

Predator-prey migration phenologies remain synchronised in a warming catchment

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SUMMARY

1. Animal migrations often evolve to exploit seasonal variation in foraging opportunities. Many migrants move among discrete habitats using environmental cues to time their arrivals with seasonal peaks in food abundance. This type of migratory behaviour has been hypothesized to be particularly vulnerable to climate change, which can generate asynchrony between the seasonal timing (phenology) of animal movements and periods of resource abundance in destination habitats.
2. While many studies have documented climate-induced mismatches between migrants and the lower trophic levels they target, virtually none have explored the consequences of altered migration phenology on the higher trophic levels that migrants often subsidise. We explored the roles of climatic variation and prey migrations in driving the seasonal migrations of predators.
3. We show that in a warming catchment where prey migrations have changed substantially over the last 4 decades, migrations of Dolly Varden (*Salvelinus malma*) (predator) remain synchronised with annually variable Pacific salmon (*Oncorhynchus* spp.) (prey) migrations and appear to be cued directly by salmon migration rather than environmental conditions.
4. In contrast to many previous studies, our results suggest that some wide-ranging predators may be resilient to altered prey phenology.

Keywords: coastal watersheds, Dolly Varden, salmon, subsidies, trophic resources

Introduction

One of the most frequently studied responses to climate change is phenology, the timing of life-cycle events in plants and animals. Phenologies may evolve to exploit temporal variation in foraging opportunities; for example, the timing of animal migrations may be linked to periods of resource abundance in destination habitats (Dingle & Drake, 2007). If changes in climate generate asynchronous responses in the phenology of consumers and their trophic resources, the resulting mismatch can potentially result in consumer population declines (e.g. Post & Forchhammer, 2008) and structural changes to the food web (e.g. Winder & Schindler, 2004). Mismatch has been hypothesized to be especially problematic for migratory consumers, which often rely on environmental cues such as temperature or photoperiod to time their

arrivals at distant feeding grounds. While a growing body of research has documented changes in the migration timing of animals, research on the trophic consequences of altered migration has mainly focused on the relationship between migrants and the in situ resources at their destinations (Durant *et al.*, 2007). However, migrants themselves offer foraging opportunities and may incite the movements of predators. Virtually no studies have explored how climate change affects the synchronisation of these predator–prey migrations.

Pacific salmon (*Oncorhynchus* spp.) are ecosystem engineers best known for their anadromous spawning migrations that transfer marine-derived energy and nutrients to less productive freshwater and terrestrial ecosystems (Gende *et al.*, 2002). Salmon subsidies provide high-quality foraging opportunities to more than fifty species of consumers, many of which are

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commercially and culturally important (Willson & Halupka, 1995). Intensified climate change in high-latitude zones, where salmon are most abundant, has resulted in some of the highest temperature increases on the planet (IPCC, 2013). Concurrent with this warming, some salmon spawning migrations are shifting in time (Taylor, 2008; Kovach *et al.*, 2013). There is a growing concern that this shifting salmon phenology may adversely affect the many consumers that exploit salmon during and after their spawning migrations.

Dolly Varden (*Salvelinus malma*) is an opportunistic predator in the family Salmonidae that exhibits diverse life-history strategies, including anadromous migration (Armstrong, 1974). Anadromous Dolly Varden migrate to coastal marine areas in the spring and return to fresh water throughout the summer months, where they eventually spawn in the autumn. Early studies of Dolly Varden found that anadromous individuals migrated to fresh water along with Pacific salmon and then capitalised on salmon subsidies throughout the summer (Everman & Goldsborough, 1907; Armstrong, 1965). Dolly Varden feed heavily on salmon eggs, sometimes preying on eggs as they are released into the nest or more typically scavenging dislodged eggs that enter the stream drift.

Where salmon remain at historical levels of abundance, Dolly Varden can acquire the majority of their annual energy intake by gorging on salmon eggs (Denton, Rich & Quinn, 2009; Armstrong & Bond, 2013). Although salmon eggs are rich in lipids and often hyper-abundant (Moore, Schindler & Ruff, 2008), the spawning window of each species of salmon may be relatively short, lasting only 2–6 weeks (Schindler *et al.*, 2013). Thus, Dolly Varden must arrive at salmon spawning sites (streams and lake shores) at particular times to fully capitalise on salmon eggs. A key question is whether Dolly Varden have been able to adjust their migration timing to track the shifting arrival timing of salmon at their spawning sites. Using daily census counts of upstream migrating fish, including four species of salmon with unique run timings, we explored how Dolly Varden migration behaviour responds to inter- and intra-annual variation in salmon migration in a warming catchment where some of the strongest changes in salmon phenology have been documented (Kovach *et al.*, 2013).

Methods

Study area and focal species

Auke Creek is the 0.5-km long outlet of Auke Lake that drains into the sheltered marine waters of the Alexander

Archipelago off the south-eastern coastline of Alaska, USA (Fig. 1a). Four temporally distinct runs of Pacific salmon return to Auke Creek each year, spawning in the following order (Fig. 1b): sockeye (*Oncorhynchus nerka*), chum (*O. keta*), pink (*O. gorbuscha*) and coho salmon (*O. kisutch*) (collectively termed, 'salmon', here). From 1980 to 2006, an annual average of 3341 sockeye, 11 041 pink, 1443 chum and 716 coho salmon entered Auke Creek (Echave, 2009). From 1997 to 2006, the period of our study, an annual average of 3973 Dolly Varden entered Auke Creek (Echave, 2009). Mature salmon either spawn in Auke creek or move upstream to spawn in Auke Lake (67 ha), Lake Creek [the primary tributary draining 648 ha (Hoover, 2008)] or Lake Two Creek (draining approximately 259 ha; Juneau Watershed Partnership, 2009; Fig. 1a).

In contrast to salmon in small coastal streams, which normally spend 0–2 years in fresh water, migrate to offshore marine waters to attain most of their size, and spawn soon after re-entering fresh water, the majority of Auke Creek Dolly Varden, and south-eastern Alaska sea-run Dolly Varden in general, spend 2–4 years in fresh water, migrate annually to saltwater in spring (peak in May; Echave, 2009) and return to freshwater streams and lakes from July to October, often weeks to months before their October–November spawning period (Armstrong, 1974; Echave, 2009). While in saltwater, Dolly Varden in the study region tend to remain in near-shore waters and do not commonly demonstrate large, open water crossings (Bernard *et al.*, 1995). Dolly Varden emigrating from catchments devoid of lakes tend to search out adjacent catchments with lakes for subsequent overwintering habitat (Armstrong, 1974; Bernard *et al.*, 1995). Throughout the summer months, many upstream migrating Dolly Varden are smaller, immature individuals, while larger individuals will migrate later in the season and spawn before overwintering (Armstrong, 1974; Lum *et al.*, 1998; Fig. 1c).

Censusing upstream migrating salmon and Dolly Varden

From 1997 to 2006, a fish collection weir was cooperatively operated by National Marine Fisheries Service (NMFS), University of Alaska Fairbanks and Alaska Department of Fish and Game (ADFG) on Auke Creek, approximately 400 m downstream of Auke Lake and slightly above mean tide level (Echave, 2009). Each year, generally from 1 July to 31 October, the weir was operated to capture all fish moving from the nearshore marine environment of Auke Bay upstream into Auke Creek. Since the weir was located at the edge of tidal

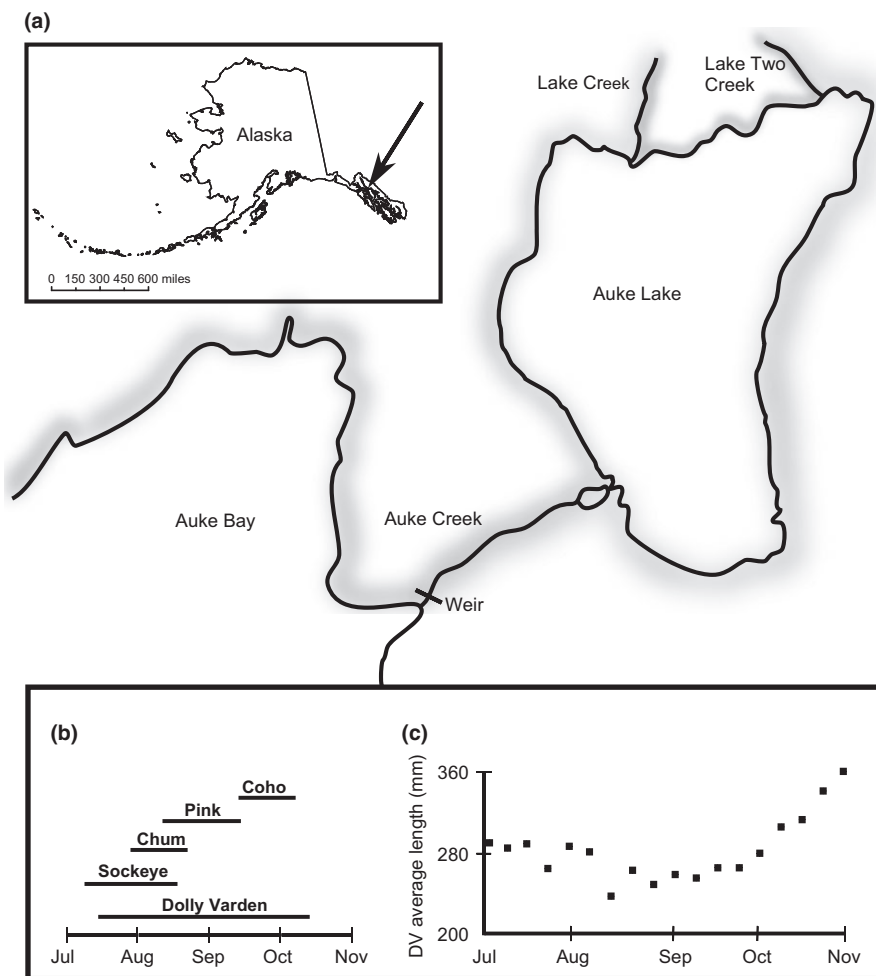


Fig. 1 Study area, migration timing by species and average Dolly Varden length. (a) Auke Creek catchment and location within Alaska, United States. (b) Migration windows (solid lines) spanning the average run timing from the first 5% of migrating individuals each year to 95% of the migrating individuals for Dolly Varden and the four species of Pacific salmon migrating into Auke Creek from 1997 to 2006. (c) In 1997, average weekly length of Dolly Varden (DV) increased markedly after 1 October (Lum *et al.*, 1998).

influence, the fish captured represented all of the fish migrating into Auke Creek. In 1997, all Dolly Varden entering the weir were measured to the nearest 5 mm. A series of annual reports composed by ADFG and NMFS biologists during the sampling years (for example, see Lum *et al.*, 1998 and Hoover, 2008) describe weir construction methods and data collection in detail. **Daily census data** used in our analyses were derived from this series of annual reports.

Correlation between salmon and Dolly Varden migration

To measure synchrony between Dolly Varden and salmon run timing, Spearman's rank correlation coefficient was calculated for **annual pairwise comparisons of daily census counts for Dolly Varden and Pacific salmon** (pooled across species) at Auke Creek weir. Daily census counts (i.e. **the number of fish entering the stream each day**) included in the analysis spanned 1 July to 30 September. For all correlation calculations and the modeling described in the next section, October counts were

not included because individual length data for Dolly Varden arriving during this period suggest October-migrating individuals are capital breeders that migrate to Auke Creek only to spawn, and fuel reproduction from energy acquired elsewhere (Fig. 1c). Effective degrees of freedom were adjusted to account for serial autocorrelation in the times series data (Pyper & Peterman, 1998).

Predicting Dolly Varden daily census counts using salmon and environmental variables

To test the hypothesis that Dolly Varden timed their upstream migrations using the presence of prey species rather than environmental signals, daily census counts of salmon and Dolly Varden were linked with corresponding environmental variables. Daily precipitation values (an index of streamflow; 1-day lag $r = 0.865$; Kovach *et al.*, 2013) from the study area were obtained through the National Climatic Data Center (Auke Bay dataset at <http://www.ncdc.noaa.gov/>). Daily water

temperature data from Auke Creek were obtained from the series of ADFG/NMFS annual reports previously referenced (Figs 2a and S1). Other predictor variables included the calendar day of the year, daily weir counts of salmon (both pooled and grouped by species), as well as daily presence/absence of salmon at the weir.

To account for the large number of zeros and the skewed distribution of Dolly Varden counts, we used negative binomial hurdle models, which allow the response to be modelled as the presence/absence, and conditional distribution representing positive counts (Zeileis, Kleiber & Jackman, 2008). We compared the data support of models with environmental variables to those with prey (salmon) variables using Akaike's information criteria (AIC). To allow for additional unexplained temporal variation in the environmental and prey models, we included year and calendar day as covariates. Year was considered separately as a factor or numeric variable in the presence/absence and count models to allow for linear trends or nonlinear variation.

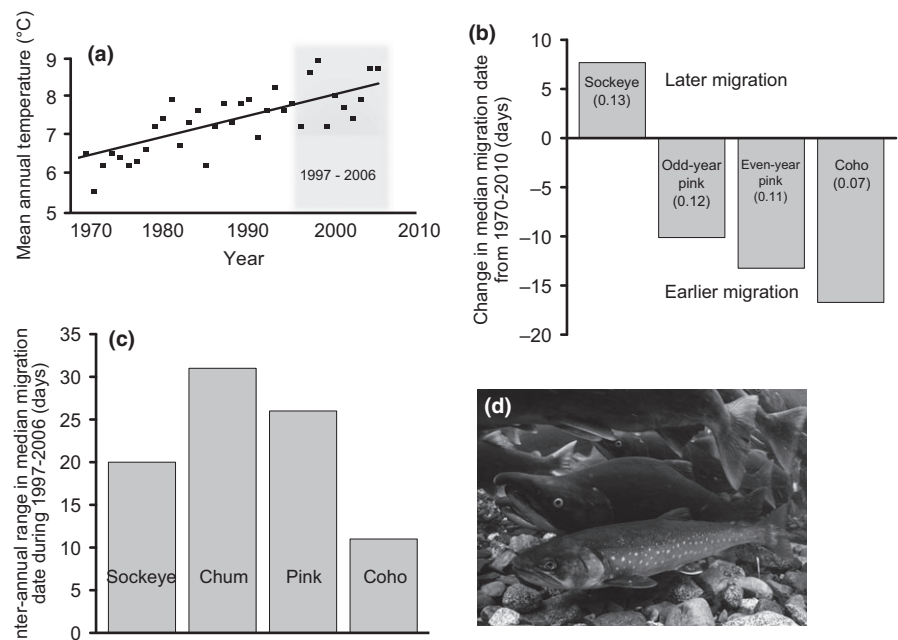
Results

During the 10 years near the end of the 40-year warming period, Dolly Varden foraging migrations were synchronised with salmon spawning migrations (Spearman's rank correlation coefficient = 0.37–0.75, $n = 10$ years significant at $\alpha \leq 0.05$; Fig. 3b). Each year, the protracted upstream migration of Dolly Varden spanned the range of salmon migration timing and closely matched the pulsed

intraspecific and interspecific variation in salmon run timing (Figs 3a and S2). The date of first entry into the stream each year for Dolly Varden closely or exactly matched the first day of entry for sockeye salmon, the earliest spawning species in Auke Creek ($n = 7$ years; Fig. 3c).

Previous studies, including ones conducted in Auke Creek, have examined environmental variables as the main factors driving the timing of upstream salmonid migrations (Davidson, Vaughan & Hutchinson, 1943; Fukushima & Smoker, 1997; Bond & Quinn, 2013). Altered environmental conditions (e.g., earlier peak temperature) are often suspected to decouple synchrony between consumer phenology and periods of prey resource abundance (Visser & Both, 2005; Scheuerell, Zabel & Sandford, 2009). **Dolly Varden appeared to avoid the potential for trophic mismatch by cueing their migrations directly from prey phenology rather than environmental conditions such as streamflow** (indicated by precipitation in our analysis) or water temperature. Our statistical modelling demonstrated that prey variables (salmon presence/absence or daily census counts) more accurately predicted Dolly Varden counts than environmental variables (temperature and precipitation; Table 1). The best positive statistical model indicated that daily census counts of Dolly Varden (i.e. the number of fish entering the stream each day) were best explained by the daily census counts of salmonid prey species (Table 1 and Fig. S3). Further, using counts of **individual salmon species was a better predictor than the aggregate (total salmon)**, indicating that salmon may

Fig. 2 Warming catchment temperature and shifting salmonid migration phenology in Auke Creek. (a) Auke Creek mean annual water temperature has risen approximately 2 °C over four decades (linear regression, $r^2 = 0.532$, $P < 0.001$; data from ref. Wing *et al.*, 2006). (b) From 1970 to 2010, adult Pacific salmon shifted median migration dates into Auke Creek (all data from Kovach *et al.*, 2013; SE of annual rate of change in parentheses). (c) During the 1997–2006 study period, salmon median migration date ranged from 11 to 31 days, depending on species. (d) Char swimming upstream alongside sockeye salmon with characteristic spawning body morphology (photo credit: J.B.A.).



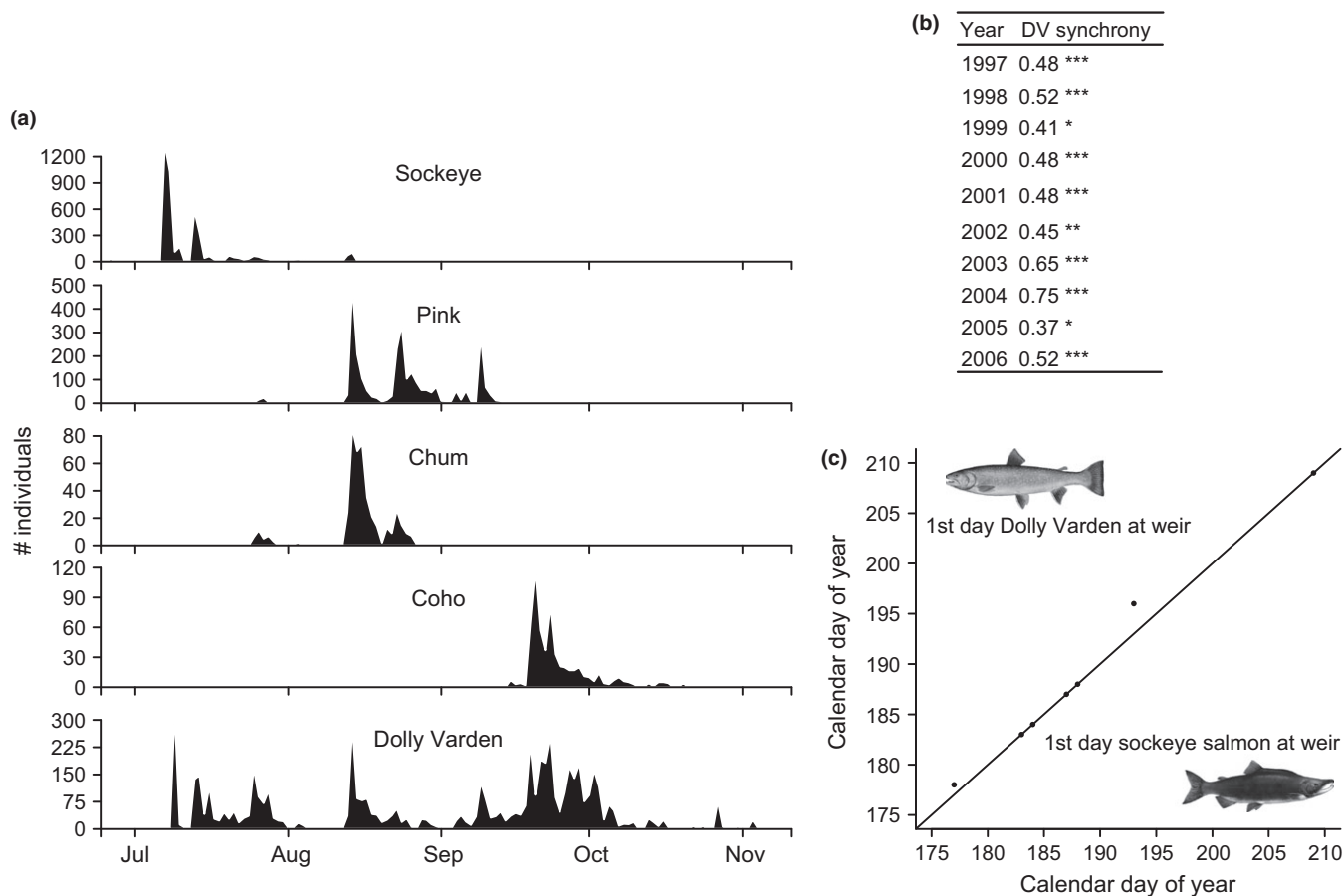


Fig. 3 Intra- and inter-annual patterns in the migration phenologies of Pacific salmon and Dolly Varden. (a) Time series of daily census counts by species for a representative year (1997; see Fig. S2 for 1998 to 2006 time series). (b) Synchrony (Spearman's rank correlation coefficients) between Dolly Varden (DV) and total salmon daily census counts from 1997 to 2006. *** $P < 0.001$, ** $P < 0.01$. * $P < 0.05$ (c) Relationship between calendar day of first salmon arrival at weir each season and first Dolly Varden; 1:1 relationship represented by solid line; years when fish were counted on the first day of weir operation ($n = 3$) were excluded from analysis; fish images from Wikimedia Commons: <http://commons.wikimedia.org/>

have species-specific effects on Dolly Varden migration dynamics (Table 1, Fig. S3 and Table S1).

Previous research in this system has demonstrated that pink and coho salmon now migrate to spawning grounds 10–17 days earlier, while sockeye salmon are migrating 8 days later (Kovach *et al.*, 2013; Fig. 2b). Remarkably, Dolly Varden remained synchronised with each upstream salmon migration, despite non-directional shifts in the timing of salmon runs (Fig. 3). This result lends further support to the hypothesis that Dolly Varden migrations are cued by salmon rather than environmental variables.

Synchrony between Dolly Varden and salmon phenology was consistently positive and statistically significant, but did vary inter-annually during our study period (Fig. 3b). On an annual timescale, the duration of the salmon run (i.e. total number of days salmon run upstream each year) appears to be negatively correlated

with the strength of predator–prey synchrony ($n = 10$, $r^2 = 0.442$, $P = 0.036$; Fig. 4a). If Dolly Varden are cued by the onset of each salmon run, a more protracted run would reduce the correlation between predator and prey migration, because the latter portion of the salmon run would entrain fewer Dolly Varden, while comprising more of the total observations. The strength of predator–prey synchrony was not correlated with water temperature ($n = 9$, $r^2 = 0.002$, $P = 0.611$; Fig. 4b), which lends further support to the conclusion that warming is not reducing the synchronicity of Dolly Varden and salmon migrations.

Discussion

Climate-induced phenological shifts of the magnitude documented in Auke Creek have decoupled consumer–resource phenologies in a variety of systems,

Table 1 Negative binomial hurdle models predicting Dolly Varden daily census counts ranked in order of highest to lowest data support. Correlation between predicted and observed values for the top prey-based model (0.76) was higher than the top environment-based model (0.58)

Hypothesis	Presence-absence model	Positive model	AIC	ΔAIC
Prey (salmon)	Year (f), tot. salmon, CD, salmon present	Year, CD, so, ch, co, pi	6841.0	0.0
	Year (f), CD, salmon present	Year, so, ch, co, pi	6881.3	40.3
	Year (f), tot. salmon, CD, salmon present	Year, so, ch, co, pi	6881.7	40.7
	Year (f), tot. salmon, CD, salmon present	Year, tot. salmon, CD, salmon present	6902.8	61.8
	Year (f), tot. salmon, CD	Year, so, ch, co, pi	6909.0	68.0
	Year (f), tot. salmon, CD	Year, tot. salmon, CD	6928.4	87.4
	Year, tot. salmon, CD, salmon present	Year, tot. salmon, CD, salmon present	6955.0	114.1
	Year (f), CD, salmon present	Year, CD, salmon present	7010.7	169.7
	Year (f), temp * CD, precip	Year, temp * CD, precip	7098.1	257.2
Environmental	Year (f), temp * CD, precip	Year, temp, CD, precip	7099.1	258.1
	Year, temp * CD, precip	Year, temp, CD, precip	7118.7	277.7
	Year (f), temp, CD, precip	Year, temp * CD, precip	7119.6	278.6
	Year (f), temp, CD, precip	Year, temp * CD, precip	7119.6	278.6

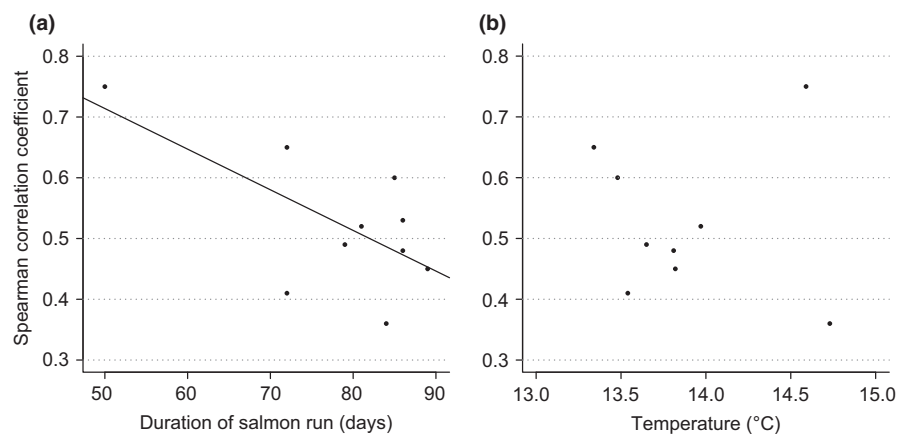
Year (f) = year as a factor variable, temp = water temperature, CD = Calendar Date, precip = precipitation (index of streamflow), and each salmon species (co = \log_e [coho + 1], ch = \log_e [chum + 1], so = \log_e [sockeye + 1], pi = \log_e [pink + 1]) represents the daily census counts for that species (i.e. the number of fish entering the stream each day).

leading to trophic mismatches (Visser & Both, 2005; Post & Forchhammer, 2008; McNeeley & Shulski, 2011). However, predator–prey migration phenologies showed no signs of reduced synchrony in our study, reducing the risk of trophic mismatch and consequent reduced growth potential for Dolly Varden. Our results provide direct evidence that Dolly Varden migration phenology tracked contemporary inter-annual variation in salmon migration phenology. While we cannot be unequivocal that Dolly Varden also tracked salmon migration phenology in the decades before and after this study, this is a reasonable conclusion considering similar short-term historical observations in other nearby catchments (Everman & Goldsborough, 1907; Armstrong, 1965) and that we found strong synchrony near the end of a long-term warming period. The alternative hypothesis, that Dolly

Varden only became synchronised with salmon after the shifts in salmon phenology, is not intuitive given that sockeye now migrate later, while coho and pink salmon migrate earlier (Kovach *et al.*, 2013).

There is probably strong selection on Dolly Varden to fully capitalise on salmon subsidies, which requires them to track substantial inter-annual variation in the arrival of salmon. This high-frequency variation may have led to adaptations that buffer Dolly Varden from the lower frequency, directional trend of climate change. This supports the hypothesis that animals from highly variable environments at high latitudes may be more resilient to future variability associated with climate change (Huey *et al.*, 2009). We therefore conclude that, in our study system, Dolly Varden migration is resilient to the effects of climate change on freshwater prey resources, following both high-frequency inter-annual

Fig. 4 Predator–prey migration synchrony may decrease with an increase in the total days salmon arrived at the weir each season. (a) Linear regression, $r^2 = 0.442$, $P = 0.036$. (b) In contrast, the average water temperature during weir operation period was not significantly correlated with synchrony (linear regression, $r^2 = 0.002$, $P = 0.899$); average temperature for 1997 was removed from the figure because of an excessive number of missing measurements.



variation in salmon migration phenology, as well as the longer term warming trends (Wing, Masuda & Taylor, 2006; Kovach *et al.*, 2013).

We did not directly study the foraging ecology of Auke Creek Dolly Varden and cannot quantify how the level of synchrony between Dolly Varden and salmon migration phenologies affects the foraging opportunities of Dolly Varden. However, we believe asynchronous migration phenologies would lead to trophic mismatches given the ephemeral nature of salmon eggs as a trophic resource (Fukushima, Quinn & Smoker, 1997) and their major contribution to Dolly Varden energy budgets. While salmon populations may be present at spawning sites for 2–6 weeks (Schindler *et al.*, 2013), females often release eggs within the first few days of breeding activity (Fukushima *et al.*, 1997; McPhee & Quinn, 1998), so foraging opportunities for egg-eating fishes are particularly transient. Gorging on eggs provides Dolly Varden enough energy stores to fuel subsequent reproduction or over-winter survival, whereas alternative in situ trophic resources, such as benthic invertebrates, are unlikely to provide even a positive energy balance (Denton *et al.*, 2009; Armstrong & Bond, 2013). From 1997 to 2006, annual median migration timing of salmon phenologies varied 11–31 days across species. In our focal system, the protracted migration of four salmon species buffers the potential penalties of trophic mismatch to some degree. However, in many systems with anadromous Dolly Varden, single species of salmon dominate; for example, sockeye dominate salmon returns in some of the large lake catchments where Dolly Varden are present (Hilborn *et al.*, 2003).

In catchments dominated by single species of salmon, population-level phenological diversity has been shown to extend the window of time when salmon are available to consumers (Schindler *et al.*, 2013). In small catchments like Auke Creek, there is limited population-level diversity and instead it is species-level diversity that extends the period of availability of salmon for consumers; from 1997 to 2006, the aggregate of salmon species in Auke Creek persisted, on average, for 34–59 days longer each year than the duration of its single species components (49–71% longer). We cannot assess whether earlier migrating Dolly Varden sequentially exploited the different salmon runs in Auke Creek, but this is likely given their potential to track variation in resource abundance across time and space. In other systems, rainbow trout (*Oncorhynchus mykiss*) have been shown to move across a stream network to track spatial variation in sockeye salmon phenology (Ruff *et al.*, 2011). Dolly Varden are more mobile than resident rainbow trout, and the

salmon breeding sites in Auke Creek are constrained within a small catchment (< 1000 ha), so Dolly Varden would expend little energy tracking inter-specific variation in salmon breeding phenologies. Dolly Varden spend variable amounts of time along the south-eastern Alaska coastline (Armstrong, 1974; Bernard *et al.*, 1995) where they exploit the abundant marine trophic resources at the expense of increased predation risk. Dolly Varden that arrive with later-spawning species of salmon may be those that have found better foraging opportunities at sea, early salmon runs in adjacent catchments, or they may represent individual variation in how migration strategies balance trade-offs between growth and survival in marine and freshwater environments.

Small to medium-sized catchments such as Auke Creek are prevalent throughout the 2500 miles of the north Pacific coastal temperate rainforest. Dolly Varden and related chars are numerous throughout these rainforest streams and provide not only an important trophic resource to terrestrial predators (Willson & Halupka, 1995), but also a valuable contribution to recreational fisheries that are increasingly important to regional economies. The productivity of Dolly Varden populations probably depends on their ability to capitalise on ephemeral salmon subsidies. Dolly Varden and other resident fishes reach the asymptote of their maximum food intake rate when feeding on salmon eggs (Bentley *et al.*, 2012; Armstrong & Bond, 2013; Armstrong *et al.*, 2013), so their growth potential is highly sensitive to the duration of time that they can exploit salmon subsidies. Climate-induced shifts in salmon phenology could seriously diminish the trophic linkage between salmon and Dolly Varden were it not for the remarkable ability of Dolly Varden to track annual variation in the timing of salmon subsidies.

It remains largely unknown whether additional consumers are able to track annual variation in the phenology of pulsed subsidies. Most salmon consumers move to salmon spawning grounds from alternative habitats. The scale of these movements ranges from hundreds of metres for small resident fishes (Armstrong *et al.*, 2013) to thousands of kilometres for migratory birds (Willson & Halupka, 1995). For these consumers to directly cue their migrations to salmon presence, as Dolly Varden appear to, their perceptual extent must overlap with the migration routes of salmon (Lima & Zollner, 1996). Although fish may not be able to perceive a large portion of the riverscape, the branched linear topology of catchments increases the probability that a fish will perceive salmon as they propagate up the river network to

spawn. Dolly Varden in south-eastern Alaska, which typically do not migrate long distances offshore and often remain near stream entrances (Bernard *et al.*, 1995), are likely to either see adult salmon entering a catchment or smell the production of salmon eggs (Quinn *et al.*, 2012). In contrast, avian consumers such as eagles and gulls are less likely to be proximate to migrating salmon, but they have large perceptual extents. Terrestrial predators such as bears and wolves probably have intermediate perceptual extents, but are highly mobile and may be able to rely on accurate biotic cues to salmon arrival, such as the large aggregations of gulls that accompany salmon spawning (Schindler *et al.*, 2013).

Prey migrations are critical features of ecosystems across the globe. Prey may evade predators in departure habitats, but become vulnerable to predators along migration routes and at destination locations (Fryxell & Sinclair, 1988). The resource subsidies triggered by prey migrations may be critical to maintaining higher levels of the food chain (Polis, Anderson & Holt, 1997), but these trophic linkages are highly vulnerable to mismatch due to their short duration. Our study provides some of the first empirical data on the bottom-up effects of altered migration phenology and suggests that some predators may be more resilient to trophic mismatch than ecologists often assume.

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References

- Armstrong J.B. & Bond M.H. (2013) Phenotype flexibility in wild fish: Dolly Varden regulate assimilative capacity to capitalize on annual pulsed subsidies. *Journal of Animal Ecology*, **82**, 966–975.
- Armstrong J.B., Schindler D.E., Ruff C.P., Brooks G.T., Bentley K.T. & Torgersen C.E. (2013) Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology*, **94**, 2066–2075.
- Armstrong R.H. (1965) Some feeding habits of the anadromous Dolly Varden *Salvelinus malma* (Walbaum) in south-eastern Alaska. *Alaska Department of Fish and Game Information Leaflet*, **51**, 1–27.
- Armstrong R.H. (1974) Migration of anadromous Dolly Varden (*Salvelinus malma*) in southeastern Alaska. *Journal of the Fisheries Research Board of Canada*, **31**, 435–444.
- Bentley K.T., Schindler D.E., Armstrong J.B., Ruff C.P. & Lisi P.J. (2012) Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. *Ecosphere*, **3**, art113.
- Bernard D.R., Hepler K.R., Jones J.D., Whalen M.E. & McBride D.N. (1995) Some tests of the “migration hypothesis” for anadromous Dolly Varden (southern form). *Transactions of the American Fisheries Society*, **124**, 297–307.
- Bond M.H. & Quinn T.P. (2013) Patterns and influences on Dolly Varden migratory timing in the Chignik Lakes, Alaska, and comparison of populations throughout the northeastern Pacific and Arctic oceans. *Canadian Journal of Fisheries and Aquatic Sciences*, **70**, 655–665.
- Davidson F.A., Vaughan E. & Hutchinson S.J. (1943) Factors influencing the upstream migration of the pink salmon (*Oncorhynchus gorbuscha*). *Ecology*, **24**, 149–168.
- Denton K.P., Rich H.B. Jr & Quinn T.P. (2009) Diet, movement, and growth of Dolly Varden in response to sockeye salmon subsidies. *Transactions of the American Fisheries Society*, **138**, 1207–1219.
- Dingle H. & Drake V.A. (2007) What is migration? *BioScience*, **57**, 113–121.
- Durant J.M., Hjermann D.O., Ottersen G. & Stenseth N.C. (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**, 271–283.
- Echave J.D. (2009) Auke Creek weir studies: 2007. Alaska Department of Fish and Game Fishery Data Series, 08-51.
- Everman B.W. & Goldsborough E.L. (1907) The fishes of Alaska. *Bulletin of the Bureau of Fisheries*, **26**, 219–360.
- Fryxell J.M. & Sinclair A.R. (1988) Causes and consequences of migration by large herbivores. *Trends in Ecology and Evolution*, **3**, 237–241.
- Fukushima M., Quinn T.J. & Smoker W.W. (1997) Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 618–625.
- Fukushima M. & Smoker W.W. (1997) Determinants of stream life, spawning efficiency, and spawning habitat in pink salmon in the Auke Lake system, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 96–104.

- Gende S.M., Edwards R.T., Willson M.F. & Wipfli M.S. (2002) Pacific salmon in aquatic and terrestrial ecosystems. *BioScience*, **52**, 917–928.
- Hilborn R., Quinn T.P., Schindler D.E. & Rogers D.E. (2003) Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 6564–6568.
- Hoover C.L. (2008) Auke Creek weir studies: 2006. Alaska Department of Fish and Game Fishery Data Series, 09-67.
- Huey R.B., Deutsch C.A., Tewksbury J.J., Vitt L.J., Hertz P.E., Perez H.J.A. *et al.* (2009) Why tropical forest lizards are vulnerable to climate change. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 1939–1948.
- IPCC (2013) *Climate Change 2013: The Physical Science Basis*. Cambridge University Press, Cambridge.
- Juneau Watershed Partnership (2009) Auke Lake Watershed Assessment. Available at: http://www.juneauwatersheds.org/publications/AUKE%20LAKE_FINAL_JWP.pdf [Accessed 11 November 2014].
- Kovach R.P., Joyce J.E., Echave J.D., Lindberg M.S. & Tallmon D.A. (2013) Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. *PLoS ONE*, **8**, e53807.
- Lima S.L. & Zollner P.A. (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*, **11**, 131–135.
- Lum J.L., Kondzela K., Jones J.D. & Taylor S.G. (1998) Dolly Varden char and sea-run cutthroat trout populations at Auke Lake, Southeast Alaska, during 1997. Alaska Department of Fish and Game Fishery Data Series, 98-43.
- McNeeley S.M. & Shulski M.D. (2011) Anatomy of a closing window: vulnerability to changing seasonality in Interior Alaska. *Global Environmental Change*, **21**, 464–473.
- McPhee M.V. & Quinn T.P. (1998) Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka*. *Environmental Biology of Fishes*, **51**, 369–375.
- Moore J.W., Schindler D.E. & Ruff C.P. (2008) Habitat saturation drives thresholds in stream subsidies. *Ecology*, **89**, 306–312.
- Polis G.A., Anderson W.B. & Holt R.D. (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology, Evolution, and Systematics*, **28**, 289–316.
- Post E. & Forchhammer M.C. (2008) Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **363**, 2369–2375.
- Pyper B.J. & Peterman R.M. (1998) Comparison of methods to account for autocorrelation in correlation analysis of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 2127–2140.
- Quinn T.P., Dittman A.H., Barrett H., Cunningham C. & Bond M.H. (2012) Chemosensory responses of juvenile Coho salmon, *Oncorhynchus kisutch*, Dolly Varden, *Salvelinus malma*, and sculpins (*Cottus* spp.) to eggs and other tissues from adult Pacific salmon. *Environmental Biology of Fishes*, **95**, 301–307.
- Ruff C.P., Schindler D.E., Armstrong J.B., Bentley K.T., Brooks G.T., Holtgrieve G.W. *et al.* (2011) Temperature-associated population diversity confers benefits to mobile consumers. *Ecology*, **92**, 2073–2084.
- Scheuerell M.D., Zabel R.W. & Sandford B.P. (2009) Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.). *Journal of Applied Ecology*, **46**, 983–990.
- Schindler D.E., Armstrong J.B., Bentley K.T., Jankowski K., Lisi P.J. & Payne L.X. (2013) Riding the crimson tide: mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters*, **9**, 20130048.
- Taylor S.G. (2008) Climate warming causes phenological shift in Pink Salmon, *Oncorhynchus gorbuscha*, behavior at Auke Creek, Alaska. *Global Change Biology*, **14**, 229–235.
- Visser M.E. & Both C. (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2561–2569.
- Willson M.F. & Halupka K.C. (1995) Anadromous fish as keystone species in vertebrate communities. *Conservation Biology*, **9**, 489–497.
- Winder M. & Schindler D.E. (2004) Climate change uncouples trophic interactions in an aquatic ecosystem. *Ecology*, **85**, 2100–2106.
- Wing B.L., Masuda M.M. & Taylor S.G. (2006) Time series analyses of physical environmental data records from Auke Bay, Alaska. NOAA Technical Memo, NMFS-AFSC-166.
- Zeileis A., Kleiber C. & Jackman S. (2008) Regression models for count data in R. *Journal of Statistical Software*, **27**, 1–25.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Mean daily temperature in Auke Creek (solid line) during the study period. Dashed line is ± 1 SD.

Figure S2. Time series of all daily census counts of salmon and Dolly Varden for all study years (1997–2006).

Figure S3. Predictions of daily census counts of Dolly Varden (gray filled circles) using the best prey-based (solid line) and environmental-based (dashed line) models.

Table S1. Results from the best statistical model predicting Dolly Varden counts. (A) Presence/absence model results (B) Positive model results.

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