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Linking Coral Reef Health and Human Welfare

A dissertation submitted in partial satisfaction of the  
requirements for the degree Doctor of Philosophy

in

Marine Biology

by

Sheila Marie Walsh

Committee in charge:

Professor Nancy Knowlton, Chair

Professor Jeremy Jackson, Co-Chair

Professor Richard Carson

Professor Theodore Groves

Professor Jennifer Smith

2009

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University of California, San Diego

2009

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Chapter 3 is currently being prepared for submission for publication as: Walsh, S.M. & Groves, T. “How and Why Alternative Incomes Fail to Reduce Fishing and Improve Human Welfare.” The dissertation author was the primary investigator and author of this paper.

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- Carilli, J.E., Norris, R.D., Black, B., **Walsh, S.M.**, & McField, M.D. (2009) Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. *Global Change Biology*. (DOI: 10.1111/j.1365-2486.2009.02043.x)
- Carilli, J.E., Norris, R.D., Black, B.A., **Walsh, S.M.**, & McField, M.D. (2009) Local stressors reduce coral resilience to bleaching. *PLoS ONE*, **4**, e6324. (DOI:10.1371/journal.pone.0006324)
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- Walsh, S.** (2000) Visualizing our environment: an exploration of the communication of environmental issues through visual arts. *Dreams and Inward Journeys* (eds J. Ford & M. Ford), pp. 562-567. Longman Publishing Group, New York.

### **Fields of Study**

Ecology  
Environmental Economics  
Development Economics

# **ABSTRACT OF THE DISSERTATION**

Linking Coral Reef Health and Human Welfare

by

Sheila Marie Walsh

Doctor of Philosophy in Marine Biology

University of California, San Diego, 2009

Professor Nancy Knowlton, Chair

Professor Jeremy Jackson, Co-Chair

Globally, ~700 million people depend on coral reef goods and services. However, over half of coral reefs are threatened due to global warming, fishing, and nutrient pollution. Using ecological and economic methods, I evaluated 1) the ecosystem-scale effects of fishing and nutrients, 2) the effects of fishing on condition and reproduction in a reef fish community, and 3) an integrated conservation and development program (ICDP). The Republic of Kiribati, Central Pacific, provided two natural experiments for this research.

A population re-settlement program and island-wake upwelling on Kiritimati Island created orthogonal gradients in fishing and nutrient inputs. Fishing sequentially down trophic levels and size-classes had an in-direct effect on the reef community because of the loss of herbivores. Herbivorous fish controlled algal overgrowth of

corals in the presence of nutrients and herbivory was enhanced under high nutrient conditions due to a shift in the algal community composition. Fishing also had individual level effects on the fish community. Under low fishing conditions (high predation conditions), prey fish species from five trophic groups (predator, benthic invertivores, planktivores, omnivores, and herbivores) had poor condition. Poor was only associated with higher reproductive effort when food resources were limiting. These results suggest that managing fishing should be prioritized.

The Government of Kiribati subsidized copra, coconut agriculture, in order to reduce fishing and improving welfare. Households had perverse and varying responses to the policy. Households that enjoyed fishing increased fishing effort. Households with little benefit from additional cash goods reduced copra effort. In aggregate, fishing labor increased 33%. Although welfare improved or was unchanged for the majority of households, future welfare losses are expected due to declines in coral reef health.

Four conclusions emerge from this research. First, there is no evidence for trophic cascades; fishing top predators will not benefit corals. Second, preferred fishing grounds, in upwelling zones or near pollution sources, may be more vulnerable to the effects of overfishing. Restoring top predators may have positive consequences for fisheries productivity by increasing prey fish reproductive effort. Lastly, fishing is not just a job. ICDPs that subsidize alternative incomes may actually be subsidizing overfishing.

# **CHAPTER 1: Ecosystem-scale Effects of Fishing and Nutrients on Coral Reefs**

## SUMMARY

1. Nutrients and fishing are the primary local causes of coral reef decline but their relative effects are poorly understood because they are typically confounded and large scale experiments are not feasible. Ecosystem-based management, however, requires information on 1) how these factors affect all ecosystem components, 2) how fishing is linked to macroalgal abundance, and 3) whether top-down control of macroalgae persists at large spatial scales.
2. Ecological surveys of the fish and benthic communities and household surveys of fishing activity were conducted on Kiritimati, Kiribati, where island-wake upwelling and a population re-settlement program create a natural experiment to test the effects of fishing and nutrients.
3. Fishing explained over 20% of the variance in top predator and carnivore biomass while nutrients explained very little (<4%). The converse was true for cover of crustose coralline algae (nutrients, 40%; fishing, 0%) and turf (nutrients, 34%; fishing, 3%). Macroalgal cover, however, was explained by both fishing (10%) and nutrients (27%).
4. The mixed gear fishery (hook & line, 50% of trips; gillnets, 26% of trips) caused an exponential decline in top predators and large-bodied fish ( $\geq 20$  cm). Herbivore and small bodied-fish biomass was mostly unaffected by fishing and then declined once top predator and large-bodied fishes biomass was low. Small-bodied fishes, however, showed some evidence of prey release.

**5.** In contrast to theoretical predictions, herbivores and nutrients had unexpected interactive effects on macroalgal cover at large spatial scales. Herbivores decreased the effect of nutrients and the effect of herbivores was greater under high nutrient conditions.

**6. *Synthesis and Applications*** Preferred coral reef fishing grounds may be more vulnerable because they are often near sources of pollution or upwelling. Protecting or restoring fisheries for top predators may mitigate the effects of nutrients because top predators effectively protect herbivores from fishing. Intact herbivore populations are critical to coral reef health because they can control macroalgae despite nutrient enrichment and are more effective grazers under high nutrient conditions.



## INTRODUCTION

Fishing (Jennings *et al.* 1995; Friedlander & DeMartini 2002; Pandolfi *et al.* 2003; Dulvy *et al.* 2004a; Newman *et al.* 2006; Newton *et al.* 2007; Sandin *et al.* 2008) and nutrient enrichment (Lapointe 1997; Bruno *et al.* 2003) or both (Sammarco 1982; McCook 1999; Smith *et al.* 2001; Lapointe *et al.* 2004; Burkepile & Hay 2006) are the most important local causes of coral reef decline. It is impossible, however, to evaluate local fishing and nutrient policies because these factors are almost always confounded and large-scale experiments are infeasible. Results from theoretical and small-scale experimental studies (typically  $<1 \text{ m}^2$ , four from 50 to 250  $\text{m}^2$  (Burkepile & Hay 2006)) suggest prioritizing management of herbivore populations because herbivores can control the effect of nutrients on macroalgae and nutrients alone are not sufficient to cause a phase shift from coral to macroalgal dominance (McCook 1999; Burkepile & Hay 2006; Crépin 2007). In order to apply these results to ecosystem-based management, information is needed on 1) how fishing and nutrients affect all ecosystem components, 2) how fishing (rather than fish exclosures) is linked to macroalgal abundance, and 3) whether top-down control of macroalgae persists at large spatial scales.

A population re-settlement program and island-wake upwelling on Kiritimati, Kiribati, (Fig. 1-1) creates a unique large-scale natural experiment. Kiritimati was permanently settled less than 150 years ago but re-settlement of people from the capital, Tarawa (~3,000 km to the west), has caused rapid population growth (66% increase from 1985 to 2005) (Asian Development Bank 2002). Island-wake upwelling

creates a zone of higher nutrients and primary production on the northwestern side of the island (Chaput, Modlin, Rydz & Budzynkiewicz, unpublished) (see Figs. A1-1 & A1-2 in Appendix). Fishing and nutrients are not confounded, however, because settlement has mostly occurred along the northern coastline and nutrient pollution is low due to low rainfall, no industrial activities, and a relatively low human population (Sandin *et al.* 2008). Birds are not thought to contribute to this trend in nutrients because they are less abundant near villages (Ane Ioran, pers. comm.). Recent studies of the reefs in the upwelling zone show that the water chemistry was more characteristic of nearshore reefs and had higher concentrations of microbes, which were associated with coral disease and fewer coral recruits (Dinsdale *et al.* 2008). These reefs also had fewer top predators and corals and more planktivores and benthic algae compared to nearby unfished reefs in less productive waters in the northern Line Islands (Sandin *et al.* 2008). The relative importance of fishing and nutrients is still uncertain, however, because these factors are confounded across the northern Line Islands.

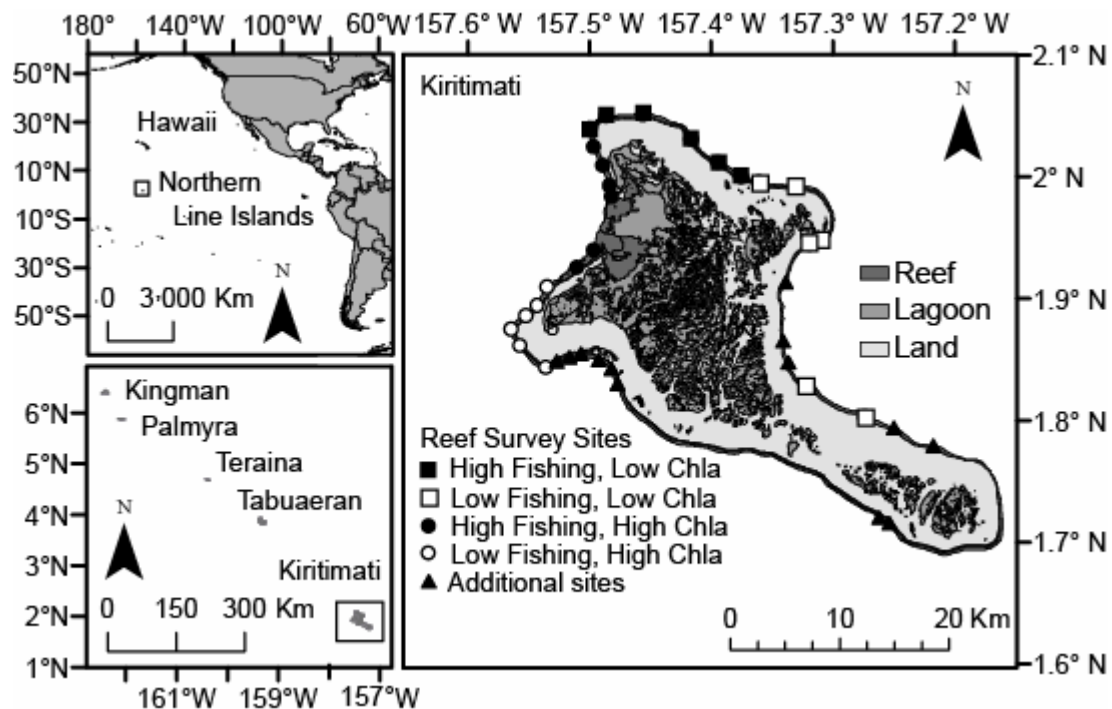


Figure 1-1. Ecological survey sites on Kiritimati, Line Islands, Republic of Kiribati. Twenty four sites were chosen to create a balanced natural factorial experimental design to test the effect of nutrients (proxied by chlorophyll a) and fishing on major ecosystem components. An additional 13 sites were chosen to capture the full fishing gradient and test mechanisms.

### Ecosystem-scale Effects

Studies of reefs in different nutrient regimes and across fishing gradients provide insight into how these factors may independently affect whole reef systems across large spatial scales, while theoretical research provides insights into their interactions at this scale. Reefs influenced by moderate upwelling and river run-off have higher abundance of benthic algae (Kinsey & Davies 1979) and phytoplankton, which supports greater herbivore (Birkeland 1987) and planktivore (Birkeland 1988) populations, respectively. Corals are still common but growth rates (Kinsey & Davies

1979) and recruitment may be lower due to competition with benthic algae (Birkeland 1977). Reefs that have been polluted by sewage have been shown to resemble reefs under naturally high nutrient conditions (Smith *et al.* 1981), suggesting that studying natural variation in nutrients may help predict responses to nutrient pollution.

Unfished reefs support fish biomass orders of magnitude greater than most reefs, with top predators accounting for more than half of the fish biomass. (Friedlander & DeMartini 2002; Newman *et al.* 2006; Stevenson *et al.* 2007; Sandin *et al.* 2008). Large-bodied herbivores are also abundant (Friedlander & DeMartini 2002; Sandin *et al.* 2008), which may explain the high abundance of reef-builders and low abundance of benthic algae (Sandin *et al.* 2008). On fished reefs, total fish biomass is much lower and dominated by small prey fishes (Friedlander & DeMartini 2002; Dulvy *et al.* 2004b; Newman *et al.* 2006; Sandin *et al.* 2008). Benthic cover is highly variable with macroalgae commonly dominating open spaces (Newman *et al.* 2006), likely due to a loss of top-down control from herbivores.

### **Linking Fishing to Macroalgal Abundance**

Controversy remains over whether reducing fishing through the creation of marine reserves will restore herbivores if top predators are also protected (Mumby *et al.* 2006). One hypothesis is that fishing removes top predators, releasing herbivores and reducing algal abundance through a trophic cascade (McClanahan *et al.* 1994; McClanahan 1997; Mumby *et al.* 2006). There is limited evidence for trophic cascades on coral reefs probably because trophic linkages are diverse, some herbivores escape

in size from predation, and many important herbivores, such as parrotfish, have similar life histories and hence vulnerability to fishing as top predators (Sandin *et al.* 2009). Alternatively, fishing may first remove large, slow growing, late maturing fish and sequentially remove less vulnerable species (Jennings *et al.* 1999). In fisheries where life history traits correspond well to specific trophic groups, this results in “fishing down the food chain” from top predators to carnivores to herbivores (Pauly *et al.* 1998), which may increase algal abundance. Evidence of a transition from gillnets (non-selective) to spearguns (selective) to handlines (selective for predators/carnivores only) from fisheries across a gradient of socio-economic development (Cinner *et al.* 2009) suggests that more developed fisheries are more likely to cause a trophic cascade, while a fishery with a diversity of gear types may mask the effects of a trophic cascade by fishing simultaneously or sequentially down the food chain or size classes.

### **Persistence of Top-down Control at Large Spatial Scales**

The relative importance of managing herbivore populations versus nutrients depends on whether herbivores exhibit top-down control at large spatial scales. Using simple Lotka-Volterra models of nutrients, autotrophs, and consumers, Gruner *et al.* (2008) predicted that top-down control (positive interactive effects) would only occur when herbivory increases proportionally with nutrient-induced increases in autotroph density. When herbivory is constant, only additive effects will occur. Constant herbivory is more likely when nutrient enrichment occurs at a large spatial scale (due

to increased resource heterogeneity and decreased edge effects) and when predators limit herbivore abundance or grazing (Gruner *et al.* 2008). Gruner *et al.* (2008), however, found no association between the spatial scale and effect size of herbivores across 191 manipulative experiments ( $<1$  to  $\sim 400 \text{ m}^2$ ). In contrast, in a fishing gradient study, Dulvy *et al.* (2002) found that predation risk structures communities at large spatial scales (4-180 km), while algal biomass structures communities at small spatial scales (0.5-10 km).

In sum, I expect that reefs with higher nutrients will have higher abundance of benthic algae, herbivores, and planktivores, while fished reefs will have lower abundance of top predators and carnivores (Table 1-1). A fishery with mixed gear types will fish down the food chain and size classes, only impacting herbivores and small-bodied fish when top predators or large-bodied fishes are not abundant (Table 1-1). Fishing of herbivores will only additively affect macroalgae. I tested my expectations for the effects of nutrients and fishing using a natural factorial experimental design (Fig. 1-1), replicating and expanding on small-scale manipulative experiments in scale and number of ecosystem components. I then tested the linkages between fishing and macroalgal abundance and the persistence of top-down control at large spatial scales using orthogonal gradients in herbivores and nutrients. These tests allowed for interpretation of the effects of fishing and nutrients in the context of ecosystem-based management.

Table 1-1. Hypotheses for Independent Effects of Nutrients and Fishing. This table shows the predicted response of fish and benthic functional groups to nutrients and fishing. Fishing may affect the fish and benthic community through four mechanisms: 1) trophic/size class cascades (TC), 2) size class cascades (SC), 3) fishing down the food chain (FDFC), and 4) fishing down the size classes (FDSS). Positive responses are indicated by +, negative responses by -, and ambiguous responses by +/- . No response is NR. Not applicable is NA. Predictions for responses to FDFC and FDSS are separated by low and high fishing pressure to distinguish between responses due to sequential fishing from high to low trophic levels or large to small-bodied fishes.

Dependent	Nutrients	TC	SC	Fishing			
				FDFC		FDSS	
				Low	High	Low	High
<i>Fish Community</i>							
Top Predators	+	-	NA	-	-	-	-
Carnivores	+	-	NA	-	-	-/+	-
Planktivores	+	+	NA	NR	-	-/+	-
Herbivores	+	+	NA	NR	-	-/+	-
Large-bodied	+	NA	-	NA	NA	-	-
Small-bodied	+	NA	+	NA	NA	NR	-
<i>Benthic Community</i>							
Coral	-	+	+/-	NR	-	-/+	-
CCA	-	+	+/-	NR	-	-/+	-
Turf	+	-	+/-	NR	+	-/+	+
Macroalgae	+	-	+/-	NR	+	-/+	+

## METHODS

### Study Area

I surveyed the benthic and fish community at 37 sites in the fore reef habitat (Fig. 1-1) from July 20 to August 10, 2007. Of these, 24 were chosen based on preliminary knowledge of upwelling and the location of human settlements to create a balanced factorial design. An additional 13 sites were chosen to capture the full fishing gradient. Sites were no less than 1 km apart with exact locations chosen

haphazardly. The south central coast was inaccessible due to a lack of roads. Data on chlorophyll a and fishing were estimated for each site (Fig. 1-2).

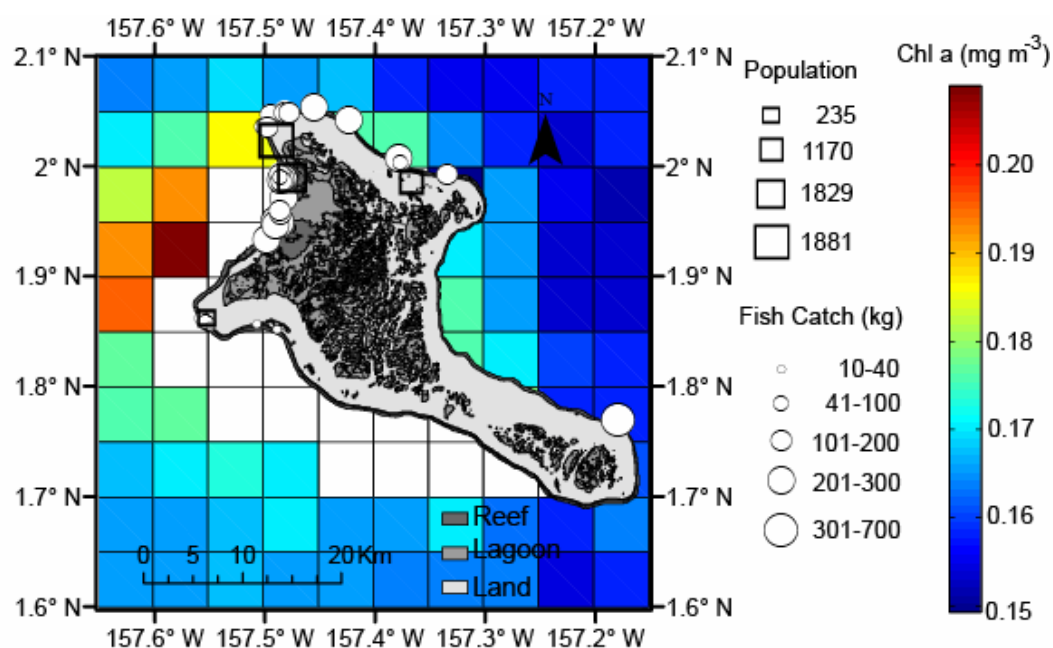


Figure 1-2. Chlorophyll a (a proxy for nutrient inputs) and fishing conditions. Island-wake upwelling in the northwest results in higher chlorophyll a concentrations (November 2002-October 2006 monthly median values). Fishing trips (represented as circles) cluster near the villages (represented as squares).

## Data Collection

### Benthic Cover

The percent cover of major benthic functional groups (coral, crustose coralline algae (CCA), turf, macroalgae, other (see Table A1-1)) was measured using the photoquadrat method along two transects, separated by approximately 10 m at 10-12 m depth (for details see Sandin *et al.* 2008). Five randomly chosen photographs from



each transect were analyzed because additional photographs were determined to not significantly change the mean benthic cover.

### Reef Fish

Data on numerical abundance and length of reef fish species were collected by a pair of divers along three transects, separated by 10 m, on an isobath between 10-12 m depth at each site (for details see Sandin *et al.* 2008). Counts were converted into biomass estimates using published length-weight parameters and summed by major functional groups (top predators, carnivores, herbivores, planktivores (see Table A1-2)).

### Fishing

Surveys of fishing activity were conducted in the four villages of Kiritimati (Fig. 1-2). The number of surveys conducted in each village was roughly proportional to the number of households in the village, except for the smallest village where a higher proportion was sampled due to the small number of households. Households were chosen haphazardly. The head of the household or other person sufficiently knowledgeable of the fishing activities of the household was interviewed after oral consent was obtained. The interviewee was asked to recall catch (kg) by family or species, effort, gear, location, and habitat for all fishing trips conducted over the previous seven days. Each trip was assigned a number, and the interviewee was asked to mark the location of each trip on a map. The fishing data were weighted by the

reciprocal of the product of the number of households surveyed in a village and the probability that the household was chosen in order to make population level estimates for each village.

### Oceanographic Data

Chlorophyll a was used as a proxy for nutrients because it is a more sensitive indicator of nutrient enrichment than nutrient concentrations themselves (Laws & Redalje 1979; Bell 1992). Data on chlorophyll a were obtained from MODIS on Aqua at a resolution of 0.05 degrees. Chlorophyll a data were collected from November 16, 2002 to October 16, 2006. Each site was assigned to the nearest cell and the median monthly value was used.

## Data Analysis

### Fishing Data

In total, 145 households were surveyed, resulting in 248 fishing trips being characterized. The fore reef habitat accounted for 23% of fishing trips (n=57) and only these trips were analyzed. Fish catch was binned by 2 km intervals along the coastline. The distance in either direction from each bin to each village was measured. An exponential function of theses distance ( $x$ ) was fit to the binned fish catch data ( $y$ ) ( $y = \beta_1 * \beta_2^x$ ) ( $R^2=0.91$ ,  $p<0.001$ ). This function was weighted by the fraction of the fish catch in either direction from each village and then used to estimate fish catch at each ecological survey site using the distance from a village to the site. The total fish

catch at a site was the sum of the fish catch from each of these village and direction specific estimates. Summary statistics on frequency of gear types and catch composition (percentage of top predator, carnivore, herbivore, and planktivore biomass) were calculated directly from the pooled catch data. Catch composition was compared across areas identified as high and low fishing for the natural factorial experiment using MANOVA (Stata v9).

### Ecosystem Structure

The differences in normalized (if needed) mean biomass of fish functional group and percentage cover of each benthic functional group were tested using two-way ANOVAs with chlorophyll a and fishing as fixed factors (Stata v9). These data were tested for independence using Moran's I since sites within a given treatment were spatially clustered. There was no evidence of spatial autocorrelation for the nine response variables within any of the four treatments, except for herbivore biomass within the low chlorophyll a/high fishing treatment (see Table A1-3). Fish catch and chlorophyll a were compared for sites within and between levels of each factor using one-way ANOVAs (Stata v9) to verify the factorial experimental design. The percentage of variance explained by each fixed factor was calculated using omega squared ( $\omega^2$ ) (Graham & Edwards 2001; Olejnik & Algina 2003). Negative values of  $\omega^2$  were set to zero because their effects were assumed to be negligible (Graham & Edwards 2001).

### Structuring Mechanisms

The full set of 37 sites were used to test 1) four mechanisms (trophic cascades, size class cascades, fishing down the food chain, and fishing down size classes) (Table 4) linking fishing to changes in top predators and herbivores and large-bodied ( $\geq 20$  cm) and small-bodied ( $< 20$  cm) fish and 2) the independent and interactive effects of herbivores and nutrients on benthic community structure (see Table A1-4). These tests were possible because chlorophyll a was shown not to affect top predator or herbivore biomass (see results, Table 1-2) and herbivore biomass and chlorophyll a were not correlated across the full range of sites (Spearman Correlation,  $\rho = -0.26$ ,  $p = 0.12$ ). Prior to model estimation, data were tested for independence using Moran's I and failed (see Table A1-3). Models were then estimated using ordinary least squares and the residuals were tested for spatial autocorrelation. If the residuals exhibited spatial autocorrelation, models were estimated using spatial simultaneous autoregressive error methods (R). The best model fit was chosen based on the corrected Akaike Information Criterion.

## RESULTS

### Fishing and Chlorophyll a Conditions

The analysis of chlorophyll a levels and fishing pressure for the sub-set of 24 sites validated the factorial experimental design. Fish catch was higher in the north near the two largest villages ( $141 \text{ kg km}^{-1} \text{ wk}^{-1}$ ), which are inside and outside of the upwelling zone, than away from the villages ( $27 \text{ kg km}^{-1} \text{ wk}^{-1}$ ) (ANOVA,  $F_{(1,22)} = 7.64$ ,

$p=0.01$ ; Fig. 1-2). However, fish catch was not significantly different across areas of high and low chlorophyll a (ANOVA,  $F_{(1, 22)}=2.49$ ,  $p=0.13$ ; Fig. 1-2). Across all sites, fish catch ranged from  $445 \text{ kg km}^{-1} \text{ wk}^{-1}$  to less than  $1 \text{ g km}^{-1} \text{ wk}^{-1}$ . Half of fishing trips used hook and line. Gillnets (26%) and spears (19%) were the next most common gear. A small percentage of fishermen (5%) used SCUBA and hand nets to collect fish for the aquarium trade. Top predators (37%) and herbivores (36%) comprised the largest percentage of the total catch by biomass. Carnivores (20%) were the next largest and planktivores (7%) were a small percentage of the total catch. Catch composition (percentage of biomass by functional group) was not different in areas with high and low fish catch (MANOVA,  $F_{(4,76)}=1.18$ ,  $p=0.32$ ).

The twelve sites along the northwestern coastline in the upwelling zone had persistently higher chlorophyll a levels ( $0.195 \text{ mg m}^{-3}$ ) compared to the twelve sites along the northeastern coastline, which is outside of the upwelling zone ( $0.171 \text{ mg m}^{-3}$ ) (ANOVA,  $F_{(1, 22)}=48.14$ ,  $p<0.0001$ ; Fig. 1-2). Chlorophyll a levels were not, however, significantly different across areas with high and low fishing levels ( $F_{(1, 22)}=0.16$ ,  $p=0.69$ ). For comparison, the global range in average annual chlorophyll a observed by MODIS is  $0.01$  to  $0.61 \text{ mg m}^{-3}$  (Dasgupta *et al.* 2009). The natural levels of chlorophyll a on coral reefs ranges from  $0.08 \text{ mg m}^{-3}$  on the oceanic atoll, Eniwetok Atoll, (Glynn 1973) to  $1.48 \text{ mg m}^{-3}$  on reefs in the Bay of Panama that experience upwelling (d'Cruz & Robertson 1997). Reefs polluted by sewage in Kaneohe, HI had chlorophyll a levels up to  $0.68 \text{ mg m}^{-3}$  (Smith 1981). When sewage was diverted, chlorophyll a dropped to  $0.55 \text{ mg m}^{-3}$ , a 19% decrease, and coral reefs recovered. This

change is comparable to the 12% change in the mean chlorophyll a level across sites categorized as high and low chlorophyll a or a 32% change from the highest to the lowest chlorophyll a levels in this study.

### **Ecosystem-scale Effects**

Fishing had the largest effect on the upper trophic levels of the fish community (Table 1-2). Top predator biomass was 75% higher at sites with low fish catch ( $0.78 \text{ mT ha}^{-1}$ ) as compared to sites with high fish catch ( $0.18 \text{ mT ha}^{-1}$ ). Carnivore biomass was 63% lower at sites with high fish catch. In contrast, planktivore biomass was only 36% lower at these sites. Herbivore biomass showed no change over the range of fish catch captured in the factorial experimental design, although parrotfish biomass was marginally lower at sites with high fish catch.

Table 1-2. Two-way analysis of variance with fishing and chlorophyll a as fixed factors and mean biomass (mT ha<sup>-1</sup>) of four fish functional groups as dependent variables.

Source	df	SS	F	p	% variance explained
<i>Fish Community</i>					
Top Predators					
Fishing	1	8.821	8.37	0.009	22.3
Chlorophyll a	1	2.304	2.19	0.155	3.6
Interaction	1	1.197	1.14	0.299	0.4
Residual	20	21.084			
Total	23	33.40			
Carnivores					
Fishing	1	2.933	7.80	0.011	22.8
Chlorophyll a	1	0.174	0.46	0.504	0
Interaction	1	0.179	0.48	0.500	0
Residual	20	7.524			
Total	23	10.810			
Planktivores					
Fishing	1	5.680	4.54	0.046	10.0
Chlorophyll a	1	11.498	9.19	0.007	23.1
Interaction	1	0.361	0.29	0.597	0
Residual	20	25.024			
Total	23	42.563			
Herbivores					
Fishing	1	0.044	1.22	0.283	1.0
Chlorophyll a	1	0.033	0.92	0.349	0
Interaction	1	0.020	0.54	0.470	0
Residual	20	0.720			
Total	23	0.816			

Chlorophyll a mainly affected the lower trophic levels of the benthic community (Table 1-3). Percent cover of both turf and macroalgae was higher at sites with high chlorophyll a, whereas CCA cover was lower. Macroalgal cover was also higher at sites with high fish catch. Although algal cover was affected by fishing and chlorophyll a, coral cover was not. The only fish group affected by chlorophyll a was

the planktivores (Table 1-2). Planktivore biomass was higher at low chlorophyll a sites, outside of the upwelling zone. Planktivores outside of the upwelling zone were mostly large bodied Fusiliers as compared to small bodied *Anthias* and *Chromis* inside the upwelling zone.

Table 1-3. Two-way analysis of variance with fishing and chlorophyll a as fixed factors and percent cover of five benthic functional groups as dependent variables.

Source	df	SS	F	p	% variance explained
<i>Benthic Community</i>					
Coral					
Fishing	1	0.000	0.00	0.977	0
Chlorophyll a	1	0.028	1.75	0.201	3.3
Interaction	1	0.000	0.05	0.821	0
Residual	20	0.315			
Total	23	0.344			
CCA					
Fishing	1	0.015	0.98	0.335	0
Chlorophyll a	1	0.279	17.56	<0.001	40.0
Interaction	1	0.029	1.84	0.190	2.0
Residual	20	0.318			
Total	23	0.641			
Turf					
Fishing	1	0.001	0.04	0.838	3.1
Chlorophyll a	1	0.219	10.24	0.004	34.1
Interaction	1	0.035	1.66	0.212	8.1
Residual	20	0.427			
Total	23	0.683			
Macroalgae					
Fishing	1	0.049	4.86	0.039	10.3
Chlorophyll a	1	0.112	11.06	0.003	26.9
Interaction	1	0.005	0.51	0.483	0
Residual	20	0.203			
Total	23	0.370			



## Structuring Mechanisms

The full set of 37 sites was used for tests of mechanisms linking fishing to changes in top predators and herbivores and large-bodied and small-bodied fishes and fishing of herbivores and nutrients to changes in benthic community structure. Fishing resulted in an exponential decline of top predators from 3.73 mT ha<sup>-1</sup> (73% of total biomass) at the least fished site to 0.02 mT/ha (6% of total biomass) at the most fished site (Table 1-4, Fig. 1-3a). Large-bodied fishes showed a similar trend from 7.61 mT ha<sup>-1</sup> (92% of total biomass) to <0.01 mT ha<sup>-1</sup> (4% of total biomass) (Table 1-4, Fig. 1-3b). Herbivores and small-bodied fishes declined less dramatically with fish catch (Table 1-4, Figs. 1-3c & 1-3d); however, both were highly variable at sites with low fish catch. This pattern may be explained by the bimodal relationships between trophic groups and between size classes. When top predator biomass is high, corresponding to low fish catch, herbivore biomass does not change with top predator biomass but then declines sharply when top predator biomass is low, supporting the fishing down the food chain hypothesis (Table 1-4, Fig. 1-3e). The high herbivore biomass observed at some sites with intermediate levels of top predators suggests that a trophic release may also be occurring but this model has <1% probability that it best explains the data (Table 1-4). Small-bodied fish biomass, however, is higher at intermediate levels of large-bodied fish biomass and lower at sites with both high and low biomass of large-bodied fishes, supporting both the cascade and fishing down hypotheses (Table 1-4, Fig. 1-3f).

Table 1-4. Models of the effects of fishing on biomass ( $\text{mT ha}^{-1}$ ) of fish trophic groups and size classes. All predictor are random variables and models were estimated using ordinary least squares. \* If residuals exhibited spatial autocorrelation, relationships were estimated using spatial autoregressive error models.

Dependent	Predictor	AICc	$\Delta$ AICc	AICc wt
<i>Trophic-based Models</i>				
ln(Top Predators)	ln(Fish Catch)	92.01	0	99.9%
	Fish Catch*	106.05	14.04	0.1%
ln(Herbivores)	ln(Fish Catch)	113.73	-	0%
	Fish Catch	-16.79	0	100.0%
Herbivores	Top Predators*	-0.86	12.61	0.2%
	1/Top Predators	-13.47	0	96.5%
	Quadratic Top Predators	-6.75	6.72	3.4%
<i>Size-based Models</i>				
ln(Large-bodied fish)	ln(Fish Catch)	98.48	0	82.5%
	Fish Catch	101.58	3.1	17.5%
ln(Small-bodied fish)	ln(Fish Catch)*	97.58	1.57	31.3%
	Fish Catch	96.01	0	68.7%
ln(Small-bodied fish)	Large-bodied fish*	98.35	6.26	4.1%
	1/Large-bodied fish*	101.24	9.15	1.0%
	Quadratic Large-bodied fish*	92.09	0	94.9%

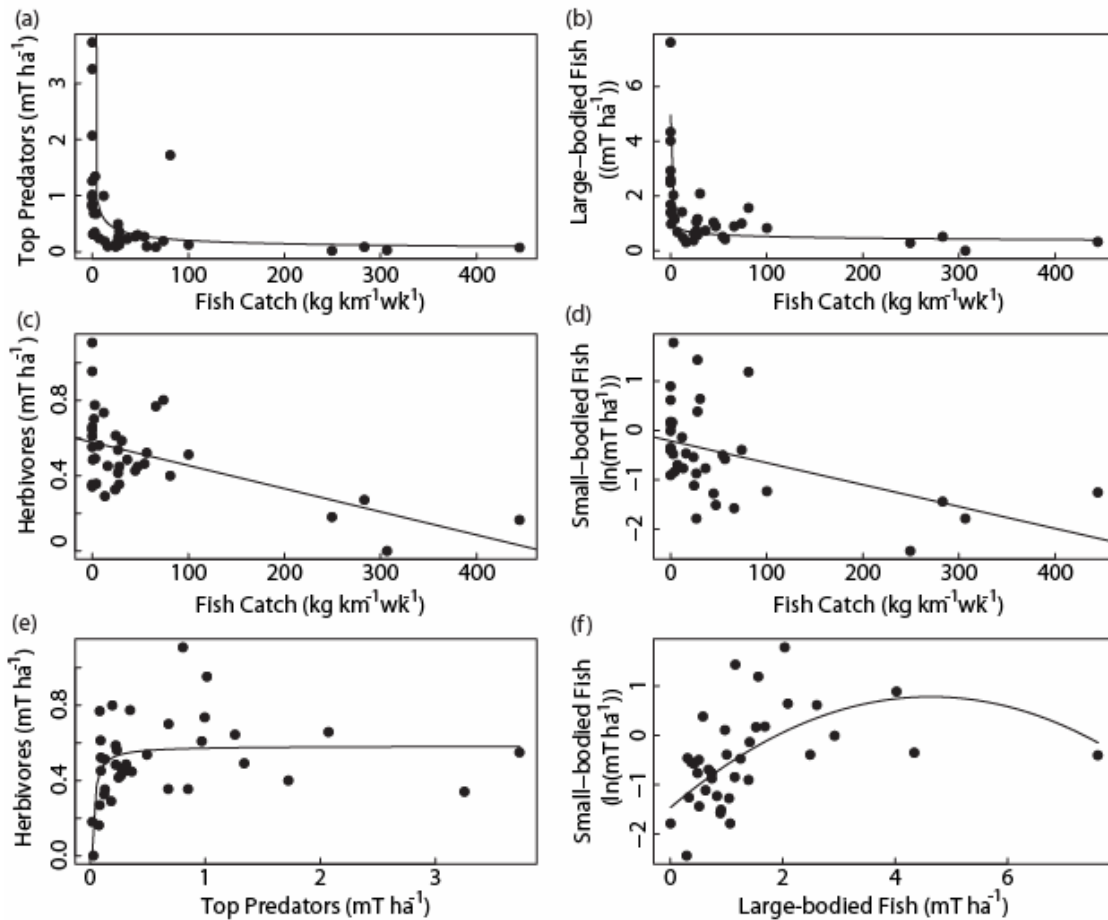


Figure 1-3. The direct and in-direct effects of fishing on top predators, herbivores, large- and small-bodied fish biomass. Fishing resulted in exponential declines in top predator (a,  $R^2=0.58$ ,  $p<0.0001$ ) and large-bodied fish (b,  $R^2=0.43$ ,  $p<0.0001$ ) biomass. Herbivores (c,  $R^2=0.30$ ,  $p<0.001$ ) and small-bodied fish (d,  $R^2=0.22$ ,  $p<0.01$ ) biomass declined linearly with fish catch. Herbivore biomass only declined when top predator biomass was low (e,  $R^2=0.26$ ,  $p<0.01$ ). Small-bodied fish biomass increased and then declined with declines with large-bodied fish biomass (f, pseudo  $R^2=0.65$ ,  $p<0.05$ )

Fishing affected the abundance of macroalgae and CCA via changes in herbivore biomass, while chlorophyll a affected the abundance of macroalgae, CCA, and turf. Coral cover was not significantly affected by herbivore biomass or chlorophyll a levels (see Table A1-4, Fig. 1-4a). CCA was highest when herbivore biomass was highest; however, chlorophyll a decreased the positive effect of herbivore biomass on CCAs (see Table A1-4, Fig. 1-4b). Herbivores had no observable affect on turf. Turf was highest when chlorophyll a was high (see Table A1-4, Fig. 1-4c). Herbivores and chlorophyll a independently and interactively affected macroalgal cover (see Table A1-4, Fig. 1-4d). The marginal effect of herbivores on macroalgae increased with increasing chlorophyll a (Fig. 1-5a), while decreasing herbivore biomass enhanced the marginal effect of chlorophyll a on macroalgae (Fig. 1-5b).

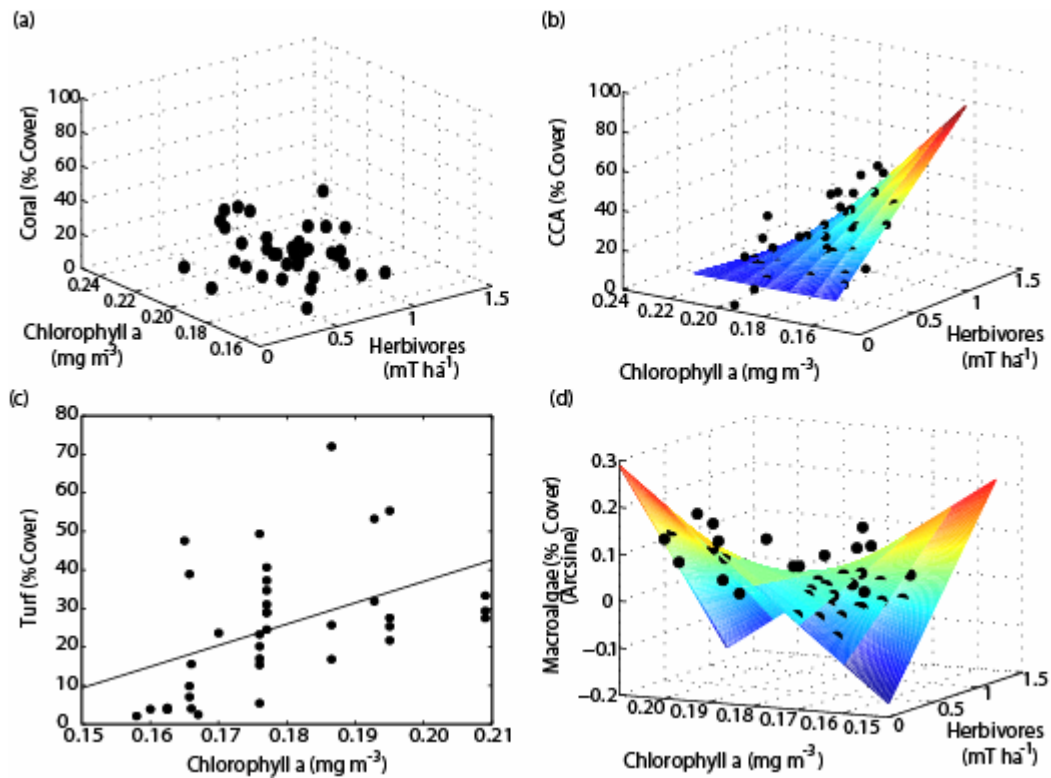


Figure 1-4. The effect of herbivores and chlorophyll a on benthic functional groups. a) Coral was not significant affected by herbivores or chlorophyll a, b) CCA and fitted values (rainbow mesh) as a function of herbivore biomass and the interaction between herbivores and nutrients (pseudo  $R^2=0.68$ ,  $p<0.10$ ), c) Turf and fitted values (black line) predicted by chlorophyll a ( $R^2=0.19$ ,  $p<0.01$ ), d) Macroalgae and fitted values (rainbow mesh) predicted by herbivores, chlorophyll a, and an interactive term ( $R^2=0.37$ ,  $p<0.001$ ).

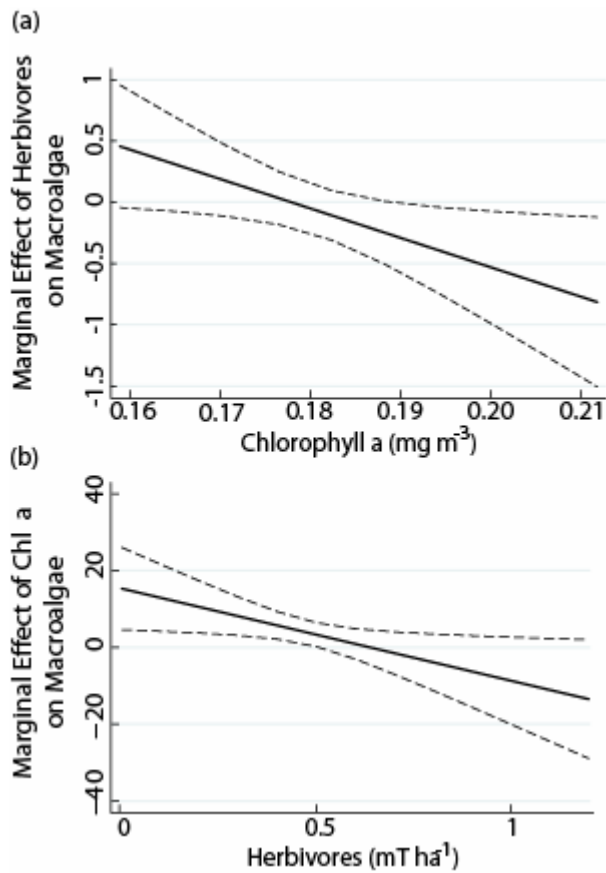


Figure 1-5. The marginal effects of herbivores (a) and chlorophyll a (b) on macroalgae estimated from the best fit model of macroalgae to herbivores, chlorophyll a, and their interaction. Dotted lines are 95% confidence intervals.

## DISCUSSION

The results of this large-scale natural experiment support those found at smaller scales, namely that herbivores and nutrients control the balance between macroalgae and reef-builders (Burkepile & Hay 2006). However, this study expands on previous research to show that 1) fishing primarily affects the fish community while nutrients affect the benthic community, 2) fishing down the food chain or size

classes are the best supported mechanisms by which fishing indirectly affects the benthos and 3) herbivores and nutrients have unexpected interactive effects on macroalgal cover at large spatial scales. The first finding generalizes our understanding of nutrients and fishing to all major ecosystem components, while the other findings have important implications for management.

Fishing significantly decreased the biomass of all fish functional groups and had the greatest effect on the upper trophic levels and large-bodied fishes. About half of fishing trips used hook and line, which selects for larger predators or carnivores. This was evidenced by the fact that almost 40% of the catch was top predators and 20% was carnivores. It is not surprising then that fishing had a strong effect on both top predator and large-bodied fish biomass. However, the precipitous decline of these groups is also probably due to their extreme vulnerability to fishing since they tend to have slow growth and late maturation (Jennings *et al.* 1999). Herbivores and small-bodied fish showed less dramatic declines with fishing. Gillnets, which are unselective and can capture small fish, were used in about a quarter of all fishing trips. Although almost 40% of the catch was herbivores, the diversity of life history may ameliorate the effects on the entire functional group. There was limited evidence that the removal of top predators resulted in a release of herbivores. However, small-bodied fishes increased in response to fishing large-bodied fishes, supporting previous findings of prey release in the smallest size classes of reef fishes (Dulvy *et al.* 2004b). Both herbivores and small-bodied fish declined once top predators and large-bodied fishes

were greatly reduced due to fishing, support the fishing down the food chain or size classes hypotheses.

Fishing of herbivores and nutrients had significant independent and interactive effects on CCAs and macroalgae, while turf was only affected by nutrients. Although coral cover was not affected by fishing or nutrients, a decline in CCAs and increase in turf and macroalgae suggests that future declines may occur due to decreased survival of recruits (Dinsdale *et al.* 2008). These results also support the hypothesis that differences in the levels of benthic algae and coral cover found for the leeward sides of the northern Line Islands must be due at least in part to differences in fishing pressure and cannot be attributed to oceanographic effects alone (Sandin *et al.* 2008).

In contrast to theoretical predictions, a significant interactive effect of herbivores and nutrients on macroalgae was found at a large spatial scale. Similar to small-scale experimental results, macroalgae only increased in response to nutrients when herbivores were low. This supports some previous results showing that herbivores are able to track resources even at larger spatial scales (Russ & McCook 1999; Williams & Polunin 2001; Levin & Hay 2002; Williams *et al.* 2002) and/or that predators have a limited ability to control herbivores (Sandin *et al.* 2009). However, unlike small-scale experimental results, herbivores had less of an effect on macroalgae when nutrients were low. One explanation may be that macroalgae is less susceptible to herbivory at lower nutrient levels due to plasticity within a species or changes in community composition (Gruner *et al.* 2008). In fact, *Peyssonellia* spp. and *Lobophora* spp., which are highly resistance to herbivory, were more abundant at sites



with lower chlorophyll *a* (Littler *et al.* 1983; Coen & Tanner 1989). This result may not be commonly reported because the time-scale of manipulative experiments may be too short to observe shifts in species composition or algal defenses (Gruner *et al.* 2008).

The common coincidence of fishing and nutrient enrichment, either due to better weather conditions for fishing in the lee of islands where island-wake upwelling occurs or the proximity of fishing grounds to sources of pollution, suggests that corals reefs in preferred fishing areas may be more sensitive to overfishing. Two management plans emerge from this study, which warrant further investigation. In the case of island-wake upwelling, reserves or spatial catch limits could shift fishing pressure away from high nutrient areas in order to reduce the risk of coral loss. Similar policies could be used in the case of nutrient pollution; however, the costs of fisheries regulations should be weighed against the benefits of reducing other economic activities, which cause nutrient pollution. Fishing regulations should specifically aim to restore fisheries for top predators since there is limited evidence that fishing top predators affects the benthos and may even effectively protect herbivores from fishing. Although managing both fishing and nutrients is important, protecting herbivore may be more cost effective since they can control macroalgae in the presence of nutrients and are more effective grazers under high nutrient conditions.

This study provides insight into how the results of small-scale experiments apply to ecosystem-based management but is limited due to examining reefs on a single island with natural rather than anthropogenic nutrient enrichment. Given that

the effects of nutrients and fishing appear to be conditional, future research, using ecological surveys, experiments, and economic valuation methods, should be conducted on reefs that represent the range of nutrient and fishing conditions to develop a set of ecosystem-based management scenarios.

### **ACKNOWLEDGEMENTS**

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## APPENDIX

Table A1-1. Assignment of benthic organisms to major functional groups.

---

Coral	
	all Scleratinian corals
CCA	
	all CCA
Turf	
	any non-encrusting benthic algae less than 1 cm in height
Macro-algae	
	<i>Halimeda</i>
	<i>Lobophora</i>
	<i>Peyssonellia</i>
	Blue-Green Algae
	Encrusting Macroalgae
	Frondose Macroalgae
Other	
	Acanthaster
	Anemone
	Bryozoan
	Sea Cucumber
	Soft Coral
	Sponge
	Tridacna
	Tunicate
	Urchin
	Zooanthid

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Table A1-2. Assignment of fish species to major functional groups.

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Top Predators
<i>Aphareus furca</i>
<i>Aprion virescens</i>
<i>Aulostomus chinensis</i>
<i>Bothus mancus</i>
<i>Carangoides ferdau</i>
<i>Carangoides orthogrammus</i>
<i>Caranx ignobilis</i>
<i>Caranx lugubris</i>
<i>Caranx melampygus</i>
<i>Caranx sexfasciatus</i>
<i>Carcharhinus amblyrhynchos</i>
<i>Carcharhinus melanopterus</i>
<i>Cephalopholis argus</i>
<i>Cephalopholis leopardus</i>
<i>Cephalopholis miniata</i>
<i>Cephalopholis urodeta</i>
<i>Elagatis bipinnulata</i>
<i>Epinephelus fasciatus</i>
<i>Epinephelus hexagonatus</i>
<i>Epinephelus macrospilos</i>
<i>Epinephelus maculatus</i>
<i>Epinephelus melanostigma</i>
<i>Epinephelus polyphekadion</i>
<i>Epinephelus retouti</i>
<i>Epinephelus spilotoceps</i>
<i>Epinephelus tauvina</i>
<i>Euthynnus affinis</i>
<i>Fistularia commersonii</i>
<i>Gracila albomarginata</i>
<i>Gymnothorax breedeni</i>
<i>Gymnothorax flavimarginatus</i>
<i>Gymnothorax javanicus</i>
<i>Gymnothorax meleagris</i>
<i>Gymnothorax monostigma</i>
<i>Gymnothorax sp</i>
<i>Gymnothorax undulatus</i>
<i>Lethrinus obsoletus</i>
<i>Lethrinus olivaceus</i>
<i>Lethrinus rubrioperculatus</i>
<i>Lethrinus sp</i>
<i>Lethrinus xanthochilus</i>
<i>Lujanus monostigma</i>

Table A1-2. Continued.

---

Top Predators

*Lutjanus bohar*  
*Lutjanus fulvus*  
*Lutjanus gibbus*  
*Lutjanus kasmira*  
*Oxycheilinus diagrammus*  
*Oxycheilinus unifasciatus*  
*Paracirrhites forsteri*  
*Paracirrhites hemistictus*  
*Pterois antennata*  
*Pterois radiata*  
*Pterois volitans*  
*Scomberoides lysan*  
*Sphyraena barracuda*  
*Sphyraena helleri*  
*Sphyraena qenie*  
*Synanceia verrucosa*  
*Synodus binotatus*  
*Synodus dermatogenys*  
*Synodus jaculum*  
*Synodus sp*  
*Synodus variegatus*  
*Thunnus albacares*  
*Triaenodon obesus*  
*Variola louti*

## Carnivores

*Aetobatos narinari*  
*Aluterus scripta*  
*Amanes scopas*  
*Anampses caeruleopunctatus*  
*Anampses melanurus*  
*Anampses meleagris*  
*Anampses twistii*  
*Apogon kallopterus*  
*Apolemichthys xanthopunctatus*  
*Arothron meleagris*  
*Arothron stellatus*  
*Balistapus undulatus*  
*Balistoides viridescens*  
*Bodianus axillaris*  
*Bodianus loxozonus*  
*Bodianus prognathus*

Table A1-2. Continued.

---

Carnivores

*Bolbometopon muricatum*  
*Cantherhines dumerilii*  
*Cantherhines pardalis*  
*Canthigaster amboinensis*  
*Canthigaster solandri*  
*Caracanthus maculatus*  
*Chaetodon auriga*  
*Chaetodon bennetti*  
*Chaetodon ephippium*  
*Chaetodon lineolatus*  
*Chaetodon lunula*  
*Chaetodon lunulatus*  
*Chaetodon meyeri*  
*Chaetodon ornatissimus*  
*Chaetodon pelewensis*  
*Chaetodon quadrimaculatus*  
*Chaetodon reticulatus*  
*Chaetodon trifascialis*  
*Chaetodon ulietensis*  
*Chaetodon unimaculatus*  
*Chaetodon vaigiensis*  
*Cheilinus chlorourus*  
*Cheilinus fasciatus*  
*Cheilinus oxycephalus*  
*Cheilinus trilobatus*  
*Cheilinus undulatus*  
*Cirrhitichthys oxycephalus*  
*Cirrhitops hubbardi*  
*Coris aygula*  
*Coris centralis*  
*Coris gaimard*  
*Diodon hystrix*  
*Diplogrammus goramensis*  
*Echidna nebulosus*  
*Echidna unicolor*  
*Enchelychore pardalis*  
*Epibulus insidiator*  
*Eviota albolineata*  
*Eviota sp*  
*Forcipiger flavissimus*  
*Forcipiger longorostris*  
*Gnathanodon speciosus*

Table A1-2. Continued.

---

Carnivores
<i>Gnathodentex aureolineatus</i>
<i>Gnatholepis</i> sp
<i>Gobiid</i> sp
<i>Gomphosus varius</i>
<i>Halichoeres hortulanus</i>
<i>Halichoeres margaritaceus</i>
<i>Halichoeres marginatus</i>
<i>Halichoeres melasmapomus</i>
<i>Halichoeres ornatissimus</i>
<i>Halichoeres trimaculatus</i>
<i>Hemigymnus fasciatus</i>
<i>Hologymnosus annulatus</i>
<i>Hologymnosus doliatus</i>
<i>Labroides bicolor</i>
<i>Labroides dimidiatus</i>
<i>Labroides pectoralis</i>
<i>Labroides rubrolabiatus</i>
<i>Macropharyngodon meleagris</i>
<i>Malacanthus latovittatus</i>
<i>Monotaxis grandoculis</i>
<i>Mulloidichthys flavolineatus</i>
<i>Mulloidichthys mimicus</i>
<i>Mulloidichthys vanicolensis</i>
<i>Neoniphon opercularis</i>
<i>Neoniphon sammara</i>
<i>Novaculichthys taeniourus</i>
<i>Ostracion meleagris</i>
<i>Paracirrhites arcatus</i>
<i>Parapercis lata</i>
<i>Parapercis millepunctata</i>
<i>Parupeneus barberinus</i>
<i>Parupeneus cyclostomus</i>
<i>Parupeneus insularis</i>
<i>Parupeneus multifasciatus</i>
<i>Parupeneus pleurostigma</i>
<i>Parupeneus</i> sp
<i>Pervagor aspricauda</i>
<i>Pervagor</i> sp
<i>Platax orbicularis</i>
<i>Plectroglyphidodon dickii</i>
<i>Plectroglyphidodon imparipennis</i>
<i>Plectroglyphidodon johnstonianus</i>

Table A1-2. Continued.

---

Carnivores

*Pomacanthus imperator*  
*Pseudobalistes flavimarginatus*  
*Pseudocheilinus hexataenia*  
*Pseudocheilinus octotaenia*  
*Pseudocheilinus sp*  
*Pseudodax moluccanus*  
*Sargocentron caudimaculatum*  
*Sargocentron ittodai*  
*Sargocentron tiere*  
*Sebastapistes coniota*  
*Sebastapistes cyanostigma*  
*Stethojulis bandanensis*  
*Sufflamen bursa*  
*Sufflamen chrysopterum*  
*Sufflamen fraenatum*  
*Synchiropus moyeri*  
*Synchiropus ocellatus*  
*Thalassoma lunare*  
*Thalassoma lutescens*  
*Thalassoma quinquevittatum*  
*Thalassoma sp*  
*Thalassoma trilobatum*  
*Valenciennea helsdingenii*  
*Valenciennea strigata*  
*Zanclus cornutus*

## Herbivores

*Acanthurus achilles*  
*Acanthurus achilles x nigricans*  
*Acanthurus blochii*  
*Acanthurus guttatus*  
*Acanthurus leucochilus*  
*Acanthurus lineatus*  
*Acanthurus maculiceps*  
*Acanthurus nigricans*  
*Acanthurus nigricauda*  
*Acanthurus nigrofuscus*  
*Acanthurus nigroris*  
*Acanthurus olivaceus*  
*Acanthurus pyroferus*  
*Acanthurus sp*  
*Acanthurus triostegus*



Table A1-2. Continued.

## Herbivores

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*Acanthurus xanthopterus*  
*Calotomus carolinus*  
*Centropyge flavissima*  
*Centropyge loricula*  
*Cetoscarus bicolor*  
*Chlorurus frontalis*  
*Chlorurus microrhinos*  
*Chlorurus sordidus*  
*Cirripectes auritus*  
*Cirripectes sp*  
*Cirripectes stigmaticus*  
*Cirripectes variolosus*  
*Ctenochaetus binotatus*  
*Ctenochaetus cyanocheilus*  
*Ctenochaetus flavicauda*  
*Ctenochaetus hawaiiensis*  
*Ctenochaetus marginatus*  
*Ctenochaetus striatus*  
*Hipposcarus longiceps*  
*Kyphosus bigibbus*  
*Kyphosus cinerascens*  
*Kyphosus sp*  
*Kyphosus vaigiensis*  
*Leptoscarus vaigiensis*  
*Naso lituratus*  
*Naso unicornis*  
*Scarus altipinnis*  
*Scarus festivus*  
*Scarus forsteni*  
*Scarus frenatus*  
*Scarus ghobban*  
*Scarus globiceps*  
*Scarus niger*  
*Scarus oviceps*  
*Scarus psittacus*  
*Scarus rubroviolaceus*  
*Scarus sp*  
*Scarus spinus*  
*Scarus tricolor*  
*Stegastes aureus*  
*Stegastes fasciolatus*  
*Stegastes nigricans*

Table A1-2. Continued.

## Herbivores

*Zebrasoma rostratum**Zebrasoma scopas**Zebrasoma veliferum*

## Planktivores

*Acanthurus albipectoralis**Acanthurus thompsoni**apogonid sp**Aspidontus dussumieri**Aspidontus taeniatus**Caesio teres**Chaetodon kleinii**Chanos chanos**Chromis acares**Chromis agilis**Chromis lepidolepis**Chromis margaritifer**Chromis vanderbilti**Chromis weberi**Chromis xanthura**Cirrhilabrus exquiritus**Dascyllus auripinnis**Decapterus macarellus**Hemitaenichthys thompsoni**Heniochus acuminatus**Lepidozygus tapeinosoma**Luzonichthys whitleyi**Manta birostris**Meiacanthus atrodorsalis**Melichthys niger**Melichthys vidua**Myripristis adusta**Myripristis amaena**Myripristis berndti**Myripristis kuntee**Myripristis murdjan**Naso annulatus**Naso brevirostris**Naso hexacanthus**Naso vlamingii**Nematoeleotris magnifica**Odonus niger*

Table A1-2. Continued.

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Planktivores
*Ostorhinchus angustatus**Ostorhinchus apogonides**Paracanthurus hepatus**Pempheris oualensis**Plagiotremus rhinorhynchos**Plagiotremus tapeinosoma**Pomacentrus coelestis**Priacanthus hamrur**Pseudanthias bartlettorum**Pseudanthias cooperi**Pseudanthias dispar**Pseudanthias olivaceus**Pseudanthias sp**Pseudocoris heteroptera**Ptereleotris evides**Ptereleotris heteroptera**Ptereleotris magnifica**Ptereleotris microlepis**Ptereleotris sp**Ptereleotris zebra**Pterocaesio lativittata**Pterocaesio tile**Thalassoma amblycephalum**Xanthichthys caeruleolineatus*


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Table A1-3. Test of independence for response variables within each treatment in the natural factorial experiment and across all sites. The unit of measure for abundance of benthic functional groups is percent cover and for fish functional groups is  $\text{mT ha}^{-1}$ .

Dependent	Moran's I		SD	p-value
	Expected	Observed		
<i>Low Fishing, Low Chl a</i>				
Coral	-0.2	-0.18	0.19	0.92
CCA	-0.2	-0.46	0.22	0.23
Macroalgae	-0.2	-0.6	0.29	0.17
Turf	-0.2	-0.11	0.18	0.63
Top Predators	-0.2	-0.03	0.17	0.32
Carnivores	-0.2	-0.41	0.26	0.44
Planktivores	-0.2	-0.25	0.19	0.78
Herbivores	-0.2	-0.41	0.27	0.44
<i>High Fishing, Low Chl a</i>				
Coral	-0.2	-0.18	0.17	0.90
CCA	-0.2	0.09	0.16	0.07
Macroalgae	-0.2	-0.28	0.15	0.60
Turf	-0.2	-0.07	0.19	0.48
Top Predators	-0.2	-0.05	0.15	0.31
Carnivores	-0.2	-0.02	0.18	0.24
Planktivores	-0.2	-0.05	0.18	0.40
Herbivores	-0.2	0.20	0.18	0.03
<i>High Fishing, High Chl a</i>				
Coral	-0.2	-0.02	0.21	0.38
CCA	-0.2	-0.04	0.15	0.29
Macroalgae	-0.2	-0.09	0.18	0.54
Turf	-0.2	-0.31	0.18	0.55
Top Predators	-0.2	0.17	0.19	0.051
Carnivores	-0.2	-0.10	0.12	0.42
Planktivores	-0.2	-0.05	0.10	0.15
Herbivores	-0.2	-0.07	0.18	0.47
<i>Low Fishing, High Chl a</i>				
Coral	-0.2	-0.12	0.13	0.54
CCA	-0.2	-0.30	0.13	0.41
Macroalgae	-0.2	-0.02	0.13	0.16
Turf	-0.2	-0.28	0.08	0.34
Top Predators	-0.2	-0.17	0.06	0.58
Carnivores	-0.2	-0.20	0.06	0.96
Planktivores	-0.2	-0.29	0.06	0.46
Herbivores	-0.2	-0.25	0.11	0.64
<i>All Sites</i>				
Coral	-0.03	0.12	0.07	0.03
CCA	-0.03	0.31	0.07	<0.001

Table A1-3 Continued

Dependent	Moran's I		SD	p-value
	Expected	Observed		
Macroalgae	-0.03	0.21	0.07	<0.001
Turf	-0.03	0.17	0.07	0.004
Top Predators	-0.03	0.21	0.06	<0.001
Carnivores	-0.03	-0.10	0.03	0.66
Planktivores	-0.03	0.12	0.06	0.016
Herbivores	-0.03	0.11	0.07	0.01

Table A1-4. Models of the effect of herbivores ( $\text{mT ha}^{-1}$ ) and chlorophyll a ( $\text{mg m}^{-3}$ ) on the percent cover of benthic functional groups. All predictor are random variables and models were estimated using ordinary least squares. However, if residuals exhibited spatial autocorrelation, relationships were estimated using spatial autoregressive error models (indicated by \*).

Dependent	Predictors			AICc	$\Delta \text{AICc}$	AICc wt
Coral	Herbivores	Chla	Interaction	-29.84	1.65	9%
	Herbivores	Chla		-30.21	1.28	11%
	Herbivores*			-31.04	0.45	8%
		Chla*		-28.14	3.35	3%
	Herbivores		Interaction	-31.18	0.31	18%
		Chla	Interaction	-31.49	0.0	21%
	Interaction*			-31.11	0.38	18%
CCA	Herbivores	Chla	Interaction*	-36.50	2.87	10%
	Herbivores	Chla*		-38.07	1.30	22%
	Herbivores*			-34.00	5.37	3%
		Chla*		-33.88	5.49	3%
	Herbivores		Interaction*	-39.37	0	42%
		Chla	Interaction*	-37.74	1.63	19%
	Interaction*			-32.27	7.1	1%
Turf	Herbivores	Chla	Interaction*	-25.22	6.08	2%
	Herbivores	Chla		-30.02	1.28	19%
	Herbivores*			-25.50	5.80	2%
		Chla		-31.30	0	37%
	Herbivores		Interaction	-29.88	1.42	18%
		Chla	Interaction	-30.06	1.24	20%
	Interaction*			-25.97	5.33	2%
Macroalgae (arcsine)	Herbivores	Chla	Interaction	-67.40	0	91%
	Herbivores	Chla		-59.68	7.72	2%
	Herbivores*			-54.74	12.66	<1%
		Chla		-61.21	6.19	4%
	Herbivores		Interaction	-54.84	12.56	<1%
		Chla	Interaction	-59.96	7.44	2%
			Interaction*	-54.68	12.72	<1%

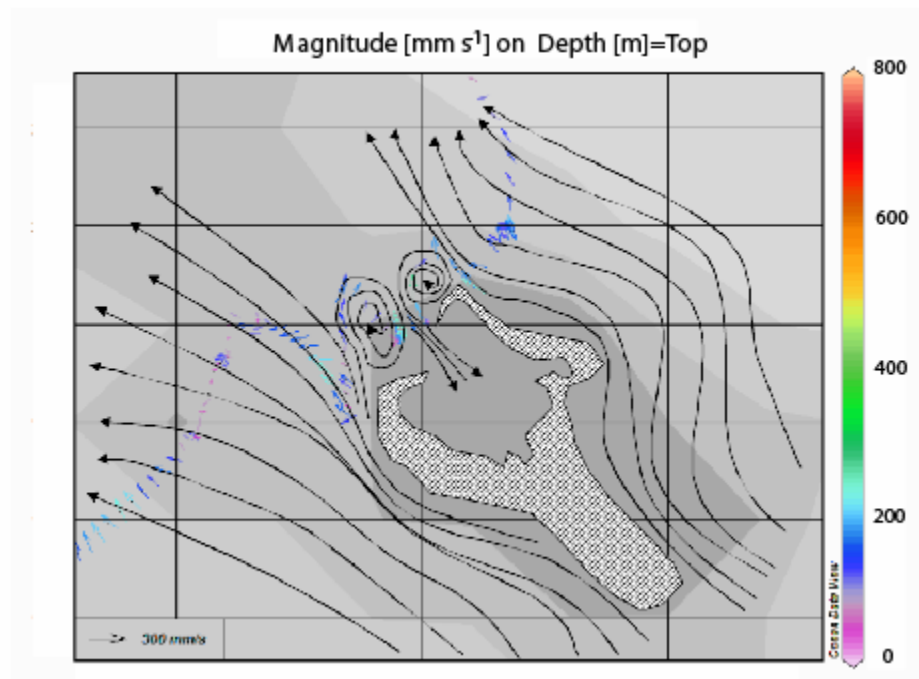


Figure A1-1. Interpolation of surface currents surrounding Kiritimati based on ADCP vector data from a single transect. Evidence of two anti-cyclonic eddies is visible in the lee of the island with an inflow of surface water to the lagoon. The prevailing current is heading Northwest. (Chaput, Modlin, Rydz & Budzynkiewicz, unpublished data).

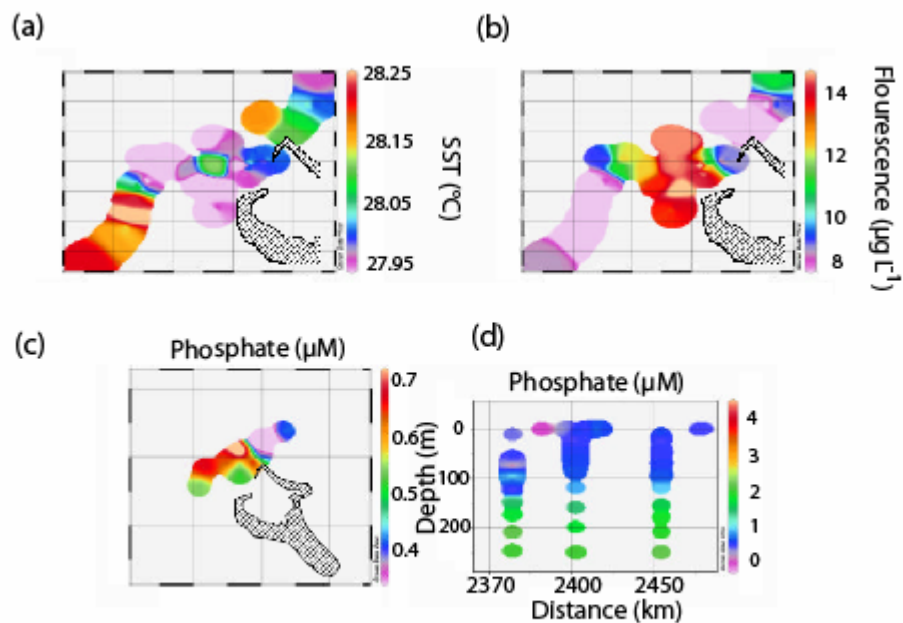


Figure A1-2. Sea Surface Temperature, Fluorescence, and Phosphate. a) Sea surface temperature data shows cooler waters inside the eddies than outside. b) Fluorescence data shows greater productivity inside the eddy, which is associated with higher phosphate levels at the surface (c) of the eddies and at depth (d). The data at distance 2370 km are within the eddy and the other data (2400 and 2450 km) are outside the eddy. (Chaput, Modlin, Rydz & Budzynkiewicz, unpublished data).



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## **CHAPTER 2: Fishing Affects Condition and Reproduction in a Reef Fish Community**

## ABSTRACT

Fishing dramatically alters fish community structure by removing top predators. Changes in the numerical abundance and biomass of prey fishes in response to the removal of top predators have been well studied. The paucity of evidence for trophic cascades in coral reef ecosystems suggests that other individual-level physiological responses may be occurring. In the northern Line Islands, we examined differences in condition and reproductive effort among five coral reef fish species (representing five major trophic groups) under high and low fishing conditions, both within and across islands. Removal of top predators through fishing was expected to be associated with greater energy storage (condition) because lower predation risk may increase foraging time and the probability of using energy stores for future reproduction. In contrast, prey fishes were expected to have lower condition when fishing was low and predation risk was high. Greater reproductive effort was expected under low fishing conditions if predation risk was sufficiently high and food resources were limiting such that the benefit of current reproduction outweighed the cost of reduced survival. We found that all species of prey fishes were in poorer condition (lower adjusted mean body weight and liver weight) in locations where fishing was low and top predator abundance was high. Reproductive effort (adjusted mean gonad weight and size at sex change) was higher under low fishing and high predation conditions for herbivorous fish only. These trends were observed within and across islands, suggesting that differences in condition and reproductive effort are not likely due to genetic differences in the populations of fishes. Changes in condition and

reproductive effort may have important implications for fisheries productivity however the net effect will depend on the relative contribution of individual somatic growth versus population growth.

## INTRODUCTION

Predation and food are primary factors affecting animal populations. Animal populations respond to predation through changes in abundance and life history parameters, such as condition and reproduction. Despite an awareness of the importance of interactions between predation and food availability, there are a limited number of studies that consider both predation and food and even fewer studies consider community-wide responses. Thus the dramatic decline of top predators on coral reefs due to fishing and the associated increase in macroalgae provide a unique opportunity to test the independent and interactive effects of predation and food on a community of animals (Jackson *et al.* 2001; Friedlander & DeMartini 2002; Newman *et al.* 2006; Stevenson *et al.* 2007; Sandin *et al.* 2008; Walsh 2009).

Top predators may have once dominated coral reef fish community biomass, but now only represent a small fraction of total fish biomass on fished reefs (Friedlander & DeMartini 2002; Newman *et al.* 2006; Stevenson *et al.* 2007; Sandin *et al.* 2008). Yet, there are surprisingly few examples of prey fishes increasing in abundance in response to fishing predators (Dulvy *et al.* 2004, Sandin *et al.* 2009). This may be because many top predators were overfished before modern coral reef



ecology began (Pandolfi *et al.* 2003; Knowlton & Jackson 2008; Sandin *et al.* 2009), the diversity of species and abundance of omnivores result in few strong trophic linkages (Jennings & Kaiser 1998; Bascompte *et al.* 2005), and fishing occurs at multiple trophic levels (Jackson *et al.* 2001; Walsh 2009). Alternatively, fishing predators may have more important non-lethal effects on prey (Lima 1998). Foraging behavior or physiological stress, for instance, change in response to predation risk and may have consequences for condition and reproduction (MacArthur & Pianka 1966; Lima 1990; Werner & Anholt 1996; Boonstra *et al.* 1998, McPeck *et al.* 2001).

High predation risk can change prey behavior, resulting in fewer food resources are obtained during foraging (e.g. Stein & Magnuson 1976; Milinski & Heller 1978; Grubb & Greenwald 1982; Holmes 1984; Schmitt & Holbrook 1985). Prey may choose habitats with lower food quality (Gilliam & Fraser 1987), reduce the amount of time spent away from shelters (Lima 1985), or reduce the distance traveled to food resources (Suhonen 1993) in order to reduce the probability of mortality. These changes in foraging behavior may reduce food intake and, consequently, energy stores, which are measured by condition (Lima 1986). Reduced condition may also result in reduced reproductive effort because less energy is available to be re-allocated between somatic stores and reproductive organs. Alternatively, reduced condition can be a consequence of increased reproductive effort under high predation risk.

High predation risk increases the value of current reproduction over energy allocation to storage for survival and future reproduction (Schaffer 1974) because current reproduction will increase fitness for individuals in populations that experience

high mortality rates. Under low predation risk, individuals have a greater expectation of surviving to the next reproductive season. Therefore, individuals living in populations with low predation risk may increase their fitness by storing ingested energy for future demands. Trade-offs between larger gonads or clutches and lower body weight and fat stores have been observed in the field for a diversity of taxa (Roff 1982, Lessells 1986, Brough & Dixon 1989, Poizat *et al.* 1999, Bety *et al.* 2003). However, a substantial number of studies have also reported no trade-off (Finke *et al.* 1987; Salvanes & Stockley 1996; Karels *et al.* 2000). Increased reproductive effort associated with high predation risk is only expected when food resources are limited (Levins 1968; Sibley & Calow 1986; Stearns 1992).

Only a few studies have examined the effect of fishing on condition and reproductive effort, despite an abundance of studies of these metrics in the fisheries literature. More often, metrics of condition or reproductive effort are measured in order to provide parameter estimates for fisheries models (e.g. Kulbicki *et al.* 1993; Green *et al.* 2006). Little consideration has been given to changes in these parameters in response to fishing and rarely have they been measured for a community of fishes. However, Begg *et al.* 2005, proposed using a multivariate index of life history parameters, including a metric of condition, to measure the performance of marine reserves. The effect of the marine reserve on the condition of two study species was mixed; one species (coral trout) showed greater mean weight at age within the reserve and the other (red throated emperor) showed no difference (Begg *et al.* 2005). Other studies have found differences in fish length-weight relationships and gonad-weight

relationships across geographic areas that cannot be explained by environmental factors alone and suggest that historical or current patterns in fishing may explain the differences (Salvanes & Stockley 1996; Brodziak 2000, Gerritsen 2007). However, fishing and predation pressure were not directly measured and the linkages to changes in condition and reproduction are somewhat unclear. There is strong evidence, however, that size at sex change in protogynous fishes decreases with fishing and predation pressure (Armstrong 2001; Petersen & Warner 2002; DeMartini *et al.* 2005; DeMartini *et al.* 2008). Males make greater gains in fertility with size and age, which suggests that a reduction in the size at sex change represents a strategy to increase reproduction (Warner & Robertson 1978; Warner *et al.* 1975).

Here we examine the effects of fishing on condition and reproduction in a community of reef fishes. We expect that high predation risk, associated with low levels of fishing, will decrease condition and increase reproductive effort when food resources are limited. In order to test this hypothesis, we surveyed and collected representative species from five trophic groups at sites representing high and low fishing pressure within and across islands. We used underwater visual survey data of the fish and benthic community to assess the level of predation, competition, and resource availability. We used household survey data of fishing activity to assess the fishing pressure. We then relate these factors to physiological responses, specifically metrics of condition (total weight, liver weight) and reproduction (gonad weight, size at sex change).

## METHODS

### Study Sites

Palmyra and Kiritimati Atolls in the northern Line Islands (Fig. 2-1, Table 2-1) provide a natural experiment to test the effect of fishing on reef fish community life history traits. No fishing occurs on Palmyra Atoll because it is a U.S. Fish and Wildlife Refuge and at most hosts 20 scientists and staff at a research station. Kiritimati Atoll has a population of 5,115 (2005), mostly recent arrivals due to a re-settlement program from Tarawa, the capital of the Republic of Kiribati (3,000 miles to the west). The population is concentrated in the north and west, leaving over 60% of the coastline uninhabited. Comparing fishes from unfished Palmyra Atoll (Pal) and the lightly fished southeastern area of Kiritimati Island (KirSE) to the northwestern heavily fished side of Kiritimati (KirNW) allowed determine whether differences in traits may be due to genetic differences between populations or plastic responses to differences in predation risk.

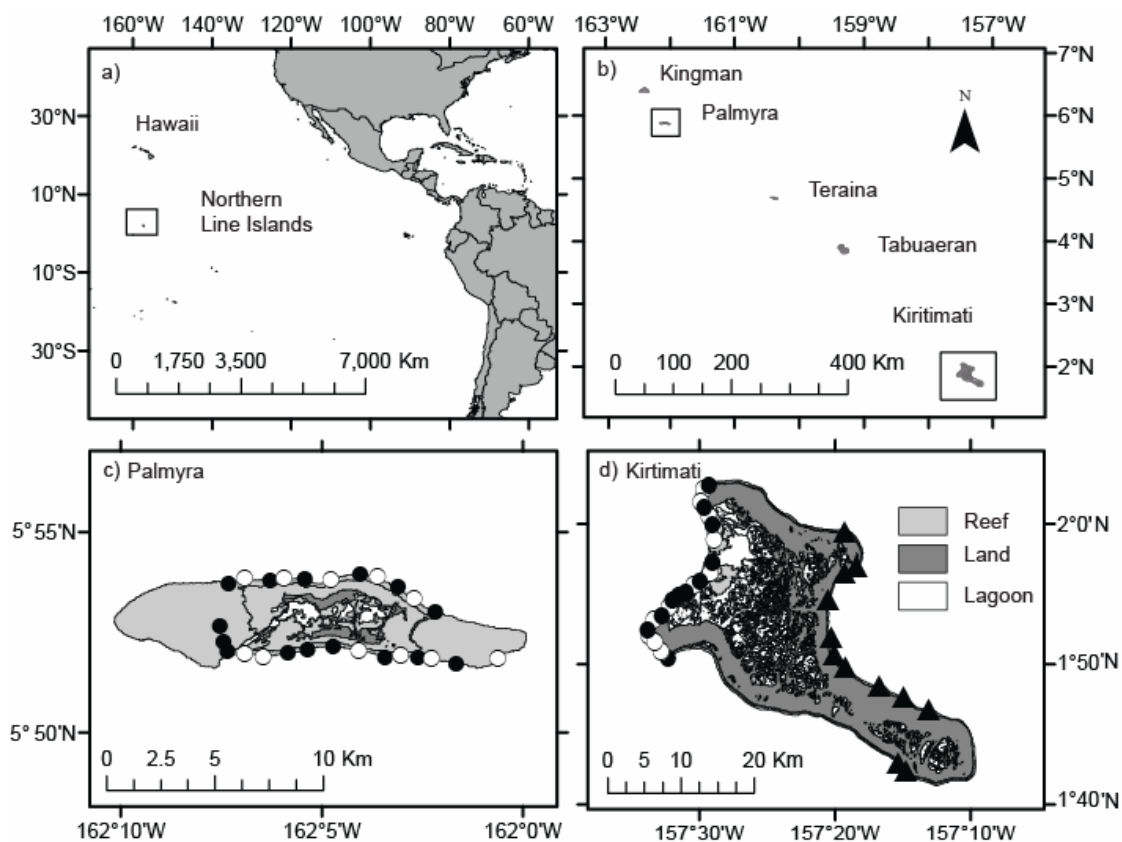


Figure 2-1. Palmyra and Kiritimati are two atolls in the northern Line Islands (a, b). Palmyra is part of the Pacific Remote Islands Marine National Monument and Kiritimati is a populated island in the Republic of Kiribati. Fish and benthic surveys were conducted on Palmyra (c) and the northwestern side of Kiritimati (d) in 2005 (black circles: fish surveys; white circles: fish and benthic surveys). Fish and benthic surveys were conducted on the southeastern side of Kiritimati in 2007 (black triangles). Fish collections were made on Palmyra in 2006, northwestern Kiritimati in 2006 and 2007, and southeastern Kiritimati in 2007.

Table 2-1. Ecosystem and Environmental Attributes (mean, standard deviation). Mean values were determined to be significantly different by t-tests with Holm's sequential Bonferroni correction are indicated by a, b, or c.

Factor	KirNW	KirSE	Pal
Fish Catch (kg/km/wk)	173.88 <sup>a</sup> (34.87)	43.62 <sup>b</sup> (15.80)	0 <sup>c</sup> -
<i>Predation pressure</i>			
Predator density (#/m <sup>2</sup> )	0.31 <sup>a</sup> (0.04)	0.19 <sup>b</sup> (0.05)	0.13 <sup>c</sup> (0.01)
Predator density (g/ m <sup>2</sup> )	24.76 <sup>c</sup> (5.05)	124.36 <sup>b</sup> (34.70)	168.43 <sup>a</sup> (24.12)
Shelter (% coral cover)	14.99 <sup>c</sup> (2. 26)	38.42 <sup>a</sup> (4.04)	20.36 <sup>b</sup> (2.67)
<i>Resource Availability</i>			
Coral cover (%)	14.99 <sup>c</sup> (2. 26)	38.42 <sup>a</sup> (4.04)	20.36 <sup>b</sup> (2.67)
Turf algal cover (%)	52.59 <sup>a</sup> (4.77)	13.37 <sup>c</sup> (3.74)	24.95 <sup>b</sup> (3.21)
Macro algal cover (%)	16.21 <sup>a</sup> (3.26)	5.82 <sup>b</sup> (0.94)	17.77 <sup>a</sup> (2.19)
<i>Resource Competition</i>			
L. bohar (#/m <sup>2</sup> )	0.02 <sup>c</sup> (0.003)	0.03 <sup>b</sup> (0.009)	0.04 <sup>a</sup> (0.005)
P. arcatus (#/m <sup>2</sup> )	0.03 <sup>c</sup> (0.004)	0.05 <sup>b</sup> (0.006)	0.08 <sup>a</sup> (0.009)
C. margaritifer (#/m <sup>2</sup> )	1.53 <sup>a</sup> (0.26)	0.59 <sup>b</sup> (0.14)	0.51 <sup>c</sup> (0.08)
P. dickii (#/m <sup>2</sup> )	0.07 <sup>b</sup> (0.01)	0.27 <sup>a</sup> (0.04)	0.03 <sup>c</sup> (0.005)
A. nigricans (#/m <sup>2</sup> )	0.02 <sup>c</sup> (0.004)	0.05 <sup>b</sup> (0.008)	0.07 <sup>a</sup> (0.008)
Apex predators (#/m <sup>2</sup> )	0.02 <sup>b</sup> (0.003)	0.07 <sup>a</sup> (0.020)	0.07 <sup>a</sup> (0.007)
Invertivores (#/m <sup>2</sup> )	1.56 <sup>a</sup> (0.11)	0.38 <sup>c</sup> (0.03)	0.62 <sup>b</sup> (0.03)
Planktivores (#/m <sup>2</sup> )	9.48 <sup>a</sup> (0.73)	4.17 <sup>b</sup> (0.70)	1.80 <sup>c</sup> (0.15)
Omnivores (#/m <sup>2</sup> )	0.07 <sup>b</sup> (0.01)	0.28 <sup>a</sup> (0.04)	0.03 <sup>c</sup> (0.005)
Herbivores+	0.55 <sup>a</sup>	0.36 <sup>b</sup>	0.38 <sup>b</sup>
Detritivores (#/m <sup>2</sup> )	(0.04)	(0.03)	(0.03)

Table 2-1. Continued.

Factor	KirNW	KirSE	Pal
<i>Oceanography</i>			
Chlorophyll a (mg/m <sup>3</sup> )	0.18 <sup>a</sup> (0.02)	0.16 <sup>b</sup> (0.01)	0.11 <sup>c</sup> (0.02)
Sea Surface Temperature (°C)	28.22 <sup>b</sup> (0.49)	28.03 <sup>c</sup> (0.17)	28.73 <sup>a</sup> (0.14)

### Fishing

Surveys (n=147) of fishing activity were conducted in the four villages of Kiritimati by two enumerators from the Kiribati Fisheries Department-Kiritimati Division in August 2007. The number of surveys conducted in each village was roughly proportional to the number of households in the village, except for the smallest village where a higher proportion was sampled due to the small number of households. Households were chosen haphazardly. The head of the household or other person sufficiently knowledgeable of the fishing activities of the household was interviewed after oral consent was obtained. The interviewee was asked to recall catch (kg) by family or species, effort (number of people and hours), gear, location, and habitat for all fishing trips conducted over the previous seven days. The fishing data were multiplied by an inflation factor, i.e. the number of households in the population that each household in the sample represents, to make population level estimates for each village.

### **Fish and Benthic Community Surveys**

To assess spatial variation in the abundance and biomass of fish communities, visual surveys of fish along three belt transects (25 m), separated by 10 m, were conducted by teams of paired divers at 25 sites in Palmyra and Kiritimati-NW during 2005 (Sandin *et al.* 2008, DeMartini *et al.* 2008) and 12 sites in Kiritimati-SE in 2007 (Walsh 2009) (Fig. 2-1). Fishes greater than or equal to 20 cm total length were counted in an 8-m wide strip as the transect was laid. Fishes smaller than 20 cm total length were counted in a 4 m wide strip in the reverse direction along the transect. Fishes were recorded to species. Sizes (total length) were estimated for every fish encountered in 5 cm size bins and sexes (initial phase females and terminal phase males) were identified for the protogynous parrotfish, *Chlorurus sordidus*. The total area surveyed per site for fishes greater than or equal to 20 cm total length was 600 m<sup>2</sup> (3 x 25 x 8 m) and 300 m<sup>2</sup> (3 x 25 x 4 m) for fishes less than 20 cm total length. Sites were no less than 1 km apart and at 10-12 m depth on the fore reef. After surveys of fish abundance and size were completed, the dive team also recorded the size and number of the initial and terminal phase parrotfish, in one-way swims over an area of ~3,000 m<sup>2</sup> (100 m x 30 m) to increase the number of males for later calculation of the size at sex change. Fish were classified to functional groups based on published diet studies (REFS) and biomass was estimated by using published length-weight relationships (Kulbicki *et al.* 2005; Froese & Pauly 2007).

The photoquadrat method was used to survey benthic cover along two transects (25 m) at 11 sites in Palmyra and 12 at Kiritimati-NW during 2005 (Sandin *et al.*



2008) and at 12 sites in Kiritimati-SE in 2007 (Walsh 2009). Photographs of a quadrat (0.9 X 0.6 m or 0.54 m<sup>2</sup>) were taken with a digital camera at ten randomly selected points along each of the two transects, for a total of 20 photographs. Percent cover of benthic functional groups was estimated by identifying the organisms under 100 random points per photograph. This information was used to assess spatial differences in percent cover of macroalgae, turf algae, crustose coralline algae, corals, and other benthic space occupying organisms at each location.

### **Oceanographic Data**

Chlorophyll a and sea surface temperature data analyses and visualizations used in this study were produced with the Giovanni online data system, developed and maintained by the NASA Goddard Earth Sciences (GES) Data and Information Services Center (DISC) (Acker & Leptoukh 2007). The MODIS/Aqua chlorophyll a and sea surface temperature monthly global 0.083° x 0.083° products were obtained for the area surrounding each study region to create area-averaged values. Areas for each study region were defined as the rectangle described by the range of the latitude and longitude of the visual survey sites +/- half of the distance of the data resolution (0.083°) (Palmyra: 5.93 N to 5.83 N, 162.15 W to 161.99 W; Kiritimati-NW: 2.08 N to 1.83 N, 157.61 W to 157.45 W; Kiritimati-SE: 2.03 N to 1.67 N, 157.37 W to 157.13 W). Monthly area-averaged values and standard deviations for chlorophyll a and sea surface temperature were averaged available and relevant time period (July 2002 through July 2007).

## Study species

Five study species were chosen to represent the major fish trophic groups (apex predators, benthic invertivores, omnivores, planktivores, and herbivores) based on abundance as assessed through visual surveys in 2005 (Sandin *et al.* 2008). The predator, *Lutjanus bohar* (snapper), mainly feeds on fish, is preyed on by reef sharks, and is a target of local fisheries (Allen 1985). It is protogynous and reproduces in mass spawning events (Allen 1985). The benthic invertivore, *Paracirrhites arcatus* (hawkfish), is typically associated with small branching corals, e.g. *Pocillopora* spp., *Acropora* spp., and *Stylophora* spp., feeds on shrimp, crabs, and other crustaceans and is known to be eaten by smaller groupers (Hiatt & Strasburg 1960; Randall & Brock 1960; Lieske & Myers 1994). The omnivore, *Plectroglyphidodon dickii* (damelfish), establishes territories on *Acropora* corals and feeds on filamentous algae, small benthic invertebrates, and occasionally small fishes (Myers 1991). The planktivore, *Chromis margaritifer* (damsel fish), feeds on zooplankton and is often found alone or in small groups near corals (Kuitert & Tono-zuka 2001; Froese & Pauly 2007). The herbivore *Acanthurus nigricans* (surgeonfish) feeds on filamentous algae and is a fishery target on Kiritimati (Choat *et al.* 2004; Walsh, pers. obs.). An additional herbivore, *Chlorurus sordidus* (parrotfish), which feeds on benthic algae, was chosen to examine spatial differences in size at sex change since it is a protogynous hermaphrodite that exhibits obvious changes in coloration between initial and terminal phases (Choat & Robertson 1975; Sano *et al.* 1984). Its known predators are snappers

and groupers and it is sometimes a target of the Kiritimati fishery (Froese & Pauly 2007; Walsh, pers. obs.).

### **Collections**

Collections of 19-109 individuals of each species (except *C. sordidus*) were made in each region using nets, spears, and hook and line. Collections were made in Palmyra during August 10-September 2, 2006 and in Kiritimati-NW during August 22-September 5, 2006. Collections were made in Kiritimati-SE during August 8-August 15, 2007. Additional individuals were collected from Kiritimati-NW to test for differences across years. Each individual was weighed, measured for length, dissected and its liver and gonad weighed following sexing.

### **Statistical Analyses**

Data from fishing surveys, underwater visual surveys and photography, and MODIS/Aqua were used to estimate mean values of fishing pressure, predation pressure, food availability, and environmental conditions for each region. Differences in these factors across regions were assessed using t-tests with Holm's sequential Bonferonni correction to account for multiple comparisons (Holm 1979).

Data from fish collection were used to estimate condition and reproductive effort for each species across regions. Condition was measured by adjusted total weight (controlling for length) and adjusted liver weight (controlling for total weight). A higher total weight for a given length, indicates that the fish have larger energy

stores (Hart & Reynolds 2002). Adjusted liver weight may be independent of adjusted total weight and indicate even higher energy stores because the liver is a storage area for fats, which may be re-allocated to gonads during reproductive periods (Delahunty & de Vlaming 1980). Gonad weight (controlling for total weight) is a typically measure of reproductive effort (Hart & Reynolds 2002). Gonad size can change seasonally and typically increases during the breeding season. To control for seasonal differences in gonad size across species, we collected individuals from each population during the same season each year. We only compared gonad weights for mature females from each population because fully matured females could be distinguish consistently in the field using macroscopic features of the oocytes. In addition to adjusted gonad weight, we estimated size at sex change for a the protogynous parrotfish, *C. sordidus*, as a additional metric of reproductive effort.

Differences in the relationship between total weight and standard length ( $\ln(W) = \ln(a) + b \ln(SL)$ ), liver weight and total weight ( $\ln(W_{liver}) = W_{total} + c$ ), and gonad weight and total weight ( $\ln(W_{gonad}) = W_{total} + c$ , females only) were estimated using generalized linear models (Stata v9) with region as factors. Models that represent all combinations (9) of effects of region on the intercept, slope, and/or both were tested (see Table A2-1). The best fit model was chosen using the Akaike information criterion corrected for small sample sizes. Adjusted means and associated standard errors and confidence intervals were then estimated using the best fit model (Sokal & Rohlf 1995). Multiple comparisons of adjusted means were conducted using t-tests with Holm's sequential Bonferonni correction (Holm 1979). The length at

which 50% of *C. sordidus* individuals were terminal phase males was estimated by fitting a logistic regression of the proportion of terminal phase males to the size class for each region.

Table 2-2. Summary of trends across regions in fishing, predation, food availability proxies, and metrics of condition and reproductive effort.

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Fishing		KirNW>>KirSE>PAL
Predation		PAL>KirSE>KirNW
Resources		
<i>Coral</i>		KirSE>PAL>KirNW
<i>Turf Algae</i>		KirNW>PAL>KirSE
<i>Macroalgae</i>		KirNW=PAL>KirSE
<i>Chlorophyll a</i>		KirNW>KirSE>PAL

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Condition		
<i>Weight</i>		
Predator	KIR-NW=PAL	
Invertivore	KIR-NW>KIR-SE>PAL	
Omnivore	KIR-NW>KIR-SE>PAL	
Planktivore	KIR-NW=KIR-SE=PAL	
Herbivore	KIR-NW>KIR-SE>PAL	
<i>Liver Weight</i>		
Predator	KIR-NW>PAL	
Invertivore	KIR-NW>KIR-SE=PAL	
Omnivore	KIR-NW=KIR-SE>PAL	
Planktivore	KIR-NW=KIR-SE=PAL	
Herbivore	KIR-NW=KIR-SE=PAL	
Reproduction		
<i>Gonad Weight</i>		
Invertivore	KIR-NW=KIR-SE=PAL	
Omnivore	KIR-NW=KIR-SE=PAL	
Herbivore	PAL>KIR-SE=KIR-NW	
<i>Size at Sex Change</i>		
Herbivore	KIR-NW>KIR-SE>PAL	

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## RESULTS

### Fishing, Predation, and Resources

The average fish catch in the Kiritimati-NW was over three times greater than in Kiritimati-SE (Table 2-1, Table 2-2). Predator biomass densities in Kiritimati-SE (124.36 g/m<sup>2</sup>) were similar to those in protected Palmyra Atoll (168.43 g/m<sup>2</sup>), whereas predator densities in Kiritimati-NW were about five times lower (24.76 g/m<sup>2</sup>) (Table 2-1, Table 2-2). Sharks were largely absent throughout Kiritimati due to shark finning, but were abundant on Palmyra. Coral cover shows the same trend as predators, suggesting that higher shelter may reduce the effective predation risk in Kiritimati-SE and Palmyra (Table 2-1, Table 2-2).

Overall cover of fleshy algae (turf and macroalgae) was highest in Kiritimati-NW (69%), intermediate at Palmyra (43%), and lowest at Kiritimati-SE (19%) (Table 2-1, Table 2-2). Numerical densities of *L. bohar*, *P. arcatus*, and *A. nigricans* decreased with increasing fishing pressure, possibly reducing competition for resources (Table 2-1). Numerical abundance of *C. margaritifer* followed patterns in chlorophyll a, with the greatest abundance in Kiritimati-NW. *P. dickii* was most abundant in Kiritimati-SE (Table 2-1, Table 2-2), where *Acroporid* coral were common.

### Condition

The predator (*L. bohar*) and the planktivore (*C. margaritifer*) showed no differences in adjusted mean weight across regions (Table 2-2, Figs. 2-2a & 2-2d).

The benthic invertivore (*P. arcatus*), omnivore (*P. dickii*), and herbivore (*A. nigricans*) had decreasing adjusted mean weight from Kiritimati-NW to Kiritimati-SE to Palmyra, correlating with decreasing fishing pressure (Table 2-2, Figs. 2-2b, 2-2c & 2-2e).



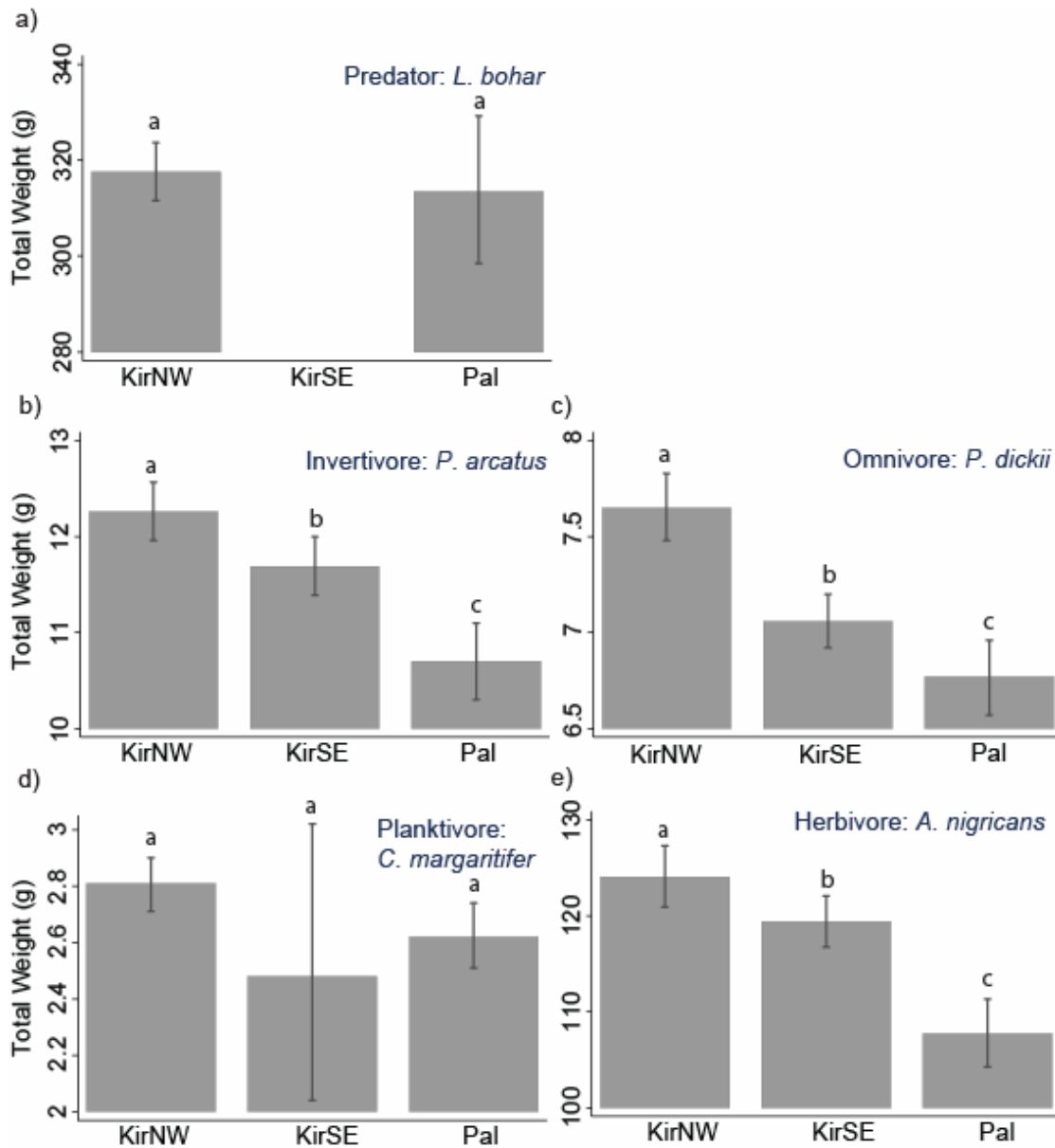


Figure 2-2. Adjusted mean total weight and 95% confidence intervals by regions from best fit models (see Table A2-2) for: a) *L. bohar* (model:  $F_{(2,111)}=7942.67$ ,  $p<0.0001$ ; KirNW,  $n=95$ ; Pal,  $n=19$ ), b) *P. arcatus* (model:  $F_{(5,215)}=866.43$ ,  $p<0.0001$ ; KirNW,  $n=71$ ; KirSE,  $n=109$ ; Pal,  $n=41$ ), c) *P. dickii* (model:  $F_{(4,186)}=375.52$ ,  $P<0.0001$ ; KirNW,  $n=64$ ; KirSE,  $n=85$ ; Pal,  $n=42$ ), d) *C. margaritifer* (model:  $F_{(5,133)}=354.78$ ,  $p<0.0001$ ; KirNW,  $n=75$ ; KirSE,  $n=25$ ; Pal,  $n=39$ ), and e) *A. nigricans* (model:  $F_{(3,234)}=1543.11$ ,  $p<0.0001$ ; KirNW,  $n=80$ ; KirSE,  $n=108$ ; Pal,  $n=50$ ). Adjusted mean weights that were determined to be significantly different by t-tests with Holm's sequential Bonferroni correction are indicated by a, b, or c.

Adjusted mean liver weight, an indication of fat stores, was lower at unfished Palmyra than at fished Kiritimati-NW for the predator, invertivore, omnivore, and planktivore (Table 2-2; Figs. 2-3a, 2-3b, 2-3c, 2-3d). Comparisons of liver weight within Kiritimati also showed lower liver weight at lightly fished Kiritimati-SE as compared to fished Kiritimati-NW for the invertivore (Table 2-2, Fig. 2-3b). The herbivore showed no differences in liver weight (Table 2-2, Fig. 2-3e), which may be due to fat storage in mesenteries surrounding the gut and in unique paired, retroperitoneal fat bodies posterior to the visceral cavity (Fishelson 1985).

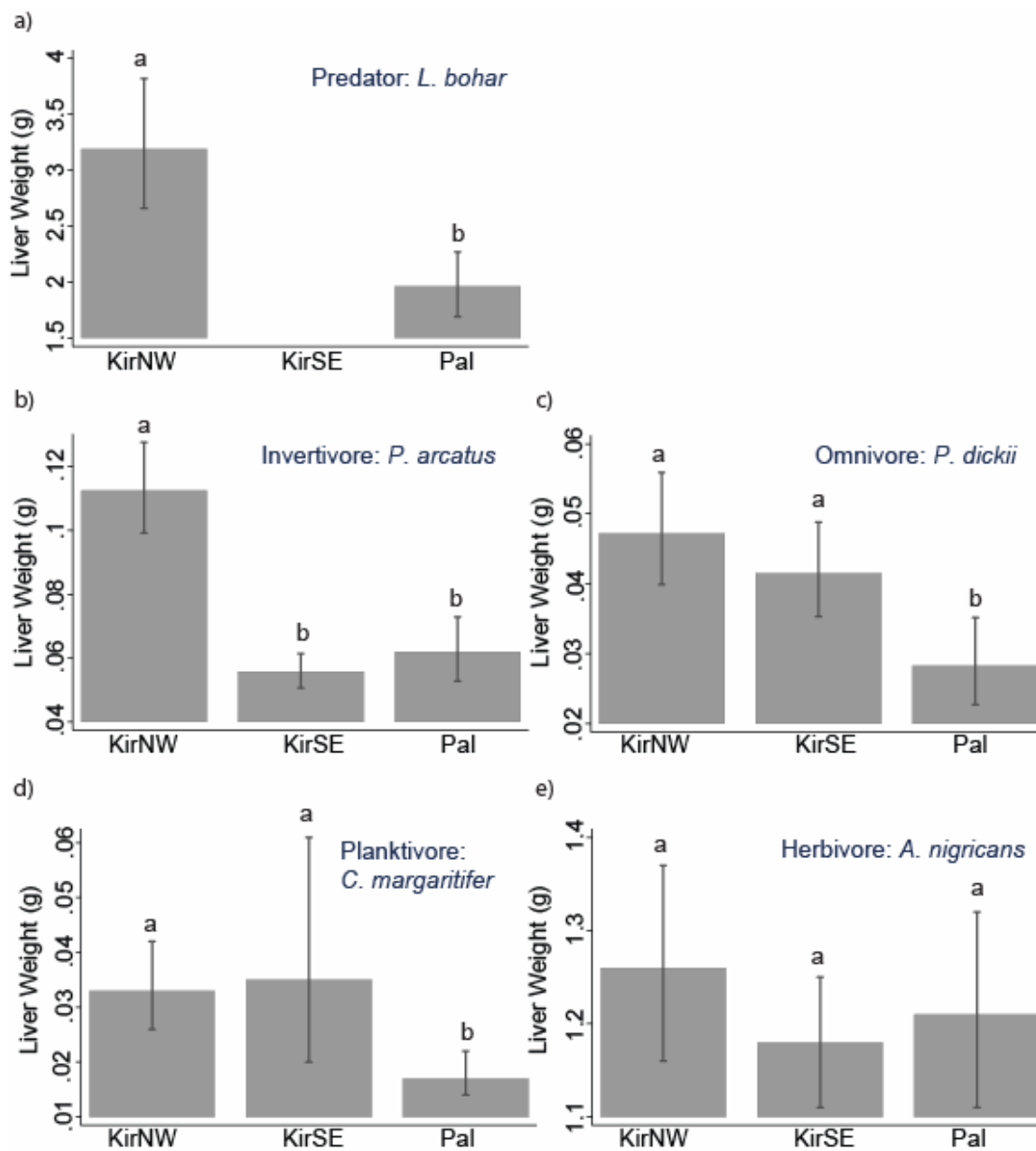


Figure 2-3. Adjusted mean liver weight and 95% confidence intervals by region from best fit models (see Table A2-3) for: a) *L. bohar* (model:  $F_{(2,66)}=131.53$ ,  $p<0.0001$ ; KirNW,  $n=54$ ; Pal,  $n=15$ ), b) *P. arcatus* (model:  $F_{(4,177)}=32.98$ ,  $p<0.0001$ ; KirNW,  $n=50$ ; KirSE,  $n=97$ ; Pal,  $n=35$ ), c) *P. dickii* (model:  $F_{(3,118)}=21.27$ ,  $p<0.0001$ ; KirNW,  $n=37$ ; KirSE,  $n=52$ ; Pal,  $n=33$ ), d) *C. margaritifer* (model:  $F_{(4,36)}=6.34$ ,  $p<0.001$ ; KirNW,  $n=12$ ; KirSE,  $n=13$ ; Pal,  $n=16$ ), and e) *A. nigricans* (model:  $F_{(4,186)}=116.27$ ,  $p<0.0001$ ; KirNW,  $n=8$ ; KirSE,  $n=44$ ; Pal,  $n=101$ ). Adjusted mean weights that were determined to be significantly different by t-tests with Holm's sequential Bonferroni correction are indicated by a, b, and c.

**Reproduction**

Only three species had sufficient numbers of reproductive females to compare differences in gonad weights. The invertivore and omnivore showed no differences in adjusted mean gonad weight across fishing regions (Table 2-2, Figs. 2-4a, 2-4b). The herbivore showed no differences in adjusted mean gonad weight across fishing regions within Kiritimati but had higher gonad weight at unfished Palmyra as compared to both regions in Kiritimati (Table 2-2, Fig. 2-4c).

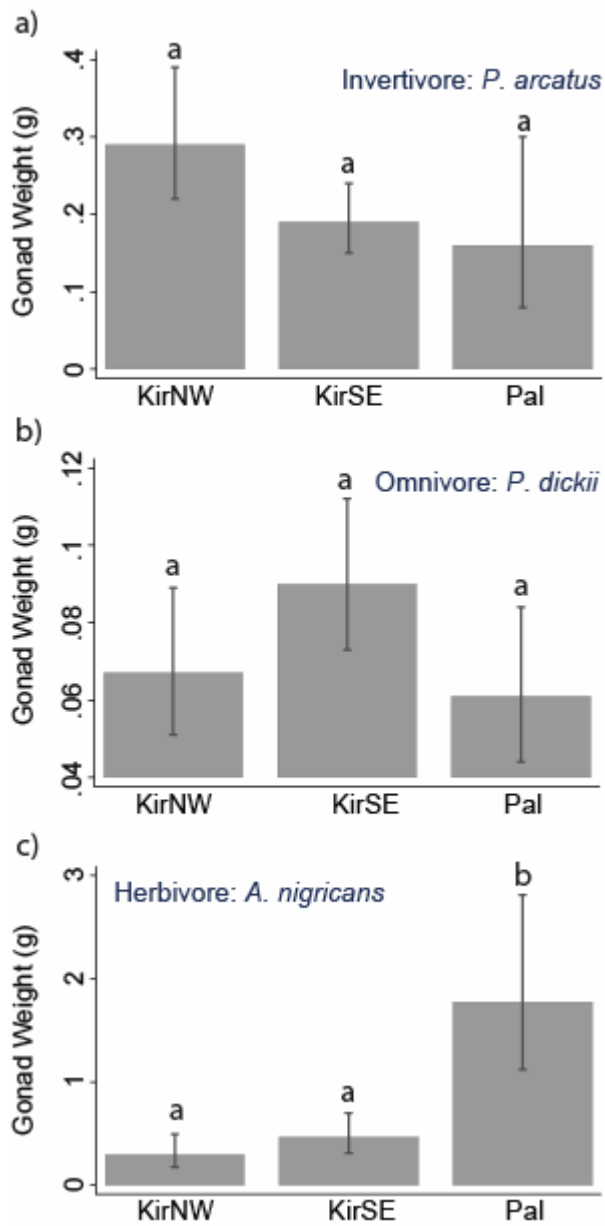


Figure 2-4. Adjusted mean gonad weight and 95% confidence intervals by region from best fit models (see Table A2-4) for: a) *P. arcatus* (model:  $F_{(3,51)}=8.85$ ,  $p<0.001$ ; KirNW,  $n=17$ ; KirSE,  $n=29$ ; Pal,  $n=9$ ), b) *P. dickii* (model:  $F_{(3,55)}=4.88$ ; KirNW,  $n=17$ ; KirSE,  $n=29$ ; Pal,  $n=13$ ), and c) *A. nigricans* ( $F_{(4,78)}=18.48$ ,  $p<0.0001$ , KirNW,  $n=16$ ; KirSE,  $n=39$ ; Pal,  $n=28$ ). Adjusted mean weights that were determined to be significantly different by t-tests with Holm's sequential Bonferroni correction are indicated by a, b, and c.

The length at which 50% of individuals are terminal phase males,  $L_{50}$ , was lowest at unfished Palmyra (21.08 cm), followed by lightly fished Kiritmati-SE (28.45 cm), and fished Kiritmati-NW (34.74 cm) (Table 2-2, Fig. 2-5).

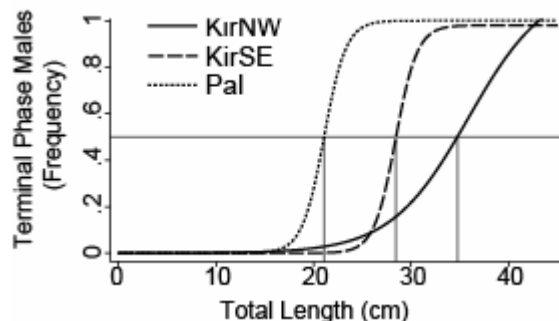


Figure 2-5. Fitted values from logistic regressions of the frequency of terminal phase males on size class for each region (all  $R^2 > 0.93$ , all  $p < 0.001$ ). Vertical lines indicate  $L_{50}$ , the length at which 50% of individuals are terminal phase males.

## DISCUSSION

All trophic groups exhibited lower condition, by at least one metric, in regions with lower fishing pressure and higher predator biomass (Table 2-2). Differences in adjusted mean weight were found between and within islands for three out of five fishes. Differences in adjusted mean liver weight between islands were found for four out of five species and differences within islands were only found in one fish. Out of the three species examined, only the herbivore showed a trade-off in condition and reproductive effort and only across islands (Table 2-2). The sex-changing herbivore had a smaller size at sex change in regions with higher fishing pressure (Table 2-2).

These findings support the hypothesis that increased predation risk on lightly fished or unfished reefs is associated with poor condition across a community of reef fishes, but trade-offs with reproduction are only observed when food resources are limited. Observable differences between and within islands also support the hypothesis that that these responses reflect plastic physiological responses rather than genetic differences between populations.

Community-wide decreases in condition in regions with little to no fishing and high predator biomass may be a consequence of changes in foraging behavior and reduced food intake due to high predation risk. A concurrent study of the behavior of representative fish species in the northern Line Islands found observable changes in behavior in association with differences in predator biomass. The time that fishes spent foraging was lower and time spent sheltering was higher when predation risk was high (Madin *et al.* 2007). Predation risk, therefore, may have indirect and negative consequences on condition by limiting foraging time and reducing the rate of food intake. In addition, different patterns of movement were associated with different levels of predators (Madin *et al.* 2007), suggesting that not only food intake but food quality may be reduced if fishes are not visiting preferred habitats. Both lower food intake and lower food quality associated with high predation risk could explain the observed patterns in condition.

Reduced condition may be associated with reduce reproductive effort because less stored energy is available to re-allocate to reproductive organs without significantly decreasing the probability of survival. However, if predation risk is

sufficiently high and food resources sufficiently limiting, reduced condition may be associated with higher reproductive effort because the benefits to current reproduction outweigh the marginal decrease in survival probability under already risky conditions. Condition and reproductive effort were negatively correlated for the herbivore, *A. nigricans*, on Palmyra but no correlation was observed for the invertivore, *P. arcatus*, and the omnivore, *P. dickii*. In Palmyra, *A. nigricans* may experience higher predation risk because it is larger-bodied than these other species and, therefore, at greater risk of predation by reef sharks. Reef sharks are abundant on Palmyra and weak or injured *A. nigricans* are quickly eaten (S. Walsh per. obs.). Lower food availability may also compound the effects of changes in foraging behavior on food intake and quality, making food resource limiting for *A. nigricans*. Turf algal cover, the primary food resource for *A. nigricans*, was lower at Kiritimati-SE (13%) and Palmyra (25%) than at Kiritimati-NW (53%). High densities of *A. nigricans* on Palmyra may increase competition for turf algae, further reducing food availability. Although we do not have a direct measure of food resources for *P. dickii* and *P. arcatus*, their food resources may be proxied by coral cover because *P. dickii* guards territories on plate corals (*Acropora* spp.) and *P. arcatus* are associated with branching corals (*Pocillopora* spp., *Acropora* spp., and *Stylophora* spp.) where it feeds on benthic invertebrates, such as stomatopods. Coral cover was lowest and plating corals were virtually absent under low predation conditions in Kiritimati-NW, indicating that food resources may have been limiting for *P. dickii* and *P. arcatus* under low predator conditions, not high predator conditions.



There are two alternative reasons why trade-offs in reproductive effort and condition were not observed in two out of three species: 1) these two species are income breeders, using energy from current food intake rather than from somatic stores of energy for reproduction or 2) intra-individual variation in resource acquisition and energy allocation is similar. Small animals with high metabolic rates may use current energy from foraging for reproduction (Sibley & Calow 1986), which would lead to no observable impact of reproductive effort on condition. For example, house wrens that had their brood size experimentally increased maintained the same body weight (Finke *et al.* 1987). In contrast, reproductive effort and condition are linked in capital breeders, organisms that use stored energy, because they draw on somatic or fat stores for reproduction. Since metabolic rate scales with body size (Gillooly *et al.* 2001) we can hypothesize that *P. dickii* (average 7.7 g, average this study) and *P. arcatus* (13.6 g, average this study) have higher metabolic rates than *A. nigricans* (133 g average this study) and are more likely to be income breeders and capital breeders, respectively.

Negative correlations in the trade-off between condition and reproductive effort are expected when the variation in resource acquisition is low relative the variation in energy allocation between individuals (Van Noordwijk & de Jong 1986). However, if variation in energy acquisition and allocation is somewhat similar across individuals, no trade-off will be observed. We have no information on variation in energy acquisition; however, the coefficient of variation in gonad weight is similar across species (*P. arcatus*, 0.56; *P. dickii*, 0.64; *A. nigricans* 0.66). Assuming equal

levels of variation in resource acquisition, these data do not support the hypothesis that the observation of a trade-off in reproduction and condition in *A. nigricans* only is explained by individual variation in resource acquisition and energy allocation. Instead, we suggest that differences in food resources and strategies of income versus capital breeders are better explanations. Although differences in the date of collection could also affect our result, this is unlikely because this would be expected to result in differences in mean adjusted gonad weight between Kiritimati-NW (August 22-September 5, 2006) and Kiritimati-SE (August 8-August 15, 2007), not between Palmyra and these regions (August 10-September 2, 2006).

Our study; however, is limited because it is a natural experiment, it may have had low power to detect differences in reproductive effort due to small sample sizes, and it used population metrics to infer changes in individual level phenomena (Stearns 1992). We have a limited ability to establish causality between fishing, predation, and resource availability and metrics of condition and reproductive effort because we did not experimentally manipulate these factors. However, the conditions in Kiritimati presents the closest example of a large-scale fishing experiment that we know of, because fishing pressure increased dramatically in recent years due to the re-settlement of people on the northern coast of Kiritimati from the Kiribati capital, Tarawa. In addition, small-scale manipulative experiments and large-scale natural experiments have linked fishing to the loss of predators and associated increase in fleshy algae (Burkepile & Hay 2006; Walsh 2009). Although our small sample sizes may have limited our ability to detect differences in reproductive effort in *P. arcatus* and *P.*

*dickii*, samples sizes for *A. nigricans* were only somewhat higher. Lastly, ideally we would measure differences condition and reproductive effort on the same individuals under different fishing, predation, and resource conditions using reciprocal transplant experiments or controlled laboratory experiments rather making measurements on different individuals. However, these methods would be infeasible for this study, though future research should consider the use of mesocosm experiments for reef fish communities. By comparing fish between and within islands, we were at least able to show that differences are likely not to be attributed to genetic differences between populations.

Despite their limitations, these results are an important first step to understanding the still unclear relationship between fishing, fish community structure and productivity (NRC 2006). Our results suggest that predators reduce condition, an indicator of somatic growth, for fishes from all trophic levels. Reduced condition may be related to enhance reproduction, especially for larger-bodied herbivorous fishes. The net impact of fishing predators on reef fisheries productivity will depend, however, on the relative contribution of and interaction between of individual somatic growth and population growth. If predators enhance fish community productivity by favoring higher reproductive effort despite decreased condition, especially productivity of herbivore populations, restoring predators may be a win-win for fisheries and conservation. Better estimates of the effect of fishing on life history parameters across reef fish communities are needed from both natural and manipulative experiments combined with careful surveys of fisheries production and

effort are needed to determine whether predators may enhance reef fisheries productivity.

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## APPENDIX

Table A2-1. Candidate Models. Candidate models with all combinations of two fixed factors (KirSE, Pal) that represent the region of collections and take values of zero and one. The natural logarithm of total weight was estimated with the natural logarithm of standard length as a covariate for all fishes. The natural logarithm of liver weight was estimated with total weight as a covariate. The natural logarithm of gonad weight was estimated with total weight as a covariate for all female fishes.

Model	Fixed Model Terms
1	KirSE+Pal+KirSE*(covariate)+Pal*(covariate)
2	KirSE+Pal
3	KirSE*(covariate)+Pal*(covariate)
4	KirSE+Pal+KirSE*(covariate)
5	KirSE+Pal+Pal*(covariate)
6	KirSE+ KirSE*(covariate)+Pal*(covariate)
7	Pal+ KirSE*(covariate)+Pal*(covariate)
8	KirSE+ Pal*(covariate)
9	Pal+KirSE(covariate)

Table A2-2. Comparison of Candidate Models for Condition. All models are specified with standard length (SL) (log transformed) as a covariate and total weight (log transformed) as the response variable. Best fit models are in bold.

Model	Fixed Model Terms	n	df	AICc
<i>L. bohar</i>				
1	Pal+Pal*ln(SL)	114	4	-219.97
2	Pal* ln(SL)	114	3	-221.96
<b>3</b>	<b>Pal</b>	<b>114</b>	<b>3</b>	<b>-221.99</b>
<i>P. arcatus</i>				
<b>1</b>	<b>KirSE+Pal+KirSE*ln(SL)+Pal*ln(SL)</b>	<b>221</b>	<b>6</b>	<b>-354.46</b>
2	KirSE+Pal	221	4	-351.5
3	KirSE* ln(SL)+Pal* ln(SL)	221	4	-353.3
4	KirSE+Pal+KirSE* ln(SL)	221	5	-352.10
5	KirSE+Pal+Pal* ln(SL)	221	5	-350.4
6	KirSE+ KirSE* ln(SL)+Pal* ln(SL)	221	5	-353.99
7	Pal+ KirSE* ln(SL)+Pal* ln(SL)	221	5	-351.59
8	KirSE+ Pal* ln(SL)	221	4	-352.4
9	Pal+KirSE*ln(SL)	221	4	-352.33

Table A2-2. Continued.

Model	Fixed Model Terms	n	df	AICc
<i>Pl. dickii</i>				
1	KirSE+Pal+KirSE*ln(SL)+Pal*ln(SL)	191	6	-365.81
2	KirSE+Pal	191	4	-366.7
3	KirSE* ln(SL)+Pal* ln(SL)	191	4	-366.16
4	KirSE+Pal+KirSE* ln(SL)	191	5	-367.84
5	KirSE+Pal+Pal* ln(SL)	191	5	-365.75
<b>6</b>	<b>KirSE+ KirSE* ln(SL)+Pal* ln(SL)</b>	<b>191</b>	<b>5</b>	<b>-367.94</b>
7	Pal+ KirSE* ln(SL)+Pal* ln(SL)	191	5	-364.79
8	KirSE+ Pal* ln(SL)	191	4	-340.04
9	Pal+KirSE*ln(SL)	191	4	-329.01
<i>C. margaritifer</i>				
<b>1</b>	<b>KirSE+Pal+KirSE*ln(SL)+Pal*ln(SL)</b>	<b>139</b>	<b>6</b>	<b>-142.20</b>
2	KirSE+Pal	139	4	-140.5
3	KirSE* ln(SL)+Pal* ln(SL)	139	4	-140.34
4	KirSE+Pal+KirSE* ln(SL)	139	5	-141.82
5	KirSE+Pal+Pal* ln(SL)	139	5	-139.28
6	KirSE+ KirSE* ln(SL)+Pal* ln(SL)	139	5	-141.06
7	Pal+ KirSE* ln(SL)+Pal* ln(SL)	139	5	-139.89
8	KirSE+ Pal* ln(SL)	139	4	-140.01
9	Pal+KirSE*ln(SL)	139	4	-140.88
<i>A. nigricans</i>				
1	KirSE+Pal+KirSE*ln(SL)+Pal*ln(SL)	238	6	-335.54
2	KirSE+Pal	238	4	-339.41
3	KirSE* ln(SL)+Pal* ln(SL)	238	4	-338.68
4	KirSE+Pal+KirSE* ln(SL)	238	5	-337.52
5	KirSE+Pal+Pal* ln(SL)	238	5	-337.60
6	KirSE+ KirSE* ln(SL)+Pal* ln(SL)	238	5	-336.94
7	Pal+ KirSE* ln(SL)+Pal* ln(SL)	238	5	-337.64
8	KirSE+ Pal* ln(SL)	238	4	-338.46
<b>9</b>	<b>Pal+KirSE*ln(SL)</b>	<b>238</b>	<b>4</b>	<b>-339.53</b>

Table A2-3. Comparison of Candidate Models for Liver Weight. All models are specified with total weight (WT) as a covariate and liver weight (log transformed) as the response variable. Best fit models are in bold.

Model	Fixed Model Terms	n	df	AICc
<i>L. bohar</i>				
<b>1</b>	<b>Pal+Pal*ln(WT)</b>	<b>69</b>	<b>4</b>	<b>70.40</b>
2	Pal* ln(WT)	69	3	81.79
3	Pal	69	3	95.66
<i>P. arcatus</i>				
1	KirSE+Pal+KirSE*ln(WT)+Pal*ln(WT)	182	6	234.79
2	KirSE+Pal	182	4	233.22
3	KirSE* ln(WT)+Pal* ln(WT)	182	4	236.53
<b>4</b>	<b>KirSE+Pal+KirSE* ln(WT)</b>	<b>182</b>	<b>5</b>	<b>232.65</b>
5	KirSE+Pal+Pal* ln(WT)	182	5	234.78
6	KirSE+ KirSE* ln(SL)+Pal* ln(WT)	182	5	239.00
7	Pal+ KirSE* ln(WT)+Pal* ln(WT)	182	5	234.88
8	KirSE+ Pal* ln(WT)	182	4	245.99
9	Pal+KirSE*ln(WT)	182	4	233.31
<i>Pl. dickii</i>				
1	KirSE+Pal+KirSE*ln(WT)+Pal*ln(WT)	122	6	195.64
2	KirSE+Pal	122	4	192.80
3	KirSE* ln(WT)+Pal* ln(WT)	122	4	192.80
4	KirSE+Pal+KirSE* ln(WT)	122	5	193.45
5	KirSE+Pal+Pal* ln(WT)	122	5	193.85
6	KirSE+ KirSE* ln(WT)+Pal* ln(WT)	122	5	195.55
7	Pal+ KirSE* ln(WT)+Pal* ln(WT)	122	5	194.92
<b>8</b>	<b>KirSE+ Pal* ln(WT)</b>	<b>122</b>	<b>4</b>	<b>192.33</b>
9	Pal+KirSE*ln(WT)	122	4	193.06
<i>C. margaritifer</i>				
1	KirSE+Pal+KirSE*ln(WT)+Pal*ln(WT)	41	6	54.64
2	KirSE+Pal	41	4	56.77
3	KirSE* ln(WT)+Pal* ln(WT)	41	4	57.95
<b>4</b>	<b>KirSE+Pal+KirSE* ln(WT)</b>	<b>41</b>	<b>5</b>	<b>52.03</b>
5	KirSE+Pal+Pal* ln(WT)	41	5	53.16
6	KirSE+ KirSE* ln(WT)+Pal* ln(WT)	41	5	53.90
7	Pal+ KirSE* ln(WT)+Pal* ln(WT)	41	5	53.23
8	KirSE+ Pal* ln(WT)	41	4	63.94
9	Pal+KirSE*ln(WT)	41	4	52.83

Table A2-3. Continued.

Model	Fixed Model Terms	n	df	AICc
<i>A. nigricans</i>				
1	KirSE+Pal+KirSE*ln(WT)+Pal*ln(WT)	191	6	142.79
<b>2</b>	<b>KirSE+Pal</b>	<b>191</b>	<b>4</b>	<b>138.63</b>
3	KirSE* ln(WT)+Pal* ln(WT)	191	4	138.99
4	KirSE+Pal+KirSE* ln(WT)	191	5	140.69
5	KirSE+Pal+Pal* ln(WT)	191	5	140.34
6	KirSE+ KirSE* ln(WT)+Pal* ln(WT)	191	5	140.34
7	Pal+ KirSE* ln(WT)+Pal* ln(WT)	191	5	216.91
8	KirSE+ Pal* ln(WT)	191	4	215.08
9	Pal+KirSE*ln(WT)	191	4	214.84

Table A2-4. Comparison of Candidate Models for Gonad Weight. All models are specified with total weight (WT) as a covariate and liver weight (log transformed) as the response variable. Best fit models are in bold. Females only.

Model	Fixed Model Terms	n	df	AICc
<i>P. arcatus</i>				
1	KirSE+Pal+KirSE*ln(WT)+Pal*ln(WT)	55	6	56.45
2	KirSE+Pal	55	4	54.15
3	KirSE* ln(WT)+Pal* ln(WT)	55	4	54.19
4	KirSE+Pal+KirSE* ln(WT)	55	5	56.46
5	KirSE+Pal+Pal* ln(WT)	55	5	53.93
6	KirSE+ KirSE* ln(SL)+Pal* ln(WT)	55	5	55.58
7	Pal+ KirSE* ln(WT)+Pal* ln(WT)	55	5	54.36
<b>8</b>	<b>KirSE+ Pal* ln(WT)</b>	<b>55</b>	<b>4</b>	<b>53.27</b>
9	Pal+KirSE*ln(WT)	55	4	55.01
<i>Pl. dickii</i>				
1	KirSE+Pal+KirSE*ln(WT)+Pal*ln(WT)	59	6	109.13
<b>2</b>	<b>KirSE+Pal</b>	<b>59</b>	<b>4</b>	<b>106.17</b>
3	KirSE* ln(WT)+Pal* ln(WT)	59	4	107.08
4	KirSE+Pal+KirSE* ln(WT)	59	5	108.36
5	KirSE+Pal+Pal* ln(WT)	59	5	106.88
6	KirSE+ KirSE* ln(WT)+Pal* ln(WT)	59	5	108.52
7	Pal+ KirSE* ln(WT)+Pal* ln(WT)	59	5	106.65
8	KirSE+ Pal* ln(WT)	59	4	106.37
9	Pal+KirSE*ln(WT)	59	4	106.74



Table A2-4. Continued.

Model	Fixed Model Terms	n	df	AICc
<i>A. nigricans</i>				
1	KirSE+Pal+KirSE*ln(WT)+Pal*ln(WT)	83	6	195.41
2	KirSE+Pal	83	4	194.10
3	KirSE* ln(WT)+Pal* ln(WT)	83	4	197.22
4	KirSE+Pal+KirSE* ln(WT)	83	5	195.93
<b>5</b>	<b>KirSE+Pal+Pal* ln(WT)</b>	<b>83</b>	<b>5</b>	<b>193.18</b>
6	KirSE+ KirSE* ln(WT)+Pal* ln(WT)	83	5	198.65
7	Pal+ KirSE* ln(WT)+Pal* ln(WT)	83	5	193.47
8	KirSE+ Pal* ln(WT)	83	4	197.94
9	Pal+KirSE*ln(WT)	83	4	193.75

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### **CHAPTER 3: How and Why Alternative Incomes Fail to Reduce Fishing and Improve Human Welfare**

## ABSTRACT

Alternative income programs are a common strategy used to reduce resource extraction and improve human welfare but it is unclear whether these programs are successful because they are rarely implemented with evaluation in mind. Taking advantage of a natural experiment in Kiribati, Central Pacific, we tested the effect of an agricultural subsidy on fishing and human welfare. We developed a model of household fishing and agricultural production and consumption. Contrary to predictions of this model and the programs aims, some households actually increased fishing and decreased agricultural labor. To explain these data, we developed an alternative model in which households also derive utility from labor in fishing. This model predicts an increase in fishing in response to the subsidy when households have a revealed preference for fishing prior to the subsidy, which was supported empirically. Conservation-development strategies therefore need to consider heterogeneity in household behavior and non-market benefits from traditional livelihoods.

## INTRODUCTION

Fishing is a primary cause of global coral reef decline (Jackson *et al.* 2001, Pandolfi *et al.* 2003). Marine reserves have been created to reduce fishing pressure; however, only 9% of reserves are successful (e.g. prevent poaching) (Mora *et al.* 2006). Improved implementation and evaluation of incentive-based conservation strategies such as enforcement, conservation payments, and alternative income

programs are needed to reduce fishing pressure on coral reefs. While there has been relative success using only enforcement for protected areas generally (Bruner *et al.* 2001), pure enforcement schemes often provoke conflict, which may undermine conservation efforts (Ferraro & Kramer 1997). Some marine reserves and other fisheries management tools are designed to compensate fishermen for their loss in fishing grounds or catch in one period by improving their total catch and profits in the long-run (Sanchirico *et al.* 2005). However, short-run and even long-run welfare losses often occur due to the environmental (e.g. very low or very high dispersal benefits relative to foregone harvest) or market setting (e.g. incomplete resource market or complete labor market) (Sanchirico & Wilen 2001, Muller & Albers 2004). Consequently, some alternate form of compensation is needed for conservation strategies to be successful (Wells *et al.* 1992, Tisdell 1995).

*Integrated conservation-development programs* (ICDP) have emerged in the last three decades in response to this need. ICDPs attempt to create or enhance alternative incomes as a way to reduce resource extraction and improve local welfare (Wells *et al.* 1992). Increasing agricultural productivity is expected to decrease reliance on natural resources and is a typical strategy used in ICDPs (OECD 1996, Wilkie & Godoy 2000, Bennett 2002). The majority of the work on agricultural development and natural resources has been in terrestrial environments, particularly tropical forests (e.g. Oates 1999). There are few examples examining the effect of alternative incomes on marine resources (Wilcox 1994, e.g. Pollnac *et al.* 2001, Sievanen *et al.* 2005, Thiele *et al.* 2005).

Reviews of ICDPs have found few successes (Wells *et al.* 1992, Smith *et al.* 1998, UNDP 2000, Hughes & Flintan 2001). The major challenge in understanding how and why ICDPs fail is that few ICDPs are designed with evaluation in mind. Data is rarely collected before and after implementation, and, more importantly, non-random implementation generates a strong selection bias. Rather than randomly selecting treatment and control villages or households so that one can estimate the effect of the treatment, controlling for other changes across time, villages or households are often chosen for political or economic reason or self-selected. In the case of self-selection, the treatment group is biased because it will contain households that are most likely to give up the resource extractive activity. Here, we were able to take advantage of a natural experiment in the Republic of Kiribati that had limited selection bias. In 2004, the government of the Republic of Kiribati subsidized the buying price of copra, a coconut product, with the aim of reducing fishing pressure on local reefs and improving welfare. Given that almost all households in Kiribati engage in fishing, own some land with coconut trees, and both fishing and copra production do not require significant capital investments, virtually all households were included in the treatment.

In this paper, we first develop a simple model of the household that represents the standard assumptions that motivate ICDPs. This model predicts that a copra price subsidy should increase labor in copra, decrease labor in fishing, and improve overall welfare. However, this model does not explain the observation of a significant number households *increasing* fishing labor and *decreasing* copra labor over the time period

covering the price subsidy increase. We thus develop an alternative model that simply assumes fishermen may enjoy fishing. This model predicts that if fishing labor is equated to leisure households will increase fishing labor in response to the price subsidy. We tested the predictions of this model on data collected from a survey of 329 households in 2007 that collected retrospective data on labor allocation, income, production, capital, household attributes, and opinions on changes in welfare and fisheries, as well as income satisfaction covering the period 2001 to 2006. Our results suggest that households respond heterogeneously to the copra subsidy and that enjoyment of fishing caused the copra subsidy to have an overall perverse effect on fishing labor. These results have important implications for ecosystem health, long-run welfare, and the design of ICDPs when significant non-monetary benefits may be derived from an occupation.

This paper is organized as follows: section two reviews the existing literature on ICDPs and non-monetary benefits of particular occupations; section three presents the models of the household and the comparative static results; section four presents the estimation strategy, section five describes the data, section six presents the empirical results; and section seven discusses the results, focusing on implications for the ecosystem, welfare, and ICDP design.

## **EXISTING LITERATURE**

Integrated conservation and development programs (ICDP) aim to fulfill both conservation and economic development goals (Worah 2000). ICDPs most often

involve a complimentary biodiversity conservation program, such as a protected area, and a rural development program (Hughes & Flintan 2001). More broadly, ICDPs are rural sustainable development programs. As of 2001, there were an estimated three hundred or more ICDPs worldwide, supported by hundreds of millions of dollars from governments and international donor (Hughes & Flintan 2001). Designing and implementing successful ICDPs has been far more difficult than marketing the idea and raising the funds (Wells *et al.* 1992). Yet, it is still unclear if ICDPs have failed and why because few ICDPs include objective evaluation components that gather empirical data on both biological and economic outcomes (Kremen *et al.* 1994, Larson *et al.* 1997, Smith *et al.* 1998).

The rural development components of ICDPs take various forms including social or infrastructure development, adding value to natural resources through marketing and ecotourism, resource access and benefit sharing, and alternative livelihoods such as agriculture, agroforestry, and crafts. In this paper, we focus on an alternative livelihood program. Alternative livelihood programs have been criticized for not providing a clear link between conservation and development and for decreasing conservation incentives by weakening the dependence on the natural resource (Hughes & Flintan 2001). Moreover, many failures have been attributed to a lack of understanding of the cultural context in which the programs are introduced.

On the positive side, alternative income programs associated with marine protected areas have been suggested to increase compliance with new regulations (Thiele *et al.* 2005, Pollnac *et al.* 2001) and to be a good predictor of various measures

of MPA success, including coral mortality, perceived resource change, infrastructure, and community empowerment (Pollnac *et al.* 2001). However, alternative incomes have been also associated with lower perceived quality of life and involvement in conservation activities (Thiele *et al.* 2005). A major problem with these studies, however, is that it is impossible to separate the effect of alternative incomes and investment in marine protected area programs broadly. Moreover, the authors of these studies did not explicitly measure changes in fishing labor allocation or fish stocks.

Sievanen *et al.* (2005) investigated whether fishermen who were encouraged to engage in seaweed farming reduced their fishing pressure. But this study is limited by the fact that it only observed fishermen who were self-selected, rather than randomly selected into the program, and did not measure any biological outcomes. The study showed that seaweed farming significantly increased income and was also associated with increased ownership of electronics and sometimes fishing capital. However, it was not associated with a decrease in the number of fishermen or fishing effort. Sievanen *et al.* (2005) argue that a lack of reduction in fishing pressure may be due to the fact that seaweed farming only requires labor periodically and that labor may be provided by women and children. Most fishermen that engaged in seaweed farming never gave up fishing entirely.

In order to understand why fishermen would not switch to an alternative livelihood that provides a much higher income, such as seaweed farming, we need to consider the non-monetary benefits associated with fishing. Wage rates in alternative livelihoods programs may understate the opportunity cost of fishing if non-monetary

benefits are significant (Berman 1997). Anthropologists (Pollnac & Poggie 1988, Gatewood & McCay 1990) suggest that the enjoyment of fishing explains why fishermen often choose fishing over other jobs with higher wages. Attitudinal surveys of fishermen in the Philippines report that fishermen will not give up fishing for other occupations (although they would consider them for supplemental income) because they enjoy the income and lifestyle associated with fishing (Pollnac *et al.* 2001, CRMP 2000). This attitude is not particular to developing countries. North American fishermen have high levels of job satisfaction that are attributed to factors that represent “self-actualization,” suggesting that fishing relates to individuals’ need to fulfill themselves, rather than just their need to sustain themselves (Smith 1976, Apostle *et al.* 1985, Pollnac & Poggie 1988). These attitudes may be associated with other types of traditional livelihoods and explain, in part, why development programs are limited in their effect on rural communities.

### **HOUSEHOLD MODEL**

We develop here a model of the household under standard assumptions and show that increasing the wage in the alternative income activity, copra production, should reduce fishing and improve welfare. We then show that observed household behavior in Kiribati is not consistent with the predictions of this model, motivating the development of an alternative model that allows analysis of possible non-monetary benefits from fishing.



### Standard Model

Consider a household that makes its living through the production of copra, the dried meat of coconuts, or other labor, primarily fishing. The local fishery is open access and fishing is mostly done on nearby coral reefs with simple technology, such as handlines, gillnets and canoes (and sometimes with small motors). Fish are either consumed by the household or sold in local markets. Coconuts are harvested from trees on household land. Little to no improvement is done to the land<sup>1</sup>. Coconuts simply fall to the ground, are collected by household members, and the meat is removed and dried. Copra is sold to local agents from the government owned copra exporting companies. Cash from copra is primarily used to purchase rice, which is imported. We will ignore capital because land and credit markets are non-existent or incomplete and instead focus on options of the household close to the extensive margin. In addition, there are no formal labor markets, so household production is almost totally dependent on household labor only.

In this economy, the standard household problem is to maximize utility from consuming rice ( $r$ ), fish ( $f$ ) and leisure ( $l$ ) subject to the household's income and their labor endowment ( $\bar{L}$ ).

$$(1) \quad \max_{r,f,l} u(r, f, l)$$

$$(2) \quad \text{s.t. } r + p^f f = p^c G(L^c) + H(L^o)$$

$$(3) \quad \bar{L} = l + L^c + L^o, l > 0, L^c > 0, L^o > 0, r > 0, f > 0$$

---

<sup>1</sup> Although copra plantations existed in Kiribati when it was a British colony, copra production since independence is done on household land and rarely involves fertilizer, clearing of undergrowth, or intentional planting of coconut trees. Coconuts are left to grow into trees or harvested opportunistically.

Total imputed household income is derived from the value of copra production ( $p^c G(L^c)$ ) and other labor ( $H(L^o)$ ), where  $p^c$  is the government purchasing price of copra,  $L^c$  is household labor in copra, and  $L^o$  is household labor in other activities. In this model, all income is spent on rice and fish and  $p^f$  is the local price for fish. We normalize on the price of rice and focus on an interior solution where households consume some rice, fish, and leisure and participate in both fishing and copra.

The first order conditions for an interior maximum are:

$$(4) \quad \frac{\partial u / \partial f}{\partial u / \partial r} = p^f$$

$$(5) \quad \frac{\partial u / \partial l}{\partial u / \partial r} = \frac{\mu}{\lambda}$$

$$(6) \quad \frac{\partial H / \partial L^o}{\partial G / \partial L^c} = p^c$$

$$(7) \quad r + p^f f = p^f F(L^f) + p^c G(L^c)$$

$$(8) \quad \bar{L} = l + L^f + L^c$$

As expected, equation (4) requires consumption decisions to be made such that the marginal rate of substitution between rice and fish is equal to the price ratio. Similarly, equation (5) requires that the consumption of rice relative to leisure is equal to ratio of the shadow price of labor and income. Labor allocation decisions are to be made such that the marginal rate of technical substitution should equal the wage ratio (6). Also, the household spends all its income on consuming rice and fish (7) and the sum of leisure and labor in fishing and copra must equal the household labor endowment (8).

### Comparative Statics

Predictions of how households will respond to a copra subsidy, which results in a higher copra purchase price,  $p^c$ , follow directly from the first order conditions. First, we assume that the marginal productivity of other labor is constant and that the marginal productivity of labor in copra is decreasing. These may be reasonable assumptions because fishing in Kiribati occurs mostly closed to shore, while extensive reef areas remain unfished or lightly fished due to distance and low technology. In contrast, land resources are very limited on Kiribati atolls and most household land can be reach on foot. Under these assumptions, if the price of copra increases, consumption of all goods will increase (assuming all goods are normal) and either the marginal productivity of copra labor must decrease or labor in copra must increase. Therefore, households would be expected to unambiguously increase copra labor at an interior solution.

Second, we assume that both marginal productivity of copra labor and all other labor is decreasing. If the price of copra increases, the consumption of all goods will increase if all goods are normal. The ratio of the marginal productivity of other labor to copra labor must increase to compensate for the increase in the price of copra. Three alternative changes in labor allocation may occur in order to make this adjustment: a) decreases in copra labor may be associated with large decreases in other labor and increases in leisure ( $L^c < 0, L^o < 0, l > 0$ ), b) increases in copra labor may be associated with decreases in other labor of similar magnitude and ambiguous changes for leisure ( $L^c > 0, L^o < 0, l ?$ ), and c) large increases in copra labor may be

associated with smaller increases other labor and decreases in leisure ( $L^c \gg 0, L^o > 0, l < 0$ ). The third scenario is eliminated if all goods, in particular leisure, are assumed to be normal.

A simple comparison of household copra labor, other labor, and leisure before (2001) and after (2006) the copra subsidy shows that the standard model predicts 23.25% of households' responses under the first set of assumptions and 28.03% of households' responses under the second set of assumptions (Table 3-1). A remaining 26.75% or 21.97% of households' responses are not predicted by the standard model (Table 3-1). Half of households' responses do not fit the assumption of an interior solution (some labor did not change over the period), which may be the result of using recall data (see section on data) (Table 3-1). Importantly, 21.97% of households increase other labor and 26.75% of households decreased their labor in copra, which was the opposite of the result intended by the copra subsidy (Table 3-1). These observations show that the standard model is insufficient to describe the observed behavior.

Table 3-1. The percentage of households by changes in copra labor, other labor and leisure between 2001 and 2006.

Case	Changes in Labor	% Households
1	$L^c < 0, L^o < 0, l > 0$	19.11
2	$L^c < 0, L^o > 0, l < 0$	3.18
3	$L^c < 0, L^o > 0, l > 0$	4.46
4.	$L^c < 0, L^o > 0, l = 0$	0
5.	$L^c < 0, L^o = 0, l > 0$	3.50
Subtotal		30.25
6.	$L^c > 0, L^o < 0, l > 0$	5.10
7.	$L^c > 0, L^o > 0, l < 0$	14.33
8.	$L^c > 0, L^o < 0, l < 0$	3.82
9.	$L^c > 0, L^o < 0, l = 0$	0
10.	$L^c > 0, L^o = 0, l < 0$	5.10
Subtotal		28.35
11.	$L^c = 0, L^o > 0, l < 0$	14.33
12.	$L^c = 0, L^o < 0, l > 0$	11.15
13.	$L^c = 0, L^o = 0, l = 0$	15.92
Subtotal		41.40
TOTAL		100.00

### Alternative Model

It seems possible that general equilibrium effects due to an increase in the price of copra could explain the increase in other labor (primarily fishing) because an increase in consumption of fish could lead to an increase in the price of fish, drawing labor back into fishing. However, in order for this to occur, the price of fish would have to increase faster than the price of copra, which we do not observe (Figure 3-1).

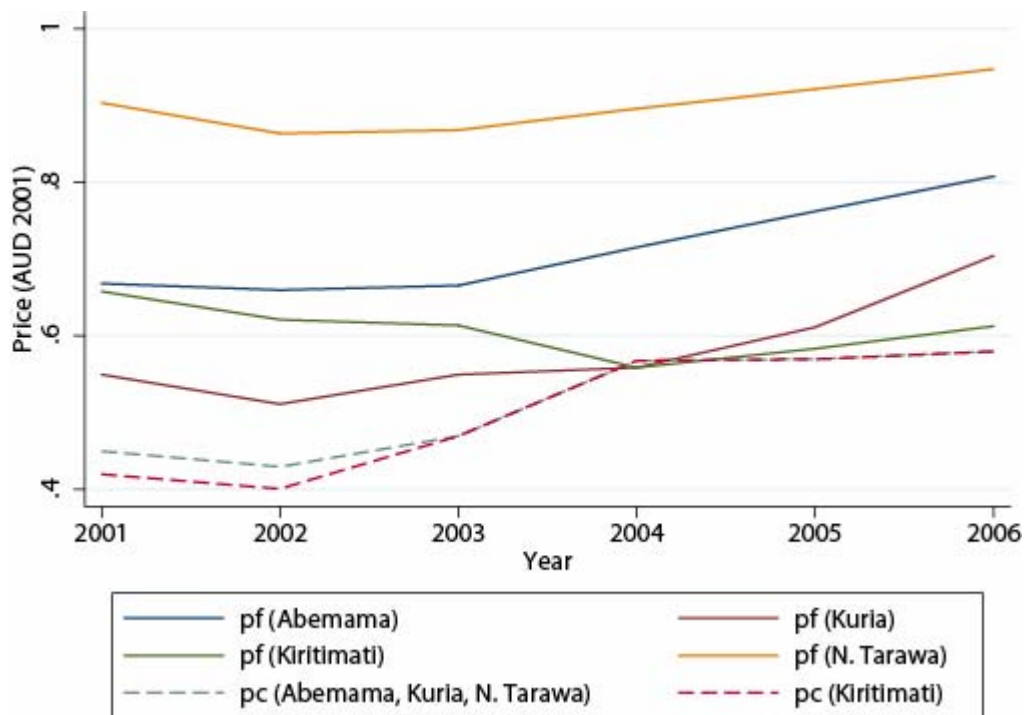


Figure 3-1. Copra and fish prices by island and year.

An alternative, more parsimonious, mechanism by which labor in fishing might increase in response to the copra price increase would be if people like to fish. Fishing produces fish but it may also provide direct benefits through the act of fishing<sup>2</sup>.

In an alternative model that includes fishing as a consumption good, the household problem is to maximize consumption from rice ( $r$ ), fish ( $f$ ), leisure ( $l$ ), and fishing labor ( $L^f$ ) subject to household income and the labor endowment ( $\bar{L}$ ).

<sup>2</sup> This seems to be a reasonable assumption that may be general to fishing, given the anthropological evidence for significant non-monetary benefits from fishing (Pollnac & Poggie 1988, Gatewood & McCay 1990), and specifically to this study, given personal observations of enumerators employed for this study complaining about not being able to fish.

$$(9) \quad \max_{r,f,l,L^c,L^f} u(r,f,l,L^f)$$

$$(10) \quad r + p^f f = p^c G(L^c) + p^f F(L^f) + \tilde{H}(L^o)$$

$$(11) \quad \bar{L} = L^c + L^f + L^o + l, L^c > 0, L^f > 0, L^o, l > 0, r > 0, f > 0$$

Assuming all goods are normal, under this model specification, we would expect that an increase in the price of copra would increase the consumption of all goods, including fishing labor. If both fishing labor and leisure increase, the sum of copra labor and all other labor must decrease. The predictive power of this model, relative to the standard model, and the expected magnitude of the change in fishing labor will depend, in part, on households' enjoyment of fishing relative to other consumption goods.

### EMPIRICAL ESTIMATION

To test the predictions of our models, we considered reduced form models of copra and fishing labor:

$$(12) \quad \ln(L_{it}^c) = \alpha_i^0 + \alpha_i^1 p_t^c + \alpha_i^2 p_t^f + \varepsilon_{it}$$

$$(13) \quad \ln(L_{it}^f) = \beta_i^0 + \beta_i^1 p_t^c + \beta_i^2 p_t^f + \varepsilon_{it}$$

where the price of copra,  $p_t^c$ , and the price of fishing,  $p_t^f$ , predict labor allocation. Ideally, we would estimate these equations for each household individually; however, given the limited data on each household we instead used household specific interaction terms to separate general responses from household specific responses. Labor allocation, for instance, responds to price changes generally and specifically based on household characteristics. Household demographics,  $D_{it}$ , are represented in

the constant terms,  $\alpha_i^0 = (\alpha^3 + \alpha^4 D_{it})$  and  $\beta_i^0 = (\beta^3 + \beta^4 D_{it})$ . Household preferences for goods that can be purchased with cash (i.e. rice) and fishing are unobservable and, hence, the fraction of labor in copra and fishing in the first time period were used to instrument for these preferences, respectively. Consequently, the response of labor in the two production activities to a change in copra price has a general component and

household specific component,  $\alpha_i^1 = \left( \alpha^5 + \alpha^6 \times \frac{L_{i0}^c}{L_{i0}^c + L_{i0}^f} \right)$  and

$\beta_i^1 = \left( \beta^5 + \beta^6 \times \frac{L_{i0}^f}{L_{i0}^c + L_{i0}^f} \right)$ . The response of labor to a change in fish price is

represented similarly,  $\alpha_i^2 = \left( \alpha^7 + \alpha^8 \times \frac{L_{i0}^c}{L_{i0}^c + L_{i0}^f} \right)$  and  $\beta_i^2 = \left( \beta^7 + \beta^8 \times \frac{L_{i0}^f}{L_{i0}^c + L_{i0}^f} \right)$ .

These models were tested using data from a household survey conducted in the Republic of Kiribati.

## DATA

Data on individual households over the period 2001-2006 was collected by implementing a national level household survey in May and June 2007. It was necessary to use retrospective data collection because the data of interest were either not collected or were only available in aggregate. The survey instrument was developed with input from officers from the Ministry of Finance and Ministry of Fisheries and pre-tested on 85 households on two islands in December 2006.



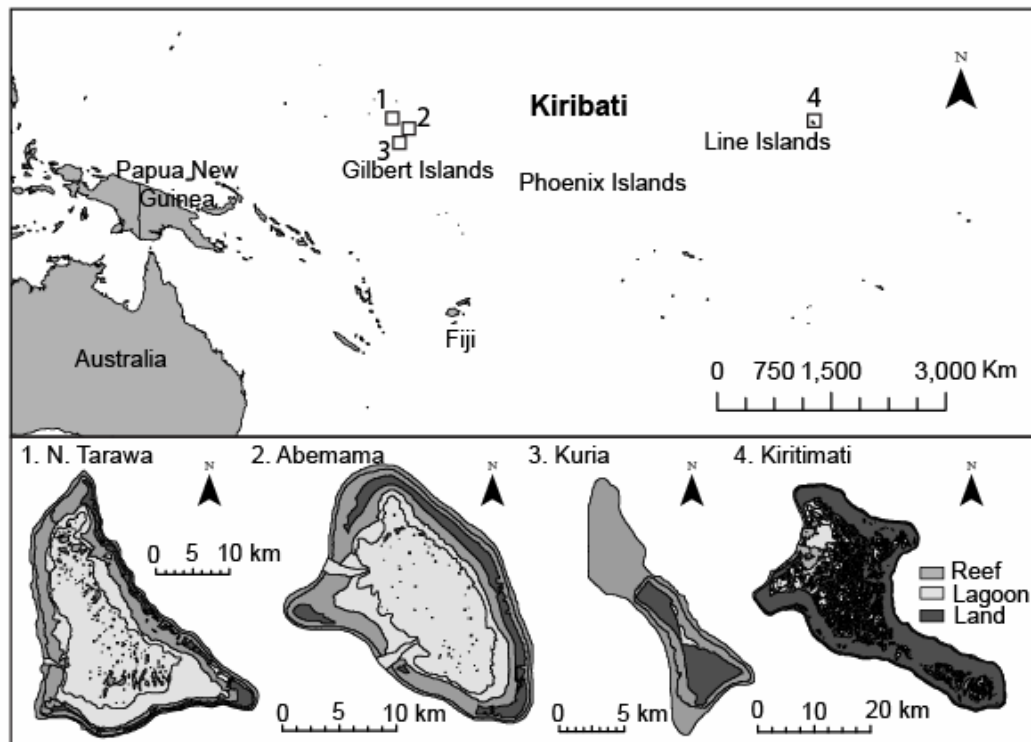


Figure 3-2. Map of study sites. The Republic of Kiribati is comprised of 33 islands in three island chains: Gilbert, Phoenix, and Line Islands. Four islands out the 20 populated islands were chosen by the probability that a household from each island would appear in a random sample of the population. The four study islands are 1) N. Tarawa, 2) Abemama, 3) Kuria, and 4) Kiritimati. Focused ecological surveys were conducted on Kiritimati.

### Sampling Design

A cluster sampling design was used for the household survey. A total of 329 households were surveyed on four islands (Figure 3-2) and asked retrospective questions covering the period 2001-2006. This resulted in a 2% sample of the population and a total of 1,974 observations. Each island was considered as a different cluster. Islands were chosen based on the probability that a household would be drawn

from a random sample of the population (households per island/total households). The target number of households surveyed at each island was proportional to the population of the island. Households from each village in a given island were surveyed in order to capture the variability within each island. Households are generally arranged linearly along the single or main road that runs the length of each island. This arrangement was used to randomly select households. A random number from 1-5 was chosen prior to entering a village and every  $n^{\text{th}}$  household was visited.

### **Survey Design**

The survey was designed to obtain data on income, labor, and production from various economics activities, income from other sources, capital related to fishing and copra, ownership of household goods, and household characteristics over the period 2001 to 2006. The survey also included discrete choice and open ended questions about welfare, income options and satisfaction, and the status of the fishery and conservation.

### **Survey Implementation**

Surveys were conducted by the author and a trained field assistant with translation by local Fisheries Assistants. Upon arriving at a household, a household head (male or female with sufficient knowledge of household activities) was identified. The purpose of the project and the nature and duration of the survey was described generally prior to asking for oral consent. Quantitative answers were

obtained for capital ownership, household goods, and household characteristics. However, for income, labor and production, quantitative data was obtained for as many years as the subject could recall and five-level Likert scale was used for the other years. The survey was followed by de-briefing questions.

## **EMPIRICAL RESULTS**

### **Household Level Effects**

The reduced form model for copra labor explained 62% of the variation in copra labor across households and time (Table 3-2). Copra price alone had a positive effect on copra labor ( $\beta = 7.46$ , Robust SE=6.43); however copra price interacted with the fraction of copra labor in 2001 had a negative effect ( $\beta = -16.25$ , SE=8.59). Fish price showed the opposite trend. Overall, the effect of the copra price on copra labor was positive when the fraction of labor in copra in 2001 was low (indicating high enjoyment of fishing) and negative when the fraction of labor in copra was high (indicating low enjoyment of fishing) (Figure 3-3a).

The reduced form model of fishing labor explained 46% of the variation across households and time and showed the opposite responses to price changes (Table 3-3). Copra price alone had a negative effect on fishing labor ( $\beta = -10.07$ , Robust S.E.=5.21), while the interaction between copra price and the fraction of labor in fishing in 2001 had a positive effect ( $\beta = 21.46$ , Robust S.E.=9.28). The effect of fish price was the opposite. The effect of the copra price conditional on the fraction of labor in fishing showed that households with a low fraction of fishing labor in 2001 (indicating low

enjoyment of fishing) decreased their fishing labor in response to the copra price increase, while households with a high fraction of fishing labor in 2001 (indicating a high enjoyment of fishing) increased their fishing labor (Figure 3-3b).

Table 3-2. Ordinary least squares estimate of copra labor (log transformed).

<i>Description of explanatory variable</i>	$\beta$	<i>Robust SE</i>
copra price	7.46	6.43
copra price* $\frac{L_{i0}^c}{L_{i0}^c + L_{i0}^f}$	-16.25	8.59
fish price	-12.90	4.30
fish price* $\frac{L_{i0}^c}{L_{i0}^c + L_{i0}^f}$	21.98	4.31
Capital		
bicycles	0.24	0.11
motorcycles	0.45	0.19
gillnet	-0.07	0.10
handlines	0.10	0.06
canoes	0.73	0.44
motor	0.17	0.31
ln(land)	0.99	0.21
Demographics		
number of household members	0.09	0.06
number of males aged 15-60	-0.05	0.08
Constant	-3.32	1.61
N	1872	
R <sup>2</sup>	0.62	

Table 3-3. Ordinary least squares estimate of fishing labor (log transformed).

<i>Description of explanatory variable</i>	$\beta$	<i>Robust SE</i>
copra price	-10.07	5.21
copra price* $\frac{L_{i0}^f}{L_{i0}^c + L_{i0}^f}$	21.46	9.28
fish price	5.46	5.33
fish price* $\frac{L_{i0}^f}{L_{i0}^c + L_{i0}^f}$	-8.24	6.34
Capital		
bicycles	0.46	0.17
motorcycles	0.88	0.35
gillnet	0.16	0.19
handlines	0.38	0.26
canoes	0.97	0.51
motor	0.15	0.14
ln(land)	0.36	0.03
Demographics		
number of household members	0.05	0.05
number of males aged 15-60	0.33	0.07
Constant	-6.78	1.88
N	1851	
R <sup>2</sup>	0.46	

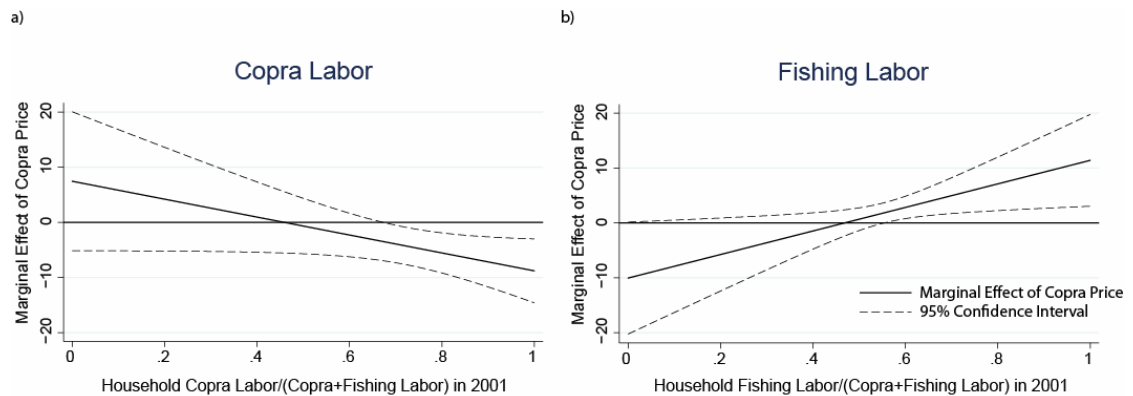


Figure 3-3. The marginal effect of a change in copra price on copra labor (a) and fishing labor (b) conditional on the fraction of labor in copra or fishing in 2001.

## Aggregate Effects

### Labor Allocation

The results of the regression analysis allowed us to estimate the aggregate effects of the copra price change on fishing and copra labor and, ultimately, on the ecosystem. The household specific coefficient on copra price in the fishing labor estimation equation was raised to the population level by an inflation factor ( $w_{ic}$ ), for household  $i$  in cluster  $c$ , by taking the product  $\hat{\beta}_i^1 = \left( \hat{\beta}^5 + \hat{\beta}^6 \times \frac{L_{i0}^f}{L_{i0}^c + L_{i0}^f} \right) \times w_{ic}$ . The inflation factor is defined as  $w_{ic} = h_c \times h_{ic}$ , the product of stage specific inflation factors. The cluster inflation factor is defined as  $h_c = (n\pi_c)^{-1}$ , where  $n$  is the number of clusters sampled,  $\pi_c$  is the probability that a cluster is selected ( $\pi_c = M_c/T$ ). The total population,  $T$ , is the sum of the population in each cluster,  $M_c$ ,  $T = \sum_{c=1}^N M_c$ . The within cluster inflation factor is defined as  $h_{ic} = (m_c\pi_{ic})^{-1}$ , where  $m_c$  is the cluster sample size, and  $\pi_{ic}$  is the probability a household is selected within a cluster, conditional on the cluster being selected.

The price elasticity of fishing labor then is  $e_i^{p^c, L^f} = \hat{\beta}_i^1 \times \bar{p}^c$ . Using the estimated price elasticity and the fishing labor in 2003 (the year before the subsidy), we calculated the aggregate change in the fishing labor that would be expected

following the price subsidy, 
$$\frac{\sum_{c=1}^n \sum_{i=1}^{m_c} (17\% \times e_i^{p^c, L^f} \times w_{i,c} \times L_{i,2003}^f)}{\sum_{c=1}^n \sum_{i=1}^{m_c} (w_{i,c} \times L_{i,2003}^f)} \times 100.$$
 A 17% increase

in the copra price ( $p_{2003}^c = 0.47$  AUD 2001/kg,  $p_{2004}^c = 0.57$  AUD 2001/kg) resulted in a 33% (95% CI: 81%, -15%) increase in fishing labor. The effect of the copra price subsidy on copra labor was estimated using the same methods and resulted in a -33% (95% CI: -79%, 13%) decrease. Although the percentage increase in fishing labor, 33%, is exactly the same as the percentage decrease in copra labor, 33%, the actual labor reallocation was not identical since the allocation of labor is not evenly divided between copra production and fishing.

### Ecosystem Effects

To estimate the effect of a change in fishing labor on the ecosystem, we used parameters from regression models of the relationships between fishing labor and various coral reef ecosystem components (total fish biomass, herbivorous fish biomass, algal cover (turf and macroalgae), and reef-builder cover (coral and coralline algae)) fitted using data from 34 ecological survey sites across an extreme gradient in fishing pressure (caused by a government re-settlement program) in Kiritimati Island, Kiribati. These results, when combined with our economic model, suggest that a 33% increase in fishing labor will result in a 14% decrease in total fish biomass (Figure 3-4a) and a 5% decrease in herbivore biomass (Figure 3-4b). Fishing has indirect effects on reef builders and algae because the consumption of algae by herbivores helps

maintain the dominance of reef-builders. We predict that a 33% increase in fishing will result in a 6% decrease in reef-builders (Figure 3-4c) and a 12% increase in algae (Figure 3-4d). The estimate of losses in reef-builders is conservative because increased fishing on Kiritimati only occurred recently and reef-builders are slower to respond to changes than algae. On historically over-fished reefs, such as in the Caribbean, sudden and almost complete losses of reef-builders have been observed following disturbances (Knowlton 1992, Hughes 1994).



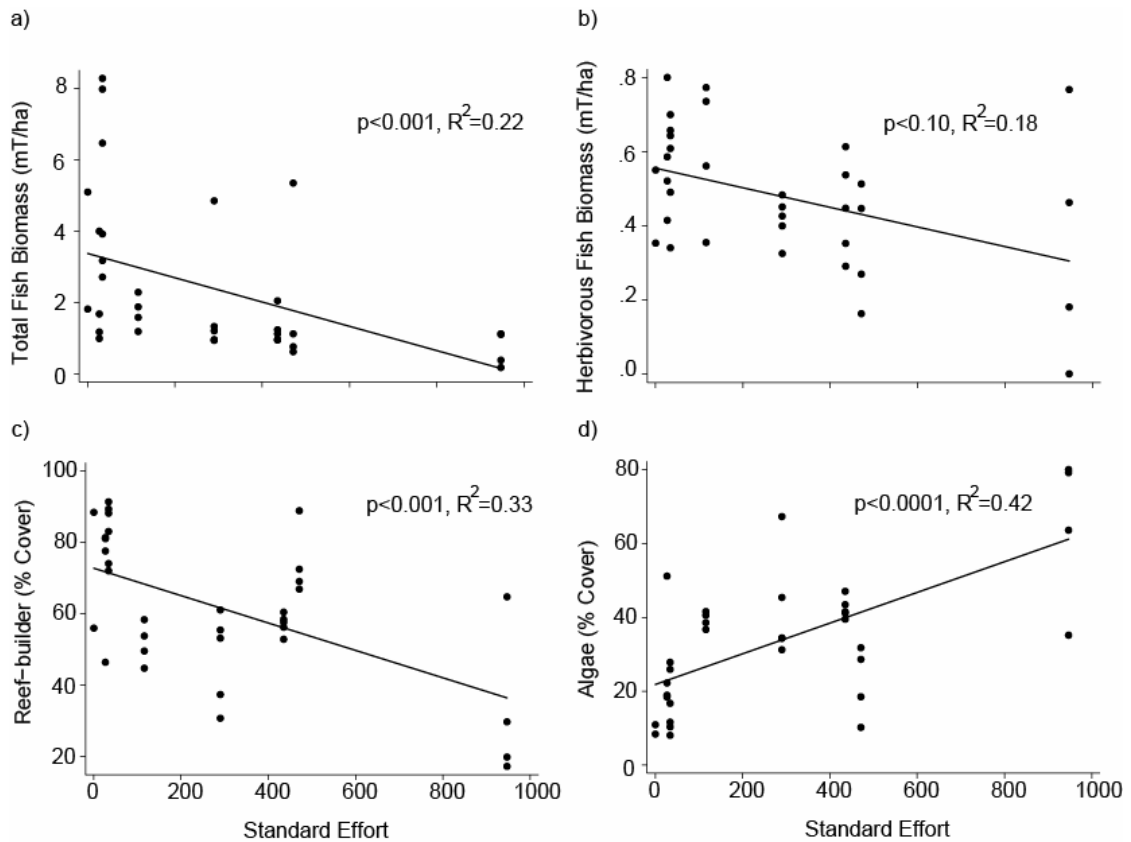


Figure 3-4. Estimates of ecological change in response to a change in fishing labor. An estimated 33% increase in fishing labor will result in a) a 1.4% decrease in total fish ( $B = -0.003$ , robust  $SE = 0.0009$ ;  $F_{1,32} = 13.32$ ,  $p < 0.001$ ,  $R^2 = 0.22$ ), b) a 5% decrease in herbivores ( $B = -0.0003$ , robust  $SE = 0.0001$ ;  $F_{1,33} = 3.26$ ,  $p < 0.10$ ,  $R^2 = 0.18$ ), c) a 6% decrease in reef-builders (coral and crustose coralline algae) ( $B = -0.0004$ ,  $SE = 0.0001$ ;  $F_{1,32} = 15.71$ ,  $p < 0.001$ ,  $R^2 = 0.33$ ), and d) a 12% increase in algae ( $B = 0.0004$ ,  $SE = 0.00009$ ;  $F_{1,32} = 23.62$ ,  $p < 0.0001$ ,  $R^2 = 0.42$ ).

We also observed the effect of a change in the copra price subsidy on the coral reef fishery using responses to a discrete choice question regarding changes in the effort required to catch fish. Of the respondents, 84% (95% CI: 76%, 93%) said that it was getting harder to catch fish, 2% (95% CI: -4%, 7%) said it was easier, and 14% (95% CI: -4%, 23%) said it was staying the same over the study period.

Households showed no shift in fishing area or gear over this period, suggesting that changes in the difficulty of fishing represent changes in the resource. In response to a binary choice question regarding the need for fisheries conservation, 91% (95% CI: 72%, 110%) households said that something needed to be done to ensure health fisheries, while only 9% (95% CI: -10%, 28%) said nothing needed to be done.

### **Welfare Consequences**

Welfare necessarily increased with an increase in the copra price (wage), although the gain may be off-set by coral reef degradation in the long-run. To measure the net effect of the copra subsidy on welfare, we used responses to a discrete choice question regarding welfare change over the study period as well as data on ownership of household amenities (tv/video players and non-kerosene or non-candle light sources). We expect that the responses to these questions give a more accurate measure of welfare than income given that non-monetary benefits associated with fishing are important. Of the respondents, 46% (95% CI: 38%, 76%) stated that welfare improved, 43% (95% CI: 27%, 59%) said that welfare did not change, and 11% (95% CI: -12%, 33%) said that welfare declined over the period. The portion of households that experienced declines in welfare typically attributed the decline to idiosyncratic events, such as deaths in the family, aging, and children leaving home. Households with more fishing labor were more likely to experience declines in welfare ( $\beta=0.59$ ,  $p<0.05$ ), while households with more copra labor were more likely to experience improvements, although this result was only marginally significant. In

contrast, households with more fishing labor were more likely to own tv/video players ( $\beta=0.86$ ,  $p<0.01$ ) or have improved lighting ( $\beta=0.74$ ,  $p<0.05$ ). There was no relationship between copra labor and ownership of these goods.

In addition, we asked households if they were satisfied with their income and if they said no, if they wanted some alternative income opportunity. Of the 318 households that responded, 36% (95% CI: 27%, 45%) were satisfied with their income and 64% (95% CI: 55%, 73%) were not. Of the 64% that were not satisfied, 58% wanted some alternative (95% CI: 49%, 67%) and 42% did not (95% CI: 32, 51%). Some respondents gave specific examples of alternative income opportunities, such as selling bread, starting a small company, or improving fishing. Of the 63 households that gave specific examples, 38% (95% CI: 28%, 38%) mentioned something related to improving fishing. Often this was related to capital improvements, such as buying a boat, engine, or new gear, but many households indicated that it was difficult to get a loan unless you were a government employee.

## **DISCUSSION**

We have shown that under standard assumptions, increasing the price of copra should decrease fishing and increase welfare. However, we observed significant numbers of households actually increasing fishing and decreasing copra labor. To explain these observations, we developed an alternative model in which households also get utility from fishing labor, representing the importance of non-monetary benefits associated with fishing that is often cited by anthropologists. This model

predicted that households would increase fishing labor, along with consumption of fish, rice, and other leisure, in response to the copra subsidy. Our empirical estimations support these predictions and show that households that have revealed a high enjoyment of fishing (instrument by the fraction of fishing labor in 2001) increased fishing. In aggregate, the 17% increase in the copra price led to a 33% increase in fishing labor and a 33% decrease in copra labor. The increase in fishing labor was estimated to have significant negative consequences for the fish stock and reef builders, which provide important goods and services such as food or protection from storms and sea-level rise. In sum, the subsidy not only failed to reduce fishing and protect ecosystem services but actually exacerbated the problem. This suggests that although the subsidy had a positive effect on welfare, these improvements will not be maintained in the long-run if the fishery and ecosystem declines.

Although there are other mechanisms that could explain an increase in fishing in response to an increase in the copra price, we find little support for these mechanisms and suggest that role of non-pecuniary benefits of fishing is the most parsimonious explanation. For instance, under the standard assumptions, an increase in copra price should lead to a decrease in fishing and an increase in consumption of all goods, including fish. This suggests that general equilibrium effects could lead to an increase in the price of fish, which would draw labor back into fishing. However, for the net effect of fishing labor to be positive, this would require the price of fish to increase at a faster rate than the price of copra, which we do not observe, or for rice to be an inferior or even a Giffen good. Given that rice is imported and fish is produced

locally, as well as the observation that eating rice is associated with wealth and status, rice is probably not an inferior or Giffen good in Kiribati. Another possible explanation would be a declining fish stock. Although there is some evidence that the fish stocks in Kiribati are declining, the rate of decline is probably much slower than the rate of increase in the copra price and cannot explain the increase in fishing labor over a short time scale.

The limited selection bias, small number of goods, and incomplete labor and resource markets made estimating the effect of the copra subsidy valid and tractable. However, these attributes also limit the generality of the results. Perfect labor markets may buffer responses to alternative income projects because new labor can come in from outside. However, if there were well functioning labor markets in Kiribati, households with lots of land might hire laborers, which would give land owners more free time that they could possibly use to go fishing. Perfect credit markets may strengthen the negative impact of the copra subsidy by enabling households to invest in boats, motors, and fishing gear. Our results suggest that a significant number of households want to invest in fishing capital but are credit constrained. With improved credit markets, fishing labor may not increase, but fishing effort would, with deleterious effects on the reefs. Lastly, there are a very limited number of goods to purchase or leisure activities in Kiribati. If more options were available, people may substitute fishing labor as leisure for other goods or activities, such as televisions and other mass consumption goods, lessening the negative impact of the copra subsidy.

An additional limitation of the study is the use of re-call data. Evaluating alternative income programs is not only challenging because they often have major issues of selection bias but because data is rarely collected over time. Moreover, the data that is collected must not only include economic data but also ecological and anthropological data. Although the small percentages of households observed changing fishing or copra labor in response to the copra subsidy is inconsistent with our model, suggesting imperfections in the recall data, evidence from island level copra production data suggests that the direction of these changes is correct. Using copra production data over the period 2001-2005 for the four islands surveyed in this study, we found that copra production actually decreased with an increase in the copra price ( $\beta=-2064$ , Robust S.E.=583).

## **CONCLUSIONS**

The results of this research suggest that investments in alternative income programs may not always return a “double-dividend” to conservation and economic development as commonly thought. Non-monetary benefits associated with fishing or other livelihoods may play a significant role and small differences in wages between alternative incomes and fishing may not be sufficient to draw labor out of fishing. Households are likely to respond differently to these programs not only based on their demographic attributes and capital endowments but based on preferences. Here, we show how a preference for fishing actually causes an alternative income program to have the perverse effect of increasing fishing. In cases where the non-monetary

benefits of traditional livelihoods are high, ICDPs need to provide alternative incomes that are similar to the traditional livelihood but have low impact (e.g. catch-and-release sport fishing), make available additional consumption goods, or develop community work programs to produce public or common resource goods.

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