CHAPTER 10

Shifting roles of abiotic and biotic regulation of a multi-host parasite following disturbance

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10.1 Background

Impacts of macroparasitic diseases can scale from the individual host to the community (Anderson and May 1978; Holmes 1982; Scott 1988; Scott and Dobson 1989), however our knowledge of the community-level mechanisms that drive macroparasite dynamics in wildlife is still limited. Even more limited is empirical evidence that shows how parasites of wildlife respond to anthropogenic disturbances. Many of the current emergent and resurgent parasitic diseases in wildlife appear to be associated with anthropogenic activities (Schrag and Wiener 1995; Harvell *et al.* 1999; Daszak *et al.* 2000), but the paucity of rigorous data on wildlife diseases in general and their ecological aspects in particular limit our ability to assess causality. There are cases in which causality can be assigned, but these generally are limited to zoonoses (e.g. Lyme disease, Spielman 1994; LoGiudice *et al.* 2003; Wasserberg *et al.* 2003) and introduced pathogens of endangered or charismatic species (e.g. malaria in Hawaiian birds (Van Riper *et al.* 1986), whirling disease in trout (Hedrick *et al.* 1998), distemper in black-footed ferrets (Thorne and Williams 1988), upper respiratory disease in desert tortoises (Jacobson *et al.* 1991)). To date, few studies rigorously test for the impacts of anthropogenic disturbances, such as habitat loss, change, and degradation, on macroparasitic diseases in wildlife.

The evidence needed to link disturbance with diseases is often anecdotal, even for well-studied human diseases (McSweegan 1996). Recent work provides clues to the importance of anthropogenic disturbance in macroparasitic diseases with complex life cycles (Wasserberg *et al.* 2003). For example, overfishing in Lake Malawi is hypothesized to increase densities of the intermediate host snail of schistosomiasis and lead to increased prevalence in humans (Stauffer *et al.* 1997). Although this is a compelling argument, the authors acknowledge that their data are anecdotal and more study is necessary to test their hypothesis. A recent paper also suggested that eutrophication could alter food webs in a cascading effect from snail hosts to parasite abundance to limb deformities in amphibians (Johnson and Chase 2004). Again, this is a compelling hypothesis that deserves further testing but the data that support the links between eutrophication, snails, and infection in amphibians is generated from different studies in different sites over different years (see Skelly *et al.*, chapter 11, this volume for a systematic study of urbanization effects on trematode infection in amphibians).

Due to the extent and severity of anthropogenic disturbances and the likelihood that they will significantly alter parasite–host dynamics, it is essential to rigorously measure the response of different types of parasites and pathogens to disturbances and then apply this knowledge in ecological restoration and conservation efforts. This chapter focuses primarily on macroparasites that are especially sensitive to disturbance due to the diversity of hosts and transmission stages necessary to complete their life cycles. In addition to their inherent sensitivity to disturbance, macroparasites can have

significant, but difficult to detect effects on their host populations. Indeed, recent work demonstrates that nematode parasites can cause population cycles in grouse (Hudson *et al*. 1998). Thus, a change in macroparasitism in response to disturbance could greatly affect host populations, and the dynamics between hosts and parasites (May and Anderson 1979).

One of the main limitations in assessing impacts of anthropogenic disturbances on parasite populations in wildlife is the inability to replicate these disturbances. Natural disturbances play a strong role in structuring patterns of species diversity and distribution (Sousa 1984, 2001; Pickett and White 1985). The effects of natural disturbances are often measured through replicated experimental manipulations within a designated temporal and/or spatial regime (Levin and Paine 1974; Sousa 1979; Hobbs and Mooney 1991). The effects of large-scale, single-point anthropogenic disturbances, such as oil spills, can be difficult to assess as they are often generated by events that are unreplicated through time or space (for review see Schmitt and Osenberg 1996). As long as care is taken in site selection, some anthropogenic disturbances, such as habitat fragmentation and road building, can be used for natural experiments; however these are the exception to the rule. In addition, understanding the effects of disturbance on epidemiology can be made more difficult due to dispersal of infected individuals, parasite stages, or vectors away from or into the site of disturbance. Parasites with complex life cycles often infect hosts that cross ecosystem boundaries, such as schistosomes in humans, or migrate long distances, such as *Nanophyetus* in salmon. The difficulty is in assessing not only the patterns of infection, but also whether and how they are affected by anthropogenic impacts.

In this chapter, I report results of a study designed to measure the effects of three levels of anthropogenic disturbance on each host and parasite stage of a macroparasite that occurs in stream communities of the Pacific Northwest, USA. The disturbance of interest is clearcut logging: a prevalent, replicated, large-scale disturbance in the northwestern United States. I chose a "closed" parasite–host system in which none of the hosts regularly disperses or migrates outside of the local watershed. This eliminates the need to estimate parasite loss due to host movement. I carefully selected 18 creeks in watersheds exposed to three levels of disturbance associated with clearcut logging. They include streams located in old growth forests without anthropogenic disturbances, streams in clearcut forests, and streams in clearcut forests that experienced severe winter flooding (debris flow) that was exacerbated by logging. I measured the effects of disturbance level on the density of each obligate host and on the prevalence, intensity, and density of each stage of the parasite. I then assessed whether disturbance alters the strength or direction of the relationship between host and parasite densities and explored the implications of these changes to parasite transmission. I interpret these results in the context of general Anderson and May (1978, 1979) models for macroparasites. These models assume mass-action transmission that results in a positive relationship between host and parasite densities with or without an upper threshold. These models are commonly used to predict the response of parasites to environmental disturbances (e.g. Lafferty and Holt 2003). Finally, I test whether disturbance shifts the role of environmental and biotic factors in the host–parasite populations.

10.2 The parasite-host system

The trematode parasite, *Cephalouterina dicamptodoni*, obligately and sequentially infects three stream-dwelling species: the Pacific giant salamander, *Dicamptodon tenebrosus*, an abundant snail, *Juga silicula*, and the stonefly, *Calineuria californica* (Fig. 10.1) (Senger and Macy 1953; Schell 1985). Adult parasites live and sexually reproduce in the intestines of their salamander hosts. Parasite eggs are released into the environment with the host's feces where they are consumed by snails and subsequently hatch into miracidia. The miracidia migrate to the snail's gonads and transform into a series of sporocyst stages. Each of these sporocysts asexually produces thousands of cercariae that are then released into the aquatic environment. To continue the life cycle, these cercariae search for the next obligate host species which is a nymphal stonefly, *C. californica*. Once found, the cercaria

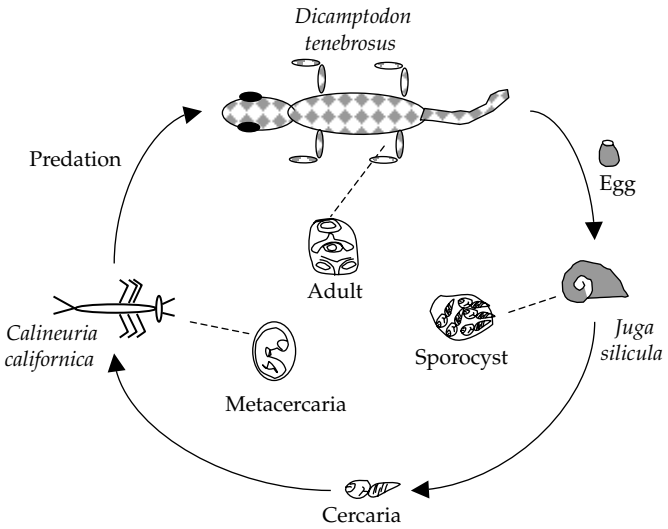

Figure 10.1 Life cycle diagram of *Cephalouterina dicamptodoni*, a trematode parasite that infects the definitive host, *Dicamptodon tenebrosus*, the first intermediate host, *Juga silicula*, and the second intermediate host, *Calineuria californica*. Free-living parasite stages transmit to the snail and stonefly host. Parasites transmit to the salamander via predation of an infected stonefly. Arrows indicate direction of transmission for each stage of the parasite between hosts.

pierces the stonefly with a scalpel-like stylet and penetrates the exoskeleton through the incision. Cercariae encyst as metacercariae in the muscle tissues of the stonefly. The life cycle of the parasite is completed when a salamander preys upon an infected stonefly and the metacercaria excysts and grows to sexual maturity.

Each host of *C. dicamptodoni* is an important component of the aquatic food web in small streams in the Cascade Mountains of Oregon. Larvae of *D. tenebrosus* often comprise the greatest vertebrate biomass in small streams throughout western Oregon and California and are voracious predators (Murphy and Hall 1981; Corn and Bury 1989). *Dicamptodon* larvae eat a wide variety of aquatic and terrestrial prey, with aquatic macroinvertebrates comprising the most significant prey base (Parker 1992). Salamander larvae of different size classes overlap significantly in the prey they consume with preference toward certain macroinvertebrates, including *Calineura* spp. During their aquatic stage, *D. tenebrosus* are territorial and cannibalistic. With the exception of neotenic individuals, larval salamanders reside in streams for 2–3 years until metamorphosis to the terrestrial adult stage (Nussbaum and Clothier 1973).

Juga silicula is an abundant aquatic snail inhabiting mid-elevation streams from northern California north to southern Washington (Burch 1982). This species often comprises the majority of total invertebrate biomass in streams, reaching densities of 1500 m^2, thus making them strong competitors with macroinvertebrate grazers, particularly Diptera (Hawkins and Furnish 1987).

Calineuria californica, the second intermediate host, is distributed from central California north through British Columbia and east to Montana (Stewart and Stark 1993). In the central Cascades, stonefly nymphs are semivoltine. *Calineuria* prey dominantly on larval Diptera and Ephemeroptera (Sheldon 1969; Peckarsky 1984).

10.3 Methods

10.3.1 Host censuses

To measure the effects of anthropogenic disturbance on patterns of parasite and host abundance, I surveyed each host species from 18 streams located in the McKenzie and Fall creek watersheds, Oregon. The streams were located in small watersheds (4–16 km^2) that had experienced one of three levels of anthropogenic disturbance associated with logging. The three categories of disturbance were: no disturbance (ND), intermediate disturbance (ID), and severe disturbance (SD). ND streams ($n = 7$) were located in watersheds covered by mature forests that were at least 80 years old. ID streams ($n = 7$) were in watersheds with at least 50% clearcuts. SD streams ($n = 4$) were in watersheds

with predominantly clearcut forests that experienced major flooding and debris flows (as defined in Leopold *et al.* 1964) 2 years prior to the survey. Clearcut watersheds were defined as having ⩽ 20-year-old clearcuts covering at least 50% of the area of the watershed. Each watershed was selected to minimize differences in logging-independent geomorphology such as stream gradient, elevation, and watershed size. Streams were randomly sampled with respect to date from June 13 through July 30, 1998.

Each stream was sampled over a 2-day period. Macroinvertebrates and physical data were collected on the first day and salamanders were collected on the second day. Streams were sampled in a stratified random manner and samples were collected every 5 m along a 150 m transect for a total of 30 surber samples per stream. *D. tenebrosus* larvae and neotenes were collected from each stream along the 150 m transect using a fish electroshocker. Seine nets were placed at least every 50 m along the transect to block individuals from escaping. All *D. tenebrosus* were counted, measured, and weighed in the field. A representative sample of larvae was euthanized, dissected (Table 10.1), and all intestinal parasites were counted and preserved.

Snails, stoneflies, and other macroinvertebrates were collected from a 30 × 30 cm quadrat using a surber sampler. All snails greater than 5 mm were dissected for sporocyst presence. Counting sporocysts was time-prohibitive so intensity of this stage was estimated based on a regression of percentage of gonad infected and gonad length (Poteet 2001). Snails smaller than 5 mm were not included in these data since prior dissections revealed that small snails were never infected (Poteet 2001). All encysted metacercariae were counted in each stonefly. To count all the metacercariae, each stonefly was digested in an HCl and pepsin bath that dissolved stonefly muscles, but not parasite cysts (Ash and Orihel 1991).

Prevalence, intensity, and density of each parasite stage were calculated following Bush *et al.* (1997). Prevalence was calculated as the proportion of hosts in the population that were infected by one parasite stage. Mean parasite intensity was measured as the number of parasites of a single stage averaged across all infected hosts in the population. Mean parasite density was calculated as the number of parasites of a single stage averaged across all hosts per square meter. For parasites in snails and stoneflies, each metric was averaged per quadrat. Stream averages were calculated as the grand mean for all quadrat means. Means for prevalence, intensity, and density of the adult parasites were averaged across all dissected salamanders and then divided by total creek area sampled. The total creek area sampled was the product of the transect distance of 150 m and the mean wetted width of the creek.

Table 10.1 Number of *D. tenebrosus* larvae captured and dissected along a 150 m transect within each creek. All captured larvae were weighed and measured in the field. Larvae that were not dissected were released in the creek from where they were captured.

Creek	Date	Disturbance	Captured	Dissected
CONE	17 June	ND	42	18
JONES	21 June	ND	74	23
SLICK	24 June	ND	12	10
SFGATE	28 June	SD	24	10
HOLDEN	1 July	ID	4	3
OSBORNE	3 July	ID	43	20
RITCHIE	6 July	ID	46	21
FINN	8 July	ID	14	10
WFNFGATE	10 July	SD	31	17
HAGAN	11 July	ND	100	30
EFNFGATE	15 July	SD	48	19
SIMMONDS	17 July	ND	38	17
ELK	19 July	ND	24	11
WFDEER	21 July	ID	46	23
EFDEER	23 July	ID	42	19
NFNFGATE	25 July	SD	21	11
MONA	28 July	ND	45	22
STURDY	31 July	ID	8	5

Disturbance levels are ND = no disturbance, ID = intermediate disturbance, SD = severe disturbance.

10.3.2 Disturbance, environmental variables, and parasitism

Logging leads to increased stream temperatures, altered stream velocity, and decreased habitat heterogeneity. Clearcuts in the Cascade mountains are associated with high rates of hillslope erosion and increased storm peak discharge (Jones and Grant 1996) that affect stream channel morphology,

particle size, and discharge. Each of these variables can significantly affect the success of parasite transmission (Chernin and Perlstein 1969; Upatham 1974; Anderson *et al*. 1982; Jewsbury 1985; Woolhouse and Chandiwana 1989; Shostak and Esch 1990; Sousa and Grosholz 1991; McKindsey and McLaughlin 1994). Along each 150 m transect, I measured a series of environmental attributes associated with logging and used these measures to correlate parasitism with disturbance-related environmental variables. These attributes included dominant substrate particle size, thalweg depth, thalweg velocity, percent channel morphology (pool, riffle, run, or cascade), and percentage of canopy cover. I also measured substrate embeddedness, or the extent to which fine sediments filled the interstitial spaces around larger substrates (Bovee 1982; Gordon *et al.* 1992). The interstitial spaces formed within creek substrates are important habitat for salamanders, stoneflies, and other stream biota. Thus, as embeddedness increases, habitat availability and biotic productivity decreases.

To standardize host and parasite density measurements across creeks, I measured bank-full width and depth and wetted-channel width. Air temperature was measured in the morning, and minimum and maximum diurnal water temperatures were measured over the 48-h sampling period. Watershed area was calculated from USGS 7.5′ topographic maps.

10.3.3 Statistical analyses

I tested for differences in host density and parasite prevalence, intensity and density across forest disturbance levels with analysis of variance (ANOVA) followed by adjusted Tukey post hoc comparisons. I regressed parasite density on host density for each host–parasite pair to test model assumptions that parasite transmission leads to positive correlation between host and parasite densities (May and Anderson 1979). All variables were transformed where necessary to meet the assumptions of homogeneity of variance and normality.

I tested for the responses of parasite density to abiotic and biotic variables with principal components analysis (PCA) followed by analysis of covariance (ANCOVA). Seven correlated abiotic variables were transformed into their principal components (Selvin 1998; S-Plus 2000). Variables used in the PCA included maximum water temperature, thalweg velocity, pool/riffle ratio, percentage canopy cover, channel shape (measured as width/depth ratio), embeddedness (Brusven Index, Gordon *et al.* 1992), and mean substrate particle size (Dunne and Leopold 1978). These variables were chosen for their high probability of affecting host or parasite populations. Before conducting the analysis, the data were transformed where necessary to meet the assumptions of normality and homogeneity of variance and all variables were standardized to a mean of 0 and unit variance to account for differing scales of measurement.

Biotic variables considered for the ANCOVA included host length, host density, parasite density and, in the case of metacercarial transmission, salamander diet (i.e. the mean number of stoneflies found in salamander stomachs per treatment, see Fig. 10.1). Abiotic variables considered for the ANCOVA included the first three principal components. Because the number of possible explanatory variables for the ANCOVA was greater than the number of replicate streams, I chose leaps and bounds analyses to select the best-fit models for each host–parasite pair (Furnival and Wilson 1974; S-Plus 2000). Leaps and bounds analysis is similar to model selection analyses that evaluate the best fit models from the full set of explanatory variables. However, unlike other model selection analyses leaps and bounds uses an algorithm developed by Furnival and Wilson (1974) that identifies the best fit by testing all possible models. The resulting best-fit models of donor-target pairs had at least four explanatory variables and thus I was unable to divide the forests into all three disturbance levels for the analyses due to low replication. The final best-fit models lumped ID with SD into a single "disturbed" category.

10.4 Results

10.4.1 Responses of host density and parasite prevalence, intensity, and density to environmental disturbance

Densities of each host species were significantly lower in logged creeks, but patterns differed by

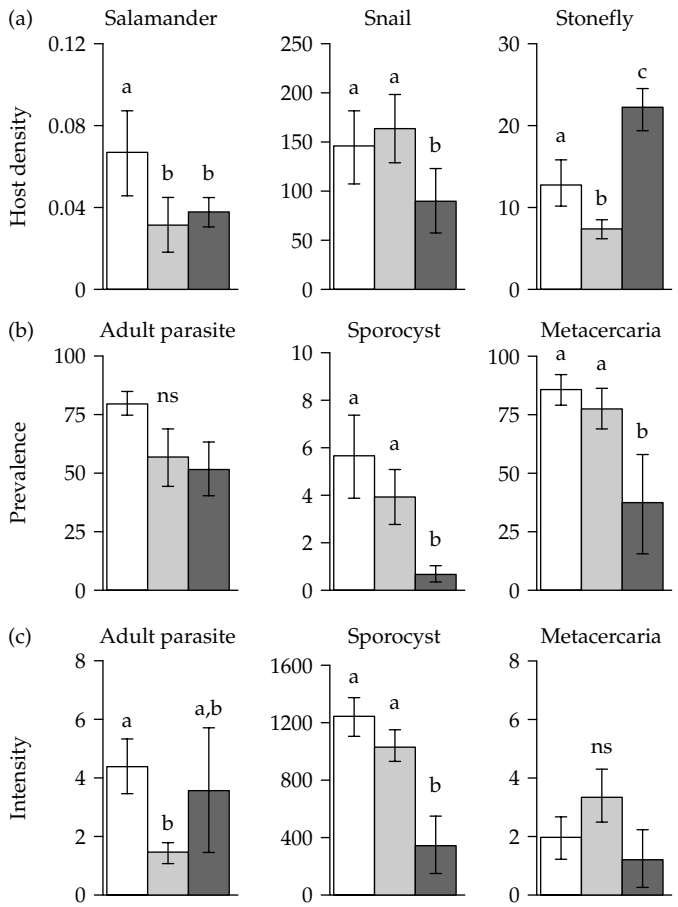

Figure 10.2 Host density, parasite prevalence, and parasite intensity for 18 streams of three disturbance intensities. (A) Host density is the mean number of hosts/m^2. (B) Prevalence is the mean proportion of hosts infected. (C) Parasite intensity is the mean number of parasites averaged across all infected hosts. Small letters denote statistical significance at the $p < 0.05$ level. Error bars are ± 1 SE. White bars = no disturbance (ND) sites, grey bars = intermediate disturbance (ID) sites, and black bars = severe disturbance (SD) sites.

host species and level of disturbance (Fig. 10.2(a)). Salamander density was similar across ID and SD creeks, but snail densities were lower only in creeks with the most severe disturbances. Stonefly densities differed across disturbance levels such that the lowest stonefly densities were found in ID streams and the highest densities were found in SD streams.

Prevalence and intensity of each parasite stage was generally lower in logged sites but did not track host density (Fig. 10.2(b) and (c)). Interestingly, adult parasite intensity recovered somewhat in severely disturbed streams even though salamander densities remained low (Fig. 10.2(a) and (c)). At the same time, prevalence of adult parasites remained constant across disturbance (Fig. 10.2(b)) leading to a recovery in the density of adult parasites in SD streams as compared to ID streams (Fig. 10.3(a)). These results run counter to many population models of macroparasite population dynamics (e.g. May and Anderson 1979) and to predictions that parasite densities will decrease following disturbances that cause decreased host densities (Lafferty and Holt 2003). This anomaly is likely explained by an increase in the rate of parasite transmission from stoneflies to salamanders that result from the predation-dependent transmission of this parasite stage (Box 10.1).

Of all stages, the sporocysts were most affected by disturbance, with significant declines in prevalence and intensity in ID and SD creeks. This density-dependent effect is partially explained by the sharp decline in snail host density in the sites with severe disturbance, but is also associated with changing abiotic conditions (see *Principal Components Analyses*, below). Intensity of metacercariae was not

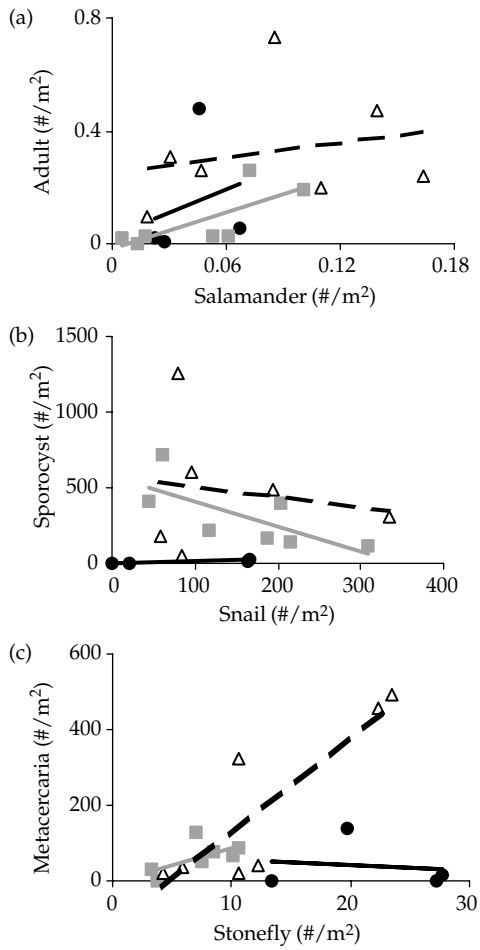

Figure 10.3 Regressions between each host and parasite pair at three levels of disturbance. Common models for macroparasite populations assume a positive correlation between parasite and host densities. These regressions demonstrate that this assumption is not valid for most of the parasite stages in areas with environmental disturbances. (a) Adult parasite in salamanders, (b) sporocyts in snails, (c) metacercariae in stoneflies. Open triangles with dashed lines = no disturbance (ND) sites, gray squares with solid gray lines = intermediate disturbance (ID) sites, and filled circles with solid black lines = severe disturbance (SD) sites.

statistically different across the disturbance gradient (Fig. 10.2(c)), but metacercarial density was lower in SD than ND sites (Fig. 10.3(c)). The low metacercarial density in SD sites was somewhat surprising since stonefly densities in these sites were the highest of the three stream types. The low density of metacercariae in SD sites was probably due to low recruitment of cercariae from small snail populations at these severely disturbed sites.

10.4.2 Environmental disturbance and model assumptions

If the assumption of mass-action transmission is correct in the general macroparasite models (May and Anderson 1979), then regressions of parasite density on host density should have positive slopes. Significantly positive regressions between parasite and host densities were found in only two cases (Fig. 10.3(a) and (c)): between salamanders and adult parasites in ID ($R^2 = 0.5584$, $F_{1,5} = 6.321$, $p = 0.054$) and between stoneflies and metacercariae in ND ($R^2 = 0.6153$, $F_{1,5} = 7.999$, $p = 0.037$). In general, the regression slope between adult parasites and salamanders trended toward positive across all disturbance levels (Box 10.1). This is not the case for the two other parasite stages. In fact, the regression between snails and sporocyst densities was significantly negative across ID sites ($R^2 = 0.6096$, $F_{1,5} = 7.806$, $p = 0.038$) and was not significantly different from 0 at ND and SD sites (Fig. 10.3(b)).

10.4.3 Physical attributes of streams: univariate analyses

When selecting streams to test for effects of environmental disturbance on parasite populations, I controlled for geographic location, watershed area, elevation, and stream gradient to minimize differences among watersheds that were not caused by disturbance. All but three streams were located in the McKenzie River watershed. The remaining three streams, Jones, Slick, and Sturdy, were in the Little Fall creek watershed, which is the drainage immediately south of the McKenzie River watershed. There were no differences in watershed area, elevation or stream gradient among streams in different forest types (basin area: $F_{2,15} = 0.271$, $p = 0.766$; elevation: $F_{2,15} = 1.743$, p=0.208; gradient: $F_{2,15} = 0.052$, $p = 0.949$).

Undisturbed streams had significantly higher pool to riffle ratios (30%) than ID (11%) or SD (2%) streams. Thalweg velocity and substrate embeddedness (Brusven Index) were higher in streams at logged sites (velocity: $F_{2,15} = 28.276$, $p = <0.001$;

Box 10.1 Transmission through predation of an obligate, intermediate host

Predicting how changes in salamander density will affect parasite dynamics is not straightforward since salamanders acquire infections by consuming infected stoneflies. Thus, transmission of metacercariae will depend upon the predator–prey functional response curve between salamanders and stoneflies. May and Anderson (1979) suggest that transmission completed through a trophic link is extremely efficient and that the threshold density of predators, in this case salamanders, required to maintain the adult parasite population is low (May and Anderson 1979). So even at extremely low salamander densities, metacercarial transmission should be successful. However, the rate of transmission will vary with the predator–prey functional response, which will depend upon the density of salamanders and stoneflies. Pacific giant salamander larvae prey disproportionately on mayflies and large predaceous insects, including stoneflies (Parker 1994). The proportion of stoneflies relative to the other prey items preferred by salamanders is not constant across forest type (M. Poteet, unpublished data). This suggests that the functional response curve is likely to be nonlinear with disturbance, either Type II or Type III, which would lead to nonlinear parasite transmission and not the linear transmission function assumed by mass-action models (e.g. Crofton 1971; Anderson and May 1978). In addition, since the salamander must eat an infected stonefly to become infected, the rate of transmission will not only be affected by the functional response of the predator, but also by the proportion of stoneflies that are infected. Thus, a transmission term that is dependent upon prevalence of infection in stoneflies would provide a better description of metacercarial transmission than would mass-action transmission. This is reminiscent of frequency-dependent models in which infection of the vector is dependent upon the frequency of infected nonvector hosts (Getz and Pickering 1983; Thrall *et al*. 1995; McCallum *et al*. 2001). One interesting outcome of frequency-dependent transmission is the lack of a host threshold, since transmission depends upon proportional infection. By this model, even if stonefly and salamander densities are extremely low, parasites should still be able to establish in salamanders. That seems to be the case in this system, where even at high levels of disturbance and low metacercarial densities (Fig. 10.3(c)) adult parasite density almost recovers to undisturbed levels (Fig. 10.3(a)). In either transmission model, decreased salamander density should result in decreased metacercarial transmission and this is the case here. At each level of disturbance, regardless of salamander density, there is a direct correlation between salamander densities and adult parasites. This is not the case for the free-living transmission stages (sporocysts and metacercariae), whose densities are affected by both environmental stressors and host density.

embeddedness: $F_{2,15} = 5.391$, $p = 0.005$). The only abiotic factor that was significantly lower at logged sites was canopy cover ($F_{2,15} = 20.770$, $p < 0.001$). The decreased canopy cover in ID and SD streams corresponded to slightly increased air temperature and maximum water temperature, though neither differed significantly with disturbance level (air temperature: $F_{2,15} = 2.667$, $p = 0.102$; water temperature: $F_{2,15} = 0.648$, $p = 0.537$).

10.4.4 Physical attributes of streams: principal components analyses

Each of the principal components described some aspect of the physical responses of streams to logging. Logging increased sediment load delivered to the creeks, increased peak storm flows (Jones and Grant 1996), and decreased canopy cover. These changes altered channel shape, increased stream velocity, and decreased streambed particle size. Each of these features is described by at least one principal component, with channel shape a significant feature in each principal component.

The first principal component (PC1) described channel shape and was composed of positive correlations between stream velocity and the ratio of bank full width to bank full depth (width/depth). This reflected higher stream velocities and wider, shallower channels following logging. The second principal component (PC2) described stream channel pool/riffle morphology. Logging increased the proportion of riffle habitat which led to greater mean channel width. Pool/riffle ratio was inversely proportional to width/depth ratio and stream temperature. The third principal component (PC3) described streambed particle size

Table 10.2 Results of ANCOVA testing for the effects of disturbance on the biotic and abiotic variables that best explain variation in each stage in the life cycle of the parasite. Best fit models were selected with the leaps and bounds method (see text for explanation)

Adult				**Sporocyst**				**Metacercaria**			
	C	***t***	***p***		***C***	***t***	***p***		***C***	***t***	***p***
ND	–0.504	–0.949	0.361	ND	–31.663	–2.25	0.059	ND	–0.987	–0.455	0.663
D	–0.469	–0.883	0.394	D	–20.61	–1.464	0.186	D	–3.476	–1.601	0.153
Salamander #/m^2 (ND)	0.236	2.224	0.046	Snail #/m^2 (ND)	8.797	2.726	0.03	Stonefly #/m^2 (ND)	3.407	3.907	0.006
Salamander #/m^2 (D)	0.179	3.554	0.004	Snail #/m^2 (D)	0.905	1.224	0.26	Stonefly #/m^2 (D)	0.858	0.946	0.376
Salamander SVL (ND)	0.274	1.912	0.080	PC3 (ND)	–4.02	–1.267	0.246	PC1 (ND)	1.468	1.578	0.159
Salamander SVL (D)	0.113	2.575	0.024	PC3 (D)	0.494	0.831	0.434	PC1 (D)	–0.217	–0.705	0.503
				PC1 (ND)	7.525	2.464	0.043	Snail #/m^2 (ND)	2.828	2.086	0.075
				PC1 (D)	–0.946	–2.943	0.022	Snail #/m^2 (D)	1.74	4.109	0.004

ND = no disturbance, or watersheds in old growth forests; D = disturbance, or watersheds in clearcut forests with and without debris flows; SVL = salamander length measured from the snout to the vent in mm; P1 = principal component 1; P3 = principal component 3; C = regression coefficients. The first two coefficients in the 'C' column are regression intercepts for the ND or D sites respectively. The remaining coefficients are regression slopes for each variable for the ND or D sites respectively.

as a function of channel shape and was composed of the pebble count, maximum water temperature, and width/depth ratio. Width to depth ratio and pebble count were positively correlated with each other and inversely related to the maximum water temperature. The first three principal components among all streams explained 76% of the variation in abiotic variables. The significant components were based on variables with loadings greater than 0.40 or less than − 0.40 (Hair *et al.* 1987; McGarigal *et al.* 2000).

10.4.5 Disturbance shifts the importance of biotic and abiotic variables

Because host density did not explain significant amounts of variability in abundance for most of the parasite stages, I expanded the regression analyses to include host density and the first three principal components. Leaps and bounds analyses selected the following explanatory variables for each parasite stage to minimize the Mallow's Cp:

- adult parasite density: salamander density and salamander length;
- sporocyst density: snail density, PC3, and PC1;
- metacercarial density: stonefly density, PC1, and snail density.

The models were analyzed with ANCOVA using forest type as a covariate. Since there were only four replicates of SD streams, I combined the ID and SD forests into a "disturbed" category (D).

In all but the adult parasite stage, disturbance switched the dominant variable that best explained parasite density (Table 10.2). Although disturbances had significant effects on the overall density of adult parasites, they did not alter the positive correlation between the parasite and its salamander host. For example, adult parasite density was positively and significantly correlated with salamander density in both logged and unlogged streams, and significantly correlated with salamander size in logged streams (Table 10.2). Adult parasite densities could not be explained by variation in abiotic variables for either logged or unlogged streams.

Unlike adult parasites, disturbance caused a significant shift in the type of variables that controlled sporocyst density. Both abiotic and biotic variables correlated with sporocyst density in unlogged streams, but only abiotic variables affected sporocyst density in logged streams. Specifically, sporocyst density was significantly and *positively* correlated with snail density and the channel shape/velocity principal component (PC1). However, in streams with disturbance, sporocyst density was significantly and *negatively* correlated with PC1 and not correlated with snail density (Table 10.2).

Disturbance caused a shift in the biotic variables controlling metacercarial densities, but as with adult parasite density, abiotic variables were not associated with metacercarial densities in logged or unlogged streams. In unlogged streams, stonefly density explained the majority of variation in metacercarial density. Disturbance shifted control over metacercarial density from stonefly hosts to snail hosts in logged streams (Table 10.2).

10.5 Discussion

Land use change and resource use by humans increasingly force species to cope with fragmented and degraded habitats that can alter infection dynamics of diseases and parasites (e.g. Dobson and Carper 1992; Lafferty and Holt 2003; LoGiudice *et al.* 2003, this volume). Although several reviews report that diseases and parasites of wildlife respond to anthropogenic disturbances (Schrag and Wiener 1995; Lafferty 1997; Daszak *et al.* 2000), most of the studies cited are either anecdotal or are not sufficiently replicated, which limits our ability to interpret them (but see Wasserberg *et al*. 2003). By measuring each stage of a macroparasite and its host species across replicated environmental disturbances, this study measures the response of parasite infection levels to disturbance and also explores the mechanisms that drive these changes.

Disturbances caused by logging led to significant declines in host density and in the prevalence, intensity, and density of infection by trematodes in these three host species. Regressions between parasite and host densities were also affected by disturbance, suggesting that disturbance

affected the success or functional form of parasite transmission. Disturbance could act directly on parasite transmission by changing abiotic factors that impact the free-living stages of the parasite, or indirectly by affecting host abundance or distribution (in space or time) (Sousa and Grosholz 1991; Sapp and Esch 1994; Marín *et al*. 1998). For example, changes in abiotic factors such as temperature and velocity can directly affect reproduction and survival of parasite transmission stages (Anderson *et al*. 1982; Evans 1985; Jewsbury 1985). Higher temperatures lead to increased reproductive rate of parasites, often at the expense of survivorship of the free-living stages (Anderson *et al*. 1982). On the other hand, increases in stream velocity result in damage to and decreased transmission success of parasite infective stages (Upatham 1974; Jewsbury 1985). Transmission of free-living stages can also be directly affected by changes in geomorphology and microhabitat heterogeneity (Chernin and Perlstein 1969, for review see Sousa and Grosholz 1991), features of streams that are often affected by logging (Dunne and Leopold 1978; Beschta *et al.* 1987; Bisson *et al*. 1987; Everest *et al*. 1987).

Indirect effects of logging on parasitism are just as likely to occur as direct effects, and will be manifest through changes in host population features including host density and size structure. Logging did have a strong effect on density of each of the three host species. In high gradient streams similar to those I censused, larval salamander and nymphal stonefly densities generally increase while snail densities generally decrease after logging (Murphy and Hall 1981; Hawkins *et al.* 1982, 1983, but Corn and Bury 1989 found decreased salamander density in logged creeks). In this study, host density responded strongly to logging both with and without debris flows but the strength and direction of the effect was dependent upon host species and severity of logging. Salamander density decreased following logging, regardless of debris flows whereas snail density did not change following logging unless it was coupled with debris flows. Stoneflies were the most sensitive to logging disturbance. Their population density decreased in logged creeks but rebounded above unlogged levels in streams with severe disturbances (debris flows). The increased abundance of stoneflies following debris flows is most likely due to the decrease in canopy cover and subsequent increase in light penetration to the stream. Increased sunlight penetration in streams leads to increased algal production (e.g. Gregory 1980; Hill and Harvey 1990), which translates into more herbivorous prey for the predaceous stoneflies (Power 1992; Hill *et al.* 1995).

The response in host densities to disturbance was not mirrored by the parasites. Different disturbance levels led to complex, noncorrelated responses among the suite of parasite stages and their hosts. This suggests that the decline in parasite infections in disturbed streams was accompanied by changes in transmission dynamics of the parasites. The simple mass-action transmission that is often used in models of parasite population dynamics assumes that the rate of transmission is directly proportional to the densities of uninfected and infected hosts or parasitic stages (e.g. Crofton 1971; Anderson and May 1978, 1979; May and Anderson 1979). These linear transmission models generally predict a threshold host density below which parasites cannot persist and a stable equilibrium in which the disease is maintained. Logging-induced disturbances in this study generated complex patterns among parasite stages and their hosts that suggest nonlinear transmission. For example, the correlations between snail and sporocyst densities in ND and ID sites (Fig. 10.3(b)) show decreasing sporocysts with increasing snail densities, suggesting density-dependent transmission. In SD sites for this same host–parasite pair, there was no significant correlation.

Unlike sporocyst–snail pairs, correlations between salamander densities and adult parasites suggest a maximum threshold of infection, possibly limited by recruitment from stoneflies (Fig. 10.3(a)). Although the salamander–adult parasite pair seems to fit the mass-action model, it also has the characteristics of frequency-dependent transmission (Box 10.1). The sporocyst–snail and metacercaria–-stonefly pairs are more likely to fit models that assume nonlinear transmission and that exhibit more complex behaviors including unstable host–parasite equilibrium points, multiple stable equilibrium points, lack of host thresholds in some cases, and limit cycles (May and Anderson 1979; Gabriel *et al.* 1981; Getz and Pickering 1983; Liu

et al. 1986; Hochberg 1991; Briggs and Godfray 1995; Dwyer *et al.* 1997; McCallum *et al.* 2001).

The sensitivity of models to transmission functions has implications for maintenance, epidemics, and invasion of disease and parasitism. Since transmission is a function of the densities of susceptible hosts and infected hosts or parasite stages, anthropogenic disturbances that alter the availability of either host or parasite will inevitably affect transmission. That is certainly the case here. Transmission dynamics can be teased apart through careful experiments to test for shifts in the functional form of transmission due to changes in the donor (infected) and target (susceptible) host species and to determine how to model these parasite dynamics to predict the effects of different disturbance levels on parasite population dynamics (Box 10.2).

Box 10.2 *In-situ* manipulations of host and parasite density to test responses of transmission to disturbance

Because the success of parasites hinges on transmission from one host to the next, disturbance-induced changes in density of infected or susceptible hosts are likely to significantly affect the rate or functional response of transmission (May 1977; May and Anderson 1979; Schwartz 1985; Hochberg 1991; Woolhouse *et al.* 1991; Anderson and May 1992; Gubbins and Gilligan 1997; Hudson and Dobson 1997). The direction and strength of these effects will depend on characteristics of the particular host–parasite association. Transmission between hosts can be accomplished by free-living stages of the parasite, consumption of parasite eggs or cysts by susceptible hosts, or through consumption of infected prey by susceptible hosts. Thus one parasite with at least three hosts could employ each mode of transmission during its life cycle. The parasite species, *C. dicamptodoni*, which I discuss in this chapter, is a good example of this. Elucidating the form of transmission is essential for building models of parasite–host dynamics and for predicting at which life-history stage and in which direction will parasites respond to disturbances.

Transmission of parasites by a free-living stage combines the processes of reproduction in and dispersal away from the infected or "donor" host, and location of and recruitment into the subsequent or "target" host. Changes in density of the donor host could thus alter reproduction of parasite recruits, whereas changes in the density of target hosts could affect the probability of locating and recruiting to a host. Parasites that transmit through predator–prey interactions will also respond to altered host densities if the trophic functional response is altered as a result of disturbance (see Box 10.1).

McCallum (2000) and McCallum *et al.* (2001) provide short reviews of empirical and analytical methods to estimate parasite transmission rates and force of infection. The following methods specifically refer to field experiments that test for the effects of disturbance on the functional form of transmission in macroparasites. The form of transmission can be measured empirically by simultaneously manipulating donor (reproduction) and target (recruitment) host densities in a fully factorial, replicated experiment (Fig. 10.4). Host densities should span the range of densities found in all sites across the disturbance gradient. Experiments should

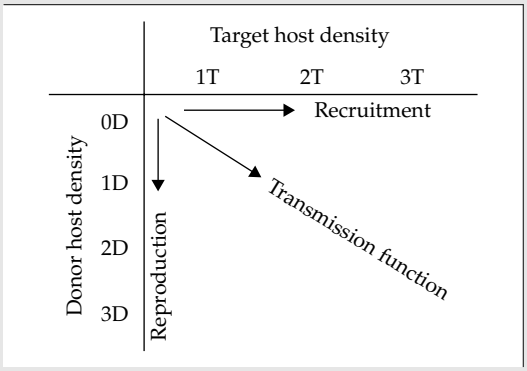

Figure 10.4 Factorial design for experimental estimation of the transmission function as it is affected by disturbance-induced changes in host densities. The response variable is parasite density in target hosts. Densities of donor (D) and target (T) hosts are selected to span the range of host densities found across the disturbance gradient. This diagram shows three densities of target hosts and four densities of donor hosts. The 0 donor host treatment is included to control for background levels of parasite reproduction in the environment. Density gradients in donor hosts with target host density held constant test for density-dependence in parasite reproduction. Density gradients in target hosts with donor host density held constant test for density dependence in parasite recruitment. The form of transmission can be estimated when donor and target host densities are manipulated simultaneously to determine the final parasite density in target hosts.

continues

Box 10.2 ***continued***

last just long enough for the parasites to recruit and mature, but not long enough for asexual reproduction to occur, if present in the parasite species. Host age or size should be standardized as appropriate. The response variable is the density of parasites that successfully recruit into the target hosts. Density of infective parasite stages can be assessed from dissections of donor hosts at the end of the experiments. While holding target host density constant, regressions of the response variable on infective parasite density provides an estimate of parasite transmission that is dependent on reproduction. While holding donor host density constant, regressions of the response variable on target host density provides an estimate of parasite transmission that is dependent on recruitment. Simultaneous analysis of the response variable across densities of infective parasites and target hosts provides a three-dimensional functional response plane for transmission across varying target and host densities. To date, I am aware of only one study that has accomplished this for all transmission stages of a single macroparasite in the field (Poteet 2001).

Experimental tests of the response of parasite transmission to changes in host density are more straightforward for parasites of small, nonmigratory hosts such as those reported in this chapter (closed system). They become more difficult for parasites that infect large, migratory, or highly mobile species such as large mammals, salmon, or birds (open system). It is feasible to cage small hosts by scaling the cage size to the organism and maintaining a gradient in natural host densities while also taking care not to alter dispersal or behavior of parasite stages or hosts (e.g. in aquatic systems, measure flow through the cage to test for changes in flow velocity). For "open" systems, the density of highly mobile donor hosts can be manipulated by placing an "attractant" within the research area. The attractant could be, for example, a scent, recorded call, food, or enhanced refugia (e.g. bird houses). For these types of manipulations, estimates of donor host density could be quite difficult and would have to be developed for each species. In addition, instead of measuring density of infectives within the donor host, it is more likely that density of infectives would be measured as number of "transmitting" parasites (e.g. through counts of eggs in feces, or number of cercariae in the environment if possible).

Robust interpretation of the data in these experiments depends on researcher acknowledgment of underlying assumptions. Assumptions inherent in these experiments include:

1. Increased donor host density correlates significantly and linearly with the number of recruits produced. This might not be the case for territorial or aggressive host species whose behavior changes at higher host densities.
2. Target hosts have equal susceptibility to hosts naturally infected in the wild. If uninfected hosts are collected from wild populations, then there could be bias toward collecting hosts that are predisposed to repel infections (see McCallum 2000 for discussion). This could underestimate transmission, but if hosts are well-mixed across replicates, it is unlikely to alter the functional form of transmission.
3. Behavior of hosts or parasites does not change with caging.
4. No parasite deaths occur in the donor host for the duration of the experiments. If deaths occur, then calculations of transmission could increase estimates of transmission per infective parasite. To solve this problem, estimate the deaths of infective parasites by subsampling parasites from a representative sample of donor hosts before and after the experiments.

In addition to the apparent nonlinearities in transmission, the relative roles of abiotic and biotic variables in this parasite–host system were disturbance-dependent. Explanatory variables for sporocyst densities switched from a positive correlation with snail densities, stream velocity, and width/depth ratio in unlogged streams (Fig. 10.5(a)) to a negative correlation with velocity and width/depth ratio (Fig. 10.5(b)). Transmission of free-living aquatic trematodes increases with velocity up to a maximum threshold. Beyond this threshold, stream velocity can result in damage to and decreased transmission success of parasite infective stages (Upatham 1974; Jewsbury 1985). Logging disturbance increased the proportion of riffle and run habitats which led to higher average stream velocities. In streams with high pool/riffle ratios and low average velocity, parasite transmission was enhanced by snail densities and stream velocity. However, in streams with low pool/riffle

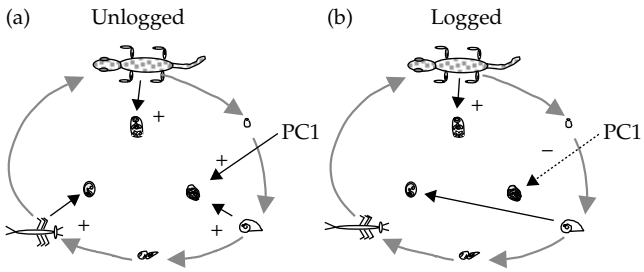

Figure 10.5 Diagram that depicts ANCOVA results of effects of disturbance on the relationship between parasite stages and the biotic and abiotic variables associated with logging. Abiotic and biotic variables that explain the majority of variation in each parasite stage differ between (a) unlogged and (b) logged sites. Gray lines show the direction of parasite transmission. Solid lines represent positive correlations. Dashed lines represent negative correlations. PC1 = principal component 1 and is composed of stream velocity and the stream width/depth ratio.

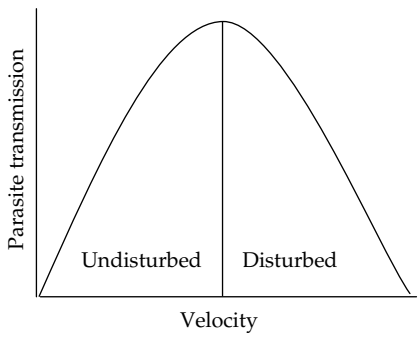

Figure 10.6 Conceptual diagram relating parasite transmission to stream velocity in undisturbed and disturbed sites.

ratios and high average stream velocity, parasite transmission was harmed by increasing stream velocity (Fig. 10.6).

As with sporocyst parasites, the explanatory variables for metacercariae switched with disturbance. In undisturbed streams metacercarial density was positively correlated with stonefly hosts (Fig. 10.5(a)), but disturbance switched the explanatory variable to snail host density (Fig. 10.5(b)). Stonefly density was high in streams that experienced the most severe disturbance and mass-action models suggest that metacercarial recruitment would respond positively to this increase. However, in SD streams snail density was at its lowest and thus snails limited the recruitment of cercariae to stoneflies and led to low metacercarial density.

The dynamics of this parasite–host system are clearly context-dependent. Parasite abundance and transmission depend on the level of disturbance and its effects on host density, stream velocity, and channel morphology. In undisturbed sites, the mass-action transmission model seems to apply. This suggests a threshold host density below which the parasite cannot persist, and a stable equilibrium between the parasite and host species. However, in disturbed sites, this model does not apply. Parasites are able to persist and transmit at low host densities (Box 10.1) and correlations among parasite stages, host densities, and abiotic variables shift in direction and strength with disturbance. The patterns and correlations in the data from these sites suggest some form of nonlinear transmission. Thus, this parasite–host system may shift from one transmission function to another based on the disturbance regime.

10.6 Conclusion

In addition to affecting the patterns of infection in each host, logging-induced disturbance changed the relationships between the parasite stages, host densities, and environmental features in the streams. Patterns in parasite infections differed with severity of disturbance and parasite stage and these differences were explained in part by transmission, host densities, and abiotic variables. But biological interactions apart from those between a parasite and its hosts are very likely to influence the response of parasites to disturbance. Each of these hosts is linked by a single parasite, but each host also interacts within the stream community through competition, predation, or herbivory. Changes in stream community composition following disturbance lead to altered relative abundance of each host species within the stream community. This in turn feeds back into changes in trophic and competitive interactions which could affect transmission of the parasite. For parasites with multiple life-history stages, complex community-level effects on parasite–host dynamics could obscure

the results of parasite population studies that consider only a single host and parasite stage. Thus, empirical examination of community-level influences on a parasite and its multiple hosts could help tease apart the mechanisms that drive complex parasite–host interactions.

An example of one scenario where community processes could affect parasite transmission is in streams that experienced logging and debris flows such that snail populations were decimated to the point of local extinction. Because snails are competitively dominant grazers, the decline in snail populations may release macroinvertebrate grazers from competition. Since many of these macroinvertebrates are eaten by stoneflies, this competitive release could increase the prey available to *C. californica*, the second intermediate stonefly host of the parasite. Stonefly densities increased significantly in creeks with severe disturbances; this suggests that the mechanism of competitive release of macroinvertebrates could be occurring. It is probably the high density of stoneflies that increases the probability that the cercariae, which are at low densities in areas with severe disturbance, will find a host. Thus, this cascading trophic effect from algae to stoneflies could ultimately influence the probability of parasite transmission.

Acknowledgments

S. Collinge and C. Ray provided helpful comments on this manuscript. I thank W. Sousa, M. Power, E. Hadly, V. Resh, and C. Bell for their discussions and support while conducting this study. Weyerhaueser Industries and E. Arnett provided generous and unlimited access to private timberlands in the McKenzie and Fall creek watersheds, Oregon. The McKenzie Ranger District provided access to public lands and logistical support. Many thanks to D. Anderson, C. Nerney, R. Wildman, S. Gregory, and the Andersons for their help and support during field work and D. Sanver, K. Rothwangl, and A. Talianchich for laboratory work. The H. J. Andrews Experimental Forest and LTER in Blue River, Oregon and the Brackenridge Field Laboratory in Austin, TX generously provided laboratory space. This research was supported by NSF dissertation grant DEB-9701128, the ARCS foundation, Inc., and the H. J. Andrews LTER.

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