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The Effect of Light Intensity, Alga Concentration, and Prey Density on the Feeding Behavior of Delta Smelt Larvae

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Abstract.—Understanding how environmental factors influence first feeding success is critical for the conservation-oriented larval culture of delta smelt *Hypomesus transpacificus*, a threatened osmerid endemic to the San Francisco Estuary. We investigated the effects of light intensity, alga concentration, and prey (rotifer) density on feeding of cultured delta smelt larvae. In one experiment, first feeding larvae were exposed to three light intensities (0.01, 0.3, and 1.9 μmoles $\cdot s^{-1} \cdot m^{-2}$) and three alga concentrations (0, 0.5, and 2 $\times 10^6$ cells/mL). Intestinal contents were examined to determine the incidence of feeding and gut fillness. Maximum feeding responses (92% feeding; 4.8 rotifers/feeding larva in 2 h) were observed at the highest light intensity and alga concentrations; feeding sharply declined with a reduction of either factor. A second experiment was performed to study the effect of alga concentration (0, 1.5, 3, and 6×10^6 cells/mL) in more detail. Feeding responses were very low without algae (13% feeding; 2.1 rotifers/feeding larva in 2 h), but dramatically increased at high concentrations (83% feeding; 5.1 rotifers/feeding larvae in 2 h). In a third experiment, the effect of prey (rotifer) density (0.1, 1, 10, and 100 rotifers/mL) was tested, which significantly enhanced feeding up to the 10/mL treatment (84% feeding; 4.2 rotifers/feeding larvae in 1 h). All three environmental factors significantly affected feeding success of larval delta smelt. Optimization of these factors has improved survival and growth during the sensitive larval period and has improved laboratory culture of delta smelt.

Introduction

Delta smelt *Hypomesus transpacificus* are small euryhaline fish endemic to the San Francisco Estuary. They inhabit low salinity estuarine areas (2–7 g/L), but adults can be found in fresh and brackish waters at salinities up to 18.4 g/L and temperatures ranging from 6°C to 28°C (Moyle 2002). Previously one of the most common pelagic fish in the San Francisco Estuary, delta smelt have dramatically declined in abundance since the 1980s and were listed as threatened in 1993 under the Federal and California Endangered Species Acts (USFWS 1993). Since, there has been continued interest to develop culture techniques to support delta smelt research. Delta smelt are an environmentally sensitive estuarine fish that can be used as an "indicator species" for the ecosystem. Understanding the causes of their decline will be helpful to the risk assessment of other native species.

Low feeding success and survival during the early larval period hampered previous efforts to culture delta smelt. Failure to establish exogenous feeding at the right time and consume adequate amounts of food results in high mortality (Hjort 1914) due to catabolism of larval body tissues (Ivlev 1961). Lack of food intake for even a short duration could lead to abnormal development and behavior of larval fish (Ivlev 1961; Gisbert and Williot 1997). The optimization of feeding conditions would help improve growth rates and reduce mortality of delta smelt during the sensitive and prolonged larval period (Mager et al. 2004, this volume).

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Many fish larvae are visual predators, and their feeding behavior is affected by light (Blaxter 1981). Reduction in light intensity below a visual threshold can impair foraging efficiency or stop feeding altogether (Blaxter 1986; Miner and Stein 1993). The density of suspended particles can influence the feeding conditions of larvae by limiting light penetration into the water column. The quality of light (light spectrum) can also influence larval feeding success (Downing and Litvak 2001). Light intensity and turbidity play important roles in feeding and survival of fish larvae under laboratory and wild conditions (Miner and Stein 1993; Cobcroft et al. 2001; Utne-Palm and Stiansen 2002).

The presence of suspended particles enhanced feeding and growth rates of rainbow smelt *Osmerus mordax* (Sirois and Dodson 2000), Pacific herring *Clupea pallasi* (Boehlert and Morgan 1985), Atlantic halibut *Hippoglossus hippoglossus,* (Naas et al. 1992), and walleye *Stizostedion vitreum* (Rieger and Summerfelt 1997). The positive effects of turbidity were associated with the visual contrast between prey and background (Boehlert and Morgan 1985), reducing feeding energy cost (Sirois and Dodson 2000), and facilitating predator avoidance (Boehlert and Morgan 1985). However, high turbidity has also had adverse effects on larval feeding of striped bass *Morone saxatilis* (Breitburg 1988) and gulf killifish *Fundulus grandis* (Benfield and Minello 1996); Chesney (1989) found no effect of turbidity (0–150 ppm kaolin) on gut fullness and growth of striped bass larvae. There is no information on the effects of turbidity on feeding behavior of larval delta smelt. However, it was reported that unicellular algae was necessary in rearing water to initiate feeding (Mager 1996).

The effect of prey density on larval feeding has been studied for many freshwater and marine species. Higher prey densities increased feeding rates of tautog *Tautoga onitis* (Schoedinger and Epifanio 1997), rainbow smelt (Sirois and Dodson 2000), Atlantic cod *Gadus morhua* (Puvanendran and Brown 1999), gilthead seabream *Sparus auratus* (Parra and Yufera 2000), and pikeperch *Stizostedion lucioperca* (Ljunggren 2002). The effect was associated with increased encounter rates between predator and prey, leading to improved growth and survival (Werner and Blaxter 1980; Kiorboe and Munk 1986). In contrast, low prey densities reduced growth rates and increased larval mortality of many fish species (Werner and Blaxter 1980; Houde 1987; Duffy et al. 1996; Puvanendran and Brown 1999).

This study was conducted to determine how three variables—light intensity, suspended alga concentration, and prey density—influence feeding incidence and gut fullness of cultured larval delta smelt at the onset of exogenous feeding.

Methods

Animals and experimental procedures

Delta smelt were obtained from the University of California at Davis's Delta Smelt Culture Facility at the State Water Project site in Byron, California. Wild-caught juveniles were reared to full sexual maturity and spawned naturally in freshwater within 1,000-L circular tanks. Fertilized eggs were collected daily from the tank bottom and incubated at 15–17°C until hatching (8–10 d). Newly hatched yolk sac larvae originated from the same mating cohort for each experiment and were maintained until 6 days posthatch (dph) in 2-L beakers (500 larvae/2-L beaker). The beakers were covered on sides and bottom with black plastic so that all light originated overhead. Water was gently aerated and changed daily. At 7 dph, the yolk sac was nearly resorbed, but the oil-globule was still present. Larvae (5–7 mm total length) were randomly distributed among treatments at a stocking density of 20/beaker (10/L). Rotifers *Brachionus plicatilis* were added as prey to each beaker to initiate the larval feeding trials. The content of each beaker was mixed with a pipette every 20 min to ensure that algae and rotifers remained well suspended. This method has been used in previous experiments (authors' unpublished data) to maintain suspension of live prey and particulate matter and does not adversely influence feeding ability. Larvae were allowed to feed for 2 h in experiments one and two and for 1 h in experiment three. At termination of feeding, beaker contents were passed through a 600-μm-mesh sieve to collect larvae, which

were immediately euthanatized (500 mg/L MS-222) and preserved in 5% neutral buffered formalin. The transparent larvae were examined under a dissecting microscope within 4–6 weeks after fixation to quantify feeding incidence (percent of larvae feeding) and the degree of gut fullness (number of rotifers consumed per larva). Rotifers were enumerated in situ, with few dissections required to verify in situ counts.

Conditions for each experiment

Three experiments were conducted during the 1999 (experiments one and two) and 2002 (experiment three) spawning seasons to evaluate the effects of light intensity, alga concentration, and prey (rotifer) density on first feeding success of delta smelt larvae.

Experiment one: effects of light intensity and alga concentration on feeding behavior of delta smelt larvae

A two-factor, crossed design incorporated three light intensities (0.01, 0.3, and 1.9 μmoles $\cdot s^{-1} \cdot m^{-2}$, or 0.1, 3.6, and 22.8 lx, conversion from Biggs 1986) and three alga concentrations (0, 0.5, and 2×10^6 cells/mL; 1, 3, and 11 NTU using a 2100P turbidity meter, HACH Company, Loveland, Colorado). Light intensity was measured at the water surface using a LI-250 light meter (LI-COR Inc., Lincoln, Nebraska). Larvae were randomly distributed among 27 beakers (three replicate beakers per treatment) and were placed in three water baths (17°C) to acclimate overnight. Light treatments (water baths with beakers) were separated with black plastic from ceiling to floor to omit extraneous lighting. Two overhead 13-W fluorescent lights installed 0.5 m above the water surface (1.9 μmoles $\cdot s^{-1} \cdot m^{-2}$) illuminated one water bath. The two remaining water baths were illuminated using one fluorescent light and were covered with layers of shade cloth to decrease the light intensity to 0.01 and 0.3 μmoles $\cdot s^{-1} \cdot m^{-2}$. Beakers in the lowest light intensity treatment investigated the ability of larvae to feed in the dark. Cryopreserved *Nannochloropsis* (Reed Mariculture Inc., San Jose, California) were added to each beaker to yield three concentrations at each light level (0, 0.5, and 2×10^6 cells/mL). Rotifers were added to each beaker (10/mL) to start the feeding trial.

Experiment two: effect of suspended algae on first feeding behavior of delta smelt larvae

Four concentrations of algae were tested under constant light intensity (0.3 μmoles $\cdot s^{-1} \cdot m^{-2}$; 13-W fluorescent bulb) to determine the effect of suspended alga particles on feeding of delta smelt larvae. Larvae were randomly distributed among 24 beakers (6 replicate beakers per treatment) and were placed in a water bath (16°C) to acclimate overnight. Cryo-preserved *Nannochloropsis* was added to the beakers to obtain four alga concentrations: 0, 1.5, 3, and 6×10^6 cells/mL (2, 10, 18, and 35 NTU), and rotifers were added to each beaker (10/mL) to initiate the feeding trial.

Experiment three: effect of prey density on first feeding behavior of delta smelt larvae

Four rotifer densities were tested to evaluate the effect of prey density on the first feeding behavior of delta smelt larvae. Larvae were randomly distributed among 16 beakers (4 replicate beakers per treatment). After acclimating for 2 h at 17°C, algae paste (*Nannochloropsis* 3600- premium fresh; Reed Mariculture Inc., San Jose, California) was added to all beakers at a level known to elicit a feeding response (6×10^6 cells/mL; 25 NTU). Analysis of data from 1999 determined that larvae fed well (>90% incidence) at a light intensity of 1.9 μmoles $\cdot s^{-1} \cdot m^{-2}$. Since then, we determined that the higher light level (6.0 μmoles $\cdot s^{-1} \cdot m^{-2}$; 25-W fluorescent bulbs) in our larval production facility does not have an adverse affect on feeding behavior, hence the higher light intensity used for this trial. Rotifers were added to the beakers at four prey densities (0.1, 1.0, 10, and 100/mL).

Statistics

Feeding responses (feeding incidence and gut fullness) were examined by analysis of vari-

ance (ANOVA) after testing for normality and homogeneity of variance (SAS/STAT; SAS Institute 1985). Feeding incidence data were $\log_{10}$-transformed in experiment one and arcsine square root-transformed in experiments two and three. A one-way ANOVA model was used to analyze gut fullness data from experiment one, due to the unbalanced design resulting from exclusion of nonfeeding groups. When the treatment effect was significant ($P < 0.05$), Tukey's test was used for the separation of means (Snedecor and Cochran 1993).

Results

The intestine of first feeding delta smelt larvae remained transparent after fixation, allowing for accurate counts of consumed prey. Use of anesthetic (MS-222) helped to relax the larvae prior to preservation resulting in straighter larvae, which were easier to process. No apparent regurgitation of ingested rotifers was observed after submersion in the anesthetic.

Delta smelt larvae were allowed to feed for 2 h in the first two experiments. Closer examination of the larvae revealed that many of the ingested rotifers were at or near the posterior end of the intestine, so there was concern that some could be lost through defecation. Consequently, the period of exposure to prey was shortened to 1 h in the third experiment, which was found sufficient to quantify feeding response.

Experiment one: effect of light intensity and alga concentration

Light intensity and alga concentration significantly influenced feeding of delta smelt larvae with a significant interaction ($P < 0.001$) between the two factors (Figure 1). Maximum feeding responses were observed at the highest alga concentration and light intensity (92% feeding; 4.8 rotifers/feeding larva in 2 h). High alga concentration did not stimulate feeding at low light intensity (3.3% feeding; 1.5 rotifers/feeding larva in 2 h). Feeding responses in clear water (no algae) were low (0–7% feeding; 0–1.2 rotifers/feeding larva in 2 h) at all light intensities, unlike the results at high alga concentration. Moreover, high intensity light appeared to inhibit feeding at the low alga concentration (0.5×10^6 cells/mL). Light and algae were both necessary in sufficient quantities (1.9 μmoles $\cdot s^{-1} \cdot m^{-2}$; 2.0×10^6 cells/mL) to elicit the best feeding response (>90% incidence). When algae or light was reduced, the response to the other variable sharply declined, which explains the observed interaction.

Experiment two: effect of suspended algae

Alga concentration had a significant ($P < 0.001$) effect on feeding incidence and gut fullness (Figure 2). A poor feeding response was observed in clear water (12% feeding; 2.1 rotifers/feeding larva in 2 h), similar to the first experiment. Most larvae in clear water occupied positions along the beaker walls, with only few larvae feeding in the center water column. Feeding increased with increasing alga cell density, reaching the highest response (82% feeding; 5.1 rotifers/feeding larva in 2 h) at 3×10^6 cells/mL; no further increase was observed at 6×10^6 cells/mL (83% feeding; 5.1 rotifers/feeding larva in 2 h). The majority of larvae in these treatments were feeding throughout the water column by coiling into an "S" shape position and thrusting forward to capture their prey.

Experiment three: effect of prey density

Prey density significantly influenced feeding incidence ($P < 0.001$) and gut fullness ($P = 0.01$) of delta smelt larvae (Figure 3). Both feeding responses increased with increasing rotifer density up to 10/mL (84% feeding; 4.2 rotifers/feeding larva in 1 h), with no further increase at the highest prey density, 100/mL (85% feeding; 3.9 rotifers/feeding larva in 1 h). Feeding responses were significantly lower at prey densities of 1/mL (49% feeding; 3.4 rotifers/feeding larvae in 1 h) and 0.1/mL (10% feeding; 2.1 rotifer/larva in 1 h).

Discussion

Successful culture of delta smelt is dependent on establishing suitable environmental con-

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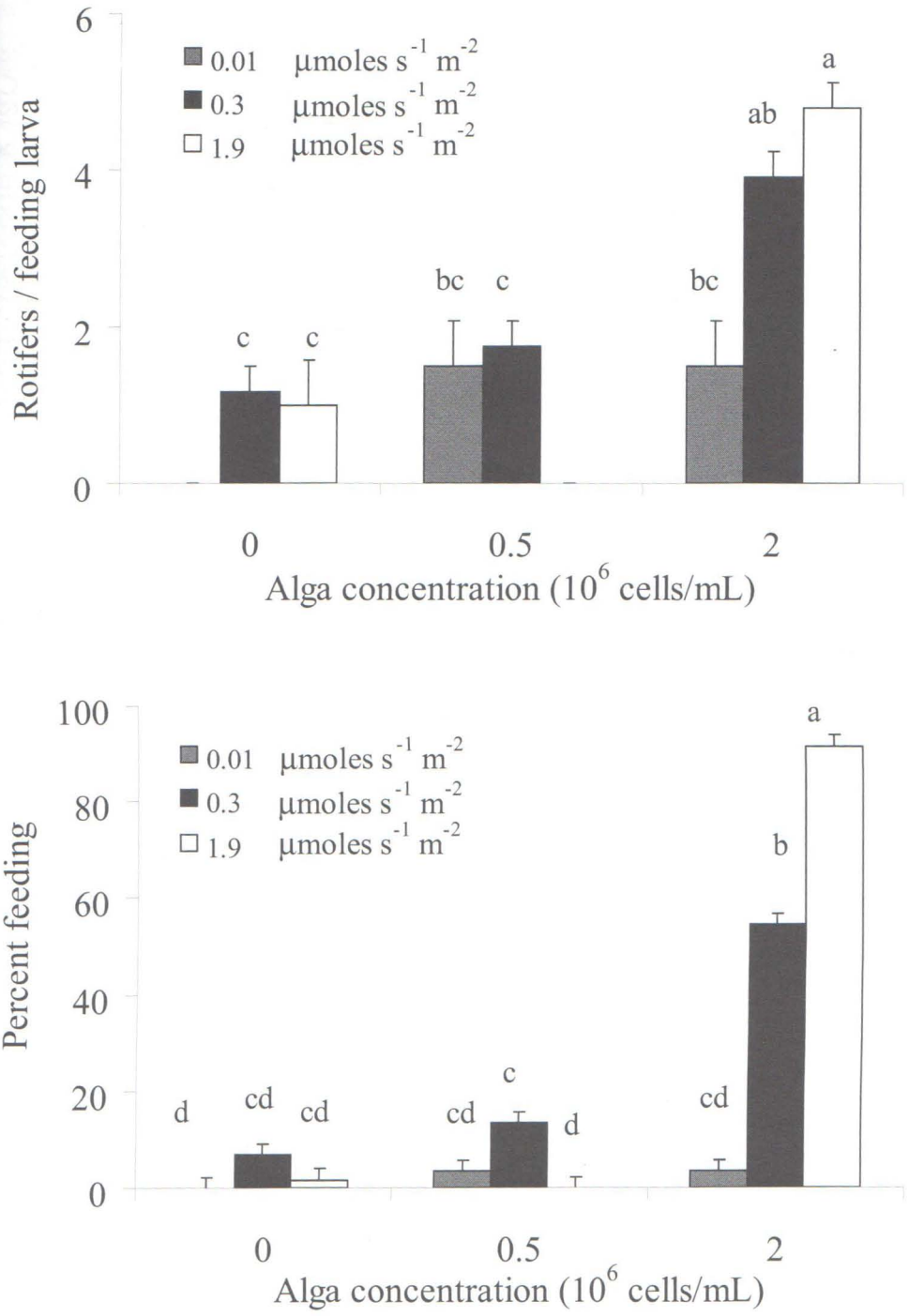


FIGURE 1. The effect of light intensity (0.01, 0.3, and 1.9 µmoles · s^{-1} · m^{-2}) and alga concentration (0, 0.5, and 2.0 × 10^6 cells/mL) on feeding incidence (percent feeding; top) and gut fullness (number of rotifers consumed per feeding larva; bottom). Values represent the treatment mean ± SE based on the ANOVA model. Delta smelt larvae were fed rotifers for 2 h at a prey density of 10/mL. Treatments with different superscripts were significantly different ($P \leq 0.05$).

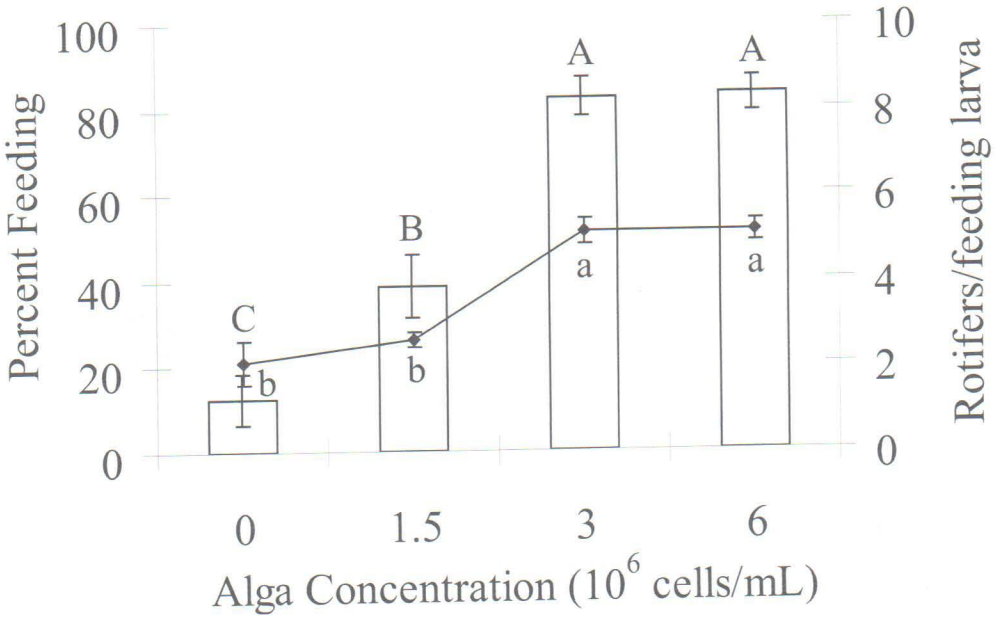


FIGURE 2. The effect of alga concentration (0, 1.5, 3, and 6 × 10^6 cells/mL) on first feeding behavior of delta smelt larvae. Values represent the treatment mean ± SE. Feeding incidence (percent feeding; bars) and gut fullness (number of rotifers consumed per feeding larvae; line) were significantly different for treatments with different uppercase and lower case letters, respectively ($P \leq 0.05$).

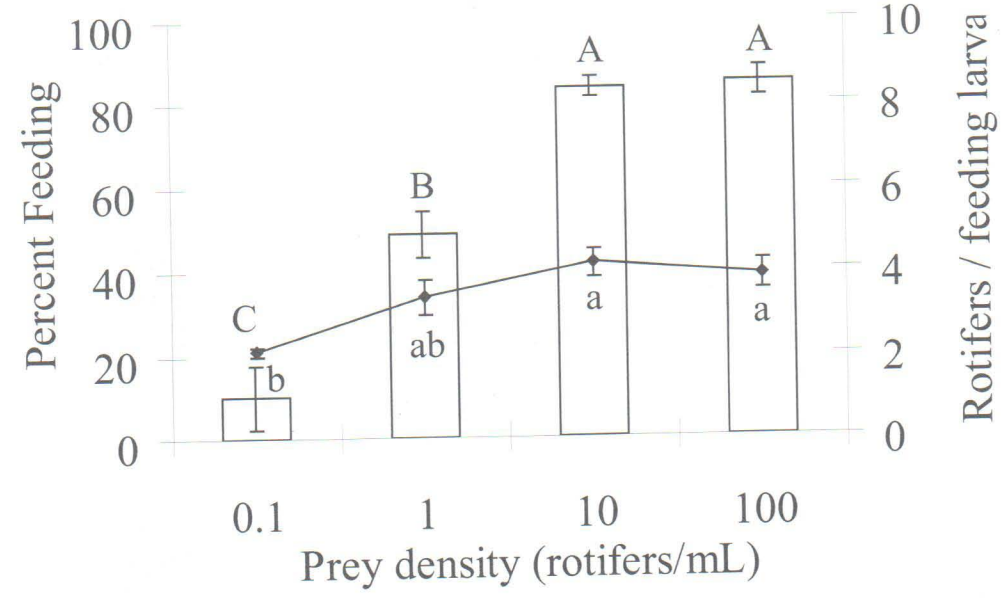
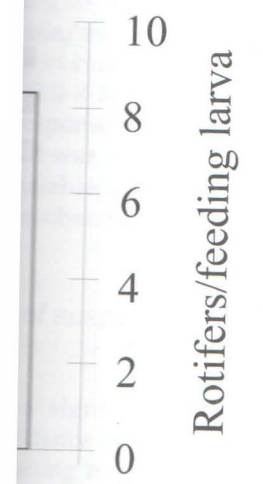


FIGURE 3. The effect of rotifer density (0.1, 1, 10, and 100 rotifers/mL) on first feeding behavior of delta smelt larvae. Values represent the treatment mean ± SE. Feeding incidence (percent feeding; bars) and gut fullness (number of rotifers consumed per feeding larvae; line) were significantly different for treatments with different uppercase and lower case letters, respectively ($P \leq 0.05$).



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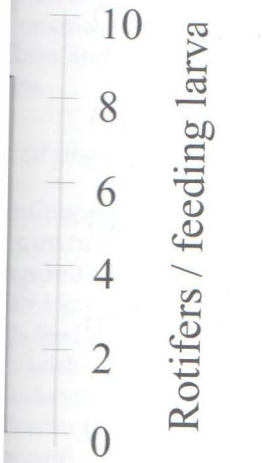

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ditions at the onset of feeding. Characteristics of the artificial habitat can be manipulated in the laboratory to test how each factor influences feeding. This study revealed that environmental conditions are critical during first feeding for delta smelt larvae. Different levels of three environmental factors (light intensity, alga concentration, and prey density) affected larval feeding success and had important roles in developing a successful culture program of this threatened species.

Adequate levels of light intensity and alga concentration were necessary to promote feeding of delta smelt larvae, and a reduction of either factor significantly affected their larval feeding ability. An interaction was also observed between these two variables as a high response to light intensity at the high alga concentration, but little or no response to light intensity at the lower alga levels. Miner and Stein (1993) reported a similar interactive effect on feeding for larval bluegill *Lepomis macrochirus*, with high water turbidity enhancing feeding at high light intensity, but inhibiting feeding at a low light intensity. The highest light intensity tested in experiment one was relatively low (1.9 μmoles $\cdot s^{-1} \cdot m^{-2}$), compared to other studies (upper limit tested usually > 20 μmoles $\cdot s^{-1} \cdot m^{-2}$; Chesney 1989; Benfield and Minello 1996; Cobcroft et al. 2001; Downing and Litvak 2001; Utne-Palm and Stiansen 2002). In contrast with these studies, practically all delta smelt in our experiment (92%) were feeding at 1.9 μmoles $\cdot s^{-1} \cdot m^{-2}$ at the highest alga concentration (Figure 1), which demonstrates that this light intensity was sufficiently above the threshold to allow most larvae to feed.

The beneficial effect of algae on feeding of delta smelt larvae, as well as many marine larvae, is not entirely understood. While algae can provide chemical cues or serve as a food supplement, their immediate effect on feeding of delta smelt appears to be related to visual mechanisms of feeding. Their limited ability to feed under low light intensity (0.01 μmoles $\cdot s^{-1} \cdot m^{-2}$), regardless of the alga concentration, suggests that they are largely visual predators. Suspended particles in the water column may provide a visual contrast enabling delta smelt larvae to better locate and ingest their prey as has been suggested for Pacific herring (Boehlert and Morgan 1985). Swimming behavior of delta smelt was also influenced by the presence of algae. Without algae, larvae aggregated along the beaker walls and were not feeding, despite the presence of prey. Immediately following the addition of algae, delta smelt larvae swam away from the tank walls and began feeding in the water column. A similar "clinging" behavior in clear water has been described for larval walleye (Bristow and Summerfelt 1994; Rieger and Summerfelt 1997).

The first experiment demonstrated that sufficient amounts of light and suspended algae were necessary to create conditions suitable to elicit a first feeding response. The effect of suspended algae was further tested in experiment two. Very few rotifers were ingested in clear water, consistent with earlier observations (Mager 1996), but feeding incidence and gut fullness increased with increasing alga concentration up to 3×10^6 cells/mL (Figure 2). Recent data supports that delta smelt remain dependent on suspended algae at 34 dph (total length 11–15 mm) and improve their foraging ability in clear water only at a more advanced stage of development (length 20 mm), when they approach metamorphosis (authors' unpublished data). Thus, suspended particles and light intensity are of concern during the entire larval period.

Sirois and Dodson (2000) reported a positive effect of turbidity on the growth of rainbow smelt larvae and attributed this increase to a reduction in energetic cost, rather than increased prey ingestion rate. In our study, with short-term exposure to turbid treatments, we observed an increase in the number of rotifers consumed with increasing alga concentration. Delta smelt are presumably well adapted to living in the mixing zone of the upper estuary where they are subjected to varying turbidity (5–100 NTU). It is not surprising that they are better able to forage under turbid conditions, which may also provide refuge from predators.

The effect of prey density on larval feeding was examined in experiment three, in order to optimize current feeding protocols at the Delta Smelt Culture Facility. This experiment utilized optimal alga concentrations, determined from the two previous experiments

and a light intensity higher than the previous experiments, but appropriate for feeding of larval delta smelt (authors' unpublished data). The increase of prey density from 0.1 to 10 rotifers/mL increased feeding incidence of delta smelt larvae from 10% to 85%. It appears that delta smelt larvae require relatively high (10/mL) concentrations of zooplankton at the onset of feeding, at least under our culture conditions. Low prey densities extended the duration of the larval period of weakfish *Cynoscion regalis* (Duffy et al. 1996) and gilthead seabream (Parra and Yufera 2000). Reduced growth rates during early life stages can result in increased cost of culture and susceptibility to disease. In intensive culture, suboptimal prey densities may result in greater variation in size and reduced survival. Feeding success at the transition from endogenous to exogenous feeding may be a valuable indicator of future survival. Parra and Yufera (2000) reported that survival of gilthead seabream juveniles was closely associated with feeding success of larvae at the onset of exogenous feeding.

In conclusion, three factors examined in this study (light intensity, alga concentration, and prey density) had significant effects on feeding success of cultured delta smelt larvae. Each of these variables significantly influenced feeding response and a low level of even one factor resulted in a poor response. Unfavorable environmental conditions during initiation of larval feeding can result in high mortality and poor recruitment to the adult stage. Optimization of feeding conditions for delta smelt during the larval period has led to the successful culture of this species and has provided considerable knowledge of their early life history.

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