

Organic and Caloric Levels of Fish Feces Relative to Its Consumption by Coprophagous Reef Fishes

T. G. Bailey¹ and D. R. Robertson²

¹ Oceanic Biology Group, Marine Science Institute, University of California; Santa Barbara, California 93106, USA

² Smithsonian Tropical Research Institute; Apartado 2072, Balboa, Republic of Panama

Abstract

Levels of protein, lipid, carbohydrate, ash, and calcium in the rectal contents of a species representative of each of four trophic groups of coral reef fishes were determined. These levels and the estimated caloric levels were related to the degree to which the feces of each species were eaten by species of coprophagous fishes and to the potential nutritional value of their non-fecal foods. The potential nutritional value of feces (based on estimated caloric content), protein and lipid levels were positively correlated with the percentage of feces eaten by coprophagous fishes. Levels of calcium and ash were negatively correlated with the percentage eaten. Fecal carbohydrate level was not correlated with the degree of ingestion. Food values of these feces were at least equal to those of non-fecal foods (i.e. zooplankton, coral tissue, algae, etc.) of the coprophages. Feces produced by the coprophagous species had even lower potential food value.

Introduction

Naturally occurring coprophagic interactions among marine macroorganisms have received little direct attention from marine ecologists. However, a number of pertinent observations have been made. Macroinvertebrates and fishes in 'no choice' situations in the laboratory will ingest invertebrate and fish feces (Johannes and Satomi, 1966; Frankenberg and Smith, 1967; Frankenberg *et al.*, 1967). Corals feed on fish feces at night (McCloskey and Chester, 1971). The feces of a laboratory-maintained macrocrustacean, two species of herbivorous shore fishes, and several midwater fish species contain significant amounts of organic material (Johannes and Satomi, 1966; Montgomery and Gerking, 1980; Robison and Bailey, in press). However, data on the extent of coprophagy in the marine environment and its potential significance in the diets of marine macroorganisms are generally lacking. In

particular, the scientific literature contains virtually no information on the occurrence or nutritional significance of coprophagic interactions among coral reef fishes.

Certain coral reef fishes at Palau, in the Western Pacific, regularly consume the feces of other reef fishes. Those coprophagic interactions occur immediately upon egestion of the fecal material (Robertson, in press). Coprophagic fishes, which included at least 45 species representing 8 families, ate the feces of at least 64 fish species belonging to 11 families. The following general coprophagic relationships were observed: (1) The feces of carnivorous fishes whose diets consisted of other fish, zooplankton, and benthic invertebrates were eaten by herbivorous fishes. (2) The feces of benthic-feeding herbivorous fishes whose diets included fleshy microalgae (principally red algae) and relatively little inorganic material (ash) were eaten by (a) benthic-feeding herbivores that consumed mainly brown algae and had low ash-content diets and (b) benthic-feeding herbivores and detritivores that had high ash-content diets. (3) The feces of fishes with low ash-content diets which consumed the tissues of hard corals were eaten by herbivorous fishes with high ash-content diets. (4) The feces of fishes with high ash-content diets were rarely, if ever, eaten by other fishes.

These observations suggest two hypotheses. First, the freshly egested feces of some coral reef fishes are relatively more nutritious than those of other reef fishes; and the degree to which a species' fecal material is consumed by other fishes is a function of its potential nutritional value. Second, interspecific coprophagic interactions are non-reciprocal because, in any pair of coprophagically interacting fishes, the potential nutritional value of the coprophage's feces is less than that of the defecator's feces. These hypotheses were tested by (a) determining the potential food value of fish feces ingested by herbivorous fishes and comparing this with the potential food value of the algae they normally eat; and (b) comparing a ranking of the potential nutritive value of the feces produced by fishes of different trophic groups with a ranking of the

relative degree to which each species' fecal material is actually eaten by other fishes. We analyzed the rectal contents of four coral reef fishes, each a different feeding type. The concentrations of protein, carbohydrate, lipid, calcium, and ash were determined for the feces of each species. The caloric content of the feces of each species was calculated from its chemical composition. In addition, we collected quantitative data on the coprophagous interactions of the four species.

Materials and Methods

Site and Fishes Studied

Observations on coprophagy were made from January through April, 1980, at Koror, Palau in the Western Caroline Islands (Lat. 7°30'N, Long. 134°30'E) in the study area described by Robertson (in press). Rectal content samples were collected during the latter half of March, 1980.

The species studied included: (1) *Chromis atripectoralis*, a small zooplanktivorous damselfish (Pomacentridae) (Allen, 1975), which was one of the most common zooplanktivorous fishes in Palau. They fed in the mid- and upper levels of the water column in intertidal and shallow subtidal areas.

(2) *Chaetodon trifasciatus* was the most abundant butterflyfish (Chaetodontidae). It fed almost exclusively on the tissues of living hard corals. Twenty-five different individuals, watched for 10 min each, took bites from the substrate at a mean rate of 13.8 (SE=0.6) min⁻¹. A mean of 99.9% (SE=0.06) of each fish's bites were from living hard corals (see also Reese, 1975).

(3) *Zebrasoma scopas*, is a small, abundant herbivorous surgeonfish (Acanthuridae), which fed primarily on fleshy red microalgae (although occasionally it ingested small crustaceans, Robertson and Gaines, unpublished data).

(4) *Scarus oviceps*, one of the most common parrotfishes (Scaridae), fed by cropping micro-algae and scraping the surfaces of coralline substrate to remove fine epilithic and presumably, endolithic microalgae. Its diet included relatively large quantities of ash (coralline substrate).

Field Observations and Sample Collection

Data on coprophagic interactions among the species within the study area were collected by following individuals of each species for periods up to one hour, and by incidental observations.

Due to the difficulty of collecting uncontaminated samples of naturally produced fresh feces, rectal contents were used for chemical analyses. We assume that these rectal samples are very similar in chemical components to feces because most nutrient absorption occurs in the proximal part of a fish's intestine (Fänge and Grove,

1979). However, the rectal samples probably contain undigested and/or unabsorbed food along with components of the gut flora (Montgomery and Gerking, 1980).

Individuals of the four species used for rectal content analyses were collected between mid-morning and mid-afternoon. They were speared, killed immediately by pithing, and then placed in a diver-towed insulated container filled with ice and brine. Fishes were transported to the laboratory in this container and either dissected immediately or kept in a freezer at -10°C and dissected later.

Chemical Analyses

Chemical analyses were performed on the rectal contents obtained by extrusion using gentle pressure along the distal half of the rectal portion of the excised fish intestine. The samples were collected in glass vials with parafilm lined screw-caps and frozen until chemically analyzed. Samples were thawed and transferred to a glass tissue grinder and homogenized in 2 ml of distilled water. The volume of the homogenate was brought up to 10 ml with distilled water and then dispensed immediately into vials for analyses.

Three 0.5-ml aliquots of each homogenate were dispensed into pre-weighed, pre-ashed aluminum weighing boats and then dried in a 60°C oven to constant weight (2-3 d). The dried samples were reweighed and then placed in a 485°C muffle furnace overnight and then weighed again to determine the ash content.

Each of the samples used in the estimation of ash was subsequently placed in a test tube containing 5 ml of 2 N HCl. The amount of calcium present was determined with a Varian Techtron Model AA6 atomic absorption spectrophotometer. Calcium chloride was used as the standard.

Two 0.5-ml aliquots of each homogenate were analyzed for protein using a modification of the Lowry method (Merchant *et al.*, 1964) with bovine serum albumin as the standard.

Two 0.5-ml aliquots of each homogenate were analyzed for carbohydrate using the method of Dubois *et al.* (1956) with glucose as the standard.

Lipid was extracted from two 0.5-ml aliquots of each homogenate using the method of Bligh and Dyer (1959). The extracts were dried under nitrogen in a 30°C water bath and then analyzed for lipid using the charring method of Marsh and Weinstein (1966) with stearic acid as the standard.

Caloric levels were estimated using the following factors: protein, 4.1 Kcal g⁻¹; carbohydrate, 2.5 Kcal g⁻¹; lipid, 8.0 kcal g⁻¹. These conversion factors were used rather than the absolute caloric value (e.g. 5.7 Kcal g⁻¹ for protein; 4.1 Kcal g⁻¹ for carbohydrate; 8.7 Kcal g⁻¹ for lipid) since they more accurately and realistically reflect the energy value of fish feces to potential consumers (Brett and Groves, 1979).

Results

Coprophagy

Chromis atripectoralis feeding in midwater produced pale, stringlike feces. Several different species of coprophagous fishes, including *Zebrasoma scopas* and *Scarus oviceps*, regularly joined schools of *C. atripectoralis* and ingested almost all of the fecal material produced by this damselfish (Table 1 and Fig. 1). The great majority of the dark, bean-shaped feces produced by territorial and schooling *Z. scopas* were eaten by other fishes (Table 1 and Fig. 1), including *S. oviceps*. The pale, semiliquid strings of feces produced by *Chaetodon trifasciatus* were frequently eaten

by other fishes (Table 1 and Fig. 1), including *S. oviceps*. The numbers of feces of *C. trifasciatus* and *Z. scopas* eaten by coprophages were not significantly different. When *Z. scopas* and *C. trifasciatus* were swimming above the substrate, coprophages often followed them and approached their vent regions even before they defecated. None of the pale, pelletoid or highly fragmentary feces produced by *S. oviceps* were eaten by other fishes (Table 1 and Fig. 1).

No instances were observed of fishes eating the feces of conspecifics (Robertson, in press). The only coprophagic interactions that occurred between the study species were those described above. Intraspecific coprophagy did occur in other species, although it was extremely rare (Robertson, in press).

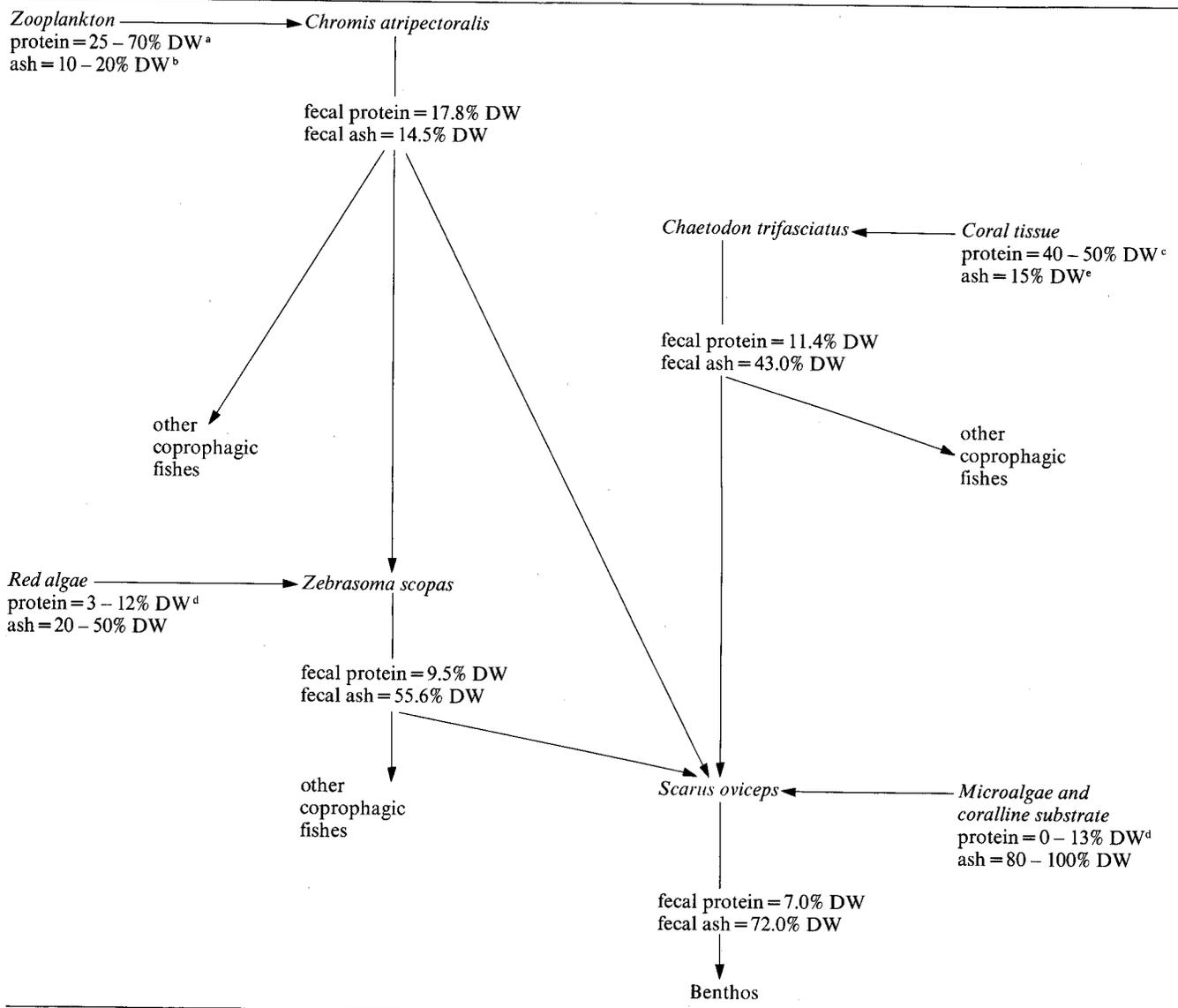


Fig. 1. Hierarchical representation of coprophagic interactions among four species of coral reef fish. Levels of protein and ash are given as indicators of the differences in potential nutritional value of feces and non-fecal food of each species. Footnotes:

- (a) Gerber and Gerber (1979) protein = nitrogen \times 6.25
- (b) Childress and Nygaard (1974)
- (c) Szmant-Froelich and Pilson (1980)
- (d) Montgomery and Gerking (1980)
- (e) R. L. Trench, personal communication

Table 1. Degree to which the feces of each species were consumed by coprophagous fishes: percentage of all observed freshly egested feces consumed by coprophages before the feces reached the bottom

Species	Percentage of feces eaten by coprophages	Number of feces
<i>Chromis atripectoralis</i>	92.4	487
<i>Chaetodon trifasciatus</i>	85.3	75
<i>Zebrasoma scopas</i>	80.8	99
<i>Scarus oviceps</i>	0	180

Chemical Composition of Feces

The levels of fecal ash ranged from 72.0% dry weight for *Scarus oviceps* to 14.5% dry weight for *Chromis atripectoralis* (Table 2). Each of the four species differed significantly from each of the others (Mann-Whitney U-test, $P < 0.01$). The level of ash in the feces of the 4 species was negatively correlated ($r = -0.780$; Snedecor and Cochran, 1967) with the degree to which the feces were consumed by coprophagous fishes (Table 1).

The level of calcium corresponded closely to the level of ash of the feces of each species, ranging from a low of 0.11% dry weight for *Chromis atripectoralis* to a high of 7.45% dry weight for *Scarus oviceps* (Table 2). Each species differed significantly from each of the other species (Mann-Whitney U-test, $P < 0.01$ for each pair of species except *Chaetodon trifasciatus* and *Zebrasoma scopas*, where $P < 0.05$). There was a strong negative correlation ($r = -0.909$) between the level of calcium in the feces and the percentage of the feces consumed by coprophagous fishes.

The level of protein ranged from 7.0% dry weight for *Scarus oviceps* to 17.8% dry weight for *Chromis atripectoralis* (Table 2). The values for *Zebrasoma scopas* and *Chaetodon trifasciatus* were not significantly different (Mann-Whitney U-test, $P > 0.05$). The value for *Z. scopas* was significantly different from that of *S. oviceps* ($0.01 < P < 0.05$) and from *C. atripectoralis* ($P < 0.01$). The value for *C. trifasciatus* was significantly different from those of *C. atripectoralis* and *S. oviceps* ($P < 0.01$). The value for *C. atripectoralis* differed significantly from those of the other three species ($P < 0.01$). The level of protein in the feces was positively correlated ($r = 0.719$) with the degree to which the feces were eaten by coprophagous fishes.

The level of carbohydrate ranged from 3.5% dry weight for *Scarus oviceps* to 15.2% dry weight for *Zebrasoma scopas* (Table 2). The value for *Z. scopas* was significantly higher than those of the other three species (Mann-Whitney U-test, $P < 0.01$). None of the other species differed significantly from one another ($P > 0.05$). There was a weak positive correlation ($r = 0.313$) between the level of carbohydrate and the percentage of feces consumed by coprophagous fishes.

The level of lipid ranged from 2.6% dry weight for *Scarus oviceps* to 33.3% dry weight for *Chromis atripectoralis* (Table 2). The value for *C. atripectoralis* was significantly higher than those of the other three species (Mann-Whitney U-test, $P < 0.01$). The value for *Chaetodon trifasciatus* was significantly higher than those of both *Zebrasoma scopas* and *S. oviceps* ($P < 0.01$). The value for *Z. scopas* was significantly higher than that of *S. oviceps* ($P < 0.05$). The level of lipid in the feces was positively correlated ($r = 0.495$) with the degree to which the feces were eaten by coprophagous fishes.

The caloric level of feces of *Chromis atripectoralis* was over 3 times that of both *Zebrasoma scopas* and *Chaetodon trifasciatus*, and almost 6 times that of *Scarus oviceps* (Table 2). There was a positive correlation ($r = 0.583$) between the estimated caloric content and the percentage of the feces consumed by coprophagous fishes.

Sums of the measured chemical constituents of the fecal samples ranged from only 65.5% dry weight for *Chaetodon trifasciatus* to 85.1% dry weight for *Scarus oviceps* (Table 2), probably resulting from several factors. First, the Lowry method probably underestimated the protein level because it measures primarily tryptophan and tyrosine. Fish feces probably contain a significant proportion of digested protein (i.e. amino acids, dipeptides, etc.) which would not be detected. Second, high-temperature ashing underestimates the ash level because some inorganic material is lost, a particular problem when samples contain large amounts of carbonate. Finally, chitin, which was not measured, ranges from 13.2 to 28.7% dry weight of the feces of midwater oceanic fishes that prey on crustaceans (Robison and Bailey, unpublished data).

Discussion

Many factors can determine the nutritional value of ingested food. Among these are the chemical composition

Table 2. Chemical composition (% dry weight) and estimated caloric content (Kcal g⁻¹ dry weight) of rectal contents of four species of coral reef fish. Numbers in parentheses are standard errors of the mean; *n* equals the number of specimens sampled

Species	<i>n</i>	Caloric content	Protein	Lipid	Carbohydrate	Ash	Calcium
<i>Chromis atripectoralis</i>	14	3.5	17.8 (1.2)	33.3 (3.2)	3.7 (0.3)	14.5 (1.8)	0.11 (0.02)
<i>Chaetodon trifasciatus</i>	14	1.1	11.4 (0.6)	6.0 (0.7)	5.1 (0.6)	43.0 (2.2)	2.81 (0.25)
<i>Zebrasoma scopas</i>	14	1.1	9.5 (0.7)	3.8 (0.3)	15.2 (1.8)	55.6 (2.3)	3.80 (0.24)
<i>Scarus oviceps</i>	14	0.6	7.0 (0.7)	2.6 (0.3)	3.5 (0.2)	72.0 (2.2)	7.45 (0.50)

of the food, the specific nutritional requirements of the consumer, and factors which affect digestion and absorption. We assume that the relative levels of organic material in feces are indicative of their nutritive value. The significance of the various levels of lipid, carbohydrate and protein in determining the nutritional value of feces as food remains to be determined.

Various aspects of the natural history and behavior of both defecators and coprophages may interact and affect the chances that feces will be eaten. Selection based on such factors as fecal size, morphology, sinking rate, abundance, availability, and nutritional value may be important in determining the degree to which a species' fecal material is eaten by coprophages (Robertson, in press). Correlations between levels of chemical constituents of feces and the degree to which they are eaten probably reflect their general nutritional value as well as the relative importance of specific nutritional components.

Fishes in general have protein requirements higher than other vertebrates (Love, 1970) and they require a variety of amino acids (Phillips, 1969; Cowey and Sargent, 1979). The positive correlation between protein level and the degree to which feces are eaten is probably the best indicator of the overall nutritional value of feces according to the data presented here.

The positive correlation of lipid level with the percentage of feces eaten may also reflect their relative nutritional value. Fishes require lipids as a source of metabolic energy and for maintenance of cellular membranes (Cowey and Sargent, 1979).

Fishes, in general, digest and utilize protein and lipid more efficiently than carbohydrate (Brett and Groves, 1979; Montgomery and Gerking, 1980). They can assimilate animal protein and lipid more efficiently than plant protein and lipid (Kapoor *et al.*, 1975; Brett and Groves, 1979; Montgomery and Gerking, 1980). If the categorical composition of feces is a reasonable indicator of their food quality, then carnivore feces have a greater food value than do herbivore and corallivore feces. The greater percentage of *Chromis atripectoralis* feces eaten by coprophages may reflect the greater nutritional value of zooplanktivore feces. The lack of correlation of carbohydrate level with degree to which feces are eaten probably reflects the low digestibility of carbohydrate relative to protein and lipid (Brett and Groves, 1979; Montgomery and Gerking, 1980).

The strong negative correlations of ash and calcium levels with fecal consumption could indicate either selection by coprophages against high levels of inorganic material or simply the low caloric levels usually concomitant with high levels of ash and calcium.

There was a positive correlation between the percentage of a species' fecal material eaten by coprophagous fishes and the caloric value of those feces. *Chromis atripectoralis* feces ranked highest both in terms of percentage eaten by other species and in terms of caloric level. The feces of *Scarus oviceps* ranked lowest in both regards.

The feces of *Zebrasoma scopas* and *Chaetodon trifasciatus* were similar in both caloric level and in the percentages consumed by coprophages. The feces of *Z. scopas* contained almost 3 times as much carbohydrate as those of *C. trifasciatus*. If we assume that carbohydrate has less nutritional value (because of its low digestibility) than either protein or lipid then, although the feces of *Z. scopas* and *C. trifasciatus* have similar caloric levels, the feces of *Z. scopas* may in fact have a lower actual food value than those of *C. trifasciatus*.

Montgomery and Gerking (1980) obtained the following range of values for chemical composition and energy content of 14 species of fleshy marine algae (reds, greens, and browns), some of which are commonly eaten by herbivorous fishes: protein, 7.7–10.2% dry weight (% DW); lipid, 2.1–4.8% DW; carbohydrate, 51.9–59.9% DW; caloric content, 2.49–3.30 Kcal g⁻¹ dry weight. Menzel (1960) obtained somewhat lower caloric, protein and lipid values for two green algae. Assuming that carbohydrate has less nutritional value than either protein or lipid, then it is clear that the nutrient and energy content of algae is less than the feces of *Chromis atripectoralis* and *Chaetodon trifasciatus*. Thus, there is a potential nutritional advantage for herbivores like *Zebrasoma scopas* and *Scarus oviceps* to ingest the feces of *C. atripectoralis* and *C. trifasciatus*.

The feces of *Chaetodon trifasciatus* are eaten by both herbivores and detritivores whose diets normally include large amounts of ash. Those coprophages, along with herbivores that have low-ash diets consisting primarily of brown macroalgae, ingest the feces of *Zebrasoma scopas*. Because of the relatively high levels of ash in algae and detritus, the potential food value of the normal diets of these coprophages is probably less than that of either *C. trifasciatus* or *Z. scopas* feces. Montgomery and Gerking (1980) suggest that herbivorous fishes generally prefer red and green algae to brown algae because the latter generally contain the highest concentrations of undigestible (i.e. structural) types of carbohydrates. Thus, although brown algae are rich in calories (Montgomery and Gerking, 1980), much of this caloric content may be unavailable to consumers.

There would appear to be no nutritional advantage for any of the study species to consume the feces of *Scarus oviceps* due to their low caloric value and very high ash level.

The correlation between the potential nutritional value of feces and the degree to which those feces are eaten, in combination with our data on coprophagic interactions, support our two hypotheses. The feces of species at different trophic levels are qualitatively different. The fecal material most commonly eaten has the highest potential food value (in calories). Feces consumed by coprophagous fishes have food values at least equal to the foods that constitute their 'normal' diet. The non-reciprocal nature of coprophagic interactions also reflects these differences. These differences in turn probably reflect differences in the food value of non-fecal material eaten by each species, i.e. zooplankton has a higher food value than plant material

and coral tissue, and coral tissue and low-ash-content plant material have higher food values than high-ash-content plant material.

Consumption of feces may be influenced by factors additional to our gross nutritional approximations. For example, microorganism-produced nutrients and vitamins, trace minerals, or specific nutrients not digested by the first fish may be significant in determining the overall nutritional value of feces to coprophages. These factors have not yet been assessed.

The relative contribution of feces to the total nutrition of coprophagous fishes also remains to be determined. Robertson (in press) found that 2 herbivorous fishes which commonly ate zooplanktivore feces consumed 3–5% and 20–25% of their own weight in feces over several hours. The variability in the relative contribution of feces to the total nutrition of coprophagic fishes is probably a function of many factors, including the relative availability of both feces and non-fecal food items. In many instances coprophagy is evidently fortuitous (Robertson, in press).

The observations of extensive coprophagic interactions among coral reef fishes, along with the knowledge that the feces of some of the more abundant species contain significant amounts of organic matter, clearly indicate the importance of coprophagy in the energetics of coral reef ecosystems in general and of coprophagy in the energetics of coral reef fishes in particular.

Acknowledgements. This research was supported financially by a Fluid Research Award from the Smithsonian Institution (to D. R. Robertson); by the Micronesian Mariculture Demonstration Center, Koror, Palau; by NSF grant OCE78-09018 (to B. H. Robison); and by the University of California Research Expeditions Program (UREP). S. Foster assisted with the collection of data on coprophagy. P. McGuire and R. L. Petty assisted with the chemical analyses. We thank B. H. Robison for his criticism of the manuscript.

Literature Cited

- Allen, G. G.: Damselfishes of the South Seas, 240 pp. Neptune City, New Jersey: T. F. H. 1975
- Bligh, E. G. and W. J. Dyer: A rapid method of total lipid extraction. *Can. J. Biochem. Physiol.* 37, 911–917 (1959)
- Brett, J. R. and T. D. D. Groves: Physiological energetics. *In: Fish physiology*, Vol. 8, pp 279–352. Ed. by W. S. Hoar, D. J. Randall and J. R. Brett. New York: Academic Press 1979
- Childress, J. J. and M. Nygaard: Chemical composition and buoyancy of midwater crustaceans as function of depth of occurrence off southern California. *Mar. Biol.* 27, 225–238 (1974)
- Cowey, C. B. and J. R. Sargent: Nutrition. *In: Fish physiology*, Vol. 8, pp 1–69. Ed. by W. S. Hoar, D. J. Randall and J. R. Brett. New York: Academic Press 1979
- Dubois, M., K. A. Gilles, J. K. Hamilton, P. A. Rebers and F. Smith: Colorimetric method for determination of sugars and related substances. *Analyt. Chem.* 28, 350–356 (1956)
- Fange, R. and D. Grove: Digestion. *In: Fish physiology*, Vol. 8, pp 162–260. Ed. by W. S. Hoar, D. J. Randall and J. R. Brett. New York: Academic Press 1979
- Frankenberg, D. and K. L. Smith Jr.: Coprophagy in marine animals. *Limnol. Oceanogr.* 12, 443–450 (1967)
- Frankenberg, D., S. L. Coles and R. E. Johannes: The potential trophic significance of *Callinassa major* fecal pellets. *Limnol. Oceanogr.* 12, 113–120 (1967)
- Gerber, R. P. and M. B. Gerber: Ingestion of natural particulate organic matter and subsequent assimilation, respiration and growth by tropical lagoon zooplankton. *Mar. Biol.* 52, 33–43 (1979)
- Johannes, R. E. and M. Satomi: Composition and nutritive value of fecal pellets of a marine crustacean. *Limnol. Oceanogr.* 11, 191–197 (1966)
- Kapoor, B. G., J. Smit and I. A. Verighina: The alimentary canal and digestion in teleosts. *Adv. mar. Biol.* 13, 109–239 (1975)
- Love, R. M.: The chemical biology of fishes, 547 pp. New York: Academic Press 1970
- Marsh, J. B. and D. B. Weinstein: Simple charring method for determination of lipids. *J. Lipid Res.* 7, 574–576 (1966)
- McCloskey, L. R. and R. H. Chester: Effects of man-made pollution on the dynamics of coral reefs. *In: Scientists-in-the-sea*, pp VI-229–VI-238. Ed. by J. W. Miller, J. G. Van Der-Walker and R. A. Waller. Washington D.C.: US Dept. Interior 1971
- Menzel, D. W.: Utilization of algae for growth by the Angelfish, *Holacanthus bermudensis*. *J. Con., Cons. int. Explor. Mer* 24, 308–313 (1960)
- Merchant, D. J., R. H. Kahn and W. H. Murphy Jr: Handbook of cell and organ culture, 269 pp. Minneapolis, Minn.: Burgess Publ. 1964
- Montgomery, W. L. and S. D. Gerking: Marine macroalgae as foods for fishes: an evaluation of potential food quality. *Env. Biol. Fish.* 5, 143–153 (1980)
- Phillips, A. M., Jr.: Nutrition, digestion, and energy utilization. *In: Fish physiology*, Vol. 1, pp 391–432. Ed. by W. S. Hoar and D. J. Randall. New York: Academic Press 1969
- Reese, E. S.: A comparative field study of the social behavior and related ecology of reef fishes of the family Chaetodontidae. *Z. Tierpsychol.* 37, 37–61 (1975)
- Robertson, D. R.: Fish feces as food on a Pacific coral reef. *Mar. Ecol. Prog. Ser.* (In press)
- Robison, B. H. and T. G. Bailey: Sinking rates and dissolution of midwater fish fecal matter. *Mar. Biol.* (In press)
- Snedecor, G. W. and W. G. Cochran: Statistical methods, 593 pp. Ames, Iowa: Iowa State University Press 1967
- Szmant-Froelich, A. and M. E. Q. Pilson: The effects of feeding frequency and symbiosis with zooxanthellae on the biochemical composition of *Astrangia danae* Milne Edwards and Haime 1849. *J. exp. mar. Biol. Ecol.* 48, 85–97 (1980)

Date of final manuscript acceptance: March 7, 1982.
Communicated by J. M. Lawrence, Tampa