[Article]

Observational Evidence of Spatial and Temporal Structure in a Sympatric Anadromous (Winter Steelhead) and Resident Rainbow Trout Mating System on the Olympic Peninsula, Washington

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Abstract.—We documented the spawning distribution and male mating tactics of sympatric anadromous rainbow trout *Oncorhynchus mykiss* (winter steelhead) and resident rainbow trout in the Calawah and Sol Duc River basins, Washington. Snorkel surveys and in situ behavioral observations were used to determine the spatial and temporal distribution patterns and male mating tactics of anadromous, resident, and hatchery residual fish across the spawning season. In general, male steelhead entered our survey reaches earlier than female steelhead, and both entered earlier than the wild resident and hatchery residual forms. Spatially, wild residents represented the greatest proportion of the population in the middle and upper survey reaches. Those differences coincided with mating attempts primarily between male and female steelhead early in the spawning season and primarily between female steelhead and wild resident males at the end of the season. Most of the mating attempts that we observed involved a single female and a single male steelhead, but attempts commonly included multiple male steelhead, wild resident males, or both, and behavioral tactics differed between forms. The patterns suggest a strong temporal structure and a lesser spatial structure to the distribution of *O. mykiss* during the spawning season, which has important implications for future studies of this complex species.

Several fishes in the family Salmonidae have evolved multiple life history forms that exploit different degrees of anadromy. Some of those species include rainbow trout *Oncorhynchus mykiss* (Neave 1944), coastal cutthroat trout *O. clarkii* (Zimmerman et al. 1997), sockeye salmon *O. nerka* (Wood 1995), Arctic char *Salvelinus alpinus* (Nordeng 1983), brown trout *Salmo trutta* (Skaala and Naevdal 1989), and Atlantic salmon *Salmo salar* (Verspoor and Cole 1989). The forms range from individuals that undertake extensive ocean migrations before returning to spawn in freshwater (anadromous form) to those that complete their entire life cycle in freshwater (nonanadromous resident form; Jonsson and Jonsson 1993; Quinn and Myers 2005). Between those extremes, fractions of each population may remain in the ocean for as little as 1 year or as long as 6 years (Groot and Margolis 1991). Of particular interest is the distribution and mating behavior of sympatric anadromous and resident forms during the spawning season (e.g., Jonsson 1985; Webb and Hawkins 1986; Wood and Foote 1996; Zimmerman and Reeves 2000), which has implications for

understanding mating systems and population structure.

Oncorhynchus mykiss is an iteroparous species that displays some of the most diverse life history strategies among Pacific salmonids *Oncorhynchus* spp. The two most common forms are steelhead (anadromous rainbow trout) and resident rainbow trout (hereafter "rainbow trout"). Steelhead generally spend 1–4 years in the ocean and spawn in freshwater, although some offspring may mature without migrating to the ocean (residual steelhead or precocious parr; Shapovalov and Taft 1954). There are two general races of steelhead: summer runs (river maturing) that typically enter rivers several months prior to spawning in a relatively immature condition, and winter runs (ocean maturing) that enter the river in a more mature state and spawn soon after (days to several weeks; Busby et al. 1996). Rainbow trout spend their entire life in freshwater and may remain relatively sedentary or undertake migrations within rivers and into and out of lakes (Behnke 2002). Steelhead and rainbow trout are sympatric in many Pacific Northwest watersheds, and knowledge of their mating system is essential to their conservation and management.

The *O. mykiss* mating system is less studied than the mating systems of semelparous Pacific salmonids (e.g.,

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Groot and Margolis 1991). Several studies indicate that steelhead and rainbow trout interbreed to varying degrees (e.g., Chilcote 1976; Currens et al. 1990; Docker and Heath 2003; Narum et al. 2004; Kuligowski et al. 2005). However, this research did not account for behavior, and the samples were often collected over a relatively short time span (days to weeks) or within a relatively short distance from one another (tens of kilometers), as opposed to over the entire temporal and spatial breadth of a spawning season. Research that does not adequately account for the variables of time and space may misrepresent the population structure and mating systems, especially in iteroparous species with protracted spawning periods (Garant et al. 2000; Hendry et al. 2002). This is because populations are composed of a mixture of individuals that reproduce at different times within a particular season or location, and these times are often heritable (Hendry and Day 2005). Therefore, an important first step in understanding population structure is determining the spatial and temporal structure of the distribution of sympatric forms during the reproductive season.

Most information about the spawning distribution and behavior of sympatric *O. mykiss* forms in the Pacific Northwest is derived from two studies that focused on populations of summer steelhead and rainbow trout in inland river basins (e.g., Columbia River tributaries). One study found that while both forms overlapped on the spawning grounds, female rainbow trout spawned slightly later than female steelhead and dug nests in different microhabitats (Zimmerman and Reeves 2000). Another study indicated that the forms spawned at the same times, although rainbow trout did spawn at slightly higher elevations than steelhead (Pearsons et al. 2003). While these studies provide some evidence for slight structure to the temporal and spatial distribution of forms during spawning, no such data are available for sympatric winter steelhead and rainbow trout.

Behavioral observations during periods of overlap between summer steelhead and rainbow trout have often documented attempts by male rainbow trout to mate with female steelhead, typically by using the sneaking tactic to counterbalance the presence of larger, guarding male steelhead (Zimmerman and Reeves 1996; Kostow 2003; Pearsons et al. 2003). Rainbow trout may rely heavily on the sneaking tactic; however, sometimes rainbow trout are the only available mates for female steelhead, and the behavior displayed by rainbow trout in those situations has not been described (Pearsons et al. 2003). There is a need to examine the different tactics smaller rainbow trout use in attempted matings with steelhead and vice versa.

Further information on the distribution patterns of different *O. mykiss* forms during spawning is necessary to better understand this complex species, especially in the case of winter steelhead. To our knowledge, no study has systematically and simultaneously examined the spatial and temporal distribution patterns of sympatric coastal winter steelhead and rainbow trout and their mating behaviors across an entire spawning season. Such basic behavioral information may provide evidence of spatial and temporal structure in the distribution of sympatric anadromous and resident *O. mykiss* during the spawning season, and is important for developing strong hypotheses for future studies examining their mating systems and population structure.

In this study, we investigated the mating system of sympatric coastal anadromous (winter steelhead) and resident rainbow trout across the spawning season in the Quileute River basin, Washington. To accomplish this task, we conducted intensive field surveys, including spatially referenced snorkel surveys, redd counts, and behavioral observations across four successive years. The objectives were to (1) determine whether anadromous and resident forms co-existed during the spawning season, (2) determine whether there was spatial and temporal structure to the distribution and spawning time of anadromous and resident forms, (3) determine whether periods of overlap resulted in attempted matings, and (4) characterize male behaviors associated with mating attempts.

Methods

Study site and population.—This study was conducted in the Calawah (190 km^2) and Sol Duc River basins (196 km^2), which lie within the Quileute River watershed (790 km^2) on the west side of the Olympic Peninsula, Washington (Figure 1). We focused on the winter steelhead in the Sol Duc and Calawah rivers, which are considered healthy among populations in the contiguous United States (Huntington et al. 1994), and the unstudied population of resident *O. mykiss* (the nonanadromous form potentially included rainbow trout and residual steelhead; J.R.M., personal observation). Mean annual escapement from 1992 to 2002 was 5,053 fish (range = 2,295–7,634 fish) in the Sol Duc River and 3,806 fish (range = 1,458–5,558 fish) in the Calawah River (WDFW 2002). They enter freshwater from December through June, and most spawn from March through June in main-stem rivers and the largest tributaries (WDFW 2002). In addition to winter steelhead, a few summer steelhead are present but little is known about the populations.

A steelhead hatchery is located 14 km downstream from our main-stem Calawah River survey reach, and a
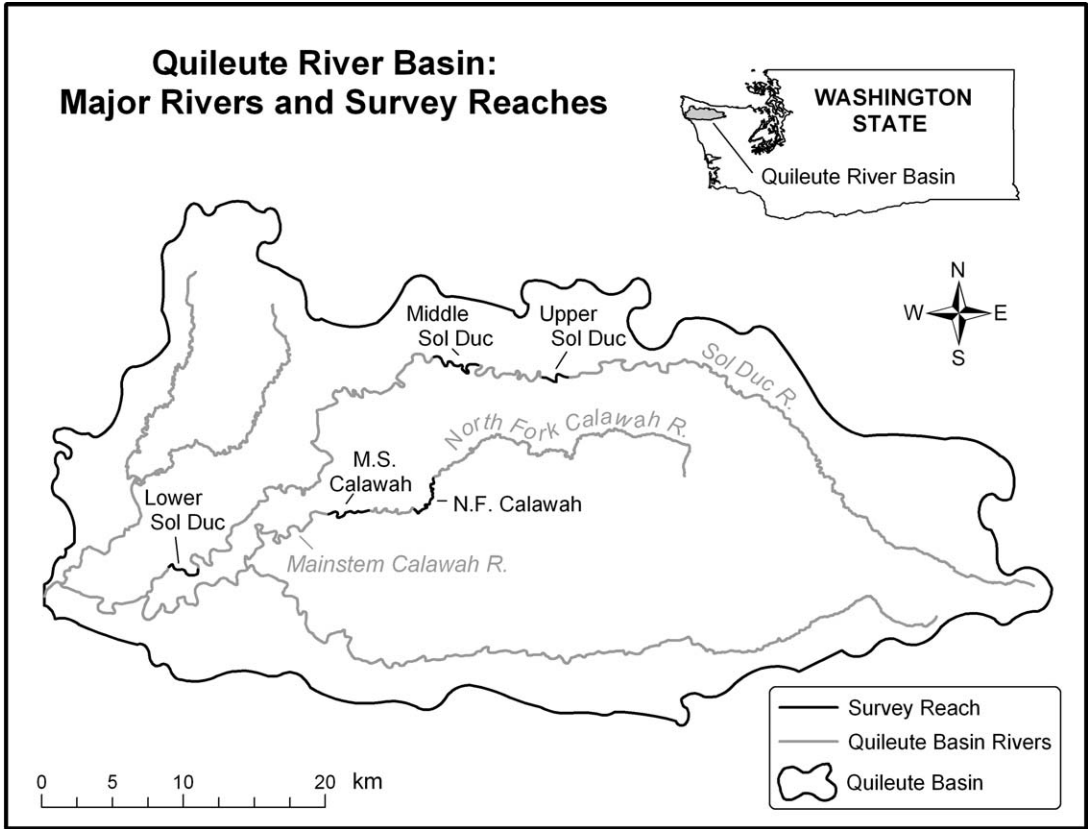
FIGURE 1.—Map of the Quileute River basin, Washington. Survey reaches are denoted by bolded lines.

juvenile rearing pond is located at the upper start point of the middle Sol Duc River reach. These facilities release approximately 55,000 summer and 190,000 winter steelhead smolts per year into the Bogachiel, Calawah, and Sol Duc rivers (WDFW 1998–2004). Low numbers of returning adult hatchery winter steelhead are harvested each year in both rivers (36–161 fish), most of which (>90%) are taken from November through January (WDFW unpublished data, 2001–2005). Although adult hatchery steelhead return at a time when wild spawning is believed to be minimal, the hatchery smolts are released in May during the peak spawn time. Precocious residual male parr are a relatively common by-product of hatcheries and may spawn with wild steelhead (Viola and Shuck 1995; Pearsons et al. 2003). More documentation is necessary to determine the extent to which these interactions occur in other populations.

Extent of surveys.—We conducted snorkel surveys, redd counts, and behavioral observations across four successive spawning seasons (1999–2003) to examine the mating system of wild winter steelhead, resident rainbow trout, and hatchery residual steelhead. Data were collected at different locations and during each month of the spawning season to capture potential variation in the distribution and timing of spawning activity. Our study locations included three survey reaches in the Sol Duc River that are roughly representative of the lower, middle, and upper river areas and one reach each in the main-stem Calawah and North Fork Calawah rivers (Figure 1). To try to reduce the possibility of counting summer steelhead and their redds, the reaches were located well below (>19 km) areas where those fish are believed to spawn (WDFW 2002). Snorkel survey reaches (2.3–5.0 km in length) were generally longer than redd count reaches (1.9–4.0 km) because stream wading was limited at higher flows whereas snorkeling was not.

The goal was to conduct one redd count and one fish survey per month across the spawning season, although stream conditions prevented monthly surveys on a few occasions. Surveys were initiated as early as stream conditions allowed, which was typically January or February, and continued until steelhead were absent

(June–July). Snorkel and redd counts were conducted by the same person (J.R.M.) to eliminate inconsistencies that can occur with multiple surveyors (Thurow 1994).

Classification of O. mykiss types.—We classified individual fish as wild anadromous males, wild anadromous females, wild residents, and hatchery residuals during snorkel surveys and behavioral observations. Adult hatchery anadromous fish were not enumerated because they were never observed spawning or attempting to mate with wild anadromous or resident fish. We used the terms "anadromous" and "resident" because we relied solely on visual identification and could not rule out the possibilities that a few steelhead were summer run fish and that some resident fish were residual steelhead or precocious parr instead of rainbow trout.

Fish that were visually estimated to be greater than 50 cm in length were classified as wild anadromous fish. Fish that were estimated to be 25–50 cm in length and with characteristic coloring and spotting patterns (e.g., red stripe, dense spots below lateral line) were classified as wild residents, and fish that had those same characteristics plus a missing adipose fin were classified as hatchery residuals. Most wild juvenile steelhead in the Quileute River basin smolt after 2 years in freshwater at a size of 15–20 cm (80%) or at age 3 at 20–25 cm (19%); the vast majority of anadromous fish (>99%) spend two or more years in the ocean and attain a very large size (75–250 cm; J.R.M., personal observation; WDFW and Quileute Tribe 2001–2005). Snorkel surveys in the Sol Duc and Calawah rivers confirmed the presence of numerous 25–50-cm fish in August and September (1998–2002), a time when winter steelhead were absent and only a few summer steelhead were present, which provides evidence for the presence of a resident form (J.R.M., personal observation). Female steelhead were distinguished from males by their blunt heads, shorter maxillaries, and consistent silvery coloration. We could not determine the sex of wild resident and hatchery residual fish during snorkel surveys, but we could during spawning observations because of the inherent behavioral differences (e.g., discharging milt versus excavating redds).

Snorkel surveys and redd counts.—Snorkeling can be an effective method for establishing presence or absence and estimating the relative abundance of salmonids if certain criteria are met (Thurow 1994). We conducted 70 snorkel surveys over an average of 81.1 km of stream (SD = 61.5) per year to enumerate the relative abundance of wild anadromous, wild resident, and hatchery residual fish. Stream discharge and visibility were scouted daily, and surveys were

only conducted when the diver could see the stream bottom in water that had a depth of 3 m or more (Northcote and Wilkie 1963; Thurow 1994). Once in the water, the diver worked downstream through all channel units in a single pass and classified fish upon observation. In a few situations, when cover was complex, the diver made multiple passes through the unit and the mean number of fish counted was used.

We conducted 97 redd counts over an average of 60.2 km of stream (SD = 33.0) per year to estimate the monthly timing of female steelhead spawning activity. All observed redds were assumed to be constructed by anadromous females rather than resident females because of the large excavation area and associate substrate size (Graybill et al. 1979; Zimmerman and Reeves 2000). Furthermore, we never observed resident-sized fish excavating redds. Redds were noted by the differences in substrate coloration or algal growth or the presence of spawning fish, and the locations were recorded in a notebook to ensure that the same redds were not counted in subsequent surveys.

Spawning behavioral observations.—We conducted one to two detailed in situ observations of attempted matings during redd counts to (1) determine whether anadromous and resident forms were attempting to mate, (2) characterize the structure of attempted mating events across the spawning season, and (3) describe the behavioral tactics used by males to orient toward females during attempted matings. The tendency of *O. mykiss* to spawn in shallow water (27–88 cm deep; Graybill et al. 1979) allowed for detailed observation of their mating behavior. Attempted matings were defined as incidents in which a male oriented toward a spawning female, mouth agape, and visibly discharged milt, followed by subsequent egg burial by the female. Attempts that did not meet these criteria were discarded.

The attempted matings were scored according to the number and life history of males orienting toward a single anadromous female: one wild anadromous male (1WAM), multiple (2–5) wild anadromous males (2WAM, 3WAM, 4WAM, or 5WAM), wild resident male (WRM), and hatchery residual male (HRM). The observations were pooled across years by month and location to assess whether the attempted matings reflected the prevailing population composition. Tactics used by males to orient toward females were classified as guarding, sneaking, or group mating tactics, the proportion of which was described monthly for different males. We defined guards as males that used aggression to monopolize access to females and sneaks as less-aggressive males that darted alongside a spawning pair (Gross 1991). Group tactics were times

TABLE 1.—Pooled fish counts for all Quileute River basin, Washington, survey reaches and *O. mykiss* types, including the number of surveys (n), wild anadromous males (WAMs), wild anadromous females (WAFs), wild residents (WRs), and hatchery residuals (HRs). Surveys were conducted during 1999–2003.

Month	n	WAM	WAF	WR	HR
Feb	10	42	27	13	1
Mar	12	37	32	15	5
Apr	13	69	89	34	0
May	16	81	132	94	13
Jun	15	9	45	121	40
Jul	4	0	5	37	15

when multiple males attempted to mate without a noticeable behavioral hierarchy. Observation times ranged from 30 min up to 2 h and ceased when fish left the area or until 2 h was up. Observations involving multiple males required more time because their intense competition often pushed females away for short periods before returning.

Data analysis.—We used the snorkel survey data to calculate the monthly abundance of each form, which was then expressed as a normalized cumulative distribution of fish counts; the counts probably consisted of both pre- and postspawn fish, so the accuracy of freshwater arrival timing is unknown. We used the cumulative redd count data to generate a similar cumulative distribution curve to examine differences in spawning activity of females between different locations because redd counts were conducted more consistently on a monthly basis than snorkel counts due to inclement stream conditions. Multiple two-sample Kolmogorov–Smirnov tests between pairs of distributions were used to test for differences in the median time of entry between forms and the median spawn time between locations and were executed in SYSTAT version 10 (SPSS, Inc., Chicago, Illinois). We defined the median time of entry as the time at which 50% of the fish counted had entered our survey reaches. Significant differences in median entry time between forms and in median spawn time between locations were assumed to represent temporal and spatial structure respectively. Given the use of multiple comparisons (10 in the case of pairwise comparisons of five different sampling sites), the statistically significant error rate per test was lowered from 0.05 to 0.005 (1 in 200); the net aggregated error rate was therefore no more than 1 in 20. In each case, the probability expresses a two-sided test given that there was no a priori expectation that any individual fish was more likely to enter the reach than any other.

Simultaneous evaluation of the effects of location, life history form, and time of year on observed fish abundances were evaluated using a linear mixed model (LMM). The model is similar to analysis of covariance (ANCOVA) but allows the explicit, simultaneous estimation of the fixed and random effects in the model. Temporal autocorrelation was evaluated and was found to be nonsignificant; therefore, repeated-measures models were not used. However, the numbers of years was small and 2001 had conspicuous values, so the power to detect autocorrelation was low. The LMM tests were performed using a procedure within SAS version 8 (Littell et al. 1996). Month, wild anadromous sex, and resident fish were treated as fixed effects since we were only prepared to draw inferences about those categories. Given our interest in the potential use of sampling locations to characterize the spatial variation within the watershed, locations were treated as random effects. Evaluation of the model's residuals revealed no significant autocorrelation or deviation from normality for the fish and redd counts; thus, the data were pooled across all years.

Results

Distribution of Different Types

Wild anadromous fish ($n = 568$) exhibited the highest abundance in our snorkel surveys, followed by wild residents ($n = 314$) and hatchery residuals ($n = 74$). The sex ratio of wild anadromous fish was female biased (42% male, 58% female). Six of the fish in the resident size-class were reclassified as wild anadromous fish because they displayed characteristics suggestive of ocean entry (e.g., silvery, few spots), which contrasted sharply with the striking lateral red stripe and dense spotting of the resident fish. No fish in the anadromous size-class were reclassified as residents. Fish counts were pooled over the 4-year survey period (see Data Analysis) and indicate that wild anadromous and wild resident individuals coexisted during each month of the spawning season (Table 1). Hatchery residual fish were present in low numbers during all months except April.

Despite extensive overlap, there was variation in the median time of entry (50%) into our survey reaches between the different types. Specifically, April was the median entry time for WAMs, April–May was the median for wild anadromous females, May was the median for wild resident fish, and June was the median for hatchery residual fish (Figure 2A). The greatest difference in entry time between WAMs and wild anadromous females was 17% ($P < 0.001$; two-sided probability), compared with 32% ($P < 0.001$) between wild anadromous females and wild residents and 25% ($P < 0.0001$) between wild residents and hatchery residual fish.

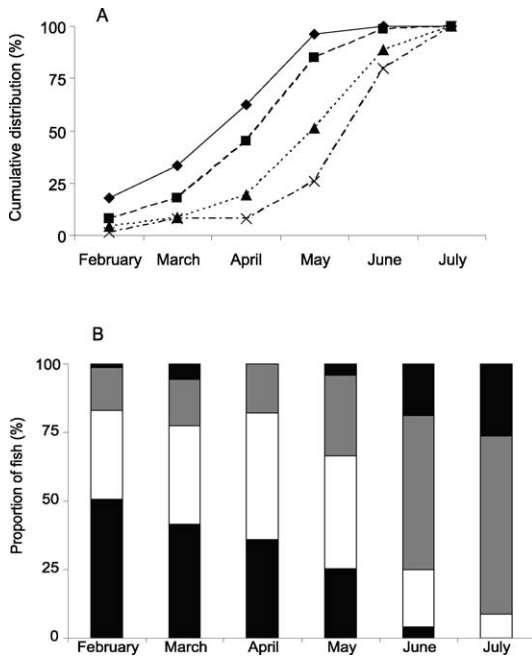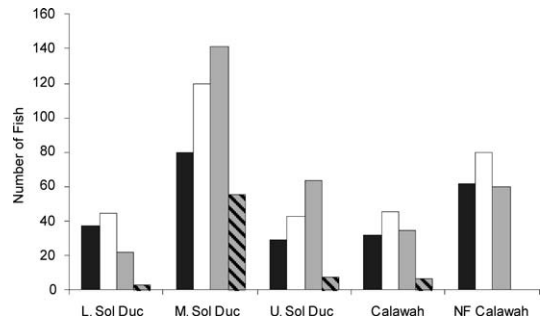As a result of the entry time differences, which

FIGURE 3.—Cumulative counts of *O. mykiss* types at each survey location within the Quileute River basin, Washington (February–July 1999–2003). Survey locations were lower (L.), middle (M.), and upper (U.) sections of the Sol Duc River and the North Fork (NF) and main stem of the Calawah River. Black = wild anadromous males, white = wild anadromous females, gray = wild residents, and hatching = hatchery residuals.

FIGURE 2.—Panel **(A)** shows the median time of freshwater entry (50%) as described by a normalized distribution of cumulative counts of *O. mykiss* types in the Quileute River basin, Washington (1999–2003). Symbols are as follows: diamonds = wild anadromous males, squares = wild anadromous females, triangles = wild residents, and *x*s = hatchery residual fish. Panel **(B)** shows the population composition for all survey reaches across the spawning season; black = wild anadromous males, white = wild anadromous females, gray = wild residents, and hatch marks = hatchery residuals.

reflected an unknown proportion of arriving and leaving fish, the population composition shifted from being predominately WAMs in February (51%) and March (42%) to being predominately wild anadromous females in April (46%) and May (41%) (Figure 2B). By June, 21% of the population consisted of wild anadromous females, but only 6% were WAMs. In comparison, wild residents accounted for less than 20% of the counts until May (26%) and were the predominant type in June (56%) and July (65%).

Spatially, wild anadromous and wild resident fish were observed at all survey reaches at some point in the spawning season (Figure 3). However, wild residents were most abundant in the middle Sol Duc, upper Sol Duc, and North Fork Calawah River reaches and were least abundant in the lower Sol Duc River. Hatchery residual fish were observed at all locations except for the North Fork Calawah River and were most abundant in the middle Sol Duc River, where the juvenile rearing facility is located.

The results of the LMM indicated that month, life history form, and the month × form interaction all influenced the relative abundance of *O. mykiss* during the spawning season (Table 2). The effect of the location × month × life history form (tertiary) interaction was highly significant ($P < 0.001$), as was location alone ($P = 0.025$) and the location × month interaction ($P = 0.028$). Location had an effect on fish counts that was on average larger than the tertiary interaction term when each was compared with the overall variance contributed by the LMM residuals (variance ratio = 0.54 versus 0.40). Thus, despite equivocal differences in pairwise comparisons of cumulative fish count distribution between locations, the sexes and forms predominated at different times within the watershed across the spawning season. This indicates a strong temporal structure and slightly weaker, though still significant, spatial structure in the distribution of spawning anadromous and resident forms.

Spawn Time

Wild anadromous females spawned over a highly protracted temporal period (January–July), and monthly redd abundance peaked in April and May (Figure 4A). Spatially, the median spawn time varied between locations, although not all differences were significant (Figure 4B). The greatest differences were observed between the upper and lower Sol Duc River at 24% ($P < 0.001$) and the North Fork Calawah and lower Sol Duc rivers at 20% ($P < 0.001$), and these differences were significant. In contrast, the greatest difference between the main-stem Calawah and North Fork Calawah rivers was 12% ($P = 0.14$), and the greatest

TABLE 2.—Results of a linear mixed model evaluation of Quileute River basin fish counts for fixed and random effects; (months: Feb–Jul; types: wild anadromous males, wild anadromous females, wild residents, and hatchery residuals; the five study locations are shown in Figure 1).

Effect	df	F_s	P	Ratio	SE	Z	One-tailed P-value
Fixed							
Month	5, 18	5.03	0.0047				
Type	3, 66	13.65	<0.0001				
Month × type	15, 66	5.78	<0.0001				
Random							
Location				0.5368	2.8188	1.27	0.0251
Location × month				0.1488	0.8132	1.22	0.0278
Location × month × type				0.4026	0.9778	2.75	0.0008
Residual				1.0000	0.7252	9.20	<0.0001

difference between the upper and middle sections of the Sol Duc River was 17% ($P = 0.02$); these differences were not significant. While the spatial differences in spawn time were not as distinct as the

FIGURE 4.—Panel **(A)** presents a box-and-whisker plot of monthly spawning activity (redds/km) by wild anadromous female rainbow trout within the Quileute River basin, Washington, 1999–2003. The squares within the boxes indicate the medians, the top and bottom lines of the boxes the 25th and 75th percentiles, and the whiskers the maximum and minimum values. Panel **(B)** shows the median time (50%) of wild anadromous female spawning activity as described by a normalized distribution of cumulative redd counts in each survey reach. The triangles, *x*s, and asterisks = the lower, middle, and upper Sol Duc River, respectively; the diamonds and squares = the main-stem and North Fork Calawah River, respectively.

temporal differences in entry time between the sexes and forms, the results provide support for some spatial structure in the spawn time of anadromous females.

Attempted Matings

In over 118 h of direct observation, we documented 169 attempted matings between WAMs and wild anadromous females, 29 attempted matings between wild anadromous females and WRMs, and 2 attempts between wild anadromous females and HRMs. The first attempted mating was observed on January 6 and the last on July 8. The greatest number of observations was recorded in April and May, and the lowest number was observed in July (Table 3). The sex ratio during those observations reflected the predominance of male steelhead (59% male, 41% female) and rose slightly to 63% male when including mating attempts with WRMs and HRMs. Most attempted matings ($n = 119$) consisted of a single wild anadromous male attempting to mate with a single wild anadromous female, while 62 involved 2WAM, 12 involved 3WAM, 6 involved 4WAM, and 1 involved 5WAM. Most attempted matings between anadromous and wild resident forms involved a single WRM ($n = 24$), and all HRM attempts involved single males ($n = 2$).

The structure of attempted matings varied temporally and spatially, generally reflecting the changing distribution of male types in space and time. While the proportion of attempted matings involving 1WAM was fairly consistent across much of the spawning season, the greatest proportion of attempts involving more than two males was greatest during the peak of the spawning season (April–May; Table 3). Wild resident males were not observed attempting to mate with wild anadromous females until April, but by June they accounted for most of the attempts and were the lone mate source for females returning in July. Spatially, anadromous female × WRM attempts accounted for the greatest proportion of attempts in the upper Sol Duc (18%), middle Sol Duc (10%), and North Fork Calawah rivers (11%) (Table 4).
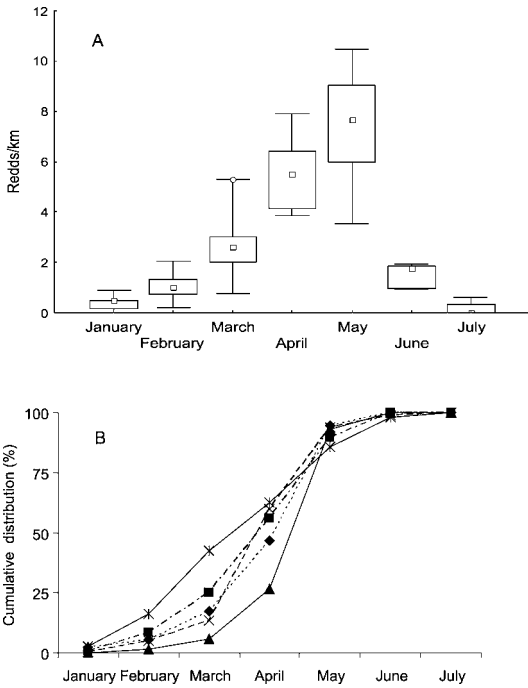
TABLE 3.—Number of attempted matings (*n*) observed across the spawning season in the Quileute River basin, Washington (1999–2003) and proportion (%) of attempts by wild anadromous males (WAMs), wild resident males, and hatchery residual males.

Month	*n*	WAMs					Wild resident	Hatchery residual
		1	2	3	4	5		
Jan	5	83	17	0	0	0	0	0
Feb	15	55	45	0	0	0	0	0
Mar	25	52	39	9	0	0	0	0
Apr	60	55	27	6	6	0	6	0
May	80	53	27	6	2	1	11	0
Jun	14	34	18	0	0	0	41	7
Jul	1	0	0	0	0	0	100	0

These same reaches contained the greatest proportion of wild resident fish during snorkel surveys. No attempted matings between forms were observed in the lower Sol Duc River, and the two attempts involving HRMs were observed in the middle Sol Duc River near the hatchery rearing ponds in May. Importantly, the onset and increase of attempted matings between forms coincided with the dramatic increase in wild residents during the latter portion of the spawning season, which is consistent with the distribution structure observed during snorkel surveys.

Male Mating Tactics

Wild anadromous males used the guarding (53%) and sneaking (47%) tactics almost equally during attempted matings. Wild resident males (90%) and HRMs (100%) relied almost exclusively on the sneaking tactic. These observations were relatively consistent across the spawning season until July, when male steelhead were absent and WRMs abandoned the sneaking tactic to use group mating (Figure 5). In those situations, two groups of two to four resident males displayed minimal aggression as different fish took turns using shudders to stimulate the anadromous female. We often observed anadromous females demonstrating aggressive behaviors toward nondomi- nant males when guards were present, but this did not happen during the group mating activity.

Discussion

Population Composition Patterns

In sympatric populations of anadromous and non-anadromous salmonids, females often predominate among the anadromous individuals and males among the residents (Jonsson and Jonsson 1993). This has been documented in Atlantic salmon (Gibson 1983), brown trout Jonsson (1985), Arctic char (Nordeng 1983), brook trout *S. fontinalis* (Wilder 1952), and sockeye salmon (McCart 1970). The predominance of females in anadromous forms (see Jonsson and Jonsson 1993) may be explained by the strong connection between reproductive fitness and size in females (e.g., egg size, fecundity; Fleming and Gross 1991). In contrast, the success of male salmonids is not as strongly linked to size because different-size males can use different behavioral tactics to achieve fertilizations (Hutchings and Myers 1985, 1988; Gross 1991). Females do predominate in some steelhead populations in the Pacific Northwest (Burgner et al. 1992; also see Kostow 2003), which is what we found in our snorkel surveys. Resident populations may include many females, as they do in inland rivers draining the Columbia River (Zimmerman and Reeves 2000;

TABLE 4.—Proportions (%) of different *O. mykiss* types, observed during attempted matings (wild anadromous females [F], wild anadromous males [M], and wild resident fish [R]) in the Quileute River basin, Washington, 1999–2003.

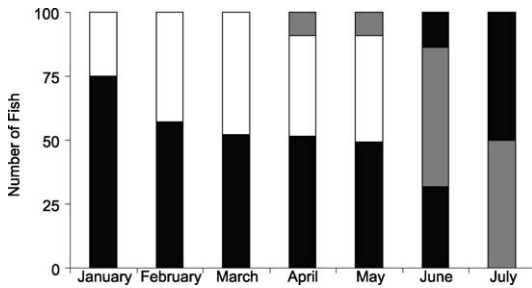| Month	Calawah River						Sol Duc River								
	North Fork			Main stem			Lower			Middle			Upper		
	F	M	R	F	M	R	F	M	R	F	M	R	F	M	R
Feb	67	33	0	50	50	0	0	0	0	67	33	0	50	50	0
Mar	73	27	0	58	42	0	0	0	0	57	32	11	60	30	10
Apr	41	47	12	55	42	3	50	50	0	57	33	10	56	39	6
May	50	41	9	60	40	0	69	31	0	40	40	20	40	40	20
Jun	25	25	50	33	33	33	50	50	0	0	50	50	10	30	60
Cumulative	51	38	11	54	41	5	63	44	0	56	34	10	45	38	18

FIGURE 5.—The relative proportions of sneaking, guarding, and group mating tactics displayed by *O. mykiss* males of different types during attempted matings with anadromous females within the Quileute River basin, Washington, 1999–2003. Symbols are as follows: black = wild anadromous male guarding, white = wild anadromous male sneaking, gray = wild resident male sneaking, stippling = wild resident male group mating, and hatching = hatchery residual male sneaking.

Pearsons et al. 2003), or they may be mostly male (Shapovalov and Taft 1954). Furthermore, the species may also display a sympatric single interbreeding population that consists of a female-dominated steelhead form and a male-dominated resident form, as found in rivers on the Kamchatka Peninsula, Russia (Savvaitova et al. 1997). We could not determine the sex of individuals within the resident population by means of snorkel surveys. However, 39 wild residents were sampled via angling during the study period, and 85% were males (J.R.M., unpublished data). Additionally, we never observed a resident-sized female excavating redds or attempting to mate with male steelhead. While confirming the sex ratio of the resident form in our study would require a more explicit analysis of sex and life history, the patterns suggest the potential for a male-dominated resident form.

Temporal and Spatial Distribution Structure

The structure in the distribution of sympatric anadromous and resident *O. mykiss* within a watershed and across a spawning season should not be considered static. We found that anadromous sexes and life history forms predominated at different times and places, and the patterns coincided with attempted matings and differences in male mating behavior; these results indicate that the mating system has a distinct structure that exists in space and time. For example, the median time of entry was April for male steelhead, and they represented over 50% of the population in February and March, while the median time of entry for females was April–May, the same as the peak spawn time. The presence of a high proportion of male steelhead early in

the spawn season suggests that anadromous males arrived in freshwater prior to females (protandry), which is relatively common in Pacific salmonids (Morbey 2000). A study of winter steelhead found small differences in the median arrival date between sexes (1–3 d; Seamons et al. 2004). However, the population was small (<160 fish) and fish were collected daily at a weir, so a direct comparison is limited.

Anadromous males may arrive earlier to try to establish dominance and maximize mating opportunities (Morbey 2000). In contrast, females of ocean-maturing life histories, such as winter steelhead, tend to arrive just prior to spawning and leave quickly thereafter (see Busby et al. 1996; Rubin et al. 2005). Seamons et al. (2004) found that winter steelhead males almost invariably arrived before the females with whom they mated (average of 15 d earlier). Despite the benefits, this behavior can have a cost. Earlier arrival and arduous competition over a lengthy spawning period can lead to male depletion at the end of the spawning season in Atlantic salmon, which display a mating system similar to that of *O. mykiss* (Moran et al. 1996; Fleming et al. 1997). Steelhead exhibited a highly protracted spawning season (6 months) in our study, and competition for females was intense in April and May. This might help explain the steep decline in the number of male steelhead at the end of the spawning season in June. Whatever the reason, the decline is noteworthy because it coincided with an increased abundance of wild residents.

Spatially, wild residents were present on the spawning grounds throughout the season, but their abundance peaked sharply in May and June, especially in the upper survey reaches. This spatial distribution is generally similar to that observed among sympatric summer-run steelhead and rainbow trout in the Yakima River basin, Washington. The study found extensive overlap between steelhead and rainbow trout, but rainbow trout were more common at higher elevations than steelhead were (see Cramer et al. 2003; Pearsons et al. 2003). The resident form may predominate at higher elevations because oversummering conditions (e.g., cooler water temperatures) are more favorable in those locations (Cramer et al. 2003). We did not have summer temperature data with which to assess this question.

The peak in the abundance of wild residents during May and June may be attributable to their later spawn time relative to that of steelhead; thus, wild residents may have occupied other locations earlier in the year. Female rainbow trout spawned slightly later than female steelhead in the Deschutes River, Oregon, although the two forms did exhibit extensive overlap (Zimmerman and Reeves 2000). However, there is an

important difference between Zimmerman and Reeves' (2000) observations and ours. We did not observe resident females excavating redds in our main-stem river reaches, as they did in the Deschutes River study. Between 20–35 km of main-stem river habitat are available in the Sol Duc and Calawah rivers above our uppermost survey reaches, so it is possible that resident females were excavating redds further upstream earlier in the year. Some resident females may also have spawned in small tributaries that we did not survey. Spawning activity outside of our survey reaches may represent a level of spatial and temporal structure that we were unable to account for in our study design.

Alternatively (a situation that is perhaps more likely considering our behavioral observations) the resident population may be composed primarily of males, which have little choice but to exploit mating opportunities with anadromous females. Their later arrival could be timed to maximize mating opportunities with anadromous females as the abundance of anadromous males declines. Such a situation would imply a high degree of movement during the spawning season. Small resident males are likely to occupy lower positions in the steelhead hierarchy. Anadromous, nondominant male Atlantic salmon have been documented to migrate more within a watershed than dominant males, possibly searching for mating opportunities where dominant males are less abundant (Webb and Hawkins 1986). A combination of these possibilities might help to explain why we found more resident fish later in the spawning season.

Attempted Mating Patterns

The sex ratio of actively spawning fish is often male biased in salmonids because competition for females is intense and multiple males tend to concentrate around a single female (Fleming and Gross 1994; Quinn et al. 1996). This was the case in our study. Nonetheless, most of the attempted anadromous × anadromous matings were associated with a single male steelhead, although attempted matings that involved multiple male steelhead were common. Most female steelhead × resident male pairings included only a single male. These results should be viewed conservatively for several reasons. First, the observations only account for attempted matings and do not represent fertilizations. Second, the number of males attempting to mate with each female is likely to be an underestimate because we only observed a short period (0.5–2 h) of their spawning process, and females often spawn over a 1–6-d period (Quinn et al. 1996; Fleming 1998). Third, we were unable to count fish under 25 cm and therefore may have missed attempts from mature male parr,

which can be an important component of the O. mykiss mating system (Seamons et al. 2004).

Despite the limitations, our observation of increased multiple-male attempted matings during the peak spawn time is largely consistent with previous research on salmonids (Quinn et al. 1996; Fleming et al. 1997). A genetic study of a winter steelhead population found that 1:1 interactions were the most common but that females did mate with multiple males (range = 0–5 males; Seamons et al. 2004). Mating with multiple males and resident forms has been invoked as a mechanism to increase effective population size (Martinez et al. 2000), genetic variability, and reproductive success in anadromous females (Foote et al. 1989; Moran and Garcia-Vazquez 1998; Garant et al. 2001).

Most matings between sympatric anadromous and resident forms appear to occur via resident males and anadromous females (Wood and Foote 1996; Garcia-Vazquez et al. 2001). This is indeed what we observed and is consistent with observations of summer steelhead and rainbow trout (Zimmerman and Reeves 1996; Kostow 2003; Pearsons et al. 2003). We did not observe male steelhead attempting to mate with resident females, and apparently the interactions are less common. Using otolith microchemistry, Zimmerman and Reeves (2000) were unable to find evidence of matings between male steelhead and female rainbow trout in the Deschutes River and found only a few offspring with resident mothers in the Babine River. Similarly, Seamons et al. (2004) found a high number of missing parents during a study of winter steelhead, most of which were male, suggesting that resident males were fathering numerous offspring. The resident males in our study appeared to provide an important mate source for female steelhead at the end of the spawning season when male steelhead were scarce or absent. Proving this would obviously require a parentage study. However, the role and importance of resident males in the mating systems of Atlantic salmon (Moran et al. 1996; Garcia-Vazquez et al. 2001) and brown trout (Jonsson 1985) provide some support for this hypothesis.

Male Mating Tactics

As expected, WAMs used the guarding and sneaking tactics, while smaller WRMs and HRMs almost exclusively used the sneaking tactic to attempt matings with anadromous females. The use of the sneaking tactic by resident males is consistent with previous observations (Kostow 2003; Pearsons et al. 2003). Guards often achieve a higher success rate in fertilization than sneaks because they maintain close proximity to females; however, smaller anadromous and resident males can be consistently successful by

employing the sneaking tactic (Maekawa and Onozato 1986; Hutchings and Myers 1988; Fleming et al. 1997; Foote et al. 1997). The tactic might help explain the behavior used by resident males to fertilize anadromous females of winter-run (Seamons et al. 2004) and summer-run steelhead (Araki et al. 2007) in studies that did not incorporate observations of spawning fish.

The fact that WRMs abandoned the sneaking tactic and adopted group mating when anadromous males were absent later in the spawning season indicates that the different behaviors are part of a conditional strategy whereby males select a tactic depending upon the number and size of competitors (Gross 1991). Small resident males are capable of stimulating larger anadromous females in Atlantic salmon when anadromous males are absent (Martinez et al. 2000), but to our knowledge this behavior is unstudied in *O. mykiss*. It is possible that use of the group mating tactic by resident males occurred because clear hierarchies were difficult to establish and maintain when numerous similarly sized males were competing for larger females.

Implications

Understanding the population and mating system structure of anadromous and resident *O. mykiss* is critical to the species' conservation and management. The temporal and spatial structure we found in the distribution of different sexes and forms during the spawning season has implications for future research. Temporal structure is important because salmonid populations often consist of a mixture of individuals that reproduce at different times within a particular season or location, and the timing of spawning is often heritable (Hendry and Day 2005). Indeed, in recent studies, the population structure of steelhead has been linked to time and space. Hendry et al. (2002) sampled summer steelhead in the Dean River, British Columbia, during different times of entry and placed individuals into one of three temporal groups (early: July 2–30; middle: July 31–September 5; and late: September 6–20); those authors found significant genetic differences between the early and late groups. This is notable because the time span between those groups was roughly the same as the monthly variation in population composition we documented, and the fish in our study spawned over a 6-month period. Similarly, Narum et al. (2006) found significant genetic differences among steelhead in different tributaries of the Klickitat River, Washington, and determined that six to seven distinct populations were present. These results, combined with our findings, suggest that genetic samples taken during different periods of the spawning season and at different locations would reveal quite

different population structures in the Sol Duc and Calawah rivers. Although collecting genetic samples across extensive temporal and spatial scales is expensive and time consuming, our results appear to justify the collection of such data if we are to truly understand the full complexity of sympatric anadromous and resident *O. mykiss*populations.

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