



## ‘Whales eat fish’? Demystifying the myth in the Caribbean marine ecosystem

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### Abstract

There has been much recent discussion about the idea that large whales are potential competitors with fisheries for available marine resources. Based on this idea, often referred to as the ‘whales eat fish’ conflict, culling whales has been proposed as a way to increase resources available for human consumption and thereby ensuring global food security. However, the scientific basis for such arguments remains unclear, especially in the Caribbean waters where baleen whales generally do not feed. In this article, we (i) develop an ecosystem model describing the trophic interactions between whales, fish and fisheries in the Caribbean waters, (ii) calculate the level of overlap between cetaceans and fisheries for food resources, and (iii) simulate the removal of cetaceans from the Caribbean waters in order to quantify the potential increase in available biomass of commercially important fish. Ten groups of cetaceans are considered in the model, including baleen whales, toothed whales and small cetaceans. Our results suggest that baleen whales are not a threat to fisheries in Caribbean waters, while toothed cetaceans seem to be more impacted by fisheries than they actually impacting them. Whales target different types of food resources and consume significantly less than what is taken by fisheries. Moreover, simulated reductions in large whale abundance do not produce any appreciable increase in biomass of the commercially important fish species. In some cases, the presence of some whales actually improves fishery yield as a result of indirect predation effects.

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## Introduction

There has been much discussion about the idea that marine mammals in general and large whales in particular are potential competitors with fisheries for available marine resources (Mori and Butterworth 2006; Jackson 2007). Based on this idea, often referred to as the 'whales-eat-fish' conflict, culling whales has been promoted as a way to increase resources available for human consumption and thereby ensuring global food security (Anonymous 2001). The scientific basis upon which these advocates of whale culling reach their conclusion remains unclear. First, although some species such as minke whales (*Balaenoptera acutorostrata*, Balaeopteridae) are perceived as important predators in their feeding areas (Schweder *et al.* 2000), there is no scientific evidence for existing large-scale competition between great whales and fisheries (Kaschner 2004; Morissette 2007). Second, it is well documented that human over-exploitation is the main cause for the depletion of world's marine resources (Pauly *et al.* 2002; Myers and Worm 2003). Finally, the unpredictable consequences of reducing predator populations could be considerable (Scheffer *et al.* 2001; Springer *et al.* 2003).

Recently, the argument has received growing attention in the scientific literature (Clapham *et al.* 2007; Gerber *et al.* 2009). Most studies investigating the ecological role of baleen whales in ecosystems have looked at the issue in terms of single predator-prey interactions (Lindstrøm *et al.* 2002) with just a few multispecies studies (Hill *et al.* 2006). However, trophic interactions between cetaceans and other marine species are complex and often indirect, and

consequently, this issue is most appropriately evaluated within an ecosystem framework (Morissette 2007). The choice of an appropriate multispecies model should ultimately be linked to scientific goals and/or management objectives. For objectives linked to broad-scale questions regarding the structure of ecosystems, ecosystem models, such as *Ecopath with Ecosim*, (*EwE*) may be a more suitable tool to use, particularly if indirect effects are to be quantified (Morissette 2007). Other models, such as minimum realistic models (MRMs) as used by Punt and Butterworth (1995), have more flexibility in modelling the dynamics of marine predators, but usually ignore indirect effects (Plagányi 2007). Other issues with the utility of the MRM approach are that there is no way of knowing *a priori* what level of complexity constitutes the 'minimum' required for a given purpose. Particularly important is the number of assumptions required to determine reliably the processes that govern the interactions between all components of a greatly reduced skeleton of the system. This is particularly important when reducing ecosystem structure from more than the 520 species found in the Caribbean to just four components or so. These issues may be the reason why most ecosystem analyses performed in the Caribbean thus far have favoured the multispecies approach to the MRMs (e.g. the LAPE project; Mohammed *et al.* 2007a).

The 'whales eat fish' debate is a global issue, but much of the debate at for example the annual meeting of the International Whaling Commission's, is focused on tropical countries that depend on marine resources for employment and food – among them many of the Caribbean nations (Fanning *et al.* 2007). While available evidence suggests that the decline of

Caribbean fisheries is likely the result of over-exploitation (Chakalall *et al.* 1998; Food and Agriculture Organization of the United Nations (FAO) 2007a), it is still proposed that whales could be the cause of such depletion. At the 58th annual meeting of the IWC in 2006, this debate led to the St. Kitts declaration, stipulating that, 'scientific research has shown that whales consume huge quantities of fish, making the issue a matter of food security for coastal nations...' (International Whaling Commission 2006). In the Caribbean area, the Japanese-funded project LAPE (Lesser Antilles Pelagic Ecosystem), led by the Food and Agriculture Organization (FAO) of the United Nations, suggested that:

Most populations of oceanic marine mammals in the region seem to be increasing. This is due to being protected from fishing through most of their ranges and efforts to reduce incidental capture in fishing gear. Cetaceans may impact fisheries by competing with other species in the ecosystem for the same prey, or directly with fisheries for the same target species

Food and Agriculture Organization  
of the United Nations (FAO) (2007b)

While many of the undersigning countries are voting in support of resuming whaling, other Caribbean nations such as Dominica now object to whaling (R. Skeritt, Dominica's Prime Minister, Roseau, Ocean Life Symposium, March 2009), pledging for a more precautionary approach on the management of their marine resources.

The Caribbean ecosystem represents an important breeding ground for many baleen whales (Stevick *et al.* 2003). In such tropical areas, most baleen whales only spend part of the year, feeding at a much reduced rate, if at all, during that time (Brown and Lockyer 1984; Corkeron and Connor 1999). The St. Kitts Declaration referenced above therefore illustrates the biased, yet widely prevailing perception of the ecology of great whales in their tropical breeding grounds. To provide a scientific basis for this discussion, in this article, we (i) develop an ecosystem model describing the trophic interactions between whales, fish and fisheries in the Caribbean, (ii) calculate the level of overlap between cetaceans and fisheries for food resources, and (iii) simulate the removal of cetaceans from the Caribbean waters in order to quantify the potential subsequent gain in biomass for commercially important fish. Finally, we discuss the potential conservation and management strategies in the Caribbean marine ecosystem.

## Material and methods

### Studied ecosystem and ecosystem modelling approach

Our study area covers the Caribbean Sea Large Marine Ecosystem, a predominantly pelagic environment. It includes the EEZs of the West Indies and the Lesser Antilles islands ranging from 9.75° N to 22.2° N latitude and from 73.25° W to 56.25° W longitude, covering a total area of 1 960 863 km<sup>2</sup> (Fig. 1). This area represents a typical tropical, pelagic environment used by many great whales during the breeding season, and includes eight adjacent ecosystems that have been modelled in the past (described in Melgo *et al.* 2009). Data from these eight models were used to establish confidence intervals for our input parameters.

The software *Ecopath with Ecosim* was used to build a food web model of the Caribbean. Methodology is described by Christensen *et al.* (2005). As with any other model, this approach presents some strengths and weaknesses (Plagányi 2007). *EwE* has been broadly used for comparative studies on a global scale (Pauly *et al.* 1998; Murawski *et al.* 2010; Worm *et al.* 2009) and is now the world's most widely used tool for ecosystem modelling; *EwE* models represent about 20% of the 4115 published 'ecosystem modelling' work in 2009 (ISI Web of Science search October 2009). Recently, it was recognized by NOAA as the one of the 10 most important scientific breakthroughs in the last 200 years (<http://celebrating200years.noaa.gov/breakthroughs/ecopath/welcome.html>), and is also considered by the European Commission as the model that best fulfils the needs for projects addressing scenarios and models of future trends of biodiversity and ecosystem services changes (2009).

Data for parameterizing our model were largely extracted from the *Lesser Antilles Pelagic Ecosystem Project* report (LAPE; Food and Agriculture Organization of the United Nations (FAO) 2003), but included additional details relevant to our specific research questions. We used a higher taxonomic resolution for cetaceans with 10 trophic groups, representing most species occurring in the area (Melgo *et al.* 2009). Species relevant to IWC discussions or with a different diet were assigned to a distinct trophic group such as minke, fin (*Balaenoptera physalus*, Balaenopteridae), humpback (*Megep-tera novaeangliae*, Balaenopteridae), sei (*Balaenoptera*



**Figure 1** Map showing the spatial boundaries of our study area. The coordinates of the Caribbean islands area are 9.75N–22.25N and 73.25W–56.25W, covering the EEZs of the Lesser Antilles and the West Indies, for a total area of approximately 1.9 million km<sup>2</sup>. The numbers shown on the map represent eight adjacent tropical models, which provided data for the confidence intervals: Bahia Ascencion [1] (Vidal and Basurto 2003); Southern Mexican Caribbean [2] (Alvarez-Hernández 2003); Grenada and the Grenadines [3] (Mohammed 2003); Colombian Caribbean Sea [4] (Duarte and Garcia 2002); Costa Rica [5] (Wolff *et al.* 1998); Caribbean coral reef [6] (Opitz 1996); Central Atlantic [7] (Vasconcellos and Watson 2004) and Eastern Tropical Pacific [8] (Olson and Watters 2003).

*borealis*, Balaenopteridae), Bryde's (*Balaenoptera edeni*, Balaenopteridae) and blue whales (*Balaenoptera musculus*, Balaenopteridae) while other species such as beaked whales, sperm whales, killer whales or dolphins were aggregated. We aggregated non-marine mammal species into 19 functional groups representing fish, cephalopods, crustaceans, benthic invertebrates, plankton and detritus. The groupings were based on similarities of food habits, habitats and biological variables. Detailed descriptions of input data and model parameterization can be found in Melgo *et al.* (2009).

Additional data for trophic groups not included in the LAPE research were compiled from existing global databases (e.g. Kaschner 2004), and from an extensive literature search for data on the abundance, diet and consumption rates of cetaceans. We also hosted a workshop in Barbados in September 2008 ([http://www.lenfestocean.org/whales\\_fisheries.html](http://www.lenfestocean.org/whales_fisheries.html)) to access local data resources and expertise and to gain feedback from local experts.

#### Information on cetaceans

Due to the lack of dedicated surveys, very few reliable abundance estimates are available for most

cetacean species in the Caribbean Sea. Biomass densities were therefore derived from a global database of marine mammal abundance converted into local densities and weighted by the species-specific relative suitability of the environment of our study area (Kaschner 2004; Kaschner *et al.* 2006). Wherever possible, we used existing estimates from surveys conducted in the vicinity of our study areas or in similar habitats to ground-truth these values (Table 1). Surveys generally only covered the northern part of the Gulf of Mexico and only provided estimates for a subset of species including killer, sperm and Bryde's whales (Davis and Fargion 1996; Davis *et al.* 2000; Mullin and Fulling 2003). Production estimates expressed as the population growth rate,  $P/B$ , in the model, were based on the assumption the  $P/B$  ratio equals total mortality (Allen 1971). Mortality estimates were available for minke, fin and sperm whales. For the remaining cetacean groups, we used  $P/B$  values published for the same species from existing EwE models (e.g. Okey 2001; Heymans 2005; Guénette *et al.* 2006).

Consumption estimates expressed as total consumption over biomass,  $Q/B$ , were estimated from a basic food consumption model derived from Trites *et al.* (1997) to generate the biomass and consump-

**Table 1** Comparison of predicted cetacean densities in Caribbean waters based on a global model developed by Kaschner *et al.* (2006) and Kaschner (2004) and observed minimum and maximum densities in similar habitats (subtropical and tropical waters).

Common name	Estimated density (animals per 1000 km <sup>2</sup> )	Observed density (animals per 1000 km <sup>2</sup> )	CV	G(0) corrected	Geographic area	Survey years	Survey type	Source
Blue whale	0.02	0.07	0.24	No	Eastern Tropical Pacific	1986–90	S	Wade and Gerrodette (1993)
Blue whale	0.02	4.96	0.13	Yes	NE Pacific, California inshore	1991–96	S	Calambokidis and Barlow (2004)
Bryde's whale	0.28	0.67	0.20	No	Eastern Tropical Pacific	1986–90	S	Wade and Gerrodette (1993)
Bryde's whale	0.28	0.04	0.85	No	NW Atlantic, northern Gulf of Mexico (GulfCet I survey)	1991–94	S	Davis and Fargion (1996)
Fin whale	0.22	1.85	0.48	No	NW Atlantic, Virginia Capes	2002	S	Garrison <i>et al.</i> (2003)
Fin whale	0.22	0.07	0.72	Yes	NE Pacific, Hawaii waters	2002	S	Barlow (2003a)
Humpback whale	6.50	0.03	0.37	Yes	NE Pacific, California offshore	1991–96	S	Calambokidis and Barlow 2004
Humpback whale	6.50	112.32	0.27	No	SW Indian Ocean, Madagascar (southern block)	1994	S	Best <i>et al.</i> 1996
Minke whale	0.73	0.93	0.51	Yes	NE Pacific, west coast US	1996	S	Barlow (2003b)
Minke whale	0.73	0.03	1.29	No	NW Atlantic, US east coast, south of Maryland	1998	S	Mullin and Fulling (2003)
Sei whale	0.05	0.10	0.73	Yes	NE Pacific, west coast US	1996	S	Barlow (2003)
Sei whale	0.05	0.03	1.01	Yes	NE Pacific, west coast US	2001	S	Barlow (2003)
Killer whale	0.06	0.14	0.98	Yes	NE Pacific, Hawaii waters	2002	S	Barlow (2006)
Killer whale	0.06	0.79	0.48	No	NW Atlantic, northern Gulf of Mexico (GulfCet I survey)	1991–94	S	Davis and Fargion (1996)
Sperm whale	1.03	0.85	0.57	No	NW Atlantic, northern Gulf of Mexico (GulfCet I EPA survey)	1996–97	S	Davis <i>et al.</i> (2000)
Sperm whale	1.03	3.80	0.23	No	NW Atlantic, northern Gulf of Mexico (SEFSC)	1996–2001	S	Mullin and Fulling (2004)

Density estimates that are corrected for animals missed on the track-line are indicated in the G(0) corrected column. All other observed estimates might represent underestimations. A, aerial surveys; S, ship-based surveys.

tion (Q/B) ratios needed for each cetacean group. For all cetaceans except baleen whales, we used an empirical model developed by Innes *et al.* (1986), which was later modified by Trites *et al.* (1997), to estimate food consumption. For baleen whales, annual food intake was estimated based on a model by Armstrong and Siegfried (1991). Except for the Bryde's whale, which are known to occur in these areas year round (Mohammed *et al.* 2007a), all other baleen whales only spend about a third of the year in their tropical breeding grounds, where they are known to either fast or feed at a considerably reduced rate (Kenney *et al.* 1997; Perry *et al.* 1999). We assumed a 90% reduction in food intake for baleen whales based on Lockyer (1981).

Some odontocetes are also migratory or undertake seasonal inshore–offshore movements but are not known to alter their feeding behaviour in tropical waters (e.g. Whitehead 2002). Published diet data were available for all fish, most invertebrates and plankton. However, for cetaceans, we found very few quantitative descriptions of diet, especially in tropical baleen whale, breeding areas such as the Caribbean. Therefore, we relied largely on published diet information for these cetaceans in the North Atlantic so long as specific criteria were met. Criteria included, in order of importance: same cetacean species, quantitative wet weight diet information (vs. frequency of occurrence), same ecosystem type (i.e. pelagic), and similar time period. The assumption that cetaceans do not change their diet and eat the same kind of fish, in terms of size and trophic level, in high latitude northern feeding grounds and tropical breeding areas is a critical aspect of our uncertainty analysis. Such an assumption might be intuitive, but because there is no published evidence for such dietary plasticity linked to migration patterns, we tested the possibility that cetaceans could be feeding at higher trophic levels in tropical breeding areas (uncertainty analysis described below). A detailed and referenced description of the diet matrix along with data sources for biomass, P/B and Q/B values is available in a report by Melgo *et al.* (2009).

#### Fisheries catch data time series

The main commercial species or trophic groups caught in the Caribbean include small and schooling pelagic fish, crustaceans and benthos, scombrids and reef fishes. Other commercial groups include tunas, dolphinfish (*Coryphaena hippurus*, Coryphae-

nidae), flyingfishes (*Hirundichthys affinis*, *Cheilopogon cyanopterus*, *Cypselurus cyanopterus* and *Parexocoetus brachypterus*, Exocoetidae), sharks and other predatory species (see detailed catch data in Melgo *et al.* 2009). As far as possible, we used data obtained from national catch statistics, which were considered to be the most reliable. Time series of total catches (in tonnes km<sup>-2</sup> year<sup>-1</sup>) from 2001–05 for Antigua and Barbuda, St. Kitts and Nevis, Dominica, St. Lucia, St. Vincent and the Grenadines, Grenada, Barbados, Trinidad, Martinique and Guadeloupe were obtained from the LAPE project (Mohammed *et al.* 2007b), compiled from international databases at the FAO and the International Commission for the Conservation of Atlantic Tunas (ICCAT) and national data holdings. For countries in our study area that were not covered by the LAPE project, which included Anguilla, British Virgin Islands, Dominican Republic, Montserrat, Puerto Rico and US Virgin Islands, we used fisheries data specified by country, geographic origin and taxon, from the *Sea Around Us Project (SAUP)* database (*Sea Around Us*, 2008; described in Watson *et al.* 2004). We also used the SAUP database to complete the LAPE with information from 1986 to 2000, and to get catches for the whole 1986–2005 period from foreign fleets, which came mainly from the USA, Puerto Rico, Venezuela, Netherlands Antilles and Colombia.

#### Analyses and simulations

Diet composition for cetacean species and fisheries catches were standardized to express proportions of different prey groups, allowing direct comparison between the diet and the catch. Similarly, we expressed estimates of total annual intake for each trophic group and predation mortality as an annual rate, which could then be compared with fishing mortality. Using output from our *Ecopath* models, we calculated the overlap in resource exploitation between cetaceans and fisheries [see Morissette (2007) using a modified version of Kaschner (2004)]:

$$\alpha_{f,m} = \left( \frac{2 \sum_k (p_{m,k} p_{f,k})}{\sum_k p_{m,k}^2 + \sum_k p_{f,k}^2} \right) \times \left( \frac{Q_m}{(Q_m + C_f)} \frac{C_f}{(Q_m + C_f)} \right) \quad (1)$$

where  $\alpha_{f,m}$  is the quantitative overlap between a fishery  $f$  and a marine mammal group  $m$  in the

ecosystem, and the first term expresses the qualitative similarity in diet/catch composition between the marine mammal group  $m$  and fisheries  $f$  sharing the resource or food type  $k$ , with  $p_{m,k}$  and  $p_{f,k}$  representing the proportions of group  $k$  in the diet of marine mammals  $m$  or the catch by fishery  $f$ . This term is multiplied by the product of the proportion of total food consumption by marine mammals  $Q_m$  and the proportion of total fisheries catches  $C_f$  in the ecosystem. This index scales from 0 showing no overlap to 0.25 when identical resources are targeted by whales and fisheries. When resource use is identical between these two groups, the first term of equation (1) is equal to 1 and each proportion of the second term is 0.5 (or 0.25 for the product).

In order to describe the overall structure and functions of the Caribbean ecosystem, we calculated the system omnivory index (SOI), which is a measure of the connectance of the food web, but weighted by the importance of each prey in its' predator diet.

We also calculated the mixed trophic impact (MTI) to assess species interactions in the ecosystem comprehensively. The MTI summarizes quantitatively both the direct and indirect effects that a small change in the biomass of a group will have on the biomass of all other groups in the system (Ulanowicz and Puccia 1990):

$$MTI_{ij} = DC_{ij} - FC_{j,i} \quad (2)$$

where  $DC_{ij}$  is the diet composition term expressing how much  $j$  contributes to the diet of  $i$ , and  $FC_{j,i}$  is a host composition term giving the proportion of the predation on  $j$  that is due to  $i$  as a predator. When calculating the host compositions, the fishing fleets are included as 'predators'.

In addition, we calculated the trophic level of cetacean consumption ( $TL_Q$ ) (Morissette 2007) to compare it with trophic level of the catch ( $TL_C$ ) (Christensen *et al.* 2005):

$$TL_Q = \sum_i \left( TL_i \left( \frac{\sum_{j=1}^n Q_{ij}}{\sum_{j=1}^n Q_i} \right) \right) \quad (3)$$

where  $Q_{ij}$  is the consumption of prey  $i$  (in tons) by cetacean  $j$ ,  $Q_j$  is the total consumption of all species by cetacean species  $j$  and  $TL_i$  is the trophic level for species  $i$ . Equation (3) represents the average trophic level at which cetaceans feed. This is the average TL of each species multiplied by their proportion in the consumption matrix

expressed as tonnes per  $km^{-2}$  per year that cetaceans consume.

#### Model parametrization and dynamics

We used the balanced Ecopath model for the Caribbean to parameterize a dynamic *Ecosim* model that attempts to reproduce the changes in trophic structure based on historical trends in fishing effort. To account for ecological differences of different trophic groups, we adjusted the vulnerability ( $v$ ) of each group based on available information about the specific ecology of each species and by fitting the model to biomass time series for those trophic groups for which such data could be obtained.

The model was fitted to independent time series of biomass data for 12 trophic groups by adjusting the vulnerabilities of all groups and other parameters representing detailed ecological features related to marine mammals: prey-switching effects, prey-handling time and changes in foraging time. The maximum relative feeding time was set from 2.0 (default) to 10.0 for all cetaceans, given that these species can spend more time searching for their prey if they are scarce (Piroddi 2008). Feeding time adjustment rate was set to 0.5 for cetaceans and to 0.0 for other groups, because cetaceans may change their feeding time as food availability varies (Heymans 2005; Piroddi 2008). Finally, assuming that cetaceans can be opportunistic foragers and adapt their diet depending on prey availability, the switching power was set to 2.0 for these groups and left at 0.0 (default) for other trophic groups (Piroddi 2008). The model was driven by fishing effort obtained from commercially important species in the Caribbean (see detailed information in Melgo *et al.* 2009).

Once the model was fitted, we used *Ecosim* to investigate how a potential harvest of whales might impact the biomass of commercially important fish. We simulated the removal of whales from the ecosystem by applying an intense exploitation pattern and using a fishing mortality value of 5. This value represents an average of 20-fold increase in fishing effort on whales and an extreme harvesting scenario for groups that were not harvested (Morissette 2007). This increase in the mortality allowed us to simulate extinction of marine mammal populations. Subsequently, we compared biomass trends over 22 years with or without whales in the system, which took us up until 2007, which is the end of our time series.

**Uncertainty**

*Model fitting to time-series data*

We validated our ecosystem model using independent time series of biomass, CPUE, and catch that we collated from the literature and from the SAUP database (Melgo *et al.* 2009) to assess how well the model replicates observed behaviour through time. The 'best' model was identified based on weighted sums of squares (SS) between observed and predicted biomass and catch data:

$$SS = \sum_{i=1}^n (X_i - \bar{X})^2 \tag{4}$$

Simulations based on the best model were driven using independent time series of effort.

We conducted extensive sensitivity analyses to test the robustness of our results to various model assumptions. To test model performance, we simulated the eradication of baleen whales under different assumptions about cetacean feeding rates, biomass and proportion of fish in the diet of the cetaceans (Table 2). For each set of assumptions, three hypothetical stages were simulated: our default value, a minimum and a maximum value. We also explored an alternative management scenario using similar assumptions but applying a fishing moratorium in which all human predators were removed. This was in place of removing whales. The increase of biomass was calculated as the average percent change in the biomass of commercially exploited fish groups after the 22-year simulation, for the different scenarios compared with the initial simulation.

**Results**

**Ability of the model to explain biomass trends**

In spite of obvious scarcity of data for the Caribbean ecosystem, the model performed relatively well at reproducing basic trends in relative biomass for most commercially important trophic groups, based on independent CPUE time series (Fig. 6a). Model fitting allowed us to minimize sum of squares (SS) by adjusting vulnerabilities, prey-switching, prey-handling and foraging for all species ( $SS_{\text{default}} = 737$ ;  $SS_{\text{fitted best model}} = 69$ ).

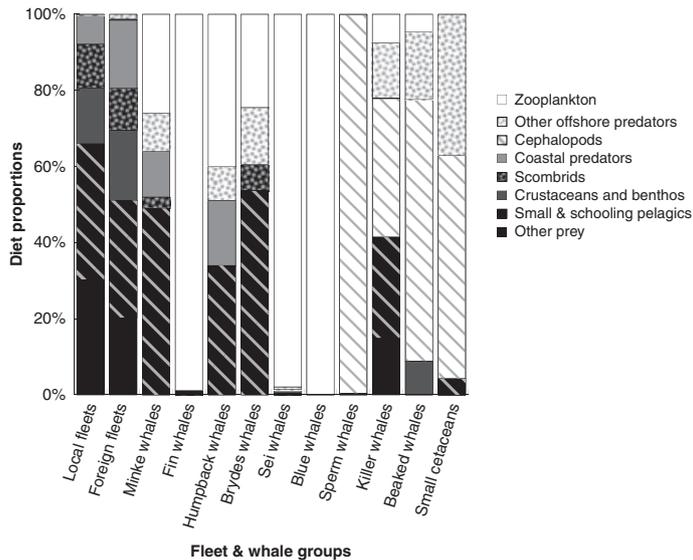
**Comparison of diets, total intakes and mortalities**

More than 75% of fisheries catch by local fleets was composed of five trophic groups: *small and schooling pelagics, scombrids, crustaceans and benthos, coastal predators* and *reef fishes*. For foreign fleets, the same five groups represented more than 90% of the catch. By contrast, cetaceans mostly consumed *zooplankton, small and schooling pelagics, reef fishes* and *scombrids*. For most mysticetes, *zooplankton* and *small and schooling pelagics* made up more than 75% of the consumption. For odontocetes, *cephalopods* and *small and schooling pelagics* were more important (Fig. 2).

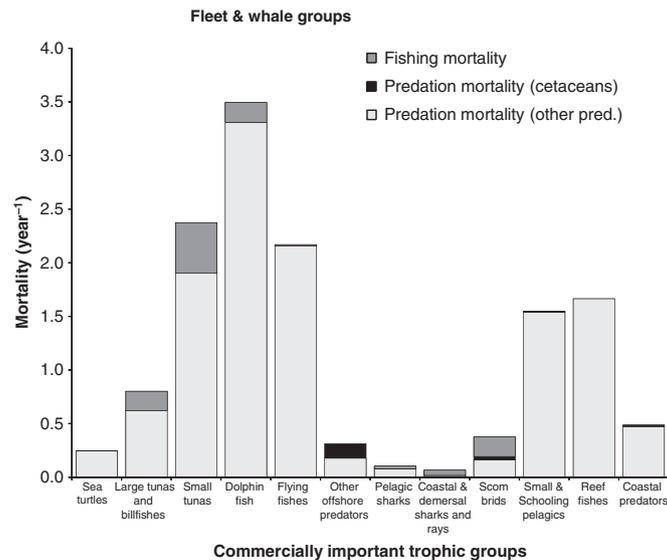
Total annual mortality varied greatly between trophic groups, but our results clearly showed that the primary source of mortality for all groups was predation by non-cetacean predators (M2, Fig. 3). Fishing was the second most important source of mortality for some trophic groups such as *small tunas, scombrids*, and *large tunas and billfishes*. By contrast,

**Table 2** Model scenarios and assumptions that were used to examine the impacts of whaling and fishing in *Ecosim*.

Assumption	Minimum	Best estimate	Maximum
Feeding rates of baleen whales in breeding areas (expressed as proportion of total annual food intake in feeding areas)	1%	10%	100%
Whale density	Calculated based on lowest abundance estimate reported in the literature for the study area or similar habitat (see Melgo <i>et al.</i> 2009)	Estimated based on Kaschner (2004) global database	Calculated based on highest abundance estimate reported in the literature for the study area or similar habitat (see Melgo <i>et al.</i> 2009)
Proportion of fish in the diet of cetaceans	50% decrease in the diet proportion of each fish group	Best available data for each cetacean species' diet	50% increase in the diet proportion of each fish group
Fishing effort	50% of original time series	Time series of <i>F</i> from best available data	150% of original time series



**Figure 2** Catch composition of local and foreign fleets vs. diet composition of the 10 marine mammal species present in the Caribbean model. Dark colours and patterns represent fish that are mainly targeted by fisheries, while light colours and patterns are prey essentially eaten by whales.



**Figure 3** Fishing mortality (F) and predation mortality (M2) from marine mammals and other predators for commercially important fish of the Caribbean ecosystem.

cetaceans had a negligible predatory impact on most commercially important fish in this system, except *other offshore predators*, for which about 40% of total mortality could be attributed to cetaceans.

The highest consumption by baleen whales occurred in Bryde's and humpback whales (in Table 3). Among toothed cetaceans, the 'small cetaceans' group showed the highest consumption of fish, by an order of magnitude greater than consumption of other cetaceans. Overall, more marine resources were taken by fisheries than any cetacean group except for small cetaceans.

### Resource overlap

We estimated overlap in resource exploitation between fisheries and cetaceans in the Caribbean

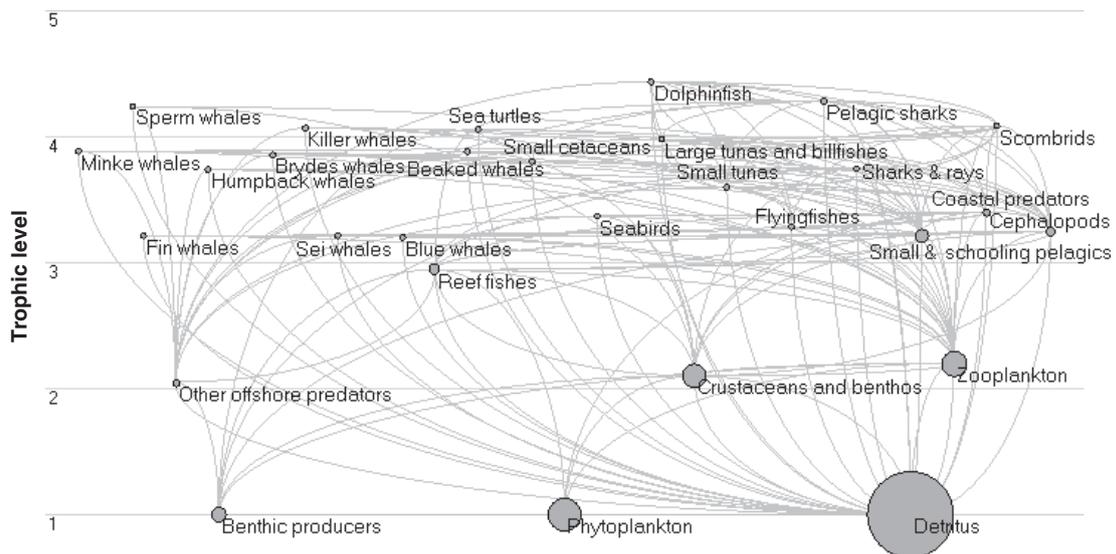
waters to be highest for humpback and Bryde's whales (Table 3). Overlap was very low for most species, but higher between cetaceans and local fleets than between cetaceans and foreign fleets (Table 3).

### Trophic structure and functions of the Caribbean ecosystem

The Caribbean area has an ecosystem dominated by pelagic organisms (Fig. 4), where most primary production was consumed by zooplankton, which is then transferred to pelagic species. The complexity of the system is relatively high with a bias towards a web of trophic interactions rather than linear links, with a system omnivory index (SOI) of 0.23. In comparison, the average complexity of marine

**Table 3** Resource overlap index, mean trophic level (TL) and mixed trophic impacts (MTI) of fisheries' catches and cetacean consumption in the Caribbean.

	Total amount taken (tonnes km <sup>-2</sup> )	Overlap index	Mean TL of the catch/consumption	Overall MTI
Fisheries	0.104	–	3.28	–1.52
Local fleets	0.097	–	3.29	–0.06
Foreign fleets	0.007	–	3.14	–1.46
Minke whales	0.004	0.025	2.88	>–0.001
Fin whales	0.003	<0.001	2.20	>–0.001
Humpback whales	0.035	0.102	2.74	–0.02
Bryde's whales	0.027	0.116	2.84	–0.03
Sei whales	<0.001	<0.001	2.20	>–0.001
Blue whales	<0.001	<0.001	2.20	0
Sperm whales	0.095	0.001	3.25	–0.02
Killer whales	0.005	0.019	3.12	–0.20
Beaked whales	0.001	<0.001	3.25	>–0.001
Small cetaceans	0.576	0.007	2.81	–0.75
Baleen whales	0.070	0.147	2.76	–0.05
Toothed whales	0.677	0.005	2.89	–0.98
All cetaceans	0.747	0.010	2.86	–1.03

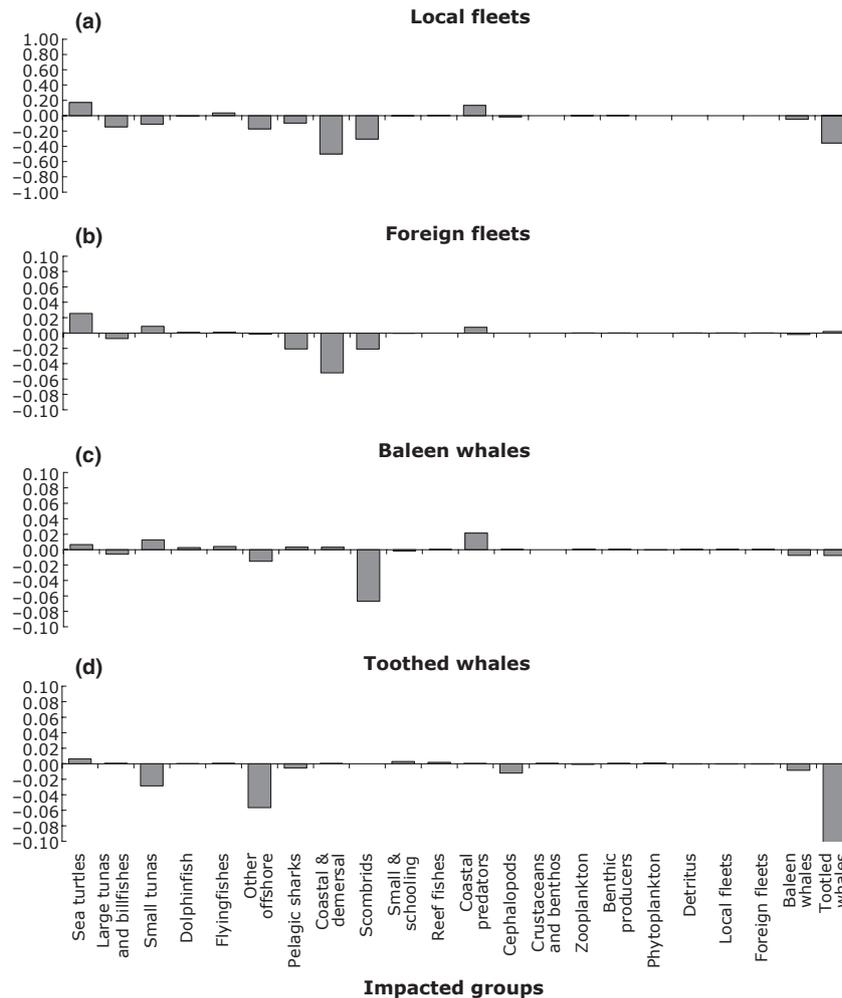


**Figure 4** Schematic representation that illustrates the primary flows of biomass in the Caribbean ecosystem. The size of each node is proportional to the group's biomass in the system.

ecosystems, as measure by the SOI, is around 0.172 (Morissette 2007). Cetaceans groups and especially those that could be targeted by whaling, occur at relatively low trophic levels (between 3 and 4) because they mostly feed on species from the second trophic level.

The MTI analysis indicated that all cetaceans and all fisheries had an overall negative impact, which implies a potential decrease in abundance,

on other groups of the Caribbean ecosystem (Table 3). However, while total MTI for baleen whales and foreign fleets were negligible and were two orders of magnitudes smaller (Fig. 5b,d) than that of toothed whales and local fisheries, both appeared to have substantial overall negative impacts (Table 3). Local fisheries not only had their greatest impact on *coastal demersal sharks and rays*, but also had a substantial negative impact on



**Figure 5** Mixed trophic impacts of local fleets (a), foreign fleets (b), all toothed whales (c) and baleen whales (d) in the Caribbean. Note that scales are an order of magnitude lower for panels b, c and d.

toothed whales in the system (Fig. 5a). Toothed whales were estimated mainly to impact themselves and appear to have little or no effect on local fisheries (Fig. 5c).

Positive effects of both types of fishery were mainly on *sea turtles* and *coastal pelagics*, while cetaceans positively impacted *coastal predators*, *sea turtles* and *flyingfishes*. Baleen whales in particular, appeared to have mostly positive, albeit small impacts on commercially important fish groups (Fig. 5d).

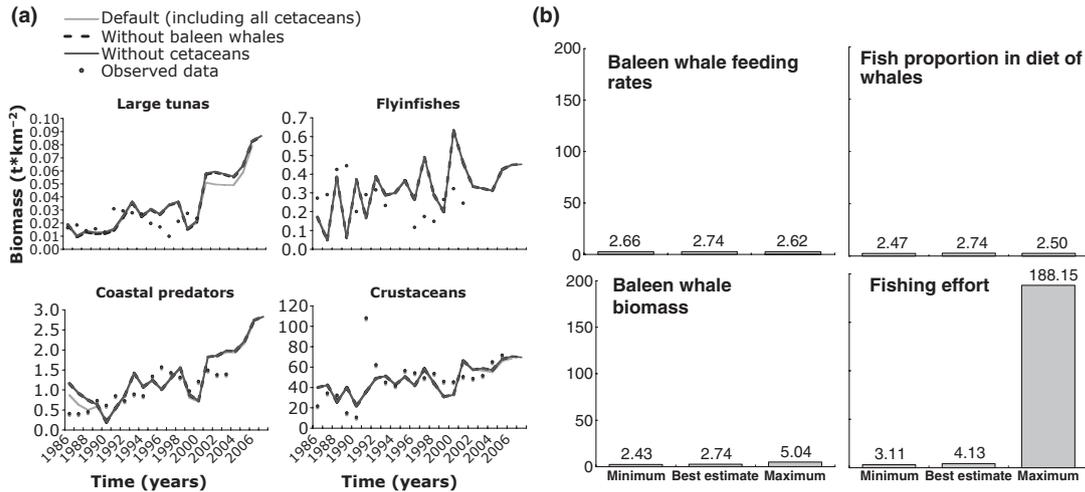
### Trophic levels

In the Caribbean ecosystem, fisheries represented the true top predator, as they targeted higher trophic level species than did any cetacean group

(Table 3). In particular, trophic levels averaged 20% higher than that of any mysticetes. Fin, sei and blue whales showed the lowest  $TL_Q$ . By contrast, sperm whales and beaked whales, which predominantly feed on *cephalopods*, had relatively similar  $TL_Q$  to that of fisheries ( $TL_C$ ).

### Simulated effects of whaling and fishing regulations

Running simulations with real time series of fishing mortality ( $F$ ) and our best model, we found that even a complete eradication of baleen whales did not lead to a measurable increase in biomass for most commercially important trophic groups in the Caribbean. This is shown by the fit for four major trophic groups in Fig. 6a. Similarly, removing all



**Figure 6** Simulations results of biomass trends over 22 years for the most commercially important species, under different whaling scenarios (eradication of baleen whales, eradications of all cetaceans or no whaling) compared with observed data trends (a), and effects of different assumptions on the overall results (b).

cetaceans from the ecosystem had only a negligible effect on fish biomass. To account for the high degree of uncertainty associated with many of our input parameters, we tested the robustness of these results to basic assumptions and default inputs. We found that if we removed whales from the ecosystem and adopted extreme assumptions about input parameters only negligible increases in the biomass of all commercially important fish resulted (Fig. 6a). By contrast, the simulated fishing moratorium under the same assumptions resulted in substantial increases in fish biomass (Fig. 6b).

## Discussion

### Understanding trophodynamics of the Caribbean ecosystem

Despite the paucity of data, our ecosystem model allowed us to develop an overview of basic trophic relations in the Caribbean ecosystem. The cetaceans groups considered in our study range from plankton-feeding primary consumers such as baleen whales, to those feeding on larger, higher trophic level fish species such as dolphins or sperm whales. The trophic role of cetaceans in the Caribbean Sea is thus very diverse and depends on the species considered, although the dearth of specific diet studies (Melgo *et al.* 2009) represented a great challenge. This lack of regional data forced us to extrapolate diet information from feeding areas outside the Caribbean, which raises a number of

cautions. Assuming a relatively high proportion of fish in the diet of some baleen whale species, such as minke whale in order to be as conservative as possible in the context of our research question, may have biased our representation of the ecosystem. Given *Ewe's* basic mass balance assumption, any predator demand has to be matched by a sufficiently high prey biomass, requiring us to increase fish biomass compared to densities reported in the original model. There is little evidence supporting our assumed proportion of fish in baleen whale diets in Caribbean waters, especially as the 2001–05 *LAPE* acoustic survey showed that the large dense aggregations of fish required by most feeding baleen whales are very rare in the Caribbean (Melvin *et al.* 2007). In addition, many prey species occurring in more polar feeding grounds are unlikely to occur in the subtropical waters of the Caribbean Sea. However, this can be expected to have little impact on our overall results, given that most whales are opportunistic feeders (Perrin *et al.* 2002), and that our diet matrix describes very general prey groups. In the light of unavailable quantitative regional diet data, our approach was to rely on the only diet information available despite the known biases and consequences during the balancing process.

### Trophic role of cetaceans in the Caribbean

Of all the great whales managed by IWC, minke whales are most often viewed as potential competi-

itors in fisheries (Vilkingsson and Kapel 2000). This is mainly not only because of their high abundance and the relative large proportion of fish known to make up their diet (Windsland *et al.* 2007), but also because of high spatial overlap of feeding areas with important fishing grounds (Kaschner 2004). In the Caribbean, we estimated resource overlap to be slight, due to low minke whale biomass in the system. Interestingly, the overlap between baleen whales and all fisheries was the highest value observed, a result that appears to be mostly driven by a high overlap between local fishing fleets and the seasonally very abundant humpback whales or the only tropical resident Bryde's whales.

The highest overlap was seen between fisheries and small cetaceans in our system. This seems realistic because this group has the greatest dietary overlap with fisheries and stays in the area year round. However, the biomass density of small cetaceans was potentially overestimated, because we had to increase its initial value [based on Kaschner's (2004) global model] by an order of magnitude to meet the predatory demands of killer whales and so balance the model. This increase was still within the range of possible values and implied the same density as used by Vidal and Basurto (2003) in their Mexican Caribbean model.

In summary, in comparison with other ecosystems, the overlap between combined cetaceans and fisheries in the Caribbean was minimal (0.01 compared to an average 0.043 for seven ecosystems; Morissette 2007).

#### **Who are the main predators in the Caribbean ecosystem?**

The mostly pelagic ecosystem surrounding the Caribbean islands is dominated by tunas, sharks, flyingfishes and other large predatory fishes. Not surprisingly, our results showed that, in terms of mortality, fish predation was greater by far than cetacean predation for commercially important species. As with all other parameters, data on fish biomass are highly uncertain. In addition to bias associated with limited availability of reliable surveys for fish in the Caribbean, the balancing process and our assumptions about whale diets and feeding rates may have contributed to the overall uncertainty by creating an artificial demand for fish by predators, thus resulting in an overestimation of these prey in the system. Nonetheless, fish predation exceeded cetacean predation by several orders of

magnitude (Fig. 3) and consequently, overall findings are unlikely to be affected by this uncertainty. The importance of fish predation is well documented by other studies (e.g. Trites *et al.* 1997) and indeed, fish are major predators of other fish in most ecosystems (Bax 1998). Interestingly, while there is a 'whales eat fish' issue, there is no equivalent counterpart for fish predation in which we would expect a highly charged political 'fish-eat-fish' debate in the Caribbean or elsewhere in the world for that matter. Ironically, the reason for the lack of such a debate might be that by fishing down the food web and greatly depleting high trophic level fish species in many marine ecosystems (Pauly *et al.* 1998; Springer *et al.* 2003), fisheries have essentially been working hard at reducing competition created by these non-cetacean predators.

Our results suggest that in the Caribbean, whales are not only eating less in terms of quantity, but they are also feeding at lower trophic levels than are exploited by fisheries. This has strong implications for the structure and function of the Caribbean ecosystem, because it seems clear that removing higher trophic levels has a stronger effect by taking much more production to maintain these trophic levels, than does targeting smaller species with lower trophic levels. This can lead to cascading effects for the entire food web (Terborg and Estes 2009).

In many cases in the Caribbean, there is a perception that competition between small odontocetes and fisheries is a predominant issue. However, while our MTI analysis showed that due to competition and the ongoing harvest of odontocetes, a high negative MTI of local fisheries on toothed whales resulted. We did not find any evidence suggesting that odontocetes have a similar impact on fisheries. The overall MTI of odontocetes was comparable with that of foreign fisheries, but this can mostly be attributed to the major negative impact of killer whales. Thus, rather than competing with fisheries, toothed whales seem to impact mainly themselves not only through predation by killer whales but also through competition between beaked whales and small cetaceans targeting the same food resources.

#### **Beneficial predation**

'Beneficial predation' is defined as a situation where a predator may have a direct negative impact on its prey, which is counterbalanced by indirect positive

effects through the consumption of other predators and competitors of the prey (Pauly *et al.* 2002). Results from our sensitivity analysis suggest that beneficial predation might be a relevant concept in the Caribbean ecosystem. In particular, our assumed increase in baleen whale feeding had a counter-intuitive effect by resulting in an increase of commercial fish biomass (Fig. 6). Given the overall uncertainty, the existence of beneficial predation is at best speculative. Nevertheless, this finding highlights the complexity of food web interactions and the importance of considering the potential unexpected consequences of reducing whale biomass in the ecosystem.

### Conclusions

Cetaceans play different roles in the Caribbean ecosystem. As predators, they not only compete with other trophic groups for food resources, but they also act as prey, and even as mutualists. In light of their high biomass, cetaceans generally represent an important component of the Caribbean ecosystem. Therefore, instead of viewing cetaceans as competitors, they should be viewed as indicators of ecosystem health and an integral part of the local marine biodiversity. Through whale-watching, they provide an alternative source of income for local fishermen. Understanding the trophodynamics of cetaceans in the Caribbean is therefore an essential first step in supporting the responsible management of fisheries in ways that will allow them to coexist sustainably in a healthy marine environment as well as enhancing the conservation of endangered cetacean species and marine biodiversity (CIESM 2004). The 'whales eat fish' issue competes unnecessarily for attention and funding with other research needs, which are important for marine biodiversity conservation and sustainable fisheries management in the Caribbean.

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