COMPARING INTER-ISLAND CONDITION, DETERMINING SPAWNING PATTERNS, AND TESTING ENVIRONMENTAL EFFECTS ON CATCH USING FISH MARKET SURVEY DATA FROM O'AHU AND MAUI (HAWAI'I, USA)

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ABSTRACT

Hawai'i's coral reef fishery is important as fishing provides both sustenance and a sense of community. Yet, Hawai'i's reefs have been depleted, especially in densely human-populated areas. Fish market surveys are important as they can be used to determine fish size and species harvested, and how catch composition differs spatially and temporally. The data used in the current study were from Poseidon Fisheries Research's Hawai'i Biosampling Project in which markets on O'ahu and Maui were surveyed from July 2018 to July 2019.

Length-weight relationships for six fish species show two consistent patterns: i) Maui fishes are generally longer than O'ahu fishes and ii) the larger size classes of O'ahu fishes outweigh Maui fishes. A potential explanation for this finding is the release of interspecific and intraspecific competition on O'ahu due to higher fishing pressure, allowing more food resources per individual fish.

Generalized additive models using moving averages with 95% confidence intervals show relative condition factor can capture spawning patterns on lunar and annual scales. Based on relative condition factor variation, all periods of inferred heightened spawning are associated with the new and full moons, with exact timing varying by species. Most species also have periods of inferred heightened spawning during Months 5 – 8 and some species with a second period during Months 1 – 3. These findings are supported by similarities in relative condition factors with gonadosomatic index patterns and in correspondence to hatch dates. The non-overlapping 95% confidence intervals of the moving averages show that relative condition factor changes significantly throughout the lunar cycle.

Principal component analyses and correlation tests show there are weak environmental relationships with fish count and median length. The number of species and the number of individual fish per species present in the markets are negatively correlated with high wind speed and positively correlated with lunar day. Other principal components for fish count and length indicate an out-of-phase relationship between herbivores and carnivores, with their number and size being negatively correlated. However, fish count and median length are not correlated to each other and differ in their sign of correlation with the environmental variables.

Comparing Inter-Island Condition, Determining Spawning Patterns, and Testing Environmental Effects on Catch Using Fish Market Survey Data from O’ahu and Maui (Hawai’i, USA)

by

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This thesis is submitted in partial fulfillment of the requirements for the degree of Master of Science in Marine Science at Hawai’i Pacific University. We the undersigned have examined this document and have found that it is complete and satisfactory in all respects, and all revisions required by the final examining committee have been made.

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Ch. 1: Hawai'i's Coral Reef Fishery and the Importance of Fish Market Surveys

The Value of Hawai'i's Coral Reef Fishery

Hawai'i's coral reef fishery has substantial commercial and non-commercial value. Between 2009 and 2013, approximately 2 million kilograms of nearshore fish were harvested with a total value between $10 million and $16 million (Grafeld et al. 2017). Nearshore fish catch alone produced 7.7 million meals per year, enough to feed each Hawai'i resident five times (Grafeld et al. 2017). Seafood is the least imported food item in Hawai'i with less than half coming from imports (Geslani et al. 2012).

The fishery also has important social and cultural implications. Fishing is of especially high importance for subsistence as people in Hawai'i consume on average 80% more fish than the U.S. average (Geslani et al. 2012). Aside from food, most non-commercial fishers utilize fishing as an activity for leisure time as well as spend time with family and friends, as about one-third of Hawai'i's 1.4 million residents are classified as fishers (Madge and Williams 2016) with 78% of those fishers sharing their catch with their community. On Kaua'i's north shore, three-quarters of an individual fisher's catch is shared (Vaughan and Vitousek 2013; Madge and Williams 2016). Sharing involves supplying sustenance, provide fish for special ceremonies, and to show gratitude to the elders who taught them the skills to fish, all of which contributes to improving community cohesion (Vaughan and Vitousek 2013).

Strong social, cultural, and substantial aspects of Hawai'i's coral reef fishery make its sustainability a top priority. The fishery prior to Western contact was completely subsistence-based and was kept sustainable with annual catches estimated around 17,000 kg/km^2/yr. based on estimates of the number of people settled in the area and the amount of fish they consumed for over 400 years (McClenachan and Kittinger 2013). Today, catch is estimated to be between 10,000 and 12,000 kg/km^2 /yr. (McClenachan and Kittinger 2013). One reason the fishery was kept sustainable was due to strict site and time-specific regulations with the people's overwhelming compliance given that the consequence for failing to comply with the regulations was capital punishment (Malo 1903).

However, both the commercialization and the abolishment of pre-contact regulations allowed for overexploitation of reef fishes, leaving Hawai'i's reefs vulnerable to overfishing. Overall, Hawai'i's reef fish populations have become heavily depleted (Friedlander et al. 2008), more so in highly populated areas (Friedlander and DeMartini 2002; Williams et al. 2008; Nadon et al. 2015; Friedlander et al. 2017). Catch varies greatly by location, with less catch in heavily populated and touristic areas and more catch in less populated areas (Delaney et al. 2017). Though it is clear the Main Hawaiian Islands (MHI) experience immense fishing pressure, the effects of such fishing pressure on the dynamics of the fishery, for example the size and species of fish being targeted, has been in question. The affect fishing pressure has on individual species is even less known. Species-specific information on fish size and harvest locations is important when assessing the effects of a given level of fishing pressure on different target fish stocks.

The Importance of Surveying Fish in the Markets

Many fish surveys conducted in Hawai'i used in-situ surveying methods, which are useful for determining fish biomass, assemblage structure, standing stock, trophic structure, and species composition of a location, or to make a comparison between multiple locations. For example, Friedlander and DeMartini (2002) compared mean fish biomass in the Northwestern Hawaiian Islands (NWHI) to the MHI and documented lower-level carnivores, herbivores, and apex predators in the NWHI having about 1.5, 2, and 65 times more biomass than in the MHI respectively, which can be attributed to fishing. Multiple studies also focused on correlations with human population density (which was used as a proxy for fishing pressure). Williams et al. (2008) showed that there is a negative correlation between population density near fish survey sites and biomass of targeted species around the MHI, but found that there was little to no effect of density on non-targeted fish species. Williams et al. (2015) investigated potential drivers of changes in fish assemblage and biomass at different islands and atolls throughout the Pacific and found that reef fish biomass was positively correlated with chlorophyll concentration but negatively correlated with human population, suggesting both primary production and fishing are affecting fish stocks. Friedlander et al. (2017) compiled several visual fish census datasets from both the NWHI and MHI to compare biomass between locations and determined reef fish biomass in the NWHI was about six times higher than that of the MHI.

While in-situ surveys give an estimate of fish biomass or community in the environment, fish market surveys can provide information of what fish species, weights, and sizes are being harvested by the fishery. Analysis of fish market data can be used to determine temporal patterns or seasonality in fishery landings and (with life history data) whether a species at a given location is being growth overfished (when fish are harvested before reaching peak growth potential, most likely before maturity as well).

Market surveys have been used to document which species were harvested, which species were preferred based on number of individuals and price, and how the price of individuals in certain species related to the number and size of individuals in the markets. Shellem et al. (2021) used species composition, size distributions, and fish prices of fish markets around the Red Sea to determine which species have higher value and thus more targeted by fishers. They found that more than half of the individuals in the markets consisted of groupers and emperors (families Serranidae and Lethrinidae, respectively), which are large-bodied, carnivorous fishes. It was also found that species with the highest prices were the largest, lowest in abundance, and most individuals in the markets were smaller than the documented size-at-maturity.

Market survey data have also been used to estimate the amount of influence environmental variability has on fishing success. For instance, higher fishing pressure was inferred to be the cause of high influences of environmental variability on fish catch in some regions in Micronesia based on available commercial catch and market data (Houk et al. 2012). It seems the lengths and number of individuals from fish market survey data could reflect some combination of fishing pressure but also current drivers of the fishery, such as fishing success due to optimal weather conditions and accessibility to preferred fishing locations. Therefore, temporal variability in fish market survey data could be a useful diagnostic of fishing pressure on an island scale.

Fish Market Surveys for Hawai'i's Biosampling Project

From July 2018 to July 2019, Poseidon Fisheries Research (Pardee and Wiley 2020) sampled several fish markets on O'ahu and Maui for the purpose of attaining missing life history data for certain species as well as size-at-catch data for the commercial fishery. Over 11,000 fish were sampled weekly for one year at six fish markets: three on O'ahu and three on Maui. Though, it should be noted that sampling on Maui was not as consistent as sampling on O'ahu due to a shortage in surveyors. Surveyors counted the number of fish per species up to 20 individuals and recorded lengths and weights of individual fish.

One major finding was that Maui fishes for five of the main market species had longer mean fork lengths than O'ahu fishes, though the analysis did not include the weights of individual fish. A preliminary examination of fish sizes between O'ahu and Maui shows that for some species included in the data, O'ahu fishes were heavier per given length than Maui fishes. This result leads to question whether O'ahu and Maui fishes grow differently.

Although changes in fish prevalence was not reported on a monthly scale, Pardee and Wiley (2020) observed there were less fish in the markets at certain times, likely in response to bad weather. For instance, the prevalence of *M. grandoculis* in the markets may be related to favorable wind and surf conditions for fishing. This observation suggests weather has a notable influence on species prevalence on a weekly or daily scale. Although it appears that weather may affect fish availability in the markets, it is unknown if it also affects the sizes of the fish harvested. Any significant results regarding the relationship between weather and fish size would be a novel finding.

These market survey data are comparable to the Commercial Marine License (CML) catch data, which is due to most species groups from the market data representing a similar proportion of the total catch weight compared to the CML data (most within a 5% difference) (Figure 1). Therefore, these market survey data are like a representation of the total commercial catch, but on a smaller scale. There was potential for the market survey data to find differences in fish size and abundance of catch by island, environmental conditions, and on the lunar and annual scales.

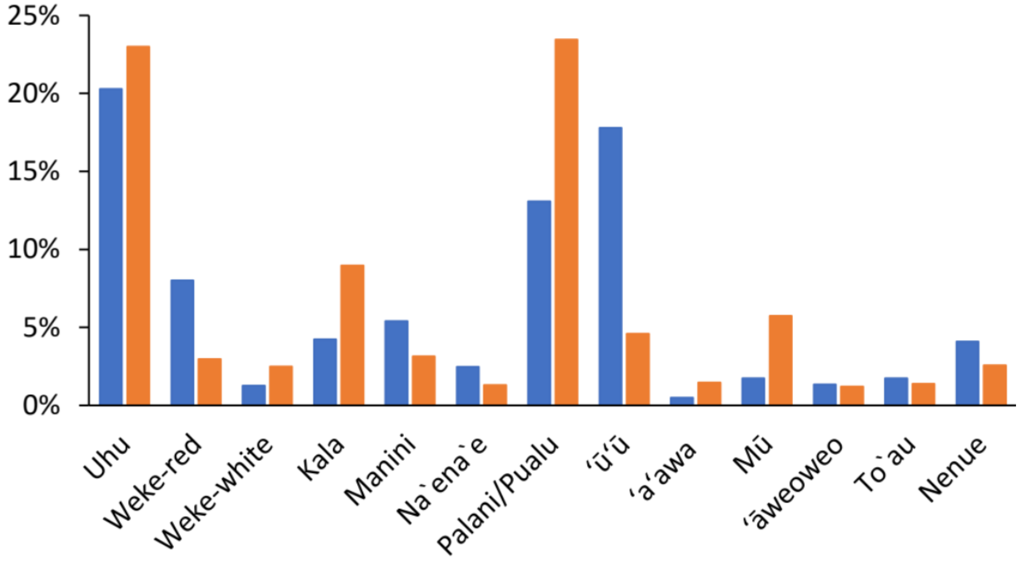

Figure 1. Proportion of catch weight for a single species to the total catch weight for several frequently observed species from the CML data (blue) and market survey data (orange). From Pardee and Wiley (2020).

References

Delaney, D. G., Teneva, L. T., Stamoulis, K. A., Giddens, J. L., Koike, H., Ogawa, T., ... & Kittinger, J. N. (2017). Patterns in artisanal coral reef fisheries reveal best practices for monitoring and management. *PeerJ Preprints*, 5, e3076v1.

Friedlander, A., Aeby, G., Brainard, R., Brown, E., Chaston, K., Clark, A., ... & Wiltse, W. (2008).

The state of coral reef ecosystems of the main Hawaiian Islands. *The state of coral reef ecosystems of the United States and Pacific freely associated states*, 17, 222-269.

Friedlander, A. M., & DeMartini, E. E. (2002). Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. *Marine Ecology Progress Series*, 230, 253-264.

Friedlander, A. M., Donovan, M. K., Stamoulis, K. A., Williams, I. D., Brown, E. K., Conklin, E. J., ... & Walsh, W. J. (2018). Human‐induced gradients of reef fish declines in the Hawaiian Archipelago viewed through the lens of traditional management boundaries. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*(1), 146-157.

Geslani, C., Loke, M., Takenaka, B., & Leung, P. (2012). Hawaiʻi's seafood consumption and its supply sources. *Joint Institute for Marine and Atmospheric Research, SOEST Publication*, 12(01).

Grafeld, S., Oleson, K. L., Teneva, L., & Kittinger, J. N. (2017). Follow that fish: Uncovering the hidden blue economy in coral reef fisheries. *PloS one*, 12(8), e0182104.

Houk, P., Rhodes, K., Cuetos-Bueno, J., Lindfield, S., Fread, V., & McIlwain, J. L. (2012). Commercial coral-reef fisheries across Micronesia: a need for improving management. *Coral Reefs*, 31, 13-26.

Madge, L., & Williams, E. T. (2016). Attitudes and preferences of Hawaii non-commercial fishermen. Volume 1: report from the 2015 Hawaii Saltwater Recreational Fishing Survey. *Pacific Islands Fisheries Center*, 2016.

McClenachan, L., & Kittinger, J. N. (2013). Multicentury trends and the sustainability of coral reef fisheries in Hawaiʻi and Florida. *Fish and Fisheries*, 14(3), 239-255.

Nadon, M. O., Ault, J. S., Williams, I. D., Smith, S. G., & DiNardo, G. T. (2015). Length-based assessment of coral reef fish populations in the Main and Northwestern Hawaiian Islands. *PLoS One*, 10(8), e0133960.

Pardee, C., & Wiley, J. (2020). Hawaii's Bio-Sampling Project, Final Technical Report. Pp. 3-4, 7-10. Western Pacific Regional Fisheries Management Council.

Shellem, C. T., Ellis, J. I., Coker, D. J., & Berumen, M. L. (2021). Red Sea fish market assessments indicate high species diversity and potential overexploitation. *Fisheries Research*, 239, 105922.

Vaughan, M. B., & Vitousek, P. M. (2013). Mahele: sustaining communities through small-scale inshore fishery catch and sharing networks1. *Pacific Science*, 67(3), 329-344.

Williams, I. D., Baum, J. K., Heenan, A., Hanson, K. M., Nadon, M. O., & Brainard, R. E. (2015). Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS One*, 10(4), e0120516.

Williams, I. D., Walsh, W. J., Schroeder, R. E., Friedlander, A. M., Richards, B. L., & Stamoulis, K. A. (2008). Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environmental Conservation*, 35(3), 261-272.

Ch. 2: Comparing Fish Condition Between O’ahu and Maui Using Length-Weight Relationship and Relative Condition Factor

Introduction

The Effects of Fishing Pressure on Fish Populations

Comparing population differences in relation to individual fish length and weight have portrayed the consequences of fishing pressure in the Main Hawaiian Islands (MHI). Higher fishing pressure in the MHI results in lower trophic diversity, overall fish biomass (referring to the total weight of all individual fish, regardless of individual weights) (Friedlander and DeMartini 2002), and smaller fish (shorter lengths) (Nadon et al. 2015) than in the Northwestern Hawaiian Islands (NWHI), where there is no fishing pressure. Fish biomass was up to six times higher in the NWHI than the MHI (Friedlander et al. 2017). However, the comparison between the NWHI and MHI reflect a fished vs. unfished dichotomy instead of a scenario comparing areas experiencing various levels of fishing pressure. Furthermore, it is not clear if fish ‘productivity’ (weight gain per individual fish) or ‘condition’ (health of an individual fish based on its weight) vary as a function of fishing pressure between greater and lesser-fished areas. Therefore, comparing variation in productivity and condition between islands with different levels of fishing pressure could potentially be used to indicate the ecological consequences of harvesting.

Smaller differences in biomass can be found within the MHI as well. Fish biomass within the MHI was negatively correlated to human population density, which was a proxy for fishing pressure (Williams et al. 2008; Williams et al. 2015; Friedlander et al. 2017), with remote and inaccessible areas having double the mean fish biomass of accessible and populous areas (Williams et al. 2008). In addition, target fish biomass, ‘prime spawner’ (defined as fish >70% the maximum length) biomass, and ‘prime spawner’ richness were two to three times greater in remote and inaccessible areas than accessible and populous areas (Williams et al. 2008). Since there was no relationship between population density and non-target species biomass (Friedlander et al. 2017), fishing was likely the main influencer of differences in target species biomass. Other effects such as pollution, runoff, and habitat loss can be ruled out since all species, regardless of being targeted by fishers, would be negatively affected.

While biomass can be a useful tool when monitoring fish stocks, biomass alone can be misleading as two locations may record the same amount of biomass, yet have different size classes and individual fish numbers. From the fish market data (Pardee and Wiley 2020), there were about six times as many manini (*Acanthurus triostegus sandvicensis*) from O’ahu surveyed as there were from Maui. Yet, mean weight for Maui manini was higher than that of O’ahu manini (182 g to 158 g respectively). Using biomass to compare O’ahu and Maui market landings also does not consider the lengths and weights of individual fish from each island.

Nadon et al. (2015) demonstrated how size classes in a stock are altered from various levels of fishing pressure. Although there was no correlation between human population density and average length, there was a negative correlation for a select group of species (*Parupeneus porphyreus*, *Aprion viscerens*, and *Caranx ignobilis*). Kūmū (*P. porphyreus*), uku (*A. viscerens*), and ulua aukea (*C. ignobilis*) are part of a group of known food and sport fishes in Hawai’i. These species also had lower average lengths and higher fishing mortality in O’ahu, the island with the largest population, than the other islands. The value of fishery-targeted species, along with the lack of effect of population density on non-target species, suggests the size differences of the target species are related to fishing pressure.

One case in the Line Islands showed non-piscivorous fishes being larger in populous areas and smaller in less-populous, remote areas. DeMartini et al. (2008) found that larger non-piscivorous fishes (e.g. herbivores, planktivores) can be observed, counterintuitively, around islands with higher human populations. Tabuaeran, one of two of majorly populous atolls, was found to have a greater median length of larger non-piscivorous fishes than any other less populous atoll. It was suggested the difference in herbivore lengths was due to high harvest selectivity for piscivores, as piscivores around the populous atolls had less biomass and smaller fish. The removal of large piscivores allowed non-piscivorous fishes to grow with less inhibition from predation. There is a possibility for larger non-piscivorous fishes to occur in areas with less predators. If so, this phenomenon would obviously be seen in areas of high fishing pressure and a strong preference for piscivores.

Length-Weight Relationship and Relative Condition Factor as Measurements of Fish Condition

Fish condition refers to the weight of an individual fish with respect to its length, but can also be used to represent an average for a stock and can be compared with conditions of other stocks during a point period when subjected to the same length-weight relationship (Froese 2006). Understanding condition can improve our understanding of the effect of environmental variability on the health of individual fish, which in turn can reflect the nutritional gain of the stock. While biomass and trophic diversity are well studied and can reflect fishing pressure, the concept of fish condition has not been frequently used in the MHI thus it is not clear how fish condition varies throughout the MHI and which factors impact it the most.

The Length-Weight Relationship (LWR) is a widely utilized method in fisheries science and can be used for determining condition, with heavier fish at a given length being in 'better condition' (Froese 2006). The LWR has several uses, including predicting both individual weight and overall biomass based on length data as well as comparing life history and morphology of populations from different regions (Petrakis and Stergiou 1995). Its equation is as follows:

$$W = aL^b, \tag{1}$$

with L being the observed length of a fish, W being the fish's predicted weight at its length, and *a* and *b* being parameters.

LWRs can also be expressed as the Relative Condition Factor (RCF), which uses this equation:

$$K = \frac{W}{aL^b} \times 100, \tag{2}$$

with K being the relative condition factor, W and L being the weight and length of an individual fish, and a and b being the parameter values determined by the corresponding LWR of the reference population. The factor of 100 centers the RCF around 1. RCFs are typically used to compare an individual fish's weight to the mean weight at a given length (Froese 2006). RCF < 1 means the individual fish is in 'worse' condition than normal and RCF > 1 being the fish is in 'better' condition.

The objective for this analysis was to compare the condition of coral reef fishes by species between O'ahu and Maui. Reasoning for this analysis was that although Pardee and Wiley (2020) found fishes of the most frequented species in the markets were longer on Maui than O'ahu, preliminary findings shown O'ahu fishes for some species were heavier per given length than Maui fishes. Fishes from one island that accumulate more weight with length would be heavier per given length and have a higher RCF than fishes from the other island.

Methods

Length-Weight Relationships

LWRs were calculated and compared for each species by island. Only species that had at least 20 individuals from both islands were used for this analysis. O'ahu fishes smaller than the smallest Maui fish were then omitted and excluded from the LWR. Excluding these fishes reduced the noise from having a disproportionally greater number of small fishes than large fishes. After omitting O'ahu fishes smaller than the smallest Maui fish, 4278 (Table 1 Final n) out of 6110 (Table 1 Initial n) fishes were used to calculate LWR relationship equations.

The data for the selected species were grouped by island, then *a* and *b* were calculated for each group independently using a linear regression model:

$$\log W = b \log L + \log a, \tag{3}$$

in which *b* is the slope of the line and *a* is 10 raised to the power of the y-intercept. The data were plotted by island along with their respective LWR curves. LWR logarithmic forms were also plotted for 95% confidence intervals as evidence for significant difference.

Mean Relative Condition Factors

Mean or median RCFs were calculated using a shared LWR for both islands. A new LWR that accounts for all fishes from both islands was calculated. RCF for each fish was then calculated using the observed weight and length, and the *a* and *b* from the shared LWR (Equation 2). RCFs for each species were tested for normality using the Shapiro-Wilk test. Species with normal data used mean RCF and t-test to test for significance while species with non-normal data used median RCF and the Wilcoxon signed-rank test. α was corrected for multiple hypothesis testing from 0.05 to 0.008, using the number of tests performed.

Results

Summary Statistics

The key parameters from six species observed in the fish markets used for this analysis are as shown in Table 1. The parameters are presented in subsets for each species by each island and each subset has a length range, weight range, median length, predicted weight at O’ahu and Maui median lengths, and the *a* and *b* parameter values.

Removal of O’ahu fishes smaller than the smallest Maui fish greatly reduced the number of individuals eligible for analysis. The number of O’ahu individuals was reduced by more than 50% for two species (*M. vanicolensis* – 70%, *N. lituratus* – 64%), but less than that amount for other species (Table 1). Even with the truncation of O’ahu fish samples, some species had as many as 10 times the amount of data for O’ahu as for Maui.

Length-Weight Relationship Comparison

LWR analysis between O’ahu and Maui fishes shows that although Maui fishes have longer mean lengths, O’ahu fishes are predicted to outweigh Maui fishes at any given length. This separation of weight is prominent at larger size classes and the margin increases with length for 5 of the 6 species. The maximum for the Maui fish length distribution exceeds that of the O’ahu fish length distribution for four of the seven species (except *A. triostegus*, *A. dussumieri*, and *M. flavolineatus*) (Figure 2). Given *A. triostegus*, *A. dussumieri*, and *M. flavolineatus* had more O’ahu fish than Maui fish, the reason for these species having higher range maximums for O’ahu than Maui is because there were many more O’ahu fish sampled than Maui fish, thus revealing a broader length distribution.

The best-fit lines for O’ahu and Maui fishes intersect at a certain length (*A. triostegus*: ~ 198 mm at 228 g, *L. kasmira*: ~ 216 mm at 203 g, *M. flavolineatus*: ~ 249 mm at 284 g, *M. vanicolensis*: ~ 229 mm at 242 g, *N. lituratus*: ~ 252 mm at 394 g) (Figure 2), meaning O’ahu and Maui fishes at this length theoretically have the same average weight. However, at longer lengths, O’ahu fish weights become heavier than Maui fish weights for four of the six species

(Figure 2). O’ahu fish weights are heavier than Maui fish weights at both Maui and O’ahu median lengths for all species except *A. triostegus* and *M. vanicolensis* (Table 1), but it should be noted that the O’ahu fishes for these species are still heavier than the Maui fishes at larger size classes. The difference in weight per given length at larger size classes is also greater in the carnivorous species (*L. kasmira*, Figure 2C; *M. flavolineatus*, Figure 2D; *M. vanicolensis*, Figure 2E) than in the herbivorous species (*A. triostegus*, Figure 2A; *A. dussumieri*, Figure 2B; *N. lituratus*, Figure 2F) as the largest differences for herbivores is 150 g and 200 g for carnivores. An exception to this pattern is with *A. dussumieri*, in which the distance between the two curves shrinks at larger size classes (Figures 2 & 3). The curve of *A. dussumieri* is likely driven by large quantities of smaller fish as well as the lack of larger fish from Maui.

LWRs for Maui fishes had smaller *b* values and smaller *a* values than those for O’ahu fishes for most species (except *A. dussumieri*), which reflects O’ahu fishes outweighing Maui fishes per given length at larger size classes (Table 1, Figure 3). Prior analysis including the smaller O’ahu fishes showed large differences in *a* values, suggesting that *a*, the predicted weight at theoretical length 0 (the y-intercept), may have been influenced by an abundance of smaller O’ahu fishes or lack thereof from Maui. Though it is not clear how *a* values would vary with the addition of smaller Maui fishes. Maui having larger *a* values than O’ahu indicate Maui fishes potentially outweighing O’ahu fishes at smaller size classes. However, due to an overlap in confidence intervals before the intersection of the best-fit lines (Figure 3), it cannot be concluded that there are differences in weight per given length between O’ahu and Maui fishes at smaller size classes. Though regardless of the values of *a*, because O’ahu fishes were represented with higher *b* values (the best-fit lines for O’ahu fishes were steeper), O’ahu fishes would eventually outweigh Maui fishes per given length after some length (where the best-fit lines intersect). *A. dussumieri* is the only exception whereby Maui fish have a smaller *a* value and larger *b* value than O'ahu fish (Table 1) and are generally predicted to outweigh Maui fish per given length (Figure 2).

Table 1. Key parameters from seven species observed in fish markets on both O'ahu and Maui that are related to length-weight relationships. Parameters for each species are given by island. *Final n* is defined as the number of individuals used for analysis after omitting outliers and O'ahu fish smaller than the smallest Maui fish. R^2 values are derived from the linear regression models used to find *a* and *b*. All p-values are < 0.001. TG = Trophic Guild; LR = Length Range; WR = Weight Range; PW = Predicted Weight; ML = Median Length

Species	**TG**	**Island**	**Initial n**	**Final n**	**LR (mm)**	**WR (g)**	**O'ahu ML (mm)**	**Maui ML (mm)**	**PW at O'ahu ML (g)**	**PW at Maui ML (g)**	**a (x10^{-5})**	**b**	**R^2**
A. triostegus (Convict Tang, Manini)	Herb.	O'ahu	1098	946	153 – 219	70 – 303	174		156	172	3.63	2.96	0.88
		Maui	158	153	153 – 215	100 – 310		180	163	178	25.7	2.59	0.73
A. dussumieri (Dussumier's Surgeonfish, Palani)	Herb.	O'ahu	272	254	245 – 441	390 – 2294	328		992	1056	3.98	2.94	0.96
		Maui	43	43	245 – 452	350 – 2450		335	876	935	1.86	3.05	0.93
L. kasmira (Blue stripe Snapper, Ta'ape)	Pisc.	O'ahu	1326	822	196 – 287	90 – 489	214		197	380	1.00	3.13	0.88
		Maui	85	85	196 – 335	140 – 730		264	197	355	5.89	2.80	0.81
M. flavolineatus (Yellow stripe Goatfish, Weke 'a)	Bent.	O'ahu	577	312	220 – 338	158 – 725	260.5		327	332	1.12	3.09	0.93
		Maui	40	39	220 – 320	210 – 460		262	313	317	200	2.15	0.82
M. vanicolensis	Bent.	O'ahu	1115	330	197 – 275	100 – 442	207		177	232	1.17	3.10	0.84

(Yellowfin Goatfish, Weke Ula)		Maui	107	106	197 – 278	150 – 410		226	187	234	24.5	2.54	0.74
N. lituratus (Orange spine Unicorn fish, Umaumalei)	Herb.	O'ahu	125	45	214 – 297	190 – 666	244		357	426	1.02	3.16	0.86
		Maui	39	39	214 - 345	260 - 900		258	363	420	19.1	2.63	0.95

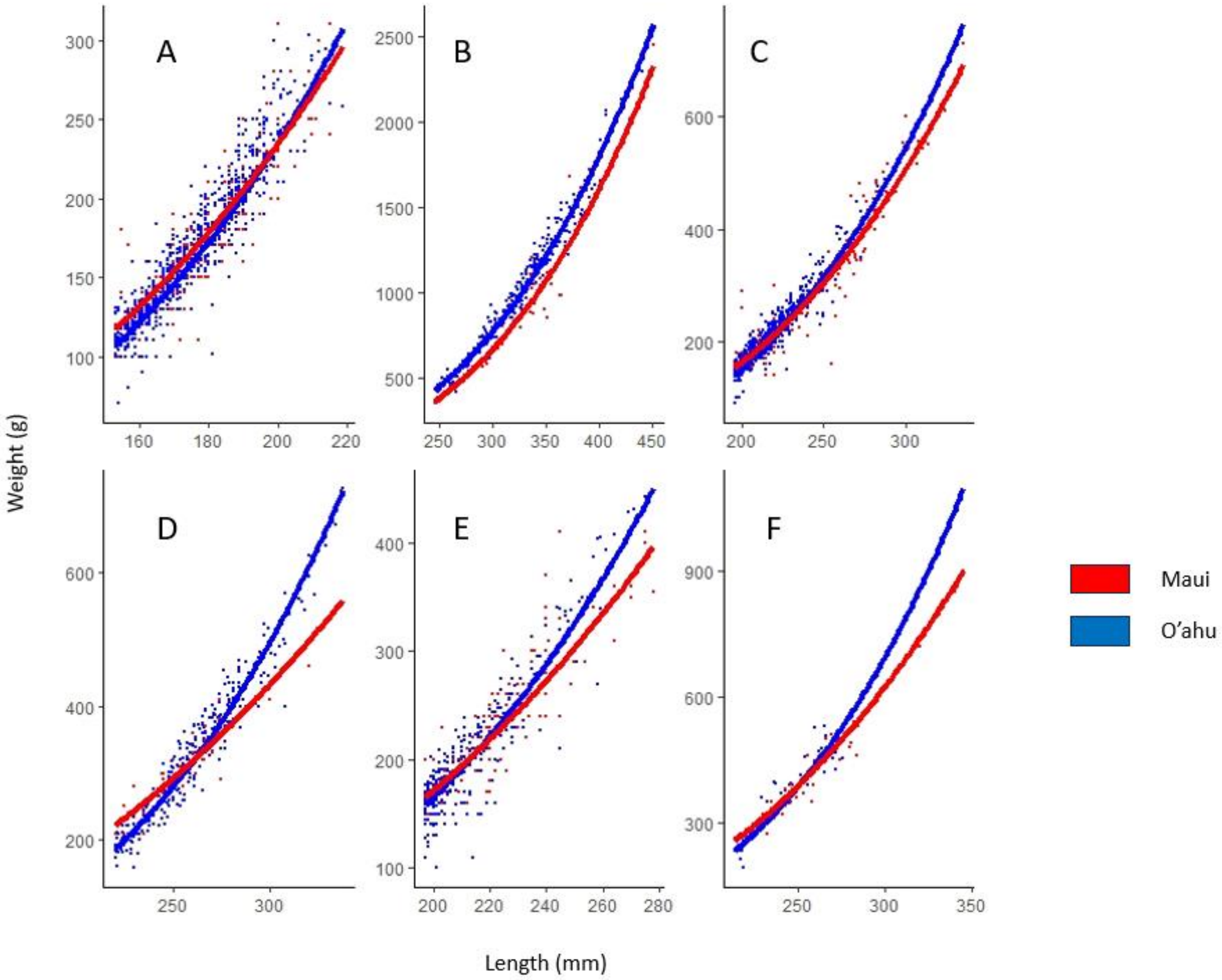

Figure 2. Length-weight curves for six species observed in fish markets on both O'ahu (blue) and Maui (red): (a) *Acanthurus triostegus*, (b) *Acanthurus dussumieri*, (c) *Lutjanus kasmira*, (d) *Mulloidichthys flavolineatus*, (e) *Mulloidichthys vanicolensis*, and (f) *Naso lituratus*. Plots are not scaled equally.

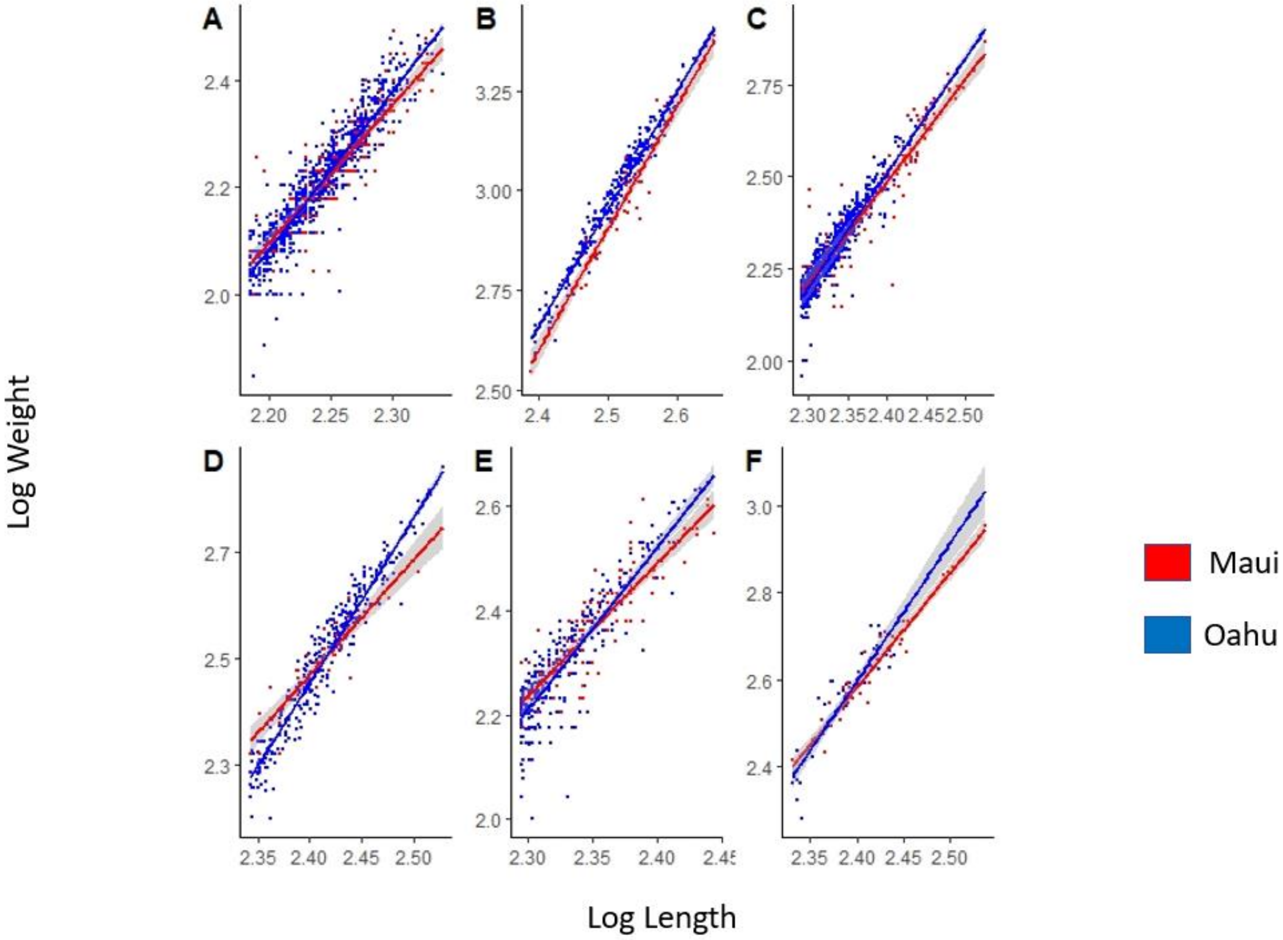

Figure 3. Logarithmic length-weight plots for six species observed in fish markets on both O'ahu (blue) and Maui (red): (a) *Acanthurus triostegus*, (b) *Acanthurus dussumieri*, (c) *Lutjanus kasmira*, (d) *Mulloidichthys flavolineatus*, (e) *Mulloidichthys vanicolensis*, and (f) *Naso lituratus*. The shaded area around the lines represents the range of the 95% confidence interval. Plots are not scaled equally.

Inter-Island Relative Condition Factor Comparison

In order to test for a difference in RCF between islands, a shared LWR among all fishes was calculated and used as the basis fo RCF estimations. O'ahu fishes had higher RCF values for 5 of the 6 species and thus are in better condition than Maui fishes (Table 2). RCF data for four species were not normally distributed and were tested with the Wilcoxon Signed Rank test, while a t-test was used for two species with normally distributed RCF data (Table 2). Means were used in the t-tests and medians were used in Wilcoxon tests. Mean or median RCF was signiicantly different between O’ahu and Maui, by which p-values were less than 0.05, with three being less than 0.001, for all except the two goatfish species, *M. flavolineatus* and *M. vanicolensis* (Table 2). *A. triostegus*, *A. dussumieri*, *L. kasmira*, and *N. lituratus* retained significance after correcting for multiple hypothesis testing (Bonferroni Correction, new α = 0.008). However, it should be noted that goatfishes *M. flavolineatus* and *M. vanicolensis* do have the largest differences in weight per given length in the larger size classes, but that most of the individuals lie in the smaller size classes where the difference in weight per given length is reduced. Therefore, the reason that the median RCFs for *M. vanicolensis* and *M. flavolineatus* are not different between O’ahu and Maui fishes may be due to the lack of large Maui fish rather than O’ahu and Maui fishes having similar weights per given length.

Table 2. Results of the Spatial Relative Condition Factor comparison between O’ahu and Maui for seven species observed in fish markets on both islands. A t-test was used for species with normal distributions and a Wilcoxon signed-rank test was used for species with non-normal distributions. Mean RCF is displayed for species that used the t-test and median RCF for those that used the Wilcoxon test. Mean or median values are followed by lower and upper 95% confidence values in (). *** indicates species with a significant difference in RCF between islands after correcting for multiple hypothesis testing.

Species	**Statistical Test Used**	**Mean/Median Maui RCF**	**Mean/Median O’ahu RCF**	**Test Statistic**	**p-value**
*A. triostegus****	Wilcoxon	98.9 (97.8, 99.1)	102.9 (102.4, 103.4)	60238	< 0.001
*A. dussumieri****	Wilcoxon	89.7 (86.8, 96.2)	101.7 (100.4, 102.7)	2280	< 0.001
*L. kasmira****	Wilcoxon	93.1 (89.4, 96.8)	100.4 (99.8, 101.0)	21706	< 0.001
M. flavolineatus	t-test	98.7 (94.0, 101.5)	97.8 (96.9, 98.6)	0.5535	0.583
M. vanicolensis	Wilcoxon	102.3 (99.7, 105.1)	105.8 (104.5, 107.3)	15332	0.056
*N. lituratus****	t-test	95.5 (92.7, 98.2)	101.3 (98.3, 104.3)	-2.850	0.006

Discussion

Why Would O’ahu Fishes Outweigh Maui Fishes per Given Length?

There are multiple possibilities for O’ahu fishes being in better condition and outweighing Maui fishes per given length. Sea surface temperature (SST) was thought to influence growth and weight gain along a latitudinal gradient, but there is no such gradient for nearshore waters. Release of interspecific and intraspecific competition and predation are more suitable explanations for O’ahu fishes outweighing Maui fishes per given length. There is density dependence for the study species as individuals usually travel and feed in groups for these species and that coral reefs provide limited space for residency and resources. Higher fishing pressure on O’ahu would reduce density dependence for O’ahu fishes since more individuals are removed.

One possible reason is that differences in SST around the islands may affect the growth rate, which would affect weight gain, for fishes and is independent of fishing pressure. *Cephalopholis argus* were found to grow slower and weigh more per given length in the northern islands, and the northern areas of the islands, than in the southern islands and the southern areas of the islands (with the exception of South Kona) (Donovan et al. 2013). Donovan et al. suggested this difference in growth and weight is due to cooler SSTs in the north. However, any effects caused by a north-south gradient would likely occur in the open ocean and not in coastal waters where a windward-leeward gradient is dominant (Figure 4). SST around the MHI has a windward-leeward gradient in which windward waters are cooler while leeward waters are warmer (Figure 4). This pattern is consistent for all islands except for those in the lee shadow of another island. Also, since Maui fishes are shorter than O’ahu fish at a given age (Donovan et al. 2013), one would expect Maui fishes to weigh more per given length than O’ahu fishes. It is unlikely for SSTs to be a major factor in explaining weight per given length between these two islands, but it can potentially explain any differences between fishes on different sides of one island (such as windward vs. leeward).

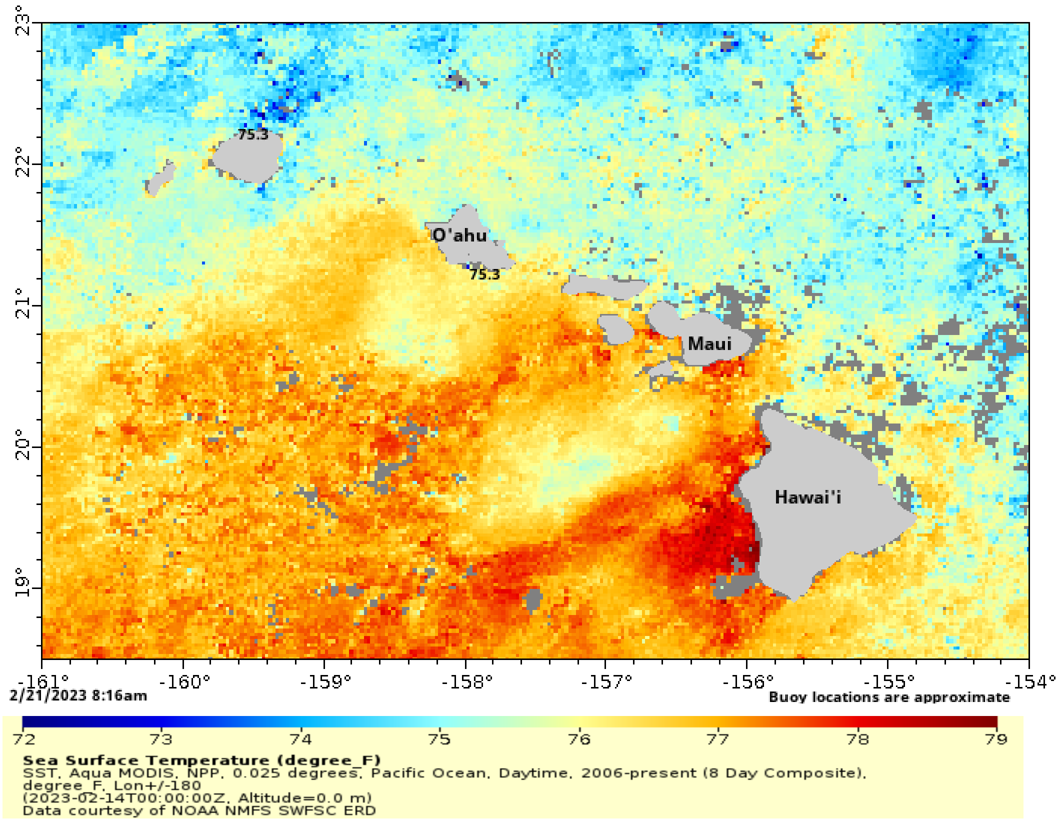

Figure 4: From Swell Matrix, which uses data from NOAA’s buoys around Hawai’i. 8-day composite SSTs of nearshore and offshore waters surrounding the MHI from 2006 to 2023.

Another reason may be from a release of interspecific or intraspecific competition due to removal of individual fishes via fishing. Greater removal of individual fishes on O’ahu would increase food availability per fish. Fishing pressure is known to be higher on O’ahu than on Maui as from 2004 – 2013 mean annual commercial catch for O'ahu was 4.5 times higher than for Maui (levels of fishing pressure have likely not changed since then) (Williams et al. 2008, McCoy et al. 2018). Larger fishes from Maui also show that there is less fishing pressure on Maui than on O'ahu (Nadon et al. 2015, Figure 2). Since Maui experiences less fishing pressure, there are more, longer individual fishes present, resulting in less food available per individual fish because there is more competition. Therefore, weight gain for Maui fish could have greater limitations due to less food being available per individual fish. Though to consider competitive release possibilities, fish diets must be clarified to confirm the assumption that species involved in the present study consume the same resources for competition to exist.

The Relationship Between Diet, Feeding, and Food Source Availability

It is important to know the diets of these fishes to understand the role of food source availability to competition. Over half of the diets of *A. triostegus* and *A. dussumieri* consist of red (Rhodophyta) and turf algae and about half of the *N. lituratus* diet are both brown (Ochrophyta), red, and turf algae (Nalley et al. 2022a; Nalley et al. 2022b; Kelly et al. 2016). Polycheate worms make up for almost the entire *M. flavolineatus* diet while portnid crabs were dominant in *M. vanicolensis* guts (polychaete worms were the third most common prey for *M. vanicolensis*) (Sorden 1982; Kolasinski et al. 2009; Schumacher 2011)*.* *L. kasmira* consumes a variety of prey items, but decapod shrimps and fish larvae were the most dominant (DeFelice and Parrish 2003; Schumacher 2011; Mablouke et al. 2013).

The species' trophic level may be a factor towards the magnitude in the difference in weight per given length between their groups from O'ahu and Maui. It was noted that the herbivores (*A. triostegus*, *A. dussumieri*, and *N. lituratus*) have less difference in weight per given length than the carnivores (*L. kasmira*, *M. flavolineatus*, and *M. vanicolensis*). Turf algae are abundant on coral reefs and are fast-growing (Kelly et al. 2016). Furthermore, the shape of the jaws and teeth, as well as the feeding motion of surgeonfishes make it difficult for fishes to completely remove algae on a natural surface (Purcell and Bellwood 1993; Schumacher et al. 2008) and leaves room for greater algal primary production (Carpenter 1986). Therefore, herbivorous fishes are not likely to be as food-limited as more algae-rich areas are available once one is outgrazed. High algal abundance, though, does not reduce competition between herbivores as there would still be more food per fish after many individuals are removed, but can explain why the herbivores have less difference in weight per given length than the carnivores.

Interspecific Competitive Release

Interspecific competitive release related to fishing of highly-targeted species has been documented to cause increases in standing stock and biomass of less-targeted and non-targeted species alike. Competitive release has been suggested to explain a decrease in standing stock of lesser-targeted small-bodied piscivores from Kiritimati and Tabuaeran, the most human-populated atolls, to Kingman and Palmyra, the least human-populated populated atolls, in the Line Islands (DeMartini et al. 2008). An increase in biomass of non-targeted elasmobranchs coinciding with a decrease of highly-targeted demersal fishes from fishing along Georges Bank was thought to be the result of reduced competition for common food sources (Fogarty and Murawski 1998).

There may be interspecific competitive release among the herbivorous species with the mass removal of *A. triostegus* benefitting *A. dussumieri* and *N. lituratus*. Since *A. triostegus* can appear in vast schools (Nalley et al. 2022b), they are more likely harvested (and thus be found in the markets) in greater numbers than species that gather in smaller groups or are solitary, such as *A. dussumieri* and *N. lituratus*. *A. triostegus* also having the least difference in weight per given length (Figure 1) and condition (Table 2) of the three herbivores shows that this species may be responsible for influencing food allocation rather than it being influenced due to their vast numbers. If food were allocated amongst the three species equally, they would have proportionaly equal differences in weight per given length and conditon. Though in slight contrast with what has been documented in the literature, all three species are highly-valued food fishes and are impacted by fishing to an extent. It would be impossible for *A. dussumieri* and *N. lituratus* to increase overall biomass or standing stock because of intense fishing pressure. However, removing many *A. triostegus* individuals may have allowed faster weight gain for *A. dussumieri* and *N. lituratus* individuals on O’ahu in a short period of time, creating larger differences in weight per given length and condition.

Intraspecific Competitive Release

Intraspecific competitive release means there are less individuals in one species consuming the same resource. Growth rate of two coral reef goby species, *Coryphopterus glaucofraneum* and *Gnatholepis thompsoni*, decreased with increasing conspecific density (Forrester et al. 2006). Forrester et al. also found that growth also decreased with increasing heterospeciality but was degrees lower than that of increasing conspecific density, suggesting intraspecific competition has a larger role in resource allocation than interspecific competition. Arctic char in Norway were found to have increased food consumption (which would lead to weight gain) and somatic growth rates after a reduction in population density from large-scale density manipulation (Amundsen et al. 2007). Amundsen et al. observed an increase in food consumption and growth rate once Arctic char were removed and found that both food consumption and growth rate are negatively correlated with population density. It is entirely possible that O’ahu fishes have undergone intraspecific competitive release after major harvesting, resulting in more food being available per individual fish on O’ahu than on Maui. More food for O’ahu fishes would allow them to gain weight faster than fishes on Maui.

In the presence of intraspecific competition, some fish will have a competitive advantage over others, even if every individual in the stock have similar phenotypic characteristics (Ward et al. 2006), which would result in these fish being slightly larger. Differences in competitive ability, in which indiviudals would be similar in size, decrease with increasing group size (Tregenza et al. 1996; Humphries et al. 1999), but the results of the present study do not reflect these findings. There are a few individuals that are heavier per given length than the majority of fishes from Maui for all species and O’ahu fishes are more similar in weight per given length

(Figure 1). It would be difficult to determine whether there is intraspecific competitive release based on length alone because there were less Maui fishes at larger size classes. Reasons for less large Maui fishes could be 1) only a handful of individuals being larger, or 2) less fish were surveyed from Maui overall. In areas with lower fishing pressure, one would assume that a single-species mass harvest would contain many indviduals of similar size but a few (the 'better competitors') would be larger. However, with a release of intraspecific competition from high fishing pressure, many individuals, including the 'better competitors,' may be removed. Intense fishing may equalize the opportunity for fishes to obtain food, thus allowing indiviudals to be similar in weight per given length.

O'ahu having about 2.5 times as much recreational catch and about 5 times as much commercial catch as Maui (McCoy et al. 2018) means there were likely more individual fishes removed from O'ahu than Maui. The data used in the present study are a representation of the number of individuals commercially harvested since it is similar to the Commercial Marine License data (data of commercial catch in Hawai'i) (Pardee and Wiley 2020).

Predatory Release

Fishes from lower trophic levels may be allowed to gain weight at a higher rate after mass removal of apex predators, causing predatory release. Biomass for non-piscivorous fishes from Kiritimati and Tabuaeran exceed that of Kingman and Palmyra as well as within Kiritimati with biomass decreasing farther from the most human-populated areas (DeMartini et al. 2008). The explanation for this finding was that primary consumers around Kiritimati and Tabuaeran were released from predation due to intense fishing for apex predators, allowing the lower trophic fishes to grow and gain weight with reduced predation risk. Maui generally has a higher apex predator biomass than O'ahu likely because of lower fishing pressure on Maui (Williams et al. 2008). With less apex predators around O'ahu, O'ahu fishes may be able to gain weight at a higher rate than Maui fishes because O'ahu fishes can divert time used for evading and hiding from predators to feeding.

Conclusion

O'ahu fishes may be in better condition and outweigh Maui fishes per given length from a release in interspecific and intraspecific competition caused by fishing, which means O'ahu reefs are capable of supporting more fish biomass but is repressed by heavy fishing.

SST may explain differences between the windward and leeward sides within an island, but is unlikely to explain difference between coastal areas around northern and southern islands. Confirming windward and leeward differences will require information on the locations where fish are harvested, which can be gathered through commercial catch data and fisher interviews.

References

Amundsen, P. A., Knudsen, R., & Klemetsen, A. (2007). Intraspecific competition and density dependence of food consumption and growth in Arctic charr. *Journal of Animal Ecology*, 149-158.

Carpenter, R. C. (1986). Partitioning herbivory and its effects on coral reef algal communities. *Ecological monographs*, *56*(4), 345-364.

DeFelice, R. C., & Parrish, J. D. (2003). Importance of benthic prey for fishes in coral reef-associated sediments. *Pacific Science*, *57*(4), 359-384.

DeMartini, E. E., Friedlander, A. M., Sandin, S. A., & Sala, E. (2008). Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific. *Marine Ecology Progress Series*, *365*, 199-215.

Donovan, M. K., Friedlander, A. M., DeMartini, E. E., Donahue, M. J., & Williams, I. D. (2013). Demographic patterns in the peacock grouper (*Cephalopholis argus*), an introduced Hawaiian reef fish. *Environmental biology of fishes*, *96*, 981-994.

Fogarty, M. J., & Murawski, S. A. (1998). Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecological Applications*, *8*(sp1), S6-S22.

Forrester, G. E., Evans, B., Steele, M. A., & Vance, R. R. (2006). Assessing the magnitude of intra- and interspecific competition in two coral reef fishes. *Oecologia*, *148*, 632-640.

Friedlander, A. M., & DeMartini, E. E. (2002). Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. *Marine Ecology Progress Series*, *230*, 253-264.

Friedlander, A. M., Donovan, M. K., Stamoulis, K. A., Williams, I. D., Brown, E. K., Conklin, E. J., ... & Walsh, W. J. (2017). Human-induced gradients of reef fish declines in the Hawaiian Archipelago viewed through the lens of traditional management boundaries. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*(1), 146-157.

Froese, R. (2006). Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. *Journal of applied ichthyology*, *22*(4), 241-253.

Humphries, S., Metcalfe, N. B., & Ruxton, G. D. (1999). The effect of group size on relative competitive ability. *Oikos*, 481-486.

Kelly, E. L., Eynaud, Y., Clements, S. M., Gleason, M., Sparks, R. T., Williams, I. D., & Smith, J. E. (2016). Investigating functional redundancy versus complementarity in Hawaiian herbivorous coral reef fishes. *Oecologia*, *182*, 1151-1163.

Kolasinski, J., Frouin, P., Sallon, A., Rogers, K., Bruggemann, H. J., & Potier, M. (2009). Feeding ecology and ontogenetic dietary shift of yellowstripe goatfish *Mulloidichthys flavolineatus* (Mullidae) at Reunion Island, SW Indian Ocean. *Marine Ecology Progress Series*, *386*, 181-195.

Mablouké, C., Kolasinski, J., Potier, M., Cuvillier, A., Potin, G., Bigot, L., ... & Jaquemet, S. (2013). Feeding habits and food partitioning between three commercial fish associated with artificial reefs in a tropical coastal environment. *African Journal of Marine Science*, *35*(3), 323-334.

McCoy, K. S., Williams, I. D., Friedlander, A. M., Ma, H., Teneva, L., & Kittinger, J. N. (2018). Estimating nearshore coral reef-associated fisheries production from the main Hawaiian Islands. *PloS one*, *13*(4), e0195840.

Nadon, M. O., Ault, J. S., Williams, I. D., Smith, S. G., & DiNardo, G. T. (2015). Length-based assessment of coral reef fish populations in the Main and Northwestern Hawaiian Islands. *PLoS One*, *10*(8), e0133960.

Nalley, E. M., Donahue, M. J., Heenan, A., & Toonen, R. J. (2022a). Quantifying the diet diversity of herbivorous coral reef fishes using systematic review and DNA metabarcoding. *Environmental DNA*, *4*(1), 191-205.

Nalley, E. M., Donahue, M. J., & Toonen, R. J. (2022b). Metabarcoding as a tool to examine cryptic algae in the diets of two common grazing surgeonfishes, *Acanthurus triostegus* and *A. nigrofuscus*. *Environmental DNA*, *4*(1), 135-146.

Pardee, C., & Wiley, J. (2020). Hawaii's Bio-Sampling Project, Final Technical Report. Pp. 3-4, 7-10. Western Pacific Regional Fisheries Management Council.

Petrakis, G., & Stergiou, K. I. (1995). Weight-length relationships for 33 fish species in Greek waters. *Fisheries research*, *21*(3-4), 465-469.

Purcell, S. W., & Bellwood, D. R. (1993). A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). *Environmental Biology of Fishes*, *37*, 139-159.

Schumacher, B. D. (2011). Habitat use and trophic ecology of the introduced snapper *Lutjanus kasmira* and native goatfishes in Hawaii (Doctoral dissertation, [Honolulu]: [University of Hawaii at Manoa], [August 2011]).

Schuhmacher, H., Krone, R., & van Treeck, P. (2009). Underestimated Eroder among Reef Fishes Experimental Comparison between *Ctenochaetus striatus* and *Acanthurus nigrofuscus* (Acanthuridae). In *Proceedings of the 11th International Coral Reef Symposium, Ft. Lauderdale, Florida July 2008 Session number 10.* (Vol. 7).

Sorden, C. T. (1982). Trophic relationships of goatfishes (family Mullidae) in the Northwestern Hawaiian Islands. University of Hawai'i at Manoa.

Tregenza, T., Hack, M. A., & Thompson, D. J. (1996). Relative competitive success of unequal competitors changes with overall density. *Oikos*, 158-162.

Ward, A. J., Webster, M. M., & Hart, P. J. (2006). Intraspecific food competition in fishes. *Fish and Fisheries*, *7*(4), 231-261.

Williams, I. D., Baum, J. K., Heenan, A., Hanson, K. M., Nadon, M. O., & Brainard, R. E. (2015).

Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS One*, *10*(4), e0120516.

Williams, I. D., Walsh, W. J., Schroeder, R. E., Friedlander, A. M., Richards, B. L., & Stamoulis, K. A. (2008). Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environmental Conservation*, *35*(3), 261-272.

Ch. 3: Using Relative Condition Factor to Determine Lunar and Annual Spawning Patterns for Coral Reef Fishes

Introduction

Coral reef fish spawning is a complex, yet important aspect to understand in managing nearshore fishery stocks. Unlike most temperate fishes, which have restricted spawning seasons, coral reef fishes tend to spawn year-round (Randall 1961; Craig 1998; Lowerre-Barbieri et al. 2011) making it difficult to determine spawning patterns. Temperate fishes often take advantage of optimal conditions, such as food availability, to have major spawning events during certain times of the year (Ward and Staunton-Smith 2002; Erisman and Allen 2006; Brosset et al. 2015). However, coral reef fishes are not limited to certain times in the year to spawn. Coral reef fishes tend to have periods of heightened spawning (i.e., when more spawning occurs than usual) on lunar and annual scales.

Known Spawning Patterns for Coral Reef Fishes Along the Lunar and Annual Cycles

Coral reef fish may spawn year-round, but there are some months throughout the year in which fishes spawn to a higher magnitude, determined by analyzing Gonadosomatic Index (GSI). *Mulloidichthys flavolineatus* in Okinawa had the highest GSIs between May and July, which declines until September (Samejima et al. 2021). Several surgeonfishes, *Acanthurus blochii, A. dussumieri, A. xanthopterus,* and *A. olivaceus*, were found to have spawning activity year-round, but *A. blochii* and *A. olivaceus* had periods of high GSI in April – August and June – September respectively (Pardee et al. 2022).

Various studies have also found different spawning patterns for some coral reef fish species in relation to the lunar cycle through direct observations using GSI, histology, and number of viewed spawns. Some patterns relate to spawning at different times before, during, and after the full moon. For instance, *Centropyge potteri* was only observed spawning the week preceding the full moon (Lobel 1978). *Psdeudobalistes flavimarginatus* in Palau spawns in sync with the full moon (Lobel and Johannes 1980). *Kuhlia sandvicensis* spawns near the time of the full moon (Tester and Takata 1953). Some species also appear to spawn around the time of the new moon. *Thallasoma hardwicke* in Moorea spawns more frequently around lunar days 30 and 1, the time of the new moon (Mitterwallner and Shima 2022).

While many species spawn either around the full or new moon, other coral reef fish species have a bimodal spawning pattern that revolves around the new and full moons. For instance, *Scarus rupripinne* in the Caribbean Sea spawn at the full and new moons (Randall and Randall 1963). *Abudefduf abdominalis* in Hawai'i spawns during the time of the full and new moons (Helfrich 1958). *Dascyllus aruanus* in Okinawa spawns 2-4 days before the new and full moons (Mizushima et al. 2000).

Coral Reef Fish Lunar Spawning Periodicity in Hawai'i

One study focused on lunar spawning periodicity on coral reef fishes in Hawai'i, but found patterns to be highly variable by location and year and had little data for many months sampled. Schemmel and Friedlander (2017) examined GSI and gonad histology for *Acanthurus triostegus sandvicensis* (convict tang, manini) throughout the lunar cycle for two years at three locations in Hawai'i: North Kaua'i, Maunalua Bay on O'ahu, and North Kona on Hawai'i Island, to determine spawning. Lunar spawning patterns for *A. triostegus sandvicensis* were found to be variable by location and year. *A. triostegus sandvicensis* spawned around both full and new moons in Maunalua Bay. However, for Maunalua Bay, less than 10 individuals sampled for many months, so it is uncertain whether true spawning patterns are truly captured. Spawning in North Kaua'i was like Maunalua Bay, but occurred slightly earlier with a smaller magnitude. In addition, North Kona did not have a clear pattern with a general decrease in 2013 and general increase in 2014. More data are needed to determine definite spawning patterns for coral reef fishes in Hawai'i, but it is not always possible to obtain enough gonads or spawn observations in a reasonable amount of time.

Why Use Relative Condition Factor to Predict Spawning?

GSI, histology, and in-situ surveying are ideal; for determining spawning patterns but are costly in time and resources. GSI and histology need many gonads that represent all developmental stages and must be kept in pristine condition from harvest to microscope. In-situ surveying requires hours of observation time, as well as the knowledge of where and how target fish species spawn.

Relative Condition Factor (RCF) only requires length and weight for analysis (refer to Equation 2). RCF can be used for areas or species with abundant length and weight data but lack data of other parameters. Also, since RCF only requires length and weight, a lot of data (which is needed to capture spawning patterns) can be gathered in a short amount of time.

RCF has been used to determine changes in condition, but its correlation to spawning is uncertain. Sardines in the Mediterranean Sea were found to have higher RCFs in the summer and was suggested to be related to higher food availability from increased primary production, but would drastically drop during the winter because of a combination of spawning and low food availability (Brosset et al. 2015). RCF and GSI for *Lutjanus vitta* in southwest India were found to have a similar trend with a decline from September to March (Ramachandran et al. 2013). Although it has been suggested that RCF may change due to spawning, no studies that use RCF as the main method to test for spawning patterns were found. RCF was also never used on a lunar scale, so it is not well known how RCF is correlated to spawning in relation to the moon, especially in Hawai'i.

However, other studies have used Fulton's Condition Factor (FCF), a formula like RCF. *Lutjanus fulviflamma* in the Persian Gulf were found to have both high FCF and GSI in May, with a decline through September (Razi and Noori 2018). However, the issue is that unlike RCF which uses the values of *a* and *b* from the length-weight relationship (Equation 1), FCF disregards *a* and sets *b* to 3, assuming length and weight gain for the studied fish stock is proportionally equal. Ultimately, FCF does not capture an individual fish's true condition based on the characteristics of its home stock because it assumes individual fish grow and gain weight at the same rate throughout the course of its life.

The objective of this analysis is to test whether RCF can be used to determine spawning patterns for coral reef fishes by observing how RCF changes throughout the lunar and annual cycles and determine whether these changes are related to spawning. If related to spawning, RCF should share a similar pattern to that of GSI and coincide with specific events related to spawning, like larvae hatching and the formation of spawning aggregations.

Methods

Fish market data were derived from Poseidon Fisheries Research's Hawai'i Biosampling Project (Pardee and Wiley 2020, refer to Ch. 1).

Calculating Relative Condition Factor

RCF was calculated based on a length-weight relationship formulated using all surveyed fish of a given species at and above the species size-at-maturity (L_{50}). Twelve species for O'ahu only from Pardee and Wiley (2020) had enough data of at least 100 observations distributed across the time series to analyze RCF across both lunar and annual cycles. Species L_{50} was derived from life history information in the current literature (Table 3). Literature from studies conducted in Hawai'i were used, when possible, but if not available literature from studies elsewhere in the tropical and sub-tropical Pacific were used. L_{50}s are in fork length in accordance with Pardee and Wiley (2020). Only mature females were used for *S. rubroviolaceus* as indicated by external color phase in the market data. To find the values for *a* and *b*, a length-weight relationship (refer to Equation 1) was formulated using the remaining mature fish. RCF was calculated for each individual fish using its observed length and weight. Each species was analyzed independently.

Moving Averages

For each species, fish were grouped into 6-day windows based on lunar day surveyed in the markets and averaged by RCF. The 6-day windows were used to 1) ensure each individual RCF had an equal weight regardless of how much data were available for a particular lunar day and 2) account for the possibility of market fish being caught 1 – 5 days prior to surveying. Fish were assigned a lunar day based on the day they were observed in the markets with a shift 3 lunar days prior to surveying due to the uncertainty of the day fish were harvested. Each fish was fit into a single 30-day lunar cycle, with Days 1 and 30 being the new moon and Day 15 being the full moon. 6-day windows were created using 6 consecutive lunar days with each window overlapping 3 days with the previous and following windows. Each window is represented by its median day. Examples of the windows are as such: Day 0.5 (Days 28-3), Day 3.5 (Days 1-6), Day 6.5 (Days 4-9), etc. Average RCF with 95% confidence intervals were calculated for each window.

Generalized Additive Models

Generalized Additive Models (GAMs) were run for both lunar and annual cycles. GAMs were used to account for the non-linearity of the lunar and annual cycles and find patterns which otherwise would not be seen by adjusting smoothing and basis functions. RCF values from individual fish were used. Model fits were adjusted separately for lunar and annual cycles. For the lunar cycle, smoothing was set to 0.2 with 5 basis functions. For the annual cycle, smoothing was auto-adjusted by R with 6 basis functions.

Results

Summary Statistics for Species Analyzed

Twelve species had at least 100 individuals at and above size-at-maturity to analyze RCF in relation to lunar day and month. 100 individuals were chosen as the minimum sample size to ensure all points in the lunar and annual cycles were evenly represented. Most of the species had more than 85% of their initial sample size at or above the given size-at-maturity (Table 3). *A. xanthopterus, M. vanicolensis, and M. grandoculis* had the lowest percentages of individuals at and above size-at-maturity at 62%, 75%, and 83% respectively.

Table 3: Size-at-maturity (L_{50}), initial sample size, and sample size at and above the L_{50} for 12 species. Literature where L_{50} was derived from is in () next to the number. FL – fork length; * - only females were used; ^ - L_{50} was from a study outside of Hawai'i

Species	**L_{50} (FL, mm)**	**Initial n**	**n at L_{50}**
Acanthurus triostegus sandvicensis	127 (Schemmel et al. 2016)	1098	1096
Mulloidicthys vanicolensis	175 (Cole 2009)	1115	837
Acanthurus xanthopterus	310.6 (Pardee et al. 2022)	639	395
Mulloidicthys flavolineatus	185 (Cole 2009)	577	485
*Scarus rubroviolaceus**	340 (Howard 2008)	593 total, 409 females	402
Acanthurus blochii	226.4 (Pardee et al. 2022)	434	402
Acanthurus dussumieri	255.3 (Pardee et al. 2022)	272	248
Lutjanus fulvus	188 (Longenecker et al. 2013)	270	265

Monotaxis grandoculis	303 (Pardee and Wiley 2022)	265	221
Naso unicornis	355 (DeMartini et al. 2014)	237	235
Acanthurus olivaceus	178 (Pardee et al. 2022)	238	209
*Naso lituratus^*	145 (Taylor et al. 2014)	131	125

Analysis of RCF Lunar and Annual Patterns for Three Focal Species

RCF in this analysis is evaluated with the purpose of determining spawning patterns, with a maximum in RCF followed by a decline indicating the onset of a major spawning period. 'Decline' will refer to the decrease in RCF from a maximum to a minimum. Figures for this analysis will feature three focal species in the body of the paper because these species have the most distinct patterns of either the lunar or annual scale. The other nine species will be presented separately in a Supplementary section.

A. triostegus sandvicensis shows maximums followed by declines in RCF around both the full and new moon on a lunar scale and declines beginning in Months 1 and 5 on an annual scale. Both moving averages (Figure 5a) and GAM (Figure 5b) show a maximum in RCF around three days before the full moon (Day 12) and at around the new moon (Day 1). The maximum at Day 12 is significantly different from the minimum at Day 22, indicating a decline in RCF in this 10-day period. Figures 4a and 4b also show a slight minimum at around Days 6 – 10, but 95% confidence intervals still overlap. There are declines in RCF occurring in both winter (Months 1 – 3) and summer (Months 5 – 8) (Figure 5c).

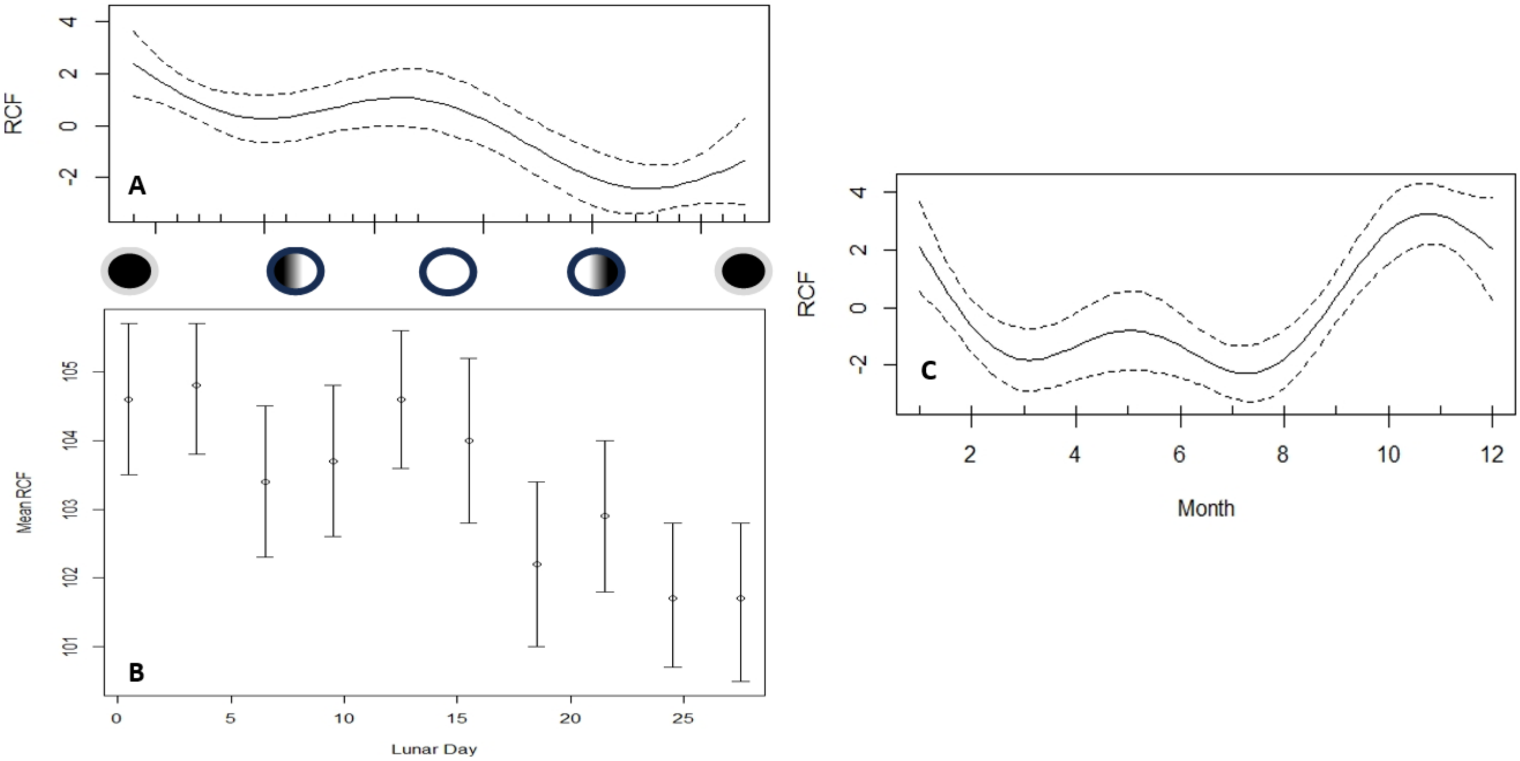

Figure 5: Lunar cycle RCF GAM (A) and moving averages (B) and annual cycle RCF GAM (C) for *A. triostegus sandvicensis.* 95% confidence limits are represented by the dotted lines (A, C) and error bars (B).

There is a decline in RCF for *M. flavolineatus* after the full moon and *M. vanicolensis* has declines both before the new and full moons on a lunar scale. *M. vanicolensis* peaks three days after the new moon (Day 3) and six days after the full moon (Day 21) with the two maximum values significantly different from the minimum value at around Day 12 (Figures 6a and 6b). *M. flavolineatus* had peak RCF about 2 days before the full moon (Figure 7b). *M. flavolineatus* had a secondary peak around 5-8 days after the full moon that appears in the moving averages (Figure 7a), but not in the GAM. In this case, it cannot be determined that there is a secondary maximum after the full moon.

However, both goatfish species share a decline in RCF on the annual scale. *M. flavolineatus* and *M. vanicolensis* have noticeable declines in RCF during the summer (Months 5 – 8) (Figures 6c and 7c). Although there are other minimums (around Month 2 in Figure 6c and between Months 12 and 1 in Figure 7c), it cannot be determined whether there are true declines in RCF because of the broad confidence ranges in which the upper or lower limit shows no such decline.

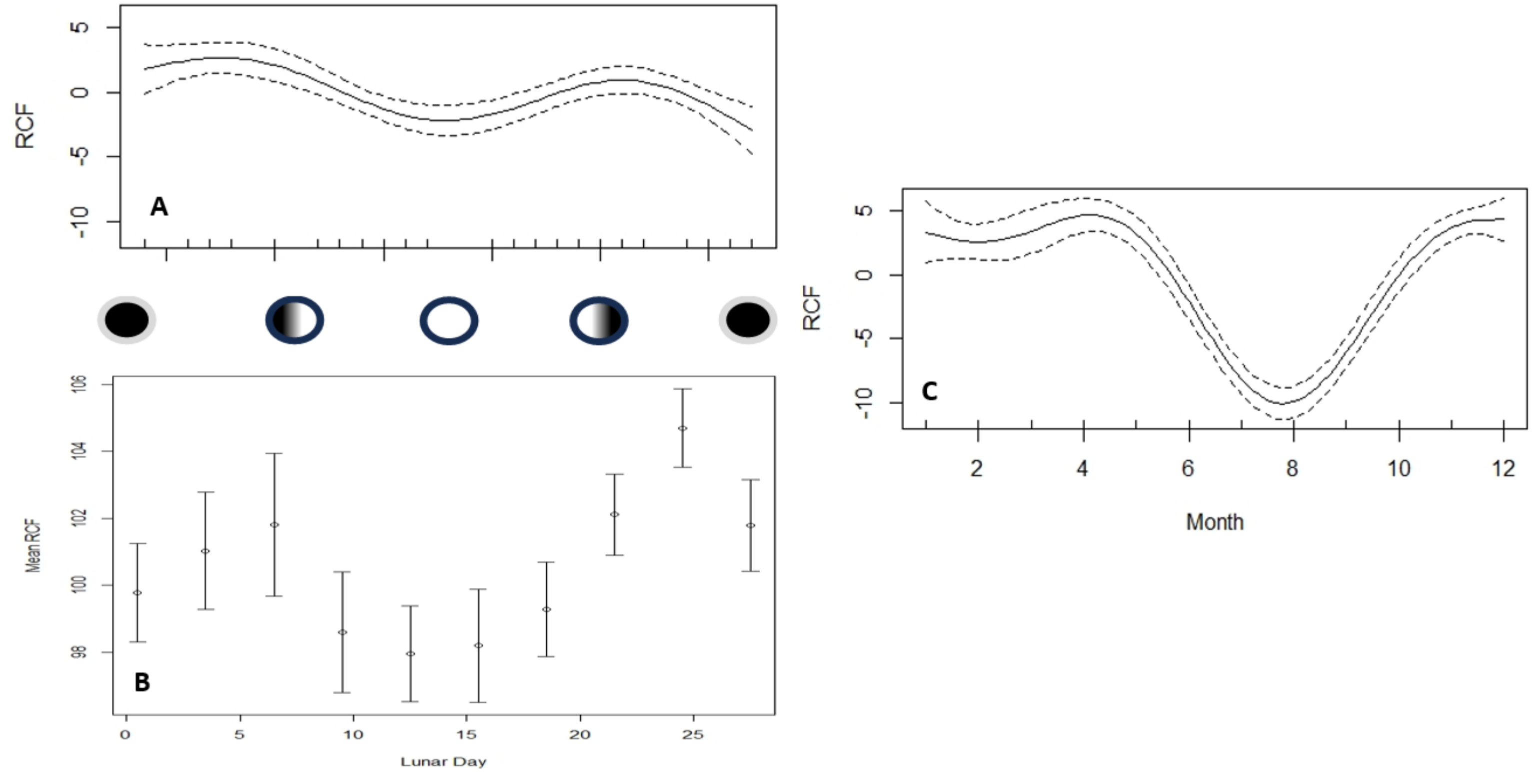

Figure 6: Lunar cycle RCF GAM (A) and moving averages (B) and annual cycle RCF GAM (C) for *M. vanicolensis.* 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

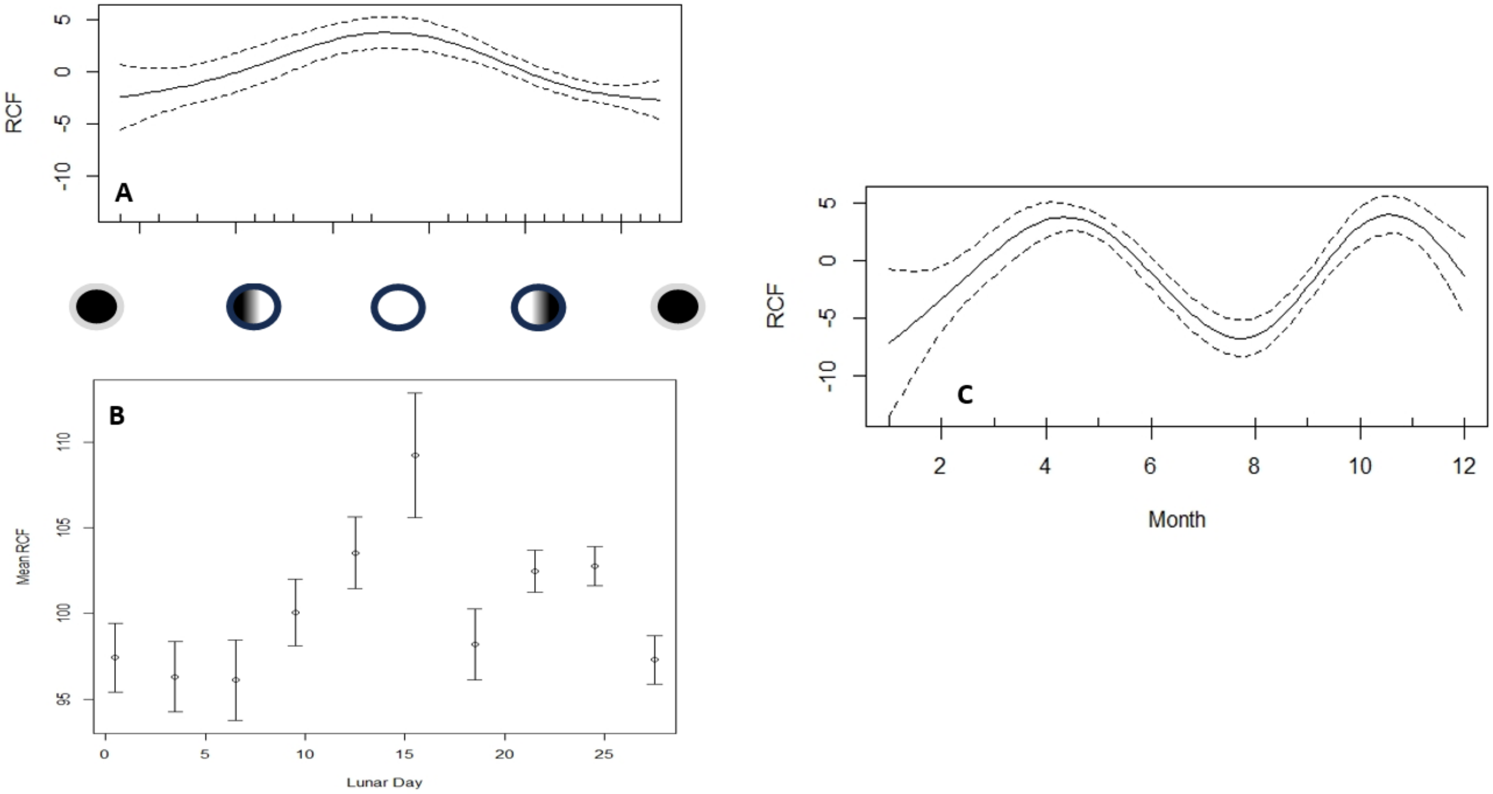

Figure 7: Lunar cycle RCF GAM (A) and moving averages (B) and annual cycle RCF GAM (C) for *M. flavolineatus.* 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

<u>Trends in Lunar RCF Patterns for Other Species</u>

RCF patterns in all nine other species show maximums followed by declines in relation to the full moon, new moon, or both. Ten of the twelve species have non-overlapping 95% confidence intervals among moving averages, showing significant differences between RCF maximums and minimums (Figures S.1 – S.9).

Two species show RCF maximums before the full moon while one species shows an RCF maximum during the full moon and two species after the full moon. *S. rubroviolaceus* had an

RCF maximum about 3 days before the full moon (Figure S.3b), but the confidence intervals of the moving averages show no significance between the maximum and the minimums around the full moon and around three days after the new moon (Figure S.2a). *A. blochii* shown an RCF maximum around 2-3 days before the full moon in the GAM (Figure S.4b), but the moving averages shows a maximum around 3 days after the full moon (Figure S.3a). *A. xanthopterus* had an RCF maximum at around the time of the full moon (Day 15). *A. dussumieri* had an RCF maximum around 2-3 days after the full moon (Figure S.4b). *N. lituratus* had an RCF maximum around 3 days after the full moon (Figure S.9b).

Three species show RCF maximums in relation to the new moon, with one species showing maximums each before, during, and after. *A. olivaceus* had an RCF maximum around 3 days before the new moon (Figure S.8b). *M. grandoulis* shows an RCF maximum around the time of the new moon (Day 1/30) (Figure S.7b), but confidence intervals from the moving averages show no difference between the maximum and the minimum around 2 days before the full moon (Figure S.6a). No clear pattern can be seen in the moving averages for *M. grandoculis* because Days 3.5 and 6.5 have high variation in mean RCF due to individuals with extreme RCF values. *N. unicornis* had an RCF maximum around 6-9 days after the new moon (Figure S.7b).

L. fulvus does not seem to have a definite pattern as shown in the GAM (Figure S.5b), but the confidence intervals in the moving averages show a significant decline from around 2-3 days after the full moon to about 6 days before the new moon (Figure S.5a)

Trends in Monthly RCF Patterns for Other Species

Monthly RCF patterns are highly variable by species, but 10 of the 12 species show a decline in RCF during the spring and summer months, many of which are from Months 5 - 8. *A. xanthopterus* had a decline in RCF from Month 6 to Month 9 (Figure S.1c). *S. rubroviolaceus* had a decline in RCF from Month 5 to Month 8 (Figure S.2c). *A. blochii, A. dussumieri, L. fulvus,* and *N. unicornis* also had declines in RCF from Month 5 to Month 8 (Figures S.3c, S.4c, S.5c, and S.7c). *M. grandoculis* had a slight decline in RCF from Month 6 to Month 12, but the broad confidence ranges make it difficult to determine if there is a true decline (Figure S.6c).

Nine of the twelve species also show an RCF decline at some point during the winter months (Months 11 – 3). *A. xanthopterus* and *L. fulvus* also had a decline in RCF from Month 1 to Month 3 (Figures S.1c and S.5c). The decline from Month 1 to Month 3 for *A. xanthopterus* may have begun at Month 11, but it is questionable since the confidence range during that time is broad and that the upper limit does not appear to show any such decline (Figure S.1c). The decline for *A. blochii* may have started in Month 1, but the disconnect in the GAM from Month 12 to Month 1 makes it difficult to determine this (Figure S.3c). *A. olivaceus* has an earlier decline in RCF than the other species which occurs from Month 1 to Month 5 (Figure S.8c). *N. lituratus* had a long decline in RCF from Month 1 to Month 8 (Figure S.9c).

Discussion

The Influence of Spawning on Relative Condition Factor

There are various reasons why RCF may be influenced by periods of heightened spawning on a lunar and annual scale. Declining RCF in both moving averages and GAMs with non-overlapping confidence intervals are key to determining spawning as the non-overlapping confidence intervals indicate significant changes in RCF over the span of the lunar cycle. These changes in RCF may suggest the onset of a period with heightened spawning beginning at the time of maximum RCF and ending at the time of minimum RCF. The decline in RCF corresponds with the decrease in gonad weight from gamete release.

Similarities Between Relative Condition Factor and Gonadosomatic Index Patterns for *A. triostegus sandvicensis* Signaling Detections of Spawning Patterns on a Lunar Scale

RCF patterns for *A. triostegus sandvicensis* correspond with GSI patterns by lunar day, suggesting RCF can determine spawning on a lunar scale. The GAMs with RCF by lunar day for *A. triostegus sandvicensis* (Figure 5b) show semilunar periodicity which occur around times of the new and full moons. This pattern is like Schemmel and Friedlander (2017)'s GAM for *A. triostegus sandvicensis* in Maunalua Bay, which also had a semilunar pattern displaying maximums in GSI around the new and full moons (Figure 8), indicating *A. triostegus sandvicensis* has heightened spawning at around the new and full moons. The similarities between RCF and GSI further supports that RCF can be an indicator of spawning patterns in relation to the moon.

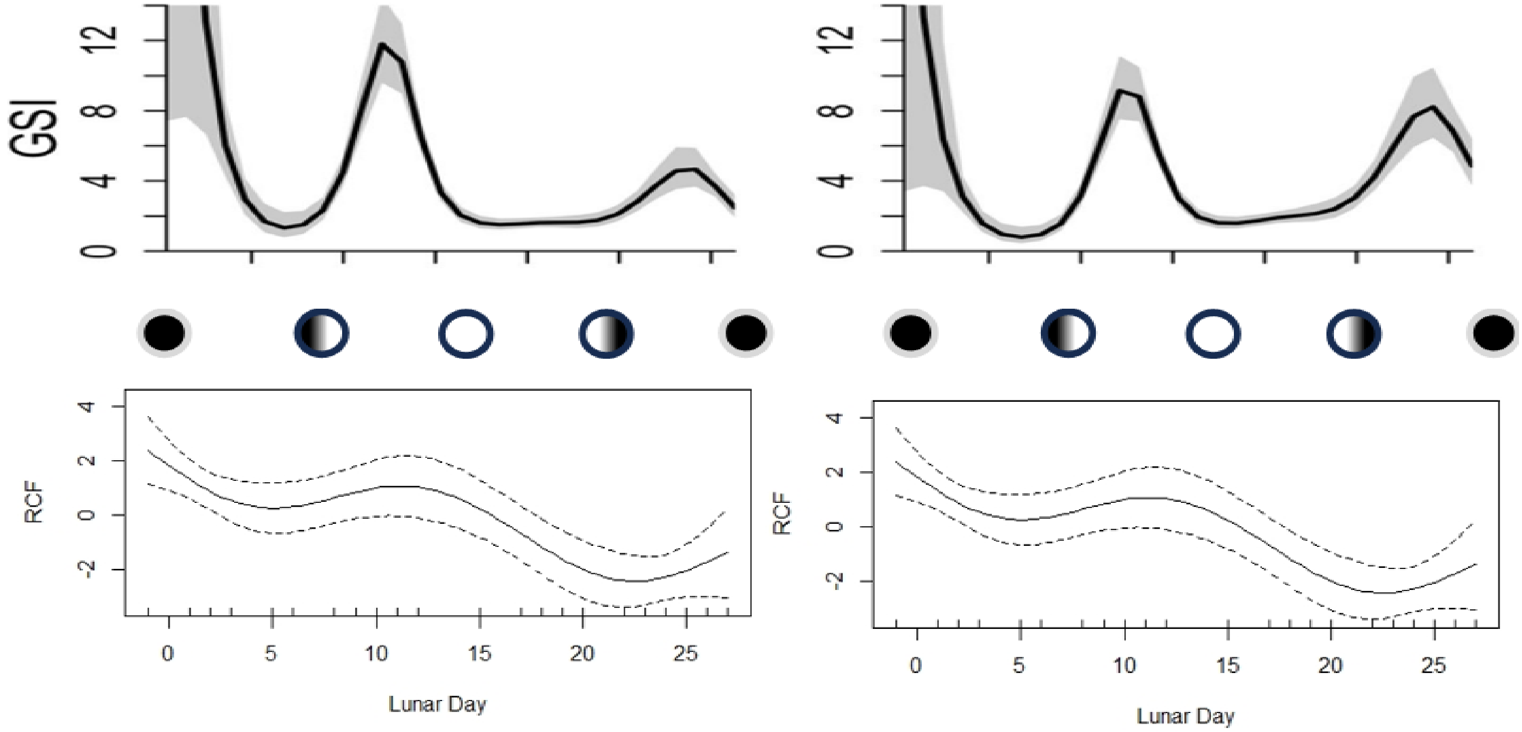

Figure 8: GSI GAMs for *A. triostegus sandvicensis* in Maunalua Bay, O'ahu along the lunar cycle in 2013 and 2014 from Schemmel and Friedlander (2017) (above) in comparison to RCF GAMs of *A. triostegus sandvicensis* from the current study (bottom).

<u>Potential Explanations for Contrasts in Relative Condition Factor Across Months</u>

There are major differences between RCF and GSI for *A. triostegus sandvicensis* on a monthly scale. Schemmel et al. (2016) analyzed mean GSI and spawning fraction by month for *A. triostegus sandvicensis.* Mean GSI and spawning fraction reach a maximum in August (Month 8) with a sharp decline and a minimum in October-November (Months 10-11), suggesting heightened spawning for *A. triostegus sandvicensis* occurs in the fall. However, the RCF GAM shows the opposite – a minimum in Month 8 with a sharp incline and maximum in Months 10-11 (Figures 5c and 9). Annual variation in spawning, external factors such as feeding rate and energy expenditure, and sea surface temperature may contribute to varying levels of annual RCF and GSI.

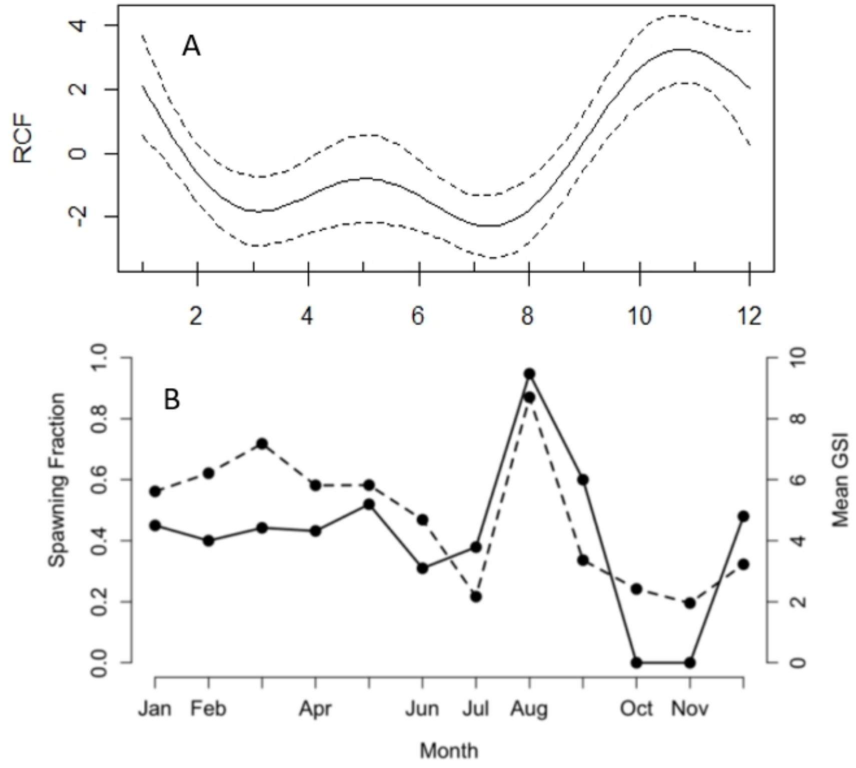

Figure 9. *A. triostegus sandvicensis* annual RCF pattern from the current study (A) and the patterns for GSI (dashed line) and spawning fraction (solid line) from Schemmel et al. (2016) (B).

The timing of annual spawning can vary by 2 - 3 months and has been observed in other coral reef fish species. *Pterocaesio pisang* in the Philippines was observed in one year to have peak spawning starting during the transition period after the northwest monsoon season and the year after to have peak spawning during the northwest monsoon season itself, though the reason for this variability is unclear (Abesamis et al. 2015). The difference in the positions of maximums for both *A. triostegus sandvicensis* and *P. pisang* are 2 - 3 months, so it is possible that the monthly RCF pattern from the current study is different from the monthly GSI pattern from Schemmel et al. (2016) because of inter-annual spawning variability.

Annual spawning variability could also be explained by differences in the timing of high and low sea surface temperatures (SSTs). Temperature may influence the onset of spawning on an annual scale for coral reef fishes (Pankhurst and Porter 2003), though it remains unclear how SST affects spawning and may vary by species' spawning preferences. Randall (1961) found *A. triostegus sandvicensis* gonads were enlarged in the fall months and that heightened spawning occurred in February – March. From the observations of enlarged gonads (Randall 1961), peak GSI (Schemmel et al. 2016), and peak RCF (Figure 6c) all occurring during the fall and winter, it is likely that *A. triostegus sandvicensis* tends to spawn more when SST is lower, which can vary year-over-year. Therefore, it is possible that the RCF pattern from the current study and the GSI pattern from Schemmel et al. (2016) did not match because *A. triostegus sandvicensis* generally spawns more when SST is cooler instead of around a set time and that the timeframe heightened spawning may begin is months long. However, there are currently no studies that describe variability in the onset of heightened spawning for *A. triostegus sandvicensis*.

Feeding rate and energy expenditure are two factors not accounted for in the current study and may influence annual RCF variability not captured during analysis. Brownscombe et al. (2017) studied spatiotemporal factors in *Albula vulpes* (bonefish, o'io) energy expenditure and found that SST was a major factor in energy expenditure in which *A. vulpes* metabolism and activity was greater in higher temperatures. *A. vulpes* also consumed more energy in shallower waters likely due to increased foraging behavior. Oliveira et al. (2023) simulated a marine heatwave event (anomalous increase in SST) with juvenile *Zebrasoma scopas* (two-tone tang) and found that energy loss via fecal and ammonia excretion and respiration increased, while energy intake decreased from the increase in SST due to the heatwave.

Another possibility for a difference in annual RCF pattern from annual GSI pattern for *A. triostegus sandvicensis* is that seasonal SSTs affected metabolism and energy intake, which would affect weight and ultimately RCF. SST in Kāne'ohe Bay in July 2018 was at around 26 °C, while in December 2018 was around 24 °C (Pacific Islands Ocean Observing System 2018). Monthly RCF for *A. triostegus sandvicensis* was low in the late spring and summer, when SST was high, and high in the early winter, when SST was low (Figure 5c). Higher SST in the summer may have increased metabolism and energy loss through excretion. The combination of higher SSTs and foraging activity may have been enough for energy lost to be greater than energy gained through feeding. Fishes may have experienced net loss of energy (and thus weight loss) resulting in a decrease in RCF, but not necessarily a change in GSI if gonad development is unaffected. However, there are no current studies on how energy expenditure affects weight for coral reef fishes in Hawai'i.

RCF Reduction Injunct with Oama Hatch Dates and Appearance Signals Monthly Spawning Patterns

Comparing annual RCF patterns of *M. vanicolensis* and *M. flavolineatus* with the hatch dates of their juveniles provides support that RCF does change due to spawning with the appearance of large oama (juvenile *M. flavolineatus* and *M. vanicolensis*) schools and the coincidence of oama hatch dates (Kamikawa et al. 2019) and decline in monthly RCF suggests

RCF changes due to spawning across months. Kamikawa et al. (2019) used oama otoliths to calculate hatch dates of individual fish by subtracting the fish's age (in days) from the date harvested in 2014 and 2015. It was found that most hatch dates for both *M. flavolineatus* and *M. vanicolensis* fell between April and August in both years (Figure 10), suggesting spawning for *M. flavolineatus* and *M. vanicolensis* occurs in the spring and summer. I have also personally observed vast schools of oama appearing in shallow nearshore waters in the summer, typically present from June to September (Months 6 – 9). Monthly RCF for both species declines drastically from Month 5 to Month 8 (Figures 6c and 7c), which coincides with the oama hatch dates. The point in time RCF reaches a minimum, in Month 8, also coincides with the presence of large oama schools in the later summer months. It should be noted that the hatch date calculations and market surveys did not occur in the same year. Knowing that large oama schools appear in the same time window every year supports the idea that the occurrence of hatch dates and decline in RCF are related to each other in terms of annual spawning. In the case of *M. flavolineatus* and *M. vanicolensis*, RCF does change due to spawning across months.

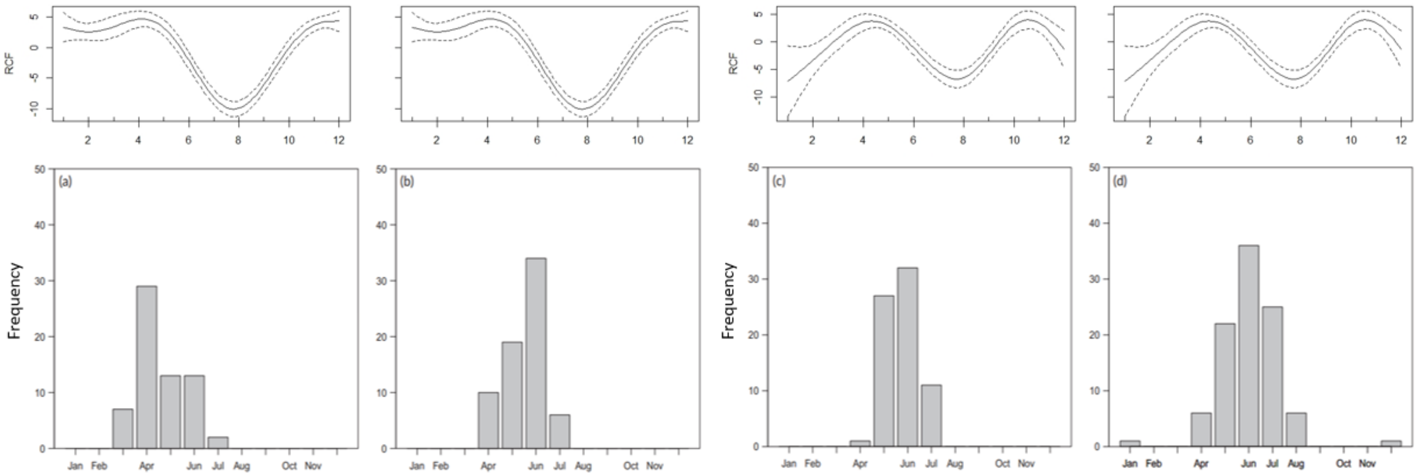

Figure 10: Frequency of oama hatch dates by month for *M. vanicolensis* in 2014 (a) and 2015 (b) and *M. flavolineatus* in 2014 (c) and 2015 (d) from Kamikawa et al. (2019) in comparison to RCF GAMs along the annual cycle from the 2018-2019 market surveys (above hatch date graphs).

Comparing Annual RCF and GSI for *N. unicornis*

The annual RCF pattern for *N. unicornis* is similar to a corresponding GSI pattern in which there is a decline in RCF occurring from Month 5 to Month 7. DeMartini et al. (2014) studied spawning seasonality of *N. unicornis* in Hawai'i and found that peak GSI occurs in Month 5, followed by a drastic decline with a minimum at Month 7, suggesting a heightened spawning period (Figure 11). Simultaneously, a maximum RCF is observed at Month 5, followed by a decline and minimum at around Month 7 (Figure 11). This comparison further supports the idea that RCF does capture spawning patterns.

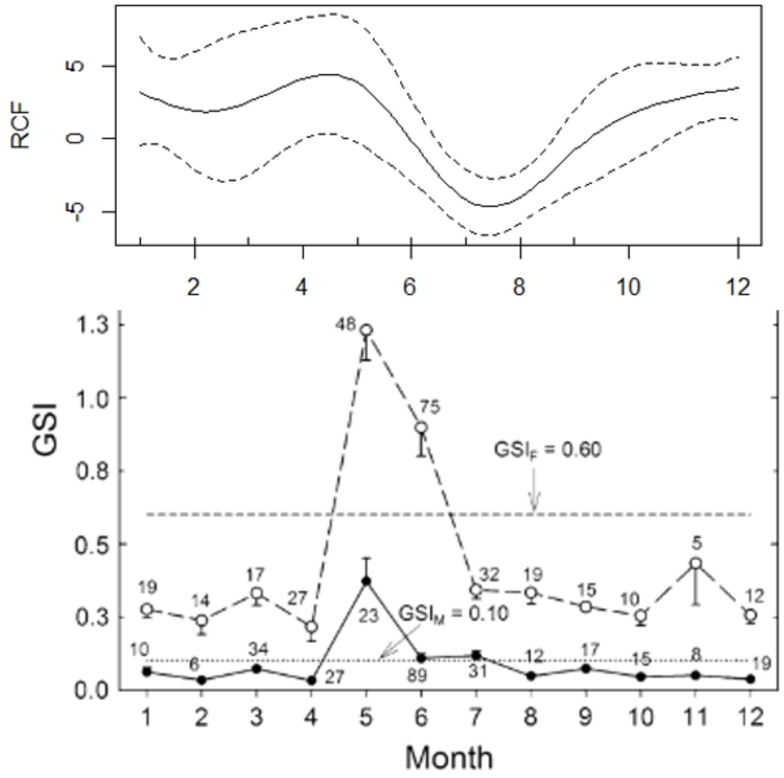

Figure 11: Comparison of the annual RCF pattern (top) to the annual GSI pattern from DeMartini et al. (2014) (bottom) for *N. unicornis*. For the GSI pattern, the dotted line with open circles represents female GSI and the solid line with filled circles represents male GSI. Numbers next to the circles are the sample size for that given point. For the RCF pattern, 95% confidence intervals are represented by dotted lines.

Coral Reef Fish Spawning in the Winter

The idea that reduced feeding leads to lower condition in the winter for coral reef fish is plausible. Two grouper species, *Cephalopholis cyanostigma* and *C. boenak* were found to consume more fish during the summer than in the winter because of a higher abundance in prey recruits in the summer (Beukers-Stewart and Jones 2004). *Sargassum* tissue removal by herbivorous fishes along the Great Barrier Reef was reduced fourfold in June and July, when it is cooler, due to poorer condition and the presence of epiphytes on the algae (Lefevre and Bellwood 2010).

However, while reduced feeding may explain a consistent decline in RCF during the winter, coral reef fish spawning in the winter has been documented before. Peak reproduction for *Centropyge potteri*, a damselfish, was found to occur from January to May (Lobel 1978). Nine coral reef fish species were found to spawn dominantly during the winter, falling between December and April (Claydon et al. 2014).

Perhaps many coral reef fish species in Hawai'i spawn in the winter for the purpose of larval retention. Many species have RCF decline during the winter months, most with the maximum occurring in Month 1 and the minimum occurring in Month 3 (Figures S.1c, S.3c, and S.5c) but also with *A. olivaceus* having a minimum between Months 4 and 5 (Figure S.8c) and *N. lituratus* having a minimum a Month 7 (Figure S.9c). Lobel (1989) found that peak spawning for four coral reef fish species occurs between January and July, particularly around March-April. It was inferred that the timing of peak spawning is associated with the state of ocean currents around the Hawaiian Islands during this time, being parallel to the islands flowing to the northwest (Barkley et al. 1964; Watson and Leis 1974). The species that exhibit high RCF during the late winter and early spring months may take advantage of the shift in current during the winter to ensure more larvae are retained around the islands, survive, and recruit back to the population.

Conclusion

Periods of decline in RCF is inferred to indicate heightened spawning on lunar and annual scales, supported by the significant difference in 95% confidence intervals between the minimum and maximum RCF values. RCF can be used for species in areas with abundant length and weight data but lacking information for other life history parameters, which is a major advancement in the use of RCF as it has never been used for the purpose of determining spawning. Based on RCF alone, many species spawn within 3 days before, during, and after the full and new moons, as well as both before and after the full moon. These findings correspond with those of past studies on coral reef fish spawning in which for all species, heightened spawning occurs around the new and full moons.

Many species also have heightened spawning periods in the late spring/early summer months (Months 5-8) and some species may have heightened spawning periods during the winter (Months 11-3).

References

Abesamis, R. A., Jadloc, C. R. L., & Russ, G. R. (2015). Varying annual patterns of reproduction in four species of coral reef fish in a monsoonal environment. *Marine biology*, *162*, 1993-2006.

Barkley, R. A., Ito, B. M., & Brown, R. P. (1964). *Releases and recoveries of drift bottles and cards in the Central Pacific* (No. 492). US Department of the Interior, Bureau of Commercial Fisheries.

Beukers-Stewart, B. D., & Jones, G. P. (2004). The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish. *Journal of Experimental Marine Biology and Ecology*, *299*(2), 155-184.

Brosset, P., Ménard, F., Fromentin, J. M., Bonhommeau, S., Ulses, C., Bourdeix, J. H., ... & Saraux,

C. (2015). Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions. *Marine Ecology Progress Series*, *529*, 219-231.

Brownscombe, J. W., Cooke, S. J., & Danylchuk, A. J. (2017). Spatiotemporal drivers of energy expenditure in a coastal marine fish. *Oecologia*, *183*, 689-699.

Claydon, J. A. B., McCormick, M. I., & Jones, G. P. (2014). Multispecies spawning sites for fishes on a low-latitude coral reef: spatial and temporal patterns. *Journal of Fish Biology*, *84*(4), 1136-1163.

Craig, P. C. (1998). Temporal spawning patterns of several surgeonfishes and wrasses in American Samoa. *Pacific Science 1998*, 35-49.

DeMartini, E. E., Langston, R. C., & Eble, J. A. (2014). Spawning seasonality and body sizes at sexual maturity in the bluespine unicornfish, Naso unicornis (Acanthuridae). *Ichthyological Research*, *61*, 243-251.

Erisman, B. E., & Allen, L. G. (2006). Reproductive behaviour of a temperate serranid fish, *Paralabrax clathratus* (Girard), from Santa Catalina Island, California, USA. *Journal of fish biology*, *68*(1), 157-184.

Helfrich, P. (1958). *The early life history and reproductive behavior of the maomao, Abudefduf abdominalis (Quoy and Gaimard)* (Doctoral dissertation, University of Hawaii).

Kamikawa, K. T., Humphreys Jr, R. L., Bowen, B. W., & Friedlander, A. M. (2019). Recruitment dynamics and fishery characteristics of juvenile goatfishes *Mulloidichthys spp*. in Hawaiʻi. *Journal of Fish Biology*, *95*(4), 1086-1093.

Lefèvre, C. D., & Bellwood, D. R. (2010). Seasonality and dynamics in coral reef macroalgae: variation in condition and susceptibility to herbivory. *Marine biology*, *157*, 955-965.

Lobel, P. S. (1978). Diel, lunar, and seasonal periodicity in the reproductive behavior of the pomacanthid fish, *Centropyge potteri*, and some other reef fishes in Hawaii. *Pacific Science 1978*, 193-207.

Lobel, P. S. (1989). Ocean current variability and the spawning season of Hawaiian reef fishes. *Environmental Biology of Fishes*, *24*, 161-171.

Lobel, P. S., & Johannes, R. E. (1980). Nesting, eggs, and larvae of triggerfishes (Balistidae). *Environmental Biology of Fishes*, *5*, 251-252.

Lowerre-Barbieri, S. K., Ganias, K., Saborido-Rey, F., Murua, H., & Hunter, J. R. (2011). Reproductive timing in marine fishes: variability, temporal scales, and methods. *Marine and Coastal Fisheries*, *3*(1), 71-91.

Mitterwallner, P., & Shima, J. S. (2022). The relative influence of environmental cues on reproductive allocation of a highly iteroparous coral reef fish. *Coral Reefs*, *41*(5), 1323-1335.

Mizushima, N., Nakashima, Y., & Kuwamura, T. (2000). Semilunar spawning cycle of the humbug damselfish *Dascyllus aruanus*. *Journal of Ethology*, *18*, 105-108.

Oliveira, H., Maulvault, A. L., Santos, C. P., Silva, M., Bandarra, N. M., Valente, L. M., ... & Anacleto, P. (2023). Can marine heatwaves affect the fatty acid composition and energy budget of the tropical fish *Zebrasoma scopas*? *Environmental Research*, *224*, 115504.

Pankhurst, N. W., & Porter, M. J. R. (2003). Cold and dark or warm and light: variations on the theme of environmental control of reproduction. *Fish Physiology and Biochemistry*, *28*, 385-389.

Pardee, C., Wiley, J., Schemmel, E., Fendrick, T., & Giglio, J. (2022). Comparative demography of four large-bodied surgeonfish. *Environmental Biology of Fishes*, *105*(2), 231-245.

Ramachandran, S., Ali, D. M., & Varghese, B. C. (2013). Age, growth, and maturity of brown stripe snapper *Lutjanus vitta* (Quoy & Gaimard, 1824) from southwest coast of India. *Journal of Marine Biological Association of India*, *55*(2), 61-68.

Randall, J. E. (1961). Contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. *Pacific Science 1961*, 215-272.

Randall, J. E., & Randall, H. (1963). The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. *Zoologica*, *48*, 49-60.

Razi, A., & Noori, A. (2018). Length-weight, Condition factor and gonadosomatic index of blackspot snapper *Lutjanus fulviflamma* (Forsskal, 1775) (Perciformes: Lutjanidae) in the northern Persian Gulf. *International Journal of Aquatic Biology*, *6*(2), 66-74.

Samejima, S., Uehara, M., & Tachihara, K. (2021). Life-history traits of a widely distributed coral reef fish, *Mulloidichthys flavolineatus* (Mullidae), Okinawa Island, southern Japan. *Environmental Biology of Fishes*, *104*(12), 1559-1574.

Schemmel, E. M., & Friedlander, A. M. (2017). Participatory fishery monitoring is successful for understanding the reproductive biology needed for local fisheries management. *Environmental Biology of Fishes*, *100*, 171-185.

Schemmel, E., Friedlander, A. M., Andrade, P., Keakealani, K., Castro, L. M., Wiggins, C., ... & Kittinger, J. N. (2016). The codevelopment of coastal fisheries monitoring methods to support local management. *Ecology and Society*, *21*(4).

Tester, A. L., & Takata, M. (1953). *Contribution to the Biology of the Aholehole: A Potential Baitfish* (No. 38). Hawaii Marine Laboratory.

Ward, T., & Staunton-Smith, J. (2002). Comparison of the spawning patterns and fisheries biology of the sardine, *Sardinops sagax*, in temperate South Australia and sub-tropical southern Queensland. *Fisheries Research*, *56*(1), 37-49.

Watson, W., & Leis, J. M. (1974). Ichthyoplankton of Kaneohe Bay, Hawaii A one-year study of fish eggs and larvae. *The University of Hawaii Sea Grant.*

Ch. 4: Effect of the Environment on Fish Present in the Markets

Introduction

The Effect of Environmental Variability on Fish Size and Prevalence

Changes in environmental conditions affect weekly availability of fish in the markets, in which there are less fish in the markets during weeks speculated to unfavorable conditions. For instance, in Micronesia, wave height and moon illumination were the most important factors in explaining variations in daily market biomass (Houk et al. 2012).

One possibility for the environment influences on fish availability in the markets is that fish are easier to catch during certain conditions. For instance, Rhodes et al. (2008) found evidence that lunar illumination is an important factor affecting fish catch since higher catch and market purchases were occurring on days of low lunar illumination in Pohnpei, Micronesia. This finding would suggest more optimal conditions to result in higher fish catch. Spear fishers use low-light conditions to reduce backlighting and fish avoidance (Rhodes et al. 2008).

Another possibility is that smaller surf and less moonlight provide optimal conditions for fishers to harvest fish or allow access to a wider range of fishing spots. For instance, in East Africa, one explanation for reduced catch during the southeast monsoon is because of reduced effort from fishers due to rough ocean conditions (McClanahan 1988). Rough ocean conditions would restrict and confine fishers to harvest fish in protected areas, resulting in reduced overall catch. During calmer conditions, fishers would have access to a larger number of areas to harvest fish that were not accessible during rough conditions, resulting in increased overall catch.

Multiple studies claim that temporally-changing environmental conditions have greater effect on catch variability at locations with denser human populations, which is likely due to greater fishing pressure (Williams et al. 2008, Williams et al. 2015, and Friedlander et al. 2017). For example, environmental variability around the Commonwealth of the Northern Mariana Islands (CNMI) accounted for approximately 3-4 times as much of the variability in daily market biomass as Yap and 1.5 times as much as Pohnpei and the CNMI's human population is about ten times the size of Yap's and twice the size of Pohnpei's (Houk et al. 2012). These findings support Houk et al.'s hypothesis that environmental variability has a tighter influence on fish catch with increasing fishing pressure. On the islands with higher fishing pressure, reduced catch would be observed on days with poor environmental conditions because there would be more fishing occurring in protected areas, hence more fish being harvested which would decrease the number of fish in these protected areas over time. Conversely, on the islands with lower fishing pressure, catch would not be affected as much by environmental variability because there would be less fishing and therefore fewer areas under high fishing pressure on days with poor conditions.

Environmental Variability in Hawai'i

The influence of environmental variability on coral reef fish catch in Hawai'i is lacking in the literature. Inn Hā'ena on Kaua'i's north shore that over half of its annual catch is during the summer months because high surf makes fishing difficult during the winter (Vaughan and Vitousek 2013). However, much of the summer catch in Hā’ena was akule (*Selar crumenophthalamus*), which form spawning aggregates during the summer (Vaughan and Vitousek 2013). Therefore, there is still considerable uncertainty in the relationship between fish catch and environmental factors in Hawai’i.

Environmental factors may also influence where fishers decide to fish at on any given day, which in turn may vary in overall fish condition. Coral reef habitats along Hawaiian shores are not uniform, nor is the weather consistent around an entire island. On O’ahu, the north and east sides of the island (the windward side) experience more wind, wind swell, and rain, while the south and west sides (the leeward side) is drier and has less wind swell. Some factors, surf being a notable one, are seasonal in which conditions occur on one side of the island throughout a given season. In Hawai’i, large surf occurs along north and west-facing shores during the winter, and along south and east-facing shores during the summer (Richmond and Mueller-Dumbois 1972).

The objective for this analysis was to determine environmental influence on coral reef fish catch for O’ahu. About 1 million of 1.5 million (~70%) Hawai’i residents live on O’ahu (U.S. Census Bureau 2020) and length for target fish species was the lowest in the most densely populated locations (i.e. O’ahu) (Nadon et al. 2015). There was expectation for the environment to influence fish catch as O’ahu has the highest level of fishing pressure in the Hawaiian Islands.

Methods

Fish market data were derived from Poseidon Fisheries Research’s Hawai’i Biosampling Project (Pardee and Wiley 2020) and environmental data were obtained from the National Data Buoy Center (Station MOKH1, https://www.ndbc.noaa.gov/station_history.php?station=mokh1; Station 51207, https://www.ndbc.noaa.gov/station_history.php?station=51207) and the U.S. Geological Survey (Makaha Stream - Station 16211600, https://waterdata.usgs.gov/monitoring-location/16211600; Kahalu’u Stream - Station 16283200, https://waterdata.usgs.gov/monitoring-location/16283200; historical data were directly sent by USGS researchers).

Defining the Parameters

Three parameters were chosen to characterize fish catch: individual fish count by species, total number of species observed, and median length by species. These fish parameters were used in place of biomass to account for differences in the number of individual fishes that are sold, as well as individual fish size and number of species sold in the markets, in which neither are detected if only utilizing biomass.

Seven parameters were chosen to characterize the environment: number of hours of high wind speed, number of hours of low wind speed, number of hours of high wave height, number of hours of low wave height, average streamflow from Kahalu’u (windward O’ahu), average streamflow from Makaha (leeward O’ahu), and lunar day. Data for the environmental parameters were taken as far as 5 days prior to the survey day being represented (excluding the survey day itself) since fish observed in the markets were likely caught between one and five days before surveying. All 120 hours (24 hours/day) were considered for the wind speed and wave height parameters. Thresholds for high and low wind speed and wave height were chosen to count the number of readings below the low threshold and above the high threshold, in which the number of hours was determined by dividing the total number of readings by the number of readings recorded in one hour. Streamflow was used in place of rainfall since rainfall is not uniform throughout the island due to its complex geography (i.e., there is more rainfall near the mountains than near the ocean). Both Kahalu'u and Makaha streamflow were used to describe windward and leeward conditions and as gauges for high and low streamflow. Lunar day was averaged and adjusted by shifting each day seven days forward so that Days 7 and 8 represented the new moon and Day 22 was the full moon, creating a linear scale. Preliminary findings showed that there was a positive relationship between lunar day and certain PCs, even when both Days 1 and 30 were new moon. By shifting each lunar day seven days, the full moon would be designated as a pseudo-maximum.

Method of Analysis

Individual fish count, species count, and median length were calculated and principal component analyses were conducted to find potential patterns in fish count and length. Principal Component Analyses (PCAs) were conducted separately for count and length. The purpose of PCAs is to simplify complex, multivariate data matrices and find patterns by creating new variables (Wold et al. 1987; Bro and Smilde 2014). PCAs were used for this analysis because there were numerous species that were analyzed with the same parameters (count, median length). Fish parameters were normalized by subtracting the observed value from the species mean, then divided by the standard deviation. By normalizing the data, the same total mean and standard deviation applied for all species, which placed all values on a common scale and eliminated extreme values that would be unequally represented in the PC loadings. PC scores for the first five PCs for each survey day were used for correlation and regression analysis. A series of correlations were conducted with the environmental parameters each for counts and median lengths of the top twelve species. Forward stepwise regressions were run for each PC that had significant correlations with two or more environmental parameters to determine the best predictor or group of predictors for that specific PC. Multiple linear regressions were run using the best predictors for each PC (for PCs with a significant correlation with one environmental parameter, a simple linear regression was done).

Results

Summary Statistics

Twelve species with the most data were used for analysis. Preliminary findings showed that the principal components (PCs) only using the species with the most data had stronger loadings and correlations than the PCs using all species.

Correlations were run between environmental parameters to determine shared variability with each other (Table 4). The purpose of this step was to ensure the high and low thresholds were different enough to capture separate high and low anomalous conditions. The thresholds were chosen as followed: high wind speed: ≥5.27 m/s; low wind speed: ≤2.57 m/s, high wave height: ≥1.83 m, low wave height: ≤1.52 m. For both wind speed and wave height, the number of hours below the low threshold had strong negative correlations with the number of hours above the high threshold (Table 4). The number of hours above the high threshold and below the low threshold for wind speed and wave height also had moderate correlations of opposite signs with the other parameter (Table 4). These findings show that the chosen thresholds successfully capture separate high and low anomalies. However, correlations between wind speed/wave height and streamflow/lunar day were weak and had similar signs, suggesting streamflow and lunar day are independent of wind speed and wave height and are completely different parameters.

Table 4: Coefficients of the correlation matrix of the environmental parameters, followed by p-values in (). All parameters are based on 1 – 5 days prior to surveying. WH = wave height; WS = wind speed

Environmental Variables	# Hours High WS	# Hours Low WS	# Hours High WH	# Hours Low WH	Kahaluu Streamflow	Makaha Streamflow
# Hours High WS						
# Hours Low WS	-0.70 (< 0.001)					
# Hours High WH	0.54 (< 0.001)	-0.35 (0.006)				
# Hours Low WH	-0.66 (< 0.001)	0.65 (< 0.001)	-0.58 (< 0.001)			
Kahaluu Streamflow	0.03 (0.837)	0.10 (0.460)	-0.07 (0.622)	-0.02 (0.886)		
Makaha Streamflow	0.13 (0.331)	0.14 (0.270)	0.22 (0.081)	-0.03 (0.808)	0.57 (< 0.001)	
Lunar Day	-0.10 (0.451)	0.08 (0.561)	-0.08 (0.545)	-0.03 (0.799)	-0.11 (0.383)	0.01 (0.916)

Principal Component Loadings

For fish count, species' loadings for PC 1, including species count, were positive apart from *M. grandoculis* (Table 5, Figure 12). Loadings for PC 2 and PC 3 were not considered since there was no strong correlation to the environment (Table 7). Loadings for PC 4 were positive for herbivorous fishes (*A. blochii, A. dussumieri, A. olivaceus, N. lituratus,* and *S. rubroviolaceus*) and negative for carnivorous fishes (*L. kasmira, L. fulvus, M. grandoculis,* and *M. vanicolensis*) (Table 5). Two exceptions are *A. triostegus* and *A. xanthopterus* which have negative loadings.

Loadings for PC 3 for length are like that of PC 4 for fish count in which loadings for herbivores are positive and are negative for carnivores, with the exceptions of *A. dussumieri* and *A. xanthopterus* (Table 6). However, PC 4 for fish count and PC 3 for length are not correlated to each other (correlation, df = 60, T = 1.06, r = -0.14, p = 0.295).

Table 5: Loading values for the first four PCs of fish count. Loadings from PCs with significant correlations with environmental parameters are bolded. 'Total Species Count' is the count of all species observed in the markets.

Species	PC 1	PC 2	PC 3	PC 4
A. blochii	**0.34**	0.03	0.02	**0.12**
A. dussumieri	**0.27**	0.24	-0.51	**0.12**
A. olivaceus	**0.27**	-0.07	0.22	**0.32**
A. triostegus	**0.30**	-0.30	-0.16	**-0.06**
A. xanthopterus	**0.25**	-0.04	-0.04	**-0.30**
L. fulvus	**0.28**	0.14	-0.43	**-0.22**
L. kasmira	**0.15**	-0.40	0.13	**-0.43**
M. grandoculis	**-0.05**	0.60	0.22	**-0.14**
M. flavolineatus	**0.41**	0.17	-0.01	**-0.09**
M. vanicolensis	**0.13**	0.36	0.35	**-0.54**
N. lituratus	**0.06**	0.32	0.01	**0.37**
N. unicornis	**0.18**	-0.19	0.20	**1.83×10^{-3}**
S. rubroviolaceus	**0.24**	-0.06	0.48	**0.26**
Total Species Present	**0.44**	0.04	0.12	**0.16**

Table 6: Loading values for the first four PCs of length. Loadings from PCs with significant correlations with environmental parameters are bolded.

Species	**PC 1**	**PC 2**	**PC 3**	**PC 4**
A. blochii	0.40	0.02	**0.05**	0.28
A. dussumieri	0.45	-0.37	**-0.03**	-0.10
A. olivaceus	-0.17	-0.41	**0.11**	0.46
A. triostegus	-0.13	-0.42	**0.33**	-0.43
A. xanthopterus	0.32	0.02	**-0.29**	-0.18
L. fulvus	0.42	-0.08	**-0.25**	0.19
L. kasmira	-0.20	-0.04	**-0.50**	-0.11
M. grandoculis	-0.06	-0.39	**0.12**	-0.21
M. flavolineatus	-0.45	-0.21	**-0.23**	0.07
M. vanicolensis	0.14	-0.31	**-0.27**	-0.25
N. lituratus	-0.10	0.45	**3.64×10^{-3}**	0.32
N. unicornis	0.04	0.05	**0.46**	0.27
S. rubroviolaceus	0.21	0.09	**0.37**	-0.38

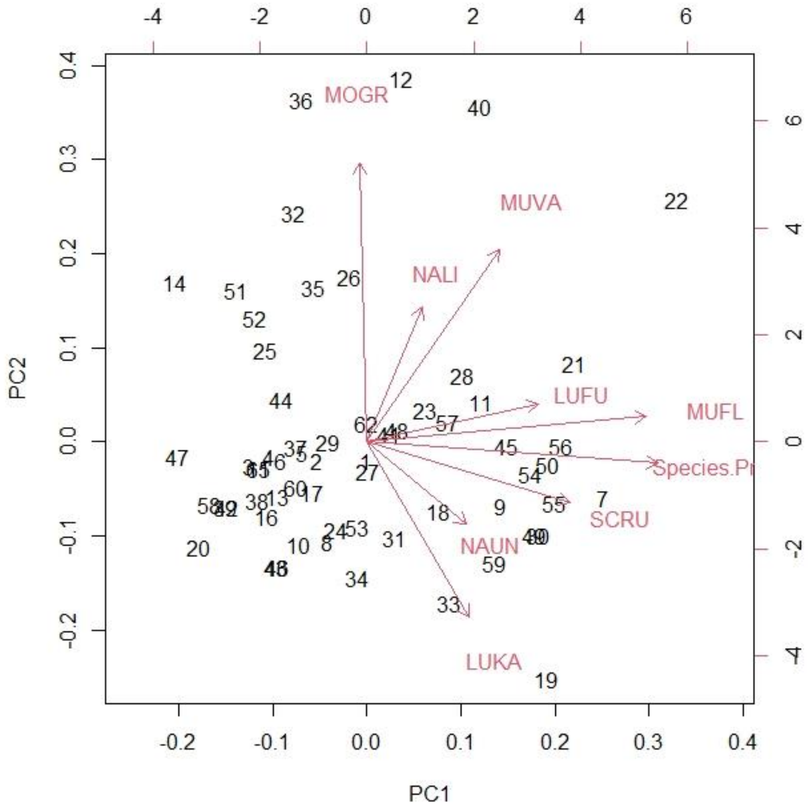

Figure 12: Biplot of PC 1 and PC 2 for fish count. Each number represents a survey day. Arrows indicate the direction of each species' loadings along the PC 1 and PC 2 axes. Species names are displayed by using the first two letters in the genus and species names (ex. LUKA = *Lutjanus Kasmira*, ACTR = *Acanthurus triostegus*).

Environmental Impact on Fish Count

PC 1 and PC 4 for fish count were significantly correlated with some environmental parameters. PC 1 was correlated with number of hours with high wind, number of hours with low surf, and lunar day with number of hours with high wind speed and lunar day being the best predictors (Tables S.1 and S.3). PC 4 was correlated with number of hours with low wind speed, number of hours with low wave height, and average Makaha streamflow with number of hours with low wave height and average Makaha streamflow being the best predictors (Tables S.1 and

S.4). Regression slopes for PC 1 against number of hours with high wind speed and lunar day are -0.02 (SE = 0.008, t = 2.36, p = 0.022) and 0.05 (SE = 0.026, t = 1.88, p = 0.065) respectively with $R^2 = 0.15$ (Table 7, Figure 13). Regression slopes for PC 4 against number of hours with low wave height and Makaha streamflow are -0.07 (SE = 0.003, t = 2.75, p = 0.008) and -0.01 (SE = 0.024, t = 2.46, p = 0.017) with $R^2 = 0.18$ (Table 7, Figure 14).

PCs 2 and 3 did not exhibit any notable patterns and were not used in tests against the environmental parameters.

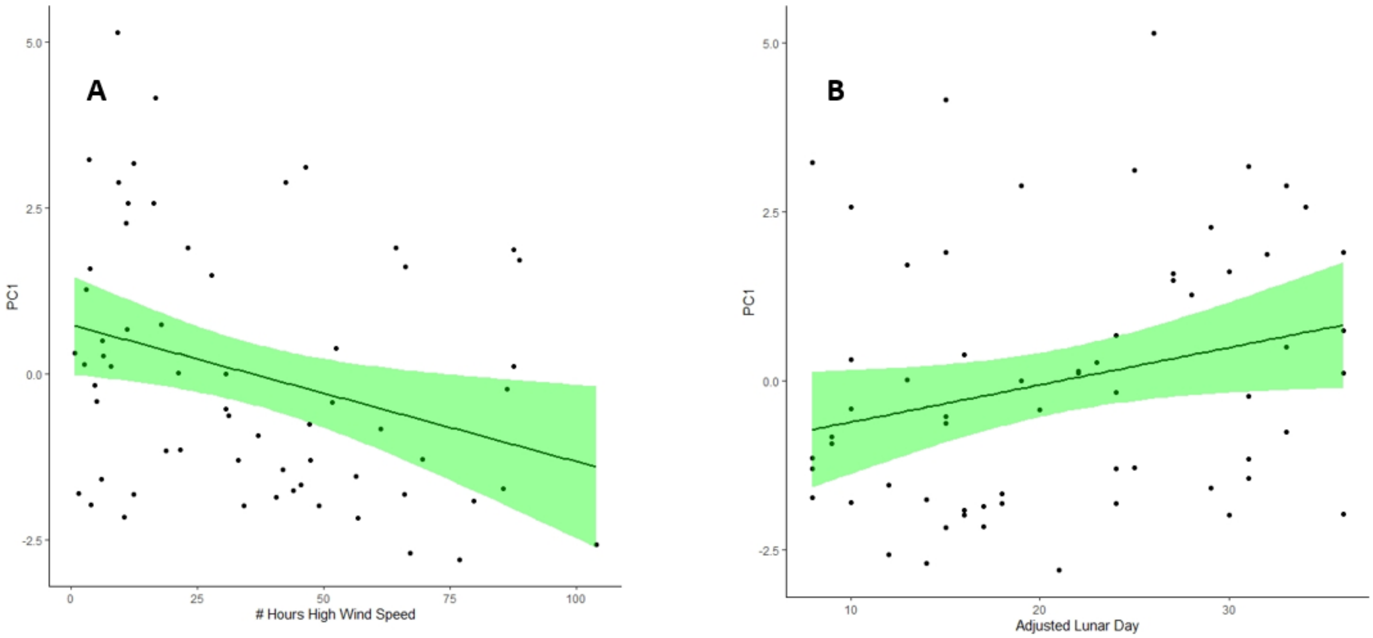

Figure 13: Scatterplots with regression lines of PC 1 for fish count vs. number of hours with high wind speed (A) and lunar day (B) ($R^2 = 0.15$, p = 0.010). The regression slope for number of hours with high wind is -0.02 and for lunar day is 0.05. The green-shaded areas around the regression line represent 95% confidence limits.

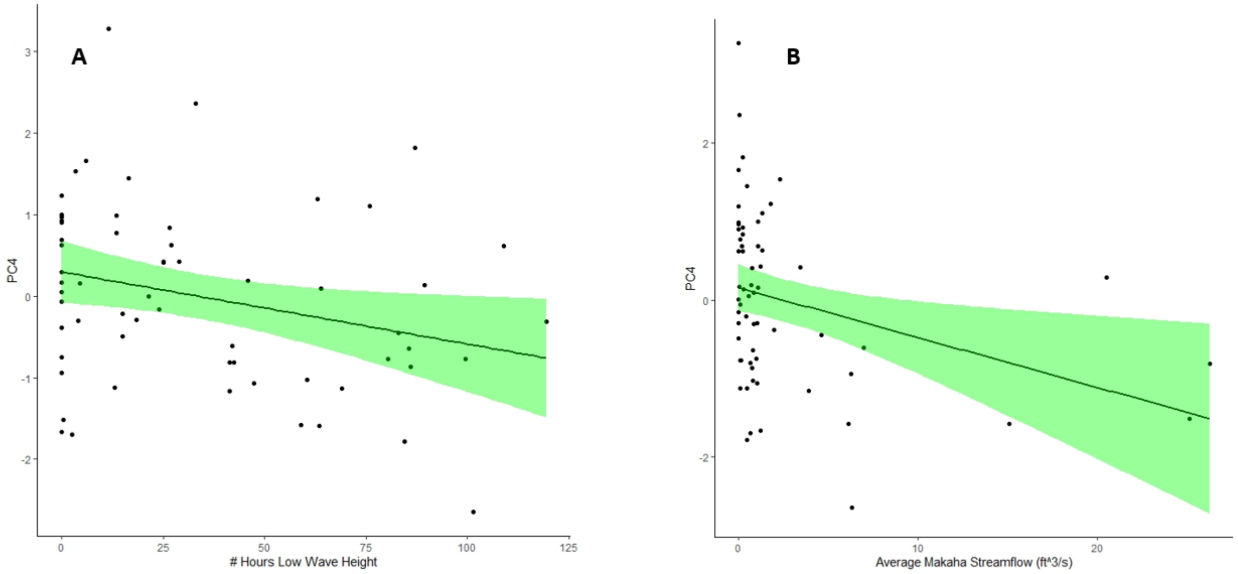

Figure 14: Scatterplots with regression lines of PC 4 for fish count vs. number of hours with low wave height (A) and average Makaha streamflow (B) ($R^2 = 0.18$, $p = 0.003$). The regression slope for number of hours with low surf is -0.07 and for average Makaha streamflow is -0.01. The green-shaded areas around the regression line represent 95% confidence limits.

Environmental Impact on Length

Correlation tests using the PCs of median length resulted in PC 3 being significantly correlated with number of hours with high wind speed, number of hours with high wave height, and number of hours with low wave height with number of hours with high wind being the sole best predictor (Tables S.2 and S.5). The regression slope for PC 3 vs. number of hours with high wind speed was 0.01 (SE = 0.005, t = 2.34, p = 0.022) with R^2 = 0.08 (Table 7, Figure 15).

PCs 1, 2, and 4 did not exhibit any notable patterns and were not used in tests against the environmental parameters.

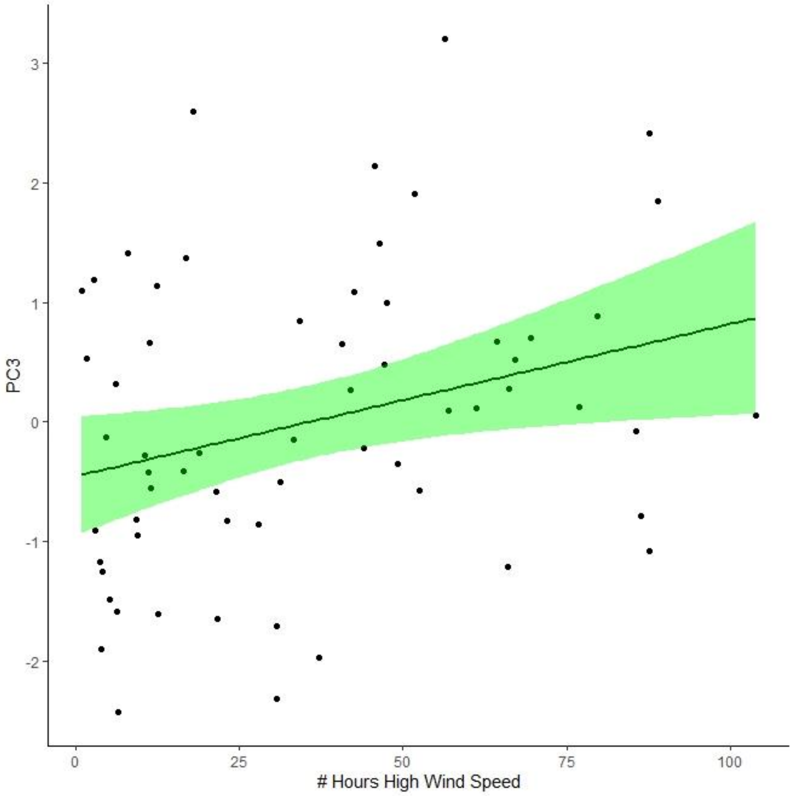

Figure 15: Scatterplot with regression line of PC 3 for length vs. number of hours with high wind (R^2 = 0.08, p = 0.022). The regression slope is 0.01. The green-shaded areas around the regression line represent 95% confidence limits.

Table 7: Linear regressions of PCs with their best environmental predictors based on selection by the forward stepwise regression. All models are significant.

Fish Parameter	**PC**	**Environmental Parameter(s)**	**df**	**R^2**	**F**	**p**	**AIC**
Count	1	# Hours High Wind Speed, Lunar Day	59	0.15	5.03	0.010	252.79
Count	4	# Hours Low Wave Height, Average Makaha Streamflow	59	0.18	6.59	0.003	183.61
Length	3	# Hours High Wind Speed	60	0.08	5.49	0.022	202.79

Discussion

Interpretation of the Principal Components and Correlations to the Environment

PC 1 for fish count showed positive signs for most species and species count (Table 6), which suggests that when there are more species in the markets, there tends to be more individuals per species in the markets as well. However, one species (*M. grandoculis*) does not follow this pattern. The loading value for *M. grandoculis* is small (-0.05, Table 5), meaning the number of *M. grandoculis* individuals is independent of how many other fishes are in the markets. Being that PC 1 is negatively correlated with number of hours with high wind speed (Figure 12a, Table S.1) and positively correlated with lunar day (Figure 12b, Table S.1), more fish tend to be in the markets when there is less wind and is closer to the full moon. This finding signifies that the environment, albeit a weak one, does influence fish catch.

Commercial fishers use different methods of harvesting fish based on the weather conditions for a given day. According to information from a fisher interview, spearfishing is done on days with less wind and surf while surround nets are used when the winds are stronger. Herbivores may be easier to spear than carnivores from being more abundant. However, when surround netting, a wider variety of fish are usually caught, including carnivores.

Both PC 4 of fish count and PC 3 for length share a similar pattern with herbivores having positive signs while carnivores have negative signs (Tables 6 & 7). This pattern suggests that when more herbivores are in the markets, there are less carnivores. Also, when there are larger herbivores in the markets, there are smaller carnivores. PC 4 of fish count is negatively correlated with number of hours with low surf and average Makaha streamflow (Figure 13), suggesting more herbivores are in the caught when there is less surf and less streamflow from Makaha while more carnivores are caught when there is more surf and more streamflow from Makaha. Since Makaha does not normally have streamflow due to its position on the leeward side of the island, any major streamflow from Makaha may be due to major storms that impact O'ahu. Alternatively, PC 3 of length is positively correlated with number of hours with high wind (Figure 14), suggesting larger herbivores are caught with more wind and larger carnivores are caught with less wind, which could be due to the type of method fishers use to harvest fish during certain conditions.

In addition, a result of spearfishing's high level of selectivity would be a shorter range of size classes that are harvested and may potentially explain the positive correlation between number of hours with high wind speed and PC 3 for length. Fishes harvested via spearfishing in Indonesia had a truncated size range leaning towards smaller size classes compared to fishes harvested via handline (Humphries et al. 2019). In this specific case, many herbivores (*A. xanthopterus, A. blochii, A. dussumieri, N. unicornis*) are larger-bodied than most of the carnivores (*L. kasmira, L. fulvus, M. vanicolensis, M. flavolineatus*). Since it appears larger carnivores are caught when there is less wind and larger herbivores with more wind (Table 6, Figure 13), it is possible that although larger carnivores are harvested during days spearfishing is utilized, the carnivores overall are not as large-bodied as the herbivores and are still relatively small.

However, since PC 4 of fish count and PC 3 of length are not correlated (correlation test, r = -0.14, df = 60, p = 0.295), these patterns may not have a clear coherent pattern in relation to one another. One may conclude that the less individuals of a given trophic guild there are in the markets, the larger each individual fish is. Though, the lack of correlation between count and length may mean the patterns for each parameter are completely independent of one another. It should be noted that most of the market catch was harvested using surround nets.

Environmental Influence in Relation to Fishing Pressure

Results from the current study were unexpected in that the R^2 values for O'ahu did not correspond that of Houk et al. (2012), in which environmental variability explained catch the most (highest R^2) for the highest populated region. The highest R^2 values are 0.18 for PC 4 and 0.15 for PC 1 of fish count (Table 5). In Houk et al. (2012), models with similar R^2 values are associated Pohnpei, with the second most populated island of all the study regions, while models from the Northern Mariana Islands (CNMI) the most populated location have R^2 values near 0.3. Given that O'ahu's population density is six times greater than that of the CNMI (reference to be added later), it would be expected for O'ahu to experience a higher level of fishing pressure and therefore observe greater impact from the environment on fish catch. Though it should be considered that different parameters were used in the current study than in Houk et al. (2012) (individual/species count and median length instead of biomass) and that while Houk et al. (2012) only used data from the summer months (when fishing was more "accessible"), the current study used data year-round.

One reason for the lack of strong correlation between fish count and length and the environment may be because people on O'ahu today do not rely as much on coral reef fish as a main food source as in Micronesia. Today, approximately 90% of Hawai'i's food is imported

(Kent 2015). Also, about 99% of O'ahu's population live in urban areas (U.S. Census Bureau 2020), meaning greater access to facilities to buy food from such as grocery stores. The reduced influence from the environment on fish catch may be due to a reduced need for coral reef fish from a vastly urbanized O'ahu.

There are other potential reasons why count and length are not strongly correlated with the environment. There may have been fish kept in freezers that are only brought out when supply for fresh fish is scarce. There was no information on how extra unsold fish is stored in the markets. The markets also do not distinguish between fresh and previously frozen local fish, so it was possible for previously frozen fish, not reflective of environmental conditions, to be sampled (Wiley, per comm.). O'ahu may also have more protected coastline making it easier for fishers to harvest on days with poor conditions and that fishers would be less confined to certain areas. Fishers on O'ahu may have higher quality gear and equipment than fishers in Micronesia and thus can catch more fish regardless of environmental conditions.

Conclusion

Results from the PCAs for fish count and median length display that when there are more species present in the markets, there are also more individual fish in the markets as well, which occurs when there is less wind and is around the time of the full moon. There are also correlations between low wave height and average Makaha streamflow with PC 4 of fish catch which can be explained by when fishers harvest fish and what methods they use to do so. Also, PC 3 for median length indicated that when there are more herbivores in the markets, there are less carnivores when there is less surf and streamflow in Makaha. However, when there are larger herbivores, there are smaller carnivores, regardless of abundance in the markets during times of less wind.

References

Bro, R., & Smilde, A. K. (2014). Principal component analysis. *Analytical methods*, *6*(9), 2812-2831.

Friedlander, A. M., Donovan, M. K., Stamoulis, K. A., Williams, I. D., Brown, E. K., Conklin, E. J., ... & Walsh, W. J. (2017). Human-induced gradients of reef fish declines in the Hawaiian Archipelago viewed through the lens of traditional management boundaries. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28(1), 146-157.

Houk, P., Rhodes, K., Cuetos-Bueno, J., Lindfield, S., Fread, V., & McIlwain, J. L. (2012). Commercial coral-reef fisheries across Micronesia: a need for improving management. *Coral Reefs*, 31, 13-26.

Kent, G. (2015). Food Security in Hawaiʻi. Thinking Like an Island: Navigating a Sustainable Future in Hawai'i. Honolulu: University of Hawaii Press. https://www. academia. edu/33166933/Food_Security_in_Hawaii. _2015.

McClanahan, T. R. (1988). Seasonality in East Africa's coastal waters. Marine ecology progress series. *Oldendorf*, 44(2), 191-199.

Nadon, M. O., Ault, J. S., Williams, I. D., Smith, S. G., & DiNardo, G. T. (2015). Length-based assessment of coral reef fish populations in the Main and Northwestern Hawaiian Islands. *PLoS One*, 10(8), e0133960.

Pardee, C., & Wiley, J. (2020). Hawaii’s Bio-Sampling Project, Final Technical Report. Pp. 3-4, 7-10. Western Pacific Regional Fisheries Management Council.

Rhodes, K. L., Tupper, M. H., & Wichilmel, C. B. (2008). Characterization and management of the commercial sector of the Pohnpei coral reef fishery, Micronesia. *Coral Reefs*, 27(2), 443-454.

Richmond, T. D. A., & Mueller-Dombois, D. (1972). Coastline ecosystems on Oahu, Hawaii. *Vegetatio*, *25*, 367-400.

U.S. Census Bureau. 2020. Hawaii, Honolulu County. https://data.census.gov/profile/Honolulu_County,_Hawaii?g=050XX00US15003

Vaughan, M. B., & Vitousek, P. M. (2013). Mahele: sustaining communities through small-scale inshore fishery catch and sharing networks1. *Pacific Science*, 67(3), 329-344.

Williams, I. D., Baum, J. K., Heenan, A., Hanson, K. M., Nadon, M. O., & Brainard, R. E. (2015). Human, oceanographic and habitat drivers of central and western Pacific coral reef fish assemblages. *PLoS One*, 10(4), e0120516.

Williams, I. D., Walsh, W. J., Schroeder, R. E., Friedlander, A. M., Richards, B. L., & Stamoulis, K. A. (2008). Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environmental Conservation*, 35(3), 261-272.

Wold, S., Esbensen, K., & Geladi, P. (1987). Principal component analysis. *Chemometrics and intelligent laboratory systems*, *2*(1-3), 37-52.

Supplementary Section

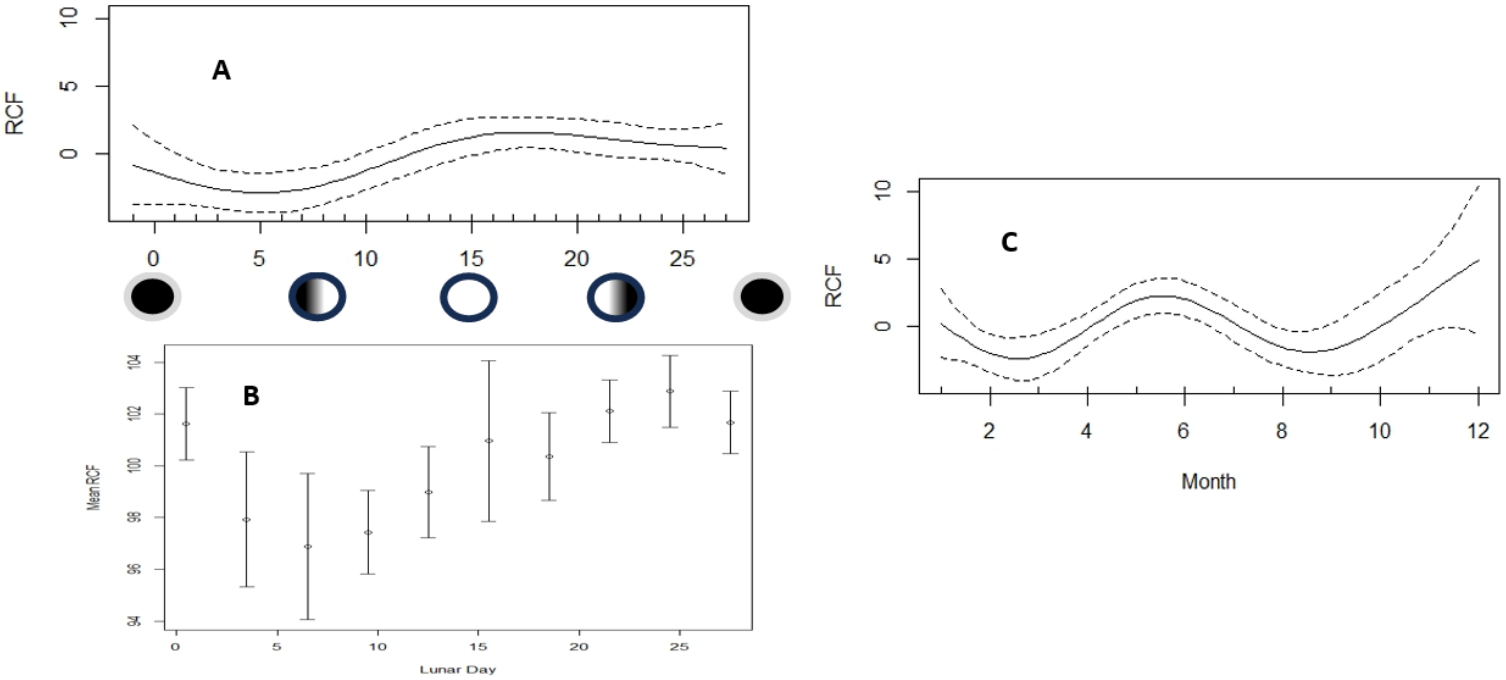

Figure S.1. Lunar RCF GAM (A) with moving averages (B) and monthly RCF GAM (C) for *A. xanthopterus*. 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

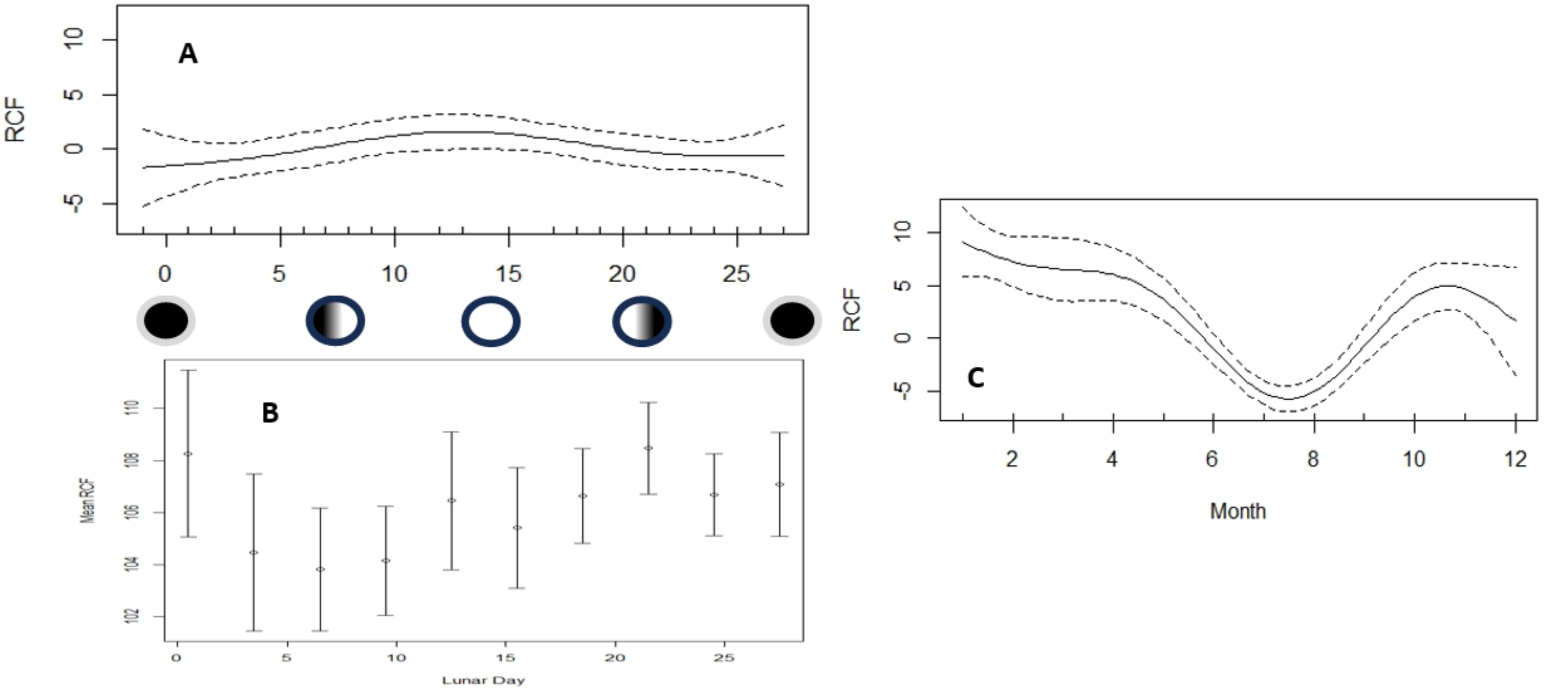

Figure S.2. Lunar RCF GAM (A) with moving averages (B) and monthly RCF GAM (C) for *S. rubroviolaceus.* 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

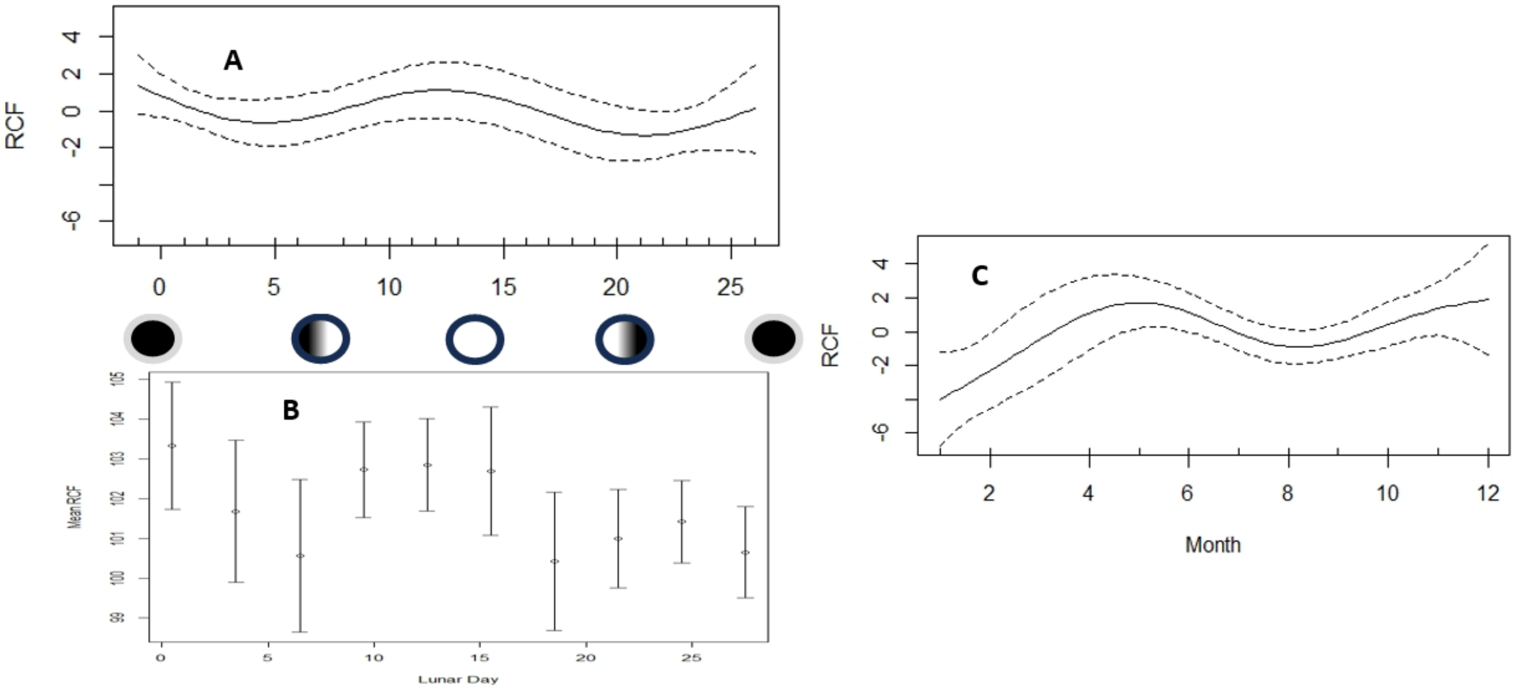

Figure S.3. Lunar RCF GAM (A) with moving averages (B) and monthly RCF GAM (C) for *A. blochii.* 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

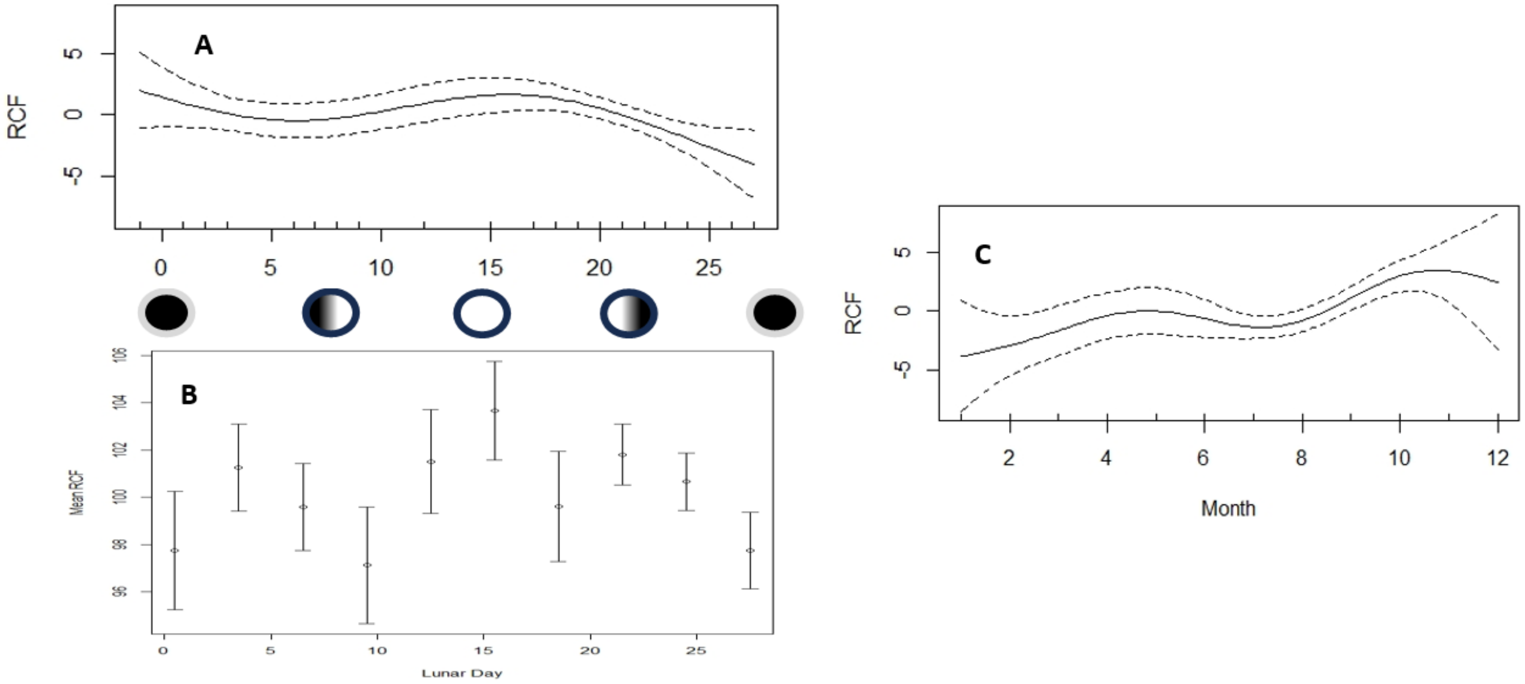

Figure S.4. Lunar RCF GAM (A) with moving averages (B) and monthly RCF GAM (C) for *A. dussumieri.* 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

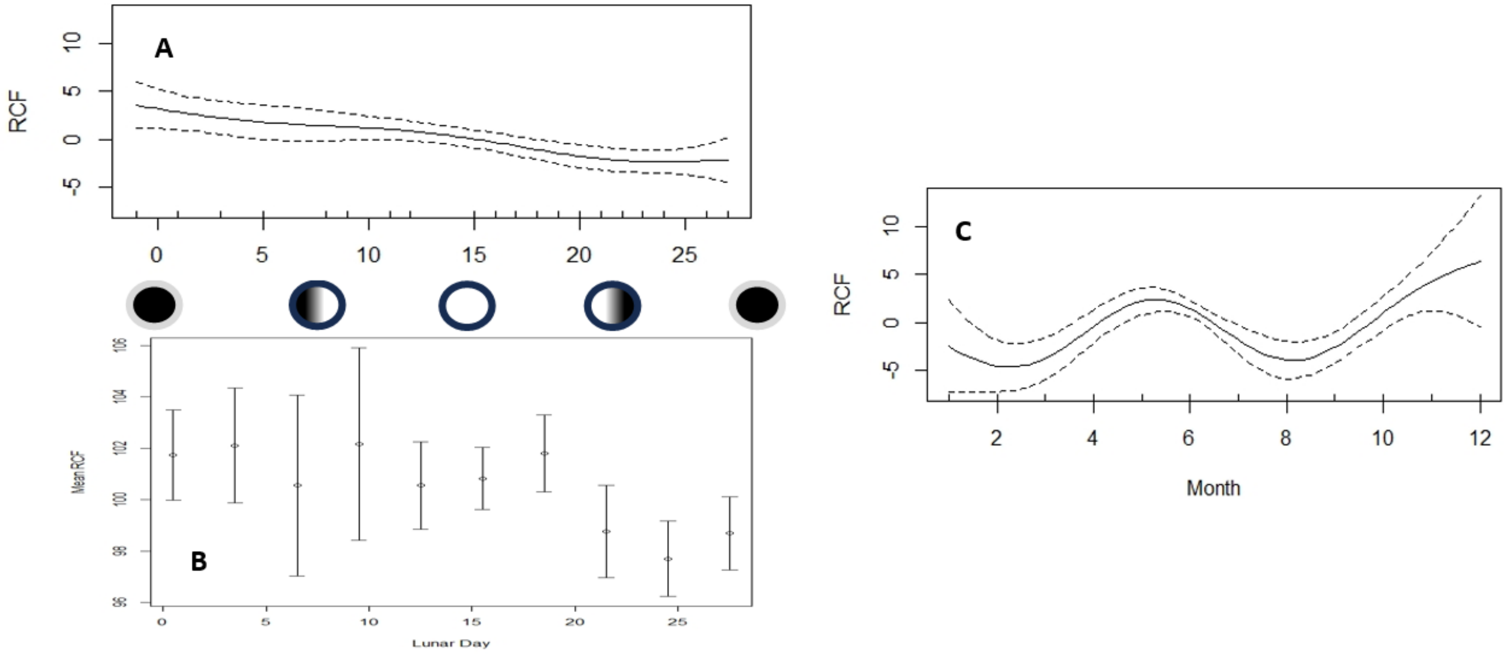

Figure S.5. Lunar RCF GAM (A) with moving averages (B) and monthly RCF GAM (C) for *L. fulvus.* 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

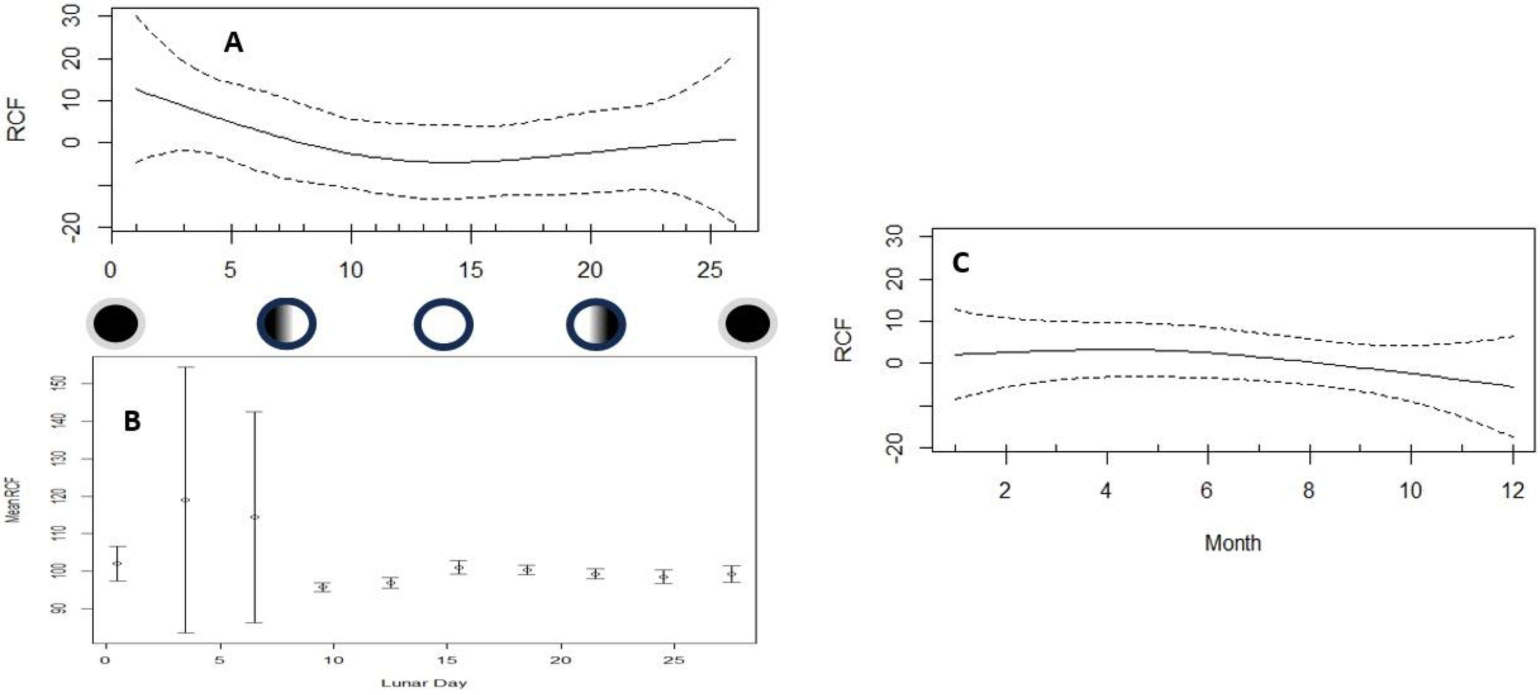

Figure S.6. Lunar RCF GAM (A) with moving averages (B) and monthly RCF GAM (C) for *M. grandoculis.*

95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

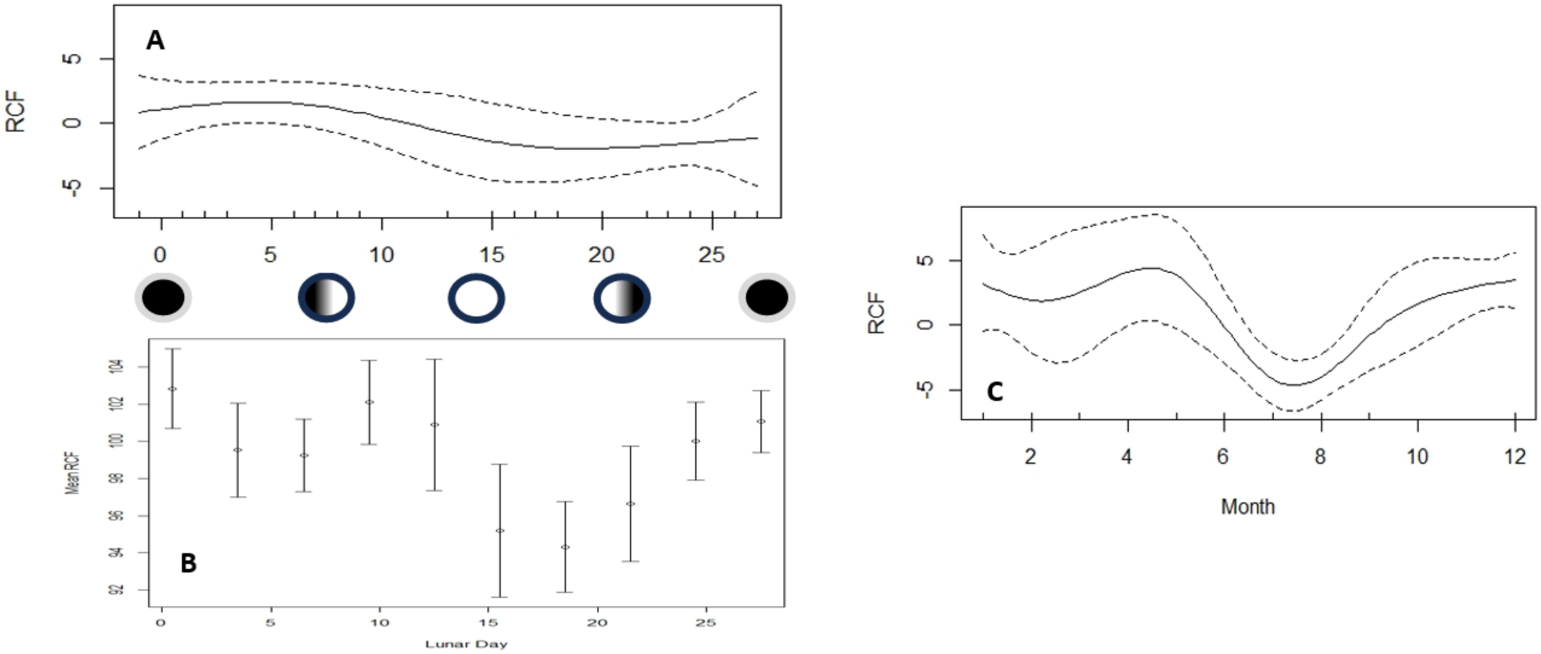

Figure S.7. Lunar RCF GAM (A) with moving averages (B) and monthly RCF GAM (C) for *N. unicornis.* 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

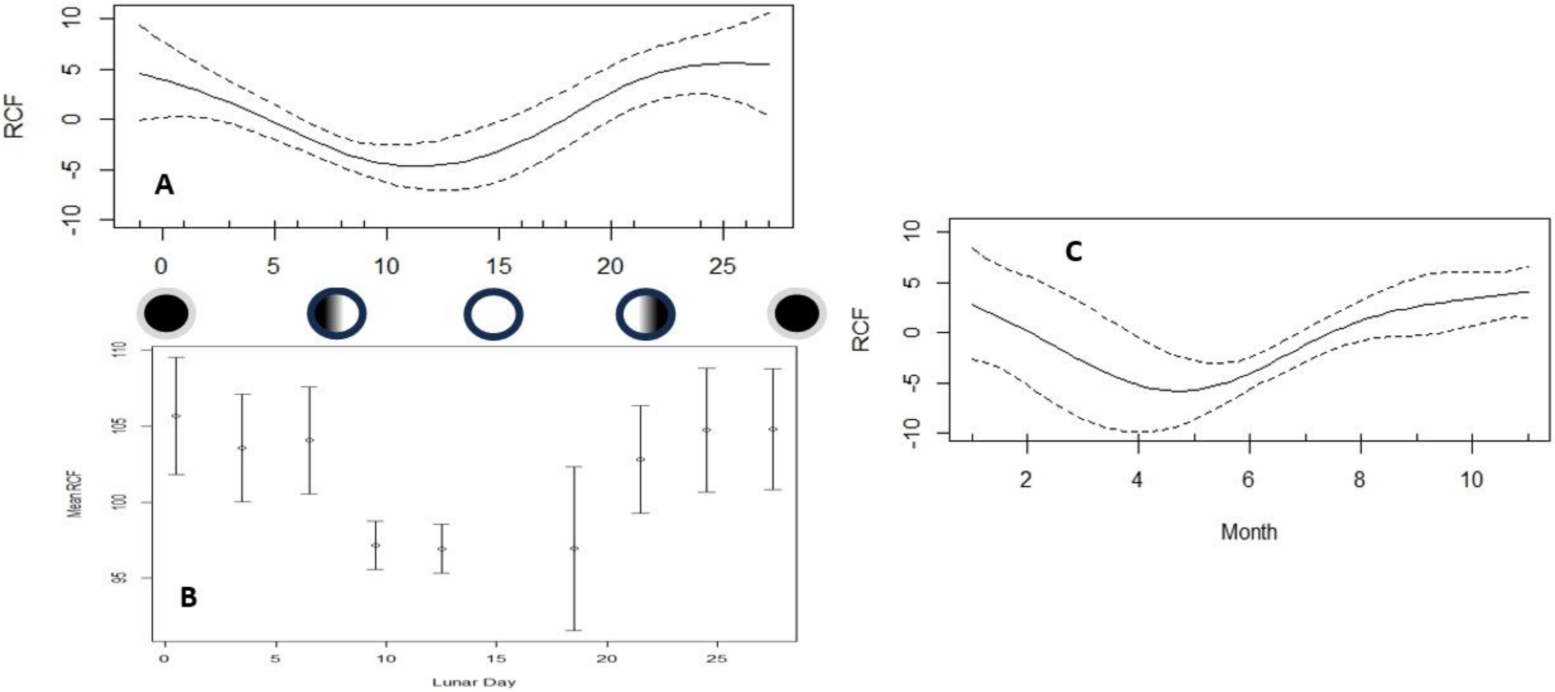

Figure S.8. Lunar RCF GAM (A) with moving averages (B) and monthly RCF GAM (C) for *N. olivaceus.* 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

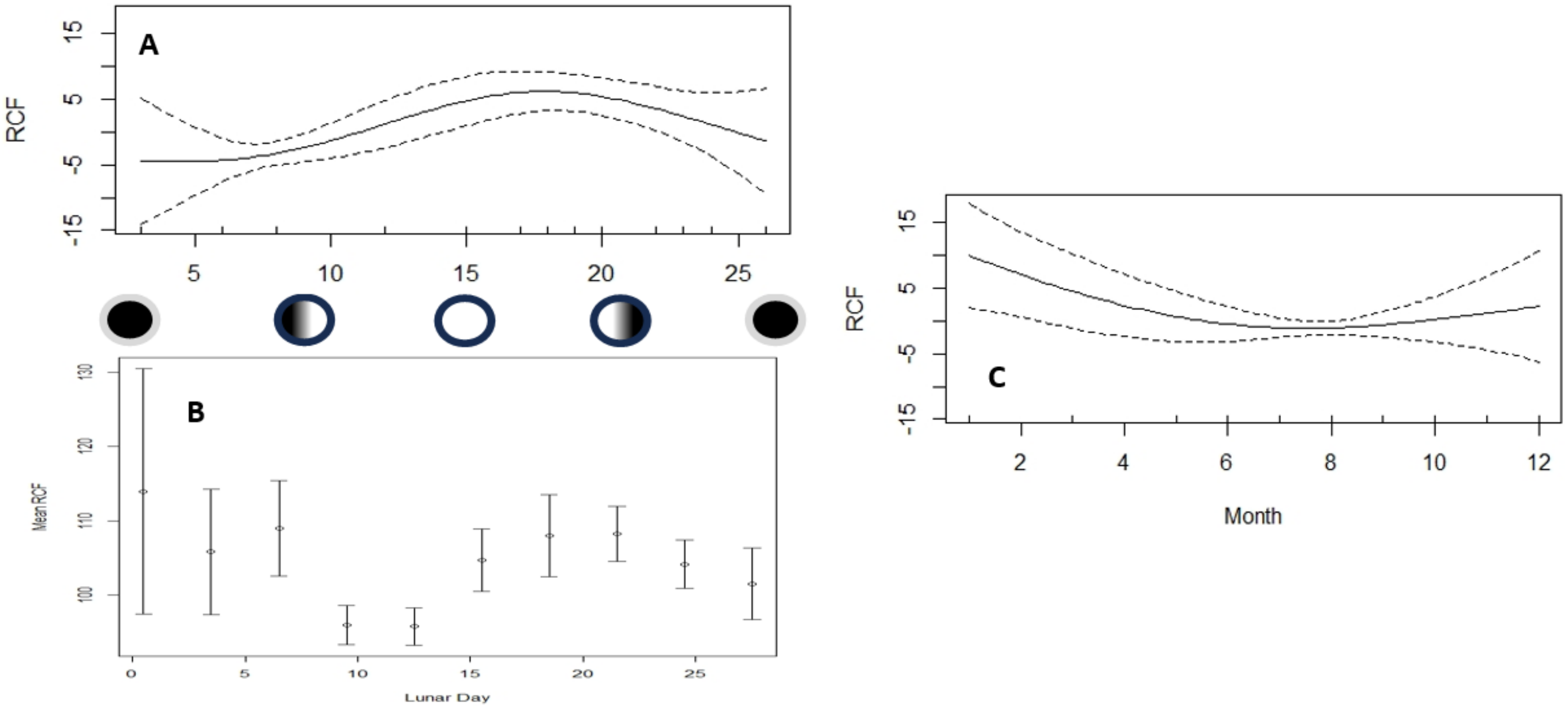

Figure S.9. Lunar RCF GAM (A) with moving averages (B) and monthly RCF GAM (C) for *N. lituratus.* 95% confidence intervals are represented by dotted lines (A, C) and error bars (B).

Table S.1. Correlations between environmental variables and principal components of fish count followed by p-values in (). Significant correlations are bolded.

PCs	# Hours High Wind	# Hours Low Wind	# Hours High Surf	# Hours Low Surf	Kahaluu Streamflow	Makaha Streamflow	Lunar Day
PC 1	**-0.31 (0.015)**	0.21 (0.103)	-0.13 (0.313)	**0.25 (0.050)**	-0.18 (0.156)	-0.02 (0.877)	**0.25 (0.046)**
PC 2	-0.18 (0.154)	0.12 (0.370)	-0.22 (0.091)	0.19 (0.147)	0.06 (0.626)	0.09 (0.470)	-0.04 (0.769)
PC 3	0.01 (0.937)	0.05 (0.684)	0.04 (0.771)	1.4 x 10^{-3} (0.991)	0.12 (0.335)	0.01 (0.937)	-0.06 (0.617)
PC 4	0.14 (0.285)	**-0.27 (0.029)**	-0.13 (0.303)	**-0.28 (0.028)**	5.7 x 10^{-3} (0.965)	**-0.31 (0.013)**	-0.23 (0.071)
PC 5	0.18 (0.152)	-0.25 (0.054)	0.21 (0.094)	-0.11 (0.385)	-0.15 (0.236)	-0.12 (0.331)	-3.1 x 10^{-3} (0.981)

Table S.2. Correlations between environmental variables and principal components of fish length followed by p-values in (). Significant correlations are bolded.

PCs	# Hours High Wind	# Hours Low Wind	# Hours High Surf	# Hours Low Surf	Kahaluu Streamflow	Makaha Streamflow	Lunar Day
PC 1	-0.12 (0.365)	0.06 (0.657)	-0.09 (0.497)	-0.06 (0.626)	0.05 (0.700)	0.11 (0.415)	-0.02 (0.864)
PC 2	0.13 (0.312)	-0.13 (0.306)	0.05 (0.695)	-0.21 (0.093)	0.03 (0.833)	-0.03 (0.800)	0.07 (0.565)
PC 3	**0.29** **(0.022)**	-0.15 (0.229)	**0.28** **(0.026)**	**-0.25** **(0.048)**	-0.12 (0.356)	0.07 (0.592)	7.7×10^{-3} (0.953)
PC 4	-0.03 (0.825)	0.02 (0.908)	1.9×10^{-3} (0.989)	-0.06 (0.908)	0.07 (0.583)	0.03 (0.801)	0.12 (0.363)
PC 5	-0.05 (0.685)	-0.03 (0.807)	0.21 (0.099)	0.03 (0.808)	0.11 (0.385)	0.01 (0.921)	-0.12 (0.347)

Table S.3. List of best models based on AIC determined by forward stepwise regression for PC 1 of fish count, with the best model bolded. Only parameters PC 1 had significant correlations to were listed.

Step	Environmental Parameters	AIC
1	High Wind Speed	76.45
2	**High Wind Speed + Lunar Day**	**74.85**
3	High Wind Speed + Lunar Day + Low Wave Height	76.21

Table S.4. List of best models based on AIC determined by forward stepwise regression for PC 4 of fish count, with the best model bolded. Only parameters PC 4 had significant correlations to were listed.

Step	Environmental Parameters	AIC
1	Average Makaha Streamflow	9.72
2	**Average Makaha Streamflow + Low Wave Height**	**5.66**
3	Average Makaha Streamflow + Low Wave Height + Low wind Speed	7.40

Table S.5. List of best models based on AIC determined by forward stepwise regression for PC 3 of median length, with the best model bolded. Only parameters PC 3 had significant correlations to were listed.

Step	Environmental Parameters	AIC
1	**High Wind Speed**	**24.84**

2	High Wind Speed + High Wave Height	25.30
2	High Wind Speed + Low Wave Height	26.38

Table S.6. Questions and responses during an interview with a commercial coral reef fisher from O'ahu.

Questions	Responses
Do you use different fishing methods? Are there certain days/weather conditions you use certain methods?	Does spearfishing, surround netting, and trapping. Spearfishes when there is good weather and flat water. Surrounds when the trade winds are stronger and during the day. Trapping is done regardless of conditions.
Which side of the island do you fish on? Do you fish on multiple sides of the island? If so, do weather conditions influence which side you fish on?	Consistently fished on the windward side of the island.
How long does it take for fish to reached the markets after being harvested?	Fish are harvested one day, brought to the market the next. Normally sent fish to the markets on Tuesdays and Thursdays.
Conditions are consistently changing hour-by-hour. If conditions on a given day start off bad, but improve later, do you go out when conditions are better or do you wait until the next day?	Went out fishing as fast as possible if conditions got better later in the day to beat other fishers to the fishing spot.