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Effects of size and light on respiration and activity of walleye pollock (*Theragra chalcogramma*) larvae

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Abstract

The respiration rate and swimming activity of walleye pollock (*Theragra chalcogramma*) larvae were measured in the laboratory to determine how these were affected by body size (measured as dry weight), and amount of light. Size influenced respiration rates, but not activity. Activity increased with increased light, and as walleye pollock larvae developed, light had an increasingly important effect on respiration rate. For older larvae, light is an important factor affecting respiration rate and this may be due to an increased sensitivity to light. Thus, in addition to size, light plays an important role in the energetics of walleye pollock larvae. © 2001 Published by Elsevier Science B.V.

Keywords: Activity; Fish larvae; Respiration; *Theragra chalcogramma*

1. Introduction

Walleye pollock (*Theragra chalcogramma*) is a commercially important fish species with annual catches in Alaska waters (Gulf of Alaska and Bering Sea) averaging 1.4 million metric tons a year (FAO, 1995). The fishery is driven by large recruitment pulses, which are largely established by the end of the larval stage (Bailey et al., 1996). Successful feeding of walleye pollock larvae to supply their energetic requirements for metabolism and growth is a critical factor in their survival (Bailey et al., 1995; Theilacker et al., 1996). Thus, knowing the energy requirements of walleye pollock larvae can provide a better understanding of how the environment affects growth,

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survival, and ultimately year–class strength. Many factors can influence energetics, but some of the important environmental factors that supply energy and affect the nutritional requirements of walleye pollock larvae include availability of prey, amount of light, and temperature.

Most fish larvae need light to feed (Blaxter, 1986), including those of walleye pollock (Paul, 1983). Light intensity influences capture success, duration of feeding bouts, and rate of prey searching (Batty, 1987). Light is also an important determinant of activity. Several studies have shown that fish larvae become more active as the amount of light increases (Batty, 1987; Olla and Davis, 1990). Studies examining the effect of light on larval walleye pollock feeding and swimming behavior have shown that as the amount of light increases above a detection threshold, the proportion of larvae feeding increases (Paul, 1983), and larvae become more active (Olla and Davis, 1990). In the dark, the activity of walleye pollock larvae is greatly reduced (Olla and Davis, 1990).

The metabolic rate of fish varies with factors such as activity, and developmental stage (Rombough, 1988). It is most often measured by the rate of oxygen consumption (Fry, 1971), and conversion factors are used to calculate the caloric equivalent of the respiration rate (Brett and Groves, 1979). Although light is known to influence activity, the effect of light on larval fish respiration is not well known, and its effect on larval walleye pollock respiration has not been studied previously. Studies using other species of fish larvae have found that light increases metabolic rate (Rombough, 1988). Oxygen consumption of Atlantic cod (*Gadus morhua*) larvae is higher for larvae held at 0.7 μmol photon m^{-2} s^{-1} than for larvae held in darkness (Solberg and Tilseth, 1984). Many studies have shown that the respiration rate of fish larvae also changes with size (e.g., Houde and Schekter, 1983; Giguere et al., 1988; Yamashita and Bailey, 1989; Oozeki and Hirano, 1994), and physiological and behavioral changes associated with development influence respiration rates as well.

Few studies have quantified the relationship between activity and respiration in fish larvae (Rombough, 1988). Activity is a very important factor affecting the metabolic rate of fish larvae (Holliday et al., 1964; Blaxter, 1969) because swimming is energetically costly for fish, but it is necessary for searching for and capturing prey, and for escaping predators (Calow, 1985). The metabolic rate of larval Atlantic herring (*Clupea harengus*) can be 9–10 times higher in active larvae compared to inactive ones (Holliday et al., 1964). Atlantic cod (*G. morhua*) larvae in the exogenous feeding stage respire more as swimming speed increases, but in the yolk-sac and mixed feeding stage there is no significant relationship between respiration rate and swimming speed (Hunt von Herbing and Boutilier, 1996). An exponential relationship between swimming speed and respiration rate has been found for roach (*Rutilus rutilus*) larvae (Kaufmann, 1990). For adult fishes, metabolic rate also increases exponentially as activity increases (Brett, 1970).

The objective of research reported here was to examine how the respiration rate and activity of fed walleye pollock larvae are affected by light, and body size. Environmental conditions that larvae could encounter during their development in the sea were simulated in the laboratory. The relationship of larval walleye pollock respiration rate and activity was also examined. Information provided by this study will be useful for energetic modeling and understanding early life history of walleye pollock.

2. Methods

2.1. Larval rearing

Adult walleye pollock were collected by trawl in Shelikof Strait, Gulf of Alaska, by the NOAA ship *Miller Freeman* during the spawning season in March 1997. Eggs from 4 to 5 females were mixed with sperm from 3 males to fertilize the eggs. Fertilized eggs were maintained aboard ship in the dark at 3°C for a few days before being moved to the Alaska Fisheries Science Center, Seattle, WA, where they were incubated at 3°C in the dark in 4 l glass jars filled with 3 l of filtered seawater (33‰ salinity). Two days prior to hatching the eggs were transferred into 120 l circular, black, fiberglass tanks (62 cm diameter, 43 cm deep) filled with 90 l filtered seawater, and maintained at a temperature of 3°±0.5°C. Two tanks with approximately 1500 to 2000 eggs each were used, and a water bath was used to control tank temperature. A 16-h light-cycle was started at hatching, and fluorescent lights illuminated the surface of the water between 3.0 and 3.5 μmol photon m^{-2} s^{-1}. In the sea, walleye pollock eggs from Shelikof Strait hatch deep in the water column (approximately 150 m) and the larvae swim up into the photic zone (Kendall et al., 1994). Approximately 2 days before first feeding, prey was added to the rearing tanks. Prey consisted of wild zooplankton (a mixture of *Acartia* sp. copepod nauplii and copepodites, and gastropod and polychaete larvae) collected from local lagoons. The density of prey in the rearing tanks was maintained between 0.5 and 1.0 prey ml^{-1}. First feeding was defined as the day at which 50% of the larvae sampled from a tank had prey in their gut. Further details on larval rearing are described in Porter and Theilacker (1996).

2.2. Respiration rate and activity experiments

Two types of experiments were conducted; one measured respiration rate (oxygen consumption) and the other measured activity. In both experiments, light levels of 0.01 (low), 0.33 (medium), and 10.25 (high) μmol photon m^{-2} s^{-1} were used, as these three levels cover the range of light estimated to occur at the depths where walleye pollock larvae are most abundant in Shelikof Strait, Gulf of Alaska (Kendall et al., 1994). The experiments were conducted at 3°C, which is a temperature that walleye pollock larvae can encounter in the Bering Sea. On the southeastern Bering Sea shelf, in the area where walleye pollock larvae are found during the spring, average sea surface temperature is between 3° and 4°C (Reed, 1995).

Three age groups of larvae were used in the experiments. One day after first feeding (DAFF) was chosen as the starting point of the experiments because at this stage larvae are dependent upon the environment for their energy needs. The remaining ages (13 and 25 DAFF) were chosen so that developmental changes in respiration rate and activity could be examined.

2.2.1. Respiration rate experiments

Oxygen consumption was used to determine the respiration rate of walleye pollock larvae. Walleye pollock larvae were held at 3°C in 60 ml Biological Oxygen Demand

(BOD) bottles (3.5 cm diameter by 6.0 cm tall) during daylight hours at the light levels previously described. BOD bottles were placed inside boxes with screened lids to control the amount of light in the bottles. Fluorescent light fixtures provided light, and it was measured using a Li-Cor model LI-189 meter and a LI-193SA spherical quantum sensor. Larvae from each rearing tank were kept in separate bottles so that tank variability could be assessed. Six treatment bottles were used for each light level, 3 bottles containing larvae from each rearing tank. The number of larvae per bottle was adjusted to ensure that no more than 10% of the oxygen in a treatment bottle was used. The number of larvae per bottle varied with age: 12 larvae per bottle for 1 DAFF; 9 larvae per bottle for 13 DAFF; and 5 larvae per bottle for 25 DAFF. Walleye pollock larvae were held with zooplankton so that their active, feeding respiration rate could be measured. Two controls were used, filtered seawater (seawater filtered through a 1 μm filter then UV treated), and filtered seawater with zooplankton. These controls were used to determine if zooplankton respiration was significantly contributing to the oxygen consumption in the experimental bottles and to calculate the amount of oxygen consumed by the walleye pollock larvae. Zooplankton were filtered through a 149-μm mesh sieve and then added to the BOD bottles to achieve a final estimated prey concentration of 0.5 ml^{-1}. Immediately following the addition of zooplankton, the bottle was capped and the experiment started. The experiments were conducted for 12 h in a temperature controlled room to minimize disturbing the larvae. At the conclusion of an experiment, the Winkler method for measuring dissolved oxygen in seawater (modified by Carritt and Carpenter, 1966) was used to determine the dissolved oxygen concentration in each BOD bottle.

A set of 10 larvae was sampled (5 from each rearing tank, kept separate) to determine mean standard length (SL) and dry weight for each age group. Larvae were placed on a microscope slide with a 10% solution of MS-222, and a dissecting microscope with an ocular micrometer was used to measure SL, then any yolk or prey was removed from the gut. Walleye pollock larvae 1 DAFF had approximately 10% of their yolk left; larvae 13 and 25 DAFF had no yolk. After a distilled water rinse, 5 larvae from the same rearing tank were placed onto a pre-weighed foil boat and then dried at 60°C for 24 h. A Cahn C-31 microbalance was used to weigh the foil boat containing the larvae to the nearest 0.1 μg.

2.3. Activity experiments

Larval walleye pollock activity in square glass tanks with approximately the same dimensions as the BOD bottles ($3.5 \times 3.5 \times 9.0$ cm, filled with 60 ml filtered seawater) was recorded using a video camera. The recording system is described in Spring (1996), the only difference being that a single camera was used. Recording was conducted at 3°C in a temperature controlled room which was lined with black plastic to minimize reflection.

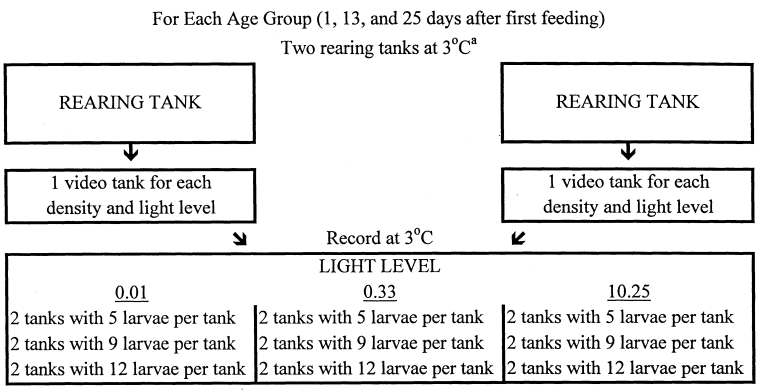
A 100-watt incandescent light bulb was suspended 48 cm above the video tanks, and light was measured with the Li-Cor light meter described earlier. A rheostat connected to the light fixture was used to adjust the amount of light in the tanks. A video camera was directed at the tanks from the side so that larvae could be observed from the top to the bottom of the tank. The amount of prey, and light levels used for the activity

measurements were the same as those used for the respiration rate experiments. Each age group was recorded at larval densities of 5, 9, and 12 larvae $tank^{-1}$ at each light level; these are the densities of larvae used in the treatment bottles for each age group in the respiration rate experiments. There were two experimental tanks for recording activity for each light level/density combination; each tank contained larvae from one of the rearing tanks (Fig. 1). Activity measurements were conducted on the same day as the respiration experiments but were done independently of them, i.e., larvae from the same rearing tanks were used but the same larvae were not used to measure both activity and respiration. Larvae were recorded for 30 min after a 2 to 3 h acclimation period in the video tank at the light level at which they would be recorded.

The number of times a larva swam during one minute (swimming was defined as when the tail started and stopped beating) was used as the measure of activity. To calculate the number of swimming events $larva^{-1}$ min^{-1} for each experimental tank, the number of swimming events occurring in a randomly chosen, 3-min sample of video sequence were counted. This value was then divided by 3 and by the mean number of larvae in the field of view during the sequence. This procedure was repeated four times for each tank, and the mean of the four measurements was used as the value for the tank. A 3-min time interval was chosen because a majority of the time walleye pollock larvae are inactive, their behavior follows a pattern of burst (i.e., brief periods of swimming), glide, and sink (Spring, 1996). Random samples of tape section were chosen without replacement so that they were independent of each other.

2.4. Data analysis

Systat 7.0 (SPSS, Inc.) was used for correlation analysis, and S-Plus 3.0 (MathSoft, Inc.) statistical software was used for analysis of variance (ANOVA) procedures.



[a]same rearing tanks used for the respiration rate experiments

Fig. 1. Experimental design of the activity experiments. The number of tanks used for each larval density at each light level are shown. Amount of light was measured in μmol photon m^{-2} s^{-1}.

3. Results

3.1. Respiration rates

3.1.1. Zooplankton contribution to oxygen consumption

For each age group the dissolved oxygen concentration in the filtered seawater control and filtered seawater with zooplankton control were compared. There was no significant difference between the two control types (ANOVA, $P > 0.05$ in all cases) so respiration due to the zooplankton was considered to be insignificant.

3.1.2. Rearing tank, body size, and light effects

There were no rearing tank effects (ANOVA, tank effect, $P > 0.20$ in all cases), so for each age and light level, treatment bottles were pooled for further analyses.

Mean respiration rate individual^{-1} (μl oxygen consumed individual^{-1} hr^{-1}) increased with dry weight (ANOVA, $P < 0.001$; Tables 1 and 2). Respiration rate was highest at the heaviest body weight and was not significantly different between the intermediate and lightest weights (Student–Newman–Keuls multiple comparison test, SNK, $P < 0.05$; Zar, 1996). The interaction between dry weight and light was significant (ANOVA, $P = 0.006$; Table 2), meaning that light may be affecting each weight group differently; therefore, each weight group was individually examined for the effect of light using the SNK test (Table 3). Light had no significant effect on respiration rate individual^{-1} at the lightest and intermediate weight groups. However, at the intermediate weight (107.1 μg), mean respiration rate individual^{-1} was lowest at the lowest light level (Table 1). At the heaviest weight group, light level significantly affected respiration rate; rates at the medium and high light levels were not significantly different, but both were significantly

Table 1
Mean respiration rates (μl oxygen consumed individual^{-1} hr^{-1}, and μl oxygen consumed mg dry weight^{-1} hr^{-1}), and standard deviations (S.D.) for various light levels, and sizes of walleye pollock (*Theragra chalcogramma*) larvae at 3°C

DAFF[a] (age)[b]	SL[c] ± S.D.	Dry weight[d]	Light level[e]	*n*	Respiration rate individual^{-1}	Weight-specific respiration rate
1 (16)	5.59±0.25	77.8±12.9	0.01	5	0.254±0.071	3.255±0.899
1 (16)	5.59±0.25	77.8±12.9	0.33	6	0.157±0.048	2.018±0.621
1 (16)	5.59±0.25	77.8±12.9	10.25	5	0.216±0.086	2.775±1.111
13 (28)	6.16±0.39	107.1±11.0	0.01	5	0.140±0.047	1.308±0.435
13 (28)	6.16±0.39	107.1±11.0	0.33	6	0.242±0.066	2.258±0.613
13 (28)	6.16±0.39	107.1±11.0	10.25	5	0.195±0.079	1.822±0.740
25 (40)	6.22±0.46	115.5±11.4	0.01	5	0.291±0.089	2.522±0.774
25 (40)	6.22±0.46	115.5±11.4	0.33	5	0.495±0.138	4.287±1.197
25 (40)	6.22±0.46	115.5±11.4	10.25	6	0.421±0.112	3.647±0.968

[a] Days after first feeding.
[b] Days after hatching.
[c] Standard length, mm.
[d] μg.
[e] μmol photons m^{-2} s^{-1}.

Table 2
Summary of the analysis of variance results for weight and light effects on the respiration rate individual^{-1} (μl oxygen consumed individual^{-1} hr^{-1}) and weight-specific respiration rate (μl oxygen consumed mg dry weight^{-1} hr^{-1}) of walleye pollock (*Theragra chalcogramma*) larvae at 3°C

Source	df	SS	MS	*F*	*P*
Respiration rate individual^{-1}					
Dry weight	2	0.440	0.220	29.842	< 0.001***
Light	2	0.037	0.018	2.486	0.10
Dry weight × light	4	0.125	0.031	4.232	0.006**
Error	39	0.288	0.007		
Weight-specific respiration rate					
Dry weight	2	22.332	11.166	15.702	< 0.001***
Light	2	1.901	0.951	1.337	0.27
Dry weight × light	4	12.878	3.219	4.527	0.004**
Error	39	27.733	0.711		

higher than respiration rate at the lowest light level (Tables 1 and 3). Results for weight-specific respiration rates (μl oxygen consumed mg dry weight^{-1} hr^{-1}) were similar for both weight and light effects (Tables 1 and 2). Therefore, for walleye pollock larvae, respiration rate increased about two fold with size (dry weight), and the effect of light on respiration rate was size dependent with respiration rate about 1.5 times higher at the highest light level for the largest larvae.

3.2. Activity (number of swimming events larva^{-1} min^{-1})

3.2.1. Density, body size, and light effects

The density of larvae in the tanks did not significantly affect activity (ANOVA, $P = 0.56$; Table 4), but overall activity between the 3 light levels was significantly different (SNK test, $P < 0.05$; Table 5). Activity was highest at the highest light level

Table 3
Summary of the Student–Newman–Keuls multiple comparison test results for the effect of light on respiration rates (μl oxygen consumed hr^{-1} individual^{-1}) for each weight group of walleye pollock (*Theragra chalcogramma*) larvae at 3°C[a]

Weight group											
77.8 μg				107.1 μg				115.5 μg			
Light level	$q_{0.33}$	$q_{10.25}$		Light level	$q_{0.01}$	$q_{10.25}$		Light level	$q_{0.01}$	$q_{10.25}$	
0.01	2.64	0.99		0.33	2.77	1.28		0.33	5.31**	2.01	
10.25	1.60			10.25	1.43			10.25	3.53*		
0.33				0.01				0.01			
Result:	0.01	10.25	0.33	Result:	0.33	10.25	0.01	Result:	0.33	10.25	0.01

[a] Amount of light was measured in μmol photon m^{-2} s^{-1}. Underlined light levels are not significantly different from each other.

Table 4
Summary of the analysis of variance results for activity (number of swimming events larva^{-1} min^{-1}) of walleye pollock (*Theragra chalcogramma*) larvae at 3°C

Source	df	SS	MS	*F*	*P*
Dry weight	2	14.356	7.178	5.993	0.009**
Light	2	34.952	17.476	14.592	< 0.001***
Density	2	1.423	0.712	0.594	0.56
Dry weight × light	4	11.391	2.848	2.378	0.08
Dry weight × density	3	5.785	1.928	1.610	0.22
Light × density	4	2.732	0.683	0.570	0.69
Dry weight × light × density	6	14.115	2.352	1.964	0.12
Error	21	25.151	1.198		

and lowest at the lowest light level (Table 6). Although ANOVA showed that dry weight had a significant effect on activity ($P = 0.009$; Table 4), the activity of the largest and smallest larvae was not significantly different (SNK test, $P > 0.05$; Table 5). Thus, activity remained constant with size, and larvae increased their swimming activity about two fold at higher light levels.

3.2.2. Relationship between respiration and activity

Since the same larvae were not measured for both respiration and activity, the mean activity and respiration rate for each age group, and light level combination were used to examine this relationship (Fig. 2). The Spearman correlation coefficient ($r_s = 0.30$) was

Table 5
Summary of the Student–Newman–Kuels multiple comparison test results for the overall effects of light (A) and size (B) on the activity (number of swimming events larva^{-1} min^{-1}) of walleye pollock (*Theragra chalcogramma*) larvae at 3°C[a]

A. Overall light effects			
Light level (μmol photons m^{-2} s^{-1})	$q_{0.01}$	$q_{0.33}$	
10.25	7.64***	3.86*	
0.33	3.79*		
0.01			
Result: All three light levels are significantly different from each other			
B. Overall size effects			
Dry weight (μg)	$q_{107.1}$	$q_{77.8}$	
115.5	3.99*	0.54	
77.8	4.23**		
107.1			
Result:	115.5	77.8	107.1

[a] Underlined values are not significantly different from each other.

Table 6
Mean activity (number of swimming events larva^{-1} min^{-1}), and standard deviation (S.D.) for various light levels, and sizes of walleye pollock (*Theragra chalcogramma*) larvae at 3°C[a]

Dry weight (μg)	Light level	*n*	Mean activity±S.D.
77.8	0.01	6	2.26±0.95
77.8	0.33	6	3.68±0.81
77.8	10.25	6	5.40±1.56
107.1	0.01	6	2.17±0.56
107.1	0.33	6	2.98±0.46
107.1	10.25	6	2.93±1.20
115.5	0.01	3[b]	2.67±1.78
115.5	0.33	3	3.52±1.45
115.5	10.25	3	5.65±2.10

[a] Amount of light is measured in μmol photons m^{-2} s^{-1}. Mean is a pooled value at each weight and light level due to insignificant density effects (see text).
[b] Only enough larvae remaining to do 3 replicates at each light level.

not significantly different from 0 ($n = 9$, $P > 0.05$; Zar, 1996). Thus, there was no relationship between swimming activity and respiration rate individual^{-1}, indicating that other factors besides activity affect respiration rate at 3°C.

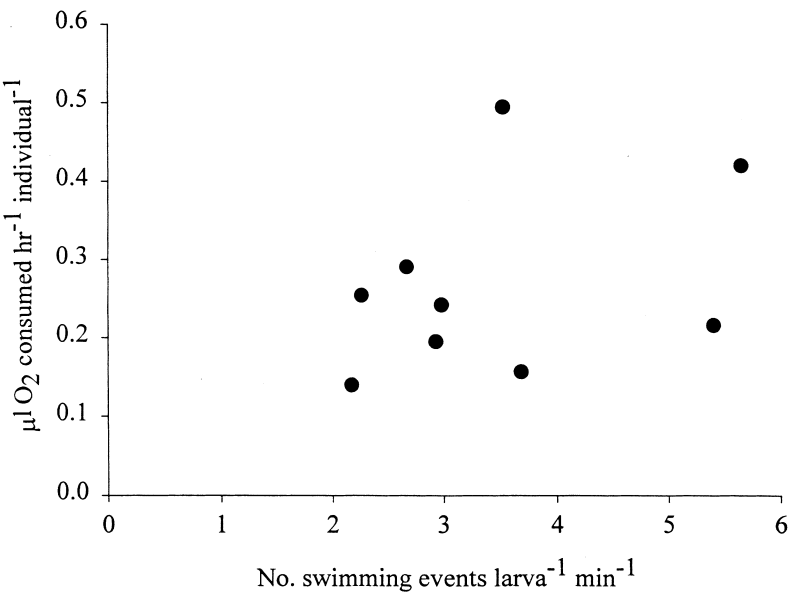


Fig. 2. The relationship between activity (number of swimming events larva^{-1} min^{-1}) and respiration rate (μl O_2 consumed hr^{-1} individual^{-1}) for walleye pollock (*Theragra chalcogramma*) larvae at 3°C. The Spearman correlation coefficient is 0.30.

4. Discussion

Body size, and light are two important factors that can affect the respiration rate of fish larvae. For walleye pollock larvae, respiration rate was influenced by the interaction of these two. Walleye pollock larvae depend on light for survival because they are visual predators (Paul, 1983). Sight is probably the most important sense walleye pollock larvae use for feeding because they do not appear to respond to chemosensory cues (Davis and Olla, 1995). The way in which respiration rate is linked to this critical environmental factor changes with size. The present study showed that as walleye pollock larvae developed, light had an increasing effect on their respiration rate. The respiration rate of the largest larvae was lowest at the lowest light level. This may be due to developmental and behavioral changes. The percentage of walleye pollock larvae that show positive phototaxis increases with age (Olla and Davis, 1990). Blaxter (1968) also showed that plaice (*Pleuronectes platessa*) larvae became more sensitive to light with age, and the amount of light required for feeding decreased with age. Furthermore, eye development and behavioral changes have been correlated (Noakes and Godin, 1988).

The lowest light level used in this study is adequate for larval walleye pollock feeding (Paul, 1983). Larval feeding was not light limited so respiration rates were similar between the light levels for younger larvae. For the oldest larvae in this study, respiration rates increased from the lowest and highest light levels, which could be an avoidance or stress response. The highest light level used in this study was nearly the level of light that walleye pollock larvae have been shown to avoid. Walleye pollock larvae swam away from the surface of the water when light levels in laboratory experiments were greater than 13 μmol photon m^{-2} s^{-1} (Olla and Davis, 1990). Likewise in the sea, walleye pollock larvae avoid bright light. In Shelikof Strait at night, 7 mm walleye pollock larvae moved up to depths that in daytime had light levels greater than 10 μmol photon m^{-2} s^{-1} (Kendall et al., 1994). The increase in respiration rate of older larvae at the higher light levels may be due to stress associated with bright light.

Light not only affected respiration rate but activity as well. Activity increased with increasing light but overall activity remained constant over the size range examined. The activity of Atlantic herring (*C. harengus*) larvae increased with light and age (Batty, 1987). In studies involving walleye pollock larvae reared at temperatures greater than 3°C, activity increased with both light (Olla and Davis, 1990) and age (Spring, 1996). Slower growth and development at 3°C could possibly explain why there was no increase in activity with size. Walleye pollock larvae reared at 6°C grow faster than those at 3°C. In the present study, growth rate was 0.026 mm day^{-1}. At 6°C, rates ranged from 0.06 mm day^{-1} for just after first feeding, to 0.12 mm day^{-1} from 12 to 17 DAFF (Yamashita and Bailey, 1989).

Studies have shown that a positive relationship exists between swimming activity and oxygen consumption in fish. For various fish species, diel rhythms in activity and oxygen consumption are similar (Sims et al., 1993; Liu et al., 1997; Thetmeyer, 1997). For Atlantic cod (*G. morhua*) larvae the relationship between activity (swimming speed) and oxygen consumption was age dependent. There was no relationship between swimming speed and respiration rate for yolk-sac cod larvae, but as the larvae developed, a positive, linear relationship between respiration and activity suggested that

activity in the older stages of cod larvae is an aerobic process (Hunt von Herbing and Boutilier, 1996). For larval and juvenile cyprinids, *Chalcalburnus chalcoides* and *R. rutilus*, an exponential relationship exists between swimming speed and oxygen consumption (Kaufmann, 1990). In the present study, the lack of correlation between activity and respiration rate may indicate that activity plays a small role in the metabolic energy budget at 3°C. Compared to 3°C, walleye pollock larvae at 6°C are more active, their respiration rate is higher, and activity and respiration rate are positively correlated (Porter, 1999). Because of low activity at 3°C (compared to warmer temperatures), activity was not strongly influencing respiration rate and hence respiration rate and activity were not statistically correlated in the present study. Alternatively, high variability among replicates could have caused low statistical power and masked a weak correlation. Other methods may give more precise measurements of oxygen consumption of fish larvae, such as an oxygen electrode connected to an experimental chamber. However, in studies that have used oxygen electrodes to measure the respiration rate of fish larvae, the respirometers constrained the larvae to a very small volume (e.g., 15 ml, Hunt von Herbing and Boutilier, 1996), and such small volumes affect larval fish activity. The Winkler method was used in the present study because of the relatively large volume of water the larvae could be put in.

Body size is an important factor determining how walleye pollock larvae respond to light. Field observations of walleye pollock larvae support this conclusion. In Shelikof Strait, small walleye pollock larvae (5 to 6 mm SL) do not vertically migrate, but larger (>7 mm) ones do (Kendall et al., 1994). Kendall et al. (1994) suggested that the reason the larvae vertically migrate is to stay in an optimal light level for feeding and to avoid predators. Although the effect of light on respiration rate is minor early in development, it should not be ignored for ecological modeling because for the energetics of larval walleye pollock it can be important.

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