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7 Title: Linking fishing pressure with ecosystem thresholds and food web

8 stability on coral reefs

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10 Short title: Ecosystem thresholds for fisheries

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20 Abstract: Managing fisheries for ecosystem resilience is essential, but practical guidance is

21 limited by food-web complexity. Processes, mechanisms, and thresholds associated with

22 ecosystem overfishing were investigated by combining traditional concepts in fisheries biology

23 with recent advances in food-web modeling. Diverse coral-reef food webs were simplified by

24 grouping species into guilds based upon the way they capture, store, and transfer energy, rather

25 than taxonomically. Biomass fluxes between the guilds were then quantified using an allometric

26 trophic model. The model was calibrated by linking parameters describing growth, predation,

27 and competition with known body-size and metabolic constraints, and then adjusting the base

28 rate of parameters to match fish biomass estimates from a 'pristine' coral-reef system.   The

29 calibrated model was then tested by replacing equilibrium fish biomasses with observations from

30 fished systems across the Pacific. Encouraging relationships were found between predicted algal

31 accumulation and field observations, and between modelled and observed guild restructuring. In

32 terms of food-web ecology, 'pristine' food webs were characterized by asynchronous population

33 dynamics between the guilds (i.e., offsetting fluctuations), which maximized their persistence

34 and the net accumulation of biomass within food webs. Beneficial, offsetting fluctuations were

35 driven by the contrasting roles of density dependence, apparent competition, and predation.

36 Fishing for predators synchronized the population fluctuations between the guilds, resulting in

37 larger amplitudes (i.e., highs and lows), and a growing dominance of small herbivores.

38 Continued fishing for large herbivores eventually led to an inflection point where algal biomass

39 accumulated exponentially, revealing an ecosystem-based fisheries benchmark. Management

40 targets that maximized fisheries yields while controlling for algal accumulation required

41 simultaneous exploitation across the guilds; a significant challenge because maximum yields of

42 predators, large herbivores, and small herbivores were magnitudes of order apart. This strategy

43 also represented a significant departure from modern commercial fisheries policies that place

44 catch quotas on entire fish families taxonomically, committing systems to smaller fish, higher

45 biomass turnover, and undesirable algal accumulation. Moving forward, the model provided a

46 flexible and repeatable framework to consider economic and ecosystem objectives of fisheries

47 simultaneously, ultimately balancing resilient food webs against higher fisheries productivity.

48

49 **Keywords:** allometric trophic model; apparent competition; coral reefs; density-dependence;

50 ecosystem-based fisheries management; food-web stability; predation

51

52 **Introduction:** Coral reefs are among the most productive marine ecosystems in the world

53 (Nixon 1982), as high productivity and efficient recycling combine to support systems with

54 abundant fish stocks in oligotrophic waters (Friedlander et al. 2010, Houk and Musburger 2013).

55 These characteristics dictate that most fishery species are long-lived, slow-growing, and provide

56 lower yields compared with less-productive temperate ecosystems (Nixon 1982, Coleman et al.

57 2000). Combined, efficient recycling and slow growth of target fishes also suggest that reef

58 ecosystems are vulnerable to harvesting. In support, associations between fishing pressure, fish

59 biomass, and indicators of ecosystem fragility persist across large spatial scales (McClanahan et

60 al. 2011, Houk et al. 2015). Associations can be used to infer causation, but deeper insight into

61 how fisheries exploitation may lead to compromised ecosystem states remains limited by food-

62 web complexity on coral reefs. Food-web complexity leads to multiple, interacting processes

63 that dictate how populations change through time, such as predation, competition, and density

64 dependence. Ultimately, uncertainty in understanding how these processes combine to drive

65 populations and entire systems limits practical guidance for ecosystem-based approaches to

66 management.

67

68 Ecosystem models that account for each species, or species group, provide ideal tools for

69 managers to consider harvest yields against system responses, but the complexity of coral reef

70 systems often extends to a complex parameterization process (McClanahan 1995, Pauly et al.

71 2000). Species-based parameters may or may not resonate with ecological laws governing their

72 body-sizes and metabolic processes (Brown 1984, Brown et al. 2004), and ecosystem models

73 often do not consider self-regulation (i.e., density dependence) or recycling between the fish

74 guilds and basal resources due to complexity. Both are especially relevant for coral reef systems

75 with low influxes of nutrients from surrounding oligotrophic waters (Hatcher 1997). The clear

76 benefits of ecosystem models are to help balance harvest against production, and predict the

77 cascading responses of both target and non-target species to harvesting. But how might entire

78 system states shift in response to harvesting? This question has typically been addressed through

79 a second line of research focused upon one, or a few, key processes, such as herbivory. Insightful

80 consumer-resource models investigating herbivory on coral reefs have been calibrated and tested

81 against field data to predict ecological phase shifts, such as coral-to-algae transitions, and offer

82 thresholds for ecosystem-based management (Bascompte et al. 2005, Hixon and Jones 2005,

83 Roff et al. 2016, Ruppert et al. 2016). Yet, predation and competition are also critical for food

84 web persistence, but uncertainty remains regarding the nature and strength of their contribution

85 to ecosystem dynamics (Hixon and Jones 2005, Roff et al. 2016, Ruppert et al. 2016). Clearly

86 there is a desire to appreciate a greater suite of processes that drive both population and

87 ecosystem dynamics on coral reefs, but reconciling ecological complexity and developing model

88 parameters is a longstanding challenge.

89

90   The present study took a novel approach to model fisheries exploitation in coral-reef systems by

91   first reducing food-web complexity, and then building a framework that simultaneously

92   examined the processes of herbivory, predation, competition, density dependence, and excretion.

93   The complexity of coral-reef systems was reduced by grouping species into guilds based upon

94   the way they capture, store, and transfer energy across trophic levels, rather than taxonomically

95   (Mouillot et al. 2014, Madin et al. 2016). Because metabolic processes are dictated by body size

96   (Brown et al. 2004), grouping species based upon their trophic level and body size can simplify

97   model parameterization by linking metabolic rates, such as growth, to a common anchor point

98   (Yodzis and Innes 1992, Brose et al. 2006). Next, guilds were organized into a generalized food-

99   web motif that has been applied to systems of both high and low diversity to investigate how

100   disturbances alter individual populations and entire systems (McCann 2011, Moore and de Ruiter

101   2012). For diverse systems such as coral reefs, generalized food-web motifs may be repetitive

102   across habitats that are coupled by a common predator pool, or vertically across trophic levels

103   (McCann et al. 1998, Bascompte and Melián 2005, Rooney et al. 2008, Stouffer and Bascompte

104   2011, Schwarzmüller et al. 2015). The present model was centered laterally on hard-bottom

105   habitats with greatest economic, ecological, and fisheries values, and vertically on the key guilds

106   driving observable patterns within coral-reef systems (Fig. 1).

107

108   We first examined whether a set of linked population growth models could depict biomass

109   restructuring within reef systems exposed to fishing, and eventually lead to compromised reef

110   states. This initial hypothesis was tested by comparing model predictions with extensive field

111   data gathered across a suite of Pacific islands with varying rates of fisheries exploitation. Given

112   correspondence, mathematical stability analyses were next performed to evaluate how ecological

113   processes interact to drive food-web resilience (i.e., stability or return times) and reactivity (i.e.,

114   population and system responses) along a gradient of fishing pressure (May 1971). Stability

115   analyses defined which ecological processes were most sensitive to fishing pressure and most

116   critical for ecosystem-based fisheries management to consider. The combined results were then

117   used to consider fishing scenarios that balanced food-web resilience with optimal harvest yields.

118

Methods: Essential components of coral-reef ecosystems and ecosystem-based fisheries management (EBFM) were captured within a representative food-web motif, including (i) a common basal resource pool, (ii) two herbivore guilds that grouped species based upon their growth rates and biomass turnover within the food web, and (iii) a common predator that represented piscivorous fishes and reef sharks combined into a single guild, essentially a mesopredator guild (A, H1, H2, P, respectively, Fig. 1b). This food-web motif was positioned across these trophic levels to focus on hard coral assemblages and key processes that link fisheries exploitation with a key attribute of ecosystem status, algal accumulation. Depending upon the question of interest, similar food-web motifs could be centered differently across trophic levels, or motifs could be expanded to include more predator groups in higher trophic levels, such as larger roving apex predators. Here, we isolated upon hard bottom substrates with herbivore and predator guilds that are primary components of reef fisheries (Houk et al. 2012), and support hard coral assemblages that support tourism economies and provide coastal protection.

The resource pool represented opportunistic turf, encrusting, and macroalgal growth on coral reefs that responds rapidly to nutrients and accumulates detritus (Wilson et al. 2003), and can ultimately impact coral abundance, diversity, and reef growth through time (Mumby et al. 2006, Houk and Musburger 2013, Perry et al. 2013). By default, calcifying corals and crustose coralline algae represented the inverse of this resource pool, implicitly considered here as the 'favorable' state of hard-bottom assemblages. Herbivores and detritivores subjected to fishing pressure on coral reefs were grouped given their mixed diets, and mixed presence of algal and detritus on the reef. Together herbivores and detritivores represented a suite of species mainly within three families (Acanthuridae, Siganidae, Kyphosidae) and one sub-family (Scarinae, family Labridae). A literature synthesis was conducted to categorize herbivores and detritivores from Pacific coral reefs into 'fast' and 'slow' energy channels based upon indicative life-history traits and extensive observation records (Appendix S1: Fig. S1). Small species with fast growth rates and high biomass turnover are quick to respond to available resources and represent preferential prey for predators (i.e., 'fast' channels; Rooney and McCann 2012, Schwarzmüller et al. 2015). This is counterbalanced by large species with slower growth rates and low biomass turnover that sequester biomass longer in the system, and are less reactive to disturbances or

system perturbations (i.e., 'slow' channels). We found evidence for a consistent ordering and separation of herbivores with respect to growth rates, maximum body sizes and weights, and size distributions recorded in catch data (Appendix S1: Fig. S1). Herein, we use the term 'herbivores' to represent the combined herbivore and detritivore guilds for brevity. Notably, the process of categorizing herbivores extended species-based resource partitioning patterns and allometric relationships that have been observed for a diversity of organisms within many ecosystems (Brown 1984), but to our knowledge, never applied to herbivores on coral-reefs. Last, predators represented piscivorous fish species and reef sharks combined into a single guild that linked the herbivores, essentially a generalist group of mesopredators that have the greatest influence on herbivore populations (Appendix S1: Table S1).

The model combined elements of logistic growth for the consumer species, mass-action terms for competition and predation, and proportional feedback rates to represent excretion that was recycled back to the resource pool. Cumulatively, we examined a system of four differential equations that represented the linked populations in terms of biomass fluxes (kg C/m^2):

$$\frac{dA}{dt} = \lambda + i_1 H_1 + i_2 H_2 + i_p P + cA - r_1 H_1 A - r_2 H_2 A - x_a A$$

$$\frac{dH_1}{dt} = r_1 H_1 A - s_1 H_1^2 - \alpha_{12} H_1 H_2 - w_1 P H_1 - f_1 H_1$$

$$\frac{dH_2}{dt} = r_2 H_2 A - s_2 H_2^2 - \alpha_{21} H_2 H_1 - w_2 P H_2 - f_2 H_2$$

$$\frac{dP}{dt} = e_1 w_1 P H_1 + e_2 w_2 P H_2 - x_p P - f_p P$$

(0.1)

where (A) was the combined resource pool of algal substrates that were consumed by both smaller-bodied (H_1) and larger-bodied (H_2) herbivore guilds, with growth rates (r) and carrying capacities (s). Additions to the basal algal resource pool came from external allochthonous inputs (λ), recycled autochthonous inputs via excretion (i), and conversion between differing forms of algae and detritus (c). Competition (α) existed among herbivores for the algal resource pool. Predators (P) assimilated herbivores based upon attack rates (w) and energy conversion efficiencies (e). Last, both natural (x) and fishing mortality (f) was applied to the harvested fish populations.

174

Parameterization and Calibration: The allometric trophic model consisted of linked rate parameters pertaining to the fish guilds: growth rates (r), carrying capacities (s), attack rates (w), and excretion rates (i). Rates were scaled by metabolic constraints associated with body sizes, and then adjusted for differing home-range sizes to yield estimates per reef area (Appendix S1: Fig. S2, Tables S1 and S2; Yodzis and Innes 1992, Brown et al. 2004, Berlow et al. 2009, Green et al. 2014). For instance, growth rates and carrying capacities for small and large herbivores scaled with the power law described by the metabolic theory of ecology, but were adjusted to account for the fact that small herbivores have a smaller home-range size compared to large herbivores (Appendix S1: Fig. S2). Similarly, predator attack rates were scaled by known body-size feeding preferences (Yodzis and Innes 1992, Berlow et al. 2009). Excretion rates were scaled by body size, home-range size, and nutrient content that is influential to algal biomass production (Vanni 2002, McIntyre et al. 2007, Burkepile et al. 2013). In sum, it was only necessary to define one rate parameter (i.e., growth), as others were anchored.

188

Next, the relative contribution of each process was determined. Growing evidence across many ecosystems supports that diverse food-web networks stably persist when competition and predation have weaker influences on population dynamics compared to density dependence (McCann et al. 1998, Neutel et al. 2002, Bascompte et al. 2005, Berlow et al. 2009), giving way to self-regulation as the primary driver of individual guilds. Thus, intraspecific density dependence was required to be stronger than interspecific competition and predation (May 1974). Last, we gave constants conservative values based upon previous studies (Appendix S1: Table S2). Changes in their values (±20%) did not shift any model outcomes so long as their relative influence remained consistent. Because productivity on coral reefs is disproportionally driven by efficient recycling via excretion between fish guilds and algal/detrital resource pools (Hatcher 1997), we set external influx rates (λ) as lowest contributions to algal resource pools, and natural losses (x) and conversion between differing forms (c) lower than additions from excretion (i). Natural mortality rates for predators (5%) were consistent with estimates from fisheries studies (Pauly 1980). Standard values of 10% were used as trophic energy conversions for predators.

204

205   Using these assumptions, the model was calibrated by solving the system of equations at

206 equilibrium in terms of parameters only, disregarding negative solutions, and adjusting the linked

207 parameters to standing stock estimates from a nearly pristine atoll in the Marshall Islands

208 (Appendix S1: Fig. S3, calibration process and sensitivity analyses; Houk and Musburger 2013).

209 Rongelap atoll has remained largely uninhabited for 57 years due to fallout from the atomic

210 bomb testing at nearby Bikini Atoll in 1954. We converted percent cover estimates of the algal

211 resource pools on Rongelap into biomass using a foundational study for nearby Eniwetok Atoll,

212 Marshall Islands, that provided conversion estimates based upon bomb calorimetry (Odum and

213 Odum 1955). Fish biomass data were derived from length estimates during underwater

214 stationary point counts, which were then converted to weight based upon length-weight

215 relationships (Appendix S1: Table S1). Fish biomass estimates were then rescaled by both the

216 survey area and their home-range size to provide consistent units of biomass density (kg C/m^2).

217 Home-range size scaling resonated with recent research that provided both theory and evidence

218 to show that inverted biomass pyramids once thought to be a feature of coral reefs should be

219 reconsidered due in large part to species home-range sizes (Trebilco et al. 2013, Bradley et al.

220 2017). Home-range size scaling had greatest implications for large species, mainly predators,

221 which have large home-ranges but may be attracted to divers conducting non-instantaneous

222 visual censuses in remote unfished areas over extended periods of time (Kulbicki 1998, Ward-

223 Paige et al. 2010). Clearly all visual census techniques for mobile fishes have biases to some

224 degree, yet we argue the scaling for home-range sizes was less of a bias and more of fundamental

225 requirement. Further, to deal with potential bias, we note that our study relied upon relative

226 comparisons derived from similar field protocols and observers (Dickens et al. 2011). Predator

227 biomasses were further adjusted to account for their energy derived from hard-bottom habitats

228 only (Fig. 1a). The parsimonious approach was to divide predator biomasses by three to account

229 for each of the habitats, supported by the limited dietary studies available that describe foraging

230 for species commonly observed (McCauley et al. 2012). Because limited data existed to verify

231 this assumption, we also calibrated the model while not making this adjustment. This assumption

232 made no difference to the model outcomes and shifted the base rate parameters by less than 10%.

233 We summarize that the most significant assumption was to scale predator biomass estimates by

234 their home range sizes, shifting the natural shape of trophic pyramids from being inverted to

235 bottom heavy, matching studies that provided compelling evidence (Trebilco et al. 2013,
236 Bradley et al. 2017).

237

238 **Field validation.** All of the assumptions made while calibrating the model were tested against an
239 expansive dataset from Micronesia, tropical North Pacific Ocean (Houk et al. 2015). A proxy to
240 fishing pressure was previously shown to be the primary driver of coral-reef ecosystem
241 conditions across Micronesia, while pollution had a secondary role that was most pronounced in
242 the few urbanized watersheds near population centers (Houk et al. 2015). Thus, it was
243 hypothesized that fishing would exert primary control over food-web structure, algal-resource
244 accumulation, and by extension ecosystem condition across a suite of islands in the tropical
245 Pacific. We populated the calibrated model with fish biomass estimates from 71 sites across
246 Micronesia, spanning 9 islands and numerous major-reef habitats (Appendix S1: Table S3). We
247 then examined the correlation between the predicted algal biomass and the field-based
248 observations at the site-and-island scale. Because wave energy has previously been shown to
249 have a positive association with coral ecosystem conditions across Micronesia due to flushing of
250 algae and detritus with high wave energy (Houk et al. 2015), we examined correlations with and
251 without site-based wave energy estimates as a covariate (Appendix S1: Table S3). In addition,
252 we set minimum limits to observed fish biomass estimates in instances where zero or trace
253 values led to unrealistic algal biomass accumulation. The alternative approach of capping algal
254 resource accumulation with a model parameter was not preferred because site-level differences
255 in wave exposure existed, and would not be accounted for consistently. Last, we appreciated that
256 disturbances can alter standing stock biomasses and induce inconsistent transient dynamics.
257 Data used to test model performance were collected prior to major natural disturbances
258 associated with the 2014-2015 global bleaching event for affected islands; other islands with data
259 during these timeframes were not impacted by the recent bleaching event.

260

261 We also tested a key finding of the calibrated model suggesting that predators facilitate a more
262 even distribution of herbivore biomass across both 'slow' and 'fast' energy channels (i.e., small
263 and large herbivores), and across species assemblages, compared to systems without predators.

264 Using field data, predator biomass was examined against the ratio of herbivore guilds, and
265 against Shannon-Weaver diversity indices using least-square regression models.

266

267 **Model analysis and fishing scenarios.** Following model validation with field data, linear
268 stability analyses were performed to assess the ecosystem consequences of fishing. Linear
269 analyses investigated the set of linked differential equations with respect to whole-system
270 stability and reactivity, which was distinguished from intra-guild stability and reactivity
271 described below. This required deriving the Jacobian matrix, or the community matrix, which
272 represented the change in populations with respect to density dependence (diagonal elements)
273 and inter-specific interactions (off diagonals). Mathematically, these terms represented partial
274 derivatives. The determinant, or linear solution of this matrix, has dominant components, or
275 eigenvalues, that are either positive or negative, with or without complex numbers that have
276 imaginary terms. Negative eigenvalues associated with Jacobian matrices described that the
277 system will return to its original equilibrium state, with the rate of return given by the eigenvalue
278 magnitude. Positive values indicate that the system will move away from equilibrium. Complex
279 numbers indicate that the system will oscillate around equilibrium. This classic form of stability
280 analysis has a counterpart, reactivity, which describes the magnitude of oscillations when
281 returning to equilibrium, known as the Hermitian part of the community matrix (Neubert et al.
282 2004). Increasing values of reactivity indicate increasing magnitudes of oscillations and
283 increasing system instability. Eigenvalues associated with both stability and reactivity represent
284 metrics that describe the net change within the whole system. Whole-system stability and
285 reactivity were estimated after each step increase in fishing pressure.

286

287 In addition, a second form of reactivity was used to assess intra-guild oscillations following
288 fishing events, or pulsed exploitation. We argue that this approach may be most relevant to
289 assess reactivity within fish populations that have discrete growth, or defined reproduction. Intra-
290 guild reactivity was assessed using the discrete, time-step version of our model to follow
291 individual populations for 10 timesteps intervals after pulsed exploitation. Correlations among
292 the guilds were then calculated to assess their synchrony.

293

294   Using the described approach, two fishing scenarios were examined. First, sequential fishing
295   pressure was applied to predators, large-bodied herbivores, and small-bodied herbivores,
296   respectively. Harvesting was simulated until each guild went functionally extinct, or caused
297   other populations to go extinct. This was defined when populations became low and fishing
298   would target other species. Mathematically, this threshold was defined when oscillations crossed
299   zero, suggesting a population was very low with the possible chance of extinction. A second
300   scenario was then considered to highlight a potential approach towards EBFM. Simultaneous
301   fishing pressure was applied so that maximum sustainable yield was attained at the same time
302   within each guild. In both instances, we used biomass accumulation within the algal resource
303   pool as an indicator of declining ecosystem states. The ratio of fished-to-unfished biomass was
304   also used as a reference point to assess ecosystem status. Previous studies have recommended
305   biomass targets between 25 to 50% of unfished biomass (0.25 to 0.5 B_0) for all fish guilds
306   grouped to prevent coral-to-algae phase shifts, yet initial changes in the structure of fish
307   assemblages began between 0.5 to 0.88 B_0 (Karr et al. 2015, McClanahan et al. 2015). These
308   guidelines were used to describe a plausible range for maximum ecological yield (MEY).

309

310   **Results.** Sensitivity analyses guided a repeatable process to calibrate the model to a 'pristine'
311   reef state (Appendix S1: Fig. S3). Parameters ranges varied by less than 10% when matching
312   biomass estimates from 'pristine' reefs. The calibrated, unfished system represented a trophic
313   pyramid dominated by basal resources, but with nearly equal contributions from herbivores and
314   predators (52%, 25%, and 23% of total food-web biomass within the algal resources, herbivores,
315   and predators, respectively), as predicted by modern theory. Observed fish biomass data from a
316   suite of islands across the Tropical Pacific were then loaded into the model, and predicted algal
317   biomasses were tested against field data. Observed algal biomasses were well predicted across
318   multiple spatial scales of investigation (r = 0.58 and 0.69, respectively for site-based and island-
319   based correlations inclusive of all islands but Rongelap where the model was calibrated,
320   P<0.001, Fig. 2a-b, Appendix S1: Table S3). Predictive relationships also persisted within
321   individual islands (mean r = 0.57 ± 0.23 SD for islands that had 6 or more sampling locations).
322   Together, these initial results suggested that basal resource standing stocks were well predicted
323   by restructuring fish assemblages, offering a unique platform to investigate how ecosystems may
324   respond to fishing.

Sequential fishing. Sequential fishing for predators, large-herbivores, and small-herbivores, respectively, was applied to characterize and contrast system responses. Stability trends were first compared within each of the three system states, representing food webs with: 1) both herbivore and predator guilds, 2) only herbivore guilds, and 3) only the small herbivore guild (Fig. 3a, left-to-right separated by vertical dashed lines). Stability analyses highlighted decreases in system resilience, or slower return times, within each system state when exposed to fishing (Fig. 3a, increases in solid lines within each window until functional extinctions or grey boxes). This was the result of diminishing direct trophic interactions as fishing reduced predation and herbivore consumption, resulting in longer time periods for the system to return to equilibrium. In contrast, comparisons across system states served to understand the beneficial roles of predators and indirect trophic interactions. Prior to applying any fishing effort, systems with predators had slower return times and greater population responses than systems with herbivores only (Fig. 3a, higher initial starting points for both solid and dashed black lines in the window with predators), unintuitively suggesting that systems with predators were less resilient and more reactive. Yet, it is important to appreciate that net-system reactivity and stability depend on the number of species, or guilds. Systems with more species will have greater net-values simply because there are more populations to fluctuate. More interestingly, the examinations of individual populations revealed that higher reactivity in systems with predators was beneficial because it was the result of offsetting, asynchronous fluctuations (Fig. 3b-c, offsetting oscillations shown for systems with predators). Offsetting fluctuations increased net system reactivity, but diminished the variability within each guild. For instance, while small herbivores had the greatest response to pulsed exploitation as expected by their higher growth rates, competition from large herbivores and preferential assimilation by predators buffered the magnitude of this oscillation, and reduced the amplitude of population fluctuations (i.e., reduced 'boom-and-bust' dynamics). Once food webs became impacted by fishing, beneficial asynchrony among the guilds decreased (Fig. 3b-c, r = -0.56 and -0.49, inter-guild correlations for 10-timestep windows following light and moderate fishing, respectively). Most significantly, once predators became functionally extinct, species responses shifted from having negative-to-positive correlations, and population fluctuations within the food webs became synchronized and larger in amplitude. We summarize that the functional extinction of predators represented a critical

356   transition point where synchronized guild responses emerged. The consequences of synchronized

357   food webs were next investigated with respect to fisheries potential and algal resource

358   accumulation.

359

360   In terms of fisheries potential, synchronized systems without predators and large herbivores were

361   clearly more productive, but higher productivity also led to larger fluctuations within fish guilds

362   and the algal resource pool (Fig. 3b-e). Interestingly, algal resources fluctuated four times as

363   much as herbivores when fishing predators towards their maximum yields (regressions between

364   percent predator removal and resultant fluctuation in herbivore guilds and algal resources;

365    $P_{\%\,decline} = 102(1 - e^{-0.55H_{\%\,change}})$, $P_{\%\,decline} = 418(1 - e^{-0.005A_{\%\,change}})$, R^2 values > 0.95, P<0.001, Fig. 3b-

366   c). Once predators were removed, apparent competition grew stronger and the ratio of small-to-

367   large herbivores increased (Fig. 3d). Empirical data served to supported this model prediction, as

368   reduced predator abundances predicted higher ratios of small-to-large-bodied herbivores across

369   the suite of Pacific islands where field data were collected ($\ln(P) = 0.50 \ln\left(\dfrac{H1}{H2}\right) 1.24$,

370   adjusted $R^2 = 0.38$, P<0.001, Fig. 2c), and reduced Shannon-Weaver herbivore diversity indices

371   as well ($\ln(P) = 3.4$ *diversity* 12.6, adjusted $R^2 = 0.42$, P=0.07, Fig. 2c-d, *see Discussion*). In

372   sum, competitive interactions among the herbivore guilds became more pronounced with

373   predator removal, and this had greatest consequences for algal resource fluctuations. Building

374   upon this finding, simultaneous fishing across all guilds was next investigated as a potential

375   means to maximize fisheries yields while minimizing algal resource accumulation in the model

376   food web.

377

378   **Simultaneous fishing.** Simultaneous fishing served to maintain the benefits of all trophic guilds

379   working together to balance the processes of predation, competition, and density dependence.

380   However, simultaneous fishing required large adjustment to fishing pressure because maximum

381   yields differed by magnitudes of order across the guilds (Fig. 3e). Adjusting fishing pressure so

382   that MSY_P and MSY_{H2} peaked simultaneously served to control algal resource accumulation and

383   enhance the yield of large herbivores relative to the sequential fishing scenario (Fig. 4).

384   Continued fishing beyond the MSY_P and MSY_{H2} peaks revealed an inflection point where algal

385   accumulation shifted from a slow asymptotic increase to an exponential rise that eventually

386   resulted in a tripling of algal biomass and unstable oscillations. This system inflection point

387   represented 60% of the unfished biomass for all guilds combined ($0.6\ B_0$). The present results

388   provided a further breakdown of unfished biomass benchmarks by guilds, representing 0.6 to 0.7

389   B_0 for predators and 0.5 to 0.75 B_0 for large herbivores. The low-to-high range in these

390   benchmarks were associated with fishing effort at 60 to 100% of their respective MSY,

391   representing conservative and aggressive thresholds respectively (Fig. 4b).

392

393   **Discussion.** The direct and indirect consequences of fishing on ecosystems have long been

394   considered in theory, especially with regards to large and long-lived fishes and their functional

395   roles (Jennings and Polunin 1997, Worm et al. 2009). Using a combination of empirical data and

396   modelling across novel trophic guilds, we quantified how natural coral-reef food webs

397   maintained offsetting ecological processes that maximized both population stability and biomass

398   accumulation. The benefits of asynchronous interactions between guilds have been considered

399   within theoretical studies (Rooney et al. 2006, Vasseur and Fox 2007), but correspondence with

400   field data and investigating both net-system stability and individual population stability offered

401   more insight. Fisheries became more productive once asynchronous dynamics within food webs

402   were removed, but synchronized 'boom-and-bust' systems provided intermittent subsidies to the

403   algal resources leading to a 1.5-fold increase in algal biomass (Fig. 4). An interesting analogy

404   and supporting evidence came from a carbon pulse-chase experiment in terrestrial systems that

405   manipulated predator abundances. Following predator addition, there was a 1.4-fold decrease in

406   carbon turnover as above-ground biomass turnover shifted towards below-ground biomass

407   sequestration (Schwarzmüller et al. 2015), due to both consumptive and non-consumptive effects

408   of predators.

409

410   Support for the hypothesized functions of predators on coral reefs has been inconsistent (Houk

411   and Musburger 2013, Ruppert et al. 2013, Rizzari et al. 2015, Roff et al. 2016, Ruppert et al.

412   2016), in part because many of the proposed functions represent indirect trophic interactions that

413   are difficult to observe and quantify, and also because predator removal is often accompanied by

414   continued fishing for herbivores. Here, the sequential fishing scenario summarized potential

415   system responses to predator removal without any confounding factors. Large herbivores were
416   most sensitive to predator removal because of their competition with small herbivores that
417   reduced their equilibrium biomass. As a result, reactive fluctuations brought them close to our
418   defined functional extinction point following disturbances (Fig. 3c). However, without sustained
419   fishing for large herbivores to augment these fluctuations, a reduction in diversity was not
420   expected (i.e., a stable equilibrium point inferring competitive exclusion). Sustained fishing
421   pressure for herbivores clearly existed across Micronesia (Houk et al. 2012), supporting the
422   positive relationship between predators and herbivore diversity indices (Fig. 2d). However,
423   diminished relationships are predicted in the absence of sustained herbivore fishing, offering
424   potential reconciliation for contrasting reports of herbivore biomass and diversity along predator
425   gradients (Jennings and Polunin 1997, Friedlander and DeMartini 2002, Houk and Musburger
426   2013, Ruppert et al. 2013, Rizzari et al. 2015). The clearer response of the herbivore community
427   to predator removal was the growing ratio of small-to-large herbivores, with less influence to
428   overall biomass retained within the combined herbivore guild. Thus, further studies investigating
429   how the guilds defined in the present study may shift along predator gradients can benefit our
430   understanding.

431

432   Logically, increases in algal resources with fishing pressure translated to decreases in corals and
433   calcifying substrates (i.e., an inverse relationship between these groups, see methods). Studies
434   across large spatial scales show that a suite of biological attributes such as coral recruitment,
435   growth, diversity, and algal abundances are sensitive to gradients of fish biomass or fishing
436   pressure (Mora 2008, McClanahan et al. 2011, Houk et al. 2015). These patterns are caused by
437   changing population interactions through time. Given the uncertain, yet influential roles of long-
438   lived predators and herbivores in driving population interactions, an evolving goal for
439   ecosystem-based fisheries management (EBFM) has been to sustain the stock structure of all
440   species simultaneously, or species-based management units, in order to maintain the suite of
441   functions fishes provide (Froese et al. 2008, Blanchard et al. 2014). This cautious approach is
442   challenging, because species-based responses to fishing pressure and species-based functional
443   roles remain poorly resolved for diverse coral reef ecosystems. The present study simplified this
444   situation by developing trophic guilds that grouped species based upon their energetic and life-

445 history characteristics, which helped to refine stock management units and inform fisheries
446 polices.

447

448 **Fisheries management**. Most fisheries management policies are rooted in the ideology of
449 compensatory density dependence that assumes reductions in adult populations create space for
450 enhanced recruitment because resource become less limiting. Building upon this concept, we use
451 the application of the Magnuson-Stevens Fishery Management and Conservation Act for coral
452 reef fisheries in the United States as an example because it represents a powerful legislative
453 basis, and a common approach towards fisheries in general (WPFMC 2011).   Under this
454 legislation, annual fish quotas were derived from optimized catch scenarios for each stock unit.
455 However, stock units are defined based upon taxonomy rather than ecological function. Species
456 within the two largest families of herbivores on coral reefs, the parrotfishes and surgeonfishes,
457 were binned into stock units that combined both slow-and-fast growing species, shown here as
458 energy channels that make strikingly different contributions to carbon storage and turnover in
459 food webs.   Even though catch limits were conservatively defined by 75% of the estimated
460 MSY, a replacement of large-bodied species by smaller-bodied counterparts would be expected,
461 an ongoing situation (Houk et al. 2012), and algal resources subsidies would be expected.
462 Policies might instead equate management units primarily to functional guilds, and secondarily
463 to taxonomy (i.e., distinguish between large-and-small-bodied parrotfishes, surgeonfishes, or
464 grouped herbivores). Then, as our knowledge of life histories grows, management units can be
465 refined to group species based upon both their functional roles and expected responses to fishing
466 pressure (i.e., group similar species of small-bodied parrotfishes into a management unit). This
467 approach would improve our ability to define and adjust ecosystem-based targets.

468

469 Based upon overall fish biomass, our ecosystem-based targets to prevent an exponential increase
470 in algal resources were slightly higher than targets required to prevent a coral-to-algae phase
471 shift in the Caribbean and Indian Oceans (0.6 B_0 versus 0.5 B_0, respectively; Karr et al. 2015,
472 McClanahan et al. 2015). However, when breaking down these targets by guilds, predators and
473 large herbivores required conservative benchmarks greater than 0.5 B_0, while fisheries centered
474 upon smaller herbivores could have attained yields that were up to one magnitude of order larger.

475   Thus, refining fisheries objectives with respect to fish guilds can help to guide the distribution of

476   fishing pressure, and eventually pave the way for detailed studies within each management unit.

477

478   **Conclusions.** We conclude that the slow but persistent expansion of coral reef fisheries over

479   decades represents a chronic threat to ecosystem resilience (Birkeland 2004, Graham et al. 2013,

480   Cuetos-Bueno and Houk 2015). The present model offered a repeatable framework to balance

481   economic and ecosystem objectives of fisheries, ultimately balancing the retention of biomass

482   needed for resilient food-web networks against higher biomass turnover needed to fuel fisheries

483   economies. Future adaptations could include covariates of fisheries production and ecosystem

484   condition. Climate change, disturbance cycles, pollution, and habitat loss all represent key

485   threats to fisheries that could be incorporated and tested within the context of our generalized

486   model of coral reef systems.

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658 participated in field data collection, unfortunately their contributions were too numerous to list
659 individually.   Jim Baldwin, Brett Taylor, several anonymous reviewers and the editor all
660 provided beneficial reviews of our modelling framework, assumptions, and manuscript drafts.
661 Data used in our analyses can be found in the supplemental materials.

662

663 **List of Figures**

664 **Figure 1**. Repetitive food-web motifs hypothesized for coral-reef ecosystems consisting of a
665 common resource pool, two consumer guilds grouped by their energy assimilation and retention
666 properties as 'fast' and 'slow' energy channels, and a generalist predator that couples both
667 consumer guilds and major habitats (a). Letters denote P-planktivores, H-herbivores and
668 detritivores, M-micro and macroinvertebrates, and I-invertivores. Numbers denote 1-'fast'
669 energy assimilation channels with lower biomass retention, and 2-'slow' energy assimilation
670 channels with higher biomass retention. The present study was centered upon hard-bottom, coral-
671 reef habitats and key guilds driving ecological dynamics on coral reefs (a, dashed box). Trophic
672 interactions within the focal motif (b) are represented by arrows linking the A-algal resource
673 pool, H1 and H2-fast and slow energy channel herbivores, and P-predators. Largest black
674 arrows represent external input, natural loss and fishing exploitation, and recycling within the
675 system. Small black arrows represent consumptive interactions.   Dashed arrows represent
676 excretion from the fish guilds back to the resource pool. Dotted arrows represent weak
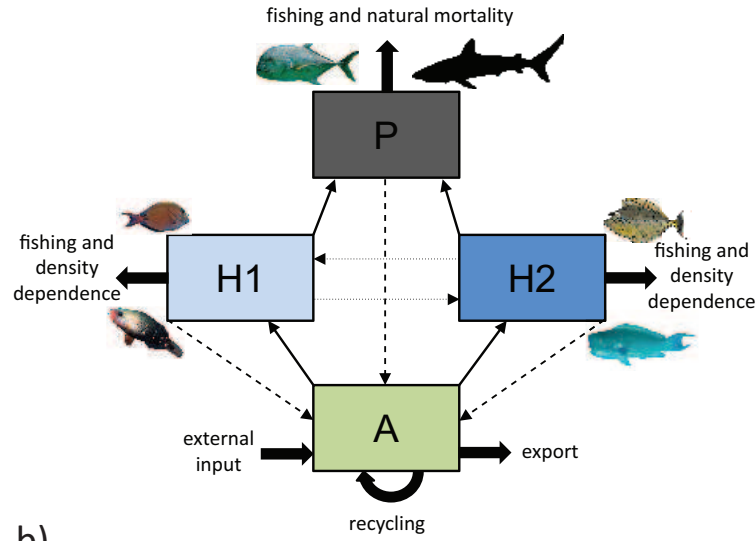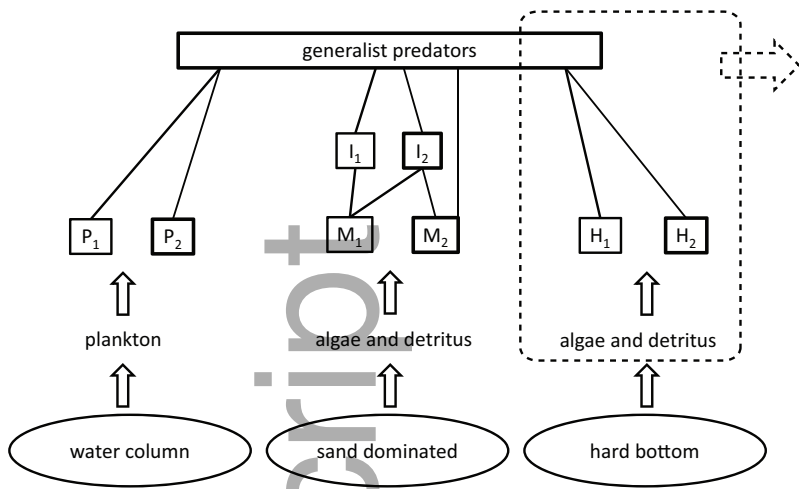677 competitive interactions.

678

679 **Figure 2.** Performance of the coral-reef food-web model based upon comparisons with empirical
680 data collected from numerous jurisdictions across Micronesia. Predicted algal biomasses (A)
681 were correlated with field-derived counterparts at both the site (a, dashed lines represent islands,
682 solid line represents the regional relationship) and island (b, grey region represents 95%
683 confidence band of the relationship) level. Field data also concurred with two additional model
684 predictions, whereby predators would (c) enhance the standing stocks of large herbivores relative
685 to small herbivores (H1/H2 ratio), and (d) increase herbivore diversity indices if herbivores were
686 targeted by artisanal fisheries. Only islands that had 6 or more samples were considered in the

687 island-level plots, (b) and (d), and grey areas represent 95% confidence intervals of the

688 relationships.

689

690 **Figure 3.** Coral-reef food-web stability, reactivity, trophic pyramids, and catch biomass along a

691 sequential fishing gradient for predators, large-herbivores, and small-herbivores, following each

692 to extinction. Net stability and reactivity within entire food webs were described by the solid

693 and dashed lines, respectively, for systems with and without predators (a, vertical dashed lines

694 representing changes in system state). In contrast to net stability and reactivity, fluctuations

695 within individual populations were also quantified in a system with light (b) and moderate (c)

696 fishing for predators. Trophic pyramids highlighted the biomass retained within each guild prior

697 to any fishing pressure (d), with windows following the same changes in system state defined in

698 (a). Solid, unidirectional arrows indicate where fishing pressure was applied, and dashed arrows

699 represent the scaled response of each guild. Fisheries yields were also depicted along the same

700 gradient of fishing within each system state (e).

701

702 **Figure 4.** Biomass retained within fish guilds (a, left y-axis), the algal resource pool (a, right y-

703 axis), and fish landings (b) along a gradient of fishing pressure (lower x-axis). The x-axis

704 denotes F-fishing pressure for each guild defined by the proportional harvest rate, a term nested

705 within the population models. In this scenario, fishing pressure was applied simultaneously

706 across the guilds so that maximum yields for large herbivores and predators peaked

707 simultaneously (b, MSY_P and MSY_{H2}, respectively). A window of potential ranges for

708 maximum ecological yield (MEY) was considered between 55 to 88% of total unfished biomass

709 (0.5 to $0.88 B_0$, Results). In all instances, A-algal resource pool, H1 and H2-fast and slow energy

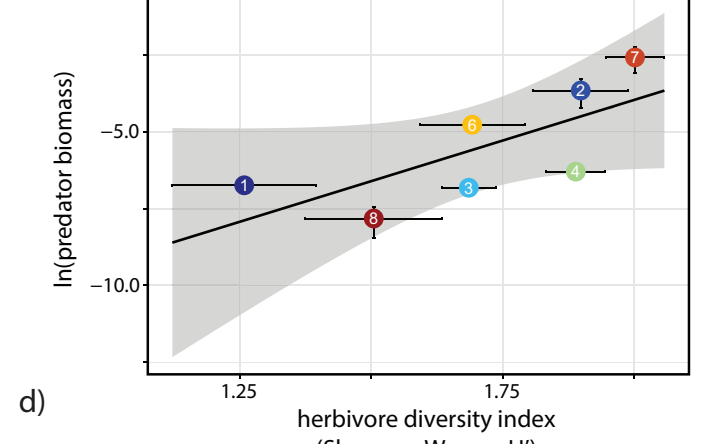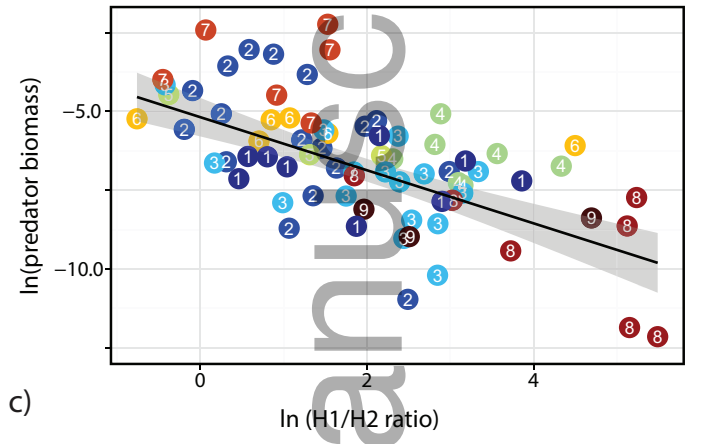710 channel herbivores, and P-predators.

a)

b)

fishing and natural mortality
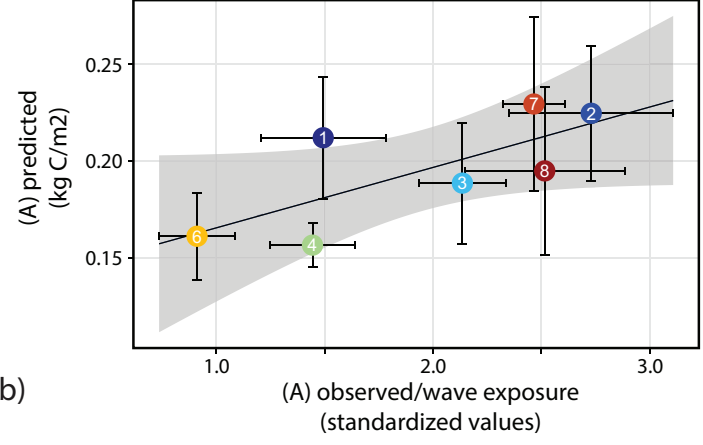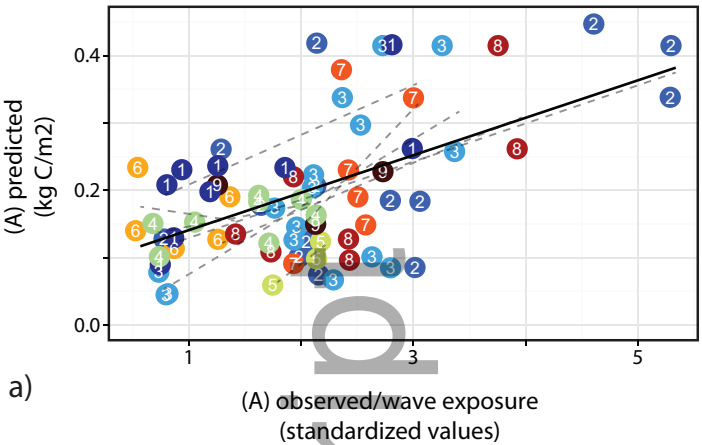
fishing and density dependence

fishing and density dependence

external input

export

recycling

ecm_1278_f1.eps

a)

b)

c)

d)

Legend:
1 Yap
2 Chuuk
3 Pohnpei
4 Kosrae
5 Majuro
6 Namdrik
7 Rongelap
8 Saipan
9 Rota

ecm_1278_f2.eps

b) Low, asynchronous modulations following perturbation (F)

c) Higher, more synchronous modulations with increase in F

A
H1
H2
P

reactive system collapse

Predators and herbivores

Small and large herbivores

Small herbivores

increased reactivity

increased stability

functional extinction

functional extinction

a)

F (predator)

F (large herbivore)

F (small herbivore)

d)

F (predator)

F (large herbivore)

F (small herbivore)

a)

Ecosystem inflection point
at MSY for P and H2

Exponential increase
to oscillations

b)

MEY
(range)

Simultaneous fishing pressure (proportional harvest rate)

FP = 0 to 0.1
FH2 = 0 to 5
FH1 = 0 to 2

A
H1
H2
P

ecm_1278_f4.eps