Are autumn-growing detritivorous mayflies most productive?

Ronald W. Griffiths and Tom G. Northcote

Introduction

Terrestrial leaf litter is known to be the prime source of organic matter for many detritivorous aquatic invertebrates (CUMMINS et al. 1989, WALLACE et al. 1999), particularly in small woodland streams (ANDERSON & SEDELL 1979). In temperate regions this detrital resource varies seasonally with the most bountiful supply occurring during autumn. Consequently, some studies assert that stream detritivores synchronize their life histories to take advantage of this "manna from the sky" (HYNES 1963, PETERSEN & CUMMINS 1974, CUMMINS et al. 1989) and thereby avoid the detritus-scarce summer season (RICHARDSON 1991).

Shredder-detritivores take direct advantage of leaf litter inputs by colonizing and consuming this leaf matter (RICHARDSON 1992), and an increased supply of leaf litter has been shown to result in higher growth rates, lower emigration rates, or higher abundances of shredders (CUMMINS et al. 1973, RICHARDSON 1991). Collector-detritivores do not directly consume leaf litter, yet they are also observed to rapidly colonize leaf litter in streams, possibly because of the accumulation of fine particulate organic matter on which they feed (SHORT et al. 1980, RICHARDSON 1992), and an increased supply of leaf litter has been shown to result in higher abundances of collectors (RICHARDSON & NEILL 1991, DOBSON et al. 1992). GRIFFITHS & NORTHCOTE (2006), however, found that an autumn-growing, detritivorous stonefly was not any more productive than a similar summer-growing species because the production resulting from the increased autumn growth rate was negated by a higher loss rate (mortality and emigration). Notwithstanding the observed positive demographic responses to an increased leaf litter supply, other components of production (HURYN & WALLACE 2000) may change in a compensatory manner to negate these benefits. Thus in stream ecosystems experiencing seasonally fluctuating conditions, synchronizing nymph growth with autumn leaf drop may simply be one of several distinct ways for detritivores to maximize production. This may help explain the temporal separation of closely allied species within a stream (HYNES 1970, BRITTAIN 1982).

This study investigates whether the autumn (leaf-drop) season provides optimal conditions for collector-detritivores by comparing the mortality, growth, development time, nymph size, and production of summer-growing and autumn-growing cohorts of *Paraleptophlebia* mayflies in a coastal headwater stream. *Paraleptophlebia* are good model species for this question because they are morphological similar, feed on fine particulate organic matter, are widely distributed throughout North America, and inhabit a range of watercourses from small streams to large rivers (WALTZ & BURIAN 2008).

Key words: detritivores, life cycle, mayflies, *Paraleptophlebia*, production, stream

Methods

This study was conducted in the headwaters of Spring Creek that drains part of the Malcolm Knapp Research Forest of the University of British Columbia, located about 60 km northeast of Vancouver (49°18'N; 122°32'W). The study site (altitude 310 m) consisted of a stream reach 37 m long averaging 3 m wide and was bounded upstream by a small dug (fire protection) pond (area = 960 m^2; maximum depth 1 m) and downstream by a road culvert that led to a steep waterfall. Similar thermal regimes were experienced during these 2 periods, although opposite in direction. Annual water temperature was estimated to be 8 °C based on monthly minimum-maximum measurements. Discharge was steady throughout the summer with minimal flows in August. A series of rainfall-generated spates occurred from September through November. GRIFFITHS & NORTHCOTE (2006) provides a detailed description of site conditions.

The benthic samples were collected on 12 dates between early May 1979 and late March 1980. Eight samples were collected using a proportional, habitat-stratified (upper riffle, pool, lower riffle) random sampling design on sampling dates from June to December. In May and March, only a single sample was collected from each habitat. Samples were collected with a Hess-type sampler that enclosed a 0.05 m^2 area and had a collecting net made from 0.471-mm mesh attached

to a removable plastic bottle with its bottom replaced with 0.153-mm mesh.

Paraleptophlebiid mayflies were removed from the debris in each sample under a low-power stereoscope, identified, and enumerated. Subsequently, the head width of all mayflies in one sample from the upper riffle, pool, and lower riffle was measured to the nearest 0.02 mm using an ocular micrometer. Because only a proportion of individuals was retained by the sampler with head widths between 0.471 and 0.153 mm, density correction factors for young instars were estimated as described in GRIFFITHS & NORTHCOTE (2006). This correction had little effect on biomass estimates because only the density of the smallest instars was adjusted.

Biomass was calculated using the head-width distribution in a sample and a regression between dry mass and head width, based on unpreserved paraleptophlebid mayflies. Individuals were killed in hot water, measured, dried at 60 °C for 24 hr, cooled in a desiccator and then weighed to the nearest 0.002 mg. The relationship between dry mass (M) in mg and head-capsule width (H) in mm was described by a power equation:

$$M = a * H^b$$

where, $a = 0.446$ and $b = 2.84$ ($n = 20$; $r^2 = 0.99$; $p < 0.001$).

Instantaneous growth rates (G) were estimated by linear regression of ln-transformed mean individual mass against time in days. The instantaneous change in density (D) was estimated by linear regression of ln-transformed mean density against time in days. Because of the upstream pond, invertebrate drift entering the study reach was minimal, restricted to days with very fast flows resulting from heavy rainfall events. Thus, D provided a good measure of instantaneous loss rate from the study reach as a consequence of mortality and emigration, except during periods of recruitment via egg hatching. Production was estimated as the product of the instantaneous growth rate and the mean biomass for each sample interval (RICKER 1975). Annual production was estimated from May 1979 to May 1980 using the biomass data from May 1979 as an estimate for May 1980. Development time was estimated as the number of days from the peak nymph density to median day of emergence.

In this study, summer refers to the 3.5-mo period from early May until mid-August, while autumn refers to the 3.5-mo period from mid-August until December. Autumn thus incorporated the period when noticeable quantities of deciduous leaf material occurred in the stream channel (personal observation; RICHARDSON 1991). This leaf material was primarily from "fast" in-stream-processing riparian species and secondarily from "medium" in-stream-processing species (CUMMINS et al. 1989).

Results

Paraleptophlebia debilis had a single generation per year (Fig. 1). Eggs likely hatched sometime during the winter
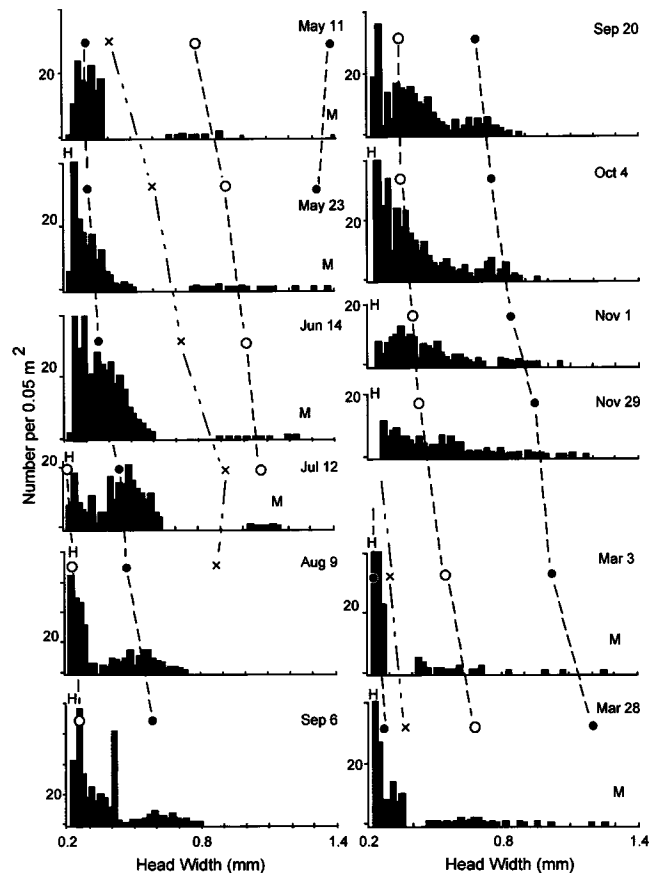

Fig. 1. Density of *Paraleptophlebia temporalis* nymphs in Spring Creek by head-width size classes over 1 yr. Median head width is indicated for *Paraleptophlebia temporalis* (summer-hatching cohort) by open circles, *Paraleptophlebia temporalis* (winter-hatching cohort) by solid circles and of *Paraleptophlebia debilis* by an "x". H indicates the presence of hatchlings (head width <0.02 mm); M indicates the presence of nymphs with black wing pads and ready to emerge.

given the size structure of nymphs observed in early March; unfortunately the specific time and duration could not be determined because the gills of young *Paraleptophlebia* instars (head width <0.32 mm) are single filaments and thus cannot be identified to species. *Paraleptophlebia debilis* nymphs grew rapidly in size from March through August. Wing pads appeared on nymphs with a head width >0.76 mm. Adults emerged from the stream likely throughout September because mature nymphs with black wing pads (maximum head width 1.12 mm) were collected from nocturnal drift samples on September 11 and 25. The absence of *P. debilis* nymphs in benthic samples during September suggests that a low density of mature individuals occurred within the study area.

Nymph abundance increased from $0 \ m^{-2}$ in late November to an observed peak of just over $2700 \ m^{-2}$ in

early March (Fig. 2); thereafter, nymph density declined. The mean D was -1.9% d^{-1} (S.E. $+/-$ 0.2; $r^2 = 0.92$) during the summer. Biomass followed a similar pattern, with a peak of 50 mg m^{-2} occurring in early March (Fig. 3). During the summer, mean individual mass increased from 0.066 to 0.31 mg (Fig. 4), and the mean G was 1.5% d^{-1} (S.E. $= +/-0.3$; $r^2 = 0.90$). Summer production was 30 mg m^{-2}; annual production was 110 mg m^{-2}.

Paraleptophlebia temporalis had a complex life cycle consisting of 2 slightly overlapping cohorts (Fig. 1). Hatchlings (nymphs with a head width <0.20 mm) of the "summer-hatching" cohort were found from July through November, suggesting a 5-mo period of egg hatching after about 4 mo of incubation. These nymphs grew continuously in size through to the following summer, about 12 mo. Wing pads were first noted in late November on individuals with a head width >0.68 mm. Adult emergence probably occurred from June into August because individuals with black wing pads (head width >1.08 mm) were found in the benthos or drift at this time. Maximum head width among mature nymphs was 1.22 mm. Eggs laid by these adults contributed to the "winter-hatching" cohort of *P. temporalis*.

Nymph abundance of the summer-hatching cohort increased from 0 m^{-2} in June to a peak of just over 7400 m^{-2}

in early September (Fig. 2). Thereafter, nymph density declined. During the autumn, D was -1.3% d^{-1} (S.E. $=$ $+/-0.4$; $r^2 = 0.76$) and during the following summer was -1.9% d^{-1} (S.E. $= +/-0.5$; $r^2 = 0.97$). Biomass followed a similar pattern, with a peak of almost 160 mg m^{-2} occurring in early October (Fig. 3). During the autumn, mean individual mass increased from 0.0085 to 0.062 mg (Fig. 4), and G was 1.5% d^{-1} (S.E. $= +/-0.2$; $r^2 = 0.96$). During the following summer, mean individual mass increased from 0.23 to 0.75 mg, and G was 1.3% d^{-1} (S.E. $= +/-0.1$; $r^2 = 0.96$). Autumn production was 190 mg m^{-2} whereas summer production was 70 mg m^{-2}. Annual production was 330 mg m^{-2}.

Hatchlings of the winter-hatching cohort were found from March through May, suggesting that eggs likely started hatching at least in February and continued for 4 mo. Nymphs grew steadily from March until the following summer, about 15 mo. Wing pads were first noted on individuals in August with a head width >0.64 mm. Adult emergence probably occurred from March until June because individuals with black wing pads (head width >1.18 mm) were found in the benthos at this time. Maximum head width among mature nymphs was 1.38 mm. Eggs laid by these adults contributed to the summer-hatching cohort of *P. temporalis*.
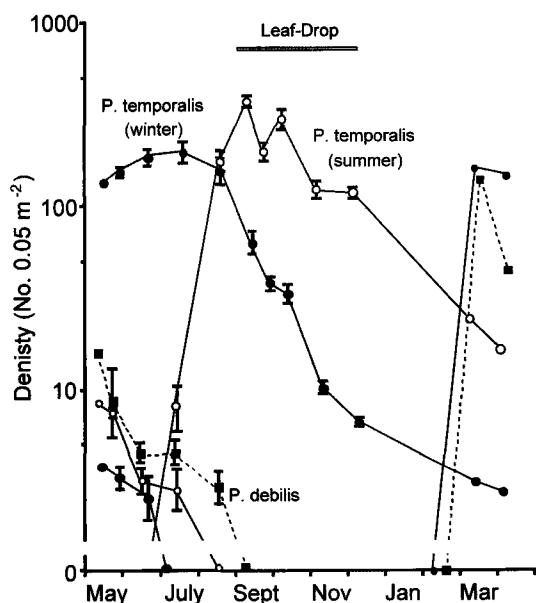

Fig. 2. Mean density of *Paraleptophlebia temporalis* (summer-hatching cohort, open circles), *Paraleptophlebia temporalis* (winter-hatching cohort, solid circles) and *Paraleptophlebia debilis* (solid squares) nymphs (± S.E.) in Spring Creek over 1 yr. The bar indicates the period of maximum leaf drop.
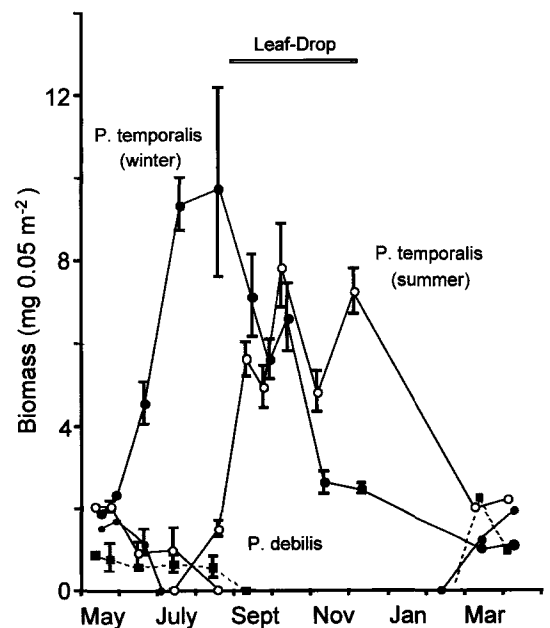

Fig. 3. Mean biomass (dry mass) of *Paraleptophlebia temporalis* (summer-hatching cohort, open circles), *Paraleptophlebia temporalis* (winter-hatching cohort, solid circles) and *Paraleptophlebia debilis* (solid squares) nymphs (± S.E.) in Spring Creek over 1 yr. The bar indicates the period of maximum leaf drop.

Nymph abundance of the winter-hatching cohort increased from 0 m^{-2} in winter to a peak of just over 3900 m^{-2} in July (Fig. 2); thereafter, nymph density declined. During the first summer, D was essentially zero; over the following autumn it was –2.8 % d^{-1} (S.E. = +/–0.2; r^2 = 0.97), and during the second summer it was –2.0 % d^{-1} (S.E. = +/–0.4; r^2 = 0.95). Biomass followed a similar pattern, increasing to a peak of more than 190 mg m^{-2} in early August and then declining (Fig. 3). During the first summer, mean individual mass increased from 0.0015 to 0.063 mg (Fig. 4), and G was 1.7 % d^{-1} (S.E. = +/–0.2; r^2 = 0.97). During the following autumn, mean individual mass increased from 0.063 to 0.44 mg, and G was 1.6 % d^{-1} (S.E. = +/–0.1; r^2 = 0.99). During the second summer, mean individual mass increased from 0.55 to 1.11 mg, and G was 1.0 % d^{-1} (S.E. = +/–0.5; r^2 = 0.76). Production during the first summer was 230 mg m^{-2}, whereas autumn production was 180 mg m^{-2}. Annual production was 420 mg m^{-2}.

Discussion

The addition of a large quantity of high quality food, primarily alder and maple leaves, during autumn (CUMMINS et al. 1989, RICHARDSON 1991) did not enhance production. Autumn production of neither P. temporalis cohort (180–190 mg m^{-2}) exceeded the summer production of the winter-hatching cohort of P. temporalis (230 mg m^{-2}). GRIFFITHS & NORTHCOTE (2006) similarly found in this same stream that the autumn production of a detritivorous nemourid stonefly (130 mg m^{-2}) did not exceed the production of those in the summer (140–210 mg m^{-2}). These observations suggest that detritivores whose growth period coincides with the high detrital resources of autumn are not necessarily more successful than others growing during a season with lower detrital resources (e.g., summer). Because production is the product of several life history characteristics (e.g., growth rate, mortality, development time, fecundity; HURYN & WALLACE 2000), our study suggests several possible ways for detritivorous species to exploit temporally varying environments, each yielding similar levels of production. This may help explain the temporal separation of closely allied species within a stream (HYNES 1970, BRITTAIN 1982).

The high leaf litter inputs of autumn also did not enhance instantaneous growth rates. The observed G for both cohorts of P. temporalis in autumn was not significantly different from that observed in the summer (t-test, p > 0.5), or from that of P. debilis during the summer (ANCOVA, p > 0.5). The average G of 1.5 % d^{-1} during
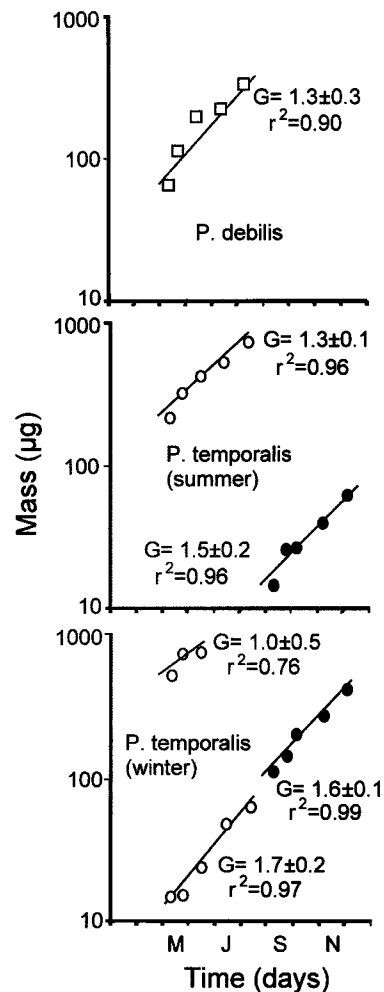

Fig. 4. Mean individual mass of *Paraleptophlebia temporalis* (summer-hatching cohort), *Paraleptophlebia temporalis* (winter-hatching cohort) and *Paraleptophlebia debilis* in Spring Creek over time. Open symbols represent summer values; solid symbols represent autumn values. Regression lines estimate instantaneous growth rates G in %d^{-1} ± S.E.

summer and autumn is within the range predicted for mayflies in a stream with an annual temperature of 8 °C (BRITTAIN 1990). In contrast, the G of the nemourid stonefly, *Zapada cinctipes*, markedly increased during the autumn leaf drop period in this stream (GRIFFITHS & NORTHCOTE 2006). The lack of a growth response by *Paraleptophlebia* may reflect the fact that they do not directly feed on leaf material, in contrast to the shredder-detritivore, *Z. cinctipes* (SHORT & WARD 1981). Although *Paraleptophlebia* does eat leaf material (MATTINGLY 1987), DIETERICH & ANDERSON (1995) and DIETERICH et al. (1997) found that *P. gregalis* could not survive by nibbling on leaf material alone, but required fine particulate organic matter (FPOM) to fully develop and thus function as a collector-gatherer. Yet *Paralep-*

tophlebia nymphs do rapidly colonize leaf litter in streams (SHORT et al. 1980, HOLOMUZKI & MESSIER 1993). We observed that noticeably more nymphs "jumped" through the anode ring of an electro-fisher when it was held over leaf litter than over an adjacent area of gravel within our stream. But RICHARDSON (1992) and SHORT et al. (1980) both noted that collector abundance in leaf packs was correlated with its FPOM content, suggesting that *Paraleptophlebia* may colonize leaf litter to feed on accumulated FPOM while also having shelter from the elements (LANCASTER & HILDREW 1993) and refuge from fish predators (HOLOMUZKI & MESSIER 1993). We observed nymphs walking over leaves near the stream edge that left a noticeable clear path behind them, suggesting they were gathering FPOM and associated matter from the leaf surface for food.

The leaf litter inputs of autumn also did not enhance survivorship of *Paraleptophlebia*. In fact, autumn was rather harsh as the instantaneous change in density or loss rate **D** was greater during autumn ($-2.8\% \ d^{-1}$) than summer ($-1.9\% \ d^{-1}$; Fig. 4). Note that continued recruitment of hatchlings to the summer-hatching cohort throughout autumn was not sufficient to prevent a decline in abundance ($-1.3\% \ d^{-1}$), whereas the winter-hatching cohort of *P. temporalis* maintained its density over the summer with just the hatchling recruitment from May. Nevertheless, these loss rates were much smaller than the -4.4 to $-4.8\% \ d^{-1}$ measured for nemourid stoneflies in this stream (GRIFFITHS & NORTHCOTE 2006). Thus, the upstream movement behavior of leptophlebiids (HAYDEN & CLIFFORD 1974) may possibly partially compensate for losses resulting from nocturnal behavioral and catastrophic drift. In addition, the movement of larger nymphs from high to low velocity habitats (LEHMKUHL & ANDERSON 1972, HOLOMUZKI & MESSIER 1993) may also reduce the risk of downstream displacement. In nearby Mayfly Creek, RICHARDSON (1991) found that an experimental increase in summer leaf litter abundance similarly did not enhance *Paraleptophlebia* survivorship.

Life cycles provide insight into the adaptive balance between maximizing seasonal benefits (e.g., food resources) and minimizing seasonal costs (e.g., avoiding harsh conditions). *Paraleptophlebia debilis* had a fast, seasonal life cycle with eggs hatching in late winter and adults emerging in late summer through early autumn, as reported elsewhere in North America (e.g., LEONARD & LEONARD 1962, LEHMKUHL & ANDERSON 1971). In contrast, *P. temporalis* had a slow, nonseasonal life cycle consisting of 2 partially overlapping cohorts, with a summer-hatching cohort emerging the following summer and a winter-hatching cohort emerging the following winter

and spring. Although previous studies (LEHMKUHL & ANDERSON 1971, HARPER et al. 1995) have inferred a univoltine life cycle, the long hatching and emergence periods and coarse size measurements made this interpretation tenuous. Because the maximum biomass of these 2 species occurred either in the winter (*P. debilis*), or summer and autumn (*P. temporalis* cohorts) seasons (Fig. 3), clearly their life cycles did not synchronize nymph growth with the autumn abundance of leaf resources. Instead this pattern infers that the supply of FPOM and associated algae, fungus, and bacteria, some of which may be derived by shredders feeding on leaf litter (SHORT et al. 1980, RICHARDSON 1992), is available throughout the year for these morphologically similar collector-detritivores. Consequently, the life cycle of each species may reflect adaptations for surviving the harsh, rainfall-generated spates of autumn that characterize coastal streams (NEGISHI & RICHARDSON 2003). The fast seasonal life cycle of *P. debilis* allowed it to avoid the effects of autumn spates as eggs. The long nonseasonal life cycle of *P. temporalis*, meanwhile, exposed nymphs of both cohorts to autumn spates. Consequently, the 5-mo hatching period of the summer-hatching cohort is a possible adaptation for survival against flashy autumn discharges. While the winter-hatching cohort avoided the first autumn as eggs, the juxtaposition of peak nymph abundance just prior to autumn is another possible adaptation for survival of autumn spates.

Finally, because **G** was similar among cohorts, the observed greater body size of mature nymphs in the winter-hatching cohort of *P. temporalis* seems to have solely resulted from a longer development period (330 days vs. 310 for the summer-hatching cohort and 200 for *P. debilis*). Because mayfly fecundity is directly related to body size (CLIFFORD & BOERGER 1974, BRITTAIN 1990), the larger size of the winter-hatching cohort females helps explain the higher density of young nymphs (maximum of 7400 m^{-2}) observed in the summer-hatching cohort of *Paraleptophlebia temporalis*, while the smaller size of the summer-hatching cohort females helps explain the lower density of young nymphs (maximum of 3900 m^{-2}) observed in the winter-hatching cohort. *Paraleptophlebia debilis* with the smallest-sized mature nymphs had the smallest population of young nymphs. The larger size of *P. temporalis* thus greatly contributes to its higher production, through both larger individual body mass and higher abundance as a consequence of egg production. This more than compensates for the greater loss of nymphs, especially during autumn, that results from its slow nonseasonal life cycle.

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Authors' addresses: Ronald W. Griffiths, Oregon State University, Oregon Hatchery Research Center, 120 Nash Hall, Corvallis, OR 97331-3803. E-mail: bugman@execulink.com.
Tom G. Northcote, 10193 Morrison Close, Summerland, BC, Canada V0H 1Z7.