Feeding performance of juvenile hatchery-reared spotted seatrout *Cynoscion nebulosus*

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The feeding performance of individual hatchery-reared (HR) and wild juvenile spotted seatrout *Cynoscion nebulosus* was compared across a series of six 1·5 h feeding exposures over a 3 day period in a controlled experiment. The predation cycle served as a context for discerning feeding performance elements. The experimental design facilitated assessments of the effects of experience, motivation due to hunger or satiation and prey density and encounter frequency. Although feeding success improved significantly across successive trials for both groups of *C. nebulosus*, wild *C. nebulosus* successfully captured and consumed significantly more *Palaemonetes* spp. prey and completed most performance metrics more efficiently than HR *C. nebulosus*. Total exposure time decreased with experience for both groups of *C. nebulosus*; however, HR *C. nebulosus* took longer to complete feeding exposures. Underpinning this difference was the time spent by HR *C. nebulosus* in non-search mode and for completing various foraging behaviours. Nevertheless, juvenile HR *C. nebulosus* exhibited sufficient foraging plasticity to switch from a pelleted diet to live novel prey.

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INTRODUCTION

The success of stock enhancement depends on the ability of hatchery-reared (HR) fishes to perform effectively in the wild (Brown & Day, 2002; Huntingford, 2004; Liao, 2004). Quick acquisition of foraging skills by newly released HR fishes ensures that energetic demands are met for maintenance, growth and predator avoidance. Successful foraging requires proficiency in a whole suite of behavioural skills including the recognition, pursuit, capture and handling of live natural prey (Sundström & Johnsson, 2001; Kelly & Brown, 2011). By quantifying differences in feeding performance between wild and naïve fishes, the capacity of HR fishes to adapt to natural conditions can be evaluated (Blankenship & Leber, 1995).

Quantifying key skills within the context of the predation cycle (Eggers, 1977), offers an approach to understanding the ontogeny of foraging behaviour of naïve fishes (Steingrund & Fernö, 1997). The predation cycle specifies the sequence of

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exclusive behaviours within a foraging event and can serve as a guide for defining feeding performance elements. An experimental design based on inputs inferred from the predation cycle facilitates the detection of effects of experience, motivation due to hunger and prey encounter frequency. Also, focal studies of individual subjects within the context of the predation cycle can reveal the development of essential feeding performance skills. Towards this end, wild fishes can serve as the standard and HR fishes as unimprinted for elucidating how foraging skills develop. An efficient forager also may benefit from foraging plasticity, wherein repeated exposure to novel prey actuates the refinement of foraging skills (Warburton, 2003). Thus, inherent foraging plasticity should also facilitate the transition from the hatchery to the natural environment (Brown & Laland, 2001; Brown *et al.*, 2003).

In Mississippi, U.S.A., the heavily exploited spotted seatrout *Cynoscion nebulosus* (Cuvier 1830) is being considered for stock enhancement as part of a comprehensive management approach. Apart from initial feeding by the earliest stages on rotifers and *Artemia* spp., HR *C. nebulosus* receive a pelleted diet in an unstructured environment. Consequently, newly released juvenile HR *C. nebulosus* lack experience in recognizing and capturing live prey. Because juvenile *C. nebulosus* occupy dynamic estuarine environments, however, this species may possess sufficient inherent plasticity to allow HR individuals to switch to a natural diet in the wild.

In this study, changes in feeding performance metrics were compared between individual naïve HR and wild juvenile *C. nebulosus* exposed to live grass shrimp *Palaemonetes* spp. over a series of repeated exposures. The use of both time-to-event and performance variables facilitated detection of possible effects of experience, motivation due to hunger or satiation and encounter frequency (prey density). The use of focal subjects within a comparative context helped to elucidate group differences in feeding performance skills and individual variability. Few existing studies examine the effects of all these factors on the development of feeding performance of HR fishes.

MATERIALS AND METHODS

All experimental HR *C. nebulosus* came from the same hatchery cohort cultured at the Cedar Point Campus of the USM GCRL in Ocean Springs, MS, U.S.A. in summer 2008. HR subjects had reached a mean of $10 \cdot 08$ cm total length (L_T) and $9 \cdot 86$ g mass. These *C. nebulosus* had been maintained on a generic pelleted diet during the rearing process. Wild *C. nebulosus* of a size range comparable to HR *C. nebulosus* (*i.e.* $10 \cdot 63$ cm mean L_T; $9 \cdot 90$ g mean mass) were collected from marsh edge habitat in Davis Bayou, Ocean Springs, MS, U.S.A. ($30 \cdot 392°$ N; $88 \cdot 899°$ W) using a $7 \cdot 62$ m long, $1 \cdot 27$ cm stretch-mesh bag seine. Ages of wild and HR *C. nebulosus* were probably not too different, as wild *C. nebulosus* would have been about 90 days old based on the age and mass relationship of Powell *et al.* (2004), and HR *C. nebulosus* were 91 days old when the experiment began.

Because diets of wild *C. nebulosus* ($n = 53$) of a comparable size (*c.* 10 cm L_T) to HR *C. nebulosus* consisted mainly of *Palaemonetes* spp. (grass shrimp) and small penaeid shrimp, live *Palaemonetes* spp. standardized to the predator–prey size ratio observed for wild *C. nebulosus* (18–22% of fish L_T) were used as prey for the experiment. *Palaemonetes* spp. for feeding trials were collected from local marsh edge habitat using a $22 \cdot 5$ cm wide, 1 mm mesh kick net.

HR *C. nebulosus* were acclimated to the laboratory by holding them in a 76 l tank for 5 days prior to the experiment. During acclimation, HR *C. nebulosus* were fed their usual $2 \cdot 0$ mm pelleted diet *ad libitum* twice daily at 0745 and 1830 hours. Wild *C. nebulosus* also

TABLE I. Definitions of predation-cycle behaviours recognized during feeding trials

Behaviour	Description	Quantifiable behaviour
Non-search	Not actively looking for prey	Lack of swimming movements and repetitive non-focused swimming
Search	Actively looking for prey	Directional, focused swimming movements
Prey recognition	First fixation on prey item	Orienting towards prey by changing angle relative to bottom of tank
Foraging event	Time from prey recognition to culmination of attack	Prey recognition, then striking (perhaps repeatedly) until successful capture or giving up on the attack
Handling time	Time from initial prey contact until resumption of respiratory gill cover movements	Return to either non-search or search behaviours

were acclimated to laboratory conditions in 76 l holding tanks until they resumed feeding on *Palaemonetes* spp. (3–4 days). After feeding resumed, wild *C. nebulosus* were held for an additional 5 days in a 76 l tank in the same way as HR *C. nebulosus,* except they were fed *Palaemonetes* spp. *ad libitum* twice daily at 0745 and 1830 hours.

Once acclimated, HR and wild subjects were randomly selected and placed on opposing sides of divided 76 l aquaria, which served as foraging arenas. Two arenas were used concurrently. No water exchange occurred across the solid tank dividers and *C. nebulosus* had no visual contact with each other. A black background with 1 cm^2 white grid lines facilitated the recognition of behaviours. Arenas were covered by glass lids and equipped with 17 W fluorescent light strips and aerated, except during feeding trials. Each arena also was surrounded by a black plastic blind with an observation window through which a video camera was positioned. Behaviours were recorded using either a Sony Handycam DCR-SR45 or a Sony HDR-SR5 video camera (www.sony.com).

Six consecutive feeding trials (*i.e.* exposures) were conducted with each subject ($n = 10$ wild *C. nebulosus*; $n = 10$ HR *C. nebulosus*) from 7 August to 19 September 2008. Each subject experienced two feeding exposures per day, at 0800 and 1630 hours, for 3 days. Five *Palaemonetes* spp. were introduced to the bottom back corner of the foraging arena by gently flushing them through a 2·54 cm diameter polyvinyl chloride (PVC) pipe which was then removed. Pilot trials determined that five *Palaemonetes* spp. were sufficient to initiate a feeding response without presenting more prey than could be readily consumed during the trials. Subjects were allowed to feed for a maximum of 1·5 h, during which time all behaviours were video recorded. After the allotted period or when no prey remained (as a result of consumption or escape of prey), the trial ceased and any remaining *Palaemonetes* spp. were carefully recovered with a small dip net. Following removal of uneaten prey, subjects remained undisturbed between exposures.

Video recordings of feeding trials were analysed using the Sony Picture Utility programme (Picture Motion Browser version 2.1.00.04170, Copyright 2006, 2007 Sony Corporation). Non-search, search, prey recognition, strike, capture and handling-time behaviours were delineated using time stamps associated with each type of behaviour (Table I). Behaviours occurring between foraging events were classified as either non-search or search. The time period between foraging events was formally defined as the time between the recognition of consecutive prey, prey capture notwithstanding. A foraging event spanned the duration from the moment of prey recognition until either the prey was captured or the *C. nebulosus* gave up the pursuit. The number of strikes per foraging event also was noted. Prey capture culminated with the consumption of the *Palaemonetes* spp., for which handling time (HT) was measured whenever possible.

DATA ANALYSIS

One-way repeated measures (RM) ANOVA (GLM procedure in SPSS version 15.0.1; www.01.ibm.com/software/analytics/spss) was used to examine the response variables: (1) total number of shrimp consumed, (2) number of strikes per foraging event, (3) number of captures per foraging event and (4) strike efficiency. The within-subjects factor (Exposure) accounted for variability and dependence among the six consecutive exposures (six levels). The between-subjects factor (Fish Type) represented Wild and HR groups. As there was no *a priori* reason to expect a particular directionality in the difference between wild and HR *C. nebulosus,* results were interpreted as two-tailed hypotheses. The RM ANOVA model also included terms for an intercept (overall mean) and for an interaction term (Exposure × Fish Type). Data were $\log_{10}$ transformed if a one-sample Kolmogorov–Smirnov (K–S) test on transformed data showed a better or as good a fit to normality as the raw data. Zero values for $\log_{10}$ transformed data were replaced with nominal values obtained by subtracting 2.5 S.D. from means of the transformed non-zero data. Box's test-of-equality-of-covariance assessed whether covariance matrices were equal across groups. Levene's test addressed whether the error variance of the dependent variable was equal across groups for each level of the within-subjects (Exposure) factor. Mauchly's test assessed the sphericity assumption for the within-subjects factor. Where sphericity was confirmed [all variables except the number of strikes per foraging event (Mauchly's, $\chi^2 = 25.85$, d.f. $= 14$, $P < 0.05$)], the standard univariate RM ANOVA F-test was used to interpret significance for the within-subjects factor (Exposure) and its interaction with Fish Type. Otherwise, the Greenhouse-Geiser corrected significance level was used. A standard F-test was used to evaluate the between-subjects factor (Fish Type). As four different responses were examined via RM ANOVA, the error rate was protected by holding α to 0.0125 for overall within and between-subjects effects. Finally, potential trends across exposures were diagnosed for the best fit by linear, quadratic, cubic or higher order (up to fifth order) polynomial contrasts.

As time is a currency within the predation cycle, time-to-event variables were important for this study. The analysis of time-to-event data is not straight-forward because of the presence of censored observations and because response time does not follow a normal distribution (Chan, 2004). Therefore, Cox regression survival analysis (SPSS version 15.0.1) was used to evaluate the effects of several covariates and their interactions on time-to-event responses. As a semi-parametric method, Cox regression does not require any specific distribution in the time-to-event response. For the response variables: (1) total time per exposure, (2) time to first prey recognition and (3) time to first prey capture, the response was represented in the model by Time, the completion status by Status (*i.e.* coded 1 when the event occurred), and the explanatory covariates by Fish Type (*i.e.* HR or Wild), Exposure (*i.e.* trials 1–6) and the Fish Type × Exposure interaction.

Three response variables: (1) mean foraging event time, (2) mean search time and (3) mean non-search time, required two additional covariates reflecting satiation and prey density. Therefore, in addition to the previously described model structure, the model for the latter response variables also included the covariates Number Of Remaining Shrimp and Number Of Shrimp Consumed, as well as the interactions Fish Type × Number Of Remaining Shrimp and Fish Type × Number Of Shrimp Consumed. Although the two additional explanatory covariates were inversely related, they theoretically represented different influences on the time-to-event responses (*e.g.* prey encounter rate and satiation). Moreover, variance inflation factors (VIF) for these two covariates [*i.e.* within the context of multiple regressions (MRs)] were considerably lower than typical VIF exclusion thresholds across the three MRs (*i.e.* VIF, range 2.06–2.29) (O'Brien, 2007). For the last three response variables, missing values were excluded from the analysis and zero values were replaced with the nominal value of 0.01 (*i.e.* true zero doubtful).

The Wald forward stepwise procedure selected combinations of covariates that best explained time-to-event responses. The contrast was set to Fish Type as an indicator. The proportional hazards function assumption was met for Fish Type in all regressions, as Fish Type lines did not intersect on log-minus-log plots.

HT was recorded only when *C. nebulosus* were oriented such that the behaviour was clearly discernable. As a result, mean HT was calculated across all trials and compared between HR and wild *C. nebulosus* via a two-tailed independent samples *t*-test (SPSS version 15.0.1).

Because the variance in HT was slightly unequal between *C. nebulosus* groups (Levene, $F_{1,63} = 4 \cdot 475$, $P < 0 \cdot 05$), the unequal variance correction was used to interpret the significance of the test.

RESULTS

Total time per exposure decreased across exposures for both HR and wild *C. nebulosus,* as their foraging skills improved (Wald $= 13 \cdot 336$, d.f. $= 1$, $P < 0 \cdot 001$) (Table II). Total time per exposure, however, was consistently higher for HR *C. nebulosus* than for wild *C. nebulosus* (Wald $= 57 \cdot 005$, d.f. $= 1$, $P < 0 \cdot 001$). Wild *C. nebulosus* took less time than HR *C. nebulosus* to consume *Palaemonetes* spp. Furthermore, the variance in total time per exposure was high and homogeneous across exposures for HR *C. nebulosus,* whereas the variance decreased markedly by the third trial for wild *C. nebulosus.* Wild *C. nebulosus* also generally consumed more prey per exposure than HR *C. nebulosus* (between-subjects $F = 18 \cdot 409$, d.f. $= 1$, $P < 0 \cdot 001$) (Table III). Both groups of *C. nebulosus* consumed more prey across exposures (within-subjects $F = 5 \cdot 581$, d.f. $= 5$, $P < 0 \cdot 001$) (Table IV). The overall trend across the six exposures was significantly linear ($F = 29 \cdot 429$, d.f. $= 1$, $P < 0 \cdot 001$). Finally, both *C. nebulosus* groups improved in a parallel manner across exposures, as demonstrated by the lack of a significant interaction (between-subjects $\times$ within-subjects $F = 1 \cdot 044$, d.f. $= 5$, $P > 0 \cdot 05$).

The predation cycle was subdivided into a sequence of performance elements (Wintzer & Motta, 2005) including search, prey recognition, strike, capture and HT. HR *C. nebulosus* took longer to perform most elements of the predation cycle and spent a much larger portion of their time in non-search mode than wild *C. nebulosus* (Fig. 1). Overall, search time decreased across subsequent exposures. During trials, search time increased relative to fewer remaining prey and, conversely, decreased relative to the number of prey consumed. Also, HR *C. nebulosus* took longer to search as the number of remaining prey decreased (Wald $= 10 \cdot 601 - 80 \cdot 462$, d.f. $= 1$, $P = 0 \cdot 001$ to $< 0 \cdot 001$) (Table II). Moreover, HR *C. nebulosus* spent considerably more time in non-search mode relative to the number of remaining prey (Wald $= 49 \cdot 658$, d.f. $= 1$, $P < 0 \cdot 001$) (Table II).

Wild *C. nebulosus* generally completed foraging events within about half the time of HR *C. nebulosus* (Wald $= 116 \cdot 897$, d.f. $= 1$, $P < 0 \cdot 001$) (Table II); however, HR *C. nebulosus* completed successive foraging events more quickly as they gained experience and improved at prey recognition [Fig. 2(a)], strike efficiency [Fig. 2(b)] and prey capture success [Fig. 2(c) and Table IV].

Time to first prey recognition decreased with experience for both *C. nebulosus* groups (Wald $= 27 \cdot 970$, d.f. $= 1$, $P < 0 \cdot 001$; Table II). HR *C. nebulosus* took longer than wild *C. nebulosus* to recognize prey during the first four exposures, but thereafter, HR *C. nebulosus* rapidly improved and converged with wild *C. nebulosus* (Wald $= 13 \cdot 932$, d.f. $= 1$, $P < 0 \cdot 001$) [Fig. 2(a)]. Furthermore, an abrupt decrease in the variance associated with the median time to first prey recognition for HR *C. nebulosus* implied that some individuals developed search images more quickly than others.

Wild *C. nebulosus* made more than twice as many strikes per foraging event than HR *C. nebulosus* (between-subjects $F = 27 \cdot 159$, d.f. $= 1$, $P < 0 \cdot 001$) [Fig. 2(b)

TABLE II. Explanatory variables contributing to final Cox regression models of time-to-event responses. All response metrics are represented by means, except for time to first prey recognition, which is represented by the median

Variable	Covariates in final model	b	S.E.	Wald	d.f.	P	Exp B	95% C.I. lower	95% C.I. upper
Total time per exposure	Fish type	−1.832	0.243	57.005	1	<0.001	0.160	0.100	0.258
	Exposure	0.229	0.063	13.336	1	<0.001	1.257	1.112	1.421
Foraging event time	Fish type	−0.948	0.088	116.897	1	<0.001	0.387	0.326	0.460
Time to first prey recognition	Fish type	−1.876	0.355	27.970	1	<0.001	0.153	0.076	0.307
	Exposure × fish type	0.305	0.082	13.932	1	<0.001	1.357	1.156	1.593
Time to first prey capture	Fish type	−1.644	0.239	47.241	1	<0.001	0.193	0.121	0.309
	Exposure	0.185	0.063	8.678	1	<0.01	1.203	1.064	1.361
Search time	Exposure	0.152	0.026	33.200	1	<0.001	1.165	1.106	1.227
	Number of remaining shrimp	0.460	0.051	80.462	1	<0.001	1.584	1.432	1.751
	Number of shrimp consumed	−0.212	0.065	10.601	1	0.001	0.809	0.712	0.919
	Fish type × Number of remaining shrimp	−0.126	0.026	24.451	1	<0.001	0.881	0.838	0.927
Non-search time	Fish type × Number of remaining shrimp	−0.175	0.025	49.658	1	<0.001	0.839	0.799	0.881

Exp B, between-group hazard ratio or the relative risk of an event occurring for every unit increase in the covariate; B, ln(B).

TABLE III. Between-subjects effects for one-way repeated measures (RM) ANOVA on performance variables

Variable	Source	Type III sum of squares	d.f.	Mean square	F	P	Partial η^2	Power
Total number of shrimp consumed per exposure	Fish type	64·533	1	64.533	18·409	<0·001	0·506	0·982
	Error	63· 100	18	3·506				
Number of strikes per foraging event	Fish type	3· 509	1	3·509	27·159	<0·001	0·601	0·998
	Error	2· 326	18	0.129				
Number of prey captures per foraging event	Fish type	8· 517	1	8·517	29·861	<0·001	0·624	0·999
	Error	5· 134	18	0.285				
Strike efficiency	Fish type	0· 404	1	0.404	3·550	>0·05	0·182	0·425
	Error	1· 821	16	0.114				

TABLE IV. Within-subjects effects for one-way repeated measures (RM) ANOVA on performance variables

Variable	Source	Type III sum of squares	d.f.	Mean square	F	P	Partial η^2	Power
Total number of shrimp consumed per exposure	Exposure	24.400	5	4.880	5.581	<0.001	0.237	0.989
	Exposure × Fish type	4.567	5	0.913	1.044	>0.05	0.055	0.357
	Error (exposure)	78.700	90	0.874				
Number of strikes per foraging event	Exposure	0.303	3.210	0.094	1.367	>0.05	0.071	0.357
	Exposure × Fish type	0.095	3.210	0.029	0.427	>0.05	0.023	0.133
	Error (exposure)	3.991	57.777	0.069				
Number of captures per foraging event	Exposure	2.894	5	0.579	6.647	<0.001	0.270	0.997
	Exposure × Fish type	0.754	5	0.151	1.732	>0.05	0.088	0.574
	Error (exposure)	7.837	90	0.087				
Strike efficiency	Exposure	1.132	5	0.226	4.662	0.001	0.226	0.968
	Exposure × Fish type	0.236	5	0.047	0.972	>0.05	0.057	0.330
	Error (exposure)	3.885	80	0.049				
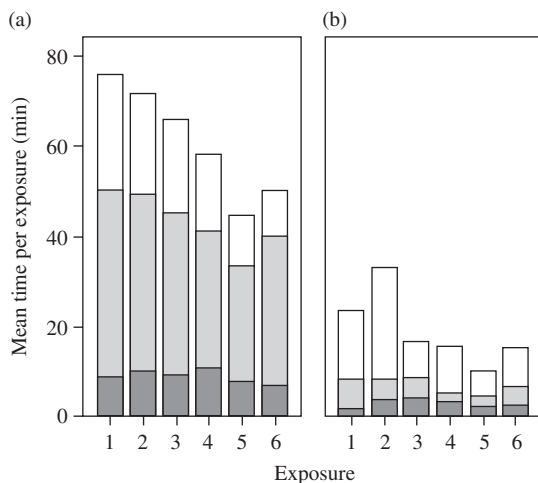
FIG. 1. Breakdown of how (a) hatchery-reared and (b) wild *Cynoscion nebulous* allocated time to search (□), non-search (▨) and foraging (▦) across the six exposures. The maximum possible total exposure time was 90 min; however, an exposure ended when no *Palaemonetes* spp. remained.

and Table III]. Generally, the number of strikes per foraging event did not increase across exposures (within-subjects $F = 1.367$, d.f. $= 3.210$, $P > 0.05$) (Table IV); moreover, neither did HR *C. nebulosus* converge towards wild *C. nebulosus* (Fish Type × Exposure $F = 0.427$, d.f. $= 3.210$, $P > 0.05$).

Prey capture success was characterized by the time-to-event variable, time to first prey capture and by the performance variables, strike efficiency and captures per foraging event. Time to first prey capture generally decreased across exposures for both *C. nebulosus* groups (Wald $= 8.678$, d.f $= 1$, $P < 0.01$), but HR *C. nebulosus* consistently took up to five times longer to initially capture prey (Wald $= 47.241$, d.f. $= 1$, $P < 0.001$) (Table II). In addition, the variance in this response was notably higher for HR *C. nebulosus* across the six exposures.

Wild *C. nebulosus* captured more prey per foraging event than HR *C. nebulosus* [between-subjects $F = 29.861$, d.f. $= 1$, $P < 0.001$; Table III; and Fig. 2(c)]. This metric improved across exposures for both fish groups (within-subjects $F = 6.647$, d.f. $= 5$, $P < 0.001$; Table IV); the form of the overall within-subjects trend was linear ($F = 32.551$, d.f. $= 1$, $P < 0.001$). Furthermore, both *C. nebulosus* groups improved in a parallel manner (Exposure × Fish Type $F = 1.732$, d.f. $= 5$, $P > 0.05$).

Strike efficiency appeared higher for wild *C. nebulosus*, but this difference was non-significant (between-subjects $F = 3.550$, d.f. $= 1$, $P > 0.05$; Table III). Strike efficiency, however, improved significantly across exposures together for both groups of *C. nebulosus* (within-subjects $F = 4.662$, d.f. $= 5$, $P = 0.001$; Table IV) and the overall trend in strike efficiency was linear ($F = 17.340$, d.f. $= 1$, $P = 0.001$). In addition, the improvement in strike efficiency was parallel between *C. nebulosus* groups (Fish Type × Exposure $F = 0.972$, d.f. $= 5$, $P > 0.05$).

Generally, HR *C. nebulosus* took significantly longer (mean ± s.d. $= 0.60 ± 0.46$ s, $n = 24$) than wild fish ($0.28 ± 0.19$ s, $n = 41$) to handle prey ($t = 3.239$, d.f. $= 27.604$, $P < 0.01$).
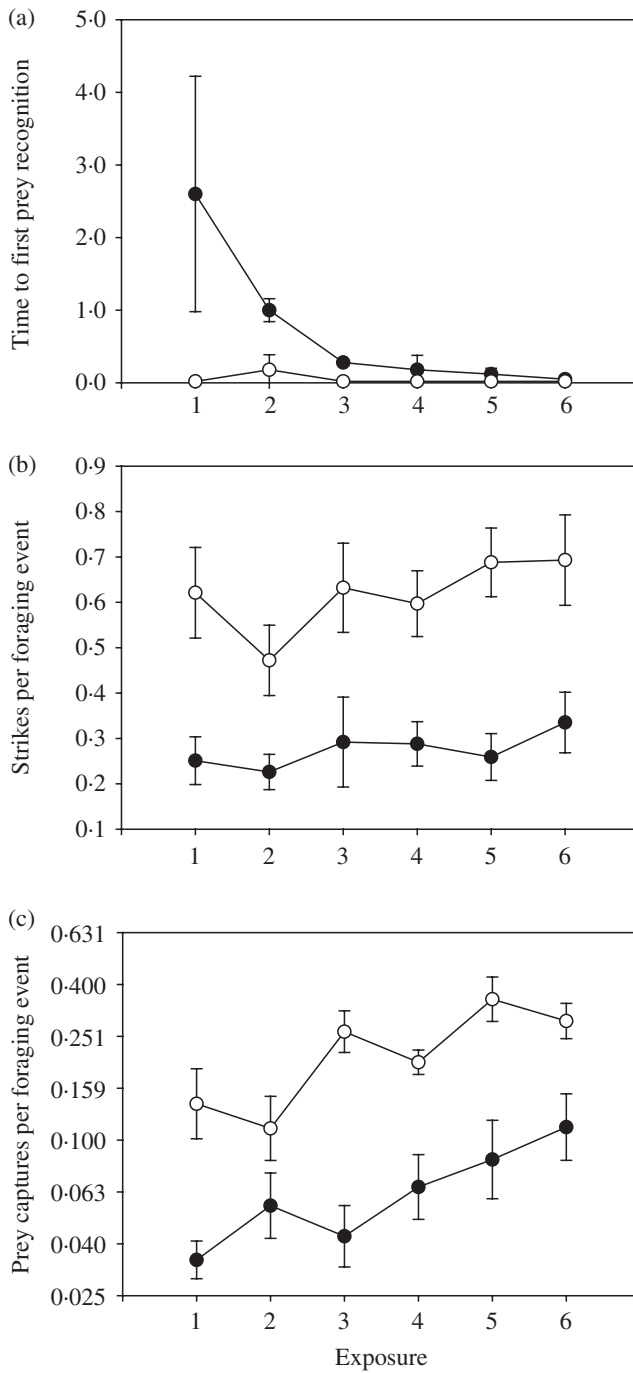
FIG. 2. Exemplary metrics illustrating convergence, lack of improvement and parallel improvement for hatchery-reared (●) and wild (○) *Cynoscion nebulosus* across exposures. Mean ± s.e. (a) time to first prey recognition (Median), (b) number of strikes per foraging event and (c) number of prey captures per foraging event.

DISCUSSION

Comparisons of HR and wild *C. nebulosus* within the context of the preda-
tion cycle elucidated differences and improvements in terms of time-to-completion
(Hughes *et al.,* 1992) and performance variables (Croy & Hughes, 1991*a*). For some
variables such as the time to first prey recognition and time to first prey capture, HR
C. nebulosus improved and converged with wild *C. nebulosus.* For other metrics,
including number of shrimp consumed per exposure, number of captures per foraging
event and total time per exposure, wild *C. nebulosus* consistently performed better
than HR *C. nebulosus,* while both groups of *C. nebulosus* improved in tandem. For
the number of strikes per foraging event, wild *C. nebulosus* performed better than
HR *C. nebulosus,* although neither group improved much despite additional expe-
rience across exposures. Finally, strike efficiency improved for both *C. nebulosus*
groups, while not differing between HR and wild *C. nebulosus.* For this skill, both
C. nebulosus groups attained comparable levels of performance within the confines
of the experimental system.

The most noticeable between-group difference in this study was in the time spent
searching for prey. Wild *C. nebulosus* spent most of their time searching between
foraging events; whereas, HR *C. nebulosus* spent most of their time in non-search
mode. Searching is mediated by experience, the prey encounter rate, hunger level,
release from the need for vigilance and social facilitation and interference (Reiriz
et al., 1998; Brown & Laland, 2001; Sundström & Johnsson, 2001; Warburton, 2003).
Search time decreased for both groups, as HR fish learned to recognize novel live prey
and wild *C. nebulosus* were probably acclimating to the artificial conditions. Search
time, however, also increased generally, and especially for HR *C. nebulosus,* as the
number of remaining shrimp decreased. This variable presumably reflected the rate of
prey encounter. Conversely, search time varied inversely with the number of shrimp
consumed, which presumably reflected the effect of satiation. HR *C. nebulosus* did
not initiate searching behaviour as readily or sustain it nearly as well as did wild *C.
nebulosus.* As the number of remaining prey decreased, HR *C. nebulosus* did not
locate prey as effectively and readily lost the motivation to search.

As the gateway to prey capture, prey recognition represents a first step towards
improved foraging efficiency. Prey recognition entails the formation of stimulus
associations contributing to the search image. These stimuli support and in turn are
reinforced by other foraging skills (Warburton, 2003). Recognition stimuli include
visual cues associated with the search image such as prey colour, size, shape or the
presence of conspicuous appendages (Howick & O'Brien, 1983; Croy & Hughes,
1991*b*; Reiriz *et al.,* 1998). Marked reduction and convergence in time to first prey
recognition across exposures suggests that HR *C. nebulosus* retained the innate abil-
ity to form search images for *Palaemonetes* spp. in this study. This effect also has
been noted in studies of the feeding ontogeny of HR coho salmon *Oncorhynchus
kisutch* (Walbaum 1792) and brown trout *Salmo trutta* L. 1758 (Paszkowski & Olla,
1985; Olla *et al.,* 1998; Sundström & Johnsson, 2001). Likewise for reared tur-
bot *Scophthalmus maximus* (L. 1758) the time to first prey recognition decreased
and converged with that of wild fish (Ellis *et al.,* 2002), implying that *S. maximus*
learned to recognize novel prey. Interestingly, an initial high variance in the median
time to first prey recognition followed by rapidly decreasing variance across expo-
sures suggested that some HR *C. nebulosus* required less experience to form search

images in this study. Early learners would presumably benefit from this ability upon release.

The act of striking at prey is a critical step linking prey recognition and capture within the predation cycle. Successful prey capture reinforces prey recognition, the motivation to strike and the probability of capturing a novel prey (Hughes *et al.*, 1992; Warburton, 2003). Although wild *C. nebulosus* struck at and captured prey more frequently than HR *C. nebulosus,* strike efficiency (*i.e.* captures per strike) was not significantly different between *C. nebulosus* groups. By contrast, prey capture efficiency improved with experience for naïve largemouth bass *Micropterus salmoides* (Lacépède 1802) when foraging on novel mosquitofish prey *Gambusia holbrooki* Girard 1859 (Wintzer & Motta, 2005). Likewise, capture efficiency was lower for reared *S. trutta,* although they still improved with experience (Sundström & Johnsson, 2001). Wild cod *Gadus morhua* L. 1758 also consumed more two-spotted gobies *Gobiusculus flavescens* (Fabricius 1779) per attack and were energetically more efficient foragers than reared *G. morhua* (Steingrund & Fernö, 1997). In this study, HR *C. nebulosus* did not appear to strike as vigorously as wild *C. nebulosus* (L.A. Jackson, pers. obs.). Similarly, Steingrund & Fernö (1997) noted that reared *G. morhua* spent more energy attacking prey than wild *G. morhua.* Such behavioural differences can indirectly affect post-release survival by making reared fishes more conspicuous to predators.

Additional experience with a novel prey type should lead to enhanced feeding profitability. In this study, the time to first prey capture was much longer for HR *C. nebulosus* during the first few exposures, but thereafter this metric rapidly converged towards the level shown by wild *C. nebulosus.* Similarly, Paszkowski & Olla (1985) found that experienced *O. kisutch* smolts captured sand shrimp *Crangon* sp. more quickly than those with less experience. Experience can enhance foraging efficiency through improvements in prey manipulation skills so as to facilitate consumption via reorientation or dismemberment of prey (Hughes *et al.,* 1992). HT potentially limits the maximum feeding rate, or energy yield per unit time (Werner & Hall, 1974). In this study, significantly higher HT for HR *C. nebulosus* probably reflected their lack of experience.

The experimental design of this study enabled the detection of effects of experience as well as effects of motivation due to satiation and the frequency of prey encounter. Prey density is an external environmental factor affecting the prey encounter rate (Eggers, 1977); whereas, satiation is an internal factor affecting hunger-related motivation (Croy & Hughes, 1991*b*). Prey encounter rate depends on the product of the ability to perceive prey and the external effect of prey density. By focusing attention on feeding, hunger imposes an internal mediating influence on foraging in addition to the cognitive effects of experience (Croy & Hughes, 1991*a*; Adriaenssens & Johnsson, 2011). Experience also reinforces the motivation to feed on novel prey. For example, Ellis *et al.* (2002) inferred marked differences between wild and reared *S. maximus* in their motivation to capture and consume novel prey. Time-to-completion metrics in this study reflected both internal and external factors that might differentially affect the motivation to feed.

Assessing the capability of HR fishes to feed on live novel prey is critical for ascertaining whether a particular species of reared fish can adapt to the natural setting. The experimental setting in this study did not duplicate many relevant aspects of the natural setting. Foraging arenas constrained prey escape while not incorporating

effects of habitat complexity as a prey refuge. In nature, predators encounter multiple prey types, each possessing unique escape abilities and defensive adaptations (Tinker *et al.,* 2009). Furthermore, under natural conditions, the development of foraging skills might be hindered by the need for vigilance against the threat of predation (Hughes *et al.,* 1992). Conversely, Hossain *et al.* (2002) found that starved Japanese flounder *Paralichthys olivaceus* (Temminck & Schlegel 1846) were more readily captured by predators than satiated *P. olivaceus.*

Although experimental conditions did not match the natural setting, the laboratory setting facilitated comparisons of well-defined foraging skills between HR and wild *C. nebulosus.* Marked improvements in foraging skills of wild *C. nebulosus,* however, probably did not reflect experience with a novel prey type, as wild *C. nebulosus* were presumably already familiar with *Palaemonetes* spp. as prey. Instead, the experimental setting probably resulted in both groups of *C. nebulosus* being confronted with unique challenges. Likewise, escape success improved for crimson spotted rainbowfish *Melanotaenia duboulayi* (Castelnau 1878) in conjunction with their familiarity relative to the experimental setting (Brown, 2001). Thus, improvements in some foraging skills may reflect responses to different challenges by wild and HR *C. nebulosus.* Moreover, improvement did not always level off for one or both groups within the experimental time frame. Thus, juvenile *C. nebulosus* possess considerable capacity to learn feeding performance skills.

In conclusion, although wild juvenile *C. nebulosus* completed most feeding performance metrics more effectively than HR *C. nebulosus, C. nebulosus* exhibited sufficient foraging plasticity to switch from a pelleted diet to feeding on live novel prey. Such flexibility requires learning capacity, which should play a key role in the post-release survival of HR fishes (Brown & Laland, 2001). The ontogeny of this inherent prey switching capacity was complex for *C. nebulosus.* Skill levels for various elements of the predation cycle improved at different rates as HR *C. nebulosus* acquired more experience across successive feeding trials. The role of foraging in mediating the survival of HR *C. nebulosus* in the natural environment is still unknown. Further research needs to examine how foraging capabilities and deficiencies of HR *C. nebulosus* might affect their survival upon release.

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