

Seasonal plasticity in telencephalon mass of a benthic fish

E. S. McCALLUM*, P. M. CAPELLE AND S. BALSHINE

Department of Psychology, Neuroscience and Behaviour, McMaster University, 1280 Main Street West, Hamilton, ON, L8S 4K1 Canada

(Received 17 April 2014, Accepted 18 July 2014)

To gain a deeper understanding of how environmental conditions affect brain plasticity, brain size was explored across different seasons using the invasive round goby *Neogobius melanostomus*. The results show that *N. melanostomus* had heavier telencephalon in the spring compared to the autumn across the two years of study. Furthermore, fish in reproductive condition had heavier telencephala, indicating that tissue investment and brain plasticity may be related to reproductive needs in *N. melanostomus*.

© 2014 The Fisheries Society of the British Isles

Key words: brain mass; reproduction; round goby; seasonality; spatial cognition.

An organism's relative investment in brain structures will be partially shaped by cognitive needs imposed by the ecological demands in their environment (*e.g.* avoiding predation, dealing with spatial complexity and locating mates) (Dukas, 1998; Sherry, 2006). As brain tissue is energetically expensive to maintain (Mink *et al.*, 1981; Soengas & Aldegunde, 2002; Chittka & Niven, 2009), the functional benefits gained from investing in larger brain structures should outweigh the associated metabolic costs (Johnston, 1982; Kotrschal *et al.*, 2013). Seasonal plasticity in brain size and shape may then arise when the environmental conditions an organism faces are not static, and for many species with seasonal foraging and mating patterns, the demands on cognition and their associated neural investment should vary with season. Seasonal plasticity in vertebrate brain morphology has provided an exciting avenue to further understand how ecological factors shape brains and behaviour.

To date, research on seasonal plasticity has been primarily confined to mammal and bird species, with heavy focus on songbirds (Tramontin & Brenowitz, 2000; Yaskin, 2011). For example, hippocampal size is known to vary seasonally with demands for caching in food-storing bird species such as the black-capped chickadee *Poecile atricapillus* and marsh tit *Parus palustris* (Smulders *et al.*, 1995; Healy & Krebs, 1996; Sherry & Hoshooley, 2009). This relationship between hippocampal size and variance in spatial demands across seasons has been similarly reported in mammals (Lavenex *et al.*, 2000; Pyter *et al.*, 2005). Male rodents with large home ranges such

*Author to whom correspondence should be addressed. Tel.: +1 519 671 9729; email: mccalles@mcmaster.ca

as meadow voles *Microtus pennsylvanicus* and montane voles *Microtus montanus* have larger hippocampi during the breeding season when compared to females that hold much smaller territories, or when compared to the males of other closely related species with smaller home ranges such as the pine vole *Microtus pinetorum* and prairie vole *Microtus ochrogaste* (Jacobs, 1996). These studies have linked seasonal variation in ecological demands on cognition to underlying neural structures and helped to show how selection processes shape brain evolution. As far as is known, however, there are no studies that have documented similar seasonal plasticity in brain size in teleosts.

Teleosts present an excellent opportunity to assess brain size variation. Unlike mammal and avian species, fishes exhibit neurogenesis broadly across the brain as adults (Kaslin *et al.*, 2008; Zupanc, 2008), as well as indeterminate growth across their lifetime (Sebens, 1987; Charnov & Berrigan, 1991). More recently, the relationship between brain structures, the environment and cognitive abilities has been investigated with specific focus on the forebrain and spatial abilities (Broglia *et al.*, 2003; Salas *et al.*, 2006; Ebbesson & Braithwaite, 2012). Functionally, the teleost forebrain, or telencephalon, is linked to spatial cognition, as fishes with ablations to this brain area fail spatial learning and memory tasks (Salas *et al.*, 1996a, b; Portavella *et al.*, 2002). From a neuroecological perspective, fish species foraging in spatially complex environments have larger telencephalons compared to related species foraging in less complex areas (Huber *et al.*, 1997; Kotrschal *et al.*, 1998; Pollen *et al.*, 2007; Costa *et al.*, 2011). This has also been shown between different populations of the same species in nine-spined sticklebacks *Pungitius pungitius* (L. 1758) (Gonda *et al.*, 2009, 2011). Moreover, under controlled laboratory conditions, Atlantic salmon *Salmo salar* L. 1758 (Näslund *et al.*, 2012; Salvanes *et al.*, 2013), coho salmon *Oncorhynchus kisutch* (Walbaum 1792) (Kotrschal *et al.*, 2012) and zebra fish *Danio rerio* (Hamilton 1822) (von Krogh *et al.*, 2010) show increased neural plasticity in the telencephalon when raised in spatially enriched *v.* barren environments; however, this relationship was not found in guppies *Poecilia reticulatus* Peters 1859 when raised under similar testing conditions (Burns *et al.*, 2009). Fishes living in seasonal climates often exhibit spatial migrations, and have demands on spatial cognition for foraging, reproduction and predator avoidance that strongly vary across time. Although it is well established that the teleost telencephalon underpins spatial cognition, few, if any studies have yet addressed the potential for seasonal plasticity in this brain region in a migrating fish.

In this study, seasonal variation in telencephalon mass was assessed in the benthic round goby *Neogobius melanostomus* (Pallas 1814) to provide an initial assessment of possible plasticity in a seasonally migrating fish. *Neogobius melanostomus* vertically migrate to and from deeper waters seasonally, inhabiting the shallow littoral zone in the spring and summer breeding season (Charlebois *et al.*, 1997; Sapota, 2004). When *N. melanostomus* migrate to shallow water, they encounter not only many species of piscivorous fishes (Dietrich *et al.*, 2006; Reyjol *et al.*, 2010; Taraborelli *et al.*, 2010), but also water snakes (King *et al.*, 2006) and aquatic birds that hunt fishes near the shore (Somers *et al.*, 2003; Jakubas, 2004; Coleman *et al.*, 2012), therefore, increasing demands on spatial cognition to locate and remember sheltered locations. Moreover, male *N. melanostomus* establish territories with nests where they guard offspring over the breeding season, while females must horizontally navigate the breeding grounds to assess potential mates and they will reproduce multiple times throughout spring and summer breeding season (Charlebois *et al.*, 1997; Corkum *et al.*, 1998). As a result of these expected spatial demands, telencephalon mass was expected to increase in the

spring (the breeding season) compared to autumn in both sexes, while whole brain mass (whole brain mass less the telencephalon mass) would remain unchanged across seasons.

Neogobius melanostomus were collected using minnow traps across 2 years from two locations in Hamilton Harbour, ON, Canada (La Salle Marina: 43° 18' N; 79° 50' W, and Pier 15: 43° 16' N; 79° 50' W). Spring samples were collected in June 2012 ($n = 51$; $n_{\text{male}} = 29$, $n_{\text{female}} = 22$) and in June 2013 ($n = 76$; $n_{\text{male}} = 41$, $n_{\text{female}} = 35$), and autumn samples were collected in October 2011 ($n = 47$; $n_{\text{male}} = 24$, $n_{\text{female}} = 23$) and in October 2012 ($n = 85$; $n_{\text{male}} = 72$, $n_{\text{female}} = 13$) [sampling procedures are given in Marentette *et al.* (2009), Young *et al.* (2010) and Marentette & Balshine (2012)]. After collection, fish were euthanized (benzocaine, Sigma Aldrich; www.sigmaaldrich.com) and transported on ice to the laboratory at McMaster University. Fish were dissected and the following morphological measurements were taken: standard length (L_S , to the nearest 0.01 cm, from the snout to the caudal peduncle), body and gonad mass (to the nearest 0.001 g). Brains were exposed by removal of the top of the skull and the entire skull was placed in a vial of 4% paraformaldehyde for 30 days. Brains were then removed from the brain cavity, and the brain stem was cut precisely 2 mm from the base of the brain. Brains were carefully patted dry using a Kimwipe (Kimberly-Clark; www.kimberly-clark.com) and immediately after the whole brain mass was measured three times on a Metler AT20 Microbalance (Metler Toledo; <http://ca.mt.com/ca/en/home.html/>) accurate to the nearest 0.0001 g. An average of the three measurements was used in subsequent analyses. The telencephalon was removed and weighed using a Metler AB204-SFact Microbalance (Metler Toledo) accurate to the nearest 0.00001 g.

All statistical analyses were performed using R 0.97.248 (R Core Team 2012; www.r-project.org). Quantile–quantile plots and residuals *v.* fitted plots were visually inspected to test the assumptions of the models. To analyse the effect of season of collection on telencephalon mass, a generalized least squares model (GLS) was implemented using the nlme package in R (Pinheiro *et al.*, 2014). In this model, ln-transformed telencephalon mass was used as the response variable, ln-transformed whole brain mass was the covariate and sampling season was the predictor variable with four levels for each sampling period (*i.e.* autumn 2011, spring 2012, autumn 2012 and spring 2013). To control for any potential effects of sex and site of collection, these variables were included in the model as fixed effects. Ln-transformed values were used because of an allometric relationship between brain size and body size in the sample (Schmidt-Nielsen, 1984). A GLS model was used because of uneven variances in the response variable across seasons of collection, facilitating a weighting of the variance by each season. The effect of season of collection on whole brain mass (where the telencephalon mass was subtracted from the whole brain mass prior to transformation) was analysed using the same statistical procedure mentioned above. Ln-transformed adjusted whole brain mass (less the telencephalon mass) was used as the response variable and ln-transformed body mass as the covariate. In both GLS models, any main effects of season were followed with *post hoc* multiple comparison tests using Tukey's HSD. To assess whether telencephalon mass predicted reproductive status, a binomial logistic regression was used. Gonad mass was used to calculate gonado-somatic index (I_G) for each fish, where males with $I_G > 1\%$ and females with an $I_G > 8\%$ were considered to be in reproductive condition (Marentette & Corkum, 2008). Reproductive status was used as the response variable (reproductive *v.* non-reproductive as given by

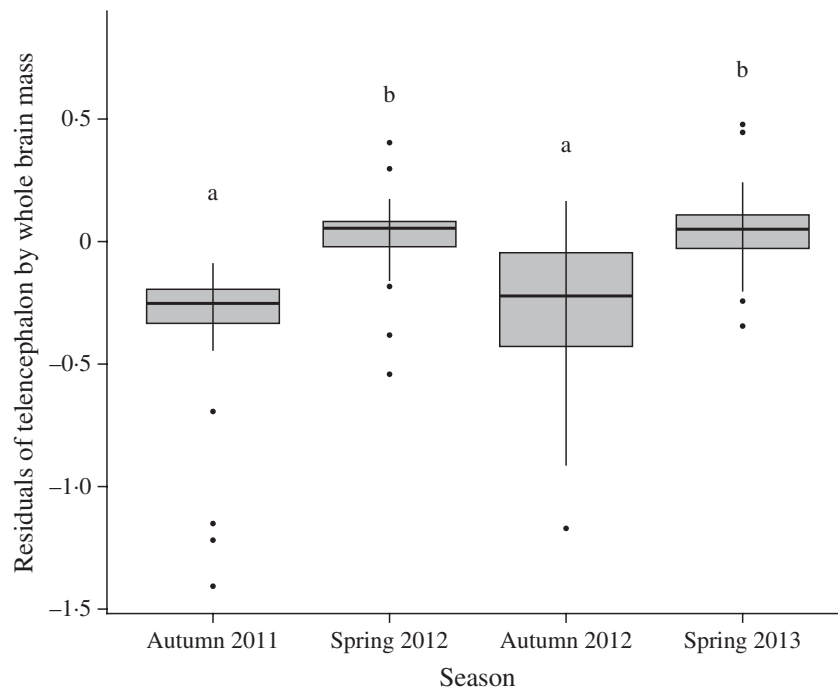


FIG. 1. Residuals of ln-transformed telencephalon mass by ln-transformed whole brain mass plotted by season. The box plot shows the median with first and third quartiles and the 95% c.i. around the mean. Different lowercase letters indicate results of *post hoc* analyses at significance $P < 0.001$.

I_G score), while the residuals of the relationship between ln-transformed telencephalon mass and ln-transformed whole brain mass were used as predictors.

Neogobius melanostomus telencephalon mass varied with season (GLS: estimate \pm s.e. = 0.130 ± 0.014 , $\chi^2_{254} = 79.29$, $P < 0.001$; Fig. 1), with heavier telencephalons in both spring seasons compared to both autumn seasons (for all comparisons, Tukey HSD: $Z > 7.80$, $P < 0.001$). There was no effect of sex (GLS: estimate \pm s.e. = 0.014 ± 0.024 , $\chi^2_{254} = 0.36$, $P > 0.05$) or collection site (GLS: estimate \pm s.e. = -0.004 ± 0.024 , $\chi^2_{254} = 0.026$, $P > 0.05$) on telencephalon mass. Whole brain mass (less the telencephalon mass) also varied across time, but in contrast did not systematically vary with season (GLS: estimate \pm s.e. = -0.021 ± 0.006 , $\chi^2_{254} = 10.05$, $P < 0.01$); fish collected in the autumn of 2011 had heavier brains compared to autumn of 2012 (Tukey HSD: $Z = -2.93$, $P < 0.05$) and to fish from the spring of 2013 (Tukey HSD: $Z = -4.24$, $P < 0.001$). Also, fish collected in spring 2012 had heavier brains compared to the fish collected in the spring 2013 (Tukey HSD: $Z = -3.37$, $P < 0.01$), suggesting that there was no effect of season. There was no effect of sex (GLS: estimate \pm s.e. = -0.020 ± 0.015 , $\chi^2_{254} = 1.68$, $P > 0.05$), but there was an effect of collection site with fish from La Salle having heavier brains compared to fish collected at Pier 15 (GLS: estimate \pm s.e. = -0.030 ± 0.013 , $\chi^2_{254} = 4.59$, $P < 0.05$). Finally, *N. melanostomus* with a larger telencephalon mass were more likely to be in reproductive condition (binomial logistic regression: estimate \pm s.e. = 5.67 ± 1.05 , $Z_{257} = 5.38$, $P < 0.001$). The covariate, body mass, did not vary with season (GLS: estimate \pm s.e. = -0.17 ± 0.17 , $\chi^2_{254} = 0.95$, $P > 0.05$), but did vary with sex, where males were heavier than females (GLS: estimate \pm s.e. = 1.74 ± 0.38 ,

$\chi^2_{254} = 17.99$, $P < 0.001$). Also, body mass varied with site, fish from La Salle were heavier than fish from P15 (GLS: estimate \pm s.e. = -1.12 ± 0.38 , $\chi^2_{254} = 8.44$, $P < 0.01$).

The results of this study confirm that *N. melanostomus* telencephalon mass was heavier in spring when compared to autumn, and are similar to previous findings of brain plasticity in other seasonal migrating species (Tramontin & Brenowitz, 2000). As the telencephalon is thought to orchestrate spatial cognition in fishes (Ebbesson & Braithwaite, 2012), the increased investment in this structure may be related to greater spatial demands experienced by *N. melanostomus* in the breeding season (*e.g.* needs to avoid predators, forage, locate and defend shelters). Additionally, *N. melanostomus* with larger telencephalon were more likely to be in reproductive condition, providing an initial link to reproductive physiology. Similar to plasticity in the song control circuitry of songbirds (Brenowitz, 2004; Pfaff *et al.*, 2007), changes in *N. melanostomus* telencephalon mass may be hormonally mediated. There was no difference in telencephalon mass between the sexes, indicating that both sexes are investing similarly in this structure and may be experiencing equal demands on spatial cognition in the breeding season. Males would need to locate a suitable nest and territory, while females need to locate shelter and potential mates (Corkum *et al.*, 1998). Both sexes also need to forage and avoid predators.

Although whole brain mass (less telencephalon mass) was expected to remain unchanged across seasons, there was variation in whole brain mass across collection times, but no systematic seasonal variation was observed (*i.e.* spring *v.* autumn). Moreover, to more rigorously explore variation in brain size across seasons, the analysis was restricted to a smaller sample of size-matched fish across seasons. After this, telencephalon size still varied with season, while whole brain mass did not. Given the large original sample size ($n = 259$) and the comparatively low effect size, the whole brain mass differences may be driven by a factor not assessed in the present work. Future analyses of how individual brain areas (*e.g.* the cerebellum, optic tectum and olfactory bulbs) change separately, or in concert, with season would provide greater resolution of what might be driving the differences in whole brain mass.

Seasonal variation in *N. melanostomus* telencephalon mass is probably associated with demands on spatial cognition, reproductive needs or a combination of these factors. As the research presented here is correlative, however, it does not provide a functional explanation or direct link between spatial or reproductive behaviours and brain plasticity. To better understand the relationship between seasonal changes in cognition and brain size in *N. melanostomus*, it would be advantageous to follow protocols from other fish species (von Krogh *et al.*, 2010; Salvanes *et al.*, 2013) and assess spatial learning in fishes raised in enriched (spatially challenging) *v.* barren (structurally simple) environments. Furthermore, it would be beneficial to assess hormone profiles and reproductive behaviour (*i.e.* nest building and defence) in conjunction with brain analyses to discern the link between brain size and reproductive condition. More precise neuroanatomical analyses should be employed to assess fine-scale fluctuations in other brain regions such as the olfactory bulb and cerebellum. Although future work is needed to disentangle the causal underpinnings of seasonal brain plasticity in *N. melanostomus*, the present work provides an important first indication that ecological factors that fluctuate with season appear to affect telencephalon size in *N. melanostomus*, and provides one of the first studies of seasonal plasticity in brain mass of a teleost.

The authors wish to thank B. Bolker, D. Champredon, C. Dey, A. Reddon and K. Cogliati for help with statistical analyses and comments on the manuscript, and S. Marsh-Rollo, E. Krutzmann and D. Tomczyk for field collection assistance. E.S.M. is supported by an Ontario Graduate Scholarship. S.B. is supported by the Canada Research Chair Programme and NSERC Discovery Programme.

References

- Brenowitz, E. A. (2004). Plasticity of the adult avian song control system. *Annals of the New York Academy of Sciences* **1016**, 560–585. doi: 10.1196/annals.1298.006
- Broglio, C., Rodríguez, F. & Salas, C. (2003). Spatial cognition and its neural basis in teleost fishes. *Fish and Fisheries* **4**, 247–255. doi: 10.1046/j.1467-2979.2003.00128.x
- Burns, J. G., Saravanan, A. & Rodd, H. F. (2009). Rearing environment affects the brain size of guppies: lab-reared guppies have smaller brains than wild-caught guppies. *Ethology* **115**, 122–133. doi: 10.1111/j.1439-0310.2008.01585.x
- Charlebois, P. M., Marsden, J. E., Goettel, R. G., Wolfe, R. K., Jude, D. J. & Rudnika, S. (1997). *The Round Goby, Neogobius melanostomus (Pallas): A Review of European and North American Literature*. Zion, IL: Jointly published by the Illinois-Indiana Sea Grant Program and the Illinois Natural History Survey.
- Charnov, E. L. & Berrigan, D. (1991). Evolution of life history parameters in animals with indeterminate growth, particularly fish. *Evolutionary Ecology* **5**, 63–68. doi: 10.1007/BF02285246
- Chittka, L. & Niven, J. (2009). Are bigger brains better? *Current Biology* **19**, R995–R1008. doi: 10.1016/j.cub.2009.08.023
- Coleman, J. T., Adams, C. M., Kandel, M. & Richmond, M. E. (2012). Eating the invaders: the prevalence of round goby (*Apollonia melanostomus*) in the diet of double-crested cormorants on the Niagara River. *Waterbirds* **35**, 103–113. doi: 10.1675/063.035.sp111
- Corkum, L. D., MacInnis, A. J. & Wickett, R. G. (1998). Reproductive habits of round gobies. *Great Lakes Research Review* **3**, 13–20.
- Costa, S. S., Andrade, R., Carneiro, L. A., Gonçalves, E. J., Kotrschal, K. & Oliveira, R. F. (2011). Sex differences in the dorsolateral telencephalon correlate with home range size in blennioid fish. *Brain, Behavior and Evolution* **77**, 55–64. doi: 10.1159/000323668
- Dietrich, J. P., Morrison, B. J. & Hoyle, J. A. (2006). Alternative ecological pathways in the eastern Lake Ontario food web-round goby in the diet of lake trout. *Journal of Great Lakes Research* **32**, 395–400. doi: 10.3394/0380-1330(2006)32[395:AEPITE]2.0.CO;2
- Dukas, R. (1998). *Cognitive Ecology: the Evolutionary Ecology of Information Processing and Decision Making*. Chicago, IL: University of Chicago Press.
- Ebbesson, L. O. E. & Braithwaite, V. A. (2012). Environmental effects on fish neural plasticity and cognition. *Journal of Fish Biology* **81**, 2151–2174. doi: 10.1111/j.1095-8649.2012.03486.x
- Gonda, A., Herczeg, G. & Merilä, J. (2009). Adaptive brain size divergence in nine-spined sticklebacks (*Pungitius pungitius*)?. *Journal of Evolutionary Biology* **22**, 1721–1726. doi: 10.1111/j.1420-9101.2009.01782.x
- Gonda, A., Herczeg, G. & Merilä, J. (2011). Population variation in brain size of nine-spined sticklebacks (*Pungitius pungitius*) local adaptation or environmentally induced variation? *BMC Evolutionary Biology* **11**, 1–11. doi: 10.1186/1471-2148-11-75
- Healy, S. D. & Krebs, J. R. (1996). Food storing and the hippocampus in Paridae. *Brain, Behavior and Evolution* **47**, 195–199. doi: 10.1159/000113239
- Huber, R., van Staaden, M. J., Kaufman, L. S. & Liem, K. F. (1997). Microhabitat use, trophic patterns, and the evolution of brain structure in African cichlids. *Brain, Behavior and Evolution* **50**, 167–182. doi: 10.1159/000113330
- Jacobs, L. F. (1996). The economy of winter: phenotypic plasticity in behavior and brain structure. *Biological Bulletin* **191**, 92–100.
- Jakubas, D. (2004). The response of the grey heron to a rapid increase of the round goby. *Waterbirds* **27**, 304–307. doi: 10.1675/15244695(2004)027[0304:TROTGH]2.0.CO;2
- Johnston, T. D. (1982). Selective costs and benefits in the evolution of learning. *Advances in the Study of Behaviour* **12**, 65–106. doi: 10.1016/S0065-3454(08)60046-7

- Kaslin, J., Ganz, J. & Brand, M. (2008). Proliferation, neurogenesis and regeneration in the non-mammalian vertebrate brain. *Philosophical Transactions of the Royal Society B* **363**, 101–122. doi: 10.1098/rstb.2006.2015
- King, R. B., Ray, J. M. & Standford, K. M. (2006). Gorging on gobies: beneficial effects of alien prey on a threatened vertebrate. *Canadian Journal of Zoology* **84**, 108–115. doi: 10.1139/Z05-182
- Kotrschal, K., Van Staaden, M. J. & Huber, R. (1998). Fish brains: evolution and environmental relationships. *Reviews in Fish Biology and Fisheries* **8**, 373–408. doi: 10.1023/A:1008839605380
- Kotrschal, A., Sundstrom, L. F., Brelin, D., Devlin, R. H. & Kolm, N. (2012). Inside the heads of David and Goliath: environmental effects on brain morphology among wild and growth-enhanced coho salmon *Oncorhynchus kisutch*. *Journal of Fish Biology* **81**, 987–1002. doi: 10.1111/j.1095-8649.2012.03348.x
- Kotrschal, A., Rogell, B., Bundsen, A., Svensson, B., Zajitschek, S., Brannstrom, I., Immler, S., Maklakov, A. A. & Kolm, N. (2013). Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. *Current Biology* **23**, 168–171. doi: 10.1016/j.cub.2012.11.058
- von Krogh, K., Sørensen, C., Nilsson, G. E. & Øverli, Ø. (2010). Forebrain cell proliferation, behavior, and physiology of zebrafish, *Danio rerio*, kept in enriched or barren environments. *Physiology and Behavior* **101**, 32–39. doi: 10.1016/j.physbeh.2010.04.003
- Lavenex, P., Steele, M. A. & Jacobs, L. F. (2000). The seasonal pattern of cell proliferation and neuron number in the dentate gyrus of wild adult eastern grey squirrels. *European Journal of Neuroscience* **12**, 643–648. doi: 10.1046/j.1460-9568.2000.00949.x
- Marentette, J. R. & Balshine, S. (2012). Altered prey responses in round goby from contaminated sites. *Ethology* **118**, 812–820. doi: 10.1111/j.1439-0310.2012.02071
- Marentette, J. R. & Corkum, L. D. (2008). Does the reproductive status of male round gobies (*Neogobius melanostomus*) influence their response to conspecific odours? *Environmental Biology of Fishes* **81**, 447–455. doi: 10.1007/s10641-007-9240-7
- Marentette, J. R., Fitzpatrick, J. L., Berger, R. G. & Balshine, S. (2009). Multiple male reproductive morphs in the invasive round goby (*Apollonia melanostoma*). *Journal of Great Lakes Research* **35**, 302–308. doi: 10.1016/j.jglr.2009.01.009
- Mink, J. W., Blumenschine, R. J. & Adams, D. B. (1981). Ratio of central nervous system to body metabolism in vertebrates: its constancy and functional basis. *American Journal of Physiology* **241**, R203–R212.
- Näslund, J., Aarestrup, K., Thomassen, S. T. & Johnsson, J. I. (2012). Early enrichment effects on brain development in hatchery-reared Atlantic salmon (*Salmo salar*): no evidence for a critical period. *Canadian Journal of Fisheries and Aquatic Sciences* **69**, 1481–1490. doi: 10.1139/f2012-074
- Pfaff, J. A., Zanello, L., MacDougall-Shackleton, S. A. & MacDougall-Shackleton, E. A. (2007). Song repertoire size varies with HVC volume and is indicative of male quality in song sparrows (*Melospiza melodia*). *Proceedings of the Royal Society B* **274**, 2035–2040. doi: 10.1098/rspb.2007.0170
- Pollen, A. A., Dobberfuhl, A. P., Scace, J., Igulu, M. M., Renn, S. C., Shumway, C. A. & Hofmann, H. A. (2007). Environmental complexity and social organization sculpt the brain in Lake Tanganyikan cichlid fish. *Brain, Behavior and Evolution* **70**, 21–39. doi: 10.1159/000101067
- Portavella, M., Vargas, J. P., Torres, B. & Salas, C. (2002). The effects of telencephalic pallial lesions on spatial, temporal, and emotional learning in goldfish. *Brain Research Bulletin* **57**, 397–399. doi: 10.1016/S0361-9230(01)00699-2
- Pyter, L. M., Reader, B. F. & Nelson, R. J. (2005). Short photoperiods impair spatial learning and alter hippocampal dendritic morphology in adult male white-footed mice (*Peromyscus leucopus*). *Journal of Neuroscience* **25**, 4521–4526. doi: 10.1523/JNEUROSCI.0795-05.2005
- Reyjol, Y., Brodeur, P., Mailhot, Y., Mingelbier, M. & Dumont, P. (2010). Do native predators feed on non-native prey? The case of round goby in a fluvial piscivorous fish assemblage. *Journal of Great Lakes Research* **36**, 618–624. doi: 10.1016/j.jglr.2010.09.006
- Salas, C., Broglio, C., Rodríguez, F., López, J. C., Portavella, M. & Torres, B. (1996a). Telencephalic ablation in goldfish impairs performance in a ‘spatial constancy’

- problem but not in a cued one. *Behavioural Brain Research* **79**, 193–200. doi: 10.1016/0166-4328(96)00014-9
- Salas, C., Rodríguez, F., Vargas, J. P., Durán, E. & Torres, B. (1996b). Spatial learning and memory deficits after telencephalic ablation in goldfish trained in place and turn maze procedures. *Behavioral Neuroscience* **110**, 965–980.
- Salas, C., Broglio, C., Durán, E., Gómez, A., Ocaña, F. M., Jiménez-Moya, F. & Rodríguez, F. (2006). Neuropsychology of learning and memory in teleost fish. *Zebrafish* **3**, 157–171. doi: 10.1089/zeb.2006.3.157
- Salvanes, A. G. V., Moberg, O., Ebbesson, L. O., Nilsen, T. O., Jensen, K. H. & Braithwaite, V. A. (2013). Environmental enrichment promotes neural plasticity and cognitive ability in fish. *Proceedings of the Royal Society B* **280**, 1–7. doi: 10.1098/rspb.2013.1331
- Sapota, M. R. (2004). The round goby (*Neogobius melanostomus*) in the Gulf of Gdańsk – a species introduction into the Baltic Sea. In *Biology of the Baltic Sea* (Kautsky, H. & Snoeijs, P., eds), pp. 219–224. Dordrecht: Springer.
- Schmidt-Nielsen, K. (1984). *Scaling: Why is Animal Size so Important?* Cambridge: Cambridge University Press.
- Sebens, K. P. (1987). The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics* **18**, 371–407. Available at <http://www.jstor.org/stable/20971371>
- Sherry, D. F. (2006). Neuroecology. *Annual Review of Psychology* **57**, 167–197. doi: 10.1146/annurev.psych.56.091103.070324
- Sherry, D. F. & Hoshoooley, J. S. (2009). The seasonal hippocampus of food-storing birds. *Behavioural Processes* **80**, 334–338. doi: 10.1016/j.beproc.2008.12.012
- Smulders, T. V., Sasson, A. D. & DeVoogd, T. J. (1995). Seasonal variation in hippocampal volume in a food-storing bird, the black-capped chickadee. *Journal of Neurobiology* **27**, 15–25. doi: 10.1002/neu.480270103
- Soengas, J. L. & Aldegunde, M. (2002). Energy metabolism of fish brain. *Comparative Biochemistry and Physiology B* **131**, 271–296. doi: 10.1016/S1096-4959(02)00022-2
- Somers, C. M., Lozer, M. N., Kjoss, V. A. & Quinn, J. S. (2003). The invasive round goby (*Neogobius melanostomus*) in the diet of nestling double-crested cormorants (*Phalacrocorax auritus*) in Hamilton Harbour, Lake Ontario. *Journal of Great Lakes Research* **29**, 392–399. doi: 10.1016/S0380-1330(03)70446-8
- Taraborelli, A. C., Fox, M. G., Johnson, T. B. & Schaner, T. (2010). Round goby (*Neogobius melanostomus*) population structure, biomass, prey consumption and mortality from predation in the Bay of Quinte, Lake Ontario. *Journal of Great Lakes Research* **36**, 625–632. doi: 10.1016/j.jglr.2010.07.011
- Tramontin, A. D. & Brenowitz, E. A. (2000). Seasonal plasticity in the adult brain. *Trends in Neurosciences* **23**, 251–258. doi: 10.1016/S0166-2236(00)01558-7
- Yaskin, V. A. (2011). Seasonal changes in hippocampus size and spatial behavior of mammals and birds. *Biology Bulletin Reviews* **72**, 27–39. doi: 10.1134/S2079086411030108
- Young, J. A. M., Marentette, J. R., Gross, C., McDonald, J. I., Verma, A., Marsh-Rollo, S. E., Macdonald, P. D. M., Earn, J. D. & Balshine, S. (2010). Demography and substrate affinity of the round goby (*Neogobius melanostomus*) in Hamilton Harbour. *Journal of Great Lakes Research* **36**, 115–122. doi: 10.1016/j.jglr.2009.11.001
- Zupanc, G. K. H. (2008). Adult neurogenesis and neuronal regeneration in the brain of teleost fish. *Journal of Physiology - Paris* **102**, 357–373. doi: 10.1016/j.jphysparis.2008.10.007

Electronic References

- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team (2014). *nlme: Linear and non-linear mixed effects models*. R Package Version 3.1–117. Available at <http://CRAN.R-project.org/package=nlme>.