Depth-specific patterns of benthic secondary production in an oligotrophic lake

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Abstract. Benthic secondary production plays an important role in the population, community, and ecosystem dynamics of lakes. However, whole-lake estimates of benthic secondary production are rare, and very little is known about intralake patterns in production. We measured benthic secondary production for the dominant macroinvertebrate taxa in Crampton Lake, a 26-ha north-temperate lake at the border of Wisconsin and Michigan, USA. Production was estimated by the size–frequency method for each taxon at each depth where it occurred. Confidence intervals for production estimates were determined by bootstrapping. A small number of taxa were responsible for most benthic secondary production, and most taxa were not highly productive. Thus, we observed a log-normal rank–production relationship. This relationship might be common in other lakes. However, production was not strongly related to abundance, a result that suggests that even rare taxa might contribute substantially to secondary production. Whole-lake benthic secondary production averaged 4.4 g dry mass $m^{-2} y^{-1}$. Across depths, confidence intervals for area-specific rates of production generally overlapped, although point estimates were somewhat higher in the littoral zone (4.8–6.5) than in the profundal zone (3.2–4.5). Despite this similarity in rates, >65% of whole-lake benthic secondary production occurred in the littoral zone because of lake morphometry. A synthesis of limited published data revealed multiple patterns in the relationship between depth and benthic secondary production in other lakes. In most lakes, area-specific rates of production either declined or remained constant as depth increased. This observation, combined with the fact that most lakes are small and predominantly littoral, suggests that littoral dominance of whole-lake benthic secondary production might be widespread, and might help explain recent findings that lake fishes rely heavily on littoral production.

Key words: secondary production, benthic macroinvertebrate, lake, littoral, food web.

Limnologists have long recognized implicitly that benthic processes play a role in lake food webs (Lindeman 1942). Only recently, however, have conceptual models of lake food webs begun to incorporate benthic pathways explicitly as key components (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002). The advent of stable-isotope methods in foodweb ecology demonstrated that fishes often rely heavily on energy derived from benthic–littoral pathways (Hecky and Hesslein 1995, Vander Zanden and Vadeboncoeur 2002, Karlsson and Bystrom 2005). Modeling studies suggest that use of littoral prey might have important consequences for population

and community dynamics (Schindler et al. 1996, Post et al. 2000, Vadeboncoeur et al. 2005, Vander Zanden et al. 2005), and empirical evidence indicates that direct predation on benthic invertebrates is the predominant pathway connecting fishes to benthic processes in most lakes and species (Vander Zanden and Vadeboncoeur 2002). These results have heightened interest in the secondary production of lake invertebrates.

Unfortunately, data describing patterns in benthic secondary production in lakes are relatively limited. Many estimates of whole-lake benthic secondary production were produced in conjunction with the International Biological Program in the 1960s and 1970s (Kajak and Hillbricht-Ilkowska 1972). However, these studies were mostly interested in energy fluxes at the ecosystem level; their methods were often designed to give only rough whole-ecosystem estimates with roughly defined uncertainties. Increasing evidence that both resource use and predation risk of zoobenthos might vary as a function of taxonomy and

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TABLE 1.   Physical characteristics of lakes for which depth-specific patterns of benthic secondary production with depth have been estimated. DO = dissolved O_2. — indicates data not available.

Lake	Country	Max depth (m)	Mean depth (m)	Bottom DO (mg/L)[a]	Mean pH	Surface area (km^2)	Trophic state	Reference
Crampton	USA	18.5	4.9	0.2	6.4	0.26	Oligotrophic	This study
Batchawana	Canada	11	—	0.08	6.1	0.058	Oligotrophic	Dermott 1988
Esrom	Denmark	22.3	13.5	—	9.2	17.3	Eutrophic	Jónasson et al. 1990
Mikolajskie	Poland	27.8	11	—	8.25	4.6	Eutrophic	Kajak 1978
Thingvallavatn	Iceland	114	34.1	—	8.5	83	Oligotrophic	Lindegaard 1992
Little Turkey	Canada	11	—	0.16	6.6	3.305	Oligotrophic	Dermott 1988
Turkey	Canada	27	—	3.7	6.7	0.52	Oligotrophic	Dermott 1988

[a] Measured in mid-August

depth (e.g., Venturelli and Tonn 2005, Hershey et al. 2006, Solomon et al. 2008) suggests that more detailed consideration of intralake patterns of secondary production will be necessary to explain fully the role of zoobenthos in lake food webs. Such detailed studies of secondary production are rare (Lindegaard 1992).

We present a whole-lake estimate of benthic secondary production for a north-temperate lake. Our study combines high taxonomic resolution, explicit consideration of biases and uncertainties, and a focus on production–depth relationships, and therefore, provides unique insights into patterns of benthic secondary production in this and other lakes.

Methods

We estimated benthic secondary production in Crampton Lake, an oligotrophic system at the University of Notre Dame Environmental Research Center on the border between Wisconsin and the Upper Peninsula of Michigan, USA (lat 46°13′N, long 89°32′W). Crampton Lake has a surface area of 26 ha, a maximum depth of 18.5 m, and a mean depth of 4.9 m. During our study period, mean Secchi depth and mixed-layer depth were 5 m and 4.4 m, respectively. Surface temperatures ranged from 20.6 to 27.5°C, mean total P was 7.6 µg/L, and mean dissolved O_2 at 4.5 m was 6.5 mg/L. The littoral zone, defined here as depths <4.5 m, makes up 52% of lake area. For additional site description, see Table 1 and Pace et al. (2007).

We sampled benthic macroinvertebrates approximately every other week from 13 June through 23 August 2005 and on additional dates in mid-September and early October, for a total of 7 sampling occasions spanning 5 mo. We did not sample during the winter, when low water temperatures result in minimal growth of invertebrates. Thus, we assumed that our October sample adequately represented the maximum size attained by taxa that overwinter as late-

instar larvae and emerge before June. On each sampling date, we used a 60-cm-long Kajak–Brinkhurst multiple corer to collect 2 replicate cores (depth of core ~20 cm, area = 4.3×10^{-3} m^2) at each of 14 sites distributed around the lake. Sampling sites were stratified by depth, so that each depth stratum was sampled in approximate proportion to its area (2 sites at 0.5 m, 3 at 1.5 m, 3 at 3.5 m, 3 at 6 m, 2 at 10 m, and 1 at 15 m). We considered all of the cores collected at a given depth and sampling date to be replicate samples of the invertebrate assemblage in that depth stratum, and calculated a single production estimate for each taxon within each depth stratum.

Substrate at the littoral sites (0.5, 1.5, and 3.5 m) consisted of sand and gravel covered by a thin (~0.5–5 cm) layer of unconsolidated organic matter; the substrate at deeper sites was predominantly unconsolidated organic matter. Substrate at our sampling locations was representative of most of the lake because there is relatively little spatial heterogeneity in substrate in Crampton Lake. Macrophytes are present in the littoral zone but do not cover a large proportion of lake area.

We sieved cores through 500-µm mesh, preserved the samples in 70% ethanol, and dyed them with rose Bengal. We removed all organisms from the preserved samples under 20 to 25× magnification and identified them to genus when possible. We excluded taxa, including tubificid worms, water mites, and ostracods, that were not sampled effectively by our mesh size. We identified chironomids based on Wiederholm (1983) and other taxa based on Merritt and Cummins (1996). We were unable to identify species from the odonate families Libellulidae and Corduliidae uniquely at the time of sampling, so we present only 1 production estimate for this group of taxa. Subsequent examination of 20 voucher specimens collected at various sites and dates suggested that ~75% of individuals in these families were *Celithemis elisa* (Hagen), with *Ladona julia*

(Uhler), *Libellula quadrimaculata* (Linnaeus), and *Cordulia shurtleffi* (Scudder) also present.

We estimated depth-specific rates of secondary production for all taxa except those that were very rare. We used an ocular micrometer to measure head capsule width or total length (to the nearest 0.01 mm for chironomids or the nearest 0.1 mm for other taxa), and converted length to mass based on the relationships published by Benke et al. (1999). Production was calculated using the size–frequency method (Benke 1984), which assumes that the mean size–frequency distribution of a taxon across sampling dates is an approximation of the survivorship curve of a hypothetical average cohort. We divided all taxa into 10 equal size classes and excluded any apparent negative production in the initial size classes from the summed production across size classes (Benke and Wallace 1980). We corrected estimates for cohort production interval (CPI; the mean duration of the aquatic stage; Benke 1979). For most taxa, we used published CPI values (Stead et al. 2005), but for Amphipoda and Sphaeriidae, we estimated CPI based on temporal series of mass–frequency histograms. The result of the size–frequency calculation is an estimate of area-specific production (g dry mass m^{-2} y^{-1}) for a taxon at a depth. We calculated area-weighted production (g dry mass/y) by multiplying area-specific production by the area of each depth stratum as derived from bathymetric mapping (N. Preston, Univ. of Wisconsin, Madison, Wisconsin, unpublished data). Thus, we assumed that our estimate of area-specific production at a particular depth was representative of all of the lake area in that depth stratum. We used the strata: 0 to 1 m, 1 to 2.5 m, 2.5 to 4.5 m, 4.5 to 8 m, 8 to 12.5 m, and 12.5 to 18.5 m.

We estimated the uncertainty in our production estimates using a bootstrap procedure (Efron and Tibshirani 1993). Bootstrap techniques have improved the estimation of uncertainty in secondary production studies by avoiding problematic assumptions about the sampling distribution of production estimates (Giberson and Galloway 1985, Morin et al. 1987, Brey 1990). Bootstrapping is now applied commonly in secondary production studies, particularly in lotic systems (Huryn 1996, Carlisle and Clements 2003, Woodcock and Huryn 2007). In our analysis, 1000 bootstrapped data sets were assembled by randomly selecting *n* cores, with replacement, from the *n* actual cores collected at each depth and sampling occasion. For each bootstrapped data set, we used the procedure described above to calculate the production of each taxon at each depth. We calculated approximately 95% confidence intervals for the production of individual taxon–depth combinations as the upper and lower 2.5[th]
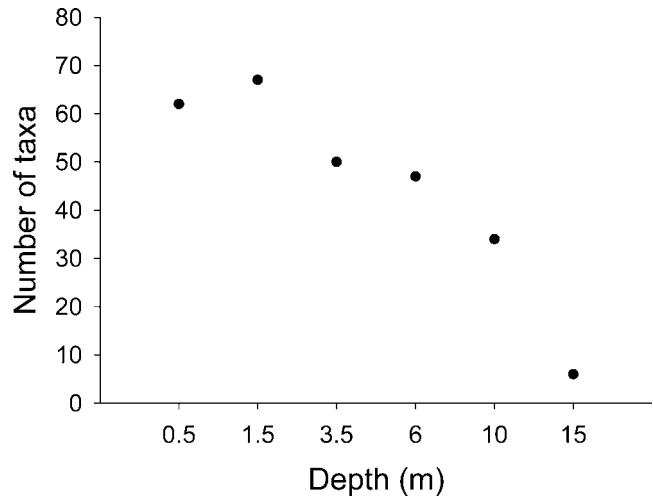

Fig. 1. Total number of benthic invertebrate taxa observed at each sampling depth across sites and dates.

percentiles of the 1000 bootstrapped production estimates for that taxon–depth combination. For aggregated production estimates (e.g., total rate of production at 1.5 m), we calculated the aggregate measure within each bootstrap, and then took the percentiles of the 1000 estimates of the aggregate measure. When comparing production rates (e.g., between 2 depth strata), we interpreted nonoverlapping confidence intervals as strong evidence for a difference in rates (Carlisle and Clements 2003, Woodcock and Huryn 2007).

We put our results in perspective by synthesizing production–depth relationships for the limited set of lakes where such data were available (Kajak 1978, Dermott 1988, Jónasson et al. 1990, Lindegaard 1992). We excluded 1 lake for which data were available (Wishart Lake; Dermott 1988) because its maximum depth (5 m) was much less than that of the other systems we considered. We expressed all production estimates as g dry mass/m^2. For estimates originally given in energetic units (kcal or kJ), we converted from kcal to g dry mass by multiplying by 0.2618 (Cummins and Wuycheck 1971).

Results

We observed 89 taxa of benthic macroinvertebrates in Crampton Lake. Taxonomic richness was highest at the shallowest sites and declined with depth (Fig. 1). We estimated secondary production at each depth for 26 of the most abundant of these taxa (total of 82 taxon-by-depth combinations; Table 2). We did not estimate production at 15 m because no taxa were sufficiently abundant at that depth to allow estimation. We assumed that the low production rates occurring in the ~5% of lake area that is in the 12.5- to 18.5-m depth

TABLE 2.   Secondary production of benthic invertebrates in Crampton Lake. For each taxon at each depth where it was observed, columns give mean biomass calculated across all sampling dates and sites (B), standard deviation of biomass (BSD), cohort production interval correction factor used in calculating production by the size–frequency method (365/CPI), point estimate of production (P), the lower and upper limits of a bootstrapped 95% confidence interval for production (low CL and high CL), the empirical estimate of the production:biomass ratio (P:B), and the mean density across all cores, sites, and dates (D). Units of mass are g dry mass.

Taxon	Depth (m)	B (g/m^2)	BSD	365/CPI	P (g m^{-2} y^{-1})	Low CL	High CL	P:B	D (ind./m^2)
Amphipoda	0.5	0.207	0.301	1.11	0.645	0.261	1.070	3.12	174
Diptera									
Ceratopogonidae									
Bezzia/Palpomyia	0.5	0.116	0.057	1.02	0.422	0.279	0.597	3.64	358
	1.5	0.170	0.118	1.02	0.800	0.551	1.030	4.71	537
	3.5	0.054	0.035	1.02	0.236	0.122	0.370	4.35	150
	6	0.035	0.034	1.02	0.119	0.021	0.178	3.40	50
Dasyhelea	0.5	0.066	0.069	1.02	0.314	0.142	0.541	4.74	972
	1.5	0.049	0.062	1.02	0.160	0.111	0.222	3.28	554
	3.5	0.013	0.014	1.02	0.037	0.021	0.056	2.82	127
Probezzia	1.5	0.037	0.019	1.02	0.126	0.065	0.203	3.44	127
	3.5	0.067	0.056	1.02	0.300	0.145	0.410	4.46	172
Chironomidae									
Ablabesmyia	0.5	0.127	0.057	1.02	0.529	0.407	0.638	4.16	798
	1.5	0.135	0.113	1.02	0.575	0.449	0.685	4.26	674
	3.5	0.086	0.079	1.02	0.355	0.246	0.442	4.11	425
	6	0.088	0.072	1.02	0.343	0.231	0.450	3.91	293
	10	0.033	0.040	1.02	0.097	0.014	0.200	2.91	174
Chironomus	6	0.048	0.047	1.23	0.218	0.126	0.332	4.55	183
	10	0.534	0.298	1.23	2.580	1.840	3.870	4.83	1146
Cladopelma	1.5	0.007	0.011	1.02	0.020	0.012	0.029	2.96	122
	3.5	0.011	0.005	1.02	0.033	0.013	0.044	3.10	127
	6	0.007	5.007	1.02	0.017	0.007	0.028	2.52	55
Cladotanytarsus	0.5	0.002	0.002	1.02	0.008	0.005	0.011	3.85	116
	1.5	0.002	0.001	1.02	0.011	0.006	0.016	4.67	133
	3.5	0.002	0.001	1.02	0.008	0.005	0.010	4.21	122
Dicrotendipes	0.5	0.033	0.042	1.02	0.165	0.096	0.226	4.94	940
	1.5	0.022	0.026	1.02	0.108	0.062	0.132	4.86	481
	3.5	0.051	0.084	1.02	0.182	0.112	0.222	3.56	421
	6	0.016	0.017	1.02	0.048	0.029	0.071	2.94	172
Lauterborniella	0.5	0.022	0.023	1.02	0.094	0.069	0.125	4.29	1712
	1.5	0.010	0.006	1.02	0.070	0.035	0.085	7.30	665
	3.5	0.004	0.004	1.02	0.014	0.008	0.021	3.40	272
Microtendipes	0.5	0.036	0.059	1.02	0.153	0.085	0.218	4.31	433
	1.5	0.048	0.055	1.02	0.196	0.134	0.244	4.09	665
	3.5	0.042	0.052	1.02	0.141	0.075	0.224	3.33	388
	6	0.019	0.024	1.02	0.050	0.026	0.081	2.58	177
Nilothauma	0.5	0.001	0.000	1.02	0.002	0.001	0.004	2.61	100
	1.5	0.001	0.000	1.02	0.002	0.001	0.003	3.18	61
Polypedilum	1.5	0.007	0.004	2.07	0.068	0.034	0.095	9.97	265
	3.5	0.026	0.034	2.07	0.284	0.117	0.392	11.1	300
	6	0.027	0.032	2.07	0.324	0.098	0.435	12.1	244
Procladius	0.5	0.036	0.024	1.02	0.186	0.109	0.241	5.20	316
	1.5	0.207	0.154	1.02	0.976	0.635	1.240	4.72	986
	3.5	0.175	0.172	1.02	0.830	0.583	0.947	4.74	642
	6	0.308	0.209	1.02	1.610	1.000	1.970	5.23	721
	10	0.120	0.099	1.02	0.401	0.241	0.618	3.34	307
Psectrocladius	0.5	0.011	0.013	1.02	0.033	0.014	0.052	3.09	150
	1.5	0.037	0.032	1.02	0.142	0.101	0.186	3.80	505
	3.5	0.027	0.031	1.02	0.110	0.075	0.137	4.10	321
	6	0.024	0.028	1.02	0.085	0.045	0.129	3.56	354
Pseudochironomus	0.5	0.027	0.023	1.02	0.150	0.058	0.218	5.64	449
	1.5	0.026	0.030	1.02	0.120	0.060	0.173	4.69	454
	3.5	0.027	0.015	1.02	0.083	0.059	0.110	3.10	199

Table 2. Continued.

Taxon	Depth (m)	B (g/m^2)	BSD	365/CPI	P (g m^{-2} y^{-1})	Low CL	High CL	P:B	D (ind./m^2)
Tanytarsus	0.5	0.036	0.023	1.02	0.145	0.098	0.206	4.04	2293
	1.5	0.013	0.006	1.02	0.057	0.038	0.071	4.54	514
	3.5	0.017	0.012	1.02	0.058	0.041	0.077	3.45	409
	6	0.063	0.099	1.02	0.225	0.095	0.551	3.58	1014
	10	0.051	0.083	1.02	0.109	0.042	0.181	2.15	665
Ephemeroptera									
Caenidae									
Caenis	0.5	0.108	0.081	1.07	0.679	0.472	0.824	6.29	2067
	1.5	0.034	0.030	1.07	0.214	0.125	0.256	6.37	686
	3.5	0.012	0.011	1.07	0.048	0.015	0.085	4.05	144
	6	0.003	0.003	1.07	0.006	0.001	0.011	1.97	39
Ephemeridae									
Hexagenia	3.5	0.230	0.183	1.02	0.788	0.400	1.270	3.43	72
Megaloptera									
Sialidae									
Sialis	1.5	0.003	0.001	0.52	0.002	0.001	0.007	0.67	17
	3.5	0.125	0.086	0.52	0.288	0.129	0.446	2.30	133
Odonata									
Coenagrionidae	0.5	0.251	0.377	1.01	0.580	0.182	0.897	2.31	83
	1.5	0.207	0.231	1.01	0.410	0.056	0.732	1.98	50
Libellulidae/Corduliidae	0.5	0.292	0.417	1.01	1.210	0.315	1.860	4.14	349
	1.5	0.503	0.516	1.01	2.020	0.743	3.060	4.02	293
	3.5	0.093	0.123	1.01	0.334	0.080	0.557	3.58	89
Trichoptera									
Hydroptilidae									
Oxyethira	0.5	0.059	0.054	0.521	0.100	0.060	0.145	1.69	440
	1.5	0.012	0.007	0.521	0.022	0.012	0.034	1.79	155
	3.5	0.014	0.011	0.521	0.022	0.014	0.035	1.52	77
Leptoceridae									
Oecetis	0.5	0.009	0.007	1.07	0.031	0.016	0.047	3.38	150
	1.5	0.014	0.014	1.07	0.067	0.034	0.095	4.71	205
	3.5	0.030	0.045	1.07	0.145	0.039	0.239	4.83	177
Polycentropodidae									
Polycentropus	1.5	0.122	0.150	1.07	0.122	0.020	0.244	1.00	28
	3.5	0.136	0.104	1.07	0.319	0.085	0.585	2.35	44
	6	0.134	0.062	1.07	0.140	0.074	0.300	1.04	28
Veneroida									
Sphaeriidae	0.5	0.035	0.018	0.667	0.092	0.069	0.124	2.62	565
	1.5	0.066	0.029	0.667	0.260	0.181	0.295	3.92	1074
	3.5	0.081	0.035	0.667	0.242	0.186	0.295	3.01	1356
	6	0.089	0.045	0.667	0.322	0.215	0.427	3.64	919
	10	0.045	0.020	0.667	0.060	0.027	0.092	1.35	166

stratum represented a negligible portion of whole-lake production.

Area-specific rates of production for the entire macroinvertebrate assemblage remained fairly constant across depths (Fig. 2A). The maximum rate was 6.5 g m^{-2} y^{-1} at 1.5 m. The minimum calculated rate was 3.2 g m^{-2} y^{-1} at 10 m, but the rate was probably even lower in the 15-m depth stratum. Between 0.5 and 10 m, the bootstrapped 95% confidence intervals for area-specific production overlapped for all depth pairs except 1.5 m and 6 m (Fig. 2A).

Despite similarities in area-specific production, littoral production dominated when area-specific rates were scaled up to area-weighted rates because the littoral zone makes up >50% of the surface area of Crampton Lake. Over 65% of the benthic secondary production in the lake occurred in the littoral zone, whereas only ~11% occurred in the 8.5- to 12.5-m depth stratum (Fig. 2B). Mean whole-lake benthic secondary production was 4.4 g m^{-2} y^{-1}, with a 95% confidence interval that extended from 3.8 to 4.6 g m^{-2} y^{-1}.

Maximum rates of production occurred in the littoral zone for most taxa (Table 2). Furthermore, many taxa maintained a rate of production near their maximum across a broad depth range in the littoral zone (Table 2). To quantify this observation, we compared the maximum and minimum rates of
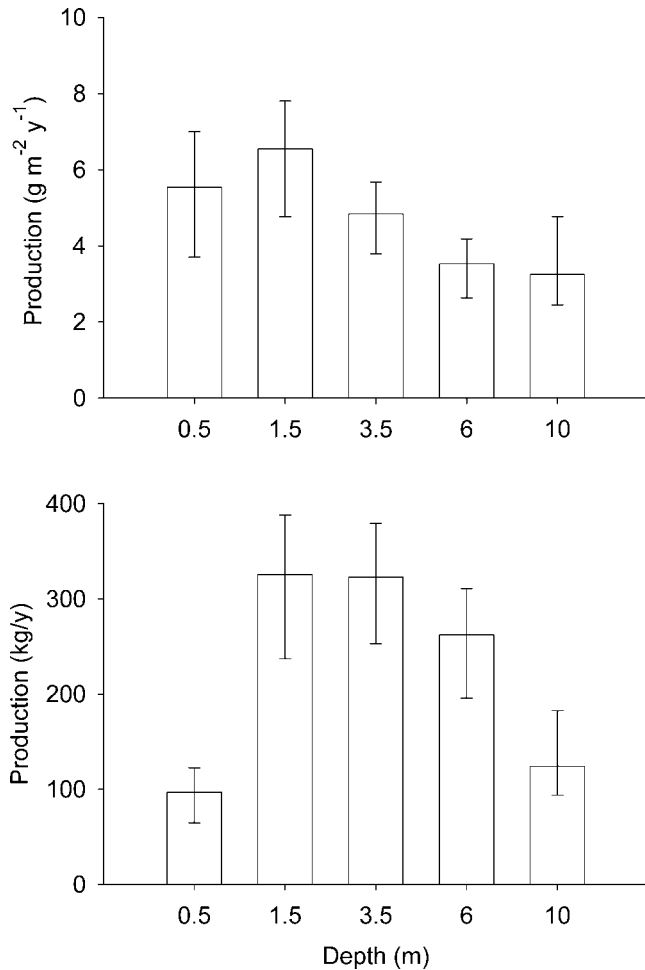
FIG. 2.   Relationship between depth and benthic secondary production in Crampton Lake. A.—Area-specific rate of production. B.—Area-weighted rate of production (area-specific rate multiplied by the total area of lake bottom in that depth stratum). Error bars show approximately 95% confidence intervals.

production for each taxon across depths. The mean taxon-specific ratio of maximum:minimum production (excluding *Sialis*, which had extremely low abundance at all but 1 depth) was 9.75 ± 24.59 (SD). However, when only littoral depths were considered the average ratio was 3.71 ± 3.11. A few taxa, particularly *Chironomus* and *Hexagenia*, were found almost exclusively at 1 depth (10 m and 3.5 m, respectively). The highest rate of production observed was 2.58 g m^{-2} y^{-1} for *Chironomus* at 10 m, and the lowest was 0.002 g m^{-2} y^{-1} for the chironomid genus *Nilothauma*. Confidence intervals for individual taxa were generally fairly wide (Table 2).

Relatively few taxa were responsible for most of whole-lake secondary production. The chironomid genera *Procladius*, *Chironomus*, and *Ablabesmyia*, and the few species of Libellulidae and Corduliidae together accounted for >50% of whole-lake production. Few taxa had high rates of production, and most species had relatively low production. Thus, the rank–production relationship for Crampton Lake benthos was log-normal (Fig. 3).

Diptera, particularly the family Chironomidae, were an important component of production at all depths. Diptera contributed >39% of total production at 0.5 m, and this contribution increased to 98% at 10 m (Fig. 4). Odonata also contributed substantially to production, particularly in the littoral zone, whereas Ephemeroptera, Megaloptera, and Trichoptera combined contributed ≤33% of the production at any depth.

Discussion

Bias and uncertainty

Whole-lake estimates of benthic secondary production are logistically difficult and subject to a number of biases and uncertainties. To facilitate comparisons between our results and those of other authors, in this section we explicitly consider important sources of bias and uncertainty that might affect our production estimates.

Our production estimates are almost certainly underestimates, for at least 3 reasons. First, we were unable to estimate length or head capsule width of some individuals in many taxa. We excluded these individuals from the size–frequency calculations because it was impossible to assign them to a size class. Second, we did not correct the masses estimated from length–weight regressions for retransformation bias (Sprugel 1983). The correction factor for this bias requires an estimate of the variance of the regression, which was not given in the summary of length–mass regressions that we used (Benke et al. 1999). Third, as have many studies, we excluded meiofauna, which might account for ~50% of total benthic production (Strayer and Likens 1986, Stead et al. 2005).

We bootstrapped our data to estimate the uncertainty associated with sampling error in our secondary production estimates. However, we did not consider at least 2 sources of uncertainty in our bootstrap procedure. First, we did not consider uncertainty in the CPI estimates that we used. It is possible to estimate this uncertainty using a parametric bootstrap (e.g., Huryn 1996), but the lack of detailed knowledge about the sampling distribution of CPI estimates limits the quantitative precision of this approach. Second, we did not consider uncertainty in the point estimates of the published regression parameters that we used to convert observed invertebrate lengths to masses.
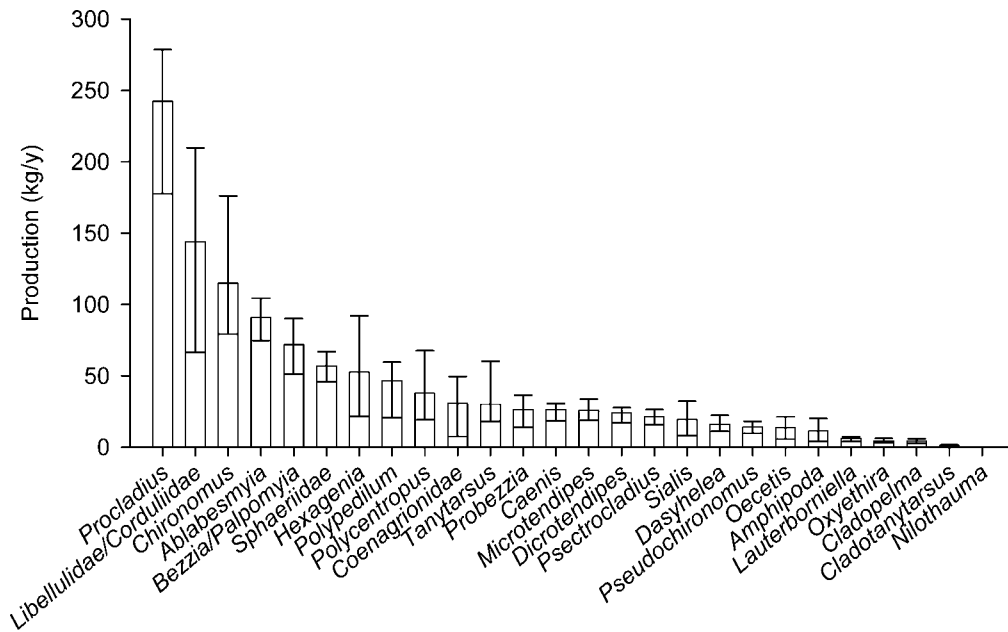
FIG. 3. Rank–production relationship for the dominant taxa in Crampton Lake. Data are total area-weighted production of each taxon across all depths. Error bars show approximately 95% confidence intervals.

Again, a parametric bootstrap based on the standard errors of these parameters could be incorporated into a bootstrap procedure. An appropriate analysis would draw values for these 2 parameters simultaneously from a bivariate normal distribution because the covariance of the slope and intercept is probably not 0. Unfortunately, the covariance of length–mass regression parameters usually is not reported. Future work to describe CPI sampling distributions and the covariances of length–mass regression parameters could lead to improved uncertainty estimates for secondary production calculations.

Taxonomic patterns in secondary production

We observed 2 particularly interesting taxonomic patterns in benthic secondary production. First, our data suggest that competition for resources might be important in limiting the rate of benthic secondary
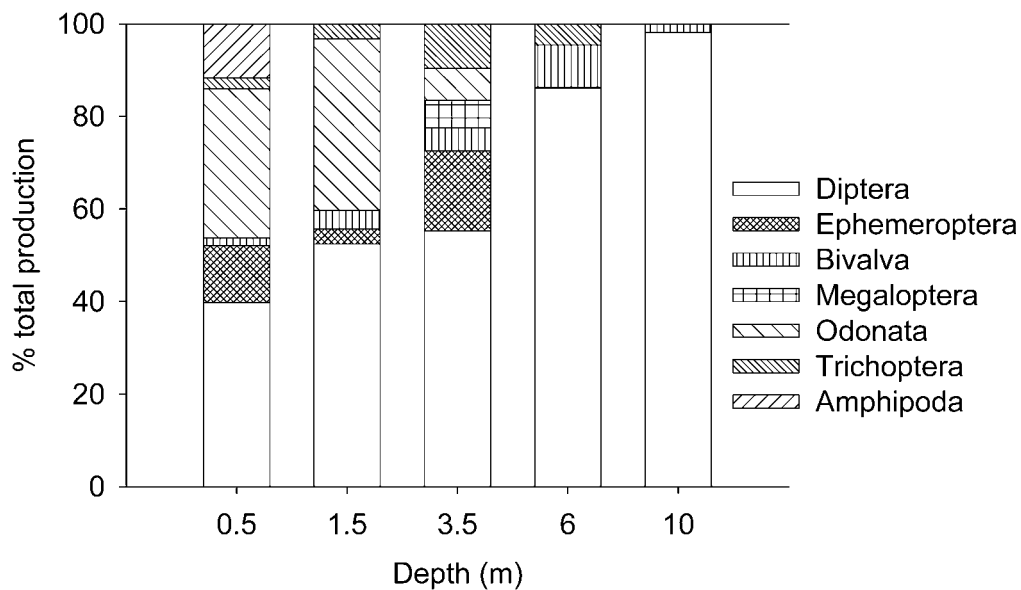
FIG. 4. Percent contribution of each taxonomic order to total benthic secondary production at each sampling depth.
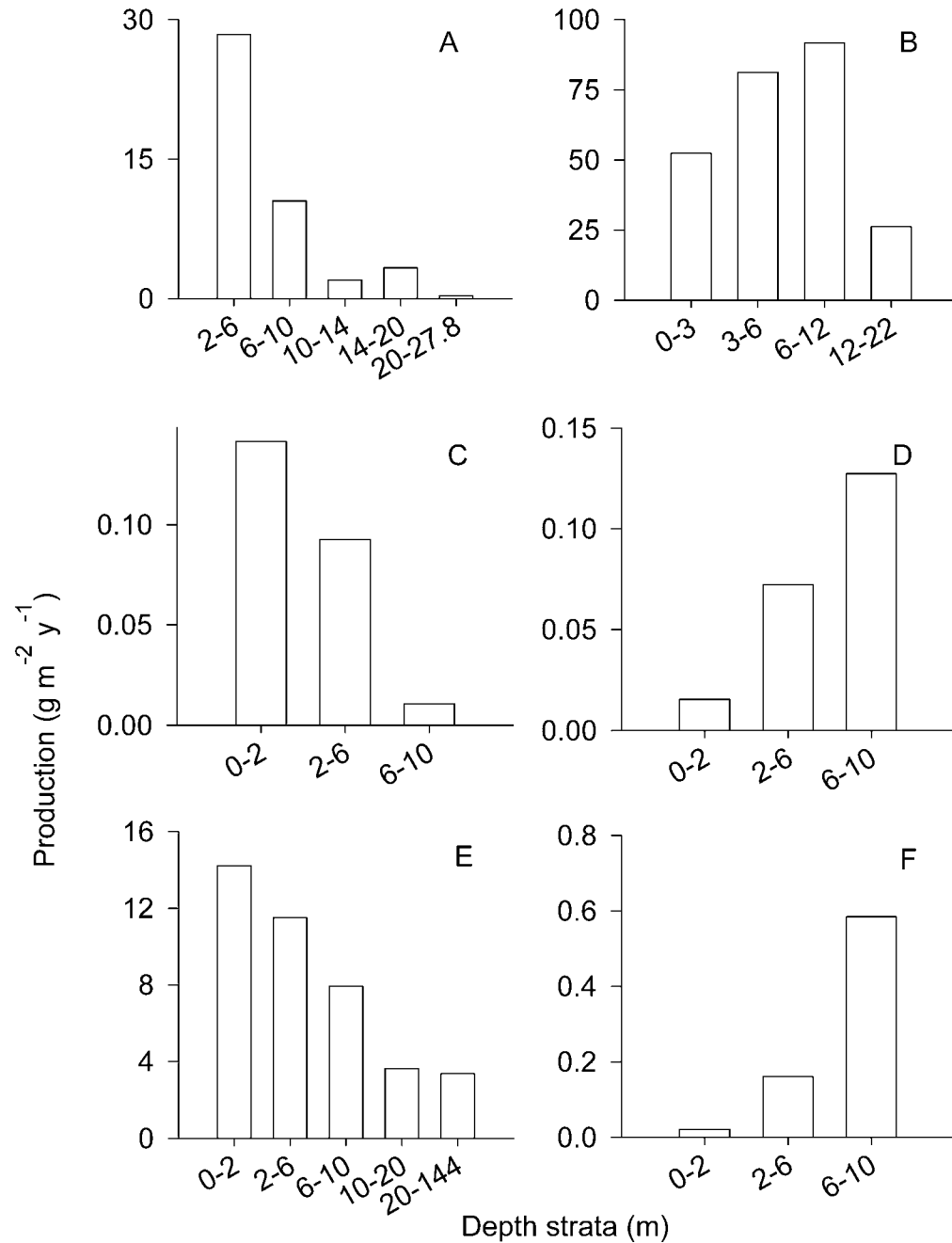
FIG. 5. Benthic secondary production by depth zone in previous studies. A.—Lake Mikolajskie (Kajak 1978). B.—Lake Esrom (Jónasson et al. 1990). C.—Batchawana Lake (Dermott 1988). D.—Turkey Lake (Dermott 1988). E.—Lake Thingvallavatn (Lindegaard 1992). F.—Little Turkey Lake (Dermott 1988).

production in Crampton Lake. Invertebrate taxonomic richness was highest at 1.5-m depth and decreased substantially with depth. This pattern is observed commonly in lakes and might result from reduced habitat and resource heterogeneity, increased abiotic stress, and other factors that change as depth increases (Brinkhurst 1974, Kajak 1978, Jónasson 1992). The

increasing dominance of production by Chironomidae with depth is also a common pattern (Jónasson 1992, Johannsson et al. 2000). However, even though fewer taxa contribute to secondary production at deeper sites (Table 2, Fig. 4), the rate of production remains nearly constant (Fig. 2A). Thus, favorable conditions at shallow sites allow the persistence of many taxa, but

this high diversity seems to result only in a more finely partitioned resource base, not in an increase in production relative to deep sites where only a few taxa can persist.

Second, we observed that most taxa have very low rates of production. Therefore, production is dominated by relatively few taxa with very high rates of production. This log-normal rank–production relationship (Fig. 3) has not been widely recognized in studies of lake benthic production, although it might be quite common. For instance, when we plotted the production data for Thingvallavatn (Lindegaard 1992), we observed a similar log-normal rank–production relationship. Log-normal rank–production relationships might be expected given that species abundances, which are an important component of production, are similarly distributed (Preston 1948). However, abundance was a strong predictor of production in Thingvallavatn, but not in Crampton Lake (linear regression of log[production] on log[abundance]: Thingvallavatn slope = 0.73, p-value for slope <0.0001, R^2 = 0.62; Crampton slope = 0.42, p-value for slope = 0.11, R^2 = 0.11). In fact, the 4 most productive taxa in Crampton Lake accounted for >50% of total production, whereas the 4 most abundant taxa accounted for only 25% of total production. The lack of correlation between abundance and production in Crampton Lake might be caused by the large number of rare taxa with unexpectedly high production. Although the most abundant taxa were often those with a broad depth distribution, many of the most productive taxa achieved very high production only within a very narrow depth range (i.e., odonates and *Chironomus*). The drivers of rank–production relationships require further investigation, but the concentration of most secondary production in a handful of taxa, some of which are disproportionately rare, might be important to understanding the impacts of local or global species loss on ecosystem processes in lakes (Loreau et al. 2002).

Littoral dominance of whole-lake benthic secondary production

We observed little or no change in area-specific rates of production between 0.5- and 10-m depth in Crampton Lake. Differences in production rates were small among the 5 depth strata that we considered, and confidence intervals for all but 1 depth pairing overlapped (Fig. 2A). Rates of production probably were significantly lower only in the ~5% of lake surface area that was in the 12.5- to 18.5-m depth

stratum, where we did not calculate production because of low invertebrate abundances.

The mean rate of production in Crampton Lake (4.4 g m^{-2} y^{-1}) is near the median of other published estimates (range = 0.05–44.3 g m^{-2} y^{-1}; Andronikova et al. 1972, Winberg et al. 1973, Potter and Learner 1974, Mason 1977, Kajak 1978, Wissmar and Wetzel 1978, Sarvala et al. 1981, Strayer and Likens 1986, Lindegaard 1992, Johannsson et al. 2000). However, changes in production with depth seem to be much more pronounced in other lakes than in Crampton Lake (Fig. 5A–F). None of these investigators estimated the uncertainty in their production estimates, so apparent patterns must be interpreted with caution. Nonetheless, in most of these lakes, point estimates of production rates showed large changes with depth. In many cases, the range of production rates over depth spans an order of magnitude, whereas in Crampton Lake this range is <2-fold.

Among the 7 lakes for which depth–production data are available (including the present study), at least 3 patterns are apparent (Figs 2A, 5A–F). In 3 lakes (Mikolajskie [Fig. 5A], Batchawana [Fig. 5C], and Thingvallavatn [Fig. 5E]), production declined monotonically with depth. In Turkey (Fig. 5D) and Little Turkey lakes (Fig. 5F), production increased monotonically with depth. In Crampton Lake (Fig. 2A) and Lake Esrom (Fig. 5B), no clear trend in production was apparent with depth. We used available descriptive data for the lakes to consider potential drivers, including lake size, trophic status, depth, and percentage of area in the littoral zone, of these different depth–production relationships. No clear pattern emerged. Lake Batchawana had high littoral production largely because it was fishless, and odonates, whose chief habitat is the littoral zone, became the top predators and were highly productive (Dermott 1988). In Lake Mikolajskie, for which the depth-specific production estimates include only nonpredaceous taxa, shallow zones were dominated by *Dreissena*, which may have driven production patterns for that system (Kajak 1978). Production was higher in the littoral zone than at greater depths in Thingvallavatn probably as a result of O$_2$-rich conditions in the surf zone (0–2 m) and low food quality and O$_2$ in the deep profundal (Jónasson 1992). Deep peaks in production are often caused by highly productive *Chironomus*. In the case of Lake Esrom, Jónasson et al. (1990) suggested that water circulation patterns and sedimentation gave filter feeders an advantage over herbivores, leading to high biomass and production in the profundal. Overall, depth–production relationships appear to be highly system specific, at least based on the data available to date. Further studies, perhaps with more

consistent methods and definitions of depth strata, are needed to understand the patterns and causes of changes in benthic secondary production across depth gradients.

Despite the minimal change in area-specific production with depth in Crampton Lake, the littoral zone dominates whole-lake benthic secondary production because most of the lake area is in the littoral zone (Fig. 2B). More than 65% of annual benthic secondary production in Crampton Lake occurred in the littoral zone. We hypothesize that littoral dominance of whole-lake benthic secondary production might be common on a global scale. Over 99% of all the lakes in the world are the size of Crampton Lake or smaller, and these lakes account for ~40% of the global total of lake area (Downing et al. 2006). Most small lakes have a high proportion of littoral area. If many lakes show either little change or monotonic decreases in area-specific production with depth, then littoral zones will tend to dominate whole-lake benthic secondary production. Such a pattern could partially explain why littoral prey is so dominant in fish diets (Vander Zanden and Vadeboncoeur 2002). Not only does the littoral zone offer favorable conditions for many fishes (e.g., high dissolved O_2, optimal temperatures for growth), it also might offer most of the available benthic secondary production.

Another hypothesized driver of the prevalence of littoral C in fishes is more efficient transfer up the food chain of benthic production than pelagic production (Hecky and Hesslein 1995). A recent analysis in Castle Lake found some support for this hypothesis. Benthic secondary production made up only 30% of whole-lake (benthic + pelagic) secondary production, but it made up 63% of the C in fish tissues (Vander Zanden et al. 2006). We suspect that a similar pattern exists in Crampton Lake. We used biweekly data from 2005 on the abundance and size of Crampton Lake zooplankton species (M. L. Pace and J. J. Coloso, Institute of Ecosystem Studies, unpublished data) and the method of Shuter and Ing (1997) to estimate zooplankton secondary production. Our estimate of 40 g m^{-2} y^{-1} suggests that benthic secondary production makes up ~12% of total secondary production in Crampton Lake. This estimate is at the low end of the range of estimates for lakes with similar mean depth (Vadeboncoeur et al. 2002). However, a study of fish diets in Crampton Lake in 2005 indicates that benthic prey items are key components of fish diets (B. C. Weidel and J. F. Kitchell, University of Wisconsin, unpublished data). Benthic organisms make up 60 to 62% of the diet (by wet mass) of juvenile and adult bluegill (*Lepomis macrochirus*), which represent ~50% of total fish biomass in the lake. Benthic organisms are similarly important for largemouth bass (*Micropterus salmoides*; 45% of total fish biomass). They directly contribute 10 to 19% of observed bass diets, and they support much of the fish production that makes up most (71–82%) of bass diets. In Crampton Lake, benthic secondary production appears to play a key role in supporting fish production even though the lake is relatively large and has much greater pelagic than benthic secondary production. Given that lake foodweb paradigms increasingly emphasize the importance of spatial connectivity (Schindler and Scheuerell 2002, Vadeboncoeur et al. 2002, Carpenter et al. 2005), further studies describing spatial patterns in secondary production will be essential for understanding trophic pathways in lake food webs.

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