

important to promote fetal brain growth during gestation [20]. While T4 is the most abundant thyroid hormone, it is directly converted to T3, which has many times the biological activity of T4 [20,21]. T3 levels are relatively slow to change when food shortages are first encountered, allowing the body to use all available fuel to search for food. If poor food conditions persist, T3 abruptly declines, lowering metabolism to prevent the body from exhausting its remaining fuel stores [21–24]. T3 may also be blunted under good food conditions when a low metabolism is needed to increase growth (e.g., to accumulate blubber stores in fall, in preparation for the relatively lean winter; [20]). In dolphins, T3 is lower in failed versus successful pregnancies at all stages of gestation [25]. T3 is relatively unresponsive to disturbance stress.

This study uses temporal patterns in P4 and T to predict pregnancy outcomes among the SRKWs and T3, GC and the T3/GC ratio to index the importance of nutritional and other stressors in their reproductive decline.

1.1 SRKW natural history

Mean reproductive maturity (age at first conception) in female SRKWs occurs at 9.8 years of age in captivity 12.1 years in the wild [10,26]. Maximum fecundity (probability of becoming pregnant in a single estrous cycle) of SRKW occurs between ages 20–22, increasing quickly during the first four years after sexual maturity, slowly declining from age 22 to 39, and then precipitously declining thereafter [4,10]. Gestation is approximately 18 months, making the prior year's salmon availability particularly important to fecundity [11,27].

During our late May through October study period, the SRKWs primarily feed on Chinook salmon, increasingly dominated by Fraser River Chinook (FRC) returning to spawn in nearby rivers [28,29]. SRKWs generally spend the remainder of the year outside the Salish Sea, moving up and down the Pacific Coast, from CA to Southeast AK [6]. K and L pods tend to spend more time further south than does J pod in winter, while J pod frequents the Salish Sea more than does K and L pods in summer and winter. Nutritional demands on SRKW are presumed to be greatest in winter when their salmonid prey are more widely dispersed, smaller in size and other non-salmonid prey appear to be a larger fraction of the diet [6,29,30]. Thermoregulatory demands may also influence nutritional demands during winter. SRKW then transition to spring, eventually subsisting on a diminishing number of spring/summer run adult Chinook salmon approaching river mouths inside and outside the Salish Sea until the Fraser River Chinook (FRC) runs peak in mid- to late-August.

Temporal patterns in fecal GC and T3 concentrations [5], combined with radio-tagging data [28], suggest that early spring interior race Columbia River Chinook (CRC) runs are also important to SRKW nutrition. The CRC run increases from mid-March to the end of May based on estimates at the Bonneville dam [31] and have some of the highest fat content of any adult salmon to support their extremely long freshwater spawning migration [32,33]. Foraging on the fat rich Columbia River Chinook in early spring was hypothesized to replenish the killer whales after the long winter and sustain them until the temporally and quantitatively variable mid to late August peak in Fraser River Chinook (FRC) occurs (S1 Fig). T3 concentrations in fecal samples collected between 2007 and 2009 were consistently at their highest when the SRKW first arrived in the Salish Sea in late spring [5]. Presumably, this occurred because the whales arrived after feeding on the fat rich Columbia River Chinook. SRKW were detected twice as frequently at the Columbia River in early spring than expected by chance [28]. This argument is further supported by increases in serum thyroid stimulating hormone, T4 and T3 in fasting humans and rats in response to leptin injections [20]. With FRC runs still quite low, T3 levels then fell precipitously. GC concentrations when the SRKWs first arrive in the Salish Sea in late spring were also relatively high, further reflecting the comparatively low FRC