ECOLOGY

Should Whales Be Culled to Increase Fishery Yield?

We examine the scientific evidence for the assertion that commercial fisheries are negatively impacted by whales in tropical breeding areas.

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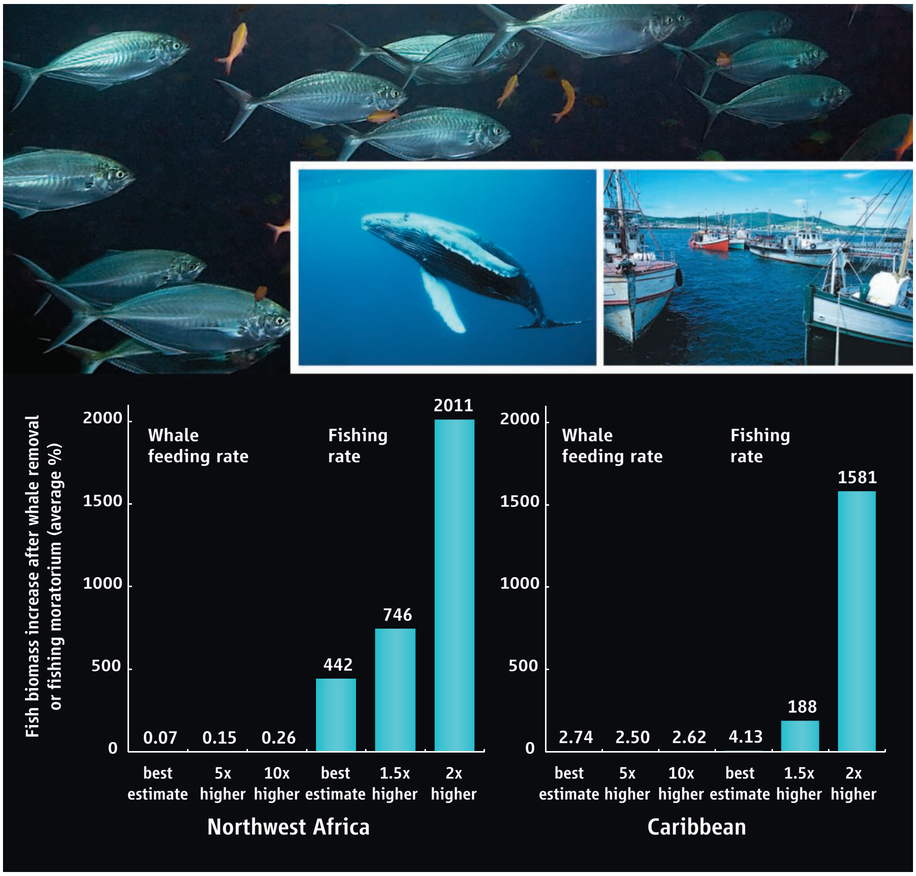
Science and international politics play complicated roles in the global arena of whale conservation and the management of the resources of the world's oceans. The International Whaling Commission (IWC), charged with the global conservation of whales and the management of whaling, introduced a moratorium on commercial whaling in 1986 because of the widespread depletion of whale species and stocks. Despite a lack of scientific data to indicate that many whale stocks have recovered, every year a heated debate takes place at the IWC meeting about the future of commercial whaling. Recently, whaling countries have introduced a new argument for resuming whaling by blaming whale populations for the decline in commercial fish stocks.

Couched in terms of "ecosystem management," whaling countries, including Japan, advocate the culling of whales as a solution to recover overexploited fish stocks and to increase fishery yield (*1*, *2*). Some developing countries, which may benefit economically and politically by supporting pro-whaling nations at IWC (*3*–*7*), have also supported the "whales-eat-fish" assertion. The Caribbean-driven St. Kitts Declaration at the 58th Annual Meeting of the IWC stated: "scientific research has shown that whales consume huge quantities of fish making the issue a matter of food security for coastal nations" (*6*). This issue was also claimed to be one of global concern at a 2008 symposium of IWC members in the Northwest Africa region (*8*).

When scientific information about the role of whales in marine ecosystems and for the economies of developing nations are considered, it becomes clear that delegates from developing countries who support the pro-whaling nations at the IWC may in fact be acting against the best interest of their countries. Whaling does not provide direct benefit to the fisheries that these countries closely depend on (*9*), but rather leads to the loss of species that are important for the structural integrity of their ecosystem (*10*–*12*). Living whales, on the other hand, may actually represent an alternative source of income through whale watching (*13*, *14*).



Negligible effects of removing whales on commercial fish biomass relative to the effect of a fishing moratorium. Estimated increases in fish biomass for best estimates of whale feeding and fishing rates, 5- and 10-fold underestimates of whale feeding, and 1.5 and 2-fold underestimates of fishing. For details, see (*9*).

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The rationale for whaling as the solution to depleted fisheries has been questioned by many in the scientific community in light of documented overfishing in oceans globally (*15*), a lack of spatially explicit overlap of resource exploitation between fisheries and whales (*2*), and the unpredictable consequences of culling (*16*, *17*). Based on stomach content analyses of whales caught during the Japanese scientific whaling program and available data on whale abundance, Japanese scientists estimate that whales consume several times as much food as the combined global fisheries catch in recent years (*18*). However, the methodology used by Japanese researchers to support their claim that whales' consumption of fish is an important component of fish declines has been repeatedly criticized (*19*–*22*). Although these discussions have been insightful, they have not stimulated movement within the IWC to break the current deadlock.

One of the obstacles in scientific studies of whales is that there are few data and models available to inform policy discussions. This is particularly true in the tropical waters bordering many of the developing countries that support the resumption of commercial

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whaling, although these areas are known to be primarily breeding (not feeding) grounds for baleen whales (*23–27*). We conducted an extensive literature search to compile and make use of all available sources of local data to provide a scientific starting point to the discussion (*9*). We also sought to actively involve scientific advisers of delegates who support Japan's position at the IWC meetings and to foster regional collaboration and active dissemination of our findings to inform discussions in local communities among scientists, managers, and other local experts (e.g., 2008 "Whales-Eat-Fish" regional workshops held in Senegal and Barbados, http://lenfestocean.org/whales_fisheries.html).

Using data available from the literature, and, e.g., the Sea Around Us Project (www.seaaroundus.org) and obtained during our regional stakeholder workshops, we developed ecosystem models to examine the potential increase in the biomass of commercially important fish stocks that would result from a reduction in whale abundance in the Northwest African and Caribbean ecosystems (*9*). Any discussion about the interactions between whales and fisheries must be considered in an ecosystem context, which allows investigation of the complex indirect effects of trophic relationships that would otherwise be very difficult to study. Although the IWC Scientific Committee maintains that "Ecosystem modelling cannot be used to predict interactions between marine mammals and fisheries" (*28–30*), other studies provide evidence to the contrary that mammals and fisheries can be studied with ecosystem models (*31–32*).

Our approach to addressing concerns about scientific uncertainty was to conduct extensive sensitivity analyses to explore the results emerging from a range of assumptions about ecosystem structure and the quality of our input data (table S2). For a wide range of assumptions about whale abundance, feeding rates, and fish biomass, even a complete eradication of baleen whales in these tropical areas does not lead to any appreciable increase in the biomass of commercially exploited fish. In contrast, just small changes in fishing rates lead to considerable increases in fish biomass (see figure, p. 880). We found little overlap between fisheries and whale consumption in terms of prey types, and we also found that fisheries remove far more fish biomass than whales consume (*9*). Moreover, because some whale prey species compete with commercially targeted fish for plankton and prey occupying a lower trophic level in the food web, it is possible that removing whales from marine ecosystems could result in fewer fish available to the fisheries (*9*).

Today, the majority of fish stocks (*33*) and many whale populations (*34*) are seriously depleted, but most available evidence points toward human overexploitation as the root of the problem. When developing tropical countries are encouraged to focus on the notion that "whales eat fish," they risk being diverted from addressing the real problems that their own fisheries face, primarily, overexploitation of their marine resources by distant-water fleets (*35*).

Here, we offer a set of recommendations for rational decision-making by effectively applying ecosystem management concepts to managing whales.

First, the question of "who is eating our fish" should be considered in a larger context (with respect to foreign fleets, ecosystem collapses, and climate change). Indirect social and economic benefits of whales in tropical ecosystems [e.g., tourism (*36*, *37*)] should also be taken into account.

Second, despite complicated politics, science should be an integral component of the discussions about managing whale and fishery interactions. An effort must be made to actively engage scientists and managers from countries that support Japan's claims (*3–5*) to help them investigate this issue within an ecosystem context in their own regions. In many cases, fisheries officers in tropical areas, such as the Caribbean, do not necessarily believe the whales-eat-fish arguments. Rather, the arguments are endorsed for reasons related to their aid relationship with Japan, especially in the fisheries sector.

Third, ecosystem modeling tools should be developed in order to bring the best available science to decision-making about the conservation of whales. Research aimed at filling the gaps on key scientific parameters (e.g., abundance, consumption rates, and diet information for key marine organisms) should be supported.

Finally, it is important to recognize that the goal of ecosystem-based management is to manage the whole system for long-term sustainability rather than modifying particular trophic levels in an attempt to maximize fishery yield (*38*). Broad-based, ecosystem management can and should increase an ecosystem's value so that it can provide benefits for future generations.

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Supporting Online Material

1. Materials and Methods

Ecosystem modelling approach

We used *Ecopath with Ecosim* (*EwE*) (*S1*) to build food web models of Northwest African and Caribbean waters. While there are a number of ecosystem modeling approaches available (*S2*), we chose *EwE* because of its representation of predator-prey interactions and the inclusion of different routines to take account of the estimated uncertainty associated with model inputs (*S3*). The *Ecopath* part of the model is based on mass balance principles (*S1*, *S4*). For any species or group of species of the system, this leads to the linear equation:

$$B_i \bullet P_i/B_i \bullet \mathrm{EE}_i - (\Sigma B_j \bullet Q_j/B_j \bullet \mathrm{DC}_{ij}) - \mathrm{Ex}_i = 0$$

where *i* indicates a component (stock, species, group of species) of the model, *j* indicates any of the predators of *i*, B_i indicates the biomass of *i*, P_i/B_i indicates the production/biomass ratio, which is equivalent to total mortality (*Z*) under most circumstances (*S5*), Q_i/B_i indicates the food consumption per unit biomass of *i*, DC_{ij} indicates the contribution of *i* to the diet of *j* (in terms of mass), EE_i indicates the ecotrophic efficiency of *i*, or the fraction of production that is consumed or caught within the system, and Ex_i indicates the export of *i* from the system (by emigration or fisheries catch).

Trophic groups

Species relevant to IWC discussions or with a distinctly different diet than other species were assigned to a unique trophic group (e.g., all great whales including minke, fin, humpback, sei, Bryde's, blue), and other species were included as aggregated groups (i.e. beaked whales, sperm whales, or small cetaceans). Sperm whales represented a special case, since they were allocated to a unique group for the Northwest African model, but were grouped together with the pygmy and dwarf sperm whales in the Caribbean ecosystem. The overall effect of this re-grouping is, however, likely to be very small since the combined biomass of pygmy and dwarf sperm whales is very small in comparison to that of the true sperm whales. To maintain the total number of trophic groups at a manageable size, we aggregated non-marine mammal trophic groups into distinct functional groups, following the criteria developed by Essington (*S6*). These groups were defined on the basis of similarities of food habits, habitats, and biological variables and include fish, cephalopods, crustaceans, benthic invertebrates, plankton, and detritus (Table S1).

Cetacean food consumption estimates

We used a basic food consumption model based on the approach of Trites *et al.* (*S7*). This model was used to generate the biomasses and consumption (*Q*/*B*) ratios needed for each *Ecopath* group. Annual food consumption was calculated as:

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

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

Cetaceans abundance and biomass estimates

Estimates of local abundance were based on the proportion of the global estimated abundance of each species that fell within the study area weighted by the relative suitability of the habitat in each of the study areas for each species (*S8*). Species-specific global abundance estimates were compiled from the literature (*S8*). Suitability of habitat for each species was predicted using a relative environmental suitability (RES) model (*S9*). Sex ratios as well as mean species and sex-specific body mass were obtained from Trites and Pauly (*S10*).

Feeding rate models

The annual food consumption calculated above also depends on the feeding rate of each species based on weight-specific daily rations (*S11*). This parameter is not only fundamental to describing animal energetics, but is also important for studies of energy flow through the food web in the ecosystem (*S12*). For all cetaceans (except baleen whales), we used the empirical model developed by Innes *et al*. (*S13*) to estimate food consumption. This model was later modified by Trites *et al*. (*S7*) to account for the difference between consumption for growth and for maintenance and then applied to all cetacean species. Food intake of specific species per day was calculated as follows:

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

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

For all baleen whales, daily food intake was estimated based on a model by Armstrong and Siegfried (*S14*) for food consumption of minke whales in the Antarctic. These authors suggested a modification to the empirical model of Innes *et al*. (*S15*) equation for baleen whales to account for larger body sizes and seasonal variation in food intake. This approach was later used to estimate food consumption of whales around Iceland (*S16*) and represents one of the methods used by Tamura (*S17*) to estimate global food intake of cetaceans. This feeding rate is calculated as:

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

Annual food consumption for each cetacean species was then divided by the biomass estimates in order to estimate consumption to biomass (*Q*/*B*) ratios, i.e. food intake expressed as percent of body mass used in the *Ecopath* model.

It is important to note that Northwest African and Caribbean waters represent a tropical breeding environment for most baleen whales (*S18–S24*). In general, most baleen whales only spend about a third of the year in their breeding grounds, where they are known to either fast or eat at a considerably reduced rate (*S18–S20*, *S22*, *S23*, *S25–S30*). To account for this reduced feeding rate, as a default we therefore set food intake in breeding areas to amount to 10% of the food intake in feeding grounds (*S20*, *S26*, *S27*), but also examined a range of assumptions for this value (Fig. 1). Although other cetacean species, such as sperm whales are also migratory; these toothed whales are not known to alter their feeding behavior in tropical waters (*S31*). Similarly, although some of the other toothed whale species might undertake small migrations or seasonal inshore-offshore movements, these are not known to be associated with changes in feeding patterns.

Diet composition

All available information on cetacean diets in our study areas was used as input for our models. However, as we found very few quantitative descriptions of diet for cetaceans in general, and especially in tropical areas such as Northwest African and Caribbean waters where these whales are generally breeding (vs. feeding), we also used diet information/studies for the same species of cetaceans in the North Atlantic. Because we assumed these diet data from feeding areas were relevant in breeding areas, we also examined this issue in the detailed uncertainty analyses conducted throughout this study (Table S2).

Dynamic simulations modeling removal of whales from the ecosystem

Ecosim provides temporal simulations using the initial parameters of the *Ecopath* master equations. This tool uses differential equations to estimate biomass fluxes as follows:

$$dB_i / dt = g_i \sum_j Qij - \sum_j Qij + I_i - (M_i + F_i + e_i) B_i$$

where dB_i/dt is the biomass growth rate of group i during the interval dt, g_i is the net growth efficiency (production/consumption ratio), I_i is the immigration rate, M_i and F_i are natural and fishing mortality rates of group i, and e_i is emigration rate (*S1*, *S4*, *S32*).

Fisheries catch data were obtained from the *Sea Around Us Project* (*SAUP*) database (*S33*) for Northwest Africa (which database have been updated in 2001 for specific NW African time series after a workshop of regional experts called *Système d'Information et d'Analyses des Pêches – SIAP*) (*S34*), and from *SAUP* and a new database from the *Lesser Antilles Pelagic Ecosystem* (*LAPE)* (*S35*) project in the Caribbean.

To account for differences in catchability of different trophic groups, we adjusted vulnerability settings based on available information about the specific ecology of each species and by fitting to time series of biomass for each species or trophic group for which data was available.

An extreme exploitation pattern was applied to our baleen whales species (minke, fin, humpback, Bryde's, sei, and blue whales) which generated a dramatic increase in their mortality to effectively simulate the removal of whales from the ecosystem. We then compared biomass trends of other trophic groups during simulations before and after the removal of whales.

Sensitivity analyses

We used different scenarios to explore the impacts of changing assumptions about feeding rates, biomass, and diet of the cetacean groups in our model on model results (Table S2). We compared alternative scenarios based on the fit of the sum of squares to the observed data. We also examined the extent to which these alternate scenarios may influence the outcomes of our analysis (i.e. if they create an increase or decrease in biomass of commercially important fish when whales are eradicated).

Fig. 1 represents an example of one scenario of our sensitivity analysis, for the feeding rate of baleen whales in tropical areas. We simulated the "eradication of baleen whales" using three hypothetical feeding rates by whales in breeding areas. These included our best estimate (the assumed 10% feeding rate in breeding areas), and 5-fold and 10-fold increases of this value. The latter value effectively corresponds to a 100% feeding rate (i.e., the extreme assumption that whales would continuously feed as much during their sojourn in breeding areas as they do in their regular feeding areas). For all scenarios, the removal of whales as predators led to negligible increases in the biomass of commercially valuable fish stocks. To illustrate just how negligible the effect of whale culling was on the recovery of fish stocks, we simulated a similar reduction in pressure on commercially exploited fish stocks by imposing a fishing moratorium (i.e., no fishing being the equivalent of no whales). We simulated the complete removal of fisheries from the system under three assumed levels of fishing pressure: our best estimate of fishing effort, based on available real time series, and 1.5 times and 2 times the default value for effort. This allowed the comparison of the effect of culling whales to a complete fishing moratorium (where the fishing effort of all fleets on all groups was set to zero) for a range of values for both whale consumption rates and fishing effort. The reason that the range of assumed predatory pressure are not identical is that any increase beyond twice our default rate of fishing caused the system to collapse and some trophic groups go extinct before the end of the 20-year simulation, such that our metric "change in biomass" was no longer meaningful.

The increase in biomass was calculated as the average percent change in the biomass of commercially exploited fish groups, for the different scenarios compared to the initial simulation (i.e., running the model without any whaling using our default feeding rate and with normal fishing effort). Even for smaller changes in basic assumptions (e.g., 2-fold increase in fishing pressure versus 10-fold increase in whale consumption in breeding areas), the magnitude of increase is much greater under an assumed fishing moratorium than for an assumed removal of all baleen whales from the ecosystem.

The unexpected effect of a decrease in the whale removal impact after increasing from 5x to 10x feeding rates seen in the Caribbean ecosystem may be explained based on a threshold effect, where indirect effects and trophic interactions are more important for whales in that area. In particular, even for a high feeding rate, the kind of fish whales eat represent competing species or prey for other predators. In such case, an eradication of great whales becomes less beneficial for fish. This effect may vary for other ecosystems (i.e., Northwest Africa) that differ in complexity, structure, and species composition (esp. for commercially important fish).

2. Supporting Tables

Table S1. List of trophic groups and species included in the *Ecopath* model for (a) Northwest Africa, and (b) the Caribbean. Species **in bold** represent to key species for each trophic group.

Table S1(a)

***Ecopath* group**	**Species**
1. Minke whales	*Balaenoptera acutorostrata*
2. Fin whales	*Balaenoptera physalus*
3. Humpback whales	*Megaptera novaeangliae*
4. Bryde's whales	*Balaenoptera brydei*
5. Sei whales	*Balaenoptera borealis*
6. Blue whales	*Balaenoptera musculus*
7. Sperm whales	*Physeter macrocephalus*
8. Killer whales	*Orcinus orca*
9. Beaked whales	*Mesoplodon densirostris*, *M. europaeus*, *Ziphius caviostris*
10. Small cetaceans	*Delphinus delphis*, *Feresa attenuata*, *Globicephala macrorhynchus*, *Grampus griseus*, *Kogia breviceps*, *Kogia simus*, *Lagenodelphis hosei*, *Peponocephala electra*, *Pseudorca crassidens*, *Sousa teuszii*, *Stenella attenuata*, *Stenella clymene*, *Stenella coeruleoalba*, *Stenella frontalis*, *Stenella longisrostris*, *Steno bredanensis*, *Tursiops truncatus*
11. Seabirds	*Actitis hypoleucos*, *Calidris ferruginea*, *Calonectris diomedea*, *Ceryle rudis*, *Chlidonias niger*, *Halcyon malimbica*, *Limosa lapponica*, *Numenius phaeopus*, *Oceanites oceanicus*, *Pagrodama nivea*, *Pelecanus rufescens*, *Phalacrocorax africanus*, *Phoenicopterus rubber*, *Pluvialis squatarola*, *Sterna caspia*, *Sterna hirundo*
12. Large pelagics	*Acanthocybium solandri*, *Brama brama*, Centrolophidae, *Coryphaena hippurus*, *Cubiceps gracilis*, Istiophoridae, *Istiophorus albicans*, *Istiophorus platypterus*, ***Katsuwonus pelamis***, *Makaira nigricans*, *Ranzania laevis*, *Ruvettus pretiosus*, *Schedophilus medusophagus*, *Tetrapturus albidus*, *Tetrapturus pfluegeri*, *Thunnus alalunga*, ***Thunnus albacares***, ***Thunnus obesus***, *Thunnus thynnus*, *Xiphias gladius*
13. Mesopelagics predators	***Aphanopus carbo***, *Astronesthes niger*, *Atherina presbyter*, *Benthosema glaciale*, *Borostomias elucens*, *Chauliodus danae*, *Diplospinus multistriatus*, *Evermannella balbo*, *Lampris guttatus*, *Lepidocybium flavobrunneum*, *Leptostomias gladiator*, *Maurolicus muelleri*, *Micromesistius poutassou*, ***Micromesistius poutassou***, *Mora moro*, Moridae, *Myctophum asperum*, *Myctophum nitidulum*, *Myctophum punctatum*, *Nealotus tripes*, *Photonectes margarita*, *Polyacanthonotus challengeri*, *Rhadinesthes decimus*, *Sternoptyx diaphana*, *Stomias boa boa*, Stomiidae, Trachichthyidae, *Trachyrincus scabrus*, *Vinciguerria nimbaria*, *Xenodermichthys copei*
14. Bathydemersal predators	*Beryx* sp., *Beryx decadactylus*, *Caelorinchus caelorhincus*

	caelorhincus, Caproidae, *Chimaera monstrosa*, *Coryphaenoides rupestris*, *Coryphaenoides zaniophorus*, Gadiformes, Gempylidae, *Helicolenus dactylopterus dactylopterus*, Lophiidae, ***Lophius budegassa***, *Lophius piscatorius*, *Lophius vaillanti*, Lotidae, Merlucciidae, ***Merluccius merluccius***, *Merluccius polli*, ***Merluccius senegalensis***, *Muraena helena*, *Nezumia aequalis*, *Nezumia sclerorhynchus*, Phycidae, *Phycis blennoides*, *Phycis phycis*, *Polyprion americanus*, *Pristis pectinata*, *Spectrunculus grandis*, *Synaphobranchus kaupii*
15. Sharks	*Alopias* sp., *Alopias superciliosus*, *Alopias vulpinus*, Alopiidae, *Carcharhinidae*, *Carcharhinus falciformis*, ***Carcharhinus limbatus***, *Carcharhinus longimanus*, *Carcharhinus obscurus*, *Carcharhinus plumbeus*, Centrolophidae, *Centrophorus granulosus*, *Centroscyllium fabricii*, *Centrophorus squamosus*, *Centrophorus uyato*, *Centroscymnus coelolepis*, *Centroscymnus cryptacanthus*, *Centroscymnus crepidater*, *Cetorhinus maximus*, *Dalatias licha*, *Deania calcea*, Elasmobranchii, Etmopteridae, *Etmopterus princes*, *Etmopterus pusillus*, *Galeorhinus galeus*, *Galeus melastomus*, *Galeus polli*, *Ginglymostoma cirratum*, *Hexanchus griseus*, *Isurus* sp., *Isurus oxyrinchus*, *Lamna nasus*, Lamnidae, *Mustelus asterias*, *Mustelus mustelus*, *Prionace glauca*, Pristidae, *Rhizoprionodon acutus*, Scyliorhinidae, *Scyliorhinus canicula*, *Scyliorhinus stellaris*, *Sphyrna lewini*, *Sphyrna zygaena*, Sphyrnidae, Squalidae, *Squalus acanthias*, *Squalus blainville*, *Squalus megalops*, *Squatina squatina*, Squatinidae, Triakidae
16. Rays	Dasyatidae, *Dasyatis margarita*, *Dasyatis pastinaca*, *Dipturus batis*, *Dipturus oxyrinchus*, *Gymnura altavela*, *Leucoraja naevus,* Myliobatidae, *Myliobatis aquila*, ***Raja clavata***, *Raja miraletus*, *Raja montagui*, *Raja straeleni,* Rajidae, Rajiformes, Rhinobatidae, *Rhinobatos cemiculus*, ***Rhinobatos rhinobatos***, *Rhinoptera bonasus*, *Rhinoptera marginata,* Torpedinidae, Torpedo sp.
17. Costal tunas	*Auxis rochei*, *Auxis thazard*, ***Euthynnus alletteratus***, *Orcynopsis unicolor*, ***Sarda sarda*,*Scomberomorus tritor***
18. Coastal demersals	Acanthuridae, *Albula vulpes*, Ammodytidae, *Anthias anthias*, *Aphia minuta*, *Apogon imberbis*, Apogonidae, *Argentina sphyraena*, *Argyrosomus regius*, *Ariomma bondi*, **Ariidae**, *Ariomma melanum*, *Arius heudelotii*, *Arnoglossus laterna*, *Aulopus cadenati*, Balistidae, *Boops boops*, *Bothidae*, *Bothus podas*, *Brachydeuterus auritus*, *Brotula barbata*, *Campogramma glaycos*, *Capros aper*, *Cepola macrophthalma*, *Chaetodon hoefleri*, *Charis charis*, *Chelidonichthys obscurus*, *Chlorophthalmus agassizi*, *Conger conger*, Congridae, *Ctenolabrus rupestris*, Cynoglossidae, *Cynoglossus senegalensis*, *Dentex angolensis*, *Dentex canariensis*, *Dentex dentex*, *Dentex gibbosus*, *Dentex macrophthalmus*, *Dentex maroccanus*, *Dicentrarchus* sp.,*Dicentrarchus labrax*, *Dicologlossa cuneata*, *Diplodus bellottii*, *Diplodus cervinus cervinus*, *Diplodus sargus*

	cadenati, Diplodus vulgaris, *Drepane africana*, Echeneidae, Emmelichthyidae, *Epinephelus marginatus*, Epinephelus aeneus, *Epinephelus goreensis*, *Eucinostomus melanopterus*, *Fistularia tabacaria*, *Gaidropsarus* sp., Galeoides sp., *Galeoides decadactylus*, *Gerres nigri*, *Gobius niger*, *Gobius paganellus*, Haemulidae, *Halobatrachus didactylus*, Labridae, *Lepidorhombus* sp., *Lepidotrigla cadmani*, *Lepidotrigla dieuzeidei*, *Lethrinus atlanticus*, *Lithognathus mormyrus*, *Liza aurata*, *Liza dumerili*, *Liza falcipinnis*, *Liza grandisquamis*, *Liza ramado*, *Lutjanus* sp., *Lutjanus goreensis*, *Macroramphosus scolopax*, *Molva* sp., *Microchirus* sp., *Microchirus boscanion*, *Microchirus variegates*, *Monochirus hispidus*, Mugilidae, *Mugil capurrii*, *Mugil cephalus*, Mullidae, *Mullus barbatus*, *Mullus* sp., *Mullus surmuletus*, Muraenidae, *Mycteroperca rubra*, *Oblada melanura*, *Plectorhinchus macrolepis*, *Pagrus* sp., *Pagrus pagrus*, *Pagrus caeruleostictus*, *Pagellus* sp., *Pagellus bellottii bellottii*, *Pagellus acarne*, *Pagellus bogaraveo*, *Pagellus erythrinus*, *Pegusa lascaris*, *Pentanemus quinquarius*, *Platichthys flesus*, *Plectorhinchus macrolepis*, *Plectorhinchus mediterraneus*, Pleuronectidae, Pleuronectiformes, *Pleuronectes platessus*, Polynemidae, Pomacentridae, *Polydactylus quadrifilis*, *Pontinus kuhlii*, *Pomadasys jubelini*, *Pomadasys incisus*, *Pomadasys perotaei*, *Pomadasys rogerii*, *Pseudotolithus typus*, *Pseudotolithus senegalensis*, *Pseudotolithus elongatus*, *Pseudotolithus senegallus*, *Pseudupeneus prayensis*, *Pteroscion peli*, *Pseudupeneus prayensis*, *Rachycentron canadum*, Sarpa salpa, Saurida brasiliensis, Scaridae, **Sciaenidae**, Sciaena umbra, *Schedophilus pemarco*, Scophthalmidae, *Scophthalmus rhombus*, Serranidae, *Selene dorsalis*, Scorpaenidae, *Scorpaena maderensis, Scorpaena notata*, *Syacium guineensis*, Soleidae, *Solea senegalensis, Solea solea*, **Sparidae**, *Sparus auratus*, Sparus caeruleostictus, *Spondyliosoma cantharus*, *Stephanolepis hispidus*, *Stromateus fiatola*, *Symphodus mediterraneus*, *Symphodus melops*, *Synagrops microlepis*, *Synaptura lusitanica lusitanica*, *Trachinus draco*, *Trachinocephalus myops*, Triglidae, Tetraodontidae, *Trisopterus minutus*, *Trisopterus luscus*, *Umbrina cirrosa*, *Umbrina canariensis*, *Zeus faber*, *Zenopsis conchifer*
19. Clupeids	*Alosa alosa*, Clupeidae, Clupeiformes, *Engraulis encrasicolus*, ***Ethmalosa fimbriata***, *Ilisha Africana*, *Sardina pilchardus, Sardinella* sp., ***Sardinella aurita***, ***Sardinella maderensis***, *Sprattus sprattus*
20. Other coastal pelagics	*Alectis alexandrinus*, *Aphanopus intermedius*, Belonidae, Carangidae, *Caranx* sp., *Caranx hippos*, ***Caranx rhonchus***, *Caranx senegallus*, *Cheilopogon heterurus*, *Chloroscombrus chrysurus*, *Decapterus* sp., *Decapterus punctatus*, *Dicentrarchus punctatus*, *Elops lacerta*, Exocoetidae, *Exocoetus obtusirostris,* Hemiramphidae, *Hemiramphus* sp., *Lepidopus caudatus*, *Lichia amia*, Pomatomus saltatrix, Promethichthys pometheus, *Regalecus glesne*, *Scomber* sp., ***Scomber japonicus***, Scomber scombrus, *Scomberesox saurus saurus*,

	Scomberomorus sp., Scombridae, *Seriola* sp., *Sphyraena* sp., *Sphyraena barracuda*, *Spicara* sp., *Trachinotus* sp., *Trachinotus ovatus*, *Trachurus* sp., *Trachurus mediterraneus*, *Trachurus picturatus*, *Trachurus trachurus*, ***Trachurus trecae***, Trichiuridae, *Trichiurus lepturus*, *Tylosurus acus acus*
21. Cephalopods	*Alloteuthis subulata*, Cephalopoda, *Illex coindetii*, Loliginidae, *Loligo* sp., ***Loligo vulgaris***, Octopodidae, ***Octopus vulgaris***, Ommastrephidae, *Sepia bertheloti*, *Sepia elobyana*, *Sepia officinalis*, *Sepia orbignyana*, Sepiidae, Teuthida, *Todarodes sagittatus*
22. Crustaceans	Aristeidae, *Aristeus antennatus*, *Aristeus varidens*, **Brachyura**, *Calappa rubroguttata*, *Cancer pagurus*, *Carcinus maenas*, *Crangon* sp., *Crangon crangon*, Crangonidae, Geryon sp., *Geryon maritae*, *Homarus gammarus*, Leucosiidae, *Maja squinado*, Metapenaeus, Munidae, Natantian decapods, *Necora puber*, *Nephrops norvegicus*, Paguridae, Palaemonidae, *Palinurus* sp., *Palinurus elephas*, *Palinurus mauritanicus*, *Panulirus regius*, *Panulirus* sp., *Parapenaeopsis* sp., *Parapenaeopsis atlantica*, ***Parapanaeus longirostris***, Penaeidae, ***Penaeus* sp.**, ***Penaeus kerathurus***, ***Penaeus notialis***, *Pleoticus robustus*, *Plesionika heterocarpus*, *Plesiopenaeus edwardsianus*, Portunidae, Scyllaridae,
23. Benthos	Anthozoa, *Arca* sp., Arcidae, Bivalvia, Cardiidae, *Cardium edule*, *Chama crenulata*, Conidae, *Crassostrea* sp., *Crepidula porcellana*, *Cymbium* sp, Donacidae, *Donax* sp., Epizoanthidae, Gastropoda, Glycymerididae, Haliotidae, *Haliotis tuberculata*, *Modiolus* sp., *Murex* sp., Muricidae, Mytilidae, Naticidae, *Ostrea edulis*, *Patella* sp., *Pecten maximus*, Pectinidae, Porifera, *Pyura dura*, *Ruditapes decussates*, *Solen* sp., Solenidae, *Tapes* sp., *Thais haemastoma*, Veneridae, *Venus rosalina*, *Venus verrucosa*, Volutidae
24. Benthic producers	Algae, benthic bacteria
25. Zooplankton	Chaetognatha, Copepoda, Euphausiacea, Hydrozoa, Hyperiidae, Mysidacea, Scyphozoa, ichtyoplankton, macroplankton, meroplankton, planktonic decabods, larvae, and eggs
26. Phytoplankton	
27. Detritus	

Table S1(b)

Ecopath group	**Species**
1. Minke whales	*Balaenoptera acutorostrata*
2. Fin whales	*Balaenoptera physalus*
3. Humpback whales	*Megaptera novaeangliae*
4. Bryde's whales	*Balaenoptera brydei*
5. Sei whales	*Balaenoptera borealis*
6. Blue whales	*Balaenoptera musculus*
7. Sperm whales	*Physeter macrocephalus*, *Kogia breviceps*, *Kogia simus*
8. Killer whales	*Feresa attenuata*, *Orcinus orca*, *Pseudorca crassidens*
9. Beaked whales	*Mesoplodon densirostris*, *Mesoplodon europaeus*, *Ziphius caviostris*
10. Small cetaceans	*Delphinus capensis*, *Delphinus delphis*, *Globicephala macrorhynchus*, *Grampus griseus*, *Lagenodelphis hosei*, *Sousa teuszii*, *Stenella attenuata*, *Stenella clymene*, *Stenella coeruleoalba*, *Stenella frontalis*, *Stenella longisrostris*, *Steno bredanensis*, *Tursiops truncatus*
11. Seabirds	*Actitis hypoleucos*, *Ajaia ajaja*, *Calidris ferruginea*, *Calonectris diomedea*, *Ceryle rudis*, *Chlidonias niger*, *Halcyon malimbica*, *Limosa lapponica*, *Numenius phaeopus*, *Oceanites oceanicus*, *Pagrodama nivea*, *Pelecanus rufescens*, *Phalacrocorax africanus*, *Phoenicopterus rubber*, *Pluvialis squatarola*, *Sterna caspia*, *Sterna hirundo*
12. Seaturtles	*Caretta caretta*, *Chelonia mydas*, *Eretmochelys imbricata*, ***Dermochelys coriacea***
13. Large tunas and billfishes	**Istiophoridae**, *Istiophorus albicans*, ***Makaira nigricans***, *Parexocoetus brachypterus*, ***Tetrapturus albidus***, *Tetrapturus pfluegeri*, ***Thunnus alalunga***, ***Thunnus albacares***, *Thunnus obesus*, *Thunnus thynnus*, ***Xiphias gladius***
14. Small tunas	***Auxis* sp., *Euthynnus alletteratus, Katsuwonus pelamis, Sarda sarda, Thunnus atlanticus***
15. Dolphinfish	***Coryphaena hippurus,* Coryphaenidae**
16. Flyingfish	***Hirundichthys affinis, Cheilopogon cyanopterus,*** *Cypselurus cyanopterus*, ***Parexocoetus brachypterus,*** Exocoetidae
17. Other offshore predators	**Alepocephalidae**, *Argyropelecus olfersi*, *Bathylagus nigribenys*, *Cyclothone* sp., **Gonostomatidae**, *Gonosthoma bathyphilum*, *Lampris guttatus*, *Lampanyctus macdonaldi*, *Lobotes surinamensis*, *Melanocetus* sp., **Moridae**, **Myctophidae**, *Pomatomus saltator*, *Ruvettus pretiosus*, *Scopelogadus beanie*, *Sternoptyx diaphana*
18. Pelagic sharks	Carcharhinidae, *Carcharhinus acronotus*, ***Carcharhinus brevipinna***, *Carcharhinus falciformis*, *Carcharhinus leucas*, *Carcharhinus limbatus*, ***Carcharhinus longimanus***, *Carcharhinus perezi*, Elasmobranchii, ***Galeocerdo cuvier***, Lamnidae, ***Lamna nasus***, ***Prionace glauca***, *Isurus oxyrinchus*, ***Isurus paucus***, *Sphyrna lewini*, Urolophidae
19. Coastal sharks and rays	*Aetobatus narinari*, Dasyatidae, ***Dasyatis americana***, ***Ginglymostoma cirratum***, *Mustelus* sp. , Myliobatidae, *Negaprion brevirostris*, *Raja* sp., Rajiformes, rays, *Rhizoprionodon terraenovae*, small/juvenile sharks, Squalidae
20. Scombrids	***Acanthocybium solandri***, ***Scomberomorus brasiliensis***,

	Scomberomorus cavalla, *Scomberomorus maculatus*, *Scomberomorus regalis*, *Scomberomorus sp.*, Scombridae
21. Small and schooling pelagics	*Ablennes hians*, *Alectis ciliaris*, *Anchoa hepsetus*, *Anchoa lucida*, *Anchoa lyolepis*, Belonidae, *Carangoides ruber*, *Caranx crysos*, *Caranx latus*, *Caranx lugubris*, *Cetengraulis edentulous*, *Cetengraulis edentulous*, Clupeidae, Clupeiformes, ***Chloroscombrus chrysurus, Decapterus macarellus, Decapterus punctatus, Decapterus* sp.**, ***Dorosoma petenense***, *Elagatis bipinnulata*, *Elops saurus*, Engraulidae, *Etrumeus teres*, ***Harengula clupeola, Harengula humeralis, Harengula* sp.**, *Hyperoglyphe bythites*, *Hypoatherina harringtonensis*, *Jenkinsia lamprotaenia*, *Lepidocybium flavobrunneum*, *Neoopisthopterus tropicus*, *Oligoplites saurus*, *Opisthonema oglinum*, *Peprilus alepidotus*, *Peprilus sp.*, *Platybelone argalus*, ***Sardinella aurita, Sardinella brasiliensis***, ***Selar crumenophthalmus***, *Selene brevoortii*, *Selene orstedii*, *Selene peruviana*, *Selene setapinnis*, *Sphyraena barracuda*, *Sphyraena* sp., Stromateidae, *Strongylura timucu*, Trichiuridae, *Trichiurus lepturus*, *Tylosurus acus*, *Tylosurus crocodilus*
22. Reef fishes	*Abudefduf saxatilis*, *Abudefduf taurus*, *Acanthostracion polygonius*, *Acanthostracion quadricornis*, *Acanthuridae*, *Acanthurus bahianus*, *Acanthurus chirurgus*, *Acanthurus coeruleus*, *Albula vulpes*, *Alphestes afer*, *Aluterus schoepfii*, *Aluterus scripta*, *Anisotremus surinamensis*, *Anisotremus virginicus*, *Antennarius striatus*, *Apogon maculates*, *Aulostomus maculatus*, *Balistes capriscus*, *Balistes vetula*, Balistidae, *Bodianus rufus*, *Bothus lunatus*, *Bothus ocellatus*, *Brotula barbata*, *Calamus bajonado*, *Calamus calamus*, *Calamus pennatula*, *Cantherhines macrocerus*, *Cantherhines pullus*, *Canthidermis sufflamen*, *Canthigaster rostrata*, *Centropomus undecimalis*, *Centropyge argi*, *Cephalopholis cruentata*, *Cephalopholis fulva*, *Chaetodipterus faber*, *Chaetodon aculeatus*, *Chaetodon capistratus*, *Chaetodon ocellatus*, *Chaetodon sedentarius*, *Chaetodon striatus*, *Chilomycterus antennatus*, *Chilomycterus antillarum*, *Chromis cyanea*, *Chromis multilineata*, *Clepticus parrae*, *Coryphopterus glaucofraenum*, *Dactylopterus volitans*, *Diodon holocanthus*, *Diodon hystrix*, *Diplectrum formosum*, *Diplodus argenteus caudimacula*, *Echidna catenata*, *Enchelycore nigricans*, *Entomacrodus nigricans*, *Ephippidae*, *Epinephelus adscensionis*, *Epinephelus itajara*, *Epinephelus morio*, *Epinephelus nigritus*, *Epinephelus niveatus*, *Epinephelus striatus*, *Equetus lanceolatus*, *Equetus punctatus*, *Eucinostomus argenteus*, *Eugerres plumieri*, *Fistularia tabacaria*, Gerreidae, *Gerres cinereus*, *Gnatholepis thompsoni*, *Gobiosoma evelynae*, *Gobiosoma horsti*, *Gramma loreto*, *Gramma melacara*, *Gymnothorax funebris*, *Gymnothorax miliaris*, *Gymnothorax vicinus*, **Haemulidae**, *Haemulon album*, *Haemulon aurolineatum*, *Haemulon carbonarium*, *Haemulon chrysargyreum*, *Haemulon flavolineatum*, *Haemulon macrostomum*, *Haemulon melanurum*, *Haemulon parra*, *Haemulon plumieri*,

	Haemulon sciurus, *Halichoeres bivittatus*, *Halichoeres garnoti*, *Halichoeres maculipinna*, *Halichoeres poeyi*, *Halichoeres radiatus*, *Hemiramphus brasiliensis*, *Holacanthus ciliaris*, *Holacanthus tricolor*, *Hypoplectrus aberrans*, *Hypoplectrus chlorurus*, *Hypoplectrus nigricans*, *Hyporhamphus unifasciatus*, *Joturus pichardi*, ***Kyphosus incisor, Kyphosus sectatrix***, Labridae, *Labrisomus guppyi*, *Labrisomus nuchipinnis*, *Lachnolaimus maximus*, *Lactophrys bicaudalis*, *Lactophrys triqueter*, *Lopholatilus chamaeleonticeps*, *Malacanthidae*, *Malacanthus plumieri*, *Melichthys niger*, *Menticirrhus littoralis*, *Micropogonias furnieri*, *Micropogonias undulates*, *Microspathodon chrysurus*, Monacanthidae, *Monacanthus ciliatus*, *Monacanthus tuckeri*, Mullidae, *Mycteroperca bonaci*, *Mycteroperca rubra*, *Mycteroperca tigris*, *Mycteroperca venenosa*, *Myrichthys breviceps*, *Myrichthys ocellatus*, *Myripristis jacobus*, *Neoniphon marianus*, *Odontoscion dentex*, *Ogcocephalus nasutus*, Ophidiidae, *Ophioblennius atlanticus*, *Opistognathus aurifrons*, *Opistognathus macrognathus*, *Opistognathus maxillosus*, *Opistognathus whitehursti*, Ostraciidae, *Parablennius marmoreus*, Paralichthyidae, *Paralichthys* sp., *Paranthias furcifer*, *Pareques acuminatus*, *Phaeoptyx conklini*, *Plectrypops retrospinis*, *Pogonias cromis*, Polynemidae, Pomacanthidae, *Pomacanthus arcuatus*, *Pomacanthus paru*, Pomacentridae, *Priacanthus arenatus*, *Pseudupeneus maculates*, *Rypticus saponaceus*, *Scaridae*, *Scartella cristata*, *Scarus coelestinus*, *Scarus coeruleus*, *Scarus guacamaia*, *Scarus iserti*, *Scarus taeniopterus*, *Scarus vetula*, *Scorpaenodes caribbaeus*, *Serranidae*, *Serranus tabacarius*, *Serranus tortugarum*, *Sparisoma aurofrenatum*, *Sparisoma chrysopterum*, *Sparisoma radians*, *Sparisoma rubripinne*, *Sparisoma viride*, *Sphoeroides spengler*, *Stegastes fuscus*, *Stegastes leucostictus*, *Stegastes planifrons*, *Stegastes variabilis*, *Stephanolepis setifer*, *Symphurus chabanaudi*, Tetraodontidae, *Thalassoma bifasciatum*, *Xanthichthys ringens*, *Xyrichtys novacula*, *Xyrichtys splendens*
23. Coastal predators	*Achirus klunzingeri*, ***Alectis ciliaris***, *Archosargus probatocephalus*, **Belonidae**, ***Caranx hippos***, ***Caranx* sp**., *Cynoponticus coniceps*, *Cynoscion* sp., *Heteropriacanthus cruentatus*, Holocentridae, *Holocentrus coruscus*, ***Elegatis bipinnulata***, **Lutjanidae**, ***Lutjanus analis, Lutjanus apodus, Lutjanus cyanopterus, Lutjanus griseus, Lutjanus jocu, Lutjanus mahogoni, Lutjanus purpureus, Lutjanus synagris***, *Megalops atlanticus*, *Mugil cephalus*, *Mugil curema*, *Mugil liza*, Mugilidae, *Mulloidichthys martinicus*, *Myrichthys breviceps*, *Myrichthys ocellatus*, *Myripristis jacobus*, *Ocyurus chrysurus*, ***Oligoplites* sp.**, *Ophichthus ophis*, *Pempheris poeyi*, *Peprilus medius*, *Peprilus snyderi*, *Pomadasys corvinaeformis*, *Pomadasys crocro*, *Rachycentron canadum*, *Rhomboplites aurorubens*, *Sargocentron vexillarium*, Sciaenidae, *Scorpaena grandicornis*, *Scorpaena inermis*, ***Seriola dumerili, Seriola rivoliana, Seriola* sp.**, *Syacium latifrons*, *Syacium ovale*, *Synodus foetens*, *Synodus intermedius*, *Trachinotus*

	carolinus, *Trachinotus falcatus*, *Trachinotus goodie*, *Trachinotus paitensis*
24. Cephalopods	*Alloteuthis subulata*, Loliginidae, *Loligo pealeii*, ***Loligo* sp.**, *Loligo vulgaris,* *Lolliguncula panamensis*, Octopodidae, ***Octopus vulgaris***, Ommastrephidae, *Sepia bertheloti*, *Sepia elobyana*, *Sepia officinalis*, *Sepia orbignyana*, Sepiidae, *Thysanoteuthis rhombus*, *Todarodes sagittatus*
25. Crustaceans and benthos	*Aristeidae*, *Arca* sp., *Arcidae*, *Aristeus antennatus*, *Aristeus varidens*, Bivalvia, *Brachyura*, *Busycon sp.*, *Calappa rubroguttata*, *Callinectes sapidus*, *Cancer pagurus*, *Carcinus maenas*, *Cardiidae*, *Cardium edule*, *Chama crenulata*, Chitonidae, Conidae, *Crangon crangon*, Crangonidae, *Crassostrea rhizophorae*, ***Crassostrea virginica***, *Crepidula porcellana*, Crustacea, *Diadema* sp., Donacidae, Echinoderms, Gastropoda, *Geryon maritae*, *Geryon quinquedens*, *Haliotis tuberculata*, *Homarus gammarus*, Leucosiidae, *Maja squinado*, *Menippe mercenaria*, Miscellaneous marine mollusks, Muricidae, Mytilidae, Naticidae, *Necora puber*, *Nephrops norvegicus*, Paguridae, Palaemonidae, *Palinurus elephas*, *Palinurus mauritanicus*, ***Panulirus argus***, *Panulirus regius*, *Panulirus* sp., *Parapanaeus longirostris*, *Parapenaeopsis atlantica*, *Pecten maximus*, Pectinidae, Penaeidae, *Penaeus kerathurus*, *Penaeus brasiliensis*, *Penaeus notialias*, ***Penaeus* sp.**, *Perna perna*, *Pleoticus robustus*, *Plesionika heterocarpus*, *Plesiopenaeus edwardsianus*, *Porifera*, Portunidae, *Portunus* sp., *Pyura dura*, *Ruditapes decussates*, Scyllaridae, Solenidae, ***Strombus* sp.**, Veneridae, *Venus rosalina*, *Venus verrucosa*, Volutidae, *Xiphopenaeus kroyeri*
26. Benthic producers	Algae, benthic autotrophs
27. Zooplankton	Chaetognatha, Copepoda, Euphausiacea, Hydrozoa, Hyperiidae, Mysidacea, Scyphozoa, ichtyoplankton, macroplankton, meroplankton, planktonic decabods, larvae, and eggs
28. Phytoplankton	
29. Detritus	

Table S2. Uncertainty analyses and different scenarios tested with our ecosystem models. Scenario 1 and 2 are highlighted in Figure 1.

Scenario	Parameter	Default (best model) setting	Type of Change
1	Feeding rate for baleen whales species	10%	Increased to 50% and 100% feeding rate (5 times and 10 times the best estimate)
2	Time series of fishing effort	100%	Increased the effort to 150% and 200% fishing effort (1.5 times and 2 times the best estimate)
2	Cetaceans biomass	100%	Increased to 1000% (10 times the default)
3	Fish biomass	100%	Decreased to 10%
4	Cetaceans diet: percent of higher trophic level fish	Based on available diet info	Doubled proportion of higher trophic level fish and adjusted the remaining diet proportions

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