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ORIGINAL ARTICLE

The role of prey concentration and size range in the growth and survival of larval cod

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Abstract

The effects of food quantity vs. food quality may be influenced by complex interactions that are difficult to isolate in trophic studies of fish larvae in the natural environment. Food quantity, or abundance, is mediated by the proportion of suitable prey available, with 'suitability' defined variously as size, species, or nutritional content. Using an experimental approach, food consumption, growth, and survival of larval cod, in response to zooplankton abundance and diversity of zooplankton sizes, were tested in a replicated land-based mesocosm (2500 l) system. Northeast Arctic cod (*Gadus morhua* L.) larvae were reared for two months with a manipulated zooplankton prey field comprised of narrow (N) or wide (W) prey spectrum (range of prey sizes), combined with high (H) or low (L) prey concentration. In the W treatments, cod larvae were fed both small and large sized zooplankton, while in the N treatments they were fed only small zooplankton. Initial prey concentration was 2000 prey l^{-1} in the H treatments and 200 prey l^{-1} in the L treatments, decreasing to 500 and 50 prey l^{-1} during the course of the experiment. Larval cod grew faster at higher prey concentrations. Prey concentration as well as spectrum affected larval feeding patterns with a wider spectrum prey size leading to the consumption of larger prey, but without a significant effect on larval growth. Survival was significantly higher in high prey concentration treatments, and also tended to be better in treatments with wider prey size diversity.

Key words: *Fish larvae, larval–zooplankton interactions, mesocosm, prey selection, prey size spectrum, zooplankton*

Introduction

The abundance, species composition, and size distribution of zooplankton may all influence the growth and the survival rates of larval fish (e.g. Cushing 1990; Puvanendran & Brown 1999; Heath & Lough 2007). The seasonal progression of prey size in the available plankton may provide an optimal situation for larval fish to utilize a succession of prey species or size ranges as the larvae grow (Pope et al. 1994; Buckley & Durbin 2006). Furthermore, ontogenetic changes in vertical distribution of larvae (Grønkjaer & Wieland 1997) and their prey (Basedow et al. 2008) can potentially mediate prey size match for larval fish. As fish larvae develop, they become better adapted to locating, catching, and digesting prey (Hunter 1980; Fuiman & Higgs 1997). Thus, prey size selectivity changes with larval size and developmental stage, and probably also with availability of suitable sized prey (Rowlands et al. 2008). Recent studies have suggested that fluctuations in the species composition and body sizes of zooplankton have an effect on survival of larval fish (Beaugrand et al. 2003; Buckley & Durbin 2006). To further understand the match between larval fish and their prey, it is necessary to separate the different effects of prey abundance (availability) and size (or composition) on the growth and survival of larval fish.

Laboratory studies have demonstrated that larval cod (*Gadus morhua* Linnaeus, 1758) are gape limited predators when feeding on *Artemia* and rotifers, where prey size increases with increasing body and gape size (Puvanendran et al. 2004). However, feeding strategies of larval cod seem to vary between the laboratory and the natural environment. Larval cod *in situ* generally feed on zooplankton considerably smaller than the maximum size available (Last

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1978). However, both laboratory and field studies show that larval cod are opportunistic and, in order to cope with lack of ideal food, cod larvae will include plankton of different types and sizes in their diet (van der Meeren & Næss 1993; Munk 1995; Rowlands et al. 2008). Thus it seems likely that zooplankton concentration, species composition and diversity of prey size (prey size breadth, or spectrum) will all have an effect on growth and survival of cod larvae.

The interaction between prey concentration and available prey size range has been poorly studied in larval fish. The objective of this experiment was therefore to contrast the effects of prey concentrations and size spectra on growth and survival of larval cod by manipulating the prey field in a replicated mesocosm design. Larval fish growth, measured as changes in the population mean size, is clearly related to food concentrations, whereas other population characteristics appear to be influenced more by the type of available prey. The presence of both larger and smaller prey items in the prey field may encourage the growth of some individuals, leading to a wider distribution of larval size-at-age within the population (Geffen 1996). The population size distribution is the raw material for many size-selective processes, including starvation-induced mortality and cannibalism (Folkvord 1997). Thus, the diversity of prey size may affect survival by controlling size-selective processes, while prey concentration is likely to have a direct effect on larval growth rates.

Material and methods

Source of eggs and larvae

The cod larvae used in this study were obtained from a Northeast Arctic cod broodstock that originated from 25 to 30 families produced at Akvaforsk in Sunndalsøra, Norway from wild fish in 2002. Most of the parental fish were second-time spawners.

Two cohorts of eggs (26,000 total), spawned 6 days apart, were incubated at 6°C in flow-through conditions, and introduced into the mesocosms two days before hatching at an approximate density of 10 larvae l^{-1}. Day 0 (dph, days post-hatching), defined by 50% hatching, was 23.04.05 for the first cohort and 29.04.05 for the second cohort. Larvae from the younger cohort were identified by their alizarin-marked otoliths (Folkvord et al. 2004). In addition, non-feeding trials were set up in the laboratory to control for hatching dates and viability of the eggs. The two larval cohorts comprised part of a parallel common garden experiment (Vollset et al. 2009), but survival of the younger cohort (0–2.2% vs. 2.8–24.6%) was not sufficient for a full inter-cohort comparison of feeding treatments and responses to the manipulated prey fields, and therefore results are reported only for responses of the older cohort.

Zooplankton prey

Zooplankton was collected from the sea using a land-based Hydrotech® filter consisting of three chambers, each containing a drum-shaped filter wheel. The filter wheels retained plankton according to mesh size, and the mesh on each wheel could be changed to select a specific range of prey size. The zooplankton was collected in two stages. First, water from the fjord (8 m depth) was pumped through the filter, retaining both small and large zooplankton. This mixed-size plankton stock was re-filtered on the following day, separated by size and stored in two separate stock tanks. These two plankton stocks were used as food for the larval fish. As the larvae grew they required bigger prey, and the filter sizes in the chambers were changed twice during the experiment to include larger zooplankton (Table I).

The feeding regimes provided for the larvae were manipulated to give an excess abundance of prey for high concentration treatments (H, 2000 prey items l^{-1}) and a suboptimal feeding regime for low concentration treatments (L, 200 prey items l^{-1}). The response of larval cod growth has been shown to differ at these prey concentrations in laboratory experiments (Puvanendran & Brown 1999). These prey concentrations were combined with two different size ranges of zooplankton: a narrow spectrum (N) and a wide spectrum (W). Mesocosms with N were supplied with only small sized plankton while mesocosms with W were fed both small- (90%) and large-sized plankton (10%), defined by the plankton stock tanks (Table I). The range of zooplankton sizes in the W treatments was potentially 1.5–3 times larger than in the N treatments. Zooplankton concentration was monitored daily and fresh zooplankton from the plankton stocks was given out in predetermined size ranges at noon. Daily additions of prey were based on the counts of remaining zooplankton in each mesocosm. At the beginning of the experiment the

Table I. Mesh size (μm) in the two chambers of the zooplankton collecting filter used to collect zooplankton for different periods during the experiment. Days post-hatching (dph) indicates larval age defining each period.

Size fraction	4–25 (dph)	25–32 (dph)	32–54 (dph)
Large	200–250	250–400	400–1000
Small	80–200	120–250	120–400

larvae were not large enough to consume the largest zooplankton, and so all were fed with small zooplankton, primarily copepod nauplii. Zooplankton was first offered to the cod larvae at 4 dph, and consisted of small fraction prey (80–200 μm). Beginning at 18 dph, larger zooplankton was added to the W treatments to give a wide range of prey sizes. Concentrations in the mesocosms were initially held at 2000 prey items l^{-1} and 200 prey items l^{-1} in high concentration (H) and low concentration (L) mesocosms, respectively. However, the concentration was lowered during the experiment (Table II), to compensate for mortality of the cod larvae and the fact that prey capture efficiencies increased as the larvae developed (Hunter 1980). At the end of the experiment the nominal prey concentrations were 500 prey items l^{-1} and 50 prey items l^{-1} in H and L treatments, respectively.

Experimental design

The experiment was conducted in outdoor, land-based mesocosms at Espegrend Marine Biological Station (University of Bergen, Norway), from 21 April 2005 to 14 June 2005. The semi-intensive system consisted of eight round plastic mesocosms (148 cm × 150 cm ~2.6 m^3), with four mesocosms contained within each of two temperature control tanks (32 m^3) (Figure 1). The experimental design comprised two replicate mesocosms and four different feeding regimes, combining high–low prey concentration and narrow–wide prey size spectra. The eight mesocosms were sampled on five dates, so that for each feeding regime there were two observation units, repeated five times.

Sampling design and analysis

The water temperature in the mesocosms was measured daily and salinity and oxygen were measured weekly with an oxygen meter (model WTW Oxi 34i) and a conductivity meter (model WTW 330).

The concentration and species composition of the zooplankton was determined from daily samples from each mesocosm and from the two different stock tanks which contained the large and small size fractions. A large-bore plastic tube (1.5 cm × 180 cm) was lowered into the tanks to collect zooplankton samples from the surface to near the bottom of each mesocosm. The volume of water sampled for the daily zooplankton counts was 0.1 l from the H treatments, 1.0 l from the L treatments, and 0.1 l from each of the two size stock tanks. The live zooplankton was classified into five main groups: rotifers, copepod nauplii, copepods, miscellaneous edible and miscellaneous non-edible.

Table II. Nominal prey concentrations (number of prey items l^{-1}) in H and L treatments during the course of the experiment. Larval age ranges in dph (days post-hatching) define each period.

	4–24 (dph)	25–33 (dph)	34–41 (dph)	42–53 (dph)
H	2000	1500	1000	500
L	200	150	100	50

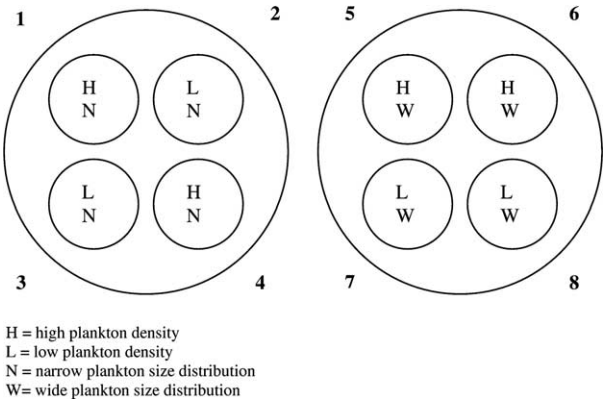

Figure 1. Experimental design. Arrangement of individual mesocosm tanks (1–8) within two larger temperature control tanks. H and L refers to high and low prey concentration treatments, W and N refers to wide and narrow prey size spectrum treatments.

Zooplankton samples were preserved daily from the stock tanks and weekly from each mesocosm for later determination of species and size composition. These samples (90 ml) were preserved with 10 ml 37.3% formaldehyde buffered with borax.

The preserved zooplankton samples from the stock tanks and mesocosms were split with a whirling vessel (Wiborg 1951), transferred to a counting chamber, photographed (Olympus Camedia 5050 zoom camera connected to a Leica MZ 95 dissecting microscope with polarization filter), and identified. From the images, the length of plankton was measured using Image-J image analysis software (Rasband, 1997–2006). Cephalosome length was measured in all copepods except harpacticoid copepods. Total length (excluding setae) was measured in nauplii, decapod, trochopore, and veliger larvae, cladocerans and harpacticoid copepods.

The cod larvae were sampled weekly, from 4 dph until the end of the experiment at 53 dph. On each occasion, 30 larvae were sampled from each mesocosm, and the stomach contents were analysed from half of these. Three techniques were used to collect the larval fish samples: (1) sampling with a large bore sampling tube with an open/close function at the bottom, (2) focal sampling, with a scoop, and (3) sampling larvae with a fine mesh dip net. The latter techniques were used when the larvae grew larger and as the concentration of fish in the mesocosms decreased.

All cod larvae were photographed live (Olympus Camedia 5050 zoom camera connected to a Nikon model C-DS dissecting microscope) and frozen individually at –18°C in Eppendorf tubes for later examination. Standard length (SL) was measured from the images using image analysis software. The frozen larvae were rinsed in distilled water, dried in an (Termax) oven at 60°C for 24 h and weighed to the nearest microgram (Sartorious M3P microbalance). Variations in dry weight were analysed and reported in Vollset et al. (2009).

After weighing, the larvae were rehydrated for stomach content analysis. The whole digestive tract was dissected away from the larval body and cut open to remove the individual prey items. The gut contents were photographed, and the zooplankton measured and identified as described previously. Most of the zooplankton in the gut contents which had been dried and rehydrated were 1–5% smaller than the zooplankton stored in formalin. Veliger larvae and cladocerans, on the other hand, were on average approximately 15% smaller after drying and rehydration than those preserved in formaldehyde. However, these accounted for only a small part of the diet of the cod larvae, and therefore the sizes were not corrected for these analyses. In total, the stomach contents of 560 larvae were analysed, and from them 5336 zooplankton prey items were measured.

Data analysis

Variations in the size of ingested prey were fitted to ANCOVA models, with log-transformed larval length as the covariate, to test effects of prey spectrum, prey concentration and the interaction of these two factors. Replicates were nested within treatments and considered as a random factor to control for tank effects. For analysis of fish length, only larvae with measurable stomach content were included. A two-way factorial ANOVA model was used to test for effects of treatment on larval size variability (CV of length) and on survival. Only main effects are reported in the absence of significant interaction effects. Unequal HSD Tukey's test was performed when significant interactions were found. Homogeneity of variance was tested with Hartley F-max. STATISTICA 7.0 was used for all ANOVA tests.

Chesson's selectivity index was calculated for 0.1mm size categories of zooplankton length. The frequency of zooplankton of each size category in the stomach contents was compared to the frequency of zooplankton of each size category in the mesocosm tanks. Chesson's index, α, was calculated following Chesson (1978):

$$\alpha = \frac{(r_i/p_i)}{\sum_i^m (r_i/p_i)}$$

where r_i is the proportion of prey type i (species or size class) found in the gut; p_i is the proportion of prey type i in the environment (the tank); and m is the number of prey types (species or size classes) in the tank. The index, α, is equal to m^{-1} when there is no selectivity for a particular prey class, and values of α greater or less than m^{-1} indicate positive or negative prey preference, respectively. In our study, the size range of zooplankton prey was divided into 16 size classes between 0.1 and 1.7 mm, plus a size class for >1.7 mm prey, thus in this study $\alpha = 0.06$.

Results

Water temperatures increased from approximately 7.5°C to around 11°C as the experiment progressed. The N mesocosms were on average 0.3°C warmer than the W mesocosms during the experiment. The salinity was generally low with an average of 29.7. Oxygen saturation was stable in all mesocosms (mean = 97.5%), with a maximum value of 105% and minimum value of 93%.

Samples from the zooplankton stock tanks were used to characterize the prey field available to the larvae in the different treatments over the course of the experiment (Figure 2). Mean edible zooplankton length increased from 0.37 to 0.89 mm in the large-fraction stock tank throughout the experiment. In the small-fraction stock tank, mean zooplankton length increased in the latter half of the experiment, and ranged from 0.21 to 0.5 mm. After the first week, the addition of zooplankton from the large-fraction stock tank provided the larvae in the W treatments with a prey size spectrum of more than double the range of larvae in the N treatments. In the stock tanks, the zooplankton species composition fluctuated throughout the experiment as the season progressed. Some species were present in the stock tanks during the whole experimental period and ranged in proportions from 8.6 to 33% of the total zooplankton sample (e.g. *Oithona* sp.), but others were found only once or twice (*Platyhelminthes*, decapod larvae) and accounted for only 0.2–0.9% of the total zooplankton sample (Table III).

Larval development and survival in the non-feeding trials confirmed that there was no influence of poor egg quality or handling. Significant differences between replicate mesocosms were observed in the larval size at age (length and weight), but this tank effect was not present on every sampling date and was not consistent with respect to mesocosm.

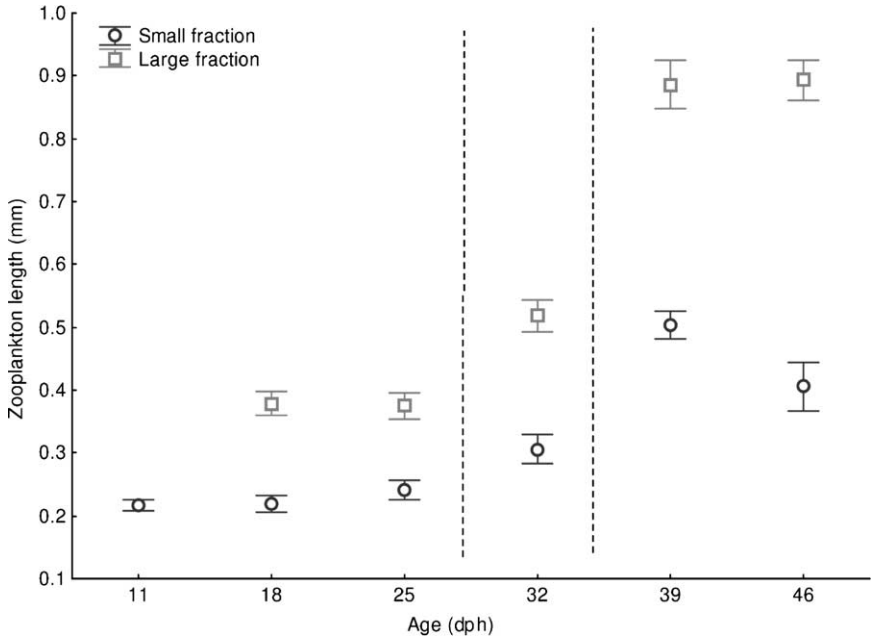

Figure 2. Mean zooplankton size (mm) from the small (open circles) and large (open squares) fraction plankton stock. Error bars indicate 95% confidence intervals around the mean. The dotted lines indicate the timing of the changes in filter mesh size. Total *n* for zooplankton = 1858.

The responses of the cod larvae to contrasting prey concentration and prey size diversity were analysed by comparing feeding patterns based on the prey length, CV of prey length, number of prey consumed, and prey size preferences. Mean prey length increased with increasing larval length (Figure 3).

Table III. Relative composition (%) of zooplankton taxa found in the small- and large-fraction stock tanks. Total sample, $n = 2107$. dph = days post-hatching.

Larval age (dph)	10	18	24	31	38	45
Calanoid copepods						
Temora longicornis	2.1	8.4	7	21.7	9.7	10.2
Acartia sp.	0	0	0	0.0	1.5	0
Centropages hamatus	0	0	0	1.0	9.2	36.3
Calanus sp.	0	0	0	0	3.5	2
Pseudocalanus minutus	0	0	0	2	16.2	1.0
Paracalanus parvus	0.4	2.5	1.3	7.9	20.3	6.1
Cyclopoid copepods			0	0	0.0	
Oithona sp.	14.3	33	30.6	8.6	10	10.7
Oncea sp.	0	0.4	0.4	0	0.2	0
Harpacticoid copepods			0	0	0	
Unident. Harpacticoids	1.8	1.7	4.8	0.7	0.3	0
Tisbe sp.	0	0	0	0.7	0	0.5
Copepod nauplii			0	0	0	
Temora nauplii	11.4	2.9	7.4	3	0.5	0.5
Other copepod nauplii	55	36	31	13.5	13.9	7.4
Cladocerans			0	0	0	
Podon sp.	0	0	0	2	2.9	11
Evadne sp.	0	0	0	8.9	4.4	1.3
Miscellaneous edible			0	0	0	
Trochopore larvae	7.5	8.8	1.3	1.3	2.4	2.3
Decapod larvae	0	0	0	0	0.9	0.5
Cirriped larvae	0	0	4.8	3.6	0.3	1.3
Veliger larvae	0.7	1.3	0	1.6	0.5	1.3
Oikopleura dioica	0	0	0	0.7	0.3	0
Miscellaneous non-edible		0	0	0		
Polychaete larvae	6.7	5	11.4	22.7	3	7.4
Others	0	0	0	0.4	0.2	0

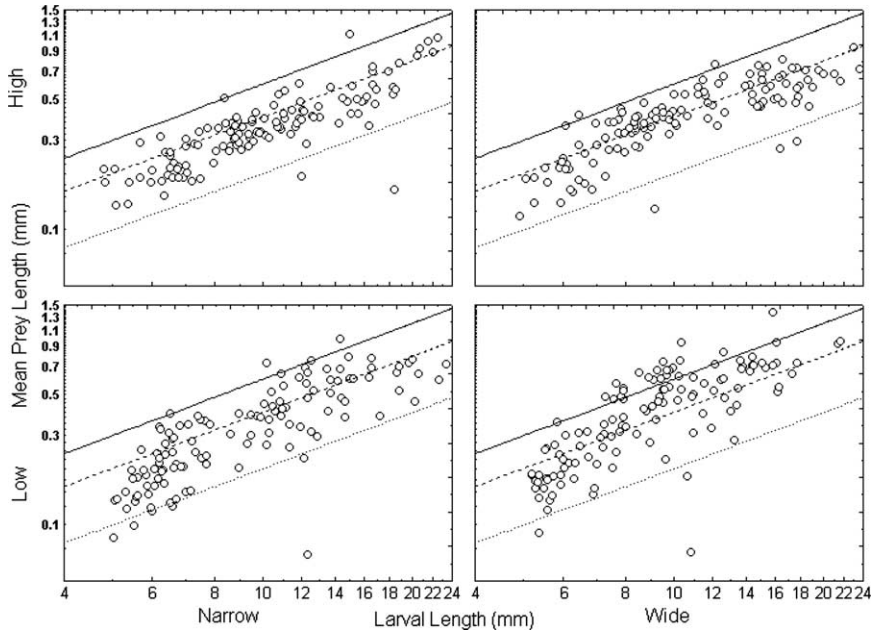

Figure 3. Mean length of zooplankton prey items consumed by individual cod larvae during the experiment, in relation to larval length. Lines indicate the prey lengths equal to 2% (dotted line, ····), 4% (dashed line,----), and 6% (solid line, ——) of larval fish lengths. Axes are plotted to logarithmic scale.

Prey spectrum significantly affected the consumption patterns, as larvae in the W treatments generally ate larger zooplankton during the experiment (ANCOVA, $p < 0.01$) (Table IV). Larvae in the H–W treatment (higher prey abundance and wider range of prey sizes) ate larger prey items (mean = 0.32 mm) than larvae in the H–N treatment (mean = 0.26 mm), and larvae in the L–W treatment (mean = 0.25 mm) generally ate larger prey items than larvae in the L–N treatment (mean = 0.18 mm). Prey concentration significantly affected the larval feeding pattern only at 25 dph (ANOVA, $p < 0.05$) when larvae in the H treatments consumed larger prey than larvae in the L treatments (Figure 4).

The CV of ingested prey length tended to increase slightly with increasing fish length in the H treatments, and was stable or decreased in the L treatments (Figure 5). With less food available, the larvae in the L treatments consumed more diverse prey (by length) than the larvae in the H treatments and generally, the larvae in the H–N treatment consumed prey of more uniform and consistent size. Smaller-sized larvae consumed a wider range of prey sizes when in conditions of low prey concentrations.

Prey consumption by cod larvae initially increased with increasing larval size in all treatments (Figure 6), and larvae in the H treatments generally ate more than larvae in the L treatments. After 32 dph, larvae in the N treatments ingested more prey items than larvae in the W treatments (ANOVA, $p < 0.05$).

Until 46 dph, cod larvae in the L–N treatment showed a strong selection for small zooplankton, based on Chesson's Index (Figure 7), but there was no consistent pattern of prey size selectivity at the end of the experiment. Larvae in the W treatments showed an increasing preference for larger zooplankton, especially after 32 dph, and those growing at lower prey concentrations (L–W) continued to select both small and large zooplankton. The prey selection pattern was reflected in the uneaten zooplankton remaining in the mesocosms. Remaining prey items

Table IV. ANCOVA test results for effects of prey concentration and prey size spectrum on the size of prey consumed by larvae, accounting for larval length. Significant interaction effects are evident.

	SS	df	MS	*F*	*p*
Intercept	153.92	1	153.92	1527.0	0.000
Size spectrum	2.73	1	2.73	27.1	0.000
Prey concentration	1.17	1	1.17	11.6	0.001
Spectrum × concentration	0.44	1	0.44	4.3	0.038
Larval length (Ln)	79.02	1	79.02	783.9	0.000
Concentration × larval length (Ln)	1.50	1	1.50	14.9	0.000
Error	47.17	468	0.10		

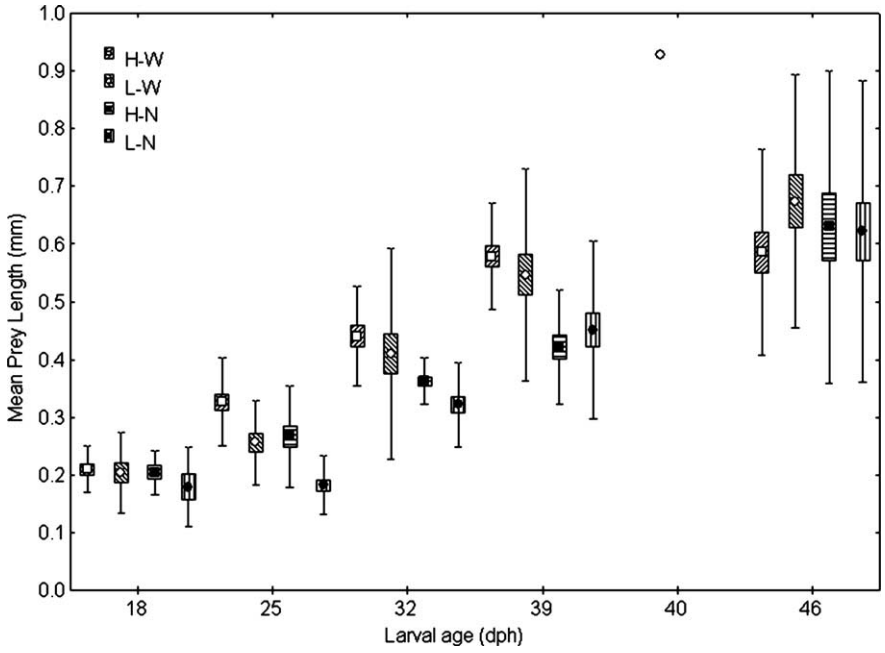

Figure 4. Mean prey size ± SE (boxes) and 1 s.d. (whiskers) in stomachs of cod larvae in the different treatments over 5 weeks. Filled symbols represent the W treatments, while open symbols represent the N treatments. Square symbols indicate low prey concentration, and circles indicate high prey concentration treatments. Symbols for each treatment are spread either side of the individual sample dates (dph) for clarity. Estimates in the plot are based on the mean prey lengths found in all larval cod. Total n for prey found in guts of the larvae = 5227. * Indicates significant effects of prey size range, and + indicates significant effects of concentration.

were larger in the L treatments than in the H treatments, because the larvae selectively fed on more of the smaller prey.

The growth, size variation, and survival of the cod larvae were significantly affected by prey concentration, but not prey spectrum. Cod larvae were generally longer at a given age in the H treatments than the L treatments (Figure 8, ANOVA, $p << 0.001$). Even though the larvae in W treatments ate larger prey than larvae in N treatments during most of the experiment, prey spectrum did not significantly affect larval growth (ANOVA,

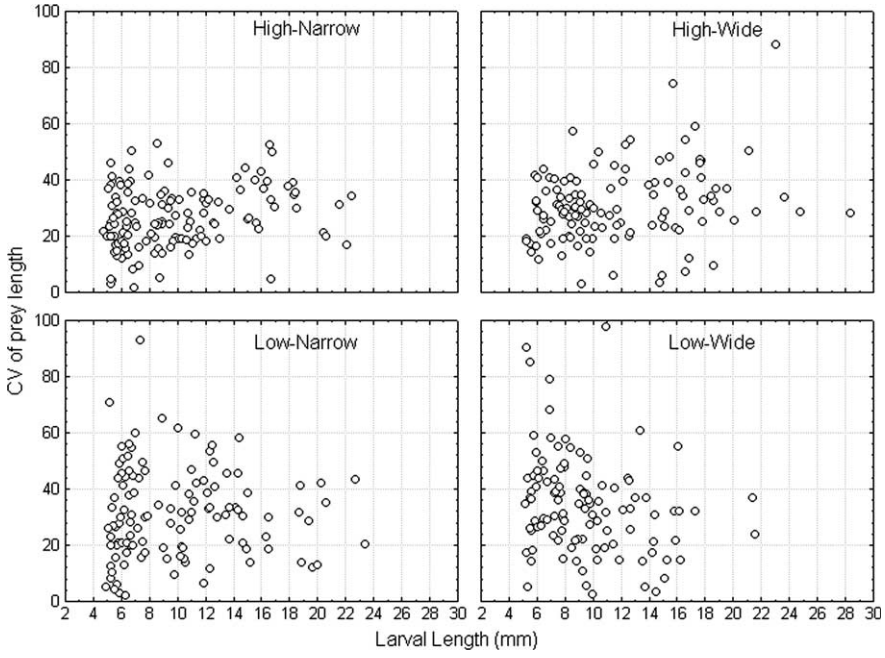

Figure 5. Coefficient of variance (CV) of prey length for zooplankton consumed by individual cod larvae during the experiment, in relation to larval length.

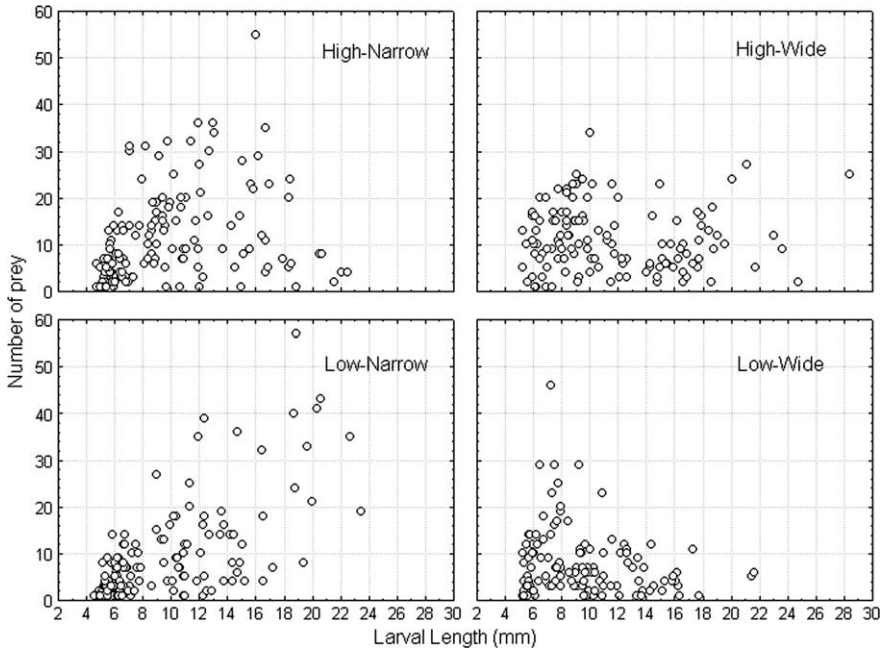

Figure 6. Mean number of prey items consumed by individual cod larvae in the different treatments during the course of the experiment, in relation to larval length.

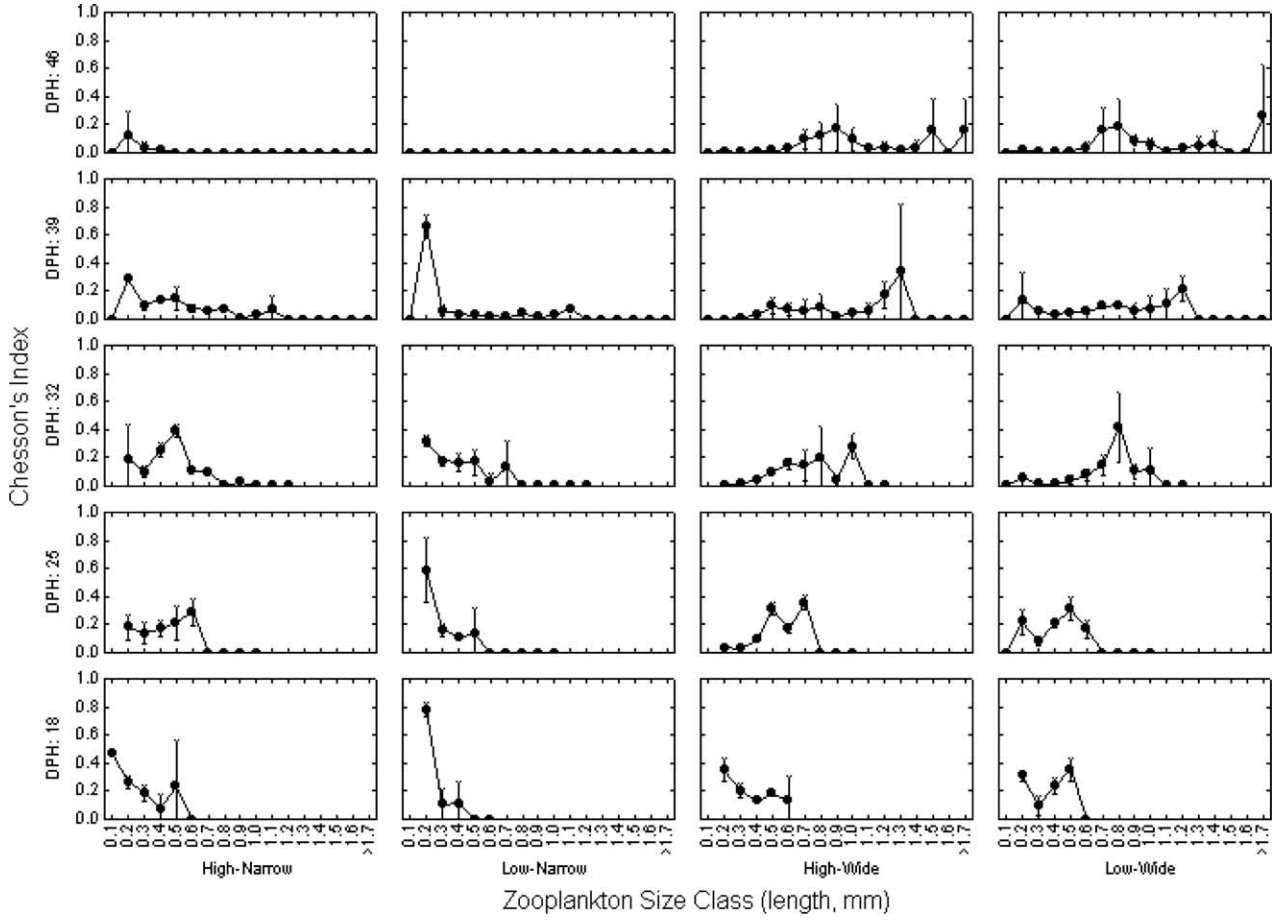

Figure 7. Patterns of feeding preferences of cod larvae in the different treatments during the course of the experiment. Chesson's index measures selectivity by comparing sizes of zooplankton consumed against the sizes of zooplankton available in the mesocosms.

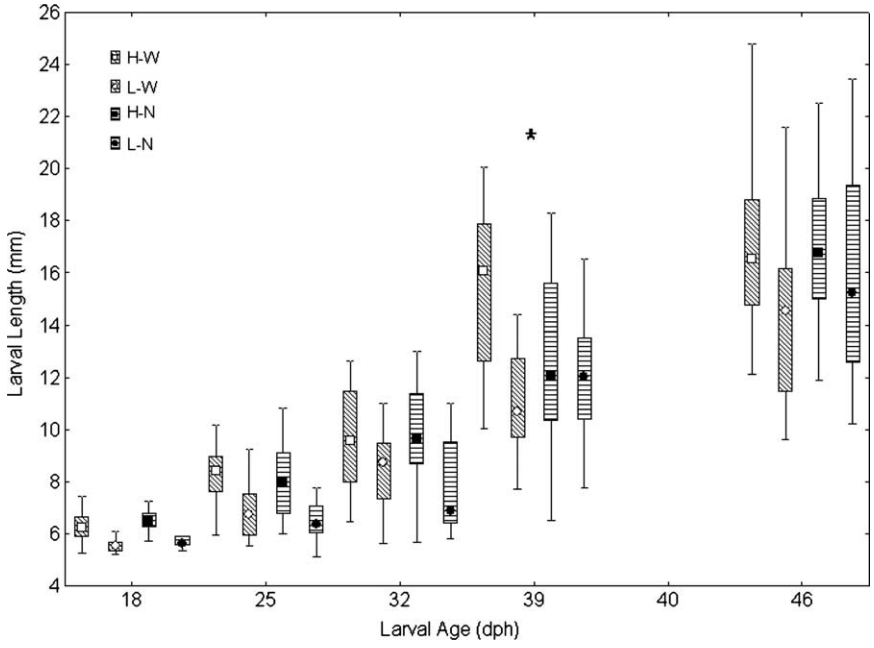

Figure 8. Standard length (SL) of cod larvae in different treatments. Filled symbols represent the W treatments, while open symbols represent the N treatments. Square symbols indicate low prey concentration, and circles indicate high prey concentration treatments. Symbols for each treatment are spread either side of the individual sample dates (dph) for clarity. *Indicates significant effect of prey concentration. Total n for larvae = 526.

$p > 0.05$). The relative variation in fish length increased until 32 dph for all treatments, and the CV of larval length tended to be higher in the H treatments compared to the L treatments (Figure 9). At the end of the experiment the larvae in the H–N treatments were significantly more variable in length than those in the L–N treatments (ANOVA, $p < 0.05$).

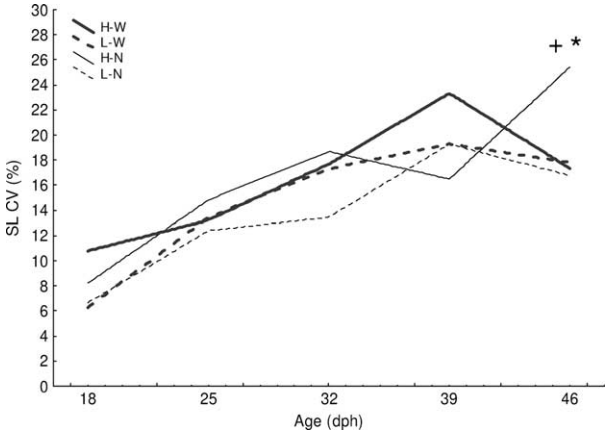

Figure 9. Coefficient of variation (CV) of standard length (SL) for cod larvae in different treatments. Thick lines indicate wide range treatments, while thin lines indicate narrow range treatments. Solid lines are for the high concentration treatments while dotted lines are for the low concentration treatments. *+ Indicate significant interaction effect between prey concentration and prey size range. Smoothing = Lowess.

Larval cod survival was significantly higher with higher prey concentrations (Table V, ANOVA, $p < 0.002$). In addition, survival was somewhat higher in the W treatments than in the N treatments, although the difference was not significant (ANOVA, $p = 0.2$).

Discussion

Prey size

Choice of prey clearly depended on the prey size availability, and larvae offered a wide size range of prey ingested larger prey than larvae offered a narrow size range. This can be predicted from optimal foraging theory as described for fish by Werner & Hall (1974), who demonstrated that adult bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819) ate the largest prey available when the encounter rate was high enough. Prey concentration had a significant effect on the size of prey consumed only on one sampling date, and there was no significant interaction between concentration and size spectrum on the size of prey ingested. This suggests that prey concentration affected size selective feeding patterns indirectly by making the cod larvae more opportunistic at low concentrations. Previous studies have shown that larval cod with access to high prey concentrations consume zooplankton in the mid-size range, while larval cod restricted to a low concentration of prey consume prey in a non-selective manner (van der Meeren &

Table V. Survival (%) of larvae in the replicate mesocosms of the different treatments, based on numbers of eggs per litre, numbers of survivors from the end of the experiment, and sampled fish during the experiment.

	Survival (%)	
Treatment	Mesocosm A	Mesocosm B
HN	15.8	11.9
LN	2.8	5.6
HW	24.6	18.0
LW	3.6	6.5

Næss 1993; Munk 1995). Larvae in the L treatments generally ate smaller prey items than larvae in the respective H treatments, and the size range (CV) of the prey they consumed was wider. During the first three weeks, the cod larvae in the L treatments, offered lower prey concentrations, consumed more miscellaneous edible prey. Since miscellaneous edible prey mainly consisted of small plankton species, larvae in low prey concentration treatments consumed more small plankton resulting in the wider size range observed in both L–N and L–W treatments.

Our results show that the size of ingested prey increased in all treatments as the larvae grew. Larval cod in all treatments generally selected larger prey than the average size available from the small fraction stock tank, but the larvae in the W treatments always ate smaller prey items than the average size available from the larger-fraction stock tank. Thus these size fractions were a suitable means of manipulating the prey field for the larvae, allowing and modifying the expression of selective feeding behaviour. Cod larvae select larger prey as their body size and gape increases (Pepin & Penney 1997; Puvanendran et al. 2004; Rowlands et al. 2008). In contrast, Thorisson (1994) suggested that metamorphosing cod larvae (10–13 mm) in the wild ingest smaller prey items than do smaller cod larvae (8–9 mm). However, the combination of few observations in this size interval together with the lack of plankton availability estimations, make those findings inconclusive. Larval cod in the Irish Sea switched to larger prey and increasingly preferred *Calanus* sp. at and after metamorphosis (Rowlands et al. 2008). Pepin & Penney (1997) also observed increased prey size, and increased variance in prey size, in larger cod larvae. In the wide size spectrum treatments (W), the mean prey size of cod at the average size of 8.4 mm was 0.41 mm while the mean prey size of cod at the average size of 11 mm (metamorphosis) was 0.54 mm. Our results confirm that larval cod eat larger and larger prey as they grow, and suggest that this consumption pattern does not change during metamorphosis.

Larval growth

The cod larvae grew faster at high prey concentrations, as expected based on previous experiments (e.g. Houde 1978; Puvanaendran & Brown 1999). Larval search volume is increased at low prey concentrations (Munk & Kiørboe 1985; Munk 1995; Puvanendran & Brown 1999), and since increased swimming activity is energetically costly for fish larvae (Kiørboe & Munk 1986), the trade-off between energy for swimming or growth could be an important factor governing growth in this experiment. Puvanendran & Brown (1999) found that cod larvae reared at low prey concentrations had a lower capture success than cod larvae reared in high concentrations during their first three weeks after hatching. The slower growth observed in the L treatments compared to the H treatments in the beginning of the experiment may have resulted from reduced feeding success. Growth was affected only by prey concentration in this experiment, and there were no significant interaction between concentration and prey size range, although Geffen (1996) found that a wide prey size range resulted in a skewed size distribution of cod larvae.

Relative variability in larval length increased in all treatments until 28 dph. There was, however, no significant difference between the treatments until the end of the experiment. If there was a higher zooplankton:fish larvae ratio in the L treatment due to mortality, especially size selective mortality, this could suppress the expected increase in larval size variation. Furthermore, more larval cod survived in the H treatments, such that smaller and slower-growing fish could have contributed to an increased relative size variation in the H treatments. Previous studies have observed both more (Houde 1977) and less (Gotceitas et al. 1996) variation in larval size in response to low prey concentrations. Vollset et al. (2009) analysed the growth and size distribution of mesocosm-reared cod larvae, including some of the material from this experiment. Based on larger sample sizes, they observed that larvae in the L treatments were more variable in weight compared to larvae in the H treatments. If more prey were available for each larva, despite the overall low prey concentrations in the L treatments, this could have led to increased variation in growth rates. Variance in weight and length may also be affected differently by factors like condition and stomach fullness, since these vary with weight but not with length. Thus trends in size variation may show some inconsistencies between studies using different measurement units.

A size- and temperature-dependent larval cod growth model (Folkvord 2005) was applied to analyse whether the observed temperature difference between

N and W mesocosms at the end of the experiment was sufficient to explain any differences in larval growth. Cumulatively the model predicted that size difference due to temperature alone would be approximately 5% after 35 dph, increasing to around 12% at the end of the experiment. The predicted differences are based on optimal feeding conditions, and temperature-dependent differences should be reduced in our experiment, especially in the L treatments. Nevertheless, there may have been some systematic bias due to temperature that obscured any significant difference in growth between N and W treatments.

Survival

Larvae survival was lower in the L treatments than in the H treatments, and was not significantly influenced by the prey size range available. Effects of prey concentration are apparent in previous studies (Houde 1978; Gotceitas et al. 1996; Puvanendran & Brown 1999). Although the prey availability in all treatments seemed to be converging during the experiment, the proportion of copepod nauplii in the uneaten plankton in the mesocosms was much lower compared to the proportion in the small fraction zooplankton stock. Hence, the competition for copepod nauplii may be the main effect governing survival in the beginning of this experiment, resulting in lower survival in the L treatments than in the H treatments.

Survival tended to be higher in the W treatments than in N treatments in this experiment. Even though the concentration of prey available did not differ between the narrow and wide range treatments, the total biomass of zooplankton available did. The average zooplankton size in the large fraction stock tank was almost twice as large as the zooplankton in the small fraction stock tank, and thus more energy was available per individual prey in the large fraction. If the zooplankton are considered as spheres, large prey account for eight times the biomass of the small prey on a per prey basis. The 10% large size fraction added to the W treatment mesocosms would then account for about 60% more biomass relative to the N treatment mesocosms. Higher final survival in the W treatments was probably a result of the availability of larger zooplankton, more zooplankton biomass, and thus less competition for prey.

The miscellaneous non-edible prey increased in the H–N treatments as the larvae grew, while in the H–W treatments this prey occurred in more or less the same proportions through the experiment. Thus selective feeding by larvae in the H–N treatment altered the remaining prey species composition to a larger extent than in the H–W treatment. Cushing (1983) suggested that growing fish larvae can exert an increasing effect on the concentration of prey. Consumption by fish larvae during their first 3 months of life (hatching to metamorphosis) can reach 50 $mgC^{-2}\ d^{-1}$, enough to cause a significant impact on zooplankton populations (Heath 2007). In addition, larvae provided with small prey items have to capture more prey to satisfy their increasing energy demands (Puvanendran et al. 2004). This was evident, as the cod larvae in N treatments ate more prey items than cod larvae in W treatment. Thus, intra-specific competition is expected to have been higher in the N treatments towards the end of the experiment, resulting in lower final survival compared to the W treatments, in particular the H treatment.

Evidence of cannibalism was found in the end of the experiment, through the presence of a vertebra in the stomach of one fish larvae in the final sample in the H-W treatment. In addition, a decrease in the CV of larval length suggests that cannibalism occurred in several mesocosms at the end of the experiment. Cannibalism should be greatest among cod juveniles at approximately 20 mm (Folkvord 1993, 1997), when the relative mouth size is largest (Otterå & Folkvord 1993). In this experiment, the average fish size never reached 20 mm, although individuals larger than 20 mm were found in all mesocosms at the end of the experiment. Because cannibalism probably occurred only at the final stage of the experiment, it is unlikely to have affected the overall pattern of the results.

Mesocosms have the advantage over smaller controlled laboratory experiments, giving the larvae a more natural environment (Solemdal 1981), and are thus more likely to produce high growth rates and survival (e.g. van der Meeren & Jørstad 2001). The use of natural zooplankton presented a challenge in controlling a manipulated feeding experiment, but produced results that are more likely to relate to natural conditions. This experiment showed that size spectrum of available prey affected the feeding patterns of the cod larvae, whereas prey concentration was an important factor in determining growth and survival. Larval growth and survival were not influenced by any significant interaction between prey concentration and prey size spectrum. Prey concentration did affect the size selective feeding patterns indirectly, by making the cod larvae more opportunistic at low concentrations. Overall, the findings from this mesocosm experiment demonstrate that prey size spectrum may play an important role where there is competition between larval fish for suitably sized prey.

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