

Spatial patterning of habitat for *Oncorhynchus mykiss* in a system of intermittent and perennial streams

Boughton DA, Fish H, Pope J, Holt G. Spatial patterning of habitat for *Oncorhynchus mykiss* in a system of intermittent and perennial streams. Ecology of Freshwater Fish 2009: 18: 92–105. No claim to original US government works. Journal compilation © 2008 Blackwell Munksgaard

Abstract – The salmonid *Oncorhynchus mykiss* tends to inhabit forested or snow-fed streams having cold reliable flows, but in the California chaparral they inhabit rain-fed stream networks with extensive areas of intermittent flow. We hypothesised that hydrological mechanisms in such watersheds tend to spatially segregate spawning and over-summering habitats, and tested the hypothesis using observations from a series of tributaries in a pristine watershed. Consistent with the hypothesis, reaches with suitably sized spawning gravels tended to occur in intermittent tributaries, and also the perennial mainstem (which was too warm for over-summering). In early summer, juvenile *O. mykiss* (<10 cm) occurred at similar densities in the intermittent and perennial tributaries, but larger fish had greater densities in perennial tributaries. Large wood debris would be expected to mitigate the spatial segregation of habitats somewhat, but was scarce, though stream-side outcrops appeared to partially compensate by forcing gravel bars in high-gradient channels.

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Key words: steelhead trout; self-fining; Mediterranean climate; California

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Accepted for publication July 4, 2008

Introduction

Intermittent streams are decidedly common, and pose obvious problems for stream-dwelling fish: Intermittency entails a seasonal shrinkage of habitats that can concentrate fish into high densities, where they are vulnerable to physiological stress, predation, and high levels of competition, and the drying of reaches restricts mobility as well as killing fish outright (Gasith & Resh 1999; Magalhaes et al. 2002; Magoulick & Kobza 2003; Matthews & Marsh-Matthews 2003; Dekar & Magoulick 2007). In parts of North America, 59% of total stream length appears to be either intermittent or ephemeral (Nadeau & Rains 2007), and occurrence of intermittency may expand in the future as climate trends convert snow-fed stream systems into rain-fed systems with reduced natural water storage and lower minimum flows. Such conversions are already in progress (Mote et al. 2005; Regonda et al. 2005; Hodgkins & Dudley 2006; Knowles et al. 2006), and are expected

to affect most of the European, Asian and American continents north of 45°N, and also mountainous areas outside this region (Etchevers et al. 2002; Mote et al. 2003, 2005; Jasper et al. 2004; Leung et al. 2004; Bradley et al. 2006; Knowles et al. 2006; Schindler & Donahue 2006).

But if intermittent streams pose obvious problems for fish, it is also true that much about their role in fish ecology is not obvious. Erman & Hawthorne (1976) observed a population of rainbow trout (*Oncorhynchus mykiss*) in which 39–47% of adults entered an intermittent mountain creek to spawn despite the ready availability of perennial habitat nearby. Ebersole et al. (2006) showed that a creek in Oregon, though nearly dry in midsummer, supported high densities of spawning coho salmon in the fall (*Oncorhynchus kisutch*). Juveniles rearing in the creek grew rapidly in winter and emigrated as larger smolts, relative to those in perennial creeks nearby. Ostrand & Wilde (2002) described a prairie river system in Texas that had intermittent upper reaches, and demonstrated that

some fish species were specifically associated with the intermittent areas.

Stanley et al. (1997) observed that in intermittent streams, unconstrained reaches tended to dry out sooner than constrained reaches, and this underscores the fact that seasonal patterns of drying are inextricably bound up with stream geomorphology and the related processes of sediment transport and deposition during high flows. This affects fish. For example, May & Lee (2004) found that bedrock pools, in which annual peak flows have sufficient power to scour away sediment, tend to reliably maintain dry-season flows and successfully support juvenile salmonids, more so than pools storing sediment. And yet many species of fish require sediment substrates – often with particular size distributions – and especially during their spawning season. At the watershed scale, geomorphic processes influence the spatial distributions of both intermittent reaches and of reaches with suitable substrates. One would thus expect them to exhibit nonindependent patterning, but the form of such patterning is unclear.

Here, we investigate such patterning for a population of *O. mykiss* inhabiting a chaparral watershed in central California. *Oncorhynchus mykiss* spawn in winter and spring on gravel deposits falling within a particular size range (Kondolf & Wolman 1993), and basin-wide sorting of sediment sizes – often called ‘self-financing’ – drives the broad-scale distribution of these gravels (Montgomery et al. 1999; Buffington et al. 2004; May & Lee 2004; Burnett et al. 2007). The self-financing process is governed by peak flows, which determine maximum stream power and interact with channel constraints to influence the competency of channels to transport and sort sediments. Basin-wide trends in competency tend to produce a general progression of coarse to fine sediments from headwater to confluence, accompanied by a predictable sequence of geomorphic channel forms (Magilligan 1992; Grimm et al. 1995; Montgomery & Buffington 1997; Knighton 1999; Brummer & Montgomery 2003; Gomez 2006). The connections between self-financing and distribution of spawning habitat have been studied in forested watersheds and snow-fed stream networks, but not in more arid situations where natural water storage tends to be lower, peak flows and stream power higher, and the potential for intermittency much broader.

Our focus here is on three alternative hypotheses for *O. mykiss* inhabiting a rain-fed stream network in the California chaparral. The first is that suitably sized spawning gravels and intermittent reaches tend to co-occur due to broad-scale fluvial and climatic processes, testable via an appropriate covariate analysis. A corollary of the hypothesis is that winter spawning and summer rearing habitat for *O. mykiss*

may tend to get segregated to different parts of a watershed. An alternative hypothesis is that broad-scale processes may dominate patterning but not segregate the two habitats; and a third alternative is that fine-scale processes could dominate, such that habitat variation is greater within streams than among them, and is not explained by covariates related to the broad scale processes. Such fine-scale processes include channel-spanning wood-jams that resist the self-financing process and maintain spawning habitat in low-order reaches (Montgomery et al. 1996; Hassan et al. 2005), local forcing of channel structure by confluences, rock outcrops, etc. and frequent inputs of hillside sediments (Benda and Dunne 1997a,b; Church 2002; Montgomery & Buffington 1997). Hill-slope inputs are especially relevant in mediterranean climates, where frequent wildfire and intense rainfall can produce geomorphic effects of comparable magnitude to sorting processes (Benda & Dunne 1997b; Keller et al. 1997).

Study area

To evaluate the hypotheses, we estimated habitat and fish distribution in the principal tributaries and mainstem of the Arroyo Seco River in central California (Fig. 1) and examined their relationships to broad-scale drivers of pattern such as clines in precipitation, drainage area and channel gradient. The basic study design was to collect observations in summer 2006 from a stratified-random sample of reaches and analyse the data using a series of multilevel Bayesian statistical models (Wyatt 2002, 2003; Gelman et al. 2004; Gelman & Hill 2007), in which regression predictors were based on existing conceptual models of self-financing (Buffington et al. 2004).

The Arroyo Seco watershed drains an undeveloped 632 km² section of the coastal Santa Lucia Mountain Range in central California. Under the hydrologic-landscape system of Wolock et al. (2004), it is classified as semiarid mountains with permeable soils and impermeable bedrock. The mainstem Arroyo Seco flows east to the Salinas River, which flows northwest to the ocean. The watershed has complex geology, a steeply dissected mixture of igneous, metamorphic and undifferentiated sedimentary rocks with much faulting. Uplift of bedrock is 0.85 mm·year⁻¹, exceeding the fluvial erosion rates by about an order of magnitude so that hillslope processes such as landslides and dry ravel are probably important components of landscape denudation (Florsheim et al. 1991; Ducea et al. 2003). Thus, the study site gives a conservative test of the hypothesis that hill-slope inputs do not overwhelm broad-scale patterning.

Montane ridges and peaks have mixed evergreen forests including the large conifers *Pinus lambertiana*,

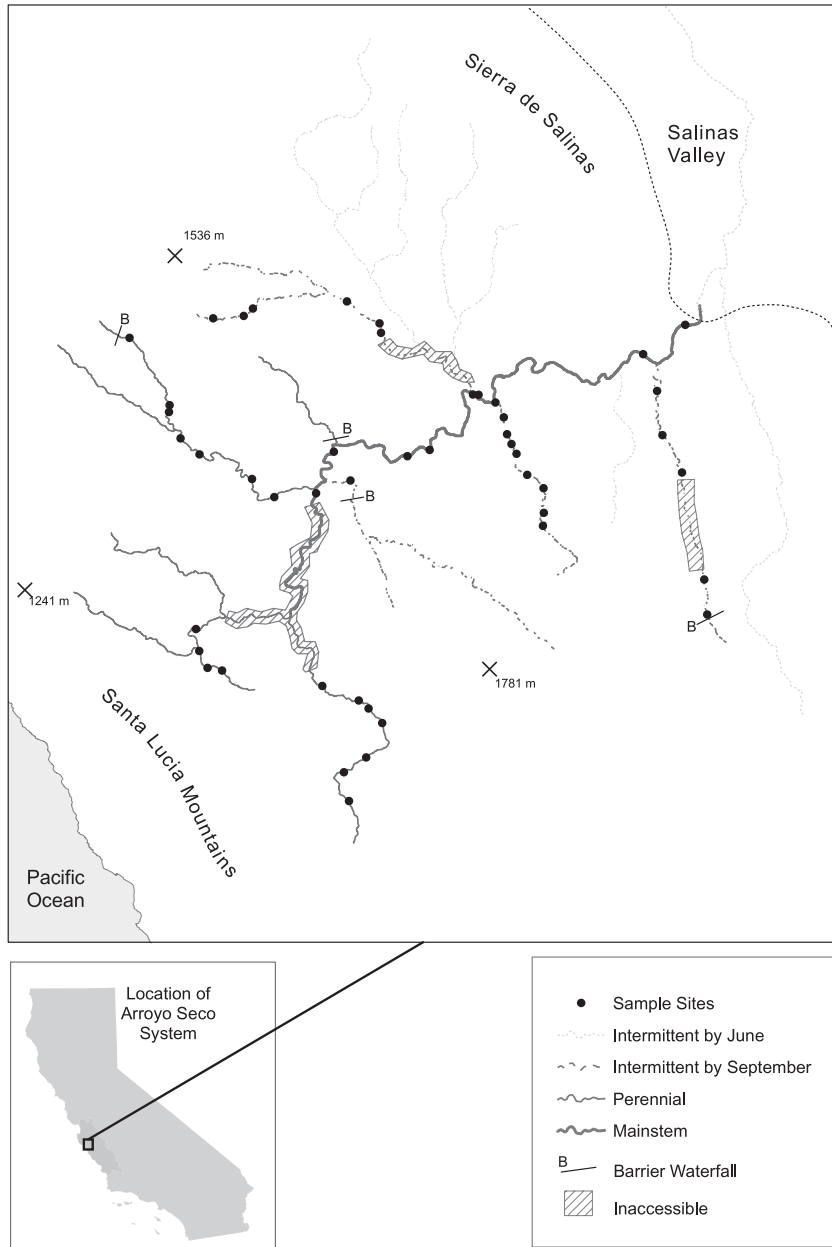


Fig. 1. Principal tributaries of Arroyo Seco, including sampling locations.

Pinus ponderosa and *Pseudotsuga menziesii*, which are Pleistocene relicts. Chaparral occurs on steep slopes with grassland and oak savannah becoming prominent in the eastern areas. The hardwoods *Quercus*, *Populus*, *Platanus* or *Acer* occur along most creeks, although some reaches have steep canyon walls preventing woody vegetation, and many unconstrained reaches are lined by thickets of *Salix*, *Alnus* and *Toxicodendron*.

Annual precipitation on the nearby coast (at Big Sur Station) was 1155 mm for the period 2002–2006, with higher precipitation on the ridge separating the coastal drainages from the Arroyo Seco watershed. A rain-shadow occurs further east, with 610 mm of precipitation near the centre of the watershed (Arroyo Seco

Ranger Station), and 207 mm near the river’s confluence with the Salinas River (CIMIS Station 114). The Arroyo Seco River is perennial in the mountains but as its name suggests, it goes dry in the Salinas Valley by June of most years, due to percolation into a large aquifer.

Virtually all precipitation falls as rain between October and May, though snow may appear briefly on high peaks in some years. The 2006 water year tended to the wet side, producing a mean annual flow in the lower mainstem of $7.39 \text{ m}^3 \cdot \text{s}^{-1}$, or 154% of the average for the years 1902–2007 (range for 1902–2007: $0.197\text{--}20.8 \text{ m}^3 \cdot \text{s}^{-1}$). The fish fauna is closely related to that of the Central Valley of California

(Moyle 2002). The Arroyo Seco system supports a discrete population of *O. mykiss* that is separated from conspecific populations by *c.* 100 km of low-gradient, warm-water channels composing the main-stem Salinas River. Both the ocean-going and the freshwater-resident forms of *O. mykiss* inhabit the watershed. Although *O. mykiss* is a well-studied species overall, its distinctive ecology in the chaparral watersheds of southern and central California is poorly understood.

Material and methods

Sampling frame

Reaches from a Geographic Information System (GIS) (Boughton & Goslin 2006) were stratified by main-stem and principal tributaries (Fig. 1) and sampled using hierarchical randomisation (Stevens & Olsen 2004). We excluded reaches above barrier waterfalls and three inaccessible areas, and in cases of branching tributaries only one branch was sampled, with sampling probabilities adjusted accordingly (Gelman & Hill 2007). During June and early July 2006, sampling sites were located in the field using a geographic positioning system with WAAS capabilities (GPSmap 60C; Garmin International, Olathe, KS, USA), and data were collected from 100-m longitudinal transects (200-m transects were used briefly at the beginning).

We also made field observations to classify streams as perennial or intermittent in the year of the study. In general, the classification of streams as ephemeral (flowing briefly after rainstorms), intermittent (flowing for much, but not all, of the year) and perennial (flowing year-round) is sensitive to the spatial and temporal scale of observations. Our field classification was based on the fact that mediterranean climates have regular annual wet and dry seasons. We considered ephemeral tributaries to be channels that did not maintain continuous surface flow between rainstorms in the wet season, and omitted them from consideration. We considered intermittent streams to be those maintaining surface flow at the outset of the dry season but with dry sections of channel by the end of the dry season (August–September), with perennial streams being those maintaining continuous surface flow through to the first rainfall. Even small sections of dry channel led us to classify a tributary as intermittent, as such interruptions in flow would completely block the movement of fish and drifting food items through the stream, with potentially large effects on habitat quality.

One principal tributary (Reliz Creek) and several minor tributaries or branches were found to be nearly dry by June (termed “early intermittent”). We surveyed *O. mykiss* occurrence in the sparse collection of residual pools in Reliz Creek, but otherwise omitted

the early intermittent creeks from sampling. In late August, we hiked large sections of the other streams and categorised them as perennial tributary, intermittent tributary or perennial mainstem. Streams were considered perennial if they had maintained continuous surface flow throughout the extent surveyed and intermittent otherwise. It is possible that some tributaries judged perennial had dry sections in unsurveyed areas or that appeared in the weeks between the survey and the first rainfall in early October. To minimise this possibility, we focused on reaches that seemed likely to go dry first (reaches with weak flows and deep, coarse alluvium) and spot-checked such reaches throughout September.

Spawning habitat

Water depth, velocity, percent fines and intragravel flow are all important characteristics of spawning habitat for *O. mykiss* (Quinn 2005), but we assumed the fundamental physical constraint to be the calibre of stream sediments, which determine whether the fish can excavate nests for spawning (Buffington et al. 2004; Davey & Lapointe 2007). We also estimated channel morphology, which interacts with discharge to structure scour depth, water depth and velocity and intragravel flow (Montgomery et al. 1999; Quinn 2005).

To quantify broad-scale patterns of sediment calibre (Montgomery & Buffington 1997; Church 2002), we estimated the median surface grain size (D_{50}) for each sampled reach using a systematic pebble count (Wolman 1954). Individual grains were sampled at 2 m intervals along a transect approximately 45° to the thalweg, reflected at the banks, which was intended to sample systematically along both the longitudinal and lateral axes of the stream. The transect was followed from one end of the site to the other (100 m), generally resulting in a sample of about 100 stones. Sizes of the medium axes of stones were estimated using a gravelometer, or for larger rocks, a tape measure or laser rangefinder.

To quantify fine-scale forcing of spawning habitat, in each sampled reach we counted the number of gravel bars that were longer than 1 channel-width and associated with one of the following forcing agents: channel-spanning woody debris (>30 cm, diameter breast-height); step-pools (see below); or a bedrock channel or bedrock outcrop at the channel margin. Bars were judged by eye to be gravel if nearly all particles fell within 2–32 mm diameter (which omits very coarse gravels) but we otherwise refrained from rating their quality as spawning habitat for *O. mykiss*. Below we refer to these as ‘force bars’ to distinguish them from the self-organising gravel bars of the pool-riffle type of channel morphology, which are associated with

the self-financing process (see below) and were not included in the counts of force bars.

Channel morphology was categorised using the system of Montgomery & Buffington (1997), whose Table 1 was converted into a field checklist. This system categorises reaches as pool-riffle, plane-bed, step pool, cascade or bedrock. Many reaches were transitional – for example, plane-bed reaches with scattered step pools were not uncommon – and were assigned a primary and secondary morphology. The data were treated as an ordinal variable, as the categories correspond to increasing levels of stream power and are expected to be related to D_{50} (Montgomery & Buffington 1997). Thus, our primary metric of the amount of spawning habitat produced by self-financing was the length of reaches having suitable D_{50} (using criteria from Kondolf & Wolman 1993), but also included a secondary metric of suitable channel morphology: specifically, the occurrence of bedform roughness (pool-riffle or step-pool morphology) (Montgomery & Buffington 1997), believed to promote beneficial water flow through gravel at spawning sites (e.g., Quinn 2005).

Summer habitat

Summer habitat was quantified directly by making summer dive counts of *O. mykiss*. Dive counts were made by observers wearing snorkel gear and crawling slowly up the channel. *Oncorhynchus mykiss* were distinguished from other species by field marks, usually parr marks. In wide reaches, two observers worked side by side and used a system of hand signals to avoid duplicate counting. Observers visually classified fish into three size categories [FL (fork length) <10 cm, 10 cm < FL < 20 cm and FL > 20 cm], with reference to a measuring scale drawn on an underwater writing tablet.

We employed dive-counting rather than electrofishing to enable a larger sample of reaches (perhaps two to five times over) under available resources. Dive counts can be precise but biased due to undercounting (detection rate less than 1) (Hankin & Reeves 1988). To estimate detection rate, at three calibration sites we paired dive-counting with standard depletion electrofishing (block-netting, three passes).

Derived observations

For each dataset, we fit a Bayesian multilevel model and used it to predict values at unsampled reaches via probabilistic imputation (Gelman et al. 2004). Bayesian analyses were conducted in the R computing environment (R Development Core Team 2006) using OpenBUGS (Sturtz et al. 2005; Thomas et al. 2006) to estimate posterior probabilities via

Markov-Chain Monte-Carlo (MCMC), and package *rv* (Kerman & Gelman 2005) to conduct probabilistic imputation.

For the counting data (dive counts, bar counts), we found the Markov chains extremely slow to converge when the analysis was coded as a single Bayesian model, so we broke such models into discrete steps, using posterior probability densities from one step as derived observations for the next (Gelman et al. 2004, p. 141; Michielsens et al. 2006). Specifically, we assumed counts Y_i to be Poisson-distributed with reference to an underlying log-density of objects y_i , according to the model

$$Y_i \sim \text{Poisson}(L_i 10^{y_i}) \quad (1)$$

where L_i is the length of the sampled reach. The prior probability density for 10^{y_i} was assumed uniform between 0 and 100 items per meter of channel length. After fitting Eqn. (1), the posterior means of the y_i were used as a derived observation in subsequent model-fitting, with sampling errors assumed to be equal to the posterior variances of y_i . This two-step model-fitting procedure will give similar results to a single full model if (i) The uncertainty in the counting procedure is independent of the multilevel model describing the densities and (ii) the posterior of y_i is well-described by a Normal distribution. Our field protocols were designed to ensure the former, and inspection of the posterior simulations indicated that the latter was a reasonable approximation.

A more complex model was necessary to derive median grain sizes from the pebble counts, as the probability distributions of grain sizes rarely conform (even approximately) to any of the standard probability distributions. Log-transformed D_{50} and its variance were estimated using a Bayesian version of the multinomial sampling model (Petrie & Diplas 2000), in which the k terms of the probability vector were specified using $k - 1$ parameters in a linear predictor constrained to sum to 1.0 (see Gelman et al. 2004, section 16.7). The priors were log-uniform over the interval $-30, 30$ relative to the k th category, which served as an intercept or reference, and the cumulative probability distribution was approximated by a series of line segments connected at the boundaries of the grain-size categories. The posterior means and variances of $\log(D_{50})$ obtained from each site's cumulative distribution were then used as derived observations in subsequent analysis.

Estimating observation rates

To estimate detection rate for the dive counts, we used data from the three sites where dive counts were followed by depletion-electrofishing. A Bayesian

depletion-estimator (Mantyniemi et al. 2005) was modified by adding terms for the dive counts, modelled as

$$Y_{w,i} \sim \text{Poisson}(R_w n_{w,i}) \quad (2)$$

where $n_{w,i}$ is the number of fish (size w) between the block nets, estimated by dive counts and depletion-electrofishing concurrently. The parameter R_w is rate of fish detected per fish in the population, given a uniform prior between 0 and 2 (i.e., completely undetectable to completely double-counted). Mantyniemi et al.'s (2005) depletion estimator has a parameter for variation in catchability, but unfortunately at least eight to ten passes are necessary to estimate this parameter, whereas our field conditions only allowed us three passes in the morning before water temperature exceeded the terms of our permit (intended to prevent unnecessary mortality of this protected fish). One alternative would have been to fit a standard depletion estimator, which assumes no variation in catchability, but we thought a more reasonable approach was to use an informative prior for the catchability parameter, derived from the *Salmo trutta* data described in Mantyniemi et al. (2005). The priors for $n_{w,i}$ were specified as in Gazey & Staley (1986). We allowed medium and large fish to have higher susceptibility to electrofishing by modelling capture probability as

$$c_S = \alpha \text{ for small fish, and}$$

$$c_{ML} = \alpha + \frac{\beta}{1 - \alpha} \text{ for medium and large fish.}$$

with α and β having uniform prior probabilities between 0 and 1. Large fish were too rare to be parameterised separately from medium. The posteriors of R_w were log-transformed and summarised as mean and variance for detection rate (\hat{r}_w and $\hat{\sigma}_{r,w}$), which were used as derived observations in the multilevel statistical models.

Multilevel statistical models

The data on channel morphology and the derived observations for D_{50} , bar density and fish density were analysed using linear models of the general form

$$y_i = \alpha + \beta X_i + \varepsilon_{i(j)} + \varepsilon_j + \varepsilon_{\text{obs},i} \quad (3)$$

where y_i is the derived observation at reach i , α is an intercept, βX_i is a vector product of covariates and regression weights (used only in the model for D_{50}) and the ε terms refer to normally distributed variation from various sources: variation among reaches within a stream [$\varepsilon_{i(j)} \sim N(0, \sigma_{\text{crk},j})$], variation among streams [$\varepsilon_j \sim N(0, \sigma_{\text{all}})$], and variation from observation error

[$\varepsilon_{\text{obs},i} \sim N(0, \hat{\sigma}_{\text{obs},i})$, where $\hat{\sigma}_{\text{obs},i}$ is the derived term for sampling error described earlier]. The term $\sigma_{\text{crk},j}$ was simplified to σ_{crk} (all creeks with same site-level variation) if warranted by model-checking. We used the models and multiple imputation to estimate the distribution of spawning habitat and summering habitat among the three categories of stream (perennial mainstem, perennial tributary and intermittent tributary). The range of values of D_{50} considered suitable for spawning steelhead were taken from Kondolf & Wolman (1993).

To evaluate the role of self-fining, we examined covariates expected to be related to $\log-D_{50}$ under a theoretical model of self-fining (Buffington et al. 2004). Specifically, choice of covariates was based on the theoretical expectation that median sediment calibre is a log-linear function of channel gradient and bank-full discharge for transport-limited reaches. As in Buffington et al. (2004), the covariates were log-transformed values of channel gradient and watershed contributing area, the latter being a proxy for bank-full discharge. We added a covariate for mean annual precipitation (log-transformed), which would also be expected to influence bank-full discharge. Covariates were estimated using the GIS (similar to the methods of Burnett et al. 2007), including a digital precipitation map obtained from the Climate Source, Corvallis Oregon (Daly et al. 1994). We had no specific prior knowledge about the strength of the covariates in chaparral watersheds and therefore assigned vague priors to their regression weights (Uniform $[-30, 30]$).

The role of downstream fining was thus judged via the strength of covariates, whereas other (competing) processes would be subsumed under the reach- and stream-specific effects of the model (parameters $\sigma_{\text{crk},j}$ and σ_{all}). These include small-scale changes in surface flow and input of coarse sediments from hillslopes and side channels (Benda and Dunne 1997a,b; Constantine et al. 2003; Davey & Lapointe 2007; Mueller & Pitlick 2005).

In the model for gravel bars produced by local-forcing rather than self-fining, the prediction of bar occurrence was conditional on reach-level D_{50} being unsuitable for steelhead spawning.

In the model for summer habitat, fish density was estimated as

$$\lambda_{w,i} = \alpha_w + \varepsilon_{w,i} + \varepsilon_{w,j} + \varepsilon_{w,\text{obs},i} + \varepsilon_{w,k} + \hat{r}_w, \quad (4)$$

where $\lambda_{w,i}$ is the log-density of fish m^{-1} of channel for size class w in reach i . The parameter \hat{r}_w is an offset to correct for imperfect detection during dive counts, and we assumed that $\varepsilon_{w,\text{obs},i} \sim N(0, \sqrt{\hat{\sigma}_{r,w}^2 + \hat{\sigma}_{\lambda,w,i}^2})$ [the second term is the posterior variance for the log-density of observed fish, from Eq. (1)]. The terms \hat{r}_w

and $\hat{\sigma}_{r,w}^2$ are mean and variance of log-detection rate estimated from calibration sites (Eq. 2). Other terms are as in Eq. (3) except as follows: covariates did not improve out-of-sample predictive power [deviance information criterion (DIC); Spiegelhalter et al. 2002] and were omitted. The term $\varepsilon_{w,k}$ was added to capture the effect of stream type (mainstem, perennial tributaries and intermittent tributaries), though a model without it gave similar predictions and had a similar DIC score.

Results

Intermittency

We field-checked intermittency of the principal tributaries of Arroyo Seco in early June of 2006 and again in late August, and found it to be related to mean annual precipitation in the contributing area of the tributary (Fig. 2). In July, we intensively explored Reliz Creek, the largest early intermittent tributary, and found only a few widely separated residual pools, all without *O. mykiss*; this creek was omitted from subsequent analysis. The other principal tributaries maintained continuous surface flow through June, and most through July, but by the end of August some had dry sections extending for many kilometres, but also sections of surface flow, particularly in bedrock areas. In these intermittent streams, we observed numerous *O. mykiss* dead in dried channels or trapped in rapidly shrinking pools.

General distribution of spawning habitat

As predicted by self-financing models, the median calibre of surface grains in stream reaches (D_{50}) was associated positively with channel gradient and negatively with contributing watershed area, but the 95% credible

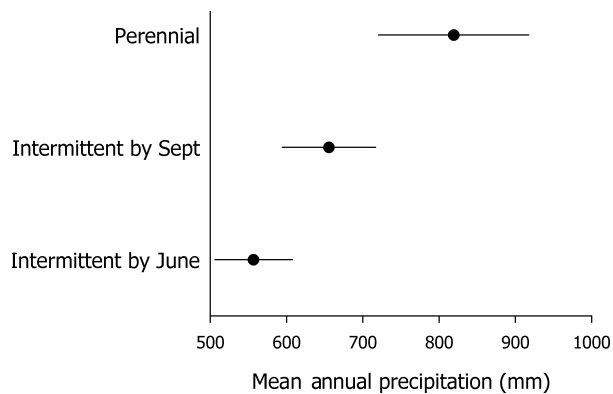


Fig. 2. Intermittency and mean annual precipitation in the contributing areas of tributaries to Arroyo Seco. The ‘intermittent by June’ category includes two large branches of an ‘intermittent by September’ tributary in the northern watershed (see Fig. 1). Bars are SD among tributaries.

intervals of the regression weights overlapped zero. In contrast, the precipitation gradient had an unambiguous positive association with median grain size (Fig. 3). The regression weights in Fig. 3 are for standardised covariates ($\mu = 0$ and $\sigma = 1$) and under-represent the influence of the precipitation gradient relative to contributing area – untransformed, the contributing areas of sample sites covered 2.4 orders of magnitude, whereas precipitation covered only 0.23 yet had a stronger association. Out-of-sample predictive power of the model (as indicated by DIC; see Spiegelhalter et al. 2002) was notably degraded by omitting precipitation, but was slightly improved by omitting contributing area (Table 1). A common assumption in the literature is that unit stream power and shear stress scale to the contributing area (Montgomery et al. 1996; Buffington et al. 2004), but our data demonstrate that precipitation gradients can be more important than drainage area in determining patterns of D_{50} . This broadened the spatial scale of patterning as drainage area varied more within the tributaries than across them, whereas precipitation varied most across the tributaries.

Predictive power was also degraded by assuming that all streams had equal variances of D_{50} among reaches – i.e., we found heterogeneity in the heterogeneity of creeks (Fig. 4). This was probably due mostly to fine-scale hillslope processes or confluence

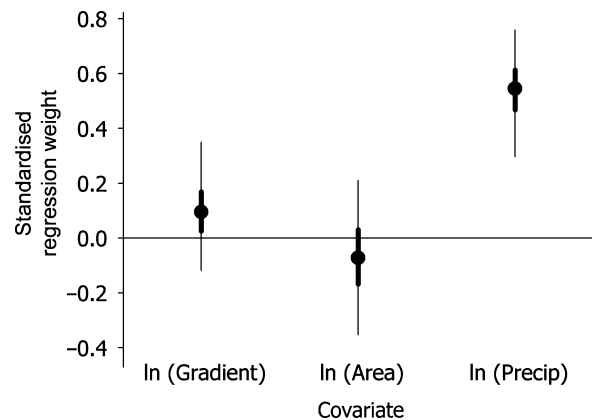


Fig. 3. Weights (betas) for covariates in the model of median surface grain size, scaled as change in $\log(D_{50})$ per unit standard-deviation change in the covariate. Symbols are medians with 50% and 95% credible intervals.

Table 1. Deviance information criterion (DIC) for competing linear models of median surface grain size (D_{50}).

Regression model	DIC
Full model	107.9
Gradient term removed ($\beta_S = 0$)	107.4
Area term removed ($\beta_A = 0$)	106.2
Precip. term removed ($\beta_P = 0$)	115.3
Equal stream variances ($\sigma_{crk,1} = \sigma_{crk,2} = \dots \sigma_{crk,j}$)	120.0

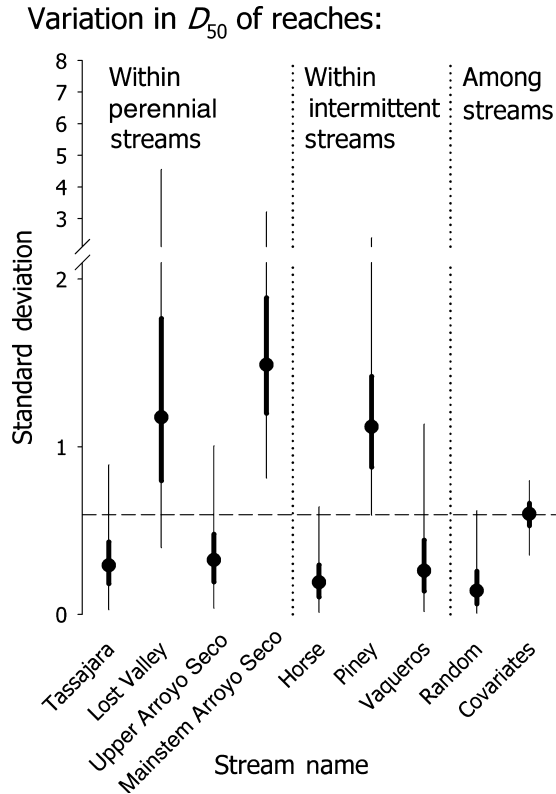


Fig. 4. Components of variance in $\log(D_{50})$ from parameters of the multilevel statistical model. The horizontal line marks the median estimate for variation due to the covariates, computed from the standard deviation of the βX_i terms of Eq. (3) using the posteriors of β . The others estimates are posteriors of $\sigma_{\text{crk } j}$ and σ_{all} . Symbols are medians with 50% and 95% credible intervals.

effects in the mainstem. Figure 4 also shows variation in $\log(D_{50})$ among creeks (including the portion attributed to the covariates). Among-creek variation was greater than within-creek variation for some tributaries but not for others, suggesting that both broad-scale and fine-scale processes influence $\log(D_{50})$. Even so, according to the full model, most of the reaches with D_{50} suitable for spawning occurred in the low-rainfall part of the watershed, indicating the overall importance of broad-scale self-finishing processes that focused spawning habitat into the intermittent tributaries and the mainstem (Fig. 5).

Bedform roughness (pool-riffle or step-pool morphology) (Montgomery & Buffington 1997), believed to promote beneficial water flow through gravel at spawning sites (e.g., Quinn 2005), was present at three-quarters of the sites with suitable D_{50} .

Also shown in Fig. 5 are predictions for the tributaries that were intermittent by June. These were not part of the original sampling frame and thus the predictions are less certain, but it is interesting that they are predicted to provide substantially more spawning habitat than either the late-intermittent or perennial tributaries.

- Perennial streams
- Intermittent by late summer
- Intermittent by early summer

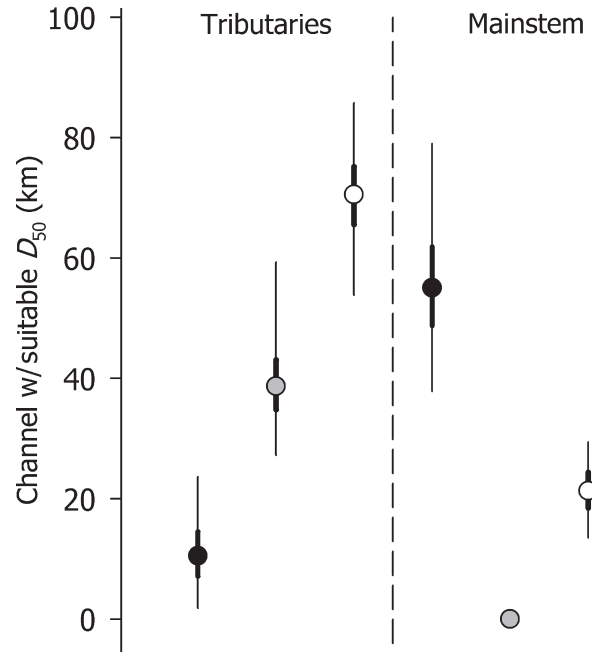


Fig. 5. Cumulative length of reaches with D_{50} suitable for steelhead spawning. Symbols are medians with 50% and 95% credible intervals.

Local-forcing of spawning habitat

Of the forced gravel bars predicted to occur in the watershed, only 17% were associated with coarse woody debris (95% CI: 11–27%). Most (61%) forced bars were associated with bedrock outcrops or channels (95% CI: 48–73%), with the remaining 21% being associated with step pools (95% CI: 14–32%). The density of gravel bars (per unit stream length) associated with bedrock was greater than the density of other types in the mainstem and perennial tributaries (Fig. 6).

The mainstem was predicted to contain about half the forced gravel bars (48%; CI 35–62%), somewhere between 2500 and 6500 separate force bars in areas where D_{50} for the reach as a whole was otherwise too coarse for spawning. The perennial creeks were predicted to contain 36% of the forced gravel bars (95% CI 26–47%), with the remaining 16% in the intermittent creeks (95% CI 11–23%).

Summertime distribution of *Oncorhynchus mykiss*

Detection rate for dive counts of *O. mykiss* was 0.87 per capita for fish <10 cm fork length (95% CI: 0.79–0.94), and 0.75 per capita for larger fish (95% CI: 0.86–1.13). The mean density of fish by body size and

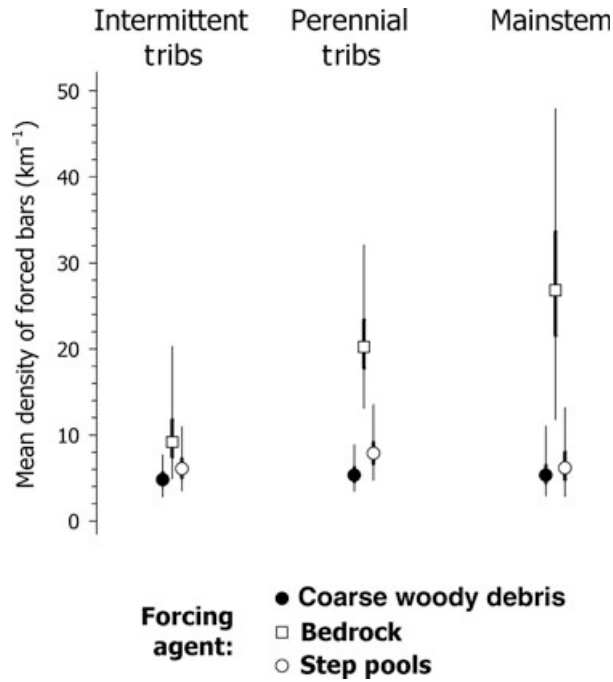


Fig. 6. Mean density of forced gravel bars for different categories of stream and forcing agent. Values for intermittent tributaries omit the ‘early intermittent’ category of stream.

stream type showed a striking pattern (Fig. 7). Mean densities of small *O. mykiss* were very similar in intermittent and perennial tributaries. The densities in intermittent streams do not represent forced aggregations due to drying, as they were standardised per unit length of channel rather than wetted area. Small fish were rare in the mainstem, where spawning habitat was most abundant but daytime water temperatures in summer were 23–28 °C (Fig. 8) and a warm-water predatory fish, *Ptychocheilus grandis*, was extremely abundant. Larger *O. mykiss* were also rare in the mainstem, and most common in the perennial tributaries (Fig. 7).

Revisiting the original general hypotheses, the data as a whole indicated broad-scale spatial patterning of habitat, such that most of the reaches with suitable D_{50} were in the intermittent tributaries or in the mainstem (Fig. 5). The patterns of intermittency and D_{50} both appeared to be related to the precipitation cline (Figs. 2 and 3). For D_{50} there was substantial variation that was not related to covariates and was potentially driven by finer-scale mechanisms such as hill-slope inputs or confluence effects, but it was not sufficient to dominate the broader scale patterning mechanisms (Table 1, Fig. 5). Other forcing mechanisms that might produce gravel bars locally were quite rare, except for rock outcrops. The force-bars associated with rock outcrops were mostly in the mainstem which, though perennial, tended to be too warm for high summer densities of

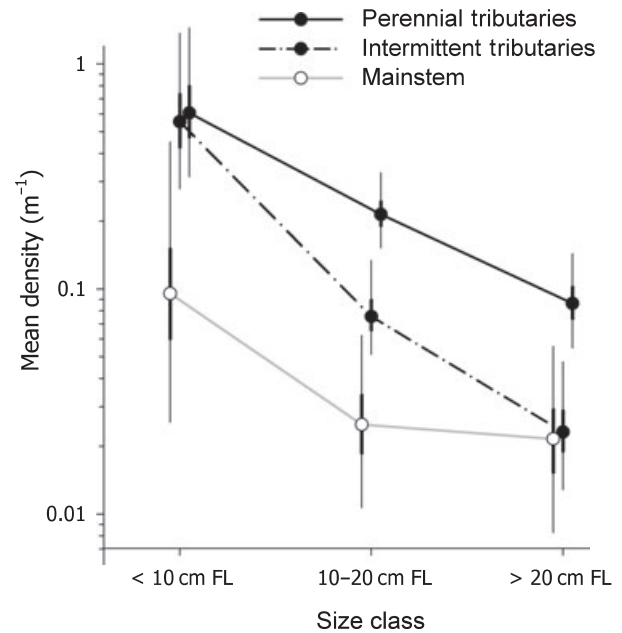


Fig. 7. Mean density of *Oncorhynchus mykiss* by stream category and fish size. Circles are median estimates of mean density; error bars denote 50% and 95% credible intervals. Means weighted by stream lengths. Values for intermittent tributaries omit the ‘early intermittent’ category of stream.

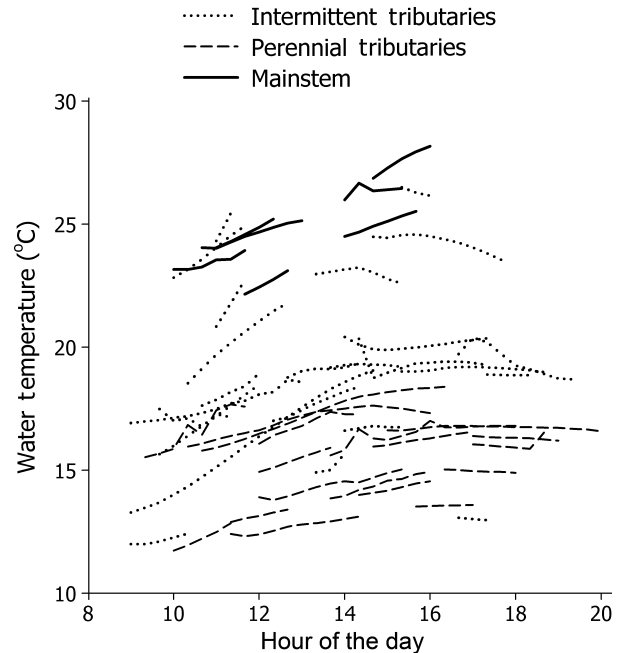


Fig. 8. Water temperatures observed at sampled reaches during dive counts. The data are from an Onset water temperature logger placed in the main current of each reach for the duration of data-collection activities at the site, typically 1–3 h.

O. mykiss (Fig. 8). In contrast to spawning habitat, the larger size classes of *O. mykiss*, most of which had probably already survived at least one summer (i.e.,

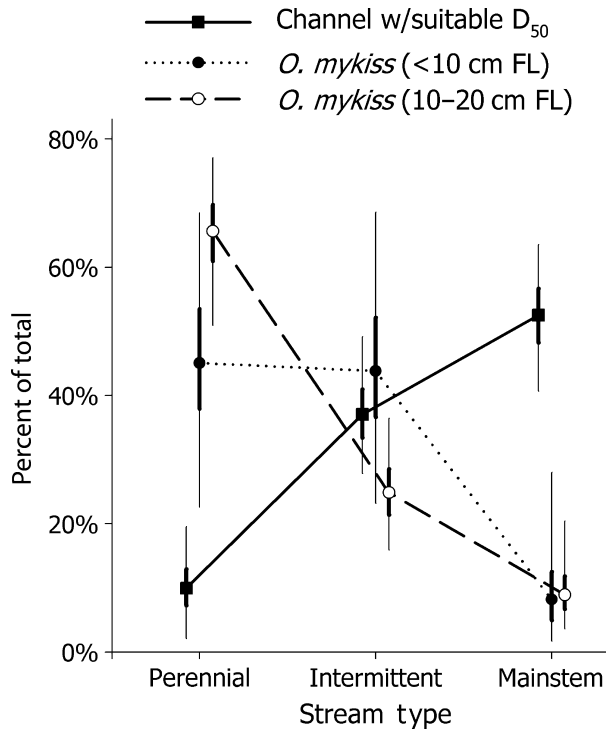


Fig. 9. Proportional abundance of spawning habitat (channel with suitable D_{50}) and summer habitat, the latter indicated by two size classes of *Oncorhynchus mykiss* in June–July 2006. Proportions were computed from abundances estimated using randomly sampled reaches, a multilevel statistical model, and multiple imputation to infer abundances at unsampled sites. Symbols are median estimates with 50% and 95% credible intervals.

were 1+), had the highest density in the perennial tributaries (Fig. 7). The predicted abundances of fish and habitat were used to estimate their proportional abundance in each stream category (Fig. 9). The proportional abundances depicted in Fig. 9 strongly support the segregation hypothesis of winter spawning and summer rearing habitats being concentrated in different parts of the watershed. The distribution of small fish, probably consisting mostly of young-of-the-year, was intermediate between that of spawning habitat and of larger fish. This strongly suggests that substantial spawning had occurred in the intermittent tributaries the previous winter.

Discussion

Geomorphic processes and Salmonid habitat

The data indicated that the largest aggregations of spawning gravel occurred in the drier eastern part of the watershed, while the cool perennial tributaries were in the western part where winter rainfall was highest and summer air temperatures were coolest. Densities of the smallest fish were similar in both types of creek, but the larger size classes tended to

occur in the perennial tributaries. These data suggest that spawning was widespread in the intermittent tributaries (and perhaps the mainstem), but that survival past the first year occurred mainly in the perennial tributaries. However, some survival may occur in perennial headwater areas of otherwise intermittent creeks. The mainstem had both spawning gravels and perennial flow but was mostly too warm for overwintering, probably due to hot air temperatures and a general lack of vegetative cover.

The results support the hypothesis of a spatial disjunction of spawning and summering habitat, maintained by climatic and geomorphic processes ultimately tied to elevation and the meteorological temperature-lapse rate. The disjunction appeared to be exacerbated by a scarcity of coarse woody debris, which in coniferous montane watersheds is common and forces pool formation and gravel retention in reaches that are otherwise too steep or exhibit bankfull discharges too great to retain significant gravel (Montgomery et al. 1996; Buffington et al. 2004). In the study area, most coniferous forests were on ridgetops and most of the instream coarse woody debris that we observed derived from hardwood species, which are less effective geomorphic agents compared to conifers (Opperman 2005). Our data suggest that bedrock outcrops and channels partly compensated for the lack of wood, especially in the perennial tributaries.

These conclusions, however, are based on a single season of observations for *O. mykiss* distribution, and a fairly simple approach to characterising the spawning habitat. Although appropriate gravel sizes and bedform roughness are important for survival of eggs and fry, so are numerous other biotic and abiotic factors which we did not attempt to quantify. More importantly, the actual usage of the habitat by spawning adults was not examined; this would be quite difficult due to turbid and hazardous water conditions and difficult access to much of the field site during the winter and spring months (large sections of the watershed are accessible only via low-water bridges or hiking up stream channels). Most of the anecdotal reports of steelhead spawning are from the eastern tributaries and mainstem, supporting our general conclusions; however, this is the only part of the watershed with year-round human residents so there is a potential observer bias. Finally, we should note that the log-normal models at the heart of our statistical analysis can have poor robustness relative to more complex mixture models (Dorazio et al. 2007).

Implications for Salmonid productivity

The most striking result was that small *O. mykiss*, probably mostly young-of-the-year, maintained very

similar densities in intermittent and perennial creeks during the first part of the summer. The species' longer-term dynamics of habitat use are not known for the study area, nor for other ecologically comparable watersheds in the region, but salmonids are known to spawn in intermittent streams (Erman & Hawthorne 1976; Ebersole et al. 2006), and more generally their reproductive behaviour and population dynamics are sensitive to stream discharge (e.g., Lobon-Cervia & Mortensen 2005; Gortazar et al. 2007; Lobon-Cervia 2007). However, we are not aware of work that has documented the use of intermittent habitats at the magnitude and scale observed in this study.

The data were consistent with the hypothesis that spawning habitat occurred in intermittent streams not by chance, but due to the combined action of orographic rainfall patterns and the self-financing process. This conclusion was based on analysis of covariates (especially an interpolated map of mean annual precipitation generated using methods of Daly et al. 1994), and there is always a possibility of a spurious correlation. This would imply an alternative explanation for the spatial pattern observed, perhaps arising from the geological structure of the range. The geology is quite complex; however, there is no obvious confounded variable, as a single rocktype, sandstone, is prominent in both the driest and the wettest parts of the watershed.

It is interesting that annual precipitation has more explanatory power for D_{50} than contributing area of the watershed, as the latter is sometimes assumed to be of primary importance in snow-fed and coniferous systems (Montgomery et al. 1996; Buffington et al. 2004). In many parts of their range, *O. mykiss* inhabit snow-fed mountain streams that more effectively store water for summer discharge than the rain-fed system observed in our study. However, many of these are expected to convert to rain-fed systems due to climate change. Under a given amount of annual precipitation, such conversion will produce larger peak flows in winter and lower minimum flows in summer, with attendant implications for a shift in self-financing processes and patterns of intermittency respectively.

In the study area, the fitness of young-of-the-year hatching in the eastern spawning areas should depend strongly on their ability to emigrate to the western perennial tributaries before they succumb to warm temperatures, predators, or stream intermittency. Extensive movements of juvenile salmonids are now recognised to be common and fitness-enhancing (e.g., Kahler et al. 2001; Bramblett et al. 2002; Ebersole et al. 2006), but Einum et al. (2006) presented data on *Salmo salar* suggesting that the ability to disperse develops progressively, as a function of body size. He proposed a general model for vertebrates with indeterminate growth, in which resource-shortages for

newly hatched juveniles result in mortality (Milner et al. 2003), but for larger juveniles they result more often in emigration or decreased growth rates (Grant et al. 1998; Keeley 2001, 2003; Sutherland & Norris 2002; Imre et al. 2004; Lobon-Cervia 2005; Einum et al. 2006). Kahler et al. (2001) found that juvenile emigration in *Oncorhynchus* tended to occur from poor (shallow) sites and resulted in enhanced growth elsewhere. One hypothesis is that such dynamics would tend to produce a behaviourally mediated 'buffer effect' on population dynamics (Grant et al. 1998; Keeley 2001, 2003; Sutherland & Norris 2002; Imre et al. 2004; Einum et al. 2006).

Our data suggest that in the chaparral watersheds of southern California, intermittency would tend to disrupt any buffer effect by fragmenting the stream network each summer; the spatial segregation of habitats would increase the fraction of affected young-of-the-year (Kocik & Ferreri 1998). Although *O. mykiss* has had much time to adapt to the environment of southern California, the historical record suggests that runs of anadromous *O. mykiss* in the region have always been exceptionally variable, and the pattern of seasonal fragmentation (a threshold effect sensitive to annual rainfall) indicates a possible mechanism. The mean density of *O. mykiss* at our sites was 0.155 fish per m^{-2} (SD = 0.178), about half the mean for the heavily forested coastal region to the north (Platts & McHenry 1988).

Significantly, some of the earliest-drying parts of the intermittent tributaries occurred just above their confluences, where they emerged from steep side canyons onto the unconstrained floodplain of the mainstem. This pattern cut off the possibility of emigration from intermittent creeks early in the seasonal drying process. This sort of bottom-up drying pattern might have greater mortality impacts than a top-down pattern, as the fish would retain a greater number of dispersal options for a longer time in the top-down pattern. On the other hand, a top-down pattern would force the fish down to warmer reaches during the height of summer, whereas the bottom-up pattern gives them a retreat to relatively cool headwater areas, and blocks immigration by warm water predators such as *P. grandis* during the late summer. In fact, during the late August reconnaissance, we sometimes observed *P. grandis* and other warm-water fish species at some of our perennial dive-count sites, from which they had obviously been absent when the dive counts were made earlier in the summer.

If there is merit to our hypothesis of a functional link between intermittency and occurrence of spawning habitat, then the disruptive pattern of habitat segregation that we observed may be more general, and perhaps would spread under scenarios of conversion of stream networks from snow-fed to rain-fed.

Ultimately, any long-term process of habitat segregation in warming mountain ranges may depend sensitively on expansion or contraction of forests at a regional scale (Hayhoe et al. 2004), as occurrence of forest places an upper bound on inputs of coarse woody debris to stream channels. Although warming and stream conversion may unfold progressively over the course of decades, the changes in habitat that it enables – redistribution of gravels and instream wood via floods and loss of conifers via die-off or wildfire – involve nonlinearities and threshold effects, storage effects, and complex interactions with topography and with each other (Macklin & Lewin 2003; Zelt & Wohl 2004; Coulthard et al. 2005; Schumacher et al. 2006; Lane et al. 2007). In short, there is great potential for surprises.

Currently, large winter peak flows and intermittent summer flows are typical for the stream networks inhabited by *O. mykiss* in the southernmost part of its natural range, and of course in other stream networks with mediterranean climates (Gasith & Resh 1999). The pattern of habitat segregation that we observed appears to be functionally related to such hydrographic patterns. It would be interesting if the functional relationship generalised to other regions with seasonally intermittent creeks and other fish species with particular substrate requirements.

Acknowledgements

We thank W. Cotton, H. Williams, C. Fischer, L. Smith, L. Gould, L. Borzini, K. Malengo and the San Francisco Zen Center for providing access to field sites. NOAA Fisheries, SW Fisheries Science Center funded the work. S.T. Lindley, D. Rundio, P. Adams, and E. Danner provided helpful comments on the manuscript.

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