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First Documented Case of Anadromy in a Population of Introduced Rainbow Trout in Patagonia, Argentina: Response to Comment

Before we respond to the Comment by R. J. Behnke regarding our article on the first documented case of anadromous *Oncorhynchus mykiss* in Patagonia (Pascual et al. 2001), we were requested by the Editors to address an issue discussed by one of the reviewers of this exchange. The reviewer noted that the existence of anadromy in Santa Cruz River rainbow trout was not demonstrated in our paper, but rather assumed, based on the analogy of scale patterns with those described for anadromous salmonids elsewhere.

In our article, we considered scale pattern analysis as supporting evidence for anadromy. The spatial and seasonal occurrence of catches of distinctively large fish observed year after year in the Santa Cruz River is consistent with that expected for an anadromous run. These fish are not found in the basin during late spring or most of the summer and appear in locations near the river mouth in late summer with typical steelhead oceanic coloration. Their abundance at these locations peaks in early fall, and catches cease after late fall. These fish are much larger than the fish that are caught in the river year round (Pascual et al. 2001; Figure 3).

New information has been collected since we published our article that provides even stronger evidence for the existence of the anadromous run and substantiates our proposed life cycle. This information is part of a manuscript submitted for publication and as a doctoral thesis in progress (C. Riva Rossi, unpublished). The principal findings are as follows: (1) Rainbow trout caught at several sites throughout the basin, including lake-dwelling populations of the upper basin, are all significantly smaller in size than those assigned to the anadromous type and have distinctive scale patterns. (2) Tracking of five fish that were radio-tagged during river entrance in early fall allowed us to characterize the in-river migration. All five fish remained in the main stem of the river, without visiting upper-basin locations and had left the river by early December. (3) The radio-tracking experiment pointed us to probable spawning grounds. Although we failed to visually detect spawning beds, gill-net sampling at one particular site (Estancia Nueva Lubeck, river km 320 [from the mouth of the river]) in the spring of 2000 and 2001 yielded mature fish that, based on size and scale patterns, can be clearly assigned to three alterna-

tive types: stream resident fish, lake resident fish, and ocean-migrating fish. This last group comprised distinctively larger fish, with sizes and scale patterns matching those of fish regularly caught at the river mouth during river entrance. (4) We received numerous reports of large salmonids being caught by sport fishermen along the Patagonian Atlantic coast as well as by coastal commercial fishing boats. We obtained samples of three of these fish captured as far north as 1,000 km from the Santa Cruz River estuary. The three fish were rainbow trout with sizes and scale patterns matching those of Santa Cruz River anadromous fish.

Behnke's Comment deals with two general subjects: the origin of the Santa Cruz River fish and the interpretation of genetic results as pertains to the relationship between anadromous and resident fish. We thank him for providing further details on the potential origins of the Patagonian populations of rainbow trout. Fish introductions in Argentina began in 1904, over a decade after the Baird Station on the McCloud River had closed, so rainbow trout eggs could not have come directly from this station. Baird Station, however, was a major source of rainbow trout used to found stocks at federal hatcheries around the United States based on an egg collection program led by the U.S. Fisheries Commission (Wales 1939; Dollar and Katz 1964; Busack and Gall 1980; Nielsen et al 1997). This total effort led many authors to believe that the Baird Station was the most likely ultimate source of introduced rainbow trout around the world (Scott et al. 1978) and led us to take it as the most likely source for Santa Cruz River fish. Nevertheless, we kindly take into consideration Behnke's observation that the parental stock could as well have included fish from southern Oregon and northern California, which at different times contributed to the establishment of hatchery stocks.

Although domestic records of rainbow trout propagation in Argentina are limited, the destination of the earliest shipments could be readily reconstructed, especially because only three federal hatcheries operated at that time (Tulian 1908; Marini and Mastrarrigo 1963). For example, the shipment made in 1908 mentioned by Behnke, which contained 300,000 fish labeled as ''steelhead,'' was destined for La Cumbre Hatchery in Cordoba province (Tulian 1908). One other shipment of fish labeled as ''steelhead'' arrived in Argentina in 1904 and was destined for the Nahuel Huapi Hatchery at Bariloche in Rio Negro province. These eggs can be considered ''lost'' because of high egg mortality. These two ''steelhead'' shipments never contributed fish to the Santa Cruz River, which is remote and was extremely inaccessible at the time. The Santa Cruz River has had a history of salmonid transplants largely independent from and less active than that experienced by less isolated northern locations, hence our interest in using it as a model for studying salmonid microevolution.

At this time, we can put forward three major statements regarding the origin of Santa Cruz River fish as it concerns the founding of novel anadromous populations: (1) As mentioned in our original paper and confirmed by Behnke, a mix of anadromous and resident fish probably constituted the parental stock of Santa Cruz River fish in particular and for Argentine fish in general, originating most likely in the Sacramento River and its tributaries or in other rivers of northern California and southern Oregon. (2) Whatever the exact origin, the same stocks were planted elsewhere in Argentina and around the world but led to documented anadromous populations only in the Santa Cruz River, which was the main interest and motivation for our research. (3) Like most transplants of salmonids in the early part of the 20th century, details of source populations for Patagonian *O. mykiss* may never be known from remaining records alone, much less which sources actually contributed to population establishment. Unless we unearth some unknown document about early fish transactions between the northern hemisphere and Patagonia, the written record will most probably prove inadequate to establish the exact origin of the Santa Cruz River fish. Molecular genetic analysis, though certainly limited, provides an indirect tool to explore sources and evolutionary history of Patagonian *O. mykiss.* These techniques have been used to investigate origins and early evolutionary history of introduced salmonids (e.g., Hendry et al. 1996; Quinn et al. 1996; Burger et al.; 2000) and other species (e.g., Argentine ants: Tsutsui et al. 2001; round gobies: Dillon and Stepien 2001).

This last point leads us to the second set of observations raised by Behnke, which concerns the power and interpretation of genetic analyses. Although evaluating the genetic and environmental bases of anadromy is at the core of our research program, the analyses presented in our paper were not intended as a tool to identify the genetic determinants of anadromy. We used population genetics of presumed neutral loci with a more modest objective in mind, which was to evaluate the existence of significant gene flow between life his-

tory forms and to search for indications of a common origin.

When we started this research project we did not know if anadromy of Santa Cruz River rainbow trout was a strategy that the fish had evolved independently after being introduced in the river or if it had resulted from a contemporary colonization of the river by anadromous fish. Given that the development of Chile's extensive net-pen aquaculture started in the early 1980s, concurrently with first catch records of anadromous fish in the Santa Cruz River, we considered this last scenario to be likely. We now believe that our results provide strong support for the first scenario.

We must note that we never claimed that anadromous and resident Santa Cruz River fish were not reproductively isolated. In fact, we clearly acknowledged in the discussion that one of the critical aspects that we did not know was to what extent the two forms were segregated. We only indicated that the two forms appear to share common ancestry, appear to exchange migrants, and may arise within a single nominative population. This population may undergo a substantial amount of assortative mating, or structuring in other ways, leading to partial isolation of the migratory forms. Indeed, in cases where resident and anadromous forms are genetically determined and exchange migrants, it is somewhat moot to argue whether one is dealing with alternate life histories within a single population or two sympatric populations with significant gene flow. The alternatives are just ''two sides of the same coin.''

Behnke's comment also suggests that because we refer to ''life history forms'' we attribute no genetic basis to the migratory forms. In truth we make no statement either way, only that the anadromous and resident forms do not appear to constitute strongly isolated populations. The tendency for residency or anadromy is likely to depend on both environmental and genetic determinants (Nordeng 1983; Thorpe 1989; Gross 1996; Parker et al. 2001) and no significant reason exists why a genetic basis for the trait would preclude both forms from existing within a common population. Claims that gene flow between forms would lead to hybrid swarms, panmixia, and loss of one of the life history forms are probably oversimplified characterizations of gene flow and its interaction with selection and the inheritance of anadromy. Resolving whether one of the life history forms ultimately predominates, whether both coexist as alternatives within a common population, or whether greater apparent isolation develops between the forms remains an intriguing prospect for future investigation in Patagonia. This uncertainty has potential significance for insights into the maintenance of sympatric anadromous and nonanadromous forms in the natural range of the species.

Our conclusions were supported by our results, and we stated them conservatively in light of the amount of data and our knowledge of the history of these fish. Our genetic results must of course be interpreted from the perspective of population genetics of presumed neutral loci. We used microsatellite variation in our study primarily to inform us about likely genetic affinities and found that the resident and anadromous forms in the Santa Cruz River are similar enough to suggest that they probably arose from a common source of introduction. Secondarily, we suggest that substantial genetic interchange probably still occurs between the forms in the Santa Cruz River, perhaps on the scale seen in many North American populations. Whether one considers such differentiation evidence of one population with partly isolated genetic life history types or two populations with extensive gene flow is largely semantic under the prevailing conditions. Management efforts should aim to preserve both types regardless of definition

The strong evidence for active gene flow between types was crucial in our present view of Santa Cruz River fish and how we recommend managers to proceed. Our results show that steelhead cannot be managed as a single, separate population and that it is imperative to look at Santa Cruz River rainbow trout as a whole. As a result, our current research concentrates heavily on characterizing the population structure of Santa Cruz River rainbow trout through a variety of techniques, including genetics, radio tracking, field sampling, and otolith chemistry (Zimmerman and Reeves 2000, cited by Behnke). Besides allowing us to go further into the problem of investigating the origin of the andromous behavior, these studies will provide us with crucial insight about what the management units should be.

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