A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies

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Abstract

A balanced trophic model of a Galápagos rocky reef system was constructed using Ecopath and Ecosim. The Ecopath approach allowed characterization of food web structure through integration of disparate ecosystem information derived from many years of study of Galápagos shallow-water rocky reefs. Ecosim and Ecospace routines enabled us to explore various hypotheses about system dynamics as well as potential solutions to conservation concerns about overfishing. A full series of functional group removal simulations resulted in estimations of interaction strengths and 'keystone' potentials for each of the 42 living functional groups in the model. Relative interaction strengths in a pristine unfished system are likely to be quite different from interaction strengths indicated by this present-day model. At present, humans extract food from very low trophic levels (mean trophic level = 2.3) in Galápagos rocky reef systems because sea cucumbers and detritivorous mullets comprised 71 and 15%, respectively, of the total fisheries catch. Catch rates of sea cucumbers (*Stichopus fuscus*; referred to here as '*pepinos*') are shown to be unsustainable, and the population should be declining rapidly. The exclusion of fishing from 23% of the total reef area, representing a hypothetical non-extractive zone, prevented the functional extinction of *pepinos* that our analysis predicted to occur with no areas protected (given 1999–2000 capture rates). Even with 23% of the hypothetical area protected, *pepinos* were predicted to decline overall to a stable 36% of their current estimated biomass. *Pepino* biomass was predicted to increase to eight times that of current levels if *pepino* fishing were stopped altogether.
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1. Introduction

The Galápagos Archipelago lies in the equatorial eastern sector of the Pacific Ocean, about 1000 km west of the coast of Ecuador, South America (between 01°40′N–01°25′S and 89°15′W–92°00′W) (Fig. 1). The archipelago consists of 13 large and 6 small islands, 42 islets, and numerous exposed rocks (Snell et al., 1995). These current islands represent the tops of relatively young volcanoes that rose from the sea between 1 and 3 million years ago, though submerged islands in the archipelago have been dated at 9 million years old, and islands might have been produced over this mantle hotspot for much longer (Christie et al., 1992). The islands rise from a relatively shallow (< 200 m) Galápagos Platform surrounded by deep waters (>1000 m).

The location of the Galápagos Archipelago, at the confluence of warm currents (26–29 °C) from the north, cool waters (20–22 °C) from the south-west, and nutrient-rich upwelling waters from the west propagating eastward, has led to complex and poorly understood marine and coastal ecosystems (Houvenaghel, 1984; Wellington, 1984; James, 1991). Between three and five major biogeographic units have been proposed for the archipelago; however, the number of units and their boundaries still require clarification (Abbott, 1966; Harris, 1969; Jennings et al., 1994; Banks, 1999; Wellington et al., 2001). The largest regional mix of marine species occurs on the central Galápagos shelf, including the study area located around the island of Floreana (Fig. 2). This area is characterized by a particularly diverse combination of warm- and cool-water biota (Witman and Smith, 2003).

The shallow-water ecosystems around Floreana Island consist primarily of sloping lava fields interspersed with sandy pocket beaches, as do most of the coastal shores of the Galápagos. These beaches are composed of both biogenic material (white and

Fig. 1. Map of the Galápagos Islands showing the coastal use-zoning scheme that has been in effect since 2000. Floreana Island is shown in the lower central part of the map. Wolf and Darwin Islands are not pictured; they are smaller and they lie to the NNW of the main islands.
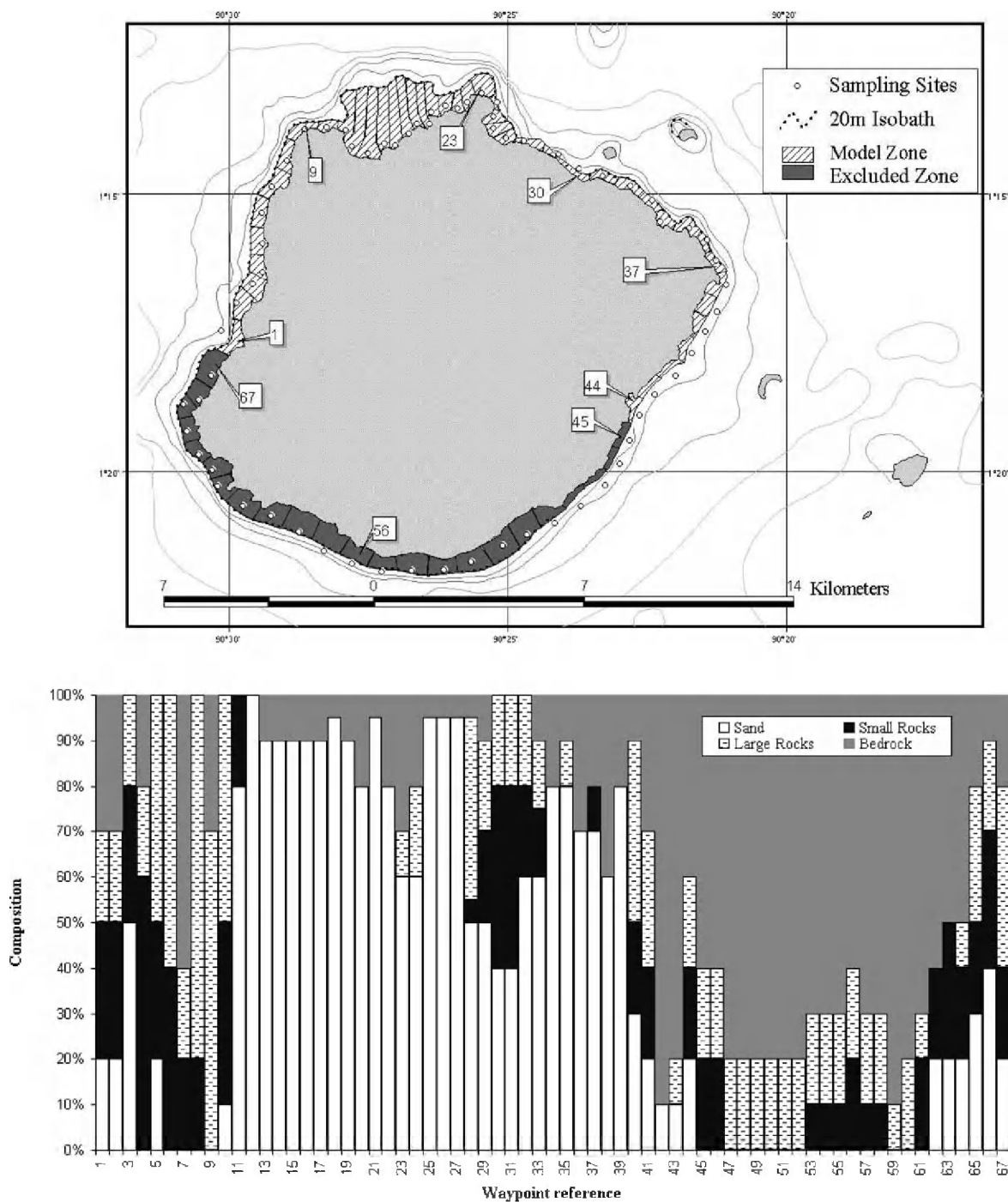
Fig. 2. A map of Floreana Island and the waypoint areas used to estimate proportions of habitat types around the island. The accompanying chart in the lower panel shows the estimated proportions of habitat types at each waypoint reference area. These relative proportions were used to estimating biomasses of various functional groups in the modeled area.

brown sand mainly from corals and echinoid tests) and pulverized lava (black sand), while sporadic mangrove forests occur in sheltered inlets. Subtidal lava reefs surround all the Galápagos Islands, and they can be subdivided into categories that include bedrock, boulders, cobbles, and sand (Fig. 2).

Cool nutrient-rich waters on the Galápagos platform support high biomasses of small pelagic fishes such as sardines, thread-herrings, anchovies, pompanos, mackerel, scads, halfbeaks, and lantern fishes, which in turn feed substantial populations of top predators such as sharks, tuna, wahoo, billfishes, jacks, barracuda, dolphinfish, seabirds, and toothed cetaceans (Feldman, 1985, 1986), many of which visit and feed actively in Galápagos rocky reef habitats.

This productive pelagic system surrounds and interfaces with the benthic rocky reef habitats fringing each island of the Galápagos Archipelago, and plankton carried by oceanic currents is a major source of primary production on the reefs. Planktivorous reef fishes inhabit the boulder strewn reef and feed in the water column. They include gringo (Paranthias colonus)—the most abundant Galápagos reef-dwelling fish species. In addition to sustaining large numbers of pelagic and reef-associated fishes and seabirds, plankton supports a high biomass of suspension- and filter-feeding invertebrates. These include the barnacle Megabalanus peninsularis, the sessile mollusc Hipponix sp., brittle stars and the black and stony corals Antipathes spp. and Pavona spp.

Benthic primary production is the other major source of primary production in this system. Galápagos rocky reefs in some areas include a foliose algal turf that, along with diatoms and other microphytobenthos, provides a large bulk of the energy supporting high biomasses of whole suites of invertebrates, fishes, and other vertebrates, including the marine iguana (Amblyrhynchus cristatus)—a unique sea-going lizard and active marine grazer that symbolizes the system's strong dependence on benthic primary production.

Three highly abundant species of sea urchins (Tripneustes depressus, Eucidaris thouarsii, and Lytechinus semituberculatus) exert intense grazing pressure on benthic primary producers (and corals), often forming extensive urchin barrens (Breen and Mann, 1976; Ayling, 1981; Himmelman and Lavergne, 1985). Herbivorous fish species include damselfish, surgeonfish and parrotfish. Herbivorous green sea turtles (Chelonia mydas) are also present, sometimes in relatively high numbers. Several species of sea cucumbers (holothurians, Spanish pepino del mar) are also very widespread and abundant, notably the slow growing Stichopus fuscus, hereafter 'pepino'.

Omnivorous reef fishes, including chubs, butterflyfish, and damselfish, consume algae and small benthic invertebrates. Small benthic invertebrate-eating fishes include grunts, small wrasses, and an angelfish. Predatory invertebrates include whelks, conch, spiny lobsters, and crabs. Upper trophic levels feature many species of piscivorous reef fishes such as groupers and snappers. Large benthic invertebrates are consumed by large wrasses and triggerfish. Other high-level predators include octopus, the Galápagos sea lion (Zalophus wollebaeki), and unique seabirds such as the Galápagos penguin (Spheniscus mendiculus) and the flightless cormorant (Nannopterum harrisi). A variety of shark species is present including the Galápagos shark (Carcharhinus galapagensis), the white-tipped reefshark (Triaenodon obesus), other reef sharks, and species that interface with pelagic systems.

Small-scale fisheries feed tourists and residents, but most of the catches in the archipelago (high-value sea cucumbers and lobsters) are exported to lucrative foreign markets (e.g. Japan, Taiwan, US). As an example, in 1999 and 2000, local fishers were paid about US$ 0.90 for every landed pepino (S. fuscus—a slow growing holothurian), although the price fell to ≈US$ 0.55 in 2001 (PIMPP, 2001).

The international fisheries markets drive the growing population of local fishers to deplete exploitable marine invertebrates (as well as illegally captured sharks), potentially shifting the structure of these ecosystems directly and indirectly, and undermining their sustainability (Constant, 1993; Camhi, 1995; Merlen, 1995). In addition, water quality is jeopardized around urban areas, and overflows from rudimentary septic tanks increase nutrient levels near the expanding population centers. Large and small spills occur occasionally when fuel is brought to the islands for delivery to tourist vessels, and visitors directly stress coastal biota. A Special Law of Galápagos was recently enacted to improve marine reserve management and enforcement, but these stresses nevertheless continue. Finally, oceanographic and climatic changes, including the El Niño/La Niña oscillations

and the potential for global climate change can profoundly influence the structure of Galápagos marine communities (e.g. Colinvaux, 1972; Houvenaghel, 1984; Glynn, 1988; Bost and Le Maho, 1993).

A provisional coastal use-zoning plan has been in place in the archipelago since 2000 (Bustamante et al., 2002; see Fig. 1). In this scheme, fully protected 'no-take' areas, i.e. areas where no entry or human uses other than scientific research are allowed, protect 8% of the island's coastlines (zones shaded in black in Fig. 1); non-extractive use areas, i.e. areas where tourism, recreation and education are allowed, cover 10% of coastlines (zones shaded in dark grey in Fig. 1); regulated extractive uses, i.e. recreational and fisheries uses, are allowed along 77% of the coastlines (zones shaded in light grey in Fig. 1); and special zones nearby the inhabited port areas, i.e. areas where the local stakeholders will define their status through a participatory process, cover the remaining 5% of the island's coastline (zones shaded in thickened light grey in Fig. 1). This zoning plan provides an opportunity to protect small and replicated portions of Galápagos coastlines, and to evaluate the potential consequences and benefits of small and large marine protected areas (Branch et al., 2002).

Although some violations of this scheme occur, fishing in the 'fisheries exclusion' zones (about one fifth of the total coastlines) is lower than in the zones open to fishing. The Charles Darwin Research Station has an ongoing marine ecological monitoring program designed to gather baseline information about these unique marine systems and to reveal any biological changes that might be related to the zoning and associated changes in human use patterns throughout the islands. The rocky reefs around Floreana Island are divided among fisheries, tourism, and fully protected zones.

The present modeling exercise complements this monitoring program in a way that allows refinement of knowledge and management through an iterative approach to learning and an adaptive (or experimental) approach to conservation and fisheries management. The purpose of the model is to provide accessible 'views' of the whole system and to predict how it might respond to changes in human actions or other stresses. The model may also provide insights into the underlying ecological mechanisms operating in the system and explore possible solutions to conservation

problems. In particular, this continually updated ecological synthesis can be used to generate hypotheses about the dynamics of this special system and to address questions such as: Which functional groups currently exert large effects on the system? What are the potential ecosystem consequences of removing particular species from the system? Are any species in this system currently being fished at unsustainable levels? To what extent will fisheries exclusion zones alleviate declines of overfished species or restore previous abundances?

2. Methods

2.1. Modeling tools: Ecopath with Ecosim

Ecopath trophic models are mass-balance models, or more accurately mass-continuity models, that account for the energy flows in a food web. The Ecosim routine expresses the mass-balance constraint in a dynamic context to explore the direct and indirect ecological effects of fisheries, perturbations, and even physical forces. For example, the relative strengths of trophic interactions among species can be estimated, and the effects of changes in a particular fishery on various biotic components can be simulated. These models are continually refined and evaluated in an iterative process. See Okey et al. (2004a) for a summary of the formulation and basic approach of Ecopath and Ecosim (also see Polovina, 1984; Christensen and Pauly, 1992; Walters et al., 1997, 1999, 2000; Christensen et al., 2000; Pauly et al., 2000; Oritz and Wolff, 2002; Christensen and Walters, 2004; and http://www.ecopath.org/).

In Ecospace, the simulated interactions among organisms occur in a spatially explicit, and habitat-based, context rather than in a single 'reaction vat' (Walters et al., 1999). Ecosim, because of simulated refugia from predation, also does not work as a simple vat. The area of interest is represented by a spatial mosaic of cells that can be designated as land and a variable number of marine habitats. For each functional group, these habitats are specified as preferred or not preferred. The dynamic redistribution of organisms in the system is based on user-specified base dispersal rates, relative movement rates in bad habitat, relative feeding rates in bad habitat, and the constantly changing

densities of predator and prey groups with which a given functional group interacts. The instantaneous dispersal rates across cell boundaries are determined by the specified base dispersal rate, the habitat type in the source cell, and the responses of functional groups to predation risk and feeding conditions in the source cell (Walters et al., 1999). Spatial variations in primary production and current advection fields can be specified, as can spatially relative fishing costs (i.e. effort) and the spatial distribution of marine protected areas (i.e. fisheries exclusion zones). Grid number and sizes can be adjusted or scaled appropriately.

2.2. Delineating Floreana rocky reefs

The region characterized in this balanced trophic model includes reefs shallower than 20-m depth along the eastern, northern and western coasts of the Floreana Island—a relatively homogeneous area that is also representative of the central Galápagos shelf region, which includes the large islands of Santiago, Santa Cruz, Santa Fé, San Cristóbal and northern Española, and the eastern coast of Isabela—the largest of the islands (Fig. 1). Because the southern coast of Floreana is much more exposed and influenced by cooler waters associated with the southern equatorial current and equatorial undercurrent, and has been little studied, that region was excluded from the model described here. Spatially, the exclusion represents an estimated 42% of the 20-m isobath (all strata) and 64% of the total rocky reef model area for the island. Reefs in water depths >20 m, and soft-sediment habitat types, were also excluded from the current model.

A combination of site aerial photography and chart bathymetric data, geo-referenced within an Arcview GIS system, was used to estimate the spatial extent of the 20-m isobath from the coast. Spatial estimations were further weighted against a modifier for estimated habitat coverage (see Fig. 2). A series of 67 observations of substrate composition were taken around the coastal perimeter of the island at approximately 500-m intervals. The spatial localization of each observation was taken as a polygonal area roughly equidistant between adjacent sampling points extending from the coast to the reported 20-m isobath. Rocky and bedrock strata estimations were grouped as representative of the model space and weighted by localized

Table 1
Model space estimations within the 0–20 m isobath

Area	Total area (km^2)	Weighted habitat modifier (%)	Corrected area (km^2)
0–20 m isobath	28.38	62.2	17.65
Southerly exclusion	11.91	94.2	11.22
Modeled rocky reef	16.47	39.1	6.44

area to give a final estimation of the entire model space (Table 1).

2.3. Defining functional groups

The 43 functional groups in the Floreana Island rocky reef model were the product of a collaborative process that defined the system. A number of experts, including the present authors, participated in several iterations of the list of functional groups. All the species in the system were aggregated into these functional groups based on similarity of ecological role, defined by similarities in diet, production and consumption rates, life history, and habitat associations, but also sometimes on value-driven criteria such as commercial status or importance for tourism.

In the final iteration, benthic invertebrates were represented by 19 functional groups; others were fishes, 13; primary producers, 3; zooplankton, 2; marine mammals, 2; marine reptiles, 2; birds, 1; and detritus, 1. Because of the nature of the Galápagos archipelago, i.e. a relatively small and narrow rocky platform surrounded by deep open-ocean waters, the model includes discrete, but interconnected, benthic- and pelagic-based subsystems.

2.4. Estimating Ecopath input parameters

Biomass estimates were derived using methods specific to each functional group. Production/biomass (P/B), consumption/biomass (Q/B), and diet compositions for each species were derived mostly from the scientific literature and with the help of FishBase (www.fishbase.org). P/B was usually estimated by assuming that it equals total mortality (Z) under the assumption of population equilibrium (Allen, 1971). Q/B was most commonly estimated from the empirical relationship proposed by Palomares and Pauly (1999), setting mean water temperatures at 22–25 °C.

Representative values for aggregated groups were derived as averages of species-specific estimates weighted by relative biomass (B) or consumption (Q) as appropriate.

Input biomass estimates of benthic and demersal fish groups and large invertebrates (>20 mm) were obtained directly from site-specific surveys of Floreana rocky reefs. These middle trophic-level groups represent the strong core of the model, and confidence in these estimates is expected to increase further as the ecological monitoring program progresses. Site-specific data were also available for pelagic fish groups, birds, turtles, sharks, and marine mammals, but resulting biomass estimates (or estimates of dietary proportions originating from the rocky reef) are more uncertain for these more mobile groups because of the haphazard nature of the existing sightings data, or knowledge of foraging patterns. Biomasses of macro-invertebrates (0.5–20 mm) and lower trophic-level groups were estimated by the model, but empirically based estimates of primary production of benthic macro-algae and phytoplankton were used to structure the base of the food web.

Missing input parameters were taken from the literature (e.g. P/B and Q/B ratios, and diet composition) and adjusted proportionally as weighted estimates for all species in a functional group whenever possible (e.g. most of the fish groups). Diet compositions were the least certain type of input parameter because of the paucity of site-specific dietary data. Examination of the knowledge gaps revealed during model construction enabled adaptive refinements to strategies for the continuing monitoring program.

2.4.1. Primary producers

Mean phytoplankton standing stock was estimated using multispectral image analysis software to extract SeaWiFS chlorophyll concentration estimates from geo-referenced 1.1-km^2 resolution localities over the eight target sites group averaged to the surrounding 10 km^2 at each point, excluding coastal overlap and cloud cover. Data were collated over the year 2000 as available from local area coverage from the NASA-PODAAC distributed data archive. Time series plots at target sites were constructed to examine seasonal and geographic variability within the model area, and averages compared against in situ samples collected during trips on May 26, 2001 and June 18, 2001. An

averaged value of 12 tonnes km^{-2} was derived from an estimation of 0.64 mg chlorophyll m^{-3} following conversion factors for phytoplankton standing stock from Durbin and Durbin (1998), Arreguín-Sánchez et al. (1993), and Pauly et al. (1993a). Macro-algal biomass on the rocky reef at Floreana Island was estimated based on measured standing wet biomass at two sites on Santa Cruz Island, and based on subtidal observations. Microphytobenthos biomass was left to be estimated by the Ecopath routine.

2.4.2. Invertebrate groups

Biomass estimates for 10 of the 15 mega-invertebrate (>20 mm) groups in the model were derived from visual line transect surveys at nine Floreana rocky reef sites sampled during 2000 and again in 2001. Twenty-five species were aggregated into these 10 sampled functional groups. At each site, a 50-m transect line was laid down along two selected depth contours, and the number of large invertebrates within one meter of each side of the line recorded as the diver moved along one side and then back along the other side of the transect. The wet masses of individuals of most mega-invertebrate species from Floreana were also measured to estimate mean wet mass. In a few cases, the maximum length (e.g. arm radius for seastars, shell for gastropods, or body for sea cucumbers) or diameters (for sea urchins) of up to 30 individuals of each invertebrate species were recorded in situ using a measuring tape for later estimation of mass using length–weight ratios. Mean densities were multiplied by mean weights to obtain biomass density estimations, and skeletal carbonate weights were subtracted as appropriate.

2.4.3. Fish groups

Biomass estimates for the 13 fish groups were derived from visual line transect surveys at nine rocky reef sites around the Floreana coastline during 2000 and 2001. At each site, divers swam at a constant speed on each side of 50-m transect lines placed along the 6- and 15-m isobaths, while recording the numbers and sizes of fish species observed within a 500 m^2 area (10 m total swathe) and 5 m above the transect line. The density of each size class for each species was transformed into biomass/area, using length–weight relationships in FishBase (www.fishbase.org). Conversion factors for related proxy species were used when

no conversion factor was available for a species. The biomass/area values of the size classes were summed for a total species biomass and these were summed for total functional group biomass estimates.

2.4.4. Higher vertebrates (sea lions, sharks, turtles, iguanas)

Biomass estimates for sharks and turtles were the products of the number of diver sightings and average mass of individuals divided by the approximate area surveyed per dive. A sightings correction factor based on the discrepancy between diver-observed sea lion biomass and sea lion biomass based on counts on rookeries was then applied to the shark and turtle visual estimates to calculate rough error-corrected biomass estimates. A corrected biomass estimate for sea lions that feed on reefs was derived by multiplying the haul-out survey biomass estimate by the proportion of the diet from reefs. The biomass estimate for marine iguanas was based on surveys on Floreana Island, and is likely an underestimate for most of the north side of the island. However, a correction factor for such a density discrepancy is not yet developed, and the density presently used is likely more representative of the archipelago in general.

2.4.5. Fisheries information

Fisheries catch and effort data for the Galápagos Archipelago have been collected since 1997 through a daily monitoring program that includes recordings of the landed catch, effort, and distributions of finfish, sea cucumbers, and lobsters. Data are collected at the three main ports in Galápagos at the islands Santa Cruz, San Cristóbal, Isabela, and occasionally in Floreana. For the calculation of the average annual catch rate for these species we divided the catches that are extracted from the Floreana area by an estimate of the modeled area. Catches were calculated for the monitored species with use of conversion factors that describe the relation between the state of the product at landing (dried, salted, gutted, etc.) and its actual fresh weight. *Pepino* catch data in numbers of individuals were converted into fresh weight with the assumption that the average length is 21.3 cm in the population around Floreana (Anon, 2001). Given the length–weight relationship for *pepino* estimated in 1999 ($n = 4363$, $R^2 = 0.355$) this length corresponds to a 333 g fresh weight. The fresh weights were

summed per functional group and an average was calculated for the period under investigation. The average monitored finfish landings were multiplied with a raising factor to convert the monitored landings into an estimate of the total landings. This conversion factor (1.66) expresses the 34% effectiveness of the monitoring program and was derived from Espinoza et al. (2001). No conversion factor was used for invertebrate catches because these are fully covered (100% monitored) through a system of export certificates. Landings per square kilometer were calculated with a fixed area of 16.47 km^2 because fishing activities around the total coast of Floreana were taken into account. The resulting estimates of fishing density are applicable to the more limited area that was modeled.

2.5. Analyses

The majority of the missing parameters left to be estimated by the Ecopath software were ecotrophic efficiency (EE) values, as empirically based estimates were available for most basic parameters in the system. However, Ecopath estimated 10 missing biomass values by specifying a reasonable EE value and solving the Ecopath master equation. One missing P/B value was estimated by additionally specifying a reasonable rate of production to consumption (P/Q). Trophic levels were calculated as the biomass weighted average of food items plus 1, and the omnivory index was the variance of the trophic levels of the prey groups (Pauly et al., 1993b). The basic flows in the system and other indices were also summarized while characterizing the system (see Christensen and Pauly, 1992; Christensen et al., 2000).

A full series of 'removal' simulations was conducted to evaluate the relative interaction strength of each species in the Floreana rocky reef food web. Additional mortality was imposed on one *pepino* group so that it declined to zero by the 10th year of the 30-year simulation. System-wide changes in biomasses resulting from the removal of a species were recorded. Mortality rates were then reset to initial levels before the next removal simulation. We used the interaction strength index (ISI), the sum of all resulting relative changes in the system (the total absolute relative changes in all but the removed group). The 'keystone' index is the ISI expressed in terms of the relative biomass of the respective groups

(see Power et al., 1996, for definition of keystone species).

Fisheries were analyzed in terms of the proportion of the total catch in the system contributed by each functional group as well as the proportion of each group's total mortality accounted for by fisheries. An analysis of the directed *pepino* fishery was conducted because it stood out as unsustainable. Biomasses and catches were plotted as a function of capture rate (annual catch/biomass) as predicted by surplus production models in hypothetical equilibrium conditions.

A simple Ecospace simulation was used to explore the potential effects of fishery exclusion zones on *pepinos* in the Galápagos Islands. The Floreana rocky reef model was re-expressed spatially using a mosaic of cells scaled to simulate Floreana Island, but the simulation was set up as a hypothetical island within the Galápagos archipelago. The area of rocky reef was exaggerated on the Ecospace base map for diagrammatic purposes (the reefs in the spatial simulation are made much wider than the actual narrow band around most Galápagos Islands; (Fig. 2). The hypothetical no-fishing zone covers approximately 23% of the coastline in the Ecospace base map reflecting the current proportion of protected coastline in the Galápagos Archipelago (18%) plus the special port areas (5%) in which local communities specify uses. This would tend to provide overly optimistic predictions of population responses to protection since local communities choose fishing. This hypothetical zone takes the form of a single no-fishing zone at one island. The simulation assumes a base dispersal rate of 5 km per year for *pepinos*, corresponding to 14 m per day. Additional simulations were performed to account for higher dispersal rates of *pepino* larvae.

3. Results

The Floreana rocky reef food web model is characterized by very high biomasses of fishes and invertebrates (Table 2). The model is unique among Ecopath mass-balanced models in that the primary and secondary production needed to support such high biomasses are specified as a net 'immigration' of phytoplankton and zooplankton delivered to these reefs by oceanic currents, assuming that oceanic islands are plankton sinks. This results in a strong system heterotrophy, as indicated in the descriptive statistics (Table 3) and visible when examining a summary of system flows (Table 4).

The 10 groups with the highest indicated interaction strengths (Table 2) were (in decreasing order): pelagic predators, large benthic invertebrate-eating fishes, shrimps and small crabs, omnivorous reef fishes, benthic algae, microphytobenthos, small benthic invertebrate eaters, other herbivorous fishes, non-commercial reef predators, and herbivorous zooplankton. Sea lions and sharks ranked 12th and 15th, respectively. The 10 groups with the highest indicated 'keystone index' values (Table 2) were (in decreasing order): toothed cetaceans, birds, sharks, sea lions, octopus, *Hexaplex* gastropods, spiny lobsters, non-commercial reef predators, pelagic predators, and large benthic invertebrate-eating fishes. Omnivorous reef fishes ranked 11th.

Specific results of the first of 43 functional group removal simulations are shown in Fig. 3. Toothed cetaceans, sea lions, and non-commercial reef predators are predicted to increase when sharks are removed, thus causing decreases in *bacalao*, i.e. the grouper *Mycteroperca olfax*, other commercial reef fishes, and small benthic invertebrate-eating fishes through increased predation or competition, or both. Sea turtles, marine iguanas, large benthic invertebrate-eating fishes, and parrotfish are also predicted to increase when sharks are removed. Some small benthic invertebrates are predicted to increase, while large benthic invertebrates are predicted to decrease, and other trophic cascades are apparent.

The model also shows the mean trophic level of the fisheries catch to be particularly low (2.3; see Table 3). Humans fill an unusually low trophic position in the Galápagos because, for example, *pepinos* comprised 71% of the fisheries catch from Floreana Island during the late 1990s and detritivorous fishes (Mugilidae) comprised 15% (Table 5).

Pepinos declined in every simulation that included status quo fishing rates, because estimated overall mortalities from fisheries, predators, and senescence exceeded this group's estimated production for the entire range of input parameters reasonable for this species. The *pepino* fishery, as executed at 1999–2000 levels, accounted for 88% of the total mortality of this species.

The current capture rate far exceeds the optimum sustainable capture rate estimated by Ecosim (Fig. 4)

Table 2
Basic parameters of the Ecopath model of the Floreana rocky reef, Galápagos[a]

Group name	Trophic level	OI	Biomass (tonnes km^{-2})	P/B (per year)	Q/B (per year)	EE	ISI	Biomass (%)	Keystone index
Sharks	**4.4**	**0.40**	0.75	0.24	4.90	**0.030**	8.6	0.03	286.7
Toothed cetaceans	**4.4**	**0.50**	0.02	0.08	14.60	**0.000**	1.6	0.001	1600.0
Bacalao grouper	**4.2**	**0.34**	7.14	0.35	4.50	**0.649**	1.0	0.27	3.6
Birds	**4.1**	**0.32**	0.01	5.40	80.00	**0.340**	0.2	0.0004	575.0
Sea lions	**4.0**	**1.27**	5.68	0.07	25.55	**0.864**	9.4	0.22	42.8
Pelagic predators	**3.9**	**1.19**	30.00	0.42	4.35	**0.282**	22.4	1.14	19.6
Non-commercial reef predators	**3.8**	**0.23**	14.86	1.03	11.07	**0.877**	11.5	0.57	20.2
Octopus	**3.5**	**0.10**	0.79	1.10	7.30	**0.511**	0.9	0.03	30.0
Pelagic planktivores	**3.4**	**0.15**	5.50	0.98	32.10	**0.353**	1.6	0.21	7.6
Other commercial reef predators	**3.3**	**0.16**	9.30	0.62	7.11	**0.557**	1.7	0.35	4.9
Large benthic invertebrate eaters	**3.3**	**0.06**	32.71	0.65	9.82	**0.658**	18.7	1.25	15.0
Planktivorous reef fish	**3.3**	**0.31**	281.13	1.50	45.07	**0.260**	7.0	10.73	0.7
Hexaplex gastropod	**3.0**	**0.02**	3.61	2.80	14.00	**0.667**	3.7	0.14	26.4
Small benthic invertebrate eaters	**3.0**	**0.31**	100.99	1.39	13.73	**0.569**	13.4	3.85	3.5
Carnivorous zooplankton	**2.8**	**0.52**	3.58	8.70	29.00	**0.475**	8.8	n/a	n/a[b]
Spiny lobsters	**2.8**	**0.26**	3.00	0.45	7.40	**0.650**	2.6	0.11	23.6
Slipper lobster	**2.7**	**0.39**	4.00	0.45	7.40	**0.722**	0.7	0.15	4.7
Omnivorous reef fishes	**2.7**	**0.29**	41.52	1.02	21.85	**0.896**	17.7	1.58	11.2
Shrimps and small crabs	**2.6**	**0.33**	**55.13**	3.60	20.45	0.950	18.0	2.10	8.6
Asteroids	**2.5**	**0.36**	10.49	0.49	3.24	**0.105**	0.4	0.40	1.0
Other herbivorous fish	**2.4**	**0.42**	200.60	0.88	25.83	**0.265**	13.4	7.66	1.7
Eucidaris urchin	**2.2**	**0.23**	104.43	1.40	2.81	**0.830**	8.4	3.99	2.1
Anemones	**2.2**	**0.26**	**79.24**	2.00	4.00	0.900	3.1	3.02	1.0
Worms and ophiuroids	**2.2**	**0.25**	**84.67**	4.14	61.60	0.950	10.3	3.23	3.2
Stony corals	**2.2**	**0.22**	**91.16**	1.09	15.00	0.900	2.6	3.48	0.7
Chitons	**2.2**	**0.29**	**2.85**	0.34	11.70	0.900	0.1	0.11	0.9
Detritivorous fish	**2.1**	**0.12**	**39.95**	**1.37**	13.70	0.095	0.6	1.52	0.4
Small gastropods	**2.1**	**0.11**	**188.05**	2.50	14.00	0.950	6.4	7.18	0.9
Sea turtles	**2.1**	**0.15**	3.02	0.15	3.50	**0.162**	0.2	0.12	1.7
Pepino sea cucumber	**2.1**	**0.07**	3.90	0.60	3.36	**0.972**	n/a[c]	0.15	0.0[c]
Other urchins	**2.0**	**0.01**	4.65	1.40	2.81	**0.755**	0.1	0.18	0.6
Parrotfishes	**2.0**	**0.00**	21.50	0.50	16.60	**0.627**	1.7	0.82	2.1
Marine iguana	**2.0**	**0.00**	0.80	0.11	15.00	**0.376**	0.1	0.03	3.3
Other sea cucumbers	**2.0**	**0.00**	3.55	0.60	3.36	**0.166**	0.1	0.14	0.7
Tripneustes urchin	**2.0**	**0.00**	48.74	1.40	9.71	**0.350**	3.9	1.86	2.1
Lytechinus urchin	**2.0**	**0.00**	8.72	1.40	2.81	**0.903**	0.5	0.33	1.5
Small crustaceans	**2.0**	**0.03**	**91.41**	9.00	125.50	0.950	0.5	3.49	0.1
Filter + suspension feeders	**2.0**	**0.08**	**367.39**	2.00	16.50	0.900	9.0	14.02	0.6
Herbivorous zooplankton	**2.0**	**0.08**	**3.19**	17.30	57.70	**0.656**	10.9	n/a	n/a[b]
Phytoplankton	**1.0**	**0.00**	12.00	70.00	–	**0.946**	3.7	n/a	n/a[b]
Microphytobenthos	**1.0**	**0.00**	**393.59**	23.70	–	0.990	16.1	15.02	1.1
Benthic algae	**1.0**	**0.00**	256.80	12.00	–	**0.986**	16.5	9.80	1.7
Detritus	**1.0**	**0.29**	500	–	–	**0.499**	n/a[c]	n/a	n/a

[a] Values in bold have been calculated with the Ecopath software; other values are empirically based inputs, or values that were adjusted from empirically based values during balancing. The omnivory index (OI) indicates dietary breadth; ecotrophic efficiency (EE) is the proportion of production not consumed or exported; P/B and Q/B are the ratios of production and consumption to biomass; ISI is the interaction strength index, which is the sum of the predicted relative change (all groups) after removal of the indicated group at the beginning of 30-year dynamic simulations. The keystone index is the ratio of the interaction strength index and the percent of the system's overall biomass that is represented by the group.

[b] ISI values and keystone indices were not estimated for the three plankton groups in the system because of high specified immigration rates.

[c] *Pepino* almost entirely disappear automatically during 30-year simulations due to unsustainable catch rates, so 'removing them' is redundant and thus no Pepino keystone effects can be estimated by this present analysis.
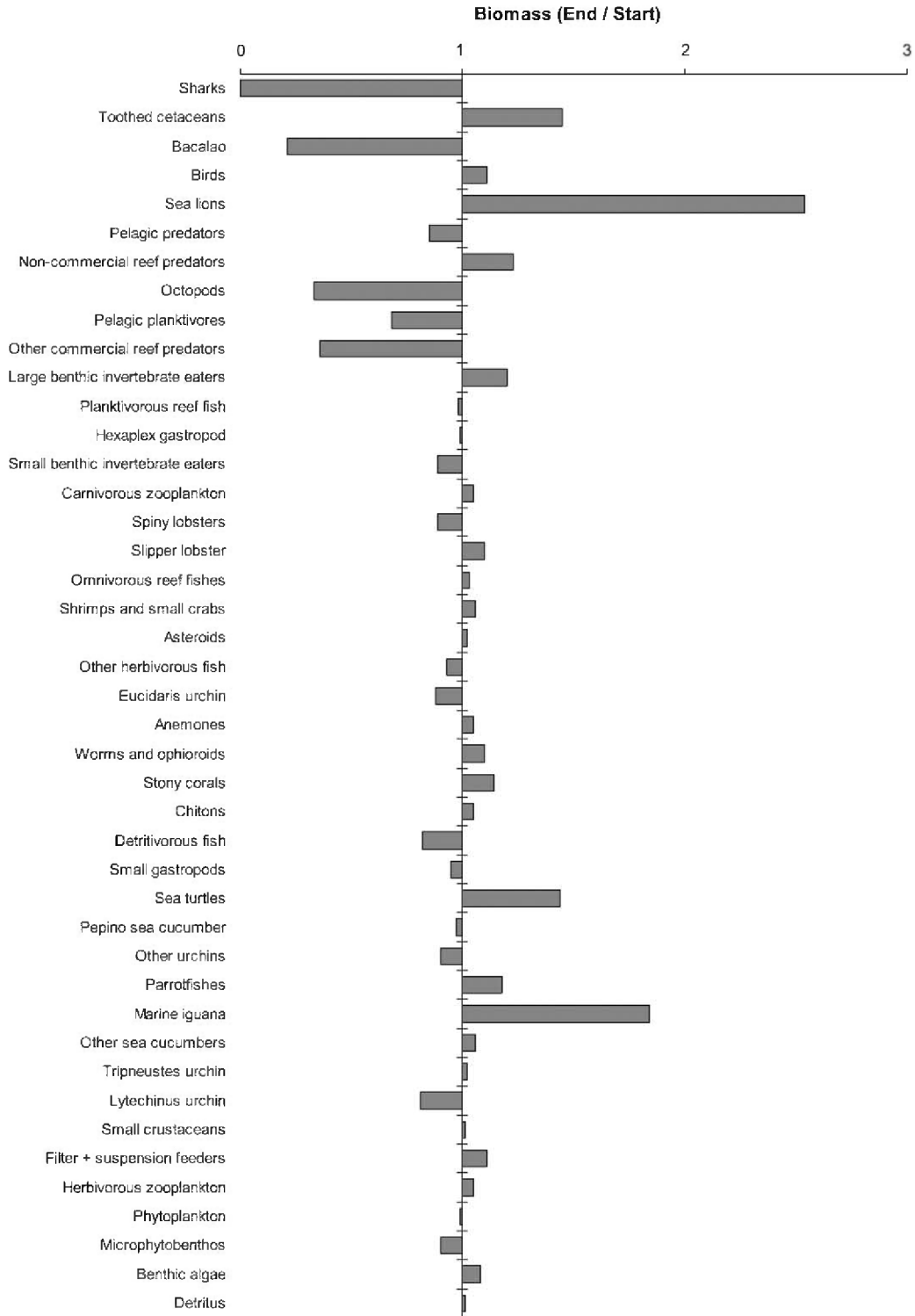
Biomass (End / Start)

Fig. 3. Predicted changes resulting from the complete removal of sharks from the present-day Floreana rocky reef trophic model. Results shown are the predicted relative change in biomasses at the end of a 30-year simulation in which sharks were removed by year 10 ($V = 0.4$).

Table 3
Basic flows and indices in the Floreana rocky reef Ecopath model[a]

Flows	(tonnes km^{-2} per year)
Calculated total net primary production	13250
Net system production	−14388
Sum of all production	17337
Sum of all consumption	51600
Sum of all exports	−5412
Sum of all respiratory flows	27638
Sum of all flows into detritus	21024
Total system throughput	94850
Total catches	4.15

Biomass	(tonnes km^{-2})
Total living biomass	2620

Indices	
Total primary production/total biomass	5.06 per year
Total biomass/total throughput	0.03 per year
Total primary production/total respiration	0.48
Proportion of flows originating from detritus	0.62
Connectance index	0.16
Mean trophic level of the catch	2.27
System omnivory index	0.25 TL units

[a] Flows and biomass are expressed in wet weight.

indicating highly unsustainable fishing pressure. On the other hand, six- to eight-fold increases in *pepino* biomass were predicted when total fishing moratoriums were simulated.

The biomass of *pepinos* was predicted to increase inside a hypothetical no-fishing zone (Fig. 5), but the overall biomass of *pepinos* is predicted to decline and
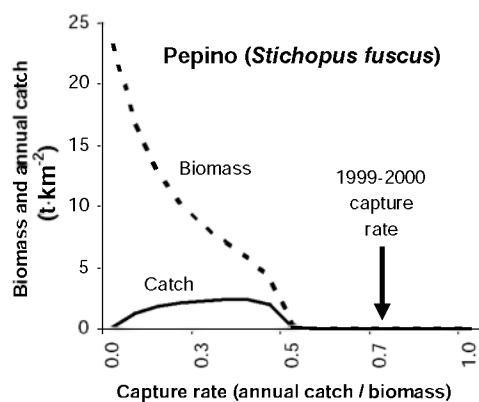
Fig. 4. Predicted catch and biomass curves for *pepino* sea cucumbers (*S. fuscus*) on the rocky reefs at Floreana Island, Galápagos. The 1999–2000 capture rate (annual catch/biomass) of this species was essentially twice that of sustainable levels. This figure represents the predicted states of the biomass and annual catch after the system reaches 'equilibrium' based on the specified biomass and production rate (*P/B*) of *pepino* and the combined effect of all sources of mortality in the system. It is possible for the actual capture rate to greatly exceed sustainable capture rates, but only if the population is rapidly collapsing.

stabilize at 36% of the 2000–2001 levels by the end of the 10 year simulation. Although the fisheries exclusion zone does not prevent overall *pepino* biomass from declining, it does prevent these intense fisheries from completely eliminating this slow-growing species. Dispersal rates higher than 14 m per day result in a larger 'spillover' effect (catchable emigration), but a lower buildup (protection) of biomass in the no-fishing zone.

Table 4
Flows from primary production and detritus[a]

TL	From primary production					From detritus				
	Consumed	Export	To detritus	Respiration	Throughput	Consumed	Export	To detritus	Respiration	Throughput
VI	0	0	0	1	1	0	0	0	1	1
V	1	0	5	15	20	1	0	4	12	16
IV	16	0	224	381	621	13	0	210	337	561
III	1099	−927	2125	3237	5533	1048	−927	1050	1684	2855
II	10276	−8843	9956	13058	24448	5086	−3648	7195	8912	17544
I	14668	−1600	155	0	13223	10490	10534	0	0	21124
Sum	26059	−11370	12465	16692	43846	16639	5959	8459	10946	42102

[a] Flows are expressed in tonnes per square kilometer per year. System imports and exports are not shown. Some flows reach trophic-level VI because some organisms within some functional groups are supported by energy that has traversed five links from primary producers.

Table 5
Percentage of total annual catch comprised by the 10 functional groups targeted in Floreana reef fisheries[a]

Functional group	TL	Catch (tonnes km^{-2} per year)	Total catch (%)	Total mortality (%)
Bacalao grouper	4.2	0.031	0.8	1.4
Pelagic predators	3.9	0.221	5.4	1.9
Non-commercial reef predators	3.8	0.067	1.6	0.5
Pelagic planktivores	3.4	0.004	0.1	0.1
Other commercial reef predators	3.3	0.037	0.9	0.6
Large benthic invertebrate eaters	3.3	0.006	0.1	0.9
Spiny lobster	2.8	0.178	4.3	13.1
Slipper lobster	2.7	0.011	0.3	0.7
Detritivorous fishes	2.1	0.621	15.2	1.2
Pepino (*S. fuscus* sea cucumber)	2.1	2.922	71.3	87.5

[a] Analysis based on data from 1997 to 2000. A great majority of the catch comprised *pepinos* and detritivorous fishes. TL is trophic level, and the final column is the percent of each group's total mortality that is directly caused by fisheries.

4. Discussion

It seems obvious after construction of the Floreana rocky reef model that the remarkably high biomasses of fishes, invertebrates, and other organisms on Galápagos rocky reefs is made possible not only by high production of macro-algae and microphytobenthos, but also because these reefs are sinks for oceanic plankton. Or put differently, it is imported food (energy) that allows the high biomass observed in Galápagos. The reefs must capture the primary and secondary production of large oceanic areas as currents continually flow past and around the islands. These large quantities of plankton are captured by high biomasses of filter- and suspension-feeding invertebrates and planktivorous reef fishes creating unusually rapid turnover of diversity and biomass, particularly in areas subjected to continual upwelling (Witman and Smith, 2003).

The importation of large quantities of carbon to rocky reefs through this planktonic–benthic linkage is discussed by Bray et al. (1981) and Bray (1981).
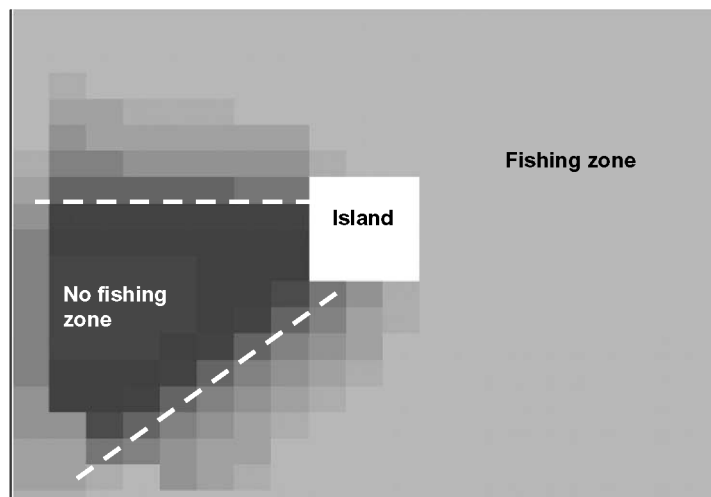
Fig. 5. A simple diagrammatic representation of the potential effects of a fisheries exclusion zone on *pepino* (*S. fuscus*) biomass at the end of a 10-year Ecospace simulation at a hypothetical Galápagos island. Darker areas represent high biomasses and lighter areas represent low biomasses. Catchable emigration of *pepinos* can be seen as dark shading outside the dotted lines that demarcate the boundaries of the hypothetical fisheries exclusion zone. *Pepinos* still decline to a biomass lower than present, but the no-fishing zone prevents the intense fishery from extirpating them.

The necessity for such importation (to support the existing high biomasses on reefs) is, however, made clear only through construction of mass-balance trophic models. One implication of this import is that secondary production and tertiary production are strongly coupled and magnified by oceanographic conditions, as discussed by Menge et al. (1997). Although trophic connections, linkages, and cascades in nearshore rocky subtidal systems can be dampened by physical oceanographic forces (e.g. Kvitek et al., 1998), there is some evidence that biological oceanographic conditions (food inputs) can strengthen trophic connections along rocky shorelines (Polis and Hurd, 1996; Menge et al., 1997; also see Oksanen et al., 1981), just as kelp subsidies can increase competition and secondary production in the rocky intertidal zone (e.g. Bustamante et al., 1995).

The changes predicted by the shark removal simulation (Fig. 3) have presumably already taken place to a much larger extent than the present-day simulation predicts. Sharks might be considerably reduced over Galápagos reefs due to unaccounted shark fisheries since the 1950s and which continue illegally today (Constant, 1993; Camhi, 1995). Indeed, the commercial reef predator groups (including groupers) make up only 1.8% of the present-day Galápagos fisheries catch (present analysis), whereas these fishes were the main target in the past (Reck, 1984; Ruttenberg, 2001). The implication is that recovery of sharks could lead to increases in other reef predators by decreasing the biomass of their respective predators.

Several functional groups in the system are likely to have lower than normal interaction strength than in the present-day system because their biomasses or size distributions (or diets) have been considerably reduced or modified. These now depleted functional groups with reduced biomass potentially include sharks, sea lions (*Z. wollebaeki*), birds, grouper (*Mycteroperca olfax*), large benthic invertebrate-eating fishes (e.g. *Bodianus diplotaenia, Semicossyphus darwini*), pepinos, spiny lobster (*Panulirus gracilis* and *P. penicillatum*), slipper lobster (*Scyllarides astori*) and stony and black corals. The situation of formerly important commercial large groupers (i.e. *Epinephelus mystacinus* and *Epinephelus cifuentesi*; Reck, 1986) is unclear, as they are confined to deeper waters, and their fishery has not been given much attention during the last decade.

Such reductions of species and functional groups can severely modify marine ecosystems (Dayton et al., 1995, 1998), especially because many of the groups removed are from upper trophic levels and have high 'keystone' values (Table 2). Local fisheries are now supported by lower trophic-level species instead of the upper trophic-level species that were preferred in the past (Table 5). Still other species may have become more abundant in response to reductions in biomasses of predators that structure the system. These species with net gain might include planktivorous reef fish (i.e. *gringo, P. colonus*), sea urchins (e.g. *E. thouarsii, T. depressus, L. semituberculatus*) and in some cases anemones (i.e. *Aiptasia* sp.). The central Galápagos rocky reefs appear to be a local example of the global pattern of 'fishing down marine food webs' (Pauly et al., 1998). Even if increases in *pepino* fishing pressure in the Galápagos is driven more by global increases in demand than local depletion of fishes like *bacalao*, the lucrative financial incentives for catching *pepinos* are arguably driven by global changes in coastal species composition (i.e. fishing down the food web) that have lead to increasing markets for holothurians and other low trophic-level organisms. The fishing down effect is however reinforced by the fact that the *bacalao* grouper, a top predator, was in the past the main target for the local and mainland salt-dried market (Reck, 1984); today, two species of planktivorous mullets (*Mugil spp.*) dominate the salt-dried landings (Espinoza et al., 2001).

Many of the changes might be exacerbated indirectly through trophic cascades. For example, Ayling (1981) suggested that the removal of large benthic invertebrate-eating fishes might have led to increases in sea urchin biomass in New Zealand. In the Galápagos, any such increase in densities of the urchin *E. thouarsii* could have contributed to the decline of stony corals and caused other changes in this benthic rocky reef system (Glynn et al., 1979). Wellington (1975) noted that a conspicuous urchin predator, the Mexican hogfish *Bodianus diplotaenia*, has declined locally. Recent data have suggested an increase in urchins and herbivorous fish resulting from the removal of such large predatory fishes during the 1970s (Ruttenberg, 2001). These ecological cascades are indicated even in the present-day shark removal simulation shown in Fig. 4.

Indeed, modifications to the Galápagos marine ecosystem have shaped a present-day marine system that is probably more removed from its pristine state than we tend to think. This puts modeling exercises at a disadvantage when the working model is based on the present-day system, because organisms that might have played a strong structuring role in the past might now have only negligible effects on the system. In the context of modified ecosystems, therefore, the only way to fairly evaluate the potential role of organisms using whole trophic modeling is to construct a past system model (*sensu* Pitcher and Pauly, 1998; Pitcher, 2001; Pitcher et al., 2003). This can be accomplished in relatively short order by using the present-day Floreana rocky reef model as a template, but only if good information about the chosen past system is available. Luckily, some information is available on past abundances of some of the organisms in question throughout the Galápagos Archipelago.

Heavy grazing by sea urchins is known to be the immediate cause of extensive 'barren grounds' where the bottom is dominated by crustose coralline algae and high abundances of urchins (Mann and Breen, 1972). Such an ecological phenomenon resembles a shift to an alternate stability domain (*sensu* Scheffer et al., 2001), though it is perhaps more accurately described as a shift to a non-trivial boundary point (Sutherland, 1974) where one or more species in the system (i.e. predators of sea urchins) are removed. Regardless of how they are categorized, such shifts generally have negative implications for diversity and ecosystem integrity. Similar shifts that are linked to removal of urchin predators are documented worldwide (Estes and Palmisano, 1974; Elner, 1990; Levitan, 1992; Estes and Duggins, 1995; McClanahan et al., 1996; Sala, 1998; Sala et al., 1998). These barren grounds are now a common feature of the seascape of Galápagos reefs (Glynn et al., 1979; Ruttenberg, 2001). In some areas, 'anemone barrens' have begun to appear, in which a single species of anemone (*Aiptasia* sp.) has replaced previously diverse shallow reef habitats (Okey et al., 2004b).

Questions surrounding the genesis of this Galápagos seascape can be explored using a model that features more pristine levels of urchin predators; i.e. lobsters and groupers. For example, why is the *bacalao* grouper indicated to have such low interaction strengths *and* such a low keystone index in the present-day model, particularly when groupers are thought to be strong shapers of reef ecosystems (Hixon and Beets, 1993)? One hypothesis is that their biomass has been considerably reduced. Another is that their size class distribution shifted to smaller individuals and they simply do not interact like the big grouper predators they once were. Both trends might be true (Ruttenberg, 2001), but explicit specification of past information (e.g. from Reck, 1984) could provide insights into this group's past role in shaping the system relative to their current role. It is tempting to suggest that *large bacalao* groupers are size-overfished (Coello and Grimm, 1993) and probably functionally extinct in the Galápagos Archipelago, but more information is needed to evaluate that question.

A 'past system' model will allow assessments of the roles of such strong interacting species, but moreover, it can be used to postulate and explore the trophic cascades and other mechanisms that changed a pristine system to a degraded system. Moreover, this approach can be used to provide potential 'roadmaps' to restoration (Pitcher, 2001), as well as helping to guide the continuing ecological monitoring of the Galápagos Marine Reserve.

Unavoidable uncertainty in the predictions of *pepino* equilibrium catch and biomass in relation to capture rate is a function of the paucity of information on stock–recruitment relationships for *pepinos*, which is probably non-linear. Theoretically, stock–recruitment relationships are implicit in the specified *pepino* production rate (P/B) of 0.6 per year, which is based on information in Pauly et al. (1993a). These authors assumed that total mortality (Z, and thus P/B) of holothurians is approximately twice that of natural mortality (M), like fishes targeted by a fishery. Opitz (1986) used a P/B of 0.29 per year as equivalent to the natural mortality of unfished Caribbean holothurians. One option for pursuing shortcomings in this analysis would be to specify split, but linked, pools for different life stages of *pepinos*. This can be done using Ecopath with Ecosim when enough information becomes available on the early life stages of this species.

The simulation of the effects of a fishery exclusion zone on *pepino* is a simplistic representation of the real dynamics of the system. For example, the exaggeration of the width of the fringing reefs was neces-

sary due to the resolution constraints of the Ecospace grid (e.g. a proportionally narrow band of reef around Galápagos islands could not be simulated with the current version of Ecospace). In the context of the spatial characteristics of these fringing reefs, there is considerable uncertainty with respect to dispersal and effort response effects, as implied above (also see Mangel, 2000). We expect that the resulting exaggerated area of the reef would overestimate the beneficial effects of the fishery exclusion zone, if anything. Size does matter when it comes to protected areas, *pepinos* or no *pepinos* (Walters et al., 1999; Martell et al., 2000; but see Halpern, 2003). Nevertheless, since overall distances across the cell matrix are scaled properly (with reference to Floreana Island), the simulation has at least made it clear that protecting small portions of reef areas (23%) is likely inadequate to prevent further overall declines of *pepino* biomass in the Galápagos Islands without considerable reductions in *pepino* capture rates. At the same time, the simulation indicated that *pepino* biomass increased in the hypothetical fishery exclusion zone, thus preventing extirpation of *pepinos*. This indicates a positive effect of the exclusion zone on the fishery —related to emigration (Walters et al., 1999) and consistent with empirical findings of Roberts et al. (2001)—despite the prediction of an overall catch decline even when implementing fishery exclusion zones. In spite of its simplicity and inherent uncertainties, these simulation results are remarkably similar to a recent empirical evaluation of the effects of a fishery and marine reserves on a closely related sea cucumber (*Parastichopus parvimensis*) in California's Channel Islands (Schroeter et al., 2001).

Our Ecospace simulation is also fully consistent with the conclusions of Allison et al. (1998) that marine reserves are necessary but not sufficient for marine conservation, and especially their conclusion that well intentioned networks of marine reserves must be complemented with strong conservation efforts in the areas *outside* the reserves (also see Murray et al., 1999). A fisheries free-for-all justified by the establishment of a network of reserves is reasonable to expect, and would quite likely prevent achievement of conservation goals.

Finally, we must stress that the present model does not represent some major areas of the archipelago. For example, the biotic communities of the central Galápagos shelf are markedly different from the commu-

nities of the more northern Wolf and Darwin Islands and the western side of Isabela and Fernandina Islands (see Fig. 1). Evidence is mounting that these latter two areas comprise discrete biogeographic zones, though separated by very short geographical distances (Abbott, 1966; Harris, 1969; Glynn and Wellington, 1984; Reck, 1986; Jennings et al., 1994; Bustamante et al., 2000; Wellington et al., 2001; Bustamante et al., 2002). This situation gives rise to several new questions: Should these differences be integrated into one model or should models of each biogeographic zone be constructed? What are the roles oceanographic forces in shaping these biotic communities relative to trophic forces? Such questions will inform the development of our ecosystem research; the results presented here constitute a first step to explore and understand the nature and dynamics of the broader Galápagos marine ecosystems.

Our continuing strategy is to evaluate and refine the Floreana Island rocky reef ecosystem model iteratively in parallel with the ongoing baseline monitoring program. Only by combining such analytical approaches with ongoing empirical field investigations can the usefulness of ecological models be truly evaluated. This adaptive approach will help evaluate the potential effects of human activities and management policies such as the effectiveness of zone-based fisheries and conservation management in the Galápagos Marine Reserve. Examination of the knowledge gaps revealed during model construction has already enabled adaptive refinements to strategies for the continuing monitoring program in the sense that the focus of this program is shifting to less certain aspects of the Galápagos subtidal rocky reef.

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