

# UC Irvine

## UC Irvine Previously Published Works

### Title

Genetic variability in krill.

### Permalink

<https://escholarship.org/uc/item/8zg7m7nb>

### Journal

Proceedings of the National Academy of Sciences of the United States of America, 73(2)

### ISSN

0027-8424

### Authors

Valentine, JW

Ayala, FJ

### Publication Date

1976-02-01

### DOI

10.1073/pnas.73.2.658

### Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

## Genetic variability in krill

(adaptive strategies/enzyme polymorphisms/environment-genotype interactions/*Euphausia*)

JAMES W. VALENTINE\* AND FRANCISCO J. AYALA†

\* Department of Geology and † Department of Genetics, University of California, Davis, Calif. 95616

Communicated by Theodosius Dobzhansky, December 19, 1975

**ABSTRACT** We have estimated genetic variability by gel electrophoresis in three species of krill, genus *Euphausia* (Arthropoda: Crustacea). Genetic variability is low where trophic resources are most seasonal, and high where trophic resources are most stable. Similar trends have been found in benthic marine invertebrates. The observed trends of genetic variability do not correlate with trends in the stability of physical environment-parameters.

We have estimated genetic variation in three species of krill of the genus *Euphausia* using standard techniques of gel electrophoresis; our procedures are described elsewhere (1, 2). The species are closely related, belonging to the same subgenus (3). In geographic distribution, however, one species is circumantarctic, another is temperate, and the third is tropical (Fig. 1).

*Euphausia superba* was collected off Palmer Peninsula, Antarctica, near 64° S, 64° W in the Circumpolar Water Mass (4). *E. mucronata* was collected off northern Chile in transition water of the Peru Current at approximately 21° S, 71° W. Two samples of *E. distinguenda* were studied from Pacific Equatorial Water over the Guatemala Basin at 7° 32' N, 92° 16' W, and at 10° N, 93° 45' W. *E. distinguenda* is restricted to tropical waters in the eastern Pacific (3, 5). The biology of *E. superba* is relatively well known (6, 7); this species is legendary for its high assimilation and biomass. The biology of the other two species is less well known.

Table 1 summarizes the electrophoretic findings. Between 28 and 36 loci were studied for each species. The best single measure of genetic variability in large outbreeding populations is the average heterozygosity. The observed frequency of heterozygous loci per individual is for *E. superba* 5.8 ±

0.4% (4), for *E. mucronata* 15.5 ± 1.0%, and for *E. distinguenda* 21.1 ± 0.4%. There is a trend from low genetic variability in the high-latitude species to high genetic variability in the low-latitude species.

There are several hypotheses that predict relations between genetic variability and stability of the environment. One, largely based on theoretical arguments (8), predicts low genetic variability on environments that are stable in physical factors such as climate. Proponents of this hypothesis have specifically predicted low levels of genetic polymorphism in tropical reef settings (9) and in the deep sea (10, 11). Various tests of this hypothesis have produced results incompatible with these predictions (12-18). We have found high levels of genetic variation in organisms from tropical reefs (average heterozygosity about 20% in two populations of the clam *Tridacna*) (13, 14) and from the deep-sea benthos (average heterozygosities about 17% in a brachiopod, an ophiuroid, and four species of starfish) (15-17). Furthermore, intermediate or low levels of genetic polymorphism have been reported in marine invertebrates from temperate waters (2, 19, 20) and from shallow antarctic waters (18). The krill data reported now are also inconsistent with the climatic stability hypothesis. *Euphausia mucronata* faces greater environmental variability in physical parameters (especially temperature) both in the region of our samples and throughout its distributional range, than does either one of the other two species. Yet, the genetic variation of *E. mucronata* is intermediate between that of *E. distinguenda* and *E. superba*.

An alternative hypothesis predicts that genetic variability should be lowest in environments that are most highly sea-

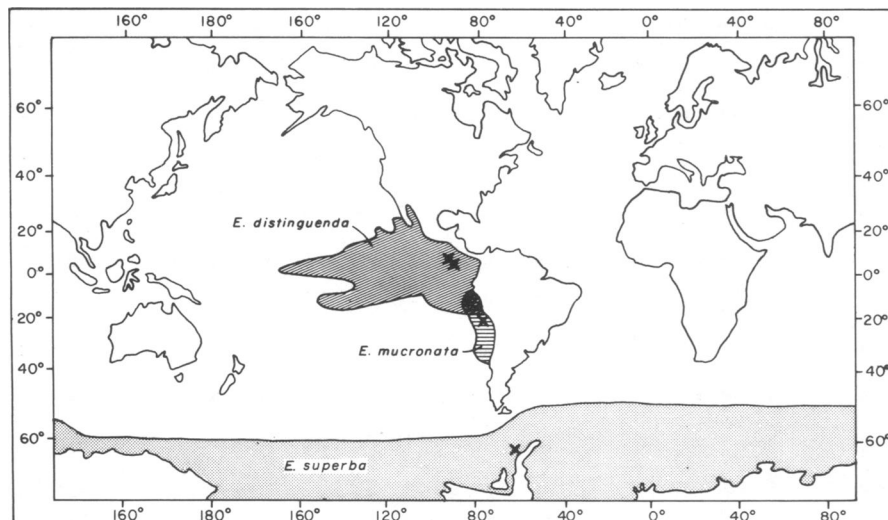


FIG. 1. Distribution of *Euphausia superba*, *E. mucronata*, and *E. distinguenda*. The approximate locations where the samples were obtained are marked by Xs.

Table 1. Genetic variation in three species of the krill *Euphausia*

Parameter	<i>E. superba</i>	<i>E. mucronata</i>	<i>E. distinguenda</i> *
Gene loci sampled	36	28	30
Individuals sampled	127	50	110
Alleles observed per locus	1.81 ± 0.14	2.54 ± 0.30	3.20 ± 0.28
Frequency of polymorphic loci†	0.139	0.571	0.700
Mean heterozygosity:			
(1) Expected (average over loci)	0.057 ± 0.019	0.141 ± 0.025	0.213 ± 0.034
(2) Observed (average over individuals)	0.058 ± 0.004	0.155 ± 0.010	0.211 ± 0.005

\* The two populations sampled have been pooled, since they are genetically very similar.

† A locus is considered polymorphic when the frequency of the most common allele ≤ 0.95.

sonal or otherwise temporally variable in trophic resources (16, 18). This hypothesis was advanced to account for the observation that genetic variability in benthonic marine species correlates with patterns of marine species diversity (21, 22). In ecosystems of rich species diversity, levels of genetic variability are generally high. Unfortunately, data on the seasonality of trophic resources are available for only a few scattered stations in the seas. General patterns of trophic stability must then be inferred from whatever data are available on productivity together with hydrographic, chemical, and meteorological information (23).

In general, the productivity of the oceans is most seasonal in the highest latitudes, where there may be only one short but pronounced bloom per year. In temperate regions blooms tend to be repeated or extended over spring and fall maxima with lower summer levels; productivity rarely approaches the near-zero level characteristic of high latitudes. In the tropics, annual variations are greatly damped; productivity, although low at any one time, tends to vary little throughout the year. Local conditions can, however, modify greatly the general picture just presented. Highly seasonal upwelling, for example, generates seasonal productivity in some tropical latitudes (23).

The general latitudinal variation appears to hold for the stations where our krill populations were sampled. Among our three species, the population (*E. superba*) from circumpolar water faces the longest period with productivity nearly or completely absent, with a brief but large spring bloom (23, 24). In the waters of the Peru Current from which *E. mucronata* was obtained, annual productivity must be very high (25). Adequately high levels of productivity have been recorded in March and April from stations within 10 miles of shore (26). These studies made in waters several degrees to the north of our krill sampling station show that upwelling generated by the prevailing winds is chiefly responsible for the high productivity; the high levels of productivity must be fairly prolonged. Thus, although the upwelling is somewhat irregular, seasonality is considerably less pronounced than in the circumantarctic waters. In the tropical eastern Pacific from which *E. distinguenda* was sampled, upwelling associated with the dynamics of the equatorial current systems raises productivity levels above the tropical average; but in spite of the perturbations, the productivity is there certainly more stable than in the waters where the other two species were sampled (23, 27).

A further complication in estimating the trophic resource regimes of animals derives from the fact that the feeding habits of particular populations may either lessen or increase

the effects of variations in primary productivity. For example, detritus feeders may exploit over long periods of time the resources generated during short bursts of production, while species that stop feeding during reproductive phases may have seasonal growth patterns even in areas of stable productivity. We have tried to minimize such effects by studying closely related krill species with similar ecological roles even though they live in water masses having different regimes of productivity.

We conclude that pelagic krill exhibit a correlation between the seasonality of productivity and the levels of genetic variation. Where trophic resources are less seasonal (= more stable) genetic variability is higher. We have previously inferred the same relationship for benthic marine invertebrates. Doubtless, levels of genetic variation are affected by a variety of factors (28, 29), but the seasonality of trophic resources appears to play a significant role. This may be because unstable resources favor generalized ecological strategies so that the occurrence of only a few flexible genotypes enhances adaptation under such conditions (30).

We thank E. Brinton, Scripps Institution of Oceanography, for providing the samples of *E. mucronata* and *E. distinguenda*, for critically reading the manuscript, and for other courtesies.

1. Ayala, F. J., Tracey, M. L., Mourão, C. A. & Pérez-Salas, S. (1972) *Genetics* 70, 113-139.
2. Ayala, F. J., Valentine, J. W., Barr, L. G. & Zumwalt, G. S. (1974) *Biochem. Genet.* 18, 413-427.
3. Brinton, E. (1975) *Euphausiids of Southeast Asian Waters, "Naga Reports," Contrib. Scripps Inst. Oceanogr.* (Univ. of Calif. Press, Berkeley, Calif.), Vol. 4, pt. 5.
4. Ayala, F. J., Valentine, J. W. & Zumwalt, G. S. (1975) *Limnol. Oceanogr.* 20, 635-640.
5. Brinton, E. (1962) *Bull. Scripps Inst. Oceanogr.* 8, 51-269.
6. Mauchline, J. & Fisher, L. R. (1969) *Adv. Mar. Biol.* 7.
7. Marr, J. W. S. (1962) "Discovery" Rept. 32, 33-464.
8. Levins, R. (1968) *Evolution in Changing Environments* (Princeton Univ. Press, Princeton, N.J.).
9. Grassle, J. F. (1973) in *Biology and Geology of Coral Reefs*, eds. Jones, O. A. & Endean, R. (Academic Press, New York), Vol. 2, pp. 247-270.
10. Grassle, J. F. (1972) *Fifth Eur. Mar. Biol. Symp.*, Piccin Editore, Padua, pp. 19-26.
11. Grassle, J. F. & Sanders, H. L. (1973) *Deep-Sea Res.* 20, 643-659.
12. Gooch, J. L. & Schopf, T. J. M. (1972) *Evolution* 26, 545-552.
13. Ayala, F. J., Hedgcock, D., Zumwalt, G. S. & Valentine, J. W. (1973) *Evolution* 27, 177-191.
14. Campbell, C. A., Valentine, J. W. & Ayala, F. J. (1976) *Mar.*

- Biol.*, in press.
15. Ayala, F. J. & Valentine, J. W. (1974) *Mar. Biol.* **27**, 51-57.
  16. Valentine, J. W. & Ayala, F. J. (1975) *Deep-Sea Res.* **22**, 37-44.
  17. Ayala, F. J., Valentine, J. W., Hedgecock, D. & Barr, L. G. (1975) *Evolution* **29**, 203-212.
  18. Ayala, F. J., Valentine, J. W., DeLaca, T. E. & Zumwalt, G. S. (1975) *J. Paleontol.* **49**, 1-9.
  19. Selander, R. K., Yang, S. Y., Lewontin, R. C. & Johnson, W. E. (1970) *Evolution* **24**, 402-414.
  20. Schopf, T. J. M. & Murphy, L. S. (1973) *Biol. Bull.* **145**, 589-597.
  21. Valentine, J. W. (1971) *Lethaia* **4**, 51-61.
  22. Valentine, J. W. (1974) *Evolutionary Paleocology of the Marine Biosphere* (Prentice-Hall, Englewood Cliffs, N.J.).
  23. Ryther, J. H. (1963) in *The Sea*, ed. Hill, M. N. (Interscience Publ., New York), Vol. 2, pp. 347-380.
  24. El-Sayed, S. Z. (1970) in *Antarctic Ecology* (Academic Press, London), Vol. 1, pp. 119-135.
  25. Posner, G. S. (1957) *Bull. Bingham Oceanogr. Collect.* **16**, 106-155.
  26. Ryther, J. H., Menzel, D. W., Hilburt, E. M., Lorenzen, C. J. & Corvin, N. (1971) *Invest. Pesq.* **35**, 43-59.
  27. Holmes, R. W., Schaefer, M. B. & Shimada, B. M. (1957) *Bull. Inter-Amer. Trop. Tuna Comm.* **4**, 129-156.
  28. Selander, R. K. & Kaufman, D. W. (1973) *Proc. Nat. Acad. Sci. USA* **70**, 1875-1877.
  29. Somero, G. N. & Soulé, M. (1974) *Nature* **249**, 670-672.
  30. Da Cunha, A. B., Dobzhansky, T., Pavlovsky, O. & Spassky, B. (1959) *Evolution* **13**, 389-404.