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Filter-feeding in *Corbicula fluminea* and its effect on seston removal

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Abstract. Factors affecting filtration rates of the Asiatic clam *Corbicula fluminea* were studied in controlled laboratory experiments, and the data were then used to illustrate the importance of clam filtering in a North Carolina river. Both temperature and food concentration significantly affected clam filtration rates. Rates measured at winter temperatures were significantly lower than summer rates, while food concentrations and filtration rates were inversely related. Filtration rates were compared among clams collected from several different habitats in North Carolina, and although shell length (SL)-dry flesh weight (DFW) relationships differed between locations, filtration rate-size relationships were not significantly different when SL was used as a measure of clam size. Extrapolation of the above relationships to a population of *Corbicula* in the upper Chowan River, North Carolina, indicated that the average number of clams in a square meter of river bottom (350) could filter a volume of water equivalent to the overlying water column (mean depth 5.25 m) every 1-1.6 days in summer, depending on seston concentrations.

Key words: *Corbicula*, Asiatic clam, bivalve, filter-feeding, seston removal, North Carolina.

Filter-feeding bivalve molluscs remove particles from the surrounding water, retaining and sorting these particles on the gills. Laboratory experiments with estuarine bivalves indicate that many species can potentially process large volumes of water, up to 1-2 L/hr per individual (Haven and Morales-Alamo 1970, Hildreth and Crisp 1976, Winter 1970). Thus filter-feeding bivalves can be important in the removal of suspended particulate matter in estuarine systems (Haven and Morales-Alamo 1966, Krauter 1976, Kuenzler 1961, Tenore and Dunstan 1973) and in shallow habitats where abundant bivalves have been implicated as the major control of seston concentrations (Cloern 1981, Officer et al. 1982, Rhoads 1974). Filtered material is sorted at several points: the gills, labial palps, and stomach (Morton 1979), so not all material removed from suspension is ingested. However, both rejected material (pseudofeces) and excreted material (feces) are deposited in the sediments, and this biodeposition may substantially accelerate natural seston deposition (Tenore and Dunstan 1973). Filter-feeding bivalves, therefore, have been considered to couple water column and benthic subsystems (Dame et al. 1980).

Among freshwater bivalves, the exotic Asiatic clam *Corbicula fluminea* (Müller) (= *manilensis*, Britton and Morton 1979) would appear to have the greatest potential for affecting sediment-

water exchanges by its filtration activities. It is the predominant benthic filter-feeder in many U.S. lakes and rivers south of 40° latitude, and densities of more than 1000 clams/m² are common (see McMahon 1983). Clams can remove particle sizes ranging from 5 to 30,000 μm² (Wallace et al. 1977), and based on limited data, recent studies have indicated that populations of *Corbicula* can significantly enhance seston removal in large rivers (Cohen et al. 1984, Lauritsen and Mozley 1983). Other freshwater filter-feeding bivalves found in the U.S. (Unionidae and Pisidiidae) have very low filtration rates (Mattice 1979) and are not usually abundant, so therefore can be expected to have less impact. For example, Hornbach et al. (1984) estimated that a pisidiid population could remove only 0.0004% of the carbon from a stream annually.

Several factors influence filtration rates in marine species, including bivalve size, food concentration, and temperature (e.g., Winter 1978). In my study, laboratory experiments were conducted to determine how each of these factors affects *Corbicula* filtration rates. I hypothesized that rates would be inversely related to food concentration, but directly related to individual size and temperature. This is the first reported work in which the importance of these factors has been tested under controlled laboratory conditions. Also, filtration rates of clams from different habitats were compared and re-

sults extrapolated to populations of *Corbicula* in a North Carolina river to estimate the potential impact they may have on removal of suspended material in a natural habitat.

Methods

Experimental organisms

Clams were collected from three locations in North Carolina: Lake Waccamaw (Columbus Co.), an artificial stream fed by a diversion from the Neuse River near New Bern (Craven Co.), and the Chowan River at Winton (Hertford Co.). Clams were held at 20°C in buckets containing at least 5 L of constantly aerated water from the collection site and a 5-cm deep layer of sand. Holding time ranged from 2 to 6 days and during this period clams were fed cultured algae, including *Chlorella vulgaris*, *Ankistrodesmus* sp., *Scenedesmus quadricauda* and *Cyclotella* sp. Details of algal culture are given in Lauritsen (1986).

Feeding experiments

Experiments were conducted at 20°C except as noted. Clams were isolated 18–24 hr in containers of filtered (Whatman GF/C filters) lake water, then acclimated 1 hr in feeding chambers which contained 1.5 L of continuously circulating, filtered water. Chambers were closed systems consisting of two compartments: (1) a chamber containing the clam, and (2) a dosing chamber made from a 2-L aquarium filter box where food was initially added and which continually circulated water through PVC pipes to (1) and back. Visual observations indicated that water movement was sufficient to keep particles suspended without disturbing clam shell gape or siphon extension.

Filtration rates were determined indirectly as changes over time in concentration of either algal chlorophyll *a* or ¹⁴C-labeled algae. To determine if the two methods gave significantly different rate estimates, an experiment was conducted using equivalent volumes (1 mm³ total) of labeled and unlabeled *Chlorella* fed to clams collected from the artificial stream. Twenty hours before feeding, two samples of *Chlorella* were removed from the same batch culture, 2 μCi of ¹⁴C bicarbonate were added to one, and both samples were placed under cool white light. One hour before feeding, each

portion was centrifuged, washed and resuspended in filtered lake water to separate labeled algae from the radioactive culture medium (Petrocelli et al. 1977). Total algal biovolume was determined for each portion with a Coulter Counter Model T_{AII}, with a 100-μm aperture (Sheldon and Parsons 1967). A randomized block design was used to assign treatments of labeled and unlabeled *Chlorella* to the clams (*n*=8 for each treatment).

Experiments ended 1 hr after the addition of food, and earlier testing indicated that no label would be respired or excreted during this time (Lauritsen 1985). Clams were removed, frozen, and dried at 60°C for 2 wk; dry flesh weight (DFW) and shell length (SL) (longest dimension) of each clam were then determined. The water containing algae not removed by clams was filtered (Whatman GF/C) to determine final algal concentrations, and 1-mm³ total volumes of labeled and unlabeled algae were filtered to determine initial concentrations of chlorophyll *a* or ¹⁴C.

After drying and fuming with HCl to remove traces of inorganic carbonate (Parsons et al. 1984), radioactive filters were placed in vials with 10 ml Scintiverse® scintillation cocktail, and counted on a Beckman LS 7000 liquid scintillation counter, using an external standard to determine counting efficiencies (Wang et al. 1975). Unlabeled filters were frozen and extracted with 90% buffered acetone, and chlorophyll *a* content determined (Wetzel and Likens 1979) with a Bausch and Lomb Spectronic 200. The same methods for sample treatment and analysis were used in all other filtration rate experiments.

Filtration rates (FR) for individual clams were calculated according to the formula (Coughlan 1969):

$$FR = \frac{\text{volume of water}}{\text{time}} \cdot \log_e \frac{\text{initial [food]}}{\text{final [food]}} \quad (1)$$

The ratio of initial to final food concentration was determined as the total amount of algal radioactivity or chlorophyll *a* dosed divided by the algal radioactivity or chlorophyll *a* remaining at the end of 1 hr. Algal settling was assumed negligible since water in feeding chambers was continuously circulated (Hildreth and Crisp 1976, Petrocelli et al. 1977) and so is not included above.

To determine the effect of food concentration on filtration rates, a randomized block design was used with four levels of food as treatments. A mixed culture of *Ankistrodesmus* and *Scenedesmus* (equal volumes of each) was fed to clams from the artificial stream at algal volumes of 0.33, 0.67, 1.33, and 2.67 mm³/L (*n*=3 clams for each treatment), and filtration rates were determined from changes in chlorophyll *a* concentration. The range of shell lengths of clams used was 21.2–24.1 mm, with a mean SL=22.7 mm (SE=0.27).

The effect of temperature on filtration rates was determined at 8°C, 20°C, and 31°C using clams collected from Lake Waccamaw in January (for 8° tests), June (for 20° tests), and August (for 31° tests) 1984. Clams were held 24–48 hr at the appropriate temperatures and filtration rates were determined from changes in concentration of ¹⁴C-labeled *Chlorella* (1 mm³ total algal volume used at each temperature). Clams of a similar size were used in these experiments (mean SL=22.4 mm, SE=0.24).

Filtration rates of clams were also compared among the three different collection sites. Rates were determined for clams collected between 13 July and 8 August 1984, from changes in ¹⁴C-labeled *Chlorella* (1 mm³ total volume).

Statistical methods

Two ANCOVAs were used to test for location differences and significance of the methods used to measure filtration rates, with clam size (either DFW or SL) used as the covariate in each case. All data were log-transformed, and treatments were first tested for parallel slopes, a prerequisite for ANCOVA, by using a multiple linear regression (Neter and Wasserman 1974, SAS Institute, Inc. 1982). ANOVA was used to determine significance of food concentration and temperature on filtering rates, and *F*_{max} tests were first used on these data to test for homogeneity of variances. A Pearson product-moment correlation was used on log-transformed data pooled from all three collection sites to determine whether shell length (SL) or dry flesh weight (DFW) was more highly correlated to clam filtration rate.

Results

Corbicula filtration rates measured using chlorophyll *a* varied more (range 109–1370 ml/

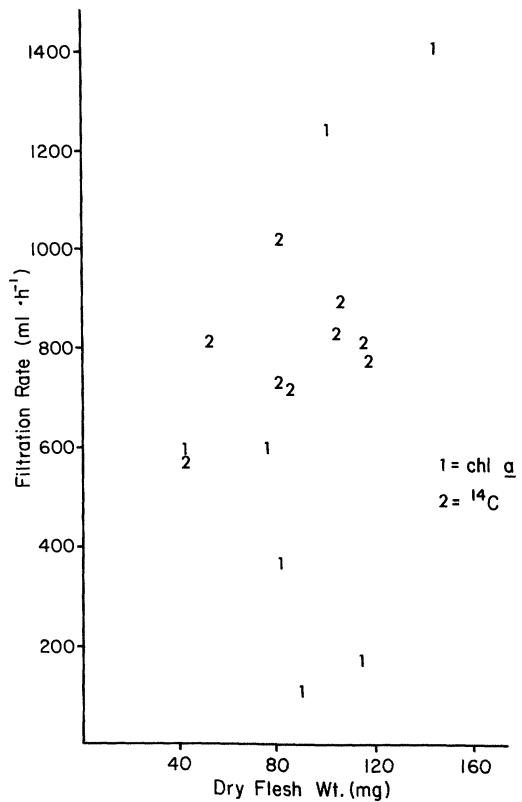


FIG. 1. Individual *Corbicula* filtration rates (ml/hr) as a function of clam dry flesh weight (mg), measured by changes in chlorophyll *a* concentration (1) and by changes in concentration of ¹⁴C-labeled algae (2). Each diet consisted of a total volume of 1 mm³ *Chlorella*.

hr) than rates measured by ¹⁴C (564–1010 ml/hr; Fig. 1), but there was no statistically significant difference in the method used (*p*=0.464, with SL as the covariate in the ANCOVA).

Food concentration had a significant effect on filtration rates (*p*<0.001). Rates per individual decreased with increasing food concentration, although the volume of algae ingested (ingestion = amount filtered because no pseudofeces were observed) increased significantly (*p*<0.0001) at higher food concentrations (Table 1).

Temperature also had a significant effect on filtration (*p*<0.001), due to the significantly lower winter rates that were measured at 8°C (a posteriori orthogonal contrast of winter vs. spring-summer (20 and 31°); *p*<0.001) (Table 2). Half of the clams tested at 8° (*n*=8) did not open their shells during the 1-hr test period so

TABLE 1. Effect of varying food concentrations (combination of equal volumes of *Ankistrodesmus* and *Scenedesmus*) on *Corbicula* mean filtration rate and mean volume ingested by the clams during the feeding period. Tests were conducted at 20°C, $n=3$ clams per treatment.

	Algal Volume (mm ³ /L)				
	0.33	0.67	1.33	2.00	2.67
Mean filtration rate (ml/hr)	782.3	656.5	489.0	420.2 ^a	277.8
1 SE	69.6	55.5	53.6		82.5
Mean volume ingested (mm ³)	0.23	0.41	0.64		0.80
1 SE	0.01	0.03	0.06		0.07

^a Algal volume used to represent summer seston concentrations in the Chowan River, obtained by extrapolation (see text).

were not included in the statistical analysis. Rates of clams collected in spring and summer were not significantly different (orthogonal contrast, $p>0.50$) (Table 2).

A comparison of filtration rates was made among clams from three locations in North Carolina. Because SL-DFW relationships in *Corbicula* vary both with season (Lauritsen 1985, Williams and McMahon 1986) and between habitats (Fig. 2), filtration rates were regressed against both SL and DFW. But since treatment slopes were not parallel in either set of regressions, ANCOVAs could not be used to test for location differences. *Corbicula* collected from Lake Waccamaw had much reduced weights for a given SL (Fig. 2) so that regressions of rates against DFW suggest a trend of location differences (Fig. 3a). Regressions of rates against SL are more similar among locations, although the Chowan slope was flatter than the other two regression lines (Fig. 3b), indicating that filtration rates increased less in larger clams. Filtration rates of clams of a given size were similar among locations (e.g., for 20-mm clams, filtration rates would be about 600 ml/hr for Cho-

wan, 620 ml/hr for Neuse artificial stream, and about 720 ml/hr for Lake Waccamaw).

Correlations using pooled data from the three collection sites indicated that filtration rate was more highly correlated to SL ($r=0.822$) than to DFW ($r=0.739$), although SL was highly correlated with DFW in the same clams ($r=0.890$). Because small clams (<13 mm SL) were collected only from Lake Waccamaw, a regression of SL and filtration rate was based on pooled data from the three sites (Fig. 3), resulting in the following allometric equation:

$$FR = 3.534SL^{1.723} \quad (2)$$

where SL is the untransformed shell length (mm) and filtration rate (FR) is expressed in ml/hr. Shell length of clams used to develop this relationship ranged from 8.3 to 27.2 mm ($n=41$).

Discussion

Filtration rates reported in the literature for average-sized (about 20 mm SL) *Corbicula* vary widely: 20–150 ml/hr (Prokopovich 1969); mean of 11 ml/hr (Habel 1970); mean of 816 ml/hr (Auerbach et al. 1977); 500–600 ml/hr (Mattice 1979); 24 ml hr⁻¹ g⁻¹ clam wt (Cohen et al. 1984). Relevant comparisons are impossible because in most cases the test conditions are not well elucidated, nor are clam sizes reported in a consistent manner. In my study, the wide range in filtration rates measured by changes in chlorophyll concentration shows how a particular method could potentially affect the results obtained.

Research with filter-feeding zooplankton as well as with marine bivalves indicates that at higher food levels, filtering rates decline while

TABLE 2. *Corbicula* mean filtration rate as a function of water temperature. Similarly sized clams (mean SL=22.4 mm) were used for testing. At 8°C, only data from clams that opened their shells were analyzed.

	Temperature		
	8°C	20°C	31°C
Mean filtration rate (ml/hr)	245.9	905.8	951.3
1 SE	47.4	43.6	78.9
n	4	4	4

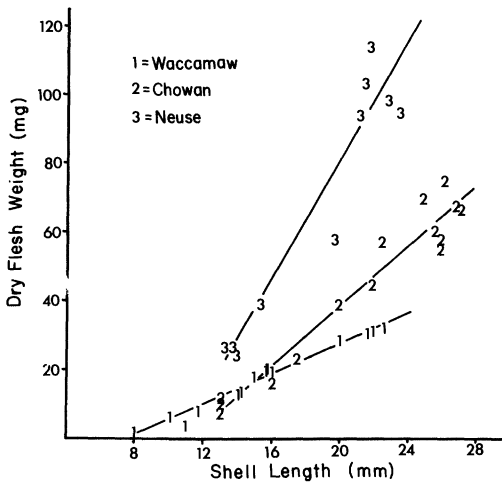


FIG. 2. Relationship between shell length and dry flesh weight of *Corbicula* collected from three different habitats in North Carolina in summer 1984: 1 = Lake Waccamaw; 2 = Chowan River at Winton; 3 = artificial stream, diversion of the Neuse River near New Bern.

rates of ingestion remain relatively constant, with a large percentage of filtered material usually being rejected by the animals (e.g., Lehman 1976 for zooplankton, Winter 1978 for marine bivalves). I observed no definitive leveling off of ingestion rate with increasing food concentrations although Table 1 suggests such a trend. Other experiments, again at food concentrations representing natural conditions, indicate that production of pseudofeces by *Corbicula* is dependent more on the type (i.e., shape, size) of algal food (Lauritsen 1985) than on concentration.

Measuring filtration rates in situ, Mattice (1979) found no significant correlation between *Corbicula* filtration rate and seston concentration over the range of 7–25 mg/L. C. B. Jørgensen (August Krogh Institute, Copenhagen, personal communication) believes that bivalves do not normally modify filtration rate in response to variations in food concentrations, so experiments that show an inverse relationship between the two are simply a reflection of less than optimum test conditions for the bivalves. Further in situ testing of *Corbicula* filtration is needed, although obviously it is difficult to control for factors other than seston concentration in such studies.

My work shows that at 20 and 31°C *Corbicula*

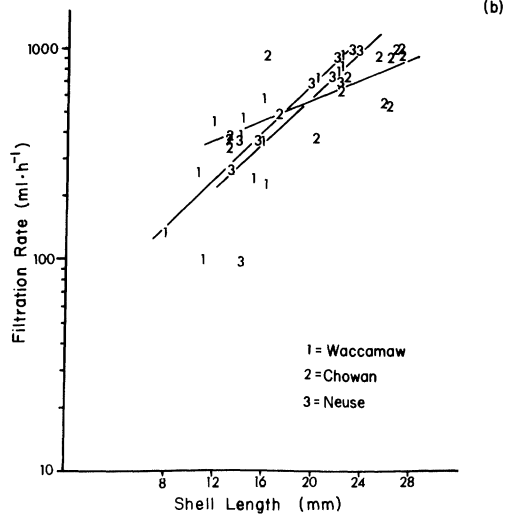
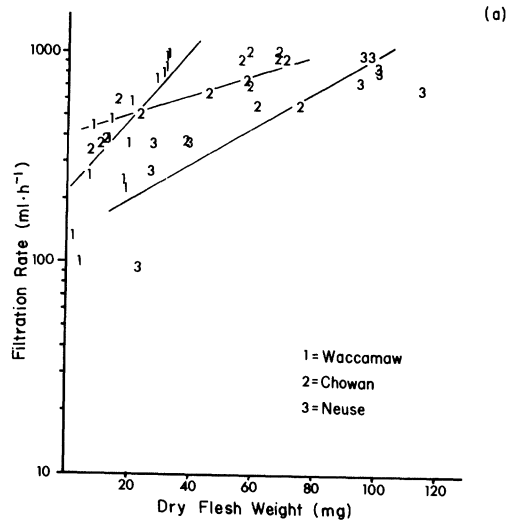


FIG. 3. Relationship between filtration rate (at 20°C) and (a) dry flesh weight, and (b) shell length, for *Corbicula* collected from: 1 = Lake Waccamaw; 2 = Chowan River at Winton; 3 = artificial stream, diversion of the Neuse River near New Bern. Individual regression lines are shown on each graph; for pooled regressions of filtration rate vs. dry flesh weight, $r=0.739$, and for pooled filtration rate vs. shell length, $r=0.822$.

filtration rates were not significantly different, while clams appear relatively inactive at winter temperatures and have very low filtration rates. Mattice (1979) measured *Corbicula* filtration rates (in situ) over the range 18–27°C and found maximum rates at 24°C (about 800 ml/hr for 22-

mm clams), with rates dropping to about 400 ml/hr at 27°C.

Dry flesh weight (DFW) is commonly used as an expression of clam size in allometric relations of physiological functions like filtration rate. But in *Corbicula*, flesh weight may vary greatly in a clam of a given SL, both seasonally within a population (Lauritsen 1985, Williams and McMahon 1986) and among populations from different habitats. *Corbicula* may actually reduce tissue weight over the course of the summer when most of their acquired energy goes into reproduction and shell growth (Williams and McMahon 1986). I have therefore suggested that SL be used as an estimator of size for filtration rate relationships.

Estimate of the importance of Corbicula filtration in a North Carolina river

The relationships described here between filtration rate and clam size, food concentration, and temperature can be used to predict the impact that *Corbicula* filter-feeding may have in the Chowan, a large Coastal Plain river. A benthic survey of the river, conducted in 1980, sampled 17 transects, with 6 sample sites at each transect (Lauritsen and Mozley 1983). The Winton transect from the upper river, used here as an example, averaged 350 clams/m² (mean SL of clams = 18.4 mm). Higher densities of clams were found in the deeper part of the channel where sediments consisted primarily of medium to coarse sand and some detritus.

I assumed that the influence of spring-summer variation in water temperatures in the Chowan (20–28°C; Kuenzler et al. 1982, NCDEM 1984) on filtration rates would be negligible. However, food concentrations (determined as chlorophyll *a* concentrations) had a significant effect on rates, so I used the spring-summer range in chlorophyll *a* values in the Chowan near Winton (<5 µg/L to 10–14 µg/L; Kuenzler et al. 1982, NCDEM 1982, 1984) to calculate a range in clam filtration rates at high (summer) and low (spring) food concentrations. Chlorophyll values represent surface water concentrations in the river, but the water column is well mixed, and surface-to-bottom chlorophyll *a* concentrations are similar (H. W. Paerl, University of North Carolina, personal communication). In filtration rate-food concentration experiments I measured both algal volume (mm³) and chlorophyll *a* content in order to

relate the two. The range in chlorophyll *a* concentration in the river was equivalent to 0.67 mm³/L of algae in spring and 2 mm³/L of algae in summer. The higher summer algal concentration would cause an estimated 64% reduction in clam filtration rates measured at 0.67 mm³/L.

Shell length-frequency data from the survey were used in conjunction with Equation 2 to determine filtration rates, then values were summed to obtain total volume of water filtered per m² of river bottom (V_T) at each of the six stations along the Winton transect:

$$V_T = \sum FR_i$$

where $FR_i = N_i \cdot [3.534SL_i^{1.723}]$ and N_i = number of clams with shell length *i*. An average (V_{Ave}) filtration rate per m² of clams at Winton was then calculated by dividing V_T by 6 (number of samples). Because the clam size-filtration rate relationship in Equation 2 was developed using 0.67-mm³/L food levels, these results (V_{Ave}) are equivalent to the population filtration estimate at low (spring) food concentrations, and the estimate for high food levels is $V_{Ave} \cdot 0.64$.

Mean monthly discharge at Winton in summer 1982 was 73.3 cm/s (Daniel 1977; U.S. Geological Survey Water Resources Division, Raleigh, North Carolina, unpublished data). Mean water depth at Winton is 5.25 m, so clams found in a square metre could filter a volume equivalent to the overlying water (5.25 m³) every 1.04 d at low chlorophyll concentrations or every 1.6 d at high concentrations. Since nothing is known of boundary layer flow rates, which would affect the amount of river water actually filtered by the clams, I make this comparison only as an illustration of the magnitude of water filtered, and do not suggest that the clams are actually filtering all of the overlying water during a certain time. In the only other assessment of the significance of filter-feeding by *Corbicula*, Cohen et al. (1984) estimated that clam populations within a stretch of the Potomac River could filter a volume of water equivalent to the volume of water contained within the stretch of river in 3–4 d. *Corbicula* densities were much higher (about 1400/m²) than in the Chowan, but the average filtration rate that the Potomac researchers used in their estimates was much lower than rates reported here (about 100 ml/hr for a 20–22-mm

SL clam, determined in laboratory experiments).

In estuarine systems, filter-feeding bivalves may deplete seston concentrations within the benthic boundary layer (Wildish 1977, Wildish and Kristmanson 1984). It is presently unknown whether seston depletion may occur where *Corbicula* beds are dense, and the premise here of a well-mixed water column in the Chowan may not represent conditions a few centimetres above the sediment surface. Clearly, the next step in evaluating the impact of filter-feeding bivalves in seston removal should be consideration of the conditions within the benthic boundary layer, and determination of how well this layer mixes with the overlying water column at different levels of flow. There appears to be a good correlation between the distribution of *Corbicula* and flow speed (in the Chowan, *Corbicula* is most abundant at estimated average flows above 0.14 cm/s; Lauritsen and Mozley 1983) and a certain minimal water velocity may be necessary to facilitate mixing between the boundary layer and the overlying water column, preventing seston depletion. Given the volume of water which can be filtered per clam and typical densities of *Corbicula* encountered in most habitats, their potential for particulate removal is significant.

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