SUSTAINABLE FISHERIES MANAGEMENT: PACIFIC SALMON

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32 Using Photosynthetic Rates to Estimate the Juvenile Sockeye Salmon Rearing Capacity of British Columbia Lakes

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Abstract.—We describe refinements to a simple sockeye salmon *Oncorhynchus nerka* rearing capacity model, the photosynthetic rate (PR) model, which was first described in an earlier paper. The model is based on a correlation between photosynthetic rate expressed as metric tons of carbon per year and sockeye salmon smolt biomass. Estimates of optimum escapements and spring fry recruitment required to produce maximum smolt numbers and biomass were taken from the Alaskan euphotic volume (EV) model. We define rearing capacity as the point at which the maximum number and biomass of smolts are produced and optimum escapement as the number of spawners that results in maximum smolt production. We compare model predictions to direct estimates of optimum escapements (developed from fry models—the relationship between numbers of spawners and numbers of fall fry) from two British Columbia (B.C.) lakes and discuss assumptions and limitations of the model. Although we currently have direct estimates of optimum escapement (e.g., fry models) for only two lakes that make up 16% of the total B.C. sockeye salmon nursery lake area, PR data are currently available for 57% of B.C.'s nursery lake area. We provide estimates of optimum escapements and smolt production from those lakes where suitable data are available. By making assumptions about productivity of lakes where PR is unknown, we also provide estimates of optimum sockeye salmon escapement to all major regions of B.C. Although more research and data are needed, the PR model is a promising tool to help managers make decisions regarding sockeye salmon escapement and enhancement.

INTRODUCTION

British Columbia (B.C.) and Alaska have highly valued stocks of Pacific salmon *Oncorhynchus* spp. Of the five salmon species which occur in western North America, sockeye salmon *O. nerka* are the most economically valuable, with an annual catch worth several hundred million dollars (Burgner 1991). Sockeye salmon are planktivorous throughout their 4–5 year life cycle and reside in lakes for 1–2 years before they migrate to the ocean. Consequently, lakes are an important nursery area for this species.

For much of the 20th century there have been efforts in many parts of B.C. to increase adult sockeye salmon numbers. Without appropriate methods to estimate rearing capacity, it was assumed that sockeye salmon numbers could be increased beyond ambient numbers to some unspecified level. In some lakes this assumption was validated by historic escapement data (returning spawners that are not caught in the fishery), while in others no data were available to indicate the lake could support additional sockeye salmon. Enhancement efforts were undertaken without a clear understanding of the

rearing capacity of a particular sockeye salmon stock's nursery lake. Sockeye salmon enhancement focused on increasing fry recruitment by increasing escapements (Roos 1989); by increasing egg-to-fry survival using spawning channels (McDonald 1969); by direct additions of sockeye salmon fry to lakes (Diewert and Henderson 1992); and by increasing freshwater growth and survival through lake fertilization (Hyatt and Stockner 1985). Enhancement efforts such as spawning channels have been highly successful in some locations and have had little or no effect on stock size in others (Hilborn 1992). Efforts to increase escapement and subsequent smolt production through harvest management have been very successful on some Fraser system stocks (Roos 1989).

Predicting the production capacity for fish in a particular body of water has long been an objective of freshwater research in North America (see Leach et al. 1987 for a review). It has relevance to management of recreational and commercial fisheries (sustainable yield) and to enhancement (amount that recruitment to a lake can be increased). There have been numerous attempts to develop empirical relationships between lake productivity and fish yield. Since a direct measure of productivity (i.e., photosynthetic rate) was not usually available, investigators used a number of other limnological variables as surrogates for photosynthetic rate (PR). These included mean depth and total dissolved solids (Ryder 1965); summer average chlorophyll concentration (Oglesby 1977; Jones and Hoyer 1982); lake area (Youngs and Heimbuch 1982); and total phosphorus concentration (Stockner 1987; Downing et al. 1990).

Fee et al. (1985) and Downing et al. (1990) reported that PR measurements were positively correlated to fish yield. Downing et al. (1990) also found that PR was more closely correlated to fish yield than some other variables commonly used as indices of lake productivity (chlorophyll, total phosphorus). While these surrogates may be correlated to PR, using abiotic or biomass variables instead of PR in empirical relationships with fish yield will introduce additional uncertainty. Furthermore, an improved understanding of energy flow between lake trophic levels is more likely when rate measurements at each trophic level are used.

Development of empirical models in earlier studies was hampered by difficulties in reliably measuring fish yield. Model development was also confounded by resident fish populations which were often multi-species, with varying life histories (i.e., different degrees of planktivory and piscivory). To a large extent, selection of lakes on which estimates of fish yield were available was done qualitatively, with the main criterion being that the lakes must have had "moderately intensive to intensive fishing effort on a spectrum of species for a number of years" (Ryder et al. 1974). If a lake met these criteria for fish yield data, two assumptions had to be made: first, that the quality of the data (e.g., creel census, commercial landings) was good enough for model development, and second, that catches actually did represent maximum sustainable yield. In most cases, these assumptions could not be tested.

When developing rearing capacity (fish yield) models, sockeye salmon nursery lakes in B.C. and Alaska offer a number of advantages over most other lakes. Adult sockeye salmon spawn in the fall, fry enter the lake the following spring, reside in the lake for 1–2 years (in B.C. lakes, residence for most sockeye salmon is 1 year), and the following spring migrate to the ocean as smolts. Prior to or during migration, numbers and biomass of juvenile sockeye salmon can be accurately estimated from midwater acoustic and trawl surveys (fry) or from counts at fences (smolts). On a given lake, if juvenile sockeye salmon numbers and biomass resulting from a wide interannual range of adult spawner escapements are available, maximum juvenile production (e.g., rearing capacity) can be determined by measuring the point where juvenile numbers and biomass are greatest. If spawner numbers increase past this point where escapements are optimum, juvenile sockeye salmon production will not increase and may decrease (Koenings and Burkett 1987; Hume et al. 1996). While sockeye salmon nursery lakes support a variety of other fish species, their biomass is often small relative to maximum juvenile sockeye salmon biomass (Hume et al. 1996). Consequently, maximum biomass of juvenile sockeye salmon is a reliable indicator of rearing capacity or annual fish yield. Sockeye salmon fry are almost exclusively limnetic planktivores, so they are more strongly coupled to limnetic zooplankton production than fish species with a wider

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dietary range that may include terrestrial and benthic organisms. In addition, determination or prediction of maximum biomass in a sockeye salmon nursery lake also permits calculation of spawner numbers required to produce that biomass (i.e., optimum escapements). Given the very high economic value of the stocks and the suitability of available data, fish yield models are perhaps an even more important management tool in sockeye salmon nursery lakes than they are in other North American lakes.

While it is generally assumed that most of the over 90 sockeye salmon nursery lakes in B.C. are recruitment limited (i.e., greater spawning escapements would produce additional smolts), some recent escapements to several major B.C. sockeye salmon lakes have been at or above optimum levels (Hyatt and Steer 1987; Hume et al. 1996). Consequently, a reliable rearing capacity model for sockeye salmon nursery lakes is of even greater importance now than it was in the past. Better predictions of optimum escapements would enable managers to determine whether current escapements are above or below optimum. If escapement of a particular stock is below optimum, the amount of feasible or desirable enhancement to bring lake production up to full rearing capacity could be quantified and the economic value of a successful enhancement program could be estimated. Conversely, the cost in lost production from not enhancing a stock could be assessed. Furthermore, when escapements exceed that required to maximize smolt production, the economic cost of the foregone catch can also be determined. In short, a reliable rearing capacity model would be a powerful tool for fisheries managers concerned with maximizing and sustaining B.C. sockeye salmon.

The euphotic volume (EV) model (Koenings and Burkett 1987; Koenings and Kyle 1997) was developed using data from a number of Alaskan lakes and was the first rearing capacity model developed specifically for sockeye salmon. It provided predictions of optimum escapement, optimum spring fry recruitment, and maximum smolt output. In Hume et al. (1996) we modified the EV model so that it could be used in B.C. lakes. Our model was based on photosynthetic rate and was called the PR model. Objectives of this chapter are to describe a revised version of the PR model, to explain its derivation from the EV model and from the original PR model, to test model predictions in B.C. lakes where appropriate sockeye salmon data are available, to discuss assumptions of the model, and to present model predictions for all B.C. lakes for which suitable data are available.

BRITISH COLUMBIA SOCKEYE SALMON NURSERY LAKES

Sockeye salmon nursery lakes occur in all regions of B.C. with the exception of the Peace River drainage basin in northeastern B.C. (east of the Cassiar mountains). Extensive dam construction in the Columbia River drainage basin has blocked access to anadromous fish in lakes in the central and eastern portion of southern B.C. (parts of the Okanagan and Kootenays), although remnant sockeye salmon stocks still reach some lakes. B.C.'s sockeye salmon nursery lakes occur in most of the province's varied climatic and geologic regions, with corresponding large variations in latitude and elevation. Some lakes occur virtually at sea level while the elevation of others exceeds 1,200 m. B.C. nursery lakes occur over a north-south range of >1,000 km. This results in wide differences in thermal regimes, water clarity, water residence times, nutrient loading, and trophic status. Surface area of the nursery lakes range over more than two orders of magnitude, from <2 km² to >400 km². Mean depths range from <6 m to >150 m and water residence times range from several days to >20 years. Trophic status ranges from ultra-oligotrophic (e.g., Chilko Lake; Stockner and Shortreed 1994) to meso-eutrophic (e.g., Fraser Lake; Shortreed et al. 1996). Some nursery lakes have very high water clarity while others are turbid from either glacial or organic inputs. Distance from the ocean is also highly variable, resulting in freshwater migration distances of <1 km for some coastal systems to >1,000 km for some interior stocks. The very wide range of lake types that sockeye salmon inhabit confirm the "elastic" nature of their habitat requirements.

The total surface area of B.C.'s approximately 90 sockeye salmon nursery lakes is about 3,800 km². The size of individual sockeye salmon stocks is highly variable. In some years adult returns (catch and escapement) to major producers such as Quesnel or Shuswap Lakes exceed 10 million and spawning escapements exceed 1 million. Returns of some smaller stocks (or of major producers in non-dominant brood years) are as low as a few hundred to a few thousand fish. The nursery lakes contain over 590 spawning streams, of which over half have less than 1,000 spawners. About 4% of the streams have peak spawning populations in excess of 100,000 (Williams and Brown 1994). The Fraser River system has nine lakes where escapements have exceeded 100,000 in recent years (Chilko, Fraser, Harrison, Lillooet, Quesnel, Shuswap, Stuart, Takla, and Trembleur). Of northern B.C. stocks, only Babine Lake on the Skeena River and Meziadin Lake on the Nass River have had recent escapements exceeding 100,000. Of coastal B.C. lakes, five (Great Central, Long, Nimpkish, Owikeno, and Sproat) have had recent escapements that exceeded 100,000.

METHODS

MEASUREMENT OF PRODUCTIVITY VARIABLES

We used data on sockeye salmon smolts and fall sockeye salmon fry to support and validate our model. Smolt data were from Alaskan lakes (Koenings and Burkett 1987) and from two B.C. lakes (Babine and Chilko). Smolt numbers and size have been determined using fence counts and mark-recapture estimates since 1949 at Chilko Lake (Roos 1989) and since 1961 at Babine Lake (MacDonald et al. 1987). Since the 1970s we have estimated sockeye fry numbers for three B.C. lakes (Fraser, Quesnel, and Shuswap) using hydroacoustic and trawl techniques as described in Hume et al. (1996). All sampling was done at night when the fish were dispersed and within the working range of the midwater trawl and hydroacoustic system (McDonald and Hume 1984; Burczynski and Johnson 1986). Hydroacoustic and trawl data presented in this chapter were collected in the fall (October and early November).

The PR data used in this chapter were collected from 33 lakes during 1977–1995. Data were collected from spring (April to May) to fall (October to November) and sampling frequency varied from once weekly to once monthly. PR data were collected using *in situ* incubations of light and dark bottles inoculated with ¹⁴C. PR data collected prior to 1994 have been reported and methods described elsewhere (Stockner and Shortreed 1979; Stockner et al. 1980; Shortreed and Stockner 1981; Hume et al. 1996; Shortreed et al. 1996). In 1994 and 1995 we sampled a number of lakes in the Skeena River drainage basin. Methods used for determination of PR were identical to those reported in earlier studies, with the following exceptions. After the 1.5–2.0-h *in situ* incubations were completed, samples were filtered onto 25-mm diameter Micro Filtration Systems GF75 glass fiber filters, which are equivalent to Whatman GF/F filters. Filters were placed in scintillation vials containing 0.5 mL of 0.5 N HCl. Lids were not put on the vials for 6–9 h. In the laboratory, 10 mL of scintillation cocktail (Fisher Scientific's Scintiverse II) were added to the vials, which were then counted in a Packard scintillation counter. Methods used to calculate volumetric, integrated, and daily (mg $C \cdot m^{-2} \cdot d^{-1}$) rates were described in the previously mentioned papers. Prior to 1980, we used scintillation cocktails which were not alkalized. Consequently, PR data we reported for those years overestimated actual PR by a factor of 1.49 (Kobayashi 1978). We divided PR data collected prior to 1980 by this factor to ensure compatibility with more recent data.

Seasonal average daily PR ($PR_{\bar{x}}$) in mg $C \cdot m^{-2} \cdot d^{-1}$ for each lake was computed by integrating daily PR (measured at least monthly from May to October) and dividing by the length of the growing season, which we defined as May 1 to October 31. Total seasonal PR in metric tons C/lake (PR_{total}) was calculated by multiplying $PR_{\bar{x}}$ by the length of the growing season and by lake area. Where multiple years of data were available for a lake, we averaged all years to obtain a single PR estimate. Alaskan PR data used in development and verification of our model were taken from Figure 9 in Koenings and Burkett (1987). In Koenings and Burkett (1987) PR data were presented

as $PR_{\bar{z}}$. To convert to PR_{total}, we multiplied $PR_{\bar{z}}$ by the length of the growing season, which we assumed extended from May 1 to October 31, and by lake area.

MODEL DEVELOPMENT

The PR model presented in this chapter has evolved from the Alaskan EV model (Koenings and Burkett 1987; Koenings and Kyle 1997) and from an earlier version of the PR model (Hume et al. 1996). The EV model is a rearing capacity model developed specifically for sockeye salmon. It uses seasonal average euphotic zone depth ($EZD_{\bar{z}}$) as an analog for seasonal average PR ($PR_{\bar{z}}$) in mg $C \cdot m^{-2} \cdot d^{-1}$ and correlates it to maximum juvenile sockeye salmon numbers and biomass and optimum escapements. This was possible because, in the Alaskan study, lakes with widely varying water clarities caused by glacial or organic stain resulted in a positive linear correlation between $EZD_{\bar{z}}$ and $PR_{\bar{z}}$. This positive correlation does not occur in most B.C. sockeye salmon nursery lakes or in most North American lakes, where lake productivity is generally negatively correlated to $EZD_{\bar{z}}$ and positively correlated with nutrient loading (Wetzel 1975; Hume et al. 1996). Consequently, in its original form, the EV model was not suitable for use in B.C. sockeye salmon lakes.

The EV model utilized EV units (1 EV unit was defined as $10^6 m^3$ of euphotic volume) which were calculated using the equation:

$$EV\ units = EZD_{\bar{x}}(Area)/10^6 \qquad (32.1)$$

where
$EZD_{\bar{x}}$ = seasonal average euphotic zone depth (m)
Area = lake surface area (m^2)

In Hume et al. (1996) we modified the calculation of EV units to use $PR_{\bar{x}}$ instead of $EZD_{\bar{x}}$, which made the EV model useful in a wider range of lake types (including B.C. lakes). We did this by using the correlation between $EZD_{\bar{x}}$ and $PR_{\bar{x}}$ in Alaskan lakes ($EZD_{\bar{x}} = 0.0583PR_{\bar{x}}+3.25$; $r^2 = 0.81$) to substitute $PR_{\bar{x}}$ for $EZD_{\bar{x}}$ in the calculation of EV units. Because the revised model calculated EV units using $PR_{\bar{x}}$ instead of $EZD_{\bar{x}}$, we renamed them PR units, and also renamed the model the PR model (Hume et al. 1996). PR units are equivalent to EV units. PR units are calculated by the equation

$$PR\ units = (0.0583PR_{\bar{x}}+3.25)Area/10^6 \qquad (32.2)$$

where
$PR_{\bar{x}}$ = seasonal average daily PR (mg $C \cdot m^{-2} \cdot d^{-1}$)
Area = lake surface area (m^2)

In the original EV model, recommended escapements were 800–900 adult spawners/EV unit, which were observed to produced an average of 23,000 smolts with a mean weight of 2.0 g (Koenings and Burkett 1987; Koenings and Kyle 1997). However, adult sockeye salmon production was greater at spawner densities approximately one half that necessary to produce 2.0-g smolts (Koenings and Burkett 1987; Koenings et al. 1993). At these lower spawner densities, juvenile sockeye salmon freshwater survival and growth were both greater, resulting in the production of similar numbers of larger (4–5 g) smolts (Koenings and Burkett 1987; Koenings et al. 1993). Since we wanted the PR model to be a method for estimating escapements that would produce maximum smolt numbers and biomass and, subsequently, optimum adult production, our PR model used the following:

Optimum escapement = 425 adult spawners/PR unit
Maximum smolt numbers = 23,000/PR unit
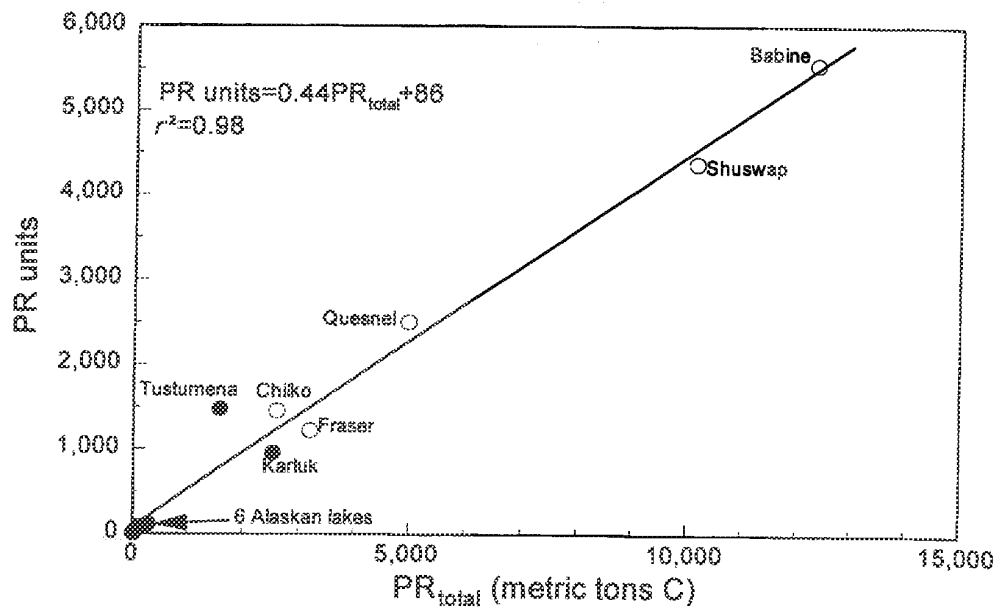Maximum smolt biomass = 103.5 kg/PR unit

FIGURE 32.1 Relationship between photosynthetic rate (PR) units and total seasonal carbon production (PR_{total}) in Alaskan (solid circles) and B.C. (open circles) lakes.

where

Optimum escapement = Number of spawners needed to maximize smolt production.
Maximum smolt numbers = Maximum number of smolts a lake can produce, based on observed maximum production in Alaskan lakes (Koenings and Burkett 1987).
Maximum smolt biomass = Maximum number of smolts × a mean smolt weight of 4.5 g, also from observed maximum production in Alaskan lakes (Koenings and Burkett 1987).

The primary reasons for developing the PR model were to simplify the use of production models and to enhance their utility for understanding energy flow between lake trophic levels. Consequently, we revised the model to use PR_{total} (units are metric tons C/lake) rather than PR units. PR units from both Alaskan and B.C. lakes were significantly correlated to PR_{total} (PR units = $0.44PR_{total}+86$; $r^2 = 0.98$; Figure 32.1). In this relationship the intercept was not significantly different than zero and forcing the intercept through zero resulted in the equation:

$$PR\ units = 0.44PR_{total} \qquad (32.3)$$

With this relationship we modified the PR model to use PR_{total} instead of PR units. Resulting predictions were

Optimum escapement = $187 \times PR_{total}$
Maximum smolt numbers = $10,120 \times PR_{total}$
Maximum smolt biomass (kg) = $45.5 \times PR_{total}$

where

PR_{total} = Total seasonal (May to October) carbon production (metric tons)

With these simple equations the revised PR model generates predictions of optimum escapement to and smolt production from any lake where suitable PR data are available.

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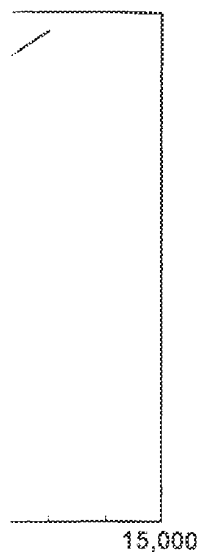15,000

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RESULTS AND DISCUSSION

TESTING THE PR MODEL

The two variables (PR$_{\overline{x}}$ and lake surface area) used in computing PR$_{total}$ strongly affect PR model predictions. Surface areas of sockeye salmon nursery lakes in B.C. vary over two orders of magnitude, while PR$_{\overline{x}}$ in lakes for which we have data varies approximately one order of magnitude. If PR$_{\overline{x}}$ was similar in all lakes then surface area alone would cause interlake variation in model predictions. Conversely, if all lakes were similar in size, then PR$_{\overline{x}}$ alone would be sufficient to explain the variation. Since variation in surface area is substantially greater than that in PR$_{\overline{x}}$, we expected it to explain a substantial proportion of the variation in model predictions and, hence, in a lake's measured rearing capacity. Youngs and Heimbuch (1982) reported that surface area alone explained 94% of the variability in fish yield for a large suite of lakes located in many different parts of the world. However, the surface area of lakes in their data set varied over four orders of magnitude. As the range in area decreases in the set of lakes being analyzed, the proportion of variation explained by area alone would also be expected to decrease.

To test the relative contribution of surface area and productivity in determining rearing capacity, we selected data from Alaskan and B.C. lakes where both PR$_{\overline{x}}$ and maximum juvenile sockeye salmon biomass were known. Data from Alaskan lakes came from Koenings and Burkett (1987). Hume et al. (1996) determined maximum fall fry biomass in two B.C. lakes. In these lakes smolt biomass was unavailable, so we assumed that smolt biomass was equal to fall fry biomass (i.e., overwintering mortality was balanced by overwintering growth). We also used data in this analysis from three additional B.C. lakes (Babine, Chilko, and Fraser) that have recently had record high numbers of adult spawners which produced record high juvenile numbers and biomass. While these three lakes have not had sufficient years of high escapements to conclusively demonstrate that maximum juvenile production has been reached, we decided that maximum recorded juvenile biomass was sufficiently high to merit being used in a test of the PR model. For these Alaskan and B.C. sockeye salmon nursery lakes, maximum observed juvenile sockeye salmon biomass was significantly correlated ($P < 0.05$, $r^2 = 0.65$) with lake area (Figure 32.2a). However, when PR$_{total}$ was used, the relationship improved substantially ($r^2 = 0.91$) (Figure 32.2b). Removing data points from the three British Columbia lakes where maximum juvenile production has not been conclusively demonstrated did not affect the significance of the relationships, but did reduce the slopes. In addition, observed and predicted (from the PR model) maximum juvenile sockeye salmon biomass were highly correlated (Figure 32.2b, $r = 0.95$, $n = 11$), although the predicted biomass slope was significantly lower (Figure 32.2b).

Further confirmation of the importance of PR in determining rearing capacity is the strong log relationship ($r^2 = 0.87$) between maximum fry or smolt biomass and total seasonal PR, when the variables are normalized to area (Figure 32.3a). Using published data from lakes covering a wide range of trophic levels, Downing et al. (1990) found that total fish production and PR were highly correlated. To compare productive capacity of North American sockeye salmon nursery lakes with data presented by Downing et al. (1990), we reproduced one of their figures and included data from Alaska and B.C. sockeye salmon nursery lakes (Figure 32.3b). Despite wide differences in techniques used in data collection, both PR and fish production in sockeye salmon nursery lakes fall near the middle of the range found in many other lakes around the world. While the slope of the relationship in Alaskan and B.C. lakes appears to differ from that for the other lakes, an analysis of covariance indicated those differences were not significant ($F = 1.82$, $P > 0.05$). However, intercepts were different ($F = 8.54$, $P < 0.05$). We do not have sufficient information to suggest reasons for the difference in intercepts.

Since PR data are positively correlated to observed maximum smolt or fry biomass, it should be possible to develop a rearing capacity model solely from B.C. data. However, for several reasons, sufficient or suitable data are not yet available to do this. First, we have data for only two B.C.

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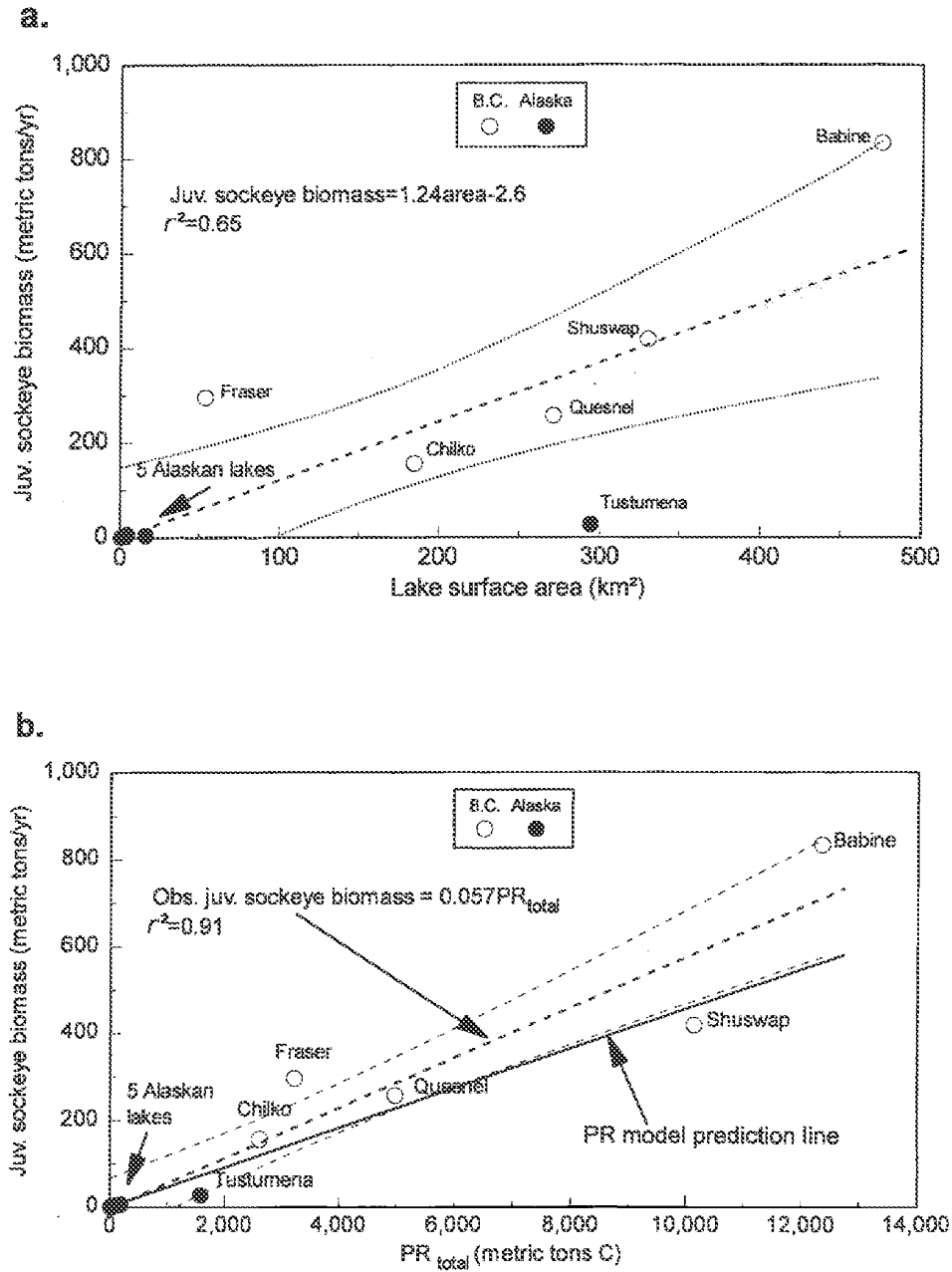
FIGURE 32.2 Observed maximum juvenile sockeye biomass correlated with (a) lake area and with (b) total seasonal carbon production (PR_{total}). Data are smolt biomass except for Fraser, Quesnel, and Shuswap lakes, which are fall fry biomass. Data for Alaskan lakes are from Koenings and Burkett (1987). The regression equation and 95% confidence intervals between biomass and area or PR are shown (dashed and dotted lines). On (b) the solid line is the predicted maximum smolt biomass from the PR model.

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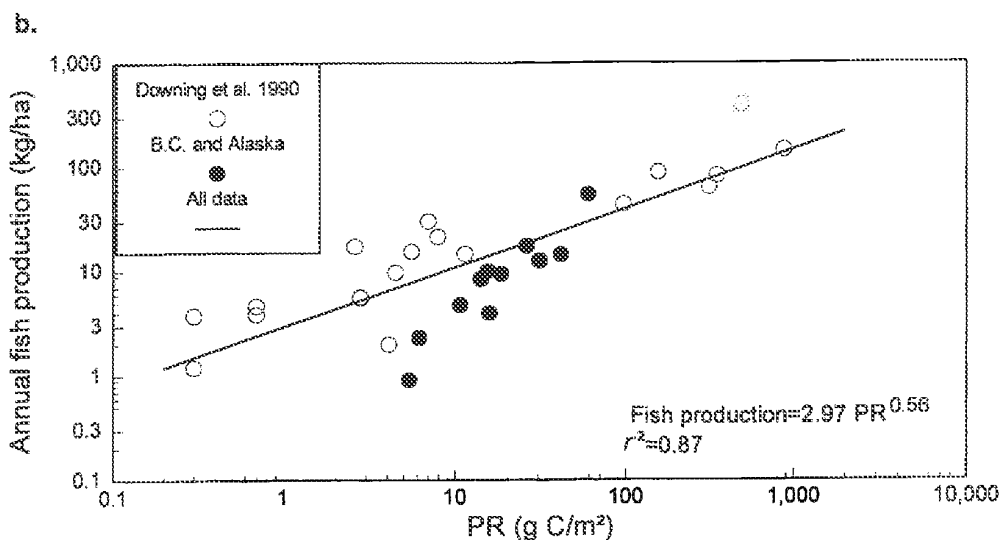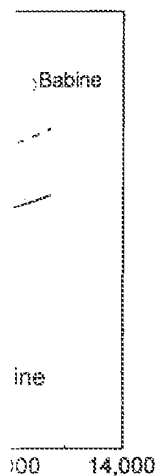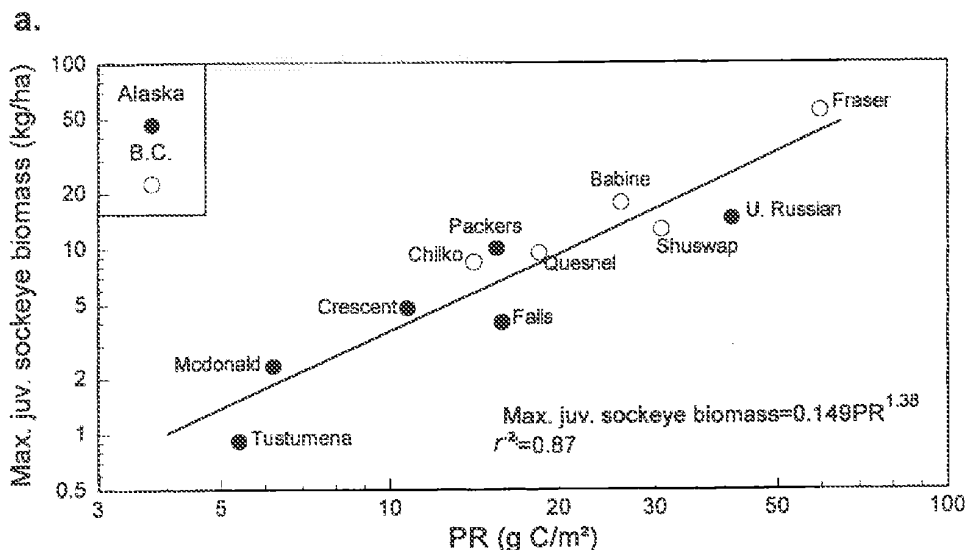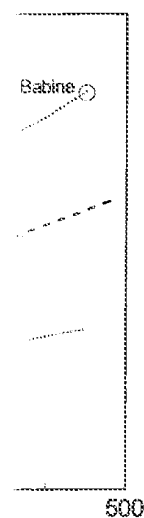
FIGURE 32.3 Variation in maximum juvenile sockeye production (kg/ha) with total seasonal PR. To standardize units with those of Downing et al. (1990), PR data are presented as g C·m⁻²·year⁻¹. Figure 32.3(a) presents data from B.C. and Alaskan lakes (Koenings and Burkett 1987) and 3(b) the same data in addition to data from lakes from a wide range of geographic areas (Downing et al. 1990).

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sockeye salmon nursery lakes (Quesnel and Shuswap) which conclusively show that maximum juvenile sockeye salmon biomass has been reached (Hume et al. 1996, Figure 32.4). Second, even on these lakes, smolt biomass was not available, so we assumed that fall fry biomass was equivalent to smolt biomass. Third, on two other B.C. lakes where smolt counts and biomass are available (Babine and Chilko), trends in the data suggest, but do not conclusively show, that maximum smolt biomass has been reached. While we believe current relationships between observed maximum juvenile biomass and PR in B.C. lakes are useful in validating the PR model, current data are too limited to allow independent development of a B.C. rearing capacity model.

The PR model also provides predictions of optimum escapements, and we wished to test these predictions in B.C. lakes. If sufficient data are available, relationships between effective female spawners (successfully spawned female sockeye salmon as determined by examination of carcasses) and fall fry numbers provide a way of estimating optimum escapements (Hume et al. 1996). Currently, we have such data for two B.C. lakes (Quesnel and Shuswap). These relationships were originally published in Hume et al. (1996), but for this chapter we added more recent data and also calculated total fry biomass (Figure 32.4). PR model predictions of optimum escapements (solid vertical lines on the figure) agree quite well with observed optimum escapements, since no increase in fry production is seen at escapements in excess of PR model predictions.

PR Model Assumptions

In the EV model, spring fry recruitment necessary to produce maximum smolt biomass and/or numbers was determined by a series of fry stocking experiments (Koenings and Burkett 1987). Spawner numbers necessary to produce this fry recruitment (e.g., optimum escapements) were determined from multiple years of data from 12 Alaskan nursery lakes (Koenings and Kyle 1997). Since sufficient data on all freshwater life-history stages of juvenile sockeye (egg deposition, spring fry recruitment, fall fry, smolt numbers) are not available for most B.C. lakes, we chose to adopt those published for Alaskan lakes and used in the EV model (Koenings and Burkett 1987; Koenings and Kyle 1997). This assumes that the components (sex ratio, fecundity, spawning success, egg-to-fry survival) of the spawner-to-fry relationship are similar (and constant) in B.C. and Alaska lakes. Undoubtedly, this assumption is not always met, since the components can vary between years for a given population and also between populations (Burgner 1991; Bradford 1995). Nevertheless, in the two B.C. lakes (Quesnel and Shuswap) where maximum fry production has been observed, PR model predictions of optimum escapement correspond closely to escapements which produce maximum fry numbers and biomass (Figure 32.4). Also, PR model equations predict smolt production of 54 smolts/adult spawner or 108 smolts/female spawner. In Chilko Lake, which has the only natural (non-enhanced) sockeye stock in B.C. with long-term data for both spawners and smolts, an average of 91 smolts/female spawner are produced at high spawner densities. Over a wide range of spawner densities, an average of 120 smolts/female spawner are produced (Hume et al. 1996).

Another assumption of the PR model is that lake rearing capacity and not spawning ground capacity controls smolt production. However, some B.C. lakes have less spawning ground capacity than lake rearing capacity. In these cases the PR model will overestimate optimum escapements and may be more useful for estimating the amount of enhancement (e.g., spawning channel construction, fry outplants) required to maximize production.

The PR model assumes that planktivores other than age-0 juvenile sockeye salmon are present in low numbers. While this is true of most nursery lakes, some contain large populations of limnetic planktivores such as kokanee (lake rearing *O. nerka*), stickleback *Gasterosteus aculeatus*, longfin smelt *Spirinchus thaleichtys*, and age-1 juvenile sockeye salmon. While other planktivores sometimes occur at higher densities than juvenile sockeye salmon (Simpson et al. 1981; Henderson et al.

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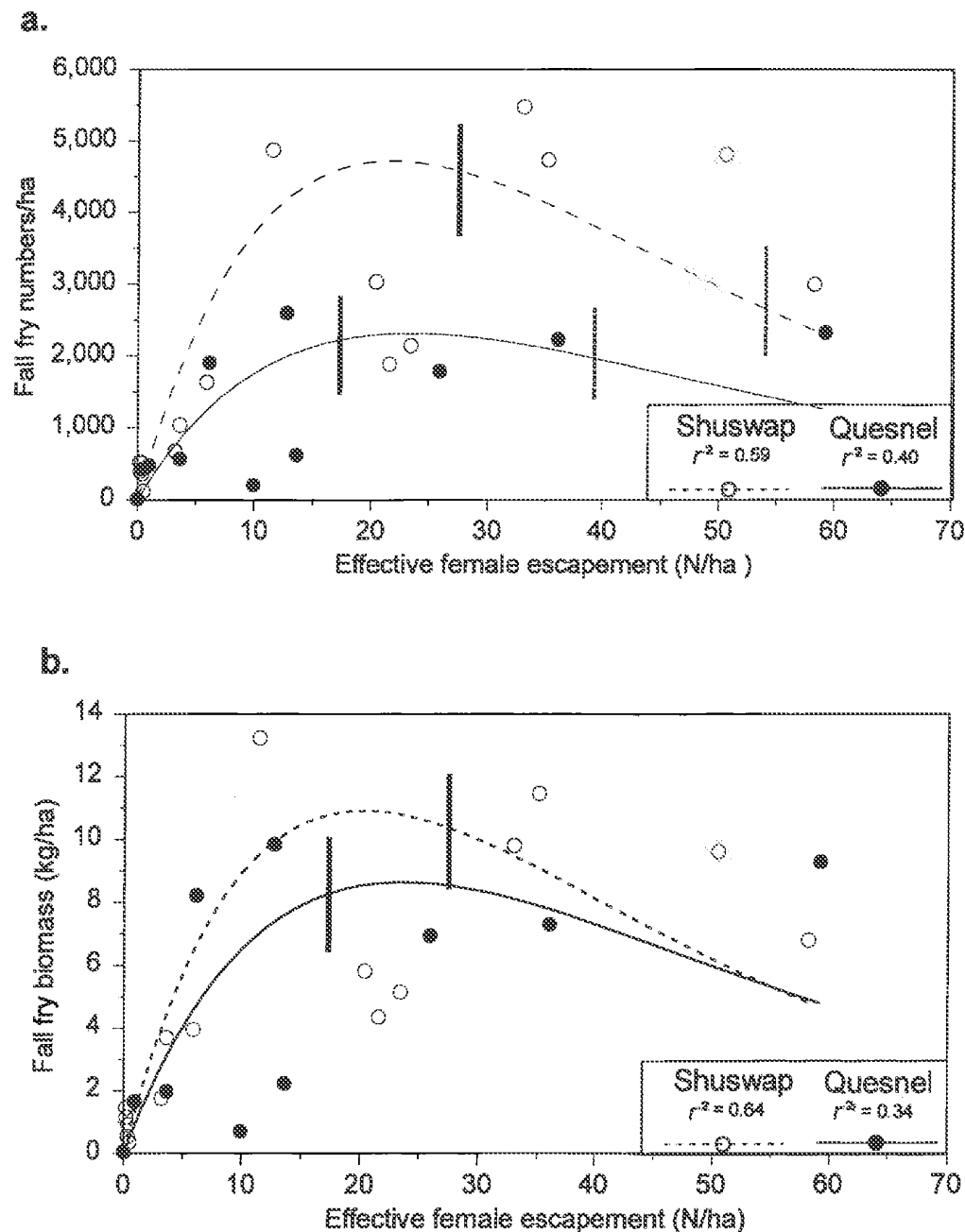981; Henderson et al.

a.

b.

FIGURE 32.4   Density (a) and biomass (b) of fall fry in Quesnel and Shuswap lakes produced by effective female spawners (Hume et al. 1996). Ricker stock-recruit functions are fitted to the data. Optimum escapement predictions from the PR model are shown by the solid vertical lines. EV model optimum escapements are indicated by the dashed vertical lines on (a).

1991), not all planktivores are competitors with juvenile sockeye salmon (Diewert and Henderson 1992). However, when competitive planktivores are numerous, estimates of optimum escapements and maximum smolt production must be reduced proportionately to the relative biomass of age-0 sockeye salmon and their competitors.

Both the PR and EV models assume that smolt weights will average 4.5 g at maximum productivity (Koenings and Burkett 1987; Koenings et al. 1993). However, some B.C. lakes do not produce smolts this large even at low escapements (Hyatt and Stockner 1985). We suggest that the models' assumption of a constant relationship between phytoplankton productivity (PR) and juvenile sockeye salmon production is not always valid. Efficiency of energy transfer from phytoplankton to zooplankton to juvenile sockeye can vary (Stockner 1987; Stockner and Shortreed 1989). However, methods to routinely quantify variation in this efficiency are not available. B.C. sockeye salmon nursery lakes for which we have data cover a relatively narrow trophic range (almost all are oligotrophic). Within this group of lakes, those with a theoretically lower energy transfer efficiency (i.e., longer food chain) are the most oligotrophic (Stockner 1987). In oligotrophic lakes, higher efficiencies occur in lakes near the upper range of oligotrophy; so varying efficiencies theoretically should affect the positive relationship between PR and sockeye production only by changing its slope. Further work is needed to incorporate varying energy transfer efficiencies into PR model predictions.

Given that zooplankton provide the linkage between phytoplankton and juvenile sockeye, some correlation should exist between zooplankton biomass and both PR and juvenile sockeye salmon production. Under some circumstances, these correlations can be detected. In lakes where planktivore densities are low, zooplankton biomass is strongly correlated to lake productivity (Hanson and Peters 1984; Shortreed and Stockner 1986; Shortreed et al. 1996). In lakes where sockeye salmon densities exhibit substantial annual variability, a negative correlation between plankton biomass and juvenile sockeye salmon numbers occurs (Hume et al. 1996). When planktivores are numerous, they can strongly influence zooplankton biomass and community composition (Kyle et al. 1988; Koenings and Kyle 1997; Hume et al. 1996). Because the zooplankton community can be suppressed by sockeye salmon grazing, we found that zooplankton biomass is most closely correlated to PR in lakes and years where grazing pressure is minimal (i.e., low planktivore densities) (Figure 32.5). If available, zooplankton biomass from years of low grazing pressure may be an indicator of underutilized rearing habitat which could support further development of rearing capacity models.

Zooplankton productivity and community structure strongly affect a lake's ability to rear juvenile sockeye. In the presence of continuous high grazing pressure, a lake may develop a predator-resistant, less productive zooplankton community (Kyle et al. 1988). This community will support fewer juvenile sockeye, even though PR remains the same. Adult escapements (800–900/EV unit) suggested in the EV model can produce this situation, with small (2.0 g) smolts, lowered freshwater and marine survival, reduced adult sockeye production, and a predator-resistant zooplankton community (Koenings and Burkett 1987; Koenings and Kyle 1997; Koenings et al. 1993). Data from B.C. lakes where high escapements have been observed support these findings, since EV model predictions of optimum escapement are much higher than those needed to maximize juvenile sockeye salmon production (Figure 32.4). Most recorded escapements to B.C. lakes have been much smaller than recommended by either rearing capacity model, and development of predator-resistant zooplankton communities has not been observed. Further, in many lakes, including those where excessive escapements have occurred (e.g., Chilko, Quesnel, Shuswap), sockeye returns tend to be cyclical, with both high and low adult returns in any 4-year cycle. Consequently, consecutive over-escapements have not occurred, allowing the zooplankton community to recover from any year of severe grazing pressure.
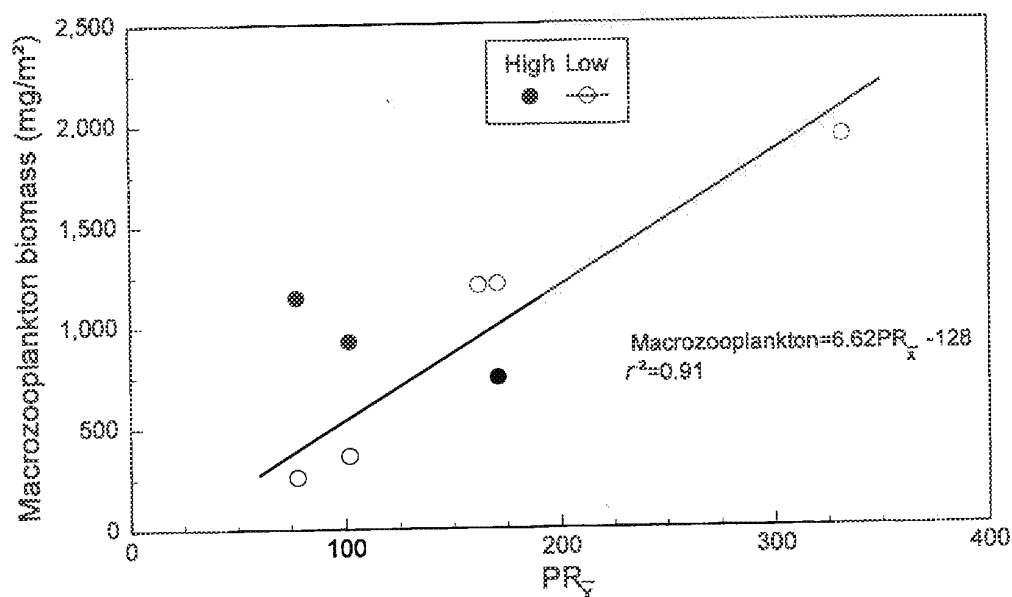
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FIGURE 32.5 Differences in the relationship between macrozooplankton and PR in high density (>14 EFS/ha) and low density (<2 EFS/ha) brood years, where EFS = effective female spawners. Data are seasonal averages from Fraser River lakes. (Hume et al. 1996 and Shortreed et al. 1996). Regression line is for low density years only.

PREDICTIONS FOR B.C. LAKES

Of the 90 B.C. sockeye salmon nursery lakes, we have data to directly estimate maximum smolt production and optimum escapements (i.e., fry models) only from Quesnel and Shuswap lakes. These lakes make up 16% of the total nursery lake surface area in B.C. and 29% of the total surface area in the Fraser River system. We have PR data for a much larger number of B.C. lakes (Tables 32.1 and 32.2). The Fraser River drainage basin is one of the world's most important sockeye salmon producers and contains 66% of B.C.'s nursery lake area (Table 32.2). Currently, PR data are available for 43% of the Fraser's nursery area. Of sockeye salmon nursery lakes in other regions of B.C., we have PR data for the majority of nursery lakes near the mainland coast, on Vancouver Island, and in the Skeena River drainage basin. No PR data are available for lakes on the Queen Charlotte Islands or for lakes north of the Nass River drainage basin (Table 32.2).

To make a first estimate of total productive capacity of B.C. sockeye salmon lakes, we assumed that lakes where no PR data were available had PR equal to the average of other lakes within the region, or of adjacent regions if no data were available within the region (Table 32.2). While this assumption may not be valid, we believed it was the best option until better data are available. This resulted in estimates of optimum escapement of 12.3 million to the Fraser River drainage basin and 16.9 million to all B.C. sockeye salmon lakes. Maximum smolt numbers (assuming 4.5-g smolts) from optimum escapements were estimated to be 667 million from the Fraser River drainage basin and 914 million from all B.C. sockeye salmon lakes (Table 32.2). If a smolt-to-adult survival of 10 to 15% is assumed (Hume et al. 1996), maximum adult returns to the Fraser system would range from 67 to 100 million. This is similar to the estimated historical return of 100 million sockeye salmon during dominant cycle years suggested by Ricker (1987). If the same survivals are assumed for all B.C. sockeye salmon, maximum adult returns would range from 91 to 137 million. Current dominant-year returns of adult sockeye salmon to the Fraser River system are 15 to 25 million (PSC 1996).

TABLE 32.1

British Columbia sockeye salmon nursery lakes where PR data are available and resulting PR model predictions (optimum escapement = $187 \times PR_{total}$; maximum smolt number = $10{,}120 \times PR_{total}$; maximum smolt biomass = $45.5 \times PR_{total}$)

Region	Lake	Surface area (km²)	PR_{total} (metric tons C)	PR model predictions		
				Optimum escapement (thousands)	Max. smolt number (millions)	Max. smolt biomass (metric tons)
Central coast	Bonilla	2.3	44	8.2	0.45	2.0
	Curtis[a]	3.0	62	12	0.63	2.8
	Devon	1.8	22	4.1	0.22	1.0
	Kitlope	12	99	19	1.0	4.5
	Long	21	240	45	2.4	11
	Lowe	3.7	52	9.7	0.5	2.4
	Owikeno	91	904	170	9.2	41
	Simpson	8.7	100	19	1.0	4.6
Fraser River	Chilko	185	2,614	490	26	119
	Francois	250	7,247	1,400	73	330
	Fraser	54	3,215	600	33	146
	Quesnel	270	4,985	930	50	227
	Shuswap	296	10,157	1,900	103	462
Nass River	Fred Wright	3.9	84	16	0.85	3.8
	Meziadin	36	991	190	10	45
Skeena River	Alastair	6.9	244	46	2.5	11
	Babine	470	12,355	2,300	125	562
	Bear	19	491	92	5.0	22
	Johanson	1.4	17	3.2	0.17	0.8
	Kitsumkalum	18	109	20	1.10	5.0
	Kitwanga	7.8	372	70	3.8	16.9
	Lakelse	13	173	32	1.75	7.9
	Morice	96	1,488	280	15	68
	Morrison	13	255	48	2.6	12
	Sustut	2.5	40	7.5	0.40	1.8
	Swan	18	369	69	3.7	17
Vancouver Isl.	Great Central[a]	51	889	170	9.0	40
	Henderson[a]	15	504	94	5.1	23
	Hobiton[a]	3.6	51	9.5	5.2	2.3
	Kennedy	64	627	120	6.4	28
	Nimpkish	37	412	77	4.2	19
	Sproat	41	325	61	3.3	15
	Woss	13	209	39	2.1	10

[a] PR estimates for these lakes were collected during whole-lake fertilization experiments. Under normal conditions all estimates would be lower.

CONCLUSIONS

The EV model is a useful predictor of rearing capacity in some Alaskan lakes. By using photosynthetic rate instead of euphotic zone depth, our PR model makes EV model predictions usable in a wider range of lakes and conditions. Although there are few B.C. lakes where predictions can be tested, in Quesnel and Shuswap lakes, where maximum sockeye production has been observed,

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Max. smolt biomass (metric tons)
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4.5
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227
462
3.8
45
11
562
22
0.8
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TABLE 32.2

Variation in total sockeye salmon nursery area within major regions or drainage basins of British Columbia, the proportion of each region where photosynthetic rate (PR) data are available, and PR model predictions for the regions. For the predictions, we assumed that PR for lakes where no data were available was similar to PR in other lakes in the region. Where no regional data were available, PR data from adjacent regions were used.

Region	Approximate total lake area (km²)	Percent of total B.C. nursery area	Percent of area with PR data	PR model predictions		
				Optimum escapement (millions)	Maximum smolt biomass (metric tons)	Maximum smolt number (millions)
Fraser River	2,501	66.3	43	12.3	3060	667
Skeena River	666	17.6	100	2.9	724	158
Vancouver Island	257	6.8	91	0.6	153	33
Central coast	172	4.6	83	0.34	86	18
Nass River	75	2.0	53	0.38	94	21
Queen Charlottes	56	1.5	0	0.11	28	6.1
Taku River	28	0.8	0	0.12	30	6.6
Stikine River	19	0.5	0	0.08	21	4.5
Total	3,774	100		16.9	4,196	914

PR model predictions correspond well to observed optimum escapements (Figure 32.4). In Chilko Lake, PR model predictions of 108 smolts/female spawner were similar to observed smolt production of 91 smolts/female spawner at maximum sockeye production.

The PR model allows predictions of optimum escapement and maximum smolt production to be made after 2–3 years of data collection. Estimates can be made with only 1 year of data (for a number of lakes we have only 1 year of PR data), but annual variability can be substantial and multiple years of data ensure greater confidence in annual estimates. Predictions can be made when the only available data on sockeye nursery lakes are seasonal carbon production and lake area, but model predictions can be readily modified and/or verified as more data are available about spawning area, rearing environment, and the life-history stages of a sockeye stock.

PR model predictions of optimum escapement are for the number of spawners required to fully utilize lake rearing capacity. These predictions must be modified if key assumptions are not met. For example, if spawning ground capacity is less than lake rearing capacity, the PR model will overestimate optimum escapements. If planktivores other than age-0 sockeye salmon are present and compete with sockeye salmon fry, model predictions must be adjusted for the proportion of the rearing capacity which they utilize. If a lake has a predation-resistant plankton community because of extreme oligotrophy (Stockner and Shortreed 1989) or because of high grazing pressure (Kyle et al. 1988), its rearing capacity may be lower than PR model predictions.

In lakes which are below rearing capacity (the majority), the amount of additional sockeye production that is biologically feasible can be estimated using the PR model. Increased production could be accomplished by increasing escapements or by some form of enhancement (e.g., spawning channels or fry stocking). In a lake which is currently producing large numbers of adult sockeye salmon, the PR model enables escapement targets to be set based on the lake's productive capacity. If escapements exceed the amount required to maximize smolt production, the economic cost of the foregone catch can be determined. The PR model would be useful in maintaining productive stocks at optimum levels and in determining the amount that unproductive stocks can be increased, making it a valuable tool in sustaining and enhancing B.C. and other sockeye salmon stocks.

ACKNOWLEDGMENTS

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