tistic are thus indicative of heterogeneity among the data sets. The multiple comparisons were performed with the use of a standard computer program (MRANK of SAS 79.5; *12*). Since unmated females might either represent "slow" females, that is, simply not inclined to mate in the 30-minute observation period, or qualitatively different "nonmaters", several samples were analyzed with the "unmated" class of females both included and deleted. The results of the Kruskal-Wallis tests for heterogeneity of sample means are presented in Table 2. The significance levels of the various tests were determined with full cognizance that multiple a posteriori comparisons have true significance levels (*p* values) somewhat higher than those determined from the standard tabled distributions of the χ^2 statistic for single a priori tests.

The 1981 test distributions of Fig. 1 present an interesting problem in interpreting the heterogeneity tests, since the two slow-mating lines S-1 and S-1-T exhibit different patterns depending on whether unmated females are included (Fig. 1B) or excluded (Fig. 1A) from the analysis. In the former case, the two controls (Salvador and K-23) are very similar, and the two slow maters (S-1 and S-1-T) are mildly different; these pairs, however, differ widely from each other [CE, HI, and (CE) (HI), respectively, in Tables 1 and 2]. With unmated females excluded, on the other hand, S-1 becomes indistinguishable from the Salvador controls while S-1-T remains significantly different (see Fig. 1A and CH, CI, right side of Table 2). It is as if the slower overall mating speed of S-1 was attributable not to a rightward shift of the whole mating time distribution, but to the mixture of two impaternate clones with different mating profiles. One of these may mate in a way similar to the controls and includes a peak of nonmaters resulting from the threshold effect of measuring mating for only 30 minutes. The other clone would appear to show little or no tendency to mate at all. Thus, S-1-T, having gone through eight generations of isogenization, may represent a pure strain of slow maters while the relatively large differences between the 1980 and 1981 tests of S-1 might be attributed to stochastic shifts in the relative number of females tested from each of the "mating" and "nonmating" clones.

The general similarity of S-1-T to S-1 permits inference of the approximate time of the major alteration of the behavior of the original S-1 females as occurring some time after the 1973 tests but before 1975, when the subsample was sent to Templeton. Contamination of the S-1 strain by another low-propensity strain can be ruled out, since each of the latter present in the laboratory was carrying a marker gene in homozygous state. Decay of mating behavior as found in the S-1 strain is not unprecedented. Incidental to another study, Henslee (*13*) noted a significant drop in mating propensity in the course of his experiments with a derivative of the unisexual stock RS-3. At the time of his work, the isogenizing nature of the genetic system operating in *D. mercatorum* was not fully understood.

Although we favor a genetic interpretation of this behavioral change, an extrinsic cause, such as a microbial infection, cannot be ruled out. We contend that unisexually reproducing stocks artificially made from bisexual ones provide an exceptional opportunity to test the genetic decay of characters pertaining to sexual reproduction. Females of *Drosophila* are well known to exercise choice in mating (*14, 15*). Permanent removal of males from the environment of females, therefore, appears to serve as a sensitive test for Muller's hypothesis, outlined earlier. A stock that is automatically isogenizing in each generation may experience a number of random mutations, some of which may be expected to be deleterious to the proper functioning of mating behavior. If they do not have dysgenic side effects, such mutants may become fixed purely by chance, since normalizing natural selection will not function to remove them. Theory relating to the fixation of neutral mutations is well developed (*16*); the present case appears to provide an example; a destructive mutation need not be deleterious and can become incorporated much as a neutral gene change would be. The "decline and fall of the female" in the S-1 strain of *D. mercatorum* serves as a useful microevolutionary model for the regressive evolution of characters to vestiges which have become functionless with regard to the Darwinian fitness of the individual.

HAMPTON L. CARSON
LINDA S. CHANG
TERRENCE W. LYTTLE

*Department of Genetics,
University of Hawaii at Manoa,
Honolulu 96822*

References and Notes

1. H. Muller, *Proc. Am. Philos. Soc.* **93**, 459 (1949).
2. H. Carson, *Genetics* **55**, 157 (1967).
3. A. Templeton, H. L. Carson, C. F. Sing, *ibid.* **82**, 527 (1976).
4. H. Carson, *ibid.* **63**, 619 (1969).
5. ———, I. Y. Wei, J. A. Niederkorn, Jr., *Proc. Natl. Acad. Sci. U.S.A.* **70**, 1772 (1973).
6. H. Carson and S. Snyder, *Egypt. J. Genet. Cytol.* **1**, 256 (1972).
7. J. Annest and A. Templeton, *Genetics* **89**, 193 (1978).
8. H. Ikeda and H. Carson, *ibid.* **75**, 541 (1973).
9. H. Ikeda *et al.*, *Behav. Genet.* **10**, 361 (1980).
10. H. Carson *et al.*, *ibid.* **7**, 189 (1977).
11. J. Bradley, *Distribution-Free Statistical Tests* (Prentice-Hall, Englewood Cliffs, N.J., 1968).
12. W. Sarle, *Statistical Analyses Systems, Technical Report X-120X* (SAS Institute, Cary, N.C., 1981).
13. E. Henslee, *Am. Nat.* **100**, 191 (1966).
14. L. Ehrman and E. Spiess, *ibid.* **103**, 675 (1969).
15. E. Spiess and H. Carson, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 3088 (1981).
16. M. Kimura and T. Ohta, *ibid.* **75**, 2868 (1978).
17. We thank J. W. Archie, C. M. Simon, A. R. Templeton, and L. T. Teramoto for comments. Supported by NSF grant DEB 7926692.

5 April 1982; revised 14 May 1982

Interoceanic Differences in the Reproduction of Coral-Reef Fishes

Abstract. *Eggs of demersal spawning coral-reef fishes of the tropical western Atlantic are smaller than those of related species in the western Pacific. Decreased egg volume may result in increased fecundity per unit body weight of Atlantic species, a factor that may underlie apparent differences in the stability of the respective coral-reef fish communities.*

Interoceanic differences in the ecology of marine animals have been suggested (*1*) but have not been widely documented. Investigators of coral-reef fishes often assume that differences between western Atlantic and western Pacific faunas are minimal (*2, 3*). This assumption is based primarily on broad systematic overlap at the generic level. Comparison of life histories to test this assumption is difficult because of the often lengthy planktonic larval stages characteristic of these fishes—a stage of development about which little is known. One aspect of reproduction, however, is amenable to comparison: the size of eggs produced by fishes from each area. Egg size has been linked to fecundity, size of newly hatched larvae, and duration of the planktonic larval stages (*4, 5*). An analysis of egg-size distributions for fishes in the two ocean regions showed that there are statistically significant differences for several important families, which might

Table 1. Mean egg volume (± standard deviation) for five families of coral-reef fishes common to the western Atlantic and western Pacific. Statistical significance (P) determined by Komolgorov-Smirnoff test.

Family	Western Atlantic		Western Pacific		P
	Egg volume (mm³)	Number of species	Egg volume (mm³)	Number of species	
		Demersal spawners			
Pomacentrinae	0.662 ± 0.21	7	1.85 ± 0.858	19	.013
Apogonidae	0.014 ± 0.01	3	0.219 ± 0.063	6	.036
Blenniidae	0.086 ± 0.03	2	0.246 ± 0.184	15	.63
		Pelagic spawners			
Pomacanthidae	0.290 ± 0.114	3	0.217 ± 0.084	7	.61
Acanthuridae	0.164 ± 0.022	2	0.122 ± 0.045	4	.71

lead to fundamental differences in the dynamics of community composition.

Data for the comparison were obtained from the literature (*6*), various investigators (*7*), and measurements of eggs at One Tree Island on the Great Barrier Reef, Australia (*8*). Calculations of egg volumes were based on the approximate shapes of the eggs—cylindrical, spherical, or hemispherical—and the lengths of the major and minor axes. If more than one value was available for a species, an average size was used. Egg volumes were analyzed for five groups (*9*) of fishes that are common to both faunas; three produce demersal eggs and two produce pelagic eggs (*6*).

Comparisons of size-frequency distributions of egg volumes (Table 1 and Fig. 1) indicate marked differences between oceans among demersal spawners; average egg volumes for western Pacific species sampled range from 280 percent (Pomacentrinae) to 535 percent (Apogonidae) larger than those for the same families in the western Atlantic. The differences are statistically significant, despite small sample sizes, for the Pomacentrinae (P = .027) and the Apogonidae (P = .036) (*10*) but not for the Blenniidae (P = .63), although the pattern of egg sizes of Blenniidae is similar to those of the other families. Egg volumes do not differ significantly between areas for the two pelagic spawning families (Acanthuridae and Pomacanthidae), nor is there evidence of a trend comparable to that apparent for demersal spawning families.

Fish egg volumes vary with water temperature (*11*), latitude (*12*), and adult size and body condition (*4, 5*), but none of these factors appeared relevant in this analysis; water temperatures during spawning periods are similar in the two regions (*13*); both areas reach their temperate limits at latitudes of approximately 25°, and adult sizes for species sampled are comparable within families (*14–16*). Body condition is difficult to quantify, but spawning adults in both oceans appeared equally healthy and well fed (*17*). Chance systematic effects or a sampling bias are unlikely sources of the differences, in view of the common pattern of the size-frequency distribution of egg volumes for at least three families and the diverse data sources.

Several investigators (*5, 18*) have suggested an optimality approach to egg size; selection is suggested to maximize some combined function of size of the newly hatched larva, which increases with egg volume, and fecundity, which decreases with egg volume (*19*). Some as yet unidentified factor or factors may be selecting for production of more, but smaller, eggs for the western Atlantic representatives of some families than for western Pacific confamilials. Size at settlement onto the reef appears to be comparable in the two areas (*20*), suggesting that the selection relates primarily to rates of egg and larval survival, larval growth rates, or duration of the planktonic larval stage. Two selective factors that have been related to egg size in fishes, water column productivity (higher productivity leads to smaller eggs) (*21*) and amount of parental care (more care coincides with larger eggs) (*4, 5*), however, do not unambiguously account for observed interoceanic differences. There is some evidence that plankton productivity is higher in the tropical western Atlantic than that in the tropical western Pacific (*22*), but why such increased productivity would affect demersal, but not pelagic, spawning families is not clear (*23, 24*). Extent of parental care within families appears equal in the two areas; for example, apogonids in both incubate their eggs in their mouths (*6*). Comparisons between families, moreover, suggest a weak relation between egg size and amount and type of parental care in reef fishes (*25*).

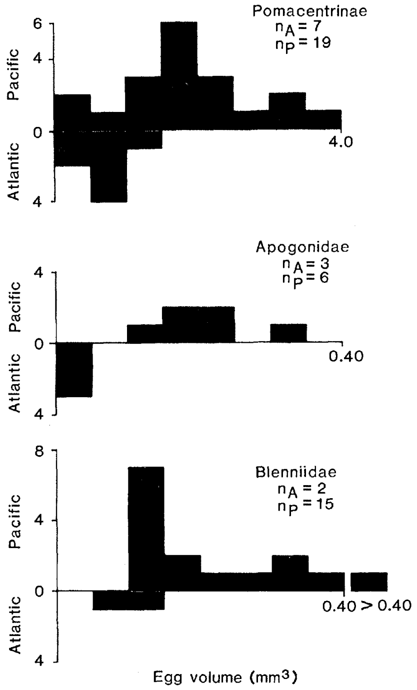

Fig. 1. Size-frequency distributions of egg volumes for three groups of demersal spawning fishes common to tropical western Atlantic and tropical western Pacific coral reefs. Sample sizes are given for the western Atlantic (n_A) and the western Pacific (n_P) oceans.

Whatever the causal factors, differences in egg volumes between the two areas may be fundamentally related to dynamics of the respective fish communities. As noted, increased egg size in fishes broadly correlates with decreased fecundity per unit of adult weight (*4, 5*). Demersal spawning species in the western Atlantic, therefore, are likely to be more fecund than western Pacific species of comparable size; data to test this possibility are not yet available. Higher fecundity, in turn, suggests that overall rates of recruitment onto the reef may be greater (*26*). If this is so, western Atlantic coral-reef fish communities may be more nearly saturated with individuals, and thus more prone to competitive interactions, than are western Pacific communities (*27*).

R. E. THRESHER*

Department of Biological Sciences,
University of Sydney,
N.S.W. 2006, Australia

References and Notes

1. G. J. Vermeij, *Biogeography and Adaptation* (Harvard Univ. Press, Cambridge, Mass., 1978) pp. 113–148.
2. G. S. Helfman, *Environ. Biol. Fish.* **3**, 129 (1978).
3. P. F. Sale, *Oceanogr. Mar. Biol. Annu. Rev.* **18**, 367 (1980).
4. J. H. S. Blaxter, in *Fish Physiology*, W. S. Hoar and D. J. Randall, Eds. (Academic Press, New York, 1969), vol. 3, pp. 171–252; R. H. K. Mann and C. A. Mills, *Symp. Zool. Soc. London* **44**, 161 (1979).
5. D. M. Ware, *J. Fish. Res. Board Can.* **32**, 2503 (1975).
6. R. E. Thresher, *Reproduction in Reef Fishes*

(Tropical Fish Hobbyist, Neptune City, N.J., in press).
7. Personal communications: P. L. Colin on western Atlantic species, M. Schmale on western Atlantic Pomacentrinae, W. Douglas on western Pacific Apogonidae, B. C. Russell and B. Carlson on western Pacific Blenniidae, and J. Moyer on western Pacific Pomacanthidae.
8. Eggs were collected from nests of 19 pomacentrins and five blenniids, and from males of two species of apogonids. A binocular microscope and a ruled ocular were used to measure live eggs. The same procedure was used by the investigators listed in (*5*).
9. Because there are statistically significant differences in the egg size of pomacentrid subfamilies (R. E. Thresher, in preparation), analysis was limited to the Pomacentrinae, the only subfamily for which good comparative data are available. All other comparisons are at the family level.
10. Komolgorov-Smirnoff test for unequal sample sizes.
11. A. J. Southward and N. Demir, in *The Early Life History of Fish*, J. H. S. Blaxter, Ed. (Springer-Verlag, New York, 1974), pp. 53–68.
12. T. S. Rass, *Jubilee Publ. Mosc. Soc. Nat.* **1** (1942).
13. R. E. Johannes, *Environ. Biol. Fish* **3**, 65 (1978).
14. Average maximum adult sizes reported are as follows: (i) Pomacentrinae, $\bar{X} = 11.8$ cm standard length (S.L.), variance = 14.8 in the western Atlantic, and $\bar{X} = 9.2$ cm S.L., variance = 10.3 in the western Pacific ($P > .10$, Mann-Whitney U test); (ii) Apogonidae, $\bar{X} = 7.6$ cm S.L., variance = 14.5 in the western Atlantic and $\bar{X} = 12.0$ cm S.L., variance = 14.8 in the western Pacific ($P > .25$); and (iii) Blenniidae, $\bar{X} = 10.9$ cm S.L., variance = 0.4 in the western Atlantic and $\bar{X} = 9.4$ cm S.L., variance = 7.0 in the western Pacific ($P > .25$).
15. The correlations between egg volume and adult size were statistically significant for both pelagic spawning families (Pomacanthidae, $r = .84$, $N = 10$; Acanthuridae, $r = .66$, $N = 5$) but not for demersal spawning families, on the basis of data for Pacific species only to avoid confounding interoceanic effects (Pomacentridae, $r = .11$, $N = 19$; Apogonidae, $r = .35$, $N = 6$; and Blenniidae, $r = .14$, $N = 13$).
16. No data are available on annual or seasonal variations in egg volume for any reef-associated species, but seasonal variation, at least, appears to be minimal.
17. R. E. Thresher, personal observations.
18. G. Svardson, *Rep. Inst. Freshwater Res. Drottningholm* **29**, 115 (1949); G. C. Williams, *Adaptation and Natural Selection* (Princeton Univ. Press, Princeton, N.J., 1966), pp. 158–192; C. C. Smith and S. D. Fretwell, *Am. Nat.* **108**, 499 (1974).
19. R. E. Johannes (*13*) and P. F. Sale (*3*) both emphasize that coral-reef fishes are apparently under strong selection to maximize fecundity.
20. For the Pomacentrinae, the only group for which such data are available, the mean size of smallest individuals for seven Atlantic species, recorded by A. R. Emery [*Bull. Mar. Sci.* **23**, 649 (1973)], is 10.9 mm S.L. with a variance of 3.05 mm; the mean size at settlement for the only three western Pacific species for which data are available is 10.0 mm S.L. with a variance of 0.65 [R. E. Thresher, personal observations and references in (*6*)].
21. D. H. Cushing, *J. Mar. Biol. Assoc. U.K.* **47**, 193 (1967); T. B. Bagenal, *J. Fish Biol.* **3**, 207 (1971).
22. T. R. Parsons *et al.*, *Biological Oceanographic Processes* (Pergamon, Oxford, ed. 2, 1977), p. 20; R. W. Sheldon, A. Prakash, W. H. Sutcliffe, Jr., *Limnol. Oceanogr.* **3**, 327 (1972).
23. The correlation between water column productivity and egg volume in reef fishes can be independently tested by measuring egg volumes in other areas of high plankton productivity, such as the Red Sea.
24. J. M. Leis and J. M. Miller [*Mar. Biol.* **36**, 359 (1976)] report that larvae of pelagic spawning and demersal spawning families at Hawaii are typically found in different planktonic environments. If a general rule, this difference might bear on the possibly different effects of plankton productivity on the two groups.
25. R. E. Thresher, in preparation.
26. The relation is probably a loose one, especially when one considers the probable complexity of interactions in the plankton and stochastic processes associated with larval survival and recruitment onto the reef.
27. Studies on the dynamics of reef-fish communities emphasize the Pomacentrinae, benthic territorial damselfishes, as key species. This emphasis may, in fact, be maximizing differences between western Atlantic and western Pacific communities.
28. I thank B. Carlson, P. L. Colin, W. Douglas, J. T. Moyer, B. Russell, and M. Schmale for invaluable information on egg sizes; A. M. Gronell for assistance throughout the study; A. Press and A. J. Underwood for advice on statistical analysis; H. Caffey for pointing out relevant literature; and P. J. Doherty, A. M. Gronell, P. F. Sale, and R. Shine for critical reviews of the manuscript. Supported by grants from the Australian Research Grants Committee, the University of Sydney, and, especially, a Queen Elizabeth II Fellowship in Marine Science. This is a contribution from the One Tree Island Field Station.

* Present address: Section of Ecology and Systematics, Cornell University, Ithaca 14853.

10 August 1981; revised 20 April 1982

Colony Defense by Africanized and European Honey Bees

Abstract. *Africanized and European honey bee (*Apis mellifera*) populations showed quantitative differences in colony defensive behavior. Africanized bees responded faster and in much larger numbers than European honey bees and produced 8.2 and 5.9 times as many stings during two different experiments. Times to react to alarming stimuli were negatively correlated with the number of bees responding and to the total number of stings. The number of bees responding was significantly correlated to the total number of stings only for the Africanized population.*

By 1990 (*1*), American agriculture may have to deal with the immigration of the Africanized bee, an insect with the potential to alter agricultural practices and significantly increase the cost of bee-pollinated food products. Honey bees (*Apis mellifera*) are not native to the Western Hemisphere, but were introduced to the Americas through importations of European stocks (*A. m. mellifera* and *A. m. ligustica*) since 1621 (*2*). In 1956, a variety from Africa, *A. m. scutellata* (formerly *adansonii*) (*3*) was introduced into Brazil for the purpose of improving honey production with a more tropically adapted bee (*4*). The variety of honey bee resulting from the interbreeding of the established European and newly imported African types, referred to as the Africanized bee, has spread through much of South America and into Panama.

The Africanized bee has received considerable coverage in the popular press, from early stories about hoards of bees stinging victims to death and the subsequent "killer bee" label to more recent reports from Brazil that the bees are no longer a problem. The tendency to sting readily is the most objectionable charac-

Table 1. Correlations between defensive behavior measures in European (E) and Africanized (A) honey bees. Data are from experiment 1 only. Pre, before testing.

Item	Time to react to		Number of bees in picture at				Total number of stings
	Pheromone	Targets	Pre	30 seconds	60 seconds	90 seconds	
Time to react to							
Pheromone							
E	1.00	.01	−.15*	−.30†	−.29†	−.28†	.02
A	1.00	.29†	−.16†	−.41†	−.42†	−.32†	−.30†
Targets							
E		1.00	−.09	−.09	−.17†	−.16†	−.38†
A		1.00	−.09	−.15†	−.16†	−.08	−.18†
Number of bees in picture							
Pre							
E			1.00	.55†	.53†	.45†	.02
A			1.00	.76†	.66†	.53†	.13*
30 seconds							
E				1.00	.93†	.80†	.04
A				1.00	.94†	.76†	.31†
60 seconds							
E					1.00	.90†	.10
A					1.00	.83†	.31†
90 seconds							
E						1.00	.19†
A						1.00	.27†
Total number of stings							
E							1.00
A							1.00

Significant at $^*P < .05$, $^\dagger P < .01$.