

APPLIED ISSUES

# Amphibians as metrics of critical biological thresholds in forested headwater streams of the Pacific Northwest, U.S.A.

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## SUMMARY

1. Amphibians are recognized both for their sensitivity to environmental perturbations and for their usefulness as cost-effective biometrics of ecosystem integrity (=system health).
2. Twenty-three years of research in headwater streams in the Klamath-Siskiyou and North Coast Bioregions of the Pacific Northwest, U.S.A., showed distinct patterns in the distribution of amphibians to variations in water temperature, % fine sediments and the amount of large woody debris (LWD).
3. Here, we review seven studies that demonstrate connections between species presence and abundance and these three in-stream variables. These data were then used to calculate realized niches for three species, the southern torrent salamander, the larval coastal tailed frog and the larval coastal giant salamander, relative to two of these environmental stressors (water temperature and % fine sediments). Moreover, multivariate generalized additive models were used to predict the presence of these three amphibians when these three stressors act in concert.
4. Stream-dwelling amphibians are shown to be extremely sensitive to changes in water temperature, amounts of fine sediment and LWD, and specific thresholds and ranges for a spectrum of animal responses can be used to manage for headwater tributary ecosystem integrity.
5. Consequently, amphibians can provide a direct metric of stream ecosystem integrity acting as surrogates for the ability of a stream network to support other stream-associated biota, such as salmonids, and their related ecological services.

*Keywords:* *Ascaphus*, biometrics, *Dicamptodon*, *Rhyacotriton*, stream health

## Introduction

Stream networks in the mountainous catchments of the Pacific Northwest, U.S.A. (PNW) are dominated by first- and second-order headwater channels (Shreve, 1969) comprising up to 80% of stream kilometres within a catchment (Dunne & Leopold,

1978). These channels form the link between aquatic and terrestrial ecosystems (Ward *et al.*, 1998; Nakano & Murakami, 2001; Wipfli, 2005), and are sources of large volumes of wood and colluvial sediment (May & Gresswell, 2003). Upland forests and their transecting headwater channels influence water quality and quantity, inputs of invertebrates and detrital matter to the system and the physical habitats throughout the catchment (Wiens, 2002; Lowe, Likens & Power, 2006). Management of headwater streams is vital for ecosystem integrity (=system health) and sustainability of these landscapes.

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Ecosystem integrity can be viewed "...as the characteristics embodied in the parts (genetic diversity, species, communities) and processes (hydrology, demography, interspecific interactions, energy flow, nutrient dynamics) of nature's legacy in a region" (Karr, 2006). For the purposes of this paper we focus on a subset of the physical attributes in this definition, water temperature, fine sediments and large woody debris (LWD), as the most critical attributes of regional tributaries because they specifically are highly vulnerable to anthropogenic disturbances and are documented to adversely impact ecosystem integrity when modified.

Maintaining aquatic and riparian environments in a healthy functioning state requires guidelines for anthropogenic practices that will preserve physical and biological linkages between channel networks, riparian zones and uplands (Independent Multidisciplinary Science Team, 1999). In PNW, such guidelines need to apply specifically to the range of available water temperatures, the amounts of fine sediments and the amounts and distribution of LWD. Here we present a case for using headwater amphibians as biometrics for assessing appropriate levels of these three attributes in headwater tributaries of PNW. Shared evolutionary histories and similar life requisites means the use of headwater amphibians as biometrics can also indicate the ability of tributary networks to support downstream biota such as salmonids.

The science behind such an approach is now conceptually well established (e.g. Spellerberg, 1991; Simon, 2003; Niemi & McDonald, 2004). However, a carefully formulated programme of biological monitoring is most cost-effective when using target organisms because organisms are the integrators of all that happens in a catchment (Karr, 2006). Given the complex nature of healthy functioning stream networks (Gomi, Sidle & Richardson, 2002; Benda *et al.*, 2004; Lowe *et al.*, 2006), it is both necessary and expedient to select biometric organisms that are not only sensitive to environmental perturbations, but ones whose life histories can also be directly linked to key system attributes and processes (Nichols & Williams, 2006). Such biometrics have enhanced value if they are relatively easy and inexpensive to measure. Most importantly, changes in their numbers should demonstrate clear thresholds relative to key ecosystem changes (Lambeck, 1997; Huggert, 2005; Groffman *et al.*, 2006).

Headwater streams typically do not support fish (but see Wigington *et al.*, 2006) but have a strong influence on downstream conditions and fish-bearing habitats (Naiman & Latterell, 2005) by affecting water temperatures (Poole & Berman, 2001; Moore, Spittlehouse & Story, 2005), sediment input (Montgomery, 1999), substratum structuring (Lisle, 1982) and large wood loads (Naiman *et al.*, 2002). However, headwater channels are hot spots of amphibian diversity, often supporting more species than any other part of the landscape (e.g. Sheridan & Olson, 2003). Headwater amphibians, with their well studied natural histories, documented sensitivities to known ecosystem perturbations, high numbers in healthy streams, high site philopatry, long lives and ease of sampling, are a cost-effective and logical choice for monitoring headwater integrity.

## Methods

We now have over 23 years of research on stream amphibians in the southern regions of PNW demonstrating their links with landscape, macro- and micro-environmental attributes and conditions. This research provides a wealth of details on assemblage composition, and for particular species, data on how their numbers relate to specific conditions in healthy (i.e. reference condition; see RCBI in Stoddard *et al.*, 2006) versus unhealthy streams. Here we review and integrate data from seven studies on amphibian population trends relative to water temperature, fine sediments and LWD, and provide detection rates and animal densities or captures per unit effort such that these amphibians can serve as metrics of headwater ecosystem integrity (i.e. targeted monitoring, *sensu* Nichols & Williams, 2006) of tributaries in the forests of the Klamath-Siskiyou and North Coast bioregions and potentially throughout the PNW.

Our approach was to illustrate how lotic amphibians could function as metrics of environmental stress by quantifying the links between species presence or abundance, and thresholds of water temperature, fine sediments and LWD. Thresholds mark key target points along continua where tributaries transition from healthy to unhealthy states (Groffman *et al.*, 2006). Here a healthy stream is one with high ecological integrity (Westra *et al.*, 2000), and is specifically defined for this paper as one containing the low water temperatures and low fine sediment loads that

support the native coldwater adapted aquatic fauna as represented by the presence of robust populations of native lotic amphibians. Furthermore, healthy streams contain sufficient LWD to maintain the vital function of creating habitat heterogeneity which contributes to a high faunal diversity as exemplified by high abundances of these same amphibians. Key aspects of the natural history of these amphibian species as it relates to these attributes are discussed below (see species accounts) as are details on how they respond to variation in these attributes based on our studies (see environmental thresholds).

We focus on three key physical attributes of the stream environment, which when altered, present in the extreme or missing, are known to create stressful stream conditions that can eliminate some or all of the native biota. Specifically defined these attributes are: (i) the water temperature regime (°C) (hereafter water temperature); (ii) the relative amounts (%) of fine sediments, which includes both silt (particles <0.06 mm) and sand (particles 0.06–2.0 mm) (silt + sand = fines) and (iii) the amount of LWD (>10 cm diameter and >1 m in length). We also evaluated fine sediment effects using the variable 'embeddedness', a visual estimate (%) of the vertical surfaces of large substrata (e.g. cobbles) buried in silt, sand or the two combined.

#### *Headwater amphibian assemblages*

The headwater amphibian assemblage at the southern end of the PNW Bioregion is comprised primarily of the different life stages of three species: the coastal (formerly Pacific) giant salamander (*Dicamptodon tenebrosus* Baird & Girard), the coastal tailed frog (*Ascaphus truei* Stejneger) and the southern torrent salamander (*Rhyacotriton variegatus* Stebbins & Lowe). These species, or their congeners, occur further north, most as far as British Columbia, where additional species are also part of the headwater amphibian assemblage (Jones, Leonard & Olson, 2004; Olson *et al.*, 2007).

*Coastal giant salamander* The coastal giant salamander is one of four species in family Dicamptodontidae (Good, 1989), all endemic to the PNW. These salamanders occur in both terrestrial and aquatic morphs (Jones *et al.*, 2004). The aquatic phase occurs from headwater tributaries down through the fish-bearing

reaches (Jones & Welsh, 2004). Recent evidence indicates they can occur 30–60 cm down in the hyporheic zone of stream channels (Feral, Camann & Welsh, 2005). The smallest size class can be significantly more abundant in intermittent headwater reaches compared with downstream perennial waters (Welsh, Hodgson & Lind, 2005a). Within small, high gradient streams they are often the dominant vertebrate predator (Hawkins *et al.*, 1983; Corn & Bury, 1989), comprising as much as 90% of total vertebrate predator biomass (Murphy & Hall, 1981; Hawkins *et al.*, 1983). Their high numbers and their predatory role (Parker, 1993, 1994) indicate that they play a significant role in converting invertebrate to vertebrate biomass in regional aquatic food webs (see Davic & Welsh, 2004). While apparently not as restricted by water temperature as torrent salamanders and tailed frogs (see below), they demonstrate a negative response to fine sediments (Ashton, Marks & Welsh, 2006) and embeddedness (Welsh & Ollivier, 1998). Unlike the torrent salamander and tailed frog, there is no apparent relationship between giant salamander abundances in streams and adjacent forest seral stage (Welsh & Lind, 2002). They do not, however, occur beyond forested portions of the PNW, and are clearly a large component of the headwater amphibian assemblage of this region.

*Coastal tailed frog* Tailed frogs are the sister taxa to the remaining frogs of the world (Ford & Cannatella, 1993), representing an extremely ancient endemic taxa in western North America, where they exist as two species, the Rocky Mountain and coastal tailed frog (Nielson, Lohman & Sullivan, 2001); the later species being the focus of our research. Adult tailed frogs are extremely intolerant of desiccating environments (Brattstrom, 1963; Claussen, 1973). The fully aquatic larvae (tadpoles), the primary focus of this paper, are found in cold, clear lower-order tributaries, with low fine sediment loads (Welsh & Ollivier, 1998; Welsh & Lind, 2002; Ashton *et al.*, 2006). Adults, active primarily nocturnally, are found in both stream and riparian habitats, taking diurnal cover under streambed substrata, logs, boulders, overhanging banks or in riparian vegetation (Welsh & Lind, 2002). Both life stages of tailed frogs show an association with environmental conditions found most reliably in mature to late-seral forests (Welsh, 1990; Welsh & Lind, 2002) (but see Diller & Wallace, 1999). Negative impacts to tailed

frog populations by timber harvesting and road-building are well documented (Corn & Bury, 1989; Welsh & Ollivier, 1998; Dupuis & Steventon, 1999; Wilkins & Peterson, 2000; Wahbe & Bunnell, 2003). Tailed frog populations occupy headwaters and further down channel networks, becoming uncommon in fish-baring reaches (H. Welsh, unpubl. data). The fully aquatic larvae reach highest densities in coarse stream substrata with numerous interstices (Welsh & Ollivier, 1998; Welsh & Lind, 2002; Ashton *et al.*, 2006). Because they are low-order specialists, tailed frogs are highly vulnerable to extirpation by isolation from habitat fragmentation due to disturbances further down the stream network that can result in cessation of gene flow (e.g. Lowe, 2002). Adults, that use both aquatic and riparian environments, are highly sensitive to microclimatic changes in both venues.

*Southern torrent salamander* The southern torrent salamander is one of four species of *Rhyacotriton*, the single genus in the family Rhyacotritonidae (Good & Wake, 1992). This is the third amphibian family endemic to the PNW. Torrent salamanders are the most evolutionarily derived of the native headwater species, with unique morphological specializations designed for a primarily aquatic existence in cold, clear, highly-oxygenated mountain brook habitats (Valentine & Dennis, 1964). Eggs are laid in slow-flowing headwall springs and seeps, the larvae are fully aquatic and the adults are semi-aquatic, leaving streams only under conditions of high ground-level ambient moisture. This species has the lowest desiccation tolerance of North American salamanders (Ray, 1958). This strictly limits the range of microenvironments that can support these salamanders, including a relatively narrow range of low water temperatures. Welsh & Lind (1996) reported signs of thermal stress in adults at 17.2 °C. Stable low water temperatures occur at the upper end of the stream continuum (e.g. a regional headwater spring measured throughout the summer had a mean of 11.0 °C and daily amplitude of <2.0 °C (Welsh, Hodgson & Karraker, 2005b). These habitats function as 'shields' that protect this salamander from natural stochastic perturbations (Shealy, 1975). These conditions are found most reliably in late-seral forests, which may explain why this species is closely associated with such forests (Welsh, 1990; Welsh & Lind, 1996; Welsh, Hodgson & Lind, 2005a; but see Diller & Wallace, 1996). Torrent

salamanders also prefer shallow, slow-flowing habitats (e.g. seeps), with a mixture of gravel and larger coarse substrata (Welsh & Lind, 1996) and show a low tolerance for sand or fine sediments (Welsh & Ollivier, 1998). This species is particularly sensitive to the impacts of timber harvesting and road-building (Welsh, Roelofs & Frissell, 2000; Welsh & Karraker, 2005). Torrent salamanders show high genetic diversity among populations across PNW (Good & Wake, 1992; Wagner, Miller & Haig, 2006). This high genetic diversity attests to a long history of isolation in headwater refugia and a high vulnerability to restricted gene flow (e.g. Lowe, 2002). Welsh & Lind (1992) and Welsh *et al.* (2005a) showed that this species has experienced additional isolation from anthropogenic disturbances in California.

#### Study area

Our focus here is on headwater stream processes in the context of forest succession because low-order channels are intimately linked with, and influenced by, surrounding forest conditions (e.g. Waters *et al.*, 2001; Sheridan & Spies, 2005), conditions which are to a large degree an expression of seral stage. A particularly significant aspect of the seral continuum for coldwater adapted amphibians requiring low temperatures and high moisture in riparian zones, are changes in microclimates toward cooler, moister, more stable states from young to late-seral forests (Chen *et al.*, 1999; Welsh, Hodgson & Karraker, 2005b). These cool, moist, stable microclimates are particularly important for species whose life cycles include time as terrestrial adults in riparian and upland forests.

The geographic scope of this paper are the North Coast and Klamath-Siskiyou bioregions of California (Welsh, 1994), and the Klamath-Siskiyou Bioregion of southern Oregon. However, most of these amphibians or closely related congeners occur across PNW into central British Columbia, Canada (Jones, Leonard & Olson, 2004), and therefore these taxa could serve as metrics of stream health throughout this greater region. We focused primarily on small colluvial channels which are mostly high gradient and directly drain steep slopes. Following Strahler (1964), the highest and smallest tributaries in a network are first-order streams, their junctions forming second-order streams, and so forth. These tributaries can comprise 80% of stream kilometres in a catchment

(Dunne & Leopold, 1978). First- and second-order channels occur at the top of the river continuum (Vannote *et al.*, 1980), in a process domain (Montgomery, 1999) distinct from, but that profoundly influences, lower gradient alluvial channels where sediments are sorted and deposited (depositional reaches; Hey, 1979; see also Benda *et al.*, 2004).

#### Data sets used

To derive amphibian detection probabilities and densities for monitoring stream health, we used data from three extensive retrospective studies conducted along the forest seral continuum of the regionally dominant Douglas-fir mixed hardwood forests: Welsh (1990) ( $n = 30$  seeps), Welsh (1993) ( $n = 53$ , 110 and  $153 \times 10 \text{ m}^2$  quadrates for torrent salamanders, tailed frogs and coastal giant salamanders, respectively), Welsh & Lind (2002) [ $n = 39$  streams with 585 bank to bank, 1.0 m wide, belts (hereafter belts)]. We also used data from a fourth study describing a natural experiment in old-growth redwood (Welsh & Ollivier, 1998) ( $n = 10$  streams with 267, 0.6 m wide, belts). Two landscape level studies, one of the Mattole catchment (Welsh, Hodgson & Lind, 2005a) ( $n = 31$  tributaries with 294 belts) and one in the South Fork Trinity (H.H. Welsh & G.R. Hodgson, unpubl. data) ( $n = 60$  tributaries with 601 belts), also provided data for this study. A seventh study of 10 streams in the Smith River drainage of northwest California contributed data to our analysis of LWD (G.R. Hodgson, unpubl. data).

Based on our research and that of others (e.g. Tang, Franklin & Montgomery, 1997), we assume that streams in late-seral forests represent the highest quality or healthiest streams in this region (i.e. reference condition; see RCBI in Stoddard *et al.*, 2006). Along with enhanced health based on physical parameters, we consistently found significantly higher amphibian diversity in old-growth streams (e.g. Welsh & Lind, 2002). These streams are followed, in decreasing states of health, by those transecting mature, young and recent clear-cut forests; streams which typically represent a temporal continuum since time of last anthropogenic disturbance. However, the disturbance to half the old-growth redwood forest streams sampled in Welsh & Ollivier (1998) consisted of increased fine sediments, indicating that even in old-growth forest, stream conditions can represent a

continuum of relative health resulting from anthropogenic disturbances (see also Ashton *et al.*, 2006).

#### Realized niche dimensions

We identify specific numbers per unit area (densities) for a range of water temperatures, fine sediment loads and amounts of LWD for particular species as determined by combining appropriate data from the studies listed above. We specifically identify dimensions of their realized niche (for discussions of the niche see Chase & Leibold, 2001; Guisan & Thuiller, 2005) as it relates to two of these physical attributes using data representing the range of available stream conditions in northwestern California and southwestern Oregon following the approach of Huff, Hubler & Borisenko (2005). Determining key thresholds for environmental attributes in the field compared with the laboratory is advantageous because only under natural conditions are important processes like predation and competition an integral part of the system such that ones' results reflect real world conditions (Welsh *et al.*, 2001; Huff *et al.*, 2005).

A species' realized niche centre (RNC) can be defined as the mean value of the physical attribute (e.g. water temperature) weighted by the species abundance, given by the formula,

$$\hat{u}_k = \frac{\sum_{i=1}^n y_{ik} x_i}{\sum_{i=1}^n y_{ik}}$$

where  $x$  = the physical attribute,  $x_i$  = the value of  $x$  in sample  $i$  and,  $y_{ik}$  = the abundance of  $k$  in sample  $i$ . A species niche width (RNW) is one standard deviation from the mean of the parameter weighted by the species relative abundance, and is given by the formula,

$$\hat{t}_k = \left[ \frac{\sum_{i=1}^n y_{ik} (x_i - \hat{u}_k)^2}{\sum_{i=1}^n y_{ik}} \right]^{1/2}$$

#### Generalized additive models

To examine the influence of the three stressor variables working in concert we used generalized additive models (GAM's; Hastie & Tibshirani, 1990), with a logit-link function using occurrence (detected or not) as the binary response. Only data sets having all five relevant variables [water temperature, LWD cover, fines (silt + sand) and embeddedness] were used. GAM's allow the data to define the functional form

(shape) of the relationship between dependent and independent variables (Yee & Mitchell, 1991). We used Akaike's information criterion (AIC) to rank competing models, reporting the best model (lowest AIC) for each species (Burnham & Anderson, 1998), and we evaluated each model's deviance reduction relative to null models with adjusted  $D^2$  (Guisan & Zimmerman, 2000). Analyses were performed using S-PLUS 2000 statistical software (MathSoft, Inc, 1999).

## Results

### *Environmental thresholds for headwater amphibians*

While there are many interacting components that contribute to a healthy functioning stream ecosystem (see Welsh *et al.*, 2000; Lowe *et al.*, 2006), here we confined our analysis to the three aspects of the stream environment that are most often altered by anthropogenic disturbances from timber harvesting and road-building.

**Water temperature (°C)** Water temperatures associated with aquatic giant salamanders indicated detections in stream reaches with a mean of 12.8 °C and range of 4.3–20.9 °C; highest detections were in reaches at 12.9 °C (RNC = 12.9 °C); RNW ranged 11.1–14.6 °C (Table 1; Fig. 1a). Temperatures for sites with larval tailed frogs indicated they occurred at sites with a mean of 11.6 °C and range of 5.7–15.8 °C; highest detections occurred at 11.7 °C (RNC = 11.7 °C); RNW ranged 9.7–13.6 °C (Table 1; Fig. 1b). Temperatures at sites with torrent salamanders indicated they occurred at sites with a mean temperature of 11.4 °C and range of 6.7–15.0 °C; highest detections were at

11.4 °C (RNC = 11.4 °C); RNW ranged 9.8–13.0 °C (Table 1; Fig. 1c).

**Fine sediments (% of surface area)** Fine substrata estimates where aquatic giant salamanders were found indicated that detections occurred at sites with a mean of 15.9%, and a range of 0.0–100%; highest detections were at 16.8% (RNC = 16.8%); RNW ranged from 0.0% to 35.4% (Table 1; Fig. 2a). Fine substrata where larval tailed frogs were found indicated detections at sites with a mean of 9.3%, and a range of 0.0–59.0%; highest detections were at 8.3% (RNC = 8.3%); RNW ranged from 0.0% to 16.9% (Table 1; Fig. 2b). Fine substrata where torrent salamanders were found indicated detections occurred at sites with a mean of 12.0%, and a range of 2.0–45.0%; highest detections were at 11.6%, (RNC 11.6%); RNW ranged from 4.0% to 19.3% (Table 1; Fig. 2c).

All three species showed significant declines in numbers with increased embeddedness (%), however, effects varied, with giant salamanders least sensitive (Fig. 3a), larval tailed frogs more sensitive (Fig. 3b) and southern torrent salamanders most sensitive, approaching zero detections at about 65% embedded (Fig. 3c). The threshold at which either the percent of fine sediments (Fig. 2, Table 1) or the percent of embeddedness (Fig. 3), actually eliminates these amphibians varies considerably by species. Our previous research indicated that it also varies by stream mesohabitat type (Welsh & Ollivier, 1998), however, in each case clearly less is better.

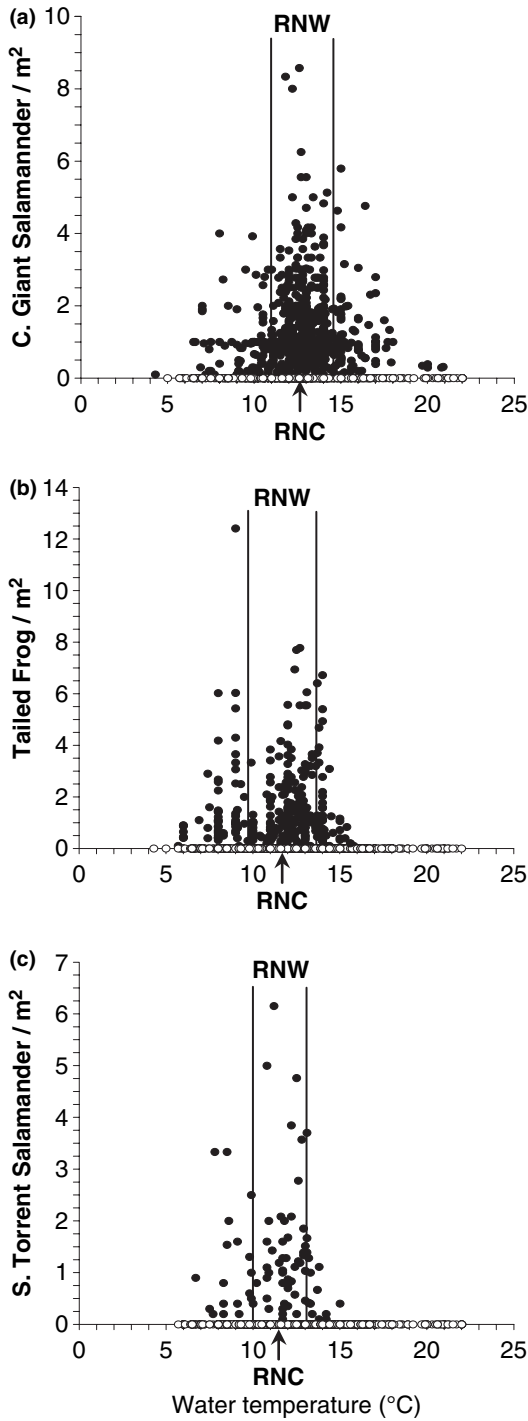
**Large woody debris** In a study of 10 tributaries of the Smith River, Del Norte County, California, we found significant positive relationships between percent of

**Table 1** Meta-analysis of water temperature (°C) and surface area (%) covered in fine substratum (fines and sand combined) as they relate to the abundances of three amphibian species

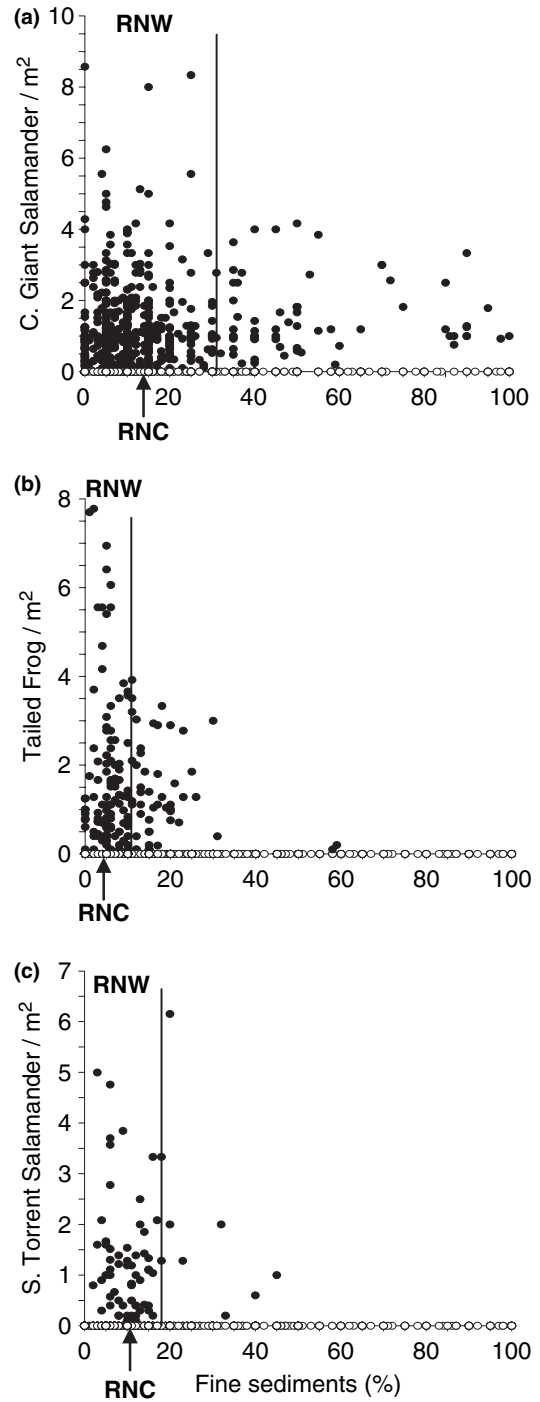
Species	No of streams and (belts)	Min.	Mean	Max.	RNC*	RNW*
<b>Water temperature (°C)</b>						
Coastal giant salamander	308 (1889)	4.3	12.8	20.9	12.9	11.0–14.6
Tailed frog	266 (1847)	5.7	11.6	15.8	11.7	9.7–13.6
S. torrent salamanders	209 (1792)	6.7	11.4	15.0	11.4	9.8–13.0
<b>Fine substratum (%)</b>						
Coastal giant salamander	264 (1307)	0.0	15.9	100	16.8	0.0–35.4
Tailed frog	226 (1269)	0.0	9.3	59.0	8.3	0.0–16.9
S. torrent salamander	172 (1215)	2.0	12.0	45	11.6	4.0–19.3

Sample sizes by stream and belt, with minimum, mean, maximum, realized thermal niche centre (RNC), and realized thermal niche width (RNW). Results are based on data collected at the belt level. See text for methods and data sources.

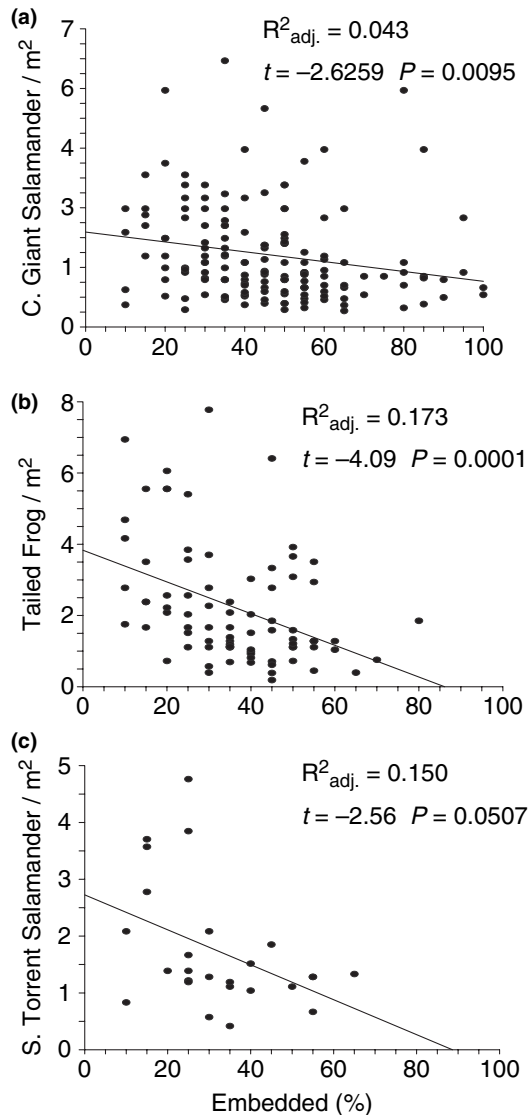
\*Realized thermal niche centre and width (formulas from Huff *et al.*, 2005).



**Fig. 1** Water temperatures (°C) and amphibian detections (closed symbols) and non-detections (open symbols) from five studies (see Methods) with stream sites across the North Coast and Klamath-Siskiyou bioregions conducted from 1984 through 2001: (a) coastal giant salamander, (b) tailed frog, (c) southern torrent salamander. See Methods for details on calculations. Data used for analyses were from the belt level.

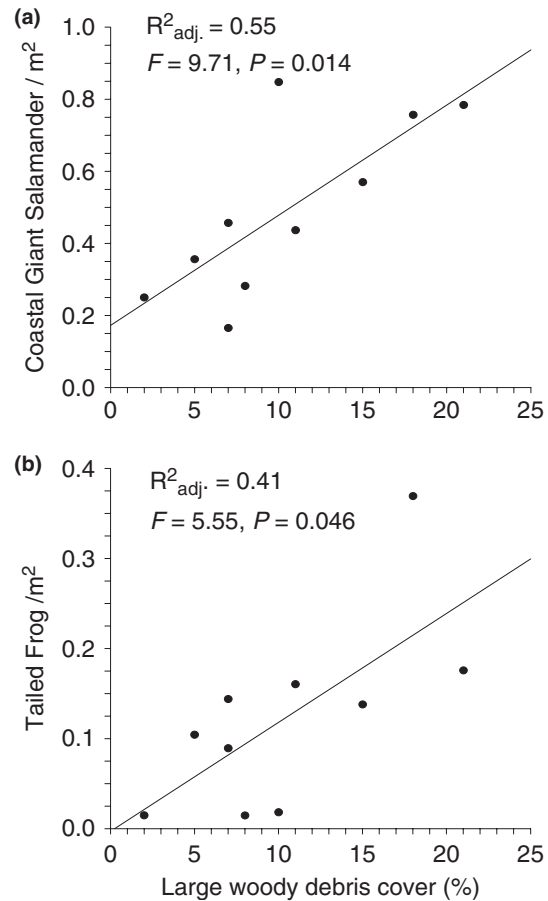


**Fig. 2** Fine sediment (silt and sand combined) estimates (per cent of surface area) and amphibian detections (closed symbols) and non-detections (open symbols) from five studies with sample sites across the North Coast and Klamath-Siskiyou bioregions conducted from 1984 through 2001: (a) coastal giant salamander, (b) tailed frog, (c) southern torrent salamander. See Table 2 for RNC and RNW values and sample sizes. For definitions see Fig. 1.



**Fig. 3** Densities of three species of headwater amphibians shown with respect to embeddedness of coarse substratum (% of surface area) by fine sediments: (a) coastal giant salamander, (b) tailed frog, (c) southern torrent salamander. Data are from 10 streams, five impacted and five unimpacted by fine sediment. Animal data were natural log transformed to derive regressions; axes were back transformed to show actual values. See Welsh & Ollivier (1998) for details.

LWD cover and densities of giant salamanders (Fig. 4a) and tailed frogs (Fig. 4b). While we lacked sufficient data to provide similar threshold values for LWD as we have with water temperature and fine sediments (Tables 1 & 2), the multivariate models below provide a first approximation of lower LWD amounts that supported each of the three species.



**Fig. 4** Relationship of amounts of large woody debris (LWD) in stream channels to amphibian densities in 10 tributary streams of the Smith River, Del Norte County, California: (a) coastal giant salamanders; (b) larval tailed frogs.

#### Multivariate models (GAM's)

The best GAM for the giant salamander showed clear thresholds for each of three environmental variables when combined, with the probability of detection significantly reduced in water temperatures  $<10.5$  and  $>17.0$  °C, where embedded  $>75.5\%$  and where LWD cover was  $>5.0\%$  (Fig. 5). Confidence intervals for LWD above 30% were too large to determine a significant relationship with occurrence. Furthermore, at this level of LWD we could not distinguish between an actual lack of animals and our inability to detect them if present. This model was most influenced by water temperature, followed by LWD and then embeddedness; it had an adjusted  $D^2$  of 0.066 (Table 2).

The best GAM for larval tailed frogs consisted of five variables, with LWD cover, water temperature,



**Table 2** Generalized additive models (GAM's) and deviance values for the best multi-parameter predictive models for the presence of three headwater amphibians

Parameter	Species		
	<i>Dicamptodon tenebrosus</i> (aquatic phase)	<i>Ascaphus truei</i> (larvae)	<i>Rhyacotriton variegatus</i>
Null deviance	1129	631	299
Null d.f.	861	861	864
Model deviance	1049	491	249
Model d.f.	856	849	857
adj $D^2$	0.066	0.212	0.164
Deviance increase (%)			
Water temperature	34 (43)	22 (15)	17 (34)
Embedded	14 (17)	7 (5)	–
Large woody debris	20 (26)	36 (25)	13 (26)
Silt	–	12 (9)	–
Sand	–	17 (12)	–
Silt and sand	–	–	23 (46)

Deviance increase resulting from removing the selected variable from the model. The percentage increase is given in parentheses.

sand, silt and embeddedness, respectively, having the greatest influence on tailed frog presence (Table 2); the adjusted  $D^2$  for this model was 0.212. The probability of detection of larvae significantly decreased in water temperatures  $>14.2$  °C, sand  $>9.0\%$  and embeddedness  $>76.8\%$ . Probability of detection decreased below 2.0% LWD, above 15% the data were not sufficient to clarify the relationship and the

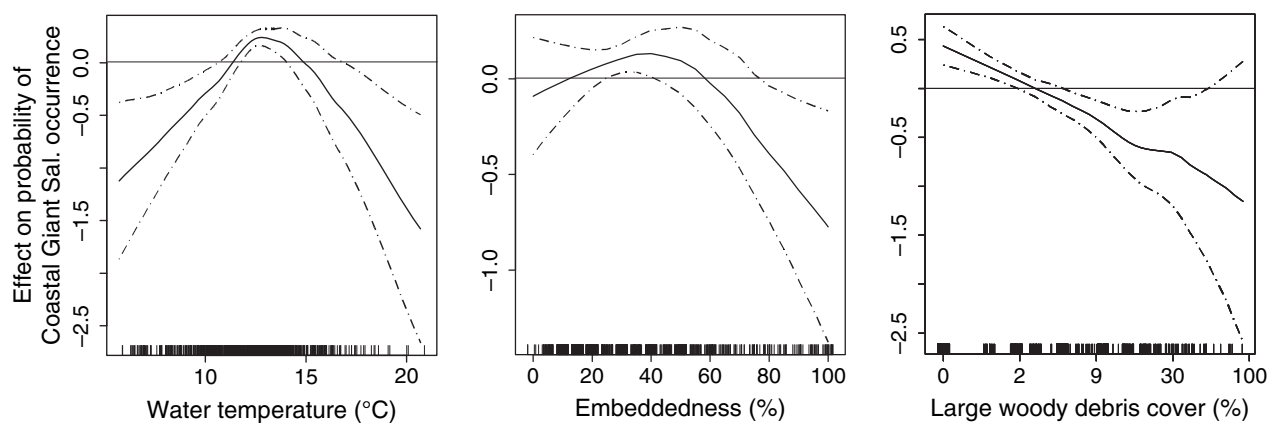
same detection problem exists as was mentioned above for the giant salamander (Fig. 6).

The best GAM for the southern torrent salamander indicated reduced probability of detections at water temperatures  $>16.0$  °C, a tolerance for fine sediments between 3.6% and 33.0% and no detections with LWD cover  $<2.8\%$  (Fig. 7). Above 12.0% LWD cover data were insufficient to determine a pattern. This model had an adjusted  $D^2$  of 0.164, with silt and sand, water temperature and LWD cover, respectively, having the greatest influence on the detection of this species (Table 2).

## Discussion

### *Water temperature, forest succession and amphibians*

Stream temperature controls the rates of many abiotic and biotic processes and can be greatly altered by streamside and upslope land uses (Johnson & Jones, 2000; Moore *et al.*, 2005; Welsh, Hodgson & Karraker, 2005b). From the perspective of water temperature, a healthy stream in the PNW is one that possesses the range of temperatures required to support self-sustaining populations of all native aquatic species. However, most aquatic organisms have a narrow range of temperatures within which they can persist and reproduce (i.e. Huff *et al.*, 2005). Historically the stream fauna of this region has been dominated by coldwater adapted life forms. Our combined data on the thermal niche (Magnuson, Crowder & Medvick,



**Fig. 5** Shape of the estimated nonparametric function (solid line) and 95% confidence intervals (dotted lines) for the best predictive model (GAM) for aquatic coastal giant salamander presence. The functional form describes the relationship of each independent variable to the probability of salamander presence given the inclusion of all other variables in the model. Model thresholds are indicated by those points where all three lines cross the zero axis. Vertical tick marks on the x-axis represent variable values for each plot. Y-axis values are on the logit-scale.

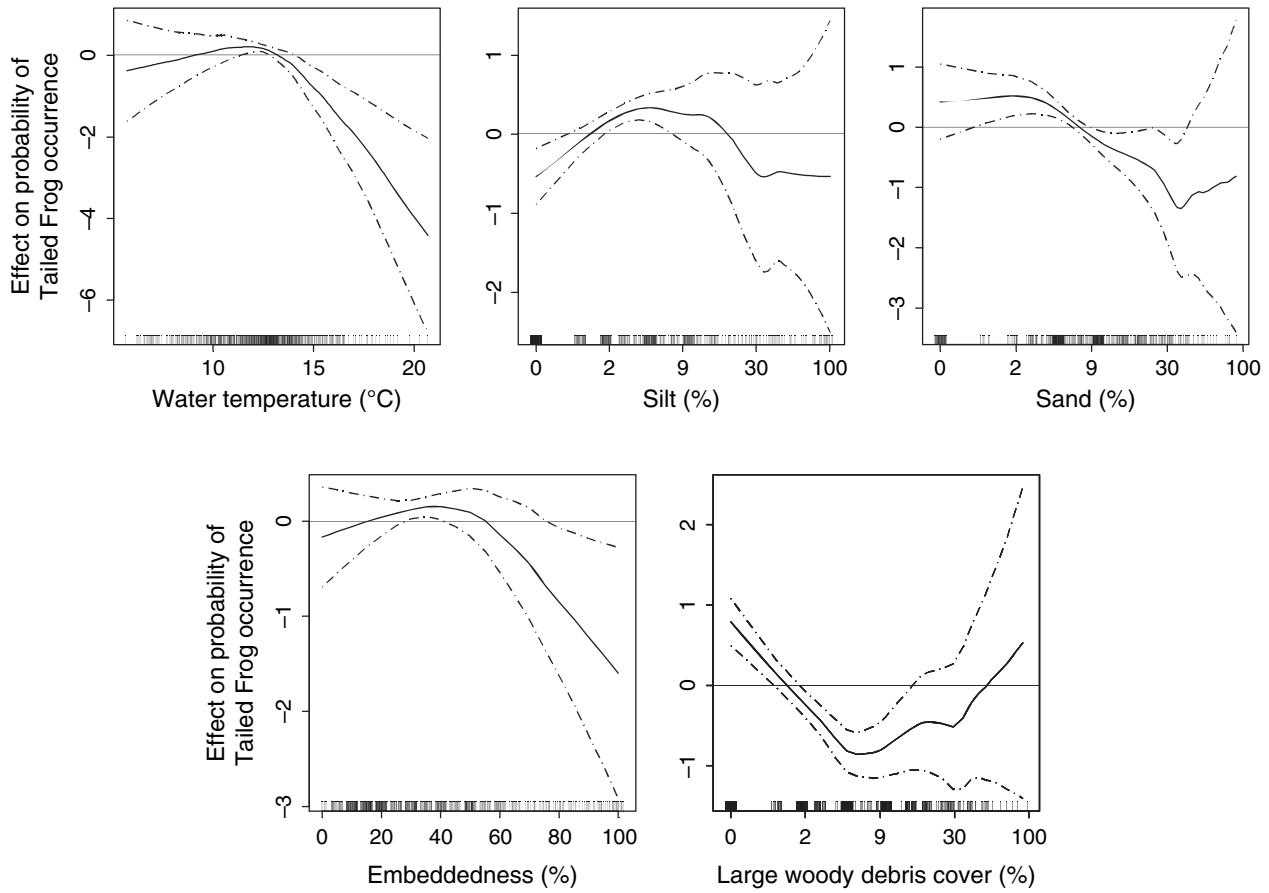


Fig. 6 Shape of the estimated nonparametric function (solid line) and 95% confidence intervals (dotted lines) for the best predictive model (GAM) for the larval tailed frog. See legend to Fig. 5 for details.

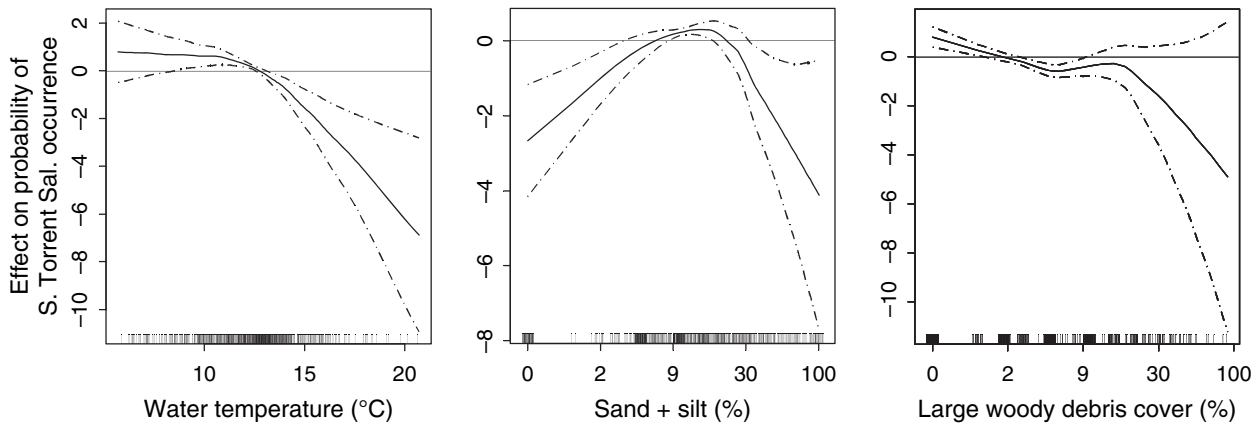


Fig. 7 Shape of the estimated nonparametric function (solid line) and 95% confidence intervals (dotted lines) for the best predictive model (GAM) for the southern torrent salamander. See legend to Fig. 5 for details.

1979) of three headwater amphibian species indicated that the southern torrent salamander occupies the narrowest range of stream temperatures, larval tailed

frogs occupy a slightly broader range and the giant salamander appears to tolerate higher water temperatures better than the other two species. Below we

briefly discuss how these water temperature regimes relate to other aquatic fauna and to common disturbance regimes like forest harvesting.

In the Mattole, we found that tributaries containing young coho salmon (*Oncorhynchus kisutch* Walbaum) had summer mean weekly maximum water temperatures (MWMT)  $\leq 18$  °C in fish-bearing reaches (Welsh *et al.*, 2001). The Mattole is heavily managed for forestry, and our research indicated that southern torrent salamanders and tailed frogs now occur almost exclusively in the few remaining late-seral headwater tributaries (Welsh, Hodgson & Lind, 2005a). We found a marked increase in water temperatures from the top of the stream continuum downstream in Mattole tributaries, reflecting a common pattern in drainage networks (Poole & Berman, 2001). An informative example of this gradient is the Little Finley Creek catchment, which was burned by a stand replacement fire in the early 1970's and now is covered in 35-year-old second-growth forest. This catchment provides a natural control for temperature variation that might result from differences in forest succession along its length. We found that torrent salamanders and tailed frogs presently exist only in the headwaters of this catchment. Water temperatures in Mattole headwaters are typically well below published thermal thresholds for the tailed frog and the torrent salamanders (18.5 and 17.2 °C, respectively; Welsh *et al.*, 2001), while downstream temperatures often exceed these thresholds in summer months. The downstream summer MWMT also exceeded the thermal limits for over-summering coho salmon (Welsh *et al.*, 2001). We previously determined that changes in stream temperature, rather than changes in adjacent forest seral stage, were the probably ultimate causal mechanism in eliminating torrent salamanders and tailed frogs from tributaries in the Mattole (Welsh, Hodgson & Lind, 2005a). However, we also found that changes in stream temperatures were the result of anthropogenic disturbance, primarily timber harvest and conversion of forest to pasture and that this catchment level disturbance was the proximate factor affecting these animal distributions through its influence on water temperature regimes (Welsh, Hodgson & Karraker, 2005b).

Subsequent to our research, the Mattole Restoration Council (MRC) and the Mattole Salmon Group surveyed 97 Mattole River tributaries for evidence of

rearing (over-summering) coho salmon using a standard 10 pool snorkelling protocol (Welsh *et al.*, 2001). They reported coho in 26 of the 97 tributaries (26.8%) (MRC, unpubl. data). Our earlier amphibian sampling (Welsh, Hodgson & Lind, 2005a) was coincidentally in nine of these 26 coho streams (34.6%), and indicated that eight of the nine streams also contained one or both torrent salamanders or tailed frogs (88%). This is the first direct evidence supporting the hypothesis that headwater amphibians are valid biometrics for the ability of streams to support coho salmon.

Given the narrow and relatively cold thermal niches of the southern torrent salamander and the tailed frog it appears that forest seral stage acts as a surrogate for conditions at a finer scale of resolution – the stream microenvironment, where these small ectothermic vertebrates are directly influenced by environmental conditions, particularly microclimates (Dunham, Grant & Overall, 1989; Huey, 1991). This hypothesis is supported by data on tailed frog from both high and low altitude sites where both stand age and stream temperatures were examined (Fig. 8). From these data it is clear that while the older stands generally contained more tailed frogs, water temperature has an over-riding influence compared with stand age, because stands over 1000 m.a.s.l. actually had the most tailed frogs, yet several of these streams were in forests <200 years of age; one stand was as young as

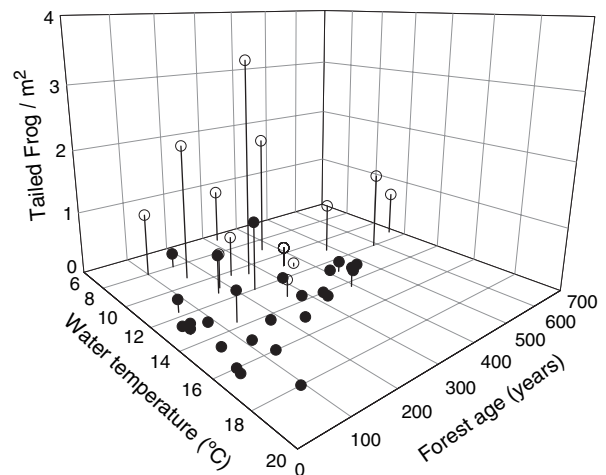


Fig. 8 Stream temperature (°C), forest age and tailed frog abundances (both life stages combined) and altitude (above or below 1000 m.a.s.l.). Figure is modified from Welsh & Lind (2002).

100 years. While the presence of late-seral forest can often assure the presence of cold water, and possibly the presence of tailed frogs or torrent salamanders, it is clearly the low water temperatures that are acting as the ultimate determinant as to whether a stream supports these amphibians. However, these two parameters are intimately linked because in many parts of their natural ranges, water temperature can exceed the tolerances of these amphibians when the late-seral forest structure is removed (Chen *et al.*, 1999).

Scrutiny of water temperature niches of headwater amphibians indicates that: (i) if there is sufficiently cold water at the headwater end of the stream continuum it can and probably will support torrent salamanders and tailed frogs; (ii) with the presence of late-seral forest at the headwaters, there is a high probability of low and suitable water temperatures and (iii) the further downstream, or the greater the proportion of the catchment, one maintains sufficient late-seral forest cover, the more likely other elements of the coldwater adapted fauna will occur downstream (e.g. Welsh *et al.*, 2001). Our findings indicate that to support viable populations of these amphibians these stream temperatures should not be exceeded: 15.0 °C for the torrent salamanders, 15.8 °C for the tailed frog and 20.9 °C for the coastal giant salamander. Data on coho salmon distributions from the Mattole support the contention that maintaining these temperatures in headwater reaches will probably provide sufficiently cold water for elements of the native fauna downstream.

#### *Fine sediments and amphibians*

Fine sediments (particles <2.0 mm diameter) comprise one of the most pervasive stressors of lotic systems worldwide (Waters, 1995). There are several recent studies showing that fine sediments have a significant negative impact on populations of headwater amphibians (Corn & Bury, 1989; Welsh & Ollivier, 1998; Ashton *et al.*, 2006). Indeed, Ashton *et al.* (2006) found significantly fewer southern torrent salamanders, tailed frogs and giant salamanders in recovering second-growth redwood forests in Humboldt County, California, 60 years after harvest. There were significant differences in fine sediments loads between reference late-seral and

second-growth forest associated streams but not in water temperatures (Ashton *et al.*, 2006). Previously, Welsh & Ollivier (1998) found that these same species were adversely affected in streams in old-growth redwood forest, where fine sediments in pool bottoms averaged  $\geq 1.5$  cm (SE = 0.36) in depth. Impacts of fines in these same streams were also determined by estimating embeddedness of stream-bed cobbles at pool tails, where these same three species were negatively impacted when embeddedness was  $\geq 62.6\%$  (SE = 3.91; Welsh & Ollivier, 1998). Fine substrata have a similar negative effect on the establishment of fish redds and the hatching success of salmonid eggs (Stouder, Bisson & Naiman, 1997), behaviours that affect individual fitness (Robertson, Scruton & Clarke, 2007), and they negatively impact the growth and survival of juvenile fishes (Suttle *et al.*, 2004).

#### *Large woody debris and amphibians*

Large woody debris has a vital role in the trapping and sorting of sediments, structuring of stream habitats (Naiman *et al.*, 2002; Montgomery *et al.*, 2003) and influencing the distribution of stream organisms. While much of the evidence for the influence of LWD on stream amphibians is anecdotal or correlative (e.g. Welsh & Ollivier, 1998; Welsh & Lind, 2002), it is clearly an important habitat element. The relationships revealed in our univariate analysis may suggest a greater influence than occurs in typical stream networks (see multivariate models) due to the dominance of bedrock reaches in the streams of the Smith River data set, resulting in low coarse substratum amounts and hence possibly greater dependence on LWD by amphibians. However, this is clearly an important aquatic habitat component for amphibians because of its role in sorting sediments and thus creating critical microhabitats. We have also observed recent metamorphs of the coastal giant salamander having left the water using LWD piles over wetted channels as cover in late summer prior to autumn rains when they are then able to disperse into the forest (H. Welsh, pers. obs.). Its importance to other elements of the stream biota is well established (see Laudenslayer *et al.*, 2002). We encourage that every effort be made to both maintain, and recruit LWD as a part of management seeking to sustain biodiversity in streams.

*Using headwater amphibian assemblages as biometrics of stream health*

The status of headwater amphibian populations as they relate to changes in these three physical attributes is viewed here as indicative of the state of health (i.e. ecological integrity) of the stream reach and a means to identify the likely mechanism(s) of both depressed amphibian populations (and probably other biota) and declines in stream health. However, because of the unique niche of each of these three species, judging the health of an entire channel or network system using their numbers would require assessments of a particular species only at appropriate locations within a stream network. For example, the southern torrent salamander is strictly a headwater specialist and its presence would only be expected in the lowest order tributaries. Therefore, we would argue that torrent salamanders be sampled only in first-order tributaries and in their other preferred microhabitats of springs and seeps (Welsh & Lind, 1996). Tailed frog larvae and larval and paedomorphic giant salamanders, while sometimes present in head waters, occur more commonly in second- to fifth-order tributaries, and should be sampled accordingly. Also, one must be aware that larval tailed frogs become increasingly rare in fish-baring reaches, a fact that could greatly modify expected values in a given reach. An effective strategy for judging the health of a stream network might be to randomly select 10 tributaries in each of several orders, including first order, and then sampling to determine presence or mean values for each species in the appropriate parts of the network to compare with reference data. For a particular tributary, a similar approach would be to randomly select a number of sample reaches along its length and do the same. If a tributary, or network, failed to meet or exceed reference values (see below) for each of these species, the lower numbers would be reflective of its relative health, and would be indicative of a compromised ability of that system to support other coldwater biota therein and downstream. Toward that end, we have compiled data from several studies indicating detection probabilities for each of the three species along the seral continuum where streams in old-growth or late-seral forests represent reference conditions or the healthiest streams (Table 3). From these data it is evident that the tailed frog and torrent salamanders occur at

higher detection rates in older forests; whereas the giant salamander does not. Once a species is present, densities for all three appear to be fairly consistent across the seral continuum. This suggests that detection rates may be a more accurate indicator of stream health than relative densities. However, the density data from the old-growth redwood forest streams (i.e. Welsh & Ollivier, 1998) indicate that all three species are more abundant in the low sediment streams. This result supports a combination of both approaches when assessing stream health, and suggests that the differences in our densities across species and stream sets, and between data sets, probably reflect real differences (or not) in the relative health of the various stream sets. The consistently low densities of giant salamanders from the Welsh (1993) study compared with the other two data sets probably results from biased sampling primarily in lower-order streams as this study was originally designed specifically to detect torrent salamanders and tailed frogs.

*Headwater amphibians and current timber harvest practices*

Welsh *et al.* (2000) presented data for southern torrent salamanders and tailed frogs from redwood forest streams in an area of commercial timberland where the headwater streams were unprotected, compared with those from parkland streams. These data indicated a mean of 0.052 (SD = 0.092) versus 0.724 (SD = 0.786) salamanders per hour (Mann–Whitney test;  $Z = 2.93$ ,  $P = 0.003$ ) and 0.108 (SD = 0.097) versus 2.40 (SD = 1.58) tailed frog larvae per hour ( $Z = 4.30$ ,  $P < 0.0001$ ) respectively. These data were from streams in coastal redwood forests where stream temperatures are often sufficiently low, even without forest canopy, to support populations of these amphibians (e.g. Diller & Wallace, 1996, 1999). Road-building and the resulting run-off of sediments are a common result of activities on commercial timberlands so fine sediments, rather than higher water temperatures, is probably responsible for the differences (e.g. Ashton *et al.*, 2006). However, examples of differences in amphibian numbers resulting from altered water temperatures (e.g. Welsh, Hodgson & Lind, 2005a) and differing amounts of LWD indicate that all three mechanisms can generate similar results. What then is the absence or depressed population of a

**Table 3** Number of stream sites sampled, proportions with detections and densities  $m^{-2}$  for sites with animals for three headwater amphibians in four forest age classes (clear-cut = 0–30 years, young = 31–99 years, mature = 100–200 years and old-growth = 200+ years) from (a) Three studies of streams that sampled the seral continuum and (b) One study comparing sediment-impacted with un-impacted streams in old-growth redwood forest

(a)												
Study	Clear-cut			Young			Mature			Late-seral		
	No. sites	Sites present (prop.)	Mean density (SD)	No. sites	Sites present (prop.)	Mean density (SD)	No. sites	Sites present (prop.)	Mean density (SD)	No. sites	Sites present (prop.)	Mean density (SD)
Coastal giant salamander												
Welsh, 1993	39	17 (0.44)	0.36 (0.47)	21	15 (0.71)	0.25 (0.12)	20	11 (0.55)	0.34 (0.36)	71	34 (0.48)	0.39 (0.34)
Welsh & Lind, 2002	–	–	–	33	5 (0.15)	1.49 (0.88)	25	5 (0.20)	1.50 (0.87)	59	11 (0.19)	1.25 (0.44)
Tailed frog												
Welsh, 1993	25	7 (0.28)	0.87 (0.78)	18	8 (0.44)	0.54 (0.55)	14	9 (0.64)	1.24 (0.96)	53	31 (0.58)	1.00 (1.52)
Welsh & Lind, 2002	–	–	–	33	5 (0.15)	1.01 (0.89)	25	11 (0.44)	1.30 (1.10)	59	36 (0.61)	0.60 (0.59)
Southern torrent salamander												
Welsh, 1993	20	5 (0.25)	0.86 (0.53)	4	4 (1.00)	0.43 (0.26)	7	5 (0.71)	0.58 (0.63)	22	18 (0.82)	0.74 (1.13)
Welsh, 1990	–	–	–	10	1 (0.10)	1.00 (–)	9	5 (0.55)	1.80 (0.83)	11	8 (0.73)	4.13 (2.18)
(b)												
Study	Unimpacted			Impacted								
	No. sites	Sites present (prop.)	Mean density (SD)	No. sites	Sites present (prop.)	Mean density (SD)						
Coastal giant salamander												
Welsh & Ollivier, 1998	130	77 (0.59)	1.98 (1.30)	137	77 (0.56)	1.40 (0.81)						
Tailed frog												
Welsh & Ollivier, 1998	130	51 (0.39)	2.39 (1.73)	137	33 (0.24)	1.94 (1.51)						
Southern torrent salamander												
Welsh & Ollivier, 1998	130	19 (0.15)	1.97 (1.24)	137	7 (0.05)	1.21 (0.36)						

Welsh (1990) data are captures per half hour timed-constrained searches.

headwater amphibian on a particular landscape indicating about stream processes and the condition of downstream reaches? We maintain that their absence or low numbers is indicative of unhealthy headwater processes (=compromised ecological integrity) resulting from changes in water temperature, fine sediments, LWD or some combination. It may take further investigation to discern the actual mechanism(s), but the result is that healthy salmonid populations and other fishes cannot be sustained downstream because they require healthy functioning headwater stream processes to maintain suitable conditions of all three attributes for hatching, rearing and foraging in these lower reaches (see Naiman & Latterell, 2005).

Recent amphibian studies indicate that forest practice regulations throughout the PNW are cur-

rently inadequate to protect headwater amphibians or the stream processes upon which they and downstream aquatic biota depend (reviewed by Olson *et al.*, 2007). It can take +200 years for the structural integrity of a headwater system in a late-seral forest to re-establish itself (Franklin *et al.*, 2000; Moeur *et al.*, 2005). Given current harvest rotations, we may never see aquatic ecosystems on commercial timberlands in PNW returned to a healthy functional state unless we actively manage for that outcome. That means incentives; legislation, regulations and actual land use practices must recognize and promote healthy forest and headwater stream networks based on the concepts of ecological sustainability and integrity (e.g. Welsh, 2000; Olson *et al.*, 2007). Managing headwaters for amphibian populations (e.g. Semlitsch, 2002;

Semlitsch & Bodie, 2003; Olson *et al.*, 2007) would go a long way toward establishing and maintaining healthy, functioning stream networks and associated biota on PNW forestlands (e.g. Labbe & Fausch, 2000) (see also Meyer *et al.*, 2003).

Our approach is based on the logic that headwater amphibians have evolved for eons in these same streams with anadromous life forms of commercial interest, and thus they share the same requirements of a healthy stream environment to exist and thrive. We would therefore argue that the combined characteristics of high sensitivity to environmental perturbations, high abundances, ease of sampling and shared evolution in headwater environments of stream networks, make amphibians excellent biometrics for the monitoring of anthropogenic stresses to these networks (e.g. Tabor & Aguirre, 2004), where stresses tend to move downstream and influence lower channel networks and their resident species (Gomi *et al.*, 2002; Benda *et al.*, 2004; Richardson *et al.*, 2005). Furthermore, an understanding of the relationships between specific environmental stressors and amphibian responses, makes tracking their assemblage composition and relative numbers in headwater streams an inexpensive and effective means of predictive monitoring (i.e. detecting undesirable effects before they have a chance to become serious) (see Nichols & Williams, 2006).

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