A Natural Experiment in Life-History Evolution: Field Data on the Introduction of Mosquitofish (Gambusia affinis) to Hawaii
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A NATURAL EXPERIMENT IN LIFE-HISTORY EVOLUTION:
FIELD DATA ON THE INTRODUCTION OF MOSQUITOFISH
(GAMBUSIA AFFINIS) TO HAWAII

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Patterns in life-history variation were first explained by differences in mode of population regulation \(r\&K\)-selection. Alternative explanations were based on differences in adult and juvenile mortality rates (Stearns, 1976). It now seems appropriate to base predictions on age-specific mortality and fecundity rates and on the cost of reproduction. Thus I agree with Schaffer (1979), Charlesworth (1980), and others who argue that \(r\&K\)-selection is inadequate and outmoded. First, density-dependent mortality applied equally to all age classes selects for early maturity, high fecundity, and a short life, just as does constant density-independent mortality. Second, fluctuations in effective reproduction (fecundity \(\times\) juvenile survival) have consequences not reflected in \(r\&K\)-selection. Third, \(r\&K\)-selection contains no trade-off between current reproduction and residual reproductive value and no age-specific effects. Thus it misleads by suggesting that the evolutionary origin of variation in life-histories resides in the mode of population regulation, whereas the directly causal mechanisms are much more precisely expressed as changes in age-specific mortality and fecundity regimes and the cost of reproduction. Those must be measured to provide a strong test of the theory.

The predictions best supported by selection experiments (Sokal, 1970; Mertz, 1975; Taylor and Condra, 1980; Barclay and Gregory, 1981) and by comparisons of wild populations (see articles reviewed in Stearns 1976, 1977, 1980) are these: (1) High, variable, or unpredictable adult mortality rates select for increased reproduction early in life. (2) High, variable, or unpredictable juvenile mortality rates select for decreased reproduction and longer adult life.

This paper begins a test of age-specific models. In designing this study, I kept in mind certain criteria for assessing life-history studies (Stearns, 1977): they should contain measurements of the environmental factors invoked as evolutionary causes, of the variation of life-history traits among populations in the field, of the genetic component of that variation measured in the laboratory under constant conditions, of the time-series of age-specific mortality rates, and of reproductive efforts. Here I report evidence bearing on the first two criteria. In Stearns (1983) I report evidence bearing on the third.

Without field data on age- and size-specific mortality rates, I cannot directly test current predictions. This paper tests assumptions about the differences between stable and fluctuating environments and evaluates alternative explanations of what causes variation among populations.

MATERIALS AND METHODS

Study Sites

In 1905, about 150 mosquito fish were introduced from Texas to Hawaii (Seale, 1905), and by 1910 their numerous descendants had been spread into reservoirs on sugar plantations. Water levels in some reservoirs fluctuated because they were used for irrigation. Other reservoirs were abandoned by 1910 because harvesting practices changed, and their water levels have fluctuated very little since then. In 1974 I collected at least 250 fish from each of 24 reservoirs, four stable and 20 fluct-
tuating in water level, and analyzed their life-history traits. I also analyzed the plantations' daily records of reservoir water levels to describe the fluctuation patterns.

All reservoirs sampled were located on Maui, Hawaii, or Oahu (Fig. 1). Their elevations ranged from 6 to 564 m. On the dates sampled, water temperatures at a depth of 45 cm ranged from 19.5 C to 25 C (Table 1).

Three stable reservoirs were on Hawaii, one on Oahu. Eighteen fluctuating reservoirs were on Maui, two on Oahu. There is no water route between the reservoirs on Oahu, or between the reservoirs on Hawaii. On Maui, the 18 fluctuating reservoirs are connected by irrigation ditches that flow right to left on Figure 1. Only Reservoirs 21, 22, and 40, which are above the other reservoirs, and Reservoir 91, with a different water source, can be considered isolated. Fish probably do not move among islands or among reservoirs on Hawaii and Oahu, but can move downstream on Maui.

**Fish Samples**

Fish were collected from 24 reservoirs in the wet season (December–February, 1973–1974) and again from six of those reservoirs at the end of the dry season (November, 1974), using a seine with a mesh size of 2.2–2.8 mm. I took five samples at all reservoirs except four of those sampled in November, at which I took three samples. Sampling sites included all obvious habitat types in the reservoir. Each sample consisted of the fish collected in enough sweeps of the seine to produce 100 fish or to exhaust the fish in the area. Thus the effort per sample varied. The fish were preserved in 10% formalin, then transferred after 2–5 weeks to alcohol.

Fifty fish were selected at random from each preserved sample. Each fish was measured (standard length) to 0.1 mm,
LIFE-HISTORY EVOLUTION

Table 1. Reservoir characteristics. Temperatures were taken at 45 cm depth. S/F indicates whether reservoir is stable or fluctuating.

<table>
<thead>
<tr>
<th>Island</th>
<th>Reservoir</th>
<th>Elev. (m)</th>
<th>Constructed</th>
<th>Sampled</th>
<th>Temp</th>
<th>S/F (1)</th>
</tr>
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<td></td>
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<tr>
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<td>Twin</td>
<td>564</td>
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<td>31 Dec 73</td>
<td>20 C</td>
<td>S</td>
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<tr>
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<td></td>
<td></td>
<td></td>
<td>27 Nov 74</td>
<td>21</td>
<td>S</td>
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<tr>
<td></td>
<td>Kay</td>
<td>503</td>
<td>Before 1910</td>
<td>5 Feb 74</td>
<td>20</td>
<td>S</td>
</tr>
<tr>
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<td></td>
<td></td>
<td>27 Nov 74</td>
<td>21</td>
<td>S</td>
</tr>
<tr>
<td></td>
<td>Kaahue</td>
<td>251</td>
<td>Before 1910</td>
<td>2 Jan 74</td>
<td>21</td>
<td>S</td>
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<tr>
<td></td>
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<td>6</td>
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<tr>
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<td>F</td>
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<tr>
<td></td>
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<td>1914</td>
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<td>21</td>
<td>F</td>
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<td>Maui</td>
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<td>Res. 22</td>
<td>258</td>
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<td></td>
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<td>117</td>
<td>Before 1907</td>
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<tr>
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<tr>
<td></td>
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<td>165</td>
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<td>Before 1910</td>
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<td>23</td>
<td>F</td>
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<td>Before 1910</td>
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<td>23</td>
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<td>F</td>
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<tr>
<td></td>
<td>Res. 91</td>
<td>53</td>
<td>Before 1910</td>
<td>21 Jan 74</td>
<td>25</td>
<td>F</td>
</tr>
</tbody>
</table>

classified as adult female, juvenile female, adult male, juvenile male, or unsexed juvenile, and, if an adult female, dissected.

Embryos were classified as uneyed small (NES), uneyed large (NEL), early-eyed (EE), late-eyed (LE), and very late-eyed (VLE). These states correspond to those of Chambolle, Cambar, and Tran (1970) as follows: NES, not yet yolked or fertilized; NEL, yolked but not yet fertilized through Stage 17 (11 to 16 days after fertilization at 25 C); EE, Stages 18 through 24 (11 to 19 days); LE, Stages 25 through 32 (16 to 25 days); VLE, Stages 33 through 35 (23 to 28 days). Fish and embryos were dried at 100 C for 6 h, then each fish and each class of embryos was weighed (±0.05 mg).

Reservoir Fluctuation Data

I got daily records of the water level at 0700 h in 18 reservoirs on Maui (January, 1959 to December, 1974 = 5,818 days) and for one reservoir on Oahu (November, 1943 to January, 1971 = 9,950 days). Plantation officials estimated the accuracy of the records at ±15 cm. On Maui, data from weekends and holidays were missing after 1965, which amounted to 31.5% of the data over that period, or 19.8% of the data from 1959 to 1974. I assumed that the reservoirs remained at the last recorded level until the night before the next recorded level. No data were missing for the reservoir on Oahu. I then converted the water levels first to volume, then to percent full.

The fluctuation data were transformed using time-series analysis (see Appendix for details). I then did a factor analysis of the derived descriptions to get a lower-dimensional description of the reservoirs in terms of water fluctuation patterns. These measurements of the physical similarities of
the reservoirs were compared with similarities in life-history traits among the fish inhabiting the reservoirs.

Statistical Analyses

The analyses aimed to answer these questions: Did the stocks differ in their life-history traits? Were there differences in the life-histories of fish from stable reservoirs and from fluctuating reservoirs? What impact did fluctuations in water level have on the expression of life-history traits in the field? All analyses of variance were done according to procedures given in Sokal and Rohlf (1981). Principle components and multiple regression analyses were done with programs P4M and P1R in the BMDP package (Dixon and Brown, 1977). Fecundity, weight, weight of embryos, and condition factors were not transformed before analysis. Reproductive allocation was first given the arcsine-squareroot transformation.

RESULTS AND DISCUSSION

One-hundred fifty generations after they shared ancestors, do populations from stable and fluctuating reservoirs differ in their life-history traits? Both stable and fluctuating classes, and individual populations, do differ significantly in important life-history traits.

In Hawaii, these fish breed in every month of the year. In the wet season, most females are pregnant and in good condition; in the dry season, the pregnancy rate drops and fish are thinner. The wet season runs from November or December through April or May. Thus the main sample came from populations in which the intensity of reproduction had recently increased with the start of the wet season. Throughout, I use the word “stock” to indicate fish from a single reservoir.

Do Stocks from Stable and Fluctuating Reservoirs Differ?

Description.—I analyzed 1,367 female mosquitofish sampled from four stable and 20 fluctuating reservoirs in January, 1974. There were 6,334 fish, but juveniles and males are not described. The average somatic dry weight of females from stable reservoirs was 154 mg, with a range of 22–589 mg; that for females from fluctuating reservoirs was 195 mg, with a range of 23–1,089 mg (Table 2). The average fecundity of females from stable reservoirs was 17 embryos, with a range of 2–66; that for females from fluctuating reservoirs was 22 embryos, with a range of 1–342 (Table 2). The average fecundity of 188 mg females (the overall average size) from stable reservoirs was 19 with a range of 6–21; that for females from fluctuating reservoirs was 22 with a range of 5–70 (Table 3). The average reproductive allocation (100 × dry weight of gonads/dry weight of soma) of females from stable reservoirs was 22, with a range of 0.2–63.7; that for females from fluctuating reservoirs was 23, with a range of 0.4–88.4. The average weight of early-eyed embryos from stable reservoirs was 1.9 mg with a range of 0.9–3.1 mg; that for early-eyed embryos from fluctuating reservoirs was 2.0 mg, with a range of 0.8–4.4 mg (Table 4).

Tables 2–4 suggest that stocks differed significantly for most, but not all, traits. Are the mean values of traits for different stocks associated in consistent patterns? The correlation matrix of stock means (Table 5) indicates that longer fish have higher somatic and regular condition factors. Fecundity correlates positively with condition factors and reproductive allocation, but negatively with weight of early-eyed embryos. In turn, the weight of early-eyed embryos correlates negatively with condition factors, fecundity, and reproductive allocation. The variation among these stocks suggests a strong trade-off between a few, large young and many, small young. Note that there is no significant correlation between length and fecundity, length and reproductive allocation, or length and weight of early-eyed embryos.

After the linear effects of length and condition were removed, the partial correlations indicated that fecundity was still very strongly correlated with reproductive allocation, and that weight of early-eyed young was still negatively correlated with
### Table 2

Description of adult females sampled in January, 1974. (1) Somatic condition factor = (dry wt of soma in mg/power of SL in mm) × 6, where power = slope of regression of log(weight) on log(length). For condition factors, values are reported for only those stocks where the amount of variation explained by that regression exceeded 75%. Sample sizes for totals are reduced accordingly. (2) Regular condition factor = (dry wt of soma and gonads/power of SL) × 10 ed. (3) Fecundity = total number of yolked or developing eggs. (4) Reproductive allocation = 100 × (dry wt of gonads/dry wt of soma). Each entry has the following format: first line—mean + 95% confidence interval; second line—minimum maximum.

<table>
<thead>
<tr>
<th>Location</th>
<th>N</th>
<th>Stan. length (mm)</th>
<th>Somatic wt (mg)</th>
<th>Somatic CF (1)</th>
<th>Regular CF (2)</th>
<th>Fecundity (3)</th>
<th>Reprod. alloc. (4)</th>
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<td>Twin Res.</td>
<td>6</td>
<td>34.3 ± 3.7</td>
<td>157.4 ± 62.8</td>
<td>3.1 ± 0.2</td>
<td>3.4 ± 0.3</td>
<td>7.7 ± 3.0</td>
<td>9.6 ± 6.1</td>
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<tr>
<td></td>
<td></td>
<td>(30.0 39.1)</td>
<td>(91.9 249.6)</td>
<td>(2.7 3.3)</td>
<td>(3.0 3.7)</td>
<td>(7.0 10.0)</td>
<td>(1.6 16.7)</td>
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<td>Kay Res.</td>
<td>205</td>
<td>34.1 ± 2.5</td>
<td>156.5 ± 10.2</td>
<td>4.0 ± 0.1</td>
<td>4.9 ± 4.1</td>
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<td></td>
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<td>(27.7 48.9)</td>
<td>(56.0 588.5)</td>
<td>(2.6 7.4)</td>
<td>(3.0 8.5)</td>
<td>(2.0 66.0)</td>
<td>(0.2 63.7)</td>
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<tr>
<td>Kaihue Pump</td>
<td>11</td>
<td>31.7 ± 4.0</td>
<td>147.0 ± 80.5</td>
<td>0.7 ± 0.1</td>
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<td>5.5 ± 2.0</td>
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<td></td>
<td></td>
<td>(23.4 43.3)</td>
<td>(38.2 415.1)</td>
<td>(0.6 0.8)</td>
<td>(0.7 0.9)</td>
<td>(2.0 12.0)</td>
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<td>Univ. Pond</td>
<td>24</td>
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<td>100.2 ± 35.1</td>
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<td>(24.7 40.7)</td>
<td>(21.5 371.6)</td>
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<td>(4.2 32.6)</td>
<td>(4.2 32.6)</td>
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<td>Wahiawa R.</td>
<td>17</td>
<td>34.8 ± 2.6</td>
<td>166.3 ± 42.6</td>
<td>5.9 ± 0.4</td>
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<td>153</td>
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<td>173.4 ± 12.5</td>
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<td>(23.2 438.9)</td>
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<td>115</td>
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<td>(33.9 1001.7)</td>
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<td>9.2 ± 0.4</td>
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<td>19.5 ± 4.2</td>
</tr>
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<td>(48.9 700.1)</td>
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<td>Res. 25</td>
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<td>(66.2 513.1)</td>
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<td>Res. 31</td>
<td>10</td>
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<td>127</td>
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<tr>
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<td>(31.8 55.2)</td>
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### Table 2. Continued.

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<th>Stan. length (mm)</th>
<th>Somatic wt. (mg)</th>
<th>Somatic CF (1)</th>
<th>Regular CF (2)</th>
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<td>(21.3 ± 24.4)</td>
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<td>(24.0 ± 48.8)</td>
<td>(43.8 ± 439.7)</td>
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<td>(8.0 ± 11.6)</td>
<td>(3.0 ± 20.0)</td>
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<td>35.4 ± 0.6</td>
<td>186.8 ± 15.3</td>
<td>13.4 ± 1.2</td>
<td>16.7 ± 1.6</td>
<td>21.5 ± 1.0</td>
<td>22.8 ± 0.6</td>
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<td>(28.4 ± 52.8)</td>
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<td>(0.3 ± 231.4)</td>
<td>(0.4 ± 275.1)</td>
<td>(1.0 ± 342.0)</td>
<td>(0.2 ± 88.4)</td>
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<tr>
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<td>4.7 ± 0.1</td>
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<td>22.0 ± 1.1</td>
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<td>(18.6 ± 55.9)</td>
<td>(23.2 ± 1,088.8)</td>
<td>(0.3 ± 231.4)</td>
<td>(0.4 ± 275.1)</td>
<td>(1.0 ± 342.0)</td>
<td>(0.4 ± 88.4)</td>
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<tr>
<td>Total</td>
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<td>22.8 ± 0.6</td>
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<td>(18.6 ± 55.9)</td>
<td>(21.5 ± 1,088.8)</td>
<td>(0.3 ± 231.4)</td>
<td>(0.4 ± 275.1)</td>
<td>(1.0 ± 342.0)</td>
<td>(0.2 ± 88.4)</td>
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<th>b</th>
<th>Fec 188 gm</th>
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<td>21.07 + 0.93</td>
<td>0.611</td>
<td>0.373</td>
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<td>0.336</td>
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<td>0.192</td>
<td>31.89 + 5.73</td>
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<td>0.089</td>
<td>18.71 + 1.15</td>
<td>0.701</td>
<td>0.492</td>
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<tr>
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<td>0.047</td>
<td>17.74 + 1.03</td>
<td>0.502</td>
<td>0.252</td>
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<td>Res. 32</td>
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<td>0.048</td>
<td>33.94 + 3.30</td>
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<td>0.113</td>
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<td>Res. 33</td>
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<td>33.24</td>
<td>0.195</td>
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<td>0.058</td>
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<td>27.29 + 2.01</td>
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<td>0.087</td>
<td>21.62 + 0.90</td>
<td>0.500</td>
<td>0.250</td>
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fecundity (Table 5). The squared multiple correlations of the dependent variables with length, somatic condition factor, and regular condition factor were 0.29 for reproductive allocation (P < .06), 0.53 for fecundity (P < .002), 0.21 for the intercept of the fecundity-weight relation (P > .10), 0.32 for the slope of the fecundity-weight relation (P < .04), and 0.34 for the weight of early-eyed embryos (P < .03). Thus length and condition explain 21–53% of variation among stocks in reproductive traits.

Analysis.—Effects of samples within reservoirs.—I first asked if samples within reservoirs differed in their life-history traits. Only in Kay Res., Opaelu Res., and Res. 's 21, 32, 35, 42, 61, and 91 were there enough pregnant females in each sample (six or more) to examine sample effects. I did a nested, two-level, unbalanced analysis of covariance (with weight as the covariate) for the effects of stocks and samples within stocks on fecundity and reproductive allocation for females from these eight reservoirs. The effects of both stocks (P < .001) and samples within stocks (P < .001) were significant. Differences among stocks accounted for 26% of the variation in fecundity and 18% of the variation in reproductive allocation; differences among samples within stocks accounted for 5% of the variation in fecundity and 3% of the variation in reproductive allocation. The significance of samples within stocks was contributed entirely by Reservoir 32. When it was removed from the analysis, stock effects remained highly significant for both fecundity (P < .001) and reproductive allocation (P < .001), but the effects of samples within stocks were no longer significant.
<table>
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<th>Very late-eyed</th>
<th>Late-eyed</th>
<th>Early-eyed</th>
<th>Large uneyed</th>
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<td>1.4 ± 0.6</td>
<td>0.4 ± 0.1</td>
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<td>(0.1 ± 3.2)</td>
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<td>(1.7 ± 3.1)</td>
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<td>(0.8 ± 2.5)</td>
<td>(0.2 ± 0.5)</td>
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<td>1.8 ± 0.3</td>
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<td>(1.7 ± 2.2)</td>
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<td>1.7 ± 0.2</td>
<td>9 ± 0.6</td>
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<td>(1.0 ± 3.1)</td>
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<td>(0.9 ± 3.0)</td>
<td>(0.3 ± 1.3)</td>
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<tr>
<td>Res. 31</td>
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<td>(1.5 ± 2.0)</td>
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<td>(0.2 ± 1.2)</td>
<td></td>
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</tr>
<tr>
<td>Res. 32</td>
<td>11</td>
<td>1.1 ± 0.2</td>
<td>8 ± 0.3</td>
<td>15 ± 0.3</td>
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</tr>
<tr>
<td></td>
<td>(0.8 ± 1.5)</td>
<td></td>
<td>(0.2 ± 1.4)</td>
<td>(0.1 ± 1.9)</td>
<td></td>
</tr>
<tr>
<td>Res. 33</td>
<td>4</td>
<td>1.8 ± 0.6</td>
<td>5 ± 0.4</td>
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</tr>
<tr>
<td></td>
<td>(1.4 ± 2.3)</td>
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<td>(0.4 ± 2.4)</td>
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<tr>
<td>Res. 35</td>
<td>3</td>
<td>1.3 ± 0.7</td>
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<td>12 ± 0.6</td>
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</tr>
<tr>
<td></td>
<td>(1.0 ± 1.6)</td>
<td></td>
<td>(0.3 ± 0.9)</td>
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</tr>
<tr>
<td>Res. 40</td>
<td>6</td>
<td>2.0 ± 0.1</td>
<td>40 ± 0.7</td>
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</tr>
<tr>
<td></td>
<td>(1.7 ± 2.6)</td>
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<td>(0.2 ± 1.3)</td>
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<tr>
<td>Res. 50</td>
<td>5</td>
<td>2.0 ± 0.4</td>
<td>4 ± 0.4</td>
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<td></td>
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<tr>
<td></td>
<td>(1.5 ± 2.4)</td>
<td></td>
<td>(0.4 ± 2.4)</td>
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<tr>
<td>Res. 60</td>
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<td>2.2 ± 1.1</td>
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<tr>
<td></td>
<td>(1.5 ± 7.0)</td>
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<td>(1.2 ± 2.7)</td>
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<tr>
<td></td>
<td>(1.3 ± 2.5)</td>
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<td>(0.8 ± 3.4)</td>
<td>(0.3 ± 1.2)</td>
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<td>1.3 ± 0.7</td>
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</tr>
<tr>
<td></td>
<td>(1.0 ± 1.6)</td>
<td></td>
<td>(1.2 ± 3.2)</td>
<td>(0.2 ± 0.8)</td>
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</tr>
<tr>
<td>Res. 81</td>
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<td>8 ± 0.4</td>
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<tr>
<td></td>
<td>(0.9 ± 1.4)</td>
<td></td>
<td>(0.1 ± 0.7)</td>
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<td>Res. 84</td>
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<tr>
<td></td>
<td>(1.5 ± 2.0)</td>
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<td>(0.2 ± 1.2)</td>
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</tr>
<tr>
<td>Res. 90</td>
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<td>19 ± 0.5</td>
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<tr>
<td></td>
<td>(1.6 ± 2.7)</td>
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<td>(0.2 ± 0.9)</td>
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<tr>
<td>Res. 91</td>
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<td>90 ± 0.7</td>
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<td></td>
<td>(1.4 ± 1.8)</td>
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<td>(1.3 ± 2.6)</td>
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<tr>
<td>Stable</td>
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<td>112 ± 0.7</td>
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<td>65 ± 0.6</td>
</tr>
<tr>
<td></td>
<td>(0.9 ± 2.0)</td>
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<td>(0.9 ± 3.1)</td>
<td>(0.1 ± 0.3)</td>
<td>(0.2 ± 0.7)</td>
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<td>Fluct.</td>
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<td>(1.0 ± 7.0)</td>
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<td>(0.8 ± 3.0)</td>
<td>(0.5 ± 3.8)</td>
<td>(0.0 ± 0.5)</td>
</tr>
<tr>
<td>Total</td>
<td>54</td>
<td>1.9 ± 0.2</td>
<td>99 ± 0.3</td>
<td>2.0 ± 0.0</td>
<td>459 ± 0.6</td>
</tr>
<tr>
<td></td>
<td>(1.0 ± 7.0)</td>
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<td>(0.8 ± 3.0)</td>
<td>(0.1 ± 3.8)</td>
<td>(0.0 ± 0.5)</td>
</tr>
</tbody>
</table>
TABLE 5.  Correlation matrices for stock means of females from January, 1974, sample. MeanLn = the mean length of pregnant females; SomCF = somatic condition factor; RepCF = regular condition factor; RepAll = dry weight of gonads/dry weight of soma; Fec188 = mean fecundity of 188 mg females; Intcpt = intercept of regression of fecundity on weight; Slope = slope of regression of fecundity on weight; WtEyed = dry weight of early-eyed embryos.  * P < .05.  ** P < .01.  N = 14, 18, or 20 stocks; only those stocks with reliable estimates of condition factors and embryo size were used (cf. Tables 2–4).

<table>
<thead>
<tr>
<th></th>
<th>MeanLn</th>
<th>SomCF</th>
<th>RegCF</th>
<th>RepAll</th>
<th>Fec188</th>
<th>Intcpt</th>
<th>Slope</th>
<th>WtEyed</th>
</tr>
</thead>
<tbody>
<tr>
<td>MeanLn</td>
<td>1.00</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SomCF</td>
<td>0.61**</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RegCF</td>
<td>0.61**</td>
<td>0.99**</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RepAll</td>
<td>0.27</td>
<td>0.51*</td>
<td>0.53*</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fec188</td>
<td>0.42</td>
<td>0.71**</td>
<td>0.73**</td>
<td>0.95**</td>
<td>1.00</td>
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<td></td>
</tr>
<tr>
<td>Intcpt</td>
<td>0.34</td>
<td>0.43</td>
<td>0.45*</td>
<td>0.60**</td>
<td>0.69**</td>
<td>-0.05</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>Slope</td>
<td>0.24</td>
<td>0.55*</td>
<td>0.56*</td>
<td>0.71**</td>
<td>0.69**</td>
<td>-0.87**</td>
<td>-0.88**</td>
<td>-0.52*</td>
</tr>
<tr>
<td>WtEyed</td>
<td>-0.10</td>
<td>-0.70**</td>
<td>-0.66**</td>
<td>-0.87**</td>
<td>-0.88**</td>
<td>-0.52*</td>
<td>-0.91**</td>
<td>1.00</td>
</tr>
</tbody>
</table>

(B. Partial correlations with linear effects of length and condition removed)

<table>
<thead>
<tr>
<th></th>
<th>RepAll</th>
<th>Fec188</th>
<th>Intcpt</th>
<th>Slope</th>
<th>WtEyed</th>
</tr>
</thead>
<tbody>
<tr>
<td>RepAll</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fec188</td>
<td>0.97**</td>
<td>1.00</td>
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</tr>
<tr>
<td>Intcpt</td>
<td>0.49*</td>
<td>0.60**</td>
<td>1.00</td>
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</tr>
<tr>
<td>Slope</td>
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<td>0.51*</td>
<td>-0.38</td>
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</tr>
<tr>
<td>WtEyed</td>
<td>-0.40</td>
<td>-0.52*</td>
<td>-0.28</td>
<td>-0.30</td>
<td>1.00</td>
</tr>
</tbody>
</table>

(P > .50, P > .10). Therefore, because sample effects were significant in only one reservoir and accounted for less than 5% of the variation, I ignored the effects of samples within stocks in analyzing the complete set of 24 stocks.

Effects of stocks and classes.—All traits differed among stocks except standard length and the weight of early-eyed eggs (Table 6). Fecundity and reproductive allocation were analyzed with a two-level, unbalanced, nested analysis of covariance with dry weight of soma as the covariate. The other traits were analyzed with a two-level, nested, unbalanced analysis of variance. Differences among stocks accounted for 80% of the variation in fecundity, for 97% of the variation in condition factors, for 18% of the variation in reproductive allocation, for about 32% of the variation (Table 6).

TABLE 6. Summary of ANCOVA’s and ANOVA’s for traits of females collected in January, 1974. (1) Analysis of covariance to test for effects of islands and stocks with weight as the covariate. (2) For this and all subsequent traits in this table, the results reported are for an unbalanced, nested, two-level analysis of variance calculated according to Sokal and Rohlfs (1981), p. 294–299.

<table>
<thead>
<tr>
<th>Trait</th>
<th>N</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>% of total variance accounted for by stocks among stocks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Island</td>
<td></td>
<td>Stock</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
<td>P</td>
<td>F</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>Fecundity (1)</td>
<td>1,367</td>
<td>5.47</td>
<td>&lt;.025</td>
<td>58.79</td>
<td>&lt;.001</td>
<td>79.1%</td>
<td></td>
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</tr>
<tr>
<td>Reprod. alloc. (2)</td>
<td>1,367</td>
<td>6.20</td>
<td>&lt;.025</td>
<td>19.11</td>
<td>&lt;.001</td>
<td>18.0%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stand. length</td>
<td>1,367</td>
<td>0.96</td>
<td>&gt;.25</td>
<td>30.65</td>
<td>&lt;.001</td>
<td>31.0%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Somatic weight</td>
<td>1,367</td>
<td>30.85</td>
<td>&lt;.001</td>
<td>34.02</td>
<td>&lt;.001</td>
<td>33.1%</td>
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</tr>
<tr>
<td>Regular CF</td>
<td>1,367</td>
<td>1,860.8</td>
<td>&lt;.001</td>
<td>1,621.27</td>
<td>&lt;.001</td>
<td>96.7%</td>
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<td></td>
</tr>
<tr>
<td>Somatic CF</td>
<td>1,367</td>
<td>1,562.5</td>
<td>&lt;.001</td>
<td>1,157.72</td>
<td>&lt;.001</td>
<td>96.6%</td>
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</tr>
<tr>
<td>Wt early-eyed embryos</td>
<td>609</td>
<td>0.28</td>
<td>&gt;.50</td>
<td>0.97</td>
<td>&gt;.50</td>
<td>0.0%</td>
<td></td>
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</tr>
<tr>
<td>Wt large uneyed embryos</td>
<td>627</td>
<td>2.48</td>
<td>&gt;.10</td>
<td>5.45</td>
<td>&lt;.001</td>
<td>11.1%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wt small uneyed embryos</td>
<td>459</td>
<td>2.00</td>
<td>&gt;.10</td>
<td>3.37</td>
<td>&lt;.001</td>
<td>9.1%</td>
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</tbody>
</table>
TABLE 7. Comparison of size structure of fish populations from six reservoirs sampled in January and November, 1974. P < .001 for all except Twin, for which 0.05 > P > 0.025. Counts include all fish caught; measure is standard length.

<table>
<thead>
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<th></th>
<th></th>
<th></th>
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</tr>
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<td>Twin</td>
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<td>23</td>
<td>90</td>
<td>63</td>
<td>27</td>
<td>25</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>238</td>
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</tr>
<tr>
<td></td>
<td>Nov</td>
<td>0</td>
<td>7</td>
<td>41</td>
<td>56</td>
<td>30</td>
<td>14</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>150</td>
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</tr>
<tr>
<td></td>
<td>Total</td>
<td>0</td>
<td>30</td>
<td>131</td>
<td>119</td>
<td>57</td>
<td>39</td>
<td>12</td>
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<td>0</td>
<td>0</td>
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<td>2</td>
<td>20</td>
<td>29</td>
<td>47</td>
<td>134</td>
<td>66</td>
<td>10</td>
<td>5</td>
<td>0</td>
<td>313</td>
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<tr>
<td></td>
<td>Nov</td>
<td>0</td>
<td>0</td>
<td>18</td>
<td>65</td>
<td>31</td>
<td>9</td>
<td>16</td>
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<td>38</td>
<td>94</td>
<td>78</td>
<td>143</td>
<td>82</td>
<td>15</td>
<td>6</td>
<td>0</td>
<td>458</td>
<td>125.62</td>
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<td>10</td>
<td>42</td>
<td>103</td>
<td>52</td>
<td>15</td>
<td>8</td>
<td>3</td>
<td>11</td>
<td>4</td>
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<td>250</td>
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</tr>
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<td>Nov</td>
<td>0</td>
<td>30</td>
<td>78</td>
<td>55</td>
<td>16</td>
<td>9</td>
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<td>11</td>
<td>4</td>
<td>2</td>
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<td>173</td>
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<td>114</td>
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<td>1</td>
<td>0</td>
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<td>8</td>
<td>48</td>
<td>79</td>
<td>10</td>
<td>2</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>150</td>
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<td>162</td>
<td>137</td>
<td>15</td>
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<td>86</td>
<td>99</td>
<td>41</td>
<td>12</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td>0</td>
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</tr>
<tr>
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<td>Nov</td>
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<td>21</td>
<td>132</td>
<td>66</td>
<td>25</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>250</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>1</td>
<td>107</td>
<td>231</td>
<td>107</td>
<td>37</td>
<td>8</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>500</td>
<td>69.25</td>
</tr>
</tbody>
</table>

in length and weight, and for 11% or less of the variation in embryo weight.

Fecundity, somatic weight, and condition factors differed significantly by F-test between stable and fluctuating classes (Table 6: I used error mean-square rather than stock mean square in the denominator because class effects were fixed, or Model I, rather than random, or Model II—cf. Brownlee, 1965 p. 508).

Thus both stocks and classes differed significantly in life-history traits. Fish from stable reservoirs were smaller, thinner, and had lower fecundities and reproductive allocations than fish from fluctuating reservoirs. However, stocks consistently accounted for more variability than did classes. The percentage of variation accounted for by classes could not be estimated reliably because of the unbalanced design.

Differences Between Samples from January and November 1974

The January sample was taken shortly after the start of the wet season, and the November sample was taken at the end of a very dry summer. Six reservoirs were sampled on both dates: Twin, Kay, 33, 41, 50, and 81. In only three of the six were there enough pregnant females on both dates to make meaningful comparisons of fecundity and reproductive allocation: Kay, 41, and 81.

In all stocks there were fewer fish shorter than 15 mm in November, indicating less reproduction, higher mortality for small fish, or both, during the summer (Table 7). In five of the six reservoirs, pregnancy rates changed from January to November. In four of the five, fewer females were pregnant; in Reservoir 41, more females were pregnant (Table 8). In all three reservoirs with adequate samples, fecundity and reproductive allocation were lower in November (Table 9). Overall, there were fewer small fish, lower pregnancy rates, lower fecundities, and lower reproductive allocations in November than in January.

These changes are consistent with plastic responses to food stress during the summer. Mosquitofish reproduce throughout the year in Hawaii but respond to dry seasons with reduced reproductive output. Allochthonous insects are probably a major food item for these fish (Stearns, 1975). They accounted for 47%
of stomach contents by count in 120 fish taken from five reservoirs in November, 1974. During the summer, fewer insects are produced, and in the fluctuating reservoirs the water recedes from the border of vegetation. Thus fewer insects are blown onto the water surface to become food for mosquitofish.

The Impact of Water Level Fluctuations

How rapidly do life-history traits change in the field? If changes take less than a generation, they must be plastic responses to short-term environmental change, rather than genetic responses to selection. With data both on reservoir fluctuation patterns and on fish phenotypes, I examined what impact the recent history of water level fluctuations had on the expression of reproductive traits. I first calculated the means and coefficients of variation in water level for the periods 1–30, 31–60, 61–90, 91–120, 121–150, and 151–180 days before the fish were sampled from each of the 18 fluctuating reservoirs on Maui. Weight-corrected fecundity was negatively correlated with mean water level, but positively correlated with the coefficient of variation in water level. Surprisingly, fecundity was more strongly correlated with measures of water level 61–150 days before the sample date than with measures 1–60 days before the sample date (Table 10).

To determine how water level affected fecundity, I did multiple regressions. I performed all analyses on six variables using random variables as substitutes for water level measures when fewer than six water level measures were independent variables. That method controlled for the increase in $r^2$ with number of independent variables.

In preparing the data, I attached the measures of water level fluctuation, which varied among but not within stocks, to the records of individual females, which varied both among and within stocks. Because fecundity varied significantly among stocks, any independent variable—even a random variable—that varied among stocks would have an apparently significant contribution to the variance explained by multiple regression. I therefore calculated the multiple $r^2$ of 30 regressions on six random variables: mean $= 0.1441$, 95% CI $= 0.0431$. That controlled for variation in fecundity among stocks that

<table>
<thead>
<tr>
<th>Name</th>
<th>Date</th>
<th>Not pregnant</th>
<th>Pregnant</th>
<th>Total</th>
<th>G</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Twin</td>
<td>Jan</td>
<td>53</td>
<td>7</td>
<td>60</td>
<td>4.89</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Nov</td>
<td>46</td>
<td>0</td>
<td>46</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>99</td>
<td>7</td>
<td>106</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kay</td>
<td>Jan</td>
<td>10</td>
<td>241</td>
<td>251</td>
<td>137.30</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>Nov</td>
<td>46</td>
<td>15</td>
<td>61</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>56</td>
<td>256</td>
<td>312</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Res. 33</td>
<td>Jan</td>
<td>8</td>
<td>29</td>
<td>37</td>
<td>25.76</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>Nov</td>
<td>22</td>
<td>3</td>
<td>25</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>30</td>
<td>32</td>
<td>62</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Res. 41</td>
<td>Jan</td>
<td>35</td>
<td>9</td>
<td>44</td>
<td>13.68</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>Nov</td>
<td>38</td>
<td>41</td>
<td>79</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>73</td>
<td>50</td>
<td>123</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Res. 50</td>
<td>Jan</td>
<td>3</td>
<td>5</td>
<td>8</td>
<td>4.43</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>Nov</td>
<td>11</td>
<td>1</td>
<td>12</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>14</td>
<td>6</td>
<td>20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Res. 81</td>
<td>Jan</td>
<td>3</td>
<td>16</td>
<td>19</td>
<td>1.45</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>Nov</td>
<td>11</td>
<td>20</td>
<td>31</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>14</td>
<td>36</td>
<td>50</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 9. Comparison of January and November, 1974, Samples. Fecundity adjusted for weight within samples, across dates. Reproductive allocation transformed with arcsine square root. * P < .05; ** P < .01; *** P < .001.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Length</th>
<th>Weight</th>
<th>Fecundity</th>
<th>Repro. Alloc.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kay Reservoir</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan 205</td>
<td>34.1 ± 0.5</td>
<td>156.5 ± 10.2</td>
<td>14.4 ± 1.2</td>
<td>26.6 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>(27.7 ± 48.9)</td>
<td>(56.0 ± 588.5)</td>
<td>(2.5 ± 62.0)</td>
<td>(2.6 ± 50.8)</td>
</tr>
<tr>
<td>Nov 11</td>
<td>40.0 ± 1.7</td>
<td>257.6 ± 31.9</td>
<td>5.5 ± 4.3</td>
<td>11.9 ± 3.2</td>
</tr>
<tr>
<td></td>
<td>(36.7 ± 43.7)</td>
<td>(198.0 ± 342.0)</td>
<td>(3.3 ± 16.7)</td>
<td>(3.2 ± 21.1)</td>
</tr>
<tr>
<td></td>
<td>t = 7.13***</td>
<td>t = 6.57***</td>
<td>t = 4.36***</td>
<td>t = 9.37***</td>
</tr>
<tr>
<td>Reservoir 41</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan 8</td>
<td>31.1 ± 3.8</td>
<td>117.0 ± 51.5</td>
<td>3.6 ± 5.8</td>
<td>31.3 ± 5.0</td>
</tr>
<tr>
<td></td>
<td>(27.2 ± 41.3)</td>
<td>(68.0 ± 263.0)</td>
<td>(4.0 ± 16.5)</td>
<td>(17.8 ± 39.5)</td>
</tr>
<tr>
<td>Nov 37</td>
<td>31.3 ± 1.3</td>
<td>113.4 ± 17.8</td>
<td>-3.4 ± 3.3</td>
<td>26.1 ± 2.6</td>
</tr>
<tr>
<td></td>
<td>(26.3 ± 40.3)</td>
<td>(48.0 ± 237.0)</td>
<td>(2.7 ± 22.4)</td>
<td>(8.1 ± 41.6)</td>
</tr>
<tr>
<td></td>
<td>t = 0.08</td>
<td>t = 0.15</td>
<td>t = 2.33*</td>
<td>t = 2.07*</td>
</tr>
<tr>
<td>Reservoir 81</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jan 16</td>
<td>35.7 ± 3.3</td>
<td>216.7 ± 60.5</td>
<td>25.6 ± 15.2</td>
<td>36.8 ± 7.0</td>
</tr>
<tr>
<td></td>
<td>(28.8 ± 45.4)</td>
<td>(100.0 ± 411.0)</td>
<td>(11.4 ± 82.2)</td>
<td>(10.5 ± 62.2)</td>
</tr>
<tr>
<td>Nov 24</td>
<td>27.8 ± 2.1</td>
<td>85.8 ± 25.4</td>
<td>-20.4 ± 1.7</td>
<td>22.4 ± 2.4</td>
</tr>
<tr>
<td></td>
<td>(21.5 ± 47.1)</td>
<td>(33.0 ± 343.0)</td>
<td>(-31.1 ± 10.0)</td>
<td>(9.6 ± 33.3)</td>
</tr>
<tr>
<td></td>
<td>t = 4.31***</td>
<td>t = 4.32***</td>
<td>t = 6.46***</td>
<td>t = 4.10***</td>
</tr>
</tbody>
</table>

had nothing to do with recent history of water levels.
I then regressed fecundity on mean water level 1–30 days before sampling, plus five random variables, then on mean water level 1–30 and 31–60 days before sampling, plus four random variables, and so forth until the regression included all six

TABLE 10. Matrix of correlation coefficients of short-term measures of water level fluctuations and fecundity. 1–30 indicates the period 1 to 30 days before the reservoir was sampled. m indicates the mean water level, in % full, for the period indicated. cv indicates the coefficient of variation in water level. Fecundity was first adjusted to remove the effects of weight. All correlations were done by attaching the measures of water level fluctuation to the records of fecundities of individual fish; thus all fish in a reservoir were associated with the water level measures for that reservoir. Total sample size = 951. Reservoirs used: All 18 Maui reservoirs, January, 1974 sample.

<table>
<thead>
<tr>
<th></th>
<th>1–30</th>
<th>31–60</th>
<th>61–90</th>
<th>91–120</th>
<th>121–150</th>
<th>151–180</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>m</td>
<td>cv</td>
<td>m</td>
<td>cv</td>
<td>m</td>
<td>cv</td>
</tr>
<tr>
<td>30 m</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 cv</td>
<td>-0.66</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>60 m</td>
<td>0.54</td>
<td>-0.28</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>60 cv</td>
<td>-0.37</td>
<td>0.24</td>
<td>-0.85</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>90 m</td>
<td>0.38</td>
<td>-0.12</td>
<td>0.90</td>
<td>-0.78</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>90 cv</td>
<td>0.01</td>
<td>0.08</td>
<td>-0.37</td>
<td>0.53</td>
<td>-0.54</td>
<td>1.00</td>
</tr>
<tr>
<td>120 m</td>
<td>0.31</td>
<td>-0.14</td>
<td>0.97</td>
<td>-0.74</td>
<td>0.89</td>
<td>-0.82</td>
</tr>
<tr>
<td>120 cv</td>
<td>0.05</td>
<td>0.06</td>
<td>-0.44</td>
<td>0.58</td>
<td>-0.47</td>
<td>0.60</td>
</tr>
<tr>
<td>150 m</td>
<td>0.31</td>
<td>-0.28</td>
<td>0.72</td>
<td>-0.67</td>
<td>0.90</td>
<td>-0.73</td>
</tr>
<tr>
<td>150 cv</td>
<td>0.33</td>
<td>-0.14</td>
<td>-0.17</td>
<td>0.28</td>
<td>-0.37</td>
<td>0.85</td>
</tr>
<tr>
<td>180 m</td>
<td>0.47</td>
<td>-0.24</td>
<td>0.90</td>
<td>-0.72</td>
<td>0.91</td>
<td>-0.27</td>
</tr>
<tr>
<td>180 cv</td>
<td>-0.06</td>
<td>0.27</td>
<td>-0.41</td>
<td>0.44</td>
<td>-0.63</td>
<td>0.55</td>
</tr>
<tr>
<td>Fecund.</td>
<td>0.01</td>
<td>0.11</td>
<td>-0.07</td>
<td>0.09</td>
<td>-0.07</td>
<td>0.32</td>
</tr>
</tbody>
</table>
means as independent variables. I repeated this procedure for the coefficient of variation in water level. The results confirmed the impression given by the correlation matrix. Only when I entered the mean water level 91–120 and 121–150 days before sampling did the regression on the means produce a multiple $r^2$ higher than the 95% CI for six random variables, and only when I entered the coefficient of variation in water level 91–121, 121–150, and 151–180 days before sampling did the multiple $r^2$ exceed that limit (Fig. 2). These results are consistent with $F$-tests for adding variables in stepwise regressions, but are more conservative because $F$-to-add often indicated that random variables had significant effects.

Water level fluctuations are correlated with something—perhaps food availability—that affects the expression of fecundity. On the day they were sampled, the fish retained the effects of events that occurred 90 to 180 days before. This does not mean that phenotypes always lag 3 to 6 months behind current events. Water levels had simply been low 3 to 6 months before sampling, and no more recent events had affected the phenotypes as strongly. Thus events in the more distant past can have a stronger effect on phenotypes than events in the more recent past. The environment can induce significant lag effects via physiological plasticity.

In a similar analysis with reproductive allocation as the dependent variable, the $r^2$ never exceeded the 95% CI for six random variables.

To summarize: both patterns of water level fluctuation and seasonal changes are correlated with changes in the expression of reproductive traits of mosquito fish in Hawaii over periods too short to be responses to selection. These fish live about a year in the field, and these changes took place within 3 to 10 months. The responses must be plastic.

**GENERAL DISCUSSION**

**Relevance to Predictions**

Life-history theory predicts that increased reproductive effort early in life should be selected by high, variable, or unpredictable adult mortality rates, whereas decreased reproductive effort and a longer life should be selected by high, variable, or unpredictable juvenile mortality rates. The observed differences suggest that adult mortality rates should be higher or more variable in the fluctuating reservoirs than in the stable reservoirs, and that juvenile mortality rates should be higher or more variable in the stable than in the fluctuating reservoirs. Mortality rates have not yet been measured directly, but analysis of stocks does permit evaluation of some of the alternative hypotheses.

**Five Alternative Hypotheses**

Five hypotheses, not mutually exclusive, could explain why stock differences, not class differences, accounted for most of the variation. First, the stable-fluctuating dichotomy could mislead. “Stable” vs. “fluctuating” is a coarse categorization of variation that spans continua in more than one dimension. Thus we might expect the rough categories to explain only a small amount of the variation. Second, the differences among stocks could be caused by the plastic responses of organisms that all
shared similar genetic potentials. Evidence presented above strongly supports this view; it needs no further discussion. Third, fluctuations in water level might not explain the expression and evolution of life-history traits in mosquitofish. We would then have to look at other environmental characteristics for the key factors. Fourth, the stocks may differ because founder effects and subsequent genetic drift could have caused divergence. Fifth, the phenotypic differences observed in the field might have been selected. In this section I evaluate the remaining three of the first four hypotheses; the companion paper (Stearns, 1983) deals with the fifth.

**Did the Stable-Fluctuating Dichotomy Mislead?**

Were there many different kinds of stable or fluctuating reservoirs? I answered this by performing Fourier transforms on the daily time-series of water levels (in percent full) of each of 19 fluctuating reservoirs (see Appendix), and taking four measures from the power spectrum of each reservoir: percent power in significant peaks, ratio of power at periods of one week to power at periods of one year, ratio of power at periods of one week to the sum of all power not in significant peaks, and ratio of power at periods of one year to the sum of all power not in significant peaks. To these four measures I added the total volume and the mean water level in the reservoir in percent full. I also added four stable reservoirs to the data set with values of 0.0 for the time-series measures, 10 million gallons for volume, and 100 for mean water level in percent full. (This move was not arbitrary. The stable reservoirs have been observed for 40 years, and no significant fluctuations in water level were remembered by plantation officials.) I then did principle components analysis on six measures for 23 reservoirs.

The correlations among the reservoirs indicated that large reservoirs have large yearly fluctuations and low mean water levels. The first PC accounted for 65% of the variation among reservoirs; reservoirs with strongly positive correlations with this factor had large yearly fluctuations and low mean water levels. The second PC accounted for another 21%; reservoirs with strongly positive correlations with this factor had small volumes, large weekly fluctuations, and high mean water levels. A plot of the reservoirs in principle component space (Fig. 3) indicates the many different kinds of fluctuating reservoirs. The four stable reservoirs necessarily occupy a single point, but the 19 fluctuating reservoirs scatter widely on both axes. If the plot were not labelled, there would be no more reason to call the stable reservoirs a separate category than there would be to call any outlying fluctuating reservoir a separate category.

Locating the reservoirs in principal component space is a more accurate way to represent variation in fluctuation patterns than any simple classification scheme (e.g., seasonal or weekly). Thus the stable-fluctuating dichotomy hides significant variability, and, at least in this sense, it misleads.

Is there any correlation between the factor scores for fluctuation patterns and the life-history traits of the fish? I did a multiple regression analysis of fecundity and reproductive allocation with factor scores,
including somatic dry weight as a covariate. In neither case did the multiple $r^2$
exceed that found for the short-term patterns. Then I did a canonical correlation
analysis of the two sets of variables, factor scores and the reproductive traits of Table
5. Again, I found no significant association between the two sets. One explana-
tion is that the phenotypic plasticity induced by recent water level fluctuations
obscures the impact of selection, and that the correlation of recent history with long-
term pattern accounts for the variation explained by long-term pattern.

**Do Water Level Fluctuations Have Significant Impact?**

Three lines of evidence suggest that they do. Fluctuations in the recent past affect
fecundity (see above). Moreover, a rapid drop in water level changed the size-struc-
ture of one stock, and prolonged low water changed the size-structure of several stocks
in the opposite direction.

On December 5, 1974, I sampled Reservoir 50 and its outlet channel when the
reservoir was half empty and later when it was nearly dry. The fish in the outlet
channel were larger than those in the reser-
voir: 24 vs. 21 mm (1130 h) and 26 vs.
21 mm (1400 h, $P < .002, t$-test). Smaller
fish remain near shore, larger fish move
offshore, and the outlet through which
water and fish leave is far from shore. Thus
rapid drops in water level select against
larger fish.

In November, 1974, after prolonged low
water, there were fewer small fish in six
stocks than in January, and pregnancy
rates, fecundity, reproductive allocation,
and regular condition factors were lower
(Tables 7–9). I set up two crowded aquar-
ia with similar size structures, let the water
level drop slowly, and restricted rations.
Twenty-three of 69 fish in each replicate
survived through 36 days. As in the field,
survival was poor for fish shorter than 15
mm (Fig. 4), which were eaten by larger
fish. In the field, cannibalism probably
contributes to the mortality of small fish, especially during the summer in fluctuat-
ing reservoirs.

![Figure 4](image)

**Fig. 4.** Comparison of the effects of summer in the field and restricted food supply in the laboratory on the size structure of mosquitofish populations. In both cases, there were fewer, larger fish in the second sample. In the laboratory, the mechanism was cannibalism.

Rapid fluctuations kill adults, and long periods of low water kill juveniles. How-
ever, water-level fluctuations do not explain all the differences among stocks. Fish
from the four stable reservoirs differ among
stocks and from January to November,
with no variation in water level in the short
or long term. Thus patterns of water level
fluctuation are not the primary environ-
mental concern for life-history evolution.
They are significant only to the extent that
they affect age-specific mortality rates and
fecundity. Other environmental factors
must also be involved.

**Did Founder Events and Drift Contribute to Divergence?**

The people who introduced mosquitofish did not record how many were put in
each reservoir. Thus I cannot assess the
importance of founder events. More direct
evidence suggests the potential impor-
tance of subsequent drift.

On three occasions, I easily got large
samples from Reservoir 81, but in June,
1980, it was clear that water had been very
low and had only recently risen. The shore
was littered with dead crayfish and decaying fish and the bottom mud was cracked
in hexagonal patterns. The clear water was
1 to 50 cm deep and rapidly rising. The
reservoir contained only two adult female
mosquitofish. Each had recently given
birth, for two broods of very small fish swam at the reservoir margin. If populations occasionally contract to such small sizes, then drift could contribute to genetic divergence among stocks in the fluctuating reservoirs.

SUMMARY

About 150 mosquito fish were introduced from Texas to Hawaii in 1905. I analyzed 1,367 pregnant females collected in 1974 from four stable and 20 fluctuating reservoirs and the time-series of water levels in the fluctuating reservoirs.

Fish from stable reservoirs had fewer offspring, lower reproductive allocations, were thinner, shorter, and weighed less, than fish from fluctuating reservoirs. Stocks differed for those traits and in weight of yolked and yolking eggs. Length and condition explain 21–53% of variation of reproductive traits among stocks. Effects of samples within stocks were only significant for one of the eight reservoirs with adequate sample sizes, and accounted for only 3–5% of variation in reproductive traits. In this case the stable-fluctuating dichotomy misled; the fluctuating reservoirs differ significantly in their fluctuation patterns, and these differences are reflected in the life-history traits of the fish living in them. Much of the variation among stocks was caused by plastic responses to short-term environmental change. The pattern of variation in water levels in the more distant past (3–6 months) had strong effects on weight-adjusted fecundity than did the more recent past (1–3 months). The environment can induce significant lag effects in less than a generation via physiological plasticity. Water level fluctuations affect the expression of life-history traits in these stocks, but they cannot account for variation among the stocks from stable reservoirs. Founder effects may contribute to divergence among all stocks, and drift may contribute to divergence among fluctuating stocks.

ACKNOWLEDGMENTS

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LITERATURE CITED


SCHAFER, W. M. 1979. The theory of life-history evolution and its application to Atlantic salmon,
LIFE-HISTORY EVOLUTION

APPENDIX

The Fourier transform can represent any time series as some linear combination of sine and cosine functions. The transform uses particular frequencies. In this case, the lowest frequency corresponded to a period of about 8 years (half the length of the series), and the highest frequency corresponded to a period of 2 days (twice the distance between adjacent data points). I used Singleton's (1969) algorithm based on the Fast Fourier Transform (FFT) proposed by Cooley and Tukey (1965) on series truncated into multiples of 2 \times 364 days. This reduced the series to 88% (Maui) and 95% (Oahu) of their original length.

The FFT calculates the coefficients (A and B) of the sine and cosine terms for each frequency. After scaling the coefficients by multiplying by \(1/2N\) (\(N = \) length of the series), one computes the power at each frequency, \(i = 1, 2, \ldots, m\) (\(m = (N/2) - 1\)), by squaring and adding the coefficients:

\[
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The power can be thought of as the amount of variation in the original series explained by sine and cosine waves at that frequency. Graphing log(power) against frequency produces the power spectrum. Then one averages the power over a small frequency band to get the 95% confidence interval for deviations from background noise. The broader the band, the smaller the confidence interval (because variance \(\times\) bandwidth = a constant, cf. Box and Jenkins, 1970). I used a bandwidth of 10 frequency intervals.