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Effects of greenwater and claywater regimes on early exogenous feeding in larval sablefish (*Anoplopoma fimbria*)

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ABSTRACT

Marine fish larvae often survive better with algae in their rearing water, but algae is expensive and cheaper alternatives should be explored. This study tested the effects of algae and clay, a less-expensive water additive, on feeding, growth and survival during the first week of exogenous feeding in sablefish (*Anoplopoma fimbria*). After three days with algae or clay, larvae with algae fed better than those with clay. On the fourth day, half of the algae tanks were transitioned to clay, and half of the clay tanks were transitioned to algae. When the transition was 90 % complete, feeding was better if algae was used for the first three days, regardless of whether the larvae were transitioning to clay on day-4 or kept on algae, so the previous water additive (algae or clay) predicted feeding rates better than the additive at the time of the feeding trial. Benefits of the first three days with algae did not last indefinitely, however, as larvae that transitioned from algae to clay on the fourth day stopped showing feeding benefits by the fifth and sixth days. In a separate experiment, different algae-clay mixtures were compared: i) 100 % clay, ii) 25 % algae / 75 % clay, iii) 50 % algae / 50 % clay, and iv) 100 % algae. The third and fourth treatments fed and survived better relative to the first treatment, and did not differ from each other. In another experiment, larval feeding was higher in 100 % algae than in 50 % algae / 0 % clay, highlighting the importance of the clay component of the 50 % algae / 50 % clay mixture. Thus, algae use during the first week of exogenous feeding was halved by using an algae-clay mixture, without impacting larval feeding, growth, or survival. This study provides methods to reduce the reliance on expensive algae during the larval period.

1. Introduction

Successful marine fish larviculture often requires expensive water additives, but cheaper substitutes have been explored. Algae is the most common water additive for marine fish larviculture (Cobcroft et al., 2001; Naas et al., 1992). Algae might provide a number of benefits, including an enhanced visual environment (Boehlert and Morgan, 1985; Utne-Palm, 2002; 2004), a direct or indirect food source (Reitan et al., 1997; van der Meeren, 1991), gut enzyme stimulation (Cahu et al., 1998), stimulation of feeding response (Lazo et al., 2000), and influences on the microbiome (Eddy and Jones, 2002). However, because algae is expensive and can contribute to detrimental bacterial growth (Attramadal et al., 2012; Dodd et al., 2020), clay has been tested as a potential substitute. Results have varied, with studies on different marine fish species finding clay to be superior, inferior, or equal to algae, in terms of effects on growth and survival (e.g., Attramadal et al., 2012; Daugherty, 2013; Koven et al., 2019; Stuart et al., 2015).

When rearing larval sablefish (*Anoplopoma fimbria*), using clay as a water additive can cause high mortality in the first week of exogenous feeding, but is a viable substitute for algae at the beginning of the second week (Lee et al., 2017, 2021; Pierce et al., 2019). Introducing clay after at least one week of exogenous feeding can result in significant cost savings over algae, without negative effects on growth or survival (Lee et al., 2021). However, rearing sablefish from first feeding to weaning onto dry feed still has the highest daily costs of the aquaculture cycle. The first week of exogenous feeding is particularly expensive because algae must be used, but also offers opportunities for further improvement. The first week of exogenous feeding is also an important period when larvae must learn to feed on live prey, and when reduced or delayed feeding can lead to developmental impairments or reduced survival (Gisbert et al., 2004; Rao, 2003; Yufera and Darias, 2007).

The main objective of this study was to determine if algae use could

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be reduced during the first week of rearing larval sablefish without compromising feeding, growth or survival. Experiment 1 tested for the relative effects of algae and clay as water additives on feeding. Experiment 2 tested the effects of different mixtures of algae and clay on larval sablefish feeding, growth, and survival, in an attempt to reduce dependence on algae. Experiment 3 tested if the reduced algae concentration in the algae-clay mixture identified in Experiment 2 could be sufficient on its own (without clay) in achieving feeding rates similar to a full-algae treatment.

2. Material and methods

2.1. Spawning, larval production, and feeding

Methods for broodstock maintenance and spawning, and rearing of embryos are detailed in Cook et al. (2015) and Goetz et al. (2021). Briefly, broodstock were collected from the Pacific Ocean off the Washington coast and manually spawned at the NOAA Fisheries, Northwest Fisheries Science Center, Manchester Research Station, in Port Orchard, WA. Embryos were held in dark 300-L incubators for 12 days and then transferred before hatching to tall dark 850-L silos, where they were held for 38 days. At yolk depletion, larvae were removed from silos and stocked into experimental tanks for first feeding with rotifers (*Brachionus plicatilis*). For all experiments, feeding consisted of adding live rotifers to the experimental tanks at a concentration of 11 rotifers per ml of tank water, once per day between 0900 h – 1100 h, unless otherwise noted.

2.2. Tanks

Cylindrical 37-L experimental tanks measured 36.5-cm diameter and 43.0-cm tall. Tanks walls were black, and bottoms were white. Water (10–12 °C) continuously flowed into each tank at a rate of 250 ml per minute, and exited through a screened center standpipe. Light was maintained at 27–32 lux, measured at the water surface.

2.3. Algae and clay

General procedures for algae and clay followed Lee et al. (2021). Algae paste (*Nannochloropsis oculata*, Reed Mariculture, Campbell, CA, USA) and Kentucky Ball Clay OM4 (Kentucky-Tennessee Clay Company, Roswell, GA, USA) were used for all experiments, at concentrations specified for each experiment below. Concentrated clay solutions were made by mixing clay and water with a blender. For all experiments, green dye ("green shade color," Esco Foods, San Francisco, CA, USA) was also added to algae and clay solutions for a final concentration in rearing tanks of 0.005 ml dye per L rearing water. Concentrated solutions of algae and clay were dosed from source tanks to experimental tanks with peristaltic pumps that were controlled by cycle timers (3-minutes on, 15-minutes off).

2.4. Experiment 1: effects of algae and clay on feeding

On March 22, 2021, 32 tanks (37 L per tank) were stocked with 500 larvae per tank (derived from three broodstock crosses). The tanks were divided into four treatments (n = 8 tanks per treatment) that differed in the application of algae or clay over the six-day experiment: 1) clay for the entire experiment, 2) clay on day 1, transitioned to algae on day 4, 3) algae for the entire experiment, 4) algae on day 1, transitioned to clay on day 4. Transitions were initiated by changing the algae or clay solutions in the source tanks that pumped into experimental tanks. The source tank contents were changed within minutes from clay to algae or algae to clay, but the change was more gradual in the experimental tanks as the peristaltic pumps slowly dosed the new water additive from the source tanks to the experimental tanks and the previous water additive was diluted out of the tank through the center standpipe. Transitions in treatments 2 and 4 were initiated early on day 4, and a feeding trial was conducted six hours later (24 hours after the previous feeding). At the time of the day 4 feeding trial, transitions were 90 % complete, based on simulations that took into account the input rate from the peristaltic pump and the overall water flow rate through each flow-through tank. That is, tanks that were transitioning from algae to clay were 90 % clay, while tanks that were transitioning from clay to algae were 90 % algae. Transitions were 100 % complete by the time of the feeding trials on days 5 and 6.

Clay concentrations in experimental tanks were maintained at 15 mg of clay per L tank water (nephelometer turbidity level of 13.9 NTU; Lee et al., 2017). Algae concentrations in experimental tanks were maintained at 1.4×10^9 cells per L tank water. These concentrations resulted in equal secchi-disk turbidities between treatments, measured with a turbidity tube (Carolina turbidity tube, Carolina Biological Supply Company, Burlington, NC, USA).

One hour after rotifer additions on days 3 through 6, ten larvae were removed from each tank and euthanized with MS-222. Young larval sablefish have transparent bodies, so the number of rotifers in each larval gut was quantified by looking through each larval body wall under a microscope (Accu-Scope Z650HR). Recently-consumed rotifers could be clearly distinguished from those consumed previously because older gut contents were mostly-digested, whereas recently-consumed rotifers were intact. For each tank, we averaged the number of rotifers per larva over the ten larvae (rotifers eaten), and counted the number of larvae that had eaten at least one rotifer (feeding incidence).

2.5. Experiment 2: algae-clay mixture effects on feeding, growth and survival

Trial 1. On April 5, 2021, 32 tanks (37 L per tank) were stocked with 300 larvae per tank (derived from two broodstock crosses in this trial and six broodstock crosses in trial 2 below). The tanks were divided into four treatments (n = 8 tanks per treatment) that tested different algae-clay mixtures: 1) 100 % of the normal clay concentration (hereafter, "0A-100C"), 2) 25 % of the normal algae concentration plus 75 % of the normal clay concentration (hereafter, "25A-75C"), 3) 50 % of the normal algae concentration plus 50 % of the normal clay concentration (hereafter, "50A-50C"), and 4) 100 % of the normal algae concentration (hereafter, "100A-0C"). "Normal" concentrations of algae and clay refer to the concentrations described for Experiment 1; the numbers before "A" and "C" refer to percentage of normal concentration, not the algae-to-clay ratio. Feeding and gut content assessment methods were identical to those described for Experiment 1. Feeding was quantified on the day after stocking (day 2), using the same methods as described for Experiment 1.

Trial 2. On April 7, 2021, the experiment was repeated to add another 8 replicates per treatment to the day-2 feeding data (n = 16 total). Additionally, instead of ending the experiment on day 2, we continued to rear the larvae for a total of nine days. Larvae were fed rotifers twice per day from day 2 to day 7, and once per day on days 8 and 9. On day 8, following a previously-published rearing protocol (Lee et al., 2017, 2021), all treatments were transitioned to clay (15 mg of clay per L tank water). On day 9, feeding data were collected as described for Experiment 1, then surviving larvae were counted and ten larvae per tank were dried in an oven and weighed.

2.6. Experiment 3: will 50 % algae generate a feeding response similar to 100 % algae?

The next experiment tested whether 50 % of the normal algae concentration could achieve feeding rates typical of 100 % algae. On May 17, 2021, 32 tanks (37 L per tank) were stocked with 300 larvae per tank (derived from three broodstock crosses). The tanks were divided into two treatments (n = 16 tanks per treatment): 1) 50A-0C, and 2) 100A-0C. Feeding methods were identical to those described for Experiment

1. Feeding was quantified on the day after stocking (day 2), using the same methods as described for Experiment 1. This trial ended after the day-2 feeding trial.

2.7. Statistics

2.7.1. Experiment 1

For day 3, a Wilcoxon test compared rotifers eaten and feeding incidence between clay and algae treatments. For days 4–6 where there were four treatments, differences were first tested with Kruskal-Wallis tests and significant results were followed with *post hoc* Tukey-Kramer HSD. Statistical tests were conducted with JMP 15 (SAS Institute, Inc., Cary, NC, USA).

2.7.2. Experiment 2

For day 2 data on rotifers eaten and feeding incidence, a mixed model tested for a treatment effect (fixed effect) on rotifers eaten and feeding incidence. Trial number was included as a random effect.

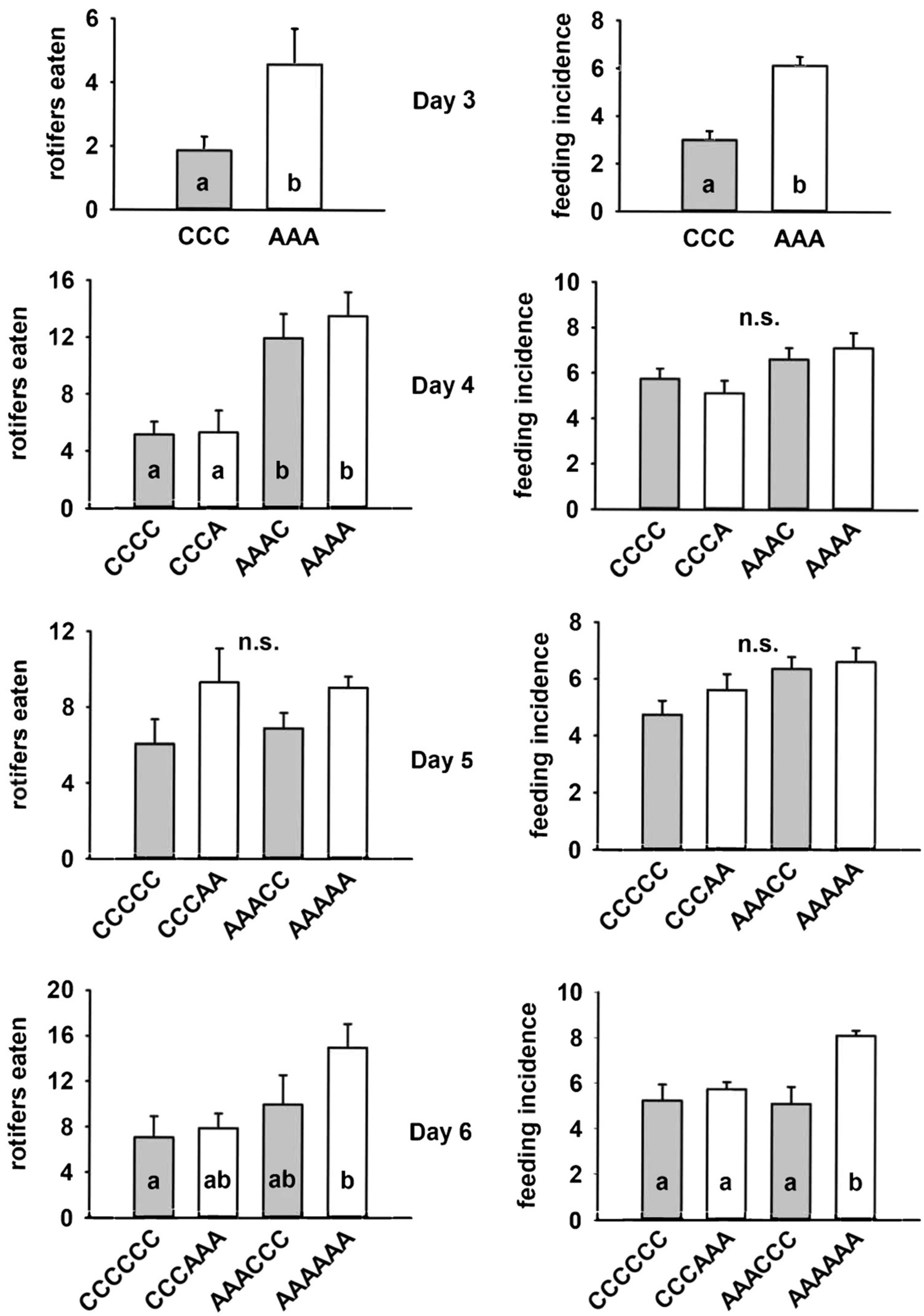

Fig. 1. Experiment 1. On day 3, larvae reared for three days in algae (AAA, n = 16 tanks) ate more rotifers and had higher feeding incidence than larvae in clay (CCC, n = 16 tanks). On day 4, half of the CCC tanks were continued on clay (CCCC, n = 8 tanks) and the other half were transitioned to algae (CCCA, n = 8 tanks). Similarly, on the fourth day, half of the AAA tanks were continued on algae (AAAA, n = 8 tanks) and the other half were transitioned to clay (AAAC, n = 8 tanks). These assignments to clay or algae continued until the end of the experiment on day 6. Capital letters under each bar indicate treatment history, with the first letter indicating treatment on day 1 and the last letter indicating treatment on the day of data collection. Different lower-case letters indicate statistically significant differences. Lack of statistical significance among any of the four treatments is indicated with "n.s." Data are presented as mean of tanks ± SEM.

Significant effects were followed with *post hoc* Tukey-Kramer HSD.

After all treatments were transitioned to clay on day 8, day 9 data on rotifers eaten, feeding incidence, survival, and dry weight were first tested with Kruskal-Wallis tests and significant results were followed with *post hoc* Tukey-Kramer HSD. Statistical tests were conducted with JMP 15 (SAS Institute, Inc., Cary, NC, USA).

2.7.3. Experiment 3

On day 2, a Wilcoxon test compared rotifers eaten and feeding incidence between treatments.

3. Results

3.1. Experiment 1: effects of algae and clay on feeding

The day before some treatments transitioned from one additive to the other (day 3), larvae reared in algae (AAA) ate more rotifers ($p = 0.018$) and had a higher feeding incidence ($p < 0.0001$) than larvae reared in clay (CCC, Fig. 1, day 3). On the day that some treatments transitioned (day 4), the number of rotifers eaten was higher in the two treatments that began on algae, regardless of whether the treatments remained on algae or transitioned to clay (AAAA versus CCCC: $p < 0.01$; AAAA versus CCCA: $p < 0.01$; AAAC versus CCCC: $p = 0.01$; AAAC versus CCCA: $p = 0.02$, Fig. 1, day 4). There were no significant differences between treatments that began on algae ($p = 0.75$), or between treatments that began on clay ($p = 0.87$). There were no significant differences in feeding incidence among treatments ($p = 0.10$, Fig. 1, day 4). On day 5, there were no significant differences in the number of rotifers eaten ($p = 0.22$) or feeding incidence ($p = 0.08$, Fig. 1, day 5). On day 6, larvae that remained on algae throughout the experiment consumed more rotifers than larvae that remained on clay throughout the experiment ($p = 0.04$, Fig. 1, day 6). Larvae that began on clay before transitioning to algae, and larvae that began on algae before transitioning to clay, did not consume a significantly different number of rotifers from each other ($p = 0.88$) or any other treatment (CCCAAA versus CCCCCC: $p = 0.73$; CCCAAA versus AAAAAA: $p = 0.08$; AAACCC versus CCCCCC: $p = 0.73$; AAACCC versus AAAAAA: $p = 0.30$, Fig. 1, day 6). Feeding incidence on day 6 was significantly higher for larvae that remained on algae throughout the experiment, compared to all other treatments (AAAAAA versus CCCCCC: $p < 0.01$, AAAAAA versus CCCAAA: $p = 0.02$, AAAAAA versus AAACCC: $p < 0.01$, Fig. 1, day 6). There were no significant differences in day-6 feeding incidence among the other treatments (CCCCCC versus CCCAAA: $p = 0.92$, CCCCCC versus AAACCC: $p = 1.00$, CCCAAA versus AAACCC: $p = 0.85$).

3.2. Experiment 2: algae-clay mixtures

On the day after stocking larvae into the rearing tanks (day 2), the number of rotifers eaten did not significantly differ among the four treatments ($p = 0.06$, Fig. 2). Feeding incidence in the 50A-50C and 100A-0C treatments, but not the 25A-75C treatment, was significantly higher than the 0A-100C treatment ($p < 0.05$, Fig. 2). Feeding incidence did not significantly differ among the 25A-75C, 50A-50C, and 100A-0C treatments ($p > 0.05$, Fig. 2).

On day 9, one day after the transition of all treatments to clay, there were no significant treatment differences in number of rotifers eaten ($p = 0.63$) or feeding incidence ($p = 0.22$, Fig. 3). Survival was significantly higher in the 50A-50C and 100A-0C treatments, than in the 0A-100C and 25A-75C treatments ($p < 0.01$, Fig. 4). There were no significant differences between the 50A-50C and 100A-0C treatments ($p = 0.69$) or between the 0A-100C and 25A-75C treatments ($p = 0.07$, Fig. 4). Dry weights did not significantly differ among treatments ($p = 0.65$, Fig. 4).

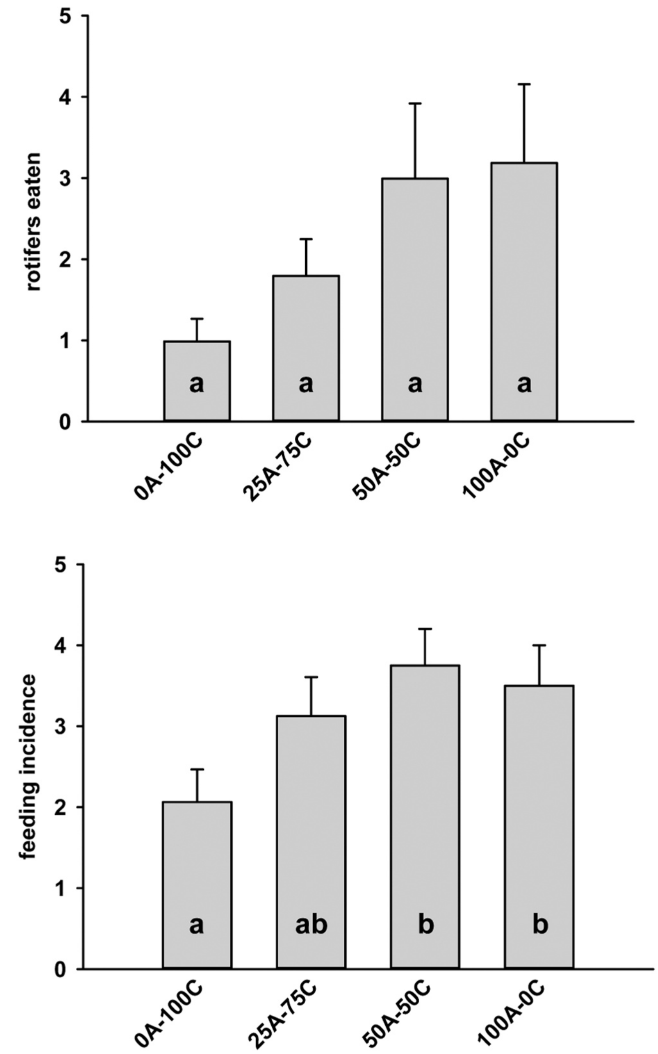

Fig. 2. Experiment 2. Feeding on day 2. There was no significant effect of clay (C) and algae (A) dosages on number of rotifers consumed ($0.05 < p < 0.06$), and a significant effect on feeding incidence. Each treatment consisted of 16 tanks ($n = 16$). Different lower-case letters indicate statistically significant differences. The numbers before "A" and "C" refer to percentage of normal concentration, not the algae-to-clay ratio. Data are presented as mean of tanks ± SEM.

3.3. Experiment 3: will 50 % algae generate a feeding response similar to 100 % algae?

On day 2, the number of rotifers eaten and feeding incidence were significantly lower for larvae in the 50A-0C treatment than for larvae in the 100A-0C treatment ($p < 0.01$, Fig. 5).

4. Discussion

This study demonstrates that algae use during the first week of exogenous feeding can be halved by substituting algae with a 50/50 mixture of algae and clay, but a full day-4 transition from algae to clay decreases feeding during the crucial first week of exogenous feeding. Previous studies have shown that clay can completely replace algae after the first week of exogenous feeding, but completely replacing algae with clay for the entire first week causes poor survival (Lee et al., 2017, 2021; Pierce et al., 2019).

First-feeding marine fish larvae are vulnerable to starvation, and poor feeding during the transition from endogenous to exogenous feeding can negatively affect development and survival (Gisbert et al.,

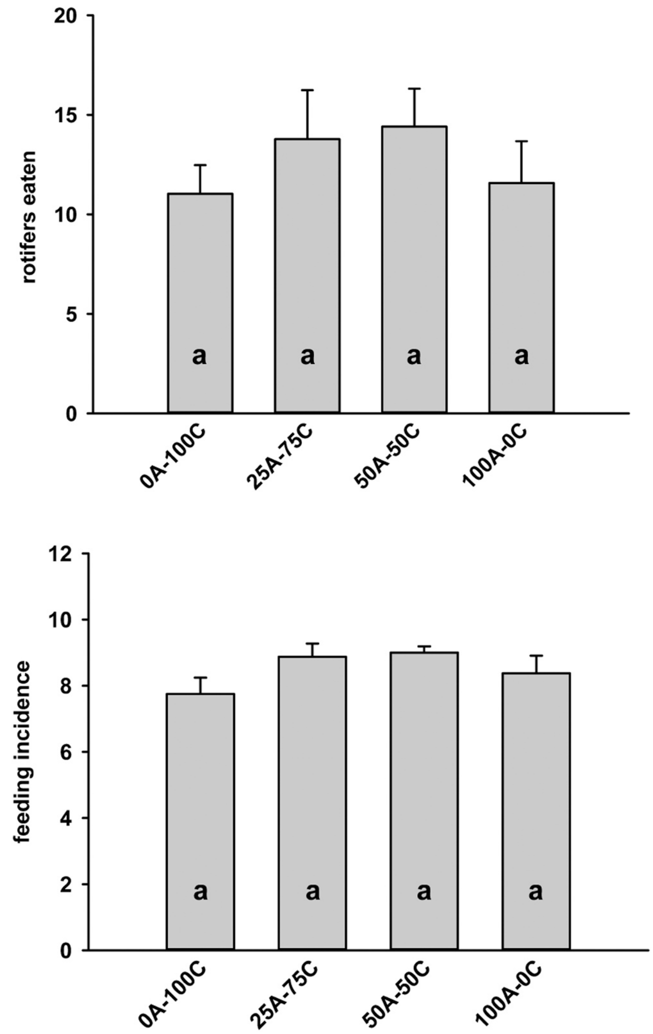

Fig. 3. Experiment 2. Feeding on day 9. All treatments were transitioned to clay on day 8 of the experiment. Treatments from days 1–7 (shown on x-axis) did not significantly affect the number of rotifers eaten or feeding incidence on day 9 ($p > 0.05$). Each treatment consisted of eight tanks ($n = 8$). Different lower-case letters indicate statistically significant differences. The numbers before “A” and “C” refer to percentage of normal concentration, not the algae-to-clay ratio. Data are presented as mean of tanks ± SEM.

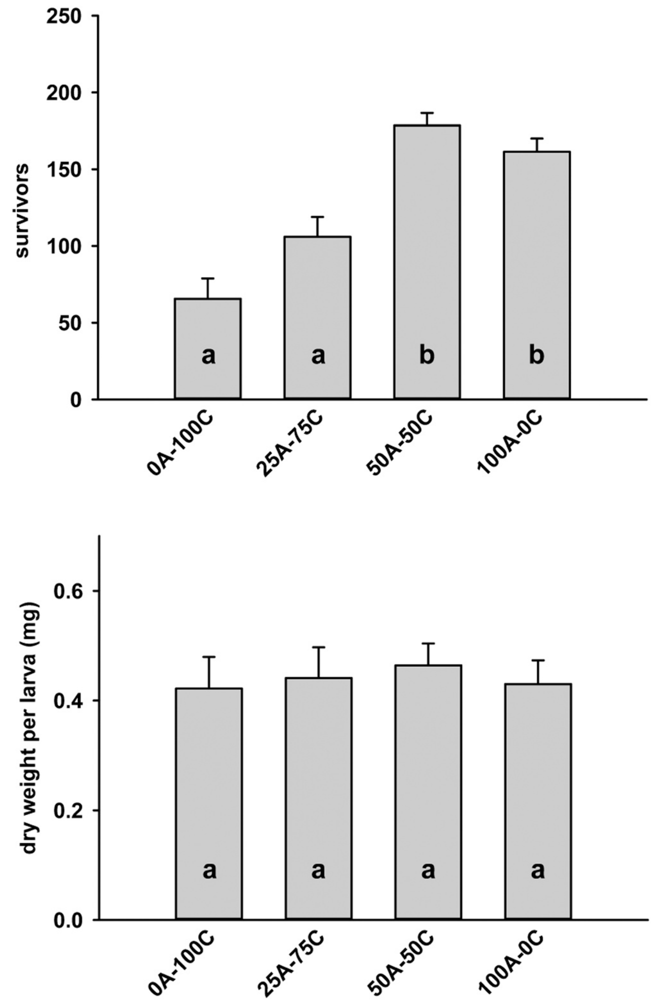

Fig. 4. Experiment 2. There was a significant effect of clay (C) and algae (A) dosages on survival, but no significant effect on dry weight ($p > 0.05$). Each treatment consisted of eight tanks ($n = 8$). Different lower-case letters indicate statistically significant differences. The numbers before “A” and “C” refer to percentage of normal concentration, not the algae-to-clay ratio. Data are presented as mean of tanks ± SEM.

2004; Yufera and Darias, 2007). Previous studies in other species have shown higher feeding rates with algae in the rearing water, compared to clay or clear water (e.g. grey mullet (*Mugil cephalus*), halibut (*Hippoglossus hippoglossus L.*), cod (*Gadus morhua L.*): Koven et al., 2019; Naas et al., 1992; van der Meeren et al., 2007). The greater feeding rate of algae-reared larvae in Experiment 1 (days 3 and 4) suggests that feeding benefits played a role in the greater survival of larval sablefish reared with algae in the first week of exogenous feeding in previous studies (Lee et al., 2017, Lee et al., 2021, Pierce et al., 2019).

The ability to switch from expensive algae to cheaper clay, without decreasing feeding, was only briefly evident on the day of the transition from algae to clay (AAAC not different from AAAA, Fig. 1). Further, algal feeding benefits were not immediately observed when larvae transitioned from clay to algae (CCCA not different from CCCC, Fig. 1). At the time of the feeding trial, transitions were only 90 % complete, but Experiment 2 showed that a 50A-50C mixture was sufficient to increase feeding, relative to 0A-100C. Thus, the lack of immediate feeding responses to transitions are more likely explanations for the results than the fact that transitions were not 100 % complete.

The most commonly-cited mechanism for why algae is superior to clear water is that algae offers a better visual environment for larvae to see prey (Naas et al., 1992), and the same mechanism has been proposed to explain better survival with algae over clay (Lee et al., 2021). However, a simple visual mechanism on day-4 is not supported, because switching from algae to clay did not immediately decrease feeding, and switching from clay to algae did not immediately increase feeding.

Providing algae during the first three days may have “preconditioned” larvae to feed better on day 4, for example by causing larvae to be in better physical condition, or physiologically priming them to feed. Potential mechanisms that could have acted during the first three days include visual benefits (Cobcroft et al., 2001; Cox and Pankhurst, 2000; Lee et al., 2021; Naas et al., 1992; Shaw et al., 2006), consumption of algae (Reitan et al., 1994, 1997; van der Meeren, 1991; van der Meeren et al., 2007), stimulation of digestive enzymes (Cahu et al., 1998), stimulation of the feeding response (Lazo et al., 2000; Lee et al., 2016), and establishment of a superior microbiome (Dodd et al., 2020; Eddy and Jones, 2002; Pierce et al., 2019). Multiple mechanisms could act simultaneously, and the importance of different mechanisms likely change through ontogeny (Koven et al., 2019; Lee et al., 2021; Pierce et al., 2019; Reitan et al., 1994; Shaw et al., 2006), particularly in sablefish where the relative effects of algae and clay on larval sablefish growth and survival change in the first few weeks of exogenous feeding

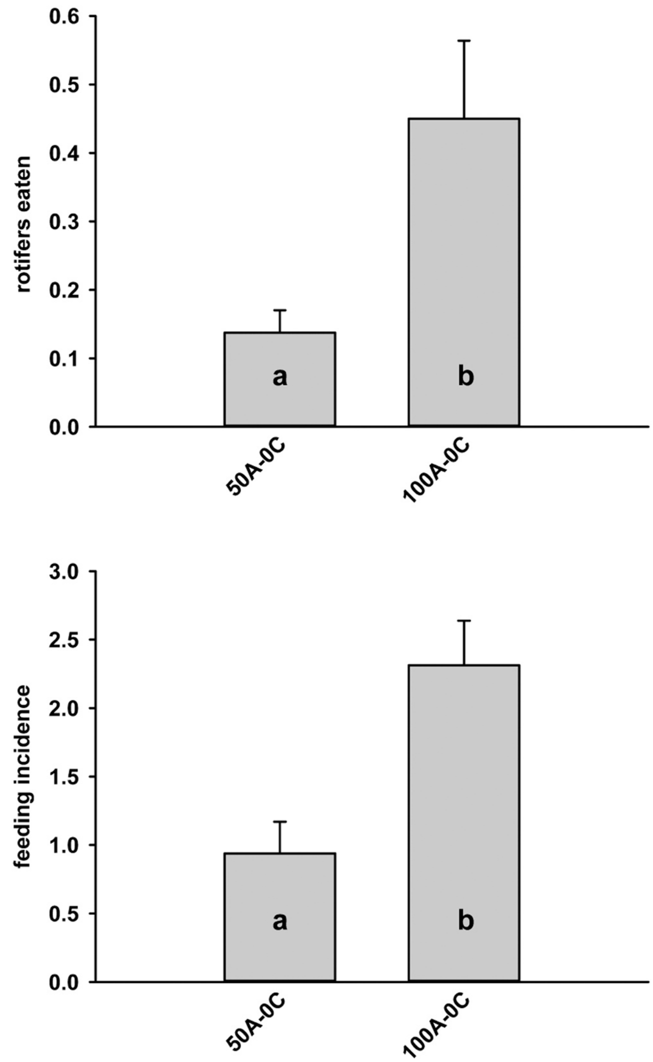

Fig. 5. Experiment 3. Larvae consumed significantly more rotifers and had higher feeding incidence in the 100 % algae treatment compared to the 50 % algae treatment ($p < 0.01$). Each treatment consisted of sixteen tanks ($n = 16$). Different lower-case letters indicate statistically significant differences. The numbers before "A" and "C" refer to percentage of normal concentration, not the algae-to-clay ratio. Data are presented as mean of tanks ± SEM.

(Lee et al., 2017, 2021). Future studies should test possible mechanisms, because understanding mechanisms would help formulate new strategies to further reduce reliance on algae while maintaining or improving feeding, growth, and survival.

Transitioning from algae to clay decreased feeding during the crucial first week of exogenous feeding, but a mixture of algae and clay reduced algae use without negative effects on feeding, growth, or survival. In Experiment 1, the algal feeding benefit in the treatment that transitioned to clay on day 4 was gone by day 5, when larvae stopped consuming significantly more rotifers than larvae reared exclusively with clay, and by day 6, when they had lower feeding incidence than algae-reared larvae. In contrast, the mixture of algae and clay (50A-50C) halved algae use, while achieving feeding and survival benefits similar to the standard (100 %) algae application. The 50A-50C and 100A-0C treatments showed higher feeding incidence than 0A-100C, whereas 25A-75C appeared intermediate, showing no significant difference from any other treatment. The survival data mirrored the feeding data, with 100A-0C and 50A-50C—but not 25A-75C—producing survival improvements relative to 0A-100C. The 50 % algae concentration is not recommended to be used without clay in week 1, because feeding in 50A-0C was inferior to feeding in 100A-0C; thus, the clay component of the 50A-50C mixture appears to be necessary.

This work provides new techniques to reduce the reliance on expensive algae for sablefish larviculture, to improve the efficiency and profitability of sablefish aquaculture. Previously-published timelines for the use of algae and clay can be modified to incorporate the 50A-50C mixture. In a previous study that compared rearing with algae to transitions from algae to clay on days 8 (day-8 strategy) and 18 (day-18 strategy), both transition dates led to improved body weight and biomass (total weight of all survivors), relative to remaining on algae, and the day-18 strategy led to higher biomass than the day-8 strategy (Lee et al., 2021). Thus, while both transition strategies led to higher growth, higher biomass, and lower costs than the traditional greenwater strategy, the day-8 strategy minimized the use of expensive algae, while the day-18 strategy maximized biomass. The 50A-50C mixture described in this current study could be used instead of algae in both strategies. At current retail prices for the algae paste ($77.25 per L) and clay ($1.12 per kg) used in this study, rearing sablefish larvae in greenwater for 35 days would cost $1703 in algae per 5000 L rearing tank, assuming a flow-through tank that turns over once every four hours. That cost decreases to $859 in algae and clay under the day-18 strategy, to $436 under the modified day-18 strategy (replacing the greenwater days with the 50A-50C mixture), to $352 under the day-8 strategy, and to $183 under the modified day-8 strategy.

CRediT authorship contribution statement

Jonathan S.F. Lee: Conceptualization, Data Curation, Formal analysis, Investigation, Methodology, Project administration, Writing—original draft. **Rachel S. Poretsky:** Funding acquisition, Project administration, Resources, Writing—review & editing. **Barry A. Berejikian:** Resources, Supervision, Writing—review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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