Coastal cutthroat trout in headwater stream networks: Distribution and abundance in space and time

Jason K. Walter

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Committee:

Christian E. Torgersen

Robert E. Bilby

Thomas P. Quinn

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University of Washington

Abstract

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Jason K. Walter

Chair of the Supervisory Committee:

Affiliate Assistant Professor Christian E. Torgersen

School of Environmental and Forest Sciences

Understanding the linkages among physical and biological processes across scales is vital to understanding the diversity and heterogeneity of headwater streams. Most research investigating fish–habitat relationships in headwater catchments has been conducted over a limited geographic extent and at small spatial scales. We conducted spatially continuous single-pass electrofishing and physical stream habitat surveys, sampling all habitat units possible, within the fish-bearing portions of 16 catchments where coastal cutthroat trout were the only salmonid species present. Each catchment was surveyed twice, first in the autumn and then again the following spring, prior to the emergence of young-of-the-year cutthroat trout. Spatial and temporal (seasonal) variability of cutthroat trout abundance within each study catchment was

assessed at coarse (catchment) and intermediate (stream segment) spatial scales. Catchment-scale cutthroat trout density in both the autumn and spring was positively correlated with catchment area, and significantly associated with catchment shape, with highest densities in heart-shaped catchments. These high densities may be associated with increased habitat heterogeneity imparted by tributary confluence effects, which tend to be greater in dendritic stream networks in heart-shaped catchments. Stream segments were identified and grouped by analyzing intermediate-scale stream channel characteristics (i.e., channel gradient and the location of significant tributary junctions) derived from high-resolution (≤2 m) LiDAR digital elevation models. Segment-scale fish density in the autumn was positively correlated with segment contributing catchment area, negatively correlated with channel gradient, and significantly associated with the interaction of the two variables ($P < 0.05$). No segment-scale variables were significant predictors of fish density in the spring. The change in predictive ability for models of cutthroat density in the spring relative to the autumn was coupled with a significant decline in fish density between the seasons ($P > 0.05$). Improved understanding of the relationships between fish abundance and stream habitat is needed to help land managers identify areas of high biological potential where specific habitat protection or restoration efforts may be warranted or most productive.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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DEDICATION

To my “Nana”, Ruth Kremer

Introduction

The organization of aquatic systems in space and time is a fundamental concept in aquatic ecology (Frissell et al. 1986). Seemingly straightforward inquiries into the distribution and abundance of organisms frequently require an understanding of the complex integration of environmental heterogeneity and the adaptation of organisms to available habitat (Gresswell et al. 2006). This may be particularly true in habitats such as headwater catchments that are highly heterogeneous in both space and time.

Headwater catchments serve a variety of key ecological functions in the maintenance of aquatic systems. They are critical to nutrient cycling, the recruitment and transport of sediment and woody debris, and in providing habitat for a variety of organisms (Meyer and Wallace 2001). In addition, Lowe and Likens (2005) estimate that headwater streams account for more than 70% of the cumulative stream channel length in mountainous catchments. Despite their prevalence on the landscape, and the fact that the physical and biological properties of these systems have been studied for decades, the importance of headwater streams within watersheds and their effect on downstream reaches are poorly understood (Gomi et al. 2002). Fausch et al. (2002) suggest that "a continuous view of rivers is essential for effective research and conservation of their fishes and other aquatic biota – a view not just of disjunct reaches but of the entire spatially heterogeneous scene of the river environment, the *riverscape*, unfolding through time". Therefore, understanding the physical and biological properties of headwater streams, and their linkage to downstream habitats and processes is vital to understanding the diversity and heterogeneity of riverine systems (Vannote et al. 1980, Gomi et al. 2002, Benda et al. 2004, Lowe et al. 2006).

There is an inherent spatial disconnect between the scale at which aquatic systems are typically studied, how they function ecologically, and how they are managed. Levin (1992) suggests that scales of investigation are often imposed on researchers not by the natural system to be studied, but instead by our perceptual capabilities or technological and logistical constraints. If a system is studied at an inappropriate scale, one may not detect its actual dynamics and patterns, but instead those that are simply artifacts of the scale of research (Wiens 1989).

The preponderance of research studying fish ecology in headwater streams has been conducted at a small spatial scale (Schlosser 1995), thereby limiting how findings and information can be accurately applied across the landscape. More recently, Fukushima (2001) reported that the majority of past research assessing physical stream habitat and subsequent linkages with fish populations has been conducted at the local, or site specific scale. Despite the fact that the importance of considering scale in ecological research has long been recognized, many studies still do not adequately take into account the discrepancy in the scale at which data are collected and the scale at which inference about a given system or population is made. Hewitt et al. (2007) report that small-scale mechanistic experiments carried out in a few randomly selected locations and analyzed with categorical statistical methods still represent the majority of ecological studies. This same basic observation was made by Levin (1992), who suggested that researchers often rely on randomly selected points across the landscape to elucidate features about a given aquatic system or population of interest. This technique may be appropriate and useful in relatively homogenous environments; however, headwater catchments are highly heterogeneous in both space and time (Gomi et al. 2002), and may not be ideal for such a sampling approach. Hewitt et al. (2007) admit that advancements have been made

through small-scale manipulative experiments, but they argue that ecological systems are not easily reduced and manipulated to fit the constraints of most study designs. These issues are not only important for the sake of academic argument, but also because scientists and natural resource managers are often asked to use the findings of small-scale research to postulate the effects of anthropogenic and landscape disturbance processes, such as forest management, on natural resources and ecosystems. Fausch et al. (2002) conclude that scientists have been largely ineffective at providing natural resource managers with information on stream fish populations at the scale needed for conservation, and that this has contributed to the demise of many populations.

Coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) occupy the habitat at the upstream extent of fish distribution in western Washington (Connolly 1997, Trotter 2000, Fransen et al. 2006), making them a logical species of interest when investigating fish population dynamics within headwater catchments in the region. These headwater habitats differ from downstream reaches, in part, by their close coupling to hill-slope processes (Gomi et al. 2002), including anthropogenic processes and disturbance associated with forest management. Current forest management practices recognize the coarse-scale differences among aquatic habitats, such as fish presence versus absence, and perennial versus seasonal flow. This approach does not address heterogeneity of headwater habitats that exists at finer scales, such as the differences between individual catchment types, or stream reaches based on channel gradient, stream size, and network geometry. As a result, forest practices may overlook the variability in biological potential of different habitat types important to fish populations within and among headwater catchments.

A number of analytical techniques are now available to assess spatial and temporal heterogeneity in ecological research. For example, the use of continuous rather than categorical data enables researchers to partition variance between a number of potentially explanatory variables (Hewitt et al. 2007). These techniques change not only the way researchers perceive the landscape but how they sample it, as well. One method for sampling and analyzing multi-scale, spatially continuous patterns of stream fish and physical habitat distribution was described by Torgersen et al. (2004) and validated by Bateman et al. (2005). To help develop a better understanding of the heterogeneity associated with patterns of coastal cutthroat trout abundance and distribution both within and among headwater catchments in space and time, this methodology was used to investigate the following research questions: (1) How do patterns of coastal cutthroat trout distribution and abundance vary in headwater stream networks over space and time? (2) How are these patterns associated with aquatic habitat at multiple spatial scales? The specific objectives of this research were to (1) identify headwater catchment and stream network characteristics associated with coastal cutthroat trout distribution and abundance, (2) assess aquatic habitat factors that are associated with trout abundance at multiple spatial scales, and (3) compare patterns of distribution, abundance, and habitat associations in autumn and spring. Hypotheses of this study were that (1) coastal cutthroat trout distribution and abundance vary with respect to headwater catchment and stream network characteristics, (2) abundance of coastal cutthroat trout within headwater stream networks is associated with specific aquatic habitat characteristics, which may vary depending on the spatial scale of analysis, and (3) coastal cutthroat trout abundance is significantly lower in the spring than in autumn; however, the spatial patterns of abundance will be consistent among seasons.

Methods

Study area

Study catchments were selected from within the ca. 236,200 ha Weyerhaeuser Vail and Longview Tree Farms in southwestern Washington (Figure 1). These timberlands are predominantly within the western foothills of the Cascade Mountains. The area is bounded by the Puget Sound lowlands to the north, Cascade Mountains to the east, the Columbia River to the south, and the Willapa Hills to the west. Major rivers draining the area include the Deschutes and Skookumchuck to the north, and the Cowlitz, Toutle, and Green rivers to the south. The tree farms are vegetated primarily with second- and third-growth stands of Douglas-fir (*Pseudotsuga menziesii*). Additional common overstory species include red alder (*Alnus rubra*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*).

The climate across this region is temperate maritime. Annual precipitation is highly variable and ranges from approximately 100 to 360 cm, with most precipitation falling between the months of November and May. The underlying geology of the region is largely Tertiary volcanic (predominantly andesite lava flows). Elevation in the study area ranges from approximately 20 to 1375 m.

Site selection

In conjunction with forest management practices, Weyerhaeuser Company has conducted fish distribution surveys on over 1450 streams within these tree farms since 1997. At the time of the current study, cutthroat trout had been identified as the only salmonid species present at the upstream extent of fish distribution in 705 of these streams. From these streams, a sample of potential study catchments was identified that included only those in areas where LiDAR

coverage was currently available and the underlying geology was Tertiary volcanic. Within the Longview Tree Farm, potential study catchments were further limited to those in the northern half of the tree farm due to logistical constraints related to travel; areas were excluded within the extent of the blast zone of the 1980 eruption of Mt. St. Helens to avoid any legacy effects of the eruption on fish distribution. From the final set of potential catchments, eight (four each from the Vail and Longview Tree Farms) were randomly selected to be sampled in the first year (2008/2009), and another eight were selected for the second year (2009/2010). Selected catchments were assigned a unique alphanumeric code starting with the letter 'V' or 'L' corresponding to the tree farm in which they were located. Each of the 16 study catchments was sampled twice, once in autumn and again the following spring to provide a means for assessing temporal changes in patterns of distribution, abundance, and habitat associations of coastal cutthroat trout.

Fish and physical stream habitat sampling

Spatially continuous, single-pass electrofishing and physical stream habitat surveys within the fish-bearing portions of each study catchment were conducted using the methodology similar to that described by Torgersen et al. (2004) and validated by Bateman et al. (2005). The downstream endpoint of each surveyed catchment was located at a physical barrier restricting access to other species of salmonids, or at a stream confluence where the resulting downstream stream order was 4^{th} order or higher, whichever was farther upstream. The upstream extent of surveyed stream length corresponded with the upstream limit of cutthroat trout distribution on all fish-bearing tributaries within the catchment, or at the point where effective sampling was no longer possible. Where habitat conditions prevented the effective sampling of any given habitat

unit(s), the length and gradient of the section of stream that could not be effectively sampled was measured so that a complete elevation profile of the surveyed portion of the study catchments could be created. In some locations, for example, the presence of large beaver ponds or large quantities of overstory blow-down from the adjacent riparian stand made effective stream sampling difficult or impossible.

Fish sampling was carried out using a Smith-Root Model LR-24 backpack electrofisher. The electrofisher setting at each site was set using the 'Quick Setup' process available on the LR-24. This process automatically sets the voltage of the electrofisher in order to produce 30 Hz, 12% duty cycle at 25 watts average output power, relative to the water being sampled. All captured cutthroat trout were measured (fork length in millimeters) and then returned to the stream where they were captured. For individual fish that were observed but not captured, an estimate of fork length was made by the electrofishing crew. To ensure that this use of ocular estimations of length was not biased, length estimates were made for a subset of captured fish for comparison with ocular estimates. The presence of any other species of fish and/or amphibian seen or captured was noted. In addition, total electrofishing time was recorded in seconds in order to provide a means to assess catch-per-unit-effort.

Concurrent with the electrofishing surveys, a spatially continuous physical stream habitat survey was conducted within each study catchment using, in part, the habitat criteria developed by Bisson et al. (1982). All sampled channel units were classified (pool, riffle, cascade, rapid or vertical step) and measured. Variables measured on channel units included length (m), wetted-width (m), bankfull-width (m), mean-depth (cm), and max-depth (cm). Gradient (%) was measured in riffle, cascade and rapid habitats, as gradient was assumed to be 0% for pools. Only the height and formative agent (e.g., wood, boulder, bedrock) for vertical steps was recorded.

Length and width measurements were taken at the lateral and longitudinal mid-point of each measured channel unit using a hand-held Tru-Pulse laser rangefinder (Laser Technology, Inc.); these measurements were recorded to the nearest 0.1 m. A single gradient measurement was recorded for the entire length of each channel unit using a hand-held clinometer, and this number was recorded to the nearest whole number (%). Channel unit depth was measured along the thalwag using a stadia-rod. Habitat survey crews also assessed (via ocular estimation) the type and percent surface area of dominant and sub-dominant substrate types, as well as the percent surface area of each habitat unit covered by large woody debris providing potential cover for fishes.

During the habitat survey, a Garmin GPSmap 60CSx was used by the survey crew to generate a track-log of the surveyed stream length in each study catchment. Waypoints were taken at landmark features that potentially could be identified later on LiDAR maps (e.g., tributary junctions, road crossings, waterfalls, and other geomorphic barriers to the upstream migration of fish).

To increase sampling efficiency, a sub-sampling technique within a subset of homogeneous stream habitat units was used. When the sampling area within an individual riffle, cascade, or rapid extended upstream for more than the length equivalent to 10 channel widths, sampling within that unit was suspended, and a portion of that habitat unit was not sampled. The section of habitat not sampled extended upstream for a length equivalent to 20 channel widths or to a point where a different habitat unit began, whichever was reached first. In the event that the original habitat unit extended upstream farther in length than the 20 channel widths that was not sampled, another section of that unit was sampled for a length of 10 channel widths, and so on. This technique was not used in pool habitats.

Data processing and GIS

Field-measured fish and physical stream habitat data at the channel unit scale were organized in relational databases. Dynamic segmentation methodology (ESRI 2008) was then used to georeference the field-measured data to LiDAR derived hydrologic networks that were created in GIS. Landmarks such as tributary junctions and road crossings that were identified and mapped with waypoints during field surveys were used as anchor points to calibrate the GIS derived stream length to the actual field surveyed stream length. Data associated with individual channel units, including habitat unit type, physical channel metrics measured in the field, and fish abundance, were then merged with the linearly referenced stream network by creating a link between the relational database and GIS (ESRI 2008).

Three-dimensional landscape terrain maps were generated for each study catchment in the ArcScene 3D analyst module of ArcGIS using data from LiDAR-derived digital elevation models (DEMs). Linearly referenced fish and habitat data were then overlaid on the three-dimensional map. Total cutthroat trout abundance within each sampled channel unit of the surveyed portion of the catchment was graphically extruded vertically on the maps to provide a visual representation of fish abundance throughout the sampled stream networks and to allow for assessment of spatial patterns in trout abundance at the catchment scale. Catchment-scale physical habitat parameters were identified and/or calculated using maps of data from the study catchments in ArcGIS (Table 1). These parameters were assessed relative to cutthroat trout abundance at the catchment scale. A descriptor of catchment shape (e.g., heart, pear, or rectangular; see Figure 2) was assigned to each of the 16 study catchments using criteria described by Benda et al. (2004). Dendritic stream networks occur primarily in heart- and pear-shaped catchments. The spatial configuration of tributary streams within these two catchment

types varies, and affects the relative influence of tributary confluences on morphological habitat heterogeneity within the catchment, with heart-shaped catchments having the greatest likelihood of confluence effects. Trellis and parallel stream networks are often associated with rectangular catchments in which tributary confluence effects are relatively less pronounced than in other catchment shapes (Benda et al. 2004).

To provide a means for assessing intermediate-scale cutthroat trout abundance and physical stream habitat relationships, the surveyed stream length within each catchment was delineated in segments based on channel gradient and the location of significant tributary junctions (stream size). Rhoads (1987) suggests that flow-related morphological changes in streams occur at tributary junctions where the ratio between tributary and mainstem size approaches 0.6 or 0.7. Very few tributary junctions within the small, headwater catchments sampled in this study met this criterion. Therefore, a more conservative and inclusive benchmark was used. A tributary junction was classified as significant if the contributing catchment area associated with the tributary stream was >25% of the total catchment area at the tributary junction, including both the mainstem and the tributary stream. Segment breaks based on gradient were associated with four distinct gradient categories identified by Montgomery and Buffington (1998). These categories included segments of stream with an average gradient of <2% (pool-riffle channels), 2-4% (plane-bed channels), 4-8% (step-pool channels), and 8-20% (cascade channels). The minimum length for a segment based on channel gradient was 100 m. Channel gradient was assessed using a method described by Torgersen et al. (2006). A channel gradient profile was generated for the surveyed stream length within each study catchment using a LiDAR-derived digital elevation model by sampling elevation every 2 m along the stream channel and then calculating gradient using a 100-m moving window. Segment-scale physical

habitat parameters were identified and/or calculated using maps of data from the study catchments in ArcGIS (Table 2). These parameters were assessed relative to cutthroat trout abundance at the segment scale.

Statistical analysis

Coastal cutthroat trout and physical stream habitat data were analyzed to assess fish abundance and distribution as it related to habitat characteristics at coarse (catchment) and intermediate (segment) scales. Data organization and exploration were performed in Microsoft Excel and Minitab 16. Modeling and regression analyses were conducted using SAS (SAS 2008).

Linear regression was used to investigate relationships between habitat variables and fish density (fish/m) at catchment and segment scales. For both scales, box-plots and ANOVA were used to assess relationships between the categorical variables (Tables 1 and 2) and fish density at the catchment scale. To address the problem of multicollinearity, an assessment of potential relationships between continuous habitat variables was completed via visual inspection of scatter plots and evaluation of a correlation matrix. Potential relationships between categorical habitat variables were assessed using contingency tables. Visual inspection of box-plots depicting the distribution of data was used to assess any potential relationships between the continuous and categorical habitat variables. For both the autumn and spring samples, a backwards elimination stepwise regression analysis with a general linear model (GLM) was performed of fish density against catchment and segment scale habitat variables. The habitat variable with the highest *P*-value in each step of the modeling processes was removed from each analysis until only significant variables remained ($\alpha = 0.05$). Residuals were plotted and visually examined. For

each model, ANOVA was used to assess the interaction between and significance of categorical variables relative to the response variable of fish density. Least-squares means were calculated and a pair-wise comparison of the resulting values was made for all categorical variables.

A paired *t*-test was used to assess change in catchment-scale fish density between the autumn and spring samples within individual catchments. Analysis of variance was used to investigate the relationship between fish density at the segment scale and stream gradient. To assess catchment-scale habitat variables associated with the percent decline in fish abundance between the autumn and spring samples, a backwards elimination stepwise regression analysis with a general linear model (GLM) was performed using the same potential explanatory variables from the catchment-scale model. The habitat variable with the highest *P*-value in each step of the modeling processes was removed from the analysis until only significant variables remained ($\alpha = 0.05$).

Results

Over the four field sampling periods in this study, approximately 22,000 coastal cutthroat trout were sampled from more than 11,000 individual stream channel units. In total, almost 100 km of stream length were surveyed. Within individual catchments, the length of surveyed stream channel ranged from 716 m in catchment V2 to 6940 m in catchment L9. The number of sampled fish within a catchment ranged from 51 individuals during the spring sample in catchment V1, to 1861 fish during the autumn sample in catchment V4 (Table 3). Percent pool habitat, derived from field survey measurements, averaged 20% across all samples, and ranged from 9% in catchment L15 to a high of 44% in catchment V2 (Table 4). A descriptor of catchment shape was assigned to each of the study catchments. Three catchments were heart shaped, seven were pear shaped, and six were rectangular. Mean catchment area for all 16 catchments was 545 ha, and ranged from 254 ha in catchment L33 to 850 ha in catchment V4 (Table 5). The percent of surveyed stream length that could be effectively sampled was 91% when averaged across all samples and catchments, and ranged from 75% for catchment L2 (autumn) to 99% for catchment V1 (spring).

Patterns of coastal cutthroat trout abundance and distribution within catchments were highly variable in both space and time. Longitudinal patterns of coastal cutthroat trout abundance within catchments included (1) increasing abundance moving upstream, (2) decreasing abundance moving upstream, (3) unimodal distribution with a peak in abundance near the midpoint of fish distribution within the catchment, (4) bimodal distribution with peaks at the upstream and downstream extents of fish distribution within the catchment, and (5) random pattern (Figure 3).

Catchment-scale fish density

Exploratory data analysis suggested that certain individual catchment-scale habitat variables were related to fish density. For example, contributing catchment area was positively correlated with fish density in autumn (Figure 4). Also, fish density within each of the catchment shape categories was significantly different in autumn (ANOVA, $P = 0.048$), with fish density averaging 0.48, 0.34, and 0.20 fish/m in heart-shaped, pear-shaped, and rectangular catchments, respectively (Figure 5).

Backwards elimination stepwise regression revealed that two variables, catchment shape and catchment area, were significant predictors of catchment-scale fish density in autumn (Table 6). The model with these two explanatory variables explained 73% of the variability in fish density (Figure 6). There was significant evidence of different intercepts among catchment shapes (ANOVA, $P = 0.007$). Pair-wise comparison of least-squares means for catchment shape indicated that autumn fish density in heart-shaped catchments was significantly higher than in pear-shaped ($P = 0.003$) or rectangular catchments ($P = 0.040$), and that fish density in pear-shaped and rectangular catchments was not significantly different ($P = 0.168$; Table 7).

Catchment shape and catchment area also were significant predictors of fish density at the catchment scale in spring (Table 6) and explained 63% of the variability in fish density (Figure 7). There was also evidence of differing intercepts among catchment shapes in spring, though the difference was not highly significant (ANOVA, $P = 0.063$). Pair-wise comparison of least-squares means for catchment shape indicated that spring fish density in heart-shaped catchments was significantly higher than in pear-shaped catchments ($P = 0.044$). The comparison of fish density in heart-shaped versus rectangular catchments was suggestive of a difference, but was not highly significant ($P = 0.055$). Spring fish density in pear-shaped and

rectangular catchments was not significantly different ($P = 0.818$; Table 7). Slopes of the trend lines comparing catchment-scale fish density relative to catchment area when grouped by catchment shape were not significantly different for the autumn (ANOVA, $P = 0.648$) or spring (ANOVA, $P = 0.464$) samples (Figure 8).

Segment-scale fish density

In the 16 study catchments, 132 segments were identified based on differences in channel gradient and locations of significant tributary junctions. Individual segments ranged from 26 m to 1678 m in length and averaged 403 m. Among the 132 segments, six were classified as pool-riffle channels (average channel gradient of <2%), 25 were plane-bed channels (average gradient of 2-4%), 56 were step-pool channels (average gradient of 4-8%), and 45 were cascade channels (average channel gradient of 8-20%). Fish density was more variable within segments than in catchments; density in segments ranged from zero fish to 1.06 fish/m.

Backwards elimination stepwise regression revealed that at the segment scale, segment contributing catchment area (SCCA) and segment gradient (SG), and their interaction (SCCA×SG), were significant predictors of fish density in autumn. Variables that were significant at the catchment scale (i.e., catchment area and catchment shape) were also included in the segment-scale model (Table 8). The model with catchment area, catchment shape, SCCA, SG, and SCCA×SG explained 54% of the variability in fish density (Figure 9). Intercepts were significantly different among catchment shapes (ANOVA, $P < 0.0001$). All pair-wise comparisons of least-squares means for catchment shape were significantly different ($P < 0.016$; Table 9). The significance of the interaction between SCCA and SG relative to fish density at

the segment scale is apparent in Figure 10. The effect of SCCA on fish density increased with channel gradient.

Catchment-scale variables, including catchment shape and catchment area, were significant predictors of segment-scale fish density in spring. Segment gradient and SCCA were not significant predictors of fish density at the segment scale; however, the interaction of these two variables, while not significant, had some explanatory value ($P = 0.083$; Table 8). The model with catchment area, catchment shape, SCCA, SG, and the interaction between SCCA×SG explained only 38% of the variation in segment-scale fish density in the spring (Figure 11). The intercepts for catchment shape were different but not highly significantly (ANOVA, $P = 0.075$). Pair-wise comparison of least-squares means for catchment shape indicated that segment-scale spring fish density in heart-shaped catchments was significantly higher than in rectangular catchments ($P = 0.048$), and was suggestive, but not conclusive of a difference between heart-shaped and pear-shaped catchments ($P = 0.055$). Fish density in pear-shaped versus rectangular catchments was not significantly different ($P = 0.884$; Table 9).

Temporal patterns

Mean fish density in all catchments decreased from 0.32 fish/m in the autumn to 0.19 fish/m in the spring; a highly significant difference (paired *t*-test, $P < 0.0001$). Within individual catchments, the amount of change between seasons was highly variable, with a minimum of 13% in catchment V2, and a high of 55% in catchment L5 (Table 10). The decrease in catchment-scale fish density between the autumn and spring samples was associated with a more consistent spatial distribution of fish with fewer locations supporting very high or low abundance, as was common in the autumn sample (Figure 12). This homogenization in the distribution of fish

between seasons resulted in 13 of the 16 catchments exhibiting a random pattern of distribution in the spring compared to only four catchments with this distribution pattern in the autumn (Figure 3; Table 10).

Mean segment-scale fish density in each of the four gradient categories in autumn ranged from 0.22 fish/m in cascade channels to 0.39 fish/m in plane-bed channels; there was a significant difference between channel types in autumn (ANOVA, $P = 0.011$). Fish density in the spring ranged from 0.15 fish/m to 0.19 fish/m, and there was no significant difference between channel gradient categories (ANOVA, $P = 0.639$; Figure13). Backwards elimination stepwise regression of percent change in catchment-scale fish density between autumn and spring revealed that none of the measured habitat variables were significantly associated with percent change in fish density ($P > 0.05$).

Discussion

Traditional means of fish sampling over large spatial extents (i.e., multiple pass removal techniques with block nets) can be extremely labor intensive, time consuming, and therefore, expensive. As a result, the spatial dynamics of aquatic systems are an important topic that has been largely ignored (Jackson et al. 2001). In addition, these constraints limit the potential scope of individual studies and have created a body of knowledge in aquatic ecology that is largely based on data collected within short fragments of habitat over short periods of time (Fausch et al. 2002). Vadas and Orth (1993) suggest that to achieve sampling at a greater extent, it may be necessary to compromise sampling intensity or to employ alternative sampling techniques.

The spatially continuous, single-pass electrofishing and physical stream habitat survey methodology (Torgersen et al. 2004, Bateman et al. 2005) used in this study was highly effective for providing a relative index of cutthroat trout abundance and for quantifying physical stream habitat data throughout entire catchments with reduced effort. Gresswell et al. (2006) used these methods to survey resident cutthroat trout populations and stream habitat in 40 basins in western Oregon and found that bedrock lithology was the dominant factor influencing the patterns of cutthroat trout abundance among catchments. In the current study, I expanded the scope of this previous work. I controlled for the effect of lithology by selecting only catchments where the underlying geology was classified as Tertiary volcanic (predominantly andesite lava flows). This allowed me to investigate the effects of habitat variables beyond the underlying geology of the catchment at multiple spatial scales. Furthermore, Gresswell et al. (2006) only enumerated fish that were greater than 70 mm in length. Thus, variability and pattern associated with the distribution of young-of-the-year fish was not considered. The life cycle of stream fishes can potentially extend over multiple spatial scales over a timeframe defined by the life history

characteristics of the species of interest (Schlosser 1995). For cutthroat trout, the habitat requirements of young-of-the-year fish may be markedly different than those for older age-classes. Moore and Gregory (1988) found that young-of-the-year cutthroat trout were often associated with the lateral margins of streams, whereas older age-classes of cutthroat trout were typically associated with pools (Bisson et al. 1988, Rosenfeld et al. 2000, Rosenfeld 2003). We sampled all coastal cutthroat trout in our study catchments, regardless of age-class, to better understand patterns of distribution and abundance of coastal cutthroat trout across the entire age-range of their population. In addition, Gresswell et al. (2006) sampled the majority of catchments only once per year, thereby limiting their ability to detect temporal patterns and variation in how and where fish were distributed. Adult cutthroat trout are known to migrate upstream in the spring (Meehan and Bjornn 1991), suggesting that the timing of a survey may be important in assessing patterns of distribution. By conducting surveys in autumn and spring within each catchment, we were able to investigate patterns of temporal variation within and among catchments.

The high resolution and spatially continuous nature of LiDAR data are well suited to capturing fine-scale habitat variability over large areas, providing the opportunity to evaluate biological and physical patterns over a wide range of spatial scales (Franklin 1992, Benda et al. 1998, Frissell and Ralph 1998, Peterson and Thomas 1998, Mertes 2002). In my study, remotely sensed LiDAR data were used to quantify three-dimensional structure and landscape patterns in selected headwater catchments. Using the channel-unit-scale habitat data collected during field surveys in conjunction with LiDAR data provided the means to investigate complex linkages between the spatial heterogeneity in cutthroat trout distribution and landscape variables at both coarse (catchment) and intermediate scales (segment).

I found that catchment shape was a significant predictor of coastal cutthroat trout abundance in both autumn and spring, and that fish density was highest in heart-shaped catchments in both seasons. According to Benda et al. (2004), heart-shaped catchments with dendritic stream networks may promote the highest likelihood of network complexity and tributary stream confluence effects, thereby increasing stream habitat heterogeneity. Increases in habitat heterogeneity have been linked to increased species richness (Huston 1994, Allan 1995) and increased availability of specialized habitats for certain species or life-stages of aquatic organisms (Reeves et al. 1995).

Cutthroat trout occupy different habitat types at as they mature. The need for various habitat types, coupled with the isolated nature of these fish populations in headwater catchments, requires not only spatial heterogeneity in habitats but also connectivity or 'complementation' of various habitat types within individual catchments. Burnett et al. (2007) showed that the spatial distribution of stream reaches with the potential to support high quality habitat for salmonids influences the status of habitats and populations over broad spatial extents. Other work in riverine systems (Scheimer et al. 1991, Dunning et al. 1992, Schlosser 1995) also suggests that habitat complementation can be a critical factor determining the size and long-term persistence of fish populations. The increased effects of tributary confluence effects associated with the stream networks in heart-shaped headwater catchments may result in within-catchment habitat complementation that is beneficial to cutthroat trout.

Catchment-scale coastal cutthroat trout abundance was significantly correlated with both catchment shape and catchment area in both autumn and spring; however, the patterns of fish abundance and distribution within catchments (Figure 3) were highly variable across all catchment shapes and sizes. No reliable method is available for assessing the size of small

streams via remote sensing. For the purposes of my study catchment area and SCCA were treated as surrogates for stream size at the catchment and segment scales respectively. Previous research on coastal cutthroat trout suggests differing views on spatial trends in abundance and the drivers that influence these patterns. For example, Trotter (2000) suggests that trout density in headwater reaches is low and declines to zero at the upstream extent of fish distribution, reflecting a steadily declining pattern in abundance in an upstream direction. In contrast, Rosenfeld et al. (2000) concluded that trout density was highest in small streams, particularly at the upstream extent of fish distribution. I observed a high degree of variation in longitudinal patterns of coastal cutthroat trout abundance among catchments; therefore, I propose that within-catchment factors other than channel size also may be influencing trout abundance and distribution at finer scales.

Segment-scale coastal cutthroat trout density in the autumn was negatively correlated with segment gradient but positively correlated with stream size, and there was a significant interaction between these two variables. Results from previous studies investigating the influence of channel gradient on fish abundance are variable. Chisholm and Hubert (1986) and Kozel et al. (1989) reported that trout density was negatively correlated with stream gradient. Isaak and Hubert (2000), on the other hand, found that stream slope had no effect on fish biomass despite the fact that lower gradient channels typically had a higher percentage of pools. I found that fish density among the four gradient categories (and associated channel types) was significantly different in autumn, with the highest densities occurring in plane-bed channel segments with an average gradient of 2-4%. The lowest fish density was observed in cascade channels with an average gradient of 8-20%. The relationship between the interaction of segment-scale gradient and stream size in relation to fish density is variable. In pool-riffle

channels where gradient is <2% there is no observed relationship between stream size and fish density. As segment gradient increases, the effect of stream size becomes more pronounced as illustrated by the increasing slopes of the trend lines in the four gradient categories (Figure 10). Thus, smaller stream channels (i.e., those with contributing catchment areas of less than ~300 ha) tended to support more fish if they were lower in gradient. In larger headwater stream channels, however, where catchment area was greater than ~300 ha, streams supported more fish at moderate to high channel gradients.

Mean coastal cutthroat trout density was significantly higher in the autumn sample (September/October) than in the spring sample (April/May) of the following year. Fish emigration out of the study catchments and over-winter mortality were both expected to decrease fish abundance; however, I did not measure either of these factors. Wyatt (1959) reported that over 95% of the cutthroat trout present in a study stream in the Cascade Mountains of Oregon were three years of age or less, suggesting that fish in headwaters may have short life spans (high annual mortality rates) or do not remain within these habitats beyond a certain life-stage. If the quality of over-winter habitat in headwater catchments is not suitable, fish may move downstream to higher quality habitats in the late autumn or winter (Meehan and Bjornn 1991). In addition to the decrease in overall fish density from autumn to spring, there was also a decrease in spatial variance (i.e., lower segment-to-segment variability) in coastal cutthroat trout distribution in 13 of the 16 catchments (Table 10). This decrease in spatial heterogeneity in fish density between autumn and spring is illustrated in Figure 12. Previous studies have described multiple potential explanations for changes in salmonid distribution among seasons, including the emergence of fry in the spring (Hartman et al. 1982), territorial behavior related to feeding or spawning (Chapman 1962), and the onset of autumn freshets (Cederholm and Scarlett 1982).

Changes in behavior by coastal cutthroat trout in the winter relative to the summer months may also partially explain this decrease in spatial heterogeneity. In the summer, fish may be feeding and selecting habitats that maximize growth, whereas in the winter, fish may seek refuge from high flow to conserve energy (Meehan and Bjornn 1991). A combination of these behavioral strategies may be reflected in the patterns of cutthroat trout distribution that I observed in this study.

Management Implications

Current forest practices to protect aquatic habitats and biota in headwater catchments potentially affected by management activities often do not explicitly consider the biological potential of different catchment- or segment-scale habitat types to fish populations. As a result, stakeholders do not always agree on the best practices for protecting aquatic systems or prioritizing restoration efforts associated with aquatic habitats. Studies investigating the effects of forest management on headwater systems report varied responses by aquatic organisms. For example, Young et al. (1999) found substantially lower summer abundances of cutthroat trout associated with logging, while De Groot et al. (2007) did not detect any logging treatment effects on relative abundance and condition of cutthroat trout populations. Murphy et al. (1981) found both higher trout abundance and biomass in stream reaches within clear-cuts than in forested stands. Latterell et al. (2003) concluded that forest management activity may not influence the upstream limit of trout distribution in headwater catchments. Decisions regarding habitat protection and restoration within headwater stream habitats are based on observations of fish presence or absence, which determine the type and level of protection afforded. Fish presence/absence in these headwater streams is typically determined using specific protocols for

conducting electrofishing surveys on forestlands in Washington State (Washington Forest Practices Board 2002). Although these protocol-based electrofishing surveys are useful for determining species occurrence, the survey techniques are time consuming, costly, and often dangerous (Fransen et al. 2006). In addition, the utility of the survey data is often limited because the protocol does not provide a reliable means of assessing relative abundance of fish or qualitatively mapping stream habitat. Therefore, the same level of protection is afforded to fish-bearing headwater stream reaches across the landscape even though the distribution and abundance of fish in these reaches is known to be highly variable. Jackson et al. (2001) suggest that determining the relative importance and timing of use by fish in various habitat types could provide resource managers with tools for minimizing potential impacts during resource exploitation. In this study, I developed an approach for identifying specific catchment- and segment-scale habitats with the greatest biological importance to coastal cutthroat trout. This approach is intended to help land managers identify areas where habitat protection and/or restoration efforts may be warranted or most productive.

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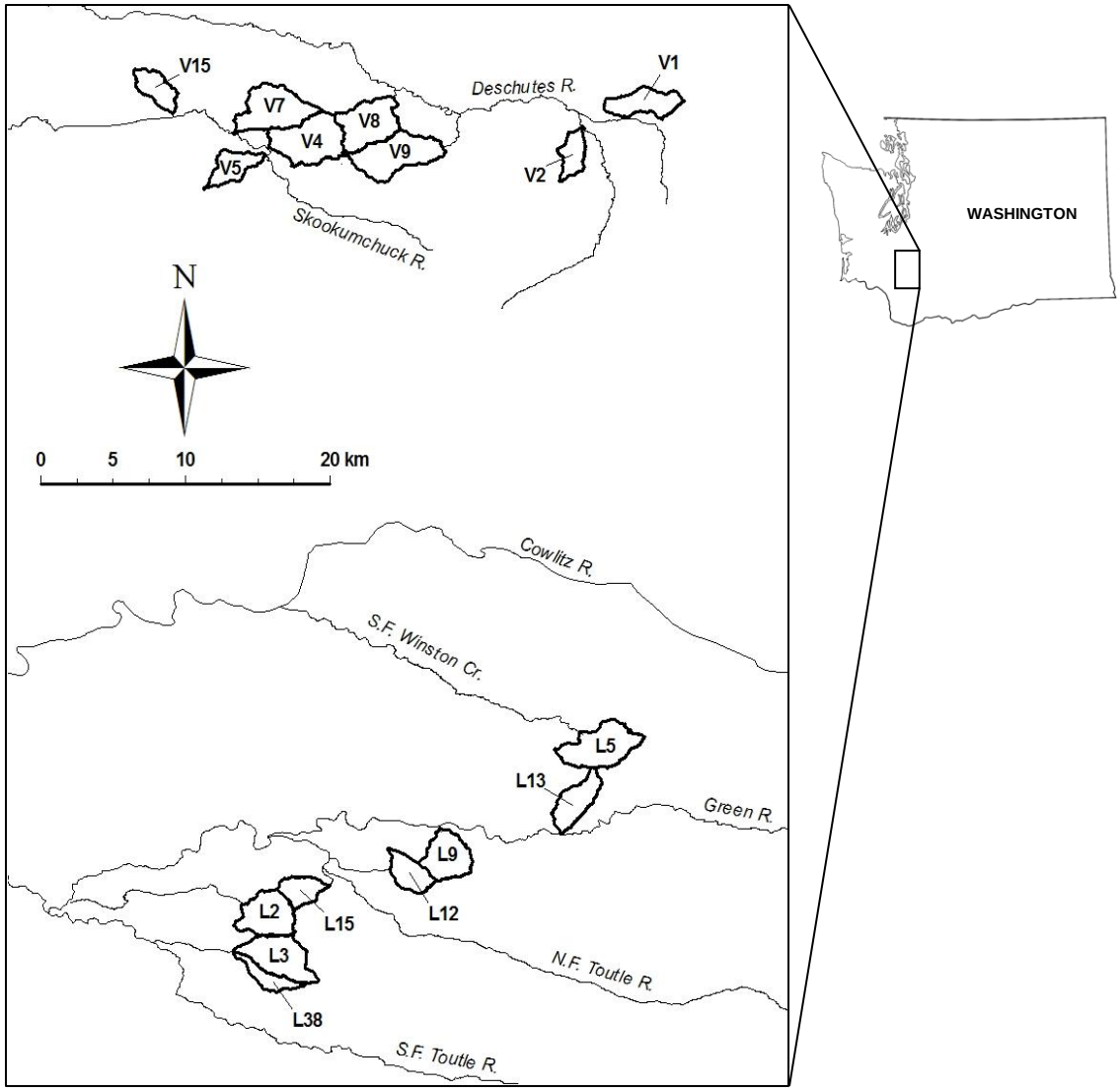

Figure 1. Locations of the 16 study catchments in southwest WA, USA, and their respective watersheds. Catchments are bordered in black and are coded with a unique alpha numeric code.

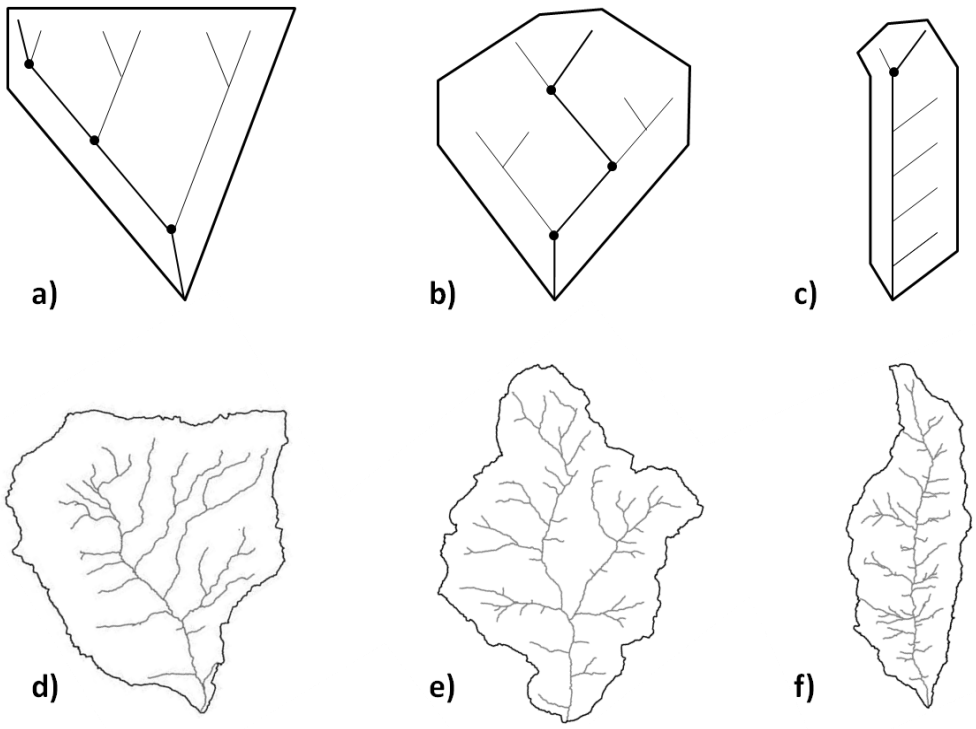

Figure 2. Theoretical headwater catchment shapes and examples from this study. Theoretical shapes include (a) heart-shaped, (b) pear-shaped, and (c) rectangular catchments (Benda et al. 2004). Examples from this study include (d) catchment L15 (heart-shaped), (e) catchment V8 (pear-shaped), and (f) catchment L13 (rectangular). On the theoretical sketches, dots indicate the locations of significant tributary junctions along the mainstem channel.

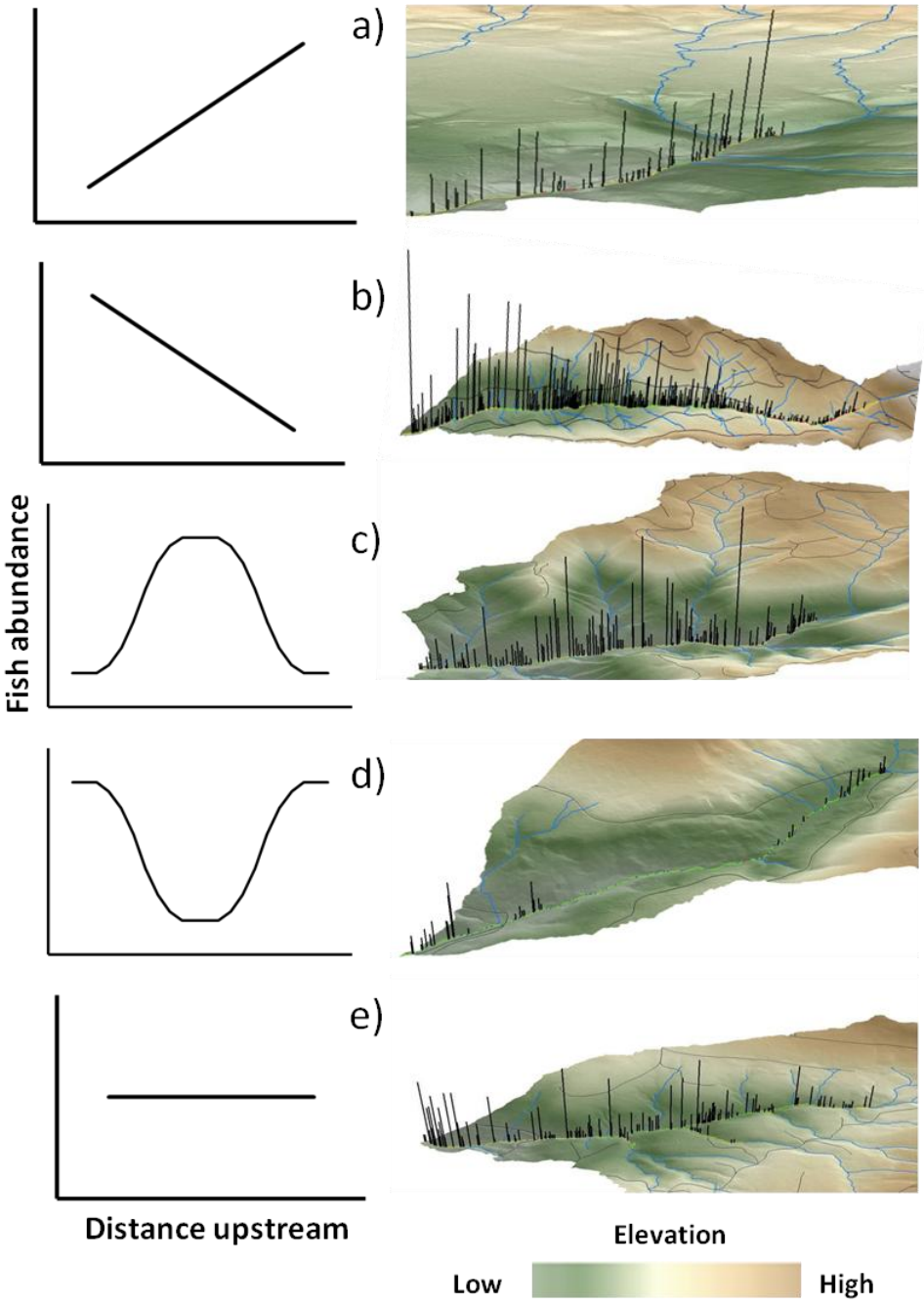

Figure 3. Theoretical longitudinal patterns of coastal cutthroat trout distribution and abundance in headwater catchments and maps with examples of patterns observed in this study. Patterns include (a) increasing abundance with distance upstream (catchment L2), (b) decreasing abundance (catchment L13), (c) unimodal distribution with a peak in abundance at the midpoint (catchment V9), (d) bimodal distribution with peaks at the upstream and downstream margins of distribution (catchment V15), and (e) a random pattern of distribution (catchment V15).

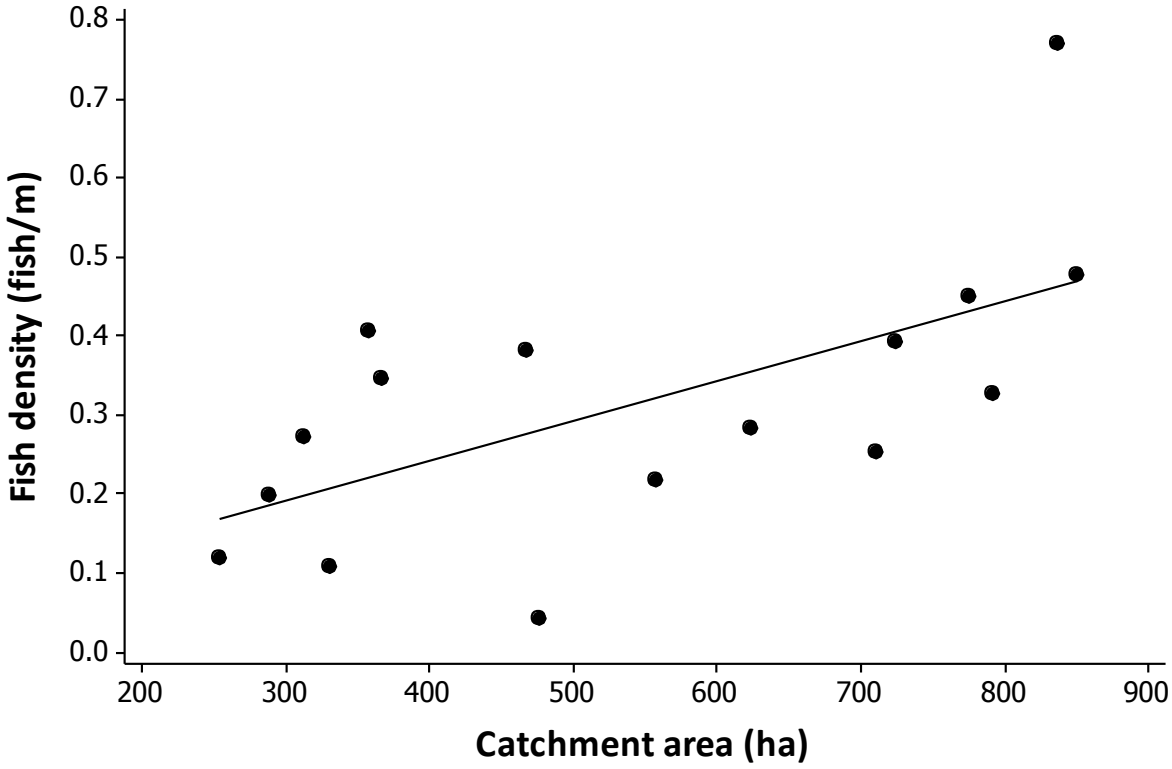

Figure 4. Bivariate scatterplot and linear regression of catchment-scale fish density and catchment area in autumn (n = 16).

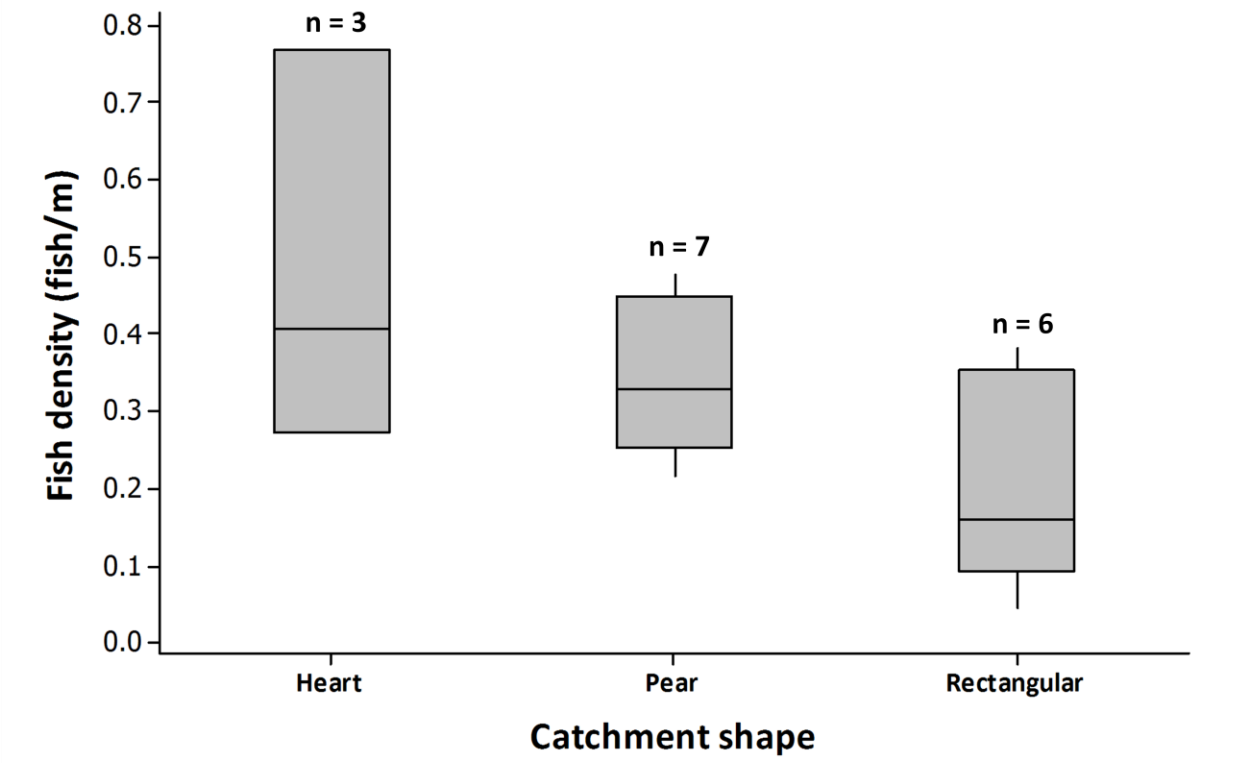

Figure 5. Box plots of catchment-scale fish density and catchment shape in autumn. Horizontal lines within the boxes represent the medians. The lower and upper limits of the boxes indicate the 25th and 75th percentiles; lines extending vertically from the boxes show the upper and lower 25% of the distribution. Mean fish density was significantly different among shapes ($P < 0.05$).

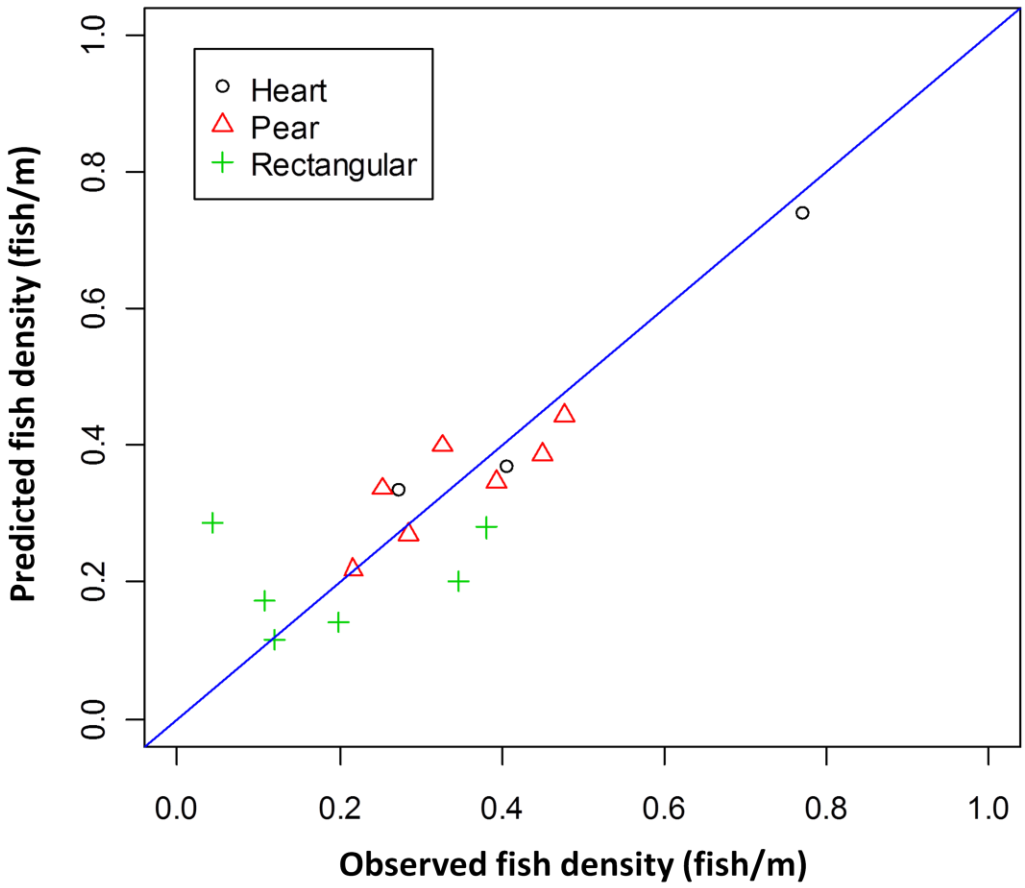

Figure 6. Predicted versus observed catchment-scale fish density in autumn ($R^2 = 0.73$). Variables included in the final catchment-scale model were catchment shape and catchment area. Symbols on the plot correspond to the different catchment shapes. The diagonal line represents a 1:1 relationship between observed and predicted fish density ($n = 16$).

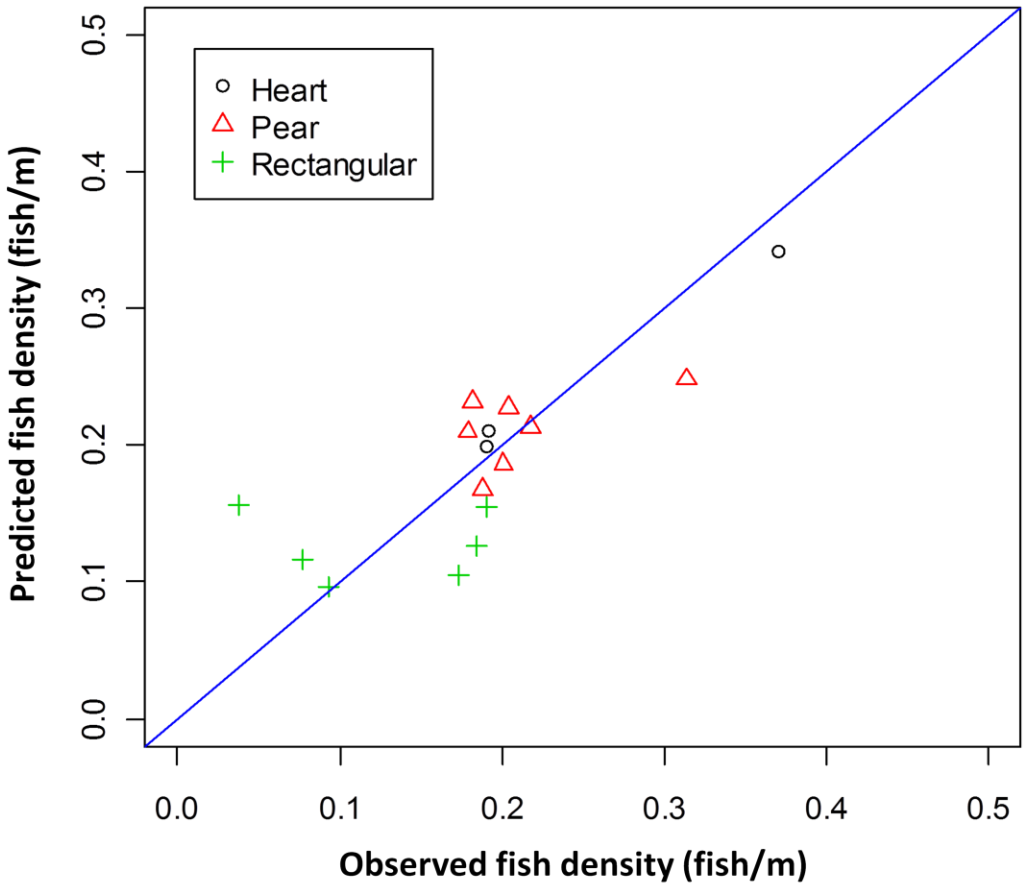

Figure 7. Predicted versus observed catchment-scale fish density in spring (R^2 = 0.63). Variables included in the final catchment-scale model were catchment shape and catchment area. Symbols on the plot correspond to the different catchment shapes. The diagonal line represents a 1:1 relationship between observed and predicted fish density (*n* = 16).

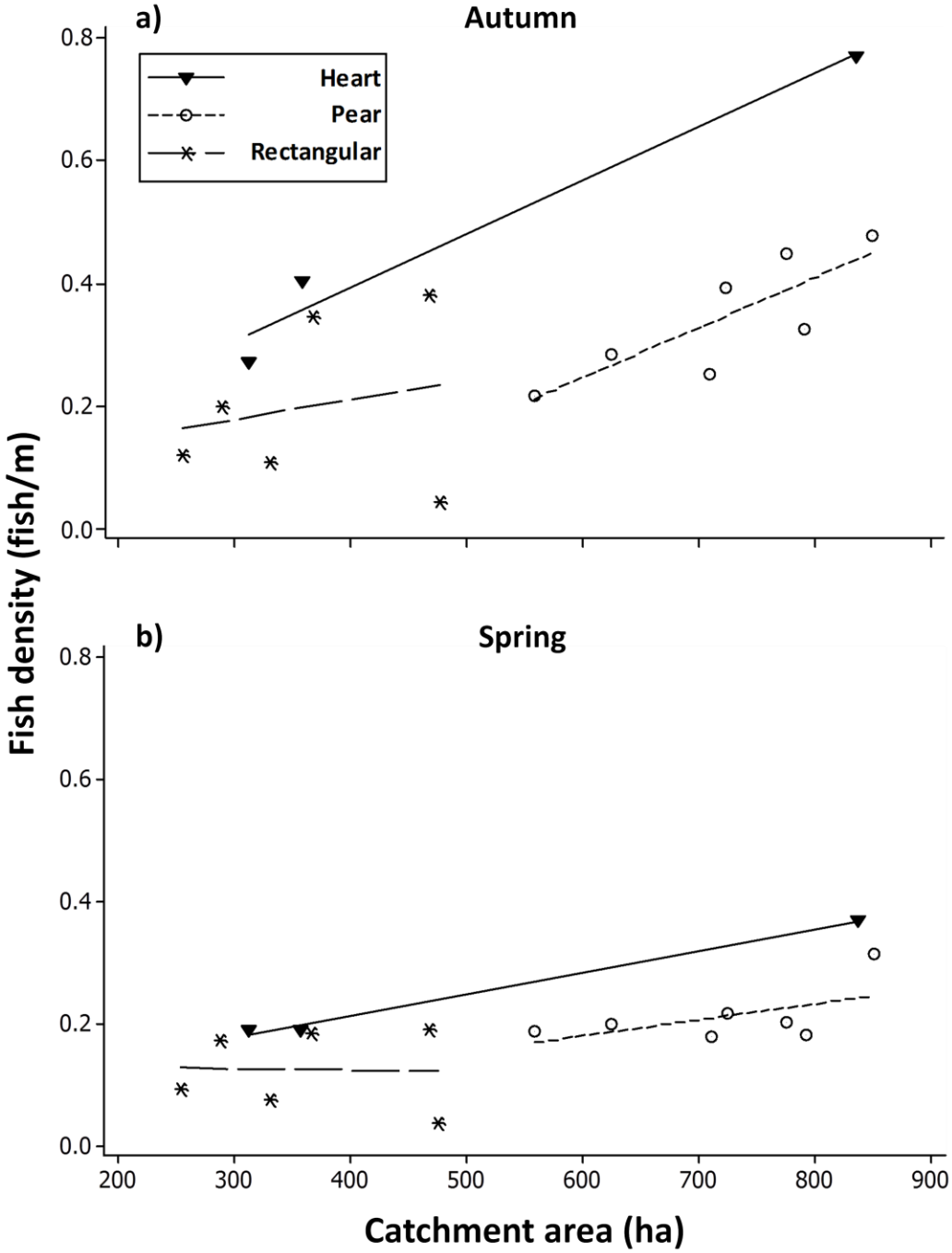

Figure 8. Catchment-scale fish density relative to catchment area in (a) autumn and (b) spring. Symbols and trend lines indicate the three catchment shapes: heart (n = 3), pear (n = 7), and rectangular (n = 6). Slopes among catchment shapes were not significantly different ($P > 0.05$) in autumn or spring.

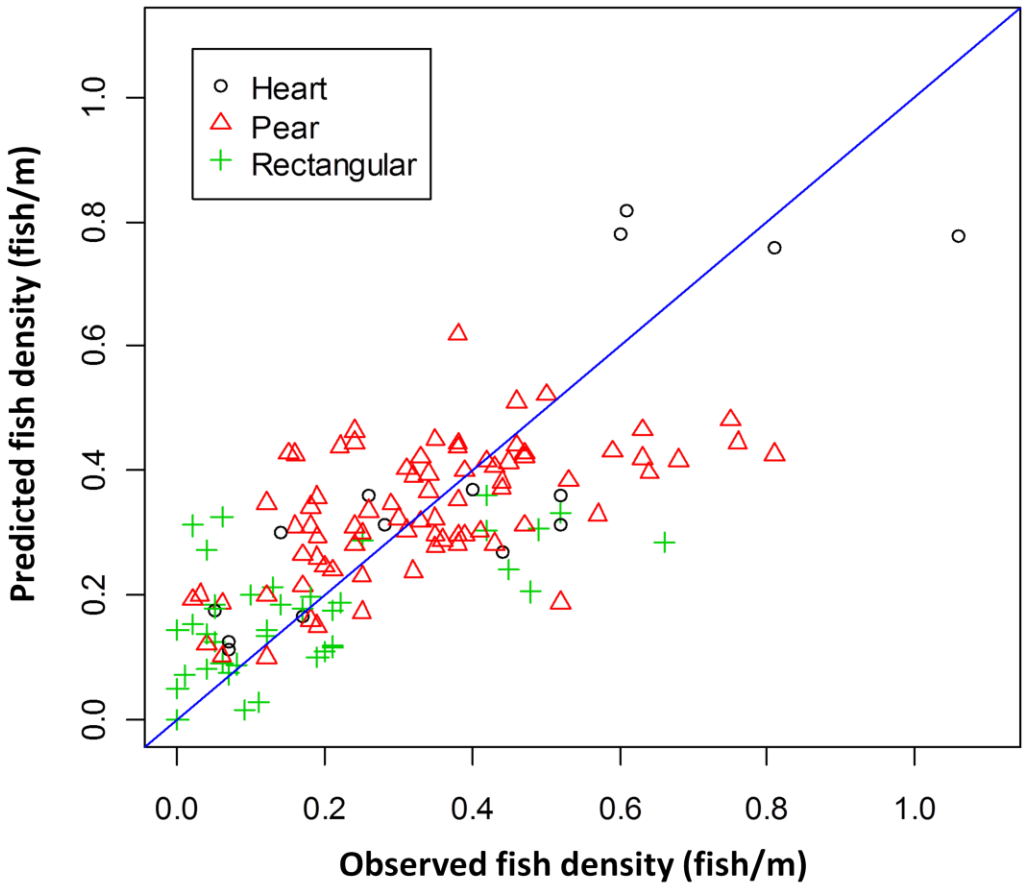

Figure 9. Predicted versus observed segment-scale fish density in autumn (R^2 = 0.54). Variables included in the final segment-scale model were catchment shape, catchment area, SG, SCCA, and SG×SCCA. Symbols on the plot correspond to the different catchment shapes. The diagonal line represents a 1:1 relationship between observed and predicted fish density (*n* = 132).

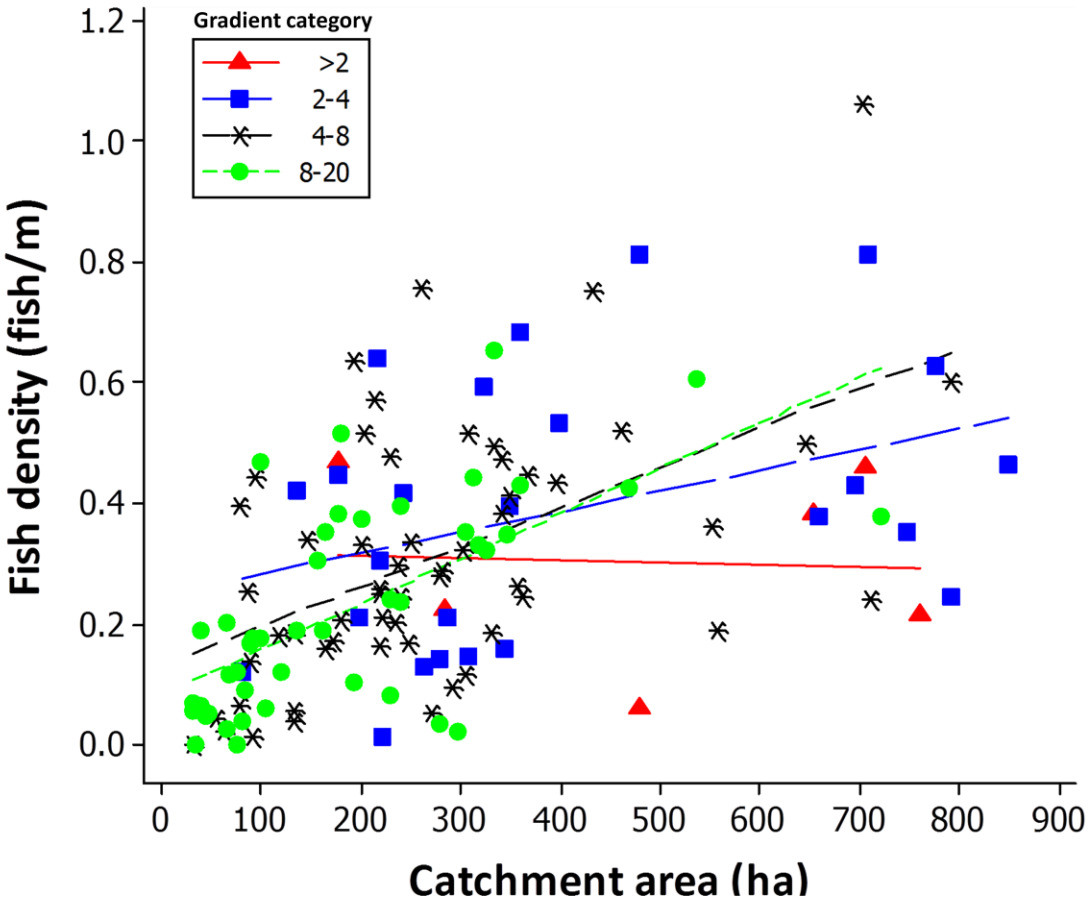

Figure 10. Interaction between segment-scale gradient (categories) and contributing catchment area (x-axis) relative to fish density (y-axis) in autumn. Different symbols and trend lines represent gradient categories that were used to identify segment breaks (n = 132).

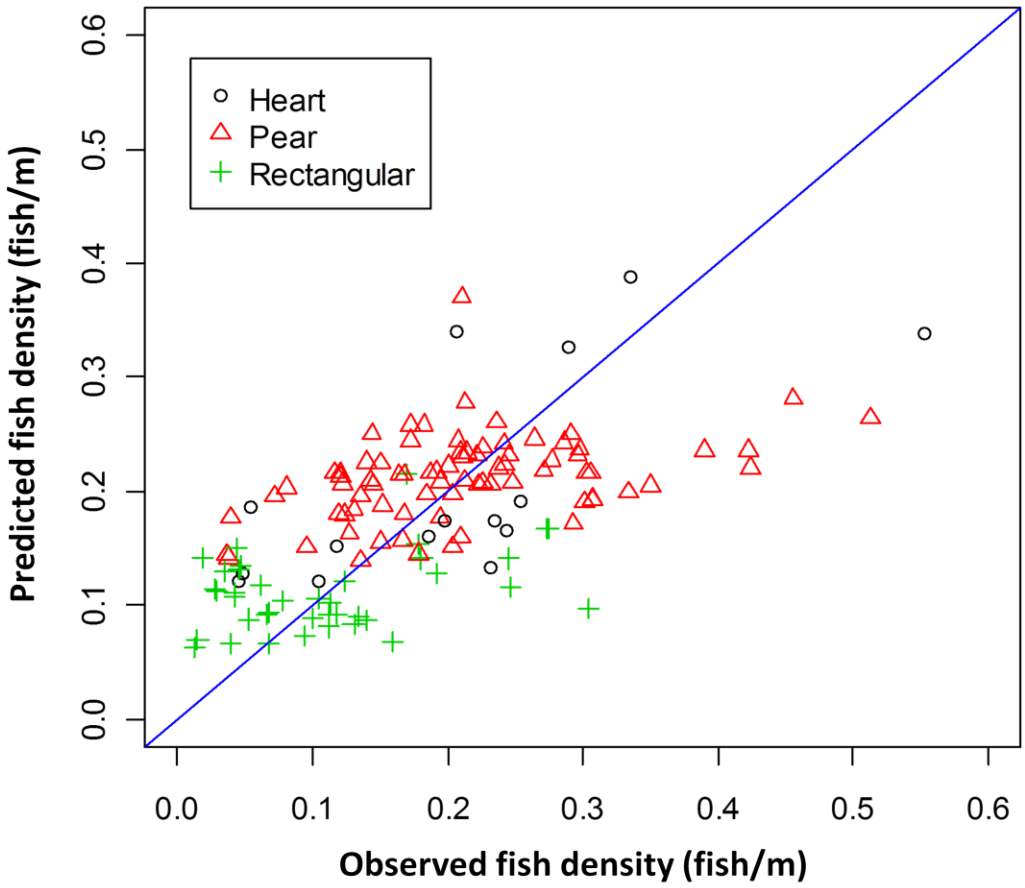

Figure 11. Predicted versus observed segment-scale fish density in spring (R^2 = 0.38). Variables included in the final segment-scale model were catchment shape, catchment area, SG, SCCA, and SG×SCCA. Symbols on the plot correspond to the different catchment shapes. The diagonal line represents a 1:1 relationship between observed and predicted fish density (*n* = 132).

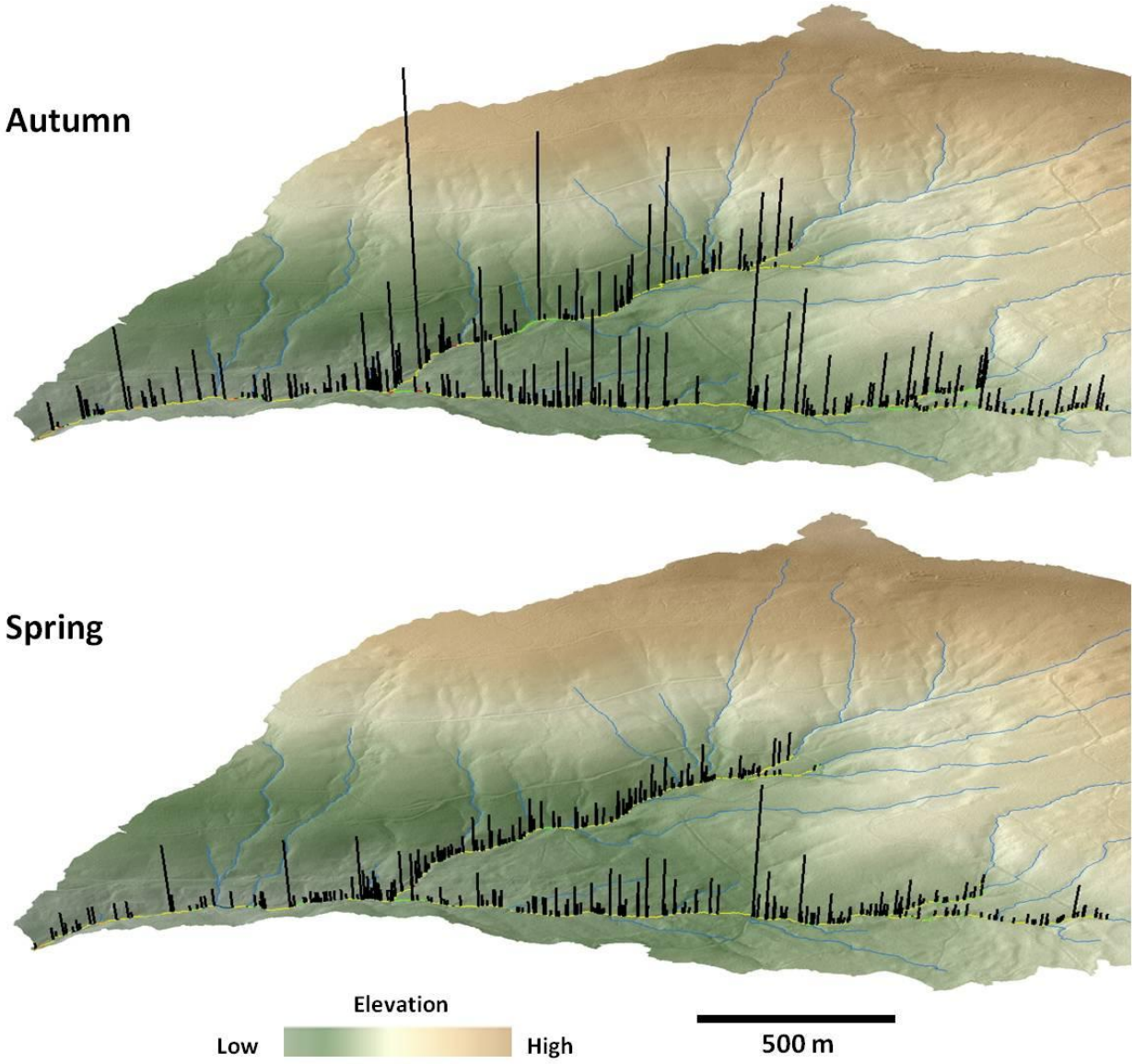

Figure 12. Comparison of coastal cutthroat trout abundance patterns between autumn and spring in catchment L3. The extruded bars on each map illustrate coastal cutthroat trout relative abundance at the channel unit scale. In this example, the pattern of distribution changed from unimodal in the autumn to random in the spring.

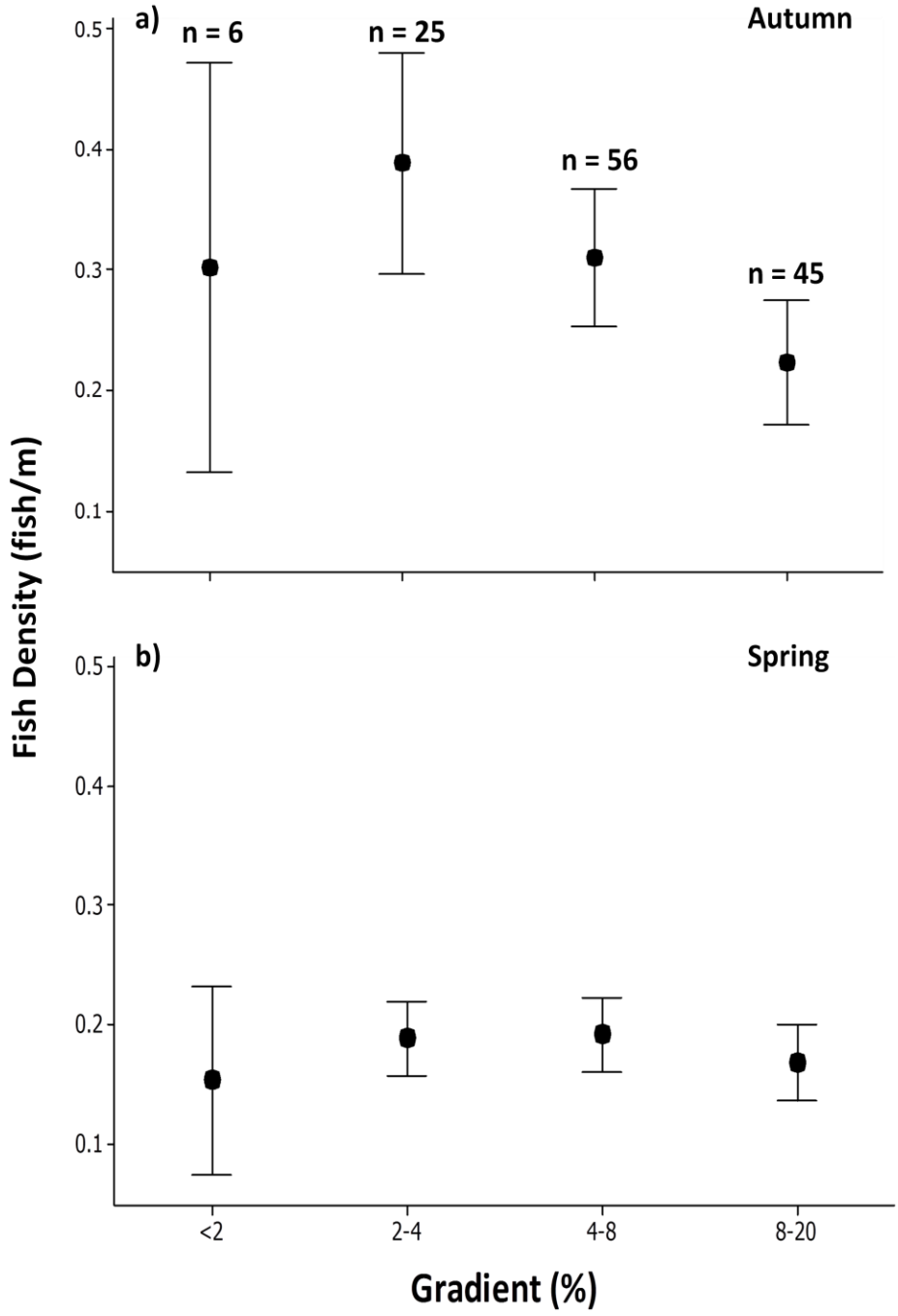

Figure 13. Mean segment-scale fish density in (a) autumn and (b) spring in each of the four segment gradient categories (Montgomery and Buffington 1998), with 95% confidence intervals. Mean fish density varied significantly among gradient categories in autumn ($P < 0.05$), but was not significantly different in spring ($P > 0.05$).

Table 1. Variables included in the catchment-scale backwards elimination stepwise regression of fish density (fish/m) in autumn and spring.

Variable	Variable type	Description
Catchment shape	Categorical	Catchment shape: heart, pear, or rectangular (sensu Benda et al. 2004)
Closed system	Binary	Denotes whether there was a permanent physical in-stream barrier to the upstream migration of fish located at the downstream initiation point of the catchment
Beaver activity	Binary	Denotes whether there was significant beaver activity at or near the upstream end of the sampled stream length on one or more of the tributary streams within the catchment
Catchment area (ha)	Continuous	Land surface area contributing to stream flow above the downstream initiation point of the catchment
Mean catchment elevation (m)	Continuous	Mean elevation for all points within the catchment
Surveyed stream length (m)	Continuous	Total length of stream surveyed within the catchment
Catchment relief ratio	Continuous	Elevation difference (m) between the highest and lowest points within the catchment, divided by the distance (m) along the longest dimension of the catchment parallel to the mainstem channel
Significant confluence density	Continuous	Number of 'significant' tributary confluences (i.e., contributing >25% of the flow at a tributary junction) in the surveyed stream length divided by the total length (km) of stream surveyed
Total confluence density	Continuous	Total number of tributary confluences divided by the total length (km) of stream surveyed
Terminal node density	Continuous	Number of terminal nodes (i.e., upstream extent of fish points) divided by total length (km) of stream surveyed
Tributary length ratio	Continuous	Total length (m) of tributary streams surveyed divided by the total length (m) of the mainstem reach surveyed

Table 2. Variables included in the segment-scale backwards elimination stepwise regression of fish density (fish/m) in autumn and spring.

Variable	Variable type	Description
Catchment shape [a]	Categorical	Catchment shape: heart, pear, or rectangular (sensu Benda et al. 2004)
Catchment area (ha) [a]	Continuous	Land surface area contributing to stream flow above the downstream initiation point of the catchment
Tributary confluence	Binary	Denotes whether the upstream end of the segment is located at a significant tributary stream junction
Segment terminal nodes	Categorical	Number of terminal nodes (i.e., upstream extent of fish points) within or upstream of the segment
Segment length (m)	Continuous	Total length of stream surveyed within the segment
Segment gradient (%)	Continuous	Elevation difference (m) between the highest and lowest points in the surveyed segment divided by the total length (m) of stream surveyed; abbreviation: SG
Segment contributing catchment area (ha)	Continuous	Catchment area upstream of the downstream end of the segment; abbreviation: SCCA
Total confluence density	Continuous	Total number of tributary confluences divided by the total length (km) of stream surveyed within the segment

[a] Catchment scale variables, catchment shape and catchment area, were included in the segment-scale model because they were statistically significant predictors of catchment-scale fish density.

Table 3. Catchment-scale summary statistics for spatially continuous surveys of coastal cutthroat trout in headwater stream networks by season. Data on terminal nodes, stream length surveyed, and total fish counts are presented for each catchment.

Catchment ID	Terminal nodes (count)[a]	Surveyed stream length (m)[b]	Fish abundance (count)		Fish density (fish/m)[c]	
			Autumn	Spring	Autumn	Spring
L15	4	2504	564	399	0.27	0.19
V5	2	1919	652	292	0.41	0.19
V9	1	1848	1382	672	0.77	0.37
L2	3	1973	394	296	0.29	0.20
L3	4	5267	1171	838	0.25	0.18
L5	3	4297	1363	679	0.45	0.20
L9	4	6940	1147	1051	0.22	0.19
V4	3	4752	1861	1226	0.48	0.31
V7	3	5105	1420	850	0.33	0.18
V8	4	4066	1291	731	0.39	0.22
L12	3	2011	527	299	0.35	0.18
L13	3	4970	1460	757	0.38	0.19
L33	2	3579	381	301	0.12	0.09
V1	2	1349	56	51	0.04	0.04
V15	1	1910	209	133	0.11	0.08
V2	1	716	115	105	0.20	0.17

[a] Upstream extent of fish distribution points

[b] Surveyed stream length includes sections of stream that could not be effectively sampled for fish abundance.

[c] Fish density was calculated from the length of stream sampled, not from the surveyed stream length.

Table 4. Catchment-scale statistics for physical habitat characteristics from the autumn survey of stream habitat.

Catchment ID	Percent pool area	Mean maximum pool depth (cm)	Percent cascade area	Average cascade gradient (%)	Percent riffle area
L15	9%	31	41%	17	43%
V5	11%	37	22%	10	58%
V9	24%	57	58%	12	15%
L2	12%	34	43%	12	19%
L3	12%	31	68%	14	16%
L5	15%	33	12%	8	50%
L9	15%	34	40%	12	31%
V4	19%	34	30%	13	40%
V7	27%	34	7%	12	53%
V8	16%	33	39%	11	35%
L12	16%	35	44%	11	24%
L13	17%	33	31%	16	36%
L33	14%	33	61%	13	20%
V1	41%	45	10%	11	47%
V15	22%	38	37%	14	24%
V2	44%	27	3%	13	40%

Table 5. Catchment-scale statistics for basin characteristics derived from LiDAR digital elevation models.

Catchment ID	Catchment shape	Catchment area (ha)	Mean elevation (m)	Relief ratio	Significant confluence density (number/km)
L15	heart	312	547	0.180	0.000
V5	heart	357	462	0.128	0.521
V9	heart	836	589	0.115	0.000
L2	pear	624	605	0.155	0.507
L3	pear	710	613	0.150	0.380
L5	pear	775	757	0.147	0.931
L9	pear	558	517	0.154	0.432
V4	pear	850	494	0.148	0.421
V7	pear	791	393	0.102	0.392
V8	pear	724	510	0.141	0.492
L12	rectangular	366	574	0.166	0.000
L13	rectangular	468	606	0.125	0.000
L33	rectangular	254	528	0.156	0.559
V1	rectangular	476	459	0.099	0.741
V15	rectangular	330	401	0.104	0.000
V2	rectangular	288	414	0.120	0.000

Table 6. Final catchment-scale general linear model parameter estimates predicting fish density in the autumn and spring.

Variable	Parameter estimate	SE	*t*	*P*
Autumn				
Intercept	0.09505	0.11372		
Catchment shape				
Pear	-0.30724	0.08163	-3.764	0.002
Rectangular	-0.17661	0.07649	-2.309	0.040
Catchment area	0.00077	0.00019	3.978	0.002
Spring				
Intercept	0.11284	0.06070		
Catchment shape				
Pear	-0.09795	0.04357	-2.248	0.044
Rectangular	-0.08675	0.04083	-2.125	0.055
Catchment area	0.00027	0.00010	2.648	0.021

Table 7. Catchment-scale least squares estimates and 95% confidence intervals for mean fish density by catchment shape in autumn and spring.

Catchment shape	Mean (fish/m)	Test at $\alpha = 0.05$[a]	Lower 95%	Upper 95%
Autumn				
Heart	0.52	a	0.39	0.65
Pear	0.21	b	0.10	0.32
Rectangular	0.34	b	0.22	0.46
Spring				
Heart	0.26	a	0.19	0.33
Pear	0.17	b	0.11	0.22
Rectangular	0.18	a,b	0.11	0.24

[a] Summarizes test results comparing means within each season. Means with the same symbol are not significantly different ($\alpha = 0.05$).

Table 8. Final segment-scale general linear model parameter estimates predicting fish density in the autumn and spring. Catchment shape and catchment area are also included in the catchment-scale models.

Variable	Parameter estimate	SE	*t*	*P*
Autumn				
Intercept	0.14590	0.08315		
Catchment shape				
Pear	-0.26050	0.05156	-5.053	<0.001
Rectangular	-0.13670	0.04613	-2.963	0.004
Catchment area	0.00073	0.00012	6.074	<0.001
Segment gradient (SG)	-2.15600	0.61840	3.485	0.001
Segment contributing catchment area (SCCA)	-0.00007	0.00013	0.595	0.553
SG×SCCA	0.00525	0.00164	3.202	0.002
Spring				
Intercept	0.06082	0.04853		
Catchment shape				
Pear	-0.05811	0.00300	-1.935	0.055
Rectangular	-0.05383	0.02690	-2.001	0.048
Catchment area	0.00026	0.00007	3.756	0.002
Segment gradient (SG)	-0.23790	0.35800	-0.665	0.508
Segment contributing catchment area (SCCA)	0.00002	0.00007	0.295	0.769
SG×SCCA	0.00160	0.00091	1.746	0.083

Table 9. Segment-scale least squares estimates and 95% confidence intervals for mean fish density by catchment shape in autumn and spring.

Catchment shape	Mean (fish/m)	Test at $\alpha = 0.05$[a]	Lower 95%	Upper 95%
Autumn				
Heart	0.49	a	0.41	0.65
Pear	0.23	c	0.18	0.32
Rectangular	0.35	b	0.22	0.46
Spring				
Heart	0.23	a	0.18	0.28
Pear	0.17	a,b	0.15	0.20
Rectangular	0.18	b	0.14	0.22

[a] Summarizes test results comparing means within each season. Means with the same symbol are not significantly different ($\alpha = 0.05$).

Table 10. Changes in catchment-scale distribution patterns and density of coastal cutthroat trout in headwater stream networks between autumn and spring. See Figure 3 for descriptions of distribution patterns.

Catchment ID	Percent decrease in fish density (fish/m)	Distribution pattern		Change in pattern
		Autumn	Spring	
L15	30%	random	random	no
V5	52%	unimodal	random	yes
V9	51%	unimodal	unimodal	no
L2	29%	increasing	random	yes
L3	29%	unimodal	random	yes
L5	54%	random	random	no
L9	13%	increasing	random	yes
V4	34%	bimodal	random	yes
V7	44%	increasing	random	yes
V8	44%	random	random	no
L12	46%	bimodal	random	yes
L13	49%	decreasing	random	yes
L33	22%	unimodal	random	yes
V1	13%	random	random	no
V15	28%	bimodal	bimodal	no
V2	13%	decreasing	decreasing	no