

Research Article

Distribution and abundance of the introduced snapper *Lutjanus kasmira* (Forsskål, 1775) on shallow and mesophotic reefs of the Northwestern Hawaiian Islands

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Abstract

The Bluestriped Snapper, *Lutjanus kasmira* (Forsskål, 1775), was intentionally introduced to the island of O‘ahu between 1955 and 1961. It quickly spread throughout the Hawaiian Islands and became highly abundant in reef slope and spur and groove habitats. Here, we investigated the distribution of *L. kasmira* on shallow and mesophotic reefs of the Northwestern Hawaiian Islands (NWHI) using fish survey data collected from 2007 to 2016. *L. kasmira* was recorded at all islands or atolls of NWHI except for Gardner Pinnacles, Maro Reef, and Laysan Island—the middle region of the NWHI. It was most abundant at French Frigate Shoals and Nihoa at the southern end of the NWHI. On mesophotic reefs, *L. kasmira* was not observed at any locations north of French Frigate Shoals, except for one individual at Lisianski Island at an upper mesophotic depth. Small-bodied individuals were found more frequently at greater depths. *L. kasmira* was often observed along with *Mulloidichthys vanicolensis* (Valenciennes, 1831), *Chromis acares* Randall and Swerdloff, 1973, and *Naso hexacanthus* (Bleeker, 1855) on shallow-water reefs. The present study indicates the potential effects of habitat types and water temperature in the vertical and horizontal distribution of *L. kasmira* in the NWHI and the possibility of differential utilization of resources by adults and juveniles.

Key words: biological invasion, fish, Papahānaumokuākea Marine National Monument

Introduction

Aquatic organisms are often accidentally or intentionally transported to new habitats through anthropogenic activities such as domestic and international shipping and aquaculture (Bax et al. 2003). Species introduced outside of their native range can pose a major threat to biodiversity by displacing native fauna and altering community structure (Molnar et al. 2008). Interactions between native and non-native species can be extremely complex, however, thus the effects of introduced species on native fauna and the exact outcomes of invasion are difficult to predict (Mills et al. 2004). While the case of an introduced

marine fish becoming a major invasive threat is rare, recent studies indicate the potential for invasive fish to have devastating effects, directly and indirectly, on coral reef ecosystems (Albins and Hixon 2013; Green et al. 2012).

The Bluestriped Snapper, *Lutjanus kasmira* (Forsskål, 1775), is a tropical species with a wide indigenous range in the Indo-Pacific. Following an initial release of fewer than 12 individuals in 1955, 2,435 individuals of *L. kasmira* were intentionally introduced from the Marquesas Islands in French Polynesia to O‘ahu, one of the inhabited Main Hawaiian Islands (MHI), in 1958 to enhance recreational and commercial fishing (Randall 1987; Schumacher and

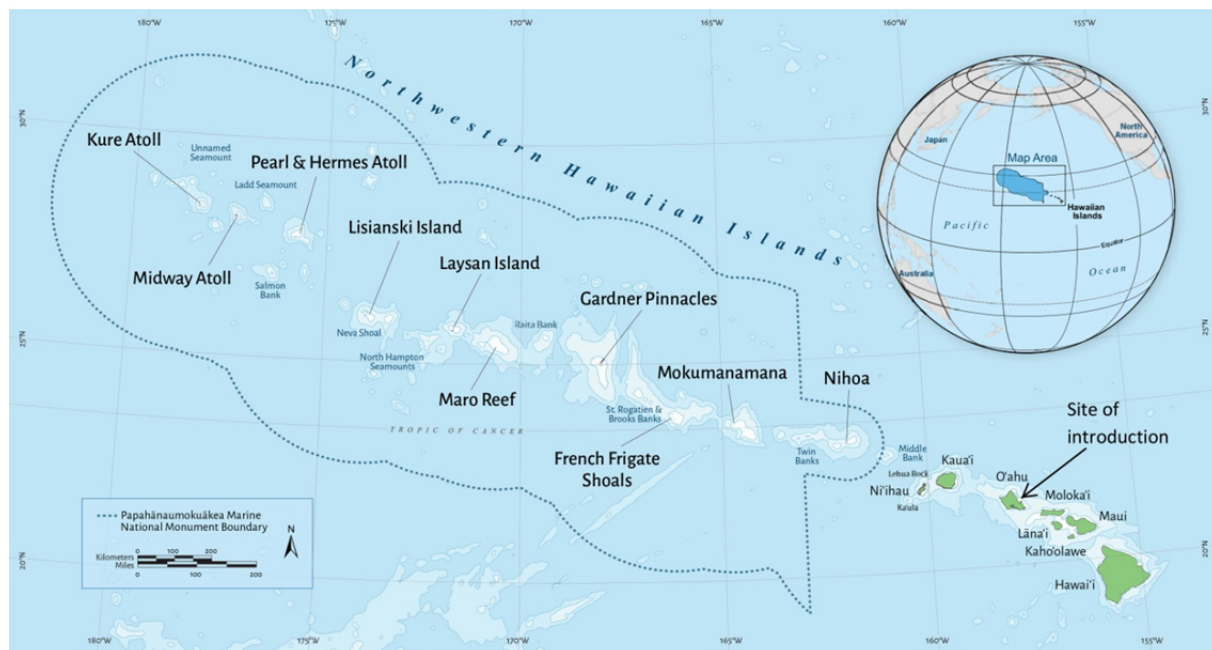


Figure 1. Map of the Hawaiian Archipelago including the Northwestern Hawaiian Islands. *Lutjanus kasmira* was intentionally introduced to the island of O‘ahu in the late 1950’s.

Parrish 2005). This introduction was followed by another introduction of 728 individuals from Moorea in the Society Islands in 1961 (Gaither et al. 2010a; Schumacher and Parrish 2005). *L. kasmira* quickly spread throughout the MHI and the Northwestern Hawaiian Islands (NWHI), and are now highly abundant in reef slope and spur and groove habitats, often occurring in large aggregations (Friedlander et al. 2002; Oda and Parrish 1981). In Hawai‘i, this species is now commonly known by its Tahitian name, *ta‘ape*. Although there is no evidence of strong ecological associations between *L. kasmira* and other fishes (Friedlander et al. 2002), previous studies have suggested that *L. kasmira* could compete with native goatfish for shelter (Schumacher and Parrish 2005) and potentially contribute to declines of some native fish species (Grigg et al. 2008).

The NWHI, located northwest of the MHI, are part of the Papahānaumokuākea Marine National Monument, a marine protected area encompassing 1,508,870 km². The NWHI consist of ten major islands or atolls that span approximately 2,000 km, from the small basaltic island of Nihoa at the southeastern end to Kure Atoll at the northwestern end (Figure 1). Islands/atolls in the NWHI provide a wide range of marine habitats for reef organisms with diverse underwater topography, habitat complexity, and benthic species compositions and coverage (Friedlander et al.

2009; Maragos et al. 2004). Due to its protected status, the coral reef ecosystem of the NWHI is considered to be a relatively pristine, predator-dominated, reef ecosystem, particularly in comparison to more heavily impacted systems of the MHI. However, despite the protected status, remoteness, and relative inaccessibility, alien species are one of the most severe threats to native fauna (Office of National Marine Sanctuaries 2009). It is, therefore, important to examine the current distribution of the introduced *L. kasmira* to assess their potential ecological impacts on native fauna.

Here, we examined the distribution of *L. kasmira* on shallow and mesophotic reefs of the NWHI using data collected for two separate projects: NWHI Reef Assessment and Monitoring Program (RAMP) that surveyed shallow-water (≤ 30 m depths) habitats and mesophotic reef characterization that surveyed deep-water (30–100 m depths) habitats. Occurrence of *L. kasmira* has previously been reported from shallow-water habitats of different locations in the NWHI including Maro Reef (Gaither et al. 2010a), Laysan Island (Oda and Parrish 1981), Midway Atoll (Randall et al. 1993) and Kure Atoll (Gaither et al. 2010a). However, their distribution across the NWHI and size distribution at each island/atoll on either shallow or mesophotic zones are poorly known. We also investigated potential associations of *L. kasmira* with other reef fish species.

Methods

Survey sites

Fish surveys were performed during summer months aboard the NOAA ship *Hi'ialakai* from 2007 to 2016. Islands and atolls in the NWHI that were visited varied between years, depending on the schedule and length of each expedition. Surveyed sites included shallow-water and mesophotic reefs of 10 islands and atolls (Figure 1): Nihoa (23°04'N; 161°55'W), Mokumanamana (23°34'N; 164°42'W), French Frigate Shoals (23°52'N; 166°17'W), Gardner Pinnacles (25°01'N; 167°59'W), Maro Reef (25°25'N; 170°35'W), Laysan Island (25°42'N; 171°44'W), Lisianski Island (26°04'N; 173°58'W), Pearl and Hermes Atoll (27°56'N; 175°44'W), Midway Atoll (28°12'N; 177°21'W) and Kure Atoll (28°25'N; 178°20'W).

Shallow-water surveys

Shallow-water surveys (0–30 m) were performed every summer from 2007 to 2015, except for 2008 and 2013. Survey sites were randomly chosen each year using GIS bathymetric and bottom composition maps, in which target hard-bottom habitats for monitoring were stratified by reef zone (backreef, forereef and lagoon) and depth range (shallow 0–6 m, mid 6–18 m and deep 18–30 m). At each site, one or two pairs of divers simultaneously performed a reef fish survey using a stationary point count (SPC) method (Williams et al. 2015). The survey consisted of an initial five-minute species enumeration period to list all species observed inside an SPC cylinder (15 m in diameter) and a following tallying period to work through the list systematically to record the numbers and sizes of individual species. If a large school of fish swam through an SPC cylinder, a surveyor of the cylinder treated the situation as if taking a snapshot and only counted individuals in the cylinder at one point in time (i.e. instantaneous count), and did not continue to count the rest of the school as it swam through. Divers remained stationary at the centers of their cylinders to avoid disturbance as much as possible, but at the end of the tallying period they swam through their plots to count small, semi-cryptic species.

Mesophotic surveys

Mesophotic surveys (30–100 m) were performed every summer by divers using open-circuit trimix systems from 2010 to 2012 and closed-circuit rebreathers from 2013 to 2016. Multibeam sonar data were used to locate potential survey areas having

hard-bottom slopes, ledges, or other distinguishing features of fish habitats within allowable diving depths (< 100 m). Survey sites were haphazardly chosen from these potential areas as randomization of site selection was extremely difficult due to both the limited area of hard-bottom habitat in appropriate depth ranges and limited availability of multibeam sonar bathymetry. At each site, divers identified, counted, and estimated size of all conspicuous, diurnally-active fishes along a 25 × 2 m belt transect (Kane et al. 2014). Unlike the SPC method, divers counted all individuals if a school of fish swam over their transects during the surveys. Mesophotic surveys consisted of one transect survey per site, except for some survey sites from 2010 to 2012 where replicate observations were made on the same day. For the purpose of comparison, we categorized the surveys into three depth ranges: upper mesophotic (< 50 m), mid (50–70 m) and deep (≥ 70 m).

Species association

Analyses of species association were done separately for shallow-water and mesophotic surveys using the software package PRIMER 7 (Clarke and Gorley 2015). For both shallow-water and mesophotic surveys, fish counts were first averaged to obtain fish abundance per survey site. Pelagic or semi-pelagic fishes, including sharks, rays, tunas, jacks, sardines, anchovies and herrings, were excluded in order to focus on non-transient, resident reef fishes.

Type 2 Similarity Profile (SIMPROF) analyses, followed by Type 3 SIMPROF, were used for formal analyses of species association as described by Somerfield and Clarke (2013). Briefly, a reduced set of 50 most-important species was obtained for each survey dataset by successively dropping species that accounted for the smallest percentage of total abundance at every site until 50 species were retained. An interspecies association matrix of these 50 species was computed using the Index of Association (IA) after standardizing the variable (i.e. species abundance) by total across all sites. Type 2 SIMPROF tested for species association among all 50 species on the basis of IA (i.e. global test). After a null hypothesis of this global test was rejected, species were divided into hierarchical groups using group-average clustering of the IA matrix. We used a sequence of Type 3 SIMPROF tests to identify groups of fishes that varied coherently across samples in order to determine which species were associated with *L. kasmira*. For both Type 2 and Type 3 SIMPROF analyses, 4999 permutations and the significance level of $\alpha = 0.05$ were used.

Table 1. Frequency of occurrence of *Lutjanus kasmira* per island/atoll for shallow-water and mesophotic surveys.

	Shallow-water			Mesophotic		
	Number of sites	Number of sites with <i>L. kasmira</i>	Frequency of occurrence	Number of sites	Number of sites with <i>L. kasmira</i>	Frequency of occurrence
Nihoa	8	2	0.250	9	3	0.333
Mokumanamana	21	1	0.048	0	–	–
French Frigate Shoals	142	58	0.408	41	16	0.390
Gardner Pinnacles	12	0	0.000	7	0	0.000
Maro Reef	81	0	0.000	9	0	0.000
Laysan Island	45	0	0.000	6	0	0.000
Lisianski Island	132	1	0.008	28	1	0.036
Pearl & Hermes Atoll	165	3	0.006	39	0	0.000
Midway Atoll	131	1	0.018	14	0	0.000
Kure Atoll	96	1	0.010	13	0	0.000

Table 2. Total numbers of *Lutjanus kasmira* in different size classes observed in each year during shallow-water surveys and the total number of SPCs per year. The size of SPC survey area was 176.6 m² (circular plot 15 m in diameter).

	2007	2009	2010	2011	2012	2014	2015
1–5 cm	0	0	0	0	0	0	0
6–10 cm	0	1	22	0	0	8	11
11–15 cm	15	0	3	1	1	4	0
16–20 cm	58	1	32	16	14	42	28
21–25 cm	95	0	27	42	16	48	4
>25 cm	14	0	6	23	15	8	0
Total SPCs	464	656	430	362	188	178	192

Table 3. Total numbers of *Lutjanus kasmira* in different size classes observed in each year during mesophotic surveys and the total number of transects per year. The size of transect survey area was 50 m² (25 × 2 m belt).

	2010	2011	2012	2013	2014	2015	2016
1–5 cm	0	1	0	0	88	0	0
6–10 cm	0	0	1	4	18	35	4
11–15 cm	0	14	0	10	2	14	120
16–20 cm	0	7	0	37	52	0	0
21–25 cm	0	75	0	0	0	0	0
>25 cm	>300	0	0	4	0	0	0
Total transects	36	33	23	16	28	22	25

Results

Shallow-water surveys

In total, 555 individuals of *Lutjanus kasmira* were recorded during 2,470 SPC surveys at 833 shallow-reef sites in the NWHI (Supplementary material Table S1). Frequency of occurrence was highest at French Frigate Shoals with *L. kasmira* present at 41% of the sites surveyed, followed by Nihoa and Mokumanamana (Table 1). At Lisianski Island, Pearl and Hermes Atoll, Midway Atoll, and Kure Atoll, *L. kasmira* was present at < 2% of the site surveyed, and none were observed at Gardner Pinnacles, Maro Reef, or Laysan Island (Table 1). Sizes of individuals ranged from 6 to 33 cm total length (TL), but nearly 90% of them were larger than 15 cm TL (Table 2, Figure 2). Small individuals (6–10 cm TL) were all found at forereef habitat at depths ≥ 18 m at French Frigate Shoals with an exception of one individual found in a lagoon at 4 m depth at Kure Atoll (Figure 3). No individual smaller than 6 cm in TL was recorded. In addition, there was no individual observed from backreef habitat at any depth.

Mesophotic surveys

In total, 486 individuals of *L. kasmira*, were observed during 182 transect surveys at 165 mesophotic reef sites in the NWHI (Table S2). In addition, a large school of *L. kasmira* consisting of ~ 300 individuals (25–30 cm TL) was recorded from a single transect at French Frigate Shoals at 57 m depth in 2010 (Figure 4). Similar to the shallow-water surveys, frequency of occurrence was highest at French Frigate Shoals with *L. kasmira* present at 39% of the sites surveyed, followed by Nihoa (Table 1). One individual was also recorded from Lisianski Island at 37 m depth in 2011. There were no mesophotic surveys at Mokumanamana. Sizes of individuals ranged from 3 to 30 cm TL (Table 3, Figure 2). At depths ≥ 70 m, all observed individuals were smaller than or equal to 15 cm TL (Figure 5). There were 88 individuals that were 3–5 cm TL recorded from 61 m depth at French Frigate Shoals in 2014 and one individual 4 cm TL from 37 m depth at Lisianski Island.

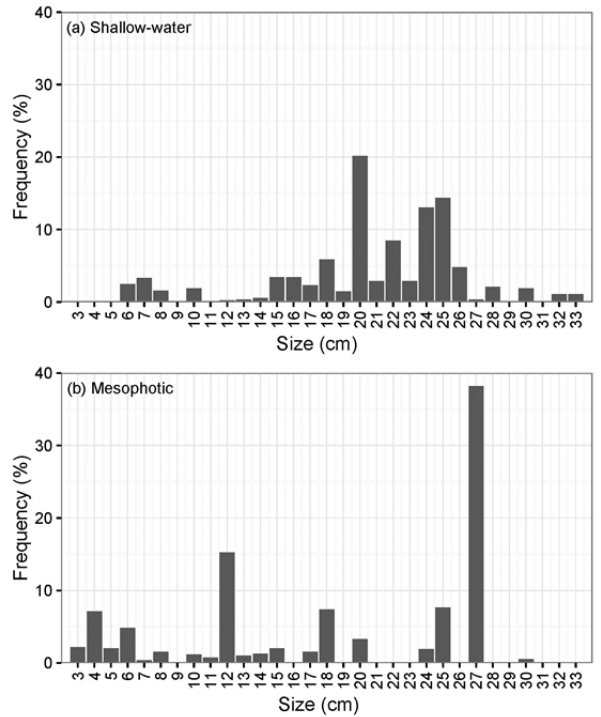


Figure 2. Size distribution of *L. kasmira* from (a) shallow and (b) mesophotic surveys in the NWHI. Note that the bar at 27 cm TL in the mesophotic surveys represents a single school of *L. kasmira* consisting of ~ 300 individuals 25–30 cm TL.

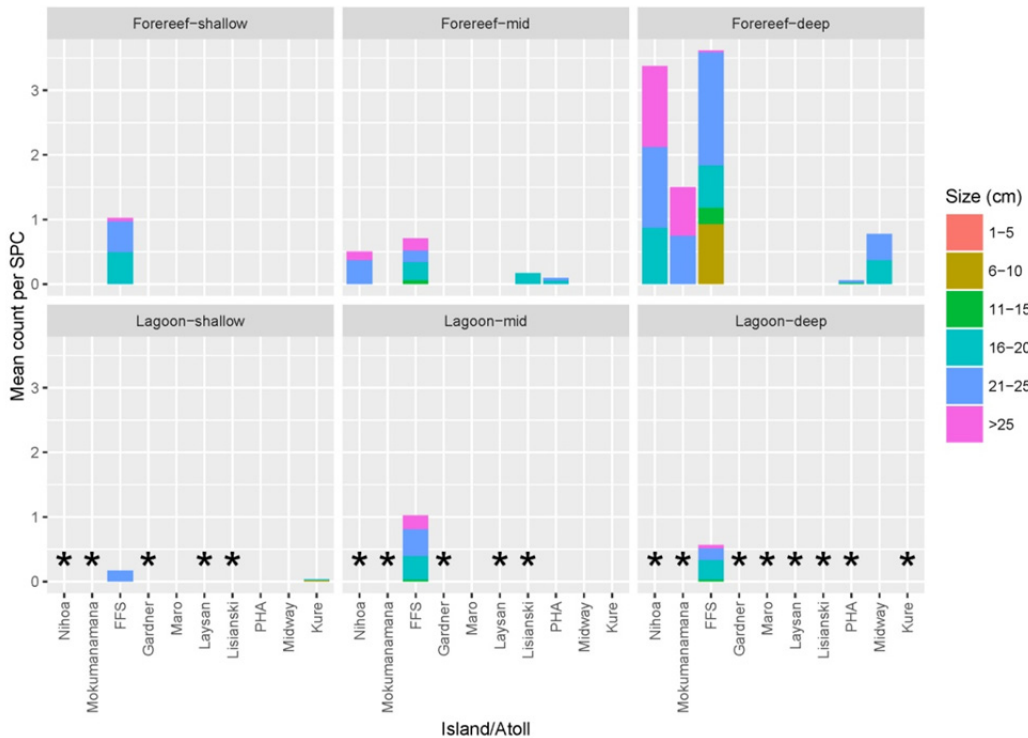


Figure 3. Average counts of *L. kasmira* per stationary point count survey and proportions of size classes in each habitat stratum at different locations of the NWHI: Nihoa, Mokumanamana, French Frigate Shoals (FFS), Gardner Pinnacles, Maro Reef, Laysan Island, Lisianski Island, Pearl and Hermes Atoll (PHA), Midway Atoll and Kure Atoll. Depth ranges are shallow 0–6 m, mid 6–18 m and deep 18–30 m. Asterisks (*) show habitat types not available at particular island/atoll. No individuals were found in backreef habitat.

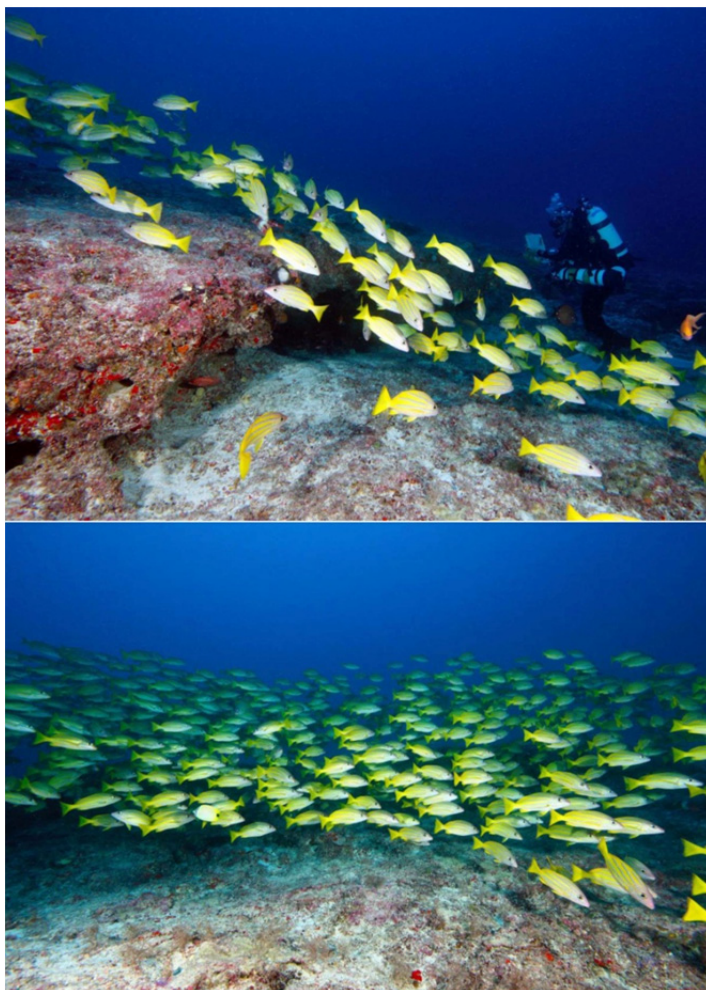


Figure 4. A large school of *L. kasmira* consisting of ~ 300 individuals at French Frigate Shoals at 57 m depth observed on August 15, 2010. Photo credit: Greg B. McFall/NOAA.

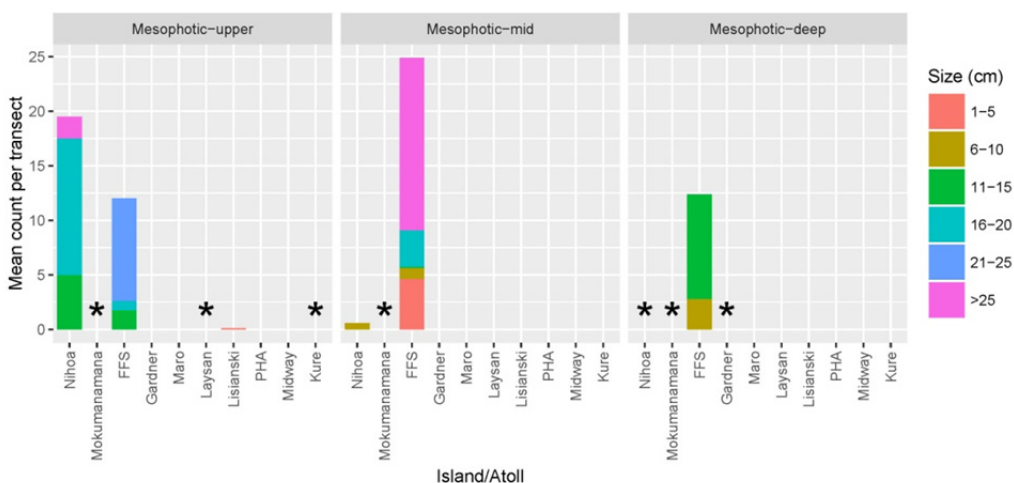


Figure 5. Average counts of *L. kasmira* per transect survey and proportions of size classes in each habitat stratum at different locations of the NWHI: Nihoa, Mokumanamana, French Frigate Shoals (FFS), Gardner Pinnacles, Maro Reef, Laysan Island, Lisianski Island, Pearl and Hermes Atoll (PHA), Midway Atoll and Kure Atoll. Depth ranges are upper mesophotic 30–50 m, mid 50–70 m and deep \geq 70 m. Asterisks (*) show depth ranges that were not surveyed at particular island/atoll.

Species association

There was a statistically significant association among species on both shallow reefs ($\pi = 1.53$, $p = 0.002$) and on mesophotic reefs ($\pi = 1.10$, $p = 0.002$). Type 3 SIMPROF tests identifying species whose abundances varied coherently across samples showed that *L. kasmira* was typically observed with *Chromis acares* Randall and Swerdloff, 1973, *Mulloidichthys vanicolensis* (Valenciennes, 1831), and *Naso hexacanthus* (Bleeker, 1855) on shallow-water reefs and with *Heniochus diphreutes* Jordan, 1903 and *Myripristis amaena* (Castelnau, 1873) on mesophotic reefs. Note, however, that despite the removal of rare species, the 50 most important species in mesophotic surveys included those relatively low in overall abundance. The mean densities of *H. diphreutes* and *M. amaena* were 0.47 and 0.13 per 50 m², respectively, while that of *L. kasmira* was 2.95 per 50 m² excluding the large school on a single transect at French Frigate Shoals.

Discussion

Lutjanus kasmira was most frequently recorded at French Frigate Shoals and Nihoa, the southern end of the NWHI, on both shallow and mesophotic reefs. Despite previous records of *L. kasmira* from Maro Reef and Laysan Island (Gaither et al. 2010a; Godwin et al. 2006; Oda and Parrish 1981), no individuals were observed at these locations, nor at Gardner Pinnacles, during either the shallow-water or mesophotic surveys. While the relatively low numbers of survey sites at these locations (Table 1) may have contributed to this absence of *L. kasmira* in our surveys, the present study showed that *L. kasmira* was much less common north of French Frigate Shoals on both shallow and mesophotic reefs. This may be due to differences in physical distances from the island of O'ahu, the site of introduction, suggesting that *L. kasmira* is still in the process of being established in northern part of the NWHI. This explanation seems unlikely because *L. kasmira* reaches sexual maturity at 1–2 years and is highly dispersive (Gaither et al. 2010b). It was also reported from Laysan Island as early as in 1981 (Oda and Parrish 1981). In addition, a previous genetic study that included individuals from the NWHI showed *L. kasmira* in the Hawaiian Islands is a single population with no genetic structure across the archipelago. This indicates that the numbers of individuals needed to maintain most of the genetic diversity colonized each island/atoll during the spread of the species from O'ahu (Gaither et al. 2010a).

Of the three locations at the southern end of the NWHI, French Frigate Shoals is a large, open atoll with basalt features that support a wide range of reef habitats including reef slopes, patch reefs and pinnacles, while Nihoa and Mokumanamana are both small basalt islands with relatively small amounts of shallow reef habitat (Friedlander et al. 2009). Accordingly, abundance and species richness of scleractinian corals are higher at French Frigate Shoals than Nihoa or Mokumanamana (Maragos et al. 2004). In particular, *Acropora* table corals, which are found only in a middle region of the NWHI from Mokumanamana to Laysan Island, reaches a maximum abundance at French Frigate Shoals (Maragos et al. 2004). A school of *L. kasmira* is often observed under or in association with these table corals during the day (Figure 6). Therefore, the higher abundance of *L. kasmira* at French Frigate Shoals, in comparison to Nihoa or Mokumanamana, is likely due to a greater diversity of habitat types, and a higher availability of preferred reef habitat for this particular species.

L. kasmira occurs from shallow water to depths > 200 m (Randall 1987) but is generally limited to depths < 150 m in Hawai'i (Parrish et al. 2000). In the present study, it was generally more abundant on shallow reefs in forereef habitat, especially at depths ≥ 18 m, than in lagoons or backreef habitat where no individuals were found (Figure 3). This was consistent with a previous study off the island of Kaua'i by Friedlander et al. (2002), in which *L. kasmira* was abundant on hard-bottom reef edges, was absent on shallow and deep reef flats, and rare on complex back reefs. On mesophotic reefs, *L. kasmira* was present at all surveyed depth ranges up to French Frigate Shoals, but north of French Frigate Shoals, only one individual was found at an upper mesophotic depth at Lisianski Island. In the NWHI, cooler water temperature in winter, in comparison to the MHI, restricts occurrence of shallow-water species that are adapted to warm water (Mundy 2005). As *L. kasmira* is a tropical species with a natural range from South Africa to the Marquesas and Line Islands in the central Pacific, it is possible that temperature gradients along depth and latitude regulate the horizontal and vertical distribution of *L. kasmira* in the NWHI. During this study, temperatures as low as 17 °C were recorded by divers at depths of 90–100 m at Pearl and Hermes Atoll, Midway Atoll and Kure Atoll.

The Hawaiian Islands support unique fauna and flora due to their isolation, and endemism of reef fish is relatively high, averaging $\sim 30\%$ in the shallow waters of the NWHI (Grigg et al. 2008). The level of endemism is even higher on mesophotic reefs



Figure 6. Photographs of *L. kasmira* under or in association with *Acropora* table corals at Rapture Reef, French Frigate Shoals at 25 m depth. Photo credit: James D. Watt/NOAA.

of the NWHI reaching as high as 100% at Kure Atoll (Kosaki et al. 2016). While mesophotic reefs have received increased attention in recent years as potential refugia and source of propagules for degraded shallow-water habitats (Baker et al. 2016; Lindfield et al. 2016), the present study suggest that mesophotic reefs of the northern part of the NWHI may also serve as potential refugia from alien species. It is also interesting to note that *Cephalopholis argus* Bloch and Schneider, 1801 and *Lutjanus fulvus* (Forster, 1801), two fishes that were also intentionally introduced to the Hawaiian Islands in the 1950's and became established (Randall 1987), were entirely absent in our mesophotic surveys, despite the presence of *C. argus* up to French Frigate Shoals on shallow reefs. Our unpublished data show the presence of these species on mesophotic reefs of the MHI, with *C. argus* at 31 m depth at Ni'ihau, the northwestern end of the MHI, and *L. fulvus* also at 31 m depth at Ni'ihau and 51 and 76 m depths at Maui.

While direct quantitative comparisons of *L. kasmira* abundance between shallow-water and mesophotic surveys are difficult due to differences in the survey methods and sampling efforts, relative abundances of

smaller individuals were generally higher at deeper depths. Individuals smaller than 11 cm TL were mostly observed at depths ≥ 18 m during the shallow-water surveys, and those smaller than 6 cm TL were only observed during the mesophotic surveys. These observations were consistent with a previous study in Kaua'i, in which solitary or small schools of large individuals were observed in shallow slope habitats while larger schools of smaller individuals were found on deep slopes (Friedlander et al. 2002). In the same study, no individuals smaller than 6 cm TL were recorded during transect surveys on shallow reefs (Friedlander et al. 2002). These findings indicate the potential for differential use of resources by adult and juvenile *L. kasmira* (i.e., nursery areas). Ontogenetic migrations often are driven by food availability and predation risk (Dahlgren and Eggleston 2000). Such migrations occur among reef fish across depth gradients, although their directions are species specific, with some migrating from shallower to deeper waters as juveniles mature (Andradi-Brown et al. 2016; Rosa et al. 2016) and others using mesophotic reefs as a nursery habitat (Brokovich et al. 2007). The higher occurrence of smaller individuals at greater

depth, however, does not necessarily mean that mesophotic reefs only support smaller individuals. This was evident in the present study where a large school of *L. kasmira* > 25 cm TL were found at 57 m depth, as well as in a previous study in Hawai'i using a submersible that reported individuals up to 30 cm TL at mesophotic depths (Parrish et al. 2000). Investigating how this introduced species uses habitat and food resources at different stages of its life cycle should help managers assess the potential for further spread of the species in the Papahānaumokuākea Marine National Monument.

Species association analyses suggested *L. kasmira* was associated with different species of fish on shallow-water and mesophotic reefs. *L. kasmira* nocturnally migrates from reefs to surrounding soft-bottom habitat for foraging (Friedlander et al. 2002) and primarily feed on benthic invertebrates, such as crustaceans and mollusks, and fish, but also eats some pelagic invertebrates (DeFelice and Parrish 2003; Oda and Parrish 1981; Parrish et al. 2000). The native invertivore *Mulloidichthys vanicolensis*, one of the three species identified in the species association analysis for shallow reefs, feeds primarily on crab megalopae and benthic invertebrates (Hobson 1974) and shows limited diet overlap with *L. kasmira* (Schumacher 2011). *M. vanicolensis* and *L. kasmira* also have similar patterns of habitat use during the day (Schumacher and Parrish 2005), but not at night when feeding (Schumacher 2011). In the study by Schumacher and Parrish (2005), these two species were both associated with the bottom when in resting schools during the day, although *M. vanicolensis* moved higher into water column away from the reefs when they co-occurred with *L. kasmira*, potentially making the native species more susceptible to predation.

The other two species (*Chromis acares* and *Naso hexacanthus*) usually found with *L. kasmira* on shallow reefs, and those on mesophotic reefs (*Heniochus diphreutes* and *Myripristis amaena*), are all planktivores. While *Myripristis* species have previously been reported to occur frequently with *L. kasmira* in Hawai'i (Oda and Parrish 1981; Parrish et al. 2000), *Myripristis amaena* mainly feeds on crab megalopae (Hobson 1974) and has little diet overlap with *L. kasmira*. *H. diphreutes* has also been reported previously resting close to *L. kasmira* at ~ 100 m depth (Parrish et al. 2000), but it is difficult to interpret this single observation of co-occurrence. In this study, *C. acares*, which is rare in the Hawaiian Islands (Randall 2007), was almost entirely recorded from forereef habitat, especially at depths \geq 18 m, with no individuals recorded from backreef. It was also numerically less abundant in the middle region than either the northern or southern end of the NWHI.

Overall, *L. kasmira* may compete with these planktivores for habitat space, but not for food resources. It should also be noted that *H. diphreutes* and *M. amaena* were relatively rare in the present study, so their apparent species association should be interpreted with caution (Sommerfield and Clarke 2013).

In conclusion, the present study confirmed that since its introduction in the late 1950's, *L. kasmira* has spread to Kure Atoll, the northwestern end of the Hawaiian archipelago. We also found that its distribution in the NWHI was primarily limited to southern part of the island chain up to French Frigate Shoals, particularly on mesophotic reefs. The distribution of *L. kasmira* is potentially affected by its habitat preference with water temperature along latitudinal and depth gradients acting as natural barriers for both vertical and horizontal distributions. *L. kasmira* is now highly abundant on both shallow and mesophotic reefs in the southern end of the NWHI, and eradicating this introduced species would be extremely difficult and too costly to justify without strong evidence of negative impacts on native fauna. Further studies on resource-uses by adult and juvenile *L. kasmira*, as well as their water-temperature tolerances, should increase our understanding of their invasion potential in northern part of the NWHI.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Records of the presence of *Lutjanus kasmira* on shallow reefs of the Northwestern Hawaiian Islands.

Table S2. Records of the presence of *Lutjanus kasmira* on mesophotic reefs of the Northwestern Hawaiian Islands.

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