Alaska
Fisheries Science
Center

National Marine
Fisheries Service

U.S DEPARTMENT OF COMMERCE

AFSC PROCESSED REPORT 2007-06

Optimization of Feeding and Growth Conditions for Walleye Pollock *Theragra chalcogramma* (Pallas) Larvae Reared in the Laboratory

July 2007

This document should be cited as follows:

S. M. Porter, and K. M. Bailey. 2007. Optimization of feeding and growth conditions for walleye pollock *Theragra chalcogramma* (Pallas) larvae reared in the laboratory. AFSC Processed Rep. 2007-06, 20 p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar, Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

Notice to Users of this Document

This document is being made available in .PDF format for the convenience of users; however, the accuracy and correctness of the document can only be certified as was presented in the original hard copy format.

Optimization of Feeding and Growth Conditions for Walleye Pollock *Theragra chalcogramma* (Pallas) Larvae Reared in the Laboratory

By

Steven M. Porter and Kevin M. Bailey

Resource Assessment and Conservation Engineering Division
Alaska Fisheries Science Center
National Marine Fisheries Service
National Oceanic and Atmospheric Administration
7600 Sand Point Way NE
Seattle, WA 98115

July 2007

ABSTRACT

A series of experiments were conducted to identify optimal rearing conditions for walleye pollock *Theragra chalcogramma* (Pallas) larvae. Experiments examined the influence of light spectrum (amount of ultraviolet (UV) light), temperature, prey type and density, first exposure to prey, and turbulence. Natural prey (zooplankton), prey density, and temperature positively affected feeding and/or growth. Moderate turbulence, and age of first exposure to prey were not important factors. UV light had a negative effect on feeding and growth. The optimum conditions for rearing walleye pollock larvae include temperatures near 10° C, a natural zooplankton diet (minimum prey density of 500 per liter), full spectrum fluorescent light bulbs, and clear, acrylic tank covers used to reduce the amount of UV light entering the tank to lessen the chance of UV light injury to the larvae. Visible light level should not exceed 13 μmol photons per m^2 per second.

CONTENTS

INTRODUCTION

Walleye pollock *Theragra chalcogramma* (Pallas) is a commercially important fish species with annual catches in Alaska waters (Gulf of Alaska and Bering Sea) averaging 1.2 million metric tons a year (FAO 2002) worth about US $300 million. There is currently no commercial aquaculture of walleye pollock, but larvae have been successfully reared since the 1980s. Small-scale laboratory rearing has been used to study various aspects of their early life history to better understand conditions that support growth and survival requirements of this species.

Factors that are most easily manipulated when rearing fish larvae in the laboratory are light, temperature, and prey type and density. Walleye pollock larvae are visual predators and require a minimum threshold light level to feed (Paul 1983). Recently, many fish have been shown to have ultraviolet-A (320 – 400 nm, UV-A) sensitive cone pigments in their eyes (Losey et al. 1999). Ability to see in the UV wavelengths may help feeding by providing higher contrast between the background and the prey (Losey et al. 1999). Temperature is an important environmental factor because of its effects on physiological processes in fish. Laboratory studies have shown that prey type can affect growth (Davis and Olla 1992), and prey density can have an effect on the timing of first feeding, the percentage of larvae feeding, and their growth, survival and ingestion rates (Parra and Yufera 2000).

This study reports on a series of experiments manipulating light spectrum (the amount of UV light), temperature, prey type and density, first exposure to prey, and turbulence to examine optimal rearing conditions for walleye pollock larvae.

MATERIALS AND METHODS

General Rearing Methods

Adult walleye pollock in spawning condition were collected by trawl or hook and line from the Bering Sea, Gulf of Alaska, or Puget Sound, Washington. Eggs from one to three females were stripped and fertilized with sperm from one to three males (Table 1). Rearing was conducted at the Alaska Fisheries Science Center in Seattle, Washington, except in 1987 where it was done at the Northwest Fisheries Science Center's facility located at Manchester, Washington. Eggs were incubated in the dark in 4 liter (L) glass jars until they were near hatching, then were transferred into circular black tanks ranging in size from 20 to 120 L. Keeping the eggs in darkness until hatching simulates natural conditions in the wild, as eggs are located deep in the water column and rise slowly towards the surface during development. A 16/8 hour light/dark cycle was started at hatching, and black screening tank covers were used to adjust the visible light level in the tanks to 2.5 μmol photons per m^2 per second using full spectrum fluorescent light bulbs (General Electric C50). A similar light level was used for all the experiments conducted in our study. The prey types used to feed walleye pollock larvae were laboratory-cultured rotifers (*Brachionus plicatilis*; cultured on a mixture of the algae *Isochrysis galbana*, and Microfeast L-10 Larval Diet (Provesta) and AquaGrow Advantage (Advanced BioNutrition) artificial feeds), and natural zooplankton (a mixture of *Acartia* sp. copepod nauplii and copedodites, and gastropod and polychaete larvae; ≤ 202 μm) collected from a local lagoon. Prey were added about 2 days before the estimated day of first feeding.

All feeding experiments presented in this report were conducted in the morning after an extended period of 12-15 hours of darkness that allowed the larvae to void their gut of prey from the previous day. Lights were turned on and the larvae fed for a specific amount of time, then the tanks were covered with black plastic to stop feeding and larvae were preserved in 5% formalin. Feeding was measured by the number of prey in the midgut; the midgut was dissected using fine needles and a dissecting microscope, and the number of prey in it was recorded. Standard length (SL) was measured to the nearest 0.08 mm using an ocular micrometer on a dissecting microscope. All statistical tests were conducted using Systat version 11 statistical software.

Experiments to Determine Optimal Rearing Conditions

Eight experiments were conducted to examine how various rearing conditions affected larval walleye pollock feeding and growth (Table 1).

Effect of different prey types on growth

All walleye pollock larvae used in this experiment were initially reared at 6° C in the same 120 L tank and fed rotifers at a density of approximately 10,000 per liter. At 24 days after hatching (dah) the experiment was started; larvae were divided between three separate 120-L tanks (1 tank for each treatment) each with 250 larvae. The experiment was run for 2 weeks (from 24 to 38 dah, which is 19 to 33 days after first feeding, respectively) using 3 different types of prey: 1) rotifers; 2) natural zooplankton (the size fraction less than 333 μm; a mixture of *Acartia* sp. copepod nauplii and copedodites, and gastropod and polychaete larvae); 3) and just-hatched *Artemia* nauplii. The mean density of each prey type in the tanks was 19,000 rotifers per liter, 1,300 zooplankton per liter, and 2,500 *Artemia* per liter. These prey levels were selected to allow the larvae to feed at maximum rate of ingestion based on our previous, unpublished work. A minimum of 10 live larvae were measured from each tank starting at the beginning of the experiment and then once each week. The data were fourth-root transformed to reduce heteroscedasticity and ANCOVA was used to compare the slopes of larval growth rate for each prey type. The Student-Newman-Kuels multiple comparison test was performed to determine differences in growth among diet types (Zar 1996).

Effect of different prey densities on growth and feeding

Prey densities of 10, 30, 50, and 500 natural zooplankton per liter (size fraction < 149 μm) were used to determine the effect of prey density on larval feeding and growth at 6° C, and to determine a minimum prey density for growth and feeding. A single 120-L tank was used for each prey density and 1,000 larvae were stocked in each tank. On the day of the experiment, 20 larvae were sampled after 0, 1.5, 3, and 6 hours of feeding. Experiments were conducted 9, 13, and 17 dah (3, 7, and 11 days after first feeding, respectively). The Kruskal-Wallis test and Dunn multiple comparison test were used to compare feeding (number of prey in the midgut) at each prey density. ANCOVA was used to examine growth rates among prey densities.

Effect of first exposure to prey on feeding

Between hatching and first feeding, two groups of larvae were reared in separate 120-L tanks at 6° C. One group was exposed to a 750 natural zooplankton per liter (size fraction < 202 μm) prey density beginning 5 days before first feeding, and the second group of larvae were not exposed to any prey. At first feeding (determined by when the larvae in the tank with prey began feeding), 100 larvae from each group were transferred into each of four replicate 20-L tanks without any prey added. One day later (9 dah, 1 day after first feeding) 500 *Acartia* sp. copepod nauplii per liter were added to each tank, the larvae were allowed to feed for 6 hours, and then all were preserved. In addition to testing for differences in the number of prey in the midgut between treatments, ANOVA was also used to test for differences in the percentage of larvae feeding (data were arcsin ($x^{0.5}$) transformed).

Effect of temperature on feeding and growth rates

Feeding -- Separate groups of larvae were reared at 2° and 6° C in four replicate 20-L tanks. Each tank was stocked with 300 larvae and 100 natural zooplankton per liter prey (size fraction < 202 μm). The experiments were conducted such that larvae at each temperature would be of similar size (length) on the day the experiment was run. At 6° C the experiment was conducted 17 dah (10 days after first feeding) and at 33 dah for the 2° C larvae (21 days after first feeding). Larvae were sampled after 0, 1 and 2 hours of feeding. Fifteen larvae were sampled from each tank at 6° C, and five larvae were sampled from each tank at 2° C due to lower numbers remaining. ANOVA was used to compare the number of prey in the midgut between temperatures.

Growth -- Walleye pollock larvae were reared at 9.9° C from hatching to first feeding in 3, 120-L tanks containing 700 larvae each. At first feeding, the temperature in one of the tanks was reduced to 7.4°, and another to 5.7° C. Larvae were fed rotifers at a density of 10,000 per liter, and standard length measurements of 5 – 10 live larvae were taken at 8, 15, and 20 dah (0, 7, and 12 days after first feeding, respectively). The fourth-root data transformation was used to reduce heteroscedasticity. Growth rates were compared using ANCOVA, and the Student-Newman-Kuels multiple comparison test.

Effect of turbulence on feeding

Two experiments were conducted to examine the effect of turbulence on larval walleye pollock feeding. A shaker table (Lab-Line Instruments, Inc., Model 3520; which moved in circular oscillations) was used to generate moderate turbulence in 4-L glass jars ¾ full of filtered seawater. Shaker table RPM was used to adjust the level of turbulence in the jars. The experimental setup was as follows: The jars contained 50 larvae and the experiments were conducted at 6° C. The treatments used were: 1) turbulence exposure for a specific number of days before the experiment was run, 2) first exposure to turbulence on the day of the experiment, and 3) no turbulence. There were three replicate jars for each treatment.

Experiment 1 -- Two days after hatching the larvae were placed into jars. The next day (3 dah) rotifers at a density of 10,000 per liter were added, and three jars were treated with turbulence (shaker table running at 60 RPM, relative centrifugal force = 0.032 g) for 12 days before the experiment was conducted. At 15 dah (7 days after first feeding), the experiment was run for 2 hours with the shaker table running at 70 RPM (relative

centrifugal force = 0.044 g) and with a prey density of 20,000 rotifers per liter. All larvae were preserved at the end of the experiment.

Experiment 2 -- Larvae were reared in a 120-L tank until 17 dah, and during this time they were fed 10,000 rotifers per liter. At 17 dah (9 days after first feeding), larvae were moved into jars containing 1,000 natural zooplankton per liter prey (size fraction less than 202 μm), and three jars were treated with turbulence (shaker table running at 50 RPM, relative centrifugal force = 0.022 g) for 5 days before the experiment was run. At 22 dah (14 days after first feeding) the experiment was conducted for 2.5 hours with the shaker table running at 70 RPM (relative centrifugal force = 0.044 g) and with a natural zooplankton density of 1,700 per liter. All larvae were preserved at the end of the experiment.

Analysis -- The percentage of larvae feeding in each treatment were compared using ANOVA after the data were arcsin ($x^{0.5}$) transformed. ANOVA was also used to compare the number of prey in the midgut among treatments.

Effect of ultraviolet (UV) light on feeding and growth

A spectraradiometer was used to measure the spectrum of light emitted from full spectrum fluorescent light bulbs (GE C50) used for rearing. Clear, acrylic tank covers (2 mm thick) were used to reduce the amount of UV light entering the tanks and black screening tank covers were used to adjust the visible light level in the tanks to 2.5 μmol photons per m^2 per second. Six 20-L tanks were stocked with 200 eggs each, and three replicate tanks were used for each treatment (reduced UV light and full UV). The experiment was conducted at 6°C. Rotifers at a mean density of 10,000 per liter were used as prey. Ten larvae were sampled from each replicate tank at 5, 9 and 15 dah (first feeding, 4, and 10 days after first feeding) to examine feeding and growth. The number of prey in the midgut for each treatment were compared using ANOVA after applying the fourth-root data transformation to make the data normally distributed. ANCOVA was used to examine growth rate.

RESULTS

Effect of different prey types on growth

Larval SL was not significantly different among diet types at the beginning of the experiment (ANOVA, $F_{2, 42} = 0.53$, $P = 0.59$). Over the time period examined the growth rates of the larvae were significantly different among diets (ANCOVA, $F_{2, 189} = 3.25$, $P = 0.04$, Fig. 1). Walleye pollock larvae that were fed zooplankton grew significantly faster than those fed rotifers ($P = 0.05$, growth rate 0.16 and 0.07 mm per day for zooplankton and rotifer diets, respectively). Larval growth rate on *Artemia* (0.11 mm per day) could not be discerned between zooplankton and rotifer diets ($P = 0.23$ and 0.18, respectively). However, there is evidence that growth on *Artemia* was more similar to that of the rotifer diet because after 2 weeks of feeding the standard length of rotifer-fed and *Artemia*-fed larvae were not significantly different (Tukey multiple comparison test, $P = 0.42$), and zooplankton-fed larvae were significantly greater in length than the larvae from either of the other two diets (Tukey multiple comparison test, $P = 0.02$ for *Artemia*, $P < 0.001$ for rotifers).

Effect of different prey densities on feeding and growth

Only the 3 and 6 hour samples were used to compare feeding at different prey densities because it takes 4 to 5 hours for walleye pollock larvae to fill their gut with prey (Canino and Bailey 1995). The mean number of prey in the midgut at time zero was subtracted from the values of the 3 and 6 hour samples.

Feeding -- Results from the experiment run at 17 dah were excluded because these larvae were not feeding well regardless of prey density; a number of larvae in the rearing tanks appeared to be starving. Additionally, larvae on Day 13 had significantly more prey in their midgut than those sampled on Day 17 for both the 50 and 500 natural zooplankton per liter treatments after 3 and 6 hours of feeding (Kruskal-Wallis test, $P < 0.05$ for all cases).

After 3 and 6 hours of feeding, larvae in the highest prey density tank had a significantly greater number of prey in their midgut than those feeding in prey densities of 50 per liter or less for both 9 and 13 dah (Kruskal-Wallis test, $P < 0.001$, Dunn multiple comparison test; Table 2). Feeding at prey densities of 50 per liter or less did not differ significantly at 9 dah (Dunn multiple comparison test; Table 2). At 13 dah after 3 hours of feeding, larvae feeding in the 50 prey per liter treatment had significantly more prey in their midgut than those feeding at 10 per liter (Kruskal-Wallis test, $P < 0.001$, Dunn multiple comparison test; Table 2). After 6 hours, feeding at 50 prey per liter was significantly higher than both 10 and 30 prey per liter, but there was no significant difference between 10 and 30 prey per liter treatments (Kruskal-Wallis test, $P < 0.001$, Dunn multiple comparison test; Table 2). For the age groups examined, walleye pollock larvae fed best at the highest prey density used (500 prey per liter), and their feeding ability improved with age.

For both age groups, the percentage of feeding larvae increased from the lowest to highest prey density. The percentage of feeding larvae also increased with age, with the highest overall percentage of feeding larvae occurring at 6 hours, 13 days after hatching.

Growth -- Walleye pollock larvae grew best at 500 prey per liter (0.04 mm per day), larvae reared at 50 and 30 prey per liter did not grow, and those at 10 per liter showed a negative growth rate indicating that they were starving (ANCOVA, $F_{3, 647} = 25.50$, $P < 0.01$; Tukey Test; Fig. 2).

Effect of first exposure to prey on feeding

There was no significant difference in the number of prey in the midgut of feeding larvae that had been exposed to prey 5 days before first feeding compared to those that had not been exposed to prey until 1 day after first feeding (ANOVA, $F_{1, 6} = 3.02$, $P = 0.13$; Fig. 3). There was also no significant difference in the percentage of feeding larvae between the two treatments (ANOVA, $F_{1, 6} = 3.02$, $P = 0.55$).

Effect of temperature on feeding and growth

Feeding -- Only healthy, feeding larvae from each temperature were used in our analysis. Using a growth rate of 0.11 mm per day for 6° C laboratory-reared walleye pollock (Yamashita and Bailey 1989), it was calculated that on the day of the experiment healthy, feeding larvae at 6° C would be of the size 6.76 mm and larger. Larvae smaller than this size were not used in the analysis. To compare larvae of the same size for each temperature, this size cut-off was also used to exclude small larvae from the 2° C

treatment. The mean number of prey in the midgut at time 0 was subtracted from the 1 and 2-hour samples.

There was no significant difference in the number of prey in the midgut between 2° and 6° C after 1 h of feeding (ANOVA, $F_{1, 6} = 4.05$, $P = 0.09$; Fig. 4), but after 2 hours of feeding there were significantly more prey in the midgut of larvae feeding at 6° C (ANOVA, $F_{1, 6} = 9.14$, $P = 0.02$; Fig. 4). At this time, larvae at 6° C had approximately 2.5 times more prey in their midgut than those at 2° C.

Growth -- Temperature had a significant effect on larval walleye pollock growth rate (ANCOVA, $F_{2, 66} = 14.11$, $P < 0.001$; Fig. 5). Growth rate of larvae at both the high (9.9° C growth rate = 0.10 mm per day) and medium (7.4° C growth rate = 0.08 mm per day) temperatures was about twice that of the low (5.7° C growth rate = 0.05 mm per day) temperature treatment (Student-Newman-Kuels multiple comparison test; $P < 0.001$ for high temperature treatment, and $P = 0.002$ for medium temperature treatment). Growth rate was not significantly different between the high and medium temperatures ($P = 0.09$).

Effect of turbulence on feeding

Both of the experiments showed that larval walleye pollock feeding was not improved at the level of turbulence tested. For Experiment 1, there was no significant difference in the percentage of larvae feeding in turbulent and non-turbulent conditions (ANOVA, $F_{2, 6} = 0.98$, $P = 0.43$; Table 3), and no significant difference in the number of prey in the midgut between conditions (ANOVA, $F_{2, 6} = 0.28$, $P = 0.76$; Table 3). For Experiment 2, larvae were feeding better in the no-turbulence treatment than either of the turbulence treatments with respect to both the percentage of larvae feeding and number of prey in the midgut (for percentage feeding ANOVA, $F_{2, 6} = 13.72$, $P = 0.006$, Tukey Test; for number of prey in the midgut ANOVA, $F_{2, 144} = 9.52$, $P < 0.01$, Tukey Test; Table 3).

Effect of UV light on feeding and growth

UV light in both the A (320 – 400 nm) and B (280 –320 nm) ranges was emitted from the light bulbs (Fig. 6A). UV light entering the tanks was reduced by adding clear, acrylic tank covers (Fig. 6B); peak UV-B light was reduced by 14% and peak UV-A light was reduced by 70%. Larvae reared in reduced UV light fed better than those in full UV light (ANOVA, $F_{1, 12} = 5.74$, $P = 0.03$; Fig. 7A). Overall, larvae feeding in reduced UV light had about 1.5 times more prey in their midgut than those feeding at the higher level. The growth rate of larvae reared in reduced UV light was 2.5 times greater then that of larvae in full UV light (ANCOVA, $F_{1, 14} = 6.78$, $P = 0.02$, Fig. 7B).

DISCUSSION

Prey type and density, temperature, turbulence, and light spectrum all had significant effects on larval walleye pollock feeding and/or growth in our study. Walleye pollock larvae grew best when fed on a diet consisting of natural zooplankton. Growth rates were lower when enriched rotifers or *Artemia* nauplii (both at higher densities) were used. Our results are similar to Davis and Olla (1992) in that walleye pollock larvae had the highest growth when fed a diet of natural zooplankton. Walleye pollock larvae may grow better on natural zooplankton because for fish larvae, copepods are easier to digest

and are higher in essential fatty acids and other important nutrients than enriched *Artemia* nauplii (Sheilds et al. 1999).

Prey density can affect when fish larvae start feeding, the percentage of larvae feeding, and their growth, survival and ingestion rates (Parra and Yúfera 2000). In our experiment, growth rate, ingestion, and the percentage of feeding larvae were greatest at the highest prey density (500 per liter). For rearing walleye pollock larvae during the first week of feeding, 500 prey per liter should be considered a minimum prey density for growth. During the first week after first feeding growth at 6º C using 500 prey per liter was 0.04 mm per day; this is lower than the 0.05 to 0.10 mm per day growth for walleye pollock larvae reared at the same temperature on a mixture of rotifers (10,000 per liter) and natural zooplankton (3,000 per liter) over the same time period (S. Porter, unpublished data). These densities are much higher than the > 20 prey per liter density suggested by Theilacker et al. (1996) as being necessary for optimal growth in the field. Prey levels needed for growth are higher in the laboratory than in the sea, and this may be due to prey in the sea being concentrated in patches or small scale turbulence aiding feeding (MacKenzie et al. 1990).

Rising temperatures have been shown to boost feeding rates in marine fish larvae (Houde 1989). In our study, increasing temperature positively affected feeding; the number of prey consumed nearly tripled for a 4º C increase in temperature. Temperature had a positive effect on growth rate also. For larvae of the reef fish *Pomacentrus coelestis*, temperature had a stronger effect on growth than prey abundance (Meekan et al. 2003). Walleye pollock larvae that have been reared at 9º C had a growth rate of 0.18 mm per day using a prey density of 30,000 to 50,000 rotifers per liter or 1,000 natural zooplankton per liter (Bailey and Stehr 1988). In our study, growth rate at 9.9º C was 0.10 mm per day; the lower prey density used in our study may have contributed to the larvae not growing as fast as those in Bailey and Stehr (1988). The growth rate between 7.4º and 9.9º C was not significantly different, which may possibly indicate that this temperature range could be approaching the high end of the temperature tolerance limit for walleye pollock larvae.

Small-scale turbulence increases contact rates between predator and prey (Rothschild and Osborn 1988), and its effect on larval fish feeding is hypothesized to be bell-shaped, with intermediate levels having the greatest positive effect on feeding (MacKenzie et al. 1994). In our study, turbulence did not improve feeding. This may be due to the level of turbulence used not being optimal for larval walleye pollock feeding. Alternatively, the benefit of turbulence is increased contact rate, but the contact rate may have been saturated due to high prey levels (as in Experiment 1), or turbulence may have been too high and consequently the larvae did not have enough time to react to the prey and capture it (as in Experiment 2). Another factor that may have affected feeding in Experiment 2 is that the type of prey was switched from rotifers to zooplankton. Prior exposure to turbulence also had no significant impact on feeding rates.

Fish larvae are visual predators that rely on sufficiently high light levels to feed (Paul 1983, Blaxter 1986). Threshold light level at which early walleye pollock larvae initiate prey capture is about 0.003 μmol photon per m^2 per second (Paul 1983). Light levels typically used for rearing walleye pollock larvae range between 1 and 4 μmol photons per m^2 per second (Bailey and Stehr 1986, Porter 2001). Having sight in the UV wavelengths can aid in identifying prey (Losey et al. 1999); however, UV light (both A

and B) also can have negative effects on fish embryos and larvae (Browman et al. 2000 and references therein). UV-B light has been shown to be harmful to fish larvae, causing lesions in the brain and retina, and reducing growth rate (Hunter et al. 1979). The effects of UV-A light are not as well understood (Browman et al. 2000). In our study the walleye pollock larvae may have suffered injuries caused by exposure to full UV light which reduced their feeding and growth.

Optimum conditions for rearing walleye pollock larvae are a natural zooplankton diet (minimum prey density of 500 per liter) and a temperature near 10º C. Clear, acrylic tank covers should be used with full spectrum fluorescent light bulbs to avoid possible UV light injury to the larvae. Visible light level should not be greater than 13 μmol photons per m^2 per second because the larvae will avoid light levels higher than this (Olla and Davis 1990).

ACKNOWLEDGMENTS

Mike Canino for providing data from temperature and prey density feeding experiments. Debbie Blood for helpful comments on an early draft of the manuscript. Susan Picquelle for statistical advice and helpful comments on an early draft of the manuscript. This research is contribution FOCI-0608 to NOAA's Fisheries-Oceanography Coordinated Investigations.

CITATIONS

Bailey K. M., and C. L. Stehr. 1986. Laboratory studies on the early life history of the walleye pollock *Theragra chalcogramma* (Pallas). J. Exp. Mar. Biol. Ecol. 99: 233-246.

Bailey K. M., and C. L. Stehr. 1988. The effects of feeding periodicity and ration on the rate of increment formation in otoliths of larval walleye pollock *Theragra chalcogramma* (Pallas). J. Exp. Mar. Biol. Ecol. 122: 147-161.

Blaxter, J. H. S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. 115: 98-114.

Browman, H. I., C. A. Rodriguez, F. Béland, J. J. Cullen, R. F. Davis, J. H. M. Kouwenberg , P. S. Kuhn, B. McArthur, J. A. Runge, J-F. St.-Pierre, and R. D. Vetter. 2000. Impact of ultraviolet radiation on marine crustacean zooplankton and ichthyoplankton: a synthesis of results from the estuary and Gulf of St. Lawrence, Canada. Mar. Ecol. Prog. Ser. 199: 293-311.

Canino M. F., and K. M. Bailey. 1995. Gut evacuation of walleye pollock larvae in response to feeding conditions. J. Fish Biol. 46: 389-403.

Davis M. W., and B. L. Olla. 1992. Comparison of growth, behavior and lipid concentrations of walleye pollock *Theragra chalcogramma* larvae fed lipid-enriched, lipid-deficient and field-collected prey. Mar. Ecol. Prog. Ser. 90: 23-30.

Food and Agricultural Organization of the United Nations (FAO). 2002. Fishery statistics catches and landings. FAO, Rome, Italy.

Houde, E. D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: Temperature and implied latitudinal effects. Fish. Bull., U.S. 87: 471-495.

Hunter, J. R., J. H. Taylor, and H. G. Moser. 1979. Effect of ultraviolet irradiation on eggs and larvae of the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*, during the embryonic stage. Photochem. Photobiol. 29: 325-338.

Losey, G. S., T. W. Cronin, T. H. Goldsmith, D. Hyde, N. J. Marshall, and W. N. McFarland. 1999. The UV world of fishes: a review. J. Fish Biol. 54: 921-943.

MacKenzie, B. R., W. C. Leggett, and R. H. Peters. 1990. Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild? Mar. Ecol. Prog. Ser. 67: 209-225.

MacKenzie, B. R., T. J. Miller, S. Cyr, and W. C. Leggett. 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. Limnol. Ocean. 39: 1790-1799.

Meekan, M. G., J. H. Carleton, A. D. McKinnon, K. Flynn, and M. Furnas. 2003. What determines the growth of tropical reef fish larvae in the plankton: food or temperature? Mar. Ecol. Prog. Ser. 256: 193-204.

Olla, B.L., and M. W. Davis. 1990. Effects of physical factors on the vertical distribution of larval walleye pollock *Theragra chalcogramma* under controlled laboratory conditions. Mar. Ecol. Prog. Ser. 63: 105-122.

Parra, G., and M. Yúfera. 2000. Feeding, physiology and growth responses in first feeding gilthead seabream (*Sparus aurata* L.) larvae in relation to prey density. J. Exp. Mar. Biol. Ecol. 243: 1-15.

Paul, A. J. 1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae *Theragra chalcogramma*. Mar. Ecol. Prog. Ser. 13: 175-179.

Porter, S. M. 2001. Effects of size and light on respiration and activity of walleye pollock (*Theragra chalcogramma*) larvae. J. Exp. Mar. Biol. Ecol. 256: 253-265.

Rothschild, B. J., and T. R. Osborn. 1988. Small-scale turbulence and plankton contact rates. J. Plank. Res. 10: 465-474.

Shields R. J., J. G. Bell, F. S. Luizi, B. Gara, N. R. Bromage, and J. R. Sargent .1999. Natural copepods are superior to enriched *Artemia* nauplii as feed for halibut larvae (*Hippoglossus hippoglossus*) in terms of survival, pigmentation and retinal morphology: relation to dietary essential fatty acids. J. Nutrit. 129: 1186-1194.

Theilacker, G. H., K. M. Bailey, M. F. Canino, and S. M. Porter. 1996. Variations in larval walleye pollock feeding and conditions: a synthesis. Fish. Ocean. 5 (Supplement 1): 112-123.

Yamashita Y., and K. M. Bailey. 1989. A laboratory study of the bioenergetics of larval walleye pollock, *Theragra chalcogramma*. Fish. Bull., U.S. 87: 525-536.

Zar J. H. 1996. Biostatistical analysis. Third edition, Prentice Hall, Upper Saddle River, New Jersey. 662 p.

Table 1.-- Summary of the experiments used to determine optimum rearing conditions for walleye pollock *Theragra chalcogramma* larvae.

Experiment	Year	Egg source[1]	No. females[2]	Tank size (L)	No. Replicate tanks	Temp. (°C)	Age[3]	Prey type[4]	Prey density (number per liter)
Growth on different prey types	2004	GOA	1	120	1	6.0	24, 31, 38	ZP, R, A	ZP = 1300, R = 19000, A = 2500
Feeding and growth at different prey densities	1993	GOA	1	120	1	6.0	9, 13, 17	ZP	10, 30, 50, 500
First exposure to prey	2000	GOA	3	20	4	6.0	9	*Acartia* sp. nauplii	500
Temperature and feeding	1996	GOA	3	20	4	2.0, 6.0	17 (6°C), 33 (2°C)	ZP	100
Temperature and growth	1987	PS	3	120	1	5.7, 7.4, 9.9	8, 15, 20	R	10,000
Turbulence and feeding (Exp. 1)	2003	BS	3	4	3	6.0	15	R	20,000
Turbulence and feeding (Exp. 2)	2003	GOA	3	4	3	6.0	22	ZP	1,700
Ultraviolet light and feeding	2004	GOA	1	20	3	6.0	5, 9, 15	R	10,000

[1]GOA = Gulf of Alaska; PS = Puget Sound, Washington State, USA; BS = eastern Bering Sea.

[2]Number of females stripped for eggs used in the experiment.

[3]Days after hatching.

[4]ZP = natural zooplankton; R = rotifers; A = *Artemia* sp. brine shrimp.

Table 2.-- Larval walleye pollock *Theragra chalcogramma* feeding at different natural zooplankton densities. Letters indicate feeding at prey densities that were not significantly different based on results from the Kruskal-Wallis test and the Dunn multiple comparison test with a 0.05 significance level.

Age (days after hatching)	Time feeding (hours)	Prey density (microzooplankton per liter)	Mean prey in gut ± standard error
9	3	10[a]	0.05 ± 0.05
		30[a]	0.08 ± 0.08
		50[a]	0.43 ± 0.19
		500	3.15 ± 0.95
9	6	10[b]	0.15 ± 0.11
		30[b]	0.15 ± 0.05
		50[b]	0.32 ± 0.12
		500	4.87 ± 1.07
13	3	10[c]	0.39 ± 0.19
		30[cd]	1.53 ± 0.73
		50[d]	2.86 ± 0.83
		500	9.01 ± 1.47
13	6	10[e]	0.98 ± 0.30
		30[e]	0.84 ± 0.26
		50	2.77 ± 0.41
		500	10.86 ± 1.52

Table 3.-- Overall percentage feeding and number of prey in the midgut for walleye pollock *Theragra chalcogramma* larvae feeding under conditions of moderate turbulence and no turbulence. For Experiment 2, larval diet was switched from rotifers to natural zooplankton 5 days before the experiment was conducted. Letters indicate treatments that were not significantly different based on results from ANOVA and the Tukey multiple comparison test with a 0.05 significance level.

	Percent feeding	Mean number of prey in the gut ± standard error
Experiment 1		
Turb. for 12 days[1]	82[a]	8.75 ± 1.21[b]
Turb. on exp. day[2]	88[a]	10.73 ± 1.28[b]
No turbulence	79[a]	9.08 ± 1.26[b]
Experiment 2		
Turb. for 5 days[3]	53[c]	2.20 ± 0.47[d]
Turb. on exp. day	64[c]	1.88 ± 0.59[d]
No turbulence	81	5.15 ± 0.67

[1]Larvae were treated with moderate turbulence for 12 days before the experiment was conducted.

[2]Larvae were treated with moderate turbulence on the day the experiment was conducted.

[3]Larvae were treated with moderate turbulence for 5 days before the experiment was conducted.

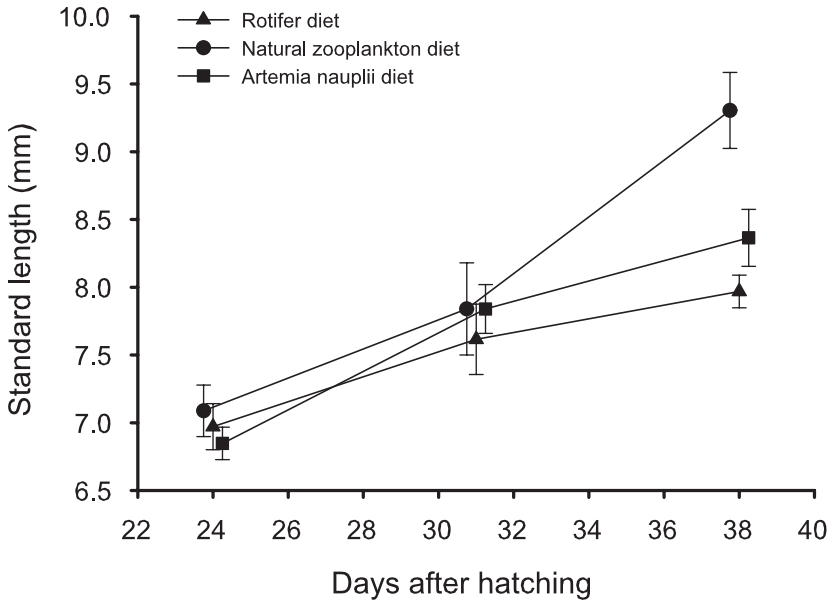

Figure 1. -- Growth of walleye pollock *Theragra chalcogramma* larvae fed diets of rotifers, natural zooplankton, or *Artemia* sp. brine shrimp nauplii. Mean ± standard error is shown.

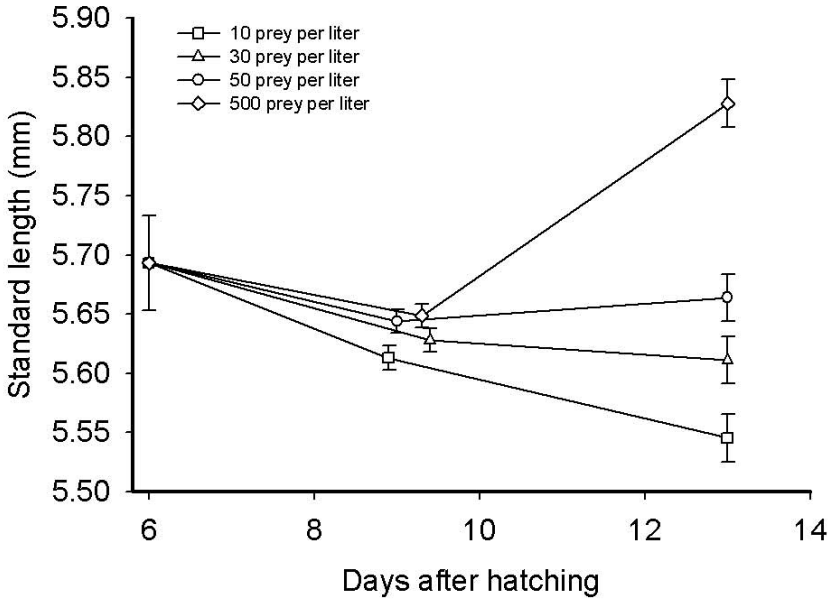

Figure 2.-- Growth of walleye pollock *Theragra chalcogramma* larvae fed different densities of natural zooplankton. Mean ± standard error is shown.

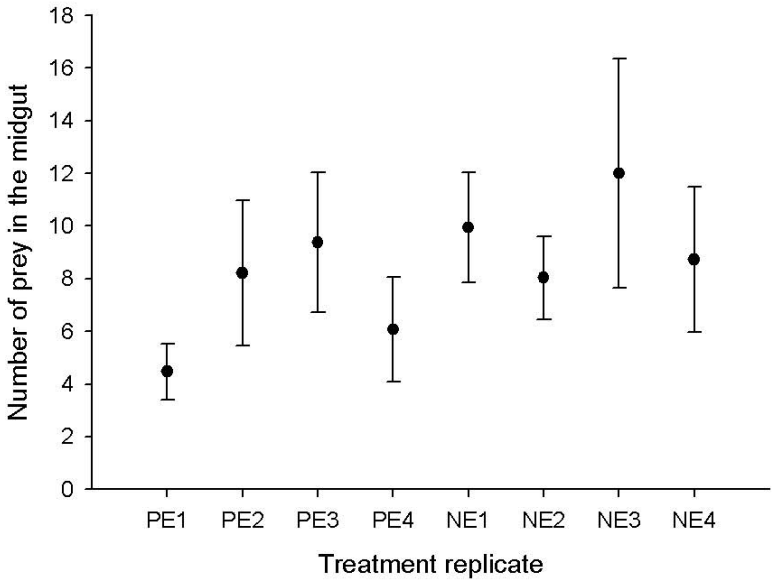

Figure 3. -- The number of prey in the midgut of walleye pollock *Theragra chalcogramma* larvae exposed to prey for 5 days prior to first feeding (PE) and at 1 day after first feeding (NE). Mean ± standard error for each replicate tank is shown.

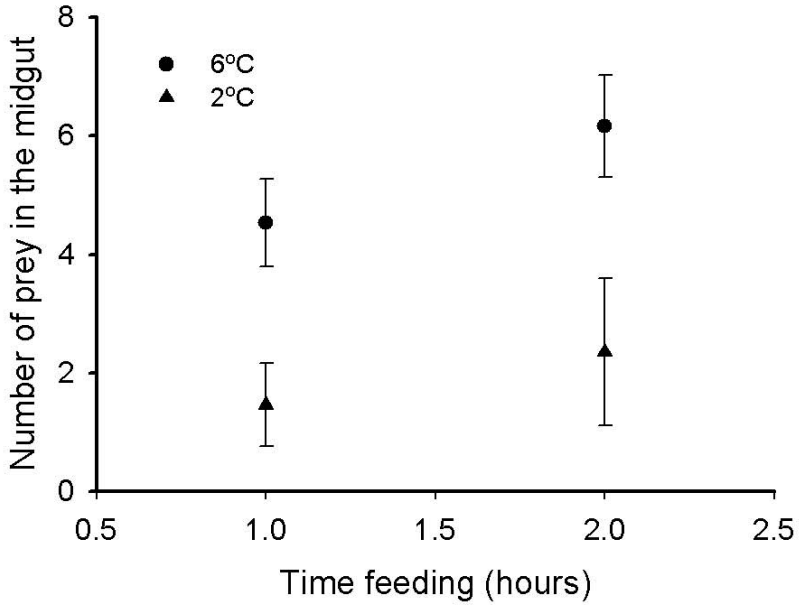

Figure 4. --Walleye pollock *Theragra chalcogramma* larvae feeding at 2º and 6º C after 1 and 2 hours of feeding. Mean ± standard error is shown.

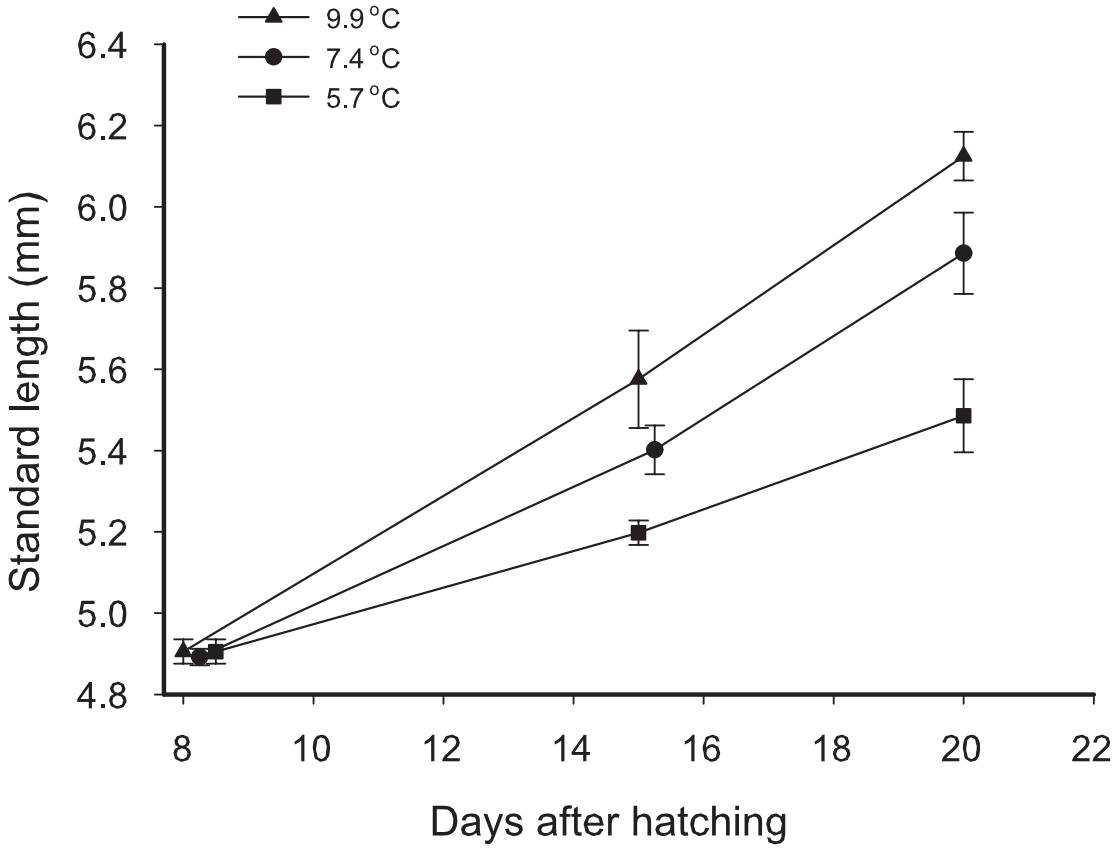

Figure 5. -- Growth of walleye pollock *Theragra chalcogramma* larvae at temperatures of 5.7º, 7.4º, and 9.9º C. Mean ± standard error is shown.

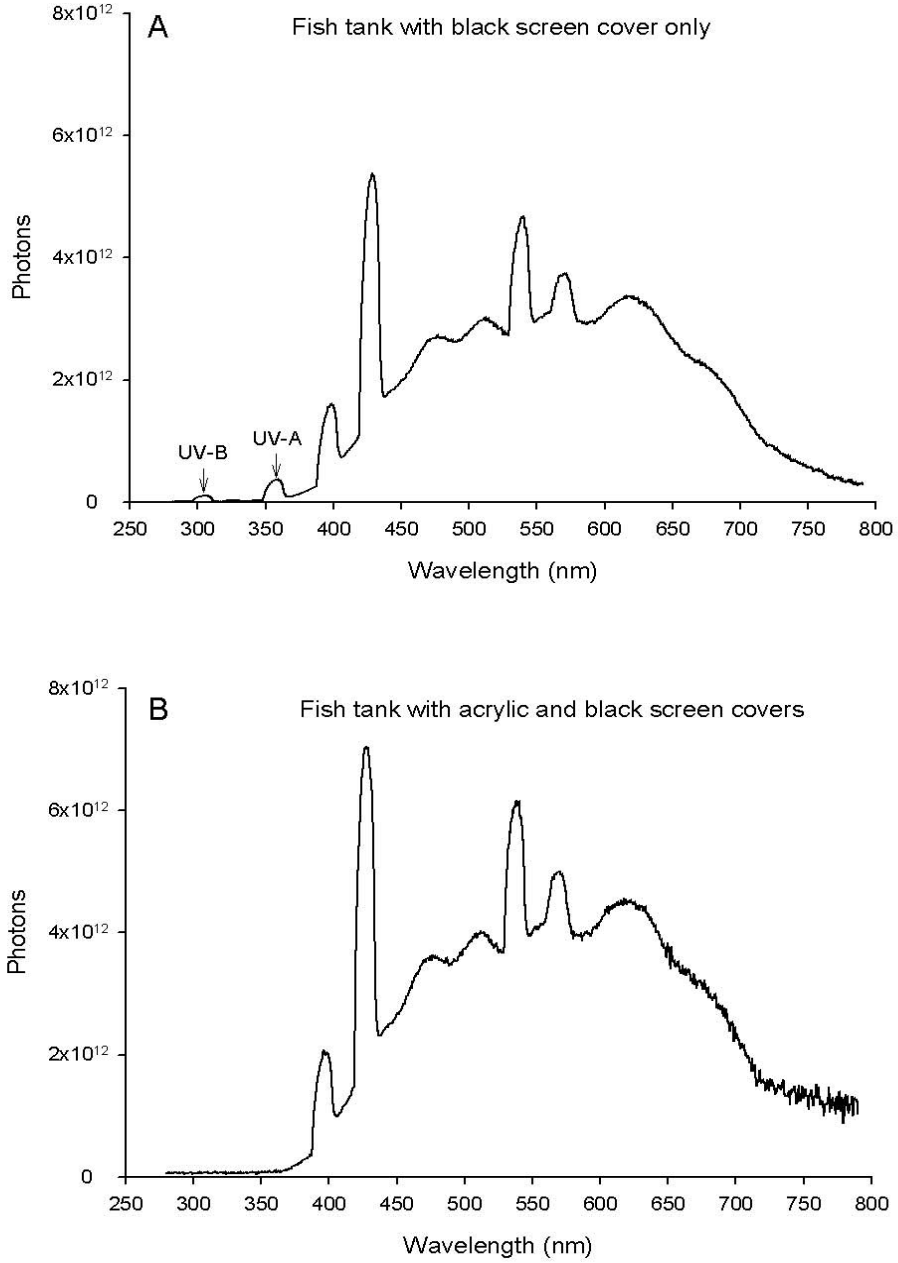

Figure 6. -- Action spectrum of light in a fish tank before (A) and after a clear, acrylic tank cover was added (B) to reduce the amount of ultraviolet (UV) light entering the tank. Black screening tank covers were used to adjust the level of visible light level in the tanks.

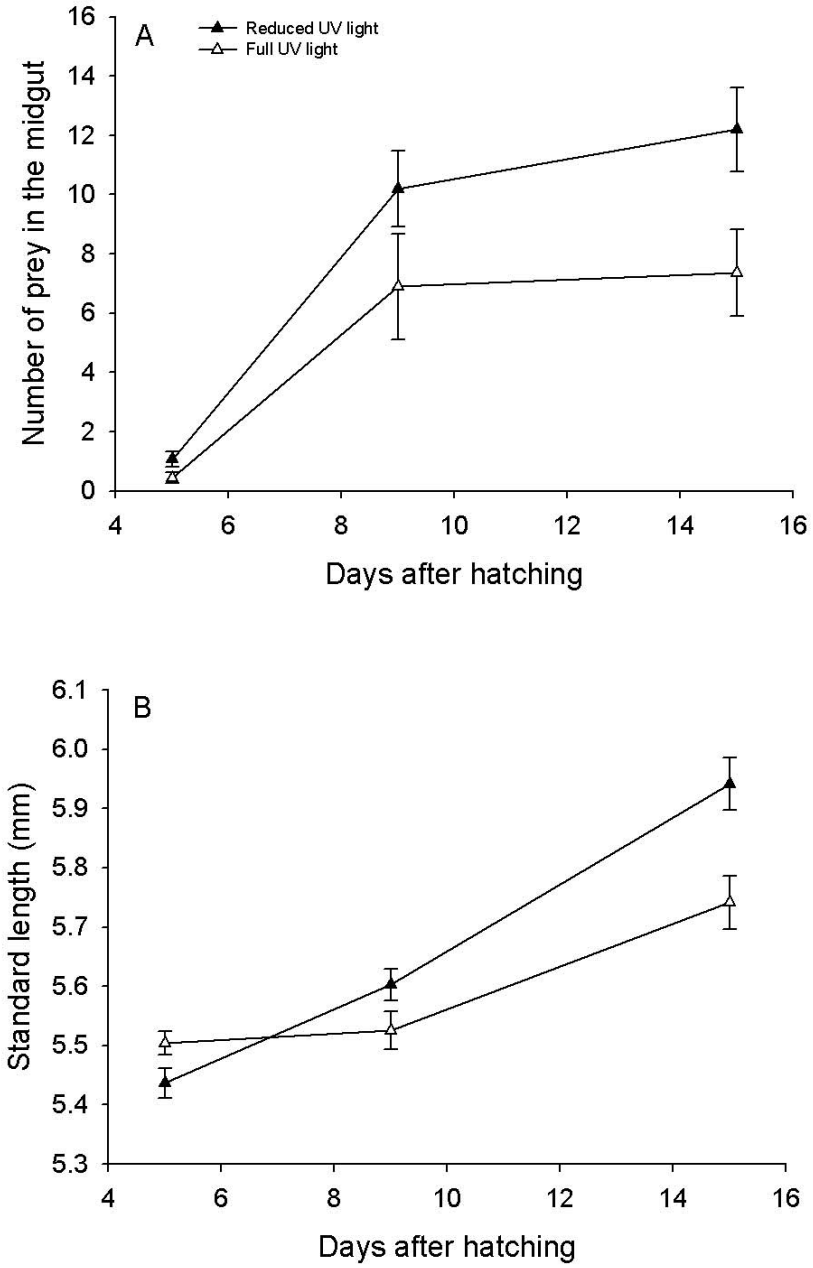

Figure 7. -- Feeding (A) and growth (B) of walleye pollock *Theragra chalcogramma* larvae reared in different amounts of ultraviolet (UV) light. Mean ± standard error is shown.