



Article Salmonid Jumping and Playing: Potential Cultural and Welfare Implications

Robert M. Fagen

Ronin Institute, Montclair, NJ 07043, USA; 8sitaya@gmail.com; Tel.: +1-907-789-4608

Academic Editor: Luis Hector Hernandez Hernandez Received: 6 March 2017; Accepted: 25 May 2017; Published: 30 May 2017

Simple Summary: Salmonids jump from the water in nature and in confinement. These behaviors are economically important and relevant to fish welfare. In net pen culture, the need to control parasitic sea lice has motivated studies of salmonid jumping behavior. Some instances of jumping in salmon may be a form of play. Indigenous and institutional science, cultural wisdom, and direct observation can aid the understanding of these behaviors.

Abstract: Salmonids of several species and other fishes can jump into the air from the water. This behavior has been used in net pen culture applications to control parasitic sea lice. The reasons that salmonids jump remain a topic for speculation. Research on these behaviors has focused on Atlantic salmon in net pen culture in Northwest Europe. Jumping in salmonids is a heterogeneous behavioral category with diverse functional outcomes. Additional research is needed from broad perspectives spanning indigenous and institutional science, cultural wisdom, and ethological direct observation. In theory and in practice, it is interesting that some salmonid jumping behavior may be a form of play.

Keywords: fish jumping; play behavior; pleasure in animals

tobu ayu no soko ni kumo yuku nagare kana ayu jump and beneath them flow the moving clouds Onitsura (1661–1738)

1. Introduction

Jumping (termed leaping by some authors) is a familiar behavior in fishes (e.g., [1] (pp. 194–195), [2–5], [6] (pp. 98–99). Jumping in immature and adult salmonids is well known (e.g., [1] (pp. 194–195), [7] (p. 175), [8] (p. 136), [9] (p. 143)). It is important in practical fish culture and management, especially in the control of sea lice [10–19] and in fishway design [20–24].

The key concept of organism-environment interaction [25] is well illustrated by salmonid ecology. In salmon ecosystems, fish, forests, interconnected waterbodies extending from glaciers and icefields to the open ocean, mycorrhizal fungi, nitrogen-fixing bacteria, myriad single-celled and multicellular species, and humans are tightly and deeply interdependent [9,26–29]. The polyrhythms of life in moving fluids [30,31] are the drumbeat for this ecological dance [32].

Worldviews that recognize eco-centric values are widely acknowledged (e.g., [33]). They serve as a basis for informed critiques of the extreme reductionist views that flourished briefly in America and Western Europe during the late 20th century [34].

On the Northwest Coast of North America and throughout northern countries worldwide, salmonids and people have lived together for millennia [26–29,32]. The welfare of salmonids and the

welfare of people are tightly linked [26–29,32]. There is a need for general theoretical treatments of salmonid culture and welfare in broad ecological contexts, as well as for practical studies that can enhance population and stock survival and sustainable harvests. Humanely ensuring survival and sustainability is equally important for salmonids and their habitats, for traditional cultures, for fishing families, and for aquaculture enterprises.

2. Materials and Methods

The materials used in this paper include traditional ecological and cultural knowledge, scientific literature, personal communications from experienced salmonid biologists, and personal experience in Alaska, Yukon, and the Pacific Northwest. The traditional ecological knowledge of Alaska, Yukon, and Pacific Northwest salmon peoples continues to inform the cultural and intellectual life of the entire region. North American ecological and environmental thought are indebted to indigenous science. The scientific study of salmon jumping is an opportunity to participate in the material and methodological convergence [35] of indigenous and Western institutional science. It also opens perspectives on broader issues of salmonid culture, welfare, and awareness.

3. Results

3.1. Descriptive Ethology of Salmon Jumps

The ethology of these jumps is well defined and clearly differentiated from the surface rolls and oriented stream ascent leaps that salmon also perform. When an Atlantic salmon (*Salmo salar*) in a net pen [4] or a Pacific salmon (*Oncorhynchus* sp.) in its natural habitat ([1] (pp. 194–195), [7] (p. 175), [8] (p. 136)) jumps from the water, it may perform one or more lateral body flexions during its ascent to a height above the water of one or more body lengths and again during its descent. The fish frequently land on their side and make an audible splash as they reenter the water. The "characteristic leaping behaviour" of pink salmon begins with a "forward leaping motion" followed by a lateral rotation that causes the fish to fall on its side or back, and "a rapid series of jumps by the same fish often takes place" [8] (p. 136).

3.2. Sea Lice, Net Pens, and Atlantic Salmon Jumps

Sea lice (*Lepeophtheirus salmonis* and *Caligus* spp.) are parasitic crustaceans (Siphonostomata: Caligidae). They represent a challenge to the net pen culture of Atlantic salmon [4,17–19]. An ingenious control scheme for this parasite [4] exploits the natural tendency of Atlantic salmon to jump out of the water. To facilitate the control of sea lice, net pen fish are induced to jump through a surface film that contains a chemical treatment that kills the lice. The natural frequency of spontaneous jumps in Atlantic salmon is low (~1 jump per individual per 2 h [4]). For this reason, managers have studied salmon jumping. Their goal is to identify factors that can be manipulated to increase the jumping frequency and, therefore, the effectiveness of the treatment regime.

3.3. Why do Salmonids Jump?

Away from work and sometimes even at work, fisheries professionals and recreational fishers often discuss the possible reasons that salmon jump. As one reviewer noted, biologists frequently go salmon fishing after work, and the highlight of most fishing stories back in camp is the vigor with which a hooked salmon leapt.

Jumping may serve to loosen egg skeins; dislodge ectoparasites; evade predators; reduce perceived crowding; communicate with conspecifics; avoid supersaturated, turbulent, hyposaline and/or turbid water; and/or refill the swim bladder with air. All of these functional hypotheses are open to discussion and investigation. For example, F.A. Beach [36] proposed that jumping functions to remove ectoparasites because he opposed the idea that fish jumping might sometimes represent play

behavior. Burghardt [3] more recently marshaled new information and deployed clearer reasoning to criticize this argument.

In the Tlingit culture of southeast Alaska, tradition offers specific insights into salmon jumping. An indigenous perspective mentioned to non-Natives by elders and culture-bearers is that a salmon jumps for the same reason that a person stands up in a boat to better see the surrounding waters and land. This hypothesis, based on indigenous science, that jumping in Pacific salmon can function to facilitate above-water visual orientation in space could productively be tested in field and experimental trials. In the Tlingit language [37,38], one of the meanings of the verb root \sqrt{TAAN} is "to jump (fish)" [38]. It would be interesting to consider other traditional cultures both on the Pacific Coast and worldwide to find traditions and linguistic terms that applied to salmon jumping.

It is also possible that some instances of salmon jumping are best categorized as play behavior. Dennis Dobson, a veteran Pacific Northwest fishing guide and outdoor journalist, argues that jumping in the fish he has observed over decades in the wild can be plausibly interpreted as play [39]. His arguments rely on extensive direct observations and experience, and his descriptions appear to fall within the scope of current scientific definitions of play. Dobson's interpretation, like other plausible hypotheses about salmon jumping, seems scientifically credible. The method of multiple working hypotheses [40] furnishes a fruitful methodological and philosophical basis for testing hypotheses about salmon jumping.

4. Discussion

That play behavior is by no means restricted to warm-blooded vertebrates has become increasingly evident. Play (including several instances of jumping, though not in salmonids) is now well documented in fishes [3], [6] (p. 94–98). Jennifer Nielsen [3] (p. 148) observed a possible instance of movement play (not involving jumping) resembling adult redd-digging behavior in juvenile coho salmon (*Oncorhynchus kisutch*). In fact, vertical leaps are a paradigmatic instance of play in nonhuman species [41]. As one referee informatively stated, "jumping for joy" is a timeless expression: Duke Ellington not surprisingly "jumped for joy" when he left Cotton Isle. So did Kingfish (Bob Weir and company) when they were "coming back to 'Frisco". Baby Roo, Tigger, and Pooh jumped for joy often.

For additional discussions of animal play behavior, see, e.g., [3,41–43].

Burghardt [3,44,45] proposed an open, inclusive definition of play. His definition has a sound basis in classical continental European ethology (e.g., [46]) and has been well received by ethologists and zoologists. Furthermore, Burghardt, Dinets and colleagues [47] have substantially enlarged the empirical basis for the belief that play behavior occurs in fishes. In turn, Marc Bekoff [48,49] has placed these and other observations in a broad ethical context relating play to animal awareness, suffering, and pleasure, and to natural principles of fairness in animal communication and sociality. (See also [50,51].)

Current views of the deep ecology of salmonids (e.g., [9]) cite holistic perspectives. Tlingit people might well recognize echoes of their own Raven ecology in these latter-day views. John Muir first encountered this traditional indigenous and ancient science of natural balance and harmony in nature when he visited Tlingit elders Daanaawaak and Lunaat' in Alaska's Chilkat-Chilkoot country. During his few days' visit with them and their people in a Tlingit village near present-day Haines, Alaska, John Muir learned the ecology lesson he would never forget [52,53]. Muir's ecological reeducation in Tlingit country would eventually influence society. Muir's ecological ideas and environmental activism grew organically from indigenous Tlingit and additional Native Alaskan and First Nations sources, spurring later mainstream North American scientific ecology and philosophical and practical environmentalism. For example [54–56], environmental ethicist and freshwater salmonid biologist J.J. Piccolo spent years with Native Americans and Alaskan Natives as a fisheries scientist on their traditional lands. He later insightfully integrated this experience with the work of scholars such as Aldo Leopold and Holmes Rolston, who had also been influenced by the Daanaawaak-Lunaat'-Muir tradition.

Alaska fisheries researcher Nicholas F. Hughes contributed paradigmatic insights into the ecology of salmonids in moving water. He provided a general framework within which ecological interactions among fish in flowing water might be profitably explored [57–59]. Reasoning based on this framework has spurred a fecund theoretical perspective termed Net Energy Intake Theory. The theory has shed light on several aspects of salmonid cognitive/social behavior, including social learning for foraging and recognition of familiar partners [60,61]. In immature salmon, the perceptual, cognitive, and sensory-locomotor salience of water streaming from hoses and pipes and splashing from buckets is a developmental and ecological puzzle. Clearly, however, considering the pervasiveness of organism-environment interactions shaped by moving water, the development of behavioral flexibility and cognitive-motor strengths and skills involving the physics and dynamics of life in moving fluids could be important for behavioral and cognitive development in salmonids beginning in early ontogeny. Indeed, species, stock, population, or strain differences having ecological, aquacultural, and welfare implications could be investigated, as each salmonid species, stock, or strain can experience different contrasting and varying flow regimes throughout its life cycle (e.g., [1,8,62]). In several mammalian species, play increases subsequent survival or components of survival such as physical capacity [63–67]. Whether play confers such benefits in nonmammalian taxa is not yet known. Subjectively, a stream of water might well represent an exciting sensorimotor and aesthetic property of the environment to a young salmonid (in the sense of Darwinist aesthetics [68]) as well as an ecologically salient feature that might stimulate it to leap repeatedly with no immediate ulterior purpose.

5. Conclusions

Jumping play in salmonids is of potential interest as a measure of well-being and as a potential component of survival and fitness. Whether salmonid play necessarily implies the ability to experience pleasure and to suffer and/or constitutes indirect evidence for consciousness may be a challenging question for the future.

Acknowledgments: John J. Piccolo, Roger Harding, Daanaawaak (Austin Hammond), Dan Henry, Koolyeikh (Roby Littlefield), Xh'unei (Lance Twitchell). I thank the three referees of this manuscript and the Editors for their assistance. Alaskan fishing families, especially the Chris McDowell, Tom Brayton, and Joyanne Bloom families, helped me learn about Alaska fisheries in ways that I would never have known as an academic fisheries scientist. The descendants of Lunaat' and of the Jacquot brothers in Haines, Wells, Klukwan and Juneau, "children of noble grandparents" including the first author of [35] and her extended family, honored me with traditional and modern stories from their Tlingit and French-Alsatian heritage, cultural wisdom, and inspiration. *Gunalchéesh* and *vielmohls mersi*.

Conflicts of Interest: The author declares no conflict of interest.

References

- 1. Berg, L.S. *Freshwater Fishes of the USSR and Adjacent Countries;* Tr. Ronen, O., Ed.; Israel Program for Scientific Translations: Jerusalem, Israel, 1962; Volume 1.
- Uchida, K.; Tsukamoto, K.; Kajihara, T. Effects of environmental factors on jumping behavior of the juvenile ayu *Plecoglossus altivelis* with special reference to their upstream migration. *Nippon Suisan Gakkaishi* 1990, 56, 1393–1399. [CrossRef]
- 3. Burghardt, G. The Genesis of Animal Play: Testing the Limits; MIT Press: Cambridge, MA, USA, 2005.
- Dempster, T.; Kristiansen, T.S.; Korsøen, Ø.J.; Fosseidengen, J.E.; Oppedal, F. Technical note: Modifying Atlantic salmon (*Salmo salar*) jumping behavior to facilitate innovation of parasitic sea lice control techniques. *J. Anim. Sci.* 2011, *89*, 4281–4285. [CrossRef] [PubMed]
- 5. Prenosil, E.; Koupal, K.; Grauf, J.; Schoenebeck, C.; Hobuck, W.W. Swimming and jumping ability of 10 Great Plains fish species. *J. Freshw. Ecol.* **2016**, *31*, 123–130. [CrossRef]
- 6. Balcombe, J. *What a Fish Knows: The Inner Lives of our Underwater Cousins;* Scientific American/ Farrar, Straus and Giroux: New York, NY, USA, 2016.
- Pravdin, I.F. Ocherk zapadno-kamchatskyogo rybolovstva. *Izv. Tikhookean. Nauchnopromysl. Stantsii* 1928, *I*, 169–259.

- Heard, W.R. Life history of pink salmon (*Oncorhynchus gorbuscha*). In *Pacific Salmon Life Histories*; Groot, C., Margolis, L., Eds.; University of British Columbia Press: Vancouver, BC, Canada, 1991; pp. 119–230.
- 9. Stokes, D.; White, D. *The Fish in the Forest: Salmon and the Web of Life;* University of California Press: Berkeley, CA, USA, 2014.
- 10. Fernö, A.; Huse, I.; Juell, J.-E.; Bjordal, Å. Vertical distribution of Atlantic salmon (*Salmo salar* L.) in net pens: Trade-off between surface light avoidance and food attraction. *Aquaculture* **1995**, *132*, 285–296.
- Birkeland, K.; Jakobsen, P.J. Salmon lice, *Lepeophtheirus salmonis*, infestation as a causal agent of premature return to rivers and estuaries by sea trout, *Salmo trutta*, juveniles. *Enviorn. Biol. Fishes* 1997, 49, 129–137. [CrossRef]
- Wells, A.; Grierson, C.E.; MacKenzie, M.; Russon, I.J.; Reinardy, H.; Middlemiss, C.; Bjørn, P.A.; Finstad, B.; Bonga, S.E.W.; Todd, C.D.; et al. Physiological effects of simultaneous, abrupt seawater entry and sea lice (*Lepeophtheirus salmonis*) infestation of wild, sea-run brown trout (*Salmo trutta*) smolts. *Can. J. Fish. Aquat. Sci.* 2006, 63, 2809–2821. [CrossRef]
- 13. Dempster, T.; Juell, J.E.; Fredheim, A.; Lader, P.; Fosseidengen, J.E. Behaviour and growth of Atlantic salmon (*Salmo salar*) in sea-cages subjected to short-term submergence. *Aquaculture* **2008**, 276, 103–111. [CrossRef]
- Dempster, T.; Korsoen, Ø.; Oppedal, F.; Folkedal, O.; Juell, J.E. Submergence of Atlantic salmon (*Salmo salar*) in sea-cages: A potential short-term solution to poor surface conditions. *Aquaculture* 2009, 288, 254–263. [CrossRef]
- Korsøen, Ø.J.; Dempster, T.; Fjelldal, P.G.; Oppedal, F.; Kristiansen, T.S. Long-term culture of Atlantic salmon (*Salmo salar* L.) in submerged cages during winter affects behaviour, growth and condition. *Aquaculture* 2009, 296, 373–381. [CrossRef]
- Korsøen, Ø.J.; Fosseidengen, J.E.; Kristiansen, T.S.; Oppedal, F.; Bui, S.; Dempster, T. Atlantic salmon adapt rapidly to re-fill their swim bladders in an underwater air filled dome. *Aquacult. Eng.* 2012, *51*, 1–6. [CrossRef]
- 17. Bui, S.; Oppedal, F.; Korsøen, Ø.; Dempster, T. Modifying Atlantic salmon behavior with light or feed stimuli may improve parasite control techniques. *Aquacult. Environ. Interact.* **2013**, *3*, 125–133. [CrossRef]
- 18. Bui, S. The Behavioural Resistance and Response of Atlantic Salmon to the Ectoparasite *Lepeophtheirus Salmonis*. Ph.D. Thesis, School of BioSciences, University of Melbourne, Melbourne, Australia, 2016.
- Dempster, T.; Bui, S.; Stien, L.; Oppedal, F. Effects of the cage-based "snorkel" sea lice barrier technology on Atlantic salmon growth, condition and behaviour. In *The Behavioural Resistance and Response of Atlantic Salmon to the Ectoparasite Lepeophtheirus Salmonis*; School of BioSciences, University of Melbourne: Melbourne, Australia, 2016; pp. 145–167.
- 20. Clay, C.H. Design of Fishways and Other Fish Facilities; CRC Press: Boca Raton, FL, USA, 1994.
- 21. Lauritzen, D.V.; Hertel, F.; Gordon, M.S. A kinematic examination of wild sockeye salmon jumping up natural waterfalls. *J. Fish Biol.* **2005**, *67*, 1010–1020. [CrossRef]
- Lauritzen, D.V.; Hertel, F.S.; Jordan, L.K.; Gordon, M.S. Salmon jumping: Behavior, kinematics and optimal conditions with possible implications for fish passageway design. *Bioinspir. Biomim.* 2010, *5*, 035006. [CrossRef] [PubMed]
- 23. Mueller, R.P.; Southard, S.S.; May, C.W.; Pearson, W.H.; Cullinan, V.I. Juvenile coho salmon leaping ability and behavior in an experimental culvert test bed. *Trans. Am. Fish. Soc.* **2008**, *137*, 941–950. [CrossRef]
- 24. Kondratieff, M.C.; Myrick, C.J. How high can brook trout jump? A laboratory evaluation of brook trout jumping performance. *Trans. Am Fish. Soc.* **2006**, *135*, 361–370. [CrossRef]
- 25. Lewontin, R.C. Organism and environment. In *Learning, Development and Culture;* Plotkin, H.C., Ed.; Wiley: New York, NY, USA, 1982; pp. 151–170.
- 26. Dauenhauer, N.M.; Dauenhauer, R. (Eds.) *Haa Shuká, Our Ancestors*; University of Washington Press: Seattle, WA, USA; Sealaska Heritage Foundation: Juneau, AK, USA, 1987.
- 27. Wolf, E.C.; Zuckerman, S. Salmon Nation; Oregon State University Press: Corvallis, OR, USA, 2003.
- 28. Thornton, T.F. *Being and Place among the Tlingit*; University of Washington Press: Seattle, WA, USA; Sealaska Heritage Foundation: Juneau, AK, USA, 2008.
- 29. Bloom, L.; Van Vactor, N.; Behnken, L. If Alaska's leaders put "fish first", we'll prosper for generations. *Alaska Dispatch News*; Anchorage, Alaska, 16 January 2016. Available online: https://www.adn.com/author/ lindsey-bloom/ (accessed on 3 March 2017).
- 30. Vogel, S. Behavior and the physical world of an animal. Persp. Ethol. 1981, 4, 179–198.

- 31. Vogel, S. *Life in Moving Fluids: The Physical Biology of Flow,* 2nd ed.; Princeton University Press: Princeton, NJ, USA, 1996.
- 32. Hayes, E. Blonde Indian; University of Arizona Press: Tucson, AZ, USA, 2006.
- 33. Washington, H.; Taylor, B.; Kopnina, H.; Ayer, P.; Piccolo, J.J. A Statement of Commitment to Ecocentrism. Available online: http://www.ecologicalcitizen.net/statement-of-ecocentrism.php (accessed on 6 May 2017).
- 34. Callicott, J.B. *Thinking Like a Planet: The Land Ethic and the Earth Ethic;* Oxford University Press: New York, NY, USA, 2013.
- 35. Ewing, L.; Fagen, B.; Gehring, B.; Symons, R. Convergence; Dream Farm Press: Juneau, AK, USA, 2016.
- 36. Beach, F.A. Current concepts of play in animals. Am. Nat. 1945, 79, 523–541. [CrossRef]
- 37. Edwards, K. Dictionary of Tlingit; Sealaska Heritage Institute: Juneau, AK, USA, 2009.
- 38. Twitchell, L. (Ed.) *Tlingit Dictionary;* University of Alaska Southeast and Goldbelt Heritage Foundation: Juneau, AK, USA, 2017.
- Dobson, D. Why Fish Jump. Available online: http://www.bigfishtackle.com/fishing_articles/Regional_ Fishing/United_States_Fishing_Articles/Oregon_Fishing_Articles/Why_Fish_Jump_457.html (accessed on 9 May 2017).
- 40. Chamberlin, T.C. The method of multiple working hypotheses. *Science* **1965**, *148*, 754–759. [CrossRef] [PubMed]
- 41. Fagen, R. Animal Play Behavior; Oxford University Press: New York, NY, USA; Oxford, UK, 1981.
- 42. Pellis, S.; Pellis, V.C. The Playful Brain; Oneworld Publications: London, UK, 2009.
- 43. Bateson, P.; Martin, P. *Play, Playfulness, Creativity and Innovation*; Cambridge University Press: Cambridge, UK, 2013.
- 44. Burghardt, G.M. Defining and recognizing play. In *The Oxford Handbook of the Development of Play;* Pellegrini, A.D., Ed.; Oxford University Press: New York, NY, USA, 2011; pp. 9–18.
- 45. Burghardt, G.M. A brief glimpse at the long evolutionary history of play. *Anim. Behav. Cogn.* **2014**, *1*, 90–98. [CrossRef]
- 46. Meyer-Holzapfel, M. Das Spiel bei Säugetieren. Handb. Zool. Berl. 1956, 8, 1–36.
- 47. Burghardt, G.M.; Dinets, V.; Murphy, J.B. Highly repetitive object play in a cichlid fish (*Tropheus duboisi*). *Ethology* **2015**, *121*, 38–44. [CrossRef]
- 48. Bekoff, M. Why Dogs Hump and Bees Get Depressed; New World Library: Novato, CA, USA, 2013.
- 49. Bekoff, M.; Pierce, J. *The Animals' Agenda: Freedom, Compassion and Coexistence in the Human Age;* Beacon Press: Boston, MA, USA, 2017.
- 50. Balcombe, J. Animal pleasure and its moral significance. *Appl. Anim. Behav. Sci.* 2009, 118, 208–216. [CrossRef]
- 51. Safina, C. Beyond Words: What Animals Think and Feel; Henry Holt and Co.: New York, NY, USA, 2015.
- 52. Heacox, K. John Muir and the Ice that Started a Fire; Lyons Press: Guilford, CT, USA, 2014.
- 53. Henry, D. Across the Shaman's River; University of Alaska Press: Fairbanks, AK, USA, 2017.
- Piccolo, J.J.; Hughes, N.F.; Bryant, M.D. Water velocity influences prey detection and capture by drift-feeding juvenile coho salmon (*Oncorhychus kisutch*) and steelhead (*Oncorhynchus mykiss irideus*). *Can. J. Fish. Aquat. Sci.* 2008, 65, 266–275. [CrossRef]
- 55. Piccolo, J.J. Stoking the "green fire": Bringing the land ethic to the water. *Fisheries* **2012**, *37*, 516–518. [CrossRef]
- Piccolo, J.J. Intrinsic values in nature: Objective good or simply half of an unhelpful dichotomy? *J. Nat. Cons.* 2017, 37, 8–11. [CrossRef]
- 57. Hughes, N.F. Ranking of feeding positions by drift-feeding Arctic grayling (*Thymallus arcticus*) in dominance hierarchies. *Can. J. Fish. Aquat. Sci.* **2008**, *49*, 1994–1998. [CrossRef]
- Hughes, N.F. Selection of positions by drift-feeding salmonids in dominance hierarchies: Model and test for Arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, interior Alaska. *Can. J. Fish. Aquat. Sci.* 2008, 49, 1999–2008. [CrossRef]
- 59. Hart, P.J.; Bergman, E.; Calles, O.; Eriksson, S.; Gustafsson, S.; Lans, L.; Österling, M. Familiarity with a partner facilitates the movement of drift foraging juvenile grayling (*Thymalus thymallus*) into a new habitat area. *Enviorn. Biol. Fishes* **2014**, *97*, 515–522. [CrossRef]
- 60. White, S.L.; Gowan, C. Brook trout use individual recognition and transitive inference to determine social rank. *Behav. Ecol.* **2013**, *24*, 63–69. [CrossRef]

- 61. White, S.L.; Gowan, C. Social learning enhances search image acquisition in foraging brook trout. *Environ. Biol. Fishes* **2014**, *97*, 523–528. [CrossRef]
- 62. Smirnov, A.I. *Biologiya, Razmnozhenie i Razvitie Tikhookeanskikh Lososei;* Moscow State University Press: Moscow, Russia, 1975.
- 63. Fagen, R.; Fagen, J. Juvenile survival and benefits of play behavior in brown bears, *Ursus arctos. Evol. Ecol. Res.* **2004**, *6*, 89–102.
- 64. Cameron, E.Z.; Linklater, W.L.; Stafford, K.J.; Minot, E.O. Maternal investment results in better foal condition through increased play behaviour in horses. *Anim. Behav.* **2008**, *76*, 1511–1518. [CrossRef]
- 65. Fagen, R.; Fagen, J. Play behavior and multi-year juvenile survival in free-ranging brown bears, *Ursus arctos*. *Evol. Ecol. Res.* **2009**, *11*, 1–15.
- 66. Lee, P.C.; Moss, C.J. African elephant play, competence and social complexity. *Anim. Behav. Cogn.* **2014**, 2, 144–156. [CrossRef]
- 67. Théoret-Gosselin, R.; Hamel, S.; Côté, S.D. The role of maternal behavior and offspring development in the survival of mountain goat kids. *Oecologia* 2015, *178*, 75–86. [CrossRef] [PubMed]
- Fagen, R. Play, five evolutionary gates, and paths to art. In *Play: An Interdisciplinary Synthesis (Play and Culture Studies, Volume 6)*; McMahon, F.F., Lytle, D.E., Sutton-Smith, B., Eds.; University Press of America: Lanham, MD, USA, 2004; pp. 213–238.



© 2017 by the author. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).