

Species interactions through ontogeny: Effects of size-selective predation by red grouper on Caribbean spiny lobster in solution holes of Florida Bay

Robert D. Ellis*

Florida State University, Department of Biological Science, Tallahassee, FL 32306, United States

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ABSTRACT

Demographic size- or stage-structure can result in significant heterogeneity in species interactions within populations and ontogenetic shifts in the strength or type of these interactions have important consequences for populations. In the case of the Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804), and red grouper, *Epinephelus morio* (Valenciennes, 1928), both are important fishery species commonly found co-occurring in Florida Bay habitats. Red grouper are known to prey upon juvenile lobsters but karst solution holes excavated by red grouper often host large groups of lobsters. A combination of experiments tested the effect of red grouper on different lobster size classes to determine how this interaction changes through lobster ontogeny: red grouper were excluded from solution holes to test the effect of grouper presence on the abundance of each lobster size class; artificial dens were constructed to test the avoidance behaviors of small lobsters to red grouper; and a tethering experiment tested how lobster survival varied across size classes. Lobster abundance in solution holes with red grouper increased more than in holes where the grouper was removed (126% versus 16.9%), but this effect was strongest on adult and large immature lobsters. Experiments with artificial dens showed no effect of caged grouper presence on the abundance of small lobsters. Survival of tethered lobsters was lowest for small juveniles but again differed significantly between size classes. Overall, the distribution of lobsters in solution holes appears to be driven primarily by asymmetrical predation risk from red grouper through lobster ontogeny. Shifts in this interaction across life stages may play an important role in structuring the Caribbean spiny lobster population in Florida Bay.

1. Introduction

Multiple biotic and abiotic factors combine to regulate the distribution and abundance of marine fishes and invertebrates. Predation, especially during recruitment, is well-known to shape the structure and alter diversity of marine communities (Hixon, 1986; Sogard, 1997; Stier et al., 2017). Generally, predation has a negative effect on the abundance of small individuals and can play a large role in the size-structure of populations (Almany and Webster, 2006; Holmes and McCormick, 2010). Likewise, the role of habitat in modifying the effects of predation has been well studied in a variety of marine ecosystems. Habitat complexity has generally positive effects on prey abundance as more complex or variable habitats are associated with reduced prey mortality (Hixon and Beets, 1993; Eggleston et al., 1997; Johnson, 2007). However, predation and habitat complexity can interact in complex ways, for example by also enhancing the efficiency of mesopredators that benefit from reduced predation or competition in more complex habitats (Grabowski and Powers, 2004). When habitat quality is variable,

predators may force prey to occupy habitats of lesser quality, resulting in trade-offs between food availability and predation risk (Heithaus and Dill, 2002). Such trade-offs can have important ramifications for population structure when they modify transition rates between stages. Similarly, intra- and inter-stage competition for resources can ultimately reduce demographic transition rates and lead to smaller populations (Samhouri et al., 2009). As individuals transition through ontogenetic stages they experience different competition and predation regimes. In some cases, the sign of interactions may change between stages and the nature of these interactions will interact to regulate the adult population size and distribution of prey species (Werner and Gilliam, 1993).

The Caribbean spiny lobster (*Panulirus argus*; referred hereafter as “lobster”) life cycle proceeds through a series of distinct ontogenetic stages differentiated by changes in morphology, behavior, and habitat associations that experience different size-selective predation regimes. Following a planktonic larval stage that can last up to 8 months (Goldstein et al., 2008), postlarval lobsters settle preferentially on red

* Corresponding author at: Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL 33701, United States.
 E-mail address: robert.ellis@myfwc.com.

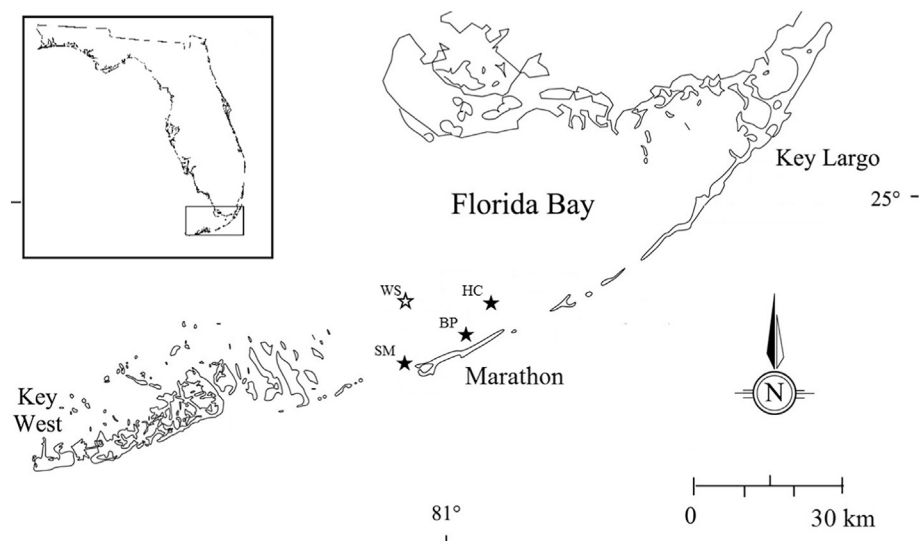


Fig. 1. Map of study area and sites used in study. Closed stars indicate observational sites: Seven-Mile Bridge (SM); Burnt Point (BP); Hawks Cay (HC). Open star indicates the experimental site: Wilkerson Bank (WS).

algae (*Laurencia* spp.) where they are solitary and feed on associated infauna until growing to around 23 mm carapace length (CL; Herrnkind and Butler IV., 1986). The transition from the algal to juvenile stage involves a noticeable change in coloration pattern and behavior as juveniles begin to aggregate with other lobsters (Childress and Herrnkind, 1996). Juvenile lobsters range in size from 24 to 45 mm CL and are typically associated with sponges, coral heads, and small crevices that are used as diurnal shelters (Bertelsen et al., 2009). Subadult and adult lobsters (> 46 mm CL) are highly gregarious and reside primarily in crevice shelters (Marx and Herrnkind, 1986; Childress and Herrnkind, 2001). Gregarious behaviors and the importance of chemical cues on aggregated shelter use increases as lobsters grow through the juvenile, subadult (large immature adult), and adult stages (Ratchford and Eggleston, 1998).

Predation on juvenile lobsters is intense, and behaviors that increase survival are likely to be under strong selection. Lobster predators include a variety of piscine and invertebrate species such as groupers (Epinephelidae), snappers (Lutjanidae), grunts (Haemulidae), triggerfish (Balistidae), toadfish (*Opsanus* spp.), sharks (e.g., *Ginglymostoma cirratum*), octopus (*Octopus briareus*), and crabs (e.g., stone crabs, *Menippe mercenaria*; Randall, 1967; Moe, 1969; Smith and Herrnkind, 1992; Mintz et al., 1994; Berger and Butler IV, 2001; Childress and Herrnkind, 2001; Bouwma, 2006). Gregarious behavior, typified by aggregation in shelters, enhances lobster survival (Smith and Herrnkind, 1992; Mintz et al., 1994). Lobsters use a variety of chemical cues to navigate their environment, and olfactory cues have been shown to be important for conspecific aggregation (Ratchford and Eggleston, 1998; Butler IV et al., 1999), avoiding diseased conspecifics (Behringer and Butler IV, 2010), and avoiding predators (Eggleston and Lipcius, 1992; Berger and Butler IV, 2001). Experiments that have tested lobster predator avoidance using mesocosms have found that lobsters will actively avoid nurse sharks (Eggleston and Lipcius, 1992) and octopuses (Butler IV and Lear, 2009), but there is no evidence to suggest that they actively avoid teleost predators.

In Florida Bay, exposed areas of the karst bottom are pockmarked with solution holes, crevice shelter habitat features used by juvenile, subadult, and adult lobsters as an important source of diurnal shelter (Herrnkind et al., 1997). Red grouper (*Epinephelus morio*), a common lobster predator found in Florida Bay, excavate sediment and detritus from solution holes, thereby increasing the amount of crevice shelter habitat available to other species (Coleman et al., 2010). Red grouper excavations are associated with more abundant and diverse faunal communities compared to solution holes without red grouper, and

surveys of lobster abundance found that red grouper presence in solution holes was also associated with increased abundance of lobsters (Ellis et al., 2017). Furthermore, the abundance of other lobster predators, including triggerfish (*Balistes capricus*), nurse sharks (*Ginglymostoma cirratum*), and goliath grouper (*E. itajara*), was greater when red grouper were also present, while other lobster predators commonly found in the bay (e.g., octopuses, toadfish) were conspicuously absent. The positive relationship between red grouper presence and lobster abundance in solution holes was true when all size classes of lobsters were grouped together. However, this relationship likely varies across lobster ontogeny, and while experiments in solution holes occupied by red grouper have found high predation risk for juvenile lobsters (Schratwieser, 1999), similar experiments have not yet been conducted for subadult and adult lobsters.

The combination of ontogenetic shifts and size-selective predation suggest that trophic interactions between lobsters and their predators may be complex and should be measured for all ontogenetic stages, not just at the species level (sensu Miller and Rudolf, 2011). In this study, I investigated the interaction between lobsters and red grouper in solution-hole habitats in Florida Bay across lobster ontogeny with a combination of observations and experiments. I monitored a fixed set of solution holes for four years to determine how red grouper presence and solution-hole size interact to control the abundance of each lobster size class. At a different set of solution holes, I experimentally manipulated red grouper presence to quantify the interaction strength between red grouper and each lobster size class. To test whether juvenile lobsters avoid dens already occupied by red grouper, I created artificial dens and tracked lobster colonization in the presence and absence of a caged grouper. Finally, I tethered lobsters adjacent to solution holes with red grouper to measure how survival in these habitats varies across lobster size. Collectively, these efforts describe how the lobster–red grouper interaction changes across lobster ontogeny.

2. Methods

2.1. Lobster abundance and size distribution in solution holes

From 2010 through 2013, I documented the abundance of lobsters found in solution holes at three sites in southwestern Florida Bay (Fig. 1). All three sites were characterized by the presence of seagrasses (mainly *Thalassia testudinum* and *Syringodium filiforme*), sponges, and octocorals interspersed with exposed limestone patches containing occasional solution holes. All solution holes were in water < 4 m deep

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