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Fishing Methods Matter: Comparing the Community and Trait Composition of the Dai (Bagnet) and Gillnet Fisheries in the Tonle Sap River in Southeast Asia

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Abstract: The Tonle Sap Lake and River ecosystem in the Lower Mekong Basin of Southeast Asia is one of the most productive inland fisheries globally but is currently threatened by overfishing, dam construction, and climate change. We compare the catch composition and amount from 2007–2013 of two fishery gear types, the bagnets of the largest commercial fishery, the Dai fishery, and gillnets, which are deployed ubiquitously by independent fishers. We found that the two methods captured a similar number of genera (81 and 88 in the Dai and gillnet). Catches of both fisheries were dominated (>75%) by three genera that migrate longitudinally, *Henicorhynchus*, *Labiobarbus*, and *Paralaubuca*. The catch of the Dai fishery followed annual variation in the flood pulse extent, but the gillnet catch did not. We used resource selection ratios to quantify selection pressure by the gillnet fishery, relative to the Dai fishery, on fish from different genera and trait groups. The gillnet selected for fish that migrate laterally from the floodplain to the main river and for higher trophic level fish. Gillnets may target groups of fish that are less impacted by the long-standing Dai fishery. For both fisheries, we note a need for monitoring fish lengths in order to understand the effects of selection on population dynamics and species-specific trait changes.

Keywords: selection; body size; trophic level; migration; flood pulse; tropical; Mekong; Tonle Sap; resource selection ratios; river flows

1. Introduction

Understanding selectivity of fishing gears on catch composition and traits in a multi-species fishery informs sustainable management [1,2]. The fisheries in the Lower Mekong basin and the Tonle Sap River provide livelihoods and food security for the local human population [3]. In the Lower Mekong Basin of Cambodia (Figure 1), more than 80% of rural households participate in fisheries [4] and inland fisheries provide 76% of animal-sourced protein [5]. The Tonle Sap is a flood pulse system, driven by rising waters in the Mekong River that expand the lake and adjacent floodplain via the Tonle Sap River in the wet season (typically June–October). In the dry season (November–May), as the Mekong River flows recede, the Tonle Sap River reverses direction to drain the lake, lowering its level on average by 10 m from the rainy season's height. The Lower Mekong Basin is a hotspot for freshwater fish biodiversity [6], and many fish depend on the lateral and longitudinal connectivity provided by the seasonal flood pulse [7–9]. This flood pulse driven ecosystem creates one of the most productive inland fisheries in the world [10] and the Tonle Sap

Lake ecosystem constitutes more than 60% of Cambodia's total inland fisheries catch [11]. However, catch per unit effort has declined in recent years [12–14], highlighting the need to understand drivers of change to the fishery in the basin.

The reliance on fish by the local people is reflected in the diversity of fishing gear and scales of operations in the Lower Mekong Basin. With a diversity of gear types, there is a corresponding diversity in catch composition, with fisheries variously targeting a single species, group of species, or entire assemblage [6,15,16]. Over 150 types of gear are used in Cambodia, including seines, net fence systems, cast-nets, and lift nets [3,17]. Many local fisheries position themselves to benefit from the flow reversal in the Tonle Sap River to capture fish as they migrate out from the flooded lake to the Mekong River in the dry season. Two important fishing types that make use of this flood-pulse driven fishery are Dai (bagnets) and stationary gillnets [17] (Figure 1). The Dai fishery was established in the late nineteenth century. Intermittent monitoring began in the 1930s and continuous monitoring began in the 1990s [18]. Accordingly, the Dai fishery has been used to make inferences about changes in the fish community and production in the Lower Mekong Basin in relation to fishing pressure and hydrology [19–21]. The fishery is considered indiscriminate regarding the size and species captured. The Dai fishery is the largest industrial-scale fishing operation in the Mekong Basin, and fishers are required to obtain a fishing license from the government through auction to operate nets. Gillnet fisheries, although individually smaller in scale and less regulated, are ubiquitous, and may collectively have a substantial effect on the fish community. Up to 80% of households use gillnets during the dry season in the Mekong basin [22]. Gillnet fisheries are likely more size selective than the Dai fishery, as fishers can match gillnet mesh sizes to the body sizes of targeted fish groups. Gillnets have been shown to be strongly size selective across systems and species [23,24]. Additionally, gillnets may capture fish from different migration guild types, even though they are deployed within the same river, because they are less dependent on water current to operate and tend to be deployed in edge habitats. Furthermore, the gillnets can operate year-round, although we only look at the dry season catches in this study to directly compare catches to the Dai fishery. Both fisheries are widespread in the Tonle Sap River and knowing the selection bias of each method will improve our understanding of the fish taxa and sizes that are targeted by these fisheries and the impacts of each to the larger Tonle Sap River fishery.

Resource selection ratios are often used to quantify how animals disproportionately use a habitat type or food item [25,26]. For example, these ratios have been employed to understand that jaguars tend to use forested areas near water within their home range [27], or that habitat selection by a marine fish, cod, varies with sea surface temperatures [28]. We employ resource selection ratios in a novel way to understand resource use by one of the top predators in the Lower Mekong Basin, human fishers. Because the Dai fishery is stationary and consistently uses relatively size-indiscriminate methods, it is the best measure of resource availability during the dry season. On the other hand, gillnets represent more dynamic resource use by human fishers, and may demonstrate selectivity by the fishermen due to changes in market forces, consumption preferences, and deployment methods.

Based on differences in the selectivity of the Dai (indiscriminate) and gillnet (more selective) fisheries, we might expect differences in both the common taxa captured and their associated traits. If so, these would be reflected in the resource selection ratios. These differences could be due to both mechanical differences in the gear and the fisher's preferences. For example, the Dai fishery tends to capture "white" fish, or fish that migrate longitudinally from the Tonle Sap Lake to the Mekong River, in the main channel current. On the other hand, gillnets may be more likely to capture fish that reside in the floodplain (referred to as "black" fish) and fish that make lateral migrations from the floodplain to the main channel ("grey" fish) because they are placed at the rivers' edge and not reliant on water flow for operation. Additionally, small-sized fish under 25 cm in total length, such as trey riel (*Henicorhynchus* spp.) and *Labiobarbus* spp., which are used to make fish paste (*prahok* in Khmer), are generally worth much less on the market than larger-bodied fish [29]. Given this difference in value, gillnets may be employed by fishers to capture relatively fewer of these small fish by altering their mesh size. Similarly, gillnet fishers may select for fish of higher trophic levels, which has been demonstrated by gillnets in African inland fisheries [30] and by developed inland fisheries in China [31]. Other fish, like the common cyprinids in the *Paralaubuca* genus, may be more frequently caught in the gillnet fishery due to their habitat use. For example, *P. typus* are surface insect feeders [32], and may be less likely to occupy the main current of the river and be pulled into the Dai nets than in the static gillnets. In summary, the differences in the location, gear, and use of the two fisheries likely result in differences in the composition of taxa and traits in the catch.

Figure 1. (**a**) Aerial view of one of the 14 rows with several bagnets in the well-established Dai fishery in the Tonle Sap River. (**b**) Fishermen hauling a net in the Dai fishery. (**c**) A fisher pulls in a gillnet, with a single fish in the net, from a slow edge habitat. (**d**) Gillnets can be spotted drying in a village. The photographs contrast the organized, industrial nature of the Dai fishery with the small-scale and independent but ubiquitous gillnet fisheries. (**e**) Map of the Dai fisheries and the monitored stationary gillnet in the Tonle Sap River within the Lower Mekong Basin. Photos by Chhut Chheana.

Even productive fisheries are vulnerable to local and global environmental change [33,34]. Major threats to fisheries in the Lower Mekong Basin include hydrologic alteration due to completed and ongoing dam construction and climate change [35–38], as well as fishing pressure [14,19,39]. The catch of many taxa, such as fish in the *Henicorhynchus* genus, has been linked to the magnitude of the flood pulse in the Dai fishery [19,20], and the flooding magnitude has been decreasing in recent years [40]. While these large disturbances influence overall fishery productivity, it is important to understand whether catch data generated using different fishing methods congruently quantifies these changes. For example, it is likely that the catch of the gillnet fishery does not respond like the Dai fishery to annual variation in the magnitude of the flood pulse because gillnets are less dependent on water velocity for operation.

The Lower Mekong River is facing increased fishing pressure, largely from small and medium-scale fisheries such as gillnets [41,42], while the Dai fishery effort has remained relatively constant. Here we compare two fisheries, the Dai and the gillnet, in order to inform future monitoring and management of the Lower Mekong Fishery. First, we examine fluctuations in catch in both fisheries in relation to annual flooding magnitude. Second, we compare the fish community that is captured by each fishery. Third, we explore if the gillnet fishery is selecting for common species and trait groups relative to the less-discriminate Dai fishery, and if selection is related to the magnitude of seasonal flooding. Finally, we examined if quantitative traits in body size and trophic level have changed over seven years in each fishery. In summary, we offer the first comparison of these two widespread fisheries in the Lower Mekong Basin and offer suggestions for further monitoring and analyses to inform sustainable management of this multi-gear and multi-species fishery.

2. Materials and Methods

2.1. Fish Catch and Trait Data

The Dai fishery is an industrial bagnet fishery that operates during the receding hydrograph and dry season, from October to March, along the lower stretch of the Tonle Sap River (Figure 1). The Dai fishery is operated during the flow recession to capture fish that are returning from the Tonle Sap Lake and floodplains to the Mekong River. The Dai is organized into 14 rows that are perpendicular to flow. The rows begin downstream of Kampong Chhang and continue towards the confluence of the Tonle Sap and Mekong Rivers. Each row is 25 m wide and is made up of two to seven nets, which are independently operated by lease holders and lifted by separate crews. The Dai nets are relatively indiscriminate with mesh sizes that taper from 15 cm down to 1 cm at their terminus (cod end). The nets encompass nearly the entire water column, with the top of the net on the water surface and the bottom weighted to the substrate, and the net is held open by the water current. See [17] (pages 228-232) for diagrams of the bagnets. We used a previously published time series on catch, which is recorded by weight, at the Dai fishery [14]. This data set was developed using a randomly stratified sampling method across several rows that is designed to estimate fishery production. Seasonal estimated catch (in biomass, kg) was used in this study. This data set excludes 25 sporadic species (e.g., estuarine and marine visitors) that made up 0.38% of the total catch.

Gillnet data were collected from June 2007 through May 2014 (366 weeks) following sampling procedures outlined by the Mekong River Commission (MRC, 2007) and as described in [43]. Briefly, three stationary gillnets were deployed daily in the Tonle Sap River for 12 ± 2 h. Gillnets were 2–3.5 m high and 120 ± 50 m long with a mesh size of 3–12 cm and are typically set perpendicular to flow. A diagram of typical gillnets can be found in [17] (pages 162–164). Captured fish were identified to species and enumerated. The mean of the daily catches (numbers of fish) of the three nets were summed to estimated weekly catch. While gillnet data are available throughout the year, here we only use weeks that overlap with the Dai fishery season to facilitate direct comparisons. For all analyses, we aggregated fish from both datasets by genus. We completed this step to avoid potential inconsistencies in species-level identification between the Dai and gillnet fisheries.

To analyze change in the trait composition of the fisheries, each species was assigned a set of traits describing migration pattern, body size, and trophic level using categorizations that are based on several sources and published in [43]. In summary, migratory guilds were assigned as white fishes (longitudinal migratory species, up and down the Mekong River), grey fishes (lateral migratory species, between the floodplain and streams or rivers), and black fishes (non-migratory, resident species). Body size groups were based on estimated maximum total lengths and were grouped as small (<25 cm), medium (26–60 cm), or large (>60 cm). Trophic position estimates were categorized into trophic group 1 (trophic level <2.75), group 2 (2.75–3.75), and group 3 (>3.75).

2.2. Comparing Annual Catch to Flooding Magnitude

We quantified annual variations in the magnitude of the flood pulse using daily water level data from 26 years (1990–2015) at the Tonle Sap River that were obtained from the Mekong River Commission. We used this data to estimate the flood pulse extent following [21], where the flood pulse extent is the multiplication of the number of days when flows exceed base flows by the average deviation from baseflows. Baseflows are defined as the mean daily flow for the time series. We compared the flood pulse extent to the net residual from the seasonal trend using Fast Fourier Transforms as described in [21]. We compared these two methods using a Pearson's correlation for the entire time series and for the seven years of fish data (Figure S1). The estimates were very similar, so we used flood pulse extent since this metric has been previously demonstrated to be important for the Mekong fishery [20].

While the productivity of the Dai fishery is known to be closely linked to the previous wet season hydrology, with flood years resulting in a more productive fishery, this pattern has not been explored for the gillnet fishery. We summed the total catch for each fishery for the dry season and compared this to the pattern of flood pulse extent in the Tonle Sap River. For each fishery, we calculated a Pearson's correlation between total seasonal catch and flood pulse extent.

2.3. Community Analyses to Compare the Dai and Gillnet Fisheries

We conducted a set of analyses to understand differences in the community of fish captured in the gillnet versus the Dai fishery. To understand how the diversity of catch was distributed across seven years in each fishery, we estimated species richness and Shannon Diversity indices for each fishery and year combination (n = 14) using the "specpool" function in the "vegan" package in R [44]. Errors in species richness estimation are driven by the presence of rare species [45]. We treat these measures of richness and evenness as observations of species with high certainty given that the few rare species were excluded for being insufficient for the linear model in the Dai dataset [14]. We also calculated the average and annual percent of catch in both fisheries that is represented by the three most common genera in both fisheries, *Henicorhynchus*, *Paralaubuca*, and *Labiobarbus.*

Next, we used nonmetric multidimensional scaling (NMDS) to visualize differences in the catch assemblage of the two fisheries. We standardized the two catch datasets using the "frequency" method in the "decostand" function in the "vegan" package R so that the two datasets were comparable. We then conducted the NMDS using the "metaMDS" function in "vegan" with Bray-Curtis dissimilarity. Finally, we conducted a permutational analysis of variance (PERMANOVA) on the Bray-Curtis dissimilarity matrices to determine if the fishery (Dai versus gillnet) and year explained a significant amount of the variance of the community structure. We performed the PERMANOVA using the "adonis2" function in "vegan" with 999 permutations.

2.4. Resource Selection Ratios to Quantify Gillnet Selectivity Relative to the Dai Fishery

Resource selection ratios are commonly used to quantify preferential use of a resource (e.g., food item or habitat type) by animals [25]. Here, we use resource selection ratios to quantify the preference for certain fish taxa and traits by the gillnet fishery in comparison to the Dai fishery. In this analysis, we treat the largely indiscriminate Dai fishery as a baseline measurement of resource availability and the gillnet fishery as the set of selections made by a predator given the available resource base. The selectivity by the gillnet fishery encompasses both differences in the gear itself, including increased size selectivity of gillnets, as well as variability in their use by fishermen. We use the resource selection ratio in [25] that is described as $w(x)$, where:

$$w(x) = f^{u}(x)/f^{a}(x) \tag{1}$$

Such that:

$$f^{u}(x) = u(x)/n \tag{2}$$

$$f^{a}(x) = a(x)/N \tag{3}$$

where $u(x)$ is the number of units used of type x, n is the total number of units used, $a(x)$ is the number of units of type x that are available, and N is the total number of units that are available. For our purposes, we use the gillnet fishery catch as the units that are used and the Dai fishery catch as the units that are available. Note that the catch of the gillnet fishery is reported in count while the catch of the Dai fishery is reported in biomass. However, these resource selection ratios are expressed as unitless ratios. Further, most of the catch (92% of the gillnet and 80% of the Dai fishery) is comprised of small-bodied fish, so we expect a minimal bias to be introduced in the calculated ratios due to this difference in the available data. Length-weight regressions or average weights do not exist for most species in our data, making any conversion between length and biomass units impossible, and demonstrating the need for additional basic and management-relevant information about the taxa in the Lower Mekong Basin.

We calculated the resource selection ratio—the selection of the gillnet fishery relative to the Dai fishery—for common genera and trait groups. We report the annual resource selection ratios for *Henicorhynchus*, *Paralaubuca*, and *Labiobarbus*. We also report annual selection for three trait groups: migration guild, body size group, and trophic group.

Next, we were interested in understanding if inter-annual variation in the flood pulse contributed to differential selection of the gillnet fishery compared to the Dai fishery. For example, high flow years may trigger more fish to migrate from the Tonle Sap Lake to the river, thus increasing the availability of white fish relative to black fish in the Dai fishery. In these years, the gillnet fishery may demonstrate a lower selectivity for white fish as they are more likely to be in the main flow of the river than in the edge near the gillnets. To test this prediction, we estimated Pearson's correlation between the flood pulse extent and the resource selection ratio for each genus (*Henicorhynchus*, *Paralaubuca*, and *Labiobarbus*) and trait group (migratory guild, body size, and trophic level).

2.5. Trait Changes in the Dai and Gillnet Fishery

Overfishing and targeted selection can cause shifts in body size and trophic level of fish communities in tropical regions [46–48]. We predicted that the more size-selective gillnet fishery would demonstrate a greater decline in traits such as body size and trophic level. For both fisheries, we estimated the annual weighted mean of maximum total length (cm) and trophic position using the trait database, weighted by catch. We estimated weighted means using the "wtd.mean" function in the "Hmisc" package in R [49]. Next, we conducted linear regressions between these two traits and year for each fishery for a total of four linear regressions.

3. Results

3.1. Comparing Annual Catch to Flooding Magnitude

The annual catch of the Dai fishery was strongly correlated with flood pulse extent (t = 2.9, df = 5, $p = 0.03$, Pearson's correlation = 0.80), and both peaked in 2011 (Figure 2). The seasonal catch of the gillnet fishery did not follow the pattern of the flood pulse extent, but peaked instead in 2009 (Figure 2), which was a year with an average flood pulse extent. Gillnet catch and flood pulse extent were not correlated ($p > 0.1$, Pearson's correlation = 0.17).

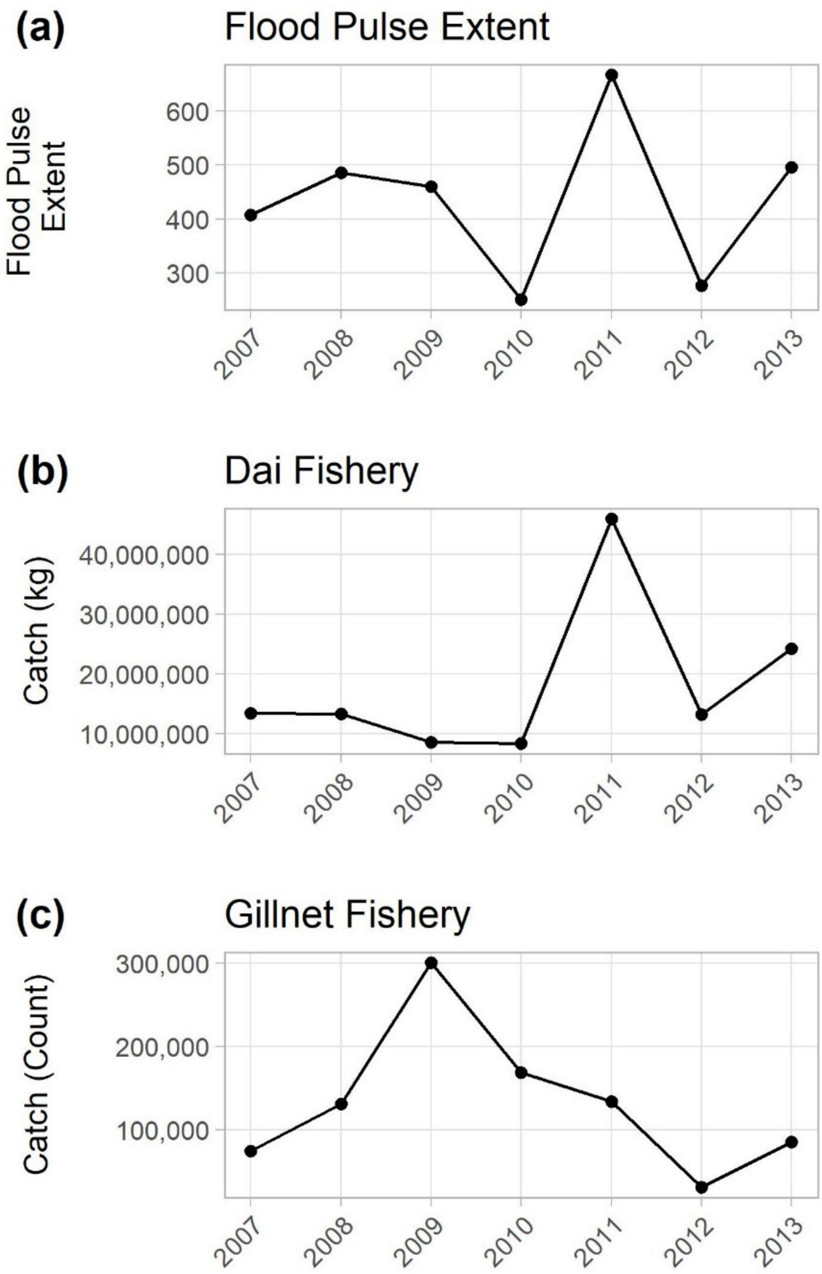

Figure 2. (**a**) Time series of the flood pulse extent (mean deviation from baseflows × number of days exceeding baseflows), (**b**) catch of the Dai fishery, and (**c**) catch of Gillnet fishery.

3.2. Community Analyses to Compare the Dai and Gillnet Fisheries

Over the seven-year record, the catch of the gillnet and Dai fisheries was represented by a similar number of unique species and genera (143 species from 88 genera in the gillnet, versus 141 species from 81 genera in the Dai). There were 26 genera in the gillnets that were not observed in the Dai and 19 genera in the Dai that were not observed in the gillnets. Within any given year, the Dai fishery consistently captured more genera (77–81) than the gillnet fishery (41–64) (Figure 3). Additionally, the Shannon index, a measure of evenness, was nearly twice as high for the Dai fishery than the gillnet fishery annually (Figure 3).

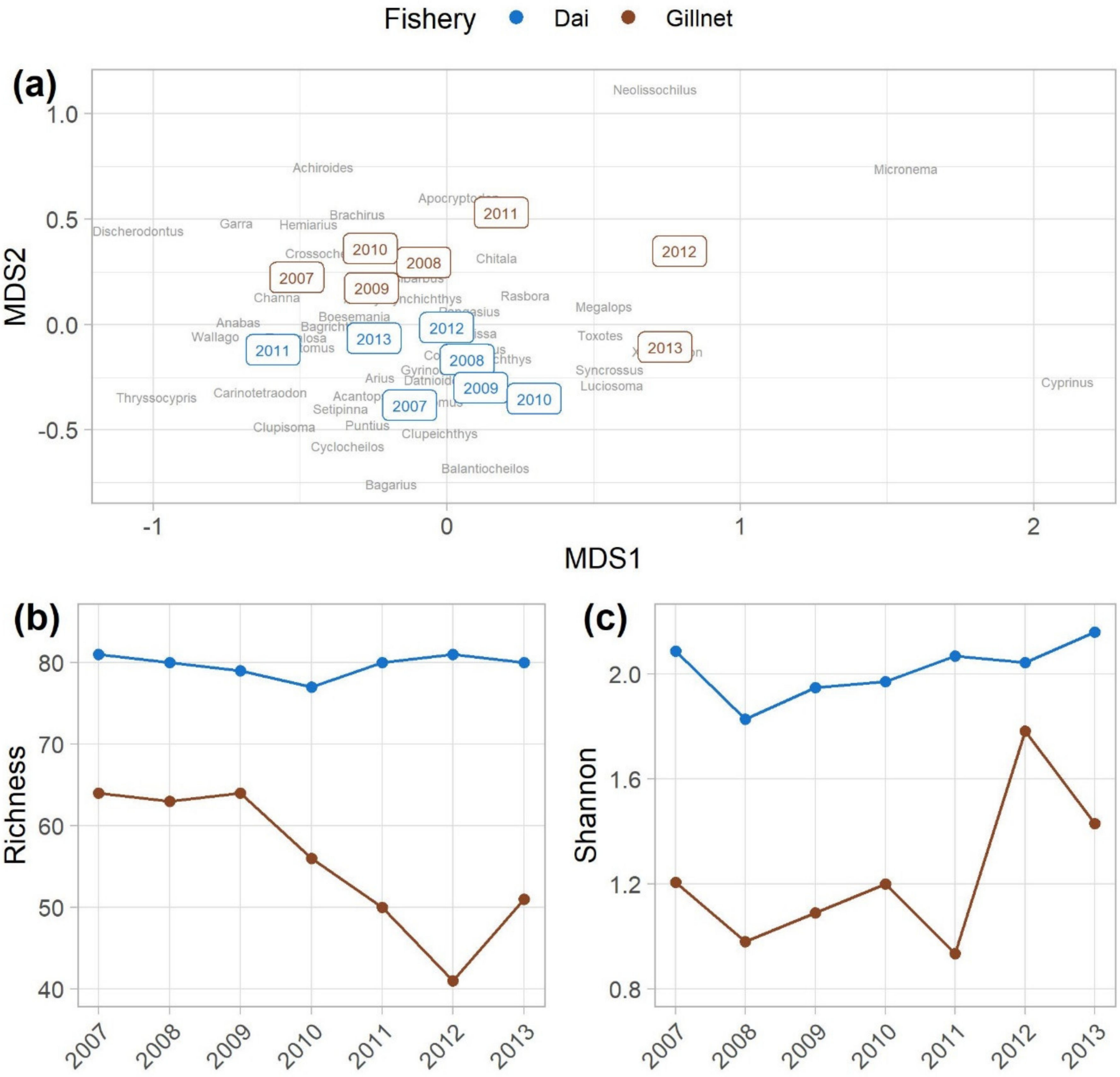

Figure 3. (**a**) Non-metric multidimensional scaling plot visualizes that the Dai fishery and gillnet fishery capture different communities of fish. The Dai fishery (**b**) captures a greater number of species and (**c**) has a higher Shannon index annually than the gillnet fishery.

The NMDS plot demonstrates that the Dai and gillnet fisheries are capturing different communities of fish, with sites separating along MDS axis 2 (Figure 3). Fishing method explained a significant amount of variance in the community structure in a PERMANOVA test ($F_{1,13} = 2.28$, $p = 0.01$), while year did not ($F_{6,13} = 0.99$, $p > 0.1$).

The three most common genera were *Henicorhynchus*, *Paralaubuca*, and *Labiobarbus* which represented 91.7% of the total catch of the gillnet fishery and 75.1% of the Dai fishery across all seven years. *Henicorhynchus* was by far the most caught taxa and represented

48.7% of the gillnet catch and 47.7% of the Dai catch. *Paralaubuca* was also common, representing 29.9% of the catch in the gillnet and 11.7% of the catch in the Dai. Lastly, *Labiobarbus* represented 13.3% of the catch in the gillnet and 15.7% of the catch of the Dai. Overall, the gillnet fishery demonstrated much higher inter-annual variability in the proportion of seasonal catch that was represented by each of these three genera (Figure S2).

3.3. Resource Selection Ratios to Quantify Gillnet Selectivity Relative to the Dai Fishery

Two of the common genera, *Henicorhynchus* and *Labiobarbus*, had resource selection ratios close to 1, indicating that the gillnet fishery catches those genera at similar proportions as the Dai fishery (Figure 4). There was some variation among years, with the resource selection ratio reaching 2.1 for *Labiobarbus* in 2011, meaning it was twice as common in the gillnet fishery compared to the Dai fishery. *Paralaubuca* had much higher resources selection ratios overall, but with great variation among years. The ratio was greater than 2 for all years except 2011 and 2012, when it was less than 1 (Figure 4). For all three genera, there was no relationship between flood pulse extent and resource selection ratios in a Pearson's correlation ($p > 0.1$ for all correlations, Figure S3).

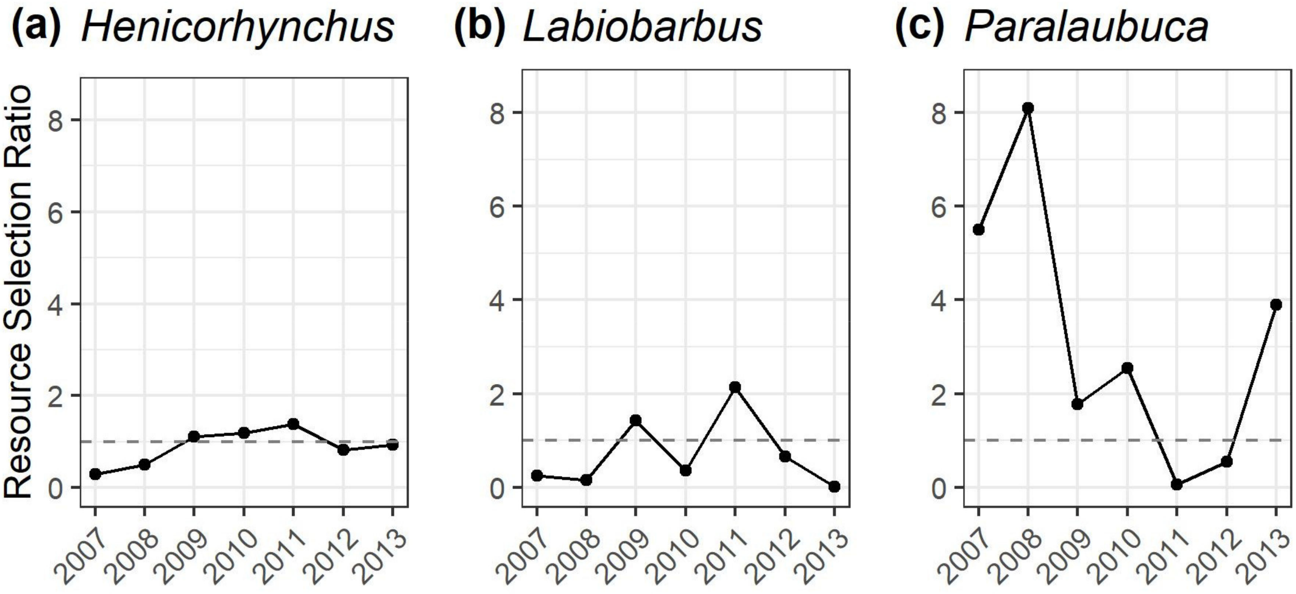

Figure 4. Resource selection ratios for the three most common genera, (**a**) *Henicorhynchus*, (**b**) *Labiobarbus*, and (**c**) *Paralaubuca*, representing selection the gillnet fishery relative to the Dai fishery. Grey dashed line is at 1, representing when the genera is caught equally in both fisheries.

Grey fish were caught at higher rates in the gillnet fishery in most years, except for 2011 and 2012 (Figure 5). White fish were half as common in the gillnet fishery than the Dai fishery in 2007–2008, while in 2007 black fish were more common in the gillnet than the Dai fishery (Figure 5). The gillnet demonstrated no strong selection for small fishes, but under-selected for large fish relative to their availability (Figure 5). Medium-sized fish were equally represented in both fisheries, except in 2012, when they were overrepresented in the gillnet fishery, with a resource selection value of 4.1 (Figure 5). Overall, the gillnets tended to select for fish of higher trophic levels. Resource selection ratios for fish in trophic group 2 were >1 for all years except 2012, and >2.5 in 2008 and 2010. Selection for fish in trophic group 3 was below 1, until 2012 and 2013, when the ratio was 3.9 and 4.2, respectively (Figure 5). For all trait groups, there was no relationship between flood pulse extent and resource selection ratios ($p > 0.1$ for all Pearson's correlations, Figure S4).

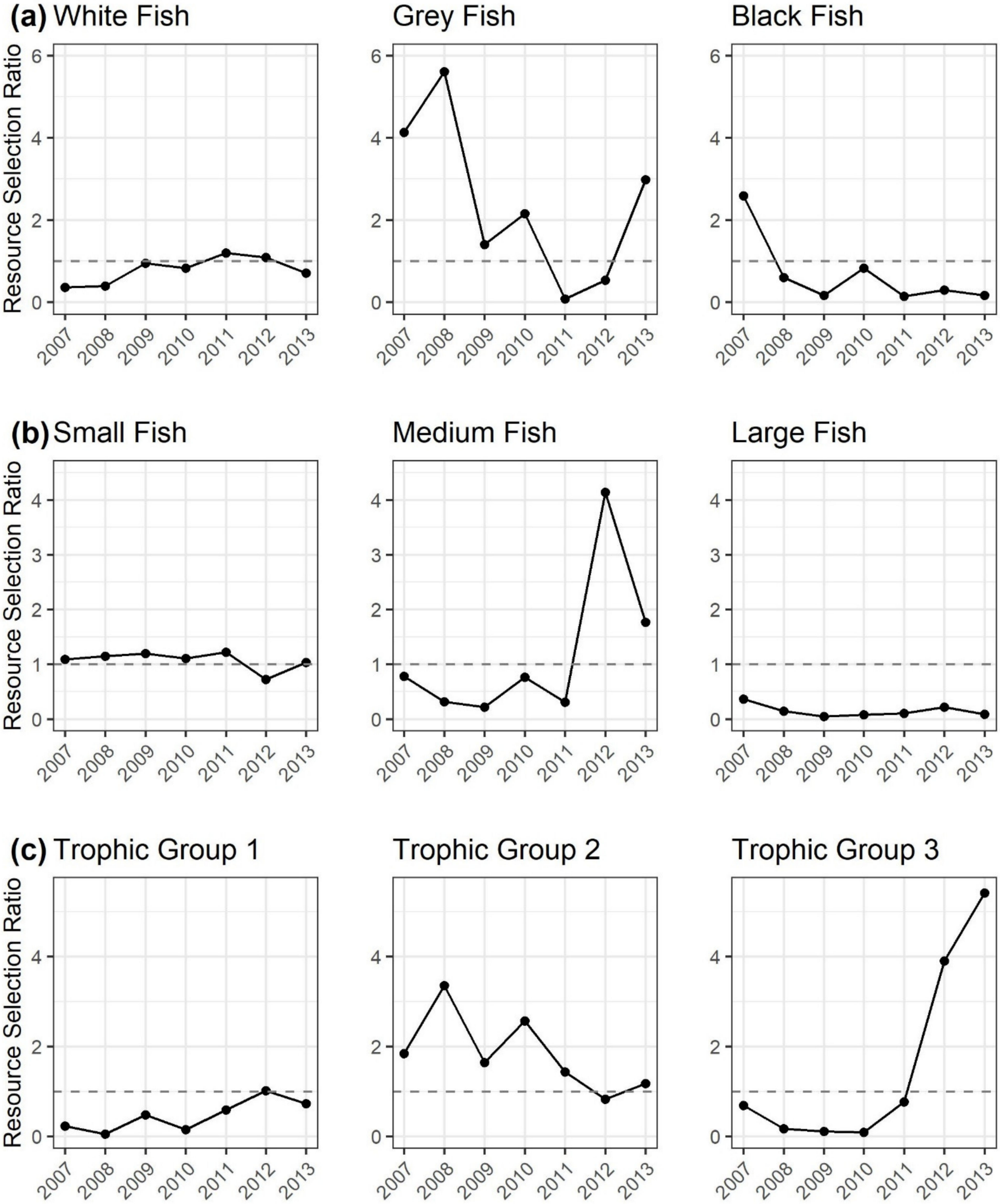

Figure 5. Resource selection ratios for the trait groups estimate selection by the gillnet fishery relative to the Dai fishery. Grey dashed line represents when the resource selection ratio equals 1, when the group is represented equally by both fisheries. (**a**) Selection for migratory guilds. "White" fish are longitudinal migrants, "grey" fish are latitudinal migrants, and "black" fish are floodplain residents. (**b**) Selection for body size groups. Small fish are <25 cm total length, medium fish are 25–60 cm, and large fish are >60 cm. (**c**) Selection for trophic level groups. Trophic group 1 are fish of trophic level <2.75, trophic group 2 are 2.75–3.75, and trophic group 3 are >3.75. Note the difference in scale on the y-axis for all trait groups.

3.4. Trait Changes in the Dai and Gillnet Fishery

We predicted that weighted mean of maximum total length and trophic level would be more likely to decline in the gillnet fishery than the Dai fishery given its greater potential for size-selectivity. We found that weighted mean of maximum total length showed no significant change in the gillnet fishery through time ($p > 0.1$ in a linear regression, Figure 6). The weighted mean of maximum total length slightly increased over the same period in the Dai fishery ($F_{1,5} = 7.9$, $p < 0.05$, slope estimate = 0.67 ± standard error = 0.24, adjusted R-squared = 0.54) (Figure 6). We found that the weighted mean of trophic position declined over seven years in the gillnet fishery ($F_{1,5} = 6.9$, $p = 0.05$, slope estimate = -0.07 ± standard error = 0.03, adjusted R-squared = 0.49), but not in the Dai fishery ($p > 0.1$) (Figure 6). Residuals did not violate a Shapiro-Wilk test for normality for all regressions ($p > 0.1$). For this dataset, body size categories include a range of trophic level groupings (Figure S5), allowing for different results for these two trait groups.

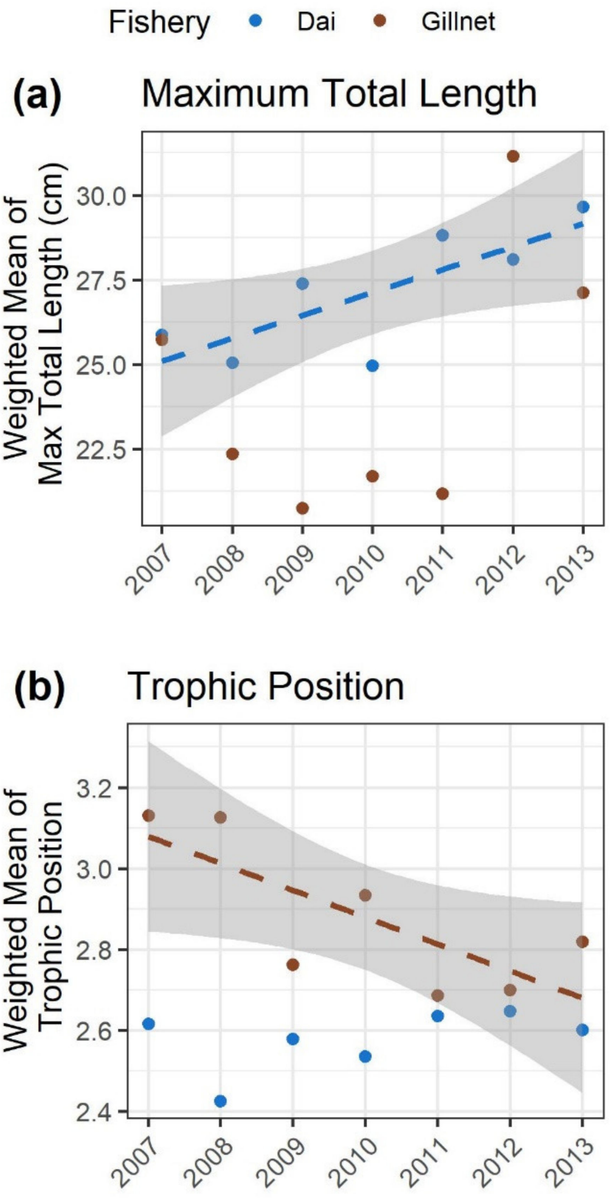

Figure 6. Changes in (**a**) weighed mean of the maximum total length and (**b**) weighted mean of trophic position over seven years in the Dai and gillnet fishery. Significant linear regressions are plotted, and grey areas represent one standard error.

4. Discussion

The Dai and gillnet fisheries demonstrated overlap in the most caught genera but responded differently to major climatic events. The catch of both fisheries was dominated by three genera that are known to migrate down the Tonle Sap River at the end of the rainy season as the lake recedes. However, the Dai catch was correlated to annual flood pulse extent, while the gillnet catch was not. The approximate total number of species and the most common genera were similar. The Dai catch was consistent, catching almost the same number of genera at similar proportions every year, whereas the gillnet catch was more variable both in terms of total number of genera and the composition. Variability in the gillnet catch is likely driven by the efficacy and use of the gear in the gillnets, as well as the ability of fishers to target certain groups in some years. Neither the Dai fishery nor gillnet fishery reliably captured rare species, or at least they were not reported, a common phenomenon which has often has substantial implications for conservation management using wildlife models [50].

Relying on just one gear type to gather information about the state of the fishery will likely lead to biased or incomplete inferences. We suggest that the Dai fishery provides a more consistent estimate for annual production, especially for white fish that migrate from the Tonle Sap Lake to the Mekong River. On the other hand, the catch of the gillnets may be more likely to pick up subtle changes in the spatial and temporal habitat use of fishes. This difference may be especially true for floodplain residents and fish that migrate from the floodplain to the river, who may be more likely to found in edge habitats. The catch in the gillnet is likely to be more variable as their deployment is more flexible and fishers can shift their target catch by changing mesh size and/or exact location. Monitoring more gillnets (>3 per day as in this dataset) may help resolve reasons for variability in the catch. As gillnets continue to grow in popularity, understanding the selectivity of this gear type will become increasingly important. Understanding shifts in taxa that are targeted by the gillnets, relative to the Dai fishery, may inform which taxa and trait groups (i.e., higher trophic level fish) are threatened and in need of new management policies. Both datasets would greatly benefit from taxa-specific length-weight information to understand potential shifts in population size and age structure. We suggest that monitoring both fisheries provides a more complete picture of the status and composition of the fish and fishers' preference in the Tonle Sap Lake and River ecosystem. Other studies have similarly identified that gillnets can complement other methods to provide a complete understanding of species composition [51,52].

The total catches of both the Dai and gillnet fisheries were dominated by fish from the same three common genera, *Henicorhynchus*, *Labiobarbus*, and *Paralaubuca*. Using the same dataset going back to 2001, Ngor et al. [14] reported that these three genera contributed 66% of the total Dai catch, while we found that from 2007–2013 the same genera contributed 75.1%, suggesting that overall, the Dai fishery is increasingly reliant on these small-bodied species [53]. Yet, remarkably, these three genera comprise 91.7% of the total gillnet harvest during this same period. Thus, gillnet fishermen are likely to be disproportionately impacted by fluctuations in these taxa. Given the increasing reliance on these three taxa, information on the size and age structure from monitoring fish length will inform if these taxa can support increased fishing pressure.

Despite the reliance of both fisheries on these three genera that migrate from the Tonle Sap Lake to the River with receding flows, the gillnet fishery was not as responsive to annual variation in the flooding extent, which is an aspect of the Dai fishery that has been repeatedly noted [18,19,21,54]. There is a need to understand why total catches of the gillnet do not follow the total catches in the Dai and variations in flood pulse extent. One reason may be that the gillnets are not continuously monitored and might "fill up" over the period of their deployment (approximately 12 h). On the other hand, the Dai fishery is constantly operated and lifted and so may be better suited to continuously harvest during periods of high fish density. However, it is possible that the gillnet gear may be more resilient to short term droughts since total catches and catches of common taxa were not driven by the flood pulse extent in this fishery. More information on factors that impact fishers' decisions on net sizing and placement will be very helpful in understanding the future resiliency of this ubiquitous fishing method.

Although the relationships between flood pulse extent and resource selection ratios for the three common taxa by the gillnets were not statistically significant (Figure S3), there are a few patterns that warrant discussion. First, the selection ratio for *Henicorhynchus* hovered near 1, while *Labiobarbus* showed slightly more variation (Figure 4). The selection ratio for *Paralaubuca*, however, was >1 for all years except 2011 and 2012, and exceeded 8 in 2008, meaning 8 times more *Paralaubuca* were caught in gillnets than in the Dai that year. Interestingly, 2011, the year with the highest flood pulse extent and highest catch in the Dai fishery (Figure 2), was the year when the resource selection ratio for *Labiobarbus* was highest, at 2.1, and for *Paralaubuca* was lowest, at 0.1. These differences may be due to slight variations in habitat use and downstream migration habits of these two taxa. *Labiobarbus* tend to occupy the midwater-to-bottom of rivers while *Paralaubuca* are found in slower, often standing water, and migrate near the surface along the riverbank. In higher flow years when water velocity increases, *Paralaubuca* may be more difficult to catch in gillnets. However, selection for *Paralaubuca* in the gillnets in the following year, in 2012, was also low, even though it was a drier year, suggesting that there are more factors aside from water velocity that determine its abundance and catchability in the gillnets.

While most of the catch was dominated by common genera in both fisheries, the rarer taxa differed in composition (Figure 3). Additionally, the Dai fishery consistently captured the same number of species throughout the seven years, and at similar proportions (evenness) as quantified by the Shannon Index. Meanwhile, the gillnet fishery demonstrated greater inter-annual variation in the number of taxa and evenness. This difference may be due to the mechanics of the nets: the Dai captures all fish that are flowing with and through the water column, while the gillnet may be more subject to variations in individual fish movements into the stationary nets. Additionally, community species composition and catch estimates of the Dai fishery are done by subsampling the catch [14] which may be prone to missing rare species. The focus of the Dai is commercial in nature and thus is more consistent. The stochasticity of the gillnets may be due to variation in their deployment by fishers, given that it is largely for subsistence purposes and thus more flexible to change with independent preferences, which could include unreported alterations in mesh size and location.

One notable difference between the two fisheries is that the gillnets selected for grey fish, the category of fish that migrates laterally between the floodplain and main river channel. Without further surveys of the fishers, we do not know if this is due to selection differences inherent to the gear types or due to preference of gillnet fishers for these fishes. More specifically, the Dai fishery is inherently better positioned to capture white fishes, but it is unclear if the gillnet fishers can make intentional adjustments in their gear and deployment to increase their catch of grey fish relative to white fish. The years of 2011 and 2012, the wet year and following dry year, were the only years when grey fish were relatively less common in the gillnets and the resource selection ratios fell below 1.0 (Figure 5). It is possible that, though brief, the reduced catch of grey fish in these two years was due to drought-associated population declines that occurred in 2010 (the driest year in our time series, Figure S1), and grey fish populations may have required multiple years to recover. Regardless, the trend that gillnet fisheries disproportionately selected for grey fish could be of great concern as it indicates that this increasingly widespread and difficult to monitor gear type is targeting a group of fish that was previously less impacted by the Dai fishery. There remains much to learn about the movement and reproductive biology of many of these intermediate migrants, and future research should seek to understand the ecological and economic impacts of overfishing grey fish in the Lower Mekong Basin.

Contrary to expectations, neither fishery demonstrated a decline in maximum body size over this seven-year time series. In fact, we observed an increase in the weighted mean of maximum total length for the Dai fishery between 2007 and 2013. The slight increase in larger-bodied fish may be related to the removal of the century-old lot fishing system in the Tonle Sap Lake in 2012, which targeted fish in the lake before they would have migrated to the Tonle Sap River. The Dai fishery, which is largely upstream of our monitored gillnet, may have enjoyed a temporary increase in large-bodied fish as a result. Additionally, the large flood pulse in 2011 may have facilitated the ability of fish to disperse from upstream habitats of the Mekong to the lower floodplain such as Tonle Sap. In the gillnet fishery, there was substantial annual variation in weighted mean of maximum lengths, ranging from 21 to 31 cm (Figure 6). This variation is likely due in part to the greater potential for variation in site selection of individual fishers relative to the Dai nets. Additionally, the two years with the highest weighted mean of maximum total length in the gillnets were 2012 and 2013, which may again be related to the removal of the lot system in the lake in 2012 and the high flood pulse in 2011.

While the increase in weighted mean of maximum body size in the Dai fishery could be interpreted as a positive sign for the overall Mekong fish community, analyses conducted over longer time series show that this trend is relatively recent, and minor compared to then longer-term decline that began at least in 2001 [14]. It is likely that the average and maximum body size of fish shifted before our time series began, as an increase in the dominance of small-sized fish in the Dai net catches was previously observed between 2000 and 2008 [29]. Larger-bodied fish species typically require multiple years to reach sexual maturity, making them particularly prone to overfishing and skewing catch towards smaller species with higher population growth rates [53]. Thus, it is highly likely that the average and maximum body sizes of fishes shifted before the earliest date in our time series (2007). Furthermore, the increase from approximately 25 to 28 cm we observed in mean catch-weighted maximum size is small relative to the reported mean catch-weighted maximum length of 55 cm reported for the Dai fishery in 2002 (Ngor et al. 2018a). This longer-term decline is largely due to a loss of large-bodied and often threatened fishes, such as giant catfishes in the Mekong River, though quantitative historic data demonstrating how common these taxa were previously are lacking [47,55,56]. In summary, major declines in fish length likely preceded the time series available for our analysis, making more recent decreases less likely and slight increases relatively minor.

Furthermore, although we observed no change in maximum body size for this time series, this result does not indicate that size selectivity is not occurring in both fisheries. Empirical data on lengths of each species in each year, rather than the groupings based on the estimated maximum length of the species that were available in this dataset, would allow for estimates of gear-specific size selectivity [24,57]. In fact, gillnets are known to be size-selective [58], and an exception in the Tonle Sap River ecosystem would be a surprise. This species-specific length data could also provide important insights into how behaviors of fishers shift in response to fish body size evolution [59,60]. Species-specific length data would also facilitate more direct comparisons between the Dai fishery and the gillnet fishery, which are currently reported in weight and number of fish, respectively. Collection of baseline monitoring data through time will be critical for developing population growth and size structured models that could help predict the potential impacts of fisheries, dams, and climate change on these important fisheries.

Our analysis showed that the gillnet fishery does not select for large fishes (Figure 5), despite their potential profitability compared to small fish [29]. In fact, large fish (>60 cm) were the only size category of fish having a resource selection ratio <1 across all years. There are at least two possible explanations for this. First, Cambodian fisheries law officially limits the size of gillnet mesh to sizes between 1.5 and 15 cm in inland waters [61]. Because gillnets are designed to entangle fish of specific body depths by using specific mesh sizes, the largest fish may be too large to become entangled or sufficiently powerful to break free from the relatively lightweight monofilament nets that are commonly used (Figure 1). The Dai nets, however, are designed not to entangle fish gills, but rather to funnel them towards the terminal trap, effectively retaining even large fish. Second, it may indicate that fishers have determined it is not profitable to deploy gillnet mesh sizes that would target larger species because they are not present at high enough densities. Instead, they target their efforts at more abundant smaller species [62], which comprised over 90% of the total gillnet catch.

Interestingly, we observed a decline in mean trophic position in the catch in the gillnet fishery. The fact that the gillnet fishery showed selection for higher trophic level fishes than the Dai fishery also supports our result that the gillnets display a change in this trait through time while the Dai does not. At the end of the time series, in 2012 and 2013, there was a simultaneous increase in the resource selection ratio for fish in trophic group 3 (>4, Figure 5) and decline in the resource selection ratios for fish in trophic group 2. This finding suggests that there may be a tradeoff in the net placement for targeting fish from higher trophic levels, or that fish in trophic group 2 became relatively less available to the gillnet fishery. Interestingly, the increase in the resource selection ratios for fish in trophic group 3 in the gillnet fishery was driven by an increase in the genus *Xenentodon*, a predatory needle fish (Figure S6). This increase was not seen in the Dai fishery (Figure S6). It is possible that the increase in *Xenentodon* in 2012–2013 in the gillnets is also related to the removal of the lot system in the Tonle Sap Lake in 2012. Continuing this time series would determine if this trend is long-term and reflects trade-offs for fishers and/or community level changes. Regardless, the potential loss of biomass of higher trophic level fish could have consequences for the entire food web of the Lower Mekong River.

We found that resource selection ratios were useful in understanding the differential resource use of gillnet fisheries relative to the Dai fishery. Resource selection ratios could be applied to further inform management strategies if data gaps are appropriately addressed. We estimated resource selection ratios for the annual catch (for the Dai fishery) and for the seasonal catch of the gillnet encompassing the same time period. As data become available at a finer scale temporal resolution, e.g., weekly, future research could ask how selectivity of the two methods differ throughout the season. For example, during the two migration pulses that are associated with the full moon and high catches in the Dai fishery [63], we might expect that the gillnets select for migrants at a higher rate. Similarly, the Dai fishery tends to capture large and medium-bodied taxa earlier in the season, in October–November [18], and the gillnet fishery may show a different pattern of selection in these months before the catch is dominated by *Henicorhynchus*. Additionally, further information on the body sizes for fish of each species that are captured would be particularly useful in understanding if the gillnets are selecting for fish of a different life stage than the Dai. For example, we might predict that the gillnets capture more juveniles, since they are located closer to the marginal riverbank habitats.

5. Conclusions

Fishing methods matter for quantifying changes in community and abundance of catches in freshwater ecosystems supporting multi-species and multi-gear fisheries. We suggest that the Dai fishery is more likely to be a better estimate of relative annual production of the fishery, since the methods are stationary and better standardized. However, because gillnets are widespread, understanding their apparent selection for fish of higher trophic level and those classified as grey fishes has implications for the entire fishery. We highlight that further data on species-specific body sizes within each fishery will be critical for guiding evolutionary-informed management in light of widespread fisheries selectivity that has been documented globally.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/w13141904/s1, Figure S1: Hydrology in Tonle Sap River, Figure S2: Interannual variation in catch represented by three common genera, Figure S3: Flood pulse extent and resource selection ratios for three common genera, Figure S4: Flood pulse extent and resource selection ratios for trait groups, Figure S5: Body size and trophic level groups in the Dai and gillnet fisheries, Figure S6: Annual catch of trophic group 3 fish in the gillnet fishery and in the Dai fishery.

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