UNNATURAL RANDOM MATING SELECTS FOR YOUNGER AGE AT MATURITY IN HATCHERY CHINOOK SALMON STOCKS

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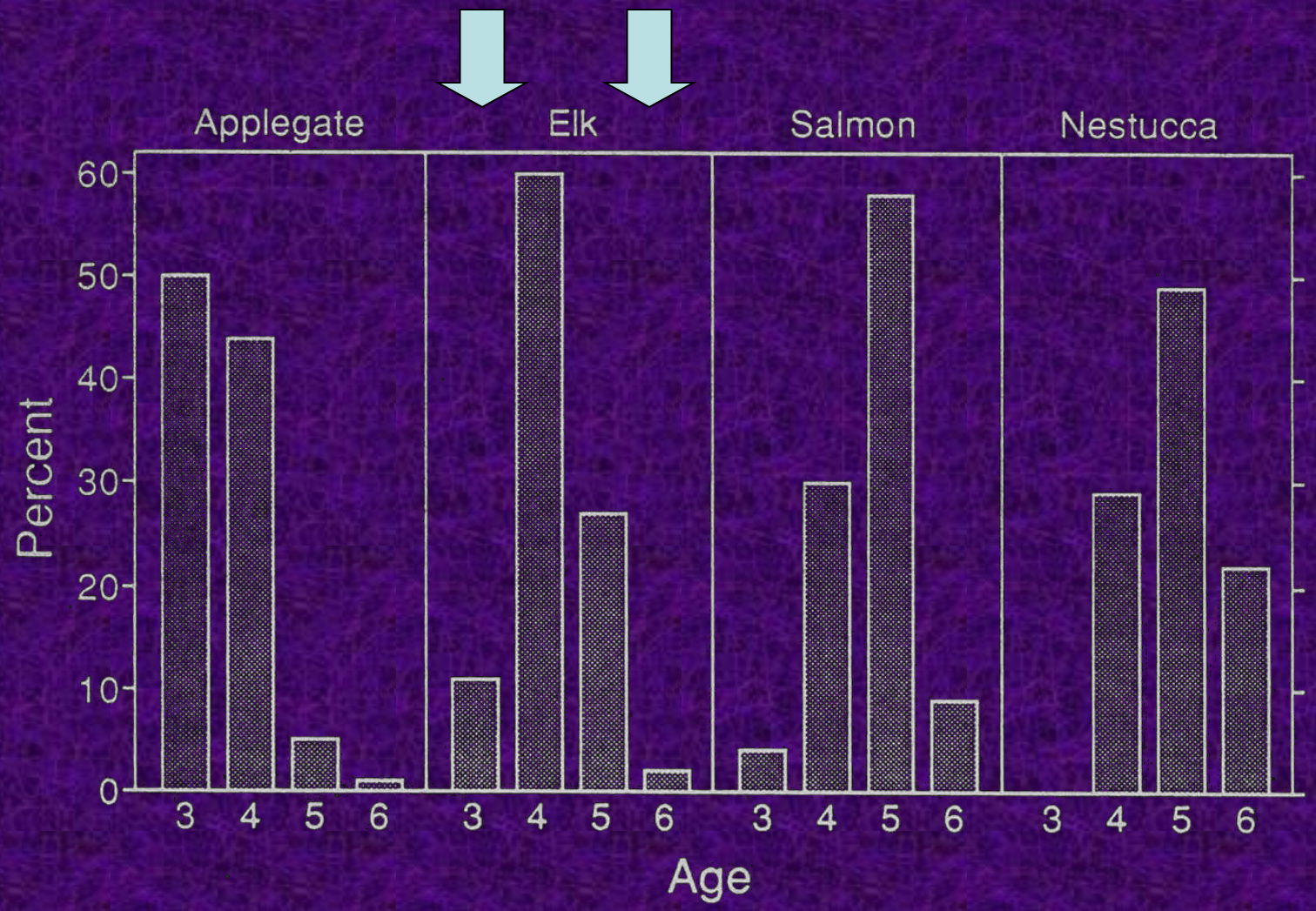
“Completely Random Mating” – Why a Possible Cause of Concern?

- Behavioral observations suggest that Chinook salmon do not mate “randomly” on the spawning grounds;
- Size-selective ocean troll fisheries shift age composition of spawners to younger ages (Ricker expressed concern circa 1980.)
- Striking evidence of inheritance of age at maturity in Chinook (Elk River Hatchery experiments, Hard’s work);

Female Age Compositions are used to Describe Stock-Specific Maturation Schedules (Early-, Mid-, and Late-Maturing). Examples from several Oregon Coastal Streams (Nicholas and Hankin 1988):

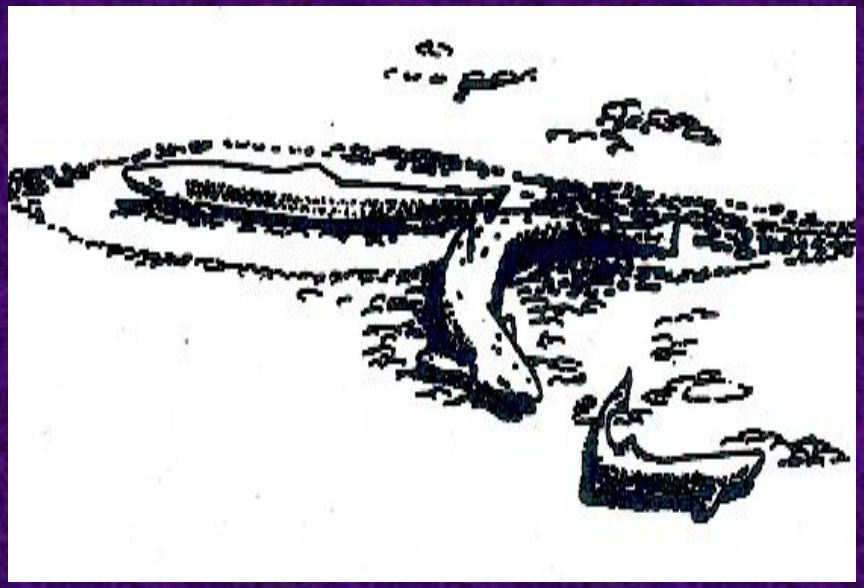


In natural populations, the percentages of males are not closely linked to the percentages of females at age.

Female Ages				Stream	Male Ages				
3	4	5	6		2	3	4	5	6
Late-Maturing									
0	20	73	7	Nehalem	4	23	31	42	0
2	33	43	32	Trask	0	12	62	20	6
4	30	58	9	Salmon	35	22	28	13	2
Early/Mid-Maturing									
11	60	27	2	Elk	52	22	19	7	1
Early-Maturing									
50	44	5	1	Applegate	33	39	26	2	0

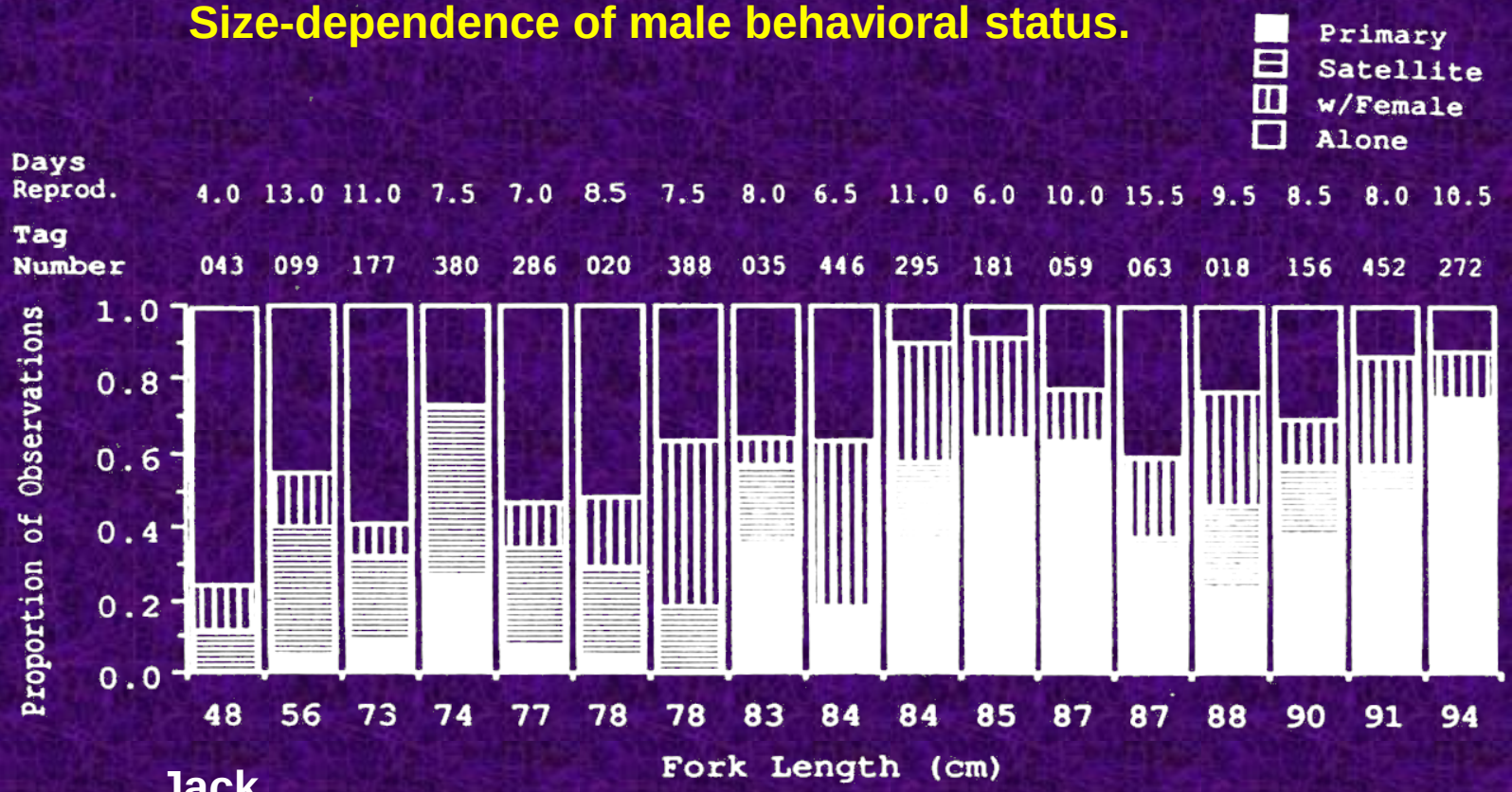
Natural Spawning Behaviors of Chinook Salmon do not Lead to Random Mating (Baxter, HSU MS Thesis 1991; other pubs, other species)

- Chinook females "prefer" mates that exceed their own size;
- Male mating success is size-dependent: largest males more often dominant, spawn with many females;



- Jacks have "sneaker" strategy, and presumably are less successful than adult males.

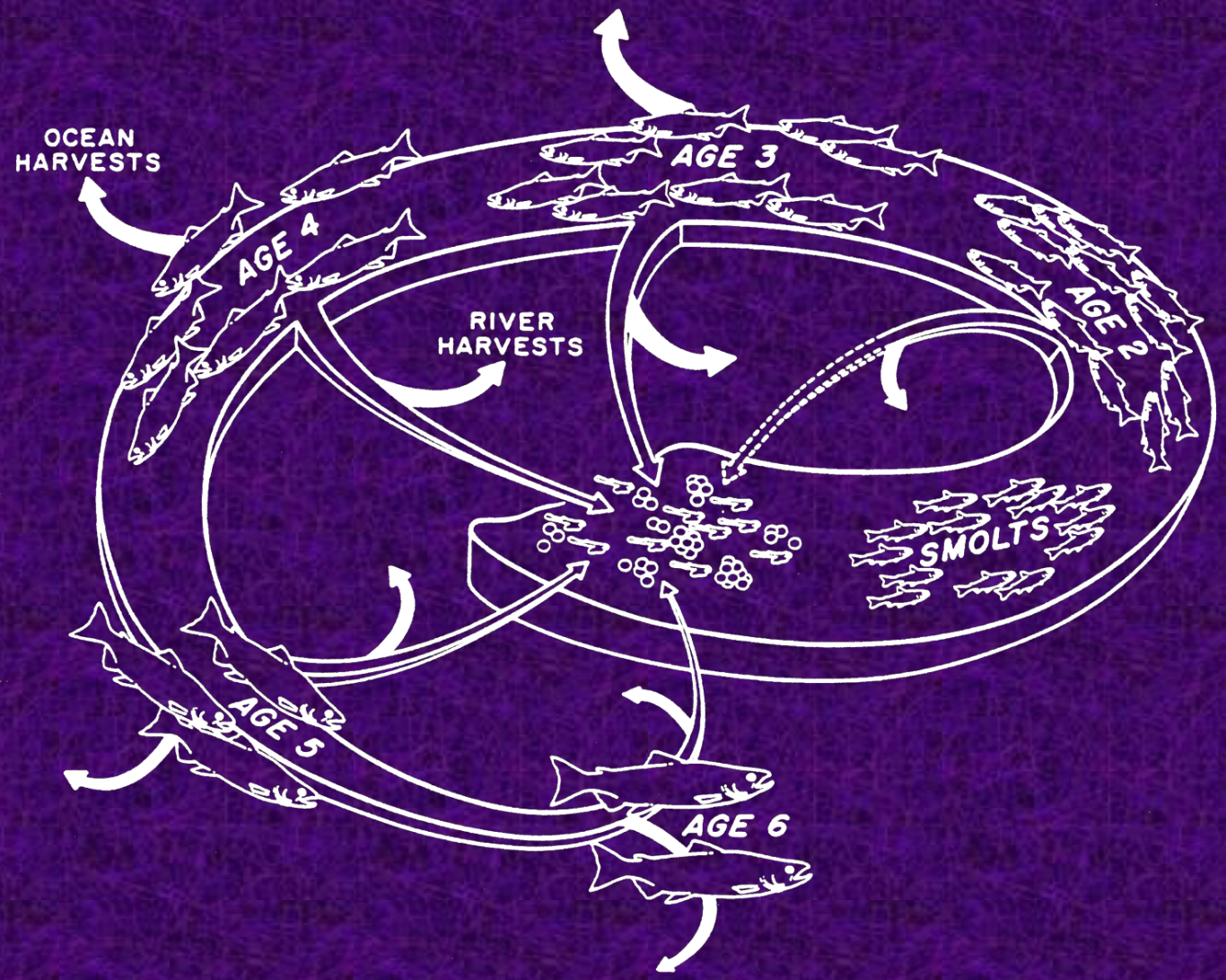
Behavioral observations from Baxter 1991: Size-dependence of male behavioral status.



Jack

The Proportion of Observations in which Each Tagged Male Was a Primary, a Satellite, with a Female (Non-courting), and Holding Alone or Wandering Arranged in Order of Increasing Male Fork Length. Tag Number and Number of Days Reproductive Are Presented for Each Male (1985 Data).

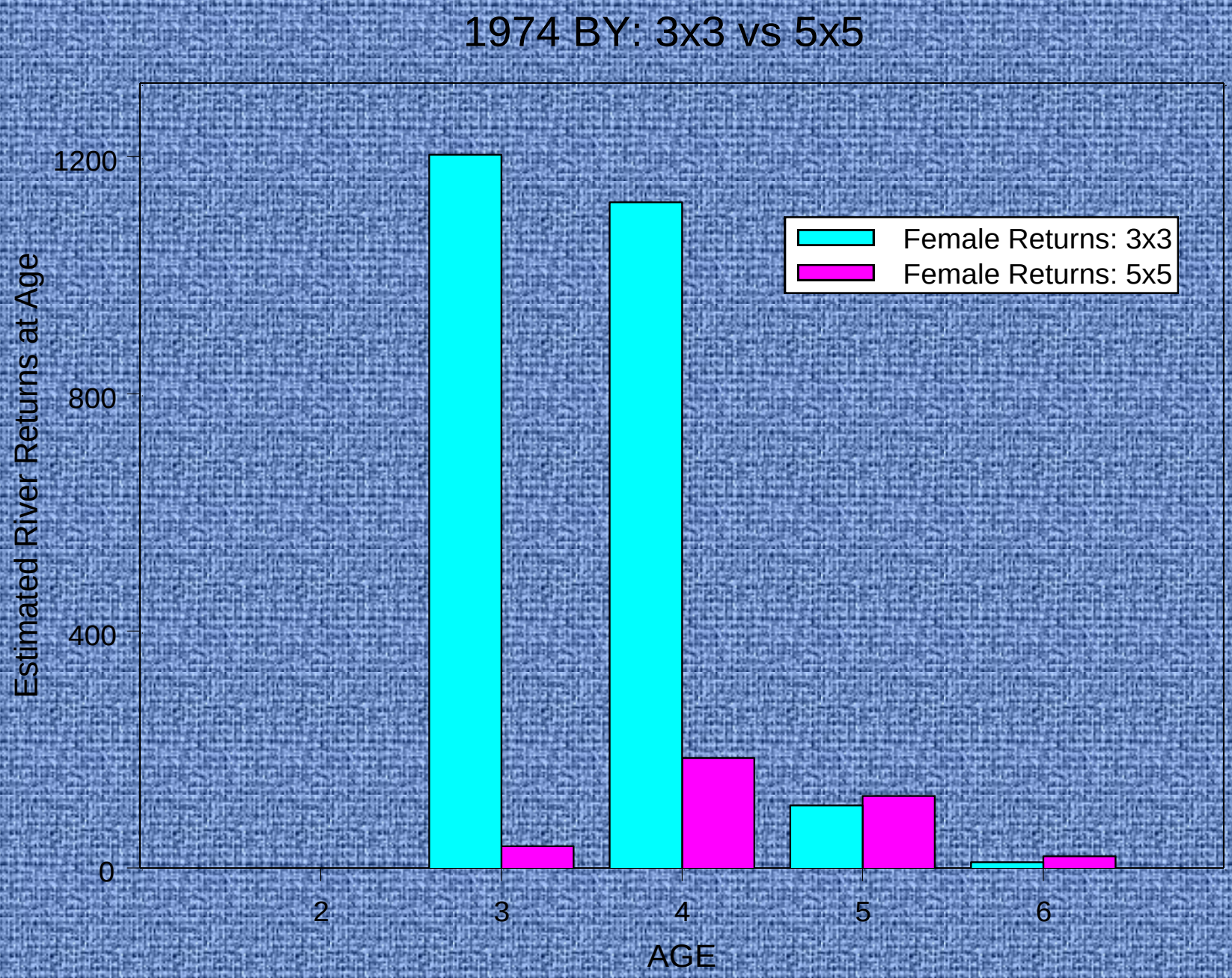
Ocean fisheries can dramatically reduce the probability of spawning at older ages

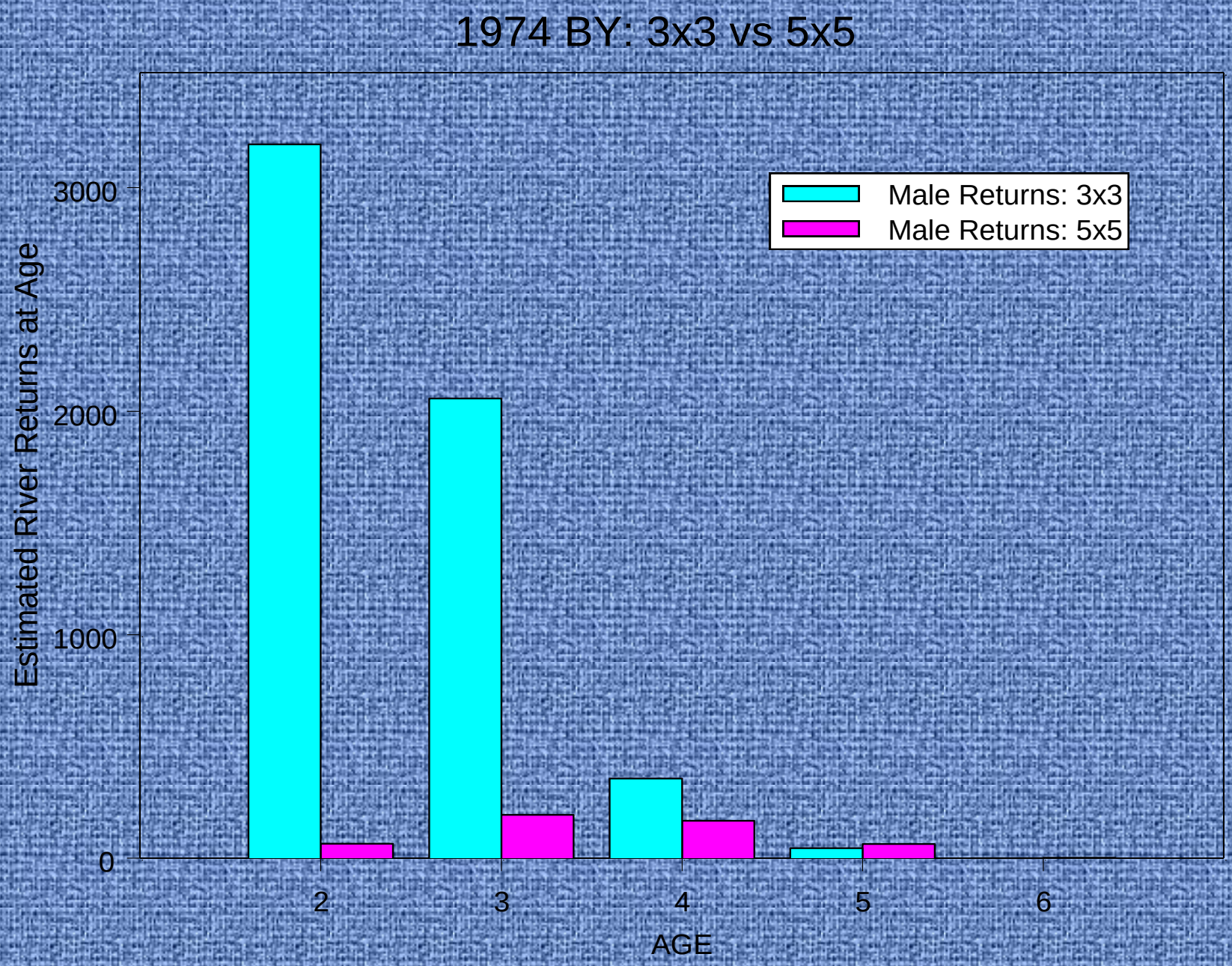


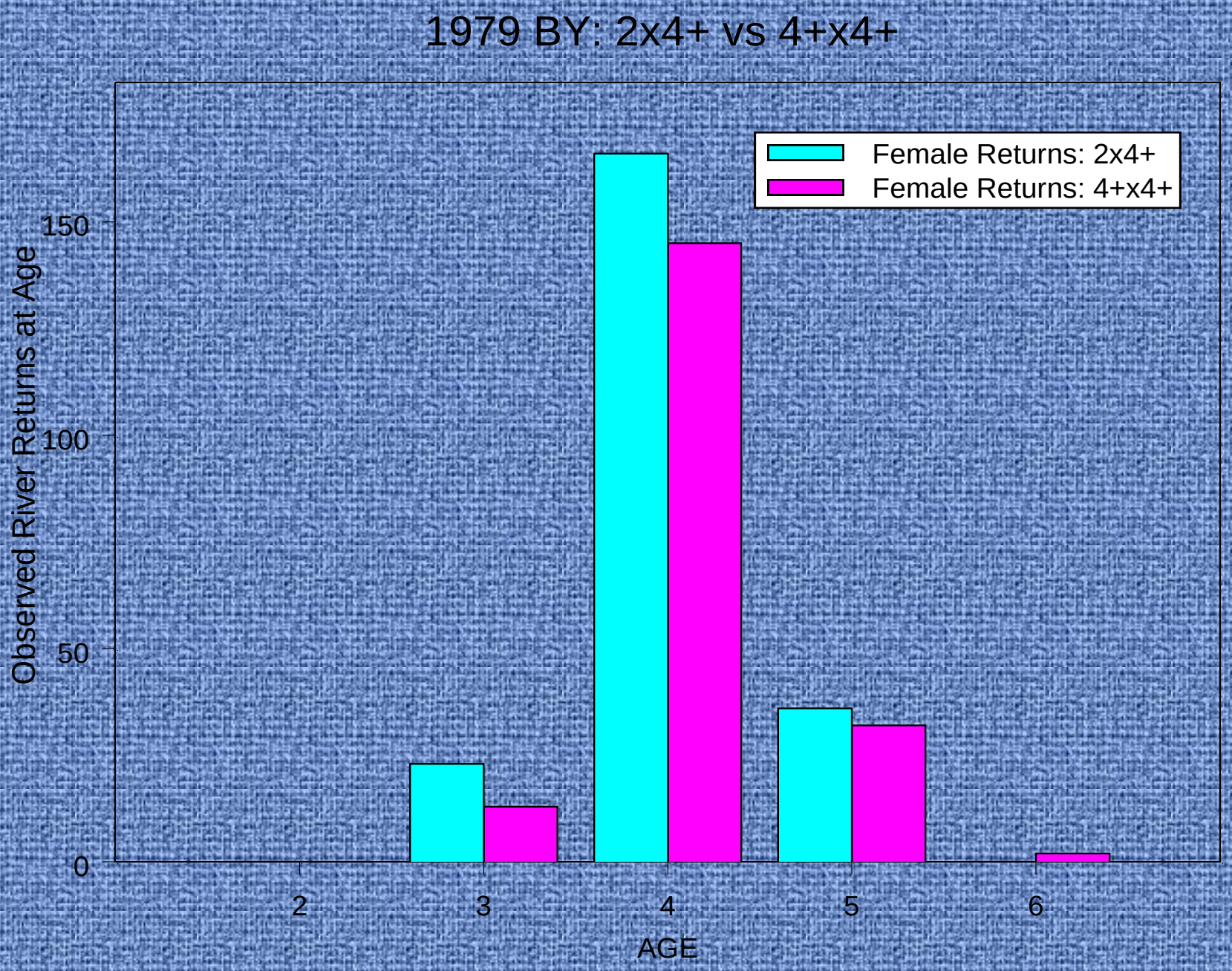
Age at maturity is a strongly inherited trait in Chinook salmon

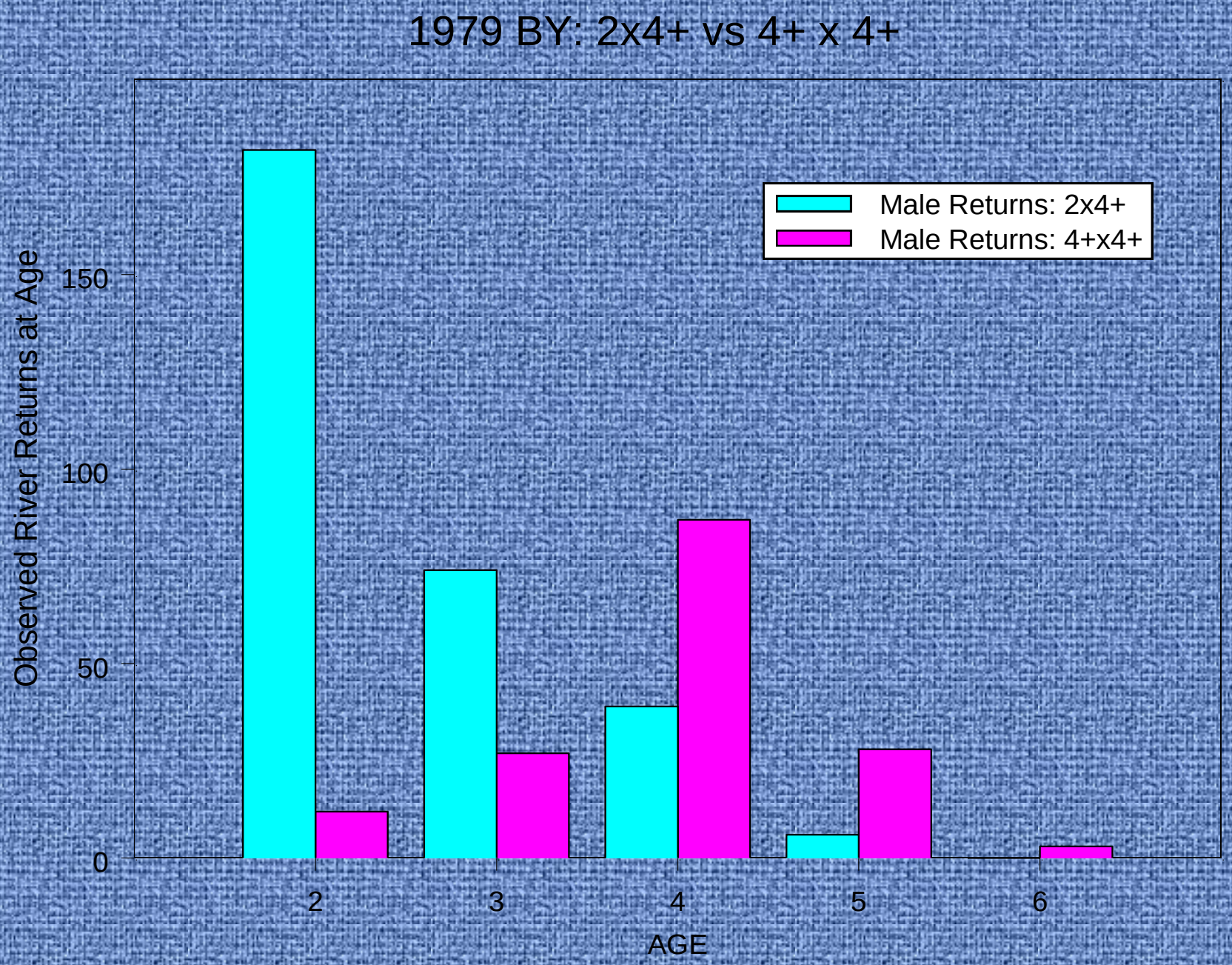
Elk River Hatchery (OR) age at maturity mating experiments (see Hankin et al. 1993): age *i* males x age *j* females

- 1974 BY: 3 x 3 vs 5 x 5
- 1979 BY: 2 x 4+ vs 4+x 4+
- 1980 BY: 2 x 4+ vs 4+x 4+


1974 BY: 3x3 vs 5x5
Estimated River Returns at Age
1200
800
400
0
2
3
4
5
6
AGE
Female Returns: 3x3
Female Returns: 5x5


1974 BY: 3x3 vs 5x5
Male Returns: 3x3
Male Returns: 5x5
Estimated River Returns at Age
3000
2000
1000
0
2
3
4
5
6
AGE


1979 BY: 2x4+ vs 4+x4+
Female Returns: 2x4+
Female Returns: 4+x4+
Observed River Returns at Age
150
100
50
0
2
3
4
5
6
AGE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AGE

MANAGEMENT ISSUES AND MODELING QUESTIONS

- Does size-selective ocean fishing, through shifting age composition of spawners to younger ages, select for earlier age at maturity (Ricker 1980, 1981; sea also Rutter circa 1900, re Sacramento gill net fishery)?
- Does random mating of hatchery fish, especially random inclusion of jacks as male parents, cause unintentional selection for earlier age at maturity (Hankin 1986-present!)?
- If hatchery mating strategies instead emulated the outcomes of natural spawnings, could such unintentional selection be avoided (Hankin 2009)?

Model-Based Assertion: Random hatchery matings generate unintentional long-term selection for younger age at maturity in hathcery Chinook salmon populations.

- Empirical Basis:
  - Elk River Hatchery Age at Maturity Experiments
- Theoretical Basis:
  - A model for inheritance of age at maturity in a hatchery Chinook population (20 yr after original idea!);
  - Alternative hatchery mating strategies;
  - Long-term equilibrium age and sex structure of modeled hatchery populations

Model Structure: Basic Features

- Age-and sex- structured representation of Chinook population dynamics, with typical assumptions;
- Models incorporate alternative hatchery mating policies & size-selective ocean fisheries;
- Computer calculations used to generate “long-term equilibrium” age and sex structure.

Key Modeling Assumption

- Simulation of “long-term” selection (due to unnatural random mating) is valid for at least ten generations given fixed “heritabilities”.
- Support for this assumption from selection experiments with rats, etc. (e.g. Falconer & Mackay).
- Model details in Hankin, Fitzgibbons & Chen. 2009. CJFAS 66: 1505-1521.

Classical Approach: Heritability

Example 10.2.

Figure 10.1 illustrates the regression of offspring on mid-parent values for wing length in *Drosophila melanogaster* (Reeve and Robertson, 1953). There are 37 pairs of parents and a mean of 2.73 offspring were measured from each pair of parents. The parents were mated assortatively, with the result that the variance of mid-parent

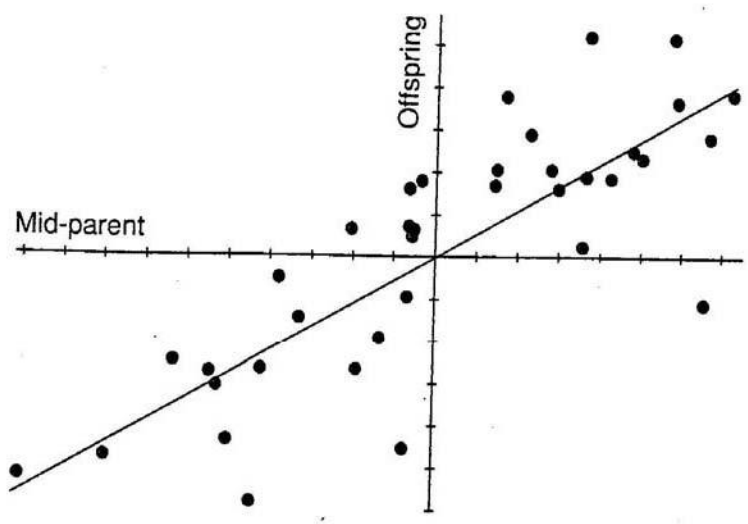


Fig. 10.1. Regression of offspring on mid-parent for wing length in *Drosophila*, as explained in Example 10.2. Mid-parent values are shown along the horizontal axis, and mean value of offspring along the vertical axis. (*Drawn from data kindly supplied by Dr E. C. R. Reeve.*)

Response to Selection

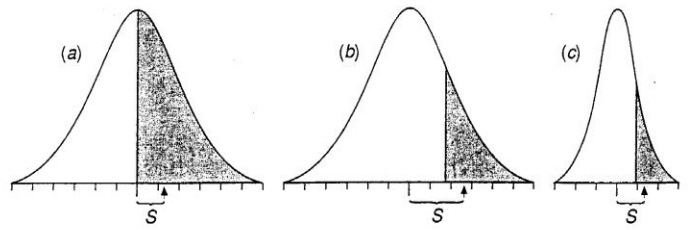


Fig. 11.2. Diagrams to show how the selection differential, S, depends on the proportion of the population selected, and on the variability of a normally distributed character. All the individuals in the stippled areas, beyond the points of truncation, are selected. The axes are marked in hypothetical units of measurement.

(*a*) 50 per cent selected; standard deviation 2 units: $S = 1.6$ units.
(*b*) 20 per cent selected; standard deviation 2 units: $S = 2.8$ units.
(*c*) 20 per cent selected; standard deviation 1 unit: $S = 1.4$ units.

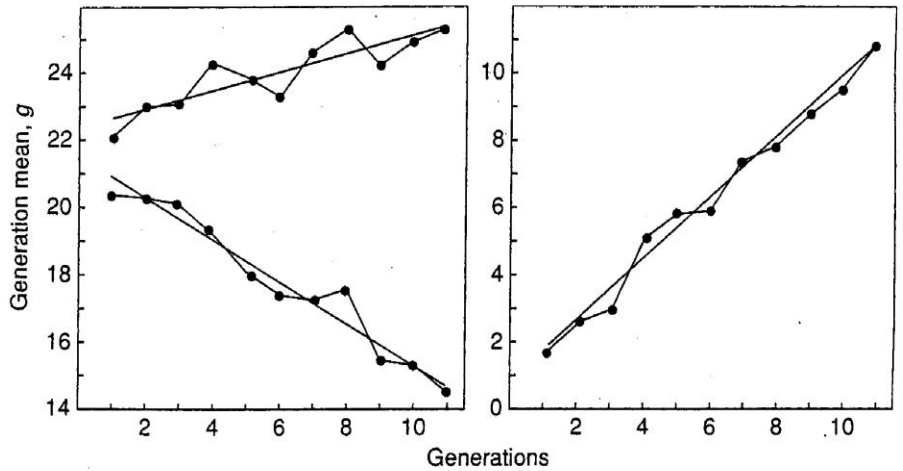


Fig. 11.4. Two-way selection for 6-week weight in mice. On the left the response of the two lines are shown separately. On the right the 'divergence' is shown, i.e., the difference between the upward- and downward-selected lines. See Example 11.4. (*Based on Falconer, 1953.*)

KEY Model Parameters: Age- and Sex-Specific *Conditional Maturation Probabilities,*

$$\sigma_{kF}(i,j), \sigma_{kM}(i,j)$$

- Definition – Probability that an age *k* female (or male), not caught and alive in the ocean at age *k,* will mature at age *k* <u>given that it had male and female parents of ages *i* and *j*, respectively.</u> (*Captures essence of inheritance of age at maturity.)*

- Parameter Values – ERH age at maturity experiments used to directly estimate a few (from cohort reconstructions); remaining are “interpolated” (“imputed”).

Example matrix of maturation probabilities: age 2 males

	Age of Male Parent				
Age of Female Parent	2	3	4	5	6
3	0.5810	0.2997	0.1786	0.0574	0.0287
4	0.5428	0.2800	0.1688	0.0536	0.0268
5	0.5280	0.2600	0.1549	0.0498	0.0249
6	0.4652	0.2400	0.1430	0.0460	0.0223

Example matrix of maturation probabilities: age 3 females

	Age of Male Parent				
Age of Female Parent	2	3	4	5	6
3	0.4026	0.3103	0.2182	0.1280	0.0604
4	0.2740	0.2122	0.1484	0.0856	0.0429
5	0.1456	0.1122	0.0789	0.0455	0.0228
6	0.0726	0.0567	0.0394	0.0228	0.0140

MODEL SCENARIOS

- Unexploited vs Exploited (ocean fishing only).

- Hatchery Mating Policies:
  1. Completely Random Mating – jacks included
  2. Completely Random Mating – jacks excluded
  3. Male Length ≥ Female Length

- Stock Type: *Mid-maturing* (Elk R., OR) and *late-maturing* (Wilson R., OR – see Chen thesis) stock types

Model Calculations of Long-Term Age and Sex Structure

1. Specify *Initial Conditions*: Begin with assumed numbers of age *k* males and females in hatchery returns for first 6 years;
2. Select hatchery mating policy;
3. Generate numbers of expected (*i,j*) matings according to mating policy and hatchery returns;
4. Use age-specific fecundities, survival from egg to age 2, and maturation probability matrixes to calculate returns at age (from each mating type) in subsequent years;
5. Impose exploitation (if exploited) to alter returns at age;
6. “Run” computer model until equilibrium reached (usually 25-50 years (6-12 generations).

Model (Simplifying) Assumptions

- Hatchery matings are all 1:1 (no pooling of sperm or eggs);
- No females mature at age 2;
- All eggs are equally likely to survive to age 2;
- Size at age *k* is independent of parental mating type;
- 50:50 sex ratio in ocean at age 2;
- No freshwater harvest; Ocean exploitation rates are independent of fish sex and do not vary across years .

A “Piece” of the Model

$$(1) \qquad N_{2M}(t) = [0.5(1-u_2)] \sum_{i=2}^{6} \sum_{j=3}^{6} [\sigma_{2M}(i,j) R_{ij}(t)]$$

$$(2) \qquad N_{3M}(t) = [0.5p_2(1-u_2)(1-u_3)] \sum_{i=2}^{6} \sum_{j=3}^{6} [\sigma_{3M}(i,j)(1-\sigma_{2M}(i,j)) R_{ij}(t-1)]$$

$$(3) \qquad N_{3F}(t) = [0.5p_2(1-u_2)(1-u_3)] \sum_{i=2}^{6} \sum_{j=3}^{6} [\sigma_{3F}(i,j) R_{ij}(t-1)]$$

$$(4) \qquad N_{4M}(t) = [0.5p_2p_3(1-u_2)(1-u_3)(1-u_4)] \cdot \sum_{i=2}^{6} \sum_{j=3}^{6} [\sigma_{4M}(i,j)(1-\sigma_{2M}(i,j))(1-\sigma_{3M}(i,j)) R_{ij}(t-2)]$$

$$(5) \qquad N_{4F}(t) = [0.5p_2p_3(1-u_2)(1-u_3)(1-u_4)] \cdot \sum_{i=2}^{6} \sum_{j=3}^{6} [\sigma_{4F}(i,j)(1-\sigma_{3F}(i,j)) R_{ij}(t-2)]$$

The expected number of age 2 ocean recruits originating from matings of age *i* males with age *j* females is:

$$R_{ij}(t) = p_1 \Theta^*_{ij}(t-2) = p_1 X_{ij}(t-2) f_j$$

$

Where:

$$\Theta^*_{ij}(t) = \frac{\Theta_{ij}(t)\Theta_{max}}{\sum_{i=2}^{6}\sum_{j=3}^{6}\Theta_{ij}(t)}$$

and Θ_{max}= maximum egg take.

The X_{ij}, the expected number of matings between age i males and age j females, depends on the mating policy. For example, for

Completely Random Mating:

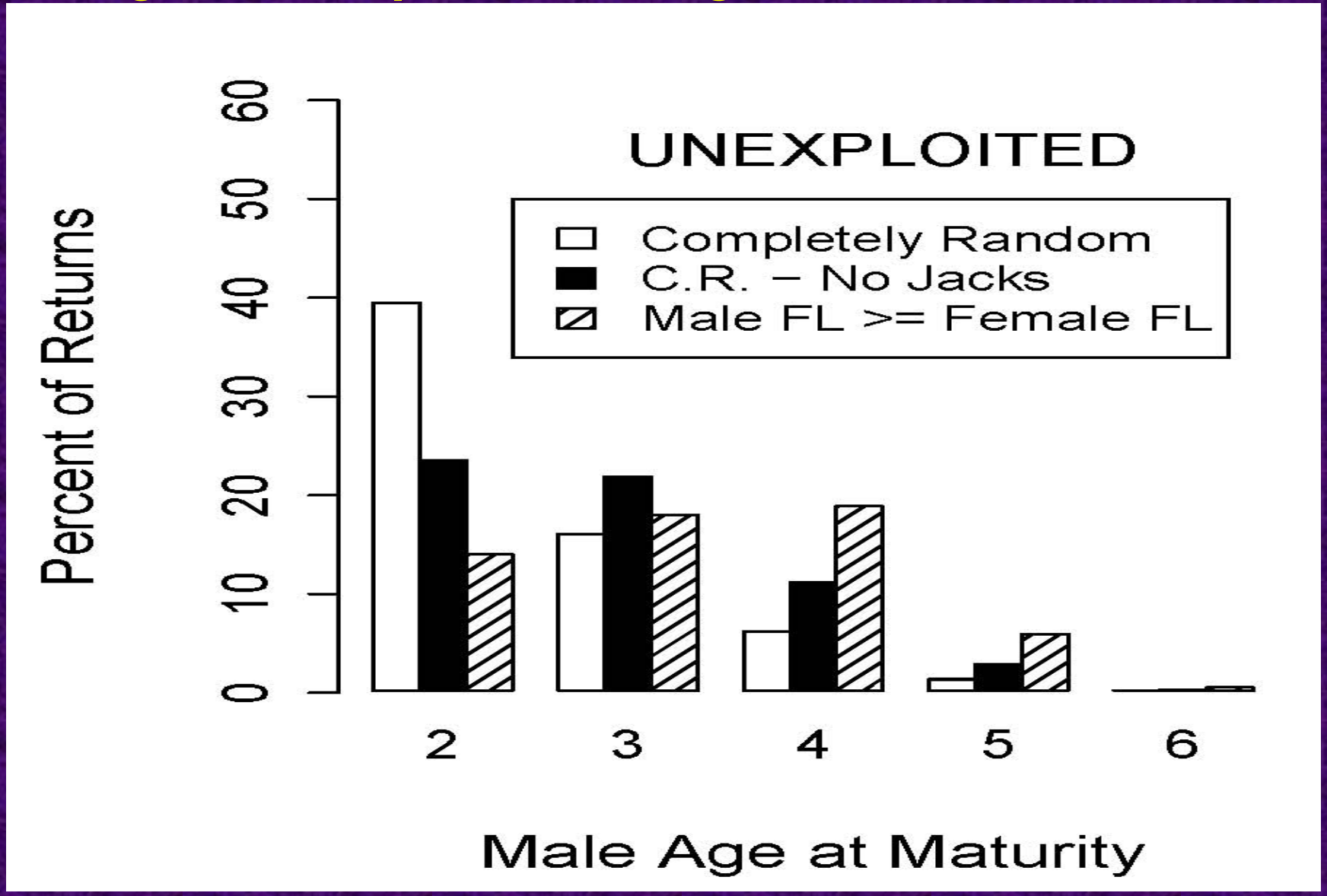
$$X_{ij}(t) = N_{jF}(t)\left[\frac{N_{iM}(t)}{N_{2M}(t) + N_{3M}(t) + N_{4M}(t) + N_{5M}(t) + N_{6M}(t)}\right]$$

Completely Random, Excluding Jacks:

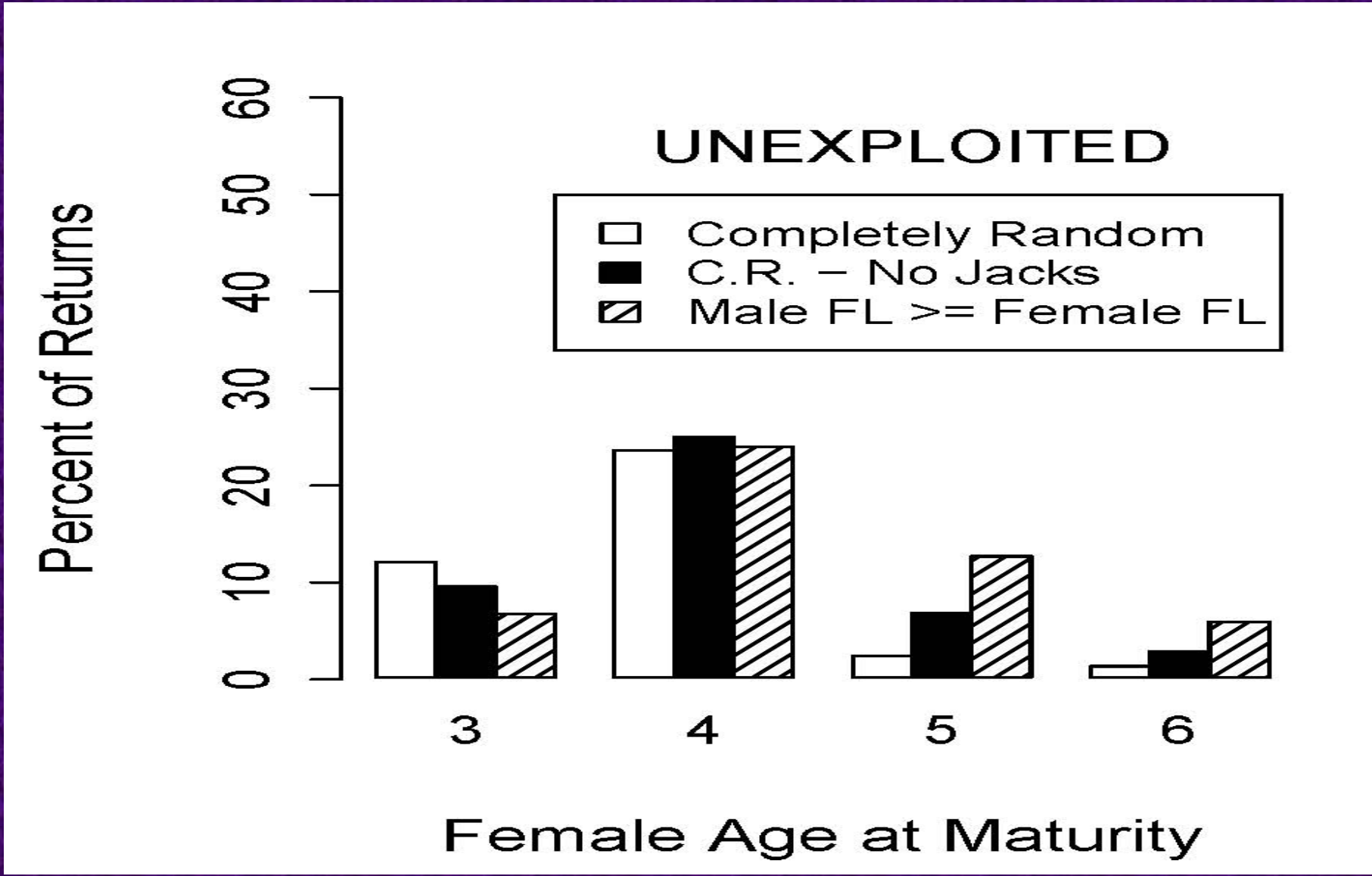
$$X_{ij}(t) = N_{jF}(t)\left[\frac{N_{iM}(t)}{N_{3M}(t) + N_{4M}(t) + N_{5M}(t) + N_{6M}(t)}\right]$$

Male Length ≥ Female Length (more complicated!)

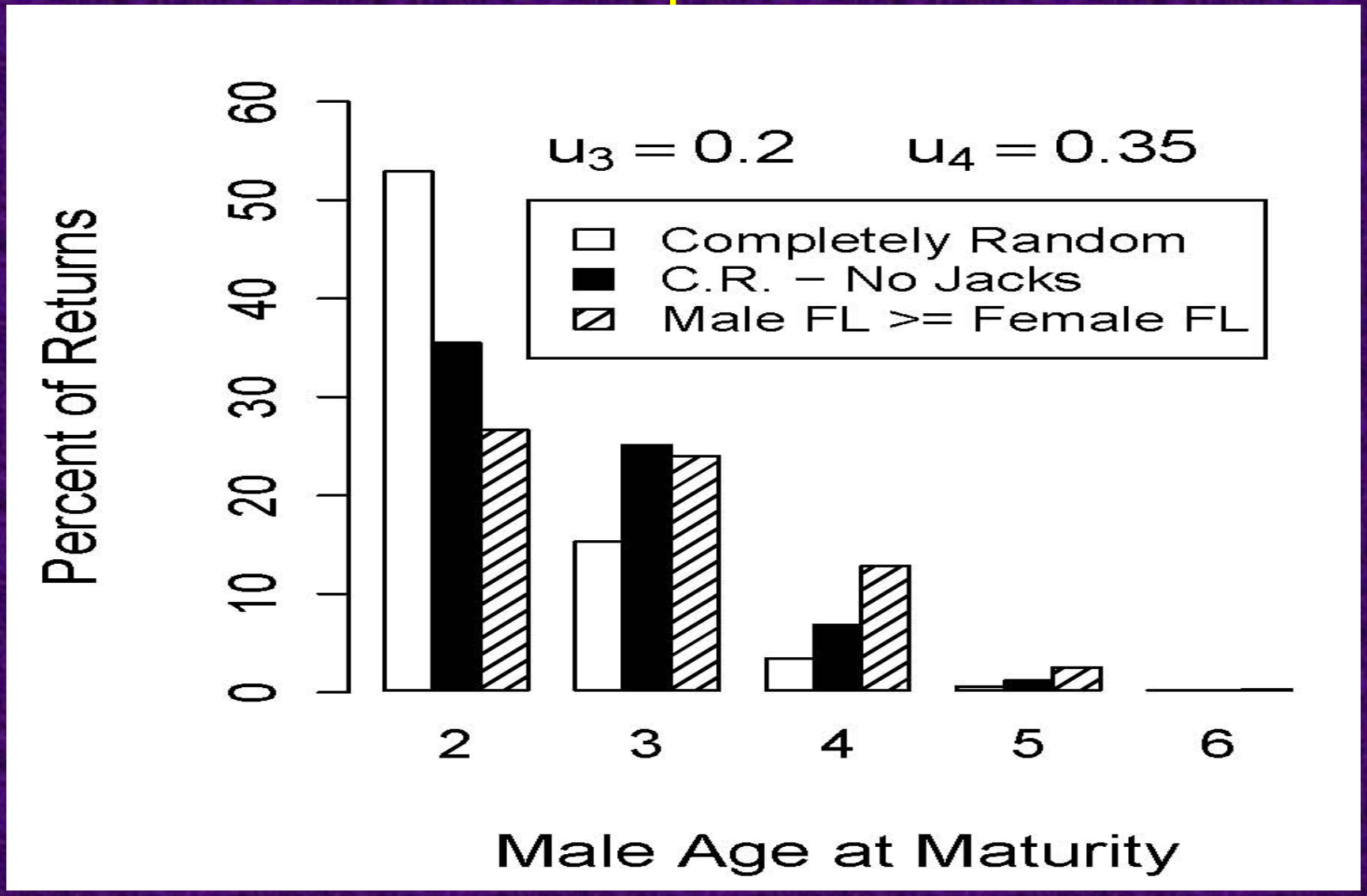
Elk River Chinook
Long-Term Equilibrium Age Structure: - Males



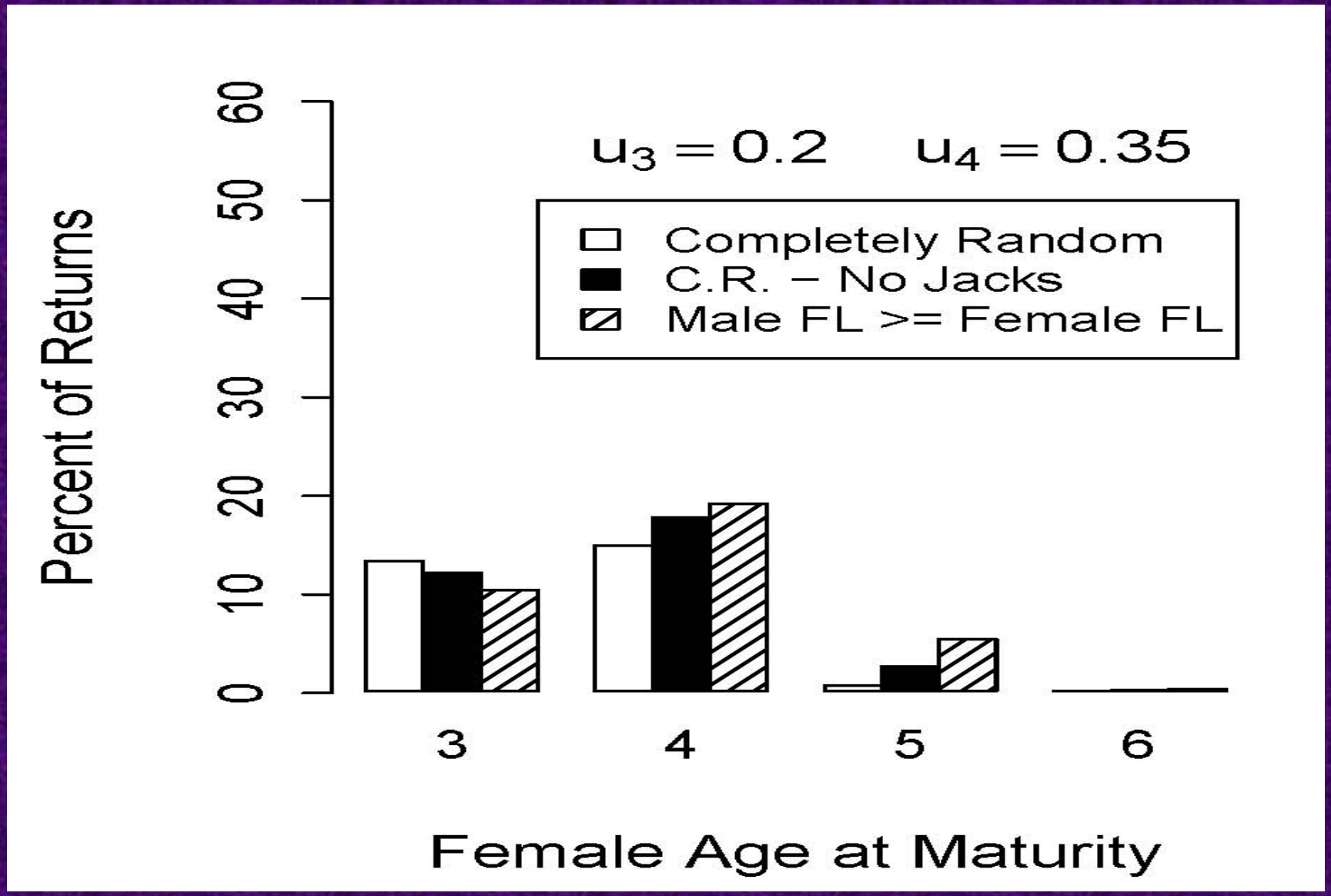
Long-Term Equilibrium Age Structure: Females



Long-Term Equilibrium Age Structure Under "Moderate" Ocean Exploitation: Males



Long-Term Equilibrium Age Structure Under "Moderate" Ocean Exploitation : Females

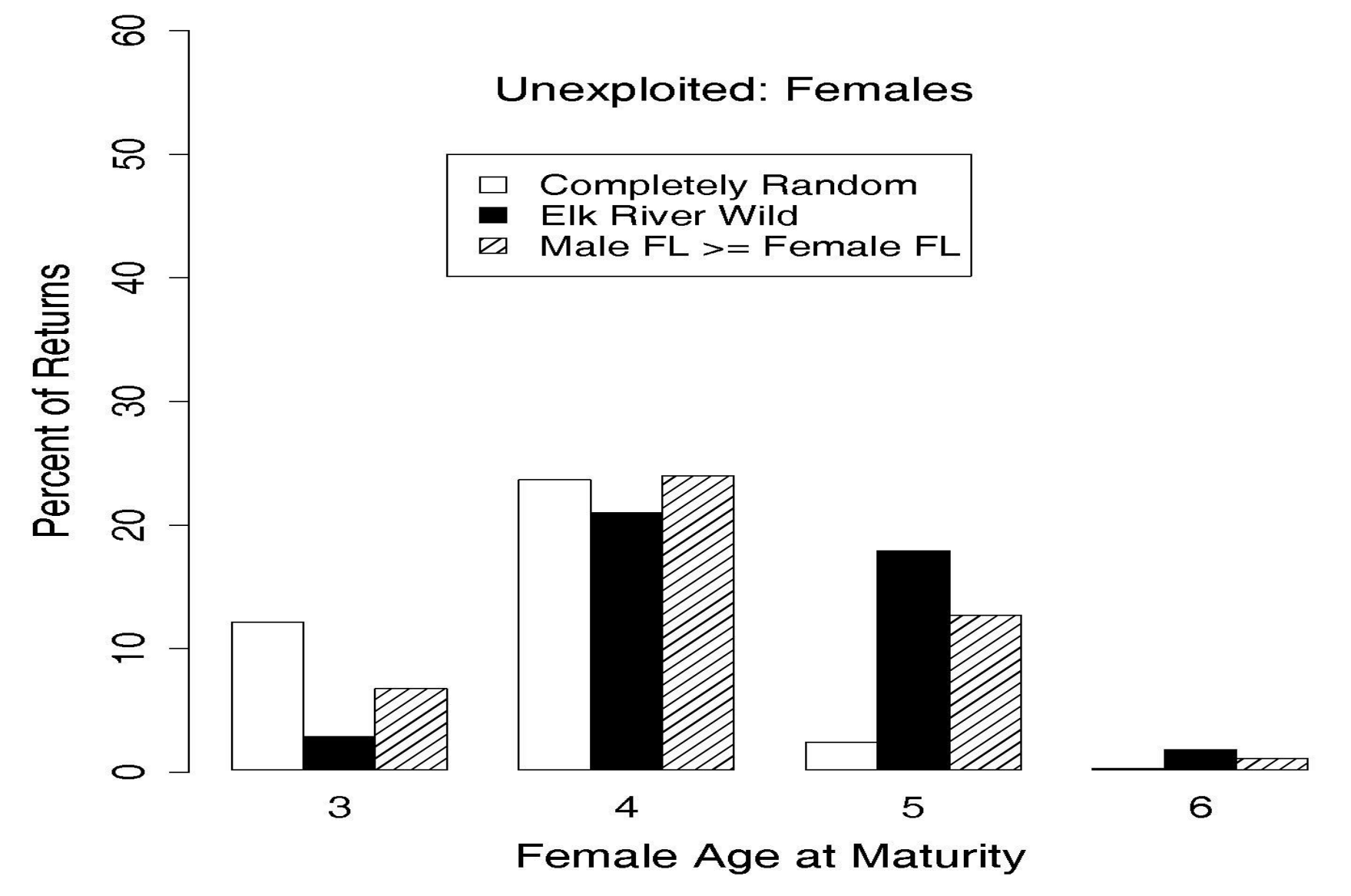


Conclusions – Elk River Chinook

- Completely random mating will result in substantial selection for younger age at maturity.
- Some jacks will continue to be produced, even if none are used as male parents.
- Partial selection against jacks (e.g., half of percentage among males) has effects intermediate to Completely Random and CR with jacks excluded.
- Exclusion of jacks reduces intensity of selection, but does not prevent selection for earlier age at maturity.
- Use of a “Male FL ≥ Female FL” mating policy may be feasible to implement at hatcheries and provides an equilibrium age and sex structure similar to a natural spawning population (next slide).

Natural vs Hatchery Age Structure: Males

Natural vs Hatchery Age Structure: Females



Additional Comments

- Results for Late-Maturing Stock Type, with very little natural jack return, are less striking. In general, degree of reduction in mean ages will depend strongly on stock type and the maturation matrixes;

- For simplified forms of the model (Lamberson et al. 2007), not all maturation maturations lead to long-term stable equilibria.

- Interesting that model generates long-term equilibrium age structure vs continued directional change (in contrast to standard selection experiments).