

NETWORK ANALYSIS REVEALS CONTRASTING EFFECTS OF INTRASPECIFIC COMPETITION ON INDIVIDUAL VS. POPULATION DIETS

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Abstract. Optimal foraging theory predicts that individuals should become more opportunistic when intraspecific competition is high and preferred resources are scarce. This density-dependent diet shift should result in increased diet breadth for individuals as they add previously unused prey to their repertoire. As a result, the niche breadth of the population as a whole should increase. In a recent study, R. Svanbäck and D. I. Bolnick confirmed that intraspecific competition led to increased population diet breadth in threespine stickleback (*Gasterosteus aculeatus*). However, individual diet breadth did not expand as resource levels declined. Here, we present a new method based on complex network theory that moves beyond a simple measure of diet breadth, and we use the method to reexamine the stickleback experiment. This method reveals that the population as a whole added new types of prey as stickleback density was increased. However, whereas foraging theory predicts that niche expansion is achieved by individuals accepting new prey in addition to previously preferred prey, we found that a subset of individuals ceased to use their previously preferred prey, even though other members of their population continued to specialize on the original prey types. As a result, populations were subdivided into groups of ecologically similar individuals, with diet variation among groups reflecting phenotype-dependent changes in foraging behavior as prey density declined. These results are consistent with foraging theory if we assume that quantitative trait variation among consumers affects prey preferences, and if cognitive constraints prevent individuals from continuing to use their formerly preferred prey while adding new prey.

Key words: clustering; complex networks; *Gasterosteus aculeatus*; individual specialization; intraspecific competition; niche variation; optimal foraging theory; resource polymorphism; threespine stickleback.

INTRODUCTION

Optimal foraging theory (OFT) has long been used to understand and predict prey choice and patch use in animal populations (Stephens and Krebs 1986). One of the key predictions of classical OFT is that when resources are abundant, foragers should concentrate on a few most-preferred prey and have narrow food niches. As these preferred prey become scarce, lower-value prey types are added to the diet and individuals should become more opportunistic (MacArthur and

Pianka 1966, Schoener 1971, Pulliam 1974). For example, the bluegill sunfish, *Lepomis macrochirus*, is highly size selective when prey are abundant, but eats prey as encountered when resources become depleted (Werner and Hall 1974). Intraspecific competition is thus expected to increase individual niche breadth by reducing the availability of preferred prey (Svanbäck and Bolnick 2005), which will ultimately lead to the population's niche expanding as well. Therefore, according to OFT, intraspecific competition is expected to increase both population and individual niche breadth.

Most models of optimal foraging implicitly assume that conspecific individuals are ecologically equivalent, having the same rank preferences for prey (Stephens and Krebs 1986). One implication of this assumption is that regardless of individual and population niche breadths,

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no among-individual variation in diet is expected. However, variation in morphological or behavioral traits can lead to among-individual variation in search efficiencies, handling times, and thus rank preferences for alternate prey (Bolnick et al. 2003). Among-individual differences in foraging efficiencies for alternate prey may reflect functional trade-offs linked to phenotypic variation. For example, it has been shown within fish species that streamlined individuals have higher foraging efficiencies on zooplankton in open water compared to deeper-bodied fish. In the structurally more complex littoral zone, on the other hand, the deeper-bodied individuals have a higher foraging efficiency (Ehlinger 1990, Schluter 1995, Robinson 2000, Svanbäck and Eklöv 2003). As a result of these trade-offs, one consumer may rank prey according to their energy per unit handling time in one order, $e_1/t_1 > e_2/t_2 > e_3/t_3$, and a second individual with a different phenotype might rank prey in a different order, $e_3/t_3 > e_2/t_2 > e_1/t_1$. Another possibility is that rank orders are the same, but some individuals might be less willing to add lower-ranked prey, $e_1/t_1 \gg e_2/t_2 \gg e_3/t_3$. Finally, both foragers may prefer prey type 1, but resort to different secondary prey, for instance if $e_1/t_1 > e_2/t_2 > e_3/t_3$ for one consumer and $e_1/t_1 > e_3/t_3 > e_2/t_2$ for another (Robinson and Wilson 1998, Svanbäck and Bolnick 2005). In each of these cases, competition leads to increased individual niche width. On the other hand, population niche breadth changes little in the first scenario (divergent preference model), and increases with competition in the second and third models (shared preferences and refuge models, respectively). The degree of among-individual variation will also tend to change due to intraspecific competition. Depending on whether individual niches expand faster or slower than the population niche, diet variation may increase or decrease as prey become scarce. For instance, in the first scenario (divergent preferences), diet variation will tend to decline, whereas in the latter two models diet variation may increase as individual niche width expands (Svanbäck and Bolnick 2005). These “pure” models, however, are not mutually exclusive and can, in principle, occur in a mixed situation in natural populations.

In a recent experiment, Svanbäck and Bolnick (2007) found that intraspecific competition led to broader population niches in threespine stickleback (*Gasterosteus aculeatus*), in accordance with OFT predictions. Interestingly, this population niche expansion was achieved via increased between-individual variation, rather than increased individual niche breadth; individual niche breadth did not differ significantly between low- and high-competition treatments, indicating that individuals do not simply add novel resources to their diets when competition is high. Because Svanbäck and Bolnick (2007) focused on testing whether competition increased niche variation among individuals, they did not address the apparent contradiction between foraging theory and their observation that individual niche

breadth remained constant. One possible explanation is that the top-ranked prey was so scarce in the high-density treatment that it no longer showed up in stomachs, although individuals would still accept it (Svanbäck and Bolnick 2007). Another possibility is that only a subset of the individuals underwent niche shifts, but when shifting to novel prey they dropped the top-ranked prey from their diets. Such a behavior would be indicative of cognitive constraints preventing individuals from exploiting different resources at the same time (Werner et al. 1981, Persson 1985).

In this paper, we reanalyze the stickleback experiment, using a new method based on complex network theory that identifies the specific patterns of prey use by individuals. Our goal is to resolve the contrast between Svanbäck and Bolnick’s (2007) results and the predictions of OFT. Our method allowed us to evaluate how competition led the stickleback population to become more generalized when individual niches remained relatively constrained. We did this by determining (1) what the top-ranked resource is and what resources are added by the population due to competition, (2) whether the top-ranked resource is still consumed by the population when competition is high, (3) whether all individuals underwent niche shifts or just a subset of individuals, (4) and whether such subsets are morphologically distinct from individuals that continued to use the original prey spectrum. We contrast these patterns with basic predictions of OFT, and propose a simple resolution.

MATERIALS AND METHODS

Data collection

The data used in the present study come from an experiment conducted in June 2005 in Blackwater Lake on northern Vancouver Island, British Columbia (Svanbäck and Bolnick 2007). We give only a brief description of the data collection procedures and refer readers to Svanbäck and Bolnick (2007) for further details. Five pairs of 9-m² enclosures made of 1.6-mm seine net were built in ~2 m deep water, and stocked with wild-caught stickleback to generate paired low-density (hereafter LD) and high-density (HD) treatments (either 30 or 90 fish per enclosure; see Plate 1). These densities fall within natural densities of threespine stickleback populations (Wootton et al. 2005). After 14 days, stickleback were trapped, anesthetized, and preserved in formalin. Stickleback were also sampled from outside each enclosure pair to serve as a natural baseline, and these samples are hereafter referred to as “controls.” Surveys by a snorkeler in Blackwater Lake in June 2007 suggest that the LD treatment is roughly similar to ambient densities (D. I. Bolnick, *unpublished data*). Comparisons of prey densities, stomach content mass, and fish growth rates confirmed that LD enclosures reflected current levels of intraspecific competition, and HD represented elevated competition (Svanbäck and Bolnick 2007). Stomach contents were identified to the lowest feasible taxonomic level.



PLATE 1. A block of four 10-m² net enclosures from an experiment in June 2007, in Blackwater Lake, British Columbia. The data described in this paper are from a June 2005 experiment with only two enclosures per block; however, the site pictured here was used for one of the blocks of enclosures in the June 2005 experiment. Photo credit: D. I. Bolnick.

Stomach contents provide a cross-sectional measure of an individual's diet, which may be biased if the forager is sampling from patchy prey, or if the stomach can only hold a few diet items at a time. However, stickleback guts usually contain many items (mean = 15 diet items, range = 1–300 items, as observed in the present study), and the small scale of the enclosures ensured that all individuals were capable of encountering all available prey in much less time than it takes to digest them (more than six hours). Consequently, the spatial scale makes it unlikely that the observed diet variation is the result of patchy resources or stochastic variation. In addition, significant correlations between stickleback morphology, stable isotopes (which integrate a consumer's diet over relatively long time scales), and diet suggest that diet variation is not due to stochastic sampling effects and can be a good guide to long-term differences in resource use (Bolnick et al., *in press*). We therefore analyzed patterns of prey use by individuals within each enclosure, using methods outlined below.

To test for associations between morphology and diet, four linear measurements were taken from the fish: body length, mouth width, mouth height, and gill raker length (all in millimeters). In addition, the fish were photographed, and 23 homologous landmarks were digitized on the left side of each fish, and used in the program TpsRelw (Rohlf 2005) to convert the landmarks to partial warps.

Data analyses

Measuring the degree of clustering.—If individuals within a population differ in their diet preferences they might be organized into discrete groups specialized on distinct sets of resources. For example, stickleback populations may be formed by a pelagic and a littoral group, so that individuals belonging to the same group greatly overlap in resource use with each other, and at the same time have negligible overlap with individuals in the other group. Such an organization is closely related to an important concept of complex network theory, namely, network clustering (Watts and Strogatz 1998). Therefore, the available metrics of the degree of clustering of networks can be a useful tool in describing intrapopulation patterns of resource use. However, before we could apply network theory to study intrapopulation resource use, we needed to develop a framework linking the two. We accomplished this by developing what we call the “individual niche overlap network” (see Appendix A), in which the elements of the network (nodes) represent individuals, and the edges connecting individuals measure the diet overlap among pairs of individuals (Fig. 1). Weights varying from zero to 1 ($0 \leq w_{ij} \leq 1$) can be associated to each edge as a measure of the pairwise diet overlap between individuals i and j , zero indicating no diet overlap and 1 indicating total overlap. The degree of diet variation in the

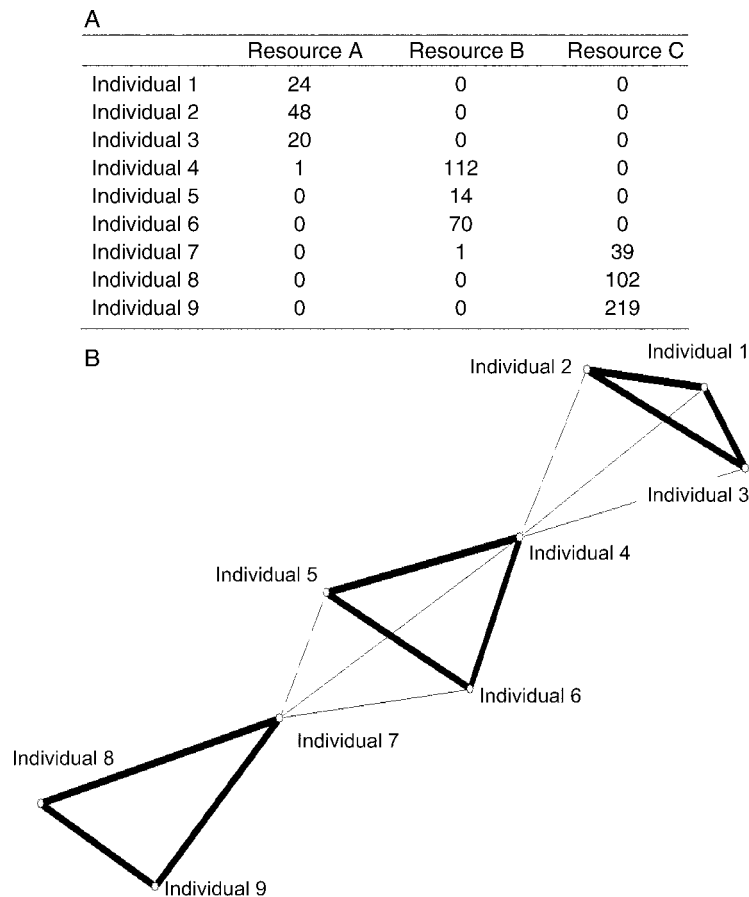


FIG. 1. The use of resources by different individuals of a hypothetical population described as (A) a matrix and (B) a network. The numbers in the Resource columns represent prey items. The widths of links in (B) are proportional to the degree of pairwise overlap between individuals (w_{ij}). The variable w_{ij} is the degree of pairwise diet overlap between individuals i and j , varying from 0 (no overlap) to 1 (total overlap). Absence of an edge between two individuals indicates no diet overlap ($w_{ij} = 0$). This network approach allows the description of previously unexplored, intrapopulation structures, such as clusters (see *Materials and methods: Data analyses: Measuring the degree of clustering* for details). For example, the depicted hypothetical population has three clusters formed by individuals 1-2-3, 4-5-6, and 7-8-9.

population can be quantified as $E = 1 - \bar{w}_{ij}$ (see Appendix A for details).

In a diet network, for a given level of diet variation (E), links may be arranged randomly among individuals, or may be organized into highly connected subgroups (clusters) that are weakly connected to each other (Fig. 1B). When analyzing diet data, clustering will occur when the population is organized into discrete groups of individuals sharing a common subset of resources and overlapping little with other such groups. Clustering also implies that there are few dietary opportunists. Based on classical foraging theory, we would not expect that intraspecific competition would increase clustering. Instead, as individuals add new resources to their diets, similarity among existing clusters should increase or stay roughly the same.

It is possible to quantify the degree of clustering of a network with clustering coefficients, which compare the overall density of connections in the network to the

density of connections around individual nodes (Watts and Strogatz 1998). We propose measuring diet clustering with the weighted clustering coefficient C_{ws} (see Appendix A). In a totally random network $C_{ws} \sim 0$, whereas C_{ws} will be positive and tend to +1 if the population is organized into clusters (Fig. 1B; the local density of connections is higher than the overall density of connections). Note that these clusters do not mean that individuals are clustered in space, but rather that individuals in the same cluster use the same subset of resources. C_{ws} can also be negative and will tend to -1 if individuals' diets are overdispersed (the local density of connections is lower than the overall density of connections in the network), indicating that each individual uses a unique combination of resources. Positive values of C_{ws} would represent discrete diet variation commonly referred to as "discrete resource polymorphism" (Skúlason and Smith 1995, Smith and Skúlason 1996), whereas negative values of C_{ws} would

represent more continuous diet variation (Bolnick et al. 2003).

In order to test the null hypothesis that $C_{ws} = 0$, a null model approach can be used to test the significance of this index. We used a bootstrap procedure in which each individual was reassigned the same number of prey items that it was observed eating, drawn randomly from the population diet distribution via multinomial sampling (Bolnick et al. 2002). Calculating C_{ws} for each resampled population (we used 10 000 iterations), the null hypothesis can be rejected if $C_{ws} > 0$ and higher than 97.5% of the null C_{ws} values, or if $C_{ws} < 0$ and C_{ws} is lower than 97.5% of the null C_{ws} values. In the former case there is significant evidence of clustering, whereas in the latter there is significant evidence of overdispersion. We calculated E and C_{ws} for the control sample, and for fish from within each enclosure. We used two-tailed, one-sample t tests to contrast the LD and HD treatments against the control and two-tailed paired t tests to contrast the LD and HD treatments. We developed a program in C, DIETA1 (see Supplement), to calculate E and C_{ws} and to perform Monte Carlo simulations.

Assigning individuals to discrete groups.—After detecting significant clustering, we determined individuals' memberships to clusters. This allowed us to identify the specific prey associated with clusters, and to test whether clusters were morphologically distinct. In the complex network literature, clusters have been defined in several different ways (e.g., *cliques*, *k-cores*, *k-plexes* [Wasserman et al. 1994]). Unfortunately, methods for defining clusters often rely on presence/absence of connections, rather than the weights of connections. As a result, very weak diet overlap between two individuals (low w_{ij}) would be treated as equivalent to high diet overlap (high w_{ij}) when assigning individuals to clusters. To overcome this drawback, we adopted an approach that has been widely used and relies on the definition of a cutoff value that defines strong edges in a given network (e.g., Costa 2004). We defined a strong edge as one whose w_{ij} is higher than the population average pairwise overlap (see Appendix A).

The simplest concept of a cluster is the *clique*, which is defined as a group of nodes in which all nodes are connected to each other. We defined a *w-clique* as a clique in which nodes are interconnected by "strong edges." We note that only a subset of the nodes are assigned to *w-cliques*, because there are nodes that cannot be unambiguously assigned to any given *w-clique* or do not meet the criterion of being connected to all the nodes comprising any given *w-clique*. Following the identification of *w-cliques*, we determined the dominant prey taxa that characterized each clique and compared the morphology among *w-clique* members.

We used DIETA1 to generate weighted and binary matrices that can be imported into commonly used programs of network analyses that draw networks and identify cliques. We used the program Pajek (Batagelj

and Mrvar 1998; *available online* for free download)⁹ to draw networks and to assign individuals to *w-cliques* in all enclosures and for all control fish. We determined the number of clusters in the control sample and each LD and HD enclosure, and also determined the functional group of prey associated with each cluster (benthic cladocerans, littoral macroinvertebrates, chironomids, pelagic cladocerans, pelagic macroinvertebrates). This allowed us to test whether the number of clusters varied between density treatments, and to identify specifically which prey were added or lost as clustering changed. We were thus able to evaluate the prediction that in variable populations clustering should decrease or should not change with competition.

Morphological analyses.—Having observed significant clustering within a given sample, we are forced to ask why individuals with access to a common set of prey would choose to consume different subsets of this prey distribution. As outlined in the *Introduction*, one possibility is that morphological variation leads to divergent prey preferences. Having identified the *w-cliques*, we tested whether the members of the different *w-cliques* were morphologically distinguishable. For the sake of statistical power, we pooled the data of all enclosures according to treatment, so that we ended up with three data sets: control, low density, and high density. Within each data set, we assigned individuals to diet clusters and then compared the morphology among the diet clusters. We used two types of morphological variables: linear distance measures and geometric shape variables. Geometric shape variables (partial warps [Bookstein 1991]) were derived from morphological landmarks archived as two-dimensional Cartesian coordinates. To test whether diet clusters are morphologically divergent subsets of the population, we applied a canonical variates analysis for linear distances, size-standardized linear distances (residuals on body length), and landmark data. We constructed 95% confidence regions around centroids for canonical axes in Matlab (MathWorks 1999) using parametric bootstrap (Ringrose 1996, Von Zuben et al. 1998). Body form changes were visualized as deformations by using the program TpsRegr (Rohlf 2000).

RESULTS

Patterns of resource use

We found high degrees of significant clustering in the control sample and in all enclosures (all $C_{ws} > +0.26$; all $P < 0.001$) with the exception of one LD enclosure ($C_{ws} = 0.0194$; $P = 0.2029$; Table 1). In the LD treatment, average clustering ($C_{ws} = +0.308$) did not differ from the control ($C_{ws} = +0.2912$; $t_4 = 0.209$; $P = 0.844$), whereas it was significantly higher in HD enclosures ($C_{ws} = +0.466$) than the control ($t_4 = 3.073$; $P = 0.037$; Table 1). In four of five enclosure pairs the HD enclosures exhibited more

⁹ (<http://vlado.fmf.uni-lj.si/pub/networks/pajek/>)

TABLE 1. The C_{ws} measure of clustering in the control, low-density (LD), and high-density (HD) treatments in a population of threespine stickleback, *Gasterosteus aculeatus*.

Treatment	Pair	Enclosure no.	N	C_{ws}^\dagger	P
LD	A	1	12	0.0194	0.2029
HD	A	2	49	0.3218	<0.001
LD	B	4	22	0.4163	<0.001
HD	B	3	39	0.3496	<0.001
LD	C	6	21	0.4554	<0.001
HD	C	5	44	0.5875	<0.001
LD	D	7	16	0.3778	<0.001
HD	D	8	48	0.4799	<0.001
LD	E	9	23	0.2692	<0.001
HD	E	10	45	0.5888	<0.001
Control	...	wild-caught	52	0.2912	<0.001

Notes: N = sample size, the number of stickleback recaptured at the end of the experiment that had any food in their guts. P values were estimated with Monte Carlo bootstraps (10 000 replicates).

† The clustering coefficient C_{ws} compares the density of connections around individual nodes with the overall network density of connections and varies from -1 to $+1$. Negative values indicate continuous diet variation, whereas positive values indicate discrete diet variation.

clustering than their LD counterparts (Table 1) and the HD enclosures exhibited marginally more clustering than their LD counterparts ($t_4 = -2.219$; $P = 0.09$). Note that because clustering is independent of the degree of diet variation (see Appendix A), these results extend rather than replicate the findings by Svanbäck and Bolnick (2007) that among-individual variation was higher in HD treatments. Using our network-based

measure of diet variation, E , we also found that the degree of diet variation was higher in HD than LD (see Appendix A).

The tendency toward higher clustering in the HD treatment was confirmed by visual inspection of the niche overlap networks. For the sake of brevity, we only show the networks for one pair of enclosures (Table 1: pair C) to illustrate this trend (Fig. 2), relegating the

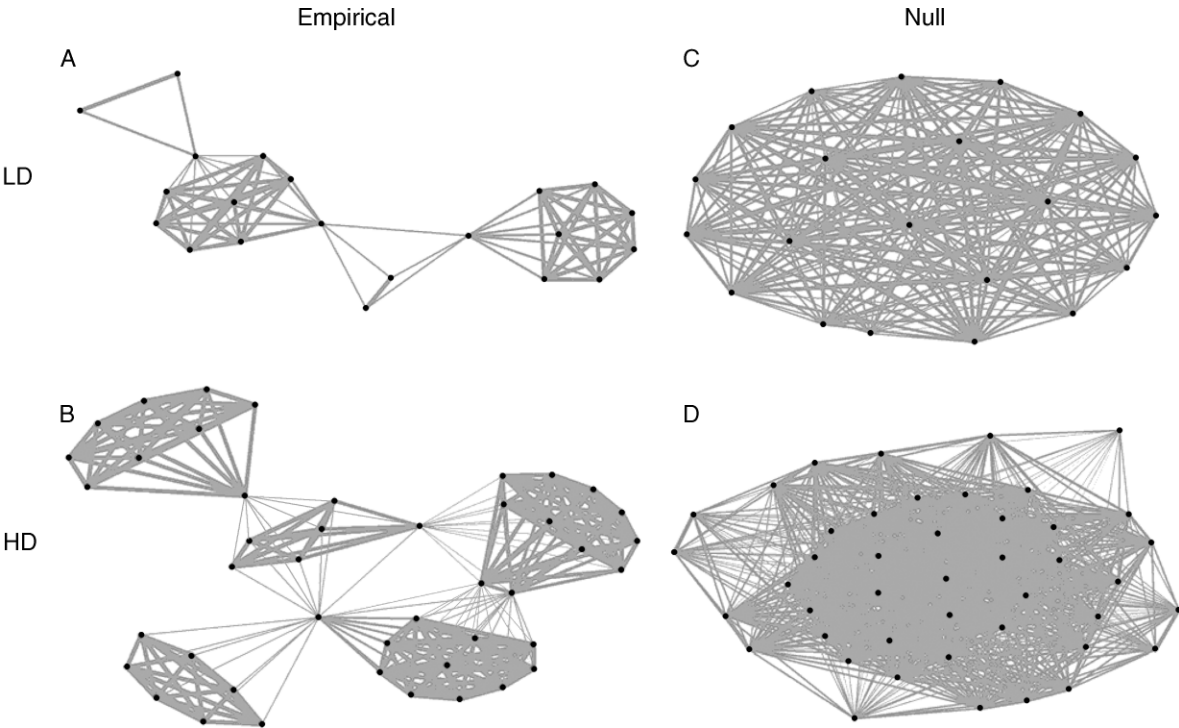


FIG. 2. Weighted networks representing the pair C of enclosures (Table 2). (A, B) Empirical networks of the low-density (LD) and high-density (HD) enclosures, respectively. (C, D) Null networks corresponding to the median C_{ws} value of a null distribution of 10 000 C_{ws} values generated by a Monte Carlo procedure. Note that the empirical networks are strikingly more clustered than their null counterparts. Individuals are connected if they consumed resources in common. The strength of the edges is a measure of the degree of pairwise niche overlap among individuals.

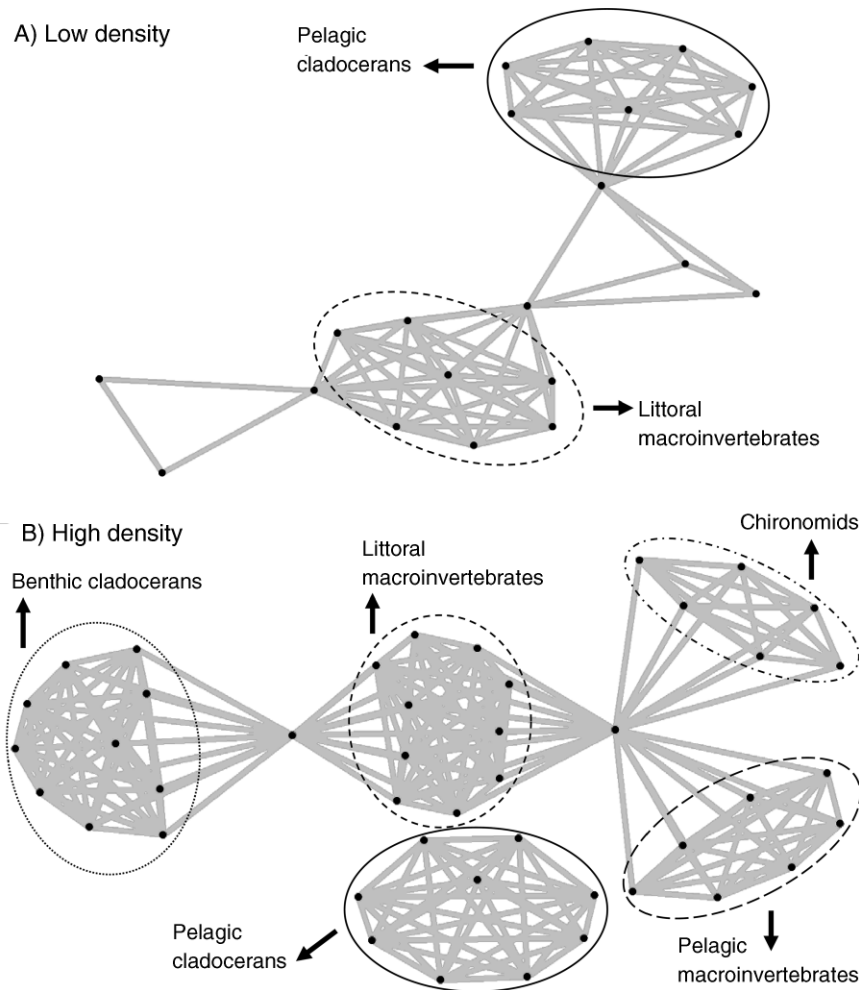


FIG. 3. Binary networks of strong connections extracted from the networks depicted in Fig. 2, showing their w -cliques (a group in which all individuals are connected to each other) and the resources consumed by each w -clique. The different line types surround different w -cliques and show the correspondence between the two cliques common to A and B. The prey type consumed by one w -clique was not consumed by another w -clique in the same network. (A) Low-density enclosure showing two w -cliques. (B) High-density enclosure showing five w -cliques. A higher number of w -cliques in the high-density treatment was a general trend among enclosure pairs (see Appendix B).

other networks to an online appendix. The contrast between LD and HD illustrated in Fig. 2 is mirrored across all HD/LD pairs (see Appendix B). Visual inspection of the networks (Fig. 2A, B) shows that increased clustering was achieved by the formation of new dietary clusters. The empirical networks in both LD and HD treatments (Fig. 2A, B) were strikingly more clustered than their null counterparts, in which individuals sample randomly from the population diet (Fig. 2C, D, respectively).

Most, but not all, individuals in a network were assigned to w -cliques (Fig. 3, Table 2). With the exceptions of enclosures 6 and 7, the percentage of individuals assigned to w -cliques was always higher than 70% (Table 2). The number of w -cliques varied from two to five (Table 2) and was consistently larger in the HD than in the LD treatments (paired t test: $t_4 = 5.880$; $P =$

0.004). For example, in enclosure pair C, we found two w -cliques in the LD enclosure and five w -cliques in the HD enclosure (Fig. 3). LD enclosures generally contained two or three w -cliques, most often with one w -clique using littoral macroinvertebrates and another using pelagic cladocerans (Fig. 3A, Table 2). We therefore conclude that these two resource types represent the basic menu for stickleback when resources are relatively abundant. Notably, this benthic/limnetic partitioning occurred even within 9-m² enclosures in 2 m deep water. In the HD enclosures, however, a subset of individuals resorted to novel resources, forming additional w -cliques that select pelagic macroinvertebrates, chironomids, and benthic cladocerans (Fig. 3B). We stress that these groups occur repeatably across replicate enclosures (Table 2), and are not a result of between-enclosure variation. Moreover, the appearance of novel

TABLE 2. The percentage of nodes that were assigned to *w*-cliques, the number of identified *w*-cliques, and the number of nodes assigned to each *w*-clique in the control, low-density (LD), and high-density (HD) treatments in a population of threespine stickleback, *Gasterosteus aculeatus*.

Treatment	Pair	Enclosure no.	% of nodes in <i>w</i> -cliques	No. <i>w</i> -cliques	No. nodes within <i>w</i> -cliques†				
					LM	PC	PM	Ch	BC
LD	A	1	92	2	6			5	
HD	A	2	84	4	10	14		6	11
LD	B	4	73	2	10	6			
HD	B	3	82	3	12	11			9
LD	C	6	48	2	7	3			
HD	C	5	95	5	10	9	7	6	10
LD	D	7	69	2	8	3			
HD	D	8	82	5	11	7	8	7	8
LD	E	9	75	3	10	5		3	
HD	E	10	93	5	11	6	6	7	12
Control	...	wild-caught	77	3	21	15	4		

Notes: The *w*-cliques (groups in which all individuals are connected to each other by strong connections) were classified according to diet: LM (littoral macroinvertebrates); PC (pelagic cladocerans); PM (pelagic macroinvertebrates); Ch (chironomids); and BC (benthic cladocerans).

† Empty cells indicate that no *w*-cliques were associated with a given food resource.

w-cliques in the HD treatment is not an artifact of larger sample sizes, since there were proportionately more individuals consuming the alternative resources in the HD than in the LD treatment in all pairs of enclosures (Fisher's exact test; all $P \leq 0.039$). We conclude that increased clustering was achieved by the addition of novel diet items to the population diet, rather than the partition of the existing diet items. This is consistent with the finding that population niche breadth increased in HD (Svanbäck and Bolnick 2007), but allows us to identify which prey were added, and which individuals performed this diet shift. Moreover, the appearance of novel clusters at high density is in direct conflict with classical foraging theory because individuals in these HD-only clusters have switched to a new prey type and ceased to use their original prey.

Morphology vs. diet

The morphological distribution in Blackwater Lake stickleback was unimodal, with no indication of discontinuities that would indicate a priori discrete resource polymorphisms (Fig. 4). In addition, Svanbäck and Bolnick (2007) found that morphological variances were similar in control, LD, and HD samples. They therefore posited that the increased diet variation (within a two-week experiment) was due to shifts in foraging behavior rather than morphology. In this study, our post hoc analysis of *w*-cliques revealed previously unsuspected diet-morphology associations. In the control sample, the analyses of linear measurements showed a clear separation between individuals feeding on benthic and on pelagic prey (Fig. 5A). As expected, the pelagic feeders were smaller and had smaller mouths and longer gill rakers compared to the benthic feeders (Fig. 5B). We found a similar pattern in both LD and HD treatments (Fig. 5C–F), but in the latter there was a finer resolution among *w*-cliques,

especially those with “pelagic” morphology (Fig. 5E, F). The same pattern held in the analyses using the size-standardized linear data, which are not shown. The finer resolution between groups at HD is consistent with the finding by Svanbäck and Bolnick (2007) that the correlation between diet and morphology was stronger in HD enclosures.

In the analyses involving the partial warps of geometric shape, we ran into singular matrices when analyzing the control and LD data sets. For this reason, we present only the results for the HD treatment. We found substantial differentiation between the groups of individuals feeding on different prey. As can be seen from the deformation grids (Fig. 6), individuals consuming cladocerans and pelagic macroinvertebrates were more slender and had more pointed snouts, whereas individuals consuming littoral prey had deeper bodies and blunter snouts (Fig. 6). Notably, we found subtle shape differences among *w*-cliques within both the littoral and the pelagic environments.

DISCUSSION

Populations of threespine stickleback became more opportunistic in response to increased intraspecific competition and reduced prey availability. Because morphological variance was equal in high- and low-density treatments (Svanbäck and Bolnick 2007), this diet variation reflects behavioral changes rather than increased morphological variation. Here, we show that the population niche expansion occurred because at high density, some individuals switched to form novel dietary groups using prey that were rarely used at low stickleback density. This was previously interpreted as a behavioral niche shift, consistent with classical optimal foraging theory (OFT). However, we find that individuals in the new dietary clusters ceased to use prey from previously dominant clusters. Dropping formerly pre-

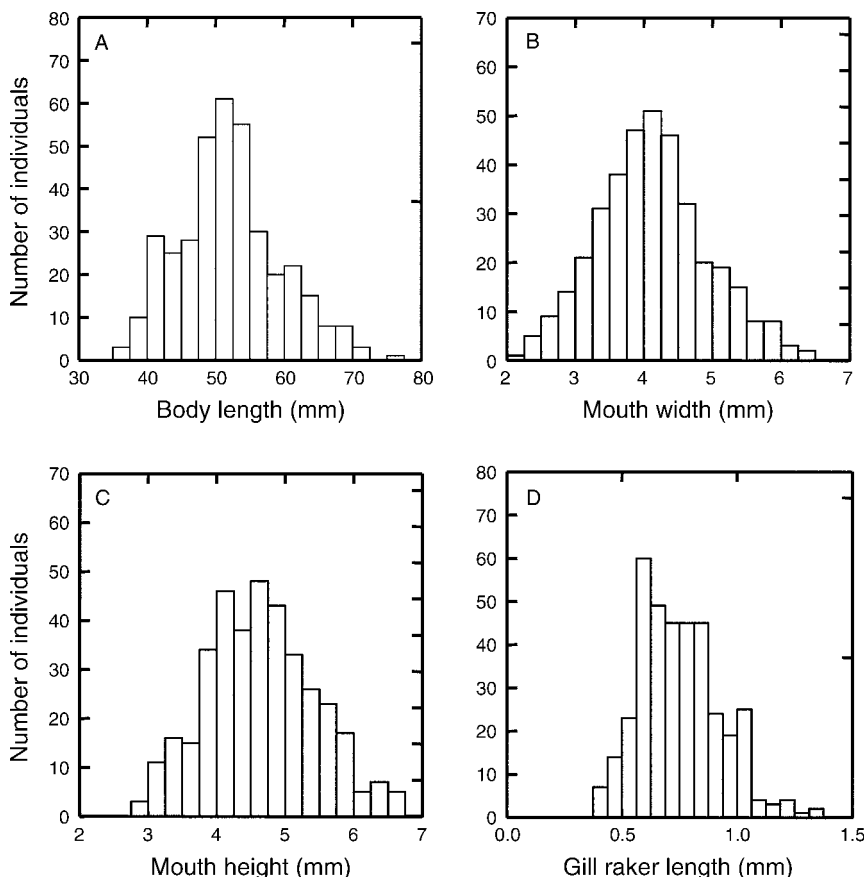


FIG. 4. Frequency distributions of linear measurements ($N = 370$ fish) for four morphological variables of a population of threespine stickleback, *Gasterosteus aculeatus*, in Blackwater Lake, on northern Vancouver Island, British Columbia. Morphological variables are (A) body length, (B) mouth width, (C) mouth height, and (D) gill raker length. Note that the morphological distribution is unimodal with respect to all four variables, allowing no a priori identification of discrete groups.

ferred prey is not consistent with foraging theory. Furthermore, our finding that these dietary clusters are morphologically distinct implies that the behavioral niche expansion is conditional on morphological variation.

Optimal foraging theory

In the present study, we found that stickleback show a complex pattern of foraging that conforms to more than one model of optimal foraging (Svanbäck and Bolnick 2005). On the one hand, the finding of two major morphologically differentiated diet clusters, one consuming littoral macroinvertebrates and the other pelagic cladocerans, among the wild-caught fish and in the LD enclosures indicates that phenotypically different stickleback have distinct diet preferences, in accordance with the distinct preferences model. Nevertheless, within those clusters individuals resort to different secondary prey when competition is high, in accordance with the competitive refuge model (Robinson and Wilson 1998, Svanbäck and Bolnick 2005). We therefore posit that stickleback represent a mixture of the models of diet variation outlined in Svanbäck and Bolnick (2005). An

important discrepancy with classical optimal foraging theory, however, was observed: at high competition some individuals virtually abandoned their previously preferred resources, completely switching to their secondary prey instead of simply adding the novel prey to their diets. Consequently, individual niche breadth did not change (Svanbäck and Bolnick 2007). Svanbäck and Bolnick attributed this constant individual niche width to a sampling artifact, namely, that when preferred prey become very scarce they do not show up in stomach contents even when the individual would accept the preferred prey. However, the present analysis shows that the original dietary clusters did not disappear at high competition, so preferred prey did not become so scarce as to disappear from individuals' diets.

A few other studies have documented similar switching from formerly preferred prey to focus on new prey. For example, in bumble bees the population as a whole became more opportunistic during strong competition, but individuals remained selective (Heinrich 1979). Selectivity resulted from the increased handling abilities of individuals on flower types after repeatedly handling them, so that individuals "majored" on different flower

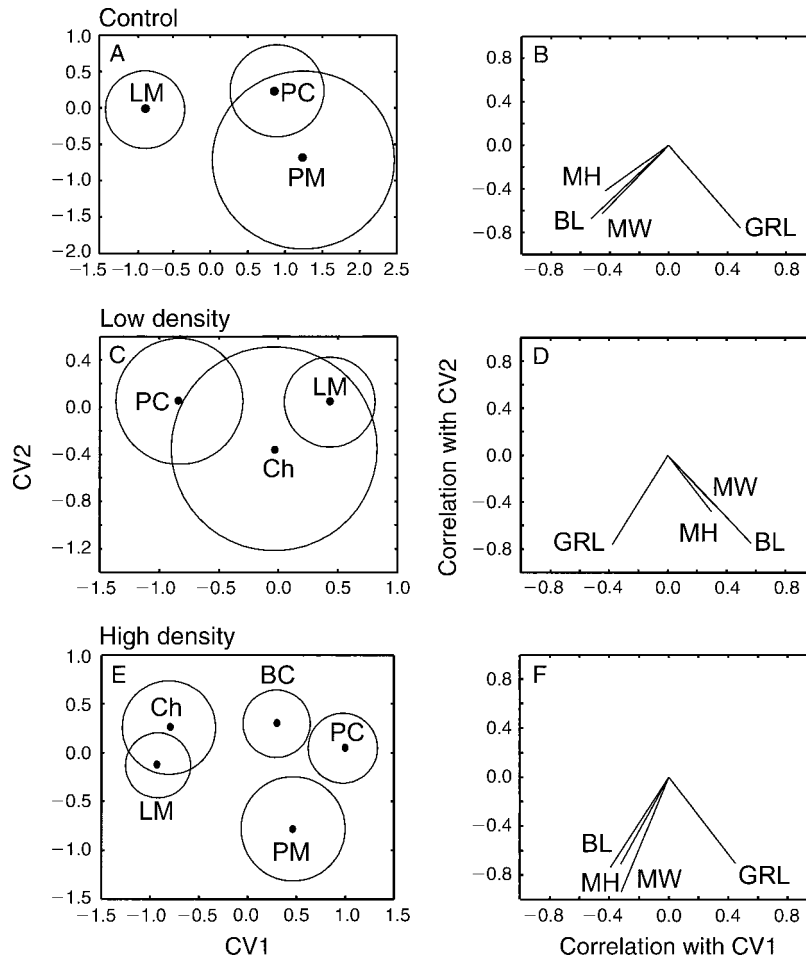


FIG. 5. Morphological variation among diet groups within control, low-, and high-density treatments, based on four linear measurements. (A, C, E) Bivariate plot of centroids (denoted as solid dots) and 95% confidence regions for canonical variates 1 and 2 (CV1 and CV2, respectively) derived from linear measurements. (B, D, F) Vectors portraying the principal directions of variation (estimated as Pearson correlation coefficients) in linear measurements in the plane of the first two canonical variates. Diet groups were: littoral macroinvertebrates (LM), pelagic cladocerans (PC), pelagic macroinvertebrates (PM), chironomids (Ch), and benthic cladocerans (BC). Linear measurements were: body length (BL), mouth height (MH), mouth width (MW), and gill raker length (GRL). Confidence regions were derived from parametric bootstrapping. No overlap of confidence regions indicates significant morphological differences. Percentage of variance explained by CV1 and CV2, respectively: (A) 92.28% and 7.72%; (C) 95.22% and 4.78%; (E) 83.65% and 14.23%.

species (Heinrich 1979). Similarly, in an experiment with feral pigeons, *Columba livia*, individuals had preference for the same type of seed. A subset of individuals nevertheless switched to prefer different types of seeds when competition reached a certain threshold and ignored previously preferred resources (Inman et al. 1987). We conclude that intraspecific competition may lead to population niche expansion, as expected under OFT, but that in some cases unknown additional factors constrain individual niche widths, in conflict with OFT.

According to OFT an individual should always attack its most-favored prey when encountered, as this high-value resource imposes no opportunity cost (Stephens and Krebs 1986). Our observations raise the intriguing question of what factor prevents an individual from using a most-favored resource when it resorts to novel

prey. Because our experimental enclosures were small, microhabitats were not spatially isolated. Consequently, the observed diet switches cannot simply be attributed to habitat switches (e.g., from open water to vegetation), as observed, for example, in the bluegill sunfish, *Lepomis macrochirus* (Werner et al. 1983). Instead, we posit that our results can be reconciled with OFT by relaxing the standard assumption that rank preferences are fixed. If resource use requires learned search images and/or capture or handling skills, individuals switching to new resources may lose their ability to efficiently use past top-ranked resources (Werner et al. 1981, Lewis 1986, Werner and Sherry 1987, Ehlinger 1990). Such cognitive constraints have previously been demonstrated in the Eurasian perch, *Perca fluviatilis* (Persson 1985). Perch become more efficient at capturing chironomids with

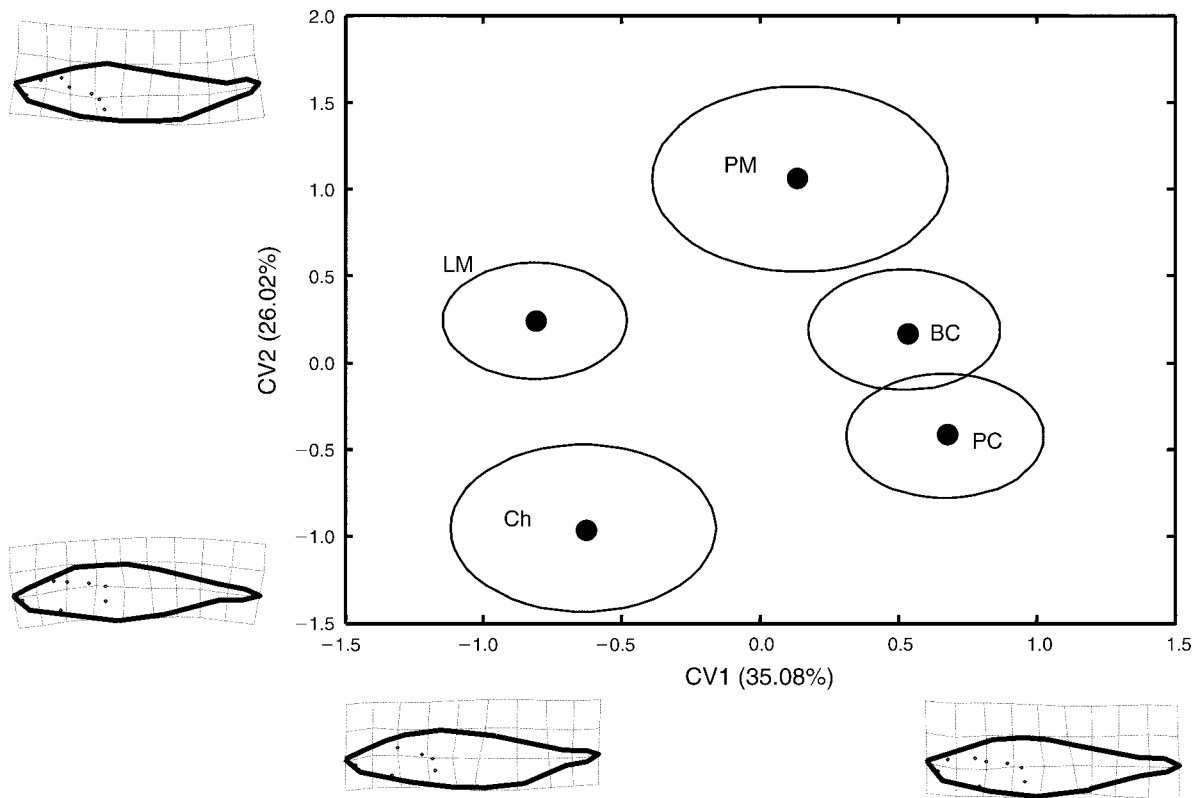


FIG. 6. Bivariate plot of centroids (denoted as solid dots) and 95% confidence regions for canonical variates 1 and 2 (and percentage of variance explained) derived from a canonical variates analysis of partial warp scores of coordinate landmark data. The deformation grid plots below and to the left of the graph are estimated changes in body shape implied by the first and second canonical variates for positive and negative deviations from the mean shape (consensus). Confidence regions were derived from parametric bootstrapping. No overlap of confidence regions indicates significant morphological differences. The deformation grid plots were exaggerated (3 \times) to make the visualization easier.

repeated exposure, but this capture success is reduced when individuals are also exposed to an alternative prey. If these learning trade-offs also occur in stickleback, individuals that switch to novel prey might lose the ability to efficiently handle formerly preferred prey. The resulting changes in rank preferences could explain, for example, why some stickleback in our study abandoned littoral macroinvertebrates (a most-favored prey at low density) when using chironomids (a secondary prey). Finally, it has been shown that limited attention may constrain an animal's ability to feed and simultaneously attend predators (Dukas 2002). If stickleback have such attention constraints, predator avoidance might further limit an individual's ability to feed on more than one prey type, which would help explain the high diet selectivity of individuals.

Ecological and evolutionary implications

The degree to which the individuals within a population are sorted into dietary clusters may have important ecological and evolutionary implications. Few models have explicitly examined the community-level effects of within-population diet variation in general (Doebeli 1997), let alone clustering in particular.

We therefore do not know how the degree of clustering might influence food web dynamics. The implications of diet variation for intraspecific competition, however, are well known. When a population is composed of ecologically divergent individuals, competition becomes frequency dependent and favors rare phenotypes. Such frequency-dependent competition may drive disruptive selection (Bolnick 2004), which can help maintain quantitative genetic variation within populations (Bolnick and Lau, *in press*). Most theoretical models of intraspecific competition, however, assume that competition between individuals falls away gradually with phenotypic difference (Roughgarden 1972, Taper and Case 1985, Dieckmann and Doebeli 1999). The existence of clusters suggests that competition interacts with phenotypic differences in a stepwise fashion, so that individuals will either overlap greatly or not at all in resource use when competition reaches a certain threshold. Our results thus suggest the need for new approaches to modeling intraspecific frequency-dependent competition. The degree of clustering may dictate the types of models one should use for studies of frequency-dependent intraspecific competition.

Frequency-dependent competition is sometimes used in models of sympatric speciation that also require strong assortative mating (Dieckmann and Doebeli 1999). Interestingly, clustering might provide a viable basis for assortative mating, if mate preferences are influenced by diet similarity. Assortative mating by diet might arise (1) via spatial segregation into different microhabitats, (2) temporal isolation if prey availability peaks at different times of the year for different groups, or (3) via direct mate choice, for instance if individuals prefer to school with conspecifics with more similar diets. The latter effect has recently been demonstrated in stickleback (Ward et al. 2004, 2005), although its effects on mating are not known. In conclusion, the degree of clustering is likely to influence the potential for evolutionary divergence in natural populations.

Resource polymorphism in lacustrine fish

Our network-based analysis found that stickleback in Blackwater Lake partition resources in accordance with the major littoral–pelagic axis already described for stickleback (Schluter and McPhail 1992) and other lacustrine fish (Skúlason et al. 1999, Robinson and Schluter 2000). This partition has been interpreted as resulting from biomechanical trade-offs associated with the use of littoral and pelagic resources (Schluter 1995, Robinson 2000). However, our results revealed some unexpected complexities to benthic/pelagic niche variation. First, this habitat-based niche partitioning was maintained even in $9 \times 9 \times 2$ m deep enclosures that removed effects of spatial segregation of prey. In such small enclosures, a given fish can readily sample any available prey in a very short time period. Second, our analysis revealed that littoral and pelagic resources may be more finely partitioned, with groups of morphologically different individuals distinguishing among different pelagic prey (zooplankton vs. macroinvertebrates) and different benthic prey (chironomids, benthic cladocerans, and benthic macroinvertebrates). This suggests the possibility of subtler, unknown functional trade-offs in resource use within the littoral and pelagic habitats that would become important under high competition. Moreover, our results indicate that these trade-offs are density dependent. We conclude that the broad categorization of resources as “littoral” or “pelagic” hides finer subdivisions that are perceived by stickleback at times of resource limitation. It remains to be seen whether this finer pattern of resource partitioning is unique to stickleback or is a more general phenomenon in lacustrine fish.

Conclusions

In this paper, we identified a previously unnoticed pattern of resource partitioning in lacustrine fish, in which individuals form dietary clusters. These clusters result from individuals switching from most-favored prey to secondary prey under high competition, suggesting the presence of subtle trade-offs precluding individuals from

broadening their niches, in contrast to the assumptions of optimal foraging models. The nature of the trade-offs is unknown, but is probably a result of an interplay between functional morphological differences and learning. Our results therefore indicate an often underappreciated role of the interaction between morphology and behavior in shaping individual and population niches. Our results also suggest the need for alteration to foraging theory models to produce prey switching patterns, rather than simple, individual niche expansion.

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APPENDIX A

Derivation of the C_{ws} index of clustering (*Ecological Archives* E089-115-A1).

APPENDIX B

Weighted networks of wild-caught (control) and low- and high-density pairs of enclosures (*Ecological Archives* E089-115-A2).

SUPPLEMENT

The computer program DIETA1.exe, its source code, and its manual (*Ecological Archives* E089-115-S1).