

# Darkness represses the onset of downstream migration in hatchery-released chum salmon, *Oncorhynchus keta*, fry

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**Abstract**—Downstream migration and plasma thyroxine ( $T_4$ ) levels in hatchery reared chum salmon, *Oncorhynchus keta*, fry were investigated late in the migration season. Groups of 1.7–6.7 million fry were discharged by opening gates of the raceways at 09:30 h for a daytime release and at 18:30 h for a nighttime release experiments. A peak in the number of migrating fry and  $T_4$  surge were detected simultaneously, 1–1.5 h after the release in the daytime release. In nighttime release, the peak of  $T_4$  surge occurred 3 h after the release, and the number of the migrating fry peaked 8 h and 11 h after the release. In dark treatment, although the control group showed peaks within 2 h of the gate opening, the downstream migration of the dark-treated fish was repressed in daytime and small number of migrating fish was observed 3 h and 10 h after the gate opening. These results suggest that darkness represses the onset of downstream migration in chum fry late in the migration season, and the  $T_4$  surge is not related to the onset of downstream migration during the night.

**Key words:** chum salmon, *Oncorhynchus keta*, downstream migration, illumination, thyroxine,  $T_4$  surge

## Introduction

Many salmonids, fish of the genera *Oncorhynchus*, *Salmo*, and *Salvelinus*, are anadromous and the juveniles migrate down to the ocean (downstream migration) after smoltification that involves morphological, physiological, and behavioral changes. Numerous studies have been conducted on the hormonal control during the smoltification process in salmonids (Hoar 1988, Boeuf 1993). Many authors have reported increasing plasma thyroxine ( $T_4$ ) levels during smoltification in fresh water (Dickhoff et al. 1982, Yamauchi et al. 1984, Boeuf et al. 1989). In the migratory season, surges of plasma  $T_4$  levels were also observed due to changes in environmental stimuli such as lunar phase and changes in freshwater quality (Grau et al. 1981, Nishioka et al. 1985, Hoffnagle and Fivizzani 1990, Specker et al. 2000, Iwata et al. 2003). Plasma  $T_4$  levels are higher in migrating fish than that of non-migrating fish (Youngson and Simpson 1984, Fujioka et al. 1990, Høgåsen and Prunet 1997, Iwata et al. 2003). These comprehensive findings suggest that salmon juveniles may require a surge of plasma  $T_4$  in the migratory season to trigger and maintain downstream migration and other behavioral changes related to migration. In a previous study, a turbid-water stimulus triggered migratory behaviors and  $T_4$  surges simultaneously. An exogenous  $T_4$  treated chum fry

showed increased plasma  $T_4$  levels; however, no effect on downstream behavior was induced. These results suggest that thyroid hormones are not the sole factor responsible for initiating migration (Ojima and Iwata 2007 in press).

The timing of downstream migration varies in different species; pink salmon *Oncorhynchus gorbuscha* and chum salmon *O. keta* are able to enter seawater soon after their emergence from river beds as fry, and hatchery-reared chum salmon fry remain in the river for only a few days after stocking (Iwata and Komatsu 1984). Sockeye salmon *O. nerka* acquire a silvery body colour late in their first spring and swim down to nursery lakes. By contrast, masu salmon *O. masou*, coho salmon *O. kisutch*, Atlantic salmon *Salmo salar*, and other species spend one or more years in freshwater, then some migrate down to the sea while others remain as river residents.

There have been many studies on the environmental factors relating to the downstream migration in salmonids. Three main environmental factors seem to dominate: diurnal light periodicity, water temperature, and water flow in onset of downstream migration (Greenstreet 1992, Hvidsten et al. 1995, Arahamiam and Jones 1997). Salmonids generally exhibit a downstream migration during the night (Aarestrup et al. 2002, Riley et al. 2002, Carlsen et al. 2004). However, Moore et al. (1995) observed a change to this pattern of nocturnal downstream migration, with late season smolts migrat-

ing during both the day and night. While hatchery reared chum salmon fry released during the daytime at the end of the migratory season migrated down river immediately (Iwata et al. 2003).

Most behavioral activities of juvenile salmon are considered to depend on a visual reaction (review by Blaxter 1970). Ali (1959) reported that salmonids begin to recognize others by vision at light intensities greater than  $10^{-3}$  lux, and expansion of cones in the retina begins at about 1 lux in smolts of coho salmon. Nearest neighbor distance (NND) in coho salmon begin to decrease at light intensities of more than 4 lux (Azuma and Iwata 1994). These results demonstrate that salmonids cannot form a school under low illumination, and suggest that the mechanism of school formation may be controlled by a different mechanism at night.

We designed two experiments in order to examine our hypothesis that downstream migration is regulated by different mechanisms during the day and night. In the first experiment, we monitored the downstream behavior and plasma  $T_4$  levels in chum salmon fry after daytime and nighttime releases. In the second experiment, we observed downstream behavior under dark treatment in daytime by covering the experimental tanks to examine the inhibitory effect of darkness on the onset of downstream migration.

## Materials and methods

### Experiment 1

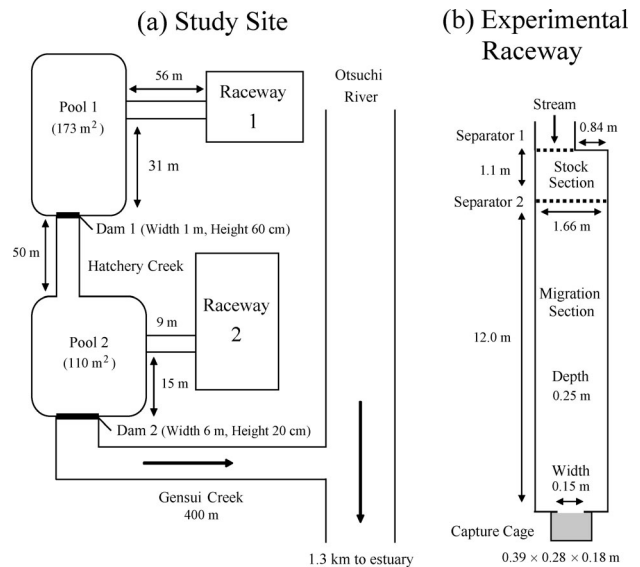
#### Fish and Study sites

Chum salmon *Oncorhynchus keta* fry were reared in the Otsuchi Salmon Hatchery, Iwate Prefecture, Japan. The fry were maintained under a natural photoperiod in the hatchery raceways and supplied with water from wells and springs in the 3-ha hatchery site. The water temperature is stable in a range of 11–12°C. The fry were fed a commercial diet after yolk absorption.

The study site comprised raceways, pools, and creeks in the Otsuchi Salmon Hatchery (Fig. 1a). The hatchery is located at the upper end of the 400-m-long Gensui Creek, a tributary of the Otsuchi River. All the hatchery water flows into the study creek, and springs are present in the sandy bottoms of the pool and the creek.

#### Releases

Groups of 1.7–6.7 million chum fry were used for the daytime or nighttime release experiments by opening the raceway gates at 18:30 h on 30 March 2004 (BW:  $1.7 \pm 0.05$  g, Raceway 2), at 18:30 h on 7 April 2004 (BW:  $1.5 \pm 0.06$  g, Raceway 1), and at 09:30 h on 30 April 2004 (BW:  $1.4 \pm 0.08$  g, Raceway 2). The fry were flushed out from the raceways and subsequently discharged into the each hatchery pool through a drain channel (Fig. 1a). The water levels of



**Fig. 1.** Figures show the study site and experimental raceway at the Otsuchi Salmon Hatchery. In the left panel (Fig. 1a), a group of 1.7–6.7 million chum salmon fry were released from Raceway 1 or Raceway 2 into the 56-m-long or 9-m-long drain channels, respectively. The fry were discharged the drains to the pools and then they began to form schools in the pools. The schools then moved over concrete Dam 1 from the Pool 1 or Dam 2 from the Pool 2 to the Gensui creek. Fish staying in the pool and moving over the dams were sampled, and the numbers of fish migrating were counted at the dams.

Right panel (Fig. 1b) shows the experimental raceway for the dark treatments. Experiment was started at 10:00 h by opening the separator 2 of the stock section, and migrating fish caught in the capture cage were counted every 20 min for 24 h. The water currents in the raceway were less than 3 cm/sec.

the pools were maintained by 60 cm (Dam 1) and 20 cm (Dam 2) high concrete dams. The fry schools moved sequentially from the pools to the Gensui Creek, Otsuchi River, and eventually to Otsuchi Bay. The distance from the hatchery to the estuary is approximately 1700 m. No fish remained in the pools on the day following release. Data on precipitation on release days in Otsuchi were obtained from the database of the Japan Meteorological Agency. The precipitation of 14 mm was observed only on 7 April. Sunrise and sunset time were 05:30 h and 17:22 h on 30 March, 05:08 h and 18:02 h on 7 April, 04:35 h and 18:25 h on 30 April, respectively. Night releases were conducted after dusk when the sky became dark. The experiments were not conducted on days of a new moon (Grau et al., 1981).

#### Number of migrants

All fry formed loose schools in the pools within minutes of release. Then the fry schools swam down the dam into the creek. The movement over Dam 1 or Dam 2 was defined as the onset of downstream migration, and the migrating fry schools were counted by the naked-eye at intervals of 20 min in the daytime, and were caught using scoop nets at the same

interval during the night.

### Blood sampling

Samples were taken from groups of 40–50 chum fry, netted from the hatchery raceways before each release, and then from the pool every 30 min or 1 h following release. The fry were transferred into a 15 L bucket containing 0.04% 2-phenoxy-ethanol. The caudal peduncle was amputated, and blood samples collected in a heparinized capillary tube. The samples were then centrifuged at 12000 *g* for 10 min. Twenty micro liters of plasma was transferred to a micro test tube and stored at  $-35^{\circ}\text{C}$  until thyroxine ( $T_4$ ) analysis.  $T_4$  was assayed by non-isotopic time-resolved fluoroimmunoassay (TR-FIA) by the method of Satoh et al. (2000).

### Experiment 2

#### Fish and Experimental tanks

The fish used in Experiment 2 were from the same strain of chum salmon fry as used in the Experiment 1. However, size of the fry was larger than that of fry in Experiment 1 (BW:  $2.6 \pm 0.10$  g), because we expected the most fish of control group fish migrate soon after the opening separator. In the present experiment and our previous study (Ojima and Iwata 2007 in press), the larger fish in late migration season are more active to migrate than small fry in early season. Downstream behaviour was observed in raceways (Fig. 1b). The raceways were divided into two sections comprising the upper fish stock section and a 12 m long migration section. A capture cage was installed at the end of each raceway to trap the migrating fry. Approximately 400 fry were placed in each stock section of the raceway 48 h prior to the start of the experiments.

#### Migration experiments

The fry were released from the stock sections by opening the separators at 10:00 h on 26 April, 29 April, and 2 May 2005. The fish trapped by the capture cage were counted every 20 min for 24 h following release. Precipitation was not observed during the experimental period. Sunrise and sunset time of the experimental periods were 04:34–04:40 h and 18:21 h–18:27 h, respectively. The experiments were not conducted on the day of a new moon.

#### Dark treatment

In order to examine the effects of darkness on the onset of downstream migration, groups of chum fry were treated with darkness by covering the experimental raceway with wooden boards and thick black sheet, except at the stock section. A control experiment was conducted in same manner but without the cover. The experiment was started by removing the raceway separator at 10:00 h on 26 April, 29 April, and 2 May 2005. Immediately after release the stock section was also covered with boards and black sheeting. Light inten-

sity was monitored on the bottom of the raceway using an illumination meter (IM-5, TOPCON, Tokyo) with reading taken every 20 min throughout the experiments.

### Statistics

The Kolmogorov-Smirnov test was applied to remove extremely high or low values in the number of migrating fish and concentrations of plasma  $T_4$  from each distribution. In Experiment 1, the means in plasma  $T_4$  levels were analyzed by ANOVA followed by Tukey's HSD test. In Experiment 2, any differences in rates of migration from the control were analyzed using a Chi-Square test.

## Results

### Experiment 1

#### Number of migrants and plasma $T_4$ levels after release

In the daytime release on 30 April, the number of fry migrating showed a peak 1 h after the gate opening, decreasing rapidly to less than one tenth of the peak level after 3 h (Fig. 2). The proportion of fish that migrated in the daytime release was greater than 95%. Plasma  $T_4$  levels showed a peak 1.5 h (11.1 ng/ml) after the release, and then decreased to the basal levels (4.1 ng/ml) after 4 h.

During the nighttime releases, on 30 March and 7 April, the number of fry migrating showed peaks 8 h and 11 h after the gate opening, respectively. With peaks in plasma  $T_4$  levels occurring 3 h (18.2 and 17.5 ng/ml) after both releases.

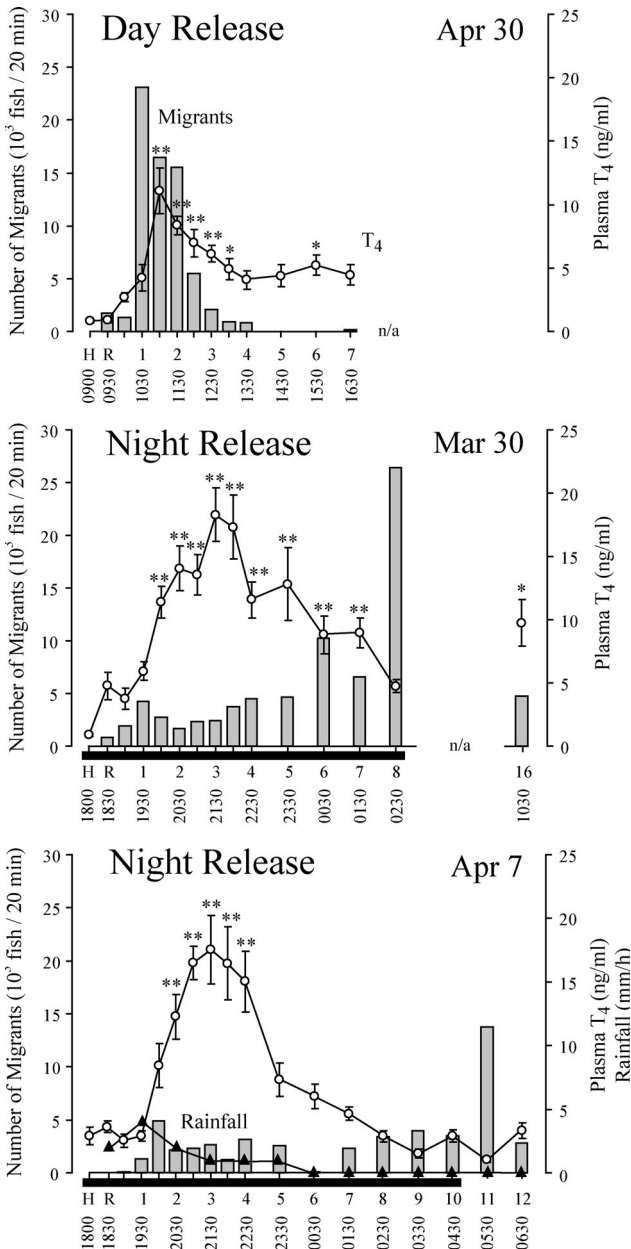
### Experiment 2

#### Downstream migration in dark treatments

The numbers of fry migrating in the dark treatments were significantly lower than those of control groups (Fig. 3). On all occasions, the control groups showed peaks of migration within 2 h of the separator opening. The dark treatments showed peaks of downstream migration 3 h (April 26) and 10 h (April 29 and May 2) after opening the separator (Fig. 4).

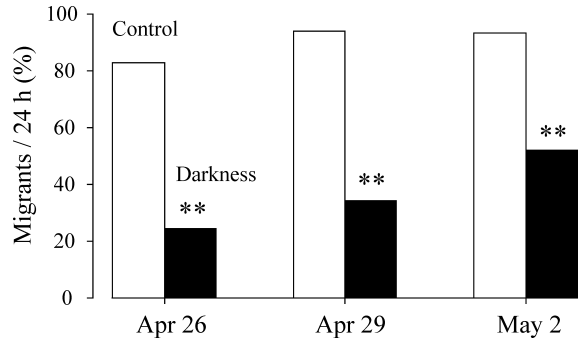
## Discussion

In the daytime releases, chum salmon fry in Experiment 1 and control fish in the dark treatments (Experiment 2) showed a single peak of downstream migration soon after opening of the raceway gates or separators (Fig. 2, 4). These results are consistent with our previous release experiments on chum fry (Iwata et al. 2003, Ojima and Iwata 2007 in press). This rapid onset of the downstream migration may reflect their physiological condition late in their migratory season. The nighttime release on 30 March, however, exhibited a second peak of migration at 02:30 h 8 hours after the release despite the darkness; another release on 7 April showed a

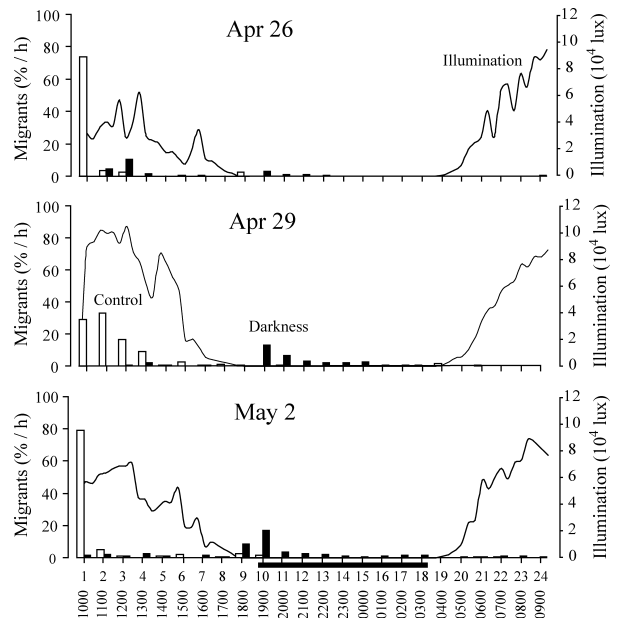


**Fig. 2.** Changes in the number of migrating chum salmon fry (columns) and plasma  $T_4$  concentrations (open circles) after the daytime and nighttime releases. Chum fry were released at 09:30 h (30 April) and 18:30 (30 March and 7 April) from the hatchery raceways to the pools. The fry formed schools in the pools and migrated out from the dams to the creek. Numbers of migrating fry were counted at the dams. Plasma samples were collected from fry in raceway before release, and then sampled from fish in the pools. Plasma  $T_4$  levels are expressed as means $\pm$ SEM ( $n=9-12$ ). Black horizontal bars indicate darkness. Asterisks indicate significant differences from the initial  $T_4$  levels sampled from hatchery raceways before each release (\* $P<0.05$ , \*\* $P<0.01$ ).

peak of migration at 05:30 h 11 hours after the release (Fig. 2). Both showed small peaks a few hours after the releases as same as the daytime release experiment. Similarly in the dark treatments, although the numbers of fry were lower than control groups, the migrations were observed 10 hours after the



**Fig. 3.** Total number of migrating chum salmon fry in the dark treatment experiment. Raceway was covered by wood boards and thick black sheet, whereas control raceway was not covered. Approximately 400 fry were placed at each stock section in the raceways. The fry were released from the stock sections by opening separator at 10:00 h. The fish moved into a capture cage and were counted every 20 min for 24 h. Asterisks indicate significant differences from control group (\* $P<0.05$ , \*\* $P<0.01$ ).



**Fig. 4.** Diurnal changes in the number of migrating chum salmon fry in the dark treatment experiment and the illumination intensities at the raceway surfaces. White and black columns indicate control and darkness groups respectively. Light intensity was monitored at floor of next tank (lines). Black horizontal bars indicate darkness.

releases on both 29 April and 2 May experiments. In wild populations, chum salmon and other salmonids generally migrate downstream after dark (Hoar 1951, Neave 1955, Aarestrup et al. 2002, Riley et al. 2002, Carlsen et al. 2004). However, Moore et al. (1995) observed a change to this pattern of nocturnal downstream migration, with late season smolts migrating during both the day and night. Chum fry is an obligatory ocean migrant the same as pink salmon *O. gorbuscha*; and begin the downstream migration following the yolk absorption. They may feed during the daytime and mi-

grate downstream at night in early migratory season (Kobayashi 1958). However, fry in the modern Japanese salmon propagation program are released several weeks after their natural migration period. At this stage of development the released fry were observed to migrate during the daytime (Iwata et al. 2003, Ojima and Iwata 2007 in press). The rapid onset of downstream migration in the daytime releases of the present study agrees with the previous studies. The nighttime releases with same group of chum fry delay the onset of migration more than several hours comparing with the daytime release without connection to the light conditions. Furthermore, the dark treatment in daytime depressed the onset migration in late migration season.

Chum salmon fry acquire the seawater adaptability as alevins weighing about 0.4 g and migrate downstream to the sea shortly after the emergence from the gravel beds and the complete absorption of their yolk. Seawater adaptability and preference in chum fry decrease during prolonged rearing in fresh water (Iwata et al. 1982, Iwata et al. 1986). Timing in the onset of downstream migration may alter from early stage to the late stage of migratory season according to the changes in their physiological condition.

Activities of juvenile salmon are considered to depend on a visual reaction (review by Blaxter, 1970). Ali (1959) reported that salmonids could recognize other individuals using vision at  $10^{-3}$  lux or higher illumination intensities, because a gradual expansion of cones in the retina begins at about 1 lux in smolts of coho salmon. Nearest neighbor distance (NND) in coho salmon smolts began to decrease in a condition that illumination increase more than 4 lux. The tight school formation that was maintained during the day was lost at night (Azuma and Iwata, 1994). These results suggest that salmonid juveniles may not be able to form schools under dark conditions. The daytime illumination may be required for the tight school formation of chum fry migrants. In this experiment, the exact illumination below  $10^{-2}$  lux was not determined. However, the night releases were conducted under darkness, following dusk, 30 min after sunset. There is a possibility that the light intensities for the night-released fry were not sufficient for school formation in the pond. In a previous study observing migrating chum schools in the Otsubuchi River, the fry formed a school of 50–100 individuals in a pond during a daytime release, the school then swam actively head downstream, in water velocities less than 30 cm/sec, and entered the estuary within a day (Iwata 1982, Iwata et al. 2003). These results show that the tight school formation characterizes the downstream migration of chum fry during the day late in the migration season. The school formation may be an indispensable factor for the downstream migration of chum salmon fry in late migration season, although the fry migrate downstream at night in early migratory season (Kobayashi 1958). The results of this study suggest that nighttime release in late migration season may re-

press school formation in the pond possibly because of the low light intensities.

In early season of migration, chum salmon fry migrate downstream to the sea soon after emergence and display tight schooling behavior as described by Hoar (1954). Although Yamagishi et al. (1981) reported aggressive behaviour for chum fry restrained in a small tank, schooling chum fry displayed the least aggressiveness when compared with other salmonid species (Hutchison and Iwata, 1997). In the present study, however, the school formation of chum fry was always observed in the hatchery tanks, the pool, and the creek without aggressive behaviors. The aggressiveness was not observed to stimulate or restrain the school formation and migration in this experiment.

In the nighttime release, a second peak of migration was observed despite the darkness. This result suggests a possible ability to synchronize downstream migration without the necessity to visually form the schools. Downstream migration in freshwater is believed to be a passive displacement by the current with smolts actively seeking higher velocities (Jonsen, 1991). It has been found in the field investigation that downstream movement of chum salmon fry takes place within 2–3 h after sunset (Hoar 1951, Neave 1955). Keenleyside and Hoar (1954) reported the mechanism of downstream migration of chum fry at night. The fry form schools in the day, after sunset the schools break up and fry move to water surface possibly as a result of impaired sight in the darkness, and are carried downstream by the surface flow. However, in the daytime, tight schools are observed migrating in the middle or deep layers of a stream; a few fry in loose schools can be observed under flashlight at night. Hence the downstream movement in certain dark conditions may be by passive displacement regardless of the school formation, and each individual may react to unknown environmental stimuli such as car light and moonlight.

In this investigation,  $T_4$  surges were observed within a few hours after the release both in the daytime and nighttime releases. This suggest that the  $T_4$  surges in the released chum fry may have been induced by the disturbance of deposited materials and sediment at the bottom of raceways and pools caused by the rapid water flows at gate opening. It has been suggested that salmon juveniles may require a surge of plasma  $T_4$  during the migratory season in order to synchronize downstream migration, maintain schooling, and activate other behaviors related to the migration (Iwata 1995). In our recent study, exogenous  $T_4$  treatments increased the plasma  $T_4$  concentrations of chum fry, however, no effect on downstream migration was detected. By contrast, endogenous  $T_4$  surges that were induced by stimuli of the release and turbid water did not result the expected migratory behaviours. These results suggest that thyroid hormones are not the sole factor that is responsible for initiating migration (Ojima and Iwata 2007 in press). In the present study, although the

downstream migration coincided with the  $T_4$  surge in the daytime release, the nighttime release delayed the migration several hours from the timing of  $T_4$  surges. These results suggest also that endogenous  $T_4$  is not always effective at triggering downstream migration, and suggest that the mechanisms controlling onset of downstream migration are repressed at night by low light intensities.

In conclusion, the present study shows that low illumination at night represses the onset mechanisms in the downstream migration of chum salmon fry at the end of migratory season. The onset mechanisms of downstream migration may also be different between day and night. The  $T_4$  surge is not related with the onset of the downstream migration at night.

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### References

- Aarestrup, K., Nielsen, C. and Koed, A. 2002. Net ground speed of downstream migrating radio-tagged Atlantic salmon (*Salmo salar* L.) and brown trout (*Salmo trutta* L.) smolts in relation to environmental factors. *Hydrobiologia* 483: 95–102.
- Ali, M. A. 1959. The ocular structure, retinomotor and photo-behavioral responses of juvenile Pacific salmon. *Can. J. Zool.* 37: 965–996.
- Aprahamian, M. W. and Jones, G. O. 1997. The seaward movement of Atlantic salmon smolts in the Usk estuary, Wales, as inferred from power station catches. *J. Fish Biol.* 50: 442–444.
- Azuma, T. and Iwata, M., 1994. Influences of illumination intensity on the nearest neighbour distance in coho salmon *Oncorhynchus kisutch*. *J. Fish Biol.* 45, 1113–1118.
- Blaxter, J. H. S. 1970. Light. *Animals. Fishes. In Marine Ecology.* Vol. 1. No. 1. Kinne, O. (Ed.), pp. 213–320, Wiley-Interscience, London.
- Boeuf, G. 1993. Salmonid smolting: a pre-adaptation to the oceanic environment. *In Fish Ecophysiology.* Rankin, J. C. and Jensen, F. B. (Eds.), pp. 105–135, Chapman & Hall, Tokyo.
- Boeuf, G., Le Bail, P. Y. and Prunet, P. 1989. Growth hormone and thyroid hormones during Atlantic salmon *Salmo salar* L., smolting and after transfer to seawater. *Aquaculture* 82: 257–268.
- Carlsen, K. T., Berg, O. K., Finstad, B. and Heggberget, T. G. 2004. Diel periodicity and environmental influence on the smolt migration of Arctic charr, *Salvelinus alpinus*, Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in northern Norway. *Environ. Biol. Fish.* 70: 403–413.
- Dickhoff, W. W., Folmar, L. C., Mighell, J. L. and Mahnken, C. V. W. 1982. Plasma thyroid hormones during smoltification of yearling and underyearling coho salmon and yearling chinook salmon and steelhead trout. *Aquaculture* 28: 39–48.
- Fujioka, Y., Fushiki, S., Tagawa, M., Ogasawara, T. and Hirano, T. 1990. Downstream migratory behavior and plasma thyroxine levels of Biwa salmon *Oncorhynchus rhodurus*. *Nippon Suisan Gakkaishi* 56: 1773–1779.
- Grau, E. G., Dickhoff, W. W., Nishioka, R. S., Bern, H. A. and Folmar, L. C. 1981. Lunar phasing of the thyroxine surge preparatory to seaward migration of salmonid fish. *Science* 211: 607–609.
- Greenstreet, S. P. R. 1992. Migration of hatchery reared juvenile Atlantic salmon, *Salmo salar* L., smolts down a release ladder. 1. Environmental effects on migratory activity. *J. Fish Biol.* 40: 655–666.
- Hoar, W. S. 1951. The behaviour of chum, pink and coho salmon in relation to their seaward migration. *J. Fish. Res. Bd. Can.* 8: 241–263.
- Hoar, W. S. 1954. The behaviour of juvenile Pacific salmon, with particular reference to the sockeye (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Can.* 11: 69–97.
- Hoar, W. S. 1988. The Physiology of smolting salmonids. *In Fish Physiology*, vol. XIB. Hoar, W. S. and Randall, D. J. (Eds.), pp. 275–343. Academic Press, Tokyo.
- Hoffnagle, T. L. and Fivizzani, A. J. 1990. Stimulation of plasma thyroxine levels by novel water chemistry during smoltification in chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* 47: 1513–1517.
- Høgåsen, H. R. and Prunet, P. 1997. Plasma levels of thyroxine, prolactin, and cortisol in migrating and resident wild arctic char, *Salvelinus alpinus*. *Can. J. Fish. Aquat. Sci.* 54: 2947–2954.
- Hutchison, M. J. and Iwata, M. 1997. Decreased aggressive behavior in masu salmon (*Oncorhynchus masou*) during the parr-smolt transformation. *Mem. Fac. Fish., Hokkaido Univ.* 44: 22–25.
- Hvidsten, N. A., Jensen, A. J., Vivås, H., Bakke, Ø. and Heggberget, T. G. 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. *Nord. J. Freshwat. Res.* 70: 38–48.
- Iwata, M. 1982. Downstream migration and seawater adaptability of chum salmon (*Oncorhynchus keta*) fry. *In Proc. No. Pac. Aquaculture Symp.* Melteff, B. R. and Neve R. A. (Eds.), pp. 51–59. Univ. Alaska, Anchorage.
- Iwata M. 1995. Downstream migratory behavior of salmonids and its relationship with cortisol and thyroid hormones: A review. *Aquaculture* 135: 131–139.
- Iwata, M. and Komatsu, S. 1984. Importance of estuarine residence for adaptation of chum salmon (*Oncorhynchus keta*) fry to seawater. *Can. J. Fish. Aquat. Sci.* 41: 744–749.
- Iwata, M., Hasegawa, S. and Hirano, T. 1982. Decreased seawater adaptability of chum salmon (*Oncorhynchus keta*) fry following prolonged rearing in freshwater. *Can. J. Fish. Aquat. Sci.* 39: 509–514.
- Iwata, M. Ogura, H., Komatsu, S. and Suzuki, K. 1986. Loss of seawater preference in chum Salmon (*Oncorhynchus keta*) fry retained in fresh water after migration season. *J. Exp. Zool.* 240: 369–376.
- Iwata, M., Tsuboi, H., Yamashita, T., Amemiya, A., Yamada, H. and Chiba, H. 2003. Function and trigger of thyroxine surge in migrating chum salmon *Oncorhynchus keta* fry. *Aquaculture* 222: 315–329.
- Jonsson, N. 1991. Influence of water flow, temperature and light on

- fish migration in rivers. Nord. J. Freshwat. Res. 66: 20–35.
- Keenleyside, M. H. A. and Hoar, W. S. 1954. Effects of temperature on the responses of young salmon to water currents. Behaviour 7: 77–87.
- Kobayashi, T. 1958. An ecological study on the salmon fry, *Oncorhynchus keta* (5). The behaviour of chum salmon fry to their seaward migration. Sci. Rep. Hokkaido Salmon Hatch. 12: 21–30 (in Japanese with English abstract).
- Moore, A., Potter, E. C. E., Milner, N. J. and Bamber, S. 1995. The migratory behaviour of wild Atlantic salmon (*Salmo salar*) smolts in the estuary of the River Conwy, North Wales. Can. J. Fish. Aquat. Sci. 52: 1923–1935.
- Neave, F. 1955. Notes on the seaward migration of pink and chum salmon fry. J. Fish. Res. Bd. Can. 12: 369–374.
- Nishioka, R. S., Young, G., Bern, H. A., Jochimsen, W. and Hiser, C. 1985. Attempts to intensify the thyroxin surge in coho and king salmon by chemical stimulation. Aquaculture 45: 215–225.
- Ojima, D. and Iwata, M. The relationship between thyroxine surge and onset of downstream migration in chum salmon *Oncorhynchus keta* fry. Aquaculture (2007 in press).
- Riley, W. D., Eagle, M. O. and Ives, S. J. 2002. The onset of downstream movement of juvenile Atlantic salmon, *Salmo salar* L., in a chalk stream. Fish. Manage. Ecol. 9: 87–94.
- Satoh, R., Yamada, H., Chiba, H., Kambegawa, A. and Iwata, M. 2000. Seasonal changes in thyroidal response to thyroid-stimulating hormone in rainbow trout *Oncorhynchus mykiss*. Fish. Sci. 66: 174–176.
- Specker, J. L., Eales, J. G., Tagawa, M. and Tyler III, W. A. 2000. Parr-smolt transformation in Atlantic salmon: thyroid hormone deiodination in liver and brain and endocrine correlates of change in rheotactic behavior. Can. J. Zool. 78: 696–705.
- Yamagishi, H., Matsushima, T. and Nakamura, M. 1981. Notes on the aggressive behaviour of juvenile chum salmon *Oncorhynchus keta* (Walbaum). Sci. Rep. Hokkaido Salmon Hatch. 35: 25–31.
- Yamauchi, K., Koide, N., Adachi, S. and Nagahama, Y. 1984. Changes in seawater adaptability and blood thyroxine concentrations during smoltification of the masu salmon, *Oncorhynchus masou*, and the amago salmon, *Oncorhynchus rhodurus*. Aquaculture 42: 247–256.
- Youngson, A. F. and Simpson, T. H. 1984. Changes in serum thyroxine levels during smolting in captive and wild Atlantic salmon, *Salmo salar* L. J. Fish Biol. 24: 29–39.