NUMERICAL, GROWTH AND SECONDARY PRODUCTION RESPONSES OF THE BENTHIC MACROINVERTEBRATE COMMUNITY TO WHOLE-LAKE ENRICHMENT IN INSULAR NEWFOUNDLAND

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Numerical, Growth and Secondary Production Responses of the Benthic Macroinvertebrate Community to Whole-Lake Enrichment in Insular Newfoundland

by

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A thesis submitted to the
School of Graduate Studies
in Partial fulfilment of the
requirements for the degree of
Master of Science

1995

St. John's Newfoundland

ABSTRACT

A whole-lake enrichment (N + P) experiment was conducted over a three-year period to evaluate the feasibility of boosting benthic productivity in insular Newfoundland lakes. Response of the benthic community to enrichment was monitored by a combination of biomonitoring (artificial substrate) and quantitative dredge sampling in both the enriched lake and two control lakes.

Observations of benthic abundance through biomonitoring approaches revealed a continuum of positive numerical responses to enrichment. Responses were most rapid in short-lived herbivores such as chironomids, gastropods and sphaeriid clams while longer-lived detritivores (mayflies, amphipods) and predators (flatworms, leeches and dragonflies) demonstrated a slower, more modest numerical response. The benthic macroinvertebrate communities of the study lakes were composed of cosmopolitan species from the North American fauna in relatively low densities. Benthic biomass was dominated by gastropoda and the odonate Cordulia. Secondary production estimates were relatively low when compared to mainland systems. Short-lived herbivores (Amnicola, Phryganea) were observed to have increased secondary production in the enriched pond. Secondary production estimates were similar in the three study ponds for the other macroinvertebrate taxa. Some of these taxa were observed to have increased growth

(Cordulia) and/or recruitment (Enallagma) late in the study. This pattern indicates that benthic macroinvertebrate community production was still increasing in the enriched pond.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Dr. Roy Knoechel, for his guidance, supervision and patience throughout the course of this project. Financial support for this project was provided through Dr. Knoechel from a Long Range Transport of Air Pollutants (LRTAP) contract, a NSERC-DFO subvention grant and a NSERC research grant.

Appreciation is extended to the members of my supervisory committee, Dr. M.H. Colbo who provided invaluable help with the identification of benthic organisms and Dr. D. Schneider who introduced me to the statistical procedure of randomization. In addition, they both constructively reviewed an earlier version of this thesis.

I would also like to thank Pat Ryan of D.F.O. who supplied several papers and his 20 years experience on the limnology of the Experimental Ponds Area. Roy Ficken provided photographic services for this thesis and a poster presented at ASLO 1994. Dr. J.J. Kerekes of the Canadian Wildlife Service supplied several papers on benthic organisms and primary production.

I would also like to thank Chris Brown who stayed sane through three years of living in a travel trailer for 4 months of the year. Chris was my field partner and aided with all facets of sample collections, which were often extremely difficult in the damp and cold conditions of Newfoundland.

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CHAPTER 1: GENERAL INTRODUCTION

Lakes were once considered isolated microcosms and therefore have long been used to test and develop hypotheses on the structure and functioning of ecosystems (Wetzel 1983). One of the more intensive areas of investigation since the 1970's has been the effect of nutrient loading (Schindler 1977). Studies of the effects of nutrient increases on lake ecosystems can be divided into two basic groups: those in which the nutrient increase resulted from land use and pollution (Cattaneo 1987, Harper and Stewart 1987, Hough et al. 1989, Dougherty and Morgan 1991, Stauffer 1991, Kumar et al. 1992), and those where nutrient levels have been experimentally manipulated to determine ecosystem responses (Stockner and Shortreed 1985, Schindler 1990, Cowell and Dawes 1991, Niederhauser and Schanz 1993).

The basic premise of any nutrient enrichment or fertilization experiment is that the artificially induced increase in nutrients will result in an increase in ecosystem productivity. This is basically a "bottom-up" view of ecosystem structure, which has been verified in the past by experiments that have linked increases in phytoplankton (Reinertsen 1982, Henry et al 1985, Stockner and Shortreed 1985, Havens and DeCosta 1986, Niederhauser and Schanz 1993) and benthic algae (Bjork-Ramberg and Anell 1985, Carrick and Lowe 1989, Bergmann and Welch 1990) to nutrient loading.

The "bottom-up" view of ecosystem structure states that community processes (i.e. predation) will work to pass the increased primary production through the food chain, thus creating a more productive ecosystem with higher biomass at all trophic levels. This has been verified by studies which have linked increased primary production to responses in the zooplankton (Langeland and Reinertsen 1982, Elser and Mackay 1989, Fairchild et al. 1989) and fish communities (Reinertsen and Langeland 1982, Hyatt and Stockner 1985, Mills 1985).

Newfoundland lakes differ from their counterparts in mainland North America and Europe in several ways. The majority of the lakes, or ponds as they are known in Newfoundland, are small bodies of acidic water surrounded by a mixture of coniferous forest and peatland. The productivity of these lakes is generally low (Kerekes 1975, Knoechel and Campbell 1988) and observations of stream and precipitation chemistry (R. Knoechel, unpub. data) suggest that the surrounding vegetation acts as a nutrient sink keeping the production of these lakes low. The main fish species are the stickleback Gasterosteus aculeatus, the brook trout Salvelinus fontinalis, and the Atlantic salmon Salmo salar. All these species appear to rely heavily on the benthic community for their food (Brown 1993; Baggs 1989; K. Clarke, unpub. data).

This benthos-based food web is fundamentally different than those in ecosystems where previous fertilization experiments have been conducted, where a more direct pelagic food chain is the norm. The benthic community has largely been overlooked in lake fertilization studies of the past, although Schindler (1987) has suggested that benthic organisms may be more responsive to nutrient loading because of accumulation of nutrients and organic matter in the sediments. The few fertilization studies which have tried to incorporate benthos (Smith 1969, Milbrink and Holmgren 1981, Aagaard 1982, Brylinsky 1993) have reported varying and ambiguous results.

The main objective of this study is to characterize the response of the benthic community to nutrient enrichment in Newfoundland lakes. Responses are evaluated in terms of numerical increases, growth rate increments and changes in population productivity through a combination of artificial substrate (Chapter 3) and quantitative dredge sampling (Chapter 4). The influence of life-cycle characteristics and feeding mode (ie. herbivore, carnivore, detritivore) on the magnitude and speed of response is also investigated.

CHAPTER 2: THE STUDY SITE

PHYSICAL CHARACTERISTICS

The study was carried out in Coles Pond (48°17.4' N 55°31' E), Spruce Pond (48°19' N 55°28' E) and Headwater Pond (48°16' N 55°29' E) at the Department of Fisheries and Oceans Experimental Ponds Area (EPA) in central Newfoundland (Figure 2.1). The EPA has served as the site of several biomonitoring projects in the past. Most recently it was a part of the Canadian Long Range Transport of Air Pollutants (LRTAP) project which involved sampling for water chemistry, phytoplankton, zooplankton and macroinvertebrates plus the estimation of salmonid populations (Ryan et al. 1994). This earlier work provided extensive background information for the present study.

The lakes in the EPA are small, shallow and dystrophic (Table 2.1), typical of lakes in the area (Ryan and Wakeham 1984, Ryan et al. 1994) and remain well mixed throughout the ice-free season. The experimental lake, Coles Pond, has a low ratio of catchment basin to surface area (Table 2.1), which results in a low summer flushing rate that makes it easier to manipulate chemically. Headwater Pond is similar to Coles Pond in that it is a headwater lake with a low summer flushing rate. It was used as one control while Spruce Pond, the second pond downstream from Headwater Pond, was used as a second control system. Spruce Pond is more similar to Coles

Table 2.1: Physical characteristics of the study ponds in the Experimental Ponds Area.

Pond	Mean depth (m)	Surface area (ha)	Catchment area (ha)	Area Ratio
Coles Pond	1.3	25.7	331	12.88
Spruce Pond	1.0	36.5	2006	54.96
Headwater Pond	1.1	76.1	596	7.83

Note: Area ratio = Catchment to surface area ratio.

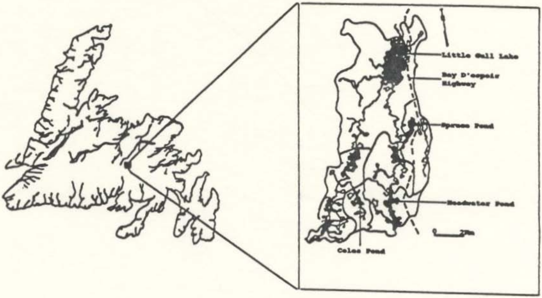

Figure 2.1: The Experimental Ponds Area of central Newfoundland highlighting the ponds used in this study.

in surface area (Table 2.1) and it has a low effective flushing rate in spite of its large catchment area. This low flushing rate is due to the adjacent location of both the major inlet and the outlet in the south end of the pond. The watershed of these lakes is made up of peatland and coniferous forest which is dominated by black spruce. The exception to this is Headwater Pond where a forest fire in 1986 left more than half of the western shoreline consisting of charred tree remains and low-lying regrowth. The major substrate of these ponds is a gelatinous brown sediment frequently referred to as 'dy' (Ruttner 1969). This loose organic substrate does not support dense aggregations of macrophytes and creates a fairly uniform substrate type across all three ponds. Near-shore areas subject to wave action have a cobble-boulder substrate, these areas are relatively limited, especially in Coles Pond.

BIOLOGICAL CHARACTERISTICS

The study ponds are typical of insular Newfoundland in that they are oligotrophic (Knoechel and Campbell 1988) and have a depauperate fauna. The resident fish populations in the Experimental Ponds Area include; brook trout (Salvelinus fontinalis), juvenile Atlantic salmon (Salmo salar), and the three spined stickleback (Gasterosteus aculeatus) (Ryan and Knoechel 1994). Limited prior benthic studies (Ryan et. al. 1985, Ryan et. al. 1990) indicate that these ponds are typical of Newfoundland systems in that the benthic community is composed of the widespread species from mainland North American fauna (Larson and Colbo 1983). These species generally occur in low densities and a detailed characterization of the macroinvertebrate fauna for these ponds is documented in this thesis (Chapter 4).

EXPERIMENTAL MANIPULATION

Coles Pond was fertilized during the summer (June-September) with nitrogen and phosphorus additions at a rate of 0.824 Kg N per day and 0.118 Kg P per day starting in the summer of 1991 and continuing in the summer of 1992. The fertilization continued in 1993 but at a three-fold greater rate. The nitrogen was supplied as pellets of either ammonium nitrate or sodium nitrate which were added to pails in a major inlet where they dissolved. The phosphorus was added in the form of phosphoric acid which was dripped directly into the pond at a location adjacent to the major inlet.

CHAPTER 3: NUMERICAL RESPONSES AS INDICATED USING BIOMONITORING TECHNIQUES (ARTIFICIAL SUBSTRATES)

INTRODUCTION

Past fertilization experiments have successfully linked experimental increases of nutrients to an overall increase in biomass for freshwater lakes (Smith 1969, Reinertsen 1982, Henry et al 1985, Stockner and Shortreed 1985, Elser and MacKay 1989). This suggests that at least in the initial stages of fertilization "bottom-up" controls are structuring the changes within the ecosystem. Thus, my working hypothesis was that an experimental increase of limiting nutrients would increase overall benthic biomass in Coles Pond.

The speed and magnitude of response to fertilization will differ among the various species populations within the benthic community and these differences should be related to the life span (Steins and Wharf 1987) and the trophic role of the organisms. It is therefore useful to summarize estimates of life span and trophic role for the populations used in this analysis (Table 3.1). It is expected that short-lived species such as chironomids should show faster responses to fertilization than longer-lived species such as dragonflies. Organisms feeding near the base of the food web such as filter feeding clams and herbivorous gastropods should show quicker responses than detritivorous mayflies and predatory leeches. The combination of life span and trophic role should be

Table 3.1: Life span and trophic role of the most abundant benthic organisms. Each taxon is typically dominated by a single genus or family as indicated in parenthesis.

Taxon	life span	Trophic role	Principle food
Diptera (Chironomidae)	+/- 1 year	mixed	diverse
Gastropoda (Amnicola)	<18 months	herbivore	periphyton
Pelecypoda (Sphaeriidae)	<18 months	herbivore	phytoplankton
Trichoptera (Oxyethira)	+/- 1 year	herbivore	filamentous algae
Amphipoda (Hyalella)	+/- 1 year	detritivore	coarse detritus
Ephemeroptera (Leptophlebia)	<2 years	detritivore	fine detritus
Turbellaria	+/- 1 year	predator	small inverts
Hirudinea (Glossiphonia) (Helobdella)	>3 years (except Helobdella)	predator	snails, chironomids
Odonata (Cordulia)	>3 years	predator	chironomids, mayflies etc.

additive, therefore short-lived herbivores should display the quickest response while long-lived predators should display the slowest.

The benthos of freshwater lakes have been found to be an effective indicator of ecosystem change because they provide a cumulative indication of conditions over time, unlike chemical data which provide a snapshot of ambient conditions (Reice and Wohlenberg 1993). An increase of limiting nutrients from fertilization should produce an increase in production and, subsequently, abundance of benthic organisms. The relationship between benthic biomass and nutrient level has been studied in the past. For example, Schell and Kerekes (1989) reported that phosphorous was significantly related to the abundance of benthic macroinvertebrates in eight Nova Scotia lakes. Fertilization experiments, however, have displayed variable results with respect to the response of benthic taxa. Smith (1961,1969) reported that fertilization of a lake increased the biomass of small, fast-growing organisms such as chironomids, amphipods, gastropods and sphaeriid clams. Peterson et al. (1993) reported that phosphorus additions to a tundra river increased insect growth rate but that abundance was held in check by community interactions such as predation. Brylinsky (1993), in contrast, did not find any significant differences in abundance of benthic organisms in four fertilized and four control wetlands in the Tobeatic Wildlife Management Area of Nova Scotia Canada.

A possible explanation for the differing results in these fertilization experiments may be the varying levels of sampling effort. Benthic sampling is expensive because of the large amount of time required for sorting and identification. Therefore most whole ecosystem studies have had a limited benthic component (Reice and Wohlenberg 1993). Various strategies were employed in the above studies to reduce the time needed to sample the benthos. Smith (1961) reduced sample processing time by using a 1mm mesh to sieve his Ekman grabs. This size mesh would pass many of the smaller organisms such as chironomids and flatworms. Brylinsky (1993) employed sweep net sampling to follow the response of the benthic communities. Sweep netting is a qualitative method of sampling which makes quantitative comparisons among sites difficult. Peterson et al.(1993) collected small numbers of samples thus reducing the power of the statistics which could be employed. The net result of any of these strategies is reduction of the sensitivity for detecting differences. An efficient method of quantitative sampling with well-defined statistical precision is required to efficiently quantify the response of the benthos to a perturbation such as fertilization.

Artificial substrates are inexpensive and have been shown to have low variability (Rosenberg and Resh 1982). This makes them ideal for following the abundance of benthic macro-invertebrates through time to highlight differences brought about because of artificial perturbation.

MATERIALS AND METHODS

Artificial substrate sampling was used to evaluate the numerical response of the benthic invertebrate community to fertilization in the present study. Sixty artificial substrates (rock-bags) were placed in both the fertilized and control ponds in the summer of 1991. These rock-bags consisted of approximately 1130 g of coarse (2.5 cm) road gravel encased by plastic vexar mesh (1.5 cm, stretch measure). Rock-bags were placed at 3 stations per pond, each station consisting of 4 lines with 5 rock-bags per line extending perpendicular from the shore and thus providing a variety of depths (Figure 3.1). The rock-bags were collected in the spring and fall of each year (1991-93) beginning in the fall 1991, shaken vigorously in a bucket of water for 40 seconds to remove organisms and then visually inspected to insure complete removal. The only item not removed with 100% efficiency was leech egg cases and these were usually empty. The rock-bags were then replaced in the pond until the next sampling. The water was filtered through a 300 um Nitex screen and all organisms retained were preserved in 95% ethanol.

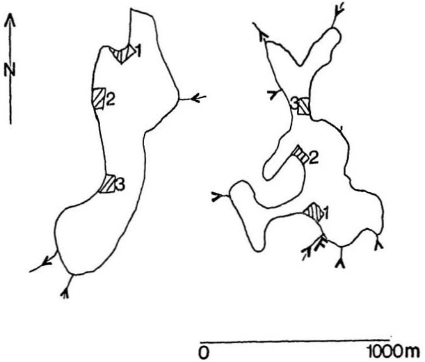

Figure 3.1: Experimental pond (Coles Pond) and control pond (Spruce Pond) with artificial substrate stations highlighted. Arrows indicate the direction of flow in the streams and 'F' denotes the site where fertilizer was added.

A sub-sample of 15 rock-bags consisting of five bags from each station and one bag from each of the near-shore to off-shore positions was selected for each pond and sampling date. Initial analysis revealed no statistically significant differences among stations and depths therefore all samples have been pooled. The specimens of these samples were sorted and identified using the following keys: aquatic insects (except Trichoptera) Merritt and Cummins (1984); Trichoptera, Wiggins (1977); all other macro-invertebrates, Pennak (1978). Graphical techniques were used to show the temporal pattern of abundance of each taxonomic group through time. Organism/rock-bag data was not normally distributed therefore 95% confidence intervals of the mean were estimated by randomization techniques. The 15 estimates of abundance were replicated 200 times to produce a population of 3000 values which were then randomly sampled in sets of 15, one thousand times. The 95% confidence intervals of the mean were then determined from this set of one thousand means. Lack of overlap of the 95% confidence interval around the mean of one set of samples with the mean of a second set thus indicates a greater than 2 standard error difference between the means defining a statistically significance of $p < 0.05$.

RESULTS AND DISCUSSION

Artificial fertilization has been repeatedly shown to increase primary productivity in freshwaters (Smith 1969, Hall et al. 1970, Peterson et al. 1993, Brylinsky 1993). It is expected that this increase in primary productivity should also lead to an increase in abundance of organisms in the benthic community.

It was expected that the speed and scale of response would be related to the life span and trophic role of the individual taxa as summarized in Table 3.1. The most pronounced response to fertilization observed in the benthic community was by the small, short-lived, herbivores such as chironomids (Figure 3.2), gastropods (Figure 3.3) and sphaeriid clams (Figure 3.4). These organisms have the ability to reproduce more than once a year and have relatively short life cycles (less than 18 months) making them ideal rapid indicators of change in the abiotic environment. These findings are similar to those of Smith (1961, 1969) who noted increases in clams and gastropods during the second and third years after fertilization. The chironomids (Figure 3.2) had the largest increase in abundance, showing almost a 6-fold increase in 1992 over 1991. The numbers dropped drastically during the winter of 1992 but rose to an even higher level by the fall of 1993. The large reduction over the winter of 1992 suggests that a large amount of chironomid biomass was shunted

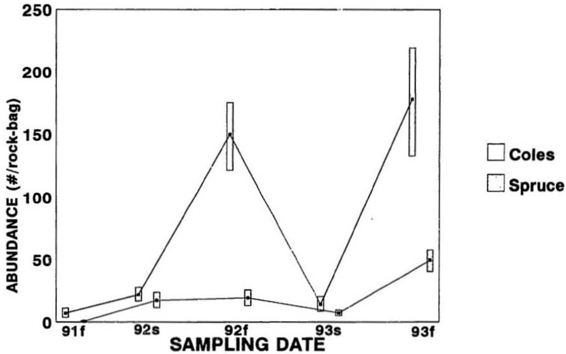

Figure 3.2: The abundance of chironomids in the enhanced pond (Coles Pond) and a control pond (Spruce Pond) during the first three years of fertilization. Bars are 95% confidence intervals of the mean.

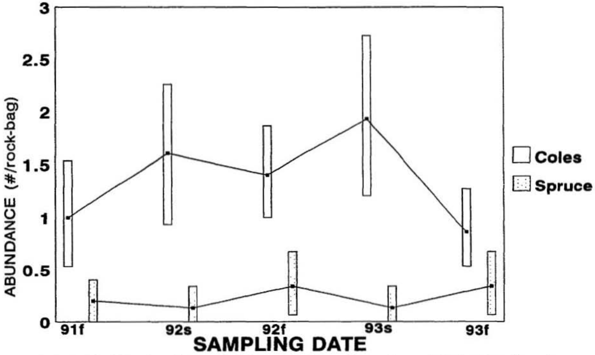

Figure 3.10: The abundance of Odonata in the enhanced pond (Coles Pond) and a control pond (Spruce Pond) during the first three years of fertilization Bars are 95% confidence intervals of the mean.

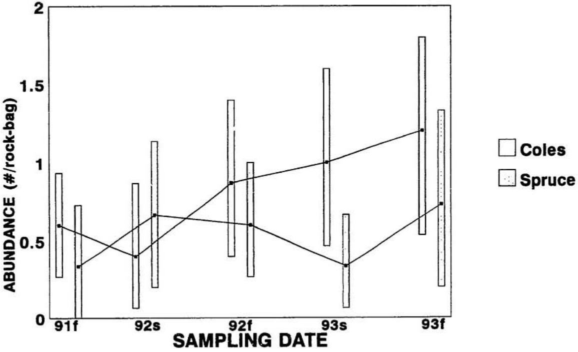

Figure 3.9: The abundance of leeches in the enhanced pond (Coles Pond) and a control (Spruce Pond) during the first three years of fertilization. Bars are 95% confidence intervals of the mean.

up the food chain (predation) or left the system through a mass emergence late in the fall or early in the spring.

Gastropod abundance (Figure 3.3) increased in the fertilized pond, except for the spring of 1993 when abundances declined in both ponds suggesting either harsh winter conditions or high winter predation rates. Sphaeriid clams (Figure 3.4) which are similar to the gastropods in life span and trophic role (Table 3.1), increased significantly in Coles Pond after the first year of fertilization (1991) and have subsequently remained at consistent, elevated levels. The clams may have been held from increasing further either by increased predation or by a reduction in their food supply. Chlorophyll levels remain elevated in Coles Pond (R. Knoechel unpub. data) however and stomach content analysis of benthic-feeding salmonids (unpub. data) and sticklebacks (Brown 1993) revealed that clams were not an important diet item. Thus the mechanism maintaining the apparent steady state abundance level is unclear.

The response of the trichopteran Oxyethira (Figure 3.5) is an exception to the general trend seen in the herbivores. There was a slight divergence between the two populations over the winter in both 1991 and 1992 suggestive of enhanced winter survival in Coles Pond. The abundance level in Coles Pond was not significantly higher until fall 1993, however. This might be attributable to a delay in the increase of filamentous

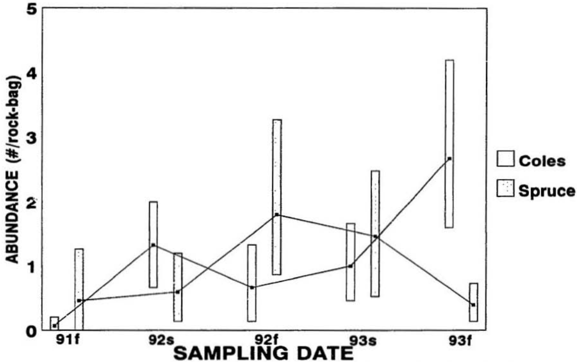

Figure 3.8: The abundance of flatworms in the enhanced pond (Coles Pond) and a control pond (Spruce Pond) during the first three years of fertilization. Bars are 95% confidence intervals of the mean.

benthic algae that these organisms feed on. Large 'clouds' of filamentous benthic algae were observed in Coles Pond in the summer of 1993 but were not obvious in 1991 or 1992.

The larger, longer-lived organisms with mainly detritus-based diets responded more slowly to fertilization. Amphipod levels (Figure 3.6) were significantly higher in Coles Pond in the fall of 1992 but the populations were at similar levels at all other sampling times. This is in contrast to the observations of Smith (1961) where amphipods showed significant, quick increases after fertilization.
Ephemeropteran abundances (Figure 3.7) remained similar in both ponds through the fall of 1992 followed by a divergence over the winter of 1992-93 with decreased abundance in Spruce Pond. Thus by the spring of 1993 the abundance in Coles Pond was significantly higher than that observed in Spruce Pond. This trend continued through the fall of 1993 and is expected to be maintained until the mayfly
population in Coles Pond stabilizes at a new equilibrium with their food supply and their predators.

The final group of organisms considered were the predators of the benthic community. The flatworms (Figure 3.8) are the smallest and have the shortest life cycle (Table 3.1) of the predators considered in this analysis. They showed significantly higher abundance in Coles Pond in the spring of 1992 but their levels were not significantly greater

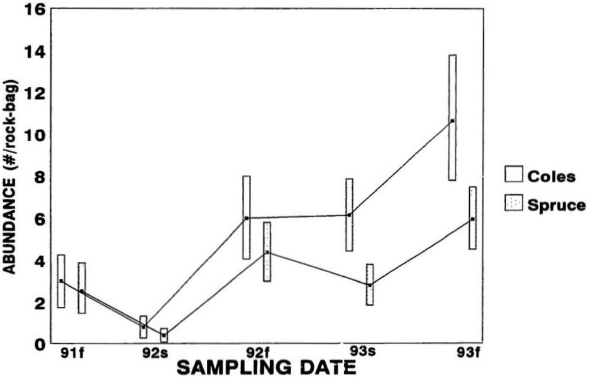

Figure 3.7: The abundance of Ephemeroptera in the enhanced pond (Coles Pond) and a control pond (Spruce Pond) during the first three years of fertilization. Bars are 95% confidence intervals of the mean.

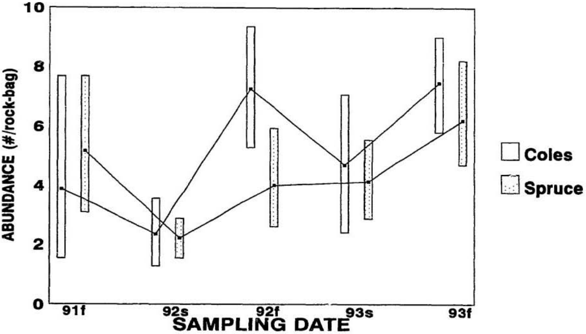

Figure 3.6: The abundance of amphipods in the enhanced pond (Coles Pond) and and a control pond (Spruce Pond) during the first three years of fertilization. Bars are 95% confidence intervals of the mean.

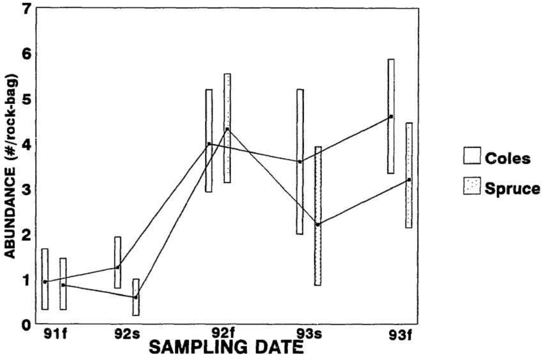

Figure 3.5 The abundance of the trichopteran *Oxyethira* in the enhanced pond (Coles Pond) and a control pond (Spruce Pond) during the first three years of fertilization. Bars are 95% confidence intervals of the mean.

again until the fall of 1993.

The leeches (Figure 3.9) have shown steady increases in abundance in Coles Pond since the spring of 1992 although the level was only significantly higher than Spruce Pond in the spring of 1993. With continued fertilization it is expected that the abundance of leeches will continue to climb and eventually maintain a level significantly higher than that observed in Spruce Pond.

The Odonata (Figure 3.10) were always significantly higher in abundance in Coles Pond than Spruce Pond. There were no significant differences in Spruce Pond abundances over time while there was a significant increase in Coles Pond by spring 1993. The subsequent sharp decline in Coles Pond was correlated with an increase in salmonid abundance that summer (Knoechel unpub. data). Odonata constitute a major portion of salmonid diets in these ponds (Clarke unpub. data).

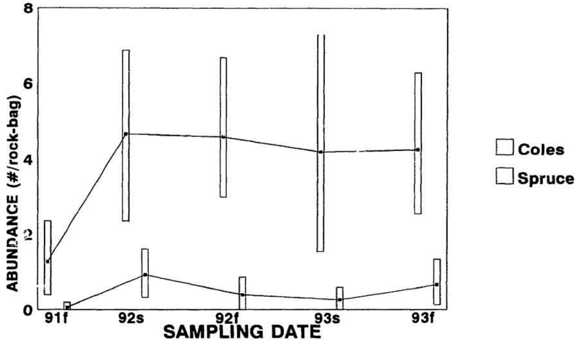

Figure 3.4: The abundance of sphaeriid clams in the enhanced pond (Coles Pond) and a control pond (Spruce Pond) during the first three years of fertilization. Bars are 95% confidence intervals of the mean.

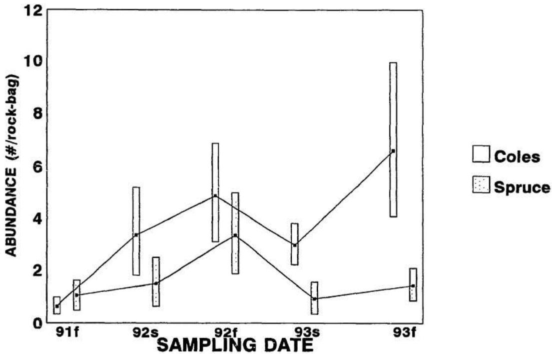

Figure 3.3: The abundance of gastropods in the enhanced pond (Coles Pond) and a control pond (Spruce Pond) during the first three years of fertilization. Bars are 95% confidence intervals of the mean.

SUMMARY

Artificial fertilization of Coles Pond has increased the abundance of several benthic macroinvertebrate taxa. The life history and feeding characteristics of the organism studied was related to both the speed and the magnitude of the response to fertilization. For example, small, short-lived herbivores (gastropods) demonstrated a quicker response than did larger, long-lived detritus feeders (mayflies) which in turn had a quicker response than did larger predators (leeches). The widening abundance differential observed for most taxa suggest that continued fertilization will increase the abundance of benthic organisms in Coles Pond until the community settles into a new equilibrium at an overall higher level of abundance and production.

CHAPTER 4: MACROINVERTEBRATE RESPONSE TO FERTILIZATION: GROWTH, DENSITY AND PRODUCTION.

INTRODUCTION

Most studies of experimental perturbation of the benthic community employ simple estimates of numerical abundance when making comparisons among treatments (Benke 1994, Rosenberg and Resh 1993). However, numerical abundance is influenced by the balance between reproduction and death, each of which may respond independently to the perturbation. Simple numerical estimates also cannot reflect differences in individual size that may result from growth rate enhancement. Secondary production estimates may be more powerful indicators of ecosystem change because they take reproduction, growth and death all into account (Benke 1994). Obtaining accurate secondary production estimates requires large sample sizes and labour-intensive weight determinations, consequently they are infrequently reported in the literature.

Benthic community production has been shown to be affected by stresses including insecticides (Lugthart and Wallace 1992), nutrient increases from agriculture (Sallenave and Day 1991) and organic enrichment (Flossner 1982, Lazin and Learner 1986, Losos 1984).

Benthic community production has usually been neglected in mesocosm fertilization experiments and benthic production estimates are almost non-existent in whole lake fertilization experiments. A computer-based search of Biological Abstracts from January 1985 to June 1994 and a subsequent review of the literature cited in the selected references obtained, revealed only two papers dealing with secondary production of the benthic community following fertilization. One of these articles (Peterson et al. 1993) dealt with a tundra river system and the other (Aagaard 1982) was a whole lake enrichment experiment but only reported production estimates for two chironomid species. Both articles (Peterson et al. 1993, Aagaard 1982) however, report conflicting results relating fertilization to benthic community production. Peterson et al. (1993) reported initial growth rate increases but total secondary production did not increase due to 'top-down' processes (predation) in the community. Aagaard (1982) reported density increases but these increases and the production estimates were reported as being within the limits expected by annual variation alone and thus the effect due to the fertilization was not clear.

The present study aims to better quantify the relationship between whole lake fertilization and its effect on benthic secondary production. Coles Pond was experimentally fertilized with inorganic nitrogen and phosphorus beginning in summer 1991 (see Chap. 2) while Spruce and Headwater ponds served as control ecosystems. The working hypothesis was that the increase in nutrient load to the enriched ecosystem (Coles Pond) would increase primary productivity which in turn would increase the productivity of the benthos. Benthic responses could be manifested as numerical increases and/or growth rate increases (larger size), both of which should be reflected in population production estimates.

MATERIALS AND METHODS

Density, biomass and production estimates for the major macroinvertebrate taxa were obtained using a quantitative sampling regime initiated in the second year of the study. Sampling started in July 1992 and was repeated four additional times throughout the study (August 1992, May 1993, July 1993 and August 1993). Samples were collected using a hand-held dredge sampler affixed with a 2 mm Nitex mesh bag designed to retain the macroinvertebrates while passing the sediment and microinvertebrates (Figure 4.1). It thus enabled sampling of the large areas necessary for quantitative description of large, low-density organisms. The larger mesh size of the dredge sampler means that the results of this sampling method are not directly comparable to those in Chapter 3 in which the artificial substrate collections were sieved using a 300 um mesh screen.

The sampler was deployed by snorkelling out and back along a 15 m transect. The sampler had a 0.25 m wide aperture

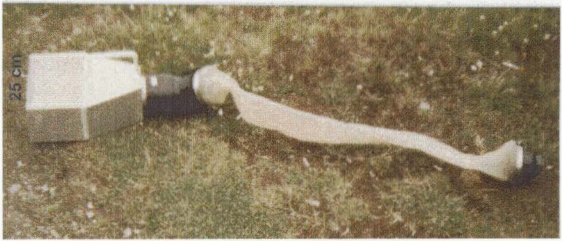

Figure 4.1: Dredge sampler used in quantitative sampling regieme. The opening at the left is 25 cm.

and thus each sample covered an area of 7.5 m^2. Samples were collected in triplicate at 3 stations per pond (Figure 4.2) and two depths (0.5 and 1.0 m) per station. This sampling regime produced 18 samples per pond per sampling date which were preserved in 95% ethanol. A sub-set of 12 samples per pond per sampling date, representing 90 m^2 of benthic substrate, were sorted and the specimens counted and identified using the keys cited in the materials and methods section of Chapter 3. Confidence intervals (95%) of the mean density were estimated using randomization techniques. The 12 estimates were replicated to produce a population of 2400 values which were then randomly sampled in sets of 12, one thousand times. The 95% confidence limits of the mean were then empirically determined from this set of one thousand means. These 95% confidence intervals are shown in all figures and sample means which lie outside the confidence interval for a given site and date were judged to be significantly different at the 5% level.

Standing stock biomass (dry wt./m^2) was calculated for use in secondary production estimates. Dry weight was obtained after drying the specimens at 60 °C for 24 hours, both clams and snails were weighted whole with shells due to the small size (< 3 mm) of the dominant species. Biomass estimates were then calculated by multiplying the average weight by the average density for taxa that displayed little

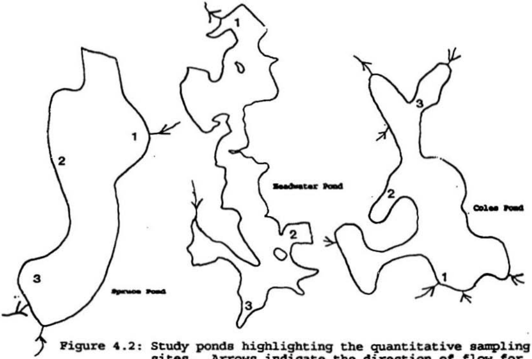

Figure 4.2: Study ponds highlighting the quantitative sampling sites. Arrows indicate the direction of flow for the major streams. Note: The ponds are not drawn to scale

range in size such as Amnicola. The average dry weight was estimated by weighing groups of 20-25 randomly selected specimens in duplicate where numbers permitted (density $>0.25/m^2$). For taxa represented by fewer than 20 specimens the number of individuals weighed can be estimated by multiplying the density, graphed in the figures, by the 90 m^2 sample size. Log length : log dry weight regressions were used to estimate the biomass of taxa that varied widely in size such as Cordulia. The regressions are presented in Appendix A.

Evaluation of the general life-history pattern for several of the more abundant taxa was investigated by plotting their average density and average weight though time. The patterns observed in these plots were interpreted using a set of simple rules. A large increase in density and/or decrease in average weight was interpreted as evidence for recruitment while a sharp decline in density indicated a period of emergence (aquatic insects) or high mortality (predation, mass die off). Growth responses of individual taxa were evaluated by comparing weight gains in the three ponds over important growing periods. Likewise, response in recruitment was evaluated by comparing the change in density in the three ponds during important recruitment periods. These analyses were only carried out if the taxon's life cycle was found to be in phase in all three ponds.

Production estimates were then calculated using one of two methods. Secondary production of populations with distinct univoltine cohorts was calculated using the increment-summation method as described by Rigler and Downing (1984) using the equation:

Eq. 1. $$P = \Sigma\ (\bar{N}(m_k\ -\ m_{k-1}))$$

where $\bar{N}$ is the average #/m^2 at time k and k-1, m_k is the average weight (mg) at time k and m_{k-1} is the average weight at the previous sampling date. When sampling dates spanned an emergence (usually denoted by a sharp decline in average individual weight) the number at k-1 for the new cohort was set at 0 and the number at k for the old cohort was set at 0 giving an estimate of production for the two cohorts (See example Appendix B). Annual production was calculated using a correction factor which was 365 divided by the days elapsed during the study. Daily secondary production for specimens where cohorts were not readily identified was calculated using the size-frequency method of Hamilton (1969) with a correction for actual cohort production interval (CPI) (Benke 1979) using the equation:

Eq. 2. $$P = (\Sigma\ P_i\ = \bar{N}_i(m_{max} - m_{min})/D_i)CPI$$

where P_i is the daily production of an arbitrary size class i, $\bar{N}_i$ is the average #/m^2 in the size class, m_{max} is the maximum weight (mg) in the size class and m_{min} is the minium weight in the size class. D_i is the average duration of each size class which is estimated by dividing 365 days by the number of size classes. Size classes were assigned arbitrarily by the histogram function in MINTAB with only one requirement, each size class had to have both a minimum and maximum observed weight (ie. there had to be more than one individual in the class and they had to vary in weight). If this requirement was not met then two or more size classes were combined to ensure a range in weights within the size class.

The estimate is then multiplied by the CPI which is a correction for actual duration of the aquatic life-cycle. This correction is necessary because the size-frequency method was formulated for organisms with a 365 day aquatic life-stage duration. The resulting production estimate was then multiplied by 365 days to give annual production in $mg.m^{-2}yr^{-1}$.

RESULTS AND DISCUSSION

BENTHIC COMMUNITY COMPOSITION

Benthic community taxonomic composition was similar among the three study ponds (Table 4.1). There were five taxa unique to Coles Pond collections and four unique to Spruce Pond but all taxa classified as abundant in any one pond were present in each of the others with the exception of the trichopteran Polycentropus, which was absent from Spruce Pond collections. Most of the taxa listed are holarctic in distribution and are typical of Newfoundland's benthic fauna

Table 4.1: List of the taxa identified from collections in the three ponds over the course of the study with the quantitative dredge sampler (* indicates presence, ** indicates abundant taxa)

SPECIMEN	COLES	SPRUCE	HEADWATER
Gastropoda			
Amnicola	**	**	**
Helisoma	**	**	**
Valvata	*	**	*
Physa	*	*	*
Gyraulus	*	*	*
Ferrissia	*		
Bivalvia			
Sphaerium	**	**	**
Anodonta		*	*
Amphipoda			
Hyalella	**	**	**
Crangonyx		*	*
Ephemeroptera			
Caenis	**	**	*
Stenonema		*	
Leptophlebia	**	**	**
Hexagenia	*		
Heptagenia	**	**	*
Eurylophella	*	*	*
Trichoptera			
Helicopsyche		*	*
Ceraclea	*	*	*
Limnephilus	*	*	*
Oxyethira	**	**	*
Mystacides	*	*	*
Oecetis	**	**	*
Leptocerus	*	*	*
Banksiola	**	**	*
Phryganea	**	**	*
Platycentropus	*	*	*
Polycentropus	**		*
Lepidostoma		*	
Anabolia		*	
Molanna		*	*

Odonata			
Cordulia	**	**	**
Aeshna	*	*	*
Enallagma	**	**	**
Diptera			
Chironomidae	**	**	**
Ceratopogonidae	**	**	**
Tabanidae	**	*	*
Annelida			
Oligochaeta	**	**	**
Hirudinea			
Placobdella	*		*
Nephelopsis	*	*	*
Glossiphonia		*	
Helobdella	**	**	**
Turbellaria	*	*	*
Hydracarina	**	**	**
Eubranchiopoda			
Conchostraca			
Lynceus	*		
Coleoptera			
Haliplidae	*		
Chrysomelidae	*		
Hemiptera			
Corixidae		*	*
Totale	38	39	38

(Larson and Colbo 1983), and have been previously catalogued in the Experimental Ponds Area (Ryan et al. 1990). The one exception is the clam shrimp (Eubranchiopoda) Lynceus brachyurus which was only collected in Coles Pond and has not been previously reported in Newfoundland. The distribution of this species is thought to be holarctic (Pennak 1978) but it has only been reported in the literature three times for all of Canada, the most easterly point being in Quebec (Martin and Belk 1988). Its discovery in insular Newfoundland supports its having a cosmopolitan distribution; its infrequent reporting may be due to difficulties in identification, as it is easily mistaken for an ostracod at first glance, or due to its very low abundance.

MACROINVERTEBRATE BIOMASS

Total benthic macroinvertebrate biomass was comparable in Coles Pond and Headwater Pond throughout the study (Figure 4.3). Biomass was initially highest in Spruce Pond but declined by August 1993 to levels similar to the other ponds. Biomass was generally dominated by gastropoda in all three ponds (Figure 4.3) with odonata, dominated by the genus Cordulia, the next most important group. Total biomass declined from July through August 1992, recovered over the winter and then declined from May through July 1993 in all three ponds. The biomass decline continued through August

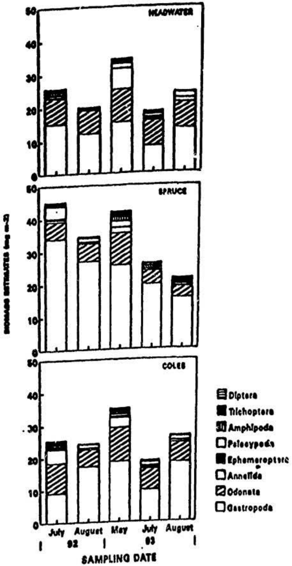

Figure 4.3: Benthic biomass estimates for the study ponds: Showing the relative importance of the major taxonomic groups.

1993 in Spruce Pond while an increase was observed in both Coles and Headwater ponds. These patterns suggest an overall decline in benthic biomass over the summer, while aquatic insects are emerging and benthic-feeding salmonids are most active, and a fall increase corresponding to the recruitment period of aquatic insects and the brook trout spawning period.

DENSITY AND GROWTH PATTERNS

Secondary production is much easier to calculate if the organism in question can be followed through time as a distinct cohort (Rigler and Downing 1984, Benke 1994). It is therefore important to have an understanding of the general biology of the organism before calculations are attempted.

Cordulia

Cordulia shurtleffi (Cordulidae:Odonata) is the dominant benthic predator (in terms of biomass) in these systems. Cordulia has been observed to have 10-14 instars in Newfoundland systems (Farrell 1985, Clarke 1992, Larson and House 1990). Laboratory experiments (Clarke 1992) and observations in the field (Clarke unpub.) suggest that it would require 4-5 years to complete this number of instars in Newfoundland. This estimate is similar to that of Cordulia aneae amureis of Northeast Asia (Ubukata 1981).

Densities of Cordulia increased significantly in Coles and Headwater ponds from August 1992 to May 1993 (Figure 4.4). Density increased in Spruce Pond over the same time period but

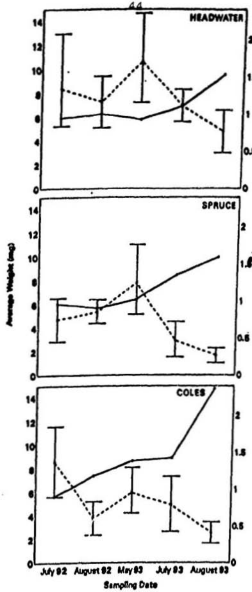

Figure 4.4: Average individual weight (—) and density (---) of the dragonfly <u>Cordulia</u>.

differences were not significant (Figure 4.4). These increases correspond to a period of recruitment in all three ponds. This recruitment was followed by a period of emergence and/or high predation pressure from May 1993 to August 1993 as indicated by the significant decline in densities (Figure 4.4). The average individual weight of Cordulia increased throughout the study in all ponds (Figure 4.4). The increasing average weight despite recruitment suggests the influence of a strong, older cohort. This is illustrated in Figure 4.5 which shows the median length continually increasing in the three ponds over the course of the study. There was an absence of smaller individuals in the August samples (Clarke unpub. data) suggesting that recruitment to catchable size is fairly synchronous and thus Cordulia may have a synchronous emergence in these ponds. This observation agrees with observations in Quebec where the same species were observed to emerge synchronously over a one week period in 1982 and a two week period in 1983 (Caron and Pilon 1990).

The average individual weight gain over the study period (July 1992 to August 1993) in Coles Pond was more than double that in Spruce and Headwater ponds (Figure 4.6). The weight gain was particularly large in Coles Pond over the July to August 1993 interval (Figure 4.4), suggesting that growth rates were still in an acceleration phase and that recruitment rates should thus increase in future years. An alternative

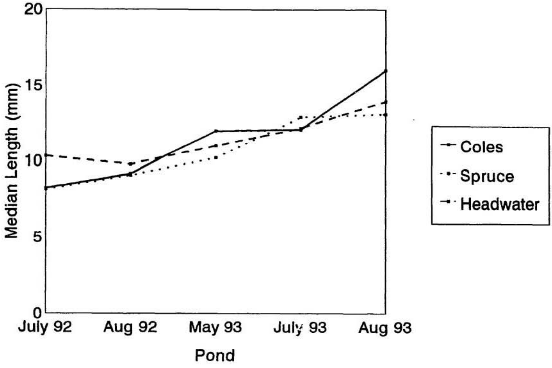

Figure 4.5: Median lengths for the dragonfly *Cordulia* in the three study ponds throughout the course of this study

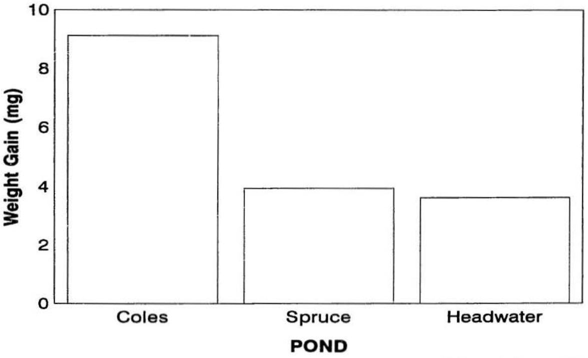

Figure 4.6: Comparison of individual weight gain of the odonate *Cordulia* (July 1992 - August 1993) among the three study ponds. Note that the greatest increase was in the fertilized pond.

mechanism behind the larger weight gain in Coles Pond could be higher rates of size-selective predation on the smaller individuals relative to the other ponds. This hypothesis however, was not supported by a salmonid stomach analysis conducted in these ponds in 1993 which revealed a preference towards larger Cordulia in salmonid diets (Clarke unpub. data).

Enallagma

Enallagma is the most abundant zygopteran (damselfly) odonate in the study systems. It is a predator of small benthic invertebrates and generally has an aquatic life stage duration of 18-24 months (Merritt and Cummins 1984).

Density increased significantly from August 1992 to May 1993 in all ponds, indicating a period of recruitment (Figure 4.7) the magnitude of which was highest in Coles Pond (Figure 4.8). This was followed by a period of emergence between May and July 1993 indicated by the significant decline in density. The average individual weight did not drop at the same time which suggests both a lack of recruitment from July to August 1993 and that emergence was not totally synchronous in the population (Figure 4.7).

Amnicola

Amnicola was the most common gastropod in the study ponds. It feeds mainly on periphyton algae and generally has a life-history duration of 12 months (Pennak 1978) although

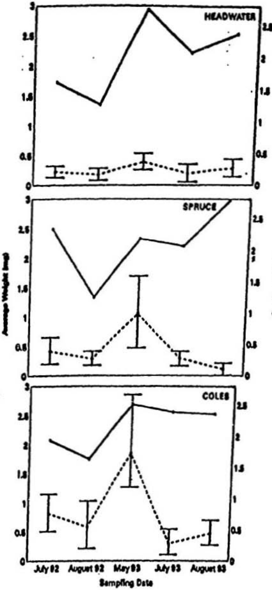

Figure 4.7: Average individual weight (—) and density (---) of the odonate Enallagma.

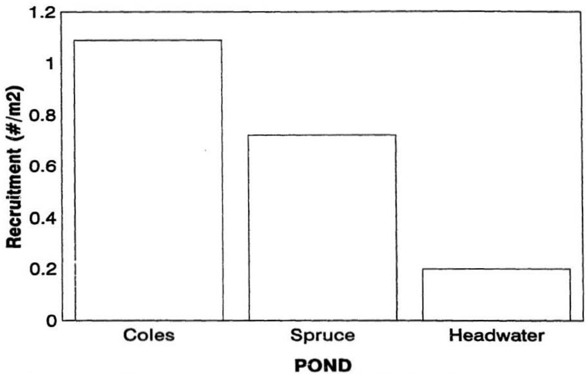

Figure 4.8: Comparison of density increases (recruitment) for the odonate *Enallagma* (August 1992 - May 1993) among the three ponds, demonstrating the highest level of increase in the fertilized pond

the life-history of Newfoundland populations has not been determined.

Density declined significantly in Spruce Pond from August 1992 to August 1993 (Figure 4.9) and significant density declines for Headwater Pond were observed from August 1992 to July 1993 with the mean for August 1992 not being significantly different from that of July 1993 (Figure 4.9). The density in Coles Pond declined significantly from May 1993 to August 1993 and the estimate for August 1992 was not significantly different from that of May 1993. These trends suggest that there is only one cohort represented in the samples from August 1992 to August 1993. This is the time period used for calculations of secondary production for this species. Small members of a new cohort would not be represented, due to the 2 mm mesh size of the sampler. The average weight of Amnicola increased throughout the course of the study in Coles and Headwater ponds as would be expected of a single cohort (Figure 4.9). The average weight in Spruce Pond declined over the first sampling interval but then followed the same pattern as in the other ponds. The annual weight gain from August 1992 to August 1993 was highest in Coles Pond (Figure 4.10). This observation was largely due to a much larger weight increase in Coles Pond from July 1993 to August 1993 as compared to the other two ponds (Figure 4.10). These observations suggest that Amnicola had enhanced growth

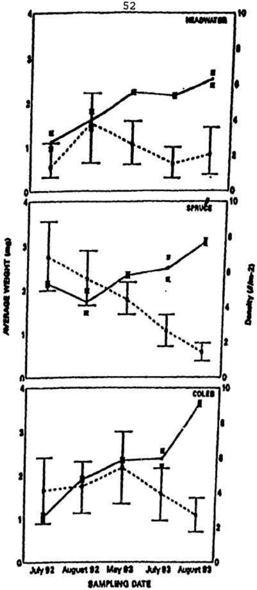

Figure 4.9: Average individual weight (—) and density (---) of the gastropod Amnicola. "*" indicates the range of replicate weight determinations.

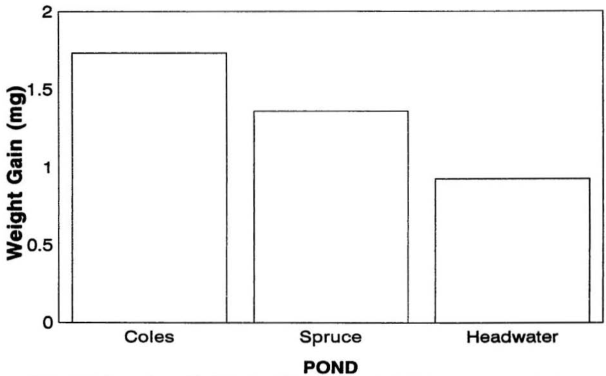

Figure 4.10: Comparison of individual weight gain of *Amnicola* (July 1992 - August 1993) among the three study ponds illustrating that the greatest increase was in the fertilizied pond.

rates in the enriched pond especially during the latter part of the study.

Helisoma

Helisoma was the second most abundant gastropod in the study ponds. It feeds on periphyton but it is much larger than Amnicola and is generally thought to have a longer life cycle (Pennak 1978).

Densities declined significantly from July 1992 to July 1993 in all ponds followed by a significant increase from July 1993 to August 1993 in Spruce and Coles ponds (Figure 4.11). A density increase was also observed in Headwater Pond for the same time period but it was not significant. The average weight also showed a general decline over the course of the study. Weight-density patterns were consistent throughout the study in that whenever the density declined the average weight increased and vice versa. This suggests that the population was going through periods where recruitment was higher than mortality followed by periods where the opposite is true. Coles Pond had the most rapid density decline and the lowest average weight which suggests that it has the highest rate of mortality (predation) and the youngest population age structure. There were no clear recruitment or growth differences among the ponds during the course of the study.

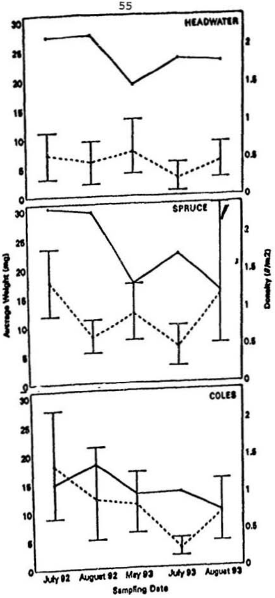

Figure 4.11: Average individual weight (—) and density (---) of the gastropod Helisoma.

Phryganea

Phryganea is a relatively large trichopteran that feeds mainly on filamentous algae (Wiggins 1978). It was the secondmost abundant trichopteran retained by the dredge sampler during this study.

Densities increased significantly from July 1992 to May 1993 in all three ponds indicating a period of recruitment (Figure 4.12). This was followed by an emergence which occurred from May 1993 to July 1993 as indicated by the rapid and statistically significant decline in density. Densities increased significantly from July 1993 to August 1993 in all three ponds suggesting a second period of recruitment (Figure 4.12). The average individual weights increased from August 1992 through July 1993 and then declined by August 1993 (Figure 4.12). The patterns in density support an interpretation of one cohort per year with the majority of emergence prior to the July sample period. However, the high average weight of those remaining indicates that not all members of the population had emerged. The weight gain from August 1992 to July 1993 was similar in all three ponds (Figure 4.13a) while recruitment from July 1992 to May 1993 was similar in Coles and Spruce ponds in both of which it was much higher than that observed in Headwater Pond (Figure 4.13b).

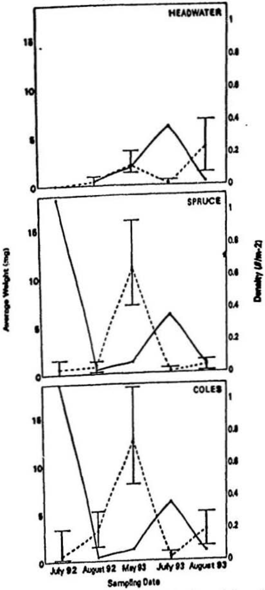

Figure 4.12: Average individual weight (—) and density (---) of the trichopteran Phryganea.

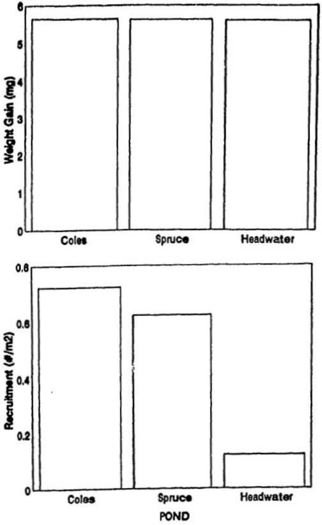

Figure 4.13 a): Average individual weight gains for August 1992 - July 1993; indicating very similar values among all ponds and b) recruitment during July 1992 - May 1993 for the trichopteran Phryganea indicting much lower recruitment in Headwater Pond.

Oecetis

Oecetis was the most abundant trichopteran retained by the dredge sampler during the study. It differs from Phryganea in that it is smaller in size and it is a predator of small invertebrates. Its aquatic life-stage duration is generally 12 months (Wiggins 1978).

Density declined in all three ponds from July to August 1992 with the differences in Headwater and Spruce ponds being significant (Figure 4.14). Density increased significantly in Spruce Pond from August 1992 to May 1993, an increase was also observed in Coles and Headwater ponds but the differences were not statistically significant. These patterns suggest recruitment occurred between August 1992 and May 1993 in all three ponds, which was followed by an emergence between May 1993 and July 1993 in Coles and Spruce ponds indicated by the decline in density (this decline was significant for Spruce Pond but not Coles Pond). This general pattern was not followed in Headwater Pond as densities continued to rise significantly through August 1993 with no indication of emergence (Figure 4.14). The large decline in average individual weight between July 1992 and May 1993 suggests a drawn-out period of summer and fall emergence, particularly in Coles Pond (Figure 4.14). The populations do not appear to be in phase in the three ponds so further analysis of growth and recruitment was not attempted.

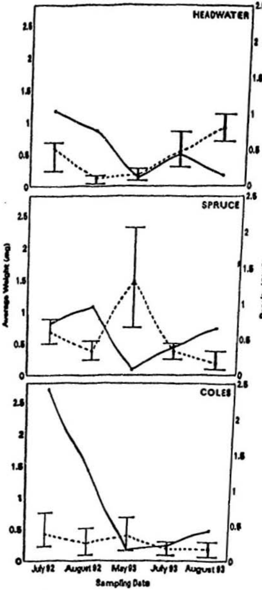

Figure 4.14: Average individual weight (—) and density (---) of the trichopteran Oecetis.

Leptophlebia

The genus Leptophlebia was the most abundant ephemeropteran collected throughout the study. Three species of this genus have been reported in the Experimental Ponds Area in the past (Ryan et. al. 1990), the specimens in the present study however, were only identified to the generic level. It is relatively large detritus-feeding ephemeropteran that generally has an aquatic life-stage duration of one year (Merritt and Cummins 1984).

Densities declined significantly from July to August in both 1992 and 1993 indicating that the dominant species has an annual life-cycle with mid-summer emergence (Figure 4.15). Growth patterns were harder to discern because of low densities which resulted in very few if any specimens to weigh at certain times of the year. Recruitment, in the dominant species, was highest in Spruce Pond from August 1992 to July 1993 followed by Coles Pond and then Headwater Pond (Figure 4.16). Recruitment seems to have been held in check in Coles Pond from May to July 1993 (Figure 4.15) suggesting higher predation pressures in the Coles Pond population. This interpretation is supported by the significant increase in brook trout, a major predator of these organisms, observed in Coles Pond over the summer of 1993 (Knoechel unpub. data).

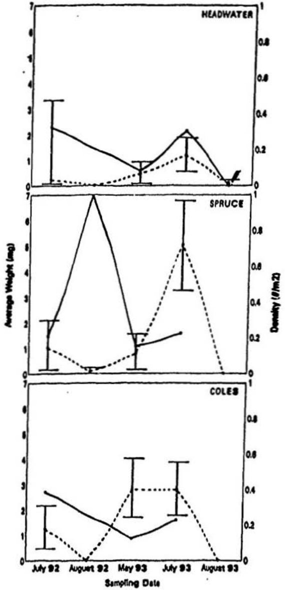

Figure 4.15: Average individual weight (——) and density (---) of the ephemeropteran Leptophlebia sp.

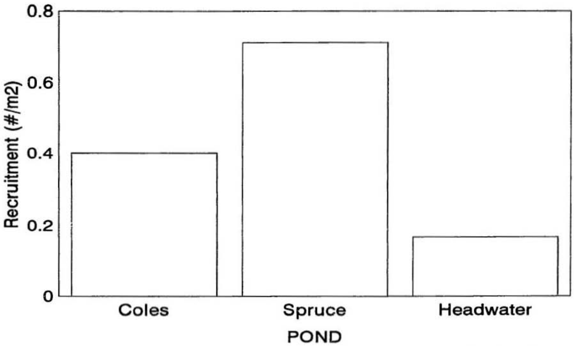

Figure 4.16: Density increases (recruitment) of the dominant *Leptophlebia* sp. August 1992 - July 1993. Illustrating the highest recruitment in Spruce Pond and the lowest in Headwater Pond

Caenis

Caenis (only C. simulans has been reported from insular Newfoundland) was the second most abundant ephemeropteran genus collected in the dredge samples. It is a small detritus-feeding organism which generally has a life-cycle of one year (Merritt and Cummins 1984). It was the smallest and lowest density organism used in production estimates and it may be that the sampling regime was inadequate to characterize its life-cycle.

The density patterns in Headwater and Spruce Ponds indicate a fall emergence in 1992 (Figure 4.17) while the 1993 patterns suggests an early summer emergence in Coles Pond and mid-summer emergences in Headwater and Spruce ponds. The populations were not in phase in the three ponds, therefore further analysis of recruitment and growth was not attempted.

SECONDARY PRODUCTION

Secondary production estimates were calculated for 10 taxa (Table 4.2). These taxa contributed 85-90% of the standing stock macroinvertebrate biomass in the ponds on all sampling dates (Figure 4.3) and should thus be good indicators of total benthic community production over the course of the study. Detailed mean weight, density and secondary production data are presented here for two taxa that contributed the major portion of the macroinvertebrate biomass and secondary

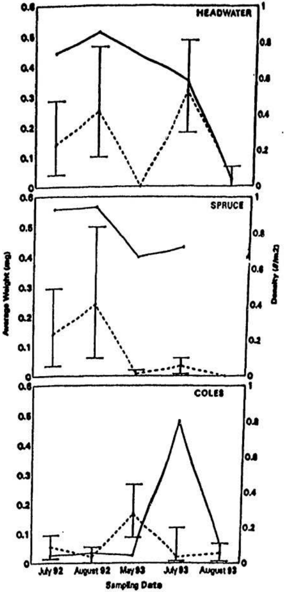

Figure 4.17: Average individual weight (—) and density (---) of the ephemeroptern Caenis.

Table 4.2 : Taxa and methods employed in secondary production estimates.

Taxon	Production Method
Amphipoda	
Hyalella	size-frequency
Gastropoda	
Amnicola	increment summation
Valvata	increment summation
Helisoma	size-frequency
Ephemeroptera	
Caenis	increment summation
Leptophlebia	increment summation
Trichoptera	
Oecetis	increment summation
Phryganea	increment summation
Odonata	
Enallagma	size-frequency
Cordulia	size-frequency

production: the gastropod Amnicola; and the odonate Cordulia. Data for the remaining taxa are contained in Appendix B.

Amnicola PRODUCTION

Amnicola is a small gastropod that feeds on epiphytic algae and it has a life-cycle of approximately one year (Pennak 1978, also see analysis above) which should make it a good indicator organism. Artificial substrate sampling indicated its abundance initially increased from 1991 to 1992 in response to fertilization (Chapter 3), following which its abundance seemed to stabilize (Figure 3.3). It is therefore a good taxon to test the ability of secondary production methodology to monitor perturbation effects, such as nutrient enrichment.

The populations of Amnicola were composed of one cohort from August 1992 to August 1993 (see above) this simplified the calculation of secondary production over this period using the increment summation method; the data needed for these calculations are summarized in Table 4.3. The 95% confidence intervals were calculated by substitution of the density confidence intervals into the increment summation method. This method of calculation assumes that the variation in weight is insignificant when compared to that observed in density. The annual secondary production estimate for Amnicola was highest in Coles Pond and lowest in Headwater

Table 4.3: Density, individual dry weight and production estimates for the gastropod Amnicola.

Pond	Sampling Date	N/m^{-2}	m (mg)	Interval Production (mg/m^{-2})
SP	18 Aug 92	5.622	1.724	NA
	22 May 93	4.433	2.335	3.067
	18 July 93	2.644	2.486	0.535
	26 Aug 93	1.422	3.084	1.203
CP	17 Aug 92	4.370	1.912	NA
	24 May 93	5.433	2.345	2.122
	17 July 93	3.944	2.388	0.202
	24 Aug 93	2.700	3.640	4.159
HWP	19 Aug 92	3.778	1.590	NA
	23 May 93	2.611	2.214	1.993
	19 July 93	1.544	2.144	- 0.108
	26 Aug 93	2.033	2.512	0.658

Ponds (Figure 4.18). The observed enhanced production of *Amnicola* in the fertilized pond (Coles) demonstrates the ability of secondary production techniques to monitor perturbation effects even after numerical responses have ceased. Headwater Pond had the lowest production estimate and further inspection of the raw data revealed that the southern basin of Headwater Pond had a very low *Amnicola* density as compared to that of the northern basin, and of the other two ponds. This low density is correlated with observations of a large amount of charcoal on the bottom at station 3 which resulted from the fire in 1986. The difference between the production in the two basins was significant ($p < 0.05$), but the removal of the southern basin data still did not bring the production estimates of Headwater Pond up to the level of Spruce and Coles ponds (Figure 4.19). This difference is thus another indication of the usefulness secondary production techniques can have in the study of perturbations in the aquatic ecosystem.

Cordulia PRODUCTION

The odonate *Cordulia* is a predator with a relatively long aquatic life stage. Investigations in Newfoundland lakes (Farrell 1985, Clarke 1992) indicate *Cordulia* has approximately 10 to 14 instars and a aquatic life-cycle duration of 4-5 years (Clarke 1992, Clarke unpub. data), hence the secondary production estimates were calculated using both

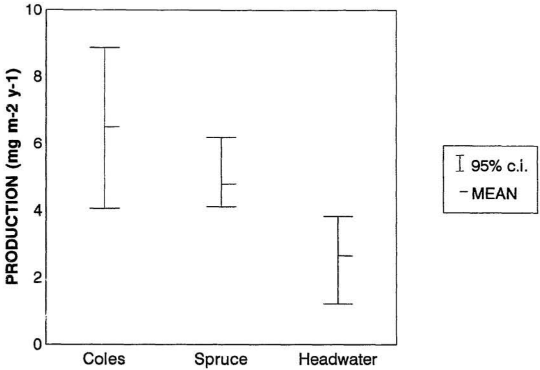

Figure 4.18: *Amnicola* production (August 1992- August 1993).

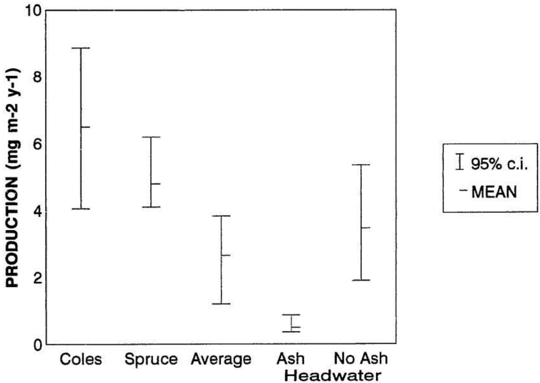

Figure 4.19: ***Amnicola*** **production (August 1992- August 1993), Illustrating the differences in the north (no ash) and south (ash) basins of Headwater Pond.**

a 4 and 5 year aquatic life stage. The long aquatic stage means that the population, was composed of several cohorts. These cohorts were difficult to separate based on size, so secondary production estimates were calculated using the size-frequency method. The data needed for these calculations are presented in Table 4.4 for Headwater Pond, Table 4.5 for Spruce Pond and Table 4.6 for Coles Pond. These calculations produce daily secondary production estimates which were multiplied by 365 to give annual secondary production.

Secondary production estimates for the Cordulia populations over the course of the study were highest in Headwater Pond followed by Coles Pond and Spruce Pond (Figure 4.20). The differences are not as pronounced as those observed for Amnicola which may reflect the long life-cycle of Cordulia.

INTERANNUAL PRODUCTION COMPARISONS FOR TAXA WITH ANNUAL LIFE CYCLES

Interannual comparison of secondary production were made for the trichopteran and ephemeropteran taxa by comparing their production estimates for July-August 1992 with the same time period in 1993 (Figure 4.21). Production estimates of the trichopteran Phryganea were higher in Coles Pond and Spruce Pond in 1993, while the estimate for Headwater Pond was lower in 1993 (Figure 4.21). The magnitude of the increase

Table 4.4: Size frequency characteristics used in the calculation of secondary production of the dragonfly Cordulia in Headwater Pond (estimates reported for an aquatic life-cycle of 4 and 5 years).

Size Class	Frequency N/m^2	Size Range m_{min} (mg)	m_{max} (mg)	Production ($mg/m^2/day$) 4 years	5 Years
1	0.2844	0.0891	1.9493	0.0058	0.0046
2	0.2911	2.0122	3.9322	0.0061	0.0049
3	0.1378	4.0304	5.9446	0.0029	0.0023
4	0.1644	6.0722	7.8918	0.0033	0.0026
5	0.0533	8.0445	9.5039	0.0009	0.0007
6	0.0467	10.2029	11.5032	0.0007	0.0005
7	0.0467	12.0912	13.7516	0.0008	0.0007
8	0.0244	14.4097	15.7852	0.0004	0.0003
9	0.0089	16.9930	17.2414	> 0.0001	> 0.0001
10	0.0089	18.5180	19.8533	0.0001	0.0001
11	0.0133	20.4040	21.2482	0.0001	0.0001
12	0.0178	22.1143	23.3036	0.0002	0.0002
13	0.0178	24.2218	25.8025	0.0003	0.0002
14	0.0111	26.4527	29.1576	0.0003	0.0002
15	0.0067	30.2154	33.5345	0.0002	0.0002
16	0.0111	36.6720	42.1578	0.0007	0.0005

Table 4.5: Size frequency characteristics used in the calculation of secondary production of the dragonfly Cordulia in Spruce Pond (estimates reported for an aquatic life-cycle of 4 and 5 years).

Size Class	Frequency N/m^2	Size Range m_{min} (mg)	m_{max} (mg)	Production ($mg/m^2/day$) 4 years	5 Years
1	0.2333	0.2716	1.9439	0.0037	0.0030
2	0.1467	2.0122	3.9322	0.0027	0.0022
3	0.5778	4.0304	5.9446	0.0011	0.0008
4	0.0467	6.0722	7.7409	0.0008	0.0006
5	0.0400	8.1990	9.8495	0.0007	0.0005
6	0.0267	10.3826	11.6972	0.0003	0.0003
7	0.0222	12.0912	13.7516	0.0004	0.0003
8	0.0333	14.4097	15.5504	0.0004	0.0003
9	0.0089	16.7469	17.7451	0.0001	0.0001
10	0.0089	18.5180	19.8533	0.0001	0.0001
11	0.0178	20.4040	23.6072	0.0005	0.0004
12	0.0089	24.2218	25.8025	0.0001	0.0001
13	0.0133	28.4656	29.1576	0.0001	0.0001
14	0.0067	30.9340	32.7779	0.0001	0.0001

Table 4.6: Size frequency characteristics used in the calculation of secondary production of the dragonfly Cordulia in Coles Pond (estimates reported for an aquatic life-cycle of 4 and 5 years).

Size Class	Frequency N/m^2	Size Range m_{min} (mg)	m_{max} (mg)	Production ($mg/m^2/day$) 4 years	5 Years
1	0.2378	0.2716	1.8876	0.0042	0.0034
2	0.1689	2.0122	3.8356	0.0034	0.0027
3	0.0689	4.0304	5.8187	0.0014	0.0011
4	0.0644	6.0722	7.4448	0.0010	0.0008
5	0.0356	8.1990	9.8495	0.0006	0.0005
6	0.0356	10.3826	11.6972	0.0005	0.0004
7	0.0222	12.2914	13.7516	0.0004	0.0003
8	0.0133	14.4097	15.5504	0.0002	0.0001
9	0.0156	16.2615	17.4921	0.0002	0.0002
10	0.0156	18.5180	19.8533	0.0002	0.0002
11	0.0067	20.4040	21.2482	0.0001	> 0.0001
12	0.0244	22.7040	23.6072	0.0002	0.0002
13	0.0267	24.2218	25.8025	0.0005	0.0004
14	0.0067	26.7817	27.4474	> 0.0001	> 0.0001
15	0.0133	29.1576	37.4845	0.0012	0.0010
16	0.0200	40.8485	45.3159	0.0010	0.0008

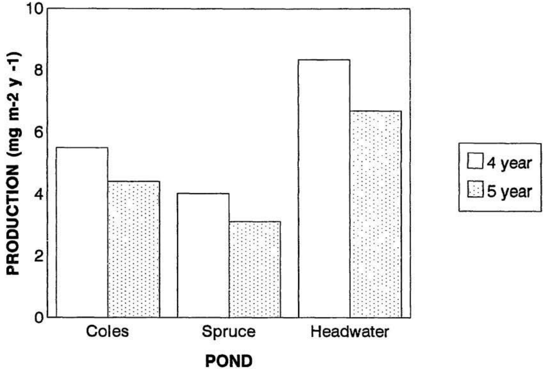

Figure 4.20: Annual secondary production of *Cordulia*: Production was calculated using both a 4 and 5 year aquatic life-stage duration.

was larger in Coles Pond and is correlated to observations of large blooms of filamentous algae in Coles Pond over the summer of 1993. These algae are the main food source for this species of trichopteran (Wiggins 1978) and blooms were not obvious in the other two ponds. The production estimates for the ephemeropteran Leptophlebia were higher in all three ponds during July-August 1993 while those of the trichopteran Oecetis were lower in all three ponds (Figure 4.21). These interannual comparisons do not indicate any clear trends in secondary production due to fertilization during the two study years for these taxa, with the possible exception of the trichopteran Phryganea which was observed to have a large increase in production in 1993 as compared to 1992.

TOTAL BENTHIC MACROINVERTEBRATE PRODUCTION

The majority of the benthic macroinvertebrate production in the EPA ponds was attributable to the gastropoda and odonata (Figure 4.22). Total benthic macroinvertebrate production was highest in Spruce Pond, followed by Coles Pond and Headwater Pond. Spruce Pond's higher production estimate was the result of a larger gastropod component, the majority of which is attributable to a large production estimate for Helisoma (Table 4.8).

Coles Pond had the highest production estimates for the amphipod and trichopteran communities while being the second

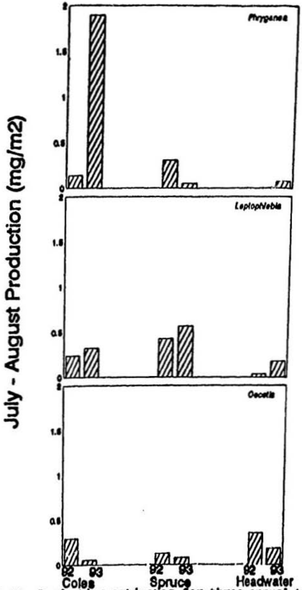

Figure 4.21: Production estimates for three annual taxa comparing the period July - August for both 1992 and 1993.

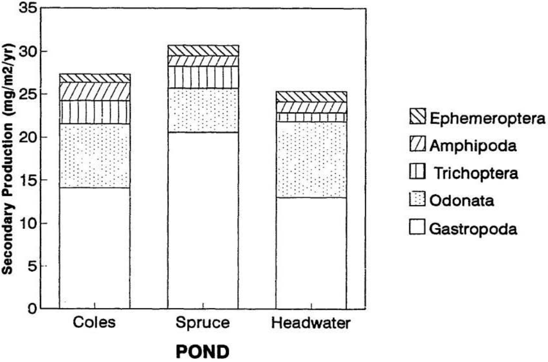

Figure 4.22: Macroinvertebrate secondary production for the three study ponds (production was corrected for an annual basis)

Table 4.7: Production estimates for the most abundant taxa from July 1992 - August 1993. Estimates are given in mg dry wt./m^2/yr. Values are given for individual orders and further subdivided to genera where necessary (e.g. the Trichoptera production of 2.6398 mg/m^2 for Coles Pond consisted of 0.3784 mg/m^2 from the genus Oecetis and 2.2614 mg/m^2 from the genus Phryganea.

Taxon	Coles	Spruce	Headwater
Amphipoda *Hyalella*	2.1697	1.2119	1.2309
Gastropoda	14.1480	20.5976	12.9900
Amnicola	6.4830	4.6750	2.6310
Valvata	-	1.2938	-
Helisoma	7.6650	14.6288	10.3590
Ephemeroptera	0.9859	1.2546	0.8065
Caenis	0.0751	0.1137	0.2805
Leptophlebia	0.9108	1.1409	0.5260
Trichoptera	2.6398	2.5912	1.0327
Oecetis	0.3784	0.6324	0.6279
Phryganea	2.2614	1.9588	0.4048
Odonata	7.7352 6.5800	5.4788 4.6020	8.1643 6.6360
Enallagma	1.9591	1.0944	0.5219
Cordulia	5.4860 4.3888	4.0234 3.1207	8.3534 6.6828
Total Production	27.3885	30.7731	24.9354

NOTE: Values for Cordulia are given for both 4 and 5 year life cycles, the total uses the estimate for the 4 year life-cycle. The production estimates that utilized the increment summation method were corrected to a annual rate by dividing the total production over the course of the study by the time elapsed from July 92-August 93.

most productive in the ephemeropteran, gastropod and odonate communities (Table 4.8). On an individual taxon basis, Coles Pond had the highest production estimates for 4 of the 9 taxa studied. Spruce Pond had the highest production estimates in 4 of the 9 taxa and Headwater Pond had the highest production estimates in only 1 of the 9 taxa (Table 4.8). Observations of accelerating growth or recruitment rates noted for several taxa in Coles Pond in August 1993 suggest that secondary production will increase further with continued fertilization.

MACROINVERTEBRATE PRODUCTION: NEWFOUNDLAND vs MAINLAND

Benthic macroinvertebrate production estimates for individual taxa in these ponds are very low as compared to published estimates from mainland North America. Benke (1976) reported a production estimate of 1927.6 $mg/m^2/yr$ for the odonate Epitheca in a eutrophic farm pond in South Carolina. The highest estimate for an odonate in this study was only 7.7 $mg/m^2/yr$ (Table 4.8). Ephemeroptera production estimates reported from the Ogeechee River, Georgia for Ephemerella argo, Tricorythodes sp. and Baetis intercalaris, were 275.9, 457.0 and 2735.3 $mg/m^2/yr$ respectively (Benke 1994), while the maximum estimate for an ephemeropteran in the present study was only 1.1 $mg/m^2/yr$. The low estimates are largely due to the low densities of benthic organisms in these systems which is correlated to the low primary production of Newfoundland

Lakes (Knoechel and Campbell 1988).

SUMMARY

The species collected in this study were typical for the Newfoundland fauna and the species assemblages were similar among the study ponds, with the more abundant taxa being present in all three lakes.

Gastropoda and Odonata made up the majority of the benthic macroinvertebrate biomass. Differences in benthic biomass for the three lakes throughout the sampling period appeared to be correlated with density and growth patterns of aquatic insects in the area. This resulted in a general trend where benthic biomass was low in the summer (July) and increased in the fall corresponding to the mid-late summer emergence of most aquatic insects in this area.

Fertilization appears to have enhanced the individual growth rates of Cordulia and Amnicola, particularly in 1993, while recruitment of Enallagma also appears to have been enhanced relative to the control ponds (Table 4.9). Growth and recruitment rates of Helisoma did not vary significantly among ponds while Phryganea and Leptophlebia demonstrated an intermediate rate of recruitment but no growth response in the enriched pond (Table 4.9). The life cycles of Oecetis and Caenis appeared to be out of phase among the ponds preventing comparison of growth and recruitment.

Table 4.8: Benthic community responses to whole-lake enrichment in Coles Pond: Summary Table.

Taxa	Recruitment	Growth	Production
Amnicola		+	+
Helisoma			
Leptophlebia	intermediate		intermediate
Caenis	NA	NA	intermediate
Oecetis	NA	NA	-
Phryganea	+ (vs HWP)		+
Enallagma	+		+
Cordulia		+	+

+ denotes an increase (relative to control ponds)

- denotes a decrease (relative to control ponds)

intermediate (increases observed but differences not large relative to control ponds)

NA Not available because distinct recruitment and growth periods could not be identified.

The macroinvertebrate taxa of Newfoundland lakes were estimated to have low secondary production. This is a general indication of the overall low production of these systems. The secondary production estimate for the gastropod Amnicola was higher in the fertilized pond as compared to the other two ponds (Table 4.9). The trichopteran and ephemeropteran communities also showed increases in secondary production in 1993 over 1992 in Coles Pond (Table 4.9).

These trends demonstrate the ability of production techniques to monitor experimental perturbations and also illustrate the positive effect fertilization is having on the macroinvertebrate community of Coles Pond.

CHAPTER 5: GENERAL SUMMARY

Biomonitoring techniques showed that the nutrient enrichment of Coles Pond increased the abundance of several components of the benthic community. The speed and magnitude of these responses appear to be closely related to the life history and trophic role of the organisms. This produced a gradient of numerical responses, where for example short-lived herbivores have increased in abundance much faster and to a larger degree than long-lived predators. For example chironomids, gastropods and sphaeriid clams demonstrated relative abundance increases of 6 fold, 4 fold and 2 fold respectively. In comparison, longer-lived higher trophic taxa such as leeches and odonata demonstrated no significant abundance differences over the 3 year fertilization period. These observations tend to support the idea that "bottom-up" and "top-down" processes are both important in structuring these ecosystems, with "bottom-up" processes causing an initial increase in herbivores directly correlated to the nutrient enrichment. This increase in abundance of food organisms in turn enhances conditions for organisms higher in the food chain and they increase in abundance with a lag.

The benthic community of these insular Newfoundland lakes is composed of a sub-set of species from the North American fauna. These species are generally holarctic in their distribution and occur in these lakes in relatively low densities. These low densities and the overall lower production of Newfoundland lakes combine to create conditions where benthic biomass and secondary production estimates are low when compared to sites in mainland North America.

Secondary production of several components of the benthic community appeared to be increased by nutrient additions to Coles Pond. These increases were most apparent in the short-lived herbivores such as the gastropod Amnicola and the trichopteran Phryganea. These organisms feed primarily on benthic epiphytic and filamentous algae, which suggests that the benthic primary production of Coles Pond has been increased significantly by fertilization.

Secondary production estimates for the other members of the benthic community were similar in Coles Pond and Spruce Pond. These organisms were generally higher in the food chain (i.e. detritivores and predators) and had a longer than one year aquatic life-stage. Some of these organisms were observed to have increased growth (e.g. Cordulia) and/or recruitment (e.g. Enallagma). These increases were more prevalent during the second half of the study (1993) suggesting that the production of these organisms was still increasing. This increased production should become more apparent in future years if the enrichment of Coles Pond is continued.

The secondary production estimate for the gastropod Amnicola in Headwater Pond was significantly lower than those observed in Coles Pond and Spruce Pond. This difference was due in large part to the low densities observed in the northern basin which were correlated with the presence of charcoal in the sediment, resulting from a fire that burned to the shoreline in 1986. The fact that the density is still low 6-7 years after the fire suggests that these ecosystems may have a long recovery period when externally perturbed.

The benthic community of Coles Pond appears to be still in the initial increasing phase brought about by "bottom-up" processes. The higher predators were beginning to show increases in growth and recruitment during the later stages of the study. It is expected that with continued fertilization benthic abundances and production will continue to climb until populations reach a new equilibrium with an overall higher production level for the ecosystem.

The nutrient enrichment of Coles Pond appears to be successfully increasing the productivity of the whole ecosystem. The process is simple and relatively inexpensive and therefore may be a realistic method of enhancing some of our 10000 small lakes. One ultimate goal of enrichment is to enhance salmonid production. Brook trout and Atlantic salmon have been observed to feed almost exclusively on benthic organisms in Newfoundland pond ecosystems (Baggs 1989, Clarke and Knoechel unpub.). A study on the effect that enrichment is having on the salmonid population of Coles Pond is ongoing. It is apparent from the present study that nutrient enrichment has produced significant increases in density (abundance), growth and production of the benthic macroinvertebrate community.

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Appendix A: Length : Dry weight regressions used in benthic biomass estimates.

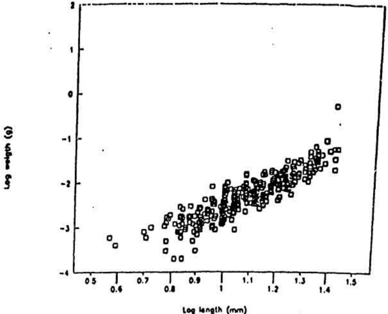

Figure A1: The length : Dry weight regression for the dragonfly <u>Cordulia</u>.

The regression equation is:

Log dry weight(g) = -5.27 + 2.75(log length (mm))

r^2 = .789

Analysis of variance

source	DF	SS	MS	F	p
Regression	1	60.264	60.264	1133.70	<.001
Error	304	16.160	0.053		
Total	305	76.424			

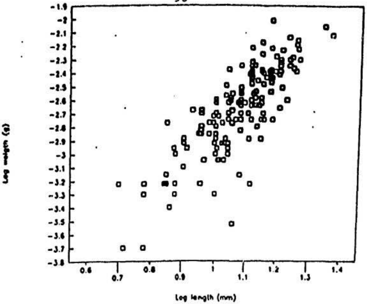

Figure A2: The length : Dry weight regression for the damselfly Enallagma.

The regression equation is:

Log dry weight(g) = -5.03 + 2.19(log length (mm))

r^2 = .655

Analysis of variance

source	DF	SS	MS	F	p
Regression	1	11.158	11.158	297.62	<0.001
Error	157	5.886	0.037		
Total	158	17.044			

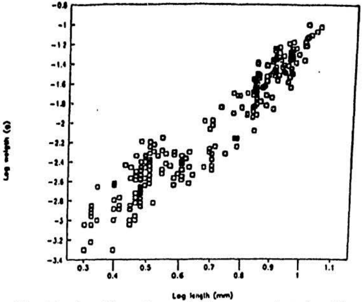

Figure A3: The length : Dry weight regression for the gastropod Helisoma.

The regression equation is:

Log dry weight(g) = -3.92 + 2.67(log length (mm))

$r^2 = .909$

Analysis of variance

source	DF	SS	MS	F	p
Regression	1	74.623	74.623	2344.78	<.001
Error	234	7.447	0.032		
Total	235	82.070			

Appendix B: Secondary Production estimates for the most abundant benthic organisms.

Table B1: Density, average individual dry weight and production estimates for the gastropod Valvata.

Pond	Sampling Date	N/m^2	m(mg)	Interval Production (mg/m^2)
SP	6 July 92	1.822	2.928	NA
	18 Aug 92	1.444	2.820	0
	22 May 93	1.644	3.264	0.6855
	18 July 93	0.967	3.466	0.2637
	26 Aug 93	0.544	4.161	0.5253

Valvata was not abundant enough in Coles Pond or Headwater Pond for the calculation of secondary production.

Table B2: Density, average individual dry weight and production estimates for the ephemeropteran Caenis.

Pond	Sampling Date	N/m^2	m(mg)	Interval Production (mg/m^2)
SP	6 July 92	0.233	0.557	NA
	18 Aug 92	0.400	0.565	0.0026
	22 May 93	0.056	0.400	0.1130
	18 July 93	0.056	0.433	0.0019
	26 Aug 93	0.000	NA	0.0121
CP	8 July 92	0.089	0.025	NA
	17 Aug 92	0.033	0.033	0.0005
	24 May 93	0.278	0.025	0.0039
	17 July 93	0.033	0.480	0.0708
	24 Aug 93	0.056	0.060	0.0096
HWP	7 July 92	0.233	0.444	NA
	19 Aug 92	0.422	0.513	0.0226
	23 May 93	0.000	NA	0.1081
	19 July 93	0.533	0.352	0.0939
	26 Aug 93	0.044	0.020	0.0943

Table B3: Density, average individual dry weight and production estimates for the ephemeropteran Leptophlebia.

Pond	Sampling Date	N/m^2	m(mg)	Interval Production (mg/m^2)
SP	6 July 92	0.144	1.469	NA
	18 Aug 92	0.011	6.975	0.4267
	22 May 93	0.111	1.071	0.0978
	18 July 93	0.722	1.572	0.2084
	26 Aug 93	0.000	NA	0.5674
CP	8 July 92	0.178	2.700	NA
	17 Aug 92	0.000	NA	0.2403
	24 May 93	0.400	0.870	0.1740
	17 July 93	0.400	1.603	0.2932
	24 Aug 93	0.000	NA	0.3206
HWP	7 July 92	0.033	2.28	NA
	19 Aug 92	0.000	NA	0.0376
	23 May 93	0.067	0.575	0.0193
	19 July 93	0.167	2.129	0.3635
	26 Aug 93	0.011	0.001	0.1777

Table B4: Density, average individual dry weight and production estimates for the trichopteran Oecetis.

Pond	Sampling Date	N/m^2	m(mg)	Interval Production(mg/m^2)
SP	6 July 92	0.611	0.815	NA
	18 Aug 92	0.333	1.075	0.1228
	22 May 93	1.322	0.088	0.2368
	18 July 93	0.333	0.433	0.2861
	26 Aug 93	0.167	0.733	0.0750
CP	8 July 92	0.378	2.700	NA
	17 Aug 92	0.244	1.433	0.2929
	24 May 93	0.356	0.180	0.0180
	17 July 93	0.167	0.240	0.0628
	24 Aug 93	0.167	0.480	0.0534
HWP	7 July 92	0.522	1.176	NA
	19 Aug 92	0.111	0.867	0.3551
	23 May 93	0.156	0.133	0.0585
	19 July 93	0.478	0.493	0.1140
	26 Aug 93	0.811	0.169	0.1863

Table B5: Density, average individual dry weight and production estimates for the trichopteran *Phryganea*.

Pond	Sampling Date	N/m^2	m(mg)	Interval Production (mg/m^2)
SP	6 July 92	0.033	18.00	NA
	18 Aug 92	0.044	0.420	0.3062
	22 May 93	0.656	1.175	0.2643
	18 July 93	0.011	6.000	1.6091
	26 Aug 93	0.044	0.900	0.0528
CP	8 July 92	0.033	18.35	NA
	17 Aug 92	0.189	0.414	0.1401
	24 May 93	0.756	1.181	0.3622
	17 July 93	0.022	6.050	1.8941
	24 Aug 93	0.189	0.950	0.1563
HWP	7 July 92	0.000	NA	NA
	19 Aug 92	0.022	0.400	0.0044
	23 May 93	0.122	1.825	0.1026
	19 July 93	0.011	6.000	0.2776
	26 Aug 93	0.233	0.367	0.0757

Table B6: Size frequency characteristics used in the calculation of secondary production of the damselfly *Enallagma* in Coles Pond (estimates reported for an aquatic life-cycle of 18 months).

Size Class	Frequency N/m^2	m_{min} (mg)	m_{max} (mg)	Production ($mg/m^2/day$)
1	0.009	0.1450	0.2162	>0.0001
2	0.051	0.2277	0.7256	0.0005
3	0.064	0.7698	1.2330	0.0006
4	0.060	1.3522	1.7457	0.0005
5	0.116	1.7809	2.2342	0.0011
6	0.067	2.2745	2.6992	0.0006
7	0.056	2.7889	3.2123	0.0005
8	0.051	3.2613	3.6161	0.0004
9	0.024	3.7742	4.1576	0.0002
10	0.024	4.3280	4.6204	0.0001
11	0.004	4.9233	6.5956	0.0001

Table B7: Size frequency characteristics used in the calculation of secondary production of the damselfly Enallagma in Spruce Pond (estimates reported for an aquatic life-cycle of 18 months).

Size Class	Frequency N/m^2	m_{min} (mg)	m_{max} (mg)	Production ($mg/m^2/day$)
1	0.049	0.2897	0.7256	0.0004
2	0.044	0.7698	1.2330	0.0004
3	0.044	1.2623	1.7457	0.0004
4	0.064	1.7809	2.2342	0.0005
5	0.027	2.3563	2.6550	0.0001
6	0.029	2.8343	3.1154	0.0001
7	0.040	3.2613	3.6684	0.0003
8	0.011	3.8817	4.1576	0.0001
9	0.011	4.4437	4.6204	>0.0001
10	0.002	5.2336	7.7275	0.0006

Table B8: Size frequency characteristics used in the calculation of secondary production of the damselfly *Enallagma* in Headwater Pond (estimates reported for an aquatic life-cycle of 18 months).

Size Class	Frequency N/m^2	m_{min} (mg)	m_{max} (mg)	Production (mg/m^2/day)
1	0.027	0.3168	0.7040	0.0002
2	0.018	0.7698	1.2330	0.0001
3	0.024	1.2919	1.6763	0.0002
4	0.033	1.7809	2.2342	0.0002
5	0.020	2.5246	2.7438	0.0001
6	0.018	2.8802	3.0675	0.0001
7	0.020	3.2613	3.7211	0.0002
8	0.013	3.8277	4.2140	0.0001
9	0.016	4.2708	5.4296	0.0003

Table B9: Size frequency characteristics used in the calculation of secondary production of the gastropod <u>Helisoma</u> in Coles Pond (estimates reported for an aquatic life-cycle 18 months).

Size Class	Frequency N/m^2	m_{min} (mg)	m_{max} (mg)	Production ($mg/m^2/day$)
1	0.058	0.7700	2.4700	0.0015
2	0.067	2.6800	7.4900	0.0048
3	0.042	7.9200	11.960	0.0025
4	0.036	13.130	15.690	0.0014
5	0.098	17.800	21.700	0.0057
6	0.029	22.540	27.030	0.0019
7	0.036	27.990	32.040	0.0022
8	0.007	33.100	42.450	0.0015

Table B10: Size frequency characteristics used in the calculation of secondary production of the gastropod <u>Helisoma</u> in Spruce Pond (estimates reported for an aquatic life-cycle 18 months).

Size Class	Frequency N/m^2	m_{min} (mg)	m_{max} (mg)	Production ($mg/m^2/day$)
1	0.093	0.7652	2.4657	0.0038
2	0.078	2.6838	7.4903	0.0090
3	0.031	8.3719	11.3964	0.0023
4	0.022	13.1327	16.3772	0.0017
5	0.024	17.8024	21.6976	0.0023
6	0.016	21.6976	26.0864	0.0016
7	0.044	28.9663	32.0372	0.0033
8	0.027	33.1042	36.4375	0.0021
9	0.073	37.5933	42.4451	0.0086
10	0.029	43.7160	46.3286	0.0018
11	0.013	49.0368	51.8418	0.0009
12	0.020	51.8418	56.2341	0.0021
13	0.007	57.7481	60.8521	0.0005

Table B11: Size frequency characteristics used in the calculation of secondary production of the gastropod Helisoma in Headwater Pond (estimates reported for an aquatic life-cycle 18 months).

Size Class	Frequency N/m²	m_{min} (mg)	m_{max} (mg)	Production (mg/m²/day)
1	0.044	0.7652	2.4657	0.0015
2	0.040	2.6838	7.4903	0.0039
3	0.042	7.9234	11.3964	0.0030
4	0.022	13.7460	16.3772	0.0012
5	0.038	17.8024	21.6976	0.0030
6	0.020	22.5351	26.0254	0.0018
7	0.058	27.9853	32.0372	0.0048
8	0.029	33.1042	36.4375	0.0020
9	0.056	37.5933	42.4451	0.0055
10	0.024	43.7160	46.3286	0.0013
11	0.013	53.2812	54.7452	0.0004

Table B12: Size frequency characteristics used in the calculation of secondary production of the amphipod *Hyalella* in Coles Pond (estimates reported for an aquatic life-cycle of 9 months).

Size Class	Frequency N/m^2	m_{min} (mg)	m_{max} (mg)	Production (mg/m^2/day)
1	0.016	0.1400	0.4500	0.0001
2	0.029	1.4290	1.6500	0.0001
3	0.187	2.2300	5.0300	0.0058

Table B13: Size frequency characteristics used in the calculation of secondary production of the amphipod *Hyalella* in Spruce Pond (estimates reported for an aquatic life-cycle of 9 months).

Size Class	Frequency N/m^2	m_{min} (mg)	m_{max} (mg)	Production (mg/m^2/day)
1	0.351	0.0813	0.3625	0.0011
2	0.076	0.4000	1.6500	0.0011
3	0.069	2.2182	3.7417	0.0012

Table B14: Size frequency characteristics used in the calculation of secondary production of the amphipod *Hyalella* in Headwater Pond (estimates reported for an aquatic life-cycle of 9 months).

Size Class	Frequency N/m^2	m_{min} (mg)	m_{max} (mg)	Production (mg/m^2/day)
1	0.504	0.2400	0.5672	0.0018
2	0.033	0.2000	1.5000	0.0005
3	0.053	2.0545	3.8600	0.0011