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Eco-evolutionary feedbacks in the functional role of a polymorphic colonizer: Arctic charr in subarctic lakes of Alaska and Iceland

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ABSTRACT

Background: The Arctic charr, *Salvelinus alpinus*, is likely to be the first fish to colonize northernmost freshwater systems. It often exhibits sympatric morphotypes.

Question: How do ecosystem characteristics and the life history of Arctic charr interact to generate food webs in subarctic lakes?

Organisms: We focus on allometric dietary patterns of Arctic charr. We compare them with selected, co-occurring fish species, including threespine stickleback (*Gasterosteus aculeatus*) among others, and both benthic and limnetic invertebrates.

Field sites: Subarctic lakes in two regions that differ greatly in colonization history (ten in Iceland and four in Alaska).

Methods: We used natural variation in the stable isotope ratios $\delta^{13}C$ and $\delta^{15}N$ to estimate trends in trophic position and relative use of benthic and limnetic carbon sources with body size among lakes and among species × morph × body size brackets within lakes.

Results: (1) In subarctic lakes with low levels of fish diversity, food chains lengthened via insertion of intermediate prey. (2) Ecosystem attributes, including the presence of competitors and competitor resource use, were associated with allometric shifts in Arctic charr resource use. (3) Species attributes, including the presence and nature of polymorphism exhibited by the Arctic charr, likewise shifted allometric trends in resource use. (4) Both the expression of resource polymorphism and interspecific interactions (i.e. predation, competition, or both) affected food web structure.

Keywords: Arctic charr, eco-evolutionary feedback, food web, resource polymorphism, subarctic lake.

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INTRODUCTION

Harsh conditions can prevent high levels of fish diversity in lakes at high latitudes (Pienitz *et al.*, 1997; Edmundson and Mazumder, 2002), while recent deglaciation, high environmental variability, and topographical features also inhibit colonization. Colonizers of such regions are thought to be particularly adaptable, and when combined with a lack of competitors, may show high ecological diversity or co-occurring morphs, such as in the Arctic charr, *Salvelinus alpinus* and the threespine stickleback, *Gasterosteus aculeatus* (Bernatchez and Wilson, 1998; Robinson and Schluter, 2000; Griffiths, 2006). Such intraspecific diversity reflects resource polymorphism – the tendency of a species to form multiple realized niches among morphs often in sympatry (Skúlason and Smith, 1995). Morphs can differ in habitat use, growth rates, maturity patterns, and timing and/or location of spawning, sometimes leading to genetic population differentiation (Kapralova *et al.*, 2011).

Although populations may become more specialized, reflecting local circumstances, together such variation results in a large intraspecific functional niche across a variety of conditions (Bernatchez and Wilson, 1998; Robinson and Schluter, 2000). A wide functional niche allows for more opportunity to overlap with co-occurring species, possibly causing interspecific competition that theoretically may lead to niche partitioning or local extinction (Holt, 2004). Intraspecific diversity, on the other hand, is promoted by frequency-dependent selection via intraspecific competition, possibly in conjunction with associated reproductive barriers (Schluter, 1996; Dieckmann *et al.*, 2004; Bassar *et al.*, 2013).

Thus, local ecological conditions can control both community ecology and the generation of intraspecific diversity. However, only recently have these fields been linked as interacting components of an ecosystem (Schoener, 2011). Recent research on eco-evolutionary feedbacks has made it clear that the traditional assumption that evolutionary dynamics act on longer time scales than ecological dynamics is invalid (Quinn *et al.*, 2001; Hairston *et al.*, 2005; Carroll *et al.*, 2007). Instead, evolutionary dynamics may drive ecological dynamics (Yoshida *et al.*, 2003; Ellner *et al.*, 2011; Kinnison *et al.*, 2015). In particular, adaptation in response to species interactions can affect community dynamics (Lawrence *et al.*, 2012; Turcotte *et al.*, 2012; Strauss, 2014). In addition, eco-evolutionary feedbacks ultimately lead to changes in ecosystem processes through changes in food web dynamics, productivity, decomposition, or nutrient cycling (Matthews *et al.*, 2011; Walsh *et al.*, 2012). The evolution of consumers co-occurring with predators or other consumers can affect the role that their trophic niches play in ecosystem processes (Palkovacs *et al.*, 2011; Lawrence *et al.*, 2012; Marshall *et al.*, 2012), as can evolutionary dynamics of trophic levels that do not even directly interact (Bassar *et al.*, 2012; Rudman *et al.*, 2015). Likewise, local adaptation or co-evolution of predators can determine prey community composition (Howeth *et al.*, 2013; Pantel *et al.*, 2015) and trait adaptations (Walsh and Post, 2011; Hiltunen and Becks, 2014). Furthermore, the evolutionary effects of intraspecific diversity on ecosystem properties can be of a similar magnitude to abiotic controlling factors (El-Sabaawi *et al.*, 2015).

Therefore, examining niche formation through the interplay of evolution and ecology is important for understanding how biodiversity generates functional diversity that impacts ecosystems (e.g. Song *et al.*, 2014; Leduc *et al.*, 2015), as well as threats to ecosystem stability or resilience due to anthropogenic losses in diversity. Functional redundancy is considered a mechanism that could increase ecosystem resilience by conserving ecosystem function (Biggs *et al.*, 2012), such as through competitor niche expansion or an increased competitor biomass after the loss of a species (Rosenfeld, 2002; Rice *et al.*, 2013; Bell *et al.*, 2014). However, the role of intraspecific divergence in promoting functional redundancy is poorly understood.

The conditions under which both intraspecific diversity and functional redundancy are generated can be highly context-specific, such as through frequency-dependent selection (Schluter, 1996; Dieckmann *et al.*, 2004; Bassar *et al.*, 2013) or predation avoidance (Bassar *et al.*, 2010, 2013). As a result, Rosenfeld (2002, p. 160) suggested that 'understanding the functional attributes of individual species is a necessary first step towards mechanistically linking the properties of species to the properties of ecosystems'.

This study follows Rosenfeld's (2002) suggestion, but extends it into the intraspecific realm, by analysing the functional role of Arctic charr in recently colonized ecosystems – subarctic lakes. Arctic charr tolerate low temperatures (Baroudy and Elliott, 1994) but have low competitive ability (Langeland *et al.*, 1991). Given their dominance as a key colonizing fish of high-latitude lakes, there is a high potential for large shifts in lake ecosystem processes if their dietary habits become altered, as new waves of colonization occur when southerly species move northward due to climate-induced changes (Vincent *et al.*, 2013). In this study, we compare allometric trends of Arctic charr in two regions (ten Icelandic and four Alaskan lakes) with similar latitudes and postglacial histories, but different colonization rates. In contrast to Alaska, Iceland has relatively depauperate flora and fauna due to geographic isolation (Jónasson *et al.*, 1998). Trends in allometry and size structure are important for understanding the development of intraspecific diversity (e.g. Snorrason and Skúlason, 2004), as well as the effects of size-structured competition on population dynamics and ecosystems (Andersson *et al.*, 2007; Bourlot *et al.*, 2014; Bassar *et al.*, 2015). Therefore, we used stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ to depict allometric trajectories in resource use, which can be thought of as the intersection between a species and its interaction with its ecosystem via the food web. On the one hand, allometric trends in resource use is a characteristic of a species (or, more accurately, a population), but on the other hand, it is a functional attribute that describes a component of the local food web. We first examined effects of an ecosystem-level property (i.e. a gradient of biodiversity) on this functional attribute of a species (i.e. allometric trends in resource use). We then reversed this paradigm to analyse the effects of the presence of resource polymorphism, a species- (or population-) level property, on food web characteristics (i.e. stable isotope values from Arctic charr, often the most dominant species), as a property of the ecosystem.

METHODS

Fish and invertebrate samples

Ten Icelandic and four Alaskan lakes were studied (Table 1). Fish were caught mostly with a combination of sinking and floating gill nets and minnow traps in the summer and fall of 2009–2010 and included Arctic charr (*Salvelinus alpinus*), threespine stickleback (*Gasterosteus aculeatus*), brown trout (*Salmo salar*), sockeye salmon fingerling (*Oncorhynchus nerka*), rainbow trout (*Oncorhynchus mykiss*), Arctic grayling (*Thymallus arcticus*), pygmy whitefish (*Prosopium coulterii*), northern pike (*Esox lucius*), and slimy sculpin (*Cottus cognatus*) [see Table S1 at evolutionary-ecology.com/data/3113Appendix.pdf (see also Denton *et al.*, 2010)]. In all Icelandic lakes, Arctic charr was polymorphic; in Alaska, only Lower Tazimina Lake contained polymorphic Arctic charr (Jónsson and Skúlason, 2000; Jónsson, 2002; Woods *et al.*, 2012a, 2013). After assignment, each morph was categorized based on expected asymptotic size (S = small, M = medium, L = large) from Woods *et al.* (2012a) and the dietary results from this or previous studies (Appendix Table S2, Benthic = generalized or

specialized benthic food consumption, Limnetic = generalized limnetic consumption, Zooplanktivorous = specialized limnetic consumption of zooplankton, Piscivorous = specialized consumption of fish prey at larger sizes). Note, however, that no attempt was made to distinguish the cause of differences in growth rates. That is, the allometric trajectory of a 'morph' may develop from genetic differences or phenotypic plasticity. Stickleback morphs were not distinguished except in Thingvallavatn, where depth of capture indicates different morphs. For Arctic charr, Arctic grayling, pygmy whitefish, and threespine stickleback, pictures were taken from which standard lengths (threespine stickleback) and fork lengths (all others) were measured using ImageJ v. 1.44o.

Stable isotope analyses

For fresh waters, the ratio of ^{13}C to its lighter isotope ^{12}C is used to distinguish benthic carbon sources, which tend to have an enriched isotope ratio relative to limnetic, terrestrial, or profundal carbon sources (Vander Zanden and Rasmussen, 1999; Jeppesen *et al.*, 2002). The ratio of ^{15}N to its lighter isotope ^{14}N reflects trophic position (Fry, 2006).

Dorsal muscle plugs or caudal fin clips (rainbow trout) were taken for isotope analyses of all species. Littoral stone and mud habitats (>1 m deep) were scoured for benthic invertebrate samples providing baseline values for stable isotope analyses (base 1 below). Zooplankton (base 2) was sampled using a 125 μ plankton tow net (Iceland) or a 153 μ tow net (Alaska). Stable isotope samples were corrected for ethanol preservation (Vander Zanden *et al.*, 2003; Ventura and Jeppesen, 2009), body length (Kelly, 2000; Schielke and Post, 2010), and normalized for lipid content (Kiljuenen *et al.*, 2006). We also corrected all $\delta^{13}C$ and $\delta^{15}N$ values for variability at the base of the food chain to allow site comparisons at higher trophic positions (Vander Zanden and Rasmussen, 1999, 2001; Post, 2002; Woods *et al.*, 2013) (see also Appendix). Trophic position (TP) and the proportion of carbon from the benthic food chain consumed (BFC, denoted a in equations) of the secondary consumer (sc) were calculated using the mixture model:

$$TP_{sc} = \lambda_{base1} \times a + \lambda_{base2} \times (1 - a) + (\delta^{15}N_{sc} - [\delta^{15}N_{base1} \times a + \delta^{15}N_{base2} \times (1 - a)]).$$

Here, λ_{base1} and λ_{base2} represent trophic positions of the samples $\delta^{15}N_{base1}$ and $\delta^{15}N_{base2}$ used to calculate the bases of the first and second food chains (e.g. limnetic and benthic), assuming a $\delta^{15}N$ fractionation of 3.4‰ with each increase in trophic position (Cabana and Rasmussen, 1996; Post, 2002). Values for $\delta^{13}C$ can then be used to calculate $a = (\delta^{13}C_{sc} - \delta^{13}C_{base2})/(\delta^{13}C_{base1} - \delta^{13}C_{base2})$. Invertebrate stable isotope values used to calculate baselines and final parameter values are given in Fig. 1 and Table 1. For statistical analyses, we used R v. 2.13.0 (R Development Core Team, 2011).

Effects of ecosystem properties on species properties

Resource partitioning and fish diversity

We compared groups (i.e. TP and BFC levels) to broadly estimate resource partitioning among sizes, species, and morphs within food webs. Species were split into three size groups (S < 20 cm; M = 20–30 cm; L ≥ 30 cm), and Arctic charr were assigned to one of four morphs: (1) small [S] benthic, which have a growth curve differentiated from (2) medium-to-large [M–L] benthic, and (3) limnetic or (4) piscivorous. Small-sized morphs were confounded with small sizes of large morphs, as small-sized Arctic charr are generally not

Table 1. Location, sampling date, and baseline values of $\delta^{15}N$ and $d^{13}C$ used for the limnetic and benthic food chains in stable isotope studies

					Limnetic base			Benthic base		
Lake	No.	Latitude	Longitude	Date	$\delta^{15}N$	$\delta^{13}C$	Group	$\delta^{15}N$	$\delta^{13}C$	Group
Hólmavatn	25	65.150	20.933	26 July 2010	7.30	−25.81	Cop	0.54	−11.02	Snail/ST
Hólsvatn	55	64.517	22.133	30 July 2010	5.57	−23.40	Cop/ST	2.85	−22.22	Snail/ST
Sauravatn	56	64.667	22.117	30 July 2010	3.44	−27.46	Mus/ST	0.45	−24.47	Snail (& Chir)
Vatnshlíðarvatn	21	65.517	19.633	17 July 2010	3.39	−25.94	Clad (& Cop)	3.43	−20.52	Snail (& Chir)
Högnavatn	37	65.800	22.167	13 Aug 2010	−0.14	−23.96	Clad (& Cop)	1.56	−14.92	Snail (& Chir)
Thríhyrningsvatn	65	65.167	15.767	7 Sept 2010	1.51	−30.47	Clad (& Cop)	0.22	−15.98	Snail/AC
Galtaból	4	65.250	19.717	27/28 Aug 2010	6.53	−23.63	Cop	2.40	−10.81	Snail/AC
Sigurðurstaðavatn	14	66.483	16.300	21/22 Aug 2010	−0.89	−19.97	Clad	0.95	−14.12	Snail/AC
Vestara-Friðmundarvatn	22	65.300	14.683	15 Sept 2010	2.38	−26.25	Mus	−0.44	−16.69	Snail/AC
Thingvallavatn	0	64.167	21.130	1/5 Sept 2010	4.61	−33.56	Cop/AC	−0.01	−8.23	Snail/AC
Summit Lake	101	59.704	−153.686	20/21 Aug 2010	2.20	−31.69	Clad	1.99	−16.87	Snail/AC
Caribou Lake	102	60.450	−154.630	8 Dec 2010	3.82	−32.63	Clad	4.49	−16.29	Snail/AC
Lower Tazimina Lake	103	59.962	−154.550	6 Dec 2010	1.74	−33.34	Clad	0.38	−13.65	Snail
Iliamna Lake	100	59.738	−154.208	23/30 Aug 2010	5.51	−29.73	Clad	3.49	−10.27	Snail/AC

Note: Icelandic lake numbers correspond with those in the ESIL database. When a base group is listed alone, it was used for both $\delta^{15}N$ and $\delta^{13}C$; otherwise, A (& B) indicates that A only was used for $\delta^{15}N$ and the average of A and B was used for $\delta^{13}C$, and A/B indicates that A only was used for $\delta^{15}N$ and B only was used for $\delta^{13}C$. Groups included copepods (Cop), cladocerans (Clad), pea clams (Mus), snails (Snail), chironomid larvae (Chir), stickleback (ST), and Arctic charr (AC).

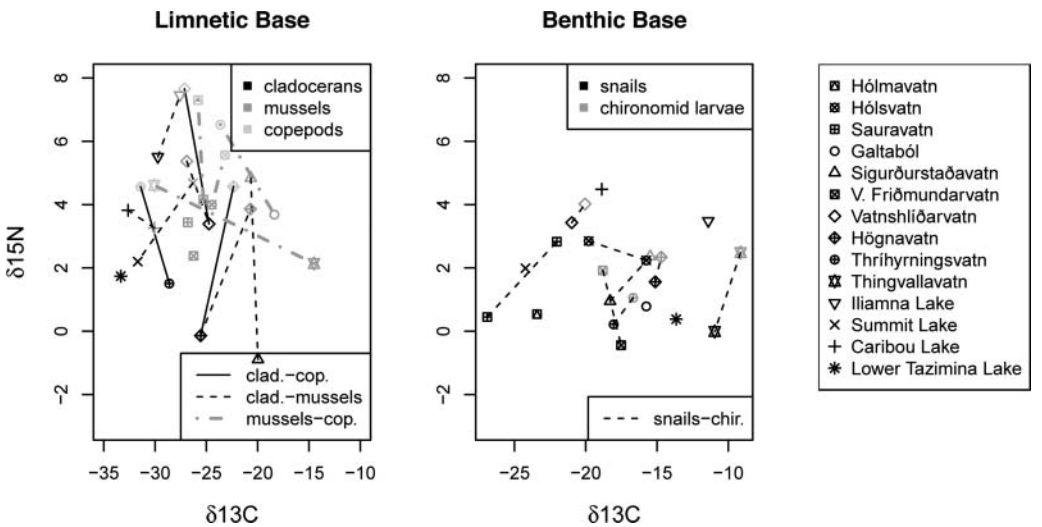

Fig. 1. Potential baseline values for the limnetic and benthic food chains. Wherever alternate baseline taxa could be considered, lines were drawn to show which samples originated within the same lake.

yet capable of becoming piscivorous due to gape restrictions, and morphological differences may be minimal. For example, in Vestara-Friðmundarvatn, the piscivorous morph was defined as having a length > 30 cm due to difficulties in distinguishing morphs, preventing any overlap in size between morphs. However, it is obvious from trophic positions that medium-sized M–L benthic forms likewise eat some stickleback, so it may contain indistinguishable medium-sized piscivorous individuals (Appendix Figs. S1 and S2).

To compare discreteness in resource use between lakes containing only Arctic charr versus more diverse lakes, we predicted TP and BFC based on species × morph × size group in linear models. M–L benthic Arctic charr represented the baseline for lakes where they occurred; in the other lakes, the large piscivorous morph was the baseline (Sigurðurstaðavatn). The large benthic morph from Thingvallavatn was not included in the analysis because this lake has more than one large morph (see also supportive gut content analyses in Appendix Table S2).

Species interactions: predation

Linear mixed effects models were used to test the effects of stickleback presence, fork length, and interactions on allometric changes in Arctic charr BFC and TP with lake as a random effect. Non-significant interactions were removed from the model. Models were run separately for Icelandic and Alaskan lakes. As threespine stickleback may be polymorphic, linear mixed effects models were used to test reciprocal effects of Arctic charr presence and stickleback length on stickleback BFC using lake as a random effect.

Species interactions: competition

To test the effect of competitor resource use on allometric trends in medium-to-large Arctic charr, we defined competitors as another species roughly within the size range of adult M–L Arctic charr (>20 cm). A linear mixed effects model was used to test for the effects of

competitor resource use and length on Arctic charr BFC and TP with lake as a random effect. Competitor resource use was summarized as the mean BFC or mean TP for individuals > 20 cm and included as a covariate. As few lakes had such competitors, only Thingvallavatn in Iceland and all but Summit Lake in Alaska were used in the same analysis. We also tested whether stickleback appeared to compete with small Arctic charr by repeating this analysis on Arctic charr < 20 cm, including four lakes from Iceland and two from Alaska. To incorporate the spatial overlap necessary for competition in Thingvallavatn, we used deep-caught (~14 m) stickleback as the competitor for piscivorous/limnetic Arctic charr, and shallow-caught (~1–2 m) stickleback as the competitor for benthic morphs.

Effects of species properties on ecosystem properties: resource polymorphism

Interactions of polymorphism type

Linear mixed effects models were used to test for the effects of the presence of polymorphism on Arctic charr BFC and TP while accounting for allometry (body length as a covariate) and lake as a random effect. Icelandic and Alaskan lakes were modelled separately. Polymorphism was then broken down by type according to Woods *et al.* (2012a): Galtaból and Thingvallavatn had both morphological and growth rate differentiation, Vatnshlíðarvatn and Thríhyrningsvatn only exhibited morphological differentiation, and Vestara-Friðmundarvatn and Högnavatn only exhibited growth rate differentiation. The effects of each polymorphism type (growth rate or morphological differentiation), the interaction between their presence, and interactions with fork length were tested. This determined whether the development of polymorphism via growth rate versus morphological differentiation (or both) resulted in similar allometric trends in resource use across lakes. Interactions were of primary interest. Only growth rate differentiation was detected in Alaskan lakes, so interactions could not be tested.

Interactions of growth rate differentiation with prey availability

The presence of growth rate differentiation and stickleback presence were then included in a linear mixed effects model to predict Arctic charr TP and BFC to test whether allometric trends of large morphs in resource use were consistent across lakes with differing prey availability. Again, the interaction was of primary interest. Due to a lack of replication, these analyses were only completed on Icelandic lakes.

RESULTS

Effects of ecosystem properties on species properties

Resource partitioning and fish diversity

All linear models testing for differences in trophic position (TP) among species × morph × size bracket combinations were significant, except in Lower Tazimina Lake and Icelandic lakes with only Arctic charr present (Table 2). Lakes with greater fish diversity had more differentiated TP values among species × morph × size brackets (Table 2). In contrast, linear models indicated that differences in the proportion of benthic food chain consumed (BFC) among species × morph × size bracket combinations were widespread but not ubiquitous,

Table 2. Results of linear models (*F*-statistic, *P*-value, and degrees of freedom) testing for differences in proportion trophic position (TP) or benthic food chain consumed (BFC) among species × morph × size brackets, compared with the lake's location and presence of other species

Lake	Location	Other species present?	TP		BFC		
			F	*P*	*F*	*P*	*df*
Thingvallavatn	Iceland	Yes	10.58	<0.0001	19.10	<0.0001	12,159
Galtaból	Iceland	Yes	14.50	<0.0001	1.862	0.111	5,77
Sigurðurstaðavatn	Iceland	Yes	8.481	<0.0001	4.542	0.006	3,56
Vestara-Friðmundarvatn	Iceland	Yes	36.74	<0.0001	12.70	<0.0001	3,60
Vatnshlíðarvatn	Iceland	No	0.381	0.767	4.103	0.013	3,40
Högnavatn	Iceland	No	2.688	0.079	1.354	0.269	2,45
Thríhyrningsvatn	Iceland	No	2.062	0.121	4.162	0.012	3,39
Iliamna Lake	Alaska	Yes	17.02	<0.0001	12.61	<0.0001	8,47
Summit Lake	Alaska	Yes	8.063	<0.0001	2.579	0.085	2,54
Caribou Lake	Alaska	Yes	44.01	<0.0001	12.26	<0.0001	6,66
Lower Tazimina Lake	Alaska	Yes	1.131	0.3483	55.55	<0.0001	9,102

with little relation to fish diversity (Table 2). The largest differences among coefficients estimated for each species × morph × size bracket can, but do not always, lie between species rather than between morphs, indicating that intraspecific dietary differences can be as extreme as interspecific dietary differences within a food web (Appendix Figs. S1–S3 and Tables S3–S5). For gut content data used to help interpret stable isotope data, see the Appendix.

Species interactions: predation

Trophic position

Stickleback TP showed no effects of Arctic charr presence ($t_5 = 0.469$, $P = 0.659$) or length ($t_{229} = 1.051$, $P = 0.294$). The linear mixed effects model used to predict Arctic charr TP in Icelandic lakes indicated that the main effect of threespine stickleback presence was not significant ($t_5 = 0.567$, $P = 0.595$), and there was a positive effect of length ($t_{320} = 2.980$, $P = 0.003$) but no interaction with stickleback ($t_{320} = 1.932$, $P = 0.054$; Fig. 2, top). In Alaskan Arctic charr, stickleback raised the trophic position of Arctic charr ($t_2 = 12.179$, $P = 0.007$), length was positively correlated with TP ($t_{195} = 4.309$, $P < 0.0001$), and the interaction was removed (not shown).

Benthic versus limnetic resource consumption

Stickleback BFC did not differ with Arctic charr presence ($t_5 = 2.267$, $P = 0.073$), although greater benthic consumption occurred at larger sizes ($t_{229} = 2.250$, $P = 0.025$, results not shown). In the linear mixed effects model predicting BFC of Icelandic Arctic charr, stickleback presence was not significant ($t_5 = 1.946$, $P = 0.109$), but length was significant ($t_{343} = 3.034$, $P = 0.003$), as was its interaction with stickleback presence ($t_{343} = -2.850$,

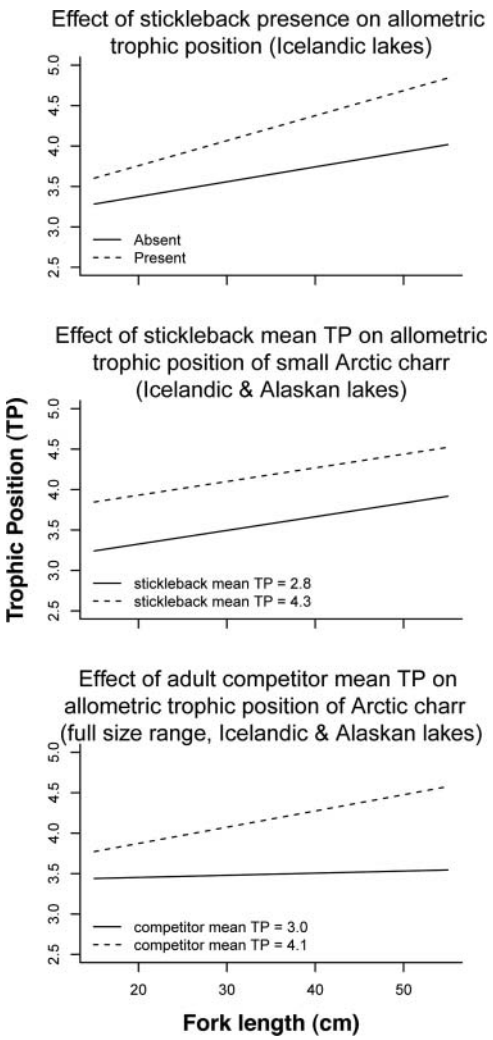

Fig. 2. Results from fitted linear mixed effects models indicated that ecosystem properties, such as the presence of stickleback (top), the mean TP of stickleback (middle), or the mean TP of co-occurring adult competitor (bottom), did not cause a large change in the allometric trajectories that predict trophic position (TP) of Arctic charr from its body size. That is, the effect of the interaction, which is indicated by comparing slopes after fixing the competitor TP predictor at a relatively high versus low value, is minimal. The values used for mean TP of stickleback (2.8 and 4.3) or the competitor (3.0 and 4.1) represent minimum and maximum values found in our data.

$P = 0.005$). Therefore, stickleback did not affect the overall BFC of Icelandic Arctic charr, but its allometric slope shifted (Fig. 3, top). For Alaskan Arctic charr, although length increased BFC significantly ($t_{195} = 7.807$, $P < 0.0001$), stickleback had no effect ($t_2 = -1.425$, $P = 0.290$), and the interaction was removed (not shown).

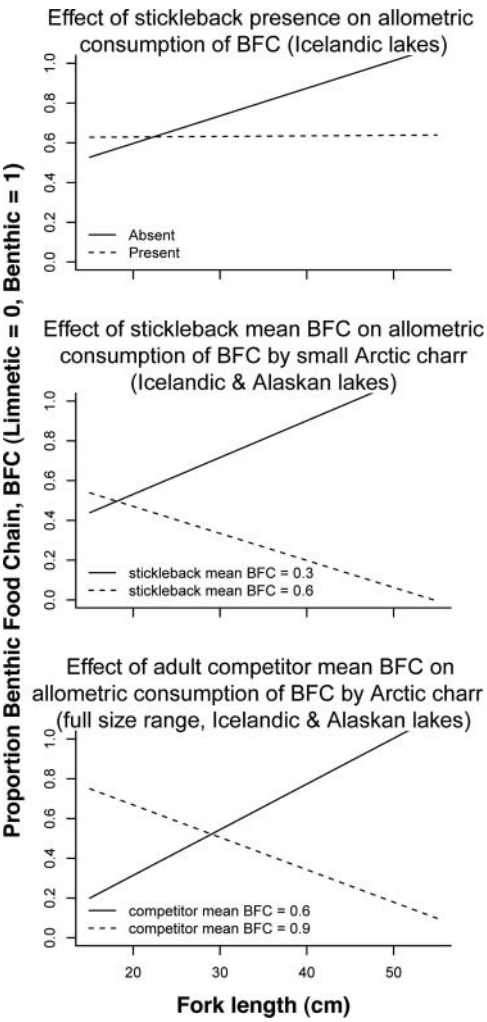

Fig. 3. Results from fitted linear mixed effects models indicate that ecosystem properties, such as the presence of stickleback (top), the mean BFC of stickleback (middle), or the mean BFC of co-occurring adult competitor (bottom), can affect species properties by changing the allometric trajectories that predict the proportion of benthic food chain consumed (BFC) by Arctic charr from its body size. That is, the effect of the interaction, which is indicated by comparing slopes after fixing the competitor BFC predictor at a relatively high versus low value, is strong. The values used for mean BFC of stickleback (0.3 and 0.6) or the competitor (0.6 and 0.9) represent minimum and maximum values found in our data.

Species interactions: competition

Trophic position

The tests here only reflect comparisons with a single competitor, although others may have been present. For example, for northern pike and rainbow trout in Iliamna Lake, rainbow trout were considered the more likely competitor due to known competitive interactions

between Arctic charr and other salmonids (Langeland *et al.*, 1991; Hesthagen *et al.*, 1997; Jansen *et al.*, 2002; Forseth *et al.*, 2003). The diet of rainbow trout can be similar to Arctic charr depending on the habitat (Arostegui and Quinn, 2018). Interaction of the competitor's mean TP with length in predicting Arctic charr TP was only marginally significant (competitor's mean TP: $t_2 = 0.198$, $P = 0.861$; length: $t_{211} = -1.398$, $P = 0.164$; interaction: $t_2 = 1.941$, $P = 0.054$), indicating little change with competitor trophic position (Fig. 2, bottom). Using stickleback as the competitor of small Arctic charr (Fig. 2, middle), there were weak positive effects of length and competitor mean TP (competitor's mean TP: $t_4 = 2.683$, $P = 0.0551$; length: $t_{112} = 1.905$, $P = 0.059$; interaction: removed).

Benthic versus limnetic resource consumption

The competitor's mean BFC value and Arctic charr length had a positive effect on Arctic charr BFC (competitor's mean BFC: $t_2 = 7.243$, $P = 0.019$; length: $t_{211} = 7.911$, $P < 0.0001$), but showed a negative interaction ($t_{211} = -7.390$, $P < 0.0001$). Therefore, in lakes where the competitor ate more benthos, so did Arctic charr, but its allometric trajectory shifted towards less consumption of benthic resources over length compared with other lakes (Fig. 3, bottom). Using stickleback as the competitor of small Arctic charr revealed the same pattern (Fig. 3, middle): positive effects of the competitor's mean BFC ($t_4 = 3.016$, $P = 0.039$) and length ($t_{111} = 2.093$, $P = 0.039$), but a negative interaction ($t_{111} = -3.145$, $P = 0.0009$).

Effects of species properties on ecosystem properties: resource polymorphism

Interactions of polymorphism type

Trophic position

The presence of polymorphism had no effect on the TP of Icelandic Arctic charr populations ($t_5 = -1.434$, $P = 0.211$). Trophic position increased with length ($t_{321} = 15.210$, $P < 0.0001$), and the interaction was removed (results not shown). Likewise, polymorphism did not affect Alaskan Arctic charr TP ($t_2 = 0.970$, $P = 0.434$), but length was positively correlated ($t_{195} = 4.260$, $P < 0.0001$, results not shown). Even when polymorphism was split by type, no significant results were observed except for a positive association with length (morphological differentiation: $t_3 = -1.665$, $P = 0.195$; length: $t_{318} = 3.501$, $P = 0.0005$; growth rate differentiation: $t_3 = -1.323$, $P = 0.278$; length × morphological differentiation: $t_{318} = -0.111$, $P = 0.911$; length × growth rate differentiation: $t_{318} = 1.110$, $P = 0.268$; growth rate differentiation × morphological differentiation: $t_3 = 1.445$, $P = 0.244$; three-way interaction: $t_{318} = -0.287$, $P = 0.774$). Therefore, only an allometric increase in TP could be detected (Fig. 4, bottom).

Benthic versus limnetic resource consumption

The BFC of Icelandic Arctic charr was not affected by polymorphism ($t_5 = 0.4300$, $P = 0.6853$) or length ($t_{321} = -0.2991$, $P = 0.7650$), and the interaction was removed (results not shown). However, a different picture emerged in Iceland when polymorphism was split by type. Morphological differentiation ($t_3 = -2.450$, $P = 0.092$), length ($t_{318} = 1.664$, $P = 0.097$), and growth rate differentiation were not significant main effects ($t_3 = 1.665$, $P = 0.195$), but there was a positive interaction of morphological differentiation with length

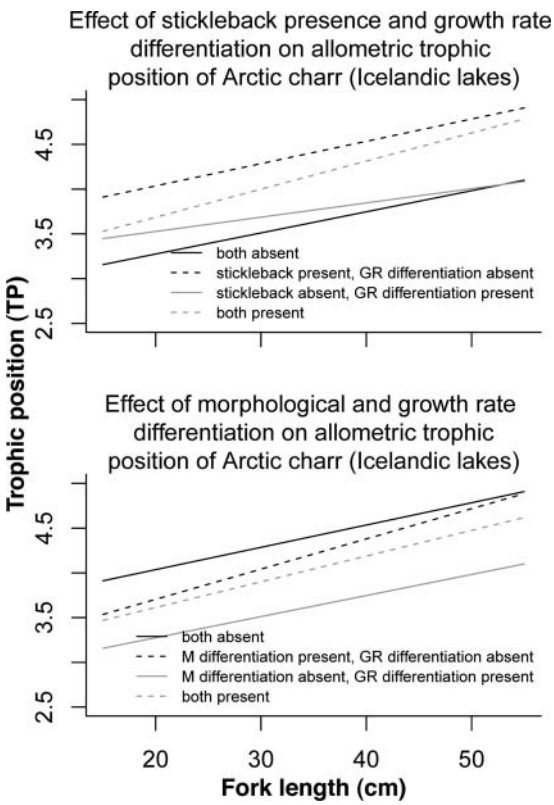

Fig. 4. Results from fitted linear mixed effects models indicate that species properties, such as Arctic charr growth rate differentiation (top and bottom) or morphological differentiation (bottom), did not have a strong effect on allometric trajectories that predict trophic position (TP) of Arctic charr from its body size, and did not interact strongly with the presence of stickleback (top). That is, the effect of the interaction was not strong, as the slopes of the lines depicted are rather similar.

($t_{341} = 3.365$, $P = 0.001$). The interaction of growth rate differentiation with length was not significant ($t_{341} = -0.425$, $P = 0.671$), but a three-way interaction among these factors and morphological differentiation was ($t_{341} = -4.638$, $P < 0.0001$). The two-way interaction between differentiation types was not significant ($t_3 = 2.606$, $P = 0.080$).

Therefore, when split by polymorphism type, polymorphism-related changes in allometric trajectories of resource use became strong (Fig. 5, bottom). In Icelandic lakes with morphological differentiation, increased benthic food consumption occurred as the fish grew, whereas lakes with growth rate differentiation between morphs showed little consistent change, and those with both types of differentiation showed instead an increased consumption of limnetic foods at larger sizes. By contrast, in Alaskan Arctic charr, BFC was not affected by length ($t_{129} = -1.484$, $P = 0.139$) or polymorphism ($t_2 = -3.779$, $P = 0.063$), but their interaction was significant ($t_{194} = 9.665$, $P < 0.0001$). However, a different trend emerged from the interaction: Lower Tazimina Lake Arctic charr, which exhibited both morphological and growth rate differentiation, tended to consume more benthic resources at larger sizes compared with their monomorphic counterparts (not shown).

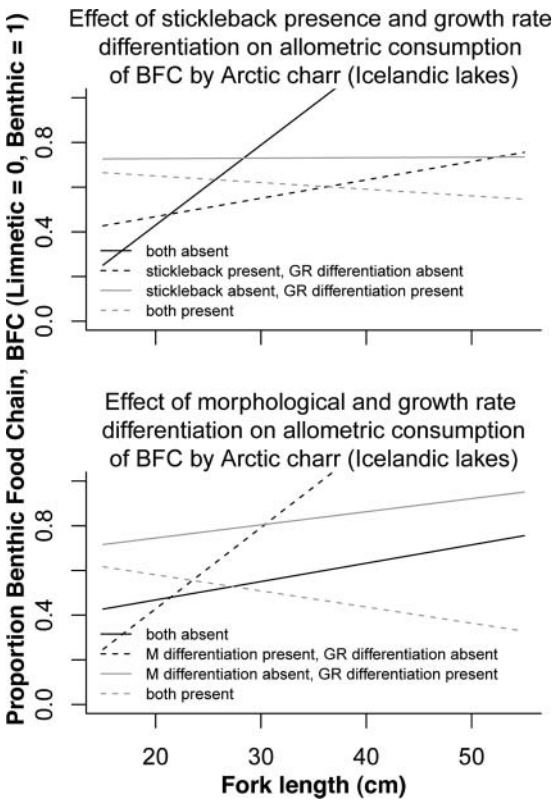

Fig. 5. Results from fitted linear mixed effects models indicate that species properties, such as Arctic charr growth rate differentiation (top and bottom) or morphological differentiation (bottom), can affect ecosystem properties by changing the allometric trajectories that predict the proportion of benthic food chain consumed (BFC) by Arctic charr from its body size and their interactions with stickleback (top). That is, the effect of the interaction was strong, as the slopes of the lines differed greatly.

Interactions of growth rate differentiation with prey availability

Trophic position

When growth rate differentiation, a type of polymorphism, and the presence of stickleback were included in a linear mixed effects model to predict Arctic charr TP (Iceland only), only an allometric increase of TP with length was detected (growth rate differentiation: $t_3 = 0.988$, $P = 0.396$; length: $t_{318} = 2.431$, $P = 0.016$; stickleback presence: $t_3 = 1.646$, $P = 0.198$; length × growth rate differentiation: $t_{318} = -0.603$, $P = 0.547$; length × stickleback presence: $t_{318} = 0.111$, $P = 0.912$; growth rate differentiation × stickleback presence: $t_3 = -1.597$, $P = 0.209$; three-way interaction: $t_{318} = 0.960$, $P = 0.338$; Fig. 4, top).

Benthic versus limnetic resource consumption

When the same model was used to predict Arctic charr BFC instead, the main effects of growth rate differentiation ($t_3 = 3.882$, $P = 0.030$) and length ($t_{341} = 5.165$, $P < 0.0001$) were

significant, but stickleback presence ($t_3 = 2.042$, $P = 0.133$) was not. However, stickleback presence had a negative interaction with length ($t_{341} = -3.214$, $P = 0.001$), as did growth rate differentiation ($t_{341} = -3.933$, $P = 0.0001$). The two-way interaction between growth rate differentiation and stickleback presence was not significant ($t_3 = -1.728$, $P = 0.182$), but the three-way interaction between these factors and length was ($t_{341} = 2.329$, $P = 0.021$). Therefore, stickleback presence and growth rate differentiation both caused a shift in allometric trend towards greater consumption of limnetic resources at larger sizes. When both were present, this effect was still present, but not as strongly as would be expected if the shifts were additive (Fig. 5, top).

DISCUSSION

As Arctic charr is the northernmost distributed fish species in fresh waters and can be anadromous, it is likely to be the first colonizer of many subarctic lakes (Klemetsen, 2010). True studies of vertebrate colonization are rare (but see Milner *et al.*, 2011), and comparing fish diversity across lakes can only partially reflect colonization, as it is confounded with other attributes of the system, such as ecosystem size and productivity (Post and Takimoto, 2007; McHugh *et al.*, 2010). However, the diversity of local responses of Arctic charr populations shown in this study can clarify the process of colonization and food web development by revealing how community ecology and evolutionary mechanisms interact to shape food web structure in species-depauperate ecosystems such as subarctic lakes. First, increased differentiation in trophic position among functional units was evident when fish communities included fish species other than Arctic charr alone, as well as generally higher trophic positions, supporting the theory that food chains increase in length with species diversity (Post and Takimoto, 2007). Results regarding trophic position indicated that the insertion of intermediate prey (stickleback) lengthened food chains at all levels of diversity, implying a need to focus beyond the apical trophic position towards intermediate trophic levels in food web studies (Post and Takimoto, 2007; McHugh *et al.*, 2010). However, the presence of an additional fish species was not associated with increased use of benthic versus limnetic resources. That is, even when Arctic charr inhabited a lake alone, they could be highly differentiated in benthic and limnetic resource use, suggesting higher functional diversity within populations. Second, Arctic charr resource use was highly dependent on resource use by others, suggesting that flexible species may consistently increase functional redundancy within food webs regardless of which other species are present, although this effect would need to be tested experimentally. In both cases, ecosystem properties (fish diversity and colonization) affected resource use by Arctic charr. In addition, the presence of polymorphism and its type affected how Arctic charr populations responded to local competitors or prey availability through allometric trends in resource use in Arctic charr. Therefore, both attributes of the ecosystem and context-specific evolutionary mechanisms for species divergence, which can be considered species or population attributes, are likely to interact in the development and stability of subarctic lake food webs.

Effects of ecosystem properties on species

Insertion of intermediate fish prey produced differentiation in resource use within Arctic charr, but not necessarily new morphs. An ontogenetic switch towards piscivory was detected in medium-to-large fish (~25–30 cm), differing slightly from other study systems

[~16 cm (L'Abée-Lund *et al.*, 1992 and Adams *et al.*, 1998); ~20 cm (Malmquist *et al.*, 1992 and Amundsen, 1994); and 35–40 cm (Hobson and Welch, 1995 and Guiguer *et al.*, 2002)]. The ecological effects of predator evolution have been considered for eco-evolutionary feedbacks (Walsh *et al.*, 2012; Howeth *et al.*, 2013; Pantel *et al.*, 2015), but the effects of intermediate prey on the predator have not been addressed, nor the propensity of a species to become a predator. Furthermore, an increase in growth rate clearly accompanies the shift towards piscivory, indicating that population dynamical effects of additional size structure within Arctic charr could likewise affect ecosystem properties (Andersson *et al.*, 2007; Bourlot *et al.*, 2014; Bassar *et al.*, 2015).

Our results regarding differentiation in benthic versus limnetic resource use were far subtler, even though polymorphism in fish is often attributed to frequency-dependent selection for benthic versus limnetic resource use (Schluter, 1996; Snorrason and Skúlason, 2004). Differences in benthic versus limnetic consumption among populations of Icelandic Arctic charr may similarly result from abiotic differences among ecosystems that control food availability (Woods *et al.*, 2012b). Some populations in which limnetic feeding declined at larger sizes (i.e. Vestara-Friðmundarvatn, Sigurðurstaðavatn, and Lower Tazimina Lake) showed an ontogenetic shift towards benthic resources that may allow for resource partitioning among size classes within Arctic charr populations (Forseth *et al.*, 1994; Byström and Andersson, 2005). However, this shift did not occur in all populations, as in lakes Galtaból and Högnavatn for example.

Differences in ontogenetic trajectories among ecosystems were also explained by the food habits of co-occurring species. In addition to becoming intermediate prey, the presence of stickleback was associated with less consumption of benthic resources at larger sizes. Lower mean consumption of benthic resources in stickleback led to greater consumption of benthic resources by small Arctic charr, suggesting that stickleback serve as a competitor to small Arctic charr. Likewise, when considering the mean proportion of benthic food consumed by large consumers (i.e. rainbow trout, Arctic grayling, brown trout), high mean benthic consumption by the competitor reduced benthic consumption by large Arctic charr.

Although transmission of a limnetic signal up the food web via piscivory can change interpretation of food web results (see Appendix), competition appears to shift allometric trends away from overlap with the competitor (Russell, 1980; Kreiner, 2006; Amundsen *et al.*, 2010; Sandlund *et al.*, 2010), especially where cohabitating with other salmonids (Langeland *et al.*, 1991; Hesthagen *et al.*, 1997; Jansen *et al.*, 2002; Power *et al.*, 2002; Forseth *et al.*, 2003; Knudsen *et al.*, 2010). Competitor diets and trophic positions also vary substantially across lakes, for example in Arctic grayling (Russell, 1980), stickleback (Jeppesen *et al.*, 2002; Jónsson, 2002; Kristjánsson *et al.*, 2002), and pygmy whitefish (Gowell *et al.*, 2012). However, the present study indicates that Arctic charr respond in a predictable manner, suggesting that Arctic charr populations readily evolve with co-occurring species (e.g. Palkovacs *et al.*, 2011; Lawrence *et al.*, 2012; Marshall *et al.*, 2012).

Effects of species properties on the ecosystem

It is clear that differences in resource use related to ecosystem properties, discussed in the previous section, are likely to cause eco-evolutionary feedbacks whereby such differences then affect ecosystem properties, for example through changes in food web structure or biogeochemical processes (Matthews *et al.*, 2011; Walsh *et al.*, 2012). However, an additional layer of complexity can be added to this one; individual properties of species themselves can exacerbate or dampen such feedbacks. Such is the case when considering resource

polymorphism as a property of the species, the expression of which depends on the local environment, such as lake depth and the presence of competitors (Woods *et al.*, 2012b), or population dynamics (e.g. Andersson *et al.*, 2007; Bourlot *et al.*, 2014). We found that the nature of Arctic charr polymorphism likewise affects allometric trends in resource use, which in turn is likely to affect food web structure. Morphological divergence was associated with a higher consumption of benthic resources while growth rate divergence showed mixed results. However, combined with either stickleback presence or morphological divergence, growth rate divergence led to increased consumption of limnetic resources by larger Arctic charr in Iceland, whereas the reverse was true of Alaska. Thus, polymorphism likely interacts with properties of the ecosystem, but the outcome varies regionally, perhaps as a result of environmental or genetic differences. Further studies could focus on how such interactions could facilitate functional redundancy or changes in food web dynamics, productivity, decomposition rates, or nutrient cycling that differ from those caused by monomorphic populations (Matthews *et al.*, 2011; Bassar *et al.*, 2012; Walsh *et al.*, 2012; El-Sabaawi *et al.*, 2015; Rudman *et al.*, 2015).

In conclusion, this study represents a rare approach of studying allometric trends to understand how ecosystem properties affect species properties and vice versa. Results demonstrate the importance of intraspecific diversity as a driver of food web structure, especially under species-depauperate conditions. Differences between Iceland and Alaska appeared to result from species interactions with Arctic charr, as well as unexplained regional differences. The apparently high functional diversity of Arctic charr may increase food web stability (Romanuk *et al.*, 2006). However, evolutionary mechanisms, such as reproductive isolation and the adaptation of traits, may have conflicting effects on ecosystem stability (Mellard and Ballantyne, 2014). Ecosystem function can be affected by the collapse of intraspecific diversity into a single morph (Rudman and Schluter, 2016). This event and shifts in allometric trends in resource use may become more frequent as global climate change increases the likelihood of successful invasion of southerly fish into northern lakes (Vincent *et al.*, 2013). Therefore, understanding the dynamics of these sensitive ecosystems is essential for conservation and management strategies.

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