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Import, export, and recycling of dissolved nutrients in the Ogeechee River estuary (Georgia, USA)

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ABSTRACT

We constructed an empirical mass balance model of nutrient fluxes in the Ogeechee River estuary (Georgia, USA) from eight surveys of seasonal estuarine nutrient concentrations during 2015 and 2016. The model results indicated a net removal of dissolved phosphorus and a net production of dissolved nitrogen (N) within the estuary over an annual cycle. During summer and autumn low flow periods, much of the dissolved N discharged to the ocean seems to be recycled into the estuary in the form of phytoplankton biomass. As a result, the outwelled N is not new nitrogen fueling coastal production but is nitrogen trapped within a recycling loop across the ocean–estuarine boundary. Higher flows in the fall and winter lead to direct discharge of nutrients with minimal recycling. A balanced N budget for the Ogeechee River estuary requires that estuarine N-fixation must exceed burial and denitrification losses within the estuary.

Keywords: estuary, nutrients, flux, nitrogen fixation, outwelling

1. Introduction

Most salt marsh estuaries export dissolved nutrients to the coastal oceans (Childers, Day, and McKellar 2000) despite high rates of internal cycling and consumption of riverborne nutrients (Bianchi 2006; Bauer and Bianchi 2011; Regnier et al. 2013; Canuel and Hardison 2016). A recent review by Herrmann et al. (2015) estimated that 60% of the terrestrial dissolved carbon flux into US East Coast estuaries is captured or respired, with the remaining 40% exported to the coastal ocean where it can provide nutritional support for coastal food webs (e.g., Turner, Woo, and Jitts 1979b; Hopkinson 1985; Savage et al. 2012). Seitzinger (1988) concluded that approximately 40% to 50% of dissolved inorganic nitrogen (DIN) inputs into (primarily temperate) estuaries were consumed by denitrification alone. Other studies have shown that efficiency with which nutrients (i.e., DIN and dissolved inorganic phosphorus) are either consumed *in situ* or passed through to the coastal ocean is a strong

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function of estuarine water residence time (e.g., Nixon et al. 1996). Longer residence times permit greater opportunities for internal nutrient cycling and losses and weaken the capacity for estuarine outwelling to enhance productivity on the adjacent shelf. Thus, in riverine estuaries where the annual range in freshwater discharge and associated nutrient and particle fluxes are large, the outwelling capacity of the estuary is likely to vary considerably over an annual cycle.

The many and varying nutrient sources and sinks within the estuary, combined with the complexities of physical circulation, mean that the proximate sources of nutrients and particles that contribute to the observed export flux cannot always be readily discerned. Though “nitrate is nitrate,” a significant fraction of the total nutrient exports from many estuarine systems are in organic form (Bianchi 2006), and the availability of those nutrients to coastal food webs will be dependent on their biological and/or photochemical lability. For example, while terrestrial dissolved organic carbon (DOC) sources usually dominate export from estuaries into the coastal ocean (Bauer and Bianchi 2011), DOC sources from salt marshes, estuarine phytoplankton, and microphytobenthos can also contribute to the observed flux (Raymond and Bauer 2001). These sources may be more readily used by coastal food webs than more refractory terrestrial carbon and nitrogen (N) (Raymond and Bauer 2000; Wang et al. 2014). Furthermore, although the primary focus of the literature on material exchange between estuaries and the adjacent ocean has been on estuarine production and export, import of materials from the oceanic endmember also contribute significantly to estuarine budgets (e.g., Smith and Hollibaugh 1997; Roegner and Shanks 2001; Buck et al. 2014).

In coastal Georgia, five rivers export material from inland watersheds to an extensive salt marsh estuarine fringe. Upland nutrient delivery to the heads of the estuaries is well constrained (Asbury and Oaksford 1997; Schaefer and Alber 2007). Productivity in the adjacent coastal ocean is high (Thomas 1966; Turner, Woo, and Jitts 1979a; Verity et al. 1993) and is dependent on delivery of nutrients from the estuary as well as local recycling (Hopkinson 1985, 1987; Hanson and Robertson 1988). However, the quantitative role of the adjacent salt marsh estuaries in modifying riverine nutrient fluxes prior to export to the Georgia coastal zone is poorly documented. In this paper we combined data from a series of seasonal longitudinal surveys of the Ogeechee River estuary (ORE) (Fig. 1), with a simple box model assessment of fluxes (Officer 1980; Cai et al. 2000) to address material processing within, and net exports from, the ORE to the coastal ocean.

2. Methods

a. Study location and attributes

The Ogeechee River watershed (Fig. 1) extends from the piedmont of middle Georgia to the lowlands of the coastal plain. It possesses most of the attributes of a coastal blackwater river, such as high concentrations of colored dissolved organic matter and low concentrations of inorganic suspended particulate matter. The total watershed area is 14,300 km², and is

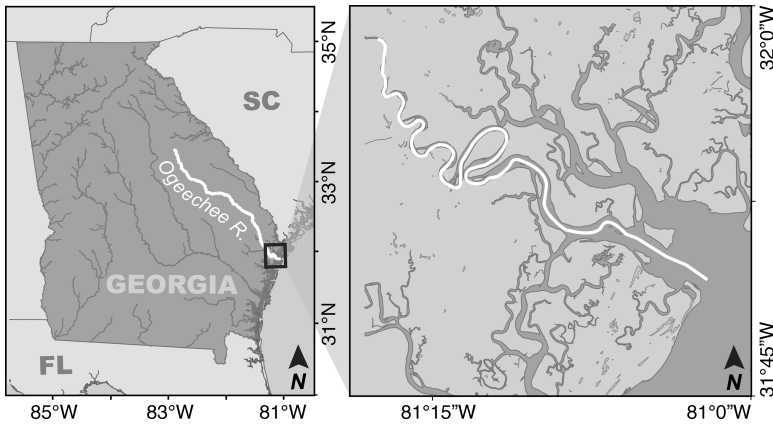


Figure 1. Ogeechee River in Georgia and its estuary. *Left*: Location of the Ogeechee River. *Right*: Path of survey transects within the estuary.

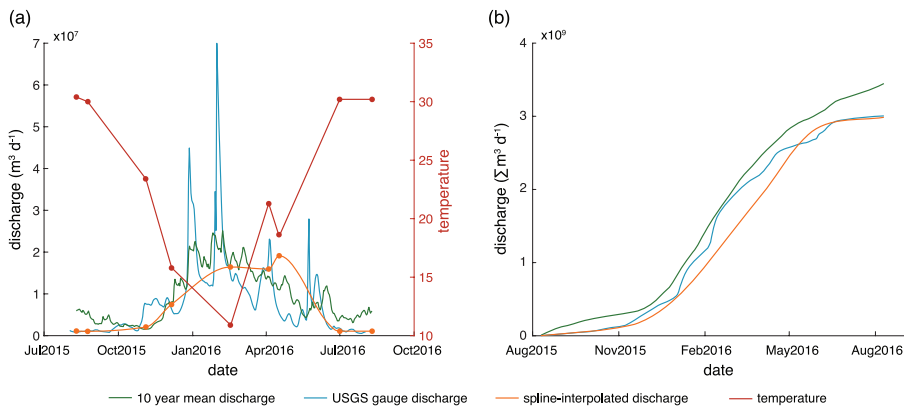


Figure 2. Ogeechee River discharge, 2015–2016. (a) Estuary temperature and Ogeechee River daily discharge. (b) Cumulative river discharge over the study period.

largely forested (40%), wetlands (24%), and agricultural (17%) (GA EPD 2001). It is undammed, and, as a result, water discharges are strongly seasonal with average winter flows approximately 10 times greater than summertime flows (Fig. 2). In the summer, salt concentrations greater than 0.1 psu extend more than 50 km up the estuary. In the winter, the 0.1 psu isohaline is less than 15 km from the coastal ocean. Changes in discharge have a large effect on freshwater residence times (Table 1; see Alber and Sheldon 1999; Sheldon and Alber 2005). The estuary is shallow, with an average depth of 4 m (Dame et al. 2000) and an average tidal range of 2.3 m. The lower reaches of the river are surrounded by extensive *Spartina alterniflora* salt marshes. The oligohaline portions of the estuary are bordered by *Spartina*, *Juncus* and *Zizaniopsis* marshes (Więski et al. 2010). The intertidal

Table 1. Freshwater residence times in the Ogeechee River estuary calculated using the date-specific method of Alber and Sheldon (1999).

Survey transect	Survey date	Ogeechee discharge (m ³ d ⁻¹)	Freshwater residence time (days)
S1	8/10/2015	1110336	36
S2	8/24/2015	1030689	43
F1	11/4/2015	2075544	23
F2	12/6/2015	7540333	11
W1	1/19/2016	17407356	4.5
W2	2/17/2016	16433970	7
Sp1	4/4/2016	15945938	6.5
Sp2	4/17/2016	19122072	5.5

Table 2. Underway sondes and sampling rates used during the Ogeechee River estuary seasonal surveys, 2015–2016.

Property	Instrument units	Sonde	Sampling rate (Hz)
GPS location	lat, long	Hummingbird 797 C25	0.2
Depth	m	Seabird SBE21 ^a	0.2
Salinity	psu	Seabird SBE 21 ^a	0.2
	psu	YSI 600 OMS ^b	0.5
Temperature	°C	Seabird SBE 21 ^a	0.2
	°C	YSI 600 OMS ^b	0.5
Oxygen	mg l ⁻¹	YSI 600 OMS ^b	0.5
Chlorophyll	ug l ⁻¹	Wetlabs FLNTU	1
Turbidity	NTU (nephelometric turbidity units)	Wetlabs FLNTU	1
		Wetlabs FLNTU	1
Dissolved organic matter fluorescence	QSE (quinine sulfate equivalents)	Wetlabs FLCD	2
		Wetlabs FLCD	2

Notes: ^aThe SBE 21 CTD sampled surface water only. ^bThe YSI 600 OMS was used for both surface sampling and profiling.

marshes comprise approximately 66% of the total estuarine area (M. Robinson, personal communication).

b. Field transects

We conducted continuous underway surveys of surface water properties on the Ogeechee mainstem (Fig. 1) using an underway flow-through sampling system and recording sondes (Table 2). Individual transects began at the mouth of the estuary at slack low tide, and the sampling proceeded upriver at approximately the rate of progression of the tidal front (13–15 km h⁻¹). Data were recorded continuously until we reached salinities less than 0.1 psu. By sampling continuously at the local low tide, we believed that we would capture a signal

that would integrate the contributions of both open water processes and processes occurring on the flooded marsh platforms during the prior high tide. Because of our frequent station stops (described below), we were unable to fully keep pace with the tidal front. By the endpoint of our surveys, we were usually sampling on a rising tide.

Four seasonal pairs of underway surveys were conducted on the Ogeechee: two transects each in late summer, fall, winter, and spring (Fig. 2 and Table 1). Sampling spanned nearly the full range of estuarine temperature and river discharge conditions (Fig. 2). Sampling location was logged continuously and timestamped by GPS. The GPS failed during the first winter transect and sample location could not be accurately determined. Data from that transect were not used in the flux analyses.

River properties measured on a continuous basis were temperature, salinity, depth, dissolved oxygen, chlorophyll fluorescence, dissolved organic matter fluorescence (fDOM), and turbidity. All data are reported in instrument units (Table 2). The sondes logged data from 0.5 to 2 Hz. At a survey speed of 13 km h^{-1} , individual samples were recorded every 2 to 7 meters of underway distance. Because of a finite turnover time of the water volume in the sampling system, the effective spatial resolution of sampling while underway was on the order of 50 to 100 m. Approximately every 3 psu salinity change we stopped to make a vertical cast with the sonde package and to collect bottle samples for nutrients. A Go-Flo bottle (General Oceanics; generaloceanics.com) was used to obtain surface and bottom water samples that were filtered while underway to obtain water for analysis of nutrients; 50 mL samples for analysis of inorganic nutrients (NO_3^- , NO_2^- , NH_4^+ , PO_4^{3-}), total dissolved phosphorus (TDP), dissolved organic carbon (DOC), total dissolved nitrogen (TDN) were syringe filtered through a $0.2 \mu\text{m}$ Target2 cellulose acetate syringe filter (ThermoFisher Scientific; thermofisher.com) into 60 mL amber HDPE bottles while underway, and the filtrates were stored on ice. On return to the lab, nutrient samples were frozen at -20°C overnight and express shipped to the JBL Analytical Services lab at the University of Georgia the following day for analysis.

Samples for fluorometric analysis of chlorophyll were collected as triplicate 40 mL aliquots and were vacuum filtered onto 25 mm ashed GF/F filters under a shroud to shield them from ambient light while underway. Samples were stored on ice in the field and were analyzed within 48 hours at the Skidaway Institute of Oceanography.

c. Laboratory analyses

i. Nutrients. DOC and TDN were analyzed by high temperature combustion on a Shimadzu TOC-V with a TN unit (Joye et al. 2004). NH_4^+ samples were analyzed colorimetrically (Solorzano 1969). NO_2^- was quantified according to the procedures outlined in Bendschneider and Robinson (1952). Total $\text{NO}_2^- + \text{NO}_3^-$ was measured as NO on an Antek detector and NO_3^- was calculated by difference. Dissolved organic nitrogen (DON) was calculated as the difference between TDN and DIN. Dissolved phosphate was analyzed colorimetrically (Strickland and Parsons 1972). Total phosphorus (P) was determined by the method of Solorzano and Sharp (1980).

ii. *Chlorophyll*. Chlorophyll was extracted from filters with 90% acetone for between 4 and 6 hours at -20°C in darkness, sonicated, and then extracted for an additional hour. Centrifuged extracts were analyzed for chlorophyll content on a Turner AU-10 fluorometer using standard protocols (Strickland and Parsons 1972). Data are presented as means of triplicate field samples.

iii. *Data analysis*. Measured nutrient concentrations were corrected for analytical and procedural blanks prior to analysis. Raw blanks for the ammonium samples were high and variable, occasionally leading to negative concentrations of blank-corrected data. At least some of the blank contamination was traced to electrical tape used to help shade the filter funnels in the field. High blanks were associated primarily with the initial filter blank and probably resulted from rinsing accumulated adsorbed ammonium from the tape onto the filter. Remaining blanks were always less than $1\ \mu\text{M}$, and using only those blanks to correct the field data assured that all samples except one had positive post-blank concentrations.

Because of interfering substances in the water, raw chlorophyll fluorescence data from the underway sondes could not be converted directly into chlorophyll biomass units using the instrument calibration factors. For each transect, we conducted a multiple linear regression analysis of laboratory determined chlorophyll data (as $\mu\text{g chl}$ per filtered volume) versus raw chlorophyll fluorescence, raw fDOM fluorescence, and turbidity. R^2 of the regression relationship was usually greater than 0.8. We used fDOM rather than DOC because the continuous fDOM data allowed the regressions results to be applied to the continuous underway fluorometer data without interpolation. The relationship between fDOM and DOC was linear during most transects, but the slope of the relationship varied greatly between them. Results of the analyses showed that fDOM (or an fDOM-correlated optical property) generally contributed significantly to the observed regression by quenching chlorophyll fluorescence. The regression relationship obtained from the analysis of 6 to 11 pointwise samples along each transect was then applied to the entire underway sonde data record for that date to obtain a continuous underway estimate of chlorophyll concentration in $\mu\text{g chl l}^{-1}$.

Each sonde survey data set was interpolated onto a common time vector with one second sampling intervals prior to further analysis. Time periods during which the survey vessel was stopped for profiling and water was not flowing through the surface mapping system were excised from the underway transect data and the gaps were linearly interpolated to obtain a continuous time and track data record for the underway sampling. Sonde data sets were smoothed using a robust locally weighted regression routine (MATLAB 'rloess'; Mathworks 2021) with a two-minute window.

iv. *Residence time*. Estuarine residence times were calculated using the fraction of fresh-water method (Dyer 1973). Daily discharges on the dates preceding sampling cruises were summed until the accumulated discharge volume equaled the calculated volume of fresh-water in the estuary (the "date-specific method"; Alber and Sheldon 1999). For each 2 km

box the amount of freshwater contained in the low tide box volume was estimated using the zero and 34 psu as the riverine and coastal ocean endmember salinities. We had no specific data from outside the estuary to constrain the seaward estimate. Coastal salinity varies seasonally with river discharge (Blanton 1981) but is always lower than continental shelf salinities (35–36 psu), because river discharge is largely confined behind a coastal salinity front (Blanton 1981, 1986). Ogeechee River discharge data were taken from the most downstream non-tidal USGS gauges in the Ogeechee and Canoochee drainages (USGS 02202680 and 02203518, respectively). The data were not corrected for any potential additional freshwater inputs between the gauges and the estuary (15 km), nor were any allowances made for time-of-travel lags between gauged discharges and actual freshwater delivery to the head of the estuary itself. We estimate that the ungauged portion of the rivers represent less than 5% of the total Ogeechee River watershed.

v. Flux estimates. Low tide river volumes were obtained for two km sections of the river from Mike Robinson at the Skidaway Institute of Oceanography. River volumes by section were calculated using the surface volume tool within the functional surface toolset of ArcGIS 10.4 3D Analyst Extension (ESRI 2020). Volumes for each raster section were calculated using a reference plane of 0.0 meters for mean lower low water (MLLW) values and using a reference plane of 2.173 meters for mean high water (MHW) values. The MHW to MLLW offset of 2.173m is referenced to the Ft. Pulaski, Georgia, tidal station.

Average values for constituent concentrations were calculated for each section. For continuous sonde data, all individual sonde readings from within the section were averaged. As discrete nutrient samples were collected at spatial intervals greater than 2 km, the data were first linearly interpolated between stations, and then the averages for each 2 km interpolated section were calculated.

Estuarine budgets were constructed by estimating riverine fluxes into the estuary and internal fluxes within the estuary. Exports from the estuary were calculated as the sum of the riverine and internal fluxes. The implicit assumption here is that over a time period equal to the freshwater residence time the import and export of nutrients within the estuary are in balance. Riverine inputs into the ORE were calculated as the product of the observed nutrient concentration at the most upstream sampling point and the USGS gage daily discharge. Internal fluxes of individual constituents were calculated using the procedures described by Officer (1980) and Cai et al. (2000). In the original model formulation, the deviation of any constituent concentration from a conservative distribution within an estuarine box was predicted from the salinity gradients among the boxes and the known fluxes of that constituent within each box: $[C] = [F] * [S_{\text{coeff}}/R]$; where $[C]$ is a vector of “excess” concentrations (i.e., observed–conservative) for the estuarine boxes, $[F]$ is a vector of constituent fluxes within the boxes, R is the river discharge, and $[S_{\text{coeff}}]$ is a vector of salinity coefficients describing the salinity gradient. We inverted this model (i.e., $[F] = [S_{\text{coeff}}/R] \setminus [C]$) in order to estimate the fluxes within each box that are necessary to support the observed estuarine distribution of each constituent C . Net fluxes for the estuary as a whole are the summation

of the flux contributions in each individual box. Total flux values (i.e., the sum of calculated within box fluxes) estimated for any given transect were sensitive to values estimated for the most seaward and landward flux boxes. These values were often large compared with flux estimated for interior boxes. There are several contributing reasons for this. At the seaward end of the transects, the influence of local artifacts due to sediment resuspension at the bar at the entrance to the estuary cannot be precluded (e.g., Verity et al. 1998). This is particularly likely for chl, where high concentrations were observed at the most seaward station on all sampling dates. Additionally, the model seems to do a poor job resolving “true” fluxes where salinity gradients between boxes are small—on the order of a few tenths of a psu or less. Under these circumstances, small changes in property concentrations can generate large swings in the magnitude of estimated fluxes. This can be observed in the large scatter in flux estimates for boxes with salinities less than 1 in the F2–Sp2 transects (see the supplemental figures), and in the large step in fluxes between the first two boxes for all properties at the landward end of the S2 transect. For the purposes of completeness and transparency, we show calculated fluxes for all of the sampled boxes. However, for the purposes of interpretation, we exclude the data from the seaward endmember and low salinity gradients at the riverine endmember except where specifically noted.

An additional idiosyncrasy of the data is the “kink” in most profiles (e.g., F2 DON at $S \sim 8$; see the supplemental figures). These kinks always correspond to the sampling stations just seaward of the apex of the loop at Nine Mile Bend. At this point there is a narrow connection with the waters of the Little Ogeechee River drainage immediately to the north of the Ogeechee. Presumably because of a tidal pressure gradient, water was always seen flowing from the Little Ogeechee into the Ogeechee mainstem at our low tide transects. At sampling stations immediately downstream of the connections we were sampling water that had a significant Little Ogeechee component that had not yet completely mixed with resident Ogeechee mainstem water. The effect was most noticeable during high flow transects because the Little Ogeechee drainage has no significant upland freshwater source and had higher salinities at that point. The skewed salinity gradients generated anomalous flux spikes in the calculations; however, the practical effects of the water exchange were minimal because the flux deviation on the downstream side was countered by a “restoring” deviation on the upstream side. The estimates for cumulative property fluxes were largely unaffected by the local crossover between the two drainages.

To estimate annualized fluxes, the nine-month sampling period (10 August 2015–17 May 2016) of this study was augmented by two extrapolated dates (S3 and S4: 1 June and 10 August 2016) to extend the time series through the summertime low-flow time period. The addition of the point of 1 June 2016, was used to force the spline fits of the data to respond more quickly to the attenuation of river flows during the summer months (Fig. 2). Numerical values for all constituents for the extrapolated summer 2016 dates were set to the means of the two summer 2015 transect values. A piecewise hermite (MATLAB PCHIP; Mathworks 2021) spline was used to interpolate daily fluxes between the sampling cruises. Total annualized fluxes were calculated as the summation of the modeled daily

fluxes. Changing the date at which the summer inflection occurs changes the absolute magnitudes of input and output fluxes by shortening or extending the duration of the spring high discharge period, but it exerts relatively little influence on the net difference between inputs and outputs because the post-inflection discharges and fluxes are assumed to be constant.

vi. Error analysis. The box model approach is fundamentally a steady-state model, whereas the actual estuary is never truly at steady state (e.g., Arndt, Regnier, and Vanderborcht 2009; Arndt et al. 2011, and Fig. 1). Instead, we have averaged flows over the freshwater residence time for each transect to establish an “average state” condition rather than a steady-state or instantaneous-state. Standard deviations of the averaged daily flows were used to estimate uncertainty in the “average state” riverine fluxes. Note that since the riverine nutrient concentration history is unknown, the nutrient concentration at the time of sampling is assumed to be constant over the averaging period.

Errors in riverine input and estuarine internal fluxes for individual transects were estimated from $n = 10,000$ Monte Carlo simulations for which error estimates for R (the standard deviation of daily river flow for the time period equal to the calculated freshwater residence time) and the analytical error associated with the nutrient measurement at the riverine endmember were permitted to vary independently. For each simulation, nutrient concentration and flow were assigned values based on the mean value plus a normally distributed error term centered on a mean of zero \pm one standard deviation. The standard errors of each of those 10^4 simulations represents the estimated error of the mean flux over the time interval represented by the freshwater residence time for each sampling date (4–40 days, Table 1). All individual errors were propagated fully through the final calculation.

Errors for the annualized fluxes were calculated similarly. For each date, the value assigned to the import and estuarine internal fluxes was the mean value plus a random value centered on a mean of zero \pm the standard error from the prior Monte Carlo simulations for each survey date. Within each simulation run, a PCHIP spline was fitted to the estimated data points and the values were summed over the year to obtain cumulative inputs and outputs. The results of $n = 10,000$ such simulations were used to obtain means and standard errors for the annualized model.

Our perforce utilization of an average state of the ORE to establish error bounds for our flux estimates does not eliminate the potential confounding effects of transient changes in estuarine storage or coastal boundary conditions on the estimated fluxes (e.g. Arndt, Regnier, and Vanderborcht 2009; Arndt et al. 2011). In both the F2 and W2 surveys for example, there were substantial changes in river flow within the averaging periods for each, and our simple model formulation is not well equipped to account fully for those perturbations.

All survey data were collected at approximately local low tide and represent an integration of processes within the ORE occurring during neap low tides. Ideally, the nutrient and salinity data would represent tidal averages, but that was not possible given our sampling constraints. Our results and conclusions are ebb-biased to an unknown degree. Additionally,

both the magnitudes and directions of fluxes of specific constituents out of the marshes and into the river potentially can vary over the spring/neap tidal cycle. Whiting et al. (1985) measured fluxes of NO_3^- , NH_4^+ , and PO_4^{3-} from three tidal streams within the North Inlet National Estuarine Research Reserve (NERR) (South Carolina) and found large differences in apparent fluxes between spring and neap tides, although the large error terms rendered their results inconclusive. We believe our analyses and models are valid within the limitations of our sampling design. Nevertheless, our conclusions must be regarded as tentative until more comprehensive data are available.

3. Results and Discussion

a. River discharge and residence time

The eight surveys bracketed the annual range of water temperature and river discharge (Fig. 2). The two summer and first fall transect occurred during a period of minimal riverine flow and warm temperatures. The winter and spring transects occurred during high flows. Note that the winter samples followed significant flood pulses. The June 2016 flood pulse (Fig. 2) was not included in the calculations because it occurred after our final transect in April 2016. Our spline interpolation of discharge is identical to the annual discharge measured by the USGS gages, but it underestimates the actual winter flows and overpredicts the spring discharge because it does not resolve flood pulses well (Fig. 2).

b. Dissolved nutrient fluxes

For all constituents, fluxes into the estuary from the Ogeechee River are mostly a function of river discharge. Net exports from the estuary into the coastal ocean, however, are mediated by processes occurring both within the estuary and the adjacent coastal ocean.

Exports of DOC were $28 \pm 1\%$ greater than riverine delivery (Fig. 3). Annual net additions of DOC within the estuary amount to $7.3 \pm .03 \times 10^8$ moles (Table 3), or $2.1 \text{ moles m}^{-2} \text{ y}^{-1}$, given a total Ogeechee River estuarine area of $349 \times 10^6 \text{ m}^2$ (M. Robinson, personal communication). Given the shape of DOC-salinity plots (see the supplemental figures), most of that addition seems to be a result of desorption of particle associated organic matter in the oligohaline portion of the estuary. The calculated production of DOC within the estuary is somewhat less but similar to estimates from some other southeastern salt marsh estuaries. Osburn et al. (2015) estimated that a North Carolina salt marsh exported $135 \text{ g (11.3 moles) m}^{-2} \text{ y}^{-1}$ of DOC. Estimates of net export fluxes from tidal channels draining salt marshes at the North Inlet, South Carolina, NERR site were from 11.4 to $21.7 \text{ moles m}^{-2} \text{ y}^{-1}$ (Gardner and Kjerfve 2006). Total DOC exports from the estuary are estimated to be $11.2 \text{ moles m}^{-2} \text{ y}^{-1}$, a value similar to some other mesotidal salt marsh estuaries. Chalmers et al. (1985) calculated whole estuary-scale exports of DOC of $9 \text{ moles m}^{-2} \text{ y}^{-1}$ in the Duplin River, Georgia. Dame et al. (1986) estimated that the North Inlet, South Carolina, marsh/creek complex exported $27 \text{ moles DOC m}^{-2} \text{ y}^{-1}$. Scheibel et al. (2018) modeled DOC exports from a New England marsh estuary to be

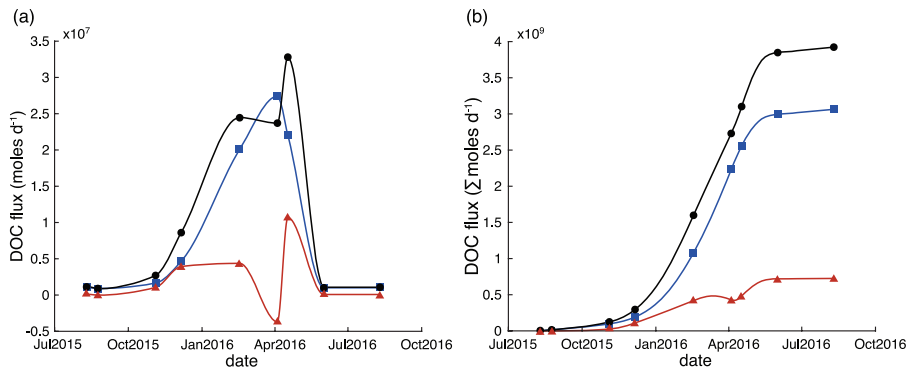


Figure 3. Modeled dissolved organic carbon (DOC) fluxes, 2015–2016. (a) Daily. (b) Cumulative. River input is blue, calculated estuarine internal production/consumption fluxes are in red, and net exports are shown in black.

Table 3. Total annual fluxes of chemical constituents derived from the Monte Carlo model simulations.

	River import		Internal production		Estuarine export	
	Mean (mol y ⁻¹)	Standard error	Mean (mol y ⁻¹)	Standard error	Mean (mol y ⁻¹)	Standard error
DOC	3.06×10^9	6.8×10^6	7.25×10^8	2.6×10^6	3.92×10^9	3.93×10^7
NO ₂ ⁻	8.81×10^5	1.97×10^3	1.05×10^5	9.13×10^3	9.85×10^5	9.31×10^3
NO ₃ ⁻	1.97×10^7	5.4×10^4	3.27×10^6	9.2×10^4	2.31×10^7	1.07×10^5
NH ₄ ⁺	2.15×10^5	5.6×10^3	2.37×10^6	3.46×10^4	4.52×10^6	3.5×10^4
DON	8.59×10^7	1.67×10^5	1.14×10^7	4.72×10^5	9.74×10^7	5.01×10^5
PO ₄ ⁻³	2.56×10^6	3.6×10^3	1.64×10^6	6.1×10^3	4.23×10^6	7.2×10^3
DOP	2.22×10^6	3.5×10^3	-1.12×10^6	9.4×10^3	1.08×10^6	1.0×10^4
CHL-C	1.96×10^7	3.75×10^5	-9.59×10^7	2.79×10^5	-7.71×10^7	2.82×10^5
CHL-N	1.23×10^6	2.34×10^4	-5.99×10^6	1.74×10^4	-4.82×10^6	1.76×10^4
CHL-P	1.85×10^5	3.54×10^3	-9.05×10^5	2.63×10^3	-7.27×10^5	2.66×10^3

Notes: DOC–dissolved organic carbon, DON–dissolved organic nitrogen, DOP–dissolved organic phosphorus, CHL–chlorophyll.

16 moles m⁻² y⁻¹ in the absence of extreme events that increased estimated DOC exports by 2 orders of magnitude during floods. In this study, the residence time averaging captures a portion of the second winter and spring flood pulses, but none of the first winter pulse (Fig. 2). The DOC export modeled for the ORE likely approximates an “event-free” background export.

There is net annual production of DIN (as NO₂⁻, NO₃⁻ and NH₄⁺) and DON within the estuary and export to the coastal ocean (Table 3; Fig. 4 a, b, d, f, and h). Maximal DIN exports lag imports during the winter/spring season. Exports of DIN + DON to the coastal ocean are

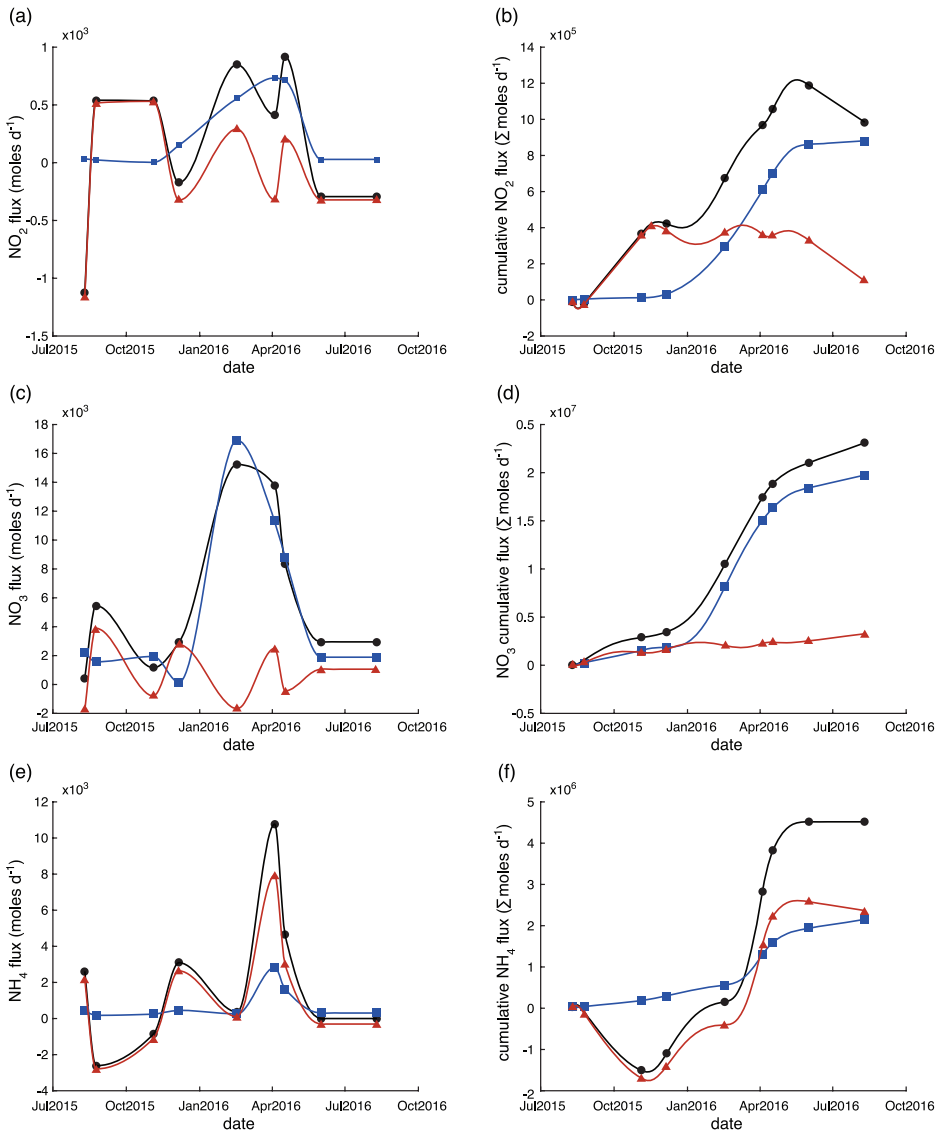


Figure 4. Modeled daily and cumulative fluxes of nitrogen species in the Ogeechee River estuary, 2015–2016. (a) Daily NO_2 . (b) Cumulative NO_2 . (c) Daily NO_3 . (d) Cumulative NO_3 . (e) Daily NH_4 . (f) Cumulative NH_4 . (g) Daily dissolved inorganic nitrogen (DIN). (h) Cumulative DIN. (i) Daily dissolved organic nitrogen (DON). (j) Cumulative DON. (k) Daily total dissolved nitrogen (TDN). (l) Cumulative TDN. River input is blue, calculated estuarine internal production/consumption fluxes are in red, and net exports are shown in black.

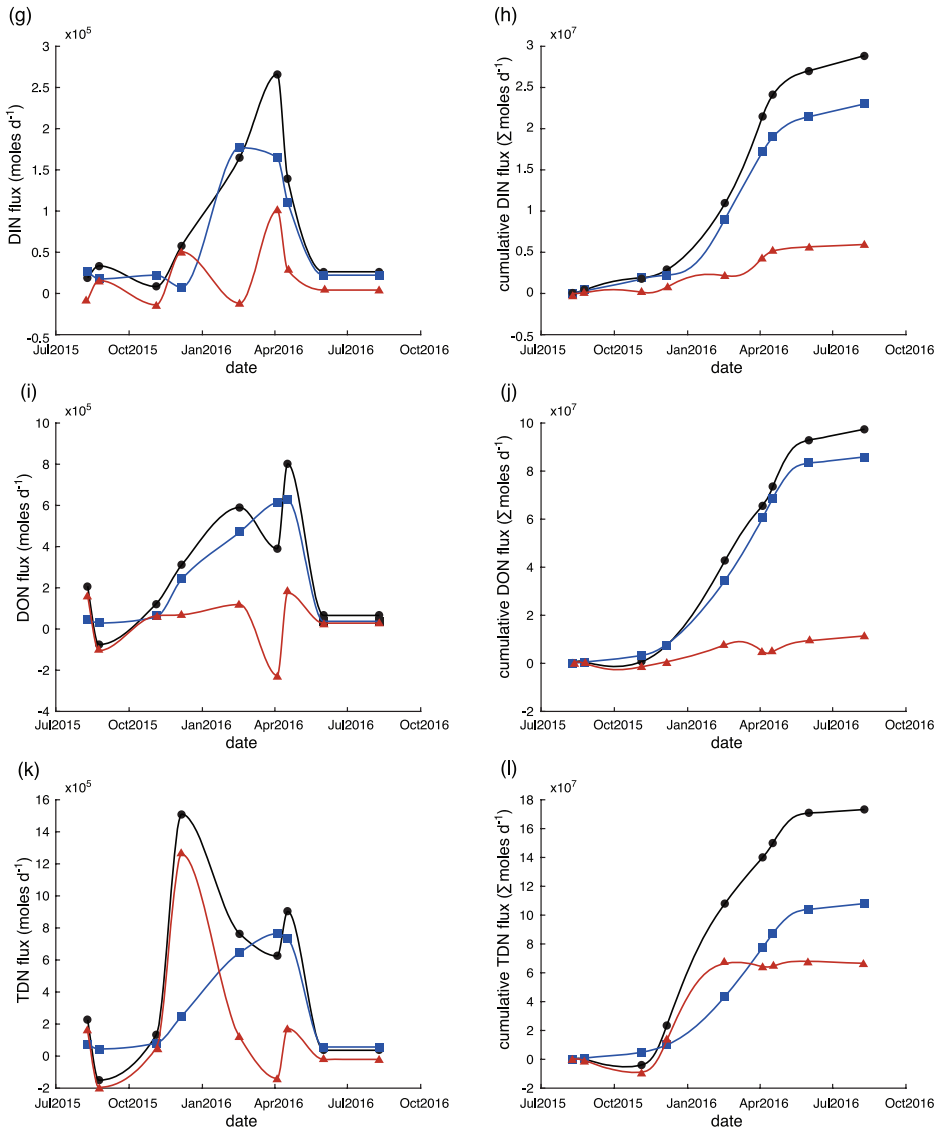


Figure 4. Continued

calculated to be 1.7×10^7 moles ($16 \pm 5\%$) greater than riverine imports. DON is the largest component of the N flux, accounting for slightly less than 80% of both imports and exports. The lesser addition of DON relative to DOC on an annualized basis could be the consequence of contributions of C-rich DOM sources or the preferential removal of N-rich DOM within the estuary. (e.g., Wiegner et al. 2006). The contribution of DON to the total N influx to the estuary varies seasonally, and is greater in the high flow winter and spring periods. Annual

net estuarine production of DON in the ORE is $33 \pm 5 \text{ mmol m}^{-2} \text{ y}^{-1}$. For comparison, Flynn (2008) estimated that the annual net addition of DON to the Mullica River–Great Bay estuary ($39^\circ 32.6' \text{ N}$, $74^\circ 24.4' \text{ W}$) was $80 \text{ mmol m}^{-2} \text{ y}^{-1}$. Both estimates are considerably lower than the values of $745 \text{ mmol m}^{-2} \text{ y}^{-1}$ produced within the Bly Creek subsystem of North Inlet, South Carolina (Dame et al. 1991). In Bly Creek, 70% of the net DON addition (excluding stream sources) was derived from export from the salt marsh (Dame et al. 1991). The differences between export estimates derived from small subdrainages such as Bly Creek relative to complete estuaries such as Great Bay or the ORE are evidence of the great extent of material reworking that must occur within the estuary prior to export to the coastal ocean. Applying Dame et al.'s (1991) estimate of the annual DON export from the Bly Creek salt marsh (3.5×10^5 moles, or 650 mmol m^{-2} salt marsh y^{-1}) to the total salt marsh area of the ORE ($230 \times 10^6 \text{ m}^2$) yields a potential marsh DON contribution to the estuary of 1.5×10^8 moles DON. That value is 1.8 times the annual DON input from the Ogeechee River and 13 times the apparent net DON production within the estuary. If similar marsh exports are assumed for the ORE, then more than 90% of the DON exported from the marsh surface must be recycled or removed before it can be exported in order to maintain mass balance.

NO_3^- is the next most abundant form of N in the ORE, comprising about 18% of the estuarine TDN export to the coastal ocean. Nitrate concentrations were greater than $10 \mu\text{M}$ throughout the estuary during the summer transects, but were 3 to $5 \mu\text{M}$ the rest of the year (see the supplemental figures). The ORE oscillated between production and consumption of NO_3^- throughout the year (Fig. 4c and d). On an annualized basis, exports exceeded imports by $17 \pm 1\%$.

NO_2^- and NH_4^+ fluxes were less than 5% of the total TDN export (Fig. 4k–l); however, 40% of the additional DIN that is generated within the estuary and contributes to the net DIN export is in the form of NH_4^+ . The largest NH_4^+ exports occurred in the spring (Fig. 4e) when river discharge was high and ammonium concentrations were in the low micromolar range. Similar to the findings of Schaefer and Hollibaugh (2017), mid-estuarine concentrations of NO_2^- reached as high as $5 \mu\text{M}$ in the summer transects (see the supplemental figures).

The estuary is also a net exporter of dissolved phosphate and a net consumer of dissolved organic P (Table 3, Fig. 5 a–d). The river contributes 2.6×10^6 moles of PO_4^{3-} to the estuary and another 2.2×10^6 moles of DOP. The estuary itself contributes another 1.6×10^6 moles of PO_4^{3-} to the total export flux while consuming 1.1×10^6 moles of organic P. The annualized net production of TDP within the ORE during estuarine transit is $6.4 \pm 6 \times 10^5$ moles, or $14 \pm 1\%$ of annual riverine inputs. Consumption of P in the ORE in the spring and summer is mostly balanced by production in the fall and winter (Table 3, Fig. 5e and f). The net consumption of PO_4^{3-} during spring months (April–June) was also noted by Wolaver and Spurrier (1988) in salt marshes in South Carolina.

A net export of dissolved nutrients from the ORE requires net diagenetic or other contributions to the estuary. Anthropogenic sources of N and P within the ORE are unlikely to

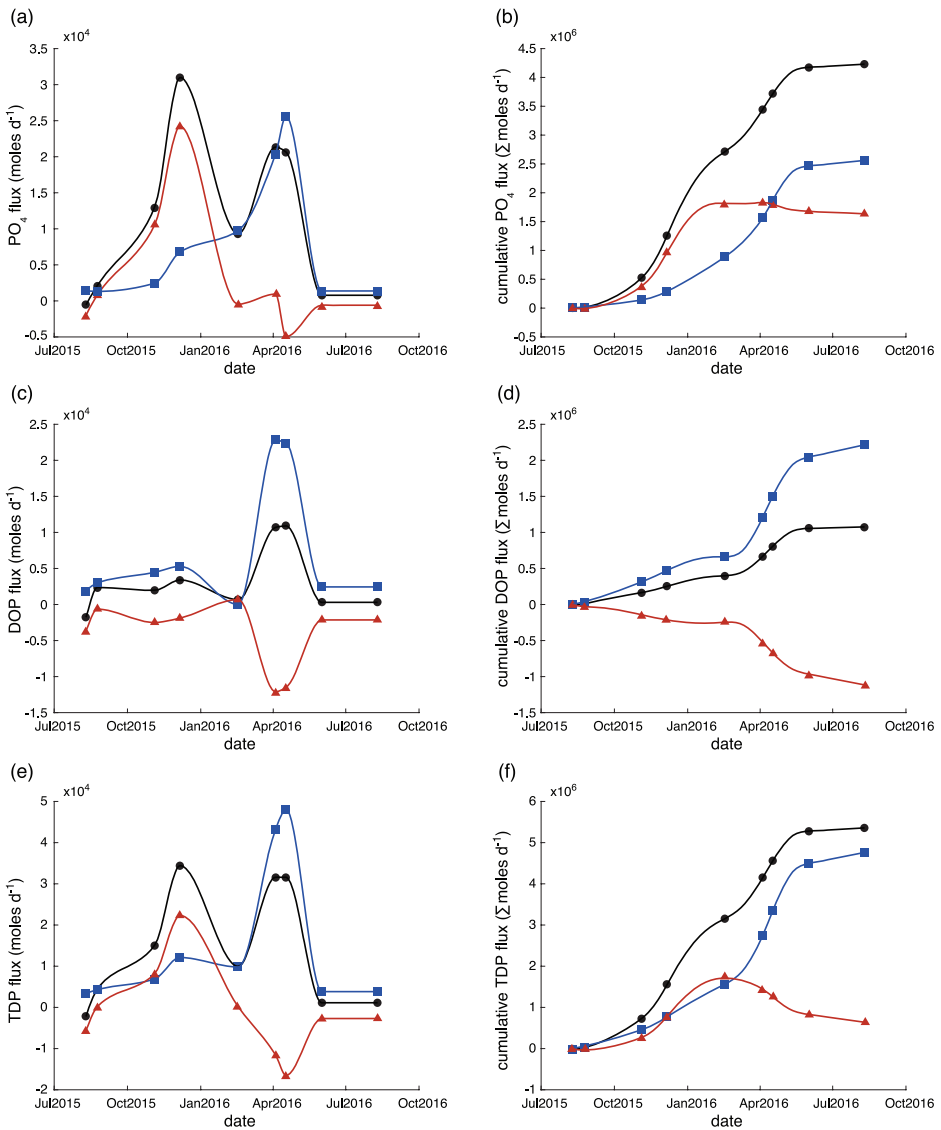


Figure 5. Modeled daily and cumulative fluxes of phosphorus species in the Ogeechee River estuary, 2015–2016. (a) Daily PO_4 . (b) Cumulative PO_4 . (c) Daily organic phosphorus (DOP). (d) Cumulative DOP. (e) Total daily phosphorus (TDP). (f) Cumulative TDP. River input is blue, calculated estuarine internal production/consumption fluxes are in red, and net exports are shown in black.

contribute significantly to the observed net export (Wang 2003). Development surrounding the shorelines of the ORE are mostly suburban. There are no major industrial discharges into the estuary itself. Point source sewage discharges for the city of Savannah (pop. 150,000)

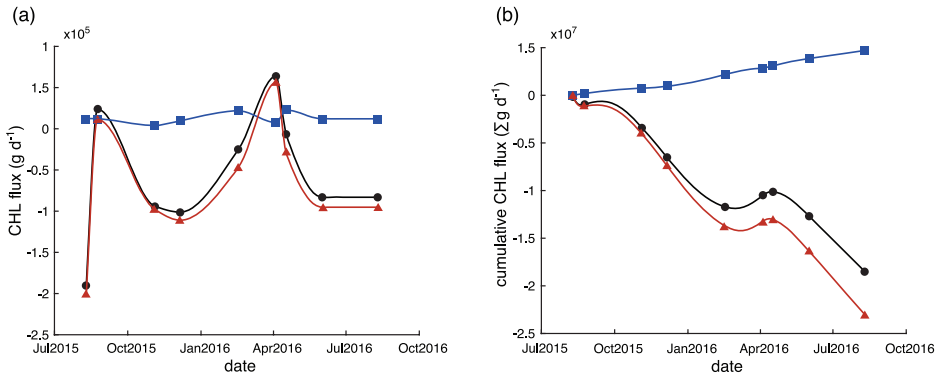


Figure 6. Modeled daily and cumulative fluxes of chlorophyll (chl) in the Ogeechee River estuary, 2015–2016. (a) Daily. (b) Cumulative. River input is blue, calculated estuarine internal production/consumption fluxes are in red, and net exports are shown in black.

on the northern fringe of the estuary are directed mostly to the Savannah River to the north. Municipal discharges for the city of Richmond Hill (pop. 12,500) on the south side of the estuary are applied to a constructed wetland and not flushed directly into the estuary. Non-point discharges from runoff and septic systems have not been quantified. Street runoff from the northern (Savannah) side of the estuary is intercepted first by the Little Ogeechee River and does not intersect the Ogeechee mainstem above about 4 km from the Ogeechee estuary mouth.

c. Particulate phytoplankton nutrients

In contrast to the dissolved nutrients, however, on an annual basis the ORE seems to be a significant sink for chlorophyll imported from both the Ogeechee River and from the coastal ocean. Seasonal chlorophyll fluxes were dominated by large imports from the coastal ocean in the summer and early fall (Fig. 6a and b). Imports from the riverine endmember were approximately constant all year, but were an order of magnitude smaller than coastal fluxes in the summer and fall. An apparent spring bloom within the estuary in the spring led to net exports of chlorophyll in that season (Fig. 6a).

The likely fate of most of the imported coastal phytoplankton biomass is to be remineralized within the estuary and contribute to dissolved nutrient pools. Using a rough estimate of 50:1 for the carbon/chlorophyll ratio of local estuarine phytoplankton—while bearing in mind that these ratios are poorly constrained and may vary with season (e.g., Jakobsen and Markager 2016)—and assuming that the biomass is remineralized in Redfield proportions, then the total potential contribution of imported phytoplankton biomass to dissolved constituent cycling and export can be estimated (Table 3). On an annual basis, import and remineralization of coastal phytoplankton potentially contributes as much as 7.7×10^7 moles of carbon, 4.8×10^6 moles of N, and 7.3×10^5 moles of P to the

Table 4. Comparisons of modeled annual coastal plankton fluxes into the Ogeechee River estuary with modeled production of DOC, TDN, and TDP within the estuary and for export from the estuary.

	Phytoplankton	Internal flux	Export flux	Constituent
Phyto-C	4.6×10^7	8.3×10^8 (6%)	4.2×10^9 (1%)	DOC
		1.8×10^7 (16%)	1.4×10^8 (5%)	TDN
Phyto-N	6.9×10^6	1.5×10^7 (46%)	1.1×10^8 (6%)	DON
		3.2×10^6 (216%)	2.6×10^7 (26%)	DIN
Phyto-P	4.3×10^5	1.4×10^6 (254%) ^a	5.0×10^6 (9%)	TDP
		8.0×10^5 (54%)	3.8×10^6 (11%)	PO4

Notes: ^aPhyto-P is 254% of ORE TDP uptake. DOC—dissolved organic carbon, TDN—total dissolved nitrogen, DON—dissolved organic nitrogen, DIN—dissolved inorganic nitrogen, TDP—total dissolved phosphorus.

ORE (Table 4). Inclusion of the import of riverine phytoplankton raises those estimates by 1.2 times. DIC fluxes were not measured but would likely represent the largest pool of remineralized phytoplankton carbon. Note that these estimates apply only to chlorophyll bearing phytoplankton and not to heterotrophic plankton biomass. If zooplankton (particularly microzooplankton) are as susceptible to grazing and/or depositional mortality as are phytoplankton (e.g., Dame et al. 1986), then the importance of particulate import from the coastal ocean into the estuary to the total dissolved export increases proportionally.

These estimates are dependent upon the assumed c:chl ratio of the plankton community. As a general rule, planktonic algae have low c:chl ratios under nutrient replete and low-light conditions (Beardall and Morris 1976; Geider 1987; Jakobsen and Markager 2016). Jakobsen and Markager (2016) found that winter minimum c:chl ratios for estuarine phytoplankton in Danish waters averaged 15:1. Annual mean c:chl was between 27 and 41. Both estimates are lower than the 50:1 value adopted here; however, it is not clear how fully the estuarine values reported by Jakobsen and Markager (2016) apply to the ORE. The coastal source plankton for import is nitrogen limited (Hanson and Robertson 1988) and, at least in the summer when the majority of import occurs, is well-lit—both of which would suggest higher c:chl ratios. Calvo-Diaz, Morán, and Suárez (2008) found that picoplankton immediately off the coast of Spain had peak summertime c:chl values of approximately 100. Verity et al. (1993) estimated summertime c:chl ratios as high as 250:1 in the coastal ocean adjacent to the mouth of the ORE. We have chosen to use a conservative intermediate c:chl ratio of 50:1. Doubling the c:chl ratio would double the estimated (Redfield) phytoplankton N and P fluxes; halving it would halve those fluxes.

d. Annual budgets

Over an annual cycle, the model indicates that total (including plankton) external N inputs and outputs are almost balanced (Table 5). The ORE exports $115 \pm 1\%$ of the nitrogen from all quantified sources that it receives from the riverine and coastal ocean endmembers.

Table 5. Relationship between estuarine residence time and the relative contribution of influx of plankton biomass to estuarine nutrient budgets.

	S1	S2	F1	F2	W2	Sp1	Sp2	S3–4	Annual
Freshwater residence time (days)	36	43	23	11	7	6.5	5.5	40	22
Coastal plankton N import/Riverine N import	201%	xp	89%	xp	4%	xp	xp	107%	6%
Coastal plankton P import /Riverine P import	210%	xp	65%	xp	20%	xp	xp	105%	7%
Coastal plankton N import/Estuarine N export	57%	xp	51%	xp	4%	xp	xp	70%	6%
Coastal plankton P import/Estuarine P export	pi	xp	28%	xp	1%	xp	xp	666%	8%

Notes: N–nitrogen, P–phosphorus, pi–total dissolved phosphorus imported from the coastal ocean, xp–biomass exported from the estuary.

Nitrogen capture efficiency is variable among and between seasons. Instances of net consumption of N (in S1 and Sp1) were associated with instances of consumption of DON within the estuary. Net export of total N was modeled for the remainder of the year. The implication of these results is that there is little apparent scope for significant burial of N or denitrification losses within the ORE. That seems unlikely. Loomis and Craft (2010) calculated an N burial rate for the Ogeechee estuary of 5.7×10^7 moles y^{-1} , which is approximately 9.5 times the value that we model for phytoplankton N flux and is 50% of our total modeled annual riverine N inputs to the ORE. Loomis and Craft's (2010) calculations are based on Schaefer and Alber's (2007) estimates of integrated annual dissolved N delivery from the watershed measured at Eden, Georgia, approximately 25 km upstream from the head of the estuary, and are almost twice our modeled estimates (2×10^8 moles y^{-1} as compared with 1.1×10^8 moles y^{-1}). Loomis and Craft (2010) calculated that 29% of riverine N delivery to the ORE was removed by burial, if both estuarine denitrification and N fixation within the estuary were ignored. Inclusion of N fixation (using data of Howarth et al. 1988 and Neubauer et al. 2005) and ambient denitrification in their estimate lowered the burial removal to -8% , implying a compensatory N fixation rate of 2.1×10^8 moles y^{-1} . That is, more N is added to the estuary by N fixation than is removed by denitrification and burial. Adding estimates of potential denitrification of 7.9×10^6 moles N y^{-1} (Craft et al. 2009) increased the estuarine N sink to 33% of riverine inputs. Direct measures of denitrification in the region are few. Porubsky, Weston, and Joye (2009) found that denitrification rates in unamended salt marsh cores were low ($1.5 \pm 1.4 \mu$ moles $m^{-2} h^{-1}$), which would correspond to only approximately 3×10^6 moles y^{-1} lost from the ORE salt marshes if those estimates could be applied globally to the estuary. Porubsky, Weston, and Joye's (2009) rates are among the lowest seen in a summation of 65 estuarine and coastal denitrification studies compiled by Joye and Anderson (2008). If those modest estimates are valid, denitrification consumes less than 3% of annual delivery

to the ORE, which is not inconsistent with the results we observe in the annual model. For contrast, using Nixon et al.'s (1996) regional regression model yields an annual residence time weighted estimate of approximately 20% losses of N to denitrification. Haines et al. (1977), working near Sapelo Island, Georgia, estimated that denitrification rates were about 1/3 greater than N fixation rates in salt marsh soils. However, studies by Hanson (1977, 1983) in the same area provide estimates of rhizospheric N fixation that are 5 times greater than those used by Haines et al. (1977) or Loomis and Craft (2010). Hanson's (1977, 1983) rate data are close to the mean of rates of thirteen *Spartina* marsh N fixation studies compiled by Hopkinson and Giblin (2008). Extrapolating Hanson's (1977, 1983) annual rates to the marsh area of the ORE gives a total annual N fixation of 2.6×10^8 moles N year^{-1} —more than enough to balance both the estimated N burial (5.7×10^7 moles y^{-1}) and potential denitrification (7.9×10^6 moles N y^{-1}) sinks reported by Loomis and Craft (2010) within the ORE. Given the apparent annual balance between N inputs and N outputs we model for the system, it would seem likely that N fixation must roughly balance both burial and denitrification losses. Kolton, Rolando, and Kostka (2020) determined that diazotrophic bacteria at a marsh site along the Skidaway River (adjacent to and connected to the ORE) were an important component of the *Spartina* rhizosphere, and were thought to be of major importance in mediating rhizosphere nutrient cycling. Since N fixation in salt marshes is largely a rhizospheric process (Nielsen et al. 2001), the large fraction of the ORE that is covered by marsh grasses, combined with N limitation of *Spartina* production (e.g., Mendelsohn and Morris 2000), may encourage net internal N fixation within the ORE. We hypothesize that this may be a fundamental difference in N cycling between marsh dominated estuaries, such as those of Georgia and South Carolina, and more open water estuaries like the Chesapeake Bay, Narragansett Bay, or San Francisco Bay that have a much smaller percentage cover of vegetation and a much greater expanse of unvegetated sediment.

The ORE captures $8 \pm 0.2\%$ (4.9×10^5 moles y^{-1}) of total annual dissolved phosphorus input, including phytoplankton-P. Exports exceed imports in the fall and winter, but the ORE is a sink for P during the remainder of the year. With the exception of the anomalously large export of P in the fall, the pattern of export efficiency corresponds with expectations based on water residence time (Table 1). We propose that the large phosphate export in the fall is due to a combination of declining light levels, which limits P uptake by phytoplankton within the estuary, combined with warm water temperatures, which facilitates intensive remineralization of stored P within estuarine waters and sediments.

Asbury and Oaksford's (1997) assessment of Ogeechee River watershed loadings yielded a total terrestrial P input to the river of 4.3×10^6 moles P y^{-1} . We have adjusted those numbers upward by 1.4 times to account for increasing loads over time (Schaefer and Alber 2007) to generate a modern delivery of P to the ORE of 6.1×10^6 moles P y^{-1} , which compares favorably with our estimate of $4.8 \pm 1 \times 10^6$ moles P y^{-1} . However, our estimate of P retention by the ORE is less than 10% of the marsh accumulation rates of total P of 5.2×10^6 moles y^{-1} reported by Loomis and Craft (2010). That total is equivalent to 88%

of our annual modeled P inputs into the ORE. Riverine and coastal import of particulate P may account for the bulk of P burial within the ORE.

On a date-by-date basis the relationship between N gains and losses and P gains and losses within the estuary can be incoherent. The ORE imports all forms of N and P, although not at Redfield ratios. Denitrification in the riverine watershed (Schaefer and Alber 2007) reduces the inorganic N:P ratio of imported material to 7.7:1, with a seasonal range of 1.3:1 (F2) to 18.4:1 (S1). The modeled N:P of the annual inorganic nutrient export flux is 6.8. On the surface this would suggest a net N loss to denitrification, whereas the model results indicate a net production of N for estuarine export, and a net consumption of P. During transects S1, F1, Sp1, and Sp2 and for the annual summation, the ORE acts as a sink for DOP while acting as a source for DON. During the F1 and W1 transects, the ORE is a source of PO_4^{-3} and a sink for DIN, whereas during the Sp1 and Sp2 transects, the estuary is a sink for PO_4^{-3} and a source of DIN. However, because of differences in intrinsic rates, pathways, and transient forcing among all of the processes involved, there is no a priori reason to believe that on any given tide the production and consumption of N and P within the estuary will be balanced. Arndt and colleagues (Arndt, Regnier, and Vanderborcht 2009; Arndt et al. 2011) have demonstrated through high-resolution modeling of the macrotidal Scheldt estuary that different time scales of biogeochemical responses to external forcing means that nutrient concentrations and nutrient ratios within the estuary are not predictable from river inputs and residence times on seasonal time scales. However, on an annually averaged basis, their models reflected long-term average values in the system. Analogously, in the ORE, significant intra- and inter-seasonal variation in fluxes are estimated for the various chemical species, reflecting proximate balances in production and consumption of various organic and inorganic species. For example, a net efflux of N in the (warming) spring may represent mobilization of organic matter banked in the estuary during the winter when temperatures are low and standing *Spartina* biomass that has not yet fully decayed. The summation of these temporally out of phase processes should still yield a flux that represents a true annual flux.

e. Environmental drivers of phytoplankton and nutrient fluxes

The apparent role that phytoplankton-bound nutrients play in the Ogeechee nutrient cycles can be explained by several features of the ecosystem. The waters of the Ogeechee are moderately colored and turbid. Secchi depths averaged less than 0.7 m (range: 1.5 m to 0.3 m). Light, rather than nutrients, is thought to limit photosynthetic rates within southeastern US estuaries (Ragotzkie 1959; Pomeroy et al. 1981; Pomeroy et al. 2000), although this proposition has not been tested extensively. The presence of moderate nutrient concentrations in the estuary ($\text{TDP} > 1 \mu\text{M}$, $\text{DIN} > 5 \mu\text{M}$) most of the year argues against significant nutrient limitation of phytoplankton. In general, nutrient concentrations were highest during the summer when estuarine primary production peaks (Turner, Woo, and Jitts 1979a). Light-limited phytoplankton within the estuary may grow relatively slowly

and be less effective at taking up nutrients from the water during estuarine passage. However, once the phytoplankton and nutrients are discharged from the estuary into the coastal ocean they experience significantly clearer water, enhanced residence times, and a burst of primary production across the inner shelf to the coastal front that separates the inner shelf from the middle shelf and confines river discharge to a narrow band adjacent to the shore (Thomas 1966; Turner, Woo, and Jitts 1979b; Bishop, Yoder, and Paffenhofers 1980; Verity et al. 1993). The standing stock of nearshore coastal phytoplankton creates a reservoir of biomass that can be advected into the estuaries on incoming tides.

Furthermore, within the estuary, because of lower, light-limited growth rates, phytoplankton loss rates to grazing and sedimentation may be greater than net in situ replacement. Phytoplankton suspended on the incoming tide is prone to predation by pelagic and benthic grazers. Lewitus, Koepfler, and Morris (1998) determined that summer phytoplankton populations in North Inlet, South Carolina, were controlled by microplanktonic grazers. The microplankton grazing foodweb favored rapid remineralization and recycling of dissolved nutrients in the water column (Dame et al. 2000). Benthic suspension feeding oysters (*Crassostrea* sp.), clams (*Mercenaria* sp.), and mussels (*Geukensia* sp.) in the ORE may also be significant sources of phytoplankton mortality, deposition, and remineralization (e.g., Jordan and Valiela 1982; Officer, Smayda, and Mann 1982; Dame, Zingmark, and Haskin 1984; Dame, Spurrier, and Wolaver 1989; Dame, Spurrier, and Zingmark 1992; Huang, Kreeger, and Newell 2003; Banas et al. 2007). Our recalculation of oyster reef filtration data presented by Dame, Zingmark, and Haskin (1984) suggests that oyster reefs in tidal creeks in South Carolina can intercept approximately 30% of the chlorophyll flowing across them over a tidal cycle. In shallow habitats in South San Francisco Bay, Alpine and Cloern (1992) demonstrated that high densities of suspension feeding clams could control phytoplankton abundance in the overlying water column. Huang, Kreeger, and Newell (2003) estimated that 21% of microalgal cells entering a salt marsh in Delaware on the flooding tide were deposited on the marsh surface prior to ebb. Similar measurements by Dame et al. (1986) in North Inlet, South Carolina, gave estimates of 35% removal over a tidal cycle. The authors attributed most of the losses to suspension feeding organisms on the marsh surface. The marsh imported chlorophyll in the summer and fall and exported it in the winter and spring. Jordan and Valiela (1982) estimated that ribbed mussels on the marsh surface at a Massachusetts salt marsh could potentially filter the volume of the entire flooded marsh volume during each tide. Mussels are native to Georgia's marshes as well, but population densities there are much lower (Smith and Frey 1985; Schalles et al. 2013). Nevertheless, they have been shown to contribute up to 100% of seasonal sediment accumulation on the marsh surface through their filtration and biodeposition activities (Smith and Frey 1985). Additionally, passive sedimentation among the upright stems of estuarine marsh vegetation may be a significant loss term for suspended phytoplankton and other particles (Chrzanowski and Zingmark 1986; Dame et al. 1991).

The large tidal range along the Georgia coast (mean amplitude = 2.3 m) generates a large tidal prism within the estuary. J. Sheldon (personal communication) has estimated

that the intertidal volume of the Ogeechee River is approximately $84 \times 10^6 \text{ m}^3$. Assuming 1.9 tides per 24 hours, the total daily volume change in the Ogeechee is 1.33 times the low tide estuary volume of $1.2 \times 10^8 \text{ m}^3$ (Mike Robinson, personal communication). That same intertidal volume change is on the order of 100 times the daily river discharge during the summer and fall and 10 times the daily river discharge during the winter and spring. Not all of the prism volume will correspond to new coastal water entering the estuary (e.g., Banas et al. 2004; Banas and Hickey 2005), but the difference in the magnitudes of the flows highlights the potential for tidal pumping of coastal water and associated coastal phytoplankton into the estuary. Dispersive mixing efficiently transports coastal water far into the estuary (e.g., Banas et al. 2004; Banas and Hickey 2005; Raimonet and Cloern 2017) and promotes a continuous movement of labile material upstream where it can be captured and remineralized. The net import of chlorophyll into estuaries from the coastal ocean has been observed in numerous estuaries in the Pacific northwest (Roegner and Shanks 2001; Martin, Fram, and Stacey 2007; Brown and Ozretich 2009; Roegner, Seaton, and Baptista 2011; Buck et al. 2014; Raimonet and Cloern 2017) as well as in Portugal (Blanton et al. 1987; Alvarez-Salgado et al. 2000; Cravo et al. 2014), and Brazil (Noriega et al. 2013). Coastal phytoplankton is transported into the estuaries by tides and dispersive mixing (Martin, Fram, and Stacy 2007; Raimonet and Cloern 2017) when river discharge is low. In most of these examples, the nutrient source driving the coastal production has its origin in deep water upwelling from offshore. Roegner, Seaton, and Baptista (2011) suggested that net import of coastal chlorophyll into estuaries was a unique feature of estuaries adjacent to eastern boundary current systems. However, this study and the results of Noriega et al. (2013) suggest that a more general condition of a gradient of increasing chlorophyll content across the estuarine-coastal transition zone, combined with a dominance of tidal exchange and dispersion over riverine advection flushing would favor net import of chlorophyll into estuarine systems. In systems with favorable conditions for growth, importation of biomass and nutrients may seed blooms within the estuary. However, where the rate of phytoplankton mortality within the estuary exceeds growth rates, the estuary will be a sink for imported cells and a source of remineralized nutrients.

Roegner and Shanks (2001) have speculated that the import of coastal phytoplankton biomass fed by upwelling of deep oceanic water supports the foodweb of estuarine suspension feeders in South Slough (Coos Bay), Oregon—and, by extension, would support production of remineralized nutrients within the estuary. However, in the ORE, the nutrients contributing to enhanced coastal production must have their origin in outwelled terrestrial/estuarine sources, whether directly from export of riverine dissolved nutrients or indirectly from regeneration from sedimentary sources (Hopkinson 1987). Upwelling does occur on the Georgia shelf, but the effects are isolated well offshore (Yoder et al. 1985, Lee, Yoder, and Atkinson 1991). The strong salinity gradient in the near-coastal ocean inhibits exchange with water offshore, trapping the production against the shore and creating a gradient that allows plankton to be readily imported into the ORE. The import of phytoplankton bound nutrients does not represent a source of new nutrients to the estuarine system, but

is part of a tight recycling loop between riverine dissolved nutrient exports and coastal particulate nutrient imports.

Coastal Georgia estuaries may have greater hydrographic similarities with estuaries of the Pacific northwest coast than with estuaries on the Gulf coast or elsewhere along the Atlantic coast. Similar to four Pacific northwest estuaries listed by Hickey and Banas (2003), Georgia estuaries (with the exception of the dammed and dredged Savannah River estuary) are shallow (< 4 m), mesotidal (range > 2 m), have large intertidal areas, and have large annual ranges in river discharge. Additionally, coastal set-up and set-down associated with downwelling and upwelling favorable winds can influence estuarine/coastal water exchange (e.g., Hickey and Banas 2003; Di Iorio and Castelao 2013). Estuaries in the northwestern and southeastern United States differ in that conditions seaward of the estuary mouths are more constant in coastal Georgia than in the Pacific northwest where upwelling and downwelling episodes can greatly alter water properties in the coastal ocean over short time scales. In both the southeast and northwest, riverine freshwater inflows to the estuaries are minimal in the summer months (Alber and Sheldon 1999; Hickey and Banas 2003). In the Pacific northwest, during low flow periods of the year, upstream diffusive transport of salt significantly exceeds downstream advective salt flux (Banas and Hickey 2005). Seim, Blanton, and Elston (2009) and Blanton et al. (2003) have investigated salt transport in the Satilla River of coastal Georgia. They found that tidal pumping of salt up the estuary was important but that it was slowed significantly by secondary circulation within curved channels.

The outwelling of nutrients from the estuary to the ocean may be highly variable along the Georgia coast. Estuaries with large watersheds and discharges, such as the Savannah and Altamaha, may be consistent exporters of nutrients to the coastal zone. Relatively blind tidal embayments without upland freshwater sources, such as Wassaw Sound or St. Catherines Sound, may be net importers of nutrients because of tidal pumping and marsh sequestration of coastal production. The remaining systems with variable discharge may alternate between export-dominated to import-dominated systems, depending on the ratio of dispersion to advection. Import-dominated systems will receive relatively low dissolved organic and inorganic nutrient loads from upland sources but will acquire a labile, near-Redfield particulate nutrient loading from coastal blooms. Export dominated systems will be more dependent on terrestrial nutrient subsidies. Differences in the magnitude and lability of nutrient fluxes in Georgia estuaries may lead to different balances between N fixation and denitrification within estuarine subsystems (e.g., Fulweiler et al. 2013).

Because of the nearshore connectivity of Georgia estuaries, the consequences of outwelling or inwelling from particular estuaries on coastal and estuarine productivity cannot be considered in isolation. Transport of coastal waters is under the control of the seasonal wind field (Blanton and Atkinson 1983; Di Iorio and Castelao 2013), and phytoplankton blooms present at the mouth of the Ogeechee may have had their origin in nutrients exported from other river basins. Thus, the consequences of anthropogenic nutrient enrichment in particular river basins may be both diluted and disguised since the biological effects of the nutrients

they deliver may be expressed throughout the nearshore coastal ocean (e.g., Verity et al. 1993) and the increased nutrient-driven production can be remineralized in adjacent basins.

4. Conclusion

On an annual basis, *total* nutrient imports and exports in the ORE are almost in balance. The modeled regeneration of inorganic nutrients within the ORE is nearly equal to the consumption of particulate nutrient packaged as phytoplankton biomass. Given the N and P burial rates measured in the ORE (Loomis and Craft 2010) and the estimates of estuarine denitrification (Haines et al. 1977; Porubsky, Weston, and Joye 2009), the modeled balance in nutrient fluxes implies a compensatory N fixation rate of at least 5.7×10^7 moles N y^{-1} ($\sim 500 \mu$ moles $m^{-2}d^{-1}$). The total P budget suggests a small net sequestration of P in the estuary. Phytoplankton P import into the estuary is $41 \pm 1\%$ greater than TDP production within the estuary, but the amount stored is only about 5% of the estimated annual P burial rate (Loomis and Craft 2010). The effect of dissolved terrestrial nutrient inputs in to the ORE is not generally to promote blooms within the estuary and subsequent export of particulate matter to the coastal ocean. Instead, nutrients delivered to the estuary from upstream effectively bypass the estuary proper and fertilize phytoplankton production in the nearshore coastal ocean (Thomas 1966; Turner, Woo, and Jitts 1979b; Bishop et al. 1980; Verity et al. 1993). Coastal phytoplankton production is promoted by the combination of nutrient availability (Bishop et al. 1980), a more favorable light environment (Turner, Woo, and Jitts 1979a; Verity et al. 1993) and a more extended residence time within the inner shelf (Atkinson, Blanton, and Haines 1978) that favors phytoplankton growth and biomass accumulation. The biomass that develops in the nearshore region is regularly re-injected into the ORE by tides where it can be captured by the native suspension feeding biota or sedimented directly onto the marsh platform surface on the high tide (e.g., Chrzanowski and Zingmark 1986; Huang, Kreeger, and Newell 2003). Remineralization of the captured biomass then contributes to the net efflux of dissolved nutrients from the estuary into the nearshore ocean.

The apparent strong recycling of material across the estuarine–coastal boundary has a distinct seasonality. Summer nearshore production is supported by both outwelled estuarine nutrients and nutrients regenerated and released from nearshore sediments (Hopkinson 1987; Hanson and Robertson 1988). Because river discharge is low, tides can mix the production back into the estuary where it is recycled rapidly. In the winter and spring production remains high in the nearshore (Verity et al. 1993), but the greater river discharge limits the capacity for dispersive mixing upstream and organic matter storage and remineralization are largely confined to the region seaward of the estuary mouth.

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Import, export and recycling of dissolved nutrients in the Ogeechee River estuary (Georgia, USA)

by William B. Savidge, Kathryn R. Doyle, and Brock Woodson

Supplemental figures S1–S11
Journal of Marine Research 78(2), 2020

Measured concentrations and modeled estimates for production and consumption of chemical species in the Ogeechee River estuary, 2015–2016. For all chemical species, the figure layouts are identical. Left-hand panels (a, c, e, g, i, k, and m) show the measured concentrations of each species at approximately 3 psu salinity intervals within the Ogeechee River estuary. The orange dashed line shows the theoretical conservative distribution. Note that the most seaward and landward points (open circles) are excluded from consideration. See text for explanation.

Right-hand panels (b, d, f, h, j, l, and n) show the modeled estimates of the production and/or consumption of each species in order to maintain the observed departure from a conservative distribution. The black line (left-hand axes) shows the within-section flux. The orange line (right-hand axes) shows the cumulative upstream–downstream summation of calculated fluxes for the individual section fluxes. As with concentrations, the most seaward and landward are excluded from the flux calculations.

For all species, the plots are ordered top to bottom in temporal order (S1, S2, F1, F2, W2, Sp1, and Sp2).

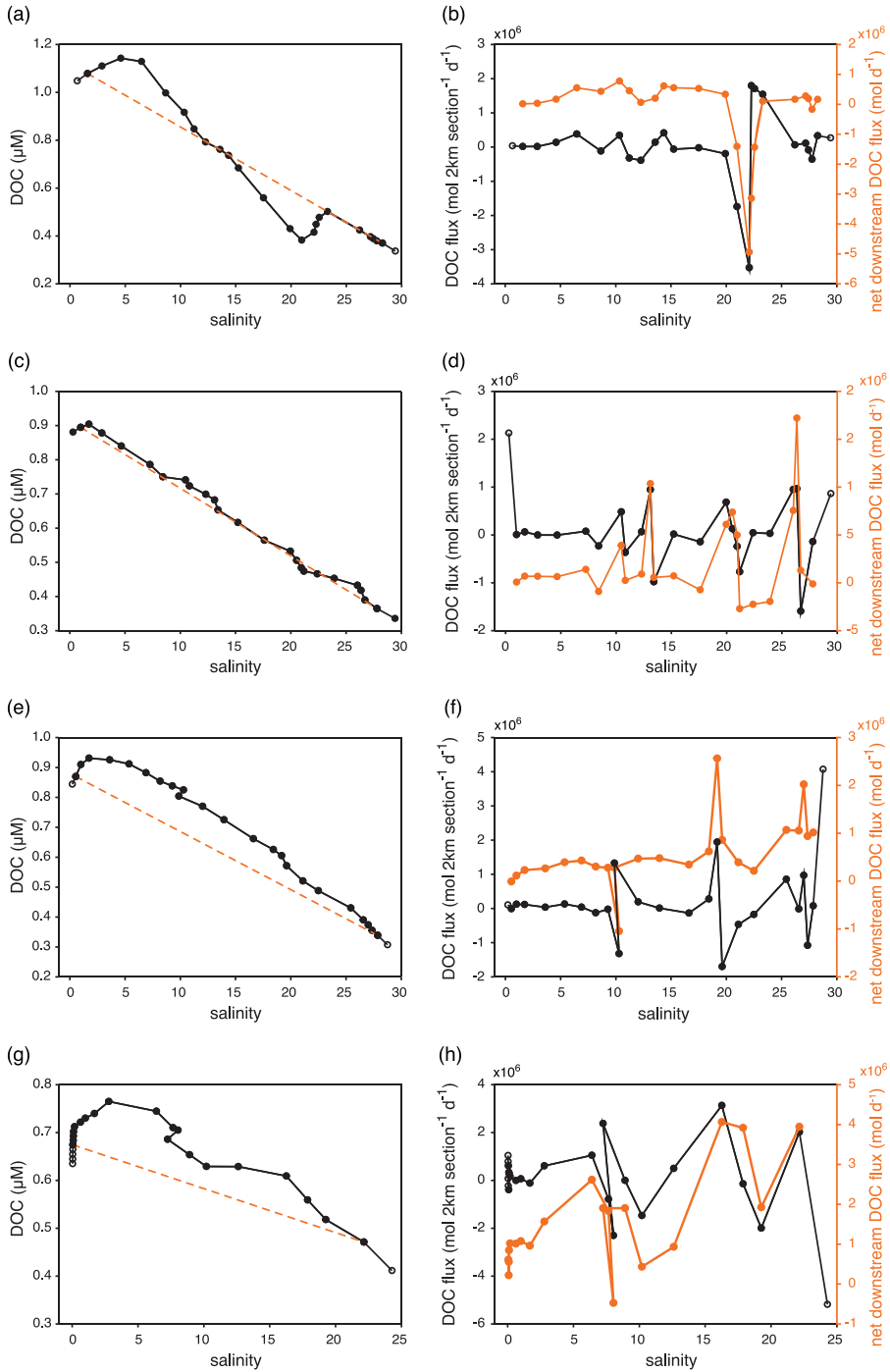


Figure S1.

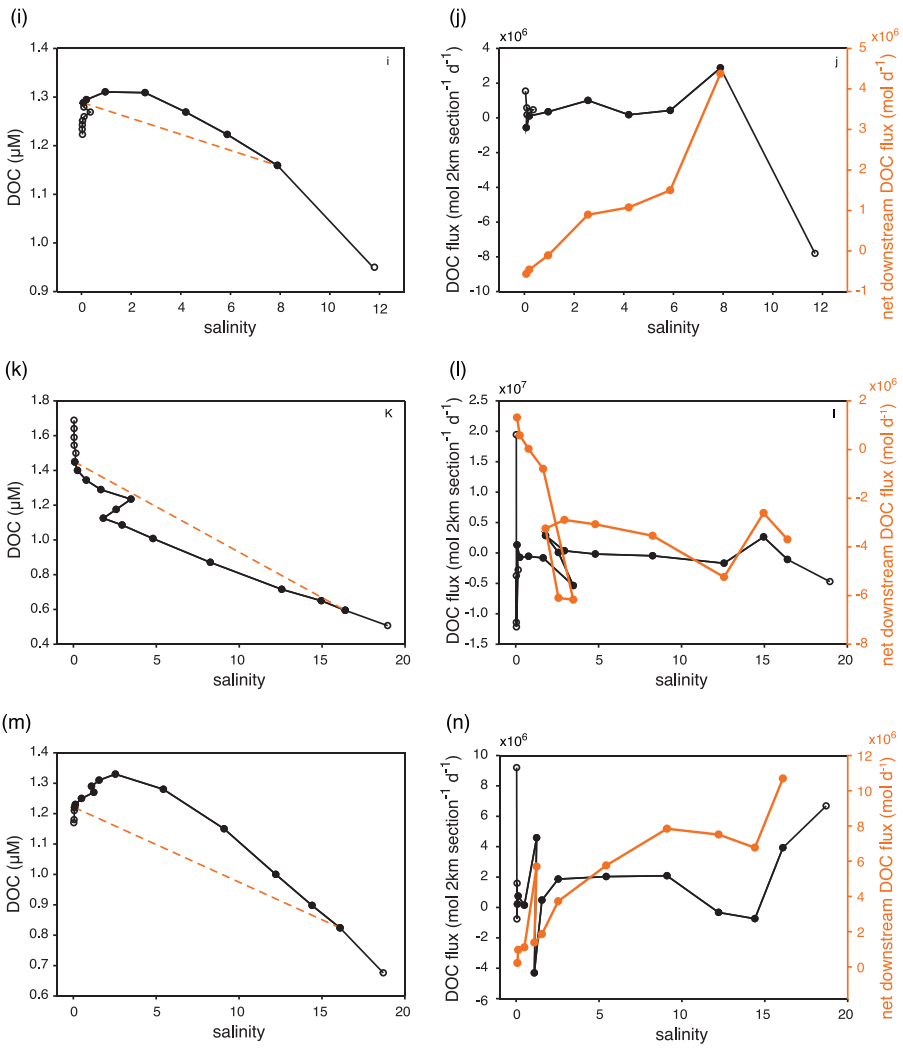


Figure S1. (continued)

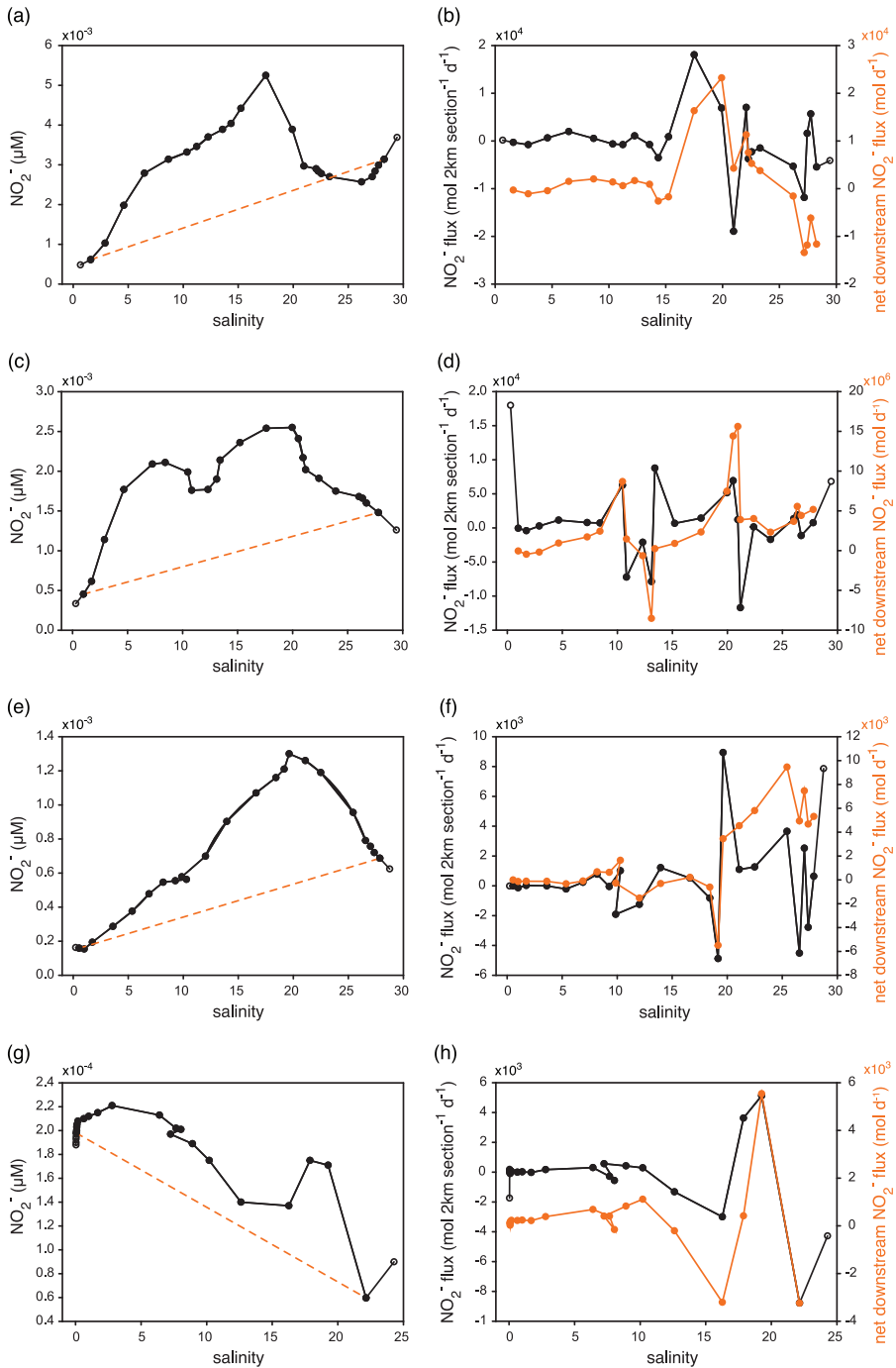


Figure S2.

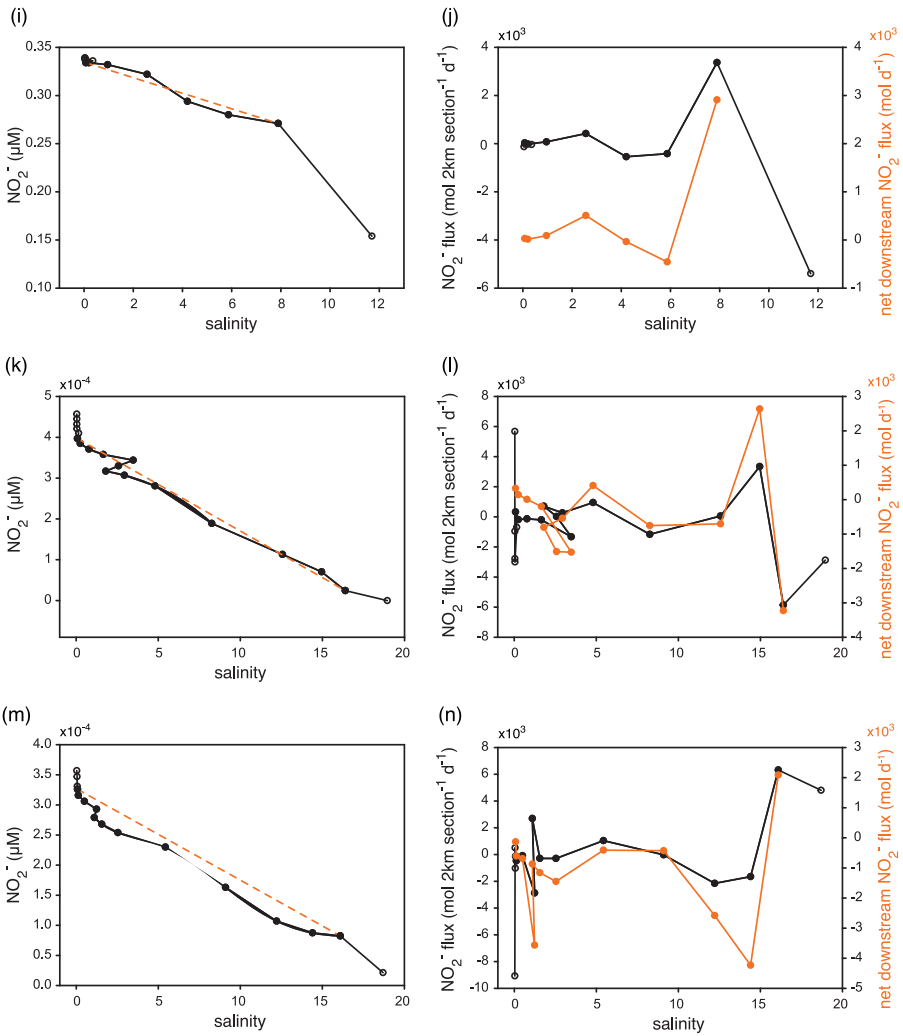


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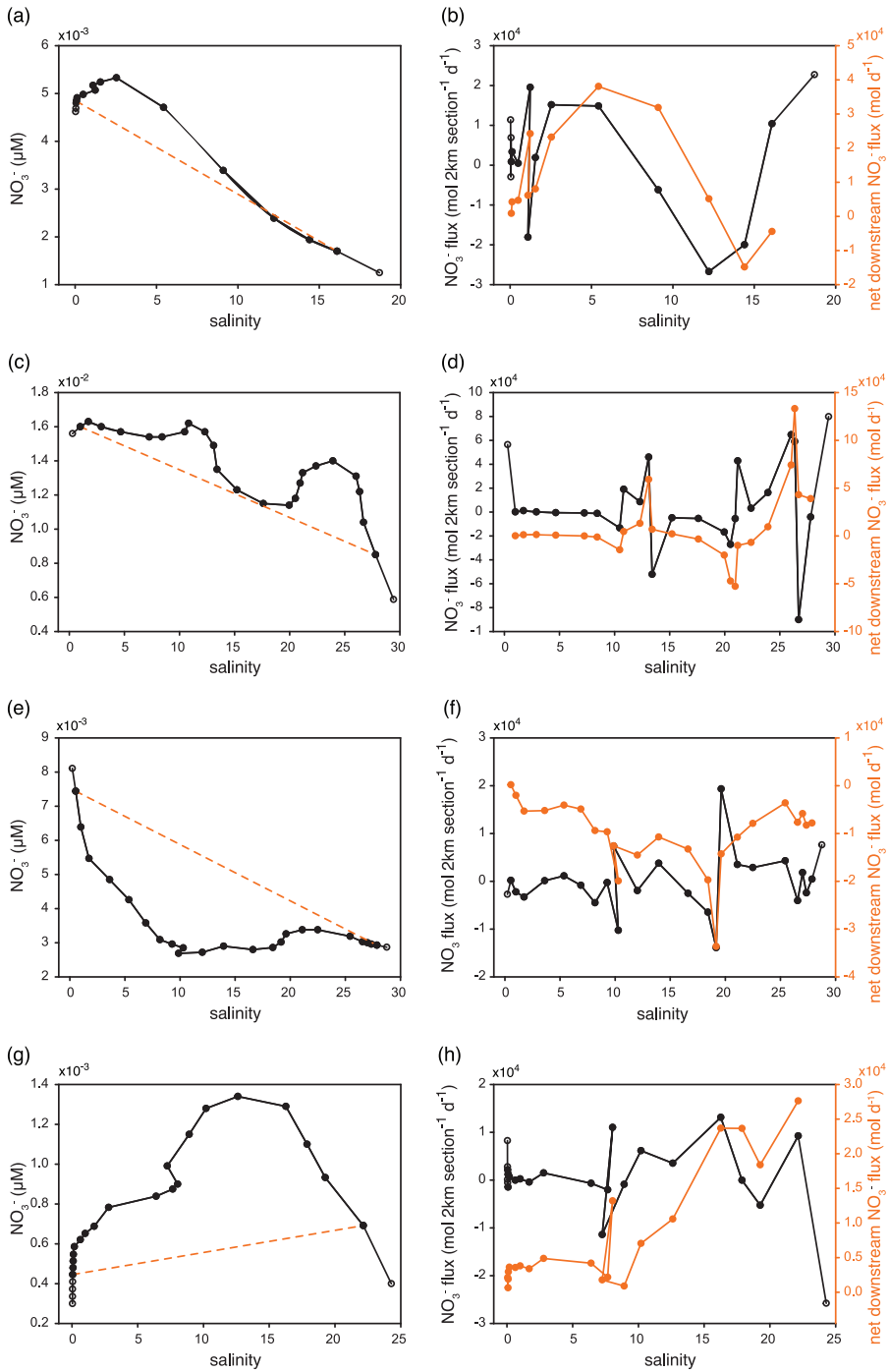


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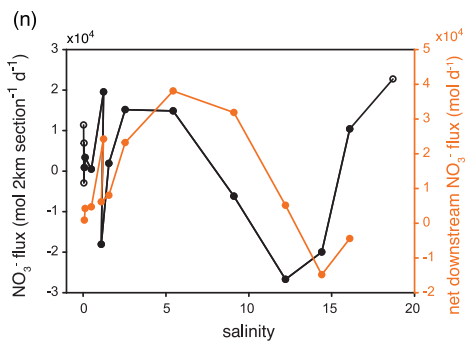
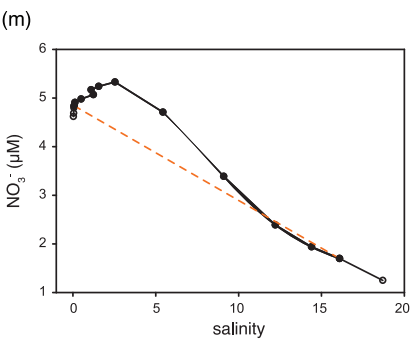
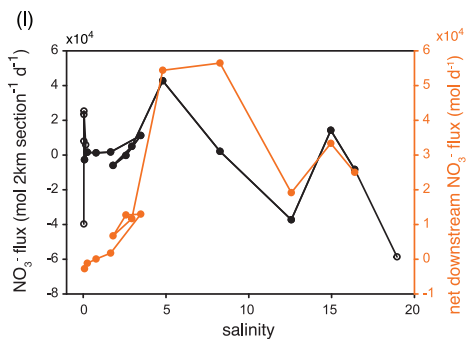
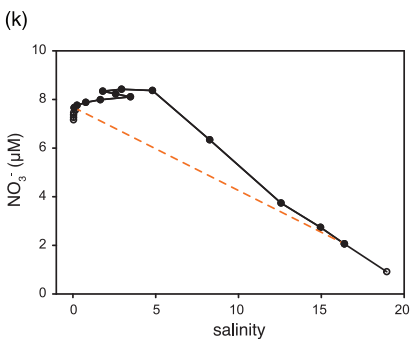
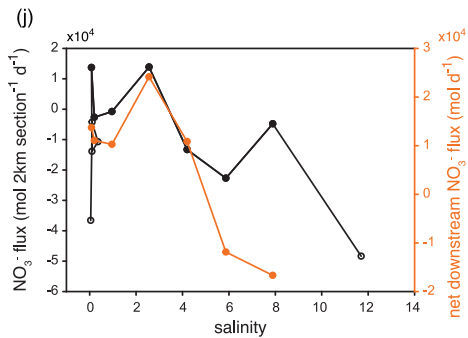
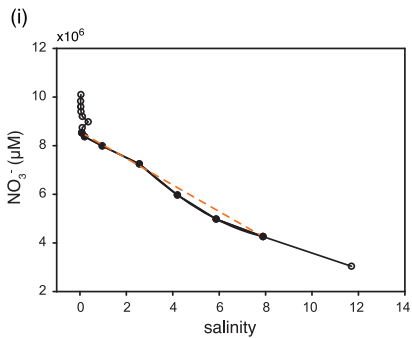


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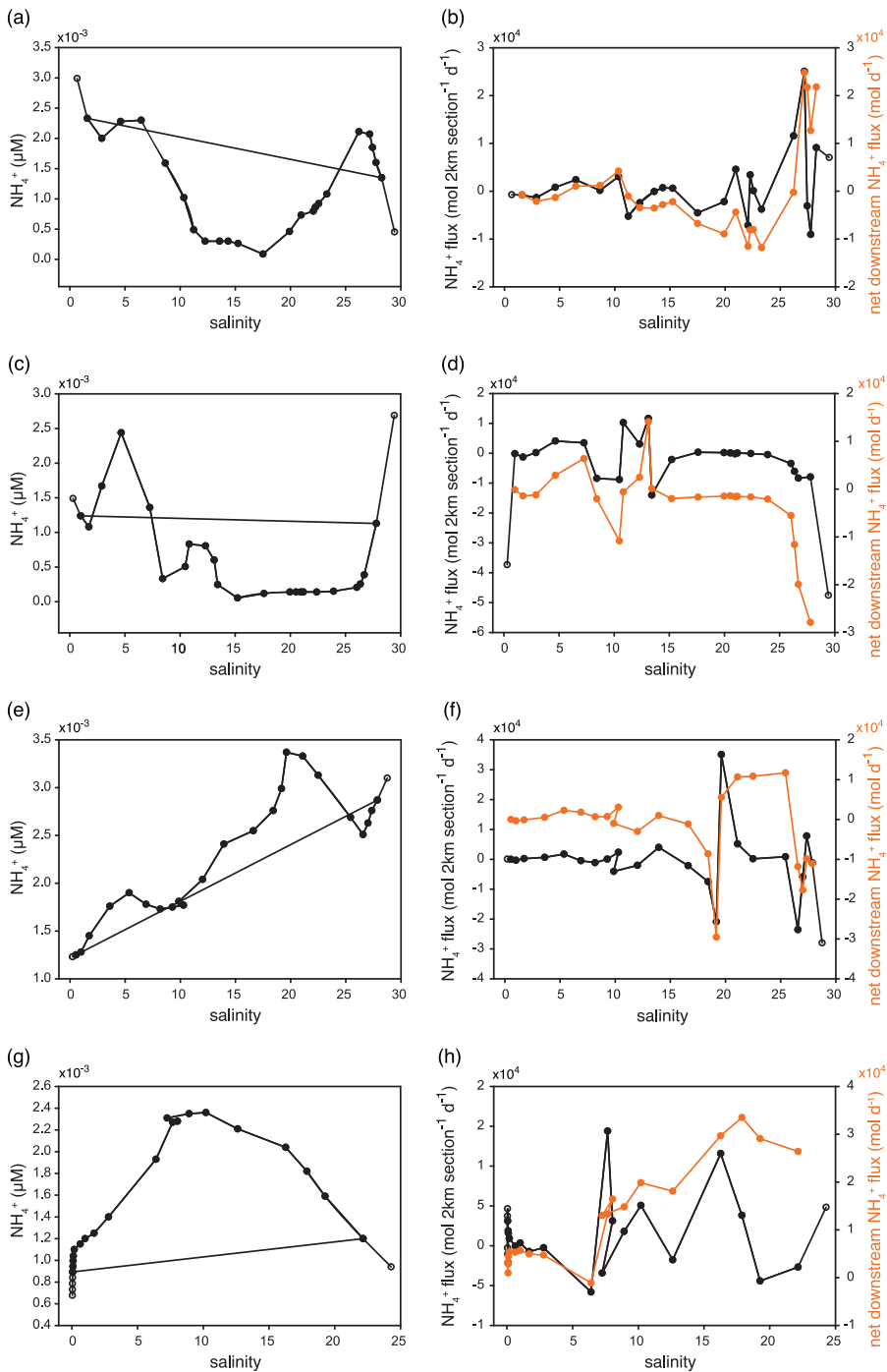


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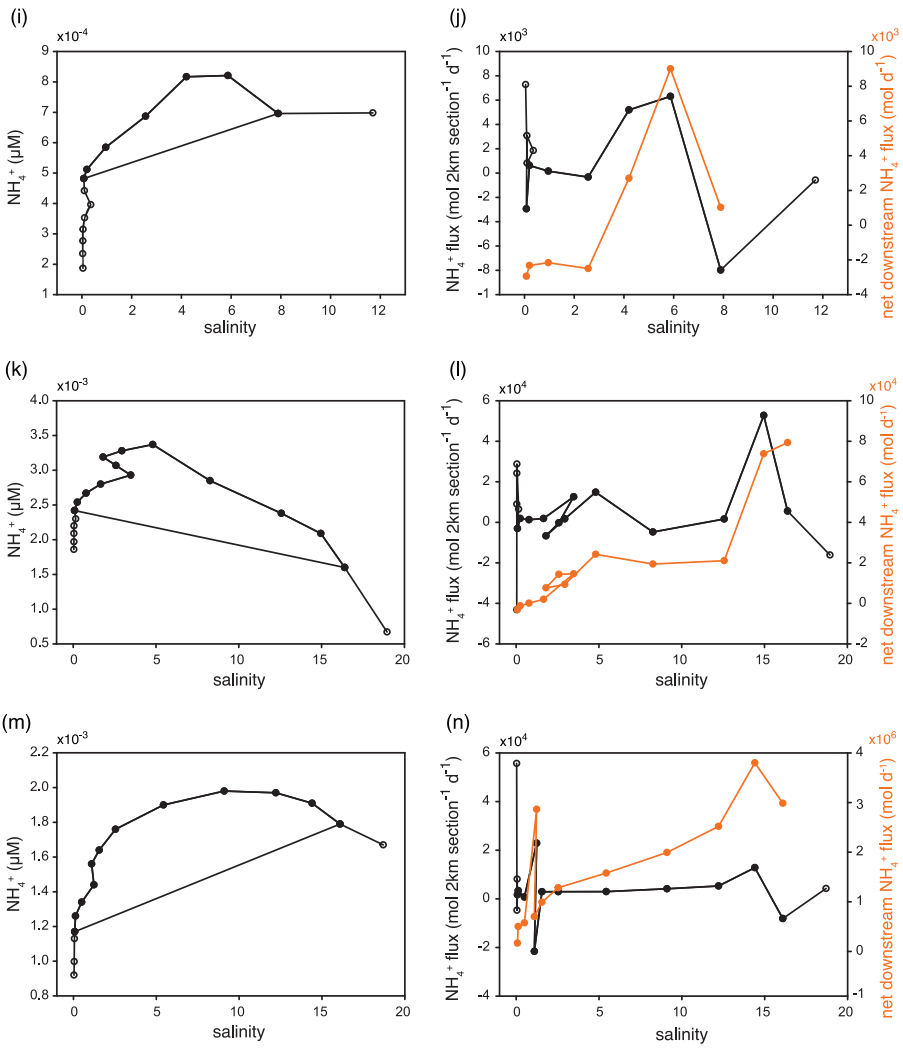


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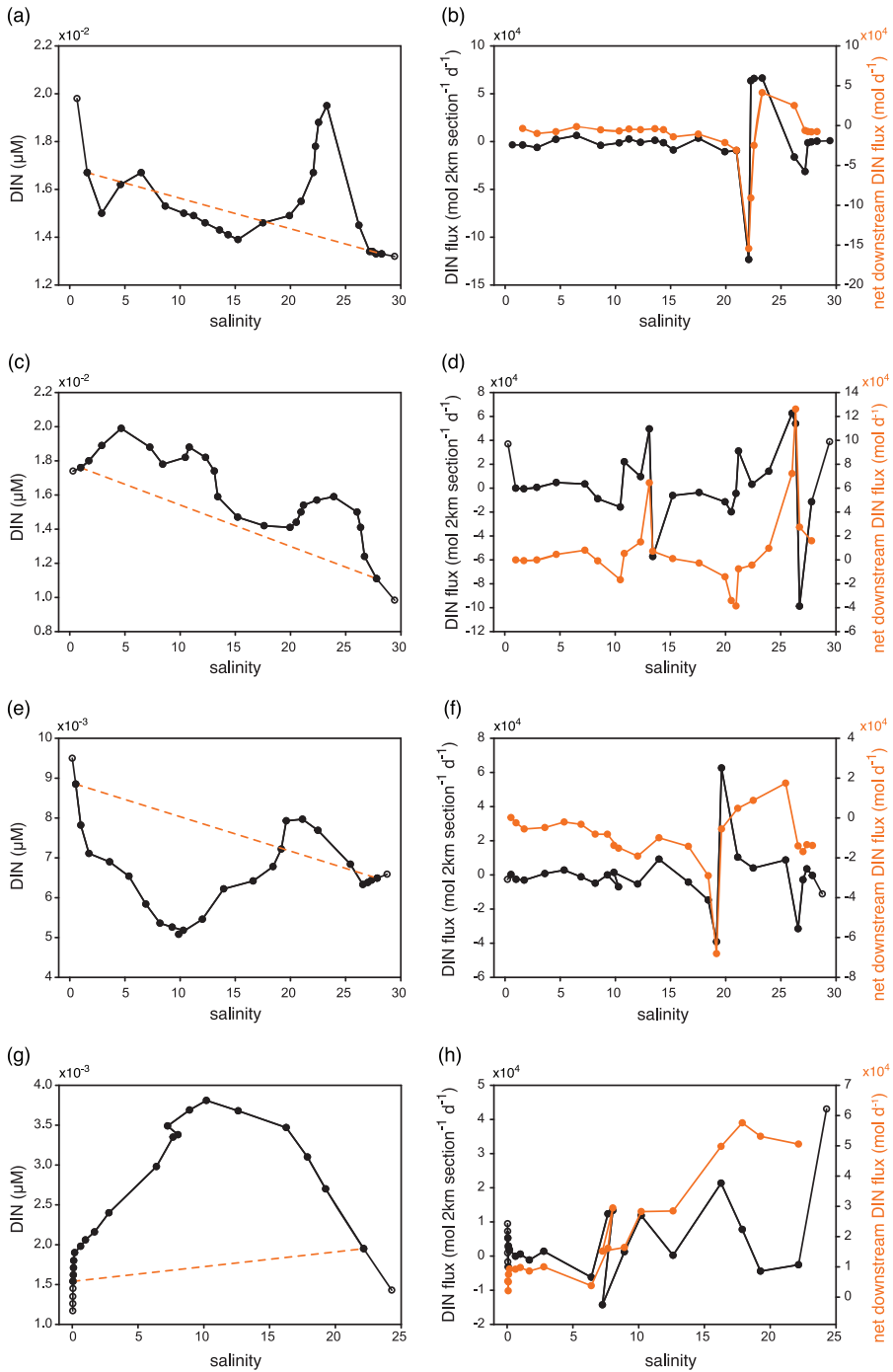


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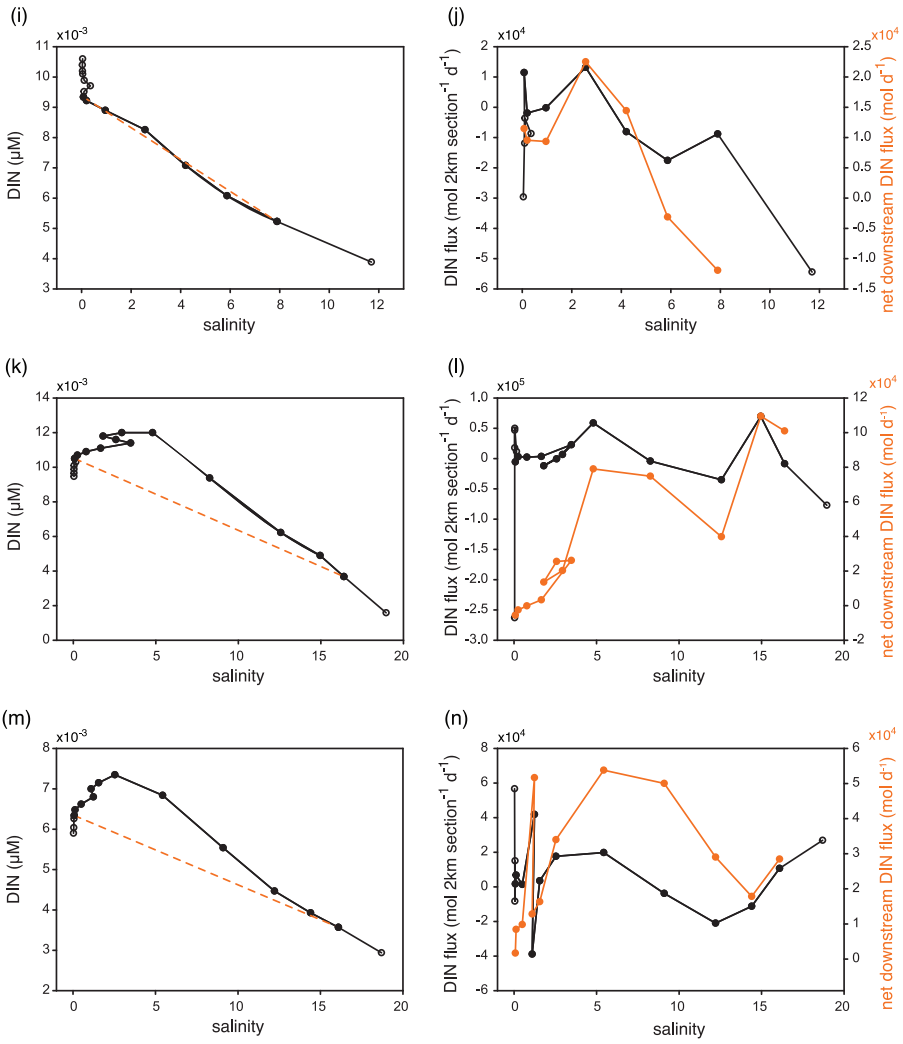


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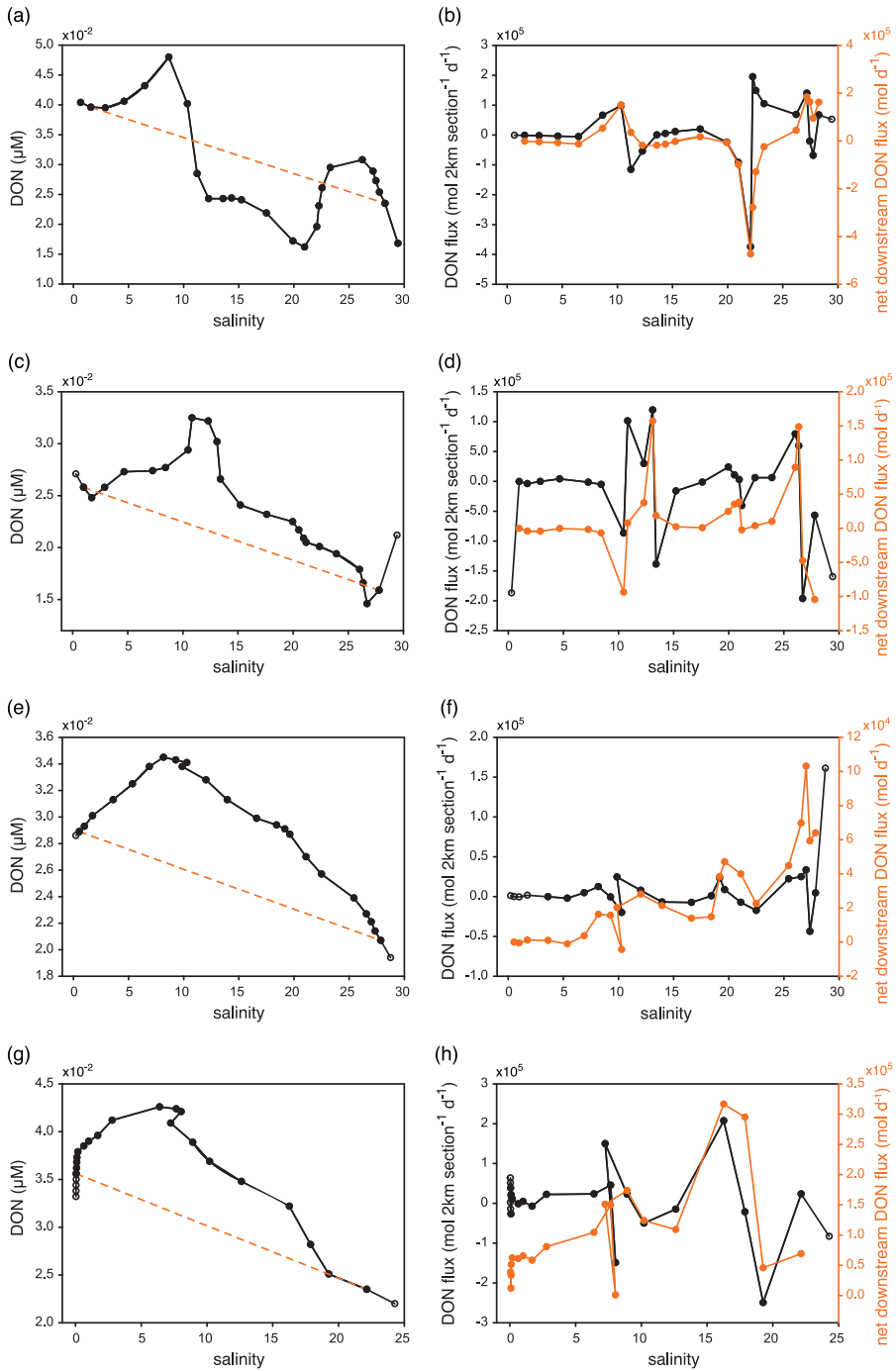


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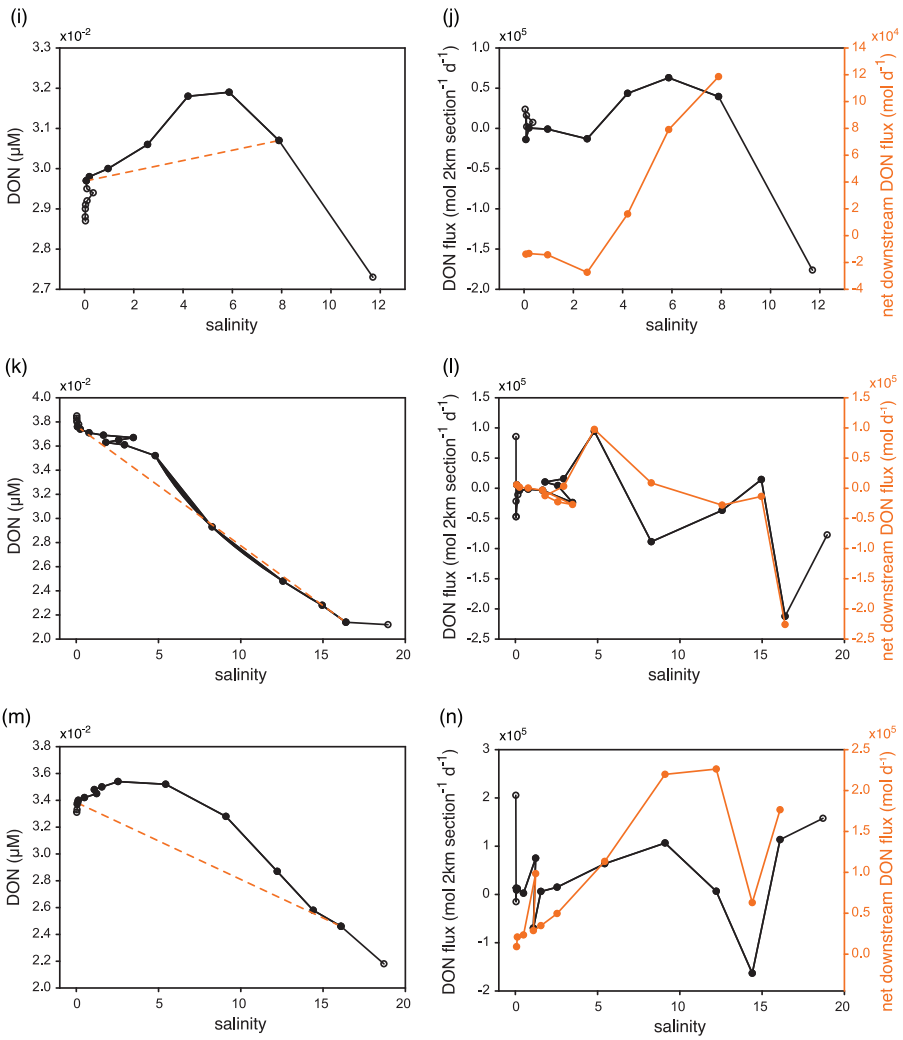


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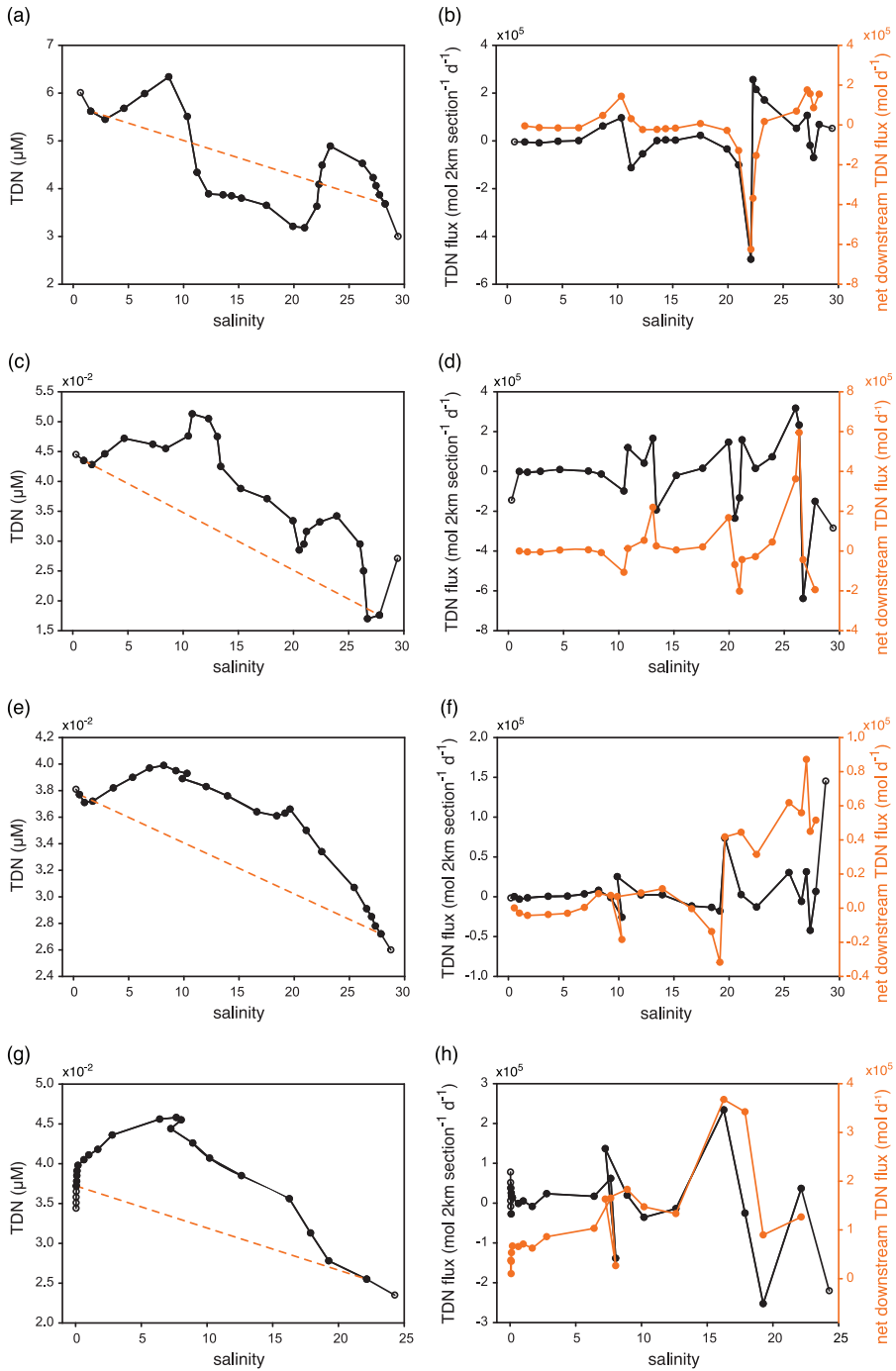


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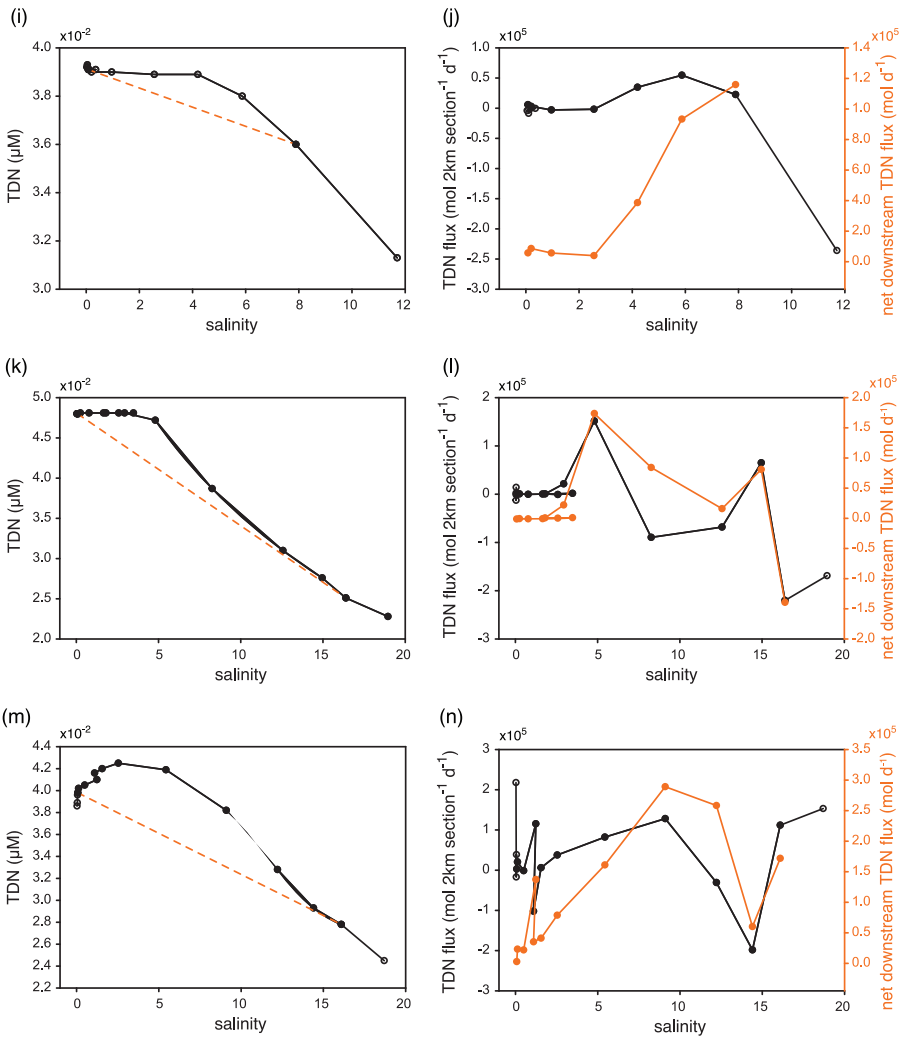


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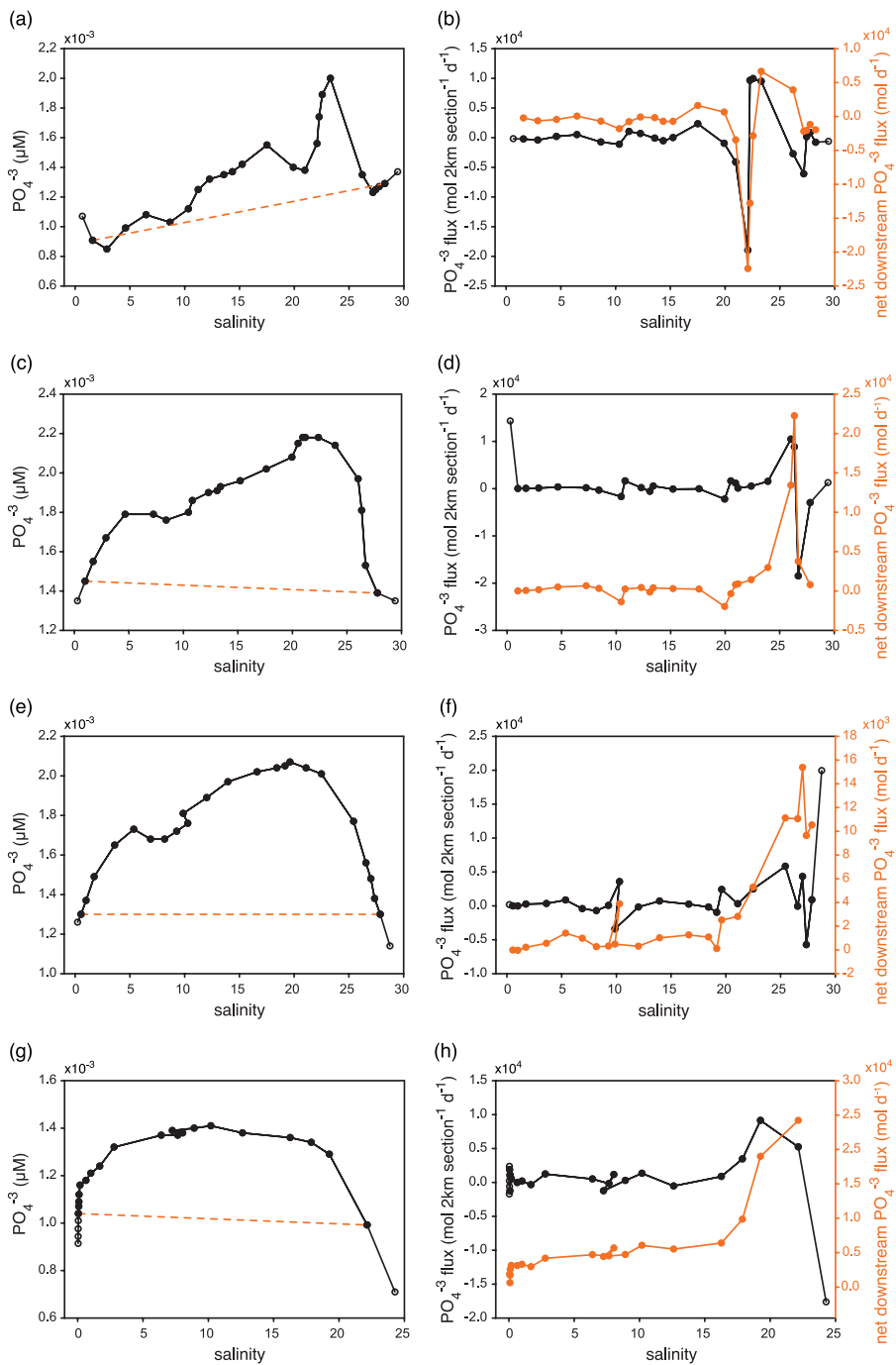


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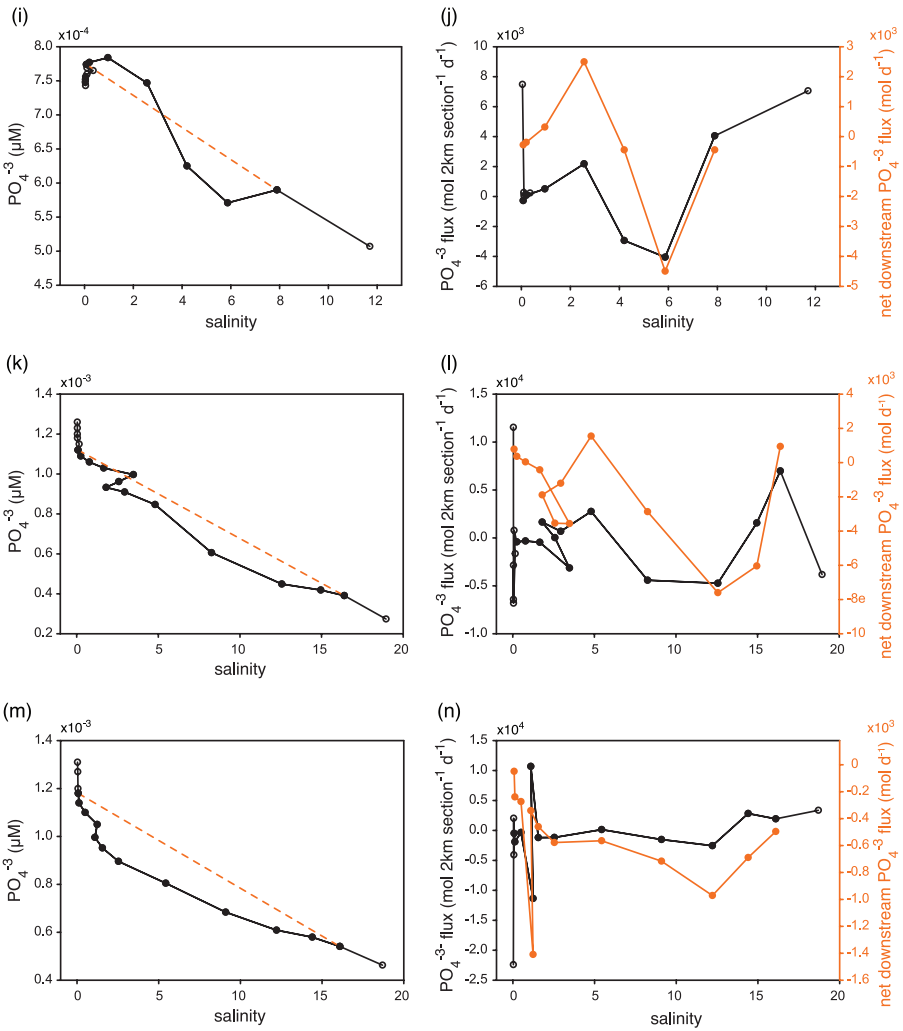


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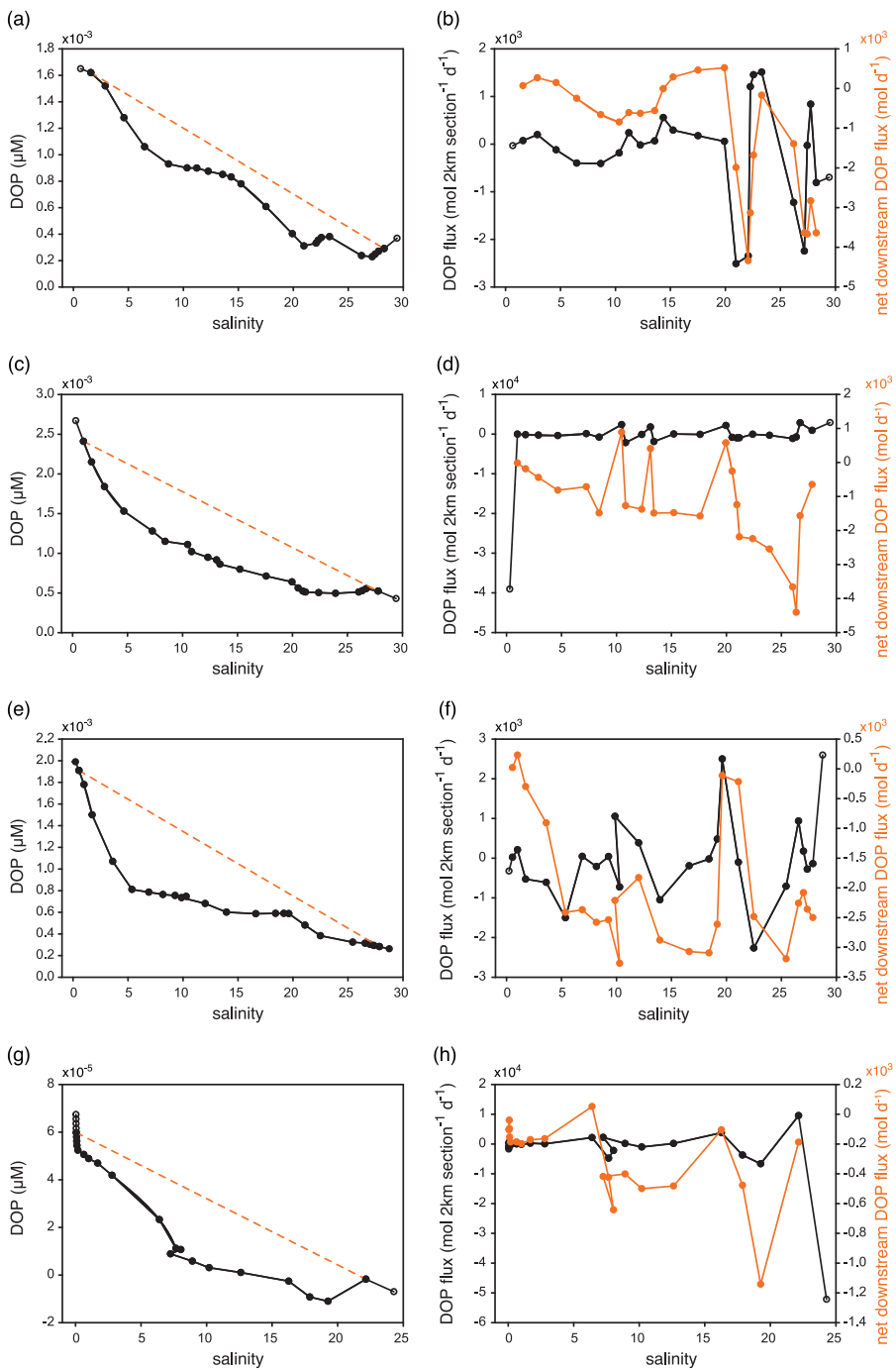


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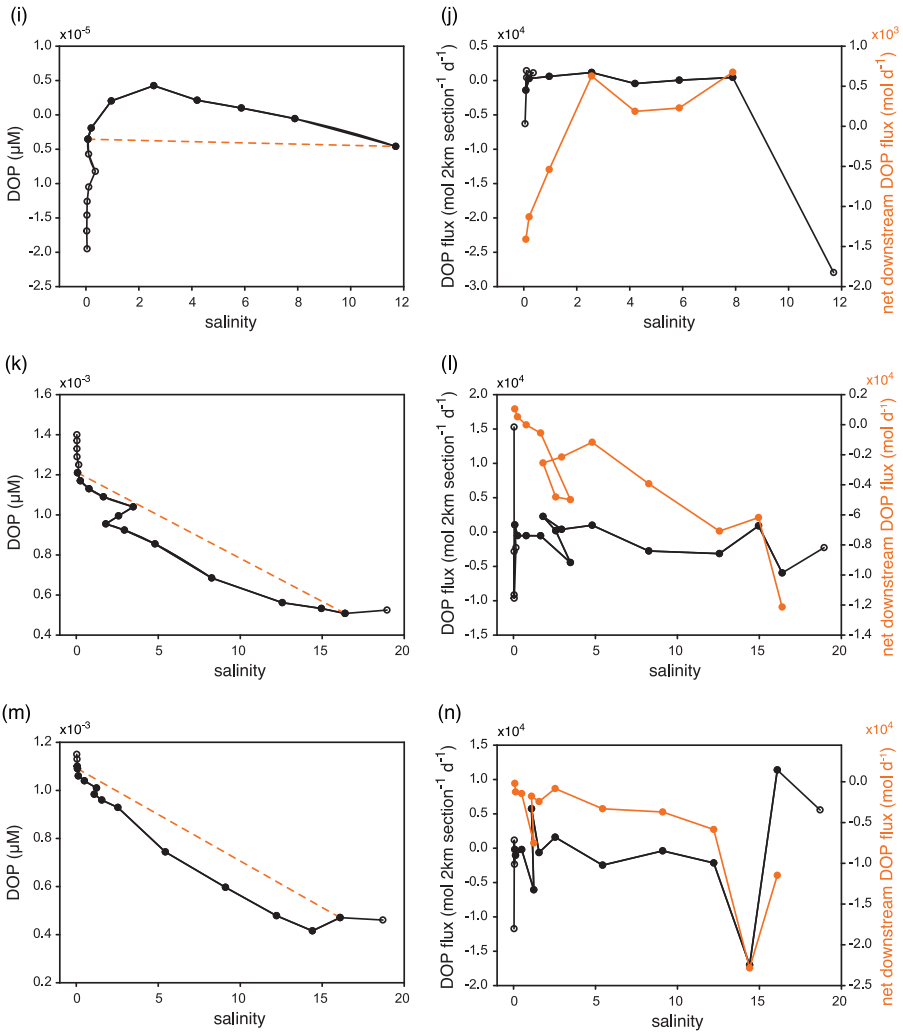


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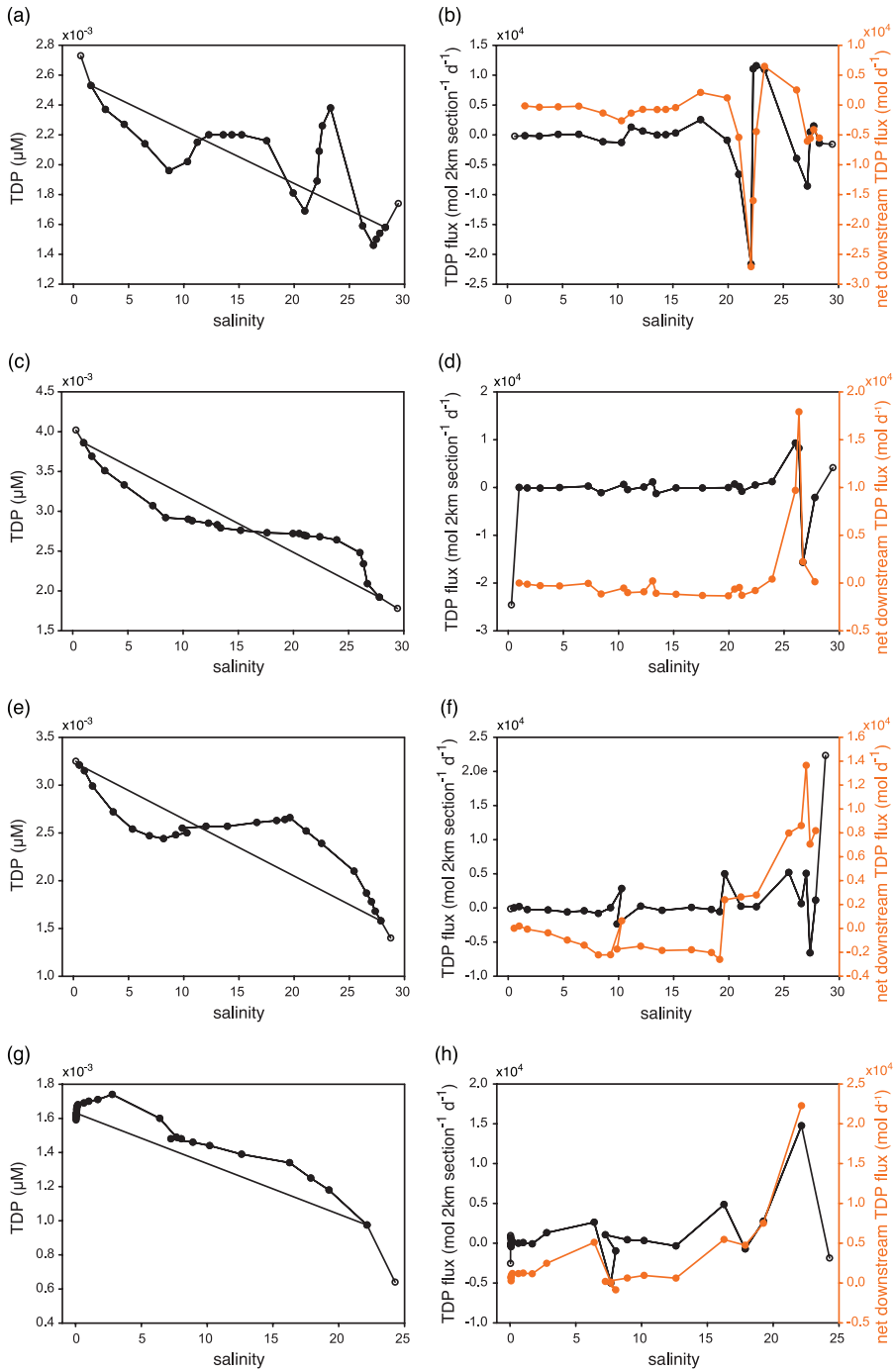


Figure S10.

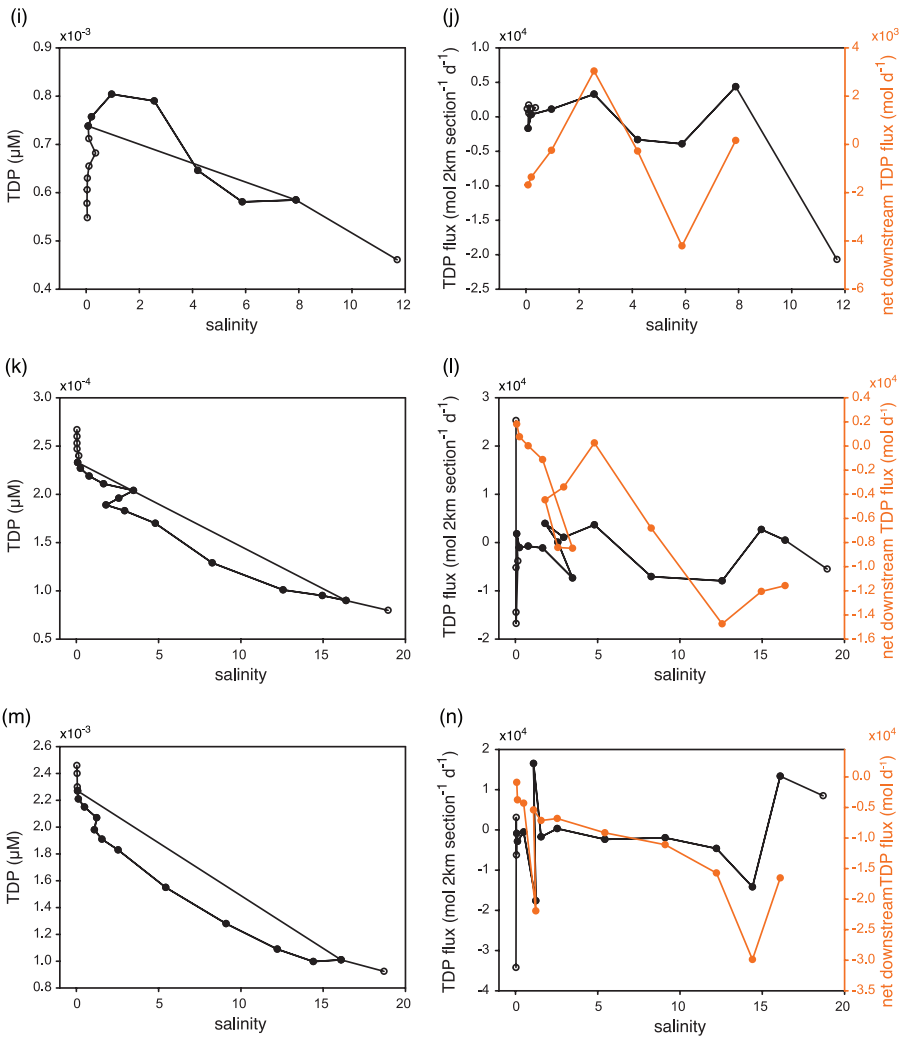


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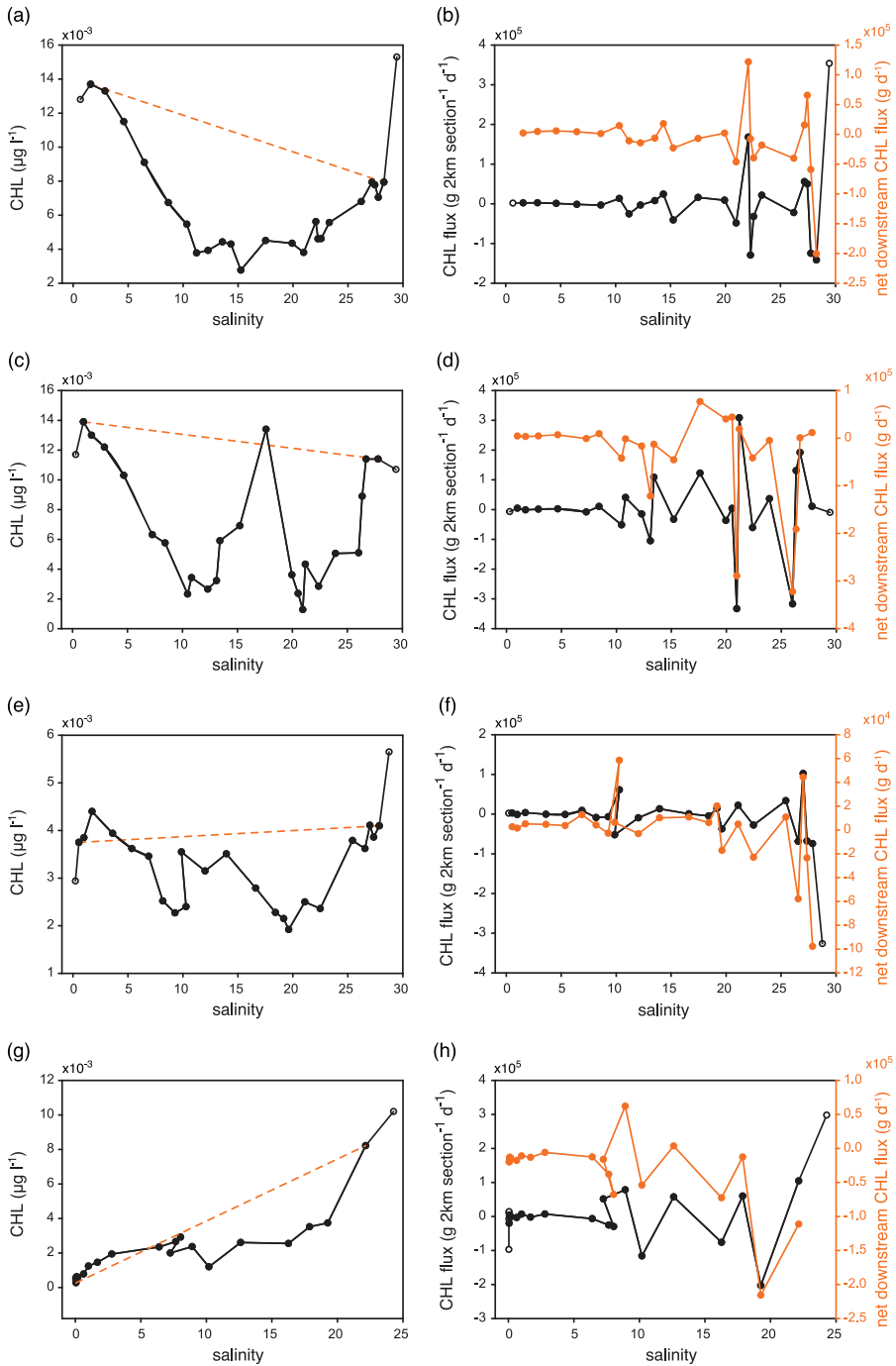


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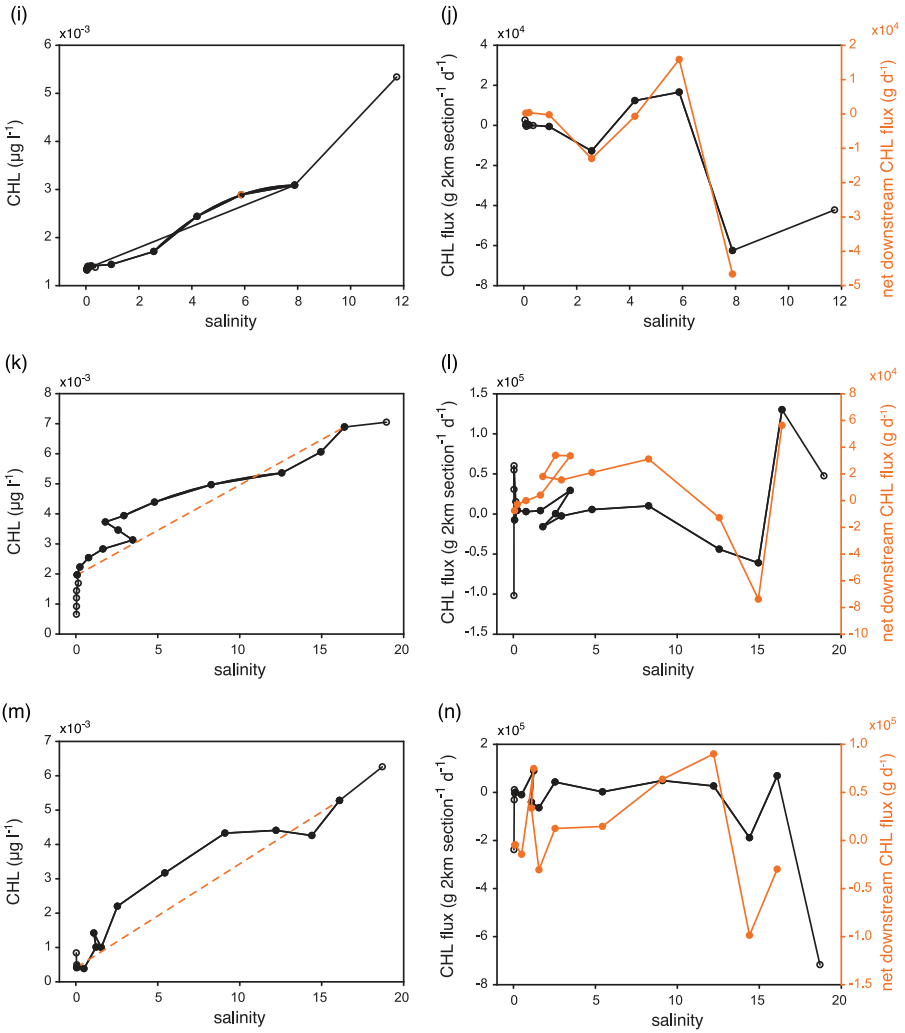


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