Abstract—Foraging behavior and prey abundance are significant factors determining the survival success of fish during the larval stage. Witch flounder (*Glyptocephalus cynoglossus*) are reported to have the longest pelagic stage of any northwest Atlantic flatfish. We used laboratory experiments to investigate the behavior and performance of witch larvae in relation to prey availability during this important life history stage. In one experiment, larvae were reared at a range of prey densities (2000, 4000, and 8000 prey per liter) and their growth and survival were monitored for 12 weeks after hatching. In a second experiment the foraging behavior of larvae was recorded during feeding trials at a range of prey densities (250, 500, 1000, 2000, 4000, 8000, and 16,000 prey per liter) during weeks 2–8 after hatching. The larval search strategy for prey appeared to change from one that was saltatory to one that was cruising, and the foraging behavior was not strongly affected by variation in prey availability. The growth rate was rapid (0.53 mm/d) and was unaffected by changes in prey density as was survival. Witch flounder larvae likely have low prey requirements compared with yellowtail flounder and Atlantic cod reared under similar laboratory conditions. The ability to forage effectively when prey is abundant or scarce and the low prey requirements of this species may be an adaptive response to the extended larval period.

The behavior, growth, and survival of witch flounder (*Glyptocephalus cynoglossus*) larvae in relation to prey availability: adaptations to an extended larval period

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The effects of prey abundance on the behavior, growth, and survival of witch flounder (*Glyptocephalus cynoglossus*, Linnaeus) larvae were examined by using laboratory experiments. Witch flounder is an interesting study organism because it displays a life history characteristic that is very different from other Pleuronectiformes. Most flatfish undergo metamorphosis at a small size and early age (see Miller et al., 1991; Osse and Van den Boogaart, 1997). Little information is available on witch flounder larval biology and ecology, and on precise length and age data at metamorphosis for witch flounder are lacking in the literature. However, field evidence indicates that witch flounder has the longest pelagic stage of any Northwest Atlantic flatfish and undergoes metamorphosis at a relatively large size (Scott and Scott, 1988). Because of their long larval period, witch flounder larvae will likely be exposed to temporal variations in prey abundance at sea. Larvae are likely able to cope with large fluctuations in prey availability and may not be as susceptible to mismatches in prey abundance or starvation in relation to other species. Unfortunately, no information is available concerning the performance of witch flounder larvae in relation to the availability of prey in the wild. Therefore, we used laboratory experiments to gain an understanding of the early biology of this species. The objective of our study was to determine the growth, survival and foraging response of witch flounder larvae to differences in prey abundance.

Materials and methods

Eggs and milt of adult witch flounder in spawning condition were collected aboard a commercial fishing vessel in the Gulf of Maine. The eggs from approximately 10 females were fertilized with milt from an equal number of males. Fertilized eggs were shipped on ice by courier to the Ocean Sciences Centre of Memorial University of Newfoundland in Logy Bay, Newfoundland. Upon arrival, the eggs were stocked in 250-L cylindroconical upwelling incubators at 12°C. Larvae hatched over a one-day period, seven days after fertilization (day 0 of the experiment). At this point, 10 larvae were sampled for morphometric measurements (defined below).

Two experiments were designed to obtain the most information possible from the limited number of larvae available. In experiment 1, larvae were reared at a range of prey densities and their growth and survival were monitored. In experiment 2, larvae were exposed to a range of prey densities and their behavior was recorded.

We recognize that designing ecologically relevant laboratory experiments is difficult (Suthers, 2000). Our rearing conditions were chosen on the basis of established techniques for other north Atlantic marine fish larvae that have resulted in high growth and survival (Puvanendran and Brown, 1999; Rabe and Brown, 2000). Although these rearing conditions do not precisely mimic a natural environment, they do enable valid comparisons of experimental

results with those for other species. One can then use this comparative evidence to make speculations concerning observations from the field. We used cultured zooplankton as live prey for the larvae. Although this is not the natural prey for larval witch flounder, it offers desirable characteristics necessary for experimentation, such as uniform shape, size, and swimming speed and although prey densities used in our experiments were typically higher than averages reported from the field (Myers et al., 1994), these levels were necessary in the laboratory to promote growth and survival (see Houde, 1978; Puvanendran and Brown, 1999).

Experiment 1: Growth and survival

Six 33-L rectangular black tanks were used for the rearing experiment. All tanks were kept in a water bath to minimize temperature fluctuations and were supplied with filtered (25 μm) seawater. Each tank was fitted with two air stones that provided light aeration to promote a homogeneous distribution of prey. The light level at the water surface was 200 lux and continuous lighting (24 h) was used. The temperature ranged from 10° to 15°C (mean 12.6°C).

On day zero, newly hatched larvae were transferred to each experimental tank to achieve a stocking density of six larvae per liter. Three replicated feeding treatments were chosen: 2000, 4000, and 8000 prey per liter. Previous results in our laboratory for other northwest Atlantic species suggested that this range of prey densities was sufficient to observe the effects of prey density on larval growth and survival (Puvanendran and Brown, 1999; Laurel et al., in press).

Rotifers (*Brachionus plicatilis*) enriched with culture selco (INVE, Belgium) or *Artemia franciscana* nauplii enriched with DHA selco (INVE, Belgium) or Algamac (Bio-Marine, Hawthorne, CA), were used as prey for the larvae. Prey densities were determined by sampling 5-mL aliquots from different depths within the tanks (below surface, mid-depth, and above bottom) and were adjusted as needed to maintain nominal densities three times a day (around 10 AM, 4 PM, and 10 PM). Microalgae (*Isochrysis* and *Nannochloropsis*) were added to the experimental tanks prior to each feeding.

At week 5, the larvae were transferred to larger 65-L circular tanks because they had grown too large for the smaller tanks; all other protocols remained unchanged. The rearing experiment was stopped at week 12. At this point most larvae had begun eye migration but were still pelagic.

Data collection   Larvae were sampled weekly for standard length (SL, measured from tip of snout to posterior end of notochord). For weeks 0–3, larvae were measured to the nearest 0.1 mm with a dissecting microscope. Standard length was measured to the nearest 1 mm after week 3. On weeks 1, 5, 8, and 12, five larvae were lethally sampled (killed by an overdose of MS-222) from each tank for determination of SL, body height (BH, myotome height posterior to anus), and dry weight (DW). These sampled larvae were kept in beakers on ice and measured immediately after

death to prevent shrinkage from dehydration. Larvae were rinsed in 3% ammonium formate, placed on preweighed aluminum foils (weighed to nearest 0.001 mg), dried at 55ºC for at least 48 hours, and reweighed. For all other weeks, the SL of ten live larvae per tank was measured.

The absolute growth rate was calculated according to the equation

$$G = (L_t - L_0)/t,$$

and the length-specific growth rate (SGR) was calculated according to the equation

$$SGR = (\ln(L_t) - \ln(L_0)/t) \cdot 100,$$

where L_t = the mean final length (mm);
   L_0 = the mean initial length; and
   t = the period of growth (days; Busacker et al., 1990).

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

Data analysis   For each growth measurement (SL, BH, DW), a mean value was calculated for each replicate and this value was used in the analysis. Growth measurements were analyzed by treatment using a model I analysis of covariance (ANCOVA, Zar, 1999) with age of the larvae (weeks after hatching) as the covariate (α=0.05). Dry weight data was logarithmically transformed to satisfy the assumptions of the ANCOVA. A one-way analysis of variance (ANOVA) was used to test for differences in survival at the end of the experiment.

Experiment 2: Behavior

Larvae were stocked into a 250-L cylindroconical upwelling tank on day zero. This tank served as a general rearing tank for larvae used for behavioral observations. The light was continuous (24 h) at an intensity of 200 lux at the surface. Preliminary results with witch flounder larvae showed that this light intensity and light regime resulted in good growth and survival (Rabe, 1999). The temperature ranged from 4–14°C (mean 12.4°C) during the 8-week experiment.

Feeding began on day 1 after hatching. Rotifers or *Artemia* nauplii, or both, were used as prey for the larvae and were enriched with commercial products as described previously. Larvae were fed three times daily at 4000 prey per liter (prey/L). The prey density in the rearing tank ranged from 0–4,000 prey/L throughout the day. Microalgae (*Isochrysis* and *Nannochloropsis*) were also added twice daily.

Data collection   Behavioral observations were conducted every 3–4 days from week 2 to 8 beginning on day 8. The prey densities used in the feeding trials were 250, 500, 1000, 2000, 4000, 8000, and 16,000 prey/L. Prior to the

Table 1

Definition of the modal action patterns (MAPs) observed in developing witch flounder larvae, after Barlow (1968).

MAP	Definition
Locomotory MAPs	
Swim:	Forward movement of the larva through the water column resulting from undulations of the caudal region.
Turn:	A rapid lateral bend initiated by the head results in rotating the body approximately 180°.
Nondirected MAPs	
Pause:	Larva is motionless (similar to "non-swimming" of Munk, 1995).
Sink:	Larva is motionless and descends through the water column, often head first.
Shake:	Rapid lateral undulations of the entire larval body.
Foraging MAPs	
Orient:	The head movement 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 MAP (Braum, 1978).
Lunge:	The larva moves towards prey from the fixate position in an attempt to capture prey (Braum, 1978).

first daily feeding, larvae were arbitrarily selected from the rearing tank and placed in 2-L glass bowls containing the appropriate density of prey. For each treatment, a total of ten larvae were serially observed for two minutes each by using the focal animal technique (Altman, 1974).

After all larvae had been observed, they were returned to the general rearing tank. The daily order of observations on prey density treatments was varied systematically over the study period. The light intensity was 200 lux during observations. On observation days, standard length was measured on 12 live larvae from the rearing tank.

Larval behaviors were categorized into modal action patterns (MAPs, Barlow, 1968). During observations, the frequency and duration of the following MAPs were recorded with an event recorder: swim, turn, pause, shake, sink, orientation, fixation, and lunge. Individual MAPs are grouped into three classes: locomotory, nondirected, and foraging (Table 1).

Data analysis The effects of prey density and larval size (mm standard length) on MAP frequency and duration were analyzed with a model III ANCOVA (Zar, 1999), with size as the covariate (α=0.05; the fixed factor was prey density and size was random). Both size and age will influence the larval response to prey density. We chose to focus on the effect of size (as a surrogate for structural characteristics), rather than age (or experience) because this factor likely has a greater effect on the foraging response to prey density during this early life history stage.

The response variable represents the mean value for the 10 individual larvae per prey density for each observation day. Means for each treatment were weighted by the inverse of the standard deviation (SD) around that mean in the ANCOVA. In cases where the SD for a treatment was zero, the mean SD for that MAP (for all prey density-size combinations) was used to weight the mean for that treatment.

A linear model was used to describe the MAPs. For the turn, pause, sink and shake duration analyses, only data

for the size range prior to the near decrease or disappearance of that MAP were used, in order to satisfy the assumptions of equal variance of the ANCOVA. For the swim duration analysis, only data for the size range prior to the larvae spending most (90%) of their time swimming were used. Most behavioral response variables were logarithmically transformed to satisfy model assumptions. Plots of residuals and predicted values were examined for heteroscedasticity and normality for each test, and ANCOVA assumptions were satisfied.

The orientation MAP frequency data could not be easily fitted to a linear or polynomial equation and were analyzed differently. An ANOVA was used to determine the effects of prey density on orientation frequency within the size range where orientation frequency was variable between treatments (10.5–20.8 mm). A Tukey test was then used to determine which treatment means differed (α=0.05).

We compared the lunge frequency of early ($\leq$2 weeks) and late ($\geq$6 weeks) stage witch flounder larvae to that of yellowtail flounder (*Pleuronectes ferrugineus*) and Atlantic cod (*Gadus morhua*) to examine differences in prey consumption rate between species. Yellowtail flounder were observed at 8000 prey/L because this prey density promotes good growth and survival for this species (Rabe and Brown, 2000). Similarly, the data used for Atlantic cod were taken from the behavioral observations conducted at 4000 prey/L presented in Puvanendran and Brown (1999). The 4000 prey/L level was the prey density that optimized growth and survival in that experiment.

Results

Experiment 1: Growth and survival

At hatching, the mean standard length of larvae was 5.62 mm ($\pm$0.12 mm SE). The standard length, dry weight, and body height of larvae did not differ between prey density

Table 2

Summary of ANOVA and ANCOVA results for growth and foraging response variables of witch flounder larvae at different prey densities (no. of prey per liter). An ANOVA was used for orient frequency within the size range 10.5–20.8 mm; for all other response variables an ANCOVA was used. Age (weeks after hatching) was used as the covariate for growth response variables, whereas size (mm SL) was used for behavioral response variables. (* denotes a significant difference at α=0.05).

MAP	Source	df	F	P
Standard length (mm)	Age	1	7041.4	<0.001*
	Prey density	2	0.85	>0.25
	Age · prey density	2	0.75	>0.25
	Error	66		
Dry weight (mg)	Age	1	2640.4	<0.001*
	Prey density	2	0.06	>0.5
	Age · prey density	2	0.21	>0.5
	Error	18		
Body height (mm)	Age	1	582.1	<0.001*
	Prey density	2	0.03	>0.5
	Age · prey density	2	0.28	>0.5
	Error	18		
Orientation frequency	Prey density	6	4.71	<0.01*
	Error	42		
Fixate frequency	Size	1	6.94	<0.05*
	Prey density	6	1.29	>0.25
	Size · prey density	6	0.52	>0.5
	Error	84		
Lunge frequency	Size	1	15.8	<0.001*
	Prey density	6	1.35	>0.25
	Size · prey density	6	0.62	>0.5
	Error	84		
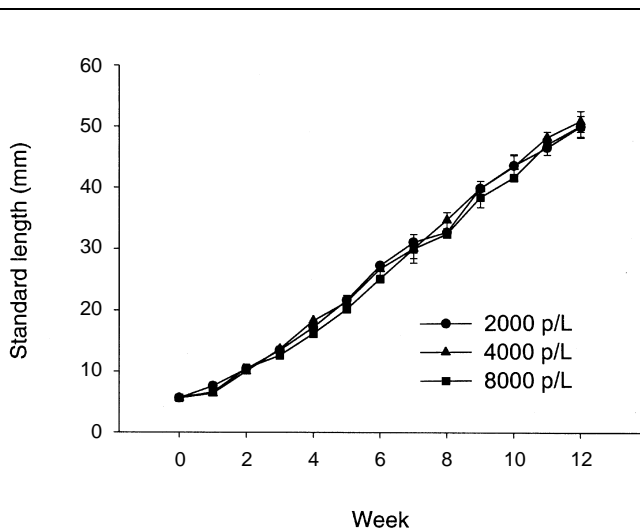
Figure 1

Mean standard length (mm) of witch flounder larvae reared at different prey densities (no. of prey per liter) over age (weeks after hatching). Values are means of the means for each replicate ±SE.

treatments (Table 2, Figs. 1 and 2). Larvae began to increase in body height around the mean size of 15 mm (Fig. 2B). The average absolute growth rate from week 0 to week 12 for all treatments was 0.53 mm/d.. The average specific growth rate (SGR) from week 0–6 was 3.68%/d and from week 0–12 was 2.61%/d.

The survival results were not corrected for fish sampled lethally (20 per tank). The survival in all treatments was similar over the course of the experiment (Table 3) and was unaffected by prey density at week 12 (ANOVA; $F_{2,3}$=2.75, P=0.210).

Experiment 2: Behavior

Larval behavior was characterized by a shift from nondirected MAPs to locomotory activities between the mean sizes of 10.5–16.2 mm (Fig. 3, A and B). The increase in locomotory activities was due to an increase in the total time spent swimming (Fig. 3A). The average duration of a swim MAP increased from 3.2 to 86.3 seconds over the study, whereas the frequency of swimming decreased significantly (Table 4). A turn MAP was used during the early stage, disappearing by the time larvae reached

10.5 mm (Fig. 3A). Pause and sink MAPs decreased when larvae reached 16.2 mm, whereas a shake MAP stopped altogether (Fig. 3B). The durations of the locomotory and nondirected MAPs changed with size (Fig. 3, A and B) but were not significantly affected by prey density (Table 4). At the end of the study there was a slight increase in pause MAPs and a concomitant decrease in the duration of swim MAPs, the result of some larvae settling during the observation periods.

Throughout the study, larvae spent between 2% and 10% of the total time observed performing foraging activities. The variation in total time spent foraging was largely due to variation in orientation duration. The duration of the fixate and lunge MAPs (<2% of total time per MAP) was relatively constant over the observation periods, whereas the duration of the orientation MAP ranged from 1% to 7% of total time (Fig. 3C).

The frequencies of the foraging behaviors were highly variable and many larvae did not forage during the observation periods. The frequency of the orientation MAP changed throughout the study period, peaking between the mean sizes of 10.5 and 20.8 mm (Fig. 4A). Within this size range, orientation frequency increased with increasing prey density. The effect of prey density on orientation frequency was significant (Table 2); the orientation frequency of larvae at 250 prey/L was significantly lower than that of larvae at 2000–16,000 prey/L within the 10.5–20.8 mm size interval (Tukey test). After 20.8 mm, the frequency of orientation was low for all sizes and treatments.

The frequencies of fixate and lunge MAPs varied from 0 to 4 per two-min observation. Larvae at higher prey densities tended to perform more fixate and lunge MAPs compared with larvae at lower prey densities (Fig. 4, B and C), although this trend was not statistically significant (Table 2). The frequencies of fixate and lunge MAPs increased significantly with increasing larval length (Fig. 4, B and C, Table 2). The average lunge frequency of early- and late-stage witch flounder larvae was lower than that of both yellowtail flounder and Atlantic cod larvae (Fig. 5).

Discussion

Witch flounder larvae grew and survived in all treatments used in our study. Our experiment is the first to examine the early growth and behavior of witch flounder larvae in relation to prey availability. Larval performance can be influenced by many factors other than prey density, including temperature (Hunter, 1981), light, (Batty, 1987; Puvanendran and Brown, 1998), prey type (Drost, 1987), and turbulence (MacKenzie and Kiørboe 1995; Browman, 1996). We used our results 1) to describe the early growth and ontogeny of the foraging behavior in this species and 2) as a preliminary step towards understanding the behavioral ecology of witch flounder larvae.
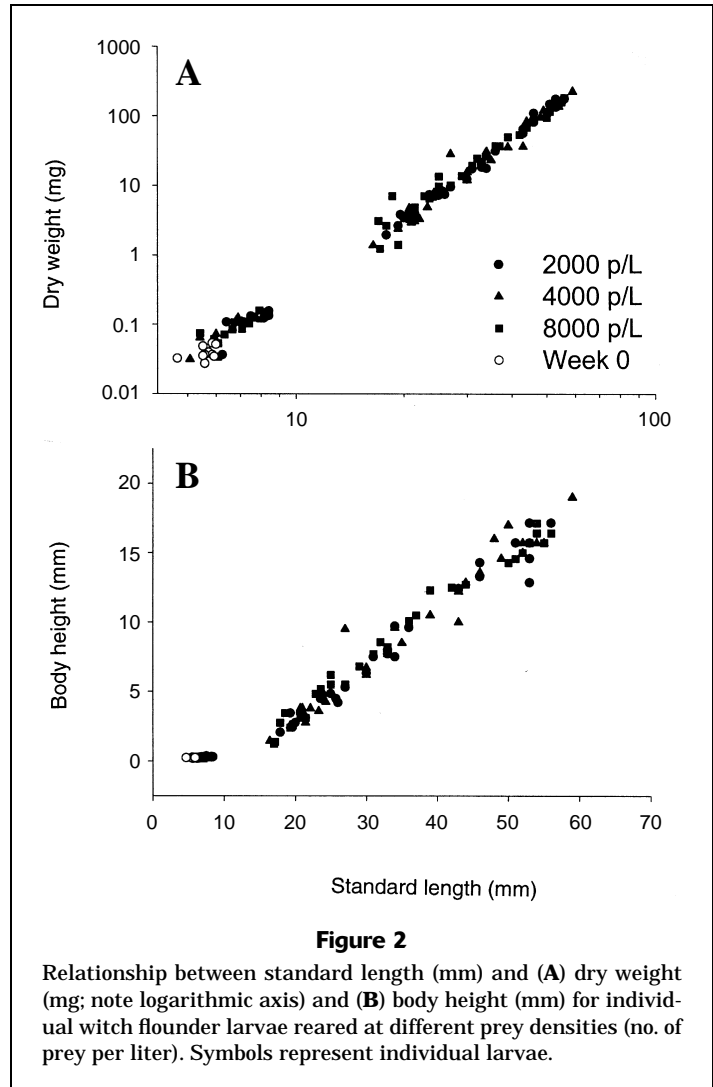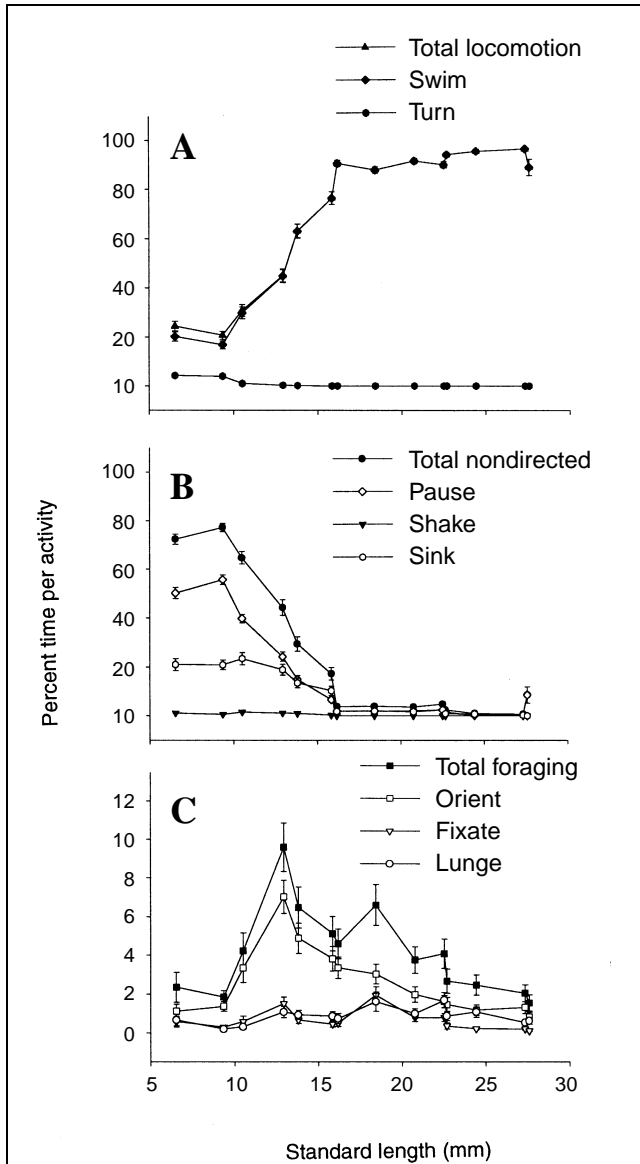

Figure 2

Relationship between standard length (mm) and (**A**) dry weight (mg; note logarithmic axis) and (**B**) body height (mm) for individual witch flounder larvae reared at different prey densities (no. of prey per liter). Symbols represent individual larvae.

Table 3

Percentage of witch flounder larvae reared at different prey densities (±SE) that survived over the experiment. Larvae sampled dead were not included in calculations.

	Prey density (no. of prey per liter)		
	2000	4000	8000
Week 2	36.15 (1.28)	30.26 (6.15)	38.20 (4.36)
Week 5	28.72 (1.54)	25.13 (5.13)	31.03 (3.85)
Week 12	14.10 (2.31)	4.62 (0.51)	8.97 (4.36)

Witch flounder grew and survived equally well at each of the prey densities tested. Although the range of prey densities used in the rearing experiment (2000–8000 prey/L) was not exhaustive, these prey densities have resulted in informative differences in growth and survival for other

Figure 3

Mean proportion (%) of time witch flounder larvae spent performing individual (**A**) locomotory, (**B**) nondirected, and (**C**) foraging MAPs over standard length (mm) during two-minute observation periods. Values are means (*n*=70 larvae per length) ±SE.

Figure 4

Frequency of (**A**) orient, (**B**) fixate, and (**C**) lunge MAPs of witch flounder larvae at different prey densities (no. of prey per liter) during two-minute observation periods over standard length (mm). Values are means (*n*=10) ±SE.

North Atlantic marine fish larvae, such as Atlantic cod (Puvanendran and Brown, 1999) and redfish (*Sebastes* sp.; Laurel et al., in press) reared under similar laboratory conditions. Therefore, we anticipated that this range of prey densities would be adequate to detect differences in growth and survival of witch flounder in relation to prey density. Furthermore, as shown in experiment 2, the lunge frequency of witch flounder was not significantly affected by prey availability, which would be expected if low prey densities (<2000 prey/L) were to reduce consumption and subsequent growth and survival.
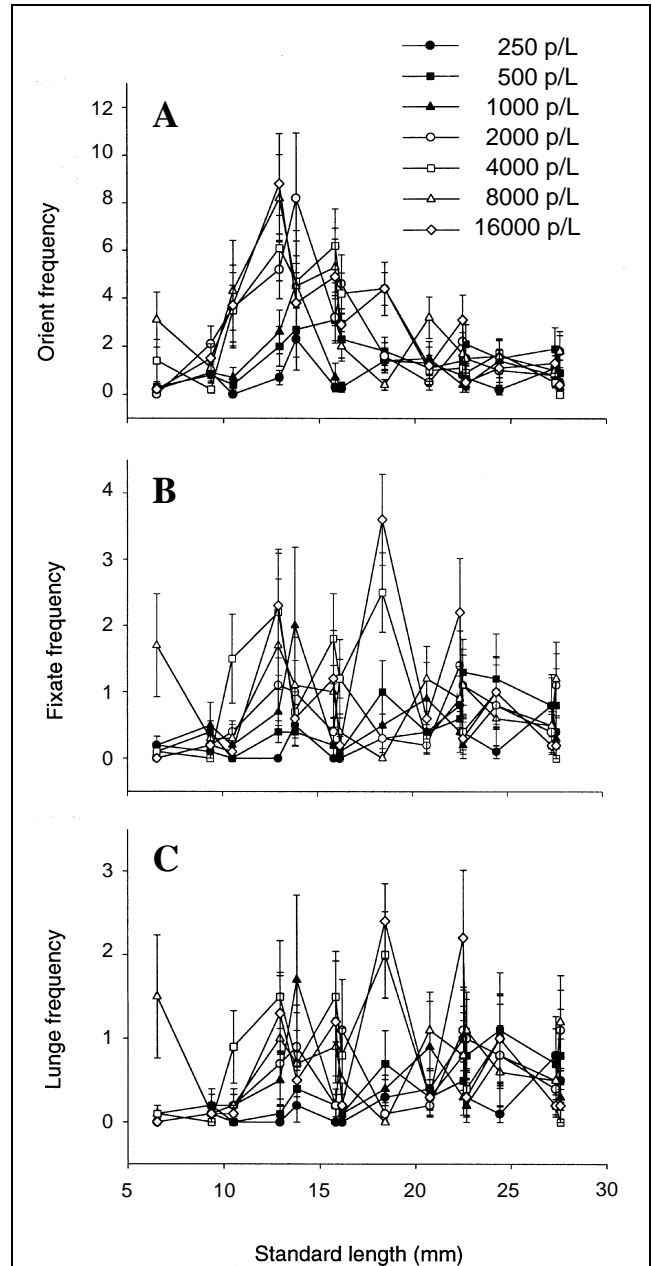
Ontogeny of behavior

Witch flounder search strategy for prey is interesting because it appeared to change from a saltatory to a cruise strategy (see O'Brien et al., 1990; Browman and O'Brien, 1992) during the study period. When larvae were less than 10 mm, foraging included many turns and brief periods of swimming that served as repositioning acts. By the time larvae reached an average size of 16.2 mm, most of their
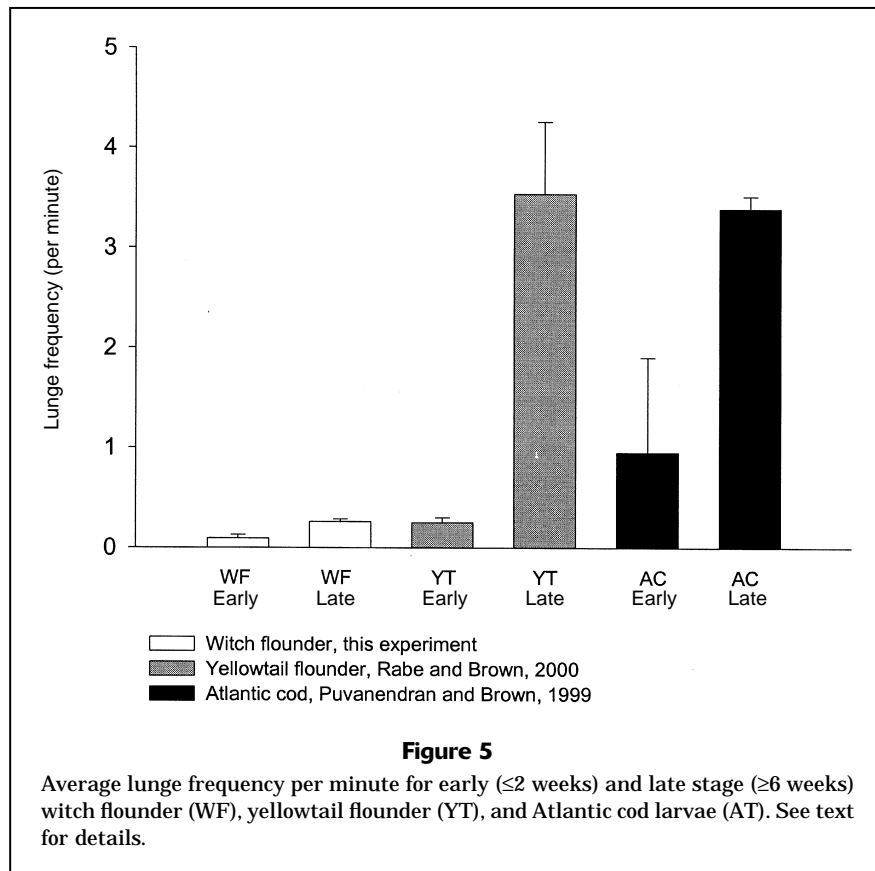
Table 4

Summary of ANCOVA results for locomotory and nondirected MAPs of witch flounder larvae at different prey densities (no. of prey per liter). Each model was run until the larval size indicated in parentheses to satisfy model assumptions. (* denotes a significant difference at $\alpha=0.05$).

MAP	Source	df	F	P
Swim frequency (20.8 mm)	Size	1	32.1	<0.001*
	Prey density	6	0.78	>0.25
	Size · prey density	6	0.42	>0.5
	Error	49		
Swim duration (20.8 mm)	Size	1	251.4	<0.001*
	Prey density	6	1.76	>0.25
	Size · prey density	6	0.17	>0.5
	Error	49		
Turn duration (13.8 mm)	Size	1	56.5	<0.001*
	Prey density	6	1.34	>0.25
	Size · prey density	6	0.82	>0.5
	Error	21		
Pause duration (20.8 mm)	Size	1	88.4	<0.001*
	Prey density	6	1.82	>0.25
	Size · prey density	6	0.26	>0.5
	Error	49		
Sink duration (18.4 mm)	Size	1	79.8	<0.001*
	Prey density	6	0.54	>0.5
	Size · prey density	6	1.35	>0.5
	Error	42		
Shake duration (16.2 mm)	Size	1	13.0	<0.001
	Prey density	6	1.13	>0.25
	Size · prey density	6	0.25	>0.5
	Error	35		

time was spent swimming, which was typically interrupted only by foraging events. During the mean size interval of 10.5–16.2 mm, the turn and shake MAPs disappeared and the frequency of pause and sink MAPs decreased. These behavioral changes were likely related to the increase in larval body height, accompanied by a substantial increase in finfold height that occurs during this time.

The nature of the nondirected MAPs shake, sink, and pause is not straightforward. Sinking has been reported in other species, such as the snapper (*Pagrus auratus*) and, like the pause MAP, has been interpreted as a resting behavior. In snapper, it occurs in yolksac larvae and in feeding larvae during night-time periods of inactivity (Pankhurst et al., 1991). Sinking is typically observed only in the early stages of other species such as the black sea bream, *Acanthopagrus schlegeli* (Fukuhara, 1987). However, Kawamura and Ishida (1985) noted that sinking occurs in both yolksac larvae and larger feeding larvae of the flounder *Paralichthys olivaceus* immediately after attacking a prey item. Observations of sinking in later-stage witch flounder larvae were not related to feeding events; the persistence of these behaviors in witch flounder was likely the result of some smaller, slower-growing individuals having been included in our observations.

Witch flounder, like other species (Holling, 1965; Houde and Schekter, 1980; Werner and Blaxter, 1980; Puvanendran and Brown, 1999), demonstrated increased foraging behavior with prey density. However, the orient MAP was the only foraging MAP statistically affected by prey density. The change in orientation frequency with size is interesting because this MAP was affected only by prey density within a limited size range. The initial low frequency of orient MAPs followed by an increase associated with greater larval size can be explained by changes in swimming speeds and encounter rates (Mittelbach, 1981). However, the decrease in orient frequency across treatments later in the study period is puzzling because larger larvae are generally competent swimmers (Rosenthal and Hempel, 1971; Laurence, 1972; Houde and Schekter, 1980) and are expected to exhibit a high prey encounter rate. This decrease in orient frequency may be due to improved foraging ability associated with greater visual acuity. Miller et al. (1993) showed that the visual angle—the smallest angle at which a stimulus may subtend the eye and remain resolvable (Neave, 1984)—decreases during the development of three species of fish larvae. Thus, the eye develops such that larvae can likely detect prey items in their periphery without turning the head and orienting themselves toward them.

Figure 5

Average lunge frequency per minute for early (≤2 weeks) and late stage (≥6 weeks) witch flounder (WF), yellowtail flounder (YT), and Atlantic cod larvae (AT). See text for details.

Behavioral ecology

The main finding of our study was that witch flounder are not affected by changes in prey availability in the same manner as other species of larvae observed under similar laboratory conditions. The typical pattern among fish larvae—that they increase their foraging behavior and prey consumption rate with increased prey density (Houde and Schekter, 1980)—was supported by our study. However, the results are unusual in that the effects of prey density on foraging behavior were not as strong as results that have been reported for other species.

The ecological implications of these results can be illustrated by a comparison of the growth and behavior of witch flounder to other northwest Atlantic species observed under similar laboratory conditions. In rearing experiments on Atlantic cod larvae, Puvanendran and Brown (1999) found that cod have specific requirements for high prey densities. Larval survival, growth rate (0.20 mm/d), and condition were highest when larvae were reared at a prey density of 4000 prey/L. Furthermore, in the same experiment, the lunge frequency (an indicator of consumption rate) of cod larvae increased from nearly 1 to 3.5 prey items per minute over the six-week study period (Fig. 5; Puvanendran and Brown, 1999). A marked increase in lunge frequency with age is also seen in yellowtail flounder, another north Atlantic pleuronectiform,

raised under similar conditions (Fig. 5; Rabe and Brown, 2000). In that study, the growth rate of yellowtail flounder was 0.34 mm/d.

Not only is the foraging behavior of witch flounder relatively unaffected by variation in prey density, but its lunge frequency is much lower, suggesting that it may have a lower consumption rate and therefore lower prey requirements compared with those of other species. The lack of a significant effect of prey density on the foraging of witch flounder is not solely a result of the larger larval size of this species. Redfish (*Sebastes*) are relatively large at extrusion (6–8.9 mm; Penny and Evans, 1985) and their foraging behavior is affected by variations in prey availability (Laurel et al., in press).

It is remarkable that the growth rate of witch flounder is faster than that of cod and yellowtail flounder, especially given the possible lower prey consumption rate of witch flounder. Two potential mechanisms that may explain this phenomenon are high assimilation efficiency and low metabolic requirements. Witch flounder are relatively large at hatching and for most of the study period were larger than other species of similar age. This size difference alone implies that its digestive system is larger, more developed, and more efficient (Govoni et al., 1986; Klumpp and von Westernhagen, 1986). Both yellowtail flounder and cod are more active and swim faster than witch flounder. Higher activity imparts a greater need for prey, which results in

larvae being more susceptible to starvation in the absence of prey (Hunter, 1981).

The ecological significance of the lack of an effect of prey density on foraging, growth, and survival found in our study may be a reflection of the life history of witch flounder. This species has an extended larval period and is committed to being in the water column much longer than other species (Bigelow and Schroeder, 1953). During this extended larval period, witch flounder larvae will likely encounter periods of high or low plankton availability, or both. The abundance of zooplankton prey for fish larvae can vary over four orders of magnitude during the year, typically reaching a peak in the warmer months and decreasing dramatically in the winter (Myers et al., 1994). Therefore, witch flounder larvae must be able to cope with this variation in prey availability to survive. This condition requires a different strategy from that of other marine fish species that have shorter larval periods and that likely rely on a "match" of spawning with plankton production to promote larval survival (Cushing, 1972). In the scope of the life history evolution of witch flounder, the long larval period and large size at metamorphosis may be a strategy to cope with intense postsettlement, size-dependent competition.

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