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PREDATION OF JUVENILE *JASUS FRONTALIS*: AN ENDEMIC SPINY LOBSTER OF THE JUAN FERNÁNDEZ ARCHIPELAGO, CHILE

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ABSTRACT This study identified and quantified in the field the natural predators of juvenile spiny lobster *Jasus frontalis*, an endemic, ecologically relevant species, and the most valuable local commercial catch of Robinson Crusoe Island. It also assessed the predation pressure that these predators exerted on juveniles lobsters and whether they showed preferences for particular body sizes within the juvenile size range. A series of tethering experiments were performed in three coastal sites of Robinson Crusoe Island (Juan Fernández archipelago, Chile). In overnight experiments, survival of juveniles decreased over time in all three sites, reaching ~50% at the end of the experiment. The evidence suggests that fish were relevant predators since mortality of lobsters was proportional to their abundance. Although video surveillances depicted numerous octopus attacks, their abundance did not exhibit a statistically significant relationship with lobster mortality. Predatory events were not selective of juvenile sizes. These results are fundamental to understand one of the key factor (i.e., predation) that affects the juvenile (and more vulnerable) benthic phase of *J. frontalis*.

KEY WORDS: predation, oceanic island, juveniles, lobsters, *Jasus frontalis*

INTRODUCTION

Predation is an important interaction in marine environment causing strong effects on the trophic structure of ecosystems (Paine 1966, Estes et al. 1978). For most marine organisms with complex life cycles there is a "critical phase," period in which the organisms are more vulnerable to predation and normally occurs during the transition from planktonic to benthic life (Steneck 2006).

For most spiny lobsters, this phase of higher vulnerability to predation occurs at the larval and juvenile stages, because the exoskeleton of these organisms becomes thicker and harder with age due to calcification and development of a greater number of spines, spinules, and setae that act as defenses from predators (Báez & Ruiz 2000). Therefore, predators mainly attack larval and juvenile stages, behavior that is directly related to their maximization of energy (Elner & Hughes 1978, Kloskowski 2011).

Previous studies on spiny lobster predation describe octopus (*Octopus vulgaris*) as one of the main predators of juvenile *Panulirus elephas* (Díaz et al. 2005), whereas coastal fishes are the main predators of juvenile *Panulirus argus* (Mintz et al. 1994, (Howard 1988). Predator pressure impacts have been well quantified and show how the abundance of recruits and juvenile lobsters can be strongly reduced in areas with high octopus abundances (Berger & Butler 2001).

Numerous studies have emphasized on the fragility of trophic assemblages and the effects that can be observed if some level of the food web is disturbed (Stevens et al. 2000, Baum & Worm 2009). A decrement of top predators, for example by overfishing, can produce a significant increase of mesopredators and, consequently, a drastic decrease of lower level prey, which in turn may represent commercially important resources (Heithaus et al. 2008, Steneck et al. 2013). On the other hand, an alleged decrease of mesopredators may increase the abundance of commercially valued resources that can now use habitat that originally belonged to their predators, in turn negatively affecting their recovery. This effect appears to be frequent in oceanic environments and strongest in some oceanic islands where species richness is commonly low (Ward & Meyers 2005, Baum & Worm 2009, Ramírez et al. 2013).

The Juan Fernández lobster *Jasus frontalis* (H. Milne Edwards, 1837) is an endemic species of the Juan Fernández archipelago (~33° 46′ S, 78° 47′ W; Robinson Crusoe, Santa Clara, and Alejandro Selkirk Islands) and the Desventuradas Islands (San Félix y San Ambrosio; ~6° 20′ S, 79° 53′ W). This sole species has represented the main fishing resource and income for the inhabitants of the archipelago since the late 19th century (Arana 2000). Therefore, better understanding of ecological processes, such as predation, which can have a significant effect on the abundance of juveniles of *J. frontalis* represents a useful knowledge when the aim is to improve the management of this species.

The main species reported to prey on adult *Jasus frontalis* are wreckfish (*Polyprion oxigeneios*), flounder (*Pleuronectes* sp.), dogfish (*Squalus fernandinus*), and other sharks (Arana 1974); however, no study refers to the identity of species that feed on juveniles of this species. Hence, there is a need for identifying the main predators that affect this early benthic juvenile phase, as well as for evaluating the predation pressure exerted on juveniles to help development of management and conservation strategies for this species.

MATERIALS AND METHODS

Experimental Design

Three tethering experiments and supporting predator surveys were performed in January of 2012 when juveniles of *Jasus*

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frontalis were exposed to predators at three coastal sites along the northern shore of Robinson Crusoe Island: El Inglés, El Palillo, and El Muelle (Fig. 1).

For each experimental trial 24 juveniles of *Jasus frontalis*, between 21 and 44 mm of cephalothorax length, were collected by means of SCUBA diving from El Muelle, located inside Cumberland Bay. Juveniles were measured to the nearest millimeter and randomly assigned to steel stakes, numbered from 1 to 24, which were driven into the sediment at each site. Individuals were tied around the cephalothorax with one end of a 1-m-long nylon monofilament (length allowing individual to move freely) and the other end to the base of the stake. At each site and by means of SCUBA, stakes were positioned at 13 m depth separated at least 3 m from one another. This experiment focused on the potential predatory pressure upon the juvenile lobsters in the field, thus no shelter was provided, which allowed us to easily identify potential predators and avoid any escape effect. A video camera (Sony Handycam DCR-HC62) in an Ikelite housing was mounted on a weighed stainless-steel frame and positioned about 3 m from a randomly selected tethering stake to record predator activity. The camera recorded the first 17 h of the experiment in a time-lapse mode. After each trial was finished divers counted missing individuals and retrieved the camera. Surviving tethered individuals were left in place and revised a second time 41 h after installed, missing individuals were counted and the experiment was finally removed.

To augment the assessment of the abundance of predatory fish at the experimental sites apart from the predation experiments, a separate half-hour stationary video surveillance sessions to identify and quantify potential predators was conducted. The video camera was positioned 30 cm off the seabed and aimed at an oblique angle to observe the foreground out to the limit of visibility. Video files were reviewed to identify and count predators at 2-min intervals over the 26 and 36 min duration of the available recordings, giving between 14 and 18 frames per trial. For each frame, fish were identified, and counted in a foreground area of approximately 10 m^2 in which they could be readily counted and identified. All fish within the field of view were quantified, although fishes less than $\sim$10 cm in length were excluded from the analysis. For each trial, predator visitation rates were calculated for each species as the average number of fish per video frame. Although the same individual fish could be repeatedly observed in many of these frames, the method provides a useful relative index of the prevalence of predatory fish at the site over the period of observation.

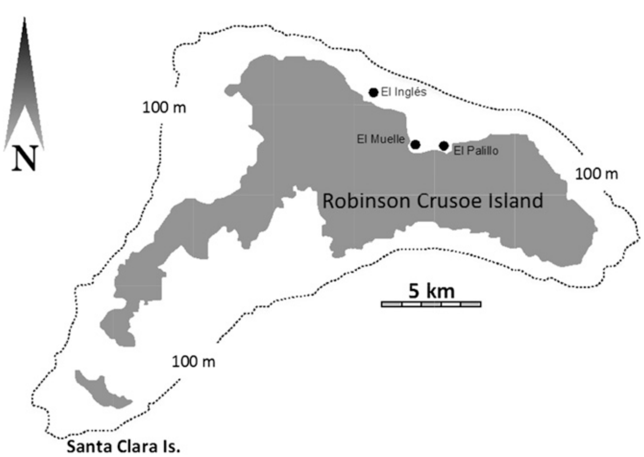

Figure 1. Robinson Crusoe Island, showing the three experimental sites along the northern shore: El Inglés, El Muelle, and El Palillo.

Finally, the abundance of octopus (*Octopus crusoe*, Vega et al. 2007, Vega 2011), known to be an important predator of lobster, was estimated at the three sites through individual counts made by a single experienced local octopus freediver, always at noon for 15 min.

Statistical Analysis

Differences among the lobster survival percentages at each site were evaluated using a generalized linear model specifying binomial distribution (McCullagh & Nelder 1989). For this statistical analysis each individual was identified with a number, 1 for predated individuals and 0 for survivors.

To determine predator's preference for any particular size of lobsters, different size ranges were exposed to predators in the field. The carapace lengths of juveniles were grouped into four size classes (18–25 mm, 26–33 mm, 34–41 mm, and 42–49 mm). The Chi-square Pearson test with 3 degrees of freedom on a two-way contingency table (Pearre 1982) was used to assess whether there were significant differences between the proportions of consumed individuals versus those available (Gaymer et al. 2001).

A one-way analysis of variance test was used to evaluate the differences between predator fish abundance at each experimental site. We applied a Tukey's honest significant difference test for the unequal sample sizes. Octopus abundances were not statically compared due to the fact that we had one single evaluation at each experimental site. The data were ln-transformed when normality and homoscedasticity criteria were not met. Normality was tested with the Kolmogorov–Smirnov test (Steel & Torrie 1985) and homoscedasticity through the Levene test (Snedecor & Cochran 1989).

RESULTS

Survival among Experimental Sites

At all three sites survival decreased over time. This was, however, significantly higher at El Palillo (72, 7%) compared with the other two sites ($P < 0.001$). No significant differences were observed between El Inglés and El Muelle (36.3% and 45.8%, respectively, Fig. 2). At the end of the experiment, including all three sites data, mortality rate averaged 50% of individuals. The smaller number of tethered lobsters at El Palillo and El Muelle (22 and 21 individuals, respectively) was due to the fact that some individuals died during the experimental setup.

Predator Abundance

During our short-term stationary video surveillance, the Juan Fernández wrasse (*Malapterus reticulatus*) was the sole species of carnivorous fish observed, and it was conspicuous and abundant at all three sites. A significantly lower abundance of Juan Fernández wrasse fish was found between El Palillo [X: 2.60 (SD = 2.22)] (MS = 5.4, DF = 2, $P < 0.5$) and El Inglés [X: 4.86 (SD = 3.23)] and El Muelle [X: 5.74 (SD = 4.24)], which in turn were not statistically different (Fig. 3). In the case of *Octopus crusoe*, we observed a higher abundance at El Muelle

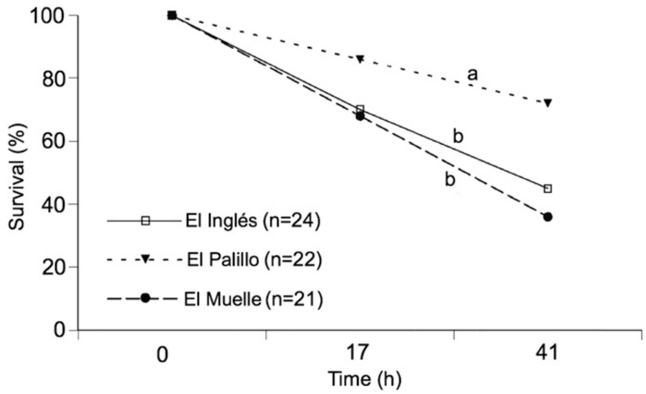

Figure 2. Survival percentage of tethered juveniles of *Jasus frontalis* at three experimental sites. Different letters above lines indicate significant difference in survival ($P < 0.05$). "n" indicates the number of lobsters that were tethered at each site.

(10 ind./m^2) followed by El Palillo (4 ind./m^2) and El Inglés (1 ind./m^2) (Fig. 3).

Potential Predators

At El Inglés the conspicuous Juan Fernández wrasse (*Malapterus reticulatus*) was observed actively attacking tethered lobsters. Further, the unfinished attack of an unidentified fish, and some monofilaments cut by fish bites were also observed. At El Inglés an individual of *Octopus crusoe* was also observed attacking a juvenile lobster. On several occasions, remains of exoskeletons around the metal stakes belonging to tethered individuals, characteristic of octopus attacks, were found.

Prey Size Selection

When comparing the sizes of juveniles consumed with respect to the availability of prey at each site no significant differences were observed. Comparing the total size spectrum consumed by predators (sum of all sites) versus its availability there was no evidence of preference for any particular size (Chi-square^2 = 1.2015, DF = 3, n = 67, P = 0.75) (Fig. 4).

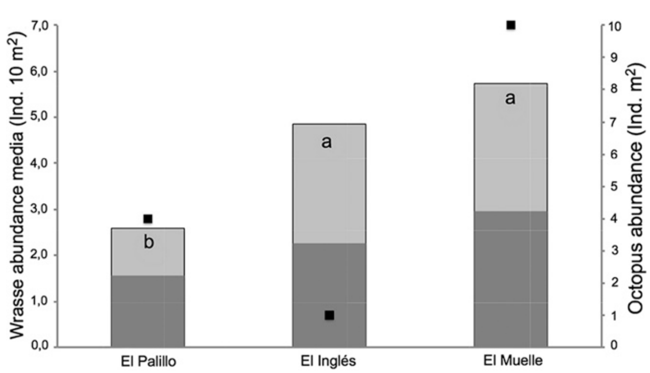

Figure 3. Octopus abundance (*Octopus crusoe*) (black squares) and predator fish abundance (gray bars) observed at each experimental site, darker portion of bars showing SD. Different letters indicate significant differences in abundance between sites ($P < 0.05$). Octopuses were quantified only once thus data were not statistically analyzed.

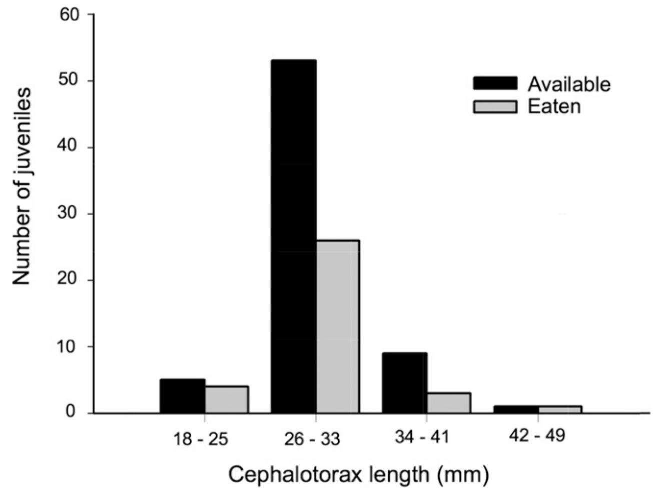

Figure 4. Consumption of juvenile *Jasus frontalis* of different sizes by predators in relation to their availability. Data from all three experimental sites (El Inglés, El Muelle, and El Palillo) were pooled.

DISCUSSION

The survival of juveniles of *Jasus frontalis* was higher at El Palillo compared with the other two study sites, which in turn did not differ significantly from each other. The lowest levels of lobster survival were observed at El Muelle where the highest predator abundance (fish and octopus) was found. It is known that predation rates are strongly influenced by the number of predators per area and the specific composition of the communities (Wooster 1994). Although there was no significant difference in fish abundance between El Palillo and El Inglés, a slightly higher number of fish was observed in the latter. This slight difference could be the reason for the higher mortality found at El Inglés.

A direct relationship between fish abundance and survival levels was found. This suggests that fish could be the main predator of juveniles of *Jasus frontalis*. In fact during one of the dives, an *in vivo* attack to a tethered lobster by the wrasse fish *Malapterus reticulatus* was observed. This fish was always abundant at the three study sites (Wahle et al., personal communication), as also noticed by Ramírez et al. (2013) who report that *M. reticulatus* is the most abundant fish of the Robinson Crusoe coastal fish assemblage. In addition to the former, several remains of monofilaments with clear evidences of fish's bites were found. Large fish such as the cod *Polyprion oxygeneios* and the dogfish *Squalus fernandinus* are described as the main predators of adult lobsters of Juan Fernández (Arana 1974). Until now, however, coastal fishes had never been described as the main predators of juvenile *J. frontalis*. These results agree with previous studies that indicated that juvenile Palinuridae lobsters are an important component of the diet of coastal reef fish of the families Lutjanidae (*Lutjanus griseus*) and Latidae (*Psammoperca waigiensis*) (Howard 1988, Mintz et al. 1994). Furthermore, Ramírez et al. (2013) indicated that decapod crustaceans are the second most important prey item in the diet of four fishes (*Malapterus reticulatus*, *Nemadactylus gayi*, *Psudocaranx chilensis*, and *Hipoplectrodes semicinctum*) of the Robinson Crusoe coastal fish assemblage, which would confirm that coastal fish are potential predators of the juvenile lobsters.

Although an octopus (*Octopus crusoe*) was observed eating a lobster and also numerous remains of empty exoskeletons (characteristic of octopus attack) around the metallic stakes were found, there were no relation between lobster survival and octopus abundance, which indicate that octopus were not the main predator of *Jasus frontalis*. Similarly to this study, Howard (1988) indicated that octopuses are not significant predators of juvenile lobsters *Panulirus cygnus* in natural habitats.

It is noteworthy that at El Inglés (site with the lowest octopus abundance) there is a small rookery of Juan Fernández fur seal (*Arctocephalus philippii*) very close to the spot where the experimental trials took place, which could have caused disturbances both in the behavior and abundance of the octopuses. It has been reported that cephalopods are a one of the main prey item of *A. philippii* at least during their reproductive period (Diaz 2007, Osman 2008).

Among the preyed juvenile lobsters no preference for size was observed, which indicates that predators fed according to prey availability. This may reflect the absence of a wide range of sizes from which to select, thus juveniles offered probably involved similar energy expenditure.

The overall juvenile mortality observed in this study (~50% of mortality after 41 h) is greater than the values found by Butler et al. (1999) for *Jasus edwarsii* in a similar tethering experiment in natural environment (30% after 48 h); however, the latter included shelters for lobsters, which could explain the difference of ~20% between both experiments. Shelters are a crucial factor in the survival of lobsters (Wharton & Mann 1981), which was reflected in a survival experiment with juveniles of *Homarus americanus*, under laboratory conditions, where they exhibited a 97% of mortality in sandy bottom compared with 69% in a habitat with shelters (Johns & Mann 2003).

The information provided herein, focused on the pressure exerted by predators upon the juvenile fraction of *Jasus frontalis* population, should be considered for better-informed management initiatives to diminish the threat of overestimation stock of this crustacean. So far, the overestimation of resource stocks has been one of the major problems around the world (Arreguin-Sanchez 2006). This problem could imply a high risk of depletion of lobsters at Juan Fernández Archipelago, where the local economy is mainly based on the extraction of this resource (Arana 2000).

Due to the economic importance of *Jasus frontalis* to Juan Fernández community, further research on the biology and ecology of juveniles of this species is needed. Among other topics we suggest studying (1) antipredator behaviors or response to predatory events (e.g., chemo-detection, camouflage, and escape from predators), (2) how shelter could influence survival rates of this lobster cohort in field tethering experiments, (3) estimating the predation pressure exerted by predators on the juveniles of *J. frontalis* in contrasting seasons, (4) studying settlement habitat selection (e.g., substrate type, shelters). This would provide a better background on the various causes that directly affect survival of juvenile lobsters. The suggested approaches could provide tools to predict fish stocks and thus help ensuring the future of this iconic artisanal fishery.

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