

- directional diapycnal mixing in the front between North and South Atlantic Central Water. *J. Geophys. Res.* **C99**: 25,175–25,280.
- KÖRTZINGER, A., L. MINTROP, AND J. C. DUINKER. 1998. On the penetration of anthropogenic CO₂ into the North Atlantic Ocean. *J. Geophys. Res.* **103**: 18,681–18,689.
- , W. KOEVE, P. KÄHLER, AND L. MINTROP. 2001. C:N ratios in the mixed layer during the productive season in the northeast Atlantic Ocean. *Deep-Sea Res. I* **48**: 661–688.
- MARTIN, J. H., G. A. KNAUER, D. M. KARL, AND W. W. BROENKOW. 1987. VERTEX: Carbon cycling in the northeast Pacific. *Deep-Sea Res.* **34**: 267–285.
- MCCARTNEY, M. S., AND L. D. TALLEY. 1982. The subpolar mode water of the North Atlantic Ocean. *J. Phys. Oceanogr.* **12**: 1169–1188.
- MILLERO, F. J., K. LEE, AND M. ROCHE. 1998. Distribution of alkalinity in the surface waters of the major oceans. *Mar. Chem.* **60**: 111–130.
- MINSTER, J.-F., AND M. BOULAHIDJ. 1987. Redfield ratios along isopycnal surfaces—a complementary study. *Deep-Sea Res.* **34**: 1981–2003.
- POLLARD, R. T., M. J. GRIFFITH, S. A. CUNNINGHAM, J. F. READ, F. F. PÉREZ, AND A. F. RÍOS. 1996. Vivaldi 1991—a study of the formation, circulation and ventilation of eastern North Atlantic Central Water. *Prog. Oceanogr.* **37**: 167–192.
- REDFIELD, A. C., B. H. KETCHUM, AND F. A. RICHARDS. 1963. The influence of organisms on the composition of sea water, p. 26–77. *In* M. N. Hill [ed.], *The Sea*. Interscience.
- RÍOS, A. F., F. FRAGA, AND F. F. PÉREZ. 1989. Estimation of coefficients for the calculation of “NO”, “PO” and “CO”, starting from the elemental composition of natural phytoplankton. *Sci. Mar.* **53**: 779–784.
- SAMBROTTO, R. N., AND OTHERS. 1993. Elevated consumption of carbon relative to nitrogen in the surface ocean. *Nature* **363**: 248–250.
- SHAFFER, G., J. BENDTSEN, AND O. ULLOA. 1999. Fractionation during remineralization of organic matter in the ocean. *Deep-Sea Res. I* **46**: 185–204.
- SPEER, K. G. 1997. A note on average cross-isopycnal mixing in the North Atlantic Ocean. *Deep-Sea Res. I* **44**: 1981–1990.
- TAKAHASHI, T., W. S. BROECKER, AND S. LANGER. 1985. Redfield ratios based on chemical data from isopycnal surfaces. *J. Geophys. Res.* **90**: 6907–6924.
- TSUCHIYA, M., L. D. TALLEY, AND M. S. MCCARTNEY. 1992. An eastern Atlantic section from Iceland southward across the equator. *Deep-Sea Res.* **39**: 1885–1917.
- WANNINKHOF, R., S. C. DONEY, T.-H. PENG, J. L. BULLISTER, K. LEE, AND R. A. FEELY. 1999. Comparison of methods to determine the anthropogenic CO₂ invasion into the Atlantic Ocean. *Tellus* **51B**: 511–530.

Received: 11 July 2000

Accepted: 17 January 2001

Amended: 29 January 2001

The influence of watershed land use on lake N:P in a predominantly agricultural landscape

Abstract—This study tests the hypothesis that lakes in watersheds dominated by row-crop agriculture (e.g., maize or soybeans) have systematically higher N:P than lakes in watersheds with large tracts of pasturelands. Current biogeochemical models of eutrophication suggest that agricultural nitrogen and phosphorus fluxes lead to a systematic decline in the N:P of receiving waters. In contrast, different agricultural activities (i.e., row-cropping vs. animal agriculture) use greatly divergent N and P amendments, and fluxes from agricultural watersheds diverge through a broad range of observed N:P (i.e., sub-Redfield to >100). Animal agriculture leads to low N:P fluxes and row-cropping to high N:P. The connection between agricultural watershed land use and lake nutrient stoichiometry was tested in a highly agricultural region of the United States (Iowa) on 113 lakes in watersheds with different amounts of row-crop (0%–95%) and pastureland (0%–36%). Multiple regression analysis shows that lakes in watersheds with large areas in pasturelands have low N:P, whereas lakes in watersheds dominated by row-cropping have systematically high N:P. Lakes in watersheds with >30% pasture had the lowest N:P, approaching Redfield levels. N:P was most frequently high (>50 as atoms) in lakes with >90% of their watersheds in row-crop agriculture. The dynamics of agricultural practice necessitates the inclusion of real-world differences among agricultural systems in nutrient stoichiometric models. Intensive row-crop agriculture yields N:P stoichiometry at high levels usually observed in pristine headwaters and open oceans, whereas increased animal agriculture will

drive N:P to low levels usually associated with cyanobacterial blooms.

Agricultural activities are a major source of nutrients to freshwater (Howarth 1996) and marine (Downing et al. 1999b) ecosystems. Nitrogen and phosphorus have been identified as leading pollutants in lakes, rivers, and estuaries (Carpenter et al. 1998). Agricultural nutrients (e.g., commercial fertilizer and animal manure) are rich in nitrogen and phosphorus and enter water bodies through surface and subsurface flow. Since nitrogen and phosphorus are the principal production-limiting nutrients in freshwater and marine systems, excessive loading of these nutrients can adversely affect receiving waters. The impacts of agricultural nutrients on freshwater and marine eutrophication worldwide are now well documented (Kronvang et al. 1993; U.S. Environmental Protection Agency 1995; Howarth et al. 1996; Downing et al. 1999a).

Both the quantity and stoichiometry of N and P influence aquatic primary production and community structure. Although N and P are essential to ecosystem function, the relative quantities (i.e., stoichiometry) of these elements are critical. When ambient nutrient supply ratios are extreme compared with biotic demand, ecosystem structure, function, and productivity are affected (Elser and Urabe 1999). In

freshwater systems, the ratio of nitrogen to phosphorus has an important impact on algae species composition (Smith 1983; Smith and Bennett 1999), productivity (Elser et al. 1990), and nutrient limitation (Elser et al. 1990; Urabe et al. 1997; Downing et al. 1999a) and influences trophic status (Downing and McCauley 1992). Because nutrient stoichiometry is important to the function and health of aquatic systems, and because agriculture is a major source of anthropogenic nutrients, it is important to understand how agriculture affects the N:P stoichiometry of receiving waters.

A recent stoichiometric model (Downing and McCauley 1992) extrapolated the prevalence of low N:P manure and generally low N:P in nonpoint agricultural fluxes (e.g., Reckhow et al. 1980) to propose that surface waters in agricultural drainage basins should have low N:P (*see also* Kronvang et al. 1993; Johnes et al. 1996). Although low aquatic N:P ratios in agriculture areas have been reported, differences among individual agriculture systems and their potential impact on nutrient export stoichiometry have often been ignored. There is ample evidence that nutrient export from agricultural crop production is high (e.g., Dillon and Kirchner 1975; Hill 1978; Neill 1989; Correll et al. 1992), but little is known about the downstream impact of divergent nutrient ratios supplied by different dominant agriculture cropping systems.

N and P stoichiometry has been observed to diverge widely among agricultural watersheds. Billen et al. (1991) reported nutrient export from agricultural watersheds to have N:P (atomic ratios) between 30:1 and 300:1. This wide range of N:P ratios in the nutrient export from agricultural watersheds may be a reflection of different agricultural production systems represented (e.g., cropland, pasture, and concentrated animal operations), yielding different ratios of major nutrients. Nutrient amendments vary among agriculture practices, as do the quantities and stoichiometry of nutrient runoff, subsurface drainage, and leachates. For example, fertilizing regimes associated with row-crop production (e.g., maize, soybeans, and wheat) are often intense, with high rates of amendment of nitrogenous fertilizers (e.g., anhydrous ammonia, ammonium nitrate, and liquid nitrogen) and low amendments of P. A recent survey of 16 maize-producing states reported that pure nitrogen fertilizers were applied to 98% of the total 1998 maize acreage at an average of 150 kg ha⁻¹ (U.S. Department of Agriculture 1999). With such intensive use of pure nitrogenous fertilizers, it is reasonable to expect that nutrient export to aquatic systems in heavily cropped watersheds would have high N:P.

In contrast, livestock operations tend to yield manure leachates with sub-Redfield N:P (Downing and McCauley 1992). Losses from animal feeding and pasture operations are therefore relatively P-enriched, so P inputs from agricultural runoff originating from these sources can hasten the eutrophication of P-sensitive waters (Daniels et al. 1998). Excessive nutrients from livestock production systems enter aquatic systems primarily through uncontrolled runoff, erosion, and leaching from manured cropland, livestock grazed pasture, confined open feedlots, and leaking earthen waste storage/treatment structures (Humenik et al. 1992). Although animal manure is variable in nutrient composition, it is relatively rich in phosphorus, compared with many other nu-

trient sources (Downing and McCauley 1992). Therefore, nutrient export to lakes in highly pastured basins would have low N:P.

Because of the frequently tight biogeochemical connection between lakes and their watersheds, aquatic systems in predominantly agricultural regions should have N:P correlated with the prevalent N:P fluxes from agricultural land use. Despite the great divergence in N:P of various sources of agricultural runoff, the impact of agricultural cropping systems on the N:P of receiving waters has seldom been examined. The purpose of this study was to examine the relationships between agricultural watershed land use (i.e., row crop vs. pastureland) and lake N:P conditions. We therefore sought to test the idea that lakes in predominantly agricultural regions have water-column N:P ratios that vary systematically with the N:P characteristics prevalent in divergent classes of agricultural land use. We studied 113 lakes in the state of Iowa, one of the most productive agricultural areas in the world, in which 90% of the total land area is under some form of agricultural use (Fig. 1).

Study area—The 113 lakes and watersheds used for this analysis are located in a highly agricultural region of the Mississippi River Basin of North America (Downing et al. 1999b; Fig. 1). Iowa has a total land area of 14.5 million ha, of which 13 million ha are in some form of agricultural use. There are roughly 10 million ha in row-crop production (predominantly maize and soybeans) and 3 million ha of pastureland (predominantly cattle and sheep, with swine feeder operations) (U.S. Department of Agriculture 1999). The lakes studied varied widely in area from 4 to 1,688 ha, and terrestrial watershed sizes range from 4 to 44,441 ha. Row-crop agriculture dominated (>50%) land use in 78% of the watersheds studied. Twenty percent of the watersheds had >20% of the total area in pastured lands. Although pasture may comprise >30% (maximum 36%) of a given watershed, there were no watersheds in this study in which pasture covered the majority of land.

Data acquisition—We studied data collected from 113 lakes in Iowa and related their average lake-water stoichiometry to drainage basin characteristics. Data were collected from mid-May through mid-August in 1990 and 1991 as part of a statewide lake survey (Bachmann et al. 1994). In each lake, samples were collected at three separate locations three times over the summer season. Sampling trips were timed to collect one sample series during early summer, one during midsummer, and one during late summer. The samples were surface mixed-zone composites collected with a piece of PVC tubing. Total phosphorus (TP) and total nitrogen (TN) samples were immediately placed into acid washed screw-top tubes for later analysis. An oxidant (sodium persulfate) was added to the TN samples within 8 h of sampling, and samples were autoclaved to convert all forms of nitrogen to NO₃-N. TP was analyzed by use of the ammonium molybdate method (Murphy and Riley 1962; Menzel and Corwin 1965), whereas TN was analyzed (after digestion) by use of second-derivative spectroscopy (Crumpton et al. 1992). The nutrient data analyzed here represent seasonal average, surface mixed-layer concentrations. The watershed character-



Fig. 1. Iowa land use (circa 1992) and outlines of lake watersheds. Land uses are coded according to the color key at lower left. The land-use map was generated and classified by use of 30-m grid Landsat Thematic Mapper data (Iowa Department of Natural Resources, Natural Resource Geographic Information System Library, Des Moines, IA). The watershed boundaries for lakes analyzed here are shown as bold black outlines. The red star on the small map in the lower right-hand corner shows the position of the state of Iowa within North America. Iowa is located in the glacial outwash plain between the Missouri and Mississippi Rivers.

istics and lake-water nutrient data used in this analysis are published elsewhere (Bachmann et al. 1994) and are available in an appendix on the L&O website (http://www.aslo.org/lo/pdf/vol_46/issue_4/0970a1.pdf).

Data analysis—We used multiple regression analysis to test the hypothesis that land use affects summer-average total N:P ratios in lake water. We tested this hypothesis with the regression model

$$\log \text{TN} = \beta_0 + \beta_1 \log \text{TP} + \beta_2 C + \beta_3 A, \quad (1)$$

where lake-water TN and TP concentrations were measured in μM , C represents the fraction of land (0–1) within each lake's watershed that was used for row crop production, and A represents the fraction of pastured lands (0–1) within each lake's watershed. In order to avoid introducing TP to both sides of the regression model, therefore risking auto-corre-

lation (i.e., regressing TN:TP as a function of TP), we analyzed TN as a function of TP and land use (i.e., Eq. 1). A relatively high concentration of TN at a given TP concentration would, for example, imply high TN:TP in this analysis. Therefore, the expected high TN:TP in row-crop-dominated watersheds would be indicated if β_2 were a significantly positive regression coefficient, whereas the expected low TN:TP in highly pasture watersheds would yield a negative regression coefficient for β_3 . Statistical significance of candidate variables was accepted at $P < 0.01$.

Results and discussion—Summer mean TN and TP concentrations in the sampled lakes were high (Table 1). Most Iowa lakes are eutrophic or hypereutrophic, with nearly all of them falling above a summer average of $1 \mu\text{M}$ of TP (Fig. 2). The nutrient concentrations in Iowa lakes are in the upper half of those seen in world lakes (Fig. 2). Although

Table 1. Statistical summary of mean summer epilimnetic total N, total P, and N:P in samples collected 1991–1992 from 113 lakes in Iowa.

	Minimum	Maximum	Mean
Total N (μM)	35	1,093	216
Total P (μM)	0.90	24	5
TN:TP (atomic)	9	219	53

the central tendency of TN and TP concentrations in Iowa lakes followed the same overall trend as other lakes (Fig. 2), the variation in TN at a given level of TP surpassed the ranges seen elsewhere in the world. Lakes in this agricultural region have among the most highly divergent patterns of TN concentrations in the world.

Multiple regression with use of backward elimination showed that TP concentration, the fraction of watershed area in cropland, and the fraction of watershed area in pastureland all had highly significant partial effects on TN:TP in Iowa lakes (Table 2). The regression equation

$$\log \text{TN} = 1.80 + 0.55 \log \text{TP} + 0.29 C - 0.71 A \quad (2)$$

indicates that TN:TP was positively correlated with the fraction of land in row-crop agriculture within the watershed and was negatively correlated with the fraction of land in pasture. This analysis thus confirms that the type of agriculture in a lake's watershed influences lake-water N:P stoichiometry. Lakes in heavily cropped watersheds have higher TN:TP

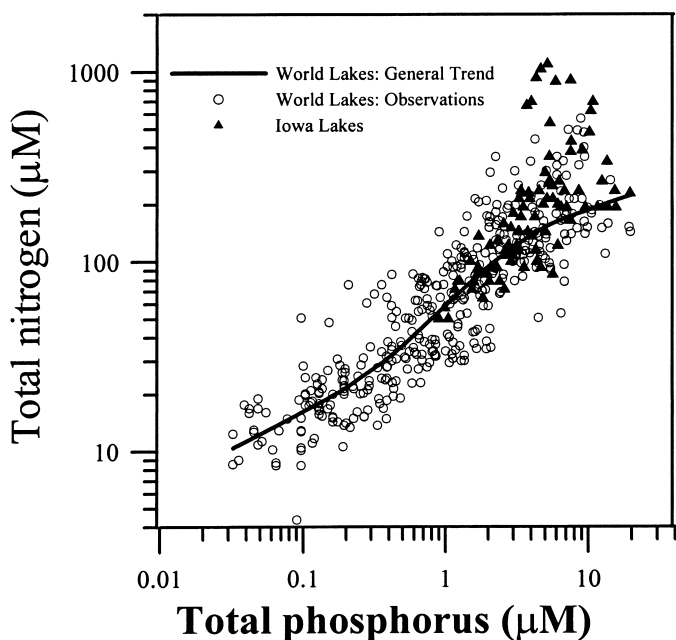


Fig. 2. Comparison of TN and TP concentrations in the lakes in Iowa's agricultural watersheds with world lakes. Data for world lakes are from Downing and McCauley's (1992) worldwide compilation of mean summer epilimnetic TN and TP concentrations. The solid line is the average trend estimated by locally weighted sequential smoothing (Cleveland 1979). The Iowa lake nutrient data are mean summer epilimnetic TN and TP from Hatch (1992) and Bachmann et al. (1994).

Table 2. The partial T values and probabilities of regression coefficients in Eq. 2. Partial T values indicate the size of statistical effect of the independent variables when all other independent variables are considered. P indicates the probability that a partial T value of equal or greater magnitude would be obtained through chance alone.

Independent variable	Partial T	P
Total P (μM)	7.35	<0.001
Fraction of watershed in row crop	3.27	0.001
Fraction of watershed in pastureland	-2.96	0.004

ratios than those found in highly pastured basins (Fig. 3). At a given TP level, watersheds dominated by row-crop agriculture yielded significantly higher lake TN:TP than watersheds with greater concentrations of pastureland. We have analyzed seasonal mean data, but it is likely that these patterns would be accentuated during spring, when runoff and loading from the watershed is high. Normal seasonal patterns of nutrient stoichiometry in row-crop-dominated lakes in this region show extreme spring N:P values that become more moderate as denitrification decreases N:P under summer stagnation (Downing unpubl. data).

Few of these lakes had sub-Redfield N:P ratios (i.e., <16:1, as moles). In spite of the high degree of agricultural activity in these watersheds and the fact that several of the watersheds had >30% pastureland, only ~5% of the lakes had TN:TP < 16. This is likely due to the great predominance of pure-N fertilizer-amended agriculture in this part of the world. N fertilization rates of these watersheds frequently run >200 kg ha⁻¹ yr⁻¹.

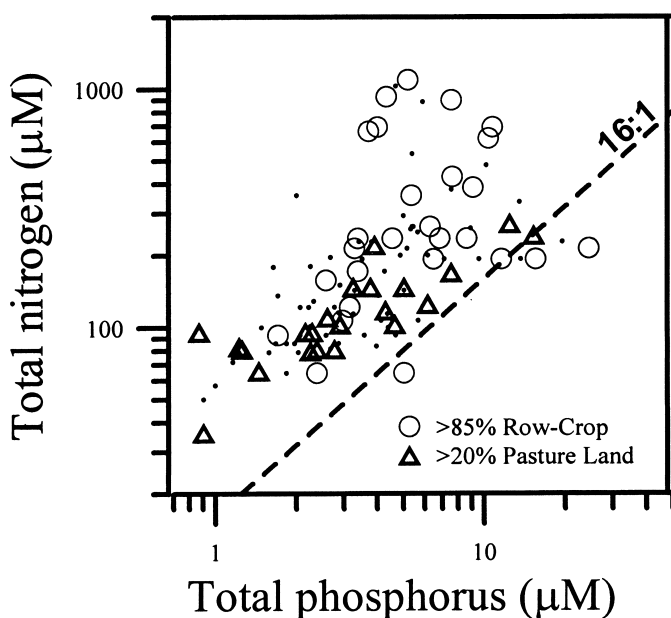


Fig. 3. TN and TP concentrations in Iowa lakes. Lakes in watersheds with >85% row-crop agriculture are indicated as open circles, lakes in watersheds with >20% pastureland are indicated as open triangles, and all other intermediate lakes, or those with other predominant land uses (e.g., urban or forest), are indicated as small dots.

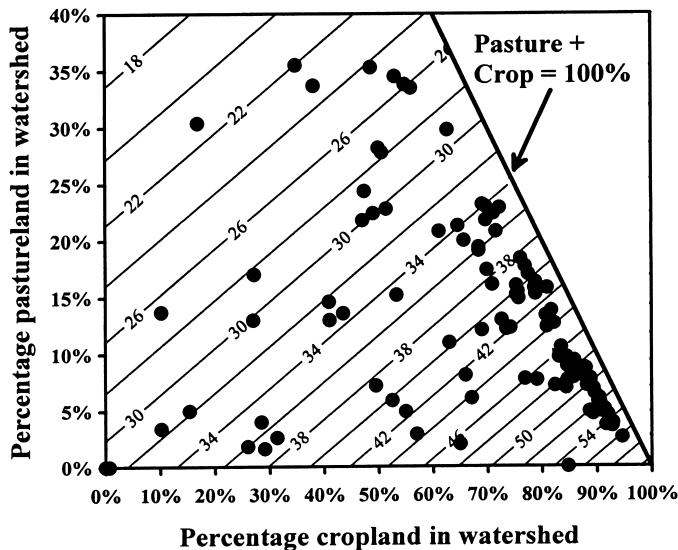


Fig. 4. Contours of predicted average atomic N:P (Eq. 2) at the average TP concentration of $4.8 \mu\text{M}$ in Iowa lakes. Dots indicate combinations of crop and pastureland use in the 113 lakes analyzed here. The limit-line to the upper right is the line indicating that the sum of crop land and pastureland would fill 100% of the watershed.

Earlier models and data collections (Downing and McCauley 1992; *see also* Reckhow et al. 1980; Kronvang et al. 1993; Johnes et al. 1996) suggest low lake TN:TP in agricultural areas but fail to account for the fact that different agricultural production systems employ practices that yield widely divergent ratios of major nutrients to receiving waters. Models based on the tenet that agriculture produces only moderately divergent ratios of major nutrients do not account for extreme nutrient inputs experienced by some agricultural systems. In regions where agricultural practices yield widely divergent ratios of nitrogen and phosphorus, where nitrogenous inputs are huge, massive nitrogen export results in high lake-water TN:TP. Lowered lake-water TN:TP in agricultural regions occurs when the agricultural practice favors animal agriculture or when the export of major nutrients is more closely aligned.

Differences in the influence of dominant agricultural systems on runoff or export N:P stoichiometry should be incorporated into models that predict lake-water N and P fluxes from watersheds in predominantly agricultural landscapes. Rearrangement of Eq. 2 allows calculation of the expected contours of lake N:P over the range of combinations of land uses present in this intensively row-cropped region (Fig. 4). This contour plot shows that considerable variation in N:P should be expected across the range of observed land use. Although the trends seen in Fig. 4 show only averaged trends predicted from the regression analyses, lakes in watersheds with $>30\%$ pastureland (near the maximum in Iowa) had the lowest lake-water TN:TP, approaching Redfield levels. The data in Fig. 4 and the analyses of Smith (1983) and Smith and Bennett (1999) suggest that noxious cyanobacteria blooms should be most prevalent in Iowa lakes that receive inputs from intensive animal agriculture (Smith 1983). On the other hand, lakes with $>90\%$ of their watersheds in row-crop agriculture had extremely high nutrient

concentrations and TN:TP most frequently $>50:1$ (as atoms). Although most lakes in Iowa were in the cyanobacteria-prone TN:TP range <64 (as moles, Smith 1983), we have observed that some of the high N:P ratio lakes in predominantly row-crop watersheds have infrequent cyanobacterial blooms, in spite of their very high P concentrations (Fig. 2), a trend that is consistent with the N:P ratio hypothesis of cyanobacterial dominance (Smith and Bennett 1999).

Agricultural activities are increasing nutrient fluxes to freshwater and marine ecosystems worldwide. Agricultural scientists in many nations are currently facing a paradigm shift away from the concept that fertilizer and manure P is immobilized in soils and is therefore of little danger to aquatic resources (e.g., Haygarth 1997). Although agriculture's role in anthropogenic eutrophication is generally well documented (e.g., Downing and McCauley 1992), past analyses have not demonstrated the divergent stoichiometric impacts specific to different agricultural systems. The dynamic nature of agriculture production systems (i.e., growth and/or changes in practice) necessitates the expansion of nutrient stoichiometric models to represent real-world differences among individual agriculture systems. In regions where intensive row-crop agricultural practices are the rule, large nitrogen fluxes into receiving waters drive N:P ratios in these aquatic ecosystems to very high levels heretofore observed in primarily pristine headwaters or open oceans (Downing 1997). At the other extreme, animal agricultural practices are associated with declining N:P ratios in receiving waters. There is currently an unprecedented increase in the amount and degree of land application of animal manure from small- and large-animal confinement facilities (i.e., animal feeding operations), implying that nutrient management for water quality protection should be increasingly based on P versus N requirements of crops. In our study region, feedlots and pastures tend to be located on steep stream valley slopes and near streams, which accentuates their impact on waters. Our analyses imply that future changes in agriculture practice are likely to result in dramatic shifts in aquatic stoichiometry and subsequent changes to aquatic communities in streams, lakes, rivers, and coastal zones.

Kelly E. Arbuckle¹ and John A. Downing²

Department of Animal Ecology
124 Science II
Iowa State University
Ames, Iowa 50011-3221

¹ Current address: Office of Environmental Services, Iowa Department of Transportation, Ames, Iowa 50010.

² Corresponding author (downing@iastate.edu).

Acknowledgments

We thank Roger Bachmann for sharing methodological details on Iowa lake sampling and analysis protocols and V. H. Smith, J. R. Jones, J. Kopaska, R. E. Hecky, and two anonymous reviewers for comments on the manuscript. This is publication J-18841 of the Iowa Agriculture and Home Economics Experiment Station (project 3423).

References

- BACHMANN, R. W., T. A. HOYMAN, L. K. HATCH, AND B. P. HUTCHINS. 1994. A classification of Iowa's lakes for restoration. Final Report. Iowa Department of Natural Resources.
- BILLEN, G., C. LANCELOT, AND M. MEYBECK. 1991. N, P, and Si retention along the aquatic continuum from land to ocean, p. 19–44. *In* R. F. C. Matoura, J. M. Martin, and R. Wollast [eds.], *Ocean margin processes in global change*. Wiley.
- CARPENTER, S. R., N. F. CARACO, D. L. CORRELL, R. W. HOWARTH, A. N. SHARPLEY, AND V. H. SMITH. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* **8**: 559–568.
- CLEVELAND, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* **74**: 829–836.
- CORRELL, D. L., T. E. JORDAN, AND D. E. WELLER. 1992. Nutrient flux in a landscape: Effects of coastal land use and terrestrial community mosaic on nutrient transport to coastal waters. *Estuaries* **15**: 431–442.
- CRUMPTON, W. G., T. M. ISENHART, AND P. D. MITCHELL. 1992. Nitrate and organic analyses with second-derivative spectroscopy. *Limnol. Oceanogr.* **37**: 907–913.
- DANIELS, T. C., A. N. SHARPLEY, AND J. L. LEMUNYON. 1998. Agricultural phosphorus and eutrophication: A symposium overview. *J. Environ. Qual.* **27**: 251–257.
- DILLON, P. J., AND W. B. KIRCHNER. 1975. The effects of geology and land use on the export of phosphorus from watersheds. *Water Res.* **9**: 135–148.
- DOWNING, J. A. 1997. Marine nitrogen:phosphorus stoichiometry and the global N:P cycle. *Biogeochemistry* **37**: 237–252.
- , AND E. MCCAULEY. 1992. The nitrogen:phosphorus relationship in lakes. *Limnol. Oceanogr.* **37**: 936–945.
- , C. W. OSENBURG, AND O. SARNELLE. 1999a. Meta-analysis of marine nutrient-enrichment experiments: Variation in the magnitude of nutrient limitations. *Ecology* **80**: 1157–1167.
- , N. N. RABALAIS, R. J. DIAZ, R. J. ZIMMERMAN, J. L. BAKER, AND T. PRATO. 1999b. Gulf of Mexico hypoxia: Land and sea interactions. Task Force Report. Council for Agricultural Science and Technology.
- ELSER, J. J., E. R. MARZOLF, AND C. R. GOLDMAN. 1990. Phosphorus and nitrogen limitations of phytoplankton growth in the freshwaters of North America: A review and critique of experimental enrichments. *Can. J. Fish. Aquat. Sci.* **47**: 1468–1477.
- , AND J. URABE. 1999. The stoichiometry of consumer-driven nutrient recycling: Theory, observations, and consequences. *Ecology* **80**: 735–751.
- HATCH, L. K. 1992. Factors affecting the trophic state of Iowa lakes. M.Sc. thesis, Iowa State Univ.
- HAYGARTH, P. 1997. Agriculture as a source of phosphorus transfer to water: Sources and pathways. *SCOPE Newslett.* **21**: 1–15.
- HILL, A. R. 1978. Factors affecting the export of nitrate-nitrogen from drainage basins in southern Ontario. *Water Res.* **12**: 1045–1057.
- HOWARTH, R. W., AND OTHERS. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to North Atlantic Ocean: Natural and human influences. *Biogeochemistry* **35**: 75–139.
- HUMENIK, F. J., AND OTHERS. 1992. Water quality: Agriculture's role. Report 120. Council for Agricultural Science and Technology.
- JOHNS, P., B. MOSS, AND G. PHILLIPS. 1996. The determination of total nitrogen and total phosphorus concentrations in freshwaters from land use, stock headage and population data: Testing of a model for use in conservation and water quality management. *Freshw. Biol.* **36**: 451–473.
- KRONVANG, B., G. ÆRTBJERG, R. GRANT, R. KRISTENSEN, M. HOVMAND, AND J. KIRKEGAARD. 1993. Nationwide monitoring of nutrients and their ecological effects: state of the Danish aquatic environment. *Ambio* **22**: 176–187.
- MENZEL, D. W., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnol. Oceanogr.* **10**: 280–282.
- MURPHY, J., AND J. P. RILEY. 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* **27**: 31–36.
- NEILL, M. 1989. Nitrate concentrations in river waters in the south-east of Ireland and their relationship to agricultural practices. *Water Res.* **23**: 1339–1355.
- RECKHOW, K. H., M. N. BEAULAC, AND J. T. SIMPSON. 1980. Modeling phosphorus loading and lake response under uncertainty: A manual and compilation of export coefficients. Publication 440/5-80-011. United States Environmental Protection Agency.
- SMITH, V. H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* **221**: 669–671.
- , AND S. J. BENNETT. 1999. Nitrogen:phosphorus supply ratios and phytoplankton community structure in lakes. *Arch. Hydrobiol.* **146**: 37–53.
- URABE, J., J. CLASEN, AND R. W. STERNER. 1997. Phosphorus limitation of *Daphia* growth: Is it real? *Limnol. Oceanogr.* **42**: 1436–1443.
- U.S. DEPARTMENT OF AGRICULTURE. 1999. National Agricultural Statistics Service. <http://www.usda.gov/nass/>.
- U.S. ENVIRONMENTAL PROTECTION AGENCY. 1995. National water quality inventory: 1994 report to congress. EPA Publication 841.

Received: 12 April 2000

Accepted: 15 January 2001

Amended: 6 March 2001