



Life History Variation and Salmonid Conservation

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To apply the conservation principle that weak salmon stocks should not be exploited, one must be able to separate stocks in mixed fisheries. The methods of Genetic Stock Identification (GSI) (Brodziak et al. 1992) are especially appropriate for separation of stocks. Results of a blind test of GSI using allozyme methods to separate mixtures by their genetic composition show errors of less than 4%. The value of GSI is to increase future options: at the end of less than 4%. The value of GSI is to increase future options: at the end of the management period there should be as many options available as at the start of the management period. This keeps the social contract (between management agencies, the public, and commercial fishers) viable. The economic value of GSI can be determined by considering a mixed stock fisher in which each stock follows its own stock-recruitment relationship. We then compare two situations: the first with GSI in which the composition of mixtures are recognized as they are being fished, and the second with no GSI in which the mixed stock is treated as if it were a single stock. The management criterion is to maximize a weighted sum of the catch over a finite period of time and the preservation value of the stock. For a two-stock situation, the value of GSI can be as large as 25% of the value of the fishery.

To understand the vulnerability of stocks we must focus on the life cycle and how actions affect the entire life cycle, not just a portion of it. This is based on the recognition that natural selection leads organisms to respond facultatively to their environment—often with unexpected results. Understanding the vulnerability of stocks is the dual recognition that biology is fundamentally nonlinear and that stages of life history are profoundly linked. Early salmonid conservationists recognized the importance of a focus on the life cycle (e.g., Clark 1928). A few conservation acts such as the Marine Mammal Protection Act (ca. 1970) and the Convention for the Conservation of Antarctic Marine Living Resources (ca. 1980) stress ecosystem considerations. The organismal equivalent of an ecosystem consideration is the life cycle (Bonner 1993).

I illustrate the life history approach by considering two examples. The first is the ontogenetic niche shift: RIVER → ESTUARY → OCEANS, of which salmon are quintessential examples. A life history principle that is often invoked to understand the ontogenetic niche shift is “minimize mortality/growth.” This can be derived in the following way: X = parr size (weight or length), T = time at which critical size for smolting is reached, $m(x)$ = mortality rate when size is x , $g(x)$ = growth

rate when size is x . Assuming the mortality is minimized we find the behaviors such that

$$\min \int_0^T m(x(t))dt, \quad (1)$$

given that $(dx)/(dt) = g(x)$. If we set $dt = (dx)/(g(x))$ and let $x(0)$ = initial size and $x(T)$ = critical size, then we have

$$\min \int_{x(0)}^{x(T)} \frac{m(x)}{g(x)} dx. \quad (2)$$

That is, we predict at each size x , the fish minimizes $m(x)/g(x)$, i.e., mortality rate divided by growth rate. However, it is generally true that smolt and adult performance depend upon the actual size at smolting, not just whether or not it exceeds the critical size needed. That is, more than $m(x)/g(x)$ is involved. We must focus on the lifetime reproductive success associated with the ontogenetic niche shift.

The approach based on lifetime reproductive success can be illustrated by considering the timing of maturity. Let $W(y)$ = weight of the fish at the time of maturation in year y , $f(w)$ = fecundity of a fish of weight w , $s(w, y)$ = survival of a fish of weight w from year y to $y + 1$, and $w'(w)$ = weight of a fish at next year's maturation point, given that its current weight is w . We can determine $f(w)$ by considering the relationship between weight, gonadal mass G , and number of eggs N . The survival of eggs to $k(N, G)$ first feeding depends upon the resources per egg, i.e., on G/N and for fixed gonadal mass usually decreases as N increases. Thus, the expected number of offspring surviving to first feeding, $Nk(N, G)$ is a "domed" function of the number of eggs N and $f(w) = \max_N Nk(N, G)$ where \max_N means that the maximum over N is taken.

We can then consider the "optimal" life history (Mangel & Clark 1988) by letting $F(w, y)$ = maximum lifetime reproductive success for a fish of weight w in year y . $F(w, y)$ satisfies the dynamic iteration equation

$$F(w, y) = \max \{f(w); s(w, y)F(w'(w), y + 1)\} \quad (3)$$

The first term corresponds to maturation in the current year and the second term corresponds to delaying maturation for another year. This equation is solved backward in time, starting at a time of senescence Y with $F(w, Y) = 0$. We can find the optimal life history (pattern of maturation) and fitness surfaces (egg number, age at maturation) that can be used to assess the reproductive success of nonoptimal patterns of development.

However, egg size affects more than survival to first feeding. It can affect the entire suite of characters associated with offspring reproductive success including fecundity, embryo survival, alevin and fry size, and developmental patterns. To incorporate this component, we must thus change Eq. 3 to

$$F(w, y) = \max \{ \max_N Nk(N, g(w))F(w_1, 1); s(w, y)F(w'(w), y + 1) \}, \quad (4)$$

where w_1 is the weight at first feeding for an offspring from an egg mass of weight g in which N eggs are laid. Because of the presence of $F(w_1, 1)$ on the righthand side of this equation, it can no longer be solved in standard ways (Mangel et al. 1994). The offspring reproductive environment is now as important as the parental reproductive environment, so we must focus on the life cycle.

In summary, we must recognize that organisms are indeed variable, that this variability is not "noise," that much of the variability can be understood, and such understanding is needed for effective conservation.

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