Lateral advection supports nitrogen export in the oligotrophic open-ocean Gulf of Mexico

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In contrast to its productive coastal margins, the open-ocean Gulf of Mexico (GoM) is notable for highly stratified surface waters with extremely low nutrient and chlorophyll concentrations. Field campaigns in 2017 and 2018 identified low rates of turbulent mixing, which combined with oligotrophic nutrient conditions, give very low estimates for diffusive flux of nitrate into the euphotic zone (< 1 µmol N m⁻² d⁻¹). Estimates of local N₂-fixation are similarly low. In comparison, measured export rates of sinking particulate organic nitrogen (PON) from the euphotic zone are 2 – 3 orders of magnitude higher (i.e. 462 – 1144 µmol N m⁻² d⁻¹). We reconcile these disparate findings with regional scale dynamics inferred independently from remote-sensing products and a regional biogeochemical model and find that laterally-sourced organic matter is sufficient to support >90% of open-ocean nitrogen export in the GoM. Results show that lateral transport needs to be closely considered in studies of biogeochemical balances, particularly for basins enclosed by productive coasts.
Conventionally, primary production is partitioned between new and regenerated production based on the source of inorganic nitrogen: new production (NP) is fueled by N (nitrogen) input from external sources (e.g., upwelled nitrate and N₂-fixation) while regenerated production (RP) comes from the internal recycling of nitrogen (e.g., ammonium). While RP often supports the vast majority of total primary production in open-ocean ecosystems, new nitrogen sources (NP) are necessary to support nitrogen and carbon export into the deep sea because the mass fluxes into and out of a system must balance when integrated over sufficiently large spatiotemporal scales. While the NP and RP dichotomy is well established in the simple biogeochemical metric of the $f$-ratio ($=\text{NP}/(\text{NP}+\text{RP})$), direct measurement of NP is complicated by the intrinsic complexities of nitrogen cycling. For example, the most common NP measurement technique, nitrate uptake incubations, assumes negligible rates of nitrification (i.e., oxidation of ammonium into nitrate) within the euphotic zone. Nitrification, which generates nitrate from ammonium, may at times be a dominant source of nitrate in surface waters 2–5, especially in oligotrophic waters where ammonium concentrations can exceed those of nitrate. Additionally, strong gradients in organic matter concentrations between coastal and offshore environments provide significant lateral transport potential. Through lateral transport, nutrients and organic matter can be carried into the offshore region, although this flux is seldom included in NP calculations. Modeling studies have suggested that net offshore fluxes can be an important addition to regional N balances, supporting 24–80% of total export in subtropical gyres 6,7. However, lateral transport is difficult to constrain because spatiotemporal scales of advection are usually poorly matched to those of direct field measurements.

While numerous biogeochemical budgets have been reported for the shallow shelves of the GoM 8–11, few studies have focused on the oceanic region that covers ~2/3rds of the GoM surface area. Data presented here were collected during two field campaigns of Bluefin Larvae in Oligotrophic Ocean Foodwebs: Investigating Nutrients to Zooplankton in the GoM (BLOOFINZ-GoM) program targeting the central GoM spawning grounds of the endangered Atlantic Bluefin tuna 12,13. Major ephuic zone C and N cycling processes were quantified during five Lagrangian studies 14–17, allowing us to compile comprehensive biogeochemical budgets. Here, we combine these in situ measurements with independent remote-sensing observations and a biogeochemical model to test alternate hypotheses that (1) locally upwelled nitrate, (2) N₂-fixation, or (3) lateral transport support N export from oligotrophic oceanic waters of the GoM.

Results and discussion

Field observations and dynamics. Nitrate+nitrite (hereafter nitrate) and ammonium were generally <100 nM throughout the euphotic zone, with nitrate concentrations between the detection limit (~10 nM) and 50 nM in the upper euphotic zone (UEZ; 0–60 m) (Fig. 1b). Nitrate concentrations remained depressed well below the lower euphotic zone (LEZ), with 2.5–12 µM concentrations at 150 m, consistent with prior characterizations of these water masses (ref. 18 and references therein). Ammonium averaged 60 nM, with no depth trend in the euphotic zone (Supplemental Fig. 1a). UEZ chlorophyll-a was consistently below 0.2 mg m⁻³ (Fig. 1c), and UEZ integrated nitrogen pools did not vary significantly throughout the Lagrangian experiments (Supplemental Fig. 1c–e). Most (62–79%) net primary production (NPP) occurred in the UEZ, with a surface maximum of 270–550 µmol C m⁻³ d⁻¹. In the LEZ, including the deep chlorophyll maximum (DCM), NPP declined to ~100 µmol C m⁻³ d⁻¹ (Fig. 1d). Nitrate uptake rates were not strongly depth-dependent, with maximum rates typically observed between 20 and 60 m and vertically integrated rates of 440–1400 µmol N m⁻² d⁻¹ in UEZ and 260–2050 µmol N m⁻² d⁻¹ in LEZ. Vertically integrated $f$-ratios were 0.04–0.14 (mean: 0.07) in the UEZ and 0.03–0.44 (mean: 0.14) for the LEZ. Although nitrification was not directly measured, ammonium-specific rates from other oligotrophic

Fig. 1 Overview of in situ data. a Study locations in the central Gulf of Mexico (GOM; colored drift trajectories) with a white outline indicating the integration volume from surface to 55 m considered as representative of the eastern Central GoM (depths >2000 m, outside the general flow of the loop current). b Vertical profiles of nitrate concentrations with inset detailing low surface concentrations. c Vertical profiles of chlorophyll concentrations as recorded by calibrated fluorometer. d Vertical profiles of net primary productivity and e vertical profiles of particulate nitrogen export at three depths: upper euphotic zone, lower euphotic zone, and 200 m. Colors correspond to Lagrangian experiments, and error bars indicate ±1 SD of means for measurements during experiments.
studies (0.02–0.5 d⁻¹; ref. 3 and references within) suggest potential nitrate sources of 1 and 30 µmol N m⁻² d⁻¹, which could supply the majority of nitrate utilized by the phytoplankton community.

Gravitational export of organic matter from the UEZ
(60 m) ranged from 590 to 1530 µmol N m⁻² d⁻¹ and generally decreased with depth (460–1140 µmol N m⁻² d⁻¹) at the base of the euphotic zone; 190–400 µmol N m⁻² d⁻¹ at 200 m; Figs. 1e and 2a). UEZ export was 164% (range: 90–330%) that of LEZ, indicating significant consumption of sinking particles within the LEZ. Active export of euphotic zone N due to ammonium excretion of migratory zooplankton at depth ranged from 0.01 to 19 trichomes L⁻¹ at 200 m; Figs. 1e and 2a). The abundance of Trichodesmium, a dominant diazotroph in the GoM, ranged from 0 to 19 trichomes L⁻¹, which based on a photo-fixation model, implies maximum N₂-fixation rates of between 0 and 0.38 µmol N m⁻³ d⁻¹ and vertically integrated fixation rates of 0.4–2.8 µmol N m⁻² d⁻¹ in the UEZ (Fig. 2a). While lower than in some other regions (up to 60 km d⁻¹), the strong coastal-offshore particulate gradients in the GoM (Supplemental Figs. 3–4). We tested this hypothesis with independent approaches of satellite remote-sensing products and a biogeochemical model tuned to the open-ocean GoM.

As vertical mixing of nitrate and N₂-fixation individually provide enough N to support <1% of sinking PON flux in our Lagrangian experiments, locally sourced new N appears insufficient to balance the measured rates of PON export. Instead, a significant role of lateral transport of organic material is suggested by the rapid horizontal displacements in our drifter experiments (up to 60 km d⁻¹) and the strong coastal-offshore particle gradients in the GoM (Supplemental Figs. 3–4).

NATURE COMMUNICATIONS | https://doi.org/10.1038/s41467-021-23678-9
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Lateral supply of nitrogen. MODIS Aqua and Terra remote-sensing products provide spatial POM data to infer lateral gradients in the GoM. Combined with a remote-sensing circulation product, OSCAR, we calculate lateral fluxes of particulate organic nitrogen (PON) in the UEZ. Independently, results from a 3D, nitrogen-currency biogeochemical model (NEMURO-GOM) are used to resolve lower trophic level dynamics in the open-ocean GoM. Notably, NEMURO-GOM was developed to accurately simulate zooplankton dynamics (and hence was primarily compared to zooplankton observations). The MODIS POM and OSCAR circulation products were not used by NEMURO-GoM.

The interannual median UEZ lateral transport of PON (i.e., organisms and detritus) into the central GoM zone (Figs. 1a and 3) is estimated to be equivalent to a flux of 1150 µmol N m⁻² d⁻¹ (IQR: 610–1530 µmol N m⁻² d⁻¹) and 1165 µmol N m⁻² d⁻¹ (IQR: 700–1725 µmol N m⁻² d⁻¹) by remote-sensing and NEMURO-GOM, respectively. Both estimates (Fig. 3) indicate that lateral transport of PON alone is sufficient to support sediment trap-derived export out of the UEZ (median: 980 µmol N m⁻² d⁻¹, range: 857–1526 µmol N m⁻² d⁻¹) and the LEZ (median: 520 µmol N m⁻² d⁻¹, range: 462–1144 µmol N m⁻² d⁻¹). DON contributed an additional ~8–46% to total UEZ lateral transport within NEMURO-GOM for any given day (Fig. 3), while lateral transport of DIN (nitrate-ammonium), generally found in diminishingly low concentrations in these waters (Fig. 1a; ref. 15), was uniformly low in the UEZ and represented ~5% of net nitrogen transport regionally. Substantial agreement between these two distinct types of models is remarkable considering that even the physical circulation fields are unique to each model (global HYCOM for NEMURO-GOM; OSCAR circulation for satellite models). Taken together, these results clearly indicate that net lateral transport of organic matter is of sufficient magnitude to support open-ocean export in the GoM.

Circulation patterns in NEMURO-GOM suggest that the open-ocean GoM is predominately a downwelling region and thus an organic nitrogen sink. In the absence of significant vertical input of subsurface nitrate into the LEZ or recently fixed nitrogen into the UEZ, particulate N export can only be supported by either lateral transport or a non-steady state drawdown of bioavailable
nitrogen. Since the latter was not observed during any of our five, 4-day Lagrangian experiments (Supplemental Fig. 1c–e), lateral input is likely to be responsible for ~100% of export out of the UEZ and >90% of export out of the LEZ (Fig. 4). While episodic transport events such as storms have been shown to be relevant in other regions, the impact of such transient processes on the N balance of open-ocean GoM is likely negligible in late spring and summer due to the very deep nitracline (80–125 m). Such second-order processes are likely more important near the shelves where nitracline and mixed layer depths are closer than in the experimental sites themselves. What is clear in the open-ocean GoM is the prevalence of mesoscale eddies formed through instabilities in the Loop Current (Supplemental Figs. 3 and 4). Previous studies have found that, through both enhanced surface velocities and long persistence, such mesoscale features can transport large volumes of water onto and off of the shelf.

These lateral fluxes likely have implications for the entire GoM food web. Organismal carbon budgets suggest that carnivorous metazooplankton in the GoM may rely on subsidies of prey advected from the coast/shelf break region. An individual-based model developed for Atlantic bluefin tuna larvae suggests that shelf break regions with strong offshore flow may be particularly important spawning locations that allow first-feeding larvae to find sufficient prey while transporting older larvae to low-predator regions. Indeed, back-trajectories showed that locations with high larval abundance on the BLOOFINZ-GoM cruises were associated with water recently advected from more productive shelf break regions. Thus, while much work is needed to elucidate relationships between specific taxa and nitrogen sources to the ecosystem, preliminary evidence shows that lateral transport is crucial to multiple trophic levels in the GoM.

**Global connections and implications.** Since the oligotrophic GoM has previously been compared to the mid-ocean gyres due to similar biogeochemical properties (e.g., DCM, oligotrophic, low biomass), it may be reasonable to consider the applicability of our results to these oceanic regions. The mid-ocean gyres are both larger than the GoM and may have less average kinetic energy (leading to circulation time-scales of months-years, rather than weeks). Consequently, lateral PON fluxes are likely weaker in gyres but may be compensated, in part, by greater DON flux contributions. Indeed, DON inputs from lateral advection, entrainment, and mixing have been shown to supply gyre interiors, and based on model results may support 40–70% of export production in the North Atlantic gyre. Furthermore, export efficiency (i.e., export/NPP) is lower in the subtropical gyres (~5%) than measured in our study (11–25%) indicating a reduced lateral input requirement to support gyre export. Taken together, these analyses suggest that lateral transport of organic matter could potentially be a dominant source of external nitrogen in the oligotrophic gyres, as it is in the GoM.
Our results highlight the importance of inter-disciplinary and integrative process studies for constraining biogeochemical fluxes. Among still unresolved issues, it is not clear whether the laterally transported organic matter was originally supported by nitrate from the shelf, upwelling at the shelf break, upwelling associated with mesoscale features, or from some combination of these. Furthermore, extrapolating our results to other time periods and conditions (e.g., winter) in the GoM should be done with caution and appropriate field measurements. Nevertheless, our results clearly highlight the importance of accounting for contributions of lateral transport to carbon and nitrogen budgets in oligotrophic ocean regions and the role that horizontal mesoscale currents have in supporting vulnerable open-ocean GoM ecosystems.

Methods

Sampling plan and environmental sampling. Data were collected during two cruises in the Northern Gulf of Mexico conducted in May 2017 and April/May 2018. Each cruise began with a bongo survey of water parcels that were identified by remote sensing as having favorable SST and vorticity for larval Atlantic Bluefin Tuna (ABT). At selected locations, a sediment trap array was deployed and a Lagrangian experiment was initiated. Over the following 3–4 days, the water parcel was repeatedly sampled for biogeochemical properties and incubations were conducted to measure process rates. Throughout an experiment, profiles of temperature and salinity were taken 3–4 times per day through the upper 200 m. Additionally, PAR profiles were conducted at least once per Lagrangian experiment around local noon. Ambient nutrient concentrations were determined from samples collected daily from 6 depths throughout the euphotic zone (same depths as incubations were conducted). The concentrations of nitrate + nitrite were measured using a chemiluminescent method, while concentrations of NH$_4^+$ were measured using the fluorescent OPA method. See Knapp et al. for details.

Trichodesmium abundance and N$_2$ fixation. Trichodesmium abundance and chlorophyll contents were assessed as reported in Selph et al. Brieﬂy, 6.6 L samples from daily noon casts at 6 depths (2–50 m) were collected and filtered through inline 8-µm, 47-mm ﬁlters, preserved (2% paraformaldehyde), and frozen (–80 °C). Trichodesmium were counted with microscopy (10–SOX magniﬁcation) under 440–460 nm excitation to detect orange–fluorescing trichomes. For chlorophyll a contents, separate samples (6.6 L) were collected onto 20 µm, 47-mm ﬁlters and frozen (–80 °C). Individual trichomes were picked from thawed ﬁlters, extracted (90% acetone), and chlorophyll fluorescence measured with 10-AU (Turner Designs) fluorometer. Chlorophyll speciﬁc N$_2$ ﬁxation rates were calculated based on the photo-ﬁxation model of Breitbarth et al. based on culture work conducted at temperatures (i.e., 26 °C) and photoperiods (i.e., 12 h) consistent with in situ conditions observed.

Productivity and nutrient dynamics. Rates of net primary production (NPP) and nitrate uptake were measured at 6 depths spanning the euphotic zone each day of a Lagrangian experiment. Incubation bottles (2.7 L) were ﬁlled with Niskin rosette and then HCO$_3^−$ (ﬁnal concentration: 154 or 196 nmol L$^−$1 on NF1704 and NF1802, respectively) and/or $^15$N$_2$ (ﬁnal concentration: 10 or 8 nmol L$^−$1 on NF1704 and NF1802, respectively) was added. Bottles were then incubated in mesh bags attached to an in situ drift array for 24 h—drift array was deployed and recovered pre-dawn, typically ~0500 local time. Upon recovery, incubation bottles were immediately ﬁltered onto pre-combusted GF/F. Filtered samples were kept at ~80 °C until analysis. In addition to in situ incubations, a series of deck-board experiments were conducted for 4–6 h to measure vertical patterns and diel variability in nitrate (same N$_2$ spike as above) and ammonium uptake (final concentration: 9.8 or 4.6 nmol L$^−$1 on NF1704 and NF1802, respectively). Samples were analyzed at the UC Davis stable isotope facility. Nutrient uptake rates and associated uncertainty were calculated as in Stukel.

Thorpe scale analysis. Proﬁles of vertical diffusivity ($K_z$) were calculated by Thorpe scale analysis of CTD-derived density proﬁles. Thorpe scale analysis estimates turbulence mixing parameters (i.e., vertical eddy diffusivity, $K_z$) based on the number and size of observed density inversions. Raw Seabird data ﬁles were processed based on the recommendations of ref. 25. Resulting proﬁles of $K_z$ were averaged across all casts during a Lagrangian experiment using the geometric mean (n = 14–26, with decreasing number of casts below the euphotic zone). Nitrate ﬂuxes ($F_N$) were then calculated using the observed vertical nutrient (N$_2$) gradients and vertical diffusivity (Eq. 1).

$$F_N = -K_z \frac{d[N_2]}{dz}$$  

Zooplankton abundance, biomass, and migrant excretion. Zooplankton were collected daily from paired day–night tows with a 4.1 m diameter ring net (200-µm mesh) towed obliquely through the euphotic zone. The tow contents were ﬁltered through stacked Nitex screens of 2, 2.1, 0.5, and 0.2-mm Nitex mesh to produce 5 size classes, and carbon, nitrogen, and dry mass for each size class were determined. Active nitrogen transport by daytime excretion of diel migrating mesozooplankton at mesoscale depths was calculated from the equations of Ikeda. Among still unresolved issues, it is not clear whether zooplankton at mesoscale depth were determined. The average C values of individual animals in each migrant size fraction, and the mean temperature in the 300–500 m depth range (~10–12 °C).

Export production by sediment trap. Each sediment trap deployment consisted of three cross-members with 12 Particle Interceptor Tubes per depth. Trap depths were selected from CTD ﬂuorescence proﬁles with one cross-member below the mixed layer and within the euphotic zone (60 m), one at the base of the euphotic zone (110–150 m), and one at 230 m. The sediment trap array included a 3-m x 1-m holey sock drogue at 15 m depth. Sediment trap tubes were ﬁlled with a poisoned brine solution. After recovery, the overlying seawater was siphoned off to within 3 cm of the brine interface. The samples were then ﬁltered through a 100-µm ﬁlter which was manually inspected under a stereo-microscope (25X) to remove zooplankton swimmers. After washing the >100-µm non-swimmer fraction back into the sample, whole tube contents were ﬁltered onto a pre-combusted GF/F for C and N isotopic analyses.

Analysis

Nitrogen isotopic signatures of new and export production. Mass balance requires that the nitrogen $^{15}$N signature of export equals the isotopic signature of the source nitrogen. N$_2$-ﬁxation supplies nitrogen with a $^{15}$N$_2$ of approximately −2% and vertical mixing of subsurface nitrate would maintain the subsurface isotopic signature: 2‰–3‰. Exported nitrogen (sinking + active transport) was observed to have a $^{15}$N$_2$ of −2.9±5‰.

Remote-sensing estimates of transport. Eight-day composites of surface PO4 concentrations estimated from Moderate Resolution Imaging Spectroradiometer (MODIS) Aqua & MODIS Terra were retrieved from the National Aeronautical and Space Administration’s (NASA) data repository for each May from 2000 to 2019. We assumed that particles had Redfield stoichiometry (106C16N, C:N, mol: mol). Remote sensing ﬁelds were binned to 8-km x 8-km resolution prior to analysis to reduce noise. Regional circulation was prescribed from OSCAR, a data-accumulating, remote-sensing data product with 1/3$^{th}$ degree spatial and 5-day temporal resolution. OSCAR circulation ﬁelds were mapped onto the remote-sensing grid using bilinear spatial interpolation and linear temporal interpolation. Fluxes between each grid cell were then calculated for each remote-sensing field (n = 80). The total net ﬂux into the control volume was divided by the area of the control volume for comparison to vertical N ﬂux measurements. Results are shown for the control volume as deﬁned in Fig. 1a.

NEMURO-GOM estimates of transport. The biochemical model NEMURO-GoM was used to provide a consistent three-dimensional perspective on nutrient uptake dynamics in the study region. The model consists of 29 z-layers with a vertical resolution of 10 m in the upper 150 m and 4-km horizontal resolution. NEMURO-GoM is run ofline within the MIT general circulation model and forced by daily averaged flow ﬁelds obtained from a data-assimilative HYbrid Coordinate Ocean Model GoM simulation. The model has been extensively validated against nutrient, biomass, and rate measurements and fully resolves a simple nitrogen cycle with 11 state variables consisting of two phytoplankton and three zooplankton functional groups. Vertical mixing in the model is parameterized based on a nonlocal K-proﬁle parameterization (KPP) mixing scheme from a bulk Richardson number approach that quantiﬁes the importance of stratiﬁcation and destabilizing shear. Daily model output for May of 1993 to 2012 were analyzed (n = 571) with ﬂux integrations performed for the same control volumes as used for the remote sensing estimations (Fig. 1a). Mesoscale eddies were identiﬁed in each resolved model ﬂow ﬁelds using the algorithm of Laxenaire et al. which utilizes surface velocities along closed contours of SSH to deﬁne eddy boundaries. Lateral eddy ﬂux (see Supplemental Discussion) was determined by calculating the net ﬂux into the control column for all model grid cells that were identiﬁed as located within an eddy (i.e., enclosed SSH contour with the greatest velocity).

Data availability

The data that support the findings of this work are available from the cited and publicly available repositories, including MODIS (NASA), OSCAR (ESR), and field data (BCO-DMO), or upon request to the author (NEMURO-GOM).

Code availability

Codes used in the preparation of this manuscript are freely available under a Creative Commons license at the following url: https://github.com/brheckel/Lateral-connectivity-in-the-gom, ref. 53, and from the author upon request.
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Acknowledgements
We thank the captain and crew of the NOAA Ship Nancy Foster for providing their assistance in conducting the fieldwork that led to this manuscript. We also thank our collaborators and colleagues at NOAA Southeast Fisheries/RSMAS/University of Miami for helping plan and carry out two successful field campaigns. We would like to thank Remi Laxenaire for his assistance in the identification of eddies. This study acknowledges BLOOFINZ Program support from National Oceanic and Atmospheric Administration awards NA15OAR4320071 (CIMEAS), NA16NMF4320058 (JIMAR), NA15OAR4320064 (CIMAS), and U.S. National Science Foundation awards OCE-1851347 and OCE-1851558. We also acknowledge support from the National High Magnetic Field Laboratory NSF/DMR-1644779 and the State of Florida.

Author contributions
T.B.K. and M.R.S. planned and synthesized the data presented here. T.B.K., M.R.L., K.E.S., T.A.S., R.K.T. and M.R.S. collected the field data. A.N.K. provided nutrient data for the analysis. T.A.S. designed the hydrodynamic model and provided output data. T.B.K. wrote the manuscript. All authors took part in editing and submission of the final manuscript.

Competing interests
The authors declare no competing interests.

Additional information
Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41467-021-23678-9.