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EDITORIAL

Advances in our understanding of the parr–smolt transformation of juvenile salmon: a summary of the 10th International Workshop on Salmon Smoltification

The 10th International Workshop on Salmon Smoltification was held in Norway from 14–August 18, 2017. Organized by L. Ebbesson, T. Nilsen, S. Stefansson and S. Handeland, the meeting was held at the University of Bergen for the first 2 days, and then at the delightful seaside resort Solstrand Hotel in Osøyro, Norway. The meeting also included an "upstream migration" to the Norwegian Wild Salmon Centre in Laerdal. The meeting was attended by 34 participants from 10 countries that included Australia, Canada, Chile, Denmark, France, Japan, Norway, Sweden, the UK and the USA.

The first International Workshop on Salmon Smoltification was held in La Jolla California and was focused on problems associated with the developing aquaculture industry, especially challenges associated with moving animals into seawater net pens. Since then the meeting has been held around the world, including Stirling in Scotland, UK, Trondheim in Norway, St. Andrews in New Brunswick, Canada, Muonio in Finland, Westport in Ireland, Tono in Japan, Corvallis in Oregon and Reykjavík and Hólar in Iceland. Over time the focus of the meeting has shifted to include hatchery fish that are part of restoration efforts, and most recently an increasing examination of fish in the wild. The emphasis on wild fish and improving hatchery conditions for mitigation of wild fish populations is especially important in light of the continuing declines in salmon populations in many areas and the looming threats of dams, climate change and other human activities that threaten the sustainability of salmon populations.

Salmon smolts make a gigantic niche shift as they migrate from freshwater rivers to the ocean, and undergo preparatory adaptations that allow them to survive and thrive in this new environment. Part of the continuing information gap for smolts is understanding the environmental factors that most contribute to fitness and survival at this critical stage. Photoperiod sets overall seasonal timing for smolting, but many of the details of photoperiod action are still unknown. There appears to be a critical photoperiod for smolt development (Strand *et al*., 2018), which may differ for different (*e.g*., more northern) populations. The extent and evolutionary flexibility of photoperiod control of smolting has important implications for the response of salmon populations to climate change, particularly given the large number of populations of salmon from the Atlantic and Pacific Oceans that are of conservation concern and supported by supplementation from hatchery-reared fish. Consequently, understanding the role early rearing environment has on development and successful transformation from parr to smolts remains an important area of investigation.

Hatchery produced smolts have been found to have lower survival compared with wild smolts, but the reasons for this remain unclear. Limitations in habitat complexity in hatcheries may result in poor learning capacity. Self *et al*. (2018a) found that artificial rearing structure provided in a hatchery setting had only minor effects on movement and predator avoidance behaviour of juvenile steelhead *Oncorhynchus mykiss* (Walbaum 1792), indicating that not all hatchery interventions will lead to improved survival. In an examination of migratory patterns of Atlantic salmon *Salmo salar* L. 1758 in a Norwegian River influenced by a large lake, Barlaup *et al*. (2018) found much later migration in hatchery reared fish compared with wild fish. This could have substantial effects on subsequent seawater survival and understanding of the reasons for these altered migratory patterns would benefit all hatchery release programmes. Effects even earlier in development, through maternal effects on size, may affect early growth and thus the demography of smolt development (Self *et al*., 2018b).

Changes to migratory corridors have the potential to affect downstream movement patterns in both hatchery and wild-reared smolts. Dams can have a dramatic effect on smolt survival, but the extent of effects is highly dependent on the height, location, turbine type and other factors. Moore *et al*. (2018) found that passage of *S. salar* smolts through an Archimedes screw hydropower turbine at a low head dam in southern England, UK, did not greatly affect migratory behaviour and survival through the rest of the fish's riverine and estuarine migration. Intercepting and tagging wild-reared smolts during migration is necessary to assess survival during the marine phase, but the effect of such procedures is largely unknown. The effect of tagging wild *S. salar* smolts caught in a small stream in southern England varied; capture of smolts following mild winters or at night decreased their probability of return as adults (Riley *et al*., 2018). This information will be important in guiding future tagging programmes to avoid artefacts and negative consequences of tagging programmes.

There is increasing evidence of population-specific migratory and physiological traits that affect fitness and survival of smolts. Masu salmon *Oncorhynchus masou* (Brevoort 1856) are largely anadromous, though landlocked, riverine populations are the rule in their more

southerly distribution in the south of Japan. Inatani *et al.* (2018) found that anadromous *O. masou* from the north of Japan had increased gill Na^+–K^+-ATPase activity and salinity tolerance in spring, whereas fish from landlocked populations in the south did not change in spring but showed modest increases in smolt appearance and salinity tolerance in autumn. It is less clear if populations in the same river catchment have evolved differential traits related to smolt development. Elsner & Shrimpton (2018) compared populations of coho salmon *Oncorhynchus kistuch* (Walbaum 1792) from high and low in the Fraser River catchment by rearing them under common conditions before and during smolt development. They did not find substantial differences in the timing or duration of gill Na^+–K^+-ATPase activity (a common indicator of smolt development), transcription levels of its isoforms or growth hormone and prolactin receptors, suggesting that the onset and duration of the smolt window may not be influenced by location in the same river system. Consistent with these findings, Bassett *et al.* (2018) found that gill Na^+–K^+-ATPase activity increased as fish moved downstream and entered the estuary, but did not find population-related differences. Further work is needed in other river systems examining other smolt-related traits to determine if within-river population differences can be found.

Successful smolting is clearly dependent on factors that the fishes experience in the freshwater environment such as pathogens and stress. The intestine is an important barrier to pathogens, but stress leads to intestinal barrier dysfunction. Sundh *et al.* (2018) found that acute stress also reduced gastrointestinal blood flow, although mechanical occlusion of blood flow to the gut did not induce barrier dysfunction. Developing therapeutic programmes that are effective and do not have a deleterious influence on the aquatic environment is often difficult. Dietary supplementation with oregano essential oil reduced infection rate of two common ectoparasites of chum salmon *Oncorhynchus keta* (Walbaum 1792) in Japan, improved growth in freshwater and resulted in higher survival rates following transfer to seawater (Mizuno *et al.*, 2018).

Ultimately the best measure of successful completion of the parr–smolt transformation is marine survival and performance following seawater entry. Given likely effects of climate change on the ocean, knowledge of how biotic and abiotic variables will influence seawater tolerance in smolts is important. Brown *et al.* (2018) found that large *S. salar* (10 fold greater than wild smolts) reared under a non-stimulatory photoperiod in which smolt development was minimized were able to acclimate to seawater, indicating that large size can help overcome the challenges of seawater exposure. Consequently, increases in temperature and potential productivity in the freshwater environment may have some benefits for smolt survival. There is also an interaction among environmental variables during seawater exposure of smolts. *Salmo salar* smolts showed greater ionoregulatory perturbations with exposure to higher salinity at warmer temperatures; effects that were not seen with just transfer to warmer water at constant high or low salinity (Vargas-Chacoff *et al.*, 2018). Along with the reduced capacity for ionoregulation in seawater at high temperatures, decreases in gill mRNA for the Na^+–K^+-ATPase α1a and α1b isoforms suggested a reduced capacity to elevate or maintain high levels of ion transporters at high temperatures. Ocean acidification due to increases in atmospheric CO_2 potentially introduces a compounding stressor for smolts entering seawater. Exposure to high CO_2 did not alter salinity tolerance in *S. salar* and growth rate in seawater was greater than under control conditions (McCormick & Regish, 2018). Significantly lower plasma chloride levels for smolts transferred into seawater with high levels of CO_2 may be associated with elevated plasma bicarbonate, a common response of fish to ocean acidification. The effects of ocean acidification, therefore, may not be all negative for salmonids to complete their anadromous life cycle. Although, much of the workshop focused on wild fish or husbandry strategies to produce competent smolts that will mimic wild-reared fish, production of aquaculture fish remains an important line of investigation. Salmon production protocols are rapidly changing towards industrialized production facilities and protocols with larger sized smolts up to 400–500 g. The rationale being that bigger fish are more robust and thus have increased performance and survival in seawater. To reach these large smolt sizes, the aquaculture industry is testing and adopting photoperiod manipulation with ever shorter winter signals, as well as use of intermediate salinities. The increased use of artificial environmental cues has raised concerns that the industry is losing or altering the timing and extent of critical smoltification traits (such as osmoregulatory ability, brain development and immune responses) that will affect post-smolt performance. For such changes to be sustainable more research and improved technological solutions will be required. Evaluation of semi-closed containment systems compared with open net pens for *S. salar* aquaculture revealed lower accumulated mortality, but the higher flow and exchange rates resulted in more small muscle fibres and cardiac hypertrophy than reference fish (Balseiro *et al.*, 2018).

Since the first smolt workshop in 1981 (and nine stimulating meetings later), our understanding of environmental effects on smolts has increased considerably, particularly with the use of new molecular tools to characterized physiological changes. In combination with these new methods, behavioural changes during the parr–smolt transformation have also been investigated revealing the complexity of responses exhibited among fish within a population. Population-specific effects have also been shown, but the genetic basis of differences in smolting are still largely unknown. Given the importance of seasonal changes in environment of stimulating the parr–smolt transformation, understanding the effects of climate changes such as temperature and ocean acidification on the life cycles is crucial to the long-term sustainability of anadromous salmonids that have so much economic and cultural importance. We expect that future lines of investigation will reveal important fitness traits for smolts under wild, hatchery-release and aquaculture settings. The interaction between behaviour and physiology will differ among rearing environments, but how domestication in the short and long-term affect these fitness traits is unclear. Understanding environmental interactions with smolts, therefore, will be critical to maintaining salmon populations in a world increasingly affected by human activity.

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REFERENCES

Balseiro, P., Moe, Ø., Gamlem, I., Shimizu, M., Sveier, H., Nilsen, T.O., Kaneko, N., Ebbesson, L., Pedrosa, C., Tronci, V., Nylund, A. & Handeland, S.O. (2018). Comparison between Atlantic salmon *Salmo salar* post-smolts reared in open sea cages and in the Preline raceway semi-closed containment aquaculture system. *Journal of Fish Biology 93*, 567–579. https://doi.org/10.1111/jfb.13659

Barlaup, B.T., Rund, H., Normann, E.S., Stranzl, S., Mahlum, S. & Vollset, K. W. (2018). Out of sync: monitoring the time of sea entry of wild and hatchery salmon *Salmo salar* smolt using floating passive-integrated transponder antennae. *Journal of Fish Biology 93*, 455–464. https://doi.org/10.1111/jfb.13648

Bassett, M.C., Patterson, D.A. & Shrimpton, J.M. (2018). Temporal and spatial differences in smolting among *Oncorhynchus nerka* populations throughout fresh and seawater migration. *Journal of Fish Biology 93*, 510–518. https://doi.org/10.1111/jfb.13678

Brown, M.S., Jones, P.L., Tromp, J.J., van Rijn, C.A., & Collins, R.A. & Afonso, L.O.B. (2018). The physiology of saltwater acclimation in large juvenile Atlantic salmon *Salmo salar*. *Journal of Fish Biology 93*, 540–549. https://doi.org/10.1111/jfb.13649

Elsner, R. A., & Shrimpton, J. M. (2018). Is the duration of the smolt window related to migration distance in coho salmon *Oncorhynchus kisutch*. *Journal of Fish Biology*, *93*, 501–509. https://doi.org/10.1111/jfb.13679

Inatani, Y., Ineno, T., Sone, S., Matsumoto, N., Uchida, K. & Shimizu, M. (2018). Assessment of the timing and degree of smolt development in southern populations of masu salmon *Oncorhynchus masou*. *Journal of Fish Biology 93*, 490–500. https://doi.org/10.1111/jfb.13647

McCormick, S.D. & Regish, A.M. (2018). Effects of ocean acidification on salinity tolerance and seawater growth of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology 93*, 560–566. https://doi.org/10.1111/jfb.13656

Mizuno, S., Urawa, S., Miyamoto, M., Hatakeyama, M., Sasaki, Y., Koide, N., Tada, S. & Ueda, H. (2018). Effects of dietary supplementation with oregano essential oil on prevention of the ectoparasitic protozoans *Ichthyobodo salmonis* and *Trichodina truttae* in juvenile chum salmon *Oncorhynchus keta*. *Journal of Fish Biology 93*, 528–539. https://doi.org/10.1111/jfb.13681

Moore, A., Privitera, L., Ives, M.J., Uzyczak, J. & Beaumont, W.R.C. (2018). The effects of a small hydropower scheme on the migratory behaviour of Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology 93*, 469–476. https://doi.org/10.1111/jfb.13660

Riley, W.D., Ibbotson, A.T., Gregory, S.D., Russell, I.C., Lauridsen, R.B., Beaumont, W.R.C., Cook, A.C. & Maxwell, D.L. (2018). Under what circumstances does the capture and tagging of wild Atlantic salmon *Salmo salar* smolts affect probability of return as adults? *Journal of Fish Biology 93*, 477–489. https://doi.org/10.1111/jfb.13655

Self, K.E., Schreck, C.B., Cogliati, K.M., Billman, E.J. & Noakes, L.G. (2018a). The effect of rearing structures on behaviour and movement of juvenile steelhead *Oncorhynchus mykiss*. *Journal of Fish Biology 93*, 449–454. https://doi.org/10.1111/jfb.13657

Self, K.E., Schreck, C.B., Cogliati, K.M., Billman, E.J. & Noakes, L.G. (2018b). Egg size and growth in steelhead *Oncorhynchus mykiss*. *Journal of Fish Biology 93*, 465–468. https://doi.org/10.1111/jfb.13764

Strand, J.E.T., Hazlerigg, D. & Jørgensen, E.H. (2018). Photoperiod revisited: is there a critical day length for triggering a complete parr–smolt transformation in Atlantic salmon *Salmo salar*? *Journal of Fish Biology 93*, 440–448. https://doi.org/10.1111/jfb.13760

Sundh, H., Gräns, A., Brijs, J., Sandblom, E., Axelsson, M., Berg, C. & Sundell, K. (2018). Effects of coeliacomesenteric blood flow reduction on intestinal barrier function in rainbow trout *Oncorhynchus mykiss*. *Journal of Fish Biology 93*, 519–527. https://doi.org/10.1111/jfb.13658

Vargas-Chacoff, L., Regish, A.M., Weinstock, A. & McCormick, S.D. (2018). Effects of elevated temperature on osmoregulation and stress responses in Atlantic salmon *Salmo salar* smolts in freshwater and seawater. *Journal of Fish Biology 93*, 550–559. https://doi.org/10.1111/jfb.13683