Abstract.–Developmental Instability (DI) has been proposed as an inexpensive, quickly applied, and sensitive indicator of stress that can be utilized in early warning and in monitoring anthropogenic impacts on fish and other animals and plants. A problem arises, however, to the extent that natural stressors confound the effects of human-induced disturbances. Our objective in this work was to investigate whether a natural stressor, in the form of El Niño conditions, contributed to DI in the Pacific hake. Right-left (fluctuating) asymmetry of otolith length, width, growth rate, and weight, as well as right-left otolith shape differences, were used as measures of DI. Results show that indeed El Niño disrupts development, indicating stress. This outcome suggests that DI, as an early warning and monitoring tool for stress, must be used with caution.

Developmental instability as an indicator of environmental stress in the Pacific hake (*Merluccius productus*)

Consuela L. Alados
Juan Escos

Estacion Experimental de Zonas Aridas
Consejo Superior de Investigaciones Cientificas
Almeria, Spain
Present Address: National Fisheries Research Laboratory
    U.S. Fish and Wildlife Service
    Naval Station Puget Sound, Seattle, WA 98115

John M. Emlen

National Fisheries Research Laboratory
U.S. Fish and Wildlife Service
Naval Station Puget Sound, Seattle, WA 98115

The viability of fish populations and the ecological communities of which they form a part is a matter of concern to fisheries managers. At present, awareness of ecological problems often occurs only when stocks have already begun to decline, when there is clear evidence of disease or morbidity, or when die-offs occur.

Much work has been done on methods to assess adverse environmental impacts on fish via physiological stress measures (Adams, 1990a). These methods can, in theory, be used to monitor problems and, possibly, act as early warning indicators. However, most of these indicators either measure short-term acute stress response (e.g., corticosteroid levels), or are expensive and laboratory-intensive. They are cost-effective only in evaluating already obvious signs that a problem exists. In economically depressed areas, including the developing nations, these methods are impractical. In addition, they generally lack ecological relevance (Adams, 1990b).

A possible alternative to these methods lies in morphological measures of developmental instability by which changes (induced by environmental or genetical stress) in the basic developmental strategy of organisms can be assessed. For example, chronic stress might aggravate right-left asymmetry in normally bilaterally symmetric structures (Soule, 1967; Valentine and Soule, 1973; Valentine et al, 1973) or increase the number of aberrations in circulus patterns on scales (Shackell and Doyle, 1990). Morphological measures are inexpensive to obtain and cause minimal or no damage to animals involved. They can be quickly and inexpensively applied not only in situations where concern has already arisen, but also as standard monitoring tools. Screening of fry might be valuable in assessing effectiveness of various hatchery practices or in evaluating smolt quality in Pacific salmon.

The efficacy of right-left, or "fluctuating" asymmetry (FA) as an indicator of both genetic and environmental stress has been well documented. Within populations, homozygosity is associated with increased FA

(Dobzhansky and Wallace, 1953; Lerner, 1954; Lewontin, 1956; Bader, 1965; Bruckner, 1976; Soule, 1979; Vrijenhoek and Lerman, 1982; Leary et al., 1983, 1984; Mitton and Grant, 1984). Increased homozygosity is one consequence of inbreeding (one form of genomic disruption). Within populations of outcrossing species, inbreeding is associated with lowered fitness (Lewontin, 1956; Charlesworth and Charlesworth, 1987). Bader (1965), Bailit et al. (1970), and Clarke (1992) have all found positive correlations among populations between inbreeding and FA.

The converse of inbreeding depression is outbreeding depression. Hybridization and subsequent introgression of sufficiently *different* populations can lead to the disruption of coadapted gene complexes and thus, in theory, promote both decreased fitness and developmental instability (Vrijenhoek and Lerman, 1982). Zakharov and Bakulina (1984) found that when individuals of similar populations of *Drosophila virilis* were crossed, no increases in FA over the parental types were observed. When more divergent strains were crossbred, FA was pronounced in the offspring. Outbreeding depression should be most apparent in interspecific hybrids. Leary et al. (1985) have found FA to be higher in laboratory hybrids of rainbow (*Oncorhynchus mykiss*) and cutthroat (*O. clarki*) trout than in either parental type.

Environmental disturbance, or deviation from the conditions to which organisms are adapted, leads to lowered fitness and developmental instability. Temperature stress causes increased FA in laboratory mice and rats (Beardmore, 1960; Siegel and Doyle, 1975, a and b; Siegel et al., 1977), in lizards (genus *Lacerta*, Zakharov 1982), and in chum salmon (*O. keta*, Beacham 1990). Audiogenic stress has the same effect on laboratory rats (Siegel and Smookler, 1973; Siegel and Doyle, 1975c). Valentine and Soule (1973) demonstrated that FA of laboratory grunion (*Leuresthes tenuis*) populations rose with concentrations of DDT. Clarke (1992) showed increased FA in pesticide-treated bush flies (*Musca vetustissima*) even at concentrations too low to produce statistically detectable changes in mortality. Zakharov and Rubin (1985) demonstrated the effects of contamination on FA in animals in the Baltic Sea. Thus FA may be an extremely sensitive indicator of stress.

Chronic stress indicators may be sensitive to naturally occurring events as well as anthropogenic disturbances. Zakharov et al. (1991), for example, found that intensified population density feedback led to increased FA during the decline phase of shrew population cycles. Data exist (Emlen, unpubl.) suggesting increased asymmetry occurs in the canine teeth of population-stressed northern fur seals. Clearly, if natural stressors are important contributors to developmental instability, then their effects must be considered when using DI as a tool for identifying or monitoring anthropogenic disturbances. In this paper we provide an example of FA responses to another natural stressor, the El Niño event of 1982–1983.

The Pacific hake (*Merluccius productus*) ranges along the Pacific coast of North America from Mexico to Alaska. Several genetic stocks can be distinguished. These include two spawning in Puget Sound, one from the Georges Straits, several from the fjords of Vancouver Island, and a so-called coastal population that ranges from San Francisco Bay to southern Baja California. Reproduction occurs from January to April, and young fish enter the fishery at about age three. Individual growth occurs largely between May and September.

Environmental conditions associated with the 1982–1983 El Niño may have caused significant dislocations of the coastal hake stock on the summer fishing grounds, since the entire population apparently moved northward (Francis and Hollowed, 1985). Length and weight information from the data set used by Francis and Hollowed and gathered by the National Marine Fisheries Service showed no significant differences between the 1980 and 1984 year classes for either sex. However, the 1980 El Niño year-class fish were slightly longer and lower in weight, and a Mann-Whitney test showed them to have significantly lower condition factor (weight/length^3) than the 1984 control year-class (respective means=0.06709, 0.07208; n=85, 63; P=0.0001). Both the dislocation in position and the diminished condition factor of population members suggest a drop in population viability and, thereby, implicate stress. Might this stress also have provoked developmental instability?

Methods

The development of otoliths, small calcareous structures used in maintaining balance in some fishes, is known to reflect growth rate and transition points in life histories (Wilson and Larkin, 1982; Volk et al., 1984; Alhossaini and Pitcher, 1988; Sogard, 1991). As such, they may be useful indicators of developmental instability. We do not suggest that otoliths fit the criteria given above for cost effectiveness and harmlessness to the organisms monitored. We use them here simply as a convenience (they were readily available and came with appropriate, attendant data on fish age, length, weight, and date of collection). The National Marine Fisheries Service, at its Alaska center in Seattle, maintains a collection of otoliths taken by scientific observers aboard commercial hake fishery boats. From this collection we obtained paired right and left

otoliths for 4-year-old hake caught in the first half of September for the years 1984 and 1988 (from the 1980 and 1984 year classes). These fish were the same from which the length and weight data, mentioned above, were taken. Individuals from the 1980 year class were in their second and third year of growth during El Niño; those from the 1984 year class were not present during the El Niño event. Time-sequential data is useful in the present context since the population was used as its own control, reducing or minimizing confounding factors of geography, genetic stock, etc.

Five otolith characters were used to assess instability: fluctuating asymmetry in weight, length, maximum width, growth rate, and right-left differences in shape (Fig. 1). For comparison of shape, one otolith was aligned with the reverse image of the other, and right-left shape differences examined. At least two means of alignment exist. Since otoliths show annual growth rings, it was possible to superimpose long axes drawn through the first growth ring. In the 1980 year class this ring was laid down just prior to the El Niño event and indicates the beginning of the period of stress. Measured differences along the outlines of the third ring, marking the end of El Niño, provide an appropriate measure of right-left differences in growth during the period. This approach was impractical.

Shape = $\Sigma_i | d_i |$/length

Figure 1
Hake *(Merluccius productus)* otoliths: **(A)** An otolith showing growth lines and the measure used to assess growth between ages 1 and 4; **(B)** Diagram of superimposed right and left otoliths showing how shape difference was characterized.

While distances between the rings could be reasonably approximated with the aid of an optical micrometer, our equipment was inadequate to permit video or photo reproduction of clear ring patterns. Accurate axes could not be drawn. Minute angular changes in axis definition generated large differences in the shape measure.

Because of these difficulties, we used an alternative approach. Equally magnified images of the two otoliths were projected onto paper and their outlines traced. One tracing was then turned over and placed atop the other. Each otolith possesses clearly marked "top" and "bottom" extreme points (Fig. 1), so alignment could be accomplished by superimposing the axes drawn through these two points. This procedure led to an almost perfect fit of the two otoliths along their straighter side and to clear pattern differences along their opposite scalloped side (Fig. 1). Nine equally spaced lines were drawn perpendicular to this axis, and, along each such line, the absolute distance between the scalloped margins of the two overlain outlines was measured. Right-left differences among the otoliths were taken as the sum of these absolute distances, normalized by dividing by the axis length. Information lost by neglecting similar differences along the straight side was negligible owing to the almost perfect fits along that margin. Growth rate was measured by the maximum distance, parallel to the straight side, between the first and the fourth otolith growth ring at the broader end of the otolith (Fig. 1).

Four-year-old fish caught in September, near the end of the growth season, may have displayed some variance in size owing to differences in date of hatching. This variance is not likely to be large because little growth occurs between earliest and latest hatching in January and April. Nevertheless, to correct for possible associations between asymmetry and early growth, we used a normalized index, $|L-R|/(L+R)$, with L and R designating left and right measures. Because collections for each of the three years were made at very nearly the same time, biases arising from possible influences of growth stage on asymmetry were minimized. The measure of right-left difference in shape is not a measure of FA in the strict sense (Palmer and Strobeck, 1986). However, an increase in the measure would indicate an increased deviation from normal developmental homeostasis. Thus it is a valid indicator of developmental instability.

Tests for fluctuating asymmetry depend on an absence of directional asymmetry (skew), anitsymmetry (bimodality or platykurtosis) and, according to one school of thought (Palmer and Strobeck, 1986), a normal distribution for $(L-R)/(L+R)$. The Shapiro-Wilk statistic (Zar, 1984, p. 95) was used to test for normality. Because of the controversy surrounding the validity of
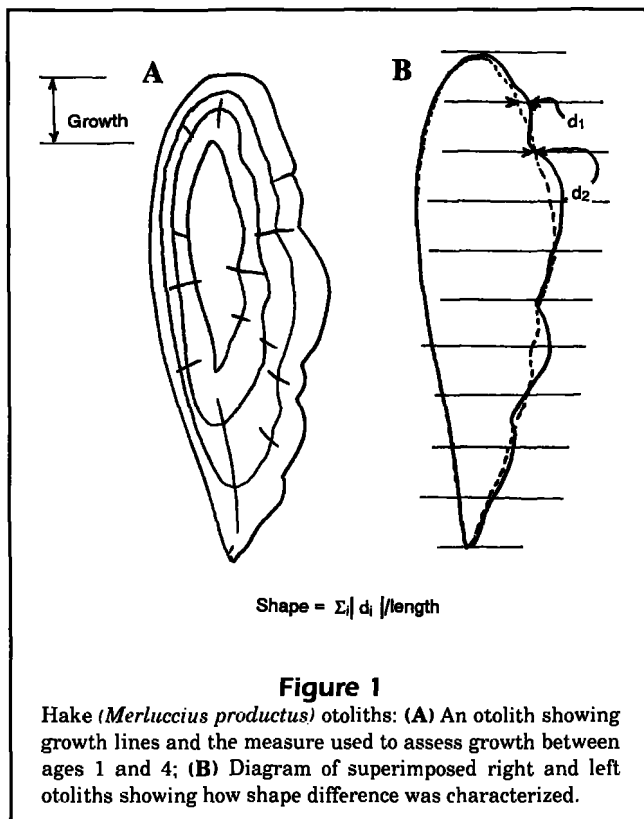
FA tests for traits not normally distributed, further analyses were carried out twice, once with and once without such traits. A second order ANOVA was applied to test for influences of sex and year class on growth rate. Finally, fish were catergorized as fast or slow growers, according to whether growth rate fell above or below the median for the year in question, and a three-way MANOVA was performed to test for effects of growth rate, sex, and year on FA and right-left otolith shape differences.

Results

For both the 1980 and 1984 year classes, we found that the distributions of weight, width, and length did not differ significantly from normality (Table 1). These variables

can, therefore, be used in analysis of FA. Growth rate was not normally distributed. The two-way ANOVA indicated no influence of sex (F=1.42; df=1, 141; P=0.234) and no significant interaction effect of sex X year (F=0.36; df=1,141; P=0.550) on growth. The main effect of year, however, was strong (F=14.20; df=1,141; P=0.0002). This last result, along with the possibility that growth rate might influence asymmetry of other characters, provided the rationale for incorporating growth rate into the three-way MANOVA, as noted above. Results were qualitatively the same— no differences with respect to which comparison deviated significantly—whether growth rate was or was not included in the MANOVA, and so only one result set, that including this variable, is presented in this paper (Table 2). There was a highly significant difference in developmental instability, but only between the years. Univariate analysis showed that FA was greater for the El Niño fish with respect to otolith weight and shape, but not width or length (Tables 3 and 4).

To examine the possibility that the between-year differences were not due to El Niño effects, we examined otoliths of 4-year-old fish from another year class (1977) unaffected by El Niño events. As with the above two groups, fish sampling took place during the first two weeks of September. These otoliths were analyzed for right-left asymmetry in weight and shape. Results of a Multiple Analysis of Variance for all three year classes, with fixed effects of year and sex, are given in Tables 5 and 6. The results, in conjunction with Tukey tests for differences among years (Table 7) show clear increases in right-left differences in both shape and weight for the 1980 El Niño year over 1984 and, in shape, over 1977 as well. Differences between the two years not affected by El Niño (1977 and 1984) were not statistically significant.

Discussion

The observation that only two of the five right-left asymmetry measures responded to stress at a statistically detectable level raises the question of consistency. If developmental instability is to be a useful indicator of stress, we need to know what measures will be relatively sensitive to stress and which will not. Highly

---

Table 1

Tests for normality of (L–R)/(L+R) for various traits used in developmental instability. (L indicates measure on the left, R the corresponding measure on the right otolith).

Width of otolith (n = 147)
Mean = 0.002
Skew = 0.184
Kurtosis = 1.333
Shapiro-Wilk W = 0.990
P = 0.9456

Weight of otolith (n = 135)
Mean = 0.003
Skew = 0.242
Kurtosis = 0.683
Shapiro-Wilk W = 0.994
P = 0.9965

Length of otolith (n = 135)
Mean = 0.001
Skew = 0.049
Kurtosis = 2.030
Shapiro-Wilk W = 0.975
P = 0.1981

Growth rate of otolith (1980 year class; n = 79)
Mean = –0.001
Skew = –1.567
Kurtosis = 6.124
Shapiro-Wilk W = 0.981
P = 0.0001

Growth rate of otolith (1984 year class; n = 69)
Mean = 0.002
Skew = –0.281
Kurtosis = 0.248
Shapiro-Wilk W = 0.981
P = 0.7044

Table 2

Multiple analysis of variance for various traits used in developmental instability analysis. Fixed effects are year, sex and growth rate. Variables are right-left differences in width, weight, length, growth rate, and shape.

Effects	Wilks Lambda	F	df	P
Year	0.8029	5.596	5, 114	0.0001
Sex	0.9509	1.176	5, 114	0.3253
Growth	0.9532	1.119	5, 114	0.3546
Year × sex	0.9407	1.438	5, 114	0.2159
Year × growth	0.9230	1.901	5, 114	0.0995
Sex × growth	0.9612	0.961	5, 114	0.4704
Year × sex × growth	0.9936	0.146	5, 114	0.9807

Table 3

Univariate breakdown of multivariate analysis of variance for various traits used in developmental instability analysis.

Fixed effect	df	SS	F	P
Variable				
Weight				
Growth rate	1	0.00001	0.26	0.608
Sex	1	0.00009	2.28	0.133
Year	1	0.00036	9.07	0.003
Growth × sex	1	0.00010	2.63	0.107
Growth × year	1	0.00001	0.35	0.554
Sex × year	1	0.00008	2.09	0.151
3-Way	1	0.00002	0.49	0.487
Error	118	0.00469		
Width				
Growth rate	1	0.00000	0.00	0.951
Sex	1	0.00003	0.88	0.350
Year	1	0.00008	2.08	0.152
Growth × sex	1	0.00001	0.32	0.574
Growth × year	1	0.00030	2.54	0.114
Sex × year	1	0.00004	1.15	0.286
3-Way	1	0.00000	0.01	0.930
Error	118	0.00456		
Growth rate				
Growth rate	1	0.00134	4.11	0.045
Sex	1	0.00058	1.77	0.186
Year	1	0.00073	2.24	0.137
Growth × sex	1	0.00000	0.00	0.998
Growth × year	1	0.00068	2.10	0.150
Sex × year	1	0.00067	2.06	0.154
3-Way	1	0.00007	0.22	0.639
Error	118	0.03837		
Shape				
Growth rate	1	0.00065	0.76	0.385
Sex	1	0.00015	0.17	0.679
Year	1	0.01856	21.79	0.000
Growth × sex	1	0.00220	2.58	0.111
Growth × year	1	0.00076	0.89	0.347
Sex × year	1	0.00292	3.43	0.066
3-Way	1	0.00006	0.07	0.753
Error	118	0.10049		
Length				
Growth rate	1	0.00002	0.60	0.440
Sex	1	0.00001	0.31	0.581
Year	1	0.00000	0.00	0.986
Growth × sex	1	0.00002	0.62	0.433
Growth × year	1	0.00009	2.66	0.106
Sex × year	1	0.00001	0.39	0.534
3-Way	1	0.00000	0.01	0.933
Error	118	0.00409		

Table 4

Means of developmental instability indices of Pacific hake *(Merluccius productus)* otoliths for 1980 and 1984 year classes.

	1980 (El Niño Group)				1984 (Non El Niño Group)			
Variable	Males	(n)	Females	(n)	Males	(n)	Females	(n)
Weight	0.0083	(36)	0.0117	(36)	0.0065	(24)	0.0065	(30)
Shape	0.0831	(36)	0.0950	(36)	0.0679	(24)	0.0603	(30)

Table 5

Multiple analysis of variance over one El Niño year (1980) and two Non-El Niño years (1977, 1984). Fixed effects are year and sex. Variables are weight and shape.

Effects	Wilks Lambda	F	df	P
Year	0.7606	11.876	4, 324	0.000
Sex	0.9930	0.574	2, 162	0.564
Year × sex	0.9577	1.770	4, 324	0.135

Table 6

Univariate breakdown of multiple analysis of variance for two traits used in developmental instability analysis over three years (1977, 1980, 1984).

Sum of squares		df	F	P
Variable = weight				
Sex	0.00002	1	0.63	0.430
Year	0.00038	2	5.01	0.008
Sex × year	0.00017	2	2.18	0.116
Error	0.00621	163		
Variable = shape				
Sex	0.00062	1	0.82	0.366
Year	0.03576	2	23.65	0.000
Sex × year	0.00285	2	1.89	0.155
Error	0.12322	163		

Table 7

Tukey test for differences among years (1977, 1980, 1984) in two measures of developmental instability. El Niño year class is 1980; Non El Niño year classes are 1977, 1984. NS = not significantly different.

Year class	Difference between means	(Sample sizes)	P
Shape			
1980–1984	0.0250	(77, 59)	<0.05
1980–1977	0.0337	(77, 25)	<0.05
1977–1984	–0.0087	(25, 59)	NS
Weight			
1980–1984	0.0033	(79, 55)	<0.05
1980–1977	0.0024	(79, 38)	NS
1977–1980	0.0009	(38, 55)	NS

Table 8

Means of asymmetry in growth rate for Pacific hake *(Merluccius productus)* in an El Niño and a non-El Niño year.

	Year	
	El Niño (1980)	Non El Niño (1984)
Growth rate		
Slow	0.0142	0.0132
Fast	0.0251	0.0157

canalized traits are unlikely to be sensitive indicators of stress. High phenotypic variance can generally be considered an indication of low canalization, and Zakharov (1989) has shown that, at least for *Lacerta* lizards, FA rises with phenotypic variability (see also Soule, 1967).

A related observation is that traits directly and strongly affecting fitness, i.e., under intense stabilizing selection and, therefore, with low heritability, should be poor candidates for detecting stress (Soule and Cuzin-Roudy, 1982). Similarly, structures whose development is affected by use may not be appropriate for FA analysis. Locomotion, for example, might discourage asymmetric growth of limb size. Long-bone length in laboratory rats shows no FA response to heat, cold, behavioral, or audiogenic stress, while long-bone density, not a size characteristic, does (Doyle et al., 1977).

In choosing measures of developmental instability, it may be useful to consider structural detail. With respect to otoliths, weight, length, width, and growth rate represent growth along a single dimension. These metrics, then, are a simple summation of one or more growth processes. Shape, on the other hand, reflects growth processes whose parts are separably measurable. Thus, shape does not compound and thereby obscure information. We might, accordingly, expect to find differences in the shapes of corresponding right and left structures to be more sensitive indicators of stress than simple metric differences, a prediction consistent with the hake otolith results presented here.

Do natural environmental stressors, as well as man-caused disturbances, result in developmental instability? The results reported here suggest an affirmative answer, namely that while DI might be usefully applied in management, it must be used with caution. Use of fin asymmetries or scale circulus aberrations in comparing hatchery stocks for smolt quality, for example, should involve only a single year class and should be given decreasing consideration as stocks diverge genetically or geo-

graphically. Suspected problems arising from water contamination in Puget Sound might be investigated or monitored by examining FA, but only so long as the control population comes also from Puget Sound.

Literature cited

Adams, S. M. (ed.).
1990a. American Fisheries Symposium 8. Am. Fish. Soc., Bethesda, MA, 191 p.
1990b. Status and use of biological indicators for evaluating the effects of stress on fish. *In* S. M. Adams (ed.) American Fisheries Symposium 8, p. 1–8. Am. Fish. Soc., Bethesda, MA, 191 p.

Alhossaini, M., and T. J. Pitcher.
1988. The relation between daily rings, body growth and environmental factors in plaice, *Pleuronectes platessa* L., juvenile otoliths. J. Fish Biol. 33:409–418.

Bader, R. S.
1965. Fluctuating asymmetry in the dentition of the house mouse. Growth 29:291–300.

Bailit, H. L., P. L. Workman, J. D. Niswander, and C. J. MacLean.
1970. Dental asymmetry as an indicator of genetic and environmental conditions in human populations. Hum. Biol. 42:626–638.

Beacham, T. D.
1990. A genetic analysis of meristic and morphometric variation in chum salmon (*Oncorhynchus keta*) at three different temperatures. Can. J. Fish. Aquat. Sci. 68:225–229.

Beardmore, J. A.
1960. Developmental stability in constant and fluctuating temperatures. Heredity 14:411–422.

Bruckner, D.
1976. The influence of genetic variability on wing symmetry in honeybees (*Apis mellifera*). Evolution 30:100–108.

Charlesworth, D., and B. Charlesworth.
1987. Inbreeding depression and its evolutionary consequences. Ann. Rev. Ecol. System. 18:237–268.

Clarke, G. M.
1992. Fluctuating asymmetry: a technique for measuring developmental stress of genetic and environmental origin. Acta Zool. Fenn. 191:31–36.

Dobzhansky, T., and B. Wallace.
1953. The genetics of homeostasis in *Drosophila*. Proc. Nat. Acad. Sci. U.S.A. 39:162–171.

Doyle, W. J., C. Kelley, M. I. Siegel.
1977. The effects of audiogenic stress on the growth of long bones in the laboratory rat (*Rattus norvegicus*). Growth 41:183–189.

Francis, R. C., and A. Hollowed.
1984. Status of the Pacific hake resource and recommendations for management in 1985. Appendix 2 *in* Status of Pacific coast groundfish fishery and recommendations for management in 1985. Pacific Fishery Management Council, Portland, Oregon.

Leary, R. F., F. W. Allendorph, and K. L. Knudsen.
1983. Developmental stability and enzyme heterozygosity in rainbow trout. Nature 301:71–72.

1984. Superior developmental stability of heteroygotes at enzyme loci in salmonid fishes. Am. Nat. 124:540–551.

1985. Developmental instability and high meristic counts in interspecific hybrids of salmonid fishes. Evolution 39:1318–1326.

Lerner, I. M.

1954. Genetic homeostasis. Oliver and Boyd, London, 134 p.

Lewontin, R. C.

1956. Studies on homeostasis and heterozygosity, I. General considerations. Abdominal bristle number in second chromosome homozygotes of *Drosophila melanogaster*. Am. Nat. 90:237–255.

Mitton, J. B., and M. C. Grant.

1984. Associations among protein heterozygosity, growth rate, and developmental homeostasis. Ann. Rev. Ecol. Syst. 15:479–499.

Palmer, A. R., and C. Strobeck.

1986. Fluctuating asymmetry: measurement, analysis, patterns. Ann. Rev. Ecol. Syst. 17:391–421.

Siegel, M. I., and W. J. Doyle.

1975a. The effects of cold stress on fluctuating asymmetry in the dentition of the mouse. J. Exper. Zool. 193:385–389.

1975b. Stress and fluctuating limb asymmetry in various species of rodents. Growth 39:363–369.

1975c. The differential effects of prenatal and postnatal audiogenic stress on fluctuating asymmetry. J. Exper. Zool. 191:211–214.

Siegel, M. I., and H. H. Smookler.

1973. Fluctuating dental asymmetry and audiogenic stress. Growth 37:35–39.

Siegel, M. I., W. J. Doyle, and C. Kelley.

1977. Heat stress, fluctuating asymmetry, and prenatal selection in the laboratory rat. Am. J. Phys. Anthro. 46:121–126.

Shackell, N. L., and R. W. Doyle.

1990. Scale morphology as an index of developmental stability and stress resistance of Tilapia (*Oreochromis niloticus*). Can. J. Fish. Aquat. Sci. 48:1662–1660.

Sogard, S. M.

1991. Interpretation of otolith microstructure in juvenile winter flounder (*Psuedopleuronectes americanus*): ontogenetic development, daily increment validation, and somatic growth relationships. Can. J. Fish. Aquat. Sci. 48:1862–1871.

Soule, M.

1967. Phenetics of natural populations, II. Asymmetry and evolution in a lizard. Am. Nat. 101:141–160.

1979. Heterozygosity and developmental stability: another look. Evolution 33:396–401.

Soule, M. E., and J. Cuzin-Roudy.

1982. Allomeric variation. 2: Developmental instability of extreme phenotypes. Am. Nat. 20:765–786.

Valentine, D. W., and M. E. Soule.

1973. Effect of p,p'-DDT on developmental stability of pectoral fin rays in the grunion, *Leuresthes tenuis*. Fish. Bull. 71:921–926.

Valentine, D. W., M. E. Soule, and P. Samollow.

1973. Asymmetry analysis in fishes: a possible statistical indicator of environmental stress. Fish. Bull. 71:357–370.

Volk, E. C., R. C. Wissmar, C. A. Simenstad, and D. M. Eggers.

1984. Relationship between otolith microstructure and the growth rate of juvenile chum salmon (*Oncorhyncus keta*) under different prey rations. Can. J. Fish. Aquat. Sci. 41:126–133.

Vrijenhoek, R. C., and S. Lerman.

1982. Heterozygosity and developmental stability under sexual and asexual breeding systems. Evolution 36:768–776.

Wilson, K. H., and P. A. Larkin.

1982. Relationship between thickness of daily growth increments in sagittae and change in body weight of sockeye salmon (*Oncorhynchus nerka*) fry. Can. J. Fish. Aquat. Sci. 39:1335–1339.

Zakharov, V. M.

1982. Analysis of developmental stability as a method of determination of the optimal conditions of development. Doklady Akad. Nauk. SSSR 267:1016–1018.

1989. Future prospects for population phenogenetics. Soviet Scientific Rev., section F, Physiology and General Biology Reviews (T. M. Turpaev and A. V. Yablokov, eds.) 4(3), 79 p.

Zakharov, V. M., and E. D. Bakulina.

1984. Disturbance of developmental stability at crossing different strains of *Drosophila virilis* (variation in the number of ovarioles taken as an example). Genetica 20:1390–1391.

Zakharov, V. M., and G. I. Rubin.

1985. The disturbance of developmental stability as an indicator of anthropogenic influence on animal populations in the Baltic Sea basin. *In* Symposium on ecological investigations of the Baltic Sea environment; Riga, USSR, 1983, 526–536 p. Valtion Painatuskeskus, Helsinki.

Zakhavor, V. M., E. Pankakowski, B. I. Shefter, A. Peltonen, and I. Hauski.

1991. Developmental instability in the common shrew. Am. Nat. 138:797–810.

Zar, J. H.

1984. Biostatistical Analysis, 2nd ed. Prentice-Hall, Englewood Cliffs, NJ, 718 p.