



Ecological Drivers of Invasive Lionfish (*Pterois volitans* and *Pterois miles*) Distribution Across Mesophotic Reefs in Bermuda

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Invasive lionfish (*Pterois volitans* and *P. miles*) are now ubiquitous throughout the Caribbean and Western Atlantic on shallow and deep reefs. Recent surveys in Bermuda have revealed dense aggregations of lionfish on mesophotic reefs (60 m depth), yet these densities are not pervasive across reefs at this depth. Using diver-led visual surveys of mesophotic reef sites, this study examines how variations in potential ecological drivers may affect lionfish distribution. Significant correlations of lionfish densities were found with prey fish density and prey fish biomass, where sites with higher abundances of prey fishes have greater densities of lionfish. Furthermore, higher densities of lionfish also correlated significantly with higher juvenile *Paranthias furcifer* biomass, a preferred prey type for lionfish. Prey fish diversity, on the other hand, was not related to lionfish density, nor did prey fish community composition differ in a way that reflected lionfish distributions. The influence of seawater temperature was found to have the strongest effect on lionfish distribution, where higher lionfish densities were found at sites with lower bottom temperature. However, temperature co-varied with prey fish density, prey fish biomass, and *P. furcifer* biomass, implying that physical parameters of the environment (i.e., temperature) likely influence ecological parameters (i.e., prey fish abundance), contributing to the structuring of lionfish distributions. We suggest, therefore, that cold-water upwelling currents may be fueling the food chain in certain locations, resulting in high abundances of prey fishes and thus lionfish. Understanding the factors that influence lionfish distributions will ultimately increase the efficacy of management strategies, which, as the data presented here suggest, must incorporate mesophotic lionfish populations.

Keywords: invasive species, mesophotic, Bermuda, prey availability, fish biodiversity, lionfish, temperature effects

INTRODUCTION

Pterois miles and *P. volitans*, collectively known as lionfish, are predatory fish belonging to the family *Scorpaenidae*, native to the Indian and Pacific oceans. The first non-native lionfish were sighted near the southeast coast of North America in 1985 (Semmens et al., 2004). Genetic evidence indicates that this popular aquarium fish was likely introduced via multiple aquarium releases off the southeast coast of Florida (Betancur et al., 2011). From there, the population spread northward along the east coast of the United States and eastward toward Bermuda, before progressing southward throughout the Caribbean, Gulf of Mexico, and western Atlantic, with lionfish reported from as far north as Rhode Island and as far south as Brazil (Schofield, 2009, 2010; Johnston and Purkis, 2011; Frazer et al., 2012; Fogg et al., 2013; Ferreira et al., 2015). A high reproductive rate coupled with the lack of native predators has allowed lionfish populations in the western Atlantic to flourish, reaching densities exceeding those found in their native habitats by a factor of 13 to 15 (Darling et al., 2011; Kulbicki et al., 2012). These high densities of lionfish indicate that they have become invasive and could potentially affect the biodiversity and structure of reef fish communities, and cause significant ecosystem change (Lesser and Slattery, 2011; Albins, 2013).

Lionfish are generalist predators with a broad diet, consuming large quantities of small and juvenile fishes, along with small invertebrates (Morris and Akins, 2009; Muñoz et al., 2011; Layman and Allgeir, 2012; Valdez-Moreno et al., 2012; Dahl and Patterson, 2014; Eddy et al., 2016; Peake et al., 2018). The relative increase of lionfish from 23 to ~40% of total predator biomass, coincident with a 65% decline in prey fish biomass between 2008 and 2010 in the Bahamas, indicates that this opportunistic generalist feeding strategy has the potential to alter reef fish communities (Green et al., 2012). While lionfish tend to be non-selective in their prey choice (Morris and Akins, 2009), contributions of various species to lionfish diets vary by location, depth, and season, indicating that lionfish may be consuming certain prey types preferentially based on their availability or ease of capture (Dahl and Patterson, 2014; Green and Côté, 2014; Eddy et al., 2016; Peake et al., 2018). It is unclear, however, if the distribution and abundance of prey types may influence lionfish abundance and distribution.

The first lionfish recorded in Bermuda was collected in 2000, yet despite being one of the first locations outside the United States to report the presence of lionfish (Smith et al., 2013), surveys indicate that the abundance of lionfish in shallow reef zones has remained relatively low (Eddy, 2016). However, lionfish populations extend well beyond shallow reefs across the invaded range, with sightings reported down to 55 m in Puerto Rico (Bejarano et al., 2014), over 100 m in The Bahamas (Lesser and Slattery, 2011), 112 m in the northwestern Gulf of Mexico (Nuttall et al., 2014), and 250 m in Honduras (Gress et al., 2017). In Bermuda, lionfish were recently sighted during submersible surveys as deep as 304 m (Gress et al., 2017). Early technical dive expeditions in Bermuda stumbled upon dense aggregations of lionfish at a few isolated deep (60 m) sites beginning in 2009. These select sites were revisited on multiple occasions over

several years and consistently yielded high catches of lionfish (pers. comm. G. Maddocks¹) leading to the presumption that they represented “hotspots” of lionfish abundance. Recent surveys of mesophotic coral ecosystems (MCEs) confirmed this assumption, reporting dense populations of lionfish on specific sites at or below 60 m in select locations around the Bermuda platform (Eddy, 2016; Andradi-Brown et al., 2017a). The average density of lionfish at these sites is roughly 250 fish ha⁻¹ (Eddy, 2016), which is similar to the densities reported at heavily invaded shallow locations in the Bahamas (Green et al., 2012). Such densities are not pervasive across this depth in Bermuda however, with observations ranging from 0 fish ha⁻¹ at some sites to 1100 fish ha⁻¹ at others (Eddy, 2016; **Figure 1**). Thus, variations in the physical environment, such as temperature (Whitfield et al., 2014) or habitat complexity (Garcia-Sais et al., 2012; Bejarano et al., 2015; Hunt et al., 2019), or in the biological community, such as availability of potential prey fish (Dahl and Patterson, 2014; Harter et al., 2017), may affect lionfish densities, resulting in higher densities of lionfish at certain locations.

A suite of variables is known to affect reef fish community structure across spatiotemporal scales, including fishing pressure, larval dispersal, habitat quality, connectivity, reef structural complexity, depth, and ecological interactions, among others (see Sale, 2002), yet the factors controlling lionfish distributions remain unclear (Benkwitt et al., 2017). The presence of biotic agents such as competitors, predators, or parasites, is hypothesized to regulate the establishment of invasive populations, such as lionfish (Keane and Crawley, 2002; Hackerott et al., 2013; Tuttle et al., 2017). However, multiple studies have found no relationship between lionfish density and native predator abundance (Anton et al., 2014; Hackerott et al., 2013; Valdivia et al., 2014), and parasites were found to have only a limited direct effect on lionfish populations (Sellers et al., 2015), suggesting instead that reduced susceptibility to parasites in the invaded range may further contribute to lionfish success (Tuttle et al., 2017). Likewise, habitat complexity has been shown to positively correlate with lionfish densities in a few studies (Garcia-Sais et al., 2012; Bejarano et al., 2015; Hunt et al., 2019), but not in others (Anton et al., 2014; Hackerott et al., 2017), and thus is not a predictable indicator of lionfish distributions over large spatial scales.

The aim of this study is to identify possible ecological drivers of lionfish distribution across MCEs in Bermuda, where lionfish have been present for nearly two decades. The long-term presence of lionfish in Bermuda may, in fact, facilitate the emergence of detectable patterns of distribution through adaptation to local conditions and prey communities. Using a series of visual censuses at mesophotic sites (60 m depth) across the Bermuda reef platform, we assess how variations in teleost (reef fish) communities and physical aspects of the environment may be influencing lionfish distribution. Understanding why high densities occur in specific locations will aid in our ability to identify and target areas for lionfish control efforts, thereby increasing the efficacy of future management.

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FIGURE 1 | Image of resident lionfish population at the XL site, showing benthic habitat as low relief hard bottom interspersed amongst rhodolith beds.

MATERIALS AND METHODS

Study Location

Located at 32°N, 64°W, 1049 km (652 nm) southeast of Cape Hatteras, United States central east coast, Bermuda's sub-tropical coral reefs represent the northernmost coral reef system in the Atlantic (Coates et al., 2013). Reefs persist in Bermuda partly due to the flow of the Gulf Stream, bringing warm water from the Gulf of Mexico (Coates et al., 2013; Locke et al., 2013b). Annual sea surface temperatures range from 15 to 30°C, which allows a variety of tropical marine organisms to live in this region, including 38 scleractinian coral species (Locke et al., 2013a).

The top of the seamount upon which Bermuda lies is a circular pseudo-atoll (~900 km²) with a total reef area of 177 km² (Coates et al., 2013). It consists of a large lagoon with thousands of patch reefs, bounded along the northern edge by a shallow annular rim reef tract that drops gradually to extensive mesophotic coral reef ecosystems (MCEs). On the southern edge, adjacent to the islands, the reefs zones are compressed and it drops quickly to the MCEs, creating a nearly continuous MCE surrounding the whole reef platform (Goodbody-Gringley et al., 2019). These MCEs are in close proximity to the shallow reefs and all reef zones are easily accessible for conducting scientific research. Shallow water coral cover in Bermuda ranks among the highest in the Caribbean and western Atlantic with an estimated mean overall cover of 38.6% (Jackson et al., 2014). Deep reef zones (below 50–60 m), such as the sites examined in the present study, are composed of extensive rhodolith beds and occasional outcroppings of hard-bottom reef with sparse scleractinian corals and low topographic complexity (Goodbody-Gringley et al., 2019).

Surveys

Surveys were performed at 11 sites at 60 m depth around Bermuda between 8 September 2013 and 26 September 2015

(Figure 2). At each site, lionfish were counted within a single 25 m × 10 m quadrat, in which a diver swam in a zigzag formation and closely examined all possible habitat for lionfish, as suggested by Green et al. (2012). While genetic evidence indicates that both *P. volitans* and *P. miles* are present in Bermuda (Betancur et al., 2011), identification to the species level is not possible *in situ*, and thus the general classification of 'lionfish' in the present study includes both species. Potential prey fish, defined as any teleost individual <15 cm in total length (TL), were surveyed within 1 m of each side of a 30 m transect tape laid adjacent to the lionfish quadrat, for a total area of 60 m² per survey (Lesser and Slattery, 2011; Pinheiro et al., 2013, 2016). Along each transect, the number of individual prey fish of each species was tallied and TL of each fish was estimated by eye and classified into 5 cm size classes. The lionfish quadrat and prey fish transects at each site were laid along the reef slope to ensure a constant depth, beginning at the closest non-living reef structure encountered to which the tapes could be secured. Bottom temperature was also recorded after a minimum of 15-min acclimation during each dive using Shearwater Petrel dive computers (precision ± 0.5°C), which continuously logged temperature throughout the dive. The number of prey fish survey transects performed at each site varied from two to six depending on the number of divers. The two sites with the highest lionfish densities (Tiger and XL) were surveyed twice, with parameters averaged across all surveys. Site names, GPS coordinates, survey dates, number of prey fish transects, lionfish density (±SE where applicable), and bottom temperature (±SE where applicable) are included in Table 1.

Statistical Analyses

Lionfish and prey fish densities were calculated as the number of fishes per hectare, where prey fish densities represent the mean across transects for each site. Mean prey fish biomass was estimated based on total length–mass relationships from

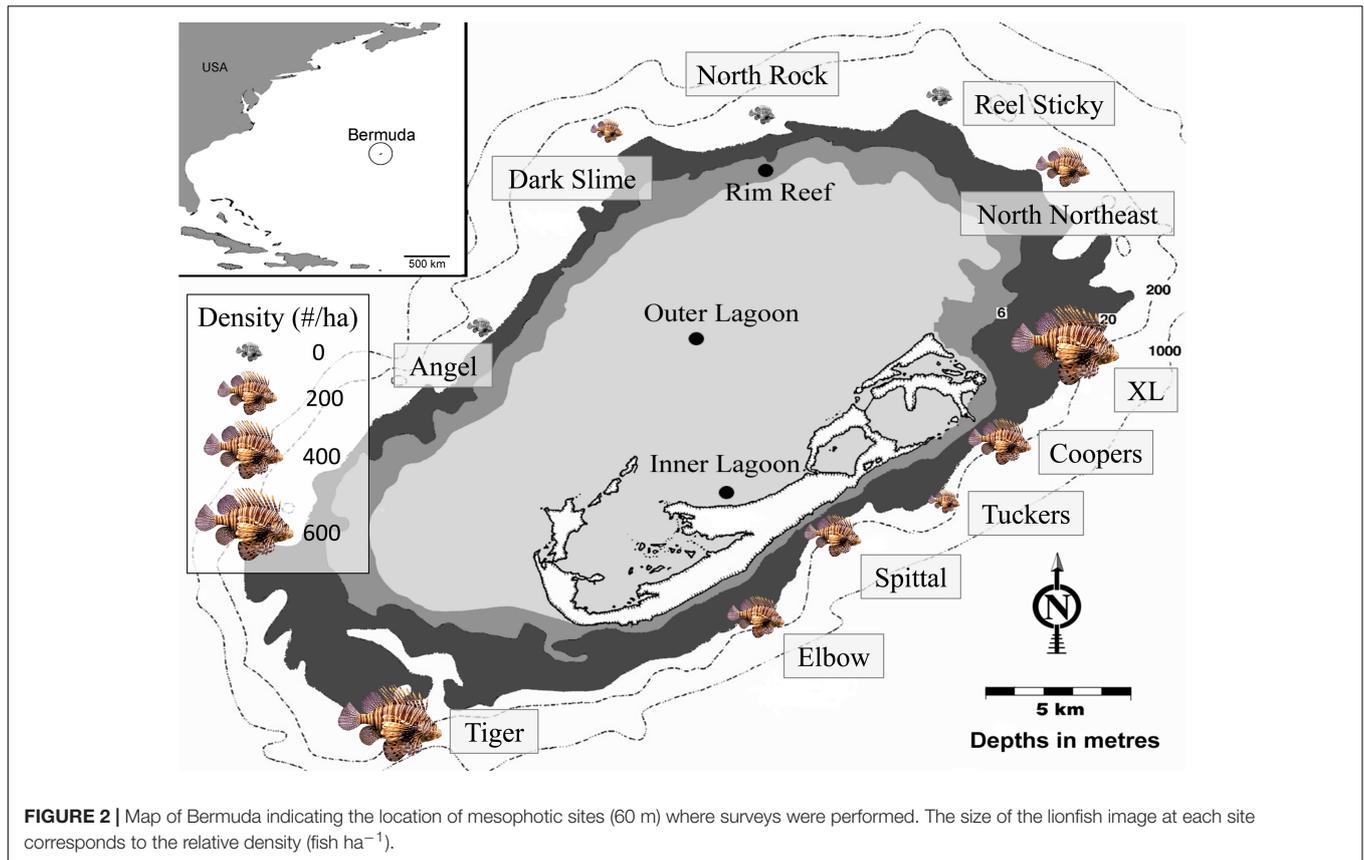


TABLE 1 | Name and GPS locations of all survey sites, including the date of each survey, the number of prey fish surveys performed, number of lionfish per hectare, and the bottom temperature (°C) recorded at the time of the survey.

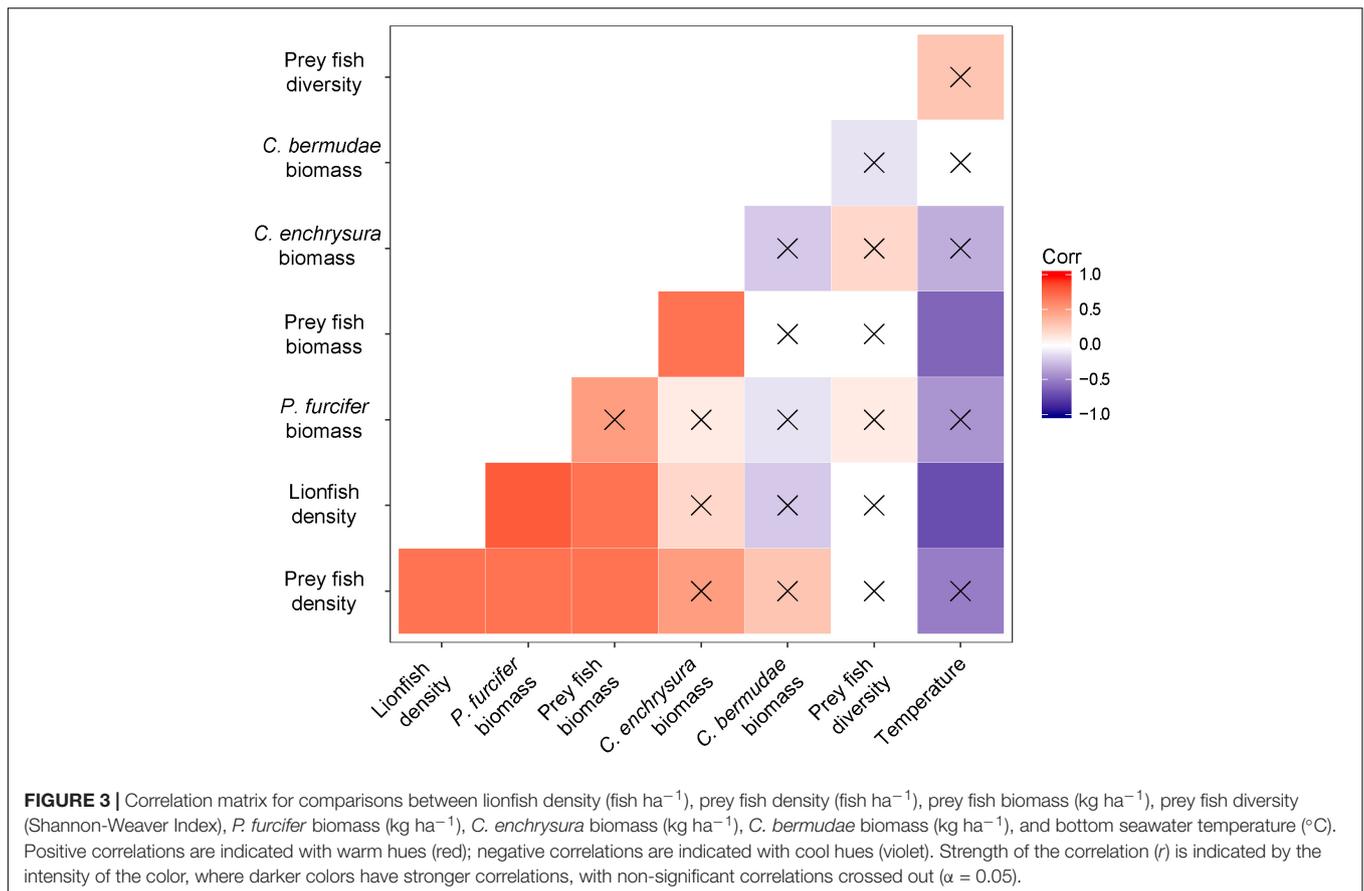
Site name	Latitude	Longitude	Survey date	Prey fish surveys	Lionfish density	Temperature (°C)
Tiger	32°11'04"N	64°58'36"W	10-Sep-14	6	653 ± 35	21.7 ± 0.0
			26-Sept-15	2		
XL	32°21'54"N	64°35'55"W	16-Sep-14	6	760 ± 272	21.1 ± 0.0
			13-Sept-15	2		
Spittal	32°17'59"N	64°42'13"W	24-Jul-14	6	160	22.2
N. Northeast	32°28'15"N	64°34'38"W	26-Jul-14	6	120	21.1
Elbow	32°14'34"N	64°46'49"W	3-Jan-15	6	160	22.2
Coopers	32°20'28"N	64°37'45"W	23-Jul-14	6	220	22.2
Tuckers	32°19'09"N	64°39'34"W	9-Sep-14	6	40	23.9
Dark Slime	32°29'23"N	64°49'13"W	23-Sep-14	6	40	22.2
Reel Sticky	32°31'02"N	64°42'13"W	26-Sep-14	6	0	22.8
Angel	32°25'39"N	64°53'41"W	2-Jan-15	4	0	22.2
N Rock	32°29'50"N	64°47'04"W	19-Sep-15	2	0	23.3

Sites surveyed on two separate dates (Tiger and XL) were averaged across both dates for the number of lionfish per hectare (±SE) and bottom temperature (±SE).

Froese and Pauly (2014), utilizing the mid-point of each 5-cm size class. When no relationship was available for a species, an average for the genus or family was applied (Froese and Pauly, 2014). Species diversity was determined using the Shannon-Weaver diversity index and averaged across transects for each site (Hill, 1973).

A correlation matrix with pairwise correlation analyses was used to compare all physical and biological parameters,

including lionfish density, prey fish density, prey fish biomass, species diversity, and bottom seawater temperature, as well as biomass of the top three most abundant species, *Paranthias furcifer*, *Chromis enchrysur*, and *Chromis bermudae*. Further comparison of the influence of potential drivers on lionfish density was examined with a Generalized Linear Model (GLM) using a gamma distribution, which resulted in normal distributions for each driver based on visualization with



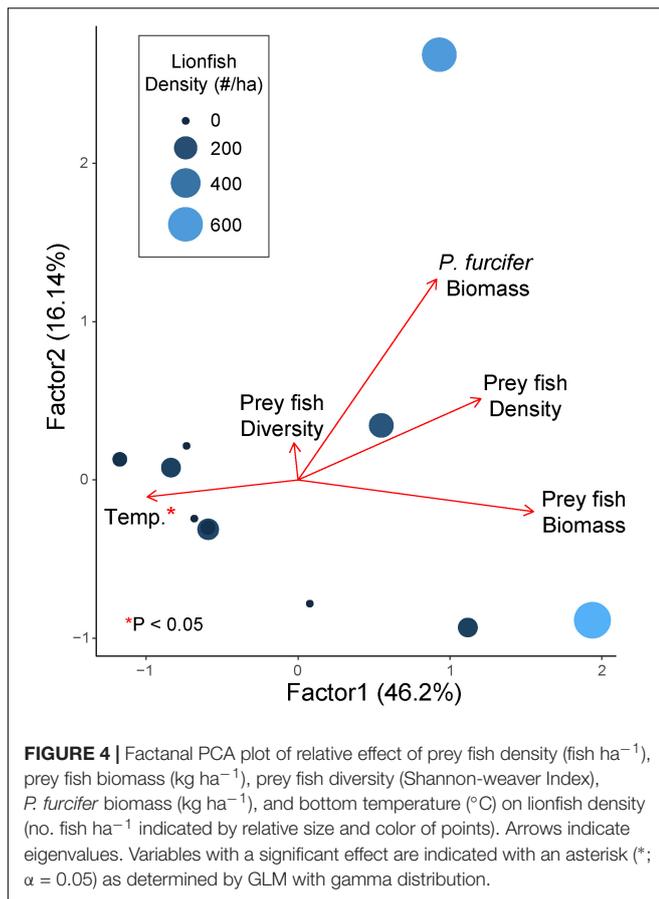
normal quantile-quantile plots (**Supplementary Figure S1**). As all factors co-varied using a single model (**Supplementary Table S1**), separate GLMs were required for each potential driver, with the best fit model determined using an Akaike Information Criterion (AIC) model selection approach (Akaike, 1974). Model results were visualized using a principal component analysis incorporating maximum likelihood factor analysis. Prey fish community composition was analyzed for percent contribution of each species across sites, with communities compared using a *k*-means cluster analysis. All statistical analyses and data visualizations were done in R version 3.4.3 (R Core Team, 2017) with RStudio 1.1.423 (RStudio Team, 2016) using the packages tidyverse (Wickham, 2017), vegan (Oksanen et al., 2018), ggplot2 (Wickham, 2009), ggbiplot (Vu, 2011), ggcorrplot (Kassambara, 2016), devtools (Wickham et al., 2018), and ggfortify (Tang et al., 2016); data and code are available on Zenodo (doi: 10.5281/zenodo.260282).

RESULTS

Significant positive correlations were found between lionfish density and prey fish density ($r = 0.7$; $p = 0.03$) and between lionfish density and prey fish biomass ($r = 0.7$; $p = 0.01$), where higher lionfish density was correlated

with higher prey fish density and higher prey fish biomass (**Figure 3**). No significant correlations were found between prey fish diversity and any other parameter (**Figure 3**; $\alpha = 0.05$). Species-specific correlations of prey fish biomass with lionfish density revealed a significant positive correlation between lionfish density and *P. furcifer* biomass ($r = 0.8$; $p = 0.006$), while correlations were not significant between lionfish density and *C. enchrysur* biomass ($r = 0.2$; $p = 0.50$) or *C. bermudae* biomass ($r = -0.2$; $p = 0.63$; **Figure 3**). Lionfish density was significantly negatively correlated with bottom temperature ($r = -0.7$; $p = 0.02$), where higher lionfish density was found at sites with lower temperatures (**Figure 3**). Likewise, a significant negative correlation was found for bottom temperature with prey fish biomass ($r = -0.6$; $p = 0.043$; **Figure 3**). However, no significant correlations were found between temperature and prey fish density or diversity (**Figure 3**).

A GLM with gamma distribution including all factors revealed covariance among factors, thereby requiring separate models for each potential driver with best fit found based on AIC model selection. Results of the GLMs show a significant effect of temperature on lionfish density, while no other comparisons were significant (**Figure 4** and **Table 2**). Furthermore, the GLM for lionfish density by temperature resulted in the lowest AIC value compared to the other models, with the closest second being prey fish biomass (+1.54 AIC), indicating that the model



for temperature as a potential driver of lionfish density was the best fit (Table 2).

Prey fish species composition differed by site (Figure 5), however, the most abundant species across sites were consistently *C. bermudae* (972 fish ha⁻¹ ± 315), *C. enchrysur* (974 fish ha⁻¹ ± 465), and *P. furcifer* (845 fish ha⁻¹ ± 499), with the next most abundant species (*Chaetodon sedentarius*) present at considerably lower densities (193 fish ha⁻¹ ± 45). Cluster analysis using *k*-means revealed two distinct communities (Figure 6), which group based on geographic location (Figure 2). The first group consists of sites that are all located along the Northeast edge of the Bermuda platform, where the dominant prey fish species was *C. bermudae* (Figures 5, 6). The latter group consists of all other sites, spanning the Southern and Western edges, where the dominant prey fish species was either *C. enchrysur* or *P. furcifer* (Figures 5, 6). Cluster analysis however, did not reveal any relationship of species assemblages and lionfish densities, as sites did not cluster relative to lionfish densities.

DISCUSSION

The present study documents significant correlations between lionfish densities and ecological as well as environmental parameters related to fish community structure, which suggest

that seawater temperatures and prey availability may affect lionfish distribution on mesophotic reefs in Bermuda. Our data show significant positive correlations between lionfish density and prey fish density as well as prey fish biomass, where an increase in lionfish density is associated with an increase in prey fish abundance (Figures 3, 4). Moreover, lionfish density and prey fish biomass were negatively correlated with bottom seawater temperature, where higher lionfish density and prey fish biomass were found in colder waters (Figures 3, 4).

Previous examinations of lionfish distribution patterns have failed to find an ecological driver for the presence of lionfish. For example, Bejarano et al. (2015) found lionfish densities in Little Cayman varied irrespective of prey fish density. Likewise, Anton et al. (2014) found no correlations between lionfish densities and prey density or predator abundance in the Bahamas. Yet, a positive relationship with food availability has been clearly defined for terrestrial predator populations, where the density of predators is known to be dependent on prey biomass (Carbone and Gittleman, 2002). This discrepancy may be due to long-term removal of fish species simultaneously from all trophic levels, which is typical of subsistence fishing practices on Caribbean coral reefs, masking our ability to track patterns of predator-prey relationships (Paddack et al., 2009; Alvarez-Filip et al., 2015). For example, Newman et al. (2006) found that while increased predator biomass was correlated with increased fish biomass across several reef sites spanning the Caribbean, predators were only abundant within large marine reserves, suggesting that populations outside of the reserves may be more strongly driven by fishing pressure than by natural fluctuations in predator-prey abundances.

MCEs are often buffered from anthropogenic impacts, including overfishing (Tyler et al., 2009; Lindfield et al., 2016; Pinheiro et al., 2016), likely because of their distance from shore in most regions, as well as the additional costs of fishing at these depths. Fish traps, traditionally used across a broad range of depths by Bermuda's commercial fishery, were banned in 1990 (Butler et al., 1993), and spear fishing, with the exception of permitted lionfish culling, is restricted to recreational users without SCUBA (Bermuda Fisheries Act, 1972; Fisheries Regulations, 2010). Thus, fishing impacts are confined to relatively shallow areas today. Indeed, fish diversity and biomass are documented to increase with increasing depth within the mesophotic range in Bermuda (Pinheiro et al., 2016). However, Stefanoudis et al. (in press) found a gradual decrease in fish biomass with depth over a broader depth range (to 90 m) on Bermuda MCEs but noted significant variability in lionfish density at 60 m within their 4 study sites, with three sites in common to this study. Thus, despite continued hook and line fisheries and occasional bycatch in lobster traps, fish communities in Bermuda in general (Paddack et al., 2009; Jackson et al., 2014), and at mesophotic depths in particular, may be less impacted by fishing pressure than those in other locations where lionfish have been studied. Hence, the positive correlation found between lionfish density and prey fish biomass in this study may be facilitated by reduced fishing pressure at the surveyed sites exposing predator-prey relationships that might be masked by the influence of overfishing in other regions. Moreover, the

TABLE 2 | Results of generalized linear models (GLM) with gamma distribution for comparisons of lionfish density with prey fish biomass (kg/ha), prey fish density (fish ha⁻¹), prey fish diversity (Shannon-Weaver index), biomass of *P. furcifer* (kg/ha), and bottom temperature (°C).

Model	df	Coefficient estimate (r)	Std. error	t-value	Pr (> t)	ΔAIC
Prey fish biomass	10	-2.59E-08	1.27E-08	-2.039	0.0718	1.54
Prey fish density	10	-1.02E-06	5.55E-07	-1.845	0.0981	2.31
Prey fish diversity	10	1.44E-03	1.04E-02	0.138	0.893	4.86
<i>P. furcifer</i> biomass	10	-4.61E-08	2.69E-08	-1.714	0.1206	2.47
Temperature	10	7.78E-03	3.13E-03	2.478	0.0351	0

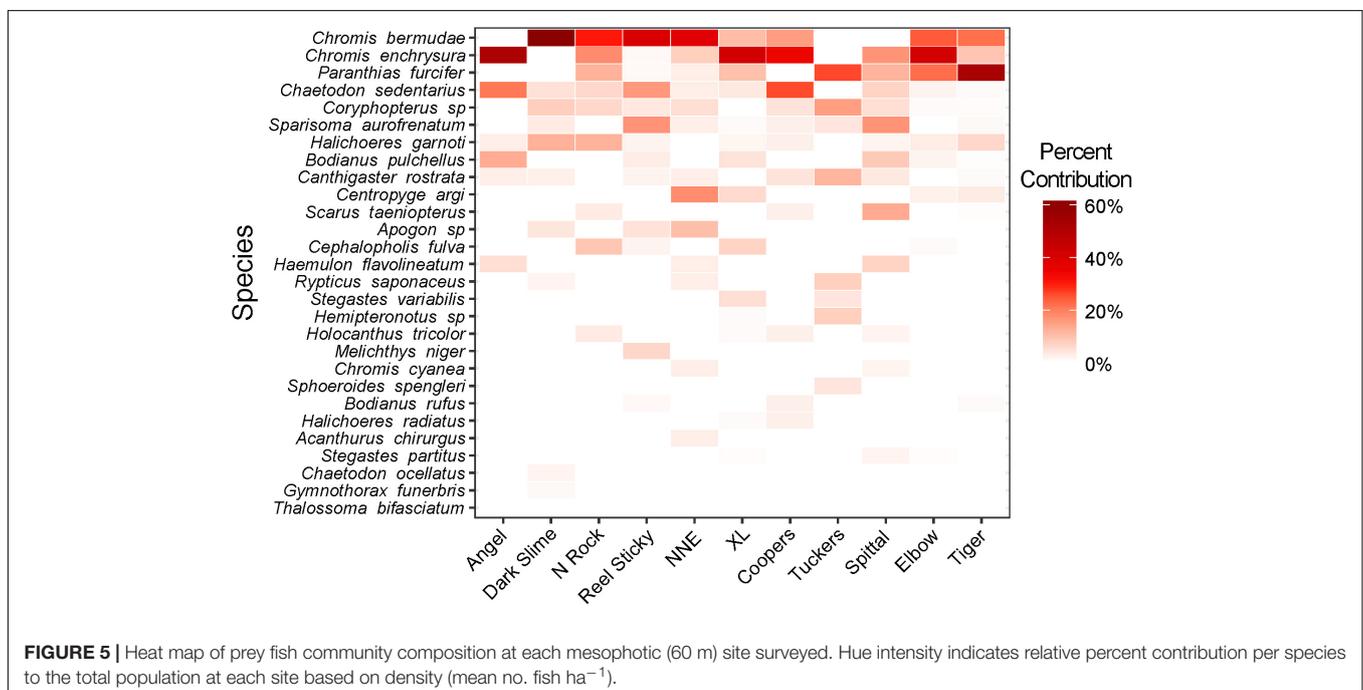
Significant relationships are indicated in bold ($p < 0.05$). The difference in Akaike Information Criterion (AIC) from the best fit model is also provided as an indication of model quality.

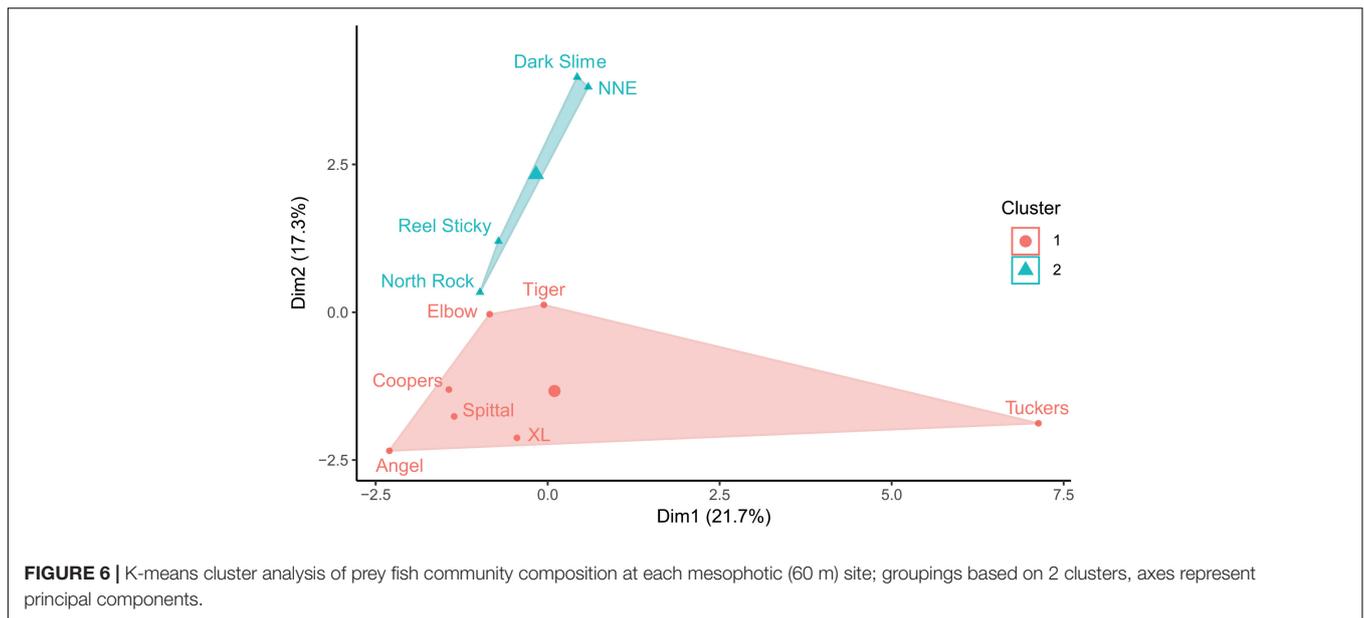
presence of lionfish in Bermuda for nearly two decades has likely allowed sufficient time for this invasive species to adapt to local conditions and distributions of prey, in turn facilitating the emergence of detectable patterns of distribution based on ecological characteristics.

Although variations in overall prey fish community assemblages between sites were not related to lionfish density (Figure 6), a significant correlation was found between lionfish density and *P. furcifer* biomass (Figure 3). *Paranthias furcifer* is the second most common teleost prey species by occurrence consumed by lionfish in Bermuda, following the top teleost prey species, *Thalassoma bifasciatum* (Eddy et al., 2016), which was not present in significant abundance at the sites surveyed for this study (<0.5% contribution to biomass; Figure 5). On the other hand, despite being the top two contributors to fish communities across the MCEs examined (Figure 5), *C. enchrysur* and *C. bermudae* biomass did not correlate significantly with lionfish density (Figure 3). In contrast, Harter et al. (2017) found *C. enchrysur* to be a significant predictor of lionfish densities on MCEs in the Pulley Ridge reef system. In Bermuda, *C. enchrysur*

and *C. bermudae* are not typically consumed by lionfish (Eddy et al., 2016), and hence the lack of correlation with these species may point to the influence of preferential feeding habits on the relationship between lionfish density and availability of preferred prey types, in this case *P. furcifer*. It is important to note, however, that a large portion of the lionfish diet in Bermuda is composed of invertebrates, such as crustaceans and mollusks, which were not included in the present study because of their diurnal crypticity, and thus the influence of these prey types on lionfish distribution remains unknown (Eddy et al., 2016). Therefore, further comparisons of feeding patterns in relation to prey availability as predictors of lionfish distribution should include a broader variety of prey types at additional locations, such as Pulley Ridge, Cayman Islands etc., in order to advance our understanding of this relationship.

The strongest driver of lionfish density, however, was found to be seawater temperature, with significantly more lionfish found at colder locations (Figures 3, 4). Previous examinations of the impact of temperature on lionfish densities have focused on the minimum temperatures at which lionfish are found,





where the minimum thermal limit for lionfish survival is 10°C and feeding ceases at 15°C, thereby limiting their latitudinal and bathymetric distribution (Kimball et al., 2004). Within the range of temperature tolerance, however, only a few studies address variations in lionfish densities in relation to seawater temperature. In their native habitat, which ranges from South Korea at 35°N to New Zealand at 34°S, higher densities of *P. volitans* are found at high latitude regions compared to low latitude locations. However, there is no correlation between temperature and lionfish density within locations across this range (Kulbicki et al., 2012). Within the invaded range, along the coast of North Carolina, Whitfield et al. (2014) found the highest densities of lionfish at the deepest sites examined (38–46 m depths), which they suggest may be related to warmer mean winter temperatures at depth, although no variation in temperature was found among sites at the time of surveys.

Temperature is documented to affect the bioenergetics of lionfish, with variations in growth and consumption rates occurring in habitats with differing temperature regimes. For example, Edwards et al. (2014) found lionfish growth rates in tropical waters near the Cayman Islands to be higher than those found by Potts et al. (2010) and Barbour et al. (2011) in temperate waters off North Carolina. Likewise, Cerino et al. (2013) found consumption rates by lionfish increase with increasing water temperature from 14 to 29.7°C. Metabolism, on the other hand, is slowed in colder temperatures for other fish species and thus assimilation may be higher, thereby reducing overall energetic costs when residing in colder waters (Bevelhimer and Adams, 1993). Previous studies have shown that fish of a particular species will spend the majority of time (75%) within a thermal range that promotes optimal physiological activities and results in maximum growth (Magnuson et al., 1979; Magnuson and Destasio, 1997). The increased density of lionfish at colder sites in Bermuda, therefore, may reflect an energy conservation strategy involving trade-offs between rates of consumption and

metabolism (Sims et al., 2006; Eddy, 2016). However, additional studies of lionfish bioenergetics are required that include seasonal variations, as anecdotal evidence in Bermuda indicates seasonal shifts in lionfish distribution to shallower reefs in winter months (pers. obs. all authors).

The presence of colder water at specific mesophotic sites might also suggest mixing of deep water at or below the thermocline, which may be promoted by site specific bathymetry, as the tidal exchange around the Bermuda Islands and over the shallow reef platform appears to promote upwelling at the eastern and western ends of the reef system (Goodbody-Gringley et al., 2019). Moore (1949) studied zooplankton horizontal and vertical distribution patterns around Bermuda and speculated on the presence of episodic upwelling to account for some patterns. Vertical mixing is typically associated with increased transport of nutrients that fuel the population growth of zooplankton species in the waters surrounding Bermuda (Bodungen et al., 1982; Sigman and Hain, 2012). For example, Jiang et al. (2007) found that a decrease in temperature by 0.4–0.8°C in the open ocean near Bermuda was correlated with an increase in zooplankton biomass at 70-m depth, which corresponds to the deep chlorophyll maximum zone (DCM) around the thermocline. Planktivores, such as *P. furcifer*, generally concentrate along the reef edge and feed mainly in midwater on zooplankton such as copepods, pelagic tunicates, and various crustacean larvae (Hobson, 1991; Rocha et al., 2008). This feeding strategy makes water currents important for supplying food to planktivores, resulting in stationary aggregations that feed around currents and then dissipate as currents slacken (Stevenson et al., 1972; Thresher, 1983; Hobson, 1991). In fact, previous studies document planktivores dominating fish community assemblages on MCEs (Colin et al., 1986; Dennis and Bright, 1988; Garcia-Sais, 2010; Bryan et al., 2013; Bejarano et al., 2014; Pinheiro et al., 2016; Rosa et al., 2016), and often cite increased abundances of zooplankton from upwelling

currents as a likely cause. Thus, increased lionfish densities associated with colder seawater temperatures may be due to the effects of vertical mixing, via upwelling, increasing local productivity and fueling the food chain at specific sites, resulting in high abundances of planktivorous prey fishes and thus in turn lionfish (**Figure 5**), particularly given that prey fish abundance and temperature were found to co-vary with lionfish density (**Figure 4**).

Importantly, temperature is not the only physical characteristic that may impact lionfish distribution. For example, despite being one of the coldest sites, the surveyed area at North Northeast did not support the highest density of lionfish (**Table 1**), which is likely attributable to the composition of the benthos at that site being dominated by beds of rhodolith balls and macroalgae, and lacking solid reef substrate or topographic complexity. Previous studies have found habitat complexity to be a strong predictor of lionfish abundances on shallow reefs, where increased lionfish density is associated with higher topographic complexity (Bejarano et al., 2015) and/or benthic community diversity (Hunt et al., 2019). However, in Bermuda, topographic complexity at the depths surveyed in this study is low overall, with sites generally dominated by rhodolith beds and occasional outcroppings of low relief reef structures (**Figure 1**; Goodbody-Gringley et al., 2019). In the northern Gulf of Mexico, lionfish are found at increased densities on artificial reef structures compared to natural reef habitat (Dahl and Patterson, 2014). Surrounded by large expanses of flat sandy bottom, these artificial reefs are thought to serve to concentrate settling juvenile lionfish that cue to high vertical relief (Dahl and Patterson, 2014). Thus, slight differences in benthic composition, such as the occasional outcropping of solid substrate within a field of rhodoliths, may also be influencing lionfish distributions in MCEs. Full characterization of the physical environment, including plankton abundance and composition, as well as benthic habitat characterization in MCEs around Bermuda would aid in such interpretations.

The extent of the lionfish invasion and the formation of reproductive populations throughout the invaded range indicates that the lionfish are established permanently in the Caribbean and Western Atlantic. While complete eradication of lionfish is unlikely, various management strategies have been proposed to reduce and/or control local populations (Albins and Hixon, 2008; Côté and Maljkovic, 2010; Arias-Gonzalez et al., 2011; Green et al., 2011; Muñoz et al., 2011; Pitt and Trott, 2014). The majority of control measures involve managed manual removal through targeted spear fishing by SCUBA and free divers and/or establishment of a commercial fishery aimed at increasing public consumption of lionfish (Muñoz et al., 2011; Frazer et al., 2012; Albins and Hixon, 2013; Gleason and Gullick, 2014). Recent work indicates that targeted removal by organized volunteers can be successful in controlling local populations, finding that continued removal of individuals from shallow populations results in an overall reduction of lionfish biomass at fished locations compared to unfished locations (de León et al., 2013; Green and Côté, 2014). However, the inability to remove individuals from deep reefs will enable continued recruitment to fished locations, as mesophotic lionfish

are highly fecund (Eddy, 2016; Andradi-Brown et al., 2017b), potentially offsetting the efficacy of local shallow water culling (Johnston and Purkis, 2015; Andradi-Brown et al., 2017a). Given the documented importance of MCEs as critical nursery habitats for several reef fish species (Lobel, 1981; Randall and Chen, 1985; Brokovich et al., 2007; Garcia-Sais, 2010; Sazima et al., 2010; Lindfield et al., 2016), it is important that lionfish populations at mesophotic depths are incorporated into management strategies. The results presented here suggest that lionfish distribution on mesophotic reefs is influenced in part by physical parameters of the environment, such as temperature, as well as ecological parameters, such as the availability of potential prey. Understanding the factors that drive lionfish distributions will ultimately aid in our ability to successfully identify and target areas with high lionfish densities, thereby increasing the efficacy of management and control efforts throughout the invaded range in order to minimize negative impacts to these threatened ecosystems.

AUTHOR CONTRIBUTIONS

All the authors developed the concept for this study, executed the field work, collected the data, and contributed to writing of the manuscript. GG-G undertook statistical analyses and composed data visualizations.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00258/full#supplementary-material>

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