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## Fishing top predators indirectly affects condition and reproduction in a reef-fish community

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To examine the indirect effects of fishing on energy allocation in non-target prey species, condition and reproductive potential were measured for five representative species (two-spot red snapper *Lutjanus bohar*, arc-eye hawkfish *Paracirrhites arcatus*, blackbar devil *Plectroglyphidodon dickii*, bicour colour chromis *Chromis margaritifer* and whitecheek surgeonfish *Acanthurus nigricans*) from three reef-fish communities with different levels of fishing and predator abundance in the northern Line Islands, central Pacific Ocean. Predator abundance differed by five to seven-fold among islands, and despite no clear differences in prey abundance, differences in prey condition and reproductive potential among islands were found. Body condition (mean body mass adjusted for length) was consistently lower at sites with higher predator abundance for three of the four prey species. Mean liver mass (adjusted for total body mass), an indicator of energy reserves, was also lower at sites with higher predator abundance for three of the prey species and the predator. Trends in reproductive potential were less clear. Mean gonad mass (adjusted for total body mass) was high where predator abundance was high for only one of the three species in which it was measured. Evidence of consistently low prey body condition and energy reserves in a diverse suite of species at reefs with high predator abundance suggests that fishing may indirectly affect non-target prey-fish populations through changes in predation and predation risk.

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Key words: energy allocation; gonad; Line Islands; liver; predation risk; prey.

### INTRODUCTION

Ecosystem-based fisheries management requires a better understanding of the indirect effects of fishing on non-target species, but these effects have been more difficult to measure than direct effects on target species (Heithaus *et al.*, 2008). One of the most

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well-documented effects of fishing is the dramatic decline in top predators, the primary target of many fisheries (Jackson *et al.*, 2001; Myers & Worm, 2003; Pandolfi *et al.*, 2003; Newman *et al.*, 2006; Stevenson *et al.*, 2007; DeMartini *et al.*, 2008; Sandin *et al.*, 2008; Walsh, 2011). Ecological theory predicts that a decline in predators should reduce predation and result in an increase in prey populations. Instances of prey release are common in systems with strong species interactions or invertebrate prey species, such as sea urchins or sea stars (McClanahan & Muthiga, 1988; Dulvy *et al.*, 2004; Borer *et al.*, 2005; Myers *et al.*, 2007; Terborgh & Estes, 2010). These examples are, however, rare in coral-reef ecosystems characterized by complex food webs (Sandin *et al.*, 2010). Although fishing top predators may not have clear effects on prey abundance in these systems, the removal of predators may still have important indirect effects on energy allocation in prey fishes (Heithaus *et al.*, 2008).

Fishing predators may indirectly increase prey-fish body condition, energy reserves and reproductive potential by reducing predator abundance and associated predation rates and predation risk. When predators are scarce, prey do not need to allocate as much energy to functions that increase survivorship and instead can direct this energy to growth, storage and reproduction (Lima, 1986; Wingfield *et al.*, 1998). Prey can spend less time avoiding predators and can forage more often and over larger areas (Skelly & Werner, 1990; Schmitz *et al.*, 1997; Madin *et al.*, 2010; Jones & Dornhaus, 2011). As a result, prey may be able to consume more food or seek out higher quality food (Werner *et al.*, 1983; Longland, 1991; Diehl & Eklöv, 1995; Morrison, 1999; Jones & Dornhaus, 2011). In addition, prey exposed to lower predation risk have lower mass-specific metabolic rates meaning that less energy is required for maintenance (Woodley & Peterson, 2003; Sunardi *et al.*, 2007; Slos & Stoks, 2008; Hawlena & Schmitz, 2010). Behavioural or physiological changes in prey under low predator conditions may result in higher net energy intake, which may translate into greater mass gain or storage of energy in fat reserves (Skelly & Werner, 1990; Hik, 1995; Boonstra *et al.*, 1998; Karels *et al.*, 2000; Garvey *et al.*, 2004; Pérez-Tris *et al.*, 2004). Higher body condition and energy reserves may lead to higher fecundity in females or competitive ability in males (Peckarsky *et al.*, 1993; Scrimgeour & Culp, 1994; Godin, 1995; Boonstra *et al.*, 1998; Kotiaho *et al.*, 1998; Karels *et al.*, 2000). For instance, females that are in good condition may make proportionally larger investments in reproduction without greatly increasing their risk of mortality (Lambert & Dutil, 2000). Females in poor condition may also, however, make large investments in reproduction even when mortality risk is high if strategies to increase survivorship and future reproduction would have limited benefits (Levins, 1968; Reznick & Endler, 1982; Sibley & Calow, 1986; Stearns, 1992).

The status of fish populations has been assessed using measures of condition and reproduction, often attributing higher condition, energy reserves and reproductive potential to lower temperatures and higher food availability (Lambert & Dutil, 1997; Froese, 2006). A growing number of studies show, however, that fishing may also affect condition and reproduction of target species. For instance, fishing may exacerbate the negative effect of poor environmental conditions on condition, energy reserves and reproductive potential (Lambert & Dutil, 1997, 2000; Ballón *et al.*, 2002), alter condition and fecundity in size-specific ways (Ballón *et al.*, 2002; Rijnsdorp *et al.*, 2010) or reduce the size or age at maturity or sex change (Armsworth, 2001; Hawkins & Roberts, 2003; Olsen *et al.*, 2004; Hamilton *et al.*, 2007). Although effects of environmental conditions and predation on condition and

reproduction in non-target species have been well studied (especially for larval or juvenile stages) (Montgomery & Galzin, 1993; McCormick & Molony, 1995; Garvey *et al.*, 2004; Hoey & McCormick, 2004; Pratchett *et al.*, 2004; Berumen *et al.*, 2005), it remains unclear how or if fishing indirectly affects condition and reproduction in non-target species through changes in predator abundance. One of the challenges in understanding this effect is that there are few places to make appropriate comparisons between fish communities where the primary difference is the fishing of predators (Heithaus *et al.*, 2008).

This study used spatial comparisons of condition and reproduction of fishes from reefs in Palmyra Atoll, south-eastern Kiritimati Atoll and north-western Kiritimati Atoll in the northern Line Islands, central Pacific Ocean, to examine the indirect effects of fishing predators on prey energy allocation. Previous studies on these reefs found that predator abundance is higher in unfished Palmyra and lightly fished south-eastern Kiritimati than in north-western Kiritimati (Stevenson *et al.*, 2007; DeMartini *et al.*, 2008; Sandin *et al.*, 2008; Walsh, 2011). These studies found, however, that fishing was not associated with a consistent pattern in biomass for any of the major prey trophic groups (DeMartini *et al.*, 2008; Sandin *et al.*, 2008; Ruttenberg *et al.*, 2011; Walsh, 2011). Studies comparing other metrics of prey fishes at Palmyra and north-western Kiritimati found that higher predator abundance was associated with smaller mean sizes and ages of prey fishes (Ruttenberg *et al.*, 2011), smaller sizes at sex change for protogynous parrotfishes (DeMartini *et al.*, 2008) and reduced prey foraging time and areas (Madin *et al.*, 2010). Building on these previous studies, this study investigated the hypothesis that body condition, energy reserves and reproductive potential may be higher for fishes under low predator conditions in fished north-western Kiritimati than for fishes under high predator conditions in lightly fished south-eastern Kiritimati and unfished Palmyra. To test this hypothesis, the body, liver and gonad mass of five representative fish species (one predator and four prey species) from reefs in the north-western and south-eastern regions of Kiritimati and in Palmyra were compared.

## MATERIALS AND METHODS

### STUDY SITES

Palmyra and Kiritimati Atolls in the northern Line Islands, central Pacific Ocean, provide a unique opportunity to test the indirect effects of fishing on prey energy allocation (Fig. 1) (Knowlton & Jackson, 2008; Sandin *et al.*, 2008). These atolls have similar species assemblages and environmental conditions because of their close proximity (*c.* 700 km), but they have very different predator populations due to fishing (Fig. 1 and Table I) (Sandin *et al.*, 2008). The fringing reefs of both islands are bathed by oligotrophic waters; however, Kiritimati has somewhat higher chlorophyll *a* concentrations and cooler waters due to regional upwelling around the equator and localized upwelling on the north-western side of the island (Table I) (Sandin *et al.*, 2008; Walsh, 2011). Palmyra has been protected from fishing by the U.S. Fish and Wildlife Service as a National Wildlife Refuge (and became part of the Pacific Remote Islands National Monument in 2009) (Federal Register, 2001; Kempthorne, 2009). Kiritimati is part of the Republic of Kiribati and has at least 5000 inhabitants (Kiribati Statistics Office, 2005). The effect of fishing on Kiritimati began relatively recently because, historically, Kiritimati had no permanent population (Sandin *et al.*, 2008). A permanent population was established for copra production (coconut agriculture) and has grown dramatically in recent decades following a population re-settlement programme that brought people from

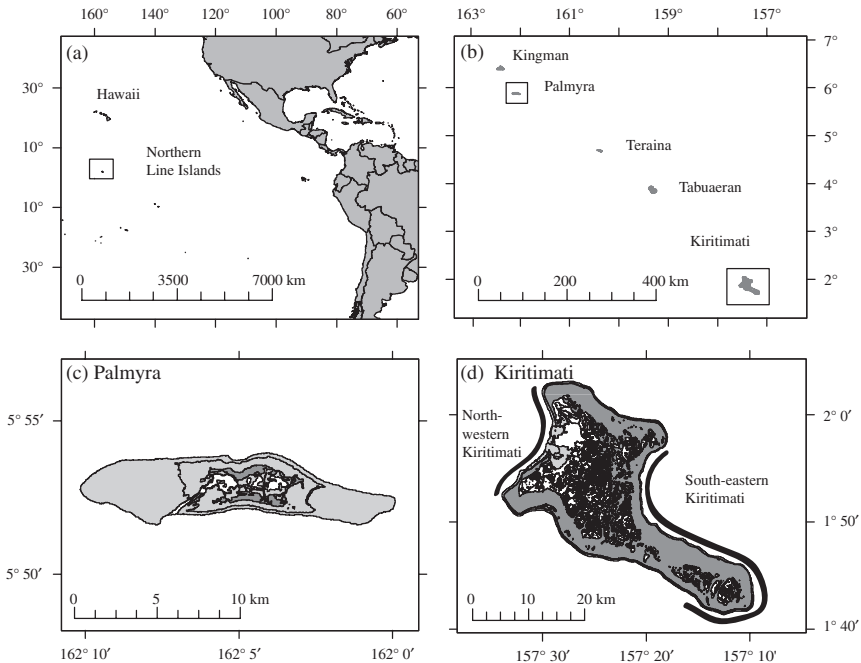


FIG. 1. Maps of the study regions in the (a and b) northern Line Islands: (c) Palmyra and (d) north-western Kiritimati and south-eastern Kiritimati (□, reef; ■, land; □, lagoon; —, subregion).

Tarawa, the capital of the Republic of Kiribati (c. 3000 km to the west) (Sandin *et al.*, 2008; Walsh, 2011).

Fishing in Kiritimati is concentrated on the leeward or north-western side of the island near the largest villages, while the windward or south-eastern coast experiences little fishing pressure because of its exposure to persistent easterly trade winds and remoteness (there are very few boats or cars in Kiritimati) (Table I) (Walsh, 2011). As a consequence, fish communities in the south-eastern side of Kiritimati more closely resemble fish communities in the protected Palmyra Atoll than fish communities in the north-western side of Kiritimati (Sandin *et al.*, 2008; Walsh, 2011). Fishing in Kiritimati has primarily affected top predators with little affect on prey fishes (except for fishing for the aquarium trade), because of the recent nature of fishing and the fact that about half of fishing trips use hook and line, which targets large predators (Table I) (Walsh, 2011). Previous studies have shown that predator biomass in Palmyra and south-eastern Kiritimati is five to seven times greater than in north-western Kiritimati and dominated by snappers, jacks, groupers and, in the case of Palmyra, sharks (DeMartini *et al.*, 2008; Sandin *et al.*, 2008; Walsh, 2011). Notably, sharks are far less abundant in south-eastern Kiritimati probably due to shark finning (Walsh, 2011). None of the major prey-fish trophic groups, however, show a pattern consistent with prey release due to fishing predators (DeMartini *et al.*, 2008; Sandin *et al.*, 2008; Walsh, 2011). Fished reefs at north-western Kiritimati also have higher algal cover (turf and macroalgae) and lower coral cover compared to lightly and unfished south-eastern Kiritimati and Palmyra, respectively (Table I) (Sandin *et al.*, 2008; Walsh, 2011).

## STUDY SPECIES

The five study species represent the five major trophic groups (predators, benthic invertivores, omnivores, planktivores and herbivores) and were among the most abundant species in these trophic groups on previous surveys of both atolls (DeMartini *et al.*, 2008; Sandin

TABLE I. Mean  $\pm$  S.D. of ecosystem and environmental attributes in the three study regions: north-western Kiritimati (KirNW), south-eastern Kiritimati (KirSE) and Palmyra (Pal) (all data except oceanographic data derived from DeMartini *et al.*, 2008; Sandin *et al.*, 2008; Walsh, 2011; Ruttenberg *et al.*, 2011)

Factor	KirNW	KirSE	Pal
Fish catch (kg km <sup>-1</sup> week <sup>-1</sup> )	173.88 $\pm$ 34.87	43.62 $\pm$ 15.80	0.00
Predation pressure			
Predator density (number m <sup>-2</sup> )	0.31 $\pm$ 0.04	0.19 $\pm$ 0.05	0.13 $\pm$ 0.01
Predator density (g m <sup>-2</sup> )	24.76 $\pm$ 5.05	124.36 $\pm$ 34.70	168.43 $\pm$ 24.12
Benthic cover			
Coral cover (%)	14.99 $\pm$ 2.26	38.42 $\pm$ 4.04	20.36 $\pm$ 2.67
Turf algal cover (%)	52.59 $\pm$ 4.77	13.37 $\pm$ 3.74	24.95 $\pm$ 3.21
Macroalgal cover (%)	16.21 $\pm$ 3.26	5.82 $\pm$ 0.94	17.77 $\pm$ 2.19
Fish abundance			
<i>Lutjanus bohar</i> (number m <sup>-2</sup> )	0.02 $\pm$ 0.00	0.03 $\pm$ 0.01	0.04 $\pm$ 0.01
<i>Paracirrhites arcatus</i> (number m <sup>-2</sup> )	0.03 $\pm$ 0.00	0.05 $\pm$ 0.01	0.08 $\pm$ 0.01
<i>Chromis margaritifer</i> (number m <sup>-2</sup> )	1.53 $\pm$ 0.26	0.59 $\pm$ 0.14	0.51 $\pm$ 0.08
<i>Plectroglyphidodon dickii</i> (number m <sup>-2</sup> )	0.07 $\pm$ 0.01	0.27 $\pm$ 0.04	0.03 $\pm$ 0.01
<i>Acanthurus nigricans</i> (number m <sup>-2</sup> )	0.02 $\pm$ 0.00	0.05 $\pm$ 0.01	0.07 $\pm$ 0.01
Oceanography*			
Chlorophyll <i>a</i> (mg m <sup>-3</sup> )	0.18 $\pm$ 0.02	0.17 $\pm$ 0.01	0.11 $\pm$ 0.02
Temperature (° C)	28.22 $\pm$ 0.49	28.03 $\pm$ 0.17	28.73 $\pm$ 0.14

\*Average of monthly values (July 2002 to June 2007) from MODIS on Aqua (Acker & Leptoukh, 2007).

*et al.*, 2008; Walsh, 2011). The two-spot red snapper *Lutjanus bohar* (Forsskål 1775) [maximum total length ( $L_T$ ): 90 cm] mainly feeds on fishes, is preyed on by reef sharks and is a target of the local fishery (Frimodt, 1995; Walsh, 2011). The arc-eye hawkfish *Paracirrhites arcatus* (Cuvier 1829) (maximum  $L_T$ : 20 cm) is typically associated with small branching corals, feeds on shrimp, crabs and other crustaceans and is prey for smaller groupers such as the peacock hind *Cephalopholis argus* Schneider 1801 (Hiatt & Strasburg, 1960; Randall & Brock, 1960; Lieske & Myers, 1994; Myers, 1999). The bicolor chromis *Chromis margaritifer* Fowler 1946 (maximum  $L_T$ : 9 cm) is a shoaling species that shelters in branching corals and reef crevices, but feeds on zooplankton in the water column (Lieske & Myers, 1994). *Chromis margaritifer* is a prey for many reef predators because of its small size and abundance (Hiatt & Strasburg, 1960). The blackbar devil *Plectroglyphidodon dickii* (Liénard 1839) (maximum  $L_T$ : 11 cm) establishes territories on *Acropora* spp. corals and feeds primarily on filamentous algae and small benthic invertebrates (Allen, 1986; Myers, 1991). The yellow-edged moray eel *Gymnothorax flavimarginatus* (Rüppell 1830) is a known predator of *P. dickii* (Hiatt & Strasburg, 1960). The whitecheek surgeonfish *Acanthurus nigricans* L. 1758 (maximum  $L_T$ : 21 cm) feeds on filamentous algae (Randall *et al.*, 1990; Choat *et al.*, 2004). Notably, only one of these species, *L. bohar*, is targeted by the fishers of Kiritimati. Fishers also target the known predators of the four prey species included in this study (*e.g.* groupers, reef sharks, eels and various piscivores).

## COLLECTIONS

Collections of 19–109 individuals of each species were made using nets, spears and hook-and-line gear from reefs that experience no fishing or low fishing in Palmyra and south-eastern Kiritimati and from reefs that experience high levels of fishing in north-western Kiritimati. Collections from Palmyra and north-western Kiritimati were made during August 2006, while collections from south-eastern Kiritimati were made during August 2007. Each individual's

total body mass ( $M_T$ ) and  $L_T$  were recorded prior to dissection. The liver ( $M_L$ ) and gonad ( $M_G$ ) mass were recorded and the sex was determined by gross examination of the gonad. The  $M_T$ , adjusted for  $L_T$ , and  $M_L$ , adjusted for  $M_T$ , using standard regression methods were used as indicators of condition and energy reserves, respectively (Lambert & Dutil, 1997). The  $M_G$  (of mature females only), adjusted for  $M_T$  using standard regression methods, was used as an indicator of reproductive potential (Lloret & Planes, 2003).

## STATISTICAL ANALYSES

To compare indicators between regions, ordinary least-squares regression was used to estimate the relationship between  $M_T$  and standard length ( $L_S$ ) ( $\ln(M_T) = \alpha_0 + \alpha_1 \ln(L_S)$ ),  $M_L$  and  $M_T$  ( $\ln(M_L) = \beta_0 + \beta_1 M_T$ ) and  $M_G$  and  $M_T$  ( $\ln(M_G) = \gamma_0 + \gamma_1 M_T$ ), where  $\alpha$ ,  $\beta$  and  $\gamma$  are coefficients. The region was included as a categorical variable that could affect the slope, intercept or both, which represented differences in the rate of somatic growth, initial size or both (e.g.  $\ln(M_T) = \alpha_0 + \alpha_1 x + \alpha_2 z + \alpha_3 x \ln(L_S) + \alpha_4 z \ln(L_S)$ , where  $x$  is south-eastern Kiritimati and  $z$  is Palmyra) (see Tables SI–SIII, Supporting information, for all model specifications). North-western Kiritimati was the reference region and, therefore, was not included explicitly as a variable in the models. The best fit model was chosen using the Akaike information criterion (AIC) corrected for small sample sizes (Hurvich & Tsai, 1989; Burnham & Anderson, 2002) (Tables SI–SIII, Supporting information). These models were used to calculate adjusted means of the dependent variables [body mass ( $\overline{M}'_T$ ), liver mass ( $\overline{M}'_L$ ) and gonad mass ( $\overline{M}'_G$ )], which were then tested for differences between pairs of regions using  $t$ -tests with Holm's sequential Bonferroni correction (Holm, 1979).

## RESULTS

Model selection procedures showed that differences in adjusted  $\overline{M}'_T$ ,  $\overline{M}'_L$  and  $\overline{M}'_G$  may be due to both allometric (differences in slope) and isometric (differences in intercept) differences across regions (Tables SI–SIII, Supporting information). In most cases, more than one of the nine candidate models considered had a similar likelihood ( $\Delta AIC_c < 2$ ) of being the best model to represent the  $M_T$ ,  $M_L$  or  $M_G$  data for each species (Tables SI–SIII, Supporting information). With few exceptions, models with a  $\Delta AIC_c < 2$  resulted in the same qualitative trends in  $\overline{M}'_T$ ,  $\overline{M}'_L$  and  $\overline{M}'_G$  across the regions. Consequently, only the estimation results and adjusted means from the models with the lowest  $AIC_c$  were presented (Tables II and III and Figs 2–4). The best models of  $M_T$  were highly significant ( $P < 0.001$ ) and explained between 89 and 99% of the variance in  $M_T$  for all species (Table II). The best models of  $M_L$  were also highly significant ( $P < 0.001$ ) but explained less of the variance in  $M_L$  (35–83%) (Table II). Far less of the variance in  $M_G$  (21–47%) was explained by the best models but these models were still highly significant ( $P < 0.01$ ) (Table II).

The  $\overline{M}'_T$  for the predator, *L. bohar*, did not differ between regions with high fishing (north-western Kiritimati) and no fishing (Palmyra) [Fig. 2(a) and Table II]. No samples were available from south-eastern Kiritimati to make comparisons. In contrast,  $\overline{M}'_T$  for three of the prey species was consistently lower in regions with low fishing and high predator abundance. The  $\overline{M}'_T$  of *P. arcatus*, *P. dickii* and *A. nigricans* was lower in Palmyra, intermediate in south-eastern Kiritimati and highest at north-western Kiritimati [Fig. 2(b), (c), (e) and Table II]. The best model of  $M_T$  for the prey species, *C. margaritifer*, showed no differences in  $\overline{M}'_T$  among these three regions [Fig. 2(d) and Table II]; however, four of the five models with a  $\Delta AIC_c < 2$



TABLE II. Estimates of mean  $\pm$  s.e. body mass ( $M_T$ ), liver mass ( $M_L$ ) and gonad mass ( $M_G$ ) from best models (Tables SI–SIII, Supporting information). Dependent variables are ln transformed (except for  $M_L$  for *Acanthurus nigricans*). The predictor variables are the regions: south-eastern Kiritimati ( $x$ ) and Palmyra ( $z$ ). The reference region is north-western Kiritimati. The covariate (CV;  $y$ ) for models of  $M_T$  is ln of standard length ( $L_S$ ) and for models of  $M_L$  and  $M_G$  is  $M_T$

Species	Variable	$M_T$	$M_L$	$M_G$
<i>Lutjanus bohar</i>	$y$	2.90 $\pm$ 0.03***	0.00 $\pm$ 0.00***	—
	$z$	0.01 $\pm$ 0.03	-0.93 $\pm$ 0.24***	—
	$x$	—	—	—
	$y \times z$	0.00 $\pm$ 0.00***	—	—
	$y \times x$	—	—	—
	Constant	—	3.31 $\pm$ 0.10***	—
	$n$	114	69	—
	$r^2$	0.99	0.84	—
<i>Paracirrhites arcatus</i>	$y$	2.64 $\pm$ 0.16***	0.03 $\pm$ 0.01**	0.06 $\pm$ 0.04
	$z$	-0.40 $\pm$ 0.25	0.60 $\pm$ 0.10***	—
	$x$	-0.58 $\pm$ 0.26*	0.37 $\pm$ 0.23	0.45 $\pm$ 0.12***
	$y \times z$	0.27 $\pm$ 0.13*	—	0.05 $\pm$ 0.02*
	$y \times x$	0.32 $\pm$ 0.13*	0.02 $\pm$ 0.01	—
	Constant	-2.86 $\pm$ 0.31***	-3.94 $\pm$ 0.21***	-3.04 $\pm$ 0.35***
	$n$	221	182	55
	$r^2$	0.95	0.43	0.34
<i>Plectroglyphidodon dickii</i>	$y$	2.96 $\pm$ 0.11***	0.06 $\pm$ 0.03*	0.11 $\pm$ 0.05*
	$z$	—	—	0.09 $\pm$ 0.21
	$x$	0.50 $\pm$ 0.25	0.13 $\pm$ 0.12	-0.30 $\pm$ 0.18
	$y \times z$	0.07 $\pm$ 0.01***	0.07 $\pm$ 0.02**	—
	$y \times x$	-0.25 $\pm$ 0.16	—	—
	Constant	-3.05 $\pm$ 0.20***	-4.16 $\pm$ 0.22***	-3.30 $\pm$ 0.41***
	$n$	191	122	59
	$r^2$	0.89	0.35	0.21
<i>Chromis margaritifer</i>	$y$	3.71 $\pm$ 0.38***	-0.13 $\pm$ 0.10	—
	$z$	0.46 $\pm$ 0.26	0.65 $\pm$ 0.17***	—
	$x$	1.22 $\pm$ 0.58*	-1.19 $\pm$ 0.68	—
	$y \times z$	-0.28 $\pm$ 0.18	—	—
	$y \times x$	-0.80 $\pm$ 0.36*	0.29 $\pm$ 0.11*	—
	Constant	-4.27 $\pm$ 0.61***	-3.48 $\pm$ 0.67***	—
	$n$	139	41	—
	$r^2$	0.93	0.41	—
<i>Acanthurus nigricans</i>	$y$	2.84 $\pm$ 0.04***	0.01 $\pm$ 0.00***	0.01 $\pm$ 0.01
	$z$	0.14 $\pm$ 0.02***	0.05 $\pm$ 0.07	-4.02 $\pm$ 1.53*
	$x$	—	0.08 $\pm$ 0.06	-0.46 $\pm$ 0.22*
	$y \times z$	—	—	0.02 $\pm$ 0.01
	$y \times x$	0.01 $\pm$ 0.01*	—	—
	Constant	-2.78 $\pm$ 0.11***	-0.29 $\pm$ 0.10**	-0.64 $\pm$ 1.39
	$n$	238	191	83
	$r^2$	0.95	0.71	0.47

$n$ , sample size; \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

for *C. margaritifer* showed that  $\overline{M}_T$  was higher in south-eastern Kiritimati than in Palmyra.

Despite a lack of differences in  $\overline{M}_T$  for *L. bohar*,  $\overline{M}_L$  was lower where there was no fishing (Palmyra) than where fishing was highest (north-western Kiritimati)

TABLE III. Paired comparisons of adjusted mean body mass ( $\overline{M}'_T$ ), liver mass ( $\overline{M}'_L$ ) and gonad mass ( $\overline{M}'_G$ ) among regions with high fishing (north-western Kiritimati, KirNW), low fishing (south-eastern Kiritimati, KirSE) and no fishing (Palmyra, Pal). Note that no collections of *Lutjanus bohar* were made on KirSE. Using Holm's sequential Bonferroni correction, differences were considered significant at  $P$  values of  $<0.05$ ,  $<0.025$  and  $<0.017$  for the three comparisons ordered from lowest to highest  $t$  statistic

Comparison	$\overline{M}'_T$			$\overline{M}'_L$			$\overline{M}'_G$		
	$t$	d.f.	$P$	$t$	d.f.	$P$	$t$	d.f.	$P$
<i>Lutjanus bohar</i>									
KirNW v. Pal	0.54	112	$>0.05$	2.76	67	$<0.01$	NA		
KirNW v. KirSE	NA			NA			NA		
KirSE v. Pal	NA			NA			NA		
<i>Paracirrhites arcatus</i>									
KirNW v. Pal	6.20	110	$<0.001$	5.81	83	$<0.001$	2.02	24	$<0.05$
KirNW v. KirSE	2.49	178	$<0.01$	8.55	145	$<0.001$	2.41	44	$<0.05$
KirSE v. Pal	3.67	148	$<0.001$	1.11	130	$>0.05$	0.61	36	$>0.05$
<i>Plectroglyphidodon dickii</i>									
KirNW v. Pal	6.54	104	$<0.001$	3.73	68	$<0.001$	0.43	28	$>0.05$
KirNW v. KirSE	5.25	147	$<0.001$	1.06	87	$>0.05$	1.72	44	$>0.05$
KirSE v. Pal	2.40	125	$<0.05$	2.85	83	$<0.01$	2.06	40	$<0.05$
<i>Chromis margaritifer</i>									
KirNW v. Pal	2.37	112	$<0.05$	3.91	26	$<0.001$	NA		
KirNW v. KirSE	1.92	99	$>0.05$	0.21	23	$>0.05$	NA		
KirSE v. Pal	0.65	62	$>0.05$	2.60	27	$<0.01$	NA		
<i>Acanthurus nigricans</i>									
KirNW v. Pal	6.63	128	$<0.001$	0.66	88	0.51	4.93	42	$<0.001$
KirNW v. KirSE	2.19	186	$<0.05$	1.24	143	$>0.05$	1.30	53	$>0.05$
KirSE v. Pal	5.12	156	$<0.001$	0.49	145	$>0.05$	4.30	65	$<0.001$

NA, not available.

[Fig. 3(a) and Table II]. Three of the four prey species (*P. arcatus*, *P. dickii* and *C. margaritifer*) had lower  $\overline{M}'_L$  where there was no fishing (Palmyra) as compared to reefs where fishing was highest (north-western Kiritimati) [Fig. 3(b)–(e) and Table II]. The  $M_L$  of these three species under intermediate fishing conditions (south-eastern Kiritimati) was not, however, distinguishable from  $M_L$  in one of the other regions (Palmyra or north-western Kiritimati) [Fig. 3(b)–(e) and Table II]. Both *P. dickii* and *C. margaritifer* had lower  $\overline{M}'_L$  at Palmyra than at north-western Kiritimati and south-eastern Kiritimati, but  $\overline{M}'_L$  in north-western Kiritimati and south-eastern Kiritimati were indistinguishable [Fig. 3(c), (d) and Table II]. In contrast, *P. arcatus* had lower  $\overline{M}'_L$  in Palmyra and south-eastern Kiritimati than in north-western Kiritimati, but  $\overline{M}'_L$  in south-eastern Kiritimati and Palmyra were indistinguishable [Fig. 3(b) and Table II]. *Acanthurus nigricans* showed no difference in  $\overline{M}'_L$  across all three regions [Fig. 3(e) and Table II].

Only three prey species (*P. arcatus*, *P. dickii* and *A. nigricans*) had sufficient numbers of gravid female fish to compare  $M_G$  across regions. The  $\overline{M}'_G$  was higher for *A. nigricans* in Palmyra than in north-western Kiritimati or south-eastern Kiritimati



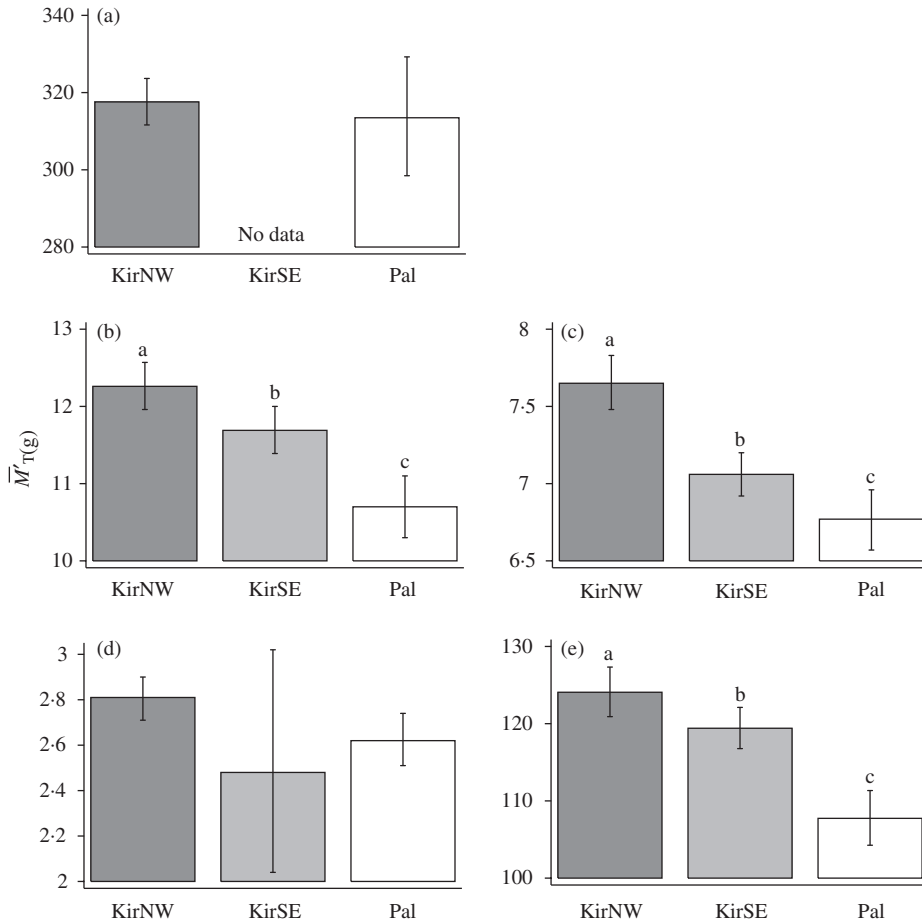


FIG. 2. Adjusted mean total body mass ( $\bar{M}_T$ ) and 95% C.I. by regions [north-western Kiritimati (KirNW), south-eastern Kiritimati (KirSE) and Palmyra (Pal)] from best fit models (Tables II and SI, Supporting information) for: (a) *Lutjanus bohar*, (b) *Paracirrhites arcatus*, (c) *Plectroglyphidodon dickii*, (d) *Chromis margaritifer* and (e) *Acanthurus nigricans*. The  $\bar{M}_T$  that were determined to be significantly different by a *t*-test with Holm's sequential Bonferroni correction are indicated by lower-case letters (Table III).

[Fig. 4(c) and Table II]. The  $\bar{M}_G$  of *P. dickii* and *P. arcatus* were not different across regions [Fig. 4(a), (b) and Table II]. Although the best model of  $M_G$  for *P. arcatus* showed no difference across regions, four of the five models with a  $\Delta AIC_c < 2$  showed that  $\bar{M}_G$  was greater in north-western Kiritimati than in south-eastern Kiritimati.

## DISCUSSION

There is a growing consensus that fishing has ecosystem-wide effects, yet the indirect effects of fishing on non-target species remain unclear (Goñi, 1998; Dayton *et al.*,

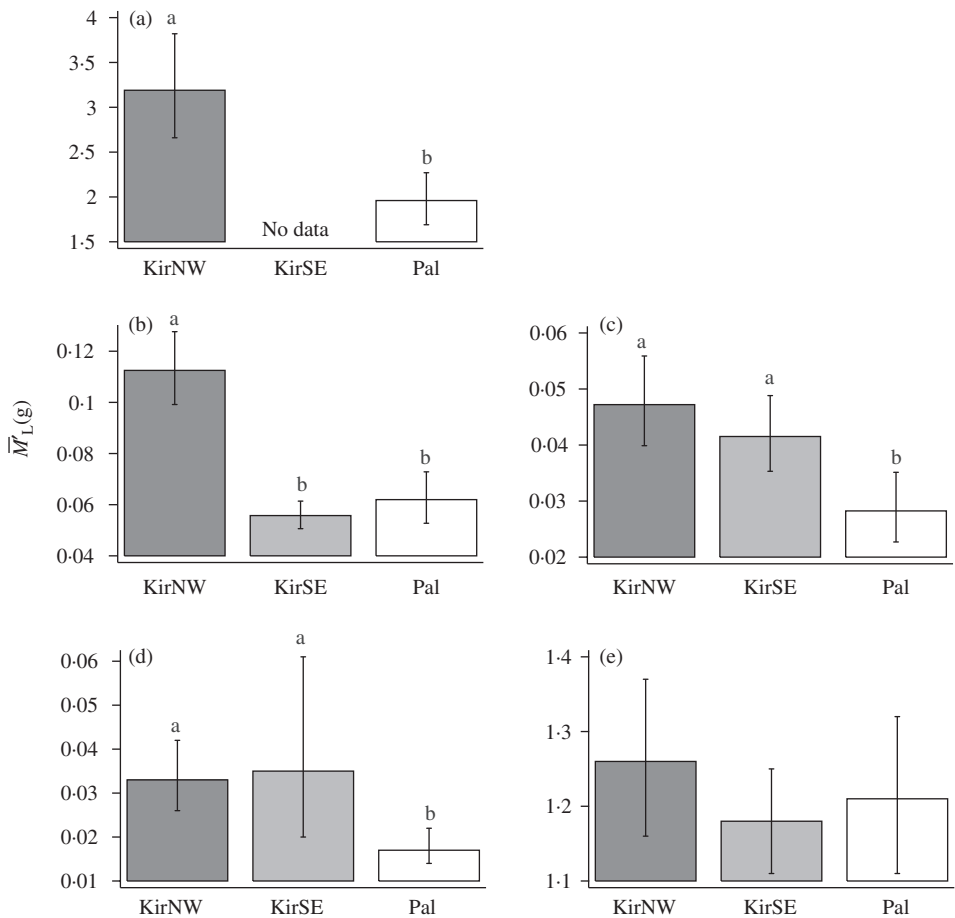


FIG. 3. Adjusted mean liver mass ( $\bar{M}_L$ ) and 95% C.I. by region [north-western Kiritimati (KirNW), south-eastern Kiritimati (KirSE) and Palmyra (Pal)] from best fit models (Tables II and SII, Supporting information) for: (a) *Lutjanus bohar*, (b) *Paracirrhites arcatus*, (c) *Plectroglyphidodon dickii*, (d) *Chromis margaritifer* and (e) *Acanthurus nigricans*. The  $\bar{M}_L$  that were determined to be significantly different by a *t*-test with Holm's sequential Bonferroni correction are indicated by lower-case letter (Table III).

2002; National Research Council, 2006). One of the main ways in which fishing may affect non-target species is by changing predator-prey interactions (Heithaus *et al.*, 2008). Fishing of top predators may lead to an increase in prey populations through prey release (Caddy & Rodhouse, 1998; Graham *et al.*, 2003; Myers *et al.*, 2007). Prey release is not, however, common in complex systems such as coral reefs (Sandin *et al.*, 2010). Predators may also have important effects on prey that do not involve changes in prey abundance (Lima, 1998), but these effects have not often been considered in the context of fishing (except the studies by DeMartini *et al.*, 2005, 2008; Stallings, 2008; Madin *et al.*, 2010; Ruttenberg *et al.*, 2011). This study tested the effect of fishing predators on prey energy allocation by comparing proxies of condition and reproductive potential in a diverse suite of species from reefs with different levels of fishing in the northern Line Islands. Fishing has resulted in

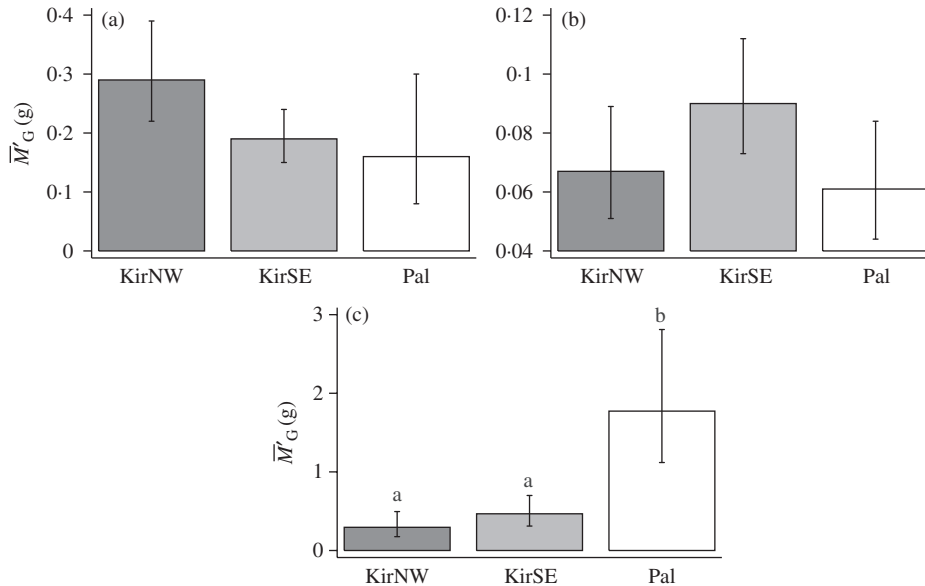


FIG. 4. Adjusted mean gonad mass ( $\bar{M}_G$ ) and 95% C.I. by region [north-western Kiritimati (KirNW), south-eastern Kiritimati (KirSE) and Palmyra (Pal)] from best fit models (Tables II and SIII, Supporting information) for: (a) *Paracirrhites arcatus*, (b) *Plectroglyphidodon dickii* and (c) *Acanthurus nigricans*. The  $\bar{M}_G$  that were determined to be significantly different by a *t*-test with Holm's sequential Bonferroni correction are indicated by lower-case letters (Table III).

five to seven-fold differences in predator abundance across these reefs (DeMartini *et al.*, 2008; Sandin *et al.*, 2008; Walsh, 2011). Although fishing predators has not been associated with a consistent increase in prey populations in the northern Line Islands (DeMartini *et al.*, 2008; Sandin *et al.*, 2008; Walsh, 2011), this study found that proxies for prey-fish condition were higher when predators were less abundant due to fishing, but that trends in prey-fish reproductive potential were inconsistent.

The differences in prey condition observed in this study may, in part, be the result of changes in predation rates and predation risk due to fishing predators. In a related study, Ruttenberg *et al.* (2011) found that the prey fishes in this study had reduced size (*P. arcatus*, *C. margaritifera* and *A. nigricans*) and longevity (*P. arcatus*, *P. dickii* and *A. nigricans*) in Palmyra, where predators are abundant, as compared to north-western Kiritimati, where fishing has reduced predator abundance. The reduced size and longevity of prey fishes in Palmyra suggest that predation rates may be higher than in north-western Kiritimati, despite no clear pattern in prey abundance. When predation rates are high, prey may allocate less energy to increasing body condition because the benefits, in terms of future reproduction, are low if prey have a high chance of being eaten (Stearns, 1992). In turn, the amount of energy available to improve body condition may be low because the energy required for behaviours that increase survivorship, such as vigilance or predator avoidance, is high (Lima, 1986; Wingfield *et al.*, 1998). Time that prey spend avoiding predators is time that cannot be spent foraging (Sih, 1980; Longland, 1991). Madin *et al.* (2010) compared the foraging behaviour of three of the species included in this study [*P. dickii*, *A. nigricans*

and *C. margaritifer*; note that *P. arcatus* and *L. bohar* were not included in the study by Madin *et al.* (2010)] at Palmyra and north-western Kiritimati and found that prey had reduced foraging areas when background predator abundance was high, predator encounters were high and model predators were introduced. Reduced foraging areas may reduce prey resource consumption and, consequently, body condition (Lima, 1998).

These studies suggest that high predation rates and predation risk may explain the lower body mass and liver mass observed in prey fishes from multiple trophic levels (*P. arcatus*, *P. dickii* and *A. nigricans*) on reefs with lower levels of fishing and higher levels of predators in this study. The lack of differences in body mass for the planktivore *C. margaritifer* and the predator *L. bohar* across reefs may, however, possibly be explained by other factors. *Chromis margaritifer* showed no evidence of differences in body mass across these reefs despite smaller foraging areas in Palmyra (Madin *et al.*, 2010). One possible explanation is that plankton may not be limiting in Palmyra and south-eastern Kiritimati, despite smaller foraging areas, because of strong currents (Hamman *et al.*, 2004; S. Sandin, pers. obs.). It is also possible that no differences in body mass were detected for these species because of insufficient statistical power. In contrast to the prey species, *L. bohar* should be directly affected by fishing rather than through changes in predation rates or predation risk. The evidence that *L. bohar* is more abundant and attains a larger size and age in Palmyra as compared to those in fished north-western Kiritimati is consistent with this hypothesis (Ruttenberg *et al.*, 2011). The lower abundance of *L. bohar* in north-western Kiritimati may, however, be expected to be associated with lower interspecific resource competition and higher body condition, if resources are limiting (Lizaso *et al.*, 2000). Unfortunately, there are no data on resource consumption for any of the species in this study.

The pattern of high prey body mass on reefs with high fishing and low predator abundance was corroborated by patterns in liver mass. The liver is an important area for energy storage and is usually the first site for lipid storage, especially in non-fatty fishes (Cowey & Sargent, 1977; Chellappa *et al.*, 1995; Pratchett *et al.*, 2004). These data suggest that prey fishes at reefs with high fishing intensity are not just heavier at a given length, but have more of their mass stored in the liver (note that liver mass was compared by controlling for total body mass). Body condition, measured by body mass and liver mass, represents the integrated energetic history of the fish (Gagliano & McCormick, 2004). The liver is, however, sensitive to short-term variation in a fish's energy balance and is affected by reproductive events (Pratchett *et al.*, 2004). For example, liver mass may vary with short-term changes in food availability and energy expenditure and it may also decrease during spawning (Eliassen & Vahl, 1982; Black & Love, 1986; Lambert & Dutil, 1997; Green & McCormick, 1999; Morgan *et al.*, 2010). Stochastic or unsynchronized changes in these factors across reefs may have obscured the effect of predator abundance (and potential predation and predation risk) on energy reserves and may explain the inconsistent pattern in prey-fish liver mass among species. In addition, liver mass is not necessarily the best indicator of energy reserves in *A. nigricans* because fishes of this genus store fat in mesenteries surrounding the gut and the visceral cavity (Fichelson *et al.*, 1985), which may explain the lack of difference in liver mass across all reefs for *A. nigricans*. Anecdotal observations made during dissections, however, revealed that fat deposits were more common in fishes from fished north-western Kiritimati, where

body mass was greater, than from lightly fished south-eastern Kiritimati and unfished Palmyra, which supports the hypothesis of higher energy reserves in locations where predators are less abundant.

Adult body mass and energy reserves should have important consequences for reproduction, yet, consistent effects have been difficult to predict and observe (Stearns, 1992; Peckarsky *et al.*, 1993; Scrimgeour and Culp, 1994; Boonstra *et al.*, 1998). Only one prey fish of the three examined showed significant differences in adjusted mean gonad mass across reefs. In Palmyra, where predator abundance is high, *A. nigricans* was in poor body condition, but exhibited elevated reproductive potential relative to south-eastern Kiritimati and north-western Kiritimati. The pattern in body mass and gonad mass suggests that there may be a trade-off in condition and reproductive potential for *A. nigricans*. Other studies have shown that these trade-offs may occur when food resources are limiting (Levins, 1968; Sibley & Calow, 1986; Stearns, 1992; Karels *et al.*, 2000). While no direct information about food resources is available, food may be more limiting in Palmyra for *A. nigricans* because of reduced foraging areas (Madin *et al.*, 2010). *Plectroglyphidodon dickii* and *C. margaritifer*, however, showed no differences in gonad mass despite also having reduced foraging areas in Palmyra (Madin *et al.*, 2010). A variety of factors may have influenced reproductive potential in these prey fishes (*e.g.* differences in food availability or energy intake and changes in reproductive timing), but unfortunately these factors cannot be evaluated in this study. Alternatively, differences in reproductive potential using gonad mass may not have been detected because this is a coarse measure and little is known of the variability in the developmental schedule of the gonads of these species in the Line Islands.

It is also possible that differences in resource competition or environmental conditions across the study sites could explain the observed patterns. Higher prey abundance may result in high resource competition and low body condition, if resources are limiting (Lizaso *et al.*, 2000). Previous studies, however, found no consistent pattern in the biomass of the major prey trophic groups (benthic invertivores, herbivores, omnivores and planktivores) that the study species represent (DeMartini *et al.*, 2008; Sandin *et al.*, 2008; Walsh, 2011). Even if fishing predators did lead to a higher abundance of prey, this mechanism would predict that prey may have lower body condition on fished reefs with low predator abundance, if resource abundance is similar, which is the opposite pattern in condition to what was observed. In addition, the consistently lower body condition found across prey species from different trophic groups on reefs with low fishing and high predator abundance suggests that the effect of predator abundance may be more important than the effect of any differences in abundance or availability of resources.

The small environmental differences among sites suggest that these factors are not wholly responsible for the observed patterns either. Kiritimati and Palmyra are relatively close together and have similar reef structures and oceanographic conditions (Sandin *et al.*, 2008). Other studies have reported differences in individual traits due to spatial variation in environmental conditions that typically span large spatial and environmental gradients (Schultz & Conover, 1997; Meekan *et al.*, 2001; Choat & Robertson, 2002; Robertson *et al.*, 2005; Ruttenberg *et al.*, 2005). In contrast, the differences in temperature (2° C) and productivity (0.07 mg m<sup>-3</sup> chlorophyll *a*) between Palmyra and Kiritimati are relatively small and may be biologically trivial compared to the magnitude of the difference in predator abundance among atolls (five

to seven-fold) (Table I). Importantly, differences in prey body mass were observed both within the island of Kiritimati and across the islands of Kiritimati and Palmyra. This suggests that differences in predator abundance within and across islands were more important than differences in environmental conditions across islands.

This study provides some of the first evidence of the indirect effects of fishing on proxies of condition and reproduction across multiple trophic levels of coral-reef fishes inhabiting predator-dominated and fished coral reefs. Fishing predators may have indirectly resulted in increased condition of prey species, but the effects on prey reproductive potential were less clear and may have been mediated by other factors. Heithaus *et al.* (2008) predicts that effects of predation risk should be more important than direct effects of predation in more complex habitats with longer lived prey species; however, this study was unable to separate the effects of predation and predation risk. Together with related studies on the effects of fishing predators in the northern Line Islands, it provides important information to help account for both the direct and indirect effects of fishing in the context of management and conservation (Stallings, 2008). A number of observational studies have documented changes in individual traits in target fishery species and related them to changes in fisheries productivity (Rijnsdorp, 1993; Lambert & Dutil, 1997; Conover & Munch, 2002; Olsen *et al.*, 2004). Understanding, however, how fishing indirectly affects these traits in communities of non-target species, the consequences for non-target species populations and feedbacks to fisheries productivity are important next steps for ecosystem-based fisheries management (National Research Council, 2006; Heithaus *et al.*, 2008; Stallings, 2008).

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## SUPPORTING INFORMATION

Supporting Information may be found in the online version of this paper:

**TABLE SI.** Comparison of candidate models for body mass. The dependent variable is total mass (log transformed). The predictor variables are the regions: south-eastern Kiritimati (KirSE) and Palmyra (Pal). The reference region is north-western Kiritimati (KirNW). All models are specified with standard length ( $L_s$ ) as a covariate. Best fit models are in bold.

**TABLE SII.** Comparison of candidate models for liver mass. The dependent variable is liver mass (log transformed, except for *Acanthurus nigricans*). The predictor variables are the regions: south-eastern Kiritimati (KirSE) and Palmyra (Pal). The reference region is north-western Kiritimati (KirNW). All models are specified with total mass ( $M_T$ ) as a covariate. Best fit models are in bold.

**TABLE SIII.** Comparison of candidate models for gonad mass. The dependent variable is gonad mass (log transformed). The predictor variables are the regions:



south-eastern Kiritimati (KirSE) and Palmyra (Pal). The reference region is north-western Kiritimati (KirNW). All models are specified with total mass ( $M_T$ ) as a covariate. Best fit models are in bold.

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