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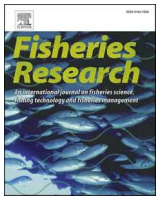

Larval ontogeny enhances resilience to a patchy planktonic food supply in the American lobster (*Homarus americanus*)

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ABSTRACT

The American lobster (*Homarus americanus*) plays an integral role in the coastal Northwest Atlantic as a benthic consumer and the target of the most valuable single-species fishery in North America. In the past decade, benthic recruitment of juvenile lobster has declined, even as egg production has increased, suggesting heightening levels of larval mortality. Recent correlative studies in the Gulf of Maine further suggest early-stage larval survival may be related to the supply and composition of planktonic foods. Despite these correlative studies and the economic importance of the species, relatively little is known about how larval lobster interacts with its prey in the pelagic environment. During these early developmental stages, lobster larvae undergo significant morphological changes which influence their ability to capture and handle prey. This study used a combination of laboratory-based feeding experiments and video recordings to examine changes in feeding behavior and ingestion rates between larval stages. Calculated Ivlev-type functional response curves were used to evaluate how larval ingestion rates vary with prey density and by larval stage on a suite of prey species. We observed dramatic stage-to-stage improvements in the capacity to pursue, capture, handle, and ingest specific prey, especially after the metamorphosis to the postlarval stage. The results highlight the vulnerability of the early life stages to low food densities. They also elucidate differences in the ability of specific prey taxa to evade predation by larval lobster. Quantifying the interactions between larval lobsters and their prey enhances our understanding of how this economically important species interacts with the pelagic food web, which fraction of available zooplankton represent viable food sources, and how lobster larvae may be impacted by altered prey availability associated with climate change.

1. Introduction

Planktonic larvae of benthic organisms (known collectively as "meroplankton"), face significant challenges prior to settling. Their survival depends on their ability to find food, avoid predators, and cope with numerous abiotic stressors such as temperature, salinity, and currents (Thorson, 1950). Mortality during this life phase is generally assumed to be extremely high, with estimates of mortality exceeding 99% (Pedersen et al., 2008). Studying planktonic larvae in the ocean can be challenging, resulting in a generally poor grasp of the mechanisms of larval trophic interactions for many species. However, we must study them to better understand the drivers of population dynamics and recruitment to adult life stages. A growing body of literature takes a more comprehensive approach to studying the ecology of marine invertebrates throughout both phases of their lifecycle by examining previously overlooked links between the ecology of planktonic larvae and the recruitment success of benthic adults (Calado and Leal, 2015).

All species of marine clawed lobster display a biphasic life cycle, with planktonic larval stages that depend on planktonic foods for their early growth, development, and survival (Wahle et al., 2012). The American lobster, *Homarus americanus*, is an exemplary model system to evaluate larval–adult linkages because all stages of the life cycle are relatively well-studied, and some populations have been monitored for many decades. The American lobster spends approximately one month developing through three larval stages in the plankton before metamorphosing to a postlarval stage that settles to the benthos (Lawton

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and Lavalli, 1995). Recent correlative evidence suggests that the abundance of certain zooplankton prey may be an important driver of lobster larval survival and benthic recruitment, which highlights a need for research into larval-zooplankton trophic interactions.

Over the past decade, recruitment or "settlement" of young-of-year lobsters to coastal nursery habitats in the Gulf of Maine has declined, despite observed increases in the broodstock and egg production that would be expected to yield higher numbers of juveniles. Carloni et al. (2018) examined several possible correlates of this decline in lobster settlement including temperature, advection, and the abundance of individual members of the zooplankton assemblage and found strong positive correlations between planktonic postlarval lobster abundance, benthic young-of-year settlement, and the abundance of the copepod *Calanus finmarchicus*. This correlation has been reinforced in a subsequent analysis of NOAA's Gulf-wide EcoMon time series of the zooplankton assemblage by Shank et al. (2024). *C. finmarchicus* is a large, lipid-rich copepod that is well known to be a key constituent of the diets of species such as the North Atlantic right whale (*Eubalaena glacialis*) and Atlantic herring (*Clupea harrengus*) (Darbyson et al., 2003, Pendleton et al., 2009). The abundance of *C. finmarchicus* has declined in the Gulf of Maine, and its center of distribution has shifted northward and earlier in the season over the last decade (Friedland et al., 2020, Ji et al., 2022), reducing the overlap between seasonal peaks in *C. finmarchicus* abundance and the larval lobster season (Carloni et al., 2024). Based on this correlation, Carloni et al. (2018) advanced the hypothesis that climate change-induced food limitation is an important driver of the disconnect between the abundances of newly hatched larvae and pre-settlement postlarval lobsters. To better understand whether lobster larvae are food-limited in the pelagic environment, more information is needed regarding their natural diets and predatory ability, as well as how these change during larval development.

Despite the economic and ecological importance of adult *Homarus americanus,* surprisingly little is known about the ingestion rates and diets of the planktonic stages of the larvae. While there is a growing body of information based on traditional gut analysis techniques and novel DNA sequencing techniques (Ascher, 2023; Juinio and Cobb, 1992), to date no study has systematically compared larval stages with respect to their prey handling abilities with different prey taxa and the response to changes in the density of planktonic foods.

In this study, we measured the ingestion rate, prey selectivity and handling time of the planktonic stages (three larval stages (SI-III) and postlarvae (SIV)) feeding on several native taxa of planktonic prey. The swimming speeds of the lobster larvae and their prey were also measured, enabling us to associate the effects of larval development and prey swimming speed with differences in capture rates. We measured prey handling times to investigate the underlying mechanisms that would impact the number of prey ingested in specific predator-prey combinations. Finally, we conducted experiments to evaluate the response of the larval and postlarval ingestion rates to varying density of several taxa of planktonic prey, and fitted estimated rates to Ivlev-type II functional response curves. We further compared the relative energetic value of the prey taxa. We hypothesized that swimming speeds and prey handling times of lobster larvae would increase and decrease, respectively, with progressive larval stages, coinciding with increased ingestion of larger and faster prey species by later stage larvae compared to early stage larvae. Our results point to dramatic ontogenetic improvements in the capacity to attack and consume prey as larvae advance to the postlarval stage that have important implications for vulnerability to food limitation in the wild during this phase of life.

2. Methods

2.1. Larval rearing

Egg-bearing female lobsters were collected from multiple locations in the midcoast and eastern Maine, USA, by our fishing industry partners, and were held in four 300 L flow-through hatchery tanks at the University of Maine's Darling Marine Center (DMC) in Walpole, Maine. The overflow was covered with a screen to retain newly hatched larvae. Larvae were collected and moved into 50 L flow-through conical rearing tanks, or transported to Bigelow Laboratory for Ocean Sciences where they were kept in 20 L buckets equipped with air pumps, and fresh seawater changes were done 1–2 times per week, as needed. Both systems were visually monitored for cleanliness and were cleaned as needed.

All larvae were fed daily using live zooplankton collected from the Damariscotta River estuary immediately adjacent to both facilities. Zooplankton were collected using a 150 μm plankton net either towed by an outboard research vessel or at the laboratory's dock in the flowing tide. Zooplankton concentrations within the rearing vessels (tanks and buckets) were kept sufficiently high (>10 individuals L^{-1}) to ensure larvae were constantly well-fed. Larval diets were supplemented with lab-reared *Artemia salina* to maintain high prey concentrations between zooplankton tows. Larvae were maintained in rearing vessels for up to one month to allow some to progress to the postlarval stage, or until use in experiments.

2.2. Prey choice feeding experiments

This experiment evaluated the hypothesis that prey preference among common prey varies with larval development. We employed a two-factor design to evaluate the separate and joint effects of larval lobster stage (4 stages) and prey species (3 taxa) on the number of prey consumed. Given the interest in *Calanus finmarchicus* as a potentially critical prey in the diet of larval lobster (Carloni et al., 2018, 2024), we conducted two sets of prey choice experiments in which *C. finmarchicus* was one of the choices among two other commonly occurring prey. In the first experiment, *C. finmarchicus* was combined with the copepods *Acartia* and *Temora* (Assemblage A). The second experiment combined *C. finmarchicus*, with the copepod *Centropages*, and native crab zoea larvae comprising a mix of *Carcinus maenas* and *Cancer* spp. but dominated by *C. maenas* (Assemblage B). Prey species in Assemblage A were selected based on abundance and co-occurrence with lobster larvae in our field surveys throughout the larval season (Wahle et al. unpublished data). Prey species in assemblage B were selected based on previous literature (Ascher, 2023; Juinio and Cobb, 1992; Ascher et al., 2024). *C. finmarchicus* was used in both assemblages A and B, and therefore served as a point of comparison across the two experiments. Assemblage A was tested during the summer of 2021 and Assemblage B was tested in the summer of 2022.

To collect zooplankton, net tows (75 cm diameter - 150 μm mesh) were conducted off the docks of Bigelow Laboratory for Ocean Sciences and the University of Maine Darling Marine Center, as well as at a site approximately 8 km offshore from Bigelow Laboratory for Ocean Sciences to obtain prey for trials. Zooplankton were sorted under a dissecting microscope (Olympus ZX-40). Fifteen individual prey of each species were pipetted into a 1 L mason jar with one lobster larva per jar for a combined density of 45 prey L^{-1}. The experimental jar was maintained at 15°C with a closed-loop water bath. Control jars with the same numbers of zooplankton but without a larva were run simultaneously. Larvae were allowed to feed for 24 hours in the dark to minimize prey aggregation. At the end of the feeding experiment the lobster larva was pipetted from the experimental jar and placed in a petri dish. The jar was poured through a 45 μm sieve into a bowl and the remaining prey items were counted under a microscope. For assemblage A, six replicates were conducted for each of the four larval stages for a total of 24 trials. For assemblage B, three replicates were conducted for each larval stage for a total of 12 trials. The lower level of replication for assemblage B was related to time constraints and availability of both larvae and prey at the time the experiments were conducted.

Statistical analyses were conducted separately for each experimental prey assemblage (A and B). The number of individuals of each of the

three prey species consumed was averaged across all replicates for the three larval lobster stages (SI-SIII) and postlarvae (SIV). Data were square-root transformed to normalize their distribution and homogenize treatment variances. A two-way ANOVA was performed in JMP Statistical Software to evaluate the main effects of lobster developmental stage and prey species and their interaction on the total prey consumed (JMP®, 2023).

2.3. Tracking free-swimming lobster larvae and their prey

Behavioral observations of free-swimming lobster larvae were conducted in a 1 L clear Plexiglas Kreisel tank connected to a small pump in a 700 mL sump to maintain constant water circulation. The shallow width of the Kreisel allowed the entire volume to be in focus in a single camera. The Kreisel was mounted on a metal track. Larvae and prey were recorded with a 3.2 megapixel black and white Flea3 USB 3.0 Camera from FLIR, with a 75 mm TV lens. The tank and sump were filled with chilled (12°C) ultra-filtered seawater (0.2 microns). A halogen microscope light with a fiber optic guide provided the "cold" light source for filming. A red filter was placed over each lamp bulb to limit any phototactic response from larvae or prey (Buskey et al., 1989; Cohen and Forward, 2002). Up to 10 early-stage lobster larvae (S1-SII) or 5 of the later stages (SIII-SIV), and numerous (species dependent) prey were placed into the Kreisel. To determine prey densities, prey items were counted using ImageJ (NIH, USA) within a selected volume of the tank which was then used to extrapolate an estimate of effective prey density. This was repeated three times for each video to obtain an average concentration.

Videos were recorded at 32 frames per second (fps) and saved directly to an external hard drive. Trials of free-swimming larvae were allowed to record for approximately 6 hours to maximize potential recordings of predatory interactions. Video analysis was conducted using the open-source particle tracking extension *TrackMate* in ImageJ. Videos were converted into image sequences. For larval stages (SI-III) we used 32fps and for postlarval lobsters we used 16 fps to account for their significantly greater swimming speeds. A scale was set within the software from a calibration ruler placed behind the filming tank. The TrackMate software was used to identify individual lobsters within the frame and track their movement over the course of the image sequence. Lobsters' average swimming speed (mm/second), maximum swimming speed, total track length (mm), net track displacement (mm), and total time of track (seconds) were recorded into a spreadsheet. Data were collected from a minimum of five unique paths for each lobster stage. Sample sizes varied between stages due to differences in the number of unique paths of sufficient length identifiable from the recordings. These data were recorded for every developmental stage, and note was made of the prey type present during the recording session. Data on track length and swimming speed were also collected for four prey species (*Pseudodiaptomus pelagicus*, *Calanus finmarchicus*, *Artemia salina*, and barnacle nauplii (*Semibalanus* sp.) and average speeds were obtained using the TrackMate extension in ImageJ. We were unable to obtain footage with clear enough swimming paths for *Parvocalanus*, *Euterpina sp*, and *Acartia* to conduct video analysis in ImageJ. Separate single factor ANOVA's were conducted to statistically compare swimming speeds across the four lobster stages and across the four prey taxa. Swimming speeds were log10 transformed prior to analysis to normalize data and equalize variances. To compare the relative swimming performance of larval predators and prey species we created a matrix tabulating differences in swimming speed for different predator stage and prey species combinations.

2.4. Prey handling by tethered larvae

Lobster larvae were tethered to a 32 gauge stainless steel wire following the methods of Fields and Yen (1993); (2002). Tethered larvae were suspended in the center of a 70 mL square chamber to video observations of the feeding behavior and handling times of *A. salina* and *C. finmarchicus* as prey. Videos were recorded at a frame rate of 32 fps and saved directly to an external hard drive. Trials of tethered larvae were limited to a maximum of 2 hours to minimize stress on tethered larvae. Approximately 20 lobster larvae were tethered, but not all tethered larvae engaged in feeding behavior during the filming period. Trials were conducted with larval stages I, III, and IV.

Video clips containing predator-prey interactions were identified and the handling time was quantified until the prey was either abandoned by the lobster or completely ingested. At least three feeding events were captured for each larval stage and prey combination, except for SIII feeding on *C. finmarchicus* where only two feeding events were observed (SI - *A. salina*: n=4; SI - *C. finmarchicus*: n=3; SIII - *A. salina*: n=4; SIII - *C. finmarchicus*: n=2; SIV - *A. salina*: n=3; SIV - *C. finmarchicus*: n=3).

A two-way ANOVA was conducted in JMP to evaluate the main effects of larval stage and prey species and their interaction on larval handling time (JMP®, 2023). Handling times were log10 transformed before the analysis to conform to normality and equal variance assumptions.

2.5. Single prey species feeding experiments- functional response

Feeding trials were conducted over a range of prey densities to evaluate the change in the ingestion rates of all four lobster stages to increasing prey density and to determine the prey density at which larvae and postlarvae reach their maximum ingestion rate. Experiments were conducted using seven different prey species: barnacle nauplii (*Semialanus spp.*), brine shrimp *Artemia salina*, copepodites and nauplii of the copepod *Euterpina acutifrons*, and adults of the copepods *Acartia tonsa*, *Parvocalanus crassirostris*, *Pseudodiaptomus pelagicus*, and *Calanus finmarchicus*. *C. finmarchicus*, *A. tonsa*, and barnacle nauplii (*Semibalanus* sp.) were collected from live zooplankton tows in the Damariscotta River estuary and sorted in the lab. *A. salina*, *E. acutifrons*, *P. crassirostris*, and *P. pelagicus* were raised in single-species cultures in the laboratory. Prey species were characterized by size, swimming behavior (i.e., slow swimmer, fast swimmer), and escape ability (slow or rapid escape response) (Table 2). Prey species were selected to span a range of sizes and swimming behaviors representative of natural prey available to lobster larvae in the Gulf of Maine. *Artemia salina* is not a naturally occurring prey, but is commonly used in hatcheries for its ease of culturing and lack of an effective escape reaction. *E. acutifrons* is also not native to the Gulf of Maine, but its nauplius and copepodite larvae are similar to other naturally occurring species, and its small size allowed us to further extend the size range of prey species.

For each set of trials, a single lobster was placed into a vessel with a prey density of either 5, 10, 20, or 50 animals L^{-1} of a single prey species in ultra-filtered seawater (0.2 μm). Larger volume vessels were used for lower prey density experiments to prevent the prey from being depleted

Table 1
Prey species used in prey choice experiments with their average dry weights and caloric contents. Data compiled from Laurence, 1976[1], McClatchie, 1985[2], McKinstry et al., 2013[3], [4]Vanhaecke et al., 1983, Hay et al. (1988)[5], and Dawirs, (1986)[6].

Species	Average dry weight (μg)	Calories/ μg dry wt	Calories/ individual
Calanus finmarchicus[1,3]	364.00	0.006425	2.3387
Centropages sp[1,2]	40.00	0.005122	0.2049
Carcinus maenas zoea[6]	20.59	0.002768	0.057
Temora longicornis[1,5]	15.05	0.004466	0.06720
Acartia sp.[1,2]	4.00	0.005160	0.02064
Artemia salina[4]	1.65	0.005953	0.00924

Table 2
Prey species used in functional response feeding experiments, arranged from small to large by average length, along with average carbon content individual^{-1} and relative swimming and escape response characteristics. Asterisk (*) denotes subset of prey taxa used to evaluate prey trait effects at maximum density (>20 prey L^{-1}; Table S2). Carbon weight data compiled from Saiz and Calbet, (2007)[1], Szyper, (1989)[2], Turner et al., 2001[3], Tande 1982[4], McKinnon and Ayukai, (1996)[5], and Uye 1983[6].

Prey Species	Average Prey Length (mm)	µg C individual^{-1}	Relative Swimming Speed	Relative Escape Response
Euterpina (copepodites and nauplii)*[2]	0.1–0.2	0.11–0.44	Slow	Slow
*Parvocalanus**[5]	0.2–0.4	0.93 ± 0.06	Fast	Rapid
*Artemia salina**[2]	0. 75	0.69–1.63	Slow	Slow
Barnacle nauplii[3]	1.0	9.80–11.10	Slow	Slow
Acartia[1]	1.0	4.00	Fast	Rapid
Pseudodiaptomus[6]	1.5	3.28–6.45	Fast	Rapid
*Calanus finmarchicus**[4]	2.0–4.0	180.00–213.00	Moderate	Rapid

during the trial. For example, at a prey density of 5 prey L^{-1}, the experiment was run in 4 L of seawater (20 prey), the 10 L^{-1} and 20 L^{-1} densities were both run in 2 L of water (20 and 40 prey, respectively), and the 50 L^{-1} density was run in 1 L of water. All trials were run for 6 hours in a 16°C water bath in the dark. After 6 hours the lobster was removed, and the contents of the jar were filtered through a 70 µm sieve (53 µm sieve used for *E. acutrifrons* due to its smaller size) and the remaining prey were counted. The ingestion rate was calculated as the number of prey consumed per hour. Both living and dead, intact, prey were included in the final prey count. Partially consumed prey (most often missing the urosome) were treated as being fully consumed. Three replicates were done for each prey species at each density using different individual lobsters. Trials were conducted with SI-IV lobsters for all prey with the exception of *A. tonsa* and barnacle nauplii as they became difficult to find in live zooplankton tows later in the summer. Only SI and SII were fed barnacle nauplii and *A. tonsa*. The majority of trials were conducted during a single larval season (summer 2021). A small subset of trials were conducted in the subsequent larval season (summer 2022) to fill in gaps where necessary and achieve three replicates of each prey, lobster stage, prey density combination.

Our early observations indicated that SIV lobsters are able to effectively forage within a much larger volume of water than the larvae. To determine the feeding rates of SIV at exceptionally low prey densities we used a set of high-volume (interior dimensions 78 × 78 × 74 cm) plastic tanks. The tanks were filled with 300 L of filtered seawater the day before the trial, and chilled overnight to 16°C. The chiller was removed from the tank just prior to the start of the trial and temperature was monitored for the duration of the 6-hour trial using a temperature probe. Water temperatures in the tank remained between 16 and 18°C over the course of the trial. Lobsters were presented with *C. finmarchicus* at concentrations of 0.50, 0.33, and 0.25 copepods L^{-1}. *C. finmarchicus* were collected from the Damariscotta River estuary via vertical plankton tows conducted onboard the Darling Marine Center's R/V Ira-C. *C. finmarchicus* were counted the day before each trial and kept in a 5°C refrigerator until the trial began. One lobster and either 75, 100, or 150 *C. finmarchicus* were placed into each experimental tank and left to feed for 6 hours. At the conclusion of the trial, lobsters were removed from the tank and tanks were then drained through a 150-um mesh filter. Copepods caught on the filter were counted under a microscope to determine ingestion. Because the large volume of water heightened risk of miscounting prey, for these trials we also ran three controls that followed the same procedures but did not include a lobster. In these trials we recovered 99.3 % of the prey released at the onset of the experiment, and we can therefore be reasonably confident that the variability in the outcome of trials including SIV is related to predation by them. To further determine whether ingestion rates depended on whether SIV were wild-caught or laboratory-reared, these trials were repeated three times at each prey density for both wild-caught and lab-reared SIV for a total of 19 trials (9 trials for wild-caught and 10 for lab-reared SIV). We used a Two-way ANOVA in JMP to evaluate the effects of source of the larvae (wild-caught versus hatchery-reared) and prey density (3 densities), and their interaction, on postlarval ingestion (JMP®, 2023).

Ingestion rates as a function of prey concentration were analyzed using Ivlev's (1961) Type II functional responses described by the general equation:

$$I = I_{max}\,(1 - e^{-bN}) \quad (1)$$

Where I is the ingestion rate (prey consumed hr^{-1}), I_{max} is the maximum ingestion rate, N is the prey density (individuals m^{-3}), and b is the proportionality constant that controls the steepness of the response curve (described as the decrease in "motivation to hunt" by Baek et al., 2009) (Parsons et al.1967). This equation enables the estimation of the theoretical maximum ingestion rate, I_{max} (i.e. the concentration at which the ingestion rate saturates) of a predator using experimental data.

To estimate the functional response curves and their parameters, the experimental data were fitted to Ivlev's Type II equation (Eq. (1)) using the least squares method in SigmaPlot 15.0. Maximum ingestion rate (Imax) and rate coefficient (b) were estimated for each larval stage and prey species combination. The strength and statistical significance of the fit were reported as R^2 and p-values, respectively. In this analysis, we further evaluated how converting consumption rates from numbers of prey to the quantity of Carbon in the prey. Initial prey concentrations (individuals L^{-1}) and ingestion rates (number of prey consumed hr^{-1}) were converted into µg C L^{-1} and µg C consumed hr^{-1}, respectively. Carbon contents for the prey species provided in Table 2 were obtained from previous studies (Tande, 1982, Uye, 1983, Szyper, 1989, McKinnon and Ayukai, 1996, and Saiz and Calbet, 2007).

To evaluate larval stage and prey trait (species, size, swimming speed, and escape response, independently) effects on larval ingestion rates. For this assessment we used four prey taxa for which data were available across all four larval stages at the higher prey densities (>20 prey L^{-1}), where food supply was least likely to be limiting. Using JMP statistical software we compared ingestion rates across larval stages and prey trait groups separately (JMP®, 2023). Table 2 lists the subset of four prey taxa used in this analysis (*Calanus, Euterpina, Artemia,* and *Parvocalanus*), along with their body size and swimming speed characteristics. An initial two-factor ANOVA indicated a very significant larval stage effect ($F = 9.117$, $df = 3$, $p < 0.0001$), a marginal prey species effect ($F = 2.717$, $df = 3$, $p = 0.05$), and no significant interaction ($F = 1.329$, $df = 9$, $p = 0.23$). In these groupings, however, data were generally not normally distributed and variances not equal. Thus, with the exception of the one comparison where we used a Student's t-test, we otherwise used a nonparametric Kruskal-Wallace test to evaluate statistical significance of one factor at a time. Where we made multiple post-hoc comparisons we applied a Bonferroni corrected alpha as appropriate to the number of comparisons (0.05/n, where n is the number of comparisons).

3. Results

3.1. Prey Choice

In the first experiment, with prey *C. finmarchicus, A. tonsa* and *T. longicornis*, all lobster stages exhibited a significant and consistent preference for *C. finmarchicus* over either *A. tonsa* or *T. longicornis* (Fig. 1a). Moreover, SIV consumed approximately twice as many prey as the three larval stages. As a result, there were strongly significant main effects of both developmental stage and prey taxa, with only a weakly

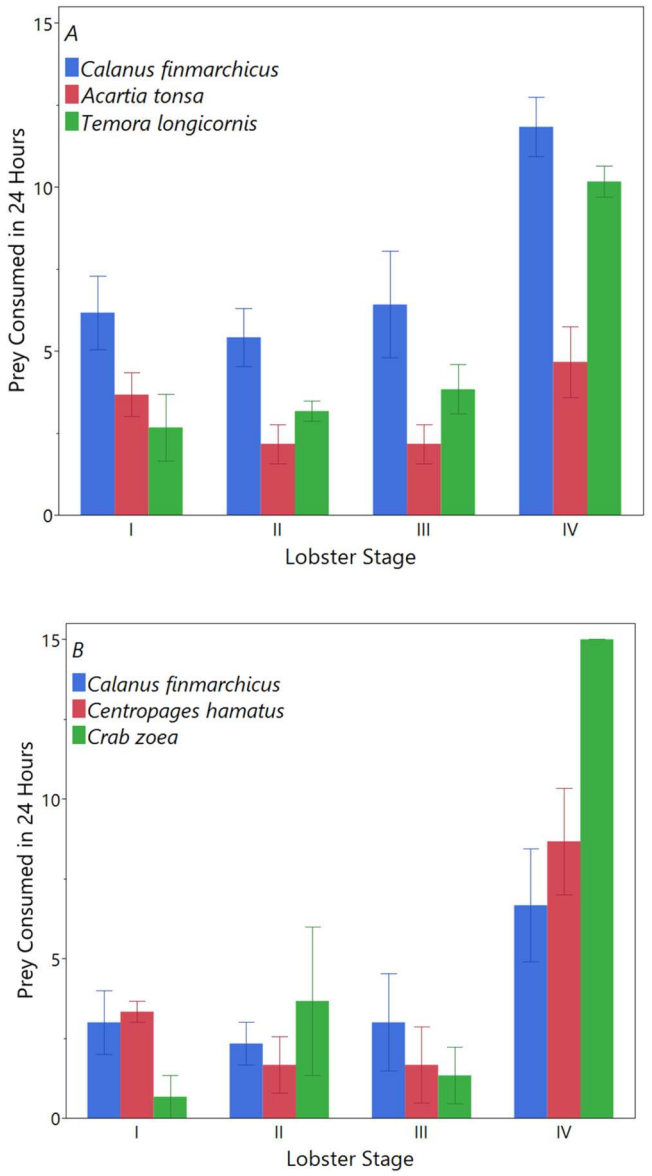

Fig. 1. (A) Average ingestion rates (± standard error) of lobster larvae and postlarvae feeding in single species treatments containing 15 individuals of *Calanus finmarchicus*, *Acartia tonsa*, or *Temora longicornis* over 24 hours (n = 6). Error bars indicate standard error. (B) Ingestion rates of lobster larvae feeding on 15 individuals of each (*Calanus finmarchicus*, *Centropages hamatus*, and crab zoea) over 24 hours (n = 3). See Table S3 for statistical analysis.

significant interaction term (Table S3a).

In the second preference experiment, lobsters' prey preferences were more variable. Comparative ingestion between *C. finmarchicus*, *C. hamatus*, and crab zoea varied between larval stages (Fig. 1b). As in the previous experiment, there was a significant developmental stage effect with SIV lobster consuming considerably more prey than the larval stages. However, we found no significant effect of prey species on the number of prey consumed, and non-significant interaction between prey species and developmental stage (Table S3b). It is noteworthy that while SI-SIII consumed the three prey in approximately equal numbers, SIV consumed almost twice as many crab larvae as the two copepod prey. In fact, SIV consumed all the crab larvae in all trials, suggesting the difference may have been even greater had more prey been provided. Because all 15 crab larvae were consumed in all three trials with SIV, the variance was zero for that treatment combination, and the assumption of equal variances among the treatments was violated. The ANOVA results therefore should be interpreted with caution. Nonetheless, a non-parametric Kruskal-Wallis test also gives a strongly significant larval stage effect (Chi-square = 17.899, df = 3, P = 0.0005) and no significant prey species effect (Chi-square = 0.279, df = 2, p = 0.869). Together the two experiments underscore the considerably greater predatory capacity of SIV lobster compared to the earlier larval stages, and that prey selectivity depends on context of available choices. The two experiments are also instructive because in one combination of prey a single prey taxon *(Calanus)* is preferred by all larval stages, whereas in another combination a clear "favorite" (crab larvae) only becomes apparent at the postlarval stage.

3.2. Predator swimming speed and prey handling behavior

Larvae became increasingly competent swimmers with development, especially at the metamorphosis to the postlarval stage (Table 3; Table S4a). At an average of approximately 120 mm s^{-1}, the SIV swimming speed was more than twenty-fold faster than SI larvae and about nine times greater than SII and SIII larvae. Larval stages II and III swam at about the same speed, which was approximately three times as fast as SI larvae.

The average swimming speeds of the four prey species also differed significantly (Table 3; Table S4b). The two copepods outperformed the larval stages of brine shrimp and barnacles. At an average speed of 9 mm s^{-1} the copepod *Pseudodioptomis* swam about 20 % faster than the other copepod, *Calanus*, but five times as fast as *Artemia* nauplii, and nearly six times as fast as barnacle nauplii.

Comparing swimming speeds of predator and prey in Table 3, makes clear the superiority of SIV lobsters relative to earlier developmental stages with respect to their potential to pursue prey. The swimming speed of SI larvae only exceeded that of brine shrimp and barnacle nauplii, and then by only by a few mm s^{-1}, but were outperformed by the two copepod species. SII and SIII larvae could outswim all four of the prey by up to tens of mm s^{-1}, but the SIV outswam all four prey by more than 100 mm s^{-1}.

As anticipated, prey handling times by larval lobster declined dramatically with advancing development, but also depended on prey type (Fig. 2; Table S5). Handling times for SI larvae ranged from about 6 min for the easy-to-handle *Artemia* nauplii to near 45 min for adult *Calanus*. SIV, by contrast, consumed *Artemia* nauplii in less than a minute and *Calanus* in only a few minutes, on average. Thus, larval developmental stage, prey type and their interaction all had significant effects on larval handling times.

3.3. Functional response

In general, we observed lobster larvae to consume increasing numbers of prey with increasing prey densities in a manner consistent with the Ivlev type II functional response curve (Fig. 3). Table 4 provides the fitted coefficients, adjusted R^2 values and significance of the fitted curves depicted in Fig. 3. Significant p-values indicate that prey density had a statistically significant effect on the ingestion rate within the domain of prey densities in the experiment. The adjusted R^2 shows the proportion of the variability in ingestion rate that is explained by prey density. Functional response curves are plotted for all four larval stages and prey combinations, except for SIII and SIV with the copepod *A. tonsa* and barnacle larvae because of limited prey availability in the field. To interpret these results it is useful to inspect the estimated coefficients in Table 4 alongside the empirical results given in Fig. 3. For instance, while most estimates of I_{max} are consistent with empirical results, in a few cases they were unrealistically high (400–3000 prey hr^{-1}).

The functional response trials show an increase in consumption rate with increasing prey density and that larvae and postlarvae quickly reached their feeding capacity over the range of prey densities offered. In general, larvae and postlarvae appeared to reach their consumption capacity at 2–6 prey hr^{-1} at prey densities above 10–20 prey L^{-1}.

Table 3
Average swimming speeds (±1SE) of lobster larvae and prey species arranged from slow to fast and relative differences. Values in matrix represent the difference between predator and prey swimming speeds (Predator speed - Prey speed). Positive values indicate that the predator's average speed is greater than the prey's, while negative values indicate that the prey's speed is greater than the predator's. See Table S4 for statistical comparison of swimming speeds across larval stages and prey species.

	Prey >	Barnacle nauplii	*Artemia salina*	*Calanus finmarchicus*	*Pseudodiaptomus pelagicus*
	Prey Speed>	1.71± 0.53 (n=7)	5.18± 0.63 (n=5)	7.52± 0.70 (n=4)	9.03± 0.63 (n=7)
Predator	**Predator Speed**				
I	5.61±3.54 (n=34)	3.9	0.43	-1.91	-3.42
II	13.97±4.86 (n=18)	12.26	8.79	6.45	4.94
III	13.82±4.302 (n=23)	12.11	8.64	6.3	4.79
IV	120.77±10.32 (n=4)	119.06	115.59	113.25	111.74

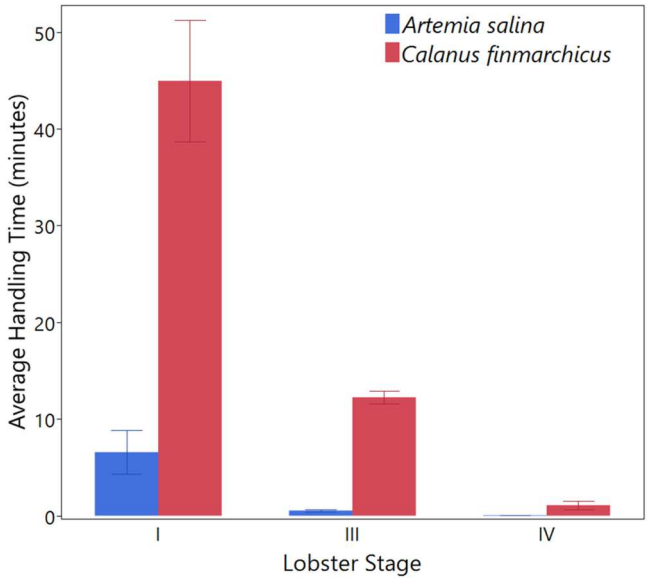

Fig. 2. Average handling times (± SE) of lobster larval stages I, II and IV feeding on *A. salina* (blue) and *C. finmarchicus* (red). See Table S5 for statistical analysis of larval stage and prey effects and their interaction.

However, in a few cases, the lobsters consumed prey at essentially the same rate across all prey densities yielding no significant relationship between consumption rate and prey density.

When we explored even lower prey densities (down to 0.25 prey L^{-1}) with SIV and *C. finmarchicus*, SIV consumption rates were still not limited by prey density. In the following paragraphs we provide a breakdown of our functional response experiment results for each prey species.

The pattern of larval functional responses was clearly not consistent across all prey species. The pattern of functional responses for the brine shrimp, *Artemia*, an intermediate-sized and slow-moving prey, was most consistent with a priori expectations in that SIV exhibited the highest consumption rates of all stages and overall prey densities. At the highest density treatment, 50 prey L^{-1}, consumption rates reached a high of nearly 4 prey hr^{-1} for SIV and a low of about 1 prey hr^{-1} for SIII larvae, with SII and SIII larvae at intermediate levels. The estimated I_{max} for SIV, 8.75 prey hr^{-1}, was three times higher than that for SII and SIII larvae (Table 4). The estimated I_{max} for SI larvae exceeded 3100 prey hr^{-1} and is regarded as unrealistic.

For *Parvocalanus* a small, fast-swimming copepod, SIV consumption rates were surprisingly lower than those for SI and higher than those for SI and SIII. Consumption rates at 50 prey L^{-1} reached a high of about 2 prey hr^{-1} for SIV and SI larvae and about 0.3 prey hr^{-1} for SII and SIII larvae (Fig. 3). Still, the estimated I_{max} for SIV, at 3.75 prey hr^{-1}, was about 50 % higher than that for SI, more than five times as high as that for SII, and nearly seven times as high as that for SIII (Table 4).

For *Euterpina*, a small, slow-swimming copepod, SIV consumption rates were also relatively low compared to those for the three larval stages, especially at the lower densities. Consumption rates at 50 prey L^{-1} reached a high of 3 prey hr^{-1} for SI larvae with the other three stages consuming prey at rates ranging from 1 to 2 prey hr^{-1} (Fig. 3). I_{max} estimates for the larval stages ranged from 0.88 for SIII, 2.12 for SII, and 4.15 for SI. The estimated I_{max} for SIV was unrealistically high at 1544 (Table 4).

For *C. finmarchicus*, a large, slow-moderate speed copepod, SIV consumption rates were nearly level across all densities at about 1.5 prey hr^{-1}, including the extra low-density treatments extending to 0.25 prey L^{-1} also relatively low compared to those for the three larval stages, especially at the lower densities. Similarly, SII consumption rates were nearly level at about 0.5 prey hr^{-1}. The earlier stage larvae, SI and SII, had gradually rising consumption rates and at the prey maximum density of 50 L^{-1} reached a high of about 0.6 prey hr^{-1} (Fig. 3). I_{max} estimates for SIV were consistent with the empirical results, with SIV feeding at 1.44 prey hr^{-1} and earlier stages ranging from 0.44 to 0.9 prey hr^{-1} (Table 4). Extending our evaluation of the functional response to very low densities (0.25–0.5 prey L^{-1}) in large volumes of seawater, we still found no significant change in the rate of prey consumption; nor did we find a significant difference in ingestion rates between laboratory-reared and wild-caught postlarvae (Table S1). Combining these results with the higher density treatments renders a virtually flat functional response across all prey densities, suggesting that even at the lowest densities of 0.25 prey L^{-1}, the ingestion rate of SIV was not

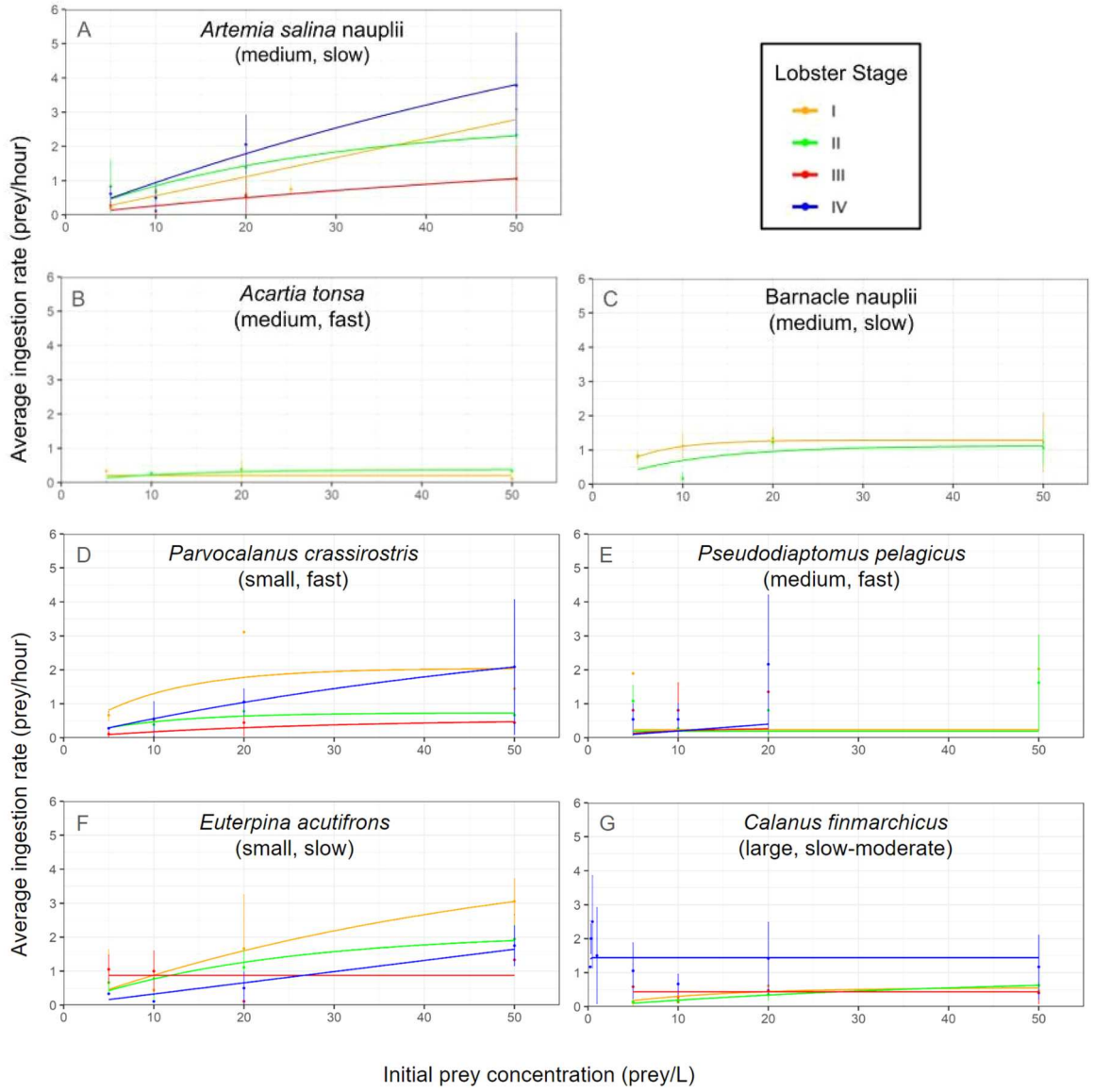

Fig. 3. Functional response curves for SI - SIV lobsters feeding on seven prey species (average ± standard error). Ingestion rates and prey concentrations are expressed as the number of individual prey. Curves are fitted to the Ivlev equation as calculated in SigmaPlot 15.0. Stage III and IV lobsters were not available for trials with *Acartia* or barnacle larvae (n = 3 for each data point).

limited by prey encounter rates (Fig. 3).

For other prey species, for which not all density treatments or larval stages were tested (*A. tonsa, P. pelagicus,* and barnacle larvae), consumption at a max density of 50 prey L^{-1} ranged from approximately 0.3 to 1.3 prey hr^{-1} (Fig. 3). Model estimates of I_{max} were consistent with these findings for larval stages subjected to the full series of density treatments.

When ingestion rates, expressed as numbers of prey (Fig. 4a, b), were adjusted for carbon content (Fig. 4c, d), carbon ingested from *C. finmarchicus* was between one and three orders of magnitude greater than carbon ingested from the other prey species tested despite the numbers of *C. finmarchicus* consumed being consistently low.

Grouping data by larval stage and by prey trait categories provided further insight into the factors affecting predation rates of the developmental stages. Fig. 5 depicts the average ingestion rates for the 93 feeding trials including all four larval stages and the four prey taxa that were run at prey densities at or above 20 prey L^{-1}.

Larval Stage effects: Pooling results from all four prey taxa, we found a significant effect of larval stage on ingestion rates (K-W test: $X^2 = 24.01$, df = 3, $p < 0.0001$), but they did not follow the expected pattern of increasing consumption with advancing development. Rather, ingestion rates of SI and SIV were similar and exceeded those of the intermediate larval stages by a considerable proportion (pairwise t-tests, Table S2a). While SIV generally consumed larger and medium size prey (*Calanus* and *Artemia*) more readily than any of the earlier larval stages, Stage I larvae, by contrast, only exceeded SIV consumption rates with the smaller prey (*Euterpina* and *Parvocalanus*) (Fig. 5, Table S2a).

Prey trait effects: Prey identity, body size and swimming speed also had significant effects on the ingestion rate at higher prey densities (Table S2b). Regardless of larval stage, ingestion rates differed significantly by prey species (K-W test: $X^2 = 16.63$, df = 3, $p < 0.0008$) in a manner generally consistent with expectations. Across all lobster stages, *Artemia*, the medium sized, slow moving prey, were consumed most readily, followed in declining order by *Euterpina*, the small, slow moving prey. *Parvocalanus*, the small faster prey, and *Calanus*, by far the largest prey (Fig. 5; Table S2b).

Parsing prey taxa into size categories, we found a statistically significant prey size effect on the number of prey ingested (K-W test: $X^2 =$

Table 4
Summary of estimated parameters and statistical significance of functional response curves fitted to Ivlev's equation from larval consumption data (Eq. (2)). Cells shaded in green indicate statistically significant p-values ($p < 0.05$) that could be tested empirically, while cells shaded in yellow indicate marginal significance ($p < 0.10$). Equation was fitted using the SigmaPlot statistical software.

Prey	Larval Stage	*Imax*	b	Adj R^2	p (model)
A. tonsa	**I**	0.21	72.99	0	1
	II	0.38	0.089	0.09	0.18
A. salina	**I**	NA	0.0000175	0.80	<0.0001
	II	2.74	0.04	0.36	0.02
	III	2.32	0.01	0.29	1
	IV	8.75	0.01	0.70	0.0004
Barnacle nauplii	**I**	1.51	0.13	0.18	0.08
	II	1.12	0.10	0.07	0.21
C. finmarchicus	**I**	0.56	0.08	0.52	0.01
	II	0.90	0.02	0.69	0.001
	III	0.44	401.10	-0.1	1.0
	IV	1.44	14.02	-0.05	0.87
E. acutifrons	**I**	4.15	0.02	0.48	0.0052
	II	2.12	0.05	0.52	0.0049
	III	0.88	979.61	-0.1	1.0
	IV	NA	0.0000213	0.68	0.0022
P. crassirostris	**I**	2.14	0.10	0.07	0.19
	II	0.73	0.10	0.26	0.05
	III	0.55	0.04	0.32	0.03
	IV	3.72	0.02	0.32	0.03
P. pelagicus	**I**	0.24	10.51	0	1.0
	II	0.19	44.02	0	1.0
	III	0.29	0.12	-0.05	0.47
	IV	NA	4.97E-05	0.22	0.1162

16.11, df = 2, p = 0.0003) consistent with the hypothesis that there is an optimum intermediate size rather than a linear progression of sizes consumed. On average, larvae consumed the intermediate size prey (*Artemia*) about 3 times as fast as the larger prey (*Calanus*) and about twice as fast as the smaller prey (*Euterpina* and *Parvocalanus*) (Fig. 5, Table S2c).

Prey swimming speed also significantly affected larval ingestion rates ($X^2 = 15.13$, df = 2, p = 0.0005). Across all larval stages, on average, larvae consumed slow prey about three times as fast as moderate speed prey, but only about 30 % more quickly than fast prey, perhaps reflecting the fact that the prey with moderate swimming speed in this analysis (*Calanus*) was also the largest prey (Fig. 5, Table S2d).

Finally, we also report a significant effect of prey escape response on larval ingestion rates (t-test: t = 3.00; df = 91; p = 0.0009). Prey, such as the copepods *Calanus* and *Parvocalanus* with a more rapid escape were ingested at a significantly lower rate than those, such as *Artemia* nauplii and the copepod *Euterpina*, with a slower response.

4. Discussion

As is true for many marine species with bi-phasic life cycles, the relatively brief period of the American lobster's planktonic larval development is arguably the most vulnerable, and also the least understood. The recently identified link between the downward trend in young-of-year lobster recruitment in the Gulf of Maine and changes in the zooplankton assemblage has motivated a closer inspection of the mechanics of larval trophic dynamics (Carloni et al., 2018, Shank et al., 2024). Our laboratory experiments reveal ontogenic changes in larval feeding ecology, especially in the transition to the postlarval stage, that shed light on, (1) why benthic young-of-year lobster recruitment in the Gulf of Maine is more strongly correlated with changes in postlarval abundance than early-stage larval or broodstock abundance, and (2) why the foundational copepod, *C. finmarchicus* figures so strongly in those correlations relative to other potential zooplankton prey (Carloni et al., 2018, Shank et al., 2024).

A central component of predator-prey interactions is the functional relationship between prey density and the number of prey consumed. Our experiments showed that regardless of prey type, the ingestion rates of the three larval stages generally increased with prey density, conforming with the standard Ivlev-type II functional response curve over a realistic natural range of prey densities we tested in the laboratory (0.25 – 50 zooplankton L^{-1}). At low prey density, predator ingestion rates are controlled by encounter rates and pursuit time. As prey density increases, ingestion rates are increasingly limited by the predator's

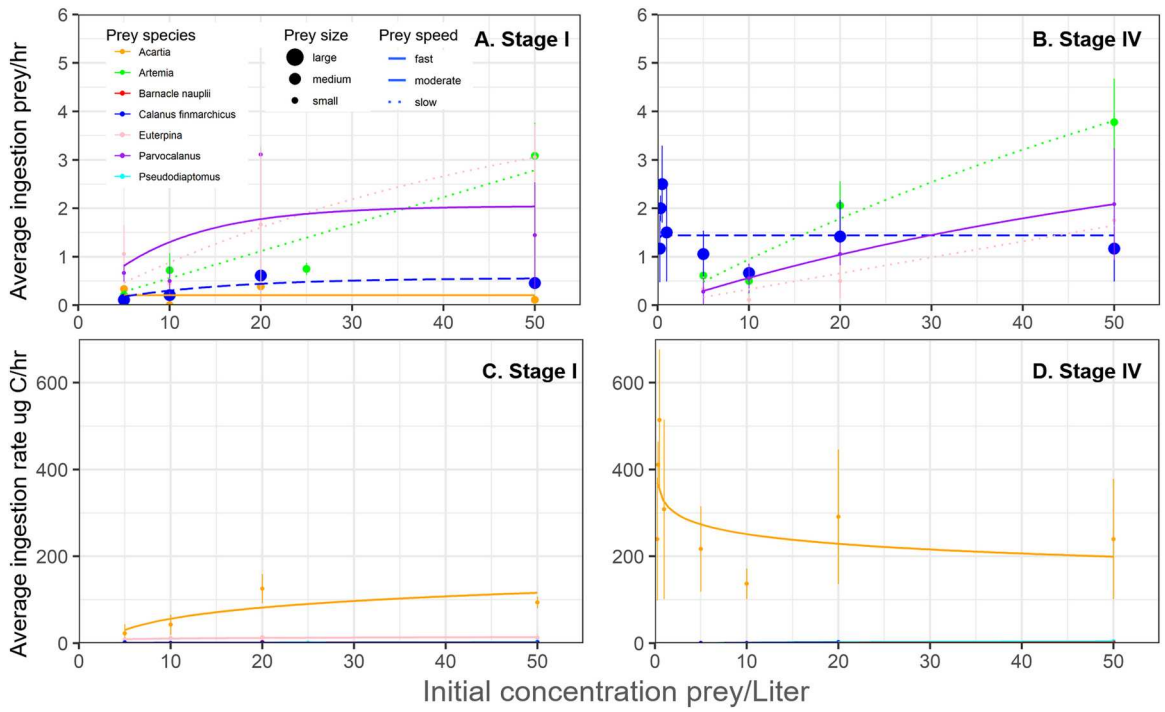

Fig. 4. Functional response curves for SI (A, C) and SIV (B, D) lobsters preying on seven different prey taxa (average ± standard error), expressed as numbers of prey (A, B), and μg Carbon (C, D) ingested hr^{-1}. Curves are fitted to the Ivlev equation and plotted together to highlight differences. See Table 4 for fitted coefficients and statistical significance. See Table 2 for average Carbon weights of individual prey taxa.

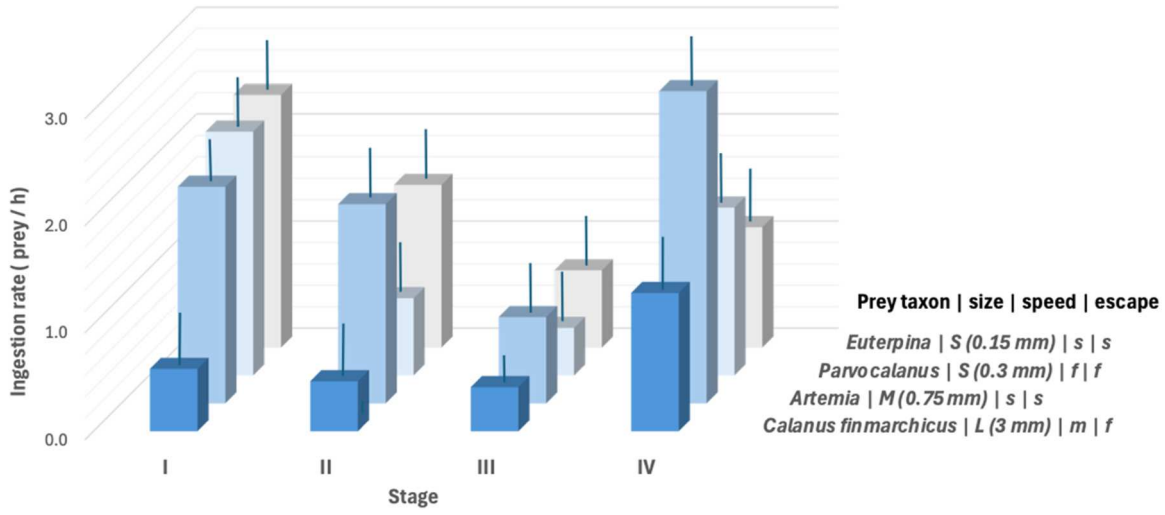

Fig. 5. Average larval lobster ingestion rates by larval stage and prey taxon for the 93 trials with prey densities at or above 20 prey L^{-1} for all stages and all prey taxa. Prey species arranged from large to small from foreground to back. See text and Table S2 for statistical analysis of larval stage and prey trait effects.

capacity to handle and process prey. By using different prey taxa, we were able to interrogate the mechanisms driving ingestion rates of each larval stage. For example, larval lobster ingestion rates on a medium-sized, slow-moving, non-native prey, such as nauplii of the brine shrimp *Artemia* (0.75 mm), increased almost linearly with prey density. In this case, ingestion rates were limited by the encounter rate with prey and the maximum feeding rates were not reached for any of the planktonic stages even at extremely high concentrations. Unlike copepods, *Artemia* exhibit no recognizable escape or avoidance reaction, largely removing prey behavior as a variable in determining ingestion rates. Ingestion rates of *Pseudodiaptomus pelagicus*, a similarly sized copepod with a strong escape response, were significantly lower. Thus, if food items are easy to catch and handle, all the planktonic stages have the capacity to exploit a patch of prey by capturing and ingesting a high number of individuals. If the prey are smaller and slow swimmers (0.15 mm: e.g., the copepod *Euterpina)* the prey are readily ingested by the early-stage larvae and appear to be largely ignored by the postlarvae. This provides evidence that size selectivity of planktonic phase lobsters increases with development as in most invertebrates with planktonic larvae (Takimoto, 2003, Schellekens et al., 2010, Calado and Leal, 2015). However, in some cases the functional response curves were relatively flat over all prey concentrations tested. This was true for postlarval lobsters feeding on *C. finmarchicus*. Even when we expanded the prey concentration to include additional low prey density treatments, the postlarvae were able to find the prey and feed at maximum ingestion rates. We likely were not able to fully capture the descending

limb of the functional response curve for the postlarvae in this instance, and it is possible that they may continue feeding at near maximum ingestion rates at prey densities much lower than what we could practically test in the laboratory. These results suggest that postlarvae may be less vulnerable to a variable planktonic food supply than earlier larval stages due to their ability to sustain high feeding rates even at the lowest prey density tested (0.25 prey L^{-1}). The greater swimming speeds and reduced handling times exhibited by the postlarvae likely contribute to their ability to effectively feed at much lower densities as compared to early stage larvae.

Temporal and spatial patchiness in the availability of zooplankton prey at scales relevant to larval lobster foraging are therefore likely to be consequential to their feeding rates. For context, the average total zooplankton density at our lobster larval sampling stations in coastal Maine was 7.06 (SD ± 3.73) animals L^{-1}, and overall copepod density was 5.03 (SD ± 3.17) animals L^{-1}, the SDs being a telling index of patchiness (unpublished data). *C. finmarchicus* was a relatively small component of the zooplankton assemblage with average densities of 0.03 (SD ± 0.07) animals L^{-1}, representing less than 1 % of the potential zooplankton prey available in these nearshore waters. Similarly, from the 30-year coastal New Hampshire zooplankton time series, Carloni et al. (2018) reported *C. finmarchicus* densities ranging between 0.002 – 0.012 L^{-1} during the larval lobster season. This means that *C. finmarchicus* typically co-exists with lobster larvae at densities approximately ten times lower than our lowest experimental density. At this concentration, at least the early-stage lobster larvae are likely to be limited in their ability to locate *C. finmarchicus* in the field of potential zooplankton prey, whereas postlarvae, appear significantly more capable to locate prey at low densities, and, we argue, much less likely to be food-limited.

Spatial patchiness of planktonic prey is difficult to quantify at scales smaller than a plankton tow (tens to hundreds of meters) because the finer scale variability that may be consequential to larval lobster feeding rates is averaged out in the process of sampling. In the field, zooplankton may form aggregations with densities orders of magnitude higher than the average density estimated from sampling large volumes of seawater with nets (Omori and Hamner, 1982). It is well known, for example, that neustonic lobster postlarvae aggregate in surface convergences and may benefit from the higher food concentrations found there (Pineda et al., 2024). Lobster larvae have been reported to stratify vertically and migrate diurnally, but the relative benefits of feeding and predator avoidance have yet to be resolved (Harding et al., 1987). Our feeding experiments suggest that, unlike the earlier larval stages, the postlarva is far better equipped to exploit prey even at very low prey densities, enabling it to capitalize on the less abundant albeit high-energy prey species, such as *C. finmarchicus,* that represents an especially valuable dietary component.

By virtue of their large body size and energetic content, *C. finmarchicus* may be a more important component of the zooplankton assemblage than their numbers in the field suggest. In terms of biomass, *C. finmarchicus* represents a much larger proportion of the available zooplankton. Our unpublished field data suggest that the average zooplankton biomass of 0.068 (SD ± 0.042) mg L^{-1}. When converted into units of carbon, the density of *C. finmarchicus* becomes 0.0069 mg C L^{-1} – roughly equivalent to 10 % of the total zooplankton biomass we observed. Thus, while planktonic lobster may be less likely to encounter *C. finmarchicus* in the plankton, the few *C. finmarchicus* they do encounter could contribute a significant amount of carbon to their diet. The high caloric content of *C. finmarchicus* is due to its large, conspicuous lipid sac. The caloric content of a single *C. finmarchicus* at 2.3 cal is equivalent to that of 113 *Acartia*, 253 *Artemia*, 41 *Carcinus maenas* zoea, 34 *Temora,* and 11 *Centropages* (Table 2). On a mass-specific basis, *C. finmarchicus* is even slightly more calorically dense than the other taxa tested (*Acartia*, *Temora*, or *Centropages*) and over twice as calorie-dense as zoea larvae of the crab, *Carcinus maenas*. Thus, while a larval lobster may be able to consume a smaller prey species more easily than *Calanus*, the return for the effort is significantly lower. We therefore infer that years of relatively high *C. finmarchicus* abundance could be an energetic windfall for larval lobsters conferring high larval survival.

While our functional response experiments illustrate the impressive ability of lobster postlarvae to pursue and handle prey at low density, we cannot rule out the possibility that laboratory artifacts may have come into play. One example is that the increased volume of the testing tank (300 L) in the low-density trials provided additional space for postlarvae to reach their maximum swimming speeds compared to the smaller 1–4 L containers used in the higher prey density trials. We suspect that postlarvae were able to achieve higher swimming speeds in the larger containers with a proportional increase in prey encounter rates. Additionally, we speculate that the increased metabolic requirements of navigating the larger volume tank may have further motivated higher consumption rates. Similar tank effects under equal prey densities have been observed in other studies (O'Brien, 1988, Dodson et al., 1997, Gorokhova and Hansson, 1997).

Our video-based measurements of larval swimming and prey handling illustrate the quantum leap in feeding performance achieved with the metamorphosis from the lobster's larval to postlarval stage. We infer that the combination of high swimming speeds and short handling times provide postlarvae a remarkable ability to find prey and attain saturated feeding rates even at extremely low prey concentrations. Indeed, the ability to reach maximum feeding capacity at prey concentrations of 0.25 prey L^{-1} reinforces the increased predatory capacity of the postlarvae.

The observed prey handling times can also be used to cross check and constrain the estimated I_{max} parameters, especially in cases where estimates seem unrealistic. For example, by video we observed SI larvae to take 7 min on average to handle and ingest a single *Artemia*. Thus, the maximum SI ingestion rate of *Artemia* nauplii would extrapolate to approximately 9 prey hr^{-1}, assuming no other constraints on ingestion rate. By contrast, from the functional response experiment at maximum prey density (50 prey L^{-1}) we estimated a somewhat lower maximum ingestion rate of 3 prey hr^{-1}, which may be a more realistic maximum reflecting other factors limiting ingestion rate such as gut capacity and evacuation rate. Similarly, from the video records SIV handling times for *Artemia* were only seconds and would translate to unconstrained ingestion rates of approximately 600 prey hr^{-1}- which is very likely to be unrealistic. By contrast, the functional response experiments yield an estimated ingestion rate of only 9 *Artemia* hr^{-1} at a density 50 prey L^{-1}, also suggesting ingestion rate may be limited by gut capacity and evacuation rates. In both instances, handling time observations add valuable context to the functional response curves.

The prey choice experiments show that patterns of selective feeding not only changed with ontogeny, but also with prey type. In the experiment where a single larva was given the choice of *C. finmarchicus* and two other prey species in equal numbers, we found that preference for *C. finmarchicus* was context-dependent: When the choice was between *C. finmarchicus* and two other copepods that co-occur in high abundance with *C. finmarchicus* in our field samples, both larvae and postlarvae selectively consumed *C. finmarchicus*. However, when the choice was between *C. finmarchicus*, and two prey that dominated larval gut contents in a previous study, a crab zoea and the copepod *Centropages* (Juinio et al., 1992), the outcome was stage dependent: stage I larvae selectively consumed the two copepods in equal amounts over the crab zoea, whereas the postlarvae consumed twice as many crab zoea as the two copepods. This supports the functional response data showing that ingestion rates of early-stage larvae were higher on small and slow-moving prey. These prey species are likely easier targets for early-stage lobsters and can be caught and consumed more readily than other larger and faster prey species.

To our knowledge, only two reports are available comparing the composition of larval lobster gut contents to that of the surrounding zooplankton assemblage (Ascher, 2023; Juinio and Cobb, 1992; Ascher et al., 2024). Both indicate the composition of larval gut contents

deviates from the surrounding prey composition, suggesting that larvae feed selectively, although biases caused by differential digestion of prey often cannot be ruled out. This is why complementing microscopy with molecular methods to detect prey in the diet can produce more robust results. Ascher, (2023); Ascher et al. (2024), for example, found that *C. finmarchicus* occurred in a larger proportion of larval lobster guts by qPCR DNA sequencing than were detected by microscopy, and that by both methods, the copepod occurrence in larval guts was disproportionately high compared to field samples of the ambient zooplankton.

The diets of larval lobsters reflect a balance between their ability to find and handle the prey and the ability of the prey to detect and avoid capture (Fields and Yen, 1996, 1997, Visser, 2007). Determining the drivers of selective feeding patterns is complex. Changes in selective feeding during ontogeny provide a framework to examine how developmental changes in the predator modify the types and abundance of prey they consume. Most decapod larval stages possess limited means for locating (Hinton and Corey, 1979) or pursuing foods in the water column (Laverack, 1988) compared to their adult counterparts (Borroni et al., 1986). We found that the pronounced developmental changes in the swimming speeds and feeding behavior of lobster's planktonic stages affect the types of prey available to the lobster (Schweikert et al., 2022). It is likely that the combination of the postlarva's larger size, increased swimming speed and capacity to handle prey, and potentially, greater visual acuity, broadens the suite of prey available and gives it an advantage over earlier stages in pursuing and capturing prey. Ontogenetic shifts in diet are common among planktonic crustaceans (Kurmaly et al., 1990, Pochelon et al., 2009) and reflect the development of the predator's physical and sensory ability. For example, the postlarva's nearly tenfold increase in swimming speed and handling capacity over the larval stages is most likely the result of the additional pleopods and changes in the coordinated use of the capture appendages that allow the later stages to swim faster and respond more quickly to escaping prey. In addition, the eye of *H. americanus* larvae increases in size at each molt through the addition of new ommatidia derived from the growth zone at the margin of the eye (Parker, 1890). The larger eye with the associated increase in sensor density presumably helps to resolve movement in lower light. We speculate that these traits also allow the later developmental stages to feed deeper in the water column or feed for a longer portion of the day (Schweikert et al., 2022).

These findings provide an interesting comparison to a similar study on the prey preferences of phyllosoma larvae of the western rock lobster, *Panulirus cygnus*, which feed preferentially on more abundant chaetognaths compared to salps or nutritionally superior krill, when given a choice of three prey species (Saunders et al., 2012). The difference in ingestion rate was greater than what could be explained by differences in encounter rates and suggested a trade-off between ease of consumption and nutritional value. Consuming krill was significantly more time-consuming due to the effort required to remove the carapace. Similarly, anatomical or behavioral prey traits may contribute to the differences in ingestion rates we observed in our prey choice experiments. *C. finmarchicus*, while more energetically valuable, is much more time-consuming to process, potentially leading lobster larvae to feed more on the less valuable crab zoea and *Centropages,* which are easier to handle. Delving further into the energetic differences between these prey species, we can see that even in trials where *C. finmarchicus* was not the most consumed prey item, it still represented the vast majority of calories consumed.

Our results also underscore how predator and prey traits influence the complexity of larval trophic interactions. Zooplankton communities in the Gulf of Maine have undergone a regime shift since 2010 due to oceanographic shifts related to climate change (Friedland et al., 2021; Pershing and Kemberling, 2023). The decline in the cold-water zooplankton assemblage, particularly *C. finmarchicus*, was found to be strongly correlated with lobster postlarval and young-of-year recruitment in the Gulf of Maine (Carloni et al., 2018, 2024, Shank et al., 2024). Modeling of copepod assemblages in the North Atlantic predicted poleward shifts of 14 major species, as well as earlier seasonal peaks in abundance as ocean temperatures increase (Villarino et al., 2015). In addition, rising temperatures may cause a shift in zooplankton community structure from primarily herbivorous copepod species to carnivorous species (McGinty et al., 2021), as well as a decrease in body size, abundance, and lipid content of large-bodied copepods such as *C. finmarchicus* (Fields et al., 2023). While greater proportions of smaller copepod species may provide *H. americanus* larvae with more easily handled prey items, the reduced return on investment of smaller prey compared to large-bodied copepods may put early larval stages at a disadvantage in fueling their development.

These results are consistent with the hypothesis that lobster year class strength may be limited by planktonic food availability to the early larval stages. By highlighting the dramatic ontogenetic enhancement in the feeding capacity of lobster planktonic stages, our results may provide an explanation for both the decoupling of larval and postlarval lobster abundance in the Gulf of Maine, as well as the strong correlation between *C. finmarchicus* and the abundance of postlarvae and benthic young-of-year lobsters (Carloni et al., 2018; 2024; Shank et al., 2024). The change in food availability coupled with changes in sea surface temperature and rising ocean acidification (Niemisto, 2019; Waller et al., 2017) may be conspiring to drive survivorship of the planktonic stage downward with important implications for future lobster recruitment.

CRediT authorship contribution statement

David Fields: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Richard Wahle:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Molly Spencer:** Investigation. **Rachel Lasley-Rasher:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Evelyn Layland:** Writing – original draft, Supervision, Methodology, Investigation, Formal analysis, Conceptualization. **Emily Patrick:** Investigation.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Evelyn Layland reports financial support was provided by NOAA National Sea Grant Office. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107179.

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