Received: 14 February 2022 | Accepted: 8 January 2023

DOI: 10.1111/1365-2656.13915

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

The costs and trade-offs of optimal foraging in marine fish larvae

Helena Hauss[1,2] | Laura Schwabe[3] | Myron A. Peck[4]

[1]GEOMAR Helmholtz Centre for Ocean Research Kiel, D-24105, Kiel, Düsternbrooker Weg 20, Germany

[2]NORCE Norwegian Research Centre, 4072, Randaberg, Mekjarvik 12, Norway

[3]Helmholtz-Zentrum Hereon, 21502, Geesthacht, Max-Planck-Straße 1, Germany

[4]Department of Coastal Systems (COS), Royal Netherlands Institute for Sea Research (NIOZ), 1790 AB, Den Burg, PO Box 59, Texel, The Netherlands

Correspondence
Helena Hauss
Email: hhauss@geomar.de

Funding information
Bundesministerium für Bildung und Forschung, Grant/Award Number: CO2MESO; German Science Foundation (DFG) AQUASHIFT Program Cluster Project RECONN, Grant/Award Number: # JO556/1-2; EU Horizon Program ACTNOW, Grant/Award Number: 101060072; ICES PICES Working Group on Small Pelagic Fish, Grant/Award Number: WGSPF/WG43

Handling Editor: Henrique Cabral

Abstract

1. In a warming world, both the metabolic rates of ectotherm predators and the phenology of their prey organisms is subject to change. Knowledge on how intrinsic and extrinsic factors govern predator–prey interactions is essential in order to understand how the environment regulates the vital rates of consumers. Controlled experiments, however, simultaneously testing behavioural and growth responses of the larvae of fish and other ectotherm organisms in different feeding regimes are scarce.
2. Prey size (*PS*) selection was determined for young Atlantic herring *Clupea harengus* L. larvae offered 100- to 850-µm copepods *Acartia tonsa* at five different concentrations. In separate, 4- (13°C) or 7-day (7°C) trials, the effect of prey size on larval foraging behaviour, specific growth rate (*SGR*) and biochemical condition (RNA:DNA, *RD*, a proxy for individual instantaneous growth) was tested.
3. Preferred (selected) *PS* was similar at all prey concentrations but increased from 3% to 5% predator length with increasing larval size. At various temperatures, dome-shaped relationships existed between *PS* and larval *RD* (and accordingly *SGR*). Compensatory changes in foraging behaviour (pause and feeding strike frequencies) existed but were not adequate to maintain positive *SGR* when available prey were substantially smaller than those preferred by larvae.
4. A physiology-based model predicted that larvae depended more heavily on optimal prey sizes at the colder versus warmer temperature to grow well and that the profitable prey niche breadth (the range in prey sizes in which growth was positive) increased at warmer temperatures.
5. Seemingly subtle match-mismatch dynamics between ectotherm predators and their preferred prey size can have large, temperature-dependent consequences for rates of growth and likely survival of the predator. To the best knowledge, this was the first study to directly quantify the "costs and trade-offs" of optimal foraging in marine fish larvae.

KEYWORDS
behaviour, growth, match/mismatch, optimal foraging, prey selection, prey size, RNA:DNA

1 | INTRODUCTION

In aquatic and terrestrial systems, rates of growth, survival, and reproductive success of secondary consumers are indelibly linked to spatial and/or temporal variability in the composition and abundance of potential prey items. Optimal foraging theory has been used to explain why changes in environment factors elicit changes in predatory behaviour in a diverse range of fauna (Mangel & Clark, 1986). In order to use prey resources in the most efficient way, many predators have developed behavioural strategies that increase their ability to obtain prey, minimize energy expenditure and/or exploit a diverse array of potential prey items (Carpenter et al., 1983; Schoener, 1971). Optimal foraging theory suggests that, for any predator size, there exists a narrow range in prey sizes that is energetically most profitable (Pyke et al., 1977) and that the selective consumption of these prey sizes is expected to yield optimal (relatively high) growth rates, andhas been widely applied as a framework to describe environmentally-driven changes in predatory behaviour within a broad range of fauna from terrestrial arthropods (Brose et al., 2008) and molluscs (Menge, 1974) to birds (Louzao et al., 2014), and teleosts (Crowder, 1985). However, very few studies have focused on optimal foraging in young fish larvae (Fortier & Harris, 1989).

Marine fish larvae are among the smallest vertebrates on the planet that grow extremely rapidly and advance through tremendously different life stages with physiological as well as behavioural consequences—starting their life as part of the drifting zooplankton, with later developmental stages transitioning to actively swimming nekton (Marshall & Morgan, 2011). Optimal foraging strategies are also likely to change during early life as larvae rapidly develop through ontogenetic stages that have very different swimming and visual capabilities (Blaxter, 1986; Moyano et al., 2016; Peck et al., 2012). Both field (e.g. Cohen & Lough, 1983; Fox et al., 1999; Voss et al., 2003) and laboratory (Checkley, 1982; Munk, 1992) studies have reported that temperate marine fish larvae often selectively feed upon specific species of calanoid copepods. As copepods develop through naupliar and copepodite stages, these animals dramatically increase in body size and swimming ability (Buskey, 1994) and, due to mortality, they decrease in concentration (Sheldon et al., 1972). Thus, larval fish are faced with obvious trade-offs in terms of their prey selection that are conceptually transferable to other communities and trophic interactions. For example, for a specific size predator, relatively large (small) prey items provide more (less) energy gain per prey item but are encountered less (more) frequently and are more difficult (relatively easy) to capture. Predators faced with such trade-offs are expected to select larger prey items only when prey concentrations are high and to exhibit more random feeding at low prey concentrations, mainly driven by the frequency of encounter events with different prey sizes/types (Werner & Mittelbach, 1981).

Many studies have estimated prey selection in larval fish (see Llopiz, 2013) but causal links between prey selection and optimal foraging remain poorly investigated. Despite the strong theoretical background of optimal foraging, to the best knowledge, no previous study has quantified the direct costs and trade-offs (in terms of growth and condition) of marine fish larvae foraging on optimal and sub-optimal prey sizes/types. This is surprising for at least two reasons. First, match-mismatch dynamics between young larval fish and their prey (i.e. the temporal overlap of first-feeding larvae with high abundance of zooplankton, for example following the spring bloom of phytoplankton in temperate and polar latitudes) forms the basis of one of the cornerstone hypotheses of marine fish recruitment (Cushing, 1990) that has fuelled a plethora of studies exploring whether larval fish growth is prey-limited (in terms of prey concentration and/or type) in the field (e.g. Buckley & Durbin, 2006; Cohen & Lough, 1983). Second, individual-based models (IBMs) that have become useful tools to predict the growth and survival of various organismsin their environment (Judson, 1994) often employ optimal foraging subroutines (for larval fish, e.g. Bils et al., 2017; Hufnagl & Peck, 2011; Kristiansen et al., 2007; Kühn et al., 2008). These IBMs appear to lack the controlled laboratory data required to validate estimates of the growth of larvae foraging in different prey fields. In one previous study on a freshwater fish, Mills et al. (1989) reported a dome-shaped relationship between specific growth rate (SGR) and prey size at low prey concentrations that disappeared at higher prey concentrations. Extrapolating those results from freshwater to marine fish species, however, is difficult due to the large differences in the foraging capacity and growth energetics that often exist between the larvae of former and latter groups (Houde, 1994).

The present study assessed prey size selection in the larvae of a marine fish and quantified the impact of different (optimal and sub-optimal) prey sizes on larval foraging behaviour, growth and nutritional condition. Larvae were feeding on natural prey that they encountered at concentrations consistent with field observations. Trials of a prey selection experiment used a wide range of prey sizes and those of a growth experiment were conducted at two temperatures and two larval body sizes to better understand the potentially dynamic costs and trade-offs of optimal foraging. We chose larvae of Atlantic herring *Clupea harengus* as a model predator due to the wealth of previous studies on larval swimming behaviour, prey perception, foraging behaviour and feeding ability (e.g.; Blaxter, 1986; Moyano et al., 2016; Munk & Kiørboe, 1985) and the use of IBMs to characterize the larval herring foraging and growth (Bils et al., 2017; Fiksen & Folkvord, 1999; Hufnagl & Peck, 2011). Moreover, our experiments filled important gaps in knowledge on the foraging and growth of the larvae of a specific population of herring (from the southwest Baltic Sea) that represents an extremely well-worked case study for marine fish recruitment processes in general (Moyano et al., 2023). Our results indicate that there are strong energetic costs associated with foraging on suboptimal prey sizes, even when prey concentrations are high, and that current foraging models lack the data needed to correctly represent how subtle changes in prey characteristics affect growth rates of marine fish larvae.

2 | MATERIALS AND METHODS

2.1 | Cultures

Copepods *Acartia tonsa* were used as prey in all laboratory trials performed in this study as they provide suitable nutrition for larval fish and are an integral part of natural zooplankton assemblages. Continuous copepod cultures were fed *Rhodomonas baltica*, a cryptophyte known to produce copepods of high nutritional value to larval fish. Copepods were maintained in semi-intensive, 300-L batch cultures (Peck & Holste, 2006). Eggs produced by *A. tonsa* were hatched and nauplii and copepodites fed to developing herring larvae. Nauplii of *A. tonsa* were grown to more advanced developmental stages and then collected via a sieve to achieve different prey sizes used in the experiments. Thus, differences in prey size also reflect differences in prey stage and age.

2.2 | Herring rearing

Ten female (mean 179 g wet mass (*WM*) and 25.3 cm standard length (*SL*) and ten male (182 g *WM*, 24.5 cm *SL*)) herring were obtained from Kiel Bight (54°22′N, 010°09′E). The eggs were strip-spawned in single rows onto white polyethylene plates, fertilized and incubated within well aerated 250-L tanks containing 16 (±0.2) psu, 10 (±0.12)°C water at a light regime of 14 h (light):10 h (dark). After hatch, larvae were reared in semi-static (30% water exchange day^{-1}) 100-L tanks (Ø 60 cm) at 17 (±0.5) psu and either 13.2 (±0.4), 10 (±0.4) or 7.2 (±0.3)°C. Tanks were "greened" with *R. baltica* (50,000 cells mL^{-1}) and larvae were fed ad libitum rations of newly-hatched *A. tonsa* nauplii which corresponded to 5 prey mL^{-1} until a larval age of 13 days post hatch (dph) and then 2 prey mL^{-1} of early and late naupliar and copepodite stages. During rearing, larval *SL*- and dry mass (*DM*)-at-age was monitored every 2 to 3 days. The same methods were used to measure individuals at the end of each trial of each experiment. Individual larvae were photographed alive for length measurements using a dissecting scope (Wild Herbrugg M3) with a camera module (Theta System CCD with PVR Plus software), dipped into distilled water and then transferred without water into a 1.5-mL cap vial and frozen at −80°C. Standard lengths were determined using Optimas® software which was calibrated in two dimensions using an object micrometre. The samples were freeze-dried (Christ Alpha 1–4 freeze-drier) at −51°C for 16 h and their mass determined (Sartorius microbalance SC2) to the nearest 0.1 µg. Based on general observations of size-at-age and feeding, the larvae were in good nutritional condition and were growing well prior to experiments. Husbandry and experimental work on larval fish were approved (G 21307/591–40.63) by the Veterinary Affairs Ethical Committee of the Authority for Justice and Consumer Protection, Hamburg.

2.3 | Selectivity experiment

Trials of a food selection experiment were repeatedly conducted using six larvae foraging within one of five different prey concentrations (0.125, 0.25, 0.5, 1.0 and 2.0 prey mL^{-1}). A total of three trials was conducted using larvae with a mean size of 10.0, 13.5 and 15 mm SL. The prey field was normalized to the body size of the larvae by calculating a relative prey size (*RPS*, %):

$$RPS = \frac{PL}{SL} \times 100, \quad (1)$$

where *PL* is prey prosome length (mm) and *SL* is larval standard length (mm). Prey were offered in six *RPS* classes (1%, 2%, 3%, 4%, 5% and 6% larval SL where, i.e. '1' includes all values between 0.5% and 1.5%). *RPS* classes were not offered at equal abundance, rather the abundance of prey decreased with increasing prey size similar to what is observed (on average) in natural marine waters supporting herring (Sheldon et al., 1972). The decrease in total abundance (AB) within increasing prey size according to a power function with slope *b* in $AB = aPL^b$ ranging from 1.5 to 2.7 and an r^2 between 0.77 and 0.89 ($p < 0.05$). Thus, the relative change in abundance of prey within each of the six *RPS* classes reflected the slopes of zooplankton size spectra commonly found in marine ecosystems (e.g. Sheldon et al., 1972).

In each selection trial, five, cylindrical 8-L (Ø 19 cm, height 30 cm) acrylic tanks were randomly positioned within a temperature-controlled room; each was filled with 16 psu filtered (0.2 µm) seawater and stocked with six herring larvae. Light intensity was ~5–10 µmol m^2 s^{-1}. Larvae were deprived of food for 3 hours and then one larva was removed from each tank and checked for gut contents under a dissecting scope. Usually, the gut contents were not entirely evacuated but prey items could never be distinguished. Copepods were added to each tank and gently mixed and larvae were allowed to feed for approximately 3 hr, less time than that required for gut evacuation / defecation of prey (Peck & Daewel, 2007). After this feeding period, larvae were individually caught with a large bore pipette, transferred into a 1.5-mL cap vial and immediately frozen in a chilled aluminium block in order to prevent defecation due to handling stress. Larvae were removed from tanks in a random order, recording the termination times for each tank. During gut content analyses, larval *SL* was determined, guts were emptied using dissecting needles and the *PL* of all ingested copepods was determined using a dissecting scope and computer image analysis.

In order to quantify the selective ingestion of a prey category relative to its abundance in the prey field, Manly's α (Manly, 1974) was calculated:

$$\alpha = \frac{r_i / n_i}{\sum_{i=1}^{k} r_i / n_i}, \quad (2)$$

where α_i is the preference index for prey type *i*, r_i is the proportion of prey type *i* in the diet ($i = 1, 2, 3, \ldots, k$), n_i is the proportion of prey type *i* in the environment, and *k* is the total number of prey categories. The α values range from 0 (complete avoidance) to 1 (exclusive preference).

Therefore α-values larger than a value of 1.0 divided by the number of available categories (i.e. ~0.17 for six prey types) indicate positive selection of a particular prey category while smaller values indicate negative selection (avoidance).

2.4 | Growth experiment

Four, short-term growth trials were conducted at two different temperatures (7 and 13°C) and two body sizes of herring larvae (~10 mm and 15 mm initial *SL*). All trials were conducted within temperature-controlled rooms for approximately 50 degree-days using a 14:10 hr L:D light regime. In each trial, a total of eleven, 16-L cylindrical (Ø 35 cm) plastic tanks was used: groups of larvae were either unfed (two tanks) or provided "small", "medium" or "large" copepod (*A. tonsa*) size fractions (three tanks at each prey size). The range of mean prosome lengths of prey items was 130 to 170 µm, 190 to 330 µm and 385 to 560 µm for "small", "medium" and "large", respectively, and these were obtained from subsequently hatched cohorts of copepods that were additionally screened through progressively smaller sieves (150, 90 and 37 µm). The variability in prey sizes within each treatment generally increased with mean prey size. Herring larvae ($n = 15–17$) were randomly loaded into tanks and into an initial group (n = 15). All tanks were gently aerated and "greened" with *Rhodomonas* to ~50,000 cells mL^{-1}. Within each trial for each prey size, ad libitum prey concentrations were provided (1 to 2 prey items ml^{-1}, re-feeding the same, previously size-fractionated copepods once at mid-trial if necessary). One tank at each of the three prey size treatments was clear allowing behavioural observations to be made. The next day and for every day afterward, observations of swimming behaviour were made which resulting in four and seven observation days at 13 and 7°C, respectively. Measurements included pause frequency (*PF*, no. s^{-1}), feeding strike frequency (*FSF*, no. min^{-1}) and pause duration (*PD*, s), which were recorded during 3 min of observations of a free-swimming larva. If a larva made contact with the tank wall or the water surface, the measurement was stopped and another larva was selected. This was repeated five times, and we attempted to choose different individuals each time. All measurements were carried out by the same observer, making them internally consistent.

At the end of each trial, copepods remaining in tanks were counted and mean *PL* was determined based on measurements made on a subsample. Dead and alive herring larvae were identified (heartbeat), counted and the *SL* measured. All living larvae were then immediately frozen at −80°C. Some weeks later, each frozen larva (from experimental tanks and initial sample) was freeze-dried, and its *DM* and biochemical condition (RNA–DNA ratio, *RD*) was measured. Concentrations of RNA and DNA were determined fluorometrically using the protocol described in Malzahn et al. (2007), using ethidium bromide as a fluorophore and digesting RNA with Ribonuclease A (bovine pancreas, Serva 34388). Nucleic acid standards were Bacteriophage λ-DNA (Roche 745782) and Ribosomal 16s, 23s RNA (*E.coli*, Roche 206936). To ensure consistency over time, two control homogenates from a pooled stock were measured within each 96-well microplate. *RD* values were standardized according to a published laboratory inter-calibration (Caldarone et al., 2006).

Specific growth rates *SGR* for dry mass (% *DM* day^{-1}) of larvae were calculated as.

$$SGR = \left(e^{Gi} - 1\right) \times 100, \quad (3)$$

where instantaneous growth rate was:

$$G_{iW} = \frac{In\ DM_{final} - In\ DM_{initial}}{t_{final} - t_{initial}}. \quad (4)$$

2.5 | Statistical analysis

Final values of the variables measured in the growth experiments were compared within a trial using one-way analysis of variance (ANOVA). In order to fulfil the assumptions required, residuals were tested for normality using Shapiro–Wilk *W* test and log-transformed if required. The homogeneity of variance was assessed using Levene's test. Tukey's HSD was used for post-hoc comparison. The swimming behaviour data were explored by assigning sampling times of approximately equal degree-day intervals (i.e. every day for trials at 13°C and every 2 days (days 2, 4 and 6) at 7°C trials). These days were considered replicates and analysed by a multivariate analysis of variance (MANOVA) with *PF*, *PD* and *FSF* as dependent variables and larval size, prey size and temperature as factors. Multiple linear regressions were used to explore the relationship between larval growth rate, *RD* and temperature. Dome-shaped relationships (3-parameter Gaussian) were explored between relative prey size as independent variable and selectivity as well as RNA–DNA ratio as a growth proxy as response variable, so that the location of the optimum is the optimal prey size PL_{MAX}. All statistical tests were considered significant at the $p < 0.05$ level. Calculations and plots were performed in R (4.1.0) and Sigmaplot 12.

2.6 | Modelling larval herring foraging and growth

To further explore the relationship between larval growth, prey size, and temperature, a *DM*-based, balanced bioenergetics budget was parameterized based upon metabolic and behavioural measurements made in this and previous studies (Table 1). Specific growth rate (*SGR*, in units *DM*) were calculated for each time step (day) using a balanced energy budget:

$$SGR = \boldsymbol{C\beta(1 - SDA) - R}, \quad (5)$$

where growth (*SGR*) is a function of consumed prey (*C*), assimilation efficiency of food (β), costs due to digestion and protein synthesis (specific dynamic action, *SDA*) and total respiration (*R*). For the range of temperatures between those investigated (7 to 13°C), we assumed an exponential relationship between feeding strike frequency and temperature, and a temperature coefficient Q_{10} of 2.2. The estimated feeding strike frequency was based on daily observations of larvae reared on a mixed prey spectrum ($FSF = 0.0038 * e^{0.2204 * T}$) and corrected for temporal variability in feeding. Initial *DM* and *SL* of larvae used in the budget were 150 µg and 10 mm, respectively. Prey length varied between 100 and 800 µm (i.e. from newly-hatched nauplii to adults of *A. tonsa*). For details on the bioenergetic parameterizations, see Hauss and Peck (2009).

TABLE 1 Parameterisations used to predict larval herring growth at different prey sizes and temperatures.

Parameter	Abbreviation	Unit	Equation
[1] feeding strike frequency	FSF	min^{-1}	$FSF = 0.07 * T - 0.35$
[2] prey capture success	CS	dimensionless	$CS = 1.1 - 13.6 * \frac{PL_{prey}}{SL_{predator}}$
[3] *Acartia tonsa* prosome length *PL* (mm) to dry weight conversion	DW	µg	$DW = 7.95 * 10^{-9} * PL^{3.31}$
[4] assimilation efficiency	β	dimensionless	$\beta = 0.7 * \left(1.0 - 0.3 * e^{(-0.003 * DW - DW_{MIN})}\right)$
[5] specific dynamic action	SDA	dimensionless	$SDA = 0.11 + 491 * 10^{-7} * DW$
[6] standard respiration	R_S	µl O_2 * h^{-1}	$R_S = 4.35 * DW^{0.82} * Q_{10}\left(\frac{(T-8)}{10}\right)$
[7] active respiration	R_A	µl O_2 * h^{-1}	$R_A = k * R_S$
[8] activity multiplier	k	dimensionless	$k = 1.9 + 0.0076 * DW_i$
[9] oxycaloric conversion		dimensionless	$0.00463 * cal * \mu l\ O_2^{-1}$
[10] calorie to larval *DW* conversion		dimensionless	$227.0 \mu g\ DW * cal^{-1}$

Note: References: [1] Peck et al. unpubl.; [2] Munk (1992); [3] Berggreen et al. (1988); [4] Buckley & Dillmann (1982); [5] Hermann & Peck unpubl.; [6] Kiørboe et al. (1987) and Peck and Daewel (2007); [8] Beyer & Laurence (1980); [9] Brett & Groves (1979); [10] Theilacker & Kimball (1984).

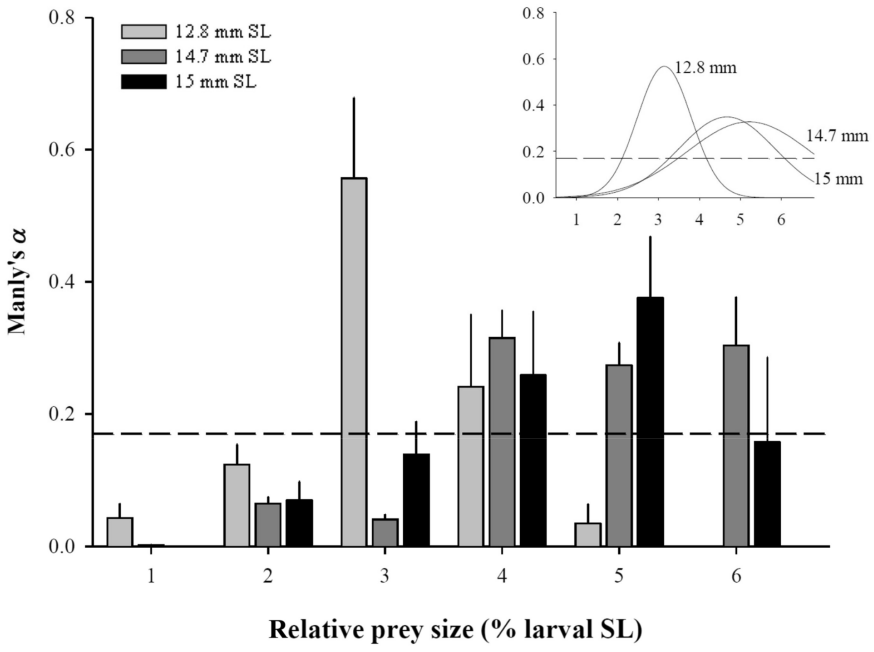

FIGURE 1 Pooled selectivity index (Manly's α) for the relative prey size classes (% larval *SL*) determined in three trials. Mean (±SE) values are shown for five prey densities Insert depicts regressions that were fitted to individual values. Dashed line indicates *k*-level (neutral selectivity at six prey categories).

3 | RESULTS

3.1 | Selectivity experiment

In all trials, intermediate size classes (3%, 4%, and 5% size bins) were positively selected while the smallest and largest prey items were avoided (Figure 1). No significant differences in prey selection were observed among the five prey concentrations. Non-linear regression analysis of these data pooled across all prey concentrations suggested that the *RPS* most frequently selected increased with increasing larval size. The most frequently selected *RPS* was 3.1 (±0.1), 5.2 (±0.3) and 4.7 (±0.3) % in 12.8, 14.7 and 15 mm *SL* larvae, respectively (Table 2). Furthermore, the range in *RPS* positively selected ($\alpha > 0.17$) by larvae increased from 2.1 (±0.5)% in the smaller larvae to 2.9 (±1.3) and 3.6 (±1.1)%, respectively, in the larger ones (Table 2).

3.2 | Growth experiment

Larval foraging behaviour during the growth experiments was significantly different in the different prey size treatments as well as with larval *SL* and/or age (Table 3). Pause duration was generally lower and both pause frequency and feeding strike frequency higher in older/larger compared to younger/smaller larvae (Tukey's HSD, $p < 0.001$). The longest pause durations were recorded for younger/smaller larvae in the "small" prey treatment. Generally, feeding

TABLE 2 Prey consumption (no. mL^{-1}) and selectivity (Manly's α) for groups of herring larvae offered a full range of relative prey sizes (*RPS*, % larval *SL*) of a copepod (*Acartia tonsa*) at five different concentrations.

	Larval herring group		
Standard length (mm)	12.8 (±1.4)	14.7 (±1.8)	15 (±1.7)
Prey concentration (no. mL^{-1})		Prey consumption rate (no. h^{-1})	
0.125	1.07	2.0 (±0.1)	1.54
0.25	2.26	3.9 (±0.1)	0.77
0.50	2.09	4.8 (±1.7)	1.86
1.0	1.54	5.0 (±0.7)	1.14
2.0	1.47	6.3 (±1.3)	0.78
Prey selection	$Manly's\ \alpha = a^{*}e^{-0.5*\left[\frac{(RPS-RPS_0)}{b}\right]^2}$		
	Parameter estimates (±SE)		
a	0.57 (±0.08)	0.33 (±0.04)	0.35 (±0.08)
b	0.66 (±0.11)	1.51 (±0.35)	1.17 (±0.36)
RPS_0 (optimal prey size, % larval *SL*)	3.14 (±0.14)	5.21 (±0.33)	4.67 (±0.32)
prey size range in positive selection	2.11 (±0.47)	3.62 (±1.13)	2.93 (±1.32)
n	30	30	30
r^2adj	0.52	0.55	0.23
p-value	<0.0001	<0.0001	0.0151

TABLE 3 Summary information for foraging-growth trials conducted on larval Atlantic herring (*Clupea harengus*). Temperature (*T*), duration, prey sizes, larval ages and tank mean values (±SD) for somatic (standard length *SL* [mm], dry mass *DM* [µg], biochemical condition [RNA–DNA ratio, *RD*]) measures and behaviour (pause frequency *PF* (s^{-1}), pause duration *PD* (s), feeding strike frequency *FSF* (min^{-1})). Letters denote significant differences among prey size treatments. "n.d." indicates not determined.

Trial				Treatment group				Atlantic herring larvae					
						Prey length					Swimming activity		
ID	T (°C)	Duration (d)	Age (dph)			Initial (µm)	Final (µm)	*SL* (mm)	*DM* (µg)	*RD* (µg µg^{-1})	*PF* (s^{-1})	*PD* (s)	*FSF* (min^{-1})
			25	Initial	(at loading)			10.4 (±0.9)	131.4 (±49.1)	2.4 (±0.46)			
1	13	4		Final	"no prey"	–	–	8.1 (±1.8)^{a}	n.d.	n.d.	–	–	–
			29		"small"	163	134	9.6 (±0.4)^{b}	n.d.	n.d.	0.14 (±0.01)	2.97 (±0.21)	0.07 (±0.07)
					"medium"	270	307	10.5 (±0.6)^{b}	n.d.	n.d.	0.16 (±0.04)	1.48 (±0.65)	1.00 (±0.54)
					"large"	384	387	10.6 (±0.3)^{b}	n.d.	n.d.	0.23 (±0.03)	1.15 (±0.28)	0.39 (±0.18)
			31	Initial	(at loading)			10.3 (±0.6)	n.d.	n.d.			
2	7	7		Final	"no prey"	–	–	9.0 (±0.6)^{a}	104.6 (±0.3)^{a}	1.2 (±0.1)^{a}	–	–	–
			38		"small"	132	139	9.8 (±0.5)^{ab}	143.8 (±5.1)^{ab}	1.8 (±0.2)^{b}	0.19 (±0.05)	2.06 (±0.55)	0.25 (±0.23)
					"medium"	201	227	10.7 (±0.2)^{b}	225.3 (±22.8)^{c}	3.1 (±0.3)^{c}	0.26 (±0.05)	1.32 (±0.18)	0.54 (±0.24)
					"large"	399	467	10.4 (±0.4)^{b}	183 (±13.6)^{b}	2.0 (±0.2)^{bc}	0.17 (±0.04)	1.86 (±0.65)	0.26 (±0.11)
			39	Initial	(at loading)			13.6 (±0.9)	399.9 (±88.5)	2.6 (±0.42)			
3	13	4		Final	"no prey"	–	–	13.6 (±0.2)^{a}	427.7 (±49.4)^{a}	1.7 (±0.1)^{a}	–	–	–
			43		"small"	n.d.	169	14.0 (±0.1)^{a}	538.0 (±33.7)^{ab}	2.3 (±0.3)^{ab}	0.23 (±0.05)	0.64 (±0.07)	5.50 (±3.27)
					"medium"	n.d.	332	14.5 (±0.5)^{a}	47.5 (±126.7)^{bc}	2.9 (±0.3)^{bc}	0.28 (±0.05)	0.86 (±0.06)	1.67 (±0.53)
					"large"	n.d.	561	14.7 (±0.3)^{a}	781.7 (±70.1)^{c}	3.5 (±0.3)^{c}	0.43 (±0.05)	0.77 (±0.1)	1.20 (±0.38)
			49	Initial	(at loading)			15.4 (±1.2)	479.9 (±189.0)	2.9 (±0.4)			
4	7	7		Final	"no prey"	–	–	13.3 (±0.4)^{a}	355.0 (±46.4)^{a}	1.8 (±0.2)^{a}	–	–	–
			56		"small"	120	140	14.7 (±0.4)^{b}	437.6 (±67.8)^{a}	1.9 (±0.2)^{a}	0.19 (±0.01)	1.02 (±0.18)	0.41 (±0.23)
					"medium"	189	194	14.7 (±0.4)^{bc}	485.8 (±82.0)^{a}	2.7 (±0.5)^{b}	0.22 (±0.02)	0.77 (±0.03)	1.91 (±0.3)
					"large"	358	413	15.9 (±0.5)^{c}	731.5 (±105.3)^{b}	3.4 (±0.1)^{b}	0.32 (±0.02)	0.87 (±0.1)	0.5 (±0.09)

strikes occurred two times more frequently at 13°C compared to 7°C (no significant difference due to high variance). Pause frequency increased significantly with prey size and tended to be inversely related to pause duration. The mean (±SE) feeding strike frequency (*FSF*) was between 0.25 (±0.23) and 5.5 (±3.7) min^{-1} (Table 3). The highest values of FSF were recorded in the 13°C trial with larger/older larvae, especially at small prey size.

Specific growth rates (% day^{-1}) in length (SGR_{SL}) determined from tank mean values increased in a linear manner with increasing RNA–DNA ratio (*RD*) (Figure 2a). SGR_{SL} at a given *RD* was generally higher at the warmer temperature (*T*) and the relationship between these variables was best described as:

$$SGR_{SL} = 1.21(\pm 0.04) * RD + 0.25(\pm 0.15) * T - 5.29(\pm 0.49), \quad (6)$$

where mean (±SE) parameter estimates are provided ($n = 33$, $r^2\text{adj} = 0.79$, $p < 0.0001$). For dry mass-specific growth rate (SGR_{DM}), a linear increase with *RD* was also observed (Figure 2b) but the slope of the increase was steeper at the warmer temperature (an interaction existed between *T* and *RD*):

$$SGR_{DM} = 1.13(\pm 0.89) * RD + 0.62(\pm 0.06) * RD^{*}T - 13.9(\pm 1.7), \quad (7)$$

where mean (±SE) parameter estimates are provided ($n = 33$, $r^2\text{adj} = 0.89$, $p < 0.0001$). These functions could thus be used to calculate growth rates (in *SL* and *DW*) of individual larvae. Larval herring survival was generally high and ranged from 69% to 96% for fed groups and between 30% and 90% for food-deprived larvae in the control tanks. Initial and final larval *SL*, *DM*, and *RD* are summarized in Table 3. In the first 13°C experiment, *DM*, *RD* and CF could not be determined due to an equipment failure, but larval *SL* was similar to the 7°C trial with younger/smaller larvae. In the two other trials, the initial size of larvae in the 7°C trial was larger than that in the 13°C trial. Larval deprived of food (in control tanks) decreased in mean *SL* by 2.7% day^{-1}. In general, the optimum relative prey size (for growth) was in the "intermediate" size treatment for younger/smaller larvae and "large" size treatment for older/larger larvae.

In each trial, the effect of *RPS* on larval biochemical condition (*RD*) was dome-shaped (Gaussian regressions, $r^2 = 0.68$ to 0.73, $p < 0.05$) and *RD* was highest at a *RPS* of 2.9 (±0.06) and 3.5 (±0.44)% in small and large larvae, respectively, and the width of the Gaussian function increased with increasing larval size (Figure 3), although there were no observations at an RPS > 4 at 13°C and the extrapolation of the curve to higher RPSs is uncertain. Given the interaction between *T* and *RD* in terms of larval growth rate, an even wider spectrum of profitable (positive growth) prey sizes was found at 13°C compared to 7°C. We explored this empirical finding using a bioenergetic model (see below; Table 4).

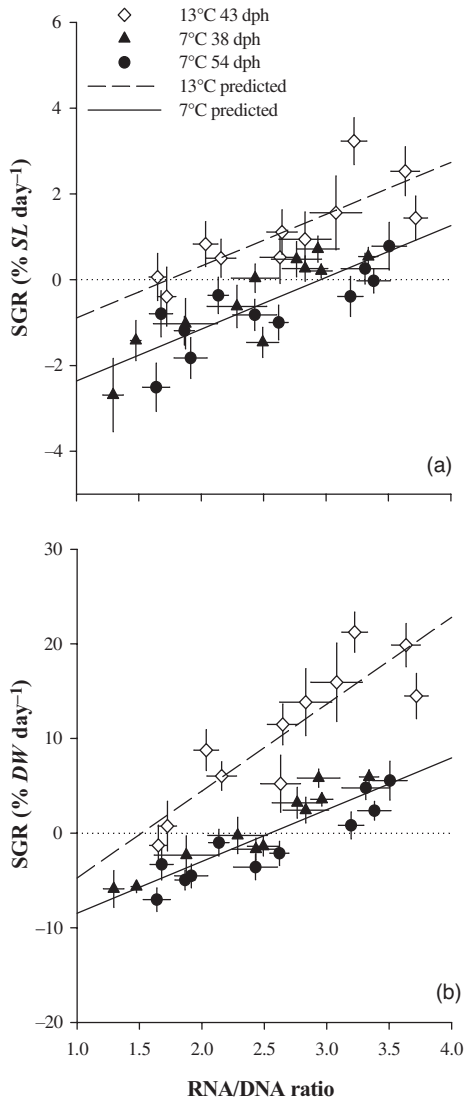

FIGURE 2 Specific growth rate SGR (% day^{-1}) in standard length *SL* (panel a) and dry weight DW (panel b) in relation to RNA–DNA ratio at two temperatures in three growth trials. Data from the two 7°C experiments were combined to fit regression. Values are tank mean (±SE) values, lines denote predictions from multiple linear regressions. Dotted line indicates zero growth. Regression equations are Panel a: $SGR_{SL} = 1.2\ (\pm 0.04)^{*}RD + 0.25\ (\pm 0.15)^{*}T - 5.29\ (\pm 0.49)$ and Panel b: $SGR_{DM} = 1.13\ (\pm 0.89)^{*}RD + 0.62\ (\pm 0.06)^{*}RD^{*}T - 13.9\ (\pm 1.7)$.

3.3 | Modelling growth of larval herring

Current parameterizations of behaviour and metabolism in larval herring result in an interaction between temperature and prey size on larval growth rate (Figure 4). The slope of the linear increase in growth rate with temperature was steepest at the optimum prey size. At the same time, larvae lost *DM* most rapidly at the warmest temperature when encountering prey of suboptimal size. When feeding on the "optimal" prey size, larvae were predicted to have a SGR_{DM} of 13.8% day^{-1} at 13°C. Likewise, *DM* loss was more rapid (−9.5% *DM* day^{-1}) for larvae foraging on the smallest prey size at the warmest temperature. A foraging model incorporating prey

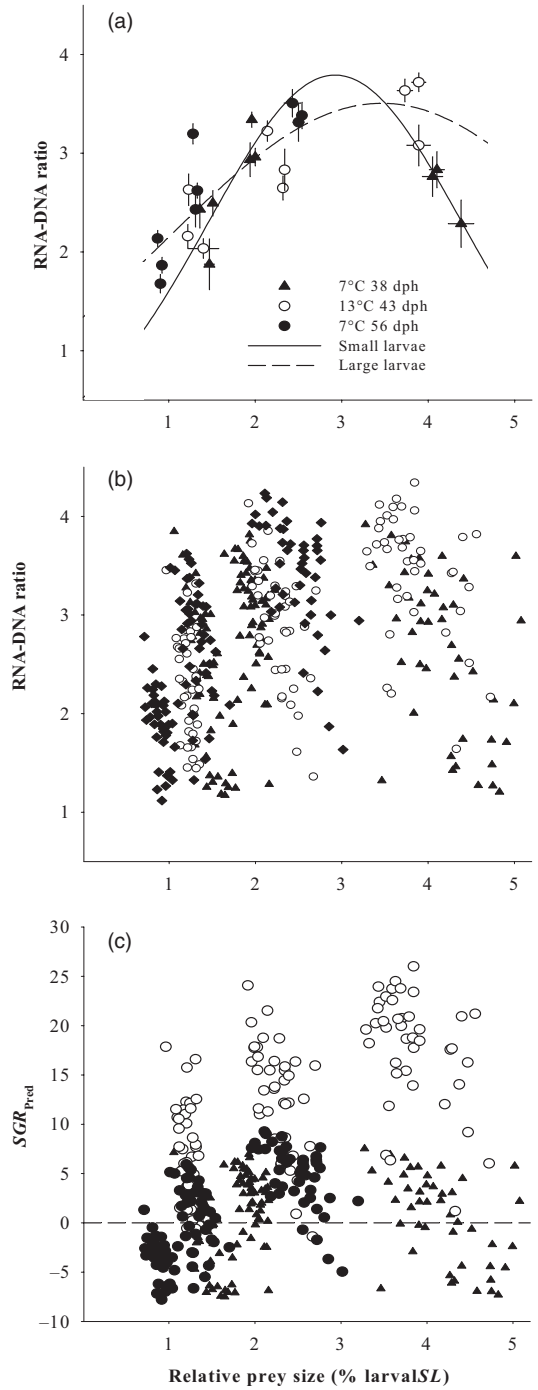

FIGURE 3 Biochemical condition (RNA–DNA ratio, panels a and b) and specific growth rate (SGR, panel c) versus relative prey length (% larval standard length SL). Values are tank means (±SE) on panel (a and b) and individual values on panel (c). Gaussian 3-parameter regressions are fitted for younger larvae (38 dph, 7°C, filled triangles $PL_{MAX}=2.9$ (±0.06), r^2adj = 0.73, $p<0.001$) and for older larvae, which were combined from two trials (43 dph, 13°C, open circles and 56 dph, 7°C, filled circles; $PL_{MAX}=3.5$ (±0.44), r^2adj = 0.68, $p<0.001$). Individual specific growth rates were calculated from RNA–DNA ratios using the regression given in Figure 2 panel b.

handling time, capture success and encounter rate estimates that the optimal prey size was 6% of the length of herring. The model results indicate that the range in prey sizes supporting a positive rate of growth is narrower at the colder temperature (note zero growth surface in Figure 4).

TABLE 4 MANOVA results for feeding behaviour. Behavioural response variables (*PD*, *PF* and *FSF*, see Table 3 for values) were used as dependent variables in the model, while the experimental variables prey size ("Prey", three levels: small, medium, large), temperature ("T", two levels: 7 and 13°C) and larval age ("Age", two levels) were entered as factors.

Factor	Wilk's λ	*df*	*p*-value
Prey	0.195	6	<0.001
T	0.673	3	0.044
Age	0.102	3	<0.001
Prey×T	0.608	6	0.108
Prey×Age	0.328	6	<0.001
T×Age	0.619	3	0.02
Prey×T×Age	0.394	6	0.003

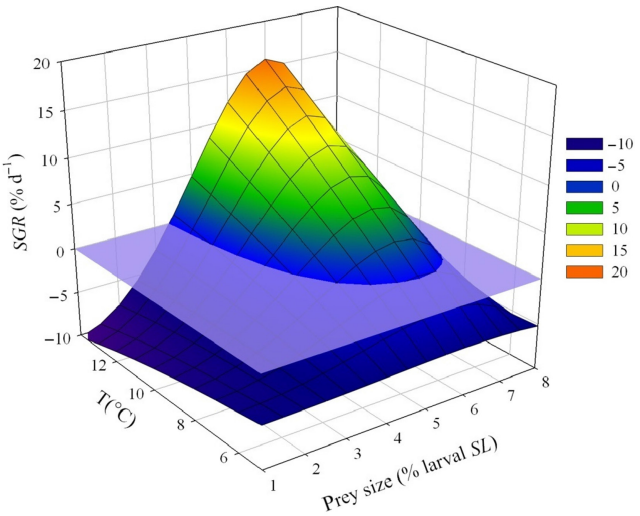

FIGURE 4 Modelled specific growth rate SGR (% day^{-1}) as a function of relative prey size (% larval standard length *SL*) and temperature (°C). Bioenergetic calculations are based on larval clupeid individual-based model (IBM) parameterisations for larval herring with a dry mass *DM* = 150 µg. Temperature-dependent feeding strike frequency is based on unpublished laboratory observations. Light blue plane represents zero growth.

4 | DISCUSSION

Rates of growth and mortality are negatively correlated during the larval period of marine fishes and mortality rates rapidly decline with increasing body size (Houde & Zastrow, 1993), thus, the ability to optimally forage and grow rapidly are expected to be of paramount importance for early life stage survival. The presence of suitable prey is considered to be a fundamental factor affecting the recruitment, or entry of immature individuals to the adult stage, as discussed in the "match-mismatch hypothesis" by Cushing (1990) and a plethora

of studies have examined prey selection by larvae in the wild (e.g. Heath & Lough, 2007; Voss et al., 2003). Thus, it is surprising that no previous studies have attempted to quantify the costs and trade-offs of feeding on prey of different size or preferred versus avoided sizes. Furthermore, optimal foraging subroutines are included in physiological-based, biophysical growth models constructed for clupeid larvae (Bils et al., 2017; Hufnagl & Peck, 2011; Kristiansen et al., 2007; Kühn et al., 2008) and those models currently lack the empirical data necessary to test their predictions. Moreover, the effects of potential interactions between prey field characteristics and other extrinsic factors such as temperature on larval growth and condition remain poorly understood (Buckley & Durbin, 2006; Llopiz et al., 2014). The present study quantified the preferred prey size of herring larvae and explored how foraging on different prey sizes affected somatic, biochemical-based, and bioenergetics-based (modelled) growth for larvae at different sizes at different temperatures.

4.1 | Preferred prey size of larval herring

Several field (e.g. Cohen & Lough, 1983; Fox et al., 1999; Voss et al., 2003) and laboratory (Checkley, 1982) studies have demonstrated that herring larvae select prey according to their type and/or size. Our laboratory trials indicated that herring larvae selected the same size of prey items over a range of prey concentrations where larvae were able to maintain relatively constant feeding strike frequencies/attack rates (MacKenzie & Kiørboe, 1995; Munk & Kiørboe, 1985). It is difficult to estimate the prey concentrations experienced by larval fish in the wild due to physical and biological processes that tend to aggregate prey at micro-(0.1–10 m) scales. For example, our prey concentrations are higher than "average" concentrations obtained using traditional nets that sample larger (100 s of m) areas (e.g. Hansen et al., 2006) but are well within the range of those obtained in situ from small-scale video imaging gear (Davis et al., 1992). Nonetheless, larval foraging may be different at lower prey concentrations or may depend upon feeding history, scenarios that were not tested in this study. Unfortunately, when offered at lower concentration, the ingestion of rare food items considerably alters the prey field composition coexisting with larvae in static laboratory tanks. Moreover, prey growth would complicate the analysis of size selection by larvae if trials were conducted over longer periods of time (days). For this and other reasons (e.g. rapid digestion rates of larvae) estimating prey selection at low prey concentrations and over longer periods of time is very challenging in marine fish larvae.

In the present study, the (relative) prey size preferred by herring larvae increased from 3% larval SL in small larvae to 4% to 5% in larger larvae. For the size of the larger larvae used in the present study, a size of 3% yielded optimal prey clearance rates in the laboratory and was most preferred by 13.5- to 45-mm herring sampled from North Sea (Munk, 1992). Some studies suggest that the relative width of the spectrum of sizes of consumed prey remains constant as larval fish increase in body length (Munk & Nielsen, 1994; Pearre, 1986) which agrees with general relationships found across taxa / habitats (Brose et al., 2008). However, this was not the case in the present study where the mean prey size that was positively selected slightly increased with larval length. In the larvae of European sprat *Sprattus sprattus*, Dickmann et al. (2007) reported that the trophic niche breadth increased markedly as larvae increased in body size from newly hatched (6 mm SL) to pre-schooling, competent foragers (16 mm SL) but remained relatively unchanged at larger body sizes. A data compilation of diet studies performed on sprat larvae indicated that the range of prey–predator size ratios (25th to 75th percentile) were 2.5% to 3.4%, 3.3% to 4.7% and 3.0% to 3.8% for 10-, 15 and 18-mm larvae, respectively (Peck et al., 2012, see their Figure 4). Prey–predator length ratios of ~2% to 3% and 1.5% to 2.6% can be calculated for 6- and 18-mm European sardine *Sardina pilchardus* larvae provided a mixture of nauplii and copepodites of *Acartia grani* in laboratory feeding trials (Caldeira et al., 2014, see their fig. 9). Based on this brief review of foraging results for the larvae of three clupeid species inhabiting European waters, it appears that generalities should not be drawn concerning the effect of body size on prey size selection during early larval life.

4.2 | Larval foraging versus prey field characteristics

Adaptive changes in behaviour allow zooplanktivorous fish to maintain consistent feeding rates across seemingly broad ranges in prey concentrations (Durbin & Durbin, 1975). Work on herring larvae has also demonstrated maintenance of relatively constant feeding strike frequencies/attack rates across different prey concentrations (MacKenzie & Kiørboe, 1995; Munk & Kiørboe, 1985). The results of the present study indicate that herring larvae foraging at different prey concentrations exhibit no compensatory changes in terms of prey size selection.

In the present study, the swimming behaviour of larvae was influenced by both larval ontogeny and prey size, with a pronounced increase in pause frequency with larval age and a decrease in pause duration, which results in older larvae spending a larger amount of time swimming (searching). Also, in the larger larvae, the prey size affected pause frequency (increasing with prey size from less than 0.2 to ~0.4 s^{-1}) more than pause duration (~1 s across all treatments), while the variability in pause frequency in the younger larvae was less distinct, and pause duration varied between 1 and 3 s. Feeding strike frequency also increased with larval age, and differed among treatments which may be due to prey perception, as swimming speed, motion patterns, and visibility in terms of contrast and image area change as copepods development from nauplii through copepodites (Buskey, 1994). In conclusion, it becomes evident that feeding behaviour is a result of many factors: larval age, prey size/type, prey concentration (both not entirely due to encounter rates), turbulence and temperature, and if foraging subroutines in mechanistic IBM are to be developed, their relative importance needs to be assessed in specifically designed experiments.

Changes in the efficiency of foraging at different temperatures are not unexpected because of the fundamental control that temperature places on rates of metabolism, swimming and even developmental characteristics of North Atlantic herring. In this study, the efficiency of foraging appears to increase with increasing temperature as the width of the range in prey sizes that enables positive growth was larger at 13°C compared to 7°C. Previous research on other fishes such as salmonids and gadoids has explored the interrelationships between temperature, foraging/feeding and growth rate. For example, Brett et al. (1969) demonstrated that temperatures supporting the highest growth rates of sockeye salmon *Oncorhynchus nerka* decreased as feeding conditions worsened, and that the range in tolerable temperatures decreased for fish that were maintained at lower feeding levels. These relationships were incorporated into a bioenergetics-based optimal foraging model for brown trout *Salmo trutta* by Elliott and Hurley (1999). Jordaan and Kling (2003) concluded that food limitation or strong competition for prey decrease the optimal temperature for growth in Atlantic cod *Gadus morhua* larvae. These studies emphasize that temperature and foraging capacity interact to constrain environmental windows permitting growth and survival in fish. The effects of various environmental factors can influence thermal growth windows within (and interactions among) species in unexpected ways as demonstrated by experiments conducted on protists (e.g. Delaney, 2003; Kimmance et al., 2006; Weisse et al., 2002). Prey size selection in predators is influenced by ambient temperature, as it impacts the metabolism of the predator as well as the phenology of the prey. For example, a study on bluefish and anchovy by Morley and Buckel (2014) found that the larger the prey size, the greater the metabolic costs for the predator, resulting in a preference for smaller prey at lower temperatures. On the other hand, the phenology of the prey also plays a role, as warmer temperatures can lead to an earlier emergence of larger prey, making them more available to the predator.

From the repeated trials of the growth experiment performed in this study, a dome-shaped relationship existed between relative prey size and larval nutritional condition, even at high (ad libitum) prey concentrations. Although the smallest prey items were always available (within the visual field of the larvae) and easily captured, increased energy losses due to the increased frequency of feeding events outweighed the energy gained by consuming many, small prey. Additionally, once captured even relatively small prey require some handling time which sets an upper limit to feeding strike frequency. Interestingly, the range of prey sizes that herring larvae could utilize to maintain a positive rate of growth increased with increasing fish size. Other studies have suggested that optimal prey sizes (Munk, 1992) and the range in relative prey sizes ('ratio-based trophic niche breadth', Pearre, 1986) remain constant with increasing larval length, which as an extension of Cushing's match-mismatch hypothesis led to the concept of "surfing the size spectrum" (e.g. Pope et al., 1994). However, for some species the trophic niche breadth may also decrease with growth when larger prey items are specifically targeted (see Uriarte et al., 2019 for bluefin tuna, *Thunnus thynnus*).

Our simple, bioenergetics-based calculations incorporating observed feeding strike frequencies and growth at 7 and 13°C and functions of metabolic loss (Hufnagl & Peck, 2011) as well as prey capture success (see Hauss & Peck, 2009) suggest that the range in prey sizes supporting a positive rate of growth for a 150-μg herring larva is narrower at the colder temperature (Figure 4). This emphasizes that two environmental factors (temperature and prey size/type) interact to constrain environmental windows within which growth is positive. Studies examining the potential effect of interactions among different environmental factors on growth rates of early life stages of marine fish species are uncommon (Llopiz et al., 2014; Peck et al., 2003). Our results imply that matches between marine fish larvae and their preferred prey are more important at colder as opposed to warmer temperatures and for smaller versus larger larvae. The former is unexpected since cold temperature offers more starvation resistance (Killen, 2014; Lear et al., 2020) while the latter is intuitive. More experimental work using a larger number of and range in temperatures is needed to better understand the functional relationship between prey size, temperature and larval growth.

5 | CONCLUSIONS

When offered a size spectrum of prey similar to that observed for zooplankton in the wild (slope of abundance versus size), herring larvae actively selected prey items that were optimal for growth and nutritional condition. Selected prey size (percentage of predator length) increased with increasing larval size/age and this was the first study designed to reveal the shape (dome-shaped) of the function describing the relationship between relative prey size and larval growth and condition. The highest growth and condition occurred when larvae consumed their preferred prey size. Although young larvae displayed flexibility in their foraging behaviour which may allow some growth compensation when encountering sub-optimal prey field characteristics (prey sizes and concentrations), performance decrements and mortality may occur if larvae experience suboptimal zooplankton size distributions, even when plankton are abundant. Furthermore, the range in profitable prey sizes (those allowing positive growth) was reduced at colder versus warmer water temperatures. Our results reveal that climate-driven changes in temperature will not only have an indirect effect on marine fish larvae by influencing the phenology and other dynamics of their prey, it also can have a direct (intrinsic, physiological) effect on the range of prey sizes that are profitable to consume (those leading to positive rates of growth). The longer-term interactions between prey size, temperature and larval growth remain to be tested. Future experiments are recommended that include rates of energy loss for a more mechanistic understanding of growth responses and foraging decisions of larvae in different prey fields that can be implemented in physiological-based models.

AUTHOR CONTRIBUTION

The authors jointly conceived the ideas and designed methodology; Myron A. Peck secured the funding; Helena Hauss and Laura Schwabe collected the data; Helena Hauss and Myron A. Peck analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank Gudrun Bening, Karolin Berg and Christian Lindemann for their help maintaining laboratory cultures. This research was supported by the German Science Foundation (DFG) AQUASHIFT Program Cluster Project RECONN (Resolving Trophodynamic Consequences of Climate Change), # JO556/1-2. H.H. acknowledges funding from the BMBF project CO2MESO. M.A.P. acknowledges funding from the EU Horizon Program ACTNOW (Grant Agreement No. 101060072). This work benefitted from discussions with members of the ICES PICES Working Group on Small Pelagic Fish (WGSPF/WG43). Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors do not have any conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available at PANGAEA https://doi.pangaea.de/10.1594/PANGAEA.940574 (Hauss & Peck, 2022).

ORCID

Helena Hauss https://orcid.org/0000-0002-0754-3388
Myron A. Peck https://orcid.org/0000-0001-7423-1854

REFERENCES

Berggreen, U., Hansen, B., & Kiørboe, T. (1988). Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. *Marine Biology*, *99*(3), 341–352. https://doi.org/10.1007/bf02112126

Beyer, J. E., & Laurence, G. C. (1980). A stochastic model of larval fish growth. *Ecological Modelling*, *8*, 109–132.

Bils, F., Moyano, M., Aberle, N., Hufnagl, M., Alvarez-Fernandez, S., & Peck, M. A. (2017). Exploring the microzooplankton-ichthyoplankton link: A combined field and modeling study of Atlantic herring (*Clupea harengus*) in the Irish Sea. *Journal of Plankton Research*, *39*(1), 147–163.

Blaxter, J. H. S. (1986). Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. *Transactions of the American Fisheries Society*, *115*, 98–114.

Brett, J. R., & Groves, T. D. D. (1979). Physiological energetics. In W. S. Hoar, D. J. Randall, & J. R. Brett (Eds.), *Fish physiology* (pp. 279–352). Academic Press.

Brett, J. R., Shelbourn, J. E., & Shoop, C. T. (1969). Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *Journal of the Fisheries Research Board of Canada*, *26*, 2363–2394.

Brose, U., Ehnes, R. B., Rall, B. C., Vucic-Pestic, O., Berlow, E. L., & Scheu, S. (2008). Foraging theory predicts predator–prey energy fluxes. *Journal of Animal Ecology*, *77*(5), 1072–1078.

Buckley, L. J., & Dillmann, D. W. (1982). Nitrogen utilization by larval summer flounder, *Paralichthys dentatus* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, *59*(2–3), 243–256. https://doi.org/10.1016/0022-0981(82)90119-8

Buckley, L. J., & Durbin, E. G. (2006). Seasonal and inter-annual trends in the zooplankton prey and growth rate of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae on Georges Bank. *Deep-Sea Research II*, *53*, 2758–2770.

Buskey, E. J. (1994). Factors affecting feeding selectivity of visual predators on the copepod *Acartia tonsa*: Locomotion, visibility and escape responses. *Hydrobiologia*, *292/293*, 447–453.

Caldarone, E. M., Clemmesen, C. M., Berdalet, E., Miller, T. J., Folkvord, A., Holt, G. J., Olivar, M. P., & Suthers, I. M. (2006). Intercalibration of four spectrofluorometric protocols for measuring RNA/DNA ratios in larval and juvenile fish. *Limnology and Oceanography: Methods*, *4*, 153–163.

Caldeira, C., Santos, A. M. P., Ré, P., Peck, M. A., Saiz, E., & Garrido, S. (2014). Effects of prey concentration on ingestion rates of European sardine (*Sardina pilchardus*) larvae in the laboratory. *Marine Ecology Progress Series*, *517*, 217–228.

Carpenter, F. L., Paton, D. C., & Hixon, M. A. (1983). Weight gain and adjustment of feeding territory size in migrant hummingbirds. *Proceedings of the National Academy of Sciences of the United States of America*, *80*, 7259–7263.

Checkley, D. M. (1982). Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. *Marine Ecology Progress Series*, *9*, 245–253.

Cohen, R. E., & Lough, R. G. (1983). Prey field of larval herring *Clupea harengus* on a continental shelf spawning area. *Marine Ecology Progress Series*, *10*, 211–222.

Crowder, L. B. (1985). Optimal foraging and feeding mode shifts in fishes. *Environmental Biology of Fishes*, *12*, 57–62.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. *Advances in Marine Biology*, *26*, 249–293.

Davis, C. S., Gallager, S. M., & Solow, A. R. (1992). Microaggregations of oceanic plankton observed by towed video microscopy. *Science*, *257*, 230.

Delaney, M. P. (2003). Effects of temperature and turbulence on the predator-prey interactions between a heterotrophic flagellate and a marine bacterium. *Microbial Ecology*, *45*, 218–225.

Dickmann, M., Moellmann, C., & Voss, R. (2007). Feeding ecology of Central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: Implications for survival. *Marine Ecology Progress Series*, *342*, 277–289.

Durbin, A. G., & Durbin, E. G. (1975). Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. *Marine Biology*, *33*, 265–277.

Elliott, J. M., & Hurley, M. A. (1999). A new energetics model for brown trout, *Salmo trutta*. *Freshwater Biology*, *42*, 235–246.

Fiksen, Ø., & Folkvord, A. (1999). Modelling growth and ingestion processes in herring *Clupea harengus* larvae. *Marine Ecology Progress Series*, *184*, 273–289.

Fortier, L., & Harris, R. P. (1989). Optimal foraging and density-dependent competition in marine fish larvae. *Marine Ecology Progress Series*, *51*, 19–33.

Fox, C. J., Harrop, R. T., & Wimpenny, A. (1999). Feeding ecology of herring (*Clupea harengus*) larvae in the turbid Blackwater estuary. *Marine Biology*, *134*, 353–365.

Hansen, F. C., Möllmann, C., Schütz, U., & Neumann, T. (2006). Spatio-temporal distribution and production of calanoid copepods in the Central Baltic Sea. *Journal of Plankton Research*, *28*, 39–54.

Hauss, H., & Peck, M. A. (2009). Comparing observed and modelled growth of larval herring (*Clupea harengus*): Testing individual-based model parameterisations. *Scientia Marina*, *73S1*, 37–45.

Hauss, H., & Peck, M. A. (2022). Growth and behaviour of Baltic spring spawning herring (*Clupea harengus*) larvae raised at two different temperatures and under different feeding regimes (prey size) using the copepod *Acartia tonsa*. *PANGAEA*. https://doi.org/10.1594/PANGAEA.940574

Heath, M. R., & Lough, R. G. (2007). A synthesis of large scale patterns in the planktonic prey of larval and juvenile cod (Gadus morhua). *Fisheries Oceanography*, *16*(2), 169–185.

Houde, E. D. (1994). Differences between marine and freshwater fish larvae: Implications for recruitment. *ICES Journal of Marine Science*, *51*, 91–97.

Houde, E. D., & Zastrow, C. E. (1993). Ecosystem-and taxon-specific dynamic and energetics properties of larval fish assemblages. *Bulletin of Marine Science*, *53*(2), 290–335.

Hufnagl, M., & Peck, M. A. (2011). Physiological-based modelling of larval Atlantic herring (*Clupea harengus*) foraging and growth: Insights on climate-driven life history scheduling. *ICES Journal of Marine Science*, *68*(6), 1170–1188.

Jordaan, A., & Kling, L. J. (2003). Determining the optimal temperature range for Atlantic cod (*Gadus morhua*) during early life. In H. I. Browman & A. B. Skiftesvik (Eds.), *The Big fish Bang* (pp. 45–62). IMR Bergen.

Judson, O. P. (1994). The rise of the individual-based model in ecology. *Trends in Ecology & Evolution*, *9*(1), 9–14.

Killen, S. S. (2014). Growth trajectory influences temperature preference in fish through an effect on metabolic rate. *Journal of Animal Ecology*, *83*(6), 1513–1522.

Kimmance, S. A., Atkinson, D., & Montagnes, D. J. S. (2006). Do temperature–food interactions matter? *Marine Ecology Progress Series*, *42*, 63–73.

Kiørboe, T., Munk, P., & Richardson, K. (1987). Respiration and growth of larval herring *Clupea harengus*: Relation between specific dynamic action and growth efficiency. *Marine Ecology Progress Series*, *40*(1), 1–10.

Kristiansen, T., Fiksen, Ø., & Folkvord, A. (2007). Modelling feeding, growth, and habitat selection in larval Atlantic cod (*Gadus morhua*): Observations and model predictions in a macrocosm environment. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*, 136–151.

Kühn, W., Peck, M. A., Hinrichsen, H. H., Daewel, U., Moll, A., Pohlmann, T., Stegert, C., & Tamm, S. (2008). Defining habitats suitable for larval fish in the German Bight (southern North Sea): An IBM approach using spatially-and temporally-resolved, size-structured prey fields. *Journal of Marine Systems*, *74*, 329–342.

Lear, K. O., Morgan, D. L., Whitty, J. M., Whitney, N. M., Byrnes, E. E., Beatty, S. J., & Gleiss, A. C. (2020). Divergent field metabolic rates highlight the challenges of increasing temperatures and energy limitation in aquatic ectotherms. *Oecologia*, *193*(2), 311–323.

Llopiz, J. K. (2013). Latitudinal and taxonomic patterns in the feeding dynamics of fish larvae: A literature synthesis. *Journal of Marine Systems*, *109-110*, 69–77.

Llopiz, J. K., Cowen, R. K., Hauff, M. J., Ji, R., Munday, P. L., Muhling, B. A., Peck, M. A., Richardson, D. E., Sogard, S., & Sponaugle, S. (2014). Early life history and fisheries oceanography: New questions in a changing world. *Oceanography*, *27*(4), 26–41.

Louzao, M., Wiegand, T., Bartumeus, F., & Weimerskirch, H. (2014). Coupling instantaneous energy-budget models and behavioural mode analysis to estimate optimal foraging strategy: An example with wandering albatrosses. *Movement Ecology*, *2*, 8.

MacKenzie, B. R., & Kiørboe, T. (1995). Encounter rates and swimming behavior of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. *Limnology and Oceanography*, *40*, 1278–1289.

Malzahn, A. M., Aberle, N., Clemmesen, C., & Boersma, M. (2007). Nutrient limitation of primary producers affects planktivorous fish condition. *Limnology and Oceanography*, *52*, 2062–2071.

Mangel, M., & Clark, C. W. (1986). Towards a unifield foraging theory. *Ecology*, *67*(5), 1127–1138.

Manly, B. F. J. (1974). A model for certain types of selection experiments. *Biometrics*, *30*, 281–294.

Marshall, D. J., & Morgan, S. G. (2011). Ecological and evolutionary consequences of linked life-history stages in the sea. *Current Biology*, *21*(18), R718–R725.

Menge, J. L. (1974). Prey selection and foraging period of the predaceous rocky intertidal snail, Acanthina punctulata. *Oecologia*, *17*, 293–316.

Mills, E. L., Pol, M. V., Sherman, R. E., & Culver, T. B. (1989). Interrelationships between prey body size and growth of age-0 yellow perch. *Transactions of the American Fisheries Society*, *118*, 1–10.

Morley, J. W., & Buckel, J. A. (2014). Effects of temperature and prey size on predator–prey interactions between bluefish and bay anchovy. *Journal of Experimental Marine Biology and Ecology*, *461*, 449–457. https://doi.org/10.1016/j.jembe.2014.08.023

Moyano, M., Illing, B., Akimova, A., Alter, K., Bartolino, V., Börner, G., Clemmesen, C., Finke, A., Gröhsler, T., Kotterba, P., Livdane, L., Mittermayer, F., Moll, D., von Nordheim, L., Peck, M. A., Schaber, M., & Polte, P. (2023). Caught in the middle: Bottom-up and top-down processes impacting recruitment in a small pelagic fish. *Reviews in Fish and Fisheries*, *33*, 55–84. https://doi.org/10.1007/s11160-022-09739-2

Moyano, M., Illing, B., Peschutter, P., Huebert, K. B., & Peck, M. A. (2016). Thermal impacts on the growth, development and ontogeny of critical swimming speed in Atlantic herring larvae. *Comparative Physiology and Biochemistry B*, *197*, 23–34.

Munk, P. (1992). Foraging behaviour and prey size spectra of larval herring *Clupea harengus*. *Marine Ecology Progress Series*, *80*, 149–158.

Munk, P., & Kiørboe, T. (1985). Feeding behaviour and swimming activity of larval herring (*Clupea harengus*) in relation to density of copepod nauplii. *Marine Ecology Progress Series*, *24*, 15–21.

Munk, P., & Nielsen, T. G. (1994). Trophodynamics of the plankton community at Dogger Bank: Predatory impact by larval fish. *Journal of Plankton Research*, *16*, 1225–1245.

Pearre, S. (1986). Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. *Marine Ecology Progress Series*, *27*, 299–314.

Peck, M. A., Buckley, L. J., Caldarone, E. M., & Bengtson, D. A. (2003). Effects of food consumption and temperature on growth rate and biochemical-based indicators of growth in early juvenile Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*. *Marine Ecology Progress Series*, *251*, 233–243.

Peck, M. A., & Daewel, U. (2007). Physiologically based limits to food consumption, and individual-based modeling of foraging and growth of larval fishes. *Marine Ecology Progress Series*, *347*, 171–183.

Peck, M. A., & Holste, L. (2006). Effects of salinity, photoperiod and adult stocking density on egg production and egg hatching success in *Acartia tonsa* (Calanoida: Copepoda): Optimizing intensive cultures. *Aquaculture*, *255*, 341–350.

Peck, M. A., Huebert, K. B., & Llopiz, J. K. (2012). Intrinsic and extrinsic factors driving match-mismatch dynamics during the early life history of marine fishes. *Advances in Ecological Research*, *47*, 177–302.

Pope, J. G., Shepherd, J. G., & Webb, J. (1994). Successful surf-riding on size spectra: The secret of survival in the sea. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *343*(1303), 41–49.

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: A selective review of theory and tests. *The Quarterly Review of Biology*, *52*, 137–154.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, *2*, 369–404.

Sheldon, R. W., Prakash, A., & Sutcliffe, W. H. (1972). The size distribution of particles in the ocean. *Limnology and Oceanography*, *17*, 327–340.

Theilacker, G. H., & Kimball, A. S. (1984). Comparative quality of rotifers and copepods as foods for larval fishes. *CalCOFi Reports*, *25*, 80–86.

Uriarte, A., Johnstone, C., Laiz-Carrión, R., García, A., Llopiz, J. K., Shiroza, A., Quintanilla, J. M., Lozano-Peral, D., Reglero, P., & Alemany, F.

(2019). Evidence of density-dependent cannibalism in the diet of wild Atlantic bluefin tuna larvae (*Thunnus thynnus*) of the Balearic Sea (NW-Mediterranean). *Fisheries Research*, *212*, 63–71.

Voss, R., Köster, F. W., & Dickmann, M. (2003). Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. *Fisheries Research*, *63*, 97–111.

Weisse, T., Stadler, P., Lindstrom, E. S., Kimmance, S. A., & Montagnes, D. J. S. (2002). Interactive effect of temperature and food concentration on growth rate: A test case using the small freshwater ciliate Urotricha farcta. *Limnology and Oceanography*, *47*, 1447–1455.

Werner, E. E., & Mittelbach, G. G. (1981). Optimal foraging: Field tests of diet choice and habitat switching 1. *Integrative and Comparative Biology*, *21*, 813–829.

How to cite this article: Hauss, H., Schwabe, L., & Peck, M. A. (2023). The costs and trade-offs of optimal foraging in marine fish larvae. *Journal of Animal Ecology*, *92*, 1016–1028. https://doi.org/10.1111/1365-2656.13915