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Title: Effects of stony coral extracts on feeding by Acanthaster planci (Linnaeus, 1758).

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The preference of the starfish Acanthaster planci for 3 species of corals which survive A. planci outbreaks (Diploastrea heliopora, Porites rus, and Coscinaraea columna), and the effects of aqueous and organic extracts of these corals on A. planci feeding, were investigated experimentally in the laboratory. In whole colony experiments, D. heliopora and P. rus were consumed significantly less than Acropora aspera. Organic extracts from D. heliopora stimulated feeding at low concentrations, but not at higher natural concentrations compared with solvent controls. Organic extracts of P. rus and C. columna did not deter or stimulate A. planci feeding at low and high natural concentrations compared with controls. Aqueous extracts from all 3 non-preferred corals tended to be feeding attractants at high concentrations relative to controls, but only aqueous extracts of P. rus at high concentrations significantly enhanced A. planci feeding significantly. When aqueous extracts of A. aspera were compared with the aqueous extracts of the 3 non-preferred

corals, A. aspera extracts were significantly preferred over D. heliopora and C. columna, but not over P. rus.

The results suggest that there is no chemical defense produced by stony corals against A. planci. Rather than defending chemically, those non-susceptible corals may avoid A. planci predation by releasing low amounts of chemical stimulants to the environment, hence A. planci would not recognize them as their prey.

Effect of stony corals extracts on feeding by *Acanthaster planci* (Linnaeus, 1758).

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INTRODUCTION

In coral reef habitats, crown-of-thorns starfish Acanthaster planci plays a very important role as a major predator of scleractinian corals (Birkeland and Lucas, 1990). Although A. planci can feed on a wide range of animals such as anemones, soft corals, and encrusting organisms (Moran 1986), field observations show that adult A. planci feed primarily on corals, and they use other food sources when scleractinian coral availability is low (Chesher 1969a). A. planci has been considered to be a specialist coral-feeder (Benson et al. 1975, Cameron and Endean 1982, Moran 1986). Predation by A. planci is known for its large scale effects on changes in species composition, trophic structure, and topography of coral reef communities (Chesher 1969a, Endean 1973, Glynn 1973, 1974, Pearson 1981, Moran 1986, Birkeland 1988). Large outbreaks of A. planci throughout the tropical Pacific and Indian Oceans are well documented (Chesher 1969a, Chesher 1969b, Endean 1973, Moran 1986, Yamaguchi 1986).

Previous feeding preference experiments and field observations indicate that A. planci has dietary preferences among the corals (Birkeland and Lucas, 1990). The dietary preference of A. planci for certain species of corals may be influenced by defensive structures such as nematocysts (Barnes et al. 1970, Goreau et al. 1972) and colony morphology (Chesher 1969b, Ormond and Campbell 1974, Menge 1982). A. planci feeding behavior in vivo is further

influenced by environmental conditions (Birkeland and Lucas 1990) such as wave action (Endean 1973, Ormond et al. 1973, Birkeland and Randall 1979), the accessibility of corals (Barnes et al. 1970, Glynn 1976, 1985a, 1985b), and the relative abundance and distribution of corals (Ormond et al. 1973, Glynn 1985a, 1985b).

The stony corals, Diploastrea heliopora, Coscinaraea spp., Galaxea spp., Turbinaria spp. and Tubastrea micrantha are reported as non-preferred prey (Barnes et al. 1970, Endean and Stablum 1973ab, Birkeland and Lucas 1990). The reasons for these corals been non-preferred prey are presently unknown. Large colonies of pocilloporids protected by crustacean symbionts are also not preyed upon (Goreau et al. 1972, Glynn 1982, 1983, 1987). However, pocilloporids without crustacean symbionts are favored prey of A. planci (Glynn 1976, 1982a, 1982b, 1987). Acroporids are also preferred prey of A. planci (Pearson and Endean 1969, Roads 1969, Garlovsky and Bergquist 1970, Branham et al. 1971, Aziz and Sukarno 1972, Goreau et al. 1972, Nishihara and Yamazato 1972, Ormond et al. 1976, Birkeland and Randall 1979, Colgan 1987).

Extracts from different species of corals are reported to elicit feeding-attraction or avoidance responses of A. planci (Brauer et al. 1970, Collins 1975b, Ormond et al. 1976). Extracts from Acropora spp. and Pocillopora spp. elicited positive feeding responses, but extracts from Porites spp. caused

avoidance responses (Brauer et al 1970). Collins (1975a) identified the substance in Fungia spp. (chemically similar to the amino acid proline) responsible for the avoidance response.

Within Guam's coral fauna, high survival rates of Coscinaraea columna, Diploastrea heliopora, and Porites rus after A. planci outbreaks have been documented (R. H. Randall and C. E. Birkeland pers. comm.). In this study, I investigated (1) the preferences of A. planci for these corals that appear to survive outbreaks of A. planci, (2) the effects of aqueous and organic extracts produced by these corals on feeding by A. planci, (3) and the effects of crushed coral tissues, which eliminates morphological features of the coral, on feeding patterns of A. planci.

I hypothesized that these corals survive outbreaks of A. planci because they are actively avoided by A. planci and that chemical defenses play an important role in the low susceptibility of these corals to predation.

MATERIALS AND METHODS

Experimental Animals

Corals and Acanthaster planci were collected from various reefs around Guam. The specimens of A. planci varied from 20 to 30 cm in diameter. These were kept in outdoor flow-through seawater tanks and fed Acropora aspera, a preferred coral, for 1 to 2 weeks before the experiments. In this study, I investigated organic and aqueous extracts of the following species of corals for their biological activities: 1) Coscinaraea columna, 2) Diploastrea heliopora, and 3) Porites rus.

Coral Extraction

Organic extracts were obtained from corals with a 1:1 mixture of dichloromethane (CH_2Cl_2) and methanol (MeOH). Aqueous extracts were obtained by soaking corals in a mixture of 1:1 MeOH and deionized water. Extracts were filtered, and solvents were evaporated with a rotary evaporator. For aqueous extracts, the remaining aqueous layers were freeze dried.

To quantify the yield of extracts per tissue weight and per surface area of corals, about 8.0 cm^2 of live coral tissue from five different colonies was waterpicked with deionized water (Johannes and Wiebe, 1970), and the waterpicked tissue was freeze dried. After obtaining the dry weight, extracts were obtained from each dried tissue sample in 100 ml of a CH_2Cl_2 / MeOH

mixture then in a MeOH / deionized water mixture as described previously. The yields were expressed in mg of extract per coral tissue area (cm^2) and mg of extract per freeze dried coral tissue weight (mg).

Feeding Preference Assays

All feeding preference assays were done in outdoor aquaria (20 cm x 95 cm x 50 cm) with constantly running seawater. In all feeding preference experiments, 20 individual A. planci were used. The duration of each assay was 6 hours. If animals did not make any choice in this time period, the results were not scored for that individual.

For whole-coral preference experiments, A. aspera and a test coral were placed at one end of the tank in alternated fashion (left vs. right) and one A. planci was placed at the other end. Corals were cut to a similar size (approximately 10 cm x 10 cm or larger surface area). Food choice was scored when an individual A. planci had spread its stomach over most of the coral. Results were scored as the number of individual A. planci selecting each coral, and were analyzed by a 2-tailed binomial test (Sokal and Rohlf, 1981).

In addition to the whole corals, the crushed coral tissues were tested. The crushed coral tissues were collected by scraping about 25 cm^2 of living surface area from corals. The crushed coral tissues were mixed with 2.5 g of carrageenan in 100 ml of deionized water. After the carrageenan mixture

hardened, it was cut into small cubes (2 cm x 2 cm x 2 cm). About 3 g of the crushed coral tissue (including some exoskeleton) was present in each carrageenan cube. In the first set of assays, crushed coral cubes were compared with control cubes containing only carrageenan and deionized water. For the second set of assays, crushed coral cubes were compared with control cubes that incorporated the same amount of crushed A. aspera tissue. These cubes and small pieces (2 cm in length) of preferred coral A. aspera were wrapped together with gauze, and gauze was held with safety pins around the coral. These gauze-wrapped corals and carrageenan cubes were placed 25 cm apart on feeding platforms (50 cm long 3/4 in. dia PVC pipe). Determination of A. planci preferences were made when an individual A.planci spread its stomach over a gauze-wrapped coral. Results were scored and analyzed with a binomial test in the same way as in the whole-coral preference experiments.

For coral-extract (organic soluble) preference experiments, extracts from corals were dissolved in ether and coated at a concentration of 0.45 mg/cm^2 and 2.7 mg/cm^2 on gauze (7.5 cm x 7.5 cm). Controls were coated with ether only. In addition to these high and low natural concentrations (Table 1), organic extracts were also tested at 1 mg/cm^2, organic extracts of A. aspera were used as a control to compare interspecific organic extract preferences. Small pieces (2cm in length) of A. aspera were wrapped with the chemically coated gauze, then offered to A. planci as described above.

Aqueous extracts from corals were tested slightly differently from organic extracts because these readily dissolve in seawater and can then be lost to solution during the experiment. To minimize this loss, aqueous extracts were tested in the ssme way as the aqueous extracts by incorporating them into carrageenan cubes. Because of their solubilities into seawater, it was very difficult to quantify natural concentrations of aqueous extracts in laboratory assays, therefore they were tested at 1% and 5% weight/volume concentrations to cover a wide range of natural concentrations (Table 2). The control cubes contained only carrageenan and distilled water. Additionally, aqueous extracts were also tested at a 2% w/v concentration compared with A. aspera aqueous extracts at 2% w/v as a control. These cubes and small pieces (2 cm in length) of A. aspera were wrapped together with gauze, then offered to A. planci as described above.

RESULTS

Coral Extraction

Based on quantitative extraction, A. aspera had the highest yield of organic and aqueous extracts per freeze- dried tissue weight. However, it had the lowest concentration of both types of extracts per surface area (Table 1, 2). Among non-susceptible corals, D. heliopora had the highest concentration of organic extracts per area as well as per freeze-dried tissue weight (Table 1). D. heliopora had the lowest amount of aqueous extract yield per tissue weight while the aqueous extracts of P. rus, C. columna, and A. aspera accounted for more than 50 % of their freeze-dried tissue weight (Table 2).

Table 1: Natural concentrations of organic extracts in corals. Values reported are mean $\pm$1 SD. N=5 for each species. Values are reported as yield per surface area (mg/cm^2 tissue) and % yield per freeze-dried tissue dry mass. Significant differences ($p<0.05$, SNK) are indicated by superscript letters for each column.

Species	mg/cm^2 tissue	% yield
Diploastrea heliopora	2.6 ± 1.4^a	10.0 ± 5.1^a
Porites rus	1.8 ± 1.0^a	7.5 ± 3.7^a
Coscinaraea columna	1.5 ± 0.4^a	4.6 ± 1.2^a
Acropora aspera	1.5 ± 0.2^a	16.8 ± 4.2^b

Table 2: Natural concentrations of aqueous extracts in corals. Values reported are mean ±1 SD. N=5 for each species. Values are reported as yield per surface area (mg/cm^2 tissue) and % yield per freeze-dried tissue dry mass. Significant differences ($p<0.05$, SNK) are indicated by superscript letters for each column.

Species	mg/cm^2 tissue	% yield
Diploastrea heliopora	8.9 ± 4.9^{ab}	32.0 ± 9.8^{a}
Porites rus	12.5 ± 3.7^{bc}	53.4 ± 6.4^{b}
Coscinaraea columna	17.2 ± 5.4^{c}	51.6 ± 13.3^{b}
Acropora aspera	5.0 ± 1.2^{a}	53.5 ± 1.7^{b}

Whole-coral Preference Assays

In the whole-coral preference experiment, Acropora aspera was preferred in most cases (Table 3). P. rus and D. heliopora were not preferred ($p=0.004$ and $p=0.041$ respectively) compared with A. aspera. However, there were no significant preferences between C. columna and A. aspera ($p=0.332$).

Table 3: Preferences of A. planci for whole-coral colonies. Values reported are number of individuals preferring each species in 3 separate choice tests. p-values were determined by 2-tailed Binomial tests.

Species	# Preferring	P-value
Diploastrea heliopora	5	0.041
Acropora aspera	15	
Porites rus	2	0.004
A. aspera	15	
Coscinaraea columna	6	0.332
A.aspera	11	

Crushed Coral Tissue Preference Assays

All of the crushed coral tissues appeared to stimulate feeding behavior (Table 4). P. rus stimulated feeding behavior the most (p=0.004) among the tested corals. These data were consistent with the 5 % (m/v) aqueous extract data (Table 10).

Table 4: Preferences of A. planci for crushed coral tissue. Values reported and determination of p-values are the same as in Table 3.

Species	# Preferring	P-value
Diploastrea heliopora	13	0.167
control	6	
Porites rus	16	0.004
control	3	
Coscinaraea columna	13	0.096
control	5	

Crushed coral tissues were also tested against crushed A. aspera as a control. A. aspera stimulated feeding significantly when compared with D. heliopora and P. rus (Table 5). These results were similar to the whole-coral preference tests (Table 3).

Table 5: Preferences of A. planci for crushed coral tissue with crushed A. aspera as the control. Values reported and determination of p-values are the same as in Table 3.

Species	# Preferring	P-value
Diploastrea heliopora	5	0.041
Acropora aspera	15	
Porites rus	4	0.019
Acropora aspera	15	
Coscinaraea columna	8	0.648
Acropora aspera	11	

Organic Extract Preference Assays

Organic extracts were tested at a concentration of 0.45 mg/cm^2 and 2.7 mg/cm^2 to cover a range of natural concentrations found in the 4 corals (Table 1). Most organic extracts at low concentration (0.45 mg/cm^2) appeared to stimulate feeding behavior of A. planci (Table 6). However, only the D. heliopora extract significantly stimulated feeding behavior and the extract from C. columna did not affect feeding. When extract concentration was increased to a 2.7 mg/cm^2 level, all test results became insignificant (Table 7). The small

size of the tanks and location of highly concentrated extracts adjacent to control corals potentially affected the ability of A. planci to distinguish between control and treated gauze-wrapped corals.

When organic extracts were tested with A. aspera organic extract as the control, there was no significant difference between the number of A. planci choosing A. aspera and D. heliopora or C. columna. However, organic extract of P. rus showed a trend of being not preferred (p=0.077) when tested against A. aspera organic extract (Table 8).

Table 6: Preferences of A. planci for coral organic extract at 0.45 mg/cm^2 concentration. Values reported are number of individuals preferring each coral extracts in 3 separate choice tests. P-values were determined by 2-tailed Binomial tests.

Species	# Preferring	P-value
Diploastrea heliopora	12	0.035
control	3	
Porites rus	12	0.238
control	6	
Coscinaraea columna	8	0.502
control	12	

Table 7: Preferences of A. planci for coral organic extract at 2.7 mg/cm^2 concentration. Values reported and determination of p-values are the same as in Table 4.

Species	# Preferring	P-value
Diploastrea heliopora	7	1.000
control	6	
Porites rus	13	0.167
control	6	
Coscinaraea columna	6	1.000
control	5	

Table 8: Preferences of A. planci for coral organic extract at 1 mg/cm^2 concentration with 1 mg/cm^2 A. aspera organic extract as a control. Values reported and determination of p-values are the same as in Table 4.

Species	# Preferring	P-value
Diploastrea heliopora	8	0.814
Acropora aspera	10	
Porites rus	4	0.077
Acropora aspera	12	
Coscinaraea columna	9	1.000
Acropora aspera	10	

Aqueous Extracts Preference Assays

Aqueous extracts were tested at 1 % (mass/volume) level and 5 % (m/v). At low concentrations (1 %), there were no significant feeding effects (Table 9). However, when the concentration was increased to a 5 % level, all aqueous

extracts seemed to stimulate feeding behavior (Table 10), especially aqueous extracts from P. rus (p=0.004).

The aqueous extracts were also tested with A. aspera aqueous extract as a control. A. aspera significantly stimulated feeding compared with D. heliopora and C. columna. However, compared with P. rus aqueous extract, there was no significant difference (Table 11).

Table 9: Preferences of A. planci for coral aqueous extract at 1 % m/v concentration. Values reported and determination of p-values are the same as in Table 4.

Species	# Preferring	P-value
Diploastrea heliopora	8	0.814
control	10	
Porites rus	6	0.454
control	10	
Coscinaraea columna	11	0.332
control	6	

Table 10: Preferences of A. planci for coral aqueous extract at 5% m/v concentration. Values reported and determination of p-values are the same as in Table 4.

Species	# Preferring	P-value
Diploastrea heliopora	12	0.238
control	6	
Porites rus	14	0.004
control	2	
Coscinaraea columna	11	0.332
control	6	

Table 11: Preferences of A. planci for coral aqueous extract at 2% m/v concentration with 2% m/v A. aspera aqueous extract as a control. Values reported and determination of p-values are the same as in Table 4.

Species	# Preferring	P-value
Diploastrea heliopora	5	0.041
Acropora aspera	15	
Porites rus	8	0.503
Acropora aspera	12	
Coscinaraea columna	5	0.041
Acropora aspera	15	

DISCUSSION

Feeding preferences of A. planci for three species of non-susceptible corals did not provide direct evidence of chemical defenses in these stony corals. However, laboratory assays indicate that A. planci has significant feeding preferences for some corals and their extracts. As whole corals, D. heliopora and P. rus were significantly less susceptible to A. planci than A. aspera (Table 3). Interestingly, under laboratory conditions, A. planci showed no difference in preference between C. columna, which is known as a non-favored prey (Birkeland and Lucas 1990), and A. aspera. When these corals were crushed and incorporated into the carrageenan cubes, then wrapped by gauze to eliminate possible differences in micromorphology and nematocysts among them, the patterns of feeding preferences (Table 5) remained identical to those of whole coral preference tests (Table 3). This result suggest that A. planci feeding preference patterns are determined neither by coral morphology nor type of nematocysts present in these three corals. This contradicts previously reported studies which suggest that coral morphology and nematocysts may affect feeding preferences of A. planci (Barnes et. al. 1970, Gorean et. al. 1972, Chesher 1969b, Menge 1982). However, colony sizes used in this experiment were relatively smaller than most of colonies in the field. Coral colonies with actual field size and growth morphology might have

different effects on feeding patterns, but it is almost impossible to conduct laboratory preference assays with full size coral colonies.

Since nematocyst effectiveness was never tested directly in the assays, possibility of defense by nematocysts can not be eliminated entirely, however further assay results suggest that feeding preference patterns are likely determined by chemical stimulants produced by these corals. Chemical extracts of live corals have long been known to induce movement and feeding responses of A. planci (Brauer et al. 1970, Collins 1970, Hanscomb 1976). In this study, almost all types of coral extracts (aqueous and organic) or crushed corals stimulated A. planci feeding behavior and in most cases acted as attractants.

Tests of organic extracts from these corals compared with solvent controls, indicate a tendency for the extracts to be attractants toward A. planci. When these organic extracts were tested with A. aspera organic extract as controls, there were no significant differences in feeding preferences between extracts from two non-susceptible corals (D. heliopora and C. columna) and A. aspera. The only exception to this was the organic extract from P. rus which was less preferred than the A. aspera extract ($p=.077$). Based on these data, organic extracts from D. heliopora, C. columna and A. aspera do not affect A. planci feeding behavior; however, organic extracts from P. rus may chemically affect A. planci feeding behavior.

All of the aqueous extracts at 5% w/v concentration from these corals tended to be attractants, especially P. rus extract (p=0.004). Tests of these extracts with A. aspera aqueous extract as a control showed that A. planci significantly preferred A. aspera aqueous extracts over D. heliopora and C. columna (p=.041 for each) but not over P. rus extract. This result can be explained by strong feeding attraction triggered by P. rus aqueous extracts (p=0.004, Table 8) acting to offset the attraction caused by A. aspera aqueous extracts (Table 9).

The best explanation for A. planci feeding preferences toward stony corals, based on this series of preference assays, is that A. planci shows "various degrees of preference" for different coral species. To summarize this, the likely order of A. planci preference for the 4 species used in this study may be ranked from most to least desired as follows: 1) A. aspera 2) C. columna 3) D. heliopora 4) P. rus. In support of this ranking; 1) whole coral or crushed A. aspera were strongly preferred over D. heliopora and P. rus, 2) A. aspera aqueous extracts were preferred over those of D. heliopora and C. columna, 3) P. rus aqueous extracts were as good an attractant as those of A. aspera, 4) there was no difference in preference for organic extracts of D. heliopora, C. columna or A. aspera, 5) P. rus organic extract was least favored, and 6) any coral extracts were better than no extracts.

This may indicate that some chemical components in the aqueous extracts are responsible for attracting A. planci. The degree of attraction toward A. planci may be influenced by quantities of these attractant chemicals in the corals. It is also possible that the quantity of the attractant chemicals varies among coral species. Such chemicals are possibly water soluble proteins, amino acids, carbohydrates or other organic molecules. Collins (1975a) and Hanscomb (1976) reported that both high and low molecular weight fractions are responsible for eliciting feeding responses. Identifying the chemical components of coral extracts that are most responsible for A. planci feeding preference could be done by separating each extract into fractions by chromatographic methods and testing them in a series of feeding preference assays.

Mechanisms responsible for high survival rates of some non-susceptible corals and avoidance of predation by A. planci are still unknown. However, possible explanations for this phenomena may be derived by analyzing preference assay data. A. planci likely select and feed on prey according to the strength of attractant chemical stimulants. D. heliopora and P. rus when undisturbed, may emit few or no feeding attractants that initiate feeding behavior of A. planci. On the other hand, other corals such as A. aspera may secrete more noticeable chemical stimulants which attract A. planci. When these non-susceptible corals are crushed or chemically extracted, the chemical

stimulants responsible for A. planci feeding behavior are enhanced. As a result they become preferred over controls.

A. planci locates prey by means of chemosensory attraction (Ormond et al. 1973, 1974). Therefore chemical stimulants play a very important role in the predator-prey relationship of A. planci and stony corals. In the field, A. planci are often attracted to damaged corals or colonies already preyed upon by other A. planci (Ormond 1973, Sloan and Campbell 1982). This feeding behavior also suggests that quantities and strengths of chemical stimulants in the environment are very important in determining dietary preferences.

Non-susceptible corals such as D. heliopora or P.rus possibly avoid A. planci predation by not sending any chemical attractants to the immediate environment. For survival of stony corals, avoiding detection by not producing chemical stimulants may be more efficient than deterring predators with chemical defenses.

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