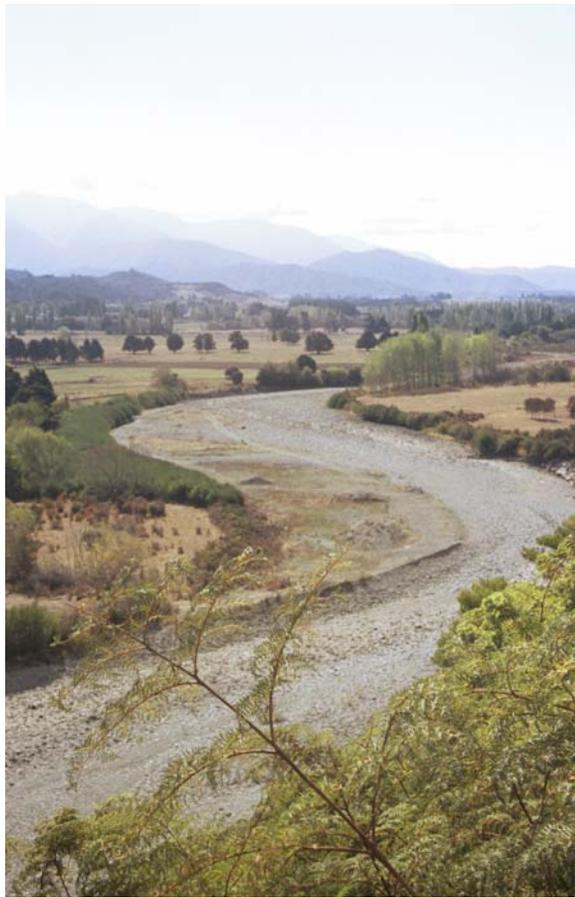


Movement of Salmonids in Response to Low Flow: A Literature Review



Prepared for

Movement of Salmonids in Response to Low Flow: A Literature Review

Prepared for

Motueka Integrated Catchment Management Programme

by

Joe Hay

Cawthron Institute
98 Halifax Street East
Private Bag 2
NELSON
NEW ZEALAND

Phone: +64.3.548.2319
Fax: +64.3.546.9464
Email: info@cawthron.org.nz

Information contained in this report may not be used without the prior consent of the client

Cover Photo: Takaka River (Dry): Cawthron 2000

EXECUTIVE SUMMARY

This report reviews the literature regarding movement and migration of salmonids in response to low stream flows.

Salmonids frequently need to move in order to avoid adverse environmental conditions, or to optimise foraging opportunities during low flow events. As well as a reduction in available wetted habitat, low flows can produce elevated water temperatures and reduced dissolved oxygen concentrations.

The evidence suggests that temperature is the most important driver of salmonid movements in response to low flow. There is a tendency for fish to migrate from adversely hot areas into deeper habitats providing cooler water temperatures (thermal refugia).

These movements take place over a range of scales, depending on the scale and magnitude of the low flow event and on the opportunity for the fish to move. At a small scale fish tend to move from riffle and run habitat into deeper water as flow declines. On a larger scale they generally move toward areas with cooler water. This often involves upstream migration to cool tributaries, but can also entail movement into lakes or the sea.

Migration distances from tens of metres to upwards of one hundred kilometres are commonly reported in the literature.

There is substantially more known about smaller scale movements from runs to pools, than there is regarding larger scale migrations prompted by low flows. This highlights a need for more research into long term, long range movements of salmonids in response to low flows.

TABLE OF CONTENTS

1.	INTRODUCTION	1
2.	LITERATURE REVIEW	1
2.1	Reasons for migration.....	1
2.2	Thermal refugia and behavioural thermoregulation	2
2.3	Scale of movement	2
2.3.1	<i>Small scale movements to pool habitat</i>	<i>3</i>
2.3.2	<i>Larger scale movements</i>	<i>4</i>
2.4	Direction of migration	5
2.5	Distance of migration	6
3.	SUMMARY	7
4.	REFERENCES.....	7

Report reviewed by:

Approved for release by:

Roger Young

Rowan Strickland

1. INTRODUCTION

Periodic reductions in flow level, as a result of prevailing weather conditions and human influences, are a prevalent feature of many riverine habitats (Armstrong and Braithwaite 1998). Low flow events obviously have the potential to interfere with fish migration, impeding their movement through affected systems (Elliott 2000). For example; when discharge fell below 0.5 litres per second in Sagehen Creek, California, downstream migrating rainbow trout (*Oncorhynchus mykiss*) fry were not able to move over shallow riffles (Erman and Leidy 1975), and in Middle Fork John Day River, Oregon, a combination of water removal for irrigation and low midsummer flows effectively made passage to headwater reaches physically impossible for salmon (Torgersen *et al.* 1999). However, low flow events also have the potential to stimulate movement of fish between habitats. This aspect of the relationship between low flows and migration remains an area in need of further research effort (Armstrong and Braithwaite 1998; Matthews and Marsh-Matthews 2003). There is a particular paucity of research focusing on fish responses to low flow in New Zealand (Jowett 1997).

This report reviews the current state of knowledge of fish movement and migrations in response to low flows, with a focus on salmonids. Since low flows are also often associated with increased water temperatures and reduced dissolved oxygen concentrations, migrations in response to these variables are also considered in this review.

2. LITERATURE REVIEW

2.1 Reasons for migration

Migrations involve directed movements between habitat types of a large proportion of an animal population, occurring with a reasonably regular periodicity, and resulting in an alternation between two or more habitats within the lifetime of the individual (Northcote 1997; Lucas and Baras 2001). Fish commonly migrate to reproductive habitat, a classic example being the well known spawning runs of anadromous salmon in the Pacific Northwest. However, fish may also migrate in search of optimal feeding habitat and food resources, or to seek refuge from adverse environmental conditions. Because environmental conditions and the distribution of resources change temporally, fish must frequently move in order to continually optimise their use of the environment (Northcote 1992).

Changes in water temperature and discharge rates are often cited as cues for migration (Jonsson 1991; Lucas and Baras 2001; Hembre *et al.* 2001). Downstream smolt runs of brown trout (*Salmo trutta*) in Norway are triggered by increased discharge and water temperature, for instance (Hembre *et al.* 2001). However, in the case of low flow events fish migration probably is driven primarily by the need for refuge from increased water temperatures and a reduction in available habitat area through drying, while also optimising feeding opportunities. Trout generally avoid high water temperatures preferring areas where temperatures remain under around 19 °C (Matthews *et al.* 1994; Garrett and Bennett 1995; Hayes and Young 2001). Extremes of elevated water temperature during low flow events can prove lethal to fish that are not able to escape

(Larimore *et al.* 1959). Jowett (1997) reported trout deaths in New Zealand rivers when temperatures exceeded 26 °C, for example.

The theory that trout move in order to avoid adverse conditions, as well as to gain access to optimal foraging positions is supported by findings of higher growth rates in mobile fish than in their resident contemporaries. Steingrimsson and Grant (2003) found that mobile fish grew as fast, or faster, than sedentary fish, as did Kahler *et al.* (2001). These findings have seen the traditional view that mobile fish were evicted subordinates give way to the idea of mobile fish seeking to optimise habitat use for their life stage (Steingrimsson and Grant 2003). However, this is not always the case. Riley *et al.* (1992) found the opposite trend in brook trout (*Salvelinus fontinalis*), with resident fish being larger than mobile trout.

2.2 Thermal refugia and behavioural thermoregulation

Although fish are not able to regulate their internal temperature physiologically, they do compensate behaviourally for adverse thermal conditions. They can respond to high temperatures by reducing their activity rate, or by moving to areas of cooler water (thermal refugia; Nielsen *et al.* 1994). There has recently been a reasonable amount of research into the use of thermal refugia in behavioural thermoregulation by river salmonids.

Baird and Krueger (2003) implanted temperature sensitive radio transmitters in brook trout and rainbow trout, allowing them to monitor both their internal temperature and position. They found that by positioning themselves in cool tributary confluences and groundwater discharges both trout species were able to maintain body temperatures below that of the river water. When the river water averaged 20 °C, or above, rainbow trout internal temperatures were 2.3 °C cooler, and brook trout were 4 °C cooler.

Ebersole *et al.* (2001) showed that mean rainbow trout abundance was negatively correlated with mean ambient stream temperature during summer in Oregon. Furthermore, many trout would move into areas of cooler water created by seeps, cool tributaries and stratification of pools when ambient temperatures rose to between 18 °C and 25 °C. The temperature in the refugia was 3-8 °C cooler than the ambient temperature in the rivers. During the warmest periods, when ambient temperatures were >22 °C, between 10 % and 40 % of trout would be aggregated in these refugia. The prevalence of use of thermal refuges was higher in warmer streams.

During low summer flows in three Californian rivers, 65 % of juvenile steelhead (*Oncorhynchus mykiss*) and many summer-run adults moved into thermally stratified pools (Nielsen *et al.* 1994). While the ambient river water temperature was 23-29 °C, cold water from tributaries and seeps kept the bottom of these pools 3 – 9 °C cooler.

These findings give an indication of the importance of water temperature to trout living in variable freshwater habitats.

2.3 Scale of movement

Movements of salmonids in response to low flow occur over a range of scales, from small scale movements between riffles and pool habitat, to larger scale movements

within rivers, and between rivers and tributaries, lakes and the sea. The current understanding of fish movement in response to low flow is mainly restricted to small scale movements over short time frames (Magoulick and Kobza 2003), which may, in part, be attributable to the methods available for studying fish movements historically (Gowan *et al.* 1995). Mark, recapture studies and those using fish traps to intercept migrating fish have limited ability to track long range movements. However, increasing use of radiotelemetry in recent times has begun to address questions of fish mobility at larger scales (Gowan *et al.* 1995). These studies have shown long range movement especially among salmonids to be more common than was traditionally believed (Young *et al.* 1997).

2.3.1 *Small scale movements to pool habitat*

As water levels fall and temperatures rise salmonids generally leave riffle and run habitats in favour of deeper water in pools (Baigun *et al.* 2000; Heggenes 2002). At a very small scale juvenile salmonids have been shown to leave their hiding places and move to deeper parts of the channel, as water levels slowly recede (Bradford *et al.* 1995).

The lower water temperature maintained in deeper pools offers a thermal refuge for trout during extreme low flow events. In a southern Californian stream where summer water temperatures typically exceed lethal limits for trout, Matthews and Berg (1997) found that trout were able to survive in pools despite the water temperatures at the surface being as high as 28 °C. The temperature in the bottom of the pools where the trout survived remained between 17.5 °C and 21 °C, although dissolved oxygen concentrations were low relative to those at the surface. Elliott (2000) also found that brown trout used pools as refugia during two drought years in Wilfin Beck, in England's Lake District. They exhibited a preference for pools with lower temperatures and higher dissolved oxygen concentrations, although temperature also appeared to have been a more important consideration than dissolved oxygen concentration in this case. Very low dissolved oxygen concentrations can impact negatively on salmonid health and even survival (Hayes and Young 2001). However, a trade off must often be made between these two variables, since cooler water in the bottom of stratified pools is likely to have low dissolved oxygen content. In both of the cases cited here temperature appears to have priority in this trade off.

Experimental flow reductions also showed that trout tend to move toward deep water habitat during low flow. When flow was experimentally reduced by 90 % for 3 months, in Blacktail Creek (Montana), to simulate summer irrigation draw-down, trout moved from runs to pools (Kraft 1972). This produced approximately a 62 % reduction in the number of brook trout older than one year in three study runs, compared with only a 20 % decrease in the control runs. Over 100 fish also tried to leave the experimental area, with emigration peaking 10 days after the flow reduction was completed. In a similar flow reduction experiment, in the regulated Shoshone River in Wyoming, flow was systematically reduced in four stages over a three month period (Dare *et al.* 2002). Both brown trout and cutthroat trout (*Oncorhynchus clarki clarki*) also showed a tendency to favour deeper water, with the majority being found in deep pools with abundant cover. Furthermore, during two experimental flow reductions in an artificial stream 80 % and 95 % of juvenile Atlantic salmon (*Salmo salar*), with feeding stations in riffles, moved into pools (Huntingford *et al.* 1999).

However, another recent experimental study, in enclosed sections of a stream, produced a somewhat equivocal response to reduced flow from Atlantic salmon parr (Armstrong and Braithwaite 1998). Although approximately half of the fish in the experimental reaches moved from riffles to pools as flow was reduced to near zero, up to half of these fish subsequently moved back into the almost dewatered riffle habitat as the drought continued. The authors suggested that remaining in riffles may be an adaptive response for fish from populations that are usually only exposed to very short term low flow events. By not vacating riffle habitat these fish might be able to maintain their territories in riffles through the drought period, while also avoiding adverse levels of competition and possibly predation risks in pool habitat.

2.3.2 *Larger scale movements*

Literature on larger scale movement of salmonids in response to reduced flow is sparse, relative to the literature focused on movement over shorter distances. As alluded to earlier, this may in part be due to technical limitations on tracking fish movements over longer distances, a problem that has recently been remedied, to some extent, by the use of radiotelemetry (Gowan *et al.* 1995).

An early application of radiotelemetry to trout movements tracked eight large brown trout for up to 346 days in the Au Sable River, Michigan (Clapp *et al.* 1990). They found that the majority of these fish moved upstream about 10 km to over-wintering habitat. However, the area used during winter was considered marginal as summer habitat, due to high water temperatures. This implies that these fish would have to migrate back downstream as water temperatures increased in summer. The upstream movement rates during autumn, of the trout in this study, appeared to be highest during periods of high flow, rather than being stimulated by low flows.

Swanberg (1997) also used radiotelemetry to track the movements of bull trout (*Salvelinus confluentus*) in Blackfoot River, Montana. He found that an upstream migration of between 42 km and 84 km was cued by a decline in discharge from the spring peak, accompanied by an increase in water temperature to ~17.7 °C. Larger fish were found to migrate earlier and at lower temperatures than smaller fish. Once again refuge from high summer temperature appears to be the main driver behind this movement. Summer water temperatures in the main stem of Blackfoot River were up to 20 °C, while the temperatures in the tributaries to which fish migrated were always ~5 °C cooler. The importance of temperature is also supported by two fish that held station near a spring with temperatures around 8 °C, and two other fish that remained near the confluence of a tributary where temperatures were around 12 °C. Upstream migration also stalled for several days in response to cooling water temperatures. Non-spawning migratory fish (67 % of all upstream migrating fish) returned downstream in August as temperatures fell to 12 °C. It is interesting to note that not all fish migrated in either of the two years of the study and that more seemed to migrate in the second summer, when summer flows were not as low as in the previous summer. The fish not taking part in the upstream migration appeared to be mainly immature fish, while the three largest non-migratory trout moved downstream, rather than migrating upstream with the majority. Swanberg noted that these results suggest that the cooler tributary habitat is important during summer, to potential spawning fish and non-spawning fish alike.

In two New Zealand radio-tracking studies large scale movements of brown trout were associated with elevated water temperatures. Upstream movements of up to 202 km were initiated by water temperatures in the lower Waikato River rising to 19 °C (Wilson and Boubée 1996). In this case the elevated temperatures were exacerbated by the discharge of powerstation cooling water into the river. A peak in downstream movement of brown trout in the Wairau River coincided with high summer water temperatures (up to 21.5 °C) and the worst drought conditions on record, at that time (Strickland *et al.* 1999). However, as the authors point out, the water temperatures in the river would have been increasing in a downstream direction, making it seem unlikely that this movement was driven by a search for thermal refugia.

There is some evidence that these large scale movements are generally more likely to occur at night. In a review of the effect of light, flow and water temperature on migration Jonsson (1991) cites numerous authors who have found that both upstream and downstream migrations of a variety of fish species show a nocturnal bias. She suggested predator avoidance as the likely reason for this. A nocturnal bias in migratory activity is supported by the findings of Swanberg (1997) and Ovidio *et al.* (1998) both of which showed that the majority of upstream migration occurred at night. Clapp *et al.* (1990) also found that brown trout were more active at night. However, this bias appears to be quite case dependent. Erman and Leidy (1975) found that downstream migration of rainbow trout fry peaked at between 9 am and 12 noon, while Jonsson (1991) also cites many cases when migratory activity is concentrated during daylight hours.

The migratory response of trout to elevated temperatures does not appear to be entirely consistent either. Young (1998) cited low year-round temperatures (<10 °C) as an explanation of the lack of movement between seasons in cutthroat trout in a Wyoming stream. In contrast, Burrell *et al.* (2000) observed that brown trout in Chattooga River, Carolina, did not seek refuge in cooler tributaries despite water temperatures exceeding 19 °C for 64 days over summer.

2.4 Direction of migration

By far the most common direction of migration in response to low flows or increased temperature is upstream. This appears to be equally true of both small scale and larger scale fish movements in response to low flows.

In the study by Huntingford *et al.* (1999), cited above, the vast majority (74 % in the first instance and 89 % in the second instance) of juvenile Atlantic salmon moving out of shallow riffle habitat during experimental flow reductions moved upstream (although 20 % of fish did not move at all in response to the flow reduction).

In Kraft's (1972) study, where flow was reduced by 90 %, movement out of the reach was monitored using fish traps. While more than 100 trout entered the upstream trap, no fish entered the downstream trap.

Upstream movement of up to 2 km was also found to be common during summer for brook trout in two Colorado streams (Gowan and Fausch 1996). This upstream migration was most pronounced as discharge approached summer baseflow, and was also more common during a dry year. They found that it was mainly the long thin fish that moved

and suggested that larger fish needed to seek out better foraging sites as foraging quality declined during summer low flows.

As outlined above, Swanberg (1997) also found the majority of migrating trout moved upstream to cooler tributaries during summer.

Kahler *et al.* (2001) report that upstream movement predominated among the juveniles of three species of salmonids in three Washington streams during summer, except where a steep pool-cascade channel form impeded upstream movement. They suggested that a rapid loss of habitat as flow declined resulted in an increase in fish mobility.

Upstream migrations of 7 to 20 km were reported by Meyers *et al.* (1992), who tracked 22 radio tagged brown trout during spring in Beaver Creek, Wisconsin. These movements were more strongly related to increased water temperature than to water level. The tagged trout were observed to move up to second order streams in the spring, then return downstream to fourth order streams in the autumn.

Using mark-recapture methods and fish weirs to monitor fish movements, Riley *et al.* (1992) found that the majority of mobile brook trout moved upstream during summer. They also noted that upstream migrants were significantly larger than those fish moving downstream. Bridcut and Giller (1993) also found predominantly upstream movement of brown trout, mainly in the early summer, using mark and recapture techniques. Unfortunately, neither of these papers gives any indication of the discharge or water temperature associated with these movements.

However, not all studies have found an upstream bias in migration triggered by increased temperature and/or low flow. For example, the movement of rainbow and brown trout, which Young *et al.* (1997) attributed to increased water temperature and summer habitat selection, did not exhibit a strong directional trend. Also, as mentioned previously, high summer temperatures and drought conditions coincided with a peak in downstream movement of brown trout in the Wairau River, despite temperature increasing downstream (Strickland *et al.* 1999).

In other cases salmonids may migrate toward refugia other than cooler tributaries or deep pools. Northcote (1992) makes reference to young brown trout migrating to the sea to avoid low summer flows in small coastal Norwegian streams. Similarly, Montgomery *et al.* (*In: Lucas and Baras 2001*) showed that six fish species, including salmonids, emigrated from the Rivière à la Truite (Quebec), simultaneously, as water levels declined. Finally, Canton *et al.* (1984) concluded that the direction of recovery of the trout population following dewatering of sections of Trout Creek, Colorado, suggested that an upstream lake acted as a refuge for trout during the preceding drought year.

2.5 Distance of migration

Gowan *et al.* (1995) suggest that seasonal movements of salmonids between freshwater habitats may be greater than 100 km. However, distances reported in the literature are commonly in the order of hundreds of metres to tens of kilometres. Two examples are; 1) upstream migrations of 5.6 to 22.95 km of brown trout, triggered by high variations in discharge and temperature in the River Ourthe, Belgium (Ovidio *et al.* 1998), 2) upstream migration of between 42 km and 84 km, cued by a decline in discharge from

the spring peak, accompanied by an increase in water temperature to ~ 17.7 °C in Montana (Swanberg 1997).

In contrast Dare *et al.* (2002) found that brown trout did not move more than 500 m during their experimental flow reduction. However, this experimental reduction of flows took place during winter. Hence, low-flow-induced increases in water temperature would not have been an issue for these fish. Gido *et al.* (2000) also reported little movement of fish during winter low flows.

There also appears to be some difference in distances moved between species and between size classes within species. For instance, rainbow trout had larger home ranges and moved greater distances than brown trout during summer (1109 m c.f. 208 m medians; Young *et al.* 1997), and larger trout tended to move further seasonally than smaller trout (Young 1999).

3. SUMMARY

Salmonids frequently appear to move in order to avoid adverse environmental conditions, or to optimise foraging opportunities during low flow events. Taken together the evidence suggests that temperature is likely to be the most important driver of these movements. There is a tendency for fish to migrate from adversely hot areas into deeper habitats providing cooler water temperatures. The general trend is for small scale movements to deeper water and for large scale movements to be in an upstream direction toward cooler tributaries. These movements take place over a range of scales, depending on the scale and magnitude of the low flow event and on the opportunity of the fish to move. There is a substantially larger body of evidence for such movements taking place at smaller scales (i.e. from runs to pools), than there is for larger scale migrations prompted by low flows. This highlights a need for more research into long term, long range movements of salmonids in response to low flows.

4. REFERENCES

- Armstrong, J. D., and Braithwaite, V. A. 1998. The response of wild Atlantic salmon parr to acute reductions in water flow. *Journal of Animal Ecology* 67: 292-297.
- Baigun, C. R., J. Sedell, and G. Reeves. 2000. Influence of water temperature in use of deep pools by summer steelhead in Steamboat Creek, Oregon (USA). *Journal of Freshwater Ecology* 15: 269-279.
- Baird, O. E., and Krueger, C. C. 2003. Behavioural thermoregulation of brook and rainbow trout: Comparison of summer habitat use in an Adirondack river, New York. *Transactions of the American Fisheries Society* 132: 1194-1206.
- Bradford, M. J., Taylor, G. C., Allan, J. A., and Higgins, P. S. 1995. An experimental study of the stranding of juvenile coho salmon and rainbow trout during rapid flow decreases under winter conditions. *North American Journal of Fisheries Management* 15: 473-479.
- Bridcut, E. G. and Giller, P. S. 1993. Movement and site fidelity in young brown trout populations in a southern Irish stream. *Journal of Fish Biology* 43: 811-960.

- Burrell, K. H., Isely, J. J., Bunnell, D. B., VanLear, D. H., and Dolloff, C. A. 2000. Seasonal movement of brown trout in a southern Appalachian river. *Transactions of the American Fisheries Society* 129: 1373-1379.
- Canton, S. P., Cline, L. D., Short, R. A., and Ward, J. V. 1984. The macroinvertebrates and fish of a Colorado stream during a period of fluctuating discharge. *Freshwater Biology* 14: 311-316.
- Clapp, D. F., Clark, R. D., and Diana, J. S. 1990. Range, activity and habitat of large, free-ranging brown trout in a Michigan stream. *Transactions of the American Fisheries Society* 119: 1022-1034.
- Dare, M. R., Hubert, W. A., and Gerow, K. G. 2002. Changes in habitat availability and habitat use and movements by two trout species in response to declining discharge in a regulated river during winter. *North American Journal of Fisheries Management* 22: 917-928.
- Ebersole, J. L., Liss, W. J., and Frissell, C. A. 2001. Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. *Ecology of Freshwater Fish* 10: 1-10.
- Elliott, J. M. 2000. Pools as refugia for brown trout during two summer droughts: trout responses to thermal and oxygen stress. *Journal of Fish Biology* 56: 938-948.
- Erman, D. C. and Leidy, G. R. 1975. Downstream movement of rainbow trout fry in a tributary of Sagehen Creek, under permanent and intermittent flow. *Transactions of the American Fisheries Society* 104: 467-473.
- Garrett, J. W. and Bennett, D. H. 1995. Seasonal movements of adult brown trout relative to temperature in a coolwater reservoir. *North American Journal of Fisheries Management* 15: 480-487.
- Gido, K. B., Larson, R. D., and Ahlm, L. A. 2000. Stream-channel position of adult rainbow trout downstream of Navajo Reservoir, New Mexico, following changes in reservoir release. *North American Journal of Fisheries Management* 20: 250-258.
- Gowan, C. and Fausch, K. D. 1996. Mobile brook trout in two high-elevation Colorado streams: Re- evaluating the concept of restricted movement. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1370-1381.
- Gowan, C., Young, M. K., Fausch, K. D., and Riley, S. C. 1995. Restricted movement in resident stream salmonids: a paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences* 51: 2626-2637.
- Hayes, J. W. and Young, R. G. 2001. Effects of low flow on trout and salmon in relation to the regional water plan : Otago. *Cawthron Report No. 615*. 27p.
- Heggenes, J. 2002. Flexible summer habitat selection by wild, allopatric brown trout in lotic environments. *Transactions of the American Fisheries Society* 131: 287-298.

- Hembre, B., Arnekleiv, J. V., and LAbeeLund, J. H. 2001. Effects of water discharge and temperature on the seaward migration of anadromous brown trout, *Salmo trutta*, smolts. *Ecology of Freshwater Fish* 10: 61-64.
- Huntingford, F. A., Aird, D., Joiner, P., Thorpe, K. E., Braithwaite, V. A., and Armstrong, J. D. 1999. How juvenile Atlantic salmon, *Salmo salar* L., respond to falling water levels: experiments in an artificial stream. *Fisheries Management Ecology* 6: 357-364.
- Jonsson, N. 1991. Influence of water flow, water temperature, and light on fish migration in rivers. *Nordic Journal of Freshwater Research* 66: 20-35.
- Jowett, I. 1997. Environmental effects of extreme flows. Pages 103-116 in M. P. Mosley and C. P. Pearson, editors. *Floods and Droughts: the New Zealand experience*. New Zealand Hydrological Society, Wellington North, New Zealand.
- Kahler, T. H., Roni, P., and Quinn, T. P. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1947-1956.
- Kraft, M. E. 1972. Effects of controlled flow reduction on a trout stream. *Journal of the Fisheries Research Board of Canada* 29: 1405-1411.
- Larimore, R. W., Childers, W. F., and Heckrotte, C. 1959. Destruction and re-establishment of stream fish and invertebrates affected by drought. *Transactions of the American Fisheries Society* 88: 261-285.
- Lucas, M. C. and Baras, E. 2001. *Migration of Freshwater Fishes*. Blackwell Science. Oxford.
- Magoulick, D. D. and Kobza, R. M. 2003. The role of refugia for fishes during drought: a review and synthesis. *Freshwater Biology* 48: 1186-1198.
- Matthews, K. R. and Berg, N. H. 1997. Rainbow trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. *Journal of Fish Biology* 50: 50-67.
- Matthews, K. R., Berg, N. H., Azuma, D. L., and Lambert, T. R. 1994. Cool water formation and trout habitat use in a deep pool in the Sierra Nevada, California. *Transaction of the American Fisheries Society* 123: 549-564.
- Matthews, W. J. and Marsh-Matthews, E. 2003. Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater Biology* 48: 1232-1253.
- Meyers, L. S., Thuemler, T. F., and Kornely, G. W. 1992. Seasonal movement of brown trout in northeast Wisconsin. *North American Journal of Fisheries Management* 12: 433-441.
- Nielsen, J. L., Lisle, T. E., and Ozark, V. 1994. Thermally stratified pools and their use by steelhead trout in Northern Californian streams. *Transactions of the American Fisheries Society* 123: 613-626.
- Northcote, T. G. 1992. Life as a trout wanderer. *Trout* 33: 60-67.

- Northcote, T. G. 1997. Potamodromy in Salmonidae – Living and moving in the fast lane. *North American Journal of Fisheries Management* 17: 1029-1045.
- Ovidio, M., Baras, E., Goffaux, D., Birtles, C., and Philippart, J. C. 1998. Environmental unpredictability rules the autumn migration of brown trout (*Salmo trutta* L.) in the Belgian Ardennes. *Hydrobiologia* 371/372: 263-274.
- Riley, S. C., Fausch, K. D., and Gowan, C. 1992. Movement of brook trout (*Salvelinus fontinalis*) in four small subalpine streams in northern Colorado. *Ecology of Freshwater Fish* 1: 112-122.
- Steingrímsson, S. O. and Grant, J. W. A. 2003. Patterns and correlates of movement and site fidelity in individually tagged young-of-the-year Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 60: 193-202.
- Strickland, R. R., Hayes, J. W., and Barter, P. 1999. Wairau River brown trout radio tracking study. *Cawthron Report No.505*. 39p.
- Swanberg, T. R. 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. *Transactions of the American Fisheries Society* 126: 735-746.
- Torgersen, C. E., Price, D. M., Li, H. W., and McIntosh, B. A. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. *Ecological Applications* 9: 301-319.
- Wilson, B. J. and Boubée, J. A. T. 1996. The seasonal movements of large brown trout in the lower Waikato River system. In: Proceedings. Lake Fisheries Workshop. Frankton, Queenstown, 1-3 April 1996. New Zealand Fish and Game Council. pp 85-101
- Young, M. K. 1998. Absence of autumnal changes in habitat use and location of adult Colorado River cutthroat trout in a small stream. *Transactions of the American Fisheries Society* 127: 147-151.
- Young, M. K. 1999. Summer diel activity and movement of adult brown trout in high-elevation streams in Wyoming, USA. *Journal of Fish Biology* 54: 181-189.
- Young, M. K., Wilkison, R. A., Phelps, J. M., and Griffith, J. S. 1997. Contrasting movement and activity of large brown trout and rainbow trout in Silver Creek, Idaho. *Great Basin Naturalist* 57: 238-244.