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Testing foraging arena theory: The effects of conspecific density and habitat type on time and energy budgets of juvenile cunner

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ABSTRACT

Density-dependent settlement, growth and mortality are often the major factors controlling recruitment success of recently-settled marine fishes. During this stage, juvenile fishes generally have spatial refuges from predation, and forage in limited but risky areas near refuges. Little is known about the mechanisms by which the tradeoff between feeding and refuge use lead to density dependent mortality. Foraging arena theory predicts that feeding activity should depend strongly on juvenile density and predation risk. Selection should act on the time that juveniles spend foraging, so as to strike a balance between growth and mortality. Because the risk of predation also varies with habitat, it is expected that variation in foraging times and resulting growth and mortality rates will be habitat-specific and density-dependent. This study tested these concepts by respirometric measurement of the metabolic cost of feeding and shelter site defense in young-of-year cunner (*Tautogolabrus adspersus*) in the northwest Atlantic. Metabolic costs were applied to time budgets measured in the field to estimate in-situ energy budgets. Contrary to expectation, time and energy spent on foraging increased as habitat complexity or conspecific density decreased. Time and energy spent on refuge defense increased with increasing predation risk (as mediated by habitat complexity) or conspecific density, highlighting the importance of refuge for a species that enters torpor at night and during the winter. Future recruitment studies should include examination of spatial habitat use by juveniles, and the behavioral and physiological mechanisms for adjusting behavior to varying food density and predation risk.

1. Introduction

The relative importance of specific life stages in determining future year-class strength of fish species depends on their duration and the respective mortality rates experienced during each stage (Sissenwine, 1984; Bradford and Cabana, 1997). Although many have argued that year class strength is set at the larval stage, more recent work has established that in species with short larval lives and/or long juvenile stage durations, year-class strength may not be established until the post-larval stage (Myers and Cadigan, 1993; Campana, 1996; Tupper and Boutilier, 1997). Because most teleost fishes produce pelagic eggs and larvae, demersal species must undergo a transition from pelagic to benthic habitats (Kaufman et al., 1992). To successfully complete the transition, fish must travel through the 'wall of mouths' near the bottom, rapidly adapt to a benthic lifestyle, and find refuge (Leis, 1991). Benthic processes may thus play as important a role in determining recruitment as events during the larval phase or adult densities (Stimson, 1990)

The transition phase is generally controlled by density dependent mortality and habitat use mediated by habitat-specific predation rates (Juanes, 2007; Schmitt and Holbrook, 2007; Hixon et al., 2012). Because juvenile fishes that remain closer to shelter can more easily escape predators, they forage in spatially and temporally restricted 'foraging arenas' (Walters and Martell, 2004; Ahrens et al., 2012). The competition in these feeding arenas results in density dependent growth and mortality as a consequence of increased risk of predation, due to higher levels of risk-taking in order to forage enough to attain a minimum viable size, leading to natural selection for restriction of foraging time in habitats with high predation risk (Walters and Juanes, 1993). Thus, survival should decrease with increasing foraging time due to predation risk, while long term survival-fecundity increases only when some minimum or threshold feeding time is exceeded because of the well-established fecundity-body size relationships in fishes (Bagenal, 1978). Because minimum feeding time is strongly and positively density dependent, selection for optimization of feeding time leads to density-dependent mortality. That is, juvenile survival should be a decreasing function of juvenile density because the minimum feeding time should increase with increasing density under constant predation risk.

Although density-dependent growth and mortality are evident in many fish populations the mechanisms underlying these processes are

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much less well understood. Various studies have concluded that although predation is the proximate cause of mortality, competition for space and/or food is likely the ultimate cause (Forrester and Steele, 2004; Hixon and Jones, 2005; Johnson, 2008). However, the role of predation risk and habitat on observed individual time and energy budgets as outlined by the foraging arena model has not been widely studied (see Biro et al., 2003; Ahrens et al., 2012 for recent reviews). In contrast, the ecosystem-scale implications of the foraging arena model have been well developed through linkages with Beverton-Holt recruitment models (Walters and Korman, 1999) and the use of ECOSIM and ECOPATH models (Walters and Martell, 2004; Ahrens et al., 2012).

The behavioral predictions of the foraging arena model were tested using young-of-year (YOY) cunner (*Tautogolabrus adspersus*, fam. Labridae). Previous work has shown that cunners exhibit density-dependent growth and mortality in the postsettlement phase when recruitment is likely determined (Levin, 1993, 1994, 1996; Tupper and Boutilier, 1995a, 1997; Nitschke et al., 2002). The goals of this study are to assess whether time and/or energy allocation differ with predation risk and/or conspecific abundance. Specific predictions are that time and energy spent foraging should decrease as a function of habitat complexity, a proxy for habitat-specific predation risk, and increase with conspecific density.

2. Materials and methods

The cunner, *Tautogolabrus adspersus* (fam. Labridae) inhabits nearshore waters from Conception Bay, Newfoundland, south to Delaware (Auster, 1989). Cunners are most abundant from the low tide mark to a depth of about 18–30 m. They are strongly associated with cover, and are found in abundance around rocky reefs, wharves and pilings or in dense vegetation. Cunners have a restricted home range, and newly settled individuals rarely move more than a few meters from their home shelter site (Green, 1975; Tupper and Boutilier, 1995a).

The cunner is a diurnally active species that undergoes a nocturnal dormant, or torpid, state. Dormancy begins 5–55 min prior to sunset and ceases 16–41 min after sunrise (Olla et al., 1975). Cunners will normally secure themselves in their home shelter site before entering dormancy. If shelter is unavailable before nightfall, cunners will enter dormancy on open bottom, thereby greatly increasing their risk of mortality (Dew, 1976). Cunners can survive a wide range of temperatures, but below 5 °C cunners become torpid and their oxygen consumption is depressed (Haugaard and Irving, 1943). During the winter months, cunners remain torpid within their home shelter site and do not feed. Activity resumes the next spring, when water temperatures reach 5–6 °C.

The study site was located in St. Margaret's Bay, Nova Scotia, an area characterized by rocky reefs formed from exposed bedrock and boulders (see Tupper and Boutilier, 1995a, 1995b, 1997 for more details on the site). Twenty YOY cunners were collected in August 1992, using stainless steel Gee™ minnow traps baited with frozen squid and soaked for 2 h. Captured cunners were transported back to the lab and kept in a flowing seawater aquarium system. Respirometry was then used to determine the metabolic rate, scope for activity, and energetic costs of foraging, resting and shelter site defense.

2.1. Experiment 1: determination of standard metabolic rate and scope for activity

The respirometry system used for all experiments in this study consisted of two identical transparent plastic containers. Each of the circular 2.5 L volume containers could be sealed with gas-tight lids and were placed in a flowing-seawater bath, the temperature of which was regulated to within ±1 °C of each experimental temperature. Grids of 1 cm squares were drawn on the bottom of the containers, allowing swimming speeds of spontaneously active fish to be measured. The water baths rested on two magnetic stir plates; stir bars on the container bottoms provided a circular water flow, which could be regulated from 1 to 20 cm/s. Flow speed was calibrated by filming dye particles at given settings of the stir plate. Flow speed was measured about 2 cm from the outside edge of the container; this was where cunner appeared to prefer to hold station. Oxygen consumption was measured with an Orion oxygen probe (model 08-97-00), which was inserted through a hole in the container lid. A rubber stopper with the center drilled out was placed around the neck of the probe and then smeared with silicone grease. This ensured a gas-tight seal between the probe and the lid.

The standard and active metabolic rate and scope for activity were determined for five individual YOY cunners. Fish of nearly identical size (45 ± 4.9 mm total length; 5.0 ± 0.7 g wet weight) were used in this experiment. Individual unfed fish were placed in the respirometer chamber at a flow speed of 1 cm/s and left overnight (16 h) to adjust to the chamber and the flow. Water temperature within the respirometer was maintained at 15 °C. Oxygen consumption was then measured in 30 min runs over a range of incrementally increased swimming speeds (1, 5, 10, 15 and 20 cm/s). Cunners swam well in the respirometer, and preferred to hold station about 2 cm from the outside edge of the chamber, where they could remain more or less parallel to the water flow. At low swimming speeds, cunners employed a labriform mode of swimming, i.e. sculling with the pectoral fins. As swimming speeds increased, cunners gradually switched to a carangiform swimming mode, utilizing their trunk and tail musculature. When the fish could no longer hold station against the current, the experiment was terminated, and the fish was removed from the respirometer and weighed. The respirometer chambers were emptied and refilled after each run. Because small environmental variations can lead to large differences within individuals in metabolic rate (Dahlhoff et al., 2002), the procedure was repeated three times per individual, with a 2-week rest in between runs on the same individual, and oxygen consumption data for each individual were pooled.

Linear regression was used to determine the relationship between oxygen consumption and swimming speed. The resulting equation was used to calculate the active metabolic rate, i.e. the oxygen consumption at the critical swimming speed (determined as per Brett (1964)), and to extrapolate the standard metabolic rate, i.e. the oxygen consumption at the y intercept of the equation. Scope for activity was calculated as the difference between active and standard metabolic rates.

2.2. Experiment 2: metabolic cost of shelter site defense

The metabolic costs of shelter site defense were estimated on three of the individual cunner that were subjected to experiment 1, so that their standard and active metabolic rates were known. Shelter sites for YOY cunner were constructed by cutting PVC pipe into 10 cm lengths of 2 cm internal diameter. Routine rates of oxygen consumption during 2 h bouts of spontaneous activity were measured for each individual (three runs per individual at 24 h intervals; fish remained in the chamber between runs) with three shelter sites placed in the respirometer chamber. Following the individual runs, a group of three individuals was placed in the respirometer chamber along with three shelter sites and the experiment was repeated. Finally, the experiment was repeated a third time with three individual cunners but only one shelter site present.

The bottom of the respirometer chamber encompassed an area of approximately 300 cm^2 (not including surface area provided by shelter sites). This approximated a density of 10 YOY individuals$\cdot m^{-2}$, which can occur in very dense natural populations (Nitschke et al., 2002). Each treatment was repeated in triplicate, using 3 different individuals per run, with a 3-day interval between treatments. For each treatment the total oxygen consumption of the group was compared to the sum of the individual oxygen consumptions of the fish making up the group. If the group oxygen consumption exceeded the sum of the

individual routine metabolic rates, it was assumed that the increased oxygen consumption resulted from interactions between individual cunner within the group. In order to support this assumption, behavior of the group was observed throughout each run, and the number of agonistic interactions over shelter sites was recorded. Oxygen consumption was compared among shelter site treatments using ANOVA.

2.3. Time budgets

At seven biweekly intervals from early September to mid-December, ten YOY cunners were captured in each of four habitat types using a 10% solution of the anesthetic Quinaldine sulfate (Sigma) in seawater, dispensed from a plastic squirt bottle. Anesthetized fish were collected with a small aquarium dip net and placed in a floating tub of seawater. The seawater tub was brought to shore, where the captured fish were measured to the nearest mm TL and marked by injecting acrylic dye of either under the eye, on the gill plate, or in both locations, either on the left or right side of the fish. The combination of different injection sites and four different colours (red, green, blue and yellow) allowed individual fish to be recognized. The tub containing marked fish was then refloated at the water's edge to maintain temperature, while a battery-powered pump was used to aerate the tub water. After 1 h, the marked fish were returned to the capture site and released.

The waters of St. Margaret's Bay are characteristically clear, with average lateral visibility about 10 m, allowing for relatively easy observation of individual cunner for prolonged periods. The tidal range in St. Margaret's Bay averages about 1.1 m. Sites were in about 1.5 m depth at low tide and about 2.5 m depth at high tide. The average depth at time of observation was approximately 2 m. Observations were made while snorkeling. This provided several advantages over the use of SCUBA, which would limit the observation time to the length of the air supply and would produce bubbles, which might disturb the fish.

Time budgets were constructed by observing an individual marked cunner for 2 h periods in four distinct habitat types: rocky reefs (most complex), cobble bottoms, seagrass (*Zostera marina*) beds, and sand (least complex) (see effects of habitat complexity below). All observations were taken from 1200 to 1400 h on partly sunny to sunny days, to avoid possible effects of light intensity, water clarity and/or circadian rhythms on activity. All activities were timed to the nearest 30 s and recorded immediately in a waterproof notebook. A total of ten observations (i.e. 20 h of total observation on 10 individuals) were made in each habitat. The timed observations were then divided into three categories:

1) Resting: The time the fish spent resting within the shelter site. It was assumed that the fish did not become dormant (i.e. maintained the standard metabolic rate) during the daylight hours (see Tupper and Boutilier, 1997), but was torpid within 1 h after sunset (Olla et al., 1975).

2) Foraging: The total time spent on prey search and feeding. Prey search was identifiable as swimming in a slightly downward-tilted plane with the eyes focused on the substrate, while feeding consisted of “pecking” motions as the cunner ingested small crustaceans or other invertebrates.

3) Defense: The total time spent on agonistic interactions involving defense of a shelter site or food supply, including all swimming involved in chasing or escaping other fish. Newly settled cunners are very site-attached (Olla et al., 1975; Tupper and Boutilier, 1995a, 1997), and the time spent swimming outside of foraging and defense was negligible.

2.4. In-situ swimming speed

In addition to quantifying the amount of time spent on each activity, swimming speed of foraging YOY cunners was also measured in situ. Since over 90% of all swimming occurred during foraging bouts, swimming speed was measured as a means of more accurately determining foraging costs. Swimming speed was estimated by recording the time it took for a marked YOY cunner to swim between two points (e.g. between a shelter site and a feeding area) and then measuring the distance between those points in cm. The swimming speed in cm/s was then converted to body lengths per second (bl/s). While this method does not account for swimming in the vertical plane, YOY cunners tended to stay very close to the substrate, minimizing the distance swum vertically. As with observations of behavioral activities, all measurements of swimming speed were conducted from 1200 to 1400 h. Swimming speed was estimated for 11 individual cunners, ranging in size from 25 to 60 mm TL.

2.5. Effects of habitat complexity on time budgets

Time budgets were constructed as above for ten individual cunners per habitat, and the mean time allocated to each category was compared between habitat treatments using analysis of variance (ANOVA). The complexity of these habitats was estimated by measuring substrate rugosity. A fine-link brass chain was fitted to the bottom contours along twelve 10 m transects in each habitat type. The total distance covered by the chain was then divided by 10 m (the horizontal transect length) to arrive at an index of substrate rugosity. It is important to note that substrate rugosity is simply a measure of the actual surface area of bottom structure available to an organism and does not account for other possible forms of shelter, such as that provided by macroalgae or seagrasses. The association of newly settled cunners with macroalgae has been well documented in the Gulf of Maine, USA (Levin, 1991, 1993, 1994). However, in St. Margaret's Bay, intense grazing by green sea urchins (*Strongylocentrotus droebachiensis*) reduced algal cover on hard bottom to a short filamentous turf. Within seagrass beds, YOY cunners were always observed in association with hard bottom (e.g., scattered small rocks, debris, empty scallop (*Placopecten magellanicus*) shells). This suggests that at these sites, vegetation is less important in providing shelter than the physical structure of the bottom per se.

To determine the role of habitat complexity in mediating predation, observations of predation by other fishes on YOY cunner were made in situ along the same 10 m transects used to estimate substrate rugosity. The observer floated motionless above the transect while recording the species and number of predators, the number of attempted strikes (lunges at a cunner), and the number of successful strikes (capture and ingestion of a cunner) over a 1 h observation period. An index of predator success was then calculated by dividing the number of successful strikes by the total number of strikes, for each of the four habitat types. Mean predator success in each habitat was calculated as the average predator success over all transects in each habitat. Among-habitat variation in predator density and capture success was determined by ANOVA. Tukey's HSD was used to determine differences among pairwise comparisons. Further details of the substrate rugosity and predation experiments can be found in Tupper and Boutilier (1997).

2.6. Effects of conspecific density on time budgets

The effects of conspecific density were quantified by experimental manipulations of cunner density. Twelve large boulders (glacial erratics), of similar size and at similar depth, and isolated from the nearest neighbouring hard bottom by at least 10 m (see Tupper and Boutilier, 1995a), were used as study reefs. The reefs were randomly divided into three groups of four, designated as low density, control and high density. On low-density reefs, the density of 1+ and older resident cunner was artificially lowered to 1 individual$\cdot m^{-2}$ by removal of individuals using anesthetic (10% solution of quinaldine sulfate (Sigma) in seawater). Individuals removed from the low-density reefs were released at a site on the far side of St. Margaret's Bay, about 3 km distant. On control reefs, natural resident density (2.4–3.2 individuals$\cdot m^{-2}$) was not manipulated. On high-density reefs, the density of 1+ and older cunner was artificially increased by transplanting cunner from

the far side of the bay. Density for this treatment was maintained at 5 individuals·m^{-2}. The density of age 1+ and 2+ cunners was manipulated because the high levels of settlement and mortality of young-of-year cunners precluded the control of their density. Moreover, the growth and survival of YOY cunners is negatively correlated with the density of age 1+ and 2+ cunners, as older cunners compete with the juveniles for food and for all but the smallest shelter sites (Tupper and Boutilier, 1995a). Larger cunners age 3 and older were not found at the study sites. Time budgets were constructed for ten individual cunners per density treatment, with the 10 individuals selected from among the four replicate reefs. Either 2 or 3 individuals were selected per reef such that all reefs were represented. The mean time allocated to each treatment was compared between density treatments using ANOVA.

2.7. Energy budgets

Energy budgets were constructed by applying the rates of oxygen consumption for each activity, as determined from the respirometry experiments, to the time budget data collected in the field. Energy budgets are simply the time budgets multiplied by these constant energetic costs (i.e. rates of oxygen consumption) for each activity.

2.8. Statistical analyses

Proportional data (percent time and energy allocated to various activities) were arcsin transformed and subjected to Levene's test for normality and Bartlett's test for homogeneity of variance (Sokal and Rohlf, 1994). Transformed data met the assumptions of parametric tests. The mean proportion of time spent on each activity was compared among habitats and among density treatments using one-way ANOVA. Post-hoc multiple comparisons were conducted using Tukey's Honest Significance Difference (HSD). The total energy expenditure (i.e. the sum of all activities) was compared among habitats and density treatments using one-way ANOVA. Total energy expenditure was also reported as a percentage of scope for activity.

3. Results

3.1. Metabolic rate and scope for activity

Fig. 1 illustrates the oxygen consumption of cunner over a range of swimming speeds, based on data pooled from each individual. The regression indicates that for cunners at 15 °C, $VO_2 = 152.4\ mg{\cdot}O_2{\cdot}kg^{-1}\ h^{-1} + 44.6$ (swimming velocity in $bl{\cdot}s^{-1}$). Standard metabolic rate is represented by the y intercept of the regression, 152.4 $mg{\cdot}O_2{\cdot}kg^{-1}\ h^{-1}$.

Table 1
Critical swimming speeds (U_{crit} in body lengths/s) measured on five 0+ cunner in the laboratory. Active metabolic rate ($mg{\cdot}O_2{\cdot}kg^{-1}\ h^{-1}$) and standard metabolic rate ($mg{\cdot}O_2{\cdot}kg^{-1}\ h^{-1}$) are estimated from inputting U_{crit} into the oxygen consumption equation ($VO_2 = 152.4\ mg{\cdot}O_2{\cdot}kg^{-1}\ h^{-1} + 44.6$, displayed in Fig. 1). Active VO_2 is the corresponding y-value for each value of U_{crit}, standard VO_2 is the y-intercept. Scope for activity is the difference between active VO_2 and standard VO_2 ($mg{\cdot}O_2{\cdot}kg^{-1}\ h^{-1}$).

Fish	U_{crit} (bl/s)	Active VO_2	Standard VO_2	Scope for activity
1	4.55	355.5	152.4	203.1
2	4.62	358.5	152.4	206.1
3	4.56	356.1	152.4	203.7
4	4.78	365.8	152.4	213.4
5	4.72	363.1	152.4	210.7
Grand mean	4.65	359.8	152.4	207.4

Table 1 lists the critical swimming speed (U_{crit}), active metabolic rate, standard metabolic rate and scope for activity of the tested five cunners. Mean U_{crit} was 4.65 body lengths per second. Inputting mean U_{crit} into the swimming speed regression yielded an active metabolic rate of 359.8 $mg{\cdot}O_2{\cdot}kg^{-1}\ h^{-1}$. The scope for activity is the active metabolic rate minus the standard metabolic rate, or 207.4 $mg{\cdot}O_2{\cdot}kg^{-1}\ h^{-1}$.

3.2. Metabolic cost of shelter site defense

Fig. 2 shows the routine metabolic rate of three cunner measured (i) individually with one shelter site each, (ii) as a group of three with one shelter site each, and (iii) as a group of three with only one shelter site among three fish. The routine metabolic rate differed significantly among the three treatments (ANOVA, $F = 185.8$, $p < 0.001$). Metabolic rate did not significantly differ between single individual cunner with one shelter site and a group of three individuals with three shelter sites (Tukey's HSD, $p = 0.72$). However, the three individuals sharing only one shelter site were observed to aggressively chase each other out of the shelter. Their metabolic rate was significantly higher (by a margin of almost 75%) than the other two treatments (Tukey's HSD, $p < 0.0001$ for all pairwise comparisons). Fig. 2 also shows the standard and active metabolic rates for these fish, as determined in Experiment 1 above. The difference between the active and standard metabolic rate is the scope for activity. Competition for shelter sites used up roughly 95% of the scope for activity when shelter was limited.

3.3. Habitat complexity and predation

Substrate rugosity, an index of habitat complexity, significantly differed among habitats and was highest on rocky reefs, followed by cobble bottoms, seagrass beds and sand (ANOVA, $F = 2.37$, $p = 0.05$; Table 2). Three sculpin species (fam. Cottidae) were observed preying

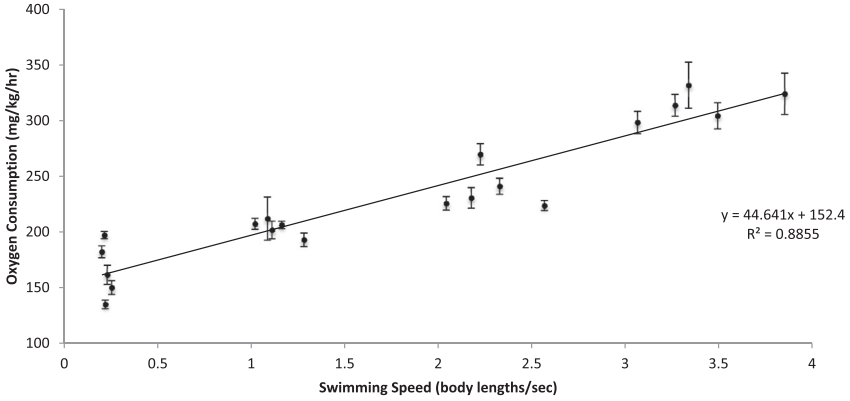

Fig. 1. Relationship between oxygen consumption ($mg{\cdot}O_2$/kg/h) and swimming speed (body lengths/s) of young-of-year cunners in the laboratory.

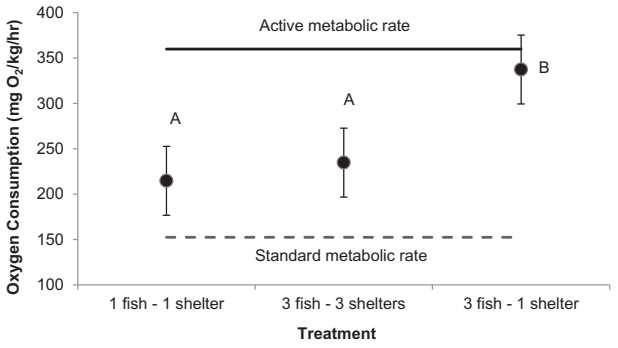

Fig. 2. Metabolic cost of shelter defense obtained in the laboratory. Data points are mean routine metabolic (oxygen consumption, mg·O_2/kg/h) rate of three cunners measured individually with one shelter site each, as a group of three with one shelter site each, or as a group of three with only one shelter site among three fish. Standard errors are displayed. Capital letters above points indicate significantly different means. Solid line represents the active metabolic rate, the dashed line the standard metabolic rate, both determined in the laboratory. The difference between the active and standard metabolic rate is the scope for activity.

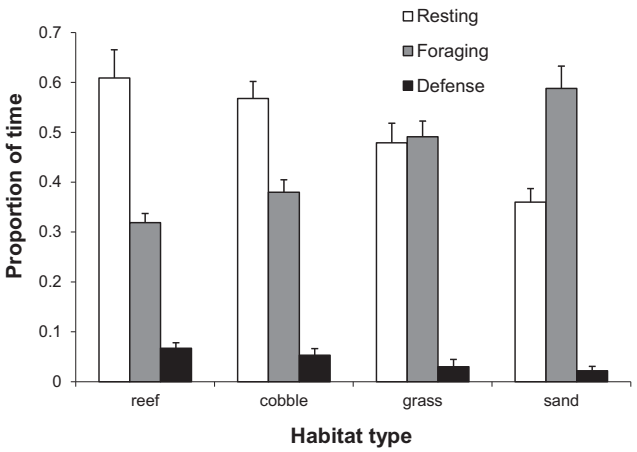

Fig. 3. Time budgets (proportion of time spent in each activity) of young-of-year cunners inhabiting different habitat types from most (reef) to least complex (sand). Standard errors are displayed. Sample sizes were 10 fish per treatment.

on YOY cunner: *Hemitripterus americanus*, *Myoxocephalus octodecemspinosus*, and *Myoxocephalus aeneus*. Total density of cottid predators did not differ among habitats (ANOVA, $F = 0.26$, $p = 0.85$; Table 2). Capture success varied significantly among habitats ($F = 364.9$, $p < 0.001$; Table 2). Capture success was highest on open sand bottoms and lowest in rocky reef habitats, and was inversely related to substrate rugosity (see Tupper and Boutilier, 1997).

3.4. Effects of habitat complexity on time budgets

The mean proportion of time spent foraging increased as habitat complexity decreased from reef (mean = 32%) to sand (59%) whereas shelter site use (61% to 36%) and defense (7% to 2%) decreased from reef to sand (Fig. 3). However in all cases, time spent in defense represented <7% of the total. The difference between habitats was significant (ANOVA, $F = 42.5$, $p < 0.001$). Time spent foraging did not differ between cunners on rocky reefs and cobble bottom (Tukey's HSD, $p = 0.23$), but cunners occupying *Zostera* beds spent significantly more time foraging than cunners on rocky reefs or cobble bottom (Tukey's HSD, $p < 0.001$ for both cases). Cunners on sandy bottoms spent more time foraging than in any other habitat (Tukey's HSD, $p < 0.001$).

Time spent defending shelter sites ranged from 1.7% on sandy bottoms to 7.3% on rocky reefs. There were significant among-habitat variations in time allocated to defense (ANOVA $F = 37.4$, $p < 0.001$). As with foraging, there was no difference between rocky reef and cobble habitats in the time spent on defense (Tukey's HSD, $p = 0.13$). There was also no significant difference between *Zostera* beds and sandy bottoms (Tukey's HSD, >0.51), although significantly less time was allocated to defense in sand and grass habitats than on rocky reefs or cobble bottoms (Tukey's HSD, $p < 0.001$ for pairwise comparisons). Similar to time spent foraging and defending shelter sites, there were significant differences across habitat types in the time spent resting within the shelter sites (ANOVA $F = 65.8$, $p < 0.0001$) and no difference between rocky reef and cobble habitats (Tukey's HSD, $p = 0.16$). In contrast to foraging, but similar to defense, cunners spent least amount of time resting in sand habitats followed by grass habitats, both significantly different from reef and cobble habitats (Tukey's HSD, $p < 0.001$ for all pairwise comparisons).

Table 2
Substrate rugosity, density per m^2 of cottid predators, and capture success of cottid predators on YOY cunner in each of four habitat types at St. Margaret's Bay, NS, Canada.

Habitat	Rugosity	Predator density	Capture success
Reef	3.86 ± 0.23	1.08 ± 0.10	0.18 ± 0.03
Cobble	3.09 ± 0.19	1.13 ± 0.09	0.26 ± 0.03
Seagrass	2.18 ± 0.23	1.07 ± 0.12	0.44 ± 0.02
Sand	1.22 ± 0.13	1.18 ± 0.12	0.67 ± 0.05

3.5. Effects of conspecific density on time budgets

The total time spent within the shelter site generally decreased as conspecific density increased (ranging from 54 to 63%, see Fig. 4). Analysis of variance indicated significant differences between density treatments in the proportion of time spent in shelter ($F = 44.9$, $p = 0.009$). However, there was no significant difference in the time spent in shelter between low density and control reefs (Tukey's HSD, $p = 0.24$), but cunners occupying high density reefs spent less time in shelter than those inhabiting low density (Tukey's HSD, $p = 0.039$) or control reefs (Tukey's HSD, $p = 0.047$).

The total time spent foraging also decreased as conspecific density increased (ranging from 18 to 37%; Fig. 4). The overall difference between treatments was significant (ANOVA, $F = 31.3$, $p < 0.001$) and all pairwise comparisons were significant (Tukey's HSD, all $p < 0.001$). In contrast, time spent defending shelter sites increased as densities increased (ranging from 1 to 28%; Fig. 4). There were significant differences between all treatments in time allocated to defense (ANOVA,

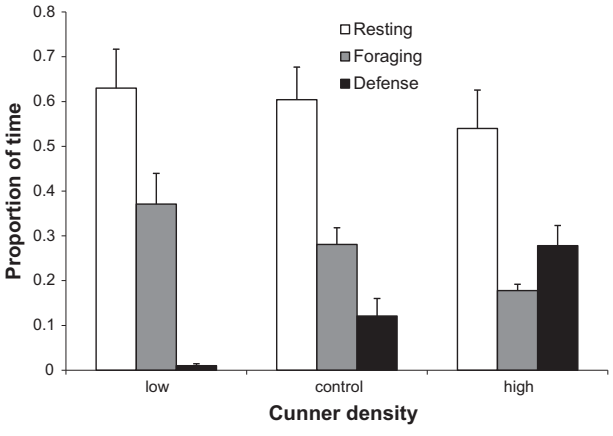

Fig. 4. Time budgets (proportion of time spent in each activity) of young-of-year cunners subjected to different conspecific densities. Low densities represent 1 individual·m^{-2}, control reefs were unmanipulated and represent natural resident density (2.4–3.2 individuals·m^{-2}). High densities represent 5 individuals·m^{-2}. Observations were carried out on rocky reef habitats only. Standard errors are displayed. Sample sizes were 10 fish per treatment.

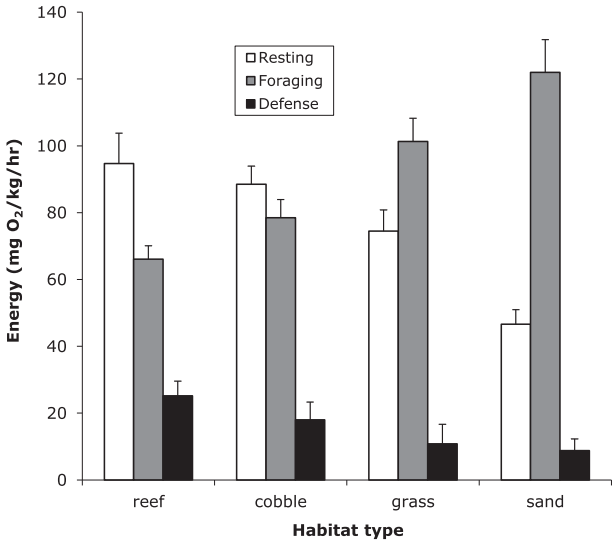

Fig. 5. Energy budgets of young-of-year cunners inhabiting different habitat types. Amount of energy ($mg \cdot O_2/kg/h$) allocated to each activity was calculated as the metabolic cost multiplied by the proportion of time spent on each activity. Standard errors are displayed. Sample sizes were 10 fish per treatment.

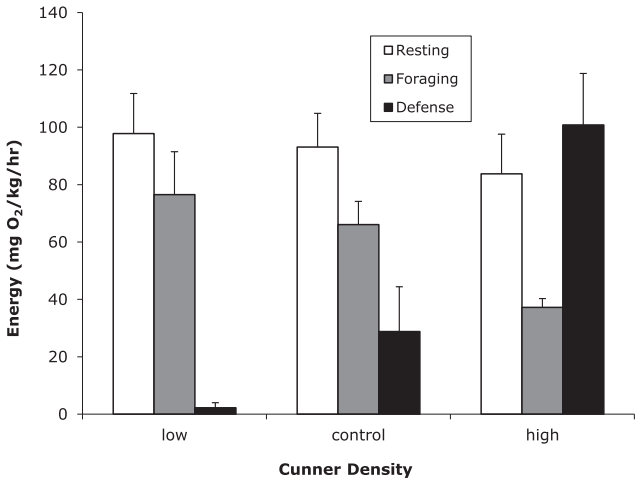

Fig. 6. Energy budgets of young-of-year cunners subjected to different conspecific densities. Amount of energy ($mg \cdot O_2/kg/h$) allocated to each activity was calculated as the metabolic cost multiplied by the proportion of time spent on each activity. Low densities represent 1 individual$\cdot m^{-2}$, control reefs were unmanipulated and represent natural resident density (2.4–3.2 individuals$\cdot m^{-2}$). High densities represent 5 individuals$\cdot m^{-2}$. Observations were carried out on rocky reef habitats only. Standard errors are displayed. Sample sizes were 10 fish per treatment.

$F = 114.5$, $p < 0.001$; Tukey's HSD, $p < 0.001$ for all pairwise comparisons).

3.6. Effects of habitat complexity on energy budgets

The metabolic rates determined by respirometry were applied to the in-situ time budgets. For resting, the standard metabolic rate of 152.4 $mg \cdot O_2/kg/h$ was used. For foraging, average swimming speed was assumed to be 1.2 bl/s, as determined from the in-situ swimming speed experiment. From the swimming respirometry, this speed equates to an oxygen consumption of 206.8 $mg \cdot O_2/kg/h$. For shelter site defense, the metabolic cost determined from the 3 fish/shelter site respirometry trial was used, which was 337.3 $mg \cdot O_2/kg/h$. When examining energy budgets the patterns are similar (i.e. energy spent foraging increased whereas defense and resting decreased as a function of habitat complexity), but the allocation of energy to defense was approximately double that represented by the time budget (Fig. 5).

The proportion of energy spent resting in shelter significantly differed between habitat types (ANOVA, $F = 65.6$, $p < 0.001$). Comparing habitat types, only cobble and reef did not differ (Tukey's HSD, $p = 0.16$). The proportion of energy spent resting in shelter differed between all other habitat types (Tukey's HSD, $p < 0.001$ for all comparisons). The proportion of energy spent on foraging differed significantly among all habitat types (ANOVA, $F = 129.6$, $p < 0.001$; Tukey's HSD, $p < 0.001$ for all pairwise comparisons). The proportion of energy spent on shelter site defense significantly differed among habitats (ANOVA, $F = 25.8$, $p < 0.001$), with the exception of reef and cobble (Tukey's HSD, $p = 0.12$ for reef vs. cobble, $p < 0.001$ for all other pairwise comparisons). Adding all activities together, there was a tendency for total energy expenditure to be higher on sand bottoms, but the difference among habitats in total energetic cost were not significantly different (ANOVA, $F = 2.7$, $p = 0.07$).

3.7. Effects of conspecific density on energy budgets

The proportion of energy spent resting in shelter did not differ significantly between density treatments (ANOVA, $F = 0.9$, $p = 0.11$) (Fig. 6). However, the proportion of energy spent on foraging decreased as density increased (ANOVA, $F = 47.2$, $p < 0.001$; and Tukey's HSD, $p < 0.001$ for all pairwise comparisons). The proportion of energy spent on shelter site defense increased markedly as density increased (ANOVA, $F = 134.1$, $p < 0.001$; and Tukey's HSD, $p < 0.001$ for all pairwise comparisons). Energy spent on defense differed by two orders of magnitude between low density and high density treatments.

4. Discussion

Recent reviews of the early life history of temperate and tropical reef fishes conclude that population regulation usually occurs soon after settlement as reflected by the substantial levels of density-dependent mortality experienced during this phase (Osenberg et al., 2002; Juanes, 2007). Much of the proximate cause of mortality is due to habitat-based differences in predation (Hixon and Jones, 2005) resulting in distributional patterns reflecting predator success (and prey response) as habitat complexity varies (e.g., Tupper and Boutilier, 1995b, 1997). What is much less well understood is how prey time and energy budgets respond to variation in habitat complexity, an index of predation risk, and to changes in conspecific densities.

Previous work on cunner and cod (*Gadus morhua* L.) in St. Margaret's Bay has shown that although settlement did not vary across habitats, the pattern of recruitment differed because survival rates were strongly habitat-dependent (Tupper and Boutilier, 1995a, 1995b, 1997). A reasonable explanation for this spatial pattern is that survival rates are mirrored by capture success rates of the major predators in each habitat. Predation risk on YOY cunners is not just a result of predator density (which did not vary between habitats) but also a strong function of habitat complexity through its effect on predator capture success and subsequent prey vulnerability (Tupper and Boutilier, 1997, this study). Habitat complexity also results in increased numbers of refuges or shelter sites, which along with the decreased predation success, leads to greater habitat suitability and decreased vulnerability to predation. How should prey daily budgets respond to these habitat-based differences in predation risk? Foraging arena theory predicts that foraging time should decrease in the face of increased predation risk and increase with density (Walters and Juanes, 1993; Ahrens et al., 2012).

Our results show that time (and energy) spent foraging increased as habitat complexity decreased. Because of the similar predator densities among habitats, predation success rates can be used as an index of habitat-dependent predation risk, resulting in a reduction of predation risk with increased habitat complexity. Thus the prediction that foraging time would decrease as a direct function of predation risk is not upheld. Instead, time spent in shelter and time spent defending the shelter

both increased as a function of habitat complexity. The contrast between foraging and defense is more marked when comparing energy budgets because of the higher energy involved in defense. Shelter site defense is energetically highly expensive and can consume the cunners' entire scope for activity. However, although there was a tendency for total energy expenditure to be higher on sand bottoms, the differences among habitats in total energetic cost were not significantly different. Because shelter quality is poor in low complexity habitats (e.g. pebbles, shell debris, or other small objects), whereas mortality is very high and strongly size-selective (Tupper and Boutilier, 1997), it may be more important to grow as fast as possible out of the vulnerability window than to use and defend poor shelters. Growth of YOY cunners was highest in eelgrass habitats compared to reef and cobble bottoms but could not be measured on sand bottoms because of the extreme mortality (or rapid emigration) suffered in this habitat (Tupper and Boutilier, 1997). Differences in foraging budgets could also have been a response to habitat-specific food availability, which wasn't measured as part of this study but is lowest in sand (Tupper, pers. observ.) and highest in eelgrass (see Sogard, 1992). In a similar study measuring growth and survival of recently settled cod (*Gadus morhua*) in St. Margaret's Bay, Tupper and Boutilier (1995b) found that cod survival was also a function of habitat complexity, lowest in sand and highest in reef/cobble, whereas growth was highest in eelgrass habitats and lowest on sand bottoms perhaps as a reflection of the higher prey densities potentially found in eelgrass beds.

Contrary to model predictions time (and energy) spent foraging decreased with increasing density. Instead, time and energy spent on shelter site defense increased with density to the point where at the highest densities more time was spent in defense than foraging. When converted to energy expenditure the trend is more extreme because of the energetic expense of defense activity. Similarly, total activity time (foraging plus defense) increased with density. This result is likely due to cunner's dependence on shelter, its site fidelity, and its need to go into torpor after dark. In contrast, in freshwater systems, various studies have shown that juvenile salmonids increase their activity (Larranaga and Steingrimsson, 2015), decrease shelter use (Armstrong and Griffiths, 2001; Davey et al., 2009), or shift how foraging time is distributed (Fingerle et al., 2016) as a function of conspecific density, but energy costs of such behaviors are rarely measured.

Cunners are active by day but enter a period of torpor at night at which time they must seek shelter or experience a very high risk of predation if found in a torpid state on an open bottom. Cunners in rocky reef habitats in St. Margaret's Bay increased their time and energy spent defending shelter sites from 2 to 7% during early afternoon (this study) to around 60% for the hour preceding dusk (Tupper, pers. observ.). Similarly, cunners become torpid in winter once temperatures reach about 5 °C when they rest in refuges until spring (Dew, 1976). This critical need for refuge likely explains the differences in time and energy spent defending the refuge across habitats, with highest expenditures in habitats with higher quality refuges. Because shelters are critical for survival, foraging time is likely sacrificed for increased shelter defense as density of conspecifics increases.

The high energy expenditure and reduced foraging of dense cunner populations results in lower growth and survival rates (Tupper and Boutilier, 1995a). The time spent active (i.e. exposed to predators) was lower at low densities. Higher survival on low density reefs may be due to the dual benefit of less time spent exposed to predation, and faster growth, which reduces the effects of size-selective mortality (Juanes, 1994; Sogard, 1997) and may lead directly to the observed density dependent mortality.

Although the specific predictions of the foraging arena model were not upheld in this study, a broader approach to the concept is suggested by considering total activity time and energy rather than just foraging time. Such an approach would lead to better predictions for species such as cunner whose recruitment is particularly sensitive to even small changes in habitat (Nitschke et al., 2002). However, very little is known about the dynamics of refuge use among prey populations (Krause et al., 2002). One exception is work on damselfishes where density dependent mortality is directly related to shelter use and is not detected during the day when fish are actively foraging (Holbrook and Schmitt, 2002). At high densities more individuals tend to be found in riskier locations near or just outside the perimeter of a refuge and thus at higher risk of predation.

Many studies have suggested that the behavioral trade-offs made between growth and survival are key to understanding population level density-dependence, but few field tests exist (Walters and Juanes, 1993; Lima and Zollner, 1996; Schmitz, 2001). More recent studies have suggested that the trade-off between growth and mortality rates leading to density dependence could be mediated by foraging activity and habitat use (Anholt and Werner, 1998a, 1998b; Nicieza, 2000; Biro et al., 2003; Johnson, 2006a, 2006b; Lindberg et al., 2006) or caused by the interplay of predation and competition (Hixon and Jones, 2005). This study extends these analyses by highlighting the importance of habitat variation in mediating time and energy budgets leading to habitat and density dependent growth and mortality. Future recruitment studies on a variety of demersal fishes should include examination of spatial habitat use by juveniles, and the behavioral and physiological mechanisms for adjusting behavior to varying food density and predation risk.

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