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Selective feeding behavior of larval naked gobies *Gobiosoma bosc* and blennies *Chasmodes bosquianus* and *Hypsoblennius hentzi*: preferences for bivalve veligers

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ABSTRACT: Naked gobies *Gobiosoma bosc*, striped blennies *Chasmodes bosquianus*, and feather blennies *Hypsoblennius hentzi* provide important intermediate links within the trophic structure of estuarine oyster reef communities. Predator-prey interactions between planktonic larvae of these fishes and larval eastern oysters *Crassostrea virginica* may influence recruitment success within oyster reef communities. These 3 species of oyster reef fish larvae were cultured from wild nests and used in multifactorial laboratory feeding experiments with larval oysters or hard clams *Mercenaria mercenaria* as well as wild plankton as prey items to determine the effects of predator age, predator concentration, and prey type on feeding selectivity of these fishes. Predator age significantly influenced feeding behavior of naked gobies and feather blennies. Predator concentration did not significantly effect feeding behavior for any of the 3 fish species. Prey type significantly affected feeding behavior of feather blennies and naked gobies. Naked gobies consumed bivalve veligers preferentially at all veliger concentrations. Feather blennies consumed veligers preferentially at concentrations as low as 12% of the available prey field. Striped blennies were less specialized in their feeding patterns but still consumed bivalve veligers preferentially at prey field concentrations as low as 11% veligers.

KEY WORDS: Larval fishes · Oyster reefs · Naked goby · Striped blenny · Feather blenny · *Crassostrea virginica* · Predator-prey interactions · Selectivity · Chesson's alpha

INTRODUCTION

On the basis of numbers alone, oyster reef fish larvae are an important component of estuarine plankton: for example, naked goby *Gobiosoma bosc* larvae seasonally dominate Chesapeake Bay ichthyoplankton collections (Shenker et al. 1983, Cowan & Birdsong 1985, Olney 1996). The local trophic effects of these planktonic predators are poorly understood. The connections between adult gobies, conspecific feather blennies *Hypsoblennius hentzi* and striped blennies *Chasmodes bosquianus* and living reefs created by eastern oysters *Crassostrea virginica* have long been acknowledged (e.g. Wells 1961, Dahlberg & Conyers 1973). Adult fishes use the heterogeneous habitat created by the matrix of adult oyster shells for shelter as well as nesting and feeding grounds.

Growth and mortality patterns for larval fishes are strongly influenced by food availability and determine observed community recruitment relationships (Shepherd & Cushing 1980, Houde 1989). Within oyster reef communities, planktonic fish larvae may be major predators on planktonic oyster larvae or 'veligers'. Temperate reef fishes and oysters spawn within the same approximate temporal or seasonal window, producing larvae that occur concurrently and undergo planktonic development followed by subsequent settlement and recruitment to the benthos. For larval fishes, abundant food supplies that are potentially available around and on oyster reefs increase growth

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rates and shorten the planktonic larval development period, reducing predation risks from pelagic invertebrate and vertebrate predators (Houde & Schekter 1980, Hunter 1981). Reduction of time to settlement potentially increases recruitment of these benthic reef fishes (Shepherd & Cushing 1980). Increased densities of benthic reef fishes provide more potential prey items for pelagic predators that use oyster reefs as feeding grounds and nursery areas.

Ichthyoplankton preference for bivalve veligers from the ambient prey field has been previously documented. Houde & Lovdal (1984) and Govoni et al. (1986) reported strong preferences for veligers by several species of larval fishes in Biscayne Bay and the Gulf of Mexico. Olney (1996) described feeding behavior and preference for veligers by larval seaboard gobies *Gobiosoma ginsburgi* collected from the Chesapeake Bay plume. Checkley's (1982) laboratory experiments with herring *Clupea harengus* larvae using wild zooplankton as prey showed significant preferences for mollusc veligers.

Breitburg (1989, 1991) conducted field and laboratory studies with pre-settlement and settlement-stage (demersal) naked goby larvae to determine feeding incidence in relation to demersal schooling behavior and settlement. Gut contents from field caught demersal naked goby larvae were dominated by crustaceans (n fishes = 22, Breitburg 1989; n fishes = 72, Breitburg 1991). Laboratory experiments testing prey selectivity of planktonic goby or blenny larvae have not been described.

The objectives of this study were to test the effects of predator age, predator concentration, and prey type on feeding selectivity using bivalve veligers as the principal prey of cultured naked goby, striped blenny, and feather blenny larvae. A selected prey item is considered to be one whose proportional occurrence in gut contents is greater than its proportion in the available prey field.

METHODS

Predators. ***Larval fish culture:*** Larval gobies and blennies used in laboratory feeding experiments were cultured using nests that were collected from naturally occurring or artificially deployed oyster shell substrate in the Piankatank and York Rivers, Virginia, USA. Fish nests were identified by egg morphology (size, color) and the identity of the guarding parents. Nests were transported to the laboratory in individual plastic bags filled with river water. In the laboratory, nests were carefully placed in 0.5 l beakers filled with a mixture of water from the field site and sand-filtered seawater. All beakers were maintained at 24°C under a 14 h light:10 h dark regime; i.e. summer field conditions.

As larvae hatched, they were moved to finger bowls filled with 1 l of sand-filtered seawater; larval densities were kept at approximately 150 per finger bowl. Larvae were fed rotifers *Branchionus plicatilis* several times daily from Day 0 post-hatching until approximately Day 8. During Days 8 to 18, larval fishes were fed a mixture of rotifers and fresh (<1 d old) *Artemia* sp. nauplii (Carolina Biological Supply, Inc.). The feeding mixture was gradually changed from 100 to 0% rotifers by Days 14 to 18 or when fishes began settlement. After 18 d, or the initiation of settlement, fishes were transferred to aquaria filled with 30 l of aerated, filtered seawater; fishes were maintained at densities <100 tank^{-1} and were fed 3 times daily with fresh *Artemia* sp. nauplii. After 21 d, clean oyster shell was placed in each tank to provide shelter and daily feedings were reduced to 2 larger portions of 2 to 3 d old *Artemia* sp. nauplii.

Preliminary laboratory feeding experiments to determine gut residence time: The results of preliminary feeding experiments to determine gut residence time were used to establish the appropriate duration for subsequent larval feeding experiments. Experiments had to be long enough to allow prey items to pass into the gut but short enough to avoid defecation. Individual striped and feather blennies of various ages were allowed to feed in chambers containing high densities of prey items (either rotifers dyed with acridine orange or *Artemia* sp. nauplii) until guts were visibly full (approximately 2 h). Individual fishes were then placed in chambers containing 0.15 l of filtered seawater. Every 30 min for 5 h, individual fishes were examined under a dissecting microscope to determine levels of gut fullness.

Multifactorial laboratory feeding experiments. Multifactorial feeding experiments were designed to test the effects of predator age and concentration on larval fish feeding and to evaluate prey selectivity with regard to bivalve veligers. To avoid potential habituation effects, cultured food organisms (rotifers or *Artemia* sp. nauplii) were never used as experimental prey items (Checkley 1982, Lindberg & Doroshov 1986, Mills et al. 1987, Connaughton & Epifanio 1993). Fishes used in any given experiment were usually from the same brood or nest. Experimental conditions were the same as fish culture conditions. Six to 8 h before an experiment (5 to 7 h before being placed in experimental chambers), larval fishes were removed from culture chambers, placed in aerated, filtered seawater at 24°C, and starved until the experiment began.

Prey items. ***Wild zooplankton prey field:*** Eight to 12 h before an experiment, 2 microplankton nets (80 µm Nytex mesh, 0.3 m diameter, 3:1 aspect ratio) were deployed in the lower York River, Virginia, USA. The lower York River supports neither oyster reefs nor

a large oyster population (Morales-Alamo & Mann 1998), thus these plankton samples are representative of conditions at sites away from oyster reefs. Nets were oriented to face into the current such that the top of the mouth support ring was within 0.1 m of the surface. The microplankton collected from each net were sieved through a 202 µm Nytex mesh to remove coelenterates and any larval fishes, taken to the laboratory, and held in 2 l of filtered, well-aerated seawater in light conditions. Debris and sediment were allowed to settle out before experimental aliquots of plankton were removed. Before plankton aliquots were added to the experimental chambers, representative aliquots were examined under a dissecting microscope to verify that the plankton were alive and swimming.

Veliger prey field: Bivalve veligers were obtained from hatchery facilities at either the Virginia Institute of Marine Science (VIMS) or VIMS Eastern Shore Laboratory (ESL) at least 18 h before an experiment. Veligers from the VIMS Hatchery required no salinity acclimatization, whereas ESL veligers (rearing salinities of 33 to 35‰) were acclimated to lower York River salinities at a rate of 1 to 2‰ per 2 h to reach an endpoint equal to ambient York River salinities (12 to 17‰). Either *Crassostrea virginica* or *Mercenaria mercenaria* veligers were used in experiments; bivalve species were never mixed. Samples of veligers were measured to the nearest 0.01 mm with a computer image analysis system before experiments. Veligers were maintained in aerated, filtered seawater post-acclimation and before addition to the experimental chambers. Veligers were fed algae (*Isochrysis galbana or Pseudoisochrysis paradoxa*) 4 to 6 h before experiments began.

Mixture of wild plankton and veligers: Wild plankton were supplemented with bivalve veligers to approximate field concentrations of veligers (38 oyster pediveligers l^{-1}, Southworth 1998) observed in proximity to restored oyster reefs in Virginia (e.g. Shell Bar Reef, Great Wicomico River) during the seasonal window when larval fishes and oyster veligers co-occur in the plankton, i.e. June to July.

Experimental protocol. Feeding experiments were conducted using 150 ml beakers as feeding chambers. Beakers were filled with 50 ml of filtered seawater at 24 to 26°C and were maintained in artificial light conditions throughout experiments. Larval fishes were added to each chamber 1 h before prey items were added. Different concentrations of fishes and different mixtures of prey items were tested for each fish species. Larval fish (predator) concentrations were 1, 3, or 5 fishes per beaker. Fishes from each predator concentration were offered bivalve veligers (veliger), wild plankton (WP), or a mixture of wild plankton supplemented with bivalve veligers (veliger + WP).

Experiments were initiated by the addition of a 5 ml aliquot of concentrated prey to each chamber. Wild plankton collections were combined to give total prey densities in each chamber of >1000 prey l^{-1} to ensure that food was not limiting (Connaughton 1994). These concentrations are similar to prey concentrations reported in other studies of larval fish feeding behavior (Mathias & Li 1982, Stoecker & Govoni 1984, Munk & Kiørboe 1985, Mills et al. 1987, Chesney 1989).

Prey density or availability was determined by enumerating individual organisms in 5 ml aliquots taken from experimental chambers and fixed in 70% ethanol. Fishes were allowed to feed undisturbed for 3 h. Experiments were ended by the removal of fishes from the chambers 3 h after prey addition. All fish were immediately placed in 10% neutral buffered formalin and saved for subsequent dissection and gut content analyses. Notochord length was determined to the nearest 0.01 mm post-preservation using an image analysis system.

Data analyses. Only fishes that had consumed at least 1 prey item were used in these analyses. The percentage of fishes feeding (Table 1) was calculated for each experimental block or predator concentration/prey type combination (e.g. 1 fish per beaker fed only veligers) by dividing the number of fish with food items in their guts by the total number of fish used in the experiment. *A priori* significance levels for statistical tests were $p = 0.05$. Assumptions of homogeneity of variance were tested using Bartlett's test (Zar 1996) while assumptions of normality were tested with the Ryan-Joiner test (similar to Shapiro-Wilks per Minitab 1995). Unless otherwise noted, data satisfied both of these assumptions. Fisher's pairwise test (Zar 1996) was used as a post-hoc multiple comparison test.

Effects of predator age, predator concentration, and prey type: Total numbers of prey items consumed by each species were transformed (reciprocal transformation, Zar 1996) to meet the assumptions of homogeneity of variance and normality. The influence of predator age, predator concentration, and prey type on feeding behavior for individual species of larval fishes were evaluated with 3-factor ANOVAs (1 per species; Table 2).

Prey selectivity: Two different graphical methods were used to qualitatively describe feeding selectivity by these reef fishes. First, percentages of prey items consumed or used by each fish species were plotted against percentages of prey available in the habitat (Fig. 1) using a modification of the technique proposed by Costello (1990). Each point on the graph represents the percentage availability in the habitat and percentage consumption by fish for a specific prey taxon. Amundsen et al. (1996) recommend another graphic

Table 1. Summary of laboratory feeding experiments to evaluate feeding preferences of larval oyster reef fishes. Bivalve veligers, wild plankton (WP), and mixtures of both were used as prey items. Treatment shows prey type and fish concentration per beaker, e.g. prey - fish concentration or Veliger -1 fish. NA: prey items not available for consumption in a particular experimental block. n: number of individual fish per treatment. Vel: bivalve veligers; Cop: copepods; Pol: polychaete larvae; Dia: diatoms

Predator **Age** Treatment	n	Mean notochord length (mm) ± SE	% fish feeding	Mean prey concentration (1000 l^{-1})	Prey field composition (% of total)				Chesson's alpha			
					Vel	Cop	Pol	Dia	Vel	Cop	Pol	Dia
Naked goby												
5 d												
Veliger - 1 fish	6	3.97 ± 0.11	33	1	100				1	NA	NA	NA
WP - 1 fish	4	3.78 ± 0.09	0	10	15	18	39	28	–	–	–	–
Veliger + WP - 1 fish	6	3.60 ± 0.06	17	6	18	28	35	18	0.6	0.4	0	0
Veliger - 3 fish	7	3.70 ± 0.07	14	1	100				1	NA	NA	NA
Veliger + WP - 3 fish	8	3.69 ± 0.06	25	4	20	22	35	22	1	0	0	0
15 d												
Veliger - 1 fish	6	4.19 ± 0.17	67	3	100				1	NA	NA	NA
WP - 1 fish	5	4.30 ± 0.14	0	11	10	43	21	26	–	–	–	–
Veliger + WP - 1 fish	6	4.16 ± 0.06	100	9	40	22	16	21	1	0	0	0
Veliger - 3 fish	17	4.14 ± 0.05	53	3	100				1	NA	NA	NA
WP - 3 fish	15	4.07 ± 0.05	13	11	10	47	26	16	1	0	0	0
Veliger + WP - 3 fish	14	4.30 ± 0.06	50	6	31	30	11	27	1	0	0	0
Feather blenny												
3 d												
Veliger - 1 fish	6	3.86 ± 0.04	83	36	100				1	NA	NA	NA
WP - 1 fish	6	3.87 ± 0.05	0	3	17	27	16	39	–	–	–	–
Veliger + WP - 1 fish	6	4.02 ± 0.08	16	18	72	7	8	12	1	0	0	0
Veliger - 3 fish	18	3.90 ± 0.03	30	29	100				1	NA	NA	NA
WP - 3 fish	18	3.87 ± 0.04	28	7	12	26	24	38	0.6	0	0.2	0.2
Veliger + WP - 3 fish	18	3.95 ± 0.08	56	22	72	10	6	11	0.9	0	0	0.1
Veliger - 5 fish	25	3.83 ± 0.04	36	25	100				1	NA	NA	NA
WP - 5 fish	30	3.89 ± 0.04	10	6	20	26	23	31	0.33	0	0.67	0
Veliger + WP - 5 fish	23	3.97 ± 0.05	39	40	78	7	4	10	0.70	0.08	0.11	0.11
5 d												
Veliger - 1 fish	6	4.01 ± 0.11	67	10	100				1	NA	NA	NA
WP - 1 fish	6	4.12 ± 0.06	33	5	36	18	20	26	0	0	1	0
Veliger + WP - 1 fish	7	3.88 ± 0.04	71	17	61	12	12	14	1	0	0	0
Veliger - 3 fish	17	3.96 ± 0.05	88	11	100				1	NA	NA	NA
WP - 3 fish	18	3.87 ± 0.03	39	7	17	21	24	37	0	0.38	0	0.62
Veliger + WP - 3 fish	17	3.82 ± 0.06	76	9	60	16	0	24	0.47	0.05	0.42	0.06
Veliger - 5 fish	20	3.89 ± 0.03	70	13	100				1	NA	NA	NA
WP - 5 fish	20	4.18 ± 0.06	35	7	0	27	17	56	0	0.14	0.71	0.14
Veliger + WP - 5 fish	20	3.95 ± 0.06	70	20	70	8	8	14	0.94	0.00	0.06	0.00
Striped blenny												
2 d												
Veliger - 1 fish	6	3.92 ± 0.08	33	3	100				1	NA	NA	NA
WP - 1 fish	5	4.34 ± 0.11	20	13	11	39	19	31	1	0	0	0
Veliger + WP - 1 fish	6	4.21 ± 0.09	33	12	33	30	16	21	0	1	0	0
Veliger - 3 fish	16	4.23 ± 0.05	25	2	100				1	NA	NA	NA
WP- 3 fish	17	4.13 ± 0.05	29	11	9	49	13	29	0.20	0.44	0.16	0.20
Veliger + WP - 3 fish	17	4.12 ± 0.06	35	16	32	34	7	27	0.53	0.19	0.28	0.00
Veliger - 5 fish	30	4.12 ± 0.03	23	8	100				1	NA	NA	NA
WP - 5 fish	30	4.15 ± 0.04	33	12	7	37	16	40	0.40	0.43	0.17	0.00
Veliger + WP - 5 fish	30	4.09 ± 0.04	43	16	30	28	15	26	0.31	0.31	0.15	0.23
5 d												
Veliger - 1 fish	6	4.46 ± 0.11	33	1	100				1	NA	NA	NA
WP - 1 fish	5	4.91 ± 0.11	20	6	24	18	37	20	0	1	0	0
Veliger + WP - 1 fish	6	4.76 ± 0.05	50	10	41	14	24	21	0.51	0	0.49	0
Veliger - 3 fish	9	4.66 ± 0.12	56	1	100				1	NA	NA	NA
WP - 3 fish	17	4.77 ± 0.07	59	6	16	25	29	29	0.03	0.65	0	0.32
Veliger + WP - 3 fish	18	4.64 ± 0.06	56	10	27	11	39	21	0.46	0.10	0.38	0.06

Table 2. Summary of ANOVAs performed on data from laboratory feeding experiments on individual species of larval fishes. *Significance at the p = 0.05 level

Species	Factors	df	p-value	Fisher's test
Naked goby	Predator age	1	0.02*	15 d > 5 d
	Predator concentration	2	0.08	
	Prey type	2	<0.001*	Veligers, Veligers + WP > WP
	Predator age × Predator concentration	1	0.08	
	Predator age × Prey type	2	0.15	
	Predator concentration × Prey type	2	0.04*	
	Predator age × Predator concentration × Prey type	2	0.01*	
Feather blenny	Predator age	1	0.04*	5 d > 3 d
	Predator concentration	2	0.82	
	Prey type	2	0.01*	Veligers, Veligers + WP > WP
	Predator age × Predator concentration	2	0.35	
	Predator age × Prey type	2	0.49	
	Predator concentration × Prey type	4	0.45	
	Predator age × Predator concentration × Prey type	3	0.91	
Striped blenny	Predator age	1	0.06	
	Predator concentration	2	0.66	
	Prey type	2	0.11	
	Predator age × Predator concentration	1	0.03*	
	Predator age × Prey type	2	0.30	
	Predator concentration × Prey type	4	0.73	
	Predator age × Predator concentration × Prey type	2	0.35	

method that relies on the variable prey-specific abundance which they suggest provides a more detailed diet description when plotted against the frequency of occurrence of a prey item. Prey-specific abundance is calculated as follows (Amundsen et al. 1996):

$$P_i = (S_i/S_{t_i}) \times 100$$

where P_i = prey-specific abundance of prey taxon i; S_i = number of prey taxon i in the stomach; and S_{t_i} = total stomach contents in only those predators with prey taxon i in their stomachs. Prey-specific abundances for the 3 predator species used in this study were calculated for bivalve veligers and plotted against the percent availability of veligers in the habitat for experimental trials with wild plankton or wild plankton supplemented with veligers (Fig. 1).

Chesson's alpha was used to quantitatively describe feeding selectivity by fishes when multiple prey types were offered (Table 1). Chesson's alpha (Chesson 1978) ranges from 1 (exclusive ingestion) to 0 (complete avoidance). Relative preference for a prey type in relation to other available prey types is inherent in the calculated alpha values. Chesson's alpha is calculated using:

$$\text{alpha} = \frac{r_i}{n_i}\left(\sum_{j=1}^{m}\frac{r_i}{n_i}\right)^{-1}$$

where r_i = portion of prey taxon i in the ingested food; n_i = portion of prey taxon i available in the habitat; and m = number of prey taxa considered.

RESULTS

Preliminary laboratory feeding experiments to determine gut residence time

Gut residence time was greater than 3 h for all ages of blennies and types of prey items; naked gobies were assumed to have similar residence times. Gobies were not tested explicitly because they were much harder to culture and all live fishes were needed to ensure adequate replication in feeding experiments. Fish age ranged from 2 through 31 d and length ranged from 2.8 to 15 mm. Although the 31 d old fishes were post-settlement and, by definition, no longer larvae, they were included in these experiments to ensure an adequate size range of animals for accurate determinations of gut residence time. All fishes were fed the prey items on which they had been cultured and >90% of the fishes tested were feeding during the window when prey were offered.

Multifactorial laboratory feeding experiments

Effects of predator age, predator concentration, and prey type

Predator age significantly affected feeding behavior of naked gobies and feather blennies (ANOVAs, $p < 0.05$; Table 2). Older fishes consumed more prey items

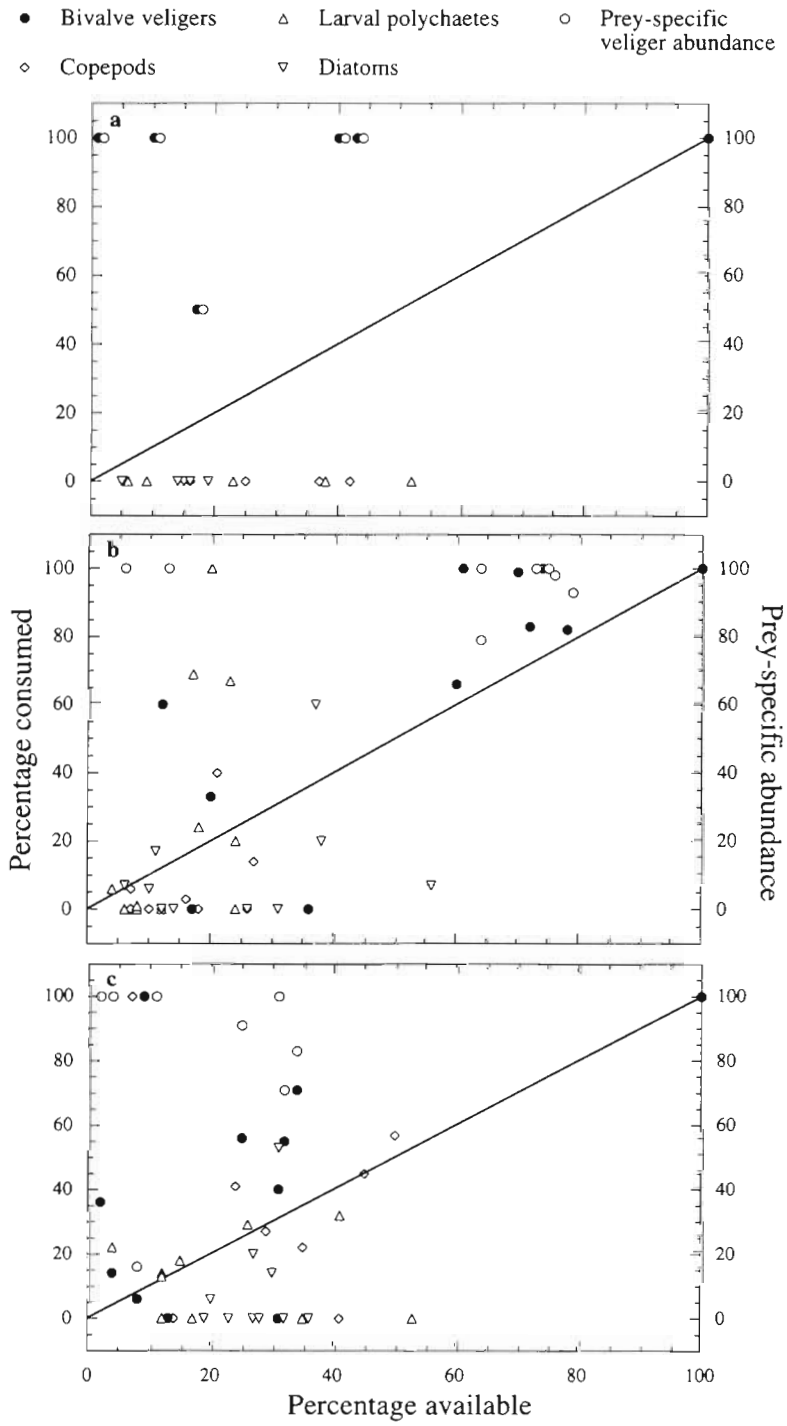

Fig. 1. Percentage consumption of prey items and prey-specific veliger abundance plotted in relation to percentage availability for laboratory feeding experiments with (a) naked gobies (n = 32), (b) feather blennies (n = 157), and (c) striped blennies (n = 82). Points above the diagonal line indicate prey items that are consumed at a higher proportion than their availability in the plankton. In cases where points representing percent bivalve veligers consumed overlapped completely with points for prey-specific veliger abundances, percent bivalve veliger abundance points were offset 1 *x*-axis unit (a percentage point) to the left and prey-specific veliger abundance points were offset 1 *x*-axis unit to the right

than younger fishes in the case of both naked gobies (15 vs 5 d old) and feather blennies (5 vs 3 d old).

Predator concentration did not significantly affect the total number of prey consumed by any larval fish species. Total prey consumption by naked gobies and feather blennies was significantly affected by the type of prey offered (ANOVAs, $p < 0.05$; Table 2). Bivalve veligers and veliger-supplemented wild plankton were consumed by naked gobies and feather blennies at significantly higher rates than were wild plankton. The interactions between prey type and predator concentration and prey type, predator concentration, and predator age were significant for naked gobies (ANOVA, $p < 0.05$; Table 2).

Prey selectivity

Larval reef fishes selectively consumed bivalve veligers from mixed prey fields. This preference is demonstrated both qualitatively (Fig. 1) and quantitatively (selectivity index values; Table 1). Specialization on a diet item is indicated graphically by points with low availability and high consumption (Costello 1990). Naked gobies showed strong preferences for bivalve veligers, regardless of their availability (Table 1, Fig. 1).

The average percentage of feeding naked goby larvae increased with age. At 5 d, 18% of the larvae fed; at 15 d, 47% of naked goby larvae fed (Table 1). The range of prey items consumed by gobies during these experiments was 1 to 7 individual prey. Feeding naked gobies preferred veligers when offered a mix of veligers and wild plankton at both predator concentrations (Table 1).

The average percentage of feeding 3 and 5 d old feather blenny larvae was 36 and 59%, respectively (Table 1). Feather blennies preferentially consumed bivalve veligers at veliger concentrations as low as 12% of the available prey field (3 d old, WP-3 fish). The maximum number of prey items consumed by an individual feather blenny, or an individual fish of any species, during the 3 h experimental window was 24 *Crassostrea virginica* veligers by a 5 d old blenny. Within the same

cohort of fish larvae during the 3 h experiment, 2 other blennies consumed 9 prey items each and a third ate 14 different prey items. Three day old feather blennies preferred veligers in all but 1 trial; larval polychaetes were preferred when wild plankton was offered at densities of 5 fish chamber^{-1} (Table 1). When veligers supplemented wild plankton, veligers were strongly preferred prey for feather blennies of both ages (Table 1). Five day old feather blenny larvae did not consume veligers in wild plankton experiments perhaps due to relatively low veliger availability (Table 1).

For striped blennies, the average percentage of feeding fish was 30% for the 2 d old larvae and 46% for the 5 d old larvae (Table 1). The number of prey consumed by an individual striped blenny during the experiments ranged from 1 to 6 prey. When veligers were offered as the exclusive prey item, they were consumed at all predator densities by both 2 and 5 d old larvae. Striped blennies consumed bivalve veligers preferentially at concentrations as low as 11% of the available prey field (2 d old, WP - 1 fish). When offered wild plankton, copepods or larval polychaetes were preferred over veligers at most predator concentrations, possibly reflecting relatively low availability of veligers in wild plankton (Table 1). When wild plankton supplemented with veligers was offered to striped blennies, veligers were selected for in all cases but one (2 d old; veliger + WP - 1 fish) where copepods were consumed exclusively (Table 1).

DISCUSSION

Larval reef fishes fed selectively on bivalve veligers in multi-factorial laboratory experiments. Diet preferences for veligers were demonstrated using qualitative (Fig. 1) and quantitative methods (e.g. selectivity indices, Table 1). These feeding patterns indicate selection for and specialization on bivalve veligers by all 3 species of larval fishes (Costello 1990, Amundsen et al. 1996). Low preference for veligers indicated by the Chesson's alpha values may be an artifact of relatively low veliger availability (Table 1) rather than active 'rejection'.

Feeding behavior of these fishes was significantly affected by age; older fishes consumed more prey items than younger fishes. Olney (1996) reports similar feeding patterns for seaboard gobies *Gobiosoma ginsburgi*. Predator concentration did not have a significant effect on larval goby and blenny feeding behavior in these experiments. Experimental chamber dimensions and volume (0.15 l) were small enough that any potential benefits offered by schooling behavior for prey location were probably negligible. Conversely, feeding behavior may have been inhibited by lack of schooling opportunities. Demersal naked gobies have been observed schooling directly above shell substrate or other structures immediately prior to settlement (Breitburg 1989). Behavior of planktonic goby and blenny larvae in relation to conspecifics is unknown. Predator concentrations in the chambers may not have been high enough (1, 2, 3, and 5 fishes) to cause competitive responses among individuals, especially in light of the high availability of food items.

Total prey concentrations were >1000 prey l^{-1} for all experiments to ensure that food was not limiting. Connaughton (1994) established 1000 prey l^{-1} as a threshold value at which the maximum number of weakfish *Cynoscion regalis* larvae had food occurring in their guts and above which consumption did not significantly increase even with an order of magnitude increase in prey availability. Natural plankton distributions are patchy (e.g. Wiebe 1970, Houde & Lovdal 1985, Owen 1989, Genin et al. 1994). Wild plankton abundance estimates may vary across several orders of magnitude depending upon the species of interest and the measurement scales used (e.g. Wiebe 1970, Gallager et al. 1996). Local concentrations of 1500 to 2000 *Pleuromamma gracilis* l^{-1} (Sixtymile Bank, CA; Genin et al. 1994), >181000 *Calanus* sp. l^{-1} (St. Margaret's Bay, Nova Scotia; Sameoto 1975), and 600000 *Limacina retroversa* l^{-1} (Great South Channel, Georges Bank; Gallager et al. 1996) have been recorded. Houde & Lovdal (1985) report concentration ranges of 31.9 to 184.4 copepod nauplii l^{-1}, 6.7 to 916.2 tintinnids l^{-1}, and 0.6 to 9.7 mollusc veligers l^{-1} for Biscayne Bay, FL. Olney (1996) provides similar mean density estimates for copepod nauplii (4.6 to 69.2 l^{-1}) and bivalve larvae (0.1 to 8.3 l^{-1}) from the Chesapeake Bay plume. Southworth (1998) reports oyster pediveliger concentrations of up to 38 l^{-1} near Shell Bar Reef, Great Wicomico River, VA, and estimates that pediveligers composed approximately 10% of the total prey field (M. Southworth pers. comm.). Although the small-scale prey abundances experienced by goby and blenny larvae in the field are unknown, it is reasonable to suggest that they may encounter differences in total prey abundance encompassing several orders of magnitude during development. In light of the natural variability observed in plankton abundances, 1000 total prey l^{-1} is a concentration threshold for optimal feeding (Connaughton 1994) as well as a reasonable representation of 'patch' abundances.

The prey items used in these experiments were small enough to be vulnerable to predation by larval reef fishes. Prey size in relation to larval fish mouth width or gape strongly influences consumption of any prey items (Hunter 1981). If a prey item is larger in all dimensions than the mouth width or height (gape) of a potential predator, its chances of being successfully captured by

that predator are small. The veligers and a large portion of wild plankton used herein were within the range of prey widths vulnerable to predation from these fishes (i.e. 0.08 to 0.3 mm, depending on the fish size).

Previous experience with a prey item, or habituation (Checkley 1982, Mills et al. 1987, Connaughton & Epifanio 1993), may also affect larval fish feeding success. None of the fishes used in these experiments had been previously exposed to either veligers or a mixture of prey types. Both Connaughton & Epifanio (1993) and Mills et al. (1987) found that habituation to a familiar prey type affects laboratory feeding results, depending on predator age and prey size. Gobies and blennies used in this study were cultured exclusively on rotifers and, subsequently, for the 15 d old naked gobies, *Artemia* sp. nauplii, effectively removing habituation to a particular experimental prey type as a potential source of experimental bias.

As visual predators, larval fishes feed during daylight when they are most likely to have a higher proportion of successful prey encounters. Variations in incident light have been correlated with reduced growth rates and/or feeding efficiency for bream *Abramis brama* (Townsend & Risebrow 1982), striped bass *Morone saxatilis* (Chesney 1989), and herring *Clupea harengus* (Batty 1987, Batty et al. 1990). Experimental chamber shape may have an effect on fish perception of prey. Bending of light through chamber corners may change perception and, subsequently, searching behavior for those fishes that rely on the dark background outside Snell's window to highlight prey (Janssen 1981). Since these experiments were conducted in full light conditions using round chambers, visual conditions were appropriate for successful predation by larval fishes.

Morphologically and behaviorally, bivalve veligers are vulnerable to predation by larval fishes. Capture success with regard to a particular prey type is a function of both predator perception and ease of handling (Hunter 1981). Bivalve veligers move slowly in the vertical plane, either actively swimming or passively sinking (Mann & Wolf 1983, Mann et al. 1991). The smooth rounded veliger morphology may make capture relatively simple for a larval fish as compared to ingestion of a prey item with multiple protruding appendages or more active swimming patterns (e.g. copepod nauplii, Van Duren & Videler 1995; or polychaete larvae, Mileikovsky 1973). As larval fishes grow and develop, they may become better suited to capture more active prey items.

High degrees of feeding specialization in fishes have been correlated with narrow niche width (Amundsen et al. 1996). While ontogeny of feeding behavior in naked gobies, feather blennies, and striped blennies may eventually reduce these high levels of specialization, in the earliest 'critical' period of larval development high abundances of preferred prey items (veligers) would facilitate growth. Larval fishes that have higher growth rates will settle more quickly thus escaping or avoiding potential larval stage mortality sources, e.g. starvation and predation (Shepherd & Cushing 1980). Selective feeding by larval reef fishes on bivalve veligers may be an important mechanism by which larval reef fishes reduce the length of their larval planktonic phase and, consequently, increase recruitment success.

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