

Transport of dissolved organic carbon through a major creek of the North Inlet Ecosystem*

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ABSTRACT: Tidal fluctuations and transports of dissolved organic carbon (DOC) were investigated at a major creek draining 1800 ha within the North Inlet Ecosystem (South Carolina, USA). Samples were collected every 1.5 h for 50 consecutive hours during neap tides (4 tidal cycles) and 50 consecutive hours during corresponding spring tides of each season. DOC concentrations were variable, ranging from 0.9 to 13.0 g m⁻³ of water with as much as 2.5 g m⁻³ of water variation during a 1.5 h period. DOC was exported from the marsh during each sampling period. Net transports ranged from approximately 5 to 480 g DOC s⁻¹. Annual budgets revealed a DOC export rate as high as 7.5 ± 1.8 × 10⁹ g C yr⁻¹ corresponding to 416 g DOC m⁻² yr⁻¹

INTRODUCTION

Movements of materials through estuaries and salt marshes have received considerable attention in the 2 decades since Teal's (1962) paper on energy flow through a salt marsh ecosystem. Much of the emphasis has been on determining net directional flows of suspended sediments (Settlemyre and Gardner, 1977), nutrients (Valiela et al., 1978), and forms of organic carbon (Woodwell et al., 1977).

Transports of particulate organic carbon (POC) have been investigated frequently and data are available for at least 8 estuaries or marsh systems (Nixon, 1980). Dissolved organic carbon (DOC) transports have not received as much attention even though concentrations can be 2 to 10 times that of POC (Happ et al., 1977). Additionally, components of the DOC pool are available to heterotrophic bacteria and the resulting particulate matter may contribute to other trophic levels (Crawford et al., 1974). In his review of DOC utilization in aquatic environments, Sepers (1977) pointed out that components of the DOC pool are available to heterotrophic bacteria and are also directly taken up by some phytoplankton and invertebrates. Recently, Manahan et al. (1982) provided con-

vincing evidence for dissolved amino acid uptake by the mussel *Mytilus edulis*.

Despite the importance of DOC as a major component of the total organic carbon (TOC) pool, annual DOC transport rates are available from only 4 marsh systems and 1 bay (Nixon, 1980). Each marsh system exported DOC at rates ranging from approximately 8 to 80 g C m⁻² yr⁻¹. The only bay system studied, Barataria Bay, exported DOC to the Gulf of Mexico; however, the export rate was considerably higher, approximately 140 g C m⁻² yr⁻¹ (Happ et al., 1977).

Apart from Barataria Bay, DOC transport data are from marshes along northern portions of the Atlantic coast. These marshes are relatively small systems within the confines of larger estuaries. Results presented herein evaluate DOC exchanges between a major creek draining a section of large, undisturbed, southeastern marsh and the Atlantic Ocean.

METHODS

Sampling was at a transect across Town Creek in the North Inlet Ecosystem (SC, USA, 33° 20' N, 79° 10' W). The creek drains much of the northern section of a 3200 ha salt marsh and forms a large section of the marsh inlet. Descriptions of the North Inlet Ecosystem and the sampling location are available (Dame et al., 1977; Chrzanowski et al., 1982a).

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Samples were collected quarterly throughout 1979 from 3 boats moored and positioned so data would accurately reflect material flow through the transects (Chrzanowski et al., 1979b; Kjerfve et al., 1981). Water was pumped (Guzzler Pump, Dart Union Corp.) from 0.2 m above bottom, 0.2 m below surface and from a midway point, collected in sterile acid-washed 500-ml glass bottles, placed on ice in the dark and immediately transported to nearby laboratory facilities. Samples were collected at 1.5 h intervals for 50 consecutive hours (4 tidal cycles) during neap and spring tides. The pump intake tubing was autoclaved between each 50 h period. During the winter, samples were collected during a mid tide instead of a neap tide.

Subsamples for DOC analysis were filtered, usually within 2 h of collection, through precombusted 47-mm glass-fiber filters (Whatman, GF/F, retention, 0.7 μm) and the filtrate collected in sterile acid-washed screw cap tubes. Filtrates were immediately frozen on dry ice and maintained at -20°C until analysis. DOC was measured using the persulfate oxidation method of Strickland and Parsons (1968). Resultant CO_2 was measured with an infrared analyser (Beckman model 215A).

Velocity measurements were taken concurrently with water samples using biplane current crosses (Pritchard and Burt, 1951). Velocity and DOC data were computer fitted to a smooth curve and new values extrapolated at 11 equispaced points from surface to bottom. For details of this procedure, methods for cross-sectional bathymetry, and tide curve construction consult Chrzanowski et al. (1979b) and Kjerfve (1975).

Instantaneous DOC transport (F) was calculated from

$$F = \sum_{j=1}^N \frac{h_j}{10} (0.5 V_{oj} W_{oj} C_{oj} + \sum_{i=1}^N V_{ij} W_{ij} C_{ij}) \quad (1)$$

where water velocity, station width, and DOC concentration at the surface of the j^{th} station are given by V_{oj} ,

W_{oj} , and C_{oj} , respectively. V_{ij} , W_{ij} , and C_{ij} are the water velocity, station width and DOC concentration at the i^{th} depth of the j^{th} station. Single tidal transports were determined by summing instantaneous transports for each tidal cycle.

Sustained rhythms in DOC transport for each consecutive four tidal cycles were described by

$$F = \mu + \alpha_1 \sin(2\pi T/24.84) + \beta_1 \cos(2\pi T/24.84) \\ + \alpha_2 \sin(2\pi T/12.42) + \beta_2 \cos(2\pi T/12.42) \\ + \alpha_3 \sin(2\pi T/6.21) + \beta_3 \cos(2\pi T/6.21) + \epsilon \quad (2)$$

This equation fits instantaneous DOC transport (F) as a function of time (T) and calculates an estimate of the average net transport (μ); α_1 , α_2 , α_3 , β_1 , β_2 , β_3 are coefficients; ϵ is a random error term. Tidal periods (24.84, 12.42, 6.21 h) are included to explain deviations from the average net transport. Sine and cosine terms reduce the standard error of the estimator of μ by accounting for variability resulting from tidal oscillations.

The equation is a form of general linear model and least squares estimates of μ and coefficients were determined using the general linear model procedures of the SAS computing package (Helwig and Council, 1979).

RESULTS AND DISCUSSION

Descriptive statistics and seasonal mean DOC concentrations are given in Table 1. Mean concentrations ranged from 2.5 g C m^{-3} of water for the winter mid tide to 4.1 g C m^{-3} of water for the fall neap tide. There was no apparent trend toward higher DOC concentrations during spring tides. Except for the fall, typical DOC ranges were between 4.5 and 7.4 g C m^{-3} of water. Data were more variable during the fall, ranging between 1.0 and 13.0 g C m^{-3} of water over a neap-spring tidal period. The concentrations are essentially the same as levels reported by Burney et al. (1981) for a Rhode Island marsh, by Shisler and Jobbins (1977) for a

Table 1. Descriptive statistics for DOC data

Season	Date	Tidal series	N	g DOC m^{-3}				Seasonal mean
				Mean	Minimum value	Maximum value	Range	
Winter	21-23	Mid	1056	2.5	1.7	6.2	4.5L	2.9
(Feb)	25-27	Spring	1056	3.2	1.7	9.1	7.4	
Spring	18-20	Neap	1056	3.5	1.6	9.0	7.4	3.4
(May)	25-27	Spring	1056	3.3	1.5	8.8	7.3	
Summer	17-19	Neap	1056	2.8	1.4	6.7	5.3	2.8
(Jul)	10-12	Spring	1056	2.9	1.4	7.7	6.3	
Fall	26-28	Neap	1056	4.1	1.0	13.0	12.0	3.9
(Oct/Nov)	2-4	Spring	1056	3.7	0.9	9.9	9.0	

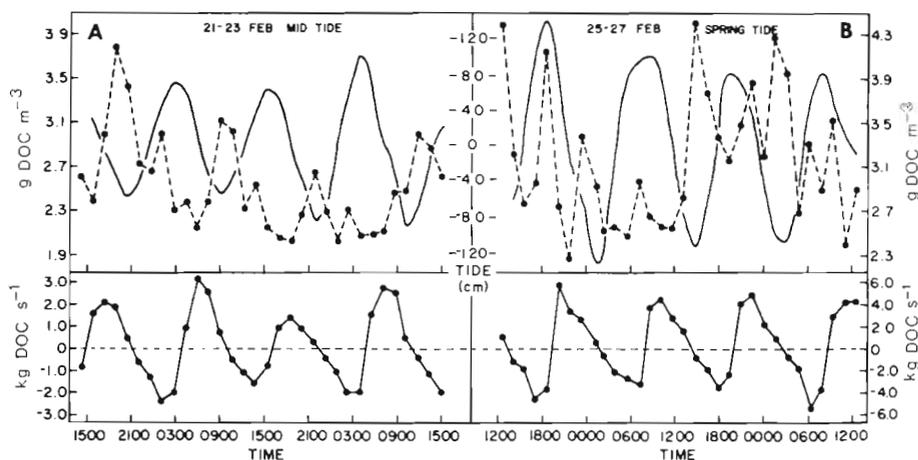


Fig. 1. Temporal fluctuations in concentration of dissolved organic carbon (●-●-●), relative tidal height (—), and instantaneous net flux (●—●) at Town Creek in February

New Jersey marsh and by Happ et al. (1977) for Baritaria Bay, but were higher than those reported by Woodwell et al. (1977) for Flax Pond.

Examples of temporal DOC fluctuations are shown relative to tidal oscillations in the upper panels of Fig. 1 and 2. DOC fluctuations were variable, ranging as much as 2.5 g C m^{-3} of water in a 1.5 h period. Tide height typically accounted for only small percentages of the variation in DOC. Coefficients of determination ranged from less than 1% during the fall to a maximum of approximately 20% during the winter spring tide. However, fluctuations during the winter mid tide were extremely regular; maximum DOC concentrations occurred at low tides with secondary concentration peaks associated with maximum water flow during rising tides. High DOC values during low tide periods and secondary concentrations peaks during maximum ebb or flood discharge occurred frequently throughout the year; but the strong tidal signature typical of winter, was only marginally apparent in other seasons. Immediately preceding the winter mid

tide there was a heavy snowfall and rapid melt resulting in a water export close to 50% of the tidal prism (Chrzanowski et al., 1982a). The distinct low tide concentration peaks during this period may represent input of DOC from terrestrial sources. Two lines of evidence support this speculation: (1) concentration peaks occurring at low tide periods are indicative of material originating within a tidally flooded system, and (2) decreasing concentration peaks on successive low tide intervals (Fig. 1A) suggest a source of decreasing intensity, as runoff.

Apart from the winter, DOC concentrations fluctuated irregularly with tidal oscillations, suggesting that DOC passing the transect normally has a patchy temporal and spatial distribution. This finding is contrary to results obtained for several particulate components. Chrzanowski et al. (1982a, b, c) previously described tidally induced fluctuations of POC, filamentous fungi, and total microbial biomass at this location and time period. They found relatively smooth fluctuation patterns indicating uniform distributions.

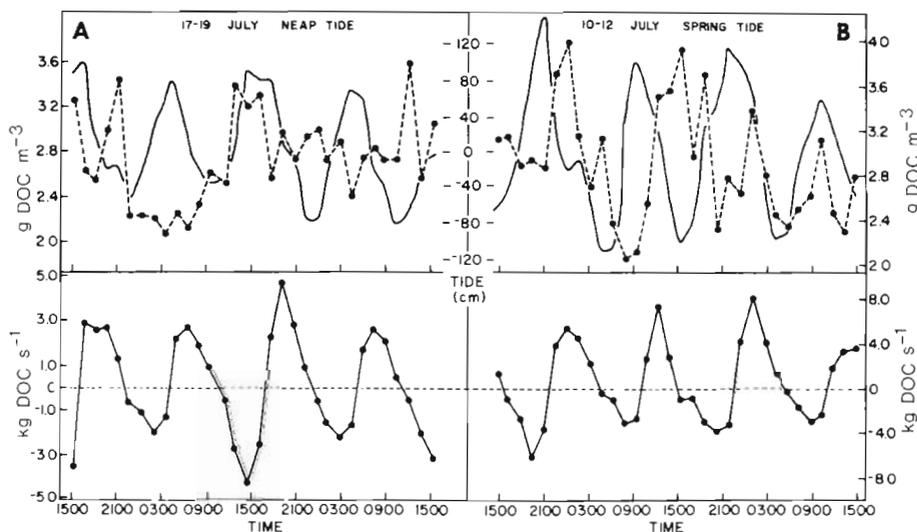


Fig. 2. Temporal fluctuations in concentration of dissolved organic carbon (●-●-●), relative tidal height (—), and instantaneous net flux (●—●) at Town Creek in July

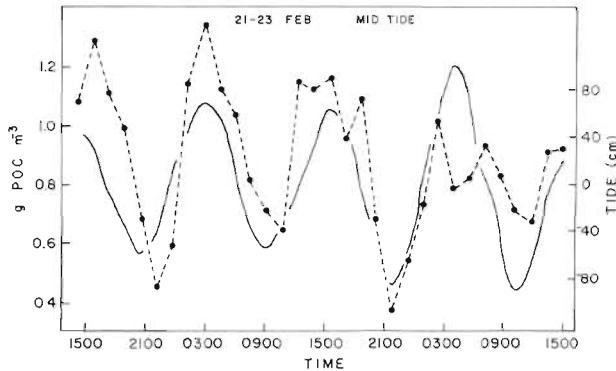


Fig. 3. Temporal fluctuations in concentration of particulate organic carbon (●- - ●), and relative tidal height (—), at Town Creek in February (adapted from Chrzanowski et al., 1982)

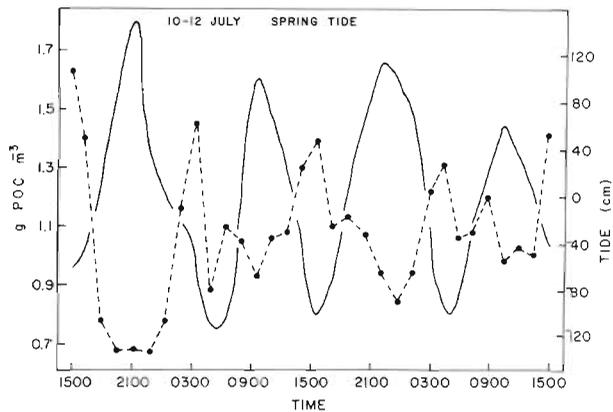


Fig. 4. Temporal fluctuations in concentration of particulate organic carbon (●- - ●), and relative tidal height (—), at Town Creek in July (adapted from Chrzanowski et al., 1982)

Occasionally, DOC fluctuations were synchronized with fluctuations of particulate components as POC, so that both variables fluctuated together or both fluctuated in opposition. Fig. 3 shows the POC fluctuation pattern for the time period corresponding to the winter mid tide DOC data shown in Fig. 1. Comparison of

fluctuation patterns shows dominant peaks of both variables fluctuated in opposition, 180° out-of-phase. Fig. 4 shows the fluctuation pattern of POC matching the spring tide DOC data in Fig. 2. In this case, fluctuation patterns were more closely aligned.

Consequences of fluctuation phasing are shown in Fig. 5 and 6, which depict TOC fluctuations (derived by addition of DOC and POC concentrations). In Fig. 5, the TOC fluctuation pattern reflects opposite fluctuation patterns in its two component variables. The distinct tidal fluctuation patterns of DOC and POC were considerably reduced following addition. In Fig. 6 the TOC fluctuation pattern reflects the more closely aligned patterns of DOC and POC. DOC and POC peaks occurring during low tides or falling tides were reinforced, their effects additive.

The overall similarity of TOC and DOC fluctuation patterns shows the dominance of DOC in the TOC pool. DOC concentrations were approximately 2.5 times greater than POC levels and, over the study period, DOC averaged 70 % of the TOC pool. Descriptive statistics for TOC data are presented in Table 2. Average TOC values ranged from 3.4 to 5.3 g C m⁻³ of water, with the greatest range during the fall.

Typical transport (mass flux) patterns for DOC and TOC are shown in the lower panels of Fig. 1, 2, 5, and 6. Occasional discontinuities were observed in transport patterns (Fig. 1A, 2A, bottom panels). The pattern of alternating peak transports appears to be caused by the semi-diurnal tide and diurnal inequality. This pattern was reported previously by Chrzanowski et al. (1982a, c) for POC and total microbial biomass and indicates the dominant role of water motion in transport determinations. In such calculations the term describing the concentration variable is often small relative to discharge, consequently concentration has little effect on the overall discharge curve. The transport curves for DOC and TOC are fairly symmetrical around zero transport, and are typical of systems hav-

Table 2. Descriptive statistics for TOC data

Season	Date	Tidal series	N	g TOC m ⁻³				Seasonal mean
				Mean	Minimum value	Maximum value	Range	
Winter (Feb)	21-23	Mid	1056	3.4	2.3	7.5	5.2	6.4
	25-27	Spring	1056	4.7	2.9	10.4	7.5	
Spring (May)	18-20	Neap	1056	5.0	2.7	10.6	7.9	7.9
	25-27	Spring	1056	4.7	2.7	10.5	7.8	
Summer (Jul)	17-19	Neap	1056	3.8	2.1	8.0	5.9	6.3
	10-12	Spring	1056	4.0	2.2	8.8	6.6	
Fall (Oct/Nov)	26-28	Neap	1056	5.1	1.7	14.2	12.5	11.1
	2-4	Spring	1056	5.3	2.3	11.9	9.6	

Table 3. Mean net export of DOC for each season

Season	Date	Tidal series	r^2	$P > T $	Net transport of DOC		
					Mean		Seasonal average 10^5 g DOC cycle $^{-1}$
					g DOC s^{-1} \pm SE**	10^5 g DOC cycle $^{-1}$	
Winter (Feb)	21–23 25–27	Mid Spring	0.93 0.91	0.015 0.022	210.6 ± 80.9 472.6 ± 192.7	94.2 211.3	152.8
Spring (May)	18–20 25–27	Neap Spring	0.94 0.89	0.971 0.048	4.8 ± 132.7 292.5 ± 140.4	2.1 130.8	66.5
Summer (Jul)	17–19 10–12	Neap Spring	0.92 0.94	0.398 0.011	108.6 ± 126.4 483.0 ± 176.6	48.6 216.0	132.3
Fall (Oct/Nov)	26–28 2– 4	Neap Spring	0.90 0.93	0.219 0.592	218.7 ± 173.4 94.7 ± 174.6	97.8 42.3	70.1

** SE = Standard error of the mean

Table 4. Mean net export of TOC for each season

Season	Date	Tidal series	r^2	$P > T $	Net transport of TOC		
					Mean		Seasonal average 10^5 g TOC cycle $^{-1}$
					g TOC s^{-1} \pm SE**	10^5 g TOC cycle $^{-1}$	
Winter (Feb)	21–23 25–27	Mid Spring	0.93 0.94	0.015 0.050	311.5 ± 118.2 497.5 ± 241.1	139.3 222.4	180.9
Spring (May)	18–20 25–27	Neap Spring	0.87 0.92	0.956 0.035	13.9 ± 250.8 416.4 ± 186.4	6.2 186.2	96.2
Summer (Jul)	17–19 10–12	Neap Spring	0.95 0.94	0.171 0.022	192.4 ± 136.4 546.2 ± 222.6	86.0 244.2	165.1
Fall (Oct/Nov)	26–28 2– 4	Neap Spring	0.92 0.95	0.161 0.479	280.8 ± 194.2 146.3 ± 203.6	125.6 65.4	95.5

** SE = Standard error of the mean

ing little or no net exchange. Peak instantaneous DOC or TOC transports were on the order of thousands of g C s^{-1} whereas net exports were on the order of tens or hundreds of g C s^{-1} .

Average net DOC and TOC transports for each tidal series are presented in Tables 3 and 4. The equation used to describe transports closely reproduced the observed transport patterns and comparison of observed and described transports generated correlation coefficients (r^2) ranging from 0.89 to 0.94 for DOC (Table 3) and from 0.87 to 0.95 for TOC (Table 4). Both DOC and TOC were exported from Town Creek during each sampling period.

Net tidal series DOC exports ranged from approximately 5 to 480 g C s^{-1} (Table 3). Spring tide exports

were greater than mid or neap tide exports on 3 of 4 occasions. Despite a net outward DOC flow, only 4 of 8 sampling series yielded net exports that were statistically different from zero flow at $\alpha = 0.05$ (two tailed T test). These transports occurred during the winter mid and spring tides, during the spring spring tides, and during the summer spring tide. Of the spring tide samplings, 75% yielded exports that differed from zero. The winter mid tide export may be the result of the rapid snow melt discussed above.

Net tidal series TOC export values ranged from approximately 14 to 550 g C s^{-1} (Table 4). The influence of DOC on the TOC flux was apparent as net tidal series TOC exports were similar to those of DOC in both magnitude and timing. As with DOC, the exports

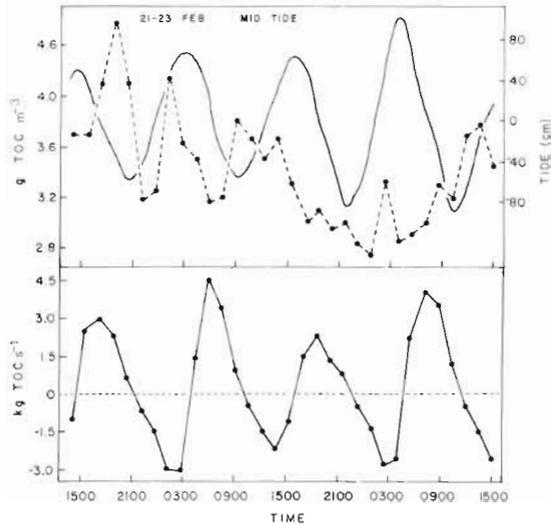


Fig. 5. Temporal fluctuations in concentration of total organic carbon (●- -●), relative tidal height (—), and instantaneous net flux (●—●) at Town Creek in February

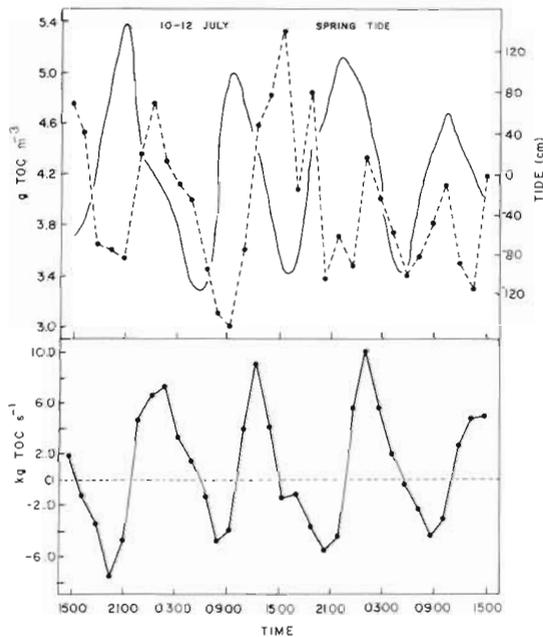


Fig. 6. Temporal fluctuations in concentration of total organic carbon (●- -●), relative tidal height (—), and instantaneous net flux (●—●) at Town Creek in July

from 50% of the sampling periods were different from zero transport. These exports matched the significant DOC export periods.

An annual transport budget may be calculated from seasonal transport data. The experimental design provided good estimates of net movements for 8 tidal cycles each season. We assume that each sampling and transport estimate are representative of the entire season. However, care must be taken in extrapolating short-term data to annual estimates, especially regarding potential problems implicit in the assumptions.

The year was divided into seasons based on monthly water temperatures for the 2 yr previous to the study, and seasonal production and mortality of *Spartina* for a nearby Georgia marsh (Gallagher et al., 1980). Months with similar features were grouped together (for details see Chrzanowski et al., 1982a). Annual net transports were calculated in 2 ways: the first method considered all data; whereas, the second method considered only data statistically different from zero. When all data were used, Town Creek exported DOC and TOC at annual rates of $7.5 \pm 1.8 \times 10^9$ and $9.6 \pm 2.2 \times 10^9$ g C yr⁻¹, respectively. These rates correspond to instantaneous rates of 237 ± 57 g DOC s⁻¹ and 304 ± 70 g TOC s⁻¹.

Annual rates based on statistically significant data were calculated by replacing nonsignificant estimates with zero. Using this method, the annual DOC export rate was $5.7 \pm 1.2 \times 10^9$ g C yr⁻¹ while TOC was exported at $6.9 \pm 1.6 \times 10^9$ g C yr⁻¹. These values correspond to instantaneous rates of 181 ± 38 g DOC s⁻¹ and 219 ± 51 g TOC s⁻¹.

Town Creek is 1 of 3 major exchange points between the North Inlet marsh and the ocean, accounting for approximately 85% of the total water flow (Chrzanowski et al., 1982a) and annually averaging 1.7×10^7 m³ of water tidal cycle⁻¹. The area of marsh drained by Town Creek, has been estimated at 1800 ha (Chrzanowski and Stevenson, 1979a). Integrating annual net fluxes over the drainage area yields annual exports equivalent to 416 g DOC m⁻² yr⁻¹ and 533 g TOC m⁻² yr⁻¹ for all data, and 317 g DOC m⁻² yr⁻¹ and 383 g TOC m⁻² yr⁻¹ for significant data.

If *Spartina* is the primary source of DOC into the North Inlet system, then comparing the exports to *Spartina* production is appropriate. Estimates of net aerial production of *Spartina* are not available for the year transport measurements were made; however, for a subsequent year net aerial production of *Spartina* was 704 g C m⁻² yr⁻¹ for creekside grass, 284 g C m⁻² yr⁻¹ for mid-marsh grass, and 499 g C m⁻² yr⁻¹ for high-marsh grass (Dame, pers. comm.). Assuming 20% of the Town Creek drainage area is covered by creekside zones and the remaining 80% is equally divided between mid-marsh and high-marsh zones, average net aerial production is about 455 g C m⁻² yr⁻¹. This rate is high for North Carolina marshes (Williams and Murdock, 1966; Stroud and Cooper, 1968), but at the low end of estimates for Georgia marshes (Gallagher et al., 1980). Net exports of DOC and TOC correspond to 91% and 117% of the *Spartina* production when all data are considered, and 70% and 84% when only significant data are used.

These export rates are unreasonable. Typical exports of DOC from marsh systems located in northern coastal regions are less than 15% of the aerial net *Spartina*

Table 5. DOC exported from marshes expressed as a percentage of aerial net *Spartina* production

Marsh location	DOC export (g m ⁻² yr ⁻¹)	Aerial net <i>Spartina</i> production (g C m ⁻² yr ⁻¹) ^b	% of production exported as DOC
New York	8.4 ^a	372.2	2.3
Delaware	38 ^c	252	15.1
Virginia	80 ^c	599.4	13.3
	25 ^c	599.4	4.2

^a Woodwell et al. (1977)
^b See citations in Nixon and Oviatt (1973); assumes a 45 % C content
^c See citations in Nixon (1980)

production (Table 5). Even if Turner's (1978) estimates for DOC input from *Spartina* leachate are added to the North Inlet production data, and if winter export rates are reduced by 50 % to compensate for atypical water export, the resultant exports would be 72 % (DOC) and 94 % (TOC) when all data are considered or 53 % (DOC) and 65 % (TOC) when significant data are used.

Since DOC concentrations, production estimates, and discharge values are reasonable we must consider alternatives to account for such extreme export rates. It is likely that the export rates result from 2 factors. Firstly, *Spartina* (net aerial) may not be the most important input of DOC to the North Inlet system. Rather, intermittent inputs from runoff or below ground stream flow, below ground *Spartina* production, phytoplankton, and edaphic and epiphytic algae may be of greater importance. Secondly, because of the highly variable nature of our DOC data, the high-density quarterly sampling scheme used in this study generated transport estimates that could not be reliably extended to annual budgets.

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LITERATURE CITED

Burney, C. M., Johnson, K. J., Sieburth, J. McN. (1981). Diel flux of dissolved carbohydrate in a salt marsh and a simulated estuarine ecosystem. *Mar. Biol.* 63: 175–187
 Chrzanowski, T. H., Stevenson, L. H. (1979a). Material fluxes through the North Inlet marsh system: short-term fluctuations of fungi and related parameters. *Mycologia* 71: 958–967
 Chrzanowski, T. H., Stevenson, L. H., Kjerfve, B. (1979b).

Adenosine 5'-triphosphate flux through the North Inlet marsh system. *Appl. environ. Microbiol.* 37: 841–848
 Chrzanowski, T. H., Stevenson, L. H., Spurrier, J. D. (1982a). Transport of particulate organic carbon through the North Inlet ecosystem. *Mar. Ecol. Prog. Ser.* 7: 231–245
 Chrzanowski, T. H., Stevenson, L. H., Spurrier, J. D. (1982b). Seasonal variability and transport of suspended microfungi in a southeastern salt marsh. *Appl. environ. Microbiol.* 43: 392–396
 Chrzanowski, T. H., Stevenson, L. H., Spurrier, J. D. (1982c). Transport of microbial biomass through the North Inlet ecosystem. *Microbiol. Ecol.* 8: 139–156
 Crawford, C. C., Hobbie, J. E., Webb, K. L. (1974). The utilization of dissolved free amino acids by estuarine microorganisms. *Ecology* 55: 551–563
 Dame, R., Vernberg, F., Bonnell, R., Kitchens, W. (1977). The North Inlet marsh-estuarine ecosystem: a conceptual approach. *Helgoländer wiss. Meeresunters.* 30: 343–356
 Gallagher, J. L., Reimold, R. J., Linthurst, R. A., Pfeiffer, W. J. (1980). Aerial production, mortality, and mineral accumulation – export dynamics in *Spartina alterniflora* and *Juncus roemerianus* plant stands in a Georgia salt marsh. *Ecology* 61: 303–312
 Happ, G., Gosselink, J. G., Day, J. W., Jr. (1977). The seasonal distribution of organic carbon in a Louisiana estuary. *Estuar. coast. mar. Sci.* 5: 695–705
 Helwig, J. T., Council, K. A. (1979). SAS user's guide. SAS Institute Incorporated, Raleigh
 Kjerfve, B. (1975). Velocity averaging in estuaries characterized by a large tidal range to depth ratio. *Estuar. coast. mar. Sci.* 3: 311–323
 Kjerfve, B., Stevenson, L. H., Proehl, J. A., Chrzanowski, T. H. (1981). Estimation of material fluxes in an estuarine cross-section: a critical analysis of spatial measurement density and errors. *Limnol. Oceanogr.* 26: 325–335
 Manahan, D. T., Wright, S. H., Stephens, G. C., Rice, M. A. (1982). Transport of dissolved amino acids by the mussel, *Mytilus edulis*: demonstration of net uptake from natural seawater. *Science, N. Y.* 215: 1253–1255
 Nixon, S. W. (1980). Between coastal marshes and coastal waters – a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In: Hamilton, R., MacDonald, K. B. (ed.) *Estuarine and wetland processes with emphasis on modeling*. Plenum Publishing Corporation, New York, p. 437–527
 Pritchard, D. W., Burt, W. V. (1951). An inexpensive and rapid technique for obtaining current profiles in estuarine waters. *J. mar. Res.* 108: 180–189
 Sepers, A. B. J. (1977). The utilization of dissolved organic compounds in aquatic environments. *Hydrobiologia* 52: 39–54
 Settlemyre, J. L., Gardner, R. O. (1977). Suspended sediment flux through a salt marsh drainage basin. *Estuar. coast. mar. Sci.* 5: 653–663
 Shisler, J. K., Jobbins, D. M. (1977). Tidal variations in the movement of organic carbon in New Jersey salt marshes. *Mar. Biol.* 50: 127–134
 Strickland, T. D. H., Parsons, T. R. (1968). A practical handbook of seawater analysis. *Bull. Fish. Res. Bd Can.* 167: 1–311
 Stroud, L. M., Cooper, A. W. (1968). Color-influenced aerial photographic interpretation and net primary productivity of a regularly flooded North Carolina salt marsh. North Carolina Water Research Institute, Raleigh, Report 12
 Teal, J. M. (1962). Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43: 614–624

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- Turner, E. R. (1978). Community plankton respiration in a salt marsh estuary and the importance of macrophyte leachates. *Limnol. Oceanogr.* 23: 442-451
- Valiela, I., Teal, J. M., Volkmann, S., Shafer, D., Carpenter, E. J. (1978). Nutrient and particulate fluxes in a salt marsh ecosystem: tidal exchanges and inputs by precipitation and ground water. *Limnol. Oceanogr.* 23: 798-812
- Williams, R. B., Murdock, M. B. (1966). Annual production of *Spartina alterniflora* and *Juncus roemerianus* in salt marshes near Beaufort, North Carolina. *Ass. Southeastern Biologist Bull.* 13: 49
- Woodwell, G. M., Whitney, D. W., Hall, C. A. S., Houghton, R. A. (1977). The Flax Pond exosystem study: exchanges of carbon in water between a salt marsh and Long Island Sound. *Limnol. Oceanogr.* 22: 823-828

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