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Colonization and Persistence of a Southern California Steelhead (*Oncorhynchus mykiss*) Population

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Abstract.—The life history and habitat interactions of southern *Oncorhynchus mykiss* populations have received less attention than their Pacific Northwest counterparts. In this article we create a conceptual model describing the factors affecting *O. mykiss* population dynamics in Topanga Creek, Los Angeles County, California to understand the process that led to extirpation following floods in 1980 and 1983, re-colonization in the late 1990's, and continued persistence. We conclude that key factors influencing population dynamics include life-history variability with both resident and anadromous individuals, population spatial structure connecting Topanga Creek with other watersheds within the metapopulation, exclusive distribution within the mainstem Topanga Creek, high-quality summer and winter rearing habit, and food availability sufficient to maintain growth at high temperatures. Protecting the population in Topanga Creek from future extirpation should include restoration of the lagoon, and preventing changes to the flow regime and water quality.

Introduction

Anadromous steelhead and resident rainbow trout in Topanga Creek belong to the federally endangered Southern California Steelhead Evolutionarily Significant Unit (now Distinct Population Segment [DPS]), as modified in July 2002. *O. mykiss* within Topanga Creek and other watersheds within the DPS are considered as part of the same metapopulation (group of sub-populations with genetic exchange). Steelhead is the term used to denote the anadromous life-history form of rainbow trout (*Oncorhynchus mykiss*). Because both anadromous and resident *O. mykiss* are found within the watershed, the term *O. mykiss* is used in situations where distinguishing juvenile steelhead from resident rainbow trout would be problematic. Preservation of both life-history forms is considered a high priority in the *Southern Steelhead Recovery Plan* (National Marine Fisheries Service 2009). *O. mykiss* stocks throughout California and in southern California in particular have substantially declined; only an estimated 500 adult steelhead remain in the Southern California DPS (National Marine Fisheries Service 2009). This DPS is considered at high risk for extinction as a result of an extirpation from much of their historical range (Boughton et al. 2005, Boughton et al. 2006); resulting in increased susceptibility to loss of genetic diversity and poor population growth rates (McElhany et al 2000).

The role of colonization and intermittent access of anadromous adults is paramount to moderating unnatural alteration of population spatial structure and mitigating the related risk of regional extinctions (Boughton et al. 2006), but is rarely documented. Challenges to colonization of new or historical habitat in southern California include highly variable flow regimes, high water temperatures, and frequent isolation from the Pacific Ocean by sandbars that develop at the mouths of most coastal streams. Few aquatic species are adapted to surviving in such conditions. *O. mykiss*, however, is a highly plastic species in terms of phenotypic and life-history variability, capable of exploiting habitats that would not sustain populations of other salmonids. Despite the contraction of southern California steelhead from their historical range, we believe that a sub-population in Topanga Creek, California has been re-established (i.e., re-colonized) within the last 20 years. Topanga Creek drains a 47 km^2 watershed within Los Angeles County and adjacent to the city of Los Angeles. Research has been ongoing for nearly a decade within a study reach that extends from the ocean upstream to the northern boundary of Topanga State Park at river kilometer (rkm) 6, which is just below the village of Topanga. Our objectives were to synthesize nine years of research on *O. mykiss* in Topanga Creek (Dagit and Reagan 2006; Dagit et al. 2007; Dagit et al. 2009; Stillwater Sciences et al. 2010) to create a conceptual model to describe the factors that resulted in extirpation, supported re-colonization, the habitat interactions affecting their current population dynamics, and management implication for protecting the sub-population from another extirpation event.

Conceptual Model

Life history

The relationships between fish exhibiting resident and anadromous life history strategies in the Topanga Creek watershed are central features of an *O. mykiss* conceptual model that could apply to many southern California coastal streams. The primary factors influencing the expression of an anadromous life history in Topanga Creek are the frequency and duration of upstream migration opportunities, which are limited by lagoon sandbar formation and other obstacles, such as a seasonally dry reach from rkm 0.5 to 1.5 and additional low-flow barriers. Adult steelhead can only enter Topanga Creek on one of the relatively rare days each year that stream flows are high enough to erode the sand bar and allow passage between the ocean and lagoon. Under current conditions resident *O. mykiss* continue to spawn and maintain a sub-population despite the absence of production from anadromous individuals. However, it is the anadromous component of the metapopulation with adults that migrate among sub-populations, and the production of anadromous smolts, which allows salmonids to persist in an environment that experiences catastrophic disturbance (Reeves et al. 1995). After *O. mykiss* were extirpated from Topanga Creek in the 1980's it was the eventual migration of adult anadromous steelhead that provided for re-colonization. The current population is now occasionally influenced by the migration of anadromous adults either from Topanga Creek, or other sub-populations (Table 1).

Colonization

Until 1980, a sub-population of *O. mykiss* was known to be present in Topanga Creek (Moyle et al. 1989; Swift et al. 1993; Dagit et al. 2005). During a February 1980 storm event 65 cm of precipitation was recorded within a week, with a peak on 16 February of 27 cm within 24 hours. The accompanying flood was estimated to be an 83-year event,

Table 1. Observations of *O. mykiss* and number of days each year that steelhead passage into Topanga Creek may be possible, 2001–2010. Anadromous adults defined as greater than 450 mm FL with silver color.

Year	Mean number observed per month (all size classes)	Numbers observed per month (range)	Smolts	Anadromous adults	Redds	Annual total rainfall (cm)	Potential passage opportunity (days)
2001	53	2–122	0	1	0	70.6	10
2002	95	8–156	0	2	0	18.4	1–2
2003	59	6–72	14	1	0	45.5	10–15
2004	103	46–209	0	0	0	33.4	<10
2005	71	49–80	0	0	0	156.4	>200
2006	75	48–409	9	1	3	53.8	<20
2007	86	30–166	0	2	0	71.2	approx. 54
2008	316	40–691	1	1	0	33.5	approx. 72
2009	207	117–323	1	0	0	42.6	approx. 50
2010	253	117–420	28	1	4	61.7	approx. 50[b]

with flows recorded over 13,000 cfs before the gage was destroyed. Massive damage resulted to the creek channel, banks, and roads along the mainstem of Topanga Creek (York 1992). Other potentially catastrophic floods took place in 1983 and 1994 (Dagit and Webb 2002). A few *O. mykiss* were reported in pools upstream of the lagoon in 1990 (Keegan 1990) but an electrofishing survey conducted by the California Department of Fish and Game in 1997 failed to observe *O. mykiss*, and it was assumed that the sub-population was extirpated (Dagit et al 2005). The extirpation of the Topanga Creek sub-population is consistent with the range contraction observed throughout the DPS, where Boughton et al. (2005) have documented that only between 58% and 65% of historic steelhead basins currently harbor *O. mykiss* populations.

During an exstensvie survey in July 1998, a single 10-cm *O. mykiss* was found in Topanga Creek. In 2000, three anadromous adult *O. mykiss* were observed, and it appeared that the habitat within Topanga Creek was in the process of being re-colonized (Dagit et al 2005). Numbers of *O. mykiss* in Topanga Creek have since increased, and monthly snorkel surveys conducted since June 2001 indicate that the sub-population is currently fairly consistent, averaging between 53–316 individuals observed per year (Table 1).

The results of a genetic analysis conducted on Topanga Creek *O. mykiss* indicate that the sub-population has very low genetic variability (Girman and Garza 2006, Stillwater Sciences et al. 2010) compared to *O. mykiss* from 60 coastal sub-populations in California (Garza et al. 2004), Topanga Creek fish exhibited about half the allelic diversity and 80% of heterozygosity. This is likely the result of founder effects; i.e., very small numbers of fish contributed to the ancestry of the Topanga Creek sub-population as a result of the recent colonization.

Subsequent to the re-colonization events the genetic composition shows a variable contribution of anadromous adults. For example, a decrease in the portion of the sub-population exhibiting hatchery ancestry between 2003 and 2006 is likely the result of a particularly wet winter and spring in 2005, when adult *O. mykiss* (of wild origins) had more opportunity to enter Topanga Creek. However, the number of tissue samples collected and analyzed between 2003 and 2008 was small, and random chance may have skewed the results, or these results may reflect random variation due to the reproductive success of a few resident *O. mykiss* during this period. Straying of adult steelhead appears to be common in southern California streams (Clemento et al. 2009; Pearse et al. 2009; Garza et al., unpubl. data, National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, California), which plays an important role in population spatial structure and genetic diversity, both which support population viability (McElhaney et al. 2000).

Factors affecting population dynamics of O. mykiss

A species' life history and the habitat available to it are among the many factors that can influence a population's ability to persist, grow, or decline. In addition, the factors affecting success vary between life-history strategies that are employed. For the anadromous portion of the population, migration opportunity, growth rate, size at ocean entry, ocean survival, and spawning success influence the dynamics of the Topanga Creek *O. mykiss* sub-population. For resident fish that produce offspring that may or may not emigrate to sea, freshwater habitat availability and predation are the main factors influencing the population. In any given year, habitat conditions may favor the relative success of one *O. mykiss* life-history type over another.

Distribution

Topanga Creek has no tributaries, and all life stages are confined to the main stem. Although in many watersheds a proportion of the *O. mykiss* will use tributaries for spawning and rearing, both Spina et al. (2005) and Boughton et al. (2009) report that, in other southern California coastal streams, summer rearing typically occurs in mainstem reaches, even if the fish spawn in tributaries. The implication for Topanga Canyon is that any disturbance to the watershed can potentially affect all life stages of the sub-population. For example, whereas the ability of salmonids to survive large floods has been documented (e.g., Bell et al. 2001), during the catastrophic 1980 and 1983 floods every individual of the *O. mykiss* sub-population would have been in the mainstem (with the exception of sub-adults or adults in the marine environment), and thus susceptible to the impacts of the floods. If Topanga Creek had tributaries that supported rearing habitat, increasing spatial distribution of individuals throughout the watershed, it would take a much more severe disturbance to eliminate the sub-population (Reeves et al. 1995).

A key component of a functioning viable salmonid metapopulation is population spatial structure (McElhaney et al. 2000). Within a functioning and viable metapopulation, when a disturbance eliminates the individuals within one sub-population, anadromous individuals from the other watersheds eventually migrate to, and re-colonize, that habitat. We believe the catastrophic disturbances such as what occurred in the 1980's in Topanga Creek are a natural occurrence (Reeves et al. 1995), and it is the spatial structure (i.e., connectedness through migration) of various watersheds in southern California that allowed the sub-population in Topanga Creek to recover, and for the DPS metapopulation to be viable over time (McElhaney et al. 2000).

Spawning

The assumption used in our general conceptual model for steelhead (and other anadromous salmonid populations) is that population growth tends to be limited by rearing habitat because the number of eggs that can be deposited in a reach (and thus the number of fry produced by spawners) is usually very high relative to the amount of

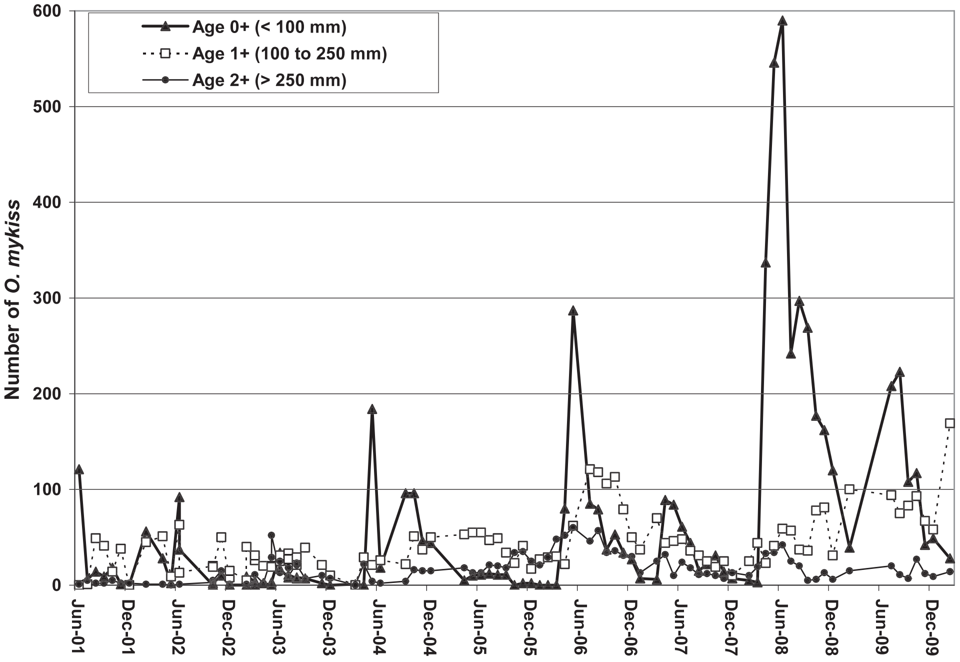

Fig. 1. Total number of *O. mykiss* observed in monthly snorkel surveys in Topanga Creek, June 2001–February 2009, by age class. Aging based on Stillwater Sciences et al 2010.

rearing habitat available as fish grow. However, in Topanga Creek, fry production does not appear sufficient to seed available rearing habitat. Because adult steelhead fecundity (usually >3,000 eggs per female) is much greater than that of resident female *O. mykiss* (usually <1,000 eggs [Moyle 2002]), population dynamics are potentially very different in years when anadromous individuals spawn versus years in which only resident *O. mykiss* spawn. Steelhead do not spawn every year in Topanga Creek. Fry production in years when adult steelhead can enter and spawn in Topanga Creek may be far greater than in years when only resident fish spawn. This phenomenon may be one reason that production of age 0 appears to fluctuate dramatically between years (Figure 1) as compared with populations in streams where anadromous individuals spawn every year.

Spawning habitat in Topanga Creek appears more than sufficient to support the relatively low numbers of resident and anadromous adults in the sub-population. Spawning gravels in Topanga Creek appear well-sorted, with embeddedness measurements generally ranging between 25 and 50%. Snorkel surveys have documented fewer than 600 age 0 in all years (Figure 1), indicating that egg-to-emergence or fry survival may be low. Observations of relatively low ratios of age 0 to age 1 juveniles (Stillwater Sciences et al. 2010) suggest that reproductive success is limiting production—even if only one or two *O. mykiss* redds were successful, age 0 fish should outnumber age 1 fish to a much greater degree than observed. Based on current spawning habitat quantity and quality, we believe that the low abundance of age 0 fish is more likely due to the fact that anadromous adults only infrequently spawn in Topanga Creek. Two other possibilities for low numbers of age 0 fish are (1) snorkel surveys are not very effective for observing this age class, and (2) age 0 fish experience high mortality rates due to occasional high spring flows (Fausch et al. 2001) or predation, as discussed below.

Access to spawning habitat

Low flows in Topanga Creek can significantly limit spawning by adult steelhead. During periods of lower flows, sediment collects at the mouth of Topanga Creek, which, paired with the action of waves, forms a sand bar that prevents steelhead access to the creek. Passage of steelhead is only possible when flows are high enough to break through the sand bar, allowing fish to migrate upstream and potentially spawn (Table 1). The lagoon channel upstream is constricted by the Pacific Coast Highway Bridge structure, which may also impede upstream passage at high flows due to high water velocity and lack of slackwater resting habitat at this location. The amount of water diverted from Topanga Creek is minimal, but seasonal low flows can also periodically restrict further upstream movement at some locations, particularly in a low-gradient reach between rkm 0.5 and 1.5 where flows are only present from the beginning of the fall rainy season until early spring. A restoration of this reach was initiated in 2008, and passage restriction in this reach is much improved under most flow conditions. Because of the above factors, passage opportunities into the upper reaches of Topanga Creek can range from fewer than 10 days in a year to more than 200 (Table 1). Presumably the timing and duration of passage opportunities during the 1980's and 1990's also limited the ability for anadromous individuals to migrate to habitat in Topanga Creek.

In 2005 more than 150 cm of rain was reported and there were at least 200 days when adult steelhead could migrate upstream into Topanga Creek. As would be expected, young-of-the-year fish were extremely abundant the following spring. Similarly, in 2007 there was relatively high rainfall and ample opportunity for passage, and the abundance of young-of-the year reported in 2008 was the highest recorded. By way of contrast, prior to 2004 upstream passage was possible fewer than 10 days each year, and the lowest numbers of age 0 were reported (Figure 1). Production in these years was presumably almost entirely (and perhaps exclusively) the product of spawning by resident fish.

Summer habitat

Summer rearing habitat has been posited to limit *O. mykiss* smolt production in some California coastal streams where a lack of habitat complexity, low pool volumes, low food availability, and excessive water temperatures may all act to reduce rearing success (e.g., Harvey et al. 2006; Stillwater Sciences 2007a). Topanga Creek appears to contain high-quality summer rearing habitat, with high pool frequency, abundant food, and ample cover supplied by interstitial spaces between cobbles and boulders in the substrate. Because food and space requirements increase as fish grow, a reach of stream will typically support far fewer age 1 than age 0 *O. mykiss* during the summer. In Topanga Creek, older age classes tend to be found in deep pools with abundant cover provided by wood or large substrate, and younger age classes in shallower step-pools and riffles (Stillwater Sciences et al. 2010). If *O. mykiss* abundance was limited by summer rearing habitat, we would expect to see higher numbers of all age classes in spring than in fall, but fall snorkel counts of age 0 fish are typically similar, if not higher, than spring counts (Figure 1), although this may be partly due to the difficulty of observing younger age classes using snorkel survey methods. In Topanga Creek it appears that shallow, structurally complex habitat is more than adequate to support numbers of age 0 fish in the summer, and sufficient deeper pool habitat is also available for over summering age 1 juveniles.

Winter habitat

In contrast to observations in many central California watersheds (Stillwater Sciences 2004, 2006, 2007b, 2009), winter habitat in Topanga Creek does not appear to limit *O. mykiss* production. As in the summer, a reach of stream in winter will typically support far fewer age 1 than age 0 *O. mykiss*. Overwintering juvenile *O. mykiss* may suffer high mortality when they are displaced by high flows, which are common in the inherently flashy Topanga Creek, where winter flows can range from a few cfs to over 10,000 cfs. Refuge from high flows requires the availability of cover similar to that used at lower flows for concealment, predator avoidance, and territorial boundaries, but access deeper into the stream bed may be necessary for avoiding displacement by turbulence near and even below the surface layer of the substrate (the potential effects of embeddedness on this are discussed later). Similar to many other southern California watersheds supporting *O. mykiss*, Topanga Creek is generally high gradient ($>3\%$), with a channel tightly confined between valley walls and few or no off-channel water bodies such as sloughs and backwaters. In general, *O. mykiss* show less propensity than other salmonid species (such as coho salmon) for using off-channel, slackwater habitats in winter, and a greater propensity for using in-channel cover provided by cobble and boulder substrates, which are common in Topanga Creek and usually immobile at all but the highest flows.

Within our conceptual model, watersheds where there are increased inputs of coarse and fine sediment to the stream channel and decreased input of large wood (often as a result of anthropogenic disturbance), there is a reduction in summer and winter carrying capacity for age 0 and age 1 *O. mykiss*. Pool frequency is reduced with the removal of large woody debris, especially in forced pool-riffle and plane-bed stream reaches (Montgomery and Buffington 1997, Harrison and Keller 2007). High gradient, confined creek channels supporting little large woody debris, such as that found in Topanga Creek are typically characterized by forced pool-riffle sequences (step pools) resulting from boulder cascade constraints. The remaining pools may become shallower as a result of aggradation and the lack of scour-forcing features such as large woody debris, and cover may also be reduced. The filling of interstitial spaces within cobble/boulder substrates by gravel and sand can also reduce summer and winter carrying capacity for both age 0 and age 1 *O. mykiss*. As a result, in many watersheds the availability of winter rearing habitat limits *O. mykiss* production. However, sediment supply to Topanga Creek is currently limited to low levels of road shoulder dry-ravel, localized eroding slope input, and infrequent natural events, and the transport capacity of the channel appears adequate to move that sediment through the system. As a result, embeddedness is generally low and interstitial spaces within cobble/boulder substrates are abundant.

Data from snorkel surveys prior to and following high winter flows indicate that abundance of juveniles and adults generally does not decline as a response to high flows (Figure 2). Under current conditions it does not appear that winter habitat is limiting the Topanga Creek *O. mykiss* sub-population from persisting. However, clearly the extreme flood events of the 1980's were of sufficient magnitude to lead the extirpation of nearly all individuals from the watershed.

Water temperature and growth

Despite relatively high summer and fall water temperatures, *O. mykiss* in Topanga Creek appear to grow quickly, rapidly attaining a size favorable for smolt survival or for resident fish to reach sexual maturity. Growth only occurs when energy input is greater

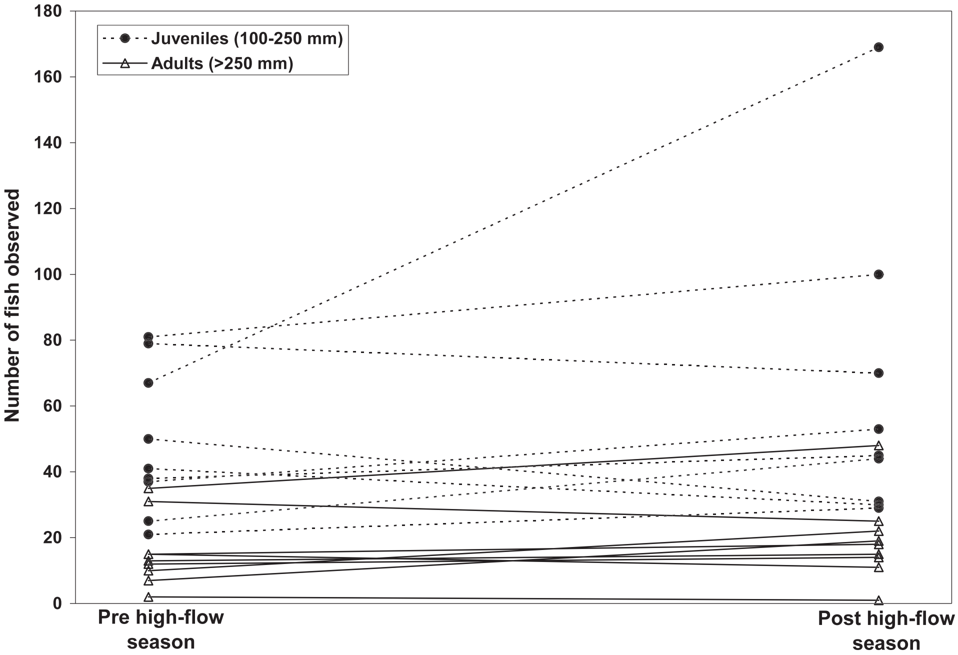

Fig. 2. Snorkel observations from pre- and post-high-flows for juvenile (100–250 mm) and adult (>250 mm) *O. mykiss*. Each line represents a separate year of observation from 2001–2009. Month of observation varies based on occurrence of peak flow event.

than energy expenditure, both of which can be affected by food availability and other environmental factors, especially water temperature (Jobling 1994).

Numerous studies have examined the relationships between water temperature and growth in *O. mykiss*. Results regarding optimal water temperatures for growth, and temperatures that may be detrimental due to increased metabolic demands, vary between study populations. Water temperatures in Topanga Creek are generally within the optimal range for *O. mykiss* growth in the spring and fall (Figure 3); however, daily maximum water temperatures over much of the summer regularly exceed species preferences and reported tolerances (>24°C) in all years monitored. It has been shown that lethal temperatures for *O. mykiss* are higher when fish have previously acclimated to high (but sublethal) temperatures (Cherry et al. 1977; Threader and Houston 1983). Further, Spina (2007) hypothesized that *O. mykiss* in Topanga Creek and other southern California streams tolerate higher water temperatures and have a higher temperature range for optimal growth than more northern populations.

O. mykiss in the southern part of their range appear able to sustain high growth rates when water temperatures are at the upper end of those considered optimal for growth, as long as food availability is high (Boughton et al. 2007). In Topanga Creek, *O. mykiss* appear to grow year-round, with potentially higher growth rates possible in spring and summer, and lower growth rates in winter (Stillwater Sciences et al. 2010). The size-at-age distribution of fish observed in Topanga Creek is consistent with the size of *O. mykiss* in comparable streams (Table 2), indicating that food availability is sufficient to counteract negative effects of increased temperatures on growth.

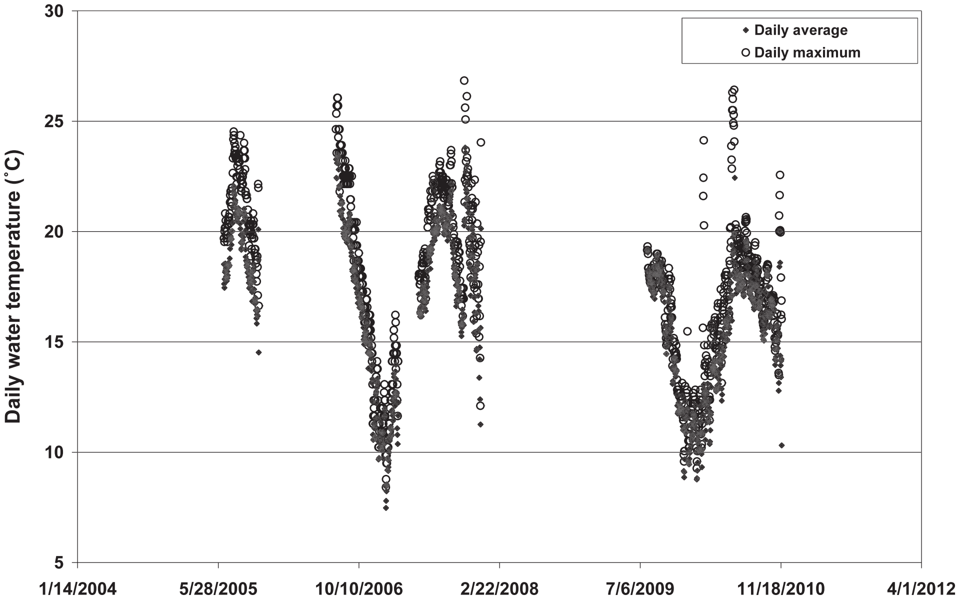

Fig. 3. Average (mean) and maximum daily water temperatures in Topanga Creek, 2005–2010.

Food availability

The ability of *O. mykiss* in Topanga Creek to grow quickly and reach large size (>250 mm) raises questions about how these fish meet their bioenergetic demands. Once salmonids reach a size of about 270–300 mm, they tend to become piscivorous regardless of habitat type, and a piscivorous or even cannibalistic diet may be necessary to maintain growth beyond this size (Bannon and Ringler 1986; Huryn 1996; Keeley and Grant 2001). Although piscivory in lake-dwelling trout populations is common, stream-dwelling resident *O. mykiss* most often feed on invertebrates and evidence of piscivory or cannibalism is rarely observed (Frost 1939; Jonsson and Sandlund 1979; Haraldstad et al. 1987, all as cited in Vik et al. 2001). Certain conditions, however, may facilitate the adoption of a piscivorous diet. For example, rainbow trout are known to prey on sockeye and chum salmon fry or smolts where such prey are concentrated, such as in small coastal streams or the outlets of lakes (McCart 1967; Hartman et al. 1967; Ginetz and Larkin 1976; Ruggerone and Rogers 1984; Fresh and Schroder 1987).

Table 2. Size of *O. mykiss* in Topanga Creek and other coastal southern California streams.

		Fork Length (mm)		
Stream	Sampling period	Mean	Range	Age class
Topanga Creek (this study)	November 2008–2009	102 (n=89)	55–125	0
		153 (n=79)	110–226	1
		222 (n=19)	170–291	2
Ventura River (Capelli 1997)	April 1995	250 (n=47)	190–395	unknown
Santa Paula Creek	November 2007 (electrofishing)	98 (n=173)	68–214	all ages

With only minor exceptions, forage fish available to adult resident *O. mykiss* in Topanga Creek are either smaller *O. mykiss* or arroyo chub (*Gila orcutti*). As mentioned above, very low numbers of age 0 trout have been observed in Topanga Creek during most years when snorkel surveys have been conducted (Figure 1). Even if only one or two redds were successful, observations of age 0 trout would be expected to be much higher than has been observed in all years, especially in years when spawning of anadromous *O. mykiss* occurs. It may be that snorkel surveys are inadequate for observing age 0 *O. mykiss*; however, their low abundance may also reflect heavy predation by resident adult *O. mykiss*. If this hypothesis is correct, the abundance of the *O. mykiss* sub-population in Topanga Creek may be limited by such predation.

Vik et al. (2001) found that cannibalism controlled brown trout mortality in a regulated stream and cites Amundsen (1994) as showing that even low rates of cannibalism (in this case, by Arctic char) may have substantial effects on recruitment. In Vik et al.'s (2001) study, cannibalism appeared to be facilitated in streams with adequate pool habitat for large individuals, but where refuge habitat for small trout was limited. Streams having coarse substrate and relatively low discharge, such as Topanga Creek, tend to exhibit these characteristics (Heggenes 1988, as cited in Vik et al. 2001). If such cannibalism is occurring in Topanga Creek, we would expect resident *O. mykiss* abundance to be limited by adult habitat (as described below) only in years when numbers of adults exceed the carrying capacity of available habitat. In addition, based on apparently very high winter and summer habitat availability in Topanga Creek, we might expect that the portion of the adult population expressing an anadromous life history could be limited by cannibalism of fry by adult resident fish, particularly if adult resident trout exhibit a functional response to the concentration of prey afforded by seasonal spawning and emergence of large numbers of *O. mykiss* fry.

Observations of arroyo chub in Topanga Creek show them to be consistently abundant, likely a result of their ability to breed almost continuously from February through August (Moyle 2002). Arroyo chub range in size from 3 to 150 mm, with approximately 10 to 50 individuals observed in nearly every pool. The high standing crop of arroyo chub suggests that either (1) predation pressure on chub is low, or (2) predation rates are high but the chub population remains high due to high rates of production. Although trout predation on arroyo chub has not been previously documented, examination of stomach contents in November 2010 revealed a mostly whole approximately 70 mm chub in the stomach of a 173 mm *O. mykiss* indicating that they may represent a potential food source for *O. mykiss* in Topanga Creek (R. Dagit, unpublished data).

Another potential food source for adult trout in Topanga Creek is the non-native red swamp crayfish (*Procambarus clarkii*). Although they had only a limited presence in Topanga Creek as recently as 2004, they are now widespread throughout the creek. Crayfish have been documented to reduce the complexity of food webs in stream ecosystems by consuming and consolidating energy from a wide variety of prey (Momot 1995). However, for the same reason, crayfish also represent high-calorie prey commonly consumed by trout (Momot 1967), and were found in three resident *O. mykiss* stomachs that were sampled in 2009 (Stillwater Sciences et al. 2010) and were also observed in two adults sampled in 2010 (R. Dagit, unpublished data). The presence of this additional high-calorie food supply in Topanga Creek could reduce cannibalism. Investigation of the diet of *O. mykiss* in Topanga Creek using gastric lavage began in November 2010 to further assess food availability and bioenergetics.

Smolt size and marine survival

The rate of growth of *O. mykiss* in fresh water has a direct effect on whether fish follow an anadromous or resident life history, as well as the ability to reach a size where they are large enough to smolt and survive in the marine environment (Satterthwaite et al. 2009). In addition, the ability of a sub-population to produce anadromous smolts is a key aspect of population spatial structure that can help increase population viability (McElhaney et al. 2000). For example, anadromous smolts may migrate to other watersheds within the metapopulation thereby increasing genetic exchange, or rear in the ocean prior to returning to spawn, thus avoiding potential disturbance events in the freshwater environment. *O. mykiss* juvenile growth rates in Topanga Creek appear sufficient to promote high ocean survival of smolts emigrating from Topanga Creek. The size of *O. mykiss* smolts has been positively correlated with marine survival, with smolts greater than 170 mm typically experiencing high survival (>10%) (Ward et al. 1989). Similarly, Bond et al. (2008) found that most adult steelhead returning to Scott Creek (central California coast) had entered the ocean as juveniles with an average fork length of just over 180 mm.

The size of smolts observed in Topanga Creek appears consistent with those observed in other southern California streams (Table 2). For example, in the Santa Clara River, most smolts measured at the Freeman Diversion Dam in 2009 were larger than 150 mm FL, averaging 185 mm FL (Steve Howard, Fisheries Biologist, United Water Conservation District, pers. comm., 2010). Kelley (2008) observed that most smolts in the Santa Clara and Santa Ynez estuaries were greater than 170 mm FL. Juvenile *O. mykiss* observed in the Ventura River during spring 1995 were all greater than 190 mm FL, and nearly all were age 2 when captured (n= 52) (Capelli 1997). Most of these fish were more than 3.2 km from the ocean, and it is not known what proportion were smolt, juvenile, or resident *O. mykiss*. Although other watersheds along the central coast of California report high growth rates of *O. mykiss* in lagoons prior to ocean entry (Smith 1990; Bond et al. 2008), poor habitat conditions in the Topanga lagoon may not be conducive to fish using this life-history strategy. Although juvenile steelhead may also remain and grow in the lagoon before entering the sea—we have rarely observed any *O. mykiss* in Topanga Lagoon. In early March 2010, we observed 28 juvenile *O. mykiss* in the Topanga lagoon but they disappeared within 24 hours following a high tide and good passage opportunity to the ocean (R. Dagit, unpublished data).

Data on the size of smolts emigrating from Topanga Creek is available from trapping conducted on an opportunistic basis, which suggests that many of the smolts are emigrating at fork lengths greater than 170 mm (Bell et al. *in press*). In addition, the trap is located at rkm 1.3, and our monitoring of PIT-tagged fish (in which there were multiple detections over several days), suggest that they migrate downstream very slowly, meaning that fish measured as smaller than 170 mm when captured in the trap may grow even larger before entering the ocean (Stillwater Sciences et al. 2010). For example, during the February 2010 snorkel survey, six smolts were observed in Topanga Creek downstream of the trap nearly a month after being observed at the trap. In other survey years, nearly all fish observed at the traps after February were larger than 170 mm, suggesting that smolts continue to grow during spring and likely enter the ocean at larger sizes than we observed at the trap in January.

Adult habitat limitations

As discussed above, resident *O. mykiss* occur in Topanga Creek. Resident *O. mykiss* are well adapted to surviving in small watersheds with high temperatures and variable flows by being highly territorial (Moyle 2002), growing at relatively fast rates (e.g., Hayes et al. 2008), reaching maturity as young as age 1 and as small as 130 mm (Moyle 2002), and by spawning multiple times. Adult habitat for resident salmonids is typically saturated if recruitment rates, even if very low, are sufficient to maintain the population (Elliot and Hurley 1998; Morita and Yokota 2002). Therefore, in most trout populations we usually assume that the resident population is limited by adult habitat; however, it is not clear that adult habitat is limiting the resident trout abundance in Topanga Creek. The most effective test to determine whether adult habitat is limiting is to increase the amount of habitat preferred by adults and observe any subsequent population response, which is often challenging, if not impossible. High flows in Topanga Creek in 2005 effectively eliminated low-flow migration barriers and adult trout were observed as far upstream as rkm 5.3 for the first time since 2000, increasing potential *O. mykiss* habitat by 900 m. The adult (age 2) population appeared to increase in that and subsequent years (Figure 1), suggesting that adult habitat had been limiting before. The apparent dramatic variability in numbers of adult trout in Topanga Creek may indicate that (1) habitat at an earlier life stage is limiting, as discussed above, (2) habitat availability changes as flows fluctuate among seasons and years, or (3) it could simply be an artifact of the challenges involved in observing *O. mykiss* during daytime snorkel surveys.

Summary

Based on nine years of data we have developed a general conceptual model for *O. mykiss* in Topanga Creek. Based on a relatively small abundance of smolts observed, the Topanga Creek sub-population is most likely an example of a "satellite" population (McElhaney et al. 2000). As a satellite population, it receives production from other sub-populations, but contributes little production to the metapopulation. Although satellite populations are more prone to extinction (as demonstrated by the temporary extirpation in the 1980's), they also buffer the metapopulation from disturbance events, can serve to increase metapopulation viability, and may become a source population in the future.

In general, the sub-population seems to be persisting since being re-colonized in the late 1990's, despite high summer water temperatures and poor habitat conditions in the lagoon. Migration from anadromous individuals in the metapopulation provided for re-colonization, and continues to influence the dynamic of the sub-population. Key factors believed responsible for supporting persistence of the sub-population are that fish can employ both resident and anadromous life histories, high-quality summer and winter rearing habitat, and food availability sufficient to maintain growth at high water temperatures. Additional data could be used to test and refine this model, focusing in particular on diet and use of the lagoon. We believe that the relatively high-quality rearing habitat in Topanga Creek should continue to be protected, especially from changes to the flow regime and increased sediment input, to guard against future extirpation. This is especially important since *O. mykiss* in Topanga Creek are exclusively distributed within the mainstem. The Topanga Creek Watershed and Lagoon Restoration Feasibility Study (Dagit and Webb 2002) outlined a series of potential actions to improve the condition of the lagoon, and prioritized the removal of the instream barrier presented by the Rodeo Grounds Berm, and streambank stabilization and channel restoration in the Narrows reach located at rkm 2–2.2. The passage problems presented by the combined constraints of the lagoon and berm were also identified as the keystone barrier for steelhead in Topanga Creek (CalTrout 2006). The Rodeo Grounds berm was removed in 2008 and passage, spawning and rearing habitat in this 1.3 km reach are much improved. The restoration of the lagoon is being considered within the revision of the Topanga Creek State Park General Plan, and the Narrows project is awaiting additional Caltrans funding. Implementation of this trio of projects would improve passage and habitat conditions throughout the entire anadromous reach to support population spatial structure.

In addition, other watersheds within the DPS that do not currently support *O. mykiss* should be recognized for their potential contribution to the metapopulation. As was demonstrated in Topanga Creek, if habitat within watersheds such as Solstice, Arroyo Sequit, Trancas, Zuma, and Ballona creeks is restored they could once again support sub-populations and increase the viability of the metapopulation.

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