BioOne COMPLETE

Temperature, Salinity, Nutrients, and the Covariation of Bacterial Production and Chlorophyll-a in Estuarine Ecosystems

Authors: Apple, Jude K., Smith, Erik M., and Boyd, Thomas J.

Source: Journal of Coastal Research, 2008(10055) : 59-75

Published By: Coastal Education and Research Foundation

URL: https://doi.org/10.2112/SI55-005.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Journal of Coastal Research	SI	55	59–75	West Palm Beach, Florida	Summer 2008

Temperature, Salinity, Nutrients, and the Covariation of Bacterial Production and Chlorophyll-*a* in Estuarine Ecosystems

Jude K. Apple[†]*, Erik M. Smith[‡], and Thomas J. Boyd[†]

[†]U.S. Naval Research Laboratory
4555 Overlook Avenue S.W.
Washington, DC 20375, U.S.A.
Jude.Apple@wwu.edu

[‡]University of South Carolina
Baruch Marine Field Laboratory
P.O. Box 1630
Georgetown, SC 29442, U.S.A.

ABSTRACT

APPLE, J.K.; SMITH, E.M., and BOYD, T.J., 2008. Temperature, salinity, nutrients, and the covariation of bacterial production and chlorophyll-*a* in estuarine ecosystems. *Journal of Coastal Research,* SI(55), 59–75. West Palm Beach (Florida), ISSN 0749-0208.

The National Estuarine Research Reserve System represents a diverse collection of ecosystems among which environmental conditions differ dramatically, making it inherently difficult to determine the extent to which patterns and properties identified in one estuary are transferable to those of any other. The primary objective of our study was to develop a multivariate classification framework for comparison of these estuaries and identify the primary sources of environmental variability in each. Using a 4-year dataset from the National Estuarine Research Reserve System-Wide Monitoring Program, combined with principal components analysis, we identified distinct patterns among 21 reserves that allowed grouping based on the primary factors shaping physicochemical variability. Salinity and temperature were the primary factors shaping variability in the reserves, an observation that was corroborated by similar multivariate analysis of data from 33 published studies of non–National Estuarine Research Reserve systems representing a wide range of coastal and estuarine waters. We then investigated the effect of temperature and salinity on biological processes in these systems by using the ratio of bacterial production to chlorophyll-*a* as a response variable. Salinity and temperature had different but significant effects on bacterial production/chlorophyll-*a* ratios, suggesting in turn that these properties contribute to the balance between autotrophic and heterotrophic planktonic processes in estuarine ecosystems. Our study confirms the universal role of salinity and temperature in shaping the variability among even the most diverse systems and provides a valuable classification framework for comparison of reserves within the context of the entire National Estuarine Research Reserve System. Use of this classification approach may provide insight into the extent to which results from investigative studies in one reserve may be applicable to others, a valuable application when the effect of environmental stressors is considered.

ADDITIONAL INDEX WORDS: *Bacterioplankton, National Estuarine Research Reserve System (NERRS), estuary, chlorophyll*-a.

INTRODUCTION

The National Estuarine Research Reserve System (NERRS) is composed of more than 4000 km^2 of protected coastal, estuarine, and wetland areas. These reserves represent a diverse collection of aquatic ecosystems that experience a wide range of environmental conditions. Significant scientific utility of the reserves has been realized through the establishment of a System-Wide Monitoring Program (SWMP) and subsequent characterization through evaluation of long-term datasets (KENNISH, 2004; WENNER *et al.,* 2004). This, in turn, has improved our understanding of the range and variability of environmental conditions in the reserves and provides the basis for comparison to other NERRS and non-NERRS estuaries.

Estuaries collectively represent a diverse array of dynamic aquatic systems that vary substantially in their state of enrichment, salinity, morphology, and hydrodynamics (KENNISH, 1992). The temporal and spatial variability of these systems is such that environmental conditions for even a single category of estuary (*e.g.,* drowned river valleys) may vary tremendously both within and among such systems (DAY *et al.,* 1989). In addition, the primary factors regulating plankton community activity and abundance are highly variable among estuarine systems and include anthropogenic nutrient inputs (REVILLA *et al.,* 2000), light availability (HARDING, MEESON, and FISHER, 1986), salinity (PRADEEP RAM, NAIR, and CHANDRAMOHAN, 2003), season, temperature, and organic matter source and quality (APPLE, DEL GIORGIO, and KEMP, 2006; LOMAS *et al.,* 2002; RAYMOND and BAUER, 2000). As a result, identifying representative estuarine systems is challenging, since the primacy of any one parameter in driving the physical and biological variability is, in itself, highly variable among systems. Yet identifying the physicochemical factors driving estuarine variability is fundamental to determining the extent to which patterns and properties identified in one location (*e.g.,* a NERRS reserve) are transferable to the understanding of any other estuary.

DOI: 10.2112/SI55-005.1.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

In studies of estuarine ecosystems, algal biomass (*i.e.,* chlorophyll-*a* concentrations) is typically used as an index of system-level productivity, trophic state, and autotrophic carbon production (CLOERN, 2001), while bacterial production (BP) is a common measure of the activity of heterotrophic microbes (KIRCHMAN, 1993) and their carbon demand (DEL GIORGIO and COLE, 1998). The relationship between BP and chlorophyll-*a* (CHLA) has been used in a number of aquatic systems as an index for heterotrophic and autotrophic coupling (*e.g.,* COLE, FINDLAY, and PACE, 1988; WHITE *et al.,* 1991). Previous studies identify a positive correlation between BP and CHLA across a wide range of systems and relate the strength of this relationship to the coherence of autotrophic and heterotrophic processes. However, these previously published studies are limited to marine and freshwater systems, and it is not altogether clear if such a relationship applies to estuaries, where inputs of allochthonous organic matter are large and often drive net ecosystem metabolism (CAFFREY, 2004; HOPKINSON and SMITH, 2005).

The primary objective of the present study is to characterize the NERRS reserves based on the primary factors driving physicochemical variability in each and develop a multivariate classification framework to facilitate comparisons among the reserves. This is accomplished by combining principal components analysis (PCA) with water quality and nutrient data collected as part of NERRS SWMP and using this analysis to establish relationships among the reserves. We then evaluate the effect of environmental factors on biological processes in estuarine ecosystems using the BP : CHLA relationship as a response variable. Data for these analyses were collected in Monie Bay and North Inlet–Winyah Bay NERRS reserves and combined with a comprehensive review of published studies conducted in other estuarine ecosystems.

METHODS

Data Collection: NERRS SWMP

A composite dataset combining measures of water quality and nutrients was generated using SWMP data available through NERRS (http://cdmo.baruch.sc.edu/). Water quality parameters included temperature (°C), salinity (psu), specific conductivity (mS cm^{-1}), dissolved oxygen (DO; in % saturation and mg L^{-1}), turbidity (NTUs), depth (m), and pH. These parameters were monitored continuously with a YSI 6600 EDS datasonde throughout the ice-free period of the year and reported at 15- to 30-minute intervals. Grab samples for nutrients typically occurred on 3- to 4-week, intervals with minimum sampled parameters including CHLA (μg L^{-1}), dissolved orthophosphate (PO_4^{3-}), ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), nitrite + nitrate (NO_x), and total dissolved inorganic nitrogen (DIN = $NH_4^+ + NO_x$). All dissolved nutrients were reported in mg (N or P) L^{-1}. Measures of phaeophyton, silicate, total suspended solids, total nitrogen, total dissolved nitrogen, total phosphorus, total dissolved phosphorus, dissolved organic nitrogen, particulate organic carbon, and dissolved organic carbon were not collected at all reserves or on all sampling events and were thus omitted from our multivariate analyses. Downloaded water quality and nutrients files for all years and reserves were date–time matched and concatenated into a single file using a Visual Basic (VB.NET version 8.0, Microsoft) parsing program written by the authors, which paired discrete nutrient sampling events with the closest continuous water quality monitoring event for each station, resulting in a minimum of 15 environmental parameters for each concatenated sampling event. Data collected as part of diel time series were not included in the analyses. Analyses focused on differences across the NERRS at the reserve level, with characterization of conditions in each reserve based on those sites for which all 15 parameters were recorded and with no attempt to differentiate sites within specific reserves. The final composite dataset represented 86 sampling stations in 21 reserves and included 2820 concatenated entries of water quality and nutrients (Table 1).

Data Collection: Published Literature

A composite dataset of literature values from 33 independent studies reporting simultaneous observations of bacterioplankton production and CHLA concentrations in estuarine, coastal, and marine surface waters was compiled. Classification of systems as estuarine, coastal, or marine (*i.e.,* open ocean) was generally provided by the author, with distinction between marine and coastal systems being based on proximity to land, potential for terrestrial influence, and water depth. This dataset included 779 paired independent measures of BP and CHLA (Table 2). When available, concurrent measures of temperature ($n = 633$), salinity ($n = 530$), and inorganic nutrient concentrations (*i.e.,* PO_4^{3-}, $n = 450$; NH_4^+, $n = 272$; NO_x, $n = 401$; DIN, $n = 314$) were also recorded. Almost all studies (>90%) were conducted in temperate estuarine and coastal systems, with the exception of one tropical estuary (BANO, MORAN, and HODSON, 1997) and four open ocean studies (BODE *et al.,* 2001; CARON *et al.,* 2000; CONAN *et al.,* 1999; SHERR and SHERR, 2001). We avoided studies reporting values for BP and CHLA that were averaged over spatial or temporal (>1 day) scales. Estimates of BP were typically reported in carbon units and converted to a standard rate of μgC L^{-1} h^{-1}. Rates of leucine and thymidine incorporation were converted to carbon units using 3.1 kg C mol Leu^{-1} (SIMON and AZAM, 1989) and 1.89 kg C mol TdR^{-1} (DUCKLOW, KIRCHMAN, and ANDERSON, 2002), respectively. Bacterial production reported as change in cell abundance was converted to carbon units using 20 fg C $cell^{-1}$ (LEE and FUHRMAN, 1987). When tabular data were not available in the published document, they were either provided by authors or extracted directly from figures using DataThief software (B. TUMMERS, http://www.datathief.org).

Field Sampling

Monie Bay is a tidally influenced subestuary of the Chesapeake Bay and one of three components of Maryland's Chesapeake Bay NERRS. This system is located on the eastern shore of Maryland and consists of a semienclosed bay and three tidally influenced creeks varying in their agricultural land use, salinity, and other watershed characteristics. North Inlet–Winyah Bay is located on the central South Carolina

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 1. *Reserves, biogeographic regions, and stations included in analysis of SWMP composite dataset with years for which data were available and total observations.*

Reserve	State	Biogeographic Region	Stations Sampled	Years	Total Obs.
Ace Basin (ACE)	SC	Carolinian	Big Bay, Fishing Creek, Mosquito Creek, St. Pierr	2002–2005	247
Apalachicola (APA)	FL	Louisianan	Cat Point, Dry Bar, East Bay surface	2002–2005	128
Chesapeake Bay, Maryland (CBM)	MD	Virginian	Iron Pot Landing, Jug Bay, Mataponi Creek, Otter Point Creek, Railroad Bridge	2003–2004	206
Chesapeake Bay, Virginia (CBV)	VA	Virginian	Clay Bank, Goodwin Island, Sweet Hall Marsh, Taskinas Creek	2002–2005	88
Delaware (DEL)	DE	Virginian	Blackbird Landing, Division Street, Lebanon Landing, Scotton Landing	2002–2005	159
Elkhorn Slough (ELK)	CA	Californian	Azevedo Pond, North Marsh, South Marsh, Vierra Mouth	2002–2005	99
Great Bay (GRB)	NH	Acadian	Great Bay, Lamprey River, Oyster River, Squamscott River	2002–2005	90
Guana Tolomato Matanzas (GTM)	FL	Carolinian	Fort Matanzas, Pellicer Creek, Pine Island, San Sebastian	2002–2005	168
Jacques Cousteau (MUL)	NJ	Virginian	Buoy 126, Buoy 139, Chestnut Neck, Lower Bank	2002–2004	98
Jobos Bay (JOB)	PR	West Indian	Station 09, Station 10, Station 19, Station 20	2002–2005	161
Kachemak Bay (KAC)	AK	Fjord	Homer Dolphin deep, Homer Dolphin surface, Seldovia deep, Seldovia surface	2004–2005	75
Narragansett Bay (NAR)	RI	Virginian	Nag Creek, Potters Cove, T-Wharf bottom, T-Wharf surface, T-Wharf	2002–2005	161
North Carolina (NOC)	NC	Carolinian	East Cribbing, Loosin Creek, Research Creek, Zeke's Basin	2002–2005	86
North Inlet–Winyah Bay (NIW)	SC	Carolinian	Clambank, Debidue Creek, Oyster Landing, Thousand Acre	2002–2005	251
Padilla Bay (PDB)	WA	Columbian	Ploeg Channel, Bayview Channel, Joe Leary Slough, Gong surface	2002–2005	268
Rookery Bay (RKB)	FL	West Indian	Middle Blackwater River, Lower Henderson Creek, Faka Union Bay, Fakahatchee Bay	2002–2005	136
Sapelo Island (SAP)	GA	Carolinian	Flume Dock, Hunt Dock, Lower Duplin, Marsh Landing, Cabretta Creek, Dean Creek	2002–2004	77
South Slough (SOS)	OR	Columbian	Charleston Bridge, Vallino Island, Winchester Arm	2002–2004	97
Tijuana River (TJR)	CA	Californian	Model Marsh, Oneanta Slough, River Channel, Tidal Linkage	2002–2004	66
Waquit Bay (WQB)	MA	Virginian	Childs River, Menauhant, Metoxit Point, Sage Lot	2002–2004	92
Wells (WEL)	ME	Acadian	Head of Tide, Inlet, Little River Mouth, Skinner Mill	2002–2005	67

coast and consists of two components: a tidally influenced lagoonal estuary (North Inlet) and a larger coastal plain estuary (Winyah Bay) that receives inputs from five coastal rivers (Buzzelli *et al.,* 2004). Sampling of Monie Bay occurred monthly during 2000–2003 and is described in detail by Apple, del Giorgio, and Newell (2004). North Inlet–Winyah Bay was sampled during July and September 2006 and followed the same protocol as that in Monie Bay. Briefly, stations were accessed via a small boat and measures of water column chemistry (*i.e.,* temperature, salinity, and Secchi depth) were recorded. Approximately 20 L of subsurface (<0.5 m) water were collected, transported back to the laboratory, and subsampled for BP, CHLA, and dissolved nutrients following standard protocols (Apple, del Giorgio, and Newell, 2004).

Statistical Analyses

All statistical analyses, including standard least squares regressions, one- and two-way analyses of variance (ANOVA), means comparisons (Tukey-Kramer honestly significant difference, or HSD; $\alpha = 0.05$), and PCA were performed using the JMP version 5.0.1 statistical software package (SAS Institute Inc., Cary, NC). Values for BP, CHLA concentrations, and dissolved nutrients were log-transformed prior to analyses. Comparison of means and PCA were also performed individually on SWMP data assigned to one of eight relevant biogeographic regions (http://nerrs.noaa.gov/), including the Acadian (WEL, GRB), Californian (TJR, ELK), Carolinian (NOC, NIW, ACE, SAP), Columbian (SOS, PDB), Fjord (KAC), Louisianan (APA), Virginian (NAR, WQB, MUL, DEL, CBV, CBM), and West Indian (JOB, RKB). (See Table 1 for explanation of abbreviations.)

RESULTS

Water Quality and Nutrient Parameters (SWMP Data)

Overall means for the entire SWMP dataset are reported in Table 3. Mean values were also calculated for each SWMP parameter in each of the 21 reserves (Table 4) and ordered using significant differences as identified by Tukey-Kramer HSD. Highest mean temperatures were recorded at JOB and RKB (28°C) and lowest at KAC (7°C). Mean salinity was highest at JOB (35) and ELK (32) and lowest at CBM (0.1) and DEL (3). Salinity and pH were positively correlated in the composite dataset, with almost neutral pH recorded in DEL (6.9), WEL (7.0), and CBM (7.0) and most alkaline conditions

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 2. *Summary of studies from which data were collected as part of our review of published literature.*

Study	System Name	System Type(s) Sampled	Total Obs.
Anderson and Taylor, 2001*	Long Island Sound	Estuarine, coastal	24
Bano *et al.,* 1997	Indus River Delta	Estuarine	52
Bjørnsen *et al.,* 1989	Denmark estuary	Estuarine	28
Blight *et al.,* 1995*	Coastal England	Estuarine, coastal	13
Bode *et al.,* 2001	Canary Islands	Coastal, open ocean	11
Caron *et al.,* 2000	Georges Bank and Sargasso Sea	Shelf, open ocean	8
Conan *et al.,* 1999	Northwest Mediterranean	Shelf, open ocean	6
Cotner *et al.,* 2000	Florida Bay	Estuarine	8
del Giorgio and Bouvier, 2001	Choptank River	Estuarine	42
Griffith *et al.,* 1994	Chesapeake Bay	Estuarine	30
Hoch and Kirchman, 1993*	Delaware Bay	Estuarine, coastal	68
Hoppe, Giesenhagen, and Gocke, 1998	Schlei estuary	Estuarine, coastal	158
Kirchman *et al.,* 1989*	Rhone River plume	Estuarine, coastal	14
Koepfler *et al.,* 1993*	James River	Estuarine, coastal	32
Kononen *et al.,* 1998	Baltic Sea	Coastal	10
Krstulovic, Solic, and Marasovic, 1997	Adriatic Sea	Coastal, shelf	5
Lancelot and Billen, 1984	North Sea	Coastal	29
Lignell, 1990	Baltic Sea	Coastal	18
Lovejoy *et al.,* 1996	St. Lawrence River	Estuarine, coastal	4
Morán *et al.,* 2002	Northeast Atlantic	Coastal, open ocean	4
Naganuma and Miura, 1997	Seto Inland Sea	Estuarine, coastal	27
Pakulski *et al.,* 2000	Mississippi and Atchafalaya rivers	Estuarine, coastal	9
Revilla *et al.,* 2000*	Urdaibai estuary	Estuarine	36
Robertson, Dixon, and Alongi, 1998	Gulf of Papua	Coastal, shelf	5
Sherr and Sherr, 2001	Northeast Pacific	Shelf, open ocean	13
Shiah and Ducklow, 1994a	Chesapeake Bay	Estuarine	12
Shiah and Ducklow, 1994b	Chesapeake Bay	Estuarine	48
Smith, 2000	Chesapeake Bay	Estuarine	5
Tuomi and Kuuppo, 1999	Gulf of Finland	Coastal	21
Van Wambeke *et al.,* 2001	Mediterranean Sea	Coastal	4
Vaqué, Casamayor, and Gasol, 2001*	Mediterranean Sea	Coastal, shelf, open ocean	6
Vincent *et al.,* 1996	St. Lawrence River	Estuarine	9
Witek *et al.,* 1997	Gulf of Gdansk	Coastal	20

* Additional unpublished data collected as part of these studies were provided by the authors.

at ELK (8.1). Percent saturation and absolute concentration (mg L^{-1}) of DO were well correlated, with the highest means recorded at KAC (106% saturation and 10.6 mg L^{-1}) and lowest recorded at TJR (61% saturation and 4.9 mg L^{-1}) and NIW (57% saturation and 4.8 mg L^{-1}). The most turbid systems were ACE, NOC, and SAP (77, 61, and 40 NTU, respectively), with the highest values consistently recorded in ACE. Least turbid were NAR and WQB (both 2.0 NTU), although mean values for these two reserves were not statistically different than the majority of the other reserves. The

Table 3. *Mean values, standard error, sample size, and range of parameters included in the SWMP composite dataset and review of published studies conducted in coastal and estuarine systems.*

	SWMP Composite Dataset			Literature Review		
Parameter	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range
Temperature (°C)	**18.1 ± 0.1**	2802	−0.9–33	13.6 ± 0.4	608	0.1–34
Specific conductivity (mS cm^{-1})	32.3 ± 0.4	2786	0.1–60	nd		
Salinity	**20.7 ± 0.2**	2786	0–40	16.0 ± 0.5	496	0–55
Dissolved oxygen (% saturation)	80.7 ± 0.6	2698	0–216	nd		
Dissolved oxygen (mg L^{-1})	7.0 ± 0.06	2693	0–21	nd		
Depth (m)	1.5 ± 0.03	2791	0–16	nd		
pH	7.5 ± 0.01	2716	4.1–9.8	nd		
Turbidity (NTUs)	23.2 ± 1.8	2599	0–2084	nd		
Phosphate (mg L^{-1})	**0.045 ± 0.003**	2665	0.0006–5.6	0.02 ± 0.008	433	0.0003–1.2
Ammonium (mg L^{-1})	0.09 ± 0.009	2651	0.0003–19	**0.22 ± 0.03**	270	0.0006–5.7
Nitrate + nitrite (mg L^{-1})	0.20 ± 0.009	2485	0.0002–8.4	**0.32 ± 0.02**	386	0.00002–2.7
Dissolved inorganic nitrogen (mg L^{-1})	0.25 ± 0.01	2129	0.0005–19	**0.61 ± 0.04**	312	0.0008–6.2
Chlorophyll-*a* (μg L^{-1})	7.8 ± 0.4	2574	0–348	**14.9 ± 0.8**	765	0.01–336
Bacterial production (μgC L^{-1} h^{-1})	nd			2.4 ± 0.2	814	0.001–55

Significantly higher means between the two datasets are indicated in bold: ANOVA and Tukey-Kramer HSD ($\alpha = 0.5$, $p < 0.0001$). nd = data not available.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

greatest water depth was recorded at KAC (6.4 m), followed by GTM (2.5 m) and PDB (2.2 m). The shallowest systems were TJR and CBV (0.3 m).

Mean CHLA was highest in DEL, CBM, and SAP (10.0, 9.0, and 7.6 μg L^{-1}, respectively) and lowest in KAC, TJR, and NAR (all <1.2 μg L^{-1}). Highest mean PO_4^{3-} occurred at TJR (0.44 mg L^{-1}), SAP (0.12 mg L^{-1}), and ACE (0.09 mg L^{-1}), while the most PO_4^{3-} deplete conditions were at MUL (0.01 mg L^{-1}) and APA (0.008 mg L^{-1}). As with PO_4^{3-}, the highest mean NH_4^+ was observed at TJR (1.25 mg L^{-1}), followed by JOB (0.16 mg L^{-1}) and NOC (0.13 mg L^{-1}). Lowest means were observed for KAC, WQB, and NAR (all <0.03 mg L^{-1}). Means in NO_x did not follow patterns in PO_4^{3-} or NH_4^+. Highest mean NO_x was recorded in CBM (0.65 mg L^{-1}) and DEL (0.75 mg L^{-1}) and lowest in JOB, RKB, and NIW (all <0.01 mg L^{-1}).

There was a highly significant effect of biogeographic region on all parameters in the composite SWMP dataset (ANOVA, $p < 0.0001$), and significant differences existed between means within all biogeographic regions (Tukey-Kramer HSD, $\alpha = 0.05$). Data from the West Indian region exhibited the highest mean temperature (27°C) and salinity (31), while lowest means for these temperature and salinity were recorded in the Fjord and Virginian regions (7°C and 13, respectively). Highest DO was recorded in the Fjord region (106% saturation and 10.6 mg L^{-1}), as was the greatest mean water depth. Reserves from the Carolinian region had the lowest DO (70% saturation and 5.1 mg L^{-1}), were the most turbid (44 NTU), and had the highest CHLA (5.2 μg L^{-1}). Lowest mean turbidity and CHLA were recorded in the Fjord region (3 NTU and 0.9 μg L^{-1}, respectively). Highest mean PO_4^{3-} (0.08 mg L^{-1}) and NH_4^+ (0.1 mg L^{-1}) occurred in the Californian region and lowest in the Louisianan (0.004 mg L^{-1}) and Fjord (0.01 mg L^{-1}) regions. The most NO_x-enriched region was Columbian (0.1 mg L^{-1}), and the most deplete region was West Indian (0.01 mg L^{-1}).

Principal Components Analysis

Principal components analysis of paired water quality and nutrients measurements derived from SWMP data identified two composite variables (hereafter PC1 and PC2) that explained 48% of the variability within the dataset ($n = 1973$), with 28% and 20% attributed to PC1 and PC2, respectively (Figure 1, Table 5). Ten parameters were used in PCA (temperature, salinity, pH, water depth, percent saturation and concentration of DO, turbidity, and dissolved concentrations of PO_4^{3-}, NH_4^+, and NO_x). Two parameters available in the composite dataset were omitted from our analyses: specific conductivity due to redundancy with salinity and DIN because it is derived from NO_x and NH_4^+ and well correlated with these parameters ($r^2 = 0.96$, $p < 0.0001$). CHLA was initially omitted from PCA because this parameter was not recorded at JOB and including CHLA would have eliminated this reserve from our comparative analyses. An additional PCA was performed including CHLA, which produced loading patterns similar to those of the first analysis and with CHLA grouping closely with NH_4^+, PO_4^{3-}, and turbidity. In both analyses, PC1 had high positive loadings for salinity and pH and was negatively correlated with NO_x, whereas PC2 was positively correlated with temperature and negatively correlated with both DO percent saturation and concentration (Figure 1, Table 5). Coordinate vectors for each parameter included in PCA (solid arrows), and mean factor loadings for each reserve (solid circles) allow visualization of the controlling environmental factors most important for each NERRS (Figure 1). Horizontal distribution of reserves (*i.e.,* along PC1) generally represented a gradient of salinity and NO_x concentrations, while vertical distribution represented one of temperature and DO. This resulted in warmer and more saline systems being located predominantly in the upper right quadrant, cooler saline systems in the lower right quadrant, and freshwater-influenced reserves to the left of the origin. Groupings of reserves generally coincided with the biogeographic region in which they were located (shaded regions in Figure 1). Mean annual temperature was well correlated with mean factor loadings from each reserve on PC2 (Figure 2; $r^2 = 0.76$, $p < 0.0001$, $n = 21$), although two reserves (KAC and TJR) deviated markedly from this general trend. Removal of these outliers from the regression analysis greatly improved the relationship (*i.e.,* $r^2 = 0.87$, $p < 0.0001$, $n = 19$).

SWMP data was divided into subsets representing each biogeographic region and evaluated using PCA. Cumulative percent variability explained by PCA for each biogeographic region was equal to or greater than that of the composite SWMP dataset and ranged from 48% (West Indian region) to 66% (Columbian region). For data from the Columbian region, all 10 water quality parameters were highly and positively correlated with either PC1 or PC2 (*i.e.,* eigenvectors ≥ 0.7). In general, analysis of data from each biogeographic region generated patterns similar that of the entire dataset, with temperature and salinity driving most of the variability and exhibiting negative correlations with DO and dissolved nutrients, respectively. Exceptions to this pattern included weaker temperature loading in Acadian, Californian, and West Indian regions (*i.e.,* eigenvectors of 0.46, 0.28, and 0.38, respectively); weak salinity loading in the Fjord region (0.46); and general absence of nutrient influence in the Carolinian region.

PCA of literature data produced loading patterns that were strikingly similar to SWMP (Table 5), with a negative correlation between heavily loaded salinity (−0.64) and dissolved nutrients (>0.77) on PC1 and a strong positive temperature loading on PC2 (0.94). PCA of literature data, including BP, also revealed a strong positive correlation between temperature and BP and heavy loading on PC2. Analysis of literature data produced negative loadings of NH_4^+ and NO_x on PC1 that were much stronger than those of SWMP data. Although loading of CHLA on PC1 and PC2 was similar to that of SWMP data, it was not as strongly correlated with dissolved nutrients. Because of limited overlap in parameters reported by published studies, literature dataset PCA included only five parameters (temperature, salinity, PO_4^{3-}, NH_4^+, and NO_x), and the dataset was much smaller ($n = 207$). This analysis explained 75% of the variability within the literature data, with 56% and 19% attributed to PC1 and PC2, respectively.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 4A. *Temperature, salinity, pH, and depth at each reserve (mean ± SE [*n*]); values are derived from analysis of the SWMP composite dataset.*

Reserve	Temperature (°C)			Salinity			pH			Depth (m)		
	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range
Ace Basin (ACE)	19 ± 0.5	(244)	5–31	19 ± 0.65	(243)	0.7–37	7.4 ± 0.03	(233)	6.7–8.3	1.6 ± 0.1	(242)	0.0–4
Apalachicola (APA)	23 ± 0.6	(125)	10–31	16 ± 0.81	(124)	0.1–34	7.8 ± 0.1	(125)	4.6–9.3	1.2 ± 0.04	(124)	0.3–2
Chesapeake Bay, Maryland (CBM)	17 ± 0.4	(205)	1–29	0.1 ± ??	(202)	0.1–0.3	7.0 ± 0.04	(199)	6.1–9.7	0.9 ± 0.04	(201)	0.0–2
Chesapeake Bay, Virginia (CBV)	18 ± 0.9	(88)	3–32	12 ± 0.85	(88)	0.1–25	7.6 ± 0.1	(88)	6.7–9.1	0.3 ± 0.02	(88)	0.0–1
Delaware (DEL)	16 ± 0.7	(159)	0–30	3 ± 0.32	(159)	0.1–20	6.8 ± 0.03	(156)	5.9–7.9	1.1 ± 0.1	(159)	0.1–3
Elkorn Slough (ELK)	18 ± 0.5	(94)	5–30	32 ± 0.34	(92)	21.3–40	8.1 ± 0.03	(85)	7.2–8.8	0.8 ± 0.1	(98)	0.0–3
Great Bay (GRB)	16 ± 0.7	(88)	0–25	14 ± 1.07	(88)	0.1–35	7.4 ± 0.1	(85)	5.9–9.4	1.7 ± 0.1	(90)	0.2–5
Guana Tolomato Matanzas (GTM)	24 ± 0.4	(168)	12–31	26 ± 0.76	(168)	0.1–38	7.6 ± 0.03	(167)	5.8–8.5	2.5 ± 0.1	(168)	0.3–5
Jacques Cousteau (MUL)	16 ± 0.7	(97)	1–27	17 ± 1.11	(97)	0–31	7.1 ± 0.1	(87)	4.1–8.2	1.9 ± 0.1	(97)	0.9–3
Jobos Bay (JOB)	28 ± 0.1	(161)	23–32	35 ± 0.19	(161)	28.4–40	7.8 ± 0.03	(160)	6.9–9.3	0.7 ± 0.02	(157)	0.3–1
Kachemak Bay (KAC)	7 ± 0.4	(75)	1–15	30 ± 0.26	(75)	19.9–33	7.9 ± 0.1	(75)	4.4–9.8	6.4 ± 0.6	(75)	0.3–16
Narragansett Bay (NAR)	13 ± 0.6	(161)	−1–29	29 ± 0.28	(157)	3.7–32	7.8 ± 0.03	(160)	6.6–8.3	2.0 ± 0.2	(161)	0.0–6
North Carolina (NOC)	20 ± 0.8	(85)	6–33	23 ± 0.64	(85)	7.3–35	8.0 ± 0.04	(84)	7.0–9.0	1.1 ± 0.05	(85)	0.3–2
North Inlet–Winyah Bay (NIW)	20 ± 0.5	(249)	4–31	24 ± 0.74	(246)	0.3–38	7.3 ± 0.02	(246)	6.4–8.1	1.0 ± 0.03	(246)	0.0–2
Padilla Bay (PAD)	12 ± 0.2	(268)	2–21	24 ± 0.66	(268)	0.2–32	7.8 ± 0.03	(259)	6.4–8.8	2.2 ± 0.1	(267)	0.0–4
Rookery Bay (RKB)	26 ± 0.3	(136)	17–33	27 ± 0.77	(136)	0.4–39	7.7 ± 0.02	(132)	7.2–8.2	0.9 ± 0.03	(136)	0.1–2
Sapelo Island (SAP)	22 ± 0.7	(77)	10–32	25 ± 0.38	(77)	10.8–29	7.5 ± 0.04	(65)	6.9–8.2	1.5 ± 0.1	(77)	0.0–4
South Slough (SOS)	13 ± 0.3	(97)	7–20	21 ± 1.21	(97)	0–34	7.5 ± 0.1	(96)	6.0–8.2	0.9 ± 0.1	(97)	0.0–4
Tijuana River (TJR)	18 ± 0.4	(66)	12–24	28 ± 1.2	(66)	1.1–40	7.7 ± 0.04	(62)	7.2–8.5	0.3 ± 0.03	(65)	0.0–1
Waquoit Bay (WQB)	14 ± 0.9	(92)	−1–29	29 ± 0.26	(90)	13.3–32	8.0 ± 0.02	(85)	7.5–8.4	0.7 ± 0.03	(91)	0.2–1
Wells (WEL)	11 ± 0.8	(67)	0–23	12 ± 1.77	(67)	0–35	7.0 ± 0.1	(67)	5.2–8.2	1.2 ± 0.2	(67)	0.0–5

Table 4B. *Dissolved oxygen, chlorophyll-*a *concentrations, and turbidity at each reserve (mean ± SE [*n*]). Values are derived from analysis of the SWMP composite dataset.*

Reserve	DO (% saturation)			DO (mg L^{-1})			Turbidity (NTU)			Chlorophyll-*a* (μg L^{-1})		
	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range
Ace Basin (ACE)	66 ± 1	(240)	7–98	5.8 ± 0.15	(240)	0.5–11	77 ± 16	(237)	4–2084	10.0 ± 1.86	(247)	1.2–348
Apalachicola (APA)	81 ± 3	(118)	2–138	6.7 ± 0.25	(117)	0.2–13	15 ± 4.5	(113)	0–500	6.2 ± 0.52	(124)	0.6–32
Chesapeake Bay, Maryland (CBM)	74 ± 2	(200)	10–137	7.3 ± 0.19	(200)	1–13	25 ± 1.9	(188)	2–200	20.4 ± 2.91	(176)	0.9–299
Chesapeake Bay, Virginia (CBV)	93 ± 3	(87)	21–171	8.6 ± 0.35	(87)	1.6–18	30 ± 3.8	(87)	0–172	4.9 ± 0.51	(88)	0.6–26
Delaware (DEL)	76 ± 2	(155)	10–155	7.9 ± 0.26	(155)	0.8–13	40 ± 2.7	(154)	2–293	16.5 ± 1.25	(159)	0.6–85
Elkorn Slough (ELK)	104 ± 4	(90)	23–191	8.3 ± 0.31	(89)	1.9–15	8 ± 0.7	(87)	1–41	5.6 ± 0.84	(93)	0.6–75
Great Bay (GRB)	98 ± 3	(83)	44–169	9.1 ± 0.33	(83)	3.7–19	22 ± 3.6	(76)	0–191	5.3 ± 0.58	(89)	0.3–38
Guana Tolomato Matanzas (GTM)	76 ± 1	(165)	24–130	5.7 ± 0.11	(165)	1.8–9	15 ± 4.4	(160)	0–699	5.6 ± 0.3	(168)	0.5–32
Jacques Cousteau (MUL)	88 ± 2	(82)	46–133	8.1 ± 0.26	(81)	3.5–14	11 ± 1.3	(67)	0–67	3.9 ± 0.34	(97)	0.03–16
Jobos Bay (JOB)	78 ± 3	(155)	4–166	5.0 ± 0.17	(155)	0.2–11	5 ± 1.2	(139)	0–139	nd		
Kachemak Bay (KAC)	106 ± 2	(72)	29–142	10.6 ± 0.24	(72)	2.6–15	3 ± 0.5	(66)	0–24	2.0 ± 0.3	(75)	0.1–11
Narragansett Bay (NAR)	90 ± 2	(155)	0–200	8.2 ± 0.24	(155)	0–21	2 ± 0.3	(160)	0–21	1.8 ± 0.15	(158)	0.1–14
North Carolina (NOC)	96 ± 3	(84)	21–216	7.9 ± 0.29	(84)	1.5–16	61 ± 18	(81)	1–1099	4.7 ± 0.61	(80)	0.6–40
North Inlet–Winyah Bay (NIW)	57 ± 1	(246)	1–97	4.8 ± 0.15	(244)	0.2–11	25 ± 5.9	(237)	1–1362	7.9 ± 0.73	(248)	0.9–135
Padilla Bay (PAD)	87 ± 2	(260)	11–159	8.0 ± 0.14	(260)	1.2–14	8 ± 0.9	(258)	0–77	3.9 ± 0.55	(268)	0.1–95
Rookery Bay (RKB)	73 ± 2	(131)	9–120	5.1 ± 0.13	(131)	0.7–9	13 ± 0.9	(127)	2–80	4.0 ± 0.27	(135)	0.5–29
Sapelo Island (SAP)	89 ± 3	(65)	46–133	6.9 ± 0.28	(65)	3.4–11	40 ± 8.1	(57)	0–298	11.1 ± 1.5	(77)	0.5–61
South Slough (SOS)	87 ± 2	(94)	6–120	8.1 ± 0.21	(94)	0.4–12	10 ± 1.7	(93)	0–131	2.8 ± 0.23	(97)	0.3–13
Tijuana River (TJR)	61 ± 7	(65)	1–189	4.9 ± 0.56	(65)	0.1–17	28 ± 12	(60)	2–748	1.9 ± 0.42	(45)	0–14
Waquoit Bay (WQB)	103 ± 2	(85)	46–156	9.2 ± 0.27	(85)	3.2–15	2 ± 0.3	(85)	0–27	7.3 ± 1.26	(83)	0–46
Wells (WEL)	84 ± 4	(66)	1–112	9.0 ± 0.48	(66)	0.1–15	3 ± 0.6	(67)	0–34	26.9 ± 5.12	(67)	0.1–223

nd = data not available.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 4C. *Dissolved nutrient concentrations at each reserve (mean ± SE [n]). Values are derived from analysis of the SWMP composite dataset.*

Reserve	Phosphate (mg L^{-1})			Ammonium (mg L^{-1})			Nitrate + Nitrite (mg L^{-1})			Dissolved Inorganic Nitrogen (mg L^{-1})		
	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range	Mean ± SE	*n*	Range
Ace Basin (ACE)	0.09 ± 0.006	(247)	0.006–0.657	0.06 ± 0.004	(239)	0.001–0.4	0.05 ± 0.004	(244)	0.0002–0.7	0.1 ± 0.01	(238)	0.00–0.7
Apalachicola (APA)	0.01 ± 0.001	(105)	0.001–0.074	0.04 ± 0.003	(122)	0.004–0.3	0.11 ± 0.01	(119)	0.007–0.4	0.1 ± 0.01	(115)	0.01–0.6
Chesapeake Bay, Maryland (CBM)	0.04 ± 0.005	(206)	0.002–0.694	0.09 ± 0.01	(204)	0.003–2.3	0.65 ± 0.03	(206)	0.012–1.8	nd		
Chesapeake Bay, Virginia (CBV)	0.02 ± 0.002	(80)	0.001–0.083	0.07 ± 0.01	(78)	0.005–0.3	0.09 ± 0.01	(73)	0.002–0.6	0.1 ± 0.02	(66)	0.01–0.7
Delaware (DEL)	0.03 ± 0.002	(151)	0.002–0.125	0.12 ± 0.01	(155)	0.007–0.5	0.75 ± 0.05	(156)	0.001–3.0	0.9 ± 0.06	(156)	0.01–3.3
Elkorn Slough (ELK)	0.06 ± 0.003	(96)	0.006–0.168	0.08 ± 0.01	(82)	0.006–0.4	0.14 ± 0.03	(87)	0.003–1.2	0.3 ± 0.05	(36)	0.02–1.2
Great Bay (GRB)	0.04 ± 0.003	(82)	0.003–0.108	0.09 ± 0.01	(84)	0.007–0.4	0.13 ± 0.01	(84)	0.003–0.6	0.2 ± 0.01	(80)	0.04–0.7
Guana Tolomato Matanzas (GTM)	0.02 ± 0.001	(164)	0.002–0.085	0.07 ± 0.004	(163)	0.009–0.3	0.02 ± 0.00	(156)	0.001–0.3	0.1 ± 0.01	(153)	0.02–0.5
Jacques Cousteau (MUL)	0.01 ± 0.002	(83)	0.001–0.06	0.03 ± 0.002	(94)	0.001–0.1	0.08 ± 0.01	(77)	0.010–0.3	0.1 ± 0.01	(77)	0.02–0.4
Jobos Bay (JOB)	0.02 ± 0.001	(152)	0.001–0.083	0.16 ± 0.01	(159)	0.008–0.6	0.01 ± 0.00	(85)	0.001–0.1	0.2 ± 0.01	(83)	0.02–0.6
Kachemak Bay (KAC)	0.04 ± 0.003	(70)	0.004–0.132	0.02 ± 0.01	(53)	0.002–0.4	0.16 ± 0.01	(63)	0.002–0.4	0.2 ± 0.01	(51)	0.01–0.4
Narragansett Bay (NAR)	0.03 ± 0.002	(161)	0.001–0.115	0.03 ± 0.004	(161)	0.001–0.3	0.05 ± 0.01	(152)	0.001–0.3	0.1 ± 0.01	(152)	0.00–0.4
North Carolina (NOC)	0.02 ± 0.003	(83)	0.001–0.129	0.13 ± 0.01	(78)	0.015–0.3	0.10 ± 0.01	(66)	0.001–0.4	0.2 ± 0.01	(60)	0.05–0.6
North Inlet–Winyah Bay (NIW)	0.02 ± 0.001	(246)	0.003–0.137	0.06 ± 0.00	(246)	0.003–0.4	0.03 ± 0.003	(243)	0.001–0.3	0.1 ± 0.01	(241)	0.01–0.5
Padilla Bay (PAD)	0.05 ± 0.001	(264)	0.001–0.079	0.09 ± 0.01	(264)	0.002–1.4	0.43 ± 0.06	(251)	0.003–8.4	0.5 ± 0.06	(251)	0.01–8.6
Rookery Bay (RKB)	0.01 ± 0.001	(129)	0.002–0.043	0.03 ± 0.003	(123)	0.004–0.1	0.02 ± 0.001	(131)	0.002–0.1	0.0 ± 0.004	(121)	0.01–0.2
Sapelo Island (SAP)	0.12 ± 0.006	(77)	0.055–0.278	0.04 ± 0.004	(71)	0.003–0.2	0.03 ± 0.004	(50)	0.005–0.1	0.1 ± 0.01	(48)	0.01–0.3
South Slough (SOS)	0.03 ± 0.002	(96)	0.002–0.062	0.05 ± 0.003	(97)	0.006–0.2	0.18 ± 0.02	(95)	0.001–0.9	0.2 ± 0.02	(95)	0.03–0.9
Tijuana River (TJR)	0.44 ± 0.1	(52)	0.020–5.6	1.25 ± 0.45	(49)	0.029–18.6	0.13 ± 0.04	(51)	0.003–1.9	1.2 ± 0.42	(45)	0.05–18.6
Waquoit Bay (WQB)	0.01 ± 0.001	(74)	0.004–0.055	0.02 ± 0.002	(75)	0.001–0.1	0.05 ± 0.01	(71)	0.001–0.5	0.1 ± 0.01	(61)	0.01–0.5
Wells (WEL)	0.04 ± 0.007	(47)	0.002–0.166	0.07 ± 0.01	(54)	0.006–0.3	0.08 ± 0.01	(25)	0.005–0.2	nd		

nd = data not available.

Covariation of BP and CHLA

The literature dataset revealed a highly significant positive relationship between BP and CHLA across a range of marine, coastal, and estuarine systems (Figure 3). Approximately 24% of the variability in BP was explained by CHLA, with a positive *y*-intercept of 0.37 μgC L^{-1} h^{-1}. Superimposed on this figure, but not included in regression statistics, are data from field sampling of Monie Bay and North Inlet conducted as part of the present study. The relationship between BP and CHLA reported in other studies was corrected for discrepancies in rate units and converted to common units of μgC L^{-1} h^{-1} prior to comparison, revealing similar slope and *y*-intercept when COLE, FINDLAY, and PACE (1988) and WHITE *et al.* (1991) were considered but steeper slope and lower *y*-intercept than those reported by MURRELL (2003). Within our dataset, open ocean systems were characterized by lower BP and CHLA, with data from studies in the Atlantic Ocean (BODE *et al.,* 2001; CARON *et al.,* 2000) exhibiting higher BP per unit CHLA relative to those from the Pacific (SHERR and SHERR, 2001). The majority of coastal and estuarine systems had higher rates of BP and higher concentrations of CHLA relative to open ocean data, with the highest values observed in estuarine systems. Paired measures of BP and CHLA from Monie Bay had a similar distribution to that of other estuarine systems but no significant relationship ($p \leq 0.6$, $n = 159$). Four systems emerged from the literature and field data that exhibited highly significant and relatively strong covariation of BP and CHLA (Figure 4), including Indus River Delta (BANO *et al.,* 1997), Urdaibai estuary (REVILLA *et al.,* 2000), Menai Strait (BLIGHT *et al.,* 1995), and North Inlet (present study).

Temperature was positively correlated with BP : CHLA and explained approximately one-third of the variability in the BP *vs.* CHLA relationship (Figure 5A). The relationship between BP : CHLA and salinity was parabolic across the entire salinity range (Figure 5B), with a second-order polynomial providing a highly significant fit (*i.e.,* $p < 0.0001$) and explaining 25% of the variability. The salinity associated with this minimum value (*i.e.,* first derivative) was 17, reflecting the relatively low values of BP per unit CHLA in mesohaline waters. We did not observe a significant relationship between BP : CHLA and ambient nutrient concentrations (*i.e.,* PO_4^{3-}, NH_4^+, NO_x, and DIN).

DISCUSSION

Principal Components Analysis

The overview of mean water quality and nutrient values presented in this study (*e.g.,* Tables 3 and 4) and others (*e.g.,* WENNER *et al.,* 2004) is useful for placing environmental conditions at any one reserve within the context of all others. However, comparisons based on a single environmental parameter cannot represent all the factors that contribute to the physicochemical character of a reserve and are thus limited in the ability to reveal the extent to which reserves are similar or may differ. In this regard, the use of PCA—and more specifically, the distribution of reserves along PC1 and PC2 axes—is a meaningful and integrative means of classi-

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

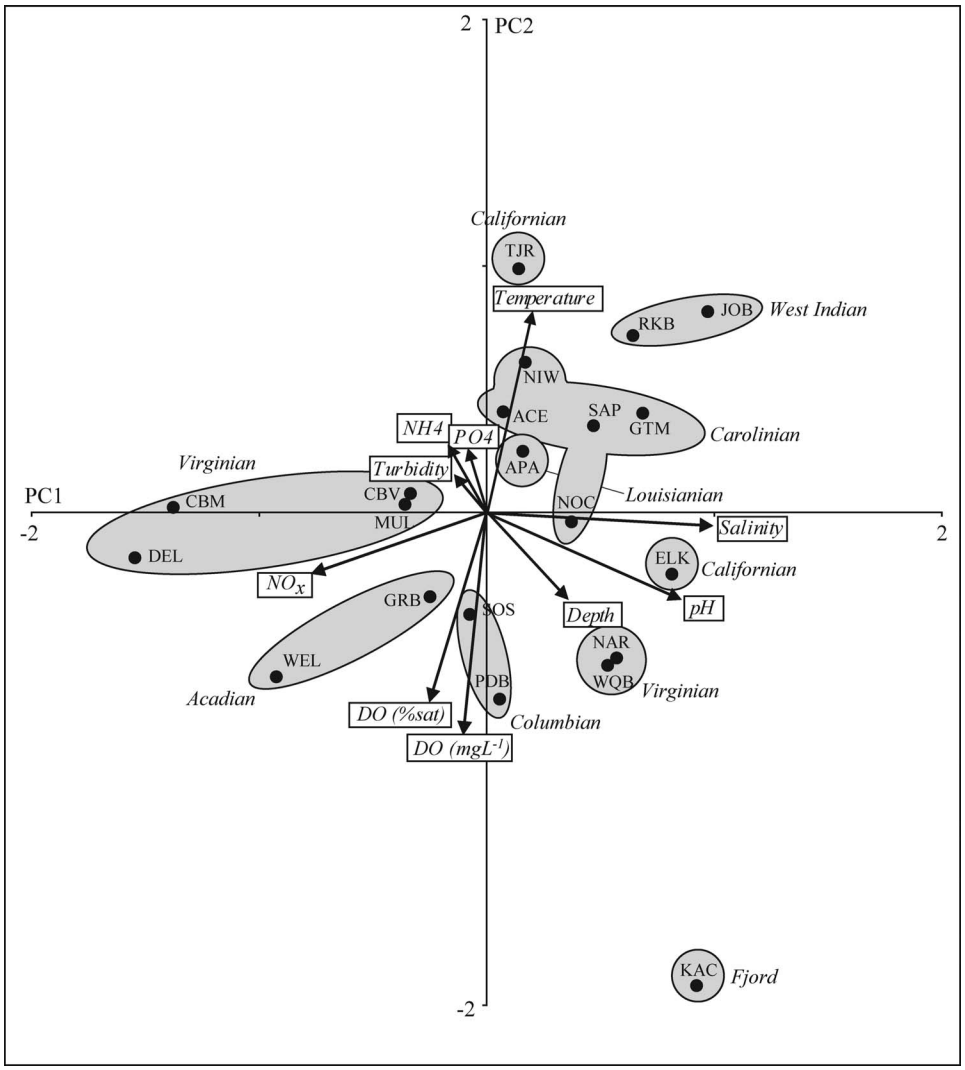


Figure 1. PCA biplot of mean factor loadings of each reserve on PC1 and PC2. Rotated eigenvectors for each parameter are indicated by arrows and italicized in boxes. Shaded regions and italics represent grouping of reserves by biogeographic region.

fying reserves based on similarities in environmental conditions. For example, reserves located in the upper right quadrant of Figure 1 represent those systems that are more saline and located in warmer climates (*e.g.,* JOB in Puerto Rico, RKB and GTM in Florida, and SAP in Georgia), while saline yet much colder systems appear in the lower left (*e.g.,* KAC in Alaska). Many reserves that share geographic proximity but differ substantially with respect to distribution of sites, hydrography, and estuary type still group closely together on the PCA biplot (*e.g.,* NAR with WQB, CBV with MUL, and DEL with CBM), suggesting that landscape-scale characteristics or regional climatological factors may often have a significant impact relative to local environmental conditions.

Salinity and Nitrogen Loading

Salinity had the greatest impact on variability in environmental conditions among the reserves, as evidenced by the strong positive loading on PC1. However, loading of other parameters (*e.g.,* NO_x and pH) on PC1 suggests that it is not salinity alone but rather the delivery of nitrogen associated with freshwater inputs that drives variability in SWMP data. This allows a more accurate characterization of physicochemical processes of these estuarine systems. The apparent influence of salinity may therefore actually be a proxy for more complex processes related to nutrient and organic matter loading in these systems. Reserves that appear to be most influenced by this phenomenon include DEL and CBM, as evidenced by their strong negative correlation with PC1. Also located along the axis of PC1 are three other mid-Atlantic reserves, including MUL in New Jersey, CBV, and NOC, suggesting that the influence of salinity and freshwater delivery of nitrogen may be a phenomena associated with climatic conditions and/or regional-scale watershed characteristics. A similar relationship between salinity and dissolved nutrient

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 5. *Results from PCA of composite SWMP (*n *= 1973) and literature review (*n *= 207) data, including eigenvalues, percent variability, and rotated eigenvectors.*

	SWMP		Literature	
	PC1	PC2	PC1	PC2
Eigenvalue	**2.8**	**2.0**	**2.8**	**1.0**
Percent variability	**27.6**	**20.1**	**55.4**	**19.4**
Cumulative percent	**27.6**	**47.7**	**55.4**	**74.8**
Eigenvectors (rotated)				
Temperature	0.21	**0.84**	0.05	**0.94**
Salinity	**0.89**	−0.06	**0.64**	0.39
Dissolved oxygen (mg/L)	−0.08	−**0.88**	nd	nd
Dissolved oxygen (% saturation)	−0.25	−**0.85**	nd	nd
Depth	0.35	−0.37	nd	nd
pH	**0.78**	−0.36	nd	nd
Turbidity	−0.12	0.15	nd	nd
Phosphate	−0.07	0.29	−**0.77**	0.11
Ammonium	−0.14	0.28	−**0.91**	−0.07
Nitrate + nitrite	−**0.70**	−0.28	−**0.88**	−0.26

Elevated loadings on each component (*i.e.,* eigenvectors ≥ 0.65) are indicated in bold. nd = data not available for entire dataset.

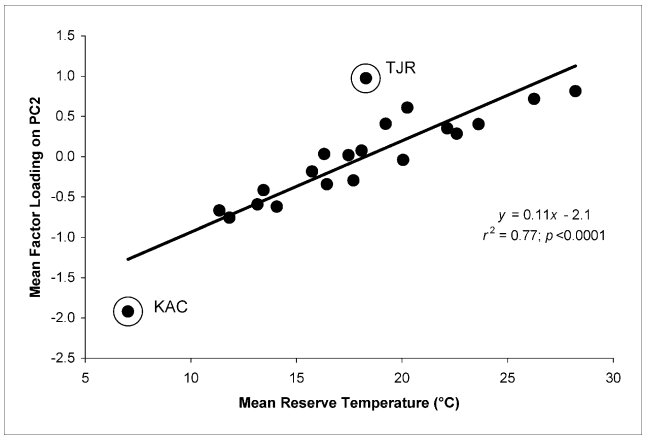


Figure 2. Relationship between mean reserve temperature and mean factor loadings on PC2.

concentrations has been observed previously in multivariate analyses of other NERRS reserve data (*i.e.,* Monie Bay; Apple, del Giorgio, and Newell, 2004) and may be a characteristic of estuarine systems with tributaries that drain agriculturally developed watersheds. Further multivariate analysis of SWMP data incorporating available information regarding watershed characteristics would provide valuable insight into the role of landscape-scale characteristics on the variability in the reserves.

Temperature and Dissolved Oxygen

Temperature was another important factor explaining variability in SWMP data, as evidenced by the positive loading of temperature on PC2 (Table 5) and highly significant correlation between mean reserve temperature and factor loadings on PC2 (Figure 2). In addition to revealing the universal effect of temperature on SWMP data, PCA provides insight into the role of temperature-dependent heterotrophic processes in regulating ambient DO concentrations. The strong negative correlation of DO (mg L^{-1}) and temperature revealed by both PCA (Table 5) and direct comparisons ($r = -0.69$, $p < 0.0001$) is not surprising, as temperature strongly dictates the physical solubility of oxygen in water. However, when expressed as percent saturation, which removes the physical effects of temperature and salinity, the strong negative correlation remains. This pattern was also observed by Caffrey (2004) in an earlier analysis of SWMP data and probably represents a general characteristic among estuarine ecosystems. Although the drivers of this phenomenon are many, it likely results from the positive effect of temperature on planktonic (Kemp *et al.,* 1992; Sampou and Kemp, 1994) and benthic (Caffrey, 2004; Cowan and Boynton, 1996) respiration, as well as the disproportionate effect of temperature on heterotrophic relative to autotrophic processes (Lomas *et al.,* 2002). Indeed, PCA of literature data revealed a strong correlation between temperature and BP but none between temperature and CHLA. The strong temperature dependence of DO—specifically, percent saturation—emphasizes the important contribution of heterotrophic processes in estuaries. Not surprisingly, these processes are subsidized by significant inputs of allochthonous organic matter that are characteristic of most estuaries and that contribute to the net-heterotrophic conditions typically encountered (*e.g.,* Hopkinson and Smith, 2005).

The temperature dependence of DO that we have observed is not absolute, and deviation of reserves from the otherwise strong positive relationship between temperature and factor loadings on PC2 (Figure 2) reveals those systems in which DO variability deviates substantially from what might typically be expected. For example, based on the relationship observed for most reserves, loading on PC2 was lower than expected (*i.e.,* DO was higher) for KAC. This system experiences some of the lowest temperatures and turbidities (and thus highest light availability) recorded in SWMP data. Higher salinities characteristic of this reserve suggest, in turn, that the role of allochthonous organic matter is minimal as a subsidy for heterotrophic activities. Thus, uncharacteristically high DO concentrations in KAC may be attributed in part to higher solubility associated with colder waters but more importantly to elevated primary production relative to temperature-dependent heterotrophic activity (Billen and Becquevort, 1990).

Tijuana River (TJR) also deviated from the otherwise strong relationship between temperature and PC2 factor loading, with higher-than-expected loadings indicating uncharacteristically low DO concentrations. In the case of TJR, the temperature dependence of DO may be more strongly influenced by factors known to drive hypoxic conditions in estuaries, such as inorganic nutrients (Kemp *et al.,* 2005; Paerl *et al.,* 1998), inputs of allochthonous dissolved organic matter, and subsequent degradation by heterotrophic microbial processes (Bano, Moran, and Hodson, 1997; Carlsson, Graneli, and Segatto, 1999). TJR is one of the most phosphate-replete reserves, having 8 of the top 10 measure-

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

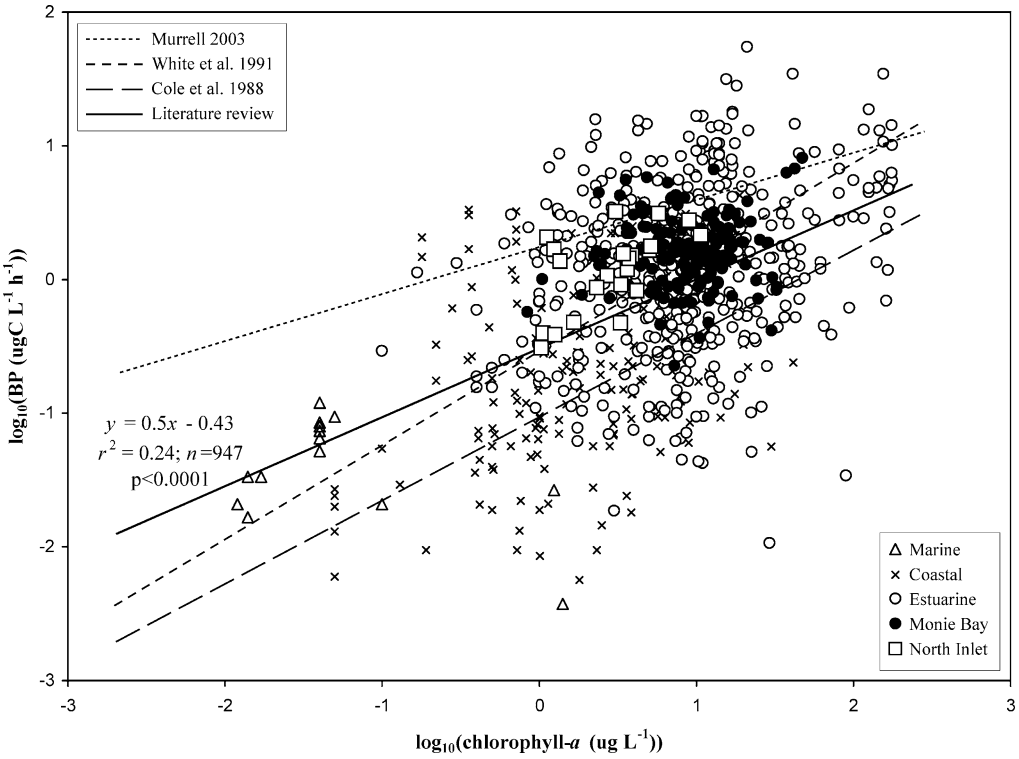


Figure 3. Relationship between BP and CHLA in marine, coastal, and estuarine systems. Data include paired measures of BP and CHLA reported in 33 published studies (Table 2) and collected as part of field sampling in Monie Bay (n = 257) and North Inlet–Winyah Bay (n = 24) reserves. Best fit from least squares regression of the entire composite dataset of literature values is shown (solid line), as are those from other studies (Cole, Findlay, and Pace, 1988; Murrell, 2003; White *et al.,* 1991).

ments for PO_4^{3-} from the entire dataset, 4 of which were in excess of 1.0 mg L^{-1}. A similar pattern was observed for ammonium in this reserve. This enrichment was reflected in DO, with over half of the 40 sampling events within the SWMP dataset that recorded extremely low DO concentrations (*i.e.,* <1 mg L^{-1}) occurring in TJR. Low DO may function as a positive feedback mechanism in this system, with reduced, hypoxic conditions causing the release of sediment-bound phosphate (Scudlark and Church, 1989) and accumulation of water column ammonium (Kemp *et al.,* 1990). Such a relationship between hypoxia and ambient NH_4^+ and PO_4^{3-} concentrations is often attributed to nutrient-driven increases in primary production and subsequent consumption of algal dissolved organic matter by heterotrophic microbes (Cloern, 2001). However, TJR experiences vigorous tidal flushing that prevents the development of persistent algal blooms (Fry, Gace, and McClelland, 2003), and most of the organic matter and nutrients delivered to this system come from raw sewage (Gersberg *et al.,* 2006). The absence of elevated concentrations of organic matter in surface waters discharged from TJR (Zeng, Khan, and Tran, 1997) indicates that most of the inputs of organic matter are removed, leading to the conclusion that low DO conditions in this system are driven by heterotrophic consumption of allochthonous organic matter that is present in the water column or that has been deposited in estuarine sediments. In this regard, TJR represents an extreme example of how excessive inputs of allochthonous organic matter and heterotrophic processes can combine to produce net-heterotrophic conditions and further degrade water quality in estuarine ecosystems.

Covariation of BP and CHLA

The scope and resolution of SWMP data are both extensive and comprehensive, yet the lack of measures of water column respiration, or another index of bacterioplankton community activity in the SWMP data, prevents us from directly addressing the magnitude of heterotrophic processes and their covariation with planktonic autotrophs within the NERRS. Instead, we investigated one aspect of this coherence in estuarine ecosystems using a synthesis of published studies reporting simultaneous measures of BP and CHLA and then compared this with patterns seen in two specific NERRS sites. Studies of the relationship between BP and CHLA have been conducted in a subtropical estuary (*e.g.,* Pensacola Bay; Murrell, 2003) and in reviews of published literature focusing on marine and freshwater systems (Cole, Findlay, and Pace, 1988; White *et al.,* 1991). These have generally reported a positive covariation, with the coherence of BP and CHLA serving as an index of ecosystem status and resource

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

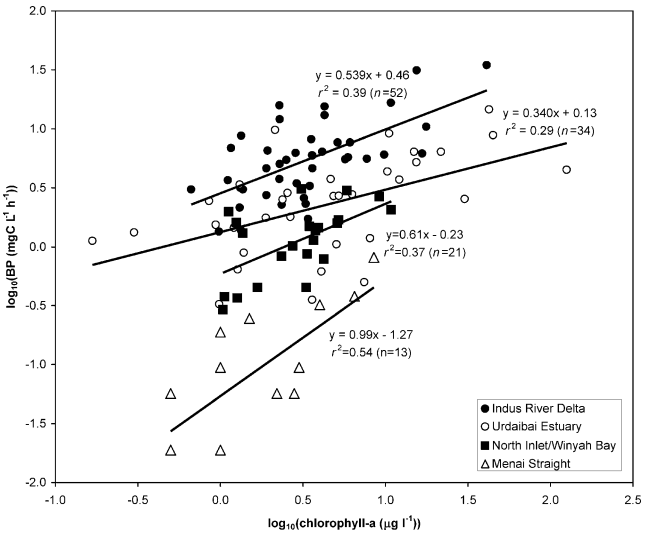


Figure 4. Estuarine systems exhibiting relatively strong covariation of BP and CHLA. All regressions are highly significant (*i.e.,* $p < 0.0001$).

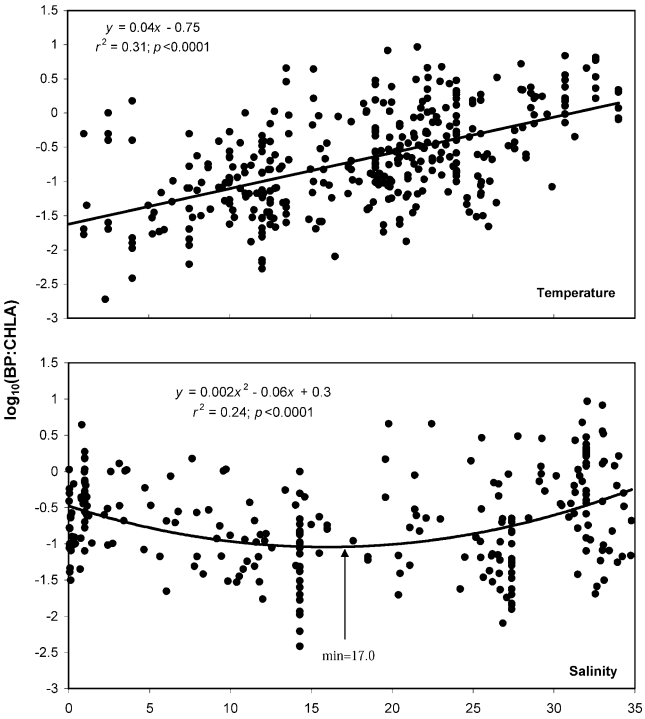


Figure 5. Relationship between log-transformed BP : CHLA ratios and (A) temperature and (B) salinity as independent variables.

supply. Our analysis of studies conducted in estuarine ecosystems also identified a highly significant positive relationship between BP and CHLA that was comparable to that reported by others (Figure 3), with one notable discrepancy being a lower *y*-intercept (*i.e.,* lower BP per unit CHLA) and greater slope when compared to those of MURRELL (2003), suggesting the influence of warmer water temperatures and more direct coupling between BP and CHLA in Pensacola Bay.

Effects of Temperature and Salinity

Based on the primacy of temperature and salinity in driving the variability of environmental conditions in SWMP data and the important role of these parameters in regulating the composition, abundance, and activity of planktonic microbes (APPLE, DEL GIORGIO, and KEMP, 2006; COTTRELL and KIRCHMAN, 2003; LOMAS *et al.,* 2002; MALONE *et al.,* 1988; SMITH and KEMP, 1995), we explored their effect on biological processes using BP : CHLA ratios as a response variable. Our analyses of literature data showed that both temperature and salinity are important factors influencing the covariation of BP and algal biomass, with no evidence that dissolved nutrient concentrations influenced this relationship (analyses not shown). Temperature had a highly significant positive relationship with BP : CHLA ratios (Figure 5A), resulting in a log-linear increase in BP per unit CHLA with increasing temperature. The decreasing exponential relationship (*i.e.,* $\beta < 1$) suggests a decrease in BP relative to CHLA at higher temperatures. Asymptotic temperature responses of BP have recently been reported in estuaries (APPLE, DEL GIORGIO, and KEMP, 2006; MURRELL, 2003) and lakes (FELIP, PACE, and COLE, 1996), which may drive the relationship between temperature and BP : CHLA values. The positive temperature response of BP : CHLA is also in general agreement with the strong temperature dependence of heterotrophic relative to autotrophic microbial processes in a range of estuarine ecosystems (HOCH and KIRCHMAN, 1993; POMEROY *et al.,* 2000; SAMPOU and KEMP, 1994; SHIAH and DUCKLOW, 1997) and the weakened coupling of BP and CHLA (*i.e.,* lower BP per unit CHLA) observed at lower temperatures (HOCH and KIRCHMAN, 1993; SHIAH and DUCKLOW, 1994a).

Salinity was also a significant factor explaining variability in the relationship between BP and CHLA (Figure 5B). The response to salinity was more complex, with a weak (*i.e.,* $r^2 = 0.24$) but significant concave parabolic relationship between salinity and BP : CHLA ratios and lower BP per unit CHLA at intermediate salinities. Based on the first derivative of the second-order polynomial describing this relationship, we estimate this minimum salinity to be approximately 17. The occurrence of lower BP : CHLA ratios at intermediate salinities may be a function of conditions in the middle to lower estuary, where phytoplankton are liberated from light limitation and respond to elevated nutrient concentrations (HARDING, 1994), resulting in an increase in CHLA relative to BP. This pattern may also be driven by lower growth efficiencies at intermediate salinities that result from elevated rates of bacterial respiration and reduced BP and are related to shifts in bacterioplankton phylogeny and/or metabolism associated with changing salinity (BOUVIER and DEL GIORGIO, 2002; CRUMP, AMBRUST, and BAROSS, 1999; DEL GIORGIO and BOUVIER, 2002; YOKOKAWA *et al.,* 2004). In Chesapeake Bay, the apparent negative effect of salinity on the

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

coherence of BP and CHLA may be attributed to the well-documented shift from net heterotrophy in the upper bay to higher phytoplankton biomass and net autotrophy in the lower bay (KEMP *et al.,* 1997). Shifts of this nature in the relationship between BP and CHLA appear to represent a recurring property along salinity gradients across a wide range of estuarine ecosystems, although the mechanisms are not well understood and may differ among estuaries.

System-Specific Patterns in the Covariation of BP and CHLA

Four estuaries emerged where the relationship between BP and CHLA was relatively strong (Figure 4): Indus River Delta (BANO *et al.,* 1997), Menai Strait (BLIGHT *et al.,* 1995), Urdaibai estuary (REVILLA *et al.,* 2000), and North Inlet–Winyah Bay NERRS (present study). These systems were generally more saline (*i.e.,* 22–37) and represent a broad geographic range and estuary types. In general, the covariation of BP and algal biomass was weaker in mesohaline systems, where alternate sources of allochthonous organic matter may undermine the reliance of bacterial metabolism on algal dissolved organic matter, and was stronger in the more saline systems, which have higher ambient water temperatures. Stronger covariation in warmer systems may reflect the important role of temperature in modulating physiological processes and may be a characteristic of the relationship between BP and CHLA in warmer, subtropical regions (MURRELL, 2003). Comparison of the four systems in Figure 4 provides compelling evidence supporting the effect of temperature on the relationship between BP and CHLA. We found a strong and highly significant correlation (*i.e.,* $r = 0.83$, $p < 0.0001$) between study latitude and *y*-intercept, with the highest BP per unit CHLA in the subtropical Indus River Delta (~24°10′ N) and lowest in Menai Strait (~53°10′ N). Despite the apparent temperature-dependent rank order among these four systems, *y*-intercepts from these regressions (including that of Indus River) remained significantly lower than those reported by MURRELL (2003), suggesting that factors other than temperature may be important in regulating the coherence of BP and CHLA in these systems.

Despite lower estimates of BP per unit CHLA, data from Menai Strait exhibited the strongest covariation of BP and CHLA ($r^2 = 0.54$). This marine-dominated system in North Wales experiences frequent phytoplankton blooms and limited inputs of allochthonous organic matter (BLIGHT *et al.,* 1995). MURRELL (2003) also observed strong coherence of BP and CHLA in Pensacola Bay, attributing this to the critical role of phytoplankton-derived substrates in supporting bacterioplankton metabolism. Indeed, the slope of the relationship between log-transformed data from this system indicates a steep increase in BP relative to CHLA at relatively low concentrations and thereby suggests a tighter coupling of BP to CHLA in this system. Similarly, we speculate that the coherence of BP and CHLA in Menai Strait represents a more direct trophic coupling of BP to algal dissolved organic matter, with the caveat that comparatively low estimates of BP per unit CHLA were observed in Menai Strait resulting from the modulating effect of lower water temperatures on the metabolic response of bacterioplankton to substrate supply (APPLE, DEL GIORGIO, and KEMP, 2006; SHIAH and DUCKLOW, 1994a). Such direct coupling did not appear to drive the covariation of BP and CHLA in other systems, where the two parameters exhibited strong coherence. Urdaibai estuary is a turbid, nutrient-enriched environment in northern Spain where bacterioplankton carbon demand is subsidized by anthropogenic inputs of organic wastes (REVILLA *et al.,* 2000). Covariation of BP and CHLA in this system most likely results from the absence of nutrient limitation for algal and bacterial growth, combined with subsidy of the latter by inputs of allochthonous organic matter. Similar conditions may exist in the eutrophic Indus River Delta in Pakistan, where over 80% of bacterioplankton carbon demand is derived from allochthonous sources (BANO *et al.,* 1997).

Comparison of Monie Bay and North Inlet

North Inlet and Monie Bay are temperate, tidally influenced coastal plain estuaries and thus share many characteristics, including an extensive network of tidal creeks, *Spartina*-dominated fringing marshes, and seasonal fluctuations in temperature characteristics of temperate climates. In this regard, the striking difference in the strength of the BP *vs.* CHLA relationship between these two systems was surprising. However, there are important contrasts between North Inlet and Monie Bay that may help explain this difference. Connectivity with coastal ocean waters is more direct in North Inlet, as indicated by its relatively high mean annual salinity (24) compared to that of Monie Bay (7.4), where water is exchanged with the mesohaline portion of Chesapeake Bay. The different water masses adjacent to Monie Bay and North Inlet lead to differences in concentration and composition of dissolved organic matter as well, with annual mean dissolved organic carbon content of floodwaters in Monie Bay being twice that of North Inlet (*i.e.,* 756 *vs.* 366 μM, respectively). Furthermore, Monie Bay drains a much more extensive and agriculturally developed upland, with dissolved organic matter absorption coefficients—an index of terrestrial organic matter (MCKNIGHT *et al.,* 2001)—being an order of magnitude higher in Monie Bay relative to North Inlet (*i.e.,* 16.1 *vs.* 1.9 m^{-1}). Monie Bay is thus a more nutrient- and organic-rich system than North Inlet, with more diverse sources of organic matter input. As a result, and despite higher annual mean CHLA in Monie Bay (10.4 μg L^{-1}) relative to North Inlet (7.9 μg L^{-1}), bacterioplankton in this resource-rich system are not metabolically linked to CHLA as tightly as in systems where autochthonous dissolved organic matter comprises a greater fraction of bacterioplankton carbon demand.

North Inlet also experiences relatively high mean tidal amplitude (1.5 m) and short residence time (~15 h), with as much as 40% of the total water volume leaving the estuary with each ebb tide (GARDNER, KJERFVE, and PETRECCA, 2006). In contrast, Monie Bay has half the mean tidal amplitude (0.7 m) of North Inlet and much longer water residence times (APPLE, DEL GIORGIO, and NEWELL, 2004). Longer residence times in Monie Bay ensure that the inputs of dissolved organic matter are also retained in the estuary lon-

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

ger. Organic matter bioavailability at the ecosystem scale is a function of its inherent decomposition rate relative its residence time in that ecosystem. Increased residence time thus extends the temporal scales beyond which BP and phytoplankton production can be linked, which may not be reflected in static observations based on CHLA. Thus, not only are the quantity and diversity of organic matter inputs greater in Monie Bay than in North Inlet but the timescale of its availability to bacterial consumers, for both autochthonous and allochthonous inputs, is also longer. Collectively, these differences in substrate availability and composition conspire to undermine the coherence of BP and CHLA in Monie Bay.

Temperature is another important difference between North Inlet and Monie Bay; as discussed earlier, it also influences the BP *vs.* CHLA relationship in these systems. A number of studies across a range of aquatic systems have reported a shift in the regulation of bacterioplankton metabolism from temperature dependence to resource dependence with increasing temperature, with the influence of resource supply being more important than the constraints of temperature above approximately 20°C (Apple, del Giorgio, and Kemp, 2006; Felip, Pace, and Cole, 1996; Hall and Cotner, 2007; López-Urrutia and Morán, 2007). This leads to the influence of organic matter quality and degradability becoming more important at warmer temperatures. In this regard, the absolute difference in mean annual temperature between Monie Bay and North Inlet may not be as relevant as the difference in the amount of time bacteria are exposed to temperatures above this threshold. Water temperatures in North Inlet were above 20°C for 49% of the year, compared to only 27% of the year in Monie Bay, resulting in a discrepancy of 84 days. Thus, bacterioplankton occurred at water temperatures where they were able to respond quickly to algal dissolved organic matter. Water temperatures were well above 20°C during the time the present data were collected for North Inlet, although continuing measurements (E.M. Smith, unpublished data) indicate the significant relationship holds across seasons as well. However, despite 2 years of biweekly sampling of Monie Bay during summer months, strong coherence of BP and CHLA was never identified, suggesting that removal of the metabolic constraints imposed by lower temperatures is not enough to induce coupling and further implicates the influence of allochthonous organic matter sources on the covariation of BP and CHLA.

Our evaluation of systems in which BP and CHLA are more coherent (Figure 4) led to the conclusion that the BP *vs.* CHLA relationship is stronger in warmer, more saline waters. The comparison of Monie Bay and North Inlet corroborates this pattern, as mean annual water temperature (*i.e.,* 20°C *vs.* 17°C) and salinity are higher in North Inlet than in Monie Bay. However, this may not necessarily result from the direct effect of salinity and temperature alone on the coherence of BP and CHLA but, rather, from the changing importance of resource supply vs. temperature in regulating bacterioplankton carbon metabolism at different temperature regimes and differences in sources of organic matter substrates between these systems.

Covariation of BP and CHLA: Additional Influencing Factors

It is generally assumed that strong covariation of BP and CHLA results from direct subsidy of bacterioplankton carbon demand by production of algal dissolved organic matter (*e.g.,* Baines and Pace, 1991), with the strength of the BP *vs.* CHLA relationship reflecting the extent of this coupling. However, covariation of BP and CHLA may also occur if both bacterioplankton metabolism and phytoplankton biomass are simultaneously yet independently regulated by an external factor, such as inorganic nutrient availability (*e.g.,* Coveney and Wetzel, 1995; Smith and Kemp, 2003; Vrede *et al.,* 1999). Under such circumstances, nutrients subsidize algal production while bacterioplankton combine nutrients with allochthonous (*i.e.,* nonalgal) sources of organic matter to fuel growth, evidence of which was observed in the studies discussed earlier (*i.e.,* Bano *et al.,* 1997; Revilla *et al.,* 2000). The independent but proportional effect of nutrients on BP and CHLA may explain why we failed to observe a relationship between dissolved nutrient concentrations and BP : CHLA ratios, because if BP and CHLA increase proportionally along a eutrophication or nutrient gradient, BP : CHLA will remain relatively unchanged. In this regard, we observed a weak but highly significant correlation between PO_4^{3-} and both BP and CHLA (*i.e.,* $r = 0.27$ and 0.22, respectively; $n = 450$), yet no relationship between PO_4^{3-} and BP : CHLA ratios. PCA revealed grouping of CHLA with NH_4^+, PO_4^{3-}, and turbidity, with NH_4^+ and PO_4^{3-} likely driving increases in CHLA concentrations and turbidity increasing as a result. The absence of a correlation between BP and dissolved nutrients in PCA of literature data attests to the overwhelming effect of temperature in driving heterotrophic relative to autotrophic processes.

The relationship observed between BP and CHLA was significant yet surrounded by considerable scatter and thus relatively weak ($r^2 = 0.24$). Although salinity and temperature explain some of this variability, there are additional factors that were not investigated as part of our study or were not included in the composite dataset that might further explain this variability. The covariation of BP to algal biomass can be influenced by temporal lags between primary production and availability of algal substrates for consumption by bacterioplankton (Billen, 1990), reliance of BP on nonalgal substrates (Baines and Pace, 1991; Bano, Moran, and Hodson, 1997), differences in extracellular organic carbon release per unit primary production (Baines and Pace, 1991), and direct (and disproportional relative to phytoplankton) effect of nutrients on bacterioplankton production (Vrede *et al.,* 1999). Coherence between BP and CHLA may also be undermined by variability in bacterial growth efficiency (del Giorgio and Cole, 1998), high turbidity (Pomeroy *et al.,* 2000), allochthonous inputs of organic matter (Hoch and Kirchman, 1993; Revilla *et al.,* 2000), and disproportionate effect of temperature on bacteria relative to phytoplankton (Shiah and Ducklow, 1994a). The extent to which measurements of CHLA accurately represent *in situ* algal biomass and production may also be compromised by variability in the carbon-to-chlorophyll ratio of phytoplankton (Cloern,

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

1995), contribution of accessory pigments to primary production (MARRA, TREES, and O'REILLY, 2007), and variability in the strength of autotrophic–heterotrophic coupling that appears to be a function of the average cell size and/or composition of the phytoplankton community (SERRET *et al.,* 2001; SMITH and KEMP, 2001). Although an investigation of these factors is beyond the scope of this study, it is important to recognize the limitations of using BP : CHLA ratios as an index of the coupling between heterotrophic and autotrophic plankton communities.

CONCLUSIONS

Our analyses identified salinity and temperature as important factors shaping the variability in both SWMP data and BP : CHLA ratios, yet the mechanisms underlying their role in shaping water quality parameters vs. the relationship between BP and CHLA are distinct. For example, the negative covariation of salinity and NO_x suggests that it is not salinity alone but also nitrogen loading associated with freshwater inputs that drive variability in SWMP data. In contrast, the influence of salinity on BP : CHLA ratios most likely reflects spatial patterns in the balance of heterotrophic and autotrophic processes along the estuarine gradient. The chemical and biological dependence of water column DO on temperature explains the primacy of this parameter as a driver of variability in SWMP data, whereas it is the disproportionate effect of temperature on heterotrophic relative to autotrophic processes that drives the temperature dependence of BP : CHLA. Inputs of allochthonous organic matter and dissolved nutrients are closely linked to salinity and temperature and subsequent changes in water quality, as these serve as tracers for inputs and drivers of metabolism, respectively. In this regard, the ability to use SWMP to track and predict aspects of water quality would be greatly enhanced by including measures of dissolved and particulate carbon, as well as total nutrients. Much greater ecological understanding would, of course, be gained through a systematic inclusion of ecologically relevant process measurements in SWMP. Given the net-heterotrophic status of most NERRS sites, integrative measures of bacterial community activity would be one logical place to begin.

Collectively, the NERRS represents a diverse array of estuaries that differ significantly with respect to the magnitude and range of *in situ* environmental conditions. It is thus difficult to categorize these systems in a manner that allows straightforward yet accurate comparisons among other reserves and other non-NERRS estuaries. Analysis of SWMP data using PCA identifies the primary sources of variability in each reserve and as such creates an integrative comparison of environmental conditions and valuable classification framework. Comparison of reserves using PCA-related analyses provides insight into the extent to which conclusions drawn from research conducted in one reserve might be applicable to another and into predicting the response of reserves to a particular stressor (KURTZ *et al.,* 2006). This framework for comparison also helps isolate outlier reserves or those exhibiting unique physicochemical properties, as with the relationship between temperature and DO in Kachemak Bay and Tijuana River. Analyses of this nature can provide a mechanism for moving from basic monitoring of the reserves into hypotheses-driven studies regarding the factors that regulate physical, chemical, and biological processes in these and other estuarine systems.

ACKNOWLEDGMENTS

This research was funded in part by grants from the NERRS Graduate Research Fellowship Program, Cooperative Institute for Coastal and Estuarine Environmental Technology, and Baruch Marine Research Institute Visiting Scientist Award. We thank D. Miller, M. Kemp, and R. Newell for revisions during the development of this manuscript and the panel of anonymous reviewers for their time, effort, and valuable contributions. We also acknowledge the contribution of additional data from D. Kirchman, P. del Giorgio, T. Bouvier, E. Koepfler, and D. Vaqué (Hivern project; Grant No. MAR98-0932 to M. Estrada).

LITERATURE CITED

ANDERSON, T.H. and TAYLOR, G.T., 2001. Nutrient pulses, plankton blooms, and seasonal hypoxia in western Long Island Sound. *Estuaries,* 24, 228–243.

APPLE, J.K.; DEL GIORGIO, P.A., and KEMP, W.M., 2006. Temperature regulation of bacterial production, respiration, and growth efficiency in estuarine systems. *Aquatic Microbial Ecology,* 43, 243–254.

APPLE, J.K.; DEL GIORGIO, P.A., and NEWELL, R.I.E., 2004. The effect of system-level nutrient enrichment on bacterioplankton production in a tidally influenced estuary. *Journal of Coastal Research,* 45, 110–133.

BAINES, S.B. and PACE, M.L., 1991. The production of dissolved organic matter by phytoplankton and its importance to bacteria: patterns across marine and freshwater systems. *Limnology and Oceanography,* 36, 1078–1090.

BANO, N.; MORAN, M.A., and HODSON, R.E., 1997. Bacterial utilization of dissolved humic substances from a freshwater swamp. *Aquatic Microbial Ecology,* 12, 233–238.

BANO, N.; NISA, M.; KHAN, N.; SALEEM, M.; HARRISON, P.J.; AHMED, S., and AZAM, F., 1997. Significance of bacteria in the flux of organic matter in the tidal creeks of the mangrove ecosystem of the Indus River Delta, Pakistan. *Marine Ecology Progress Series,* 157, 1–12.

BILLEN, G., 1990. Delayed development of bacterioplankton with respect to phytoplankton: a clue for understanding their trophic relationships. *Archiv für Hydrobiologie Beiheft Ergebnisse der Limnologie,* 34, 191–201.

BILLEN, G. and BECQUEVORT, S., 1990. Phytoplankton–bacteria relationship in the Antarctic marine ecosystem. *Polar Research,* 10, 245–253.

BJØRNSEN, P.K.; RIEMANN, B.; POCK-STEEN, J.; NIELSEN, T.G., and HORSTED, S.J., 1989. Regulation of bacterioplankton production and cell volume in a eutrophic estuary. *Applied and Environmental Microbiology,* 55, 1512–1518.

BLIGHT, S.P.; BENTLEY, T.L.; LEFEVRE, D.; ROBINSON, C.; RODRIGUES, R.; ROWLAND, J., and WILLIAMS, P.J.L.B., 1995. Phasing of autotrophic and heterotrophic plankton metabolism in a temperate coastal ecosystem. *Marine Ecology Progress Series,* 128, 61–75.

BODE, A.; BARQUERO, S.; VARELA, M.; BRAUN, J.G., and DE ARMAS, D., 2001. Pelagic bacteria and phytoplankton in oceanic waters near the Canary Islands in summer. *Marine Ecology Progress Series,* 209, 1–17.

BOUVIER, T.C. and DEL GIORGIO, P.A., 2002. Compositional changes in free-living bacterial communities along a salinity gradient in

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

two temperate estuaries. *Limnology and Oceanography,* 47, 453–470.

Buzzelli, C.; Akman, O.; Buck, T.; Koepfler, E.; Morris, J., and Lewitus, A., 2004. Relationships among water-quality parameters from the North Inlet–Winyah Bay National Estuarine Research Reserve, South Carolina. *Journal of Coastal Research,* Special Issue No. 45, pp. 59–74.

Caffrey, J.M., 2004. Factors controlling net ecosystem metabolism in U.S. estuaries. *Estuaries,* 27, 90–101.

Carlsson, P.; Graneli, E., and Segatto, A.Z., 1999. Cycling of biologically available nitrogen in riverine humic substances between marine bacteria, a heterotrophic nanoflagellate and a photosynthetic dinoflagellate. *Aquatic Microbial Ecology,* 18, 23–36.

Caron, D.A.; Lim, E.L.; Sanders, R.W.; Dennett, M.R., and Berninger, U.G., 2000. Responses of bacterioplankton and phytoplankton to organic carbon and inorganic nutrient additions in contrasting oceanic ecosystems. *Aquatic Microbial Ecology,* 22, 175–184.

Cloern, J., 1995. An empirical model of the phytoplankton chlorophyll:carbon ratio: the conversion factor between productivity and growth rate. *Limnology and Oceanography,* 40, 1313–1321.

Cloern, J., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series,* 210, 223–253.

Cole, J.J.; Findlay, S., and Pace, M.L., 1988. Bacterial production in fresh and saltwater ecosystems: a cross system overview. *Marine Ecology Progress Series,* 43, 1–10.

Conan, P.; Turley, C.; Stutt, E.; Pujo-Pay, M., and Van Wambeke, F., 1999. Relationship between phytoplankton efficiency and the proportion of bacterial production to primary production in the Mediterranean Sea. *Aquatic Microbial Ecology,* 17, 131–144.

Cotner, J.B.; Sada, R.H.; Bootsma, H.; Johengen, T.; Cavaletto, J.F., and Gardner, W.S., 2000. Nutrient limitation of heterotrophic bacteria in Florida Bay. *Estuaries,* 23, 611–620.

Cottrell, M.T. and Kirchman, D.L., 2003. Contribution of major bacterial groups to bacterial biomass production (thymidine and leucine incorporation) in the Delaware estuary. *Limnology and Oceanography,* 48, 168–178.

Coveney, M.F. and Wetzel, R.G., 1995. Biomass, production, and specific growth rate of bacterioplankton and coupling to phytoplankton in an oligotrophic lake. *Limnology and Oceanography,* 40, 1187–1200.

Cowan, J.L.W. and Boynton, W.R., 1996. Sediment–water oxygen and nutrient exchanges along the longitudinal axis of Chesapeake Bay: seasonal patterns, controlling factors, and ecological significance. *Estuaries,* 19, 562–580.

Crump, B.C.; Armbrust, E.V., and Baross, J.A., 1999. Phylogenetic analysis of particle-attached and free-living bacterial communities in the Columbia River, its estuary, and the adjacent coastal ocean. *Applied and Environmental Microbiology,* 65, 3192–3204.

Day, J.W.J.; Hall, C.A.S.; Kemp, W.M., and Yanez-Arancibia, A., 1989. *Estuarine Ecology.* New York: John Wiley and Sons.

del Giorgio, P.A. and Bouvier, T.C., 2002. Linking the physiologic and phylogenetic successions in free-living bacterial communities along an estuarine salinity gradient. *Limnology and Oceanography,* 47, 471–486.

del Giorgio, P.A. and Cole, J.J., 1998. Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics,* 29, 503–541.

Ducklow, H.W.; Kirchman, D.L., and Anderson, T.R., 2002. The magnitude of spring bacterial production in the North Atlantic Ocean. *Limnology and Oceanography,* 47, 1684–1693.

Felip, M.; Pace, M.L., and Cole, J.J., 1996. Regulation of planktonic bacterial growth rates: the effects of temperature and resources. *Microbial Ecology,* 31, 15–28.

Fry, B.; Gace, A., and McClelland, J.W., 2003. Chemical indicators of anthropogenic nitrogen loading in four Pacific estuaries. *Pacific Science,* 57, 77–101.

Gardner, L.R.; Kjerfve, B., and Petrecca, D.M., 2006. Tidal fluxes of dissolved oxygen at the North Inlet–Winyah Bay National Estuarine Research Reserve. *Estuarine Coastal and Shelf Science,* 67, 450–460.

Gersberg, R.M.; Rose, M.A.; Robles-Sikisaka, R., and Dhar, A.K., 2006. Quantitative detection of hepatitis a virus and enteroviruses near the United States–Mexico border and correlation with levels of fecal indicator bacteria. *Applied and Environmental Microbiology,* 72, 7438–7444.

Griffith, P.; Shiah, F.K.; Gloersen, K.; Ducklow, H.W., and Fletcher, M., 1994. Activity and distribution of attached bacteria in Chesapeake Bay. *Marine Ecology Progress Series,* 108, 1–10.

Hall, E.K. and Cotner, J.B., 2007. Interactive effect of temperature and resources on carbon cycling by freshwater bacterioplankton communities. *Aquatic Microbial Ecology,* 49, 35–45.

Harding, L.W., 1994. Long-term trends in the distribution of phytoplankton in Chesapeake Bay: roles of light, nutrients and streamflow. *Marine Ecology Progress Series,* 104, 267–291.

Harding, L.W.; Meeson, B.W., Jr., and Fisher, T.R., Jr., 1986. Phytoplankton production in two East Coast estuaries: photosynthesis–light functions and patterns of carbon assimilation in Chesapeake and Delaware bays. *Estuarine Coastal and Shelf Science,* 23, 773–806.

Hoch, M.P. and Kirchman, D.L., 1993. Seasonal and interannual variability in bacterial production and biomass in a temperate estuary. *Marine Ecology Progress Series,* 98, 283–295.

Hopkinson, C.S., Jr., and Smith, E.M., 2005. Estuarine respiration: an overview of benthic, pelagic and whole system respiration. *In:* del Giorgio, P.A. and Williams, P.J.B., (eds.), *Respiration in Aquatic Ecosystems.* Oxford: Oxford University Press, pp. 122–146.

Hoppe, H.G.; Giesenhagen, H.C., and Gocke, K., 1998. Changing patterns of bacterial substrate decomposition in an eutrophication gradient. *Aquatic Microbial Ecology,* 15, 1–13.

Kemp, W.M.; Boynton, W.R.; Adolf, J.E.; Boesch, D.F.; Boicourt, W.C.; Brush, G.; Cornwell, J.C.; Fisher, T.R.; Glibert, P.M.; Hagy, J.D.; Harding, L.W.; Houde, E.D.; Kimmel, D.G.; Miller, W.D.; Newell, R.I.E.; Roman, M.R.; Smith, E.M., and Stevenson, J.C., 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series,* 303, 1–29.

Kemp, W.M.; Sampou, P.; Caffrey, J.; Mayer, M.; Henriksen, K., and Boynton, W.R., 1990. Ammonium recycling versus denitrification in Chesapeake Bay sediments. *Limnology and Oceanography,* 35, 1545–1563.

Kemp, W.M.; Sampou, P.A.; Garber, J.; Tuttle, J., and Boynton, W.R., 1992. Seasonal depletion of oxygen from bottom waters of Chesapeake Bay: roles of benthic and planktonic respiration and physical exchange processes. *Marine Ecology Progress Series,* 85, 137–152.

Kemp, W.M.; Smith, E.M.; Marvin-Dipasquale, M., and Boynton, W.R., 1997. Organic carbon balance and net ecosystem metabolism in Chesapeake Bay. *Marine Ecology Progress Series,* 150, 229–248.

Kennish, M.J., 1992. *Ecology of Estuaries: Physical and Chemical Aspects.* Boca Raton, Florida: CRC Press.

Kennish, M.J., 2004. NERRS research and monitoring initiatives. *Journal of Coastal Research,* Special Issue No. 45, pp. 1–8.

Kirchman, D.L., 1993. Leucine incorporation as a measure of biomass production by heterotrophic bacteria. *In:* Kemp, P.F.; Sherr, B.F.; Sherr, E.B., and Cole, J.J. (eds.), *Handbook of Methods in Aquatic Microbial Ecology.* Boca Raton, Florida: CRC Press, chapter 58.

Kirchman, D.L.; Soto, Y.; Van Wambeck, F., and Bianchi, M., 1989. Bacterial production in the Rhone River plume: effect of mixing on relationships among microbial assemblages. *Marine Ecology Progress Series,* 53, 267–275.

Koepfler, E.T.; Kator, H.I.; Wetzel, R.L.; Haas, L.W., and Webb, K.L., 1993. Spatial and temporal bacterioplankton dynamics during destratification of the James River estuary, Virginia, U.S.A. *Marine Ecology Progress Series,* 102, 229–244.

Kononen, K.; Haellfors, S.; Kokkonen, M.; Kuosa, H.; Laanemets, J.; Pavelson, J., and Autio, R., 1998. Development of

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

a subsurface chlorophyll maximum at the entrance to the Gulf of Finland, Baltic Sea. *Limnology and Oceanography,* 43, 1089–1106.
KRSTULOVIC, N.; SOLIC, M., and MARASOVIC, I., 1997. Relationship between bacteria, phytoplankton and heterotrophic nanoflagellates along the trophic gradient. *Helgolander Meeresuntersuchungen Hamburg,* 51, 433–443.
KURTZ, J.C.; DETENBECK, N.D.; ENGLE, V.D.; HO, K.; SMITH, L.M.; JORDAN, S.J., and CAMPBELL, D., 2006. Classifying coastal waters: current necessity and historical perspective. *Estuaries and Coasts,* 29, 107–123.
LANCELOT, C. and BILLEN, G., 1984. Activity of heterotrophic bacteria and its coupling to primary production during the spring phytoplankton bloom in the Southern Bight of the North Sea. *Limnology and Oceanography,* 29, 721–730.
LEE, S. and FUHRMAN, J.A., 1987. Relationships between biovolume and biomass of naturally derived marine bacterioplankton. *Applied and Environmental Microbiology,* 53, 1298–1303.
LIGNELL, R., 1990. Excretion of organic carbon by phytoplankton: its relation to algal biomass, primary productivity and bacterial secondary productivity in the Baltic Sea. *Marine Ecology Progress Series,* 68, 85–99.
LOMAS, M.W.; GLIBERT, P.M.; SHIAH, F., and SMITH, E.M., 2002. Microbial processes and temperature in Chesapeake Bay: current relationships and potential impacts of regional warming. *Global Change Biology,* 8, 51–70.
LÓPEZ-URRUTIA, Á. and MORÁN, X.A.G., 2007. Resource limitation of bacterial production distorts the temperature dependence of oceanic carbon cycling. *Ecology,* 88, 817–822.
LOVEJOY, C.; LEGENDRE, L.; KLEIN, B.; TREMBLAY, J.E.; INGRAM, R.G., and THERRIAULT, J.C., 1996. Bacterial activity during early winter mixing (Gulf of St. Lawrence, Canada). *Aquatic Microbial Ecology,* 10, 1–13.
MALONE, T.C.; CROCKER, L.H.; PIKE, S.E., and WENDLER, B.W., 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. *Marine Ecology Progress Series,* 48, 235–249.
MARRA, J.; TREES, C.C., and O'REILLY, J.E., 2007. Phytoplankton pigment absorption: a strong predictor of primary productivity in the surface ocean. *Deep Sea Research Part I: Oceanographic Research Papers,* 54, 155–163.
MCKNIGHT, D.M.; BOYER, E.W.; WESTERHOFF, P.K.; DORAN, P.T.; KULBE, T., and ANDERSON, D.T., 2001. Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material and aromaticity. *Limnology and Oceanography,* 46, 38–48.
MORÁN, X.A.G.; ESTRADA, M.; GASOL, J.M., and PEDROS-ALIO, C., 2002. Dissolved primary production and the strength of phytoplankton bacterioplankton coupling in contrasting marine regions. *Microbial Ecology,* 44, 217–223.
MURRELL, M.C., 2003. Bacterioplankton dynamics in a subtropical estuary: evidence for substrate limitation. *Aquatic Microbial Ecology,* 32, 239–250.
NAGANUMA, T. and MIURA, S., 1997. Abundance, production and viability of bacterioplankton in the Seto Inland Sea, Japan. *Journal of Oceanography,* 53, 435–442.
PAERL, H.; PINCKNEY, J.; FEAR, J.M., and PEIERLS, B., 1998. Ecosystem responses to internal and watershed organic matter loading: consequences for hypoxia in the eutrophying Neuse River estuary, North Carolina, U.S.A. *Marine Ecology Progress Series,* 166, 17–25.
PAKULSKI, J.D.; BENNER, R.; WHITLEDGE, T.C.; AMON, R.; EADIE, B.; CIFUENTES, L.A.; AMMERMAN, J.W., and STOCKWELL, D., 2000. Microbial metabolism and nutrient cycling in the Mississippi and Atchafalaya river plumes. *Estuarine Coastal and Shelf Science,* 50, 173–184.
POMEROY, L.R.; SHELDON, J.E.; SHELDON, W.M.; BLANTON, J.O.; AMFT, J., and PETERS, F., 2000. Seasonal changes in microbial processes in estuarine and continental shelf waters of the southeastern U.S.A. *Estuarine Coastal and Shelf Science,* 51, 415–428.
PRADEEP RAM, A.S.; NAIR, S., and CHANDRAMOHAN, D., 2003. Bacterial growth efficiency in the tropical estuarine and coastal waters of Goa, southwest coast of India. *Microbial Ecology,* 45, 88–96.
RAYMOND, P.A. and BAUER, J.E., 2000. Bacterial consumption of DOC during transport through a temperate estuary. *Aquatic Microbial Ecology,* 22, 1–12.
REVILLA, M.; IRIARTA, A.; MADARIAGA, I., and ORIVE, E., 2000. Bacterial and phytoplankton dynamics along a trophic gradient in a shallow temperate estuary. *Estuarine Coastal and Shelf Science,* 50, 297–313.
ROBERTSON, A.; DIXON, P., and ALONGI, D., 1998. The influence of fluvial discharge on pelagic production in the Gulf of Papua, northern Coral Sea. *Estuarine Coastal and Shelf Science,* 46, 319–331.
SAMPOU, P. and KEMP, W.M., 1994. Factors regulating plankton community respiration in Chesapeake Bay. *Marine Ecology Progress Series,* 110, 249–258.
SCUDLARK, J.R. and CHURCH, T.M., 1989. The sedimentary flux of nutrients at a Delaware salt-marsh site: a geochemical perspective. *Biogeochemistry,* 7, 55–75.
SERRET, P.; ROBINSON, C.; FERNANDEZ, E.; TEIRA, E., and TILSTONE, G., 2001. Latitudinal variation of the balance between plankton photosynthesis and respiration in the eastern Atlantic Ocean. *Limnology and Oceanography,* 46, 1642–1652.
SHERR, E.B. and SHERR, B.F., 2001. Mesoscale variability in bacterial activity in the northeast Pacific Ocean off Oregon, U.S.A. *Aquatic Microbial Ecology,* 25, 21–30.
SHIAH, F.K. and DUCKLOW, H.W., 1994a. Temperature regulation of heterotrophic bacterioplankton abundance, production, and specific growth rate in Chesapeake Bay. *Limnology and Oceanography,* 39, 1243–1258.
SHIAH, F.K. and DUCKLOW, H.W., 1994b. Temperature and substrate regulation of bacterial abundance, production and specific growth rate in Chesapeake Bay, U.S.A. *Marine Ecology Progress Series,* 103, 297–308.
SHIAH, F.K. and DUCKLOW, H.W., 1997. Bacterioplankton growth responses to temperature and chlorophyll variations in estuaries measured by thymidine:leucine incorporation ratio. *Aquatic Microbial Ecology,* 13, 151–159.
SIMON, M. and AZAM, F., 1989. Protein content and protein synthesis rates of planktonic marine bacteria. *Marine Ecology Progress Series,* 51, 201–213.
SMITH, E.M., 2000. Factors regulating respiration and its coupling to primary production in a coastal planktonic community. College Park: University of Maryland, 285p.
SMITH, E.M. and KEMP, W.M., 1995. Seasonal and regional variations in plankton community production and respiration for Chesapeake Bay. *Marine Ecology Progress Series,* 116, 217–231.
SMITH, E.M. and KEMP, W.M., 2001. Size structure and the production/respiration balance in a coastal plankton community. *Limnology and Oceanography,* 46, 473–485.
SMITH, E.M. and KEMP, W.M., 2003. Planktonic and bacterial respiration along an estuarine gradient: responses to carbon and nutrient enrichment. *Aquatic Microbial Ecology,* 30, 251–261.
TUOMI, P. and KUUPPO, P., 1999. Viral lysis and grazing loss of bacteria in nutrient- and carbon-manipulated brackish water enclosures. *Journal of Plankton Research,* 21, 923–937.
VAN WAMBEKE, F.; GOUTX, M.; STRIBY, L.; SEMPERE, R., and VIDUSSI, F., 2001. Bacterial dynamics during the transition from spring bloom to oligotrophy in the northwestern Mediterranean Sea: relationships with particulate detritus and dissolved organic matter. *Marine Ecology Progress Series,* 212, 89–105.
VAQUÉ, D.; CASAMAYOR, E.O., and GASOL, J.M., 2001. Dynamics of whole community bacterial production and grazing losses in seawater incubations as related to the changes in the proportions of bacteria with different DNA content. *Aquatic Microbial Ecology,* 25, 163–177.
VINCENT, W.F.; DODSON, J.J.; BERTRAND, N., and FRENETTE, J., 1996. Photosynthetic and bacterial production gradients in a larval fish nursery: the St. Lawrence River transition zone. *Marine Ecology Progress Series,* 139, 227–238.
VREDE, K.; VREDE, T.; TISAKSSON, A., and KARLSSON, A., 1999. Effects of nutrients (P,N,C) and zooplankton on bacterioplankton

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

and phytoplankton: a seasonal study. *Limnology and Oceanography,* 44, 1616–1624.

WENNER, E.; SANGER, D.; ARENDT, M.; HOLLAND, A.F., and CHEN, Y., 2004. Variability in dissolved oxygen and other water-quality variables within the National Estuarine Research Reserve System. *Journal of Coastal Research,* Special Issue No. 45, pp. 17–38.

WHITE, P.A.; KALFF, J.; RASMUSSEN, J.B., and GASOL, J.M., 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. *Microbial Ecology,* 21, 99–118.

WITEK, Z.; OCHOCKI, S.; MACIEJOWSKA, M.; PASTUZAK, M., and NAKONIECZNY, J., 1997. Phytoplankton primary production and its utilization by the pelagic community in the coastal zone of the Gulf of Gdansk (southern Baltic). *Marine Ecology Progress Series,* 148, 169–186.

YOKOKAWA, T.; NAGATA, T.; COTTRELL, M.T., and KIRCHMAN, D.L., 2004. Growth rate of the major phylogenetic bacterial groups in the Delaware estuary. *Limnology and Oceanography,* 49, 1620–1629.

ZENG, E.Y.; KHAN, A.R., and TRAN, K., 1997. Organic pollutants in the coastal marine environment off San Diego, California: 3. Using linear alkylbenzenes to trace sewage-derived organic materials. *Environmental Toxicology and Chemistry,* 16, 196–201.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Coastal-Research on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use