UC Berkeley

Student Research Papers, Fall 2007

Title

Feeding behavior of the Yellowtailed Coris (Coris gaimard) in the lagoons of Moorea, French Polynesia

Permalink

https://escholarship.org/uc/item/6081t0kc

Author

Strausser, Matthew

Publication Date

2007-12-16

FEEDING BEHAVIOR OF THE YELLOWTAIL CORIS (*Coris gaimard)* IN THE LAGOONS OF MOOREA, FRENCH POLYNESIA

MATTHEW W. STRAUSSER

Department of Integrative Biology, University of California, Berkeley, California, USA
Strausser@berkeley.edu

Abstract. Animals must be locally adapted to their habitat to optimize use of available resources. In highly variable environments, behavioral change allows animals to optimize resources quickly enough to keep pace with their environment (Luttbeg 1999). The factors that determine the animal's behavior are often difficult to uncover. *Coris gaimard* (Quoy and Gaimard 1824), a species of wrasse, exhibits different foraging frequencies across its range. This study attempts to determine what biotic factors may affect the foraging behavior. The study compares the behavior of two populations of *C. gaimard* in two similar lagoons around the island of Moorea, French Polynesia and a population in a previous study done in Japanese waters (Shibuno et al. 1994). Standardized timed observations from Moorea showed an increase in the amount of foraging behavior at the site with a smaller prey base. The behaviors, however, maintained the same relative frequency as the behaviors in the prey rich site. This frequency differed greatly from the relative frequency of behaviors seen in Japanese waters where the prey base was larger, but had a different species composition. These observations indicate that prey quantity determines the amount of foraging, but the type of available prey determines the foraging strategy. Additionally, *C. gaimard* engages in heterospecific feeding relationships, but the presence of other foraging species does not significantly affect its foraging behavior. These results indicate that prey populations are a major biotic factor in determine foraging strategies.

Key words: Coris gaimard, *Yellowtailed Coris; foraging; phenotypic plasticity; optimal foraging; feeding behavior; interspecific foraging*

INTRODUCTION

On a species level, animals are adapted to fill specific feeding niches in a habitat. However, these habitats can be highly variable across the animal's range. Animals must then be locally adapted to their habitat to optimize use of locally available food resources. Species that have phenotypically plastic behaviors can develop individual optimized strategies in response to resources in its specific environment (Houston 1992). In highly variable environments, these responses are usually behavioral changes that allow animals to optimize resources quickly enough

to keep pace with their environment (Luttbeg 1999). The optimization of feeding behavior should follow optimal foraging theory to make best use of the local resources (MacArthur 1966). To determine the optimal forage strategy, the individual must respond to signals in the environment that affect feeding (Luttbeg 1999). The factors that determine the animal's feeding behavior are often difficult to uncover, but they are important to understanding behavioral choices.

This study examines the feeding behavior choices of a wrasse species, part of the family Labridae. The members of the

family Labridae, which also include parrotfish, are among the most diverse and abundant fishes in the coral reef ecosystem (Wainwright and Westneat 2004, Aronson 1987). Composed of more than 580 species, this family of fish appears in nearly all coral and rocky reefs worldwide (Wainwright and Westneat 2004). This great diversification is at least partially due to their exceptional range of trophic habits. Among the labrids are herbivores, planktivores, piscivores, ectoparasite feeders, durophagist, and carnivores (Wainwright and Westneat 2004). This great variety makes them attractive study subjects because they have unique feeding behaviors. Although the diet and feeding mechanics of many coral reef wrasses have been well studied, little is known about the feeding ecology and behavioral interactions of many of these fishes (De Pirrott 1999). Because most of this great variety of feeding habits is easily observable in tropical lagoons, labrid fish are ideal study subjects for observing a host of variations in foraging strategies and feeding behaviors.

One such wrasse, the Yellowtail Coris, *Coris gaimard* (Quoy and Gaimard), exhibits a rare foraging behavior of overturning coral rubble with its mouth to access the marine macroinvertebrate prey that hide underneath (Jennson 2005, Shibuno et al. 1994). The mechanics of this behavior are unique. However, other wrasses including *Coris aygula*, *Thalassoma pavo,* and *Novaculichthys taeniourus* also move pieces of coral substrate with their mouths in different ways for feeding or construction of sleeping mounds (Kabasakal 2001, Takayanagi 2003).

This rock flipping behavior varies in frequency across its range compared to the fish's other feeding behaviors. *C. gaimard* has an extensive range spanning from the Red Sea east to the Hawaiian archipelago (Shibuno et all. 1994). In waters off Kuchierabu-jima, Japan, *C. gaimard* has been observed scavenging for prey on the tops of coral rubble and feeding behind scarid fishes in addition to flipping rubble (Shibuno et al. 1994). *C. gaimard* populations off Moorea, French Polynesia,

employ these scavenging methods with different frequencies. Additionally, the Moorea populations exhibit two feeding behaviors not observed in Japan. This study attempts to understand the biotic factors that account for the differences in foraging methods and their frequency.

Two hypotheses are proposed. The first hypothesis indicts interspecies interactions as a major factor in determining foraging strategies. *C. gaimard* engages in heterospecific feeding relationships with goatfish species and other wrasses. Goatfish (Mullidae) use sensitive barbels to troll through lose sand substrates in coral lagoons (McCormick 1994). This behavior attracts a variety of attendant species that attempt to eat prey that escapes the mullid's initial attack (McCormick 1994, Strand 1998, Silvano 2001). *C. gaimard* can act as an attendant species to a foraging goatfish. Similarly, several goatfish species were observed following behind *C. gaimard* as it flipped over coral rubble. The goatfish was observed sifting through the recently exposed sand that had been uncovered by the flipping of a piece of rubble. This feeding relationship may motivate *C. gaimard* to flip coral rubble more often in waters to attract mullid fishes from whom it can then feed behind. This hypothesis can only be true if there is a mutualistic relationship and, more over, it occurs frequently enough to significantly affect *C. gaimard's* feeding behavior.

A second hypothesis claims that a difference in prey quantity will result in a difference in feeding behavior. As prey availability increases, less energy expensive behavior (flipping rubble) will be preferred. *C. gaimard* is a dietary generalist preying on gastropods, polychaetes, foraminifera, crabs, amphipods, stomatopods, chitons, and a variety other marine macroinvertebrates (Shibuno et al. 1994, Hiatt and Strasburg 1960). Therefore, in any tropical reef, *C. gaimard* has a host of possible prey items. This host of prey, in combination with several foraging methods, gives *C. gaimard* multiple

available foraging strategies of which one must then be the most efficient. The determination of optimal foraging will depend on the caloric value of the prey and the ease of capturing it, according to optimal foraging theory (MacArthur 1966). Because prey varies with location, so then to must the foraging strategy.

The testing of these hypothesizes will attempt to determine the effect of biotic factors on fish behavior. This determination will lead to a better understanding of foraging theory choices and the mechanisms that control it.

METHODS

Feeding behavior

The study will attempt to account for variation in foraging behavior with a corresponding variation in biotic factors. To determine the variation in frequency of feeding behaviors, *C. gaimard* adults were observed in the field using snorkeling mask and fins. Individuals were observed no more than once a day and only between 0900 hours and 1600 hours, when the fish is known to be active and feeding. The total length (TL) of the fish was visually estimated to within 2.5 cm and identifying marks were noted to prevent sampling the same individual again that day. Identifying marks most often included tail injuries and the presence of a red outline on the end of the tail. During the ten minute observation time, the observer recorded the number of times the individual attempted the following behaviors: flipping over an object, biting prey off an object it had flipped, biting prey off a surface that it did not flip, digging in the sand for prey, and feeding in the wake of a goatfish trolling through the sand. Observations were performed in two coral rubble bottomed lagoons surround the island of Moorea, French Polynesia: Temae Public Beach (17° 29' 53.2" S, 149 °45 '21.7" W) and Motu Tiahura (17° 29' 19.0" S, 149° 54' 51.5" W) (Figure 1). Both lagoons had similar depths, similar substrates of coral rubble, and a nearly equal presence of

live coral along the edges of large beds of rubble. The two populations of *C. gaimard* were sampled 20 times between 8 October 2007 and 14 November 2007. Additional observations were done offshore from Opunahu Public Beach (17° 29' 17.4" S, 149° 51' 10.7" W) during the same time period.
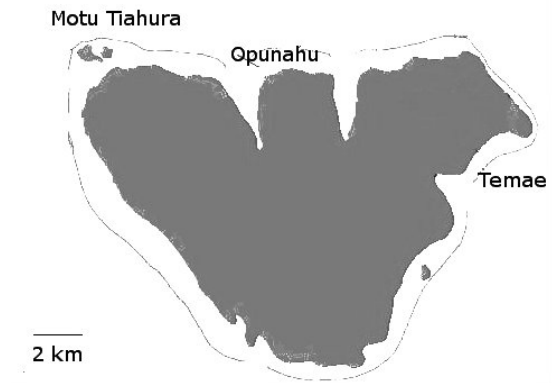

Fig 1: Map of Moorea, French Polynesia with the three study sites

Interspecies interactions

To measure the effects of interspecific feeding relationships, the frequency of feeding relationships between *C. gaimard* and other fishes were measured. All feeding relationships exhibited during the ten-minute observations were noted. Fish species feeding on rubble flipped or sand expose by *C. gaimard* were identified and recorded. These observations included all mullid fishes trolling through freshly exposed sand and other wrasses feeding off flipped rubble. Fish feeding off of flipped rubble more than 30 second after it was flipped were not included.

Rubble mass

The size of coral rubble is sometimes correlated with the amount of invertebrate prey that associates with it (Shibuno et al. 1994). Variation in the size of flipped coral rubble may correspond to a variation in prey or foraging strategy. To measure variation in the size of rubble *C. gaimard* flips, coral rubble

flipped during the ten-minute observations was collected. Coral rubble was only collected when it was possible to do so without risking losing sight of the fish and after the fish had moved over 1 m away from the rubble. The flipped rubble was brought back to the lab and weighed with a spring scale to the nearest 10 grams and then returned to the site where it was collected.

Pairing frequency

Although not hypothesized to affect feeding behavior, association with other *C. gaimard* individuals may attract more interspecific feeders. Pairing behavior was noted to discount the presence of interspecific feeders when the observed fish may not be the only factor attracting other foraging fish. To determine the frequency which *C. gaimard* pairs with other *C. gaimard* individuals, it was noted when an individual paired for 30 second or more during the ten-minute observation times. Pairing was classified as two *C. gaimard* individuals swimming within about .5 m of each other at the same speed and maneuvering around obstacles using the same path. Pairing individuals were not observed consecutively so as to not overestimate the frequency of the behavior.

Prey survey

To determine the relative abundance of prey items on the coral rubble, samples of flipped coral rubble were collected and the crustaceans living on the rubble were measured in a method outlined by an earlier study on *C. gaimard* behavior (Shibuno et al. 1994). Samples were gathered by covering a piece of rubble a *C. gaimard* individual had flipped with a 10 cm by 10 cm by 10 cm plastic box with an open bottom. The box covered the sample and was sunken 2 cm into the sand. A plastic slate was slid underneath the box. The sand and gravel was transferred to a plastic bag and brought back to the lab. At the lab, the sample was soaked in 90% ethanol. Using

tweezers, a dissecting scope, and calipers, animals > 0.2 mm in the sample were removed, measured, and categorized. The mass and diameters of the rubble was measured to the nearest 1 gram and 1 millimeter using a spring scale and calipers. Sample collecting was haphazard. Rubble was chosen by either sampling the first piece of rubble flipped after the fish's ten-minute observation or by taking the first piece of rubble flipped one full minute after the fish was spotted. Individuals were sampled no more than once per day. Twenty crustacean samples were analyzed for each observation site.

Description of behaviors

To describe the behaviors cataloged in this study, all behaviors were recorded in the field using a digital camera with underwater housing set to video mode. The videos were then slowed down using Windows Movie Maker software and still shots of the behavior were taken separately, but with similar equipment.

RESULTS

Feeding behavior and Prey survey

In the ten-minute observation data set, all data were grouped by location. In comparing sites, a Students T-test revealed no significant difference in estimated total length of observed fish between the sites (p = 0.222). Additionally, except for two observations of males at the Motu site, all fish observed were female between 10 and 35 cm TL. At the Motu sites, 192 flipping events were recorded— a mere 41.5% of the 462 flipping events recorded at the Temae site (Figure 2). An unequal variance T-test showed significantly more flipping at the Temae site (p = 0.005). The fish were observed flipping not only dead coral rubble, but also occasionally turned over clam shells, live coral pieces, rocks, large snail shells, and live hermit crabs.
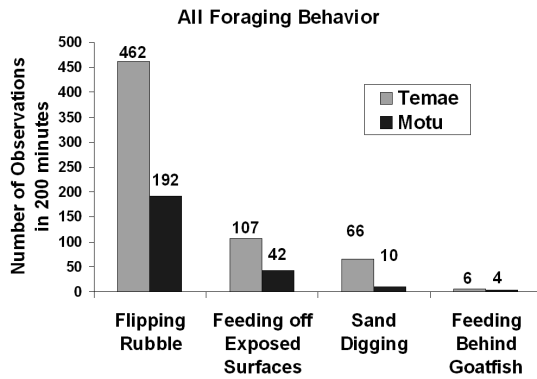
All Foraging Behavior

Fig 2: All foraging behaviors observed in standardize timed observations by site.

The number of bites taken on flipped rubble was also higher at Temae. At the Motu site, 139 bites on flipped rocks were observed resulting in a ratio of 0.556 bites per flip. That is less that the 0.724 bites per flip recorded on the Motu (derived from the 257 observed bites there) although this difference was not significant (p = .260). The number of bites at the Motu is 39.3% of the number of bites at Temae, a similar ratio to the number of flips between the two sites.

At the Temae site, the prey reward for flipping rubble was less consistent with flipping effort. The number of flips was poorly correlated (R^2 = 0.108) with the amount of bites taken on flipped rocks. At the Motu, however, increased flipping correlated much better with increased in bites on flipped rubble (R^2 = 0.511).

The more rare feeding behaviors of feeding behind goatfish and digging in the sand also were more common at the Temae site than at the Motu although significant difference could not be determined on such rare behaviors because of low sample sizes. Sand digging was observed 66 times at Temae and only 10 times at the Motu. Feeding behind a goatfish was observed a mere 6 times at Temae and 4 times at the Motu.

Regardless of the differences in number of foraging behaviors, proportionally there was little difference between foraging

behavior at the Temae site and at the Motu site (Figure 3). Flipping accounted for 72.1% and 77.4% of the feeding behaviors at each site respectively. Biting prey off non-flipped surfaces accounted for 16.7% of the feeding behaviors at Temae and 16.9% at the Motu. Sand digging and feeding behind goatfish accounted for the remaining behaviors.
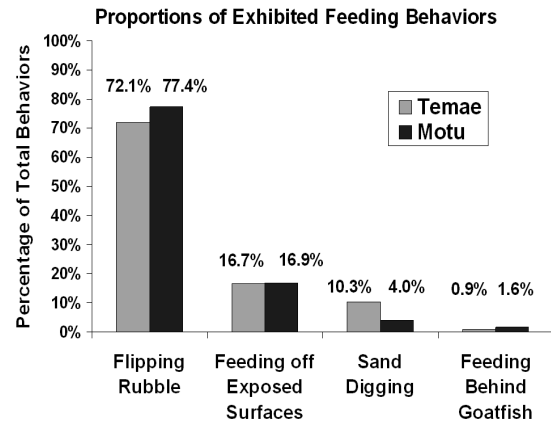

Fig 3. Relative proportions of each feeding behavior exhibited in 200 minutes of standardized observations.

Interspecies interactions

C. gaimard was observed feeding with 8 other fish species including most commonly other wrasses (Labridae), goatfish (Mullidae), and much more rarely trigger fish (Balistidae) and jacks (Caranx). No difference was observed in the frequency of these interactions between study sites. Other species of wrasse were the most commonly associated fish. They appeared in 61.9% of all observations (57.1% at Temae and 68.4% at the Motu). The most commonly associated wrasse was *Halichoeres trimaculatus* observed in 57.1% of all observations (57.1% at Temae and 57.9% at the Motu). Other wrasses observed feeding with *C. gaimard* including *Thallasoma hardwicki* and *Halichoeres hortulanus*. Both were recorded in less than 10% of the observations. All wrasses were observed feeding off the flipped coral rubble

after the *C. gaimard* individual had finished searching it for prey. However, outside of the standardized observation times, several wrasses were noticed capturing prey before the *C. gaimard* had finished searching the flipped rock.

Goatfish were the next most common associated species recorded in 47.8% of all observations (47.6% at Tamae and 55.0% at the Motu). Four species were identified and occurred in the observation time in various frequencies: *Parupeneus multifasciatus* (35.7%), *Mulloides flavoleatus* (11.9%), *Parupeneus barberinus* (7.1%), and *Parupeneus cyclostomus* (4.8% and only in juvenile stage). Combining interspecies data with foraging observations, one can deduce that in observations when *C. gaimard* was associated with a goatfish, *C. gaimard* flipping significantly more pieces of rubble (18.5 average) than when it was not associated (10.4 average) (p = 0.024).

Caranx sp. and *Rhinecanthus aculeatus* (Balistidae) were observed feeding with *C. gaimard* twice each. In contrast to the wrasses and goatfish, *Caranx* sp. and *Rhinecanthus aculeatus* only appeared when they were the only other associated fish.

Rubble mass

Three hundred pieces of coral rubble that were flipped by *C. gaimard* were retrieved and weighed totaling nearly 25 kg. They came from fish from 11 size classes estimated between 8 cm and 35 cm TL. Rubble ranged from less than 10 g to 590 g (Figure 4).
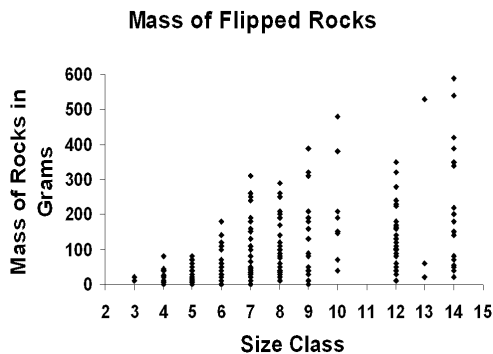

Mass of Flipped Rocks

Fig 4. Mass of Flipped Rubble by Size Class

The maximum mass flipped correlated with the TL of the fish ($R^2 = 0.894$, p < 0.001) (Figure 5).

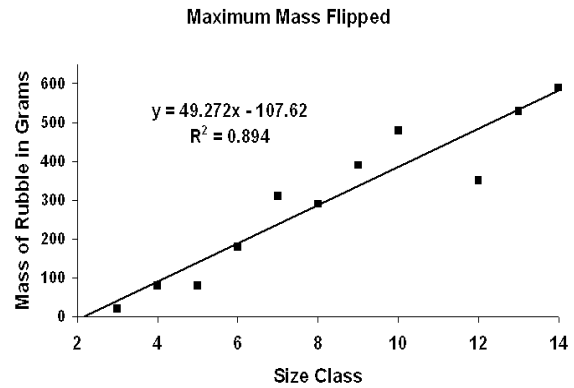**Maximum Mass Flipped**

$y = 49.272x - 107.62$
$R^2 = 0.894$

Fig 5. The maximum mass flipped by any member of the size category increase as the size category increases.

However, the minimum mass flipped by the fish remained around 10g regardless of size class. Between sites there was no significant difference in the size of rubble flipped when comparing fish in the same size classes.

Pairing frequency

Individuals often were seen accompanied by other *C. gaimard* as they foraged. In 52.0% of the observations, individuals swam together for at least 30 seconds at least once during the ten minutes. *C. gaimard* individuals were never observed feeding together or feeding behind another feeding *C. gaimard* individual. On several occasions a large male would charge smaller females, but the attack rarely lasted for more than a few seconds. Both individuals swam away following an initial charge. All observed pairs were composed of two females.

Prey survey

Twenty crustacean samples were performed at each site. The samples were collected haphazardly, and there was no significant

difference in the mass or diameters of the collected rubble pieces (p = 0.351, p = 0.862 respectively). Samples were grouped together by site. The Motu contained far more prey items than the Temae site. 463 prey items were discovered on the rubble pulled from the Motu compared to only 130 from Tamae. The Motu had more prey items in every category, especially in the category of crabs, whose biomass surpassed any other prey category (Figure 6).
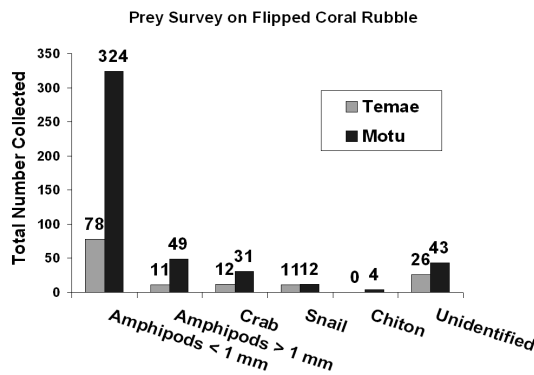
Prey Survey on Flipped Coral Rubble

Fig. 6. The results of the prey survey of all the prey items on 20 flipped rocks at each site.

Description of behaviors

Only adult *C. gaimard* were observed flipping objects. Juveniles were observed only searching sandy surfaces and algae covered rubble for food. Several videos taken of the *C. gaimard* flipping were analyzed. Five distinct steps were present in all samples. First, the fish positions itself about 30 - 45 degrees from the substrate and straightens its body (Figure 7a). During this step, the individual positions its snout just under the piece of rubble as its tail sticks up in the water column pointing away from the rubble. Second, the individual folds itself into a U shape using the force of its bending body to lift the rubble on end (Figure 7b). The fish bends in such a way so that its tail it is now pointing towards the rubble. The fish is not making contact with the substrate and is only pushing the rubble with the teeth on its lower jaw, not its snout. Third, by

swinging its tail around, the fish straightens its body, which provides the necessary force to overturn the rubble (Figure 7c). In this step it is most evident that only the jaw, not the fish's face or scales, is coming into contact with the often rough or sharp rubble pieces. Fourth, the fish will search the newly exposed substrate and the bottom of the flipped rubble for prey items (Figure 7d).

A.
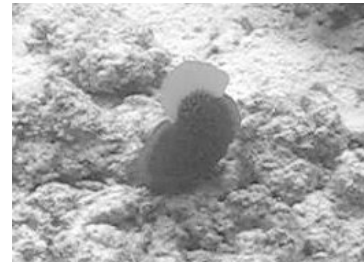
B.

C.

D.

Fig. 7 Four steps *C. gaimard* performs to overturn coral rubble

Similar video analysis was done for *Novaculichthys taeniourus* and *Coris aygula*, two somewhat related species that perform similar foraging behaviors.

DISCUSSION

Feeding behavior

This study investigates what biotic factors may influence the foraging behavior of the wrasse *Coris gaimard*. A variation in foraging behavior of *C. gaimard* was observed between two lagoons around the island of Moorea, French Polynesia. There are two proposed explanations for this variation: a variation in prey presence or the effects of interspecies interactions. The *C. gaimard* individuals at the first site, the Motu site, performed 58.5% less foraging behaviors than a similar population at second, the Temae site. This difference can be simply explained by the large difference in prey items available between the sites. A prey survey of available prey items at the sites revealed that there is 71.9% less prey available at the Temae site. This means that the fish would need to exert more foraging effort to get its required amount of food to live and reproduce. This shows that the biotic factor of prey abundance affects the amount that *C. gaimard* forages. The mechanism driving this increased amount of foraging can be assumed to be caloric demands. It seems that a fish will continue to forage until it has a sufficient food resources.

Looking only at the behavior of flipping rocks over: when the number of bites off of flipped rubble was calculated, it was poorly correlated with the number of flipped rocks at the Temae site ($R^2 = 0.108$). The amount of bites off flipped rubble was more closely correlated with the amount of flipped rubble at the Motu ($R^2 = 0.511$). This indicates that the prey was not only less common, but also less evenly distributed. Fish flipping rubble at the Temae site then had to forage longer to find prey rich patches to feed in. This

will also increase the amount of forage behaviors as the fish seeks out prey rich rocks.

Though the amount of foraging *C. gaimard* does increased, the strategies that both populations employed were strikingly similar. "Strategy" is defined here as the proportion of effort the fish spends on each foraging behavior. Both populations expended about 75% of their foraging behaviors flipping rocks. Both populations dug in the sand for 16% of their foraging behaviors. This ratio is not a species characteristic. *C. gaimard* populations elsewhere do not exhibit these behavior frequencies (Figure 8).
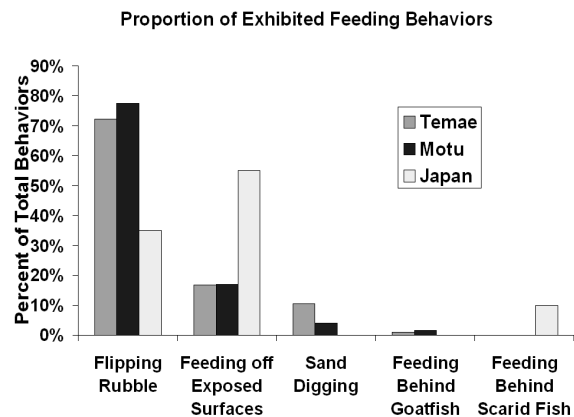
Fig. 8. Relative proportion of observe feeding behaviors in Moorea and those reported by in Japan by Shibuno et al. 1994. Note: The largest size class was used to estimate the frequencies from Japan.

In Japanese waters, a similar study of *C. gaimard* observed fish searching for exposed prey for greater that 50% of its observed foraging events (Shibuno et al. 1994). Additionally, the Japanese population was never observed feeding behind goatfish or sand digging, but instead it observed *C. gaimard* feeding behind scarid fish (Shibuno et al. 1994). The change in foraging strategies is due then, not to crustacean abundance, but instead of crustacean types. The Japanese population fed from a different crustacean food base, which many more mollusks and

crabs available to feed on (Shibuno et al. 1994). I hypothesize that the prey in those waters are more apt to be found on the surface of the substrate. *C. gaimard* then does not need to go through the energy expensive behavior of flipping rocks to uncover its required amount of prey. Different prey items demand different strategies to maximize caloric input. *C. gaimard* strategy for foraging then is not based on abundance of prey, but on composition. This variation in strategy also demonstrates that the fish has a phenotypic plasticity in its behavioral strategy. This plasticity makes it locally adapted to its habitat. This increases its fitness because it maximizes the use of variable habitats and expands its range of viable habitats. *C. gaimard* ranges throughout the tropical Pacific and Indian Oceans (Shibuno et al. 1994). This large variation can be partial explained by its ability to adapt its behavior in response to the variation in prey that is present across its range.

Interspecies interactions

An alternative hypothesis is that *C. gaimard*'s behavior was altered in Moorea by the presence of heterospecific feeding relationships. *C. gaimard* played an important role in heterospecific feeding by disturbing the substrate by turning over rubble. This exposes previously covered sand and exposes the underside of the flipped rubble. *C. gaimard* searches both the sand and the exposed rubble for prey. However, when *C. gaimard* finishes searching, goatfish would often sift the freshly exposed sand for hidden benthic invertebrate prey. Wrasses would often scavenge the newly exposed face on the rubble for prey that *C. gaimard* may have missed. These three roles: "substrate disturber", "sand sifter", and "scavenger" were filled by many different species (Figure 9).

This relationship is made more complex by three important observations. One, all three roles do not have to be filled for any of the species to forage. Occasions where only two of the roles were fill were often observed.

All species were also seen feeding alone and do not seem to require the others presence. Scavenging wrasses often find food on exposed surfaces; goatfish often troll in open sand beds; and substrate-disturbing species often turn over rubble and sand unaccompanied. Two, goatfish forage after other foraging goatfish (McCormick 1994). A foraging goatfish provides enough of a substrate disturbance to attract other goatfish and scavengers. Three, *C. gaimard* can fill the role of both substrate-disturber and scavenger.
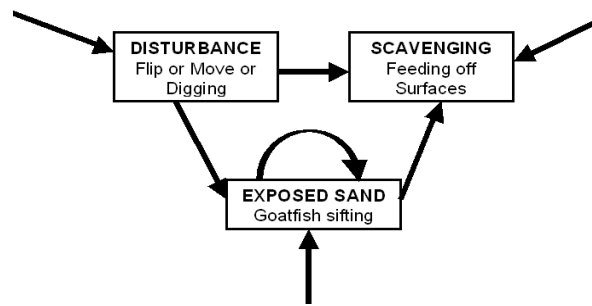

Fig 9. A conceptual diagram of roles in the heterospecific feeding relationships with *C. gaimard*

These heterospecific feeding relationships occur with notable frequency. *C. gaimard* individuals were accompanied by foraging goatfish in 47.8% of the observations and accompanied by scavenging wrasses in 61.9% of the observations. *C. gaimard* individuals accompanied by goatfish flipped significantly more rubble than those foraging alone. Goatfish are attracted to the disturbed substrate where previously covered sand is now exposed (McCormick 1994). Therefore, goatfish were more likely to find *C. gaimard* when it was flipping more often. The presence of a goatfish may provide *C. gaimard* with an additional motivation to flip over rocks. *C. gaimard* can feed after a trolling goatfish that is stirring up the sandy substrate and uncovering benthic invertebrate prey. *C. gaimard* scavenges the sand after the goatfish finish searching for prey. The proposed mutualistic relationship where *C. gaimard* over turns rocks to reveal fresh sand and a

goatfish sifts through that sand did not occur with any significant frequency. *C. gaimard* fed behind goatfish very rarely, about 1% of the time even though it was accompanied by goatfish in 47.8% of the observations. In heterospecific relationships, it is often hard to distinguish between mutualistic relationships and commensal relationships (Morse 1977). However, it does not seem that *C. gaimard* is rewarded by foraging with a goatfish for the presence of the goatfish to significantly affect its amount of prey captured. Although *C. gaimard* captured more prey when goatfish are around that is due to the fact that *C. gaimard* flipped more rocks when the goatfish was attending. The goatfish attending *C. gaimard* and *C. gaimard* attending a goatfish seem to be two separate commensal relationships that occur in different frequencies. Furthermore, this commensal relationship is not species specific to *C. gaimard*, nor is its specific to wrasses or even to fish; a diver kicking up sand easily attracts scavengers and goatfish.

Among the goatfish species that attend *C. gaimard*, there seems to be no species that associates more strongly. *Parupeneus multifasciatus* attended *C. gaimard* most often (35.7%). However, this may be a result of *P. multifasciatus* being a habitat generalist and being able to use area of reef that is covered by coral rubble and therefore preferred by *C. gaimard* (McCormick 1994). *Parupeneus barberinus* and *Mulloides flavolineatus* attended *C. gaimard* less frequently (7.1% and 11.9% respectively). These species more often select sandy habitats and are therefore less likely to encounter *C. gaimard*, which is almost always observed over coral rubble (McCormick 1994). *Parupeneus cyclostomus* juveniles attended *C. gaimard* only 4.8% of the time. Although *P. cyclostomus* is a habitat generalist like *P. multifasciatus*, it is very rare on the study sites (McCormick 1994). *P. cyclostomus* was only seen twice at the study sites and never as an adult. This lack of species specificity further indicates that there is no mutualistic relationship between the goatfish and *C. gaimard.* Therefore, there is no reason for *C.*

gaimard to alter its foraging behavior in the presence of goatfish.

Scavenging wrasses like goatfish did not provided a significant benefit to *C. gaimard*. In some rare cases, wrasses were observed scavenging off flipped rocks before the *C. gaimard* individual had done so. This relationship is then at most a mildly parasitic one. However, there is no significant difference in the behavior of *C. gaimard* individuals that were accompanied by scavenging wrasses. Therefore, interspecies interactions did not play an important role in the foraging strategy of *C. gaimard.*

Rubble mass

The masses of the rubble that *C. gaimard* individuals flipped did not significantly vary between study sites. This is important for two reasons. First, this similarity shows that the foraging strategies between the Motu and Temae did not vary in this way. The fish were not selecting larger or smaller rocks depending on prey abundance. This may be because there is no benefit in selecting different sized rocks or because there is limited plasticity in the fish's behavior. Second, it demonstrated that the fish were expending on average a similar amount of effort per flip. This is important in evaluating the cost to benefit ratio of a foraging behavior, which in this case for rock flipping would be lower at the Motu sites where there was more prey items. This lower cost per benefit means that the behavior is more beneficial. This information could be applied to optimal foraging theory if more data was collected on prey consumption and search times.

Pairing frequency

Individuals swimming in pairs did not perform any foraging behavior. However, there was no significant difference between the amounts of pairing behavior between the sites. For this reason, the pairing behavior

does not account for any variation in feeding behavior. The motivation to swim in pairs is unknown. It was only observed with two females participating, which suggests it is not a mating display. However, because it is a protogynous species, it may be a method that females use to constantly measure their dominance against other females. There is currently no research on this species reproduction and interspecies interactions. This may be partial due to the fact that the species was previously reported as solitary (Shibuno et al. 1994).

Description of behaviors

The analysis of several video tapes of the behavior suggest that regardless of location, size, or sex, the general method of flipping rubble was consistent. This behavior is also similar to that of *Novaculichthys taeniourus*, a related wrasse that inhabits the same habitat as *C. gaimard*. Similar video analysis of *N. taeniourus* rock moving shows a similar behavior with several key differences. First, *N. taeniourus* begins the behavior in the water column above the rubble, not next to it, nearly perpendicular to the substrate. *N. taeniourus* then grabs the rubble in its jaws. Finally, it performs a similar body folding and straightening before opening its jaws and releasing the rubble a small distance away.

The sand digging behavior of *C. gaimard* is exactly mimic by *Coris aygula*. Both species shovel sand to the side with their snouts as they swim upright roughly 45 degrees from the bottom of the lagoon.

Feeding behind a goatfish like feeding off exposed surfaces is a behavior common to several wrasse species. All seem to position themselves a few centimeters above the substrate around the head of the goatfish catching whatever prey items might be thrown into the water.

The similarities in feeding behaviors with related species suggests that there may be overlapping feeding niches. This would suggest competition between *C. gaimard* and these fish. The abundance of fish that compete for a feeding niche may the affect the foraging behavior of *C. gaimard* because *C. aygula* or *N. taeniourus* may out compete *C. gaimard* for prey captured by moving rocks or digging in sand. Similarly, scavenging wrasse may clean all the prey items off the surface of rocks. Future research should attempt to quantify the influence of these fish in foraging strategies. Both substrate-disturbing species and scavenging species occurred at both sites on Moorea, but with unknown abundances.

Conclusion

Biotic factors were found to influence the behavioral choices of *C. gaimard*. However, some biotic factors such as presence of goatfish, scavenging wrasses, and other *C. gaimard* individuals were found to have no significant effect on foraging strategies. These results suggest that *C. gaimard* is a phenotypically plastic species that takes cues only from its foraging success to choose a foraging strategy. This adaptability may help the species have an extensive range and live in environments that are spatial and temporally variable. The limits to this plasticity are unknown. The similarities between the two studied populations may be due to strategic choices or plasticity limitation. Further research in the topic must test the limitations of the fish's ability to adapt. Alteration of habitat or replacement studies may reveal how quickly and how much an individual can adapt its behavior. Additionally, such a study would reveal what other factors, other than frequency and amount of behavior can be modified. Future research should also include a more complete analysis of the species optimal foraging strategy. Because the fish adapts to its locality, it should then exhibit the most efficient foraging strategy possible.

LITERATURE CITED

Aronson R. B., S. L. Sanderson. 1987. Benefits of heterospecific foraging by the Caribbean wrasse, Halichoeres garnoti. Environ.Biol.Fishes **18**:303-308.

De Pirrott M., G. M. Marchetti, and G. Chelazzi. 1999. Foraging interactions among three benthic fish in a *Posidonia oceanica* reef lagoon along the Tyrrhenian Coast. Journal of fish biology **54**:1300-1309.

Hiatt R. W., D. W. Strasburg. 1960. Ecological Relationships of the Fish Fauna on Coral Reefs of the Marshall Islands. Ecological Monographs 30:65-127.

Jensen G. C. 2005. A Unique Feeding Method by a Teleost Fish, the Fourhorn Poacher Hypsagonus quadricornis (Agonidae). Biological Bulletin **209**:165-167.

Kabasakal H. 2001. Description of the feeding morphology and the food habits of four sympatric labrids (Perciformes, Labridae) from south-eastern Aegean sea, Turkey. Netherlands Journal of Zoology **51**:439-455.

Luttbeg B., R. R. Warner. 1999. Reproductive decision-making by female peacock wrasses: Flexible versus fixed behavioral rules in variable environments. Behavioral Ecology **10**:666-674.

MacArthur R. H., E. R. Pianka. 1966. On optimal use of a patchy environment. Am. Nat. **100**:603-609.

McCormick M. I. 1994. Fish feeding on mobile benthic invertebrates: influence of spatial variability in habitat associations. Marine Biology **121**:627-637.

Mcnamara J. M., A. I. Houston. 1992. State-Dependent Life-History Theory and its Implications for Optimal Clutch Size. Evolutionary Ecology **6**:170-184.

Morse D. H. 1977. Feeding Behavior and Predator Avoidance in Heterospecific Groups. Bioscience **27**:332-339.

Shibuno T., H. Hashimoto, and K. Gushima. 1994. Changes with growth in feeding habits and gravel turning behavior of the wrasse, Coris gaimard. Japanese Journal of Ichthyology **41**:301-306.

Silvano R. A. M. 2001. Feeding habits and interspecific feeding associations of Caranx latus (Carangidae) in a subtropical reef. Environmental Biology of Fishes **60**:465-470.

Strand S. 1988. Following Behavior: Interspecific Foraging Associations among Gulf of California Reef Fishes. Copeia **1988**:351-357.

Takayanagi S., Y. Sakai, H. Hashimoto, and K. Gushima. 2003. Sleeping mound construction using coral fragments by

the rockmover wrasse. Journal of fish biology **63**:1352-1356.

Wainwright P. C., D. R. Bellwood, M. W. Westneat, J. R. Grubich, and A. S. Hoey. 2004. A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. Biological Journal of the Linnean Society **82**:1-25.