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The effect of prey density on foraging mode selection in juvenile lumpfish: balancing food intake with the metabolic cost of foraging

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Summary

1. In many species, individuals will alter their foraging strategy in response to changes in prey density. However, previous work has shown that prey density has differing effects on the foraging mode decisions of ectotherms as compared with endotherms. This is likely due to differences in metabolic demand; however, the relationship between metabolism and foraging mode choice in ectotherms has not been thoroughly studied.
2. Juvenile lumpfish *Cyclopterus lumpus* forage using one of two modes: they can actively search for prey while swimming, or they can 'sit-and-wait' for prey while clinging to the substrate using a ventral adhesive disk. The presence of these easily distinguishable foraging modes makes juvenile lumpfish ideal for the study of foraging mode choice in ectotherms.
3. Behavioural observations conducted during laboratory experiments showed that juvenile lumpfish predominantly use the 'cling' foraging mode when prey is abundant, but resort to the more costly 'swim' mode to seek out food when prey is scarce. The metabolic cost of active foraging was also quantified for juvenile lumpfish using swim-tunnel respirometry, and a model was devised to predict the prey density at which lumpfish should switch between the swim and cling foraging modes to maximize energy intake.
4. The results of this model do not agree with previous observations of lumpfish behaviour, and thus it appears that juvenile lumpfish do not try to maximize their net energetic gain. Instead, our data suggest that juvenile lumpfish forage in a manner that reduces activity and conserves space in their limited aerobic scope. This behavioural flexibility is of great benefit to this species, as it allows young individuals to divert energy towards growth as opposed to activity. In a broader context, our results support previous speculation that ectotherms often forage in a manner that maintains a minimum prey encounter rate, but does not necessarily maximize net energy gain.

Key-words: behaviour, fish, optimal foraging, physiological ecology, trade-offs.

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Introduction

In many foraging models, the energetic cost of locomotion is either ignored or treated as a constant. However, it is now becoming clear that animals will alter their prey search tactics in response to certain environmental variables, thus altering the amount of energy spent on activity while foraging (O'Brien, Evans & Browman 1989; Bautista, Tinbergen & Kacelnik 2001). In particular, individuals of some species are capable of switching between foraging modes, usually alternating between 'active' and 'ambush' search strategies (McLaughlin 1989; Helfman 1990). Active foragers (also referred to as 'pursuit' or 'wide-ranging' foragers) move about their environment in search of prey, while ambush foragers (also referred to as 'sit-and-wait' foragers) remain relatively immobile, and will only attack prey that move into their field of view. It is generally assumed that active foragers spend more energy on movement, but capture increased numbers of prey, whereas ambush foragers capture less prey, but spend less energy in doing so.

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The foraging method utilized is an important consideration when evaluating foraging models as the energy required for locomotory activity can be substantial (Bishop 1999; Weibel & Hoppeler 2005). Moreover, total aerobic scope (i.e. the difference between minimal and maximal metabolic rates) often constrains the simultaneous usage of oxygen consuming physiological functions, which in addition to activity, include growth, maintenance, and digestion (Jobling 1983; Priede 1985; Bishop 1999). Assuming that the budgeting of metabolic costs is additive, the energetic demands of activity are in direct competition with these other physiological functions for allocation within an animal's energy budget. Indeed, empirical evidence suggests there is a trade-off between activity and other physiological functions such as growth, as individuals displaying elevated levels of activity have also been found to have decreased growth rates (Huey & Pianka 1981; Koch & Weiser 1983; Nagy, Huey & Bennett 1984; Secor & Nagy 1994; Rennie *et al.* 2005).

One of the most important factors affecting foraging mode appears to be prey density. Norberg (1977) originally considered foraging mode in birds and mammals under time constraints, and theorized that individuals should switch to the more energetically costly mode as prey density increases. Subsequent tests of this hypothesis using endothermic species have generally supported Norberg's predictions (e.g. Rudolph 1982), but experiments performed with ectotherms have instead shown that individuals use low cost strategies at high prey densities and switch to active foraging at low densities (Formanowicz 1982; Grant & Noakes 1987). Findings such as these prompted Helfman (1990) to speculate that the relatively low metabolic demands of ectotherms may allow them to switch foraging modes in a manner opposite to that of endotherms. Specifically, he hypothesized that while endotherms must choose the foraging mode that maximizes the ratio of energy intake to energy spent (to support their increased metabolic demands), ectotherms need only maintain a minimal prey encounter rate. More recent work has generally supported Helfman's predictions (Fausch, Nakano & Kitano 1997). However, it has been difficult to confirm the influence of metabolism on foraging mode choice in ectotherms, as most studies examining the effects prey density have not quantified the energetic demands of standard and active metabolism in the species examined.

This study examines the choice of foraging mode in juvenile lumpfish *Cyclopterus lumpus* Linnaeus 1758. Members of the family Cyclopteridae possess a ventral adhesive disc with which they adhere to rocks, vegetation, and other available substrates (Brown 1986; Moring 1989). Previous observations have shown that for young lumpfish, this disc is important in the expression of two alternate foraging modes (Brown 1986): (1) an ambush strategy, where individuals remain fixed to the substrate and display relatively little movement except to attack passing prey items, and (2) an active foraging strategy, in which individuals swim through the water in search of prey. These radically different foraging modes make juvenile lumpfish well suited for studying the energetics of foraging mode selection. Specifically, our goals were to examine the effects of prey density on foraging mode choice in juvenile lumpfish, and to quantify the metabolic cost of active foraging in this species. This allowed us to develop a preliminary model for predicting the prey density at which lumpfish should switch between the two foraging modes. Also, by combining behavioural observations of foraging activity with measures of metabolic rate, we hoped to gain a better understanding of the mechanisms governing foraging mode choice in juvenile lumpfish, and ectotherms in general.

Methods

Masses of lumpfish *Cyclopterus lumpus* eggs were collected by SCUBA in June of 2005 and transported to the Ocean Sciences Centre (OSC) in Logy Bay, Newfoundland. Experiments were performed with a mixture of eggs from four families. Once at the OSC, the eggs were placed in aerated incubators supplied with fresh seawater and maintained at 11 °C. Immediately following hatching, larvae were carefully transferred to holding tanks that were maintained at the same temperature, and fed enriched *Artemia* nauplii three times daily (750 *Artemia* L^{-1}) until they were 11 weeks of age. At this time the lumpfish had fully developed fins and cutaneous pigmentation consistent with the juvenile stage of development.

BEHAVIOURAL OBSERVATIONS

At 11 weeks of age, individuals were transferred to experimental tanks (10 lumpfish per tank), which were flow-through 40 L glass aquaria with darkened sides ($50 \times 26 \times 30$ cm). After a 1-week acclimation period, tanks (three tanks per treatment) were randomly designated to receive prey densities of either 75 or 750 *Artemia* L^{-1} (added three times daily). *Artemia* were added to each tank by mixing the appropriate number of *Artemia* (the total amount to be added to a particular tank during that feeding period) in 1 L of seawater, and then dispersing this mixture evenly across the surface of the tank. The *Artemia* were then quickly mixed throughout the water column by the current created by an airstone placed in each tank. As such, the distribution of *Artemia* throughout the tank quickly became homogeneous. *Artemia* were observed to be swimming in the water column at all times during the day. Any excess prey and faecal matter at the bottom of the tanks were removed by siphoning at the end of each day. All experimental tanks were exposed to a 16 h : 8 h light : dark photoperiod.

Observations of foraging behaviour were performed twice a week for a 6-week period, beginning 1 week after individuals were transferred to the experimental tanks. After a 2-min acclimation period following the addition of the prey *Artemia*, the focal animal technique

Table 1. General Linear Model results for proportion of time spent clinging for juvenile lumpfish *Cyclopterus lumpus* exposed to two different prey densities (75 and 750 *Artemia* L^{-1}), and the proportion of fish in each treatment observed to be clinging before, and 8–10 min after, the addition of the prey *Artemia*. For the proportion of time spent clinging, the model included the explanatory variables of prey density and week (representing time over the duration of the study which was a categorical variable). For the proportion of fish clinging before and after the addition of *Artemia*, the factor 'feeding' was also included in the model (to represent the effect of food addition)

Response variable	Source	d.f.	*F*	*P*
Time spent clinging	density	1	285·57	< 0·0001*†
	week	5	3·36	0·0054*†
	density × week	5	2·99	0·0116*
	residuals	414		
Proportion of fish clinging	density	1	518·83	< 0·0001*†
	week	5	17·30	< 0·0001*†
	feeding	1	92·41	< 0·0001*†
	density × week	5	9·14	< 0·0001*
	density × feeding	1	33·27	< 0·0001*
	week × feeding	5	1·43	0·2168
	residuals	125		

*Indicates a significant effect ($P < 0·05$).
†Indicates a lower order term that cannot be evaluated independently because of a significant interaction term.

(Altmann 1974) was used to observe lumpfish behaviour. Using this technique, the behaviours of one individual are recorded over a specific length of time (1 min in the present study). As described by Brown (1986), the foraging behaviour of lumpfish includes two easily distinguishable foraging modes: *Cling* and *Swim*, and each have associated modal action patterns (MAPs; Barlow 1968; Table 1). Of interest to the present study were: (1) *Bite*, in which the individual made a rapid forward movement in an attempt to capture an *Artemia* in its mouth (could be performed while clinging or swimming), and (2) *Hop*, in which an attached individual would temporarily leave the surface of the substrate to bite at a passing *Artemia* (could only be performed while clinging). Using these measures, we created a category called *Capture* for use in the analysis (equal to *Bite* for the swim mode, and *Hop* + *Bite* for the cling mode). Behaviours were recorded and tabulated using a hand-held Psion event recorder and associated software (The Observer 3·0, Noldus Information Technology Inc., the Netherlands).

During each observational period, behavioural observations were performed for six individuals per tank. Further, an effort was made to initiate observations with three fish that were swimming and three fish that were clinging, but this was not always possible, particularly in the high density treatments where it was rare to see individuals use the swim foraging mode. However, fish were free to move throughout the experimental tanks, and over the course of a given observation, it was common for individual lumpfish to switch between the cling and swim modes. In these cases, observations were divided into time intervals representing the time spent either clinging or swimming. The frequencies of the event MAPs (bites, hops and captures) were then converted to counts/minute spent in each mode. To avoid biases caused by disproportionate counts of behaviours while in a given mode for a short duration, intervals were not included in the final analysis if the focal lumpfish spent less than 5 s performing that mode. Also for each tank, the proportion of individuals clinging was estimated by performing a scan count of the number of fish that were in the clinging posture. This was done twice – once before the addition of *Artemia* (prior to the observations of foraging behaviour for that tank), and once after observations for that tank had concluded (approximately 8–10 min after the addition of *Artemia*).

GROWTH MEASUREMENTS

At the beginning and end of the experiment, five lumpfish were haphazardly selected from each tank ($n = 15$ per treatment), anaesthetized using MS-222, and measured for total length and wet mass. Length measurements were made using Matrox Inspector 3·0 image analysis software on images captured using a digital camera (Pixera PVC 100C). Following image capture, fish were quickly dried with a lint-free paper towel, and placed on dry, tared weigh-foils. Their wet mass was then measured using a microbalance (APX-60, Denver Instrument Co.).

RESPIROMETRY

Lumpfish used for measures of oxygen consumption were reared in two 60-L holding aquaria that were separate from the experimental tanks described above. To help determine the effects of body size on energy expenditure during foraging in young lumpfish, two size classes were used for measurements of metabolic rate: a 'small' class (207·9 ± 0·01 mg wet mass, 2·14 ± 0·08 cm total length; $n = 9$), and a 'large' size class (594·0 ± 0·04 mg wet mass, 2·96 ± 0·06 cm total length; $n = 9$).

To prevent individuals from adhering to the inside of respirometers (see below), fish were lightly anaesthetized

using MS-222 and a thin film of adhesive (VetBond® 3M Tissue Adhesive) was applied to their ventral disk with the aide of a dissecting microscope (this was done 12–15 h prior to the initiation of measurements). After being revived in aerated 11 °C seawater, fish were carefully placed in the respirometer (one individual per trial), and subjected to a brief 'training' trial (approximately 5 min) where they were exposed to low current velocities (0·5–1·5 body lengths (BL) s^{-1}) so they could orient against the current and acclimate to changes in water velocity. Individuals were allowed to acclimate overnight, and no mortalities resulted from the above procedure. To limit disturbance to the fish during the acclimation and measurement periods, the top portion of the swim tunnel was covered with a sheet of dark plastic. However, each fish's swimming behaviour was observed using a mirror placed below the swim tunnel.

Lumpfish oxygen consumption at various swimming speeds was measured using a glass Blazka-type respirometer (total volume of the respirometer and external circuit containing the oxygen sensor = 57 mL; Killen, Costa, Brown & Gamperl 2007). Oxygen concentrations within the respirometer were measured using a flow-through fibre-optic oxygen sensor (Presens, Germany), according to the methods of Killen *et al*. (2007). To maintain the temperature of the water in the respirometer, and to maintain oxygen concentrations in the water supplying the respirometer, an external circuit delivered aerated seawater to the respirometer from a reservoir located in a water bath set at 11 °C. However, as measurements of oxygen consumption could only be made when the circuit from this external reservoir was closed, the entire system was located in a cold-room set to 11 °C. To minimize the amount of background bacterial oxygen consumption, all seawater was sterilized with ultraviolet radiation, and the system was cleansed daily with absolute ethanol. In addition, blank measurements of background oxygen consumption were conducted immediately following each trial, and when necessary, this oxygen consumption was subtracted from the experimental measurements.

Measures of active metabolic rate (and metabolic scope) were obtained for individual fish by performing a modified U_{crit} test as described by Brett & Glass (1963). Using this protocol, measurements of oxygen consumption were performed at increasing water velocity increments of 0·5 body lengths per s (BL s^{-1}). For the small size class, measurements of active metabolism began at 1·0 BL s^{-1}, and for the large size class, measurements began at 0·5 BL s^{-1} (below these speeds, the current was too slow to cause fish to consistently leave the bottom of the swim-tunnel and orientate against the current). The time spent at each experimental current speed was 15 min, with oxygen measurements lasting 8–12 min and commencing 3 min after each speed increase. The trial was stopped when the fish was exhausted, as indicated by an inability to escape contact with the rear grid of the swim tunnel for at least 20 consecutive seconds. It is often difficult to obtain measures of oxygen consumption while swimming in larval and juvenile fish as they are generally averse to continuous swimming in respirometers for extended time periods (even when swimming at low velocities; Kaufmann 1990). For this reason, individuals were given a 1-min 'rest' period between each stepwise increase in current speed.

VIDEOGRAPHY

To estimate the routine swim speed of lumpfish during active foraging, groups of lumpfish were transferred to plastic containers located in a cold-room held at 11 °C (10 lumpfish per trial). The bottom of each container was marked with 1 cm gridlines, and fish were videotaped as they foraged using a video camera (JVC GR-D250V Digital Video Camera) suspended above the container. To stimulate foraging activity, prey were added to the container (at either 75 or 750 *Artemia* L^{-1}), and recordings were initiated after a 5-min acclimation period. Trials were performed for two different size classes of lumpfish ('small' 1·99 ± 0·04 cm total length, and 'large' 2·87 ± 0·07 cm total length), to match the size classes used in the measurements of active metabolism. Three trials were performed for each size class-prey density combination. Recordings were reviewed using frame-by-frame analysis (Adobe Premier Version 6·0, Adobe Systems Inc.). Swim speeds of individual fish were obtained at four separate times during the recording, and combined to calculate a mean swim speed for that fish.

DATA ANALYSIS

All statistical analyses were performed with Minitab version 13·1 (Minitab Inc.), and the level of significance for all tests was $\alpha = 0{\cdot}05$. Data are presented as means ± SEM.

Behavioural observations

We recognize that tank effects are a potentially confounding factor, and for behavioural observations and growth parameters we performed statistical analyses to examine these effects. These analyses consisted of a two-way ANCOVA within each prey density treatment for growth data and prey capture frequencies, and a two-way ANOVA for the proportion of time spent clinging. Each test used all of the observations conducted for each week, and contained the explanatory variables of tank and study duration (in weeks; used as a covariate in each ANCOVA). In all cases, tank effects and the tank × duration interactions were nonsignificant ($P > 0{\cdot}50$ in all cases). Owing to the high number of observations performed for each tank during this study, this method is a highly sensitive test for tank effects. For this reason, the data from the individual tanks were pooled within each treatment, and the effects of rearing tanks were not used in subsequent analyses.

Differences in capture frequency (while clinging, while swimming, and total captures per minute) between

prey density treatments were detected using General Linear Models with normal error structure. Model suitability (in terms of normality, homogeneity, and independence of residuals; Sokal & Rohlf 1995) was verified with the use of residual-fit plots. Models were constructed using the explanatory variables of prey density and study duration (used a covariate), and also included a term for the interaction between these two variables. To identify differences in the proportion of time spent clinging, and in the proportion of fish that were clinging before and after the addition of *Artemia* for each observation, similar models were used except that the duration of the study was designated as a categorical variable instead of a covariate (because the data could not be fit using a linear regression). To identify significant differences between treatments during each week of the study, we also performed unpaired *t*-tests for all behaviours during each week.

Respirometry

Rates of oxygen consumption (mg O_2 h^{-1}) were calculated for each trial from the decrease in water oxygen content per unit time using linear regression. Power curves were then fitted to the relationship between oxygen consumption and swim speed, and standard metabolism (MO_{2stan}) was determined as the *y*-intercept of this relationship. Metabolic intensity (mass-specific metabolic rate), was determined by dividing measures of oxygen consumption for each fish by that individual's wet mass. The absolute aerobic scope (in terms of both mg O_2 g^{-1} h^{-1} and mg h^{-1}) for each fish was calculated for each size class by subtracting MO_{2stan} from the maximal oxygen consumption (MO_{2max}). Factorial aerobic scope was obtained by calculating the ratio of MO_{2max} : MO_{2stan} (this ratio is identical when calculated using either metabolic rate or metabolic intensity). Total cost of transport (in kcal kg^{-1} km^{-1}) was calculated using an oxycaloric coefficient of 3·25 cal mg O_2^{-1} (Parsons & Sylvester 1992). A second-order quadratic regression was then fitted to the relationship between swim speed (BL s^{-1}) and total cost of transport. Differences between size classes for absolute aerobic scope, factorial aerobic scope, minimum cost of transport, and swim speed at minimum cost of transport were examined using unpaired *t*-tests. Differences in swim speeds during foraging (as observed using videography) were detected using a two-way ANOVA with the factors of prey density and size.

Behavioural modelling

Using our behavioural observations and measures of metabolic rate, we then calculate models for predicting the prey densities at which lumpfish should switch between foraging modes (assuming the decision is based on maximizing net energy gain). By examining these models from the perspective of optimality, we were able to compare our data with the original speculation of Norberg (1977), who stated that animals should switch foraging modes in a manner that maximizes their net energy intake. First, the possible net energy gain was calculated for each foraging mode (swimming and clinging) at each experimental prey density (75 and 750 *Artemia* L^{-1}) using the following equation (similar to that described by Ware 1975):

$$\mathbf{E} = \mathbf{I}\boldsymbol{ps} - \mathbf{A} \qquad \text{eqn 1}$$

Where **E** is the net energy gained while either clinging or swimming; **I** is the total energy (cal h^{-1}) ingested while using either the swimming or clinging foraging mode; ***p*** is an assimilation factor representing the proportion of ingested energy that is digested (i.e. not lost as faeces or urine); ***s*** is a factor accounting for specific dynamic action (SDA; the rise in metabolic rate during the processing and digestion of food), and is expressed as a proportion of ingested energy; and **A** is the energy spent on locomotory activity (cal h^{-1}). Values for **I** were calculated by converting the average captures min^{-1} for each foraging mode over the study to total calories ingested per hour (using 0·0068 cal *Artemia*$^{-1}$; determined for samples of *Artemia* using bomb calorimetry). We estimated ***p*** using the non-ash composition of Salt Lake strain *Artemia salina* (approximately 62% protein, 31% lipid and 7% carbohydrates; Dhont & Van Stappen 2003), and previously published assimilation factors for each class of nutrient (Ware 1975; Morais *et al*. 2004). For *Artemia*, approximately 60% of the energy from protein is recovered during digestion (***p*** for protein portion = 0·60; Morais *et al*. 2004). Lipid and carbohydrate assimilation factors specific to *Artemia* are unavailable, thus we used general estimates for each nutrient class, provided for fish by Ware (1975; ***p*** = 0·85 for lipids, and 0·40 for carbohydrates). Using this information, the overall value for ***p*** was calculated to be 0·66. The exact proportion of ingested energy representing SDA in lumpfish is unknown, but SDA in juvenile coregonids fed *Artemia* has been observed to account for 28% of ingested energy (Dabrowski & Kaushik 1984). Using this as an estimate of SDA yields a value for ***s*** of 0·72 for the lumpfish. Values for **A** were determined from the relationships between metabolic rate and swim speed for each lumpfish size class. For swimming lumpfish, metabolic rate at the average foraging speed (as determined by videography) was used for **A**. For clinging fish, we assumed no activity, and standard metabolic rate was thus used for **A** (although it should be noted that this is likely to be a slight underestimate of **A** for the cling mode, as lumpfish did display occasional movements even while clinging).

Results

BEHAVIOUR

Overall, lumpfish at the high prey density spent significantly more time clinging than those at the low prey

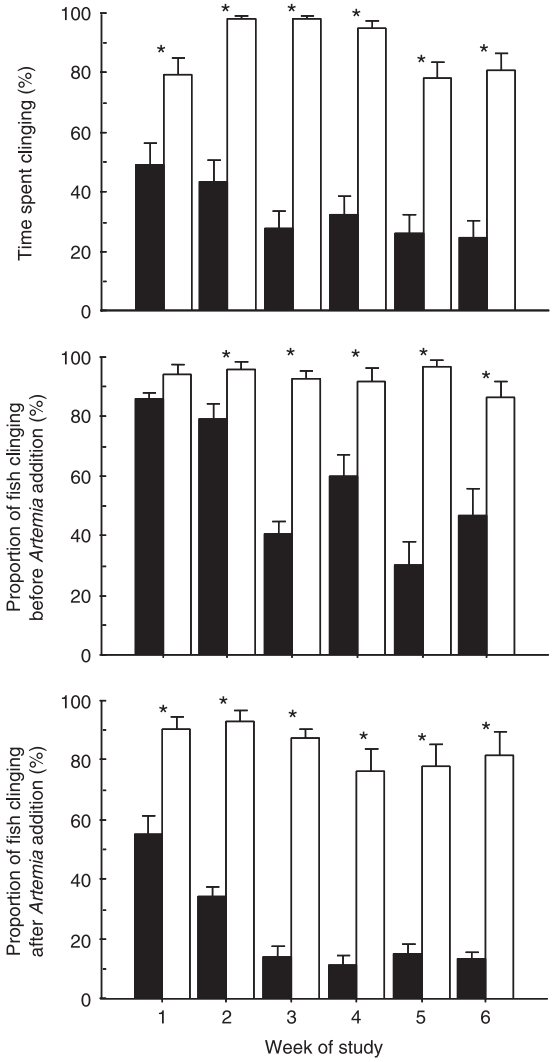

Fig. 1. Top panel: proportion of time spent clinging by juvenile lumpfish *Cyclopterus lumpus* exposed to low (75 *Artemia* L^{-1}; dark bars) and high (750 *Artemia* L^{-1}; light bars) prey densities. Middle and bottom panels: the proportion of juvenile lumpfish clinging before the addition of *Artemia* (at the beginning of the observational period), and after the addition of *Artemia* (count conducted at the end of the behavioural observations for a particular tank, approximately 8–10 min after the beginning of the observation). Data are mean ± SEM. *Represents a difference between the two treatments for observations conducted during a particular week (unpaired *t*-test, $P < 0{\cdot}05$). Details for overall statistical modelling are given in Table 1.

density (Table 1, Fig. 1). However, the time spent clinging at the low density decreased from 49·08 ± 7·39% during week 1 to 24·47 ± 5·99% during week 6. In contrast, the proportion of time spent clinging by lumpfish at the high density remained relatively constant. The proportion of individual lumpfish that were clinging in each tank generally decreased after the addition of *Artemia* (especially at the low prey density, Table 1, Fig. 1). Moreover, both before and after the addition of *Artemia*, there were generally more lumpfish clinging at the high prey density (except before *Artemia* addition during week 1 of the study).

While clinging, lumpfish at the high prey density were able to capture about 2·5 times more prey than individuals at the low prey density (5·90 ± 0·22 and 2·34 ± 0·21 captures min^{-1}, respectively, Table 2, Fig. 2). However, while swimming, there was no significant difference in the amount of prey captured, with lumpfish at the low density performing 5·29 ± 0·15 captures min^{-1}, and those at the high density performing 5·25 ± 0·56 captures min^{-1}. In total, lumpfish at the high prey density were able to capture significantly more prey (6·16 ± 0·20 captures min^{-1}) than those at the low prey density (4·57 ± 0·14 captures min^{-1}; 34·8% more captures overall at the high prey density). Total capture rates increased significantly over the course of the study, although the number of *Artemia* captured while either clinging or swimming did not change. This suggests that the increase in total captures over the 6-week study was due to a shift towards more time spent swimming (particularly for lumpfish in the low density treatment; Fig. 1).

There were no significant differences in total length (unpaired *t*-test, $t = -0{\cdot}463$, $P = 0{\cdot}647$, d.f. = 28; Table 3) or wet mass ($t = -0{\cdot}728$, $P = 0{\cdot}473$, d.f. = 28) between the two prey density treatments at the start of the study. However, by the end of the study, lumpfish at the high prey density had total length and wet mass values that were 29·1% and 2·5-fold greater, respectively, than those at the low prey density ($t = -9{\cdot}539$, $P \leq 0{\cdot}0001$, d.f. = 28; and $t = -8{\cdot}375$, $P \leq 0{\cdot}0001$, d.f. = 28).

RESPIROMETRY

For both size classes, metabolic intensity (expressed in mg O_2 g^{-1} h^{-1}) and metabolic rate (mg h^{-1}) increased in a curvilinear manner with swim speed (Fig. 3). Standard metabolic rate and standard metabolic intensity (i.e. the *y*-intercepts of the relationships between swim speed and oxygen consumption) for the small size class were 0·052 mg O_2 h^{-1} (0·169 cal h^{-1}) and 0·265 mg O_2 g^{-1} h^{-1}, respectively, whereas these values for the large size class were 0·133 mg O_2 h^{-1} (0·430 cal h^{-1}) and 0·217 mg O_2 g^{-1} h^{-1}.

Standard metabolic intensity was not significantly different between the large and small size classes, but the large lumpfish had significantly higher values for standard metabolic rate (ANCOVA, $F = 46{\cdot}48$, $P \leq 0{\cdot}0001$, d.f. = 17). Further, although absolute aerobic scope ($MO_{2max} - MO_{2stan}$) was not different between size classes when calculated using metabolic intensity, it was significantly greater for large lumpfish when calculated using absolute metabolic rate (Table 4). Factorial aerobic scope (MO_{2max}/MO_{2stan}) showed no difference between size classes. Minimum cost of transport was significantly greater for the small size class (6·17 ± 0·24 kcal kg^{-1} km^{-1}, Fig. 4) as compared with the large size class (4·28 ± 0·31 kcal kg^{-1} km^{-1}; unpaired *t*-test, $t = -4{\cdot}765$, $P = 0{\cdot}0003$, d.f. = 17). Moreover, the swim speed at minimum cost of transport for the small size class (2·48 ± 0·04 BL s^{-1}) was significantly greater as

Table 2. General Linear Model results for total captures per minute, captures while clinging, and captures while swimming for juvenile lumpfish *Cyclopterus lumpus*. The model included the explanatory variables of prey density and week (representing time over the duration of the study; was used as a covariate)

Response variable	Source	d.f.	*F*	*P*
Total captures	density	1	18·41	< 0·0001*
	week	1	4·92	0·027*
	density × week	1	3·40	0·66
	residuals	423		
Captures while clinging	density	1	26·42	< 0·0001*
	week	1	1·21	0·273
	density × week	1	0·93	0·335
	residuals	320		
Captures while swimming	density	1	0·95	0·331
	week	1	2·24	0·135
	density × week	1	0·99	0·321
	residuals	239		

*Indicates a significant effect ($P < 0·05$).

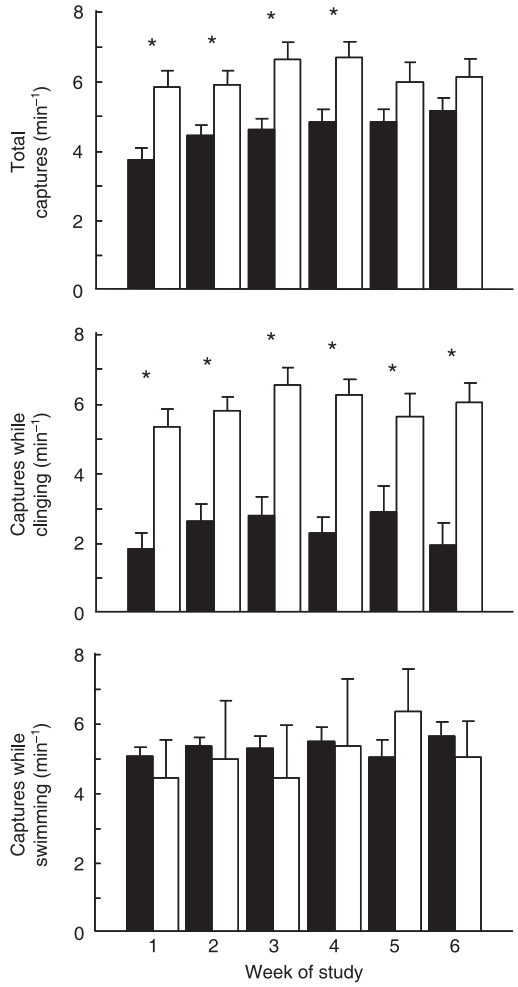

Fig. 2. Frequencies of total prey captures (top panel), and those performed while either clinging (middle panel), or swimming (bottom panel) for juvenile lumpfish *Cyclopterus lumpus*. Dark bars represent individuals in the low prey density treatment (75 *Artemia* L^{-1}), while the light bars represent those at the high prey density (750 *Artemia* L^{-1}). Data are mean ± SEM. *Represents a difference between the two treatments for observations conducted during a particular week (unpaired *t*-test, $P < 0·05$). Details for overall statistical modelling are given in Table 2.

Table 3. Measures of total length and wet mass for juvenile lumpfish *Cyclopterus lumpus* before and after the 6-week study

	Prey density (*Artemia* L^{-1})	Total length (mm)	Wet mass (mg)
Initial	75	14·4 ± 0·3	120·3 ± 1·3
	750	14·6 ± 0·4	119·2 ± 1·4
Final	75	18·9 ± 0·3	201·6 ± 1·1
	750	24·5 ± 0·5*	584·2 ± 1·5*

*Indicates a significant difference between the prey density treatments ($P < 0·05$, unpaired *t*-test).

compared with the large size class (1·90 ± 0·05 BL s^{-1}; $t = –9·033$, $P \leq 0·0001$, d.f. = 17).

Average swim speeds while foraging obtained from video analyses were not dependent on size class (ANOVA, $F = 0·00018$, $P = 0·989$, d.f. = 1, 40), but were significantly affected by prey density (ANOVA, $F = 4·823$, $P = 0·0339$, d.f. = 1, 40). For the small size class, mean swim speeds were 0·996 ± 0·11 BL s^{-1} at the high prey density (0·183 cal h^{-1}; 8·3% above standard), and 1·197 ± 0·08 BL s^{-1} at the low prey density (0·189 cal h^{-1}; 11·8% above standard). For the large size class, mean swim speeds were 0·989 ± 0·04 BL s^{-1} at the high density (0·459 cal h^{-1}; 6·7% above standard), and 1·206 ± 0·09 BL s^{-1} at the low density (0·474 cal h^{-1}; 10·2% above standard).

Values for net energy gained while either swimming or clinging were plotted against prey density (Fig. 5). Assuming a linear relationship between net energy gain and prey density for each foraging mode, a foraging strategy to maximize net energy gain would dictate that lumpfish should switch modes at the density where these linear relationships intersect. For the small size class, this potential switch-point occurs at approximately 620 *Artemia* L^{-1}, and for the large size class, it occurs at approximately 600 *Artemia* L^{-1}.

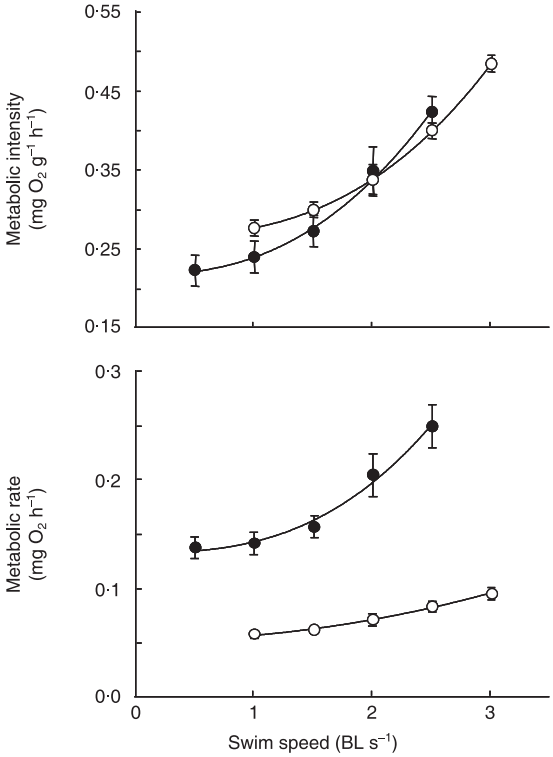

Fig. 3. Relationship between metabolic intensity and swim speed (top panel) and metabolic rate and swim speed (bottom panel), in juvenile lumpfish *Cyclopterus lumpus* at 11 °C. Open circles represent the 'small' size class (207·9 ± 0·01 mg) and filled circles represent the 'large' size class (594·0 ± 0·04 mg). Regression equations for metabolic intensity are as follows: small size class: $y = 0{\cdot}011x^{2{\cdot}72} + 0{\cdot}265$, $r^2 = 0{\cdot}99$; large size class: $y = 0{\cdot}022x^{2{\cdot}45} + 0{\cdot}217$, $r^2 = 0{\cdot}99$. Regression equations for metabolic rate are: small size class: $y = 0{\cdot}004x^{2{\cdot}17} + 0{\cdot}052$, $r^2 = 0{\cdot}99$; large size class: $y = 0{\cdot}0085x^{2{\cdot}88} + 0{\cdot}133$, $r^2 = 0{\cdot}99$. Standard rates of oxygen consumption are represented by the y-intercept for each equation. Regression lines were calculated using individual data points, but for simplicity, only the mean values of the data are shown in each figure (± SEM).

Table 4. Absolute and factorial aerobic scope for juvenile lumpfish *Cyclopterus lumpus* of two size classes (small: 207·9 ± 0·01 mg; and large: 594·0 ± 0·04 mg). Aerobic scope is shown in terms of both metabolic intensity and metabolic rate ($MO_{2max} - MO_{2stan}$)

	Absolute scope		
Size class	(mg O_2 g^{-1} h^{-1})	(mg h^{-1})	Factorial scope
Small	0·218 ± 0·01	0·042 ± 0·01	1·82 ± 0·03
Large	0·205 ± 0·02	0·166 ± 0·02*	1·94 ± 0·09

*Indicates a significant difference between size classes.

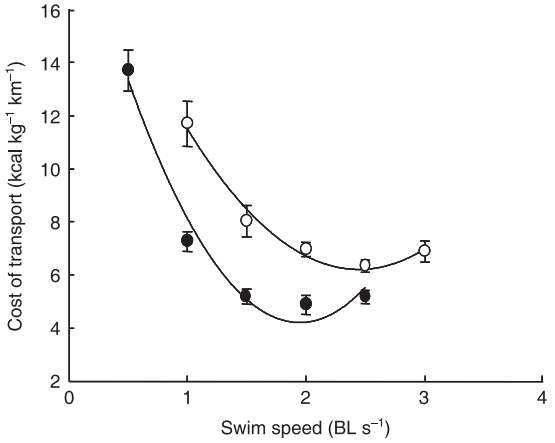

Fig. 4. Cost of transport for juvenile lumpfish *Cyclopterus lumpus*. Open circles represent the 'small' size class (207·9 ± 0·01 mg) and dark circles represent the 'large' size class (594·0 ± 0·04 mg). Regression equations are as follows: small size class: $y = 21{\cdot}34 - 12{\cdot}38x + 2{\cdot}53x^2$, $r^2 = 0{\cdot}98$; large size class: $y = 20{\cdot}67 - 16{\cdot}91x + 4{\cdot}34x^2$, $r^2 = 0{\cdot}97$. Regression lines were calculated using individual data points, but for simplicity, only the mean values of the data are shown in each figure (± SEM).

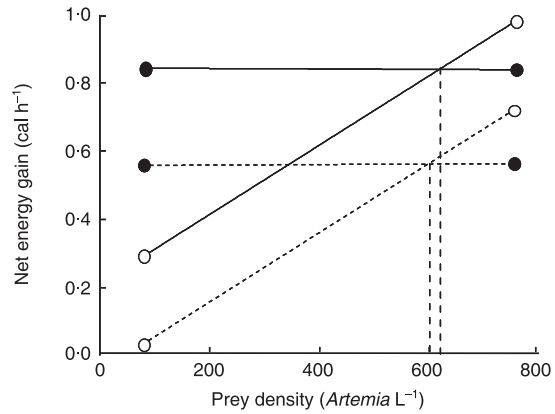

Fig. 5. Potential net energy gain by juvenile lumpfish *Cyclopterus lumpus* foraging by either clinging (open circles) or swimming (filled circles). Lumpfish acting to maximize their net energy gain should switch foraging modes at the prey density at which the net energy gain obtained by swimming and clinging intersect. According to these assumptions, smaller juveniles (solid lines) should switch at approximately 620 prey L^{-1}, and larger juveniles should switch at approximately 600 prey L^{-1} (dotted lines).

Discussion

Our results indicate that prey density is an important factor in determining the foraging mode utilized by juvenile lumpfish. Lumpfish at the high prey density spent a greater proportion of time clinging, while those at the low prey density spent more time swimming. This is contrary to early predictions regarding alternate foraging modes by Norberg (1977), but support Helfman's (1990) later hypothesis regarding foraging mode choice that was specific to ectotherms. Norberg (1977) stated that ambush foraging should be used at low prey densities because the energetic costs of activity will easily outweigh food intake when prey is scarce. However, Norberg's theoretical work mainly focused on mammals and birds, for which the energetic cost of activity may be five to 50 times resting metabolic rate (Bishop 1999; Weibel & Hoppeler 2005). In contrast, Helfman (1990) suggested that the lower metabolic rate of ectotherms might allow them to actively forage at

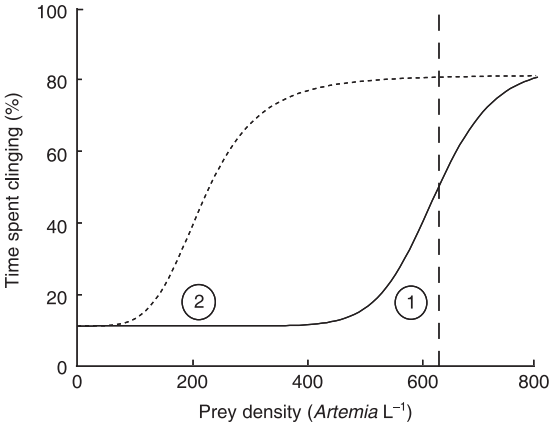

Fig. 6. Potential behavioural responses (proportion of time spent clinging) of juvenile lumpfish *Cyclopterus lumpus* to changes in prey density. Scenario 1 (solid sigmoidal curve) indicates a response that would maximize net energy gain, and agree with the model described in Fig. 5 (for the small size class). According to this scenario, the cling mode would be the dominant foraging strategy (individuals would spend greater than 50% of their time clinging) at prey densities above 620 prey L^{-1} (the switch-point that is predicted by the model for the small size class; is indicated by the vertical dashed line). Scenario 2 would indicate that juvenile lumpfish switch to the cling mode at prey densities much lower than is predicted by the model, and would suggest that lumpfish act to maintain some minimum prey encounter rate (and not to maximize net energy gain).

low prey densities and switch to an ambush strategy when prey is abundant. Our results support this reasoning, as the energetic cost of locomotion in actively foraging lumpfish is only 6–12% higher than at rest (depending on size and prey density). This relatively low cost of activity for lumpfish allows an active foraging strategy at low prey densities to still be energetically profitable.

Based on the hypothesis that juvenile lumpfish switch foraging modes to maximize their net energy intake, we devised a model for predicting the prey density at which they should switch between the swim and cling foraging modes. According to this model, lumpfish acting to maximize their net energy gain should only cling at relatively high prey densities, and should spend the majority of their time swimming at all lower prey densities (Fig. 6, scenario 1). The same conclusion might be reached after simply considering the low cost of swimming activity in the lumpfish (i.e. given the low cost of activity, why don't lumpfish swim all the time?). However, the limited information available for young lumpfish suggests they do not follow this pattern of behaviour. For example, larval and juvenile lumpfish in the laboratory predominantly use the cling mode at densities as low as 250 *Artemia* L^{-1} (Williams & Brown 1991). Furthermore, in the wild, young lumpfish are known to spend large amounts of time attached to substrates or seaweed (Moring 1989; Moring & Moring 1991), even though summer and fall zooplankton densities off the coast of Newfoundland are generally less than 100 individuals L^{-1} (Dower, Pepin & Leggett 2002).

This apparent discrepancy between the model predictions and lumpfish behaviour could be explained by the model's assumption that lumpfish act to maximize net energy intake. The observation that lumpfish behaviour does not fit the model may allow us to reject this assumption, and instead support Helfman's (1990) speculation that ectotherms act to maintain a minimum prey encounter rate, and *not* necessarily to maximize net energy gain. Given that the cling position seems to be the 'default' foraging mode of young lumpfish, we propose that they aim to reduce swimming whenever possible, but possess the behavioural flexibility to switch to the swim mode at very low prey densities (Fig. 6, scenario 2). As is indicated by our model, lumpfish will still receive a net energetic gain if they use the cling mode at intermediate and perhaps even low densities, even though they would not be maximizing the gains that would be possible by swimming at these same densities. Only the large size class in our study would receive extremely low net energy gains via clinging at the lowest prey densities, and so it is possible that larger juvenile lumpfish will switch to active foraging at a higher prey density relative to smaller individuals.

The question, however, still remains: why wouldn't lumpfish act to maximize their net energy gains? First, it should be noted that numerous studies have observed that animals often behave as energy satisficers when foraging and not optimizers (Ward 1992; Nolet, Gyimesi & Klaassen 2006), and an important aspect of satisficing is that an animal forages only enough to fulfil some minimal requirement (Ward 1992). However, this threshold is difficult to define (Nonacs & Dill 1993), especially for juvenile fishes, which must not only satisfy maintenance requirements, but also obtain surplus energy that can be used for some amount of growth. Owing to the extreme importance of growth during the early life stages of fishes (mainly to avoid size-dependent predation; Bailey & Houde 1989; Fuiman 1994), it is somewhat surprising that juvenile lumpfish do not maximize net energy gains while foraging. It should be emphasized, however, that ectotherms have low metabolic demands in comparison with endotherms, and so even during the juvenile stage they may be able to support their metabolism through ambush foraging alone while exposed to high and intermediate prey densities. In addition, the reduced energy intake resulting from ambush foraging may be offset by the benefits that come with reduced exposure to predators. For lumpfish, swimming would make an individual more obvious to predators, and larval lumpfish have been observed to increase the amount of time spent clinging when in the presence of a predator (Williams & Brown 1991). The presence of predators could cause active foraging to be detrimental to overall fitness, except at very low prey densities.

However, from an energetics perspective, reduced activity may also be beneficial for ectotherms because it allows them to conserve their limited aerobic scope

for other physiologically demanding processes such as growth and digestion (and not simply because it reduces energy expenditure *per se*). Fish face an increased risk of mortality when operating near the upper limit of their aerobic scope (Wood, Turner & Graham 1983; Wood 1991), and there is powerful selection for individuals that can reduce their power requirements so that they do not approach this upper limit (especially for slow swimming fish or those with a limited aerobic capacity; Priede 1985). Owing to their small size and high metabolic intensity, young fish have a reduced aerobic scope compared with adults, and must fit the demands of growth, digestion and activity into an extremely tight energy budget (Weiser *et al*. 1988; Kaufmann 1990; Weiser & Medgyesy 1990; Post & Lee 1996; Killen *et al*. 2007). This appears to be an especially important concern for juvenile lumpfish, as our data show that lumpfish have a very limited aerobic scope (factorial aerobic scope = 1·80–1·95) even when compared with juvenile fish of other species, such as Danube bleak *Chalcalburnus chalcoides* and roach *Rutilus rutilus* (2·5–4; Kauffman 1990); Atlantic cod *Gadus morhua* (2·5; Soofiani & Priede 1985); and pike *Esox lucius* (2·7; Weiser, Laich & Medgysey 1992). Thus, it is likely that young lumpfish use the cling posture as a means to reduce activity and preserve space within their narrow energy budget for other physiological processes. In particular, they may prioritize growth, which is important during the early life stages of fish (Bailey & Houde 1989; Fuiman 1994).

Additional evidence that juvenile lumpfish do not forage in a way that maximizes net energy gains comes from the observation that, even when actively foraging, they swim at speeds different from that which minimizes their cost of transport. Although the speed that minimizes the cost of transport in fish is typically greater than that which provides the minimum cost per unit time (Priede 1985; Gamperl *et al*. 2002), foraging at this increased swim speed will actually decrease overall energy expenditure because individuals will have increased prey encounter rates (Ware 1975; Pyke 1984), and will therefore need to forage for a shorter duration to capture the same amount of food. However, if lumpfish were to forage at this increased swim speed, the rate of energy expenditure while swimming would comprise a significant portion of their available aerobic scope. For example, the lumpfish in our study swam at speeds of 0·99–1·21 BL s^{-1} (depending on prey density and size), which equates to between 7 and 15% of their absolute aerobic scope. On the other hand, if juvenile lumpfish were to swim at the speed that minimizes their cost of transport (1·90 BL s^{-1} for the large size class, and 2·48 BL s^{-1} for the small size class), this activity would comprise approximately 46–70% of their absolute aerobic scope. Therefore, although swimming at these speeds would decrease foraging times and reduce overall energy expenditure, it would greatly constrain the ability of lumpfish to simultaneously perform additional physiological functions while swimming.

Lumpfish clinging at the high prey density were able to capture 2·5-fold more prey than those clinging at the low density. This supports the contention that the low cost foraging mode is usually the least efficient at decreased prey densities (Norberg 1977), and highlights why lumpfish may switch to active foraging when prey is scarce. Interestingly, the number of prey captured between treatments was not significantly different among fish that were swimming. This result was unexpected, as the prey intake rates of young fish that forage while swimming usually increase with prey density (Houde & Schekter 1980; Munk 1995). In contrast, lumpfish seem to respond to increases in prey availability by adopting the cling posture (as opposed to increasing their prey intake while swimming). This supports the view that the cling position is the 'default' foraging mode of young lumpfish, and that they aim to reduce swimming whenever possible.

In summary, the foraging mode utilized by juvenile lumpfish is heavily influenced by prey density. Model predictions that assume that lumpfish act to maximize their net energy intake do not match previous observations of lumpfish behaviour, suggesting that this species instead switches foraging modes to maintain some minimum level of prey intake. However, although juvenile lumpfish do not appear to optimize their energy intake while foraging, they may be maximizing their overall fitness as adopting a 'cling' posture allows lumpfish to conserve space in their extremely limited aerobic scope (< 2-fold). Future experiments should attempt to confirm this hypothesis by determining the precise density at which juvenile lumpfish increase the proportion of time spent clinging, and by examining how other factors (e.g. the presence of a predator) may represent a further constraint on foraging mode choice beyond the effects of prey density alone.

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