If grazers benefit from both epibiota and *Thallasia*, they may pursue one of two foraging strategies to satisfy their nutrient requirements. Grazers may feed selectively on leaves with moderate epibiotic cover, presumably maximizing nutrient uptake from both the leaf and the epibiota. Alternatively, grazers may feed on leaves with a range of epibiotic cover, thereby minimizing energy costs of grazing selectivity. Our results seem to support the latter prediction, though future study should examine the relationship of *Thallasia* and epibiota nutrient contents to grazer foraging behavior. More specifically, future study should investigate (1) the nutrient content of leaves with varying degrees of epibiotic growth, (2) the nutrient requirements of parrotfishes and sea urchins, and (3) the grazers' capacity to digest and take up nutrients from epibiota relative to their capacity to digest and take up nutrients from *Thallasia*. These studies may help to explain the apparent lack of selectivity in the foraging behavior of parrotfishes and sea urchins.

LITERATURE CITED

Berry, M. E., D. Gardella, A. Swanson. 1994. The importance of visual cues in Scaridae selection of *Thallassia testudinum* blades. *In* J. Bykowski, ed. Dartmouth Tropical Studies. Hanover, NH, USA

Fry, B. 1984. $^{13}C/^{12}C$ ratios and the trophic importance of algae in Florida *Syrmojadium filiforme* seagrass meadows. Marine Biology 29: 11-19.

Kikuchi, T. 1980. Faunal Relationships in temperate seagrass beds. Pages 153-172 *in* R. C. Phillips and C. P. McRay, ed. Handbook of seagrass biology. Garland STPM Press, New York.

Ogden, J. C. 1980. Faunal relationships in Caribbean seagrass beds. Pages 172-198 *in* R. C. Phillips and C. P. McRay, ed. Handbook of seagrass biology. Garland STPM Press, New York.

Stewart, I. J., V. R. Levesque. 1995. Grazer selection for inverted *Thallasia testudinum* blades. Dartmouth FSP 95. pages 147-149 *in* C. D. Wray, ed. Dartmouth Tropical Studies. Hanover, NH, USA

Tomasko, D. A., B. Lapointe. 1991. Productivity and biomass of *Thallasia testudinum* as related to water column nutrient availability and epiphyte levels. Mar. Ecol. Prog. Ser. 75:9-17.

THE FEEDING BEHAVIOR OF THE FACULTATIVE CLEANERFISH, *THALASSOMA BIFASCIATUM*

NINA E. PERLROTH AND MARC A. GINSBURG

Abstract. We examined the effects of the introduction of a preferred food resource on the cleaning behavior of the facultative cleanerfish, *Thalassoma bifasciatum* (bluehead wrasse). We hypothesized that, as the net energy return of cleaning might decrease relative to that of foraging on the introduced food resource, overall cleaning activity would decrease. Furthermore, we hypothesized that bluehead wrasse would selectively clean certain host species, and that cleaner selectivity would increase with the introduction of the preferred food resource. Finally, because ectoparasite load may be unevenly distributed on a host's body, and because ectoparasite distribution may vary between host species, we predicted that (1) bluehead wrasse would exhibit preferences for certain body parts, and (2) these preferences would vary between host species. Cleaning activity decreased upon addition of the alternate food source in terms of number of encounters per five minutes in the afternoon and number of nips and cleaners per encounter in the morning. Bluehead wrasse appear to prefer princess parrotfish in terms of percent of encounters initiated by the cleaner, and number of nips and cleaners per encounter. Likewise, blue chromis appears to be a non-preferred species. Bluehead wrasse clean the main body of the host more often than any other body part. Cleaning selectivity of the bluehead wrasse reflects a facultative foraging strategy and suggests possible competition for hosts and host body parts with other cleaner species.

INTRODUCTION

Although cleaning symbioses between fish species occur in the majority of freshwater and marine ecosystems (Losey 1974), the feeding strategies of facultative cleanerfish are poorly documented. Facultative cleaners are carnivores that do not depend on ectoparasites to satisfy their nutrient requirements (Itkowitz 1978). The bluehead wrasse (BHW), *Thallasoma bifasciatum*, is a facultative cleaner that feeds on small benthic animals and free-living zooplankton in addition to ectoparasitic crustaceans of fishes (Randall 1967). Optimal foraging theory suggests that BHW should only feed on ectoparasites when the net energy return equals or exceeds that of alternate food resources.

We examined the effects of an introduced, preferred food source on the cleaning behavior of BHW. Assuming that the net energy return of cleaning is less than the increased net foraging return associated with the introduction of a preferred food resource, we hypothesized that the introduction of a preferred food source would result in a decrease in overall cleaning activity. Furthermore, as ectoparasite load varies between host species (Losey 1974), we hypothesized that BHW would selectively clean certain hosts and predicted that the introduction of a preferred food resource would result in an increase in BHW cleaning selectivity. Assuming the energy return of cleaning preferred hosts is high, we expected no change in cleaner activity on preferred species. However, assuming the energy return of cleaning non-preferred hosts is less than the increased net energy return associated with the introduction of the preferred food, we expected a decrease in cleaner activity on non-preferred hosts.

Finally, if host ectoparasite load is unevenly distributed on a host's body, cleaners may maximize energy return by selectively feeding on certain host body parts. If ectoparasite distribution varies between host species, cleaners may also benefit from differential cleaning strategies for different hosts. We predicted that (1) cleaners would exhibit preferences

for specific body parts, and (2) body part preferences of cleaners would vary between host species.

METHODS

We conducted our experiment at five to six meters depth in the forereef of Discovery Bay, Jamaica, from 3-7 Mar 1995. We surveyed the area for bluehead wrasse cleaning activity and marked four active cleaning stations, all within 15 m of one another. An active station was defined as a site where we observed at least two bluehead wrasse cleaning encounters during our preliminary survey. Three of the sites were on coral promontories (heights~1.5 m). The fourth was over rocky substrate on the reef floor (area~3 m^2). The abundance of bluehead wrasse at each site was generally greater than 20 individuals, but ranged from 5-30 individuals during sampling periods.

We observed each site for four 20 mn periods: early morning (3 Mar, 0900-1000), late morning (6 Mar, 1100-1200), early afternoon (4 Mar, 1400-1500), and late afternoon (3 Mar, 1600-1700). During each sampling period we recorded all cleaning encounters. For each encounter, we recorded host species, whether the encounter was initiated by the host (host pose) or by the cleaner (no host pose), the number of bluehead wrasse cleaners per encounter, the total number of bluehead wrasse nips on the host, and the location on the host of each bluehead wrasse nip (head, gills, mouth, body, pectoral fins, dorsal fins, ventral fins, tail fins). In addition, we recorded host species each time a host posed but was not cleaned.

We collected a large sea urchin, a preferred food resource of bluehead wrasse (Itzkowitz 1978), from the Discovery Bay forereef. On the afternoon of our first experimental sampling period, we made a concentrated mull of the urchin's gut. We filled four petri dishes (6.5 cm diameter) with urchin mull, covered each dish with 1.5 mm nylon mesh, and sealed each dish with an elastic band. Each petri dish was weighted with a metal bolt which we attached to the underside of the dish.

We conducted two 20 min experimental trials at each site: early morning (7 Mar, 0900-1000) and late afternoon (6 Mar, 1500-1600). At the beginning of each trial, we placed one petri dish on a coral or rock outcrop at the edge of the cleaning station. Each petri dish was approximately equidistant from the center of cleaning activity at each site. Urchin mull slowly diffused through the nylon mesh throughout the experimental sampling period. For each cleaning encounter, we again recorded host species, whether the encounter was host initiated or cleaner initiated, number of bluehead wrasse per encounter, number of bluehead wrasse nips per encounter, and location on host of each bluehead wrasse nip. We again recorded host species of individual hosts that posed but were not cleaned.

For analysis, we used number of encounters per five minutes, number of cleaners per encounter, and number of nips per encounter as measures of cleaning activity. We used number of cleaners per encounter, number of nips per encounter, and % cleaner initiated encounters as measures of host selectivity.

RESULTS

The average number of encounters per five minutes (ENC5) varied with time of day ($F=11.576$, $df=3,12$, $p=0.005$). ENC5 for morning controls were less than those for afternoon controls (mean ± SE; morning 2.3 ± 0.3 ENC5; afternoon 5.2±0.7ENC5; LSD means comparison, $p<0.04$).

ENC5 did not differ significantly between the control and experimental mornings ($p=0.964$). ENC5 was higher in the control afternoon than experimental afternoon ($t= -3.743$, $df=10$, $p=0.004$).

The average percent of encounters initiated by cleaners (PIC) did not differ significantly between (a) control morning and afternoon, (b) control morning and experimental morning, or (c) control afternoon and experimental afternoon ($p_{(a)}=0.297$; $p_{(b)}=0.09$; $p_{(c)}=0.099$).

The average number of nips per encounter (NPE) was higher in the control morning than control afternoon ($t=2.054$, $df=175$, $p=0.041$). NPE was higher in the control morning than experimental morning ($t=2.326$, $df=110$, $p=0.022$). There was no significant difference in NPE between control afternoon and experimental afternoon ($p=0.276$).

The average number of cleaners per encounter (CPE) did not differ significantly between the control morning and afternoon ($p=0.619$). CPE was higher in the control morning than experimental morning ($t=2.064$, $df=129$, $p=0.041$). There was no significant difference in CPE between control afternoon and experimental afternoon ($p=0.276$).

We observed encounters with 12 different host species (princess parrotfish, yellowtail damselfish, redband parrotfish, striped parrotfish juveniles, cocoa damselfish, blue chromis, brown chromis, stoplight parrotfish adults and juveniles, ocean surgeon, blue tang, sharp nose puffer and doctor fish). PIC differed among host species ($kw=26.09$, $df=12$, $p=0.01$). We had insufficient data to compare PIC between specific host species or between control and experiment for specific host species.

NPE differed among host species ($kw=37.582$, $df=12$, $p<0.0001$). Results of a Tukey means comparison of NPE for princess parrotfish, yellowtail damselfish, redband parrotfish, striped parrotfish juveniles, blue chromis, ocean surgeon, and sharp nose puffer appear in Fig 2. NPE for princess parrotfish was higher than that for blue chromis ($p<0.0001$). There was no significant difference in NPE between control and experimental mornings for princess or redband parrotfish, but NPE for blue chromis was higher in the control morning ($p_{PrPa}=0.265$; $p_{RBPa}=0.398$; $p_{BC}=0.015$). There was no significant difference in NPE between control and experimental afternoons for princess parrotfish or blue chromis ($p_{PrPa}=0.221$: $p_{BC}=0.616$).

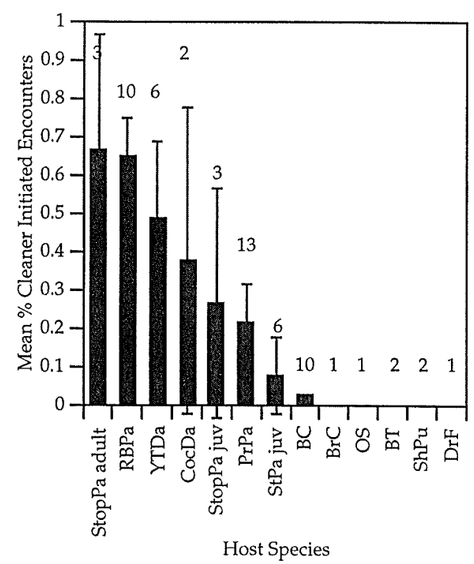

FIG. 1. Mean (± SE) percent of encounters initiated by the cleaner for each of the host species. Numbers above the means represent sample size.

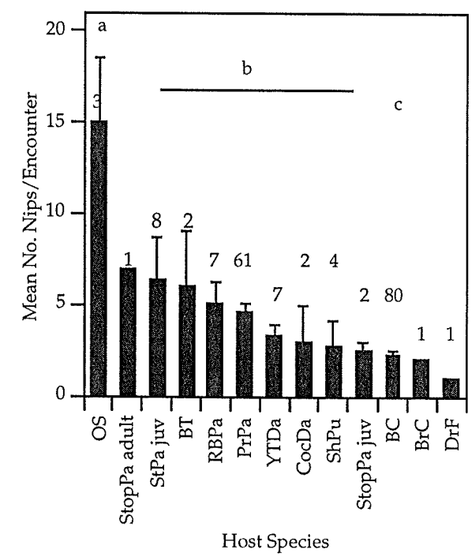

FIG. 2. Mean (± SE) number of nips per encounter for each of the host species. Numbers above the means represent sample size. Means under different letters are significantly different (Tukey means comparison, $p<0.008$).

CPE differed among host species (kw=73.724, df=12, p<0.0001). Results of a Tukey means comparison of CPE for princess parrotfish, yellowtail damselfish, redband parrotfish, striped parrotfish juveniles, cocoa damselfish, and ocean surgeon appear in Fig 3. CPE for princess parrotfish was higher than that for blue chromis (p<0.0001). There was no significant difference in CPE between control and experimental mornings for princess parrotfish, redband parrotfish, or blue chromis (p_{PrPa}=0.422; p_{RBPa}=0.726; p_{BC}=0.111). There was no significant difference in CPE between control and experimental afternoons for princess parrotfish or blue chromis (p_{PrPa}=0.465; p_{BC}=0.464).

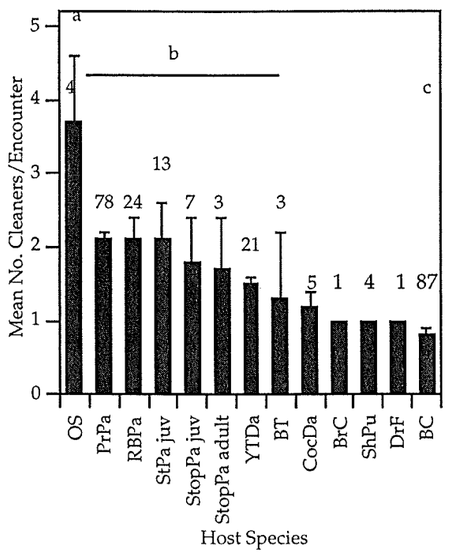

FIG. 3. Mean (±SE) number of cleaners per encounter for each of the host species. Numbers above the means represent sample size. Means under different letters are significantly different (Tukey means comparison, p<0.024).

There was a significant association between host species and specific body parts cleaned (X^2=144.2677, df=42, p<0.0001, Table 2). The average number of encounters in which a specific body part was cleaned differed among body parts (F=2.3321, df=6,42, p=0.0493). The main body was cleaned more often than any other body part (LSD means comparison, for all significant differences p<0.0151).

DISCUSSION

Bluehead wrasse forage in two broadly defined "patches": (1) cleaning stations, where they eat the ectoparasites on host fish, and (2) the surrounding area, where they eat small benthic animals and zooplankton (Randall 1967). Optimal foraging theory predicts that the level of blue headed wrasse feeding activity in each of these patches should vary with the relative food availability between the two patches. If the amount of food in the area surrounding a cleaning station increases, then blue headed wrasse feeding activity might increase in the surrounding area and decrease in the cleaning station. Likewise, if the number of hosts visiting a cleaning station increases (i.e. food availability increases), then feeding activity in the cleaning station might increase.

The higher ENC5 in the afternoon suggests that either host availability or cleaning activity (or both) is higher in the afternoon than morning. Since NPE was higher in the morning than afternoon, and CPE was the same in the morning and afternoon, cleaning activity by individual BHW appears to be higher in the morning. Therefore, the lower ENC5 in the morning probably stems from a lower host availability in the morning than afternoon.

A high host availability in the afternoon might reduce the effect on cleaning activity of adding food to the area surrounding the cleaning station. BHW foraging in the cleaning station "patch"" should continue foraging there as long as food (host) availability remains high. A low host availability in the morning might cause the BHW to drastically reduce their cleaning activity when food is added to the surrounding area. Feeding on the experimental food would probably provide higher net energy rewards than exerting more effort cleaning a lower number of hosts in the morning.

ENC5 decreased in the afternoon and remained at the low morning level when we added food to the area surrounding the cleaning station (Table 1). NPE decreased in the morning and remained at the low afternoon level. In terms of ENC5 and NPE, cleaning activity ended up at similar low levels in both the morning and afternoon experiments. Since CPE decreased in the morning but remained constant in the afternoon between control and experiment, the overall decrease in cleaning activity was higher in the morning than afternoon. As expected, the effect on cleaning activity of increasing another food resource was higher when host availability was lower.

The difference in PIC, NPE and CPE among host species suggests bluehead wrasse may prefer certain host species. Since princess parrotfish had high PIC, NPE, and CPE while blue chromis had low PIC, NPE and CPE, princess parrotfish appeared to be a preferred host while blue chromis appeared to be a non-preferred host (Fig 1,2,3). Dupré (1989) also found that parrotfish appeared to be a preferred host for BHW. Since parrotfish have higher ectoparasite loads than blue chromis (Losey, 1974), parrotfish offer greater food rewards to cleaners, and the effect on parrotfish cleaning activity of increasing another food resource should be lower than that for blue chromis. Overall, selectivity of host species should increase when an alternate food resource becomes more available.

The only change in cleaning activity on princess parrotfish and blue chromis from control to experiment was a decrease in NPE for blue chromis in the morning. As expected, BHW continue to actively clean the preferred host despite the increased availability of another food resource, and reduce their cleaning activity on the non-preferred host species. The alternate food resource appeared to make BHW more selective cleaners.

If ectoparasite load varied among different host body parts, BHW may also selectively clean certain body parts. The apparent preference for the main body of the host suggests that the main body carries the largest ectoparasite load. The main body moves less than the fins and mouth, so ectoparasites might settle more often on the main body.

Preference for certain hosts and host body parts might also represent niche specialization under competition for hosts among different cleaner species. Future studies should investigate competitive interactions between BHW and other cleaner species to better address the causes of BHW cleaning selectivity.

LITERATURE CITED

Dupré, M. and M. Kocher. 1989. An analysis of fish interactions in cleaning symbiosis. Dartmouth Tropical Studies. Hanover, NH, USA.

Itkowitz, M. 1979. The feeding strategies of a facultative cleanerfish, *Thalassoma bifasciatum*. Pages 403-413 in Zoology (87). London.

Losey, G. S. 1974. Cleaning symbiosis in Puerto Rico with comparison to the tropical Pacific. Pages 960-970. COPEIA (4).

Randall, J. E. 1967. Food habits of reef fishes of the West Indies. Pages 665-847 in Studies in Tropical Oceanography (5).

TABLE 1. Means (±SE) for control and experimental mornings and afternoons of the number of encounters per five minutes, the percent of encounters initiated by cleaners, the number of nips per encounter and the number of cleaners per encounter. Means with the same letter (a,b) in each row are significantly different.

	control AM	experimental AM	control PM	experimental PM
no. enc/5 min	2.3±0.3[a]	1.8±0.7	5.2±0.7[a,b]	1.1±0.5[b]
percent cleaner initiated	27.5±4.8	15.0±10.0	36.2±6.[8]	46.0±14.0
no. nips/enc	4.3±0.5[a,b]	2.5±0.8[b]	3.2±0.3[a]	4.1±0.6
no. cleaners/enc	1.6±0.1[b]	1.1±0.2[b]	1.8 ± 0.2	2.1±0.3

TABLE 2. Bluehead wrasse preferences for different body parts of host fishes. (+) average number of nips is greater than expected; (-) average number of nips is less than expected; (0) average number of nips does not deviate from expected based on G-test results.

Host species	head	gills	mouth	main body	pectoral fin	dorsal fin	ventral fin	tail fin
princess PF	0	0	-	0	0	+	+	-
yellowtail dml	0	0	0	-	+	0	0	-
redband PF	0	0	0	+	+	0	+	-
striped PF	0	0	0	+	0	0	0	-
blue chromis	+	0	+	-	-	-	-	+
stoplight PF	0	0	0	+	0	0	0	0
ocean surgeon	0	0	0	0	0	0	0	0