Title
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Journal
Ambio, 49(1)

ISSN
0044-7447

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Publication Date
2020

DOI
10.1007/s13280-019-01154-5

Peer reviewed

Ambio 2020, 49:130–143
https://doi.org/10.1007/s13280-019-01154-5

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RESEARCH ARTICLE

Perceptions and responses of Pacific Island fishers to changing coral reefs

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Received: 1 August 2018 / Revised: 25 November 2018 / Accepted: 21 January 2019 / Published online: 7 March 2019

Abstract The transformation of coral reefs has profound implications for millions of people. However, the interactive effects of changing reefs and fishing remain poorly resolved. We combine underwater surveys (271 000 fishes), catch data (18 000 fishes), and household surveys (351 households) to evaluate how reef fishes and fishers in Moorea, French Polynesia responded to a landscape-scale loss of coral caused by sequential disturbances (a crown-of-thorns sea star outbreak followed by a category 4 cyclone). Although local communities were aware of the disturbances, less than 20% of households reported altering what fishes they caught or ate. This contrasts with substantial changes in the taxonomic composition in the catch data that mirrored changes in fish communities observed on the reef. Our findings highlight that resource users and scientists may have very different interpretations of what constitutes 'change' in these highly dynamic social–ecological systems, with broad implications for successful co-management of coral reef fisheries.

Keywords Coral reef resilience · Disturbance · Fisheries · Local knowledge · Selectivity · Social–ecological feedbacks

INTRODUCTION

Coral reef ecosystems are under significant anthropogenic pressures from overfishing, pollution, sedimentation, ocean acidification, and rising seawater temperatures (Bellwood et al. 2004; Hughes et al. 2018), resulting in unprecedented levels of coral mortality (Hughes et al. 2017) and shifts from coral-dominated to macroalgae-dominated community states (Rogers and Miller 2006). Beyond biodiversity loss, degraded reefs present challenges for millions of coastal dwellers who rely on healthy reef ecosystems for food, income, and their personal and cultural identities. This has prompted research examining how local communities and resource users perceive, adapt to, and manage coral reefs in the Anthropocene (McClanahan and Cinner 2012; McMillen et al. 2014), including a focus on adaptive co-management, whereby management is implemented and adapted based on knowledge about feedbacks between resource users and shifting local ecosystems (Hughes et al. 2005).

The Pacific Islands region represents an ideal context to investigate how local communities and changing coral reefs interact. Island peoples have shown the capacity to adapt, cope, and innovate in the face of social–ecological change, with positive and negative outcomes for coral reef health (Johannes 2002). In some Pacific Islands, such as Fiji, Vanuatu, and the Solomon Islands, marine resources have been effectively managed over long periods through periodic fishing ground closures, gear restrictions, and other socially enforced constraints on harvesting (Cinner et al. 2006). Elsewhere, local responses to changing conditions have had negative ecological outcomes, as with poison and dynamite fishing (McManus et al. 1997). The effectiveness of adaptive responses is shaped by local cultural values and power relations that inform decision-making and the range of possibilities available (Cinner et al. 2018).

Effective adaptive management requires that resource users detect or anticipate shifts in the local environment and alter their activities accordingly. Some empirical studies have demonstrated that Pacific islanders can detect

Electronic supplementary material The online version of this article (doi:https://doi.org/10.1007/s13280-019-01154-5) contains supplementary material, which is available to authorized users.

rapid shifts in benthic communities disrupted by tsunamis (Lauer and Matera 2016), in addition to more gradual changes such as expanding seagrass beds (Lauer and Aswani 2010). Numerous questions remain, however, about the sensitivity of local resource users to change, and in particular whether ecosystem disturbances identified by ecologists are similarly perceived by Pacific islanders.

We addressed these issues for a small-scale reef fishery on the island of Moorea, French Polynesia. Social and ecological surveys explored how communities perceived and responded to changes in fishery resources associated with a crown-of-thorns sea star (COTS) outbreak followed by a destructive cyclone. In 2004, coral cover around Moorea was near the highest levels observed in the past half century (Trapon et al. 2011; Lamy et al. 2016), but an outbreak of corallivorous COTS that peaked in 2009, followed by Cyclone Oli in early 2010, reduced live coral cover by $> 95\%$ (Adam et al. 2011; Trapon et al. 2011; Adam et al. 2014; Lamy et al. 2015). Dead coral skeletons and cleared reef substrates provided substantial free space for growth of macroalgae, raising the possibility that a macroalgal phase shift could occur. However, benthic community changes were rapidly followed by changes in the fish assemblage, with roving herbivorous fishes such as parrotfishes doubling in density and tripling in total biomass (Han et al. 2016), thus preventing macroalgae from establishing. Moreover, in the years since the disturbances, coral cover has increased and even exceeds predisturbance levels in some areas (Holbrook et al. 2018). Despite intensive ecological study, it is not known if these changes in the fish assemblages have altered fishable resources, the activities of reef fishers, or how local people perceived the changes. Because spearfishing—a highly selective method—is common in Moorea, a shift in the abundances of fishable resources provides an opportunity to assess whether fishers alter what they catch as their resource environment changes.

This study addressed four questions: (1) How did residents of Moorea perceive the shifts documented in ecological studies? (2) Do they report changing their fishing behavior or seafood consumption in response to the shift? (3) How did the changes in the fish assemblage affect the availability and taxonomic composition of fishable biomass? and (4) Is there evidence for changes in fishing behavior (such as taxonomic selectivity) over time?

To answer these questions, we conducted 351 household surveys documenting fishers' perceptions of the changes and their potential responses via alteration in fishing practices or fish consumption. We analyzed a time series of catch data ($\sim$ 18 000 identified and measured fishes) collected before and after the disturbances, spanning a 9-year time period, to determine changes in targeted fish species and sizes, including key groups of herbivores crucial to recovery and resilience of the coral state. Finally, we compared the catch data with extensive surveys that estimated abundances and biomass of fishes on the reef throughout the same time frame.

MATERIALS AND METHODS

Ecological and social contexts

Moorea (17°32′S, 149°50′W) is a volcanic 'high' island 60 km in perimeter with an offshore barrier reef that encloses a shallow lagoon (Fig. 1a). The island has three types of reef habitats: within the lagoon, there are fringing reefs and back reefs, while outside the barrier reef crest, there is a steeply sloping fore reef. Moorea has over 17 000 inhabitants (Institut de la statistique de la Polynésie française 2012) residing in five *communes associées*: Afareaitu, Ha'apiti, Paopao, Papetoai, and Teavaro. It has undergone substantial economic development over the last half-century, including becoming a major international tourist destination. Communal land has been supplanted by private land ownership, and the state declared that all lagoon and marine areas are public property, meaning that customary sea tenure is nonexistent.

Reefs in Moorea continue to be the focus of widespread fishing activity, although major economic and social changes have shifted household livelihoods away from direct dependence on marine resources for food or income toward wage-earning employment. Over half of households fish, with free-dive spearfishing as the preferred method (Leenhardt et al. 2016). Most people fish so they can eat and share fresh reef fishes, a fundamental marker of Polynesian life. Reef fishes constitute the bulk of the catch and are prized as symbols of Polynesian identity and cultural pride. It is notable that Moorea's households are less dependent on marine resources for food security or income than is common in other regions in the Pacific. As citizens of France, they have access to state-subsidized healthcare, education, and social services, so poverty levels are lower than in most of Oceania. Although most households contain fishers, only a small number of fishers fish full-time solely for income.

Household surveys and key informant interviews

In 2014–2015, we interviewed 351 (approximately 20%) households in the communes of Afareaitu, Papetoai, and Haapiti. On each day of sampling within a commune, the researcher chose two starting locations within the village boundaries based on a stratified approach, so that starting locations were distributed roughly evenly within the village. Starting from one location in the morning, and the

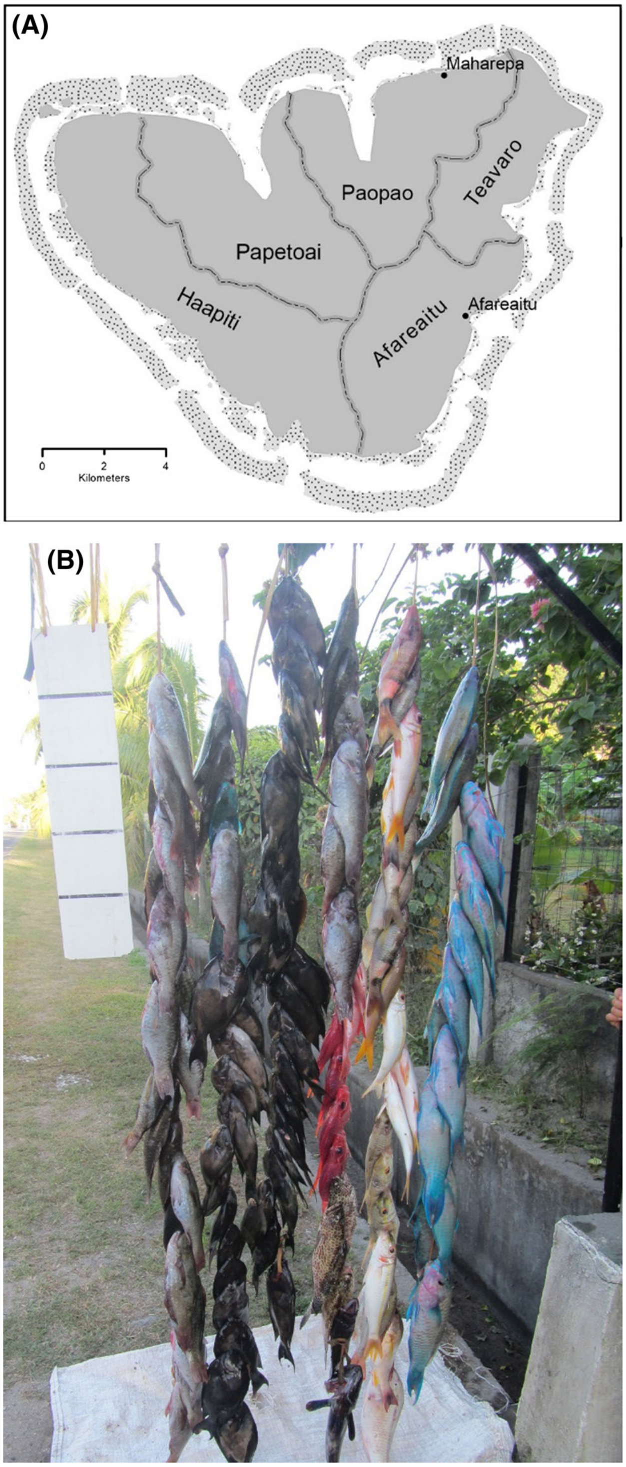

Fig. 1 **a** Map of the island with the focal regions of Afareaitu, PaoPao, and Teavaro marked. **b** Photo of fish being sold by the roadside (note the 0.5 m sizing bar)

second in the afternoon, the researcher systematically approached nearby houses and conducted an interview in each household in which an adult was willing to be interviewed. The result was a sampling design that was spatially unbiased, although necessarily biased toward those willing to be interviewed. The 60–80-min survey interviews were conducted in French or Tahitian, with local Tahitians assisting in the surveys and translating for household heads more comfortable speaking in Tahitian. Interview topics included basic demographic information, fishing effort, livelihoods, catch preferences, consumption patterns, and perceptions of resource conditions. Standardized questions allowed for later comparison, but more open-ended questions were used to discuss important issues and perceptions. Sample size for the standardized questions varied, since not every question was relevant for all respondents. We also conducted 15 semistructured interviews with fishers from around the island, who were considered highly knowledgeable local experts. In 2018, follow-up interviews were carried out with nine key informants to whom results from this paper were presented. Questions explored respondents' perceptions of postdisturbance changes in the fish assemblages.

Fish-seller surveys

The sale of most reef fishes takes place from small roadside stands along the perimeter road of the island (which has no fish markets). Fresh reef fishes are strung through the gills and hung from racks (Fig. 1b, Table S1). Each string of fish is sold as a unit, known in Tahitian as a *tui*. A seller, often the fisher, assembles each *tui* and 10 or more may be hung for sale. Any single *tui* may contain a few larger fishes or many small ones of different species. Most fish stands are active early in the morning, and by mid-morning most have sold their catch.

To sample the fishes being sold at these roadside stands, a researcher drove Moorea's ring road early in the morning on weekends, typically the busiest times for fish sales. At each stand, the rack of *tui* was photographed with a scale bar of known size (0.5 m), and the seller was briefly interviewed. Photographed fishes were later identified to the lowest taxonomic level possible, and the length of each was estimated by comparison with the scale bar (Schneider et al. 2012).

Catch surveys were conducted in five different years during 2007–2015 (2007, 2008, 2012, 2014, 2015; Table 1). Three of the five *communes associées* were sampled in all 5 years (Afareaitu, Paopao, and Teavaro), and so only data from these regions were analyzed to maintain consistent geographical coverage through time, with data pooled across regions in all analyses.

Reef surveys

We assessed reef fish populations using data from the NSF-funded Moorea Coral Reef Long Term Ecological

Table 1 Number of fish observed in the reef surveys and in the catch, by year

Year	Fish counted on reef	Fish sampled in catch
2007	32 131	1878
2008	34 255	4309
2009	41 538	–
2010	30 013	–
2011	24 231	–
2012	25 963	2435
2013	29 330	–
2014	30 430	4319
2015	23 995	4836

Research (MCR LTER) project that collects time series data at 18 locations around Moorea (Brooks 2017), and the SO CORAIL-PGEM monitoring program that collects data from 13 locations around the island (Lamy et al. 2015). Here we used data collected annually from 2007 to 2015 (Table 1), and included data only from transects located on reefs offshore of the three focal *communes* (Afareaitu, Paopao, Teavaro), as most targeted fishes are territorial, and most fishers fish near where they live.

The MCR LTER surveys are conducted by SCUBA divers between 0900 and 1600 h during late July or early August. Abundances of all mobile taxa of fishes observed are recorded on fixed 5 m × 50 m transects that extend from the surface of the reef through the water column. The abundances of all nonmobile or semicryptic taxa of fishes are also counted along the same transect lines in a 1 m wide transect. The total length of each fish observed is estimated to the nearest 0.5 cm. The SO CORAIL-PGEM monitoring program has sampled similar habitats in each of these years, counting and estimating sizes of all fishes within 5 m × 25 m transects. Fish biomass (kg) is calculated based on species-specific scaling parameters (Brooks 2011).

Fishing selectivity and fishable biomass

Spearfishing is a highly selective fishing method in which the size and species of targets can be observed before they are harvested. We tested for selectivity in size by comparing the fishes being sold by the roadside to the sizes of fishes observed during reef surveys (pooling data across the 5 years for which we have catch data). We defined a minimum fishable size (15 cm) across all species based on sizes observed in the catch (< 2% of fishes were below this size).

We determined which taxa were targeted based on the relative abundances of each genus observed in the catch and on the reef. We defined fished taxa as genera making up more than 0.1% of the total catch, which included 23 genera, constituting 99% of all fishes and 95% of all biomass being sold. Parrotfishes from the genera *Scarus* and *Chlorurus* were combined in all analyses because species from these genera often could not be reliably distinguished in our photographs of *tuis*. We note that some excluded species may be highly prized but rare in the catch because they are rare on the reef. Subsetting the ecological survey data based on our list of 23 targeted genera and the minimum fishable size, we calculated how the total fishable biomass and the fishable biomass of different targeted groups changed from 2007 to 2015.

Taxonomic composition of the catch

We evaluated the degree to which variation in the biomass of each taxon on the reef predicts variation in the taxonomic composition of the catch by comparing the relative biomass of the seven most common taxa in the catch with their relative biomass on the reef. We excluded soldierfishes (*Myripristis* spp.) from this analysis because they are nocturnal and were poorly sampled in our (diurnal) reef surveys, when they shelter within reef structures. Other species may shift habitats on a daily cycle, but any such movements are well within the spatial scale of our sampling. Because sampling effort of the catch (during roadside surveys) was not consistent over time, we cannot determine how total catch changed.

RESULTS

Household surveys and interviews

The household surveys revealed that a substantial majority of households reported regular consumption of fish, with 67% reporting that they eat fish at least three times per week, and more than half of those eating fish six to seven times per week. Most households (76%) reported at least one member who actively participated in the local reef fishery. There was great consistency in the species that households preferred to eat and preferred to catch (Table 2). All of these species are commonly caught and highly prized for the taste and texture of their meat. An exception to the focus on reef fishes is tuna (*thon* in French), which has become an increasingly important component of diets in Moorea but which is caught by a small number of pelagic fishers operating with specialized boats offshore.

There was considerably more variability in how households reported any changes in their behavior in response to the outbreak of COTS (*taramea* in Tahitian) and the

Table 2 Fish most frequently reported eaten or caught in household surveys (N = 326 surveys)

Tahitian name	Scientific name	Reported commonly eaten (%)	Reported commonly caught (%)
Thon (French)	*Thunnus* spp.	17	4
Pa'ati[a]	*Scarus/Chlorurus* spp.	15	12
Pahoro	*Scarus/Chlorurus* spp.	11	6
I'ihi	*Myripristis* spp.	8	13
Tarao	*Epinephelus* spp.	8	8
Pa'aihere	*Caranx* spp.	6	9
Ume	*Naso* spp.	6	6
Maito	*Acanthurus/Ctenochaetus* spp.	4	3
Ature	*Selar crumenophtalmus*	3	4
Roi	*Cephalopholis* spp.	2	4
To'au	*Lutjanus fulvus*	2	4

[a] This term denotes terminal phase fish

Table 3 Percentage of households who responded affirmatively to the questions related to the COTS outbreak and Cyclone Oli

	Answered 'yes' (%)
Do you remember any taramea (COTS) outbreaks? (N = 348)	40
Did taramea outbreaks change how, what, or where you fished? (N = 339)	13
Did it change what fish you ate or bought to eat? (N = 194)	1.5
Do you remember Cyclone Oli? (N = 348)	100
Did Cyclone Oli change how, what, or where you fished? (N = 310)	19
Did Cyclone Oli change what fish you ate or bought to eat? (N = 350)	10

cyclone (Table 3). Although 40% remembered the COTS outbreak and 100% remembered Cyclone Oli, few reported modifying the kinds of fishes they ate or bought (1.5% and 10%, respectively). Of those that reported responding to the COTS outbreak, responses included removing COTS from the reefs (30%), avoiding fishing in COTS-dominated areas (18%), or changing their fishing areas (6%). Of those that reported responding to Cyclone Oli, responses included waiting until the lagoon was clean from runoff before resuming fishing (30%), fishing in different locations because the fishes moved to different areas of the lagoon (16%), fishing less in the lagoon than prior to the cyclone (13%), or fishing less overall after the cyclone (10%).

In-depth interviews with expert fishers revealed that they are aware of COTS outbreaks and they recognize that COTS kill coral. Two expert fishers described how in the past, parts of the sea stars' bodies were applied as garden pesticide. Other expert fishers mentioned that the Papetoai school and local fisher organizations (in Haapiti and Afareaitu) organized outings where local people removed COTS from the reefs. One fisher noted that this practice was "a new thing" and that "the oldtimers never mentioned this kind of practice happening in the past." Most fishers acknowledged a relationship between live coral cover and reef fish abundance. However, few indicated that the dramatic loss of live coral cover caused by the COTS outbreak or Cyclone Oli had an impact on the composition of fish assemblages or the relative abundances of the main targeted taxonomic groups.

Fishing selectivity

Roadside fish sellers mostly caught fishes on the reef (77%), largely from the lagoon (69%), and the most common gear used was the spear gun (83%), followed by fishing with nets (11%) and hook and line (5%). Fishes sold in the morning were mostly caught at night (90% between 1800 and 0600 h), so our surveys of fishes sold by the roadside (hereafter, "the catch") may not be representative of fishing activities undertaken at other times.

Fishes in the catch represent a nonrandom distribution of sizes relative to those observed on the reef (Fig. 2). Harvested fishes were significantly larger on average than fishes on the reef (23 vs. 8 cm; $P < 0.0001$, Wilcoxon rank-sum test). More than 98% of fishes in the catch were at least 15 cm in length, suggesting this is a minimum bound on the size of fishes that are targeted. The relative abundance of taxa observed in the catch also diverged substantially from the community found on the reef, even when only individuals of fishable size were considered. More than 99% of the fishes in the catch were from 23 genera (Table 4) with almost 60% of the catch made up of unicornfishes (*Naso* spp.), parrotfishes (*Scarus* and *Chlorurus* spp.), soldierfishes (*Myripristis* spp.), and rabbitfishes (*Siganus* spp.). The composition of the catch

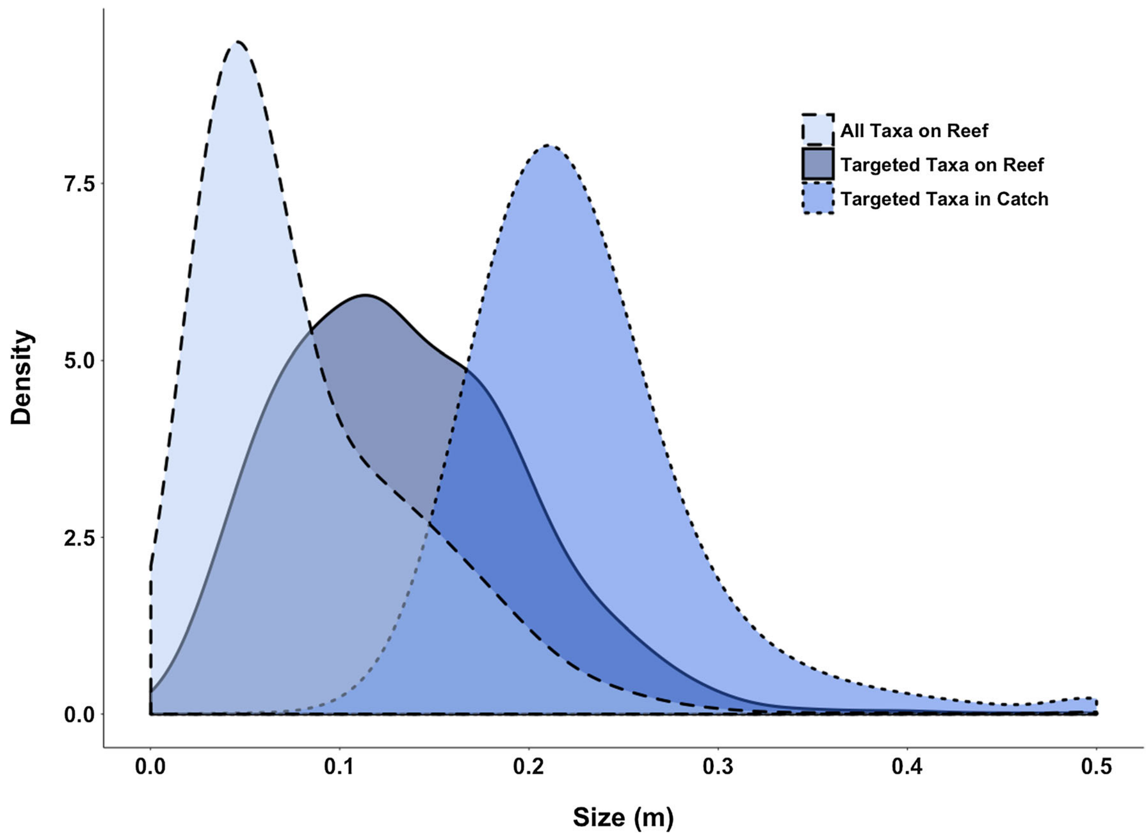

Fig. 2 Size distributions of all fish taxa observed on the reef, the subset of targeted taxa on the reef, and the taxa found in the catch. Curves are kernel density estimations (bandwidth smoothing parameter = 0.02)

contrasted with the most abundant taxa on the reef (based on fishable sized individuals; Table 4, Table S1). In particular, while *Scarids* and *Naso* were both abundant on the reef, *Myripristis* and *Siganus* were rarely observed in the reef surveys (the 38th and 29th most abundant taxa, respectively; Table S1). Furthermore, several of the most abundant taxa on the reef were completely absent from the catch, most notably surgeonfishes from the genus *Ctenochaetus* (25% of fishes on the reef).

Fishable biomass

The amount of fishable biomass (fishes $>$ 15 cm in length from 23 targeted genera) on the reef was relatively stable from 2007–2015. Although there was some variation from year to year (Fig. 3), including a spike in 2010, there was no sustained shift in fishable biomass coinciding with the disturbances that occurred in 2009–2010. By contrast, there was substantial change in the abundances of some taxonomic groups on the reef over the time period. Most dramatically, *Naso* biomass fell from 21 to $\sim$ 4 kg ha^{-1}. This decline was offset to some degree by an increase in the biomass of parrotfishes of the genus *Scarus*. While the biomass of other taxa varied substantially from year to year, there was no apparent secular trend in their abundances.

Taxonomic composition of the catch

The changes in the taxonomic composition on the reef were roughly mirrored by trends in the catch (Fig. 4). For example, *Naso* comprised more than a third of the catch prior to the disturbances, and less than 10% after. By contrast, the proportion of the catch composed of parrotfishes from the genera *Chlorurus* and *Scarus* increased over time from 56 to 66%. *Naso, Chlorurus* and *Scarus* collectively composed the bulk of the fishable biomass on the reef (48–66%) and a roughly similar total proportion of the catch (43–65%).

For the taxa that were well sampled in our reef surveys, there was a surprisingly high correlation between the biomass of each taxon on the reef and its annual contribution to the catch, with high correlations observed for the most common taxa (Fig. 5). Indeed, the correlation for unicornfishes is above 0.99, which suggests both that our reef surveys captured variation in their abundances over time and that the variation in the abundance within the ecological community may explain the observed pattern of variation in catch.

Table 4 Relative abundance of taxa observed in the catch and their corresponding % contribution to abundance on the reef (considering only fish of targetable size, > 0.15 m). The top 23 genera observed in the catch are listed, representing more than 99% of the catch. The genera *Chlorurus* and *Scarus* have been combined because they can be difficult to distinguish in the photos of the catch. Stars (*) indicate taxa reported commonly eaten in more than 5% of household surveys

Genus	% abundance in catch	% biomass in catch	% fishable size abundance on reef	% fishable size biomass on reef
*Chlorurus-Scarus**	26.5	35	20.9	22.8
*Naso**	18.5	16.1	5.5	4.2
*Myripristis**	15.5	10	0.2	0.1
Siganus	8.9	4.5	0.4	0.2
Mulloidichthys	6.4	5.1	3.4	2.1
Parupeneus	5.4	5.4	1.5	0.9
*Epinephelus**	3.2	3.1	0.4	0.3
Selar	2.9	1.2	0	0
Cypselurus	2.2	0.9	0	0
Acanthurus	1.8	1.6	10.1	8.5
Cephalopholis	1.4	1.8	3.8	3.3
Cheilopogon	1.4	0.5	0	0
Sargocentron	1.1	0.9	0.6	0.3
Lutjanus	0.8	0.9	0.3	0.2
Monotaxis	0.7	1.4	0.4	0.5
*Caranx**	0.5	3.1	0.2	1.1
Lethrinus	0.4	1.3	0.1	1
Calotomus	0.3	0.5	0	0
Heteropriacanthus	0.3	0.2	0	0
Cheilinus	0.2	0.4	0.5	0.8
Gnathodentex	0.2	0.1	2.5	1.5
Kyphosus	0.2	0.4	0	0

DISCUSSION

In this study, we coupled data from intensive sampling of both the ecological community and human resource users to provide new insights into how fishes and Pacific Island fishing communities interact during periods of substantial ecological change, and how the fishing communities perceive the changes. Each method provided a different view of these feedbacks. Household surveys confirmed that residents of Moorea were aware of the major disturbances that occurred on the reef, but revealed that little explicit change occurred in fishing behavior or perceptions of resources harvested. This contrasts with the marked shifts in the taxonomic composition of the catch that we observed, particularly the significant decrease of *Naso* spp., one of the most highly prized fishes due to its palatability. Those taxonomic shifts mirrored changes we observed in fish communities on the reef, implying that the composition of the catch is highly dependent on reef state despite the high selectivity of the fishery and local perceptions that fishing and fished resources had not changed.

Fishing selectivity

Our results revealed high selectivity in the Moorea reef fishery, both in terms of body size and taxonomy, consistent with observations of other spearfishing-focused fisheries in the Pacific (Dalzell et al. 1996). Fishers showed a preference for fishes that are larger on average than those encountered on the reef. Even when size selectivity was accounted for, we found strong taxonomic selectivity for a handful of taxa, with some being disproportionately abundant in the catch relative to their abundances on the reef (e.g., *Naso* spp. and *Myripristis* spp.) while others were greatly under-represented in the catch (e.g., *Ctenochaetus* spp.). This high degree of size and taxonomic selectivity is not surprising given the prevalence of spearfishing on the island. Spearfishers visually identify and evaluate each fish before it is harvested (Frisch et al. 2008). The resultant selectivity affords them greater latitude for adapting to ecological shifts than other capture techniques, such as hook and line or gill netting, in which the fishes are invisible to the fisher before capture.

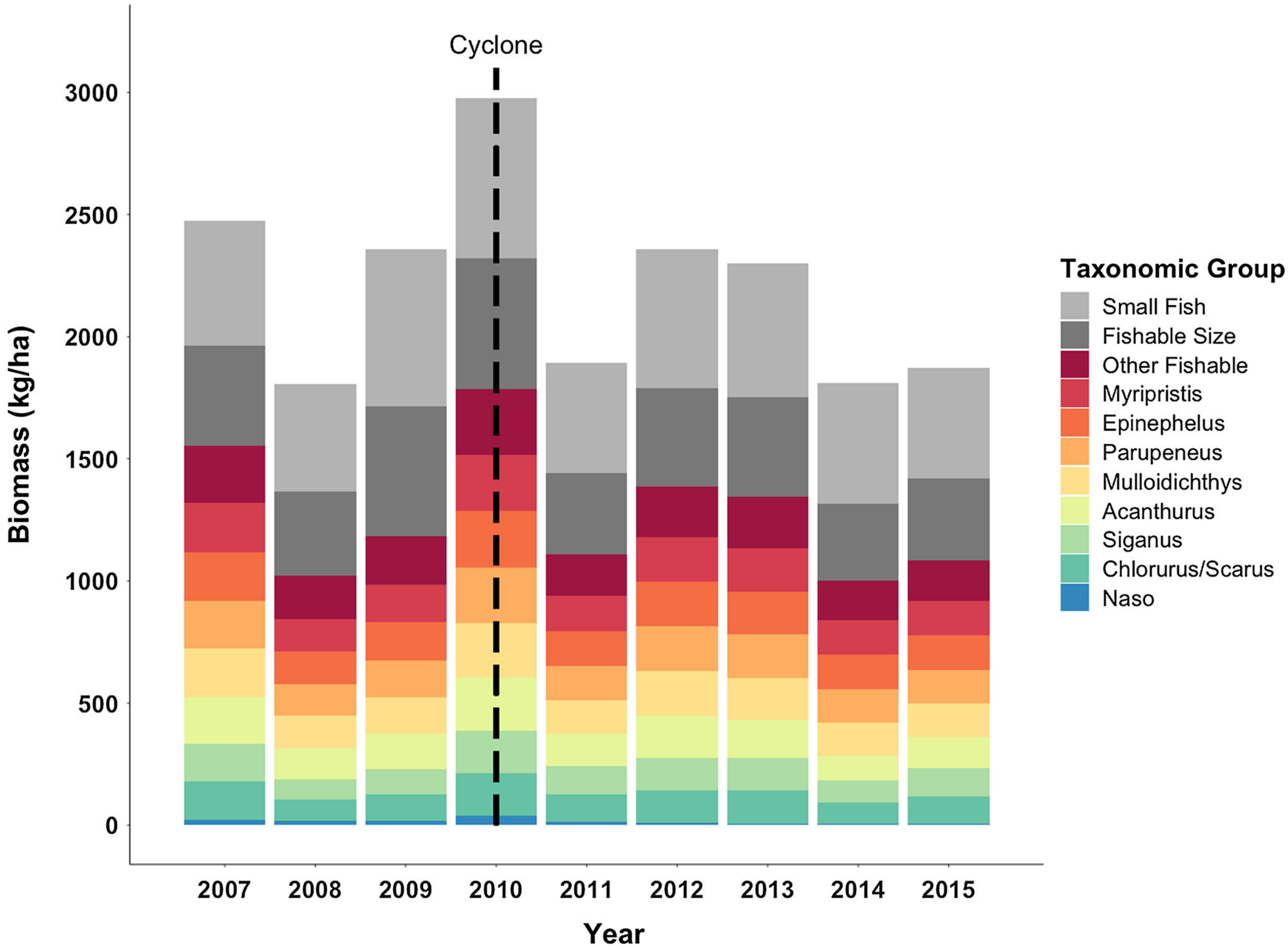

Fig. 3 Fish biomass on the reef through the time period spanning the 2009–2010 disturbances. "Small Fish" indicates biomass of fish smaller than 0.15 m, while "Fishable Size" represents larger (> 0.15 m) fish from nontargeted taxa. The remaining areas represent biomass of fish > 0.15 m which are commonly found in the catch (Table 4), with 8 taxa broken out, and the remainder combined into "Other Fishable." The timing of the peak disturbance is indicated with a dashed line

The suite of preferred species on Moorea is not limited to larger-bodied species. Soldierfishes (*Myripristis*), for example, are relatively small-bodied but represent the third most fished genus (in terms of numbers and biomass in the catch), as they are prized for the taste and the texture of their meat rather than their large filets. In commercially oriented fisheries, size selectivity can be linked to higher market demand or value for fishes of particular sizes, e.g., large enough to filet or sized to fit on a dinner plate (Reddy et al. 2013). In Moorea, spearfishers commonly describe their fishing decisions through idioms of cooking and eating, and will seek out certain species based on how they want to cook their meal that day, underscoring the noneconomic nature of the fishery.

Elsewhere, Pacific Islanders commonly target piscivores, such as emperors and groupers, but in fisheries where spearfishing is the primary mode of capture, herbivorous fishes such as unicornfishes and parrotfishes often dominate the catch (Jennings and Polunin 1995; Gillett and Moy 2006). Contemporary reef fish preferences in Moorea may be the result of the gear type used or an outcome of overfishing and fishing down the food web (Pauly et al. 1998) from piscivores to herbivores. More historical work could shed light on this possibility by detailing the trajectory of taxonomic selectivity over the last several centuries. We also note that Moorea fishers show a strong selectivity against harvesting *Ctenochaetus* and *Acanthurus* (*maito* in Tahitian) even though they are some of the most abundant species on the reef. These fish are known to be ciguatoxic, and the sale of *Ctenochaetus* was banned by the territorial government in the 1960s (Walter 1968).

Taxonomic composition on the reef and in the catch over time

Our roadside surveys indicate that the taxonomic composition of the catch shifted substantially after the disturbance (Fig. 4). Changes in the catch largely correlated with shifts

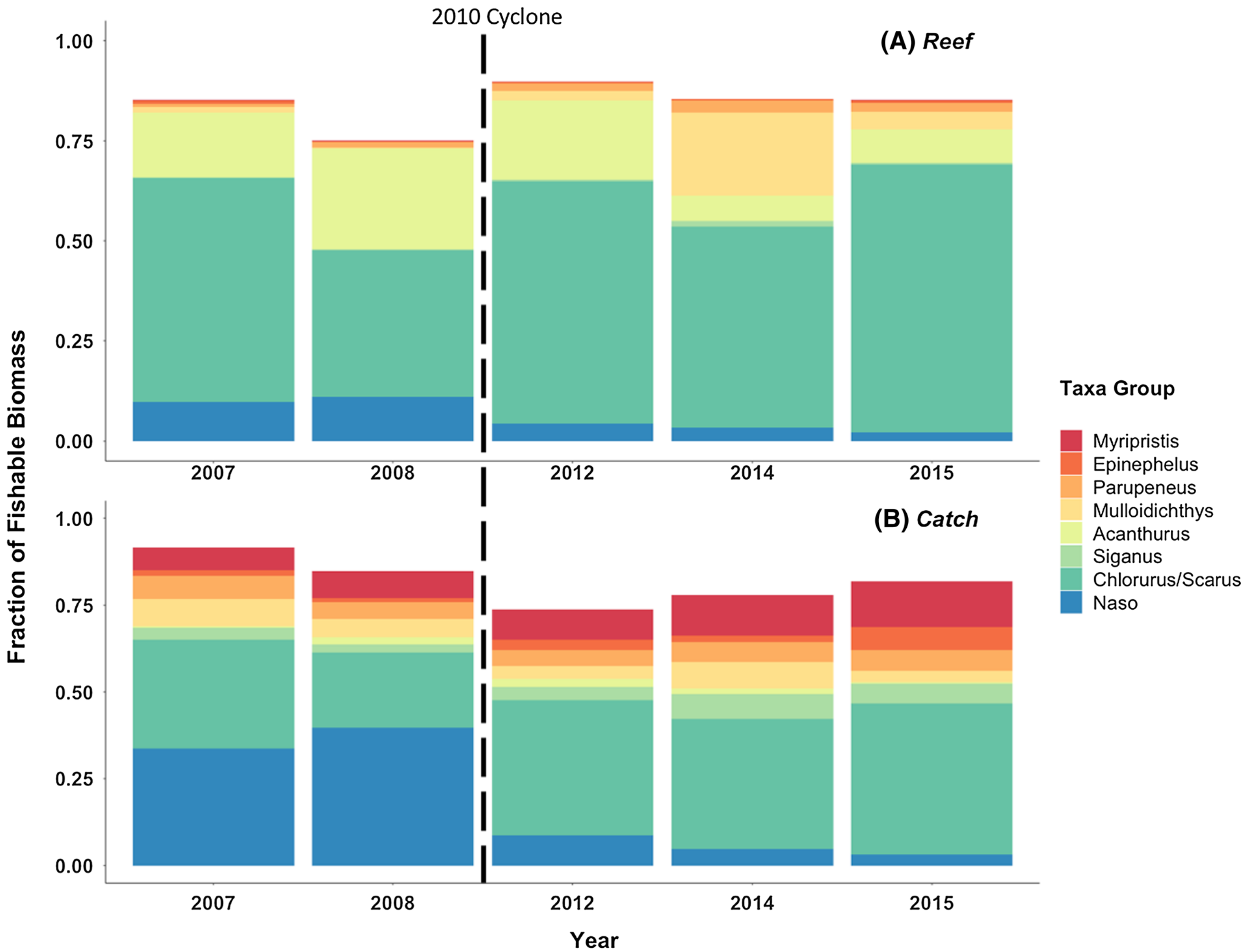

Fig. 4 The relative biomass of fishable taxa (including only individuals > 15 cm) on the reef (**a**) and in the catch (**b**). The timing of the peak disturbance is indicated with a dashed line

in the taxonomic composition of the reef community, particularly for species that made up a substantial proportion of the catch (Fig. 5). However, there is wide variation in the strength of this relationship. The unexplained variation may stem from analyzing catch at the genus level, likely combining species of different desirability within the same category. For example, dynamics on the reef and in the catch were poorly correlated for *Acanthurus*. There are five species commonly observed in the catch within this genus; if some of these are targeted and some are not (possibly based on ciguatera risk), then trends in the biomass of the genus on the reef may not represent trends in the preferred species within that genus, obscuring a tighter relationship at the species level. By contrast, one species (*Naso lituratus*) makes up more than 90% of the fishable-size individuals of that genus on the reef, so variation in the abundance of that species translates more directly to our genus-level analyses.

The composition of the catch is a joint product of the availability of resources and the demand for each from the fishing communities. If the catch primarily reflects demand for different species, we might expect to see little change in the composition of the catch as the ecosystem changes, particularly in such a highly selective fishery. Instead, the high correlations between biomass on the reef and in the catch for unicornfishes (*Naso* spp.) and parrotfishes (*Scarus* spp./*Chlorurus* spp.) indicate that shifting relative abundances result in different compositions of the catch, and suggest that there is considerable flexibility in harvest and consumption behaviors.

Perceptions of change

Our household surveys and key informant interviews suggest that Moorea's fishers generally were aware of the COTS outbreak and Cyclone Oli and that they understood

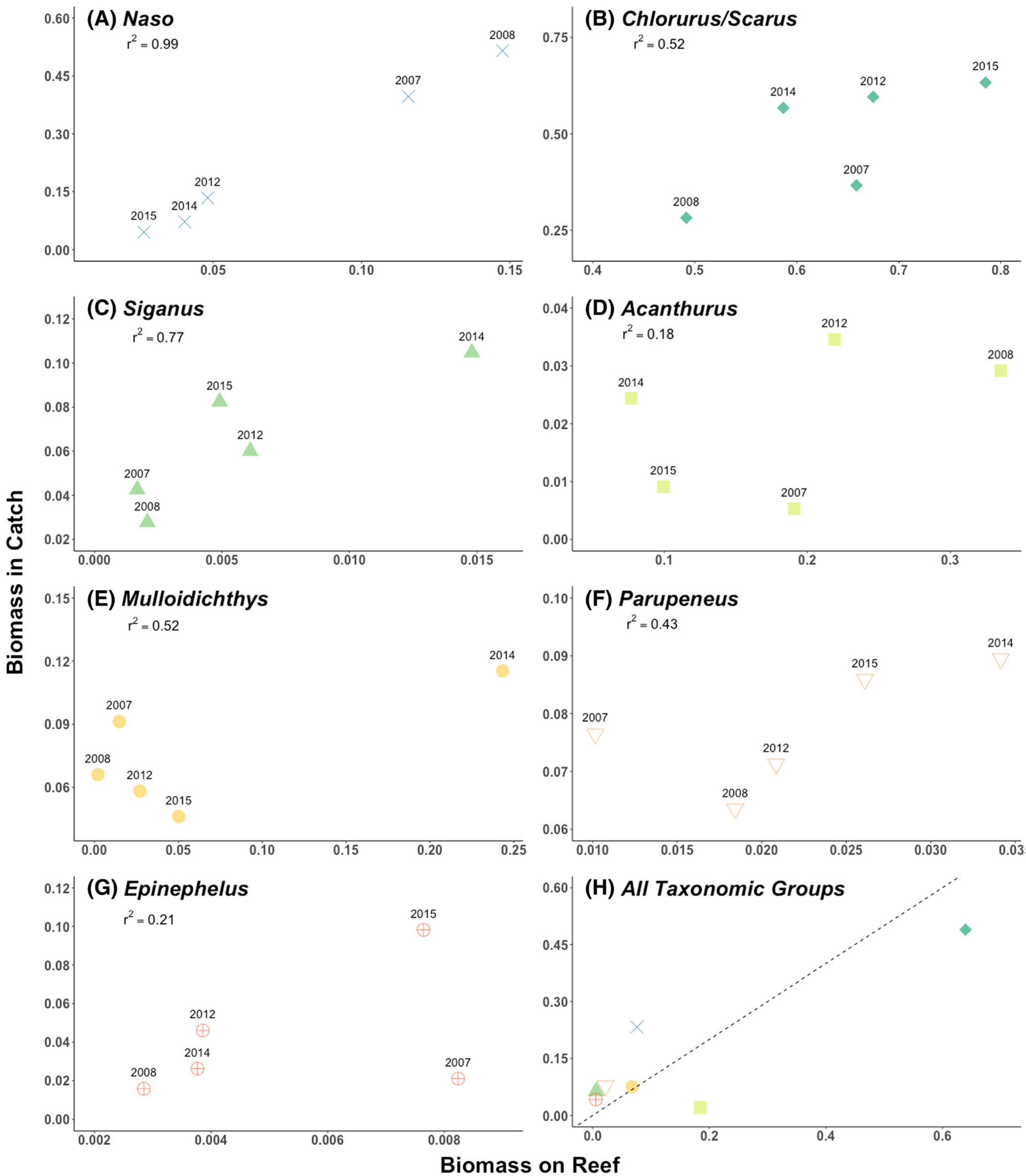

Fig. 5 The relationship between the relative biomass of each taxonomic group on the reef and the relative biomass of that group in the catch plotted by year. The time-averaged biomasses in the catch and on the reef for each taxon are also plotted (**h**). In this latter panel, the symbols for each species match those in **a**–**g** and the 1:1 line is plotted

the ecological impacts of these disturbances. This in-depth understanding is not surprising given most engage in fishing on a regular basis and thus have frequent experiential contact with the marine environment. It is widely acknowledged that in Pacific Island contexts where communities depend on marine resources, islanders maintain rich, site-specific knowledge of the marine environment as well as sophisticated understanding of ecological processes (Johannes 1981; Lauer 2017). Despite their awareness of the disturbances, few households saw these as a change that warranted modification of their fishing strategies, or altering what species of fish they ate. This narrative is in striking contrast to the shifts we documented with our roadside surveys conducted before and after the disturbances. Most surprisingly, the significant decrease of *Naso* spp. in the reef counts, while reflected in the catch, was not expressed in informants' responses. There are several possible explanations for this apparent discrepancy. For one, the relative abundances of species shifted after the disturbances, but the suite of species caught did not, with the same top five species caught before and after the disturbances. It may be that Moorea fishers would only report a more radical shift (e.g., the complete disappearance of a targeted fish) in the taxonomic composition of their diet and catch. Furthermore, fishers speak less of shifts in abundance per se but rather about changes in fishes' behaviors and their habitat choices. When asked about the decline in abundance of *Naso* spp. in the catch surveys, several fishers stated that unicornfishes have learned, as a result of heavy fishing pressure, to swim into deeper waters. Yet these behavioral changes of *Naso* spp. do not necessarily result in fewer fish caught for the best spearfishers. As one fisher stated, "a good spearfisher will find and catch the fish he desires."

The discrepancy between what constitutes noteworthy changes for Moorea's fishers and western scientists could also be related to the different ways each group conceptualizes marine environments (Johannes 1981; Hviding 1996). Ethnographic material indicates that Pacific Islanders cognize marine and terrestrial environments holistically, with more attention focused on the components and interactions of an integrated whole, than on discrete ecological attributes. The most vivid Islander expressions of this ecosystem-like understanding are the wedge-shaped, ridge-to-reef resource management units that have been described across Oceania (Ruddle et al. 1992; Lauer 2016). These land–sea concepts emphasize the intrinsic entangling of physical and biological components with the social and cultural world.

In addition to a holistic worldview of coral reef social–ecological systems, island societies like Moorea also emphasize the unpredictability and unknowability of these systems. In fact, many nonwestern societies, including those in Oceania, grasp the nature of ecosystems in ways similar to nonequilibrium ecosystem science, a framework that emphasizes surprise and nonlinearity, threshold effects, and systems flips instead of predictability, stable states, and homeostasis. The magnitudes of ecological and fishing changes we observed likely fall within the bounds of Pacific Islanders' cultural expectations for normal fluctuations in their diets and catch. In other words, the disturbances deemed dramatic from a Western scientific perspective, and perceived as significant events to fishers, are also inscribed for Pacific Islanders within a 'normal' cyclical pattern of disturbances and recoveries. Indeed, the ecological observations of the COTS outbreak and Cyclone Oli span relatively short timeframes (barely a decade) relative to individuals' own lifespans. In addition, the fore reef of Moorea has proven very resilient to disturbances that reduce coral cover, with several major disturbance events and subsequent recovery of the reef since the 1970s (Adam et al. 2011; Trapon et al. 2011; Holbrook et al. 2018). In the case of the most recent disturbances considered here, many areas of the fore reef regained their pre-disturbance levels of live coral within 5 years (Holbrook et al. 2018). The resilience of the reef ecosystem, when considered at the scale of the individuals' lifespans, may contribute to the perceptions of our informants (whose mean age = 47 years) of the limited impacts the disturbances had on their fishing behavior and dietary choices. Future archeological research, similar to that carried out on Hawaii and Rapa Nui (Kirch and Hunt 1997), exploring the long-term socioecological dynamics on Moorea, could shed light on the scale and intensity of social–ecological changes on Moorea in the context of disturbance frequency.

CONCLUSIONS

Although this study focuses on fisher–fish interactions in Moorea, our results are of general relevance for coral reef ecosystems. Coral reefs globally are experiencing increasing disturbances, in many cases causing major changes in benthic and fish communities (Holbrook et al. 2008). Understanding how fishers conceive and respond to these ecological changes is crucial to predicting how social–ecological feedbacks might enhance or erode ecosystem resilience (Leenhardt et al. 2016, 2017). Such feedbacks are particularly likely in places like Moorea where the most commonly targeted fishes are herbivores, which control macroalgae and confer resilience on the coral-dominated reef state (Mumby et al. 2007; Holbrook et al. 2016). Fishing on such species has often been linked to switches between coral and algal community states (Hughes et al. 2007; Rasher and Hay 2010), and thus the details of fishing behavior may be critical for understanding the resilience of these alterative states.

More broadly, our analysis has implications about researching knowledge production and formulating management initiatives in socioecological systems. The disconnect between Moorea's fishers' reporting of changes, those apparent in the catch data, and the characterizations of reef change offered by ecologists, highlights a critical issue—western scientists and other stakeholders may produce knowledge grounded in different epistemological and ontological assumptions about the world and what constitutes ‘change’ (Barnes et al. 2013). In complex social–ecological systems like the one studied here, we should not expect singular, incontrovertible knowledge about the system, and there will be significant differences between and gaps within both local and ecological knowledge that may only widen with the uncertainty of the Anthropocene era. Thus, it is likely to be increasingly useful to understand how all stakeholders (e.g., scientists, conservation practitioners, fishers, tourist operators, etc.) produce in situ site-specific knowledge and form social–ecological relations. Scientist–resource user collaborations for research and resource monitoring can increase trust between stakeholders, improve adaptive management strategies, and help keep pace with unforeseen social–ecological transformations of the Anthropocene.

Acknowledgements We thank T. Atger, M. Strother, A. Bunnell, C. Hunter, and O. L. Lenihan for leading anthropological field work; K. Seydel, J. Verstaan, A. Dubel, P. Germain, L. Thiault, and R. Terai for technical assistance; the staff of University of California Berkeley Gump Research Station including Ms. Hinano Murphy for logistic support; René Galzin for initiating the roadside surveys; and Dr. Jean-Yves Meyer for assistance with permits. We gratefully acknowledge the support of the National Science Foundation (OCE 1637396, OCE 1325652, BCS 1714704), the Gordon and Betty Moore Foundation, and the Agence Nationale de la Recherche (ANR-14-CE03-0001-01). Permits for field work were issued by the Haut-commissariat de la République en Polynésie Française (DRRT) (Protocole d’Accueil 2005–2006, 2006–2007, 2007–2008, 2008–2009, 2009–2010, 2010–2011, 2011–2012, 2012–2013, 2013–2014, and 2014–2015 to RJS and SJH) for research associated with the US NSF Moorea Coral Reef Long Term Ecological Research project. Service d’Observation CORAIL from CRIOBE kindly provided ecological monitoring data.

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Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

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