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Report

Reverse Evolution of Armor Plates in the Threespine Stickleback

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Summary

Faced with sudden environmental changes, animals must either adapt to novel environments or go extinct. Thus, study of the mechanisms underlying rapid adaptation is crucial not only for the understanding of natural evolutionary processes but also for the understanding of human-induced evolutionary change, which is an increasingly important problem [1–8]. In the present study, we demonstrate that the frequency of completely plated threespine stickleback fish (*Gasterosteus aculeatus*) has increased in an urban freshwater lake (Lake Washington, Seattle, Washington) within the last 40 years. This is a dramatic example of "reverse evolution," [9] because the general evolutionary trajectory is toward armor-plate reduction in freshwater sticklebacks [10]. On the basis of our genetic studies and simulations, we propose that the most likely cause of reverse evolution is increased selection for the completely plated morph, which we suggest could result from higher levels of trout predation after a sudden increase in water transparency during the early 1970s. Rapid evolution was facilitated by the existence of standing allelic variation in *Ectodysplasin* (*Eda*), the gene that underlies the major plate-morph locus [11]. The Lake Washington stickleback thus provides a novel example of reverse evolution, which is probably caused by a change in allele frequency at the major plate locus in response to a changing predation regime.

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Results and Discussion

Reverse Evolution of Armor Plates in Lake Washington Sticklebacks

The threespine stickleback (*Gasterosteus aculeatus*) provides a good model system for elucidation of the ecological and genetic mechanisms underlying phenotypic evolution [12, 13]. One dramatic and prevalent phenotypic change in these fish is the reduction of armor plates, which cover the lateral body surface, that occurred repeatedly after freshwater colonization 12,000 years ago [10]. Whereas ancestral marine sticklebacks typically have a continuous row of lateral plates (completely plated morph), freshwater sticklebacks usually have a reduction in lateral plates resulting in a gap in the middle part of the plate row (partially plated morph) or a loss of both the middle and posterior plates (low-plated morph). The major gene responsible for reduction of the stickleback lateral plates across the world is *Ectodysplasin* (*Eda*) [11]. There are two major alleles of *Eda* found in stickleback populations, and they are here referred to as the complete allele and the low allele. Most marine sticklebacks are homozygous for the complete allele, although marine sticklebacks that are heterozygous carriers of the low allele are found at a low frequency [11]. It is proposed that when marine sticklebacks colonize freshwater environments, strong selection results in an increase in the frequency of the low *Eda* allele, leading to the prevalence of low-plated fish in freshwater.

In contrast to the prevalence of the low-plated morph in many freshwater environments [10, 11], we found a high frequency of completely plated sticklebacks in Lake Washington, an urban freshwater lake in Seattle [14–16]. In 2005, we found that all three lateral-plate morphs were present, with 49% completely plated morphs, 35% partially plated morphs, and 16% low-plated morphs (Figures 1A and 2C). Although a previous study had also shown that all three morphs were present in Lake Washington in 1968–1969, only 6% were classified as completely plated morphs (Figure 1A) [17]. Instead, the low-plated morph, with a mode of seven plates, was the most common morph until the late 1960s (Figures 1B and 1C). In 1976, bimodal peaks appeared, one corresponding to fish with seven plates and another corresponding to fish with 32 plates (Figure 1C) [18]. The frequency of fish with 33 plates was even higher in the 2005 sample (Figure 1C). The increase in completely plated fish in the 2005 sample did not reflect bias in the sampling methods ($n = 322$, $\chi^2 = 6.6949$, d.f. = 4, $p = 0.1529$) or in the seasonal (Figure S1, available online) or geographical (Figure 2C) distribution of differently plated sticklebacks. These data demonstrate that the frequency of plate-morph phenotypes has changed dramatically in Lake Washington within the past 40 years, which is equivalent to 40 generations in this stickleback population [18].

Genotyping of the 2005 samples at the *Eda* locus revealed a strong association between plate phenotype and *Eda* genotype in Lake Washington ($n = 196$, $\chi^2 = 227.0$, d.f. = 4, $p < 10^{-47}$) (Figure S2, Table S1). By ANOVA, the *Eda* genotype explains 75.2% of the variance in plate number in the Lake Washington

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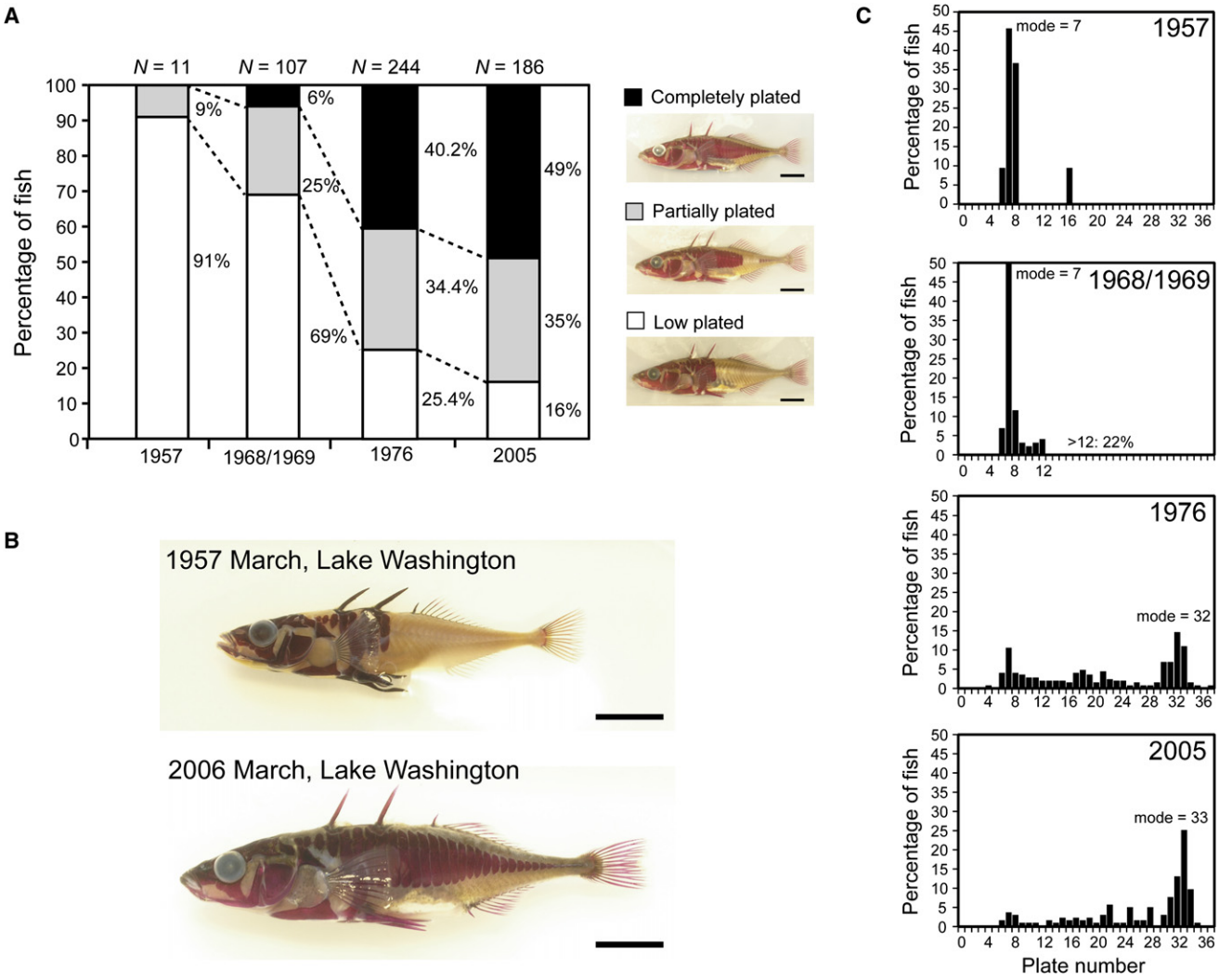

Figure 1. Lateral-Plate Evolution in the Lake Washington Stickleback

(A) Temporal change in the frequency of the completely plated (black bar), partially plated (gray bar), and low-plated (white bar) morphs in Lake Washington sticklebacks. Sample sizes are shown above the graph. Right panels show representative images of the three stickleback morphs. Skeletal structures are visualized by alizarin red staining. Scale bars represent 10 mm.

(B) Representative images of sticklebacks collected via midwater trawling during March 1957 and March 2006 in the northern pelagic zone of Lake Washington.

(C) Histograms of lateral-plate number for sticklebacks collected in 1957, 1968–1969, 1976, and 2005. Sample sizes are the same as those in Figure 1A. The most-common plate number is also shown in each panel as a mode. Among sticklebacks collected in 1968–1969, 22% had more than 12 plates, but the individual plate counts for each fish are not available [17]. Plate number was counted from the left side of the fish except in the 1976 sample, for which only right-side plate-number data were available [18]. For the 1957 data, museum specimens in the University of Washington Fish Collection were analyzed. The frequency of morph was significantly different between successive sampling time points ($p < 0.05$) except between 1957 and 1968–1969 samples ($\chi^2 = 2.375$, $p = 0.305$).

stickleback. This is close to the percentage of phenotypic variance in plate number explained by the *Eda* locus in laboratory crosses (76.9%) [19]. Thus, the increase in the completely plated phenotype in Lake Washington is probably the result of an increase in the frequency of the *Eda* complete allele, given the previously established link between plate phenotype and *Eda* genotype in stickleback populations across the world [11].

Gene Flow is Not the Primary Cause of Armor-Plate Evolution in Lake Washington Sticklebacks

Most marine sticklebacks in Puget Sound are completely plated (Figure 2C), with high frequencies of the complete *Eda* allele (Figure 2D). Because marine sticklebacks can now migrate into the lake through the Lake Washington Ship Canal (Figure 2B and Figure S3), which was built in 1917 [14], an increase in migration might have contributed to the increase of lateral plates in the Lake Washington stickleback. In order to test this hypothesis, we collected sticklebacks in neighboring marine environments (Puget Sound), in multiple points in Lake Washington, and in neighboring streams (Figure 2) and genotyped them with 15 microsatellite markers (Table S2). Genetic data were then analyzed with the Bayesian-clustering software STRUCTURE [20]. Within the marine, lake, and stream fish that were genotyped, the most probable number of genetic clusters (K) was three (Figure S4). Estimation of ancestry for each

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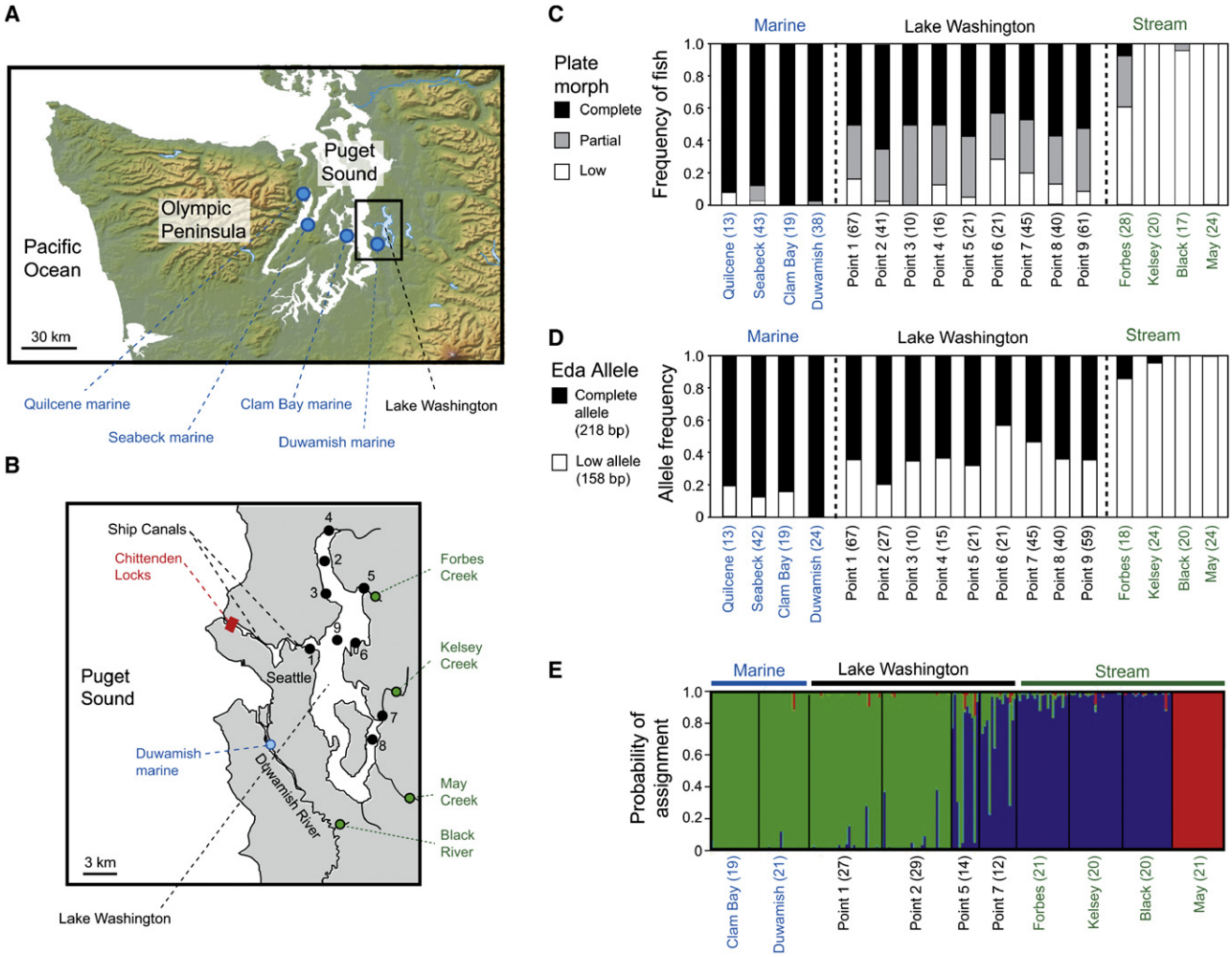

Figure 2. Genetic and Morphological Variation around Lake Washington

(A) Map of Washington State. Blue dots indicate the collection sites of marine stickleback from Puget Sound. Lake Washington is highlighted by a square and magnified in Figure 2B.

(B) Map of Lake Washington and neighboring streams. Numbers indicate the sampling sites in Lake Washington: Point 1: Union Bay; Point 2: northern pelagic zone (Area 1 in [17]); Point 3: Matthews Beach; Point 4: Tracy Owen Park; Point 5: Juanita Beach; Point 6: Yarrow Bay; Point 7: Mercer Slough; Point 8: east channel; Point 9: northern pelagic zone (Area 2 in [17]).

(C) Variation in plate-morph frequencies among populations. Each column indicates the frequency of the completely plated (black bar), partially plated (gray bar), and low-plated (white bar) morphs for each stickleback population. Numbers in parentheses indicate sample size. The frequency of different morphs was not significantly different among different points within Lake Washington ($n = 322$, $\chi^2 = 17.0$, d.f. = 14, $p = 0.255$).

(D) Variation in the allele frequency of *Eda* among populations. The black bar indicates the frequency of the complete *Eda* allele, and the white bar indicates the frequency of the low *Eda* allele at *Stn382*. Numbers in parentheses indicate sample size.

(E) Genetic structure of sticklebacks collected in Lake Washington, Puget Sound and neighboring streams. The three different genetic clusters are shown in different colors. Each individual is represented by a thin column that is partitioned into colored segments indicating the estimated proportion of ancestry from each cluster. Numbers in parentheses indicate sample size.

individual revealed that the sticklebacks in Lake Washington have two main genetic sources (Figure 2E). Sticklebacks sampled from areas near the ship canal were genetically similar to marine sticklebacks (indicated with green in Figure 2E), whereas those sampled from areas close to the streams were more similar to neighboring stream sticklebacks (indicated with blue in Figure 2E). However, there was no significant correlation between probability of marine ancestry and plate number (Pearson correlation $r = 0.005$, $p = 0.967$) (Figure S5). Multidimensional scaling of the genetic-distance matrix also confirmed the lack of association between genotypes at neutral loci and plate number (Figure S6). Thus, the increase in armor plates in Lake Washington sticklebacks does not result simply from the presence of marine sticklebacks in the lake.

It might be still possible that an increase in long-term migration from Puget Sound has contributed to the overall increase in the completely plated morph in the lake. To test this possibility, we first estimated migration rates (m; fraction of migrants per generation) from the genetic data and then examined whether the empirically estimated m can explain the observed plate evolution. We used both Isolation with Migration (IM) and LAMARC software [21–23] to estimate the m between a Lake Washington population and a Puget Sound marine

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Table 1. Estimation of the Strength of Selection (s) for the Completely Plated Morph

	Dominance of Plate-Morph Fitness		
Time Period	$h = 0$	$h = 0.5$	$h = 1$
1969–1976	$s = 0.708/0.720$	$s = 0.597/0.606$	$s = 0.582/0.591$
1976–2005	$s = 0.013/0.015$	$s = 0.017/0.020$	$s = 0.026/0.031$

Values of *s* during different time periods were calculated for different values of the dominance of plate-morph fitness (*h*). Migration rates estimated by LAMARC (left side in each cell) and IM (right side in each cell) were used. Frequencies of 6%, 40.2%, and 49.0% completely plated morphs were used for 1969, 1976, and 2005.

population (Table S3). The *m* of Puget Sound sticklebacks into Lake Washington was estimated as 3.03×10^{-4} (IM) or 1.77×10^{-3} (LAMARC), whereas the *m* of Lake Washington sticklebacks into Puget Sound was estimated as 6.43×10^{-4} (IM) or 1.20×10^{-3} (LAMARC). Then, we developed deterministic numerical simulations to calculate the *m* required for the observed change of plate phenotype under different selection regimes (Figure S7). In the absence of selection ($s = 0$), migration would need to be 0.148 to explain the observed change from 1969 to 1976 and 0.035 to explain the observed change from 1969 to 2005. These values are inconsistent with our low ($m < 10^{-3}$) migration-rate estimates, suggesting that there was a period of selection that favored the completely plated morph in Lake Washington.

Changes in Selection Regime in Lake Washington

By using the empirically estimated values of *m*, we found that a selection coefficient *s* (strength of selection for the completely plated morph) of 0.58–0.72 (Table 1) can explain the evolutionary shift from 1969 to 1976 (from 6% completely plated morphs to 40.2% completely plated morphs) (Figure 1A). This suggests that the complete morph had 58%–72% greater fitness than that of the low-plated morph during this period. To explain the transition between 1976 and 2005 (from 40.2% completely plated morphs to 49% completely plated morphs), an *s* of 0.01–0.03 is required (Table 1). We thus conclude that there was a period of very intense selection for the completely plated morph between 1970 and 1976, followed by a persistent low-level fitness advantage (1%–3%) of the completely plated morph over the low-plated morph.

One of the dramatic ecological changes that occurred in Lake Washington during the early 1970s is increased water transparency as a result of the mitigation of eutrophication in the late 1960s. Water transparency in the lake was 1–2 m Secchi depth (the maximum depth at which a white Secchi disk is visible from the water surface) during 1955–1971, and it increased to 3.4 m in 1973 and then to 6–7 m from 1976 to the present [14, 15]. Previous behavioral experiments have demonstrated that an increase in water transparency significantly increases the reaction distance of visual predators to their prey, thus leading to increased predation pressure on prey fish [24]. Cutthroat trout (*Oncorhynchus clarki*) are visual predators, extremely sensitive to subtle changes in water transparency [24], and are the primary predators of threespine sticklebacks in both the littoral and pelagic zones of Lake Washington [16, 25, 26]. Therefore, we used a visual-foraging model, which calculates the search volume by cutthroat trout as a function of light intensity and turbidity [27, 28], to investigate a possible change in the stickleback predation regime. This analysis demonstrated that the increase in lake transparency created an 8-fold increase in the visual-search volume of cutthroat trout and also expanded the depth range over which effective visual foraging could occur (Figure 3). Most of the expanded search volume was achieved during 1972–1975, when the mean Secchi-disk transparency increased to 3.4 m. Although the cutthroat trout population in Lake Washington did not increase between 1971 and 2006 (Figure S8), our model suggests that an increase in lake transparency could have changed the predation regime by increasing encounter rates between sticklebacks and cutthroat trout.

Predation by toothed predators, such as cutthroat trout, is thought to favor completely plated sticklebacks because the posterior lateral plates can protect the stickleback from being injured and swallowed [29, 30]. Reimchen predicted that the completely plated morph would occur in open-water habitats of high clarity where capture rather than pursuit defenses predominate [30]. Consistent with this hypothesis, we have shown that the increase in the frequency of completely plated morphs occurred during the time when the water clarity increased dramatically in Lake Washington, a relatively deep and large lake (with a surface area of 8.76×10^7 m^2 and a maximum depth of 65.2 m). Further supporting the hypothesis that an increase in predation by cutthroat trout has contributed to the rapid evolution of Lake Washington stickleback, recent stickleback samples are larger than historical stickleback samples (Figure 1B and Table S4). Larger body size can protect against predation by gape-limited predators such as cutthroat trout [31, 32]. Although salinity and water temperature have also been proposed as factors contributing to lateral-plate evolution [33, 34], we can exclude a role for these abiotic factors in the evolution of Lake Washington sticklebacks (Supplemental Discussion).

Conclusions

We have reported a dramatic example of "reverse evolution" [9], in which there has been an increase in completely plated sticklebacks in a freshwater lake. Our data demonstrate that selection for the complete morph was particularly strong during the early 1970s, suggesting that the main increase in the frequency of completely plated fish might have occurred during a time period of less than a decade. Armor reduction has also been shown to occur within only a few decades after the introduction of marine sticklebacks into freshwater [35–37]. Thus, sticklebacks can respond to environmental changes by either an increase or a decrease in lateral plates within a few decades. Rapid phenotypic evolution in sticklebacks provides us with a great opportunity to further investigate the mechanisms by which animals can respond to rapidly changing environments [38].

The rapid evolution of armor plates in Lake Washington sticklebacks might have been enabled by the presence of standing genetic variation at the major plate locus [11]. Without standing variation, a sudden increase in predation might have led to population extinction before a new mutation appeared [6, 39]. Although an increase in gene flow was not the primary cause of armor evolution, gene flow from the marine population might have enabled rapid armor evolution by contributing to standing genetic variation within the lake [7, 40]. This work provides an example of a rapid phenotypic change that does not result from phenotypic plasticity, which has been proposed as a major mechanism of contemporary evolution [4, 8]. Thus, investigation of the genetic mechanisms that underlie adaptive phenotypes is essential

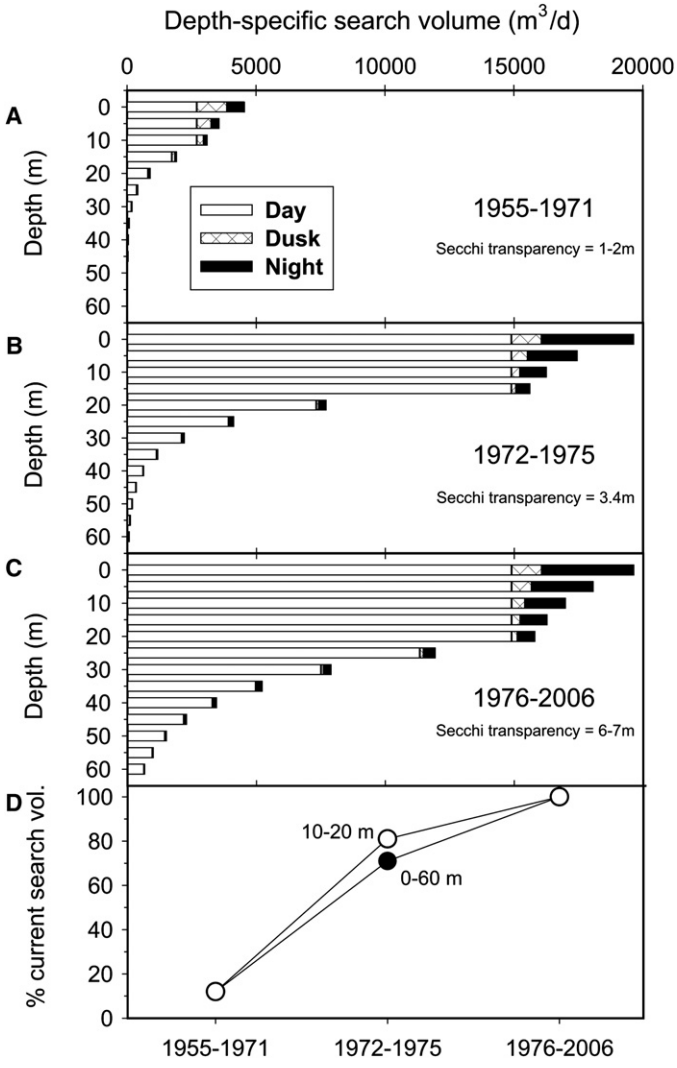

Figure 3. Changes in Cutthroat-Trout Foraging Volume in Lake Washington

(A–C) Depth-specific search volumes of cutthroat trout are shown during peak eutrophication, from 1955–1971 (A); during initial recovery, from 1972–1975 (B); and during the current transparency regime, from 1976–2006 (C). Different diel periods are indicated with white bars for day, hatched bars for dusk, and black bars for night.

(D) Changes in the search volume by trout are shown as the percentage of the current search volume. Black and white circles indicate the search volumes at the depths of 0–60 m and 10–20 m, respectively.

for a better understanding of rapid evolutionary change [2, 4, 8, 41].

Although we suggest that reverse evolution in the Lake Washington sticklebacks is probably attributable to the change in water clarity, we still lack direct evidence for this hypothesis, and additional factors might have also contributed. As in many other cases of rapid evolution [5], it is often difficult to tease apart all the potential factors that contribute to phenotypic evolution. We demonstrated, however, that changes in water clarity are able to influence predator-prey interactions; further attention should be given to the influence of water clarity on predator-prey interactions and animal evolution. In addition, this work highlights the importance of investigation of the relationships between environmental changes, species interactions, and the genetic basis of phenotypic evolution, both to better understand the mechanisms of animal evolution and to inform conservation efforts.

Supplemental Data

Detailed experimental procedures, a supplemental discussion, eight figures, and five tables are available with this paper online at http://www.current-biology.com/cgi/content/full/18/10/■■■/DC1/.

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