

## LETTER

# Effects of size selection versus density dependence on life histories: A first experimental probe

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**Abstract**

When prey experience size-based harvesting by predators, they are not only subject to selection due to larger individuals being preferentially harvested but also selection due to reductions in population density. Density-dependent selection represents one of the most basic interactions between ecology and evolution. Yet, the reduction in density associated with exploitation has not been tested as a possible driving force of observed evolutionary changes in populations harvested size-dependently. Using an artificial selection experiment with a mixture of *Daphnia* clones, we partition the evolutionary effects of size-based harvesting into the effects of removing large individuals and the effects of lowering the population density. We show that both size selection and density-dependent selection are significant drivers of life-history evolution. Importantly, these drivers affected different life-history traits with size-selective harvesting selecting for slower juvenile growth rates and a larger size at maturity, and low-density selecting for reduced reproductive output.

**KEYWORDS**

*Daphnia*, density-dependent selection, harvesting, rapid evolution, size selection

**INTRODUCTION**

The rapid evolution of key life-history traits in harvested populations has been documented repeatedly across a range of species (Haugen & Vøllestad, 2001; Walsh et al., 2006). Although this phenomenon is particularly concerning in economic contexts such as fisheries, we lack a mechanistic understanding of what drives these rapid evolutionary changes. One such mechanism is size selection, which occurs, for example when harvesting or predation leads to greater losses of larger individuals thereby shifting the distribution of prey to smaller sizes (Brooks & Dodson, 1965). Another mechanism is density-dependent selection, defined as occurring when different genotypes are favoured as population density changes (Travis et al., 2013). Here, we focus on density-dependent selection due to intraspecific competition, e.g. per-capita availability of resources increases due to a reduction in their population size. For example this form of density-dependent selection is responsible for some of

the phenotypic differences in Trinidadian guppies at low and high predation sites (Travis et al. 2014). Despite this evidence for both forms of selection, their relative importance for natural systems is not well understood.

Both observation and theory have focused almost exclusively on size selection by predators and other agents as being the major selective mechanism of life-history evolution in harvested populations (Haugen & Vøllestad, 2001; Kuparinen & Merilä, 2007; Walsh et al., 2006), even though the accompanying reduction in prey population density could be equally or more important. Although the latter has been mentioned in conceptual discussions of this issue (Abrams & Rowe, 1996; Reznick et al., 2002; Walsh et al. 2013) and investigated empirically in one system (Bassar et al., 2012; Walsh & Reznick, 2008), it has never been experimentally manipulated along with size selection. Determining the relative magnitude of these effects has many practical implications, for example whether to set size limits and/or catch limits for harvested populations.

Models of size selection, in which mortality of large individuals increases, predict some combination of a reduction in age or size at maturity, an increase in reproduction, or a reduced growth rate, but exactly which traits evolve depends on which traits are flexible and what trade-offs exist among them (Abrams & Rowe, 1996; Williams, 1966). Density-dependent selection may also promote these same traits, favouring current investment over future investment if it increases mortality of adults or all age classes (Charlesworth, 1980; Reznick et al., 2002). But density dependence can also act to increase mortality of juveniles, reduce growth rates or reduce fecundity.

Here we examine the evolutionary impact of density-dependent selection and size selection on life-history traits using a controlled selection experiment in the zooplankton *Daphnia melanica*, collected from a fishless lake. *Daphnia* are particularly suited to studies documenting genetically based trait changes because of their clonal nature and short generation time. Also, zooplankton are a classic example in which the presence of fish predators leads to smaller body size (Brooks & Dodson, 1965), and *Daphnia* in particular are known to show life-history evolution in response to introduced fish predators (Fisk et al., 2007). We raised eight populations and subjected them to culling treatments over several generations. We initiated all populations with identical mixtures of eight clones, thereby controlling for any confounding effects of initial differences in genetic composition that would be present among natural populations, and we manipulated size selection by removing either large individuals or randomly selected individuals and density-dependent selection by maintaining a high or low density. Subsequent to these manipulations, we raised the surviving clones individually for two generations before phenotyping to reduce maternal and grand-maternal effects. This approach allowed us to separate the two selective forces predators impose on prey. Furthermore, by comparing phenotypic differences between populations, we quantified the extent to which both density-dependent selection and size selection lead to the evolution of life-history traits.

## METHODS

### Sample collection

To inoculate our microcosms, we collected *Daphnia melanica* from the fishless lake Gable 4 (Sierra Nevada, CA 37°19'41.4"N, 118°41'17.4"W). We chose to use a source population that lacked fish predators to eliminate the possibility that the population had already been subjected to predator-imposed selection. Each field-collected gravid female was placed into its own beaker and allowed to reproduce clonally. From these females,

eight clonal lines were established and maintained for 5–6 generations before the start of the selection experiment. To propagate lines across generations, neonates from the second or third clutch were taken and reared individually in 100 ml containers. No males or resting eggs were observed in the clonal lines prior to or during the experiment, suggesting that individuals only reproduced clonally. By genotyping at five microsatellite loci, we confirmed that the clonal lines were genetically diverse, consisting of five unique multilocus genotypes (supplementary material, Table S1). Lines belonging to the same multilocus genotype are potentially unique but indistinguishable across our microsatellite loci. We verified that our lines were clonal by genotyping 3–6 individuals per line. There was no indication of contamination ( $N = 39$ ). All *Daphnia* were maintained in FLAMES media (Celis-Salgado et al., 2008) under constant temperature (16°C) and light (16L:8D) and fed with *Cryptomonas* every other day.

To understand the initial variation among clonal lines, we phenotyped the life-history traits of multiple individuals per clonal line (see *Phenotyping* below). We reared six individuals from each clonal line. As six individuals died before reaching reproductive maturity, sample sizes for the eight clonal lines were as follows: 6, 6, 6, 4, 3, 5, 6 and 6 individuals. We observed variation among clonal lines in all traits (Figure S1), with reproduction having the highest coefficient of variation (CV = 0.32), followed by growth rate (CV = 0.19), age at maturity (CV = 0.11), maximum size (CV = 0.05) and size at maturity (CV = 0.03).

### Experimental conditions

We experimentally partitioned the effects of size selection, density-dependent selection and their interaction using genetically identical populations raised in microcosms. We initiated eight one-litre microcosms, split into two blocks. After enough neonates had been birthed from each clonal line to create genetically identical starting populations, blocks were started two days apart. These starting populations consisted of an equal number of individuals from our eight clonal lines. We manipulated the effect of density-dependent selection by initiating populations with either 16 or 72 neonates per litre. While we do not have a density measure from this lake due to weather conditions, we found density ranges from 0.1 per litre to 100 per litre in lakes in the same species in the same region. More broadly, *Daphnia* in lakes can reach densities up to 4000 per litre (Kvam & Kleiven, 1995) but are not typically that high. Neonates were between 36 and 48 hours old when placed in the mesocosms. All mesocosms were fed the same amount, so that individuals in the high-density treatment were competing more strongly for food. Previous studies have shown that *Daphnia* are typically food-resource limited

(McCauley et al., 1988), although other negative effects of crowding have also been documented (Burns, 2000).

To manipulate the effect of size selection, we artificially selected out and discarded 20% of adults, either based on size or at random on days 7, 14 and 21. For the size-selective culling, we measured all adults using an ocular micrometre to sort individuals based on size into 0.2 mm increments and disposed of the top 20%. When populations became larger than roughly 150 individuals, we split the mesocosm into two and the process was repeated for both halves to reduce the time spent out of the environmental chamber. Because mesocosms differed in *Daphnia* density, we removed a different number of individuals from each. Doing so was likely one reason the density treatment did not last very long, as we removed more individuals from the high-density treatments than the low-density treatments.

Although *Daphnia* populations in all microcosms increased over time, the high- and low-density treatments persisted for the first 11 days, but thereafter densities were volatile, with high-density populations generally, but not always, having higher densities than low-density populations (supplementary material, Figure S2). We stopped the experiment once the populations began declining. Given that *D. melanica* on average reproduce at 14 days old but can reproduce as young as 10 days old, the experiment lasted one to two generations but may have been as long as three generations. No males nor resting eggs were observed throughout the experiment, suggesting that individuals only reproduced clonally. At the end of the 21-day period, low-density populations ranged from 102 to 180 individuals (mean  $\pm$  SD = 140  $\pm$  37), and high-density populations ranged from 130 to 253 individuals (mean  $\pm$  SD = 217  $\pm$  58). We then propagated an average of 10.5 individuals (SD = 0.93, min = 10, max = 13) from each experimental population individually for three additional generations after the end of the 21-day period, from each of which we measured traits.

## Phenotyping

We measured the life-history traits of the third generation in a controlled environment using standard methods (Lynch, 1989). Neonates aged 36–48 hours were taken from the mother's second clutch and reared individually. For 30 days, each individual's size and reproductive status (including the number of eggs) was captured with photographs every other day (when media and algae were replaced) with a Cannon EOS Rebel T3i mounted to a microscope at 20x magnification. The size was measured manually using ImageJ by drawing a line segment from the base of the tail to the top of the eye. Measurements were calibrated using photographs of a micrometre taken under the same conditions. We measured the same image 10 times, repeated for three images to obtain measurement error (SD = 0.009 mm). To find error due to our

photographing method, we took two photographs of the same individual on the same day, repeated for five individuals, and found the average of the five ranges was 0.08 mm. To determine age at maturity, we recorded the day of the first photo in which eggs appeared, then classified the stage of those eggs as early or late. Early-stage eggs are round, whereas late-stage eggs are oblong with an eyespot. Reproduction was measured as the sum of all eggs produced by Day 30. Ten individuals died before reaching maturity and were excluded from the analysis. In block 1, the sample sizes were seven from the randomly culled low-density treatment, nine from the large-size culled low-density treatment, 11 from the randomly culled high-density treatment and six from the large-size culled high-density treatment. Sample sizes for block 2 were nine the randomly culled low-density treatment, nine from the large-size culled low-density treatment, nine from the randomly-culled high-density treatment and 10 from the large-size culled high-density treatment.

## Statistical analysis

To estimate the juvenile growth rate and maximum size, an asymptotic regression model was fit to the time series of an individual's growth over time using `SSAsympOrig` function in the `nlme` package in R version 3.3.3 (Pinheiro & Bates, 2000). The `SSAsympOrig` function is  $size = Asym * (1 - e^{-lrc * day})$ , where  $lrc$  is the natural log of the growth rate constant and  $Asym$  is the asymptotic (maximum) size. Because the parameter  $lrc$  is not an intuitive measure of growth, we transformed  $lrc$  to the time in days to reach half maximum size, i.e.  $\frac{\log 2}{lrc}$ . Note that this measure of growth rate is, in part, dependent on the maximum size of an individual. We also assess an alternate measure of growth rate (i.e. the size on the fourth measurement minus size on the first measurement divided by six) and alternate measure of maximum size (i.e. the maximum size observed on any day). These results are reported in Table S2.

To test for differentiation in traits between high-density and low-density treatments, and between randomly and size-based culling treatments, we performed a two-sided three-way MANOVA using the `manova` function in R version 3.3.3. There was no indication of a deviation from normality. We report the phenotypic correlation structure among traits in Table S3. This was followed by two-sided univariate three-way ANOVAs. For all models, we included density treatment, culling treatment, the interaction between density and culling treatment, and block as our predictor variables.

## RESULTS

The density treatment, culling treatment and block were significant explanatory variables for the combined set of

life-history traits (MANOVA in Table 1). The interaction between density and culling treatment was not significant. Individual tests (ANOVA in Table 1) showed density had a significant effect on reproduction, but not on the juvenile growth rate, age at maturity, size at maturity or maximum size. Culling treatment had a significant effect on juvenile growth rate and size at maturity, but not on age at maturity, reproduction, nor maximum size. Neither block nor the interaction between culling and density treatments was significant in any of the univariate tests.

Individuals in the size-based culling treatment evolved slower juvenile growth rates and a larger size at maturity (Figure 1a and d). The alternate measure of juvenile growth similarly showed size-based culling slowed juvenile growth rate (Table S2). The less expected outcome of our study is that individuals in the high-density treatment evolved increased reproductive output (Figure 1c).

## DISCUSSION

While density-dependent selection and size selection are likely operating concurrently in many systems, the evolutionary effects of each have not been partitioned. We found density-dependent selection and size selection have different effects on different life-history traits. Also, we found the two types of selection differ in their magnitude of effects. Density-dependent selection led to moderately significant differences in reproduction ( $p < 0.05$ ). Size-selection led to very significant differences in growth rate ( $p < 0.001$ ), and, to a lesser extent, differences in size at maturity ( $p < 0.05$ ). These results may reflect differences in the selection intensity on each trait and the amount of initial genetic variation in

each trait. Because reproduction was so variable among clonal lines, it is perhaps not surprising that density selection resulted in significant differences. Similarly, the growth rate had the second-highest coefficient of variation and showed significant effects of size selection. Size at maturity did not vary much among lines but showed significant effects of size selection. It is unlikely growth rate and size at maturity jointly evolved because of linkage disequilibrium, as these traits have a correlation of  $-0.05$ .

The evolutionary predictions of density-dependent selection rely on knowing the age(s) at which competition causes increased mortality or reduced fecundity (Charlesworth, 1980). We observed the evolution of a higher reproductive rate in the high-density selection treatment. Theory predicts that a greater investment in reproduction is favoured when competition increases mortality across all age classes (Reznick et al 2002). The biological intuition is if a high-density environment increases mortality on all stages, the chance of surviving to an older age is lowered; therefore, those able to invest more in offspring will be favoured. However, if there was increased mortality in all age classes, we would also predict that an earlier age at maturity would be favoured, which is not observed in our data.

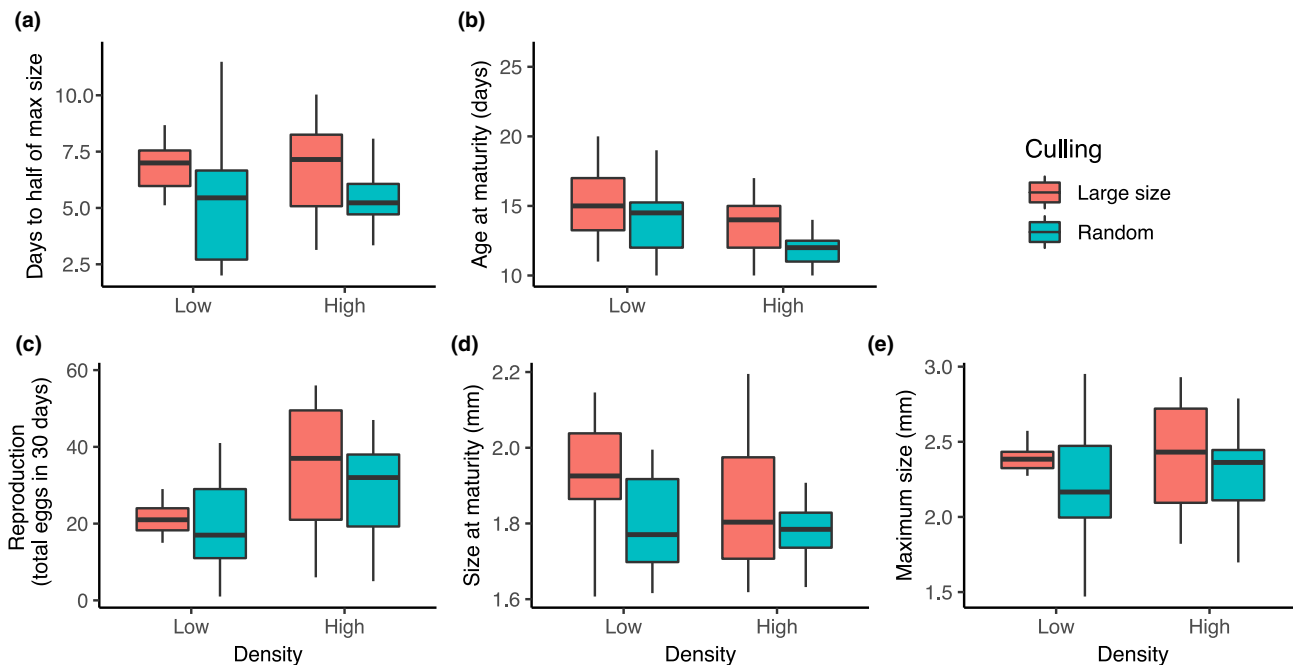
The direction of evolution in response to our treatments which mimic harvesting is sometimes but not always the same as the evolutionary effect of harvesting found in other taxa as follows. Previous research by Edley and Law (1988) simulating fish predation in *Daphnia* similarly found culling large individuals favoured slower-growing clones. While that study did not separate the effects of size selection and density selection, our results suggest that their finding was the result of size selection. One explanation for the size-selection-driven

TABLE 1 Statistical analysis of life-history traits

	Density			Culling			Density × Culling			Block		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
MANOVA (Wilk's)	3.28	5	<b>0.01</b>	3.90	5	<b>0.004</b>	0.55	5	0.73	2.40	5	<b>0.05</b>
ANOVAs												
Growth rate (lrc)	0.29	1	0.59	9.94	1	<b>0.002</b>	1.42	1	0.24	3.23	1	0.08
Age at maturity (days)	2.72	1	0.10	1.97	1	0.17	0.09	1	0.77	0.75	1	0.39
Reproduction (eggs in 30 days)	8.81	1	<b>0.004</b>	1.16	1	0.29	0.13	1	0.72	2.07	1	0.15
Size at maturity (mm)	1.31	1	0.26	6.66	1	<b>0.01</b>	1.18	1	0.28	1.46	1	0.23
Maximum size (mm)	0.56	1	0.46	3.45	1	0.07	1.10	1	0.30	1.18	1	0.28

Results of the MANOVA and univariate linear models, testing for the effect of density treatment, culling treatment, the interaction between density and culling treatment and block on life-history traits. P-values marked in bold indicate numbers that are significant at the 0.05 level or below. Effect sizes for the MANOVA, calculated as Wilks' Lambda, the multivariate partial  $\eta^2$  are  $\eta^2 = 0.23$  for density,  $\eta^2 = 0.25$  for culling,  $\eta^2 = 0.27$  for block and  $\eta^2 = 0.05$  for the interaction of density and culling.





**FIGURE 1** Comparison between low- and high-density treatments and large-size-culling and random-culling treatments for (a) days to half maximum size, (b) age at maturity, (c) reproduction, (d) size at maturity and (e) maximum size. The horizontal line in each grey box is the median, the boxes extend to the first and third quartiles and the whiskers extend 1.5 times the interquartile range from the boxes. Sample sizes for block 1 are low density/random culling ( $N = 7$ ), low density/large size culling ( $N = 9$ ), high density/random culling ( $N = 11$ ) and high density/large size culling ( $N = 6$ ). Sample sizes for block 2 are low density/random culling ( $N = 9$ ), low density/large size culling ( $N = 9$ ), high density/random culling ( $N = 9$ ), high density/large size culling ( $N = 10$ ).

slower juvenile growth rates is that organisms should linger in stages that have lower mortality rates (Williams, 1966), which in our experiment are the younger stages. A similar response to artificial size selection was found in the males of Mozambique tilapia (*Tilapia mossambica*) that evolved reduced growth rates compared to those harvested randomly (Silliman, 1975). In another empirical test of size-selective harvesting, Atlantic silversides (*Menidia menidia*) evolved slower juvenile growth rates and reduced fecundity (Conover & Munch, 2002; Walsh et al., 2006), although these results differ from what has been observed in fisheries data (Hilborn, 2006). In sum, across the various empirical studies of size selection, a common outcome has been observed, i.e. slower growth rates.

In contrast, there have been few empirical studies of density-dependent selection. We found *Daphnia* evolved increased reproduction in response to density-dependent selection. Our result differed from that of an experiment evaluating density-dependent selection in Trinidadian guppies (*Poecilia reticulata*), which showed that individuals mature later and have fewer offspring in a high-density, low-predation environment (Bassar et al., 2012, Travis et al. 2014). High-density environments can reduce fecundity or increase mortality in specific age classes, which will depend on how intraspecific competition acts within the species. Because of these variable impacts of density on different ages or stages, predictions of life-history evolution by density-dependent selection

are particularly sensitive to the specifics of a system. In a review of studies testing density regulation in vertebrates, Bassar et al., (2010) found that reduced fecundity was more common than reduced juvenile survival, which was more common than reduced adult survival, and that most studies found significant effects on more than one demographic variable. Therefore, the effects of density-dependent selection and size selection in other natural systems may strengthen one another, cancel one another out, or, as we observed, affect different traits. Thus, a major future challenge is understanding how life-history traits of different populations and species of *Daphnia* as well as of different taxa respond to both forms of selection.

### Implications for eco-evolutionary feedbacks, food webs and harvesting

Our findings have important implications for eco-evolutionary feedbacks, food web dynamics and fisheries management.

First, density-dependent selection represents a direct link between evolution and population dynamics. This link has two components: population density influences the relative fitness of different individuals, and the absolute fitness of individuals influences population growth rate and population size. When population size and fitness influence each other, there is the potential

for eco-evolutionary feedback loops (Kokko and López-Sepulcre 2007). Thus far, there are few complete empirical demonstrations of these feedback loops (Schoener, 2011; Schoener, 2013; Schoener et al., 2014). Here, we have shown the first condition, in which changes in an ecological variable, i.e. population density, drive evolutionary changes in life-history traits. The next step to complete the feedback loop is to show the second condition; that evolutionary changes in life-history traits (which translate into changes in absolute fitness) drive ecological changes at the population level. We believe this condition is likely to be satisfied. In particular, we hypothesize that the higher reproductive rates that evolved in the high-density treatment would increase population-level growth rates and increase density, triggering subsequent evolution in life-history traits.

We did not find any significant interactions between density and culling treatments. If this lack of interaction occurs for harvested fish species, fisheries would be able to manage these two selective mechanisms separately. The absence of an interaction term, however, need not exclude eco-evolutionary feedbacks involving both density-dependent selection and size selection. For example the life-history changes of reduced growth rate and a larger size at maturity induced by size selection will likely impact ecological processes such as population growth rate and population density. More work is needed to understand how far the effects of size selection might also indirectly lead to density-dependent selection.

Second, the joint effects of density-dependent selection and size selection may propagate through the food web with unexpected consequences. For example in a previous study (Pantel et al., 2015) *Daphnia* that were locally adapted to conditions with or without fish significantly altered zooplankton community assembly. In another study (Park et al. 2018) *Daphnia* that diverged in life history in response to fish predation not only increased their resistance to being eaten but also had distinct grazing preferences. Hence, density-dependent selection and size selection acting on a single species has the potential to change the composition of primary producers and reduce the abundance of their consumers. Both of these changes can have cascading effects on species in other trophic levels of the community (Ripple et al., 2016; Wootton & Power, 1993).

Third, our results have implications for how we think about the evolutionary effects of harvesting. Previous work has advocated that the evolutionary effects of size-based harvesting should be considered in the management of exploited systems (Kuparinen & Merilä, 2007). Changes in life-history traits have been repeatedly documented in harvested populations (Edley & Law, 1988; Haugen & Vøllestad, 2001; Walsh et al., 2006). This harvest-induced change is often a combination of a plastic and evolutionary response (Eikeset et al., 2016; Gislason et al. 2018, Wilson et al., 2019). There has been some debate over whether some of the best-known examples of harvesting-induced changes are evolutionary

versus demographic and over the speed at which evolution is taking place. For example Traill et al., (2014) argue that smaller body mass and horn size in trophy-hunted bighorn sheep were mostly demographic responses rather than evolutionary (see however Pigeon et al., 2016) and that the speed of evolution was likely slower than empirically reported (Coulson et al., 2018). In light of this debate, our study offers one example that documents a rapid evolutionary effect of simulated harvesting, which occurs over a very short amount of time and has been separated from any potential demographic effects. Here, we show a reduction in population size can lead to evolutionary changes in a harvested population. Therefore, not only do we need to consider the evolutionary effects of which size classes are removed in an exploited population, but also the evolutionary effects of reducing density.

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## AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and contributed to the design. KL collected and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

The data have been deposited on Dryad. <https://doi.org/10.25338/B8H62Z>.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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