

The Case for Conserving Threespine Stickleback Populations: Protecting an Adaptive Radiation

ABSTRACT

The threespine stickleback (*Gasterosteus aculeatus*) comprises a complex of geographically differentiated populations, including some that are clearly separate biological species. The complex includes marine and anadromous forms thought to represent the phenotypes that have given rise post-glacially to widely distributed, differentiated, freshwater isolates. The relative uniformity of the marine and anadromous forms permits determination of the direction of evolutionary change in the freshwater radiation. A second feature that is exceptionally valuable for evolutionary inference is the repeated, independent evolution of similar phenotypes under similar ecological conditions. This property of the radiation facilitates evaluation of the causes of evolutionary diversification and speciation. We argue that the value of individual populations of this fish is elevated by their membership in the adaptive radiation, and that each population must be viewed as an integral part of this system, rather than just as a population whose properties are replicated in other lakes. This view requires special conservation status for the stickleback radiation as a whole, and we suggest procedures for protecting this adaptive radiation that we view as reasonable, given that we cannot hope to preserve every population in its pristine state.

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Introduction

The threespine stickleback (*Gasterosteus aculeatus*) is a small prey fish that provides an essential food resource for predatory fishes, and for migratory and resident piscivorous birds throughout its range (Reimchen 1994). The impact of predators is readily apparent in the heavy armoring of this stickleback in oceanic habitats, and in the frequency with which armor has been lost in freshwater habitats devoid of predatory fishes (Figure 1, Bell and Foster 1994a). The diversity of armor phenotypes is only one aspect of the variation that exists among freshwater populations (reviews in Bell and Foster 1994b)—variation that resulted in the naming of more than 40 species before most were synonymized, leaving the taxon to be treated as a single, extremely variable species (Wootton 1976).

Only recently has the true nature of variation in the threespine stickleback species complex been recognized. In a seminal paper, Hagen and McPhail (1970) described *G. aculeatus* as a complex of differentiated freshwater populations and species derived post-glacially from oceanic ancestors. Much of the variation in freshwater populations identified at that time and in the following three decades is

demonstrably adaptive and divergent from the oceanic phenotype (reviewed in Bell and Foster 1994a). This diversification is thus an adaptive radiation. The threespine stickleback species complex subsequently has become a model system for evolutionary study, whose importance is likely to increase due to current interest in the genetic architecture underlying features that vary across populations (Carroll et al. 2001; Peichel et al. 2001).

Our primary goals in this article are to describe the unusual features of the post-glacial threespine stickleback adaptive radiation and to make recommendations for the conservation of this species complex. The radiation is unusual in two important ways. First, freshwater isolates are thought to have evolved from a relatively uniform oceanic ancestor like that existing today. This ancestral type can thus be compared to derived freshwater populations to infer the direction of evolutionary change in the radiation. Second, freshwater populations have evolved similar, derived characteristics independently under similar environmental conditions. Thus, similar ecotypes have evolved independently, and repeatedly, from a relatively uniform ancestor.

The features of the threespine stickleback radiation that make it valuable for evolutionary study also present several unusual conservation challenges. Foremost among these is the fact that the value of individual populations of sticklebacks is elevated by their membership in the larger radiation. Although sticklebacks in different freshwater populations may be superficially similar, each may have arisen from the common oceanic ancestor through different genetic modifications, and even as a consequence of different evolutionary processes. Thus, all have the potential to offer unique insights into the evolutionary process



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The threespine stickleback (*Gasterosteus aculeatus*) provides an essential food resource for migratory and resident piscivorous birds.

when contrasted with oceanic ancestors and other derived freshwater isolates, and all merit protection. On the other hand, protection of all freshwater populations of threespine stickleback is clearly unrealistic. The challenge is then, to devise a strategy by which evolutionarily significant populations can be identified and protected.

Following a description of the threespine stickleback radiation, we present a four-point plan that represents an initial effort to develop sound conservation and management strategies that will protect critical elements of this radiation before they are imperiled. We challenge those responsible for managing aquatic habitats and fisheries resources to take a proactive approach to protecting this remarkable adaptive radiation. Only by doing so can we be assured that this unusually informative species complex will be available for study by future generations of scientists.

The threespine stickleback species complex

The threespine stickleback is a temperate to subarctic species complex made up of marine, anadromous, and resident freshwater populations. Marine and anadromous (hereafter, oceanic) populations vary little across their holarctic range (Figures 1

and 2, Baker 1994; Foster et al. 1998; Walker and Bell 2000). They are also essentially “living fossils” that have changed little morphologically over the last 10 million years (Bell 1988). Taken together, these features of oceanic threespine sticklebacks suggest relatively uniform characteristics of oceanic populations can be interpreted as the ancestral features that gave rise to the diversity of freshwater derivatives. We can thus infer the direction of evolutionary change in each case.

This evolutionarily static oceanic ancestor has given rise repeatedly to freshwater isolates that have undergone rapid diversification (Figure 1, Bell 1988, 2001; Bell and Foster 1994a). The most recent period of freshwater colonization and radiation began as glaciers started to recede 22,000 years ago (Figure 2, reviewed in Bell and Foster 1994a; Bell 2001). Although there certainly exist older freshwater populations in Quaternary refugia and parts of the range not subjected to glaciation, most extant freshwater populations are post-glacial (Bell and Foster 1994a; Ortí et al. 1994). Within this post-glacial radiation, similar, derived suites of characteristics (ecotypes) have evolved many times independently, under similar conditions. These ecotypes offer insight into the causes of adaptive divergence, and, because similar species pairs have also arisen in parallel, the radiation additionally

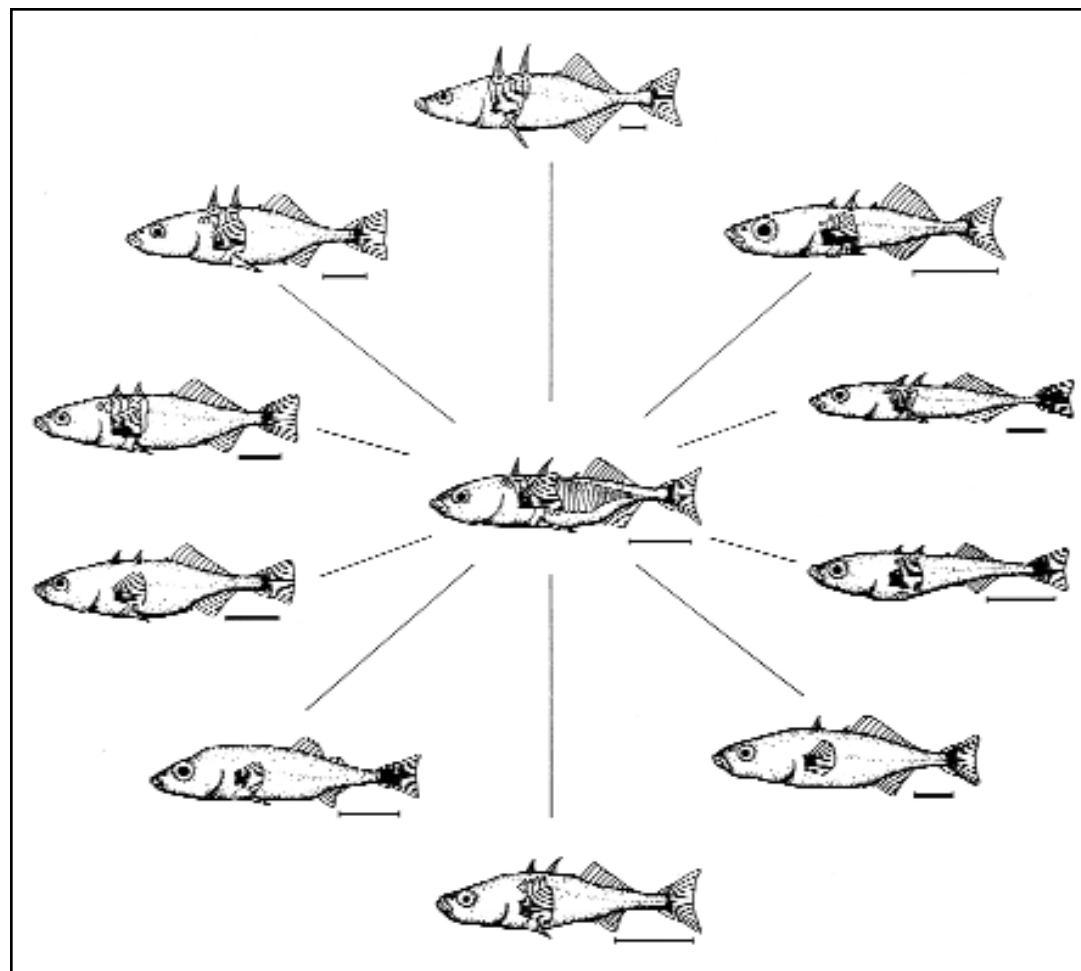


Figure 1. Variation in body form and external features among North American populations of *Gasterosteus aculeatus*. Peripheral forms are from freshwater populations. That in the center is the typical oceanic form. The scale bars are 1 cm. (Reprinted from Figure 1.2 in Bell and Foster 1994a with permission from Oxford University Press.)

offers a unique window into the speciation process (McPhail 1994; Foster et al. 1998; McKinnon and Rundle 2002).

Direction of evolutionary change and adaptive inference

Comparisons among populations of threespine stickleback demonstrate that a wide array of traits has differentiated alone, or in combination (Table 1). Rather than providing an exhaustive description, we offer two examples that illustrate the way in which the unusual features of this radiation can be used to understand evolutionary pattern and process. The first of these involves evolutionary reduction of antipredator armor, and the second, divergence of a suite of traits forming distinct ecotypes specialized for feeding in open water (limnetic ecotype) or in the shallow littoral zone of lakes (benthic ecotype).

Armor reduction

Oceanic threespine sticklebacks possess as many as 36 bony lateral plates on each side of the body (Figure 1, central image). The posterior plates typically are lost or reduced in freshwater (Figure 1, peripheral images), and significant loss can occur in as little as five generations following colonization of a new freshwater habitat by oceanic fish (Reimchen 1994; Bell 2001). In contrast,

the anterior plates are usually retained. These plates link two robust dorsal spines to a bilaterally symmetrical pelvic girdle that supports a pair of pelvic spines. These four spines lock in an erect position, increasing the difficulty of ingestion by predatory vertebrates (Reimchen 1994 for review).

Reduction and loss of the pelvic girdle are reported from lake populations in Scotland and North America (reviewed in Bell 1988; Bell et al. 1993). In the Cook Inlet region of Alaska, 40 populations with substantial pelvic reduction (>5%) were discovered (Bell and Ortí 1994). All are in lakes that lack native predatory fishes and that have low ionic strength water (Bell et al. 1993), suggesting that loss of the pelvic girdle can occur only under these circumstances. The majority of these populations are likely to have evolved pelvic reduction independently because they inhabit widely dispersed lakes lacking inlet or outlet streams (Bell et al. 1993). These data therefore offer compelling evidence of adaptive evolution.

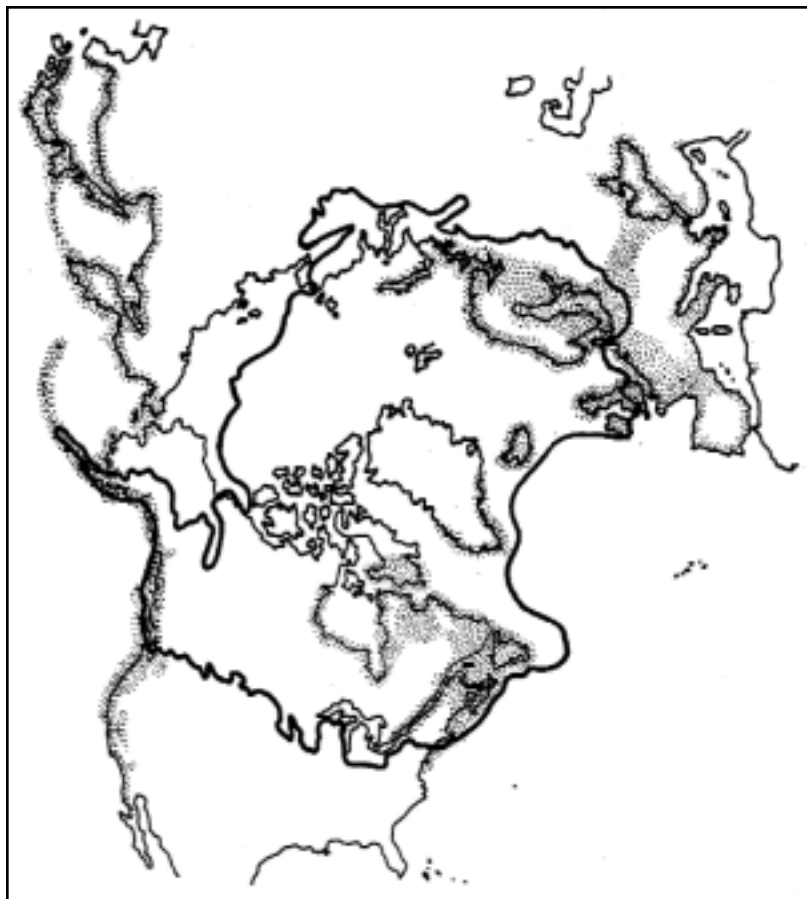
In this example, the direction of change is based on the robust construction of this feature in fossil and extant oceanic forms. Although this conclusion might have been reached without knowledge of the ancestral state (because repeated loss of a complex structure is much more likely than repeated acquisition), the inference is better supported with knowledge of the primitive condition. For attributes like color, behavior, and life history that may be equally likely to evolve in alternative directions, knowledge of the ancestral

character state is crucial for understanding the pattern of evolutionary change, and for testing evolutionary hypotheses (e.g., Bell and Foster 1994a; Foster et al. 1998).

Trophic ecotype divergence

In the Pacific northwest of North America, lacustrine populations of threespine stickleback inhabiting small, shallow lakes are specialized for feeding on benthic invertebrates (benthic ecotype), while those in deeper, more oligotrophic lakes are specialized for feeding on plankton in open water (limnetic ecotype, Figure 3, Lavin and McPhail 1985; Schluter and McPhail 1993; Walker 1997; Foster et al. 1998).

Figure 2. North polar projection of the world showing the distribution (stippled) of the *Gasterosteus aculeatus* complex. The heavy line is the approximate southern limit of continuous continental glaciation and permanent sea ice during the last glacial advance.





Photographer Alexandra Tzarougian at Cook Inlet, Alaska.

These ecotypes represent extremes of a continuum (Lavin and McPhail 1985), that are probably found throughout the range of the threespine stickleback (Hart and Gill 1994).

Molecular and geographic data indicate that these two ecotypes have evolved repeatedly and independently within regions and drainages (Thompson et al. 1997; Taylor and McPhail 2000; Cresko 2000). Both are found in lakes with and without predatory fishes, although the presence of predators promotes differentiation (Walker 1997). Behavior has diverged in concert with shifts in morphology and diet. Oceanic and benthic sticklebacks forage in large groups that destroy nests guarded by males, and cannibalize any young within them. In these populations males perform displays that divert the cannibalistic groups from nests, retain drab coloration during courtship, and perform much less conspicuous courtship than do those in limnetic populations (Foster 1994; 1995; Foster et al. 1998). These ecotypes clearly represent complexes of co-adapted traits that are favored by differences in local environments.

Speciation

Two distinct species of threespine stickleback co-occur at a number of sites scattered throughout the range of this fish (reviewed in McKinnon and Rundle 2002). These species pairs consist of differentiated forms that overlap during the breeding season in all or part of their ranges, yet mate assortatively. Six types of pairs have been identified, three of which have evolved repeatedly in parallel. These are (1) limnetic-benthic lacustrine pairs, (2) anadromous-freshwater pairs, and (3) lake-stream pairs (McPhail 1994; McKinnon and Rundle 2002). The benthic-limnetic pairs are the best studied.

Benthic-limnetic pairs of sticklebacks are restricted to the Strait of Georgia in southern British Columbia, Canada (McPhail 1994), and seem to have evolved only in lakes where the only other fish species is cut-throat trout (*Onchorynchus clarkii*; Vamosi, in press). The benthic member of each pair is thought to have arisen through independent, initial colonization of small, shallow lakes by oceanic sticklebacks as glaciers

receded. A subsequent, local geological disturbance then resulted in a second wave of colonization by oceanic sticklebacks, which gave rise to the limnetic form (McPhail 1994; Taylor and McPhail 2000). Additional divergence occurred subsequently through the processes of character displacement and reinforcement (Schluter and McPhail 1992; Schluter, D. and McPhail, J. D. 1993; Rundle et al. 2000). This process was repeated four times, once on Vancouver Island (the Enos Lake pair), twice on Texada Island (Paxton Lake pair, and the pair found in three lakes in the Vananda drainage), and once on Lasqueti Island (Hadley Lake pair).

An unusual property of this system for the study of speciation is that benthic and limnetic sticklebacks exist in allopatry, and as species pairs. Unique insights into ecological speciation are possible because we can compare character evolution in replicated types (including rare within-population polymorphisms; Cresko and Baker 1996) to ascertain, for example, characteristics of oceanic and benthic types at the time of secondary contact and the nature of subsequent divergence (Foster et al. 1998). Parallel exploration of the causes of divergence in the other types of replicated species pairs should offer insights like those that have made the benthic-limnetic species pairs models for the study of ecological speciation (McKinnon and Rundle 2002). Clearly, the species pairs and their allopatric counterparts are unique and valuable resources that merit protection.

Threats to the stickleback radiation

The threats potentially facing threespine stickleback populations inhabiting small lakes and streams include nearly all of the factors presently known to alter the structure or functioning of aquatic ecosystems: sedimentation, reduction of water quality or quantity, eutrophication, and the introduction of competitors or predators. These ecosystem changes are often traced indirectly to human activities such as logging, water withdrawal, and urbanization (Walker et al. 1993; Paterson et al. 1998; Nicholls et al. 2000.). Although the demise of a particular population is difficult to attribute unambiguously

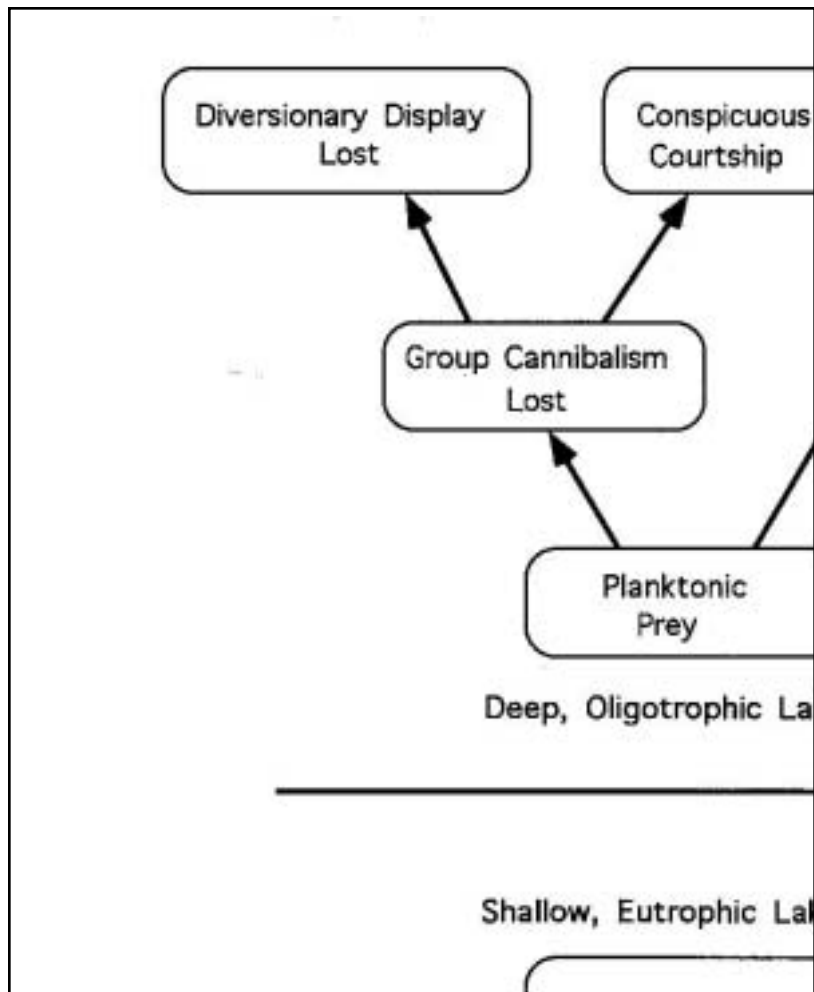
Table 1. Phenotypic traits known to vary across populations or species within the threespine stickleback complex.

Morphology
Armor structures
Body form
Trophic structures
Life history
Adult size
Age at first reproduction
Egg size
Clutch size
Allometric relationships of reproductive traits with body size
Behavior
Courtship
Nest site selection
Male parental care
Foraging
Anti-predator
Schooling
Coloration
Male nuptial/aggressive signal
Female reproductive receptivity signal
Crypsis
Melanism
Host-parasite relationship
Variable reduction of egg size
Infection avoidance/resistance?
Reproduction when infected

endangered species feature

to any of these causes, there is reason to be concerned about all of these factors in loss of unusual stickleback populations, as we describe below. The situation already is critical for the benthic-limnetic stickleback pairs. Sticklebacks are extinct in Hadley Lake following an introduction of the brown bullhead (*Ameiurus nebulosus*, Hatfield 2001a). This nocturnal predator has caused the extinction of other stickleback populations, apparently by consuming young in nests guarded by males (McPhail 1989). In Enos Lake, sticklebacks are still present, but as a single intermediate type (Kraak et al. 2001; D. Schluter, University of British Columbia, Canada, pers. comm.). The cause of this change is unknown, but it was coincident with the introduction of the signal crayfish (*Pacifastacus leniusculus*; D. Schluter pers. comm.) and with increased land development and associated turbidity (Kraak et al. 2001; Wood, this issue). Finally, the Vananda pair of sticklebacks is now threatened by forest harvesting, an activity that would likely increase turbidity in lakes that already have been substantially altered by human activity (Hatfield 2001b; Wood, this issue). This leaves only the Paxton pair free from immediate threat, though its vulnerability is highlighted by the listing of the remaining pairs in Canada as “endangered” and globally as “critically imperiled” (Wood, this issue).

Figure 3. Evolutionary consequences of planktivory (limnetic form) and benthic feeding (benthic form). Both morphology and behavior display ecotypic variation.



Freshwater populations at the southern edges of the species range seem to be particularly imperiled. The danger signs first appeared many years ago. In southern California, USA, the “unarmored threespine stickleback” *G. a. williamsoni* was once abundant and widespread in coastal streams around Los Angeles, but now is represented only by relict populations that are threatened by urbanization and introduction of exotic species (Ono and Williams 1983). Populations have also declined or become extinct in some European sites where they once were common, a problem that is particularly acute in Spain (Lelek 1987). They also have nearly disappeared from the Dutch sites that supplied specimens for classical ethological experiments (J. van Alphen, Leiden University, The Netherlands, pers. comm.).

Nowhere is the problem more serious than on Honshu Island, Japan (S. Mori, Gifu-Keizai University, Japan, pers. comm.), again at the southern limit of the species range. Here, the first report of a threatened population (Mie Prefecture Fisheries Station) was published by Ikeda in 1933, and the population became extinct in the 1950s. Fish subsequently were transplanted to this site from a drainage in the Gifu Prefecture, one of only two Japanese drainages that are home to low plated threespine sticklebacks. In this region, threespine sticklebacks are restricted to relatively cool, spring-fed water bodies that are vulnerable in the face of development. Many habitats originally occupied by sticklebacks have disappeared, or decreased substantially in size as a consequence of diversion and water table change. The causes of loss echo those in Southern California, and are problems only likely to increase as development encroaches upon the native habitats of this fish, and as water temperature increases with global warming. Indeed, as development and global warming continue, we can expect these problems to impact populations farther north as well.

In Japan, anadromous sticklebacks have also been negatively affected by construction of river mouth blockades, declines in flow, and water quality deterioration (S. Mori, pers. comm.). In combination, these human modifications have resulted in dramatically decreased breeding populations. We consider it likely that anadromous sticklebacks have been similarly affected in other regions where dams have been built and river mouths modified, but that the declines have not been reported. Such declines could have negative impacts on predatory fish and birds that depend upon stickleback as seasonal prey.

A final example from relatively pristine habitat in Alaska illustrates the subtlety of threats. In this region non-native salmonids are routinely stocked to enhance sport fishing. Recently, concern over the spread of non-native stocks has halted stocking in some lakes, or shifted stocking to more expensive triploid fish. Lakes without surface inlets or outlets continue to be stocked because risk of salmonid migration to other lakes is low. Unfortunately, these lakes

contain stickleback populations that can be most vulnerable to the introduction of predators, because such lakes do not support salmonid populations. These are the populations likely to have the most strongly reduced anti-predator armor.

We have followed nine such populations since 1990, and all have exhibited dramatic fluctuations in size (Elsemore 2000, unpublished). One is now extinct and two others may be. Five similar populations not subject to stocking are stable. Three of the pelvic-reduced populations have evolved in response to stocking. Their mean pelvic expression has increased significantly, with one approaching fixation of the full pelvic girdle. In another, the first complete pelvic girdle has just been detected. The remaining populations are devoid of functional pelvic girdles and have therefore not responded evolutionarily, or they have become extinct (Elsemore 2000, unpublished data). The evolutionary response to introductions is disturbing because, although sticklebacks still are present, they are losing their unique character, and we are losing the ability to study these unusual and important populations. A similar evolutionary response to trout introductions was observed in British Columbia (Hagen and Gilbertson 1973). In this instance however, the number of lateral plates increased. Although such rapid change in the character of these populations might seem surprising, we now have ample evidence of rapid microevolutionary change in this taxon (Bell 2001). Typically caused by human activity, alterations such as these change the fundamental nature of the affected populations, resulting in the loss of their unique characters.

There can be little question that introductions of non-native predators are among the greatest threats to populations of stickleback. In addition to the examples above, introduction of the pumpkinseed sunfish (*Lepomis gibbosus*, Kynard 1979) and of the signal crayfish (Foster, pers. observ.) have been associated with drastic population declines. The non-indigenous pike (*Esox lucius*) is spreading quickly in south central Alaska (see www.state.ak.us/adfg/adfghome.htm), and has been implicated in the loss of at least one population (unpublished data). Although these predators pose a threat to stickleback populations, so can the use of ichthyocides to eradicate them. Although British Columbia and Alaska have halted the use of ichthyocides to remove sticklebacks from lakes before stocking, these products can still be used to eliminate unwanted introductions, along with all remaining native fish.

In summary, we consider many unique and poorly characterized populations to be under threat now, and we expect that with future introductions of non-native species, continuing water table declines, watershed modification, and global warming, the threat will only increase.

Conservation Recommendations

Although there can be little question that the lacustrine species pairs of threespine stickleback merit special status for conservation due to small population size, restricted range, and resultant vulnerability (McPhail 1989, 1994; Hatfield 2001a,b; Hatfield and Ptolemy 2001; Wood, this issue), conservation of the radiation as a whole requires that allopatric populations within the complex be identified for special protection as well. Population units given high priority for conservation are termed evolutionarily significant units (ESUs; Ryder 1986), and are identified on the basis of ecological or genetic distinctiveness (Crandall et al. 2000).

A recent suggestion for diagnosing ESUs that encompasses most concerns is one in which populations are evaluated from the perspective of ecological or genetic exchangeability (Crandall et al. 2000). The concept of ecological exchangeability is that populations capable of occupying the same ecological niches or exposed to similar selective regimes are not sufficiently distinctive to merit special management concern. There can be little question that many ecotypically similar populations would be considered to have similar fundamental adaptations and to serve similar ecological functions. Theoretically, using the ecological exchangeability criterion alone, a single population of an ecotype would not be eligible for protection, except that single, isolated populations are so vulnerable to extinction through habitat alteration.

Incorporation of the genetic exchangeability criterion alters this interpretation. Populations are considered genetically exchangeable if gene flow is high ($Nm > 1$, where Nm is the effective number of migrants per generation). Grounds for rejection of genetic exchangeability include the presence of unique alleles in individual populations and phylogenetic divergence that is concordant with geographic barriers (Crandall et al. 2000). The distribution of allele frequencies of six microsatellite loci among nine populations in the Cook Inlet region of Alaska, revealed evidence of significant gene flow between the two anadromous populations only. Nm values did not differ significantly from one for any pair of the seven lacustrine populations (Cresko 2000). This contrast included three morphologically benthic populations and three that were morphologically limnetic, supporting



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Preserving (above) and shipping stickleback collections (below).



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the geographical and historical evidence that ecotypically similar populations often have independent origins from oceanic ancestors. The same results have been obtained for anadromous and freshwater stickleback populations in southern British Columbia (Taylor and McPhail 2000, and references therein), indicating the generality of this process.

These data suggest that even ecotypically similar freshwater populations must be considered candidates for special management because they are likely to have evolved phenotypic similarities independently in the time since colonization. Genetic diversity is very high in anadromous populations, indicating that future evolutionary potential (Moritz 1994) can be maintained by conserving marine and anadromous populations. The alleles that are present in freshwater populations seem to be subsets of those in ancestral populations, presumably because some genetic diversity was lost when they were founded, and there has been so little time for the appearance of new mutations (Taylor and McPhail 2000; Cresko 2000). Although the alleles present in freshwater populations are primarily subsets of those in oceanic populations, ecotypically similar freshwater populations probably have reached similar phenotypic solutions to similar local ecological conditions via different genetic pathways, and are therefore worth conserving as independently evolved, genetically unique members of this radiation.

The general procedure we propose to safeguard the threespine stickleback radiation parallels that used by many governmental agencies to protect species that are endangered, threatened, or otherwise of special concern. An example is the U.S. Endangered Species Act of 1973, which laid out guidelines to define the status of a species or population, delineate and protect critical habitat, and so forth. The procedure requires the development of four features (Table 2). We briefly elaborate on these features below.

Minimally, in order to protect the stickleback radiation, a list of the populations known to possess

unusual features, or to be specially related to populations that possess such features, must be assembled and maintained. This list would provide notice to potential developers that alteration of the land around a listed population, or of its aquatic habitat, must be shown unlikely to affect the demography of a population or its phenotypic composition. A wide variety of development activities could cause such ecological changes, such as withdrawal or discharge of water, land development (e.g., timber harvest, road building, agriculture, housing), or any activities that could cause introduction of exotic species, including species in adjacent bodies of water. Many stickleback populations will not possess attributes that would initially place them into a protected category. Thus, it is in the interests of both biologists and potential developers that the list has information on all known stickleback populations, not just those of special concern. The minimal list (Feature 2, below) thus becomes a more complete compendium (Feature 1).

Virtually every jurisdictional entity has a list of biotic constituents (species, habitats, etc.) of special concern. Feature 2 would be such a list, comprising available information on all threespine stickleback populations that are in any way unusual, unique, rare, or otherwise special. The list would provide all available information on each population, and it would highlight its particular attribute of interest. Included in this list should be information on whether the population represents the last known example of some attribute or phenomenon. For example, there should be a means of classifying populations and increasing the level of protection afforded members of a rare class when the class is depleted. The last benthic-limnetic pairs, for example, should receive special consideration as the others are gone. Authority for the special recognition would be provided, along with specification of publications relevant to the classification.

A formal, scientifically sound procedure (Feature 4) is required for assessing the salient biological features of any “new” population (one for which no, or insufficient information is available within the compendium). In most cases this procedure will be used in situations in which a population is potentially threatened by development. Nevertheless, it may also be used as a guide by biologists pursuing evolutionary or ecological studies. Finally, we propose that a framework be designed in order to permit potential developers to rapidly determine the status of any particular stickleback population of interest to them (Feature 4). Numerous formal procedures have been developed to guide governmental and consulting biologists in making assessments for specific purposes (e.g., the Index of Biotic Integrity [IBI], Angermeier and Schlosser 1987). The framework would be designed for use by trained biologists, but would not necessarily require the services of a stickleback specialist. In principle, the thrust would be similar to that of the general procedures (above) for making ecosys-

Table 2. Major features of a conservation plan to preserve the value of the threespine stickleback complex as a resource for studying evolution.

<p>Feature 1: Compendium of information</p> <ul style="list-style-type: none"> • Compilation of current information into a centralized data base • Regular updating of the data base by the addition of data on “new” populations, and addition of previously lacking information on listed populations <p>Feature 2: Classification of populations and environments</p> <ul style="list-style-type: none"> • Designation of populations under immediate threat • Designation of populations of particular interest • Identification of environments likely to harbor particularly unusual populations <p>Feature 3: Development of a “rapid-action” practical protocol</p> <ul style="list-style-type: none"> • Specification of methods for quickly characterizing key attributes of “new” stickleback populations to determine their value to the complex • Identification of methods for preliminarily assessing threats to individual stickleback populations <p>Feature 4: Development of “in-depth” protocols</p> <ul style="list-style-type: none"> • Used for detailed assessment of the biology and population phenomena of specific populations whose environments are presently threatened, or whose environments may be threatened by proposed or ongoing development • May also be used as a methodological guide for pure science using stickleback

tem- or assemblage-level assessments, but would include such features as morphology, male courtship behavior, and female reproductive traits important to a population-level assessment. Such a framework would provide not only the attributes that should be assessed, but also outline methods for making accurate assessments. Of course, all such newly gained data would become part of the growing compendium.

Conclusions

The threespine stickleback species complex affords us the opportunity to take a proactive, rather than a reactive, approach to conservation of an adaptive radiation that has the potential to contribute uniquely to our understanding of an array of phenomena including microevolution, speciation, and developmental genetics. Although some populations are presently threatened, and many have been lost, the majority inhabit relatively pristine sites that can be protected. However, most of these populations are poorly, or not at all characterized. We believe that a systematic effort to catalog population properties to determine which

are of particular value, in combination with policy changes aimed at protecting such populations, is the only means by which the critical elements of this remarkable adaptive radiation will be saved for future study.

We end by noting that phenotypic diversification like that observed in threespine sticklebacks is known in other northern fishes (Bell and Andrews 1997), such as Arctic charr (*Salvelinus alpinus*), sockeye salmon (*Oncorhynchus nerka*), lake whitefish (*Coregonus clupeaformis*), smelt (*Osmerus mordax*), and lampreys (*Lampetra* species). Although the threespine stickleback radiation has some important advantages over these for the study of evolutionary processes, these other divergent taxa are equally deserving of protection for their unique attributes. Lessons learned from protecting the stickleback radiation may well be valuable in protecting these, and as yet undiscovered radiations. We urge those responsible for managing and protecting our aquatic resources to implement the procedures we suggest, not only with the goal of protecting stickleback populations, but also to identify and protect unusual populations of other taxa that may be threatened by human activity. ■

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John Baker observes courtship in a typical stickleback breeding habitat.

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