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Spatial relationships between an introduced snapper and native goatfishes on Hawaiian reefs*

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Abstract

It has been suggested that the introduced blueline snapper (*Lutjanus kasmira*, Family: Lutjanidae) may adversely affect populations of native fishery species in Hawai'i through competition for spatial or dietary resources, or through predation on young fish. We studied the habitat use patterns of *L. kasmira* and several native reef fish species using direct observation by SCUBA divers. Habitat use patterns of the yellowtail goatfish (*Mulloidichthys vanicolensis,* Family: Mullidae) were most similar to those of *L. kasmira*. Both species were primarily found low in the water column and were closely associated with areas of vertical relief. Individual *M. vanicolensis* were found higher in the water column when *L. kasmira* were present, but *L. kasmira* were not similarly affected by *M. vanicolensis*. This finding suggests asymmetrical competition for shelter, in which the dominant *L. kasmira* displaces *M. vanicolensis* farther into the water column. This displacement from the protection of the reef could increase the vulnerability of *M. vanicolensis* to predators and fishers.

Introduction

Investigators in the 1950s from the Division of Fish and Game (DFG) of the Territory of Hawai'i concluded that the 'Hawaiian fish fauna is unbalanced' (Takata 1956) and is dominated by herbivorous fishes that are 'a useless end in the food chain' (Kanayama and Takata 1972). Notably absent from the fish assemblage of Hawai'i are native shallow-water snappers (Family: Lutjanidae) and groupers (Family: Serranidae). To increase recreational and commercial food fishing opportunities, and to fill a perceived vacant ecological niche, DFG staff made collections of 11 species of snappers and groupers from Mexico, Kiribati, the Marquesas Islands and Mo'orea and introduced them to Hawai'i. Three species became established: the grouper *Cephalopholis argus* and the snappers *Lutjanus fulvus* and *L. kasmira*. *C. argus* is now common in many reef areas in Hawai'i, and studies are beginning to clarify the importance of its role as a piscivore. *L. fulvus* is not abundant anywhere in Hawai'i. Although its ecology and behavior have been little studied, it is not generally perceived to be a threat to the native ecosystem. *L. kasmira* has become highly abundant in many locations throughout the Hawaiian Archipelago, and has become the focus of considerable attention in the scientific and recreational community as a potential threat to native fishes.

On four occasions between 1955 and 1961, *L. kasmira* were introduced from French Polynesia to O'ahu, Hawai'i. Fewer than 12 fish were released at Barber's Point on 1 December 1955; 1400 and 1035 individuals were released in Kane'ohe Bay on 23 and 24 June 1958, respectively; and 728 were released in Maunalua Bay on 1 December 1961 (Figure 1). Within two decades, the fish spread from the three introduction sites on O'ahu to all the other high, inhabited Hawaiian Islands. Shortly thereafter, they were reported from locations in the remote Northwestern Hawaiian Islands (Oda and Parrish 1982). They have subsequently been reported as far from the introduction sites as Midway Atoll, near the northwestern end of the archipelago (Randall et al. 1993). Despite their striking abundance and availability to fishers, initial hopes that *L. kasmira* would become a valuable food resource species have not been realized. Their penetration into local markets has been marginal, and many fishers consider them a nuisance, at best. While the range and population size of *L. kasmira* were expanding, local fishers reported that catches, and presumably population sizes, of other reef fishes declined. This correlation led to the popular assertion that *L. kasmira* was responsible for these declines.

Small and isolated ecosystems such as those in Hawai'i are generally less biologically diverse than larger ecosystems or those that are closer to continental landmasses, and other potential sources of colonization (MacArthur and Wilson 1967). Because of their relatively low level of diversity, utilization of resources on isolated islands is often incomplete, and competition is therefore less intense (Elton 1958; MacArthur and Wilson 1967). Interspecific competition is believed to be an important mechanism of biological resistance to invaders (Elton 1958; Case 1991; Baltz and Moyle 1993). A high level of competition leaves few resources available for an alien species to easily exploit, and evolutionary pressures encourage the development of efficient native competitors that can more effectively exclude aliens (Elton 1958; MacArthur and Wilson 1967). Research in a variety of systems suggests that more diverse ecosystems and those with higher levels of competition are less easily invaded (Ross 1991; Stachowicz et al. 1999; Levine 2000; Naeem et al. 2000). Hawai'i is the most isolated archipelago in the world, and has

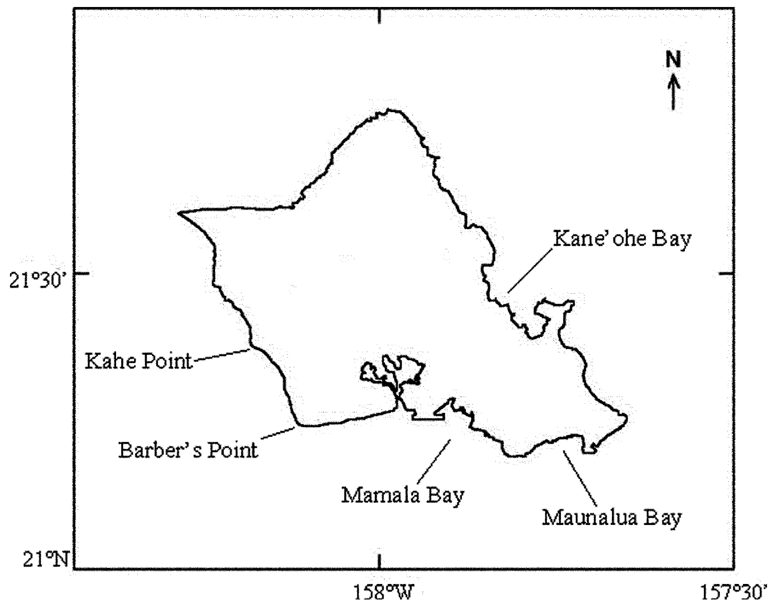

Figure 1. Locations of introductions and study sites. The snapper *Lutjanus kasmira* was introduced on the windward (NE) coast of O'ahu in Kane'ohe Bay, on the southern coast at Maunalua Bay, and on the leeward (SW) coast at Barber's Point. Study sites were established on the southern coast at Mamala Bay, and the west coast at Kahe Point.

low biodiversity relative to other ecosystems in the tropics. Therefore competition is less likely to effectively exclude invaders and prevent their deleterious effects.

High overlap between species in use of space, use of time, or in diet indicates high potential for intense competitive interactions (Ross 1986; Piet et al. 1999). Like many tropical reef species, *L. kasmira* schools near areas of hard substrate and high vertical relief during the day, and is believed to disperse at night to feed over adjacent sedimentary habitats (Hobson 1972, 1974; Holland et al. 1993; Meyer et al. 2000; Friedlander et al. 2002; DeFelice and Parrish 2003). This behavioral similarity, along with some apparent broad similarities in diet (Hiatt and Strasburg 1960; Oda and Parrish 1982; Sorden 1982; Haight et al. 1993; Friedlander et al. 2002; DeFelice and Parrish 2003; J.D. Parrish, unpubl. data) support the possibility that *L. kasmira* might contribute to declines in populations of some native fish species through competition for limited food and/or spatial resources. However, comprehensive studies of spatial, temporal and dietary interactions are necessary to clarify the ecological relationships between the alien *L. kasmira* and native reef fishes species, such as goatfishes (Family: Mullidae). Here we report on findings from our investigation of daytime spatial interactions of *L. kasmira* and several native goatfishes. We focused on (1) the degree of association of these fishes with the bottom and with areas of vertical relief, (2) the way in which different species and size classes use space in their habitat, (3) abiotic factors that may influence the distribution of these fishes, and (4) potential interspecific competitive displacements.

Materials and methods

Descriptive study

Study sites were established in Mamala Bay, off the south shore of O'ahu, Hawai'i, and off the west shore of O'ahu at Kahe Point (Figure 1). Both sites feature outfall pipes armored with stone riprap that support healthy benthic communities, and provide notable topographic relief in areas of primarily sandy substrate where suitable natural habitat for reef fishes is not otherwise available. These outfall structures constitute the primary reef in our study areas, and their complex, three-dimensional development provides valuable habitat for a number of reef fish species. Many species of reef fishes populate these sites and use them for aggregation during the day and shelter at night.

Transects were established along the pipe at these sites, arranged in groups of five (Figure 2). Transects were oriented parallel to the reef interface with the natural substrate (e.g., sand), and were 3 m wide and 50 or 100 m long, depending on the length of the reef. In each group, they were centered at the apex of the reef, at the reef/sand interface, and at 3, 6 and 9 m away from the reef. Transect groups were established in depths ranging from 5 to 30 m of water, and in locations with different substrate types adjacent to the reef (e.g., sand, rubble).

Divers using SCUBA swam the transects and recorded the number of individuals of *L. kasmira* and any goatfish observed, their length, and their height in the water column. All transects in a given transect group were sampled the same day. Because of the large numbers of fish encountered on many transects (at times as many as 1000 individuals), density was recorded in numbers of fish in 10-cm size groups per transect. Heights of fish above the substrate were also recorded in three categories: fish $< 1/2$ m above the substrate were considered to be closely associated with the bottom; those between 1/2 and 2 m, moderately associated with the bottom; those between 2 and 5 m, loosely associated; and those > 5 m, not associated. Presence and direction of currents were also recorded. Densities of fish were log transformed to improve normality and analyzed using nested and crossed MANOVA, with group (equivalent to substrate type in most analyses), site, depth and current as factors. Univariate analysis with ANOVA was also done on counts of individual size categories of fishes within species.

Correlative study

This portion of the project was initiated because of substantial spatial overlap between *L. kasmira* and *M. vanicolensis* shown by the descriptive study (see Results), and focused on detailed spatial interactions between these species. Divers

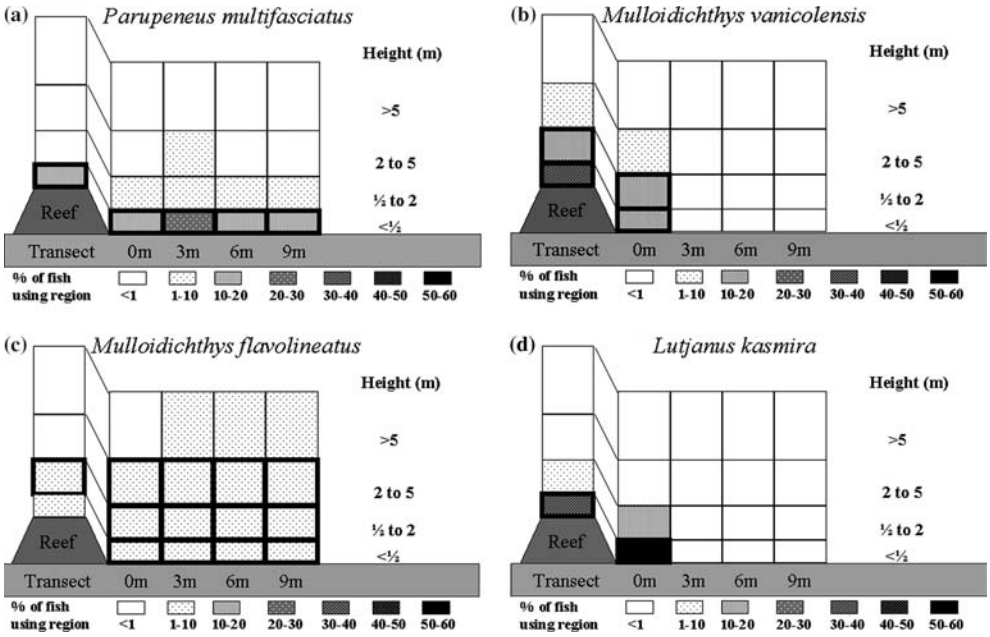

Figure 2. Primary habitat use of three native goatfish species and an introduced snapper. (a) *Parupeneus multifasciatus;* (b) *Mulloidichthys vanicolensis;* (c) *M. flavolineatus;* (d) *Lutjanus kasmira*. For each species, boxes with bold outline indicate the smallest portion of the water column where a minimum of 80% of the fish counted in a transect group were found. Intensity of shading indicates relative frequency of occurrence in that region.

monitored sections of reef divided into three 2-m wide portions (Figure 3). Outer portions were designated as 'buffer zones' and the central portion was designated the 'focal zone.' At 1-min intervals, divers recorded the social situation and visually estimated the height above the substrate of the highest and lowest individuals of both species. Three categories of social interaction were used: (1) if only one species was present in both the focal and buffer zones (Figure 3a), the species was considered to be at a low level of interspecific social interaction, and the estimated heights of the highest and lowest individuals were recorded (A and C, Figure 3a); (2) if one species was present only in the focal zone and the other only in the buffer zones (Figure 3b), the level of social interaction was designated as intermediate, and the heights of the highest and lowest individuals of the species in the focal zone (A and C, Figure 3b), and of the species in the buffer zone (B and D, Figure 3b) were recorded; (3) if both species were present in the focal zone (Figure 3c), the level of social interaction was designated as high, and the heights of the highest and lowest individuals of both species in the focal zone were estimated (A and C; B and D, Figure 3c). In the latter case, other individuals present were not considered, because the study was focused on those fish experiencing the strongest social influence. Data were log transformed to improve normality and correct for heteroscedasticity, and analyzed using *t*-tests. *P*-values were Bonferonni corrected (Bonferroni 1936).

Results

Descriptive study

General trends

Data were compiled from 297 transect swims. Alien *L. kasmira* and seven of the ten species of goatfish native to Hawai'i were recorded on our transects. *Parupeneus multifasciatus, M. flavolineatus* and *M. vanicolensis* were the most commonly observed species of goatfish. *P. porphyreus, P. pleurostigma, P. cyclostomus* and *P. bifasciatus,* were recorded only rarely, precluding detailed analysis

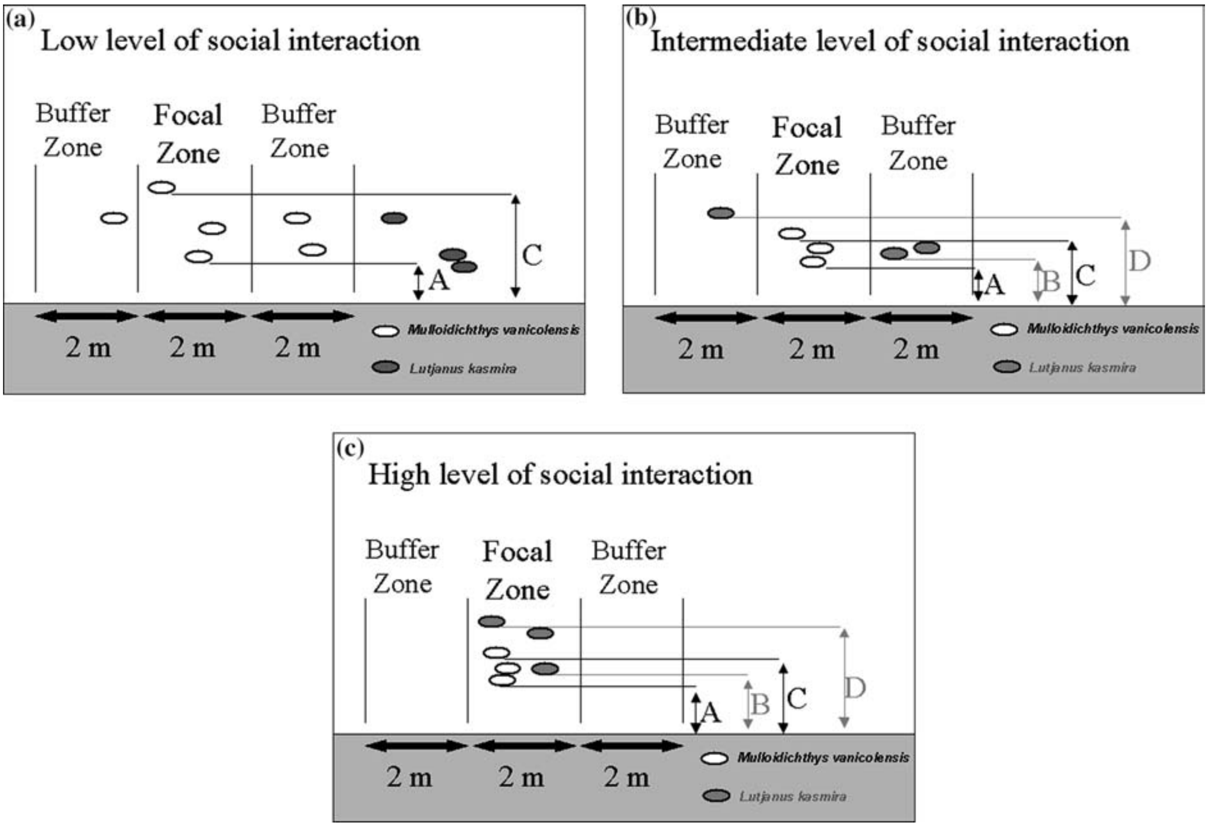

Figure 3. Correlative study. (a) Low level of social interaction; observers record the height of the highest and lowest individuals in the focal zone (A, C); (b) Intermediate level of social interaction; observers record height of the highest and lowest individuals of the species in the focal zone, and the species in the buffer zone (A, B, C, D); (c) High level of social interaction; observers record the height of the highest and lowest individuals of both species in the focal zone (A, B, C, D).

of their habitat use patterns. *P. porphyreus* and *P. bifasciatus*, when present, were always seen near the primary reef structure, and low in the water column (< 2 m above the substrate). These fish were recorded only on transects on the reef itself, or on those at the reef interface. *P. porphyreus* commonly made use of small caves and other subterranean features in the primary reef for shelter. *P. cyclostomus* was also found low in the water column, but was not exclusively associated with the primary reef. It was recorded on all transects, using habitat away from the reef as well as the reef itself. Unlike many of the more common goatfish species, it was not found in large aggregations. *P. pleurostigma* was the fourth most common goatfish, and was observed in habitat similar to that of *P. multifasciatus*. The two species were commonly seen in close association, and often formed multispecies shoals during feeding activities.

P. multifasciatus was most commonly found low in the water column in close association with the substrate. More than 80% of the individuals observed were < 1/2 m above the substrate (Figure 2a). *P. multifasciatus* was not particularly closely associated with the primary reef and was found on all transects in similar numbers. *M. vanicolensis* was also generally found low in the water column, but was concentrated on transects on the reef itself or at the reef interface (Figure 2b). It was closely to moderately associated with the substrate; 80% of recorded individuals were found < 2 m above the substrate. *M. flavolineatus* was found relatively evenly distributed in nearly all parts of the water column surveyed (Figure 2c). It was loosely associated

Table 1. Results of MANOVA for factors significantly affecting abundance of native goatfishes and an introduced snapper.

FACTOR	SPECIES			
	Parupeneus multifasciatus	*Lutjanus kasmira*	*Mulloidichthys vanicolensis*	*Mulloidichthys flavolineatus*
SITE	***	NS	*	NS
DEPTH	**	***	***	***
GROUP	*	NS	NS	NS
CURRENT	***	***	***	***
SITE*CUR	NS	**	***	NS

Asterisks indicate the level of significance of factors included in the model.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

with the substrate and the primary reef; 80% of recorded individuals were found within 5 m of the substrate, and this species was found on all transects in similar numbers. The snapper *L. kasmira*, like *M. vanicolensis*, was found low in the water column, and in appreciable numbers only on transects on the primary reef and at the reef/sand interface (Figure 2d). It was also closely associated with the substrate; 80% of the individuals of this species were recorded within 1/2 m of the substrate on these transects.

Statistical analysis

Results of analysis of the log number of fish recorded in each transect group using MANOVA are reported in Table 1. The presence of a current was an important factor for all species, and fish densities were dramatically lower on the lee side of the reef. Depth was also an important factor, with all species more dense at deeper transect groups within sites. Site was a significant factor for *P. multifasciatus* and *M. vanicolensis*; both species were found at higher densities at the Mamala Bay site. Densities of other species were not significantly different between sites. A significant interaction was found between site and current factors for *L. kasmira* and *M. vanicolensis*. Transect group, which indicates differences in the type of substrate adjacent to the reef, was a significant factor only for *P. multifasciatus*. Univariate analysis on individual size classes of species did not reveal any additional significant factors, and trends were consistent with those derived from MANOVA.

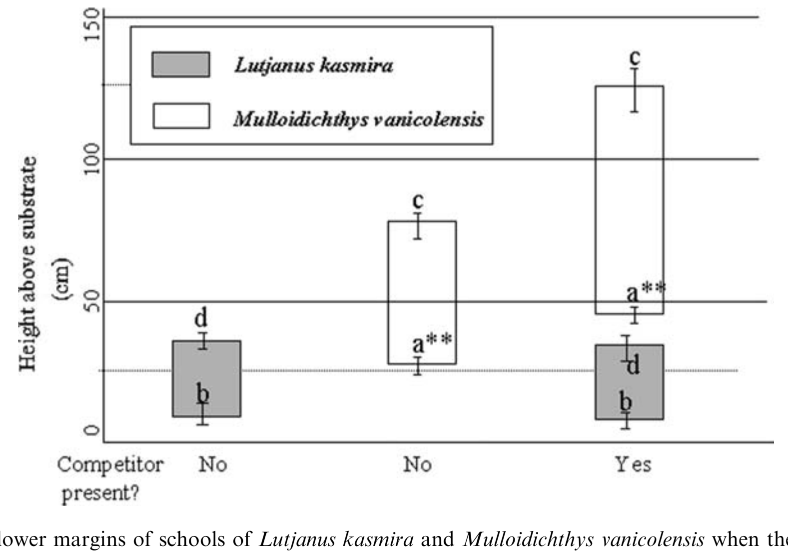

Figure 4. Upper and lower margins of schools of *Lutjanus kasmira* and *Mulloidichthys vanicolensis* when their potential competitor was and was not present. Error bars indicate one standard error. Margins that were tested against each other are indicated by matching lower case letters. Asterisks indicate margins significantly different at $P < 0.05$.

Correlative study

Observations of *L. kasmira* and *M. vanicolensis* at an intermediate level of social interaction were too few to be included in the analysis, so statistical comparisons were only made for these two species at low vs high levels of social interaction (Figure 4). Mean height in the water column of *L. kasmira* was not affected by social interaction with the goatfish *M. vanicolensis* for either the lowest *L. kasmira* individuals (7.50 cm ± 5.57 SD, $n = 46$ when goatfish were present vs 8.07 cm ± 7.17 SD, $n = 86$ when goatfish were absent; $P = 0.615$), or the highest *L. kasmira* individuals (32.4 cm ± 45.6 SD, $n = 46$ when goatfish were present vs 34.6 cm ± 23.1 SD, $n = 86$ when goatfish were absent; $P = 0.769$). By contrast, the mean height of the lowest individuals of *M. vanicolensis* increased significantly in the presence of the snapper *L. kasmira* (26.8 cm ± 33.1 SD, $n = 47$ when *L. kasmira* were not present vs 44.3 cm ± 39.6 SD, $n = 46$ when *L. kasmira* were present; $P = 0.004$, sequential Bonferroni corrected for $n = 4$ *t*-tests). However, any change in the height of the highest *M. vanicolensis* individuals was marginal (78.3 cm ± 52.6 SD, $n = 47$ when *L. kasmira* were not present vs 126.0 cm ± 116.0 SD, $n = 46$ when they were present; $P = 0.051$, sequential Bonferroni corrected for $n = 4$ *t*-tests (Holm 1979; Rice 1989).

Discussion

The more abundant native goatfishes included in this analysis appear to overlap one another only superficially in their use of space in the water column, and show different degrees of association with primary reef and the substrate (Figure 2). *P. multifasciatus* and *M. vanicolensis* both use lower portions of the water column, but the latter concentrate near the primary reef, while the former are common for at least 10 m away from it. Also, *P. multifasciatus* was found in higher densities in areas where substrate adjacent to the primary reef was mixed sand and hard bottom or rubble. When this type of substrate was not available, they tended to remain closer to the reef itself. None of the other species studied appeared to be influenced by the type of substrate adjacent to the reef. Of the species studied, *M. flavolineatus* is perhaps the most different from *P. multifasciatus*. Whereas *P. multifasciatus* usually occurred singly or in small groups and low in the water column, *M. flavolineatus* was found in large, diffuse schools (often > 1000 individuals) high in the water column. Relative to other species in the family, it was not closely associated with the bottom while in these daytime resting schools. Although they were not closely associated with the primary reef, the density of *M. flavolineatus*, like that of the other species studied, declined notably beyond the swath that we sampled quantitatively. This trend was readily apparent after initial surveys of the site, and led us to focus our study on the band of substrate adjacent to the reef itself. Whereas native goatfish species have segregated daytime microhabitats, *L. kasmira* shows substantial spatial overlap with these goatfishes, and with *M. vanicolensis* in particular.

The portion of the water column where *M. vanicolensis* is most concentrated completely overlaps the portion that *L. kasmira* uses (Figures 2b, d). Depth was consistently a significant factor influencing fish density (Table 1), particularly for *M. vanicolensis* and *L. kasmira*. On 55 censuses of 300 m^2 transects at the shallower transect group in Mamala Bay, *M. vanicolensis* was never recorded, and only two individuals of *L. kasmira* were recorded. At the deeper 300 m^2 transects, however, *M. vanicolensis* was recorded in densities between 55 and 1045 individuals ($x = 415.4 \pm 307.4$ SD), and *L. kasmira* between 1 and 275 individuals ($x = 90.7 \pm 71.5$ SD).

The height of *L. kasmira* above the substrate was not significantly affected by the presence of *M. vanicolensis*, either at the upper or lower margin. The lowest *M. vanicolensis* in a school were found to be significantly higher in the water column when *L. kasmira* was present, but the heights of the uppermost individuals did not increase significantly. Power analysis indicated that the inherent variability in the upper margins of schools gives the *t*-test low power to resolve differences between mean heights of the uppermost individuals ($P = 0.51$). Variability of lower margins is constrained because minimum values are bound by the substrate, but the upper margin has no comparable natural barrier to its variability. In any case, it seems that when *L. kasmira* is present, a larger proportion of the *M. vanicolensis* occurs higher in the water column, and away from the relative protection of the reef (Figure 4). These results are consistent with expectations of relationships between species undergoing asymmetrical competition for space (Ricklefs and Miller 2000), i.e., of a competitively subordinate *M. vanicolensis* displaced farther from the reef and into a higher portion of the water column, and of a competitively dominant *L. kasmira* that is not influenced by the presence of the *M. vanicolensis*.

These results of the analysis support previous observations by our divers, that schools of *M. vanicolensis* close to the substrate moved higher into the water column as a group of *L. kasmira* approached and moved underneath them. Fish higher in the water column and farther from shelter would be at greater risk from predators and fishers. Most fishing in the environments where these fish occur is done with spears and nets, making access to shelter important to evade capture. Piscine predators such as the goatfish *P. cyclostomus* and *Seriola dumerili* (Family: Carangidae) are commonly seen in the area, and large *P. cyclostomus* (70 cm) have been observed making predatory runs at *M. vanicolensis*.

Competition between reef fishes for shelter space has been shown to increase predatory mortality for subordinate competitors in other tropical reef systems (Schmitt and Holbrook 1999; Holbrook and Schmitt 2002). Also, subordinates may suffer from chronic stress (Alanara 1997), which can depress their immune responses, making them more susceptible to pathogens (Mazeaud et al. 1977). Stress responses also depress subordinates' feeding while simultaneously increasing their metabolic rates, leading to depressed growth rates (Abbott and Dill 1989; Wang et al. 2000; Sloman and Armstrong 2002). Slower-growing fish would spend more time at sizes vulnerable to predation, compounding the effects of their spatial displacement. The lower fecundity of smaller fish would reduce the ability of the population to offset increased predatory mortality with its reproductive output.

This new evidence of potentially detrimental interactions of introduced coral reef fishes on natives, underscores the need for further study of such behavioral and ecological relationships. Future investigations should illuminate larger-scale and longer-term patterns of habitat use, and reveal how those habitat use patterns relate to feeding patterns. Ongoing investigations of goatfish and snapper diets will permit a more comprehensive evaluation of impacts that the introduced *L. kasmira* may have on its host ecosystems in Hawai'i.

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References

Abbott JC and Dill LM (1989) The relative growth of dominant and subordinate juvenile steelhead trout (*Salmo gairdneri*) fed equal rations. Behaviour 108: 104–113

Alanara A (1997) Feeding behaviour and growth performance of fish within a dominance hierarchy. In: Houlihan D, Kiessling A and Boujard T (eds) Proceedings Workshop on Voluntary Food Intake in Fish, p. 10. Aberdeen, United Kingdom

Baltz DM and Moyle PB (1993) Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecological Applications 3: 246–255

Bonferroni CE (1936) Teoria statistica delle classi e calcolo delle probabilit à. Pubblicazioni del R Istituto Superiore di Scienze Economiche e Commerciali di Firenze 8: 3–62

Case TJ (1991) Invasion resistance, species build-up, and community collapse in metapopulation models with interspecies competition. Biological Journal of the Linnean Society 42: 239–266

DeFelice RC and Parrish JD (2003) Importance of benthic prey for fishes in coral reef-associated sediments. Pacific Science 57: 359–384

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Methuen, London, 181 pp

Friedlander AM, DeFelice RC and Parrish JD (2002) Ecology of the introduced snapper *Lutjanus kasmira* (Forsskal) in the reef fish assemblage of a Hawaiian Bay. Journal of Fish Biology 60: 28–48

Haight WR, Parrish JD and Hayes TA (1993) Feeding ecology of deepwater lutjanid snappers at Penguin Bank, Hawai'i. Transactions of the American Fisheries Society 122: 328–347

Hiatt RW and Strasburg DW (1960) Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecological Monographs 30: 65–127

Hobson ES (1972) Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. Fishery Bulletin 70: 715–740

Hobson ES (1974) Feeding relationships of teleostean fishes on coral reefs in Kona, Hawai'i. Fishery Bulletin 72: 915–1031

Holbrook SJ and Schmitt RJ (2002) Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology 83: 2855–2868

Holland KN, Peterson JD, Lowe CG and Wetherbee BM (1993) Movements, distribution and growth rates of the white goatfish *Mulloides flavolineatus* in a fisheries conservation zone. Bulletin Marine Science 52: 982–992

Holm S (1979) A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics 6: 65–70

Kanayama RK and Takata M (1972) Introduction of marine game fishes from areas in the Pacific, Job 1 (Study XII) of Statewide Dingell-Johnson program, Project F-9-2 to the State of Hawai'i DFG

Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. Science 288: 852–854

MacArthur RH and Wilson EO (1967) Island Biogeography. Princeton University Press, Princeton, New Jersey, USA, 203 pp

Mazeaud MM, Mazeaud F and Donaldson EM (1977) Primary and secondary effects of stress in fish: some new data with a general review. Transactions of the American Fisheries Society 106: 201–212

Meyer CG, Holland KN, Wetherbee BM and Lowe CG (2000) Movement patterns, habitat utilization, home range size and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. Environmental Biology of Fishes 59: 235–242

Naeem S, Knops JMH, Tilman D, Howe KH, Kennedy T and Gale S (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos 91: 97–108

Oda DK and Parrish JD (1982) Ecology of commercial snappers and groupers introduced to Hawaiian reefs. Proceedings 4th International Coral Reef Symposium 1: 59–67

Piet GJ, Pet JS and Van Densen WLT (1999) Resource partitioning along three niche dimensions in a size structured tropical fish assemblage. Canadian Journal of Fisheries and Aquatic Sciences 56: 1241–1254

Randall RE, Earle JL, Pyle RL, Parrish JD and Hayes T (1993) Annotated checklist of the fishes of Midway Atoll, Northwestern Hawaiian Islands. Pacific Science 47: 356–400

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43: 223–225

Ricklefs RE and Miller GL (2000) Ecology, 4th edn. W.H. Freeman & Co., New York, 822 pp

Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. Copeia 2: 352–388

Ross ST (1991) Mechanisms structuring stream fish assemblages: are there lessons from introduced species? Environmental Biology of Fishes 30: 359–368

Schmitt SJ and Holbrook RJ (1999) Settlement and recruitment of three damselfish species: larval delivery and competition for shelter space. Oecologia 118: 76–86

Sloman KA and Armstrong JD (2002) Physiological effects of dominance hierarchies: laboratory artifacts or natural phenomena? Journal of Fish Biology 61: 1–23

Sorden CT (1982) Trophic relationships of goatfishes (Family Mullidae) in the Northwestern Hawaiian Islands. MS thesis, University of Hawai'i, Honolulu, Hawai'i, 86 pp

Stachowicz JJ, Whitlach RB and Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286: 1577–1579

Takata M (1956) Introduction of marine game fishes from areas in the Pacific, Report on Job (9) of Reef and inshore game fish management research, Project F-5-R to the Territory of Hawai'i DFG

Wang N, Hayward RS and Noltie DB (2000) Effects of social interaction on growth of juvenile hybrid sunfish held at two densities. North American Journal of Aquaculture 62: 161–167