



Discriminating Catch Composition and Fishing Modes in an Artisanal Multispecies Fishery

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Many small-scale fisheries are multi-species, and the catch composition can vary according to available habitats, fishing modes, and fisher groups. Here, we applied novel analyses for understanding the factors affecting differences in catch composition among fishers, which should be useful for planning regulatory measures and fishery development initiatives. Interviews with 235 artisanal fishers in Fiji were used to analyse how fishers' catch composition of 22 species of sea cucumbers varied across geographic scales (locations and villages within locations), genders, and fishing modes. Venn diagrams illustrated that gleaning and SCUBA diving were practiced to varying extents among locations and genders, whereas fishers used breath-hold diving more uniformly across the fishery. Segmented bubble plots revealed spatial variations in catch composition across the fishery. A PERMANOVA analysis found that species catch composition varied most across the two geographic scales and, secondarily, among fishing modes and between men and women. Gendered differences in catch composition were variable from one village to another, and so should not be generalized. SIMPER analyses showed that gleaners and SCUBA divers caught significantly different suites of sea cucumber species. Species threatened with extinction were among those typifying catches of SCUBA divers. Our novel graphical techniques are useful for visualizing fishing modes and catches across other fisheries. Artisanal fisheries may exhibit strong heterogeneity in catches at multiple spatial scales. Planning of regulatory measures that limit certain fishing modes or species should take into account the likely differential impacts on different fishing communities and genders.

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INTRODUCTION

Artisanal and small-scale fisheries are a significant source of food, employment, tradition and cultural identity in coastal communities around the world (Berkes et al., 2001; Kittinger, 2013; Batista et al., 2014). Small-scale fisheries make up 25% of the world's catch and have grown rapidly in the last decades (Pauly and Charles, 2015; Zeller et al., 2015). These fisheries have the potential to seriously deplete nearshore marine resources (Bender et al., 2014; Purcell et al., 2014b; Samoilys et al., 2017), despite unsophisticated fishing gears and vessels compared to commercial fisheries (Piroddi et al., 2015; Munga et al., 2016). An artisanal fishery is a type of small-scale fishery in which simple or traditional fishing methods are used (Berkes et al., 2001; Batista et al., 2014). Artisanal fisheries include examples for which the catch is sold for domestic or international markets.

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Typically, artisanal fisheries use multiple gears and fishing strategies, at the same or different times of the year, to target a wide variety of invertebrates and demersal and pelagic fishes (McClanahan and Mangi, 2004; Batista et al., 2014). Many of these multispecies fisheries have operated for millennia, with various degrees of sustainability (Cesar et al., 1997; Campbell and Pardede, 2006; Tuda and Wolff, 2015). Understanding species targeted in different locations by different types of fishers will pinpoint populations of species that might be more overexploited or known to be at risk of extirpation.

The capacity to withstand ongoing fishing pressure varies among wild stocks, and some species are known to be vulnerable to extinction (Dulvy et al., 2003). Hence, there is a general consensus that multispecies fisheries should be managed with regulations that are species-specific, such as catch quotas and minimum legal size limits (Jennings and Polunin, 1996; Purcell, 2010; Samoilys et al., 2017). Clearly, data on who is catching which species are valuable for communicating such regulations to the right user groups and for understanding the impacts of regulations on different types of fishers.

A few management measures are already widespread in small-scale fisheries, including marine reserves, promotion of alternative livelihoods, and gear-based management (McClanahan and Mangi, 2004; Cinner et al., 2009; Jennings, 2009). However, measures must be appropriate to the specific characteristics, needs, and challenges of the fishery (Samoilys et al., 2017). Fishing mode, fishing gear, gender, age group, and trip frequency all affect the magnitude and species composition of the catch, and should be understood if management is to be effective (Pelletier and Ferraris, 2000; Kittinger et al., 2015; Olopade et al., 2017).

Gear types and fishing modes can also vary significantly between genders and regions, even when the same species are being targeted (Isaac et al., 2015; Rahman et al., 2016). Moreover, these factors tend to interact. For instance, the type of vessel will affect the fishing grounds that can be accessed, and therefore also the species composition of the area fished (Pennino et al., 2016). In many cultures, men and women tend to use different methods and gears, influencing the species they can access (Lambeth et al., 2014; Santos, 2015; Purcell et al., 2016a).

Here, we present novel graphical and analytical approaches to assess variations in catch composition among fishers in a multispecies artisanal fishery linked to international markets: the sea cucumber fishery in Fiji. Sea cucumbers are harvested worldwide, predominantly in small-scale artisanal fisheries, as a high-value commodity for export to Asian dried seafood markets (Purcell et al., 2013; Eriksson et al., 2015). They are an ideal case study to develop diagnostic tools to assess catch composition because multiple species are often targeted in the same region, using multiple methods (Toral-Granda et al., 2008; Eriksson et al., 2010; Purcell et al., 2016a). Fishing methods include gleaning (collection by hand in shallow water), breathhold diving and SCUBA diving (Choo, 2008; Eriksson et al., 2010; Muthiga and Conand, 2014; Purcell et al., 2016a). Such methods are typical of some artisanal shellfish fisheries in Latin America (Castilla and Defeo, 2001; Naranjo Madrigal and Salas Márquez, 2014) and in the Pacific Islands (Gillett, 2011).

The sea cucumber fishery in Fiji is operated by men and women fishers using artisanal fishing strategies (Purcell et al., 2016a), and fishery-dependent and fishery-independent data indicate over-exploitation of stocks (Pakoa et al., 2013; Mangubhai et al., 2017). Previously, we showed that men and women used gleaning, breath-hold diving and SCUBA diving with differing frequency across the Fijian fishery as a whole; a higher proportion of women gleaned than men, and very few women used SCUBA (Purcell et al., 2016a). Catch composition tended to differ between men and women, although the effects of fishing modes and finer geographic scales on catch composition were not examined.

The Fijian sea cucumber fishery has been one of the largest among Pacific Islands in terms of production volume (Kinch et al., 2008). Exports of dried sea cucumber (bêche-de-mer) have averaged ~250 tones p.a. over the past 15 years prior to a fishery moratorium in 2017 (Pakoa et al., 2013; Govan, 2017). Nearly all of the harvested sea cucumbers are exported and only a small amount of certain species (e.g., *Holothuria scabra*) are sold and consumed locally (Pakoa et al., 2013; Mangubhai et al., 2016; Purcell et al., 2016b). Tropical sea cucumbers occupy a range of reef and shallow lagoon habitats, accessible by the different fishing modes, and sale prices vary greatly among species (Purcell et al., 2012, 2017; Mangubhai et al., 2016). As with many other sea cucumber fisheries in Oceania, the products constitute a primary or secondary income source for a majority of fishers who collect them (Purcell et al., 2016b).

In this study, we interviewed 235 fishers to gather data on the frequency of catch of 22 species of sea cucumbers in Fiji. Our novel graphical approaches offer a more informative way to conceptualize spatial variations in fishing modes and catch composition than traditional graphs or tables. We then applied multivariate analyses to examine factors most affecting the variations in catch composition among fishers. Further analyses typify the species caught by fishers in distinguishable groups. By examining catch composition across multiple spatial scales, fishing modes and gender, the study contributes to an understanding of differential fishing impacts among fishers and informs management decisions for these and other small-scale fisheries.

METHODS

Fishery Context and Study Sites

The sea cucumber fishery in Fiji was operated solely by artisanal fishers operating predominantly from rural villages. Previously, we showed that fishers had a wide range of ages, and consisted of men and women using gleaning, breath-hold diving and SCUBA diving to collect sea cucumbers by hand (Purcell et al., 2016a). A total of 27 sea cucumber species were harvested in the fishery, and fishers always collected multiple species based on availability of habitats and their fishing strategies (Pakoa et al., 2013; Purcell et al., 2016a). Sea cucumbers are not by-catch or discards of other fisheries in this case because they exist in reefal areas inaccessible to trawls and other mobile fishing gears. The fishery was regulated by a single minimum legal size limit across all species and a prohibition on the use of SCUBA gear to collect

sea cucumbers, except for fishers in some villages that had been granted exemptions by the Ministry of Fisheries (Pakoa et al., 2013).

In consultation with Fiji's Ministry of Fisheries, eight locations (sub-regions) were chosen to give a broad sampling design: Yasawa group, Bua, Cakaudrove, Vanua Balavu, Lau group (south), Kadavu, Taveuni and Ra. We collected data in 35 villages (between 3 and 5 villages within each location) in which fishers were collecting sea cucumbers. Due to fears of resource depletion, the fishery was closed in 2017 by a long-term national moratorium.

Sampling and Data Collection

Data were collected from February–September 2014 using questionnaire-based interviews. Apart from consulting the village headman and village elders, a "snowball" technique was used to locate current sea cucumber fishers. We also used a gender-inclusive approach, in which women fishers were interviewed where possible to ensure their representation in surveys. At the time of the study, best estimates indicated that around 8,000 fishers were collecting sea cucumbers in Fiji (Purcell et al., 2018a). Fishers were interviewed irrespective of their age, whether they fished part-time or full-time or just collected sea cucumbers when fishing other resources, and the fishing mode(s) they used. An average of 6.7 fishers (± 1.8 s.d.) were interviewed in each village, with a total of 235 fishers across all locations.

The interview surveys of fishers were approved (Southern Cross University: ECN-13-279) for ethical human research and overseas research in accord with the Australian National Statement on Ethical Conduct in Human Research 2007. In Fiji, the Ministry of Education, Heritage and Culture granted an additional approval (RA01/14). In each village we also sought and obtained authorisation from the chiefs or village headmen for conducting the interviews. An information sheet, given to each interviewee, explained the project, funding, research uses of data, and that their responses were voluntary and confidential. Fishers gave written consent prior to the interviews.

Questions from a structured questionnaire (see Purcell et al., 2016a, Supplementary Material therein) were posed to fishers during the interviews, which lasted 40-60 min. Interviews took place in fishers' homes or in an open place within villages. To make sure fishers had understood the questions we repeated or asked them in an alternative way, and photographic identification sheets of all harvestable species were used to confirm local names of sea cucumber species used by fishers. An interpreter translated questions and responses when a foreign researcher conducted the interview. Among other questions, the questionnaire asked about how frequently they caught each of 22 species of sea cucumber, on a scale of "often," "sometimes," "seldom," or "never," which were later converted to rank frequencies of 3, 2, 1, and 0, respectively. We asked fishers about the fishing mode(s) they used to harvest sea cucumbers within the past year, which could be one or a combination of gleaning (wading on sand flats and reef flats), breath-hold diving, and SCUBA diving. Hookah gear was not used by any fisher in Fiji. Given the guarantee of confidentiality, fishers disclosed their illegal use of SCUBA gear to collect sea cucumbers in some areas where it was prohibited.

Data Analyses

Fishers might have practiced gleaning, breath-hold diving, SCUBA diving or a combination of two or three of these fishing modes in the year prior to the interviews. Thus, we constructed Venn diagrams to illustrate spatial variations in the proportion of fishers using different fishing modes in each location. Varying sizes of bubbles simultaneously illustrate the proportions of fishers in each location practicing each fishing mode and the various combinations of modes. We firstly tabulated the numbers of fishers using each fishing mode (SCUBA, gleaning, breathhold diving) and combinations of modes in each location. These location totals were entered into the fields in the online web application BioVenn (Hulsen et al., 2008) to generate the Venn diagrams for each location. Transparency of the diagrams was adjusted using Photoshop CS5.1, and each was sized to a common scale on a map. We used Venn diagrams as a novel method for visualizing variations in the use of three fishing modes among locations in a fishery. This graphical tool is useful when 2-4 fishing modes are used and shows the proportion of fishers using one or more modes; this overlap is otherwise difficult to visualize with graphics such as histograms.

Segmented bubble plots were prepared using PRIMER v7 software to illustrate the average catch frequencies of the most commonly caught sea cucumber species from each location. This graphical tool "displays several variables on the same plot as different sized segments of a circle, in differing color and segment position for the differing variables" (Clarke and Gorley, 2015)in this case species of sea cucumbers. Average frequency ranks for each species within each location were calculated (see Table S1) and the 10 species caught in greatest frequency among locations were selected. More than 10 species would have yielded unwieldy plots. The Bray-Curtis resemblance matrix of capture frequency data from the 10 species was ordinated using a metric Multi-Dimensional Scaling (mMDS) within PRIMER7 based on the Kruskal fit scheme and 50 repeats (Clarke and Gorley, 2015). Metric MDS was suited because, in this case, the segmented bubble plots illustrate the average values of ranks for each species in each location (Clarke and Warwick, 2014). The segmented bubbles for each location in geographical space were of interest here, rather than the ordination plot itself in multidimensional space which would likely be confusing to resource managers. Input data for the overlay bubble segments were the ranked frequency of capture for each species of sea cucumber for each fisher. The segmented bubbles for each location were then adjusted for transparency in Photoshop CS5.1 and overlaid on a map.

Statistical analyses were undertaken using PRIMER7 software (Clarke and Gorley, 2015). Not all species were harvested by fishers at all sites and we did not find women to interview in some villages and locations, but PERMANOVA is robust for such data (Anderson et al., 2008). A six-factor PERMANOVA analysis was conducted on the Bray-Curtis resemblance matrix from the original data on rank frequencies of each of the 22 species in our questionnaires. We employed Type III sums of squares, which is suited for designs with nested factors (Clarke and Gorley, 2015). Data among species were on the same rank scale and were not skewed, so needed no standardization or transformation. The

fixed factors were gleaning, breath-hold diving, SCUBA diving, gender, and location, while village was a random factor nested within locations. Some interaction terms were not testable owing to insufficient data combinations for those tests.

Following significant results ($\alpha = 0.05$) from the PERMANOVA analysis, one-way Similarity of Percentages (SIMPER) analyses were conducted to determine the sea cucumber species characterizing the catch within each location, and to characterize fishers who used gleaning or not, and fishers who used SCUBA diving or not. For each analysis, the cumulative contribution cut-off was specified as 50%.

RESULTS

Spatial Variation in Fishing Modes

Use of the three different fishing modes by fishers clearly varied significantly among the eight locations in Fiji (**Figure 1**). Breathhold diving was by far the most commonly used fishing mode, and was practiced by most men and most women. Fishers who used SCUBA tended, on average, to be younger (33 y \pm 1 y s.e.) than fishers who did not use SCUBA (38 y \pm 1 y s.e.). The depth range for breath-hold divers was about 1–20 m, whereas SCUBA divers told us they frequently dived to depths of 20–50 m (also see Pakoa et al., 2013).

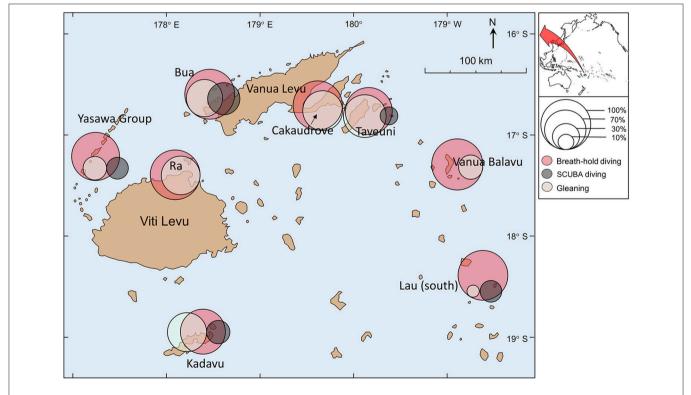
Gleaning was used by 45% of fishers overall, and was employed by few fishers (<10%) in the southern Lau group. In that

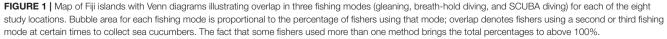
area, islands were relatively small and the reef habitats were chiefly subtidal. Similarly, relatively few fishers (10–30%) used gleaning on islands around Vanua Balavu and the Yasawa Group (**Figure 1**). In only one of the eight locations (Kadavu) was gleaning used as the sole method by a substantial proportion of fishers. Our graphical analysis shows that fishers who gleaned tended to also use breath-hold diving to collect sea cucumbers at some times, but individual fishers rarely (only 5 cases) reported catching sea cucumbers by both gleaning and SCUBA diving.

SCUBA diving was most commonly used in Bua province, where 39% of fishers used this method. SCUBA diving was used by a small proportion (<20%) of fishers in in the Yasawa group of islands, Taveuni, Lau group and Kadavu. Based on our sampling, SCUBA diving apparently was not used by sea cucumber fishers in Ra, Cakaudrove, or Vanua Balavu (**Figure 1**). Some fishers used more than one method, which brings the total percentages of the three fishing modes to more than 100%.

Variation in Catch Composition

While the 10 most commonly harvested species in Fiji (mentioned earlier) were collected in all eight study locations, the average contribution of each species to catches varied significantly among locations (**Table 1**, **Figure 2**). For example, on average, *Holothuria coluber* and *H. edulis* were caught "rarely" in Vanua Balavu and southern Lau Group, but fishers in the north-western locations reported catching them "sometimes" to





Source	df	SS	MS	Pseudo-F	P(perm)
Gleaning (Gl)	1	16,555	16,555	9.77	0.001
Breath-hold diving (Br)	1	1,234	1,234	1.29	0.097
SCUBA diving (SC)	1	13,721	13,721	6.12	0.001
Gender (Ge)	1	9,892	9,892	6.64	0.001
Location (Lo)	7	39,802	5,686	3.52	0.001
Village within Location [Vi(Lo)]	26	40,609	1,562	3.71	0.001
$GI\timesBr$	1	1,281	1,281	1.75	0.104
$GI\timesSC$	1	771	771	0.98	0.447
$GI\timesGe$	1	314	314	0.61	0.489
$GI\timesLo$	7	5,730	819	1.58	0.054
$Br\timesGe$	1	820	820	1.23	0.304
${\rm Br} \times {\rm Lo}^{**}$	5	4,074	815	1.27	0.278
$SC\timesGe$	1	802	802	1.23	0.279
$\mathrm{SC} \times \mathrm{Lo}^{**}$	4	3,575	894	1.13	0.407
${\rm Ge} \times {\rm Lo}^{**}$	6	3,434	572	0.76	0.761
$\text{GI} \times \text{Vi(Lo)}^{\star\star}$	17	8,132	478	1.14	0.214
${\rm Br} \times {\rm Vi(Lo)^{**}}$	6	3,628	605	1.44	0.078
$\text{SC} \times \text{Vi(Lo)}^{**}$	4	2,857	714	1.70	0.051
$\text{Ge} \times \text{Vi(Lo)}^{\star\star}$	7	5,993	856	2.04	0.004
GI × Ge × Lo**	1	531	531	1.07	0.429
GI × Ge × Vi(Lo)**	2	1,033	517	1.23	0.273
Res	133	55,957	421		
Total	234	220,750			

TABLE 1 | Statistical results from PERMANOVA analysis of catch composition among fishers with different fishing modes, genders, and among locations and villages within locations.

Only the testable main effects and interactions are included. Significant p-values are in bold. **Denotes interactions for which one or more levels of one of the factors is not included in the test because data did not exist (i.e. women fishers or a fishing mode was not present in one or more locations or villages).

"often"; *H. coluber* had the largest range of ranks (0.2-3.0). *Bohadschia vitiensis* were collected at a similar frequency over all eight locations (range of ranks: 2.3–2.9). *Holothuria lessoni*, a species list as Endangered by the IUCN, were collected at the lowest frequency throughout most locations (0.1-0.3; only Ra had a rank of 0.6); while *H. atra*, a low-value species, was collected with high frequency (1.5-3.0) in most locations (Table S1, **Figure 2**). The different sea cucumber species are not seasonally abundant (as with some finfish) but fishing strategies might differ seasonally somewhat for certain fishers. So some caution is needed since the inherent bias of different times in which surveys are conducted could potentially influence the differences among locations.

The PERMANOVA analysis of all 22 sea cucumber species revealed significant differences (p < 0.001) in catch composition between fishers who gleaned and those who did not, between fishers who used SCUBA gear and those who did not, and

between locations and villages within locations. Breath-hold diving was not compared in further analyses because the use of this fishing mode did not significantly discriminate catches among fishers (p = 0.097; **Table 1**). There were significant differences in average catch composition between men and women but those differences varied among villages (interaction-p = 0.004) (**Table 1**). The PERMANOVA indicated that 14% of the overall variation in catch composition was explained by fishing methods, 18% by differences among locations and 18% by differences among villages (combined difference of 50%).

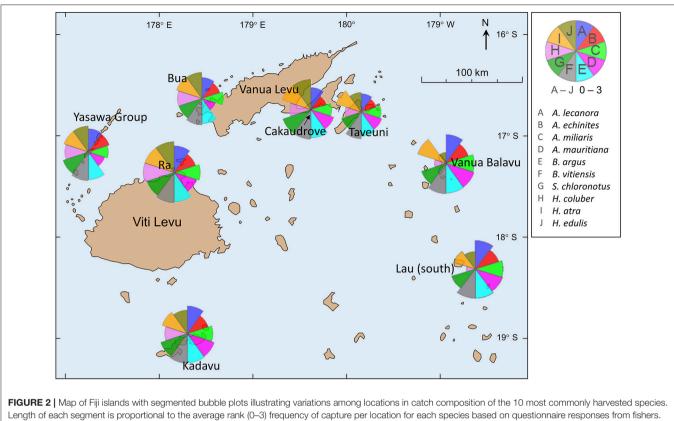
The SIMPER analyses of fishing methods revealed that *Holothuria atra, H. edulis*, and *Stichopus chloronotus* were three species typifying catches of fishers who gleaned for sea cucumbers and distinguished them from non-gleaners (**Table 2**). The non-gleaners were distinguished most by catching *Actinopyga lecanora* and *A. miliaris*, which were harvested infrequently by gleaners; *A. miliaris* was also harvested infrequently by SCUBA divers, and typified catches of breath-hold divers. Fishers using SCUBA diving were distinguished most by harvesting *A. lecanora, H. fuscogilva, T. ananas*, and *T. anax*, which are species mostly inhabiting deeper waters. Fishers using SCUBA gear also had the highest group similarity (65%) in catch (frequency) composition— i.e., they tended to catch similar species to one another, more so than fishers within other fishing-mode groups.

We also found large variation in group similarities of fishers within locations (**Table 3**). At the extremes, catch frequencies of fishers in Vanua Balavu were 79% similar to other fishers in that location, whereas catch frequencies were just 48% similar among fishers in Taveuni. Species typifying the catches differed among locations, but *H. atra, B. vitiensis, B. argus* were nearly always among the key species contributing to the similarity of catches among fishers within each location (**Table 3**).

DISCUSSION

Understanding Fishing Modes in Artisanal Fisheries

This study illustrates that even within a small-scale multispecies fishery, fishing modes can vary greatly among locations and genders. Geographic variation in fishing modes is partly explained by variation in nearby habitats accessible to village fishers, and also by differences in fishing history, socioeconomic factors, and management contexts among locations. In other fisheries, the type of vessel available to fishers determines their fishing grounds and fishing strategies (Isaac et al., 2015). We found that the use of gleaning and SCUBA diving was location- and gender-specific. Many of the commercially important sea cucumber species occupy shallow subtidal habitats in 1-10 m depth (Purcell et al., 2012). The prevalence of animals in depths that can be accessed by breath-hold diving and the extensive shallow fishing grounds in Fiji explains the relatively uniform use of this fishing mode across fishers.



Refer to Supplementary Material Table S1 for the full list of species.

TABLE 2 | SIMPER analysis showing species responsible for the first 50% of similarities between fishers who used or did not use gleaning or SCUBA methods.

Species	Similarity contribution (%)				
	Gleaners	Non- gleaners	SCUBA fishers	Non-SCUBA fishers	
Holothuria atra	14.4	7.0		11.9	
Bohadschia vitiensis	12.8	12.7	10.1	13.1	
Bohadschia argus	10.9	11.7	12.0	11.1	
Stichopus chloronotus	10.7	6.0		9.6	
Holothuria edulis	9.0			7.0	
Actinopyga lecanora		9.7	10.6		
Actinopyga miliaris		7.5			
Holothuria fuscogilva			8.1		
Thelenota ananas			7.9		
Thelenota anax			6.5		
Average group similarity (%)	59.0	62.1	64.8	60.6	

The average similarity of all samples within each grouping is given in the bottom row.

Our findings suggest that regulatory measures that control one fishing mode will probably affect fishers in different locations to varying extents within small-scale fisheries. This is true of regulations that affect specific gears and vessel types, as well as

area closures (Pennino et al., 2016; Samoilys et al., 2017). For example, the use of SCUBA for collecting sea cucumbers was fully banned in Fiji after our surveys (Mangubhai et al., 2017) and our study informs us that fishers would be mostly affected in Bua. In contrast, fishers in Ra, Cakaudrove, and Vanua Balavu, where SCUBA diving is rarely used, would have been unaffected by that regulation. SCUBA is often used in locations where shallow stocks of sea cucumbers have been depleted (Eriksson et al., 2010; Friedman et al., 2011) and can itself exacerbate over-exploitation across all fishery (Eriksson et al., 2012; Pakoa et al., 2013). Thus, the frequency of use of SCUBA across locations in a fishery (while of course considering habitat availability) offers insights to areas where depletion of resources is most likely.

Assisting fishers to cope with changes in fishery regulations is important for compliance (Arias et al., 2015), and an understanding of variations in gear use among fisher groups should inform this process. The large geographic and gendered variation in fishing modes in this study implies that management measures restricting certain fishing modes will inconsistently affect different villages. Understanding where different fishing modes are used should help managers to gauge likely socioeconomic impacts of management regulations. The full ban on SCUBA in Fiji after our surveys would have mostly affected young men, since they were the primary users of this fishing mode. Knowledge about gendered variation in fishing modes aids the design of training programs on fishing (Katikiro

TABLE 3 | SIMPER analyses of catch similarities within study locations.

Region	Group similarity (%)	Key species	Similarity contribution (%)
Ra	71.19	H. coluber	10.03
		H. edulis	9.98
		H. atra	9.96
		B. vitiensis	9.65
		S. herrmanni	8.99
		B. argus	8.54
Kadavu	61.56	B. vitiensis	11.37
		B. argus	10.58
		A. mauritiana	10.14
		S. chloronotus	9.15
		A. lecanora	8.34
		H. atra	0.97
Bua	56.87	H. atra	11.56
		B. vitiensis	10.83
		H. edulis	9.85
		B. argus	9.49
		S. chloronotus	9.33
Cakaudrove	72.76	H. atra	13.55
		H. edulis	13.05
		B. vitiensis	11.74
		S. chloronotus	11.64
		B. argus	9.98
Taveuni	47.93	B. vitiensis	16.67
		H. atra	15.76
		B. argus	11.89
		A. mauritiana	7.93
Lau Group (south)	64.56	B. argus	14.36
		B. vitiensis	13.06
		A. lecanora	11.78
		A. mauritiana	10.14
		A. miliaris	9.75
Yasawa Group	65.79	B. vitiensis	13.13
		B. argus	11.52
		S. chloronotus	9.25
		H. edulis	7.77
		H. atra	7.53
		S. herrmanni	6.45
Vanua Balavu	79.42	B. vitiensis	9.97
		B. argus	9.35
		A. mauritiana	9.24
		H. atra	9.14
		A. miliaris	8.17
		A. lecanora	8.07

et al., 2015). For example, the results of our survey show that awareness programs about SCUBA should mostly be targeted at men, and training or awareness about damage to reefs from gleaning (e.g., turning over boulders in search of animals) should not only be targeted at women. The Venn diagram approach used in this study could be used to illustrate variation in the use of gleaning, breath-hold diving, and compressed-air diving in other fisheries (e.g., Castilla and Defeo, 2001; Eriksson et al., 2010; Naranjo Madrigal and Salas Márquez, 2014). Similarly, the approach could serve in illustrating variations in the use of fishing gears for finfish such as speargun, hand line, traps, and net gears in East African artisanal fisheries (Davies et al., 2009; Daw et al., 2011), and gleaning, hook-and-line, and spearfishing in Pacific Island fisheries (Gillett, 2011).

Correlates of Catch Composition in Artisanal Fisheries

Significant variation in catch composition of sea cucumber species at small spatial scales (among villages within locations), genders and fishing modes shows that fishers within multispecies small-scale fisheries can have widely differing impacts on different species. Indeed, a fishery in southern Portugal found that gill nets and longlines caught significantly different compositions of species within similar fishing grounds (Erzini et al., 2010). Since different fish and invertebrate species attract a broad spectrum of different sale prices (Thyresson et al., 2013; Purcell et al., 2017), variation in catch composition also flows to variation in incomes and fishing strategies chosen by fishers. This is common to many small-scale multi-species artisanal fisheries. For example, in the elasmobranch fishery in Baja California, longlived species with lower fertility have largely disappeared from catches, and fishing modes have been adapted to catch smaller species that remain abundant (Smith et al., 2009). In our study, the species most typifying the catches reported by gleaners are known to be shallow-water species (Conand, 1989; Purcell et al., 2012) that tend to have a relatively low market value (Purcell et al., 2018b). In contrast, species found to typify catches of SCUBA divers were deeper water species, and most are moderateto high-value. Thus, SCUBA divers might not need to fish as often as gleaners to earn the same income. Similar trends were found for spearfishers who used hookah, rather than snorkel, to catch finfish in Chile (Godoy et al., 2016).

Understanding the species harvested most frequently by fishers presents one useful basis for planning lists of permissible species as a regulatory measure (Purcell et al., 2014a; Mangubhai et al., 2017). Species permissible for exploitation should ideally include some accessible to each fishing mode allowed in the fishery, so that each fisher group still has some species they can harvest. In this case study, fishery managers could, for example, select the top six species contributing most to similarity in catch among gleaners, non-gleaners, SCUBA divers and non-SCUBA divers as the candidates for a shortlist of permissible species in the fishery.

In data-poor fisheries, where fishery-dependent data from landing surveys or interviews with fishers are lacking, predicting the impact of management measures on catches is difficult (Kittinger et al., 2015). For example, certain species might be banned for collection or excluded from shortlists of permissible species, differentially affecting men, and women fishers in different areas. Our findings support the idea that stocks of different species will be impacted to varying extents based on the fishing modes used by fishers. Bans on SCUBA have been advocated in sea cucumber fisheries, such as the one in Fiji, in order to limit health risks to fishers and the depth range that species can be collected (Pakoa et al., 2013). Our analysis shows that such bans will also ease fishing pressure on certain species and shift pressure on other species if fishers revert to other fishing modes rather than exit the fishery.

This analysis helps to identify how different groups of fishers affect sea cucumber species of conservation interest. None of the species most typifying catches of gleaners and non-SCUBA divers are listed by the IUCN as threatened with extinction, whereas three species typifying catches of SCUBA divers (Holothuria fuscogilva, Actinopyga miliaris, Thelenota ananas) are either vulnerable or endangered with extinction (Conand et al., 2014). Similarly, fishers using SCUBA or hookah were targeting deepwater species of high value such as white teatfish H. fuscogilva in Papua New Guinea (Friedman et al., 2011), and small-scale fishers use SCUBA gears to target other endangered species such as black teatfish H. nobilis in fisheries off the coast of East Africa (Eriksson et al., 2012). Since four of the seven endangered species are considered deep-water species, the strong impact of SCUBA diving on threatened species should justify bans on compressed-air diving to collect sea cucumbers. Sea cucumbers may have different sensitivities to environmental stress and recruitment fluctuations, and some species have particular habitat requirements that makes them naturally rarer than others (Conand et al., 2014). How the vulnerability of individual species to other stresses interacts with fishing pressure

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remains to be resolved. This study provides clear justification that regulations on fishing modes could, in part, act as conservation measures.

AUTHOR CONTRIBUTIONS

SP, WL, and ST conceived the research. SP, WL, and ST conducted the fieldwork. SP and NF analyzed the data. SP, ST, NF, WL, and DC wrote the manuscript.

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SUPPLEMENTARY MATERIAL

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