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What is the fitness outcome of crossing unrelated fish populations? A meta-analysis and an evaluation of future research directions

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Abstract Outbreeding has been shown to decrease fitness in a variety of species, including several species of fish. An understanding of the general outcomes following outbreeding is required in order to understand the consequences of conservation-related actions and hybridization in aquaculture. A meta-analysis was conducted on outbreeding studies in fishes using 670 comparisons between parent populations and their hybrid progeny. Five hundred and seventy-six comparisons involved first generation hybrids (F1), and a much smaller number (94) involved second generation hybrids (F2). The overall response to outbreeding in the F1 and F2 generations was positive and significant (F1: $d^*_{i+} = 0.425 \pm 0.121$; F2: $d^*_{i+} = 0.548 \pm 0.295$, where d^*_{i+} is the effect size of studies within generations); however, responses differed when studies were separated into groups describing the experimental environment, taxon, or trait. Findings may be biased by a few studies of large effect. Genetic distance explained little of the variance in effect sizes across studies. Results of the meta-analysis suggest that there is no reliable predictor for the effects of outbreeding in fishes, although inconsistencies in experimental design were noted across studies. Future research should include comparisons in both parental environments in order to detect the underlying mechanisms of outbreeding depression, and should focus on measurement of equivalent sets of fitness-related traits. Experimental design should permit estimation of genetic distances based on quantitative traits, which may in turn be meaningful predictors of the outcomes of outbreeding depression. Concerted and consistent research in this area will provide information of relevance to conservation, aquaculture and evolutionary studies.

Keywords Hybridization · Outbreeding · Outbreeding depression · Fitness · Meta-analysis

Introduction

Hybridization, or outbreeding, is often used as a technique to recover inbred wild populations (Heschel and Paige 1995; Westemeier et al. 1998; Land and Lacy 2000; Tallmon et al. 2004) or to enhance desired traits in commercially managed stocks (for example Hedgecock and Davis 2000; Hayward and Wang 2002). In nature, some of the barriers to gene flow, and hence outbreeding, may be removed through anthropogenic factors. For example, removal of natural barriers may lead to introgression or gene flow may be increased through transfer of individuals between populations, either as a recovery effort or as part of a commercial enterprise (Waples 1991; Rhymer and Simberloff 1996; Linder et al. 1998). Unfortunately, the consequences of outbreeding are not always beneficial and may be difficult to predict (Edmands 2002).

Hybridization has several genetic outcomes that can be advantageous. Outbreeding between two individuals may produce beneficial overdominant or dominant interactions at a locus, which may confer a heterozygote advantage in the former case or mask a deleterious allele in the latter (Falconer and Mackay 1996). Hybridization may also generate new genotypic variation ultimately leading to local adaptation or

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population differentiation (Dowling and Secor 1997; Gerber et al. 2001). On the other hand, hybridization may also lead to outbreeding depression. This specific outcome has been identified as one of nine major genetic issues in conservation biology (Frankham 1999). Simply put, outbreeding depression is the reduction in fitness that occurs following mating between unrelated or distantly related individuals (Lynch 1991). This loss of fitness may be seen in the first hybrid generation or may be delayed until subsequent hybrid or backcrossed generations, and results from one or both of two mechanisms (Templeton 1986): loss of local adaptation (known as extrinsic outbreeding depression) or disruption of co-adapted gene complexes (intrinsic outbreeding depression).

Local adaptation is a process that increases the frequency of traits enhancing survival or reproductive success within a population in response to a particular environment (Taylor 1991; Carvalho 1993). Typically, species distributed over a varied geographic area and isolated by distance may show local adaptations (Templeton et al. 1986; Waser 1993). Hybrids receive only half the allelic combinations present in either parent populations, and thus may be unsuited to either of the parental environments (Waser 1993; Frankham et al. 2002). Outbreeding depression in this case is often ascribed to the loss of favorable genetic interactions within and between loci (additive and dominance interactions). Loss of fitness due to loss of local adaptation can be expressed as early as the F1 generation of hybrids (Waser et al. 2000).

Another mechanistic cause of outbreeding depression is the disruption of epistatic interactions in co-adapted gene complexes. A group of loci is said to be co-adapted if increased fitness depends on the specific interactions of those loci, and thus allele frequencies at one locus will change in response to changes at other loci (Wallace 1968). Co-adaptation is maintained because alleles which affect the same trait tend to be inherited together in order to maintain increased fitness at that trait (Templeton et al. 1986). It has been suggested that outbreeding depression will be influenced by the number and physical linkage of genes comprising a co-adapted complex (Edmands 1999). Thus, co-adapted complexes of few, tightly linked genes are less likely to be disrupted by recombination than will larger complexes or complexes where genes are more distantly located. Disruption of epistatic interactions may result in a loss of local adaptation if gene complexes are no longer expressed as trait values suitable for parental environments. Loss of fitness may be evident even in benign environments or in environments to which parents have no specific adaptation (Templeton 1986) and is usually not seen until the F2 hybrid generation. The recombination of parental genomes during meiosis occurs first in the F1, and thus epistatic interactions between co-adapted loci may be perturbed, resulting in a loss of fitness in subsequent generations (Burton 1987; Falconer and Mackay 1996; Edmands 1999). It is important to note that in this case, it may not be possible to predict the loss of fitness in the second outbred hybrid generation by observing the first hybrid generation (Edmands 1999).

Many authors have attempted to predict the outcomes of outbreeding, because such an understanding clarifies evolutionary processes and has clear management applications. In Emlen's model on the incidence of outbreeding depression (Emlen 1991), distance between parental populations (defined as the relative fitness of parents raised in the other parent's native location) is related to the fitness of hybrids over subsequent generations. As geographical distance (and presumably parental divergence) increases between mating individuals, reductions in fitness would be manifest in the F1 generation. Empirical studies in plants bear out this prediction (Fenster and Galloway 2000; Waser et al. 2000), but the use of geographic distance as a measure for genetic distance is not necessarily reliable (Quilichini et al. 2001). Genetic distances based on molecular markers may prove more dependable. For example, in a study on copepods, Edmands (1999) demonstrated that offspring of parents with greater sequence divergence showed a greater negative response to outbreeding. More recently, Edmands and Timmerman (2003) extended the model of Emlen (1991) by examining other genetic factors that may affect the outcomes of outbreeding. Their simulations showed that the scale of outbreeding depression increased with genetic distance, that a fitness decline was particularly prolonged if the underlying cause was due to a disruption of co-adapted complexes, and that severity varied with recombination and mutation rates.

Other researchers have attempted to define factors that may affect the scale and duration of outbreeding depression empirically. Several experiments have focused on the relationship between genetic distance and outbreeding depression (for example Edmands 1999; Pelabon et al. 2005; Willi and Van Buskirk 2005). There are also indications from studies in *Drosophila* (Aspi 2000; Andersen et al. 2002) that the observed effect of outbreeding varies across traits. Finally, the magnitude of outbreeding depression may also depend on prevailing environmental conditions (Lynch 1991; Gharrett et al. 1999; Waser et al. 2000; Montalvo and Ellstrand 2001; Gilk et al. 2004).

A greater understanding of the potential results of outbreeding in fishes is important for management of artificially propagated fish stocks as well as for conservation efforts. The management of fishes is unusual compared to other species in that there are many large-scale cultivation programs that take place in the presence of wild populations. The aims of these programs differ, and vary from the production of food fishes, to the release of hatchery-reared populations intended to support commercial and recreational fisheries, to supportive breeding of endangered populations in the wild. These aims may result in the use of cultivated fishes that differ in their genetic composition relative to the local wild populations with which they interact (Waples 1991). Many cultured stocks are deliberately bred for specific desirable traits (for example Marengoni et al. 1998) while others experience inadvertent domestication selection as they respond to the relaxed selective pressure of a hatchery environment (for example Petersson et al. 1996; Reisenbichler and Rubin 1999). Sometimes, non-indigenous fish are stocked for recreational opportunities, and these fish may hybridize with native species (Leary et al. 1985). Numerous examples exist of net-pen escapements or stock transfers (Gausen and Moen 1991; Hindar et al. 1991; Matthews et al. 2000) bringing genetically distinct fish populations into contact with each other. On the other hand, the introduction of genetically diverse individuals may provide a means of recovering an endangered inbred population. In a recent review, Tallmon et al. (2004) stressed the importance of developing predictive approaches to understanding the results of outbreeding, in attempt to understand whether this action could lead to the "genetic rescue" of a population or to losses due to outbreeding depression.

Meta-analysis is a method for quantitatively synthesizing the outcomes from many studies and is particularly useful in biology for comparing processes and trends across a range of conditions or environments (Hedges and Olkin 1985; Osenberg et al. 1999). Meta-analysis has been used in the natural sciences to examine a diverse array of topics including correlations between genetic diversity measured using molecular and quantitative methods (Reed and Frankham 2001), inbreeding depression in wild populations (Crnokrak and Roff 1999; Coltman and Slate 2003), competition between species (Gurevitch et al. 1992), and heritability estimates of developmental stability (Moller and Thornhill 1997).

Here, we use a meta-analysis to examine the fitness outcomes of outbreeding among fish populations, with the aim of identifying differential responses in the quantitative traits measured and examine relationships, if any, between outbreeding depression and genetic distance.

Methods

Literature search

Literature searches were performed in both the BIOSIS and ASFA databases using the key words "fish*" and one or more of the following phrases: "outbreeding," "outbreeding depression," "hybrid AND cross," "crossbreed*," "hybridization," "heterosis," "hybrid vigor," "postzygotic reproductive isolation" and "intrinsic postzygotic isolation." Additional references were obtained from the papers found during the search. The search included papers published prior to March of 2006. Information on genetic distance was found independently of the literature search terms where necessary. Criteria for inclusion in the meta-analysis were as follows: (1) at least one hybrid generation was compared to one or both parental populations; (2) comparisons were performed on intraspecific hybrids; (3) traits measured were quantitative in nature; (4) the means and variance (or SD) for both hybrid and parental traits were available. This last criterion was deemed necessary because the model used specifically incorporates the means and SD of parent and progeny groups in calculating the test statistic, *d*. Some authors were contacted directly with requests for additional data. Where data was available in a graphical format only, the digitizing software Engauge Digitizer v2.14 (Mitchell 2002; available online at http://www.digitizersourceforge.net) was used to determine means and variances for experimental and control groups. Particular effort was made to use all available studies in which F2 hybrids were examined as these studies comprised a relatively small proportion of the total number of comparisons. Thirty-four studies were used for subsequent analyses (Table 1).

Effect size

The methods used for calculating effect size and fitting a model to the data follow the example presented in (Gurevitch and Hedges 2001). Briefly, an effect size, *d*, was calculated based on the standardized mean difference between the experimental (or hybrid) group and the control (or parental group). Negative effect sizes occur when hybrids have reduced trait values compared with parents. Comparisons where authors noted outbreeding depression had negative effect sizes. Hybrids were compared to each parental population

Table 1 Number of comparisons by trait, taxon and generation for each of the studies used in the meta-analysis

References	Traits (no. comparisons)	Taxon (Family)	Generation
Bams (1976)	LH: survival (1)	Salmonidae	F1
Chiyokubo et al. (1998)	P: salinity tolerance (4)	Poeciliidae	F1; F2
Clarke et al. (1992)	M: weight (16); length (16) LH: growth rate (16) P: salinity tolerance (16)	Salmonidae	F1
Cooke et al. (2001)	P: swimming speed (12); oxygen consumption (12); ventilation rate (12)	Centrarchidae	F1
Cooke and Philipp (2005)[a]	P: cardiac variables (72)	Centrarchidae	F1
Einum and Fleming (1997)[a]	M: weight (4); length (4) LH: growth rate (6) B: aggression (4); response to predation (2)	Salmonidae	F1
Fleming et al. (2000)[a]	M: length (6)	Salmonidae	F1
Foote et al. (1992)	M: weight (4); length (4) P: salinity tolerance (4)	Salmonidae	F1
Gharrett and Smoker (1991)	M: weight (2); length (2)	Salmonidae	F1; F2
Gharrett et al. (1999)	M: length (2) LH: asymmetry (8)	Salmonidae	F1; F2
Gjerde et al. (2002)	M: weight (48)	Cyprinidae	F1
Granath et al. (2004)	LH: egg survival (12)	Salmonidae	F1
Hatfield (1997)	M: gill raker number (8); gill raker length (8); plate number (8); pelvis spine length (8)	Gasterosteidae	F1; F2
Hatfield and Schluter (1999)	LH: survival (8); fertilization success (8) M: length (2); weight (8); body depth (2); mouth width (2)	Gasterosteidae	F1; F2
Johnsson et al. (1993)[a]	LH: growth rate (10)	Salmonidae	F1
Lachance and Magnan (1990)	M: weight (6)	Salmonidae	F1
Leberg (1993)	LH: fecundity (4) M: length (4)	Poeciliidae	F1
Marengoni et al. (1998)	LH: survival (12); growth rate (12) M: weight (12); length (12)	Cichlidae	F1
McClelland et al. (2005)	LH: growth rate (8) M: weight (10); length (10) P: conversion efficiency (8)	Salmonidae	F1; F2
Miller et al. (2004)	M: length (8)	Salmonidae	F1
Nakadate et al. (2003)	LH: survival (4) M: length (8); undwarf rate (4) P: salinity (4) and temperature (4) tolerance	Poeciliidae	F1
Nguenga et al. (2000)	LH: survival (4); growth rate (4); fertilization rate (4); hatching success (4) M: weight (4)	Clariidae	F1
Nilsson (1993)	M: weight (12)	Salmonidae	F1
Quinton et al. (2004)	LH: spawn date (24)	Salmonidae	F1
Rogers et al. (2002)[a]	B: swimming behavior (12)	Salmonidae	F1
Sheffer et al. (1999)	LH: survival (8); asymmetry (7); fecundity (4) M: length (8)	Poeciliidae	F1; F2
Shikano and Taniguchi (2002a)	LH: survival (24)	Poeciliidae	F1
Smoker et al. (2004)[a]	LH: survival (24)	Salmonidae	F1; F2
Tave et al. (1990)	M: weight (16); length (16)	Cichlidae	F1; F2
Tymchuk and Devlin (2005)[a]	LH: growth rate (12) M: length (6); weight (6)	Salmonidae	F1
Tymchuk et al. (2006)[a]	LH: growth rate (12) M: length (6); weight (6) B: response to predation (6)	Salmonidae	F1
Vamosi et al. (2000)[a]	LH: growth rate (2)	Gasterosteidae	F1
Wangila and Dick (1988)	M: weight (4)	Salmonidae	F1
Wessel et al. (2006)	B: aggression (14)	Salmonidae	F1; F2

Taxa are listed at the family level. F1 refers to the first hybrid generation and F2 to the second hybrid generation. Trait classes are abbreviated B (behavioral); LH (life history); M (morphological); and P (physiological)

[a] Digitizing software was used to obtain data

separately because some studies may show a change in a trait value relative to one, but not both, parental populations, and we deemed it necessary to discriminate these cases. Effect sizes were summed across all studies to estimate an overall response to outbreeding in fishes, d_{++} (that is, the effect size for all comparison within every class). For large sample sizes, the effect size d is normally distributed; an adjustment term, J was used to correct bias due to small sample sizes, where

$$J = 1 - \frac{3}{4N_{\mathrm{tot}} - 9}$$

and N_{tot} is the total number of comparisons in the meta-analysis, (Hedges and Olkin 1985).

Combining data and hypothesis testing

A mixed effects model was used to sum effect sizes and test hypotheses (Gurevitch and Hedges 2001), because this model is most useful when there is no a priori expectation of homogeneity among classes. In this analysis, the mixed effects model produced a more conservative result than a fixed effect model; that is, there were fewer examples of significant responses to outbreeding under the former than under the latter. The calculated effect sizes for studies were pooled into classes within categories (Table 2). The statistic Q_{B}^{*} was then used to quantify between-class homogeneity within each category. Q_{B}^{*} is equal to the square of the weighted effect sizes within each class subtracted from the weighted sum of squares of those same comparisons (for equations see Gurevitch and Hedges 2001). The Q_{B}^{*} statistic follows a χ^2 distribution with degrees of freedom equal to the total number of classes minus 1; a χ^2 test can thus be used to test the null hypothesis that there was a common mean effect size within a category regardless of class (Gurevitch and Hedges 2001). A 99% confidence interval (CI) was calculated around the average effect size d_{i+}^{*} (the effect size of all comparisons within the ith class) for each class. Throughout the paper, results are presented as $d_{i+}^{*} \pm 99\%$ CI. Categories that show non-homogenous effects across classes are of special interest because this result implies that fishes respond to outbreeding differently due to some characteristic of that category. It should be noted here that different values of d_{++}^{*} can be obtained using the same studies but grouped into different categories, since this value is affected by the number of classes within a category and the variances of those classes.

Fail-safe N

One common problem encountered in meta-analysis is that of publication bias, because studies with outcomes of non-significance are frequently not published. However, while individual studies may show a small or insignificant result, the data may reveal a significant effect when studies are analyzed together (Hedges and Olkin 1985). Additionally, there are published studies which did not fit the criteria outlined above and were thus not included in this analysis although they contain information on the response of hybrids to outbreeding. Therefore, a "fail-safe N" was calculated, which serves as a measure of the robustness of the meta-analysis to missing studies. The fail-safe value is the number of additional comparisons of no effect ($d = 0$) necessary to reduce the observed effect size to a given criterion level (Orwin 1983; Wolf 1986). The fail-safe value, N_{fs}, was calculated using the following equation:

$$N_{\mathrm{fs}} = \frac{N\left(\bar{d} - \bar{d}_{\mathrm{c}}\right)}{\bar{d}_{\mathrm{c}}}$$

where N is the number of comparisons included in the meta-analysis, $\bar{d}$ is the absolute value of the average effect size for the comparisons in question and $\bar{d}_{\mathrm{c}}$ is the

Table 2 Traits, taxa, origin of populations, and hybrid rearing environments used to group effect size data

Category		
Trait	Taxa	Origin and rearing
Class		
Life-history (survival, fecundity, asymmetry, fertilization, growth rate, time to hatching, fitness, spawn date)	Centrarchidae	Wild origin/wild rearing
Behavioral (swimming characteristics, aggression, predator avoidance, stray rate, depth selection)	Cichlidae	Captive origin/captive rearing
Morphological (length, weight, undwarf rate, meristic traits)	Clariidae	Wild origin/captive rearing
Physiological (oxygen consumption, salinity and temperature tolerance, ventilation rate, conversion efficiency, disease resistance, cardiac output, blood cortisol level)	Gasterosteidae Poeciliidae Salmonidae	Captive origin/wild rearing

criterion value (Orwin 1983). The criterion level was set at $\bar{d}_c = 0.2$ (Cohen 1969). Fail-safe values were calculated for the entire data set and for each class within a category. Effect size estimates were considered robust to publication bias if the number of additional comparisons of null effect need to reduce the effect size to the critical level is greater than or equal to a tolerance limit of $5k + 10$ where k is the number of comparisons used in the meta-analysis (Rosenthal 1991). Comparisons of the actual number of studies within a class to the fail-safe value does not determine if there is publication bias, neither do they provide a measure of the magnitude of publication bias, but rather suggest whether the issue of publication bias can be ignored (if a bias exists) (Rosenberg 2005).

Non-independence of data

Since hybrids were compared to both parent populations, two comparisons of a trait were possible for each hybrid observation within a given study. While using several measures from the same study may introduce bias due to non-independence of data (Hedges and Olkin 1985), failure to use multiple comparisons will exclude valuable information from the meta-analysis (Hedges and Olkin 1985; Gurevitch and Hedges 2001). To avoid problems of non-independence to the greatest extent possible, some comparisons from the data set were eliminated. Measures which are highly correlated do not contribute much additional information for the meta-analysis, so it is reasonable to discard such measures (Hedges and Olkin 1985). We eliminated comparisons if the trait was derived from other traits measured in the same study (e.g.: combined fitness, condition factor, and aggressive behavior summed over several observations). Removal of some comparisons does not eliminate all non-independent data, and incorporation of this data will most likely result in an underestimation of the variance around the cumulative effect size, with a corresponding increase in the number of classes having a significant response to outbreeding (Gurevitch and Hedges 1999). To reduce type I error, statistical results for every factor were tested at a more conservative significance level of $\alpha = 0.01$ (or with a 99% CI) as suggested by Hedges and Olkin (1985).

Categorizing studies

In order to discriminate all factors that may affect the outcomes of outbreeding and hence the results of the analysis, we categorized studies by trait; taxon at the family level; and the environment of the parental population and the experimental rearing environment (from here on, origin and rearing); as shown in Table 2. Many traits were measured in only one study (e.g.: cardiac performance), and thus traits were combined into the larger trait categories using the classification of Roff and Mousseau (1987), namely; "life history," "behavioral," "physiological" and "morphological" (Table 2). Differences in trait response within each of these categories were assessed in the F1 and F2 hybrid generations. Comparisons represented 28 traits grouped into the four trait classes listed above. Seven taxa were represented, of which Salmonidae was the biggest taxonomic family. Thirty-four studies (576 comparisons) examined the first generation of hybrids, the F1 and 11 studies (94 comparisons) examined the second generation of hybrids, the F2 (Table 1).

Effect of experimental environment

Many of the studies compared hybrid and parental performance in only one of the two parental environments, and the combination of all results in a single meta-analysis would confound any outcomes that may be specific to a particular hybrid–parental comparison. For example, if hybrid and wild parents were compared in a domestic environment, the outcomes of hybridization may be masked by the comparison of hybrid with domestic parents in the same domestic environment. Thus, the studies were divided into two groups. Group I includes studies in which hybrids and parents were compared in the parental environment (e.g., hybrids and wild parents in the wild); Group II includes studies which hybrid and parents were compared in an environment different from the one in which the parent originated (e.g., hybrids and wild parent in captivity). Throughout the remainder of the paper Group I will be described using the abbreviated phrase "*Hyb-P1 in P1E*" and Group II will be described as "*Hyb-P1 in nonP1E*", where *Hyb* is the hybrid line, *P1* is the parental line, *P1E* and *nonP1E* are the experimental environments in which the lines were compared.

Genetic distance

Pairwise G_{ST} values (Chakraborty and Leimar 1987) were used as a measure of genetic distance between populations as considerably more data was available on G_{ST} measures between populations than any other measure of differentiation. In a model based study, Kalinowski (2002) suggests that G_{ST} is an appropriate measure to use in estimating population divergence. Additionally, it should be noted that variation in effect sizes is large for any one study so small changes in genetic distance measures are unlikely to affect the significance

Table 3 Genetic distance, G_{ST}, between parental populations and average heterozygosity, H_e, within populations

Hybridized populations	Taxon	GST	H_e	Genetic distance reference	Outbreeding reference
Threespine stickleback (*Gasterosteus aculeatus* complex) limnetic and benthic forms	Gasterosteidae	0.213	Limnetic: 0.743 Benthic: 0.531	Tayler and McPhail (2000)[b]	Hatfield (1997) Hatfield and Schluter (1999)
Threespine stickleback (*G. aculeatus* complex) limnetic and benthic forms	Gasterosteidae	0.213	Limnetic: 0.743 Benthic: 0.531	Tayler and McPhail (2000)[b]	Vamosi et al. (2000)
Silver Bluff and Savannah River Site mosquito fish (*Gambusia holbrooki*) populations	Poeciliidae	0.058	Silver Bluff: 0.112 Savannah River 0.101	Leberg (1993)	Leberg (1993)
Silver Bluff and Cohen Bluff mosquito fish (*G. holbrooki*) populations	Poeciliidae	0.103	Cohen Bluff: 0.219		
Domestic guppy strains (*Poecilia reticulata*)	Poeciliidae	0.428	F22: 0.112; S3HR: 0.263	Shikano and Taniguchi (2002b)[b]	Chiyokubo et al. (1998)
Domestic guppy strains (*P. reticulata*)	Poeciliidae	0.428	F22: 0.112; S3HR: 0.263	Shikano and Taniguchi (2002b)[b]	Nakadate et al. (2003)
Various domestic guppy strains (*P. reticulata*)	Poeciliidae	0.425	S: 0.216; S3HR: 0.263; SC:0.272; F22: 0.112	Shikano and Taniguchi (2002b)[b]	Shikano and Taniguchi (2002a)
Topminnow (*Poeciliopsis o. occidentalis*) Cienega Creek vs. other strains	Poeciliidae	0.223	Cienega: 0.263	Parker et al. (1999)[b]	Sheffer et al. (1999)
Topminnow (*P. o. occidentalis*) Monkey Creek vs. other strains	Poeciliidae	0.466	Monkey: 0.202		
Topminnow (*P. o. occidentalis*) Sharp Creek vs. other strains	Poeciliidae	0.223	Sharp: 0.281		
Topminnow (*P. o. occidentalis*) Bylas Creek vs. other strains	Poeciliidae	0.479	Bylas 0.075		
Quesnal and Conuma River chinook salmon (*Oncorhynchus tshawytscha*)	Salmonidae	0.169	Quesnal: 0.092 Conuma: 0.079	Teel et al. (2000)[a]	Clarke et al. (1992)
Sympatric kokanee and sockeye (*O. nerka*)	Salmonidae	0.181	Kokanee: 0.228 Sockeye: 0.232	Foote et al. (1989)[a]	Foote et al. (1992)
Odd and even year pink salmon (*O. gorbuscha*)	Salmonidae	0.020	Odd yr: 0.116 Even yr: 0.150	Beacham et al. (1988)[a]	Gharrett and Smoker (1991) Gharrett et al. (1999)
Coho salmon (*O. kisutch*) stocks from Satsop River and Domsea Farm	Salmonidae	0.089	Satsop: 0.732 Domsea: 0.687	McClelland (unpublished data)[b]	McClelland et al. (2005)
Hatchery and naturalized rainbow trout (*O. mykiss*)	Salmonidae	0.054		Krueger et al. (1994)[a]	Miller et al. (2004)
Tagwerker and Mount Lassen strains of rainbow trout (*O. mykiss*)	Salmonidae	0.018	Tagwerker: 0.367 Mt. Lassen: 0.425	Wangila (1994)[a]	Wangila and Dick (1988)
Lake whitefish ecotypes (*Coregonus clupeaformis* Mitchill)	Salmonidae	0.240		Rogers et al. (2002)[b]	Rogers et al. (2002)

[a] G_{ST} was calculated from data as $G_{ST} = 1 - \bar{H}_S/\bar{H}_T$ (Chakraborty and Leimar 1987)

[b] G_{ST} from microsatellite loci (for other studies allozyme data was used)

Table 4 Meta-analysis of F1 hybrids, where hybrids and parental lines were reared in the parental environment (Group I; *Hyb-P1 in P1E*). Effect sizes, 99% confidence limits, and failsafe values for classes within the following categories: (A) taxa; (B) traits; (C) origin and rearing

Class	Number of comparisons (n)	Cumulative effect size (d^*_{i+})	99% CI	Fail-safe value (N_{fs})	N_{fs} Critical level
(A) Taxa					
Cichlidae[a, b]	56	2.024	1.640–2.409	511	290
Cyprinidae	12	0.241	– 0.599–1.082	3	70
Gasterosteidae	8	0.630	– 3.80–1.658	17	50
Poeciliidae[a]	50	0.660	0.251–1.069	115	260
Salmonidae	101	– 0.142	– 0.428–0.144	0	515
Mean effect size[a, b]	227	0.616	0.425–0.807	3647	1145
All classes, Q^*_B	137.14 ($P < 0.001$; df = 4)				
(B) Trait					
Behavioral	4	0.070	– 1.596–1.736	0	30
Life-history	119	0.261	– 0.047–0.569	36	605
Physiological	12	0.474	– 0.483–1.431	16	70
Morphological[a]	92	1.188	0.838–1.538	454	470
Mean effect size[a, b]	227	0.643	0.421–0.865	2035	1145
All classes, Q^*_B	27.44 ($P < 0.001$; df = 3)				
(C) Origin and rearing					
Wild origin and rearing	19	0.475	– 0.270–1.221	26	105
Captive origin and reading[a]	208	0.641	0.414–0.868	458	1050
Mean effect size[a]	227	0.627	0.410–0.844	1040	1145
All classes, Q^*_B	0.30 ($P = 0.584$; df = 1)				

[a] d^*_{i+} or d^*_{++} value for class is significant at $\alpha = 0.01$ level

of results. G_{ST} was calculated from allozyme data in six studies, and microsatellite data in eight studies using published sources or from requested data (Table 3). The non-parametric Spearman's rank correlation was used to test the relationship between effect size and genetic distance over all data sets. Studies were then grouped by generation, trait or taxon, and correlations were estimated for each subset of the data.

Results

Response to outbreeding

Overall response

We observed a significant and positive effect size across all cross types (F1; $d^*_{i+} = 0.425 \pm 0.121$, $n = 576$; F2; $d^*_{i+} = 0.548 \pm 0.295$, $n = 94$). In addition, the null hypothesis of homogeneity of effect size across generations could not be rejected ($Q^*_B = 0.98$, $P = 0.320$). It should be noted that data on the F2 represent only 14% of the total comparisons which may explain the lack of heterogeneity across generations.

Data were treated sequentially in order to determine the most likely explanation for these results. First, the data were separated by hybrid generation. Second, data were divided into groups I *(Hyb-P1 in P1E)* and II (*Hyb-P1 in nonP1E*) for the reasons given in the methods section. Third, data were separated into classes within categories as described in Table 2. Individual class and overall category effect sizes were tested for significance using 99% confidence limits, and the fail-safe value was used to determine sensitivity to publication bias. Finally, if a class was shown to be significant, it was removed from the analysis in order to determine the effect of this class on the value of the mean effect size d^*_{++}, and between-class homogeneity Q^*_B across the remaining data.

The effects of outcrossing in the first hybrid generation

Group I comparisons: F1 hybrids and parental lines when both lines are raised in the parental environment

Certain comparisons within this group yielded effect sizes that indicated a positive response to outbreeding. There was a significant d^*_{++} over all taxa; however, results varied and individual d^*_{i+} were only significant in the family Cichlidae and Peociliidae (Table 4A). An additional 511 comparisons were needed to reduce the observed effect size of the Cichlidae class to the d_c value of 0.2, but the Poeciliidae class was not robust to publication bias. The null hypothesis of homogeneity across taxa was rejected ($Q^*_{\mathrm{B}} = 137.14$, $P < 0.001$). Removal of these two taxa resulted in an overall effect size that was no longer significant ($d^*_{++} = -0.059 \pm 0.226$, $n = 121$) and homogeneity of mean effect size could not be rejected ($Q^*_{\mathrm{B}} = 4.42$, $P = 0.036$).

Only the morphological class of traits demonstrated a significant and positive response to outbreeding ($d^*_{i+} = 1.188 \pm 0.350$, $n = 92$; Table 4B). This result appears to be explained by the responses exhibited by length and weight (their exclusion resulted in $Q^*_{\mathrm{B}} = 0.647$, $P = 0.886$ across taxa, and $d^*_{i+} = 0.122 \pm 0.595$, $n = 12$ for morphological traits). Further, removal of the cichlids and poeciliids resulted in non-significant trait responses (life history $d^*_{i+} = -0.210 \pm 0.314$, $n = 67$; behavioral $d^*_{i+} = 0.070 \pm 1.263$, $n = 4$; physiological $d^*_{i+} = -0.167 \pm 1.755$, $n = 2$; morphological $d^*_{i+} = 0.145 \pm 0.378$, $n = 48$). When the comparisons of morphological traits were, in turn, removed from the analysis of taxonomic classes, cichlids still had a significant response to outcrossing ($d^*_{i+} = 1.339 \pm 0.493$, $n = 24$) but poeciliids did not ($d^*_{i+} = 0.393 \pm 0.400$, $n = 38$).

Studies categorized according to differences in origin and rearing had a significant d^*_{++} (Table 4C); the null hypothesis of homogeneity of effect sizes could not be rejected ($Q^*_{\mathrm{B}} = 0.30$; $P = 0.584$). This result may be explained by the significant d^*_{i+} for studies where parental lines had been reared in captivity for at least one generation, and were compared with hybrids in captivity. However, this outcome may be a result of the difference in sample size between the two classes (Table 4C). Tellingly, neither class had an N_{fs} that exceeded the critical limit.

Group II comparisons: F1 hybrids and parental lines when both lines are raised in the non-parental environment

Results in this group of comparisons yielded the greatest number of significant results. The null hypothesis of homogeneity in effect sizes across taxa was rejected ($Q^*_{\mathrm{B}} = 13.22$; $P = 0.021$; Table 5A). There was a significant and positive response to outcrossing across the taxon category. The N_{fs} for d^*_{++} exceeded the critical level, and at least part of this result appears to be explained by the Centrarchids and Salmonids ($d^*_{i+} = 0.395 \pm 0.227$, $n = 108$; $d^*_{i+} = 0.332 \pm 0.179$, $n = 147$, respectively). The null hypothesis of homogeneity could not be rejected for either the trait or origin and rearing categories (Table 5B, C), although the overall mean effect size for these categories was significant (but not robust to publication bias). These results appear to be largely explained by studies in the

Table 5 Meta-analysis of F1 hybrids where hybrids and parental lines were reared in the non-parental environment (Group II; *Hyb-P1 in nonP1E*). Effect sizes, 99% confidence limits, and failsafe values for classes within the following categories: (A) taxa; (B) traits; (C) origin and rearing

Class	Number of comparisons (n)	Cumulative effect size (d^*_{i+})	99% CI	Fail-safe value (N_{fs})	N_{fs} Critical level
(A) Taxa					
Centrarchidae[a]	108	0.395	0.168–0.629	106	550
Clariide	20	0.563	− 0.228–1.354	36	110
Cyprinidae	36	− 0.029	− 0.402–0.344	0	190
Gasterosteidae	14	− 0.207	− 0.829–0.413	0	80
Poeciliidae	24	0.059	− 0.403–0.521	0	130
Salmonidae[a]	147	0.332	0.153–0.512	37	745
Mean effect size[a]	349	0.275	0.152–0.399	1594	1755
All classes, Q^*_{B}	13.22 ($P = 0.021$; df = 5)				
(B) Trait					
Behavioral	16	− 0.011	− 0.561–0.539	0	90
Life-history[a]	67	0.438	0.140–0.736	80	345
Physiological[a]	130	0.297	0.083–0.512	63	660
Morphological[a]	136	0.480	0.055–0.441	34	690
Mean effect size[a]	349	0.285	0.159–0.411	1347	1755
All classes, Q^*_{B}	3.93 ($P = 0.269$; df = 3)				
(C) Origin and rearing					
Wild origin with captive rearing[a]	336	0.292	0.165–0.420	155	1690
Captive origin with wild reading	13	0.12	− 0.496–0.736	0	75
Mean effect size[a]	349	0.285	0.161–0.410	371	1755
All classes, Q^*_{B}	0.50 ($P = 0.481$; df = 1)				

salmonid and centrachid categories; removal of these studies reduced the number of categories, and remaining trait categories had non-significant effect sizes (life-history: $d^*_{i+} = -0.052 \pm 0.503$, $n = 37$; morphological: $d^*_{i+} = 0.074 \pm 0.358$, $n = 57$). Overall effect size d^*_{++} was significant when studies were grouped according to their origin and rearing environments; this result was primarily explained by comparisons between wild-origin fish and their hybrids in a captive environment, which was also the largest sample group (Table 5C). Again, the N_{fs} fell below the critical level.

The effects of outcrossing in the second hybrid generation

Group I comparison: F2 hybrids and parental lines when both lines are raised in the parental environment

Again, we observed a positive response to outbreeding in this group of comparisons. Both d^*_{++} and Q^*_B were significant across all taxa ($Q^*_B = 289.14$; $P < 0.001$, $d^*_{++} = 0.364 \pm 0.221$, $n = 57$; Table 6A) and N_{fs} exceeded the critical level. The result appears to be largely explained by the cichlid studies; their removal from the analysis resulted in a non-significant d^*_{++} (where $d^*_{++} = -0.129 \pm 0.228$, $n = 49$). Further, d^*_{++} and Q^*_B were also significant across traits (Table 6B). Findings were similar to those observed in the F1 Group I studies; the significant d^*_{i+} for morphology appears to be explained by length and weight. Their removal resulted in a $d^*_{i+} = 0.293 \pm 0.889$ ($n = 8$) for morphology and a $d^*_{++} = -0.017 \pm 0.332$ ($n = 30$) for traits, neither of which were significant. Again, the studies on cichlids appear to have a large effect on the findings. Their exclusion resulted in $Q^*_B = 2.05$; $P = 0.562$ and the class "morphology" no longer had a significant value for d^*_{i+} (where $d^*_{i+} = -0.072 \pm 0.499$, $n = 17$). The values for Q^*_B and d^*_{++} were not significant for the origin and rearing category (Table 6C).

Group II comparisons: F2 hybrids and parental lines when both lines are raised in the non-parental environment

We observed no significant response to outbreeding in comparisons across this group of studies. Values for Q^*_B and d^*_{++} were not significant across taxa or traits in the F2 (taxa: $Q^*_B = 3.39$, $P = 0.184$, $d^*_{++} = 0.505 \pm 0.555$, $n = 37$, Table 7A; traits: $Q^*_B = 7.09$, $P = 0.069$, $d^*_{++} = 0.506 \pm 0.519$, $n = 37$, Table 7B). All of the group II studies performed on the F2 generation compared hybrids with wild–origin parents in captivity, and therefore no heterogeneity analysis could be performed on origin and rearing, and no significant response to hybridization was found within this single grouping (Table 7C).

Table 6 Meta-analysis of F2 hybrids where hybrids and parental lines were reared in the parental environment (Group I; *Hyb-P1 in P1E*). Effect sizes, 99% confidence limits, and failsafe values for classes within the following categories: (A) taxa; (B) traits; (C) origin and rearing

Class	Number of comparisons (n)	Cumulative effect size (d^*_{i+})	99% CI	Fail-safe value (N_{fs})	Critical level
(A) Taxa					
Cichlidae[a]	8	4.721	4.024–5.419	9	50
Gasterosteidae	8	0.267	– 0.247–0.780	0	50
Poeciliidae	2	0.217	– 0.729–1.164	0	20
Salmonidae	39	– 0.148	– 0.390–0.093	0	205
Mean effect size[a,b]	57	0.364	0.143–0.506	1308	295
All classes, Q^*_B	289.14 ($P < 0.001$; df = 3)				
(B) Trait					
Behavioral	8	– 0.105	– 0.956–0.746	0	50
Life-history	20	0.164	– 0.413–0.740	0	110
Physiological	4	– 0.430	– 1.628–0.768	5	30
Morphological[a]	25	1.249	0.737–1.762	131	135
Mean effect size[a]	57	0.540	0.205–0.876	193	295
All Classes, Q^*_B	23.68 ($P < 0.001$; df = 3)				
(C) Origin and rearing					
Wild origin reared in wild	7	– 0.032	– 0.961–0.897	0	45
Captive origin reared in captivity[a]	50	0.594	0.258–0.930	98	260
Mean effect size[a]	57	0.522	0.206–0.837	103	295
All classes, Q^*_B	2.66 ($P = 0.103$; df = 1)				

[a] d^*_{i+} of d^*_{++} value for class is significant at α = 0.01 level

Table 7 Meta-analysis of F2 hybrids where hybrids and parental lines were reared in the non-parental environment (group II; *Hyb-P1 in nonP1E*). Effect sizes, 99% confidence limits, and failsafe values for classes within the following categories: (A) taxa; (B) traits; (C) origin and rearing

Class	Number of comparisons (n)	Cumulative effect size (d^*_{i+})	99% CI	Fail-safe value (N_{fs})	Critical level
(A) Taxa					
Gasterosteidae	6	0.097	– 1.309–1.504	0	40
Poecliidae	11	0.322	– 1.018–1.083	0	65
Salmonidae[a]	20	0.858	0.111–1.605	66	110
Mean effect size	37	0.505	– 0.054–1.063	145	195
All classes, Q^*_B	3.39 (P = 0.184; df = 2)				
(B) Trait					
Behavioral	8	0.124	– 0.972–1.221	0	50
Life-history[a]	15	0.928	0.099–1.756	55	85
Physiological	2	– 1.304	– 3.496–0.887	11	20
Morphological	12	0.571	– 0.337–1.480	22	70
Mean effect size	37	0.506	– 0.013–1.025	22	195
All classes, Q^*_B	7.09 (P = 0.069; df = 3)				
(C) Origin and rearing					
Wild origin reared in captivity	37	0.496	– 0.066–1.058	54	195
Captive origin reared in wild	0	–	–	–	–
Mean effect size	37	0.496	– 0.066–1.058	54	195
All classes, Q^*_B	–				

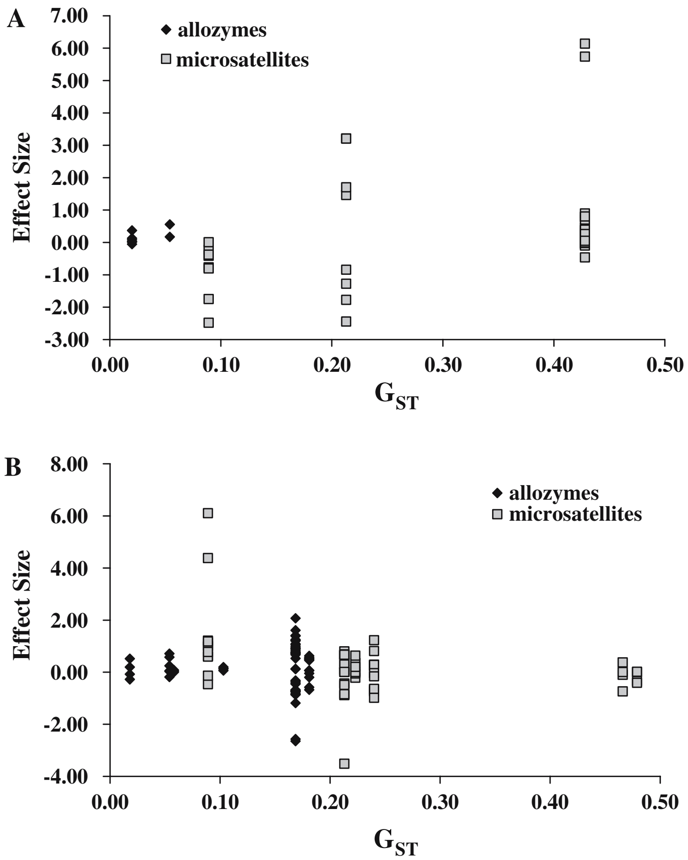

Fig. 1 Relationship between effect size and genetic distance for F1 hybrids separated into (**A**) group I studies (*Hyb-P1 in P1E*) and (**B**) group II studies (*Hyb-P1 in nonP1E*). Each point represents the effect size for one trait within one study. Studies were further separated by the type of marker used to calculate G_{ST}: allozymes or microsatellites. Points clustered at the same genetic distance are from the same study populations (Table 1)

Genetic distance

Genetic distances were obtained for 249 comparisons (Table 3). Comparisons were divided into groups I and II and further subdivided by generation, following procedures described previously. Several authors have argued that genetic distances computed using allozymes and microsatellites are not comparable (Hedrick 1999; de Innocentiis et al. 2001), and thus the effect of marker type was further considered. In the group I studies, G_{ST} and effect size, d^*_{i+}, were positively correlated in the F1, and this relationship was significant ($r = 0.353$, $P = 0.002$, $n = 75$, number of studies = 8; Fig. 1A). Correlation between G_{ST} and d^*_{i+} for studies based on microsatellites was also significant ($r = 0.409$, $P = 0.001$, $n = 66$) but not for studies based on allozyme data ($P > 0.05$). It is important to note that the number of studies represented decreased in the latter two analyses (five for microsatellites, three for allozymes). No significant correlation was observed in the group I F2 studies, regardless of marker type ($P > 0.05$, Fig. 2). Analyses of Group II studies on the F1 generation, in which all marker types were used, resulted in a significant, negative correlation between G_{ST} and d^*_{i+} ($r = -0.221$, $P = 0.013$, $n = 124$, number of studies = 10; Fig. 1B). Similarly, G_{ST} estimates based on microsatellites were negatively correlated with d^*_{i+} in both the F1 and F2 (F1: $r = -0.428$, $P = 0.001$, $n = 54$, number of studies = 5, Fig. 1B; F2: $r = -0.420$, $P = 0.037$, $n = 25$, number of studies = 3, Fig. 2), and again, the number of studies represented decreased.

Effect size values derived from certain studies on the poeciliids yielded the greatest G_{ST} values (two studies with 65 comparisons had values of $G_{\mathrm{ST}} > 0.4$) and may have affected the results. Removal of these comparisons from the analysis resulted in non-significant correlations between genetic distance and the group I F1 and group II effect sizes (G_{ST} values based on microsatellites; group I F1: $r = 0.163$, $P = 0.547$, $n = 16$; group II F2: $r = -0.430$, $P = 0.125$, $n = 14$) but the group II F1 correlation was still significant ($r = -0.459$, $P = 0.004$, $n = 38$). The group I studies for which G_{ST} values were available comprised comparisons where hybrids were reared in captivity and compared to a captively reared parental line. In group II studies with G_{ST} values, eight studies examined hybrids of two populations of wild fish reared in captivity and two studies compared hybrids of captive and wild populations reared in captivity. No significant relationship was observed when effect sizes were partitioned into any other categories including generation, trait or taxa ($P > 0.05$).

Discussion

The results of this analysis suggest that there are no clear and predictable outcomes following outbreeding between fish populations. Overall, a significant and positive response was observed across studies performed on F1 and F2 hybrid generations and there was no correlation between genetic distance and effect size. However, responses differed when studies were separated into groups describing the experimental environment, taxon, trait or population histories.

Within studies in which hybrid and parent comparisons were performed in the parental environment (here, Group I), a significant positive response was observed across all hybrid categories. Results in the F1 and F2 hybrid category appear to be largely explained by studies performed on a cichlid species, *Oreochromis niloticus*, in which captive strains derived from different geographic areas were crossed with each other. Most of the positive response was seen in morphological traits; specifically, length and weight. It is important to note that very distantly related poeciliid strains (with a G_{ST} value of around 0.4) also contributed to the positive result in the F1. The most interesting results

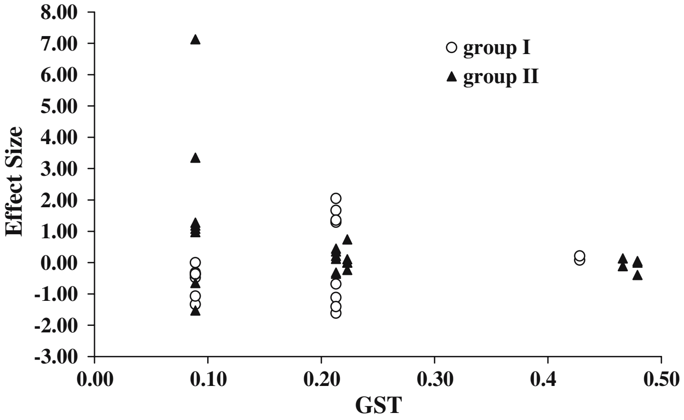

Fig. 2 Relationship between effect size and genetic distance for F2 hybrids separated into group I studies (*Hyb-P1 in P1E*) and group II studies (*Hyb-P1 in nonP1E*). Each point represents the effect size for one trait within one study. Only studies using microsatellite data to calculate G_{ST} are shown here since only one study used allozyme data. Points clustered at the same genetic distance are from the same study populations (Table 1)

were observed in studies in which hybrids and parents were compared in the non-parental environment (here, Group II). The mean effect sizes were positive and significant across taxa, traits, and origin and rearing in the F1 hybrids. Many of these results can be explained by studies in the centrarchids and salmonids, although it is noteworthy that these two taxa represent the greatest number of comparisons. However, it is important to point out that none of these findings were robust to publication bias. Results were generally not significant in the F2 hybrid generation, but individual classes (salmonids and life history traits) exhibited a significant and positive response to outbreeding. All studies in this hybrid generation involved comparisons between hybrid and wild origin parental lines in a captive environment.

Response to outbreeding differed between taxa. The cichlids, represented in the group I studies only, show a significant and positive response to outbreeding in both the F1 and F2 generation despite a small samples size in the F2. Both of the studies on cichlids utilized laboratory strains which were expected to exhibit heterosis upon crossing (Tave et al. 1990; Marengoni et al. 1998). Likewise, three of the five studies on poeciliids, *Poecilia reticulata*, were performed on strains with low heterozygosity (Chiyokubo et al. 1998; Shikano and Taniguchi 2002a; Nakadate et al. 2003). Heterozygosity was increased in the inbred populations following strain crossing, and thus heterosis was the predicted outcome (Shikano and Taniguchi 2002a). Both cichlids and poecilids exhibited a similar response, but this response appears to be a result of the demographic history of the populations in the study. It is interesting to note that salmonids comprised the greatest number of studies in all categories (nine species within four genera), and an examination of the findings within this taxon may demonstrate whether the meta-analysis was appropriately directed at the correct taxonomic grouping. Salmonids exhibited a significant response to outbreeding in the group II, but not group I, comparisons across both the F1 and F2 generation. However, a high degree of variation was seen in effect sizes across traits within the taxon; d^*_{ij} ranged from -4.365 to 1.857 for group I comparisons and from -3.092 to 9.697 for group II comparisons. The group Salmonidae was not robust to publication bias in any of the analyses; possibly a result of this high degree of variation in effect size. Thus, no strong conclusions could be made about the response of salmonids to outbreeding.

While the analyses are largely inconclusive and biased by few studies of large effect, the response to outbreeding observed in the F1 hybrids was intriguing. Loss of local adaptation is frequently implicated as the most common cause of outbreeding depression (e.g., Allendorf et al. 2001), and declines in fitness in this case are typically ascribed to the fact that hybrids have only half the adaptive alleles present in the parental populations (more specifically, extrinsic outbreeding depression would be due to the loss of additive or dominance interactions (e.g., McClelland et al. 2005; Tymchuk et al. 2006). Thus, if loss of local adaptation were the prevailing mechanism for outbreeding depression, it might be expected that the performance of F1 hybrids relative to the parental lines would be lower in parental environments (here, Group I comparisons) than in the non-native environment (Group II comparisons). However, the meta-analysis did not demonstrate a decline in hybrid performance in the former case (group I: *Hyb-P1 in P1E*). Rather, results suggest that morphological traits in particular have a strong positive response to outbreeding. Results in this case were biased by a few studies in which small inbred strains were subject to a line cross analysis, and outbreeding may have to lead to heterosis in both the F1 and F2 generation. In contrast, F1 hybrid performance across a range of traits fitted the predictions because it did improve in the latter case (group II: *Hyb-P1 in non-PE*). The majority of studies in this group compared wild and hybrid offspring in a captive environment. The findings may imply that hybrids perform better if the environment is novel to one of the parents, because hybrids have at least half of the alleles suited to that environment. Again, interpretation of the results should be viewed with caution in light of issues of publication bias raised earlier. It is also important to recognize that studies in fishes have demonstrated a range of genetic mechanisms underlying outbreeding depression (Gharrett et al. 1999; Gilk et al. 2004; McClelland et al. 2005; Tymchuk et al. 2006) and thus generalizations are not informative for any one case. For example, in an experiment on pink salmon performed with populations returning to the same environment but during different years, a decrease in survival was attributed to disruption of co-adapted gene complexes (Gharrett and Smoker 1991; Gharrett et al. 1999). In contrast, growth in coho salmon has been shown to be primarily controlled by additive (Tymchuk et al. 2006) or additive and dominance interactions (McClelland et al. 2005). It is possible that combining effect sizes controlled by different types of genetic interactions may confound the meta-analysis, particularly in instances where some traits or taxa exhibit losses of local adaptation in the first hybrid generation while others do not, but these populations might in turn demonstrate disruption of epistatic interactions in later generations.

Perhaps the greatest difficulty associated with this meta-analysis is that of sample size. For example, it should be noted that a high fail-safe number does not address all issues associated with publication bias. The fail-safe number is a function of sample size and effect size; large effect sizes (such as that noted for the studies on *O. niloticus*; Tave et al. 1990; Marengoni et al. 1998) can counter small sample size in calculations of fail-safe values. This value gives some indication of whether publication bias (due to omission of both published and unpublished studies) is a concern, but it is not indicative of the number of studies necessary for a robust analysis (Rosenberg 2005). On the other hand, it could be argued that the number of comparisons in this study equals or exceeds that of comparable meta-analyses (Moller and Thornhill 1997; Reed and Frankham 2001; Coltman and Slate 2003). Meta-analytic techniques can be successfully applied to as few as two studies; the main statistical issue associated with small sample size is lack of power to detect significance (Rosenthal 1995; Gurevitch and Hedges 2001). Thus, failure to detect outcomes of outbreeding in the F2 generation may be due to the general paucity of studies; F2 hybrids were represented in 10 studies, compared to 33 available for the F1 generation (14% of all comparisons). While the few significant findings in this study are likely valid, results cannot be claimed as being predictive and should be interpreted cautiously.

The relationship between effect size and genetic distance could not be readily determined because many of the comparisons lacked sufficient sample size, especially after grouping distance measures based on different marker types. However, the effect sizes were positively correlated with genetic distance in the F1 hybrids in those studies that compared hybrids and parents in the parental environment (Group I: *Hyb-P1 in P1E*) and negatively correlated in studies that were conducted in non-parental environments (Group II: *Hyb-P1 in non-PE*). In the latter case, the effect size was greatest at smaller genetic distances, decreasing to zero with increasing genetic distance. It is important to note the caveats associated with these relationships. First, the correlation coefficients associated with the analyses are small; in other words, much of the variance in the effect sizes cannot be explained by genetic distance. Second, genetic distances such as G_{ST} are affected by heterozygosity (Chakraborty and Leimar 1987; Hedrick 1999); it was noted that studies with the some of the lowest heterozygosities within strains (likely a result of close inbreeding and small population sizes; Chiyokubo et al. 1998; Sheffer et al. 1999; Shikano and Taniguchi 2002a; Nakadate et al. 2003) yielded the highest G_{ST} values. Their exclusion reduced the significance of the F1 group I studies. Third, correlations were examined across a range of traits, and in the meta-analysis we observed that traits may vary in their response to outbreeding; trait measurement was not consistent across all studies. Analyses across single traits resulted in non-significant correlations.

The most likely explanation for the inconclusive results reported here is that the outcomes of outbreeding cannot be easily predicted and that even if there were a method of doing so, combining all measures into a single meta-analysis may have ‘‘swamped’’ any meaningful results. It has been suggested that it might be unreasonable to make general rules about the results of outbred matings (Lynch 2000). Mutation and fixation processes are random, and thus interactions between species or population pairs can be expected to be unique (Lynch 2000). In contrast, simulations (Edmands and Timmerman 2003) and empirical studies (Templeton 1979; Edmands et al. 2005) have shown that there is significant merit in understanding the long-term effects of outbreeding, especially within a single species. The most useful aspect of this meta-analysis has been the identification of gaps in the understanding of the outcomes of outbreeding in fishes, which in turn provides strong guidance for consistent objectives and experimental design in future research efforts. Here, we attempt to describe gaps in the following areas: (1) response to outbreeding beyond the F1 generation; (2) response of traits, particularly fitness related traits, within one species; (3) the influence of the environment on hybrid response; (4) understanding of the relationship between the response to outbreeding and genetic distance at both neutral and quantitative traits; and (5) the effect of other genetic factors, specifically maternal effects and ploidy level, on response to outbreeding.

A significant proportion of studies examined here were limited to the measurement of fitness traits in the first hybrid generation, thus failing to observe outbreeding effects in later generations. Ideally, hybrids should also be assessed in both parental environments; the meta-analyses revealed some significant effects in the F1 generation in one of the two environments. The increase in the number of studies that consider these elements in the experimental design will facilitate a greater understanding of the genetic mechanisms underlying outbreeding and will provide insight into the long-term consequences of hybridization.

Theoretical treatments indicated that loss of local adaptation generally led to rapid declines in fitness (Edmands and Timmerman 2003) although, in some cases, hybridization led to heterosis. In simulations where hybridization was always deleterious, recovery of fitness following loss of local adaptation was rapid, perhaps because selection quickly eliminates the hybrids (Edmands and Timmerman 2003). Additionally, population size affected the duration and magnitude of extrinsic outbreeding depression with larger populations having a higher baseline fitness but exhibiting a greater relative loss of fitness and longer time to recovery than small populations (Edmands and Timmerman 2003). In contrast, recovery following reductions in fitness resulting from the disruption of favorable epistatic interactions depended upon the recombination rate, although such rates are often difficult to assess and may be highly variable between species (Lynch and Walsh 1998). Empirical studies in this category are rare, but in copepods recovery of fitness following changes in epistatic interactions have been observed over approximately 24 generations (Edmands et al. 2005). Finally, simulations have also shown that response to outbreeding was highly variable at smaller genetic distances (Edmands and Timmerman 2003).

The meta-analysis showed that certain results varied across trait classes. For example, morphological traits had a significant and positive response in the F1 generation and in the F2 group I comparisons. Life-history traits, those considered a direct measure of fitness, on the other hand, had significant *positive* response in the F1 group II comparisons but a significant *negative* response in the F2 group II comparisons. This latter result may indicate that there are greater constraints on life-history characters, as compared to other traits, so that there are less extrinsic differences between populations; loss of local adaptation would not be expected for these traits. However, a decrease in fitness in the F2 hybrids might result from disruption of coadapted genes leading to intrinsic outbreeding depression (Templeton 1986). The differences observed in trait response raise the issue that many of the studies evaluated here may have omitted measuring traits susceptible to outbreeding depression. Some responses were significant, suggesting that certain traits are more likely to respond to outbreeding, although in most cases publication bias may be a concern. Specific studies support this finding. Gharrett et al. (1999) report significant decreases in survival of F2 hybrids of odd and even year pink salmon (*Oncorhynchus gorbuscha*) but no increase in asymmetry (an indication of problems during development) in the same hybrids. Some hybrids between some populations of topminnow experienced reduced growth in the F1 generation only, others showed reduced growth in the F2 only and some had no evidence of outbreeding depression despite high genetic differentiation between all populations studied (Sheffer et al. 1999).

It is also important to note that the choice of traits measured was inconsistent across studies, and did not allow a comprehensive analysis of whether specific traits respond in a predictable way to outbreeding. This inconsistency is not surprising, given the range of objectives of the studies analyzed here. Morphological measurements are more appropriate to aquaculture, whereas life-history traits are directly relevant to an individual's fitness and are important for understanding the role of hybridization in evolution and conservation. Further, the relationship between the traits measured in most of the studies and lifetime fitness is not clear. For example, many of the studies incorporated in the analysis examined hybrids in a cultured setting and examined traits (particularly growth related traits) for which increases were desirable. An increase in growth rate may not always be related to fitness, particularly in wild environments. Lifetime fitness traits, such as reproductive success or survivorship, are likely directly related to individual fitness (Roff and Mousseau 1987) and would be best incorporated in those studies seeking to understand the fitness consequences of outbreeding. However, this goal may be difficult to study in most experimental situations, because the design would necessarily incorporate mate choice and would be dependent on rearing populations in the wild environment. Thus, several authors have incorporated a suite of traits as indirect measures of fitness. For example, female size (a morphological trait) is closely correlated with fecundity in salmon (Fleming and Gross 1990). Growth rate at critical periods has been shown to affect age at maturation (Shearer and Swanson 2000) and also has a significant relationship to smolt-to-adult survival in salmon (Beckman et al. 1998). Future studies aimed at applications in conservation should endeavor to prioritize fitness-related characters. It would be particularly useful to examine cumulative fitness to gauge the full impact of hybridization on a population, although we recognize the limitations of measuring such a parameter.

In several organisms, it has been shown that environmental conditions may modify the level of outbreeding detected in hybrids (Burton 1987; Waser et al. 2000; Montalvo and Ellstrand 2001). For example, the more stressful conditions experienced in the wild can result in lower fitness of outbred progeny

(Montalvo and Ellstrand 2001). However, studies of fish populations in multiple environments are rare. It was possible to perform only broad comparisons across captive and wild environments in the meta-analyses; any comparisons in these categories would reflect both demographic history (possibly inbreeding) and the influence of the rearing environment. It should be noted that there were few cases in this meta-analysis where hybrids were raised in both parental environments, so the full extent of environmental influences (Lynch and Walsh 1998) could not be assessed. In those studies in which hybrids were examined in both parental environments, results were again quite variable. For example, in a study on stickleback that assessed hybrid performance in both parental environments, hybrids performed poorly compared to the parental types in both habitats (Hatfield and Schluter 1999). In contrast, hybrids between farmed and native Atlantic salmon had a higher growth rate than both parents in the wild but a lower growth rate than both parents in a hatchery setting (Einum and Fleming 1997). Examining responses of fish populations across different environments may be beneficial, depending on the primary concern of the researchers. Given that outbreeding experiments can be used to assess impacts of stock transfers or to preserve endangered species, greater emphasis should be placed on experiments conducted on wild fish populations for addressing conservation-based questions.

Contrary to model-based predictions (Emlen 1991; Edmands et al. 2005), there was no defensible relationship between genetic distance and effect size in either the F1 or F2 hybrid generations and large variations were seen in effect size at each G_{ST} value. In a recent review, Edmands (2002) reported a positive relationship between reproductive incompatibility (defined as loss of viability or sterility in hybrid offspring) and genetic divergence. It is important to note, however, there was substantial variation within the broad pattern of increased outbreeding with increased distance, and that differentiation was a poor predictor of reproductive performance in general (Edmands 2002). It is possible that the taxonomic level used here may be an inappropriate category in which to determine the outcomes of outbreeding—such an approach may be better directed within a single species. As an example of a useful experimental approach within a single species, Gharrett and colleagues have attempted to examine the relationship between evolutionary distance and outbreeding depression in a series of studies on pink salmon. This work has been achieved by examining populations separated by strict life histories (returning in the odd-year or even-year; Gharrett and Smoker 1991; Gharrett et al. 1999); by geographic distance within the same year class (Gilk et al. 2004) and, more recently, by return timing within the same drainage system (research ongoing).

Genetic distances based on neutral molecular markers likely reflect population demographic processes within each species, rather than divergence in fitness traits (McKay and Latta 2002), and between-species comparisons of genetic distance may be uninformative. Experimental design should be based on quantitative genetic principles that permit estimation of a genetic distance based on quantitative traits, Q_{st} (Pfrender et al. 2000), which may be a more meaningful evolutionary distance. Creation of hybrid half-sib families, or use of circular mating designs, permits the estimation of the additive variance in a trait (e.g., Edmands and Harrison 2003; O'Hara and Merila 2005; Perry et al. 2005). This information can in turn be used to estimate the divergence of two populations at quantitative traits that have been subject to selection (Spitze 1993). Incorporation of this distance measure will also partly address the concern raised earlier; namely, that the relationship between traits that are typically measured in hybridization studies and lifetime fitness is not clear. Estimates of Q_{st} for individual traits will provide information on those traits that have diverged between two populations and thus provide guidance on the appropriate experimental design.

Other genetic factors, which were not tested directly in this meta-analysis, might also influence the response to outbreeding. For example, by using hybrid backcrosses of *O. niloticus*, Tave et al. (1990) were able to determine that increases in fitness beyond the first hybrid generation were a product of maternal heterosis. Maternal heterosis refers to a phenomenon where characters with a strong maternal component will manifest changes in fitness a generation after other traits (Falconer and Mackay 1996). In traits that have a large maternal component, such as yolk mass, F1 hybrids will be affected by the mother's fitness, but subsequent hybrid generations might experience changes of fitness in that trait following hybridization. In *O. niloticus*, the length and weight of the F2 progeny of outbred dams was greater than F1 hybrids because outbred dams (F1s) exhibited heterosis in egg cytoplasm allocation (Tave et al. 1990). Another example of a confounding genetic factor might be ploidy level in salmonids (Allendorf and Thorgaard 1984). The Salmonidae are residual tetraploids and some loci still exist as duplicate pairs (Devlin 1993; Hordvik et al. 1997). Additive, dominance and epistatic interactions may involve a greater number of loci than in diploid organisms and the results of the disruption of such interactions may be less predictable. Although it would be difficult to establish an experimental design taking into account these effects from the outset, both maternal heterosis and ploidy levels may warrant experimentation beyond the second hybrid generation.

In summary, future experimental designs should seek to determine the underlying genetic mechanisms of outbreeding, and hence the long-term fate of hybrids. Such designs necessarily require more than one generation of study and experiments should ideally be carried out in both parental environments. Despite a growing interest in conservation-related management approaches, there is a paucity of information on the outcomes of outbreeding in wild fish populations, and emphasis should be placed on natural environments. Assessment of cumulative fitness may provide more relevant and consistent results for determining the outcome of hybridization. Finally, careful experimental design can permit estimation of genetic distances based on Q_{ST}, which may lead to more meaningful and predictive results. The standardization of experimental approaches towards determining the outcomes of outbreeding will provide much needed information that is important for the management of aquaculture strains and populations of conservation interest, and we strongly advocate such efforts.

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