

Article

Mugilids Display Distinct Trait-Mediated Patterns with a Reinvasion of Para Grass *Urochloa mutica* in a Tropical Estuary

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Abstract: Aggressive invasions by species such as para grass *Urochloa mutica* (Forssk.) are pervasive throughout the tropics, but the impacts on estuarine habitats and biota are poorly understood. After weed control was reduced in a tropical estuary, *U. mutica* reinvaded this area composed of two contiguous habitats: a shallow pond and a deeper river. These habitats are especially important for *Mugil cephalus*, a culturally prized native mullet, and introduced *Moolgarda engeli* not targeted in the fishery. We investigated the potential impacts of *U. mutica* on juvenile and adult mullets by comparing the catch per unit effort (CPUE) of the two mullet species and the physiochemical measurements from the two contiguous habitats during different stages of its reinvasion. Overall, negative effects on the CPUE of *M. cephalus* and *M. engeli* were found as a result of the *U. mutica* reinvasion. The *M. cephalus* CPUE was consistently higher in the shallow pond habitat compared to the deeper river habitat. It decreased after *U. mutica* was established, correlative to the invasive grass canopies smothering the shallow habitat favored by juveniles. The *M. engeli* CPUE significantly declined during the initial periods of *U. mutica* reinvasion, but did not decline further after the grass became established. No differences in the *M. engeli* CPUE between habitats were found, indicating that *M. engeli* are habitat generalists. These findings are among the first in an insular tropical estuary demonstrating a negative relationship between an invasive grass and relative abundances of two confamiliar fish, while revealing distinct patterns attributed to species-specific traits. Importantly, the broad overlapping biogeographic distribution of *M. cephalus* and *U. mutica*, and the negative relationship between these species, raises widespread concern for this mullet as a globally important fisheries species.

Keywords: *Moolgarda engeli*; *Mugil cephalus*; *Urochloa mutica*; tropical island estuaries; fisheries

1. Introduction

Coastal and inland fish interact with aquatic plants, especially habitat-forming plant species. Vegetated habitats, overall, have been shown to support higher densities of fish than open habitats, because aquatic plants provide ecological services that benefit fish, and thus the productivity of fisheries [1–3]. In particular, vegetated aquatic habitats improve the water quality by releasing photosynthetically-derived oxygen, trapping sediments and stabilizing banks [4–6], and support communities of macroinvertebrates and periphyton that are important in fish diets [7]. However,

in cases where the aquatic plant is an exotic species, challenges arise for the conservation of biological diversity, environmental policy, and fisheries management. Introduced macrophytes compete in new ecosystems to the extent that exotic plants routinely displace those which are native, reducing plant diversity and richness [8], while potentially altering ecosystem processes [9]. After native vegetation is outcompeted, it is critical to understand whether the invasive plant provides ecological services that benefit fish populations in the recipient communities or whether the systems are degraded by the introduced aquatic plant.

Previous studies on aquatic plant invasions have primarily focused on freshwater habitats, highlighting the complexity of factors that contribute to the success and effects of such invasions [10,11]. For example, dense canopies of the grass family Poaceae have been shown to reduce fish abundances, richness, species diversity, and habitat availability in the Neotropics [12,13]. Significant changes in habitat complexity and structure caused by invasive macrophytes have also been shown to affect the behavior of freshwater game fish by reducing their foraging efficiency [14,15]. In addition, canopies of invasive macrophytes can cause significant reductions in water flow, open water, and light availability, thus leading to lower dissolved oxygen levels, reduced periphytic production, and an altered trophic structure [16]. Yet, others have reported a lack of effects by macrophytic invasions on freshwater faunal communities in the tropics [17–20], confirming that the biological effects from macrophytic invasions are condition-specific, species-specific, and variable among recipient communities. In estuarine habitats, however, these types of invasive plant-animal interactions are understudied.

Invasive aquatic plants that negatively affect native fish possess traits such as allelopathy, phenotypic plasticity, and rapid growth that results in dense, monospecific canopies [10]. Found in both freshwater and estuarine habitats, para grass *Urochloa mutica* (Forssk.) TQ Nguyen is a semi-aquatic species that possesses these invasive plant traits. *Urochloa mutica* aggressively invades lowland areas, storm canals, wetlands, streams, estuaries, and other low energy habitats throughout many tropical regions including northern Australia, coastal Asia, southeastern North America [21–23], and many Pacific Islands, including Hawaii [24–28]. In particular, the salinity tolerance of *U. mutica* [29] and its proliferation in calm waters with especially fast-spreading fronts [30,31] put warm water estuaries at risk because it commonly displaces native vegetation.

Estuaries are highly productive ecosystems that serve critical ecological functions and services [32], including the provision of a habitat for recreationally, commercially, and ecologically important species [33], nursery areas for juvenile fishes [34], and passageways for amphidromous species [35,36]. One species that uses estuaries throughout its cosmopolitan range, particularly in shallow habitats, is the piscine herbivore striped mullet *Mugil cephalus* Linnaeus, 1758, [37–39]. This species is prized as a sport fish and food fish [40], as well as being highly esteemed for its historical and cultural value in Hawaii [41].

The *M. cephalus* population in Hawaii now co-occurs with an invasive mullet known as kanda mullet *Moolgarda engeli* (Bleeker, 1858). Although *M. engeli* was unintentionally introduced to Hawaii in 1955, this species has successfully established in estuaries statewide [42,43] and has surpassed *M. cephalus* in numerical abundance [41]. Both of these mullet species primarily graze on microphytobenthos that is prolific in shallow open habitats. Therefore, if such habitats become limited, competition for both food and habitats between these mullet species may increase [43,44]. *M. engeli* has displayed, however, more generalist traits by readily feeding on a broader variety of algae [45], and it is apparent that the invasive mullet is free of fishing pressure due to their smaller size and lower commercial value. This translates to the invasive mullet population having at least two competitive advantages over the native mullet population in Hawaii.

Hawaii's Division of Aquatic Resources (DAR) conducted a bimonthly mullet monitoring program using cast-nets (0.6 cm and 1.0 cm meshes) between 2005 and 2014 (see Section 4.3 for details), and observed a *U. mutica* reinvasion within the sampling site that consisted of a shallow estuarine pond, Waiakea Public Fishing Area (PFA), and a deeper connected estuarine river, Wailoa River, in Hilo, HI, USA (Figure 1). Previously, invasive vegetation along the banks of the sampling site was

regularly controlled with herbicide and trimming, but these efforts were reduced due to logistical and funding constraints ca. 2007. Based on the observations recorded by DAR staff, we determined that at the sampling site, *U. mutica* was rare at the land-water interface prior to September 2007 (invasion status: “pre-invasion”). Some rooted canopies (Figure 2) of *U. mutica* invaded the shoreline of the site between September 2007 and March 2010 (invasion status: “detected”), followed by an expansion of rooted canopies into floating canopies and drifting mats (Figure 2) after May 2010 (invasions status: “established”). Further, the expansion rates and its invasion potential (based on the bathymetric characteristics of the estuary and habitat preference of *U. mutica*) were notably different between these estuarine habitats, with the shallower Waiakea PFA experiencing a faster and more extensive invasion compared to the deeper Wailoa River (Figure 1, Table S1, Figure S1).

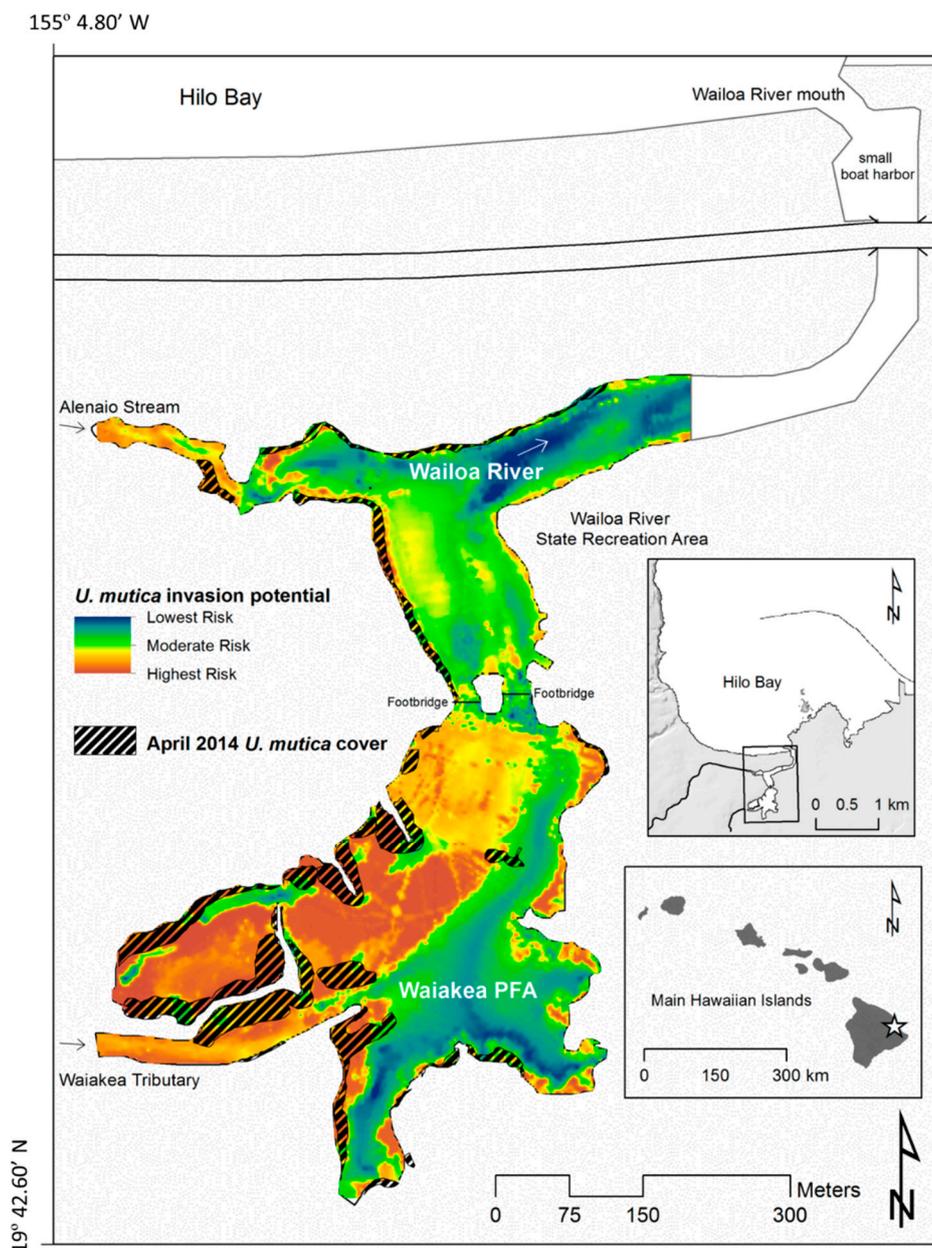


Figure 1. Map depicting the areal coverage of *Urochloa mutica* in April 2014 and its invasion potential based on the bathymetric characteristics of the Waiakea Public Fishing Area (PFA) and Wailoa River in Hilo, HI, USA. Invasion potential is based on a negative relationship between the existing *U. mutica* invasion and water depth (Figure S2).

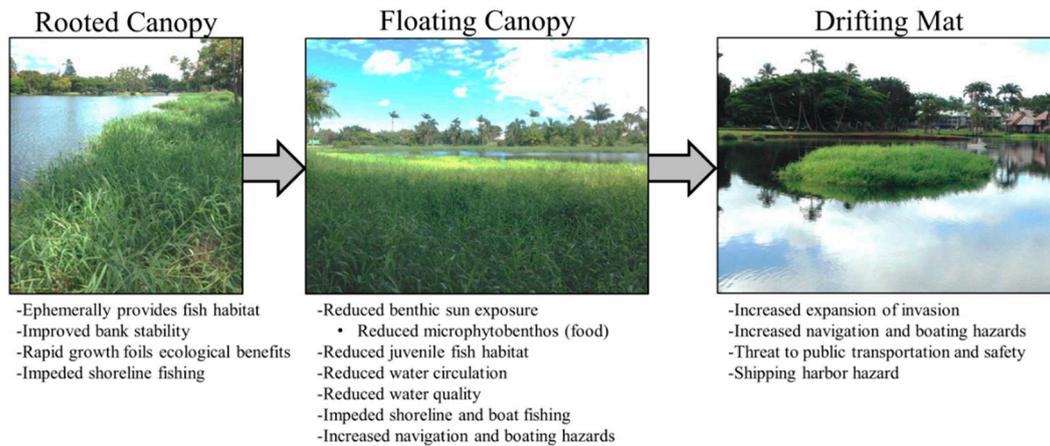


Figure 2. Schematic of a successive triphasic *Urochloa mutica* invasion and the potential effects per phase in the Waiakea Public Fishing Area and Wailoa River, Hilo, HI, USA.

Here, we examined a reinvasion of *U. mutica* in a Hawaiian estuary—a critical habitat for both juvenile and adult *M. cephalus* and *M. engeli*—to understand the invasive plant’s effects, and any potentially associated effects, on the relative abundance of both mullet species. To examine if *U. mutica* affected the mullet abundance in shallow water, we used the nine-year catch-per-unit-effort data set that serendipitously monitored the relative abundance of *M. cephalus* and *M. engeli*, as well as physiochemical characteristics, every two months inside the Waiakea PFA and Wailoa River during three periods of the reinvasion: pre-invasion (*U. mutica* rare); detected (some rooted canopies present); and established (rooted canopies, floating canopies, drifting mats present). As an introduced species that is widely established throughout the Hawaiian Islands, we hypothesized that *M. engeli*, as juveniles and adults, would be a habitat generalist and therefore not have any detectable response to the reinvasion of *U. mutica*. In contrast, because shallow water is both the preferred habitat by *M. cephalus* and highly susceptible to invasion by *U. mutica*, we hypothesized that the overgrowth of dense canopies of invasive grass would negatively affect *M. cephalus*, especially as juveniles. From this investigation, we intend to provide insight into the biological and physical effects of aquatic grass invasions in tropical estuaries and its repercussions on inhabiting native fishes and supported fisheries.

2. Results

2.1. Shoreline Physiochemical Characteristics

Dissolved oxygen (DO) concentrations (mg L^{-1}) were significantly different across invasion statuses (Table 1). Specifically, DO was significantly higher during the pre-invasion period compared to either the detected or established period (pairwise comparisons, $p < 0.02$, Figure 3A). In addition, DO concentrations were significantly higher throughout sampling stations in Waiakea PFA compared to Wailoa River (Table 1). In Waiakea PFA, the average DO (\pm standard error - SE) was $8.87 \pm 0.19 \text{ mg L}^{-1}$ during pre-invasion, $7.46 \pm 0.12 \text{ mg L}^{-1}$ during the detected period, and $7.61 \pm 0.13 \text{ mg L}^{-1}$ during the established period. In Wailoa River, the DO averaged $8.44 \pm 0.10 \text{ mg L}^{-1}$ during pre-invasion, $7.16 \pm 0.11 \text{ mg L}^{-1}$ during the detected period, and $7.33 \pm 0.09 \text{ mg L}^{-1}$ during the established period. No significant interaction effect was found between the habitat and invasion status on DO concentrations.

A significant interaction effect between the habitat and invasion status was found for water temperature (Table 1). Water temperature in Waiakea PFA decreased by an average (\pm SE) difference of $0.63 \pm 0.13 \text{ }^\circ\text{C}$ from pre-invasion to established periods, whereas the water temperature in Wailoa River was notably more stable, with an average difference of $-0.002 \pm 0.16 \text{ }^\circ\text{C}$ during the same periods. Further, the water temperature was consistently lower in Waiakea PFA ($21.42 \pm 0.06 \text{ }^\circ\text{C}$)

than in Wailoa River (22.14 ± 0.07 °C) (Figure 3B). Salinity (Practical Salinity Scale—PSS) was also significantly different between the habitats. In particular, salinity was consistently and significantly higher in Wailoa River than in Waiakea PFA (Table 1, Figure 3C). In Wailoa River, salinity averaged 3.3 ± 0.08 PSS, whereas in Waiakea PFA, salinity averaged 2.12 ± 0.09 PSS. No main effect from the invasion status or interaction effects were found on salinity.

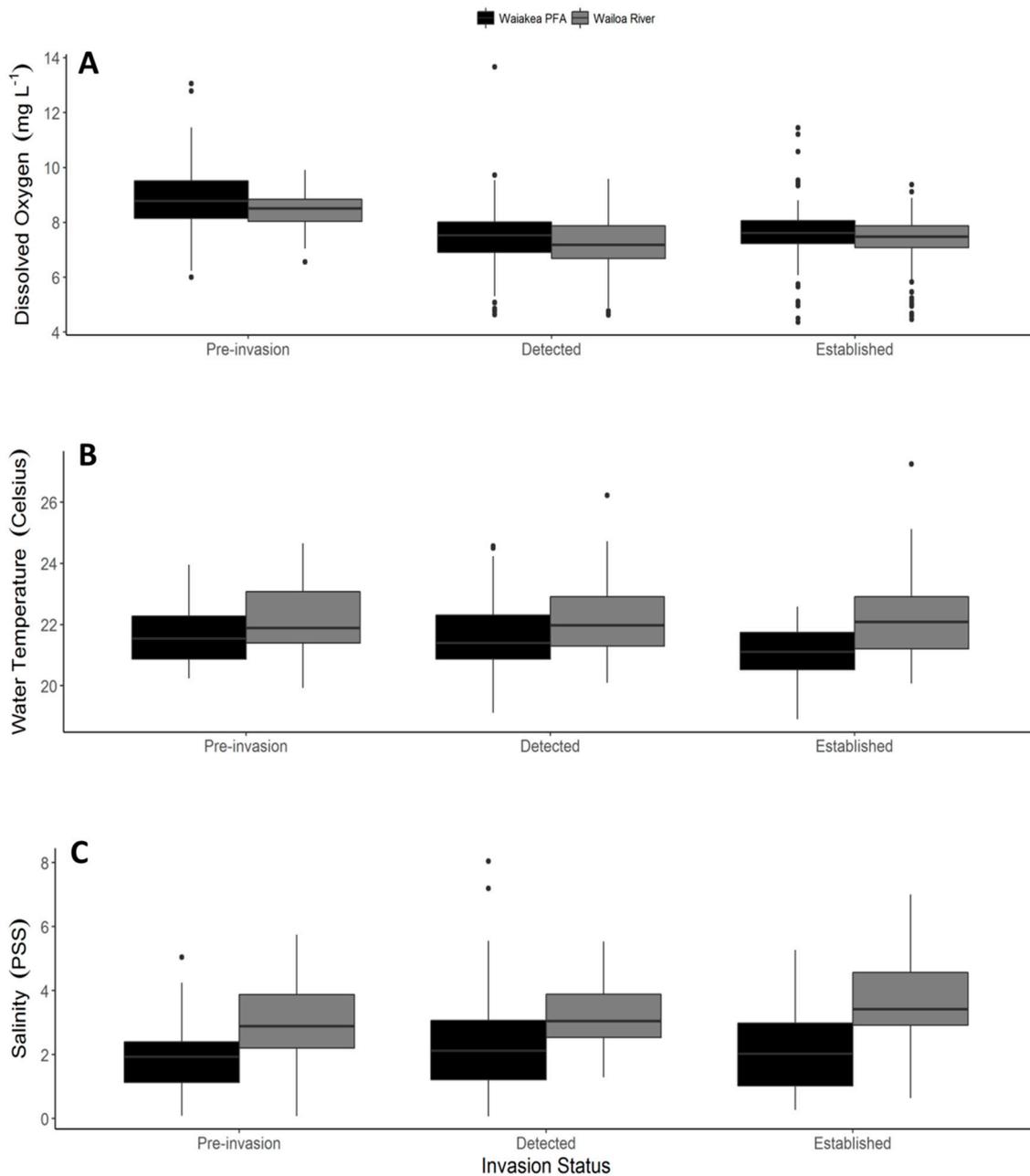


Figure 3. Box plot of (A) dissolved oxygen concentrations (mg L^{-1}), (B) water temperature ($^{\circ}\text{C}$), and (C) Salinity (Practical Salinity Scale - PSS) in Waiakea PFA (black bars) and Wailoa River (grey bars) across invasion statuses (Pre-invasion, Detected, and Established). Horizontal lines are median concentrations, shaded boxes indicate the interquartile range, whiskers indicate the upper and lower quartile limits, and points represent outliers.

Table 1. Type III ANOVA table for dissolved oxygen concentration (mg L^{-1}), water temperature ($^{\circ}\text{C}$), and salinity (PSS), showing fixed-effect terms: habitat (Waiakea PFA vs. Wailoa River), invasion status (pre-invasion, detected, and established), and interaction between habitat and invasion status. Each model also included two random-effect terms, the sampling period and interaction between the sampling period and habitat, to account for any effects of temporal variability. The model for salinity estimated a variance component of zero for the interaction between the sampling period and habitat, and this term was thus removed from the model. Bolded p values indicate significant effects.

Dissolved Oxygen (mg L^{-1})						
Source	¹ SS	² MS	³ _{num} DF	⁴ _{den} DF	F	⁵ p
Habitat	0.074	0.074	1	41.98	8.735	0.0051
Invasion status	0.092	0.046	2	43.07	5.469	0.0076
Habitat: Invasion status	0.0005	0.0003	2	42.17	0.0298	0.97
Water Temperature ($^{\circ}\text{C}$)						
Source	¹ SS	² MS	³ _{num} DF	⁴ _{den} DF	F	⁵ p
Habitat	0.079	0.079	1	40.76	44.76	<0.001
Invasion status	0.0031	0.0016	2	41.58	0.89	0.42
Habitat: Invasion status	0.016	0.0079	2	41.06	4.46	0.018
Salinity (PSS)						
Source	¹ SS	² MS	³ _{num} DF	⁴ _{den} DF	F	⁵ p
Habitat	16.68	16.68	1	434.08	126.94	<0.001
Invasion status	0.31	0.16	2	42.12	1.20	0.31
Habitat: Invasion status	0.70	0.35	2	434.13	2.67	0.07

¹SS = sums of squares, ²MS = mean square, ³_{num}DF = numerator degrees of freedom, ⁴_{den}DF = denominator degrees of freedom, ⁵ p = calculated probability.

2.2. *M. cephalus* Catch per Unit Effort (CPUE)

For *M. cephalus* young-of-year (YOY) and smaller juveniles (0.6 cm mesh cast-net samples), temporal variability explained the greatest variation in the log-transformed CPUE, followed by the habitat and invasion status (Figure 4). Generally, the *M. cephalus* CPUE was greater during late spring and summer sampling periods (Figure 5A). After controlling for the effects of invasion status and temporal variability, the mean CPUE was 1.7 (habitat effects, 95% confidence interval—CI = 1.3–2.2) times higher in the estuarine pond habitat (Waiakea PFA) than in the estuarine river habitat (Wailoa River). For the entire study site, the conditional mean CPUE was relatively stable from the pre-invasion status to the detected period (initial invasion effects 1.22, 95% CI = 0.75–1.89), but decreased from the detected period to the established period (post-invasion effects 0.56, 95% CI = 0.35–0.85).

The importance of temporal variability was reduced when the CPUE of larger juveniles and adults were examined (1.0 cm mesh cast-net samples), with the habitat explaining the greatest variation, followed by the invasion status and temporal variability (Figures 4 and 5B). Overall, the mean CPUE was 1.7 (95% CI = 1.2–2.3) times higher in Waiakea PFA than Wailoa River. There was no strong evidence for changes in the conditional mean CPUE from the pre-invasion status to the detected period (initial invasion effects 1.31, 95% CI = 0.86–1.96), but it decreased from the detected period to the established period (post-invasion effects 0.61, 95% CI = 0.42–0.86).

The estimated mean CPUE based on the habitat and invasion status effects confirmed these patterns, showing a consistently higher CPUE in Waiakea PFA than Wailoa River for both 0.6 and 1.0 mesh-size nets throughout all periods of the grass reinvasion and clear decreases from the detected to established periods in both habitats (Figure 6). Further, patterns in the CPUE were consistent across invaded and uninvaded areas of Waiakea PFA and Wailoa River, reflecting the overall CPUE characteristics in these habitats, respectively.

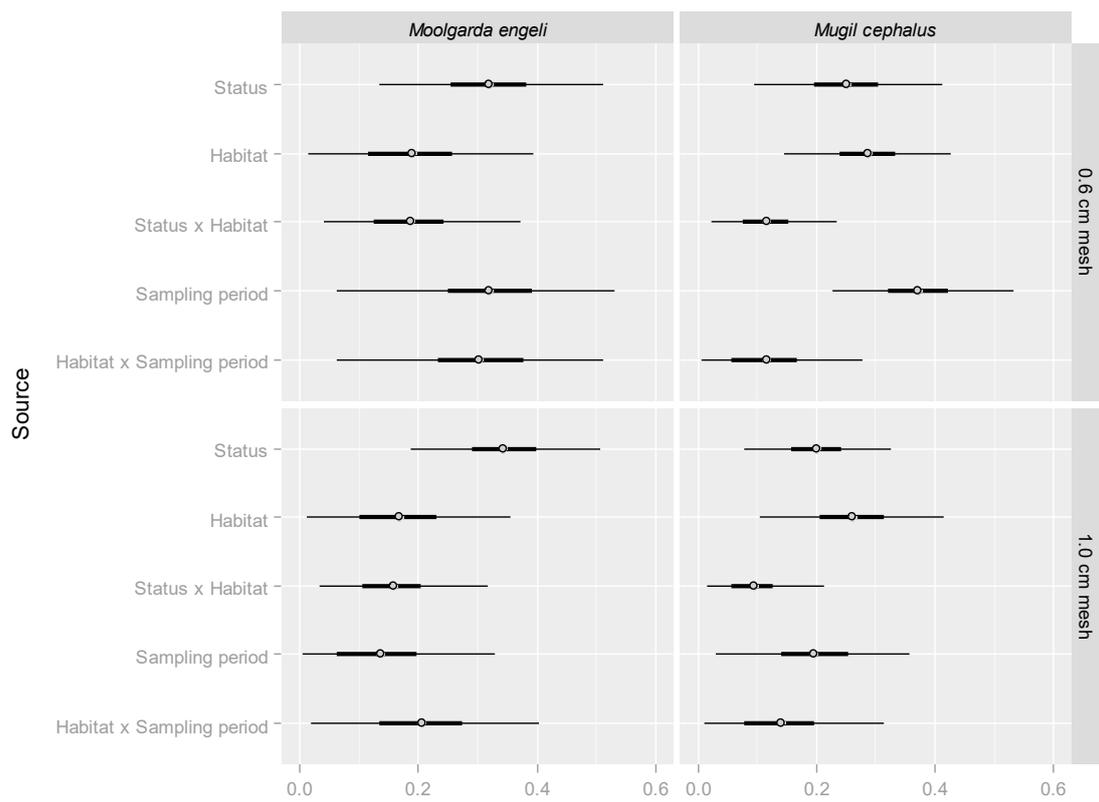


Figure 4. Variance component estimates per factor combination. Status = *Urochloa mutica* invasion status (pre-invasion, detected, established); Habitat = Pond vs. River; Sampling Period = month and year. Bars display 50% and 95% credible intervals.

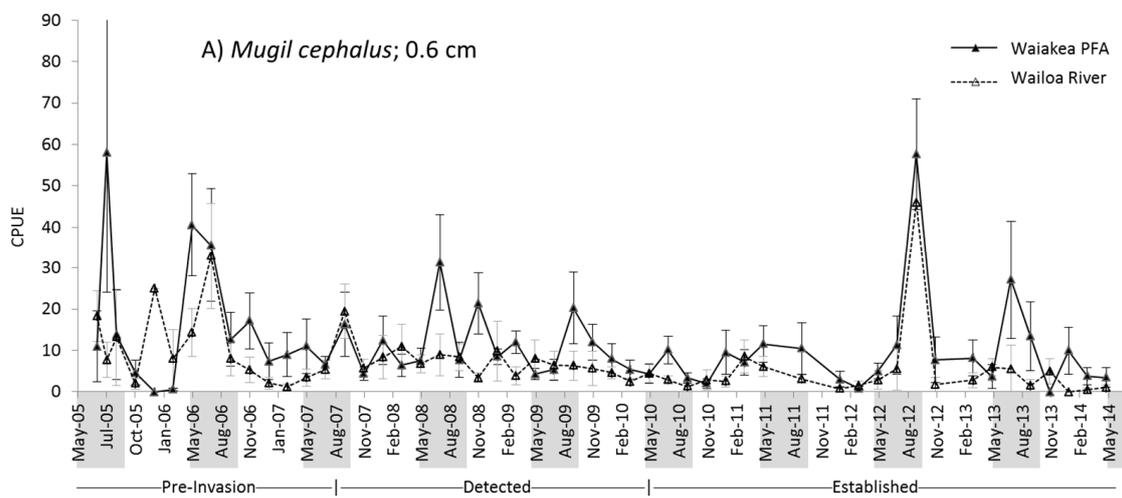


Figure 5. Cont.

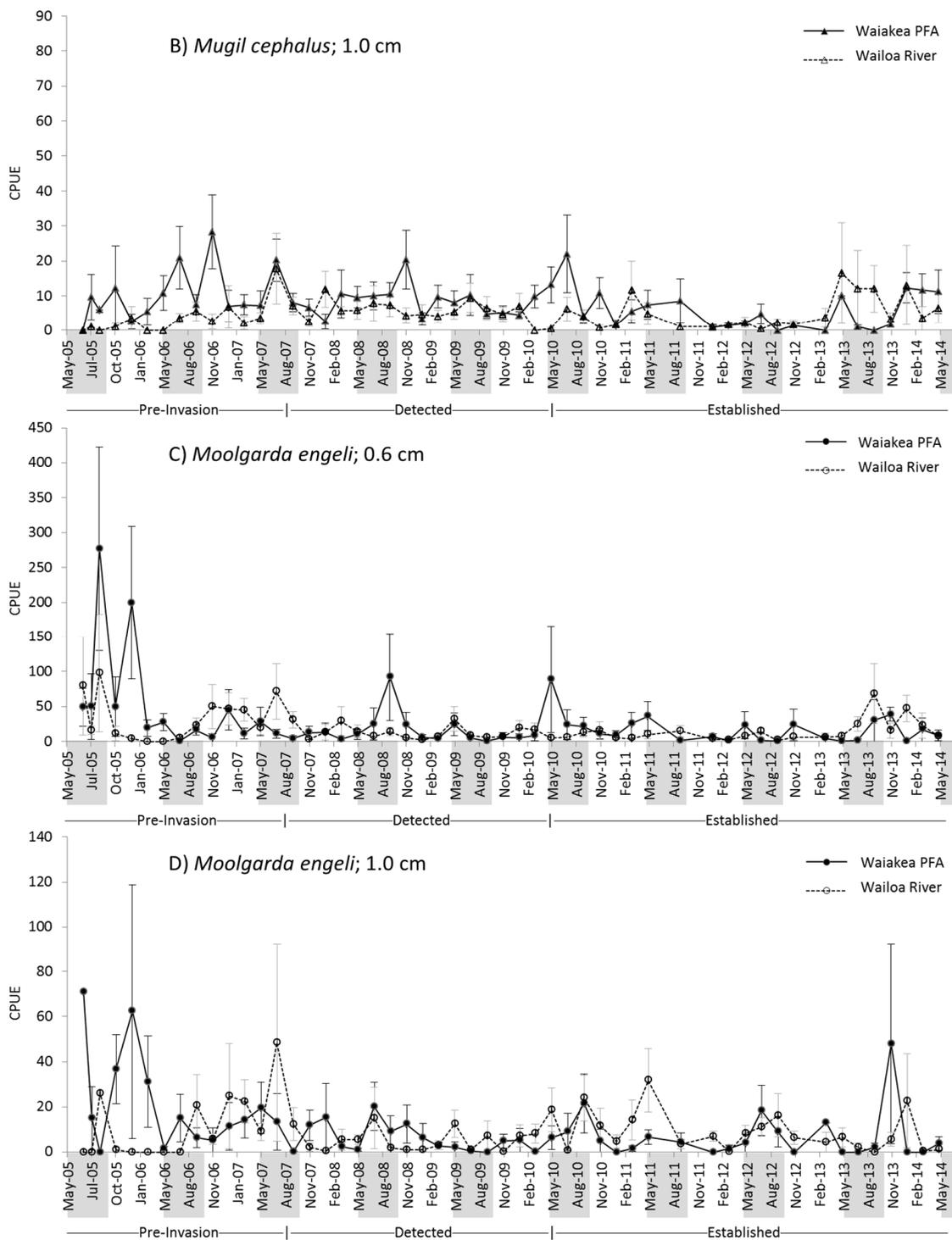


Figure 5. Mean CPUE of *M. cephalus* ((A): 0.6 cm mesh cast net; (B): 1.0 cm mesh cast net) and *M. engeli* ((C): 0.6 cm mesh cast net; (D): 1.0 cm mesh cast net) across sampling dates (month-year), across periods of *U. mutica* invasion (pre-invasion, detected, and established), and between the pond and river habitat (Waiakea PFA and Wailoa River). Shaded dates indicate late spring and summer months. Error bars are ± 1 standard error.

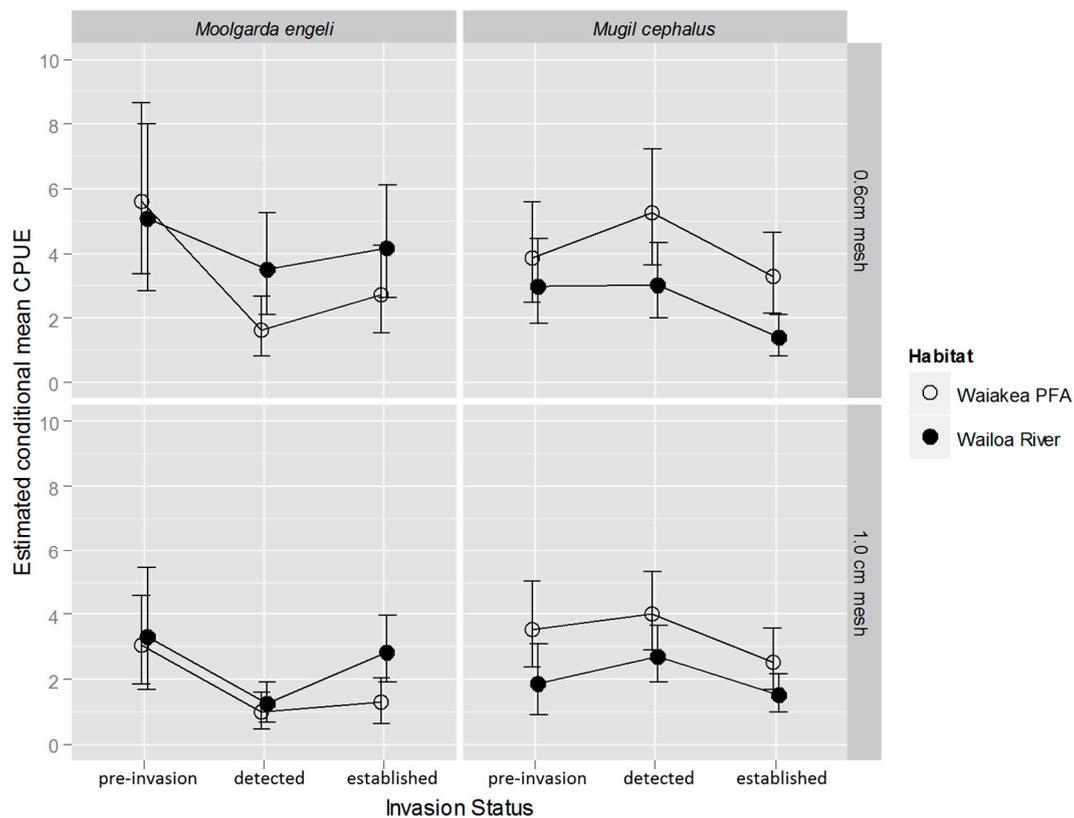


Figure 6. Estimated conditional mean CPUE of mullets per factor combination: habitat (pond vs. river) and invasion status (pre-invasion, detected, established). Error bars are ± 1 standard error.

2.3. *M. engeli* CPUE

For *M. engeli* YOY and smaller juveniles (0.6 cm mesh cast-net samples), the invasion status and temporal variability were the most important factors in explaining the variation in the log-transformed CPUE (Figure 4). Like *M. cephalus*, the *M. engeli* CPUE was generally greater during late spring and summer sampling periods (Figure 5C). After controlling for the effects of habitat and temporal variability, the conditional mean CPUE decreased from the pre-invasion to detected periods (initial invasion effects 0.47, 95% CI = 0.27–0.75), but there was no strong evidence for changes in the CPUE from the detected to established periods (post-invasion effects 1.43, 95% CI = 0.86–2.27). In addition, the variance component associated with the interaction effects between the habitat and sampling period was relatively high, showing habitat effects that were not consistent from one sampling period to another.

Similar to *M. cephalus*, the importance of temporal variability was reduced when the CPUE values of larger juveniles and adults (1.0 cm mesh cast-net samples) were considered, with the invasion status explaining the greatest variation in the log-transformed CPUE of *M. engeli* (Figures 4 and 5D). The conditional mean CPUE decreased from the pre-invasion to detected periods (initial invasion effects 0.36, 95% CI = 0.21–0.58) and then increased from the detected to established periods (post-invasion effects 1.82, 95% CI = 1.11–2.85).

The estimated mean CPUE based on the habitat and invasion status effects showed clear decreases in the conditional CPUE from the pre-invasion to detected periods for both mesh-sizes (Figure 6). Although the 95% credible intervals were relatively wide, the model also showed, on average, a higher CPUE from the 0.6 mesh-size nets in the estuarine river habitat than the pond habitat during the detected and established periods. The increase in the mean CPUE from the detected to established period for the 1.0 cm mesh-size was, on average, larger in the river habitat than the pond habitat.

3. Discussion

We demonstrated that while the relative abundances of *M. cephalus* and *M. engelii* decreased with the unconstrained spread of *U. mutica* in an insular tropical estuary, the two mullet species displayed distinct patterns with the reinvasion. On one hand, *U. mutica* negatively impacted the nursery habitat for *M. cephalus*, a valued gamefish; on the other hand, there was a more nuanced plant-animal interaction with *M. engelii*, an accidental introduction to Hawaiian waters. Specifically, with *M. cephalus* showing a strong preference for shallow water—consistent with previous findings [46–49]—the CPUE of this game fish decreased during the spread of *U. mutica* (detected to established period). Importantly, this result was consistent for both the YOY/larger juveniles and adults sampled. In contrast, all sizes of *M. engelii* displayed a more immediate reduction in CPUE from the onset of the *U. mutica* reinvasion, while larger juveniles and adults later displayed an increase in CPUE, despite *U. mutica* becoming established in the estuary.

Previous studies that examined the impacts of invasive macrophytes arrived at conflicting conclusions. Perna et al. [50] and Carniatto et al. [12] showed indiscriminate reductions in fish abundances and richness caused by exotic plant invasions. This, however, is not always the case, as others report a lack of effects, negative or positive, across aquatic faunal communities [17–20]. Our results partially agree with both of these conclusions because the *U. mutica* reinvasion response was species-specific, with *M. cephalus* experiencing a more clearly defined reduction in relative abundance, while *M. engelii* displayed a more size-specific interaction.

3.1. *M. cephalus*

As a well-studied food fish, *M. cephalus* recruits are known to prefer shallow habitats in estuaries [46–49]. In addition, smaller juvenile fishes have been shown to be in greater abundance in low-gradient shallow habitats along banks compared to altered shorelines where habitat gradients are steeper and more abrupt [51]. Consistent with this, the CPUE of the *M. cephalus* sampled with both 0.6 and 1.0 cm mesh nets was higher in Waiakea PFA, where the shallow habitat gradient is low and extensive relative to Wailoa River. The shallow, sheltered waters of Waiakea PFA also supported the growth of extensive canopies of *U. mutica* because its floating stolons grow well in this type of habitat [52]. Understanding the mutual habitat requirements of both *M. cephalus* and *U. mutica*, which is detrimental to this mullet species, is critical for the management of this important fishery. In addition, extensive areas of shallow water in Waiakea PFA have a high probability for the expansion of *U. mutica* (Figure 1), meaning that if growth continues unrestrained, this fishery resource is expected to diminish further as a result.

Using monitoring data, albeit long-term, and the biased sampling design to assess this plant-animal interaction means that determining causal agents is speculative for this study. Nevertheless, there are several plausible explanations for the negative interaction, primarily because *U. mutica* canopies are known to broadly degrade aquatic habitats [22,53]. For example, floating canopies observed during the established period may alter the foraging of *M. cephalus* because shallow water provides one of their primary food sources, microphytobenthos (MPB). Within the study area, the shallow-water diatom *Melosira moniliformis* [54] makes up the majority of the MPB, as well as the gut composition of the *M. cephalus* population under study [45]. Dense canopies of floating macrophytes, such as those formed by *U. mutica*, intercept light resulting in diminishing MPB, and in particular, *M. moniliformis*. Water depth influences light attenuation and, consequently, biofilm growth [55]. Therefore, deeper parts of the estuary are expected to have reduced MPB standing biomass relative to shallower areas that characteristically receive more photosynthetically active radiation. For this reason, we hypothesized that deep-water habitats in estuaries are less suitable for foraging by *M. cephalus*. This was supported by the lower abundances of juveniles and adults found in Wailoa River throughout the nine-year study. In addition, visual observations in deeper parts of the study site away from the shoreline have indicated notably fewer occurrences of juvenile mullets, particularly *M. cephalus*.

In addition to shading, the established period of *U. mutica* invasion, characterized by thick floating canopies, may leave juvenile *M. cephalus* vulnerable to predation. Although many plant species provide a habitat complexity that can be used as refuge from predation, an especially important function in nursery areas [56,57], *U. mutica* forms dense and nearly impenetrable canopies [24,50], and is known to be a less favorable habitat for native fishes [58]. This canopy structure may force juvenile mullet to use deeper water along the vegetation front of *U. mutica*, which exposes the juveniles to higher predation than in shallower water—similar to the effects of an armored shoreline [51]. Yet, this valid hypothesis remains to be tested.

Bunn et al. [53] described the altered ecosystem function and benthic communities associated with the reduced water quality and habitat caused by *U. mutica*. The monospecific canopies of *U. mutica* are also linked to degraded water quality through several mechanisms [21–24,27,28,59]. In addition to reduced MPB, the food availability and conditions of the benthic habitat may be further exacerbated by the high plant standing crop of *U. mutica* that contributes excessive amounts of organic material to the aquatic systems, leading to the decomposition of that material by bacteria that have high oxygen demands. Hyland [60] noted persistently low levels of dissolved oxygen (<2 ppm) in shallow wetland habitats dominated by *U. mutica*, resulting in conditions that can be stressful for fish. Our results align with these findings as measureable decreases in DO in Waiakea PFA and Wailoa River were found after the reinvasion of *U. mutica*. Therefore, *M. cephalus* may be negatively affected by this invasive plant, contributing to degraded water quality, especially as estuarine fishes in general are notably stressed by hypoxia [61,62]. However, it is important to consider that the decreased CPUE of *M. cephalus* may be a response to the additive effects of reduced food availability, increased predation pressure, and hypoxia, instead of these potential stressors separately, especially as CPUE patterns were delayed until *U. mutica* became established, despite the decrease in DO in both habitats in the detected period.

3.2. *M. engeli*

Monitoring *M. engeli* over nine consecutive years showed that this invasive species is a habitat generalist in this recipient community, with juveniles and adults showing no habitat preference in a tropical estuary. For this mullet species, there appears to be less stringent preferences and requirements for the habitat condition than *U. mutica*, as *M. engeli* may readily occupy other habitats, such as deeper parts of the estuary or other connected habitats within Hilo Bay [41]. This may explain how the population fluctuations of *M. engeli* described here showed a distinctly different pattern compared to those of *M. cephalus*. Specifically, *M. engeli* showed a clear decline in relative abundance from *U. mutica* pre-invasion to the detected period. However, larger juveniles and adults of *M. engeli* were not measurably affected by the spatial expansion of *U. mutica* by showing a relative increase in CPUE from the detected to established period. As available shallow habitats along the shoreline were reinvaded by *U. mutica*, competition for limited habitat and food resources may have increased between *M. engeli* and *M. cephalus*. Therefore, this may have stimulated *M. engeli*, as a generalist, to relocate to a habitat with less competition. This may also explain the relative increase in the adult and larger juvenile *M. engeli* CPUE from detected to established periods, as the relative abundance of *M. cephalus* decreased during this period, thereby reducing competition for food and the habitat. Yet, possible explanations for changes in the population of the smaller juveniles during the monitoring period are tentative due to limited research on the ecology and life history of *M. engeli*. This is attributable to this species having little economic value in its native range because of its comparatively smaller size to larger and more desirable food fishes. As an invasive species, this mullet is also understudied because there is only a single exotic population reported, which is restricted to the Hawaiian Islands [42]. Nonetheless, the apparent adaptability of larger juveniles and adults of *M. engeli* to the *U. mutica* reinvasion revealed another competitive advantage that this invasive mullet has over *M. cephalus* when food and habitat resources become limited.

While further research is needed for *M. engeli*, there is anecdotal evidence that shows that the juveniles of this species, particularly newer recruits, have a lower sub-lethal threshold for hypoxia than *M. cephalus*. Consistent with reports by Randall [43], our observations confirmed that *M. engeli*, especially YOY and juveniles, were notably more sensitive to oxygen stress than *M. cephalus* when temporarily held in buckets during sampling. This was evident by a quicker loss of equilibrium and more labored opercular movement by *M. engeli* compared to *M. cephalus*. Consequently, combined with a potential increase in interspecific competition for resources with *M. cephalus*, changes in physiochemical conditions caused by *U. mutica* may partially explain why the *M. engeli* CPUE declined during the detected period of the macrophyte reinvasion. For this reason, it is important to note that *U. mutica* was not present in Waiakea River during the detected period, as the invasion status of *U. mutica* was collectively determined for the entire study site and not separately for the two connected habitats. Therefore, the reinvasion of *U. mutica* may have affected the entire study site along the shoreline and became a relatively less suitable habitat for *M. engeli*. This was supported by the significant and overall reduction in DO in Waiakea PFA and Waiakea River after the *U. mutica* reinvasion began. Further, consistent reductions in DO throughout both habitats, particularly at the surface, may be explained by the fact that water from Waiakea PFA feeds directly into Waiakea River and is the primary source of water flowing through the entire site.

Despite the significant relationships between DO and the *U. mutica* reinvasion, and significant patterns in mullet CPUE, we remain cautious and inclusive when considering what caused, directly or indirectly, the significant patterns in the relative abundances of these mullets. For instance, although the DO significantly declined after *U. mutica* reinvasion, DO concentrations in the water column remained $>7 \text{ mg L}^{-1}$, which is still well above the sub-lethal hypoxic threshold for marine fish [63]. Instead of a direct effect from *U. mutica*, reductions in DO may be a reflection of reduced productivity by MPB caused by shading from *U. mutica*; the latter of which may also explain the reduction in water temperature in Waiakea PFA after the reinvasion. We must therefore consider that any or all of these possible factors, as well as others not measured in this study, can collectively have an influence on the behavior of *M. engeli* and *M. cephalus*.

4. Materials and Methods

4.1. Site Description

The survey site is located on the east shore of Hawaii Island and consists of two connected habitats, Waiakea PFA (estuarine pond habitat) and Waiakea River (estuarine river habitat) (Figure 1). Both habitats are primarily fed by groundwater discharge, and occasionally by flashy intermittent streams. Water conditions are generally calm, with surface salinities ranging between 0 and 10 [64], although a tidal salt wedge penetrates daily, raising the salinity levels to as high as 34 in deeper parts of the estuary [65]. Water temperature averages $21.8 \text{ }^{\circ}\text{C} \pm 1.2 \text{ SD}$ year round, and the benthos primarily consists of fine sediments, rocks, and boulders covered with epiphytic microalgae. Background nutrient concentrations ($\text{NO}_3^- + \text{NO}_2^-$) are relatively high, consistently exceeding the Hawaii Department of Health's mean standard ($5.0 \text{ } \mu\text{M}$) for rivers during wet conditions [66]. Together, Waiakea PFA and Waiakea River provide a premier estuarine pond and river habitat, respectively, for juvenile and adult *M. cephalus*, and as such, support a pole-and-line *M. cephalus* fishery unique to the area [41].

4.2. *U. mutica* Expansion Rates and Potential

The expansion rates and potential of *U. mutica* were examined using ArcInfo 10.0 GIS software (ESRI, Redlands, California, USA). Emergent stands, floating mats, and drifting mats of *U. mutica* were mapped throughout the survey site using the tracking feature of a GPS unit (Garmin® GPSMAP 62, Olathe, Kansas, USA) during the established period of the reinvasion on three dates: 15 April 2013, 26 November 2013, and 24 April 2014 (Figure S1). However, the spatial extent of the observed *U. mutica* canopies prior to 2013, during pre-invasion and detected periods, or any historical invasions, was not

measured. All recorded GPS tracks were converted into line feature classes by mapping the date and a polygon feature class of *U. mutica* cover was created, excluding riparian coverage on land. The total areal coverage (ha) of *U. mutica* on each of the mapping dates was calculated as the total area of all polygon features. Expansion rates ($\text{m}^2 \text{day}^{-1}$) of *U. mutica* were calculated by dividing increases in the total areal coverage of *U. mutica* by the number of days since the previous mapping date.

The relationship between *U. mutica* invasion and water depth was visually examined by creating a bar chart showing water depths and the percent occurrence of invasion at a given depth. For this, we used bathymetry data collected between March and June 2011 from a boat using a Humminbird® 998c SI Combo depth sounder (Humminbird, Eufaula, Alabama, USA). All sounding data were tide-corrected to the nearest 0.3 cm using tide levels and times from TideComp software ver. 8.00 (Pangolin Communications, Bristol, UK). Water depths were binned into 0.2 m depth intervals, and the percent occurrence of invasion at each depth category (i.e., areal coverage of *U. mutica* at each depth category divided by the total areal coverage of *U. mutica*) was calculated based on *U. mutica* cover on 24 April 2014.

A map was created to visualize the invasion potential of *U. mutica* throughout Waiakea PFA and Wailoa River according to the percent occurrence of invasion at each depth category and the bathymetric characteristics of the study site (See Supplementary Materials). We classified an invasion potential gradient from “lowest risk”, based on areas with water depths where the lowest percent occurrence of *U. mutica* invasions occurred, to “highest risk”, as areas where the highest percent occurrence of *U. mutica* invasions occurred.

4.3. Mullet Sampling

We used the catch per unit effort (CPUE) as a proxy for the relative abundance of juvenile and adult mullet for both *M. cephalus* and *M. engeli*. The CPUE of each species was calculated using catch data from the shoreline cast-net mullet sampling program by DAR from July 2005 to May 2014 in Waiakea PFA and Wailoa River. The mullet sampling methods were adapted from methods described in Nishimoto et al. [41] and conducted every two months. Schools of mullets were targeted and collected from the shore using 0.6 cm and 1.0 cm mesh cast-nets (4.9 m diameter). Primarily, YOY and smaller juvenile mullets (≤ 100 mm FL) were targeted with 0.6 cm mesh nets, while larger juveniles and adults (>100 mm FL) were targeted with 1.0 cm mesh nets.

The banks of Waiakea PFA and Wailoa River were each divided into six sampling stations, averaging a 389 ± 33.02 m linear distance to ensure that cast-net sampling was well-spaced throughout the survey site. Two surveyors each made a maximum of two casts per mesh size anywhere within each station from shore. Sampling was limited to the shoreline as to primarily target juveniles of each mullet species, which were most prevalent in these areas of the survey site. Deeper areas offshore were not conducive towards cast net sampling, particularly to target juvenile fish. Also, as mentioned previously, visual observations confirmed fewer occurrences of juvenile *M. cephalus* away from the shoreline and in deeper parts of the study site. Each cast was geo-referenced, and all individuals caught per cast were identified to species, counted, and measured for the fork length (FL) to the nearest mm. Each surveyor was limited to 20 min to visually find the largest schools of juvenile or adult mullet that were within a station. Surveyors were allowed discretion to not cast on a school of mullet only if obstructions or objects (e.g., tree branches, large boulders) were present that would considerably inhibit fish captures and net retrieval, and therefore, confound sampling efforts. In this regard, marginal habitats along canopies of *U. mutica* did not inhibit cast net sampling, and mullet schools found within these marginal habitats were also sampled if no cast-net obstructions were present. If no individuals of either mullet species were caught within a cast, the abundance was recorded as 0 for that cast and species, and included as such in the CPUE calculations. In order to reduce the inherent variability in using cast-nets, sampling was conducted by the same two individuals, or by samplers with an equal skill at using the cast net. The CPUE for each mullet species was calculated as the total number of mullets (by species) caught per individual cast. In addition to cast-net sampling, physiochemical

parameters were concurrently measured at the surface from shore at each sampling station within Waiakea PFA and Wailoa River during each sampling effort. The dissolved oxygen concentration (mg L^{-1}), water temperature ($^{\circ}\text{C}$), and salinity (PSS) were measured using a Hydrolab Quanta.

4.4. Statistical Analyses

Three-factor mixed effects models were used for formal statistical analyses of physiochemical parameters and mullet CPUE data. The factors considered were: the habitat (fixed with two levels: shallow estuarine pond, Waiakea PFA, and estuarine river, Wailoa River); *U. mutica* invasion status (fixed with three levels: pre-invasion, detected, and established); and sampling period (month and year when samples were collected, random factor nested in invasion status).

For the physiochemical parameters, models included three fixed-effect terms (invasion status, habitat, and interaction between invasion status and habitat), as well as two random-effect terms (sampling period and interaction between sampling period and habitat) to account for any effects of temporal variability. The DO concentration, water temperature, and salinity were separately analyzed according to the full three-factor design. The dissolved oxygen concentration and water temperature were first log-transformed ($Y' = \log(Y)$), and salinity was square-root-transformed. An examination of the transformed data showed no significant violations to the assumptions of ANOVA. Each model was constructed using the function `lmer()` in the `lme4` package of the statistical software R version 3.3.2 [67] and for each model, an ANOVA table of Type III was obtained for fixed effects using the function `anova()` in the `lmerTest` package [68]. When statistically significant effects were detected for fixed effects, post-hoc pairwise comparisons were done by the use of the `lsmeans` and `multcomp` packages.

Due to inconsistency in the cast net samples, an overall design for mullet sampling was highly unbalanced, with some of the sampling periods not having data from 1.0 cm mesh-size nets. In addition, the cast-net data for this analysis was used opportunistically and was the only dataset available to statistically assess any interaction between *U. mutica* reinvasion and estuarine fishes in the area. To work with this unbalanced design, we employed ANOVA using a hierarchical Bayesian framework [69]. In order to explicitly model changes in the CPUE of each mullet species during the grass reinvasion at the two habitats, CPUE data were separately analyzed for *M. cephalus* (0.6 cm and 1.0 cm mesh cast-nets) and *M. engelii* (0.6 cm and 1.0 cm mesh cast-nets), according to the full three-factor design. These four response variables were first log-transformed ($Y' = \log(Y + 1)$) to avoid high skewness and heterogeneity.

The analyses were done using a Markov chain Monte Carlo methodology with the software JAGS 3.4.0 [70] run from within program R by the use of the `rjags` and `R2jags` packages. For each of the four CPUE response variables, the linear predictor of the ANOVA model for the log-transformed CPUE in Habitat i (H_i), Invasion Status j (S_j), and sampling period T_k (nested in Invasion Status) was $Y'_{ijk} = \beta_0 + H_i + S_j + (\text{HS})_{ij} + T_{k(j)} + (\text{HT})_{ik(j)}$, in which β_0 was the overall mean. The parameterization of model terms followed the methods described in Smith et al. [71]. For a fixed factor with m levels, a sum-to-zero constraint was used, and prior distributions of coefficients β were $\beta \sim \text{Normal}(0, 100)$ for β_1 to β_{m-1} , and $\beta_m = -(\beta_1 + \dots + \beta_{m-1})$. For interactions between fixed and random factors, the same constraint was used for the fixed factor within each level of the random factor. For a random factor, prior distributions of coefficients β were $\beta \sim \text{Normal}(0, \sigma^2)$ with a standard non-informative hyper-prior $\sigma \sim \text{Uniform}(0, 10)$, where σ^2 is the variance component for the factor. The variance component estimates for fixed factors were sums of squared fixed effects (β_1 to β_m) divided by the appropriate degrees of freedom [69]. Each analysis was run with three chains, each with 100,000 iterations, from which 50,000 were discarded as a burn-in. The thinning rate of each chain was one in six. Convergence was assessed using the Brooks-Gelman-Rubin diagnostic (R hat; [72]).

In order to visually identify the source of variation in the mullet CPUE, variance components, expressed as the estimate of the standard deviation among levels, were plotted for each of the four analyses (ANOVA display; [69]). We also derived the following ratios of conditional means as part of the ANOVA analyses: the ratio of the conditional mean CPUE in the estuarine pond habitat vs.

the river habitat (habitat effects), the ratio of the conditional mean CPUE in the pre-invasion vs. detected periods (initial invasion effects), and the ratio of the conditional mean CPUE in the detected vs. established period (post-invasion effects). The estimated conditional mean CPUE values based on both the Habitat and Invasion Status effects ($Y_{(H^*S)ij} = e^{\beta_0 + H_i + S_j + (HS)_{ij}} - 1$) were also obtained and plotted with their 95% credible intervals (95% CI) for each of the four analyses.

5. Conclusions

While we have a nascent understanding of the interaction between plant invasions and fish, we have provided a clearer picture of the different traits of a native and invasive mullet of contrasting value, and the potential effects of a macrophytic invasion on these fish and their habitat. Although by using monitoring data direct causation could not be demonstrated, there was a negative relationship between *U. mutica* invasion and the *M. cephalus* CPUE, insofar as not having any positive relationship with the *M. engelii* CPUE. We may also consider that notable differences in mullet CPUE patterns correlating to the *U. mutica* reinvasion and physiochemical characteristics were caused by species-specific traits, diverging among habitat fidelity, food preference and availability, refuge from predation, and physiological resilience to oxygen stress. These findings underscore the need to further examine the potential interactive effects of macrophyte invasions on coastal nekton communities and native coastal ecosystems. This is especially important for tropical estuaries inhabited by invasive species that transcend physical and ecological barriers, which may overwhelm the resilience of native fish.

Supplementary Materials: The following are available online at www.mdpi.com/2410-3888/2/2/7/s1, Assessment of *Urochloa mutica* expansion and invasion potential in Waiakea PFA and Wailoa River in Hilo, Hawaii USA, Table S1: *Urochloa mutica* cover and expansion rates in Waiakea Public Fishing Area (PFA) and Wailoa River, Figure S1: Maps of Waiakea PFA and Wailoa River prior to *Urochloa mutica* invasion, and *U. mutica* areal coverage across three dates, Figure S2: Percent (%) distribution of total *Urochloa mutica* cover vs. water depth (*m*) in Waiakea PFA and Wailoa River.

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