genetic discontinuity may provide evidence of discreteness.

The commenters also stressed that the ESA's definition of "species" focuses solely on reproductive exchange. Section 3(16) of the ESA defines the term species as including any "distinct population segment of any species of vertebrate fish or wildlife which *interbreeds when mature*"; emphasis added). The commenters argued that the additional considerations provided in the DPS policy (including marked separation as a consequence of physical, physiological, ecological, and behavioral factors) are supplemental to the primary consideration of reproductive isolation required under the ESA.

Response: The ESA requirement that a group of organisms must interbreed when mature to qualify as a DPS is a necessary but not exclusive condition. Under the definition, although all organisms that belong to a DPS must interbreed when mature (at least on some time scale), not all organisms that share some reproductive exchange with members of the DPS must be included in the DPS. The DPS policy outlines other relevant considerations for determining whether a particular group should be delineated as a DPS (*i.e.*, "marked separation" as a consequence of physical, physiological, ecological or behavioral factors).

Although the DPS and ESU policies are consistent, they will not necessarily result in the same delineation of DPSs under the ESA. The statutory term "distinct population segment" is not used in the scientific literature and does not have a commonly understood meaning. NMFS' ESU policy and the joint DPS policy apply somewhat different criteria, with the result that their application may lead to different outcomes in some cases. The ESU policy relies on "substantial reproductive isolation" to delineate a group of organisms, and emphasizes the consideration of genetic and other relevant information in evaluating the level of reproductive exchange among potential ESU components. The DPS policy does not rely on reproductive isolation to determine "discreteness," but on the marked separation of population groups as a consequence of biological factors.

Despite the apparent reproductive exchange between resident and anadromous *O. mykiss*, the two life forms remain markedly separated physically, physiologically, ecologically, and behaviorally. Steelhead differ from resident rainbow trout physically in adult size and fecundity, physiologically by undergoing smoltification, ecologically in their preferred prey and principal predators, and behaviorally in their migratory strategy. Where the two life forms co-occur, adult steelhead typically range in size from 40–72 cm in length and 2–5 kg body mass, while adult rainbow trout typically range in size from 25–46 cm in length and 0.5–2 kg body mass (Shapovalov and Taft, 1954; Wydoski and Whitney, 1979; Jones, 1984). Steelhead females produce approximately 2,500 to 10,000 eggs, and rainbow trout fecundity ranges from 700 to 4,000 eggs per female (Shapovalov and Taft, 1954; Buckley, 1967; Moyle, 1976; McGregor, 1986; Pauley *et al.*, 1986), with steelhead eggs being approximately twice the diameter of rainbow trout eggs or larger (Scott and Crossman, 1973; Wang, 1986; Tyler *et al.*, 1996). Steelhead undergo a complex physiological change that enables them to make the transition from freshwater to saltwater (smoltification), while rainbow trout reside in freshwater throughout their entire life cycle. While juvenile and adult steelhead prey on euphausiid crustaceans, squid, herring, and other small fishes available in the marine environment, the diet of adult rainbow trout is primarily aquatic and terrestrial insects and their larvae, mollusks, amphipod crustaceans, fish eggs, and minnows (LeBrasseur, 1966; Scott and Crossman, 1973; Wydoski and Whitney, 1979). These differences in diet are a function of migratory behavior and the prey communities available to resident and anadromous *O. mykiss* in their respective environments. Finally, steelhead migrate several to hundreds of miles from their natal streams to the ocean, and spend up to 3 years in the ocean migrating thousands of miles before returning to freshwater to spawn (Busby *et al.*, 1996). Some fluvial populations of rainbow trout may exhibit seasonal migrations of tens of kilometers outside of their natal watersheds, but rainbow trout generally remain associated with their natal drainages (Meka *et al.*, 1999). Given the marked separation between the anadromous and resident life-history forms in physical, physiological, ecological, and behavioral factors, we conclude that the anadromous steelhead populations are discrete from the resident rainbow trout populations within the ranges of the DPSs under consideration.

Comment 5: Several commenters were critical of the evidence we provided that co-occurring resident and anadromous *O. mykiss* are markedly separate ("discrete"). Commenters felt that we exaggerated and oversimplified the differences between anadromous and resident *O. mykiss*, and that much of the evidence presented in support of their "marked separation" is not illustrative of traits unique to a given life-history form. The commenters felt that the majority of the phenotypic differences cited are inconsistent, overlap considerably between the two life forms, and are predominantly caused by environmental factors.

Several commenters were critical of the physical factors we cited as evidence of marked separation between the two life forms. The commenters documented overlap in the size and fecundity ranges of resident and anadromous *O. mykiss* in the same watersheds, and concluded that our assertion that steelhead are generally larger and more fecund than rainbow trout does not hold true. The commenters felt that fish size and fecundity are largely a function of food supply, rather than being a trait inherent to anadromy. The commenters cited examples where, provided sufficient food resources, rainbow trout achieve similar sizes and fecundity as steelhead.

Commenters were critical of the ecological factors we cited. The commenters felt that it is inappropriate to distinguish between the two forms on the basis of diet, as it is a function of prey availability in different environments rather than reflecting intrinsic differences in prey preference. They noted that when steelhead and rainbow trout are in the same freshwater environment, individuals of similar size and life-history stage have similar prey preferences.

Commenters were critical of the behavioral factors we cited. The commenters argued that the two life forms are not "markedly separated" in terms of migratory behavior. The commenters cited several scientific studies documenting migratory behavior in non-anadromous *O. mykiss* including: movement within a river system (potadromy); movement from lakes into rivers for spawning (limnodromy); and movement to the estuary/lagoon for growth and maturation (partial anadromy). Although commenters generally acknowledge that only the anadromous form migrates to the open ocean, they contended that this does not represent a truly discrete difference. The commenters described the life history of the *O. mykiss* species as a continuum of migratory behaviors, with anadromous and resident fish representing points on this continuum.

Commenters were also critical of the physiological factors we cited. Commenters argued that resident and