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A nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flow in a New England salt marsh[1]

Thomas E. Jordan[2] *and Ivan Valiela*

Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543

Abstract

The annual nitrogen budget of a mussel (*Geukensia demissa* = *Modiolus demissus*) population in a salt marsh was determined and compared to the nitrogen budget of the marsh. During each tidal cycle in summer, the mussels filter a volume of water in excess of the tidal volume of the marsh. Yearly, the mussels filter 1.8 times the particulate nitrogen exported from the marsh by tidal flushing. Half the nitrogen filtered is absorbed by the mussels and half deposited as feces and pseudofeces (biodeposition). Of the nitrogen absorbed, 55% is excreted as ammonia. As a result, the mussel population releases more ammonia into the marsh water than does any other population in the marsh. Four percent of the nitrogen absorbed by the mussels is secreted in byssal threads, 20% invested in growth, and 21% released in gametes. Gametes are the largest component of mussel production to enter the food web, because mortality of adult mussels is very low.

Geukensia demissa (=*Modiolus demissus*: *see* Blackwell et al. 1977) is commonly found in the intertidal zone of salt marshes. Kuenzler (1961*a*,*b*) showed the importance of these mussels in the flow of phosphorus and energy in a Georgia salt marsh. They daily filter about a third of the particulate phosphorus suspended in the marsh water and deposit most of it as feces and pseudofeces. By filtering suspended particles, mussels may reduce the export of particulate organic matter by salt marshes. Such export may represent a significant proportion of the production of marshes and may be important to the food webs of coastal waters (Teal 1962; Odum and de la Cruz 1967; Valiela et al. 1978), but the mechanisms controlling export are not well understood. Woodwell et al. (1979) found net import and Heinle and Flemer (1976) very little export of suspended matter by salt marshes. Material filtered by mussels and delivered to the sediments may be a source of food for deposit feeders (Kuenzler 1961*b*; Haven and Morales-Alamo 1966; Kraeuter 1976).

We investigated the role of mussels in the nitrogen cycle, because nitrogen is important in controlling both autotrophic and heterotrophic production in salt marshes. Increasing the nitrogen supply to marsh plants increases their productivity (Tyler 1967; Pigott 1969; Valiela et al. 1976) and secondarily results in increased production of herbivores (Vince 1979), detritivores, and predators (W. Wiltse in prep.). Nitrogen also limits the productivity of nearshore waters (Ryther and Dunstan 1971). Measurements of exchange of nitrogen between nearshore waters and Great Sippewissett Marsh (Valiela et al. 1978), where our study was done, provide useful comparisons with nitrogen flow through the mussel population.

Nitrogen absorbed by mussels—filtered but not deposited—is excreted as ammonia or dissolved organic nitrogen (DON) or used for production of flesh, shell, byssal threads, or gametes. Ammonia and DON excreted by mussels may be an important source of nitrogen to nearshore waters (Nixon et al. 1976; Bayne et al. 1976*b*). Nitrogen used in production of flesh is eventually consumed by predators or decomposers, but nitro-

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[2] Present address: Chesapeake Bay Center for Environmental Studies, Smithsonian Institution, Edgewater, Maryland 21037.

gen used in production of shell and byssal threads is probably consumed only by decomposers. Most of the nitrogen invested in gametes enters the food web because the mussel larvae suffer heavy predation (Bayne 1976).

To evaluate the mussels' role in nitrogen flow, we determined a nitrogen budget by much the same approach as Kuenzler (1961*b*) used to evaluate their role in phosphorus flow. We measured rates of filtration of suspended particles, biodeposition, excretion of ammonia and DON, secretion of byssal threads, gamete production, and growth. Several of these rates have been measured before (reviewed by Bayne et al. 1976*a*,*b*), but not all in units of nitrogen throughout the year. We measured seasonal nitrogen flow through mussels of various sizes throughout the intertidal zone and then determined a nitrogen budget for the entire population using measurements of mussel distribution, abundance, mortality, and recruitment.

S. Volkmann helped in analysis of the data and S. Tracey in the census of the mussel population. J. Hobbie and J. Teal helped edit the manuscript. The Gifford family and Salt Pond Sanctuaries granted permission to carry out the fieldwork in Great Sippewissett Marsh. A fellowship from the Friendship Fund supported T. E. J. during this study.

Methods

Distribution and abundance—The densities of *G. demissa* were measured in random 1-m^2 quadrats in areas of short and tall *Spartina alterniflora*. On the creekbanks, densities were measured in random 0.5-m quadrats extending 1 m parallel to the bank and 0.5 m into the grass. Elevations of all quadrats were measured, as were other elevations, by comparing their depth under water at a specific time with the depth vs. time record from a nearby tide gauge. The total extent of vegetated areas is from Valiela and Teal (1979). Creekbanks were divided into three categories according to mussel density and the extent of each mapped.

Mortality and recruitment—Mortality and recruitment were measured by comparing numbers of mussels in quadrats in July 1976 with numbers in adjacent quadrats in October 1978. Since only mussels longer than 30 mm could be sampled quantitatively, we calculated mortality of the cohort that had been longer than 30 mm in 1976 by using measurements of growth (*see below*) to predict the length attained in 1978 by mussels that had been 30 mm long in 1976. The number of mussels longer than this predicted length in 1978 was then subtracted from the number of mussels longer than 30 mm in 1976 to calculate mortality. Net recruitment was calculated as the number of mussels of all sizes in 1978 minus the number in 1976 plus the mortality of mussels that were longer than 30 mm in 1976.

Filtration—Filtration by mussels was measured by comparing the rate of disappearance of suspended particles in jars of seawater with and without mussels. First, mussels collected from a low elevation (submerged 17 h per day) and from a high elevation (submerged 8 h per day) were placed posterior end up in plastic vials (3.5-cm diam × 2–5 cm high) held in wooden frames near where they had been collected. The mussels attached themselves to the vials with byssal threads and were acclimated for at least 2 weeks. We then transferred the mussels along with their attached vials to glass jars (16-cm diam × 25 cm high) without destroying the byssal threads. Pairs of similar-sized mussels from a given elevation were placed in each jar, which was filled with 3 liters of freshly collected marsh water, inside of smaller jars (6-cm diam × 11 cm high) to prevent feces and pseudofeces from being stirred into suspension. One control jar was set up exactly like those containing mussels but with empty mussel shells; another contained only water. Results of both controls were identical.

The jars of marsh water with and without mussels were placed in wooden boxes with wire mesh bottoms which were then floated in a marsh creek so that tem-

perature in the jars matched ambient temperature. The water in the jars was vigorously aerated by an air stone to reduce settlement of suspended particles.

Thirty-milliliter samples were taken from the jars at the start of the experiment and at 1-h intervals for 3 h. The 3-h duration of the experiment was timed to coincide with high tide in case filtration showed a tidal rhythm (Nagabushanam 1963). The water samples were kept on ice through the experiment and then returned to the laboratory where the concentration of particles about 5–15 μm in diameter was measured with a Coulter Counter. The volume of water cleared of these particles per unit time was calculated by the method of Fox et al. (1937).

At least two experimental artifacts are possible: the mussels may not begin filtering as soon as they are placed in the jars, and they may slow their filtering when suspended particles become scarce (Winter 1978). Since both could underestimate filtration rates, we chose the highest rate measured to represent the natural rate.

Excretion of ammonia and dissolved organic nitrogen—The rates of excretion of ammonia and dissolved organic nitrogen (DON) were measured by comparing the accumulation of ammonia and DON in flasks of seawater with and without mussels. The mussels were first acclimated in plastic vials at two elevations as above. Then we rinsed the mussels and their attached vials with seawater and placed them in 1-liter Erlenmeyer flasks containing 900 ml of freshly collected marsh water. Two to four similar-sized mussels from a particular elevation were placed in each flask. Again one control flask contained empty shells and another contained only water, and again the results of the two controls were identical. All flasks were placed in wooden boxes with wire mesh bottoms and the boxes floated in a creek as above. The water in the flasks was aerated with air stones.

At the beginning and end of a 3–4-h period coinciding with high tide, water samples were taken from the flasks. The samples were then returned to the laboratory, filtered with 0.45-μm Millipore filters, and analyzed for ammonia (Solórzano 1969). Portions of the samples were stored frozen and later analyzed for DON by Kjeldahl digestion (Strickland and Parsons 1968) and ammonia determination in the neutralized digestate (Solórzano 1969).

Biodeposition—Biodeposition rates were measured by collecting mussel feces and pseudofeces with sediment traps consisting of widemouth glass jars (11 cm high × 4.9-cm inside mouth diameter). The traps contained three to four mussels of similar size, posterior end up. The traps were placed at elevations that were submerged for 6, 12, and 16 h per day and contained mussels collected from the same elevations. The mussels attached themselves to the traps with byssal threads. Water in the traps drained out at low tide through a 6-mm hole drilled in the side 2 cm from the bottom; this left the mussels partially out of water at low tide as they would be in the natural situation. Control traps containing empty mussel shells with their valves glued together were placed at the same locations.

After two tidal cycles the material that had accumulated in the sediment traps was removed by rinsing with filtered seawater, collected on Gelman glass-fiber filters, and the filters dried at 60°C and weighed. To correct the weights for salt left on the filter and sediment after drying, we used a regression of weight of salt vs. weight of sediment and salt on the filter. The amount of biodeposits was calculated by subtracting the average amount of sediment in three control traps from the amount of sediment and biodeposits in each trap containing mussels. Biodeposition rates were expressed per hour of submersion, measured from records from a nearby tide gauge.

Secretion of byssal threads—Secretion of byssal threads was measured by placing mussels with their byssal threads removed in glass jars and weighing the byssal threads produced in the jars after 21, 41, and 59 days. The jars were held in wooden frames at elevations submerged

Table 1. Distribution and abundance of mussels. Average mussel densities are given ±SE; in parentheses—numbers of replicates. Elevations are ranges represented by quadrats sampled. Mean high water is about 130 cm above mean low water (MLW).

Habitat	Submergence ($h \cdot d^{-1}$)	Elevation (cm above MLW)	Area (m^2)	Mussels · m^{-2}	Millions of mussels
Creekbanks					
High density	10.3–15.3	88.3–61.4	790	734±24 (2)	0.6
Low density	8.6–13.8	97.3–69.5	5,180	364±160 (3)	1.9
S. alterniflora					
Tall	8.3–15.9	99.0–58.3	85,130*	140±43 (6)	11.9
Short	6.5–9.5	109.0–92.5	122,500†	34±7.5 (6)	4.2
					18.6

* Area of tall *S. alterniflora* zone (Valiela and Teal 1979) minus area classified as creekbank.
† From Valiela and Teal 1979.

8 and 17 h per day. Carbon and nitrogen in byssal threads was determined with a Perkin-Elmer CHN analyzer.

Growth—Growth was determined by placing mussels in wooden frames at different elevations in the marsh and measuring the length of their shells about every 50 days from April to December. Growth in terms of nitrogen in flesh, shell, and liquor (liquid trapped between the shell and mantle) was calculated from length–weight regressions and percent nitrogen values. Nitrogen in shells was determined with a Perkin-Elmer CHN analyzer and nitrogen in liquor by the method used for DON analysis. Carbon in flesh was determined with a LECO carbon analyzer, nitrogen in flesh by the Kjeldahl method (Wilde et al. 1972).

Results

Distribution and abundance—Mussel densities are highest on the creekbanks, lowest in the short *S. alterniflora* zone, and intermediate in the tall *S. alterniflora* zone (Table 1). Mussels are unevenly distributed along creekbanks, being most abundant near the mouths of creeks or in wide cul de sacs, least abundant in backwaters and on banks subject to erosion. Although densities are highest on creekbanks, the total number of mussels on creekbanks is less than in the other habitats having greater areas. Most mussels live in the tall *S. alterniflora* zone (Table 1).

Mussels were found in areas submerged from 3 to 17 h per day. Densities tend to increase with decreasing elevation (Table 1), as also shown by Kuenzler (1961*a*), Cerwonka (1968), and Lent (1969). The maximum densities in Great Sippewissett Marsh (about $800 \cdot m^{-2}$) are higher than those observed by Kuenzler (1961*a*) in a Georgia marsh (about $50 \cdot m^{-2}$), perhaps because mussels in Great Sippewissett Marsh live where they are submerged for 17 h per day, while in Georgia they only range down to where they are submerged 8 h per day.

Mortality and recruitment—The cohort of mussels that were longer than 30 mm in 1976 did not show a significant change in number by 1978 (paired *t*-test). Therefore, there was little or no mortality of mussels longer than 30 mm between summer 1976 and summer 1978. Inaccuracies in determining growth rates introduce little error into the measurement of mortality. At high elevations, 30-mm mussels grew very little in 2 years (Table 2). At low elevations, mussels shorter than 30 mm were very scarce in 1976 and in 1978 recruits formed an easily distinguishable peak (Fig. 1). Errors due to patchiness of distribution were largely overcome by comparing numbers of mussels in adjacent quadrats; variability in numbers between adjacent quadrats was much less than among nonadjacent ones (Table 2).

Areas having high densities of mussels in 1976 showed the greatest increase in density by 1978 (Table 2). Spat may settle preferentially in areas where adult mussels are abundant. The abundance of

Table 2. Net recruitment and mortality measured by comparing mussel densities in adjacent quadrats sampled in 1976 and 1978. Quadrats in creekbank habitat were 0.5 m²; quadrats in tall and short *S. alterniflora* habitats were 1 m². *L*—Predicted length of a mussel in 1978 that was 30 mm long in 1976.

Submerged (h·d⁻¹)	No.·quadrat⁻¹ 1976	No.·quadrat⁻¹ 1978	Net recruitment	*L* (mm)	No. > 30 mm, 1976	No. > *L* mm, 1978
			Creekbank			
12.7	251	379	128	49.6	226	223
12.3	69	138	69	47.8	69	88
11.9	46	71	25	46.5	46	64
			Tall *S. alterniflora*			
11.0	88	100	12	43.0	88	96
14.1	144	257	113	53.4	144	141
9.0	22	10	−12	39.1	22	10
12.5	126	171	45	48.7	124	114
14.3	22	48	26	53.7	22	43
			Short *S. alterniflora*			
7.4	28	38	10	36.1	21	29
6.8	21	37	16	34.7	20	31
9.1	43	64	21	39.3	39	57
6.9	16	28	12	34.6	16	25
7.0	15	7	−8	35.0	13	5

adult mussels must however ultimately be determined by the settlement and survival of spat, because mortality of large mussels is very low. Since the mortality of large mussels is low and recruitment increased as density increased, it is evident that the densities had not reached the maximum supportable.

Size frequency distributions indicate that recruitment varied substantially from year to year (Fig. 1). Mussels shorter than 30 mm were scarce in 1976, but were abundant in 1978 at low elevations. One or two years of similarly high recruitment before 1975 may account for the single mode in the size distributions

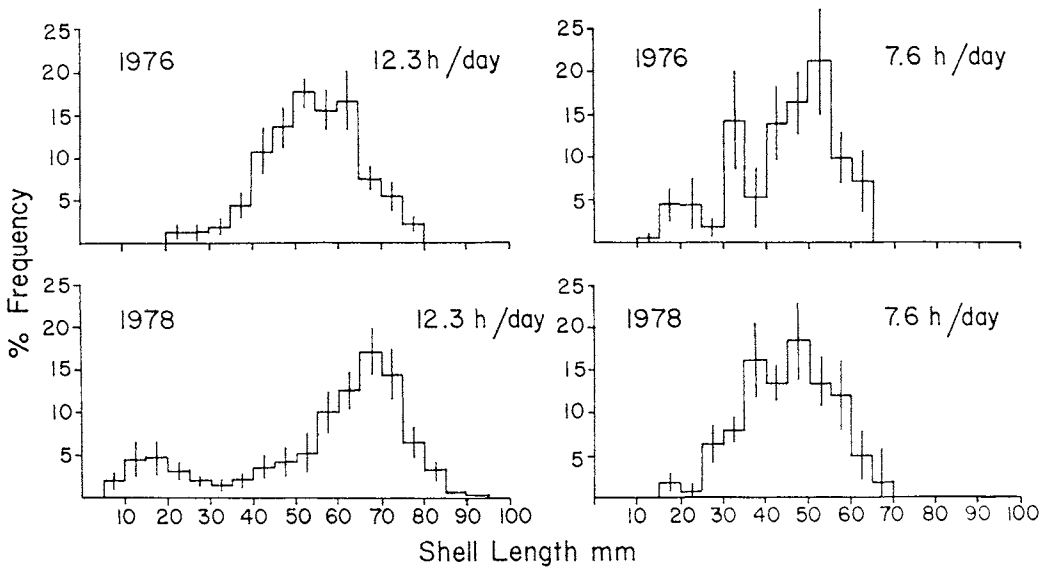

Fig. 1. Size frequency histograms for mussels from two elevations in 1976 and 1978. Vertical bars are ±SE of mean of frequency in each size class for several quadrats. Average hours submerged per day indicated for each elevation.

Table 3. Seasonal constants for regression equations for physiological rates vs. dry flesh weight. Filtration is in liters per hour submerged and other rates are in micrograms nitrogen per hour submerged. Rate = $A \cdot (\text{wt, g})^B$.

	Filtration	Ammonia excretion	Biodeposition	Byssal thread secretion, $h \cdot d^{-1}$ submerged	
				17	8
			Spring		
A	—	13.8	29.8	—	—
B	—	0.417	0.839	—	—
r	—	0.610	0.651	—	—
n	—	18	24	—	—
			Summer		
A	3.48	33.7	78.0	3.21	4.39
B	0.385	0.473	0.856	0.742	0.661
r	0.640	0.894	0.747	0.826	0.468
n	18	20	169	28	28
			Fall		
A	1.41	11.8	24.5	—	—
B	0.404*	0.400*	0.770	—	—
r	0.409	0.404	0.616	—	—
n	20	10	48	—	—

* Not significantly different from zero.

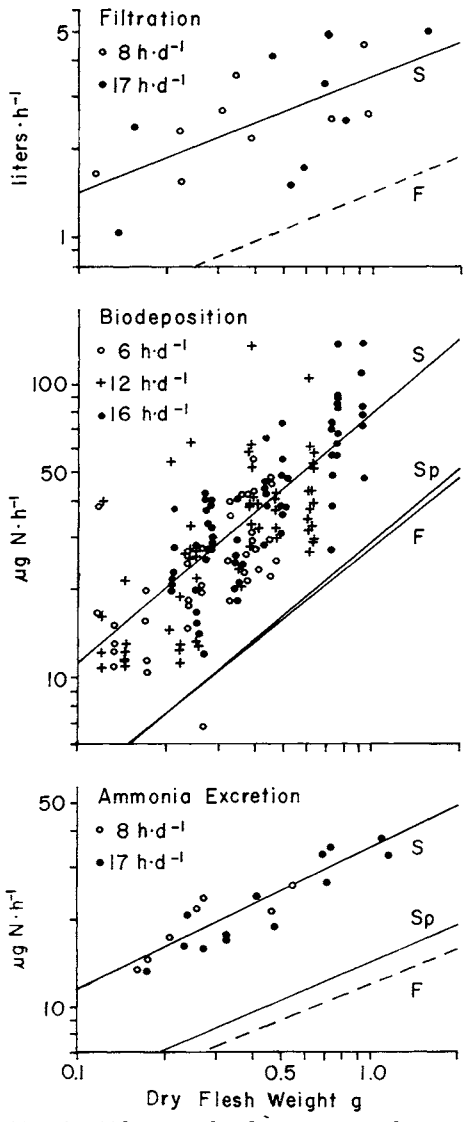

Fig. 2. Filtration, biodeposition, and ammonia excretion per hour submerged vs. dry flesh weight. Summer data points plotted with hours submerged per day indicated. Lines are regressions of summer (S), spring (Sp), and fall (F) data. Slopes of dashed lines are not significantly different from zero. Constants for regressions given in Table 3. Biodeposition was converted to units of nitrogen using measured nitrogen content of 1.2% (SE = 0.076, $n = 6$).

of mussels longer than 30 mm. The fact that this mode shifted between 1976 and 1978 indicates that the mussels of modal size were still growing and that the mode was not simply an accumulation of fully grown animals. If recruitment is generally sporadic, very low or sporadic mortality of large mussels may be enough to maintain the population at a steady state for a long time.

Physiological activities—The rates of physiological activities are generally power functions of the mussel's flesh weight (Table 3). Rates of filtration, biodeposition, and ammonia excretion rates are highest in summer (Fig. 2). The effect of season on these rates is proportionally the same for mussels of different weights, and the ratios of the rates remain constant throughout the seasons for mussels of a given weight. Our summer measurements agree with other measurements of filtration (Kuenzler 1961*b*), biodeposition (Haven and Morales-Alamo 1966), and ammonia excretion. Our measurement of lower filtration rates in fall than in summer contrasts Widdows and Bayne's (1971) finding that the rate of filtration by *Mytilus edulis* does not vary with temperature between 5° and 20°C. The seasonal trend of ammonia excretion, however, agrees with the finding of Bayne and Scullard (1977) that ammonia excre-

tion by *M. edulis* decreases as temperature decreases and shows no temperature acclimation.

The effect of mussel weight on summer filtration rates is highly significant ($P < 0.005$) in spite of relatively high variance in the data (Fig. 2). Variance is higher in fall than in summer because filtration is slower in fall. The effect of weight is not significant in fall, but the fall rate-weight regression parallels that of summer, which suggests that weight has a real effect. Laboratory measurements of bivalve filtration may be more precise (e.g. Winter 1978), but our measurements may be more accurate for predicting filtration in the field since we simulated field conditions and used mussels acclimated to the field.

The relative proportions of different rates vary with the size of the mussel (Fig. 2). For example, for small mussels the rates of ammonia excretion and biodeposition in units of nitrogen are about equal, while for large mussels the rate of biodeposition is much greater than the rate of ammonia excretion; also, the biodeposition to filtration ratio is lower for small than for large mussels. These observations suggest that small mussels have higher metabolic rates and digestive efficiencies than large mussels, probably consequences of their higher surface to volume ratios.

The elevation of *G. demissa* in the intertidal zone does not affect filtration, biodeposition, or ammonia excretion rate per hour of submergence (Fig. 2). In contrast, *Mytilus californianus* filters faster at low elevations than at high elevations (Segal et al. 1953). Our finding that elevation does not affect ammonia excretion rate suggests that mussels do not accumulate ammonia while exposed during low tide. If they did, mussels from high elevations would release ammonia faster while submerged than would mussels from low elevations. Bayne et al. (1975*a*) found that *M. californianus* accumulates ammonia during low tide at only 5% the rate of ammonia excretion during immersion.

Unlike the other physiological functions mentioned, secretion of byssal threads per hour of submergence is greater at high than at low elevations (Fig. 3). We tested the significance of this effect by regressing pooled measurements from both elevations against flesh weight and comparing the residuals of the measurements from the two elevations by the Mann-Whitney U-test ($P < 0.01$). Although mussels from the high elevation secrete signficantly more byssal threads per hour submerged, they secrete fewer per day than those from the low elevation. Mussels at high elevations secreted so few byssal threads during sampling periods that precision in measuring secretion was low. Nevertheless, the effect of weight on secretion rate was significant at both elevations ($P < 0.025$, high elevation; $P < 0.001$, low elevation). Removal of pre-existing byssal threads does not seem to stimulate initially high rates of secretion of new ones because the rates were the same during 21-, 41-, and 59-day periods after removal.

We could detect no excretion of dissolved organic nitrogen (DON) during summer, presumably the time when it

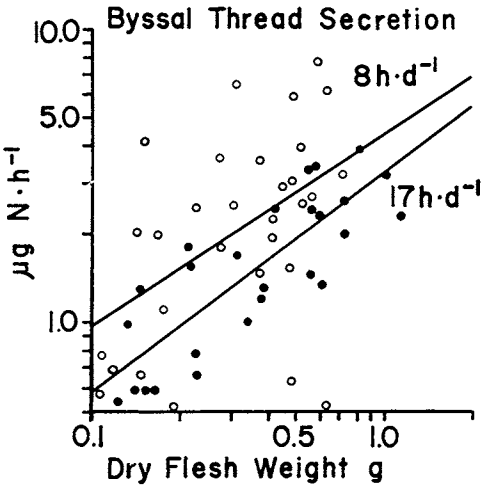

Fig. 3. Secretion of byssal threads per hour submerged vs. dry flesh weight. ○—Mussels submerged 8 $h \cdot d^{-1}$; ●—mussels submerged 17 $h \cdot d^{-1}$. Constants for regression lines given in Table 3. Weights of byssal threads were converted to units of nitrogen using measured nitrogen content of 13.33% (SE = 0.202, $n = 7$).

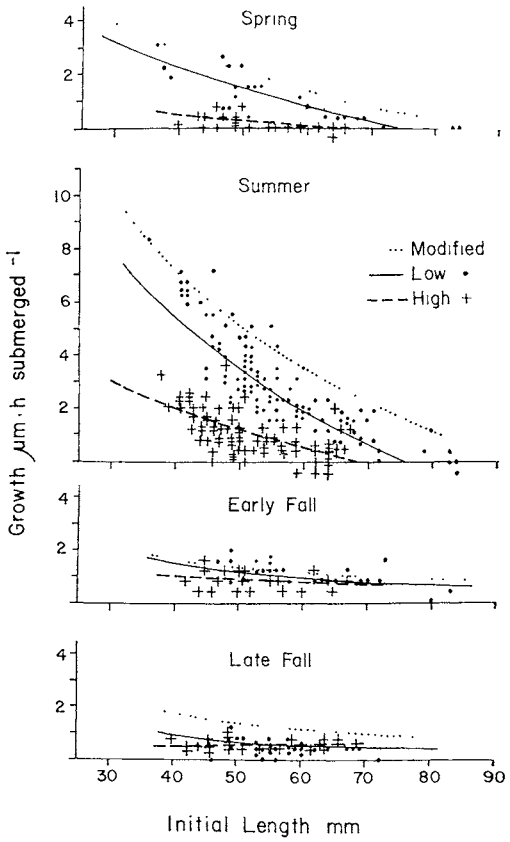

Fig. 4. Shell growth rate vs. initial shell length for four periods at high elevation, submerged 8 $h \cdot d^{-1}$ (+), and low elevation, submerged 17 $h \cdot d^{-1}$ (●). Solid and dashed lines fit by regressing growth rate against log of initial shell length for low and high elevation. Dotted lines represent modified regressions (*see text*). Constants for regressions given in Table 4.

Table 4. Seasonal constants for regression equations for growth in micrometers length per hour submerged vs. initial shell length. Growth = $A \cdot$(ln initial length, cm) + B.

	Submerged ($h \cdot d^{-1}$)		Modified regression, submerged 17 $h \cdot d^{-1}$
	17	8	
	Spring		
A	3.68	0.97*	3.68
B	15.81	4.02	16.46
r	0.774	0.517	—
n	30	20	—
	Summer		
A	8.50	3.70	8.50
B	36.74	15.61	38.42
r	0.847	0.645	—
n	119	80	—
	Early fall		
A	0.962*	0.675*	0.94
B	4.606	3.528	4.86
r	0.488	0.254	—
n	29	20	—
	Late fall		
A	0.534*	0.183*	0.94
B	2.451	0.128	4.86
r	0.346	0.166	—
n	30	20	—

* Not significantly different from zero.

would be highest. Other workers have found that mussels excrete significant amounts of DON, primarily as amino acids (Bayne and Scullard 1977; Lum and Hammen 1964). Wright and Stephens (1978) have shown that *G. demissa* can take up amino acids at concentrations similar to those in its natural environment, so that there may actually be a net uptake although we did not detect it.

Growth—The rate of shell growth decreases with increasing mussel size (Fig. 4). This trend is strongest during summer when shell growth is fastest. During winter (December–mid-April) there is no growth. During spring and summer, shell growth per hour of submergence is less at high than at low elevation. Others (reviewed by Seed 1976) have found that mussels grow less per day at high than at low elevations, but growth per hour of submergence has not been investigated before.

We used regressions of the log of initial length vs. growth per hour submerged (Fig. 4, Table 4) for predicting growth of 30-mm mussels to calculate mortality of mussels that were 30 mm or longer in 1976 (*see above*). These regressions provided the best fit to the data, although the von Bertalannfy model of growth predicts a linear relationship between growth and initial length (Yamaguchi 1975).

The relationship between the length of the shell and the weight of the flesh changes seasonally. Although the slopes of the length–weight regressions do not change seasonally, the adjusted means of weight do change (ANCOVA) and are

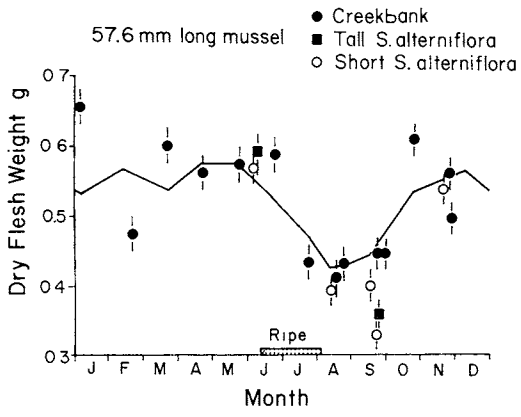

Fig. 5. Weight of 57.6-mm-long mussels from three habitats through year. Points are adjusted mean weights calculated by ANCOVA of ln length vs. ln weight. Mean length of measured mussels is 57.6 mm. Slope of ln length vs. ln weight regressions is 2.395. Vertical lines through points are ±SE of adjusted means. Line through points connects three-point running means for creekbank. Shaded bar—ripe gonads observed.

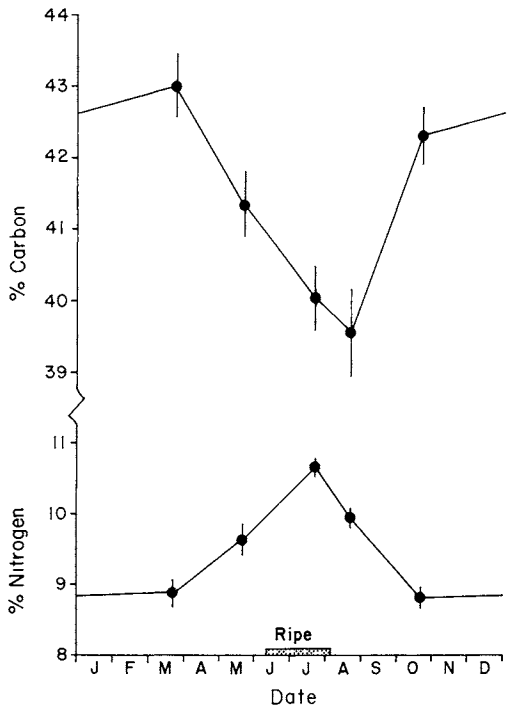

Fig. 6. Percent carbon and percent nitrogen in mussel flesh through year. Points are averages for mussels of different sizes. Vertical lines are ±SE. Shaded bar—ripe gonads observed.

lowest in August and September (Fig. 5). This means that mussels of a given length have the lowest flesh weight in August and September. In June and July the flesh of female mussels is brown, indicative of ripe gonads (Cerwonka 1968). Thus the decline in weight to a minimum in August and September probably results from consumption of fat and glycogen reserves during gametogenesis (Gabbott 1976) and from subsequent release of gametes. Mussels from high elevations may either release more gametes or consume more energy reserves than those from low elevations, since in September mussels from high elevations weigh less than those of the same lengths from low elevations. Mussels at all elevations recover lost weight in September and October, possibly due to production of fat and glycogen.

Percent carbon in mussel flesh was lowest (39.5%) and percent nitrogen highest (19.7%) just after gametogenesis (Fig. 6), reflecting consumption of stored carbohydrates. Percent nitrogen decreased during fall (Fig. 6) as did shell growth (Fig. 4), but growth in terms of nitrogen was highest in September due to the increase in flesh weight relative to shell length (Fig. 5).

Although our direct measurements of shell growth (Fig. 4, Table 4) reflect trends due to season, elevation, and the size of the mussel, they may generally underestimate growth. Shell growth estimated from the shift in the size frequency of mussels between 1976 and 1978 was higher than predictions based on our direct measurements (Jordan 1980). Therefore, we modified the regression equations used to predict growth of mussels at low elevation (Fig. 4, Table 4), so that the predicted growth of modal-sized mussels in 1976 was consistent with the mode observed in 1978. Growth of mussels at high elevations was calculated by difference for the nitrogen budget (*see below*).

Production of gametes—Measurement of the drop in nitrogen in the flesh of mussels during spawning provided a way

of calculating gamete production. First, we used the modified regression equations for growth (Table 4) to predict the lengths of mussels at low elevations throughout the seasons. Then we found the amount of nitrogen in the flesh from seasonal regressions of length vs. weight (Fig. 5) and percent nitrogen values (Fig. 6). Finally, we subtracted the measured amount of nitrogen in the flesh after gametes had been released from the amount of nitrogen estimated if gametes had been retained. We made a lower estimate of nitrogen lost as gametes by assuming that, if gametes had been retained, nitrogen in flesh would have increased at a constant rate between pre- and postreproductive periods and an upper estimate by assuming that, if gametes had been retained, nitrogen in the flesh would have increased during the spawning period at the same rate it actually increased in September, immediately after release of gametes. The upper and lower estimates differed by an amount equal to their mean, and we used the average of the two.

Although the effect of elevation on gamete production was not directly measured, other effects of elevation suggest that yearly gamete production is constant with elevation. Filtration, biodeposition, and ammonia excretion per hour of submergence are constant with elevation, while secretion of byssal threads per hour of submergence increases as elevation increases. Consequently, mussels at high elevations have less nitrogen per hour of submergence available for growth and gamete production than do those at low elevations. If yearly gamete production were constant with elevation, then gamete production per hour of submergence would increase as elevation increases leaving less nitrogen available for growth per hour of submergence at high than at low elevations. Since direct measurements indicated that growth per hour of submergence is, in fact, lower at high than at low elevations (Fig. 4) and since this difference in growth cannot be accounted for by the difference in byssal thread production, we concluded that yearly gamete production is probably constant with elevation.

Discussion

The nitrogen budget—From the above data we calculated the nitrogen budget for the mussel population. The population was divided into high and low elevation components (submerged 7.6 and 12.3 h per day) and the year divided into four periods, spring (17 April–15 June), early summer (16 June–9 August), late summer (10 August–30 September), and fall (1 October–29 November). Secretion of byssal threads during spring and fall was estimated by assuming that the ratio between secretion of byssal threads and excretion of ammonia was constant with season. Growth at the low elevation was calculated from the modified regression equations for growth (Fig. 4, Table 4). Filtration was calculated as the sum of biodeposition, ammonia excretion, byssal thread secretion, gamete production, and growth. Since filtration per hour of submergence is the same at high and low elevations, we could calculate growth at the high elevation by difference from other components of the budget.

We calculated the number of liters of water filtered by the mussels on the basis of our measurements of filtration rate (Fig. 2, Table 3), assuming filtration rates in spring to be the same as in fall. If liters filtered is converted to nitrogen filtered using a concentration of 90 μg of particulate nitrogen per liter for marsh water (unpubl.), the resulting estimate of the amount of nitrogen filtered is about three times that calculated by summing other nitrogen flows in the budget. For example, a mussel of 0.46 g of flesh weight submerged 12.3 h per day filtered 4,650 liters of water or 419 mg of particulate nitrogen yearly. However, when the amount of particulate nitrogen filtered by the same mussel is calculated by summing all other nitrogen flows in the budget, it amounts to only 143 mg for the year. One possible explanation for this discrepancy is that the concentration of particulate nitrogen in water entering the incurrent siphons is lower than the con-

centration in the water away from the mussels. This could result from mussels refiltering water in their vicinity. Such refiltration should be most pronounced where mussels are crowded or where water currents are too slow to replace already filtered water with unfiltered water. Therefore, refiltration could account for Stiven and Kuenzler's (1979) finding that crowding reduces the growth of *G. demissa*.

We estimated the standard errors of the yearly rates of filtration (in liters), biodeposition, and ammonia excretion by adding the variances of the rates predicted from their seasonal rate–weight regressions. Since the regressions were log-log, the standard errors could be expressed as percentages of the rates. The standard errors are 15% for filtration, 11% for ammonia excretion, and 12% for biodeposition. The standard error of yearly secretion of byssal threads is based on variances of predicted rates of both secretion of byssal threads and ammonia excretion, because calculation of yearly secretion of byssal threads relies on measurements of both rates. The standard error of yearly secretion of byssal threads is 14% for the low elevation and 17% for the high.

The main source of error in estimating nitrogen flows at the population level is in determining population size. Random variations in densities among quadrats result in a standard error for the total population of about 20% (Table 1). Thus, nitrogen flows through the entire population have standard errors of at least 20%.

Filtration and biodeposition are the major pathways of nitrogen flow through the mussel population (Fig. 7). Biodeposition is 50% of filtration, indicating that the mussel population absorbs half of the nitrogen it filters from suspension. Kuenzler (1961*b*) found that the biodeposition of phosphorus is 94% of filtration, suggesting that the mussels absorb only 6% of the phosphorus they filter. There are two reasons for the difference between his phosphorus budget and our nitrogen budget. First, he calculated filtration by measuring the concentration of

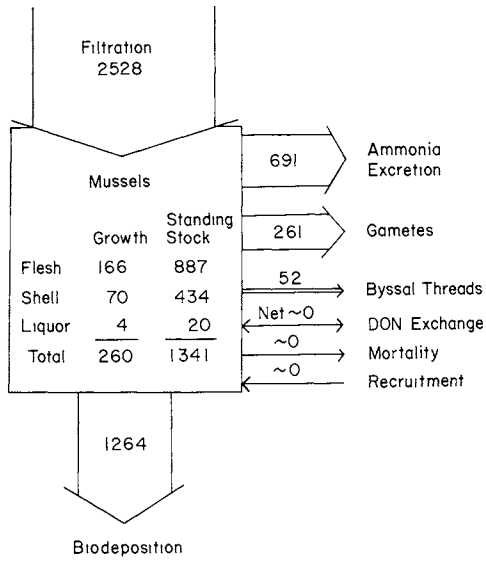

Fig. 7. Nitrogen flow through mussel population (units: kg N·yr^{-1}, except standing stock which is kg N). Width of arrows is proportional to flow.

suspended particulate phosphorus and multiplying by the volume of water filtered; an analogous calculation with our data overestimates filtration by a factor of three, possibly because mussels refilter the water in their vicinity. An overestimation of filtration in Kuenzler's budget would cause an overestimation of biodeposition because he found production of pseudofeces by difference from other parts of the budget. Although the population densities he measured were less than those we measured, mussels often occur in clumps where refiltration could be significant. The second reason for the difference between Kuenzler's budget and ours is that the concentration of suspended particles is higher where he worked than where we did. Suspended particulate nitrogen is about 290 μg·liter^{-1} in the Sapelo Island marsh (Haines 1977) and only about 90 in Great Sippewissett Marsh (unpubl.). Since filtration rate in units of water volume is equal in both marshes, the mussels in the Sapelo Island marsh filter more particulate matter and, consequently, produce more pseudofeces than do those in Great Sippewissett Marsh.

Since the C:N ratio in suspended matter (about 9:1; unpubl.) is about the same as in biodeposits, the mussels must absorb about 50% of the carbon as well as the nitrogen that they filter. Their assimilation efficiency must then be >50%, because they ingest less than they filter and because energy loss via excretion is minimal when ammonia is the primary waste product. By comparison, the assimilation efficiency of *M. edulis* varies from 20–90%, decreasing with increasing food intake (Thompson and Bayne 1972). Despite its variability, the assimilation efficiency of mussels is generally higher than the 5–20% efficiencies of many detritivores (Welch 1968; Heiman and Knight 1975). This suggests that mussels ingest food of higher quality than do most detritivores, although suspended detritus probably constitutes a significant part of it.

Although the proportion of carbon to nitrogen absorbed may be constant, the proportion of carbon dioxide released to ammonia excreted increases with the elevation of the mussel. This is because the mussels produce little or no ammonia during aerial exposure although, based on oxygen consumption measurements (Kuenzler 1961*a*), they release carbon dioxide during exposure at half the rate during immersion. Consequently, the ratio of net assimilation of nitrogen to net assimilation of carbon increases with elevation. This may reflect the increase in gamete production relative to growth as elevation increases, assuming that gametes are richer in nitrogen than the rest of the tissues. The ratio of oxygen consumed to nitrogen excreted (O:N) may also reflect the balance of catabolism of proteins, carbohydrates, and lipids: lower O:N ratios indicate proportionally more protein catabolism and are often produced by reduced food intake (Bayne et al. 1976*b*). Paradoxically, mussels at high elevations have higher O:N ratios although they feed less than mussels at low elevations. Apparently the alteration of metabolic pathways during aerial exposure makes O:N ratios difficult to interpret.

Of the nitrogen absorbed by the mussels, 55% is excreted as ammonia (Fig. 7). Kuenzler (1961*b*) found that 83% of the phosphorus absorbed by mussels is excreted as phosphate. This suggests that *G. demissa* is more efficient at conserving nitrogen than phosphorus. It may also mean that the food supply meets the phosphorus demands better than the nitrogen demands.

Production of gametes represents an output of 21% of the nitrogen absorbed by the mussels (Fig. 7). Little of this investment in gametes is returned to the population via settlement of larvae. Even if the number of larvae settling per year were 100 times the number of current adults, the resulting input of nitrogen would be only about 14 g yearly for the entire marsh, assuming that a *G. demissa* larva contains 0.007 μg of nitrogen as does a *M. edulis* larva (Bayne et al. 1975*b*). Most of the nitrogen in gametes probably enters the food web. Mussel gametes may be eaten by filter feeders, meiofauna, and microorganisms; mussel larvae may have an even wider range of predators. Predation on adult mussels is apparently minimal; mortality of mussels longer than 30 mm is undetectable. Furthermore, potential predators on adult mussels are apt to consume only the flesh, leaving the shell, liquor, and byssal threads. Since production of gametes exceeds production of flesh (Fig. 7), much more nitrogen enters the food web via predation on gametes and larvae than via predation on adult mussels. Mussels, then, are analogous to fruit trees: the fruits are eaten, not the trees.

Significance of mussels in nitrogen flow in the salt marsh—To evaluate the role of mussels in the nitrogen cycle of the salt marsh, we must compare nitrogen flow through the mussel population with that through the marsh ecosystem. In Great Sippewissett Marsh the mussel population has the highest biomass of any animal population and releases more ammonia into the water than any population of either plants or animals (Table 5). Ammonia excreted by mussels accounts for 31% of the total ammonia re-

Table 5. Release of ammonia into marsh water during summer by major marsh organisms. Excretion assumed to proceed 24 $h \cdot d^{-1}$ except for *G. demissa*. Biomass does not include shell weight for organisms having shells. Biomass of grasses is aboveground only. Biomasses of bivalves other than *G. demissa* estimated from population densities measured by others prorated by area of sandy creeks (Valiela and Teal 1979), the presumed habitat of the bivalves.

	Biomass (kg)	Release ($\mu g\ NH_3\text{-}N \cdot h^{-1}$)	Σ release ($kg\ NH_3\text{-}N \cdot d^{-1}$)
Bivalves			
Geukensia demissa	8,900	42	4.5
Mercenaria mercenaria	1,800 (Hibbert 1977)	42*	1.8
Mya arenaria	1,000 (Brousseau 1978; Edwards and Heubner 1977)	30 (Emerson 1969)	0.73
Gemma gemma	460 (Green and Hobson 1970)	42*	0.46
Grasses			
Spartina alterniflora	130,000 (Unpubl.)	0.90 (Unpubl.)	2.8
Spartina patens	36,000 (Unpubl.)	0.42 (Unpubl.)	0.40
Fish			
Menidia menidia	240 (C. Werme pers. comm.)	180 (Nixon et al. 1976)	1.1
Fundulus heteroclitus	490 (Unpubl.)	65 (Nixon et al. 1976)	0.76
Fundulus majalis	120 (C. Werme pers. comm.)	160 (Nixon et al. 1976)	0.47
Arthropods			
Uca pugnax	3,600 (Krebs 1976)	11†	1.0
Carcinas maenas	410 (Unpubl.)	11 (Needham 1957)	0.11
Orchestia spp.	140 (W. Wiltse pers. comm.)	11†	0.04
Snails			
Melampus bidentatus	460 (W. Wiltse pers. comm.)	19‡	0.21
Ilyanassa obsoleta	55 (B. Howes pers. comm.)	19 (Nixon et al. 1976)	0.02

* Excretion assumed equal to that of *G. demissa*.
† Excretion assumed equal to that of *C. maenas*.
‡ Excretion assumed to equal to that of *I. obsoleta*.

leased into the marsh water in summer by the major marsh organisms (Table 5). Although about 14 kg of ammonia nitrogen per day is released into the marsh water in summer (Table 5), 4–8 kg per day is imported to the marsh during the same time (Valiela et al. 1978). Apparently less ammonia is released by organisms in summer than is removed from the water by microorganisms and autotrophs. This is consistent with the finding of Nixon et al. (1976) that ammonia excreted in a salt marsh does not cause detectable changes in ammonia concentration in the water. They attributed the uptake of ammonia in the marsh mainly to bacteria and fungi growing on *Spartina* detritus with low nitrogen content. Thus, ammonia excreted by mussels or other organisms is probably recycled by decomposers within the marsh.

Mussels filter 1.8 times as much particulate nitrogen as is exported from the marsh per year (Fig. 8). However, it is not clear whether particles filtered by mussels would otherwise have been exported or sedimented, because sedimentation is 13.5 times net export. Much of this may result from resuspended particles rapidly settling out of suspension. Since particles which tend to remain in suspension are most subject to both filtration and export, filtration by mussels is likely to reduce significantly the amount of particulate matter exported from the salt marsh.

During summer, the mussels filter about 250,000 m^3 of water per tidal cycle. This is more than the tidal volume of the marsh (about 200,000 m^3: Valiela et al. 1978). Since most of the water in the marsh is exchanged with the tides, the mussels can potentially filter all the water in each tidal cycle. The amount of water filtered once by mussels is probably less than this because the mussels may refilter water in their vicinity.

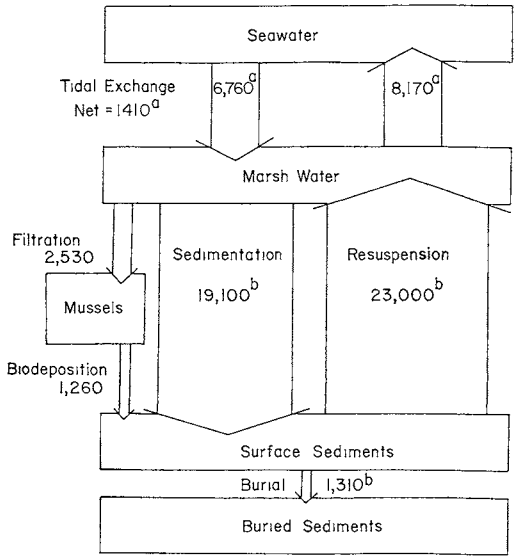

Fig. 8. Flow of particulate nitrogen in the salt marsh (units: kg $N \cdot yr^{-1}$). Width of arrows is proportional to flow. Superscript a—data from Valiela et al. 1978; superscript b—data from Jordan 1980.

Since resuspension exceeds gross tidal import of particles (Fig. 8), a significant proportion of the particles filtered by the mussels probably originates from the marsh sediments. The exact proportion cannot be determined, because the relative tendency for resuspended vs. imported particles to remain in suspension determines their relative concentrations in suspension. The amount of resuspended matter filtered by mussels also depends on the amount of resuspension occurring in the vicinity of the mussels.

Biodeposition of nitrogen is about equal to burial of nitrogen in sediment (Fig. 8), but some of the biodeposits may be resuspended. Both pseudofeces and feces, however, are larger and more prone to sedimentation than the particles from which they are formed. As a result, biodeposition delivers fine particles to the sediment where they may be ingested by deposit feeders. Although biodeposition by mussels is small in relation to total sedimentation, it could be an important source of particulate matter for deposit feeders in areas where mussels are abundant. For example, in the creek-bank habitat, where mussel densities are highest, biodeposition rate is about equal to sedimentation (Jordan 1980).

The major role of mussels in nitrogen flow in a salt marsh is to increase retention of nitrogen within the marsh by filtering particulate nitrogen from suspension. Other filter-feeding bivalves in the marsh (*Mercenaria mercenaria, Mya arenaria,* and *Gemma gemma*) play a similar role, but since mussels comprise about three-quarters of the total biomass of bivalves in the marsh (Table 5), they are responsible for most of the total filtration by bivalves. The magnitude of filtration by mussels in Great Sippewissett Marsh demonstrates the degree to which suspended particles in nearshore waters may be exploited by bivalve populations. If the particulate nitrogen filtered by mussels were instead exported from the marsh, export would be 2.8 times the present amount. Such an increase in export would significantly alter the nitrogen budget of the salt marsh, because export of particulate nitrogen represents one of the major losses of nitrogen from the marsh (Valiela and Teal 1979). Since nitrogen limits productivity in salt marshes (Valiela and Teal 1979), increased retention of nitrogen due to filtration by mussels may ultimately enhance the productivity of the marsh.

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