A Review of Caribbean Ecosystems and Fishery Resources Using ECOPATH Models

Un examen des écosystèmes caribéens et des ressources halieutiques avec l’utilisation des modèles de relations trophiques ECOPATH

S.G. Smikle, V. Christensen and K.A. Aiken
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Acknowledgements

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Introduction

1 Since the 1990’s a number of global initiatives have promoted the importance of an ecosystem approach to fisheries management (EAFM) including: the Global Plan of Action for the Protection of the Marine Environment; the Convention on Biological Diversity (UN 1992); the International Coral Reef Initiative; the Large Marine Ecosystems concept; and the FAO Code of Conduct for Responsible Fisheries, are just a few.

2 The EAFM has been aided with the proliferation of research devoted to the development of multispecies models describing the status of trophic interactions in aquatic ecosystems. Christensen and Pauly (2004) notes that this development has been made possible to a large degree by the formulation and dissemination of the ecosystem modelling approach and software tools Ecopath and Ecopath with Ecosim (Polovina and Ow 1983; Christensen and Pauly 1992; Christensen, Walters, and Pauly 2005). Christensen
and Pauly further notes that the Ecopath software has been widely distributed since 1990, and in 2004 had more than 2500 registered users in 124 countries while more than 150 models of aquatic ecosystems have been published.

This paper provides a review of ecosystems modelling within the Caribbean using the Ecopath approach and software tools. The review is not intended to provide a direct comparison of the modelled ecosystems attributes and performance, as this would require having access to the models and the data sets used to build the models. Rather, a general comparison is made of the outputs of the models and the various authors’ descriptions of ecosystem attributes.

1. Description of the study area: the Caribbean

1.1. Profile

The Caribbean refers to that area of the Americas that is enveloped by the Caribbean Sea (latitude: 9 to 22 N and longitude: 89 to 60 W) and is bounded by North America (South Florida), Central and South America, and the Antilles chain of islands (Heileman and Mahon 2009). Throughout this document, Caribbean countries or states refers to those countries or parts of countries that have land masses wholly within the Caribbean Sea, or have coastlines juxtaposing the Caribbean Sea. Also included are those Antillean islands which may not have Caribbean coasts but are geo-politically associated with the Caribbean (Figure 1).

The area encompasses some 35 countries including 27 island states – some of which are politically independent states and some are overseas territories (dependent islands) of France, The Netherlands, United Kingdom and USA (Singh and Mee 2008). This makes for a region that is geographically highly complex, with perhaps the greatest concentration of countries and associated states anywhere in the world (Chakalall et al. 2007). Wikipedia (2009) estimates that as of October 2006 the population the Caribbean was a little over 238 million – including Mexico, Colombia and Venezuela, but not the United States. Average per capita income (purchasing power parity, PPP) for the region is estimated at US$10,709 per year (USAID 2009).
1.2. Ecology

The Caribbean Sea is considered as the second largest sea in the world (Richards and Bohnsack 1990) with an area of approximately 3,274,085 square kilometres (Sea Around Us 2009). A large volume of water enters the Caribbean via the nutrient poor North Equatorial current through the passages between the Lesser Antilles and is transported by the Caribbean current into the Gulf of Mexico (Heileman and Mahon 2009). This nutrient poor water is partly responsible for the moderately productive ecosystem with primary production being approximately 456 mgC / m² / day (Sea Around Us 2009).

There is some enrichment via runoff from two of the largest river systems in the world – the Amazon and the Orinoco, as well as from several other large rivers that dominate the South American coast (Müller-Karger 1993). Areas of highest productivity are the mixing zones where the rivers meet the sea, localised upwelling areas and coral reefs, nearshore wetlands and seagrass beds (Richards and Bohnsack 1990).

The Caribbean has 7.64% of the world’s coral reefs (Sea Around Us 2009) and is biogeographically distinct in that most of the corals and associated species are endemic (Spalding, Ravilious, and Green 2001), (Wilkinson 2002). The region also includes the second largest barrier coral reef in the world – the Meso-American Barrier Reef off the coast of Caribbean Mexico and Belize (Heileman and Mahon 2009). Corals were dominated by species of Acropora, however a wide diversity of other species are also supported. The Caribbean marine ecosystem supports over 500 fish species (Randall 1983) and numerous other non-fish taxa.
1.3. Fisheries

Fisheries is a mainstay of many coastal communities within the region and perhaps support well over 2 million people (FAO 2000). The majority of fisheries activities are artisanal or small scale (SSF) operations with little changing over the centuries aside from the use of motorised boats and modern materials (Johannes 1997). There are, however, a few industrial or semi-industrial operations within the region that involves local fleets, and oftentimes fleets from industrialized nations such as Korea, Japan and the USA. The most important fish groups caught in commercially quantities are medium-sized pelagic fish, shrimps, lobster, and benthic molluscs (Table 1). Landings have increased more than fourfold from the average of approximately 80,000 tonnes reported in the 1950’s. Current production has levelled off somewhat now averaging around 330,000 tonnes for the five-year period between 2000 and 2004 (Sea Around Us 2009).

Table 1. Production in metric tons for the most important fish groups landed commercially

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Landings (t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sardinella aurita</td>
<td>Round sardinella</td>
<td>2,790,770</td>
</tr>
<tr>
<td>Opisthonema oglinum</td>
<td>Atlantic thread herring</td>
<td>242,769</td>
</tr>
<tr>
<td>Selar crumenophthalmus</td>
<td>Bigeye scad</td>
<td>99,470</td>
</tr>
<tr>
<td>Auxis</td>
<td>Frigate tuna</td>
<td>43,731</td>
</tr>
<tr>
<td>Scomber japonicas</td>
<td>Chub mackerel</td>
<td>33,220</td>
</tr>
<tr>
<td>Carangidae</td>
<td>Jacks and pompanos</td>
<td>23,897</td>
</tr>
<tr>
<td>Sphyraena</td>
<td>Barracudas</td>
<td>16,809</td>
</tr>
<tr>
<td>Penaeoida &amp; Penaeus</td>
<td>Shrimps &amp; prawns</td>
<td>945,349</td>
</tr>
<tr>
<td>Panulirus argus</td>
<td>Caribbean spiny lobster</td>
<td>1,127,725</td>
</tr>
<tr>
<td>Arca</td>
<td>Arc clams</td>
<td>545,553</td>
</tr>
<tr>
<td>Strombus spp</td>
<td>Conchs</td>
<td>480,455</td>
</tr>
</tbody>
</table>

The landings represent the totals caught since 1950. The first seven species are categorised as medium-sized pelagic (adapted from Sea Around Us 2009).

Figure 2. Reported historical landings (1950 to 2004) for the fish producing nations within the Caribbean.
For the period 2000 to 2004 production has averaged around 330,000 tonnes (Sea Around US 2009).

2. Ecopath with Ecosim Models of Caribbean Ecosystems

2.1. Methodology

A search was done for available publications of Ecopath models within the Caribbean using the University of British Columbia’s search tools of the library’s database as well as online databases. The free internet search tool Google Scholar was also used to search for available publications. In both cases the search terms were “Caribbean Ecosystem Studies” and “Caribbean Ecopath Models”, separately and with terms combined.

The searches found 53 published papers with references to ecosystem studies within the Caribbean. Of this number only nine were actually publications of studies that used the Ecopath approach and software in an ecosystem study. Of the nine papers found, 8 were among a list of 16 studies reported by Morissette (2007) as either underway or completed where EwE was used to construct marine ecosystem models within the Caribbean. One study (in the Mexican Caribbean) reported as in progress by Morissette had no author information and was therefore not included in this review. The 9th paper was published in 2009 and based on a zooplankton study in Jamaica (Persad and Webber 2009), and as such would likely not have been available to Morissette. A listing of the publications found is provided in Table 2 and shown graphically in Figure 3.

The format of the reviews follows a common structure. First, a description of the study area or location is provided. This is followed by a summary of the species described and
the categorisation into functional groups. The review then looks at the model outputs and reports on key findings of the authors.

9 Definitions for several of the ecosystem attributes generated by the models are provided below:

a. Total System Throughput (TST) represents the size of the entire ecosystem in terms of flow (Ulanowicz 1986). Calculated as the sum of all flows in a system such that:

\[ TST = \text{Total consumption} + \text{total export} + \text{total respiration} + \text{total flows to detritus} \]

b. System Primary Production to Respiration ratio (Pp/R). Defined as the ratio between total primary production and total respiration in a system (Christensen, Walters and Pauly 2005).

c. Finn's Cycling Index, was developed by Finn (1976) and is defined as the fraction of an ecosystems throughput that is recycled.

d. Transfer Efficiency (TE), expresses how efficiently flows are transferred from one discrete trophic level to the next. Calculated as:

\[
\frac{(\text{Sum of the exports from a given trophic level} + \text{The flow that is transferred from said trophic level to the next})}{\text{(The throughput on the trophic level)}}
\]

TE is expressed as a percentage (Christensen, Walters and Pauly 2005).

e. Ascendency measures the average mutual information in a system, scaled by the system throughput (Ulanowicz and Norden 1990). See Christensen (1995) for details of calculation.

f. System omnivory index is defined as the average omnivory index of all consumers weighted by the logarithm of each consumer’s food intake. The consumer omnivory index is calculated as the variance of the trophic level of a consumers prey group (Christensen, Walters and Pauly 2005).

Table 2. List of 16 Ecopath modelling studies within the Caribbean

<table>
<thead>
<tr>
<th>Model Geographic Area</th>
<th>Model Area</th>
<th>Author/Citation</th>
<th>Date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bahamas</td>
<td>Bimini</td>
<td>Grant</td>
<td>2001</td>
</tr>
<tr>
<td>Belize</td>
<td>Calbash Cay</td>
<td>Deehr et al.,</td>
<td>2007</td>
</tr>
<tr>
<td>BVI &amp; Puerto Rico</td>
<td></td>
<td>Searles</td>
<td>2004</td>
</tr>
<tr>
<td>Colombia</td>
<td>Guajira Peninsular</td>
<td>Criales-Hernández, García and Wolff</td>
<td>2006</td>
</tr>
<tr>
<td>Colombia</td>
<td></td>
<td>Duarte and García</td>
<td>2004</td>
</tr>
<tr>
<td>Cuba</td>
<td>Batabano Bay</td>
<td>Wolff et al.,</td>
<td>In prep.</td>
</tr>
<tr>
<td>Eastern Caribbean</td>
<td>Grenada &amp; Grenadines</td>
<td>Mohammed</td>
<td>2003</td>
</tr>
<tr>
<td>Eastern Caribbean</td>
<td>Lesser Antilles</td>
<td>FAO</td>
<td>In prep.</td>
</tr>
<tr>
<td>Florida</td>
<td>Looe Key</td>
<td>Venier and Pauly</td>
<td>1997</td>
</tr>
</tbody>
</table>
2.2. Model Reviews

Of the fourteen Ecopath studies that were completed only 11 publications were accessible to this author. All eleven were included in this review: (Alvarez-Hernández) 2007; Duarte and García 2004; Manickchand-Heileman et al. 2004; Mendoza 1993; Mohammed 2003; Opitz 1996; Persad and Webber 2009 and; Venier and Pauly 1997. The reviews are done in order from oldest to most recent. Figure 4 shows a map of the Caribbean with the locations of the (11) Ecopath studies.
Figure 3. Plot of the reported Ecopath models for Caribbean ecosystems

Those models reported as still in progress were assigned the year 2010. BB = Bimini; BCC = Calabash Cay; CGP = Guajira Peninsula; CGS = Gulf of Salamanca; CBB = Batabano Bay; ECGG = Grenada & Grenadines; ECLA = Lesser Antilles; FLK = LOOE Key; JDB = Discovery Bay; MSKQ = Sian Kaan, Quintana Roo; MSQ = South Quintana Roo; PRVI = PRVI Shelf; TVGP = Gulf of Paria; VNES = North Eastern Shelf.
Discussion

Many persons think of Caribbean marine biogeography of being based on reef systems. However, although coral reef ecosystems were the dominant feature of the models presented, there was clearly heterogeneity in the ecosystems represented. The models based on the South American shelf had, as expected, somewhat different habitat assemblages (estuaries, upwelling zones and mixing zones with river plumes) and species organisation, with fewer functional groups than the reef and oceanic based models of the Island ecosystems. Many of the same species were however represented in all models.

The classification of functional groups varied from simple broad groupings to more detailed groups based on family classifications. For example, Yucatan, and Colombia models have broad categories (give detail). On the other hand Opitz, Mohammed and Machinand give more details. This was symptomatic of an important limitation during the comparisons presented here in that not all models report on the same system attributes, particularly with maturity measures as discussed below.

Fisheries

Alvarez-Hernandez (2003) found that the estimated fish biomass for the southern reef of 204.6 t/km², though higher than that reported for the USVI (Randall 1963), was similar to that of the Great Barrier reef of Australia (Talbot and Goldman 1972).

Arrias-Gonzalez et al. (2004) found that the reef models were sensitive to small changes in fish biomass production and exploitation. Respectively (table 2) is an indication of the
sensitivity of the food web structure to changes in biomass of the top consumer groups (Post 2002).

Duarte and Garcia (2000, 2002, 2004) found that the key feature for small pelagic fish to affect the upper part of the food web is to have bottom up control of at least one top predator group that has a diverse diet. Contrary to expectations Duarte and Garcia (2000, 2002, 2004) found that wasp - waist type control (Rice 1995) is not exerted by the small pelagic fish group. Changes in the biomass of said groups propagated changes in the biomass or trophic flows in the upper trophic levels. However the lower trophic levels remained relatively unchanged. Given similar findings in some other trophic upwelling ecosystems (Mackinson et al. 1997), Duarte and Garcia (2000, 2002, 2004) were able to suggest that the crucial wasp waist role of intermediary trophic levels occupied by small pelagic fish in temperate and sub-tropical highly productive upwelling regions, may not be fully equivalent in tropical less productive upwelling ecosystems.

With respect to the impact of fisheries on the ecosystems, three models reported on the effective mean trophic level at which the fishery was equivalent to a predator. Trophic level of the fisheries lowest in Gulf of Paria (2.9) highest in Eastern Caribbean (4.3). The mainly offshore fisheries of the Grenada and Grenadines model targets medium-to-large pelagics and similar apex level predators, hence the high trophic level reported for this model in comparison to the others. In the Gulf of Paria, the fisheries target shrimp (detritivores) and demersal species between trophic levels II and III. Given the different ecosystem represented by the Grenada and Grenadines, Quintanaroo and Gulf of Paria models, and without additional information one cannot argue that the extent of fishing may have contributed to the different trophic levels observed. Most of the other fisheries were reef based and are probably similar to the 3.4 reported for the Yucatan.

**System Size**

The sizes of the ecosystems in terms of total energy flows were also highly variable. The total system throughput for the PRVI model was much larger than those reported from the other models with differing scales of magnitude (Table 3.).

**Ecosystem Maturity**

Caribbean reef strategy is to build up biomass through the maintenance of short cycles for an effective recycling of matter back to the detrital pool – a strategy to survive in nutrient poor waters (Opitz 1996). Evidence is the low mean transfer efficiencies reported for the models (TE = 10% – 12% Table 2). This fits with the average TE expected for ecosystems generally as reported by Pauly and Christensen (1995) with a range of 2% to 34%.

In estuarine areas, Machinand-Heileman et al. (2004) found that the detrital pathway dominated the grazing pathway. This was similar to many other esuarine systems (Day Jr. et al. 1989) with benthic invertebrates transferring much of the system energy from detritus to higher consumer levels. Other studies (e.g. Smayda 1966) have found that pelagic herbivory tend to account for no more than 10 – 20% which Machinand-Heileman et al. found was similar to that within the Gulf of Paria. Machinand-Heileman et al. also found that the detritus and other lower level trophic groups exerted bottom-up control of
the food web. Supports Odum’s (1969) suggestion that as a system matures they become more dependent on detritivory rather than herbivory.

17 Alvarez-Hernandez (2003). With PP/R less than one, the south Yucatan model represents a possible heterotrophic ecosystem with strong tendency for storage of organic matter. Concludes that the low A/C found by the model suggests that the Yucatan may have a high level of system maturity, perhaps in keeping with some literature reports of greater maturity for the Caribbean reefs (Stehli and Wells 1971) in comparison to the Pacific. Another level of comparison was that of system maturity. Odum (1969) suggests that ecosystems evolve towards maturity in a process that involves structural changes that are ordered and directional, culminating in stable systems with maximum biomass and/or information content (Christensen 1995). Odum (1969) further describes 24 attributes that characterises ecosystem development and maturity. Several of the summary statistics produced by Ecopath may be used to assess the relevant attribute of system maturity as described by Odum. These include: the system primary production to respiration ratio (Pp/R); Finns Cycling Index (FCI); system omnivory index (OI) and; Ascendency. Christensen (1995) cautions however, that ecologists have still not been able to conclusively define system maturity or stability, and that the validity of Odum’s attributes of mature ecosystems is still being challenged. Christensen further notes that these attributes may well be a measure of stability more so than maturity, and still provides a means for consistent comparison of ecosystems.

18 During the early development stage of an ecosystem, Pp/R is expected to be greater than 1 as production exceeds respiration. In systems suffering from organic pollution, the ration is expected to be less than 1. In mature systems, the energy that fixed is balanced by the cost of maintenance and so the ratio is expected to approach 1 (Christensen, Walters and Pauly 2005; Odum 1971). Grenada and Grenadines (Pp/R = 1) and Quintanaroo (Pp/R = 1.28) seem to be approaching maturity. Gulf of Paria (Pp/R = 3.77) reflects a system that is polluted, perhaps mainly due to runoff during the rainy season from several large rivers draining into the Gulf. These rivers include the Orinoco and San Juan rivers from South America, and the Caroni river from Trinidad. Pollution in the Gulf may also be influenced from waste coming from the highly industrialised west coast of Trinidad.

Table 3 shows three models reporting FCI with PRVI seemingly more stable than South Quintana Roo and Gulf of Paria respectively. Recall that the PRVI model assumed no fishing impact (Opitz 1996) while South Quintana Roo is less heavily fished (artisanal only) than the Gulf of Paria (industrial and artisanal fisheries). The level of fishing may explain why less of the throughput is recycled through the ecosystems. In terms of the other attributes of system maturity or stability, not enough models reported on these attributes to make comparisons meaningful.

**General findings**

19 Ecosystem modelling activity within the Caribbean has certainly increased since the early work of Mendoza (1993) and Opitz (1996). However, this modelling activity is not in keeping with the global growth rate of 23% per annum reported by Christensen and Walters (2005b). Figure 3 shows that growth has been flat with practically one model produced per year since 1993, excepting for a flurry of published models between 2003 and 2004.
The lack of research in the area of ecosystem modelling in the Caribbean is surprising given that there are many research institutions within the region (Velho 2005) and this count does not include those from the United States. As Velho (2005) explains, universities and public research institutions within Latin America and the Caribbean, have, largely not created mechanisms to identify national or regional needs and set their research agenda on the basis of scientific criteria in line with international mainstream science. There is a tendency for individual researchers or departments to select research themes on the basis of their perception of scientific importance, normally taking the lead from international scientific activity (Velho 2005).

Despite the relatively large number of practising research institutions within the region, there are very few that carry fisheries research agenda, and as Salas et al. (2007) confirmed there is limited capability within fishery research institutions within the region today. Ecosystem modelling within the Caribbean may therefore continue to rely on the ad hoc interventions of international organisations.

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ABSTRACTS

This paper provides a review of ecosystems modelling within the Caribbean using the Ecopath approach and software tools. The review is not intended to provide a direct comparison of the modelled ecosystems attributes and performance, as this would require having access to the models and the data sets used to build the models. Rather, a general comparison is made of the outputs of the models and the various authors’ descriptions of ecosystem attributes.

L’article présente une revue des écosystèmes marins et des ressources halieutiques de la zone Caraïbe en utilisant l’approche Ecopath pour la modélisation des interactions au sein des
Écosystèmes. En dépit des nombreuses recherches déjà réalisées, la modélisation des écosystèmes marins de la Caraïbe est parcellaire et nécessite des investigations conséquentes.

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Geographical index: Caraïbes
Mots-clés: ecopath, modélisation, écosystème marin, pêche
Keywords: modelling, marine ecosystem, fishery

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