

Ole Kristian Berg¹, Department of Zoology, Norwegian University of Science and Technology, N-7034 Trondheim, Norway

Milo D. Adkison², School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau Center for Fisheries and Ocean Sciences, 11120 Glacier Highway, Juneau, Alaska 99801

and

Thomas P. Quinn³, School of Fisheries, University of Washington, Box 357980, Seattle, Washington 98195

Bilateral Asymmetry, Sexual Dimorphism, and Nematode Parasites in Mature Male Sockeye Salmon *Oncorhynchus nerka*

Abstract

The extent of bilateral asymmetry of 310 mature male sockeye salmon (*Oncorhynchus nerka*) from 6 Alaskan populations was determined to investigate the relationship between fluctuating asymmetry in paired morphological characters and physical traits (body size and shape) that seem to signal male quality. There was marked variation within and among populations in body size and morphology (e.g., body depth), but no differences in the overall level of asymmetry were detected among the populations, nor between the two systems investigated (lakes Aleknagik and Iliamna). The counts or measurements of a number of the traits evaluated for asymmetry varied among populations, but most differences were attributable to population-specific variation in body size. The six populations exhibited marked similarities in the patterns of asymmetry. Three paired characters (length of pectoral fins, number of branchiostegals, and number of teeth) were directionally asymmetric, indicating a genetic basis for asymmetry rather than an environmental influence. Two other paired characters (ventral fin length and number of enlarged teeth) were bilaterally variable but not correlated with any attribute of male quality.

Based on the low variation between the different populations in level of asymmetry, we conclude that either stress does not influence asymmetry levels in sockeye salmon or that these populations are under similarly low levels of stress.

We also explored the relationship between biomass of a nematode parasite (*Philonema oncorhynchi*) and asymmetry. The weight of parasites was related to fluctuating asymmetry in the ventral fin length but was not related to fluctuating asymmetry in number of large teeth.

Introduction

There is an ever increasing demand for better understanding of biological diversity and its assessment and maintenance. In plants and animals bilaterally symmetric morphological characters demonstrate fluctuating asymmetry when symmetry is the rule and there is no tendency for the trait value of one side to be larger than that on the other side. The determination that bilateral symmetry is related to the developmental stability has provided a way to assess environmental impacts on the individual developmental programs in biological systems, complementing data from genetic surveys (Sarre et al. 1994; Alados et al. 1995; Wagner 1996; Møller 1996).

Deviations from bilateral asymmetry are common and are usually characterized by a frequency distribution of right (R) minus left (L) measurements (e.g. Palmer and Strobeck 1986). The three currently accepted forms of bilateral asymmetry are fluctuating asymmetry, characterized by a

normal distribution of the individual R-L values with a mean of zero, directional asymmetry, characterized with a mean significantly different from zero and antisymmetry, which arises as a genetic predisposition of an individual towards asymmetry, but without a specific bias to left or right. In the last case, the mean deviation of the individual R-L is zero, but the distribution is platykurtic (Palmer and Strobeck 1986; Palmer 1996).

Asymmetric features may have a negative effect on behavioral patterns associated with reproduction (e.g., Møller 1992a; Balmford and Thomas 1992; Balmford et al. 1993) thus reducing reproductive success, and asymmetry appears to have low heritability and appears largely to be caused by disruption of developmental processes (Clarke 1995).

Semelparous Pacific salmon (*Oncorhynchus* spp.) have a number of life history traits which make them favorable for tests of hypotheses of sexual dimorphism and mate choice. The lifetime

reproductive effort of individuals takes place over about 2-3 weeks at population-specific spawning sites. Maturation leads inevitably to death; postponement of resources to future reproduction is thus impossible. Salmon develop dramatic secondary sexual characters at maturity. The most conspicuous features are the extended snout with large teeth and the exaggerated dorsal hump of males. The salmon must invest energy to develop these features, and they may thus signal the male's energetic status or other indices of quality. These secondary sexual features are developed late in the life cycle with the limited energy resources acquired at sea and in conflict with other energetic demands as migration and gonad development. The extent of development of these features also varies among genetically distinct populations within species (Beacham 1985; Beacham and Murray 1987; Beacham et al. 1988; Blair et al. 1993).

Quinn and Foote (1994) reported that the size of certain sexually dimorphic features (body depth and, to a lesser extent, jaw length) was positively correlated with male social status and access to females, independent of body length in sockeye salmon *O. nerka* Walbaum. Body depth was closely correlated with condition factor (weight/length ratio) and the dorsal hump seems to be used in male-male displays. Jaw size, also correlated with condition factor, affects the male's ability to gape over a competitor, and thus the effectiveness of the jaws as a weapon. The development of the secondary sexual characteristics is rapid and takes place just prior to the spawning period. Fish with pronounced secondary characteristics may therefore either have a relatively large index of asymmetry due to inappropriate developmental resources or a relatively low value if indicators of sexual quality such as the size of sexual characteristics and level of asymmetry are correlated. No specific relationship between the size of secondary sexual characteristics and level of asymmetry can thus be predicted.

Hamilton and Zuk (1982) hypothesized that there is a negative correlation between parasite load and secondary sexual characteristics. No correlation was detected between the size of the secondary sexual characteristics of sockeye salmon and weight of the dominant parasite, a nematode *Philonema oncorhynchi* Kuitunen-Ekbaum in several Alaskan populations (Berg et al. 1995). However, the interrelationships between parasites,

asymmetry and secondary sexual characteristics were not explored. The purpose of this study was to assess the amount of asymmetry, primarily fluctuating asymmetry, of a number of populations of sockeye salmon from a relatively unpolluted and pristine area and correlate the asymmetry with parasite load and accepted predictors of male social status.

Methods

We compared indicators of male quality (the length of the male and the extent of development of secondary sexual characteristics), with the degree of asymmetry in several morphological traits in 310 male sockeye salmon from two oligotrophic Alaskan lakes, Lake Aleknagik and Iliamna Lake (Fig. 1). We also compared the degree of asymmetry with parasite load in 255 of the fish (Berg et al. 1995). The sockeye salmon in these lakes were selected for study because there is a large amount of information on the populations, including age structure (Rogers 1987; Blair et al. 1993), morphology (Bishop 1990; Wetzel 1993; Blair et al. 1993) and spawning behavior (Quinn and Foote 1994; Quinn et al. 1996). The study populations are very abundant and productive, and are not on the periphery of the species' range, and therefore were probably not under extreme environmental stress.

The fish were collected immediately before spawning with beach seines or gill nets on or near their spawning grounds between July 25 and August 20, 1993. Sockeye salmon from two small creeks draining into Lake Aleknagik, Yako Creek and Happy Creek, were collected as they schooled just outside the creek mouths. Sockeye from Hansen Creek, also on Lake Aleknagik, were largely sampled among sockeye killed by brown bears *Ursus arctos* L., but not eaten. In Iliamna Lake, samples were collected at Finn Bay, Knutson Bay, and Woody Island (for details see Berg et al. 1995). We attempted to sample the salmon at the peak of their development of secondary sexual characteristics (Quinn and Blair 1992) but the Finn Bay fish were not fully mature in comparison to the other Iliamna Lake populations. Fish were processed as quickly as possible after capture.

The size or count of several bilateral characters was recorded to indicate asymmetry. The number of branchiostegals (rays attached anteriorly to the hyoid bones, ventral to the gill cover)

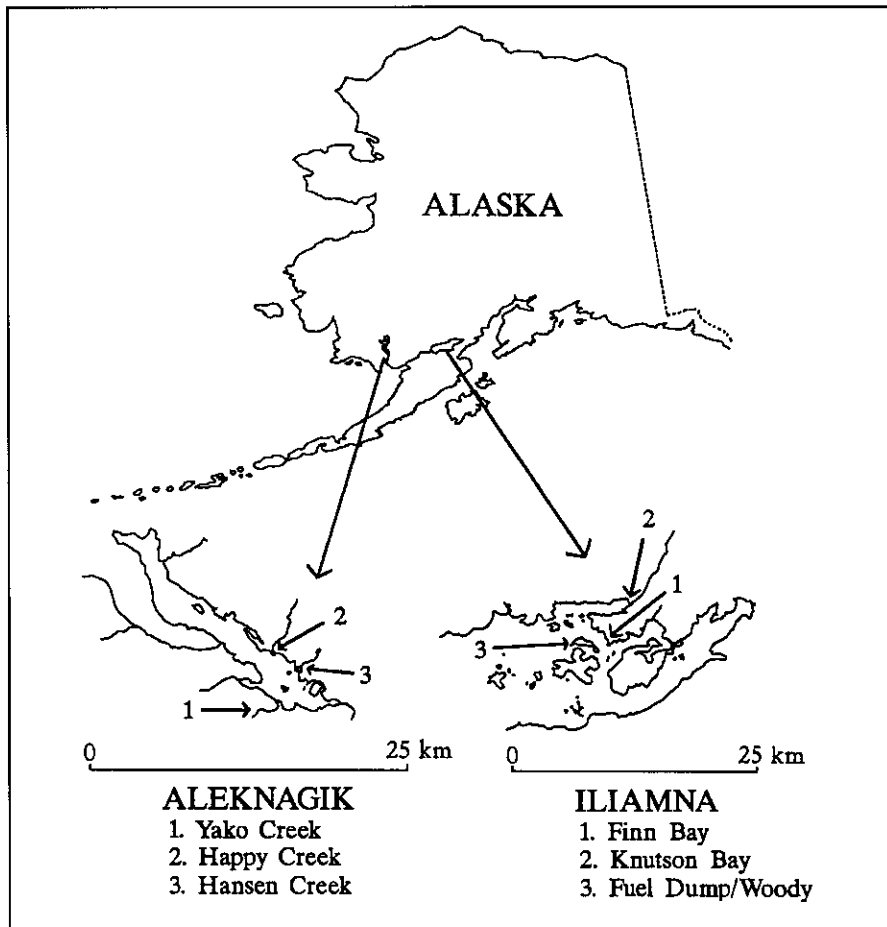


Figure 1. Map of Alaska, showing the sampling locations.

is apparently set early in life (Gharrett and Smoker 1991), and these were counted on both sides. We also measured several characters whose size or number is more likely to be affected by environmental conditions throughout development, including pectoral and ventral fin lengths, and the number of teeth on the upper and lower jaws. The length of each pectoral fin was measured with calipers as the distance (in mm) between the outer margin of the pectoral fin and the distant edge between the base of the fin and scapula (shoulder bone). The length of each ventral fin was determined between the outer margin of the fin along the inner edge to the papilla at the base of the fin. In the upper jaw there was a distinct gap in dentition about one-third of the way along the jaw from the front. The number of teeth was determined in this well-defined anterior area. These upper

jaw, frontal teeth should be of importance for fighting capacity of males. We also counted the number of large teeth (> 3 mm). The enlargement of some teeth is a secondary sexual characteristic developed just prior to spawning.

Asymmetry of a character was calculated as the absolute difference in the length (or count) of the character between the right (R) and left (L) sides. R-L distributions that depart significantly from the statistical criteria for ideal fluctuating asymmetry (mean of zero, normal distribution) are unsuitable as descriptors of developmental stability because a part of the asymmetry variation may have a genetic basis (Palmer and Strobeck 1992). Three characters (pectoral fin length, number of branchiostegals, total number of teeth) exhibited significant directional asymmetry and were therefore not utilized as indices of fluctuating

asymmetry (Palmer and Strobeck 1992). Two other characters (ventral fin length, number of big teeth) showed no directional asymmetry or antisymmetry, and were used to characterize fluctuating asymmetry. Seven extreme observations out of a total of 4,960 (310 fish x 16 morphological measurements) were discarded, as they were thought to be either recording errors or physical deformities unrelated to fluctuating asymmetry.

We selected several morphological features for measurement on the basis of their involvement in male displays, aggression, and social status (Quinn and Foote 1994). These included length (from the middle of the eye to the end of the hypural plate), and three secondary sexual characteristics: body depth (perpendicular to the long axis of the fish from the anterior insertion of the dorsal fin to the belly), snout length (mid-eye to tip of upper jaw), consistent with Quinn and Blair (1992) and Quinn and Foote (1994), and the number of large teeth. As all three secondary sexual characteristics were correlated with fish length, we substituted the residuals of site-specific regressions of these characters on body length for their raw values (Quinn and Foote 1994).

Parasite load was measured as the wet weight of the dominant macroparasite in these populations, the nematode *Philonema oncorhynchi*. Parasites within the abdomen were readily visible and easily collected for later assessment (Berg et al. 1995). The distribution of parasite weights was highly skewed, accordingly, the natural logarithm of parasite load was used for all analyses. Only 1 of 255 fish assessed for parasites had none, to permit log transformation, the smallest observed

parasite load was substituted for this observation. We calculated all possible correlations between the four signals of male quality (length and the residuals of the three secondary sexual characteristics) and the hypothesized predictors of male quality (fluctuating asymmetry and parasite load). We also calculated the correlations between parasite load and the degree of fluctuating asymmetry.

Results

There was marked variation within and between sites in the size of morphometric or number of meristic traits (Table 1). Continuous characters (body depth, snout length, fin lengths) were strongly positively correlated with body length ($p < 0.001$). The number of small and large teeth in the upper jaw was significantly correlated with length ($p < 0.001$). The numbers of lower jaw teeth count had correlations with length with p ranging between 0.15 (not significant) and 0.01 among the populations. Branchiostegal number was not correlated with body length. The populations differed in mean length and many of the inter-population differences disappeared when fish length was accounted for. Analysis substituting sea age (where most growth occurs) for body length yielded similar patterns of correlation and of statistical significance. Nevertheless, some traits varied between Lake Aleknagik and Iliamna Lake, notably body depth even after the effects of size were removed ($p < 0.05$).

There were a number of inter-trait correlations between the different characters within the pooled material such as between number of upper (and lower) jaw teeth and both pectoral and ventral fin

TABLE 1. Pooled (common) mean length/count of the different characters from the different sites. Fish, pectoral and ventral fin lengths are in mm, while other characters are counts.

	Length of fish	Pectoral fin length	Ventral fin length	Branchiostegals	Upper big teeth	Upper total teeth	Lower big teeth	Lower total teeth	Sample size*
Yako	449	83.8	61.3	13.2	2.7	7.6	3.4	17.6	50
Happy	468	89.4	63.9	13.1	3.2	7.8	3.7	18.5	52
Hansen	449	82.7		11.9	3.2	7.7	3.3		55
Aleknagik	455	85.3	62.7	12.7	3.0	7.7	3.5	18.1	157
Finn Bay	462	88.1	63.8	12.3	3.1	7.1	3.8	19.4	32
Knudson	498	96.2	68.9	12.6	3.3	7.7	3.5	17.5	60
Fuel Dump	459	88.7	66.6	13.2	3.0	7.1	3.6	17.7	61
Iliamna	475	91.8	67.1	12.8	3.1	7.4	3.6	17.8	153

* maximums—not all measurements were obtained for every fish

TABLE 2. Pooled (common) mean difference (right—left side) for measured bilateral characters in the different populations

	Pectoral fin length	Ventral fin length	Branchio-stegals	Big teeth	Total teeth
Yako	-2.4	-1.0	-0.9	-0.1	0.1
Happy	-1.7	-0.2	-0.6	0.2	0.4
Hansen	-0.4		-0.8	-0.2	
Aleknagik	-1.5	-0.6	-0.8	0.0	0.2
Finn Bay	-0.5	-1.0	-1.5	0.3	0.5
Knudson	-0.5	-0.1	-1.4	0.0	1.2
Fuel Dump	-0.8	0.5	-1.2	0.4	1.2
Iliamna	-0.6	0.0	-1.3	0.2	1.1
All	-1.1*	-0.2	-1.0*	0.1	0.7*

* mean differs significantly from 0 (Mann-Whitney U test, $p < 0.05$)

size ($p < 0.05$). Three paired characters were directionally asymmetric (Table 2) implying a partial genetic basis to the asymmetry rather than pure environmental influences (Palmer and Strobeck 1992). Pectoral fin length and the number of branchiostegals were greater ($p < 0.0001$, Mann-Whitney U-test) on the left than on the right side, whereas the total number of teeth was greater ($p < 0.002$, Mann-Whitney U-test) on the right side. Ventral fin length and number of large teeth were thus the two characters left where fluctuating asymmetry could be detected and the six populations exhibited similar patterns of asymmetry in the measured traits.

Fluctuating asymmetry in ventral fin length was weakly but significantly ($p < 0.02$) negatively correlated with the length of male sockeye (Table 3) and a similar but positive correlation ($p < 0.02$) was found between another index of condition, residual body depth, and fluctuating asymmetry in the number of large teeth. Other correlations between indices of condition and the degree of asymmetry varied in sign, but were not significant, though there was a nearly significant negative relationship between the number of large teeth and the asymmetry in their counts ($p < 0.06$). Overall, there was no consistent pattern of correlations between signals of male quality and fluctuating asymmetry. There were no correlations ($p > 0.05$) between the logarithm of parasite *Philonema oncorhynchi* weight and the four indices of male condition (Table 3). Parasite load was related to fluctuating asymmetry in the ventral fin length ($p < 0.05$, $r = 0.17$) but was not related to fluctuating asymmetry in number of large teeth ($p > 0.05$, $r = 0.08$).

TABLE 3. Correlation (r) between indices of male quality and fluctuating asymmetry or parasite load

Indices of male quality	FA in ventral length	FA in # big teeth	ln (Parasite load)
Length	-0.13*	0.01	-0.04
Residual Hump	0.02	0.13*	0.07
Residual Snout	0.08	-0.03	-0.03
Residual # Big Teeth	0.04	-0.12	0.01

* = $p < 0.05$

Discussion

Fluctuating asymmetry is considered to be an epigenetic measure of the ability of individuals to undergo identical development of a bilaterally symmetrical character. The present study was designated to get a reliable estimate of fluctuating asymmetry in a number of characters. A large number of measurements (nearly 5000) should provide a basis for a discussion of asymmetries among the selected populations. Several authors agree that antisymmetry and directional asymmetry may have a partial genetic basis, rendering these forms of asymmetry useless for studies of developmental instability (see e.g. Palmer & Strobeck 1986; Graham et al. 1993). Of five characters investigated, three were directionally asymmetric. Such parameters are not used in the statistical basis for fluctuating asymmetries, as the difference between sides probably reflect more than simple developmental noise (e.g. Palmer 1996). Further comparisons among populations of sockeye at more marginal areas of their range should be performed with a wider character set, where other (fluctuating) asymmetric characters could be included.

The body length, weight and particularly body depth varied between the populations from Lake Aleknagik and Iliamna Lake. Such an effect may be explained by the fact that the Aleknagik populations we sampled were creek-spawners, whereas the populations sampled from Iliamna Lake spawn on beaches. The limited access to shallow creeks by deep-bodied males and size-selection predation by bears (Hanson 1992) have been hypothesized to influence population-specific patterns of size and morphology (Rogers 1987; Blair et al. 1993; Quinn and Foote 1994).

Substituting sea age for body length did not alter the significant correlations nor the interaction between the factors. The results were therefore given as relationships with body size and not with the factor sea age which is intercorrelated with size.

Genetic surveys of natural populations may be insufficient to identify populations with genetic problems or to detect the impact of environmental stress on the population. The possibility that a morphological approach using the frequency and size of asymmetries can complement the biochemical techniques for assessing components of adaption of natural populations (e.g. Sarre et al. 1994) is very attractive. A rapidly growing literature indicates a correlation between developmental instability and asymmetry, implying that asymmetry might also be used as an indicator of environmental stress (e.g. Soule 1967; Palmer and Strobeck 1986; Parsons 1990; Møller 1992a,b; Emlen et al. 1993), although some authors have cautioned about comparisons between taxonomic groups (Clarke 1997) or to the widespread use of fluctuating asymmetry in a variety of comparisons (Palmer 1996). The populations that we investigated showed similar levels of asymmetry. We conclude that either stress does not influence asymmetry in sockeye salmon or these populations are under similar levels of stress.

The question of honest signalling (i.e., whether individually variable traits reflect indices of fitness like condition, energetic content or parasite infection load of the animal) in mate choice situations has been treated in a number of investigations (e.g. Balmford et al. 1993; Evans 1993; Møller and Pomiankowski 1993; Evans et al. 1995; Folstad et al. 1996). Most studies have shown positive correlations between presumably beneficial physical characters and reproductive success, but few

experimental studies have been performed. Wiley (1991) reviewed some of the experimental studies and concluded that behavior patterns rather than morphology might explain differences in reproductive success.

Quinn and Foote (1994) found that body length and especially body depth of Woody Island male sockeye salmon were associated with spawning ground status and reproductive opportunity. The fitness of an individual is affected by many factors, and the size of morphological traits and levels of asymmetry may correlate with fitness. Fitness is, however, also influenced by vigor and fish with relatively large investments in secondary characters may have less energy left for the demanding reproductive behavior patterns. Some of the morphological characters, notably teeth counts, are developed at a late stage, when the other secondary sexual characteristics are also developed. The development of these features may stress the fish, thus increasing asymmetry. Enlargement of the frontal teeth into secondary sexual characteristics occurs at what could be a stressful period in the life cycle, when salmon are migrating from saltwater to freshwater, undergoing major environmental, physiological and morphological changes. Body depth becomes exaggerated at this time and deep-bodied males had less symmetrical counts of large teeth than small males. However, Clarke (1995) reviewed the evidence and concluded that there was inadequate evidence to support any application of fluctuating asymmetry as a fitness measurement. He further questioned whether fluctuating asymmetry should be used as a substitute for conventional fitness measurements within conservation programmes. Our results are consistent with those conclusions.

Parasite load and the degree of fluctuating asymmetry in ventral fin length were significantly correlated, but not with asymmetry in the number of large teeth. The parasites were acquired by juvenile salmon while they are rearing in freshwater prior to seaward migration (Berg et al. 1995). There was no relationship between parasite load and indices of male condition. Correlations were weak and sometimes even positive, despite a wide range in parasite loads (0–28 g; Berg et al. 1995). The maximum weight of parasites observed (28 g) was less than 1% of the weight of the average salmon, however, these loads constituted a large fraction

of the space available in the body cavity, obscuring many of the organs. Parasite weight of *Philonema oncorhynchi* is not a useful indicator of stress during the buildup of the secondary sexual characteristics of the salmon.

Studies have reported positive and negative evidence for relationships between parasite load or fluctuating asymmetry and indices of fitness (Holmes and Zohar 1990; Folstad and Karter 1992; Alados et al. 1995; Folstad et al. 1996; review by Møller 1996) and meta-analysis has indicated considerable variation in support for such hypotheses (e.g., Hamilton and Poulin 1997). The absence of correlations in our study may contribute to an assessment of the overall prevalence of such phenomena as they provide a balance to the "positive" results that are more readily published. We

conclude with Csada et al. (1996) and Palmer (1996) that it is important to report results such as ours that do not conform to current research trends.

Acknowledgements

Many people assisted with the sample collection but we especially thank Michelle Cox, Andrew Hendry, Tanya Hibbing, Frank Leonetti, Paul Schlenger and Michael Ward. Frode Killingberg is thanked for drawing assistance, while Peder Fiske, John Emlen, Robert L. Burgner and an anonymous referee are thanked for improvements of the manuscript. This research was made possible by support from the Pacific Seafood Processor's Association, Norwegian Research Council and from the Nansen Endowment.

Literature Cited

- Alados, C.L., J. Escós, and J.M. Emlen. 1995. Fluctuating asymmetry and fractal dimension of the sagittal suture as indicators of inbreeding depression in dama and dorcas gazelles. *Can. J. Zool.* 73:1967-1974.
- Balmford, A., and A.R.L. Thomas. 1992. Swallowing ornamental asymmetry. *Nature* 359:487.
- Balmford, A., I.L. Jones, and A.R.L. Thomas. 1993. On avian asymmetry: evidence of natural selection for symmetrical tails and wings in birds. *Proc. R. Soc. Lond. B.* 252:245-251.
- Beacham, T.D. 1985. Meristic and morphometric variation in pink salmon *Oncorhynchus gorbuscha* in southern British Columbia and Puget Sound. *Can. J. Zool.* 63:366-372.
- Beacham, T.D., and C.B. Murray. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon *Oncorhynchus keta* in British Columbia. *Can. J. Fish. Aquat. Sci.* 44:244-261.
- Beacham, T.D., R.E. Withler, C.B. Murray, and L.W. Barner. 1988. Variation in body size morphology, egg size, and biochemical genetics of pink salmon in British Columbia. *Trans. Amer. Fish. Soc.* 117:109-126.
- Berg, O.K., C.J. Foote, and T.P. Quinn. 1995. Fish age, nematode (*Philonema oncorhynchi*) infection, and development of sexual dimorphism by the adult male sockeye salmon, *Oncorhynchus nerka*, in western Alaska. *Can. J. Zool.* 73:1999-2004.
- Bishop, S.M. 1990. Morphometric differences among spawning populations of sockeye salmon *Oncorhynchus nerka* in the Wood River Lake system. Master's thesis. Univ. of Washington. Seattle.
- Blair, G.R., D.E. Rogers, and T.P. Quinn. 1993. Variation in life history characteristics and morphology of sockeye salmon *Oncorhynchus nerka* in the Kvichak River system, Bristol Bay, Alaska. *Trans. Amer. Fish. Soc.* 122:550-559.
- Clarke, G.M. 1995. Relationship between fluctuating asymmetry and fitness: how good is the evidence? *Pacific Conserv. Biol.* 2:146-149.
- Clarke, G.M. 1997. The genetic stability and molecular basis of developmental stability: the *Lucilia* story. *Trends Ecology Evolution* 12:89-91.
- Csada, R.D., P.C. James, and R.H.M. Espie. 1996. The "file drawer problem" of non-significant results: does it apply to biological research? *Oikos* 76:591-593.
- Emlen, J.M., D.C. Freeman, and J.H. Graham. 1993. Non-linear growth dynamics and the origin of fluctuating asymmetry. *Genetica* 89:77-96.
- Evans, M.R. 1993. Fluctuating asymmetry and long tails: the mechanical effects of asymmetry may act to enforce honest advertisement. *Proc. R. Soc. Lond. B.* 253:205-209.
- Evans, M.R., T.L.F. Martins, and M.P. Haley. 1995. Inter- and intra-sexual patterns of fluctuating asymmetry in the red-billed streamertail: should symmetry always increase with ornament size? *Behav. Ecol. Sociobiol.* 37:15-23.
- Folstad, I., and A.J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* 139:603-622.
- Folstad, I., P. Arneberg, and A.J. Karter. 1996. Antlers and parasites. *Oecologia* 105:556-558.
- Gharrett, A.J., and W.W. Smoker. 1991. Two generations of hybrids between even- and odd-year pink salmon *Oncorhynchus gorbuscha*: a test for outbreeding depression? *Can. J. Fish. Aquat. Sci.* 48:1744-1749.
- Graham, J.H., D.C. Freeman, and J.M. Emlen. 1993. Antisymmetry, directional asymmetry, and dynamic morphogenesis. *Genetica* 89:121-137.
- Hamilton, W.D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? *Science (Washington D.C.)* 218:384-387.
- Hamilton, W.J. and R. Poulin. 1997. The Hamilton and Zuk hypothesis revisited: a meta-analytical approach. *Behaviour* 134:299-320.

- Hanson, R. 1992. Brown bear (*Ursus arctos*) predation on sockeye salmon (*Oncorhynchus nerka*) spawners in two tributaries of the Wood River Lake system, Bristol Bay, Alaska. M.S. thesis, University of Washington, Seattle.
- Holmes, J.C. and S. Zohar. 1990. Pathology and host behaviour. -In: C.J. Bernard, and J.M. Behnke, (eds.), Parasitism and host behaviour. Taylor and Francis, London, pp. 34-59.
- Møller, A.P. 1992a. Female swallow preference for symmetrical male sexual ornaments. *Nature* 357:238-240.
- Møller, A.P. 1992b. Patterns of fluctuating asymmetry in weapons: evidence for reliable signalling of quality in beetle horns and bird spurs. *Proc. R. Soc. Lond. B.* 248:199-206.
- Møller, A.P., and A. Pomiankowski. 1993. Fluctuating asymmetry and sexual selection. *Genetica* 89:267-279
- Møller, A.P. 1996. Parasitism and developmental instability of hosts: a review. *Oikos* 75:189-196
- Palmer, A.R., and C. Strobeck. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Ann. Rev. Ecol. Syst.* 17:391-421
- Palmer, A.R., and C. Strobeck. 1992. Fluctuating asymmetry as a measure of developmental stability: implications of non-normal distributions and power of statistical tests. *Acta Zoologica Fennica* 191:57-72.
- Palmer, A.R. 1996. Waltzing with asymmetry. *BioScience* 46:518-532.
- Parsons, P.A. 1990. Fluctuating asymmetry: an epigenetic measure of stress. *Biol. Rev.* 65:131-145.
- Quinn, T. P., and G.R. Blair. 1992. Morphological changes in senescing adult male sockeye salmon *Oncorhynchus nerka* Walbaum. *J. Fish Biol.* 41:1045-1047.
- Quinn, T. P., and C.J. Foote. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon *Oncorhynchus nerka*. *Anim. Behav.* 48:751-761.
- Quinn, T.P., M.D. Adkison, and M.B. Ward. 1996. Behavioral tactics of male sockeye salmon *Oncorhynchus nerka* under varying operational sex ratios. *Ethology* 102:304-322.
- Rogers, D.E. 1987. The regulation of age at maturity in Wood River sockeye salmon *Oncorhynchus nerka*. *Can. Spec. Publ. Fish. Aquat. Sci.* 96:78-89.
- Sarre, S., J.M. Dearn, and A. Georges. 1994. The application of fluctuating asymmetry in the monitoring of animal populations. *Pacific Cons. Biol.* 1:118-122.
- Soule, M.E. 1967. Phenetics of natural populations. II. Asymmetry and evolution in a lizard. *Amer. Nat.* 101:141-160
- Wagner, E.J. 1996. History and fluctuating asymmetry of Utah salmonid broodstocks. *Prog. Fish-Cult.* 58:92-103.
- Wetzel, L.A. 1993. Genetic, morphometric and life history characteristics of sockeye salmon *Oncorhynchus nerka* in the Wood River Lake system, Bristol Bay, Alaska. Master's thesis. Univ. of Washington. Seattle.
- Wiley, R. H. 1991. Lekking in birds and mammals: behavioral and evolutionary issues.- In: P.J.B. Slater, J.S. Rosenblatt, C. Beer, and M. Milinski (eds.), *Advances in the study of behavior*, 20. Academic Press, London, pp. 201-291.

Received 16 May 1997

Accepted for publication 25 August 1997