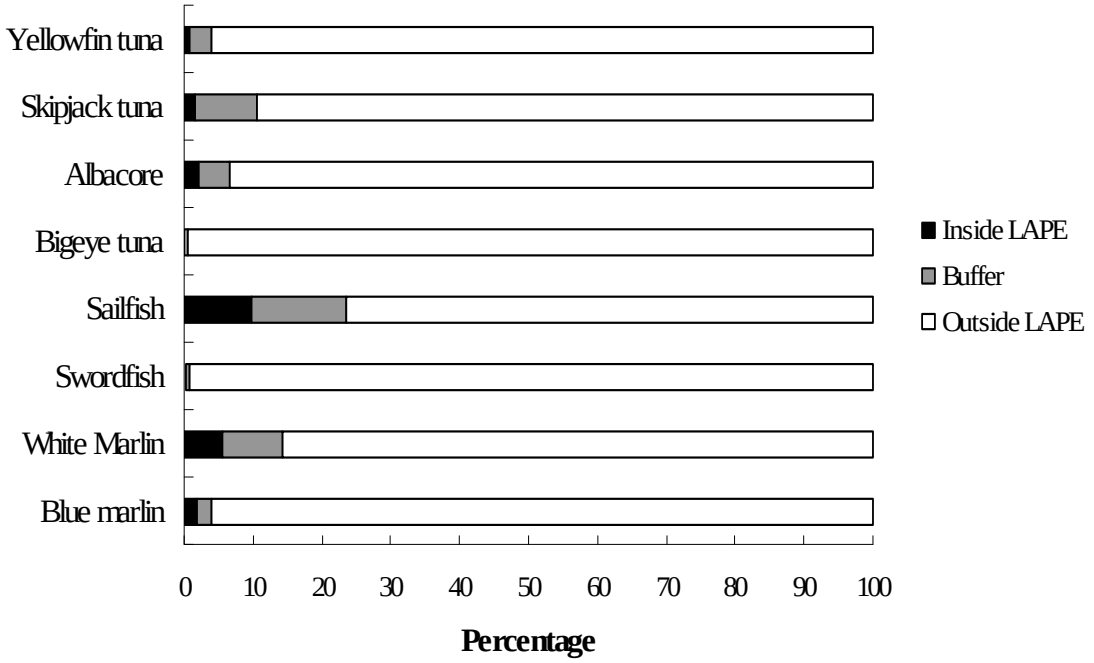

Figure A1- 2 Percentage of the biomass of main tuna and billfishes by each LAPE spatial units.

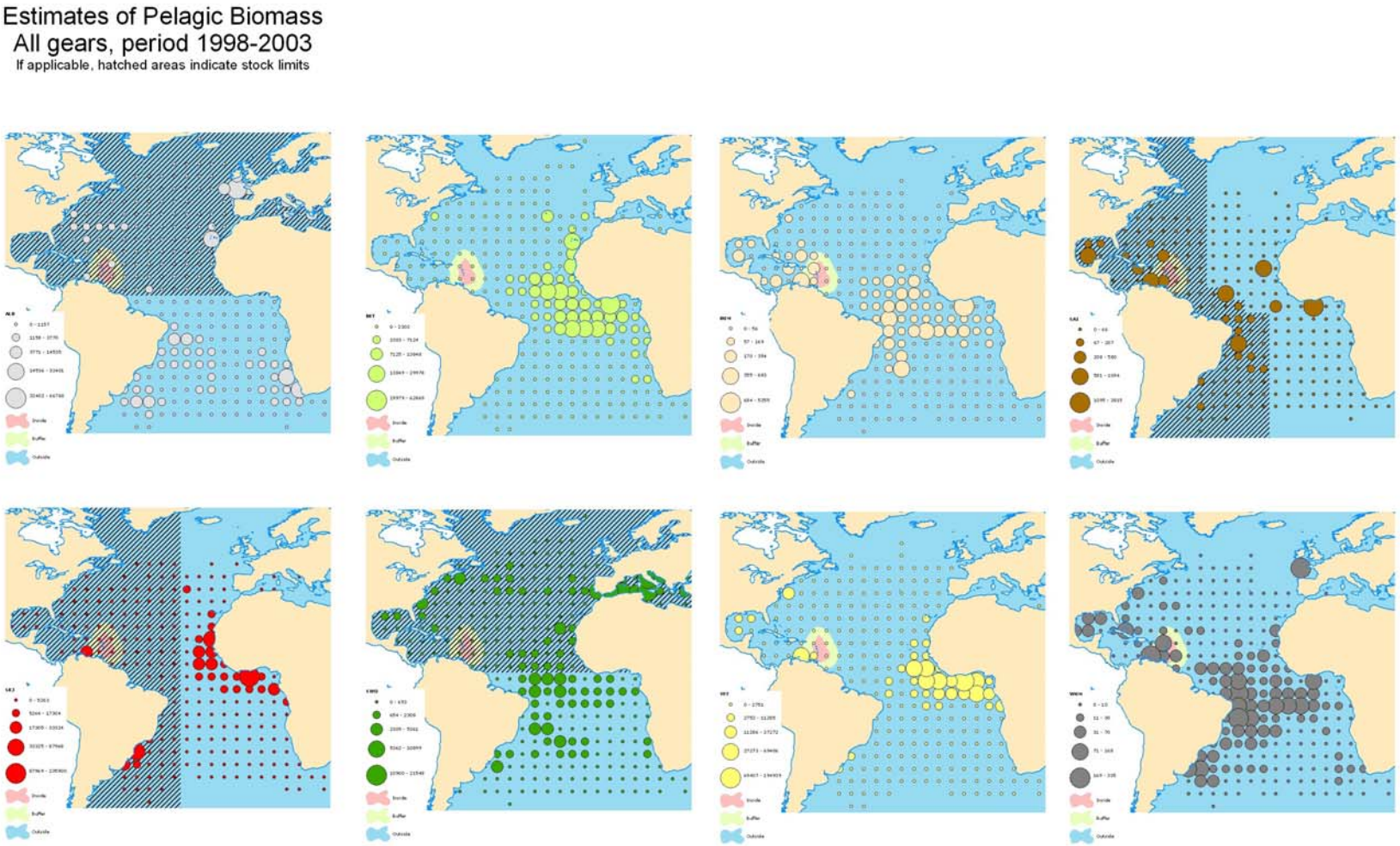

Figure A1- 3 Abundance index of main tuna and billfishes species by 5° spatial cells. The areas highlighted indicate the management unit boundaries of the stocks occurring in the LAPE (source ICCAT).

APPENDIX 2 FUNCTIONAL GROUPS PRESENT IN THE LAPE MODEL.

Group Number	Functional Group	Common Name	*Scientific Name*
1	**Seabirds**	Black-capped petrel	*Pterdroma hasitata*
		Brown pelican	*Pelacanus occidentalis*
		Cayenne tern	*Sterna eurygnatha*
		Common tern	*Sterna hirundo*
		Gull-billed tern	*Galechelidon nilotica*
		Royal tern	*Sterna maxima*
		Least tern	*Sterna antillarum*
		Sandwich tern	*Sterna sandvicensis*
		Roseate tern	*Sterna dougalli*
		Bridled tern	*Sterna anaethetus*
		Sooty tern	*Sterna fuscata*
		Laughing gulls	*Larus atricilla*
		Black noddy	*Anous minutus*
		Masked booby	*Sula dactylatra*
		Red-footed booby	*Sula sula*
		Brown noddy	*Anous stolidus*
		Red-billed tropicbird	*Phaethon aethereus*
		White-tailed tropicbird	*Phaethon lepturus*
		Audubon's shearwater	*Puffinus lherminieri*
		Magnificent frigatebird	*Fregata magnificens*
2	**Baleen whales**	Bryde's whale	*Balaenoptera edeni*
3	**Deep-diving whales**	Sperm whale	*Physeter catodon*
		Gervais' beaked whale	*Mesoplodon europaeus*
4	**Killer whales**	False Killer whale	*Pseudorca crassidens*
		Killer whale	*Orcinus orca*
		Pygmy killer whale	*Feresa attenuata*
5	**Shallow-diving small cetaceans**	Shortfin pilot whale	*Globicephala macrorhynchus*
		Atlantic Spotted Dolphin	*Stenella frontalis*
		Bottlenose dolphin	*Tursiops truncatus*
		Spinner dolphin	*Stenella longirostris*
		Pantropical spotted dolphin	*Stenella attenuata*
		Fraser's dolphin	*Lagenodelphis hosei*
		Striped dolphin	*Stenella coeruleoalba*
		Melon-headed whale	*Peponocephala electra*
		Clymene dolphin	*Stenella clymene*
		Rough-tooth dolphin	*Steno bredanensis*
6	**Swordfish**	Swordfish	*Xiphias gladius*
7	**Other Billfishes**	Atlantic blue marlin	*Makaira nigricans*
		Atlantic white marlin	*Tetrapturus albidus*
		Atlantic sailfish	*Istiophorus platypterus*
		Black marlin	*Makaira indica*
		Longbill spearfish	*Tetrapturus pfluegeri*
8	**Yellowfin tuna**	Yellowfin tuna	*Thunnus albacares*
9	**Skipjack**	Skipjack	*Katsuwonus pelamis*
10	**Albacore**	Albacore	*Thunnus alalunga*
11	**Bigeye**	Bigeye	*Thunnus obesus*
12	**Blackfin tuna**	Blackfin tuna	*Thunnus atlanticus*
13	**Other offshore predators**	Atlantic bonito	*Sarda sarda*
		Bullet tunas	*Auxis spp.*
		Little tunny	*Euthynnus alletteratus*
		Spotted oceanic triggerfish	*Canthidermis maculata*
		Ocean triggerfish	*Canthidermis sufflamen*

Group Number	Functional Group	Common Name	*Scientific Name*
14	**Mackerels**	Serra Spanish mackerel	*Scomberomorous brasiliensis*
		King mackerel	*S. cavalla*
		Cero mackerel	*S. regalis*
		Spanish mackerel	*S. maculatus*
15	**Wahoo**	Wahoo	*Acanthocybium solandri*
16	**Dolphinfish**	Common dolphinfish	*Coryphaena hippurus*
		Pompano dolphinfish	*Coryphaena equiselis*
17	**Pelagic sharks**	Blue shark	*Prionace glauca*
		Bigeye thresher	*Alopias superciliosus*
		Thintail thresher	*Alopias vulpinus*
		Longfin mako	*Isurus paucus*
		Shortfin mako	*Isurus oxyrhinchus*
		Bluntnose sixgill shark	*Hexanchus griseus*
		Great hammerhead	*Sphyrna mokarran*
		Porbeagle	*Lamna nasus*
		Smooth hammerhead	*Sphyrna zygaena*
		Tiger shark	*Galeocerdo cuvier*
		Blacktip shark	*Carcharhinus limbatus*
		Oceanic whitetip	*Carcarhinus longimanus*
		Silky shark	*Carcharhinus falciformis*
		Sandbar shark	*Carcharhinus plumbeus*
		Spinner shark	*Carcharhinus brevipinna*
18	**Flyingfish**	Fourwing flyingfish	*Hirundichthys affinis*
		Margined flyingfish	*Cheilopogon cyanopterus*
		Sailfin flyingfish	*Parexocoetus brachypterus*
19	**Coastal predators**	Keeltail needlefish	*Platybelone argalus argalus*
		Redfin needlefish	*Strongylura notata notata*
		Agujon needlefish	*Tylosurus acus acus*
		Atlantic needlefish	*Strongylura marina*
		Blue runner	*Caranx crysos*
		Black jack	*Caranx lugubris*
		Hound needlefish	*Tylosurus crocodilus*
		Crevalle jack	*Caranx hippos*
		Bar jack	*Caranx ruber*
		African pompano	*Alectis ciliaris*
		Yellowtail amberjack	*Seriola lalandi*
		Rainbow runner	*Elegatis bipinnulata*
		Leatherjacks	*Oligoplites* spp.
		Amberfish	*Seriola dumerili*
		Great barracuda	*Sphyraena barracuda*
		Guachanche barracuda	*Sphyraena guachancho*
		Sennet	*Sphyraena picudila*
		Common snook	*Centropomus undecimalis*
		Yellowtail snapper	*Ocyurus chrysurus*
		Tripletails (Lobotidae)	*Lobotidae*
		Bermuda sea chub	*Kyphosus sectatrix*
		Palometa pompano	*Trachinotus goodei*
		Permit	*Trachinotus falcatus*
		Pompano	*Trachinotus carolinus*
20	**Small offshore pelagics**	Includes juveniles of several pelagic species identified in other functional groups as well as juveniles of reef species while in the pelagic state (listed in the Ecosystem Survey report)	

Group Number	Functional Group	Common Name	*Scientific Name*
21	**Small coastal pelagics**	Atlantic bumper	*Chloroscombrus chrysurus*
		Mackerel scad	*Decapterus macarellus*
		Round scad	*Decapterus punctatus*
		Bluntnose jack	*Hemicaranx amblyrhynchus*
		Bigeye scad	*Selar crumenophthalmus*
		Threadfin scad	*Dorosoma petenense*
		False herring	*Harengula clupeola*
		Redear herring	*Harengula humeralis*
		Scaled herring	*Harengula jaguana*
		Spratt	*Harengula pensacolae*
		Dwarf round herring	*Jenkinsia lamprotaenia*
		Atlantic thread herring	*Opisthonema oglinum*
		American coastal pellona	*Pellona harroweri*
		Yellowfin herring	*Pliosteostoma lutipinnis*
		Round sardinella	*Sardinella aurita*
		Brazilian sardinella	*Sardinella brasiliensis*
		Broad-striped anchovy	*Anchoa hepsetus*
		Little anchovy	*Anchoa parva*
		Common halfbeak	*Hyporhamphus unifasciatus*
		Sargassum pelagicus	*Syngnathus pelagicus*
		Balao halfbeak	*Hemiramphus balao*
		Ballyhoo	*Hemiramphus brasiliensis*
		American harvestfish	*Peprilus paru*
22	**Small Mesopelagic fish**	(lanternfish)	*Diaphus dumerilii*
		Topside lanternfish	*Notolychnus valdiviae*
		(lanternfish)	*Lepidophanes guentheri*
		(lanternfish)	*Lampanyctus alatus*
		Warming's lanternfish	*Ceratoscopelus warmingi*
23	**Large Mesopelagic fish**	Snake mackerel	*Gempylus serpens*
		Longnose lancetfish	*Alepisaurus ferox*
		Oilfish	*Ruvettus pretiosus*
		Atlantic pomfret	*Brama brama*
24	**Leatherback turtles**	Leatherback turtles (entirely pelagic, feed on gelatinous zooplankton)	*Dermochelys coriacea*
25	**Other turtles**	Hawksbill (juveniles pelagic 1-2 yrs)	*Eretmochelys imbricata*
		Loggerhead	*Caretta caretta*
		Olive ridley (juveniles pelagic)	*Lepidochelys olivacea*
		Green turtle (juv.pelagic 2-4 yrs)	*Chelonia mydas mydas*
26	**Small squid**	Gonatidae (Mantle Length < 50 cm)	
27	**Large squid**	Onychoteuthidae and Architeuthidae Mantle Length > 50 cm	
28	**Small Zooplankton**	micro-meso-plankton (< 3-4 cm) copepods, small euphausids, etc.	
29	**Large Zooplankton**	macroplankton (> 4 cm)	
		Decapods	
		Large euphausiids	
		Mysids	
		Gelatinous plankton	
30	**Phytoplankton**		
31	**Detritus**		

APPENDIX 3 LAPE MODEL INPUT DATA SUMMARY.

	Group * biomass re-estimated in model balancing)	Biomass ($t \cdot km^{-2}$)	Method/Data Source	P/B (yr^{-1})	Method/Data Source	Q/B (yr^{-1})	Method/Data Source
1	Seabirds	2×10^{-5}	N x W (N: Schrieber and Lee, 2000; w - Vasconcellos and Watson (2004) and Mackinson *et al*. (2005); 0.5 estimate for West Indies	0.13	Vasconcellos and Watson (2004); weighted by biomass	73.69	Vasconcellos and Watson (2004); weighted
2	Baleen whales	2.51×10^{-2}	N x W (N: LAPE Cetacean Surveys; w - Trites and Pauly, 1998)	0.04	NOAA (2003)	12.19	Average from several sources: Trites and Heise, 1996; Okey, 2002; Okey and Pauly, 1998; Trites *et al*., 1999; Bundy *et al*., 2000; Zeller and Freire, 2002
3	Deep-diving whales	1.45×10^{-2}	N x W (N: LAPE Cetacean Surveys; w - Trites and Pauly, 1998)	0.04	NOAA (2003)	5.44	Daily ration (Trites *et al*., 1997; Innes *et al*., 1976)
4	Killer whales	1.58×10^{-3}	N x W (N: LAPE Cetacean Surveys; w - Trites and Pauly, 1998)	0.02	Trites and Heise (1996)	9.64	Average from several sources: Trites and Heise, 1996; Okey, 2002; Martell *et al*., 2002
5	Shallow-diving small cetaceans	3.36×10^{-2}	N x W (N: LAPE Cetacean Surveys; w - Trites and Pauly, 1998)	0.05	Assumed	13.5	Average from several sources: Browder, 1993; Bundy *et al*., 2000; Buchary *et al*., 2002; Fullton and Smith, 2002

	Group * biomass re-estimated in model balancing)	Biomass (t ·km^{-2})	Method/Data Source	P/B (yr^{-1})	Method/Data Source	Q/B (yr^{-1})	Method/Data Source
6	Swordfish	8.98 x 10^{-4}	proportion of total biomass in LAPE (from Appendix 1) and total biomass estimated by ICCAT (2006); N. Atlantic	0.372	P/B = F + M (ICCAT, 2006)	5.31	Empirical equation:Palomares and Pauly (1989)
7	Other billfishes *	5.5 x 10^{-3}	Blue and white marlin - proportion of total biomass in LAPE (from Appendix 1) and total biomass estimated by ICCAT (2006); Black marlin, sailfish and spearfish B = C/F; F from Brown *et al*. (1991)	0.42	P/B = F + M (ICCAT 2001,2006; Brown *et al*., 2001); weighted by biomass	4.59	Cox *et al*., 2002; weighted by biomass
8	Yellowfin tuna *	1.24 x 10^{-2}	At equilibrium B = C/F Catch from LAPE F from ICCAT (2004)	1.36	P/B = F + M (ICCAT, 2004, 2006)	15.53	Mean in Menard *et al*. (2000) and Cox *et al*. (2002)
9	Atlantic skipjack	1.19 x 10^{-2}	At equilibrium B = C/F Catch from LAPE F from Hampton (2000)	1.8	Mean of estimate in Hampton (2000) and Empirical equation after Pauly (1980)	19.61	Menard *et al*. (2000)
10	Albacore	9.7 x 10^{-3}	At equilibrium B = C/F Catch from LAPE F assumed = M; M estimated using Empirical equation after	0.6	P/B = F + M (see L.H.S.)	7.8	Mean of Cox *et al*. (2002) and estimate from Empirical equation after Palomares and Pauly (1989)

	Group * biomass re-estimated in model balancing)	Biomass (t ·km^{-2})	Method/Data Source	P/B (yr^{-1})	Method/Data Source	Q/B (yr^{-1})	Method/Data Source
			Pauly (1980)				
11	Bigeye tuna	1.68 x 10^{-3}	proportion of total biomass in LAPE (from Appendix 1) and total biomass estimated by ICCAT (2005);	0.74	P/B = F + M (ICCAT, 2005)	17.59	Menard *et al*. (2000)
12	Blackfin tuna *	2.1 x 10^{-3}	At equilibrium B = C/F Catch from LAPE F assumed same as that for wahoo (similar fishery) Not considered in ICCAT Task I, assumed proportion in LAPE = inside LAPE catch/total catch	1.85	P/B = F + M (F same as wahoo; M using Empirical equation after Pauly, 1980)	9.89	Empirical equation after Palomares and Pauly, 1989
13	Other offshore predators (small tunas & triggerfish)	2.3 x 10^{-3}	At equilibrium B = C/F Catch from LAPE F assumed same as that for wahoo (similar fishery) Not considered in ICCAT Task I, assumed proportion in LAPE = inside LAPE catch/total catch	1.87	P/B = F + M (F same as wahoo; M using Empirical equation after Pauly, 1980); weighted by biomass	7.44	Empirical equation after Palomares and Pauly, 1989; weighted by biomass

	Group * biomass re-estimated in model balancing)	Biomass (t ·km^{-2})	Method/Data Source	P/B (yr^{-1})	Method/Data Source	Q/B (yr^{-1})	Method/Data Source
14	Mackerels	7.8 x 10^{-3}	At equilibrium B = C/F Catch from LAPE F (Martin and Nowlis, 2004) Not considered in ICCAT Task I, assumed proportion in LAPE = inside LAPE catch/total catch	1.09	P/B = F + M (F and M from Martin and Nowlis, 2004 for Serra Spanish mackerel and Ortiz, 2004 for king mackerel; M using Empirical equation after Pauly, 1980); weighted by biomass	10.31	Empirical equation after Palomares and Pauly, 1989; weighted by biomass
15	Wahoo *	7.43 x 10^{-4}	At equilibrium B = C/F Catch from LAPE F (St Lucia - Murray and Sarvay, 1987; Murray and Joseph, 1996) Not considered in ICCAT Task I, assumed proportion in LAPE = inside LAPE catch/total catch	1.64	P/B – F+M (F and M estimates from St Lucia, see L.H.S.)	31.81	Empirical equation after Palomares and Pauly, 1989
16	Dolphinfish	1.2 x 10^{-3}	At equilibrium B = C/F Catch from LAPE F (Oxenford, 1999 – E. Caribbean) Not considered in ICCAT Task I, assumed proportion in LAPE = inside LAPE catch/total catch	4.72	Average of estimate from several sources: Oxenford, 1985; Murray, 1985; Bentivoglio, 1988 and Parker *et al*., 2000	20	Kitchell *et al*. (1999)

	Group * biomass re-estimated in model balancing)	Biomass (t ·km^{-2})	Method/Data Source	P/B (yr^{-1})	Method/Data Source	Q/B (yr^{-1})	Method/Data Source
17	Pelagic sharls		Estimated by Ecopath; assuming EE = 0.99	0.18	P/B = F + M (estimates for the north Atlantic stock of blue shark and shortfin mako, ICCAT 20050; weighted and assumed representative of the group	10	Stillwell and Kohler 1992
18	Flyingfish	1.37 x 10^{-3}	Oxenford *et al*., (1995); N per square area for each transect; total area surveyed based on Mahon (pers. com); assumed 10% *H. affinis* take to flight and 20% other 2 species; N converted to weight using max length in Samlalsingh and Pandohee, 1992 and FishBase with L/W relationship;	5.65	P/B = Z; Z for *H. affinis* from Samlalsingh and Pandohee, 1992; other 2 species not exploited; M estimated using Empirical equation after Pauly, 1980; estimate weighted assuming *H. affinis* contributes 95% to catch and *P. brachypterus* and *C. cyanopterus* only 2.5% each	24.76	Empirical equation after Palomares and Pauly, 1989; weighted by proportion to overall catch assumed
19	Coastal predators (mainly needlefishes, barracudas, large jacks, snappers) *		Estimated by Ecopath; assuming EE = 0.95	0.72	P/Q = P/B ÷ Q/B; used Q/B on R.H.S. and assumed P/Q of 0.1	7.22	Empirical equation after Palomares and Pauly (1989), as indicated in Garcia and Duarte (2002); weighted by catch

	Group * biomass re-estimated in model balancing)	Biomass (t ·km^{-2})	Method/Data Source	P/B (yr^{-1})	Method/Data Source	Q/B (yr^{-1})	Method/Data Source
20	Small offshore pelagics	7.394	LAPE Ecosystem Survey	2.15	P/Q = P/B ÷ Q/B; used Q/B on R.H.S. and assumed P/Q of 0.147, mean estimate from other models (Arreguín-Sanchez *et al*., 1993; Mendoza, 1993; Vega-Cendejas *et al*., 1993; Opitz, 1996; Manickchand-Heileman *et al*., 1998 apud Mohammed, 2003)	14.64	Empirical equation after Palomares and Pauly (1989), as indicated in Garcia and Duarte (2002); weighted by catch
21	Small coastal pelagics	12.2	LAPE Ecosystem Survey; applicable to shelf area (2% of total area)	2.15	P/Q = P/B ÷ Q/B; used Q/B on R.H.S. and assumed P/Q of 0.147, mean estimate from other models (Arreguín-Sanchez *et al*., 1993; Mendoza, 1993; Vega-Cendejas *et al*., 1993; Opitz, 1996; Manickchand-Heileman *et al*., 1998 apud Mohammed, 2003)	14.64	Empirical equation after Palomares and Pauly (1989), as indicated in Garcia and Duarte (2002); weighted by catch
22	Small mesopelagic fish *	19.36	LAPE Ecosystem Survey	3.76	Vasconcellos and Watson (2004)	18.25	Vasconcellos and Watson (2004)

	Group * biomass re-estimated in model balancing)	Biomass (t ·km^{-2})	Method/Data Source	P/B (yr^{-1})	Method/Data Source	Q/B (yr^{-1})	Method/Data Source
23	Large mesopelagic fish	10.83	LAPE Ecosystem Survey	0.15	Asymptotic weight and aspect ratio from FishBase (www.fishbase.org; Froese and Pauly, 2000)	3.55	Empirical equation after Palomares and Pauly (1989)
24	Leatherback turtles		Estimated by Ecopath; assuming EE = 0.99	0.15	Opitz (1993)	3.5	Opitz (1993)
25	Other turtles		Estimated by Ecopath; assuming EE = 0.99	0.15	Opitz (1993)	3.5	Opitz (1993)
26	Small squids *	1.51 x 10^{-2}	LAPE Ecosystem Survey	4.6	Species of small (I. illecebrosus and Todarodes sp.) and large (Dosidicus gigas) squids have an estimated life span of 1 year (Mangold, 1987; Arguelles *et al*., 2002). Assuming that 99% of squids in a population die after 1 year, with an exponential decrease in numbers, the natural mortality rate was estimated	15.86	P/Q = P/B ÷ Q/B; used P/B on L. H.S. with gross food conversion efficiency (P/Q) at 29% (Amaratunga, 1983; O'Dor and Wells, 1987)
27	Large squids	1.771 x 10^{-1}	LAPE Ecosystem Survey	4.6		15.86	

	Group * biomass re-estimated in model balancing)	Biomass ($t \cdot km^{-2}$)	Method/Data Source	P/B (yr^{-1})	Method/Data Source	Q/B (yr^{-1})	Method/Data Source
28	Small zooplankton *	3.9×10^{-3}	LAPE Ecosystem Survey	54.75	Assuming a daily turnover rate of 0.15 after Longhurst and Pauly (1987) range of 0.15 to 0.62	228.125	P/Q = P/B ÷ Q/B; used P/B on L. H.S. with P/Q of 0.24 from Optiz (1996)
29	Large zooplankton *	4.2×10^{-3}	LAPE Ecosystem Survey	40	Opitz (1993, 1996)	166.6666667	
30	Phytoplankton	21.825	LAPE Ecosystem Survey, Forget, 2007	42.8	LAPE Ecosystem Survey, Forget, 2007	NA	NA
31	Detritus	15.075	Empirical equation proposed by Pauly *et al*., (1993) with the mean estimate of primary production using the subregional and nearest neighbour approaches after Forget (2007) and a euphotic depth of 85 m from Rajendra *et al*.(1991).	NA	NA	NA	NA

APPENDIX 4 INPUT DIET COMPOSITION MATRIX FOR LAPE MODEL.

Group	Functional Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Seabirds															
2	Baleen whales															
3	Deep-diving whales															
4	Killer whales															
5	Shallow-diving small cetaceans				0.3000	0.0001										
6	Swordfish															
7	Other Billfishes									0.0017			0.0039			
8	Yellowfin tuna						0.0016	0.0070		0.0080		0.0120				
9	Skipjack						0.0016	0.1135	0.0929	0.0092		0.0120				
10	Albacore						0.0016	0.0070	0.0111	0.0080		0.0120				
11	Bigeye						0.0016	0.0185	0.0111	0.0091						
12	Blackfin tuna						0.0016	0.0070	0.0111	0.0080		0.0120			0.0006	
13	Other offshore predators		0.0750				0.0017	0.2317	0.1681	0.1007		0.0120			0.0010	0.2872
14	Mackerels		0.0750				0.0269	0.0070	0.0111	0.0080		0.0120			0.0019	0.0004
15	Wahoo						0.0016	0.0070	0.0111	0.0080		0.0120			0.0006	0.0004
16	Dolphinfish						0.0015	0.0325	0.0065	0.0008		0.0269				
17	Pelagic sharks															
18	Flyingfish	0.0826					0.0032	0.0470	0.0144	0.0281		0.2500	0.0415		0.0053	0.0330
19	Coastal predators	0.0133					0.1097	0.0604	0.0857	0.0465	0.0012	0.0028	0.1586	0.0001	0.0360	0.0195
20	Small offshore pelagics	0.1799	0.1452	0.0019	0.0968	0.2248		0.1322	0.0471	0.1918	0.0075	0.0248	0.4971	0.0535	0.8726	0.1540
21	Small coastal pelagics	0.0059	0.0048	0.0001	0.0032	0.0074	0.1225	0.0044	0.0016	0.0063	0.0002	0.0008	0.0164		0.0288	0.0051
22	Small Mesopelagic (forage) fish		0.1500	0.0080	0.1500	0.1037	0.0355	0.0002	0.0138	0.0896	0.0880	0.1081				0.0012
23	Large Mesopelagic (forage) fish			0.0120	0.1500	0.1037	0.1237	0.1370	0.1330	0.1702	0.4788	0.3946	0.0223		0.0000	0.1732
24	Leatherback turtles															
25	Other turtles															
26	Small squid	0.5431		0.0080	0.1750	0.3067	0.3930	0.1259	0.1678	0.0905	0.0901	0.0226	0.0682	0.7509	0.0153	0.1458
27	Large squid			0.0500	0.1250	0.2511	0.0231	0.0005	0.0028		0.0103					0.0028
28	Small Zooplankton	0.0057							0.0021	0.0008			0.0912	0.1116	0.0143	0.0027
29	Large Zooplankton	0.0061	0.3000				0.0175	0.0009	0.0678	0.0197	0.0306	0.0358			0.0042	
30	Phytoplankton															
31	Detritus															
	Imports	0.1633	0.2500	0.9200		0.0027	0.1262	0.0613	0.1411	0.1949	0.2934	0.0498	0.1008	0.0839	0.0187	0.1747
	SUM	1.0000	1.0000	1.0000	1.0000	1.0002	0.9938	1.0009	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.9993	1.0000

Input diet composition matrix for LAPE model.(continued)

Group	Functional Group	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	Seabirds		0.0055												
2	Baleen whales														
3	Deep-diving whales														
4	Killer whales														
5	Shallow-diving small cetaceans		0.0094												
6	Swordfish		0.0167												
7	Other Billfishes	0.0120	0.0150												
8	Yellowfin tuna		0.0008												
9	Skipjack	0.0007	0.0004												
10	Albacore		0.0004												
11	Bigeye		0.0004												
12	Blackfin tuna	0.0102	0.0004												
13	Other offshore predators	0.0115	0.0011		0.0001				0.0001			0.0080			
14	Mackerels	0.0103	0.0178		0.0002							0.0080			
15	Wahoo	0.0102	0.0004												
16	Dolphinfish	0.2115	0.0003												
17	Pelagic sharks		0.0438												
18	Flyingfish	0.1999	0.0001		0.0066				0.1791				0.0835		
19	Coastal predators	0.2258	0.2147		0.0679				0.0124			0.0080	0.0835		
20	Small offshore pelagics	0.0698	0.0476						0.0056						
21	Small coastal pelagics	0.0023	0.0016		0.3885				0.0002						
22	Small Mesopelagic (forage) fish	0.0014	0.0045		0.0010			0.0096	0.0056			0.2860	0.1670		
23	Large Mesopelagic (forage) fish	0.0028	0.0662						0.3513			0.0240			
24	Leatherback turtles		0.0000												
25	Other turtles		0.0006												
26	Small squid	0.0774	0.1638		0.0109			0.0044	0.0981			0.1140	0.1670		
27	Large squid		0.0000						0.0050				0.1670		
28	Small Zooplankton	0.0291	0.0000	1.0000	0.0430	0.5587	0.5587	0.9876	0.1075	0.0200	0.0500	0.1410		0.1000	1.0000
29	Large Zooplankton	0.0288	0.0006		0.0020	0.0011	0.0011		0.0700	0.9800	0.0500	0.3880	0.1670		
30	Phytoplankton					0.0239	0.0239							0.8000	
31	Detritus		0.0044		0.0013	0.0016	0.0016							0.1000	
	Imports	0.0936	0.3791		0.4785	0.4147	0.4147	0.0012	0.1650		0.9000	0.0240	0.1670		
	SUM	0.9973	0.9956	1.0000	1.0000	1.0000	1.0000	1.0028	1.0000	1.0000	1.0000	1.0010	1.0020	1.0000	1.0000

APPENDIX 5 CATCH DATA (TONNES) BY FLEET INCORPORATED IN THE LAPE MODEL.

Group Number	Functional Group	Beach Seine	Decked inboard (troll, longline, gillnets)	Longliners	Open outboard (other)	Open-outboard (troll, longline, gillnets)	Marine Mammal SVG	Marine Mammal STL	Open outboard (other)	Recreational	Outside LAPE
4	Killer whales						5.628	0.319			
5	Shallow-diving small					0.593	0.508	15.670			
6	Swordfish		0.016	1.487		0.030					92.677
7	Other Billfishes	0.015	1.462	48.517		7.668	0.004			0.653	679.777
8	Yellowfin tuna	0.003	1.125	42.099		5.275	0.048	0.001		0.002	4938.687
9	Skipjack	0.004		14.637		11.605	0.239				2887.955
10	Albacore		0.083	3.310		0.618	0.013	0.020			1771.779
11	Bigeye		0.011	0.111		0.008					347.225
12	Blackfin tuna	0.009		0.023		723.664	0.397	3.053		0.010	687.671
13	Other offshore predators	24.276	26.182	11.983		628.306	0.009	0.085		0.022	886.070
14	Mackerels	3.587		0.095	0.157	1221.220	0.006	0.165	0.157	0.131	3334.436
15	Wahoo	0.016	18.124	98.935		217.739	1.456	7.144		1.832	153.457
16	Dolphinfish	0.413	333.244	31.251	0.108	992.989	1.221	10.526	0.108	1.213	828.872
17	Pelagic sharks		8.940	68.524	0.135	891.763	0.216	0.442	0.135	0.040	760.800
18	Flyingfish	0.339	1392.180	59.540		211.939		6.740			
19	Coastal predators	204.093	2.920		0.433	381.048	0.517		0.433		
21	Small coastal pelagics	3289.864	14.720		0.223	230.565	2.036		0.223		
24	Leatherback turtles	1.279				2.136					
25	Other turtles	1.346			6.800	12.514	0.106	0.434	6.800	0.106	
27	Large squid					4.000					

Catches are re-scaled based on the associated proportion of total biomass inside and outside the LAPE and the associated component of fishing mortality assumed proportional to relative catches in the two regions. The re-scaled catch input is represented per unit area (LAPE area = 610,000 km^2).

APPENDIX 6 AVERAGE EX-VESSEL PRICES (US$/KG) OF FUNCTIONAL GROUPS IN THE LAPE (2001-2005).

Group Number	Functional Group	Average Unit Price (US$/kg)
4	Killer whales	3.71
5	Shallow-diving small cetaceans	3.68
6	Swordfish	3.96
7	Other Billfishes	4.22
8	Yellowfin tuna	4.51
9	Skipjack	3.92
10	Albacore	3.85
11	Bigeye	4.44
12	Blackfin tuna	4.47
13	Other offshore predators	2.84
14	Mackerels	3.65
15	Wahoo	5.05
16	Dolphinfish	5.42
17	Pelagic sharks	1.27
18	Flyingfish	1.22
19	Coastal predators	2.56
21	Small coastal pelagics	2.39
24	Leatherback turtles	1.30
25	Other turtles	3.82
27	Large squids	2.06

APPENDIX 7 DIET ODDITIES

Several odd observations have been detected arising from the diet compositions estimated for the various functional groups. These should be addressed in future versions of the LAPE trophic model.

Functional Group		Issue
1	Seabirds	Phytoplankton in diet?
2	Baleen whales	Eat mackerel and other offshore predators? But don't eat any squid?
8	Yellowfin	Skipjack a key predator of billfish, yelllowfin, skipjack, albacore, blackeye, blackfin.
9	Skipjack	Yellow is top predator of skipjack
14	Mackerels	Small squids cause the second highest mortality of mackerel? Cannibalism is the highest mortality
16	Dolphinfish	Cannibalism eclipses all other predation mortality
17	Pelagic sharks	Cannibalism highest mortality. This probably OK – but consequences for dynamics
20	Small offshore pelagics	Small mesopelagics – largest predation mortality. 4th most important predator is large zooplankton?
21	Small coastal pelagics	5th most important predator is large zooplankton?
23	Large mesopelagics	Cannibalism dominates predation mortality. Prey groups include coastal predators and other offshore predators?
26	Small squids	Cannibalism dominates mortality. Prey items include mackerels, other offshore predators and coastal predators
27	Large squids	Cannibalism dominates predation
28	Small zooplankton	Cannibalism about equal to predation by large zoops.
29	Large zooplankton	Prey upon small offshore and coastal pelagics

APPENDIX 8 SOCIO-ECONOMIC DATA FOR SELECTED FISHERIES IN THE LESSER ANTILLES.

COUNTRY SOURCE	ST VINCENT & GRENADINES Sophia Punnett		
Currency: EC dollar	Fleet		
	Open outboard (troll, palangue, longline)	Open outboard (gillnets)	Beach seines
Number of boats	337	22	102
# Engines used per boat	1	1	1
# of fishing trips per year	220	265	265
Duration of each trip (days)	1	1	1
Total fishing days	220	265	265
Vessel cost	$ 27 000	$ 9 000	$ 15 000 for large vessel, $ 8 000 for engine boat, $ 3 000 for small boat (therefore cost of 1 fleet = $ 26 000)
Engine cost	$ 12 500	$ 8 000	$ 6 700
Annual gear cost	Trolling: $ 2 500, Palangue: $ 5 000	$ 1 500	$ 6 000
Other investment costs (vehicle, ice plant, refrigerated bait container)			
Jobs: fishers per boat	3	5	10
Average cost per unit per year			
Vessel maintenance	$ 5 000	$ 1 200	$ 3 000
Engine maintenance	$ 2 200	$ 1 500	$ 1 500
Gear maintenance	Troll: EC$ 500, Palangue: EC$ 500	$500	$500
Equipment			
Insurance	No insurance	No insurance	No insurance
Satellite communication, accounting services, storage, port/dry docking fees, vessel repair facilitites, office rental etc.			
License Fees	No fees	No fees	No fees
Market Fees	Varies per species;$ 0.20 per lb dolphin, kingfish, tuna. $ 0.10 per lb of skipjack.	$ 0.08 per lb	0.08 to 0.10 per lb
Subsidies	Duty-free concession for import of boats and engines		

COUNTRY SOURCE	ST VINCENT & GRENADINES Sophia Punnett		
Currency: EC dollar	Fleet		
	Open outboard (troll, palangue, longline)	Open outboard (gillnets)	Beach seines
Loan repayment	(14% interest repayment fee) Avg $700 per month, difficult to determine what % of fishers have loans		
Average cost per unit per trip			
Fuel	$675 (60 gallons at $11.25 a gallon)	$90	$90
Oil	$87	$14.50	$14.50
Bait	Troll: $40. Palange: $80	0	0
Ice	Most boats do not carry ice		
Food	$75	Each person provides their own. Max. $10.00 each	
Overall average cost per trip			
Share	1 share for boat owner, 1 for engine, 1 for each crew, 1 for captain	50% for owner, 50% for crew after $20.00 for every $100 is given to the diver	50% for the owner, 50% for the crew
Management and monitoring cost (Division's associated budget component)	Unable to allocate costs to the different fleets, however the annual general running costs of Fisheries Division (salaries, operating costs of Division's office, vessel maintenance, project costs etc.) = $1 500 000.00		

COUNTRY SOURCE	GRENADA Sandra Grant				
Currency: US dollars	Fleets				
DETAILS	Open outbaord pirogue (troll)	Cabin Pirogue (longline); 6-9 m	Open Pirogue (longliner); <5m	Longliner medium (7-15m)	Seine boats
Number of boats	245	200		207	37
# Engines used per boat		2 outboard engines: 40-90 Hp (each)	One outboard engine: 15-75 Hp	One (1) inboard diesel: 7--350 Hp	
# of fishing trips per year		74	89	35	
Duration of each trip (days)		1	1	5	
Total fishing days		74	89	180	
Vessel cost					
Engine cost					
Annual gear cost					
Other investment costs (vehicle, ice plant, refrigerated bait container)					
Vessel + Engine + Gear cost		$18,000	$6,000	$120,000	
Jobs: fishers per boat		2 crew + 1 helper	2 crew + 1 helper	3 persons/ boat + 2 helpers +1 cleaner	
Average cost per unit per year					
Vessel maintenance					
Engine maintenance					
Gear maintenance					
Equipment					
Vessel + Engine maintenance		$1,920	$1,200	$3,000	
Insurance				$744	
Satellite communication, accounting services, storage, port/dry docking fees, vessel repair facilitites, office rental etc.					
License Fees					
Market Fees					
Subsidies		$1,554	$534	$4,865	
Loan repayment		$2,484	$1,200	$6,600	
Average cost per unit per trip					
Fuel					
Oil					

COUNTRY SOURCE	GRENADA Sandra Grant				
Currency: US dollars	Fleets				
DETAILS	Open outbaord pirogue (troll)	Cabin Pirogue (longline); 6-9 m	Open Pirogue (longliner); <5m	Longliner medium (7-15m)	Seine boats
Bait					
Ice					
Food					
Overall average cost per trip		$9,490	$6,230	$28,875	
Share		50% to owner and 25% to each crew	50% to owner and 25% to each crew	50% to owner, 17% each to crew	
Management and monitoring cost (Division's associated budget component)					

COUNTRY SOURCE	BARBADOS: Christopher Parker			
Currency Units Barbados dollars	Fleets			
DETAILS	Moses (gillnets)	Dayboats (troll, gillnets)	Iceboats (troll, gillnets)	Longliner large (>15m)
Number of boats	485		414	37
# Engines used per boat	1	1	1	1
# of fishing trips per year	?	125	15	?
Duration of each trip (days)	<1	<1	7	10
Total fishing days		<125	105	
Vessel cost		$55 000	$200 000	$425 000
Engine cost				
Annual gear cost		$1 000	$4 000	$25 000
Other investment costs (vehicle, ice plant, refrigerated bait container)				
Jobs: fishers per boat	2	2	3	3
Average cost per unit per year				
Vessel maintenance				
Engine maintenance				
Gear maintenance				
Equipment				
Vessel + Engine maintenance		$2 000	$6 000	$10 000
Insurance		$2 000	$5 000	$10 000
Satellite communication, accounting services, storage, port/dry docking fees, vessel repair facilitites, office rental etc.				
License Fees				
Market Fees		Market tolls paid		
Subsidies		Duty free concessions		
Loan repayment		$8 300	$24 000	$5 000
Average cost per unit per trip				
Fuel		$200	$300	$450
Oil		$50	$100	$150
Bait				
Ice		0	$1 000	$1 200

COUNTRY SOURCE	BARBADOS: Christopher Parker			
Currency Units Barbados dollars	Fleets			
DETAILS	Moses (gillnets)	Dayboats (troll, gillnets)	Iceboats (troll, gillnets)	Longliner large (>15m)
Food		$30	$315	$450
Overall average cost per trip				
Share				
Management and monitoring cost (Division's associated budget component)				
Barbados: loan repayment for iceboats and longliners - loan repayed in 7 years - 13% interest per annum				
Barbados: loan repayment for dayboats - loan repayed in 7 years - 13% interest per annum				

COUNTRY SOURCE	TRINIDAD Martin *et al.*, 2004
Currency US dollars	Fleet
DETAILS	Longliners (14 - 24 m)
Number of boats	10
# Engines used per boat	Inboard diesel engines between 160 - 400 Hp
# of fishing trips per year	14
Duration of each trip (days)	18
Total fishing days	182
Vessel cost	$134 921
Engine cost	
Annual gear cost	$659
Other investment costs (vehicle, ice plant, refrigerated bait container)	
Jobs: # of fishers employed per boat	4
Average cost per unit per year	
Vessel maintenance	$ 11 830
Engine maintenance	
Gear maintenance	
Equipment	
Insurance	$ 6 947
Satellite communication, accounting services, storage, port/dry docking fees, vessel repair facilitites, office rental etc.	
License Fees	
Market Fees	
Subsidies	
Loan repayment	
Average cost per unit per trip	
Fuel	$635
Oil	$79
Bait	$1 349
Ice	$357

COUNTRY SOURCE	TRINIDAD Martin *et al.*, 2004
Currency US dollars	Fleet
DETAILS	Longliners (14 - 24 m)
Food	$345
Overall average cost per trip	
Share	Owner receives 55% earnings and crew 45% after deduction of trip expenses
Management and monitoring cost (Division's associated budget component)	