Marine Biology 58, 173–179 (1980)

MARINE BIOLOGY

Digestion in a Subtidal Population of *Mercenaria mercenaria* (Bivalvia)*

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Abstract

The digestive processes of *Mercenaria mercenaria* (Linn.) were studied in a natural subtidal population. Hourly sampling of 4 to 5 quahogs was conducted over one 25 h period in August, 1978, at Woods Hole, Ma., USA. Crystalline style length did not vary significantly with time, tide, particulate C, N or suspended material in the water. Changes in secretory activity of the style sac epithelium were not evident from histological sections. Based on cellular morphological differences, digestive tubules were individually classified into one of 4 categories, indicative of the state of intracellular digestion within the digestive cells. All 4 tubule types were present in individuals from each sample hour, signifying that intracellular digestion occurs continually within the digestive gland. A 3 h time lag is evident between times of peak C, N or suspended materials and apparent peak levels of absorptive (Type II) tubules.

Introduction

Ever since the high intertidal clam *Lasaea rubra* provided evidence of cyclic digestive activity in lamellibranch bivalve molluscs (Ballantine and Morton, 1956; Morton, 1956; McQuiston, 1969), the traditional view that digestion in this class is a continuous process has been increasingly criticized. Numerous studies have shown that a variety of bivalve digestive processes are discontinuous and often cyclic under natural or quasi-natural environmental conditions. Supporting evidence has come primarily from studies on intertidal bivalves such as *Cardium edule* (Morton, 1970a; Owen, 1970), *Macoma balthica* (Morton, 1970b), *Ostrea edulis* (Langton and Gabbott, 1974), *Mytilus edulis* (Langton, 1975, 1977), *Geloina proxima* (Morton, 1975) and *Venerupis decussata* (Mathers *et al.*, 1979). In each of these cases, the digestive processes have closely followed some aspect of the tidal cycle. Freshwater bivalves *Dreissena polymorpha* (Morton, 1969), *Unio pictorum* and *Anodonta cygnea* (Morton, 1970c), have also shown discontinuous patterns of digestion. With the exception of *A. cygnea*, these freshwater species have demonstrated a possible circadian digestive cycle.

More complexity has been found in the digestive processes of subtidal species. Laboratory studies have demonstrated changing enzyme levels in *Ostrea edulis*, *Crassostrea angulata* (Mathers, 1973) and *Arctica islandica* (Palmer, 1979) following feeding. Evidence of a diphasic rhythm of intracellular digestion, correlating with tidal alternations, has been presented for *Pecten maximus* (Mathers, 1976) and *Chlamys varia* (Mathers *et al.*, 1979). On the other hand, an apparently monophasic digestive cycle has been described for *O. edulis* which closely followed local tidal fluctuation (Morton, 1971). Tidal periodicity of style secretion was not observed in oysters maintained under a continuous laboratory regime, but could be mimicked by feeding oysters discontinuously (6 h fed, 6 h, not fed) (Langton and Gabbott, 1974). A similar dependency on food was observed for the morphological changes in the digestive glands of *O. edulis* from a natural population by Wilson and LaTouche (1978).

The results of the majority of these studies are consistent with the hypothesis of discontinuous, and in many cases cyclic, digestion (Purchon, 1971; Morton, 1973), but the importance of food availability rather than the tidal cycle *per se* on the digestive processes has rarely been addressed (Langton and Gabbott, 1974; Wilson and Latouche, 1978). In addition, few studies have attempted to quantitate the intracellular digestive processes as reflected by the changing morphology of the digestive gland tubules (Langton, 1975; Wilson and La Touche, 1978). Toward both these aims, the present study was undertaken to investigate the digestive

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0025-3162/80/0058/0173/$01.40

processes of subtidal quahogs, *Mercenaria mercenaria* (Linn.) in relation to tidal parameters and available food.

Materials and Methods

Quahogs were collected from a natural population located in 6 to 8.5 m of water, approximately 30 m off of the National Marine Fisheries Service Pier, Woods Hole, Ma, USA. Beginning at 1500 hr, 10 August 1978, 4 to 5 quahogs were removed from the study area by SCUBA divers each hour, for 25 h. The divers attempted to remain on the downstream side of the collection site in order that disrupted bottom silt would not influence the normal filtration and digestive activity of the other quahogs. Bottom water temperatures were recorded by the divers each hour. Tidal height was calculated from the Tide Tables (U.S. Dept. of Commerce, NOAA and NOS, 1977).

Quahogs were immediately dissected after recording length, width and total wet weight (shell, tissue and mantle cavity sea water). The crystalline style was removed, length measured to the nearest 0.5 mm, and frozen. Style dry weights were later determined after drying at 100 °C overnight. Two pieces of tissue from the left lobe of the digestive gland and the entire style sac were dissected out, fixed and stored in Bouin's fixative. Tissues were subsequently dehydrated, embedded in polyester wax (Steedman, 1960) and sectioned at 7 μm. Cross sections were cut from 2 separate areas of the style sac. Slides from adjacent sections were stained in Alcian blue-PAS (Pearse, 1968) and mercuric bromophenol blue (Humason, 1972). Digestive gland sections were stained with Heidenhain's Azan (Humason, 1972).

Two photomicrographs were taken at random of each of the 2 pieces of digestive gland removed from each quahog using an Olympus Vanox microscope (33 x magnification). The resulting photomicrographs were thoroughly shuffled and each digestive tubule assigned to one of 4 tubule types (Type I, normal or holding phase; Type II, absorptive phase; Type III, disintegrating phase; Type IV, reconstituting phase), similar to the classification and methodology of Langton (1975). The percentage of each tubule type was calculated for each sample hour. In all, 16 to 20 photomicrographs (4 to 5 quahogs) containing 206 to 334 graded tubules ($\bar{x}$ = 289; SD = 31.7) were analyzed for each hourly sample.

Statistical tests of the tubule grading procedure reveal that the technique is consistent and reproducible. Significant differences were not obtained when the photomicrographs from the same 3 sampling hours were graded on 2 separate occasions ($P>0.05$; 2 counts x 3 tubule types Chi square contingency table). Additionally, both authors graded the same photomicrographs from 2 of the sample hours similarly ($P>0.05$; 2 counts x 3 tubule types Chi square contingency table).

Water samples were collected, in duplicate, every 2 h by divers who manually tripped 2 l PVC Niskin bottles held approximately 30 cm off the bottom. In the lab, the samples were poured through 125 and 63 μm U.S. Standard stainless steel sieves to remove large particulates. Five hundred milliliter subsamples were filtered at 5 psi vacuum through Millipore AS40-024-05 glass fiber filters which had previously been ignited at 550 °C for 18 h and stored under vacuum with silica gel dessicant. Following filtration, the filters were dried at 60 °C overnight, weighed, and stored dessicated under vacuum. Carbon (μg C l^{-1}) and nitrogen (μg N l^{-1}) analyses were later conducted on each filter with a Perkin-Elmer 240 elemental analyzer using acetanilide as a standard. The mean soluble organics level, determined for 3 filtered-seawater treated filters, was subtracted from each sample value. The mean weight ($\bar{x}$ = 0.0354 gms; SD = 0.0012 g) of 25 preignited glass fiber filters was subtracted from the weights of filters from each bihourly sample to yield a dry weight of suspended sediment (mg l^{-1}). Salinity of each sample was determined using a Bausch and Lomb refractometer calibrated with a known serial dilution of seawater.

Results

Quahogs (N = 121) ranged from 44.5 to 108.8 mm in length ($\bar{x}$ = 88.0 mm; SD = 7.4 mm) and 26.0 to 61.6 mm in width ($\bar{x}$ = 49.7 mm; SD = 4.2 mm). Total wet weights (shell, tissue and mantle cavity seawater) ranged from 33.92 to 488.13 gm ($\bar{x}$ = 270.22 gms; SD = 58.88 gms). From allometric data subsequently obtained on a subsample of the same population, these wet weight values represent 0.73 to 12.23 gms dry tissue weight.

The morphology of the digestive gland of *Mercenaria mercenaria* corresponds to that of other eulamellibranchs. The digestive tubules display morphological variations which reflect differences in the state of absorption of food material and intracellular digestion within the digestive cells which make up the tubule (Owen, 1955, 1966, 1974). These morphological variations can be recognized as 4 distinct tubule types (Types I, II, III, and IV: Fig. 1), similar to those previously described in a variety of bivalves (Morton, 1956; Morton, 1970a,b; Platt, 1971, Langton, 1975; Mathers, 1976). All 4 tubule types can be found in every individual, although Types III and IV are not always present in the graded photomicrographs. Due to the cluster arrangement of a number of digestive tubules around a secondary duct, the tubules within the same cluster generally receive food material at approximately the same time and as a result, display a similar morphological appearance. However, all clusters would not necessarily receive food material simultaneously (Langton, 1975).

Each tubule type can be readily identified in either cross or longitudinal Bouin-fixed tissue sections. Type I tubules (normal or holding phase tubules; Fig. 1A) possess a spacious lumen. In this phase, the digestive cells are columnar, 19 to 49 μm tall ($\bar{x}$ = 30.3 μm; SD = 5.5 μm; N = 175) and present a flat luminal surface with a distinct microvillar border, much shorter

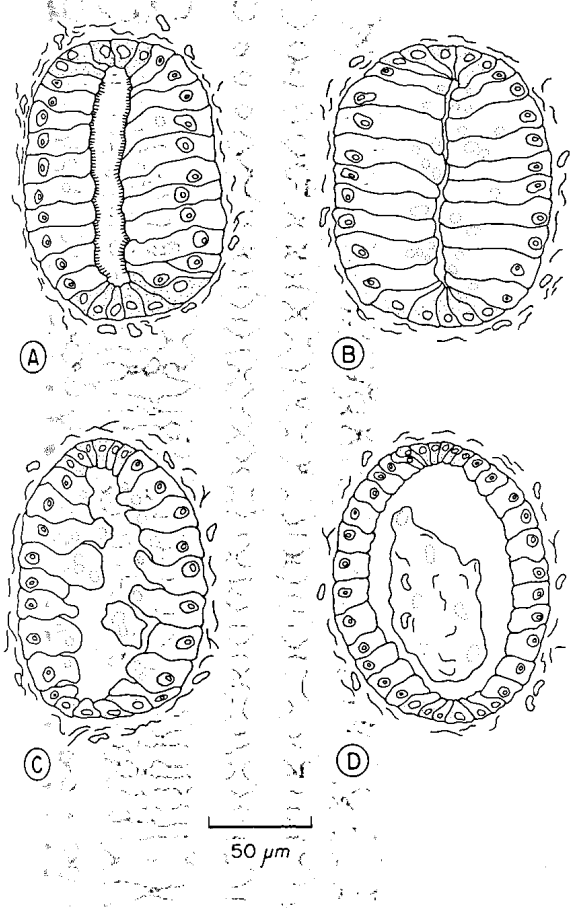

Fig. 1. Four morphologically distinct tubule types in the digestive gland of *Mercenaria mercenaria*. (A) Type I, normal or holding phase; (B) Type II, absorptive phase; (C) Type III, disintegrating phase; (D) Type IV, reconstituting phase

Table 1. Percentages of Type I–IV graded tubules from the digestive glands of *Mercenaria mercenaria* sampled hourly during the 25-hour field study

Time	Quahogs sampled	% Type I	% Type II	% Type III	% Type IV	Tubules graded
1500	4	62	29	7	2	215
1600	4	70	28	1	1	284
1700	5	56	38	5	1	312
1800	5	61	33	4	2	325
1900	5	66	29	4	1	329
2000	4	55	43	2	0	266
2100	4	64	34	2	0	206
2200	5	57	38	3	2	277
2300	5	67	29	3	1	323
2400	5	53	42	3	2	313
0100	5	63	32	4	1	282
0200	5	60	36	4	0	279
0300	5	67	26	5	2	307
0400	5	59	39	2	0	270
0500	5	47	49	4	0	300
0600	5	70	28	2	0	334
0700	5	59	38	3	0	300
0800	5	67	32	1	0	292
0900	5	60	37	3	0	287
1000	5	62	31	4	3	258
1100	5	59	37	3	1	284
1200	5	66	29	4	1	305
1300	5	62	32	5	1	296
1400	5	47	48	4	1	312
1500	5	53	42	3	2	258

than that of the secondary ducts. The digestive cells of Type II tubules (absorptive phase tubules; Fig. 1B) are taller, 23 to 61 μm, ($\bar{x}$ = 39.4 μm; SD = 7.1 μm, N = 121) and more vacuolated distally. The mean height of Type II digestive cells is significantly different from that of Type I (Student's *t*-test; t = 11.848; df = 216; P<0.01). The distal luminal surface of these cells is generally convex in shape, extending into the lumen of the tubule. In advanced stages of absorption, the lumen is often entirely occluded. Type III tubules (disintegrating phase; Fig. 1C) contain digestive cells whose distal tips appear to be breaking off from the rest of the cell. Apical cellular membranes are often indistinct. Cell size varies, depending on the degree of fragmentation. The final tubule type, Type IV (reconstituting phase, Fig. 1D), reflects the culmination of the breakdown process. Digestive cells are short, almost cuboidal, 8 to 18 μm tall ($\bar{x}$ = 12.7 μm; SD = 3.3 μm; N = 25). The luminal border is distinct and vacuolar inclusions are absent. Debris is often present in the lumen, in marked contrast to the situation found in *Mytilus edulis* (Platt, 1971; Langton, 1975).

Percentages of tubule types counted for each of the 25 sample hours are presented in Table 1. These proportions appear to vary appreciably over time. For each of the hourly samples, more Type I tubules are present than any of the other 3 types in all but 2 cases. Types III and IV tubules occur very infrequently, never amounting to more than 10% of the total tubules counted each hour. Percentages of Type II tubules (absorptive phase) are higher at 2000, 2400, 0500 and 1400 hr. Since an increase in the degree of intracellular digestion is reflected by greater numbers of Type II tubules (Owen, 1974; Langton, 1975; Morton, 1973; Wilson and LaTouche, 1978), these 4 peaks represent 4 heights of digestive activity during the 25 h study. One-way ANOVA (analysis of variance) however, reveals that higher variances from the mean percentage of Type II tubules occur within the hourly samples of 4 to 5 quahog digestive glands than between the hourly samples. Statistical significance can, therefore, not be placed on the apparent fluctuations of the percentages of each tubule type counted per hour due to the high degree of variability within an individual digestive gland.

Firm, well formed crystalline styles were present except in 12 of the 121 quahogs sampled (2300, 0100, 0700, 0800, 1100, 1300, 1400 hrs, 2 at 2000 hrs and 3 at 1000 hrs). No pattern of fluctuation in style size was evident from either regression analysis of normalized style size data (style length/quahog length *vs* time; style

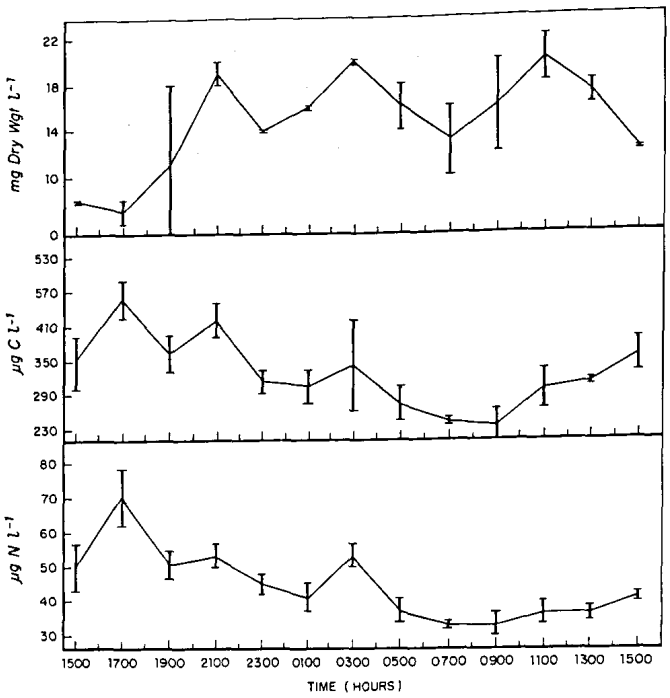

Fig. 2. The changing levels of suspended materials, particulate carbon and particulate nitrogen present in bottom water samples during the 25 h sampling period. Ranges are indicated by bars

dry wt./total quahog wet wt. *vs* time) or analysis of covariance (ANCOVA = style length against time with quahog length as a co-variate). ANCOVA indicated that a highly significant influence of body length on style length was present ($F_{(1,83)} = 95.251$; $P < 0.01$), but that hourly effects were insignificant ($F_{(24,83)} = 0.642$; $P > 0.05$). The majority of the differences in style size were therefore attributable to differences in quahog size rather than digestive state. Histological evidence from 30 quahogs (6 successive sample hours) revealed no individual differences in secretory activity. The B-cell layer (Kato and Kubomura, 1954) stained PAS(+) in all specimens, but appreciable activity was not detected in the A-cell layer. Protein secretion could not be discerned with mercuric bromophenol blue staining.

During the sampling period, both temperature and salinity varied at irregular intervals. Bottom water temperatures fluctuated between 20.7° to 24.9°C ($\bar{x}$ = 21.8°C; SD = 0.9°C; N = 25). Salinity ranged from 31.5 to 34.0 ppt ($\bar{x}$ = 32.3; SD = 0.7 ppt; N = 13). Neither fluctuations in temperature nor salinity correlated with tidal height.

The level of suspended materials, carbon (C) and nitrogen (N) changed appreciably over the sampling period (Fig. 2). ANOVA tests on C,N and suspended material levels against time revealed overall significant differences between hourly samples (for C, $F_{(12,13)} = 3.23$; $P<0.05$; for N, $F_{(12,13)} = 6.91$; $P<0.01$; and for suspended material, $F_{(12,13)} = 2.72$; $P<0.05$). Three peaks of suspended materials were apparent (2100, 0300 and 1100 hrs), whereas high levels of carbon and nitrogen were detected at 1700, 2100 and 0300 hrs. Levels of suspended material and C-N did not correlate with the tidal cycle.

These peaks of C, N and suspended materials correlate with the highest hourly mean percentage of Type II (absorptive) tubules (Fig. 3). With one exception, all peaks of absorption by the digestive tubules occurred 3 h after peaks of C-N or suspended matter. The 0300 hrs suspended material and C-N peaks were followed by a peak

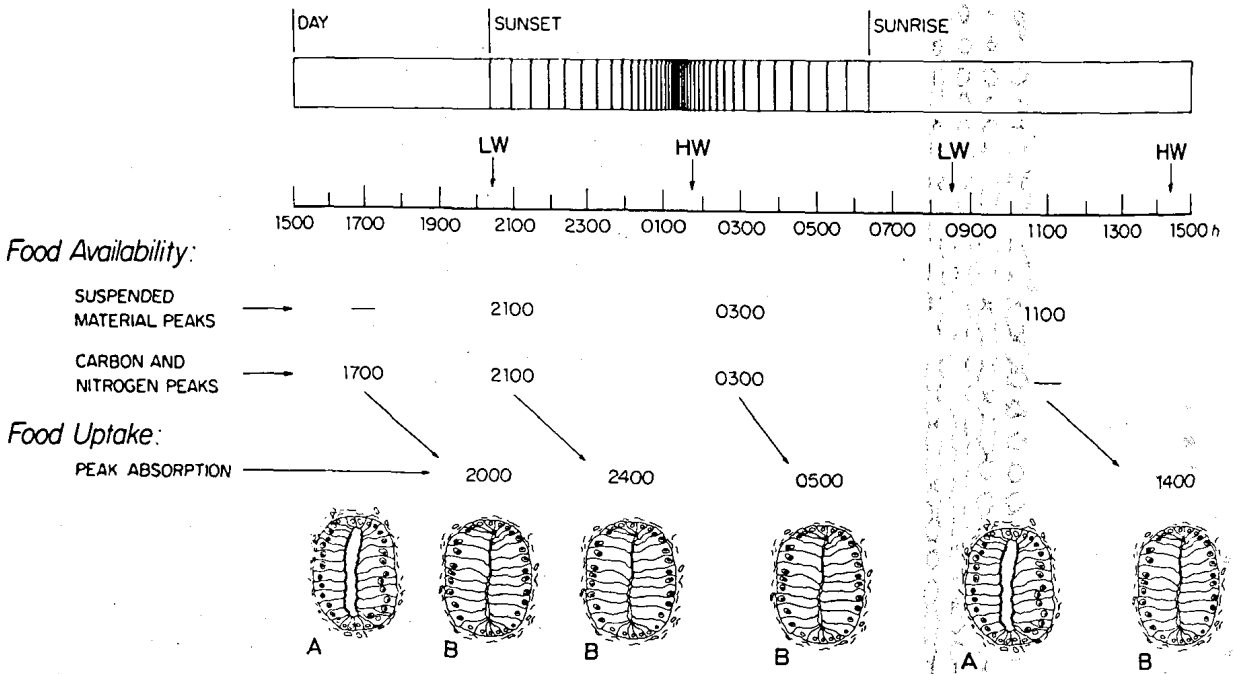

Fig. 3. The relationships between solar day, tidal cycle, food availability and food uptake within the digestive gland for the natural population of *Mercenaria mercenaria* over the 25 h sampling period. Characteristic tubule types for the respective periods are illustrated

of absorptive activity after only 2 h. Since water samples were taken bihourly, the peak of food availability could actually have occurred at 0200 hrs, triggering the absorptive peak 3 h later.

Discussion

All 4 tubule types were present in each quahog sampled, regardless of the sample time or tidal stage, indicating that some intracellular digestion occurred at all times. Similar heterogeneity in the digestive gland has been described for other species of bivalves although the finding has not been emphasized and the conclusion that intracellular digestion is continuous has generally not been made. For example, Morton's (1956) work on the high intertidal *Lasaea rubra* showed that all tubules were not in the same phase, but that a predominance of one particular tubule type was observed at any given time. McQuiston (1969) confirmed this basic finding for *L. rubra*, but reported that approximately 50% of the tubules were in a "digestive" phase while the remainder were in a "regeneration" phase at all times over the tidal cycle in the population he studied. All 4 tubule types could therefore be observed at all times. Owen (1972) has stated that the digestive glands of intertidal *Cardium edule* and *Mytilus edulis* were almost homogeneously composed of holding phase tubules at the start of a feeding period just before the individuals were covered by the incoming tide. As food arrives in the individual clusters of tubules, the digestive cells absorb the nutrients and later fragment and reconstitute. Complete disintegration of all digestive cells of an individual was rarely, if ever, seen. As long as food was available, it was ingested and digested intracellularly by digestive cells. However, the cells in different groups of tubules pass through the digestive cycle at different rates depending on the degree of absorption and the arrival of food in the tubule lumen. A jumbled picture of tubule types was therefore present whenever the individual was covered by water and feeding. On exposure again, the tubules eventually reverted back to their homogeneously appearing state. Langton (1975) however, never observed homogeneously composed digestive glands in mid-tidal *Mytilus edulis*. His data on tubule type counts of mussels collected hourly over a 26 h period revealed that all 4 tubule types were always present, but the majority of the tubules were in the absorptive phase of the digestive cycle throughout the sampling period.

Subtidally, *Pecten maximus* and *Chlamys varia* were also found to display a high degree of heterogeneity in the composition of the tubules in their digestive glands (Mathers, 1976; Mathers *et al.*, 1979). Approximately half of the tubules were in the holding state while the remainder were in the "digestive" or absorptive state. A similar heterogeneous makeup, with supporting numerical data, has been described for 2 subtidal populations of *Ostrea edulis* (Wilson and LaTouche, 1978). Although all 4 tubule types were present in each oyster, the majority of the tubules were in the absorptive state at one of 2 stations studied but in the holding stage at the other. Wilson and LaTouche observed that increases in the number of absorptive (Type II) tubules were related to higher levels of suspended sediment in the surrounding water.

Morton (1969, 1970a,b, 1971, 1967, 1977), however, has repeatedly described homogeneous tubule states within the digestive gland of a variety of bivalves living intertidally, subtidally or in freshwater. Although minor variation was acknowledged among the tubules of each individual and between the digestive glands of different individuals, the vast majority of tubules were reported to be in one phase alone and to proceed through their digestive cycles synchronously. Morton's data has suggested that in *Crassostrea gigas, Ostrea edulis, Macoma balthica* and *Cardium edule*, one or more of the 4 tubule types were absent during some sampling hours. There were periods in which absorption apparently did not occur, and others where holding phase tubules were not found.

In addition to the heterogeneous state of the digestive gland of *Mercenaria mercenaria*, a number of other factors suggest that digestion in this subtidal bivalve is a relatively continuous process, at least under the environmental conditions present during the study period. First of all, the amount of material found in the stomach during dissection did not vary noticeably over time. Similarly, the intestine was generally filled to the same degree in most bivalves.

Secondly, the crystalline style data indicate that secretion and dissolution occur relatively continually in each individual or, at least, asynchronously within the population. Crystalline styles were rarely lacking. In addition, the extreme between-quahog variations in style size connotes the absence of synchronous secretion and dissolution. Neither the incidence of missing styles nor the average hourly style sizes correlate with any of the environmental parameters which were measured. Similarly, individuals of *Crassostrea gigas* show no indication of cyclic variation in style size when submerged and actively feeding (Bernard, 1973). Intertidal individuals, however, lose their styles when exposed (Bernard, 1973; Morton, 1977). The situation in *Mercenaria mercenaria* contrasts with that found in other intertidal and subtidal bivalves, where distinct fluctuations in style size have correlated with the tidal cycle (Morton, 1956; Morton, 1971, 1976; Langton and Gabbott, 1974; Mathers, 1976; Langton, 1977). The latter studies have shown that style size increases during times when the bivalves are covered and actively feeding. In *Macoma balthica* and *Abra nitida*, dissolution of the style as well as secretion, occur only when the bivalves are feeding (Kristensen, 1972). Cyclic feeding activity, therefore, has a marked effect on style size.

Finally, the small but fairly constant number of Type III (disintegrating phase) tubules present at all times may contribute to constant extracellular digestion. Fragmentation spherules, derived from the nipped-off tips of the Type III tubule digestive cells may release

extracellular enzymes once they arrive in the stomach (Owen, 1955, 1966; Morton, 1973; Palmer, 1979). A small, steady stream of these spherules would insure a continuous supply of extracellular enzymes.

The results presented here necessitate the adoption of the traditional view that digestion in *Mercenaria mercenaria* is a continuous process. Equally as important however, is the correlation shown between high levels of either C, N or suspended matter and the peaks of intracellular digestion 2 to 3 h later. This points out the influential effect of food availability on the digestive processes. It may be better to think of eulamellibranchs, in general, as opportunistic feeders which feed and digest whenever they are exposed to suitable environmental conditions. The potential mechanisms needed for continuous digestive activity, both intra- and extracellular, have been shown to be available to bivalves (Owen, 1955, 1966, 1972, 1974), yet environmental conditions which affect the available food supply may mandate cyclic, intermittent or discontinuous digestion. Tidal exposure is the most obvious constraint for filter feeders. Other environmental factors such as vertical migration of plankton, local cycles of upwelling and tidal current influences on food concentration, may limit digestive activity in subtidal species as well. From an energetic standpoint, food levels, either in the surrounding water or within the stomach, may at times be too low for efficient processing and digestion. A period of inactivity would be expected to follow until the level of available food reaches some threshold value. The particular feeding/digestive strategy which a species of bivalve adopts, whether it be continuous or discontinuous, cyclic or intermittent, should serve to maximize energy gain in the face of the particular set of imposed environmental conditions.

Acknowledgements. We thank the M.U.R.T. Dive Team, Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, Ma, USA, for collecting the quahogs and generally assisting with the sampling. Our thanks are also extended to Dr. M. R. Pennington for help with the statistical analyses, and to Drs. M. P. Morse, N. W. Riser and D. S. Wethey for helpful suggestions and critical review of the manuscript. Special thanks are given to Mrs. J. Cusack for untiringly typing each draft of this paper.

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Date of final manuscript acceptance: June 25, 1980.
Communicated by I. Morris, West Boothbay Harbor