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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