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# Novel life history tactic observed in fall-run Chinook Salmon

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Life history diversity allows species from bacteria to trees to persist through disturbance and competition (Cole 1954). Diversifying risk through various life history strategies across space and time maintains genetic diversity, population persistence, and range and habitat expansion. Here, we observed for the first time, a novel life history tactic in age 1 (~ 1 yr post fertilization) Chinook salmon (*Oncorhynchus tshawytscha*), attempting to spawn in the wild alongside large adult (3 yr old) fish that returned from the ocean (Fig. 1). Pacific salmon (*Oncorhynchus* spp.) have plastic life history tactics that depend on genotype and environmental conditions (Taylor 1990, Gross 1991, Quinn 2005, Bourret et al. 2016). Environmental conditions that dictate these tactics are often associated with growth by a specific time of the year and include factors such as latitude, water temperature, parental spawn timing, nutrients, and food source (Taylor 1990). A "decision" on which tactic to pursue likely happens annually when salmon either remain in freshwater, migrate to the ocean, return to freshwater to spawn, or remain in the ocean for another year (Bourret et al. 2016).

Chinook salmon juveniles typically express one of two life history tactics across populations: migrate to the ocean during their first year (ocean type) or remain in freshwater and emigrate during the second year or later (stream type; Quinn 2005). Juveniles that remain in freshwater may also express a third life history tactic, maturation during their second summer as age 2 parr to spawn with returning adults from the ocean, sometimes referred to as precocious parr or microjacks (Quinn 2005). There is also a fourth tactic, where male parr mature in their first summer in their natal stream and spawn with returning adults. This fourth tactic has not been directly observed in the wild before now; instead, it has been described through circumstantial evidence of mature juveniles or mortalities during spawning surveys (Rutter 1903, Rich 1920, Gebhards 1960, Flain 1970, Mullan et al. 1992, Johnson et al. 2012).

For this study, snorkel surveys were conducted in the Shasta River, California over a six-year period from 2006 to 2012. During these surveys, mature Chinook salmon parr (age-1; ~1 yr post fertilization) were observed spawning for the first time in the wild. Although the majority of the Chinook salmon leave as age-0 fry during the spring, approximately 4% of juvenile Chinook salmon remained in the Shasta River throughout the summer months (California Department of Fish and Wildlife, *unpublished mark–recapture data*). A portion of the fish that remained apparently matured and spawned with large adult females after their first summer and without leaving their natal stream. To better understand how mature parr were spawning, underwater cameras were placed adjacent to active redds and approximately 400 min of recordings were made. During snorkel surveys, the most parr observed at a single redd was two, but from the video footage, as many as four parr were present in or near a single redd while spawning activities were taking place. A hierarchy was often observed among mature parr near the redd. A dominant parr, generally the largest, would chase other parr away when they would attempt to enter the redd. After chasing subordinate parr away, the dominant parr would return to

Fig. 1. Photo of a wild mature male Chinook salmon parr expressing milt.

the center of the redd. This behavior was very similar to that of the adult male salmon in and near the same redd. Large males ignored the parr except for rare times where the adult would chase a parr out of the redd, only to let him immediately return with no further response. The dominant parr was generally found directly underneath or behind the dominant male. When the dominant adult would chase other adult males from the redd, the parr would remain and the adult would return to above the parr in the middle of the redd behind the female. In contrast, when juvenile steelhead entered a redd, the adult would chase them off immediately.

On several occasions, parr would vibrate alongside the female similar to adult males in an apparent attempt to stimulate egg deposition. Observation of egg fertilization by parr was not possible because as many as eight adult males surrounding a single female. When the female would begin to drop eggs, all males in the local vicinity would surround her. When this happened, parr would join the rest of the males to position themselves to fertilize eggs. However, mature parr can be observed spawning after the adult males leave. At that time, the mature parr remain under the female and appear to be releasing milt with a rigid body position and gaped mouth similar to when adult males release milt (Video S1). The location of the parr directly under the spawning female salmon suggest that they are not feeding on eggs or dislodged invertebrates as optimal location for these food resources would be downstream of the spawning adults.

Spawning behavior of mature parr in this study was very similar to that of returning adult males. During all of these behaviors, almost no aggression was shown toward the mature parr by the dominant adult male in the redd. Interestingly, the mature parr may actually be competing for reproduction, yet that does not appear to be recognized by the adult male. Mature Chinook salmon parr in hatchery settings produced viable offspring, so it is assumed that these parr are likely competing for fertilization of the eggs (Robertson 1957, Unwin 1997). It is unknown why the mature parr are basically ignored by the dominant male, because steelhead of similar size to the mature parr were chased out of the redd immediately by the dominant adult male salmon.

Physical conditions within aquatic environments dictate the growth potential for organisms that reside within streams and rivers. The unique water chemistry and consistent temperature of springs in Shasta River were likely the largest contributing factors to high growth rates and early maturation. Ancient marine sediments overlain by volcanic rock in the Shasta Valley provide nitrogen and phosphorus that is incorporated into the groundwater that eventually emerges in the Big Springs Complex (Nathenson et al. 2003). In addition to enhancing nutrient availability in the Shasta River, the large groundwater inputs strongly buffer water temperatures. This moderation of stream temperatures maintains conditions in a more biologically advantageous range for juvenile Chinook salmon.

Growth in freshwater is likely the largest factor in maturation of Chinook salmon parr during the first year, although genetic predisposition may also contribute (Clarke and Blackburn 1994). Observation of mature parr in the wild has generally been associated with spring-fed systems that allow for rapid development while eggs are still in the redd due to relatively warm winter water temperatures (Rutter 1903, Rich 1920, Gebhards 1960). Age-0 Chinook salmon PIT tagged (passive integrated transponder for unique individual identification) and recaptured in the Big Springs Complex grow an average of 0.50 mm/d during the spring and summer months, compared to 0.17 mm/d for the adjacent surface water-fed Scott River (California Department of Fish and Wildlife 2008, *unpublished data*). These conditions allow for early emergence and hatched fry were captured in the Shasta River rotary screw trap as early as 16 January and thus provides more time for growth and maturation during the first year in fresh water before adults return from the ocean in September and October. Spring-fed systems also provide constant water temperatures, providing high-quality growing conditions for rearing fry/parr. It is these conditions, constant temperature and abundant food causing high growth rates that likely cause early maturation in the hatchery environment (Larsen et al. 2006). By providing stable water temperatures, abundant nutrients, and a highly abundant food source of up to 80,000 invertebrates/m$^2$ (Jeffres et al. 2009), the Shasta River meets all of the criteria to produce mature parr.

Future work should focus on determining if the mature male parr are in fact successful at fertilization and producing viable offspring. Investigations into competition between parr and adult milt may help to assess contributions that mature male parr have to the population. With recent genetic advances, testing reproductive success using parental based genetic tagging (e.g., RAPTURE; Ali et al. 2016) could provide a whole population genetic assignment if all adult fish were sampled at an adult weir and non-assigned juveniles could then be attributed to mature parr. If indeed these mature parr are contributing significantly to the population, this life history tactic may be a mechanism to stabilize declining populations, particularly in systems where migrations are long and migratory conditions unpredictable due to anthropogenic habitat alteration and climatic conditions. Maturation during the first year may also help to ameliorate potential reduced recruitment by increasing intra-cohort genetic diversity. Determining if wild mature male parr survive spawning, as observed in the hatchery environment (Robertson 1957, Unwin et al. 1999), is also important. If parr do indeed survive in the wild after spawning, it would overturn the traditional thinking that Pacific salmon only spawn during a single event and die afterward, these mature parr may indeed be contributing more than once to the population.

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