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Emigration patterns of age 0 and age 1 potamodromous rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* from two Missouri River tributaries, Montana, USA

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Abstract. Daily emigrations of non-native age 0 and age 1 potamodromous (fluvial) rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* were investigated in two Missouri River tributaries, USA over the period 1998-2002. The patterns of emigration for both age 0 and age 1 fish of both species were highly variable, sometimes showing bimodal (spring and fall) emigrations and other times less well defined patterns. Peak timing of age 0 emigration was also highly variable among years (up to 5 months) and more variable than the timing of age 1 emigrations (more than two months). Emigrations were preferentially associated with increasing photoperiod before June 22, with water temperatures from 7.5 to 12.5 °C, and often followed sudden increases in stream discharge. More emigrations were associated with the new moon phase as opposed to the full moon phase. In an analysis of models of emigration (2 rivers × 2 species × 2 ages/species × 31 model combinations for five categorical variables – year, temperature, discharge, moon phase, and photoperiod) using the information-theoretic approach, none of the models were especially effective at explaining emigrations; for the 16 models (i.e. the two with the lowest AIC per river, species and age), no corresponding multiple linear regression model explained more than 41 % of the emigration, and most other models explained considerably less. Results of this study suggest that emigrations of both brown and rainbow trout as part of their fluvial life histories are potentially influenced by a variety of environmental factors, and can be expected to show considerable variation yearly based on the complex, poorly defined genetic origins of the fish and the highly variable climatic conditions associated with the Missouri River Basin.

Key words: salmonid, migration, lunar, discharge, temperature, photoperiod

Introduction

Populations of trout (Salmonidae) in freshwater exhibit a wide range of life history variations, including resident and potamodromous (fluvial and adfluvial) forms (Behnke 1992, Rieman & Dunham 2000). The fluvial life history, involving early rearing in small streams and tributaries and subsequent emigration to larger rivers (e.g. Hogen & Scarnecchia 2006, Watry & Scarnecchia 2008), has been less studied and consequently is less understood than most other life history patterns. Successful management of fluvial populations requires an understanding of the complete life history and habitat requirements, which can exist over a broad landscape in rivers of different orders.

One important aspect of trout fluvial life history is age-specific emigration timing from natal streams into the larger rivers where they grow more rapidly and mature. Emigration from streams into large rivers or other more productive waters may result from a combination of adaptive responses to past selective pressures as well as more immediate responses to density-related food and space limitations (Chapman 1966, Mason 1976, Bilby & Bisson 1987). In general, the timing and variation of emigration from smaller to larger flowing waters may reflect the effects of past selective processes that have balanced greater mortality risk against maximizing growth potential in a more favorable habitat (Godin 1981, Riddell & Leggett 1981, Holtby et al. 1989). Understanding environmental factors affecting the timing can provide insight into the adaptive advantages of the emigrations and result in important information for harvest and habitat management of the stocks.

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Variations in the magnitude and timing of salmonid emigrations may be related to a wide range of factors, including the species, spawning and rearing densities, fish size, fish age, and a host of environmental factors such as stream discharge, temperature, photoperiod, and lunar cycle (Godin 1981). Roper & Scarnecchia (1999) investigated the relations of stream discharge, temperature, photoperiod, and lunar cycle on emigration timing of Chinook salmon *Oncorhynchus tshawytscha* and found a significant relationship to stream temperature and lunar phase but not to changes in discharge. Investigations of emigration magnitude and timing usually involve the use of one or more downstream traps (Thedinga et al. 1994), and, where incomplete collection occurs, the use of trap efficiencies in estimating the magnitude of the emigration (Roper & Scarnecchia 2000).

Introduced fluvial rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* inhabit the River Dearborn and Little Prickly Pear Creek, two Missouri River tributaries in Montana. The two streams act as spawning and rearing tributaries (Grisak 1999, Grisak et al. 2012a, b), and also contribute juvenile fish to a highly-regarded (Class 1/"blue-ribbon") trout fishery in the Missouri River downriver of Holter Dam (Munro 2004, Fig. 1). Grisak et al. (2012b) reported that "The trout assemblage is about 83 % percent rainbow trout … and 17 % brown trout … . Brown trout and rainbow trout stocking began in 1928 and 1933, respectively, and continued intermittently through 1973, (when) … Montana instituted a statewide wild fish management policy and discontinued stocking in most rivers and streams" (p. 3). The populations and the successful fishery for them have been sustained by wild reproduction since that time.

Studies were initiated on trout life history in both tributaries in the late 1990s in an effort to better understand how specific rainbow trout life history types might be affected by the potential effects of *Myxobolus cerebralis*, the causative agent of whirling disease (Leathe et al. 2001, 2002). Munro (2004) found that in general, fish in this section of the River Missouri reared for at least one year in the tributaries before moving into the River Missouri. Although relationships between *M. cerebralis* infection and the general fish life history were never ascertained in the study (Leathe et al. 2002), detailed information was collected on fish emigrations of fluvial rainbow and brown trout.

The objectives of this paper were to 1) characterize the magnitude and timing of emigrations of age 0 and age 1 rainbow and brown trout from two Missouri River sub-basins (the River Dearborn and Little Prickly Pear Creek) in Montana and 2) use the detailed information collected on emigrations to relate emigration timing to four environmental factors: stream temperature, changes in stream discharge, lunar cycle, and photoperiod. For the environmental factors, our null hypotheses were similar to those of Roper & Scarnecchia (1999), i.e. percentages of the total emigrations would occur in proportion to the frequencies of occurrence of specific stream temperatures, daily changes in discharge, phases of the lunar cycle, and photoperiod.

Material and Methods

Study site

The study was conducted over the period 1998-2002 in the River Dearborn and Little Prickly Pear Creek, two streams draining into the River Missouri, Montana USA within the 56.2 km portion of the River Missouri between Holter Dam and the town of Cascade (Fig. 1). The underlying geology and attributes of the rivers were described by Munro (2004), who reported that mean annual discharge of the River Missouri mainstem below Holter Dam over the period 1946-2000 was 155.1 m^3/s (range: 89.2-237.7 m^3/s). Little Prickly Pear Creek, the smaller of the two study streams, enters the River Missouri at river kilometer 4.3 below Holter Dam. Mean annual discharge over the period 1963-2000 was 2.5 m^3/sec (range 0.9-5.2

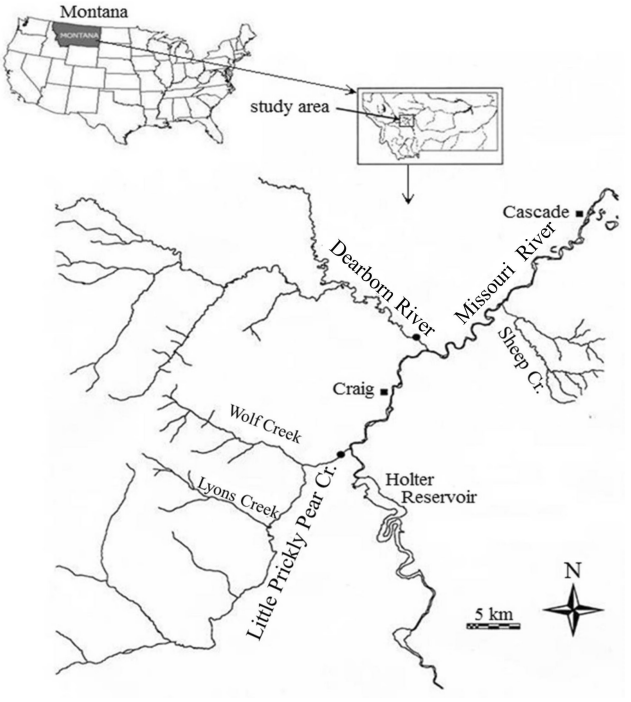


Fig. 1. Map of study area on the River Missouri, Holter Dam to Cascade, Montana, USA, including location of rotating screw traps (●) in upper Missouri River and tributaries.

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m^3/sec). In 1988, an estimated 15000 rainbow trout spawned in the lower 32 km of Little Prickly Pear Creek (Leathe et al. 1988). Rainbow trout also spawn in Lyons Creek and Wolf Creek, two tributaries of Little Prickly Pear Creek (Grisak 1999). The River Dearborn is 113 km long and joins the River Missouri at river kilometer 26.2, near the town of Craig. Mean annual discharge over the period 1946-2000 was 5.9 m^3/sec (range 1.6-10.1 m^3/sec). Based on a helicopter survey in 1988, an estimated 20000 rainbow trout migrated up the River Dearborn to spawn, primarily between river kilometers 16 to 64 (Munro 2004).

Fish trapping, population estimation and emigration timing

Rotary screw traps (1.52 m diameter, Volkhardt et al. 2007) were used to estimate age 0 and age 1 trout emigrant abundance on each of the two streams as described by Leathe et al. (2001). The traps were located 0.8 km above the mouth of Little Prickly Pear Creek and 1.9 km above the mouth of the River Dearborn. For assessing trout emigration patterns, the location of the trap used for monitoring the emigration must sometimes be taken into account, as when fish move below the trap but remain within the river (Roper & Scarnecchia 1999). The downriver positioning of the two traps avoided this potential problem. To improve trap efficiency and operation, rocks and bags of washed gravel were placed upstream from the traps during low-flow conditions to funnel the flow and the fish into a more concentrated area.

Both traps were typically operated from Sunday afternoon through Friday afternoon (5 days per week) on each stream. The duration of sampling varied slightly among years but extended from about April 1 through September, October or November, depending on the year (Tables 1, 2). Traps were operated until fish captures in autumn were at or near zero for several days. In 2000, a year of extremely low flows, no sampling was conducted on the River Dearborn from July 29 through October 4, or on Little Prickly Pear Creek from July 14 through October 4, resulting in this year being excluded from some analyses. Because traps were typically operated five days each week, catches for remaining two days were estimated by using the average of daily catches from two days before and two days after the days with missing data. For example, if six daily counts or frequencies for age 0 fish were 10, 16, ., ., 13, and 17, then 14 or (10 + 16 + 13 + 17)/4 was used to replace two missing daily frequencies and result in six daily frequencies of 10, 16, 14, 14, 13, and 17. For each trout species, weekly length frequency distributions of captured fish were used to classify fish caught each week as either age 0 or age 1. Adequate separation in lengths made classification straightforward. Nearly all of the emigrants were of those ages and they were the only fish considered in this analysis.

Trap efficiencies for age 0 and age 1 rainbow and brown trout were estimated at varying intervals from weekly to longer by releasing previously caught, fin-clipped juvenile trout between 90 and 150 meters above the trap sites. This distance was more than the 2 pool-riffle sequence distance recommended by Volkhardt et al. (2007) and selected to provide for a natural distribution of fish across the channel by the time they re-encountered the trap. Fin clips were changed weekly to better distinguish fish marked in a given week Roper & Scarnecchia (2000). Automatic fish release devices were placed at release sites (Miller et al. 2000). Fish were released 1-2 hours after sunset to mimic natural emigration patterns since prior trap catches had indicated that most fish emigrated during darkness (Leathe et al. 2001). For each estimate, batch-marked juveniles were released on the first 1-3 nights of trap operation to allow at least two full nights of trap operation after the final release of fin-clipped fish. This approach was implemented because preliminary results early in the study indicated that emigration of marked fish was typically rapid and most marked fish were recaptured within a week of when they were marked. During periods when recaptures were few or none, however, several weeks' recapture data were sometimes combined to obtain the best available estimate of trap efficiency over the interval. In other instances, efficiencies applied to adjacent periods were used when no efficiency estimates were made over a period. In general, recaptures of age 1 fish of both species were irregular each year, resulting in fewer estimates of trap efficiencies than for age 0 fish. Estimates of total daily emigration were obtained directly based on daily counts and trap efficiencies as described in Roper & Scarnecchia (2000). The available efficiency estimates were then matched to the actual daily catches, resulting in the following six fish variables: estimated daily emigration of age 0 rainbow trout and brown trout, actual catch and estimated daily emigration of age 1 rainbow trout, and actual catch and estimated daily emigration of brown trout. Efficiency estimates were used in estimating total emigrations. Because catches and recaptures of age 1 fish were typically lower than for age 0 fish, analyses against environmental factors were conducted with both actual daily catches and

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estimated daily emigrations. Confidence intervals were not calculated because although total daily catches were available in the data set, accurate daily numbers of total marked and recaptured fish were not always available, e.g. during periods when no efficiency estimates were made.

Table 1. Mean fish length (mm), standard deviation, minimum and maximum length for age 0 and age 1 each species on corresponding observed peak emigration dates each year at the River Dearborn (DB) and Little Prickly Pear Creek (LPP).

Species/Age	Site	Peak migration date	N	Mean	Std. Dev.	Minimum	Maximum
brown trout age 0	DB	Jun 17,1998	17	54.9	6.00	44.0	67.0
		Jun 08,1999	8	32.5	6.70	25.0	46.0
		Jun 12,2000	7	41.7	5.88	36.0	51.0
		Jun 28,2001	8	59.0	6.07	53.0	72.0
		Aug 09,2002	35	68.8	5.82	55.0	80.0
	LPP	Oct 05,1998	105	112.2	10.88	84.0	150.0
		Jun 11,1999	88	46.1	5.23	34.0	59.0
		Apr 21,2000	532	27.1	1.90	23.0	52.0
		Jun 18,2001	47	44.8	4.66	38.0	57.0
		Jul 04,2002	63	52.2	4.85	40.0	64.0
age 1	DB	Apr 24,1998	3	118.7	21.50	95.0	137.0
		May 04,1999	73	138.8	23.15	84.0	180.0
		Apr 25,2000	13	126.9	23.23	84.0	165.0
		May 07,2001	27	98.6	15.62	64.0	135.0
		Apr 08,2002	62	97.4	13.57	77.0	145.0
	LPP	Jun 17,1998	51	146.5	17.88	106.0	188.0
		May 05,1999	29	134.8	22.56	70.0	166.0
		Jun 01,2000	45	132.8	19.65	95.0	175.0
		Apr 27,2001	25	91.7	22.40	62.0	145.0
		Apr 09,2002	177	95.3	14.82	70.0	145.0
rainbow trout age 0	DB	Sep 22,1998	54	79.4	7.73	63.0	94.0
		Aug 13,1999	154	55.9	7.14	33.0	76.0
		Jun 19,2000	51	27.3	2.75	23.0	37.0
		Jun 25,2001	56	30.1	3.31	25.0	40.0
		Sep 09,2002	205	66.6	7.33	48.0	89.0
	LPP	Jun 30,1998	81	28.7	2.21	24.0	40.0
		Jul 09,1999	238	27.3	3.54	21.0	45.0
		Jul 10,2000	168	41.9	10.36	23.0	61.0
		Jun 18,2001	79	28.2	1.61	25.0	31.0
		Aug 08,2002	117	51.9	7.94	27.0	78.0
age 1	DB	Apr 24,1998	430	86.0	11.79	59.0	158.0
		May 06,1999	397	93.4	17.17	62.0	151.0
		Apr 24,2000	826	83.7	12.04	55.0	152.0
		Jun 13,2001	200	97.3	13.37	73.0	142.0
		Apr 09,2002	299	76.8	11.27	50.0	114.0
	LPP	Jun 04,1998	297	101.4	21.65	65.0	178.0
		Jun 14,1999	68	106.4	17.87	66.0	153.0
		Jun 02,2000	112	91.0	17.32	62.0	155.0
		May 30,2001	29	112.5	13.90	80.0	132.0
		Jul 03,2002	112	101.1	20.42	73.0	179.0

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Table 2. Akaike's information criterion for negative binomial regression models (NB AIC) of brown or rainbow trout estimated counts at the River Dearborn (DB) and Little Prickly Pear Creek (LPP) on the five factors: four years (YEAR), five categories of changes in water discharge (DISC), five categories of changes in water temperature (TEMP), four moon phases (MOON), and three photo periods (PHOP). Based on NB AIC, model probability (MP) provides a measure of the strength of evidence for each model relative to the whole set of 31 candidate models for each count using the five factors. AICs obtained from multiple linear regression (MLR AIC) models are also listed for comparison.

			brown trout								rainbow trout							
			Age 0				Age 1				Age 0				Age 1			
Site	Model	k	NB AIC	ΔAIC	MP	MLR AIC	NB AIC	ΔAIC	MP	MLR AIC	NB AIC	ΔAIC	MP	MLR AIC	NB AIC	ΔAIC	MP	MLR AIC
DB	YEAR	6	3411	11	0.002	5811	2923	115	0.000	6618	8123	382	0.000	9664	10732	421	0.000	11406
DB	DISC	7	3436	36	0.000	5863	2954	146	0.000	6637	8171	430	0.000	9781	10768	457	0.000	11435
DB	TEMP	7	3420	20	0.000	5846	2865	57	0.000	6620	8021	280	0.000	9626	10656	345	0.000	11358
DB	MOON	6	3433	33	0.000	5862	2970	162	0.000	6671	8174	433	0.000	9784	10820	509	0.000	11518
DB	PHOP	5	3411	11	0.002	5829	2828	20	0.000	6597	8045	304	0.000	9635	10625	314	0.000	11339
DB	YEAR-DISC	11	3415	15	0.000	5806	2918	110	0.000	6592	8121	380	0.000	9649	10677	366	0.000	11328
DB	YEAR-TEMP	11	3412	12	0.001	5787	2841	33	0.000	6562	7974	233	0.000	9492	10497	186	0.000	11221
DB	YEAR-MOON	10	3417	17	0.000	5801	2931	123	0.000	6620	8112	371	0.000	9653	10736	425	0.000	11408
DB	YEAR-PHOP	9	3406	6	0.029	5770	2822	14	0.001	6544	7944	203	0.000	9475	10397	86	0.000	11216
DB	DISC-TEMP	12	3424	24	0.000	5844	2868	60	0.000	6599	8022	281	0.000	9620	10636	325	0.000	11321
DB	DISC-MOON	11	3436	36	0.000	5855	2959	151	0.000	6639	8173	432	0.000	9774	10772	461	0.000	11438
DB	DISC-PHOP	10	3414	14	0.001	5826	2831	23	0.000	6584	8012	271	0.000	9634	10604	293	0.000	11304
DB	TEMP-MOON	11	3419	19	0.000	5840	2854	46	0.000	6622	8009	268	0.000	9618	10654	343	0.000	11359
DB	TEMP-PHOP	10	3409	9	0.006	5835	2830	22	0.000	6589	7929	188	0.000	9617	10535	224	0.000	11256
DB	MOON-PHOP	9	3415	15	0.000	5823	2813	5	0.045	6599	8017	276	0.000	9627	10630	319	0.000	11341
DB	YEAR-DISC-TEMP	16	3415	15	0.000	5789	2844	36	0.000	6548	7978	237	0.000	9489	10485	174	0.000	11192
DB	YEAR-DISC-MOON	15	3421	21	0.000	5796	2925	117	0.000	6594	8115	374	0.000	9638	10678	367	0.000	11331
DB	YEAR-DISC-PHOP	14	3407	7	0.018	5770	2823	15	0.000	6535	7930	189	0.000	9474	10382	71	0.000	11183
DB	YEAR-TEMP-MOON	15	3415	15	0.000	5780	2834	26	0.000	6563	7961	220	0.000	9480	10495	184	0.000	11221
DB	YEAR-TEMP-PHOP	14	**3400**	**0***	**0.582**	**5774**	2817	9	0.006	6540	7794	53	0.000	9467	10316	5	0.038	11131
DB	YEAR-MOON-PHOP	13	3411	11	0.002	5762	**2808**	**0***	**0.548**	**6547**	7909	168	0.000	9463	10400	89	0.000	11217
DB	DISC-TEMP-MOON	16	3424	24	0.000	5837	2859	51	0.000	6600	8012	271	0.000	9614	10634	323	0.000	11323
DB	DISC-TEMP-PHOP	15	3410	10	0.004	5833	2836	28	0.000	6576	7888	147	0.000	9610	10526	215	0.000	11239
DB	DISC-MOON-PHOP	14	3418	18	0.000	5818	2820	12	0.001	6586	7999	258	0.000	9627	10610	299	0.000	11306
DB	TEMP-MOON-PHOP	14	3409	9	0.006	5828	2818	10	0.004	6590	7892	151	0.000	9608	10533	222	0.000	11257
DB	YEAR-DISC-TEMP-MOON	20	3419	19	0.000	5781	2837	29	0.000	6549	7967	226	0.000	9479	10482	171	0.000	11193
DB	YEAR-DISC-TEMP-PHOP	19	**3402**	**2***	**0.214**	**5775**	2821	13	0.001	6531	7773	32	0.000	9464	10316	5	0.038	11116
DB	YEAR-DISC-MOON-PHOP	18	3413	13	0.001	5760	2813	5	0.045	6537	7906	165	0.000	9463	10385	74	0.000	11185
DB	YEAR-TEMP-MOON-PHOP	18	3404	4	0.079	5766	**2809**	**1***	**0.332**	**6541**	**7752**	**11**	**0.004**	**9455**	**10311**	**0***	**0.462**	**11131**

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DB	DISC-TEMP-MOON-PHOP	19	3411	11	0.002	5825	2826	18	0.000	6578	7859	118	0.000	9602	10524	213	0.000	11241
DB	YEAR-DISC-TEMP-MOON-PHOP	23	3405	5	0.048	5765	2815	7	0.017	6532	**7741**	**0***	**0.996**	**9453**	**10311**	**0***	**0.462**	**11117**
LPP	YEAR	6	9984	68	0.000	9820	6641	278	0.000	7365	7972	307	0.000	10529	8423	267	0.000	8361
LPP	DISC	7	10098	182	0.000	9919	6677	314	0.000	7368	7999	334	0.000	10549	8422	266	0.000	8348
LPP	TEMP	7	10049	133	0.000	9876	6600	237	0.000	7352	7845	180	0.000	10495	8402	246	0.000	8314
LPP	MOON	6	10097	181	0.000	9920	6710	347	0.000	7423	8011	346	0.000	10556	8467	311	0.000	8412
LPP	PHOP	5	10064	148	0.000	9887	6493	130	0.000	7234	7910	245	0.000	10491	8337	181	0.000	8277
LPP	YEAR-DISC	11	9990	74	0.000	9819	6597	234	0.000	7305	7960	295	0.000	10514	8372	216	0.000	8293
LPP	YEAR-TEMP	11	9927	11	0.003	9777	6470	107	0.000	7250	7804	139	0.000	10454	8324	168	0.000	8253
LPP	YEAR-MOON	10	9981	65	0.000	9816	6633	270	0.000	7361	7969	304	0.000	10522	8426	270	0.000	8362
LPP	YEAR-PHOP	9	9971	55	0.000	9780	6446	83	0.000	7164	7831	166	0.000	10453	8223	67	0.000	8221
LPP	DISC-TEMP	12	10055	139	0.000	9876	6581	218	0.000	7294	7853	188	0.000	10494	8379	223	0.000	8272
LPP	DISC-MOON	11	10099	183	0.000	9918	6678	315	0.000	7366	8001	336	0.000	10544	8424	268	0.000	8349
LPP	DISC-PHOP	10	10070	154	0.000	9889	6485	122	0.000	7205	7895	230	0.000	10487	8321	165	0.000	8240
LPP	TEMP-MOON	11	10048	132	0.000	9875	6601	238	0.000	7347	7839	174	0.000	10489	8405	249	0.000	8312
LPP	TEMP-PHOP	10	10046	130	0.000	9868	6478	115	0.000	7226	7745	80	0.000	10487	8288	132	0.000	8186
LPP	MOON-PHOP	9	10062	146	0.000	9886	6492	129	0.000	7230	7875	210	0.000	10485	8343	187	0.000	8278
LPP	YEAR-DISC-TEMP	16	9936	20	0.000	9777	6443	80	0.000	7193	7810	145	0.000	10451	8297	141	0.000	8207
LPP	YEAR-DISC-MOON	15	9987	71	0.000	9816	6592	229	0.000	7302	7961	296	0.000	10508	8372	216	0.000	8294
LPP	YEAR-DISC-PHOP	14	9974	58	0.000	9782	6402	39	0.000	7132	7822	157	0.000	10447	8199	43	0.000	8180
LPP	YEAR-TEMP-MOON	15	**9920**	**4**	**0.116**	**9773**	6461	98	0.000	7242	7794	129	0.000	10446	8325	169	0.000	8251
LPP	YEAR-TEMP-PHOP	14	9925	9	0.009	9769	6379	16	0.000	7149	7706	41	0.000	10445	8167	11	0.003	8122
LPP	YEAR-MOON-PHOP	13	9966	50	0.000	9777	6431	68	0.000	7159	7809	144	0.000	10446	8227	71	0.000	8222
LPP	DISC-TEMP-MOON	16	10054	138	0.000	9875	6585	222	0.000	7291	7848	183	0.000	10488	8380	224	0.000	8270
LPP	DISC-TEMP-PHOP	15	10054	138	0.000	9870	6476	113	0.000	7194	7741	76	0.000	10485	8285	129	0.000	8163
LPP	DISC-MOON-PHOP	14	10069	153	0.000	9887	6486	123	0.000	7203	7872	207	0.000	10482	8327	171	0.000	8241
LPP	TEMP-MOON-PHOP	14	10045	129	0.000	9868	6481	118	0.000	7221	7716	51	0.000	10481	8292	136	0.000	8185
LPP	YEAR-DISC-TEMP-MOON	20	9929	13	0.001	9774	6439	76	0.000	7188	7801	136	0.000	10444	8297	141	0.000	8205
LPP	YEAR-DISC-TEMP-PHOP	19	9932	16	0.000	9771	**6364**	**1***	**0.377**	**7117**	7698	33	0.000	10442	**8156**	**0***	**0.728**	**8096**
LPP	YEAR-DISC-MOON-PHOP	18	9969	53	0.000	9778	6396	33	0.000	7128	7805	140	0.000	10441	8201	45	0.000	8181
LPP	YEAR-TEMP-MOON-PHOP	18	**9916**	**0***	**0.854**	**9766**	6377	14	0.001	7143	**7666**	**1***	**0.378**	**10438**	8170	14	0.001	8121
LPP	DISC-TEMP-MOON-PHOP	19	10053	137	0.000	9870	6480	117	0.000	7191	7718	53	0.000	10480	8289	133	0.000	8161
LPP	YEAR-DISC-TEMP-MOON-PHOP	23	9924	8	0.016	9768	**6363**	**0***	**0.622**	**7112**	**7665**	**0***	**0.622**	**10435**	**8158**	**2***	**0.268**	**8094**

k = Number of parameters estimated for NB regression model. NB AIC = AIC obtained from NB regression model. ΔAIC = (NB AIC) – (minimum of 31 NB AIC) for each count estimate. For the minimum, ΔAIC = 0. *ΔAIC < 2 suggests evidence for the NB regression model. Model probability (MP) or Akaike weight = the chance of being the best one among the above 31 models. MLR AIC = AIC obtained from MLR model.

Migration timing

Timings of annual age 0 and age 1 emigrations from the two streams were characterized by the date of peak migration and the dates of the 25th percentile, median, and 75th percentile emigration for age 0 and age 1 fish each year. Only peak emigration timings were obtained in the two streams in 2000 because of missing observation periods.

Environmental factors

Four environmental factors were investigated in relation to emigration timing: change in discharge, water temperature, lunar cycle and photoperiod. Daily mean discharge and daily mean water temperature were obtained from United States Geological Survey gaging stations on the River Dearborn (USGS 06073500) and Little Prickly Pear Creek (06071300). Moon phases for the periods were downloaded from the NASA web site (http://eclipse.gsfc.nasa.gov/phase/phasecat.html). Photoperiod was characterized using the equinox and solstice.

Categories were established for each of the four variables: discharge (change), temperature, lunar cycle, and photoperiod. Daily mean discharges were used to construct a variable indicating percent discharge change from the previous day. Five categories of changes in discharge were constructed: (1) rapidly decreasing: discharge was > 10 % less than that of previous day, (2) slowly decreasing: discharge was > 1 % to 10 % less than that of the previous day, (3) no perceptible change: discharge was within 1 % of that of the previous day, (4) slowly increasing: discharge was > 1 % to 10 % more than that of the previous day, and (5) rapidly increasing: discharge was > 10 % more than that of the previous day. Five categorical ranges for daily mean water temperature (°C) were set: (1) < 7.5, (2) 7.5 to < 10, (3) 10 to < 12.5, (4) 12.5 to < 15, and (5) ≥ 15. Four codes for moon phase were defined: 1) new moon phase, 2) waxing phase (first quarter), 3) full moon phase, and 4) waning phase (last quarter). For example, if the 10th and 17th day of a month were new moon and first quarter, respectively, then new moon phase was assigned to the seven days of 7, 8, 9, 10, 11, 12, and 13, and waxing phase to the following seven days 14, 15, 16, 17, 18, 19, and 20. Observed photoperiod each year was divided into three sub periods as (1) before June 22: increasing day length, (2) from June 22 to September 22: decreasing day length, and (3) after September 22: increasing night length.

Data were analyzed to assess potential relations between emigration and each of the four environmental factors. For each of the six migration counts (i.e. brown trout age 0 estimate, brown trout age 1 count, brown trout age 1 estimate, rainbow trout age 0 estimate, rainbow trout age 1 count, and rainbow trout age 1 estimate), we compared observed frequencies of fish emigrating in each category of environmental factor with their expected frequencies assuming that fish would emigrate in proportion to the frequency of occurrence of each category of each factor each year (Roper & Scarnecchia 1999). For example, if stream temperatures during a given sampling season in one stream occurred in the five temperature categories in the proportions 10 %, 20 %, 40 %, 20 %, and 10 %, the null hypothesis would be that frequencies of fish emigration for each migration group would have the same proportions. Similarly, for lunar cycle, the null hypothesis was that the emigrations would occur in proportion to the frequencies of each lunar phase, which in this case are nearly equal. For the analysis, a total of 192 Chi-square tests were run (2 streams × 4 years × 4 environmental factors × 6 migration groups). In all tests, a $p \leq 0.05$ was required for significance.

In addition, the relations between the estimated numbers of migrating age 0 and age 1 brown and rainbow trout and the five categorical variables (year, temperature, discharge, lunar phase, photoperiod) were evaluated with multiple linear regression and negative binomial regression methods. In all, 31 combinations of models were evaluated (from single variable models to a five-variable model) for

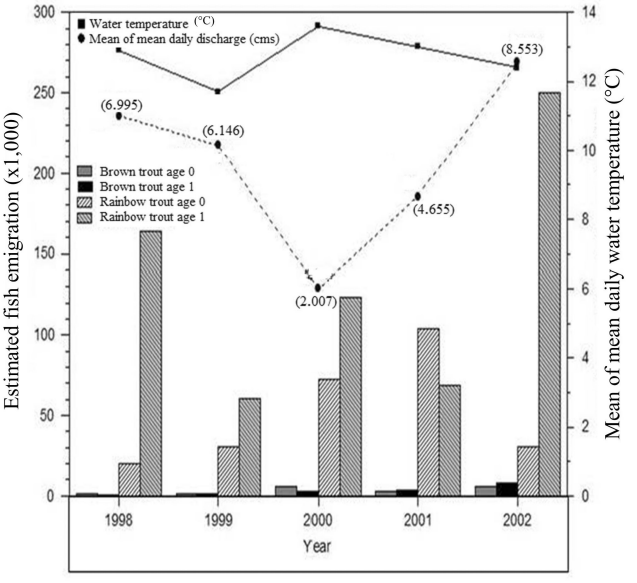


Fig. 2. Estimated number of fish emigrating from the River Dearborn, mean of mean daily water temperature, and mean of mean daily discharge from 1998 to 2002. The estimate for year 2000 is a partial estimate over the periods Apr 4-Jul 28 and Oct 5-Oct 27.

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each year class in each river in each of the multiple linear and negative binomial regressions (2 rivers × 2 species × 2 ages/species × 31 model combinations for the five categorical variables or 248 models in all). The negative binomial regression was selected based on preliminary assessment that it was generally well suited to the distribution of the migration data. The strengths of the 248 models were assessed using information-theoretic criteria (AIC, Burnham & Anderson 2002, SAS Institute 2011).

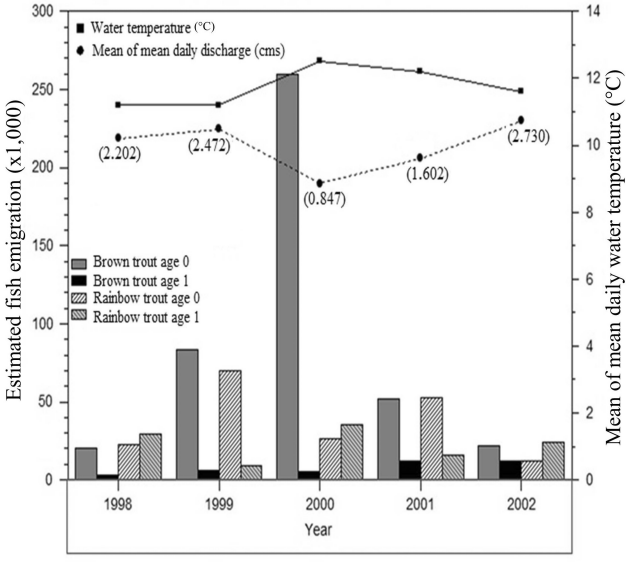


Fig. 3. Estimated number of fish emigrating from Little Prickly Pear Creek, mean of mean daily water temperature, and mean of mean daily discharge from 1998 to 2002. The estimate for year 2000 is a partial estimate over the periods Apr 4-Jul 13 and Oct 5-Oct 27.

Results

Total emigrations

The River Dearborn – for rainbow trout, estimated age 0 emigrations ranged from 19904 in 1998 to 103816 in 2001. Estimates for 1999 and 2002 were about 30000 fish. Estimated age 1 rainbow trout emigrations ranged from 60500 in 1999 to 250273 in 2002. In both cases, based on emigrations, the 1998 year class was the smallest and the 2001 year class the largest (Fig. 2).

Brown trout emigrations from the River Dearborn were much smaller than for rainbow trout. Maximum estimated age 0 brown trout emigration was 5.4 % of maximum estimated age 0 rainbow trout emigration; maximum estimated age 1 brown trout emigration was 3 % of maximum estimated age 1 rainbow trout emigration. For brown trout, estimated age 0 emigrations ranged from 1064 in 1999 to 5617 in 2002. Age 1 emigration estimates ranged from 520 in 1998 to 7652 in 2002 (Fig. 2). Based on emigration, the 2001 and 2002 cohorts appeared to be the strongest of the four for which estimates were available. Although 2000 was the lowest of the five flow years investigated (and low flows prevented trap operations for some weeks), no strong patterns were apparent between size of the emigration year classes and flows (Fig. 2).

Little Prickly Pear Creek – for rainbow trout, the estimated number of age 0 emigrating ranged from 11959 fish in 2002 to 69930 in 1999, the estimated number of age 1 fish emigrating ranged from 9350 in 1999 to 29159 in 1998. The strongest cohorts appeared to be 1998 and 1999. Unlike the River Dearborn, where brown trout emigrations were a small fraction of rainbow trout emigrations, rainbow and brown trout populations had comparable emigrations in Little Prickly Pear Creek. Maximum estimated age 0 brown trout emigration was 119 % of maximum estimated age 0 rainbow trout emigration; maximum estimated age 1 brown trout emigration was 42 % of maximum estimated age 1 rainbow trout emigration. For brown trout, estimated age 0 emigrations ranged from 20246 in 1998 to 83428 in 1999. Age 1 estimates ranged from 3180 in 1998 to 12166 in 2002. The 1999 and 2001 year classes appeared to be the strongest among the four for which estimates were available (Fig. 3). A strong emigration of age 1 brown trout was associated with the low discharge and high water temperature in 2000 (Fig. 3).

Total trap efficiencies varied from 1.6 % for age 0 brown trout in 2000 to 35 % for age 1 rainbow trout in 1998. In the River Dearborn, efficiencies ranged from 1.6 % to 13.6 % for age 0 brown trout, from 6 % to 33 % for age 1 brown trout, from 4.3 % to 7.4 % for age 0 rainbow trout, and from 3.8 % to 10.3 % for age 1 rainbow trout. In Little Prickly Pear Creek,

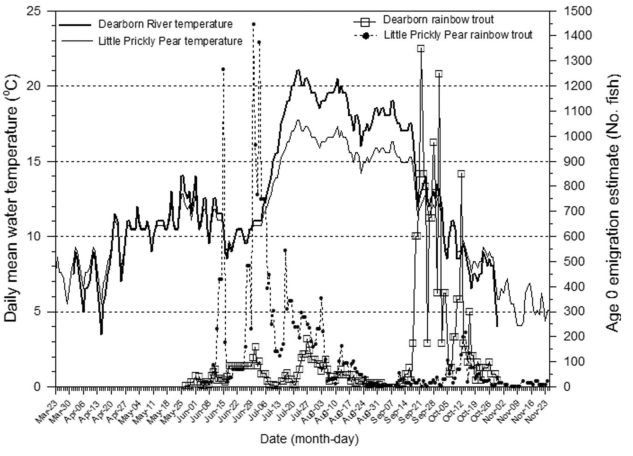


Fig. 4. Daily mean water temperature and estimated rainbow trout age 0 emigrations from the River Dearborn and Little Prickly Pear Creek, 1998.

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efficiencies ranged from 2.3 % to 23.1 % for age 0 brown trout, from 6.4 % to 17.7 % for age 1 brown trout, from 3.4 % to 12.5 % for age 0 rainbow trout, and from 5.9 % to 35 % for age 1 rainbow trout.

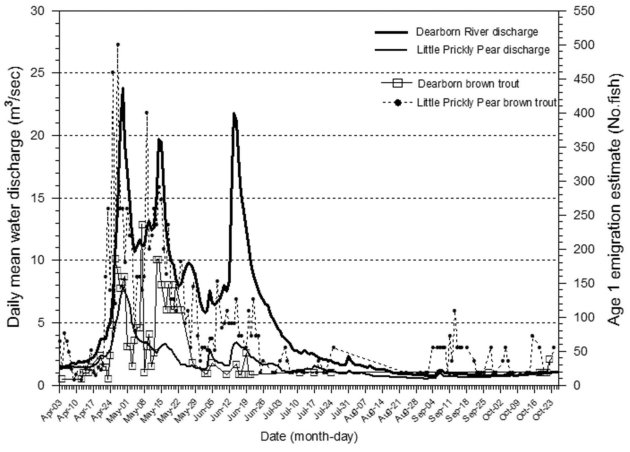


Fig. 5. Daily mean discharge and estimated brown trout age 1 emigrations from the River Dearborn and Little Prickly Pear Creek, 2001.

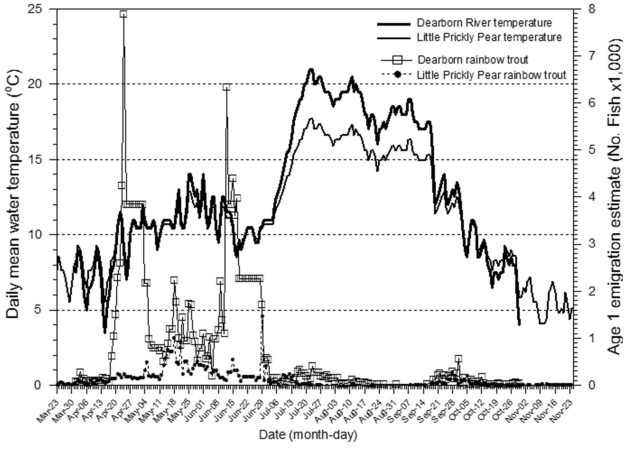


Fig. 6. Daily mean water temperature and estimated rainbow trout age 1 emigrations from the River Dearborn and Little Prickly Pear Creek, 1998.

Emigration timing

Great variation was shown in patterns of emigration for both age 0 and age 1 fish of both species. The two streams also differed in their emigration patterns. For age 0 rainbow trout in 1998, for example, most Little Prickly Pear Creek emigrants left in June and July, with a small pulse in late October, whereas most Dearborn River emigrants left in September (Fig. 4). Overall, age 0 rainbow trout emigrations from Little Prickly Pear Creek occurred earlier than from the River Dearborn.

Peak timing of age 0 emigration was highly variable among years (up to 5 months) and more variable than the timing of age 1 emigrations (slightly more than two months). For example, peak timing of age 0 brown trout emigration in Little Prickly Pear Creek ranged between April 21 (2000) and October 5 (1998). Peak timings of age 1 brown trout emigrations from Little Prickly Pear Creek always occurred in spring and ranged between April 9 (2002) and June 17 (1998). Median emigration dates (50th percentiles) for age 0 fish were also more variable than for age 1 fish.

Consistent with the great variation in peak migration timing was the great variation in mean size of emigrating fish. Earlier peak migration timings were typically associated with a smaller size of migrant fish (Table 1). In addition, a large emigration of small age 0 brown trout (compared to the other four years) occurred from Little Prickly Pear Creek in 2000 (Fig. 3, Table 1), which had the lowest peak flow of the five years.

A distinct difference was observed between the two rivers in most probable age at emigration. Based on ratios of emigrant numbers (age 0/age 1) for the two brood years for which both age 0 and age 1 emigration data were available (1998 and 2001), fish of both species from little Prickly Pear were more likely to emigrate in both years (1998 and 2001, respectively) as age 0 (brown trout: 3.19 age 0/age 1 and 4.24 age 0/age 1, rainbow trout: 2.42 age 0/age 1 and 2.16 age 0/age 1), whereas fish from the River Dearborn were comparatively more likely to emigrate as age 1 fish (brown trout: 1.35 age 0/age 1 and 0.39 age 0/age 1, rainbow trout: 0.32 age 0/age 1 and 0.41 age 0/age 1).

Environmental factors and emigrations

Higher brown trout emigrations for both age 0 and age 1 fish tended to be associated with generally increasing discharge from base flows in spring for both rivers. Increased emigrations commonly occurred following a sudden increase in discharge (e.g. Fig. 5) and a decrease in water temperature (Fig. 6).

Temperature – the temperature category associated with observed migrations differed greatly from what would be expected under the null hypothesis that temperature had no association with migration timing. Of the 48 comparisons conducted between temperature and migration, all but two were highly significant ($p < 0.001$). In Little Prickly Pear Creek, age 0 brown trout, age 1 brown trout (observed and estimated), and age 1 rainbow trout migrated preferentially in the two temperature categories from 7.5 to 12.5 °C. Age 0 rainbow trout, however, migrated preferentially in the two categories 12.5 °C and above. Patterns were similar in the River Dearborn, with age 0 rainbow trout preferentially migrating at the higher water temperatures.

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Discharge – the change-in-discharge category associated with migrations differed greatly from what would be expected under the null hypothesis that changes in discharge had no association with migration timing. Of the 48 comparisons conducted between change-in-discharge and migration, all but four were significant ($p < 0.05$). The four non-significant relationships were in Little Prickly Pear Creek. No distinct preferential patterns for increasing or decreasing discharge were detected, however; fish moved during both increasing and decreasing discharges. In Little Prickly Pear Creek, daily movements were associated with rapidly decreasing discharges, whereas in the River Dearborn, movements were associated with rapidly increasing discharges.

Lunar phase – the lunar phase category associated with migrations differed from what would be expected under the null hypothesis that moon phase had no association with migration timing. Of the 48 comparisons conducted between moon phase and migration, all but 13 were significant ($p < 0.05$). This variable was the most appropriate for comparing with migration timing because phases were uniformly distributed throughout the migration season. In particular, only three of 48 relationships during the full moon differed positively from expected, whereas 27 of 48 during the new moon differed positively from expected, indicating that migrations were much more likely during the darker, new moon phase than the more lighted, full moon phase.

Photoperiod – the photoperiod category associated with migrations differed greatly from what would be expected under the null hypothesis that changes in photoperiod had no association with migration timing. Of the 48 comparisons conducted between photoperiod and migration, all but one were significant ($p < 0.05$). In both rivers, movements were most strongly associated with the increasing period before June 22 and least associated with the decreasing photoperiod after September 23.

Negative binomial models of migration

For the River Dearborn, the negative binomial regression resulted in models that fit the data better than the multiple linear regression approach in all cases (Table 2). The best overall fitting model (lowest AIC: 2808) was for yearling brown trout in relation to year, lunar phase, and photoperiod. Age 0 brown trout

Table 3. Two best selected models among 31 models for each trout species/age count data at the River Dearborn (DB) and Little Prickly Pear Creek (LPP). Selection was based on AIC obtained from fitting negative binomial (NB) regression models. For each selected, summary of number of parameters, AIC and R-square (r^2) from fitting multiple linear regression (MLR) model were also listed for comparison.

			NB model				MLR model		
			Model						
Species/age	Location	MODEL	P_1	AIC	ΔAIC	prob.**	P_2	AIC	r^2
brown trout age 0	DB	YEAR-TEMP-PHOP	14	3400	0*	0.582	10	5774	0.131
		YEAR-DISC-TEMP-PHOP	19	3402	2*	0.214	14	5775	0.139
	LPP	YEAR-TEMP-MOON-PHOP	18	9916	0*	0.854	13	9766	0.191
		YEAR-TEMP-MOON	15	9920	4	0.116	11	9773	0.180
brown trout age 1	DB	YEAR-MOON-PHOP	13	2808	0*	0.548	9	6547	0.156
		YEAR-TEMP-MOON-PHOP	18	2809	1*	0.332	13	6541	0.170
	LPP	YEAR-DISC-TEMP-MOON-PHOP	23	6363	0*	0.622	17	7112	0.337
		YEAR-DISC-TEMP-PHOP	19	6364	1*	0.377	14	7117	0.327
rainbow trout age 0	DB	YEAR-DISC-TEMP-MOON-PHOP	23	7741	0*	0.996	17	9453	0.367
		YEAR-TEMP-MOON-PHOP	18	7752	11	0.004	13	9455	0.359
	LPP	YEAR-DISC-TEMP-MOON-PHOP	23	7665	0*	0.622	17	10435	0.170
		YEAR-TEMP-MOON-PHOP	18	7666	1*	0.378	13	10438	0.160
rainbow trout age 1	DB	YEAR-TEMP-MOON-PHOP	18	10311	0*	0.462	13	11131	0.396
		YEAR-DISC-TEMP-MOON-PHOP	23	10311	0*	0.462	17	11117	0.412
	LPP	YEAR-DISC-TEMP-PHOP	19	8156	0*	0.728	14	8096	0.331
		YEAR-DISC-TEMP-MOON-PHOP	23	8158	2*	0.268	17	8094	0.337

P_1 and P_2 are number of parameters estimated for NB and MLR model, respectively. ΔAIC = (NB AIC) – (minimum of 31 NB AIC) for each count estimate. For the minimum, ΔAIC = 0. *ΔAIC < 2 suggests evidence for the NB regression model. **Model probability (or Akaike weight) for the chance of being the best one among the 31 models.

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estimated emigrations were best described (lowest AIC: 3400) by a model involving year, temperature, and photoperiod. Age 0 rainbow trout estimated emigrations were best described (lowest AIC: 7752) by a model involving all five variables (year, discharge, temperature, lunar phase, and photoperiod). Age 1 rainbow trout estimated emigrations were best described (lowest AIC: 10311) by either of two model involving year, temperature, moon phase, and photoperiod and the model involving all five variables. As in the preceding Chi-square analysis approach, it was apparent that none of the models were especially effective at explaining emigrations; for the eight models (i.e. the two selected with the lowest AIC per species and age), no corresponding multiple linear regression model explained more than 41 % of the emigration (Table 3), and most other models explained considerably less (Table 2).

For Little Prickly Pear Creek, the negative binomial regression results in models that did not fit the data better than the multiple linear regression approach in all cases (Table 2). The best fitting negative binomial regression model (lowest AIC: 6363) was for yearling brown trout in relation to all five variables (year, discharge, temperature, lunar phase, and photoperiod). Age 0 brown trout estimated emigrations were best described (lowest AIC: 9916) by a model involving year, temperature, moon phase, and photoperiod. Age 0 rainbow trout estimated emigrations were best described (AIC: 7665) by a model involving all five variable. Age 1 rainbow trout estimated emigrations were best described (lowest AIC: 8156) by a model involving year, temperature, discharge, and photoperiod. As in the River Dearborn, it was apparent that none of the models were especially effective at explaining emigrations; for the eight models (i.e. the two with the lowest AIC per species and age), no corresponding multiple linear regression model explained more than 34 % of the emigration (Table 3), and most other models explained considerably less (Table 2).

Discussion

Although great variation in emigration patterns were observed between years, ages, and species, two or more pulses of fish were commonly observed, one or more in spring or early summer, and one or more in the fall (e.g. Fig. 4). A bi-seasonal response (spring and fall) has been commonly observed in other studies in non-smolting salmonids (Bjornn 1971, Bilby & Bisson 1987), and was present in some years in this study. Downs et al. (2006) found that adfluvial bull trout *Salvelinus confluentus* in Trestle Creek, Idaho, showed both spring and fall pulses into Lake Pend Oreille. Kruzic (1998) found that age 0 coho salmon *Oncorhynchus kisutch* showed similar downstream movements and suggested that it was associated with movement to more favorable habitats for rearing. Mason (1975) observed only a spring emigration for coho salmon and found that emigrants were smaller than those remaining in the stream he studied, supporting the idea that emigrants had been at a competitive disadvantage against those remaining. Bjornn (1971) hypothesized that age 0 fish emigrating in fall were finding the stream environment unsuitable as winter approached. Depending on habitat condition, fish densities, and other factors, the age 0 or age 1 fish may be compelled to leave at various times during the year as habitat conditions deteriorate. For example, the large emigration of small age 0 brown trout in 2000 from Little Prickly Pear Creek (Fig. 3) occurred earlier than the other four years, associated with not only the lowest of the five peak flows but the lowest peak flow over the period 1962-2011. In our study, maximum emigrations of age 0 fish could occur over a five month period, i.e. either in spring or fall, suggesting that age 0 emigrations were motivated by necessity. Stream discharge, temperature and other aspects of habitat vary from year to year and would result in fish leaving the tributaries at different times as space and food become competitively limiting. The result would be emigrations that vary greatly and may not be strongly correlated with the same factor in each year or at different fish densities. In Dearborn and Little Prickly Pear Creeks, emigrations tended to be more variable in time and conditions than in anadromous stocks. For example, Jonsson & Ruud-Hansen (1985) reported that more than 90 % of the smolts descended the River Imsa in Norway during one month in spring. Whalen et al. (1999) reported a similar narrow window of emigration for Atlantic salmon smolts in a Vermont River. Because of the physiological changes and known evolutionary advantages associated with smoltification and anadromy, smolt emigrations in anadromous stocks may be more finely adapted a consistent, focused seasonal response to specific cues than would be expected in the non-obligatory movements of many non-anadromous fish.

For age 1 fish, in contrast, the maximum emigration for both species occurred before low summer flows. Evidently there was less advantage of age 1 fish remaining in the streams through the low flow period or into a second winter than in emigrating in spring. As fish get larger, demands for adequate space and food will increase (Chapman 1966), as may emigrations

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to any larger, more productive waters such as the River Missouri mainstem. Very few adults have been observed in our two study streams after spawning (G. Grisak, pers. comm.). Godin (1981) reviewed the factors influencing the wide variation in emigration timing observed among salmonids and suggested that it was a result of genetic adaptation to predictable annual variations in a variety of environmental factors. Results of this study showed a clear relationship between greater tendency to emigrate during a new moon as opposed to a full moon, consistent with some studies (Pritchard 1944, Mason 1975, Youngson et al. 1983, Roper & Scarnechia 1999), but not with others (Hartman et al. 1982, Jonsson & Ruud-Hansen 1985, Bilby & Bisson 1987). Mason (1975) found that spring emigrations of coho salmon were highest during periods of low moonlight. Youngson et al. (1983) found that emigrations of Atlantic salmon smolts were reduced during the full moon phase. In contrast, other studies found no correlation with moon phase (McMahon & Holtby 1992). However, numerous other studies have found that night-time emigrations are typically larger than emigrations during the day for a variety of salmonid species (Godin 1981), suggesting that light level is a factor influencing emigration timing. There may also be a number of different factors affecting the observed emigration patterns in addition to lunar phase. Mason (1975) suggested, for example, that in streams with greater freshets, responses to flow or low water clarity may mask response to moon phase, whereas in more stable streams, the effects of moon phase may be detected. Responses may differ depending on site specific climatic patterns or differential selective pressures such as predation on emigrating fish. Because of the ease of obtaining lunar phase data, and the plausible hypothesis that fish may suffer lower mortality when emigrating during darker periods (Godin 1981), the possible effect of moon phase is worth examining during all emigration studies.

In contrast, it was difficult to interpret the observed significant associations of temperature and photoperiod with emigration. Clearly the observed emigration frequencies differed from the expected frequencies of occurrence of specific temperature and photoperiod categories (Figs. 4-6). However, because the temperatures and photoperiods were not evenly distributed as the season progressed (in contrast to the lunar cycle), the causal relation between temperature, photoperiod and emigration could not be evaluated as clearly as lunar cycle. What was clear was that overall, fish tended to migrate preferentially in the two temperature categories (from 7.5 to 12.5 °C) and during the increasing photoperiod (before June 22). Similar results are commonly observed worldwide in salmonids associated with the high production in the receiving waters in spring. Jonsson & Ruud-Hansen (1985) reported that timing of seaward migrating Atlantic salmon *Salmo salar* smolts over an 8-year period was most closely related to water temperatures in spring. However, they found a specific correlation between variations in water temperature between April 9 and 16 and the date of 50 % cumulative smolt descent. The river they studied had no definable spring freshets as would occur from snowmelt, but were rain-influenced, so that water temperatures did not drop as flows increased as commonly occurred in spring in our streams. Österdahl (1969) found that Atlantic salmon smolts tended to emigrate when water temperatures were about 10 °C, but found no specific indication that peak emigration at that specific temperature was more than coincidental. These results suggest that the exact relations between water temperature and emigration timing may differ among streams with different hydrographs and snowmelt inputs in spring, so that it would not be expected that temperature would correlate with emigrations in the same way in different streams. In the River Dearborn and Little Prickly Pear Creek, an exact linkage between water temperature and emigration timing was not identifiable.

Results of this study suggest that emigrations of the non-native, potamodromous, fluvial brown and rainbow trout are influenced by a variety of environmental factors, and show considerable inter-annual variation. Although the causes of this great variability remain unknown, both genetic and environmental factors probably contribute. Grisak et al. (2012b) reported that the original rainbow trout stocking was an undesignated strain, and that since stocking ceased in 1973, the rainbow trout population in the River Missouri mainstem below Holter Dam (the river section into which the River Dearborn and Little Prickly Pear Creek drain) has been influenced by at least 12 strains of rainbow trout stocked into upstream reservoirs. They found that radio-tagged rainbow trout in this system showed low inter-annual spawning site fidelity, and suggested that "the consequences of such a stocking history may be a population that lacks distinct behavior patterns and the genetic predisposition to spawning site fidelity" (p. 21, Grisak et al. 2012b). Further research is needed to determine if the observed highly variable emigration patterns of the juveniles is also evidence of a lack of finely tuned behavior patterns. In future studies, it

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would be important in understanding the emigration behavior observed in this study and the migratory and site fidelity results of Grisak et al. (2012b) by obtaining (1) a better understand of the imprinting process of age 0 and age 1 fish of both species and (2) contributions of age 0 and age 1 fish to the fishery and spawning stocks. Munro (2004) reported that, based on scale patterns, age 0 fish from tributaries were not strong contributors to adult fish harvested in the River Missouri section below Holter Dam. This result needs to be confirmed for a period of years. In addition, the relation between age at emigration and spawning site fidelity should be clarified. If age 0 rainbow trout emigration early in the year (as opposed to later in the year or as age 1 fish) results in less specific imprinting to natal streams but still results in some survival, it may in part explain the lack of selection for site fidelity observed in Grisak et al. (2012b).

The observed variability and flexibility in emigration timing response may also reflect a genetically mixed population only weakly adapted to a variable environment. The fishery is targeting a complex mixture of hatchery rainbow trout strains existing in the highly variable intra-annual and inter-annual conditions of the Missouri River basin (Thornthwaite 1941). The observed variability in their life histories may also prove in the long run to be increasingly beneficial, not only in relation to reducing overall susceptibility to *M. cerebralis* infection, as suggested by Grisak et al. (2012b), but also in response to changing the River Missouri mainstem and tributary habitats and inter-annual variations in temperature, precipitation and other aspects of weather and climate in this century.

This study was oriented and designed to assess potential impacts of *M. cerebralis* in relation to the life histories of the two salmonid species (Leathe et al. 2002). Follow-up studies to this one on these and other populations would benefit from more detailed assessments of the individual life histories and the specific factors leading to the observed emigrations, including the relations of fish emigrant abundance and timing to rearing stream habitat carrying capacity, fish physiological state, imprinting, age-specific emigrant contribution to fisheries, and possible ecological and physiological threshold levels inducing emigration (Taylor 1991, Thorpe et al. 1998). In addition, more effort should be expended to assess factors affecting inter-annual variations in year class strengths. For example, although the data from this study suggested a link between increased age 0 brown trout emigration from Little Prickly Pear Creek and low river discharge (and high water temperatures) in 2000, too few years of data were available for any statistically valid conclusions to be drawn. Such studies should preferably be conducted for at least a decade to sort out key variables and combinations affecting migrations. The long-term trapping and enumeration of emigrants, although very labor intensive, obviously should also be looked upon as only one of several study components needed to understand complex life history strategies of migratory salmonids.

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