Movement patterns and relative abundance of coastal tailed frogs in clearcuts and mature forest stands

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Abstract: Age-specific movements, abundance, and capture rates of coastal tailed frogs (*Ascaphus truei* Stejneger) were compared between clearcuts and mature forests in southwestern British Columbia, Canada, during 1998 and 1999 using pitfall traps and drift-fence arrays. Total frog abundance was similar in both habitat types. More adults were caught in mature stands than in clearcuts, but there was no significant difference for immatures. Analysis of numbers of frogs captured indicated that the direction of movement did not differ between habitat types for any age-class. Frogs were captured at similar frequencies across distance from stream in both habitats. These findings suggest that there are age-specific differences in tailed frog abundance in clearcuts along streams without riparian reserves relative to mature forests. Variation among sites had a greater influence than habitat type on the number of immatures. Low proportions of adults in clearcuts suggested that immatures may be transient or that they incurred high rates of mortality. Age-specific differences in habitat use by tailed frogs indicated that total numbers alone are insufficient to determine the effect of forest management on habitat suitability for tailed frogs.

Résumé : Les déplacements, l'abondance et les taux de capture par classe d'âge de la grenouille-à-queue (*Ascaphus truei* Stejneger) dans des coupes à blanc et des forêts matures du sud-ouest de la Colombie-Britannique, au Canada, ont été comparés en 1998 et 1999 en utilisant des pièges-fosses et des clôtures de dérivation. L'abondance totale de grenouilles était semblable dans les deux types d'habitat. Plus d'adultes ont été capturés dans les peuplements matures que dans les coupes à blanc, mais il n'y avait pas de différence significative dans le cas des grenouilles immatures. L'analyse du nombre de grenouilles capturées a montré que la direction des déplacements ne différait pas selon le type d'habitat peu importe la classe d'âge. Dans les deux habitats, la fréquence de capture des grenouilles était semblable peu importe la distance du ruisseau. Ces résultats indiquent qu'il y a des différences d'abondance selon l'âge des grenouilles-à-queue entre les forêts matures et les coupes à blanc sans forêt rémanente en bordure des ruisseaux. Chez les grenouilles immatures, la variation entre les sites était plus importante que la variation entre les types d'habitat. La faible proportion d'adultes dans les coupes à blanc suggère que les jeunes pourraient soit être de passage, soit avoir subi un taux de mortalité plus élevé. Les différences dans l'utilisation de l'habitat selon l'âge des grenouilles-à-queue montrent que l'analyse des nombres totaux n'est pas suffisante pour déterminer les effets de l'aménagement forestier sur la qualité de l'habitat de la grenouille-à-queue.

[Traduit par la Rédaction]

Introduction

To effectively manage forest ecosystems for activities such as timber harvesting, a sound understanding of the linkages between the forest and its biota are required to delineate potential impacts. For amphibians, the effects of timber harvesting vary with stand age and the quantity of affected microhabitat (deMaynadier and Hunter 1995). Significant differences in abundances of amphibians have been found between clearcuts and old-growth or maturing forests (e.g.,

Aubry and Hall 1991; Corn and Bury 1991; deMaynadier and Hunter 1995; Dupuis et al. 1995; Welsh 1990). However, findings vary making interpretations difficult, and they are further confounded when broken down by gender, size, age-class, or season. For example, larval amphibian densities may be greater in clearcut streams than in forested streams (Hawkins et al. 1983; Richardson and Neill 1998; Mallory and Richardson 2005), which could result in more of the terrestrial-stage amphibians remaining closer to streams in clearcuts (Johnston and Frid 2002).

Assessing differences in amphibian movements in various habitats (i.e., harvested versus maturing forest sites) helps to determine the effectiveness of conservation and management applications, particularly in areas with anthropogenic disturbance (Johnston and Frid 2002). If postdisturbance movement patterns change between habitats such as riparian and upland areas, then the presence of only one suitable habitat type may not be sufficient for the needs of the species.

Disturbances from timber harvesting have a variety of impacts on a forest ecosystem. Definitions of a disturbance

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vary (e.g., Townsend and Hildrew 1994). For this study, disturbance was defined as the disruption of an ecosystem, a community, or a population structure combined with changes in available resources, substrate availability, or the physical environment (Krebs 1994; White and Pickett 1985). Whereas timber harvesting may be a direct disturbance, it can also lead to environmental perturbations such as erosion, slope failure, and windthrow. These effects vary in magnitude and frequency and depend on the scale and generation time of the organism(s) concerned (Townsend and Hildrew 1994).

The coastal tailed frog (*Ascaphus truei* Stejneger) of the Pacific Northwest is a stream- and riparian-dependent species and is considered to be primarily associated with old-growth and mature forests. Logging practices are linked with lower larval and adult populations (Aubry and Hall 1991; Blaustein et al. 1995; Bull and Carter 1996; Bury and Corn 1988; Bury et al. 1991; Corn and Bury 1989, 1991; Dupuis and Steventon 1999), although it is not known whether this is due to habitat loss or degradation, disrupted immigration, or other causes. However, there is considerable variation across their range in the magnitude and direction of effects linked with forest harvesting (Richardson and Neill 1998; Biek et al. 2002). A combination of factors may affect population responses, and in the absence of long-term data, the extent of such impacts will not be fully understood.

Seasonal or directional movements in tailed frogs are not known. No studies have assessed whether movement may be stage dependent, although prereproductive individuals have been observed to move greater distances than adults (Daugherty and Sheldon 1982). These knowledge gaps may have bearing on population demography, as age- and sex-specific movement rates and direction may indicate critical life stages for population maintenance (Mduma et al. 1999).

Given that postmetamorphic tailed frogs depend on riparian habitat for at least some part of their life cycle to develop and that alteration of this habitat may impact populations, the following predictions were made: (1) *Ascaphus truei*'s upstream and downstream movements are restricted closer to the streamside (i.e., within 25 m of streams) in clearcuts than they are in less disturbed, mature forest stands. (2) *Ascaphus truei* abundance is lower in clearcuts than in intact forest. (3) Adults are more philopatric along streams in both habitats (Daugherty and Sheldon 1982), with prereproductive frogs being the main dispersers.

Conversely, strong directional movement was not expected to occur in mature forest stands with intact overhead canopy. Testing these predictions shed light on processes that potentially impact *A. truei* populations, thus allowing the application of management practices that will minimize such impacts. To date, this is the first quantitative comparison of how adult and juvenile numbers may be affected by habitat alteration.

Materials and methods

Study area

Three replicate study sites were established in clearcut habitats (<5 years old at time of study; formerly western redcedar (*Thuja plicata* Donn ex D. Don), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.); replanted in 1996 with Douglas-fir and western redcedar), and another three

Fig. 1. Schematic of the layout of a single pitfall station relative to streamflow. There were 16 stations in each study grid arranged in a 4 × 4 grid pattern. Stations consisted of a pitfall trap in the centre of each crotch (four drift fences and four pitfall traps at each station). Trap position reflected the direction of movement by the frog.
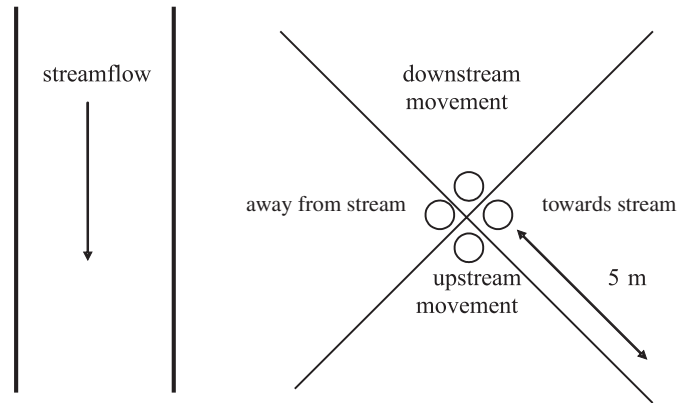
replicates were established in mature, second-growth sites (>81 years; dominated by Douglas-fir or western redcedar and broadleaf maple (*Acer macrophyllum* Pursh)). All study sites were located in the Chilliwack River valley of southwestern British Columbia, Canada. This area lies within the Coastal Western Hemlock biogeoclimatic zone of British Columbia (Meidinger and Pojar 1991), within the Cascade Range approximately 120 km east of Vancouver. Study sites were selected based on access and feasibility of installing drift-fence arrays with pitfall traps (Corn and Bury 1990) alongside nonfish-bearing streams <3 m wide, where preliminary surveys revealed the presence of *A. truei* larvae.

Experimental design

Sixteen drift-fence arrays were established in each study site, spaced 20 m apart in a 4 × 4 grid pattern. Each array consisted of clusters of four pitfall traps quartered by four guiding "drift" fences arranged in an "X" pattern, such that the direction of movement could be determined as upstream, downstream, towards the stream, or away from the stream (Fig. 1). Study trap grids were located beside creeks in mature forest stands and in clearcut sites without riparian reserves. Arrays closest to the streams were within 5 m of the stream margin. If an array could not be established owing to barriers such as stumps or trees, the location was shifted slightly around the barrier, with the pitfall station still within 3 m of its originally designated location. Obstacles blocking drift fences such as logs or rocks were removed or cut wide enough to allow passage of the drift fence and a corridor on either side. Where necessary, drift fences were diverted slightly around large, nonmovable obstacles such as stumps and trees. Fences were constructed of medium weight, clear polyfilm plastic sheets 25 cm high, and they extended 5 m out from the centre of the trap station. The bottom 5 cm of each fence was buried, and fences were stapled onto 40 cm wooden stakes pounded into the ground at intervals sufficient to prevent sagging. Pitfall traps were fashioned from 40-cm lengths of polyvinyl chloride (PVC) piping (15.2 cm diameter) buried upright with tops flush with the surrounding soil. Bottoms were cut from 3 mm thick sheets of black PVC and glued with nontoxic aquarium caulking (General Electric RTV silicone rubber adhesive sealant) onto the bottom of each PVC

pipe. Approximately five to eight holes (3 mm diameter) were drilled in each bottom to allow drainage while preventing amphibian escape. Plastic margarine containers (No. 2 size, 907-g capacity; Granpac, Wetaskiwin, Alberta), with bottoms cut out, were wedged into the top inner portion of each trap, with tops flush with the top of each trap to provide a "lip" to prevent amphibians from escaping. A length of biodegradable heavy jute twine (Bridgeline Ropes, Trenton, Ontario) extended to the bottom of each trap and was fastened to the top by tying a knot in the end and wedging it into a slit cut in the top of the margarine container. This twine allowed small mammals to climb out and potentially reduced predation on amphibians, yet minimized the chances of amphibian escape. Although traps were deep enough to provide sufficient shade to maintain relatively cool temperatures, pieces of moss were placed in the bottom of each trap and moistened with stream water to provide cover and reduce vulnerability to desiccation. Sites were monitored from June to September 1998 and during May 1999.

A total of 384 pitfall traps and drift fences were used across the six study sites. Owing to driving distances between sites, only three trap grids were opened at a time (either two clearcut sites and one mature-stand grid, or two mature-stand grids and one clearcut site) for three consecutive nights and checked each morning. Traps were then closed, and the other three sites were monitored for three days and nights. This cycle continued from June to September 1998 and during May 1999. Traps were checked within 24 h to minimize disturbance effects from observer visitations while decreasing the likelihood of amphibians becoming desiccated or being predated during prolonged periods in the traps. Pitfall traps were closed by fastening plastic lids onto the margarine containers, then securing the container in place with rocks or logs. With the onset of increased precipitation and cool weather in October and November 1998, all trap grids were continually left open at all sites and checked approximately once every 4 days. Sampling effort was equal among all six study sites in both habitat types.

All frogs were weighed (±0.05 g) using an Ohaus® SC2020 (Pine Brook, New Jersey) electronic balance and were measured for length to the nearest 1 mm. A 20-g Pesola® (Baar, Switzerland) hand-held scale was also used during times of heavy rainfall or wind, or when batteries in the balance failed. Body mass was used in this study, as snout-to-vent and snout-to-tail length measurements were found to be prone to greater variation. Frogs weighing >4.0 g were considered to be adults (reproductive), subadults (breeding capacity unknown) were 1.76–3.99 g, and immatures (prereproductive) were ≤1.75 g. Captured frogs were visually determined to be male, female, or unknown (e.g., immatures) and classed by age (based on mass and size). For pitfall captures at each site, the number of frogs in each age category was recorded for each direction (upstream, downstream, away from stream, towards stream) and distance from stream (5, 25, 45, 65 m). To distinguish new individuals from previously captured individuals, all frogs were marked by injecting a coloured, nontoxic elastomer dye (Northwest Marine Technology, Inc., Olympia, Washington) under the ventral skin surface of the hind leg, then individually marked by toe clipping (Ferner 1979; Sutherland 1996). Only first-time captures were used in the analysis. Frogs captured in pitfall traps were released in the quadrant

opposite to where they were caught at least 1 m away and facing away from the traps, as this was the presumed original direction of movement. Individuals caught outside the pitfall traps were released at their point of capture.

Larval surveys

For each stream, intensive surveys of larval abundance were conducted along 100-m reaches every 2 months to estimate the potential numbers of frogs metamorphosing at each site. The stream was divided into ten 10-m sections, each of which was intensively surveyed using standard methods (Corn and Bury 1990). All captured larvae were measured, weighed, and then returned to their respective stream sections after the survey. The number of larvae per metre length of stream provided a measure of the potential population size at a site to control for differences in stream productivity.

Data analysis

For all statistical analyses, critical significance level of tests was set at $\alpha = 0.05$. The dependent variables were the number of frogs in each age-class caught at a given distance from the stream (six sites by four distances) or moving in a particular direction (six sites by four directions). Most data were $\ln(x + 1)$ transformed to achieve normality. Although $\ln(x + 1)$ transformed data used in the analysis of variance (ANOVA) did not meet all the assumptions of normality for adults, the departure from normality was not considered to be extreme ($p = 0.03$), so the level of significance and the power of the test may still be considered valid (Neter and Wasserman 1974). In the case of subadults, the count data were sparse and not normally distributed (based on Wilk's λ), thus data were rank transformed to obtain normality. General linear models (PROC GLM; SAS® version 8.02, SAS Institute Inc., Cary, North Carolina) were used to analyse the data. Frog captures in each age-class were assessed for differences in movement direction using a two-way, nested ANOVA, with site nested within habitat type crossed with movement direction. Capture numbers within each age-class were contrasted with distance from the stream in a one-way, nested analysis of covariance (ANCOVA, with distance from stream as the covariate). A posteriori tests of specific differences were made using the Bonferroni comparison. A t test of $\ln(x + 1)$ transformed proportions was used to test for differences in total numbers per site between habitat types.

Results

Abundance

Total *A. truei* captures were similar between habitat types during the study period, with 88 *A. truei* captured in mature stands and 87 captured in the clearcut sites (Table 1). The ANOVA indicated that the total number of frogs, especially the number of adults and subadults, was significantly higher in mature stands when variation due to movement direction and site differences were included (Table 2). The ANCOVA showed that there were significantly more adults in the mature sites when site and distance were accounted for, but that the total number of frogs was not significantly different between habitats (Table 3). Both of the above analyses include additional sources of variation, and a simple t test of the three mature sites versus the three clearcut sites did not reveal significant differences in numbers of frogs between habi-

Table 1. Total number of frogs captured in pitfall traps in each age-class per site and habitat type throughout the study period.

Site name	Age-class			Site total
	Adults	Subadults	Immatures	
Clearcut sites				
McGuire	2	0	2	4
McTam	4	0	2	6
Tamihi	7	4	66	77
Clearcut total	13	4	70	87
Mature stands				
Elk	13	13	25	51
Ford	5	1	7	13
Vedder	8	3	13	24
Mature total	26	17	45	88

tats ($t = -0.713$, $p = 0.515$). Additionally, 7 amphibian species were caught in clearcuts, and 10 species were caught in mature stands (see Appendix A).

On average, adults were twice as abundant in the mature stands than in the clearcut sites. This difference was significant in both the ANOVA (which assessed movement direction) and the ANCOVA (which assessed distance from stream) ($p = 0.05$ and 0.03, respectively; Tables 2 and 3). There was no significant effect of site within habitat type on adult numbers (Tables 2 and 3).

Subadult captures in both habitat types were substantially lower than captures in other age-classes (Table 1). The ANOVA indicated a significant effect of habitat type and site within habitat type, but this was not the case in the ANCOVA (Tables 2 and 3).

Although immature frogs accounted for 80% of the total captures in clearcuts and 51% in mature stands (Table 1), this difference was not significant, in part owing to the large variation resulting from site within habitat type (Tables 2 and 3). Both the ANOVA and ANCOVA indicated that the number of immatures was weakly associated with habitat type, although there was a significant effect of site within habitat type. For immatures, the Bonferroni comparison indicated that significantly more frogs were caught at Tamihi than at all other sites, except Elk (Table 1). Within the mature stands, there was no difference in the number of immatures captured among the sites. Similarly, the Bonferroni test indicated that significantly more subadults were caught at Elk than at McTam ($p = 0.002$) and McGuire ($p = 0.002$). No other site comparisons were significant.

Larval surveys

For clearcuts, regression analysis revealed a strong positive relationship between the numbers of frogs caught by pitfall traps at each site and the number of tadpoles caught in the corresponding stream during stream surveys ($r^2 = 0.99$). Mature stands had no significant relationship ($r^2 = 0.002$). Thus, the relation across all sites was a result of the positive relation for the clearcut sites.

Direction of movement

Frequency of the four movement directions was compared at each site (upstream, downstream, towards the stream, away from the stream). A greater proportion of frogs moved paral-

lel to streams (upstream, downstream) than perpendicular (towards, away), regardless of habitat type (Fig. 2). However, there were no significant age- or habitat-specific differences in movement directions (ANOVA, Table 2).

Distance from stream

The ANCOVA indicated that there were no significant differences in capture frequencies across distance from stream for any age-class. However, the total number of frogs and the number of immatures were more affected by site than by habitat type (Table 3), and the Bonferroni comparison indicated that the Tamihi site had significantly higher numbers than all other sites, except Elk (Table 1). With the exception of Tamihi and Ford, where immature capture rates increased slightly with distance from stream, most capture rates decreased with increasing distance from the stream, regardless of habitat type (Fig. 3).

Discussion

This study indicates that age-specific differences in relative abundance and movements can occur in different habitats, which may have important implications for *A. truei* populations. The two principal findings were that clear-cut harvesting did not strongly influence *A. truei* movements or their proximity from streams, regardless of habitat type. However, adults were less abundant in the clearcut sites. The larger proportion of prereproductive frogs at the clearcut sites may indicate higher postmetamorphosis mortality or greater movement and dispersal.

Age- and habitat-specific differences in habitat use may have ramifications on population dynamics over time, particularly if small populations become more sensitive to environmental stochasticity (Schaffer 1981). Assessing survival and mortality rates of different age-classes and (or) sexes may provide insight on demographic responses to land use, including which age-class or life stage may be the most sensitive determinant of *A. truei* population dynamics (Sutherland 2000).

Larval surveys

Although the analysis for the clearcut sites indicated a strong relationship between the number of frogs caught in the pitfall traps and the number of tadpoles caught in the corresponding stream during stream surveys, no significant relationship existed for the mature stands. Thus, the overall relationship was driven by clearcuts, which suggest that tadpole densities alone were not good predictors of numbers of postmetamorphic life stages when all sites were combined. There is no reason a priori to expect that the two adjacent habitats (i.e., stream and terrestrial) would have similar habitat capacity for *A. truei*, in tadpole and postmetamorphic stages, respectively. However, the relation between relative abundances of tadpoles versus postmetamorphic *A. truei* at clearcut sites, in contrast to the lack of a relation at mature sites, suggests some differential processes affecting survival rates, emigration rates, or both in the two habitat types. One such possibility is habitat-specific resistance to movement, as demonstrated for other amphibians (Rothermel and Semlitsch 2002), but studies of such movements were beyond the scope of our study.

Table 2. Probabilities (p values) of differences in movement directions and habitat type using $\ln(x + 1)$ transformed number of frog captures in each age-class.

	df	Total frogs	Adults	Subadults	Immatures
Habitat type	1	0.04	0.05	0.04	0.36
Direction	3	0.06	0.09	0.32	0.06
Direction × habitat type	3	0.22	0.31	0.09	0.25
Site(habitat type)	4	<0.01	0.09	0.02	<0.01
Error	12				

Note: Only the data for pitfall captures were used. There were three replicate sites within each habitat type (clearcuts or mature forest) and four movement directions (upstream, downstream, towards the stream, or away from the stream).

Table 3. Probability (p values) of effects of habitat type and distance from stream based on $\ln(x + 1)$ transformed number of frog captures for each age-class.

	df	Total frogs	Adults	Subadults[a]	Immatures
Habitat type	1	0.09	0.03	0.18	0.22
Distance	1	0.12	0.56	0.99	0.11
Distance × habitat type	1	0.35	0.19	0.67	0.20
Distance × site(habitat type)	4	0.30	0.10	0.81	0.03
Site(habitat type)	4	0.04	0.18	0.53	0.01
Error	12				

Note: Only the data for pitfall captures was used. There were three sites within each habitat type (clearcuts or mature forest). Capture distances from stream were 5, 25, 45, and 65 m.
[a]Data were rank transformed to meet assumptions of normality.

Tamihi Creek had a relatively high abundance of immature *A. truei*. Stream productivity in clearcuts is enhanced owing to greater light penetration and increased algal production immediately following logging (Murphy and Hall 1981; Hawkins et al. 1983; Richardson and Neill 1998; Kiffney et al. 2003), so it is possible that high tadpole densities translate into high densities of metamorphs. However, habitat suitability for tadpoles does not necessarily reflect suitability in a direct way for other life stages (Van Horne 1983; Winker et al. 1995), and only multiyear monitoring could assess long-term suitability as conditions shift over time. Changes in survival rates over different age-classes could make a difference between a population that is increasing or declining, similar to changes in birth rates (Hastings 1998). Large numbers of young of the year in a site may also be deceptive as not all young of the year may originate from the same source (Seburn et al. 1997). Dispersing young of the year can thus make it appear that the site is successful when it in fact may not be. Ultimately, survival of individuals in a site is the best gauge of habitat suitability and its capacity (Winker et al. 1995).

Abundance, movement direction, and distance from streamside

The significant among-site variation in the number of immatures was likely influenced by the high proportion of immatures caught at Tamihi. The stream flowing through Tamihi was no larger than the other clearcuts streams and had no visible surface flow during August. However, the stream may be highly productive for larval development owing to more exposure to sunlight leading to increased algal growth (Kiffney et al. 2004; Mallory and Richardson 2005). It may also be that immatures moved through the Tamihi site from other origins, and the high captures reflected a larger spatial scale that could not be delineated from this study.

As a dispersal mechanism, juvenile movement may be selectively advantageous in discovering food, shelter, and favourable breeding grounds (Daugherty and Sheldon 1982). If unoccupied patches of habitat are available and mortality of migrating individuals is low, then immature dispersal will be beneficial when leaving degraded habitats, high density areas (Gill 1978), or areas subjected to fragmentation (Berven and Grudzien 1990; deMaynadier and Hunter 1999).

If seasonal variation becomes more pronounced as a result of habitat alteration, then this may increase activity levels or create a greater need for habitat mosaics to deal with changing conditions (Law and Dickman 1998), particularly if current habitat conditions become unfavourable. Dispersal is theoretically favoured in variable habitats (McPeek and Holt 1992). "Wanderers" may experience higher mortality rates than sedentary individuals owing to the increased likelihood of encountering predators (Rappole et al. 1989). For smaller frogs (i.e., immatures), there is also a greater susceptibility to desiccation. Thus, logging effects may contribute to density-dependent factors acting on immature survival that are otherwise not a problem under ideal conditions. Over time, gene flow may decrease if dispersal and colonization rates are reduced as a result of clear-cutting, as Berven and Grudzien (1990) observed with wood frogs (*Rana sylvatica*).

For immatures, the greatest proportion of frogs was caught furthest from the stream in clearcuts, which supported the findings of Daugherty and Sheldon (1982) that prereproductive *Ascaphus* move greater distances than adults. In clearcuts, it may be possible that immatures are moving greater distances to seek out appropriate habitat conducive to postmetamorphosis survival.

For disturbances such as clear-cutting, movements and life-history strategies of newly metamorphosed individuals may differ in sensitivity relative to those of other age-classes within the same species (deMaynadier and Hunter 1999).
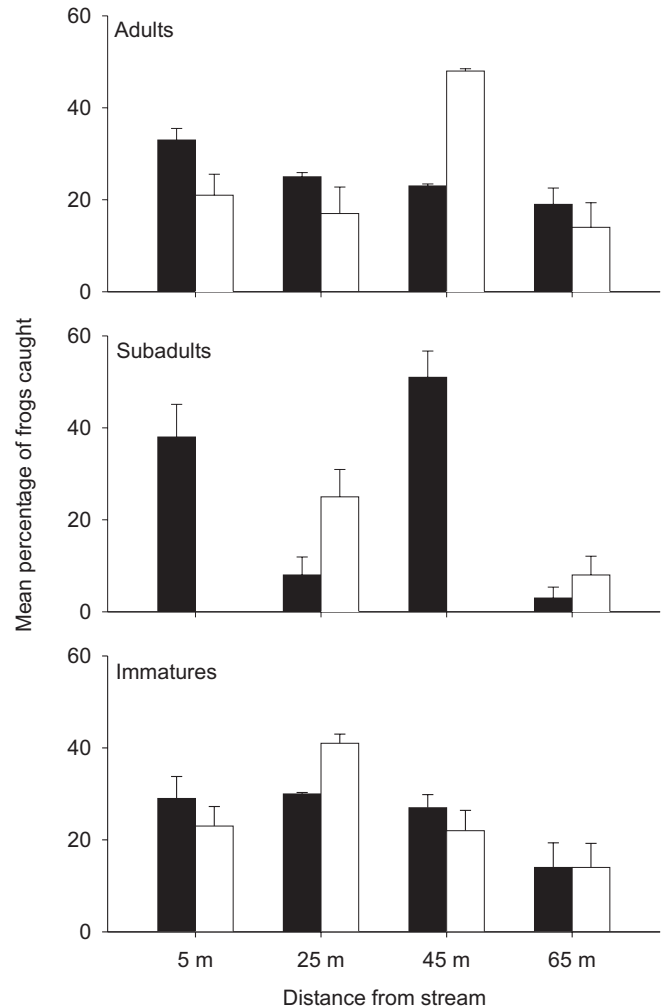
Fig. 2. Mean percentage of frogs captured in each habitat (+ standard error, $n = 3$ sites per habitat) for each direction of movement. Filled bars are for mature stands, and open bars are for clearcut sites. All captures were pooled from each array for a given direction at each site to obtain a single value. Proportion of frogs caught moving in each direction was relative to overall captures at the site.

Fig. 3. Mean percentage of frogs captured in each habitat (+ standard error, $n = 3$ sites per habitat) for each distance from the stream. Filled bars are for mature stands, and open bars are for clearcut sites. All captures were pooled from each distance at each site to provide four values per site. Proportion caught at each distance was relative to overall captures at the site.
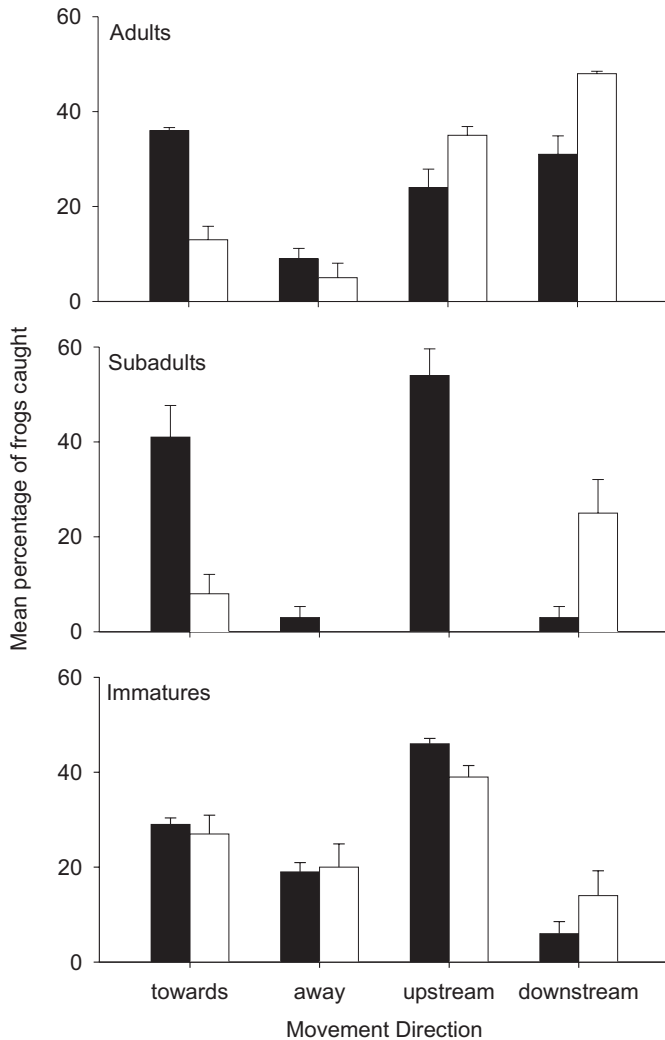
For this study, isolating the most significant factors affecting *Ascaphus* metamorphosis is difficult given the variation in environmental factors even amongst the sites within the same habitat type. Greater sensitivity to environmental cues may trigger rapid metamorphosis before drought within 1 year (Bury and Adams 1999), and this may be the case with the Tamihi clearcut site.

Owing to the time constraints, only a small number of sites could be assessed in this study, and the variation among sites resulted a statistical power that was too low to test many hypotheses (Peterman 1990). Interpretations should thus be made with caution. Forestry impacts can be measured at various scales (Bunnell and Huggard 1999), and while the site scale used in this study was considered appropriate to assess movement and responses to habitat disturbance, it may be insufficient to reveal larger scale population-level responses (deMaynadier and Hunter 1999). Seasonal shifts in activity and (or) abundance occurred in this study, but it is uncertain

as to whether these shifts are infrequent or cyclic without long-term monitoring. Pitfall-trap captures allow only assessment of frogs moving terrestrially and may not reflect animals moving via other routes, such as along or through streams.

With regard to the original predictions of this study, these findings indicated that *A. truei* did not become restricted to upstream and downstream movement in riparian corridors in clearcuts; immatures were actually found throughout the clearcut sites. Total *A. truei* abundance was not significantly lower in clearcuts. In some cases (i.e., immatures), abundance was higher in clearcuts. While prereproductive frogs may have been the main dispersers (in clearcuts), adult philopatry to streams was not detected in either habitat.

It is difficult to determine whether increased captures indicated increased abundance, increased movement, or both. Habitat-specific differences in movement rates may also affect residence time in a site and relative abundance. Amongst-site variation, even within similar habitats, had greater bearing on frog movement and relative abundance than did differ-

ences in habitat type. Distance from stream was also influenced more by site than habitat type, and capture rates generally decreased as distance from stream increased, regardless of site or habitat type. The differences in adult abundance hints that juveniles may simply move through clearcut sites without establishing residency, or have higher mortality rates, which could reduce local abundance through lower rates of reproduction in streams flowing through clearcuts.

Acknowledgements

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Appendix A

Table A1. Number of amphibian species (excluding tailed frogs) captured in pitfall traps in each site from June to September 1998 and during May 1999.

Species	Mature forest sites				Clearcut sites			
	Elk	Ford	Vedder	Total	McGuire	McTam	Tamihi	Total
Western toad (*Bufo boreas*)	150			150	2	20		22
Red-legged frog (*Rana aurora*)	2			2	2			2
Pacific treefrog (*Hyla regilla*)		2		2				0
Coastal giant salamander (*Dicamptodon tenebrosus*)	19	1	4	24				0
Northwestern salamander (*Ambystoma gracile*)	1			1	42	17		59
Long-toed salamander (*Ambystoma macrodactylum*)	2		7	9	27	5		32
Ensatina (*Ensatina eschscholtzi*)	2	51	35	88	2	1		3
Western red-backed salamander (*Plethodon vehiculum*)	8	18	115	141		1		1
Roughskin newt (*Taricha granulosa*)	1			1				0
Site total	236	85	185	506	79	50	77	206

Note: Sampling effort was similar across all six study sites. Numbers reflect total captures only and do not account for age-class or gender. Transect captures and larval frog and salamander captures from stream surveys are not included.