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Environmental factors influencing larval walleye pollock *Theragra chalcogramma* feeding in Alaskan waters

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ABSTRACT: This study examines potential interactions among the environmental variables likely to affect larval walleye pollock *Theragra chalcogramma* feeding in the sea. Walleye pollock larvae were sampled from Shelikof Strait, Gulf of Alaska, and from the eastern Bering Sea, with corresponding environmental data. Variables used in our study were time spent feeding, seawater temperature, light, prey density, wind speed and standard length of the larvae. We applied an additivity test to detect the presence of potential interactions among these variables and adopted an expansion of generalized additive models (GAMs) that allowed the inclusion of interaction terms in a non-parametric regression analysis. After testing all possible 2-way interactions among these variables, we found 4 significant terms: (1) time feeding–standard length, (2) temperature–light, (3) light–wind speed and (4) prey density–standard length. The most influential interaction term was the light–wind speed interaction, which caused a decrease of the model-generalized cross-validation (GCV, whereby lower values indicate more parsimonious models) from 0.0402 (for a model with all variables but no interaction term) to 0.0290 (for a model with all variables and this interaction), and an increase of the model explained variance by 7% ($R^2 = 0.89$ versus 0.82). This result indicates that the effect of wind speed (turbulence) on larval walleye pollock feeding is dependent upon the amount of light available. This may be due to vertical movements in the water column by both walleye pollock larvae and their prey in response to turbulence.

KEY WORDS: Larval fish feeding · Walleye pollock larvae · Generalized additive models

INTRODUCTION

The match–mismatch of feeding readiness of marine fish larvae to their prey availability in space (Lasker 1975) and time (Cushing 1975) is one of the most revered paradigms in marine ecology. However, it has become increasingly obvious that the feeding of marine fish larvae is not a simple function of prey abundance or spatial and temporal overlap (MacKenzie et al. 1990, 1994, Leggett & Deblois 1994, Lough & Mountain 1996), but a complex and dynamic process with many, often interacting, factors. Insights into the effects of environmental variability on larval fish feeding-success may offer an improved understanding of larval growth and survival processes, and ultimately help elucidate the factors responsible for recruitment variability. The relationship between fish larvae and their prey is influenced by biotic and abiotic factors, including species-specific differences in sensitivity to prey, size and development of the fish larvae, prey

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density and composition, light, temperature, small-scale turbulence and water turbidity, as well as interactions between these variables (Houde 1987, Fortier et al. 1996, Lough & Mountain 1996, Dower et al. 1998, 2002, Fiksen et al. 1998, Utne-Palm 1999, Hillgruber & Kloppmann 2000, Kloppmann et al. 2002).

Growth and developmental rates of marine fish larvae are relatively high and result in rapid changes in swimming speed, visual acuity and digestive efficiency. These ontogenetic changes can be indirectly observed by increased feeding rates and broadened prey-size spectra, as well as enhanced vertical migration behavior. First-feeding walleye pollock *Theragra chalcogramma* larvae initiate exogenous feeding on copepod eggs and small naupliar stages (Canino et al. 1991, Hillgruber et al. 1995), but quickly expand their prey field to include copepodite stages and adult copepods (Nishiyama & Hirano 1985, Kendall et al. 1987, Grover 1990). In addition, their ability to respond to physical variables, such as light and turbulence, equally increases as swimming performance improves with increasing size (Olla & Davis 1990, Davis & Olla 1995).

Fish larvae are visual predators that rely on sufficiently high light levels to detect prey (Paul 1983, Blaxter 1986). The threshold light level at which early walleye pollock larvae initiate prey capture is about 0.003 µmol photon m^{-2} s^{-1} (Paul 1983). Because of this dependence on sufficient illumination, larval feeding is, in general, severely diminished at night or ceases altogether, but picks up again soon after sunrise, resulting in a diel pattern in terms of quantity and composition of prey items ingested (e.g. Last 1980, Hillgruber & Kloppmann 2000). However, in addition to the direct effect of light on feeding incidence, changes in irradiance coupled with ontogenetic changes or turbulence can dramatically impact larval feeding rates (Fiksen et al. 1998).

Turbulence may play a major role in regulating the amount and the type of prey available to fish larvae (Dower et al. 1997). A comparison between predicted ingestion rates of fish larvae in the sea with those derived from laboratory experiments showed that feeding rate at lower prey densities was higher (near maximal ingestion) in the sea than in the laboratory (MacKenzie et al. 1990). It was suggested that small-scale turbulence could explain this discrepancy (MacKenzie et al. 1990). Small-scale turbulence introduced to the mixed layer of the water column may increase contact rates between predator and prey (Rothschild & Osborn 1988) and thereby increase the effective prey concentration available to larval fishes. Alternatively, strong mixing events may disrupt layers of high prey density, dissipate prey concentrations and, as a consequence, lead to reduced larval feeding incidence and rates (Peterman & Bradford 1987). To date, however, studies testing the effect of turbulence on larval feeding success have yielded complicated and often contradictory results (Landry et al. 1995, Dower et al. 1998, Hillgruber & Kloppmann 2000). The effect of turbulence on larval fish feeding is further complicated by interacting factors such as light, larval developmental stage and size (Fiksen et al. 1998, Fiksen & Folkvord 1999, Utne-Palm & Stiansen 2002), and search strategy (MacKenzie & Kiørboe 1995). In addition, the effect of turbulence should be diminished if prey density is at saturating levels (Dower et al. 2002).

The objective of the present study was to explain variability of *in situ* feeding of larval walleye pollock. Walleye pollock spawn in the Bering Sea and Gulf of Alaska during springtime (Kendall et al. 1996), and the larvae begin feeding about 1 wk after hatching. The range of environmental conditions that walleye pollock larvae experience is highly variable. Shelikof Strait (one of the major habitat areas for walleye pollock larvae in the Gulf of Alaska) is characterized by highly variable wind patterns, with intense storms and periods of calm during the time when walleye pollock larvae are present (Stabeno et al. 2004). Strong wind-mixing events during the time of first feeding have been associated with lower than expected survival of walleye pollock larvae; this may be partly the effect of turbulence on prey availability (Bailey & Macklin 1994, Ciannelli et al. 2004).

Previous studies of larval walleye pollock feeding in Alaskan waters have shown a relationship between prey abundance and feeding success (Canino et al. 1991, Bailey et al. 1995). However, for marine fishes in general there is a lack of field studies that quantitatively address the potential interaction among the environmental covariates that affect larval fish-feeding. In the present study we applied an additivity test to detect the presence of potential interactions among the variables that can affect larval feeding. In addition, we adopted an expansion of generalized additive models (GAMs) that allows the inclusion of interaction terms in a non-parametric regression model. To our knowledge, this is the first study that explicitly addresses and models the non-additive effects of environmental variables on larval feeding. We sampled walleye pollock larvae over an extremely broad range of environmental conditions, which were selected for this study because they are easily measured and commonly utilized in recruitment analyses. Larval feeding can be examined on different scales ranging from fine-scale studies of larval behavior in patches of prey to large-scale comparisons of seasonal prey production and feeding success; in this study, environmental parameters were integrated over scales relevant to the daily feeding range and survival of larvae.

MATERIALS AND METHODS

Data collection. Walleye pollock larvae were collected from 8 research cruises in Shelikof Strait, Gulf of Alaska (1989 to 1996) and from 2 cruises in the eastern Bering Sea (1992 and 1994). Altogether, 33 larval walleye pollock collections were made (Table 1). All larvae used in the analysis were collected from sunrise to approximately 6 h later (Table 1). Our intent was to examine the factors related to the process of gut-filling. After about 5 to 6 h larvae begin to egest prey, and the egestion rate depends on the rate of gut-filling (Canino & Bailey 1995); therefore gut samples collected later in the day may not reflect feeding rates. In Shelikof Strait, samples were collected with a 60 cm diameter bongo sampler towed vertically from 60 m depth to the surface using either 333 or 505 µm mesh nets (Table 1). Bering Sea collections were made with a 1 m^2 MOCNESS using either 335 or 505 µm mesh nets, and larvae from either 70 and 90 m depth, or 30 and 40 m depth, were pooled and used in the analysis (Table 1). Although MOCNESS tows are usually conducted in vertical series, the tows available for analysis were conducted within specific depth strata in horizontal series. Thus, only MOCNESS collections within the 5 to 6 h after sunrise time constraint were used in our analysis, which limited us to the use of tows from the above depth strata. We assumed that there was no

Table 1. *Theragra chalcogramma*. Field data used to model larval feeding in Alaskan waters. Except where noted otherwise, samples were collected by 60 cm Bongo net with either 333 or 505 µm net, towed vertically from 60 m to surface, in Shelikof Strait. N: no. of larvae examined for gut content

Year	Date	N	Feeding period (h after sunrise)	Temperature (°C)	Surface light (µmol photon m^{-2} s^{-1})	Wind speed (m s^{-1})	Prey density (ind. l^{-1})	Standard length (mm)	Prey in gut (n)
1989	28 Apr	20	5.15	3.70	1006.44	9.27	7.60	6.12–6.97	2.75
		20	6.27	3.70	1177.92	7.21	7.60	6.12–8.21	1.65
	18 May	10	0.81	3.88	313.12	10.30	14.38	6.12–8.21	1.90
		10	4.06	3.84	769.72	10.30	14.38	6.20–8.44	9.70
1990	11 May	10	4.67	4.67	524.92	7.21	25.00	6.63–8.40	6.20
1991	4 May	10	5.53	3.38	809.75	20.61	1.70	5.86–7.78	2.20
1992	20 Apr[a,b,c]	64	5.82	3.53	857.13	7.20	14.70	5.04–7.53	0.14
1993	13 May	20	0.20	5.30	0.00	8.24	24.50	6.17–9.03	0.55
		10	1.98	5.30	155.14	9.27	24.50	6.69–9.55	3.90
		10	2.85	5.30	243.26	8.24	24.50	5.39–10.59	3.80
		20	4.52	5.30	378.53	8.76	26.50	5.73–8.42	4.85
	30 May[b]	20	0.10	6.04	0.00	6.18	22.53	7.47–10.24	0.50
		20	1.38	6.04	244.85	6.18	22.53	7.99–11.54	8.85
		20	3.28	6.19	650.10	3.09	28.20	6.86–10.41	12.40
		20	4.10	6.03	767.17	4.12	29.20	7.29–10.93	20.95
	31 May[b]	10	0.63	6.25	37.54	4.12	20.39	7.12–9.46	9.90
		20	2.03	6.28	403.62	5.15	18.65	7.47–10.24	28.55
		20	3.35	6.27	661.51	5.15	18.65	7.99–10.33	34.85
1994	21 Apr[a,d]	53	5.03	3.52	863.51	7.20	14.80	6.34–9.92	2.89
	22 Apr[a,d]	60	4.70	3.70	794.22	3.09	15.40	6.34–9.16	3.63
1995	26 May[b]	20	0.77	4.85	0.00	10.30	7.90	8.33–11.11	0.90
		20	1.85	4.91	107.58	9.27	8.80	6.95–10.59	3.10
		20	2.88	4.78	217.12	11.33	8.80	6.86–10.33	3.30
		20	3.85	4.91	305.65	12.36	10.60	7.81–10.15	5.65
		20	4.77	4.87	375.18	11.33	11.80	7.03–11.28	10.90
		20	5.85	4.87	437.48	12.36	11.80	7.73–10.76	12.20
1996	4 May	20	0.00	4.76	0.00	15.45	25.50	5.94–10.40	1.80
		20	2.57	4.84	436.39	10.30	26.60	6.63–10.09	5.70
		20	4.83	4.79	691.90	9.27	23.10	6.63–9.25	5.75
	8 May	20	0.00	4.32	39.11	7.73	19.20	7.40–10.02	0.15
		20	1.75	4.28	312.12	5.15	20.20	7.32–9.63	2.85
		20	3.70	4.27	581.58	5.15	20.60	6.71–9.71	4.10
		20	5.83	4.36	863.16	5.15	16.50	7.40–10.09	5.45

[a]MOCNESS (1 m^2 samples from Bering Sea); [b]mesh size 505 µm; [c]70 and 90 m depth; [d]30 and 40 m depth

sampling bias between the 2 gear types, since walleye pollock larvae are captured equally well by bongo and Tucker tows (the latter has a towing configuration similar to that of the MOCNESS; Shima & Bailey 1994). Immediately after retrieval of the sampling gear, the codend contents were sorted for walleye pollock larvae, which were subsequently preserved in 5 or 10% buffered formalin-seawater solution. At the laboratory, larvae were measured with an ocular micrometer to the nearest 0.08 mm standard length (SL) with a dissecting microscope. The midgut was dissected and the total number of prey items recorded. Preserved SL (Table 1) was adjusted for shrinkage arising from both net damage and preservation using equations described by Theilacker & Porter (1995).

The following biological and physical environmental variables were measured at or near the time of larval collection and were used as independent variables in our study (Table 1). These were integrated over the depth range of the larval collections. Note that over the 6 h period of collections, a 6 mm larva cruising at 1 body length s^{-1} can swim about 130 m, and in fact a significant portion of this displacement can be vertical over a fairly short period (Kendall et al. 1994); therefore, the depth and environmental conditions in which it captured prey during the preceeding 6 h are unknown.

Seawater temperature (temp): Temperature was measured using a Seabird CTD system. For samples collected using bongo tows, the mean temperature between 0 and 60 m depth was calculated because most feeding-stage walleye pollock larvae are encountered in this depth interval (Kendall et al. 1994). For the MOCNESS samples, mean temperature for the sampling depth interval was calculated.

Prey density (prey): Microzooplanktonic prey were sampled either with a rosette sampler equipped with 10 l Niskin bottles at discrete depths or with a CalVET net vertically towed from a depth of 60 m to the surface. Canino et al. (1991) reported that mean prosome length of prey in the larval walleye pollock gut is approximately 200 µm, so microzooplankton <350 µm were used to calculate prey density (in most cases this included all copepod nauplii, copepodites and invertebrate eggs). For the larval samples collected using bongo tows, the mean prey density refers to the 0 and 60 m depth layer, while for the MOCNESS collections, mean prey density refers to the sampled depth interval.

Wind speed (lnws3): Wind speed was measured with a ship-based anemometer. For the formulation of the models, wind speed was cubed and used as an index of turbulence. Wind speed cubed is approximately proportional to the turbulent dissipation rate ε (Oakey & Elliot 1982). The natural log data-transformation was applied to these data.

Light anomaly (light): Photosynthetically active radiation at the sea surface at the time of larval sampling was estimated from a numerical model based on atmospheric conditions, date, time of day, and latitude and longitude (Gregg & Carder 1990). The estimated irradiance values were pooled and regressed against h after sunrise (the time when the larvae were collected), and the residuals were used as the values of light in the GAM analysis. This helped to avoid multicollinearity with time feeding, which was used as another independent variable in the GAM (see next subsection). The newly calculated light values indicated whether the light level at the sea surface at the time of sampling was higher or lower for that time of day based on all the data.

Time feeding (feed.time): This was defined as the number of hours from sunrise to the time of larval collection (Table 1), and was also included as an independent variable. This definition is reasonable since walleye pollock larvae are visual predators that cease feeding during the night (Paul 1983, Canino & Bailey 1995).

From each collection, 10 to 64 larvae were examined and the mean number of prey in the gut (NPG) and the mean SL (used as an independent variable) were used as the value for each collection to avoid pseudoreplication. Normal probability plots indicated that the dependent variable NPG (Table 1) was not normally distributed, so the fourth root data-transformation was used.

Data analysis. We used non-parametric regression models (i.e. GAMs) to isolate the factors affecting larval feeding (NPG) in the field: 2 different model formulations were adopted, an additive and a non-additive formulation. Prior to analysis, the data were weighted by the number of larvae examined from each station. For the additive GAM formulation, our model selection criterion was based on a step-wise approach, aimed at removing covariates with a p-value >0.05 and minimizing the model-generalized cross-validation (GCV; Wood 2000). The GCV is a measure of the predictive error of the model and thus takes into account not only the fit, but also the model complexity (i.e. degrees of freedom). We initially included all the covariates (without interaction terms) in the GAM model of feeding by larval walleye pollock. We then eliminated, one by one, all the covariates whose partial effect had the lowest significance level (i.e. the covariate with a p-value typically >0.05 was removed). This process was repeated until the model GCV was minimized, which also coincided with all covariates having a p-value ≤ 0.05.

We applied the additivity test developed by Chan et al. (2003) to detect the presence of potential interactions between the covariates retained in the final additive GAM formulation. The additivity test was limited to second-order terms (i.e. 2-way interactions). The rejection level (i.e. significant interaction) was set at a p-value ≤0.05. Significant second-order interaction terms were included in the non-additive GAM formulation, and the validity of the model was re-assessed adopting the step-wise procedure previously described for the additive GAM formulation. To avoid problems with model over-parameterization we never included more than 1 interaction term in a single non-additive model formulation. Thus, the non-additive terms, as detected from the additivity test, were assessed in multiple GAM models. The inclusion of the interaction term in a GAM formulation adopted the multiplicative approach described by Hastie & Tibshirani (1990) and applied by Ciannelli et al. (2004). Specifically, the interaction term was formed by the product between the 2 standardized and shifted interacting covariates. Covariates were shifted (i.e. a constant added to their standardized series) so that their value was ≥0, and consequently their product was a monotonic increasing function.

RESULTS

Additive GAM

All the inspected independent variables were retained in the final additive model formulation of larval feeding; the GCV score was 0.0402, and 82% of the variance was explained. Each variable had a positive effect on NPG, although some effects were nonlinear (Fig. 1). NPG increased from sunrise to approximately 4 h after sunrise and remained at a nearly constant level thereafter, presumably due to the onset of digestive processes (Canino & Bailey 1995). Temperature had a strong, positive, linear effect on feeding. The effects of both light anomaly and wind speed were nonlinear and most pronounced at the highest values of each factor. For integrated prey density, NPG increased up to maximum level at approximately 18 prey l^{-1}. For larvae between 6 and ~8.5 mm in length, NPG increased with increasing larval size. Thus,

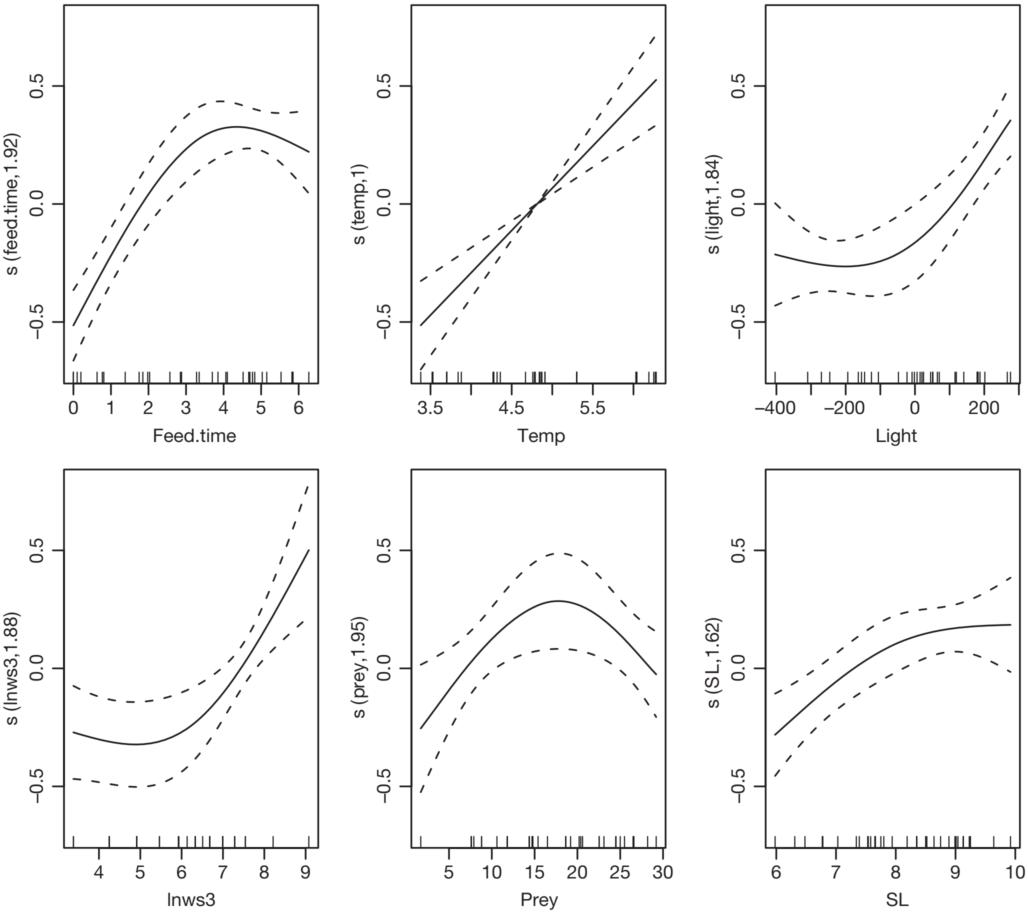

Fig. 1. *Theragra chalcogramma*. Partial additive effect on larval feeding of each environmental variable included in generalized additive model. Predicted result (no. of prey in gut, NPG) at specified level of an environmental variable is given by sum of partial effects of each variable plus a model constant. Dashed lines: ±2 SE of mean estimated effect (continuous line). Whiskers on *x*-axis: locations of measurements for that covariate. s (*y*-axis): estimated degrees of freedom for each partial effect, where <0 indicate that variable has negative effect on NPG and values >0 indicate positive effect. SL: standard length; lnw3: wind speed

according to our additive model, walleye pollock larvae initiate feeding after sunrise and need approximately 4 h to fill their guts. Best feeding conditions occur when light levels and wind speeds are high, and the integrated prey density is near 18 l^{-1}. The results also showed that larvae rapidly improve their feeding ability between 6 and 8.5 mm SL, possibly due to rapid development of swimming and feeding structures during early fish ontogeny (i.e. Hunt von Herbing et al. 2001). The GCV of a model with no independent variables (i.e. NPG was modeled by a constant) was 0.2106, which is higher than the 0.0402 for the final additive model, indicating that the observed effects are likely to be real.

Because of concern that different samples obtained by bongo and MOCNESS tows could influence the results, we also ran the model without the MOCNESS data. The only difference in the results was that length (SL) dropped out as a significant factor. This appears to be the result of the inclusion of a smaller size range of larvae in the MOCNESS samples. Since all environmental factors remained significant, we opted to include the MOCNESS data in further model-testing to increase sample size and to include the broader length range of larvae.

Additivity test

After testing all possible 2-way interactions between the variables included in the additive GAM, it was determined that 4 of the 2-way interactions were significant at the 0.05 rejection level (Table 2). The significant interactions were time feeding–SL, temperature–light anomaly, light anomaly–wind speed, and prey density–SL.

Table 2. *Theragra chalcogramma*. Results of additivity test (Chan et al. 2003) used to determine significant 2-way interactions between all independent variables used in generalized additive model, GAM. *,**Significant at p = 0.05 and p = 0.01 level, respectively

Independent variables tested	p-value
Time feeding, temperature	0.19
Time feeding, light anomaly	0.61
Time feeding, prey density	0.10
Time feeding, standard length	0.03*
Time feeding, wind speed	0.46
Temperature, light anomaly	0.002**
Temperature, prey density	0.09
Temperature, standard length	0.98
Temperature, wind speed	0.24
Light anomaly, prey density	0.24
Light anomaly, standard length	0.37
Light anomaly, wind speed	0.03*
Prey density, standard length	0.03*
Prey density, wind speed	0.06
Standard length, wind speed	0.09

Inclusion of an interaction term in additive GAM

There was no improvement in the additive GAM with the inclusion of the temperature–light anomaly interaction (p-value = 0.30, model GCV = 0.0427); thus its effect on larval feeding was not further explored. The inclusion of time feeding–SL or prey density–SL as an interaction term resulted in further improvement of the model GCV (Table 3, Models A,B). The single variable SL became non-significant in both of these non-additive models and was removed. All other additive variables had similar effects to those already described for the additive model formulation (Fig. 1). The effect of the interaction terms was explored with 3D graphs, in which the non-additive models were used to predict NPG. The 2 interacting covariates were varied throughout their entire range, while all other non-interacting covariates were kept constant at their mean value. From these 3D plots, we interpreted the time feeding–SL and prey density–SL interactions as ontogenetic changes in feeding ability (Fig. 2). As prey density and time spent feeding increase, larger larvae are

Table 3. *Theragra chalcogramma*. GAM analysis of larval feeding, with 1 interaction term added. Model A: NPG (no. of prey in gut) = constant + time feeding + temp + light + lnws3 (wind speed) + prey + feeding time × SL (standard length); GCV (generalized cross-validation) score = 0.0347, $R^2 = 0.84$. Model B: NPG = constant + time feeding + temp + light + lnws3 + prey + prey × SL; GCV score = 0.0397, $R^2 = 0.82$. Model C: NPG = constant + time feeding + temp + light + lnws3 + prey + SL + light × lnws3; GCV score = 0.0290, $R^2 = 0.89$

Model	Variable	Estimated df	p
A	Time feeding	1.61	0.01
	Temperature	1.00	3.69×10^{-11}
	Light	2.00	2.43×10^{-6}
	lnws3	1.91	0.002
	Prey	1.99	0.02
	Time feeding × SL	1.67	1.23×10^{-5}
B	Time feeding	1.93	8.17×10^{-13}
	Temperature	1.00	1.34×10^{-7}
	Light	2.00	3.40×10^{-5}
	lnws3	1.93	0.003
	Prey	1.79	0.01
	Prey × SL	1.78	0.001
C	Time feeding	1.97	$<2.22 \times 10^{-16}$
	Temperature	1.31	1.30×10^{-9}
	Light	2.00	1.26×10^{-5}
	lnws3	1.99	2.12×10^{-7}
	Prey	1.97	0.0001
	SL	1.08	6.60×10^{-6}
	Light × lnws3	1.02	0.0004

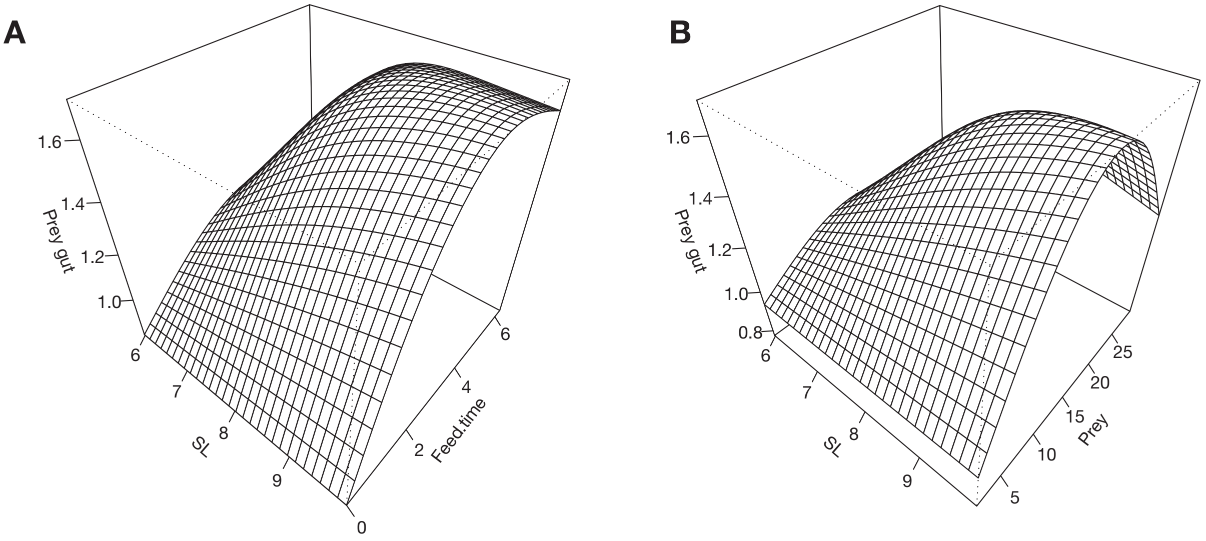

Fig. 2. *Theragra chalcogramma*. Predicted larval feeding (NPG) as a function of interacting covariates. In model predictions, interacting covariates span their entire range, while all other covariates (not shown) retain their mean value; prey gut = predicted NPG. (A) Standard length and time spent feeding interaction (Table 3, Model A); (B) standard length and prey–density interaction (Table 3, Model B)

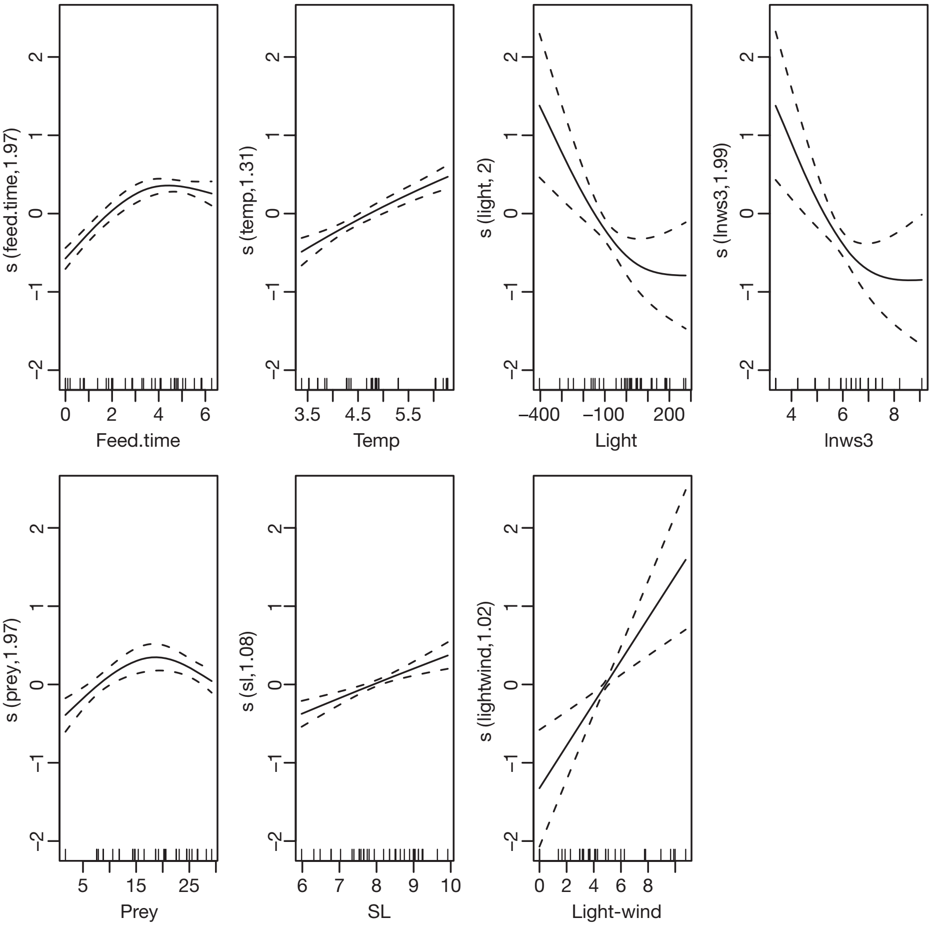

Fig. 3. *Theragra chalcogramma*. Partial additive effect on larval feeding for model that includes light and wind-speed interaction (Table 3, Model C). Further details as in Fig. 1

able to consume more prey than smaller ones.

The inclusion of the light anomaly–wind speed interaction term in the additive formulation resulted in a further improvement of the model (Table 3, Model C). All the additive variables also contributed toward a reduction of the model GCV. Most of the non-interacting covariates had similar positive effects on NPG as the additive formulation (Fig. 3). However, the additive effect of light anomaly and wind speed became negative (Fig. 3). This change in the effect of light and wind speed from positive to negative, when comparing the additive to the non-additive model formulations, is probably due to their strong interacting effect. In fact, the 3D plot showed that the effect of turbulence on feeding cannot be assessed in isolation but is dependent upon the amount of light (Fig. 4). At higher light levels, feeding improves as wind speed increases. At lower light levels, feeding conditions degrade as wind increases.

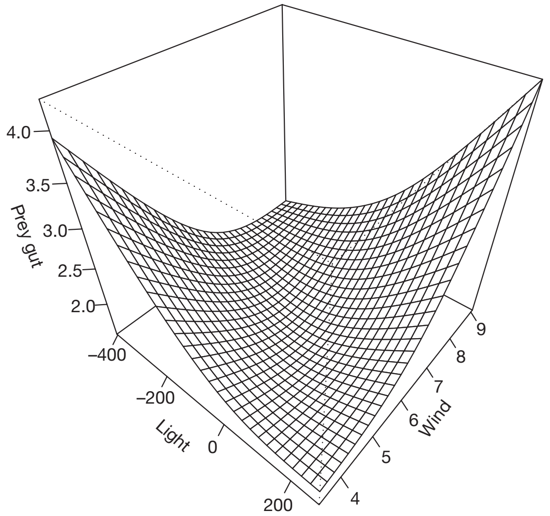

Fig. 4. *Theragra chalcogramma*. Predicted larval feeding (NPG) as a function of interaction between light and wind speed (Table 3, Model C). In model predictions, interacting covariates span their entire range, while all other covariates (not shown) retain their mean value; prey gut: predicted NPG

Among the 3 inspected models with interaction terms, the most parsimonious (i.e. best fit with least number of parameters) was the one that included the light–wind speed interaction. Compared to the additive model, the non-additive model with this interaction decreased the model GCV from 0.0402 to 0.0290, and increased the model explained variance by 7% (R^2 = 0.89 versus 0.82), making it the best overall model.

DISCUSSION

Our results indicate that feeding in walleye pollock larvae is a complex process depending not only on individual physical and biological factors, but on the interaction of these factors as well. Our best model explained a substantial portion of the variance (89%) and included an interaction between light and wind speed. This interaction had a greater effect on larval walleye pollock numerical feeding intensity than prey density over the range of values sampled. Our model showed increasing prey in the gut up to about 4 h after sunrise. This result corresponds well with the 4 to 5 h described for field collected walleye pollock (Canino & Bailey 1995). Optimal prey density for feeding was predicted to be between 15 and 20 l^{-1}, which is slightly lower than the proposed prey densities (>20 prey l^{-1}) required for walleye pollock larvae in Shelikof Strait, Gulf of Alaska, to be in healthy condition (Theilacker et al. 1996). The model also predicted increased numerical feeding intensity with increasing larval size, indicating that the predatory performance of larval walleye pollock might improve with progressing ontogeny. This is in agreement with other studies that have shown that shortly after hatching fish larvae dramatically improve their functional morphology, physiology and subsequent behavioral patterns resulting in advanced swimming performance and foraging success (Osse 1990, Porter & Theilacker 1999, Hunt von Herbing & Gallager 2000, Hunt von Herbing 2001). Similarly, increases in feeding were predicted under conditions of rising temperature, which has been shown to boost feeding rates in other studies on marine fish larvae (Houde 1989, Meekan et al. 2003). The observed positive effect of temperature on feeding success might be the result of temperature affecting not only the larval physiology and therefore swimming performance but also the physics of the surrounding environment by decreasing its viscosity (Hunt von Herbing 2002).

Wind-induced small-scale turbulence increases the contact rate between predator and prey and can thus increase larval ingestion rates. This relationship has been hypothesized to be dome-shaped rather than linear (MacKenzie et al. 1994); according to this model, maximum feeding rates occur at intermediate levels of turbulence, while highly turbulent conditions will reduce the rate of successful larval prey capture, which will lead to an overall decrease in ingestion rates. Our model predicted higher feeding rates under high turbulence levels; it did not show a decrease over the range of values observed (the maximum wind speed measured in our study was approximately 20 m s^{-1} (a speed estimated to reduce ingestion in Atlantic cod *Gadus morhua* larvae; MacKenzie et al. 1994), possibly because walleye pollock larvae avoid high turbulence situations by moving deeper down the water column (Olla & Davis 1990, Kendall et al. 1994). However, marine fish larvae are visual predators, and must rely on sufficient illumination to detect and successfully ingest prey (Paul 1983, Blaxter 1986). Thus, larval ingestion rates should be a function of not only turbulence but also light intensity, possibly with interacting effects. In a modeling study on larval Atlantic herring *Clupea harengus* and Atlantic cod *G. morhua*, both turbulence and light had a strong effect on larval ingestion rates (Fiksen et al. 1998). This is in agreement with our results, where under high-light conditions feeding improved as wind speed increased. Laboratory studies have also shown an interaction between light levels and turbulence for feeding of larval herring *C. harengus* (Utne-Palm & Stiansen 2002).

In the present study, the factors having the most influence on larval walleye pollock feeding success were light and wind speed (turbulence), with the amount of light mediating the effect of turbulence on feeding. Since turbulence may cause both fish larvae (Olla & Davis 1990, Kendall et al. 1994, Lough & Mountain

1996) and the developmental stages of copepods (Lagadeuc et al. 1997, Incze et al. 2001) to dwell deeper in the water column, one effect of turbulence may be the concentration of both predators and prey in deeper waters. This has been hypothesized by Franks (2001) in a modeling study that concluded that turbulence-avoidance behavior can lead to significant increases in predator–prey concentrations below the mixed layer. Similar avoidance behavior was reported for other marine fish larvae; namely, in Atlantic herring *Clupea harengus* larvae, high wind velocities caused a dispersion of the larval population and an increase in mean depth distribution (Heath et al. 1988). The distribution of blue whiting *Micromesistius poutassou* larvae also appeared to be deeper during high-wind than during low-wind conditions (Hillgruber & Kloppmann 2000). Organisms that would most benefit from this turbulence avoidance behavior are older larvae and zooplanktonic prey that swim sufficiently fast to be capable of leaving the mixed layer quickly after the onset of wind-mixing. Since pollock larvae are visual predators, they may need more surface downwelling light to successfully feed deeper in the water column. Therefore, increased turbulence will be most beneficial for walleye pollock larvae at high surface-light levels. When turbulence increases and light levels are low, feeding success of larvae at depth will decrease accordingly. In a modeling study, Heath (1989) found that a similar interaction between high turbulence and low light reduced feeding in larval herring *C. harengus*. Alternatively, switching to a different-sized prey or a different prey type may be a strategy to feed at low light and high turbulence. For example, radiated shanny *Ulvaria subbifurcata* larvae tended to ingest fewer, but larger, prey items under turbulent conditions (Dower et al. 1998). However, since our data only provide numerical feeding intensity, we lack the resolution necessary to identify any prey–shift behavior in walleye pollock larvae. As a data exploration technique, the GAM results suggest interesting ramifications of potential turbulence-avoidance behavior of walleye pollock larvae, warranting finer-scale sampling studies.

Our results also indicate that larval feeding decreases in the presence of high light and low wind. This may be a consequence of a lack of spatial overlap between larval walleye pollock and their prey during these conditions. Walleye pollock larvae avoid light levels above 13 µmol photon m^{-2} s^{-1} by moving deeper into the water column (Olla & Davis 1990). Thus, under conditions of high light and low turbulence, walleye pollock larvae might move deeper, resulting in reduced feeding if their copepod prey remain at shallower depths. Alternatively, feeding could simply be reduced at high light intensities, as has been shown for larval Atlantic cod *Gadus morhua* (Huse 1994).

There were some assumptions and sources of variability that could not be controlled in the present study. In simulated net-capture experiments there was no significant loss of gut contents of walleye pollock larvae (Canino & Bailey 1995), so it was assumed for the present study that loss of gut contents during collection was negligible. The period of time that the larvae experienced the environmental conditions in which they were collected could not be determined, but conditions probably do not radically change over the 6 h period of accumulation of prey in their gut. Also, wind speed was used as a measure of turbulence. Dower et al. (1998) have cautioned about using wind speed in this manner due to the complexity of turbulent regimes in coastal areas, i.e. there are factors in addition to wind speed that can affect turbulence in the water column. Furthermore, turbulent energy-dissipation rates calculated from wind speeds may not equal the values measured *in situ* (Reiss et al. 2002). In general though, where complex mixing conditions are not known to occur, wind-based models explain a high proportion of the variability in surface-layer turbulent dissipation rates (MacKenzie & Leggett 1993). In our study, we sampled in relatively deep water (bottom depth >100 m) and were mainly interested in the impact of passing storms on larval feeding; under these conditions, wind speed seems to comprise a reasonable proxy for turbulence, although we recognize that other factors may influence the level of turbulence at depth. We also assumed an even distribution of walleye pollock larvae and prey throughout the upper 60 m of the water column, even though ichthyoplankton and zooplankton distributions are typically vertically structured (e.g. Folt & Burns 1999, Napp et al. 2000). In addition to numerical feeding intensity used as a measure of larval feeding success, turbulence can also modify larval feeding behavior at other levels, such as alteration of swimming behavior, or changes in prey size or prey-taxa composition. However, our diet data did not provide the resolution necessary to determine these changes in feeding behavior. How turbulence affects prey also should be considered. For example, the copepod *Acartia clausi* is more active under turbulent conditions (Saiz & Alcaraz 1992), which could make them more vulnerable to predation. Finally, irradiance in our study was not measured, but was estimated from a model; it is recognized that there are many factors that can influence the transmission of light through the water column and also larval feeding (e.g. water clarity). Our intent was to examine common and easily measured environmental factors often used in recruitment analyses to determine which may be important to larval feeding success.

Larval feeding in relation to environmental conditions can be studied on different scales. We encourage fine-scale sampling of larvae and environmental conditions, and believe that other important factors will emerge under closer observation. However, swimming may displace larvae from the environment in which they fed, uncoupling the gut contents at the time of capture from environmental conditions under which feeding occurred. Kendall et al. (1994) demonstrated that the mean depth of larvae can change by up to 30 m during relatively short time periods during daylight intervals. We integrated sampling over the potential depth range of feeding walleye pollock larvae, as it is uncertain where in the water column larvae had actually captured prey in the previous 6 h.

Despite the listed sources of variability and the vertical integration of our samples, our model explained 89% of the observed variance in feeding, a result enabled by the wide range of the environmental conditions sampled. The results of the fitted models conform to theoretical expectations from known parameters influencing larval feeding, and provides new information on the interacting role of environmental variables. We demonstrate that for walleye pollock larvae, feeding success cannot be inferred from prey density alone. Additionally, the exploratory models presented here clarify the role of turbulence and its interdependence with light intensity on larval feeding, and lead to new hypotheses on the role of light and turbulence that can be field-tested.

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