PART II: ECOSYSTEM MODELS

A Generic Marine Ecosystem Model for the Southeastern Caribbean in the Late 1990s: Application to Grenada and the Grenadines.

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ABSTRACT

A generic ecosystem model was constructed for the southeastern Caribbean region using the Ecopath with Ecosim software, covering the late 1990s. It integrates available ecological, biological and fisheries related information for the region. The model was adjusted to the Exclusive Economic Zone (EEZ) of Grenada and the Grenadines by inclusion of the respective habitat areas and fisheries catches in 1999. Model parameterization, preliminary results, knowledge gaps and future research are discussed.

INTRODUCTION

The collapse of many fisheries worldwide has prompted scientists to re-examine the methodologies used for assessing and managing fish stocks. Failure to reliably predict stock responses to increasing fishing pressure is often attributed to single-species approaches to assessment. These traditional approaches usually consider individual species in isolation from the surrounding environment, thereby neglecting the important inter-specific interactions (e.g. competition and predation) and environmental impacts on fisheries resources, as well as the impacts of fisheries on the ecosystem. Traditional single-species assessments, however, provide essential biological (e.g., growth) and fishery related (e.g., fishing mortality) information that can be used in models depicting the multi-species nature of the fisheries and resources. The importance of traditional assessments thus remains undisputed. However, a framework is required for integrating these estimates and examining their biological and ecological compatibility, and the overall fishing impacts on both target and non-target species. This has contributed to the development of ecosystem-based management, as called for in the United Nations Convention on the Law of the Sea (United Nations, 1983), the 1992 Convention on Biological Diversity (UNEP, 1992), the 1995 United Nations Fish Stock Agreement (United Nations, 1995), the FAO Code of Conduct for Responsible Fisheries (FAO, 1995) and more recently, the 2001 Reykjavik Conference on Responsible Fisheries in the Marine Ecosystem (Nuengsigkapian, 2002). The inshore reef and shelf resources of the southeastern Caribbean islands are overexploited (Mahon, 1993; Singh-Renton and Neilson, 1994). Rebuilding of these depleted resources can form the basis for an ecosystem-based fisheries management approach. These fisheries remain the main source of income for the majority of fishers without the financial resources to invest in semi-industrial longline vessels for exploiting the offshore pelagic fishery. These resources have also supported ‘buffer fisheries’ ensuring a continued livelihood for fishers during the pelagic ‘off-season’. Until recently, inshore fisheries have been the main fisheries in the Grenadines. While future efforts are directed at increasing exploitation of offshore, highly migratory, large pelagic resources, stock assessments by the International Commission for Conservation of Atlantic Tunas (ICCAT) indicate that many large tunas and billfishes are already over-exploited. Hence the prospects for development are limited. The status of smaller pelagics (e.g., mackerels) is unknown.

The main objective of the present study was to integrate available ecological, biological and fisheries related information for resources in the southeastern Caribbean in a generic, preliminary marine ecosystem model for the region, and present a case example for one country. This may allow estimation of the available resources and flows within the ecosystem, and hence contribute to a better understanding of ecosystem structure and function.

METHODS

The marine ecosystem model was constructed using Ecopath with Ecosim (Christensen *et al.*, 2000, Pauly *et al.*, 2000). The software allows for construction of mass-balance trophic models (Christensen *et al.*, 2000; www.ecopath.org). It was first developed by Polovina (1984) for estimating biomass of species groups on the French Frigate Shoals in the north-west Hawaiian Islands. Subsequently, various routines implementing theoretical approaches in ecology (e.g., Ulanowicz, 1986) were incorporated into Ecopath (Christensen *et al.*, 2000), enabling detailed analysis of flows between groups in the system. The software is comprised of three components: a static mass-balance snap-shot of the system (Ecopath); a time dynamic simulation module for policy exploration (Ecosim, Walters *et al.*, 1997); and a spatial and temporal dynamic module for exploring optimum placement and relative size of protected areas on the resources within the ecosystem (Ecospace, Walters *et al.*, 1999). In the present study, only Ecopath was used.

Habitat area

The Ecopath parameter called 'habitat area' refers to the fraction of the total area covered by a model in which a given functional group occurs (Christensen *et al.*, 2000). The area being modeled for this case study of Grenada and the Grenadines (Figure 1) comprises the EEZ of 25,957 km^2 (Global Maritime Boundaries Database: Veridian MRJ Technology Solution, 2000), containing reef areas of 209 km^2 (Oliver and Noordeloos, 2002; Bacon *et al.*, 1984) and non-reef shelf areas of 1,595 km^2 (Mahon, 1993). Thus, habitat area fractions of 0.931, 0.008 and 0.061 were estimated for pelagic, inshore reef and shelf species, respectively. The distribution of pelagic species, which also feed on reef species, was assumed to cover the reef and outer EEZ (0.939 of total habitat area). A habitat area of 0.069 was estimated for the snapper, grouper, shark, spiny lobster and queen conch groups (see below), which are distributed across both the shelf and reef areas. It was assumed that juveniles of predatory pelagic species and small coastal pelagics were confined to shelf areas. Turtles were assumed confined to reef areas. Cephalopods and phytoplankton are distributed throughout the EEZ and reef areas, microfauna and detritus throughout the shelf and reef areas and zooplankton are present in all three areas.

Functional groups

The model comprises 50 functional groups, plus detritus. Three are mammals, 33 are fish groups (including several groups split into adults and juveniles), eight are invertebrates, three are primary producers, plus zooplankton, seabirds and sea turtles. A complete list of the species assigned to each fuctional group and associated parameters can be obtained from the author.

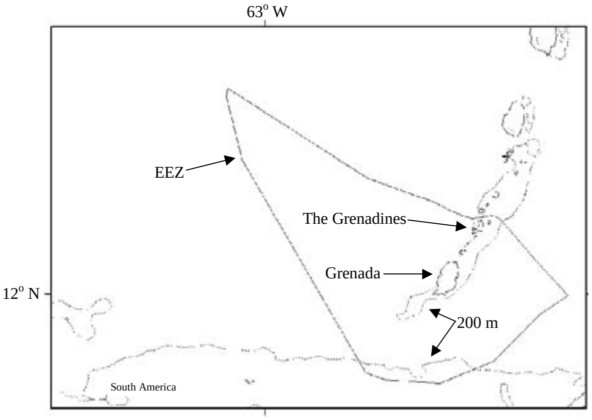

Figure 1. Map of Grenada and the Grenadines, showing the EEZ as well as the 200 depth contour.

Marine mammals

A list of marine mammals present in the Caribbean Province (Longhurst *et al.*, 1995) was assembled from the distributional information of Jefferson *et al.* (1993). This list comprises seven species of baleen whales, 12 species of toothed/beaked whales and 11 species of dolphins. Others (Reeves, 1988; Levenson and Leapley, 1978; Gordon *et al.*, 1998; Mattila *et al.*, 1994; Winn *et al.*, 1975) have listed additional marine mammal species in the southeastern Caribbean region. However, the species incorporated in this model are confined to those for which information is available.

Fish groups

Using a species list generated for the Caribbean from FishBase (Froese and Pauly, 2000; www.fishbase.org), individual species were assigned functional groups based on similarities in habitat, diet type and maximum size of fish species in the ecosystem. Because of data limitations, only 379 of the 1,072 species listed were included in the model. Exploited groups, identified based on catch statistics supplied by the Grenada Department of Fisheries, were explicitly represented to facilitate future examination of the impacts of fishing on the ecosystem. Since catches of reef and demersal shelf species of snappers (Lutjanidae) were all reported under the general heading 'snappers', and similarly for groupers (Serranidae) and sharks, it was not possible to represent these groups separately by habitat in the grouping. Further, since shark landings were not identified to the species level, thereby enabling assignment to the pelagic or demersal habitat, it was assumed that only pelagic sharks are landed as by-catch of the longline fishery.

To reduce instances of cannibalism, the adults and juveniles of top predators with ontogenetic shifts in diet and differences in growth and mortality were represented in separate groups, which also avoids the appearance of spurious cycles in Ecosim simulations (Christensen *et al*., 2000). Here, sharks, mackerels, snappers, groupers and jacks, were split into separate adult and juvenile components.

Functional groups were assigned names reflective of the most important commercial species they included. Non-exploited groups were assigned general names. This generated 33 fish groups, seven of which comprised the juveniles of predatory species, and 22 of which are exploited commercially.

Non-fish consumers and primary producers

Based on diet composition data in FishBase (Froese and Pauly, 2000; www.fishbase.org), for the respective fish groups, 11 non-fish groups, excluding detritus, were identified. The spiny lobster (*Panulirus argus*) and queen conch (*Strombus gigas*) were explicitly represented because of their commercial importance (Mahon, 1993). The other groups were organized according to Opitz (1996), and included cephalopods, benthic crustaceans, molluscs and worms, echinoderms, and zoobenthic sessile animals. Four species of marine turtles are exploited in the region (Rebel, 1974): loggerhead turtle (*Caretta caretta*); green turtle (*Chelonia mydas*); hawksbill turtle (*Eretmochelys imbricata*) and leatherback turtle (*Dermochelys coriacea*). These were all represented in one general group. All seabirds were also pooled into one group. Primary producers consisted of three groups: seagrasses and seaweeds, symbiotic algae, and phytoplankton.

Model parametrization

Two related models were consulted for model parameterization, the coral reef model of the US Virgin Islands constructed by Opitz (1996), and the pelagic ecosystem model for the central Pacific constructed by Kitchell *et al.* (1999). These models were used to assess the suitability of input parameters for similar functional groups in the present model. Input parameters were reviewed for ecological validity according to Christensen *et al.* (2000). These included a specified range for the production/consumption ratio (0.05 to 0.3) and estimates of total mortality which exceed natural mortality for exploited species. For cannibalistic species, the associated proportion of the diet should be less than 20%; for groups feeding at trophic levels higher than themselves the associated component of the diet should be less than 10%. Initial and balanced input values are listed in Table (1).

Biomass

Marine mammals

An estimate of biomass was derived for the entire Caribbean region using data in Trites *et al.* (1997), adjusted for the Caribbean Province (4.48 x 10^6 km^2) after Longhurst *et al.* (1995). Data were available for seven baleen, 12 toothed/beaked whales and 11 dolphin species occurring in the Province (Table 2).

Fish groups

Large tunas and other pelagics

Singh-Renton and Neilson (1994) presented estimates of maximum sustainable yield (MSY), computed by the International Commission for the Conservation of Atlantic Tunas (ICCAT), for several highly migratory pelagic species in the Atlantic Ocean (Table 3). Using the estimated MSY for yellowfin tuna (*Thunnus albacares*), albacore (*Thunnus alalunga*), bluefin tuna (*Thunnus thynnus thynnus*) and bigeye tuna (*Thunnus obesus*) for the respective distribution ranges, and assuming even distribution, the potential yield per unit area was estimated. Christensen (1996) estimated that approximately 25 per cent of fish production goes to catches or potential yield. Hence B * (P/B) * 0.25 = Potential Yield (where B is the biomass and P/B the production/biomass ratio). Using the estimate of P/B below (1.23 year^{-1}), and potential yield per unit area, total biomass of large tunas was estimated at 0.021 t·km^{-2}. This is comparable to biomasses estimated for similar species in the central Pacific (Kitchell *et al.*, 1999).

Mackerels

In this model landings were treated synonymous with yield although it is understood that yield also includes catches which are not landed. Hence, biomass estimates based on landings are considered minimum estimates. George *et al.* (2001) estimated fishing mortality rate for *Acanthocybium solandri* at 3.98 year^{-1}, the difference between total mortality (4.612 year^{-1} from catch curve analysis) and natural mortality (0.63 year^{-1}, using Pauly, 1980). The estimated total mortality, however, seems quite high, implying a fishing mortality rate of more than six times natural mortality. Thus, a fishing mortality equivalent to twice the natural mortality rate (1.26 year^{-1}) was assumed representative for the group.

The combined catch of all mackerel species in Grenada and the Grenadines was 50.74 t in 1997 (Grenada Fisheries Department, unpublished data). Assuming that the catches were taken within the EEZ area (24,153 km^2), the estimated biomass is 0.00167 t·km^{-2}.

Small tunas, barracudas and other pelagics

Biomass of small tunas, barracudas and other pelagics was estimated using the method described for large tunas, the estimate of P/B derived below and a catch estimated at 0.0013 t·km^{-2} for skipjack tunas (Table 3), using data from Singh-Renton and Neilson (1994). The resulting biomass estimate is 0.006 t·km^{-2}. Since data for barracudas and other pelagics are not considered, this biomass should be considered a very low estimate.

Coryphaena spp.

Parker *et al.* (2001) estimated fishing mortality (5.27 year^{-1}) for *Coryphaena hippurus* in the eastern Caribbean. This was taken as the difference between the estimated total mortality (5.98 year^{-1}) from catch curve analysis and natural mortality (0.71 year^{-1}) estimated by the authors using Pauly (1980). The overall catch of *Coryphaena* spp. within the EEZ (24,153 km^2) of Grenada and the Grenadines is 132 t. The estimated biomass is 0.001 t·km^{-2}.

Four-winged and other flyingfishes

Oxenford *et al.* (1995) reported on visual surveys to estimate abundance of the four-winged flyingfish (*Hirundichthys affinis)* and other flyingfishes (*Parexocoetus brachypterus* and *Cypselurus cyanopterus*) in the southeastern Caribbean region. The total number of fish of each species sighted was estimated as the product of the mean number of each species sighted per 0.5 nautical mile transect, and the total number of such transects surveyed (Table 4). Using length-weight conversion parameters and maximum length from Samlalsingh and Pandohee (1992), and FishBase (Froese and Pauly, 2000), the corresponding weight of each species sighted over the entire survey area was estimated. Zuyev and Nikol'skiy (1980) estimated that about 20% of flyingfish take to the air within 25m of an approaching vessel. However, Oxenford *et al.* (1995) suggested a lower percentage for *H. affinis* which is distributed deeper than the other species. Therefore, it was assumed that 10% of the number of *H. affinis* took to flight while 20% each of the remaining two species did the same. This assumption was used to adjust the estimated number taking to flight to the total number existing in the survey area. The area surveyed was estimated as the product of transect length (0.5 nm), number of transects surveyed and a total horizontal distance of 10 m surveyed by observers on either side of the research vessel (R. Mahon, pers. comm.). Biomass estimates of 0.0011 t·km^{-2} and 0.0002 t·km^{-2} were computed for the four-winged flyingfish and other flyingfishes, respectively. These estimates, however, seem low, especially since these species are the major prey for *Coryphaena* spp., and are also eaten by tunas.

An alternative estimate was derived using B = Y/F with estimates of annual catch (Y = 433 t) and fishing mortality (F = 3.3 year^{-1}) after Samlalsingh and Pandohee (1992) for *H. affinis* off Tobago. A fishing area of 250 km^2 was assumed based on the fishing area map provided by the authors. The estimated biomass is 0.524 t·km^{-2}. This is comparable to the corresponding group in the Central Pacific (Kitchell *et al.*, 1999). Using a raising factor equivalent to the ratio of biomass estimated for the four-winged flyingfish from Oxenford *et al.* (1995) and Samlalsingh and Pandohee (1992), the biomass estimate for 'other flyingfish' after Oxenford *et al.* (1995) was adjusted to 0.116 t·km^{-2}.

Demersal and reef sharks

Based on information in Saetersdal *et al.* (1999) and a personal communication from Mr Oddgeim Alvheim, who provided data from the NanSis Database (documenting survey results of R/V *Dr Fridtjof Nansen* off the South American shelf in 1988), biomass of demersal and reef sharks was estimated at 0.385 t·km^{-2} for the areas off the north coast of Trinidad. A similar biomass was assumed for the group in Grenada. However, because of the greater shelf area off Trinidad and the higher nutrient inflow from discharges of the Orinocco and Amazon rivers, it can be expected that biomass of demersal species is greater off Trinidad than around the oceanic islands further north.

Reef fishes (reef jacks, groupers, etc.)

Corless *et al.* (1997) estimated densities for several reef species in St Lucia. From these, the corresponding length-weight relationship from various sources in FishBase (Froese and Pauly, 2000), and the mean common length from Humann (1991), estimates of biomass were derived for selected species (Table 5). The estimate for *Caranx ruber* (4.45 t·km^{-2}) was taken as representative for Carangidae, similarly for the other groups listed. However, since other species of the group are not included, this estimate should be considered a minimum. Biomass of triggerfish and similar species was estimated using data for *Mulloidichthys martinicus* (11.9 t·km^{-2}; Table 5) and an estimate of 0.0116 t·km^{-2} for grunts off Trinidad's north coast (NanSis Database, Mr Oddgeim Alvheim, pers. comm.). The combined estimate (11.91 t·km^{-2}) was used as representative of this group.

Other carnivorous demersals

Manickchand-Heileman (1994) examined the distribution and abundance of flatfish on the South American shelf from Colombia to Suriname. Data on density and the associated mean individual weight of demersal species of the families Bothidae, Cynoglossidae, Pleuronectidae and Soleidae were presented for four separate surveys of the same area, with mean biomass of 0.141 t·km^{-2}. This was a minimum estimate, as the group comprises several other species besides those of the families listed.

Croakers, snooks and other carnivorous/omnivorous demersals

A biomass estimate of 2.032 t·km^{-2} for croakers off the north coast of Trinidad, was taken from the NanSis Database (Mr Oddgeim Alvheim, pers. com.) and used as the group representative. It was assumed that the biomass of other omnivorous demersals was the same as for other carnivorous demersals.

Non-Fish Groups

Cephalopods

A mean biomass estimate for squids (0.023 t·km^{-2}) off the north coast of Trinidad, obtained from the NanSis Database, was used as the group representative.

Queen conch

Several estimates of abundance and biomass were available for queen conch (CFMC and CFRAMP, 1999). The biomass estimate of 2.739 t·km^{-2} (Appeldoorn, 1995), for the artisanal zone of the Pedro bank (Jamaica) was used in the model. This estimate was selected because of the similarity of Jamaican to Grenada fisheries, and because the estimate was derived for 1997, closest to the time period (1999) covered in this model.

Echinoderms

A biomass estimate of 3.24 t·km^{-2}, derived under the Caribbean Coastal Marine Productivity Network, for *Diadema* spp. in Barbados was used as the group representative (CARICOMP, 2001).

Seagrasses, seaweeds and other autotrophs

The mean biomass of 3167.15 t·km^{-2} estimated for turtle grass and other autotrophs in Barbados under the CARICOMP programme was used (CARICOMP, 2001).

Phytoplankton

Primary productivity (PP) estimates used are based on SeaWiFS satellite data analyzed by the Institute for Environment and Sustainability of the EC Joint Research Centre (www.me.sai.jrc.it). These relied on chlorophyll, photosynthetically active radiation, and sea surface temperature maps to estimate PP from the model of Behrenfeld and Falkowski (1997). The resulting PP maps are available on a monthly and quarterly basis, but for the present study a one-year production average representing 1999 was used. Using the estimate of primary production (272.58 gC·m^{-2}·year^{-1}) after Behrenfeld and Falkowski (1997), a conversion factor of 9 gww/gC, and a production/biomass ratio of 70 year^{-1} (Opitz, 1996), phytoplankton biomass was estimated at 35.05 t·km^{-2}.

Detritus

Detritus biomass was estimated based on an empirical model in Pauly *et al.* (1993), which uses primary production (272.58 gC·m^{-2}) and euphotic depth (85 m; from Rajendra *et al.*, 1991) to predict detritus concentration of 37.89 gC·m^{-2}. However, estimates ranged between 23.93 and 51.03 gC·m^{-2} when the range of 50 to 120 m for the euphotic depth (Rajendra *et al.*, 1991) is used in the calculation.

Production/biomass ratio (P/B)

Marine mammals

A P/B ratio of 0.02 per year, half the maximum rate of population increase for cetaceans (Trites and Heise, 1996), was assumed for baleen and toothed whales. A slightly higher estimate (0.03 year^{-1}) was assumed for dolphins.

Fish Groups: Exploited

For exploited fish groups, the production/biomass ratio is considered equivalent to the instantaneous rate of total mortality (Allen, 1971).

Billfishes

Total mortality (1.13 year^{-1}) of billfishes was estimated from mean lengths using Beverton and Holt (1957), using, for billfishes in Grenada, length data provided by Eric Prince of the Billfish Foundation. Parameters for converting pre-pectoral fin length (PFL) to lower jaw forked length (LJFL) were derived (Table 6) and used to estimate missing values of lower jaw forked length. Table (7) presents the input parameters and estimated total mortality for the respective species. The overall total mortality for the group was taken as the mean of the individual species estimates.

Pelagic sharks

A consumption/biomass ratio of 0.069 for adult sharks in the central Pacific (Kitchell *et al.*, 1999) was used to estimate production/biomass ratio via an assumed value of P/Q. However, the resulting P/B ratio (0.16 year^{-1}) was lower than the estimated natural mortality (0.22 year^{-1}) for this exploited group. Therefore a consumption/biomass ratio of 0.11 was assumed, leading to an estimated P/B ratio of 0.255 year^{-1}. For the corresponding juvenile group, production/biomass ratio was computed at 0.58 year^{-1}, assuming a consumption/biomass ratio of 0.125 (similar to juvenile sharks; see Kitchell *et al.*, 1999), and a consumption/biomass ratio twice that of the adults.

Large tunas and other pelagics

Total mortality (3.06 year^{-1}) was estimated for yellowfin tuna (*Thunnus albacares*) using Beverton and Holt (1957), with L_∞ = 169 cm and K = 0.627 year^{-1} (Hennemuth, 1961), and length data provided by the CARICOM Fisheries Large Pelagic and Reef Fish Resource Assessment Unit. A mean and minimum length in the catch of 52.8 cm and 29.0 cm for the fishery in Grenada were used, respectively. The estimate of total mortality obtained is high. Natural mortality was estimated at 0.41 year^{-1} using Pauly (1980). This implies a fishing mortality in excess of six times natural mortality. This high estimate is possibly a result of hook selection resulting in a slope of the descending limb of the catch curve suggesting a higher rate of mortality than exists in the actual population. Therfore, it was assumed that fishing mortality was twice the computed natural mortality; the resulting total mortality (P/B) was assumed to be 1.23 year^{-1}.

Mackerels

As mentioned above, the estimated total mortality after George *et al* (2001) is considered too high for this group. Thus, total mortality was estimated as the sum of assumed fishing mortality (1.26 year^{-1}) and natural mortality (George *et al.*, 2001), leading to 1.89 year^{-1}, which satisfies the consumption/biomass ratio constraint. For the juvenile group, the production/biomass ratio (6.224 year^{-1}) was estimated assuming a production/consumption ratio of 0.2 and a consumption/biomass ratio twice that of the adults.

Small tunas, barracudas and other pelagics

The mean estimate of total mortality (0.886 year^{-1}) for the blackfin tuna, *Thunnus atlanticus* (0.31 year^{-1}) and skipjack tuna, *Katsuwonus pelamis* (1.48 year^{-1}) computed using Beverton and Holt (1957) was assumed representative of small tunas, barracudas and other pelagics. Mean length in the catch of 47.8 cm and 49.5 cm, and minimum length in the catch of 25 cm and 34 cm were used for blackfin and skipjack tuna, respectively, based on length data for the fishery in Grenada, provided by the CARICOM Fisheries Large Pelagic and Reef Fish Resource Assessment Unit. Growth parameters were computed from Garcia-Coll *et al.* (1984) and Claro and Garcia-Arteaga (1994) for blackfin tuna, and Claro and Garcia-Arteaga (1994) and Erzini (1991) for skipjack tuna.

Coryphaena spp.

The estimated total mortality for dolphinfish, *Coryphaena hippurus* (5.98 year^{-1}) in the southeastern Caribbean was used (Parker *et al.*, 2001). This estimate is very similar for the species in the central Pacific (5.0 year^{-1}; Kitchell *et al.*, 1999). However, a review of input parameters for *Coryphaena* spp. prior to model balancing indicated violation of the gross-food conversion efficiency constraint (0.05-0.3) with existing estimates of production/biomass and the below estimated consumption/biomass. Two options for adjustment were possible: accept the estimated total mortality from Parker *et al.* (2001) and adjust the consumption/biomass ratio to achieve a gross food conversion efficiency of 0.25 (Kitchell *et al.*, 1999); or accept the consumption/biomass ratio from Palomares and Pauly (1998) and adjust the production/biomass ratio with the same gross food conversion efficiency constraint. Since the estimate of total mortality (after Parker *et al.*, 2001) was tentative (S. Singh-Renton, pers. comm.; K. Cochrane, pers. comm.), this parameter was selected for adjustment, i.e., total mortality (production/biomass) was reduced from 5.98 year^{-1} to 2.12 year^{-1}.

Pelagic jacks, needlefish

Assuming a production/consumption ratio of 0.1 and 0.2 for the adults and juveniles, respectively, and using the computed consumption/biomass ratio below, production/biomass ratios of reef jacks and similar species were estimated at 0.944 year^{-1} and 3.776 year^{-1} for adults and juveniles, respectively.

Four-winged flyingfish

The estimated total mortality for Hirundicthys affinis (5.8 year^{-1}) off Tobago was used (Samlalsingh and Pandohee, 1992).

Reef jacks, tilefish, barracudas etc.

Initially the production/biomass ratio of reef jacks, tilefish, barracudas etc., was estimated as natural mortality (0.75 year^{-1}) using Pauly (1980), and the estimate for the corresponding juvenile group (2.396 year^{-1}) estimated assuming production/consumption ratio of 0.2.

Groupers

Straker *et al.* (2001) estimated total mortality (2.78 year^{-1}) for red hind, *Epinephelus guttatus,* in the eastern Caribbean. The species was considered representative of all adult groupers. Total mortality of the corresponding juvenile group (2.94 year^{-1}) was estimated assuming a production/consumption ratio of 0.2. However, a review of input parameters for adult groupers prior to model balancing indicated violation of the gross-food conversion efficiency constraint (0.05-0.3) with existing estimates of production/biomass and the below estimated consumption/biomass. Since the estimate of production/biomass after Straker *et al.* (2001) was tentative (based on the nature of estimates for other species derived at the same workshop), the production/biomass ratio was reduced from 2.78 to 0.84 year^{-1}, giving a production/consumption ratio of 0.12, as computed for similar groups by Opitz (1996).

Snappers

Total mortality of snappers was estimated as the mean estimate (1.068 year^{-1}) for *Etelis oculatus* in St Lucia (1.873 year^{-1}; Murray and Moore, 1992), *Lutjanus synagris* in Trinidad (0.76 year^{-1}; Dass, 1983) and *Lutjanus purpureus* in Tobago (0.57 year^{-1}; Manickchand-Heileman and Philip, 1996). Total mortality of the corresponding juvenile group (2.180 year^{-1}) was estimated assuming a production/consumption ratio of 0.2.

Squirrelfish and other small reef carnivores

Initially, the production/biomass ratio of other small reef carnivores was left for estimation by Ecopath, with an assumed ecotrophic efficiency of 0.95. However, following initial balancing of the model, the estimated production/consumption ratio (0.007) was exceedingly low, as was the production/biomass ratio (0.114 year^{-1}) compared to the estimate of natural mortality (1.73 year^{-1}; after Pauly 1980) for this exploited group. As a result, the same production/consumption ratio as ‘other carnivorous reef species’ (0.125 year-1) was assumed and the resulting production/biomass estimated at 2.013 year^{-1}. Ecotrophic efficiency was therefore left for estimation by Ecopath.

Triggerfish, grunts, porgies, angel fish, butterflyfish and other omnivorous reef species

Initially the production/biomass ratio of other omnivorous reef species was estimated as natural mortality (1.06 year^{-1}) using Pauly (1980). The group however, is exploited, and the P/B ratio was adjusted during balancing (Table 1).

Parrotfish, surgeonfish, triggerfish etc.
Initially the production/biomass ratio of parrotfish etc. was left for estimation by Ecopath, with an assumed ecotrophic efficiency of 0.95. However, the resulting production/biomass ratio of 0.008 year^{-1} was much lower than the natural mortality (1.05 year^{-1}) estimated after Pauly (1980) for this exploited group. As a result a P/Q of 0.23 (Van Rooij *et al.*, 1998) was assumed and P/B estimated at 5.83 year^{-1}.

Croakers, snooks and other carnivorous/omnivorous demersals
Estimates of total mortality were not available for this group. Assuming the same estimate for the production/consumption ratio (0.12) as for similar species in other models (Arreguín-Sanchez *et al.*, 1993 a, 1993 b; Mendoza, 1993; Vega-Cendejas *et al.*, 1993; Manickchand-Heileman *et al.*, 1998 a, 1998 b), the production/biomass ratio was estimated at 1.03 year^{-1}, using the consumption/biomass ratio estimated below. This estimate compares well with the natural mortality (0.98 year^{-1}) estimated using Pauly (1980).

Small coastal pelagics
Total mortality of small coastal pelagics (3.471 year^{-1}) was estimated using the consumption/biomass ratio estimated below and an assumed production/consumption ratio of 0.147, based on the mean for similar species in other models (Arreguín-Sanchez *et al.*, 1993 a, 1993 b; Mendoza, 1993; Vega-Cendejas *et al.*, 1993; Opitz, 1996; Manickchand-Heileman *et al.*, 1998 a, 1998 b).

Total mortality estimates of other exploited groups were left for estimation by Ecopath, assuming ecotrophic efficiency of 0.95.

Fish Groups: Unexploited
The production/biomass ratio of unexploited fish groups was estimated as the natural mortality rate using Pauly (1980), growth parameters from FishBase (Froese and Pauly, 2000), and an estimated mean habitat temperature of 28°C (Opitz, 1996).

Other flyingfishes
A review of input parameters for other flyingfishes prior to model balancing indicated violation of the gross-food conversion efficiency constraint (0.05-0.3) with existing estimates of production/biomass and the below estimated consumption/biomass computed using empirical equations. There was little basis for selecting one parameter over the other for modification. The production/biomass ratio was reduced from 4.00 to 3.80 year^{-1} (P/Q = 0.29).

Demersal and reef sharks
Assuming a consumption/biomass ratio of 0.069 and 0.125 for adult and juvenile sharks, respectively, and using the consumption/biomass estimated below, production/biomass ratio was estimated at 0.320 year^{-1} and 1.188 year^{-1} for the respective groups.

Small herbivorous/detritivorous reef species
The production/biomass ratio of small herbivorous/detritivorous reef species was initially estimated at 2.21 year^{-1} based on estimates for similar groups in other models (Aliño *et al.*, 1993; Vega-Cendejas *et al.*, 1993; Opitz, 1996; Venier and Pauly, 1997; Manickchand-Heileman *et al.*, 1998 a, 1998 b). However, a review of input parameters resulted in modification of the consumption/biomass ratio (to 33.39 year^{-1}) for this group, and an assumed production/consumption ratio of 0.15. Therefore, the production/biomass ratio (5 year^{-1}) was re-estimated as the product of consumption/biomass and production /consumption.

Mullets and other herbivorous/detritivorous coastal pelagics and demersals
A review of input parameters for mullets and other herbivorous/detritivorous coastal pelagics prior to model balancing indicated violation of the gross-food conversion efficiency constraint (0.05-0.3), while the estimated production/consumption ratio was very low (0.057), as perhaps befits detritivorous and herbivorous fish. To overcome the constraint, a production/consumption ratio of 0.15 from other models was assumed and the production/biomass ratio re-estimated at 3.033 year^{-1}.

Non-Fish Groups
Production/biomass ratio for all non-fish groups except lobster, queen conch and seagrasses were taken from Opitz (1996). However, since turtles are exploited in the southeastern Caribbean, the estimate for this group should be considered a minimum, as Opitz (1996) did not consider turtles to be exploited.

Spiny lobster

The estimate of total mortality (1.475 year^{-1}) for spiny lobster was based on the average for Pedro Bank, Jamaica (2.5 year^{-1}; Haughton and King, 1992) and the reefs of the US Virgin Islands (0.45 year^{-1}; Opitz, 1996). However, lobster were not fished in the Opitz model, while exploitation on the Pedro Bank is believed to be higher than in the southeastern Caribbean. Nevertheless, the computed P/B falls within the range specified (0.5-1.5 year^{-1}) in Munro (1983) for the species in Jamaica during 1979.

Queen conch

The mean of annual estimates of total mortality for conch between 1994 and 1998 (0.53 year^{-1}) in Jamaica (CFMC and CFRAMP, 1999) was taken as representative of P/B for the species in the southeastern Caribbean region.

Seagrasses, seaweeds and other autotrophs

The mean biomass turnover of turtle grass was estimated at 3.28% per day for Barbados and 3.71% per day for Tobago (CARICOMP, 2001). Using the mean turnover rate per day and the biomass estimated previously, production/biomass ratio was calculated as 12.76 year^{-1}. This estimate is within the range provided by seagrasses (8.43 year^{-1}) and seaweeds (15.34 year^{-1}) by Aliño *et al.* (1993), and close to the value for autotrophs (13.25 year^{-1}) in Opitz (1996).

Consumption/biomass ratio (Q/B)

Marine Mammals

Consumption was computed using Trites *et al.* (1997), based on daily ration size for individual species after Innes *et al.* (1987), and initial consumption/biomass ratios were computed (Table 8). A comparison of estimates for similar groups in Trites and Heise (1996) indicated tremendous under-estimation of this parameter for baleen whales and over estimation for toothed whales and dolphins. While consumption at higher latitudes is greater for these groups, and in particular large whales which migrate to breeding and calving grounds in the Caribbean, it is here difficult to resolve this problem. As a result, consumption/biomass ratio estimates from Trites and Heise (1996) were used (Table 1).

Fish Groups

The consumption/biomass ratio was estimated using one of two empirical equations depending on the availability of input parameters. In the absence of information on caudal fin aspect ratio, Pauly *et al.* (1990) was used to estimate Q/B; otherwise the model of Palomares and Pauly (1989) was used. A mean habitat temperature of 28°C after Opitz (1996) was used, along with estimates of asymptotic weight and aspect ratios taken from FishBase (Froese and Pauly, 2000). The consumption rate of all juvenile fish groups was assumed to be twice the estimate derived for the corresponding adult group.

For the following groups, the estimated consumption/biomass ratio using the equations after Palomares and Pauly (1989) and Pauly *et al.* (1990) were not comparable to estimates for similar species in other models, and were also considered inappropriate when the activity levels of the respective species were considered:

Billfishes

The initial estimated consumption/biomass ratio of billfishes (2.44 year^{-1}) was considered low for this group. The mean estimate for similar species in the central Pacific (Kitchell *et al.*, 1999) was 4.67 year^{-1}. However, the Pacific species are not as heavily exploited as in the Atlantic. As a result, a value of 6 year^{-1} was assumed here (Table 1).

Large tunas and other pelagics

The initial estimate of consumption/biomass ratio of large tunas and other pelagics (5.17 year^{-1}) was considered too low to support the high activity levels of these fishes. As a result, the consumption/biomass ratio estimate for the same species groups in the central Pacific (15.33 year^{-1}; Kitchell *et al.*, 1999) was used.

Small tunas, barracudas and other pelagics

The initial estimate of consumption/biomass ratio for small tunas and related species (4.37 year^{-1}) was considered low when compared to estimates for skipjack tuna in the central Pacific (20 year^{-1}; Kitchell *et al.*, 1999) and for little tunny (*Euthynnus alletteratus;* 13.4 year^{-1}; García and Duarte, 2002). The average consumption/biomass ratio estimate from these two sources (16.7 year^{-1}) was used here.

Coryphaena spp.

Initially, a consumption/biomass ratio of 3.05 year^{-1} was estimated for *Coryphaena* spp. using the growth parameters in Oxenford (1985), close to the value of 3.9 year^{-1} estimated by García and Duarte (2002). These estimates differ markedly from the estimates of 20 year^{-1} of Kitchell *et al.* (1999) and even of 8.47 year^{-1} by Palomares and Pauly (1998). The latter estimate was used here since the lower estimates do not adequately explain the fast growth of this species, while the estimate by Kitchell *et al.* (1999) would imply a metabolic rate greater than that of tunas.

Non-Fish Groups

Except for the queen conch, all estimates of consumption/biomass ratio were taken from Opitz (1996). The consumption/biomass ratio of queen conch was left for estimation by Ecopath.

Ecotrophic efficiency

Ecotrophic efficiency is an emergent property of the ecosystem; it cannot be estimated from field studies, and is usually estimated by Ecopath during balancing. For many groups, however, one of the three parameters (B, P/B or Q/B) was not available. As a result, the missing parameter was left for estimation by Ecopath, and assumptions were made on the most likely input estimates of ecotrophic efficiency for the respective groups. In most instances an ecotrophic efficiency of 0.95 was assumed (Christensen *et al.*, 2000), except for seabirds for which an ecotrophic efficiency of 0.2 was assumed. Since ICCAT stock assessments indicate over-exploitation of billfishes, an ecotrophic efficiency of 1.0 was assumed for this group. Generally, sharks are at risk of over-exploitation because of their slow growth rates and late maturity. Pelagic sharks have been recorded as by-catch of longline fleets operating in the Atlantic, prompting international concerns (IUCN, ICCAT). As a result an ecotrophic efficiency of 1.0 was assumed for both adult and juvenile pelagic sharks.

Diet composition

Initial inputs for the diet matrix for this model can be obtained form the author. There was extensive modification to the components and proportions of the diet during balancing, leading to the final diet composition as illustrated in Table (9).

Marine Mammals

The diet composition of marine mammals was taken from Pauly *et al.* (1998), and was adjusted to the present group configuration. Since the marine mammals tend to be migratory and spend only a portion of the year in Caribbean waters, it was assumed that baleen and toothed whales derive only 10% of their diet each year from the study region, the other 90% of the diet was specified as import. The actual species in the diet were extensively adjusted during balancing.

Fish Groups

The main source for diet data of fishes was FishBase (Froese and Pauly, 2000). Some information was available for 87% of the species in the model. Diet compositions were available for 280 species and information on food items for another 46 species. In the latter case, all listed food items were assumed to contribute equally to the diet of the predator.

The invertebrate components of the diet were available in considerable detail, but the fish components were highly aggregated (e.g., nekton, finfish, or unidentified fish). This contributed to high uncertainty in diet composition. When diet was specified as an aggregate category without specific species or family names, diet was apportioned equally to all other functional groups in the system, with reference to the habitat and relative size of the predator. For reef species, Munro (1983) was consulted for identification of associated predator and prey species.

Prey items and contributions to diet were assumed for juvenile pelagic sharks, juvenile reef sharks and juvenile groupers. Diet composition of juvenile mackerels was from Finucane *et al.* (1990) for corresponding species in the Gulf of Mexico and South Atlantic. Diets of juvenile *Caranx hippos* and *Caranx latus* were considered representative of juvenile pelagic jacks and juvenile reef jacks, respectively, while juvenile *Lutjanus apodus*, *L. griseus* and *L. jocu* were considered representative of the juvenile snapper group (Austin and Austin, 1971). Diet composition for billfishes, large tunas and other bathypelagics were taken from Júnior (2000) for the respective species off Brazil, for *Coryphaena* spp. information was from Oxenford and Hunte (1998), while diet composition of the four-winged flyingfish was estimated from food items given in Gillet and Lanelli (1991) for the species in the Pacific.

Non-Fish Groups

The diet matrix from Opitz (1996) was used for the following groups: zooplankton, microfauna, zooobenthic sessile animals, echinoderms, molluscs and worms, benthic crustaceans, spiny lobster, cephalopods, turtles and seabirds. Diet composition of queen conch was based on Mahon (1987) and Tewfik (1997). Both authors indicated the predominance of benthic and epiphytic macroalgae, occassional ingestion of seagrasses, with juveniles relying more on detritus and as a consequence ingesting small benthic animals as well. Furthermore, queen conch and the spiny lobster were not listed explicitly in the diets of many predators (except for consumption of spiny lobsters by turtles and other crustaceans in Opitz, 1996). A list of predators was derived from Idyll (1971) and Tewfik (1997) for spiny lobster and queen conch, respectively. The proportion in the diets of these predators attributed to crustaceans, molluscs and worms was thought to implicitly include spiny lobsters and queen conch. It was assumed that spiny lobsters and queen conch accounted for 50% of the proportion of diet attributed to the respective broader group.

Rebel (1974) gave details on the food of marine turtles. The hawksbill turtle diet comprises algae, barnacles, other small sessile animals, fish and sea urchins. Green turtles feed on marine grasses, but also feed on algae, yet are not entirely restricted to a vegetarian diet, with small mollusks and crustacea also featuring in their food. Loggerhead turtles sometimes eat marine grasses, but not to the extent of the other two turtle species. Adults eat mainly conchs, shellfish and barnacles but also feed on fish, sponges, jellyfish, crabs and sea urchins. Leatherbacks feed mainly on jellyfish, but the diet is also known to include sea urchins, squids, crustaceans, tunicates, fish, blue-green algae, and floating seaweed (US Fish and Wildlife Service, 1991). Opitz (1996) did not include small fish, queen conch and cephalopods in the diets of turtles. Here, it was assumed that small fish contributed a very small portion (0.0004) to the diet, while queen conch and cephalopods each contributed 0.001 to total diet, and the overall diet was normalized to one.

Cannibalism and feeding at higher trophic levels

Given the uncertainties in diet composition, an automated routine was used to check the proportion of the diet of top predators and reduce cannibalism to 20% of used production for groups with exceedingly high cannibalistic pressure. Though it is possible for a species to feed on organisms that occur at a higher trophic level than itself, usually such organisms do not comprise a large portion of the diet (Daniel Pauly, pers. comm.) An automated routine identified such inconsistencies and reduced this proportion to 10% of the diet, while redistributing the remaining proportion equally among other organisms in the diet.

Fisheries catches

Time series catch data for the period 1942 - 2000 were reconstructed from historical and administrative reports, published papers and information from the Fisheries Department's Fisheries Statistical Database (Mohammed and Rennie, this volume), and are summarized in Table (10).

Uncertainty in input parameters

The 'pedigree' in Ecopath allows consideration of uncertainty in input parameters (Christensen *et al.*, 2000). Specification is based on the data origin and associated default confidence intervals. Pedigree index values range from zero to one, with uncertainty expressed as confidence intervals expressed as percent of central values. An overall index of model quality is computed, with the highest quality being for a model constructed from precise parameter estimates for the system being modeled. Consideration of uncertainty in input parameters in the automated mass balance routine recently incorporated in EwE (Kavanagh *et al.*, 2004) is facilitated through use of the pedigree to specify the sampling/resampling ranges for biomass and diet composition. The lowest confidence interval (Table 11) was used in assigning pedigrees for input parameters estimated from data sources of varying levels of uncertainty.

Model balancing

The model was balanced manually according to Christensen *et al.* (2000). An automated mass-balance routine of Kavanagh *et al.* (2004) was used when ecotrophic efficiencies in excess of one could no longer be reduced manually. This routine changes input diet compositions and biomass until both Ecopath master equations indicate that mass balance has been achieved throughout the system. Conversion to a solution was achieved when a multiplier factor of 1.5 times the input confidence intervals (Table 11) was used.

PRELIMINARY RESULTS

The balanced model parameters and diet matix are presented in Tables (1) and (9), respectively. A comparison of the initial diet estimates with the associated outputs of the balanced model indicates considerbale modification in terms of the food items and relative proportions. Biomass per unit area in the balanced model ranged between 0.001 t·km^{-2} (juvenile mackerels, juvenile demersal and reef sharks and other omnivorous demersals) and 0.541 t·km^{-2} (other bathypelagics). All production of billfishes, pelagic sharks, large tunas etc., mackerels and *Coryphaena* spp. are utilized in the system (ecotrophic efficiency of 1.00). Small ecotrophic efficiencies were estimated for flyingfishes (0.509), demersal and reef sharks (0.006), squirrelfish and other small reef carnivores (0.197), parrotfish, surgeonfish and triggerfish (0.122) as well as croakers, snooks etc. (0.165).

The percentage change in initial biomass inputs to achieve mass balance varied between –400% and +100% (Table 12). Biomass of *Coryphaena* spp. was reduced by 400% while biomass of snappers, squirrelfish and parrotfish was increased by 100%. Generally predation mortality accounted for the greatest proportion of total mortality (Table 13), ranging from 0.03% (juvenile jacks) to 99.5% (small herbivorous/ detritivorus reef species) for fish groups. Fishing mortality contributed over 30% to total mortality for billfishes, large tunas etc., pelagic sharks, small tunas etc., mackerels, *Coryphaena* spp., the fourwing flyingfish, snappers, groupers and turtles.

Basic summary statistics of the model are provided in Table (14). The mean transfer efficiency is 10.3% and gross efficiency (catch/net primary production) is 2.6 x 10^{-5}. The total system throughput (the sum of all concumption, exports, respiratory flows and flows to detritus) is 14,332 t·km^{-2}. Approximately 21.7% of throughput goes to respiration and 35.8% to detritus.

DISCUSSION

This study represents the first attempt at parameterization and construction of an ecosystem model for the southeastern Caribbean. Thus, the model is preliminary in nature. Several other models have been constructed for areas in the Caribbean region (Browder, 1993; Mendoza, 1993; Arregúin-Sanchez *et al.*, 1993 a and b; Aliño *et al.*, 1993; Vega-Cendejas *et al.*, 1993; Opitz, 1996; Venier and Pauly, 1997; and Manickchand-Heileman *et al.*, 1998 a, 1998 b). These focus mainly on continental shelf, coral reef or coastal ecosystems, with little emphasis on the large pelagic component of the systems. In contrast, given the design of the present model, it lends itself well for addressing questions related to large pelagic fisheries.

Output parameters of the balanced model

Compared to corresponding groups in the US Virgin Islands model (Opitz, 1996), the present model for Grenada and the Grenadines indicates exceedingly low fish biomass in the respective habitats, ranging from 0.001 tkm^{-2} to 0.541 tkm^{-2}. Opitz (1996) however, modelled a smaller, more highly productive area and assumed zero fishing. In the present model, all production by billfishes, pelagic sharks, large tunas, mackerels and *Coryphaena* spp. is utilized in the system. This is consistent with reports of overfishing of these groups in the region (Mahon, 1990; Mahon, 1996; Singh-Renton and Mahon, 1996). The low ecotrophic efficiencies of other groups (e.g., EE = 0.509 for flyingfishes), however, require further investigation as they seem not realistic. Small pelagics such as flyingfishes do not die of old age, as most are subject to intense predation mortality (Christensen *et al.*, 2000).

Generally, predation mortality accounted for the major part of total mortality. Top predators, such as large pelagic species, which have few predators, usually are the exceptions. However, predation mortality for pelagic jacks (0.836 year^{-1}, Table 13) seems high. This requires further investigation to assess the validity of model estimates. Juveniles of large pelagics are also subjected to high predation mortality. Apart from large pelagic species, turtles were the only species for which fishing mortality exceeded the predation mortality. Fishing mortality for groupers was, however, also quite high.

The model indicates that the fishery catch has a mean trophic level of 4.3. This is reflected in the high proportion of large, migratory pelagic species in the catch. The gross efficiency of the fishery (2.6 x 10^{-5}) is low, primarily because the fishery is concentrated on apex predators. This parameter has a wide range between different systems, with high values characteristic of fisheries relying on fish low in the food web (e.g., in upwelling systems) and low values characteristic of fisheries concentrating on apex predators (e.g., tunas). The weighted global average is about 0.0002 (Christensen *et al.*, 2000). Mean transfer efficiency (10.3%) is consistent with estimates in the literature (Christensen *et al.*, 2000), while total system throughput (14,332 $t \cdot km^{-2}$) is small compared to the estimate for the US Virgin Islands coral reef model (Opitz, 1996). However, Opitz (1996) considered 6.34 km^2 of highly productive reef area compared to the present model (total area of 25,957 km^2), where only 7% of the total modelled area represented the reef component of the entire ecosystem. The overall system omnivory index, which characterizes the extent of web-like features of the system, is 0.26. The ratio of the total primary production to total respiration is one, indicating that the marine ecosystem (EEZ, reef, shelf and slope areas) off Grenada and the Grenadines is in a mature state. However, this and related model outputs are yet to be validated and other characteristics of the ecosystem indicative of maturity (Christensen, 1995) examined before such a conclusion can be considered as established.

Study limitations

The quality of the present model is affected by the uncertainty in the input estimates. This has resulted in repeated violations of ecological constraints for several groups, and violation of the Ecopath equation for some groups. Modifications to input parameters were necessary to achieve mass balance. Hence this model will benefit considerably from future, area specific research.

Data limitations are discussed in detail in Mohammed (2002). No input estimate in the existing model was specific to Grenada and the Grenadines. A general lack of biomass estimates prompted assumptions about ecotrophic efficiency (actually an emergent property estimated by Ecopath) and the use of estimates from other areas in the southeastern Caribbean. Assumptions for over-exploited groups e.g., pelagic sharks and large tunas, were well justified and supported by the literature. However, for many other groups, 95% of production was assumed utilized in the system (Christensen *et al.*, 2000). It was necessary to use estimates from other areas in the Caribbean though distinct differences in oceanographic conditions, species abundance, primary productivity and exploitation levels exist among these countries. The same concerns relate to the use of estimates of production/biomass ratio derived for similar functional groups in other islands. Estimates of production/biomass ratio were available only for a few species of commercial importance from other islands. Since each functional group comprised several species of similar diet, habitat and activity level, equal susceptibility to fishing gear, predation and mortality were assumed, and total mortality of individual species assumed representative of the group. Consumption of marine mammals within the study region is also not known. The estimate used from Trites and Heise (1996) for the British Columbian shelf is quite likely an over-estimate for the southeastern Caribbean region given the reported reduced feeding during breeding and calving in the area (Whitehead and Moore, 1982). Lack of data also resulted in the use of information for time periods that differ considerably from the model base year (1999). An additional limitation was the underutilization of some studies which did not meet the data requirement standards of Ecopath e.g., abundance surveys for flyingfish (Oxenford *et al.*, 1995), diet composition of flyingfish (Hall, 1955; Lewis *et al.*, 1962) and abundance estimates for marine mammals (Winn *et al.*, 1975; Levenson and Leapley, 1978; Mattila and Clapham, 1989; Matilla *et al.*, 1994).

Catch statistics also did not adequately represent all fisheries types. Catches of specific inshore species groups, e.g., lobster, conch and reef species, have not been adequately covered in the data collection programme (Mohammed *et al.*, 2003). Based on the Fisheries Department’s knowledge of local fisheries, a fixed raising factor for adjusting recorded data to total catches has been used since 1978. It has been adjusted to reflect recent developments in the offshore fishery, but does not consider changes in the inshore fishery. Since catch data are aggregated across gear and fishery types (inshore and offshore), the proportion of large pelagics captured in the inshore fishery is unknown. Inshore catches likely include juveniles, and can impact on the offshore fishery targeting adults of the respective species. Foreign and non-commercial catches are also not included in the statistics (Finlay *et al.*, 1988; Murray *et al.*, 1988).

Future analyses and use of the preliminary model

Further examination of the input data, as well as outputs and dynamic behaviour is required to assess the biological and ecological validity of this model. Given the general high uncertainty of input parameters an investigation of the associated model sensitivity is required for consideration in future policy exploration using Ecosim. Additionally, model predictions can be validated by fitting simulation results to time series data on catch per unit effort of the four-wing flyingfish (*Hirundichthys affinis*) and the dolphinfish (*Coryphaena hippurus*), the only two species for which such data are available in the southeastern Caribbean. This preliminary model of the southeastern Caribbean region can be adjusted to increase understanding of functional relationships and ecosystem properties of inshore or offshore systems, and to address specific national and regional management related issues.

Future studies should include application of Ecosim to explore management policy options for the flyingfish and associated large pelagic fishery undertaken by Grenada, Barbados and Trinidad and Tobago. Flyingfish are caught commercially mainly by Barbados and Tobago, but have also increased in importance as bait for the developing longline fleets. Additionally, flyingfish is a natural component in the diet of large pelagic species, especially the dolphinfish. Management recommendations thus far have identified consideration of the predator-prey interactions as high priority in arriving at an appropriate mangement strategy (Oxenford *et al*., 1993).

Furthermore, several islands in the southeastern Caribbean have embarked on setting up Marine Reserves since the late 1980s. The application of Ecospace can be used to assess the usefulness of these reserves in rebuilding of inshore resources and to test the placement and appropriate size of reserves in achieving this.

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Table 1: Basic parameters of the preliminary ecosystem model for the southeastern Caribbean: Case study Grenada and the Grenadines. Values in brackets were final values for balanced model.

Group No.	Group Name	Trophic Level	Biomass (Habitat)	Biomass		P/B		Q/B		EE		P/Q
				initial	final	initial	final	initial	final	initial	final	
1	Baleen whales	*(3.80)*	*(0.931)*	0.060	*(0.105)*	0.020		14.60			*(0.008)*	*(0.001)*
2	Toothed whales	*(5.06)*	*(0.004)*	0.014	*(0.003)*	0.020		9.80			*(0.502)*	*(0.002)*
3	Dolphins	*(5.07)*	*(0.001)*	0.005	*(0.001)*	0.030		9.80			*(0.784)*	*(0.003)*
4	Billfishes	*(4.91)*	*(0.016)*		*(0.015)*	1.130		6.00		1.000		*(0.188)*
5	Pelagic sharks	*(5.22)*	*(0.004)*		*(0.004)*	0.255		2.32	*(3.70)*	1.000		*(0.069)*
6	Juvenile Pelagic sharks	*(4.64)*	*(0.059)*		*(0.004)*	0.580		4.64	*(7.50)*	1.000	*(0.506)*	*(0.077)*
7	Large tunas and other pelagics	*(4.71)*	*(0.027)*	0.021	*(0.026)*	1.230	*(0.765)*	15.33			*(1.000)*	*(0.050)*
8	Mackerels	*(4.22)*	*(0.004)*	0.002	*(0.003)*	1.890		15.56			*(1.000)*	*(0.121)*
9	Juvenile mackerels	*(4.63)*	*(0.018)*		*(0.001)*	6.224	*(6.220)*	31.12		0.950	*(0.971)*	*(0.200)*
10	Small tunas & other pelagics	*(4.30)*	*(0.013)*	0.006	*(0.012)*	0.885		16.70			*(0.992)*	*(0.053)*
11	Coryphaena spp.	*(4.94)*	*(0.005)*	0.001	*(0.005)*	2.120		8.47		1.000		*(0.250)*
12	Pelagic jacks & other carn pelagics	*(4.53)*	*(0.022)*		*(0.021)*	0.944		9.44		0.950	*(0.961)*	*(0.100)*
13	Juvenile pelagic jacks, needlefish	*(4.18)*	*(0.257)*		*(0.016)*	3.776		18.88		0.950	*(0.953)*	*(0.200)*
14	Four-wing flyingfish	*(3.80)*	*(0.006)*	0.524	*(0.005)*	5.800		25.30			*(0.998)*	*(0.229)*
15	Other flyingfishes	*(3.63)*	*(0.029)*	0.116	*(0.027)*	3.800		12.70			*(0.509)*	*(0.299)*
16	Other bathypelagics	*(3.71)*	*(0.577)*		*(0.541)*	0.830		7.16		0.950	*(0.971)*	*(0.116)*
17	Demersal and reef sharks	*(4.32)*	*(0.096)*	0.385	*(0.007)*	0.320		4.75			*(0.006)*	*(0.067)*
18	Juvenile demersal and reef sharks	*(4.47)*	*(0.013)*		*(0.001)*	1.188		9.50		0.950	*(0.928)*	*(0.125)*
19	Reef jacks, tilefish, barracudas etc.	*(4.07)*	*(3.839)*	4.450	*(0.031)*	0.750	*(1.120)*	5.96		0.950	*(0.987)*	*(0.188)*
20	Juvenile reef jacks etc.	*(3.85)*	*(0.756)*		*(0.006)*	2.396	*(2.390)*	11.98		0.950	*(0.975)*	*(0.199)*
21	Groupers	*(4.33)*	*(0.095)*	0.950	*(0.007)*	0.840		5.61			*(0.989)*	*(0.150)*
22	Juvenile groupers	*(3.83)*	*(0.243)*		*(0.017)*	2.940		14.70		0.950	*(0.992)*	*(0.200)*
23	Snappers	*(4.24)*	*(0.052)*	48.690	*(0.004)*	1.068		5.45			*(0.964)*	*(0.196)*
24	Juvenile snappers	*(3.83)*	*(0.340)*		*(0.024)*	2.180		10.90		0.950	*(0.985)*	*(0.200)*
25	Squirrelfish & small reef carn.	*(4.07)*	*(7.785)*	31.140	*(0.063)*		*(2.013)*	16.10		0.950	*(0.197)*	*(0.125)*
26	Other carnivorous reef species	*(4.08)*	*(10.6610*		*(0.086)*	1.080		8.66		0.950	*(0.955)*	*(0.125)*
27	Triggerfish etc.	*(3.63)*	*(12.144)*	11.910	*(0.098)*	1.590		15.26			*(0.952)*	*(0.104)*
28	Other omnivorous reef species	*(3.53)*	*(6.572)*		*(0.053)*	2.210		23.24		0.950	*(0.971)*	*(0.095)*
29	Parrotfish etc.	*(2.39)*	*(11.845)*	47.380	*(0.096)*	5.830		25.34		0.950	*(0.122)*	*(0.230)*
30	Small herb./detr. reef species	*(3.05)*	*(4.646)*		*(0.038)*	5.000		33.39		0.950	*(0.995)*	*(0.150)*
31	Other carnivorous demersals	*(4.04)*	*(0.131)*	0.141	*(0.008)*	0.610		7.56			*(0.975)*	*(0.081)*
32	Croakers & other demersals	*(3.45)*	*(0.508)*	2.032	*(0.031)*	1.030		8.58			*(0.165)*	*(0.120)*
33	Other omnivorous demersals	*(3.52)*	*(0.017)*	0.141	*(0.001)*	3.340		22.32			*(0.841)*	*(0.150)*
34	Mullets & other herb/det.	*(2.03)*	*(7.094)*		*(0.436)*	3.033		20.22		0.950	*(0.969)*	*(0.150)*
35	Other carnivorous benthopelagics	*(3.80)*	*(1.068)*		*(0.066)*	0.620		2.96		0.950	*(0.974)*	*(0.209)*
36	Small coastal pelagics	*(3.64)*	*(2.915)*		*(0.179)*	3.471	*(3.470)*	23.61		0.950	*(0.970)*	*(0.147)*

Table 1: cont'd.

Group No.	Group Name	Trophic Level	Biomass (Habitat)	Biomass		P/B		Q/B		EE		P/Q
				initial	final	initial	final	Initial	final	Initial	final	
37	Sea birds	*(4.59)*	*0.002*		*(<0.001)*	5.400		80.00		0.200	(0.161)	*(0.068)*
38	Turtles	*3.11*	*0.527*		*(0.004)*	0.150		3.50		0.950	(0.970)	*(0.043)*
39	Cephalopods	*4.29*	*0.040*	0.023	*(0.038)*	2.340		12.73			(0.992)	*(0.184)*
40	Spiny lobster	*3.74*	*7.423*		*(0.516)*	1.475		7.40		0.950	(0.961)	*(0.199)*
41	Other crustaceans	*2.85*	*108.580*		*(7.546)*	1.840		25.37		0.950	(0.963)	*(0.073)*
42	Queen conch	*2.07*	*0.842*	2.739	*(0.059)*	0.530			(4.42)		(0.997)	*(0.120)*
43	Molluscs and worms	*2.25*	*37.336*		*(2.595)*	4.140		61.60		0.950	(0.996)	*(0.067)*
44	Echinoderms	*2.36*	*0.810*	3.240	*(0.056)*	0.730		6.84			(0.952)	*(0.107)*
45	Zoobenthic sessile animals	*2.29*	*344.394*		*(23.935)*	1.360		12.00		0.950	(0.956)	*(0.113)*
46	Microfauna	*2.00*	*35.386*		*(2.442)*	195.000		2050.00		0.950	(0.931)	*(0.095)*
47	Zooplankton	*2.80*	*2.472*		*(2.472)*	40.000		165.00		0.950	(0.681)	*(0.242)*
48	Seagrasses & other autotrophs	*1.00*	*3483.865*	3167.150	*(27.871)*	12.760					(0.273)	
49	Symbiotic algae	*1.00*	*2800.199*		*(22.402)*	10.200				0.950	(0.398)	
50	Phytoplankton	*1.00*	*38.551*	35.060	*(36.199)*	70.000					(0.080)	
51	Detritus	*1.00*	*37.892*	37.892	*(2.615)*						(0.999)	

Table 2: Estimated biomass of marine mammals in the Caribbean province (area = 4.48 x 10^6km^2).

Common Name	Population Numbers[a]		Mean Mass (kg)[b]		Population biomass		Total Biomass (tkm^{-2}) in Caribbean Province[c]
	Female	Male	Female	Male	Female	Male	
Northern right whale	4	4	24960	21805	91	80	0.000038
Blue whale	112	112	110126	95347	12281	10633	0.005115
Fin whale	923	923	59819	51361	55191	47388	0.022897
Sei whale	288	288	17387	16235	5010	4678	0.002162
Bryde's whale	1055	1055	16905	15381	17833	16225	0.007602
Minke whale	6867	6867	7011	6121	48144	42034	0.020129
Humpback whale	176	176	32493	28323	5721	4987	0.002390
Baleen Whales							**0.060334**
Sperm whale	1547	1547	10098	26939	15624	41682	0.012791
Pygmy sperm whale	83	83	177	177	15	15	0.000007
Dwarf sperm whale	83	83	101	101	8	8	0.000004
Cuvier's beaked whale	75	75	886	771	66	57	0.000028
Blainville's beaked whale	8	8	390	508	3	4	0.000002
Gervais' beaked whale	270	270	496	289	134	78	0.000047
True's beaked whale	6	6	473	416	3	2	0.000001
Killer whale	618	618	1974	2587	1219	1598	0.000629
Short-finned pilot whale	842	842	467	819	393	689	0.000242
False killer whale	851	851	464	692	395	588	0.000220
Pygmy killer whale	92	92	78	117	7	11	0.000004
Melon-headed whale	102	102	105	104	11	11	0.000005
Toothed whales							**0.013978**
Tucuxi	1118	1118	39	39	43	43	0.000019
Rough-toothed dolphin	89	89	88	96	8	9	0.000004
Risso's dolphin	773	773	211	236	163	182	0.000077
Bottlenose dolphin	33633	33633	172	203	5781	6835	0.002816
Pantropical spotted dolphin	9678	9678	59	72	572	694	0.000283
Atlantic spotted dolphin	30123	30123	68	65	2034	1970	0.000894
Spinner dolphin	9574	9574	40	43	379	413	0.000177
Clymene dolphin	345	345	47	47	16	16	0.000007
Striped dolphin	8663	8663	115	117	992	1011	0.000447
Common dolphin	8106	8106	68	92	553	746	0.000290
Fraser's dolphin	114	114	95	95	11	11	0.000005
Dolphins							**0.005019**

[a]Fisheries Centre Marine Mammal database; www.fisheries.ubc.ca. [b] Trites and Pauly, 1998. [c] Longhurts *et al*., 1995.

Table 3: Estimated biomass of tuna.

Country	Species (stock)	Area (km^2)	MSY (mt)[a]	MSY ($t \times 10^{-4} km^{-2}$)[b]	Biomass ($t \times 10^{-4} km^{-2}$)
Antigua	Yellowfin (all)	32,560,045	149,000	45.76	
Barbados	Albacore (north)	35,953,074	24,700	6.87	
Jamaica	Bluefin tuna (west)	23,751,216	2,660	1.12	
St Kitts and Nevis	Bigeye tuna	56,507,011	61,200	10.83	
Sum Large Tunas				64.58	**210.02**
St Vincent and Grenadines	Skipjack (west)	23,555,462	31,300	13.29	
Sum Small Tunas				13.29	**59.99**

[a] Singh-Renton and Neilson (1994); [b] based on Christensen (1996)

Table 4: Estimated biomass of flyingfish. Source: Oxenford *et al.* (1995). Maximum length of *H. affinis* from Samlalsingh and Pandohee (1993), and for *P. brachypterus* and *C. cyanopterus* from FishBase (Froese and Pauly, 2000). Constants of the length-weight relationship for *H. affinis* taken from Samalalsingh and Pandohee (1993) and assumed the same for *P. brachypterus* and *C. cyanopterus*.

Transect Number	Number of 0.5 nautical miles surveyed	Mean number of fish counted per 0.5 nm			Estimated total number of fish counted			Area surveyed
		H. affinis	***P. brachypterus***	***C. cyanopterus***	***H. affinis***	***P. brachypterus***	***C. cyanopterus***	**(m^2)**
9	64	8.67	4.16	0.32	554.88	266.24	20.48	1185280
10	3	13.97	4.89	1.40	41.91	14.67	4.20	55560
11	72	3.85	21.67	0.32	277.20	1560.24	23.04	1333440
12	24	2.21	3.26	0.19	53.04	78.24	4.56	444480
13	73	3.67	2.14	0.10	267.91	156.22	7.30	1351960
14	17	2.91	10.02	2.44	49.47	170.34	41.48	314840
15	66	5.5	2.97	0.45	363.00	196.02	29.70	1222320
16	24	2.53	2.73	0.10	60.72	65.52	2.40	444480
18	60	3.05	3.36	0.30	183.00	201.6	18.00	1111200
19	42	1.6	0.73	0.25	67.20	30.66	10.50	777840
21	84	8.82	5.50	0.10	740.88	462.00	8.40	1555680
22	30	9.7	14.49	0.17	291.00	434.70	5.10	555600
23	79	14.81	8.68	0	1169.99	685.72	0	1463080
24	79	2.06	15.71	0.08	162.74	1241.09	6.32	1463080
25	24	28.47	11.25	0.03	683.28	270.00	0.72	444480
26	26	8.04	4.80	0.06	209.04	124.80	1.56	481520
27	60	24.11	7.03	0.09	1446.60	421.80	5.40	1111200
28	40	0.39	0.85	0.03	15.60	34.00	1.20	740800
29	60	0.83	2.91	0.01	49.80	174.60	0.60	1111200
30	6	0.43	0.57	0	2.58	3.42	0	111120
31	87	1.37	5.29	0.01	119.19	460.23	0.87	1611240
33	80	9.02	21.02	0.24	721.60	1681.60	19.20	1481600
34	36	3.11	3.55	0.29	111.96	127.80	10.44	666720
35	66	1.34	5.69	0.17	88.44	375.54	11.22	1222320
37	93	1.47	0.05	0.03	136.71	4.65	2.79	1722360
38	19	5.36	0	0	101.84	0	0	351880
39	92	3.37	5.18	0	310.04	476.56	0	1703840
Total area surveyed								26039120
Total number of fish counted					8279.62	9718.26	235.48	
Assumed percentage taking to flight					10	20	20	
Estimated number of fish in surveyed area					82796.20	48591.3	1177.4	
Estimated weight (g) (number x Wmax); where Wmax = aLmax[b]					29235	5491	865	
Biomass (gm^{-2})					0.001123	0.000211	0.000033	

Table 5: Biomass estimates for selected reef species.

Group Name	Species	Density 50 m^2 [a]		Length [b]	Length-Weight parameters			Reference	Common Weight (g)	Biomass (tkm^{-2})
		NRA	NRB	(cm)	*a*	*b*	Locality			
Reef jacks etc.	*Caranx ruber*	0.87	0.24	27.94	0.021	2.954	USVI	Bohnsack & Harper 1988	400.47	4.45
Total biomass										**4.45**
Groupers	*Cephalopholis cruentata*	0.35	0.21	20.32	0.008	3.024	Jamaica	Thompson & Munro 1983b	68.48	0.38
	Cephalopholis fulva	0.22	0.17	20.32	0.017	3.000	USVI	Bohnsack & Harper 1988	145.99	0.57
Total biomass										**0.95**
Snappers	*Ocyurus chrysurus*	2.04	0.84	45.72	0.015	3.032	Jamaica	Thompson & Munro 1983a	1566.07	45.10
	Lutjanus mahogoni	0.74	0.72	24.13	0.043	2.719	S Florida	Bohnsack & Harper 1988	245.82	3.59
Total biomass										**48.69**
Squirrelfish etc.	*Holocentrus rufus*	1.56	2.60	12.70	0.017	3.000	Jamaica	Bohnsack & Harper 1988	34.82	1.45
	Holocentrus marianus [c]	0.18	0.00	22.86	0.017	3.000	Jamaica	Wyatt,1983	203.08	0.37
	Myripristis jacobus	23.10	11.90	11.43	0.111	2.720	Columbia	Duarte *et al.* 1999	83.79	29.33
Total biomass										**31.14**
Triggerfish, grunts etc.	*Mulloidichthys martinicus*	4.99	0.58	22.86	0.009	3.223	Jamaica	Munro,1983	213.64	11.90
Total biomass										**11.90**
Parrotfish, surgeonfish etc.	*Sparisoma aurofrenatum*	1.22	1.36	21.59	0.013	3.110	Jamaica	Reeson 1983a	182.02	4.70
	Sparisoma viride	0.96	1.16	38.10	0.054	2.740	Jamaica	Reeson 1983a	1152.68	24.44
	Scarus taeniopterus	0.43	0.72	22.86	0.018	3.000	USVI	Bohnsack & Harper 1988	211.45	2.43
	Scarus vetula [d]	0.43	0.72	35.56	0.014	3.000	S. Florida	Bohnsack &Harper 1988	607.04	6.98
	Acanthurus bahianus	1.35	0.96	22.86	0.019	3.080	Jamaica	Reeson,1983b	293.08	6.77
	Acanthurus coeruleus	0.18	0.80	19.05	0.031	3.000	USVI	Bohnsack & Harper 1988	210.86	2.07
Total biomass										**47.38**

[a] Data source: Corless *et al.* (1997) with mean density in numbers per 50 m^2 in non-reserve areas; [b] Mean common length (Human 1991); [c] Data not available, information for *Holocentrus rufus* used; [d] Data for *Scarus taeniopterus*.

Table 6: Conversion parameters for billfishes in Grenada. LJFL: Lower jaw fork length (cm); PPL: Pre-pectoral length (cm); R^2: correlation coefficient; N: Number of fish measured.

Species	Sex	Estimated Equation	R^2	N
Atlantic sailfish	Female	LJFL = 0.9565 PPL + 45.85	0.732	1774
	Male	LJFL = 0.9427 PPL + 46.61	0.702	1203
	Both	LJFL = 0.9684 PPL + 43.91	0.743	2977
Atlantic blue marlin	Femaile	LJFL = 1.3819 PPL - 9.14	0.937	131
	Male	LJFL = 1.1624 PPL + 22.61	0.961	90
	Both	LJFL = 1.2903 PPL + 4.40	0.939	221
Atlantic white marlin	Female	LJFL = 1.0239 PPL + 38.34	0.840	27
	Male	LJFL = 1.3077 PPL + 4.69	1.000	2
	Both	LJFL = 1.0343 PPL + 37.20	0.845	29

Table 7: Growth parameters and lengths used to estimate total mortality for billfishes around Grenada.

Species	L_∞ (cm)	K	Growth Reference	Mean length in population (cm)	Mean length at capture (cm)	Total mortality ($year^{-1}$)
Atlantic sailfish	242	0.6945	Sakagawa and Bell, 1980; Beverton and Holt (1959)	169	77	0.5511
Atlantic blue marlin	210	1.5330	Prince, 1991	189	111	0.4127
Atlantic white marlin	261	0.5800	Pauly, 1978	160	136	2.4408

Table 8: Consumption/biomass estimates for marine mammals. Average estimates for each group in bold. Sources: Inness *et al.* (1987), Trites *et al.* (1997).

Species	**Population consumption (kg day^{-1})**		**Total consumption (kg year^{-1})**	**Total biomass (kg)**	**Q/B (year^{-1})**
	Female	**Male**			
Northern right whale	0	0	0	170633	0.00
Blue whale	341	379	262726	22914439	0.01
Fin whale	2683	2615	1933951	102579368	0.02
Sei whale	941	1196	780016	9687823	0.08
Bryde's whale	76992	54776	48095537	34057508	1.41
Minke whale	63812	72334	49693466	90178149	0.55
Humpback whale	271	277	199890	10708130	0.02
Baleen Whales					**0.30**
Sperm whale	1671393	1489406	1153691734	57305326	20.13
Pygmy sperm whale	508	580	397185	29202	13.60
Dwarf sperm whale	32330	32885	23803271	16746	1421.42
Cuvier's beaked whale	112	105	79293	123564	0.64
Blainville's beaked whale	23	23	16509	7548	2.19
Gervais' beaked whale	1035	1035	755361	211788	3.57
True's beaked whale	6	5	4110	5048	0.81
Killer whale	792	913	622467	2816965	0.22
Short-finned pilot whale	2178	2484	1701879	1082392	1.57
False killer whale	3174	3174	2317333	983678	2.36
Pygmy killer whale	543	363	330717	17988	18.39
Melon-headed whale	166	166	121512	21354	5.69
Toothed whales					**124.22**
Tucuxi	11736	9307	7680947	86351	88.95
Rough-toothed dolphin	313	555	316993	16396	19.33
Risso's dolphin	33449	41532	27367880	345640	79.18
Bottlenose dolphin	62929	76868	51025598	12616815	4.04
Pantropical spotted dolphin	149848	112636	95806892	1266318	75.66
Atlantic spotted dolphin	550584	773862	483422986	4004508	120.72
Spinner dolphin	280015	226519	184885041	791471	233.60
Clymene dolphin	0	0	0	32279	0.00
Striped dolphin	78799	71505	54860997	2002979	27.39
Common dolphin	33660	33186	24398883	1298796	18.79
Fraser's dolphin	13560	12165	9389268	21697	432.74
Dolphins					**100.04**

Table 9: Diet matrix for balanced preliminary model of the southeastern Caribbean; case study for Grenada and the Grenadines.

Group No.	Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13
1	Baleen whales	-	-	-	-	.001	-	-	-	-	-	-	-	-
2	Toothed whales	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Dolphins	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Billfishes	-	-	-	.010	.069	-	-	-	-	-	.022	-	-
5	Pelagic sharks	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Juvenile pelagic sharks	-	-	-	-	.076	-	-	-	-	-	-	-	-
7	Large tunas and other pelagics	-	-	-	.003	.021	-	.001	-	-	-	-	-	-
8	Mackerels	-	-	.009	.014	.023	-	.003	-	-	-	.002	-	-
9	Juvenile mackerels	-	.012	.072	.042	.071	.010	-	.010	-	-	-	-	-
10	Small tunas, barracudas and other pelagics	-	.004	.066	.003	.071	-	-	.020	-	.007	.021	-	-
11	Coryphaena (Mahi mahi)	-	.001	.025	.009	.058	-	-	.009	-	.002	.012	-	-
12	Pelagic jacks, needlefish	-	.012	.072	.020	.071	-	-	.017	-	.002	.098	-	-
13	Juvenile pelagic jacks, needlefish	-	.012	.072	.020	.071	-	-	.017	-	-	-	.268	-
14	Four wing flyingfish	-	.012	.072	-	.071	-	-	.024	-	.002	.429	-	-
15	Other flyingfihses	-	.012	.072	.022	-	-	.121	-	-	.002	.023	-	-
16	Other bathypelagics	-	.012	.072	.408	-	-	.610	-	-	.462	.029	-	-
17	Demersal and reef sharks	-	-	-	-	-	-	-	-	-	-	-	-	-
18	Juvenile demersal and reef sharks	-	-	-	-	-	-	-	-	-	-	-	-	-
19	Reef jacks, tilefish, barracudas, etc.	-	-	-	.019	-	-	-	-	-	-	-	-	-
20	Juvenile reef jacks, tilefish	-	-	-	-	-	-	-	-	-	-	-	-	-
21	Groupers	-	-	-	-	-	-	-	-	-	-	-	-	-
22	Juvenile groupers	-	-	-	-	-	-	-	-	-	-	-	-	-
23	Snappers	-	-	-	-	-	-	-	-	-	-	-	-	-
24	Juvenile snappers	-	-	-	-	-	-	-	-	-	-	-	-	-
25	Squirrelfish and other small reef carnivores	-	-	-	.013	-	-	.024	.032	.006	.015	.004	-	-
26	Other carnivorous reef species	-	-	-	.006	-	-		.044	.006	-	-	-	-
27	Triggerfish, grunts, porgies, angelfish	-	-	-	.023	-	-	.037	.006	.011	-	-	-	-
28	Other omnivorous reef species	-	-	-	.026	-	-	.002	.038	.046	.005	.080	-	-
29	Parrotfish, surgeonfish, triggerfish, etc.	-	-	-	.002	-	-	.002	.044	.005	.005	-	-	-
30	Small herb/det reef species	-	-	-	-	-	-	-	.044	-	-	-		-
31	Other carnivorous demersals	-	-	-	-	-	-	-		-	-	.004		-
32	Croakers, snooks, & other carn/omn demersals	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 9: (cont'd)

Group No.	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	.002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	.017	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	-	-	-	.030	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	-	-	.002	.024	-	-	-	.051	-	.001	-	-	-	-	-	-	-	-	-
20	-	-	-	-	-	.076	-	-	-	-	-	-	-	-	-	-	-	-	-
21	-	-	-	.023	-	-	-	-	-	-	-	-	-	-	-	-	-	.012	-
22	-	-	-	-	.129	-	-	.051	-	.061	-	-	.060	-	-	-	-	-	-
23	-	-	-	.021	-	-	-	.020	-	-	-	-	-	-	-	-	-	.012	-
24	-	-	-	.048	.129	-	-	.051	-	.061	-	-	.060	-	-	-	-	-	-
25	-	-	.002	.024	-	-	-	.052	-	.016	-	-	-	-	-	-	-	-	-
26	-	-	-	.024	.129	.076	-	.051	-	.061	-	.062	-	.002	-	-	-	.021	-
27	-	-	.026	.035	-	.076	-	.039	-	.008	-	-	-	-	-	-	-	.001	-
28	-	-	-	.048	.129	.076	-	.051	-	.061	-	.067	.015	.002	-	-	-	.021	-
29	-	-	.011	.022	-	.076	-	.051	-	.061	-	-	-	-	-	-	-	-	-
30	-	-	-	.114	.129	.076	-	.051	-	-	-	.067	.119	.002	.003	-	-	-	-
31	-	-	.001	-	.096	-	-	.001	-	-	-	-	-	-	-	-	-	.001	.003
32	-	-	-	.117	-	-	-	.009	-	.002	-	-	-	-	-	-	-	-	-

Table 9: (cont'd)

Group No.	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
28	.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
30	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32	-	-	.005	-	-	-	-	-	-	-	-	-	-	-	-

Table 9: (cont'd): Diet matrix for balanced preliminary model of the southeastern Caribbean; case study for Grenada and the Grenadines.

Group No.	Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13
33	Other omnivorous demersals	-	-	-	-	-	-	-	-	-	-	-	-	-
34	Mullets & other herb/det coastal pel & dem	-	-	-	-	-	-	-	.044	-	-	.006		-
35	Other carnivorous benthopelagics	-	-	-	.007	-	-	-	.044	-	-	.004	.188	-
36	Small coastal pelagics	-	.012	.042	.155	-	.990	.037	.382	.911	.040	.004	.194	.420
37	Sea birds	-	-	-	-	.008	-	-	-	-	-	-	-	-
38	Turtles	-	-	-	-	.017	-	-	-	-	-	-	-	-
39	Cephalopods	-	.010	.370	.194	.277	-	.091	.001	.010	.039	-	-	-
40	Spiny lobster	-	-	-	-	-	-	-	-	-	-	-	-	-
41	Other crustaceans	-	-	-	.003	.058	-	.046	.004	.001	.034	-	.211	.580
42	Queen conch	-	-	-	-	-	-	-	-	-	-	-	-	-
43	Molluscs and worms	-	-	.058	-	.002	-	-	.002	.003	.229	-	-	-
44	Echinoderms	-	-	-	-	-	-	-	-	-	-	-	-	-
45	Zoobenthic sessile animals	-	-	-	-	-	-	-	-	-	-	-	.005	-
46	Microfauna	-	-	-	-	-	-	-	-	-	-	-	-	-
47	Zooplankton	.100	-	-	-	.021	-	-	.117	-	.080	-	.134	-
48	Seagrasses, seaweeds and other autotrophs	-	-	-	-	.003	-	.006	-	-	-	-	-	-
49	Symbiotic algae	-	-	-	-	-	-	-	-	-	-	-	-	-
50	Phytoplankton	-	-	-	-	.011	-	-	.100	-	-	-	-	-
51	Detritus	-	-	-	-	-	-	-	-	-	-	-	-	-
Import		.900	.901	-	-	-	-	-	-	-	-	-	-	-
Sum		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 9 (cont'd): Diet matrix for balanced preliminary model of the southeastern Caribbean; case study for Grenada and the Grenadines.

Group No.	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
33	-	-	-	-	.129	-	-	-	-	-	-	-	-	-	-	-	-	.031	-
34	-	-	-	.117	.129	-	-	.051	-	.061	-	-	-	-	-	-	-	.021	.159
35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
36	.005	-	-	-	-	-	-	-	-	-	-	-	-	.001	.040	-	-	.062	-
37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
38	-	-	-	.002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
39	-	-	.002	.064	-	.005	-	-	-	-	-	-	-	-	-	-	-	.006	-
40	-	-	-	.127	-	.120	-	.182	-	-	-	.156	.221	-	-	-	-	.251	-
41	-	-	.652	.127	-	.120	1.00	.182	.974	.262	.974	.368	.338	.443	.292	.027	.212	.251	.433
42	-	-	-	.003	-	.074	-	-	-	.001	-	-	.001	.001	-	-	-	.067	.033
43	-	-	.286	.003	-	.074	-	.016	.026	.019	.026	.054	.020	.169	.132	.111	.028	.067	.033
44	-	-	-	-	-	.012	-		-	.003	-	-	.001	.013	.001	-	-	.014	
45	-	.334	-	.014	-	.036	-	.003	-	.017	-	-	-	.241	.216	.056	.439	.038	.082
46	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
47	.995	.666	-	-	-	.094	-	.086	-	.042	-	.221	.109	.081	.238	.073	.028	.093	.162
48	-	-	-	.011	-	.007	-	-	-	-	-	-	-	.013	.048	.733	.293	-	-
49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
50	-	-	-	-	-	-	-	-	-	-	-	-	-	.017	-	-	-	-	-
51	-	-	-	-	-	-	-	-	-	-	-	.006	.055	.014	.029	-	-	.026	.094
Import	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 9: (cont'd)

Group No.	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**
33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
34	.001	-	.271	.027	-	-	-	-	.006	-	-	-	-	-	-
35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
36	.020	-	.271	.027	.950	-	.175	-	-	-	-	-	-	-	-
37	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
39	-	-	-	-	-	.001	.016	-	-	-	-	-	-	-	-
40	-	-	.001	-	-	.075	.322	-	.001	-	-	-	-	-	-
41	.384	-	.264	.268	-	.159	.320	.945	.015	.013	-	.038	-	-	-
42	.025	-	.001	-	-	.001	.001	-	-	-	-	-	-	-	-
43	.156	.023	.002	.069	-	.001	.001	-	.030	.013	.014	.002	.001	-	-
44	.012	-	-	-	-	.002	-	-	-	.013	-	.028	-	-	-
45	.175	-	.054	.015	-	.466	-	-	.154	.013	-	.070	-	-	-
46	-	-	-	-	-	-	-	-	.286	-	.186	.097	.113	-	.800
47	.158	-	.131	.520	.050	-	.164	-	.159	-	.027	.034	.100	-	-
48	-	.298	-	.001	-	.295	-	.055	.006	.050	.016	.211	-	.018	-
49	-	-	-	-	-	-	-	-	-	-	-	-	.316	-	-
50	-	-	-	.073	-	-	-	-	.097	.798	.382	.074	.146	-	.200
51	.067	.679	-	-	-	-	-	-	.247	.100	.374	.446	.323	.982	-
Import	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 10: Catches of fishing fleets in Grenada and the Grenadines (1999). Catches of mackerels, reef jacks, and snappers by canoes/dories and seine boats, and catches of pelagic jacks and needlefish by canoes/dories and double-enders were assumed to be juveniles of the respective groups.

Functional Group	Catch (t)				
	Canoe/ Dory	Double Ender	Semi-industrial boats	Pirogue	Seine boat
Billfishes	3.15	5.64	92.49	253.34	0.76
Large pelagic sharks	-	-	24.98	-	-
Large tunas and other pelagics	-	9.51	180.54	288.86	-
Juvenile large tunas and other pelagics	0.48	-	-	-	0.19
Mackerels	-	0.26	3.43	86.73	-
Juvenile mackerels	0.48	-	-	-	2.78
Coryphaena spp.	0.07	0.26	6.91	156.60	0.01
Small tunas, barracudas and other pelagics	-	0.48	4.74	133.47	-
Juvenile small tunas, barracudasa and other pelagics	0.97	-	-	-	0.14
Pelagic jacks, needlefish	-	-	10.70	26.93	-
Juvenile large jacks, needlefish	0.29	0.03	-	-	-
Four wing Flyingfish	-	-	108.00	150.00	-
Reef jacks, tilefish, barracudas, etc.	-	38.07	-	-	-
Juvenile large reef jacks, tilefish	2.53	-	-	-	1.66
Groupers	-	-	2.69	101.29	-
Juvenile groupers	-	-	-	-	-
Snappers	-	-	0.08	39.68	-
Juvenile snappers	1.11	-	-	-	0.08
Squirrelfish and other small reef carnivores	-	-	-	2.33	-
Triggerfish, grunts, porgies, angelfish	-	-	-	3.85	-
Parrotfish, surgeonfish, triggerfish etc	-	-	-	62.24	-
Croakers, snooks and other carn/omn demersals	-	-	-	-	1.01
Small coastal pelagics	-	23.98	9.05	133.47	13.81
Turtles	-	-	-	8.36	-
Cephalopods	-	-	0.18	0.18	-
Spiny lobster	1.78	-	0.13	80.02	-
Queen conch	-	-	-	10.19	-

Table 11: Confidence intervals assigned by author to input parameters based on data sources.

Group No.	Functional Group	Confidence Interval (+/- %)				
		Biomass	**P/B**	**Q/B**	**Diet[a]**	**Catch**
1	Baleen Whales	50-80	80	50	50	
2	Toothed Whales	50-80	80	50	50	
3	Dolphins	50-80	90	50	50	
4	Billfishes	*	90	80	40	50
5	Pelagic sharks	*	90	50	50	50
6	Juvenile pelagic sharks	*	90	90	80	>80
7	Large tunas and other pelagics	80	90[a]	80	40	50
8	Mackerels	80	90	50	50	50
9	Juvenile mackerels	*	90	90	40	>80
10	Small tunas, barracudas and other pelagics	80	50	80	50	50
11	*Coryphaena* spp.	50-80	90[s]	50	40	50
12	Pelagic jacks, needlefish & other carn. pelagics	*	90	50	50	50
13	Juvenile pelagic jacks, needlefish	*	90	90	40	>80
14	Four wing Flyingfish	50-80	20	50	50	50
15	Other Flyingfishes	50-80	90[a]	50	50	
16	Other bathypelagics	*	80	90	80	
17	Demersal and reef sharks	50-80	80	50	50	
18	Juvenile demersal and reef sharks	*	90	90	80	
19	Reef jacks, tilefish, barracudas, etc.	50-80	90	50	50	50
20	Juvenile reef jacks, tilefish	*	90	90	40	>80
21	Groupers	50-80	90[a]	50	50	50
22	Juvenile groupers	*	90	50	80	>80
23	Snappers	50-80	30	50	50	50
24	Juvenile snappers	*	90	90	80	>80
25	Squirrelfish and other small reef carnivores	50-80	90[a]	50	50	50
26	Other carnivorous reef species	*	50	50	50	
27	Triggerfish, grunts, porgies, angelfish	50-80	90[a]	50	50	50
28	Other omnivorous reef species	*	50	50	50	
29	Parrotfish, surgeonfish, triggerfish etc	50-80	90[a]	50	50	50
30	Small herb/det reef species	*	90[a]	50	50	
31	Other carnivorous demersals	50-80	50	50	50	
32	Croakers, snooks and other carn/omn demersals	50-80	*	50	50	50
33	Other omnivorous demersals	80	50	50	50	
34	Mullets and other herb/det coastal pel and dem	*	90[a]	50	50	
35	Other carnivorous benthopelagics	*	50	50	50	
36	Small coastal pelagics	*	50	50	50	
37	Sea birds	*	80	80	80	
38	Turtles	*	80	80	80	50
39	Cephalopods	50-80	80	80	80	
40	Spiny lobster	*	20	80	80	50
41	Other crustaceans	*	80	80	80	
42	Queen conch	50-80	20	*	80	50
43	Molluscs and worms	*	80	80	80	
44	Echinoderms	50-80	80	80	80	
45	Zoobenthic sessile animals	*	80	80	80	
46	Microfauna	*	80	80	80	
47	Zooplankton	*	80	80	80	
48	Seagrasses, seaweeds and other autos	40	30			
49	Symbiotic algae	*	80			
50	Phytoplankton	40	80			
51	Detritus	40				

* Parameter estimated by Ecopath; [a] Parameter adjusted manually during balancing process.

Table 12: Change in input biomass (%) undertaken to achieve mass balance.

Group Number	Group Name	% biomass change
1	Baleen whales	-75
2	Toothed whales	79
3	Dolphins	80
7	Large tunas and other pelagics	-24
8	Mackerels	-50
10	Small tunas, barracudas and other pelagics	-100
11	*Coryphaena* spp.	-400
14	Four-wing flyingfish	99
15	Other flyingfishes	77
17	Demersal and reef sharks	98
19	Reef jacks, tilefish, barracudas etc.	99
21	Groupers	99
23	Snappers	100
25	Squirrelfish and other small reef carnivores	100
27	Triggerfish, grunts, porgies, angelfish	99
29	Parrotfish, surgeonfish, triggerfish etc.	100
31	Other carnivorous demersals	94
32	Croakers, snooks & other carn/omn. demersals	98
33	Other omnivorous demersals	99
39	Cephalopods	-65
42	Queen conch	98
44	Echinoderms	98
48	Seagrasses, seaweeds and other autotrophs	99
50	Phytoplankton	-3
51	Detritus	93

Table 13: Mortality rates (year^{-1}) of functional groups in the preliminary ecosystem model for Grenada and the Grenadines.

Group Number	Group name	Total mortality (Z)	Fishing mortality (F)	Predation mortality (P)
1	Baleen Whales	0.020	0.000	0.000
2	Toothed Whales	0.020	0.000	0.010
3	Dolphins	0.030	0.000	0.024
4	Billfishes	1.130	0.939	0.191
5	Pelagic sharks	0.255	0.254	0.001
6	Juvenile pelagic sharks	0.580	0.000	0.294
7	Large tunas and other pelagics	0.765	0.724	0.041
8	Mackerels	1.890	1.010	0.880
9	Juvenile mackerels	6.220	0.111	5.929
10	Small tunas etc.	0.886	0.436	0.443
11	*Coryphaena* spp.	2.120	1.281	0.839
12	Pelagic jacks, needlefish	0.944	0.071	0.836
13	Juvenile pelagic jacks, needlefish	3.776	0.001	3.599
14	Four wing Flyingfish	5.800	1.815	3.972
15	Other Flyingfishes	3.800	0.000	1.933
16	Other bathypelagics	0.830	0.000	0.806
17	Demersal and reef sharks	0.320	0.000	0.002
18	Juvenile demersal and reef sharks	1.188	0.000	1.102
19	Reef jacks, tilefish, barracudas, etc.	1.120	0.047	1.059
20	Juvenile reef jacks, tilefish	2.390	0.026	2.303
21	Groupers	0.840	0.609	0.222
22	Juvenile groupers	2.940	0.000	2.917
23	Snappers	1.068	0.428	0.602
24	Juvenile snappers	2.180	0.002	2.145
25	Squirrelfish & other small reef carnivores	2.013	0.001	0.394
26	Other carnivorous reef species	1.080	0.000	1.031
27	Triggerfish, grunts, porgies, angelfish	1.590	0.002	1.512
28	Other omnivorous reef species	2.210	0.000	2.146
29	Parrotfish, surgeonfish, triggerfish etc	5.830	0.025	0.688
30	Small herb/det reef species	5.000	0.000	4.975
31	Other carnivorous demersals	0.610	0.000	0.595
32	Croakers and other carn/omn demersals	1.030	0.001	0.168
33	Other omnivorous demersals	3.340	0.000	2.810
34	Mullets & other herb./det. etc.	3.033	0.000	2.939
35	Other carnivorous benthopelagics	0.620	0.000	0.604
36	Small coastal pelagics	3.470	0.039	3.327
37	Sea birds	5.400	0.000	0.868
38	Turtles	0.150	0.075	0.070
39	Cephalopods	2.340	0.000	2.321
40	Spiny lobster	1.475	0.006	1.412
41	Other crustaceans	1.840	0.000	1.772
42	Queen conch	0.530	0.007	0.522
43	Molluscs and worms	4.140	0.000	4.123
44	Echinoderms	0.730	0.000	0.695
45	Zoobenthic sessile animals	1.360	0.000	1.301
46	Microfauna	195	0	181.559
47	Zooplankton	40	0	27.255
48	Seagrasses and other autotrophs	12.76	0	3.485
49	Symbiotic algae	10.2	0	4.056
50	Phytoplankton	70	0	5.63

Table 14: Summary statistics for the balanced preliminary model for Grenada and the Grenadines

Parameter	Value	Units
Sum of all consumption	6086.60	t·km^{-2} year^{-1}
Sum of all exports	2.81	t·km^{-2} year^{-1}
Sum of all respiratory flows	3116.56	t·km^{-2} year^{-1}
Sum of all flows into detritus	5126.14	t·km^{-2} year^{-1}
Total system throughput	14332.00	t·km^{-2} year^{-11}
Sum of all production	3755.00	t·km^{-2} year^{-1}
Mean trophic level of the catch	4.34	
Gross efficiency (catch/net p.p.)	0.000026	
Calculated total net primary production	3118.06	t·km^{-2} year^{-1}
Total primary production/total respiration	1.00	
Net system production	1.49	t·km^{-2} year^{-1}
Total primary production/total biomass	24.33	
Total biomass/total throughput	0.009	
Total biomass (excluding detritus)	128.17	t·km^{-2}
Total catches	0.08	t·km^{-2} year^{-1}
Connectance Index	0.18	
System Omnivory Index	0.26	