

Variation in the degree of silvering of wild coho salmon, *Oncorhynchus kisutch*, smolts migrating seaward from Carnation Creek, British Columbia

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Degree of silvering (colouration) is often used as an index of the degree of smoltification in salmonids. To judge the reliability of silvering as an indicator of migratory readiness, we examined the silvering of wild coho salmon, *Oncorhynchus kisutch*, smolts upon entry into the Carnation Creek, British Columbia, estuary. Silvering of migrants was greater in larger fish and increased over the course of the migratory period. Photoperiod appeared to account for most of the observed increase in silvering over time; increased silvering was not correlated with temperature or lunar phase. Overall, 50% of seaward migrants were completely silvered, 45% were in a transitional phase, and 5% still retained colouration characteristics of parr. Colouration thus appears to have limited utility as a reliable indicator of migratory readiness. Our findings suggest that estuarine residence is important for completion of parr-smolt transformation and that acclimation of hatchery smolts in brackish water prior to sea water entry may enhance their survival.

I. INTRODUCTION

Anadromous salmonids that grow through juvenile stages in fresh water for extended periods undergo a series of marked morphological, physiological and behavioural changes in preparation for entry into the ocean (Hoar, 1976; Wedemeyer *et al.*, 1980). Prominent among these changes is a distinct change in colouration from that cryptic for life in streams (vertical bars or 'parr marks'; Donnelly & Dill, 1984) to that cryptic for life in schools in the open ocean (silvery, reflective sides; Denton, 1971). In the transition from the freshwater parr to the seaward-migrating smolt phase, environmentally cued, hormonally regulated pigment changes in the skin and scales result in a loss of parr marks, silvering of sides, and blackening of fin margins (Wedemeyer *et al.*, 1980; Gorbman *et al.*, 1982).

Because the parr-smolt colouration change is so obvious, it is commonly used as an index of other, less visible changes that occur during smoltification (i.e. migratory behaviour, ability to osmoregulate in sea water), particularly in culture operations where it has been used in determining when to release smolts (Mahnken & Waknitz, 1979). Although silvering, increased salinity tolerance and migration generally coincide (e.g. Rodgers *et al.*, 1987), silvering may not be a reliable indicator of smolt status (Kato, 1972; Wedemeyer *et al.*, 1980). In some populations, seaward migration occurs prior to complete silvering or sea water adaptation (Mitans, 1967, 1970; Clarke *et al.*, 1978). In laboratory studies, Johnston & Eales

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(1968, 1970) found that the rate of silvering of Atlantic salmon, *Salmo salar*, smolts was affected by temperature, fish size and photoperiod (see also Kazakov & Kozlov, 1985). Moreover, it has been noted that smolts migrating late in the run are often more silvery than earlier migrants (Solomon, 1978; Rodgers *et al.*, 1987). Variation in the degree of silvering of seaward migrants thus appears common; however, few measurements of the degree of colour variation present in wild smolts have been reported (e.g. Mitans, 1967; Kazakov & Kozlov, 1985). In this paper we describe the colour variation of coho salmon, *Oncorhynchus kisutch*, juveniles migrating seaward from Carnation Creek, and attempt to account for the observed effects of size and time of migration on the silvering process. Our main objective was to judge the reliability of silvering as an indicator of migratory behaviour in juvenile coho salmon. We also aimed to increase present knowledge of the smoltification process in wild coho salmon and therefore provide a firmer basis for designing strategies to maximize survival of hatchery-released smolts.

II. STUDY AREA

Carnation Creek, a small (7.6 km long) stream that empties into Barkley Sound on the west coast of Vancouver Island, is accessible to anadromous coho and chum, *Oncorhynchus keta*, salmon and steelhead, *Salmo gairdneri*, and cutthroat, *Salmo clarki*, trout. The area is the site of a long-term study to examine the effects of logging on coastal rain-forest streams (Scrivener & Andersen, 1984).

Juvenile coho salmon spend 1–2 years in Carnation Creek prior to migrating to the sea as smolts in the spring. Since 1971, an average of 3000 smolts have migrated downstream from late April to early June (Andersen, 1987).

III. MATERIALS AND METHODS

Seaward migrating coho salmon were captured in fan-traps attached to a permanent fish-counting fence located near the mouth of Carnation Creek at the uppermost limit of tidal influence. All migrant fish were captured until stream-flows exceeded $6 \text{ m}^3 \text{ s}^{-1}$; subsamples were obtained at higher flows (Andersen, 1987). Beginning 1 March, fish were removed from traps every morning (08.00–10.00 hours) with more frequent removals during periods of high stream-flow or high fish numbers. Fish were anaesthetized in a 2-phenoxyethanol solution (1:4000), their colouration examined, and fork-length (F.L.) measured to the nearest mm. The anaesthetic had no detectable effect on colouration. Colouration (degree of silvering, fin colour, presence/absence of parr marks) of migrants was categorized according to visual criteria adapted from those described and illustrated in Gorbman *et al.* (1982):

parr—orange fin colour; parr marks dark and clearly evident; little or no silvering of sides.

transitional—sides silvery but parr marks still visible; fin colour clear or yellowish [also referred to as silvery parr e.g. Johnston & Eales (1970)].

'true' smolt—parr marks almost or completely obscured by silvering; caudal and dorsal fins clear with black, well-defined margins; eyeball diameter smaller, with surrounding integument silvery.

The colouration of 1449 (73%) of all migrants was examined; the remaining 27% consisted of fish which were removed from traps at night when colouration could not be

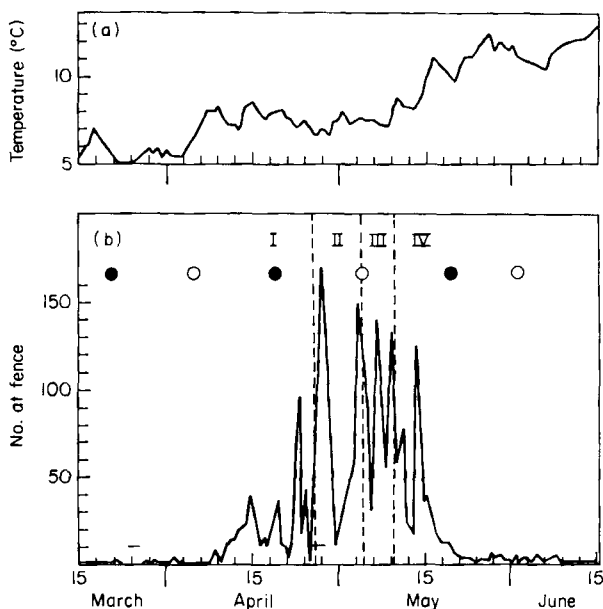


FIG. 1. Timing of seaward migration of juvenile coho salmon from Carnation Creek. (a) Average daily water temperature. (b) Number of migrants at counting fence. Total number of fish captured = 1977. Horizontal bars indicate periods when only subsamples were obtained, due to high flows. Numerals I-IV represent quartiles of migrant numbers (I = 15 March-26 April; II = 27 April-4 May; III = 5 May-10 May; IV = 11 May-9 June). Lunar phase is shown as full moon (○) and new moon (●).

accurately assessed. To compare changes in colouration of migrants over time, the percentages and length-frequencies of fish in each colouration category were determined for each quartile of the total run. A 'silvering index' was determined for each quartile by scoring parr-coloured as 1, transitional-coloured as 2, and smolt-coloured migrants as 3.

Water temperature during the migration period was recorded continuously at the hydrological weir located 500 m above the fish-counting fence.

IV. RESULTS

Migration of juvenile coho salmon began in mid-April and peaked in early May (Fig. 1). The silvering index of migrants increased for each successive quartile of the run (Fig. 2). Colouration-frequency distributions for each quartile were significantly different (χ^2 tests $P < 0.05$ to 0.001). In the first half of the run, the increase in silvering was due primarily to a decrease in the number of parr- and an increase in the number of transitional-coloured fish. In the second half, a progressive decline and increase in the number of transitional- and smolt-coloured migrants, respectively, accounted for most of the increase in silvering. Overall, 50% of migrants were completely silvered (smolt-coloured), 45% were in a transitional phase, and 5% still retained colouration characteristics of parr.

Size-related differences in the colouration of migrant fish were also apparent (Fig. 2). In each quartile, parr-coloured migrants were significantly smaller (> 5 mm differences) than transitional-coloured fish which, in turn, were significantly smaller than completely silvered fish (t -tests, $P < 0.05$). Over the entire run, the majority (86%) of migrants < 85 mm F.L. were parr-coloured whereas the

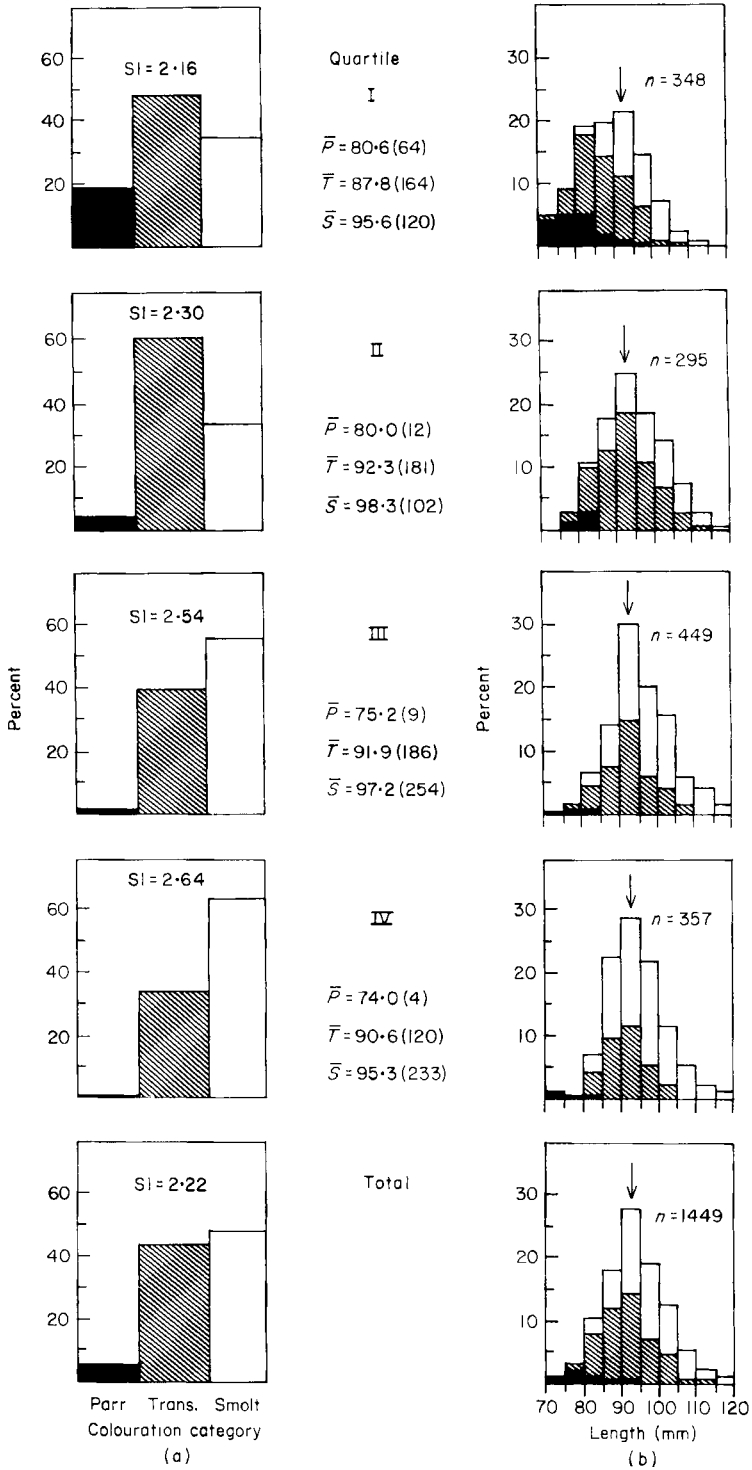


FIG. 2. The percentages (a) and length-frequencies (b) of migrants within each colouration category for each quartile and for the total run. \bar{P} , \bar{T} , \bar{S} represent mean lengths of fish in each category (parr, trans., smolt); numbers of fish in each category are shown in parentheses. Vertical arrows indicate the mean length and n denotes the total number of migrants examined in each quartile. SI is the 'silvering index'.

majority (83%) of fish >105 mm were smolt-coloured. The mean lengths of migrants increased significantly from quartile I to II ($t=4.78$, $P<0.01$) and quartile II to III ($t=2.05$, $P<0.005$), but not in quartile III to IV (Fig. 2). Thus, increased silvering over time could not be attributed solely to an increased number of fish above a certain length. Rather, silvering of fish within the 85–105 mm size range increased as the run progressed, e.g., the percentage of fish 85–90 mm in length classified as smolt-coloured increased from 22% (15 of 67) in quartile I to 56% (44 of 79) in quartile IV. Differences in the rate of silvering between age 1 and 2 migrants were unknown, but age probably had a relatively minor effect on the silvering patterns we observed, since scale analyses revealed that age 2 fish comprised only 9.6% of the total number of migrants (Andersen, 1987).

The silvering index of migrants was not correlated with either average water temperature per quartile ($r=0.86$, d.f. = 2, $P>0.05$) or average water temperature per day ($r=-0.25$, d.f. = 32, $P>0.20$). Temperatures fluctuated between 6.5 and 8.5° C when most of the migration (and hence most of the increase in silvering) occurred (Fig. 1).

The increased silvering of migrants during the run showed no obvious relationship to lunar phase. The silvering index of migrants increased from about 2.2 to 2.4 in the 2 weeks following the new moon (20 April) and from 2.4 to 2.6 in the 2 weeks following the full moon (4 May) (Fig. 1).

V. DISCUSSION

Colouration was not a reliable indicator of migratory behaviour in Carnation Creek coho salmon: seaward migrants showed considerable variation in silvering, with only 50% of the fish completely silvered upon entry into the estuary. Our findings corroborate previous observations (Johnston & Eales, 1970; Solomon, 1978; Rodgers *et al.*, 1987) that the parr-smolt colouration change occurs non-uniformly among seaward-migrating salmonids: silvering proceeds faster in larger fish and is more prevalent later in the run. Our results concur with those of Gorbman *et al.* (1982) who found that variation in the rate and timing of parr-smolt transformation in coho salmon is a normal characteristic among individuals in a population.

The causes of this size and time-related variation in silvering are not well understood. Larger fish may silver faster due to a more functional endocrine system that is more responsive to the environmental cues controlling the parr-smolt colouration change (Hoar, 1965, 1976). Growth is also known to accelerate smoltification processes (Clarke *et al.*, 1978), but the lack of a consistent relationship between increased silvering and increases in mean length of migrants in our study suggests that factors other than growth were involved. Silvering is known to be under strong endogenous control, with photoperiod and temperature the major environmental factors regulating the timing and rate of colouration change (Clarke *et al.*, 1978). The increase in silvering over time, in the absence of a strong correlation with temperature, supports Hoar's (1965) findings that photoperiod is relatively more important than temperature in controlling the rate of silvering in coho salmon (cf. Johnston & Eales, 1968). A link between lunar phase and migration and silvering of Pacific salmon has been hypothesized by Grau *et al.* (1981) and Grau (1982). However, we found no apparent influence of lunar phase

on either the increase in silvering or in the number of migrants (Figs 1, 2). Thus, fish size and photoperiod appeared to account for most of the variation in colouration of migrating coho salmon; genetic differences (Gorbman *et al.*, 1982) among migrants in the rate and timing of parr-smolt transformation, however, could also have influenced the patterns in silvering that we observed.

A number of studies have noted a positive correlation between degree of silvering and sea water tolerance. When transferred directly to sea water, parr- and transitional-coloured coho salmon have much poorer survival and growth than those completely smolt-coloured (Mahnken & Waknitz, 1979; Folmar *et al.*, 1982), apparently as a result of an incompletely developed osmoregulatory capacity (Clarke & Nagahama, 1977). Clarke & Shelbourn (1986) found that laboratory-reared coho with a mean silvering index of 2.2 had lower osmoregulatory capacity and much poorer growth upon transfer to sea water than did those with a mean silvering index >2.5 . These data correspond to the mean silvering indices we calculated for the first and second half, respectively, of the Carnation Creek smolt run (Fig. 2) and imply that 50% of Carnation Creek coho salmon enter sea water before complete sea water tolerance has developed. However, underwater observations of coho salmon in the Carnation Creek estuary in 1985 during and after the smolt run revealed that many of them resided in the estuary for at least several days prior to moving out to sea (McMahon, unpubl. data). Increased sea water tolerance following exposure to brackish water in the estuary has been documented for young coho salmon in Carnation Creek (Tschaplinski, 1982) and we hypothesize that estuarine residence is important for completion of silvering and other smoltification processes. Another possibility is that incompletely smolted fish do not migrate to the sea but return to fresh water for another year. However, two observations indicate that nearly all coho salmon migrants that enter the estuary in the spring do not re-enter fresh water: (1) only 1 of the 1977 fish that passed through the counting fence in spring 1985 was observed in the estuary after 1 June; (2) only 14 juveniles were captured in an upstream trap that was operated at the counting fence from 17 March to 1 August 1974 (Carnation Creek unpubl. data). Mitans (1967, 1970) also found that *S. salar* migrants are incompletely silvered upon entry into the Baltic Sea; only after a period of estuarine residence is smoltification completed. McCormick *et al.* (1985) observed a similar pattern for anadromous brook trout, *Salvelinus fontinalis*, entering the Moisie and Matamek River estuaries (Quebec) and presented evidence that exposure to the brackish waters in the estuary promoted sea water tolerance. Estuarine residence thus appears important for completion of silvering and other parr-smolt transformation processes in at least some salmonids (Tytler *et al.*, 1978; but see Fried *et al.*, 1978 and McCormick *et al.*, 1985 re. Atlantic salmon). The 'parr-reversion' that commonly occurs when incompletely smolted hatchery fish are transferred directly to sea water (Folmar *et al.*, 1982) may therefore be, in part, an artifact resulting from a lack of an acclimation period in estuarine waters prior to sea water entry. Since in experimental releases of hatchery smolts the degree of smoltification at sea water entry has been positively correlated to the length of seaward migration (Loyenko & Chernitskiy, 1984), we postulate that estuarine residence may be particularly important for completion of smoltification in coho salmon populations inhabiting short coastal streams like Carnation Creek.

In light of the accumulating evidence for variation in the patterns of parr-smolt transformation between different species (McCormick *et al.*, 1985), populations (Ewing & Birks, 1982; Kazakov & Kozlov, 1985) and individuals within populations (Gorbman *et al.*, 1982; this study), the use of silvering or other indices to determine the status of smolts (which tend to obscure these differences—Brannon *et al.*, 1982) becomes limited without prior testing of their reliability (Clarke, 1982). These findings also suggest that culture practices which allow the natural patterns of variation in parr-smolt transformation to be expressed may serve to increase the survival of hatchery smolts. Volitional, rather than mass, forced release of hatchery smolts, for example, allows for variation in timing of smoltification and migratory readiness among individuals and may account, at least in part, for higher returns of hatchery coho salmon (Brannon *et al.*, 1982). A common procedure of ocean ranching operations is the transfer of smolts directly from freshwater hatcheries to seawater net-pens, but instances in which up to 50–85% of fish died or ceased to grow have been reported (Mahnken & Waknitz, 1979; Nishioka *et al.*, 1982). However, if estuarine residence is important for the completion of smoltification in at least some species or populations of salmonids, as our results and those of Mitans (1967, 1970) and McCormick *et al.* (1985) suggest, then acclimation in brackish water prior to sea water entry may enhance survival of hatchery smolts. Studies demonstrating increased survival (Loyenko & Chernitskiy, 1984) and returns of hatchery-reared Atlantic salmon smolts (Jensen, 1979) exposed to brackish waters prior to release provide some evidence in support of evaluating such a practice for culture operations.

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References

- Andersen, B. C. (1987). Fish populations of Carnation Creek and other Barkley Sound streams 1985–1986. *Can. Data Rep. Fish. Aquat. Sci.* **553**, 59 pp.
- Brannon, E., Feldman, C. & Donaldson, L. (1982). University of Washington zero-age coho salmon smolt production. *Aquaculture* **28**, 195–200.
- Clarke, W. C. (1982). Evaluation of the seawater challenge test as an index of marine survival. *Aquaculture* **28**, 177–183.
- Clarke, W. C. & Nagahama, Y. (1977). Effect of premature transfer to sea water on juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* **55**, 1620–1630.
- Clarke, W. C., Shelbourn, J. E. & Brett, J. R. (1978). Growth and smolting of under-yearling coho salmon in relation to photoperiod and temperature. *Can. J. Zool.* **56**, 2413–2421.
- Clarke, W. C. & Shelbourn, J. E. (1986). Delayed photoperiod produces more uniform growth and greater seawater adaptability in under-yearling coho salmon (*Oncorhynchus kisutch*). *Aquaculture* **56**, 287–299.
- Denton, E. (1971). Reflectors in fishes. *Scient. Am.* **224**, 65–72.
- Donnelly, W. A. & Dill, L. M. (1984). Evidence for crypsis in coho salmon, *Oncorhynchus kisutch* (Walbaum), parr: substrate colour preferences and achromatic reflectance. *J. Fish Biol.* **25**, 183–195.
- Ewing, R. D. & Birks, E. K. (1982). Criteria for parr-smolt transformation in juvenile chinook salmon (*Oncorhynchus tshawytscha*). *Aquaculture* **28**, 185–194.

- Folmar, L. C., Dickhoff, W. W., Mahnken, C. V. W. & Waknitz, F. W. (1982). Stunting and parr-reversion during smoltification of coho salmon, *Oncorhynchus kisutch*. *Aquaculture* **28**, 91–104.
- Fried, S. M., McCleave, J. D. & LaBar, G. W. (1978). Seaward migration of hatchery-reared Atlantic salmon, *Salmo salar*, smolts in the Penobscot River estuary. *J. Fish. Res. Bd Can.* **35**, 76–87.
- Gorbman, A., Dickhoff, W. W., Mighell, J. L., Prentice, E. F. & Waknitz, F. W. (1982). Morphological indices of developmental progress in the parr-smolt coho salmon, *Oncorhynchus kisutch*. *Aquaculture* **28**, 1–19.
- Grau, E. G., Dickhoff, W. W., Nishioka, R. S., Bern, H. A. & Folmar, L. C. (1981). Lunar phasing of the thyroxine surge preparatory to seaward migration of salmonid fish. *Science* **211**, 607–609.
- Grau, E. G. (1982). Is the lunar cycle a factor timing the onset of salmonid migration? In *Proceedings of the Symposium on Salmon and Trout Migratory Behavior* (E. L. Brannon and E. O. Salo, eds), pp. 184–189. Seattle: University of Washington.
- Hoar, W. S. (1965). The endocrine system as a chemical link between the organism and its environment. *Trans. R. Soc. Can.* **3**, 175–200.
- Hoar, W. S. (1976). Smolt transformation: evolution, behavior, and physiology. *J. Fish. Res. Bd Can.* **33**, 1233–1252.
- Jensen, K. W. (1979). Saltwater releases and saltwater adaptation of smolts of Atlantic salmon. *Int. Coun. Explor. Sea Anad. Catad. Fish Committee C.M. 1979/M:8*. 10 pp (mimeo).
- Johnston, C. E. & Eales, J. G. (1968). Influence of temperature and photoperiod on guanine and hypoxanthine levels in the skin and scales of Atlantic salmon (*Salmo salar*) during parr-smolt transformation. *J. Fish. Res. Bd Can.* **25**, 1901–1909.
- Johnston, C. E. & Eales, J. G. (1970). Influence of body size on silvering of Atlantic salmon (*Salmo salar*) at parr-smolt transformation. *J. Fish. Res. Bd Can.* **27**, 983–987.
- Kato, T. (1972). Artificial silvering of rainbow trout reared in a blue tank. *Bull. Freshwat. Res. Lab. Tokyo* **22**, 39–47.
- Kazakov, R. V. & Kozlov, V. V. (1985). Quantitative estimation of degree of silvering displayed by Atlantic salmon (*Salmo salar* L.) juveniles originating from natural populations and from fish-rearing farms. *Aquaculture* **44**, 213–220.
- Loyenko, A. A. & Chernitskiy, A. G. (1984). Factors influencing downstream migration of young Atlantic salmon, *Salmo salar* (Salmonidae), released from hatcheries. *J. Ichthyol.* **24**, 39–48.
- Mahnken, C. V. W. & Waknitz, F. W. (1979). Factors affecting growth and survival of coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) in seawater net-pens in Puget Sound. *Proc. Wild Maricult. Soc.* **10**, 280–305.
- McCormick, S. D., Naiman, R. J. & Montgomery, E. T. (1985). Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* **42**, 529–538.
- Mitans, A. R. (1967). Uslovia smoltifikatzii, dinamika skata i chislenosti pokatnikov lososja na ribovodnikh Zavodakh. *Baltnirkh, Riga*, 35 pp.
- Mitans, A. R. (1970). The feeding of Baltic salmon smolts in the river and the sea. *J. Ichthyol.* **10**, 89–95.
- Nishioka, R. S., Bern, H. A., Lai, K. V., Nagahama, Y. & Grau, E. G. (1982). Changes in the endocrine organs of coho salmon during normal and abnormal smoltification—an electron-microscope study. *Aquaculture* **28**, 21–38.
- Rodgers, J. D., Ewing, R. D. & Hall, J. D. (1987). Physiological changes during seaward migration of wild juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **44**, 452–457.
- Scrivener, J. C. & Andersen, B. C. (1984). Logging impacts and some mechanisms that determine the size of spring and summer populations of coho salmon fry (*Oncorhynchus kisutch*) in Carnation Creek, British Columbia. *Can. J. Fish. Aquat. Sci.* **41**, 1097–1105.
- Solomon, D. J. (1978). Migration of smolts of Atlantic salmon (*Salmo salar* L.) and sea trout (*Salmo trutta* L.) in a chalkstream. *Env. Biol. Fish.* **3**, 223–229.

- Tschaplinski, P. J. (1982). Aspects of the population biology of estuary-reared and stream-reared juvenile coho salmon in Carnation Creek: a summary of current research. In *Proceedings of the Carnation Creek Workshop, a 10-year Review*. (G. Hartman, ed.), pp. 289–305. Nanaimo, British Columbia: Pacific Biological Station.
- Tytler, P., Thorpe, J. E. & Shearer, W. M. (1978). Ultrasonic tracking of the movement of Atlantic salmon smolts (*Salmo salar* L.) in the estuaries of two Scottish rivers. *J. Fish Biol.* **12**, 575–586.
- Wedemeyer, G. A., Saunders, R. L. & Clarke, W. C. (1980). Environmental factors affecting smoltification and early marine survival of anadromous salmonids. *Mar. Fish. Rev.* **42**, 1–14.