

Ecosystem structure and processes at Kaloko Honokōhau, focusing on the role of herbivores, including the green sea turtle *Chelonia mydas*, in reef resilience

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ABSTRACT: The formal protection of the Hawaiian green turtle *Chelonia mydas* in the 1970s has led to significant increases in the number of individuals recorded throughout the archipelago. Reduced growth rates and poor body condition of individuals at a number of foraging sites, including Kaloko-Honokōhau National Historical Park (Kaloko), suggest that some aggregations have reached carrying capacity. To better understand the ecological structure and processes of the reef system at the park, we developed an ecosystem model that synthesized available data on Kaloko for the year 2005 and included 26 groups, spanning the entire trophic web. Model results showed that the combined grazing pressure of the different herbivore functional groups (i.e. reef fish, sea urchins, and green turtles) in Kaloko matched total algal production. Sea urchins exerted the strongest control over algal resources, partly because of their large biomass in park waters. Results confirmed that the Kaloko green turtle aggregation has reached carrying capacity. Green turtles help maintain low algal cover, and thus resilience of reefs in the face of disturbance, and should be explicitly included in studies of ecosystem dynamics on reefs. Our work also provides a 'current-condition' baseline for Kaloko, and a valuable tool for the assessment of the future marine ecosystem impacts of projected urban expansion plans around the park.

KEY WORDS: Marine turtles · Ecosystem-based management · Ecopath · Coral reef · Herbivory · Phase shift · Nutrient enrichment · Kona coast · Hawaii

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INTRODUCTION

Grazing by herbivores is one of the major processes structuring benthic coral reef communities. Studies highlighting the role of herbivores in promoting reef resilience and recovery to coral-dominated states,

where disturbance has led to increased algal biomass (e.g. Bellwood et al. 2004), have focused almost exclusively on fish and sea urchins (Hay 1984a, Carreiro-Silva & McClanahan 2001, Mumby et al. 2006a, Paddack et al. 2006, Albert et al. 2008). Numerous Caribbean reefs have transitioned from

coral to algal-dominated states (Gardner et al. 2003) following either a dramatic reduction in fish stocks that limited the distribution, abundance, and production of algae (Ogden & Lobel 1978, Hay 1981, Lewis 1986), or the region-wide loss to disease of an important echinoid herbivore (*Diadema antillarum*) in systems that had previously seen a shift from fish-dominated to echinoid-dominated herbivory (Lessios 1988, Mumby et al. 2006b). At some locations, increased anthropogenic nutrient loading has further increased the abundance of primary producers (Burkepile & Hay 2006, Littler & Littler 2007). Few studies have looked at the role of green sea turtles *Chelonia mydas* in maintaining coral reef resilience. This is understandable in the Caribbean where green turtles mostly forage on seagrass (Bjorndal 1980, Mortimer 1981, Thayer et al. 1984) and thus predominantly have an indirect impact on the trophodynamics of reef ecosystems (Valentine et al. 2002, Heck & Valentine 2006, Wabnitz 2010).

In Hawai'i, situated in the North Pacific, although the majority of reefs are not as severely impacted as those throughout the Caribbean region (Brainard et al. 2002, Waddell & Clarke 2008), several locations have shown increasing signs of stress as a result of mounting anthropogenic pressures on the coastal zone through development and runoff, tourism and recreation activities, and overfishing (Grigg 1994, Hunter & Evans 1995, Friedlander et al. 2008, Williams et al. 2008). Unlike in the Caribbean region, green turtles in Hawai'i feed primarily on algal species that commonly occur on the reef (McCutcheon et al. 2003, McDermid et al. 2007, Arthur & Balazs 2008, Russell & Balazs 2009). They may therefore play a direct role in maintaining the resilience of reef ecosystems. The fact that green turtles feed on non-native algae, *Acanthophora* spp. and *Hypnea* spp. (Doty 1961, Russell 1992, Russell & Balazs 1994, Arthur & Balazs 2008, Russell & Balazs 2009), further highlights their contribution to the promotion of reef resilience.

Since turtle harvesting ended in the late 1970s (Witzell 1994), an approximately linear increase in the abundance of nesting females has occurred at French Frigate Shoals (Balazs & Chaloupka 2004a, 2006), which accounts for >90% of all nesting within the Hawaiian Archipelago (Balazs 1980). This increase in abundance is interpreted as a recovery trend because the Hawaiian nesting population has been continuously monitored using dependable methodology for several decades (Balazs & Chaloupka 2004a, Chaloupka et al. 2008) and is considered 'self-contained' (Dutton et al. 2008). Population trends at a number of foraging grounds that also have been subject to long-term monitoring seem to mirror this trajectory (Chaloupka & Balazs 2007).

An understanding of the ecological role of green turtles as grazers on reefs requires a process-oriented approach that assesses, preferably quantitatively, the relative contributions of all herbivore functional groups (i.e. fish, sea urchins, and green turtles). Such an approach is currently lacking, though it may provide significant insights into the need for, and consequences of, improved turtle conservation and management.

Ecological modeling has developed ways to mathematically describe the complexity and non-linear behavior of ecological systems. Ecopath with Ecosim is a freely available, widely used software for describing the structure of ecosystems and their food webs. It was recently named as one of the 10 major scientific breakthroughs in the 200 yr history of the US National Oceanographic and Atmospheric Administration (NOAA; see <http://celebrating200years.noaa.gov/breakthroughs/welcome.html>). Rather than providing outputs at the population level of biological organization, typical of many models, the Ecopath with Ecosim approach provides outputs at the ecosystem level, reflecting food-web linkages, energy cycling, and changes in biomass of each species group defined in the model (Christensen 2008). Although determining carrying capacity of a system has been highlighted as one of the uses of this software, few studies have explored this aspect through the use of Ecopath with Ecosim (but see Christensen & Pauly 1998).

We developed an Ecopath trophic model to investigate the role that green turtles play in the coral reef ecosystem of Kaloko-Honokōhau National Historical Park (Kaloko). Located on the west coast of Hawai'i Island (the 'Big Island'; Fig. 1), the park supports a healthy and relatively diverse coral habitat with little evidence of non-native species of macroalgae or diseased coral (Gibbs et al. 2007). It has low fish biomass, but high fish diversity (Parrish et al. 1990, Beets et al. 2010). The park also has a resident foraging population of immature green turtles that has been the subject of a mark-recapture study by the NOAA National Marine Fisheries Service and the US National Park Service since 1999. Three lines of evidence suggest that this foraging population has reached carrying capacity: (1) The significant increase in green turtle abundance throughout the archipelago over the last 10 to 20 yr has been associated with a significant decrease in somatic growth rates at many foraging grounds around the Main Hawaiian Islands, including the west coast of the Big Island (Balazs & Chaloupka 2004b), possibly the result of density dependence (Bjorndal et al. 2000); (2) Field measurements of body volume and mass as an index of body condition have shown that turtles at foraging locations near Kaloko have lower body condition indices than green turtles at other sites

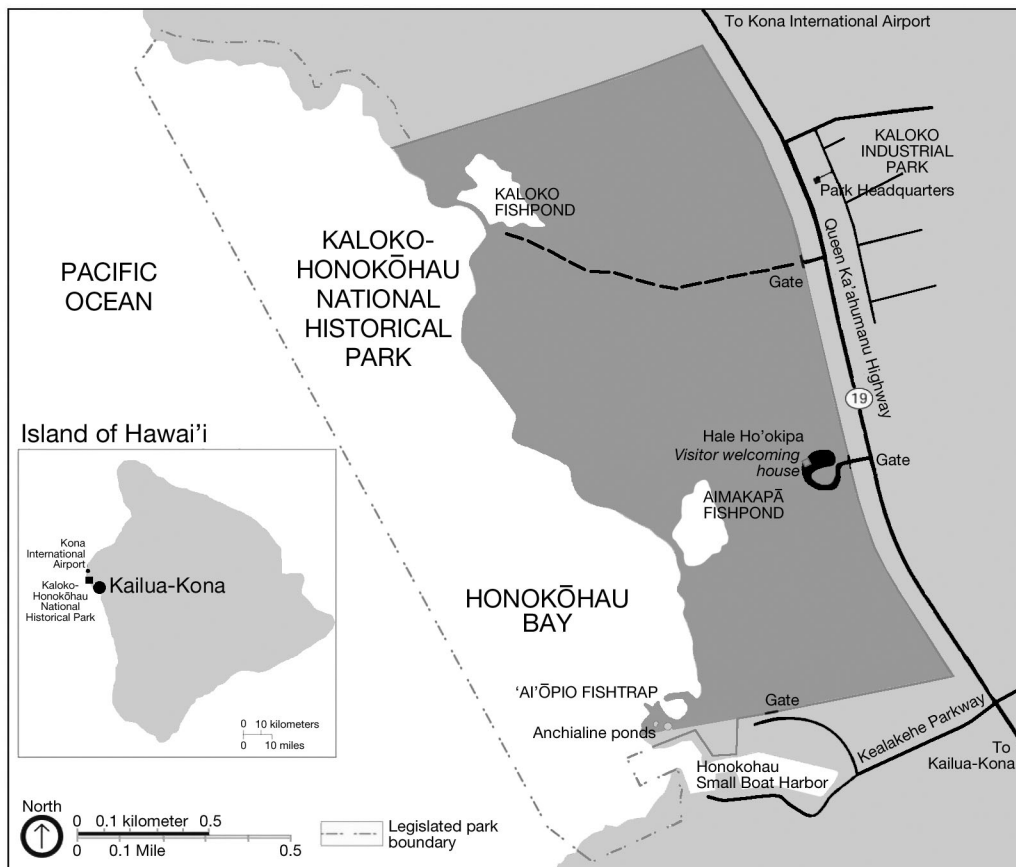


Fig. 1. Kaloko-Honokōhau National Historical Park (Kaloko), located on the west coast of the Big Island, Hawai'i, USA

on the Island of Hawai'i (Kubis et al. 2008); and (3) Recent necropsy reports cite emaciation as a probable contributor in the death of a number of green turtles found stranded at foraging locations along the west coast of the Hawai'i Island (or Kona Coast) (Work 2007, 2008a,b).

The trophic model is also intended as a 'baseline' of ecosystem state for Kaloko prior to major developments projected for areas around the park. Concern has been expressed over the future health of Kaloko's coastal resources given proposed plans for the development of lands adjacent to the south boundary of the park, including a 300% expansion of a small-boat harbor, and construction of hotels, condominiums, and a light industrial park (Gibbs et al. 2007). Expected impacts include a reduction in groundwater flow, an important feature at Kaloko, with a concomitant increase in groundwater loads of sediment, nutrient, and chemical pollutants (Oki et al. 1999, Paytan et al. 2006, Johnson et al. 2008).

The goals of this study were therefore 3-fold: (1) To develop an ecosystem model of the marine portion of the park, synthesizing available data and describing the ecological structure and processes of the reef sys-

tem at Kaloko; (2) To ascertain whether Kaloko green turtles are at carrying capacity, by determining whether grazing by green turtles and other reef herbivores matches overall algal production; (3) To provide the management community with a tool that can simulate the effects of increased urban development in the Kaloko area, as well as compare the outcomes of a range of potential management scenarios.

MATERIALS AND METHODS

Study area. Kaloko-Honokōhau National Historical Park was established in 1978 and spans 5.17 km², of which 2.48 km² is marine (Gibbs et al. 2007). The park is bordered to the south by the Honokōhau Small-Boat Harbor, and there are large scale industrial/commercial developments to the east. The terrestrial portion includes more than 180 anchialine (brackish) pools, 2 large ponds and wetlands modified for fish production by early Hawaiians, and a fish trap (Kaloko, 'Aimagapā and 'Ai'ōpio respectively; Fig. 1). The coastal waters and reefs of Kaloko are within the West Hawai'i Fisheries Management Area and are currently

managed by the State of Hawai'i. The legislated park boundary extends offshore for about 1000 m at the widest point and to maximum depths of ca. 70 m (Parish et al. 1990). Past this boundary the seabed drops off to depths >180 m. Approximately 73% of the marine section of the park is hardbottom. The remaining 27% comprises unconsolidated sediment and artificial/historical features. Most of the hardbottom area has 10 to <50% coral cover, and ca. 12% has 50 to 100% coral cover (Gibbs et al. 2007). Benthic habitats are considered relatively healthy, with no signs of diseased corals or non-native algal species (Marrack et al. 2009, Weijerman et al. 2009). Low sedimentation rates and the presence of relatively high coral cover in protected locations suggest that currently, the reef habitat in Kaloko is primarily controlled by natural wave-induced stresses (DeVerse 2006).

Modeling approach. We used Ecopath with Ecosim (EwE), software version 5.1.208 (Christensen & Walters 2004, Christensen et al. 2005, www.ecopath.org). The Ecopath component of any EwE model provides a quantitative representation of an ecosystem for a defined time period. In other words, it is a snapshot of the resources in an ecosystem and their interactions, represented by trophically linked mass-balanced biomass 'pools' (Polovina 1984, Christensen & Pauly 1992). The biomass pools, hereafter referred to as functional groups, consist of a single species, or species groups representing ecological guilds. The idea behind the mass-balance approach is that 'at any time within the system, and within the elements of that system, the amounts of matter that flow in must balance the amount that goes out plus the change in biomass' (Pauly & Christensen 2002 p. 215). Ecopath therefore operates under 2 main assumptions:

(1) That biological production within a functional group equals the sum of mortalities (i.e. on an annual basis, biomass and energy in an ecosystem are conserved; Walters et al. 1997, Walters & Martell 2004). This relationship can be expressed as follows:

$$B_i \cdot (P/B)_i = \sum_{j=1} B_j \cdot (Q/B)_j \cdot DC_{ji} + Y_i + E_i + BA_i + B_i \cdot (P/B)_i \cdot (1 - EE_i) \quad (1)$$

where B_i and B_j are biomasses of prey (i) and predator (j), respectively; $(P/B)_i$ is the production to biomass ratio, equivalent to total mortality (Z) under most circumstances (Allen 1971); $(Q/B)_j$ is the food consumption per unit biomass of (j); DC_{ji} is the fraction of prey (i) in the average diet of predator (j); Y_i is the total fishery catch rate of group (i); E_i is the net migration rate (emigration – immigration); BA_i is the biomass accumulation rate of group (i); and EE_i is the ecotrophic efficiency, defined as the fraction of production that is consumed within the system or is removed by fishers; and

(2) That consumption within a group equals the sum of production, respiration, and unassimilated foods. This relationship can be expressed as follows:

$$B \cdot (Q/B) = B \cdot (P/B) + (1 - GS) \cdot Q - (1 - TM) \cdot P + B \cdot (Q/B) \cdot GS \quad (2)$$

where GS is the proportion of unassimilated food, and TM is the trophic mode expressing the degree of heterotrophy of groups represented within the system, with 0 representing autotrophs, 1 heterotrophs, and intermediate values facultative consumers.

Ecopath then uses a set of algorithms to simultaneously solve n linear equations of the form in Eq. (1), where n is the number of functional groups. For each functional group, 3 of the basic parameters: B_i , $(P/B)_i$, $(Q/B)_i$ or EE_i must be known, in addition to the fisheries yield (Y_i), and the diet composition. Units of the model are expressed in $t \text{ km}^{-2} \text{ yr}^{-1}$ wet weight for flows and $t \text{ km}^{-2}$ wet weight for biomasses. Production per unit biomass (P/B) and consumption per unit biomass (Q/B) have the dimension yr^{-1} . For a review of EwE's capabilities and limitations see Christensen & Walters (2004), Plaganyi & Butterworth (2004), and Plaganyi (2007).

To balance the model, changes were first made to the diet matrix, as diet compositions represent only snapshots of the feeding habits of individual species and are likely to be relatively variable based on location and time periods of data collection. The model required only minor adjustments and was considered balanced when: (1) The model produced realistic ecotrophic efficiencies ($EE < 1$); (2) Values of the production to consumption ratio (P/Q) for functional groups were between 0.05 and 0.35, with the exception of groups with fast growth rates (higher ratios), and top predators (lower values) (Christensen et al. 2005).

Model parameters and functional groups. The model represented an annual average situation of ecosystem conditions in the marine portion only (i.e. to the exclusion of the anchialine pools, fish ponds, and fish traps) of Kaloko in 2005. We defined a total of 26 functional groups, 8 of which were fish, spanning the main trophic components of the ecosystem (including detritus; Table 1, Fig. 2). The 8 fish groups represented the aggregation, based on ecological and biological similarities (e.g. diet, size, habitat, mortality), of 106 fish species recorded during underwater visual census studies (Beets et al. 2010; see Table S1 in the supplement at www.int-res.com/articles/suppl/m420p027_supp.pdf).

Biomass estimates for individual species were based on values from field studies, local expert opinion, or from the literature. For species with data reported only from selected habitats, biomass values were extrapolated to the entire park by calculating an area-

Table 1. Trophic parameters for all functional groups of the balanced Kaloko model. Model outputs are presented in **bold**. *B*: biomass; *TL*: trophic level; *P/B*: productivity to biomass ratio; *Q/B*: consumption rate; *EE*: ecotrophic efficiency; *P/Q*: production to consumption ratio or gross efficiency; *P/R*: production to respiration ratio; MIF: mobile invertebrate feeders; SIF: sessile invertebrate feeders; Zoo: zooplanktivorous species; CCA: crustose coralline algae; turf_{LB}: turf algae growing on the nearshore lava bench

Group name	<i>TL</i>	<i>B</i> (t km ⁻²)	<i>P/B</i> (yr ⁻¹)	<i>Q/B</i> (yr ⁻¹)	<i>EE</i>	<i>P/Q</i>	<i>P/R</i>	Catch (t km ⁻² yr ⁻¹)
1 Spinner dolphins	3.21	2.7400	0.151	11.519	0.007	0.013	0.017	–
2 Monk seals	3.89	0.1790	0.121	11.508	0.033	0.011	0.013	–
3 Sea birds	3.17	0.0024	0.127	76.515	0.012	0.002	0.002	–
4 Rays	3.15	4.2330	0.200	3.100	0.002	0.065	0.065	–
5 Sharks and jacks	3.53	0.0700	1.058	5.100	0.453	0.207	0.350	0.030
6 Hawksbill sea turtles	3.18	0.0540	0.100	3.500	0.066	0.029	0.029	–
7 Green sea turtles	2.00	1.5910	0.109	6.764	0.039	0.016	0.021	–
8 Reef fishes - piscivores	3.39	1.7295	0.615	6.121	0.527	0.100	0.144	0.003
9 Reef fishes - herbivores	2.02	20.3350	1.400	27.149	0.205	0.052	0.069	0.162
10 Reef fishes - corallivores	2.60	0.5417	2.100	12.918	0.547	0.163	0.255	–
11 Reef fishes - detritivores	2.00	2.2598	1.900	32.272	0.282	0.059	0.079	0.018
12 Reef fishes - MIF	3.13	9.7610	0.950	8.108	0.394	0.117	0.172	0.130
13 Reef fishes - SIF	2.84	0.5440	1.700	9.581	0.224	0.177	0.285	–
14 Reef fishes - Zoo	2.85	3.0460	1.450	13.378	0.585	0.108	0.157	0.004
15 Urchins	2.00	280.0000	0.484	8.547	0.056	0.057	0.076	–
16 Crown of thorns	2.59	0.1170	0.411	9.000	0.007	0.046	0.061	–
17 Benthic invertebrates	2.18	42.5381	2.910	15.250	0.950	0.191	0.313	–
18 Corals	1.58	130.0000	0.140	2.100	0.594	0.067	0.075	–
19 Octocoral	2.07	2.9000	0.200	4.630	0.484	0.043	0.054	–
20 Macroalgae	1.00	22.6910	9.824	–	0.925	–	–	–
21 CCA	1.00	37.8180	1.770	–	0.358	–	–	–
22 Turf algae	1.00	128.7800	19.000	–	0.942	–	–	–
23 Turf _{LB}	1.00	3.0650	25.000	–	0.921	–	–	–
24 Zooplankton	2.02	1.2400	219.000	949.000	0.979	0.231	0.625	–
25 Phytoplankton	1.00	3.2900	325.458	–	0.984	–	–	–
26 Detritus	1.00	100.0000	–	–	0.694	–	–	–

weighted biomass for each species relative to the proportion that each benthic habitat category covered within park waters (the latter based on Gibbs et al. 2007). For instances where *P/B* was equal to only natural mortality (*M*), estimates were taken directly from the literature, or derived using the empirical formula of Pauly (1980). For exploited species, fishing mortality values were based on Friedlander & Parrish (1997) (see below). Where possible, the consumption rate for each functional group was obtained through field studies; otherwise it was estimated from empirical equations such as those available in FishBase (www.fishbase.org) for all finfish. The diet matrix was constructed using data from field studies in Hawai'i, preferentially the west coast of the Big Island. Where no such data were available, the matrix was complemented with information obtained from the literature for the same species in similar ecosystems. Details of data sources and estimation methods for all parameters are given in Table S2 in the supplement.

Fisheries. Kaloko's waters were designated as a Fish Replenishment Area on 31 December 1999, effectively banning the harvest of live reef fish for the aquarium trade, in response to declines of species targeted by

collectors (Tissot et al. 2004). Biomass of targeted species may have responded to the closure, and because fishing pressure for ornamentals has been removed, *P/B* was set to *M* for all formerly collected species.

The park is a popular location for subsistence fishing and shoreline gathering, traditional activities that are permitted as long as they are consistent with state law and park mandates (i.e. with legal fishing gear for personal consumption; DeVerse 2006). Harvesting is done primarily from shore using several methods, such as throw nets, spear, and pole and line fishing. Gill, or 'lay' netting, a serious threat to marine resources including marine mammals and sea turtles, was restricted within park waters in August 2005 to locally constructed, handmade nets of natural fibers. The State of Hawai'i does not have recreational and subsistence permitting or reporting requirements (Friedlander & Parrish 1997), despite surveys in the late 1980s indicating that 19 to 35% of residents fish (Smith 1993), and recent studies concluding that these fisheries dominate the catch of coral reef species (Zeller et al. 2005, Williams et al. 2008). Although several studies conducted throughout the Hawaiian Archipelago have assessed the importance of fishing impacts on coral reef

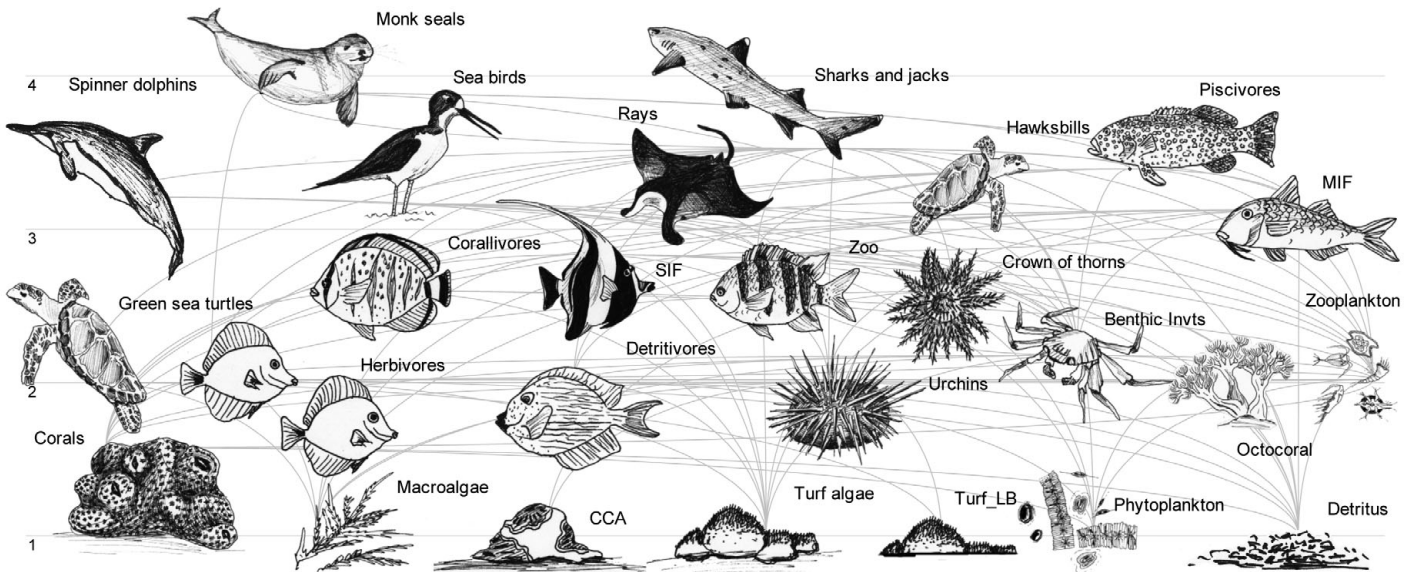


Fig. 2. Trophic flows within the Kaloko reef ecosystem. Each functional group is identified here by an illustration (© M. Bailey); where relevant, an image of a species representative of its guild is depicted. Images are not drawn to scale or proportional to the group's biomass. The light grey horizontal lines and associated numbers represent trophic levels; lines connecting individual functional groups represent trophic links. Zoo: zooplanktivorous reef fish; MIF: mobile invertebrate feeding reef fish; SIF: sessile invertebrate feeding reef fish; Turf_{LB}: turf algae growing on the nearshore lava bench; CCA: crustose coralline algae; Benthic Invts: benthic invertebrates

fish assemblages (e.g. Tissot et al. 2004, 2009, Williams et al. 2008, the Hawai'i Division of Aquatic Resources (DAR) unpubl. data in Weijerman et al. 2009), few data exist to quantify fishing mortality along the western shores of the Big Island. In the absence of catch or effort data specific to Kaloko, we assumed catch data to standing stock proportions in the park to be comparable to those in Hanalei Bay, Kauai (Friedlander & Parrish 1997), and adjusted values to reflect species known to be targeted at Kaloko. As no data were available on macroinvertebrates in Kaloko (with the exception of sea urchins), nor information regarding whether fishing occurs on those groups in the park, no catch was allocated to the 'benthic invertebrates' functional group.

We divided existing fisheries into 2 'fleets,' one targeting 'sharks and jacks' specifically, and a recreational/subsistence fishery representing fishers operating mainly from shore, and targeting small reef fish. We calculated the ratio of catch to standing stock for fish families targeted by fishers from Friedlander & Parrish (1997), and doubled them, given that fishing pressure is likely to be higher now than it was in 1997 (DAR unpubl. data in Weijerman et al. 2009). We then applied these indices to fish families harvested in Kaloko (E. Brown unpubl. data). For species groups targeted in Kaloko, but for which data were not available from Friedlander & Parrish (1997), we applied the same value as for fish families in the same functional group. Fishing mortality for individual species/

functional groups was calculated using $F = \text{catch}/\text{biomass}$.

Model analysis, indices, and uncertainty around input data. We quantified total trophic flows within the ecosystem in terms of consumption, production, respiration, exports and imports, and flow to detritus ($\text{t km}^{-2} \text{yr}^{-1}$). We then used ecological indices as obtained through ecological network analysis (ENA) to evaluate the food web (Wulff et al. 1989, Christensen & Pauly 1993). ENA is a modeling technique used for understanding the structure and flow of material between components of an ecosystem (Ulanowicz 1997). As integrated in Ecopath, ENA allows for the calculation of ecosystem macro-descriptors that quantify trophic structure, organic matter recycling, and ecosystem size and organization. These descriptors include total system throughput, ascendancy, development capacity, and the relative overhead. Throughput describes the size of a system and represents a measure of its metabolism (Christensen & Pauly 1993). Ascendancy integrates both size and organization of a given system (Christensen 1995). The development capacity (C) quantifies the upper limit to ascendancy, whereas the system's overhead (O) is complementary to the ascendancy and measures the level of 'redundancy' of particular links (Heymans 2003). The relative overhead (O/C ratio) was proposed by Heymans (2003) as an index of the resilience of the system (i.e. an index of the system's ability to withstand disturbance; Ulanowicz 1997). ENA further

allows the derivation of transfer efficiencies (TE), summarizing the proportion of consumption that is passed up a food web. The TE is the ratio between the production of a given trophic level and the preceding trophic level (Pauly & Christensen 1995). Finally, we ran the mixed trophic impact (MTI), or ecological input-output, analysis (Ulanowicz & Puccia 1990), which describes how any functional group impacts, directly and indirectly (i.e. both predatory and competitive interactions), all other functional groups within the food network. In other words, this analysis provides a first-order quantification of the beneficial and negative impacts of one functional group on another (scaled between -1 and 1). The MTI for living groups is calculated by constructing an $n \times n$ matrix, where the interaction between the impacting group (j) and the impacted group (i) is represented as follows (Christensen & Walters 2004):

$$MTI_{ji} = DC_{ji} - FC_{ij} \quad (3)$$

where DC_{ji} , as in Eq. (1) above, is the diet composition term expressing how much (i) contributes to the diet of predator (j), and FC_{ij} is a host composition term giving the proportion of the predation on (i) that is due to (j). For detritus groups, the DC_{ji} term in Eq. (3) above is set to 0.

Any ecosystem model realization requires acknowledging the large amount of data required in its development, and the difficulty in quantifying the flows between the food web's individual functional groups. Functional group dynamics can be verified by fitting model data to actual population trends over time. Such time series data do not exist for Kaloko. To address model uncertainties, probability distributions for all Ecopath input parameters were entered through the 'pedigree' (Funtowicz & Ravetz 1990) function of Ecopath (Pauly et al. 2000). Using a Monte Carlo re-sampling routine, the 'Ecoranger' module of Ecopath draws random input variables from within the confidence intervals defined for each parameter type in the pedigree tables and uses these as prior probability distributions for all input data. This approach leads to a large number of model realizations that are evaluated for their conformity to user-defined criteria as well as physiological and mass-balance constraints. The results include probability distributions for the estimated parameters along with distributions of parameters in the accepted model realizations. This routine can be run for the model overall, as pedigrees are associated with all input parameters. However, given our primary goal to determine whether green turtles are at carrying capacity at Kaloko we focused on sources of uncertainty associated with: estimates of green turtle biomass, P/B , and Q/B ; the proportion of sea urchins' diet that was derived from turf algae growing on the nearshore lava bench ($turf_{LB}$); and variability associated with $turf_{LB}$ biomass and P/B .

RESULTS

Trophic parameters and the diet matrix for the 26 groups of the final balanced Ecopath model for Kaloko are presented in Tables 1 & 2. Trophic flows between all functional groups are depicted in Fig. 2. Sea urchins (*Tripneustes gratilla*, *Echinometra mathaei*, *Heterocentrotus mammilatus*, and *Echinothrix* spp.) accounted for the largest proportion of total living biomass in the system (40%). Green turtles and reef fish groups, including 'sharks and jacks,' only represented 0.2 and 5.5% of total biomass, respectively. Reef fish functional groups were dominated by herbivorous and mobile invertebrate feeding species. Not surprisingly, consumption by sea urchins had the biggest impact (45%) on available resources at Kaloko, whereas fish accounted for 14.4% and green turtles for 0.2% of total consumption. Total fisheries catches represented less than 1% of total fish biomass (Table 1). Sharks and jacks were caught in larger quantities compared with their relatively low biomass in the assemblage. Mean trophic level of the total fisheries catch was 2.59 (Table 3).

Ecotrophic efficiency (EE) values (the proportion of a functional group's production used within the system) were lowest for some of the highest trophic levels, including 'spinner dolphins,' 'monk seals,' and 'sea birds,' as well as 'crown of thorns starfish,' 'hawksbill turtles,' 'green turtles,' 'sea urchins,' and 'corals' (Table 1). For the first 3 groups, this valuation is due to these species deriving a significant proportion of their food from outside park waters. They were included chiefly to ensure that the model was representative of the system at Kaloko (i.e. to acknowledge that these species occur in the park, and may at some point in the future suffer from indirect effects of park development, even if they do not feed exclusively or primarily in park waters). For the 5 other groups, the low EE values are a result of low predation and fishing pressure being exerted on these species. Fish groups, overall, also had relatively low EE values, with higher values registered by those species pools that were subject to higher fishing mortality. This valuation suggests that the system generates a reasonable amount of surplus secondary production. Indeed, the largest component of the mortality coefficients within the system was due to predation mortalities, with the exception of 'sharks and jacks,' for which the fishing mortality rate was greater than predation mortality. In contrast, most of the production by the macro- and turf algal groups, 'zooplankton,' 'benthic invertebrates,' and 'phytoplankton' was accounted for through consumption by other trophic groups within the model ($EE > 90\%$). In other words, sea urchins, herbivorous fish, and green turtles maintained all algae at Kaloko in a cropped state.

Table 2. Diet composition matrix for the functional groups in the balanced model for Kaloko. Groups 8 through 14 refer to reef fish as detailed in Table 1. 'Import' refers to food derived from outside of the modeled area. MIF: mobile invertebrate feeders; SIF: sessile invertebrate feeders; Zoo: zooplanktivorous fishes; invert.: invertebrates; CCA: crustose coralline algae; Turf_{I,B}: turf algae growing on the nearshore lava bench. For detailed information that was used to construct the diet matrix, see Table S2 in the supplement at www.int-res.com/articles/suppl/m420p027_supp.pdf. Numbers above columns correspond to numbers in the first column

Prey	Predator																							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	24				
1. Spinner dolphins	-	-	-	-	0.008	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
2. Monk seals	-	-	-	-	0.002	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
3. Sea birds	-	-	-	-	<0.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
4. Rays	-	-	-	-	0.005	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
5. Sharks and jacks	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
6. Hawkbills	-	-	-	-	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
7. Green sea turtles	-	-	-	-	0.019	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
8. Piscivores	-	0.200	-	-	0.110	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-			
9. Herbivores	-	0.050	-	-	0.206	-	-	0.400	-	-	0.010	-	-	-	-	-	<0.001	-	-	-	-			
10. Corallivores	-	-	-	-	0.040	-	-	0.050	-	-	0.001	-	-	-	-	-	-	-	-	-	-			
11. Detritivores	-	-	-	-	0.085	-	-	0.100	-	-	<0.001	-	-	-	-	-	<0.001	-	-	-	-			
12. MIF	-	0.080	-	-	0.120	-	-	0.200	-	-	0.010	-	0.010	-	-	-	-	-	-	-	-			
13. SIF	-	-	-	-	0.062	-	-	0.010	-	-	0.001	-	-	-	-	-	-	-	-	-	-			
14. Zoo	0.010	-	0.010	-	0.051	-	-	0.100	-	-	0.010	-	0.009	-	-	-	<0.001	-	-	-	-			
15. Urchins	-	-	-	0.050	0.010	-	-	-	-	-	0.085	0.032	-	-	-	-	-	-	-	-	-			
16. Crown of thorns	-	-	-	-	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-			
17. Benthic invert.	0.190	0.107	0.578	0.500	0.070	0.894	-	0.129	0.004	0.074	-	0.814	0.420	0.100	-	-	0.046	-	-	-	-			
18. Corals	-	-	-	-	-	0.001	-	-	0.001	0.865	-	0.005	0.450	-	<0.001	0.961	<0.001	-	-	-	-			
19. Octocoral	-	-	-	-	-	-	-	-	-	-	-	-	0.025	-	-	0.038	<0.001	-	-	-	-			
20. Macroalgae	-	-	-	-	-	<0.001	0.001	-	0.050	-	0.001	0.001	0.001	0.001	0.070	-	0.017	-	-	-	-			
21. CCA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.010	0.001	-	-	-	-	-			
22. Turf algae	-	-	0.010	-	-	-	-	-	0.782	0.050	0.300	0.032	0.050	0.050	0.745	-	0.098	-	-	-	-			
23. Turf _{I,B}	-	-	-	-	-	-	0.998	-	-	-	-	-	-	-	0.025	-	-	-	-	-	-			
24. Zooplankton	-	-	0.001	0.050	0.050	0.005	0.001	0.001	0.013	0.011	-	0.030	0.023	0.316	-	-	0.120	0.500	0.350	0.020	-			
25. Phytoplankton	-	-	0.001	-	-	-	-	-	-	-	0.005	-	-	0.050	-	-	0.120	0.100	0.380	0.800	-			
26. Detritus	-	0.001	-	-	0.005	-	-	-	0.150	-	0.695	0.001	-	0.014	0.150	-	0.598	0.330	0.250	0.175	-			
Import	0.800	0.563	0.399	0.400	0.145	0.100	-	-	-	-	-	-	-	0.450	-	-	-	0.070	0.020	0.005	-			

Table 3. Summary of outputs from the ecological network analysis (ENA)

Sum of all consumption	5332.03	t km ⁻² yr ⁻¹
Sum of all exports	520.07	t km ⁻² yr ⁻¹
Sum of all respiratory flows	3477.31	t km ⁻² yr ⁻¹
Sum of all flows into detritus	1700.15	t km ⁻² yr ⁻¹
Total system throughput	11030.00	t km ⁻² yr ⁻¹
Calculated total net primary production	3895.09	t km ⁻² yr ⁻¹
Total primary production/total respiration	1.12	
Total biomass (excluding detritus)	699.53	t km ⁻²
Total catches	0.35	t km ⁻² yr ⁻¹
Mean trophic level of the catch	2.59	
Throughput cycled (excluding detritus)	54.52	t km ⁻² yr ⁻¹
Finn's cycling index	6.13	% of total throughput
Ascendency	31.50	%
Relative overhead (O/C)	68.50	%

Reef-building corals, octocorals, benthic invertebrates, and zooplanktivorous fish were the main predators of zooplankton, while zooplankton consumed most of the phytoplankton production in the system. Benthic invertebrates were preyed upon mostly by MIF reef fish and species within the benthic invertebrate group itself.

Throughput (total flows) values for each functional group highlighted the importance of turf algae, zooplankton, phytoplankton, and sea urchins in system structure. The high *EEs* attained for all algal groups indicated that the system was at carrying capacity with respect to grazing, including for green turtles. The pri-

mary producers' high *EEs* were also reflected in the low production/respiration ratio of 1.12 for the system overall (Table 3).

Focusing on green turtles, urchins, and herbivorous reef fish in the system only, the MTI routine highlighted the resource competition both within and among all 3 groups (Fig. 3). Sea urchins were responsible for the largest among-group effect, impacting negatively on both herbivorous reef fish and green turtles, and overall had the largest impact on algal and detrital resources (not shown). Given green turtles' feeding preference on turf_{LB}, they were the

group most impacted by changes in turf_{LB} (Fig. 3).

When accounting for the uncertainty around parameters affecting consumption of turf_{LB}, *EE* values of turf_{LB} in successfully balanced model runs ranged between 0.416 and 0.998.

The mean *TE* in the ecosystem as a whole was 4.6%, with a value of 4.5% for flows originating from primary producers and 4.7% from the detritus. This low efficiency was due to consumption dominating total system throughput for the lower trophic levels, whereas respiration and flow to detritus dominated the higher trophic levels in the model (Fig. 4). This result is to be expected in a system with low biomass

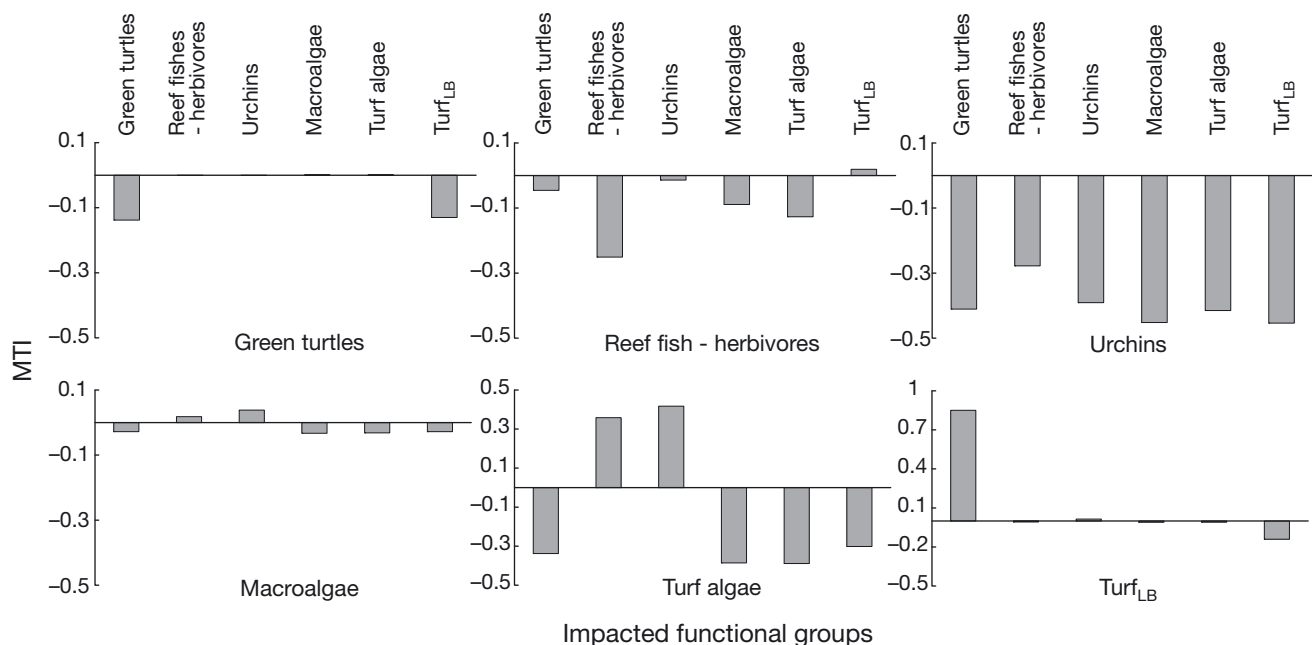


Fig. 3. Mixed trophic impact (MTI) analysis for all herbivores at Kaloko. Impacts of increases in the biomass of a particular group (impacting) on another (impacted), resulting in an increase in the latter's biomass, are recorded as a positive on the y-axis. Impacts resulting in a decline of the impacted group are recorded as a negative value. Group names along the upper x-axis represent the impacted groups. The impacting group is indicated below individual graphs

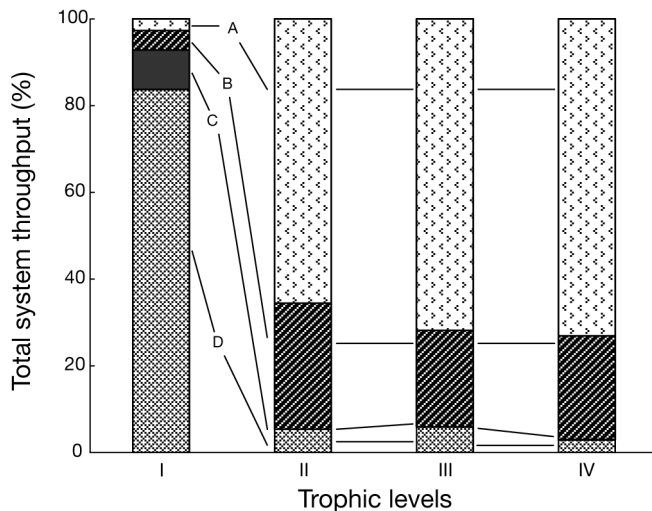


Fig. 4. Fate of total system throughput (A: respiration, B: flow to detritus, C: export, D: consumption by predator) in percentage-per-integer trophic level

at the highest trophic levels. Some upper trophic level species, such as trevally (also locally known as 'ulua' or 'jacks'), are highly vagile. As a consequence, although not being heavily fished for in park waters, their abundance may still be depressed due to high fishing pressure along the remainder of the Kona Coast. Ascendancy was 31.5% of capacity and relative overhead was 68.5% (Table 3), 46% of which was attributable to internal flows, indicating that the system contains a number of 'redundant' trophic linkages. These observations are consistent with a system exhibiting relatively high resilience to perturbation with respect to energy flows, or a high system stability sensu Odum (1971).

Net primary productivity was $3895 \text{ t km}^{-2} \text{ yr}^{-1}$ and was accompanied by a high flow to the detritus pool (Table 3). Turf algae (including turf_{LB}) and phytoplankton accounted for 57 and 24% of total production in the system, or 65 and 27% of total primary production, respectively. Sea urchins (38%) were the major contributor to the detrital pool, followed by zooplankton (28%), while the combined fish groups (mainly herbivores) contributed 11% of all flows to the detritus. The ratio between primary production and respiration (PP/R) indicates that the system was at a low developmental stage sensu Odum (1969, 1971). This finding was corroborated by the low Finn's cycling index, showing that only a small fraction of the throughput (including detritus) was recycled (6%; Table 3). The proportion of flows originating from the detritus was 0.27%.

The overall pedigree (i.e. 'quality') index of the model (0.539) was high in comparison to 50 other models for which pedigree values ranged between 0.164 and 0.676 (Morissette 2007).

DISCUSSION

Description of the Kaloko reef system

Quantitative descriptions of the flux of matter and energy can provide significant insights into the fundamental structure of ecosystems. The Kaloko system is dominated by primary production (PP), 27% of which is contributed by phytoplankton and 65% by algal turfs, which is slightly lower than other published estimates for primary producers in tropical systems (e.g. Wanders 1976, Adey & Steneck 1985, Adey & Goertemiller 1987). The trophic networks at Kaloko were dominated by grazing, with herbivores accounting for 43% of all living biomass within the system, of which 93% was sea urchins. This grazer dominance was further highlighted by the high EEs achieved for the main PP functional groups, including phytoplankton. Results from rapid assessment surveys throughout the State confirm that sea urchins in particular, and herbivorous fish, are common on reefs in Hawai'i (Rodgers et al. 2004). In contrast, relatively low EEs of higher trophic level functional groups indicate that the foraging activities of herbivores are not limited by predation pressure, as demonstrated by our analysis of total system throughput (Fig. 4). Indeed, few predators commonly occur in the park, and fewer still have been observed feeding in the park. Therefore, as highlighted by the model's average TE of 4.6%, much lower than the mean of 10% obtained for various other ecosystems (Christensen & Pauly 1993), only a small proportion of production is being transferred up the food chain. Comparison between 2 sets of underwater visual census data (E. Brown & National Park Service unpubl. data) showed a 5-fold increase in piscivore biomass between 2005 and 2007. This inter-annual difference may have been due to real differences between the 2 datasets, possibly reflecting the restrictions on gillnetting in park waters implemented in August 2005. Differences in species biomass and composition may also reflect either variability in survey accuracy for species displaying vagile (e.g. *Caranx melampygus*) or cryptic behavior (e.g. *Gymnothorax flavimarginatus*, *G. meleagris*, *Cephalopholis argus*), or seasonal changes (Friedlander & Parrish 1998, Vitousek et al. 2009), as the 2005 and 2007 datasets were collected in April and October, respectively. Future surveys should therefore focus on good intra-annual coverage to represent seasonal variation.

Phytoplankton and zooplankton had some of the highest EEs . The waters around Hawai'i are generally oligotrophic (Bienfang et al. 2009), and consequently low biomass of phytoplankton and zooplankton is to be expected. Reef environments along the Kona coast are close to the deep slope of the Pacific and subject to

strong wave action and currents along the shore (Presto et al. 2007). Therefore, we assumed that zooplanktivores on the reef derive a substantial portion of their diet from open-ocean plankton. We further assumed that ocean plankton contributes to the energy intake of benthic invertebrates and other functional groups that feed on plankton. Experiments should be conducted to ascertain the proportion of ocean plankton in the diet of reef organisms at Kaloko, or other similar systems in Hawai'i.

At 42.54 t km^{-2} , the model's benthic invertebrate (excluding sea urchins) biomass was similar to estimates provided for models in Raja Ampat, Indonesia (51.68 t km^{-2} ; Ainsworth et al. 2007), and the Great Barrier Reef, Australia (61.41 t km^{-2} ; Tudman 2001), but substantially lower than estimates for barrier reefs and fringing reefs in Moorea, French Polynesia (198.26 and 322.8 t km^{-2} respectively; Arias-González 1994, Arias-González et al. 1997). Few studies have investigated the composition of benthic invertebrates on reefs, yet they are an important prey for certain groups of reef fish (e.g. Hobson 1974) and can represent an important fishery (Friedlander & Parrish 1997). Given that benthic invertebrates accounted for 6% of total system biomass, species composition and their relative contribution to total group biomass of the benthic invertebrate community of Kaloko should be determined.

Sea urchin densities at Kaloko (ca. 5 ind. m^{-2} for *Echinometra mathaei* and $<1 \text{ ind. m}^{-2}$ for all other species) were comparable to sea urchin densities recorded on reefs throughout the State of Hawai'i (Rodgers et al. 2004) and similar to, or lower than, those reported from other reef locations, e.g. 5 to 6.8 ind. m^{-2} (chiefly *E. mathaei* and *Tripneustes gratilla*) at La Réunion (Naim et al. 1997) and 2 to 4 ind. m^{-2} (*Echinometra*) in Fiji (Appana & Vuki 2006). Current sea urchin densities at Kaloko are also comparable to those recorded in the 1970s (Ebert 1971). These similarities suggest that high sea urchin densities are natural and do not represent a release from predation pressure due to increased fishing pressure in the last 30 yr, as noted at a number of locations along the coast of Kenya (Muthiga & McClanahan 1987, McClanahan 1998).

Turtles at carrying capacity

Green turtles are at carrying capacity at Kaloko based on (1) their biomass estimates and consumption rates, (2) estimates of turf_{LB} as well as the primary production rates of these algae, and (3) the high degree to which sea urchins feed on the green turtles' main food resource. Balanced model outputs under Ecoranger, taking into account the uncertainty surrounding these

input parameters, showed that the *EE* of turf_{LB} could range between 0.416 and 0.998. Specifically, it reflects the wide range in published biomass and mass-specific productivity rates for turf algae. For example, biomass was found to vary between 230 g m^{-2} (T. Sauvage pers. comm.) and 600 g m^{-2} (Smith et al. 2001) in Hawai'i alone, 78 g m^{-2} in the Solomon Islands (Albert et al. 2008), and 850 g m^{-2} in the Caribbean (Bruggemann et al. 1994). Even greater ranges in productivity have been recorded for the different algal groups that constitute 'turf,' particularly in relation to depth and seasonal cycles (Payri 2000). An evaluation of algal turf productivity and consumption rates by green turtles at Kaloko would help refine the estimates presented here.

Results from the MTI analysis highlighted the strong competition for the same resource between sea urchins, herbivorous reef fish, and green turtles. Grazing pressure exerted by herbivorous fish does not occur uniformly on a reef. Grazing may be reduced in places where reef structure affords little refuge from predation (Lewis 1986). However, this may not be a significant factor at Kaloko where overall predation pressure is limited due to the low abundance of piscivores. Foraging efficiency may also be reduced on shallower portions of the reef due to relative high wave intensity and potential exposure of animals when water levels are low. We therefore assumed that fish at Kaloko graze chiefly on reef turf algae rather than on turf_{LB} specifically (Table 2). Recent evidence from the South Pacific demonstrates that few of the fish species previously classified as 'herbivores' are indeed exclusively herbivorous (Choat et al. 2002, Cvitanovic et al. 2007). Many appear to predominantly feed on detritus, only incidentally removing turf from the reef in the process (Crossman et al. 2001, 2005). Data on the extent of algae removed but not consumed are needed to correct our current assumption that all algal material removed by herbivorous fish was ingested. MTI results reflected resource competition between turtles and fish primarily for macroalgae, which appeared 'magnified' as macroalgae biomass overall in the park is low. As sea urchins occur in the shallows (M. Weijerman pers. comm., L. Marrack pers. comm.), probably emerging at night to feed (Mills et al. 2000, Vaitilingon et al. 2003), a small proportion of turf_{LB} was included in the echinoids' diet matrix (Table 2). Quantification in the field of this overlap and the extent to which relative densities among the 3 herbivore functional groups may change with time would help refine carrying capacity estimates for green turtles. Clarification of the extent to which sea urchins feed on turf_{LB} also has implications for their role in maintaining low algal biomass levels in the face of increased nutrient input associated with urban development activities around the park (see below).

Observations that Kaloko green turtles appear unusually 'skinny' (Kubis et al. 2008) and exhibit low growth rates (Balazs & Chaloupka 2004b) compared with turtles at a number of other Hawaiian foraging grounds support input parameters within the range used in our model (Table 1). A key difference between individual foraging sites that may help explain variations in observed growth rates is that green turtles at Kaloko forage on turf, the dominant algal group on the central Kona Coast, whereas other foraging grounds throughout the Hawaiian Archipelago have macroalgae available as forage (Arthur & Balazs 2008). Until recently, turtles tagged at Kaloko were rarely found outside of park waters, and therefore it is unlikely they were obtaining food from outside the modeled area. However, new observations have indicated a behavioral shift in the green turtles' foraging patterns. Fewer individuals are utilizing the shallow reef area in the summer months than they did prior to ca. 2006 (S. Beavers unpubl. data). More human interactions, resulting from recent increases in visitors to the park, may be partly responsible for this change in behavior (S. Beavers unpubl. data). Greater turtle movement possibly away from Kaloko further strengthens the case for carrying capacity having been reached at the park because of limited available forage.

Turf algae growing on the lava bench close to shore and in the intertidal area were included in the model as a separate functional group, as resident green turtles at Kaloko have been seen to concentrate their grazing on this portion of the park. Such focused foraging behavior may occur for 3 reasons:

(1) By focusing their feeding activities on shallow portions of the reef, individuals exert less effort foraging, as the lava bench supports a highly productive algal mat that can grow unrestricted by space competition with live coral. Were turtles to forage on deeper sections of the reef, for a similar intake of algae, animals would have to roam over wider areas and pick algae from in and around coral heads, resulting in greater energy expenditure. More energy would also have to be expended by animals in having to come to the surface to breathe. Our results, corroborated by local observations of turf algae throughout the park being closely cropped (F. Parrish pers. comm.), indicated that the system was also close to carrying capacity for overall turf algae, making foraging by green turtles in deeper reef sections even less energy efficient. 'True' carrying capacity of turf algae on the reef may actually be realized at lower *EE* values, because where turf algae are laden with sediment, much of the algae may not be available to grazers.

(2) Green turtles may prefer to forage on the lava bench because of the protection afforded by the shallows against predation by tiger sharks. Sharks are

regularly sighted at Kaloko (e.g. see www.state.hi.us/dlnr/Chairpio/HtmlNR/01-46.htm and <http://starbulletin.com/2005/07/01/news/index5.html>), and a log of necropsies performed on turtles at Kaloko indicates that shark attacks were responsible for the death of 4 turtles since 1992 (obviously, attacks that resulted in the complete ingestion of turtles by sharks cannot be monitored; G. Balazs unpublished data). Thus, the distribution of turtles, and the algae they consume, may be affected by differential vulnerability of green turtles to shark predation in different habitats (Heithaus et al. 2002, 2006). Nutritionally profitable microhabitats at Kaloko also appear to be low risk from a predation perspective.

(3) The repeatedly grazed turf_{LB} may be more palatable to green turtles than algae growing on deeper sections of the reef. The area where turtles tend to aggregate to feed is located close to 'Ai'ōpio fish trap, an area of considerable groundwater discharge (Johnson et al. 2008). As groundwater is the only conduit for nutrients into the coastal zone, the nutritional content of algae in this specific location may be significantly different from algae on the remainder of the reef.

Potential threats and impacts on natural resources due to urban development

On many coral reefs near human population centers, benthic community composition has shifted from coral-dominated to macroalgae-dominated (Hughes 1994, Hunter & Evans 1995, McClanahan & Mangi 2001). These shifts, often termed 'phase shifts' (Done 1992), have been attributed to increased anthropogenic nutrient input (e.g. Lapointe 1997) and/or to reductions in the abundance of herbivores (e.g. Hay 1984b). Studies investigating changes in grazing intensity at sites that have undergone such phase shifts (e.g. Kāne'ohe Bay, Hawai'i), have focused primarily on the role of herbivorous reef fish, and to a lesser extent small, often invertebrate, herbivores (Cheroske et al. 2000) and sea urchins (Hunter & Evans 1995, Stimson et al. 2001, Smith et al. 2008). As our results clearly demonstrate, future studies need to explicitly consider green turtles because of their important role as herbivores. Their consumption of non-native algae, including *Gracilaria salicornia* (Russell & Balazs 2009), abundant at a number of locations across Hawai'i, including Kāne'ohe Bay, further highlights their role in promoting reef resilience.

Ongoing and planned urban development activities, and associated population growth, around Kaloko will likely have significant and diverse impacts on the condition of nearby reefs. Expected impacts include, but are not restricted to: (1) A reduction in groundwater

discharge quality (i.e. increased nutrient loading), which could lead to increased macroalgal growth and the subsequent deterioration in the health of corals (e.g. Fabricius 2005, Smith & Smith 2006), particularly if combined with a reduction in the urchin population; and (2) An increase in fishing pressure and a resulting decrease in the herbivorous fish population, which could lead to an increase in the abundance of macroalgae (Stimson et al. 2001, Williams et al. 2007). Based on our findings, some key points emerge that should be taken into account if dynamic simulations of various 'impact scenarios' are run in the future.

Increased nutrient input and higher fishing pressure may lead to an increase in the proportion of macroalgal cover at Kaloko and potential forage for resident herbivores. In 2008, the NPS initiated a long-term marine water quality monitoring program (quarterly sampling), which includes optical chlorophyll sampling. Additionally, plans are underway through a partnership between the NPS and the US Geological Survey to use stable isotope tracers to identify sources of nutrient inputs to park groundwater. The NPS, in partnership with the University of Hawai'i at Hilo, recently also initiated a pilot fisheries harvest monitoring program to identify and quantify fishing pressure within the park; this should be a long-term initiative. Nutrient levels and fisheries' catch time series in conjunction with regular monitoring of algal cover within the different habitats at Kaloko, and the Ecopath model developed herein, may help to determine the impacts of such changes at the ecosystem level. Based on our model, we would expect the following responses to 2 scenarios:

(1) Increased nutrient delivery to the reef system without changes in fishing pressure. Under conditions of nutrient enrichment and intense herbivory, algal productivity may be high while biomass remains low (Hatcher & Larkum 1983). Our results demonstrate that current rates of herbivory, sea urchins, fish, and green turtles maintain all algal groups closely cropped and may therefore be able to consume increases in algal production. This grazing disturbance in turn limits the establishment of macroalgae (Lewis 1986, Williams et al. 2001, Paddack et al. 2006), implying that the current system is relatively resilient to change (as indicated by Kaloko's O/C ratio). Indeed, it is the synergy of these 3 herbivorous functional groups that makes Kaloko an interesting case study. The 'redundancy' in herbivory at Kaloko stands in contrast to areas of the Caribbean, where sea urchin biomass remains low 20 yr after the region-wide loss of the key echinoid herbivore to disease (Mumby et al. 2006b), and where, due to high fishing pressure, the ability of herbivorous fish to maintain a high proportion of reef area free of macroalgae may be limited. Some evidence suggests that even

robust herbivorous reef fish populations may be capable of maintaining only 50 to 65 % of the substratum in a cropped state (Williams et al. 2001). Although herbivorous fish may be capable of increasing their grazing rates and/or population sizes in response to higher algal production, evidence for this in the published literature is limited (McClanahan et al. 1999, Williams et al. 2001, Garpe et al. 2006). Moreover, herbivorous reef fish, with the exception of *Naso* spp. (Choat et al. 2002), all prefer turf algae over other algal resources, and frequently avoid macroalgae (Bellwood & Choat 1990, Bruggemann et al. 1994). Green turtles and sea urchins, on the other hand, commonly feed on macroalgae, highlighting their respective roles in maintaining reef resilience (Nystrom 2006).

(2) Increased nutrient delivery to the reef system with increase in fishing pressure. Herbivorous fish and sea urchins play different and complementary roles in maintaining low algal cover on reefs in the face of disturbance (e.g. Morrison 1988). Under a scenario of higher fishing pressure, model parameterization indicates that sea urchin abundance may increase as a direct response to more abundant forage on the reef and reduced predation pressure due to harvesting of the urchins' predators. Sea urchins, when abundant, can have a considerable impact on benthic ecology. Healthy populations of sea urchins have been associated with reductions in macroalgal cover and increased coral recruitment (Edmunds & Carpenter 2001, Carpenter & Edmunds 2006). Typically, sea urchins will consume a greater diversity of algae than herbivorous reef fish and, as such, they will be more effective than the latter at controlling algal growth in the event of increased nutrient levels. Alternatively, as some species of echinoids can remove a large amount of calcium carbonate while foraging (Hutchings 1986, Carreiro-Silva & McClanahan 2001), an overabundance of sea urchins can lead to rapid erosion of the reef framework (McClanahan & Kurtis 1991, Bak 1994, Mapstone et al. 2007). For example, *Echinothrix diadema* and *Echinometra mathaei* typically erode 20 % of the calcium carbonate accreted (Carreiro-Silva & McClanahan 2001). However, the relative contributions of grazing and bioerosion are species-dependent. *Tripneustes gratilla* predominantly browses on macroalgae, suggesting that this species would have less of an impact on the reef framework (Mills et al. 2000).

Currently, sea urchin densities are greatest in the shallows, while reef fish dominate grazing processes at depth (F. Parrish & M. Weijermann pers. comm.). Higher fishing pressure may reduce fish grazing intensity on deeper reef sections. In response to reduced predation, competition, and increased forage availability, sea urchins could increase in abundance at greater depths. Similarly, green turtles may also displace some of their foraging activities to deeper reef areas to take

advantage of increased algal biomass (i.e. profitable, high-risk microhabitat sensu Heithaus et al. 2007). Increases in algal biomass would further be exacerbated if mixing carries nutrients to those deeper sections of reef.

CONCLUSIONS

Our model evaluates the trophic linkages and flows on a Hawaiian near-shore reef. Our study is unique in its detailed analysis of herbivory levels and its focus on the role of herbivores to determine whether a given functional group, in this instance green turtles, is at carrying capacity. Integration of additional quantitative field data on biomass, distribution, consumption rates, and diet selection of the 3 herbivore functional groups would clarify the proportion and type of algae consumed by sea urchins and green turtles versus herbivorous fish on a Hawaiian reef and further elucidate their respective roles in, and contribution to, reef resilience (Nystrom & Folke 2001, Bellwood et al. 2004).

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