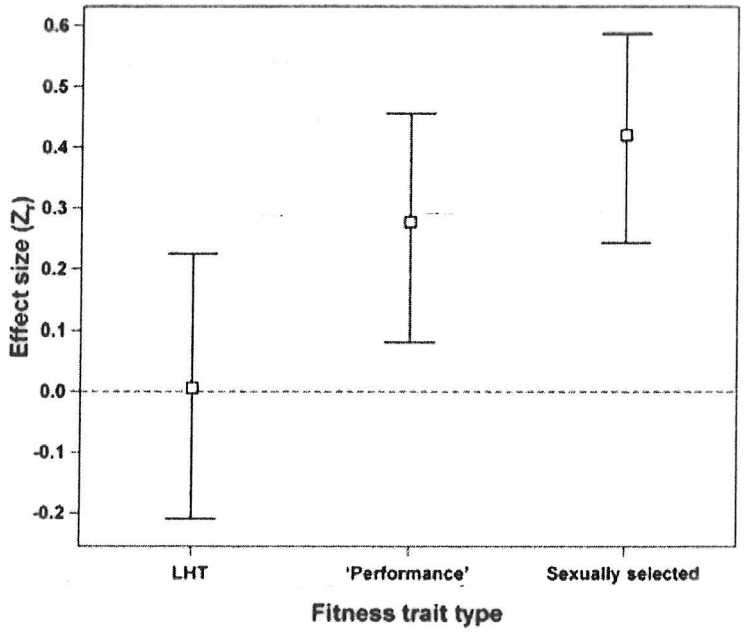
UNIVERSITE DE NANTES **FACULTE DES SCIENCES**

M1 BE Bioproduction des écosystèmes

GENETIQUE ET DYNAMIQUE DES POPULATIONS

Illustrations cours Génétique

Prof. P. G. Beninger



M1 GENETIQUE ET DYNAMIQUE DES POPULATIONS

Objectifs

(1) Présenter les principaux concepts et approches de la génétique des populations, sa relation avec l'écologie des populations et la micro-évolution.

(2) Présenter les bases biologiques quantitatives nécessaires à l'étude et la gestion des populations, avec accent sur les prévisions. Les exemples sont souvent tirés de la gestion des populations marines, mais l'application des concepts à d'autres types de populations est toujours indiquée.

Répartition des enseignements

28-8-12

Contenu des CM

1. Génétique des populations

1.1 Principaux thèmes en génétique des populations :

(I) utilisation des séquences génomiques dans l'étude des populations (délimitation, migrations, flux génique, dispersion larvaire)

(II) Etude des variations génotypiques significatives au sein d'une population : évolution

1.2 Evolution et spéciation

1.2.1 La systématique et la phylogénie aujourd'hui : importance et approches

1.2.2 Macro- vs. Micro-évolution ; relation écologie – micro-évolution

1.2.3 Mécanismes de la micro-évolution

- L'équilibre Hardy-Weinberg et ses considérants ; test pour des écarts significatifs ; allèles multiples ; taille effective de population
- écarts de l'équilibre H-W : micro-évolution

- mécanismes de la micro-évolution : (I) Producteurs de variations : Mutations, brassage des gènes, vigueur hybride, recombinaisons –transpositions (II) Réducteurs de variations : Dérive génique, fixation d'allèles, consanguinité, effet fondateur, types et mécanismes de sélection naturelle, sélection sexuelle, , compétition spermique et assurance de paternité, sélection dirigée, sélection par activités de chasse et de pêche
- norme adaptative, fardeau génétique, interaction variabilité – environnement

1.2.4 La spéciation

-critères de la spéciation
-mécanismes d'isolement sexuel
-spéciation sympatrique et allopatrique
- compétition spermique / pollénique et spéciation

1.3 Références :

Beninger, P.G. Recueil d'illustrations, Génétique et biologie des populations. *Disponible auprès de Mad. Aumaille, technicienne*
Campbell, N.A. Biologie. De Boek éditeurs. Chap. 12, 13, 14, 20, 21, 22. *Disponible BU.*
Mettler, L.E. et Gregg, T.G. Population genetics and evolution. Prentice-Hall Ltd.

2. Dynamique des populations

2.1- Concepts préalables
- Unités d'étude : espèce, population, stock
- les modèles de croissance d'une population

2.2- Paramètres biologiques et démographiques
- répartition et distribution spatiale
- nombres – recensement
- sex – ratio
- fécondité et natalité
- croissance et âge : détermination, modèles de croissance individuelle
- mortalité naturelle (M)
- détermination de M
- sources de M non-modifiables et modifiables : la prédation

2.3 - Paramètres d'exploitation
-effort et prise par unité d'effort (pue)
-utilisation de pue comme indice d'abondance et d'évolution des nombres
- puissance de pêche

2.4 – Paramètres d'un stock exploité
- recrutement, relation stock-recrutement
- vulnérabilité, phase disponible, phase exploitée
- sélectivité
- mortalité par pêche (F) et mortalité totale (Z)
- détermination de F

2.5 – Intégration – application des paramètres précédents à des données récoltées
- analyse par cohorte
- la prévision des captures
- la prévision du rendement
- taux maximal / optimal d'exploitation – courbes de Schaefer
- modèles globaux et modèles structuraux

Marine Biology (2000) 137: 953–961

M. P. Hare · S. R. Palumbi · C. A. Butman

Single-step species identification of bivalve larvae using multiplex polymerase chain reaction

Received: 30 March 2000 / Accepted: 10 July 2000

Abstract One of the biggest obstacles to studying recruitment variation in marine bivalves is the need to collect and process large numbers of plankton samples. Larval bivalves are notoriously difficult, if not impossible, to identify to species using morphological criteria alone. Remote time-series collections could satisfy the sampling challenge, but efficient identification techniques must be developed to obtain species-specific data. Thus, we have developed a multiplex polymerase chain reaction (PCR) identification assay in which a single reaction is capable of accurate and efficient discrimination of five target bivalve species based on the size of cytochrome oxidase I products. The assay was tested with cultured and field-sampled larvae as well as adult genomic DNAs. Using a single whole larva as template, multiplex PCR reactions were capable of discriminating among the commercially important bivalves: *Mercenaria mercenaria*, *Argopecten irradians*, *Mulinia lateralis*, *Spisula solidissima* and *Mya arenaria*. Overall accuracy was 92%, including very few false positives. The efficiency of this assay stems from its ability to discriminate multiple target species with a single molecular step that ultimately can be automated to process large numbers of larvae.

Table 3 Accuracy of multiplex PCR assay for identification of five target bivalve species using two different molar ratios, 3:1 and 2:1, of ribosomal 18S and COI primer pairs (see "Results"). Subset of PCR results using wild larvae were followed up with sequencing of 18S product. False negative (*neg.*) and false positive (*pos.*) results are defined in "Materials and methods"; they sum with the number of correct identifications to sample size [*No. PCR* for cultured larvae, No. sequenced (*No. seq.*) for wild-caught larvae] in that row (*WHOI* Woods Hole Oceanographic Institute, Massachusetts; *IOS* Isle of shoals, New Hampshire) Blank PCR results still produced amplifiable 18S product in some cases

Sample	No. PCR	PCR identification	No. seq.	18S sequence identification	False neg.	False pos.	Correct
3:1 Primer mix							
Cultured	7	*Mercenaria mercenaria*			0	0	7
	6	*Argopecten irradians*			3	0	3
	6	*Mulinia lateralis*			0	0	6
	6	*Spisula solidissima*			0	0	6
	7	*Mya arenaria*			0	0	7
Wild WHOI	3	*Spisula solidissima*	3	*Spisula* spp.	0	0	3
	3	*Argopecten irradians*	3	*Argopecten* spp.	0	0	3
	9	Nontarget	1	*Spisula* spp.	1	0	0
			5	*Ensis directus*	0	0	5
			2	Mytilidae	0	0	12
			1	Veneroida	0	0	1
	1	Blank	1	Mytilidae	–	–	–
IOS 5/99	24	Nontarget	1	*Mya arenaria*	1	0	0
			15	Veneroida	0	0	15
IOS 7/99	31	Nontarget	15	Mytilidae	0	0	15
	3	Blank	3	Mytilidae	–	–	–
Totals	106		50		5	0	73
Proportions					6.3		93.6
2:1 Primer mix							
Cultured	8	*Mercenaria mercenaria*			0	0	8
	8	*Argopecten irradians*			3	0	5
	8	*Mulinia lateralis*			1	0	7
	8	*Spisula solidissima*			0	0	8
	8	*Mya arenaria*			0	0	8
Wild WHOI	3	*Mercenaria mercenaria*	1	*Mercenaria mercenaria*	0	0	1
	2	*Argopecten irradians*	1	*Argopecten irradians*	0	0	1
	21	*Spisula solidissima*	5	*Spisula solidissima*	0	0	5
	1	*Spisula solidissima*	1	*Ensis directus*	0	1	0
	1	*Spisula solidissima*	1	Veneroida	0	1	0
	74	Nontarget	3	*Ensis directus*	0	0	3
			4	Veneroida	0	0	4
			2	Mytilidae	0	0	2
			1	Unionidae	0	0	1
			1	Pterioida	0	0	1
			1	Corbulidae	0	0	1
	1	Blank			–	–	–
Totals	142		21		4	2	55
Proportions					6.6	3.3	90.2

Marine Biology (2000) 137: 811–818

A. L. Martel · L. M. Auffrey · C. D. Robles · B. M. Honda

Identification of settling and early postlarval stages of mussels (*Mytilus* spp.) from the Pacific coast of North America, using prodissoconch morphology and genomic DNA

Received: 10 November 1999 / Accepted: 6 September 2000

Abstract Detailed inventories of the benthos and field studies of the settlement and recruitment processes of marine benthic invertebrates require accurate identification of newly settled larvae and early juvenile stages. We provide morphological criteria, visible under a good quality dissecting stereomicroscope, by which to discriminate between species of the settling larval and early postlarval stages (~250 to 700 μm shell length) of mussels of the genus *Mytilus* on the west coast of Vancouver Island and Southern California. Compared to the bay mussel (*M. trossulus*), the sea mussel (*M. californianus*) has: (i) a shallower and flatter umbo, the latter corresponding to a significantly less pronounced prodissoconch I (PI) curvature and (ii) a greater PI length; as well as (iii) a wider separation between the provincular lateral teeth (PLT). The PLT distance is a new term denoting the separation between the midpoint of two reddish pigment spots of the provinculum (larval hinge apparatus) region of settling larvae and early postlarvae of *Mytilus* spp. from the East Pacific Coast. These spots mark the larger provincular lateral teeth, situated at either end of the provinculum. We confirmed the validity of morphological criteria by comparing PCR products of genomic DNA of provisionally identified postlarvae. Furthermore, measurements of PI lengths and PLT distance from well-preserved postlarvae of sea mussels (*M. californianus*) and of bay mussels (*M. galloprovincialis*) from Southern California indicate that the PI morphology and morphometry, and PLT distance criterion apply for that region as well. The criteria presented here can also apply to the advanced (competent) veliger stages, as the latter may settle (i.e. become the "settling" stage) upon encountering a suitable substrate. Our present and previously published work provide economical and effective identification methods that can be used to discriminate among early life history stages (~250 μm to 5.0 mm shell length) of *Mytilus* spp. along the west coast of North America.

SEX REDUCES GENETIC VARIATION: A MULTIDISCIPLINARY REVIEW

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For over a century, the paradigm has been that sex invariably increases genetic variation, despite many renowned biologists asserting that sex decreases most genetic variation. Sex is usually perceived as the source of additive genetic variance that drives eukaryotic evolution vis-à-vis adaptation and Fisher's fundamental theorem. However, evidence for sex decreasing genetic variation appears in ecology, paleontology, population genetics, and cancer biology. The common thread among many of these disciplines is that sex acts like a coarse filter, weeding out major changes, such as chromosomal rearrangements (that are almost always deleterious), but letting minor variation, such as changes at the nucleotide or gene level (that are often neutral), flow through the sexual sieve. Sex acts as a constraint on genomic and epigenetic variation, thereby limiting adaptive evolution. The diverse reasons for sex reducing genetic variation (especially at the genome level) and slowing down evolution may provide a sufficient benefit to offset the famed costs of sex.

> Genome theory, where whole genomes serve as the informational unit, maintains that sex should reduce variation at the genome level.

> . . . we assert that there are two distinctive functions of sex and that the main one is to ensure the existence of a given species by maintaining genome system identity. In contrast, the increased diversity at the gene level by meiosis is secondary, as the combination of genes contributes to new features of existing systems rather than altering the system in a fundamental way. Clearly, if it was merely just for increasing genetic diversity, sex would not have evolved in the first place insofar as asexual systems display much higher levels of genetic diversity. Although meiotic crossing-over recombination provides new allelic combinations, it does not alter loci or even the physical order of loci.

Evolution 65-4: 1088–1098

Journal of Shellfish Research, Vol. 18, No. 1, 147–153, 1999.

FOUNDER EFFECT, GENETIC VARIABILITY, AND WEIGHT IN THE CULTIVATED PORTUGUESE OYSTER *CRASSOSTREA ANGULATA*

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ABSTRACT Existence of genetic variability is a prerequisite for successful implementation of breeding programs, and clarification of the relationships in such programs to quantitative traits is of great economic interest. We have studied the relationship between multilocus heterozygosity and/or allozyme genotypes and weight in the Portuguese oyster *Crassostrea angulata* (Lamark). Two cohorts were obtained in a commercial hatchery by mass-spawning from wild oysters. Loss of genetic variability was shown in cultured oysters as compared with the wild population because of a founder effect caused by a low effective population size. Significant effects on growth rate were detected for the *Me-2, Xdh, Lap, Pgm,* and *Est* loci. However, these effects were not retained in the two cohorts, nor in the two ages of the same cohort, nor were differentiated effects detected in weight classes of the same age. At the same time, differences between genotypes were not associated with differences between heterozygous and homozygous genotypes. Positive correlations between multilocus heterozygosities and growth rate, as well as significant differences between mean body weights for different degrees of heterozygosity, were found only in the largest weight class. Moreover, significant results were obtained when the mean weight of different heterozygosity classes for total weight, body weight, and shell weight were compared only in the oysters selected for their larger size. This result points to the isozymes as markers for quantitative traits and confirms the existence of heterosis in *C. angulata*, indicating the possibility of establishing breeding programs based on the maintenance of inbred lines and crossing them to obtain hybrid vigor.

KEY WORDS: oysters, genetic variability, weight, *Crassostrea angulata*, isozymes

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Genetic variation of wild and hatchery populations of the Pacific oyster, *Crassostrea gigas* (Thunberg), in Australia

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Abstract

Pacific oysters were introduced to Tasmania about 50 years ago from Japan; fears had been expressed that they would have lost genetic variation during their subsequent naturalisation. Using 17 allozyme loci, three hatchery and four naturalised populations of *Crassostrea gigas* (Thunberg) in Australia were compared with one another and with two endemic Japanese populations. All populations showed a high degree of genetic variability. The percent of polymorphic loci ranged from an average of 70.6% (hatcheries) through 73.5% (naturalised and Japan). Mean observed heterozygosities ranged from 0.267 (naturalised) through 0.285 (hatcheries) to 0.291 (Japan). Mean numbers of alleles per locus ranged from 3.0 (hatcheries) through 3.3 (naturalised) to 3.5 (Japan). Most loci and populations showed good fits to Hardy–Weinberg expectations; the few significant exceptions were heterozygote deficiencies. Allele-frequency differences among populations were minor, although sometimes statistically significant; only about 1% of the allele frequency variation could be attributed to among-population differences. The introduced oysters appear to have retained most of the genetic variation present in the Japanese populations.

Keywords: *Crassostrea gigas*; Heterozygosity; Allozymes; Oysters; Australia; Japan

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Likelihood of bottleneck event in the history of the Australian population of Atlantic salmon (*Salmo salar* L.)

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Abstract

Previous microsatellite DNA analyses suggested a small overall loss of genetic variation in Tasmanian cultured Atlantic salmon when compared to a sample from the progenitor Canadian population. Here, 15 loci (eight microsatellite and seven allozyme) were examined in an additional sample from Tasmania and a sample from New South Wales (site of original importation to Australia in the mid-1960s from which the Tasmanian population was founded). Significant allele frequency differences were observed between samples for both microsatellite and allozyme loci. The greater allelic variation at microsatellite loci provided more information than allozyme loci on differences between samples from the progenitor and derived populations. A significant reduction in microsatellite heterozygosity, but non-significant loss of microsatellite alleles was observed between the Canadian and Australian samples. Comparison of observed heterozygosities with that expected under a two-phased model of mutation did not support the hypothesis of a severe bottleneck in the Australian population. However, low estimates of per-generation effective population sizes (80–90 over 11 generations) are consistent with a short-term moderate bottleneck in the Australian population of Atlantic salmon early in its introduction. Despite this the breeding population has been sufficiently large to maintain most pre-existing genetic variation in the Australian population.

Keywords: Microsatellites; Allozymes; Heterozygosity; Effective population size; Genetic drift

Table 1
Observed number of alleles (a), number of individuals scored (n), observed (H_o) and Hardy–Weinberg expected (H_e) heterozygosity estimates, and probabilities of genotype conformance to Hardy–Weinberg equilibrium (P) for the eight microsatellite loci in the four Atlantic salmon samples (allele frequencies available from authors)

Locus	R. Philip[a]	Gaden	Tasmania 1[a]	Tasmania 2
cmrSs1.10				
a	3	2	2	3
n	62	97	62	100
H_o	0.177	0.000	0.016	0.110
H_e	0.166	0.098	0.016	0.123
P	1.000	<0.001	1.000	0.012
cmrSs1.14				
a	5	4	4	5
n	65	98	61	100
H_o	0.692	0.653	0.541	0.700
H_e	0.680	0.640	0.526	0.656
P	0.034	0.237	0.579	0.187
cmrSs1.22				
a	12	20	10	12
n	62	95	62	100
H_o	0.919	0.822	0.726	0.820
H_e	0.866	0.854	0.703	0.826
P	0.001	0.991	0.043	0.425
20.19				
a	4	4	4	4
n	64	100	63	100
H_o	0.766	0.663	0.524	0.530
H_e	0.580	0.693	0.647	0.533
P	0.022	0.497	0.137	0.776
5.27				
a	2	2	2	2
n	64	88	62	100
H_o	0.313	0.352	0.355	0.290
H_e	0.266	0.370	0.401	0.326
P	0.214	0.776	0.505	0.383
D30				
a	6	4	2	3
n	64	98	61	98
H_o	0.578	0.480	0.410	0.449
H_e	0.535	0.502	0.485	0.550
P	0.634	0.001	0.297	0.108
F43				
a	4	3	4	4
n	61	87	66	98
H_o	0.377	0.207	0.303	0.306
H_e	0.676	0.432	0.536	0.599
P	<0.001	<0.001	<0.001	<0.001

Zaykin, D.V., Pudovkin, A.I., 1993. Two programs to estimate significance of χ^2 values using pseudo-probability tests. J. Hered. 84, 152.

J. Mar. Biol. Ass. U.K. (2004), 84, 1051–1056
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Genetic diversity of European populations of the invasive soft-shell clam *Mya arenaria* (Bivalvia)

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The genetic diversity of the soft-shell clam *Mya arenaria* from seven locations in Europe (two stations in the southern Baltic Sea (the Gulf of Gdansk) and two in the North Sea (Veerse Meer and Oosterschelde), and three additional stations in the Denmark Straits and Bay of Biscay) was determined using starch gel electrophoresis of allozymes. The results showed a low level of genetic variability and a lack of genetic differentation among the populations studied. Basic polymorphism characteristics calculated for populations from the North Sea estuaries and the Gulf of Gdansk were: He 0.094–0.145, Ho 0.092–0.130, percentage of polymorphic loci 33 (0.95 criterion), mean number of alleles per locus 2.0–2.7. The mean value of F_{ST} was 0.0133 and not significant. It is concluded that in spite of a low level of genetic polymorphism the soft-shell clam is a successful colonizer. The genetic homogeneity among the populations reflects rapid population extension, alleles neutrality and a high gene flow.

INTRODUCTION

The soft-shell clam *Mya arenaria* originated on Pacific coasts in the Miocene. In the late Miocene it extended its range to the west coasts of the Atlantic. In Europe, the soft-shell clam appeared in the late Pliocene. It has remained in America since the Pliocene whereas it died out in Europe at the beginning of the Pleistocene. According to Peterson et al. (1992), who dated shells from Kattegat, the soft-shell clam reinvaded Europe in the 13th Century and might have been transported from North America by the Vikings. It reinvaded the Pacific east coast probably through oyster transplants from the Atlantic to San Francisco Bay prior to 1874. The last step in the invasion history of the soft-shell clam was the unintentional introduction from the Baltic Sea to the Black Sea around 1960. Today *Mya arenaria* is widely distributed over boreal waters and is often a dominant species in local shallow water benthic communities. It has also an important commercial value in some regions of North America. The soft-shell clam is a relatively large (60–100 mm, maximally 150 mm) and long-lived bivalve. It inhabits mainly intertidal and shallow subtidal waters but has been found even at a depth of 192 m. Depending on the geographical region soft-shell clams spawn once or twice per year. The fecundity value for one spawning period can vary between 120 thousand to three million eggs. The larval phase usually lasts for 2–3 weeks. *Mya arenaria* is an eurytopic species. It lives in the salinity range 4–35 psu and can easily survive salinity fluctuations of 15 psu. The southern limit of distribution is determined probably by a temperature of 28°C. A temperature of 10–12°C for spawning and 12–15°C for succesful larval development determines the northern limit of distribution (see Strasser, 1999 for references).

Even though the soft-shell clam is such a common species, very little is known about its population genetics. Recent studies on the genetics of the soft-shell clam concerned only populations from the Atlantic coasts of North America and revealed a low level of allozyme variation in this species (Levinton, 1973; Morgan et al., 1978), which is in contrast to the hypothesis that animals living in an unstable, heterogeneous environment and able to colonize new habitats should possess high genetic variability (Hedrick et al., 1976; Ehrlich, 1986). The present paper is believed to be the first on the genetic diversity of European populations of *Mya arenaria*. This is especially surprising since *Mya arenaria* was probably the first species introduced into Europe by man. Colonization of a new area may be connected with processes causing a drastic decrease in population polymorphism, as predicted by theory (Chakraborty & Nei, 1977) and observed in many species (e.g. Gallardo et al., 1995). Another theory predicts little influence of founding events on populations (Nei et al., 1975). Similarly, two different models concerning population structuring after founder events exist, predicting strong genetic structuring or reducing of genetic differentation between populations (Alvarez-Buylla & Garay, 1994).

The aim of this study was to determine the level of genetic variation of some European populations using allozymes and characterize population structure at a macrogeographical scale with respect to historical and contemporary processes.

MATERIALS AND METHODS

Samples, consisting mainly of animals with a length of 10–30 mm, were collected in autumn 2001 from seven locations (Table 1, Figure 1). Animals were held alive in aquaria at 10°C or frozen at −70°C until processed. Due to the very low number of individuals in the French and Swedish populations, the genetic structure has been discussed mainly on the basis of the results obtained for the Dutch and Polish populations.

Fig. 3.8. The percentage of homozygous offspring from systematic matings with different degrees of inbreeding. After S. Wright, *Genetics*, 6 (1921), 111–78.

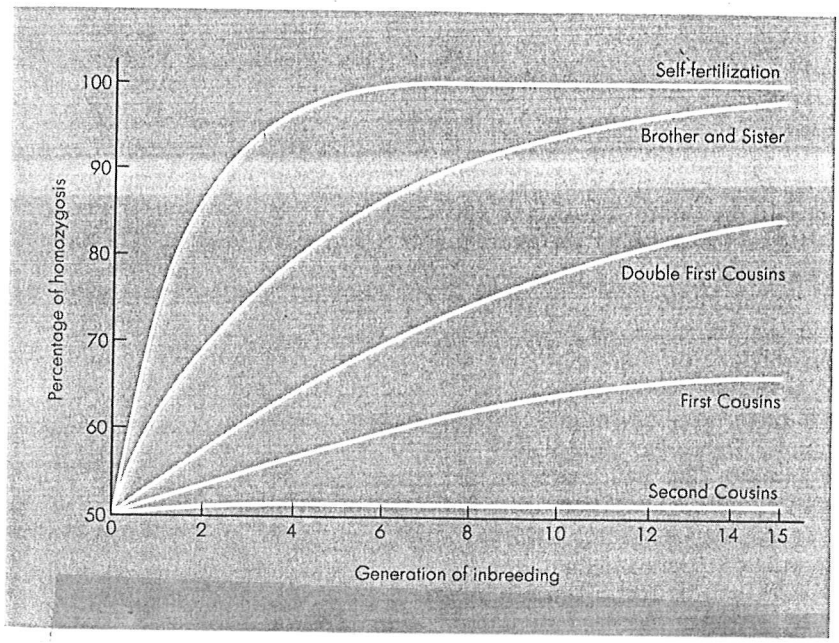

Table 3.5. The genotypic frequencies in random-mating populations with no inbreeding, partial inbreeding, and complete fixation

		Genotype frequencies		
Generations of inbreeding	F	A/A	A/a	a/a
None (Hardy-Weinberg)	$F=0$	p^2	$2pq$	q^2
One or more (Wright's equilibrium formula)	$1>F>0$	p^2+Fpq	$2pq-2Fpq$	q^2+Fpq
Infinite number (complete homozygosity)	$F=1$	p^2+pq	0	q^2+pq

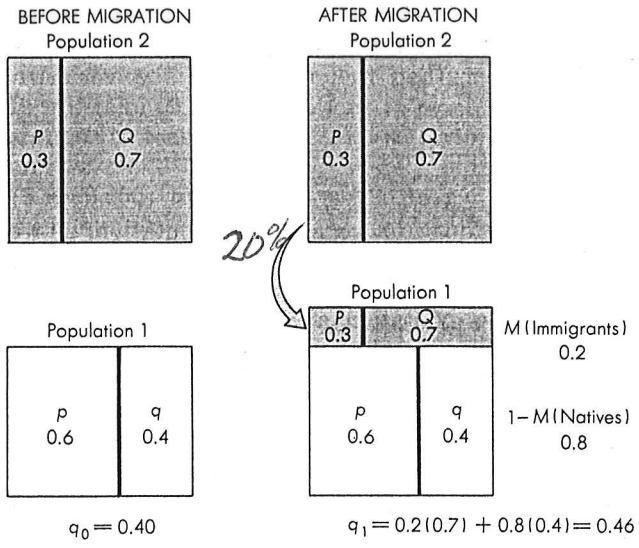

Fig. 4.8. Diagram showing the effects of migration on gene frequencies. It is assumed that the gene frequencies in population 1 and population 2 are different and that migration occurs from population 2 into population 1. After migration, population 1 will consist of 1 — M natives having gene frequencies like those of population 1 before migration occurred, and M migrants having gene frequencies characteristic of population 2.

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ORIGINAL ARTICLE

Relative risks of inbreeding and outbreeding depression in the wild in endangered salmon

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Abstract

Conservation biologists routinely face the dilemma of keeping small, fragmented populations isolated, wherein inbreeding depression may ensue, or mixing such populations, which may exacerbate population declines via outbreeding depression. The joint evaluation of inbreeding and outbreeding risks in the wild cannot be readily conducted in endangered species, so a suggested 'safe' strategy is to mix ecologically and genetically similar populations. To evaluate this strategy, we carried out a reciprocal transplant experiment involving three neighboring populations of endangered Atlantic salmon (*Salmo salar*) now bred in captivity and maintained in captive and wild environments. Pure, inbred, and outbred (first and second generation) cross types were released and recaptured in the wild to simultaneously test for local adaptation, inbreeding depression, and outbreeding depression. We found little evidence of inbreeding depression after one generation of inbreeding and little evidence of either heterosis or outbreeding depression via genetic incompatibilities after one or two generations of outbreeding. A trend for outbreeding depression via the loss of local adaptation was documented in one of three populations. The effects of inbreeding were not significantly different from the effects of outbreeding. Hence, at the geographic scale evaluated (34–50 km), inbreeding for one generation and outbreeding over two generations may have similar effects on the persistence of small populations. The results further suggested that outbreeding outcomes may be highly variable or unpredictable at small genetic distances. Our work highlights the necessity of evaluating the relative costs of inbreeding and outbreeding in the conservation and management of endangered species on a case-by-case basis.

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Inbreeding depression and growth heterosis in larvae of the purple sea urchin *Stronglyocentrotus purpuratus* (Stimpson)

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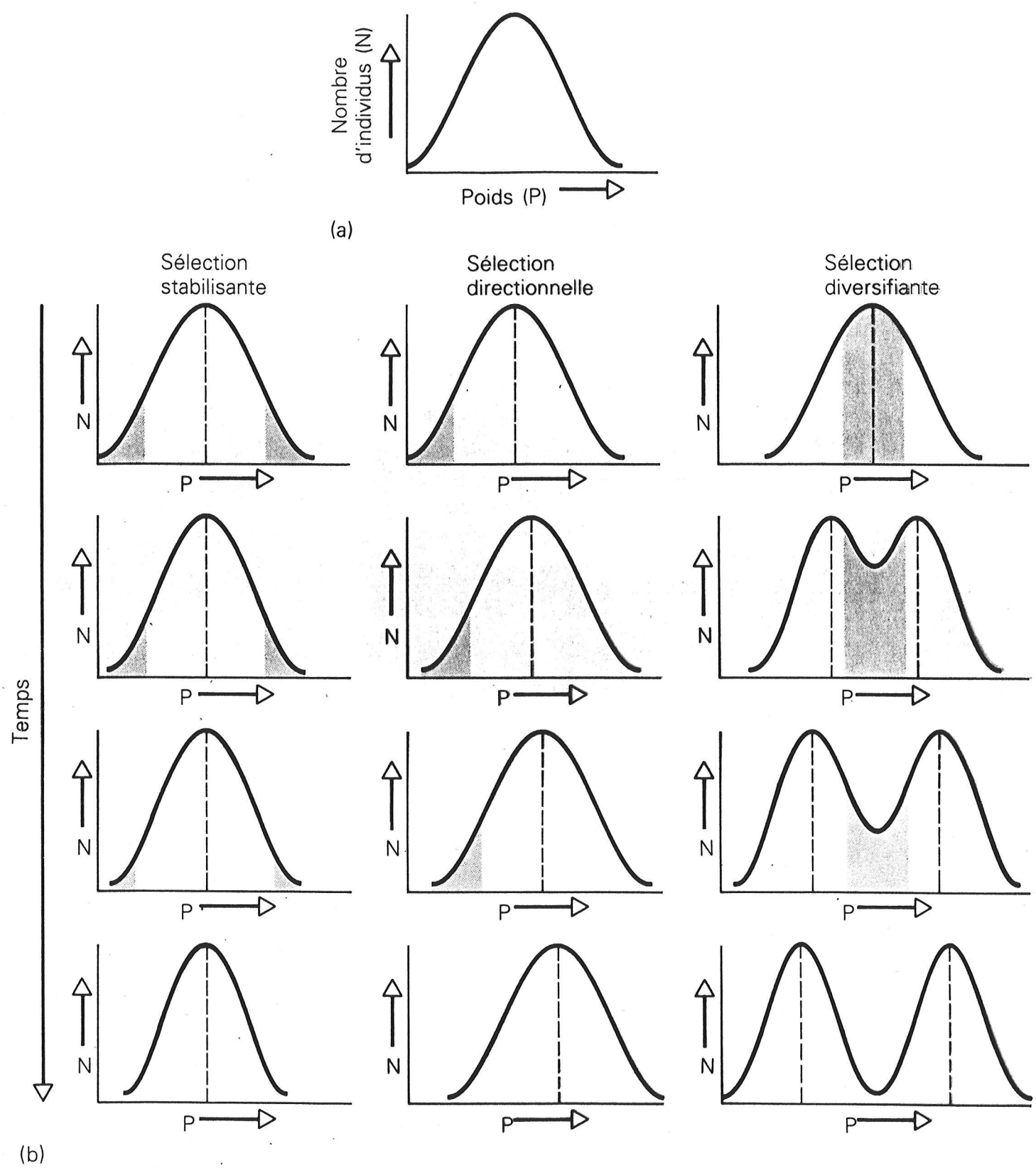
ABSTRACT

Effects of inbreeding and crossbreeding in the purple sea urchin *Stronglyocentrotus purpuratus* were examined by means of a controlled factorial cross of adult urchins from two full-sib families, which produced inbred ($f=0.25$) and crossbred offspring ($f=0$). Larvae were reared in two different culture systems: static 20-l bucket cultures and replicated 8-l buckets in a shared flow-through water system. The square root of larval area, measured by image analysis, was taken as a measure of size at one and two weeks of age. Linear models explained 60–80% of size variance in these experiments. Inbred larvae were significantly smaller and had greater coefficients of size variance than crossbred larvae, in both systems and at both time points. At week 1, the worst-performing crossbred family in the 8-l system was 33 μm greater than the best inbred family ($P \ll 0.001$); at week 2, the worst-performing crossbred family was 28 μm greater than the best-performing inbred cross ($P \ll 0.001$). The cost of inbreeding, δ/f, at week 1, was 1.0 and, at week 2, 0.8, suggesting severe inbreeding depression; the number of detrimental equivalents for larval size ranged from 0.89 to 1.32, with an average dominance of 0.06. These results, together with previous evidence for inbreeding depression of larval survival, suggest that the purple sea urchin has a large load of recessive deleterious mutations and that inbreeding and inbreeding depression could pose significant risks for hatchery-based stock enhancement or aquaculture programs, as well as for declining natural populations.



Tome I
28. Figure 12-10 **Effet des divers types de sélection sur un caractère polygénique**

Journal of Shellfish Research, Vol. 10, No. 1, 199–202, 1991.

NEGATIVE LARVAL RESPONSE TO SELECTION FOR INCREASED GROWTH RATE IN NORTHERN QUAHOGS *MERCENARIA MERCENARIA* (LINNAEUS, 1758)

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ABSTRACT F_1 offspring of wildstock *Mercenaria mercenaria* from Georgia were subjected to truncation selection (16% intensity level). Larval (F_2) progeny of *M. mercenaria* selected for rapid growth rate were significantly smaller (shell length) than larval progeny of control parents at both 10 and 18 days of age in two experimental trials. Survival rates were similar for both progeny lines from 2 to 18 days of age. Earlier studies by our group have demonstrated significantly higher embryonic mortality rates (2 days) in the progeny of parents selected for rapid growth. Control line progeny in both experiments set earlier (10–14 days) than those of the select line parents (14–18 days). This negative larval response for increased growth rate (in 3 year old adults) brings into question the merits of hatchery culling practices for smaller larvae. A long term approach to the study of the reproductive potential of bivalve brood-stock lines selected for increased rate of growth is called for on the basis of these results.

KEY WORDS: *Mercenaria mercenaria*, selection, larvae, aquaculture

TABLE 2.

Larval shell length (SL) data from two experimental trials comparing the offspring (F_2) of Select and Control Groups. Group A Control and Select lines (F_1) spawned July 6 and 7, 1989, respectively. Group B Control and Select lines (F_1) spawned June 13 and 14, 1989, respectively.

	SL (μm)		Analysis of Variance		
	Mean	Range	df	F	p
Day 2					
Group A					
Select	99.6	(97.7–103.3)			
Control	95.1	(88.0–102.3)	1	13.037	<0.001
Group B					
Select	93.9	(90.7–97.3)			
Control	98.1	(93.3–101.7)	1	7.746	<0.006
Day 10					
Group A					
Select	192.1	(177.3–203.7)			
Control	205.8	(195.3–217.7)	1	20.917	<0.0001
Group B					
Select	183.5	(171.0–192.3)			
Control	206.7	(187.0–220.0)	1	65.088	<0.0001
Day 18					
Group A					
Select	314.7	(248.3–370.0)			
Control	397.1	(369.3–425.3)	1	311.241	<0.0001
Group B					
Select	265.8	(238.7–289.7)			
Control	375.0	(329.3–415.7)	1	194.935	<0.0001

Journal of Shellfish Research, Vol. 23, No. 3, 753–757, 2004.

SELECTION RESPONSE FOR GROWTH RATE (SHELL HEIGHT AND LIVE WEIGHT) IN THE CHILEAN BLUE MUSSEL (*MYTILUS CHILENSIS* HUPE 1854)

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ABSTRACT The parental stock was taken from the 1999 natural spatfall of *Mytilus chilensis* collected in the Yaldad Bay of southern Chile. From the 22-mo-old cohort 5,688 mussels were monitored for live weight and shell length. Selection was carried out by applying a selection intensity of 1.755 for the trait "live weight". Five selected lines and five lines of an unselected control group were conditioned in seven 150-L tanks. Juveniles from the 3 selected and 2 control lines were individually tagged and transferred to three geographically distant mussel farms in southern Chile. Live weight and shell length were monitored after 10, 14, 18, and 22 months of age in all experimental mussels. The ANOVA results showed a significant difference, in both traits, between the selected and control groups at every age and location. Realized heritabilities for the trait "live weight" ranged between $h^2 = 0.35$ and $h^2 = 0.54$, whereas those for the trait "shell height" ranged between $h^2 = 0.32$ and $h^2 = 0.49$. Genotype-environment interactions were not apparent for either trait, indicating that similar selection pressures result in similar phenotypic changes for these traits across environments. These results suggest that mass selection for the improvement of the traits live weight and shell height would be effective in the Chilean mussel broodstocks.

TABLE 4.

Mytilus chilensis. Realized heritability estimates (h^2) and their standard errors (±SE) for the traits "shell height" and "live weight" at 22 months old grown at 3 geographically separated mussel farms.

	Shell Height h^2 SE	Live Weight h^2 SE
Hueihue	0.32 ± 0.017	0.38 ± 0.020
Putemun	0.49 ± 0.024	0.54 ± 0.018
Quetalmahue	0.48 ± 0.016	0.35 ± 0.015

Journal of Shellfish Research, Vol. 17, No. 4, 1171–1175, 1998.

CULTURED OYSTERS, *CRASSOSTREA VIRGINICA*, GENETICALLY SELECTED FOR FAST GROWTH IN THE DAMARISCOTTA RIVER, MAINE, ARE RESISTANT TO MORTALITY CAUSED BY JUVENILE OYSTER DISEASE (JOD)

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Orono, Maine 04469

ABSTRACT Growth and mortality of hatchery-produced juvenile oysters, *Crassostrea virginica,* selected for fast growth were compared with unselected, wild oysters at sites in Maine (Damariscotta River) and Massachusetts (North Bay) where Juvenile Oyster Disease (JOD) is enzootic. Over the course of the study, JOD occurred primarily in Maine, even though prevailing temperature and salinity at both sites were conducive for JOD development. From July to November 1996, mean shell height of selected oysters was greater than that of wild oysters at both sites. At the end of the study, mean shell height of both selected and wild oysters was greater in Massachusetts than in Maine. Mean cumulative mortality of both groups was greater in Maine than Massachusetts. Only in Maine was mean cumulative mortality of wild oysters greater than that of selected oysters. Differences in growth and mortality of oysters between sites were due primarily to the differential timing and severity of JOD occurrence. In addition, the difference in survival between selected and wild oysters in Maine was not related to differences in size between groups at the time of initial exposure to JOD. Thus, we conclude that occurrences of JOD are site specific (not dependent on source of seed), and that under challenge from JOD, selected oysters not only grow faster than wild (unselected) oysters, but exhibit a genetically based tolerance of this disease.

KEY WORDS: *Crassostrea virginica,* selection, Juvenile Oyster Disease, growth, mortality

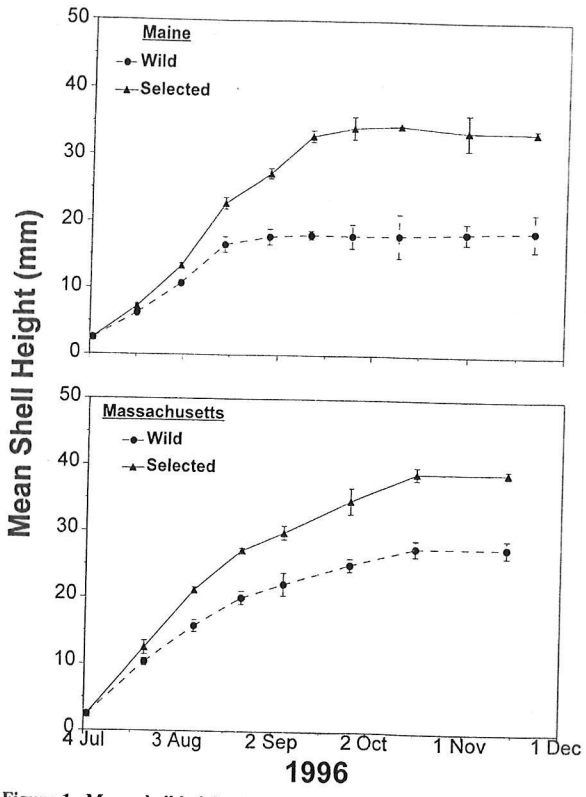


Figure 1. Mean shell height (mm, ±1 SD) of selected and wild oysters, *C. virginica,* at North Bay, Massachusetts and Damariscotta River, Maine sites.

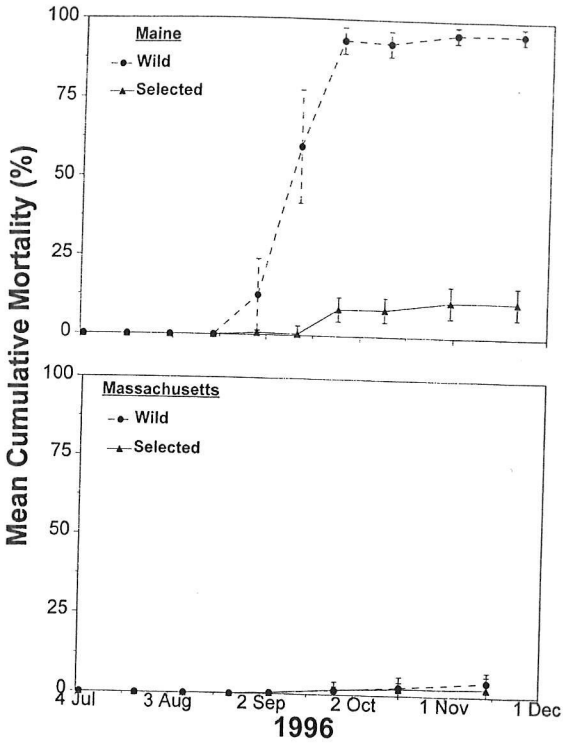
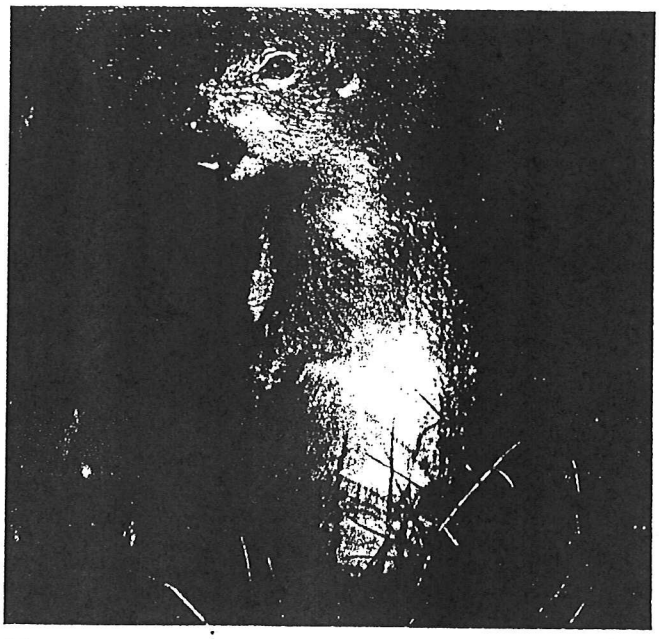
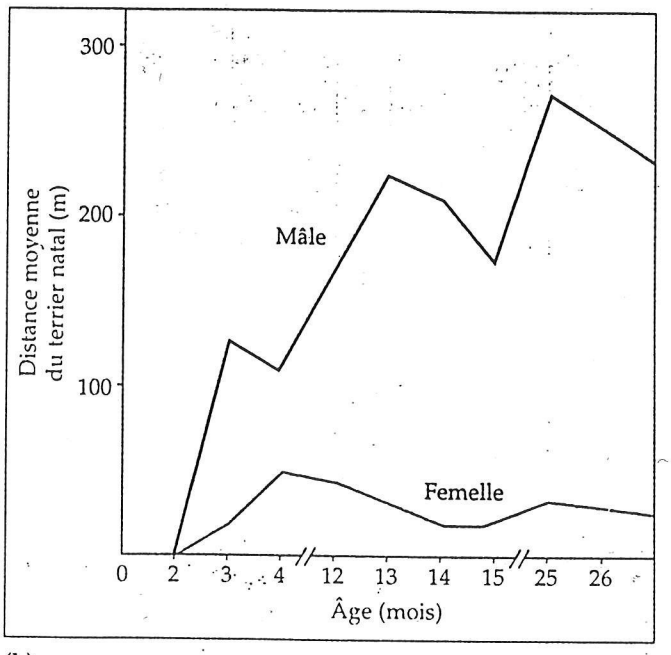


Figure 2. Mean cumulative mortality (%, ±1 SD) of selected and wild oysters, *C. virginica,* at North Bay, Massachusetts and Damariscotta River, Maine sites.



(a)



(b)

Figure 50.24
Expression de l'altruisme chez les mâles et les femelles. (a) En jetant un cri d'alarme, ce Spermophile avertit ses congénères d'un danger, de l'approche d'un prédateur par exemple. Presque tous les cris d'alarme sont émis par des femelles. (b) Le graphique explique les différences entre les Spermophiles mâles et les Spermophiles femelles en matière de comportement altruiste. Une fois sevrés, les mâles s'établissent loin de leur lieu de naissance, tandis que les femelles restent à proximité. Par conséquent, les femelles sont plus susceptibles que les mâles de côtoyer des parents proches, et elles augmentent leur valeur adaptative particulière en les prévenant du danger.

EIGHT CRITICISMS NOT TO MAKE ABOUT GROUP SELECTION

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Group selection, which was once widely rejected as a significant evolutionary force, is now accepted by all who seriously study the subject. There is still widespread confusion about group selection, however, not only among students and the general public, but among professional evolutionists who do not directly study the subject. We list eight criticisms that are frequently invoked against group selection, which can be permanently laid to rest based upon current knowledge. Experts will always find something to critique about group selection, as for any important subject, but these eight criticisms are not among them. Laying them to rest will enable authors to openly use the term group selection without being handicapped during the review process.

Group selection is the evolution of traits based on the differential survival and productivity of groups. It was first proposed by Darwin (1871), who observed that social adaptations frequently are not locally advantageous. The paradigmatic example is altruism, which is good for the group but vulnerable to more selfish behaviors within the group. How can a behavior evolve in the total population when it is selectively disadvantageous within each and every group? Only if it is selectively advantageous at a larger scale. Groups with more altruists robustly outcompete groups with more selfish individuals, which can counterbalance the selective disadvantage of altruism within groups. Sober (2011) has recently cataloged Darwin's thoughts on group selection in the entire corpus of his work.

Group selection appeared to be authoritatively rejected in the 1960s, as every student of evolutionary biology knows. The verdict was that group selection is theoretically possible but that in reality, selection within groups is almost invariably stronger than selection among groups. As George C. Williams (1966, p. 93) put it in *Adaptation and Natural Selection*, "group-related adaptations do not, in fact, exist." Following the rejection of group selection, what looked like altruism was explained in terms of individual or genetic self-interest, based on theoretical frameworks such as inclusive fitness theory, evolutionary game theory and selfish gene theory (reviewed by Sober and Wilson 1998).

All of these theoretical frameworks were regarded as alternatives to group selection until George Price convinced W.D. Hamilton that Darwin's explanation was embedded in inclusive fitness theory.

Since then, it has become clear that Hamilton's revised interpretation of inclusive fitness theory applies to all evolutionary theories of social behavior. All assume that social interactions take place in groups that are small compared to the total population, that traits termed "altruistic" and "cooperative" are selectively disadvantageous within groups, and require the differential contribution of groups to the total population to evolve. The reason that the logic of multilevel selection is not transparent is because selection differentials are typically calculated at the level of the total population, by averaging the fitness of individuals or genes across groups, without also calculating selection differentials within groups. What evolves in the total population is then labeled individually or genetically advantageous, as if group selection need not be invoked, when in fact group selection is the force that provides the selective advantage. It is impossible to evaluate whether a given trait evolves by group selection unless local and global selection differentials are compared to each other.

Group selection is often portrayed as a subject that remains controversial after many decades. It would be more accurate to say that group selection remains confusing to many people after many decades. To anyone with a basic understanding of multilevel selection theory, the core question of whether a trait can evolve on the strength of between-group selection, even when selectively disadvantageous within groups, was definitively answered long ago.

Peter,

Thanks for the kind words. The interesting thing about multilevel selection is that the individual or even gene view as the unit of selection is not entirely lost. All the multilevel selection perspective does is show that the fitness of the individual or gene is based on competition/selection at multiple level. I have attached my paper as well as 2 papers by D.S. Wilson and E.O. Wilson which provide great summaries to catch anyone up to speed (these two Wilson andWilson papers are essentially 2 different versions, a more detailedand a more simplistic one). Cheers,

omar

THE EVOLUTION OF TEACHING

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[2]*Centre for the Study of Cultural Evolution, Stockholm University, Sweden*

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Teaching, alongside imitation, is widely thought to underlie the success of humanity by allowing high-fidelity transmission of information, skills, and technology between individuals, facilitating both cumulative knowledge gain and normative culture. Yet, it remains a mystery why teaching should be widespread in human societies but extremely rare in other animals. We explore the evolution of teaching using simple genetic models in which a single tutor transmits adaptive information to a related pupil at a cost. Teaching is expected to evolve where its costs are outweighed by the inclusive fitness benefits that result from the tutor's relatives being more likely to acquire the valuable information. We find that teaching is not favored where the pupil can easily acquire the information on its own, or through copying others, or for difficult to learn traits, where teachers typically do not possess the information to pass on to relatives. This leads to a narrow range of traits for which teaching would be efficacious, which helps to explain the rarity of teaching in nature, its unusual distribution, and its highly specific nature. Further models that allow for cumulative cultural knowledge gain suggest that teaching evolved in humans because cumulative culture renders otherwise difficult-to-acquire valuable information available to teach.

Dear Dr. Beninger,
Professor Laland forwarded your email to me. Please find a copy of our paper on the evolution of teaching attached.
With regard to group selection, one of the most interesting findings we made during this project was that the invasion of teachers into a population of non-teachers raises the absolute fitness of the whole population, teachers and non-teachers alike. We suspect that this will enable groups of individuals containing teachers to out-compete groups of only non-teachers in many circumstances. We are currently working on an extension of the model presented in this paper that we hope will allow us to investigate multilevel effects of the invasion of teachers much more thoroughly. I agree that it is a very interesting area to explore.
I hope you enjoy the paper - If you have any more questions please do not hesitate to contact us again.
All the Best,
Laurel

--
Laurel Fogarty
Laland Lab,
School of Biology,
University of St.Andrews

Female sticklebacks count alleles in a strategy of sexual selection explaining MHC polymorphism

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The origin and maintenance of polymorphism in major histocompatibility complex (MHC) genes in natural populations is still unresolved[1]. Sexual selection, frequency-dependent selection by parasites and pathogens, and heterozygote advantage have been suggested to explain the maintenance of high allele diversity at MHC genes[2–4]. Here we argue that there are two (non-exclusive) strategies for MHC-related sexual selection, representing solutions to two different problems: inbreeding avoidance and parasite resistance. In species prone to inadvertent inbreeding, partners should prefer dissimilar MHC genotypes to similar ones. But if the goal is to maximize the resistance of offspring towards potential infections, the choosing sex should prefer mates with a higher diversity of MHC alleles. This latter strategy should apply when there are several MHC loci, as is the case in most vertebrates[2,5]. We tested the relative importance of an 'allele counting' strategy compared to a disassortative mating strategy using wild-caught three-spined sticklebacks (*Gasterosteus aculeatus*) from an interconnected system of lakes. Here we show that gravid female fish preferred the odour of males with a large number of MHC class-IIB alleles to that of males with fewer alleles. Females did not prefer male genotypes dissimilar to their own.

Sexual selection, the preference of certain mating partners over others, is ubiquitous among animals[6,7]. The choosing sex may be able to increase the attractiveness of offspring, or gain direct benefits such as parental care[8]. Another function of mate choice is to increase the fitness of offspring by either choosing 'good genes', or avoiding incompatible 'bad genes'—for example in matings with close kin. Particularly suited for testing the idea of choosiness with respect to genes is the MHC, a multigene family that is important in controlling the vertebrate immune system by presentation of self and foreign peptides to T cells[2]. MHC alleles confer specific resistance against pathogens and parasites. Therefore, mate choice should increase the fitness of offspring by maximizing the heterozygosity at MHC loci[1,4,9,10], allowing a wider spectrum of pathogens to be recognized during early infection.

The focus of previous studies was disassortative mating, that is, the preference of dissimilar males or females as a mating partner[11–13], as a means of inbreeding avoidance, or in order to increase the heterozygosity at MHC loci[3,14]. In the context of sexual selection, it has not been taken into account that most vertebrates possess several MHC loci[5]. As a result, there are many possible combinations of alleles at different loci[2]. The chances of choosing a partner with identical MHC haplotypes become very unlikely because the combination of alleles at multiple loci renders the expected likelihood of existing MHC genotypes very small, even under linkage disequilibrium. A mechanism of sexual selection focusing on the distinction between similar and dissimilar MHC genotypes becomes inefficient when increasing parasite resistance is important. Females should rather choose partners that maximize the number of different MHC alleles in their offspring[3].

We studied populations of the three-spined stickleback (*Gasterosteus aculeatus*) where we identified high MHC diversity for partial sequences of MHC class-IIB loci, coding for the peptide-binding region. At an estimated six loci[15], we identified 24 distinct sequences in only eight fish from a system of interconnected populations, and many more alleles were identified on the basis of single-strand conformation polymorphisms (SSCP) in a total of 144 fish. We also observed marked differences in the number of different alleles per individual fish, varying between two and eight detectable alleles across all loci (Fig. 1). For one location (Schöhsee) we calculated that the chance a female has of mating with an MHC-identical male is only 1% if she mates at random. But the probability of choosing a mate with fewer alleles is 46% under random expectations (see Methods). Therefore, we predicted that females

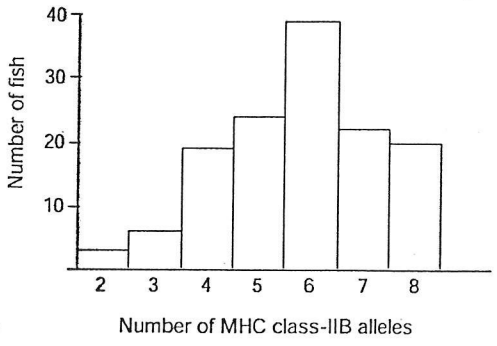

Figure 1 Frequency distribution of the number of MHC class-IIB alleles (peptide-binding region) detectable by SSCP in 144 fish from one population (Schöhsee). The mean number of MHC alleles ± s.e. was 5.8 ± 0.13.

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ORIGINAL PAPER

Ornamental comb colour predicts T-cell-mediated immunity in male red grouse *Lagopus lagopus scoticus*

Francois Mougeot

Abstract Sexual ornaments might reliably indicate the ability to cope with parasites and diseases, and a better ability to mount a primary inflammatory response to a novel challenge. Carotenoid-based ornaments are amongst the commonest sexual signals of birds and often influence mate choice. Because carotenoids are immuno-stimulants, signallers may trade-off allocating these to ornamental colouration or using them for immune responses, so carotenoid-based ornaments might be particularly useful as honest indicators of immuno-compentence. Tetraonid birds, such as the red grouse *Lagopus lagopus scoticus*, exhibit supra-orbital yellow–red combs, a conspicuous ornament which functions in intra- and inter-sexual selection. The colour of combs is due to epidermal pigmentation by carotenoids, while their size is testosterone-dependent. In this study, I investigated whether comb characteristics, and in particular, comb colour, indicated immuno-competence in free-living male red grouse. I assessed T-cell-mediated immunity using a standardised challenge with phytohaemagglutinin. Red grouse combs reflect in the red and in the ultraviolet spectrum of light, which is not visible to humans but that grouse most likely see, so I measured comb colour across the whole bird visible spectrum (300–700 nm) using a reflectance spectrometer. I found that males with bigger and redder combs, but with less ultraviolet reflectance, had greater T-cell-mediated immune response. Comb colour predicted T-cell-mediated immune response better than comb size, indicating that the carotenoid-based colouration of this ornament might reliably signal this aspect of male quality.

Carotenoid maintenance handicap and the physiology of carotenoid-based signalisation of health

Michal Vinkler · Tomáš Albrecht

Abstract Despite a reasonable scientific interest in sexual selection, the general principles of health signalisation via ornamental traits remain still unresolved in many aspects. This is also true for the mechanism preserving honesty of carotenoid-based signals. Although it is widely accepted that this type of ornamentation reflects an allocation trade-off between the physiological utilisation of carotenoids (mainly in antioxidative processes) and their deposition in ornaments, some recent evidence suggests more complex interactions. Here, we further develop the models currently proposed to explain the honesty of carotenoid-based signalisation of heath status by adding the handicap principle concept regulated by testosterone. We propose that under certain circumstances carotenoids may be dangerous for the organism because they easily transform into toxic cleavage products. When reserves of other protective antioxidants are insufficient, physiological trade-offs may exist between maintenance of carotenoids for ornament expression and their removal from the body. Furthermore, we suggest that testosterone which enhances ornamentation by increasing carotenoid bioavailability may also promote oxidative stress and hence lower antioxidant reserves. The presence of high levels of carotenoids required for high-quality ornament expression may therefore represent a handicap and only individuals in prime health could afford to produce elaborate colourful ornaments. Although further testing is needed, this 'carotenoid maintenance handicap' hypothesis may offer a new insight into the physiological aspects of the relationship between carotenoid function, immunity and ornamentation.

META-ANALYSIS SUGGESTS CHOOSY FEMALES GET SEXY SONS MORE THAN "GOOD GENES"

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Female preferences for specific male phenotypes have been documented across a wide range of animal taxa, including numerous species where males contribute only gametes to offspring production. Yet, selective pressures maintaining such preferences are among the major unknowns of evolutionary biology. Theoretical studies suggest that preferences can evolve if they confer genetic benefits in terms of increased attractiveness of sons ("Fisherian" models) or overall fitness of offspring ("good genes" models). These two types of models predict, respectively, that male attractiveness is heritable and genetically correlated with fitness. In this meta-analysis, we draw general conclusions from over two decades worth of empirical studies testing these predictions (90 studies on 55 species in total). We found evidence for heritability of male attractiveness. However, attractiveness showed no association with traits directly associated with fitness (life-history traits). Interestingly, it did show a positive correlation with physiological traits, which include immunocompetence and condition. In conclusion, our results support "Fisherian" models of preference evolution, while providing equivocal evidence for "good genes." We pinpoint research directions that should stimulate progress in our understanding of the evolution of female choice.

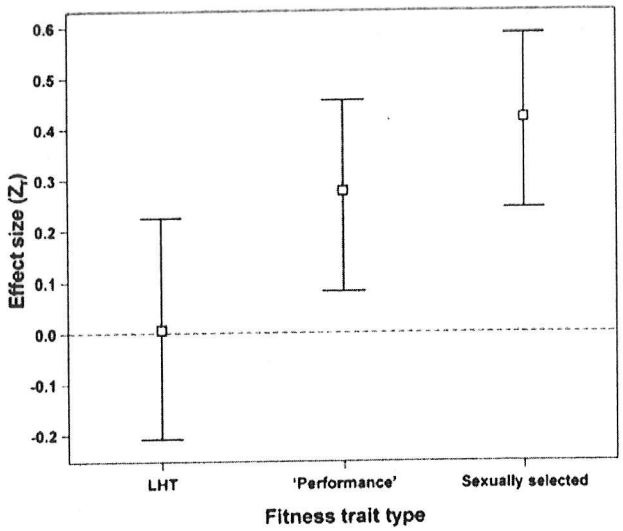

Figure 1. Mean effect sizes with confidence intervals for life history (LHT), 'performance' and sexually selected traits, estimated with model 12 fitted to the D1 dataset (see also Table S2).

Human predators outpace other agents of trait change in the wild

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The observable traits of wild populations are continually shaped and reshaped by the environment and numerous agents of natural selection, including predators. In stark contrast with most predators, humans now typically exploit high proportions of prey populations and target large, reproductive-aged adults. Consequently, organisms subject to consistent and strong 'harvest selection' by fishers, hunters, and plant harvesters may be expected to show particularly rapid and dramatic changes in phenotype. However, a comparison of the rate at which phenotypic changes in exploited taxa occurs relative to other systems has never been undertaken. Here, we show that average phenotypic changes in 40 human-harvested systems are much more rapid than changes reported in studies examining not only natural (n = 20 systems) but also other human-driven (n = 25 systems) perturbations in the wild, outpacing them by >300% and 50%, respectively. Accordingly, harvested organisms show some of the most abrupt trait changes ever observed in wild populations, providing a new appreciation for how fast phenotypes are capable of changing. These changes, which include average declines of almost 20% in size-related traits and shifts in life history traits of nearly 25%, are most rapid in commercially exploited systems and, thus, have profound conservation and economic implications. Specifically, the widespread potential for transitively rapid and large effects on size- or life history-mediated ecological dynamics might imperil populations, industries, and ecosystems.

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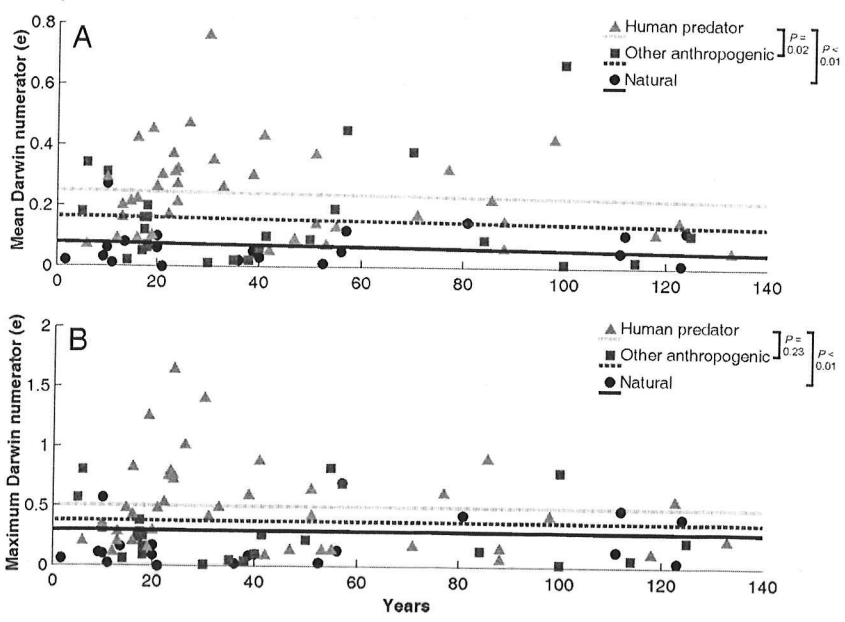

Fig. 1. Human predators outpace natural and other human-driven agents of phenotypic change. (*A*) Mean and (*B*) maximum phenotypic change (Darwin numerator) in 'natural' (n = 20 systems), 'other anthropogenic' (n = 25) and 'human predator' (n = 40) contexts with respect to the mean interval per study system. *Context* × *Years* interactions were not significant (both $P > 0.38$), so slopes were defined by *Years* coefficients and intercepts by *Context* coefficients. Shown are P values for Least Significant Difference Tests comparing marginal means between *Contexts*. One outlier datum in B (70 years, 2.57 e, other anthropogenic) not shown.

Annu. Rev. Ecol. Syst. 1999. 30:479–513

DO PLANT POPULATIONS PURGE THEIR GENETIC LOAD? EFFECTS OF POPULATION SIZE AND MATING HISTORY ON INBREEDING DEPRESSION

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Key Words mating system, genetic load, purging, self-fertilization, genetic effects of small population size

■ **Abstract** Inbreeding depression critically influences both mating system evolution and the persistence of small populations prone to accumulate mutations. Under some circumstances, however, inbreeding will tend to purge populations of enough deleterious recessive mutations to reduce inbreeding depression (ID). The extent of purging depends on many population and genetic factors, making it impossible to make universal predictions. We review 52 studies that compare levels of ID among species, populations, and lineages inferred to differ in inbreeding history. Fourteen of 34 studies comparing ID among populations and species found significant evidence for purging. Within populations, many studies report among-family variation in ID, and 6 of 18 studies found evidence for purging among lineages. Regression analyses suggest that purging is most likely to ameliorate ID for early traits (6 studies), but these declines are typically modest (5–10%). Meta-analyses of results from 45 populations in 11 studies reveal no significant overall evidence for purging, but rather the opposite tendency, for more selfing populations to experience higher ID for early traits. The likelihood of finding purging does not vary systematically with experimental design or whether early or late traits are considered. Perennials are somewhat less likely to show purging than annuals (2 of 10 vs. 7 of 14). We conclude that although these results doubtless reflect variation in population and genetic parameters, they also suggest that purging is an inconsistent force within populations. Such results also imply that attempts to deliberately reduce the load via inbreeding in captive rearing programs may be misguided. Future studies should examine male and female fitness traits over the entire life cycle, estimate mating histories at all levels (i.e. population and families within populations), report data necessary for meta-analysis, and statistically test for purging of genetic loads.

Annu. Rev. Ecol. Syst. 1999. 30:109–32

CONSPECIFIC SPERM AND POLLEN PRECEDENCE AND SPECIATION

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Key Words fertilization, gametic incompatibility, reproductive barrier, reproductive isolation, sperm competition

■ **Abstract** The evolution of reproductive isolation is perhaps the most significant stage in the process of species formation, and the study of reproductive barriers currently dominates investigations of speciation. The discovery that conspecific sperm and pollen precedence play an important role in the reproductive isolation of some closely related animals and plants is one of the real surprises to emerge from this field in recent years. This review begins with a brief history of the study of reproductive isolation with the aim of understanding why conspecific sperm and pollen precedence were generally overlooked in early work on reproductive barriers. It then examines: case studies, the prevalence of conspecific sperm and pollen precedence, the isolating potential of this class of reproductive barriers, the mechanisms that account for the operation of these barriers, and potential explanations for the rapid divergence of populations in traits related to fertilization. Conspecific sperm and pollen precedence appear to be quite effective in limiting gene exchange; these barriers are widespread although not universal in animals and plants, and they operate through a number of different mechanisms. Much more work remains to be done on a number of fronts to elucidate the processes responsible for the evolution of these reproductive barriers.

Genetic Evidence for Local Retention of Pelagic Larvae in a Caribbean Reef Fish

Michael S. Taylor* and Michael E. Hellberg

The pelagic larvae of many marine organisms can potentially disperse across hundreds of kilometers, but whether oceanographic or behavioral mechanisms can constrain dispersal over periods sufficient for the evolution of genetic differentiation remains unclear. Here, we concurrently examine larval duration and genetic population differentiation in a cleaner goby, *Elacatinus evelynae*, a member of the most species-rich genus of Caribbean reef fishes. Despite evidence for extended pelagic duration (21 days), populations of *E. evelynae* show strong genetic differentiation: among color forms (1.36 to 3.04% divergent at mitochondrial cytochrome b) and among island populations within color forms (Φ_{ST} up to 70%). These results suggest that marine populations can remain demographically closed for thousands of generations despite extended larval duration, and that recognition cues such as color may promote speciation when geographic barriers are transient or weak.

SCIENCE VOL 299 3 JANUARY 2003

Major Ecological Transitions in Wild Sunflowers Facilitated by Hybridization

Loren H. Rieseberg,[1]* Olivier Raymond,[2] David M. Rosenthal,[3] Zhao Lai,[1] Kevin Livingstone,[1] Takuya Nakazato,[1] Jennifer L. Durphy,[1] Andrea E. Schwarzbach,[4] Lisa A. Donovan,[3] Christian Lexer[1]

Hybridization is frequent in many organismal groups, but its role in adaptation is poorly understood. In sunflowers, species found in the most extreme habitats are ancient hybrids, and new gene combinations generated by hybridization are speculated to have contributed to ecological divergence. This possibility was tested through phenotypic and genomic comparisons of ancient and synthetic hybrids. Most trait differences in ancient hybrids could be recreated by complementary gene action in synthetic hybrids and were favored by selection. The same combinations of parental chromosomal segments required to generate extreme phenotypes in synthetic hybrids also occurred in ancient hybrids. Thus, hybridization facilitated ecological divergence in sunflowers.

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Journal of Experimental Marine Biology and Ecology
302 (2004) 177–188

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Hybridisations between *Mytilus edulis* and *Mytilus galloprovincialis* and performance of pure species and hybrid veliger larvae at different temperatures

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[a] *School of Ocean Sciences, University of Wales, Bangor, Menai Bridge, Gwynedd LL59 5EY, UK*
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Abstract

The mussels *Mytilus edulis* L. and *Mytilus galloprovincialis* Lamark hybridise naturally in the wild along the Atlantic coast of Europe producing a patchwork of mixed pure species and hybrid populations. Individuals of both species were spawned in the laboratory and were hybridised in a series of reciprocal crosses. After 72 h, the proportion of eggs which developed into larvae (%yield) and the proportion of those larvae which had a normal veliger morphology (%normality) were estimated and compared between pure species and hybrid families. There were no significant differences in %yield or %normality between pure species and hybrids, but significant differences were evident between the offspring from different parents irrespective of whether they were hybrids or pure species. Therefore confirmation of hybrid heterosis in laboratory studies should not be based on a single, or a few reciprocal crosses. Hybrid and pure species veliger larvae were grown for approximately 4 weeks at 10, 14 or 20 °C. In all trials, pure *M. galloprovincialis* larvae grew significantly faster at 20 °C than either reciprocal hybrid or pure *M. edulis* larvae. Irrespective of temperature, in general, hybrid larvae grew slower than larvae of either pure species. Increased exposure to planktonic predation due to slow growth can be interpreted as selection against hybrids and this may play a role in the structure and distribution of mixed pure species and hybrid populations.

(1) Hybrides naturellement courants
(2) Hybrides moins 'aptes'
(3) Tend vers la conservation des spp. distinctes

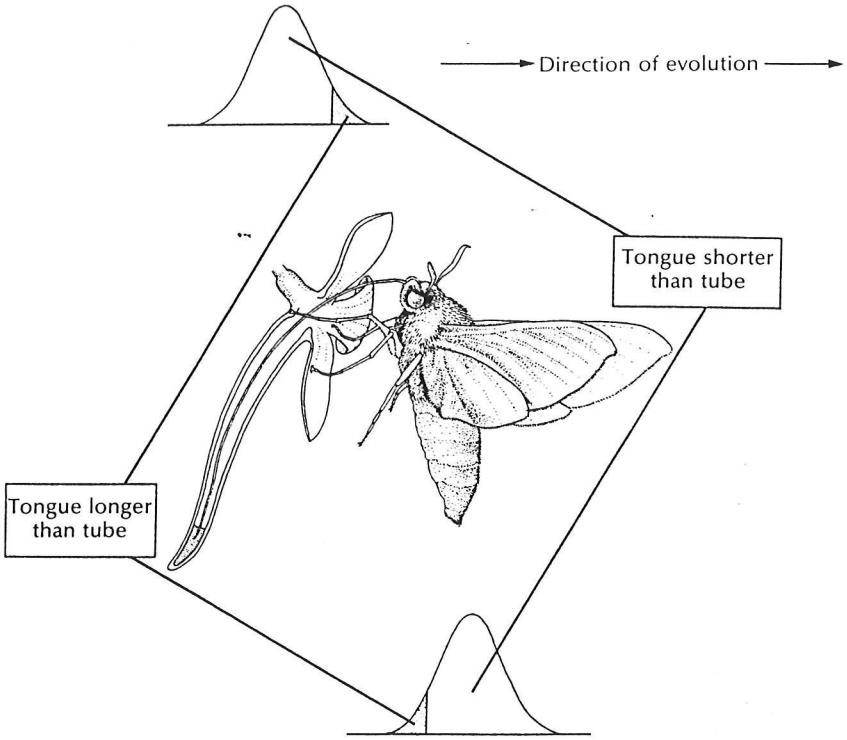
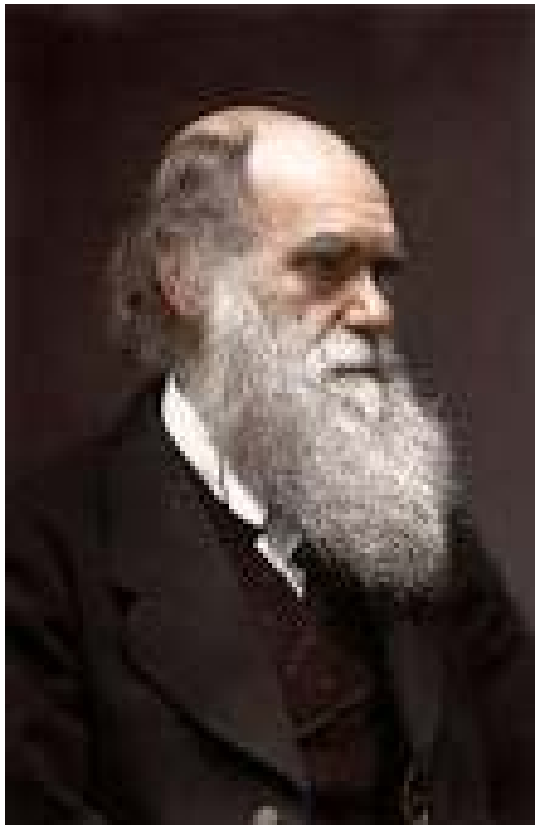


Fig. 5.3 Nilsson's (1988) modification of Darwin's hypothesis for the evolution of flowers with deep corolla tubes. Long-tongued pollinators need not contact the sexual organs in individuals with short tubes, so long tubes are favoured by selection. Short tongues will not reach the nectary, so longer tongues are selected.



THE

DESCENT OF MAN,

AND

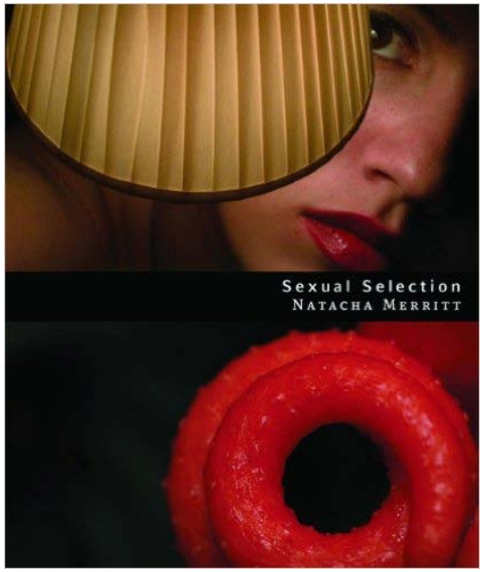
SELECTION IN RELATION TO SEX.

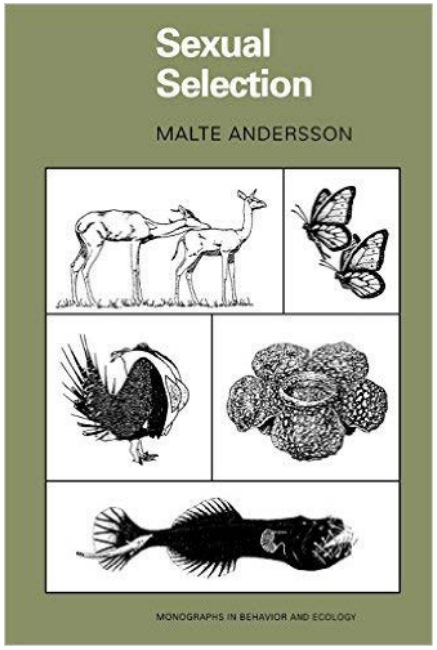
By CHARLES DARWIN, M.A., F.R.S., &c.

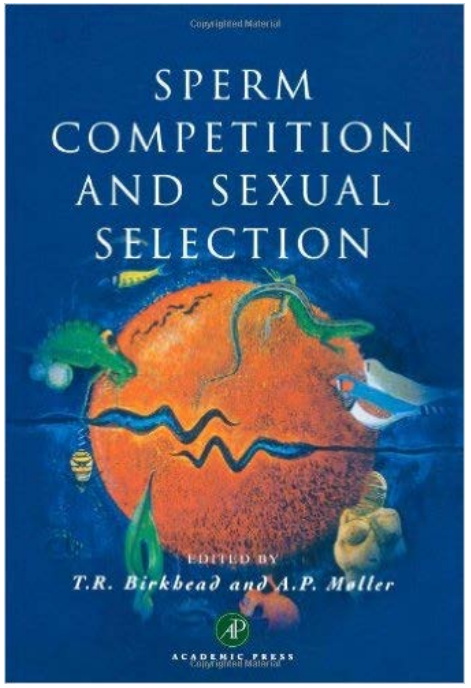
IN TWO VOLUMES.—Vol. I.

WITH ILLUSTRATIONS.

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1871.


Sexual Selection
Natacha Merritt


Sexual Selection
MALTE ANDERSSON
MONOGRAPHS IN BEHAVIOR AND ECOLOGY


SPERM COMPETITION AND SEXUAL SELECTION
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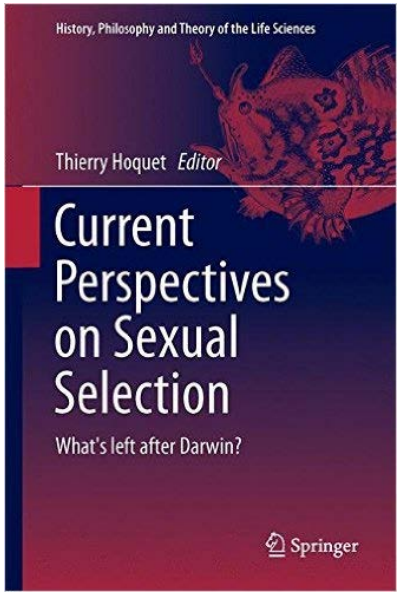
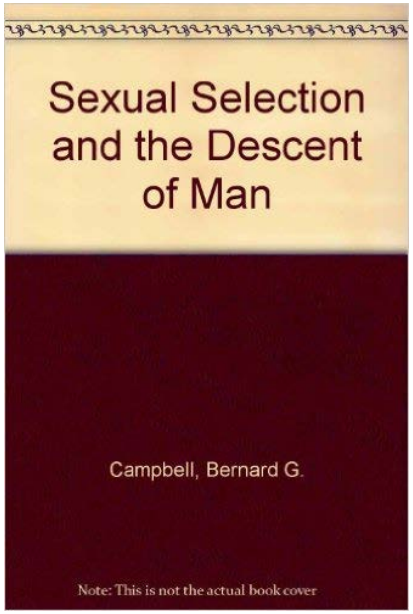
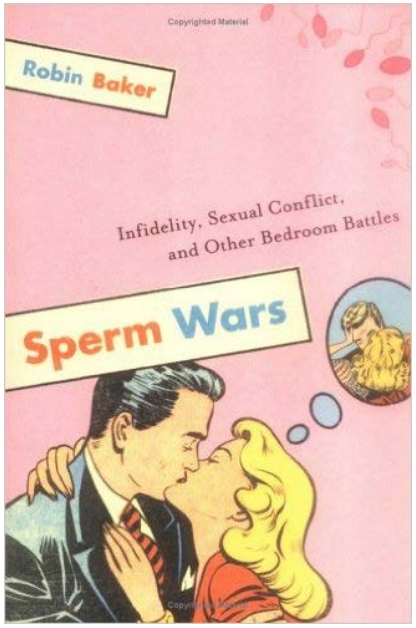

History, Philosophy and Theory of the Life Sciences
Thierry Hoquet Editor
Current Perspectives on Sexual Selection
What's left after Darwin?
Springer


Sélection naturelle et sélection sexuelle


Sexual Selection and the Descent of Man
Campbell, Bernard G.
Note: This is not the actual book cover


Robin Baker
Infidelity, Sexual Conflict, and Other Bedroom Battles
Sperm Wars

Sélection intersexuelle = choix d'un partenaire pour la reproduction

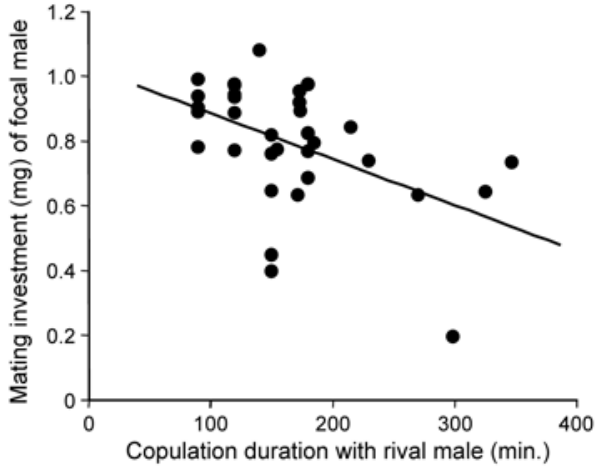
Conséquence: dimorphisme sexuel

Objectif ♀: 'Aptitude' du ♂

- Critères de santé
- Critères de force, robustesse
- Critères de position sociale
- Critères d'investissement démontré ou potentiel dans progéniture
- Critères d'investissement démontré ou potentiel dans ♀

♂ **jugé sub-optimal**:

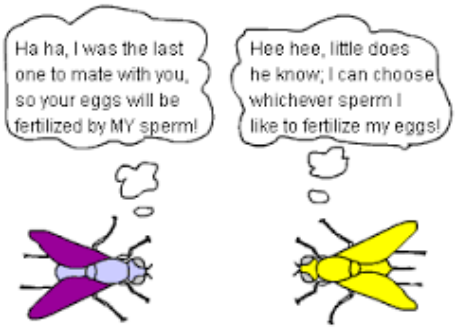
- Rejet éjaculat
- Pluri-andrie cryptique
- Sélection spermique cryptique

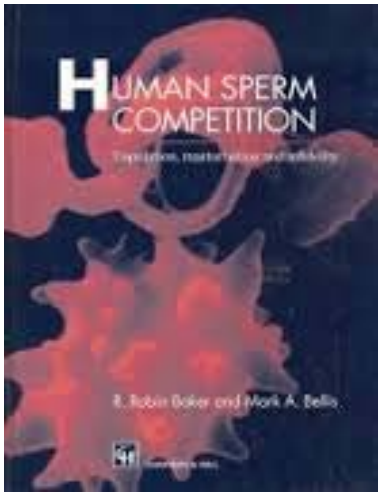


Mating investment = cadeau de nourriture

Compétition spermique:
compétition entre spermatozoïdes de ♂ différents dans le gonoducte ♀

♂ ET ♀ peuvent influencer probabilité de fécondation





Objectif ♂ : augmenter probabilité de transfert de gènes dans F1, elle-même réussie

2 exigences:

‘Aptitude’ de la ♀

Assurance de paternité

Echec partiel ou total si les 2 exigences ne sont pas remplies

Exigence ♂ 1: ‘Aptitude’ de la ♀

- Critères de fécondité
- Critères de santé
- Critères d’investissement dans progéniture

Exigence ♂ 2: Assurance de paternité

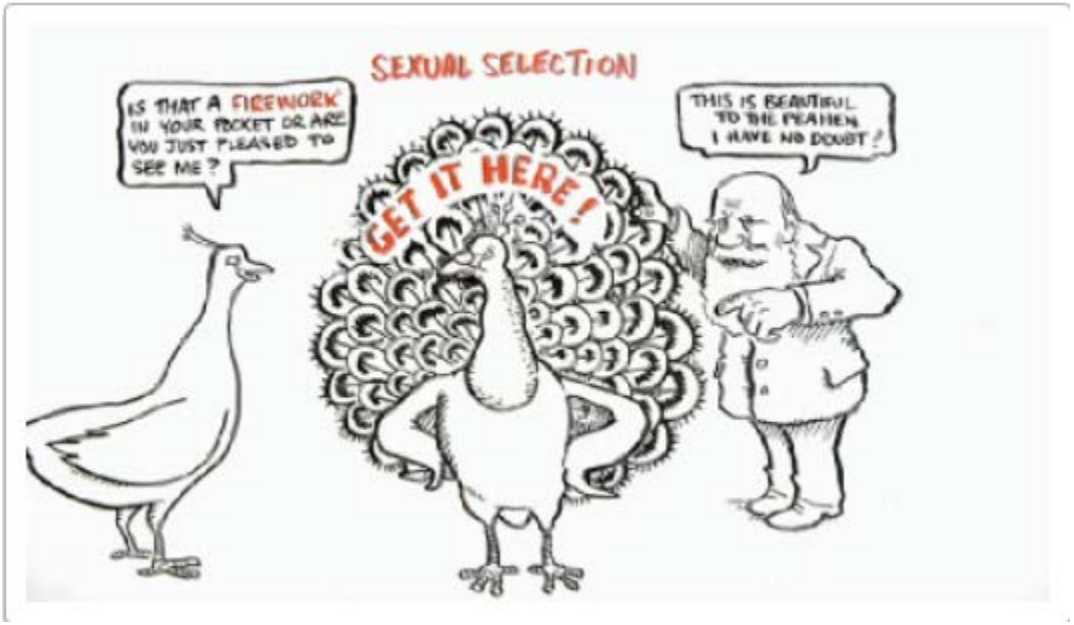
Stratégies défensives:
se réserver l'accès aux ovocytes

- Séquestration de la ♀ (embrasse pré, post-copulatoire)
- Obstruction du gonoducte ♀ après transfert des spermatozoïdes (bouchon spermique)

Stratégies offensives:
surmonter défenses, additionner les probabilités

- Comportement aggressif pour accès aux ♀ (combats)
- Fécondation à l'insu du ♂ 'titulaire' (sneak spawners/copulators)
- Retrait des obstructions du gonoducte (gonopodes spécialisés)
- Retrait des spermatozoïdes rivaux (gonopodes spécialisés)
- Partenaires ♀ multiples


Oooh Baby


SEXUAL SELECTION
IS THAT A FIREWORK IN YOUR POCKET OR ARE YOU JUST PLEASED TO SEE ME?
GET IT HERE!
THIS IS BEAUTIFUL TO BE HEAVEN I HAVE NO DOUBT

Sélection intrasexuelle = competition pour accès aux gametes opposés

Compétition entre 2 ♂ pour accès à une femelle

The Coolidge Effect: decreased copulatory motivation following successful copulation; increased motivation when presented with a new female.

derived from a story of President Calvin and Mrs. Coolidge, who visited a chicken yard where a rooster was often mating. Mrs. Coolidge learned from a worker that this happened many times a day, and said 'Tell that to the President.' After he was told, the President asked 'Same hen every time?' The worker said no, and he replied 'Tell that to Mrs. Coolidge.'

President USA 1923-29

The Coolidge Effect and strategic allocation of sperm…

- Allocation to ‘same’ and ‘new’ ♀
- Allocation to perceived ‘higher quality’ ♀