

# Fish fecal pellets are a source of minerals for inshore reef communities\*

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**ABSTRACT:** Fecal pellets of temperate and tropical reef fishes of the genus *Chromis* contained high concentrations of minerals, many of which are considered 'essential' for organismic growth. The concentrations of most elements were substantially higher in the feces than in undigested food recovered from the stomach. Large numbers of feces-associated bacteria, apparently derived from the gut microbial population, may have contributed to the high phosphorus levels in fresh feces. Phosphorus flux to inshore reefs via defecation of fecal pellets by the blacksmith *C. punctipinnus* in nocturnal shelters was comparable to estimates of phosphorus transport through surface waters by sinking zooplankton feces. Resistance of fecal pellets to degradation during long-term *in situ* incubation in nocturnal shelters suggests that bacteria do not play a significant role in controlling accumulation of fish feces on the reef.

## INTRODUCTION

Understanding of the pathways of elemental transfer in the marine environment is one of the basic goals of oceanographic research. The role of particulate matter in the movement of nutrient and trace elements from surface to deep water or bottom sediments has been demonstrated in a number of instances (Menzel and Goering, 1966; Bishop et al., 1977; Lal, 1977). Sinking fecal pellets of zooplankton have been shown to be an important vehicle for transporting a variety of elements through the water column (Small and Fowler, 1973; Fowler, 1977; Urrere and Knauer, 1981). Very little information exists, however, on the contribution of fish feces to element cycling.

Recently, Robison and Bailey (1981) presented evidence indicating that midwater fish fecal matter represent a major source of organic transfer between pelagic and benthic communities. From excretion studies, Bray et al. (1981) estimated that blacksmith *Chromis punctipinnis* imported approximately 8 g of carbon<sup>-1</sup>

m<sup>-2</sup> d<sup>-1</sup> to nocturnal shelters on rocky reefs off southern California. Although fecal pellets were found on the bottom of the shelters, they did not accumulate with time.

Reef fishes have been shown to feed on each other's feces (Robertson, 1982). Demersal zooplankton that emerge from sandy substrates at night may also feed on fish feces deposited in reef crevices (Hamner, 1981). Most nutritional studies of feces as a food source for marine organisms, however, have focused on their carbon and nitrogen content and, in some instances, on their protein, carbohydrate, and lipid composition (Johannes and Satomi, 1966; Robison and Bailey, 1981; Madin, 1982). In addition to the 'bulk' elements, there are likely to be significant levels of other essential elements in fish fecal material. Micronutrients such as phosphorus and silicon and numerous nanonutrients such as copper, iron, manganese, zinc, nickel, and chromium may also be important in establishing the suitability of feces as a food source for detritivores. To our knowledge, there is no information on the levels of micronutrients or nanonutrients in feces excreted by marine teleosts in the marine environment.

This paper presents concentration data for a variety of elements (many of which are required for growth) recovered from the feces of important reef fish of the genus *Chromis*. Species of *Chromis* were chosen for

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this study because their documented behavior of feces excretion in nocturnal shelters facilitates the estimation of allocthonous nutrient transport to inshore reefs.

## MATERIALS AND METHODS

### Feces collection and processing

Blacksmith *Chromis punctipinnis* were obtained from nocturnal shelters along the rocky bottom (10 m depth) off Santa Catalina Island, USA, 35 km southwest of Los Angeles during July 1981. Brown chromis *Chromis multilineatus* were collected at the head of the Salt River Submarine Canyon off St. Croix, US Virgin Islands, at a depth of approximately 15 m. All fish were collected at dusk by SCUBA with the aid of the anesthetic quinaldine and immediately placed in 20 l plastic buckets with lids that were fitted with 1 mm netting to allow water exchange. Each bucket contained a 1 cm plastic grid suspended approximately 10 cm off the bottom. This feature minimized disruption of the feces once they sank to the bottom. The buckets, which contained from 1 to 10 fish, were anchored at the collection site. At dawn the following morning (7 to 8 h after collection) the fish were released and the buckets containing fecal pellets excreted by the fish during the night were brought to the surface. The intact pellets were transferred to GF/C filters with clean Teflon-coated forceps and either dried to constant weight at 60 °C or transferred to diffusion chambers and placed on the bottom in nocturnal shelters.

Diffusion chambers were used to determine whether the elemental composition of the fecal pellets was affected by exposure to seawater or microorganisms. The diffusion chambers were similar to those described by Fliermans and Gordon (1977), consisting of 45 mm diameter Plexiglas cylinders enclosed at each end by polycarbonate membranes (0.2 µm pore size, Nuclepore Corp.) with 2 sampling ports sealed with neoprene septa on the side. Feces (3 to 4 g wet weight) placed inside the chambers containing filter-sterilized seawater were thus protected from physical disturbances while incubating on the sea floor but still exposed to seawater in constant exchange with the external environment. Free exchange of dissolved substances across the membranes was demonstrated by loading separate chambers with ammonium chloride and Blue Dextran (MW,  $2 \times 10^6$  daltons), placing them in nocturnal shelters, and following the diffusion of these substances out of the vessels. Ammonia concentration was determined with Nessler's reagent (American Public Health Association, 1971). Blue Dextran concentration was determined by absorption at 620 nm

using a spectrophotometer. The time required for each of these substances to achieve one-half ( $t_{1/2}$ ) their initial concentration in the chambers was 3.5 h and 140 h, respectively.

Chambers containing the feces were retrieved at intervals and the particulate material transferred to GF/C filters and dried to constant weight at 60 °C. Fecal particles were pulverized in an acid-washed glass tissue homogenizer and the powder stored in new polyethylene vials in a desiccator for subsequent analysis.

Stomach contents were obtained from fish captured at dusk. The undigested food was collected by dissection and excision of the stomach wall with a sterile scalpel blade. The material was squeezed through the excision onto a GF/C filter, dried, pulverized, and stored as described above.

### Elemental analysis

Multielement analysis of the feces and stomach contents was carried out by optical emission spectrometry using the analytical scheme of Alexander and McAnulty (1981). Briefly, 3 to 7 mg of pulverized solid was quantitatively weighed into a graphite electrode. The sample was then volatilized and excited in a DC arc and the resulting light, which contained the spectral lines of the various elements present, was separated into its components by a diffraction grating spectrometer. The intensity of each component wavelength was measured quantitatively by a separate photomultiplier. The net signal was obtained by subtracting various background components from the total signal. Interference from signals of atomic lines of other elements in the sample was corrected for by analyzing standards of the interfering element. An on-line computer was employed for the calculations, providing a concentration value for each of 26 to 29 elements included in the polychrometer array. When background and interferences were determined, the sensitivity was limited to 0.1 to 1.0 µg g<sup>-1</sup> for most elements. For zinc and phosphorus, the limit was 3 to 5 and 50 to 80 µg g<sup>-1</sup>, respectively (Alexander and McAnulty, 1981).

### Bacterial enumeration

To estimate bacterial densities, samples of fecal pellets were transferred directly from the buckets at the surface to a sterile, tared aluminum weighing dish and the wet weight determined after removal of excess water with sterile pasteur pipettes. The contents of the dish were aseptically homogenized with 5 ml of filter-sterilized seawater in a micro-container (Eberback

Corp.). The homogenate was serially diluted in filtered seawater and 0.5 ml of a 100  $\mu\text{g ml}^{-1}$  filter-sterilized aqueous solution of 4'6-diamidino-2-phenylindole (DAPI) was added to each dilution to stain the bacteria. After 5 min, 0.5 ml of a 50 % glutaraldehyde solution was added to preserve the stained cells. Two-ml volumes of the appropriate dilution were aseptically filtered through a 0.2  $\mu\text{m}$  polycarbonate membrane and the trapped bacteria on the surface of the membrane enumerated by epifluorescence microscopy using a filter combination (Zeiss 48-77-02) optimized for DAPI fluorescence. Bacterial densities were estimated from counts made on 20 randomly chosen microscope fields delineated by an eyepiece gradicule. Dilutions were selected which produced 10 to 100 bacteria field $^{-1}$ . Bacterial densities were expressed on a dry weight basis after independent determinations of the dry weight : wet weight ratio ( $0.15 \pm 0.05$ ,  $n = 17$ ) were made on the fecal pellets.

Intestinal contents, extruded through the anus by applying hand pressure to the sides of the captured fish, were processed in the same manner as the fecal pellets for bacterial density determinations.

## RESULTS

### Nanominerals

Nanomineral concentrations in fresh blacksmith feces recovered from buckets containing captive fish ranged from 16  $\mu\text{g g}^{-1}$  dry weight for Cu to 7,170  $\mu\text{g g}^{-1}$  dry weight for Fe (Table 1). The concentrations of all elements tested were higher in fecal material than in undigested food removed from the gut (Table 1). In the case of Pb, over 2,000 times greater concentrations were found in fresh fecal pellets than in gut material. Iron was also highly concentrated in the feces. The lowest concentration ratios were exhibited by Zn, Cu, and Sr.

Fresh feces obtained from brown chromis in tropical waters contained lower concentrations of Cr, Fe, Mn, Si and Pb but higher concentrations of Cu, Zn and Sr than fresh blacksmith feces collected in temperate waters off southern California (Table 1). Lead and Fe were noticeably less concentrated in brown chromis fecal pellets. The large standard deviation in Pb concentration values, however, indicates possible contamination or a highly heterogeneous distribution of the metal in the feces.

In view of the rapid change in elemental concentrations of undigested food during passage from the gut of the fish into the surrounding seawater as feces, a study was conducted to evaluate the extent to which elements were adsorbed by the pellets from the seawater.

Table 1. Trace element concentrations in feces of reef fishes of the genus *Chromis*

Sample	# of samples	Element									
		Cr	Cu	Fe	Mn ( $\mu\text{g g}^{-1}$ dry weight*)	Ni ( $\mu\text{g g}^{-1}$ dry weight*)	Pb	Zn	Sr	P ( $\text{mg g}^{-1}$ dry weight*)	Si
Blacksmith stomach	2	< 1	13 $\pm$ 2	130 $\pm$ 18	2.8 $\pm$ .4	1.0 $\pm$ .3	< 1	27 $\pm$ 3	293 $\pm$ 73	5.3 $\pm$ 0.1	1.4 $\pm$ 0.1
Blacksmith fresh feces	2	42 $\pm$ .7	16 $\pm$ .1	7,170 $\pm$ 1,316	92 $\pm$ 7	24 $\pm$ 4	2,039 $\pm$ 398	78 $\pm$ 12	514 $\pm$ 57	15 $\pm$ 1.9	13 $\pm$ 5.3
Blacksmith 10 d feces	3	35 $\pm$ 4	38 $\pm$ 4	2,652 $\pm$ 496	26 $\pm$ 9	25 $\pm$ 4	700 $\pm$ 167	113 $\pm$ 22	258 $\pm$ 14	6.4 $\pm$ 2.6	9.1 $\pm$ 1.1
Blacksmith 29 d feces	2	80 $\pm$ 18	78 $\pm$ 7	6,856 $\pm$ 2,285	114 $\pm$ 13	37 $\pm$ 13	607 $\pm$ 102	389 $\pm$ 175	240 $\pm$ 75	11 $\pm$ 3.4	21 $\pm$ 3.1
Blacksmith 62 d feces	3	146 $\pm$ 36	76 $\pm$ 26	11,914 $\pm$ 3,940	222 $\pm$ 77	53 $\pm$ 13	930 $\pm$ 189	703 $\pm$ 320	272 $\pm$ 64	15 $\pm$ 5.2	35 $\pm$ 5.0
Blacksmith 130 d feces	2	240 $\pm$ 47	53 $\pm$ 6	15,650 $\pm$ 1,344	337 $\pm$ 96	65 $\pm$ 18	1,778 $\pm$ 1,051	139 $\pm$ 30	-	16 $\pm$ 1.0	59 $\pm$ 12
Brown chromis fresh feces	5	16 $\pm$ 9	36 $\pm$ 14	1,320 $\pm$ 594	47 $\pm$ 21	22 $\pm$ 5	327 $\pm$ 282	122 $\pm$ 39	688 $\pm$ 211	17 $\pm$ 6.6	4.9 $\pm$ 3.6

\* Values are expressed as  $\pm$  1 SD

An increase in concentration of most trace elements was observed with time when fresh blacksmith feces were incubated in dialysis chambers that had been placed in the nocturnal shelters of the fish. Chromium levels increased approximately 6-fold over a 130 d period (Table 1). The possibility of contamination of the feces by elemental leaching from the Plexiglas chamber was minimized by the constant exchange of water across the membrane. In fact, several of the elements (Fe, Mn, Pb, and Sr) exhibited a substantial decrease in concentration during the first 10 d of feces incubation. Adsorption of elements from the surrounding seawater, therefore, did not appear to be sufficient to account for the concentration differences observed between stomach contents and fresh fecal pellets.

### Microminerals

Phosphorus and silicon were present in similar concentrations in fresh blacksmith feces, contributing from 10 to 15 mg g<sup>-1</sup> dry weight (Table 1). As in the case of nanominerals, undigested food removed from the guts of fish contained considerably lower concentrations of P and Si than fresh fecal pellets. The P concentrations in freshly collected brown chromis feces were comparable to that of blacksmith. Silicon concentrations were slightly lower in feces of brown chromis than blacksmith.

Incubation of the blacksmith feces in dialysis chambers maintained in nocturnal shelters for up to 130 d resulted in little change in fecal P concentrations. However, fecal Si concentrations increased 4.5-fold during this period.

Table 2. *Chromis* spp. Bacterial densities associated with gut contents and fecal pellets

Sample	# of samples	Cells g <sup>-1</sup> dry weight*
Blacksmith intestinal contents	2	3.5 ± .14 × 10 <sup>10</sup>
Fresh blacksmith feces	4	5.6 ± 3.5 × 10 <sup>10</sup>
Blacksmith feces after 9 d in chambers	2	6.3 ± 1.2 × 10 <sup>10</sup>
Blacksmith feces after 30 d in chambers	2	6.7 ± .64 × 10 <sup>10</sup>
Brown chromis intestinal contents	2	8.6 ± .64 × 10 <sup>10</sup>
Fresh brown chromis feces	4	6.2 ± 3.5 × 10 <sup>10</sup>
Brown chromis feces after 5 d in chambers	3	1.8 ± .57 × 10 <sup>10</sup>

\* Values are expressed as ± 1 SD

### Bacteria

Undigested food in the intestines of blacksmith and brown chromis contained very high densities of bacteria, ranging from 3.5 × 10<sup>10</sup> to 8.6 × 10<sup>10</sup> cells g<sup>-1</sup> dry weight, respectively (Table 2). Fresh *Chromis* fecal pellets contained bacterial densities similar to intestinal material. Blacksmith feces, incubated in shelters but protected in the chamber from the foraging activities of reef organisms, exhibited bacterial densities similar to fresh fecal pellets. In spite of the high bacterial densities, visual inspection indicated no noticeable physical change in fecal pellet consistency over 130 d of incubation. Bacterial density in fecal pellets of brown chromis decreased during 5 d incubation in the tropical waters off St. Croix (Table 2). The reason for the observed decrease is at present not known.

### DISCUSSION

*Chromis* fecal pellets contained an abundance of minerals, many of which are considered 'essential' for growth of living organisms (Mertz, 1981). The mineral concentrations in fresh blacksmith feces collected *in situ* were generally different from the levels found in feces of marine invertebrates. Fowler (1977) found higher concentrations of Cu, Fe, Mn, and Zn but lower concentrations of Pb and Sr in the feces of freshly caught euphausiids (*Meganyctiphanes norvegica*) than we detected in *Chromis* fecal pellets. The feces of algal-fed crabs (*Pugettia producta*), maintained under laboratory conditions, contained lower concentrations of Cr, Fe, Pb, and Zn than *Chromis* feces (Booth and Knauer, 1972).

The enrichment of minerals in *Chromis* feces relative to gut contents suggests that mineral requirements are easily satisfied by the fish diets. This is consistent with studies on marine invertebrates (Booth and Knauer, 1972; Fowler, 1977) and indicates that like primary consumers, secondary consumers assimilate only a small portion of the total mineral content of their food. Alternatively, feces may be a more important route of disposal for some elements than for others. For instance, the higher concentrations of Fe in feces than in the food, gut contents, or body parts of organisms (Booth and Knauer, 1972; Fowler, 1977) could be due to specific elimination of Fe-containing bile pigments through the intestine. Further characterization of the concentration and flux of Fe and other elements that are concentrated in the feces of these fish should provide a better understanding of the mechanisms involved.

The concentrations of Cu, Fe, Mn, Ni, Pb, Zn, and Sr in stomach contents of the fish were very similar to the

levels of these elements reported in zooplankton collected in Monterey Bay, California (Martin and Knauer, 1973). Since the latter are consumed by blacksmith (Hobson and Chess, 1976; Bray, 1981), trace element composition of the gut contents may be useful in food source identification.

Phosphorus levels in the fresh fish feces were similar to those found in feces of the omnivorous marine crustacean *Palaemonetes pugio* (Johannes and Satomi, 1966). The significance of the P levels observed in the feces is more apparent when expressed in terms of carbon and nitrogen. Previous analysis of samples of fresh blacksmith feces collected from the fish at the same time and place as the samples reported here indicated an organic carbon content of 12.7 % and a C:N g atom ratio of 8:1 (Bray et al., 1981). On the basis of the P concentration obtained for fresh blacksmith feces (Table 1), the C:N:P ratio is 22:2.8:1. This is much lower than that characteristic of living plankton (106:16:1) and indicates that the feces are enriched approximately 5-fold in P relative to the food of the fish which consists of drift zooplankton. Fecal pellets of gelatinous zooplankton exhibit a C:N:P ratio of 118–138:18.9–25:1 (Bruland and Silver, 1981) and ratios of suspended particles in upwelling areas have been reported to be 180:18:1 (Knauer et al., 1979). Others, however, have obtained ratios as low as 40:8:1 for particles in Antarctic waters where there is an abundance of P in the seston (Copin-Montegut and Copin-Montegut, 1978).

The P enrichment in blacksmith feces relative to zooplankton suggests that selective absorption of C- and N-containing compounds may occur during food digestion by these fish. Alternatively, feces may be a more important route for P elimination than for that of C and N.

The C:P ratio in bacteria can be as low as 30:1 (Atlas and Bartha, 1981). Our detection of very high densities of bacteria in fresh blacksmith and brown chromis fecal pellets is consistent with previous bacteriological data on gut and fecal flora of these fish (Ruby and Morin, 1979). The low C:P ratio exhibited by fresh *Chromis* feces may therefore have been at least in part due to the large numbers of bacteria present.

The data suggest that fresh blacksmith feces also serve as a rich source of Si. Using the previously determined carbon content indicated above, the feces exhibited a Si:C ratio of 0.043. This value is higher than the average ratio (0.016) obtained by Copin-Montegut and Copin-Montegut (1978) and Lisitzin et al. (1966) for particles obtained from regions of the Indian Ocean. Diatom and silicoflagellate remains, detected during microscopic examination of the fish feces, may have contributed to the silicon concentrations obtained in the pellets. Quartz, which has been shown to be a

Table 3. Comparison of elemental deposition rates on inshore reefs by blacksmith fecal pellets with elemental flux in water column via zooplankton feces

Element	Blacksmith <sup>a</sup>	Flux ( $\mu\text{g m}^{-2} \text{d}^{-1}$ )	
		Zooplankton <sup>b</sup> offshore <sup>c</sup>	nearshore <sup>d</sup>
P	2,720	–	–
Si	2,360	–	–
Fe	1,300	37,599	26,400
Pb	370	53	37
Sr	93	122	86
Mn	17	380	266
Zn	14	1,492	1,045
Cr	8	–	–
Cu	5	354	249
Ni	4	31	22

<sup>a</sup> Elemental deposition rate based on importation of 181.5 mg dry weight feces  $\text{m}^{-2} \text{d}^{-1}$  (Bray et al., 1981)

<sup>b</sup> Mineral fluxes contributed by zooplankton fecal pellets estimated from elemental concentrations of euphausiid fecal pellets ( $\mu\text{g g}^{-1}$  dry weight feces) as determined by Fowler (1977)

<sup>c</sup> Feces flux estimates calculated from total volumes (30.9  $\text{mm}^3$ ) of zooplankton fecal pellets collected 100 km off Monterey, California at 35 m depth (Urrère and Knauer, 1981)

<sup>d</sup> Feces flux estimates calculated from total pellets (120,000 specimens  $\text{m}^{-2} \text{d}^{-1}$ ) using an average pellet weight of 9.3  $\mu\text{g}$  (Dunbar and Berger, 1981). Samples collected in Santa Barbara Basin at 341 m depth

component of fecal pellets collected in sediment traps in coastal waters (Dunbar and Berger, 1981), may also have contributed to the silicon in the fish feces. It remains to be determined whether the silicon excreted in the blacksmith shelters is taken up by living cells such as benthic diatoms or incorporated into bottom deposits of the reef.

Mineral fluxes to inshore reefs via blacksmith fecal pellets were estimated from previous feces importation data (Table 3). It is important to recognize that the values represent a net influx to the reef community since the fish feed in the water column during the day (Bray, 1981). Furthermore, it is unlikely that the fecal pellets are subject to resuspension by water movement since they exhibit negative buoyancy (Bray et al., 1981) and the shelters are generally located in crevices in the reef.

Evaluation of the relative significance of mineral deposition by blacksmith is difficult since there is very little information on other mineral importation processes. Some comparisons can be made, however, with mineral flux mediated by particles sinking through the water column. The 2.7 mg  $\text{P m}^{-2} \text{d}^{-1}$  imported as blacksmith feces to inshore reefs represents approximately 45 % of the total P (6 mg  $\text{P m}^{-2} \text{d}^{-1}$ ) transported

from surface waters to a depth of 50 m by sinking particulate matter in an area of coastal upwelling (Knauer et al., 1979). Trace mineral deposition as blacksmith feces was generally lower than mineral fluxes computed for fecal pellets of zooplankton from the water column in sediment traps off the California coast (Table 3). The latter must be viewed with caution, however, since it is not yet possible to eliminate the possibility of contamination during the collection of zooplankton fecal pellets. In addition, mineral content varies greatly among plankton species and within species in different geographical areas (Mayzaud and Martin, 1975).

Recent studies also suggest that the chemical composition of the blacksmith food varies to some extent on a seasonal basis (Escandon and Bray, unpubl.). However, unlike other vectors of mineral flux described to date, blacksmith fecal pellet deposition is predictable in time and space due to the daily homing and defecation pattern displayed by the fish (Bray et al., 1981).

Long term *in situ* incubation resulted in little dissolution of the fecal pellets when they were protected from scavenging organisms. These observations are consistent with the fact that although large numbers of bacteria were recovered from the feces, they exhibited very little activity based on the relatively constant cell densities and P concentrations. These results are supported by recent evidence that in nature, fecal pellet microbial populations are largely dormant (D. M. Karl, pers. comm.).

Pomeroy and Deibel (1980) found that, while bacterial densities were initially low in freshly collected feces of pelagic tunicates, a succession of microbial populations occurred with subsequent incubation under laboratory conditions which indicated the presence of active bacteria. The cohesive nature of the fish fecal pellets indicated that they were surrounded by a peritrophic membrane which may have rendered them resistant to bacterial attack. It is unlikely therefore that dissolution through microbial action controlled the accumulation of the fecal pellets in the shelters. Current studies indicate that the fate of the fish feces may be determined by the foraging activities of reef detritivores (Rothans and Miller, unpubl.).

Although reliable data on the quantities of fecal material excreted by brown chromis in tropical reef shelters is as present not available, the lower fish densities (Bray et al., unpubl.) and smaller fish size indicate that their contribution to mineral flux is less than that of their temperate water counterpart. Unlike reefs off southern California, tropical reefs contain several species of fish which feed in the water column during the day and return to nocturnal shelters at night (Hobson, 1972). Thus, fish defecation may still repre-

sent an important pathway of mineral importation to tropical reef communities despite the low contribution made by a single species.

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