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Aquaculture 191 (2000) 289–302

Aquaculture

www.elsevier.nl/locate/aqua-online

A pulse feeding strategy for rearing larval fish: an experiment with yellowtail flounder

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Received 19 August 1999; received in revised form 2 May 2000; accepted 18 May 2000

Abstract

Providing a good foraging environment for the larviculture of marine fish must take into account a number of factors including water temperature, light intensity, prey type, prey density, and frequency of feeding. We designed an experiment to determine if larvae require continuous exposure to live prey, or if feeding in "pulses" is adequate to promote good growth and survival. Larvae of yellowtail flounder (*Pleuronectes ferrugineus*) were fed once (1×, at 10 AM), twice (2×, at 10 AM and 10 PM), four times (4×, at 10 AM, 4 PM, 10 PM and 4 AM), or continuously (by automatic feeder) at 8000 prey per liter (p/l). Larval growth, survival, and foraging behavior were monitored during weeks 1–7 post-hatch. Larval growth rate was significantly reduced in the 1× treatment. The growth rate of larvae was similar in other treatments. Larval survival was lowest in the 1× treatment, but was not significantly affected by feeding frequency. The consumption rate of larvae in the 1× and 2× treatments was significantly higher than that of larvae in the continuous treatment. This behavioral response to hunger probably enabled larvae in the 2× treatment to grow as rapidly as larvae in the continuous prey treatment. It is concluded that yellowtail flounder larvae do not require continuous exposure to high prey densities and there may be potential to reduce the cost of live food and labor in the culture of this and possibly other species.

Keywords: Feeding frequency; Prey density; Growth; *Pleuronectes ferrugineus*; Fish larvae

1. Introduction

Marine fish larvae are often fed at high prey densities during larviculture. Higher prey densities serve to increase the encounter rate between predator and prey, and an

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0044-8486/00/$ - see front matter
PII: S0044-8486(00)00434-8

increase in consumption rate with prey density has been observed for many species (Houde and Schekter, 1980; Munk and Kiørboe, 1985; Klumpp and von Westernhagen, 1986; Puvanendran and Brown, 1999). Given the rapid growth of larvae, it is often assumed that they must maintain optimal feeding rates in order to grow and survive. Therefore, a great deal of attention is invested in the monitoring and maintenance of prey densities. Greater feeding rates typically result in rapid growth and development, enhanced larval condition, and ultimately high survival.

While it is recognized that larvae require high prey densities to feed efficiently, the required frequency of exposure to high prey availability has received little research interest (but see Houde and Schekter, 1978). However, this is a relevant issue as laboratory and field evidence suggests that larvae may not require the constant exposure to high prey densities often used in larviculture. In this paper, larvae of yellowtail flounder (*Pleuronectes ferrugineus*) were offered live prey continuously and at different feeding frequencies to determine if constant high levels of prey are necessary to promote good growth and survival. Yellowtail flounder is a candidate species for aquaculture in Atlantic Canada (Brown et al., 1995).

A culture protocol that alters the exposure of larvae to prey has an ecological basis, as data from field observations suggests that fish larvae encounter prey on a scale that is spatially and temporally variable (Arthur, 1977; Owen, 1989). It is reasonable to assume that larvae are both behaviorally and physiologically adapted to conditions of varying prey availability (Brown et al., 1997). For example, northern anchovy (*Engraulis mordax*) and herring (*Clupea harengus*) larvae decreased their search area at high prey density, in an apparent attempt to stay within a patch of prey (Hunter and Thomas, 1974; Gallego, 1994). Houde and Schekter (1978) found that only 3 h of exposure to high prey density is required by larvae of sea bream (*Archosargus rhomboidalis*) in order to obtain the same high survival observed when reared at constant high prey density.

Continuous feeding may be harmful as well as unnecessary. There is evidence that prolonged feeding periods and high rations decrease digestive efficiency as they increase evacuation rate (Boehlert and Yoklavich, 1984). Johnston and Mathias (1994) showed that apparent digestibility increased with gut retention time in larval walleye (*Stizostedion vitreum*). As gut evacuation time is shorter in continuously feeding fish (Canino and Bailey, 1995), it is predicted that larvae in a constant prey treatment will have reduced absorption efficiency compared to pulse-fed larvae. Furthermore, feeding and digestion require energy. For example, an increase in oxygen consumption was observed in sea bream juveniles offered higher rations (Guinea and Fernandez, 1997). Because the consumption of excess food decreases absorption efficiency and increases the energy required for digestion, and because live food is expensive, continuous feeding may not be an optimal strategy for larval rearing.

It has been suggested that the undifferentiated digestive system of larval fish is adapted to exploit high-density patches of prey (Govoni et al., 1986; Klumpp and von Westernhagen, 1986). Although absorption efficiency decreases at high feeding rates, Boehlert and Yoklavich (1984) have calculated, using the ingestion rates of Werner and Blaxter (1980), that the increase in prey consumed at high prey density more than compensates for the overall decrease in assimilation efficiency for larval herring. Larvae may therefore maximize growth rate rather than growth efficiency. However, in aquacul-

ture, as in many industries, it may be desirable to favor efficiency rather than absolute growth (Klumpp and von Westernhagen, 1986). Live food for fish larvae is costly, and maintaining high prey densities may be wasteful. Therefore, the aim of this experiment was to determine if it is possible to reduce the amount of prey offered to the larvae, without significantly decreasing growth and survival.

2. Materials and methods

2.1. Experimental design

Eggs and milt were collected from captive broodstock maintained at the Ocean Sciences Centre, Memorial University of Newfoundland, Logy Bay, Newfoundland. Fertilized eggs were incubated in a 250-l cylindro-conical upwelling tank. The eggs hatched over a 24-h period. Larvae were sampled for initial morphometric measurements (described below) after most ($> 90\%$) of the eggs had hatched and this was considered day 0 of the experiment.

Larvae were reared in rectangular 33-l black glass tanks. All tanks were kept in a water bath and were supplied with filtered (25 μm) seawater in a flow-through system. Two air stones were used per tank to provide gentle aeration and to promote a homogeneous distribution of prey. The light intensity at the water surface was approximately 13.3 μmol s^{-1} m^{-2} (750 lx; 150 W General Electric bulbs) and continuous lighting (24 h) was used. The temperature ranged from 11.5°C to 14.5°C (mean = 12.8°C) throughout the experiment. The experiment lasted 7 weeks, as yellowtail flounder undergo metamorphosis around this time.

Larvae were stocked into experimental tanks on day 1 post-hatch at a density of 60 larvae/l. Feeding began on day 2 and all treatments were fed at 8000 prey per liter (p/l), adjusted three times daily (around 10 AM, 4 PM, and 10 PM), from days 2 to 10 in order to establish feeding in all tanks. The prey density of 8000 p/l was chosen because it was found to promote good growth and high survival of this species at our research facility (Puvanendran, unpubl. data). On day 11, the different feeding treatments were initiated. Rotifers (*Brachionus plicatilis*), enriched with culture selco (INVE, Belgium) and *Artemia franciscana* nauplii, enriched with DHA selco (INVE, Belgium) or Algamac (Bio-Marine, USA) were used as prey for the larvae. Larvae were fed rotifers exclusively until the end of week 4. Weaning to *Artemia* was complete by the end of week 5 and *Artemia* were fed exclusively thereafter.

The four treatments used in this study were feeding once ($1\times$, at 10 AM), twice ($2\times$, at 10 AM and 10 PM), four times ($4\times$, at 10 AM, 4 PM, 10 PM, and 4 AM), and continuously (by automatic feeder) at 8000 p/l. Two replicate tanks were used per treatment. An automatic feeder consisted of a reservoir for live prey and a solenoid attached to a timer. Aeration within the reservoir kept the prey evenly distributed. When the feeding treatments were initiated (day 11), the flow rates in all tanks were increased so that within 2 h after feeding, the prey availability had dropped to < 4000 p/l and within 6 h, it had been reduced to < 1000 p/l. The automatic feeder was programmed to deliver prey to the continuously fed tanks every 2 h to make up for prey lost in the

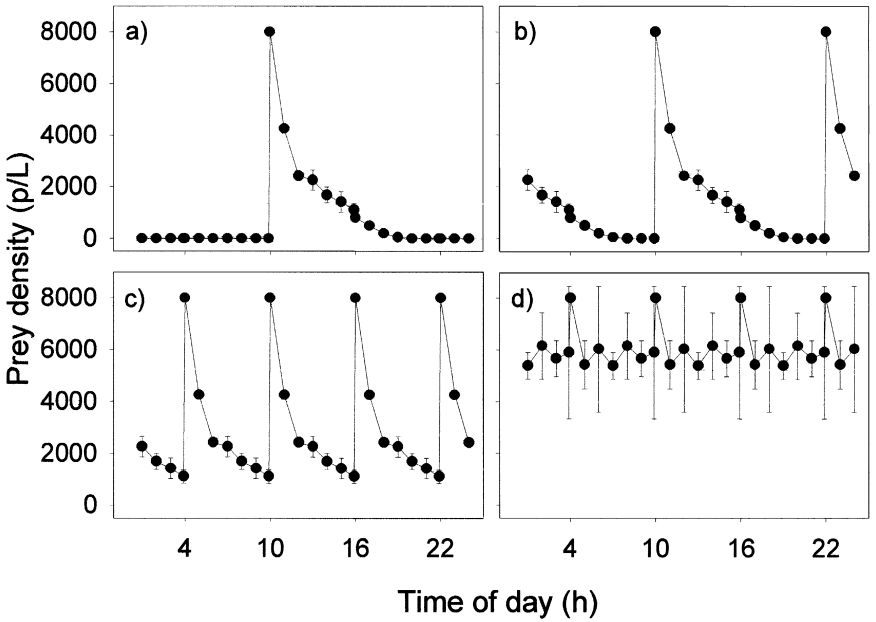

Fig. 1. Prey densities (p/l) in experimental treatments (±S.E.) over a typical 24-h period: (a) 1×, one feeding per day, (b) 2×, two feedings per day, (c) 4×, four feedings per day, (d) continuously fed. See text for details.

outflow. To ensure that the prey densities decreased as desired, prey densities were measured hourly for 6 h following the 10 AM feeding, four times during the course of the experiment. Prey densities for the measured 6-h period were then averaged and extrapolated over the 24-h day (Fig. 1).

Prey densities were determined by sampling 5 ml aliquots from different depths within the tanks (below surface, mid-depth, and above bottom) prior to the 10 AM, 4 PM, and 10 PM feedings. The total number of prey items in each sample was counted and the prey density was adjusted as required. Microalgae (*Isochrysis* and *Nannochloropsis*) were also added to all tanks at 10 AM, 4 PM, and 10 PM. Algae for each

Table 1
Definition of the MAPs observed in developing yellowtail flounder larvae, after Barlow (1968)

MAP	Definition
Swim	Forward movement of the larva through water column resulting from undulations of the caudal region.
Pause	Larva is motionless (similar to "non-swimming" of Munk, 1995).
Orient	The head moves towards a prey item (similar to "orientation" of Brown and Colgan, 1985).
Fixate	The larva is stationary and bends its caudal region into an "S" shape position, typically follows orient (Braum, 1978).
Lunge	The larva moves towards prey from the fixate position in an attempt to capture prey (Braum, 1978).

Table 2
Summary of ANCOVA results for standard length (mm), dry weight (mg), and ash-free dry weight (mg) response variables for yellowtail flounder larvae reared at different feeding frequencies

Response variable	Source	*df*	*F*	*P*
Standard length (mm)	Age	1	1197.8	0.000
	Treatment	3	0.89	0.456
	Age × treatment	3	3.55	0.021
	Error	48		
Dry weight (mg)	Age	1	2101.0	0.000
	Treatment	3	0.67	0.574
	Age × treatment	3	1.04	0.385
	Error	48		
Ash-free dry weight (mg)	Age	1	1962.4	0.000
	Treatment	3	0.62	0.607
	Age × treatment	3	1.84	0.477
	Error	48		

experimental tank was harvested from the same culture cylinder during the log phase of growth and added to each tank at the same time in order to standardize turbidity between tanks. Prey densities were not counted prior to the 4 AM feeding. The prey densities in the continuously fed tanks were monitored at 10 AM, 4 PM, and 10 PM. However, for all other feedings for this treatment and for the 4 AM feeding, it was assumed that prey densities had decreased as expected.

Because the nutritional content of live prey changes with time in enrichment medium, an attempt was made to control for differential enrichment of live food. This was especially important because of the different feeding schedules of the live food (rotifers enriched four times daily, *Artemia* fed once daily) and larvae. Rotifers were collected

Table 3
Summary of ANCOVA results for one-tailed pairwise comparisons between treatments for standard length at age

Constant treatment vs.	Source	*df*	F	*P*
1×	Week	1	818.0	0.000
	Treatment	1	0.15	0.701
	Week × treatment	1	11.2	0.003
	Error	24		
2×	Week	1	753.3	0.000
	Treatment	1	0.38	0.546
	Week × treatment	1	0.11	0.739
	Error	24		
4×	Week	1	558.3	0.000
	Treatment	1	1.18	0.289
	Week × treatment	1	0.01	0.926
	Error	24		

All treatments are compared to the constant prey treatment. 1× = one feeding per day, 2× = two feedings per day, 4× = four feedings per day.

from live food culture tanks around 10 AM and maintained in microalgae for 6–24 h prior to feeding, depending on treatment. For most feedings, *Artemia* were taken directly from enrichment tanks. However, for the 4 AM feeding *Artemia* were maintained in microalgae for 6 h. Microalgae were also added to *Artemia* in the automatic feeder reservoir. The volume of microalgae added was approximately 20% of the rotifer or *Artemia* volume.

2.2. Data collection

Larvae were sampled weekly to measure growth. Five larvae from each tank were sampled for standard length (mm) and then pooled for a measurement of dry weight (mg) and ash weight (mg). Larvae were kept on ice and measured immediately after death to prevent shrinkage due to dehydration. A dissecting microscope was used to

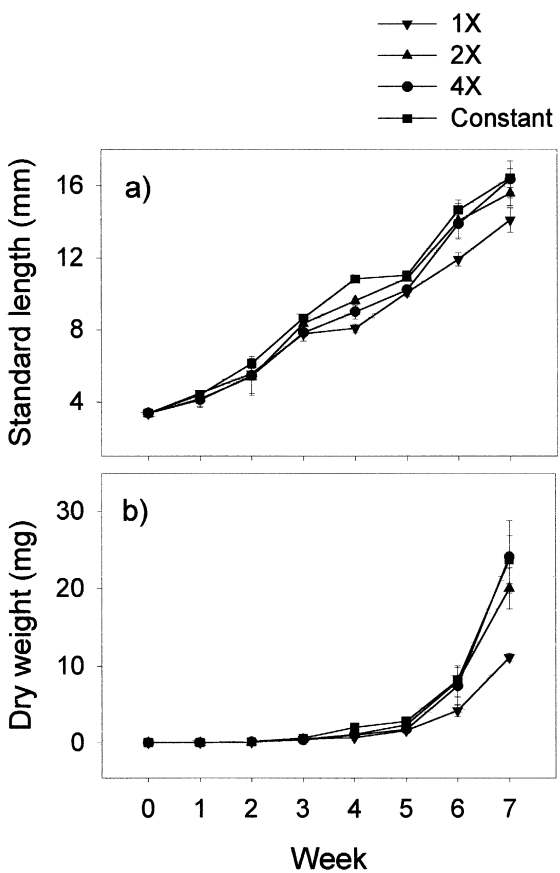

Fig. 2. Mean (a) standard length (mm), and (b) dry weight (mg) of yellowtail flounder larvae reared at different feeding frequencies over age (weeks post-hatch). Symbols are means of the means for each replicate ±S.E.

measure larvae to the nearest 0.1 mm. Larvae were rinsed in 3% ammonium formate, placed on preweighed aluminum foils (weighed to nearest 0.001 mg), dried at 55°C for at least 48 h, and reweighed. Larvae were then burned in a muffle furnace at 400°C for

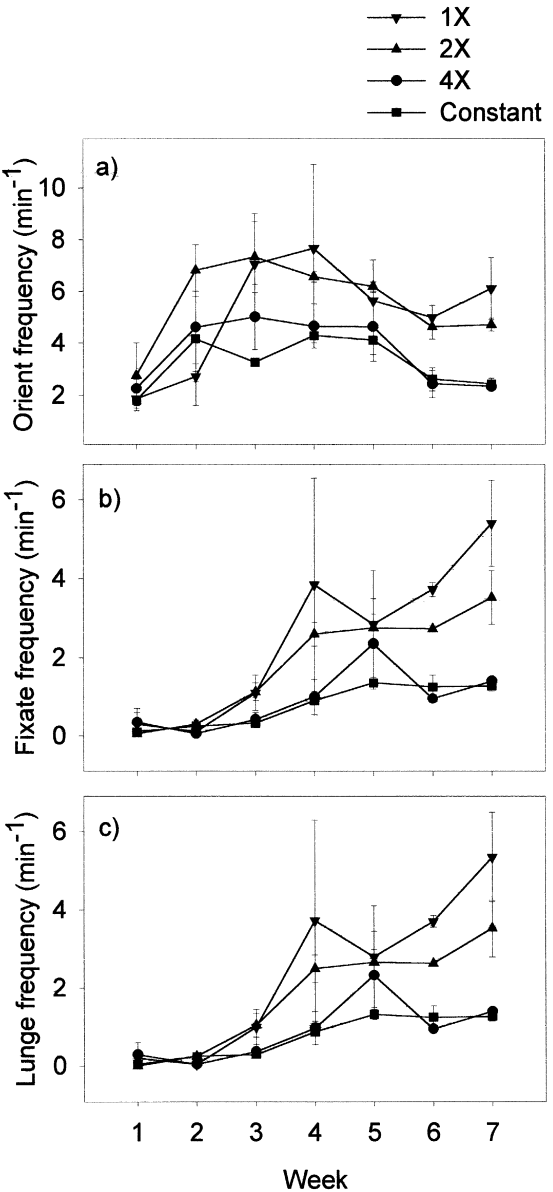

Fig. 3. Mean (a) orient frequency (min^{-1}), (b) fixate frequency (min^{-1}), and (c) lunge frequency (min^{-1}) of yellowtail flounder larvae reared at different feeding frequencies during 1 min observation periods over age (weeks post-hatch). Symbols are means of the means for each replicate $\pm$S.E.

12 h and ash weights were measured. On day 0, four sets of five larvae each were sampled from the incubation tank. On the final sampling day (day 49, week 7), three sets of five larvae each were sampled from each tank, except for one of the 1× replicates where only two fishes remained.

All tanks were examined for mortalities twice daily from day 14. Dead larvae decompose too quickly to be observed prior to this time. At the end of the experiment, the number of surviving larvae in each treatment was recorded.

Behavioral observations on larvae were conducted once weekly during weeks 1 and 2, before the different feeding treatments began, and twice weekly during weeks 3–7. All tanks were observed following the first (10 AM) meal of the day. The order of tanks observed was changed systematically on each observation day. Observations on larvae began 5 min following the adjustment of prey densities to 8000 p/l. The focal animal technique (Altman, 1974) was used to observe 10 arbitrarily chosen larvae in each tank for 1 min each. During each observation, the frequency and duration of the following Modal Action Patterns (MAPs; Barlow, 1968) were recorded using an event recorder: swim, pause, orient, fixate, and lunge (Table 1). Only two larvae remained in one of the 1× replicates during week 7. Observations on these larvae are not included in the analysis.

2.3. Data analysis

The effects of feeding frequency and age on growth indices and behavioral data were analyzed using analysis of covariance (ANCOVA), with week as the covariate ($P =$

Table 4
Summary of ANCOVA results for behavioral response variables for yellowtail flounder larvae reared at different feeding frequencies

Response variable	Source	*df*	*F*	*P*
Orient frequency	Week	1	39.8	0.000
	Week^2	1	35.9	0.000
	Treatment	3	0.65	0.588
	Week × treatment	3	0.19	0.900
	Week^2 × treatment	3	0.03	0.992
	Error	43		
Fixate frequency	Week	1	113.1	0.000
	Treatment	3	0.25	0.860
	Week × treatment	3	4.27	0.010
	Error	47		
Lunge frequency	Week	1	125.7	0.000
	Treatment	3	0.40	0.751
	Week × treatment	3	4.76	0.006
	Error	47		
Swim duration	Week	1	89.9	0.000
	Treatment	3	1.99	0.129
	Week × treatment	3	0.48	0.698
	Error	47		

Week^2 is the square of larval age in weeks; for orient frequency, a polynomial term was used in the model.

0.05). For each response variable (growth or behavioral measurement), the mean value for each replicate tank was calculated and this value was used in the analysis. When significant results were obtained from the ANCOVA model (at $P = 0.05$), planned one-tailed pairwise comparisons between treatments were performed to determine which treatments differed ($P = 0.10$; Sokal and Rohlf, 1995). Three planned comparisons were chosen, as three treatment degrees of freedom were available. In these comparisons, all treatments were compared to the constant prey treatment (1× vs. constant, 2× vs. constant, 4× vs. constant).

In order to fit the assumptions of ANCOVA, it was necessary to logarithmically transform some response variables. In most cases, a linear model was adequate to describe the results. However, a second-order polynomial was fitted to the orient frequency data. Plots of residuals and predicted values were examined for heteroscedasticity and normality for each analysis, and model assumptions were satisfied.

A one way analysis of variance (ANOVA) was used to test for differences in survival between treatments. The number of larvae alive prior to the final morphometric sampling (week 7) was used to calculate percent survival at the end of the experiment.

3. Results

The standard length of the larvae was significantly affected by the interaction of age and feeding frequency (Table 2). Pairwise comparisons of standard length-at-age between treatments show that the growth rate of larvae in the 1× treatment was significantly lower than the growth rate of larvae fed continuously (Table 3, Fig. 2a). Dry weight of the larvae was not significantly influenced by feeding frequency

Table 5
Summary of ANCOVA results for one-tailed pairwise comparisons between treatments for lunge frequency at age

Constant treatment vs.	Source	*df*	*F*	*P*
1×	Week	1	63.7	0.000
	Treatment	1	0.62	0.439
	Week×treatment	1	8.61	0.007
	Error	23		
2×	Week	1	133.8	0.000
	Treatment	1	0.23	0.638
	Week×treatment	1	10.4	0.004
	Error	24		
4×	Week	1	41.2	0.000
	Treatment	1	0.07	0.791
	Week×treatment	1	0.00	0.957
	Error	24		

All treatments are compared to the constant treatment. 1× = one feeding per day, 2× = two feedings per day, 4× = four feedings per day

(Table 2). However, by week 7, larvae in the 1 × treatment weighed less than larvae in all other treatments (Fig. 2b). A similar pattern is seen for ash-free dry weight (Table 2).

Survival results were not adjusted for the 30 larvae removed per tank prior to the final sampling day. Survival to day 14 was low and variable in all tanks (1.4–17.3%) and was not dependent on treatment (ANOVA: $F_{3,4} = 2.17$, $P = 0.234$). Survival from weeks 2 to 7 was 21.8% (±13.8), 47.3% (±1.5), 32.8% (±2.5) and 43.6% (±11.9) in the 1 ×, 2 ×, 4 × and constant treatments, respectively. Survival from weeks 2 to 7 was not significantly affected by treatment (ANOVA: $F_{3,4} = 1.55$, $P = 0.333$).

Orient frequency increased early in the study, peaked during weeks 3–5, and then declined later in the study for all treatments (Fig. 3a). The frequency of orient in the 1 × and 2 × treatments was always higher than in the 4 × and constant treatments after week 2. However, orient frequency was not significantly affected by feeding frequency (Table 4). The frequencies of the foraging MAPs fixate and lunge were similar and

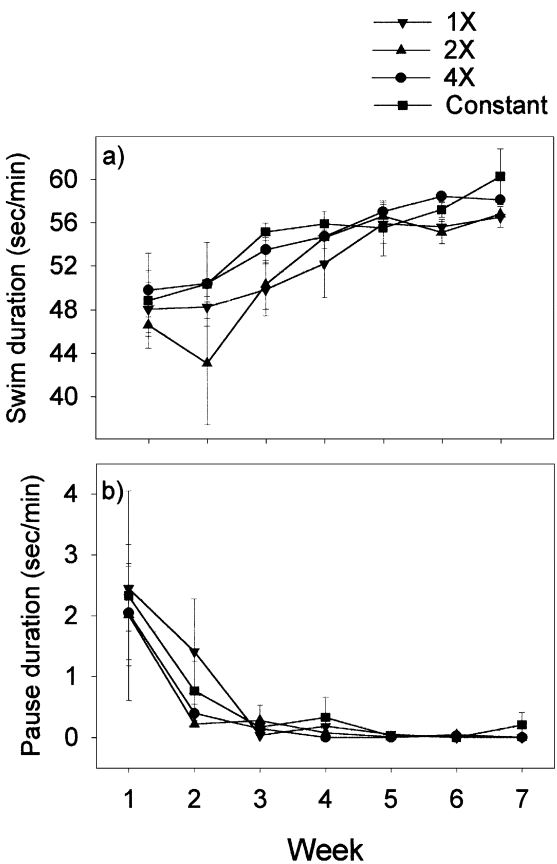

Fig. 4. Mean (a) swim duration (s/min) and (b) pause duration (s/min) of yellowtail flounder larvae reared at different feeding frequencies during 1 min observation periods over age (weeks post-hatch). Symbols are means of the means for each replicate ±S.E.

increased throughout the study period (Fig. 3b,c). The frequencies of fixate and lunge were significantly affected by the interaction of age and feeding frequency (Table 4). Pairwise comparisons show that the 1× and 2× treatments have a significantly greater increase in lunge frequency with age compared to the constant treatment (Table 5). Swim duration increased during the study period (Fig. 4a) and there was a significant effect of age on swim duration (Table 4). The pause MAP only occurred in early stage yellowtail flounder larvae (Fig. 4b) and was not analyzed statistically.

4. Discussion

Yellowtail flounder larvae grew and survived in all treatments used in this study. The results demonstrate that yellowtail flounder larvae do not require constant, high densities of prey. Larvae grew and survived when offered prey only once per day. However, a feeding frequency of 2× caused a significant increase in growth rate and an increase in survival compared to 1×. Increasing feeding frequency above 2× did not result in a further increase in growth or survival.

Different periods in microalgae enrichment may have caused differences in the quality of live prey fed to the different treatments. Thus, if prey quality decreases after 24 h in algal enrichment, the 1× treatment may have been disadvantaged as it was only fed prey that had been enriched for 24 h, due to the experimental enrichment and feeding schedule. We did not conduct an intensive chemical analysis of the live prey. However, we consider that if differences in prey quality existed, they were masked by the large differences in prey quantity offered to the larvae. Furthermore, the temperatures in our experimental tanks were approximately 10°C below the culture temperatures of the algae and live prey. This would have resulted in lower rates of chemical (fatty acid) and physiological (metabolism) change in the feed organisms and reduced any absolute differences in prey quality among the treatments. However, we cannot rule out that there may have been differences in prey quality between treatments and that these could have contributed somewhat to our results.

The survival in all treatments was low and was not significantly affected by feeding frequency. However, survival was lowest in the 1× treatment. The relatively low survival in all treatments is likely to be due to poor egg quality. The eggs used in this study were collected late in the spawning season when temperatures were high and many curled larvae were observed at hatching. Most mortality (> 80%) occurred before the experimental feeding regimes were established, suggesting that the high mortality was due to a general failure to initiate feeding and not due to the different treatments.

The behavioral data can aid in interpreting the observation that larvae in the 2×, 4× and constant treatments had similar growth rates and survival, despite wide differences in amount of prey offered to the larvae. The lunge frequency for the 2× treatment is nearly twice as high as that for the constant treatment for all weeks. This increase in consumption rate in the 2× treatment probably enabled these larvae to obtain an adequate ration when prey were available, and grow and survive as well as larvae in the 4× and constant treatments. Furthermore, despite lower consumption rates of larvae in the 4× and continuous treatments when prey were available, larvae in these

treatments probably consumed a greater total amount of prey compared to larvae in the 2 × treatment, and may have suffered from reduced assimilation efficiency.

The differences in lunge frequency between feeding frequency treatments is a departure from an accepted model of consumption by larval fish. Previous descriptions of predation describe the consumption rate of larvae at different prey densities as a functional response (Holling, 1965; Houde and Schekter, 1981). The consumption rate of many species of larval fish has been shown to increase towards an asymptote with increasing prey density (Houde and Schekter, 1981; Munk and Kiørboe, 1985; Klumpp and von Westernhagen, 1986; Miller et al., 1992). The theoretical interpretation of larval feeding behavior assumes that the observed consumption rate is a physiological and/or behavioral response to the prey density alone. However, in this experiment, yellowtail flounder larvae fed at the same prey density did not exhibit the same consumption rate. Instead, they altered their consumption rate in response to feeding history, or degree of hunger, suggesting that this must be considered in analyses of the functional response.

In his study on cod (*Gadus moruha*) larvae, Munk (1995) also observed an apparent behavioral response to hunger that was independent of prey density. Larval cod decreased their search effort as they became satiated. In his study, the time spent swimming and searching for prey decreased as the number of prey items in the gut increased. The results for yellowtail flounder differ in that significant differences in the time spent swimming between treatments were not detected. This may be a result of the different prey search behaviors of cod and yellowtail flounder. Cod are saltatory searchers, which search for prey during the motionless periods that punctuate swimming events. If prey is not located, they swim a short distance and scan again (Browman and O'Brien, 1992). For a saltatory searcher, swimming duration can thus be used as an indicator of search effort. Yellowtail flounder are cruise searchers and spend most of their time swimming (J.R., pers. observ.). The time that yellowtail flounder spend performing foraging behaviors therefore makes up little of the total observation period relative to swimming duration. Consequently, differences between treatments in the total time spent swimming should be small, and detecting them may be limited by the observer's reflexes.

The growth results are similar to those of Houde and Schekter (1978) who showed that there was a minimum period of high prey availability (3 h) that resulted in survival rates of sea bream larvae approaching those observed when larvae were reared at a constant high prey density. However, the yellowtail flounder data differ from the results of Brown et al. (1997), who examined the effects of feeding frequency on growth and foraging behavior of lumpfish (*Cyclopterus lumpus*) larvae. Their results demonstrated that lumpfish larvae grow faster when fed in discrete meals compared to continuously. The observation that lumpfish growth is inhibited by continuous feeding and yellowtail flounder growth is not may be explained by differences in digestive physiology between the two species.

The results of this study demonstrate that yellowtail flounder larvae do not require constant high prey densities during larviculture. Feeding larvae twice a day at high prey density provided an adequate ration, as similar growth and survival were observed between the 2 × and continuously fed treatments. This may be explained by a behavioral response of increased consumption rate in larvae fed twice a day or a

physiological response of decreased assimilation efficiency in larvae fed continuously. The behavioral data illustrate that larvae exhibit plasticity in responding to their foraging environment, depending on feeding history. The similar growth between larvae in the $2\times$ and constant treatments demonstrates that there is potential to reduce the live food and labor cost in larviculture. It is not necessary to maintain constant high prey densities in the rearing of yellowtail flounder, provided larvae are offered prey at high density at least twice a day. Because different species vary both physiologically and behaviorally, it may not be possible to universally apply these findings to the larviculture of other species.

Acknowledgements

We are grateful to Danny Boyce, Dena Wiseman, Olav Lyngstad, Donna Sommerton, Trevor Keough, Ralph Pynn, and Tracy Granter for technical assistance and live food production. Velmurugu Puvanendran generously shared his unpublished data. Funding for this research was provided by the Canadian Centre for Fisheries Innovation and a Memorial University Graduate Fellowship.

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