DYNAMICS AND DRIVERS OF COMMERCIAL CORAL-REEF FISHERIES IN POHNPEI

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ABSTRACT

Island societies are reliant upon sustainable coral-reef fisheries for food and ecosystem services. Pohnpei is typical of many small island nations in that evidence points towards unsustainable harvesting regimes over the last decades. Yet, species-level monitoring of fisheries landings remains rare despite their fundamental need for improving management. Extensive sampling of landings coupled with socioeconomic surveys of commercial fishing activities provided new insights into Pohnpei's reef fisheries. Pohnpei's commercial landings were dominated by only a few species, the use of nighttime spearfishing, and by a small community of fishers. These characteristics suggest a strong, targeted economic reliance currently exists for a few species by a subset of fishers. Further, strong dependence was found between fishing effort and catch composition, upon favorable fishing conditions associated with conditions of low wind/swell and lunar phases. Modern landings were suggestive of fishing "down" and "throughout" the food web dynamics, as they were dominated by species with higher resilience (high turn-over rates and density-dependence mechanisms), while less resilient components of the fishery have become rare in modern landings. Overall, our findings confirm declines of fisheries resources for over the last few decades in Pohnpei. While modern fisheries dominated by more resilient species may provide for maintained landings in the medium-term, undesired long-term effects for both ecosystems and fisheries are occurring under the current fisheries regimes. Our findings provide an improved foundation for tailored management actions that would maximize returns given challenging resources limitations.

KEYWORDS: *Coral-reef fisheries, favorable fishing conditions, resilient species*

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1. **INTRODUCTION**

Coral-reef fisheries support the social and economic wellbeing for over five hundred million people in nearly 100 coastal countries worldwide, providing financial support to over 6 million fishers and their families. Coral-reef fisheries also contribute over USD $6 billion annually to the world economy (Barnes-Mauthe et al., 2013; Cesar et al., 2003; Teh and Sumaila, 2013). However, the economic contribution is likely not as significant as the contribution to food security and poverty alleviation, particularly for small island nations that are highly dependent on their coastal resources (Bell et al., 2009; Hughes et al., 2012; Kent, 1997). In addition to the social and economic benefits, coral-reef fisheries also provide a strong cultural identity to small island nations where fisheries have been a central part of daily life for generations (Johannes, 1981; Krämer, 1917).

The proximity of human communities to coastal ecosystems can cause ecological disturbances, such as fisheries overexploitation (Brewer et al., 2009; Cinner et al., 2013; McLean et al., 2016; Mora et al., 2011). Historical records report localized depletions in reef fisheries since the 1950s (Cuetos-Bueno and Houk, 2015; Jackson et al., 2001; Pauly et al., 2002; Zeller et al., 2006). In turn, fisheries depletions have caused both social and ecological problems. The social cost of depleting fisheries is proportional to the level of dependence placed upon them (Silverstre and Pauly, 1997; Pitcher et al. 2000; Rosenberg 2005). Small and remote island nations within the Pacific Ocean are particularly sensitive to fisheries declines because reef fish constitute the main source of accessible animal protein (Bell et al., 2009; Cesar et al., 2003). Fish commercialization strongly drives fisheries decline on island nations, defined by a growing fishing footprint to meet both commercial demands and fishers income (Cinner et al., 2013; Cuetos-Bueno and Houk, 2018; Kent, 1997; Rhodes et al., 2014). In turn, one main consequence of commercialization has been the displacement of subsistence fishers because of the ability to expand to new fishing grounds is limited compared to commercial operations that can cope with rising costs (Cuetos-Bueno et al., 2018; Swartz et al., 2010; Watson and Pauly, 2001). This situation has been described as a social ratchet because of the negative feedback loops between growing commercial fishing, localized depletions, declining fisheries, and ultimately reduced fish diets for societies that replace local fish diets with cheaper processed foods (i.e., canned fish and meats) (Birkeland, 2017; Sheppard et al. 2012). Reduced fish diets can ultimately lead to a higher prevalence of diseases, such as diabetes (Corsi et al., 2008; Kaufer et al., 2010).

The ecological consequences of declining fisheries are equally severe. Commercial coral-reef fisheries preferentially target large, slow-growing predators and herbivores because of increased profit margin and catch biomass-per-effort (Hawkins and Roberts, 1995; Januchowski-Hartley et al., 2011; Rhodes et al., 2008). Additionally, many of these species are specifically targeted during dormancy (Hamilton et al. 2016) or critical life history events, such as spawning aggregations where a substantial proportion of the reproductive population can be rapidly removed (Hamilton et al., 2012; Sadovy de Mitcheson and Erisman, 2012). As these species become depleted, landings shift to smaller fish in lower trophic levels with faster biomass turnover (Anderson et al., 2008). This trend has been observed across many Micronesian islands whereby fish assemblages can become dominated by a suite of herbivores and detritivores that grow rapidly but have limited ecological functions (Cuetos-Bueno and Houk, 2018; Houk et al., 2018, 2010; Houk et al., 2017a; Rhodes et al., 2018). Because ecological processes such as grazing, predation, and nutrient distribution are exponentially related to fish size (Birkeland and Dayton, 2005; Lokrantz et al., 2008), selective fishing can alter entire food webs and ecosystem stability (Boudreau et al., 1991; Houk et al., 2017). In sum, small fish with high biomass turnover rates provide less resilience to disturbances, which are increasing in frequency with climate change (Hughes et al., 2003). Lastly, faster growth and biomass turnover means that fish populations track environmental cycles more closely, leading to larger population fluctuations that diminish population, ecosystem, and economic resilience (Anderson et al., 2008; Rouyer et al., 2012).

1.1 **Fisheries assessment**

Clearly, improving fisheries management is essential, but efforts to gather fisheries-dependent data to support policy recommendations is a constant challenge (Pauly and Zeller, 2014; Wright and Hill, 1993). Stock assessments are one fundamental approach to evaluate the status of individual fish populations (Dalzell et al., 1996). Yet, most stock assessment models are difficult to apply to coral-reef systems because of their diversity and the complex biological interactions that accompany high diversity systems (Dalzell et al., 1996; Pauly et al., 2002). In response, data-poor approaches for multi-species stock assessments have emerged to help evaluate species status by coupling extensive size data with limited age data (Nadon et al., 2015; Prince et al., 2015). The common assumption for these approaches is that exploited fish populations will diminish in size and age with growing exploitation, and evaluating fishing-versus-natural mortality and spawning potential ratios can define a conservative benchmark for each species (Ricker, 1981). Yet, recent studies have found that while many target species do have primary responses to their size and age structure with exploitation, many others show primary responses to their percent contribution and tended to disappear from landings with exploitation more than shift their sizes (Houk et al., 2018; Houk et al., 2017; Rhodes et al., 2018). These findings existed across a suite of species with similar maximum body sizes, suggesting that variability in density dependence is an influential species-based characteristic that should be taken into account when making species assessments (Rose et al., 2001). Thus, tracking species sizes and ages, as well as proportional contributions is desirable. However, time series data are rarely available for coral reef fisheries, and methods to substitute space for time are required.

In lieu of time series data, one approach to evaluate the status of fisheries is to better appreciate the spatial dynamics of fishing effort. Localized fisheries depletions are typically followed by spatial expansions. Fishers must catch more in shorter, opportunistic windows to maintain their profit margins because costs to travel to further fishing grounds may be significant (i.e., fuel) (Birkeland, 2004). Studies have found that similar shifts in catch composition and overall landings that occur through time can also occur across environmental gradients (Boss and Gumanao, 2012; Houk et al., 2012, 2017b; Cuetos-Bueno et al., 2018). Thus, capturing these gradients could provide one ideal indicator of fisheries status. For these reasons fisher interviews are also very important to fisheries assessment studies (Bunce et al., 2008; Tesfamichael et al., 2014; Fisher et al., 2015). While fish biomass and overall size spectra are commonly used biological metrics to assess fisheries status (Lindfield et al., 2015), fisher interviews represent complimentary data to understand how biological metrics may differ across environmental gradients, including distance from markets, lunar phases, wave energy and seasons (Teh et al., 2007; Rhodes et al., 2008; Houk et al., 2015; McLean et al., 2016; Cuetos-Bueno et al., 2018). For example, coral reef fisheries in the Commonwealth of the Northern Mariana Islands (CNMI) had daily landings that were significantly related to environmental factors, with highest catches associated with low wave energy that provided better access to fishing grounds along the windward coast (Houk et al., 2012). This assumption was supported by a more recent study that showed the ratios between landings during the calm summer months and rough winter months have been growing significantly through time (Cuetos-Bueno et al., 2018). Elsewhere, fishing pressure in Kosrae, Micronesia, became concentrated on the windward, eastern coast of the island when the calm spring season began (Houk et al., 2017). In sum, fisher interviews are an ideal means to record fishing effort (e.g. number of fishers involved, fishing technique, and time involved in each fishing event) with respect to time and geographic location (e.g. reefs location, type of reef, biomass extracted per reef, spatial fisheries expansions). In turn, the way fishing effort and catch success is distributed across these environmental regimes provides a useful indication of fishery status.

The present study will characterize the dynamics and drivers associated with one of the largest coral-reef fisheries in Micronesia. Both catch and effort data were collected from the coral-reef fishery in Pohnpei across one year. Data collection included fisher interviews, coupling photographic monitoring of species-based catches (sizes and species identifications), and daily market landings records. These data were used to 1) characterize daily catch and effort trends with respect to environmental gradients, 2) describe how catch and effort may shift across both geographic sectors and seasons in relation to these gradients, and 3) describe species-specific responses to fishing pressure.

2. MATERIALS AND METHODS

2.1. Study area

Pohnpei is one of four states belonging to Federated States of Micronesia, with a population of 33,000 residents dispersed among five municipalities (Fig 1). Pohnpei is surrounded by both a lagoon and a barrier reef totaling 154 km^2 of habitat, which provide a range of habitats and resources for fisheries (Rhodes et al., 2014). Fisheries have been a central part of life for many generations, not only for their sustenance but also for their cultural values (Hanlon, 1988). Modern commercial fisheries now play important economic roles for society (Rhodes et al., 2014). Yet, the growing commercialization has led to some potentially unsustainable harvesting practices such as modern nighttime spearfishing (Bejarano et al., 2013), undersized catches (juveniles), and overexploitation of large, slow-growing predators (Rhodes et al., 2018). Given their importance and their recent trends, understanding the current state and dynamics of the fishing resources in Pohnpei is a priority. This situation provided the basis for the present project that characterized and evaluated the current state of the fishery across a 1-year study period (2014-2015).

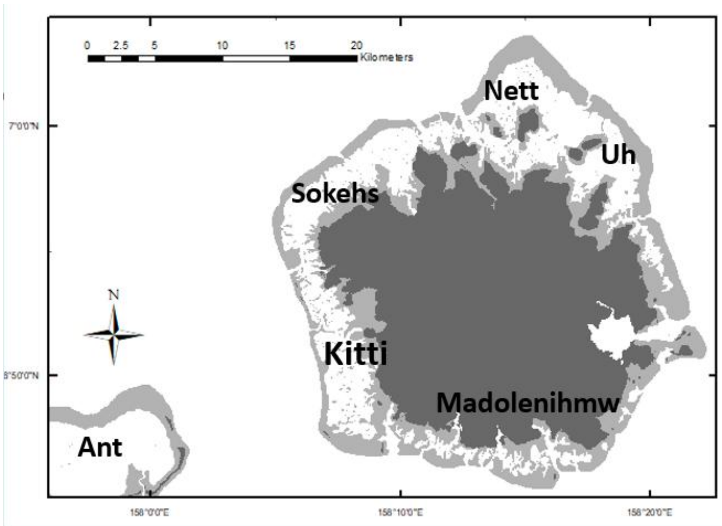

Figure 1. Map of Pohnpei highlighting the five municipalities and nearby Ant Atoll (where a considerable amount of fishing also occurs).

2.2. **Data collection**

2.2.1**. Fisheries-dependent data**

Daily commercial coral-reef fisheries surveys were conducted in Pohnpei during 12 consecutive months (04 February 2014 to 12 February 2015) to generate data on catch, effort, and species composition. Three different fisheries-dependent datasets were generated: 1) species-based catch composition from a subset of daily landings, 2) fisher interviews that were mostly linked with species-based catch composition data, and 3) records of total landings from all commercial markets.

Daily (Tuesday to Saturday) visits to the main markets in Nett, Sokehs and Kitti municipalities were conducted between 0600 and 1200 when fresh coral-reef fish were delivered to the markets (Rhodes et al., 2008). An opportunistic subset of fisher catches were selected for species-based monitoring each day. For each catch event, fish were individually placed on a standardized measuring board with a camera mounted on top. For each catch, a monitoring code was use to link individual catches to fisher interviews, thereby allowing a detailed examination of the fishery. Photographs were taken of all fish within individual catches, with a total of 50,197 fish photographs during the study period. Data were entered into a Microsoft Access database (author JCB) and photos were evaluated to determine species identification and fish length (as fork length, FL) to the nearest 1 cm. Fisher interviews (n=1,470) were conducted during daily markets visits, either at the same time as catch composition surveys were conducted or independently where catch surveys were not possible. Interviews consisted of a short questionnaire to obtain fishing information including fisher location, fisher origin, method(s) used, length of trip, number of fishers, fishing location, and some economic data. Lastly, total daily market landings were collected weekly by gathering standardized logbook records from all fish markets around the island (n=21) throughout the course of the study.

2.3. **Environmental data**

Environmental data were collected for analyses that included wind speed, lunar phase, and rainfall. For the analyses, environmental data represented independent variables to predict the variation in biological and socioeconomic data using an array of statistical approaches. Daily environmental variations were previously reported as primary drivers of fisheries in Pohnpei and elsewhere in Micronesia (Houk et al., 2012). Wind and rain data were collected from NOAA National Center for Environmental Information (https://www.ncdc.noaa.gov/cdo-web/datatools/findstation). Lunar data were collected from United States Naval Observatory (www.usno.navy.mil/USNO). Wind, rain, and lunar data were binned into groups prior to analysis (i.e., 1km/h groups for wind, 1 inch for rainfall). Cutoffs for data binning were derived from a Jenk's Natural Breaks procedure that minimized inter-group variance (Crawley. 2013). Daily wind categories were defined for some analyses to distinguish between calm and windy days, and wet and dry days. The threshold for wind categories was monthly mean wind speed values above or below 9.36 km hr^{-1}, while the thresholds for rainfall was above or below 37 in mo^{-1}. Lastly, three categories were defined for lunar phases based on moon illumination (new lunar phase:0-33, half lunar phase: 34-66, and full lunar phase: 67-100).

2.4. **Analysis**

First, the commercial fisheries sector was characterized for the study year by extrapolating values for annual biomass landings and the associated economic value to account for data gaps (e.g. missing records). Annual landings were extrapolated by multiplying the average daily landings per market by the average weekly frequency of market activity. Landings were then expanded across the entire year by multiplying across the number of operational weeks during the study period, and added across all markets. Economic value of the fishery was estimated by multiplying annual landings by average retail prices of reef fish (US$2.50 kg^{-1}).

Percent contributions of each fishing method to overall landings were next calculated using data from fisher interviews describing fishing methods and total catch from the gear-specific fishing units. Only interviews with one type of fishing method were used in these analyses, which represented 90% of the total interviews, with the remaining 10% representing mixed-gear fishing. Next, a geographic map of fish landings was created to visually display extraction trends across Pohnpei Island and nearby Ant Atoll (where considerable fishing also occurred).

First, landings for each reef section were estimated from fisher interview location and total catch data. For this process, the island was separated into 4 major sectors (northeast, northwest, southeast and southwest) associated with distinct fishing grounds. Relative geographic gradients of actual landings were made using a kriging extrapolation in ArcGIS followed by a smoothing function that takes the average of eight surrounding pixels to create a gradient.

Next, statistical differences in proportional contributions to daily landings by method, sector, lunar phase, wind and rainfall were assessed. ANOVA analyses, with crossed designs (when necessary), followed by Tukey's post-hoc tests were used to assess differences when comparing continuous data in differing categorical bins. Statistical testing for proportional contributions to daily landings was conducted on data derived from both fisher interviews and daily market landings. Tests were run for total landings and for landings associated with spearfishing that the dominant gear type.

Similarly, fishing effort data were analyzed across the same environmental factors using log-linear analyses with Pearson's coefficients that compared categorical versus categorical data. Statistical testing for fishing effort used only interview data that had fishing location associated with it.

Last, primary target species that contributed >1% to spearfishing daily landings were analyzed using the same methods described above. In addition, size-structure for those same set of species were examined to asses potential size-responses to fishing pressure (i.e. density-dependence), as skewed size distributions highlight populations disproportionally dominated by smaller individuals (Cuetos-Bueno et al., 2018; Houk et al., 2017). Species were classified as skewed if 5% percentile of skewness estimations (10,000 loops with 10% replacement) was greater than zero.

3. RESULTS

3.1 **Characterization**

Mean daily commercial landings were estimated at 584±22 kg over the study period. Annual landings were estimated at 228±36 mt yr^{-1}, which translates to a local economic value of USD $752,000. The annual economic value was distributed among fish market owners (13%), fishers (65%), and other businesses (22%) supplying fishing-associated necessities, such as gas and ice. Mean daily catch per fisher was estimated at 18.7±0.3 kg $fisher^{-1}$ $trip^{-1}$, translating to a profit of $38.1±1.0 $fisher^{-1}$ $trip^{-1}$ after accounting for fishing costs. The prevalent fishing method was spear fishing (87% of landings), followed by bottom fishing (8%) and net fishing (4%). Mean daily catch differed by fishing gear and was estimated at 19.3±0.3 kg $fisher^{-1}$ $trip^{-1}$ for spearfishing, 17.5±0.7 kg $fisher^{-1}$ $trip^{-1}$ for bottom fishing, and 13.9±0.8 kg $fisher^{-1}$ $trip^{-1}$ for net fishing. Gear-specific profits also differed and were estimated at $40.0±1.1 $fisher^{-1}$ $trip^{1}$

for spear, \$33.0±2.2 fisher^{-1} trip^{-1} for bottom fishing, and \$28.4±2.8 fisher^{-1} trip^{-1} for net.

Fisher interviews suggested that landings were not extracted homogeneously across the island reefs. From highest to lowest among sector, landings were extracted from the southwest (42%), northeast (32%), northwest (12%), Ant Atoll (7%), and lastly southeast (7%) (Figure 1). Broken down by major reef types, most landings were extracted from the barrier reef (93%), especially from the outer part of the barrier reef (69%) as opposed to the inner lagoon (24%). Landings from patch reefs and fringing reefs were disproportionate lower, accounting for only 5% and 2% respectively. Fishers from all five municipalities within Pohnpei participated in the commercial fishery, yet their contribution was not homogenous. Fishers from Kitti Municipality disproportionally accounted for 73% of landings (Figure 1 MAP), following by Nett (15%), Sokehs (6%), Madolenihmw (5%), and Uh (1%).

3.2. **Environmental factors**

Wind speed and lunar phases influenced daily commercial landings in Pohnpei. In contrast, rain had no significant relationship with daily landings. Given that spearfishing was the main fishing method used, all of the analyses performed with spearfishing landings mirrored the trends shown for total landings. Daily landings were 43% higher during days of low wind speed compared to days with higher wind speed (674±32 kg compared to 472±27 kg) (F-Statistic = 17.06, df = 1, P <0.001, ANOVA, Figure 2a). In terms of lunar phase, daily landings were highest during the new lunar phase (712±40 kg), moderate during half lunar phase (560±45 kg), and lowest during the full lunar phase (476±30 kg) (F-Statistic = 8.98, df = 2, P <0.001, ANOVA; post-hoc comparisons new lunar phase vs full lunar phase; P <0.001, Figure 2b).

Interestingly, daily wind speed and lunar phases did not influence spearfishing success (fisher catch per trip), as mean daily catch success did not significantly differ across these environmental factors. Thus, differences in daily commercial landings, noted above, were attributed to differences in fishing effort as documented below. Spearfishing catch success was mostly homogenous across geographical sectors, but not across islands. Mean fisher landings from Ant (93±7 kg $fisher^{-1}$ $trip^{-1}$) were significantly higher than those from all sectors in Pohnpei island except the southeast (F-Statistic = 4.45, df = 4, P <0.001, ANOVA test, post-hoc comparisons NE P = 0.04, NW P = 0.03 and SE P <0.001). Within Pohnpei Island, only mean fisher landings between southeast and southwest sections were significantly different, as those from the former were 20% higher than those of the later (22.6±1.5 kg $fisher^{-1}$ $trip^{-1}$ vs 18.7 ±0.5kg $fisher^{-1}$ $trip^{-1}$; post-hoc comparison P=0.04).

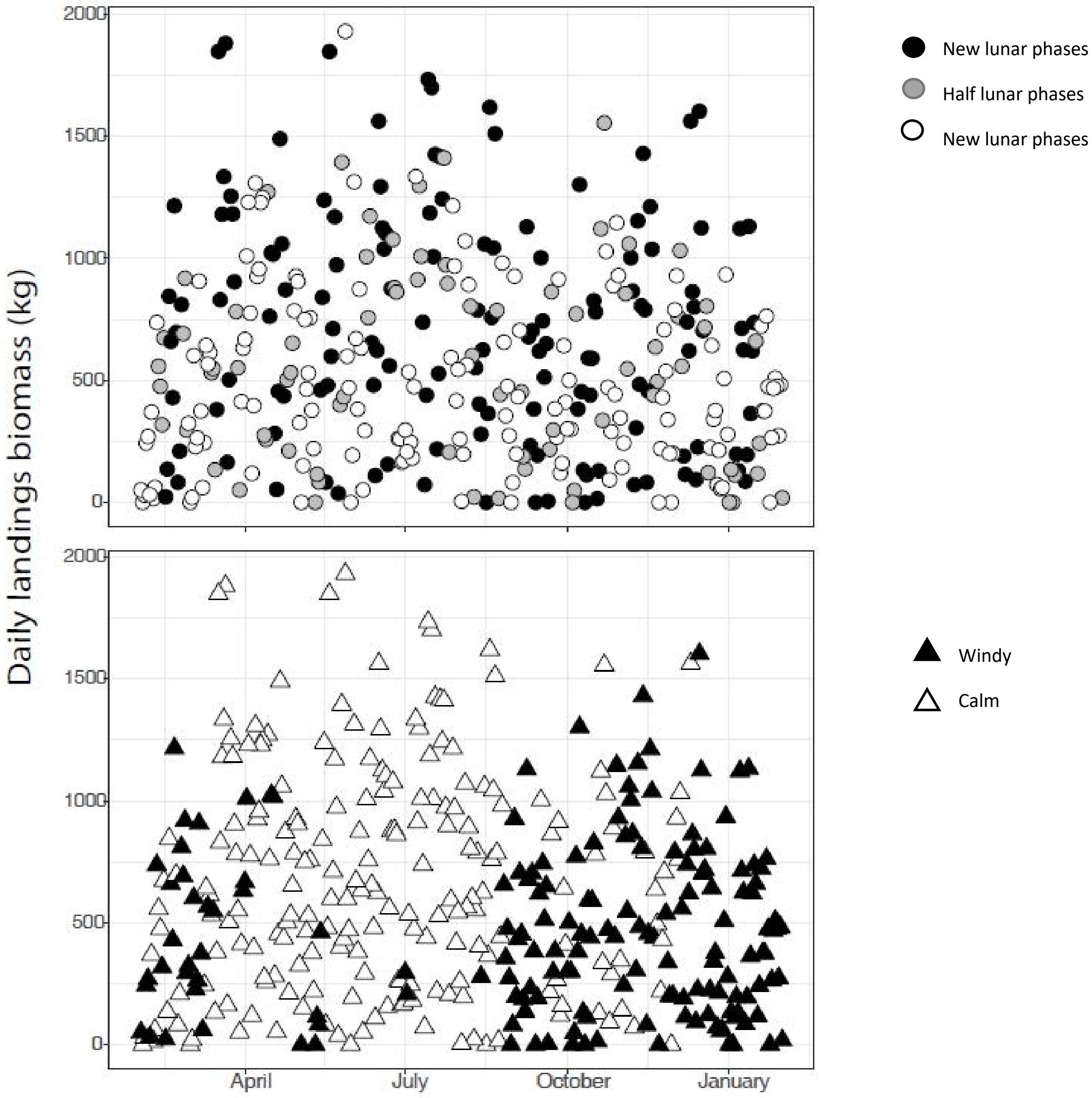

Figure 2. Trends of total daily landings of commercial coral reef fisheries in Pohnpei. Total annual landings related with different lunar phases (upper) and wind speed (lower). Circles and triangles represent the biomass captured per day for each environmental variable.

3.4. **Fishing effort**

Fishing effort trends closely aligned with total commercial landings trends. Spearfishing effort was disproportionally dominated by trips to the southwest sector (47%), followed by northeast (27%), northwest (12%), Ant (7%), and southeast (7%). Clear influences of wind speed and lunar phase on fishing effort were found. Mean number of daily spearfishing trips (trips day^{-1}) during calm days (5.6±2.6) were 47% higher than during windy days (3.8±2.2 F-Statistic =30.93, df=1, P < 0.001, ANOVA test), and 36-38% higher during new and half-lunar phases (5.3±2.6 and 5.4±2.5, respectively) than during full-lunar phases (3.9±2.3; F-Statistic =10.25, df=2, P < 0.001, ANOVA test, post-hoc comparisons new lunar vs. full lunar P <0.001; half lunar vs. full lunar P = 0.001). Incorporating the three significant factors of geography, lunar phase, and wind speed suggested significantly more fishing effort was conducted in the southwest and Ant sectors during windy days and full lunar. In contrast, lower than expected effort was found for the northeast and northwest sectors under these same conditions. Higher than expected effort was also found during calm days and half-lunar in the northeast section (Figure 3; Pearson's residuals >2, P <0.001, log-linear models). In sum, results showed that higher fishing effort and landings were focused on the most favorable locations and conditions, and therefore effort shifted significantly with lunar and wind.

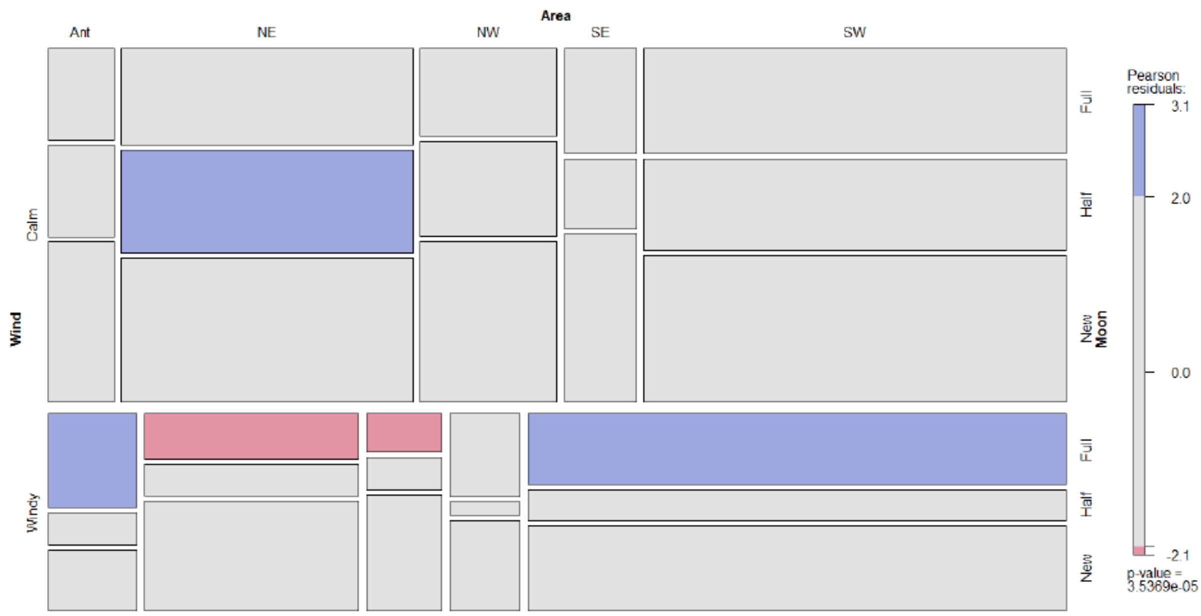

Figure 3. Spearfishing effort by significant environmental factors (wind and lunar phase) and geographic sectors. The size of each tile is proportional to fishing event

frequencies during the study period. Blue tiles indicate higher than expected fishing frequencies within each environmental factors and geographic sectors. Red tiles represent less than expected, and gray tiles are not difference that expected by chance.

3.5. **Species trends**

A total of 163 species belonging to 22 families were recorded in this study, but just 9 families comprised 95% of overall landings. Acanthuridae (Surgeonfishes and unicornfishes = 34%), Scaridae (Parrotfishes = 17%), Epinephelidae (Groupers = 11%), Siganidae (Rabbitfishes = 8%), Lethrinidae (Emperors = 7%), Lutjanidae (Snappers = 6%), Kyphosidae (Rudderfishes = 5%), Holocentridae (Soldierfishes and squirrelfishes = 4%), and Carangidae (Jacks and trevally = 4%) were most frequently caught. There were 22 species that individually contributed more than 1% of total biomass landings. These 22 top species together accounted for 75% of total landings, while just eight species represented 50% of total landings. The emblematic *Naso unicornis* was the most frequently caught species, representing 19% of the total landings, followed by the *Hipposcarus longiceps* (9%), *Acanthurus lineatus* (6%), *Naso lituratus* (4%), *Plectropomus areolatus* (4%), *Lutjanus gibbus* (3%), *Siganus doliatus* (3%), and *Kyphosus vaigiensis* (3%; Figure 4).

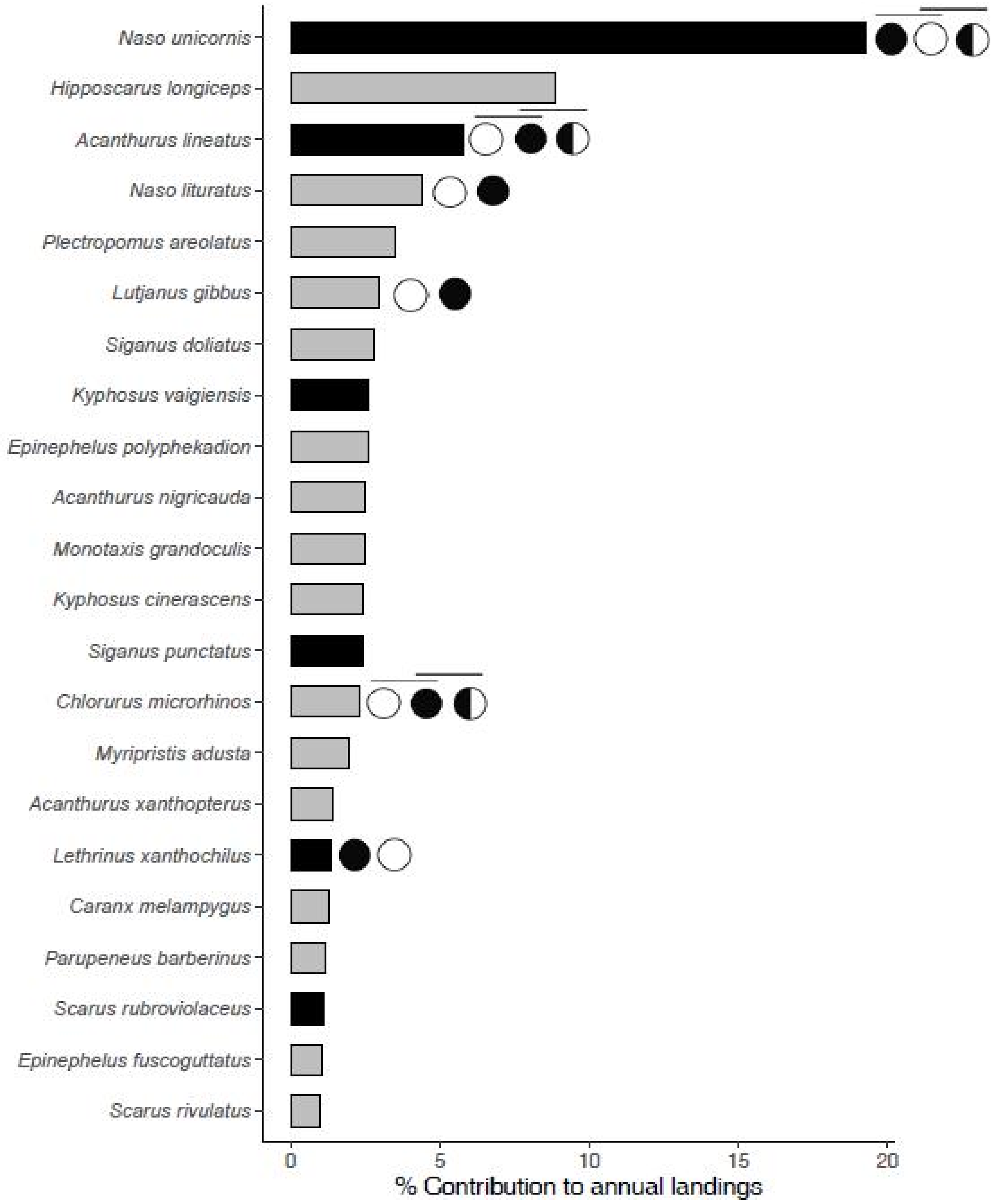

Figure 4. Twenty-two species that represented 75% of annual coral-reef fish annual biomass landings. Gray bars indicate positively skewed sized structures, while lunar phases (white, black and mix circles mean new, full and half lunar phases respectively*) depict the dependence of proportional contributions on specific lunar periods (left-to-right, from highest to lowest). Lines represent statistical groupings.*

Lunar phases had significant effects on the proportional contribution of these top 22 species that cumulatively accounted for 75% of overall landings. For instance, the new lunar phase was a primary driver for *Naso unicornis* daily landings accounting for more than twice as many landings compared to the full lunar phase (23.2±2.5 %compared to 11.4±2.3% of total landings; F-Statistic = 10.34 df = 2, P <0.001, ANOVA, post-hoc comparisons: new lunar phase vs. full lunar phase, P <0.001). A similar significant effect was found for *Lethrinus xanthochilus*, whose landings were 4.9 times higher during new lunar phase (2.0±0.3% compared to 0.4±0.2% of total landings; F-Statistic = 12.68, df = 2, P <0.001, ANOVA, post-hoc comparisons: new lunar phase vs. full lunar phase P <0.001). In contrast, full lunar phases were associated with higher landings of *Acanthurus lineatus* (11.8±2.1% compared to 3.2±0.6% of total landings; F-Statistic = 9.09 df = 2, P <0.001, ANOVA, post-hoc comparisons: full lunar phase vs. new lunar phase: P <0.001; full lunar phase vs. half lunar phase: P <0.004), *Naso lituratus* (8.0±1.0% compared to 4.4 ±0.5% of total landings; F-Statistic = 6.65 df = 2, P <0.001, ANOVA, post-hoc comparisons: full lunar phase vs. new lunar phase P <0.001), *Lutjanus gibbus* (2.0±0.3% compared to 1.7±0.3% of total landings; F-Statistic = 3.16 df = 2, P <0.001, ANOVA test, post-hoc comparisons: full lunar phase vs. new lunar phase P = 0.03), *and Chlorurus microrhinos* (3.2±0.6% compared to 2.0±0.4% of total landings; F-Statistic = 4.56 df = 2, P < 0.001, ANOVA, post-hoc comparisons: full lunar phase vs. new lunar phase P = 0.01 and full lunar phase vs. half lunar phase P <0.004). In summary, landings of six species that accounted for 36% of overall landings were significantly driven by lunar phases. Geographical effects on proportional contribution to landings also existed, but were driven mainly by differences between landings from Pohnpei and nearby Ant Atoll. Lastly, small but significant effects of wind speed were found for just two species (*Naso unicornis* and *Scarus rubroviolaceus*).

Analyses of size-frequency distributions for the same 22 species revealed skewed size-frequency distributions for 16 out of the 22 species, which together accounted for 43% of overall landings. Many of the species with higher skewness values (landings dominated by smaller individuals) were mid-size species prevalent in landings (e.g. *Lutjanus gibbus* and *Hippocarus longiceps*) and have been identified as having strong density-dependent response to fishing characterized by populations and landings increasingly dominated by small/younger fish alongside fishing pressure (Cuetos-Bueno et al., 2018; Cuetos-Bueno and Houk, 2018; Houk et al., 2017).

4. DISCUSSION

4.1. **Characterization**

Coral-reef fisheries are essential food and income sources for island nations. Yet, they are generally perceived as less important and given lower management priority compared with industrial pelagic fisheries, as their economic contributions are not always obvious (Zeller, Booth and Pauly, 2006; Teh and Pauly, 2018). This study revealed that Pohnpei is one of the most important commercial coral-reef fisheries in Micronesia. The 228 mt of annual landings are only second to those of Chuuk (265 mt), providing for a substantial direct economic value of USD $752,000 to Pohnpei's society (Cuetos-Bueno and Houk, 2014; Houk et al., 2017; Cuetos-Bueno et al., 2018). Contrary to economic benefits of industrial pelagic fisheries in the form of fishing fees that go directly to central governments with little benefits cascading down to the communities (Barclay and Cartwright, 2007), commercial coral-reef fisheries support both livelihoods and economic security to some of the most vulnerable communities and households where limited livelihood options are available. This highlights the key role of coral-reef fisheries for island societies, and the need for management that maximizes sustainable societal returns.

However, and like in most other island societies across the Pacific, commercial landings represent only a fraction of overall landings, as non-commercial extraction for subsistence purposes remain dominant in some locales, accounting for an estimated three times the amount of commercial fisheries, which could translate in Pohnpei to 500-800 mt, valued at over $2 million per year (Gillett, 2016).

Nighttime spearfishing has become the dominant fishing method across Micronesia and the wider Pacific since the introduction of the underwater flashlight (Gillet and Moy, 2006). In Pohnpei, landings caught by nighttime spearfishing accounted for 87% of the total landings, representing a dominance that has been reported for other Micronesia islands as well (e.g. Chuuk = 86%: Cuetos-Bueno et al., 2018; Yap = 80%: Houk et al., 2012). The growing prevalence of nighttime spearfishing has been linked to its efficiency even as stocks become compromised (Ennis and Aiken, 2014). This study reported higher financial returns to nighttime spearfishers compared to other gears. Yet, growing evidence continues to highlight undesirable changes in fish assemblages with a growing dependence on this method (Godoy et al., 2010; Hamilton et al., 2012; Rhodes et al., 2018). Some of the reasons for the high financial return despite stock declines are low entry and operational cost, the capacity to target a wide range of species and sizes, and the ability to target species while dormant (Frisch et al., 2012; Nunes et al., 2012; Lindfield, McIlwain and Harvey, 2014). The present study revealed several signs of growing instability in the Pohnpei fishery that resonated and added to these concepts: (i) increasing fishing effort and shifting fishing locations to areas with calm winds to maintain fisher income and daily landings, (ii) higher daily landings with favorable lunar phases and low winds, and (iii) many popular species disproportionally captured during specific environmental timeframes when they are most susceptible (i.e., both new and full lunars, species-specific). These concepts are expanded on below.

4.2 **Environmental factors and fishing effort**

Environmental influences on fishing activities and landings are a well-known natural phenomenon. Calm weather and distinct lunar phases have long been noted for their importance to island fishing culture and individual species reproduction cycles (Johannes, 1981). However, growing evidence suggests that the magnitude of dependence on favorable environmental regimes to maintain landings and fisher profits leads to increased instability as stocks become compromised (Cuetos-Bueno and Hernandez-Ortiz, 2018) In Pohnpei, daily landings were significantly higher during low wind (43% higher) and new lunar phase (50% higher compared with full lunar phase), driven by fishing effort that nearly doubled (the number of trips during low wind speed and new and half-lunar phases days were 47% and 36-38% higher, respectively). The large differences in fishing effort and daily landings with environmental factors highlights high instability in Pohnpei fisheries. Elsewhere, similar instability was also noted among seasons (i.e. wind speed) and lunar phases in Kosrae and Saipan where a smaller amount of reef per human population exists compared to Pohnpei. Meanwhile stable landings were found in Chuuk, characterized by a moderate human presence and a large reef system (Cuetos-Bueno et al., 2018; Houk et al., 2017). Further, seasonal instability was observed to grow through time in both Saipan and Palau where unique temporal datasets exist (Cuetos-Bueno et al., 2018). The findings herein summarize that Pohnpei likely represents a situation in between the observed extremes, whereby landings are moderately driven by both wind and lunar phases, with trends expected to grow through time.

Increased variability in landings even if overall annual landings are maintained has profound implications to societies. Fishers need stable income that is less dependent on seasonal or lunar cycles. Variability in income for fishers, markets and other beneficiaries increases economic uncertainty, and income to support households becomes unreliable. Further, unreliable amounts of fish available for consumption is a concern for island societies with limited supply chains and a high dependence on fishing for food security (Bell et al., 2009; Bell et al., 2018).

Recent fisheries-independent studies in Pohnpei have revealed gradients in fish biomass that closely contrast with fishing access gradients, as reefs with higher biomass were found alongside the north and east coast that is more exposed to trade winds and further away from many popular boat access points on the west coast (Houk et al., 2015). The geographical shifts in fishing effort and stock status reported for Pohnpei have also been recorded elsewhere in Micronesia. Commercial fishing effort around Kosrae, Saipan, and Guam shifted predictably to the exposed reefs during the calm wind periods, a pattern that was linked to higher fish stocks in exposed reefs in comparison with leeward counterparts (Houk et al., 2012; Taylor et al., 2014; Houk et al., 2017; Trianni et al., 2018).

4.4. **Species trends**

Understanding the current status of primary target species within multi-species coral-reef fisheries is essential to maintaining economic, ecological, and social needs. However, traditional stock assessment methods are complex and unrealistic for most tropical nations with limited resources and capacity. Alternatively, this study further explored an established, data-poor approach to assess species and provide management guidance based on: i) the proportional contribution of each species among landings, ii) evidence highlighting the degree of size/age-based truncation associated with density-dependence responses, and iii) the relationship between fishing success and environmental factors.

Pohnpei fish landings were dominated by small-and-medium-sized species within low trophic levels (i.e., herbivores accounted for 57% of landings). These broad trends provided a first sign of fishing-down-the-food-web as mid-and-large species higher in the trophic chain (secondary and tertiary) only accounted for <20% of overall landings by volume. Many of the most frequently landed species exhibited a size/age truncated base upon positively skewed size-frequency distribution (16 species that made up for 43% of overall landings). This suggested that species with strong compensatory density dependence are now becoming dominant, while other larger species higher in trophic level are becoming less common and slowly disappearing from landings.

In addition to evidence of ongoing fishing-down-the-food-web trends and the growing dominance of species with strong density-dependence responses, we also found that favorable catches for many species were dependent upon favorable environmental conditions (six species accounting for 37% of total landings were dependent upon factors like lunar phases for favorable landings). This was another problematic sign for fish stocks, especially for four key species that showed both types of responses (skewness and dependence upon environmental factors). Dependence on environmental factors enhances variability in landings and can eventually lead to localized depletions and spatial stock segregation (Cuetos-Bueno et al., 2019; Rhodes et al., 2018; Taylor et al., 2014).

5. CONCLUSIONS

Overall, our study aligns with previous studies documenting the decline of fisheries resources over the last decades in Pohnpei (Rhodes et al., 2018). The conclusions are that: i) less resilient components of the fishery are becoming rare in modern landings, ii) modern fisheries are dominated by species with higher resilience (high turn-over rates and density-dependence mechanisms), and iii) that while overall landings may be maintained in the medium-term, undesired long-term effects for both ecosystems and fisheries are occurring under the current fisheries regimes.

In addition to providing insights into the potential status of species stocks, the results also provide valuable guidance for tailored management. First, focused management efforts on species that dominate landings provides for opportunities to maximize returns from management given limited capacity and resources of local management agencies. Evidence of density-dependence responses by many dominant species suggests size limits (minimum, maximum, or slots) may be a preferred management policy for those species in order to ensure population replenishment. Alternatively, species whose landings strongly depend on favorable environmental and/or geographical gradients may benefit form area/gear/temporal management policies. Our study further highlights the need to move beyond traditional management approaches in multi-species coral-reef fisheries, as variable species-specific response to fishing pressure and complex inter-species interactions limit effectiveness of traditional approaches (i.e. blanket size limits) and can commit to species replacements (i.e. taxonomic grouping of species), eventually leading to undesired socio-ecological impacts.

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7. **SUPPLEMENTARY MATERIAL**

Hypotheses

- $H0_1$: Biomass of daily fishing landings will not be predicted by lunar, wind, rain, or season.
    - $H0_1$ will be rejected if mixed regression analyses show biomass of daily markets records or catch data are dependent on environment factors.
- $H0_2$: Proportional contribution of daily fish landings is similar for each fishing method.
    - $H0_2$ will be rejected if ANOVA and post-hoc analyses show differences in proportion biomass contribution of fishing landings based upon fishing methods.
- $H0_3$: Fish landings associated with fishing methods that contributed >25% to daily landings will not differ across lunar phases, wind speeds, rainfall, or seasons.
    - $H0_3$ will be rejected if mixed regression analyses show the percent catch biomass by all dominant fishing methods is dependent on environmental factors.
- $H0_4$: The distribution of daily landings or fishing effort across four major geographic sectors will not shift across seasons.
    - $H0_{4:}$ will be rejected if ANOVA or log- linear analyses show spatial differences in daily landings or fishing effort between the windy and calm seasons.

- $H0_5$: For all dominant fishing methods, the proportional contributions of target species that individually contribute to >1% of annual landings will be the same across lunar, wind, rain or season.
    - $H0_5$: will be rejected if mixed regression analyses show differences across lunar, wind, rain or season for target species.
- $H0_6$: For all dominant fishing methods, the size-structure of target species that individually contribute to >1% of annual landings will have a non-skewed distribution.
    - $H0_6$: will be rejected if skewness analyses show skewed size-structures for target species.