

# THE POTENTIAL TROPHIC SIGNIFICANCE OF *CALLIANASSA MAJOR* FECAL PELLETS<sup>1</sup>

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## ABSTRACT

The trophic significance of the fecal pellets of *Callianassa major* was investigated by measuring 1) the rates at which fecal material was produced, 2) its organic carbon and nitrogen content, and 3) its ingestion by other animals. Our results indicate that  $456 \pm 118$  fecal pellets are produced per burrow per day and from  $175 \pm 46$  to  $2,600 \pm 670$  pellets  $m^{-2} day^{-1}$ , depending on population density, and that an entire *C. major* population occupying an area of about 200,000  $m^2$  produces about  $280 \times 10^6$  pellets/day. The carbon and nitrogen contents of the pellets were 3 and 0.3% of their dry weight. Aging the pellets had no effect on their carbon content but halved the nitrogen content in 48 hr. Ingestion experiments indicated that fecal pellets were eaten by hermit crabs, probably by blue crabs, and possibly by several other beach inhabitants.

The results were used to calculate the rate at which organic carbon is made available in fecal pellets, and this rate was compared to production rate measurements for local primary producers. The potential quantitative significance of fecal pellets as a food source is discussed.

## INTRODUCTION

Recent studies have shown that fecal pellets of some marine invertebrates contain assimilable organic matter and may be eaten by the species that produced them or by other species (Newell 1965; Johannes and Satomi 1966). The latter authors estimate that more of the organic matter ingested by marine herbivores is channeled into the production of fecal pellets than goes into the production of new herbivore tissue. Fecal pellets may, therefore, provide a quantitatively significant source of food in marine ecosystems.

The abundance of fecal material in benthic marine habitats is well known (Moore 1931; Manning and Kumpf 1959; Haven and Morales-Alamo 1966; and others), and several authors have suggested that this material plays a role in the trophic relationships of the sea (Moore 1931; Mare 1940; Conover 1964; Newell 1965; Johannes and Satomi 1966). This study was designed to evaluate the trophic role of the fecal pellets of the burrowing shrimp *Callianassa major* in a sand beach community at Sapelo

Island, Georgia. Trophic relationships in sand beaches are especially interesting because dense animal populations occur (Fox 1950; Pearce, Humm, and Wharton 1942) despite the shifting substrate which is usually inimical to effective colonization by primary producers. It has been suggested that the majority of beach animals derive their nourishment from marine detritus carried to the beach and worked into it by wave action (Hedgpeth 1957), but it seemed to us that fecal pellets might be an additional food source.

The present study was designed to investigate: 1) how much fecal material is produced; 2) its potential nutritive value; and 3) its use as food by other animals. Laboratory and field experiments were conducted during the summer and fall of 1965.

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*Natural history and observations on  
C. major*

*C. major* is a macruran decapod crus-

taccan inhabiting deep burrows along the southeastern seacoast of the United States. It ranges from Beaufort, North Carolina, to eastern Florida, and Grand Terre Island to Timbalier Island, Louisiana (Williams 1965). It is quite common, but has received little attention from ecologists, probably because of its burrowing habits and consequent inaccessibility. It ranges up to 95 mm long, (Lunz 1937) and its burrows occur in densities up to  $0.44/m^2$  in North Carolina (Pohl 1946),  $0.27$  to  $0.38/m^2$  in South Carolina (Lunz 1937) and  $16.3/m^2$  in Georgia. These burrows are usually found below the mid-tide line on sand beaches facing or close to the open ocean. Willis (1942) found that in Louisiana the burrows extend into the subtidal zone to 34 m from shore.

The burrow consists of three parts, a narrow, thin-walled upper section extending for 5 to 20 cm at right angles to the beach surface, a gradually widening and thicker-walled middle part 10 to 15 cm long, and a wide (up to 2-cm diam), thick-walled lower section extending deep into the beach. The entire burrow has an average length of 140 cm with a range from 60 to over 210 cm (Pohl 1946). The thick wall of the burrow is easily fossilized because it consists of sand particles cemented together by an amorphous brown material. The opening of the burrow onto the beach is usually small and inconspicuous.

The most obvious surface indications of *C. major* are its fecal pellets. These are dark brown cylinders about 0.75 mm diameter and about 2 mm long. On the beach at Sapelo Island, the pellets are quite uniformly  $2.1 \pm 0.3$  mm long, with a wet weight of  $2.2 \pm 1.3$  mg and a dry weight of  $1.4 \pm 0.6$  mg. The pellets are often abundant; Ellis (cited in Lunz 1937) observed areas where  $46.5 m^2$  of beach surface was covered to a depth of 0.64 cm with pellets, and many authors have commented on the characteristic ring of pellets deposited around burrow openings at low tide. The abundance of these pellets on the beach at Sapelo Island led to their selection as the material for this study.

The methods used evolved from information obtained from field observations of burrows and pellet production. Early observations indicated that only a small fraction of burrow openings actually produced fecal pellets, suggesting that each burrow had more than one opening. This was investigated by pumping air into flooded burrows and counting the nearby openings emitting air bubbles. It was indicated that two to 10 openings were connected beneath the surface. However, this conclusion could not be directly validated by digging because of the rapid caving of beach sands. Other observations indicated that fecal pellet production stopped soon after the burrow openings were exposed by a receding tide. It was also observed that the receding tide washed away most pellets, leaving only a few of the producing burrows marked with a ring of fecal pellets. It was clear that any estimate of fecal pellet production rate must include the pellets produced during both flooded and exposed portions of the tidal cycle and that extrapolation of data to areal or population production estimates must be based on the number of burrows actually producing pellets rather than on the total number of burrow openings or on the number of openings marked with fecal pellet rings.

#### MATERIALS AND METHODS

##### *Fecal pellet production rate of C. major*

The production rate of fecal pellets was estimated from the study of single producing burrows and extrapolated to areal and total population estimates.

The production rate for producing burrows was determined by combining estimates of fecal pellet production during flooded and exposed portions of the tidal cycle. The rate for the exposed portion was estimated by counting the number of pellets in rings around producing burrows, and dividing this number by the number of hours the burrows were exposed. This was feasible as our observations had shown that fecal pellet production ceased soon after a burrow opening was exposed, consequently the ring of pellets surrounding

an exposed burrow represented the total pellet production of that burrow during the entire exposed portion of the tidal cycle. The number of pellets in rings around 100 randomly selected burrows was determined at the rate of 20 burrows per day for five days. *C. major* inhabits only the lower half of the intertidal zone (Weimer and Hoyt 1964), so an average burrow is exposed only while the tide is in its lowest quarter. Local tide gage data indicate that the tide is in its lowest quarter for 32% of its cycle or 4.03 hr.

The rate of pellet production from flooded burrow openings was measured in a tide pool on the lower portion of the beach. Wave action and turbidity made it impossible to measure this rate directly while burrows were flooded at high tide. Pairs of burrows were randomly selected with one member of the pair in the tide pool, and the other on the exposed beach. After a minimum of 2 hr, the number of pellets surrounding each burrow was counted. No pellets are produced around exposed burrows soon after exposure, so we assumed that any additional pellets around the flooded burrow had been produced subsequent to cessation of production from the exposed burrow. This assumption seemed justified as the pellets were produced around both burrows during the same time period—all other pellets having been removed by wave action—and as the pellets produced around the tide pool burrows remained close to the burrow from which they were produced. The difference between the number of pellets surrounding the two burrows was divided by the number of hours between exposure and counting to estimate the hourly production rate for the flooded burrow. Seventy pairs of burrows were evaluated in this manner, and the mean hourly production rate calculated. This rate was used to estimate the number of pellets produced during the 68% of the tidal cycle that the average burrow was flooded. The estimates of the pellet production rates for the exposed and flooded portions of the tidal cycle were

added to obtain a production estimate for the entire tidal cycle.

The pellet production rate for single producing burrows was extrapolated to estimate production rates for a square meter of the *C. major* population and for the entire population. These estimates were based on a survey of the density and the total number of *C. major* burrows along 10 transects, divided by the fraction of burrows from which pellets were actually produced. Each transect ran from the low tide line to the highest point where *C. major* occurred. Quadrats, 0.1 m<sup>2</sup>, were laid out every meter along the transects, the sand excavated to 10 to 20 cm, and the number of burrows counted. The data obtained were pooled to evaluate the density of burrows along the transect, and transect data were used to calculate the number of burrows within the area one-half the distance from each transect to the neighboring transects. Totaling the data from the 10 areas gave an estimate of the number of burrows in the area. The fraction of burrows from which pellets were actually being produced was determined by observing burrow openings during falling tides. The total number of burrow openings and number of producing openings were counted within each of 100 randomly laid out 0.1 m<sup>2</sup> quadrats. The burrows from which pellets were produced were marked with stakes and their percentage of the total calculated. Later, each quadrat was reexamined to determine the number of burrow openings marked with rings of fecal pellets and the percentage of total and producing burrows so marked was calculated.

In addition to estimating the production rate of fecal pellets, their distribution on the beach was evaluated. Concentrations were observed to be of two types: rings of pellets around burrows and concentrations of pellets left by the backwash of waves. The pellets in rings around burrows were counted and their areal concentration was calculated by multiplying their number by the average density of burrows marked with the rings. The density of pellets in backwash concentrations was determined

by collecting short vertical cores with plastic tubing of known area, counting the pellets contained above the sand surface, and calculating the concentration on an areal basis. Six such collections were analyzed during August 1965.

#### *Composition of fecal pellets of C. major*

Fecal pellets were dried at 105°C and analyzed for organic carbon and nitrogen. Organic carbon was determined using a Coleman carbon-hydrogen analyzer after treating the pellets with 5% nitric acid to remove carbonates. The method entails burning the sample in a stream of oxygen at about 1,000°C. The CO<sub>2</sub> evolved is absorbed by Ascarite and the weight gain of the Ascarite is used to calculate the carbon content of the sample. Nitrogen content was determined by Law and Co., Atlanta, using the Kjeldahl method.

#### *Ingestion of C. major fecal pellets*

To determine whether *C. major* fecal pellets are consumed by other beach fauna, specimens of various beach animals and a number of *C. major* fecal pellets were isolated in a container, and any decreases in the number of pellets were observed. When there were decreases, it was determined if the pellets were being broken up or eaten. Controls consisted of similar containers containing fecal pellets but no animals. The containers were either 12.7 cm finger bowls or 20 by 25 cm rectangular Pyrex dishes, and contained 1 cm of beach sand and 2 to 4 cm of seawater. To decrease extraneous food supplies, the sand was oven-dried at 105°C for 24 hr, and the seawater was filtered. The species used included the decapods *Pagurus* sp. and *Callinectes sapidus*, the amphipods *Parahaustorius longimerus* and *Neohaustorius schmitzi*, the isopod *Chiridotia stenops*, and the pelecypod *Mulinia lateralis*. Three experiments were run on each species. The numerical ratio of fecal pellets to experimental animals was as follows: *Pagurus* sp., 4 : 1; *C. sapidus*, 7.5 : 1; *P. longimerus*, and *N. schmitzi*, 1 : 1; *C. stenops*, 3 : 2; and *M. lateralis*, 1 : 1. The number of pellets remaining in the experi-

mental containers was determined after 4, 8, 16, 20, 24, and 48 hr. The results were expressed as percentage of pellets utilized. Utilization rates of freshly collected and aged *C. major* fecal pellets were also compared. Pellets were aged in finger bowls containing natural beach sand and seawater. The experimental conditions were as described above, and *Pagurus* sp. was used as the experimental animal. Fresh and aged pellets were placed at opposite ends of a dish, and the number of each type remaining after 4, 8, 16, 20, and 24 hr was determined. Twenty-nine experiments were run comparing fresh pellets with those aged for 24 hr, and 16 comparisons were made between fresh and 48-hr-old pellets. Organic carbon and nitrogen contents of fresh and aged feces were also compared.

## RESULTS

#### *Fecal pellet production rate*

The fecal pellet production rate for the exposed portion of the tidal cycle was  $23 \pm 1.9$  pellets burrow<sup>-1</sup> hr<sup>-1</sup>. The number of pellets in the rings around exposed burrows varied in response to weather conditions and ranged from  $37 \pm 12.5$  on a cloudy day following heavy rains to  $121.1 \pm 15.4$  on a clear day preceded by 48 hr of clear skies.

The production rate of fecal pellets for the flooded portion of the tidal cycle was  $17.2 \pm 6.8$  pellets burrow<sup>-1</sup> hr<sup>-1</sup>. This rate was multiplied by 8.64 hr (68% of a 12.7 hour tidal cycle) to obtain an estimate of  $148 \pm 56$  pellets produced during the flooded portion of the tidal cycle.

The total production rate for the entire tidal cycle is thus estimated to be  $241 \pm 64$  pellets/burrow, or  $19 \pm 5$  pellets burrow<sup>-1</sup> hr<sup>-1</sup>, or  $456 \pm 118$  pellets burrow<sup>-1</sup> day<sup>-1</sup>.

The survey indicated that *C. major* inhabited an area of about 200,000 m<sup>2</sup> on the Sapelo Island beach. The density ranged from 1.1 to 16.3 burrows/m<sup>2</sup>, with highest densities along the most directly exposed beach. The data were used to estimate the number of burrows on the beach by weighting the density differences of differ-

TABLE 1. Carbon and nitrogen in *Callinassa* major fecal pellets (per cent dry weight)

Pellet type	Carbon (%)	Nitrogen (%)
Fresh	2.8	0.32
	3.0	0.25
Aged 24 hr	2.9	0.20
	3.0	0.23
Aged 48 hr	2.9	0.14
	3.0	0.17

ent areas. The total number of burrows in the area inhabited by *C. major* was estimated to be about 1,900,000. The data from quadrat observations indicated that pellets were produced from only about  $35 \pm 5\%$  of these burrows, and only 28% of these (10% of the total number) were ringed with fecal pellets at low tide.

The areal population rate was estimated to range from  $175 \pm 46$  pellets  $m^{-2}$   $day^{-1}$  in areas where the density of *C. major* was lowest to  $2,600 \pm 670$  pellets  $m^{-2}$   $day^{-1}$  in areas of highest density. The total population was estimated to produce about  $(280 \pm 73) \times 10^6$  pellets/day.

The density of pellets in rings around burrow openings, calculated from the burrow density, the percentage of burrows surrounded by pellets, and the number of pellets in the rings, indicated that in the area of minimum *C. major* density one could expect only  $10 \pm 0.8$  pellets/ $m^2$  to be distributed in rings around burrow openings, and only  $140 \pm 11$  pellets/ $m^2$  in areas of maximum density. In areas where wave action had concentrated the pellets, however, the density was estimated to be  $770,000 \pm 320,000$  pellets/ $m^2$ .

#### Composition of fecal pellets

The organic carbon content of freshly produced feces was about 2.9%. There was no measurable change in organic carbon when the feces were held in seawater for 48 hr, although the nitrogen content decreased significantly (from 0.29 to 0.16%) in 48 hr (Table 1).

Microscopic examination of fresh feces indicated that the bulk of the organic material present consisted of bacteria adhering

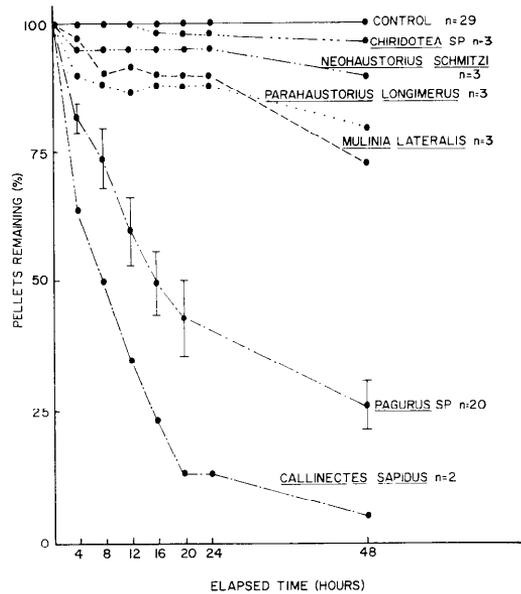


FIG. 1. Ingestion of *Callinassa major* fecal pellets.

in dense clusters to claylike particles a few microns in diameter. (The ceramiclike nature of the fecal residue after ashing also suggested that the inorganic matter in the feces was largely clay.) Under fluorescence microscopy, chlorophyll or phaeophytin, or both, in diatoms and other algal cells and cell fragments could be seen. These algae appeared to constitute only a small fraction of the organic matter in the pellets.

#### Ingestion of *C. major* fecal pellets

Fig. 1 is a plot of the percentage of fecal pellets remaining in experimental vessels against elapsed time of the experiments. All values represent the average percentage based on several replications, except that the *Pagurus* sp. data are plotted as the mean of the 20 experiments with vertical lines representing one standard error above and below the mean.

The studies indicate that the decapods *C. sapidus* and *Pagurus* sp. ingest *C. major* fecal pellets extensively, and that some other species may ingest them occasionally. Pagurid crabs were observed eating fecal pellets, but we have no data to indicate

TABLE 2. Organic carbon production by various ecosystem components

Producing unit	Season	Production g C m <sup>-2</sup> day <sup>-1</sup>	Reference
<i>C. major</i> feces	Aug	0.06	This report
Phytoplankton (estuary)	Aug	0.2	Ragotzkie 1959
Phytoplankton (estuary)	Aug	2.5	Schelske and Odum 1961
Phytoplankton (6.4 km offshore)	Aug	2.07	Thomas 1966
Marsh			
<i>Spartina alterniflora</i>	Yearly avg	ca. 4.5	Odum 1959
<i>S. alterniflora</i> detritus exported from marsh	Summer	0.3	de la Cruz 1965
Benthic algae	Summer	0.6	Pomeroy 1959
Benthic diatoms	"Warm weather"	0.1	Williams 1962
Phytoplankton-offshore waters			
Tropics	Yearly avg	0.05	Ryther 1963
Temperate	Yearly avg	0.33	Ryther 1963

that the crabs were able to assimilate the organic material in the pellets. We did not observe *C. sapidus* consuming fecal pellets.

There were no significant differences among the rates at which *Pagurus* sp. ingested fresh pellets and those aged for 24 and 48 hr.

#### DISCUSSION

The results can be used to calculate production rate of carbon in the fecal pellets in comparison with primary production of carbon compounds. These calculations indicate that the *C. major* population makes organic carbon available in its fecal pellets at a rate ranging from 0.007 to 0.109 g C m<sup>-2</sup> day<sup>-1</sup>. The mean rate for the entire population was 0.06 g C m<sup>-2</sup> day<sup>-1</sup> for a total of 11,700 g C/day.

Table 2 compares this rate with the rates at which organic carbon is made available in other forms. The data from other authors have been recalculated to express all figures in similar units.

The data in Table 2 indicate that organic carbon is made available as *C. major* fecal pellets at a rate ranging from 2.4% (Schelske and Odum) to 28% (Ragotzkie) of the rate it is made available by local estuarine phytoplankton populations. Similar comparisons indicate that carbon is made available as *C. major* fecal pellets at a rate 10% of that for benthic algae, 60% of that for benthic diatoms, 1.3% of that for *Spartina alterniflora*, 20% of that for exportable marsh detritus, 100% of that for offshore

tropical phytoplankton, 18% of that for temperature zone offshore phytoplankton, and 2.8% of that for local coastal phytoplankton.

The trophic role of fecal pellet carbon remains to be evaluated fully. It may be that the majority of this fecal carbon is not used directly as food by other animals. Newell (1965) indicates that *Hydrobia ulvae* fecal pellets are reingested only after their nitrogen content has been increased as a result of the activities of microorganisms. Johannes and Satomi (1966) report that *Palaemonetes pugio* reingests its own fecal pellets soon after their defecation, although "doubly-digested" feces were not re-eaten for several days. In either event, the fact that fecal pellets make available large quantities of carbon, even if only to microorganisms, indicates that these pellets may play a major role in the trophic relationships of the sea. This role may be especially important in benthic habitats where large quantities of fecal pellets are concentrated. Fecal pellets might have a faster sinking rate than other carbon sources and thus might reach the bottom with a greater percentage of their initial carbon (Gauld 1957). This carbon could then serve as food for benthic microorganisms that could, in turn, serve as food for benthic invertebrates.

Fecal material may thus concentrate carbon in a readily exportable state. It seems clear that the majority of the *C. major* fecal pellets are exported from the beach into

TABLE 3. *Composition of marine invertebrate fecal pellets*

Species	Carbon content (% dry weight)	Nitrogen content (% dry weight)	Reference
<i>Littorina planaxis</i>	2.0		North 1954
<i>Cirriformia tentaculata</i>	2.1		George 1964
<i>Hydrobia ulvae</i>			
fresh pellets	10.75	0.02	Newell 1965
pellets aged 3 days	9.68	1.7	Newell 1965
<i>Macoma baltica</i>			
fresh pellets	8	0.03	Newell 1965
pellets aged 3 days	7	1.2	Newell 1965
<i>Palaemonetes pugio</i>			
fresh pellets	20	4.48	Johannes and Satomi 1966
pellets aged 4 days	9	1.6	Johannes and Satomi 1966
<i>Crassostrea virginica</i>			
fresh pellets	4.6-6.1		Haven and Morales-Alamo 1966
<i>Balanus eburneus</i>			
fresh pellets	5.5-6.8		Haven and Morales-Alamo 1966
<i>Mya arenaria</i>			
fresh pellets	5.3		Haven and Morales-Alamo 1966
<i>Modiolus demissus</i>			
fresh pellets	4.4-5.6		Haven and Morales-Alamo 1966
<i>Molgula manhattensis</i>			
fresh pellets	5.4		Haven and Morales-Alamo 1966
<i>Callinassa major</i>			
fresh pellets	2.9	0.28	This report
pellets aged 2 days	2.9	0.15	This report

the subtidal zone. This export is apparent from observations, and also from comparisons of production estimates and the amounts of fecal material present on the beach. We estimate that a minimum of 70% of the total feces produced, or 7,840 g of organic carbon per day, are exported into the subtidal zone. This is also the region where the greatest densities of pagurid crabs and *C. sapidus* occur. It thus appears that the organic carbon in *C. major* feces may be of greater trophic significance to subtidal organisms than to beach species, although detritus of fecal origin could be redeposited on the beach surface after the pellets have been destroyed by wave action and beach species could then utilize it as food.

It also appears that the fecal pellets of different species contain differing amounts of organic carbon and that even the pellets of an individual species may contain differing amounts of carbon at different periods (Haven and Morales-Alamo 1966). The fecal pellets (Table 3) of *C. major* have an organic carbon content similar to the pellets

of the polychaete *Cirriformia tentaculata* and the gastropod *Littorina planaxis* but lower than pellets of the gastropod *Hydrobia ulvae* or the decapod *Palaemonetes pugio*.

Table 3 also indicates that the nutritive changes undergone with the aging of fecal pellets do not follow a single pattern. Thus Newell (1965) reported that *H. ulvae* and *Macoma baltica* fecal pellets decrease slightly in organic carbon content and increase significantly in nitrogen content when held for three days. The pellets of *H. ulvae* are initially unacceptable as food for this species but become acceptable after being held. *P. pugio* fecal pellets are initially accepted as food and lose both organic carbon and nitrogen fairly rapidly for several days, presumably becoming less nutritious (Johannes and Satomi 1966). In our experiments, fresh *C. major* fecal pellets, which were ingested by a variety of detritus feeders, decreased in nitrogen content but did not change appreciably in organic carbon content nor apparent attractiveness as food when held for 48 hr.

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