uOttawa

L'Université canadienne
Canada's university

FACULTÉ DES ÉTUDES SUPÉRIEURES ET POSTOCTORALES

uOttawa

L'Université canadienne
Canada's university

FACULTY OF GRADUATE AND POSDOCTORAL STUDIES

Jaynie Stephenson
AUTEUR DE LA THÈSE / AUTHOR OF THESIS

Ph.D. (Biology)
GRADE / DEGREE

Department of Biology
FACULTÉ, ÉCOLE, DÉPARTEMENT / FACULTY, SCHOOL, DEPARTMENT

Algal, Invertebrate, and Fish Production in Headwater Streams along a Forested Gradient

TITRE DE LA THÈSE / TITLE OF THESIS

Antoine Morin
DIRECTEUR (DIRECTRICE) DE LA THÈSE / THESIS SUPERVISOR

CO-DIRECTEUR (CO-DIRECTRICE) DE LA THÈSE / THESIS CO-SUPERVISOR

EXAMINATEURS (EXAMINATRICES) DE LA THÈSE / THESIS EXAMINERS

D. Allan (teleconference)

J. Kerr

F. Chapleau

F. Pick

L. Fahrig

Gary W. Slater
Le Doyen de la Faculté des études supérieures et postdoctorales / Dean of the Faculty of Graduate and Postdoctoral Studies

Algal, Invertebrate, and Fish Production in Headwater Streams along a Forested Gradient

Jaynie M. Stephenson

Thesis submitted to the
Faculty of Graduate and Postdoctoral Studies
In partial fulfillment of the requirements for the
Ph.D. degree

Ottawa-Carleton Institute of Biology

Thèse soumise à
Faculté des études supérieures et postdoctorales
Université d'Ottawa
en vue de l'obtention du doctorat

L'Institut de biologie d'Ottawa-Carleton

Ottawa, Ontario, Canada

Your file Votre référence
ISBN: 978-0-494-32421-9
Our file Notre référence
ISBN: 978-0-494-32421-9

Abstract

As urban populations increase globally, the conversion of natural land cover to anthropogenic land use is on the rise. Diffuse perturbations that accompany such land use changes are considered a chief threat to headwater streams, which provide habitat for diverse faunas of macroinvertebrates, fish, and amphibians and are important sources of sediments, nutrients, and organic matter for downstream systems. Although environmental assessments of stream ecosystems generally measure responses to these perturbations as shifts in community structures, functional rather than structural properties may provide a better indicator of land use impacts since measures of ecosystem function can reveal more about the mechanisms that alter running water ecosystems. The primary objective of this thesis was to quantify stream productivity along a gradient of forest cover and assess bottom-up and top-down mechanisms for observed patterns in stream productivity. In the first chapter, I quantified algal, invertebrate, and fish biomass, the single best correlate of productivity, at 38 first-third order streams along a forest cover gradient at 55 spatial scales and determined that subcatchment forest cover was consistently the best predictor of biomass at all trophic levels in terms of the variation explained by forest cover and the unexplained residual variance. When considering the independent effects of forest cover on biomass at three coarse scales, subcatchment forest cover was the only significant predictor of biomass, suggesting that the common practice of maintaining riparian buffers is an ineffective management practice for protecting stream function from catchment-wide impacts. In the second chapter, I developed two time-saving approaches for processing benthic invertebrate samples that reduced laboratory processing time by 37% and 82% and

provided production estimates that were strongly related to production estimates obtained from standard processing techniques. These time-saving approaches were used in chapter 3 so that I could measure algal, invertebrate, and fish production at 12 sites along a gradient of subcatchment forest cover, which I determined to be the most influential spatial scale on biomass in chapter 1. Total nitrogen was a significant bottom-up force that explained 34-83% of the variation in stream productivity at all three trophic levels. However, consumer production to consumption ratios indicated that predators and grazers can potentially deplete their food sources, and that top-down forces are therefore also important contributors to observed patterns in productivity and biomass along the forested gradient.

Résumé

L'accroissement des populations urbaines entraîne une augmentation de la superficie des terres modifiées par les activités humaines. Les perturbations diffuses associées à la conversion des habitats naturels sont considérées comme l'une des menaces les plus importantes aux ruisseaux d'amont qui abritent une faune diversifiée d'invertébrés, de poissons et d'amphibiens et qui sont une source importante de sédiments, nutriments et de matière organique pour les systèmes en aval. La réponse de ces écosystèmes aux perturbation est généralement évaluée par l'étendue du changement de la structure des communautés qui y vivent. Il est possible, cependant, que les propriétés fonctionnelles soient de meilleurs indicateurs que les propriétés structurelles puisque les mesures fonctionnelles de l'écosystème peuvent révéler plus d'information quant aux mécanismes qui altèrent les écosystèmes d'eau courante. L'objectif principal de cette thèse était de quantifier la productivité des ruisseaux le long d'un gradient de couvert forestier et d'évaluer les mécanismes de bas en haut (bottom-up) et de haut en bas (top-down) pour expliquer les tendances observées de la productivité des ruisseaux. Dans le premier chapitre, j'ai quantifié la biomasse des algues, des invertébrés et des poissons à 38 sites sur des ruisseaux d'ordre 1 à 3 formant un gradient de couvert forestier qui a été quantifié à 55 échelles d'observations différentes. Cette analyse a révélé que le couvert forestier à l'échelle du bassin versant était systématiquement le meilleur prédicteur de la biomasse à tous les niveaux trophiques en termes de proportion de la variance expliquée. L'analyse de l'effet indépendant du couvert forestier à 3 échelles a de plus révélé que seul le couvert forestier à l'échelle du bassin versant complet avait un effet partiel significatif sur la biomasse, ce qui suggère que la pratique courante de protéger des bandes riveraines ne

permet pas de protéger le fonctionnement des ruisseaux des impacts diffus dans le bassin versant. Dans le second chapitre, j'ai développé deux méthodes pour traiter les échantillons d'invertébrés benthiques qui permettent une économie de 37% et 82% par rapport aux méthodes usuelles, tout en menant à des estimés de production très fortement corrélés aux estimés obtenus par les méthodes usuelles. Ces méthodes rapides ont été utilisées au chapitre 3 pour mesurer la production des algues, invertébrés, et poissons à 12 sites le long d'un gradient de couvert forestier à l'échelle du bassin versant, déterminée au premier chapitre comme étant la plus importante. L'azote total a expliqué de 34-83% de la variabilité de la productivité des ruisseaux aux 3 niveaux trophiques et cela a indiqué un important effet de bas en haut (bottom-up). Toutefois, les rapports production: consommation ont indiqué que les prédateurs et les herbivores peuvent potentiellement surexploiter leurs sources de nourriture et donc que les forces de haut en bas (top-down) jouent également un rôle important sous-jacent aux patrons de productivité et de biomasse le long du gradient de couvert forestier.

Acknowledgements

I am grateful for the support of many people during the long and arduous yet rewarding path toward this Ph.D. I would first like to thank my supervisor, Antoine Morin, whose logical and thoughtful approach to science has taught me the importance of carefully considering where to place the most effort to maximize the likelihood of answering the question at hand. Antoine has critically commented on numerous drafts of papers and in doing so has improved my critical thinking and writing skills. His consistently quick turn-around of comments, especially most recently in this last stretch, is greatly appreciated. In addition to his contributions as a mentor, I am thankful to Antoine for bringing together the "benthological sirens" in his lab and for capturing wonderful moments in time through his photography. I would also like to thank the members of my thesis committee, including François Chapleau, Lenore Fahrig, and Frances Pick, whose individual expertise and critical comments and questions have contributed to this thesis.

Geneviève Carr and I began this adventure in the same year, and quickly became and still remain close friends. During the 4.5 years that we shared an office and still today, Gen has willingly discussed my research or helped me to answer questions with her invaluable statistical knowledge. I am thankful to Uta Gruenert and Jessica Strike for their help in the field and in the lab, and more importantly for their lasting friendships. I also thank my current officemate and friend, Jennifer Lento, for enjoyable and insightful discussions regarding our research, deadlines, and life in general; David Vaillancourt and Yuan Yao for their field and/or lab assistance; and Brian Giles, another supportive friend, who has assisted with improving some of the figures in my thesis.

I greatly appreciate the support of my family. My mother, Mary Stephenson, has always believed in me throughout every academic endeavor. Most recently, she has stayed with us for months at a time to help look after my daughter while I worked on my thesis. I am grateful to my brother and his wife, Charlie and Annie Stephenson, for their consistent and genuinely kind support. Likewise, I thank my husband's family and Emilie's granny Mary Higgins in particular, for their support and understanding of how busy times like this can be, especially in these last few weeks that my husband and daughter have spent with them. I must also include Sue Szaboo in this section, as she is like family to me, and was a wonderful caregiver to my daughter for 15 months and has always encouraged me. They have all been "rooting" for me, and it is greatly appreciated.

Finally, I would like to thank my husband, Michael Higgins, my best friend and confidant. In the 9 years that I have known Mick, I have been working on a masters or a Ph.D. thesis. Like my mom, Mick has supported me in countless ways, by accompanying me in the field on hot summer days to providing a sounding board for research ideas. Since our daughter was born, Mick has completed most of the family tasks, so that I could work on my thesis, and he has always done so without complaints, even encouraging me to work at times when I had little thesis energy and would rather have helped him. Thank you Mick, for helping me in every way possible to complete this PhD.

I dedicate this thesis to my daughter Emilie Mary Higgins, who has always been a welcomed distraction.

Table of Contents

List of Tables

List of Figures

A Note on Style

This thesis is comprised of three research articles that have been prepared for publication in scholarly peer-reviewed journals. Each chapter therefore contains its own introduction, methods, results, discussion, acknowledgements, literature cited, tables, and figures. Because the research articles in this thesis are intended for publication under joint authorship with my supervisor, Dr. Antoine Morin, each chapter was written in the style of first-person plural. However, the general introduction and conclusion of this thesis, which are not intended for primary publication, were written in the style of first-person singular.

General Introduction

Diffuse perturbations from anthropogenic land uses have been targeted by governments as a leading threat to aquatic ecosystem health (MWLA 1999, USEPA 2002). Concerns regarding diffuse perturbations are predicated on rapidly increasing urban populations (U.N. Population Division 2005) and associated urban sprawl and agricultural demands, along with studies demonstrating strong correlations between urban and agricultural land use intensifications and reduced water quality, habitat, and biological integrity in aquatic systems (Crosbie and Chow-Fraser 1999, Cuffney et al. 2000, Harding et al. 1998, Jones and Clark 1987, Soranno et al. 1996, Wang et al. 1997).

Impairment of headwater streams is of particular concern (Meyer et al. 2003) because these first to third order streams provide habitat for diverse faunas of macroinvertebrates, fish, and amphibians (Meyer and Wallace 2001) and are vital for the functioning of larger aquatic and terrestrial ecosystems (Gomi et al. 2002). Composing at least 70% of the total catchment area draining a given watershed (Hynes 1970, Meyer and Wallace 2001, Sidle et al. 2000), headwater streams are important sources of sediments, nutrients, and organic matter for downstream systems (Newbold et al. 1983, Rice et al. 2001, Wipfli and Gregovich 2002, Wipfli and Musslewhite 2004). Headwater streams also contribute to the productivity of riparian ecosystems by converting low-quality, allochthonous material into high-quality foods for terrestrial vertebrates through insect emergence (Gray 1993, Jackson and Fisher 1986). Since impacts to headwater streams can be propagated throughout the entire stream network as well as to adjacent riparian zones, understanding how anthropogenic land uses alter the ecosystems of

headwater streams is imperative for protecting our water supplies and the organisms that depend upon them (Meyer et al. 2003).

Currently, most best management practices for the protection of lotic systems focus on physical habitat at the reach scale and riparian vegetation (Brown 2000, Bernhardt et al. 2005), although stream ecosystems respond to disturbances at multiple spatial scales (Allan 2004, Frissell et al. 1986, Paul and Meyer 2001). Numerous multiple-scale studies have demonstrated strong correlations between structural characteristics of running water ecosystems and land use within riparian buffers (Lammert and Allan 1999, Fitzpatrick et al. 2001, Sponseller et al. 2001, Rios and Bailey 2006), and/or the entire subcatchment (Stewart et al. 2001, Strayer et al. 2003, Weigel et al. 2003, Roth et al. 1996, Morley and Karr 2002, Hession, 2003a, b, Wang et al. 2003, Freeman and Schorr 2004). Since management scenarios that match the scale of disturbance should be more effective (Walsh et al. 2005), an understanding of how land use impacts lotic ecosystems at multiple spatial scales is necessary before establishing best management practices for the preservation and restoration of urban and agricultural streams.

Environmental assessments of stream ecosystems generally measure responses to perturbations as shifts in community structure (Rosenberg and Resh 1993). Given that functional rather than structural properties reveal more about the mechanisms that alter running water ecosystems, however, ecosystem function responses to land use change may provide a more relevant basis for the development of best management practices to mitigate land use impacts (Bunn et al. 1999, Harris 1994). Energy flow in lotic systems is an essential aspect of the functioning of aquatic ecosystems (Benke 1993), and

measurements of production for entire communities at each trophic level are required to fully understand how changing land use alters the flow of energy within aquatic food webs (Huryn and Wallace 2000). However, few studies have simultaneously measured production of entire communities of algae, invertebrates and fish in streams (Huryn 1996, Huryn 1998), and none have done so at multiple streams along a gradient of anthropogenic land use (Allan 2004, Paul and Meyer 2001).

The primary objectives of this thesis are to quantify algal, invertebrate, and fish production in small headwater streams along a forested gradient and to illustrate potential mechanisms for observed patterns in stream productivity along the forested gradient. Rather than considering multiple types of anthropogenic land use, I chose forest cover as this independent variable provides a univariate measure of all undisturbed land cover in the region. I first quantified algal, invertebrate, and fish biomass, the single best correlate of production (Benke 1993), at 38 first-third order streams along a forest cover gradient at multiple scales so that I could determine the spatial scale at which forest cover has the greatest influence on stream biomass and empirically assess whether forest cover within narrow local and riparian buffers is an effective tool for mitigating catchment-wide impacts. In the second chapter, I developed two methods to reduce the time spent processing benthic invertebrate samples in the laboratory to estimate secondary production, and quantified their accuracy, precision, and efficiency. Finally in chapter 3, using the coarse-sieve method (developed in chapter 2) for processing benthic invertebrate samples and published empirical models that predict primary and secondary production (Morin and Dumont 1994, Morin et al. 1999, Randall and Minns 2000), I quantified daily algal, invertebrate, and fish production throughout the growing season at

12 streams along a gradient of forest cover within subcatchments, which was found to be the most influential scale on stream biomass (chapter 1). I then illustrated the bottom-up and top-down roles of nutrients and fish consumption in regulating algal and invertebrate production along the forested gradient. Results from this research will demonstrate patterns in stream productivity with forest cover and suggest potential mechanisms that regulate stream productivity (chapters 1 and 3), as well as elucidate the appropriate spatial scale for stream management scenarios in this study area (chapter 1) and reduce laboratory processing time of benthic samples so that future production studies at multiple trophic levels and streams are more feasible (chapter 2).

Literature Cited

Allan, J. D. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35: 257-284.

Benke, A. C. 1993. Edgardo Baldi Memorial Lecture: Concepts and patterns of invertebrate production in running waters. Verhandlungen. Internationale Vereinigung für Limnologie. 25: 15-38.

Bernhardt, E.S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake P.S., R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and O. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308: 636-637.

Brown, K. B. 2000. Urban stream restoration practices: an initial assessment. Center for Watershed Protection, Ellicott City, Maryland.

Bunn, S. E., T. D. Mosisch, and P. M. Davies. 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. Freshwater Biology 41: 333-345.

Crosbie B., and P. Chow-Fraser. 1999. Percentage land use in the watershed determines the water and sediment quality of 22 marshes in the Great Lakes basin. Canadian Journal of Fisheries and Aquatic Sciences 56: 1781-1791.

Cuffney, T. F., M. R. Meador, S. D. Porter, and M. E. Gurtz. 2000. Responses of physical, chemical, and biological indicators of water quality to a gradient of agricultural land use in the Yakima River Basin, Washington. Environmental Monitoring and Assessment 64: 259-270.

Fitzpatrick, F. A., B. C. Scudder, B. N. Lenz, and D. J. Sullivan. 2001. Effects of multi-scale environmental characteristics on agricultural stream biota in eastern Wisconsin. Journal of the American Water Resources Association 37: 1489-1507.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. Environmental Management 10: 199-214.

Gomi, T., R. C. Sidle, and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems. BioScience 52: 905-916.

Gray, L. J. 1993. Response of insectivorous birds to emerging aquatic insects in riparian habitats of a tallgrass prairie stream. American Midland Naturalist 129: 288-300.

Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream biodiversity: The ghost of land use past. Proceedings of the National Academy of Sciences of the United States of America 95: 14843-14847.

Harris, G. P. 1994. Pattern, process and prediction in aquatic ecology. A limnological view of some general ecological problems. Freshwater Biology 32: 143-160.

Hession, W.C., D. D., Hart, R. J. Horwitz, D. A. Kreeger, D. J. Velinsky, J. E. Pizzuto, D. F. Charles, and J. D. Newbold. 2003a. Riparian reforestation in an urbanizing watershed: effects of upland conditions on instream ecological benefits. Final report. number R825798. US Environmental Protection Agency, National Center for Environmental Research. (Available at: cfpub.epa.gov/ncer_abstracts/index.cfm/fuseaction/display.abstractDetail/abstract/182/report/F)

Hession, W.C., J. E. Pizzuto, T. E. Johnson, and R. J. Horwitz. 2003b. Influence of bank vegetation on channel morphology in rural and urban watersheds. Geology 31: 147-150.

Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. Limnology and Oceanography 41: 243-252.

Huryn, A. D. 1998. Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. Oecologia 115: 173-183.

Huryn, A. D., and J. B. Wallace. 2000. Life history and production of stream insects. Annual Review of Entomology 45: 83-110.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press.

Jackson, J. K., and S. G. Fisher. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran Desert stream. Ecology 67: 629-638.

Jones, R. C., and C. C. Clark. 1987. Impact of watershed urbanization on stream insect communities. Water Resources Bulletin 23: 1047-1055.

Lammert, M. and J. D. Allan. 1999. Assessing biotic integrity of streams: Effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environmental Management 23: 257-270.

Meyer, J.L., L. A. Kaplan., D. Newbold, D. L. Strayer, C. J. Woltemade., J. B. Zedler, R. Beilfuss, Q. Carpenter, R. Semlitsch, M. C. Watzin, and P. H. Zedler. 2003. Where rivers are born: the scientific imperative for defending small streams and wetlands. American Rivers and Sierra Club. (available at : http://www.sierraclub.org/cleanwater/reports_factsheets/)

Meyer, J. L., and J. B. Wallace. 2001. Lost linkages and lotic ecology: Rediscovering small streams, p. 295-317. *In* M. C. Press, N. J. Huntly and S. Levin [eds.], Ecology: Achievement and Challenge. Blackwell Scientific.

Morin, A., and P. Dumont. 1994. A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. Journal of the North American Benthological Society 13: 357-367.

Morin, A., W. Lamoureux, and J. Busnarda. 1999. Empirical models predicting primary productivity from chlorophyll *a* and water temperature for stream periphyton and land and ocean phytoplankton. Journal of the North American Benthological Society 18: 299-307.

Morley, S. A., and J. R. Karr. 2002. Assessing and restoring the health of urban streams in the Puget Sound Basin. Conservation Biology 16: 1498-1509.

MWLA. 1999. Tackling Non-Point Source Water Pollution in British Columbia: An Action Plan. Ministry of Water, Land and Air Protection.

Newbold, J. W., J. W. Elwood, R. V. O'Neill, and A. L. Sheldon. 1983. Phosphorus dynamics in a woodland stream ecosystem: a study of nutrient spiralling. Ecology 64: 1249-1265.

Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32: 333-365.

Randall, R. G., and C. K. Minns. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Canadian Journal of Fisheries and Aquatic Sciences 57: 1657-1667.

Rice, S. P., M. T. Greenwood, and C. B. Joyce. 2001. Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems. Canadian Journal of Fisheries and Aquatic Sciences 58: 824-840.

Rios, S. L., and R. C. Bailey. 2006. Relationship between riparian vegetation and stream benthic communities at three spatial scales. Hydrobiologia 553: 153-160.

Rosenberg, D.N. and V. H. Resh 1993. Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11: 141-156.

Sidle, R. C., Y. Tsuboyama, S. Noguchi, I. Hosoda, M. Fujieda, and T. Shimizu. 2000. Streamflow generation in steep headwaters: A linked hydro-geomorphic processes. Hydrological Processes 14: 369-385.

Soranno P.A., S. L. Hubler, S. R. Carpenter, and R. C. Lathrop. 1996. Phosphorus loads to surface waters: A simple model to account for spatial pattern of land use. Ecological Applications 6: 865-878.

Sponseller, R.A., E. F. Benfield, and H. M. Valett H.M. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. Freshwater Biology 46: 1409-1424.

Strayer,D.L., R. E. Beighley, L. C. Thompson, S. Brooks, C. Nilsson, G. Pinay and R. J. Naiman. 2003. Effects of land cover on stream ecosystems: Roles of empirical models and scaling issues. Ecosystems 6: 407-423.

Stewart, J. S., L. Wang, J. Lyons., J. A. Horwatich. and R. Bannerman.2001. Influences of watershed, riparian-corridor, and reach-scale characteristics on aquatic biota in

agricultural watersheds. Journal of the American Water Resources Association 37: 1475-1487.

U.N. Population Division. 2005. World Urbanization Prospects: The 2005 Revision, Executive Summary, ESA/P/WP.200. New York: United Nations.

USEPA. 2002. National Water Quality Inventory: 2000. Office of Water, Environmental Protection Agency.

Walsh, C. J., T. D. Fletcher, and A. R. Ladson. 2005. Stream restoration in urban catchments through redesigning stormwater systems: Looking to the catchment to save the stream. Journal of the North American Benthological Society 24: 690-705.

Wang, L., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries 22: 6-12.

Weigel, B.M., L. Wang, P. W. Rasmussen, J. T. Butcher, P. M. Stewart, T. P. Simon, and M. J. Wiley. 2003. Relative influence of variables at multiple spatial scales on stream macroinvertebrates in the Northern Lakes and Forest ecoregion, U.S.A. Freshwater Biology 48: 1440-1461.

Wipfli, M. S., and D. P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: Implications for downstream salmonid production. Freshwater Biology 47: 957-969.

Wipfli, M. S., and J. Musslewhite. 2004. Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. Hydrobiologia 520: 153-163.

Chapter 1: Algal, invertebrate, and fish biomass along a forested gradient at multiple spatial scales

Abstract

We measured water quality and quantified algal, invertebrate, and fish biomass at 38 small headwater streams in the National Capital Region of Canada along a forest cover gradient to determine characteristic scales of biomass response at multiple trophic levels. We considered 55 scales of forest cover including several buffer widths (10-320 m) and distances (10-1280 m, entire riparian distance) and entire subcatchments. Variation in biomass explained by forest cover generally increased with increasing scale at each trophic level, suggesting that catchment-wide disturbances are the most influential determinants of stream biomass. Subcatchment forest cover explained more variation in algal and invertebrate biomass than fish biomass. Subcatchment forest cover was just as effective a predictor of biomass as locally measured water quality parameters. When considering the independent effects of forest cover on biomass at three coarse scales (reach, riparian, and the entire subcatchment), subcatchment forest cover was the only significant predictor of biomass, suggesting that maintenance of reach and riparian buffers are ineffective at protecting stream function from catchment-wide impacts. Since most stream restoration programs stipulate riparian buffer conservation as a primary tool for mediating watershed disturbance, this study has implications for altering the way we manage streams.

Introduction

Responsible and sustainable land use implies that ecosystems are not altered sufficiently by human activities to impair function. Proper management of the levels and types of human activities therefore requires quantification of ecosystem responses to changes in land use. Multiple studies have demonstrated strong correlations between structural characteristics of running water ecosystems and land use within riparian buffers (Lammert and Allan 1999, Fitzpatrick et al. 2001, Sponseller and Benfield 2001, Rios and Bailey 2006), and/or the entire subcatchment (Stewart et al. 2001, Strayer et al. 2003, Weigel et al. 2003, Roth et al. 1996, Morley and Karr 2002, Hession 2003a, b, Wang et al. 2003, Freeman and Schorr 2004). However, few studies have examined functional responses of stream and river ecosystems to changes in land use (Houser et al. 2005, Meyer et al. 2005, Bunn et al. 1999), and it is still unclear if the characteristic scales of structural responses described by most studies are congruent with the scales at which functional responses occur.

The issue of the characteristic scale at which running water ecosystems respond to land use is central to proper management. Indeed, a recent study demonstrating the significance of effective imperviousness within the entire catchment on stream health suggests that the common riparian buffer protection approach is unlikely to be sufficient because it does not match the scale of disturbance (Walsh et al. 2005). Identifying the extent of land use influences on running water ecosystem structure or function, and assessing the effect of riparian buffer protection relative to protection of land elsewhere in catchments, are necessary steps towards effective management.

In practice, most running water management programs and restoration projects focus on physical habitat at the reach scale and on the protection of riparian vegetation (Brown 2000, Bernhardt et al. 2005). Widespread usage of riparian buffers as a management tool has been predicated on observations showing that riparian buffers of only 30-50 m can significantly reduce the amount of non-point source pollution entering streams (Swift and Norton 1993, Mayer et al. 2006). Riparian buffers are attractive because they require preserving relatively small amounts of land, typically less than 5% of the land within catchments (FISRWG 1998). However, riparian buffer protection and in-stream interventions at the reach scale are effective only if the ecosystem responds more to local conditions and proximal land use than to the overall land use in the catchment basin.

Previous studies that measured the effectiveness of buffer protection and/or empirically quantified the relationships between structural properties of running water ecosystems (biotic indices, species richness, etc.) and land use (Rios and Bailey 2006, Strayer et al. 2003, Morley and Karr 1999) have used varying and arbitrary widths for the riparian zone. In cases where multiple buffer widths and scales have been examined, for example in the studies by Wang et al. 2001 and Lammert and Allan 1999, it has been difficult to assess the independent effects of land use in riparian buffers and in the entire catchment because of strong correlations. When addressing the influence of each scale on biota, the variation in land use at each scale and the independent contributions of each scale are often neglected. The choice of buffer widths and distances can alter land use compositions within buffers, thereby weakening or strengthening correlations between land use and stream biota (Frimpong et al. 2005). Variation in forest cover at each scale

may also impact results as scales with greater ranges in land use may appear to be more influential on stream biota (Lammert and Allan 1999). Further, since land use compositions are typically correlated at multiple scales, the influence of each scale must be quantified independently of each other before making conclusions regarding the importance of multiple scales.

In this study, we quantify algal, invertebrate, and fish biomass at 38 small headwater streams along a forest cover gradient at multiple scales. We choose biomass at these 3 trophic levels because it is the single best correlate of biological productivity (Benke 1993) and only requires a fraction of the inordinate effort to quantify production. We considered percent forest cover within 55 scales including several buffer widths and distances and the entire subcatchment. Our objectives were to determine the scale at which forest cover has the greatest influence on benthic biomass, characterize patterns in algal, invertebrate, and fish biomass at the optimal scale of forest cover, and empirically assess whether forest cover within narrow local and riparian buffers is an effective tool for mitigating catchment-wide impacts on stream biomass.

Methods

Study Area

The study was performed in the National Capital Region of Canada, located in Eastern Ontario and Western Québec (45°N 75°W, Fig. 1.1). Historically this portion of Canada was entirely covered by forest, primarily composed of red pine, eastern white pine, eastern hemlock and various ashes, maple, and oak species (Hosie 1979). Today, however, 52% of the forest cover within the National Capital Region has been replaced with urban and agricultural land uses (NCC 1999). A population of 1.1 million people

resides in the National Capital Region, which consists of an area of 5,318.36 square kilometers that straddles the boundary between the provinces of Ontario and Québec (2006 Canadian Census).

Site Selection

During late spring and early summer 2001, we surveyed potential sites within the Gatineau Park, previous sampling sites in Québec (Bourassa and Morin 1995) and sites routinely monitored for water quality by the Regional Municipality of Carleton and Ottawa (RMOC 1999). A total of 38 sites were deemed appropriate for this study as they contained riffle and run habitats, 2-7 meters widths, relatively convenient accessibility, and an extensive range in forest cover.

Quantifying Forest Cover at Multiple Scales in a GIS

Typical multiple-scale studies consider 3 broad scales, including reach (local), riparian (regional), and subcatchment scales (for example see Morley and Karr 2002). However, the choice of buffer widths and distances is often arbitrarily decided upon and can alter land use compositions at local and riparian scales, potentially weakening or strengthening correlations between land use and stream biota (Frimpong et al. 2005). Therefore, we used a fine gradient of scale size, quantifying the upstream proportion of forest cover for each of the 38 study sites at 55 spatial scales, including several buffers widths (doubling from 10-320 m) and distances (doubling from 10-1280 m and the entire upstream riparian length) within subcatchment boundaries, and subcatchments. We chose 320 m as the maximum buffer width since the areas of the 320-m riparian buffers nearly covered the entire subcatchment areas. We chose 1280 m as the maximum

distance since the minimum riparian length of our streams was just over a kilometer. Forest cover was quantified in a GIS using ArcMap™ 8.2 (ESRI, Redlands, California) and 1:50,000 vector topographic maps displaying streams, rivers, lakes, and forest cover (NRC 1991). Buffers were delineated using the Buffer Wizard extension of ArcMap. We delineated subcatchments by modifying existing catchment basins provided by the RMOC (2004) to include only the portion upstream of each sampling point in Ontario. Québec subcatchments were determined from a grid (built from a digital elevation map at 10-m intervals (NCC 2001) using watershed commands with the sampling sites designated as pourpoints within the Spatial Analyst extension of ArcMAP (ESRI, Redlands, California).

To assess the accuracies of small-scale forest cover obtained from the 1:50,000 digital maps, we ground-truthed forest cover within buffers that were 10, 20, and 40 m wide and at distances that were 10, 20, and 40 m upstream (9 buffers) of each of the 38 sampling sites and compared these "real-world" contemporary values of forest cover with digital forest cover.

Field Methods

Chlorophyll *a*, benthic invertebrates, and fish were sampled at the 38 study sites during July and August of 2001 and 2002. Upon arrival at each site, two seines were erected to demarcate a 10-m section of each stream that included riffle and pool areas. We felt it was important to contain the fish immediately so that they could not escape from the sampling area while we collected water quality and cobble samples.

Average temperature was obtained from triplicate temperature measurements taken within the stream at each site. For water quality monitoring sites in Ontario, we

used averages from summer (June, July, and August) water quality parameters, including alkalinity, chloride ions, dissolved organic carbon, nitrate, total kjeldahl nitrogen, sulfate ions, conductivity, total phosphorus, total nitrogen, and pH, collected by the Regional Municipality of Ottawa and Carleton. For Québec sites, we collected triplicate water samples before sampling for biota and placed these in dark coolers with ice packs. Water quality samples were submitted to the Robert O. Pickard Environmental Centre Laboratory of the City of Ottawa for analysis within 24 hours.

Six replicate cobble samples (8-25 cm in diameter) were collected from riffle areas, before sampling for fish so that the electroshocking did not disturb the invertebrates on the cobbles. Average velocity was determined from 6 velocity measurements taken at approximately 60% of the depth of the stream where each of the 6 cobbles were collected. Each cobble sample was carefully placed in a whirl pack bag with 95% ethanol and stored in a dark cooler with ice packs. Fish were collected by backpack electroshocking along the 10-meter transect of the stream using the removal method (Zippen 1958). The identification, standard length, fork length, and maximum width of live fish were determined in the field after each electroshocking pass. Fish that could not be identified in the field were preserved in ethanol and returned to the lab for further analysis.

Laboratory methods

After returning to the lab, the cobble samples were placed in a dark and cool (6°C) refrigerator. 24-48 hours later, 15 ml of ethanol was removed from each bag and periphyton chlorophyll *a* per cobble was determined spectrophotometrically using methods described by Ostrofsky and Rigler (1987). Invertebrates from the cobbles were

then collected in a 2-mm sieve, sorted, and measured along their central axis to the nearest 0.01 mm using an image analysis system. The cleaned cobble was retained and its area was determined from the weight of aluminum foil required to completely cover it (Reice 1980).

Data analyses

Algal biomass in mg m^{-2} was estimated from the amount of chlorophyll *a* on the entire cobble, assuming that chlorophyll *a* composed 4% of algal dry mass (Morin and Nadon 1991). Dry mass (mg) of invertebrates retained in the 2 mm sieves was estimated from taxon-specific length (mm) to weight (mg) regressions (Benke et al. 1999). A published sieve retention probability accounted for dry mass lost through 2 mm sieves (Morin et al. 2004), and biomass of invertebrates per cobble was calculated as the sum of the corrected dry mass per cobble in mg m^{-2}. We used fish fork lengths (mm) in taxon-specific length-weight regressions (Randall and Minns 2000) to calculate the wet mass (g) of fish. Fish biomass (in mg dry mass m^{-2}) was then calculated from individual fish lengths and wet mass using PopPro (Kwak 1992), assuming that fish dry mass comprised 20% of fish wet mass (Kushlan et al. 1986). Prior to data analyses, we added one half of the minimum non-zero fish biomass to fish biomass, and normalized all biomass and water quality data using a $\log_{10}$ transformation.

Searching for Biomass Patterns along a Forested Gradient at Multiple Scales

We modeled the response of algal, invertebrate, and fish biomass to the proportion of forest cover within buffers or subcatchments using Lowess functions and generalized additive models (GAM's) that allow for nonlinearity of data in S-PLUS 7

(Insightful, Seattle, Washington). GAM's are appropriate models for detecting patterns in stream conditions as responses to increasing land use gradients are typically nonlinear (Allan 2004). To detect patterns in the variation explained by the GAM's (r^2's) and the unexplained variation (residual mean squares, RMS) among multiples scales, we then plotted the r^2 values against 54 scales of forest cover, including buffer widths (10-320 m) and distances (10-1280 m and riparian) for each trophic level. In these plots, we assigned 20,000 m as the distance for each of the riparian buffers so that we could include riparian buffers despite variable riparian lengths among sites. We considered the optimal scale of forest cover for predicting biomass to be the scale that explained the most variation in biomass (i.e. highest r^2 value) and contained the least unexplained variation (i.e. lowest RMS value). We then looked for significant differences in the precision of these models at multiple scales by comparing the residual variation (i.e. RMS) in models using the optimal scale and the remaining scales. We also compared model results using the optimal scale of forest cover at each trophic level to assess the relative importance of forest cover in determining algal, invertebrate, and fish biomass.

So that we could test the effectiveness of narrow local and riparian buffers at mitigating the effects of catchment-wide disturbance on biomass, we partitioned the variance in biomass independently explained by forest cover obtained from GAM's at 3 broad scales similar to those used by Morely and Karr (2002): reach (40-m buffer width and 10-m buffer distance), riparian buffer (40-m buffer width and entire riparian distance), and the entire subcatchment, following the approach of Whittaker (1984). We chose a 40-m buffer width for reach and riparian scales since this is the closest buffer width in our study to the minimal buffer width recommended by reviews on buffer

effectiveness to effectively reduce impacts from catchment-wide disturbance (DCE 1990, FISRWG 1998, Broadmeadow and Nisbet 2004, Lee et al. 2004, Mayer et al. 2006). Because independent variation explained by a single term is calculated as the difference in variation explained by the remaining terms and their interactions, and is presented as the proportion of the total variance, this approach allows for the percent of variation explained by each term to be negative. This approach has been used in ecological studies to quantify unique and shared effects that explain univariate data (He et al. 1996, Grover and Chrzanowski 2004, Gusewell et al. 2005), similar to the commonly used partitioning of variance for ecological multivariate data by Borcard et al. (1992).

Lastly, we reduced the water quality data into a few uncorrelated principal components to predict stream biomass in GAM's using the Lowess function to smooth data. Water quality regression results were then compared with the optimal forest cover regressions to determine if locally measured physical factors or forest cover are better determinants of stream biomass. Only 35 sites were used for water quality and forest cover comparisons, as 3 of the 38 sites were missing water quality data.

Results

Algal biomass ranged from 96 (± 23 SE) to 7,325 (± 3,243 SE) mg dry mass m^{-2}, while invertebrate biomass ranged from 55 (±38 SE) to 22,386 (± 6756 SE) mg dry mass m^{-2} and fish biomass ranged from 0 to 10,506 (± 308) mg dry mass m^{-2} (Table A.2). There was a broad range of forest cover at most scales (10-320-m buffers at 10-1280-m distances: 0 to ≤ 98%), with a slightly lower range of forest cover within riparian buffers and subcatchments (minimum forest cover: 5-12%, maximum forest cover: 90-98%, Table A.7). Subcatchments and riparian buffers contained the lowest variation in forest

cover among sites (CV = 43-59%), and variation in forest cover increased as buffer distances became shorter (CV > 115% at 10-m distances, Table A.7). Not surprisingly, as buffer widths and distances increased, the distribution of forest cover became progressively more similar to the distribution of forest cover within subcatchments, (range in Pearson's r = 0.30-0.98, Table A.7).

Biomass Response to Forest Cover at Multiple Scales

In general, biomass at the three trophic levels was more strongly correlated with land use within the entire subcatchment than at smaller distances. The amount of variation in algal biomass explained by forest cover generally increased with increasing scale size (from 24 to 60%), excluding relatively higher variation explained by local scales (≤ 40 m; digital forest cover r^2 = 0.28-0.35, ground-truthed forest cover r^2 = 0.35-0.53; Fig. 1.2). The amount of variation in invertebrate biomass explained by forest cover also increased with increasing scale size (r^2 = 0.18-0.56), excluding relatively higher variation explained by local scales (≤20 m, digital forest cover r^2 = 0.24-0.29; ≤ 40 m, ground-truthed forest cover r^2 = 0.33-0.48). Subcatchment forest cover predicted algal (RMS=0.083) and invertebrate (RMS=0.162) biomass significantly more precisely than forest cover within 10-20-m buffers at several distances where r^2 values were less than 0.3 (Fig. 1.2; algal RMS ≥ 0.147, $F_{37,37} \geq 1.776$, $p < 0.05$; invertebrate RMS ≥ 0.285, $F_{37,37} \geq 1.76$, $p < 0.05$). Similar to algal and invertebrate biomass, forest cover explained more variation in fish biomass with increasing scale size (r^2 = 0.04-0.40), excluding relatively higher variation explained by local scales (r^2 digital forest cover within buffers and distances ≤ 40 m = 0.10-0.22, r^2 ground-truthed forest cover within 10-m buffers and 20-40-m distances and 20-40-m buffers at 40-m distances= 0.10-0.28; Fig. 1.2). Despite

increasing r^2 values with scale size, however, subcatchment forest cover (RMS = 0.34) was not a significantly better predictor of fish biomass than forest cover at smaller scales (RMS $\leq$ 0.549, $F_{37, 37} \leq 1.594$, $p \geq 0.08$).

Biomass Response to the Optimal Scale of Forest Cover

Figure 1.3 shows patterns in algal, invertebrate, and fish biomass along a gradient of forest cover at the scale where forest cover explained the most variation in biomass. Algal biomass slightly increased from 988 mg m^{-2} to 7325 mg m^{-2} as subcatchment forest cover increased from 6% to 45%, with the exception of relatively low algal biomass (325 mg m^{-2}) at Ruisseau des Fées. Invertebrate biomass was also relatively high (1131-22,386 mg m^{-2}) at sparsely forested sites, with the exception of relatively low invertebrate biomass at Ruisseau des Fées (55 mg m^{-2}) and Graham Creek (217 mg m^{-2}). When forest cover comprised more than 45% of the subcatchment, both algal and invertebrate biomass steadily declined to 96 and 308 mg m^{-2}, respectively, with increasing forest cover. Contrary to patterns in algal and invertebrate biomass, fish biomass was relatively high, but quite variable (400-10,506 mg m^{-2}), at sites with subcatchments predominantly covered by forest. Fish biomass began to decline with decreasing forest cover when forest cover was less than 45%. Four of the 7 sites with less than 20% subcatchment forest cover contained no fish.

Subcatchment forest cover explained more variation in algal ($r^2 = 0.58$), and invertebrate ($r^2 = 0.56$) biomass than fish biomass ($r^2 = 0.40$; Fig. 1.3). Models predicting algal (RMS = 0.083) biomass were significantly more precise than models that predicted invertebrates (RMS = 0.162, $F_{37, 37} = 1.950$, p=0.02) and fish (RMS = 0.344, $F_{37, 37} =$

4.154, $p<0.001$), while models predicting invertebrate biomass were significantly more precise than models that predicted fish biomass ($F_{37, 37} = 2.130$, $p=0.01$).

Shared and Unique Variation in Biomass explained by Local, Riparian, and Subcatchment Forest Cover

Table 1.1 gives the results from the partitioning of variance in biomass explained independently by local, riparian, and subcatchment scales and their interactions. Subcatchment forest cover was the only scale to significantly predict biomass when partialing out the effects of the other scales, despite slightly lower variation explained by subcatchment forest cover than local forest cover. Riparian forest cover consistently explained less variation in biomass at each trophic level than did forest cover at local and subcatchment scales.

Influence of Local Water Quality Factors vs. Subcatchment Forest Cover on Biomass

Subcatchment forest cover was significantly negatively correlated with alkalinity, chloride, nitrate, conductivity, total nitrogen, and pH (Table 1.2). Algal and invertebrate biomasses were significantly positively correlated with alkalinity, chloride, conductivity, total nitrogen, and pH, whereas fish biomass was not significantly correlated with water quality parameters.

Water quality explained slightly more variation in invertebrate and fish biomass than subcatchment forest cover, whereas subcatchment forest cover explained slightly more variation in algal biomass than water quality parameters (Table 1.3). However, there were no significant differences in the fits of the models that used water quality parameters or forest cover to predict biomass ($F_{34, 34} < 1.77$, $p > 0.05$; Table 1.2).

Discussion

The Importance of Subcatchment Forest Cover

The repeated pattern at each trophic level of increasing variation in biomass explained by forest cover with increasing scale observed in this study (Fig. 1.2) supports recent studies demonstrating the importance of large-scale impacts to streams (Taylor et al. 2004, Houser et al. 2005, Morgan and Cushman 2005) . However, since local effects of forest cover were also evident in our study, it is clear that that land use is operating at multiple scales, perhaps by influencing nutrients and hydrology at the subcatchment scale and habitat, stream temperature, and substratum characteristics at local scales (Frissell et al. 1986, Allan et al. 1997, Sponseller et al. 2001, Allan 2004, Taylor et al. 2004).

Previous multiple-scale studies that have also considered the impacts of local habitat on benthic community structures and fish have found local habitat to be more influential than catchment or riparian land use (Richards et al. 1997, Lammert and Allan, 1999, Roy et al. 2003, Death and Joy 2004, Lehane et al. 2004). In contrast, Taylor et al. (2004) found catchment scale variables, including storm water drainage connections and imperviousness, as well as total phosphorus, which was strongly correlated with catchment scale variables, to be the primary determinants of algal biomass rather than substrate type or light availability. While habitat features were most significant, Wang et al. (2003) found watershed variables to have an increasing influence on the abundance of fish in less pristine areas. Although we cannot assess the influence of reach-scale habitat features and locally controlled physical parameters that were not measured in our study, subcatchment forest cover was consistently the best predictor of biomass suggesting that catchment-wide land use plays a primary role in determining stream biomass.

Is maintenance of riparian vegetation an effective management strategy?

Patterns in variation of biomass explained by forest cover with scale size and results from previous studies (Richards et al. 1996, Roth et al. 1996, Houser et al. 2005, Roy et al. 2006) made us question the efficacy of watershed management scenarios that stipulate maintenance of riparian buffers to mitigate agricultural, urban, and forestry impacts on aquatic systems (Hubbard and Lowrance 1994, Brown 2000, Miltner et al. 2004). However, in our dataset the distribution of forest cover at multiple scales was correlated, as is true for many catchments (Allan 2004). Admittedly, matched pairs of study sites with and without riparian forest along our forested gradient similar to the study design of Hession et al. (2003a, 2003b) would have allowed a more powerful test of the effectiveness of riparian buffers to alter the functional response of streams to land use at the catchment scale. Nevertheless, partitioning the unique and shared variation in biomass explained by forest cover at multiple scales did reveal that only subcatchment forest cover significantly predicted biomass when partialing out the effect of reach and riparian forest cover (Table 1.1), thereby suggesting that buffer maintenance alone may not be a sufficient best management practice in our streams. In congruence with our results, Hession et al. (2003a, 2003b) found that metrics of algal, macroinvertebrate, and fish community structure, excluding algal biomass, were not significantly altered by the presence of riparian forest independently of urban land use.

Variation in Forest Cover at Multiple Scales

In multiple-scale studies, scales with smaller ranges in land use/land cover can misleadingly appear to be less influential on biotic communities than scales with greater ranges in land use/land cover (Lammert and Allan 1999, Stauffer et al. 2000). In our

study, however, the range of forest cover (0 to ≤ 98%) did not vary with scale, excluding relatively smaller ranges within riparian buffers and subcatchments (minimum forest cover: 5-12%, maximum forest cover: 90-98%), and forest cover became less variable with increasing distances (CV >115% to 43%) but did not vary with buffer widths, although forest cover was generally a better predictor of biomass with increasing buffers and distances (Fig. 1.2). Exceptions to these patterns include somewhat lower r^2 values for models predicting algal and invertebrate biomass from forest cover within narrow riparian buffers (≤ 40 m) than for the same buffer widths at slightly shorter distances, which may be due in part to the relatively small range (10-96%) in forest cover within these narrow riparian buffers.

Accuracy of digital maps

Furthermore, the observed patterns in r^2 values could be due to maps that are too coarse to accurately define forest cover at small scales or changes in land use occurring after the aerial photographs of forest cover were taken. It is unlikely that the resolution of our maps greatly affected the amount of variation in biomass explained by forest cover; however, since digital forest cover at the smallest scales explained slightly more variation in biomass than slightly larger scales (Fig. 1.3). In addition, the precision of models using ground-truthed forest cover was never significantly higher than those that used digital forest cover at small scales (≤ 40 m: $F_{36, 36} \geq 0.82$, $p \geq 0.72$), despite slightly higher variation explained by ground-truthed forest cover than digital forest cover (Fig 1.3). What's more, the overall patterns in r^2 and RMS with forest cover did not change when using ground-truthed or digital data at small scales (Fig. 1.3). Therefore, we feel

inaccuracies in digital forest cover maps contributed minimally to the observed patterns in r^2 with scale size.

Lower variation in fish biomass explained by subcatchment forest cover

Unlike Fitzpatrick et al. (2001), who found that metrics of fish community structure were more sensitive than algal and invertebrate community structure metrics to land cover, forest cover at multiple scales in our models explained more variation in algal and invertebrate biomass than in fish biomass. Greater unexplained variation in fish biomass along our forested gradient could have been due to a relatively small range in fish biomass or poor sampling precision of fish biomass estimates. However, the range and variation in fish biomass (0-10,506 mg m^{-2}, CV=1.06) was similar to algal (5-7,325 mg m^{-2}, CV=0.83) and invertebrate (55-22,386 mg m^{-2}, CV = 1.02) biomass. The sampling precision of our fish biomass estimates was also greater than for algae and invertebrates as indicated by the narrower standard errors bars in Fig. 1.3, which were also generally less than the difference between observed and predicted fish biomass.

While we do not know the accuracy of biomass estimates, we suspect that an estimate of biomass on a given date is a poorer estimate of summer biomass for fish than for algae or invertebrates as fish are more mobile than benthic algae and invertebrates, and fish abundance is potentially more temporally variable. However, results from a concurrent study considering a subset of the sites in this study (n = 12) on three dates during 2002 indicate that the temporal variability of fish biomass estimates (RMS = 0.40) was not significantly greater ($F_{11, 35} = 1.31$, $p = 0.26$) than the unexplained variation (RMS = 0.30) in average fish biomass (n = 12) along a gradient of subcatchment forest

cover, indicating that temporal variability had little impact on observed patterns in fish biomass along the forested gradient.

Therefore, since it appears that the range, precision, and temporal variability of fish biomass did not contribute to the relatively lower variation explained by forest cover, factors other than forest cover may be more influential on fish biomass. In this study, water quality parameters were correlated with forest cover (Table 1.2), and similar to the significantly weaker response of fish biomass to forest cover, models predicting fish biomass from water quality parameters contained significantly weaker fits than models predicting algal or invertebrate biomass from water quality parameters (Table 1.3). Perhaps, habitat or hydrology, which were not measured in this study, play important roles in determining fish biomass in addition to forest cover or water quality. Although these factors may also be related to forest cover within subcatchments, point sources, such as stormwater drainage connections, can also alter habitat and hydrology (Taylor et al. 2004, Walsh et al. 2005) and presumably impact fish biomass as well. Indeed, multiple-scale studies have found reach-scale habitat variables to be more influential on fish community structure than catchment land use (Lammert and Allan 1999, Wang et al. 2003, Lehane et al. 2004).

Conclusions

Forest cover within subcatchments explained more variation in biomass than forest cover at smaller scales. Since the range and precision of forest cover at each scale did not appear to impact the ability of forest cover to predict biomass, we believe that catchment-wide forest cover was a better predictor of biomass because it best matched the scale of disturbance. Fits of models using forest cover within subcatchments or

locally measured water quality parameters to predict biomass were significantly better for algae and invertebrates than for fish. The range, precision, and temporal variability of fish biomass estimates did not appear to contribute to the greater unexplained variance in fish biomass, suggesting that factors other than forest cover and water quality parameters measured in this study may also contribute to the variation in fish biomass.

As recommended by Walsh et al. (2005), we believe that stream restoration techniques should focus on catchment-wide remediation, since it is at this scale that disturbances most impact water quality and ultimately the benthos, and riparian buffers were not effective at mitigating catchment-wide impacts. Providing a more parsimonious measure of disturbance that is just as good at predicting benthic biomass as routinely monitored water quality parameters, catchment-wide land use/land cover measured in a GIS should aid benthic ecologists and conservation biologists in developing effective stream restoration techniques as well as working proactively with urban planners to protect the ecological conditions of streams.

Acknowledgements

This study was supported by an NSERC Grant (R GPIN-42799-2001) to A.M. We thank J. Strike for invaluable assistance in the field and laboratory and data analysis suggestions made by M. Fortin. We greatly appreciate water quality data and digital catchment maps provided by the Regional Municipality of Ottawa and Carleton.

Literature Cited

Allan, J. D. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. Annual Review of Ecology, Evolution, and Systematics 35: 257-284.

Allan J. D., D. L. Erickson and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology 37: 149-161.

Benke, A. C. 1993. Edgardo Baldi Memorial Lecture: Concepts and patterns of invertebrate production in running waters. Verh.Internat.Verein.Limnol. 25: 15-38.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18: 308-343.

Bernhardt, E.S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz., G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and O Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308: 636-637.

Borcard, D., P. Legendre, and P. Drapeau.. 1992. Partialling out the spatial variation of ecological variation. Ecology 73: 1045-1055.

Bourassa, N., and A. Morin A. 1995. Relationships between size structure of invertebrate assemblages and trophy and substrate composition in streams. Journal of the North American Benthological Society 14: 393-403.

Broadmeadow, S., and T. R. Nisbet. 2004. The effects of riparian forest management on the freshwater environment: A literature review of best management practice. Hydrology and Earth System Sciences 8: 286-305.

Brown, K. B. 2000. Urban stream restoration practices: an initial assessment. Center for Watershed Protection, Ellicott City, Maryland.

Bunn, S.E., T. D. Mosisch and P. M. Davies. 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. Freshwater Biology 41: 333-345.

Death, R.G., and M. K. Joy 2004. Invertebrate community structure in streams of the Manawatu-Wanganui region, New Zealand: The roles of catchment versus reach scale influences. Freshwater Biology 49: 982-997.

DCE. 1990. Environmental guidelines for river management works. Department of Conservation and Environment . Office of Water Resources, Government Printing Office, Melbourne, Victoria.

FISRWG. 1998. Stream Corridor Restoration: Principles, Processes, and Practices. number GPO Item No. 0120-A; SuDocs No. A 57.6/2:EN 3/PT.653. ISBN-0-934213-59-3. Federal Interagency Stream Restoration Working Group. (available at http://www.nrcs.usda.gov/technical/stream_restoration/newgra.html)

Fitzpatrick, F. A., B. C. Scudder, B. N. Lenz, and D. J. Sullivan. 2001. Effects of multi-scale environmental characteristics on agricultural stream biota in eastern Wisconsin. Journal of the American Water Resources Association 37: 1489-1507.

Freeman, P.L., and M. S. Schorr. 2004. Influence of watershed urbanization on fine sediment and macroinvertebrate assemblage characteristics in Tennessee Ridge and Valley streams. Journal of Freshwater Ecology 19: 353-362.

Frimpong, E.A., T. M. Sutton, K. J. Lim, P. J. Hrodey, B. A. Engel., T. P. Simon, J. G. Lee, and D. C. Le Master. 2005. Determination of optimal riparian forest buffer dimensions for stream biota-landscape association models using multimetric and multivariate responses. Canadian Journal of Fisheries and Aquatic Sciences 62: 1-6.

Frissell, C.A., W. J. Liss., C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. Environmental Management, 10, 199-214.

Griffith, J.A. 2002. Geographic techniques and recent applications of remote sensing to landscape-water quality studies. Water, Air, and Soil Pollution, 138, 181-197.

Grover, J.P., and T. H. Chrzanowski. 2004. Limiting resources, disturbance, and diversity in phytoplankton communities. Ecological Monographs 74: 533-551.

Gusewell, S., K. M. Bailey, W. J. Roem, and B. L. Bedford. 2005. Nutrient limitation and botanical diversity in wetlands: Can fertilisation raise species richness? Oikos 109: 71-80.

He, F., P. P. Legendre, and J. V. laFrankie. 1996. Spatial pattern of diversity in a tropical rain forest in Malaysia. Journal of Biogeography 23: 57-74.

Hession, W.C., D. D. Hart, R. J. Horwitz, D. A. Kreeger, D. J. Velinsky, J. E. Pizzuto, D. F. Charles, and J. D. Newbold. 2003a. Riparian reforestation in an urbanizing watershed: effects of upland conditions on instream ecological benefits. Final

report. number R825798. US Environmental Protection Agency, National Center for Environmental Research. (Available at: cfpub.epa.gov/ncer_abstracts/index.cfm/fuseaction/display.abstractDetail/abstract/182/report/F)

Hession, W.C., J. E. Pizzuto, T. E. Johnson, and R. J. Horwitz. 2003b. Influence of bank vegetation on channel morphology in rural and urban watersheds. Geology 31: 147-150.

Hosie, R.C. 1979. Native Trees of Canada. Fitzhenry and Whiteside Ltd., in cooperation with the Canadian Forest Service (Environment Canada) and the Canadian Government Publishing Centre, Supply and Services, Don Mills, Ontario.

Houser, J.N., P. J. Mulholland, and K. O. Maloney. 2005. Catchment disturbance and stream metabolism: Patterns in ecosystem respiration and gross primary production along a gradient of upland soil and vegetation disturbance. Journal of the North American Benthological Society 24: 538-552.

Hubbard, R.K. and R. R. Lowrance. 1994. Riparian forest buffer system research at the coastal plain experiment station, Tifton, GA. Water, Air, and Soil Pollution 77: 409-432.

Kushlan, J. A., S. A.Voorhees, W. F. Loftus and P. C. Frohring. 1986. Length, mass, and calorific relationships of everglades animals. Florida Scientist 49: 65-79.

Kwak, T. J. 1992. Modular microcomputer software to estimate fish population parameters, production rates, and associated variance. Ecology of Freshwater Fish 1: 73-75.

Lammert, M. and J. D. Allan. 1999. Assessing biotic integrity of streams: Effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environmental Management 23: 257-270.

Lee, P., C. Smyth and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management 70: 165-180.

Lehane, B.M., P. S. Giller, J. O'Halloran and P. M. 2004. Relative influences of catchment geology, land use and in-stream habitat on brown trout populations in south-western Ireland. Proceedings of the Royal Irish Academy - Section B Biology and Environment 104: 43-54.

Mayer, P.M., S.K. Reynolds, M.D. McCutchen, and T.J. Canfield. 2006 Riparian buffer width, vegetative cover, and nitrogen removal effectiveness: A review of current science and regulations. number EPA/600/R-05/118. Environmental Protection Agency, Cincinnati, OH, U.S. (available at http://www.epa.gov/ada/download/reports/600R05118/600R05118.pdf)

Meeuwig, J. J. and R. H. Peters. 1996. Circumventing phosphorus in lake management: a comparison of chlorophyll *a* predictions from land-use and phosphorus-loading models. Canadian Journal of Fisheries and Aquatic Sciences, 53, 1795-1806.

Meyer, J. L., M. J. Paul and W. K. Taulbee. 2005. Stream ecosystem function in urbanizing landscapes. Journal of the North American Benthological Society 24: 602-612.

Miltner, R. J., D. White and C. Yoder. 2004. The biotic integrity of streams in urban and suburbanizing landscapes. Landscape and Urban Planning 69: 87-100.

Morgan, R.P. and S. F. Cushman. 2005. Urbanization effects on stream fish assemblages in Maryland, USA. Journal of the North American Benthological Society 24:643-655.

Morin, A. and Nadon D. 1991. Size distribution of epilithic lotic invertebrates and implications for community metabolism. Journal of the North American Benthological Society 10: 300-308.

Morin, A., J. Stephenson, J. Strike, and A. G. Solimini. 2004. Sieve retention probabilities of stream benthic invertebrates. Journal of the North American Benthological Society 23: 383-391.

Morley, S. A. and J. R. Karr . 2002. Assessing and restoring the health of urban streams in the Puget Sound Basin. Conservation Biology 16: 1498-1509.

NCC. 1999. 1:2000 Scale Topographic Mapping (Ottawa-Hull). National Capital Commission, Ottawa, Canada.

NCC. 2001. Digital Elevation Model Data: Ottawa-Hull and Gatineau Park. National Capital Commission, Ottawa, Canada.

NRC. 1991. National Topographic DataBase, 1:50 000, version 3.10. Ottawa: Natural Resources Canada, Geomatics Canada.

Ostrofsky, M.L., F. H. Rigler . 1987. Chlorophyll-phosphorus relationships for subarctic lakes in western Canada. Canadian Journal of Fisheries and Aquatic Sciences 44: 775-781.

Randall, R. G., and C. K. Minns. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Canadian Journal of Fisheries and Aquatic Sciences 57: 1657-1667.

Reice, S.R. 1980 The Role of Substratum in Benthic Macroinvertebrate Microdistribution and Litter Decomposition in a Woodland Stream. Ecology 61: 580-590.

Richardsd C., R. J. Haro, L. B. Johnson, and G. E. Host G.E. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshwater Biology 37: 219-230.

Richards, C., L., B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53: 295-311.

Rios, S.L., and R. C. Bailey. 2006. Relationship between riparian vegetation and stream benthic communities at three spatial scales. Hydrobiologia, 553: 153-160.

RMOC. 1999. 1998 Baseline Programme. Surface Water Quality Branch, Environment and Transportation Department, Regional Municipality of Ottawa-Carleton.

Roth, N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11: 141-156.

Roy, A.H., M. C. Freeman, B. J. Freeman, S. J. Wenger, J. L. Meyer and W. E. Ensign. 2006. Importance of riparian forests in urban catchments contingent on sediment and hydrologic regimes. Environmental Management 37: 523-539.

Roy, A. H., J. B. Wallace, A. D. Rosemond, M. J. Paul and D. S. Leigh. 2003. Stream macroinvertebrate response to catchment urbanisation (Georgia, U.S.A.). Freshwater Biology 48: 329-346.

Schueler, T. 1994. The Importance of Imperviousness. Watershed Protection Techniques 1: 100-111.

Sponseller, R.A., E. F. Benfield, and H. M. Valett H.M. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. Freshwater Biology 46: 1409-1424.

Stauffer, J.C., R. M. Goldstein and R. M. Newman. 2000. Relationship of wooded riparian zones and runoff potential to fish community composition in agricultural streams. Canadian Journal of Fisheries and Aquatic Sciences 57: 307-316.

Stewart, J. S., L. Wang, J. Lyons., J. A. Horwatich. and R. Bannerman.2001. Influences of watershed, riparian-corridor, and reach-scale characteristics on aquatic biota in agricultural watersheds. Journal of the American Water Resources Association 37: 1475-1487.

Strayer,D.L., R. E. Beighley, L. C. Thompson, S. Brooks, C. Nilsson, G. Pinay and R. J. Naiman. 2003. Effects of land cover on stream ecosystems: Roles of empirical models and scaling issues. Ecosystems 6: 407-423.

Swift, D. W. and R. L. Norton. 1993. Measures for Protecting Upland Water Quality: Assessment of Forestry Buffer Strips. Final R&D report to the Scotland and Northern Ireland Forum for Environmental Research. SNIFFER, Edinburgh, UK.

Taylor, S. L., C. J. Walsh, B. E. Hatt and S. C. Roberts. 2004. Catchment urbanisation and increased benthic algal biomass in streams: Linking mechanisms to management. Freshwater Biology 49: 835-851.

Walsh, C. J., T. D. Fletcher, and A. R. Ladson. 2005. Stream restoration in urban catchments through redesigning stormwater systems: Looking to the catchment to save the stream. Journal of the North American Benthological Society 24: 690-705.

Wang, L., J. Lyon, P. Rasmussen, P. Seelbach, T. Simon, M. Wiley, P. Kanehl, E. Baker, S. Niemela and P. M. Stewart. 2003. Watershed, reach, and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 60: 491-505.

Weigel, B.M., L. Wang, P. W. Rasmussen, J. T. Butcher, P. M. Stewart, T. P. Simon, and M. J. Wiley. 2003. Relative influence of variables at multiple spatial scales on stream macroinvertebrates in the Northern Lakes and Forest ecoregion, U.S.A. Freshwater Biology 48: 1440-1461.

Whittaker, J. 1984. Model interpretation from the additive elements of the likelihood fucntion. Applied Statistics 33: 52-64.

Zippen, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22: 82-90.

Table 1.1. Unique and shared variance in algal, invertebrate, and fish biomass explained by ground truthed forest cover within reach buffers (40-m wide and 10-m distance) and riparian buffers (40-m wide and entire riparian distance), and digital forest cover within the entire subcatchment. Variances in bold indicate that the component in the generalized additive model that significantly predicted biomass ($p<0.05$).

Component	Algae	Invertebrate	Fish
residuals	24.6%	49.6%	42.8%
reach	13.8%	14.4%	12.5%
riparian	1.8%	3.7%	3.8%
subcatchment	**8.0%**	6.0%	**38.1%**
reach x riparian	1.3%	-1.3%	-2.0%
reach x subcatchment	6.9%	12.1%	-5.6%
riparian x subcatchment	16.6%	1.6%	11.4%
reach x riparian x subcatchment	27.0%	14.0%	-1.0%
Total variance	100.0%	100.0%	100.0%

Table 1.2. Comparing water quality and physical parameters with subcatchment forest cover (%), and algal, invertebrate, and fish biomass (log_{10} (mg m^{-2}), n = 35 sites) using Pearson product moment correlations. Water quality parameters included: alkalinity, chloride ions (Cl^-), dissolved organic carbon (DOC), NO_2 + NO_3 (NO_x), total kjeldahl nitrogen (TKN) , sulfate ions (SO_4), conductivity (cond.), total phosphorus (TP), total nitrogen (TN), pH, water velocity, and temperature (temp.). Correlations in bold are significant ($p < 0.004$, two-tailed test, Bonferroni adjusted critical p value for 12 multiple comparisons).

	alkalinity (mg L^{-1})	Cl^- (mg L^{-1})	DOC (mg L^{-1})	NO_x (mg L^{-1})	TKN (mg L^{-1})	SO_4 (mg L^{-1})	cond, (µs cm^{-1})	TP (mg L^{-1})	TN (mg L^{-1})	pH	velocity (m sec^{-1})	temp. (°cel.)
forest (%)	**-0.79**	**-0.81**	0.00	**-0.61**	-0.39	**-0.65**	**-0.83**	-0.47	**-0.63**	**-0.73**	-0.21	-0.39
algae	**0.75**	**0.71**	0.25	0.38	0.45	**0.52**	**0.74**	0.39	**0.54**	**0.64**	0.22	0.24
invertebrate	**0.60**	**0.48**	0.22	0.24	0.32	0.38	**0.51**	0.36	**0.49**	**0.70**	0.10	0.42
fish	-0.16	-0.33	0.31	-0.47	0.05	-0.38	-0.32	-0.14	-0.24	-0.08	0.06	0.24

Table 1.3. Comparing r^2 and RMS values from generalized additive models that used reduced water quality and physical parameters or forest cover within subcatchments to predict algal, invertebrate, and fish biomass (n = 35 sites). Principal components analysis was used to reduce log (base 10)-transformed water quality parameters into 3 factors: PC_1 = + conductivity, alkalinity, chloride ions, pH, total nitrogen, NO_3 + NO_2, sulfate ions, total kjeldahl nitrogen, total phosphorus, temperature; and PC_2 = + dissolved organic carbon, and PC_3 = - velocity. Factor loadings from the principal components analysis are given in Table A.8.

Biomass	$PC_1 + PC_2 + PC_3$	$PC_1 + PC_2 + PC_3$	Subcatchment Forest Cover	Subcatchment Forest Cover
(log_{10} (mg m^{-2}))	r^2	RMS	r^2	RMS
algae	0.68	0.10	0.71	0.06
invertebrate	0.58	0.16	0.47	0.14
fish	0.54	0.41	0.45	0.33

Figure 1.1. The National Capital Region of Canada, i.e. the study area, is represented by the gray polygon in Ontario and Québec. Map inset shows the study area where algal, invertebrate, and fish biomass were quantified at 38 streams along a forested gradient during July and August of 2001 and 2002.

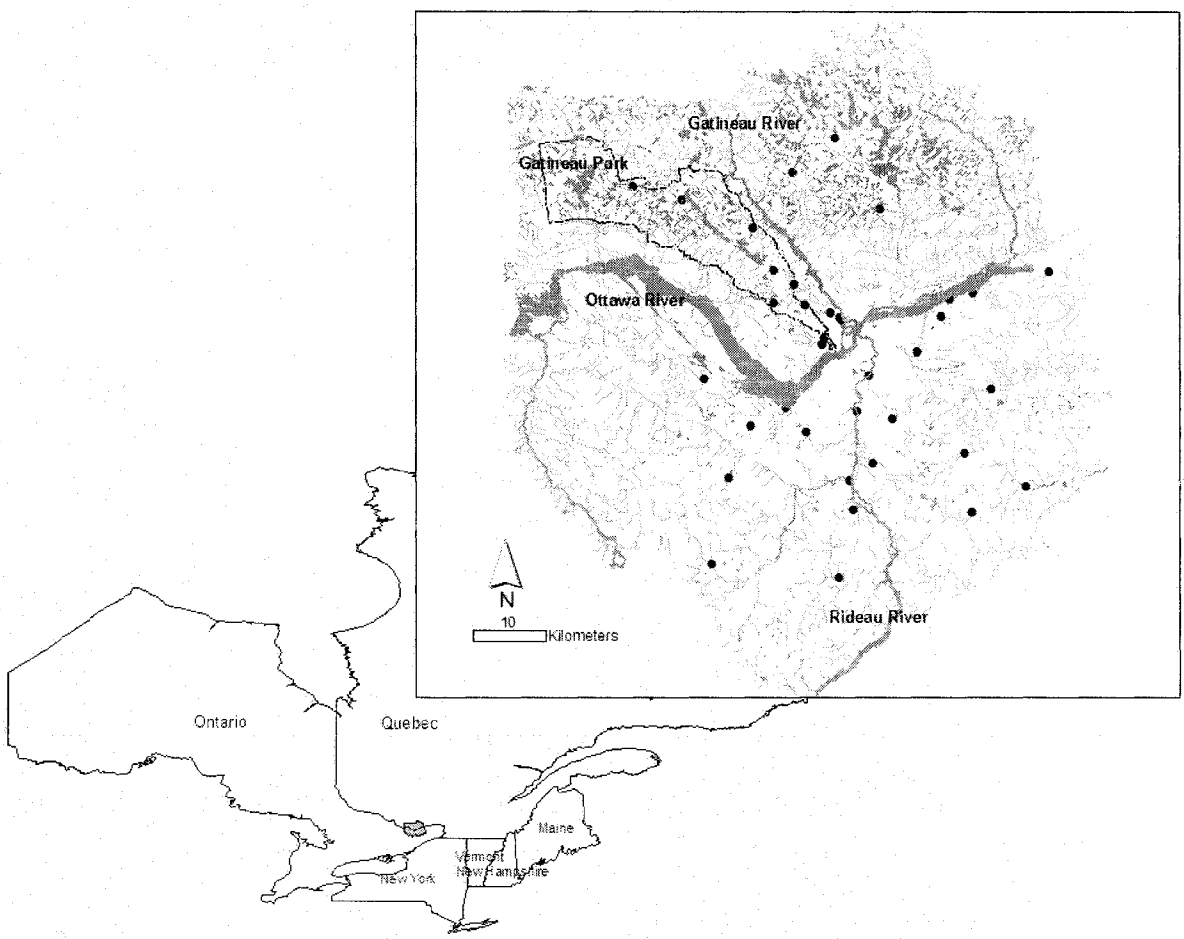


Figure 1.2. Comparing variation in algal (a), invertebrate (b), and fish (c) biomass explained by percent forest cover (r^2) at multiple scales (n = 54). r^2 values from generalized additive models (using digital (GIS) or ground-truthed (GT) forest cover at small scales ($\leq$ 40 m)) are plotted as a function of the 54 scales, i.e. buffer width and buffer distance in meters. At scales where r^2 values were $\leq$ 0.3, forest cover predicted biomass significantly less precisely than subcatchment forest cover as explained in the text.

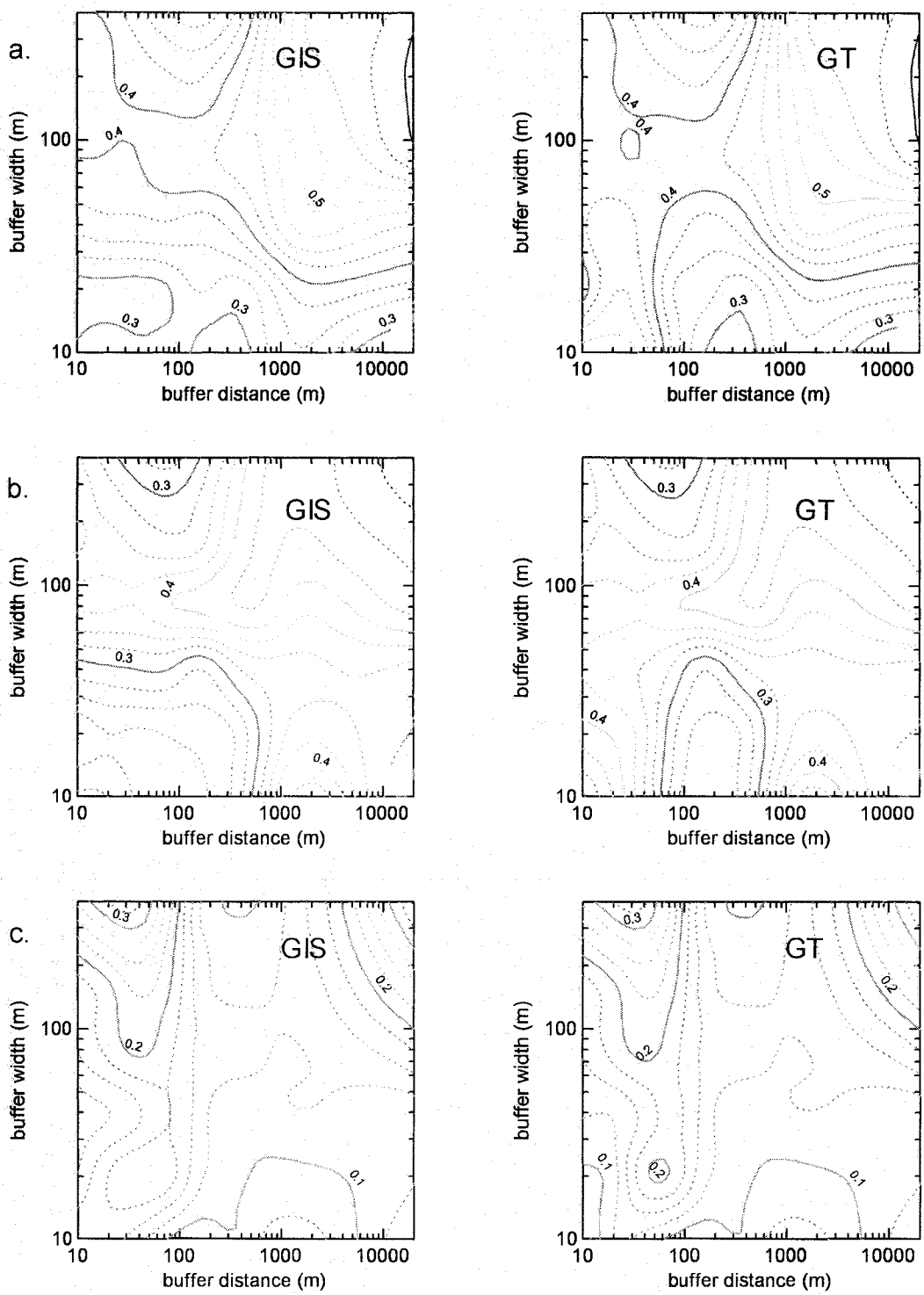
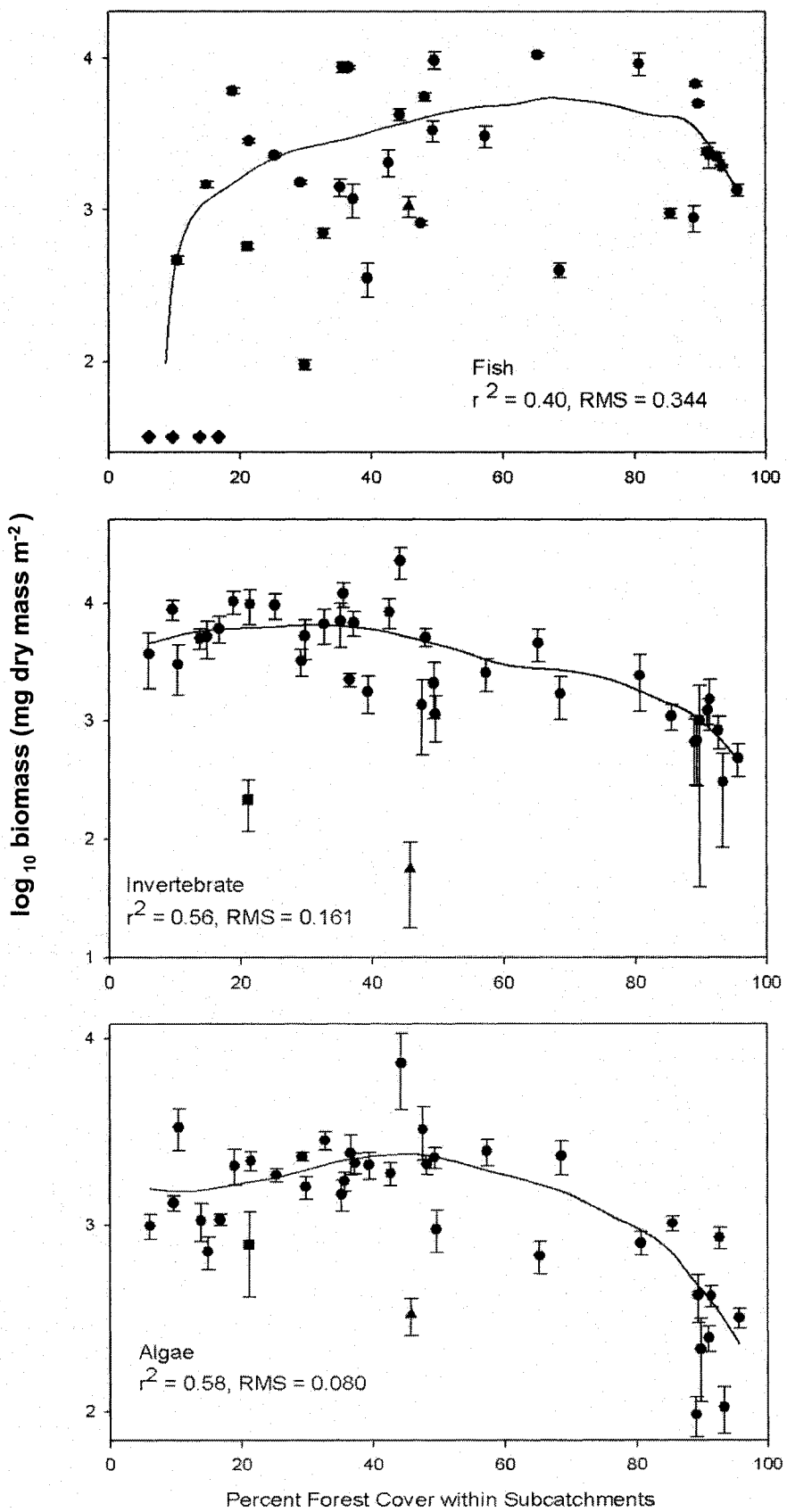


Figure 1.3. Algal, invertebrate, and fish biomass ± 1 SE along a forested gradient (n = 38 sites). Biomass was predicted from subcatchment forest cover (%) using generalized additive models and lowess functions (tension = 0.5). Relatively low algal and/or invertebrate biomass was found at Ruisseau des Fées (▲) and Graham Creek (■), but as explained in the text, all outliers were included in the analyses. No fish were found at four sites (♦).



Chapter 2: Evaluation of two timesaving techniques for processing benthic invertebrate samples to estimate secondary production

Abstract

We compared the accuracy, precision, and efficiency of two timesaving techniques for processing benthic samples for estimating secondary production to a standard laboratory procedure. In the coarse-sieve approach, production was quantified from invertebrate biomass collected in a 2-mm sieve corrected for retention probabilities of individual organisms. In the sieve-fractionated approach, production per sieve was quantified from the total biomass and average body mass of organisms collected in a geometric series of nine sieves. Production estimates from both approaches for the entire assemblage (coarse-sieve: $r^2 = 0.96$, sieve-fractionated: $r^2 = 0.99$, n = 57) and for individual taxa (coarse-sieve: $r^2 = 0.84$, n = 308, sieve-fractionated: $r^2 = 0.99$, n = 544) were strongly related to production estimates derived from standard processing techniques. The analytical error introduced by coarse-sieve (entire assemblage RMS = 0.014, individual taxa RMS = 0.001) and sieve-fractionated (entire assemblage RMS = 0.070, individual taxa RMS = 0.0004) approaches was insignificant relative to the variance of production estimates among replicates (entire assemblage = 0.150, individual taxa = 0.329). Coarse-sieve and sieve-fractionated methods for sample processing required on average only 18% and 63% of the time required for standard processing, respectively, yet coefficients of variation for production means of the entire community using standard and streamlined approaches differed by < 1%. These timesaving techniques for processing benthic samples make studies of secondary production that require multiple sampling sites and dates more feasible, and thus should further our understanding of the mechanisms that control stream productivity.

Introduction

Benthic invertebrates transfer energy and matter from in-stream primary producers or allochthonous organic matter to top predators (Wallace and Webster 1996). Quantifying and understanding energy flow in lotic systems therefore requires accurate measurements of biomass and productivity of benthic invertebrates (Benke 1993). Moreover, secondary production estimates are an essential component of effective fisheries management (Wallace and Webster 1996) and can provide a more accurate measure of benthic response to disturbance than indices of community structure (Lugthart and Wallace 1992), which are sometimes used as surrogates for benthic production when assessing stream health (Rosenberg and Resh 1993, Wallace et al. 1996). However, relatively few secondary production studies have estimated production of entire benthic communities at multiple streams, sites, or years along environmental gradients (e.g., Krueger and Waters 1983, Lugthart and Wallace 1992, Wallace et al. 1999, Morin et al. 2001, Shieh et al. 2002, Carlisle and Clements 2003, Sheih et al. 2003).

The scarcity of community production studies at multiple streams, sites, or years is likely due to the high costs of measuring invertebrate production. For instance, quantifying annual production of a single species at just one site typically requires at least 36 samples (3 replicates x 12 dates, if samples are collected monthly). Describing the response of annual production to only one environmental variable requires at least 3-5 streams (i.e. 108-150 samples) to even minimally assess a gradient in the variable of interest. Therefore, assuming 8 hours to process each sample using standard processing techniques (Stephenson unpublished data), we estimate that 864-1200 laboratory-processing hours are required to assess how production of a single species responds to

one environmental variable. Production estimates of multiple species require even more laboratory-processing hours.

Various calculation methods have been proposed to reduce the costs of obtaining production estimates. The size-frequency method (Hynes and Coleman 1968, Hynes 1980) was developed to estimate production of an entire asynchronous invertebrate community to eliminate the need for time consuming taxonomic identifications, although it is more commonly applied to individual species (Benke 1993). Further, when semivoltine or multivoltine species are considered, annual production estimates must be corrected for cohort production intervals, which requires knowledge of life cycle lengths (Benke 1979). More recently, empirical models aimed at circumventing direct measurements of growth rates required for invertebrate production estimates have been proposed (Banse and Mosher 1980, Huryn and Wallace 1986, Hauer and Benke 1987, 1991, Morin et al. 1988, Stites and Benke 1989, Benke and Parsons 1990, Huryn 1990, Morin and Bourassa 1992, Morin and Dumont 1994). Although these developments in the computational components of production estimates have reduced the need for field data on growth rates, the high cost of processing samples to estimate numbers and sizes of organisms remains.

Techniques to reduce laboratory-processing time of benthic samples are desirable if they do not affect the quality of the data, or if savings in time and money outweigh reductions in precision and accuracy. Morin et al. (2004) developed a coarse-sieve processing technique and showed that biomass estimates for entire assemblages were not significantly different from those based on invertebrates retained in 1-mm sieves and corrected for invertebrates lost through 1-mm sieves. Ramsay et al. (1997) showed that a sieve-fractionated technique allowed for accurate measurements of biomass and size

distributions from the average size of a small number of invertebrates and the total number of invertebrates retained in a geometric series of sieves. Both of these techniques could be used to streamline processing of samples for estimating production. However, it is not obvious whether the savings of such streamlined techniques are sufficient to offset the loss of precision and accuracy of the resulting production estimates. Moreover, there is a risk of missing taxa using coarse-sieve techniques, and that risk has not yet been quantified.

Here, we assess the accuracy (i.e. the magnitude of systematic bias), the precision (i.e. the added variability), and the efficiency (i.e. the reduction in processing time) of two techniques to reduce laboratory processing time of benthic invertebrate samples to estimate secondary production of entire assemblages and individual taxa. We compare the performance of the two timesaving techniques to standard laboratory procedures for processing benthic samples used for production estimates, and quantify the risk of not detecting taxa when using only coarse sieves.

Methods

Field and lab procedures

Six replicate cobbles (8-25 cm in diameter) were collected from the riffle areas of 10 headwater streams in southeastern Ontario, Canada during July and August 2001 (n = 57 [6 cobbles * 10 streams – 3 damaged samples]). Each cobble sample was placed in a plastic bag with 95% ethanol and stored in a dark refrigerator (6°C) upon returning to the lab. Three cobbles were not used because sample bags leaked during transport from the field to the lab. Invertebrates from the samples were then collected in a geometric series of 9 sieves with mesh apertures ranging from 0.063 to 16 mm. The stacked sieves were

placed in a sink with the largest sieve (16 mm) at the top, smaller sieves in order of decreasing size beneath the top sieve, and the finest sieve (0.063 mm) on the bottom. The contents of each sample bag were carefully poured into the 16-mm sieve, and the cobble was gently brushed over the series of stacked sieves to remove attached material. The sample material on the top sieve was gently washed with tap water until all material finer than 16 mm passed through the top sieve. The remaining material in the top sieve was placed in a sample jar. The top sieve was then removed, and the finer fractions remaining in the stack of sieves were processed similarly. Invertebrates collected in each sieve were sorted, assigned to one of 22 taxonomic groups, (Turbellaria, Gastropoda, Ephemeroptera (Baetidae, Heptageniidae, Leptophlebiidae, Tricorythidae, Caenidae), Coleoptera (Elmidae, Psephenidae), Diptera (Tipulidae, Simuliidae,Chironomidae), Plecoptera (Perlidae), Trichoptera (Philopotomatidae, Hydropsychidae, Polycentropodidae, Limnephilidae, Leptoceridae, Helicopsychidae), Lepidoptera (Pyralidae), Isopoda, Amphipoda), and measured along their central axis to the nearest 0.01 mm using a digital analysis system. The cleaned cobble was retained and its area determined from the weight of aluminum foil required to completely cover it (Reice 1980).

Production estimates

Standard processing technique.-To estimate the accuracy and precision of coarse-sieve and sieve-fractionated approaches for processing benthic samples, we compared production estimates obtained from our timesaving techniques to production estimates obtained using standard laboratory processing techniques where all invertebrates collected in a 63-μm sieve are sorted, identified, and measured in the laboratory.

Invertebrate dry mass (M, in mg) was calculated from taxon specific (i.e., family or order) length-mass regressions (Benke et al. 1999). Mass specific growth rates (g [d^{-1}]) were estimated for the average water temperature across all sites (20°C) at the time of collection using an empirical model developed for stream invertebrates (Morin and Dumont 1994):

$$\log_{10} g = -2.09 - 0.27 \log_{10} M + 0.025 T. \quad (1)$$

We used order-level taxon specific models for Diptera, Ephemeroptera, Plecoptera, and Trichoptera, and the general model given in equation 1 for all other orders from Morin and Dumont (1994) to estimate growth rates when calculating taxon specific production. Standard production [mg m^{-2} day^{-1}] for each sample was calculated as:

$$\text{Standard Production} = \sum_{i=1}^{n} \frac{M_i \; g_i}{A} \quad (2)$$

where M_i is the dry mass (mg) of each invertebrate, g_i is the mass specific growth rate of each invertebrate calculated from Eq. 1, A is the surface are of the cobble (m^2) and n is the total number of invertebrates collected from the sample. Although using empirical models to estimate growth rates is not a standard method for estimating benthic invertebrate production, we define "standard production" for comparative purposes in this study as production that was quantified from samples that were processed using standard laboratory techniques.

Coarse-sieve and sieve-fractionated processing techniques.-In the coarse-sieve approach, we used only the invertebrates retained in the 2-mm or larger sieves and assumed that those caught in sieves larger than 2 mm would be caught in a 2-mm sieve. We then used a sieve retention probability model to account for organisms lost through the 2-mm sieve (Morin et al. 2004). Production per cobble was calculated for the entire

benthic community and also for individual taxa from the 24 taxonomic groups listed above as:

$$\text{Coarse-sieve Production} = \sum_{i=1}^{n} \frac{M_i g_i}{A p_i} \quad (3)$$

where p_i is the probability that the i^{th} organism is retained in a 2-mm sieve, and n is the number of invertebrates retained in a 2-mm sieve. To determine p for each invertebrate retained in a 2-mm sieve, we first calculated logit p from Morin et al. (2004) as:

$$\text{logit p} = -2.84 + 5.8 \text{ Log}_{10} \text{RL} - 3.18 \text{ Log}_{10} \text{RL} * \text{Log}_{10} \text{mesh size}, \quad (4)$$

where relative length (RL) is the ratio of invertebrate body length (mm) to the 2-mm sieve mesh size. We then calculated p as $e^{(\text{logit p})} / (1 + e^{(\text{logit p})})$. For simplicity, rather than using taxon specific sieve retention models, we also used the general sieve retention model (Eq. 4) when quantifying taxon specific production, as Morin et al. (2004) found taxon specific models only increased the explained variation in sieve retention by < 2%.

In the sieve-fractionated approach, we estimated production per sample from biomass (B_j [mg m^{-2}]) and average body mass ($\overline{M}_j$ [mg]) for each of the j sieve fractions. The number of invertebrates in each sieve (n_j) was counted, and total dry mass per sieve (B_j) was estimated to obtain average body mass per sieve ($\overline{M}_j$). Because we used the same samples to calculate production using standard and timesaving processing techniques for comparative purposes, we were unable to actually weigh the dry mass of each sieve fraction. This negates the need to identify and measuring individual invertebrates, unless this method was being used to obtain taxon specific production, in which case samples would still require individual identifications but not body length measurements. Consequently, we assumed that the sum of individual dry mass obtained

from length-weight regressions was equivalent to weighing the organisms retained in a sieve after drying. The average growth rate per sieve (g_j) was determined from the $\overline{M}_j$ using the model (Eq. 1) of Morin and Dumont (1994). Taxon specific growth rate models from Morin and Dumont (1994) were used to calculate g_j when quantifying sieve-fractionated production of individual taxa. Production was then quantified for each sieve and the total production of each sample was determined as the sum of production from the 9 (= m) sieves as:

$$\text{Sieve-Fractionated Production} = \sum_{j=1}^{m} B_j g_j \qquad (5)$$

Sample processing time

We estimated the laboratory processing time of each technique from a random subset of replicate samples from each site (26 of the 57 processed cobbles). Total processing time included sorting and measuring the lengths of all individuals retained in a cobble sample for the standard processing technique and in a 2-mm subsample for the coarse-sieve technique, and we assumed that the manipulation time to sieve each sample was negligible. For the sieve-fractionated technique, we only included time spent sorting invertebrates from each sieve fraction per cobble sample and assumed that the time required to sieve, dry, and weigh the organisms collected in each sieve fraction was negligible. We then predicted the time it took to process a given number of invertebrates using standard, coarse-sieve, and sieve-fractionated techniques, and used analysis of covariance (ANCOVA) to determine if the slopes and y-intercepts significantly differed among the three regressions.

Accuracy and precision of timesaving approaches

We examined the accuracy of the two timesaving techniques by comparing standard production (Eq.2) to production estimated from coarse-sieve fractions and sieve-fractionated subsamples (Eq.3 and Eq.5) for the 57 cobbles. We compared the relative analytical precision of each technique by examining the residual variance between standard production and coarse-sieve or sieve-fractionated production, i.e. the residual mean squares (RMS) in regressions predicting standard production from production estimates using coarse-sieve and sieve-fractionated techniques. To quantify the analytical error introduced by these new approaches for processing benthic samples relative to the natural spatial variance of standard production, we then compared the unexplained error of both approaches (RMS) with the variance of standard production among replicates.

Probability of detecting taxa in sieve fractions

The probability that at least one individual of a taxon was retained in a sieve fraction when the entire sample contained n individuals of the taxon was calculated as:

$$1 - \prod_{i=1}^{n} (1 - p_i) \qquad (6)$$

where p_i is the probability that each individual i is retained by the sieve as predicted by the sieve retention probability model of Morin et al. (2004; Eq. 4). To assess the validity of this estimate of taxa retention probability, we compared the calculated values from equation 6 to the observed detections in the 2-mm sieve fraction for each taxon found on individual cobbles.

Results

We collected 15,406 invertebrates from 57 cobble samples. The numbers of invertebrates collected per sample ranged from 49 to 1485 invertebrates and standard production per sample ranged from 4.8 – 691.5 mg m^{-2} day^{-1}.

Accuracy and precision for total production

Production estimates for entire assemblages from coarse-sieve fractions and sieve-fractionated subsamples were strongly related to standard production (coarse-sieve: $r^2 = 0.96$, sieve-fractionated: $r^2 = 0.99$; Fig.1). However, only the regression predicting standard production from production estimates using the coarse-sieve approach did not significantly differ from the 1:1 line between production using standard and timesaving techniques (coarse-sieve: $F_{1,56} = 0.95$, $p = 0.34$; sieve fractionated: $F_{1,56} = 420.99$, $p < 0.001$). The sieve-fractionated approach, on the other hand, consistently overestimated standard production by ~5%.

The coarse-sieve approach (RMS = 0.014) was significantly less precise ($F_{55,55} = 14$, $p < 0.001$) at estimating standard production than the sieve-fractionated approach (RMS = 0.001; Fig.1). Nonetheless, sampling error due to the natural spatial variation in standard production (variance among replicates = 0.150) was significantly larger than the analytical error (i.e. RMS) introduced by both approaches (coarse-sieve: $F_{47,55} = 10.71$, $p < 0.001$; sieve-fractionated: $F_{47,55} = 150$, $p < 0.001$).

Accuracy and precision for production of individual taxa

Production estimates for individual taxa obtained by the two timesaving techniques were strongly correlated to standard production (coarse-sieve: $r^2 = 0.84$ n =

308; sieve-fractionated: $r^2 = 0.99$, n = 544; Fig.2) although small-bodied taxa, especially rare ones, were often not detected by the coarse-sieve technique. There was no statistically significant bias introduced by either technique, and the fitted regressions were almost perfectly superimposed on the 1:1 line between production estimates from standard and streamlined processing techniques.

The coarse-sieve technique (RMS = 0.07) was significantly less precise ($F_{306,542}$ = 175, $p < 0.001$) at estimating standard production than the sieve-fractionated technique (RMS = 0.0004; Fig.2). However, spatial variance in individual taxa production (variance among replicates = 0.329) was twice that for total production and again significantly larger than the analytical error (i.e. RMS) introduced by both approaches (coarse-sieve: $F_{306,393}$= 4.71, $p < 0.001$; sieve-fractionated: $F_{393,542}$ = 822, $p < 0.001$). The coarse-sieve technique (RMS = 0.07) was significantly less precise ($F_{542,306}$ = 175, $p < 0.001$) at estimating standard production than the sieve-fractionated technique (RMS = 0.0004; Fig. 2.2). However, spatial variance in individual taxa production (variance among replicates = 0.329) was twice that for total production and again significantly larger than the analytical error (i.e. RMS) introduced by both approaches (coarse-sieve: $F_{306,393}$= 4.71, $p < 0.001$; sieve-fractionated: $F_{542,393}$ = 822, $p < 0.001$).

Efficiency of coarse-sieve and sieve-fractionated approaches and precision of production means

Coarse-sieve and sieve-fractionated approaches required significantly less processing times for a given number of invertebrates than standard processing techniques, and there was no significant interaction between the number of invertebrates and the three processing techniques (Fig. 3). On average, the 2-mm sieve retained 18% of the

invertebrates that were present on a cobble. Therefore, the coarse-sieve approach required sorting and measuring 18% of the total number of invertebrates per sample, resulting in an 82% reduction in laboratory-processing time. Forgoing measurements of individuals entirely, the sieve-fractionated approach simply required the sorting of invertebrates and reduced laboratory-processing time by 36%. Although both approaches substantially reduced the number of hours required to process 6 replicate cobbles (standard = 33 hours ± 6 SE, coarse-sieve = 6 hours ± 1 SE, sieve-fractionated = 21 hours ± 4 SE), the average coefficients of variation (CV) for production means varied among the three approaches by ≤ 1% (standard CV = 30% ± 4 SE, coarse-sieve CV = 31% ± 4 SE, sieve-fractionated CV= 30% ± 4 SE).

Detection of taxa in the 2-mm and above sieve fraction

On average, each of the 57 cobbles harbored 9.54 taxa and there were 544 observations where a taxon present on the cobble could be either observed (1) or not observed (0) in the 2-mm and above sieve fraction. On average, the 2-mm and above sieve fraction contained only 5.4 taxa per cobble. Taxa lost were typically small (average body length = 1.8 mm, range = 0.4-8.2 mm) and not numerous (average total number on the cobble = 4.8, range = 1-62). The proportion of taxa detected in the coarse sieve fraction increased with increasing length and number of individuals, and was accurately predicted by the sieve retention probability model of Morin et al. (2004) (Fig. 4).

Discussion

Total assemblage production

The analytical error of the coarse-sieve approach was significantly greater than that of the sieve-fractionated approach, indicating that the error associated with estimating biomass lost through coarse sieves was greater than the error introduced by estimating average growth rates for each sieve fraction. Indeed, sieve retention probabilities for correcting biomass estimates obtained from the coarse-sieve approach overestimated the amount of biomass that passed through 2-mm sieves by as much as 612% and underestimated biomass that passed through 2-mm sieves by as much as 65%, yet average growth rates predicted from average size classes per sieve using sieve-fractionated techniques overestimated average P:B ratios per sieve by at most 63%.

The systematic overestimation of production using sieve-fractionated approach for the entire assemblage results from the shape of the size distribution of organisms in sieve fractions. The right skewed distribution of individual size in each sieve fraction, approaching that of a lognormal distribution, is what we typically observed and was also observed by Morin et al. (2004; their Fig. 6). Most of the biomass found in a sieve is made up of relatively few large individuals that have, because of their size, a much lower mass-specific growth rate than the bulk of the remaining smaller individuals. However, the growth rate used to calculate production for the sieve fraction is based on the average individual mass and does not take into account the mixture of sizes of organisms retained in a sieve. For right skewed distributions like that of individual sizes in a sieve, this leads to an overestimation of the biomass-weighted growth rate, and hence of the production estimate for the sieve fraction. Short of measuring individuals retained in a sieve (which

would defeat the purpose of the sieve-fractionated approach), correction of the bias would require using more sieves or making assumptions about parameters of the size distributions of organisms in a sieve. Given the small bias observed here (~5%), we doubt that this would be worth the effort. However, reducing the number of sieves used to save even more time should be avoided because it would necessarily increase the inaccuracy of the sieve-fractionated approach. Nonetheless, the analytical error introduced by both approaches was insignificant relative to the natural spatial variance of standard production estimates within each site. The coarse-sieve approach, followed by the sieve-fractionated approach, resulted in less variation in production estimate means for a given amount of laboratory-processing time than production means obtained from standard processing techniques.

Production of individual taxa

Sieve-fractionated production estimates of individual taxa are unbiased and precise, more so than for the entire assemblage. As the number of individuals in each sieve fraction decreases, the sieve-fractionated estimate converges towards the standard production estimate because, at the limit where each sieve contains only one individual, the calculations become the same. The odds of observing a heavily right skewed size distribution in a sieve fraction decrease when a single taxon is considered rather than the entire assemblage because there are fewer individuals. Consequently, the bias described above is reduced. Further reductions in processing times may be achievable without introducing objectionable bias by reducing the number of sieves used when few individuals are present. However, we suspect such savings would be small, as samples containing few individuals can often be processed very quickly.

For moderately abundant taxa, the coarse-sieve approach can be used to estimate production almost as precisely as standard processing techniques in much less time. For less common or smaller taxa, we recommend the use of a finer mesh size to decrease the odds that a taxon is not detected. Obviously, if no individuals of a rare and/or small taxon are retained in a coarse sieve, then the resulting production estimate by the coarse-sieve technique will be 0. The simple solution is to use a finer mesh sieve for these small and rare taxa if they must be detected. Since the sieve retention probability model of Morin et al. (2004) can be used to estimate the probability that a taxa present in a sample is detected in the 2-mm and above fraction (Fig. 4), it is possible to determine the appropriate mesh size given the size of the organisms and the numbers of individuals expected in replicate samples (Fig. 5).

Applications and limitations

Because the coarse-sieve approach provided accurate and precise estimates of standard production with less effort than sieve-fractionated techniques, we recommend the coarse-sieve approach for processing benthic samples to estimate secondary production of moderately abundant taxa, functional feeding groups, or the entire community at multiple sites and dates. The coarse-sieve technique will be especially useful in large scale studies that assess how secondary production responds to a gradient of disturbance or other environmental factors (e.g., Morin et al. 2001). Rather than using indices of benthic invertebrate community structure that are typically used in lotic bioassessments (Rosenberg and Resh 1993), coarse-sieve techniques for processing benthic samples will make quantitative measures of food availability for fish consumption in biomonitoring studies more feasible by reducing costly laboratory

processing time of benthic samples. Further, coarse-sieve techniques provide secondary production estimates for the entire sample, thereby avoiding discrepancies resulting from production samples collected in sieves with different mesh sizes which have previously limited the suitability of secondary production estimates in bioassessments (Bonada et al. 2006). However, for production studies of small taxa where few individuals are retained by 2-mm sieves, precision of production estimates using the coarse-sieve approach will be low unless finer meshed sieves are used. Alternatively, in such cases, the sieve-fractionated approach will save a third of the processing time required by traditional methods.

Our assessment of the two timesaving techniques is based on instantaneous production estimates from a single sampling date. Since seasonal or annual production estimates integrate several instantaneous production estimates over time, our general conclusions regarding the relative merits of the different techniques should hold when using the instantaneous growth method (Ricker 1946, Clarke et al. 1946, Allen 1949) to estimate annual production. The coarse-sieve technique could also greatly reduce the significant laboratory processing time required to estimate annual production using increment-summation (Waters 1977), removal-summation (Waters 1977), Allen curve (1951) and size frequency (Hynes and Coleman 1968, Hynes 1980) methods by correcting for the density, dry mass, and biomass lost through a 2-mm sieve with retention probabilities (Morin et al. 2004).

Conclusions

Using the coarse-sieve and sieve-fractionated techniques, the influence of one environmental variable on invertebrate production can be accurately and precisely

quantified in only 151-210 and 540-750 processing hours, respectively, much less than the 864-1200 hours required by standard laboratory procedures. Time saved by processing benthic samples with coarse-sieve and sieve-fractionated techniques allows for increases in the number of sampling sites, dates, and replicates in production studies to allow for a better understanding of the mechanisms that govern stream production. The substantial savings associated with these approaches can make it economically more feasible to assess how eutrophication, deforestation, invasive species, channel alterations, and other anthropogenic impacts to freshwater habitats affect secondary production.

Acknowledgements

This study was supported by an NSERC Grant (RGPIN-42799-2001) to AM. We thank Y. Yao for her help with sample processing and data entry. We also thank J. Holomuzki, M. R. Whiles, and two anonymous reviewers for their time and valuable suggestions that have greatly improved this paper.

Literature Cited

Allen, K. R. 1949. Some aspects of the production and cropping of fresh waters. Report, Sixth science Congress, 1947. Transactions of the Royal Society of New Zealand 77:222-228.

Allen, K. R. 1951. The Horokiwi Stream. A study of a trout population. New Zealand Marine Department Fisheries Bulletin 10:1-238.

Banse, K., and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecological Monographs 50:355-379.

Benke, A. C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnology and Oceanography 24:168-171.

Benke, A. C. 1993. Edgardo Baldi Memorial Lecture: Concepts and patterns of invertebrate production in running waters. Verhandlungen Internationale Vereinigung für Limnologie 25:15-38.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308-343.

Benke, A. C., and K. A. Parsons. 1990. Modeling black fly production dynamics in blackwater streams. Freshwater Biology 24:167-180.

Bonada, N., N. Prat, V. H. Resh, and B. Statzner 2006. Developments in aquatic insect biomonitoring: A comparative analysis of recent approaches. Annual Review of Entomology 51:495-523.

Carlisle, D.M., and W. H. Clements. 2003. Growth and secondary production of aquatic insects along a gradient of Zn contamination in Rocky Mountain streams. Journal of the North American Benthological Society 22:582-597.

Clarke, G. L., W. T. Edmondson, and W. E. Ricker. 1946. Mathematical formulation of biological productivity. Ecological Monographs 16:336-337.

Cooper, W. E. 1965. Dynamics and production of a natural population of a fresh-water amphipod, *Hyallela azeteca*. Ecological Monographs 35: 377-194.

Hauer, F. R., and A. C. Benke. 1987. Influence of temperature and hydrograph on black fly growth rates in a subtropical river. Journal of the North American Benthological Society 6:251-261.

Hauer, F. R., and A. C. Benke. 1991. Rapid growth of snag-dwelling chironomids in a blackwater river: the influence of temperature and discharge. Journal of the North American Benthological Society 10:154-164.

Huryn, A. D. 1990. Growth and voltinism of lotic midge larvae: patterns across and Appalachian Mountain basin. Limnology and Oceanography 25:339-351.

Huryn, A. D., and J. B. Wallace. 1986. A method for obtaining in situ growth rates of larval Chironomidae (Diptera) and its application to studies of secondary production. Limnology and Oceanography 31:216-222.

Huryn, A. D., and J. B. Wallace. 2000. Life history and production of stream insects. Annual Review of Entomology 45:83-110.

Hynes, H. B. N. 1980. A name change in the secondary production business. Limnology and Oceanography. 25:778.

Hynes, H. B. N., and M. J. Coleman. 1968. A simple method of assessing the annals production of stream benthos. Limnology and Oceanography 13:569-573.

Krueger, C. C., and T. F. Waters. 1983. Annual production of macroinvertebrates in three streams of different water quality. Ecology 64:840-850.

Lugthart, G. J., and J. B. Wallace. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. Journal of the North American Benthological Society 11:138-164.

Mackay, A. P. 1977. Quantitative studies on the Chironomidae (Diptera) of the Rivers Thames and Kennet. IV. Production. Archiv für Hydrobiologie 80: 327-348.

Morin, A., and N. Bourassa. 1992. Empirical models of annual production and the p-b productivity-biomass ratio of benthic invertebrates of flowing water. Canadian Journal of Fisheries and Aquatic Sciences 49:532-593.

Morin, A., N. Bourassa, and A. Cattaneo. 2001. Use of size spectra and empirical models to evaluate trophic relationships in streams. Limnology and Oceanography 46:935-940.

Morin, A., M., Constantin, and R. H. Peters. 1988. Allometric models of simuliid growth rates and their use of estimation of production. Canadian Journal of Fisheries and Aquatic Sciences 45:315-324.

Morin, A., and P. Dumont. 1994. A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. Journal of the North American Benthological Society 13:357-367.

Morin, A., J. Stephenson, J. Strike, and A. G. Solimini. 2004. Sieve retention probabilities of stream benthic invertebrates. Journal of the North American Benthological Society 23:383-391.

Ramsay, P. M., S. D. Rundle, M. J. Attrill, M. G. Uttley, P. R. Williams, P. S. Elsmere, and A. Abada. 1997. A rapid method for estimating biomass size spectra of benthic metazoan communities. Canadian Journal of Fisheries and Aquatic Sciences 54:1716-1724.

Reice, S. R. 1980. The Role of Substratum in Benthic Macroinvertebrate Microdistribution and Litter Decomposition in a Woodland Stream. Ecology 61:580-590.

Ricker, W. E. 1946. Production and utilization of fish populations. Ecological Monographs 16:373-391.

Rosenberg, D. N., and V. H. Resh. 1993. Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York.

Shieh, S. H., J. V. Ward, and B. C. Kondratieff. 2002. Energy flow through macroinvertebrates in a polluted plains stream. Journal of the North American Benthological Society 21:660-675.

Shieh, S. H., J. V. Ward, and B. C. Kondratieff. 2003. Longitudinal changes in macroinvertebrate production in a stream affected by urban and agricultural activities. Archiv Fur Hydrobiologie 157:483-503.

Stites, D. L., and A. C. Benke. 1989. Rapid growth rates of chironomids in three habitats of a subtropical blackwater river and their implications for P:B ratios. Limnology and Oceanography 34:1278-1289.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409-442.

Wallace, J. B., J. W. Grubaugh, and M. R. Whiles. 1996. Biotic indices and stream ecosystem processes: Results from an experimental study. Ecological Applications 6:140-151.

Wallace, J. B., and Webster J. R. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology 41:115-139.

Waters, T. F. 1977. Secondary production in inland waters. Advances in Ecological Research 10:91-164.

Figure 2.1. Comparison of standard production estimates for entire assemblages (P) with estimates ($\hat{P}$) obtained from coarse-sieve fractions (A) and sieve-fractionated subsamples (B) collected at 10 sites (n = 57 cobbles). The dashed line represents the 1:1 line between the two estimates of production and the solid line is the regression through the data.

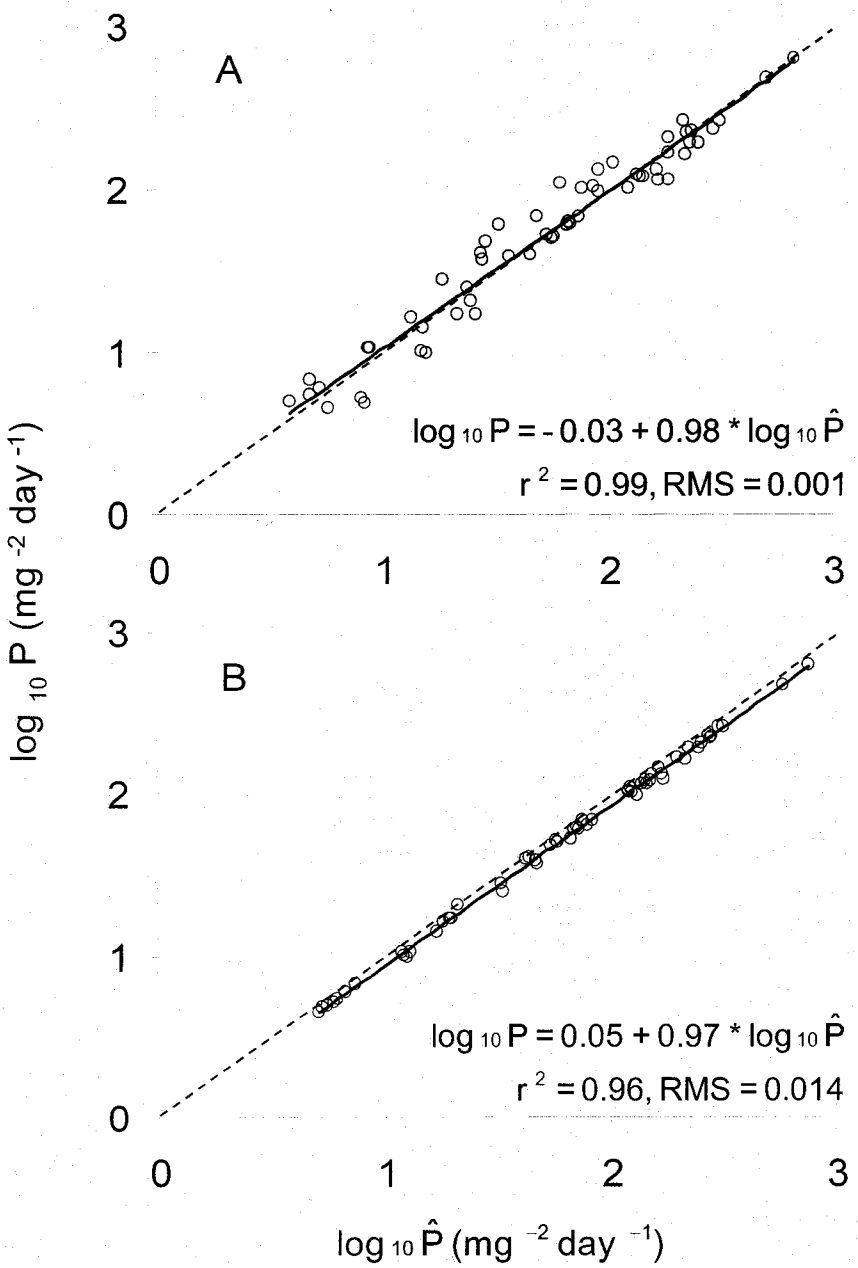


Figure 2.2. Comparison of standard production estimates for individual taxa (P) with estimates ($\hat{P}$) obtained from coarse-sieve fractions (A, n = 308) and sieve-fractionated subsamples (B, n = 544). The dashed line represents the 1:1 line between the two estimates of production and the solid line is the regression through the data.

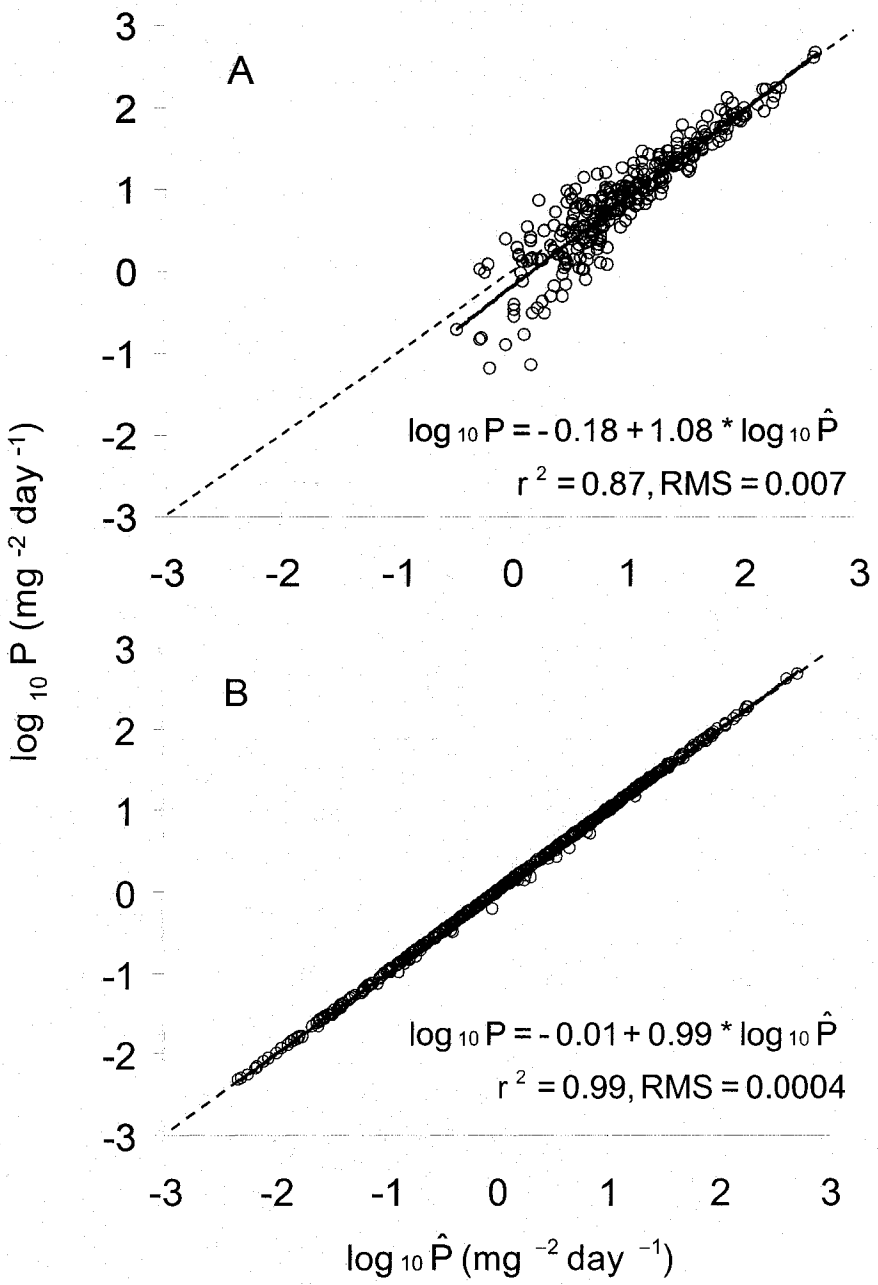


Figure 2.3 Time (hours) to process a given number of invertebrates to obtain production estimates (n = 26 cobbles from a subset of sampling sites) using standard (•), coarse-sieve (Δ) and sieve-fractionated (□) laboratory processing techniques. Y-intercepts significantly varied among the three regressions ($F_{2,74} = 107$, $p < 0.001$), whereas differences in slopes were insignificant ($F_{2,72} = 0.2$, $p = 0.84$).

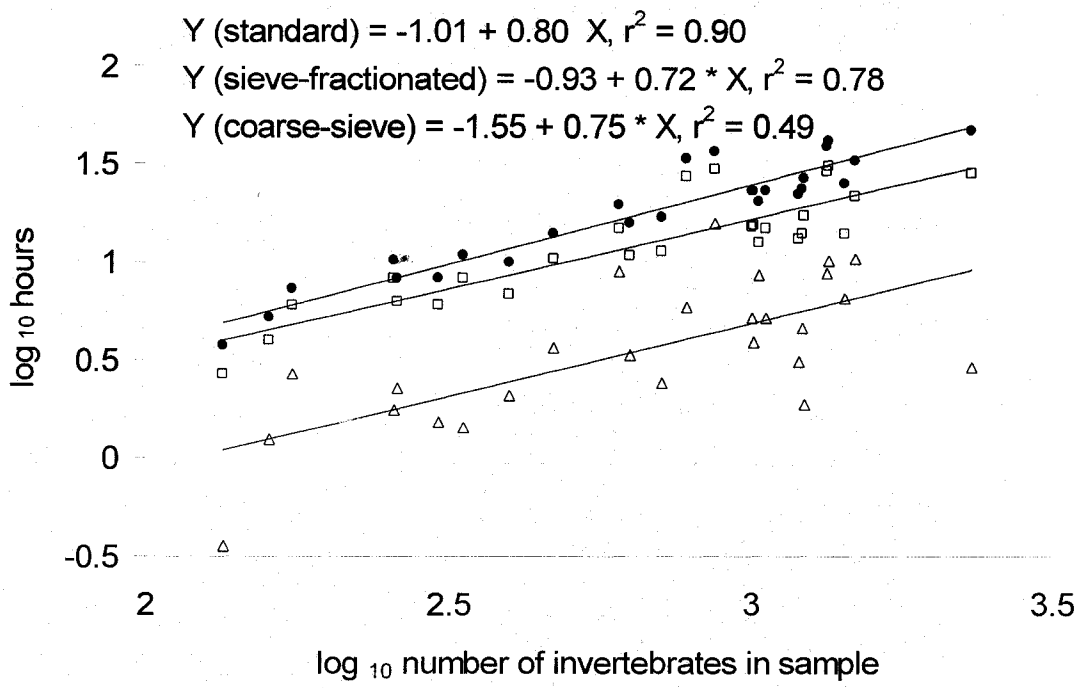


Figure 2.4. Proportion of observations where a taxon present on a cobble was detected in the 2-mm sieve fraction as a function of the predicted detection probability in the 2-mm sieve using the model of Morin et al. (2004). Circles correspond to the presence (1) or absence (0) of a taxon in the 2-mm sieve when it was present in the cobble sample (n = 544). The solid line is the lowess fit (tension = 0.3) through the observed data and the dashed line is the 1:1 line between predicted and actual detection probabilities.

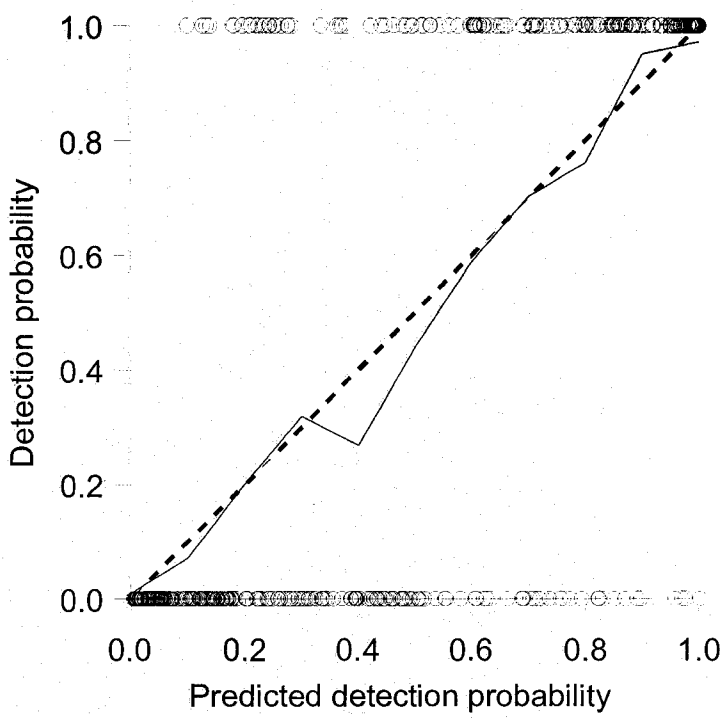
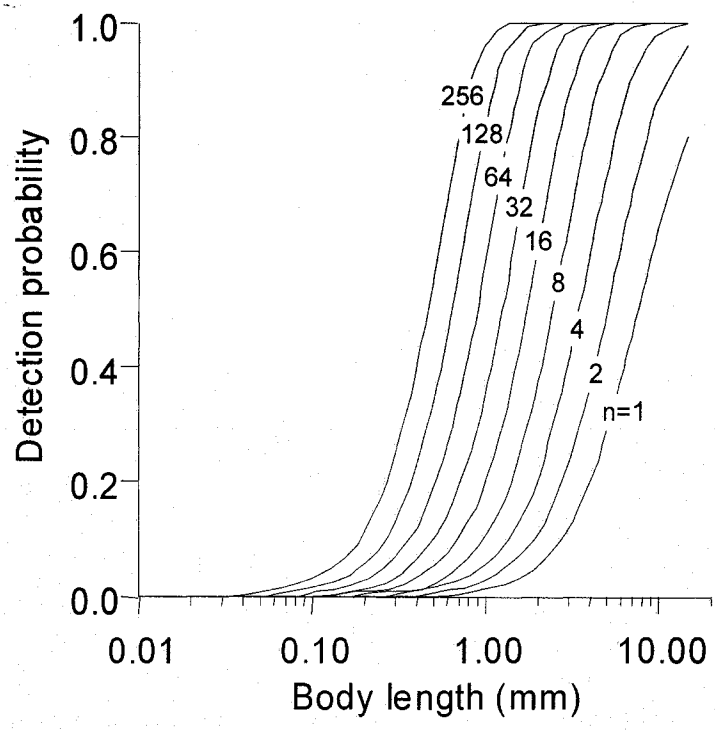


Figure 2.5. Probability that a taxon represented by n individuals in a sample is detected in the 2-mm and above sieve fraction. Probabilities (p) for n = 1 are calculated from the sieve retention probability model of Morin et al. (2004). For larger n, they were calculated as $1-(1-p)^n$.



Chapter 3: Bottom-up and top-down controls of algal, invertebrate, and fish production along a forested gradient

Abstract

We quantified algal, invertebrate, and fish production (mg dry mass m^{-2} day^{-1}) at 12 small headwater streams along a forested gradient. We hypothesized that nutrients and fish consumption were bottom-up and top-down forces that regulated production at each tropic level in our streams. The trophic structures of the streams in our study consisted of three levels: primary producers and allochthonous organic matter, primary consumers (non-predatory invertebrates and fish), and secondary consumers (predatory invertebrates and fish). Production of invertebrate functional feeding groups consisted primarily of scrapers, collector-gatherers, and collector-filterers, whereas shredders and predators made up less than 10% of invertebrate production at most sites. The majority of fish production was comprised of invertivorous production at each site, whereas detritivorous and planktivorous production composed less than 20% of fish production at all sites. Algal and invertebrate production increased significantly with total nitrogen and/or phosphorus, whereas daily fish production was unrelated to total phosphorus and was relatively high when total nitrogen was < 1000 $\mu g\ L^{-1}$, at which point fish productivity significantly declined. Fish consumption relative to invertebrate production did not significantly alter patterns in size spectra of benthic invertebrates, suggesting that fish consumption of invertebrates was not size-selective or that size-selective fish consumption was not sufficient to shift invertebrate size distributions. Although bottom-up forces appeared to be the dominant drivers of stream productivity in our streams, ratios of grazer removal to primary production and fish consumption to invertebrate production suggest that fish and invertebrates have the potential to deplete their food sources and therefore contribute to the observed patterns in stream productivity.

Introduction

Previous empirical studies have documented correlations between structural properties of stream communities and land use at both the catchment scale and in the riparian zone (Morley and Karr 2002, Sponseller et al. 2001, chapter 1). These studies have shown that stream communities are also correlated to nutrients, hydrology, substrate size, and/or temperature and suggest that land use changes at different scales alter different water quality parameters, and ultimately the stream communities. However, the actual mechanisms for the observed patterns in community structure at multiple trophic levels have not been unambiguously identified as they could result from both bottom-up (van Valen 1973) and top-down pressures (Fretwell 1977, Hairston et al. 1960).

Bottom-up factors such as nutrients, light availability, and substrate size, and top-down factors including fish or invertebrate predation and grazer removal, can simultaneously alter the abundance, biomass, taxonomic composition, and/or size distribution of algae, macroinvertebrates, and fish in streams (Flecker et al. 2002, McIntosh et al. 2005, Power 1990, Rosemond et al. 1993). The relative importance of bottom-up and top-down pressures may also change with different aspects of community structure or function (Nystrom et al. 2003, Rosemond et al. 2001). Annual production is an important aspect of aquatic ecosystems that incorporates seasonal changes (Benke 1993) and may provide a more explanatory measure of ecosystem response to bottom-up and top-down forces when measured at multiple trophic levels as it is a measure of the total food available at a given trophic level and sets rates of resource removal at lower trophic levels (Huryn and Wallace 2000). By quantifying production and consumption at multiple trophic levels in two streams with different strengths of bottom-up or

top-down forces, empirical and experimental evidence has demonstrated simultaneous bottom-up and top-down effects on stream productivity (Huryn 1998, Wallace et al. 1999).

We suspect that nutrients and consumption by fish are regulating stream productivity along the forested gradient in our study area. In this study, we quantify algal, invertebrate, and fish production throughout the growing season at 12 of the 38 sites where we measured biomass along a forested gradient. We then consider algal, invertebrate, and fish production as a function of both total nitrogen and total phosphorus to determine if nutrients are significant bottom-up predictors of stream productivity. We also quantify predatory fish and invertebrate consumption and grazer removal of periphyton production to explore the potential for consumers to deplete their food sources. By examining production of invertebrates and fish within functional feeding groups, we can detect responses to bottom-up and top down controls that are specific to functional feeding groups, as has been found in previous studies on trophic structure (Rosenfeld 2000, Wallace et al. 1999). If top-down pressures of fish are sufficient in our streams, trophic levels may be alternately dominated by relatively larger and smaller organisms (Brooks and Dodson 1965, Hall et al. 1976). To test if fish consumption significantly alters invertebrate size distributions in our streams, we examine the response of invertebrate size spectra along the observed gradient in fish consumption.

Methods

Study Area

The study was performed in the National Capital Region of Canada, located in Eastern Ontario and Western Québec (45°N 75°W). Historically this portion of Canada was entirely covered by forest, primarily composed of red pine, eastern white pine, eastern hemlock and various ashes, maple and oak species (Hosie, 1979). Today, however, 52% of the forest cover

within the National Capital Region has been replaced with urban and agricultural land uses (NCC, 1999). A population of 1.1 million people resides in the National Capital Region, which consists of an area of 5,318.36 square kilometers that straddles the boundary between the provinces of Ontario and Québec (2006 Canadian Census).

Site Selection

During the summers of 2001 and 2002, we quantified biomass at 38 sites along a forested gradient (chapter 2). The biomass sites were chosen because they provided relatively easily accessibility, riffle and run habitats, 2-7 meter widths, and an extensive range of forest cover. Making sure that we maintained an extensive range in forest cover, we chose 12 of the 38 biomass sites for this study on production.

Field Methods

During the growing season of 2002 (May-October), chlorophyll *a* and benthic invertebrates were sampled monthly, and fish were sampled seasonally (spring, summer, and fall) at the 12 study sites. Upon arrival at each site, two seines were erected to isolate a 10-m section of each stream that included riffle and pool areas. We felt it was important to contain the fish immediately so that they could not escape from the sampling area while we collected water quality and cobble samples.

Since our sites in Ontario were also water quality monitoring sites, we used averages from total nitrogen and phosphorus values that were collected throughout the growing season (May-October) by the Regional Municipality of Ottawa and Carleton. For Québec sites, we collected triplicate water samples before sampling for biota and placed these in dark coolers with ice packs. Water quality samples were submitted to the Robert O. Pickard Environmental Centre Laboratory of the City of Ottawa for analysis within 24 hours.

Six replicate cobble samples (8-25 cm) were collected from riffle areas, before sampling for fish so that the electroshocking would not disturb the invertebrates on the cobbles. Each cobble sample was carefully placed in a whirl pack bag with 95% ethanol and stored in a dark cooler with ice packs. Fish were collected by backpack electroshocking along the 10-meter transect of the stream using the removal method (Zippen 1958). The identification, standard length, fork length, and maximum width of live fish were determined in the field after each electroshocking pass. Fish that could not be identified in the field were preserved in ethanol and returned to the lab for further analysis.

Laboratory methods

After returning to the lab, the cobble samples were placed in a dark and cool (6°C) refrigerator. Some 24-48 hours later, 15 ml of ethanol was removed from each bag and periphyton chlorophyll *a* per cobble was determined spectrophotometrically using methods described by Ostrofsky and Rigler (1987). Invertebrates from the cobbles were then collected in a 2-mm sieve, sorted, identified to family or order, and measured along their central axis to the nearest 0.01 mm using an image analysis system. The cleaned cobble was retained and its area was determined from the weight of aluminum foil required to completely cover it (Reice, 1980).

Quantifying Production at Each Trophic Level

Algal production in mg dry mass m^{-2} day^{-1} per cobble was quantified from the amount of chlorophyll *a* on the entire cobble, and an empirical model that predicted algal production per cobble from chlorophyll *a* and stream temperature (°C) (Morin et al. 1999). Algal production (mg dry mass m^{-2} day^{-1}) per date was calculated as the mean of 6 cobble replicates from each site and date, assuming that carbon accounts for 50% of the ash-free dry mass of algae (Reynolds 1984). So that we could compare algal, invertebrate, and fish production for the entire 10-m

sampling transect among sites, we used the average of the algal production from the May-October sampling dates and expressed annual average algal production as mg of dry mass per m^2 of stream bottom per day, assuming that the ratio of rock total surface area per planar area of stream bottom was three (Morin et al. 1988).

The instantaneous growth rate method was used to quantify invertebrate production per date, where individual production is the product of a mass specific growth rate (day^{-1}) and individual biomass (mg m^{-2}) and production per cobble in mg m^{-2} day^{-1} is the sum of individual production per cobble. Estimates of mass specific growth rates were obtained from an empirical model that predicts growth rates from stream temperature (°C) and individual invertebrate dry mass (mg) (Morin and Dumont 1994). Dry mass of invertebrates retained in the 2 mm sieves was estimated from taxon-specific length (mm) to weight (mg) regressions (Benke et al. 1999). A published sieve retention probability accounted for invertebrate production lost through 2 mm sieves (Morin *et al.*, 2004). Using coarse-sieve methods to process benthic samples for estimating production saves considerable laboratory-processing time without sacrificing precision of production estimates (chapter 2). Mean invertebrate production per date was calculated as the average of three replicate cobble samples per date, since only 3 of the 6 cobble samples were processed for invertebrate production estimates. As with algal production, we used the average of invertebrate production per date and multiplied invertebrate production per cobble by 3 to obtain annual average invertebrate production in mg of dry mass per m^2 of the stream bed per day. We also classified invertebrates into functional feeding groups (Merritt and Cummins 1996), and estimated average daily production of invertebrates in each functional feeding group as the sum of individual production per functional feeding group.

The instantaneous growth rate method was also used to quantify fish production but for the entire year, where production of each species is the product of the annual average biomass (g

wet mass m^{-2}) per species and a mass specific growth rate (g wet mass year $^{-1}$), based on the mass of each fish species at maturity. For each sampling date, fish biomass per species (in g wet mass m^{-2}) was calculated from individual fish lengths (cm) and individual wet masses (g, predicted from fork length (cm), (Randall and Minns 2000) using Microfish (Vandeventer 1986). The mass of each fish species at maturity was predicted from the maximum fish wet weight (g) for each species throughout the entire growing season (Randall and Minns 2000). Total fish production was then calculated as the sum of fish production per species and expressed in mg of dry mass per m^2 of stream bottom per day, assuming that fish dry mass comprised 20% of fish wet mass (Kushlan *et al.*, 1986) and that the growing season in our study region per year comprises 6 months of the year, the period for which we sampled. We also classified fish into functional feeding groups (Halliwell et al. 1999, Goldstein and Simon 1999, Scott and Crossman 1973), and estimated average daily production of fish in each functional feeding group as the sum of species production per functional feeding group. Several fish were omnivorous, being both invertivores and detritivores or invertivores and planktivores. For these omnivorous fish, we assigned ½ of their production to each functional feeding group. Obviously, this is a coarse estimate of a fish's diet, but this is the best estimate we could use since we did not perform dietary gut analyses, and stable isotope analysis of potential food sources in a concurrent study did not provide conclusive results. Since smallmouth bass (*Micropterus dolomieu*), rock bass (*Ambloplites rupestris*), and brook trout (*Salvelinus fontinalis*) that were found at 4 sites never reached the length at which these fish become piscivores (Scott and Crossman 1973) and since nitrogen signatures of these fish measured in a concurrent study (unpublished data) suggest that they are secondary consumers, we classified these fish as invertivores.

Estimating grazer removal of periphyton production and secondary consumption

Grazer removal per day was estimated from density and body mass of grazer taxa (Baetidae, Deuterophlebiidae, Elmidae, Helicopsychidae, Heptageniidae, Hydroptilidae, Othocladiinae, Pshephenidae, and *Physa*), by the use of the empirical model of Cattaneo and Mousseau (1995). Since we did not directly measure consumption of invertebrates by secondary consumers, we used published ecological efficiency values and an empirical model to estimate consumption by predatory invertebrates and fish. We measured consumption by invertebrate predators as the product of the reciprocal of gross production efficiency (GPE) and predator production as described by Benke and Wallace (1980) and Huryn (1996). GPE is the product of assimilation efficiency (AE = assimilation: consumption) and net productivity efficiency (NPE = production: assimilation). Similar to Benke et al. (2001), we used values of 70% for the AE of invertebrate prey (Benke and Wallace 1980, Wallace et al. 1987) and 40% for the NPE of small invertebrate predators (Wallace et al. 1987), including predaceous Diptera , and 55% for the NPE of large invertebrate predators (Smith and Smock 1992, Smock and Roeding 1986), including predaceous Plecoptera, Coleoptera, Odonata, and Megaloptera. We estimated fish consumption per year using an empirical model based on average annual fish biomass (Liao et al. 2005). We calculated total fish consumption of invertebrates as the sum of invertivorous fish consumption. We then divided total fish consumption of invertebrates per year by the number of days in the growing season (182.5), to obtain fish consumption of invertebrates on a daily basis.

To explore the potential for depletion of a consumer's food source, we also considered ratios of predator consumption to prey production and grazer removal to periphyton production. We quantified ratios of fish consumption to invertebrate production (FC:IP) as total daily fish consumption over the average invertebrate production per area of stream bed. Ratios of predator invertebrate consumption to primary consumer invertebrate production (SIC:PIP) and grazer

removal to primary production (GR:PP) were quantified per cobble, and the means of these ratios were used to represent the average depletion of invertebrate production by invertebrate predators and the average depletion of periphyton by invertebrate grazers.

We also examined invertebrate size distributions and fish consumption relative to invertebrate production (FC:IP) at each site to determine if top-down pressures were sufficient to alter patterns in size distributions of invertebrates. Size spectra were constructed at each site by displaying the average density of invertebrates (3 replicates * 6 dates) within logarithmic size classes, corresponding to a doubling of individual dry mass (μg) in each class. We then predicted average density in each size class from size class, FC:IP, and the interaction between size class and FC:IP in a least squares regression. If FC:IP is found to be a significant negative term in the model, this suggests that fish consumption relative to invertebrate production results in significant decreases in the abundance of invertebrates in each size class. A significant interaction term between FC:IP and size class indicates that FC:IP impacts densities in each size class differently, i.e. FC:IP results in significant shifts in size distributions, implying that fish consumption of invertebrates is size-selective.

Results

Algal, invertebrate, and fish production

The trophic structures of the streams in this study consist primarily of three levels: primary producers and allochthonous organic matter, primary consumers (non-invertivorous fish and non-predatory invertebrates), and secondary consumers (invertivorous fish and predatory invertebrates). Primary production of periphyton (mean = 542 mg dry mass m^{-2} day^{-1}, range 168-782 mg dry mass m^{-2} day^{-1}) was consistently higher at each site than average daily invertebrate production (mean = 129 mg dry mass m^{-2} day^{-1}, range 30-463 mg dry mass m^{-2} day^{-1}, Table 3.1). Similarly, invertebrate production was higher at most sites than fish production

(mean = 21 mg dry mass m^{-2} day^{-1}, range 13-36 mg dry mass m^{-2} day^{-1}), excluding 2 sites of intermediate trophy where fish production (55-71 mg dry mass m^{-2} day^{-1}) was relatively high and similar to invertebrate production (47-91 mg dry mass m^{-2} day^{-1}). Scrapers (mean = 41%, range = 16-70%), collector-filterers (mean = 32%, range = 2-55%), and collector-gatherers (mean = 19%, range = 4-80%) comprised the largest component of invertebrate production. Shredders and predators, on the other hand, each composed less than 10% of invertebrate production, excluding one of the oligotrophic forested streams (Ruisseau Blackburn, Table 3.1), where predators made up 30% of invertebrate production. Invertivores made up by far the majority of fish production at all sites (mean = 96%, range = 81-100%), whereas production of planktivores (mean = 2%, range = 0-11%) and detritivores (mean = 2%, range = 0-16%) constituted only a small proportion of total fish production

Production of algae, invertebrates, and fish as a function of total nitrogen and total phosphorus

Algal production was significantly greater at sites with higher concentrations of total nitrogen and total phosphorus, whereas invertebrate production only significantly correlated with total nitrogen (Fig. 3.1). Fish production increased slightly with total nitrogen at sites which were relatively oligotrophic, i.e., when total nitrogen was less than 1000 $\mu g\ L^{-1}$, and fish production significantly declined with total nitrogen at more eutrophic sites. Fish production was unrelated to total phosphorus. Since total nitrogen appeared to be more of a limiting nutrient in our steams than total phosphorus, production of invertebrate and fish functional feeding groups as a function of total nitrogen,is given in Figures 3.2 and 3.3, respectively. Production of collector-gatherers, collector-filterers, scrapers, and shredders was greater at sites with higher concentrations of total nitrogen, but only production of collector-gatherers was significantly greater ($p=0.04$), whereas predator production decreased at sites with higher concentrations of total nitrogen, but this pattern was not significant. Making up more than 80% of fish production

at all sites, invertivorous fish production responded to total nitrogen in a similar fashion as total fish production, whereas planktivorous and detritivorous fish production were not surprisingly unrelated to total nitrogen (Fig. 3.2).

Top-down forces of consumers and grazers as a function of total nitrogen and total phosphorus

Grazers had the potential to deplete periphyton at all sites (GR:PP = 2.0-30.8) and GR:PP was significantly lower at sites with greater concentrations of total phosphorus, whereas depletion of primary consumer invertebrates by predatory invertebrates seemed possible only at Ruisseau Blackburn (SIC:CIP = 2.0) where predators made up 30% of invertebrate production. Both GR:PP and SIC:CIP did not vary significantly with total nitrogen or total phosphorus (Fig. 3.4). Fish consumption, on the other hand, had the potential to nearly deplete invertebrate production at 6 of the 12 sites (FC:IP = 0.8-3.2) where total nitrogen was less than 1000 $\mu g\ L^{-1}$, and FC:IP significantly decreased with total nitrogen. Both SIC:PP and FC:IP were significantly lower at sites with greater concentrations of total nitrogen.

Invertebrate Size Spectra and Fish Consumption

The shape of the invertebrate size spectra were quite variable among the 12 streams and did not seem to vary with fish consumption (Fig 3.5). At 5 of the 12 streams, densities peaked near the 10 ug size class, whereas average densities at the remaining sites were greater within a broader range size classes, including 0.1-100-mg size classes. Not surprisingly, average densities in size classes were significantly lower at sites where fish consumed a large portion of available invertebrate production (i.e., FC:IP), but the interaction between fish consumption and size classes was not significant in the fitted model indicating that shifts in size spectra were unrelated to FC:IP (Table 3.2).

Discussion

Significant patterns in productivity at each trophic level with total nitrogen and/or total phosphorus (Fig. 3.3) suggest that nutrients are, at least in part, driving stream productivity along the gradient of forest cover in our study. The range in periphyton production (98-783 mg dry mass m^{-2} day^{-1}, Table 3.1) and the results from nutrient models predicting periphyton productivity (TP model $r^2 = 0.66$, TN model $r^2 = 0.42$, Fig.3.1) are similar to those obtained in a concurrent study in this region (epilithic algal production range: 53-872 mg dry mass m^{-2} day^{-1}, Carr et al. 2005) that found total nitrogen explained more variation in periphyton production ($r^2 = 0.72$) than total phosphorus ($r^2 = 0.51$). In contrast, however, another study in this region (Chetelat et al. 1999) found that total phosphorus ($r^2 = 0.56$) than total nitrogen ($r^2 = 0.50$) in epilithic algal biomass. Although we observed a much wider range in invertebrate production (18 - 463 mg dry mass m^{-2} day^{-1}, Table 3.1), our patterns in production concur with results from Shieh et al (2002, 2003) who measured invertebrate production at 6 sites along a longitudinal stream gradient with differing land use impacts and found invertebrate production to be the highest (170-mg dry mass m^{-2} day^{-1}) at a site with high inorganic nutrients and lowest at a site least impacted by humans (26 mg dry mass m^{-2} day^{-1}). Though they did not measure fish production or fish consumption, the authors suggested that higher macroinvertebrate production at agricultural and urban sites resulted from relatively low invertebrate predation pressure and high nutrient availability. Similarly, results from a logging study found that macroinvertebrate production was significantly greater at a logged section of a stream (112 mg dry mass m^{-2} day^{-1}) than at an unlogged section of the same stream (69 mg dry mass m^{-2} day^{-1}) which they attributed to greater periphyton growth (Kedzierski and Smock 2001).

We suspected that production of invertebrate shredders and detritivorous fish might be less coupled with nutrients than scrapers and invertivorous fish since they feed primarily on

allochthonous detritus, and that production shredders would be more strongly affected by top-down pressures of fish consumption. In detrital based food webs, Rosenfeld (2000) found that detritivorous invertebrates were primarily influenced by concentrations of organic detritus, whereas grazers were more strongly influenced by top-down effects of fish predation. Similarly, removal of detritus in experimental streams resulted in significant decreases in the biomass and abundance of invertebrate shredders, gatherers, total primary consumers, and predators, whereas no significant differences were found in scraper and filterer functional groups (Wallace et al. 1999). Since we did not quantify the relative contributions of each invertebrate functional feeding group to fish consumption, we cannot asses whether top-down pressures were greater on shredder production than scraper production in our study. However, patterns in dominant invertebrate and fish functional feeding groups with total nitrogen were similar to those observed for total invertebrate and fish production (Fig. 3.2), and total nitrogen explained even more variation in invertebrate shredder production ($r^2 = 0.30$) than it did for invertebrate scraper production ($r^2 = 0.24$) suggesting that production of shredders was not less coupled with total nitrogen than scrapers. Although total nitrogen did explain more variation in invertivorous fish than detritivorous fish (Fig. 3.3), the small r^2 values for detritivores may actually be due to the rarity of detritivores at all sites rater than to decreased bottom-up pressures on detritivores.

We cannot compare production of fish in our streams with other studies as we found no study that has quantified fish production in small streams along a trophic or land use gradient (but see deBruyn et al. 2003, Poff and Huryn 1998). However, contrary to a study of 79 North American streams which found that fish biomass significantly increased with total phosphorus (Hoyer and Canfield 1991), fish production in our streams was unrelated to total phosphorus and appeared to only benefit from moderate increases in total nitrogen. Perhaps negative effects from other factors not measured in this study, including flashiness of stream flow and

degradation of habitat which are important determinants of fish compositions, abundance and richness (Lammert and Allan 1999, Lehane et al. 2004, Roy et al. 2005), covary with high total nitrogen concentrations and outweigh the benefits of increased trophy. Indeed, flow variability (unpublished data) was greatest at 3 of the 4 streams where total nitrogen concentrations were greater than 1000 $\mu g\ L^{-1}$, the point at which fish production began to decline.

Since fish consumption relative to invertebrate production decreased with total nitrogen, invertebrate production at eutrophic sites appears to benefit from a release of fish predation (Fig. 3.4). Previous experimental and empirical studies have documented simultaneous bottom-up and top-down effects on invertebrate production (Flecker et al. 2002). Benthic invertebrate production was significantly lower in an experimental stream where leaf litter and snags were removed than in the control stream, while benthic invertebrate predators consumed a large portion of their prey, indicating that bottom-up and top-down pressures simultaneously control stream productivity (Wallace et al. 1999). By measuring algal, invertebrate, and fish production in two adjacent streams, Huryn (1998) empirically documented the importance of bottom-up and top-down controls of ecosystem production, which were dependent upon the predatory behavior of the top predator. However, unlike predatory invertebrates in the study by Wallace et al. (1999), benthic invertebrate predators in our streams provided little evidence for top-down control as they could potentially deplete invertebrate prey at only one forested site where perlid stonefly predators comprised 30% of invertebrate production, and no patterns were found with nutrients and ratios of predatory invertebrate consumption to primary invertebrate production (Fig. 3.4). The lack of impact by invertebrate predators is not surprising since predators comprised less than 10% total invertebrates at all other sites.

Patterns in invertebrate size distributions at our streams did not vary significantly with fish consumption relative to invertebrate production, suggesting that fish consumption of

invertebrates was not size-selective or that size-selective fish consumption was not sufficient to shift invertebrate size distributions (Fig. 3.5, Table 3.2). These results are contrary to previous studies demonstrating size selective pressures on invertebrates by fish (Bechara et al. 1993, Bechara et al. 1992, Bowlby and Roff 1986, McIntosh 2002, Peckarsky et al. 2001, Rosenfeld 2000). However, size classes of invertebrates in these studies were compared in the presence or absence of brown trout (*Salmo trutta*) or brook trout (*Salvelinus fontinalis*), which are much more aggressive predators than the invertivorous fish in our streams that consisted primarily of relatively small cyprinids and centrarchids.

Admittedly by collecting cobbles from riffle areas only, we did not sample invertebrate biomass within all habitats available for fish consumption within the 10-m transect of fish sampling area. However, since densities of macroinvertebrates tend to be significantly greater in riffles than in pools (Logan and Brooker 1983), our estimates of invertebrate production per area of stream bed may slightly overestimate the availability of invertebrate production, making our estimates of fish depletion quite conservative. Although macroinvertebrates supplied much of the food for trout, Huryn (1996) emphasized the importance of considering the production of hyporheic and terrestrial invertebrates when quantifying food availability for fish. Given that the stream bottoms in our study region are made of clay or bedrock we expect that contributions of hyporheic insects to fish prey are minimal to nil. Since fish consumption exceeded invertebrate production at forested sites, we suspect that invertivorous fish at these sites supplemented their diet with terrestrial invertebrates, as has been found by other studies (Edwards and Huryn 1996, England 2004, Huryn et al. 2001).

In congruence with a similar study investigating trophic relationships at five of the same streams as in our study (Morin et al. 2001), grazer consumption was of the same order of magnitude as primary production, suggesting that herbivores in this region do deplete epilithic

primary production (Fig. 3.4). Fish consumption of invertebrates did not appear to create trophic cascading impacts on algal productivity as grazers seemed to be able to deplete algal production even at sites with relatively low total nitrogen where fish consumption could potentially deplete invertebrate production (Fig. 3.4). Furthermore, the slope for invertebrate production as a function of variation in total nitrogen among sites was not significantly greater than the slope for algal production as a function of total nitrogen (TN coefficients = 0.87 and 0.83, Fig. 3.1) suggesting that algal and invertebrate production benefited equally from a reduction in fish consumption at eutrophic sites.

Conclusions

Algal and invertebrate production significantly increased with total nitrogen, whereas only algal production was significantly related to total phosphorus. Since fish production only increased with total nitrogen at oligotrophic and mesotrophic sites, factors other than nutrients that were not measured in this study, such as hydrology or habitat, may be more important determinants of fish production, especially at eutrophic sites. Although bottom-up forces appeared to be the primary forces driving stream productivity, ratios of grazer removal to primary production and fish consumption to invertebrate production suggest that fish and invertebrates have the potential to deplete their food sources and therefore contribute to the observed patterns in stream productivity. We found no evidence of size selectivity of predators or a trophic cascade, which may be related to the types of fish present in our streams. Future ecosystem production studies at multiple streams which contain fewer or greater trophic levels, such as fishless streams or streams with piscivorous fish, may help us to better understand how higher trophic levels modulate bottom-up effects on energy flow in streams along forested or trophic gradients.

Acknowledgements

This study was supported by an NSERC Grant (R GPIN-42799-2001) to A.M. We thank J. Strike for invaluable assistance in the field and laboratory. We greatly appreciate water quality data and digital catchment maps provided by the Regional Municipality of Ottawa and Carleton.

Literature Cited

Bechara, J. A., G. Moreau, and L. Hare. 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community: the role of spatial and size refugia. Journal of Animal Ecology 62: 451-464.

Bechara, J. A., G. Moreau, and D. Planas. 1992. Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. Canadian Journal of Fisheries and Aquatic Sciences 49: 2093-2103.

Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18: 308-343.

Benke, A. C. 1993. Edgardo Baldi Memorial Lecture: Concepts and patterns of invertebrate production in running waters. Verh.Internat.Verein.Limnol. 25: 15-38.

Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology 61: 108-118.

Benke, A. C., J. B. Wallace, J. W. Harrison, and J. W. Koebel. 2001. Food web quantification using secondary production analysis: Predaceous invertebrates of the snag habitat in a subtropical river. Freshwater Biology 46: 329-346.

Bowlby, J. N., and J. C. Roff. 1986. Trophic structure in southern Ontario streams. Ecology 67: 1670-1679.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.

Carr G.M., Morin A. and Chambers P.A. 2005. Bacteria and algae in stream periphyton along a nutrient gradient. Freshwater Biology, 50, 1337-1350.

Cattaneo, A., and B. Mousseau. 1995. Empirical analysis of the removal rate of periphyton by grazers. Oecologia 103: 249-254.

Chetelat J, F. R. Pick , A. Morin, and P. B. Hamilton.1999. Periphyton biomass and community composition in rivers of different nutrient status. Canadian Journal of Fisheries and Aquatic Sciences 56:560-569.

deBruyn, A. M. H., D. J. Marcogliese, J. B. Rasmussen. 2003. The role of sewage in a large river food web. Canadian Journal of Fisheries and Aquatic Sciences 60:1332-1344.

Edwards, E. D., and A. D. Huryn. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. Hydrobiologia 337: 151-159.

England, L. E., A. D. Rosemond. 2004. Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams. Freshwater Biology 49: 721-734.

Flecker, A.S., B. W. Taylor, E. S. Bernhardt, J. M. Hood, W. K. Cornwell, S. R. Cassatt, M. J. Vanni, and N. S. Altman. 2002. Interactions between herbivorous fishes and limiting nutrients in a tropical stream ecosystem. Ecology 83: 1831-1844.

Fretwell, S. D. 1977. The regulation of plant communities by the food chains exploiting them. Perspectives in Biology and Medicine 20: 169-185.

Goldstein, R. M., and T. P. Simon. 1999. Toward a united definition of guild structure for feeding ecology of North American freshwater fishes. Pages 123-202 in T.P. Simon, editor. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94: 421-425.

Hall, D. J., J. S. T. Threlkeld, C. W. Burns, and P. H. Crowley. 1976. The size efficiency hypothesis and the size structure of zooplankton communities. Annual Review of Ecology and Systematics 7: 177-208.

Halliwell, D. B., R. W. Langdon, R. A. Daniels, J. P. Kurtenbach, and R. A. Jacobson. 1999. Classification of freshwater fish species of the northeastern United States for use in the development of IBIs, p. 301-337. *In* T. P. Simon [ed.], Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, Florida.

Hosie, R.C. 1979. Native Trees of Canada. Fitzhenry and Whiteside Ltd., in cooperation with the Canadian Forest Service (Environment Canada) and the Canadian Government Publishing Centre, Supply and Services, Don Mills, Ontario.

Hoyer, M. V., and J. H. E. Canfield. 1991. A phosphorus-fish standing crop relationship for streams? Lake and Reservation Management 7: 25-32.

Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. Limnology and Oceanography 41: 243-252.

Huryn, A. D. 1998. Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. Oecologia 115: 173-183.

Huryn, A. D., R. H. Riley, R. G. Young, C. J. Arbuckle, K. Peacock, and G. Lyon. 2001. Temporal shift in contribution of terrestrial organic matter to consumer production in a grassland river. Freshwater Biology 46: 213-226.

Huryn, A. D., and J. B. Wallace. 2000. Life history and production of stream insects [Review]. Annual Review of Entomology 45: 83-110.

Kedzierski, W.M. and L. A. Smock 2001. Effects of logging on macroinvertebrate production in a sand-bottomed, low-gradient stream. Freshwater Biology 46: 821-833.

Kushlan, J. A., S. A.Voorhees, W. F. Loftus and P. C. Frohring. 1986. Length, mass, and calorific relationships of everglades animals. Florida Scientist 49: 65-79.

Lammert, M., and J. D. Allan. 1999. Assessing biotic integrity of streams: Effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environmental Management 23: 257-270.

Lehane, B. M., P. S. Giller, J. O'Halloran, and P. M. Walsh. 2004. Relative influences of catchment geology, land use and in-stream habitat on brown trout populations in south-western Ireland. Proceedings of the Royal Irish Academy - Section B Biology and Environment 104: 43-54.

Liao, H., C. L. Pierce, and J. G. Larscheid. 2005. An empirical model for estimating annual consumption by freshwater fish populations. North American Journal of Fisheries Management 25: 525-532.

Logan, P., and M. P. Brooker. 1983. The macroinvertebrate faunas of riffles and pools. Water Research 17: 263-270.

McIntosh, A.R. 2002. Impact of introduced trout on Nesameletus mayfly populations easured using electrofishing. Archiv fur Hydrobiologie, 154, 375-392.

McIntosh, A.R., H. S. Greig , S. A. Mcmurtrie., P. Nystrom, and M. J. Winterbourn. 2005. Top-down and bottom-up influences on populations of a stream detritivore. Freshwater Biology, 50, 1206-1218.

Merritt, R. W., and K. W. Cummins. 1996. An introduction to the aquatic insects of North America, 3rd ed. Kendall/Hunt Publishing Company.

Morin, A., C. Back, A. Chalifour, J. Boisvert, and R. H. Peters. 1988. Effect of black fly ingestion and assimilation on seston transport in a Quebec lake outlet. Canadian Journal of Fisheries and Aquatic Sciences 45: 705-714.

Morin, A., N. Bourassa, and A. Cattaneo. 2001. Use of size spectra and empirical models to evaluate trophic relationships in streams. Limnology and Oceanography 46: 935-940.

Morin, A., and P. Dumont. 1994. A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. Journal of the North American Benthological Society 13: 357-367.

Morin, A., W. Lamoureux, and J. Busnarda. 1999. Empirical models predicting primary productivity from chlorophyll *a* and water temperature for stream periphyton and land and ocean phytoplankton. Journal of the North American Benthological Society 18: 299-307.

Morin, A., J. Stephenson, J. Strike, and A. G. Solimini. 2004. Sieve retention probabilities of stream benthic invertebrates. Journal of the North American Benthological Society 23: 383-391.

Morley, S. A., and J. R. Karr. 2002. Assessing and restoring the health of urban streams in the Puget Sound Basin. Conservation Biology 16: 1498-1509.

NCC. 1999. 1:2000 Scale Topographic Mapping (Ottawa-Hull). National Capital Commission, Ottawa, Canada.

Nystrom P., McIntosh A.R. and Winterbourn M.J. 2003. Top-down and bottom-up processes in grassland and forested streams. Oecologia, 136, 596-608.

Ostrofsky, M.L., F. H. Rigler . 1987. Chlorophyll-phosphorus relationships for subarctic lakes in western Canada. Canadian Journal of Fisheries and Aquatic Sciences 44: 775-781.

Peckarsky B.L., Taylor B.W., McIntosh A.R., McPeek M.A. and Lytle D.A. (2001) Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology, 82, 740-757.

Poff, N. L., and A. D. Huryn. 1998. Multi-scale determinants of secondary production in Atlantic salmon (Salmo salar) streams. Canadian Journal of Fisheries and Aquatic Sciences 55: 201-217.

Power, M. E. 1990.Effects of fish in river food webs. Science, 250, 811-814.

Randall, R. G., and C. K. Minns. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Canadian Journal of Fisheries and Aquatic Sciences 57: 1657-1667.

Reice, S.R. 1980 The Role of Substratum in Benthic Macroinvertebrate Microdistribution and Litter Decomposition in a Woodland Stream. Ecology 61: 580-590.

Reynolds, C. S. 1984. The ecology of freshwater plankton. Cambridge University Press.

Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53: 295-311.

Rios, S. L., and R. C. Bailey. 2006. Relationship between riparian vegetation and stream benthic communities at three spatial scales. Hydrobiologia 553: 153-160.

Rosemond, A.D., P. J. Mulholland, and J. W. Elwood. 1993 Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. Ecology, 74, 1264-1280.

Rosemond, A. D., C. M. Pringle, A. Ramirez, and M. J. Paul. 2001. A test of top-down and bottom-up control in a detritus-based food web. Ecology 82: 2279-2293.

Rosenfeld, J. 2000.Effects of fish predation in erosional and depositional habitats in a temperate stream. Canadian Journal of Fisheries and Aquatic Sciences, 57, 1369-1379.

Roy, A. H., S. J. Wenger, J. L. Meyer, M. C. Freeman, B. J. Freeman, and W. E. Ensign. 2005. Investigating hydrologic alteration as a mechanism of fish assemblage shifts in urbanizing streams. Journal of the North American Benthological Society 24: 656-678.

Scott, W. B., and E. J. Crossman. 1973. Freshwater Fishes of Canada. Bulletin 184. Fisheries Research Board of Canada.

Shieh S.H., Ward J.V. and Kondratieff B.C. 2002. Energy flow through macroinvertebrates in a polluted plains stream. Journal of the North American Benthological Society, 21, 660-675.

Shieh S.H., Ward J.V. and Kondratieff B.C. 2003. Longitudinal changes in macroinvertebrate production in a stream affected by urban and agricultural activities. Archiv fur Hydrobiologie, 157, 483-503.

Smith, L. C., and L. A. Smock. 1992. Ecology of invertebrate predators in a Coastal Plain stream. Freshwater Biology 28: 319-329.

Smock, L. A., and C. E. Roeding. 1986. The trophic basis of production of the macroinvertebrate community of a southeastern USA blackwater stream. Holarctic Ecology 9: 165-174.

vanValen, L. V. 1973. Pattern and the balance in nature. Evolutionary Theory 1: 31-49.

vanDeventer, J. S., and W.S. Platts. 1986. MicroFish 3.0. United States Departmnet of Agriculture.

Wallace, J. B., A. C. Benke, A. H. Lingle, and K. Parsons. 1987. Trophic pathways of macroinvertebrate consumers in subtropical blackwater systems. Archiv Fuer Hydrobiologie Supplement 74: 423-451.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409-442.

Wang, L., J. Lyons, and P. Kanehl. 2001. Impacts of urbanization on stream habitat and fish across multiple spatial scales. Environmental Management 28: 255-266.

Wang, L., J. Lyons, P. Kanehl, and R. Gatti. 1997. Influences of watershed land use on habitat quality and biotic integrity in Wisconsin streams. Fisheries 22: 6-12.

Zippen, C. 1958. The removal method of population estimation. Journal of Wildlife Management 22: 82-90.

Table 3.1. Location and average total nitrogen (TN), total phosphorous (TP), periphyton production (PP), invertebrate production (IP), and fish production (FP) during May-October 2002 at 12 sites along a forested gradient.

SITE	Coordinates	Subcatchment Forest Cover (%)	TN ($\mu g\ L^{-1}$)	TP ($\mu g\ L^{-1}$)	PP ($mg\ m^{-2}\ day^{-1}$)	IP ($mg\ m^{-2}\ day^{-1}$)	FP ($mg\ m^{-2}\ day^{-1}$)
Sawmill Creek downstream	45°23'N 75°41'W	29	1663.33	82.43	624.75	104.74	15.10
Voyageur Creek	45°28'N 75°33'W	30	2654.44	42.83	772.79	162.20	0.46
Mosquito Creek	45°17'N 75°40'W	35	843.75	40.40	609.64	228.26	35.70
Ruisseau Leamy downstream	45°27'N 75°44'W	39	1340.00	163.25	782.48	86.29	12.52
Harwood Creek	45°23'N 75°58'W	48	776.25	17.25	766.60	463.33	22.76
Sawmill Creek upstream	45°20'N 75°38'W	49	771.33	60.43	679.36	90.66	55.64
Ruisseau Leamy midstream	45°28'N 75°45'W	50	874.17	111.75	470.74	46.82	71.24
Poole Creek	45°16'N 75°56'W	69	1367.78	17.20	547.98	117.72	4.55
Ruisseau Blackburn	45°38'N 75°49'W	89	349.17	11.33	98.08	18.49	7.79
Ruisseau Chelsea	45°30'N 75°49'W	89	495.56	20.00	203.52	30.04	22.06
Ruisseau laPeche	45°37'N 76°06'W	91	477.42	32.67	340.01	35.84	24.48
Ruisseau Corriveau	45°41'N 75°44'W	96	312.50	10.00	167.29	48.72	16.11

Table 3.2. Regression results from a model predicting invertebrate density within invertebrate size classes from $\log_{10}$ dry mass of each size class, $\log_{10}$ ratio of fish consumption (mg dry mass m^{-2} day^{-1}) to invertebrate production mg dry mass m^{-2} day^{-1}), (CF:IP) and the interaction between $\log_{10}$ dry mass and $\log_{10}$ CF:IP (n = 12 sites).

independent variables	coefficient (SE)	p value
intercept	1.95 (0.08)	0.00
$\log_{10}$ dry mass (ug)	0.54 (0.06)	0.00
($\log_{10}$ dry mass)^2	- 0.40 (0.02)	0.00
$\log_{10}$ CF:IP	- 0.35 (0.07)	0.00
$\log_{10}$ CF:IP * $\log_{10}$ dry mass	0.01 (0.04)	0.80

Figure 3.1. Periphyton production (PP, ▲), invertebrate production (IP, ●), and fish production (FP, □) as a function of variation in total nitrogen and total phosphorus among sites (n = 12).

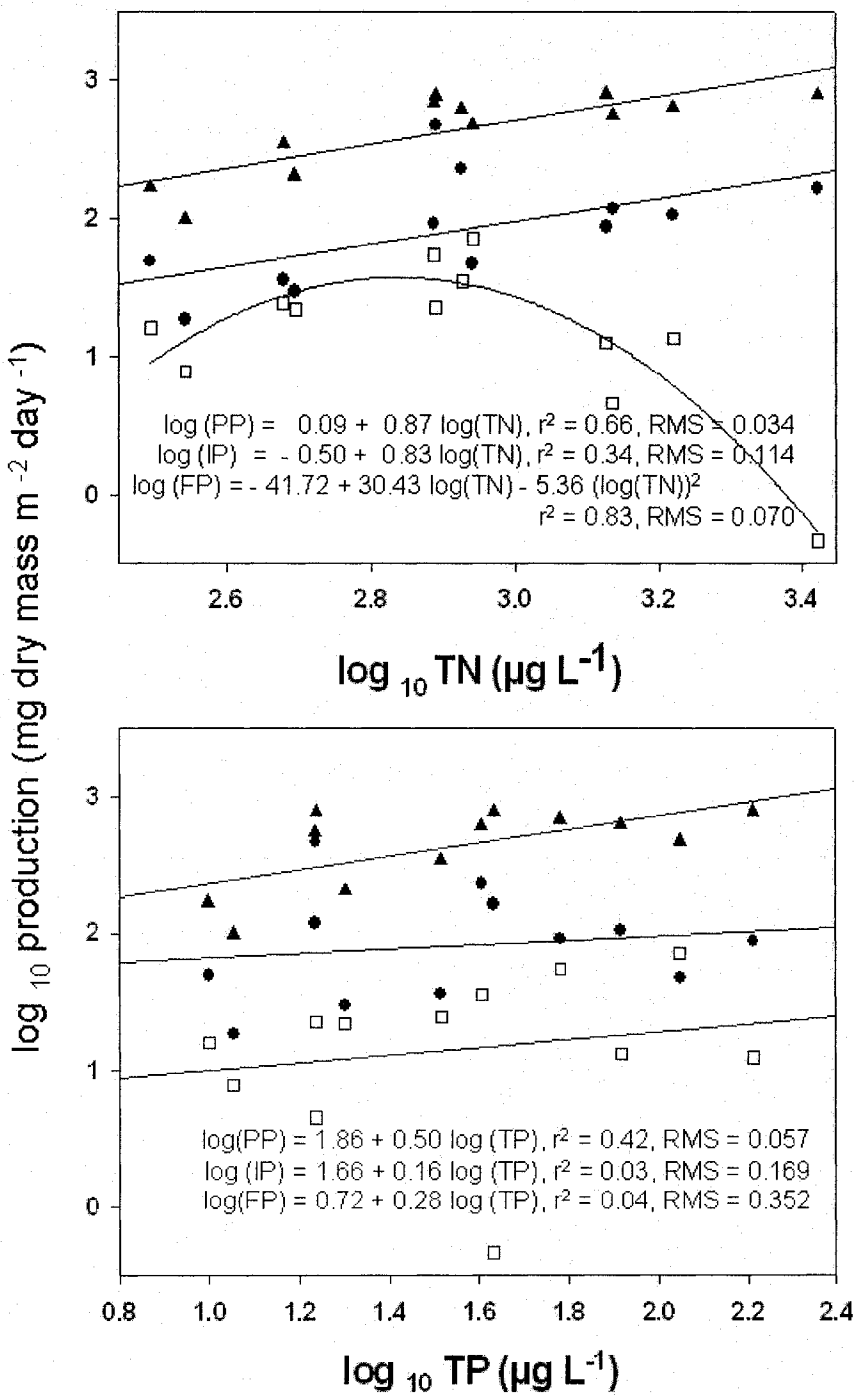


Figure 3.2. Production of invertebrate functional feeding groups as a function of variation in total nitrogen (TN) among sites (n = 12). Invertebrate functional feeding groups included scrapers (SC), collector-gatherers (CG), collector-filterers (CF), shredders (SH), and predators (PR).

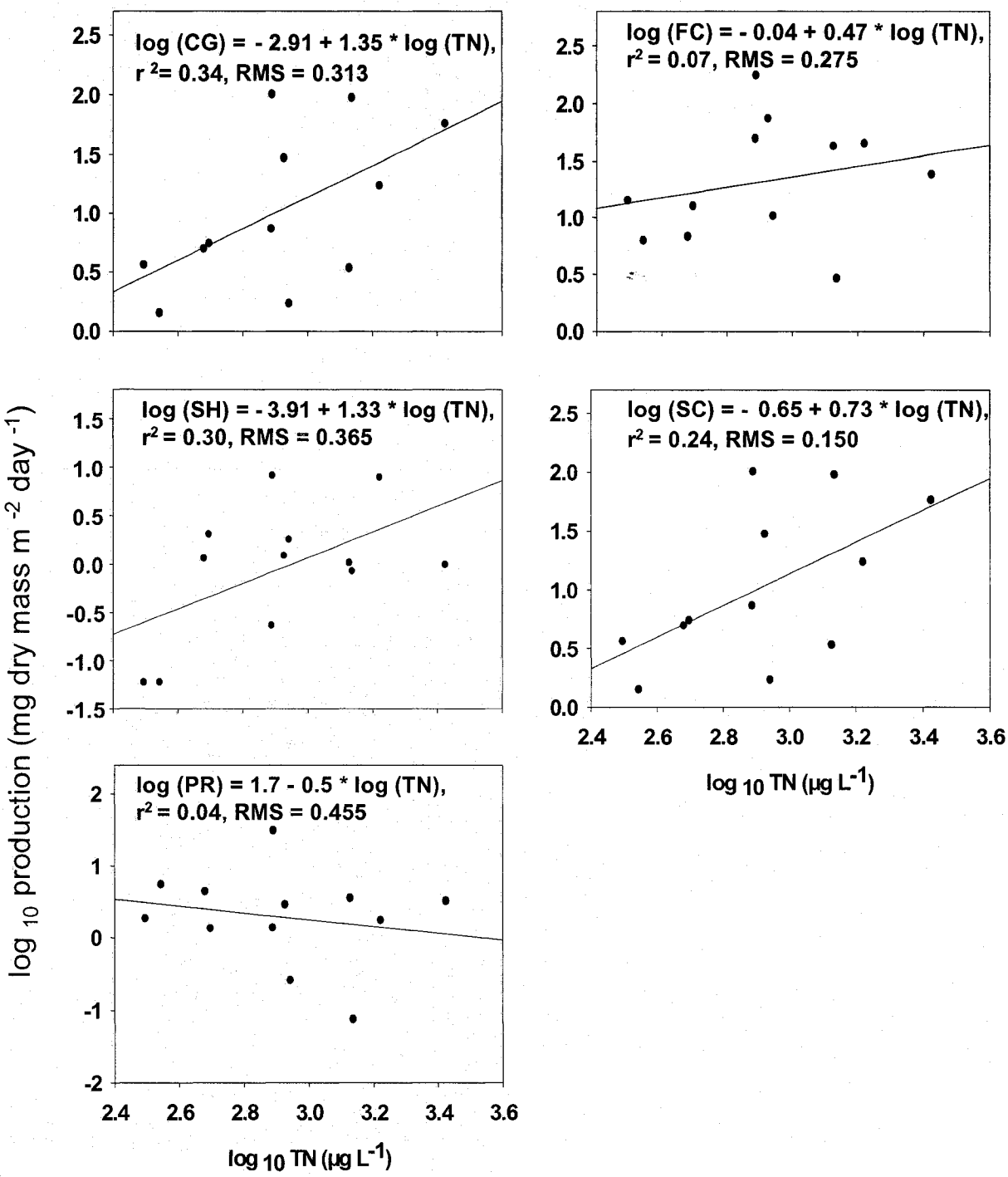


Figure 3.3. Production of fish functional feeding groups as a function of variation of total nitrogen (TN) among sites (n = 12). Fish functional feeding groups included invertivores (IN), planktivores (PL), and detritivores (DE).

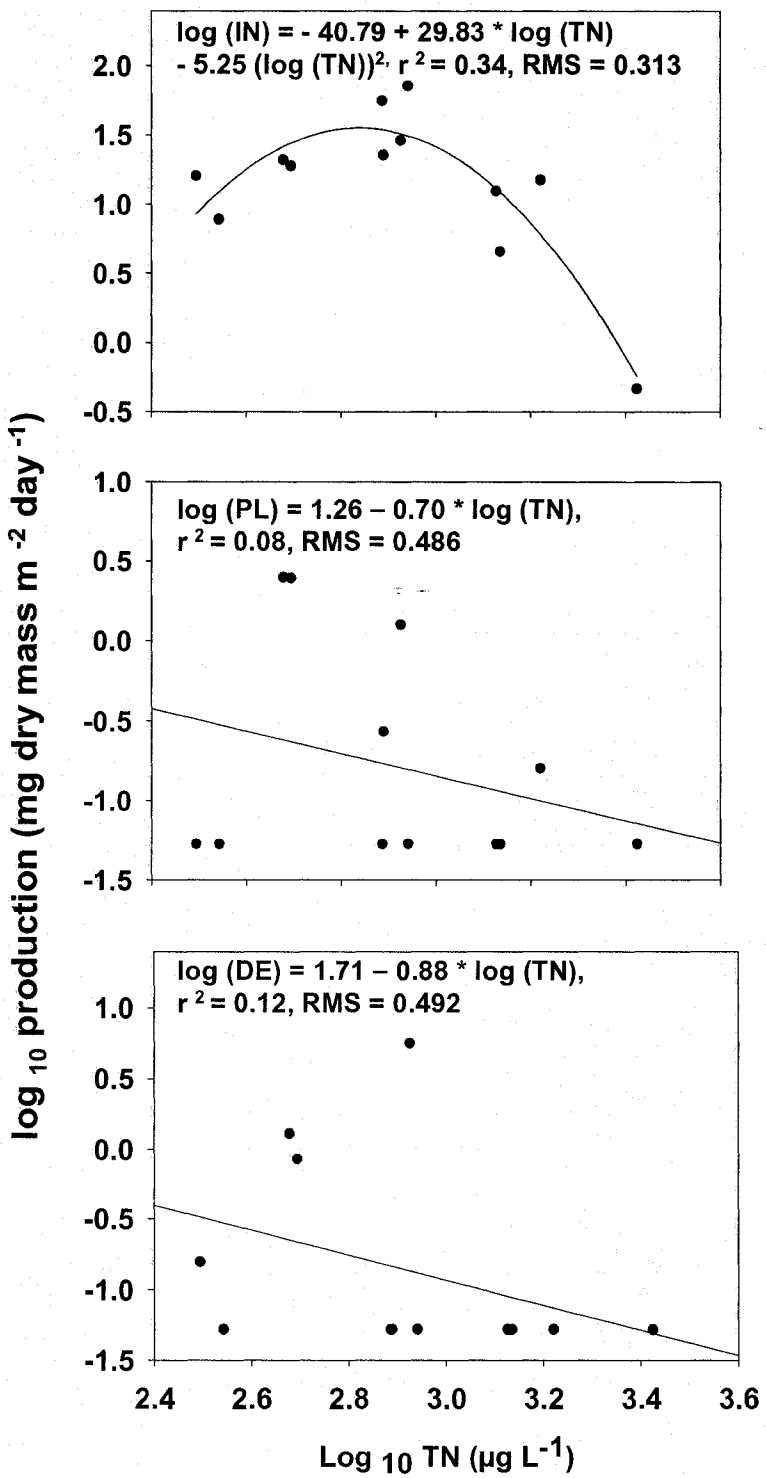


Figure 3.4. Ratios of grazer removal to periphyton production (GR:PP, ▲), secondary consumer invertebrate consumption to primary consumer invertebrate production (SIC:PIP, ●), and fish consumption to invertebrate production (CF:IP, □) as a function of variation in total nitrogen (TN) and total phosphorus (TP) among sites (n = 12).

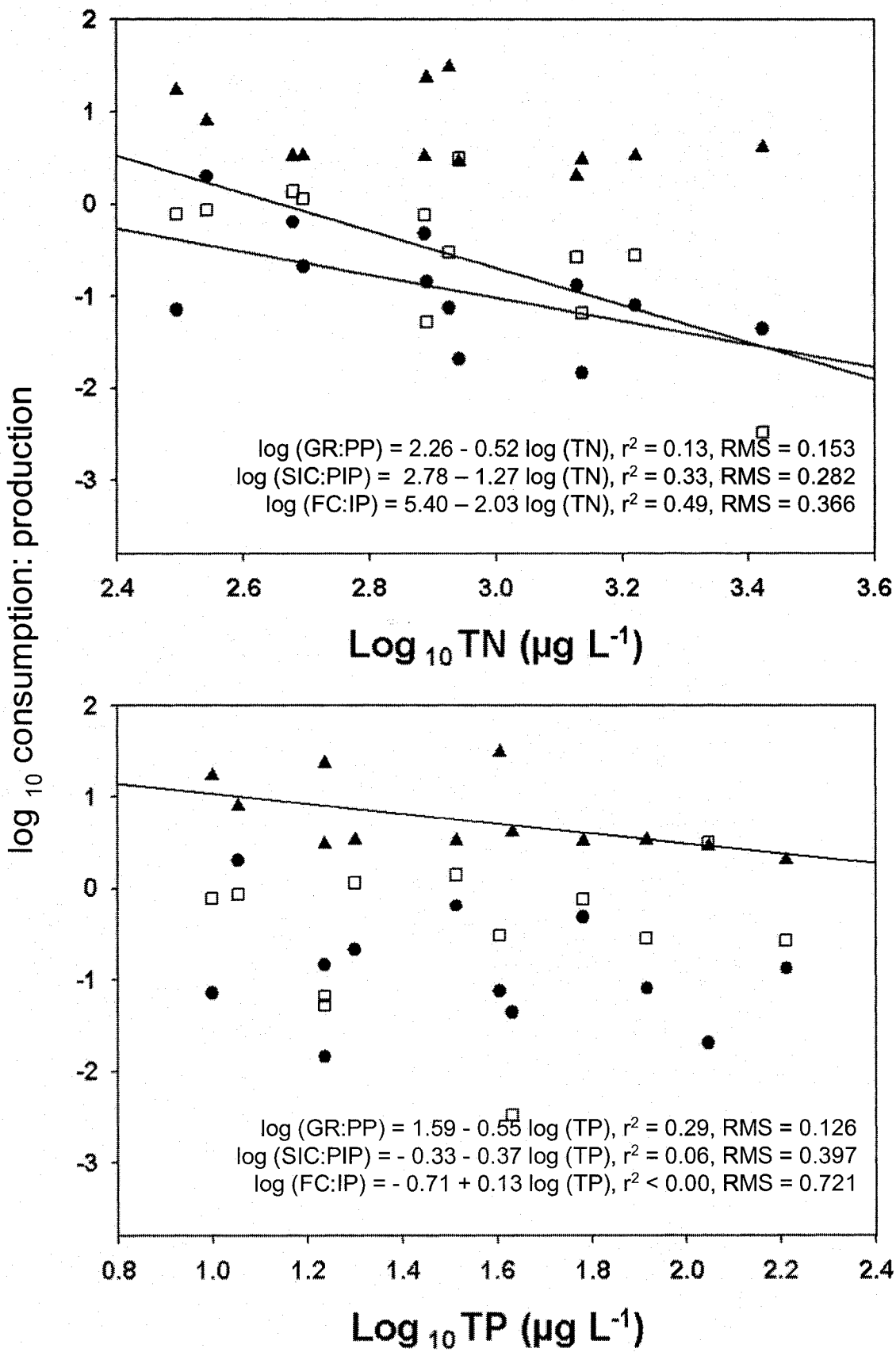
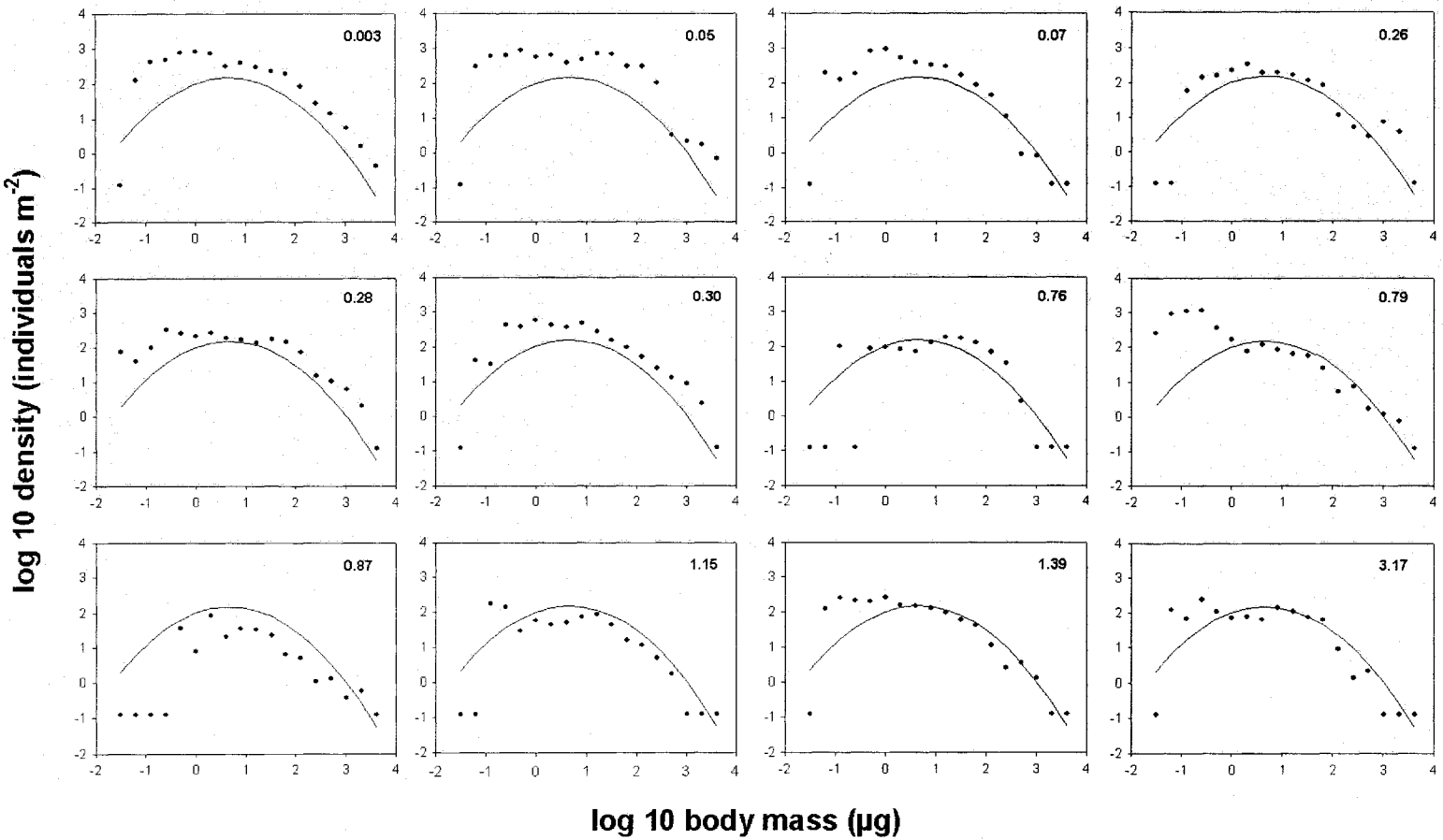


Figure 3.5. Average density (number m^{-2}) of size classes ($\log_2$ dry mass (ug)) at 12 streams (n per size class = 3 replicates * 6 dates) along a gradient of forest cover. The number above each figure is a ratio of fish consumption (mg dry mass m^{-2} day^{-1}) to invertebrate production (CF:IP) at each site.



General Conclusions

The overall purpose of this research was to determine how forest cover impacts stream ecosystem productivity. Although structural properties are typical measures of stream ecosystem response to disturbance (Rosenberg and Resh 1993), functional properties of running waters, such as stream productivity, may provide a more relevant basis for the development of best management practices (Bunn et al. 1999, Harris 1994). In this thesis, I examined multiple spatial scales of forest cover and developed time-saving methods for measuring secondary production so that I could quantify algal, invertebrate, and fish production in small headwater streams along a forested gradient and examine bottom-up and top-down mechanisms for observed patterns in stream productivity.

To determine the most influential spatial scale of forest cover on stream productivity, I quantified algal, invertebrate, and fish biomass, the single best correlate of productivity (Benke 1993), at 38 first-third order streams along a forest cover gradient at 55 spatial scales in chapter 1. Forest cover within subcatchments was consistently the best predictor of biomass at each trophic level in terms of the variance in biomass explained by forest cover and the unexplained residual variance, and the only significant predictor of biomass when considering the independent effects of forest cover on biomass at three coarse scales (within 40-m reach, riparian buffers, and the entire subcatchment).

Energy flow in lotic systems is an important aspect of stream ecosystem function (Benke 1993), and benthic invertebrates are key players in stream food webs as they transfer energy and matter from primary producers or allochthonous organic matter to top

predators (Wallace and Webster 1996). However, a review of secondary production literature revealed that only a minority of benthic invertebrate production studies has quantified production for entire invertebrate assemblages, even fewer have done so at multiple streams, and none have also included primary and tertiary production at multiple streams, which is likely due at least in part to the high costs of measuring invertebrate production. In the second chapter, I developed two approaches for processing benthic samples for estimating secondary production that reduced laboratory processing time by 37% and 82% and provided production estimates that were strongly related to production estimates obtained from standard processing techniques, with introduced analytical errors that were insignificant relative to the natural spatial variance of production.

Finally in chapter 3, using a time-saving approach for processing benthic invertebrate samples (developed in chapter 2) and published empirical models that predict primary and secondary production (Morin and Dumont 1994, Morin et al. 1999, Randall and Minns 2000), I quantified daily algal, invertebrate, and fish production throughout the growing season at 12 streams along a gradient of forest cover within subcatchments, the most influential scale on stream biomass (as determined in chapter 1). Total nitrogen explained 34-83% of the variation in algal, invertebrate, and fish production, whereas total phosphorus was only a significant predictor of algal production, suggesting the total nitrogen is a crucial bottom-up force regulating stream productivity at all three trophic levels along the forest cover gradient. However, similar to previous empirical and experimental studies investigating bottom-up and top-down forces of stream productivity (Wallace et al. 1999, Huryn 1996, Huryn 1998), the potential for

depletion or near depletion of food resources by consumers suggest that top-down forces also play an important role in regulating stream productivity.

Diffuse perturbations are considered to be a chief threat to aquatic systems (MWLA 1999, USEPA. 2002). Results from this thesis suggest that total nitrogen in particular is an important determinant of stream productivity in the National Capital Region of Canada. Given that this thesis has shown that forest cover within subcatchments was consistently the most influential scale on stream biomass at multiple trophic levels and was the only spatial scale to significantly explain independent components of the variation in stream biomass, it is unlikely that the common practice of riparian buffer maintenance is a sufficient strategy for mitigating catchment-wide disturbances on stream productivity within this region. Management scenarios that address the source of diffuse perturbations, such as careful land use planning and efforts to reduce impervious cover, or effective impervious cover, i.e. the proportion of a catchment covered by impervious surfaces that is directly connected to streams by stormwater drainage pipes (Walsh et al. 2005), are more likely to reduce watershed impacts on streams in this region.

This is the first study that I know of that has measured primary, secondary and tertiary production at more than 3 streams. By considering functional aspects of benthic and fish communities at multiple streams, I was able to show how bottom-up as well as top-down forces regulate stream productivity, which directly impacts the functioning of larger aquatic and terrestrial ecosystems that depend upon production from these headwater streams (Gomi et al. 2002). The time-saving methods for processing benthic samples developed in this thesis should make ecosystem production studies at multiple

streams more feasible so that future studies can investigate mechanisms for functional changes along gradients of disturbance. Future multiple-spatial scale studies will also help to ensure that stream management scenarios match the scale of disturbance, and are therefore more effective at protecting the ecosystems of running water systems.

Literature Cited

Benke, A. C. 1993. Edgardo Baldi Memorial Lecture: Concepts and patterns of invertebrate production in running waters. Verh.Internat.Verein.Limnol. 25: 15-38.

Bunn, S. E., T. D. Mosisch, and P. M. Davies. 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. Freshwater Biology 41: 333-345.

Gomi T., R. C. Sidle, and J. S. Richardson. 2002. Understanding processes and downstream linkages of headwater systems. Bioscience 52: 905-916.

Harris, G. P. 1994. Pattern, process and prediction in aquatic ecology. A limnological view of some general ecological problems. Freshwater Biology 32: 143-160.

Huryn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. Limnology and Oceanography 41: 243-252.

Huryn, A. D. 1998. Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. Oecologia 115: 173-183.

Rosenberg , D. N. and V. H. Resh. 1993. Freshwater biomonitoring and benthic macroinvertebrates. Chapman and Hall, New York.

Morin, A., and P. Dumont. 1994. A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. Journal of the North American Benthological Society 13: 357-367.

Morin, A., W. Lamoureux, and J. Busnarda. 1999. Empirical models predicting primary productivity from chlorophyll *a* and water temperature for stream periphyton and land and ocean phytoplankton. Journal of the North American Benthological Society 18: 299-307.

MWLA. 1999. Tackling Non-Point Source Water Pollution in British Columbia: An Action Plan. Ministry of Water, Land and Air Protection.

Randall, R. G., and C. K. Minns. 2000. Use of fish production per unit biomass ratios for measuring the productive capacity of fish habitats. Canadian Journal of Fisheries and Aquatic Sciences 57: 1657-1667.

US E PA. 2002. National Water Quality Inventory: 2000. Office of Water, Environmental Protection Agency.

Wallace, J. B., S. L. Eggert., J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69: 409-442.

Wallace, J. B., and J. R. Webster J. R. 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology 41: 115-139.

Walsh, C. J., T. D. Fletcher, and A. R. Ladson. 2005. Stream restoration in urban catchments through redesigning stormwater systems: Looking to the catchment to save the stream. Journal of the North American Benthological Society 24: 690-705.

Appendix A. Site, Biomass, Water Quality, and Forest Cover Data used in Chapter 1

Table 1.1. Name and location of 38 sites in the National Capital Region where stream biomass was measured in chapter 1. Station codes are given for biomass sites that were also monitored for water quality by the Regional Municipality of Ontario and Carleton.

SITE	Name	RMOC station code	Pro-vince	Lattitde	Longitude	Location
BEA	Bear Brook Creek	CK31-01	ON	45.3750	-75.4592	Russell Road (RR#26), near Samure Road (RR#37)
BEC	Beckett's Creek	CK25-001	ON	45.5203	-75.3582	Hwy 17 (RR#174), upstream of culvert
BIL	Billberry Creek	CK22-001	ON	45.487	-75.5343	250 meters downstream of Bilberry Drive N. (dead end)
BLA	Ruisseau Blackburn		QU	45.6413	-75.815	downstream of chemin de la Colonie; ~0.5 km north of 366
BRA	Brassil's Creek	CK44-02	ON	44.9850	-75.8012	Dwyer Hill Road, near Donnelly Road
CHE	Ruisseau Chelsea		QU	45.5021	-75.8115	at Chelsea picnic area in the Gatineau Park downstream of walking bridge
COR	Ruisseau Corriveau		QU	45.6845	-75.7395	parallel to chemin Corriveau, ~1.5 km west of 307
DESF	Ruisseau des Fees		QU	45.4371	-75.7558	upstream of promenade de la Gatineau in the Gatineau Park; ~1km sout of Gamelin Road
DEST	Ruisseau des Trembles		QU	45.4286	-75.7611	Downstrem of rue des Noisetiers, in Parc des Noisetiers, access from apartment parking lot
FOR	Ruisseau Fortune		QU	45.5195	-75.8483	at Dunlop picnic area downstream of picnic tables on chemin du Lac-Meech in the Gatineau Park
GRAD	Graham Creek downstream	CK8-01	ON			mouth of creek at Ottawa River in Andrew Hayden Park
GRAU	Graham Creek upstream	CK8-35	ON	45.3196	-75.7865	Graham at Siskin Court
GRE	Green Creek	CK21-003	ON	45.4204	-75.5922	Innes Road Bridge (RR#30), upstream of culvert
HAR	Hardwood Creek	CK65-04	ON	45.3837	-75.9709	Dunrobin Road, near River Road
HUN	Hunt Club Creek	CK19-01	ON	45.3465	-75.6963	200 meters downstream of Riverside Drive (southbound lane), between CNR tracks and Nelligan Drive
JR-01	Jock River upstream	JR-01	ON	45.2599	-75.7096	Prince of Wales (RR#73)
JR-20	Jock River downstream	JR-20	ON	45.1559	-75.954	Munster School Road
KIN	Ruisseau Kingsmere		QU	45.4803	-75.8491	tributary of Kingsmere Lake in the Gatineau Park

SITE	Name	RMOC station code	Pro-vince	Lattitde	Longitude	Location
LAP	Ruisseau la Peche		QU	45.6212	-76.0999	Upstream of chemin de Eardley-Maschem in the Gatineau Park; ~1.5 km south of 366
LDS	Leamy downstream		QU	45.4624	-75.7298	downstream of snowdump
LMS	Leamy midstream		QU	45.4674	-75.7470	behind Phelemon Wright high school
LUS	Leamy upstream		QU	45.4772	-75.7912	Downstream of Rue du Quartz off of chemin de la Mine
MCR	M. Castor River	CK63-265	ON	45.2222	-75.4931	Hwy 31 (RR#31), 0.5KM south of Victoria Rd (RR#6)
MEE	Ruisseau Meech		QU	45.5710	-75.8872	in the Gatineau Park
MNCR	Middle North Castor Rivers	CK63-266	ON	45.2547	-75.3968	intersection of Gregorie Rd (RR#41) and Victoria Road (RR#6)
MOS	Mosquito Creek	CK20-10	ON	45.2830	-75.6683	Limebank Rd.
MUD	Mud Creek	CK41-01	ON	45.2237	-75.7019	Bankfield Road, upstream of culverts (RMU-01)
NCR	N. Castor River	CK63-206	ON	45.2956	-75.5055	8th Line Road (RR#27), 1KM south of Mitch Owens Rd (RR#8)
PHI	Ruisseau Lac Phillipe		QU	45.6047	-76.0132	tributary of Lac Phillipe in the Gatineau Park
POO	Poole Creek	R010-32	ON	45.2624	-75.9256	Main Street (Stittsville), upstream of culvert
RAI	Ruisseau Rainville		QU	45.5963	-75.6586	Downstream of chemin Paiment
SAWD	Samill Creek downstream	CK18-Q	ON	45.3899	-75.6762	Riverside Drive west bound lane (downstream); near Harvey's restauran
SAWU	Sawmill Creek upstream	CK18-03-00	ON	45.3379	-75.6335	northeast tributary, at Lester and Albion Roads (8.7km upstream of confluence)
TAY	Taylor Creek	CK23-001	ON	45.4937	-75.4927	North Service Road (Jeanne D'Arc Extension), upstream of culvert
TAYD	Taylor Drain	CK42-05-03	ON	45.1399	-75.7267	Fourth Line Road (RR#5), between Roger Stevens Road and Phelan W.
UNA	unnamed		QU	45.4597	-75.7243	downstream of walking path Parc écologique due Lac-Leamy, ~0.5 km south of dirt road,
VOY	Voyageur Creek	CK35-004	ON	45.4651	-75.5485	Youville Drive (downstream of culvert)
WAT	Watts Creek	CK6-312	ON	45.3263	-75.8877	Upstream of March Road, northwest of HWY 417

Table 1.2. Biomass (mg m^{-2}) of periphyton and invertebrates per cobble, and velocity (m second $^{-1}$), which was measured at approximately 60% of the depth of the stream where the cobble was collected.

Site	Date	month	year	Rep	Periphyton Biomass	Invertebrate Biomass	Velocity
BEA	26-Jul-01	7	2001	1	21602.98	30982.86	0.11
BEA	26-Jul-01	7	2001	2	626.43	3277.83	0.34
BEA	26-Jul-01	7	2001	3	9398.36		0.11
BEA	26-Jul-01	7	2001	4	1988.38	39891.85	0.11
BEA	26-Jul-01	7	2001	5	1651.73	10348.72	0.16
BEA	26-Jul-01	7	2001	6	8681.71	26471.99	0.18
BEC	15-Jul-02	7	2002	1	1890.26	3848.93	0.59
BEC	15-Jul-02	7	2002	2	2534.78	23697.92	0.39
BEC	15-Jul-02	7	2002	3	2308.63	5085.74	0.18
BEC	15-Jul-02	7	2002	4	1355.32	11511.51	0.22
BEC	15-Jul-02	7	2002	5	3202.29	4913.22	0.42
BEC	15-Jul-02	7	2002	6	1941.28	7851.89	0.42
BIL	09-Jul-02	7	2002	1	4937.10	367.50	0.16
BIL	09-Jul-02	7	2002	2	6207.80	1168.30	0.11
BIL	09-Jul-02	7	2002	3	2872.76	265.61	0.33
BIL	09-Jul-02	7	2002	4	3565.52	1614.81	0.23
BIL	09-Jul-02	7	2002	5	1522.13	7130.61	0.17
BIL	09-Jul-02	7	2002	6	857.41	7194.40	0.33
BLA	29-Aug-01	8	2001	1	171.73	53.24	0.32
BLA	29-Aug-01	8	2001	2	56.91	0.00	0.31
BLA	29-Aug-01	8	2001	3	11.43	264.56	0.23
BLA	29-Aug-01	8	2001	4	106.64	2282.21	0.33
BLA	29-Aug-01	8	2001	5	91.16	37.09	0.11
BLA	29-Aug-01	8	2001	6	139.04	1262.56	0.27
BRA	18-Jul-01	7	2001	1	490.95	9193.79	0.32
BRA	18-Jul-01	7	2001	2	561.57	20.46	0.39
BRA	18-Jul-01	7	2001	3	1039.56	3255.12	0.37
BRA	18-Jul-01	7	2001	4	527.17	2930.02	0.37
BRA	18-Jul-01	7	2001	5	300.87	3840.28	0.21
BRA	18-Jul-01	7	2001	6	1148.28	7129.96	0.29
CHE	10-Aug-01	8	2001	1	102.05	478.21	0.11
CHE	10-Aug-01	8	2001	2	123.70	77.11	0.12
CHE	10-Aug-01	8	2001	3	584.23	89.96	0.33
CHE	10-Aug-01	8	2001	4	509.51	622.18	0.33
CHE	10-Aug-01	8	2001	5	297.20	2618.84	0.11
CHE	10-Aug-01	8	2001	6	870.65	114.94	0.15
COR	27-Aug-01	8	2001	1	245.90	222.63	0.33
COR	27-Aug-01	8	2001	2	429.80	291.77	0.22
COR	27-Aug-01	8	2001	3	258.87	550.65	0.25

Site	Date	month	year	Rep	Periphyton Biomass	Invertebrate Biomass	Velocity
COR	27-Aug-01	8	2001	4	209.75		0.25
COR	27-Aug-01	8	2001	5	313.17	1010.63	0.11
COR	27-Aug-01	8	2001	6	423.87	691.94	0.25
DESF	28-Aug-01	8	2001	1	342.10	67.03	0.23
DESF	28-Aug-01	8	2001	2	313.43	0.00	0.11
DESF	28-Aug-01	8	2001	3	93.35	16.00	0.12
DESF	28-Aug-01	8	2001	4	410.80	0.00	0.38
DESF	28-Aug-01	8	2001	5	610.74	0.00	0.29
DESF	28-Aug-01	8	2001	6	180.54	234.74	0.46
DEST	09-Aug-01	8	2001	1	2727.65	1885.11	0.20
DEST	09-Aug-01	8	2001	2	1037.53	3290.49	0.32
DEST	09-Aug-01	8	2001	3	1485.03	1711.24	0.27
DEST	09-Aug-01	8	2001	4	4265.13	1972.37	0.13
DEST	09-Aug-01	8	2001	5	1149.32	1440.89	0.42
DEST	09-Aug-01	8	2001	6	3911.29	2501.31	0.27
FOR	16-Aug-02	8	2002	1	682.39	0.00	0.14
FOR	16-Aug-02	8	2002	2	109.19	0.00	0.12
FOR	16-Aug-02	8	2002	3	59.69	5862.99	0.09
FOR	16-Aug-02	8	2002	4	260.06	0.00	0.32
FOR	16-Aug-02	8	2002	5	146.24	21.66	0.40
FOR	16-Aug-02	8	2002	6	18.55	176.85	0.05
GRAU	21-Jul-02	7	2002	1	2570.45	6130.39	0.71
GRAU	21-Jul-02	7	2002	2	1887.77	12582.18	0.42
GRAU	21-Jul-02	7	2002	3	3254.89	7045.97	0.47
GRAU	21-Jul-02	7	2002	4	1572.77	2341.06	0.30
GRAU	21-Jul-02	7	2002	5	1988.91	2717.54	0.30
GRAU	21-Jul-02	7	2002	6	1603.33	9317.02	0.23
GRAD	23-Jul-02	7	2002	1	2668.12	154.68	0.41
GRAD	23-Jul-02	7	2002	2	311.69	160.27	0.96
GRAD	23-Jul-02	7	2002	3	752.34	11.29	0.53
GRAD	23-Jul-02	7	2002	4	324.63		0.84
GRAD	23-Jul-02	7	2002	5	364.83		0.31
GRAD	23-Jul-02	7	2002	6	308.17	496.88	0.37
GRE	13-Jul-01	7	2001	1	2306.75	500.21	0.42
GRE	13-Jul-01	7	2001	2	1344.98	8789.04	0.16
GRE	13-Jul-01	7	2001	3	1736.28	12237.02	0.45
GRE	13-Jul-01	7	2001	4	2231.75	5317.89	0.63
GRE	13-Jul-01	7	2001	5	1511.12	14828.23	0.52
GRE	13-Jul-01	7	2001	6	1982.11	14462.98	0.23
HAR	15-Aug-02	8	2002	1	1469.91	3855.92	0.00
HAR	15-Aug-02	8	2002	2	1404.10	678.28	0.00
HAR	15-Aug-02	8	2002	3	8125.20	173.55	0.00
HAR	15-Aug-02	8	2002	4	3170.61		0.00
HAR	15-Aug-02	8	2002	5	3233.64		0.00
HAR	15-Aug-02	8	2002	6	2045.47	671.17	0.00
HUN	21-Jul-02	7	2002	1	987.30	7371.04	0.23

Site	Date	month	year	Rep	Algal Biomass	Invertebrate Biomass	Velocity
HUN	21-Jul-02	7	2002	2	743.92	3813.07	0.16
HUN	21-Jul-02	7	2002	3	1080.19	1572.15	0.13
HUN	21-Jul-02	7	2002	4	1224.61		0.25
HUN	21-Jul-02	7	2002	5	1228.15	10616.09	0.10
HUN	21-Jul-02	7	2002	6	1132.18	6112.80	0.11
JR-01	27-Jul-01	7	2001	1	2166.03	5652.88	0.36
JR-01	27-Jul-01	7	2001	2	2662.26	1658.68	0.21
JR-01	27-Jul-01	7	2001	3	1506.23	7396.62	0.26
JR-01	27-Jul-01	7	2001	4	2947.03	5575.32	0.49
JR-01	27-Jul-01	7	2001	5	1464.08	3351.05	0.44
JR-01	27-Jul-01	7	2001	6	1892.66	5985.15	0.69
JR-20	16-Jul-02	7	2002	1	2955.89	2401.22	1.00
JR-20	16-Jul-02	7	2002	2	3821.85	4438.23	0.31
JR-20	16-Jul-02	7	2002	3	1726.77	1200.15	1.07
JR-20	16-Jul-02	7	2002	4	1337.23	5081.73	0.64
JR-20	16-Jul-02	7	2002	5	1879.31	966.51	0.35
JR-20	16-Jul-02	7	2002	6	3072.03	787.31	0.75
KIN	27-Aug-02	8	2002	1	300.21	474.11	0.10
KIN	27-Aug-02	8	2002	2	179.34	207.15	0.29
KIN	27-Aug-02	8	2002	3	385.89	1424.52	
KIN	27-Aug-02	8	2002	4	265.07	2304.68	
KIN	27-Aug-02	8	2002	5	214.90	1301.02	0.22
KIN	27-Aug-02	8	2002	6	124.32	1469.87	0.24
LAP	23-Aug-01	8	2001	1	519.62	3531.29	0.17
LAP	23-Aug-01	8	2001	2	287.76	1784.01	0.19
LAP	23-Aug-01	8	2001	3	597.13	119.82	0.21
LAP	23-Aug-01	8	2001	4	253.53	3446.52	0.11
LAP	23-Aug-01	8	2001	5	375.11	43.65	0.27
LAP	23-Aug-01	8	2001	6	444.29	19.38	0.19
LDS	20-Aug-01	8	2001	1	1227.44	1529.39	0.41
LDS	20-Aug-01	8	2001	2	2352.81	794.46	0.39
LDS	20-Aug-01	8	2001	3	1911.66	2204.97	0.57
LDS	20-Aug-01	8	2001	4	1071.00	517.72	0.27
LDS	20-Aug-01	8	2001	5	2868.02	701.49	0.68
LDS	20-Aug-01	8	2001	6	3097.34	4562.70	0.39
LMS	28-Aug-01	8	2001	1	740.52	230.62	0.46
LMS	28-Aug-01	8	2001	2	138.11	63.90	0.53
LMS	28-Aug-01	8	2001	3	882.82	155.49	0.44
LMS	28-Aug-01	8	2001	4	1908.06	1382.96	0.15
LMS	28-Aug-01	8	2001	5	765.56	2038.63	0.61
LMS	28-Aug-01	8	2001	6	1267.42	2858.95	0.50
LUS	20-Aug-01	8	2001	1	885.36	500.32	0.23
LUS	20-Aug-01	8	2001	2	548.72	295.82	0.11
LUS	20-Aug-01	8	2001	3	771.93	2038.41	0.23
LUS	20-Aug-01	8	2001	4	740.02	1017.60	0.21
LUS	20-Aug-01	8	2001	5	335.07	8191.96	0.15

Site	Date	month	year	Rep	Algal Biomass	Invertebrate Biomass	Velocity
LUS	20-Aug-01	8	2001	6	996.74	2061.10	0.15
MCR	15-Jul-02	7	2002	1	1873.89	2787.69	0.15
MCR	15-Jul-02	7	2002	2	2476.87	14274.84	0.27
MCR	15-Jul-02	7	2002	3	2523.78	6336.02	0.44
MCR	15-Jul-02	7	2002	4	754.45	1058.91	0.29
MCR	15-Jul-02	7	2002	5	1910.21	13570.31	0.44
MCR	15-Jul-02	7	2002	6	1749.99	11152.61	0.66
MEE	27-Aug-02	8	2002	1	1295.29	218.44	0.12
MEE	27-Aug-02	8	2002	2	814.21	1717.30	0.43
MEE	27-Aug-02	8	2002	3	1226.68		0.58
MEE	27-Aug-02	8	2002	4	1022.41	913.16	0.67
MEE	27-Aug-02	8	2002	5	682.51	1023.25	0.65
MEE	27-Aug-02	8	2002	6	1078.82	1450.26	0.65
MNCR	15-Jul-02	7	2002	1	2785.90	10186.68	0.49
MNCR	15-Jul-02	7	2002	2	2122.40	2284.64	0.52
MNCR	15-Jul-02	7	2002	3	3947.38	4962.57	0.54
MNCR	15-Jul-02	7	2002	4	3610.58	1912.33	0.44
MNCR	15-Jul-02	7	2002	5	2241.50	15610.22	0.54
MNCR	15-Jul-02	7	2002	6	2236.03	3845.28	0.52
MOS	15-Jul-01	7	2001	1	1947.00	1584.07	0.45
MOS	15-Jul-01	7	2001	2	1203.30	3990.74	0.33
MOS	15-Jul-01	7	2001	3	595.41	2136.86	0.26
MOS	15-Jul-01	7	2001	4	1083.07	2408.87	0.24
MOS	15-Jul-01	7	2001	5	1446.62	19130.12	0.19
MOS	15-Jul-01	7	2001	6	2474.07	12309.63	0.39
MUD	23-Jul-02	7	2002	1	2014.15	4300.66	0.41
MUD	23-Jul-02	7	2002	2	1699.14	9674.82	0.57
MUD	23-Jul-02	7	2002	3	1134.44	3571.37	0.29
MUD	23-Jul-02	7	2002	4	1200.57	13613.92	0.73
MUD	23-Jul-02	7	2002	5	4140.73	18471.25	0.59
MUD	23-Jul-02	7	2002	6	2273.03	10444.73	0.60
NCR	20-Jul-01	7	2001	1	1350.27	4223.89	0.29
NCR	20-Jul-01	7	2001	2	2149.82	23283.14	0.47
NCR	20-Jul-01	7	2001	3	2040.21	8029.38	0.33
NCR	20-Jul-01	7	2001	4	919.47	8725.22	0.43
NCR	20-Jul-01	7	2001	5	2068.07	12938.33	0.42
NCR	20-Jul-01	7	2001	6	1757.12	12699.98	0.39
PHI	28-Aug-02	8	2002	1	50.29	165.60	0.29
PHI	28-Aug-02	8	2002	2	95.54	0.0	0.28
PHI	28-Aug-02	8	2002	3	30.41	68.55	0.16
PHI	28-Aug-02	8	2002	4	117.76	0.00	0.20
PHI	28-Aug-02	8	2002	5	235.41	170.29	0.14
PHI	28-Aug-02	8	2002	6	102.70	1409.89	0.06
POO	29-Aug-02	8	2002	1	2487.30	827.15	0.25
POO	29-Aug-02	8	2002	2	4378.34	235.47	0.55
POO	29-Aug-02	8	2002	3	921.82	1500.91	0.14

Site	Date	month	year	Rep	Algal Biomass	Invertebrate Biomass	Velocity
POO	29-Aug-02	8	2002	4	2642.27		0.22
POO	29-Aug-02	8	2002	5	1976.31	1601.07	0.28
POO	29-Aug-02	8	2002	6	1539.62	4172.29	0.42
RAI	28-Aug-01	8	2001	1	986.80	337.97	0.23
RAI	28-Aug-01	8	2001	2	508.71	520.85	0.11
RAI	28-Aug-01	8	2001	3	1216.09	416.68	0.29
RAI	28-Aug-01	8	2001	4	950.87	469.55	0.31
RAI	28-Aug-01	8	2001	5	536.89	1965.00	0.11
RAI	28-Aug-01	8	2001	6	936.78	1186.93	0.11
SAWD	17-Jul-01	7	2001	1	2175.56	905.09	0.57
SAWD	17-Jul-01	7	2001	2	2480.98	5878.62	0.35
SAWD	17-Jul-01	7	2001	3	2073.18	1791.01	0.37
SAWD	17-Jul-01	7	2001	4	2877.12	3473.52	0.54
SAWD	17-Jul-01	7	2001	5	2127.19	4783.79	0.28
SAWD	17-Jul-01	7	2001	6	2145.62	1803.21	0.45
SAWU	15-Jul-02	7	2002	1	2902.23	3773.90	0.28
SAWU	15-Jul-02	7	2002	2	956.55	540.20	0.23
SAWU	15-Jul-02	7	2002	3	2299.01	1461.96	0.11
SAWU	15-Jul-02	7	2002	4	2554.24		0.28
SAWU	15-Jul-02	7	2002	5	2882.05		0.25
SAWU	15-Jul-02	7	2002	6	2196.86		0.41
TAY	27-Jul-01	7	2001	1	1497.63	5342.86	0.33
TAY	27-Jul-01	7	2001	2	921.80		0.36
TAY	27-Jul-01	7	2001	3	1691.33	5906.71	0.41
TAY	27-Jul-01	7	2001	4	1458.90	6228.10	0.39
TAY	27-Jul-01	7	2001	5	1275.33	11439.76	0.33
TAY	27-Jul-01	7	2001	6	994.10	12776.82	0.48
TAYD	19-Jul-01	7	2001	1	248.87	4324.34	0.19
TAYD	19-Jul-01	7	2001	2	959.11	2087.10	0.26
TAYD	19-Jul-01	7	2001	3	881.61	1956.37	0.21
TAYD	19-Jul-01	7	2001	4	624.41	8042.27	0.43
TAYD	19-Jul-01	7	2001	5	1179.07	1167.31	0.43
TAYD	19-Jul-01	7	2001	6	412.36	12522.36	0.21
UNA	22-Aug-01	8	2001	1	1074.54	796.35	0.20
UNA	22-Aug-01	8	2001	2	1070.13	3837.29	0.28
UNA	22-Aug-01	8	2001	3	1152.27	1603.35	0.35
UNA	22-Aug-01	8	2001	4	325.05		0.51
UNA	22-Aug-01	8	2001	5	1430.52	10562.98	0.16
UNA	22-Aug-01	8	2001	6	875.47	1029.14	0.33
VOY	25-Jul-01	7	2001	1	2014.58	913.80	0.37
VOY	25-Jul-01	7	2001	2	1114.50	3881.87	0.63
VOY	25-Jul-01	7	2001	3	1613.36	12652.85	0.38
VOY	25-Jul-01	7	2001	4	2007.48	4347.25	0.49
VOY	25-Jul-01	7	2001	5	2020.87	4957.93	0.18
VOY	25-Jul-01	7	2001	6	744.30	2375.62	0.33
WAT	16-Jul-02	7	2002	1	990.21	2053.99	0.19
WAT	16-Jul-02	7	2002	2	1367.17	8208.37	0.30

Site	Date	month	year	Rep	Algal Biomass	Invertebrate Biomass	Velocity
WAT	16-Jul-02	7	2002	3	1456.98	2068.68	0.19
WAT	16-Jul-02	7	2002	4	1775.60	6135.41	0.29
WAT	16-Jul-02	7	2002	5	221.40	5624.94	0.32
WAT	16-Jul-02	7	2002	6	539.03	5120.50	0.33

Table 1.3. Number in each pass (P1-P4), estimated total number (N), catchability (P), estimated density (D), mean weight (w), and estimated biomass (B) of fish and their variances in size classes at 38 sites in the National Capital Region, July and August of 2001 and 2002, obtained from lengths and weights of fish using PopPro as explained in chapter 1.

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
BEA	0	0.0-1.9	0	0	0		0.00	0.00	0.00		60	0.00	0.00	0.00	0.00	0.00	0.00
BEA	1	2.0-3.9	1	0	0		1.00	0.00	1.00	0.00	60	0.02	0.00	123.66	0.00	2.06	0.00
BEA	2	4.0-5.9	18	6	7		38.11	47.47	0.43	0.02	60	0.64	0.01	864.06	3506.41	548.95	11262.96
BEA	3	6.0-9.9	9	3	3		17.58	12.99	0.47	0.03	60	0.29	0.00	2770.24	262764.81	811.63	50252.91
BEA	4	10.0-15.9	4	0	2		7.58	12.26	0.41	0.10	60	0.13	0.00	11545.84	4900828.50	1459.21	532330.50
BEA	5	16.0-17.9	2	0	0		2.00	0.00	1.00	0.00	60	0.03	0.00	22071.86	1629776.38	735.88	1811.59
BEA	6	18.0-21.9	2	1	0		3.07	0.13	0.71	0.08	60	0.05	0.00	21655.74	11090982.00	1110.05	45838.24
BEA	7	22.0-23.9	0	0	0		0.00	0.00	0.00	0.00	60	0.00	0.00	0.00	0.00	0.00	0.00
BEA	8	24.0-25.9	1	0	0		1.00	0.00	1.00	0.00	60	0.02	0.00	70341.44	0.00	1172.59	0.00
BEA	total										60	1.17	0.02			5840.36	641496.19
BEC	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	26	0.00	0.00	0.00	0.00	0.00	0.00
BEC	1	2.0-3.9	1	0	0		1.00	0.00	1.00	0.00	26	0.04	0.00	96.04	0.00	3.63	0.00
BEC	2	4.0-5.9	8	2	2		13.07	3.28	0.57	0.03	26	0.49	0.01	375.04	2130.92	185.00	1175.41
BEC	3	6.0-7.9	18	8	4		33.34	11.90	0.54	0.01	26	1.26	0.02	969.50	8037.92	1219.99	28665.31

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
BEC	4	8.0-9.9	13	2	1		16.17	0.24	0.78	0.01	26	0.61	0.00	1717.27	18559.92	1048.15	7920.00
BEC	5	10.0-11.9	1	1	0		2.18	0.55	0.57	0.20	26	0.08	0.00	3352.85	376021.97	275.65	11291.69
BEC	6	12.0-13.9	1	0	0		1.00	0.00	1.00	0.00	26	0.04	0.00	4069.65	0.00	153.59	0.00
BEC	7	14.0-15.9	0	0	0		0.00	0.00	0.00	0.00	26	0.00	0.00	0.00	0.00	0.00	0.00
BEC	8	16.0-17.9	1	0	0		1.00	0.00	1.00	0.00	26	0.04	0.00	23348.49	0.00	881.17	0.00
BEC	total										26	2.56	0.02			3767.16	49052.40
BIL	0	0.0-1.9	0	0	0	0	0.00	0.00	0.00	0.00	14	0.00	0.00	0.00	0.00	0.00	0.00
BIL	1	2.0-3.9	0	0	0	0	0.00	0.00	0.00	0.00	14	0.00	0.00	0.00	0.00	0.00	0.00
BIL	2	4.0-5.9	0	0	0	0	0.00	0.00	0.00	0.00	14	0.00	0.00	0.00	0.00	0.00	0.00
BIL	3	6.0-7.9	3	1	1	0	5.16	0.28	0.58	0.05	14	0.37	0.00	1067.78	49440.34	393.25	8316.31
BIL	4	8.0-9.9	1	0	0	0	1.00	0.00	1.00	0.00	14	0.07	0.00	2099.38	0.00	149.96	0.00
BIL	total										14	0.44	0.00			543.21	8316.31
BLA	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
BLA	1	2.0-3.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
BLA	2	4.0-5.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
BLA	3	6.0-11.9	1	1	0		2.18	0.55	0.57	0.20	17	0.13	0.00	3744.77	3929911.25	489.46	94725.59
BLA	4	12.0-13.9	1	0	0		1.00	0.00	1.00	0.00	17	0.06	0.00	8930.22	0.00	535.81	0.00
BLA	total										17	0.19	0.00			1025.27	94725.59

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
BRA	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	34	0.00	0.00	0.00	0.00	0.00	0.00
BRA	1	2.0-3.9	41	15	16		89.35	121.92	0.42	0.01	34	2.65	0.11	247.87	619.47	657.76	10969.68
BRA	2	4.0-5.9	77	35	40		225.54	1241.75	0.31	0.01	34	6.70	1.10	625.23	1538.27	4188.07	497201.97
BRA	3	6.0-7.9	47	21	7		80.32	14.20	0.60	0.00	34	2.39	0.01	1076.76	6866.55	2568.51	53589.27
BRA	4	8.0-9.9	21	7	3		32.56	3.49	0.64	0.01	34	0.97	0.00	2474.84	99140.92	2393.23	111582.53
BRA	5	10.0-11.9	11	1	2		14.43	0.79	0.69	0.02	34	0.43	0.00	6518.23	180190.23	2793.49	62608.84
BRA	6	12.0-13.9	6	0	0		6.00	0.00	1.00	0.00	34	0.18	0.00	11631.80	2870016.75	2072.79	91138.07
BRA	7	14.0-15.9	1	0	0		1.00	0.00	1.00	0.00	34	0.03	0.00	19250.98	0.00	571.75	0.00
BRA	total										34	13.34	1.22			15245.58	827090.44
CHE	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	24	0.00	0.00	0.00	0.00	0.00	0.00
CHE	1	2.0-3.9	0	0	0		0.00	0.00	0.00	0.00	24	0.00	0.00	0.00	0.00	0.00	0.00
CHE	2	4.0-5.9	43	29	13		104.74	133.43	0.43	0.01	24	4.33	0.23	1038.60	3265.07	4500.26	307641.94
CHE	3	6.0-7.9	32	13	9		61.85	34.28	0.50	0.01	24	2.56	0.06	1804.45	13963.15	4616.89	282444.31
CHE	4	8.0-9.9	16	8	0		24.60	1.02	0.71	0.01	24	1.02	0.00	2513.83	74098.45	2558.26	87826.29
CHE	5	10.0-11.9	1	1	0		2.18	0.55	0.57	0.20	24	0.09	0.00	3855.69	360757.28	347.48	16834.59
CHE	total										24	8.00	0.29			12022.88	694747.13
COR	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	31	0.00	0.00	0.00	0.00	0.00	0.00
COR	1	2.0-11.9	18	8	5		35.70	21.27	0.49	0.02	31	1.16	0.02	2303.41	98243.03	2681.56	253155.95
COR	total										31	1.16	0.02			2681.56	253155.95

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
DESF	0	0.0-1.9	0	0	0	0	0.00	0.00	0.00	0.00	19	0.00	0.00	0.00	0.00	0.00	0.00
DESF	1	2.0-5.9	1	3	3	0	14.51	468.33	0.15	0.08	19	0.74	1.23	511.67	4338.21	380.92	325326.00
DESF	2	6.0-7.9	4	1	2	0	7.40	0.93	0.52	0.04	19	0.38	0.00	1100.21	21252.43	418.10	6037.52
DESF	3	8.0-9.9	1	0	0	0	1.00	0.00	1.00	0.00	19	0.05	0.00	2147.09	0.00	110.19	0.00
DESF	4	10.0-11.9	1	0	0	0	1.00	0.00	1.00	0.00	19	0.05	0.00	6198.91	0.00	318.13	0.00
DESF	5	12.0-13.9	1	0	0	0	1.00	0.00	1.00	0.00	19	0.05	0.00	8145.94	0.00	418.05	0.00
DESF	total										19	1.28	1.24			1645.39	331363.53
DEST	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	26	0.00	0.00	0.00	0.00	0.00	0.00
DEST	1	2.0-5.9	49	28	12		102.81	63.76	0.49	0.01	26	3.90	0.09	679.92	5726.36	2654.23	129758.55
DEST	2	6.0-7.9	18	6	3		28.63	4.01	0.62	0.01	26	1.09	0.01	2087.28	36276.97	2269.35	68045.30
DEST	3	8.0-9.9	40	19	9		76.13	30.50	0.53	0.01	26	2.89	0.04	3637.18	27664.01	10514.38	812978.06
DEST	4	10.0-11.9	3	1	0		4.04	0.06	0.78	0.05	26	0.15	0.00	5688.93	347336.72	873.36	10979.29
DEST	total										26	8.04	0.14			16311.31	1021761.19
FOR	0	0.0-3.9	3	7	2		38.29	8064.61	0.12	0.10	27	1.42	11.06	413.41	9818.15	586.35	1910714.50
FOR	1	4.0-5.9	104	80	16		226.53	107.71	0.51	0.00	27	8.39	0.15	995.63	3762.19	8354.13	411364.84
FOR	2	6.0-11.9	11	5	1		17.81	1.76	0.64	0.02	27	0.66	0.00	2453.89	239625.84	1618.58	118810.54
FOR	total										27	10.47	11.22			10559.05	2440889.75
GRAU	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	24	0.00	0.00	0.00	0.00	0.00	0.00

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
GRAU	1	2.0-3.9	17	30	10		133.68	7972.77	0.17	0.02	24	5.52	13.61	156.48	1587.50	864.38	381759.34
GRAU	2	4.0-5.9	2	5	1		18.51	1041.18	0.17	0.13	24	0.77	1.78	582.31	8075.73	445.46	607502.06
GRAU	3	6.0-7.9	3	0	1		4.36	1.09	0.57	0.10	24	0.18	0.00	1980.03	174644.98	356.45	12976.03
GRAU	4	8.0-9.9	2	0	0		2.00	0.00	1.00	0.00	24	0.08	0.00	3937.11	879931.00	325.36	6009.37
GRAU	total										24	6.55	15.39			1991.65	1008246.75
GRAD	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	64	0.00	0.00	0.00	0.00	0.00	0.00
GRAD	1	2.0-3.9	33	9	3		46.12	1.92	0.71	0.01	64	0.72	0.00	139.17	1350.06	100.33	710.75
GRAD	2	4.0-5.9	17	6	2		26.09	2.28	0.65	0.01	64	0.41	0.00	576.25	2248.58	234.94	558.37
GRAD	3	6.0-7.9	6	4	0		10.43	0.91	0.65	0.03	64	0.16	0.00	1185.91	56829.65	193.40	1824.19
GRAD	4	8.0-11.9	5	5	0		10.89	2.73	0.57	0.04	64	0.17	0.00	1807.24	35008.51	307.67	3194.88
GRAD	total										64	1.46	0.00			836.34	6288.18
GRE	1	2.0-3.9	1	0	0		1.00	0.00	1.00	0.00	77	0.01	0.00	328.24	0.00	4.24	0.00
GRE	2	4.0-5.9	5	6	0		12.33	5.01	0.52	0.04	77	0.16	0.00	708.42	19225.28	112.92	908.83
GRE	3	6.0-7.9	40	5	0		45.05	0.05	0.90	0.00	77	0.58	0.00	2084.21	8994.27	1214.01	3089.92
GRE	4	8.0-9.9	16	6	0		22.31	0.45	0.76	0.01	77	0.29	0.00	3508.46	47307.13	1011.86	4852.60
GRE	5	10.0-11.9	4	4	0		8.71	2.19	0.57	0.05	77	0.11	0.00	5103.86	205009.16	575.03	12122.40
GRE	6	12.0-13.9	2	2	0		4.36	1.09	0.57	0.10	77	0.06	0.00	6665.41	320705.53	375.49	9136.08
GRE	7	14.0-15.9	1	0	0		1.00	0.00	1.00	0.00	77	0.01	0.00	9012.86	0.00	116.54	0.00

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
GRE	8	16.0-17.9	1	0	0		1.00	0.00	1.00	0.00	77	0.01	0.00	17793.52	0.00	230.07	0.00
GRE	total										77	1.24	0.00			3640.15	30109.83
HAR	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	20	0.00	0.00	0.00	0.00	0.00	0.00
HAR	1	2.0-3.9	88	49	0		141.22	7.75	0.69	0.00	20	7.04	0.02	226.48	558.14	1594.08	28639.29
HAR	2	4.0-5.9	8	2	0		10.06	0.07	0.82	0.02	20	0.50	0.00	609.81	9005.13	305.66	2328.45
HAR	total										20	7.54	0.02			1899.74	30967.74
HUN	total	0	0	0	0		0.00	0.00	0.00	0.00	15	0.00	0.00	0.00	0.00	0.00	0.00
JR01	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	107	0.00	0.00	0.00	0.00	0.00	0.00
JR01	1	2.0-3.9	6	1	0		7.02	0.02	0.87	0.02	107	0.07	0.00	495.17	1401.60	32.58	6.45
JR01	2	4.0-5.9	111	70	47		313.13	1004.45	0.35	0.00	107	2.94	0.09	938.56	2623.45	2756.67	100482.38
JR01	3	6.0-7.9	21	18	7		60.66	141.69	0.38	0.01	107	0.57	0.01	1537.76	8895.06	874.97	32359.45
JR01	4	8.0-9.9	41	27	11		94.44	87.87	0.45	0.01	107	0.89	0.01	3265.07	19447.30	2892.47	97679.45
JR01	5	10.0-11.9	16	9	1		27.35	3.05	0.63	0.01	107	0.26	0.00	4168.19	120463.86	1069.13	12590.95
JR01	6	12.0-13.9	4	3	1		9.61	9.45	0.45	0.07	107	0.09	0.00	5652.78	697267.38	509.67	32227.61
JR01	7	14.0-15.9	2	0	1		3.79	6.13	0.41	0.20	107	0.04	0.00	11065.05	75899.71	393.44	66114.09
JR01	8	16.0-19.9	1	1	0		2.18	0.55	0.57	0.20	107	0.02	0.00	25177.24	14293568.00	514.46	36447.36
JR01	total										107	4.86	0.11			9043.40	377907.69
JR20	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	58	0.00	0.00	0.00	0.00	0.00	0.00
JR20	1	2.0-3.9	121	66	32		255.09	175.48	0.48	0.00	58	4.40	0.05	210.68	411.72	926.50	10277.49

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
JR20	2	4.0-5.9	10	4	7		44.04	1584.62	0.19	0.05	58	0.76	0.47	510.65	16111.46	387.72	132103.08
JR20	3	6.0-7.9	17	14	7		54.00	221.84	0.33	0.02	58	0.93	0.07	1976.28	27279.93	1839.84	281160.25
JR20	4	8.0-11.9	7	6	4		30.78	537.38	0.24	0.05	58	0.53	0.16	3336.59	81721.10	1770.65	1801144.50
JR20	total										58	6.62	0.75			4924.71	2224685.25
KIN	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
KIN	1	2.0-3.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
KIN	2	4.0-5.9	4	0	0		4.00	0.00	1.00	0.00	17	0.24	0.00	552.43	4925.77	132.58	283.72
KIN	3	6.0-7.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
KIN	4	8.0-9.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
KIN	5	10.0-11.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
KIN	6	12.0-13.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
KIN	7	14.0-15.9	1	0	0		1.00	0.00	1.00	0.00	17	0.06	0.00	15034.62	0.00	902.08	0.00
KIN	8	16.0-17.9	0	0	0		0.00	0.00	0.00	0.00	17	0.00	0.00	0.00	0.00	0.00	0.00
KIN	9	18.0-19.9	2	0	0		2.00	0.00	1.00	0.00	17	0.12	0.00	23054.87	5364222.50	2766.58	77244.81
KIN	total										17	0.42	0.00			3801.24	77528.53
LAP	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	21	0.00	0.00	0.00	0.00	0.00	0.00
LAP	1	2.0-7.9	5	4	2		15.34	54.97	0.34	0.06	21	0.72	0.12	678.14	30489.54	491.30	72421.41
LAP	2	8.0-9.9	3	0	1		4.36	1.09	0.57	0.10	21	0.21	0.00	4196.02	22320.85	863.60	43890.21

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
LAP	3	10.0-11.9	6	3	1		10.89	2.73	0.57	0.04	21	0.52	0.01	5742.73	101022.29	2954.84	227845.38
LAP	total										21	1.45	0.13			4309.75	344157.00
LDS	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	24	0.00	0.00	0.00	0.00	0.00	0.00
LDS	1	2.0-3.9	0	0	0		0.00	0.00	0.00	0.00	24	0.00	0.00	0.00	0.00	0.00	0.00
LDS	2	4.0-9.9	6	2	0		8.09	0.12	0.78	0.02	24	0.34	0.00	1744.96	142837.17	587.98	16850.80
LDS	total										24	0.34	0.00			587.98	16850.80
LMS	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	34	0.00	0.00	0.00	0.00	0.00	0.00
LMS	1	2.0-3.9	0	0	0		0.00	0.00	0.00	0.00	34	0.00	0.00	0.00	0.00	0.00	0.00
LMS	2	4.0-5.9	13	12	9		82.39	5662.58	0.16	0.03	34	2.40	4.81	938.31	4869.82	2251.92	4258490.00
LMS	3	6.0-7.9	59	34	16		128.39	100.95	0.47	0.00	34	3.74	0.09	2255.67	9127.13	8435.97	563507.38
LMS	4	8.0-9.9	19	13	11		75.19	1091.41	0.25	0.02	34	2.19	0.93	3798.36	16865.45	8319.74	13442578.00
LMS	total										34	8.33	5.82			19007.63	18264576.00
LUS	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	30	0.00	0.00	0.00	0.00	0.00	0.00
LUS	1	2.0-3.9	17	7	8		43.90	139.77	0.35	0.02	30	1.46	0.16	289.42	1130.98	423.51	15427.97
LUS	2	4.0-5.9	15	13	7		53.86	374.02	0.30	0.02	30	1.80	0.42	788.63	4322.28	1415.66	272341.94
LUS	3	6.0-7.9	17	27	10		121.61	6060.21	0.18	0.02	30	4.05	6.73	1767.26	10060.17	7163.29	21191378.00
LUS	4	8.0-9.9	7	8	3		28.17	216.77	0.29	0.04	30	0.94	0.24	3083.70	47406.35	2894.80	2331678.25
LUS	5	10.0-13.9	7	4	1		13.07	3.28	0.57	0.03	30	0.44	0.00	5820.08	578538.75	2535.43	233179.92

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
LUS	6	14.0-15.9	3	1	1		5.86	4.33	0.47	0.10	30	0.20	0.01	12020.53	1174477.38	2347.15	739698.94
LUS	total										30	8.88	7.55			16779.84	24783704.00
MCR	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	34	0.00	0.00	0.00	0.00	0.00	0.00
MCR	1	2.0-3.9	4	3	3		27.51	3218.53	0.14	0.11	34	0.80	2.72	204.12	4698.39	163.26	116331.93
MCR	2	4.0-5.9	13	7	6		36.50	137.46	0.34	0.03	34	1.06	0.12	562.08	4735.41	596.37	42030.16
MCR	3	6.0-7.9	6	3	3		17.54	87.43	0.32	0.06	34	0.51	0.07	1236.48	39421.32	630.47	123206.46
MCR	4	8.0-11.9	6	3	1		10.89	2.73	0.57	0.04	34	0.32	0.00	2851.14	152284.36	902.76	34037.95
MCR	5	12.0-13.9	1	1	0		2.18	0.55	0.57	0.20	34	0.06	0.00	7483.34	5747.68	473.89	25885.34
MCR	total										34	2.75	2.91			2766.75	341491.84
MEE	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	44		0.00	0.00	0.00	0.00	0.00
MEE	1	2.0-3.9	1	1	0		2.18	0.55	0.57	0.20	44	0.05	0.00	534.25	2363.39	26.21	84.79
MEE	2	4.0-5.9	11	2	0		13.04	0.04	0.86	0.01	44	0.29	0.00	918.95	15185.84	269.76	1326.08
MEE	3	6.0-7.9	12	5	4		25.07	23.01	0.45	0.03	44	0.57	0.01	2118.43	17315.56	1196.19	57882.78
MEE	4	8.0-9.9	3	1	0		4.04	0.06	0.78	0.05	44	0.09	0.00	3701.85	99324.72	337.06	1239.49
MEE	total										44	1.00	0.01			1829.22	60533.14
MNCR	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	88	0.00	0.00	0.00	0.00	0.00	0.00
MNCR	1	2.0-3.9	0	0	0		0.00	0.00	0.00	0.00	88	0.00	0.00	0.00	0.00	0.00	0.00
MNCR	2	4.0-5.9	11	1	0		12.01	0.01	0.92	0.01	88	0.14	0.00	850.92	8982.38	116.67	169.42
MNCR	3	6.0-7.9	7	5	0		12.59	1.31	0.64	0.03	88	0.14	0.00	1517.69	13331.58	218.24	670.04

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
MNCR	4	8.0-9.9	2	2	0		4.36	1.09	0.57	0.10	88	0.05	0.00	3353.12	568765.88	166.83	3010.67
MNCR	5	10.0-11.9	5	3	0		8.28	0.55	0.67	0.03	88	0.10	0.00	4362.13	777566.81	412.71	8327.52
MNCR	total										88	0.43	0.00			914.45	12177.65
MOS	0	0.0-1.9	13	6	0		19.40	0.66	0.72	0.01	50	0.39	0.00	12.90	8.74	4.97	1.34
MOS	1	2.0-3.9	75	17	14		111.54	12.64	0.63	0.00	50	2.22	0.01	89.40	177.67	198.13	912.64
MOS	2	4.0-5.9	22	9	3		36.01	4.87	0.62	0.01	50	0.72	0.00	416.13	1542.80	297.74	1122.62
MOS	3	6.0-7.9	13	8	2		25.37	8.01	0.55	0.02	50	0.50	0.00	1436.11	26326.39	724.05	13213.24
MOS	4	8.0-11.9	3	0	2		8.35	93.84	0.26	0.17	50	0.17	0.04	4091.90	612142.19	678.65	637153.38
MOS	5	12.0-13.9	1	0	0		1.00	0.00	1.00	0.00	50	0.02	0.00	10635.46	0.00	211.33	0.00
MOS	total										50	4.01	0.05			2114.88	652403.19
MUD	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	32	0.00	0.00	0.00	0.00	0.00	0.00
MUD	1	2.0-3.9	0	0	0		0.00	0.00	0.00	0.00	32	0.00	0.00	0.00	0.00	0.00	0.00
MUD	2	4.0-5.9	12	7	3		25.56	17.06	0.48	0.02	32	0.81	0.02	536.77	6173.02	432.64	8898.04
MUD	3	6.0-7.9	29	5	5		40.50	2.99	0.67	0.01	32	1.28	0.00	1562.91	34018.52	1995.79	62736.40
MUD	4	8.0-9.9	23	12	6		47.41	29.76	0.49	0.01	32	1.50	0.03	3776.33	22792.71	5644.73	472801.03
MUD	5	10.0-11.9	9	3	2		15.25	3.83	0.57	0.03	32	0.48	0.00	5308.92	54913.72	2552.49	119881.32
MUD	total										32	4.06	0.05			10625.64	664316.81
NCR	0	0.0-7.9	28	37	13		133.50	1724.67	0.25	0.01	45	2.95	0.84	1127.34	14396.17	3320.13	1191526.63
NCR	1	8.0-9.9	26	31	7		85.43	220.20	0.37	0.01	45	1.89	0.11	3417.88	39520.00	6441.63	1392197.38

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
NCR	2	10.0-13.9	16	8	7		41.85	117.74	0.36	0.02	45	0.92	0.06	5642.08	175086.81	5208.49	1973145.75
NCR	3	14.0-17.9	1	1	0		2.18	0.55	0.57	0.20	45	0.05	0.00	8850.34	3970927.00	425.31	30001.45
NCR	total										45	5.80	1.00			15395.55	4586871.50
PHI	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	51	0.00	0.00	0.00	0.00	0.00	0.00
PHI	1	2.0-3.9	0	0	0		0.00	0.00	0.00	0.00	51	0.00	0.00	0.00	0.00	0.00	0.00
PHI	2	4.0-5.9	3	2	0		5.22	0.46	0.65	0.06	51	0.10	0.00	869.61	16577.43	88.97	305.85
PHI	3	6.0-7.9	6	5	1		13.85	8.50	0.49	0.04	51	0.27	0.00	1354.43	29099.96	367.89	8143.92
PHI	4	8.0-9.9	1	0	0		1.00	0.00	1.00	0.00	51	0.02	0.00	2294.65	0.00	45.00	0.00
PHI	5	10.0-11.9	0	0	0		0.00	0.00	0.00	0.00	51	0.00	0.00	0.00	0.00	0.00	0.00
PHI	6	12.0-13.9	0	0	0		0.00	0.00	0.00	0.00	51	0.00	0.00	0.00	0.00	0.00	0.00
PHI	7	14.0-15.9	0	0	0		0.00	0.00	0.00	0.00	51	0.00	0.00	0.00	0.00	0.00	0.00
PHI	8	16.0-17.9	0	0	0		0.00	0.00	0.00	0.00	51	0.00	0.00	0.00	0.00	0.00	0.00
PHI	9	18.0-19.9	1	0	0		1.00	0.00	1.00	0.00	51	0.02	0.00	25590.66	0.00	501.83	0.00
PHI	10	20.0-21.9	2	0	0		2.00	0.00	1.00	0.00	51	0.04	0.00	36542.23	260624.22	1433.19	400.89
PHI	total										51	0.45	0.00			2436.87	8850.66
POO	0	0.0-1.9	0	0	0	0	0.00	0.00	0.00	0.00	22	0.00	0.00	0.00	0.00	0.00	0.00
POO	1	2.0-3.9	2	1	0	1	4.88	5.39	0.35	0.10	22	0.22	0.01	267.80	27453.42	59.42	2149.91
POO	2	4.0-7.9	10	2	3	1	16.81	1.74	0.53	0.02	22	0.76	0.00	767.03	104762.77	585.89	63233.99

Site	size class	lengt	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
POO	3	8.0-9.9	1	0	0	0	1.00	0.00	1.00	0.00	22	0.05	0.00	3408.04	0.00	154.90	0.00
POO	total										22	1.03	0.02			800.21	65383.90
RAI	0	0.0-1.9	0	0	0	0	0.00	0.00	0.00	0.00	60	0.00	0.00	0.00	0.00	0.00	0.00
RAI	1	2.0-3.9	9	27	5	1	50.08	43.11	0.37	0.01	60	0.84	0.01	332.65	1628.96	277.68	2460.58
RAI	2	4.0-5.9	33	101	22	17	250.77	1122.69	0.25	0.00	60	4.18	0.31	701.37	1839.94	2931.96	185623.84
RAI	3	6.0-7.9	6	13	0	0	20.04	2.33	0.52	0.01	60	0.33	0.00	2176.95	11723.90	727.22	4370.74
RAI	4	8.0-11.9	1	1	1	0	3.72	4.75	0.34	0.13	60	0.06	0.00	3712.07	434550.00	229.99	19869.25
RAI	total										60	5.41	0.33			4166.85	212324.41
SAWD	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	41	0.00	0.00	0.00	0.00	0.00	0.00
SAWD	1	2.0-3.9	6	5	0		11.72	1.82	0.61	0.03	41	0.29	0.00	320.23	1357.29	92.25	225.69
SAWD	2	4.0-5.9	8	3	0		11.15	0.22	0.76	0.02	41	0.27	0.00	612.42	23693.05	167.95	1832.48
SAWD	3	6.0-7.9	13	2	0		15.03	0.03	0.88	0.01	41	0.37	0.00	1482.08	32563.79	547.66	4486.75
SAWD	4	8.0-9.9	13	4	0		17.15	0.21	0.79	0.01	41	0.42	0.00	3485.03	67331.50	1470.06	13501.24
SAWD	5	10.0-11.9	1	1	0		2.18	0.55	0.57	0.20	41	0.05	0.00	5160.57	3359.27	276.44	8809.97
SAWD	total										41	1.41	0.00			2554.36	28856.13
SAWU	0	0.0-3.9	23	28	25	14	208.72	11240.80	0.13	0.01	11	18.31	86.50	179.17	729.92	3280.47	3021340.75
SAWU	1	4.0-5.9	8	6	4	3	28.16	71.46	0.29	0.02	11	2.47	0.55	837.59	4666.26	2068.80	414237.72
SAWU	2	6.0-7.9	2	0	1	0	3.14	0.28	0.54	0.09	11	0.28	0.00	1512.79	80992.09	416.15	11047.61
SAWU	total										11	21.05	87.05			5765.42	3446626.00

Site	size class	length	P1	P2	P3	P4	N	Var-iance (N)	P	Var-iance (P)	fish area (m^2)	D	Variance (D)	W	Variance (W)	B	Variance (B)
TAY	total	0	0	0	0		0.00	0.00	0.00	0.00	23	0.00	0.00	0.00	0.00	0.00	0.00
TAYD	0	0.0-1.9	0	0	0		0.00	0.00	0.00	0.00	22	0.00	0.00	0.00	0.00	0.00	0.00
TAYD	1	2.0-3.9	23	14	2		41.67	6.98	0.60	0.01	22	1.87	0.01	370.55	3253.12	691.37	13246.43
TAYD	2	4.0-5.9	14	15	3		39.88	56.76	0.42	0.02	22	1.79	0.11	722.04	5164.55	1289.58	75812.53
TAYD	3	6.0-7.9	5	3	0		8.28	0.55	0.67	0.03	22	0.37	0.00	1290.00	93370.34	478.58	14689.45
TAYD	4	8.0-9.9	3	0	0		3.00	0.00	1.00	0.00	22	0.13	0.00	2533.32	122050.45	340.33	2202.67
TAYD	total										22	4.16	0.13			2799.86	105951.09
UNA	total	0	0	0	0		0.00	0.00	0.00	0.00	30	0.00	0.00	0.00	0.00	0.00	0.00
VOY	0	0		0	0		0.00	0.00	0.00	0.00	27	0.00	0.00	0.00	0.00	0.00	0.00
VOY	1	2.0-3.9	0	0	0		0.00	0.00	0.00	0.00	27	0.00	0.00	0.00	0.00	0.00	0.00
VOY	2	4.0-5.9	0	0	0		0.00	0.00	0.00	0.00	27	0.00	0.00	0.00	0.00	0.00	0.00
VOY	3	6.0-7.9	2	0	0		2.00	0.00	1.00	0.00	27	0.08	0.00	1630.35	101625.02	122.28	571.64
VOY	total	0	0	0	0		0.00	0.00	0.00	0.00	27	0.08	0.00			122.28	571.64
WAT	total	0	0	0	0		0.00	0.00	0.00	0.00	44	0.00	0.00	0.00	0.00	0.00	0.00

Table 1.4. Water quality parameters measured at 38 sites in the National Capital Region during July and August of 2001 and 2002 included: alkalinity (mg L^{-1}), chloride ions (Cl^-, mg L^{-1}), dissolved organic carbon (DOC, mg L^{-1}), $NO_3 + NO_2$ (NO_x, mg L^{-1}), total kjeldahl nitrogen (TKN, mg L^{-1}), total nitrogen (TN, mg L^{-1}), sulfate ions (SO_4, mg L^{-1}), conductivity (cond., µs L^{-1}), total phosphorus (TP, mg L^{-1}), and pH.

SITE	DATE	ALK	CL	DOC	NOx	TKN	TN	SO4	COND.	TP	pH
BEA	05-Jul-01	198	101	9.8	0.03	0.8	0.83	41	770	0.047	8.44
BEA	08-Aug-01	182	92	8.4	0.03	0.7	0.73	44	710	0.039	8.2
BEC	05-Jul-01	220	41	5	0.52	0.59	1.11	25	600	0.054	8.53
BEC	08-Aug-01	230	39	4.7	0.02	0.52	0.54	20	580	0.098	8.35
BEC	08-Jul-02	250	34	5	0.31	0.48	0.79	21	600	0.061	8.44
BEC	12-Aug-02	230	27	3.6	0.07	0.36	0.43	20	550	0.043	8.37
BIL	08-Jul-02	320	430	4	1.41	0.65	2.06	111	2100	0.133	8.22
BIL	12-Aug-02	260	330	3.8	1.03	0.53	1.56	87	1650	0.113	8.21
BLA	08-Jul-02	29	0.8	7.8	0.01	0.36	0.37	4.1	72	0.01	7.7
BLA	08-Jul-02			6.1			0				
BLA	08-Jul-02		0.8	5.9	0.01	0.38	0.39	4.2		0.01	
BLA	13-Aug-02	31	1	7.6	0.02	0.37	0.39	4.4	79	0.01	7.77
BLA	13-Aug-02			7.4			0				
BLA	13-Aug-02		1	7.6	0.02	0.37	0.39	4.4		0.01	
BRA	10-Jul-01	184	23	14.9	0.006	0.79	0.796	1.3	420	0.018	8.53
BRA	15-Aug-01	80	12.8	7.8	0.003	0.63	0.633	6.7	220	0.028	8.28
BRA	10-Jul-02	199	10.2	13	0.006	0.75	0.756	1	390	0.012	8.15
BRA	14-Aug-02	220	12.3	13.5	0.02	0.82	0.84	1	430	0.016	8.39
CHE	08-Jul-02	80	44	6.6	0.12	0.42	0.54	11	320	0.016	8.01
CHE	08-Jul-02			5.8			0				
CHE	08-Jul-02		43	5.8	0.12	0.58	0.7	11		0.045	
CHE	13-Aug-02	91	38	6.7	0.05	0.63	0.68	7.7	320	0.032	8.1
CHE	13-Aug-02		38	6.8	0.05	0.5	0.55	7.7		0.019	
CHE	13-Aug-02			7.1			0				
COR	08-Jul-02	32	1	3.5	0.08	0.28	0.36	4.9	81	0.017	7.36
COR	08-Jul-02			3.5			0				
COR	08-Jul-02		0.9	3.3	0.08	0.23	0.31	5		0.01	
COR	13-Aug-02	39	1.1	2.7	0.18	0.29	0.47	4.9	97	0.017	7.6
COR	13-Aug-02			2.4			0				
COR	13-Aug-02		1.1	2.7	0.18	0.18	0.36	4.9		0.005	
FOR	27-Aug-02	108	26	3.1	0.26	0.18	0.44	8.1	320	0.006	8.03
FOR	27-Aug-02			3.3			0				
FOR	27-Aug-02		26	3.2	0.26	0.19	0.45	8.1		0.005	
GRAU	04-Jul-02	200	67	5.6	2.8	0.56	3.36	54	730	0.046	8.28
GRAU	06-Aug-02	200	157	4.5	1.71	0.56	2.27	63	1010	0.034	8.16
GRAD	04-Jul-01	210	260	3.1	1.58	0.45	2.03	73	1320	0.024	8.38

SITE	DATE	ALK	CL	DOC	NOx	TKN	TN	SO4	COND.	TP	pH
GRAD	10-Jul-01	107	112		0.56	0.46	1.02	33	650	0.043	8.05
GRAD	17-Jul-01	210	240		0.84	0.46	1.3	72	1260	0.039	8.18
GRAD	01-Aug-01	210	240		1.27	0.53	1.8	67	1220	0.036	8.09
GRAD	08-Aug-01	220	260		0.08	0.54	0.62	76	1330	0.035	8.27
GRAD	09-Aug-01	220	260	3.7	1.09	0.45	1.54	72	1280	0.039	8.33
GRAD	17-Aug-01	137	105		1.13	1.32	2.45	42	710	0.107	7.73
GRAD	04-Jul-02	230	170	4.2	2.5	0.48	2.98	71	1130	0.047	8.23
GRAD	06-Aug-02	230	220	2.8	1.38	0.36	1.74	68	1220	0.018	8.21
GRE	05-Jul-01	94	141	4.7	1.08	1.15	2.23	50	760	0.149	8.04
GRE	19-Jul-01	200	350		0.08	0.57	0.65	142	1700	0.031	8.44
GRE	07-Aug-01	178	290		0.08	0.58	0.66	121	1390	0.032	8.46
GRE	08-Aug-01	191	330	5.1	0.08	0.5	0.58	145	1570	0.034	8.27
GRE	13-Aug-01	197	310		0.08	0.57	0.65	148	1650	0.049	8.31
GRE	21-Aug-01	156	200		0.13	0.58	0.71	86	1120	0.062	8.14
GRE	08-Jul-02	220	320	8.7	0.51	0.82	1.33	179	1720	0.034	8.42
GRE	12-Aug-02	200	330	5	0.08	0.4	0.48	183	1760	0.022	8.28
HAR	04-Jul-01	210	230	7.1	0.03	0.89	0.92	34	1160	0.071	8.54
HAR	07-Aug-01	164	520	5.2	0.08	0.88	0.96	26	1950	0.046	8.3
HAR	04-Jul-02	194	58	6.8	0.02	0.5	0.52	21	590	0.052	8.24
HAR	06-Aug-02	220	240	7.6	0.03	0.99	1.02	29	1160	0.109	8.01
HUN	09-Jul-01	220	103	4.7	0.38	0.56	0.94	65	860	0.042	8.32
HUN	22-Aug-01	199	90	5.6	0.09	0.47	0.56	62	800	0.044	8.25
HUN	15-Jul-02	220	133	4.4	0.74	0.49	1.23	69	960	0.036	8.12
HUN	07-Aug-02	210	127	4.4	0.26	0.62	0.88	68	930	0.049	8.14
JR-01	03-Jul-01	181	81	9.2	0.48	1.05	1.53	30	640	0.076	8.38
JR-01	01-Aug-01	177	88	7.5	0.02	0.61	0.63	27	650	0.032	8.31
JR-20	09-Jul-02	183	26	22	0.63	1.25	1.88	8.8	450	0.051	8.13
JR-20	13-Aug-02	184	26	27	0.02	1.58	1.6	4.8	440	0.074	8.1
KIN	27-Aug-02	85	4.6	2.7	0.17	0.78	0.95	7.2	200	0.103	7.81
KIN	27-Aug-02			2.5			0				
KIN	27-Aug-02		4.7	2.7	0.16	0.17	0.33	7.2		0.007	
LAP	08-Jul-02	37	1	13	0.03	0.51	0.54	2.7	85	0.026	7.7
LAP	08-Jul-02		0.8	8	0.03	0.95	0.98	2.7		0.108	
LAP	08-Jul-02			7			0				
LAP	13-Aug-02	44	1.5	6.2	0.05	0.45	0.5	2.1	100	0.017	7.81
LAP	13-Aug-02			6			0				
LAP	13-Aug-02		1.5	6.5	0.04	0.45	0.49	2.1		0.022	
LDS	08-Jul-02	137	17	25	0.03	2.3	2.33	3	880	0.23	7.49
LDS	08-Jul-02			27			0				
LDS	08-Jul-02		17	25	0.03	2.4	2.43	3		0.27	
LDS	13-Aug-02	191	310	4.1	0.59	0.61	1.2	47	1420	0.115	8.09
LDS	13-Aug-02			4.1			0				
LDS	13-Aug-02		310	4.2	0.63	0.82	1.45	47		0.163	
LMS	08-Jul-02	174	14	10	0.03	1.45	1.48	3	860	0.18	7.86
LMS	08-Jul-02			10			0				
LMS	08-Jul-02		14	11	0.03	1.7	1.73	3		0.17	
LMS	13-Aug-02	220	290	3.5	0.18	0.53	0.71	50	1400	0.088	8.1

SITE	DATE	ALK	CL	DOC	NOx	TKN	TN	SO4	COND.	TP	pH
LMS	13-Aug-02			3.5			0				
LMS	13-Aug-02		280	3.5	0.21	0.48	0.69	50		0.05	
LUS	18-Aug-03	145	5.5	7.8	0.09	0.74	0.83	0.01	290	0.04	8.09
LUS	18-Aug-03	145	5.5	7.9	0.1	0.74	0.84	0.011	290	0.04	8.11
LUS	18-Aug-03	146	5.1	7.7	0.09	0.75	0.84	0.012	290	0.046	8.09
MCR	05-Jul-01	194	63	8.7	0.03	0.59	0.62	73	710	0.029	8.38
MCR	08-Aug-01	188	97	5.2	0.03	0.48	0.51	61	760	0.036	8.11
MCR	08-Jul-02	230	48	15.3	0.29	0.87	1.16	65	710	0.029	8.26
MCR	12-Aug-02	197	75	5.2	0.03	0.39	0.42	68	750	0.033	8.24
MEE	27-Aug-02	38	1.1	3.9	0.02	0.23	0.25	5.3	98	0.013	7.54
MEE	27-Aug-02			3.2			0				
MEE	27-Aug-02		1.1	3.2	0.02	0.24	0.26	5.2		0.013	
MNCR	05-Jul-01	210	89	8.9	0.03	0.65	0.68	165	960	0.037	8.41
MNCR	08-Aug-01	210	116	8.3	0.03	0.65	0.68	103	910	0.065	8.19
MNCR	08-Jul-02	240	69	10.5	0.33	0.75	1.08	101	870	0.048	8.21
MNCR	12-Aug-02	197	84	9.6	0.03	0.75	0.78	124	870	0.055	8.22
MOS	09-Jul-01	210	69	8.7	0.02	0.76	0.78	20	650	0.071	8.27
MOS	22-Aug-01	181	22	12.2	0.02	0.8	0.82	13.4	450	0.118	8.12
MOS	15-Jul-02	184	46	13.8	0.02	0.86	0.88	27	550	0.082	8.19
MOS	07-Aug-02	200	26	12.7	0.02	0.78	0.8	16	480	0.107	8.11
MUD	09-Jul-01	220	74	3.7	0.38	0.52	0.9	54	760	0.04	8.18
MUD	22-Aug-01	190	66	3.3	0.12	0.4	0.52	37	660	0.027	8.18
MUD	15-Jul-02	280	65	6.8	1.67	0.78	2.45	73	860	0.033	8.24
MUD	07-Aug-02	230	64	3.5	0.43	0.49	0.92	38	690	0.033	8.11
NCR	05-Jul-01	210	98	6.8	0.25	0.57	0.82	220	1070	0.035	8.4
NCR	08-Aug-01	230	139	5.8	0.03	0.77	0.8	124	1030	0.044	8.29
PHI	27-Aug-02	45	1.2	6.3	0.003	0.51	0.513	3.3	105	0.023	7.61
PHI	27-Aug-02			5.9			0				
PHI	27-Aug-02		1.2	6.5	0.003	0.49	0.493	3.3		0.022	
POO	04-Jul-01	310	101	4.3	1.66	0.61	2.27	158	1150	0.015	8.2
POO	07-Aug-01	310	98	4.7	1.35	0.63	1.98	175	1170	0.028	8.27
POO	04-Jul-02	270	73	12.1	0.91	0.83	1.74	52	840	0.021	7.91
POO	06-Aug-02	300	93	4.9	1.15	0.59	1.74	119	1040	0.023	8.03
SAWD	09-Jul-01	240	270	4.4	0.78	0.65	1.43	122	1500	0.057	8.27
SAWD	22-Aug-01	188	172	7.5	0.37	0.64	1.01	87	1080	0.114	8.17
SAWD	15-Jul-02	250	240	4.5	0.91	0.45	1.36	121	1450	0.061	8.21
SAWD	18-Jul-02	260	250		0.88	0.63	1.51	126	1410	0.089	8.27
SAWD	23-Jul-02	230	210		0.66	1.02	1.68	103	1200	0.139	8.04
SAWD	07-Aug-02	250	240	4.2	0.56	0.42	0.98	116	1390	0.061	8.27
SAWD	16-Aug-02	192	174		0.63	1	1.63	86	1000	0.2	7.97
SAWD	29-Aug-02	220	240		0.38	0.33	0.71	111	1380	0.035	8.29
SAWU	09-Jul-01	250	135	7	0.03	0.46	0.49	91	1060	0.013	8.16
SAWU	22-Aug-01	250	140	8	0.03	0.33	0.36	98	1080	0.014	8.32
SAWU	05-Jul-02	250	95		0.26	0.46	0.72	71	880	0.009	8.13
SAWU	15-Jul-02	250	75	6.4	0.1	0.31	0.41	71	830	0.007	8.12
SAWU	18-Jul-02	240	82		0.2	0.32	0.52	73	840	0.005	8.36
SAWU	07-Aug-02	250	60	5.2	0.13	0.29	0.42	70	780	0.005	8.16

SITE	DATE	ALK	CL	DOC	NOx	TKN	TN	SO4	COND.	TP	pH
SAWU	16-Aug-02	240	71		0.09	0.27	0.36	69	780	0.008	8.23
TAY	05-Jul-01	79	54	4.5	0.72	0.85	1.57	22	400	0.147	8.02
TAY	08-Aug-01	250	260	3.4	0.08	0.47	0.55	81	1290	0.07	8.32
TAYD	09-Jul-01	250	26	13.9	0.18	0.98	1.16	23	590	0.057	8.32
TAYD	22-Aug-01	250	37	18	0.02	1.26	1.28	15.4	610	0.092	8.44
TAYD	15-Jul-02	290	21	17.7	2.3	1.36	3.66	18.6	650	0.065	8.19
TAYD	07-Aug-02	290	25	19.6	0.02	1.14	1.16	15.4	610	0.109	8.15
UNA	18-Aug-03	210	280	3.8	1.27	0.51	1.78	52	1340	0.097	8.38
UNA	18-Aug-03	210	280	3.8	1.27	0.54	1.81	52	1340	0.106	8.4
UNA	18-Aug-03	210	290	3.6	1.21	0.6	1.81	51	1340	0.108	8.4
VOY	05-Jul-01	175	151	5.8	1.39	0.66	2.05	57	910	0.094	8.31
VOY	08-Aug-01	280	320	5.3	0.79	0.48	1.27	108	1630	0.021	8.33
VOY	08-Jul-02	290	300	5.1	2.7	0.53	3.23	110	1690	0.04	8.29
VOY	12-Aug-02	260	310	6	1.84	0.46	2.3	105	1640	0.013	8.31
WAT	04-Jul-02	240	240	3.5	3.6	0.46	4.06	74	1370	0.0415	8.23
WAT	06-Aug-02	230	270	3	2.1	0.56	2.66	69	1400	0.093	8.26

Table 1.5. Stream temperature (° C) measured at 38 biomass sites in the National Capital Region during July and August of 2001 and 2002.

Site	month	year	Temperature
BEA	7	2001	21.5
BEA	7	2001	22.2
BEA	7	2001	21.8
BEA	7	2001	2.4
BEA	7	2001	22.4
BEA	7	2001	21.7
BEC	7	2002	25
BIL	7	2002	15.5
BIL	7	2002	19.5
BRA	7	2001	28.3
BRA	7	2001	27.4
BRA	7	2001	28
BRA	7	2001	28.8
BRA	7	2001	28.3
BRA	7	2001	28.8
GRA	7	2002	22
GRA2	7	2002	22
GRA2	7	2002	19
GRA2	7	2002	22
GRE	7	2001	19
GRE	7	2001	18.9
GRE	7	2001	18.6
GRE	7	2001	18.8
GRE	7	2001	18.3
GRE	7	2001	18.3
HUN	7	2002	20
JR-01	7	2001	22.5
JR-01	7	2001	23
JR-01	7	2001	23
JR-01	7	2001	22.8
JR-01	7	2001	22.7
JR-01	7	2001	22.8
JR-20	7	2002	28
JR-20	7	2002	28
MCR	7	2002	20
MNCR	7	2002	20
MOS	7	2001	23.2
MOS	7	2001	23.2
MOS	7	2001	23.2
MOS	7	2001	23.5
MOS	7	2001	23.4
MOS	7	2001	23.2

Site	month	year	Temperature
MUD	7	2002	22
NCR	7	2001	23
NCR	7	2001	23.4
NCR	7	2001	23
NCR	7	2001	22.9
NCR	7	2001	22.7
NCR	7	2001	23.3
SAWD	7	2001	21.7
SAWD	7	2001	21.7
SAWD	7	2001	21.7
SAWD	7	2001	21.7
SAWD	7	2001	21.5
SAWD	7	2001	21.6
SAWU	7	2002	20
SAWU	7	2002	14
TAY	7	2001	19.8
TAY	7	2001	19.6
TAY	7	2001	19.5
TAY	7	2001	19.4
TAY	7	2001	19.3
TAY	7	2001	20.2
TAYD	7	2001	22.9
TAYD	7	2001	22.5
TAYD	7	2001	22.7
TAYD	7	2001	22.7
TAYD	7	2001	22.9
TAYD	7	2001	22.9
VOY	7	2001	20.2
VOY	7	2001	20.2
VOY	7	2001	20.4
VOY	7	2001	19.9
VOY	7	2001	19.9
VOY	7	2001	20.4
WAT	7	2002	20
WAT	7	2002	14
BLA	8	2001	17
BLA	8	2001	17
BLA	8	2001	17
BLA	8	2001	17
BLA	8	2001	17
BLA	8	2001	17

Site	month	year	Temperature
CHE	8	2001	26.6
CHE	8	2001	26.5
CHE	8	2001	26.4
CHE	8	2001	26.3
CHE	8	2001	26.1
CHE	8	2001	26.4
COR	8	2001	13
COR	8	2001	13
COR	8	2001	13
COR	8	2001	13
COR	8	2001	13
COR	8	2001	13
DESF	8	2001	16
DESF	8	2001	16
DESF	8	2001	16
DESF	8	2001	16
DESF	8	2001	16
DESF	8	2001	16
DEST	8	2001	23.5
DEST	8	2001	23.2
DEST	8	2001	22.8
DEST	8	2001	22.6
DEST	8	2001	22.7
DEST	8	2001	23
FOR	8	2002	22
HAR	8	2002	24
KIN	8	2002	15
LAP	8	2001	12
LAP	8	2001	12
LAP	8	2001	12
LAP	8	2001	12
LAP	8	2001	12
LAP	8	2001	12
LDS	8	2001	16.5
LDS	8	2001	16.3
LDS	8	2001	16.4
LDS	8	2001	16.5
LDS	8	2001	16.4
LDS	8	2001	16.3
LMS	8	2001	17.8
LMS	8	2001	17.9
LMS	8	2001	17.7
LMS	8	2001	17.7
LMS	8	2001	17.7
LMS	8	2001	17.8

Site	month	year	Temperature
LUS	8	2001	17.5
LUS	8	2001	17
LUS	8	2001	17
LUS	8	2001	17
LUS	8	2001	17.3
LUS	8	2001	17
LUS	8	2001	17.4
MEE	8	2002	16
PHI	8	2002	16
POO	8	2002	16
RAI	8	2001	16
RAI	8	2001	16
RAI	8	2001	16
RAI	8	2001	16
RAI	8	2001	16
RAI	8	2001	16
UNA	8	2001	21.2
UNA	8	2001	21.4
UNA	8	2001	21
UNA	8	2001	21.2
UNA	8	2001	21.1
UNA	8	2001	21.1

Table 1.6. Ground truthed (GT forest) and digital forest (forest) cover at 38 biomass sites in the National Capital Region quantified at 55 spatial scales using topographic maps (RMOC 1994) in ArcGIS 8.2 (ESRI, Redlands, California) and methods described in chapter 1. Buffer widths and distances are in meters and forest cover is a percentage.

Site	buffer width	distance	GT Forest	Forest
BEA	10	10	0.00	57.90
BEA	20	10	0.00	59.14
BEA	40	10	0.00	59.14
BEA	80	10	59.14	59.14
BEA	160	10	59.14	59.14
BEA	320	10	59.07	59.07
BEA	10	20	0.00	54.70
BEA	20	20	0.00	54.89
BEA	40	20	5.00	54.88
BEA	80	20	54.89	54.89
BEA	160	20	54.89	54.89
BEA	320	20	54.88	54.88
BEA	10	40	5.00	54.80
BEA	20	40	5.00	59.90
BEA	40	40	15.00	68.69
BEA	80	40	68.73	68.73
BEA	160	40	68.73	68.73
BEA	320	40	68.73	68.73
BEA	10	80	53.10	53.10
BEA	20	80	65.18	65.18
BEA	40	80	79.19	79.19
BEA	80	80	83.19	83.19
BEA	160	80	83.19	83.19
BEA	320	80	83.19	83.19
BEA	10	160	53.27	53.27
BEA	20	160	67.51	67.51
BEA	40	160	82.29	82.29
BEA	80	160	89.18	89.18
BEA	160	160	91.22	91.22
BEA	320	160	91.22	91.22
BEA	10	320	39.91	39.91
BEA	20	320	53.84	53.84
BEA	40	320	70.34	70.34
BEA	80	320	77.94	77.94
BEA	160	320	79.53	79.53
BEA	320	320	80.82	80.82
BEA	10	640	32.26	32.26
BEA	20	640	50.48	50.48

Site	buffer width	distance	GT Forest	Forest
BEA	40	640	66.87	66.87
BEA	80	640	75.16	75.16
BEA	160	640	76.97	76.97
BEA	320	640	77.35	77.35
BEA	10	1280	32.83	32.83
BEA	20	1280	47.83	47.83
BEA	40	1280	60.16	60.16
BEA	80	1280	64.59	64.59
BEA	160	1280	63.54	63.54
BEA	320	1280	64.14	64.14
BEA	10	20000	49.81	49.81
BEA	20	20000	51.10	51.10
BEA	40	20000	51.66	51.66
BEA	80	20000	50.53	50.53
BEA	160	20000	48.69	48.69
BEA	320	20000	48.45	48.45
BEA	20000	20000	44.32	44.32
BEC	10	10	5.00	0.00
BEC	20	10	25.00	0.00
BEC	40	10	40.00	0.00
BEC	80	10	0.00	0.00
BEC	160	10	0.00	0.00
BEC	320	10	0.00	0.00
BEC	10	20	5.00	0.00
BEC	20	20	25.00	0.00
BEC	40	20	40.00	0.00
BEC	80	20	0.00	0.00
BEC	160	20	0.00	0.00
BEC	320	20	0.00	0.00
BEC	10	40	10.00	0.00
BEC	20	40	25.00	0.00
BEC	40	40	40.00	0.00
BEC	80	40	0.00	0.00
BEC	160	40	0.00	0.00
BEC	320	40	0.00	0.00
BEC	10	80	0.00	0.00
BEC	20	80	0.00	0.00
BEC	40	80	0.00	0.00
BEC	80	80	0.00	0.00
BEC	160	80	0.00	0.00
BEC	320	80	0.00	0.00
BEC	10	160	32.18	32.18
BEC	20	160	31.18	31.18
BEC	40	160	26.86	26.86
BEC	80	160	18.25	18.25
BEC	160	160	14.40	14.40
BEC	320	160	14.40	14.40

Site	buffer width	distance	GT Forest	Forest
BEC	10	320	66.08	66.08
BEC	20	320	65.50	65.50
BEC	40	320	53.81	53.81
BEC	80	320	42.97	42.97
BEC	160	320	30.40	30.40
BEC	320	320	34.10	34.10
BEC	10	640	82.34	82.34
BEC	20	640	82.48	82.48
BEC	40	640	74.65	74.65
BEC	80	640	59.54	59.54
BEC	160	640	41.47	41.47
BEC	320	640	36.19	36.19
BEC	10	1280	91.59	91.59
BEC	20	1280	91.60	91.60
BEC	40	1280	87.90	87.90
BEC	80	1280	77.65	77.65
BEC	160	1280	60.20	60.20
BEC	320	1280	51.23	51.23
BEC	10	20000	30.83	30.83
BEC	20	20000	30.15	30.15
BEC	40	20000	27.95	27.95
BEC	80	20000	23.08	23.08
BEC	160	20000	19.83	19.83
BEC	320	20000	19.81	19.81
BEC	20000	20000	21.46	21.46
BIL	10	10	0.00	100.00
BIL	20	10	0.00	100.00
BIL	40	10	25.00	100.00
BIL	80	10	100.00	100.00
BIL	160	10	99.67	99.67
BIL	320	10	83.79	83.79
BIL	10	20	0.00	100.00
BIL	20	20	0.00	100.00
BIL	40	20	10.00	100.00
BIL	80	20	100.00	100.00
BIL	160	20	99.10	99.10
BIL	320	20	82.77	82.77
BIL	10	40	5.00	100.00
BIL	20	40	5.00	100.00
BIL	40	40	20.00	100.00
BIL	80	40	99.98	99.98
BIL	160	40	98.95	98.95
BIL	320	40	81.93	81.93
BIL	10	80	99.79	99.79
BIL	20	80	99.81	99.81
BIL	40	80	91.38	91.38
BIL	80	80	95.02	95.02

Site	buffer width	distance	GT Forest	Forest
BIL	160	80	93.57	93.57
BIL	320	80	80.10	80.10
BIL	10	160	66.61	66.61
BIL	20	160	69.49	69.49
BIL	40	160	72.41	72.41
BIL	80	160	78.38	78.38
BIL	160	160	83.02	83.02
BIL	320	160	76.58	76.58
BIL	10	320	45.90	45.90
BIL	20	320	43.26	43.26
BIL	40	320	38.50	38.50
BIL	80	320	37.30	37.30
BIL	160	320	41.68	41.68
BIL	320	320	44.37	44.37
BIL	10	640	74.71	74.71
BIL	20	640	72.66	72.66
BIL	40	640	64.11	64.11
BIL	80	640	48.64	48.64
BIL	160	640	40.18	40.18
BIL	320	640	40.03	40.03
BIL	10	1280	74.68	74.68
BIL	20	1280	71.92	71.92
BIL	40	1280	61.76	61.76
BIL	80	1280	41.25	41.25
BIL	160	1280	30.14	30.14
BIL	320	1280	27.68	27.68
BIL	10	20000	77.03	77.03
BIL	20	20000	74.27	74.27
BIL	40	20000	65.49	65.49
BIL	80	20000	46.48	46.48
BIL	160	20000	30.26	30.26
BIL	320	20000	21.22	21.22
BIL	20000	20000	10.42	10.42
BLA	10	10	100.00	100.00
BLA	20	10	75.00	100.00
BLA	40	10	90.00	100.00
BLA	80	10	100.00	100.00
BLA	160	10	100.00	100.00
BLA	320	10	95.08	95.08
BLA	10	20	100.00	100.00
BLA	20	20	75.00	100.00
BLA	40	20	90.00	100.00
BLA	80	20	100.00	100.00
BLA	160	20	100.00	100.00
BLA	320	20	95.27	95.27
BLA	10	40	100.00	100.00
BLA	20	40	75.00	100.00

Site	buffer width	distance	GT Forest	Forest
BLA	40	40	90.00	100.00
BLA	80	40	100.00	100.00
BLA	160	40	100.00	100.00
BLA	320	40	95.88	95.88
BLA	10	80	100.00	100.00
BLA	20	80	100.00	100.00
BLA	40	80	100.00	100.00
BLA	80	80	100.00	100.00
BLA	160	80	100.00	100.00
BLA	320	80	96.41	96.41
BLA	10	160	100.00	100.00
BLA	20	160	100.00	100.00
BLA	40	160	100.00	100.00
BLA	80	160	100.00	100.00
BLA	160	160	100.00	100.00
BLA	320	160	96.90	96.90
BLA	10	320	93.16	93.16
BLA	20	320	93.20	93.20
BLA	40	320	96.71	96.71
BLA	80	320	98.48	98.48
BLA	160	320	99.34	99.34
BLA	320	320	97.62	97.62
BLA	10	640	77.10	77.10
BLA	20	640	84.71	84.71
BLA	40	640	92.41	92.41
BLA	80	640	96.30	96.30
BLA	160	640	98.27	98.27
BLA	320	640	97.92	97.92
BLA	10	1280	79.05	79.05
BLA	20	1280	86.45	86.45
BLA	40	1280	93.25	93.25
BLA	80	1280	96.67	96.67
BLA	160	1280	98.38	98.38
BLA	320	1280	98.43	98.43
BLA	10	20000	79.27	79.27
BLA	20	20000	84.98	84.98
BLA	40	20000	90.66	90.66
BLA	80	20000	94.62	94.62
BLA	160	20000	96.99	96.99
BLA	320	20000	98.06	98.06
BLA	20000	20000	89.02	89.02
BRA	10	10	0.00	0.00
BRA	20	10	5.00	14.22
BRA	40	10	10.00	24.62
BRA	80	10	11.67	11.67
BRA	160	10	3.25	3.25
BRA	320	10	6.46	6.46

Site	buffer width	distance	GT Forest	Forest
BRA	10	20	0.00	8.02
BRA	20	20	5.00	20.48
BRA	40	20	15.00	28.33
BRA	80	20	13.69	13.69
BRA	160	20	4.08	4.08
BRA	320	20	7.07	7.07
BRA	10	40	5.00	49.09
BRA	20	40	10.00	44.68
BRA	40	40	20.00	44.51
BRA	80	40	21.38	21.38
BRA	160	40	6.96	6.96
BRA	320	40	8.10	8.10
BRA	10	80	75.39	75.39
BRA	20	80	67.35	67.35
BRA	40	80	55.03	55.03
BRA	80	80	28.91	28.91
BRA	160	80	10.92	10.92
BRA	320	80	9.71	9.71
BRA	10	160	88.16	88.16
BRA	20	160	82.89	82.89
BRA	40	160	69.78	69.78
BRA	80	160	35.63	35.63
BRA	160	160	14.89	14.89
BRA	320	160	12.05	12.05
BRA	10	320	76.43	76.43
BRA	20	320	79.32	79.32
BRA	40	320	68.08	68.08
BRA	80	320	34.91	34.91
BRA	160	320	14.83	14.83
BRA	320	320	12.35	12.35
BRA	10	640	74.97	74.97
BRA	20	640	80.20	80.20
BRA	40	640	76.08	76.08
BRA	80	640	47.25	47.25
BRA	160	640	23.19	23.19
BRA	320	640	16.26	16.26
BRA	10	1280	88.16	88.16
BRA	20	1280	90.58	90.58
BRA	40	1280	88.42	88.42
BRA	80	1280	71.54	71.54
BRA	160	1280	55.33	55.33
BRA	320	1280	49.06	49.06
BRA	10	20000	74.67	74.67
BRA	20	20000	75.38	75.38
BRA	40	20000	75.79	75.79
BRA	80	20000	74.90	74.90
BRA	160	20000	71.55	71.55

Site	buffer width	distance	GT Forest	Forest
BRA	320	20000	65.91	65.91
BRA	20000	20000	65.27	65.27
CHE	10	10	100.00	100.00
CHE	20	10	100.00	100.00
CHE	40	10	100.00	100.00
CHE	80	10	92.43	92.43
CHE	160	10	91.32	91.32
CHE	320	10	70.75	70.75
CHE	10	20	100.00	100.00
CHE	20	20	100.00	100.00
CHE	40	20	100.00	100.00
CHE	80	20	93.39	93.39
CHE	160	20	92.07	92.07
CHE	320	20	71.77	71.77
CHE	10	40	100.00	100.00
CHE	20	40	100.00	100.00
CHE	40	40	100.00	100.00
CHE	80	40	94.25	94.25
CHE	160	40	93.02	93.02
CHE	320	40	73.96	73.96
CHE	10	80	100.00	100.00
CHE	20	80	100.00	100.00
CHE	40	80	100.00	100.00
CHE	80	80	95.82	95.82
CHE	160	80	94.15	94.15
CHE	320	80	77.10	77.10
CHE	10	160	100.00	100.00
CHE	20	160	100.00	100.00
CHE	40	160	100.00	100.00
CHE	80	160	97.14	97.14
CHE	160	160	93.85	93.85
CHE	320	160	80.13	80.13
CHE	10	320	100.00	100.00
CHE	20	320	100.00	100.00
CHE	40	320	100.00	100.00
CHE	80	320	90.85	90.85
CHE	160	320	80.23	80.23
CHE	320	320	76.65	76.65
CHE	10	640	100.00	100.00
CHE	20	640	100.00	100.00
CHE	40	640	97.34	97.34
CHE	80	640	87.83	87.83
CHE	160	640	82.07	82.07
CHE	320	640	81.88	81.88
CHE	10	1280	100.00	100.00
CHE	20	1280	100.00	100.00
CHE	40	1280	98.47	98.47

Site	buffer width	distance	GT Forest	Forest
CHE	80	1280	91.85	91.85
CHE	160	1280	87.48	87.48
CHE	320	1280	87.68	87.68
CHE	10	20000	76.37	76.37
CHE	20	20000	78.94	78.94
CHE	40	20000	82.85	82.85
CHE	80	20000	85.93	85.93
CHE	160	20000	87.79	87.79
CHE	320	20000	90.15	90.15
CHE	20000	20000	89.35	89.35
COR	10	10	100.00	100.00
COR	20	10	100.00	100.00
COR	40	10	100.00	100.00
COR	80	10	100.00	100.00
COR	160	10	100.00	100.00
COR	320	10	100.00	100.00
COR	10	20	100.00	100.00
COR	20	20	100.00	100.00
COR	40	20	100.00	100.00
COR	80	20	100.00	100.00
COR	160	20	100.00	100.00
COR	320	20	100.00	100.00
COR	10	40	100.00	100.00
COR	20	40	100.00	100.00
COR	40	40	100.00	100.00
COR	80	40	100.00	100.00
COR	160	40	100.00	100.00
COR	320	40	100.00	100.00
COR	10	80	100.00	100.00
COR	20	80	100.00	100.00
COR	40	80	100.00	100.00
COR	80	80	100.00	100.00
COR	160	80	100.00	100.00
COR	320	80	100.00	100.00
COR	10	160	100.00	100.00
COR	20	160	100.00	100.00
COR	40	160	100.00	100.00
COR	80	160	100.00	100.00
COR	160	160	100.00	100.00
COR	320	160	100.00	100.00
COR	10	320	100.00	100.00
COR	20	320	100.00	100.00
COR	40	320	100.00	100.00
COR	80	320	100.00	100.00
COR	160	320	100.00	100.00
COR	320	320	100.00	100.00
COR	10	640	82.96	82.96

Site	buffer width	distance	GT Forest	Forest
COR	20	640	83.13	83.13
COR	40	640	84.57	84.57
COR	80	640	91.79	91.79
COR	160	640	95.85	95.85
COR	320	640	97.85	97.85
COR	10	1280	83.41	83.41
COR	20	1280	86.25	86.25
COR	40	1280	89.50	89.50
COR	80	1280	94.44	94.44
COR	160	1280	97.05	97.05
COR	320	1280	98.27	98.27
COR	10	20000	87.69	87.69
COR	20	20000	90.55	90.55
COR	40	20000	93.62	93.62
COR	80	20000	96.67	96.67
COR	160	20000	98.18	98.18
COR	320	20000	98.89	98.89
COR	20000	20000	95.71	95.71
DESF	10	10	100.00	100.00
DESF	20	10	100.00	100.00
DESF	40	10	100.00	100.00
DESF	80	10	100.00	100.00
DESF	160	10	89.38	89.38
DESF	320	10	63.56	63.56
DESF	10	20	100.00	100.00
DESF	20	20	100.00	100.00
DESF	40	20	100.00	100.00
DESF	80	20	100.00	100.00
DESF	160	20	88.89	88.89
DESF	320	20	63.84	63.84
DESF	10	40	100.00	100.00
DESF	20	40	100.00	100.00
DESF	40	40	100.00	100.00
DESF	80	40	100.00	100.00
DESF	160	40	88.02	88.02
DESF	320	40	65.86	65.86
DESF	10	80	100.00	100.00
DESF	20	80	100.00	100.00
DESF	40	80	100.00	100.00
DESF	80	80	100.00	100.00
DESF	160	80	90.47	90.47
DESF	320	80	69.83	69.83
DESF	10	160	100.00	100.00
DESF	20	160	100.00	100.00
DESF	40	160	100.00	100.00
DESF	80	160	100.00	100.00
DESF	160	160	88.45	88.45

Site	buffer width	distance	GT Forest	Forest
DESF	320	160	70.23	70.23
DESF	10	320	99.40	99.40
DESF	20	320	97.98	97.98
DESF	40	320	96.51	96.51
DESF	80	320	95.30	95.30
DESF	160	320	88.74	88.74
DESF	320	320	75.60	75.60
DESF	10	640	99.40	99.40
DESF	20	640	97.89	97.89
DESF	40	640	94.41	94.41
DESF	80	640	84.48	84.48
DESF	160	640	69.45	69.45
DESF	320	640	63.99	63.99
DESF	10	1280	79.20	79.20
DESF	20	1280	76.96	76.96
DESF	40	1280	71.81	71.81
DESF	80	1280	63.12	63.12
DESF	160	1280	50.93	50.93
DESF	320	1280	48.43	48.43
DESF	10	20000	51.44	51.44
DESF	20	20000	49.33	49.33
DESF	40	20000	43.80	43.80
DESF	80	20000	38.18	38.18
DESF	160	20000	34.90	34.90
DESF	320	20000	38.22	38.22
DESF	20000	20000	45.75	45.75
DEST	10	10	0.00	0.00
DEST	20	10	0.00	0.00
DEST	40	10	0.00	0.00
DEST	80	10	0.00	0.00
DEST	160	10	13.24	13.24
DEST	320	10	8.81	8.81
DEST	10	20	0.00	0.00
DEST	20	20	0.00	0.00
DEST	40	20	0.00	0.00
DEST	80	20	0.00	0.00
DEST	160	20	12.09	12.09
DEST	320	20	8.06	8.06
DEST	10	40	0.00	0.00
DEST	20	40	0.00	0.00
DEST	40	40	0.00	0.00
DEST	80	40	0.00	0.00
DEST	160	40	9.92	9.92
DEST	320	40	5.86	5.86
DEST	10	80	0.00	0.00
DEST	20	80	0.00	0.00
DEST	40	80	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
DEST	80	80	0.00	0.00
DEST	160	80	6.66	6.66
DEST	320	80	4.23	4.23
DEST	10	160	0.00	0.00
DEST	20	160	0.00	0.00
DEST	40	160	0.00	0.00
DEST	80	160	0.00	0.00
DEST	160	160	5.01	5.01
DEST	320	160	3.38	3.38
DEST	10	320	9.02	9.02
DEST	20	320	7.07	7.07
DEST	40	320	5.04	5.04
DEST	80	320	4.87	4.87
DEST	160	320	6.96	6.96
DEST	320	320	4.61	4.61
DEST	10	640	36.00	36.00
DEST	20	640	33.48	33.48
DEST	40	640	30.28	30.28
DEST	80	640	25.91	25.91
DEST	160	640	25.15	25.15
DEST	320	640	28.36	28.36
DEST	10	1280	72.55	72.55
DEST	20	1280	67.82	67.82
DEST	40	1280	60.21	60.21
DEST	80	1280	49.79	49.79
DEST	160	1280	39.07	39.07
DEST	320	1280	30.94	30.94
DEST	10	20000	56.84	56.84
DEST	20	20000	55.76	55.76
DEST	40	20000	52.61	52.61
DEST	80	20000	47.42	47.42
DEST	160	20000	40.56	40.56
DEST	320	20000	37.37	37.37
DEST	20000	20000	36.64	36.64
FOR	10	10	100.00	100.00
FOR	20	10	100.00	100.00
FOR	40	10	100.00	100.00
FOR	80	10	100.00	100.00
FOR	160	10	100.00	100.00
FOR	320	10	100.00	100.00
FOR	10	20	100.00	100.00
FOR	20	20	100.00	100.00
FOR	40	20	100.00	100.00
FOR	80	20	100.00	100.00
FOR	160	20	100.00	100.00
FOR	320	20	100.00	100.00
FOR	10	40	100.00	100.00

Site	buffer width	distance	GT Forest	Forest
FOR	20	40	100.00	100.00
FOR	40	40	100.00	100.00
FOR	80	40	100.00	100.00
FOR	160	40	100.00	100.00
FOR	320	40	100.00	100.00
FOR	10	80	100.00	100.00
FOR	20	80	100.00	100.00
FOR	40	80	100.00	100.00
FOR	80	80	100.00	100.00
FOR	160	80	100.00	100.00
FOR	320	80	100.00	100.00
FOR	10	160	100.00	100.00
FOR	20	160	100.00	100.00
FOR	40	160	100.00	100.00
FOR	80	160	100.00	100.00
FOR	160	160	99.91	99.91
FOR	320	160	99.85	99.85
FOR	10	320	100.00	100.00
FOR	20	320	100.00	100.00
FOR	40	320	100.00	100.00
FOR	80	320	100.00	100.00
FOR	160	320	100.00	100.00
FOR	320	320	100.00	100.00
FOR	10	640	100.00	100.00
FOR	20	640	100.00	100.00
FOR	40	640	100.00	100.00
FOR	80	640	100.00	100.00
FOR	160	640	100.00	100.00
FOR	320	640	100.00	100.00
FOR	10	1280	91.24	91.24
FOR	20	1280	91.52	91.52
FOR	40	1280	92.21	92.21
FOR	80	1280	92.42	92.42
FOR	160	1280	91.57	91.57
FOR	320	1280	88.17	88.17
FOR	10	20000	79.43	79.43
FOR	20	20000	82.14	82.14
FOR	40	20000	86.67	86.67
FOR	80	20000	90.95	90.95
FOR	160	20000	92.99	92.99
FOR	320	20000	92.64	92.64
FOR	20000	20000	89.76	89.76
GRA	10	10	50.00	0.00
GRA	20	10	50.00	0.00
GRA	40	10	50.00	0.00
GRA	80	10	0.00	0.00
GRA	160	10	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
GRA	320	10	0.00	0.00
GRA	10	20	40.00	0.00
GRA	20	20	50.00	0.00
GRA	40	20	40.00	0.00
GRA	80	20	0.00	0.00
GRA	160	20	0.00	0.00
GRA	320	20	0.00	0.00
GRA	10	40	40.00	0.00
GRA	20	40	40.00	0.00
GRA	40	40	35.00	0.00
GRA	80	40	0.00	0.00
GRA	160	40	0.00	0.00
GRA	320	40	0.00	0.00
GRA	10	80	0.00	0.00
GRA	20	80	0.00	0.00
GRA	40	80	0.00	0.00
GRA	80	80	0.00	0.00
GRA	160	80	0.00	0.00
GRA	320	80	0.00	0.00
GRA	10	160	0.00	0.00
GRA	20	160	0.00	0.00
GRA	40	160	0.00	0.00
GRA	80	160	0.00	0.00
GRA	160	160	0.00	0.00
GRA	320	160	0.00	0.00
GRA	10	320	0.00	0.00
GRA	20	320	0.00	0.00
GRA	40	320	0.00	0.00
GRA	80	320	0.00	0.00
GRA	160	320	0.00	0.00
GRA	320	320	0.00	0.00
GRA	10	640	0.00	0.00
GRA	20	640	0.00	0.00
GRA	40	640	0.00	0.00
GRA	80	640	0.00	0.00
GRA	160	640	0.00	0.00
GRA	320	640	0.00	0.00
GRA	10	1280	0.00	0.00
GRA	20	1280	0.00	0.00
GRA	40	1280	0.00	0.00
GRA	80	1280	0.00	0.00
GRA	160	1280	0.00	0.00
GRA	320	1280	0.00	0.00
GRA	10	20000	38.17	38.17
GRA	20	20000	39.50	39.50
GRA	40	20000	41.30	41.30
GRA	80	20000	42.47	42.47

Site	buffer width	distance	GT Forest	Forest
GRA	160	20000	41.65	41.65
GRA	320	20000	37.44	37.44
GRA	20000	20000	37.24	37.24
GRA2	10	10	0.00	0.00
GRA2	20	10	0.00	0.00
GRA2	40	10	0.00	0.00
GRA2	80	10	0.00	0.00
GRA2	160	10	0.00	0.00
GRA2	320	10	0.00	0.00
GRA2	10	20	0.00	0.00
GRA2	20	20	0.00	0.00
GRA2	40	20	0.00	0.00
GRA2	80	20	0.00	0.00
GRA2	160	20	0.00	0.00
GRA2	320	20	0.00	0.00
GRA2	10	40	0.00	0.00
GRA2	20	40	0.00	0.00
GRA2	40	40	0.00	0.00
GRA2	80	40	0.00	0.00
GRA2	160	40	0.00	0.00
GRA2	320	40	0.00	0.00
GRA2	10	80	0.00	0.00
GRA2	20	80	0.00	0.00
GRA2	40	80	0.00	0.00
GRA2	80	80	0.00	0.00
GRA2	160	80	0.00	0.00
GRA2	320	80	0.00	0.00
GRA2	10	160	0.00	0.00
GRA2	20	160	0.00	0.00
GRA2	40	160	0.00	0.00
GRA2	80	160	0.00	0.00
GRA2	160	160	0.00	0.00
GRA2	320	160	0.00	0.00
GRA2	10	320	0.00	0.00
GRA2	20	320	0.00	0.00
GRA2	40	320	0.00	0.00
GRA2	80	320	0.00	0.00
GRA2	160	320	0.00	0.00
GRA2	320	320	0.00	0.00
GRA2	10	640	0.00	0.00
GRA2	20	640	0.00	0.00
GRA2	40	640	0.00	0.00
GRA2	80	640	0.00	0.00
GRA2	160	640	0.00	0.00
GRA2	320	640	0.00	0.00
GRA2	10	1280	0.00	0.00
GRA2	20	1280	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
GRA2	40	1280	0.00	0.00
GRA2	80	1280	0.00	0.00
GRA2	160	1280	0.00	0.00
GRA2	320	1280	0.00	0.00
GRA2	10	20000	14.84	14.84
GRA2	20	20000	15.55	15.55
GRA2	40	20000	16.30	16.30
GRA2	80	20000	14.79	14.79
GRA2	160	20000	13.73	13.73
GRA2	320	20000	13.83	13.83
GRA2	20000	20000	21.15	21.15
GRE	10	10	10.00	0.00
GRE	20	10	5.00	0.00
GRE	40	10	5.00	0.00
GRE	80	10	23.53	23.53
GRE	160	10	23.72	23.72
GRE	320	10	4.05	4.05
GRE	10	20	10.00	0.00
GRE	20	20	5.00	0.00
GRE	40	20	5.00	0.00
GRE	80	20	16.67	16.67
GRE	160	20	18.08	18.08
GRE	320	20	4.08	4.08
GRE	10	40	5.00	0.00
GRE	20	40	5.00	0.39
GRE	40	40	15.00	4.75
GRE	80	40	12.04	12.04
GRE	160	40	12.47	12.47
GRE	320	40	3.77	3.77
GRE	10	80	13.10	13.10
GRE	20	80	16.15	16.15
GRE	40	80	20.09	20.09
GRE	80	80	18.35	18.35
GRE	160	80	12.70	12.70
GRE	320	80	5.24	5.24
GRE	10	160	42.42	42.42
GRE	20	160	36.32	36.32
GRE	40	160	38.63	38.63
GRE	80	160	28.71	28.71
GRE	160	160	16.98	16.98
GRE	320	160	8.19	8.19
GRE	10	320	22.71	22.71
GRE	20	320	28.42	28.42
GRE	40	320	49.10	49.10
GRE	80	320	41.33	41.33
GRE	160	320	23.38	23.38
GRE	320	320	11.66	11.66

Site	buffer width	distance	GT Forest	Forest
GRE	10	640	17.21	17.21
GRE	20	640	26.14	26.14
GRE	40	640	42.58	42.58
GRE	80	640	37.25	37.25
GRE	160	640	21.47	21.47
GRE	320	640	10.72	10.72
GRE	10	1280	11.91	11.91
GRE	20	1280	22.20	22.20
GRE	40	1280	38.75	38.75
GRE	80	1280	36.16	36.16
GRE	160	1280	21.84	21.84
GRE	320	1280	12.13	12.13
GRE	10	20000	25.50	25.50
GRE	20	20000	26.92	26.92
GRE	40	20000	29.52	29.52
GRE	80	20000	30.00	30.00
GRE	160	20000	28.45	28.45
GRE	320	20000	28.17	28.17
GRE	20000	20000	25.30	25.30
HAR	10	10	100.00	0.00
HAR	20	10	80.00	3.01
HAR	40	10	80.00	26.46
HAR	80	10	26.01	26.01
HAR	160	10	26.01	26.01
HAR	320	10	25.44	25.44
HAR	10	20	80.00	0.00
HAR	20	20	50.00	1.93
HAR	40	20	60.00	16.61
HAR	80	20	17.32	17.32
HAR	160	20	17.32	17.32
HAR	320	20	16.99	16.99
HAR	10	40	50.00	15.85
HAR	20	40	25.00	17.40
HAR	40	40	30.00	26.11
HAR	80	40	30.01	30.01
HAR	160	40	31.47	31.47
HAR	320	40	31.47	31.47
HAR	10	80	49.39	49.39
HAR	20	80	47.96	47.96
HAR	40	80	51.64	51.64
HAR	80	80	56.33	56.33
HAR	160	80	55.98	55.98
HAR	320	80	55.98	55.98
HAR	10	160	75.50	75.50
HAR	20	160	74.43	74.43
HAR	40	160	76.43	76.43
HAR	80	160	75.88	75.88

Site	buffer width	distance	GT Forest	Forest
HAR	160	160	56.76	56.76
HAR	320	160	51.55	51.55
HAR	10	320	86.48	86.48
HAR	20	320	85.87	85.87
HAR	40	320	87.14	87.14
HAR	80	320	87.31	87.31
HAR	160	320	70.68	70.68
HAR	320	320	63.67	63.67
HAR	10	640	70.90	70.90
HAR	20	640	70.37	70.37
HAR	40	640	71.28	71.28
HAR	80	640	74.16	74.16
HAR	160	640	71.71	71.71
HAR	320	640	65.77	65.77
HAR	10	1280	57.67	57.67
HAR	20	1280	57.06	57.06
HAR	40	1280	57.37	57.37
HAR	80	1280	58.92	58.92
HAR	160	1280	57.85	57.85
HAR	320	1280	54.18	54.18
HAR	10	20000	30.38	30.38
HAR	20	20000	31.17	31.17
HAR	40	20000	32.49	32.49
HAR	80	20000	36.15	36.15
HAR	160	20000	39.07	39.07
HAR	320	20000	41.55	41.55
HAR	20000	20000	47.62	47.62
HUN	10	10	100.00	0.00
HUN	20	10	50.00	0.00
HUN	40	10	25.00	0.00
HUN	80	10	0.00	0.00
HUN	160	10	0.00	0.00
HUN	320	10	0.00	0.00
HUN	10	20	50.00	0.00
HUN	20	20	25.00	0.00
HUN	40	20	10.00	0.00
HUN	80	20	0.00	0.00
HUN	160	20	0.00	0.00
HUN	320	20	0.00	0.00
HUN	10	40	75.00	0.00
HUN	20	40	10.00	0.00
HUN	40	40	0.00	0.00
HUN	80	40	0.00	0.00
HUN	160	40	0.00	0.00
HUN	320	40	0.00	0.00
HUN	10	80	0.00	0.00
HUN	20	80	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
HUN	40	80	0.00	0.00
HUN	80	80	0.06	0.06
HUN	160	80	0.03	0.03
HUN	320	80	0.02	0.02
HUN	10	160	0.00	0.00
HUN	20	160	0.00	0.00
HUN	40	160	2.61	2.61
HUN	80	160	11.79	11.79
HUN	160	160	14.12	14.12
HUN	320	160	10.21	10.21
HUN	10	320	0.00	0.00
HUN	20	320	0.00	0.00
HUN	40	320	1.59	1.59
HUN	80	320	11.29	11.29
HUN	160	320	16.24	16.24
HUN	320	320	11.28	11.28
HUN	10	640	8.71	8.71
HUN	20	640	7.79	7.79
HUN	40	640	6.08	6.08
HUN	80	640	10.57	10.57
HUN	160	640	10.98	10.98
HUN	320	640	7.99	7.99
HUN	10	1280	6.06	6.06
HUN	20	1280	5.40	5.40
HUN	40	1280	4.18	4.18
HUN	80	1280	7.45	7.45
HUN	160	1280	7.79	7.79
HUN	320	1280	5.80	5.80
HUN	10	20000	34.32	34.32
HUN	20	20000	32.83	32.83
HUN	40	20000	29.05	29.05
HUN	80	20000	26.98	26.98
HUN	160	20000	23.48	23.48
HUN	320	20000	22.07	22.07
HUN	20000	20000	16.76	16.76
JR-01	10	10	0.00	0.00
JR-01	20	10	0.00	0.00
JR-01	40	10	0.00	0.00
JR-01	80	10	13.97	13.97
JR-01	160	10	9.42	9.42
JR-01	320	10	5.30	5.30
JR-01	10	20	0.00	0.00
JR-01	20	20	0.00	2.64
JR-01	40	20	0.00	4.41
JR-01	80	20	14.44	14.44
JR-01	160	20	9.55	9.55
JR-01	320	20	5.42	5.42

Site	buffer width	distance	GT Forest	Forest
JR-01	10	40	25.00	0.00
JR-01	20	40	25.00	7.46
JR-01	40	40	25.00	13.57
JR-01	80	40	21.15	21.15
JR-01	160	40	11.95	11.95
JR-01	320	40	6.90	6.90
JR-01	10	80	5.04	5.04
JR-01	20	80	20.37	20.37
JR-01	40	80	28.31	28.31
JR-01	80	80	31.82	31.82
JR-01	160	80	19.56	19.56
JR-01	320	80	11.32	11.32
JR-01	10	160	4.08	4.08
JR-01	20	160	31.07	31.07
JR-01	40	160	45.98	45.98
JR-01	80	160	45.84	45.84
JR-01	160	160	33.55	33.55
JR-01	320	160	22.73	22.73
JR-01	10	320	3.55	3.55
JR-01	20	320	33.94	33.94
JR-01	40	320	56.77	56.77
JR-01	80	320	63.27	63.27
JR-01	160	320	52.82	52.82
JR-01	320	320	40.55	40.55
JR-01	10	640	13.68	13.68
JR-01	20	640	25.63	25.63
JR-01	40	640	35.82	35.82
JR-01	80	640	41.23	41.23
JR-01	160	640	39.04	39.04
JR-01	320	640	31.08	31.08
JR-01	10	1280	14.65	14.65
JR-01	20	1280	22.45	22.45
JR-01	40	1280	28.87	28.87
JR-01	80	1280	30.96	30.96
JR-01	160	1280	26.51	26.51
JR-01	320	1280	20.74	20.74
JR-01	10	20000	53.62	53.62
JR-01	20	20000	53.09	53.09
JR-01	40	20000	91.20	91.20
JR-01	80	20000	48.29	48.29
JR-01	160	20000	44.21	44.21
JR-01	320	20000	41.87	41.87
JR-01	20000	20000	48.17	48.17
JR-20	10	10	0.00	0.00
JR-20	20	10	0.00	0.00
JR-20	40	10	0.00	0.00
JR-20	80	10	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
JR-20	160	10	0.00	0.00
JR-20	320	10	1.41	1.41
JR-20	10	20	0.00	0.00
JR-20	20	20	0.00	0.00
JR-20	40	20	0.00	0.00
JR-20	80	20	0.00	0.00
JR-20	160	20	0.00	0.00
JR-20	320	20	1.34	1.34
JR-20	10	40	0.00	0.00
JR-20	20	40	0.00	0.00
JR-20	40	40	0.00	0.00
JR-20	80	40	0.00	0.00
JR-20	160	40	0.00	0.00
JR-20	320	40	1.25	1.25
JR-20	10	80	0.00	0.00
JR-20	20	80	0.00	0.00
JR-20	40	80	0.00	0.00
JR-20	80	80	0.00	0.00
JR-20	160	80	0.00	0.00
JR-20	320	80	1.12	1.12
JR-20	10	160	6.21	6.21
JR-20	20	160	8.96	8.96
JR-20	40	160	9.43	9.43
JR-20	80	160	5.94	5.94
JR-20	160	160	2.68	2.68
JR-20	320	160	2.23	2.23
JR-20	10	320	41.71	41.71
JR-20	20	320	44.90	44.90
JR-20	40	320	45.91	45.91
JR-20	80	320	38.92	38.92
JR-20	160	320	22.74	22.74
JR-20	320	320	15.84	15.84
JR-20	10	640	32.54	32.54
JR-20	20	640	36.76	36.76
JR-20	40	640	40.43	40.43
JR-20	80	640	35.22	35.22
JR-20	160	640	22.73	22.73
JR-20	320	640	21.16	21.16
JR-20	10	1280	16.12	16.12
JR-20	20	1280	18.86	18.86
JR-20	40	1280	22.37	22.37
JR-20	80	1280	20.74	20.74
JR-20	160	1280	14.36	14.36
JR-20	320	1280	14.14	14.14
JR-20	10	20000	73.04	73.04
JR-20	20	20000	72.00	72.00
JR-20	40	20000	70.01	70.01

Site	buffer width	distance	GT Forest	Forest
JR-20	80	20000	66.02	66.02
JR-20	160	20000	60.29	60.29
JR-20	320	20000	55.56	55.56
JR-20	20000	20000	57.37	57.37
KIN	10	10	100.00	100.00
KIN	20	10	100.00	100.00
KIN	40	10	100.00	100.00
KIN	80	10	100.00	100.00
KIN	160	10	100.00	100.00
KIN	320	10	100.00	100.00
KIN	10	20	100.00	100.00
KIN	20	20	100.00	100.00
KIN	40	20	100.00	100.00
KIN	80	20	100.00	100.00
KIN	160	20	100.00	100.00
KIN	320	20	100.00	100.00
KIN	10	40	100.00	100.00
KIN	20	40	100.00	100.00
KIN	40	40	100.00	100.00
KIN	80	40	100.00	100.00
KIN	160	40	100.00	100.00
KIN	320	40	99.99	99.99
KIN	10	80	100.00	100.00
KIN	20	80	100.00	100.00
KIN	40	80	100.00	100.00
KIN	80	80	100.00	100.00
KIN	160	80	100.00	100.00
KIN	320	80	99.98	99.98
KIN	10	160	100.00	100.00
KIN	20	160	100.00	100.00
KIN	40	160	100.00	100.00
KIN	80	160	100.00	100.00
KIN	160	160	100.00	100.00
KIN	320	160	99.98	99.98
KIN	10	320	100.00	100.00
KIN	20	320	100.00	100.00
KIN	40	320	100.00	100.00
KIN	80	320	100.00	100.00
KIN	160	320	100.00	100.00
KIN	320	320	97.87	97.87
KIN	10	640	98.69	98.69
KIN	20	640	99.34	99.34
KIN	40	640	99.67	99.67
KIN	80	640	99.84	99.84
KIN	160	640	99.91	99.91
KIN	320	640	98.07	98.07
KIN	10	1280	88.65	88.65

Site	buffer width	distance	GT Forest	Forest
KIN	20	1280	94.04	94.04
KIN	40	1280	96.99	96.99
KIN	80	1280	98.38	98.38
KIN	160	1280	99.00	99.00
KIN	320	1280	97.21	97.21
KIN	10	20000	88.10	88.10
KIN	20	20000	93.15	93.15
KIN	40	20000	96.35	96.35
KIN	80	20000	97.79	97.79
KIN	160	20000	98.02	98.02
KIN	320	20000	96.98	96.98
KIN	20000	20000	91.00	91.00
LAP	10	10	0.00	100.00
LAP	20	10	10.00	100.00
LAP	40	10	10.00	100.00
LAP	80	10	100.00	100.00
LAP	160	10	100.00	100.00
LAP	320	10	99.91	99.91
LAP	10	20	40.00	100.00
LAP	20	20	50.00	100.00
LAP	40	20	35.00	100.00
LAP	80	20	100.00	100.00
LAP	160	20	100.00	100.00
LAP	320	20	99.90	99.90
LAP	10	40	70.00	100.00
LAP	20	40	80.00	100.00
LAP	40	40	50.00	100.00
LAP	80	40	100.00	100.00
LAP	160	40	100.00	100.00
LAP	320	40	100.00	100.00
LAP	10	80	100.00	100.00
LAP	20	80	99.57	99.57
LAP	40	80	97.86	97.86
LAP	80	80	93.32	93.32
LAP	160	80	97.52	97.52
LAP	320	80	98.92	98.92
LAP	10	160	66.68	66.68
LAP	20	160	52.92	52.92
LAP	40	160	51.06	51.06
LAP	80	160	65.76	65.76
LAP	160	160	83.77	83.77
LAP	320	160	91.73	91.73
LAP	10	320	47.64	47.64
LAP	20	320	49.35	49.35
LAP	40	320	51.57	51.57
LAP	80	320	61.44	61.44
LAP	160	320	79.63	79.63

Site	buffer width	distance	GT Forest	Forest
LAP	320	320	89.31	89.31
LAP	10	640	59.80	59.80
LAP	20	640	61.42	61.42
LAP	40	640	63.41	63.41
LAP	80	640	71.28	71.28
LAP	160	640	85.77	85.77
LAP	320	640	92.27	92.27
LAP	10	1280	78.38	78.38
LAP	20	1280	80.82	80.82
LAP	40	1280	84.22	84.22
LAP	80	1280	88.19	88.19
LAP	160	1280	93.66	93.66
LAP	320	1280	96.62	96.62
LAP	10	20000	81.37	81.37
LAP	20	20000	83.71	83.71
LAP	40	20000	87.70	87.70
LAP	80	20000	92.24	92.24
LAP	160	20000	95.23	95.23
LAP	320	20000	96.33	96.33
LAP	20000	20000	91.39	91.39
LDS	10	10	50.00	0.00
LDS	20	10	25.00	0.00
LDS	40	10	10.00	0.00
LDS	80	10	0.00	0.00
LDS	160	10	0.00	0.00
LDS	320	10	0.00	0.00
LDS	10	20	40.00	0.00
LDS	20	20	20.00	0.00
LDS	40	20	10.00	0.00
LDS	80	20	0.00	0.00
LDS	160	20	0.00	0.00
LDS	320	20	0.00	0.00
LDS	10	40	20.00	0.00
LDS	20	40	10.00	0.00
LDS	40	40	5.00	0.00
LDS	80	40	0.00	0.00
LDS	160	40	0.00	0.00
LDS	320	40	0.00	0.00
LDS	10	80	0.00	0.00
LDS	20	80	0.00	0.00
LDS	40	80	0.00	0.00
LDS	80	80	0.00	0.00
LDS	160	80	0.00	0.00
LDS	320	80	0.00	0.00
LDS	10	160	0.00	0.00
LDS	20	160	0.00	0.00
LDS	40	160	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
LDS	80	160	0.00	0.00
LDS	160	160	0.00	0.00
LDS	320	160	0.00	0.00
LDS	10	320	0.00	0.00
LDS	20	320	0.00	0.00
LDS	40	320	0.00	0.00
LDS	80	320	0.00	0.00
LDS	160	320	0.00	0.00
LDS	320	320	0.00	0.00
LDS	10	640	0.00	0.00
LDS	20	640	0.00	0.00
LDS	40	640	0.00	0.00
LDS	80	640	0.00	0.00
LDS	160	640	0.00	0.00
LDS	320	640	0.00	0.00
LDS	10	1280	0.00	0.00
LDS	20	1280	0.00	0.00
LDS	40	1280	0.00	0.00
LDS	80	1280	0.00	0.00
LDS	160	1280	0.00	0.00
LDS	320	1280	0.00	0.00
LDS	10	20000	57.86	57.86
LDS	20	20000	58.46	58.46
LDS	40	20000	57.27	57.27
LDS	80	20000	54.47	54.47
LDS	160	20000	52.34	52.34
LDS	320	20000	48.45	48.45
LDS	20000	20000	39.43	39.43
LMS	10	10	100.00	99.39
LMS	20	10	80.00	63.93
LMS	40	10	75.00	26.46
LMS	80	10	15.10	15.10
LMS	160	10	8.89	8.89
LMS	320	10	5.59	5.59
LMS	10	20	100.00	94.85
LMS	20	20	60.00	62.91
LMS	40	20	50.00	29.33
LMS	80	20	16.91	16.91
LMS	160	20	10.08	10.08
LMS	320	20	6.23	6.23
LMS	10	40	80.00	82.08
LMS	20	40	40.00	56.25
LMS	40	40	25.00	27.14
LMS	80	40	14.07	14.07
LMS	160	40	6.89	6.89
LMS	320	40	3.36	3.36
LMS	10	80	86.46	86.46

Site	buffer width	distance	GT Forest	Forest
LMS	20	80	61.41	61.41
LMS	40	80	32.83	32.83
LMS	80	80	17.92	17.92
LMS	160	80	9.07	9.07
LMS	320	80	4.44	4.44
LMS	10	160	86.85	86.85
LMS	20	160	64.08	64.08
LMS	40	160	37.99	37.99
LMS	80	160	20.55	20.55
LMS	160	160	9.75	9.75
LMS	320	160	4.88	4.88
LMS	10	320	82.18	82.18
LMS	20	320	67.43	67.43
LMS	40	320	43.91	43.91
LMS	80	320	23.92	23.92
LMS	160	320	13.16	13.16
LMS	320	320	7.69	7.69
LMS	10	640	57.55	57.55
LMS	20	640	48.76	48.76
LMS	40	640	37.99	37.99
LMS	80	640	29.62	29.62
LMS	160	640	18.92	18.92
LMS	320	640	11.98	11.98
LMS	10	1280	73.11	73.11
LMS	20	1280	68.66	68.66
LMS	40	1280	62.69	62.69
LMS	80	1280	59.10	59.10
LMS	160	1280	46.15	46.15
LMS	320	1280	30.86	30.86
LMS	10	20000	62.66	62.66
LMS	20	20000	63.44	63.44
LMS	40	20000	61.03	61.03
LMS	80	20000	60.13	60.13
LMS	160	20000	57.74	57.74
LMS	320	20000	55.13	55.13
LMS	20000	20000	49.73	49.73
LUS	10	10	0.00	55.59
LUS	20	10	0.00	77.36
LUS	40	10	0.00	88.70
LUS	80	10	92.76	92.76
LUS	160	10	96.73	96.73
LUS	320	10	96.92	96.92
LUS	10	20	0.00	22.90
LUS	20	20	0.00	47.47
LUS	40	20	0.00	68.70
LUS	80	20	80.65	80.65
LUS	160	20	93.35	93.35

Site	buffer width	distance	GT Forest	Forest
LUS	320	20	93.52	93.52
LUS	10	40	0.00	9.41
LUS	20	40	0.00	20.81
LUS	40	40	0.00	40.86
LUS	80	40	57.44	57.44
LUS	160	40	78.98	78.98
LUS	320	40	76.48	76.48
LUS	10	80	10.97	10.97
LUS	20	80	19.71	19.71
LUS	40	80	41.41	41.41
LUS	80	80	57.90	57.90
LUS	160	80	73.69	73.69
LUS	320	80	71.39	71.39
LUS	10	160	15.29	15.29
LUS	20	160	28.15	28.15
LUS	40	160	55.17	55.17
LUS	80	160	75.35	75.35
LUS	160	160	85.96	85.96
LUS	320	160	89.98	89.98
LUS	10	320	21.84	21.84
LUS	20	320	37.75	37.75
LUS	40	320	58.38	58.38
LUS	80	320	75.39	75.39
LUS	160	320	86.21	86.21
LUS	320	320	90.33	90.33
LUS	10	640	55.01	55.01
LUS	20	640	61.83	61.83
LUS	40	640	69.03	69.03
LUS	80	640	76.80	76.80
LUS	160	640	87.27	87.27
LUS	320	640	91.75	91.75
LUS	10	1280	41.50	41.50
LUS	20	1280	43.30	43.30
LUS	40	1280	42.40	42.40
LUS	80	1280	42.75	42.75
LUS	160	1280	58.15	58.15
LUS	320	1280	70.96	70.96
LUS	10	20000	63.76	63.76
LUS	20	20000	69.05	69.05
LUS	40	20000	72.18	72.18
LUS	80	20000	74.39	74.39
LUS	160	20000	80.91	80.91
LUS	320	20000	85.87	85.87
LUS	20000	20000	80.69	80.69
MCR	10	10	50.00	0.00
MCR	20	10	50.00	0.00
MCR	40	10	30.00	0.00

Site	buffer width	distance	GT Forest	Forest
MCR	80	10	6.29	6.29
MCR	160	10	10.95	10.95
MCR	320	10	4.00	4.00
MCR	10	20	50.00	0.00
MCR	20	20	50.00	0.00
MCR	40	20	30.00	0.00
MCR	80	20	5.35	5.35
MCR	160	20	9.35	9.35
MCR	320	20	3.70	3.70
MCR	10	40	50.00	0.00
MCR	20	40	50.00	0.00
MCR	40	40	40.00	0.00
MCR	80	40	4.11	4.11
MCR	160	40	7.55	7.55
MCR	320	40	3.16	3.16
MCR	10	80	0.00	0.00
MCR	20	80	0.00	0.00
MCR	40	80	0.00	0.00
MCR	80	80	2.92	2.92
MCR	160	80	5.53	5.53
MCR	320	80	2.53	2.53
MCR	10	160	0.00	0.00
MCR	20	160	0.00	0.00
MCR	40	160	0.00	0.00
MCR	80	160	0.00	0.00
MCR	160	160	1.05	1.05
MCR	320	160	1.57	1.57
MCR	10	320	0.00	0.00
MCR	20	320	0.00	0.00
MCR	40	320	0.00	0.00
MCR	80	320	0.93	0.93
MCR	160	320	1.78	1.78
MCR	320	320	0.84	0.84
MCR	10	640	13.02	13.02
MCR	20	640	14.41	14.41
MCR	40	640	15.07	15.07
MCR	80	640	12.63	12.63
MCR	160	640	8.51	8.51
MCR	320	640	4.70	4.70
MCR	10	1280	12.26	12.26
MCR	20	1280	12.72	12.72
MCR	40	1280	10.88	10.88
MCR	80	1280	8.40	8.40
MCR	160	1280	5.93	5.93
MCR	320	1280	3.22	3.22
MCR	10	20000	48.51	48.51
MCR	20	20000	48.31	48.31

Site	buffer width	distance	GT Forest	Forest
MCR	40	20000	48.03	48.03
MCR	80	20000	47.22	47.22
MCR	160	20000	45.51	45.51
MCR	320	20000	43.43	43.43
MCR	20000	20000	42.67	42.67
MEE	10	10	0.00	0.00
MEE	20	10	0.00	0.00
MEE	40	10	0.00	0.00
MEE	80	10	0.00	0.00
MEE	160	10	1.46	1.46
MEE	320	10	33.00	33.00
MEE	10	20	0.00	0.00
MEE	20	20	0.00	0.00
MEE	40	20	0.00	0.00
MEE	80	20	0.00	0.00
MEE	160	20	1.34	1.34
MEE	320	20	32.52	32.52
MEE	10	40	0.00	0.00
MEE	20	40	0.00	0.00
MEE	40	40	0.00	0.00
MEE	80	40	0.00	0.00
MEE	160	40	1.33	1.33
MEE	320	40	30.42	30.42
MEE	10	80	0.00	0.00
MEE	20	80	0.00	0.00
MEE	40	80	0.00	0.00
MEE	80	80	0.00	0.00
MEE	160	80	28.68	28.68
MEE	320	80	28.38	28.38
MEE	10	160	0.00	0.00
MEE	20	160	0.00	0.00
MEE	40	160	0.00	0.00
MEE	80	160	0.00	0.00
MEE	160	160	0.64	0.64
MEE	320	160	24.17	24.17
MEE	10	320	0.00	0.00
MEE	20	320	0.00	0.00
MEE	40	320	0.00	0.00
MEE	80	320	0.00	0.00
MEE	160	320	0.40	0.40
MEE	320	320	20.58	20.58
MEE	10	640	5.96	5.96
MEE	20	640	6.57	6.57
MEE	40	640	7.80	7.80
MEE	80	640	11.31	11.31
MEE	160	640	24.18	24.18
MEE	320	640	41.78	41.78

Site	buffer width	distance	GT Forest	Forest
MEE	10	1280	13.45	13.45
MEE	20	1280	14.28	14.28
MEE	40	1280	15.50	15.50
MEE	80	1280	18.33	18.33
MEE	160	1280	29.38	29.38
MEE	320	1280	46.26	46.26
MEE	10	20000	69.76	69.76
MEE	20	20000	71.07	71.07
MEE	40	20000	73.41	73.41
MEE	80	20000	76.14	76.14
MEE	160	20000	79.56	79.56
MEE	320	20000	84.73	84.73
MEE	20000	20000	85.49	85.49
MNCR	10	10	0.00	0.00
MNCR	20	10	0.00	0.00
MNCR	40	10	0.00	0.00
MNCR	80	10	0.00	0.00
MNCR	160	10	0.00	0.00
MNCR	320	10	0.00	0.00
MNCR	10	20	0.00	0.00
MNCR	20	20	0.00	0.00
MNCR	40	20	0.00	0.00
MNCR	80	20	0.00	0.00
MNCR	160	20	0.00	0.00
MNCR	320	20	0.00	0.00
MNCR	10	40	0.00	0.00
MNCR	20	40	0.00	0.00
MNCR	40	40	0.00	0.00
MNCR	80	40	0.00	0.00
MNCR	160	40	0.00	0.00
MNCR	320	40	0.00	0.00
MNCR	10	80	0.00	0.00
MNCR	20	80	0.00	0.00
MNCR	40	80	0.00	0.00
MNCR	80	80	0.00	0.00
MNCR	160	80	0.00	0.00
MNCR	320	80	0.00	0.00
MNCR	10	160	0.00	0.00
MNCR	20	160	0.00	0.00
MNCR	40	160	0.00	0.00
MNCR	80	160	0.00	0.00
MNCR	160	160	0.00	0.00
MNCR	320	160	0.00	0.00
MNCR	10	320	0.00	0.00
MNCR	20	320	0.00	0.00
MNCR	40	320	0.00	0.00
MNCR	80	320	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
MNCR	160	320	0.00	0.00
MNCR	320	320	0.00	0.00
MNCR	10	640	8.56	8.56
MNCR	20	640	10.47	10.47
MNCR	40	640	11.74	11.74
MNCR	80	640	13.20	13.20
MNCR	160	640	12.93	12.93
MNCR	320	640	12.21	12.21
MNCR	10	1280	7.66	7.66
MNCR	20	1280	9.68	9.68
MNCR	40	1280	12.87	12.87
MNCR	80	1280	16.24	16.24
MNCR	160	1280	18.18	18.18
MNCR	320	1280	17.33	17.33
MNCR	10	20000	34.49	34.49
MNCR	20	20000	34.88	34.88
MNCR	40	20000	34.72	34.72
MNCR	80	20000	33.63	33.63
MNCR	160	20000	31.85	31.85
MNCR	320	20000	30.45	30.45
MNCR	20000	20000	32.77	32.77
MOS	10	10	0.00	100.00
MOS	20	10	0.00	100.00
MOS	40	10	0.00	100.00
MOS	80	10	84.51	84.51
MOS	160	10	27.92	27.92
MOS	320	10	8.69	8.69
MOS	10	20	0.00	100.00
MOS	20	20	0.00	100.00
MOS	40	20	0.00	100.00
MOS	80	20	82.61	82.61
MOS	160	20	30.41	30.41
MOS	320	20	10.05	10.05
MOS	10	40	0.00	100.00
MOS	20	40	0.00	100.00
MOS	40	40	0.00	100.00
MOS	80	40	83.58	83.58
MOS	160	40	32.27	32.27
MOS	320	40	10.90	10.90
MOS	10	80	100.00	100.00
MOS	20	80	100.00	100.00
MOS	40	80	100.00	100.00
MOS	80	80	89.99	89.99
MOS	160	80	45.69	45.69
MOS	320	80	17.77	17.77
MOS	10	160	100.00	100.00
MOS	20	160	100.00	100.00

Site	buffer width	distance	GT Forest	Forest
MOS	40	160	95.18	95.18
MOS	80	160	76.59	76.59
MOS	160	160	42.20	42.20
MOS	320	160	21.03	21.03
MOS	10	320	86.52	86.52
MOS	20	320	87.26	87.26
MOS	40	320	80.13	80.13
MOS	80	320	63.85	63.85
MOS	160	320	37.71	37.71
MOS	320	320	23.37	23.37
MOS	10	640	76.75	76.75
MOS	20	640	74.36	74.36
MOS	40	640	64.59	64.59
MOS	80	640	47.83	47.83
MOS	160	640	27.52	27.52
MOS	320	640	17.03	17.03
MOS	10	1280	39.53	39.53
MOS	20	1280	38.52	38.52
MOS	40	1280	34.43	34.43
MOS	80	1280	25.65	25.65
MOS	160	1280	14.54	14.54
MOS	320	1280	8.77	8.77
MOS	10	20000	33.95	33.95
MOS	20	20000	35.16	35.16
MOS	40	20000	36.57	36.57
MOS	80	20000	37.39	37.39
MOS	160	20000	37.66	37.66
MOS	320	20000	36.00	36.00
MOS	20000	20000	35.24	35.24
MUD	10	10	0.00	100.00
MUD	20	10	0.00	100.00
MUD	40	10	25.00	55.62
MUD	80	10	17.49	17.49
MUD	160	10	4.74	4.74
MUD	320	10	2.92	2.92
MUD	10	20	0.00	73.18
MUD	20	20	5.00	66.39
MUD	40	20	25.00	39.72
MUD	80	20	21.96	21.96
MUD	160	20	6.31	6.31
MUD	320	20	3.49	3.49
MUD	10	40	0.00	100.00
MUD	20	40	5.00	100.00
MUD	40	40	50.00	73.23
MUD	80	40	29.00	29.00
MUD	160	40	9.20	9.20
MUD	320	40	4.60	4.60

Site	buffer width	distance	GT Forest	Forest
MUD	10	80	100.00	100.00
MUD	20	80	100.00	100.00
MUD	40	80	74.10	74.10
MUD	80	80	33.78	33.78
MUD	160	80	11.74	11.74
MUD	320	80	5.63	5.63
MUD	10	160	100.00	100.00
MUD	20	160	100.00	100.00
MUD	40	160	100.00	100.00
MUD	80	160	54.04	54.04
MUD	160	160	33.53	33.53
MUD	320	160	15.26	15.26
MUD	10	320	100.00	100.00
MUD	20	320	100.00	100.00
MUD	40	320	91.93	91.93
MUD	80	320	73.13	73.13
MUD	160	320	39.73	39.73
MUD	320	320	19.45	19.45
MUD	10	640	68.29	68.29
MUD	20	640	67.13	67.13
MUD	40	640	61.38	61.38
MUD	80	640	48.78	48.78
MUD	160	640	31.01	31.01
MUD	320	640	17.13	17.13
MUD	10	1280	49.27	49.27
MUD	20	1280	48.44	48.44
MUD	40	1280	44.15	44.15
MUD	80	1280	33.94	33.94
MUD	160	1280	22.01	22.01
MUD	320	1280	14.06	14.06
MUD	10	20000	20.75	20.75
MUD	20	20000	20.97	20.97
MUD	40	20000	19.96	19.96
MUD	80	20000	17.42	17.42
MUD	160	20000	15.29	15.29
MUD	320	20000	14.70	14.70
MUD	20000	20000	18.92	18.92
NCR	10	10	0.00	0.00
NCR	20	10	30.00	0.00
NCR	40	10	75.00	0.00
NCR	80	10	0.00	0.00
NCR	160	10	0.00	0.00
NCR	320	10	0.00	0.00
NCR	10	20	0.00	0.00
NCR	20	20	30.00	0.00
NCR	40	20	75.00	0.00
NCR	80	20	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
NCR	160	20	0.00	0.00
NCR	320	20	0.00	0.00
NCR	10	40	40.00	0.00
NCR	20	40	50.00	0.00
NCR	40	40	90.00	0.00
NCR	80	40	0.00	0.00
NCR	160	40	0.00	0.00
NCR	320	40	0.00	0.00
NCR	10	80	0.00	0.00
NCR	20	80	0.00	0.00
NCR	40	80	0.00	0.00
NCR	80	80	0.00	0.00
NCR	160	80	0.00	0.00
NCR	320	80	0.00	0.00
NCR	10	160	0.00	0.00
NCR	20	160	0.00	0.00
NCR	40	160	0.00	0.00
NCR	80	160	0.00	0.00
NCR	160	160	0.00	0.00
NCR	320	160	0.00	0.00
NCR	10	320	0.00	0.00
NCR	20	320	0.00	0.00
NCR	40	320	0.00	0.00
NCR	80	320	0.00	0.00
NCR	160	320	0.00	0.00
NCR	320	320	0.00	0.00
NCR	10	640	0.00	0.00
NCR	20	640	0.00	0.00
NCR	40	640	0.00	0.00
NCR	80	640	0.00	0.00
NCR	160	640	0.00	0.00
NCR	320	640	0.00	0.00
NCR	10	1280	0.00	0.00
NCR	20	1280	0.00	0.00
NCR	40	1280	0.00	0.00
NCR	80	1280	0.07	0.07
NCR	160	1280	0.33	0.33
NCR	320	1280	5.85	5.85
NCR	10	20000	39.64	39.64
NCR	20	20000	39.53	39.53
NCR	40	20000	39.16	39.16
NCR	80	20000	38.71	38.71
NCR	160	20000	37.73	37.73
NCR	320	20000	36.63	36.63
NCR	20000	20000	35.69	35.69
PHI	10	10	20.00	0.00
PHI	20	10	25.00	0.00

Site	buffer width	distance	GT Forest	Forest
PHI	40	10	30.00	0.00
PHI	80	10	2.15	2.15
PHI	160	10	9.19	9.19
PHI	320	10	10.90	10.90
PHI	10	20	10.00	0.00
PHI	20	20	20.00	0.00
PHI	40	20	40.00	0.00
PHI	80	20	3.89	3.89
PHI	160	20	10.99	10.99
PHI	320	20	12.22	12.22
PHI	10	40	10.00	0.00
PHI	20	40	30.00	0.00
PHI	40	40	30.00	0.00
PHI	80	40	8.04	8.04
PHI	160	40	15.02	15.02
PHI	320	40	15.36	15.36
PHI	10	80	0.00	0.00
PHI	20	80	0.00	0.00
PHI	40	80	0.56	0.56
PHI	80	80	11.67	11.67
PHI	160	80	18.56	18.56
PHI	320	80	17.79	17.79
PHI	10	160	0.00	0.00
PHI	20	160	0.00	0.00
PHI	40	160	1.49	1.49
PHI	80	160	16.02	16.02
PHI	160	160	28.41	28.41
PHI	320	160	26.57	26.57
PHI	10	320	13.00	13.00
PHI	20	320	13.30	13.30
PHI	40	320	22.05	22.05
PHI	80	320	40.57	40.57
PHI	160	320	49.28	49.28
PHI	320	320	45.76	45.76
PHI	10	640	52.66	52.66
PHI	20	640	54.69	54.69
PHI	40	640	60.75	60.75
PHI	80	640	69.72	69.72
PHI	160	640	73.56	73.56
PHI	320	640	70.10	70.10
PHI	10	1280	74.29	74.29
PHI	20	1280	76.25	76.25
PHI	40	1280	79.39	79.39
PHI	80	1280	81.17	81.17
PHI	160	1280	82.29	82.29
PHI	320	1280	82.95	82.95
PHI	10	20000	88.15	88.15

Site	buffer width	distance	GT Forest	Forest
PHI	20	20000	89.74	89.74
PHI	40	20000	91.69	91.69
PHI	80	20000	93.79	93.79
PHI	160	20000	95.29	95.29
PHI	320	20000	96.38	96.38
PHI	20000	20000	93.36	93.36
POO	10	10	0.00	0.00
POO	20	10	10.00	0.00
POO	40	10	10.00	0.00
POO	80	10	0.00	0.00
POO	160	10	0.00	0.00
POO	320	10	0.00	0.00
POO	10	20	0.00	0.00
POO	20	20	5.00	0.00
POO	40	20	5.00	0.00
POO	80	20	0.00	0.00
POO	160	20	0.00	0.00
POO	320	20	0.00	0.00
POO	10	40	0.00	0.00
POO	20	40	5.00	0.00
POO	40	40	5.00	0.00
POO	80	40	0.00	0.00
POO	160	40	0.00	0.00
POO	320	40	0.00	0.00
POO	10	80	0.00	0.00
POO	20	80	0.00	0.00
POO	40	80	0.00	0.00
POO	80	80	0.00	0.00
POO	160	80	0.00	0.00
POO	320	80	0.99	0.99
POO	10	160	28.85	28.85
POO	20	160	23.11	23.11
POO	40	160	18.80	18.80
POO	80	160	10.18	10.18
POO	160	160	6.01	6.01
POO	320	160	7.46	7.46
POO	10	320	63.51	63.51
POO	20	320	57.15	57.15
POO	40	320	47.95	47.95
POO	80	320	29.83	29.83
POO	160	320	21.11	21.11
POO	320	320	21.49	21.49
POO	10	640	68.70	68.70
POO	20	640	64.23	64.23
POO	40	640	52.91	52.91
POO	80	640	33.35	33.35
POO	160	640	20.77	20.77

Site	buffer width	distance	GT Forest	Forest
POO	320	640	16.02	16.02
POO	10	1280	51.31	51.31
POO	20	1280	49.43	49.43
POO	40	1280	42.06	42.06
POO	80	1280	28.16	28.16
POO	160	1280	21.81	21.81
POO	320	1280	27.30	27.30
POO	10	20000	83.47	83.47
POO	20	20000	83.49	83.49
POO	40	20000	82.63	82.63
POO	80	20000	79.94	79.94
POO	160	20000	76.80	76.80
POO	320	20000	73.69	73.69
POO	20000	20000	68.62	68.62
RAI	10	10	0.00	100.00
RAI	20	10	0.00	82.05
RAI	40	10	0.00	61.81
RAI	80	10	53.98	53.98
RAI	160	10	64.93	64.93
RAI	320	10	72.48	72.48
RAI	10	20	5.00	100.00
RAI	20	20	5.00	87.83
RAI	40	20	5.00	70.42
RAI	80	20	60.46	60.46
RAI	160	20	68.90	68.90
RAI	320	20	75.99	75.99
RAI	10	40	10.00	100.00
RAI	20	40	5.00	92.23
RAI	40	40	5.00	78.84
RAI	80	40	68.34	68.34
RAI	160	40	74.11	74.11
RAI	320	40	80.46	80.46
RAI	10	80	100.00	100.00
RAI	20	80	95.20	95.20
RAI	40	80	85.78	85.78
RAI	80	80	76.41	76.41
RAI	160	80	80.03	80.03
RAI	320	80	85.37	85.37
RAI	10	160	100.00	100.00
RAI	20	160	97.37	97.37
RAI	40	160	91.66	91.66
RAI	80	160	84.88	84.88
RAI	160	160	87.09	87.09
RAI	320	160	92.37	92.37
RAI	10	320	100.00	100.00
RAI	20	320	98.67	98.67
RAI	40	320	95.59	95.59

Site	buffer width	distance	GT Forest	Forest
RAI	80	320	91.30	91.30
RAI	160	320	91.80	91.80
RAI	320	320	95.07	95.07
RAI	10	640	100.00	100.00
RAI	20	640	99.32	99.32
RAI	40	640	97.68	97.68
RAI	80	640	95.31	95.31
RAI	160	640	95.43	95.43
RAI	320	640	96.93	96.93
RAI	10	1280	80.37	80.37
RAI	20	1280	84.07	84.07
RAI	40	1280	84.83	84.83
RAI	80	1280	83.99	83.99
RAI	160	1280	82.68	82.68
RAI	320	1280	79.37	79.37
RAI	10	20000	83.84	83.84
RAI	20	20000	86.28	86.28
RAI	40	20000	89.50	89.50
RAI	80	20000	93.27	93.27
RAI	160	20000	95.93	95.93
RAI	320	20000	97.10	97.10
RAI	20000	20000	92.72	92.72
SAWD	10	10	25.00	0.00
SAWD	20	10	10.00	0.00
SAWD	40	10	5.00	0.00
SAWD	80	10	0.00	0.00
SAWD	160	10	0.00	0.00
SAWD	320	10	0.00	0.00
SAWD	10	20	20.00	0.00
SAWD	20	20	10.00	0.00
SAWD	40	20	5.00	0.00
SAWD	80	20	0.00	0.00
SAWD	160	20	0.00	0.00
SAWD	320	20	0.00	0.00
SAWD	10	40	10.00	0.00
SAWD	20	40	5.00	0.00
SAWD	40	40	0.00	0.00
SAWD	80	40	0.00	0.00
SAWD	160	40	0.00	0.00
SAWD	320	40	0.00	0.00
SAWD	10	80	0.00	0.00
SAWD	20	80	0.00	0.00
SAWD	40	80	0.00	0.00
SAWD	80	80	0.00	0.00
SAWD	160	80	0.00	0.00
SAWD	320	80	0.00	0.00
SAWD	10	160	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
SAWD	20	160	0.00	0.00
SAWD	40	160	0.00	0.00
SAWD	80	160	0.00	0.00
SAWD	160	160	0.00	0.00
SAWD	320	160	0.07	0.07
SAWD	10	320	0.00	0.00
SAWD	20	320	0.86	0.86
SAWD	40	320	9.82	9.82
SAWD	80	320	15.59	15.59
SAWD	160	320	24.74	24.74
SAWD	320	320	20.19	20.19
SAWD	10	640	24.05	24.05
SAWD	20	640	24.33	24.33
SAWD	40	640	28.43	28.43
SAWD	80	640	28.65	28.65
SAWD	160	640	26.79	26.79
SAWD	320	640	17.67	17.67
SAWD	10	1280	63.89	63.89
SAWD	20	1280	63.05	63.05
SAWD	40	1280	61.00	61.00
SAWD	80	1280	44.42	44.42
SAWD	160	1280	32.95	32.95
SAWD	320	1280	21.87	21.87
SAWD	10	20000	49.01	49.01
SAWD	20	20000	47.49	47.49
SAWD	40	20000	42.95	42.95
SAWD	80	20000	36.21	36.21
SAWD	160	20000	32.32	32.32
SAWD	320	20000	27.88	27.88
SAWD	20000	20000	29.26	29.26
SAWU	10	10	50.00	17.50
SAWU	20	10	50.00	13.12
SAWU	40	10	50.00	12.21
SAWU	80	10	6.81	6.81
SAWU	160	10	3.52	3.52
SAWU	320	10	1.65	1.65
SAWU	10	20	50.00	27.85
SAWU	20	20	50.00	28.25
SAWU	40	20	50.00	21.20
SAWU	80	20	12.32	12.32
SAWU	160	20	9.83	9.83
SAWU	320	20	4.68	4.68
SAWU	10	40	50.00	51.34
SAWU	20	40	50.00	45.40
SAWU	40	40	50.00	35.43
SAWU	80	40	22.21	22.21
SAWU	160	40	28.24	28.24

Site	buffer width	distance	GT Forest	Forest
SAWU	320	40	12.91	12.91
SAWU	10	80	64.99	64.99
SAWU	20	80	60.01	60.01
SAWU	40	80	58.93	58.93
SAWU	80	80	58.52	58.52
SAWU	160	80	65.30	65.30
SAWU	320	80	41.53	41.53
SAWU	10	160	81.06	81.06
SAWU	20	160	75.45	75.45
SAWU	40	160	63.08	63.08
SAWU	80	160	67.79	67.79
SAWU	160	160	75.13	75.13
SAWU	320	160	52.23	52.23
SAWU	10	320	90.29	90.29
SAWU	20	320	83.80	83.80
SAWU	40	320	69.46	69.46
SAWU	80	320	71.41	71.41
SAWU	160	320	71.63	71.63
SAWU	320	320	48.66	48.66
SAWU	10	640	90.58	90.58
SAWU	20	640	84.26	84.26
SAWU	40	640	71.33	71.33
SAWU	80	640	74.39	74.39
SAWU	160	640	74.20	74.20
SAWU	320	640	53.42	53.42
SAWU	10	1280	90.39	90.39
SAWU	20	1280	84.26	84.26
SAWU	40	1280	71.33	71.33
SAWU	80	1280	74.39	74.39
SAWU	160	1280	74.20	74.20
SAWU	320	1280	53.42	53.42
SAWU	10	20000	90.40	90.40
SAWU	20	20000	84.26	84.26
SAWU	40	20000	70.76	70.76
SAWU	80	20000	74.38	74.38
SAWU	160	20000	74.35	74.35
SAWU	320	20000	53.42	53.42
SAWU	20000	20000	49.43	49.43
TAY	10	10	0.00	100.00
TAY	20	10	10.00	100.00
TAY	40	10	25.00	99.59
TAY	80	10	64.25	64.25
TAY	160	10	51.64	51.64
TAY	320	10	22.68	22.68
TAY	10	20	0.00	100.00
TAY	20	20	10.00	100.00
TAY	40	20	25.00	99.67

Site	buffer width	distance	GT Forest	Forest
TAY	80	20	62.71	62.71
TAY	160	20	49.86	49.86
TAY	320	20	22.65	22.65
TAY	10	40	5.00	100.00
TAY	20	40	15.00	100.00
TAY	40	40	30.00	99.76
TAY	80	40	61.05	61.05
TAY	160	40	47.05	47.05
TAY	320	40	22.62	22.62
TAY	10	80	100.00	100.00
TAY	20	80	100.00	100.00
TAY	40	80	99.85	99.85
TAY	80	80	61.10	61.10
TAY	160	80	43.48	43.48
TAY	320	80	22.86	22.86
TAY	10	160	100.00	100.00
TAY	20	160	100.00	100.00
TAY	40	160	99.50	99.50
TAY	80	160	58.75	58.75
TAY	160	160	38.80	38.80
TAY	320	160	22.75	22.75
TAY	10	320	100.00	100.00
TAY	20	320	100.00	100.00
TAY	40	320	96.87	96.87
TAY	80	320	58.66	58.66
TAY	160	320	35.67	35.67
TAY	320	320	19.65	19.65
TAY	10	640	93.06	93.06
TAY	20	640	91.12	91.12
TAY	40	640	86.87	86.87
TAY	80	640	51.42	51.42
TAY	160	640	29.42	29.42
TAY	320	640	16.46	16.46
TAY	10	1280	89.12	89.12
TAY	20	1280	87.02	87.02
TAY	40	1280	81.30	81.30
TAY	80	1280	52.31	52.31
TAY	160	1280	31.12	31.12
TAY	320	1280	17.44	17.44
TAY	10	20000	89.12	89.12
TAY	20	20000	87.02	87.02
TAY	40	20000	81.30	81.30
TAY	80	20000	52.31	52.31
TAY	160	20000	31.12	31.12
TAY	320	20000	17.44	17.44
TAY	20000	20000	9.70	9.70
TAYD	10	10	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
TAYD	20	10	0.00	0.00
TAYD	40	10	0.00	0.00
TAYD	80	10	0.00	0.00
TAYD	160	10	0.00	0.00
TAYD	320	10	0.00	0.00
TAYD	10	20	5.00	0.00
TAYD	20	20	20.00	0.00
TAYD	40	20	25.00	0.00
TAYD	80	20	0.00	0.00
TAYD	160	20	0.00	0.00
TAYD	320	20	0.00	0.00
TAYD	10	40	25.00	0.00
TAYD	20	40	25.00	0.00
TAYD	40	40	40.00	0.00
TAYD	80	40	0.00	0.00
TAYD	160	40	0.00	0.00
TAYD	320	40	0.00	0.00
TAYD	10	80	0.00	0.00
TAYD	20	80	0.00	0.00
TAYD	40	80	0.00	0.00
TAYD	80	80	0.00	0.00
TAYD	160	80	0.00	0.00
TAYD	320	80	0.00	0.00
TAYD	10	160	0.00	0.00
TAYD	20	160	0.00	0.00
TAYD	40	160	0.00	0.00
TAYD	80	160	0.00	0.00
TAYD	160	160	0.00	0.00
TAYD	320	160	0.00	0.00
TAYD	10	320	0.00	0.00
TAYD	20	320	0.00	0.00
TAYD	40	320	0.00	0.00
TAYD	80	320	0.00	0.00
TAYD	160	320	0.00	0.00
TAYD	320	320	0.00	0.00
TAYD	10	640	0.00	0.00
TAYD	20	640	0.00	0.00
TAYD	40	640	0.00	0.00
TAYD	80	640	0.00	0.00
TAYD	160	640	0.00	0.00
TAYD	320	640	0.00	0.00
TAYD	10	1280	0.00	0.00
TAYD	20	1280	0.00	0.00
TAYD	40	1280	0.00	0.00
TAYD	80	1280	0.00	0.00
TAYD	160	1280	0.00	0.00
TAYD	320	1280	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
TAYD	10	20000	19.74	19.74
TAYD	20	20000	20.06	20.06
TAYD	40	20000	19.42	19.42
TAYD	80	20000	19.59	19.59
TAYD	160	20000	19.30	19.30
TAYD	320	20000	16.28	16.28
TAYD	20000	20000	14.93	14.93
UNA	10	10	0.00	0.00
UNA	20	10	0.00	11.74
UNA	40	10	10.00	27.46
UNA	80	10	18.32	18.32
UNA	160	10	7.05	7.05
UNA	320	10	7.60	7.60
UNA	10	20	0.00	0.00
UNA	20	20	0.00	13.88
UNA	40	20	10.00	29.09
UNA	80	20	22.10	22.10
UNA	160	20	9.26	9.26
UNA	320	20	9.64	9.64
UNA	10	40	10.00	9.28
UNA	20	40	10.00	26.33
UNA	40	40	20.00	40.10
UNA	80	40	37.83	37.83
UNA	160	40	21.95	21.95
UNA	320	40	22.14	22.14
UNA	10	80	82.20	82.20
UNA	20	80	84.64	84.64
UNA	40	80	87.42	87.42
UNA	80	80	86.90	86.90
UNA	160	80	76.96	76.96
UNA	320	80	77.36	77.36
UNA	10	160	82.00	82.00
UNA	20	160	83.14	83.14
UNA	40	160	83.74	83.74
UNA	80	160	76.83	76.83
UNA	160	160	61.59	61.59
UNA	320	160	61.80	61.80
UNA	10	320	61.05	61.05
UNA	20	320	61.68	61.68
UNA	40	320	61.59	61.59
UNA	80	320	55.82	55.82
UNA	160	320	40.13	40.13
UNA	320	320	27.10	27.10
UNA	10	640	43.41	43.41
UNA	20	640	43.53	43.53
UNA	40	640	44.24	44.24
UNA	80	640	42.64	42.64

Site	buffer width	distance	GT Forest	Forest
UNA	160	640	32.41	32.41
UNA	320	640	27.05	27.05
UNA	10	1280	29.77	29.77
UNA	20	1280	29.30	29.30
UNA	40	1280	28.78	28.78
UNA	80	1280	26.29	26.29
UNA	160	1280	18.67	18.67
UNA	320	1280	13.94	13.94
UNA	10	20000	29.73	29.73
UNA	20	20000	29.26	29.26
UNA	40	20000	28.74	28.74
UNA	80	20000	26.25	26.25
UNA	160	20000	18.66	18.66
UNA	320	20000	13.94	13.94
UNA	20000	20000	6.00	6.00
VOY	10	10	0.00	0.00
VOY	20	10	0.00	0.00
VOY	40	10	0.00	0.00
VOY	80	10	0.00	0.00
VOY	160	10	0.00	0.00
VOY	320	10	0.00	0.00
VOY	10	20	0.00	0.00
VOY	20	20	0.00	0.00
VOY	40	20	0.00	0.00
VOY	80	20	0.00	0.00
VOY	160	20	0.00	0.00
VOY	320	20	0.00	0.00
VOY	10	40	0.00	0.00
VOY	20	40	0.00	0.00
VOY	40	40	0.00	0.00
VOY	80	40	0.00	0.00
VOY	160	40	0.00	0.00
VOY	320	40	0.00	0.00
VOY	10	80	0.00	0.00
VOY	20	80	0.00	0.00
VOY	40	80	0.00	0.00
VOY	80	80	0.00	0.00
VOY	160	80	0.00	0.00
VOY	320	80	0.00	0.00
VOY	10	160	0.00	0.00
VOY	20	160	0.00	0.00
VOY	40	160	0.00	0.00
VOY	80	160	0.00	0.00
VOY	160	160	10.47	10.47
VOY	320	160	6.89	6.89
VOY	10	320	0.00	0.00
VOY	20	320	0.00	0.00

Site	buffer width	distance	GT Forest	Forest
VOY	40	320	0.00	0.00
VOY	80	320	0.00	0.00
VOY	160	320	4.81	4.81
VOY	320	320	12.02	12.02
VOY	10	640	26.41	26.41
VOY	20	640	25.03	25.03
VOY	40	640	23.18	23.18
VOY	80	640	21.13	21.13
VOY	160	640	20.84	20.84
VOY	320	640	18.29	18.29
VOY	10	1280	70.83	70.83
VOY	20	1280	69.35	69.35
VOY	40	1280	67.88	67.88
VOY	80	1280	63.25	63.25
VOY	160	1280	54.31	54.31
VOY	320	1280	41.80	41.80
VOY	10	20000	83.19	83.19
VOY	20	20000	79.96	79.96
VOY	40	20000	71.58	71.58
VOY	80	20000	55.16	55.16
VOY	160	20000	38.94	38.94
VOY	320	20000	27.46	27.46
VOY	20000	20000	29.85	29.85
WAT	10	10	50.00	0.00
WAT	20	10	60.00	0.00
WAT	40	10	75.00	0.00
WAT	80	10	0.00	0.00
WAT	160	10	0.00	0.00
WAT	320	10	0.07	0.07
WAT	10	20	25.00	0.00
WAT	20	20	40.00	0.00
WAT	40	20	50.00	0.00
WAT	80	20	0.00	0.00
WAT	160	20	0.00	0.00
WAT	320	20	0.05	0.05
WAT	10	40	10.00	0.00
WAT	20	40	20.00	0.00
WAT	40	40	35.00	0.00
WAT	80	40	0.00	0.00
WAT	160	40	0.00	0.00
WAT	320	40	0.54	0.54
WAT	10	80	0.00	0.00
WAT	20	80	0.00	0.00
WAT	40	80	0.00	0.00
WAT	80	80	0.00	0.00
WAT	160	80	0.00	0.00
WAT	320	80	0.34	0.34

Site	buffer width	distance	GT Forest	Forest
WAT	10	160	0.00	0.00
WAT	20	160	0.00	0.00
WAT	40	160	0.00	0.00
WAT	80	160	0.00	0.00
WAT	160	160	0.00	0.00
WAT	320	160	0.26	0.26
WAT	10	320	0.00	0.00
WAT	20	320	0.00	0.00
WAT	40	320	0.00	0.00
WAT	80	320	0.00	0.00
WAT	160	320	0.00	0.00
WAT	320	320	0.16	0.16
WAT	10	640	0.00	0.00
WAT	20	640	0.00	0.00
WAT	40	640	0.00	0.00
WAT	80	640	0.00	0.00
WAT	160	640	0.00	0.00
WAT	320	640	0.09	0.09
WAT	10	1280	7.01	7.01
WAT	20	1280	7.12	7.12
WAT	40	1280	7.38	7.38
WAT	80	1280	5.34	5.34
WAT	160	1280	3.51	3.51
WAT	320	1280	8.19	8.19
WAT	10	20000	11.52	11.52
WAT	20	20000	11.33	11.33
WAT	40	20000	10.41	10.41
WAT	80	20000	7.40	7.40
WAT	160	20000	5.51	5.51
WAT	320	20000	9.25	9.25
WAT	20000	20000	13.85	13.85

Table 1.7 The range and coefficient of variation (CV) in percent forest cover at 55 scales (n = 38 sites) using ground truthed (GT) and digital (GIS) forest cover data. The correlation between percent forest cover at its largest scale (i.e. subcatchment) and the remaining 54 scales is also given as Pearson's *r*.

buffer width	buffer distance	Range in forest cover (GT)	Range in forest cover (GIS)	CV in forest cover (GIS)	CV in forest cover (GIS)	Correlation with subcatchment forest cover (GT)	Correlation with subcatchment forest cover (GIS)
10	10	0-100	0-100	126	132	0.38	0.33
20	10	0-100	0-100	122	122	0.38	0.38
40	10	0-100	0-100	120	113	0.40	0.32
80	10	0-100	0-100	122	122	0.47	0.47
160	10	0-100	0-100	128	128	0.54	0.54
320	10	0-100	0-100	134	134	0.65	0.65
10	20	0-100	0-100	127	131	0.39	0.45
20	20	0-100	0-100	121	119	0.40	0.47
40	20	0-100	0-100	120	110	0.42	0.42
80	20	0-100	0-100	122	122	0.48	0.48
160	20	0-100	0-100	128	128	0.55	0.55
320	20	0-100	0-100	134	134	0.66	0.66
10	40	0-100	0-100	119	117	0.37	0.46
20	40	0-100	0-100	115	117	0.36	0.53
40	40	0-100	0-100	113	104	0.37	0.39
80	40	0-100	0-100	115	115	0.46	0.46
160	40	0-100	0-100	121	121	0.55	0.55
320	40	0-100	0-100	128	128	0.65	0.65
10	80	0-100	0-100	107	107	0.31	0.31
20	80	0-100	0-100	105	105	0.31	0.31
40	80	0-100	0-100	103	103	0.33	0.33
80	80	0-100	0-100	105	105	0.41	0.41
160	80	0-100	0-100	108	108	0.52	0.52
320	80	0-100	0-100	117	117	0.57	0.57
10	160	0-100	0-100	96	96	0.31	0.31
20	160	0-100	0-100	94	94	0.30	0.30
40	160	0-100	0-100	92	92	0.31	0.31
80	160	0-100	0-100	94	94	0.43	0.43
160	160	0-100	0-100	100	100	0.52	0.52
320	160	0-100	0-100	107	107	0.60	0.60
10	320	0-100	0-100	91	91	0.36	0.36
20	320	0-100	0-100	86	86	0.38	0.38
40	320	0-100	0-100	82	82	0.42	0.42
80	320	0-100	0-100	83	83	0.52	0.52
160	320	0-100	0-100	90	90	0.62	0.62
320	320	0-100	0-100	97	97	0.71	0.71
10	640	0-100	0-100	74	74	0.45	0.45
20	640	0-100	0-100	71	71	0.47	0.47

buffer width	buffer distance	Range in forest cover (GT)	Range in forest cover (GIS)	CV in forest cover (GIS)	CV in forest cover (GIS)	Correlation with subcatchment forest cover (GT)	Correlation with subcatchment forest cover (GIS)
40	640	0-100	0-100	69	69	0.52	0.52
80	640	0-100	0-100	72	72	0.63	0.63
160	640	0-100	0-100	82	82	0.72	0.72
320	640	0-100	0-100	91	91	0.77	0.77
10	1280	0-100	0-100	71	71	0.44	0.44
20	1280	0-100	0-100	69	69	0.48	0.48
40	1280	0-98	0-98	68	68	0.53	0.53
80	1280	0-98	0-98	71	71	0.64	0.64
160	1280	0-99	0-99	79	79	0.75	0.75
320	1280	0-98	0-98	85	85	0.83	0.83
10	riparian	12--90	12--90	43	43	0.68	0.68
20	riparian	11--93	11--93	44	44	0.73	0.73
40	riparian	10--96	10--96	45	45	0.79	0.79
80	riparian	7--98	7--98	49	49	0.92	0.92
160	riparian	6--98	6--98	55	55	0.96	0.96
320	riparian	9--99	9--99	60	60	0.99	0.99
subcatchment		6--96	6--96	59	59	n/a	n/a

Table A.8. Results from principal components analysis which reduced log (base 10) - transformed water quality and physical parameters into 3 components (n = 38 sites). Water quality parameters included: alkalinity (mg L^{-1}), chloride ions (Cl^-), dissolved organic carbon (DOC, mg L^{-1}), $NO_3 + NO_2$ (NO_x mg L^{-1}), total kjeldahl nitrogen (TKN, mg L^{-1}), sulfate ions (SO_4, mg L^{-1}), conductivity (μs L^{-1}), total phosphorus (TP, mg L^{-1}), total nitrogen (TN, mg L^{-1}), pH, water velocity (meters second $^{-1}$), and temperature (temp., ° C).

Parameter	Factor1	Factor2	Factor3
conductivity	0.94	0.22	0.10
alkalinity	0.94	0.06	-0.01
Cl^-	0.92	0.26	0.06
pH	0.84	0.04	-0.25
TN	0.80	-0.20	0.25
NO_x	0.65	0.48	0.08
SO_4	0.63	0.47	-0.09
TKN	0.60	-0.71	0.15
TP	0.53	-0.46	0.45
temp.	0.46	-0.26	-0.70
DOC	0.22	-0.85	-0.17
velocity	0.14	-0.02	-0.71

Appendix B. Site and Production Data used in Chapter 2

Table 2.1. Name and location of 10 streams where invertebrate production was measured in chapter 2. Station codes are given for sites that were also routinely monitored for water quality by the Regional Municipality of Ontario and Carleton and the City of Waterloo.

Station	Region	lattitude	longitude	Name	Location
CK18-Q	Ottawa	45.38999	-75.67619	Sawmill Downstream	Riverside Drive west bound lane (downstream);near Harvey's restaurant
CK24-002	Ottawa	45.492664	-75.47075	Leonard/Cardinal Creek	Queen Street (RR#34)
CK42-07	Ottawa	45.089755	-75.79119	Steven Creek	Roger Stevens Road (RR#6), as it exits the Marlborough Forest (approx.2km west of Malakoff Road)
CK44-02	Ottawa	44.98498	-75.80118	Brassil's Creek	Dywer Hill Road, near Donnelly Road
C2	Waterloo	43.629	-80.011	Black Creek	First concession, upstream of Limehouse
G1	Waterloo	43.343	-80.532	Alder Creek	first concession S of New Dundee
G21	Waterloo	43.894	-80.3	Grand River	East Luther and Amaranth Township line
G4	Waterloo	43.616	-80.56	Canagagigue Creek	first concession N of Elmira
T1	Waterloo	43.365	-81.018	Avon River	Lorne Avenue, Stratford
T5	Waterloo	43.044	-80.82	Folden's Creek	Concession Road No. 3 West Oxford Township

Table 2.2. Benthic invertebrate production (mg m^{-2} day^{-1}) per cobble for 5-6 replicates at 10 streams in Ottawa and Waterloo regions, where P is production obtained using standard processing techniques, P coarse is production obtained from coarse-sieve methods, and P sum sieve is production obtained from sieve-fractionated techniques for processing benthic samples as described in chapter 2.

Station	Replicate	P	P Coarse	P Sum Sieve
CK24-002	1	98.94	91.10	132.17
CK24-002	2	24.94	23.71	33.55
CK24-002	3	37.17	27.42	47.47
CK24-002	4	52.77	53.19	66.49
CK24-002	5	225.78	225.47	275.96
CK24-002	6	210.27	184.51	254.14
CK18-Q	1	16.96	25.64	19.77
CK18-Q	3	6.76	4.69	7.42
CK18-Q	4	10.03	15.39	12.38
CK18-Q	5	5.48	4.71	6.08
CK18-Q	6	13.99	14.92	17.04
CK44-02	1	105.92	86.88	120.24
CK44-02	2	68.61	74.17	75.03
CK44-02	3	17.15	21.53	19.36
CK44-02	4	10.08	14.66	12.10
CK44-02	5	16.38	13.31	18.12
CK44-02	6	5.97	5.23	6.62
CK42-07	1	4.85	8.30	5.29
CK42-07	2	5.20	7.91	5.88
CK42-07	3	20.58	24.30	21.04
CK42-07	4	4.57	5.65	5.12
CK42-07	5	10.77	8.58	12.92
CK42-07	6	10.55	8.74	11.81
G4	6	51.70	57.27	57.45
G4	5	39.84	44.86	42.36
G4	4	265.59	214.73	301.44
G4	1	168.78	186.46	195.59
G4	3	635.37	677.36	758.24
T1	2	116.04	185.47	137.60
T1	3	62.93	68.31	70.82
T1	1	134.32	164.52	167.95
T1	5	193.88	250.74	244.39
T1	4	117.14	166.70	143.99
T1	6	165.90	218.60	213.89
C2	5	121.84	139.82	143.81
C2	3	232.35	236.71	281.11

Station	Replicate	P	P Coarse	P Sum Sieve
C2	1	40.59	27.12	43.48
C2	6	147.76	105.02	163.17
C2	4	134.70	90.68	153.13
C2	2	61.88	32.86	68.84
G21	5	69.04	48.49	83.21
G21	3	124.13	133.86	171.46
G21	2	51.31	55.95	58.34
G21	4	64.04	66.51	78.29
G21	1	27.96	18.46	32.64
G21	6	102.94	76.69	120.90
G1	6	196.46	233.38	221.85
G1	3	121.38	144.71	151.35
G1	2	102.21	124.28	124.81
G1	4	265.59	312.05	315.16
G1	5	237.72	292.91	272.01
T5	2	48.29	28.72	54.09
G1	1	483.06	505.22	581.18
T5	5	61.24	65.98	73.05
T5	4	39.08	36.38	46.36
T5	3	110.49	60.95	123.33
T5	6	5.02	3.83	5.50

Appendix C. Site, Production, Total Nitrogen, and Total Phosphorus Data used in Chapter 3

Table 3.1 . Daily production (mg m^{-2} day^{-1}) of periphyton (PP) and invertebrates (PP) per cobble at 12 sites in the National Capital Region throughout the growing season as explained in chapter 3.

Site	Date	Replicate	PP	IP
BLA	12-May-02	1	26.49	8.15
BLA	12-May-02	2	25.97	6.38
BLA	12-May-02	3	56.01	7.32
BLA	12-May-02	4	10.41	
BLA	12-May-02	5	29.76	
BLA	12-May-02	6	33.07	
BLA	12-Jun-02	1	66.65	0.00
BLA	12-Jun-02	2	88.70	0.00
BLA	12-Jun-02	3	50.14	0.00
BLA	12-Jun-02	4	64.99	
BLA	12-Jun-02	5	55.50	
BLA	12-Jun-02	6	102.65	
BLA	10-Jul-02	1	38.81	2.09
BLA	10-Jul-02	2	17.48	7.39
BLA	10-Jul-02	3	45.30	20.75
BLA	10-Jul-02	4	52.52	
BLA	10-Jul-02	5	31.96	
BLA	10-Jul-02	6	14.56	
BLA	12-Aug-02	1	20.41	31.87
BLA	12-Aug-02	2	18.10	10.42
BLA	12-Aug-02	3	34.95	4.89
BLA	12-Aug-02	4	16.02	
BLA	12-Aug-02	5	15.66	
BLA	12-Aug-02	6	12.56	
BLA	08-Oct-02	1	12.67	4.34
BLA	08-Oct-02	2	7.04	0.45
BLA	08-Oct-02	3	12.39	1.05
BLA	08-Oct-02	4	7.59	
BLA	08-Oct-02	5	11.58	
BLA	08-Oct-02	6	0.87	
CHE	15-May-02	1	30.77	2.82
CHE	15-May-02	2	42.65	4.82
CHE	15-May-02	3	26.28	2.93
CHE	15-May-02	4	28.84	
CHE	15-May-02	5	30.60	
CHE	15-May-02	6	17.12	
CHE	15-Jun-02	1	41.81	8.30
CHE	15-Jun-02	2	81.65	9.63
CHE	15-Jun-02	3	45.47	
CHE	15-Jun-02	4	11.72	

Site	Date	Replicate	PP	IP
CHE	15-Jun-02	5	37.40	
CHE	15-Jun-02	6	64.88	
CHE	08-Jul-02	1	58.76	20.28
CHE	08-Jul-02	2	52.17	35.77
CHE	08-Jul-02	3	72.14	6.17
CHE	08-Jul-02	4	69.35	
CHE	08-Jul-02	5	80.93	
CHE	08-Jul-02	6	64.23	
CHE	13-Aug-02	1	75.63	2.50
CHE	13-Aug-02	2	135.93	37.93
CHE	13-Aug-02	3	80.15	11.51
CHE	13-Aug-02	4	56.02	
CHE	13-Aug-02	5	113.28	
CHE	13-Aug-02	6	122.76	
CHE	01-Oct-02	1	47.94	4.41
CHE	01-Oct-02	2	31.14	1.78
CHE	01-Oct-02	3	48.62	8.12
CHE	01-Oct-02	4	369.58	
CHE	01-Oct-02	5	56.28	
CHE	01-Oct-02	6	41.11	
COR	12-May-02	1	43.76	0.41
COR	12-May-02	2	15.09	1.62
COR	12-May-02	3	8.34	6.56
COR	12-May-02	4	29.50	
COR	12-May-02	5	28.57	
COR	12-May-02	6	25.98	
COR	12-Jun-02	1	70.57	13.70
COR	12-Jun-02	2	51.95	0.00
COR	12-Jun-02	3	27.15	4.03
COR	12-Jun-02	4	103.06	
COR	12-Jun-02	5	70.36	
COR	12-Jun-02	6	91.74	
COR	08-Jul-02	1	37.89	27.04
COR	08-Jul-02	2	97.77	38.16
COR	08-Jul-02	3	51.00	14.10
COR	08-Jul-02	4	37.02	
COR	08-Jul-02	5	41.01	
COR	08-Jul-02	6	37.88	
COR	12-Aug-02	1	134.02	42.16
COR	12-Aug-02	2	120.59	62.74
COR	12-Aug-02	3	99.25	31.78
COR	12-Aug-02	4	64.42	
COR	12-Aug-02	5	88.32	
COR	12-Aug-02	6	57.96	
COR	08-Oct-02	1	33.70	9.58
COR	08-Oct-02	2	31.15	5.36
COR	08-Oct-02	3	42.88	10.08

Site	Date	Replicate	PP	IP
COR	08-Oct-02	4	66.63	
COR	08-Oct-02	5	28.45	
COR	08-Oct-02	6	36.88	
HAR	18-May-02	1	91.69	56.03
HAR	18-May-02	2	56.94	13.90
HAR	18-May-02	3	36.79	32.64
HAR	18-May-02	4	100.10	
HAR	18-May-02	5	38.21	
HAR	18-May-02	6	111.90	
HAR	10-Jun-02	1	97.87	52.73
HAR	10-Jun-02	2	124.45	168.46
HAR	10-Jun-02	3	93.43	78.12
HAR	10-Jun-02	4	113.74	
HAR	10-Jun-02	5	175.63	
HAR	10-Jun-02	6	141.77	
HAR	16-Jul-02	1	356.14	349.84
HAR	16-Jul-02	2	307.64	185.13
HAR	16-Jul-02	3	210.25	727.95
HAR	16-Jul-02	4	443.88	1213.63
HAR	16-Jul-02	5	190.34	629.60
HAR	16-Jul-02	6	152.91	
HAR	15-Aug-02	1	394.99	330.29
HAR	15-Aug-02	2	381.83	28.00
HAR	15-Aug-02	3	1308.35	10.65
HAR	15-Aug-02	4	674.45	
HAR	15-Aug-02	5	684.82	
HAR	15-Aug-02	6	497.77	40.81
HAR	05-Oct-02	1	72.95	90.89
HAR	05-Oct-02	2	201.30	0.56
HAR	05-Oct-02	3	129.32	12.09
HAR	05-Oct-02	4	152.29	
HAR	05-Oct-02	5	124.10	
HAR	05-Oct-02	6	200.17	
LAP	12-May-02	1	30.28	5.01
LAP	12-May-02	2	36.01	5.25
LAP	12-May-02	3	49.56	16.12
LAP	12-May-02	4	25.49	
LAP	12-May-02	5	41.71	
LAP	12-May-02	6	31.44	
LAP	12-Jun-02	1	123.41	25.77
LAP	12-Jun-02	2	99.82	9.32
LAP	12-Jun-02	3	142.38	20.07
LAP	12-Jun-02	4	226.27	
LAP	12-Jun-02	5	219.20	
LAP	12-Jun-02	6	57.21	
LAP	10-Jul-02	1	191.34	12.68
LAP	10-Jul-02	2	121.76	42.99

Site	Date	Replicate	PP	IP
LAP	10-Jul-02	3	153.23	10.72
LAP	10-Jul-02	4	262.25	
LAP	10-Jul-02	5	221.45	
LAP	10-Jul-02	6	228.11	
LAP	13-Aug-02	1	124.07	21.78
LAP	13-Aug-02	2	128.30	4.10
LAP	13-Aug-02	3	127.02	10.62
LAP	13-Aug-02	4	87.42	
LAP	13-Aug-02	5	118.81	
LAP	13-Aug-02	6	99.08	
LAP	08-Oct-02	1	74.82	4.60
LAP	08-Oct-02	2	103.83	8.97
LAP	08-Oct-02	3	79.59	1.72
LAP	08-Oct-02	4	58.23	
LAP	08-Oct-02	5	67.62	
LAP	08-Oct-02	6	70.36	
LDS	15-May-02	1	128.28	13.86
LDS	15-May-02	2	155.31	2.02
LDS	15-May-02	3	140.09	13.21
LDS	15-May-02	4	47.65	
LDS	15-May-02	5	75.97	
LDS	15-May-02	6	74.34	
LDS	15-Jun-02	1	57.17	1.42
LDS	15-Jun-02	2	157.54	2.97
LDS	15-Jun-02	3	99.33	1.02
LDS	15-Jun-02	4	28.09	
LDS	15-Jun-02	5	161.02	
LDS	15-Jun-02	6	83.59	
LDS	10-Jul-02	1	379.15	36.05
LDS	10-Jul-02	2	376.59	138.56
LDS	10-Jul-02	3	432.78	78.07
LDS	10-Jul-02	4	388.00	
LDS	10-Jul-02	5	289.01	
LDS	10-Jul-02	6	381.58	
LDS	13-Aug-02	1	449.00	5.52
LDS	13-Aug-02	2	423.32	25.13
LDS	13-Aug-02	3	768.57	34.17
LDS	13-Aug-02	4	487.58	
LDS	13-Aug-02	5	519.30	
LDS	13-Aug-02	6	779.98	
LDS	01-Oct-02	1	183.90	19.54
LDS	01-Oct-02	2	115.91	9.79
LDS	01-Oct-02	3	163.17	53.53
LDS	01-Oct-02	4	181.48	
LDS	01-Oct-02	5	159.89	
LDS	01-Oct-02	6	137.19	
LMS	17-May-02	1	57.63	0.44

Site	Date	Replicate	PP	IP
LMS	17-May-02	2	46.02	0.27
LMS	17-May-02	3	47.83	0.25
LMS	17-May-02	4	46.71	
LMS	17-May-02	5	39.53	
LMS	17-May-02	6	35.91	
LMS	17-Jun-02	1	55.51	1.09
LMS	17-Jun-02	2	9.63	0.00
LMS	17-Jun-02	3	19.25	1.34
LMS	17-Jun-02	4	9.45	
LMS	17-Jun-02	5	47.29	
LMS	17-Jun-02	6	33.84	
LMS	10-Jul-02	1	295.82	52.22
LMS	10-Jul-02	2	185.64	16.15
LMS	10-Jul-02	3	282.23	24.66
LMS	10-Jul-02	4	238.60	
LMS	10-Jul-02	5	369.88	
LMS	10-Jul-02	6	316.11	
LMS	13-Aug-02	1	324.23	15.03
LMS	13-Aug-02	2	328.78	32.28
LMS	13-Aug-02	3	401.22	103.86
LMS	13-Aug-02	4	225.32	
LMS	13-Aug-02	5	242.35	
LMS	13-Aug-02	6	361.31	
LMS	02-Oct-02	1	84.25	2.59
LMS	02-Oct-02	2	100.78	1.19
LMS	02-Oct-02	3	94.48	12.91
LMS	02-Oct-02	4	117.23	
LMS	02-Oct-02	5	165.18	
LMS	02-Oct-02	6	125.41	
MOS	08-May-02	1	150.88	61.02
MOS	08-May-02	2	299.71	76.88
MOS	08-May-02	3	191.02	81.26
MOS	08-May-02	4	239.28	
MOS	08-May-02	5	193.58	
MOS	08-May-02	6	262.06	
MOS	12-Jun-02	1	180.02	55.93
MOS	12-Jun-02	2	195.35	13.29
MOS	12-Jun-02	3	163.26	39.75
MOS	12-Jun-02	4	246.03	
MOS	12-Jun-02	5	140.90	
MOS	12-Jun-02	6	234.11	
MOS	15-Jul-02	1	400.81	197.98
MOS	15-Jul-02	2	212.91	242.62
MOS	15-Jul-02	3	332.27	73.50
MOS	15-Jul-02	4	377.34	
MOS	15-Jul-02	5	336.11	
MOS	15-Jul-02	6	369.31	

Site	Date	Replicate	PP	IP
MOS	14-Aug-02	1	222.58	81.86
MOS	14-Aug-02	2	162.54	92.88
MOS	14-Aug-02	3	141.23	34.79
MOS	14-Aug-02	4	178.83	
MOS	14-Aug-02	5	319.23	
MOS	14-Aug-02	6	208.70	
MOS	07-Oct-02	1	54.16	109.84
MOS	07-Oct-02	2	26.29	8.33
MOS	07-Oct-02	3	85.29	40.75
MOS	07-Oct-02	4	68.30	
MOS	07-Oct-02	5	60.85	
MOS	07-Oct-02	6	43.48	
POO	18-May-02	1	77.66	4.55
POO	18-May-02	2	124.00	13.94
POO	18-May-02	3	54.67	10.22
POO	18-May-02	4	96.94	
POO	18-May-02	5	72.10	
POO	18-May-02	6	111.75	
POO	10-Jun-02	1	195.88	17.54
POO	10-Jun-02	2	258.51	17.20
POO	10-Jun-02	3	238.98	12.70
POO	10-Jun-02	4	237.01	
POO	10-Jun-02	5	159.30	
POO	10-Jun-02	6	205.22	
POO	29-Aug-02	1	273.30	21.81
POO	29-Aug-02	2	406.77	12.46
POO	29-Aug-02	3	136.58	84.68
POO	29-Aug-02	4	286.81	
POO	29-Aug-02	5	232.46	86.32
POO	29-Aug-02	6	195.28	209.54
POO	02-Oct-02	1	204.91	20.52
POO	02-Oct-02	2	230.85	38.54
POO	02-Oct-02	3	107.39	7.14
POO	02-Oct-02	4	182.40	
POO	02-Oct-02	5	205.62	
POO	02-Oct-02	6	89.48	
SAWD	08-May-02	1	306.05	17.12
SAWD	08-May-02	2	161.59	27.24
SAWD	08-May-02	3	155.51	32.68
SAWD	08-May-02	4	213.46	
SAWD	08-May-02	5	165.30	
SAWD	08-May-02	6	160.51	
SAWD	10-Jun-02	1	320.68	55.40
SAWD	10-Jun-02	2	244.89	60.29
SAWD	10-Jun-02	3	177.01	81.23
SAWD	10-Jun-02	4	270.79	
SAWD	10-Jun-02	5	166.50	

Site	Date	Replicate	PP	IP
SAWD	10-Jun-02	6	267.87	
SAWD	11-Jul-02	1	189.61	17.88
SAWD	11-Jul-02	2	129.21	10.98
SAWD	11-Jul-02	3	126.87	17.31
SAWD	11-Jul-02	4	128.37	
SAWD	11-Jul-02	5	132.21	
SAWD	11-Jul-02	6	106.09	
SAWD	29-Aug-02	1	444.74	11.21
SAWD	29-Aug-02	2	325.76	14.72
SAWD	29-Aug-02	3	215.47	5.26
SAWD	29-Aug-02	4	330.20	
SAWD	29-Aug-02	5	336.61	
SAWD	29-Aug-02	6	373.80	
SAWD	29-Sep-02	1	106.53	45.95
SAWD	29-Sep-02	2	141.33	36.54
SAWD	29-Sep-02	3	119.52	56.08
SAWD	29-Sep-02	4	146.72	
SAWD	29-Sep-02	5	175.89	
SAWD	29-Sep-02	6	108.44	
SAWU	27-Jun-02	1	320.19	29.03
SAWU	27-Jun-02	2	126.64	16.52
SAWU	27-Jun-02	3	215.83	3.54
SAWU	27-Jun-02	4	173.17	
SAWU	27-Jun-02	5	111.00	
SAWU	27-Jun-02	6	135.67	
SAWU	15-Jul-02	1	334.56	130.93
SAWU	15-Jul-02	2	153.99	20.99
SAWU	15-Jul-02	3	284.27	61.80
SAWU	15-Jul-02	4	306.05	
SAWU	15-Jul-02	5	332.75	
SAWU	15-Jul-02	6	275.30	
SAWU	05-Oct-02	1	111.32	3.69
SAWU	05-Oct-02	2	222.17	1.82
SAWU	05-Oct-02	3	207.84	3.67
SAWU	05-Oct-02	4	272.56	
SAWU	05-Oct-02	5	261.05	
SAWU	05-Oct-02	6	231.81	
VOY	10-May-02	1	208.45	21.42
VOY	10-May-02	2	152.52	4.34
VOY	10-May-02	3	150.05	3.08
VOY	10-May-02	4	192.46	
VOY	10-May-02	5	231.26	
VOY	10-May-02	6	172.16	
VOY	10-Jun-02	1	306.60	81.71
VOY	10-Jun-02	2	506.55	106.04
VOY	10-Jun-02	3	268.91	24.24
VOY	10-Jun-02	4	290.97	

Site	Date	Replicate	PP	IP
VOY	10-Jun-02	5	199.59	
VOY	10-Jun-02	6	185.11	
VOY	09-Jul-02	1	701.10	80.28
VOY	09-Jul-02	2	315.27	120.67
VOY	09-Jul-02	3	293.77	136.86
VOY	09-Jul-02	4	318.90	
VOY	09-Jul-02	5	208.07	
VOY	09-Jul-02	6	260.04	
VOY	28-Aug-02	1	414.17	79.70
VOY	28-Aug-02	2	300.03	45.09
VOY	28-Aug-02	3	210.88	39.32
VOY	28-Aug-02	4	307.14	
VOY	28-Aug-02	5	276.17	
VOY	28-Aug-02	6	313.34	
VOY	29-Sep-02	1	245.05	53.78
VOY	29-Sep-02	2	98.21	17.52
VOY	29-Sep-02	3	230.97	43.91
VOY	29-Sep-02	4	106.84	
VOY	29-Sep-02	5	104.94	
VOY	29-Sep-02	6	158.37	

Table 3.2. Daily production (mg m^{-2} day^{-1}) of invertebrates (IP)within functional feeding groups (FFG) per cobble at 12 sites in the National Capital Region throughout the growing season as explained in chapter 3. FFG's included scrapers (SC), collector-gatherers (CG), collector-filterers (CF), shredders (SH), and predators (PR).

Site	Date	Replicate	FFG	IP
BLA	13-May-02	1	CG	0.46
BLA	13-May-02	1	CF	5.44
BLA	13-May-02	1	PR	0.96
BLA	13-May-02	1	SC	1.29
BLA	13-May-02	2	CG	0.58
BLA	13-May-02	2	CF	1.33
BLA	13-May-02	2	PR	1.42
BLA	13-May-02	2	SC	3.04
BLA	13-May-02	3	CF	6.33
BLA	13-May-02	3	none	0.00
BLA	13-May-02	3	SC	0.99
BLA	12-Jun-02	2	none	0.00
BLA	12-Jun-02	3	none	0.00
BLA	10-Jul-02	1	CG	0.41
BLA	10-Jul-02	1	PR	1.68
BLA	10-Jul-02	2	CG	1.13
BLA	10-Jul-02	2	CF	1.54
BLA	10-Jul-02	2	SC	4.71
BLA	10-Jul-02	3	CF	16.32
BLA	10-Jul-02	3	SC	4.43
BLA	12-Aug-02	1	CG	1.41
BLA	12-Aug-02	1	CF	1.75
BLA	12-Aug-02	1	PR	28.70
BLA	12-Aug-02	2	CG	2.07
BLA	12-Aug-02	2	CF	1.58
BLA	12-Aug-02	2	PR	0.81
BLA	12-Aug-02	2	SC	5.96
BLA	12-Aug-02	3	CG	1.59
BLA	12-Aug-02	3	CF	1.30
BLA	12-Aug-02	3	SC	2.00
BLA	08-Oct-02	1	SC	4.34
BLA	08-Oct-02	2	CG	0.45
BLA	08-Oct-02	3	CF	1.05
CHE	15-May-02	1	CG	0.29
CHE	15-May-02	1	SC	2.53
CHE	15-May-02	2	CG	0.70
CHE	15-May-02	2	CF	2.21
CHE	15-May-02	2	PR	0.15

Site	Date	Replicate	FFG	IP
CHE	15-May-02	2	SC	1.75
CHE	15-May-02	3	CG	1.45
CHE	15-May-02	3	SC	1.48
CHE	14-Jun-02	1	CG	2.21
CHE	14-Jun-02	1	CF	0.72
CHE	14-Jun-02	1	PR	1.07
CHE	14-Jun-02	1	SC	4.29
CHE	14-Jun-02	2	CG	1.16
CHE	14-Jun-02	2	SC	8.47
CHE	08-Jul-02	1	CG	6.58
CHE	08-Jul-02	1	CF	4.92
CHE	08-Jul-02	1	SC	7.76
CHE	08-Jul-02	1	SH	1.03
CHE	08-Jul-02	2	CG	4.33
CHE	08-Jul-02	2	CF	29.46
CHE	08-Jul-02	2	SC	1.98
CHE	08-Jul-02	3	SC	4.57
CHE	08-Jul-02	3	SH	1.60
CHE	13-Aug-02	1	CG	0.45
CHE	13-Aug-02	1	SC	2.04
CHE	13-Aug-02	2	CG	3.43
CHE	13-Aug-02	2	CF	33.71
CHE	13-Aug-02	2	SC	0.79
CHE	13-Aug-02	3	CG	3.85
CHE	13-Aug-02	3	CF	2.40
CHE	13-Aug-02	3	PR	5.25
CHE	01-Oct-02	1	CG	1.97
CHE	01-Oct-02	1	PR	0.19
CHE	01-Oct-02	1	SC	0.72
CHE	01-Oct-02	1	SH	1.53
CHE	01-Oct-02	2	CG	0.50
CHE	01-Oct-02	2	SC	0.97
CHE	01-Oct-02	2	SH	0.31
CHE	01-Oct-02	3	CG	1.06
CHE	01-Oct-02	3	CF	1.09
CHE	01-Oct-02	3	PR	0.40
CHE	01-Oct-02	3	SC	2.78
CHE	01-Oct-02	3	SH	2.79
COR	13-May-02	1	SC	0.41
COR	13-May-02	2	CF	0.88
COR	13-May-02	2	SC	0.74
COR	13-May-02	3	SC	6.56
COR	12-Jun-02	1	CG	1.70
COR	12-Jun-02	1	CF	6.84
COR	12-Jun-02	1	SC	5.16
COR	12-Jun-02	2	none	0.00
COR	12-Jun-02	3	SC	4.03

Site	Date	Replicate	FFG	IP
COR	08-Jul-02	1	CG	12.52
COR	08-Jul-02	1	CF	6.92
COR	08-Jul-02	1	PR	1.60
COR	08-Jul-02	1	SC	5.99
COR	08-Jul-02	2	CG	1.42
COR	08-Jul-02	2	CF	23.15
COR	08-Jul-02	2	PR	5.13
COR	08-Jul-02	2	SC	8.45
COR	08-Jul-02	3	CG	0.35
COR	08-Jul-02	3	CF	5.60
COR	08-Jul-02	3	SC	8.15
COR	12-Aug-02	1	CG	2.04
COR	12-Aug-02	1	CF	0.77
COR	12-Aug-02	1	PR	1.70
COR	12-Aug-02	1	SC	37.65
COR	12-Aug-02	2	CG	3.88
COR	12-Aug-02	2	PR	2.91
COR	12-Aug-02	2	SC	55.96
COR	12-Aug-02	3	CF	11.56
COR	12-Aug-02	3	SC	20.22
COR	08-Oct-02	1	CF	4.89
COR	08-Oct-02	1	SC	4.69
COR	08-Oct-02	2	CF	0.71
COR	08-Oct-02	2	SC	4.66
COR	08-Oct-02	3	CF	9.45
COR	08-Oct-02	3	SC	0.64
HAR	08-May-02	1	CF	0.47
HAR	08-May-02	1	PR	6.08
HAR	08-May-02	1	SC	28.13
HAR	08-May-02	1	SH	21.36
HAR	08-May-02	2	CF	0.28
HAR	08-May-02	2	SC	13.62
HAR	08-May-02	3	CF	11.52
HAR	08-May-02	3	PR	1.57
HAR	08-May-02	3	SC	10.82
HAR	08-May-02	3	SH	8.73
HAR	10-Jun-02	1	CF	1.42
HAR	10-Jun-02	1	SC	51.31
HAR	10-Jun-02	2	CG	2.02
HAR	10-Jun-02	2	SC	166.44
HAR	10-Jun-02	3	CG	5.36
HAR	10-Jun-02	3	CF	0.73
HAR	10-Jun-02	3	SC	72.03
HAR	16-Jul-02	1	CG	31.32
HAR	16-Jul-02	1	CF	271.34
HAR	16-Jul-02	1	PR	6.82
HAR	16-Jul-02	1	SC	40.36

Site	Date	Replicate	FFG	IP
HAR	16-Jul-02	2	CG	28.89
HAR	16-Jul-02	2	CF	67.85
HAR	16-Jul-02	2	PR	20.77
HAR	16-Jul-02	2	SC	66.76
HAR	16-Jul-02	2	SH	0.85
HAR	16-Jul-02	3	CG	90.67
HAR	16-Jul-02	3	CF	272.43
HAR	16-Jul-02	3	PR	39.79
HAR	16-Jul-02	3	SC	325.07
HAR	16-Jul-02	4	CG	154.74
HAR	16-Jul-02	4	CF	946.47
HAR	16-Jul-02	4	PR	36.19
HAR	16-Jul-02	4	SC	76.24
HAR	16-Jul-02	5	CG	168.73
HAR	16-Jul-02	5	CF	181.56
HAR	16-Jul-02	5	PR	24.09
HAR	16-Jul-02	5	SC	255.22
HAR	15-Aug-02	1	CG	155.17
HAR	15-Aug-02	1	CF	3.30
HAR	15-Aug-02	1	PR	125.00
HAR	15-Aug-02	1	SC	46.82
HAR	15-Aug-02	2	CG	26.16
HAR	15-Aug-02	2	PR	1.84
HAR	15-Aug-02	3	PR	10.65
HAR	15-Aug-02	6	CG	10.87
HAR	15-Aug-02	6	SC	29.95
HAR	05-Oct-02	1	CG	76.19
HAR	05-Oct-02	1	SC	7.46
HAR	05-Oct-02	1	SH	7.24
HAR	05-Oct-02	2	CG	0.56
HAR	05-Oct-02	3	CG	8.19
HAR	05-Oct-02	3	SC	2.06
HAR	05-Oct-02	3	SH	1.84
LAP	13-May-02	1	CG	0.20
LAP	13-May-02	1	CF	4.52
LAP	13-May-02	1	SC	0.28
LAP	13-May-02	2	CG	0.69
LAP	13-May-02	2	CF	1.25
LAP	13-May-02	2	SC	2.68
LAP	13-May-02	2	SH	0.63
LAP	13-May-02	3	CG	2.33
LAP	13-May-02	3	CF	10.25
LAP	13-May-02	3	SC	3.20
LAP	13-May-02	3	SH	0.34
LAP	13-Jun-02	1	CG	6.66
LAP	13-Jun-02	1	PR	0.99
LAP	13-Jun-02	1	SC	17.08

Site	Date	Replicate	FFG	IP
LAP	13-Jun-02	1	SH	1.04
LAP	13-Jun-02	2	CG	1.09
LAP	13-Jun-02	2	SC	8.23
LAP	13-Jun-02	3	CG	4.69
LAP	13-Jun-02	3	SC	15.38
LAP	10-Jul-02	1	CG	0.54
LAP	10-Jul-02	1	SC	12.14
LAP	10-Jul-02	2	CG	3.90
LAP	10-Jul-02	2	CF	15.97
LAP	10-Jul-02	2	PR	3.15
LAP	10-Jul-02	2	SC	16.40
LAP	10-Jul-02	2	SH	3.57
LAP	10-Jul-02	3	CG	0.76
LAP	10-Jul-02	3	PR	4.03
LAP	10-Jul-02	3	SC	5.93
LAP	13-Aug-02	1	CG	6.01
LAP	13-Aug-02	1	CF	5.57
LAP	13-Aug-02	1	PR	6.37
LAP	13-Aug-02	1	SC	3.84
LAP	13-Aug-02	2	CG	0.82
LAP	13-Aug-02	2	PR	1.32
LAP	13-Aug-02	2	SC	1.96
LAP	13-Aug-02	3	CG	0.52
LAP	13-Aug-02	3	PR	0.80
LAP	13-Aug-02	3	SC	9.31
LAP	08-Oct-02	1	CG	0.42
LAP	08-Oct-02	1	SC	4.18
LAP	08-Oct-02	2	CG	0.16
LAP	08-Oct-02	2	CF	1.54
LAP	08-Oct-02	2	PR	5.01
LAP	08-Oct-02	2	SC	2.26
LAP	08-Oct-02	3	CG	0.30
LAP	08-Oct-02	3	SC	0.94
LAP	08-Oct-02	3	SH	0.49
LDS	17-May-02	1	CG	6.44
LDS	17-May-02	1	CF	1.46
LDS	17-May-02	1	PR	0.58
LDS	17-May-02	1	SC	5.38
LDS	17-May-02	2	CG	0.12
LDS	17-May-02	2	SC	1.90
LDS	17-May-02	3	CG	4.21
LDS	17-May-02	3	CF	6.63
LDS	17-May-02	3	SC	2.37
LDS	13-Jun-02	1	SC	1.42
LDS	13-Jun-02	2	SC	2.97
LDS	13-Jun-02	3	SC	1.02
LDS	10-Jul-02	1	CF	5.59

Site	Date	Replicate	FFG	IP
LDS	10-Jul-02	1	PR	0.81
LDS	10-Jul-02	1	SC	29.65
LDS	10-Jul-02	2	CG	3.36
LDS	10-Jul-02	2	CF	34.34
LDS	10-Jul-02	2	PR	2.18
LDS	10-Jul-02	2	SC	96.86
LDS	10-Jul-02	2	SH	1.83
LDS	10-Jul-02	3	CG	4.81
LDS	10-Jul-02	3	CF	24.13
LDS	10-Jul-02	3	SC	46.77
LDS	10-Jul-02	3	SH	2.37
LDS	13-Aug-02	1	PR	5.52
LDS	13-Aug-02	2	CF	9.73
LDS	13-Aug-02	2	PR	5.40
LDS	13-Aug-02	2	SC	10.00
LDS	13-Aug-02	3	CG	0.69
LDS	13-Aug-02	3	CF	20.04
LDS	13-Aug-02	3	PR	6.78
LDS	13-Aug-02	3	SC	6.28
LDS	13-Aug-02	3	SH	0.37
LDS	01-Oct-02	1	CG	0.08
LDS	01-Oct-02	1	CF	18.67
LDS	01-Oct-02	1	PR	0.13
LDS	01-Oct-02	1	SH	0.65
LDS	01-Oct-02	2	CF	6.88
LDS	01-Oct-02	2	SC	2.91
LDS	01-Oct-02	3	CG	0.37
LDS	01-Oct-02	3	CF	53.16
LMS	17-May-02	1	SC	0.44
LMS	17-May-02	2	SC	0.27
LMS	17-May-02	3	SC	0.25
LMS	13-Jun-02	1	SC	1.09
LMS	13-Jun-02	2	none	0.00
LMS	13-Jun-02	3	SC	1.34
LMS	10-Jul-02	1	CG	1.56
LMS	10-Jul-02	1	CF	10.27
LMS	10-Jul-02	1	SC	40.38
LMS	10-Jul-02	2	CF	9.90
LMS	10-Jul-02	2	SC	4.92
LMS	10-Jul-02	2	SH	1.33
LMS	10-Jul-02	3	SC	23.16
LMS	10-Jul-02	3	SH	1.50
LMS	13-Aug-02	1	CF	4.24
LMS	13-Aug-02	1	SC	10.79
LMS	13-Aug-02	2	CG	1.95
LMS	13-Aug-02	2	CF	1.82
LMS	13-Aug-02	2	PR	0.68

Site	Date	Replicate	FFG	IP
LMS	13-Aug-02	2	SC	22.39
LMS	13-Aug-02	2	SH	5.42
LMS	13-Aug-02	3	CG	5.04
LMS	13-Aug-02	3	CF	23.06
LMS	13-Aug-02	3	PR	0.87
LMS	13-Aug-02	3	SC	73.43
LMS	13-Aug-02	3	SH	1.46
LMS	01-Oct-02	1	CF	0.59
LMS	01-Oct-02	1	SC	1.63
LMS	01-Oct-02	1	SH	0.37
LMS	01-Oct-02	2	CG	0.87
LMS	01-Oct-02	2	SC	0.32
LMS	01-Oct-02	3	CF	5.89
LMS	01-Oct-02	3	SC	7.02
MOS	08-May-02	1	CG	3.26
MOS	08-May-02	1	CF	17.29
MOS	08-May-02	1	PR	0.70
MOS	08-May-02	1	SC	39.77
MOS	08-May-02	2	CG	6.31
MOS	08-May-02	2	CF	42.00
MOS	08-May-02	2	SC	28.57
MOS	08-May-02	3	CG	3.30
MOS	08-May-02	3	CF	48.12
MOS	08-May-02	3	SC	29.59
MOS	08-May-02	3	SH	0.25
MOS	14-Jun-02	1	CG	5.23
MOS	14-Jun-02	1	CF	8.03
MOS	14-Jun-02	1	PR	12.06
MOS	14-Jun-02	1	SC	30.61
MOS	14-Jun-02	2	CG	0.28
MOS	14-Jun-02	2	SC	13.01
MOS	14-Jun-02	3	CG	3.25
MOS	14-Jun-02	3	CF	0.99
MOS	14-Jun-02	3	PR	2.25
MOS	14-Jun-02	3	SC	33.26
MOS	15-Jul-02	1	CG	19.01
MOS	15-Jul-02	1	CF	155.45
MOS	15-Jul-02	1	PR	0.19
MOS	15-Jul-02	1	SC	22.81
MOS	15-Jul-02	1	SH	0.52
MOS	15-Jul-02	2	CG	24.55
MOS	15-Jul-02	2	CF	150.91
MOS	15-Jul-02	2	SC	63.22
MOS	15-Jul-02	2	SH	3.93
MOS	15-Jul-02	3	CG	23.10
MOS	15-Jul-02	3	CF	8.07
MOS	15-Jul-02	3	PR	0.52

Site	Date	Replicate	FFG	IP
MOS	15-Jul-02	3	SC	40.61
MOS	15-Jul-02	3	SH	1.20
MOS	14-Aug-02	1	CG	25.75
MOS	14-Aug-02	1	SC	56.11
MOS	14-Aug-02	2	CG	21.00
MOS	14-Aug-02	2	SC	71.88
MOS	14-Aug-02	3	CG	4.21
MOS	14-Aug-02	3	SC	30.58
MOS	07-Oct-02	1	CG	11.91
MOS	07-Oct-02	1	CF	4.79
MOS	07-Oct-02	1	PR	0.17
MOS	07-Oct-02	1	SC	92.69
MOS	07-Oct-02	1	SH	0.29
MOS	07-Oct-02	2	CG	2.15
MOS	07-Oct-02	2	SC	6.18
MOS	07-Oct-02	3	CG	5.85
MOS	07-Oct-02	3	CF	3.24
MOS	07-Oct-02	3	PR	0.77
MOS	07-Oct-02	3	SC	30.62
MOS	07-Oct-02	3	SH	0.26
POO	18-May-02	1	CG	0.37
POO	18-May-02	1	PA	0.10
POO	18-May-02	1	SC	4.07
POO	18-May-02	2	CG	4.00
POO	18-May-02	2	CF	0.31
POO	18-May-02	2	SC	9.63
POO	18-May-02	3	CG	3.59
POO	18-May-02	3	CF	5.06
POO	18-May-02	3	SC	1.27
POO	18-May-02	3	SH	0.29
POO	10-Jun-02	1	CG	13.41
POO	10-Jun-02	1	SC	2.51
POO	10-Jun-02	1	SH	1.62
POO	10-Jun-02	2	CG	9.96
POO	10-Jun-02	2	SC	7.23
POO	10-Jun-02	3	CG	12.11
POO	10-Jun-02	3	SC	0.59
POO	29-Aug-02	1	CG	7.40
POO	29-Aug-02	1	CF	2.54
POO	29-Aug-02	1	PA	0.29
POO	29-Aug-02	1	SC	11.58
POO	29-Aug-02	2	CG	9.46
POO	29-Aug-02	2	SC	3.00
POO	29-Aug-02	3	CG	72.12
POO	29-Aug-02	3	SC	12.56
POO	29-Aug-02	5	CG	62.75
POO	29-Aug-02	5	SC	23.57

Site	Date	Replicate	FFG	IP
POO	29-Aug-02	6	CG	190.26
POO	29-Aug-02	6	SC	16.91
POO	29-Aug-02	6	SH	2.37
POO	04-Oct-02	1	CG	16.48
POO	04-Oct-02	1	CF	1.72
POO	04-Oct-02	1	SC	2.32
POO	04-Oct-02	2	CG	35.97
POO	04-Oct-02	2	CF	0.51
POO	04-Oct-02	2	SC	2.07
POO	04-Oct-02	3	CG	4.86
POO	04-Oct-02	3	CF	2.28
SAWD	08-May-02	1	CG	1.96
SAWD	08-May-02	1	CF	9.48
SAWD	08-May-02	1	PA	0.67
SAWD	08-May-02	1	PR	3.76
SAWD	08-May-02	1	SC	1.25
SAWD	08-May-02	2	CG	3.06
SAWD	08-May-02	2	CF	12.76
SAWD	08-May-02	2	SC	3.41
SAWD	08-May-02	2	SH	8.02
SAWD	08-May-02	3	CG	2.47
SAWD	08-May-02	3	CF	25.53
SAWD	08-May-02	3	SC	2.69
SAWD	08-May-02	3	SH	2.00
SAWD	10-Jun-02	1	CG	5.92
SAWD	10-Jun-02	1	SC	49.49
SAWD	10-Jun-02	2	CG	19.44
SAWD	10-Jun-02	2	CF	9.96
SAWD	10-Jun-02	2	SC	29.44
SAWD	10-Jun-02	2	SH	1.45
SAWD	10-Jun-02	3	CG	51.41
SAWD	10-Jun-02	3	CF	0.42
SAWD	10-Jun-02	3	PR	0.48
SAWD	10-Jun-02	3	SC	27.65
SAWD	10-Jun-02	3	SH	1.27
SAWD	11-Jul-02	1	CG	0.32
SAWD	11-Jul-02	1	SC	17.56
SAWD	11-Jul-02	2	CG	0.65
SAWD	11-Jul-02	2	SC	10.33
SAWD	11-Jul-02	3	CF	1.30
SAWD	11-Jul-02	3	SC	16.01
SAWD	29-Aug-02	1	CF	10.91
SAWD	29-Aug-02	1	SC	0.30
SAWD	29-Aug-02	2	CF	5.06
SAWD	29-Aug-02	2	SC	9.66
SAWD	29-Aug-02	3	CF	1.93
SAWD	29-Aug-02	3	SC	1.98

Site	Date	Replicate	FFG	IP
SAWD	29-Aug-02	3	SH	1.35
SAWD	29-Sep-02	1	CG	2.93
SAWD	29-Sep-02	1	CF	33.07
SAWD	29-Sep-02	1	PR	0.90
SAWD	29-Sep-02	1	SC	3.52
SAWD	29-Sep-02	1	SH	5.52
SAWD	29-Sep-02	2	CG	1.84
SAWD	29-Sep-02	2	CF	24.99
SAWD	29-Sep-02	2	PA	1.43
SAWD	29-Sep-02	2	SC	4.45
SAWD	29-Sep-02	2	SH	3.82
SAWD	29-Sep-02	3	CG	4.77
SAWD	29-Sep-02	3	CF	40.16
SAWD	29-Sep-02	3	PR	0.56
SAWD	29-Sep-02	3	SC	3.48
SAWD	29-Sep-02	3	SH	7.11
SAWU	27-Jun-02	1	CG	7.83
SAWU	27-Jun-02	1	SC	21.19
SAWU	27-Jun-02	2	CG	1.40
SAWU	27-Jun-02	2	PR	0.13
SAWU	27-Jun-02	2	SC	14.99
SAWU	27-Jun-02	3	CG	1.66
SAWU	27-Jun-02	3	SC	1.89
SAWU	15-Jul-02	1	CG	1.59
SAWU	15-Jul-02	1	CF	102.44
SAWU	15-Jul-02	1	SC	26.90
SAWU	15-Jul-02	2	CG	1.07
SAWU	15-Jul-02	2	CF	10.70
SAWU	15-Jul-02	2	PR	0.86
SAWU	15-Jul-02	2	SC	8.36
SAWU	15-Jul-02	3	CG	2.96
SAWU	15-Jul-02	3	CF	37.03
SAWU	15-Jul-02	3	PA	0.09
SAWU	15-Jul-02	3	PR	0.33
SAWU	15-Jul-02	3	SC	21.38
SAWU	05-Oct-02	1	CG	1.59
SAWU	05-Oct-02	1	PR	1.58
SAWU	05-Oct-02	1	SH	0.52
SAWU	05-Oct-02	2	CG	1.82
SAWU	05-Oct-02	3	CG	2.15
SAWU	05-Oct-02	3	PA	0.17
SAWU	05-Oct-02	3	PR	1.00
SAWU	05-Oct-02	3	SC	0.35
VOY	10-May-02	1	CG	17.45
VOY	10-May-02	1	CF	0.80
VOY	10-May-02	1	SC	3.17
VOY	10-May-02	2	CG	1.60

Site	Date	Replicate	FFG	IP
VOY	10-May-02	2	SC	2.73
VOY	10-May-02	3	CG	1.20
VOY	10-May-02	3	SC	1.88
VOY	10-Jun-02	1	CG	13.23
VOY	10-Jun-02	1	CF	40.78
VOY	10-Jun-02	1	SC	26.62
VOY	10-Jun-02	1	SH	1.09
VOY	10-Jun-02	2	CG	19.18
VOY	10-Jun-02	2	CF	1.88
VOY	10-Jun-02	2	SC	84.26
VOY	10-Jun-02	2	SH	0.72
VOY	10-Jun-02	3	CG	0.29
VOY	10-Jun-02	3	CF	4.46
VOY	10-Jun-02	3	SC	19.50
VOY	09-Jul-02	1	CG	6.27
VOY	09-Jul-02	1	SC	74.02
VOY	09-Jul-02	2	CG	42.34
VOY	09-Jul-02	2	CF	5.70
VOY	09-Jul-02	2	SC	72.63
VOY	09-Jul-02	3	CG	67.71
VOY	09-Jul-02	3	CF	5.31
VOY	09-Jul-02	3	SC	62.37
VOY	09-Jul-02	3	SH	1.48
VOY	28-Aug-02	1	CG	9.66
VOY	28-Aug-02	1	CF	58.65
VOY	28-Aug-02	1	PR	0.73
VOY	28-Aug-02	1	SC	10.66
VOY	28-Aug-02	2	CG	37.23
VOY	28-Aug-02	2	PA	4.56
VOY	28-Aug-02	2	PR	1.07
VOY	28-Aug-02	2	SC	2.02
VOY	28-Aug-02	2	SH	0.22
VOY	28-Aug-02	3	CG	12.05
VOY	28-Aug-02	3	CF	2.87
VOY	28-Aug-02	3	PR	1.07
VOY	28-Aug-02	3	SC	23.15
VOY	28-Aug-02	3	SH	0.19
VOY	29-Sep-02	1	CG	46.31
VOY	29-Sep-02	1	CF	0.64
VOY	29-Sep-02	1	PA	3.85
VOY	29-Sep-02	1	PR	0.41
VOY	29-Sep-02	1	SC	1.75
VOY	29-Sep-02	1	SH	0.82
VOY	29-Sep-02	2	CG	2.18
VOY	29-Sep-02	2	CF	8.88
VOY	29-Sep-02	2	SC	6.31
VOY	29-Sep-02	2	SH	0.15

Site	Date	Replicate	FFG	IP
VOY	29-Sep-02	3	CG	11.30
VOY	29-Sep-02	3	CF	3.40
VOY	29-Sep-02	3	PR	1.92
VOY	29-Sep-02	3	SC	27.29

Table 3.3. Estimated total wet weight (mass) in grams for each fish species, site, and date during spring, summer, and fall of 2002, obtained from lengths and wet weights of individual fish captured at 12 sites in the National Capital Region during each pass using Microfish as explained in chapter 3. Functional feeding groups (FFG) include invertivores (I), planktivores (P), and detritivores (D).

Site	Date	Fish	Species	Common Name	FFG	Mass
BLA	12-May-02	none				0.0
BLA	12-Aug-02	RB	*Ambloplites rupestris*	rock bass	I	59.8
BLA	12-Aug-02	SMB	*Micropterus dolomieui*	smallmouth bass	I	8.8
BLA	08-Oct-02	RB	*Ambloplites rupestris*	rock bass	I	33.9
BLA	08-Oct-02	SMB	*Micropterus dolomieui*	smallmouth bass	I	17.0
CHE	01-May-02	none				0.0
CHE	13-Aug-02	CC	*Semotilus atromaculatus*	creek chub	I	161.3
CHE	13-Aug-02	FF	*Semotilus corporalis*	fallfish	IP	34.7
CHE	13-Aug-02	LND	*Rhinichthys cataractae*	longnose dace	I	334.0
CHE	13-Aug-02	LP	*Percina caprodes*	logperch	I	2.0
CHE	13-Aug-02	RBD	*Phoxinus eos*	northern redbelly dace	IP	166.9
CHE	13-Aug-02	WS	*Catostomus commersonii*	white sucker	ID	78.8
CHE	01-Oct-02	CC	*Semotilus atromaculatus*	creek chub	I	32.1
CHE	01-Oct-02	FF	*Semotilus corporalis*	fallfish	IP	4.7
CHE	01-Oct-02	LND	*Rhinichthys cataractae*	longnose dace	I	191.3
CHE	01-Oct-02	RBD	*Phoxinus eos*	northern redbelly dace	IP	12.5
CHE	01-Oct-02	WS	*Catostomus commersonii*	white sucker	ID	14.8
COR	13-May-02	AC	*Salvelinus fontinalis*	brook trout	I	26.7
COR	08-Jul-02	AC	*Salvelinus fontinalis*	brook trout	I	7.5
COR	08-Jul-02	BNM	*Pimephales notatus*	bluntnose minnow	ID	2.8
COR	08-Jul-02	CC	*Semotilus atromaculatus*	creek chub	I	96.6
COR	08-Oct-02	AC	*Salvelinus fontinalis*	brook trout	I	26.1
COR	08-Oct-02	CC	*Semotilus atromaculatus*	creek chub	I	159.4
HAR	18-May-02	none				0.0
HAR	15-Aug-02	CC	*Semotilus atromaculatus*	creek chub	I	62.7
HAR	15-Aug-02	KF	*Fundulus diaphanus*	banded killifish	I	3.7
HAR	15-Aug-02	SB	*Culaea inconstans*	brook stickleback	I	123.7
HAR	05-Oct-02	BG	*Lepomis macrochirus*	bluegill	IP	3.1
HAR	05-Oct-02	CC	*Semotilus atromaculatus*	creek chub	I	31.2
HAR	05-Oct-02	SB	*Culaea inconstans*	brook stickleback	I	61.7
LAP	13-May-02	CC	*Semotilus atromaculatus*	creek chub	I	22.2
LAP	13-May-02	ID	*Etheostoma exile*	Iowa darter	I	23.2

Site	Date	Fish	Species	Common Name	FFG	Mass
LAP	13-May-02	RBD	*Phoxinus eos*	northern redbelly dace	IP	6.0
LAP	13-May-02	WS	*Catostomus commersonii*	white sucker	ID	21.1
LAP	13-Aug-02	CC	*Semotilus atromaculatus*	creek chub	I	66.0
LAP	13-Aug-02	FF	*Semotilus corporalis*	fallfish	IP	7.3
LAP	13-Aug-02	ID	*Etheostoma exile*	Iowa darter	I	4.9
LAP	13-Aug-02	KF	*Fundulus diaphanus*	banded killifish	I	11.6
LAP	13-Aug-02	LP	*Percina caprodes*	logperch	I	0.7
LAP	13-Aug-02	MT	*Noturus gyrinus*	tadpole madtom	I	1.6
LAP	13-Aug-02	RBD	*Phoxinus eos*	northern redbelly dace	IP	5.1
LAP	08-Oct-02	CC	*Semotilus atromaculatus*	creek chub	I	535.4
LAP	08-Oct-02	FF	*Semotilus corporalis*	fallfish	IP	78.3
LAP	08-Oct-02	ID	*Etheostoma exile*	Iowa darter	I	1.2
LAP	08-Oct-02	KF	*Fundulus diaphanus*	banded killifish	I	12.6
LAP	08-Oct-02	MT	*Noturus gyrinus*	tadpole madtom	I	1.0
LAP	08-Oct-02	PS	*Lepomis gibbosus*	pumpkinseed	IP	18.2
LAP	08-Oct-02	WS	*Catostomus commersonii*	white sucker	ID	64.3
LDS	15-May-02	none				0.0
LDS	13-Aug-02	CC	*Semotilus atromaculatus*	creek chub	I	1.2
LDS	13-Aug-02	LND	*Rhinichthys cataractae*	longnose dace	I	194.1
LDS	01-Oct-02	LND	*Rhinichthys cataractae*	longnose dace	I	78.0
LMS	17-May-02	CC	*Semotilus atromaculatus*	creek chub	I	42.5
LMS	17-May-02	LND	*Rhinichthys cataractae*	longnose dace	I	223.9
LMS	17-May-02	SB	*Culaea inconstans*	brook stickleback	I	4.0
LMS	09-Aug-02	CC	*Semotilus atromaculatus*	creek chub	I	13.6
LMS	09-Aug-02	LND	*Rhinichthys cataractae*	longnose dace	I	1263.7
LMS	02-Oct-02	LND	*Rhinichthys cataractae*	longnose dace	I	990.3
MOS	08-May-02	CC	*Semotilus atromaculatus*	creek chub	I	64.6
MOS	08-May-02	JD	*Etheostoma nigrum*	johnny darter	I	38.1
MOS	08-May-02	LND	*Rhinichthys cataractae*	longnose dace	I	26.1
MOS	08-May-02	SB	*Culaea inconstans*	brook stickleback	I	32.2
MOS	08-May-02	WS	*Catostomus commersonii*	white sucker	ID	359.0
MOS	14-Aug-02	BNM	*Pimephales notatus*	bluntnose minnow	ID	114.2
MOS	14-Aug-02	CC	*Semotilus atromaculatus*	creek chub	I	381.2
MOS	14-Aug-02	FF	*Semotilus corporalis*	fallfish	IP	43.9
MOS	14-Aug-02	JD	*Etheostoma nigrum*	johnny darter	I	0.7
MOS	14-Aug-02	LND	*Rhinichthys cataractae*	longnose dace	I	17.7
MOS	14-Aug-02	LP	*Percina caprodes*	logperch	I	51.3
MOS	14-Aug-02	RB	*Ambloplites rupestris*	rock bass	I	85.4
MOS	14-Aug-02	SB	*Culaea inconstans*	brook stickleback	I	10.4
MOS	14-Aug-02	SMB	*Micropterus dolomieui*	smallmouth bass	I	14.8
MOS	14-Aug-02	WS	*Catostomus commersonii*	white sucker	ID	18.2
MOS	07-Oct-02	BNM	*Pimephales notatus*	bluntnose minnow	ID	46.6
MOS	07-Oct-02	CC	*Semotilus atromaculatus*	creek chub	I	307.2

Site	Date	Fish	Species	Common Name	FFG	Mass
MOS	07-Oct-02	FF	*Semotilus corporalis*	fallfish	IP	8.1
MOS	07-Oct-02	JD	*Etheostoma nigrum*	johnny darter	I	1.3
MOS	07-Oct-02	LND	*Rhinichthys cataractae*	longnose dace	I	15.3
MOS	07-Oct-02	LP	*Percina caprodes*	logperch	I	8.0
MOS	07-Oct-02	RB	*Ambloplites rupestris*	rock bass	I	33.1
MOS	07-Oct-02	RBD	*Phoxinus eos*	northern redbelly dace	IP	16.9
MOS	07-Oct-02	SMB	*Micropterus dolomieui*	smallmouth bass	I	69.8
MOS	07-Oct-02	WS	*Catostomus commersonii*	white sucker	ID	132.1
POO	18-May-02	CC	*Semotilus atromaculatus*	creek chub	I	5.0
POO	18-May-02	JD	*Etheostoma nigrum*	johnny darter	I	3.8
POO	28-Aug-02	CC	*Semotilus atromaculatus*	creek chub	I	56.9
POO	28-Aug-02	JD	*Etheostoma nigrum*	johnny darter	I	2.9
POO	04-Oct-02	CC	*Semotilus atromaculatus*	creek chub	I	27.2
POO	04-Oct-02	JD	*Etheostoma nigrum*	johnny darter	I	1.2
SAWD	08-May-02	CC	*Semotilus atromaculatus*	creek chub	I	33.2
SAWD	08-May-02	JD	*Etheostoma nigrum*	johnny darter	I	13.1
SAWD	08-May-02	LND	*Rhinichthys cataractae*	longnose dace	I	126.6
SAWD	11-Jul-02	FF	*Semotilus corporalis*	fallfish	IP	5.2
SAWD	11-Jul-02	JD	*Etheostoma nigrum*	johnny darter	I	27.1
SAWD	11-Jul-02	LND	*Rhinichthys cataractae*	longnose dace	I	344.2
SAWD	11-Jul-02	LP	*Percina caprodes*	logperch	I	28.8
SAWD	29-Sep-02	JD	*Etheostoma nigrum*	johnny darter	I	68.7
SAWD	29-Sep-02	LND	*Rhinichthys cataractae*	longnose dace	I	117.8
SAWD	29-Sep-02	LP	*Percina caprodes*	logperch	I	3.3
SAWD	29-Sep-02	RB	*Ambloplites rupestris*	rock bass	I	12.2
SAWU	18-Jul-02	CC	*Semotilus atromaculatus*	creek chub	I	43.4
SAWU	18-Jul-02	JD	*Etheostoma nigrum*	johnny darter	I	19.0
SAWU	18-Jul-02	KF	*Fundulus diaphanus*	banded killifish	I	0.5
SAWU	18-Jul-02	SB	*Culaea inconstans*	brook stickleback	I	189.8
SAWU	05-Oct-02	JD	*Etheostoma nigrum*	johnny darter	I	10.9
SAWU	05-Oct-02	KF	*Fundulus diaphanus*	banded killifish	I	5.6
SAWU	05-Oct-02	SB	*Culaea inconstans*	brook stickleback	I	121.8
VOY	10-May-02	none				0.0
VOY	09-Jul-02	CC	*Semotilus atromaculatus*	creek chub	I	1.3
VOY	29-Sep-02	CC	*Semotilus atromaculatus*	creek chub	I	5.6

Table 3.4 . Total nitrogen (TN) and total phosphrus (TP) in μg L^{-1} at 12 production sites in the National Capital Region from water quality samples collected during 2002 as explained in chapter 3.

SITE	DATE	TN	TP
BLA	15-May-02	0.25	0.008
BLA	15-May-02	0.26	0.005
BLA	15-May-02	0.3	0.006
BLA	12-Jun-02	0.33	0.015
BLA	12-Jun-02	0.38	0.028
BLA	12-Jun-02	0.38	0.012
BLA	08-Jul-02	0.37	0.01
BLA	08-Jul-02	0.39	0.01
BLA	13-Aug-02	0.39	0.01
BLA	13-Aug-02	0.39	0.01
BLA	09-Oct-02	0.34	0.01
BLA	09-Oct-02	0.41	0.012
CHE	13-Jun-02	0.43	0.017
CHE	13-Jun-02	0.43	0.017
CHE	13-Jun-02	0.44	0.016
CHE	08-Jul-02	0.54	0.016
CHE	08-Jul-02	0.7	0.045
CHE	13-Aug-02	0.55	0.019
CHE	13-Aug-02	0.68	0.032
CHE	02-Oct-02	0.34	0.009
CHE	02-Oct-02	0.35	0.009
COR	15-May-02	0.2	0.008
COR	15-May-02	0.24	0.009
COR	15-May-02	0.27	0.008
COR	12-Jun-02	0.23	0.011
COR	12-Jun-02	0.27	0.012
COR	12-Jun-02	0.35	0.011
COR	08-Jul-02	0.31	0.01
COR	08-Jul-02	0.36	0.017
COR	13-Aug-02	0.36	0.005
COR	13-Aug-02	0.47	0.017
COR	09-Oct-02	0.33	0.005
COR	09-Oct-02	0.36	0.007
HAR	12-Feb-02	0.71	0.014
HAR	06-Mar-02	0.82	0.018
HAR	25-Apr-02	0.42	0.019
HAR	22-May-02	0.43	0.018
HAR	12-Jun-02	1.23	
HAR	04-Jul-02	0.52	
HAR	06-Aug-02	1.02	

SITE	DATE	TN	TP
HAR	10-Sep-02	1.06	
LAP	15-May-02	0.29	0.017
LAP	15-May-02	0.31	0.024
LAP	15-May-02	0.34	0.014
LAP	12-Jun-02	0.383	0.019
LAP	12-Jun-02	0.393	0.018
LAP	12-Jun-02	0.423	0.018
LAP	08-Jul-02	0.54	0.026
LAP	08-Jul-02	0.98	0.108
LAP	13-Aug-02	0.49	0.022
LAP	13-Aug-02	0.5	0.017
LAP	09-Oct-02	0.49	0.041
LAP	09-Oct-02	0.59	0.068
LDS	15-May-02	0.88	0.11
LDS	15-May-02	0.91	0.112
LDS	15-May-02	0.95	0.114
LDS	12-Jun-02	0.76	0.19
LDS	12-Jun-02	1.07	0.26
LDS	12-Jun-02	1.76	0.2
LDS	08-Jul-02	2.33	0.23
LDS	08-Jul-02	2.43	0.27
LDS	13-Aug-02	1.2	0.115
LDS	13-Aug-02	1.45	0.163
LDS	02-Oct-02	1.16	0.096
LDS	02-Oct-02	1.18	0.099
LMS	15-May-02	0.35	0.034
LMS	15-May-02	0.35	0.031
LMS	15-May-02	0.35	0.031
LMS	12-Jun-02	0.8	0.19
LMS	12-Jun-02	0.96	0.19
LMS	12-Jun-02	1.24	0.25
LMS	08-Jul-02	1.48	0.18
LMS	08-Jul-02	1.73	0.17
LMS	13-Aug-02	0.69	0.05
LMS	13-Aug-02	0.71	0.088
LMS	02-Oct-02	0.87	0.053
LMS	02-Oct-02	0.96	0.074
MOS	22-Jan-02	1.02	0.032
MOS	21-Feb-02	1.02	0.032
MOS	30-Apr-02	0.74	0.04
MOS	21-May-02	0.77	0.035
MOS	05-Jun-02	0.85	0.063
MOS	15-Jul-02	0.88	
MOS	07-Aug-02	0.8	
MOS	11-Sep-02	0.67	
POO	08-Jan-02	1.39	0.019
POO	12-Feb-02	1.39	0.02

SITE	DATE	TN	TP
POO	05-Mar-02	1.38	0.019
POO	24-Apr-02	1.05	0.015
POO	22-May-02	1.03	0.013
POO	12-Jun-02	1.11	
POO	04-Jul-02	1.74	
POO	06-Aug-02	1.74	
POO	09-Sep-02	1.48	
SAWD	21-Feb-02	2.74	0.122
SAWD	30-Apr-02	1.55	0.034
SAWD	21-May-02	1.83	0.025
SAWD	23-May-02	1.6	0.032
SAWD	05-Jun-02	1.83	0.08
SAWD	06-Jun-02	1.73	0.064
SAWD	12-Jun-02	2	0.22
SAWD	20-Jun-02	2.37	
SAWD	15-Jul-02	1.36	
SAWD	18-Jul-02	1.51	
SAWD	23-Jul-02	1.68	
SAWD	07-Aug-02	0.98	
SAWD	16-Aug-02	1.63	
SAWD	29-Aug-02	0.71	
SAWD	11-Sep-02	1.43	
SAWU	22-Jan-02	0.75	0.023
SAWU	21-Feb-02	1.6	0.133
SAWU	30-Apr-02	0.81	0.103
SAWU	21-May-02	0.61	0.02
SAWU	23-May-02	0.75	0.016
SAWU	05-Jun-02	0.54	0.02
SAWU	12-Jun-02	1.49	0.108
SAWU	20-Jun-02	1.12	
SAWU	25-Jun-02	0.89	
SAWU	05-Jul-02	0.72	
SAWU	15-Jul-02	0.41	
SAWU	18-Jul-02	0.52	
SAWU	07-Aug-02	0.42	
SAWU	16-Aug-02	0.36	
SAWU	11-Sep-02	0.58	
VOY	21-Jan-02	2.4	0.076
VOY	25-Feb-02	2.43	0.042
VOY	18-Mar-02	2.91	0.049
VOY	22-Apr-02	3.2	0.028
VOY	15-May-02	2.77	0.034
VOY	06-Jun-02	2.66	0.028
VOY	08-Jul-02	3.23	
VOY	12-Aug-02	2.3	
VOY	20-Sep-02	1.99	