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Ecological traits of Caribbean sea anemones and symbiotic crustaceans

P. Briones-Fourzán[1,*], M. Pérez-Ortiz[2], F. Negrete-Soto[1], C. Barradas-Ortiz[1], E. Lozano-Álvarez[1]

[1]Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo 77580, Mexico

[2]Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, México, Distrito Federal 04360, Mexico

ABSTRACT: In Caribbean coral reefs, many crustacean species associate with sea anemones, but only a few are anemone symbionts. We examined several ecological traits of 3 anemone species (*Bartholomea annulata*, *Condylactis gigantea*, *Lebrunia danae*) and their crustacean symbionts (6 species) on a coral reef at Puerto Morelos, Mexico. On average, *C. gigantea* was the largest and *B. annulata* the most abundant of the 3 anemone species. Season did not affect the density distribution of any species, whereas reef zone (back reef, fore reef, reef channels) significantly affected density and mean size of *B. annulata* and *C. gigantea*, but only density of *L. danae*. The probability of harboring crustaceans increased with anemone size in all species, but varied with reef zone and season in *B. annulata* only. These patterns may be due to different microhabitat requirements, reproductive strategies, or photosynthetic plasticity of dinoflagellate endosymbionts among hosts, and different flow regimes among reef zones. *Alpheus armatus* and *Ancylomenes pedersoni* were strongly associated with *B. annulata*, and *Periclimenes rathbunae* with *L. danae*. *Thor amboinensis* and *Mithraculus cinctimanus* occurred more often in *C. gigantea*, while *P. yucatanicus* was more evenly associated with the 3 hosts. Only *Ancylomenes pedersoni* and *T. amboinensis* occurred in conspecific groups more often than expected by chance. Commensal complexes of up to 3 symbiont species occurred in all host species, with symbionts that typically used different parts of the host coexisting more frequently. These results provide a baseline to assess the potential influence of local and global anthropogenic stressors on anemone–crustacean symbioses.

KEY WORDS: Symbiosis · Coral reef · Mexico · Commensal complex · Puerto Morelos

INTRODUCTION

Coral reefs support the highest biodiversity of all marine ecosystems, with invertebrates contributing dominantly to this condition (Reaka et al. 2008). In the complex community networks typical of coral reefs, an important ecological role is played by many invertebrates that may serve as 'habitat providers' (i.e. species that offer structure or substrate that other species may live in or on). Habitat providers are ubiquitous and include numerous species of sponges, hard and soft corals, tube-dwelling polychaetes, ascidians, echinoderms, molluscs, and sea anemones. Equally diverse are the organisms that live in or on habitat providers, which include a vast array of invertebrates and fishes (review in Glynn & Enochs 2011).

Organisms that associate with habitat providers ('hosts') may obtain a variety of benefits, including physical shelter from predation, camouflage, stability, range expansion, or advantageous positioning. For example, the nematocyst-armed tentacles of sea

*Email: briones@cmarl.unam.mx

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Influence of local habitat features on disease avoidance by Caribbean spiny lobsters in a casita-enhanced bay

Patricia Briones-Fourzán[1,*], Rebeca I. Candia-Zulbarán[1], Fernando Negrete-Soto[1], Cecilia Barradas-Ortiz[1], Juan P. Huchin-Mian[2], Enrique Lozano-Álvarez[1]

[1]Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. Prol. Av. Niños Héroes s/n, Puerto Morelos, Quintana Roo 77580, Mexico

[2]Laboratorio de Inmunología y Biología Molecular, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional-Unidad Mérida, Km 6 Antigua Carretera a Progreso, CORDEMEX, Mérida, Yucatán 97310, Mexico

ABSTRACT: In Bahía de la Ascensión, Mexico, 'casitas' (large artificial shelters) are extensively used to harvest Caribbean spiny lobsters *Panulirus argus*. After the discovery of a pathogenic virus, *Panulirus argus* virus 1 (PaV1), in these lobsters, laboratory experiments revealed that PaV1 could be transmitted by contact and through water, and that lobsters avoided shelters harboring diseased conspecifics. To examine these issues in the context of casitas, which typically harbor multiple lobsters of all sizes, we examined the distribution and aggregation patterns of lobsters in the absence/presence of diseased conspecifics (i.e. visibly infected with PaV1) in 531 casitas distributed over 3 bay zones, 1 poorly vegetated ('Vigía Chico', average depth: 1.5 m) and 2 more extensively vegetated ('Punta Allen': 2.5 m; 'Los Cayos': 2.4 m). All zones had relatively high indices of predation risk. Using several statistical approaches, we found that distribution parameters of lobsters were generally not affected by the presence of diseased conspecifics in casitas. Interestingly, however, in the shallower and less vegetated zone (Vigía Chico), individual casitas harbored more lobsters and lobsters were actually more crowded in casitas containing diseased conspecifics, yet disease prevalence was the lowest in lobsters of all sizes. These results suggest that (1) investment in disease avoidance by lobsters is partially modulated by local habitat features, (2) contact transmission rates of PaV1 may be lower in nature than in the laboratory, and (3) water-borne transmission rates may be lower in shallow, poorly vegetated habitats more exposed to solar ultraviolet radiation, which can damage viral particles.

KEY WORDS: *Panulirus argus* · *Panulirus argus* virus 1 · PaV1 · Casitas · Marine vegetation · Predation risk · Habitat features

INTRODUCTION

The spiny lobster *Panulirus argus* (Latreille, 1804) is a valuable fishing resource across the wider Caribbean region and accounts for approximately 50% of the world catch of spiny lobsters (Phillips & Melville-Smith 2006). Around 2000, wild populations of *P. argus* began being affected by a pathogenic virus, *Panulirus argus* virus 1 (PaV1) (Shields & Behringer 2004), which is currently widespread across the Caribbean (review in Behringer et al. 2011). Lobsters visibly infected with PaV1 (i.e. diseased) exhibit a white, milky hemolymph that fails to clot and, occasionally, a reddish discoloration over the exoskeleton (Shields & Behringer 2004, Lozano-Álvarez et al. 2008). Highly infected lobsters become lethargic and eventually die from metabolic waste (Shields 2011). To date, no other hosts or reservoirs

*Email: briones@cmarl.unam.mx

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Variability in clinical prevalence of PaV1 in Caribbean spiny lobsters occupying commercial casitas over a large bay in Mexico

Rebeca I. Candia-Zulbarán, Patricia Briones-Fourzán*, Fernando Negrete-Soto, Cecilia Barradas-Ortiz, Enrique Lozano-Álvarez

Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Prol. Av. Niños Héroes s/n, Puerto Morelos, Quintana Roo, 77580 Mexico

ABSTRACT: In Bahía de la Ascensión, Mexico, the fishery for spiny lobsters *Panulirus argus* is based on the extensive use of casitas, large artificial shelters that can harbor the full size range of these highly gregarious lobsters. The discovery of a pathogenic virus in these lobsters (*Panulirus argus* virus 1, or PaV1) has raised concern about its potential effects on casita-based fisheries. Because in Bahía de la Ascensión visibly infected lobsters represent an immediate loss of revenue, we examined variability in clinical prevalence of PaV1 (percentage of lobsters visibly infected) in thousands of lobsters sampled from the commercial catch at the onset of 3 consecutive fishing years, and from 530 casitas distributed over 3 zones within the bay during 2 fishing and 2 closed seasons. In the commercial catch (lobsters 67 to 147 mm carapace length [CL]), clinical prevalence of PaV1 was low and was not affected by year or sex. In lobsters (9.2 to 115.0 mm CL) that occupied casitas, clinical prevalence of PaV1 varied with sampling season and was always higher in juveniles than in subadults or adults, but was consistently lower in one zone relative to the other 2 zones. The average clinical prevalence of PaV1 in this bay was statistically similar to the average clinical prevalence reported in Cuba, where casitas are also used, and in Florida Bay, USA, where casitas are not used. To date, PaV1 has had no discernible impact on the lobster fishery in Bahía de la Ascensión, suggesting that clinical prevalence is not influenced by the use of casitas per se.

KEY WORDS: *Panulirus argus* virus 1 · PaV1 · Artificial shelters · Casitas · Clinical prevalence · Bahía de la Ascensión · Mexico

INTRODUCTION

Spiny lobsters (Palinuridae) represent valuable fisheries resources in all tropical and temperate seas of the world, and the Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) constitutes nearly 50% of the world catch (Phillips & Melville-Smith 2006). Throughout the Caribbean region, fishers use a vast array of fishing methods to catch *P. argus*. In particular, in certain areas of Cuba and the Bahamas, and in 2 bays located on the Caribbean coast of Mexico (Bahía de la Ascensión and Bahía Espíritu Santo), large artificial shelters called 'casitas' are extensively used to commercially harvest lobsters (Briones-Fourzán et al. 2000, Cruz & Phillips 2000, Ehrhardt et al. 2010). Basically, a casita is a flat slab separated from the substrate by a few centimeters, thus creating a large 'crevice' that can harbor multiple lobsters (Briones-Fourzán et al. 2000).

With the exception of the smallest benthic juveniles, *Panulirus argus* show a strong tendency to aggregate in diurnal crevice-type shelters (Childress

*Corresponding author. Email: briones@cmarl.unam.mx

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Physiological and immunological characterization of Caribbean spiny lobsters *Panulirus argus* naturally infected with *Panulirus argus* Virus 1 (PaV1)

Cristina Pascual Jiménez[1,*], Juan Pablo Huchin-Mian[2], Nuno Simões[1], Patricia Briones-Fourzán[3], Enrique Lozano-Álvarez[3], Ariadna Sánchez Arteaga[1], Juan Antonio Pérez-Vega[2], Raúl Simá-Álvarez[2], Carlos Rosas Vazquez[1], Rossanna Rodríguez-Canul[2]

[1]Universidad Nacional Autónoma de México, Facultad de Ciencias, Unidad Académica Sisal, Puerto de Abrigo Sisal S/N. Yucatán 97355, Mexico

[2]Laboratorio de Inmunología y Biología Molecular. Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Unidad Mérida, Km. 6 Antigua Carretera a Progreso, CORDEMEX, Mérida, Yucatán 97310, Mexico

[3]Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales Puerto Morelos. Prol. Av. Niños Héroes s/n, domicilio conocido, Puerto Morelos, Quintana Roo 77580, Mexico

ABSTRACT: The present study compares 13 physiological and immunological variables between a group of healthy *Panulirus argus* lobsters and a group of lobsters naturally infected with *Panulirus argus* Virus 1 (PaV1). Viral infection was determined through histopathology and PCR. Ten of the 13 variables differed significantly between the 2 groups. Using these variables, a principal component analysis yielded 2 separate clusters: one corresponding to the healthy group and the other corresponding to the infected group. In particular, infected lobsters exhibited significantly lower levels of osmotic pressure, total hemocyte counts, plasmatic proteins, and total phenoloxidase (PO) activity in plasma, as well as significantly higher levels of cholesterol and acylglycerides. These features are consistent with metabolic wasting, hyperlipidemia, and presumed immune suppression. Infection with PaV1 appears to increase the susceptibility of lobsters to some other opportunistic pathogens, as 61.1% of infected lobsters presented infestations of ciliate epibionts (*Epystilis* and *Zoothamniun*) in the gill chamber compared with 11.5% lobsters in the healthy group. Infected lobsters also showed significantly higher levels of total PO activity in degranulated hemocytes and trypsin inhibitor activity, potentially indicating activation of immune response by the PO system during the systemic infection with PaV1.

KEY WORDS: Phenoloxidase · Hemocyte · *Panulirus argus* · Immunology · Hemolymph component

INTRODUCTION

The Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) supports valuable commercial fisheries through the wider Caribbean region (Holthuis 1991). Since the last decade, this species has been affected by a highly pathogenic virus known as *Panulirus argus* Virus 1 (PaV1) (Behringer et al. 2011). PaV1 was first detected in juveniles of *P. argus* from the Florida Keys (Shields & Behringer 2004), and then in juvenile lobsters from the Caribbean coast of Mexico (Huchin-Mian et al. 2008). Currently, PaV1 appears to be widespread throughout the Caribbean (Butler et al. 2008, Huchin-Mian et al. 2009, Cruz Quintana et al. 2011) and, given its high level of pathogenicity, this virus is considered a potential

*Email: pascual.cristina@gmail.com

Does size always matter? Mate choice and sperm allocation in *Panulirus guttatus*, a highly sedentary, habitat-specialist spiny lobster

Erika Magallón-Gayón, Patricia Briones-Fourzán[1)]
& Enrique Lozano-Álvarez

(Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México. Prol. Av. Niños Héroes s/n, Domicilio Conocido, Puerto Morelos, Quintana Roo 77580, Mexico)

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Summary

Spotted spiny lobsters, *Panulirus guttatus*, are small, obligate reef-dwellers that exhibit a highly sedentary lifestyle and a low tendency to aggregate with conspecifics, and that reproduce asynchronously year-round. Individual females can produce multiple clutches per year but have a short receptivity per clutch. As in most spiny lobsters, females of *P. guttatus* mate only once per clutch and resist further mating attempts, features that may favour development of female mate choice but limit the potential for sperm competition. We separately examined mate choice by large and small mature females through laboratory experiments that controlled for effects of male–male competition, quality of shelter, and mere social attraction. Only large females expressed preference for larger males relative to their own size, suggesting that only large females that mate with small males risk sperm limitation on fecundity success. In couples that mated, males deposited rather small, thinly spread spermatophores on the sterna of females. Spermatophore area (considered as a proxy measure of sperm content) increased with male size and showed no relationship with female size, suggesting that males of *P. guttatus* have a short sperm-recovery period or do not exhibit strategic sperm allocation in a non-competitive context. A comparison of average sperm allocation between *P. guttatus* and its sympatric species, *P. argus* (a much larger, highly mobile, and highly social species with more seasonal reproductive periods and a longer receptivity of females per clutch), suggests that males of *P. guttatus* allocate proportionally less sperm to females, on average, than males of *P. argus* do. According to predictions of across-species risk models, this result suggests that males of *P. guttatus* perceive lower average levels of sperm competition risk than males of *P. argus* do, implying that different *Panulirus* species may exhibit

[1)] Corresponding author's e-mail address: briones@cmarl.unam.mx

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Influence of shelter availability on interactions between Caribbean spiny lobsters and moray eels: implications for artificial lobster enhancement

E. Lozano-Álvarez[1,*], P. Briones-Fourzán[1], L. Álvarez-Filip[1], H. M. Weiss[2], F. Negrete-Soto[1], C. Barradas-Ortiz[1]

[1]Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Unidad Académica Puerto Morelos, PO Box 1152, Cancún, Quintana Roo 77500, México

[2]Project Oceanology, Avery Point, Groton, Connecticut 06355, USA

ABSTRACT: The Caribbean spiny lobster *Panulirus argus* is a valuable fishing resource, but local populations may be limited by availability of crevice shelter on juvenile (seagrass) habitats. This has prompted research into the potential density enhancement of juvenile lobsters with 'casitas', large (1.1 m^2 surface area) but low-lying (3.8 cm entrance height) artificial shelters that exclude large predators. Moray eels (Muraenidae), however, fit into casitas and could therefore pose a threat to lobster enhancement. In a shelter-poor reef lagoon, we examined potential interactions between juvenile lobsters and the locally dominant morays *Gymnothorax vicinus* and *G. moringa* in the absence (four 1 ha control sites) and presence of casitas (five 1 ha 'casita sites', each with 10 casitas), before (6 surveys) and after (22 surveys) deployment. Morays and lobsters did not interact as predator–prey, as morays neither consumed nor intimidated co-occurring lobsters. Rather, the 2 taxa appeared to compete for limited shelter on the reef lagoon, as suggested by a significant increase in density and mean size of both taxa on casita sites after deployment. Casitas significantly increased cohabitation of morays and lobsters, yet they tended to co-occur less often than expected by chance, but this result likely reflects behavioral differences between the highly gregarious, more numerous lobsters and the typically solitary, cannibalistic morays. Our study exemplifies the influence of habitat complexity on the nature of interspecific interactions and shows that *G. vicinus* and *G. moringa* would not pose a threat to lobster enhancement with casitas.

KEY WORDS: Artificial shelters · Casitas · Competition · Environmental context · Interspecific interactions · Predation · Reef lagoon

INTRODUCTION

Communities are structured by interactions between coexisting species. Interactions are positive (e.g. mutualism) when one species improves another species' environment, or negative (e.g. predation or competition) when one species detracts from the environment of other species or has an impact on its components or fitness, such as survival, growth, or reproduction. However, interspecific interactions may be conditional, potentially shifting from negative, to neutral, to positive, depending on the environmental context (Stachowicz 2001, van Baalen & Jansen 2001, Hay et al. 2004). In particular, habitat complexity may have a profound influence on the nature and outcome of interactions between local species (Forrester & Steele 2004, Grabowski 2004, Hixon & Jones 2005) because high complexity habitats provide a greater spectrum of resources and more refuges that provide protection from predators than low complexity habitats (Sih 1984, Almany 2003, Lozano-Álvarez et al. 2007).

*Email: elozano@cmarl.unam.mx

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DEEP-WATER SHRIMP (CRUSTACEA: PENAEOIDEA) OFF THE YUCATAN PENINSULA (SOUTHERN GULF OF MEXICO): A POTENTIAL FISHING RESOURCE?

ADOLFO GRACIA,[1]* ANA ROSA VÁZQUEZ-BADER,[1] ENRIQUE LOZANO-ALVAREZ[2] AND PATRICIA BRIONES-FOURZÁN[2]

[1]*Unidad Académica de Ecología Marina, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, PO Box 70-305, México, D.F., 04510, México;* [2]*Unidad Académica Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, PO Box 1152, Cancún, Q.R., 77500, México*

ABSTRACT Shrimp fisheries in the Mexican Gulf of Mexico are limited to the 100-m-depth contour. We investigated potential penaeoidean shrimp resources on the continental slope of the Yucatan Peninsula (southern Gulf of Mexico) during 2 research cruises conducted during spring 1999 (cruise 1; number of hauls, 21; depth range, 300–599 m) and 2007 (cruise 2; number of hauls, 27; depth range, 300–999 m). During both cruises, the catch included 6 penaeoidean species: *Aristaeomorpha foliacea*, *Aristaeopsis edwardsiana*, *Pleoticus robustus*, *Aristeus antillensis*, *Penaeopsis serrata*, and *Parapenaeus politus*. The first 3 species constituted 85% and 91% of the total catch in weight obtained during cruise 1 and cruise 2, respectively. During cruise 1, the mean (± SE) biomass (1.05 ± 0.25 kg/ha) and catch per unit effort (CPUE: 3.21 ± 0.75 kg/h) of the combined species did not differ significantly between 100-m-depth strata. During cruise 2, by contrast, mean biomass and CPUE differed significantly between strata, with the highest mean values at the 600–699-m stratum (biomass, 1.37 ± 0.61 kg/ha; CPUE, 5.14 ± 2.30 kg/h) and the lowest at the 300–499-m stratum (biomass, 0.03 ± 0.01 kg/ha; CPUE, 0.10 ± 0.04 kg/h). High CPUE values (≥5.0 kg/h) were more prevalent at depths of 400–499 m during cruise 1 and 600–699 m during cruise 2. Mean size of shrimp differed significantly between and within species, except for *A. foliacea*. On average, our CPUE values compare with values obtained in fisheries for deep-water penaeoideans around the world, and also with current CPUE values from the shallow-water shrimp fisheries in the southwestern Gulf of Mexico, suggesting that these deep-water shrimp represent a potential fishing resource.

KEY WORDS: continental slope, deep water, fisheries, Gulf of Mexico, Penaeoidean shrimp

INTRODUCTION

Shallow-water shrimp of the superfamily Penaeoidea are the most important fishing resource in Mexico. At least 15 species occur along the Mexican Gulf of Mexico (Vázquez-Bader & Gracia 1994, Gracia & Hernández-Aguilera 2005), but the fisheries target 6 species of greatest abundance and commercial value: *Farfantepenaeus aztecus* (Ives, 1891) (brown shrimp), *F. duorarum* (Burkenroad, 1939) (pink shrimp), *Litopenaeus setiferus* (Linnaeus, 1767) (white shrimp), *F. brasiliensis* (Latreille, 1917) (spotted pink shrimp), *Sicyonia brevirostris* Stimpson, 1871 (rock shrimp), and *Xiphopenaeus kroyeri* (Heller, 1862) (seabob shrimp).

After the exploitation of shrimp resources in the Mexican Gulf of Mexico began during the early 1950s, the shallow-water shrimp fisheries underwent rapid development. In coastal lagoons and shallow coastal areas the fisheries are still mainly artisanal, but there is an industrial offshore trawl fishery limited to the 100-m-depth contour (Gracia et al. 1997). During the 1970 and 1980s, the most important fishing grounds were located on the Campeche Bank. Average maximum annual yields of these fisheries, which were directed to the pink and white shrimp, were of 7,000 tons. These high exploitation rates resulted in recruitment overfishing for both species and also in growth overfishing for pink shrimp (Gracia 2004), causing a drop in yield to 1,700 tons (Gracia & Vázquez-Bader 1999). Consequently, the overall shrimp production of the Mexican Gulf of Mexico underwent a drastic decline, and the fishery industry currently targets brown shrimp, with main grounds along the western Gulf. Given the heavy fishing activity, unexploited grounds are unlikely to occur over the continental shelf.

Deep-water penaeoidean shrimp (families Solenoceridae, Penaeidae, and Aristeidae) are commercially exploited around the world (Holthuis 1980). For example, along the eastern Atlantic Ocean, including the Mediterranean Sea, there are extensive deep-sea fisheries for species of the genera *Aristeus*, *Aristaeomorpha*, *Plesiopenaeus*, and *Parapenaeus* (Ragonese & Bianchini 1996, Figueiredo et al. 2001, Papaconstantinou & Kapiris 2003). In the western Atlantic, deep-water penaeoidean shrimps are currently exploited in the U.S. portion of the Gulf of Mexico and in French Guyana, Venezuela, and Brazil (Guéguen 1997, Tavares 2002, Pezzuto et al. 2006, Stiles et al. 2007). In contrast, there are currently no deep-sea fisheries in the Mexican portion of the Gulf of Mexico, where potential shrimp grounds have been poorly surveyed, if at all. In particular, the continental slope around the Yucatan Peninsula is probably the least studied deep-sea area in the Gulf of Mexico (Wicksten & Packard 2005). Therefore, the aim of the current study was to conduct a preliminary study of the species composition, distribution, abundance, and mean size of deep-water penaeoidean shrimp on the upper continental slope off the Yucatan Peninsula (southern Gulf of Mexico) as part of an ongoing investigation into the benthic fauna and potential resources of this poorly studied area.

MATERIAL AND METHODS

We conducted 2 research cruises on the *R/V Justo Sierra* (Universidad Nacional Autónoma de México) during the boreal spring to collect shrimp from the upper continental slope. Cruise 1 (Biota de los Arrecifes de la Plataforma y del

* Corresponding author: E-mail: gracia@unam.mx

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Reproductive traits of tropical deep-water pandalid shrimps (*Heterocarpus ensifer*) from the SW Gulf of Mexico

Patricia Briones-Fourzán*, Cecilia Barradas-Ortíz, Fernando Negrete-Soto, Enrique Lozano-Álvarez

Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica Puerto Morelos. Ap. Postal 1152, Cancún, Quintana Roo 77500, México

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ABSTRACT

Heterocarpus ensifer is a tropical deep-water pandalid shrimp whose reproductive features are poorly known. We examined reproductive traits of a population of *H. ensifer* inhabiting the continental slope (311–715 m in depth) off the Yucatan Peninsula, Mexico (SW Gulf of Mexico). Size range of the total sample ($n=816$) was 10.4–38.9 mm carapace length. Females grow larger than males, but both sexes mature at 57% of their maximum theoretical size and at ~30% of their total lifespan. Among adult females, the proportion of ovigerous females was high in all seasons, indicating year-round reproduction. Most females carrying embryos in advanced stages of development had ovaries in advanced stages of maturation, indicating production of successive spawns. In the autumn, however, the proportion of ovigerous females and the condition index of these females were lower compared to other seasons. This pattern potentially reflects a reduction in food resources following the summer minimum in particulate organic carbon flux to the deep benthos, as reported in previous studies. Spawns consisting of large numbers (16024 ± 5644, mean $\pm$ SD) of small eggs (0.045 ± 0.009 mm^3) are consistent with extended planktotrophic larval development, an uncommon feature in deep-water carideans. Egg number increased as a power function of female size but with substantial variability, and egg size varied widely within and between females. There was no apparent trade-off between egg number and egg size and neither of these two variables was influenced by female condition. These results indicate iteroparity and a high and variable reproductive effort, reflecting a reproductive strategy developed to compensate for high larval mortality. The present study provides a baseline to compare reproductive traits between Atlantic populations of this tropical deep-water pandalid.

1. Introduction

The family Pandalidae (Crustacea: Decapoda: Caridea) is a cold-water family of mainly epibenthic shrimps occurring from shallow depths in boreal waters to depths of about 2000 m in tropical regions (Holthuis, 1980; Chace, 1985; Bauer, 2004). Reproductive strategies differ widely between pandalid species as they exhibit a variety of sexual systems (gonochorism, protandrous hermaphroditism, or partial protandric hermaphroditism with primary males or primary females) and types of reproduction (semelparity vs. iteroparity), even within the same genus (e.g., *Pandalus*) (Correa and Thiel, 2003; Bauer, 2004). However, the species grouped in the tropical deep-water genus *Heterocarpus* are gonochoristic (King and Moffit, 1984) and typically iteroparous (King and Butler, 1985; Dailey and Ralston, 1986; Roa and Ernst, 1996).

The type-species of the genus is *Heterocarpus ensifer* A. Milne Edwards, 1881, which was originally described from specimens collected at a depth of ~400 m off the Caribbean island of Barbados (Milne Edwards, 1881). In the western Atlantic, this species occurs at depths of 170–885 m from North Carolina (USA) to Brazil, including the Gulf of Mexico and Caribbean sea (Holthuis, 1980; Lozano-Álvarez et al., 2007, and references therein). In the eastern Atlantic, it occurs at depths of 88–1278 m from the Iberian peninsula to the Congo, including the archipelagos of Azores, Madeira, Canaries and Cape Verde, and in the Spanish Mediterranean (Tuset et al., 2009, and references therein). *H. ensifer* has also been reported as occurring in the Indo-west Pacific and southwestern Indian oceans (Holthuis, 1980; Crosnier, 1988; Poupin, 1994); however, based on extensive morphological comparisons, several authors have concurred that only the specimens from the Atlantic and the SW Indian ocean (and possibly also those from Hawaii, Kiribati, and the Marquesas in the Pacific) correspond to the species described by Milne Edwards (Crosnier and Forest, 1973; Chace, 1985; Crosnier, 1988;

Abbreviations: BW, body weight; CL, carapace length; CL_{max}, size of largest specimens in the sample; CL_{50}, size at which 50% of females are ovigerous; CL_{∞}, maximum theoretical size; SOM, size at the onset of sexual maturity; RSOM, relative size at the onset of sexual maturity ($=SOM/CL_{\infty}$); ES, egg size; EMV, egg-mass volume; IRP, index of reproductive potential; PI, productivity index; RO, reproductive output.

* Corresponding author. Tel.: +52 998 871 0367x145; fax: +52 998 871 0138.
E-mail address: briones@cmarl.unam.mx (P. Briones-Fourzán).

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Estimación de crecimiento, movimientos y prevalencia de PaV1 en juveniles de langosta *Panulirus argus* en la Reserva de la Biósfera Banco Chinchorro (Quintana Roo, México) a partir de datos de marcado-recaptura

Aurora Elba Ramírez-Estévez,[*] Gloria Verónica Ríos-Lara,[**] Enrique Lozano-Álvarez,[***] Patricia Briones-Fourzán,[***] Carlos Aguilar-Cardozo,[****] Gabriel Felipe Escobedo,[****] Fabio Figueroa-Paz,[****] Víctor Sosa-Mendicuti[****] y Juan de Dios Martínez-Aguilar[****]

Entre junio de 2005 y agosto de 2007 se llevó a cabo un experimento de marcado-recaptura de juveniles de langosta *Panulirus argus* en la Reserva de la Biósfera Banco Chinchorro (Caribe mexicano), con el objeto de estimar sus tasas de crecimiento, su ámbito de movimientos y la prevalencia de la enfermedad causada por el virus patógeno *Panulirus argus* Virus 1 (PaV1). Las langostas fueron marcadas en sitios fijos de muestreo (cuadrantes de 3 600 m^2) alrededor de Cayo Norte y Cayo Centro, dentro de la laguna arrecifal del Banco. Se marcó un total de 1 060 langostas ≥20 mm de longitud cefalotorácica (LC) y fueron recapturadas 404 (38%), algunas hasta en siete ocasiones. Se estimaron las tasas de crecimiento semanales de las langostas recapturadas y se compararon entre sitios de muestreo, sexos y diferentes épocas del año. Se estimaron los parámetros K y L_∞ y se ajustó la curva de crecimiento de von Bertalanffy. Las langostas juveniles presentaron un crecimiento rápido, alcanzando la talla mínima legal de captura (~74 mm LC) en alrededor de 1.3 años a partir de su asentamiento como postlarvas (6 mm LC). La mayoría de las langostas recapturadas se movió dentro de su cuadrante de origen o entre cuadrantes, pero algunas lo hicieron entre los cayos y otras fueron recuperadas lejos de los sitios de muestreo por pescadores. La distancia de los movimientos (en línea recta) varió entre 11 m y 4.2 km, con recorridos extremos de 16, 19 y 37 km. De las langostas, 2.23% presentó signos clínicos de la enfermedad causada por el virus PaV1. Esta prevalencia se considera baja en comparación con la presencia encontrada en otros lugares del Caribe.
Palabras clave: Langosta, *Panulirus argus*, crecimiento, movimientos, PaV1, marcado-recaptura.

Estimation of growth, movements and prevalence of PaV1 in juvenile spiny lobsters *Panulirus argus* from Banco Chinchorro Biosphere Reserve (Quintana Roo, Mexico) based on mark-recapture data

Between June 2005 and August 2007, a mark-recapture experiment was conducted in Banco Chinchorro Biosphere Reserve (Mexican Caribbean) to estimate growth rates and movement ranges of juvenile spiny lobsters *Panulirus argus*, as well as the prevalence of the disease caused by the pathogenic virus *Panulirus argus* Virus 1. Within the reef lagoon, lobsters were marked on fixed sampling sites (3 600 m^2 quadrants) located around Cayo Norte and Cayo Centro. In total, 1 060 lobsters ≥20 mm carapace length (CL) were marked and 404 (38%) were recaptured, some of them up to seven times. The weekly growth rates were estimated and compared between sampling sites, sexes, and seasons. Parameters K and L_∞ of von Bertalanffy's growth equation were estimated and used to construct a growth curve. Juvenile lobsters dwelling in reef lagoon grow rapidly, reaching the minimum legal size (~74 mm CL) in approximately 1.3 years after settling as postlarvae (6 mm CL). Between recaptures, most lobsters moved within their original quadrant or between quadrants, but some lobsters moved between cays, and a few were recovered by fishermen far from the sampling sites. Distance moved by individuals (over a straight line) varied between 11 m and 4.2 km, with some extreme movements of 16, 19, and 37 km. Clinical signs of the PaV1 disease were observed in 2.23% of juvenile lobsters. This is a low prevalence compared with other Caribbean locations.
Key words: Spiny lobster, *Panulirus argus*, growth, movements, PaV1, mark-recapture.

* Centro Regional de Investigación Pesquera-Puerto Morelos INAPESCA. Puerto Morelos, Quintana Roo, México. elbaurora@hotmail.com.
** Centro Regional de Investigación Pesquera-Yucalpetén, INAPESCA. A. P. 73. Progreso, Yucatán. CP 97320. México. g_veronicar@yahoo.com.
*** Unidad Académica Puerto Morelos, Instituto de Ciencias del Mar y Limnología, UNAM. A.P. 1152. Cancún, QR, CP 77500. México.
**** Estación de Investigación Pesquera del CRIP-Puerto Morelos en Isla Mujeres INAPESCA. Isla Mujeres, QR México.

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A first glimpse into the transcriptomic changes induced by the PaV1 infection in the gut of Caribbean spiny lobsters, *Panulirus argus* (Latreille, 1804) (Decapoda: Achelata: Palinuridae)

Ioreni Margarita Hernández-Velázquez [a], Jesús Alejandro Zamora-Briseño [a,b], Alejandro Pereira-Santana [c], Juan Pablo Huchin-Mian [d], Carlos Eduardo González-Penagos [a], Juan Antonio Pérez-Vega [a], Enrique Lozano-Álvarez [e], Patricia Briones-Fourzán [e,*], Rossanna Rodríguez-Canul [a,*]

[a] *Laboratorio de Inmunología y Biología Molecular, Departamento de Recursos del Mar, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional-Unidad Mérida, Km 6 Antigua Carretera a Progreso, CORDEMEX, Mérida, Yucatán CP 97310, México*

[b] *Current affiliation: Laboratorio de Entomología Molecular. Red de Estudios Moleculares Avanzados, Clúster Científico y Tecnológico BioMimic®. El Instituto de Ecología, Carretera antigua a Coatepec 351, El Haya, Xalapa, Veracruz CP 91070, México*

[c] *CONACyT-Centro de Investigación y Asistencia en Tecnología y Diseño del estado de Jalisco, División de Biotecnología Industrial, Camino Arenero 1227, El Bajío, Zapopan, Jalisco CP 45019, México*

[d] *Departamento de Biología, División de Ciencias Naturales y Exactas, Universidad de Guanajuato, Noria Alta S/N, Guanajuato 36050, México*

[e] *Unidad Académica de Sistemas Arrecifales de Puerto Morelos, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, México*

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ABSTRACT

The Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804) supports important fisheries in the Caribbean region. This species is affected by a deadly virus, Panulirus argus Virus 1 (PaV1), the only known pathogenic virus for this species. As infection progresses, the effects of PaV1 on its host become systemic, with far reaching impacts on the host's physiology, including structural injuries to its gastrointestinal organs, such as the hepatopancreas and the gut. This last one becomes highly compromised in the last stages of infection. Since the gut is a key organ for the physiological stability of lobsters, we compared the transcriptomic changes in the gut of juvenile individuals of *Panulirus argus* naturally infected with PaV1. In the RNA-Seq analysis, we obtained a total of 485×10^6 raw reads. After cleaning, reads were de novo assembled into 68,842 transcripts and 50,257 unigenes. The length of unigenes ranged from 201 bp to 28,717 bp, with a N50 length of 2079, and a GC content of 40.61%. In the differential gene expression analysis, we identified a total of 3405 non redundant differential transcripts, of which 1920 were up-regulated and 1485 were down-regulated. We found alterations in transcripts encoding for proteins involved in transcriptional regulation, splicing, postraductional regulation, protein signaling, transmembrane transport, cytoskeletal regulation, and proteolysis, among others. This is the first insight into the transcriptomic regulation of PaV1-*P. argus* interaction. The information generated can help to unravel the molecular mechanisms that may intervene in the gut during PaV1 infection.

1. Introduction

The Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804), supports economically relevant fisheries across its natural distribution area, which encompasses the wider Caribbean Region (Shields and Behringer, 2004). This species is being affected by a lethal, pathogenic virus known as *Panulirus argus* virus 1 (PaV1), an unenveloped, icosahedral, double stranded DNA virus placed in the family Mininucleoviridae (Shields and Behringer, 2004; Lozano-Álvarez et al. 2008; Huchin-Mian et al. 2009; Subramaniam et al. 2020). Although this virus was originally discovered in the Florida Keys in 1999, it has spread along the natural distribution areas of *P. argus*. Therefore, PaV1 is considered a threat for the stability of wild populations of Caribbean spiny lobsters (Shields and Behringer, 2004; Candia-Zulbarán et al. 2019).

* Corresponding authors.
E-mail addresses: briones@cmarl.unam.mx (P. Briones-Fourzán), rossana.rodriguez@cinvestav.mx (R. Rodríguez-Canul).

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Metamorphosis of spiny lobsters (*Panulirus argus* and *Panulirus guttatus*) in the Yucatan Current as inferred from the distribution of pueruli and final stage phyllosomata

Patricia Briones-Fourzán,[1]* Julio Candela,[2] Laura Carrillo,[3] Alí F. Espinosa-Magaña,[1,4] Fernando Negrete-Soto,[1] Cecilia Barradas-Ortiz,[1] Edgar Escalante-Mancera,[1] Rubén Muñoz de Cote-Hernández,[1,5] Rogelio Martínez-Calderón,[1] Enrique Lozano-Álvarez[1]

[1]Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Mexico
[2]Departamento de Oceanografía Física, Centro de Investigación Científica y Educación Superior de Ensenada, Ensenada, Mexico
[3]Departamento de Observación y Estudio de la Tierra, la Atmósfera y el Océano, El Colegio de la Frontera Sur, Chetumal, Mexico
[4]Present address: Centro Universitario de la Costa, Universidad de Guadalajara, Puerto Vallarta, Mexico
[5]Present address: Grupo Interdisciplinario de Gestión Ambiental, A.C., Ciudad de México, Mexico

Abstract

For spiny lobsters (Palinuridae), the co-occurrence of final-stage larvae (phyllosomata) and postlarvae (pueruli) in sampling stations over oceanic waters is indicative of metamorphosis zones, some of which have been found in boundary currents. We hypothesized that metamorphosis of *Panulirus argus* and *P. guttatus* off the Mexican Caribbean coast, which has a very narrow shelf, occurs in the swift Yucatan Current (YC). During two cruises conducted in autumn 2012 and spring 2013, a mid-water trawl and a neuston net were simultaneously towed in night samplings along transects up to ~ 100 km across the YC. Hydrographic and current fields were derived from Conductivity, Temperature and Depth, and altimetry data. Metamorphosis occurred mainly within the YC core. However, velocity and distance to the coast of the YC varied with cruise, and features that may favor retention (a persistent coastal eddy and a countercurrent) were detected. Despite differences in size and condition of pueruli between cruises, their energy stores did not appear to decline during the shoreward migration, suggesting that metamorphosing within strong boundary currents may increase the chances of pueruli arriving more quickly to a shore. Based on previously reported current features and swimming speeds, pueruli metamorphosing up to 12 km offshore are more likely to reach the Mexican Caribbean coast without much loss of energetic reserves. This could also occur for some pueruli metamorphosing up to 30 km offshore if encountering the features favoring retention. In contrast, pueruli metamorphosing > 30 km offshore are more likely to be carried into the Gulf of Mexico and elsewhere.

Spiny lobsters (Crustacea: Decapoda: Achelata: Palinuridae) are an important component of tropical and subtropical benthic communities and constitute valuable fishing resources wherever they occur (Briones-Fourzán and Lozano-Álvarez 2013). These lobsters have a peculiar type of planktotrophic larva, known as "phyllosoma" (from the Greek "leaf-shaped body"), which develops in oceanic waters over an exceptionally long period (> 5 months). The lengthy larval duration confers these lobsters a great potential for dispersal (Phillips et al. 2006*a*). The final phyllosoma undergoes a complete metamorphosis into the postlarva, known as "puerulus," which is morphologically like an adult lobster but is completely transparent. Importantly, pueruli do not feed (Lemmens 1994), that is, they constitute a secondary lecithotrophic phase in the life cycle of spiny lobsters (McWilliam and Phillips 1997). After metamorphosis, the puerulus actively swims toward the shore, where it settles in shallow coastal habitats and begins its benthic life.

The Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) and the spotted spiny lobster *Panulirus guttatus* (Latreille, 1804) co-occur throughout the wider Caribbean region. The former sustains valuable fisheries across the region, whereas the latter is a much less important resource due to its smaller size and habitat specialization. Although both species reproduce year-round, *P. argus* exhibits a major reproductive peak in spring and a minor peak in autumn (Padilla-Ramos and

*Correspondence: briones@cmarl.unam.mx

diversity

MDPI

Article

Diversity and Distribution of Mid- to Late-Stage Phyllosomata of Spiny and Slipper Lobsters (Decapoda: Achelata) in the Mexican Caribbean

Rubén Muñoz de Cote-Hernández †, Patricia Briones-Fourzán *, Cecilia Barradas-Ortiz, Fernando Negrete-Soto and Enrique Lozano-Álvarez

Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos 77580, Mexico; rub.hhe.n@gmail.com (R.M.d.C.-H.); barradas@cmarl.unam.mx (C.B.-O.); fnegrete@cmarl.unam.mx (F.N.-S.); elozano@cmarl.unam.mx (E.L.-Á.)

* Correspondence: briones@cmarl.unam.mx

† Current address: Grupo Interdisciplinario de Gestión Ambiental, A.C., Ciudad de México 04909, Mexico.

Abstract: Achelata (Palinuridae and Scyllaridae) have a flat, transparent, long-lived planktonic larva called phyllosoma, which comprises multiple stages and has a duration from a few weeks (some scyllarids) to >20 months (some palinurids). The larval development of many Achelata occurs in oceanic waters, where conventional plankton nets usually collect the early- to mid-stages but not the later stages, which remain poorly known. We examined the diversity and distribution of mid- and late-stage phyllosomata in the oceanic waters of the Mexican Caribbean, where the swift Yucatan Current is the dominant feature. The plankton samples were collected at night with a large mid-water trawl in autumn 2012 (55 stations) and spring 2013 (34 stations). In total, we obtained 2599 mid- and late-stage phyllosomata (1742 in autumn, 857 in spring) of five palinurids (*Panulirus argus*, *Panulirus guttatus*, *Panulirus laevicauda*, *Palinurellus gundlachi*, *Justitia longimana*) and three scyllarids (*Parribacus antarcticus*, *Scyllarides aequinoctialis*, *Scyllarus chacei*). Overall, the mid-stages were ~2.5 times as abundant as the late stages. The palinurids far outnumbered the scyllarids, and *P. argus* dominated over all the other species, followed at a distance by *P. guttatus*. The densities of all the species were generally low, with no clear spatial pattern, and the phyllosomata assemblage composition greatly overlapped between seasons. These results suggest the extensive mixing of the organisms entrained in the strong Yucatan Current, which clearly favors the advection of the phyllosomata in this region despite the presence of some local sub-mesoscale features that may favor short-term retention.

Keywords: decapods; spiny lobsters; slipper lobsters; phyllosoma; Caribbean Sea; Yucatan Current

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1. Introduction

The decapod crustacean infraorder Achelata comprises two families: Palinuridae (spiny lobsters) and Scyllaridae (slipper lobsters) [1,2]. Palinurids are characterized by their long and spiny second antennae, whereas the second antennae of scyllarids are modified as a hinged series of five flat plates. Both families share a distinctive type of planktonic, transparent larva called "phyllosoma" (plural: phyllosomata), which differs broadly in morphology from the benthic juveniles and adults. The term phyllosoma ("leaf body" in Greek) refers to the extremely flattened body of this larva. The duration of the larval phase varies with species but may encompass 4 to 22 months in Palinuridae and 30 days to 9 months in Scyllaridae [3,4].

The adaptations of phyllosomata to a long life in oceanic waters include a virtually transparent body that helps to avoid predation and the development of long and narrow pereopods with numerous setae and exopods that are used for flotation and to swim well enough to catch and retain prey [3,5]. The final stage metamorphoses into a nektonic postlarva, known as puerulus in Palinuridae and nisto in Scyllaridae, which swims back

Climate drives the geography of marine consumption by changing predator communities

Matthew A. Whalen[a,b,c,1], Ross D. B. Whippo[c,d], John J. Stachowicz[e], Paul H. York[f], Erin Aiello[g,2], Teresa Alcoverro[h,i], Andrew H. Altieri[j,k], Lisandro Benedetti-Cecchi[l,m], Camilla Bertolini[n], Midoli Bresch[a,3], Fabio Bulleri[l,m], Paul E. Carnell[o], Stéphanie Cimon[p], Rod M. Connolly[q], Mathieu Cusson[p], Meredith S. Diskin[r,s], Elrika D'Souza[i], Augusto A. V. Flores[t], F. Joel Fodrie[u], Aaron W. E. Galloway[d], Leo C. Gaskins[v], Olivia J. Graham[w], Torrance C. Hanley[x], Christopher J. Henderson[y], Clara M. Hereu[z], Margot Hessing-Lewis[a,aa], Kevin A. Hovel[bb], Brent B. Hughes[cc], A. Randall Hughes[x], Kristin M. Hultgren[dd], Holger Jänes[o,4], Dean S. Janiak[ee], Lane N. Johnston[ff], Pablo Jorgensen[gg], Brendan P. Kelaher[hh], Claudia Kruschel[ii], Brendan S. Lanham[jj,5], Kun-Seop Lee[kk], Jonathan S. Lefcheck[c], Enrique Lozano-Álvarez[ll], Peter I. Macreadie[o], Zachary L. Monteith[a], Nessa E. O'Connor[n], Andrew D. Olds[y], Jennifer K. O'Leary[g,mm], Christopher J. Patrick[nn,6], Oscar Pino[oo], Alistair G. B. Poore[pp], Michael A. Rasheed[f], Wendel W. Raymond[qq], Katrin Reiss[rr], O. Kennedy Rhoades[e,ee], Max T. Robinson[ss], Paige G. Ross[tt], Francesca Rossi[uu], Thomas A. Schlacher[y], Janina Seemann[k,7], Brian R. Silliman[v], Delbert L. Smee[r,s], Martin Thiel[oo,vv,ww], Richard K. F. Unsworth[ss], Brigitta I. van Tussenbroek[ll], Adriana Vergés[pp], Mallarie E. Yeager[bb,8], Bree K. Yednock[xx], Shelby L. Ziegler[u], and J. Emmett Duffy[c]

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The global distribution of primary production and consumption by humans (fisheries) is well-documented, but we have no map linking the central ecological process of consumption within food webs to temperature and other ecological drivers. Using standardized assays that span 105° of latitude on four continents, we show that rates of bait consumption by generalist predators in shallow marine ecosystems are tightly linked to both temperature and the composition of consumer assemblages. Unexpectedly, rates of consumption peaked at midlatitudes (25 to 35°) in both Northern and Southern Hemispheres across both seagrass and unvegetated sediment habitats. This pattern contrasts with terrestrial systems, where biotic interactions reportedly weaken away from the equator, but it parallels an emerging pattern of a subtropical peak in marine biodiversity. The higher consumption at midlatitudes was closely related to the type of consumers present, which explained rates of consumption better than consumer density, biomass, species diversity, or habitat. Indeed, the apparent effect of temperature on consumption was mostly driven by temperature-associated turnover in consumer community composition. Our findings reinforce the key influence of climate warming on altered species composition and highlight its implications for the functioning of Earth's ecosystems.

latitudinal gradients | trophic processes | seagrass | biogeography | macroecology

Latitudinal diversity gradients have stimulated decades of research, much of it invoking a decline from tropics to poles in rates of key biological processes and species interactions (1–3). General explanations for ecological patterns across latitude, however, remain elusive in part because so many environmental and biological variables change in parallel with latitude. As a result, the connections between ecological patterns and processes at global scales remain controversial (4–6). This uncertainty has recently been amplified by demonstrations that diversity of many modern and ancient lineages peaks at midlatitudes rather than at the equator, particularly in the ocean (7, 8).

Temperature is among the environmental factors that vary most consistently with latitude, and is a fundamental driver of biological processes. Metabolic theory mechanistically links environmental temperatures to a suite of biological processes, including metabolism and trophic transfer (9–12). For example, metabolic theory predicts that per-capita consumption rates of ectothermic consumers should follow increased metabolic needs and activity, and increase with rising temperature (13). But the traits of consumers, their abundance, and the resources available

Significance

Consumption transfers energy and materials through food chains and fundamentally influences ecosystem productivity. Therefore, mapping the distribution of consumer feeding intensity is key to understanding how environmental changes influence biodiversity, with consequent effects on trophic transfer and top–down impacts through food webs. Our global comparison of standardized bait consumption in shallow coastal habitats finds a peak in feeding intensity away from the equator that is better explained by the presence of particular consumer families than by latitude or temperature. This study complements recent demonstrations that changes in biodiversity can have similar or larger impacts on ecological processes than those of climate.

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The authors declare no competing interest.

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[1]To whom correspondence may be addressed. Email: mawhal@gmail.com.

[2]Present address: Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064.

[3]Present address: First Nations Fisheries Council of British Columbia, Vancouver BC V6P 6G5, Canada.

[4]Present Address: Estonian Marine Institute, University of Tartu, 12618 Tallinn, Estonia.

[5]Present address: Department of Biological Sciences, Macquarie University, Sydney, NSW 2000, Australia.

[6]Present address: Department of Biological Sciences, Virginia Institute of Marine Science, Gloucester Point, VA 23062.

[7]Present address: International Climate Initiative, Zukunft – Umwelt – Gesellschaft gGmbH, 10963 Berlin, Germany.

[8]Present address: Marine Science Center, Northeastern University, Nahant, MA 01907.

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RESEARCH ARTICLE

Do ecological characteristics drive the prevalence of *Panulirus argus* virus 1 (PaV1) in juvenile Caribbean spiny lobsters in a tropical reef lagoon?

Charlotte E. Davies[¤], Patricia Briones-Fourzán*, Cecilia Barradas-Ortiz, Fernando Negrete-Soto, Gema Moo-Cocom, Enrique Lozano-Álvarez

Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Puerto Morelos, Quintana Roo, Mexico

¤ Current address: Department of Biosciences, College of Science, Swansea University, Singleton Park, Swansea, Wales, United Kingdom.
* briones@cmarl.unam.mx

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Abstract

PaV1 is a pathogenic virus found only to infect Caribbean spiny lobsters *Panulirus argus*, a major fishing resource. *P. argus* is a benthic mesopredator and has a complex life history, with several ontogenetic habitat changes. Habitat characteristics and species diversity of surrounding communities may have implications for disease dynamics. This is of more concern for juvenile lobsters, which are more susceptible to PaV1 and are far less mobile than adult lobsters. We targeted a population of juvenile *P. argus* in a reef lagoon in Mexico, where PaV1 was first observed in 2001. Prevalence has been since irregularly assessed, but in 2016 we began a more systematic assessment, with two sampling periods per year (June and November) in three different zones of the reef lagoon. To examine the relationship between PaV1 prevalence and potential ecological determinants, we assessed habitat complexity, cover of different substrates, and invertebrate community composition in all zones during the first four sampling periods (June and November 2016 and 2017). Habitat complexity and percent cover of some substrates varied with zone and sampling period. This was the case for seagrass and macroalgae, which nevertheless were the dominant substrates. The invertebrate community composition varied with sampling period, but not with zone. Probability of infection decreased with increasing lobster size, consistent with previous studies, but was not affected by zone (i.e., variations in ecological characteristics did not appear to be sufficiently large so as to influence prevalence of PaV1). This result possibly reflects the dominance of marine vegetation and suggests that lobsters can be sampled throughout the reef lagoon to assess PaV1 prevalence. Prevalence was higher in only one of seven sampling periods (November 2017), suggesting that the pathogen has leveled off to an enzootic level.

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Alterations in the gut-associated microbiota of juvenile Caribbean spiny lobsters *Panulirus argus* (Latreille, 1804) infected with PaV1

Jesús Alejandro Zamora-Briseño[a], Daniel Cerqueda-García[a], Ioreni Margarita Hernández-Velázquez[a], Rafael Rivera-Bustamante[b], Juan Pablo Huchín-Mian[c], Patricia Briones-Fourzán[d], Enrique Lozano-Álvarez[d], Rossanna Rodríguez-Canul[a,*]

[a] Departamento de Recursos del Mar, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional-unidad Mérida, Km. 6 Antigua Carretera a Progreso, CORDEMEX, Mérida, Yucatán CP. 97310, Mexico
[b] Dirección, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional-unidad Mérida, Km. 6 Antigua Carretera a Progreso, CORDEMEX, Mérida, Yucatán CP. 97310, Mexico
[c] Departamento de Biología, División de Ciencias Naturales y Exactas, Universidad de Guanajuato, Noria Alta S/N, Guanajuato 36050, Mexico
[d] Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Puerto Morelos, Quintana Roo 77580, Mexico

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ABSTRACT

The spiny lobster *Panulirus argus* (Latreille, 1804) is currently affected by an unenveloped, icosahedral, DNA virus termed *Panulirus argus* virus 1 (PaV1), a virulent and pathogenic virus that produces a long-lasting infection that alters the physiology and behaviour of heavily infected lobsters. Gut-associated microbiota is crucial for lobster homeostasis and well-being, but pathogens could change microbiota composition affecting its function. In PaV1 infection, the changes of gut-associated microbiota are yet to be elucidated. In the present study, we used high-throughput 16S rRNA sequencing technology to compare the bacterial microbiota in intestines of healthy and heavily PaV1-infected male and female juveniles of spiny lobsters *P. argus* captured in Puerto Morelos Reef lagoon, Quintana Roo, Mexico. We found that basal gut-associated microbiota composition showed a sex-dependent bias, with females being enriched in amplicon sequence variants (ASVs) assigned to *Sphingomonas*, while males were enriched in the genus *Candidatus Hepatoplasma* and *Aliiroseovarius* genera. Moreover, the alpha diversity of microbiota decreased in PaV1-infected lobsters. A significant increase of the genus *Candidatus Bacilloplasma* was observed in infected lobsters, as well as a significant decrease in *Nesterenkonia*, *Caldalkalibacillus*, *Pseudomonas*, *Cetobacterium* and *Phyllobacterium*. We also observed an alteration in the abundances of *Vibrio* species. Results from this study suggest that PaV1 infection impacts intestinal microbiota composition in *Panulirus argus* in a sex-dependent manner.

1. Introduction

The Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804) is an important natural resource with high economic and ecological importance along its geographic distribution in the wider Caribbean region (FAO/WECAFC, 1997; Briones-Fourzán et al., 2003). This species is currently affected by *Panulirus argus* Virus 1 (PaV1), the only known pathogenic virus of *Panulirus argus* (Shields and Behringer, 2004; Huchin-Mian et al., 2008; Lozano-Álvarez et al., 2008). PaV1 is a double-stranded DNA virus that is icosahedral in shape (Li and Shields, 2007; Behringer et al., 2011). PaV1 has been classified recently within a new family named *Mininucleoviridae*, because its replication occurs in the nucleus rather than in the cytoplasm of infected cells (Subramaniam et al., 2020). The typical clinical signs of the disease includes a milky haemolymph that lacks coagulation, a reddish discoloration of the carapace, anorexia, and moult impairment resulting in fouling of carapace by epibionts (Li and Shields, 2007; Huchin-Mian et al., 2008; Behringer et al., 2011; Pascual-Jiménez et al., 2012). In the final stage of PaV1 infection, lobsters become lethargic, presumably due to metabolic wasting and tissue ischemia (Behringer et al., 2008). At this stage, food intake is reduced, and the nutritional condition of heavily infected lobsters is lower than that of healthy lobsters, and juvenile lobsters experience a generalised metabolic failure resulting in death (Li and Shields, 2007; Behringer et al., 2011; Herrera-Salvatierra et al.,

* Corresponding autor at: Laboratorio de Inmunología y Biología Molecular, CINVESTAV-IPN Unidad Mérida, Antigua carretera a Progreso Km 6, CP 97310 Mérida, Yucatán, Mexico.
E-mail address: rossana.rodriguez@cinvestav.mx (R. Rodríguez-Canul).

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iTRAQ-Based Proteomic Profile Analysis of the Hepatopancreas of Caribbean Spiny Lobsters Infected With *Panulirus argus* Virus 1: Metabolic and Physiological Implications

*Jesús Alejandro Zamora-Briseño[1], Eliel Ruiz-May[2], José Miguel Elizalde-Contreras[2], Ioreni Margarita Hernández-Velázquez[1], Ariadne Hernández-Pérez[3], Ana Guadalupe Fuentes-García[1], Nancy Herrera-Salvatierra[1], Patricia Briones-Fourzán[4], Cristina Pascual-Jiménez[5], Enrique Lozano-Álvarez[4] and Rossanna Rodríguez-Canul[1]**

[1] Laboratorio de Inmunología y Biología Molecular, Departamento de Recursos del Mar, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional-Unidad Mérida, Mérida, Mexico, [2] Instituto de Ecología, Red de Estudios Moleculares Avanzados, Clúster Científico y Tecnológico BioMimic®, Xalapa, Mexico, [3] Department of Comparative Physiology, Uppsala University, Norbyvägen, Sweden, [4] Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Mexico, [5] Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, Sisal, Mexico

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***Correspondence:**
Rossanna Rodríguez-Canul
rossana.rodriguez@cinvestav.mx

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The Caribbean spiny lobster *Panulirus argus* (Latreille, 1084) sustains economically valuable fisheries throughout the wider Caribbean region. This species is currently affected by the pathogenic virus *Panulirus argus* Virus 1 (PaV1) that causes a systemic and chronic-degenerative infection in juvenile spiny lobsters *P. argus*. To date, there is no available information regarding the host alterations induced by this pathogen at the molecular level. In the present study, comparative proteomic analyses of the changes in the hepatopancreas between infected and non-infected juvenile lobsters were analyzed by isobaric tags for relative and absolute quantitation (iTRAQ) coupled to synchronous precursor selection (SPS)-based MS^3. We identified a total of 636 proteins, being 68 down-regulated and 71 up-regulated proteins. Among the down-regulated proteins, we identified several enzymes involved in the metabolism of hormones and lipids, digestive proteases and glycosidases, while proteins associated with the histone core, protein synthesis, immune response and RNA regulation were up-regulated. Several misregulated enzymes involved in the regulation of neuromodulators were also identified. RT-qPCR assays were used to validate the expression of transcripts encoding for selected differential proteins that were in concordance to proteomic data, as well as the tendency observed in the enzymatic activities of trypsin, chymotrypsin, and glycosidase. In a similar way, we observed glycogen reduction in muscle, and an increase in plasma acylglycerides and glucose, which may be explained by proteomic data. This

diversity

MDPI

Article

Diversity of Seagrass-Associated Decapod Crustaceans in a Tropical Reef Lagoon Prior to Large Environmental Changes: A Baseline Study

Patricia Briones-Fourzán *, Luz Verónica Monroy-Velázquez, Jaime Estrada-Olivo † and Enrique Lozano-Álvarez

Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de Mexico, Puerto Morelos, 77580 Quintana Roo, Mexico; plesionika.vmv@gmail.com (L.V.M.-V.); jest9mx@gmail.com (J.E.-O.); elozano@cmarl.unam.mx (E.L.-Á.)

* Correspondence: briones@cmarl.unam.mx

† Current address: Calle Trasatlántico SM-18, Mz 24, Lote 12; Villas Morelos, Puerto Morelos, 77580 Quintana Roo, Mexico.

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Abstract: The community composition of decapods associated with subtidal tropical seagrass meadows was analyzed in a pristine reef lagoon on the Mexican Caribbean coast in the summer of 1995 and winter of 1998. The macrophyte community was dominated by *Thalassia testudinum* followed by *Syringodium filiforme*, with interspersed rhyzophytic macroalgae and large patches of drift algae. In each season, 10 one-min trawls were made with an epibenthic sled (mesh aperture 1 mm) during the day and 10 during the night on each of five sites. In all, 53,211 decapods belonging to 119 species were collected. The most diverse taxa were Brachyura and Caridea, but the most abundant were Caridea and Anomura. Dominance was high, with three species (*Latreutes fucorum*, *Cuapetes americanus*, and *Thor manningi*) accounting for almost 50% of individuals, and 10 species accounting for nearly 90% of individuals. There was great similarity in community composition and ecological indices between seasons, but significantly more individuals and species in night versus day samples. In the 20+ years elapsed since the samples were taken, the reef lagoon has undergone substantial environmental changes due to extensive coastal development and, more recently, the decay of massive beachings of floating *Sargassum* macroalgae. This study constitutes a valuable baseline for future studies investigating the potential impact of these stressors on tropical seagrass-associated communities.

Keywords: crustaceans; invertebrates; shrimps; crabs; hermit crabs; tropical seagrass ecosystems

1. Introduction

Seagrass ecosystems occur in many coastal regions of the world, where they provide valuable ecosystem functions. Seagrasses stabilize sediments and coastlines, sequester carbon, filter water, and provide habitat for a wide variety of species, including virtually all major groups of invertebrates as well as juveniles of many fishery resources (e.g., [1–5]). However, recent reviews [6,7] have revealed that more information on the relative importance of different groups is available for temperate zones than for the tropics, from the intertidal than for the subtidal, for large species than for the small to very small, and for those associated with the seabed or swimming in the water column than for those living on the seagrass leaves.

Crustaceans are one of the most abundant groups of epifauna in all marine ecosystems, including seagrass meadows, in terms of diversity, abundance, biomass, and energy flow [8–11]. Within this group, dominant taxa include the decapods, which have an important regulatory function in seagrass

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Analysis of fatty acids to examine larval and settlement biology of the Caribbean spiny lobster *Panulirus argus*

Patricia Briones-Fourzán[1,*], Alí F. Espinosa-Magaña[1,3], Enrique Lozano-Álvarez[1], Andrew Jeffs[2]

[1]Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo 77580, Mexico

[2]Institute of Marine Science & School of Biological Sciences, University of Auckland, Auckland, 1010, New Zealand

[3]*Present address:* Centro Universitario de la Costa, Universidad de Guadalajara, Puerto Vallarta, Jalisco 48280, Mexico

ABSTRACT: Spiny lobsters have an extended pelagic larval development in oceanic waters, ending in a non-feeding post-larva that swims to coastal habitats to settle and molt to a benthic juvenile. The accumulation of energetic reserves by larvae is thought to be challenging, especially in tropical waters. We examined changes in fatty acid (FA) composition of the tropical Caribbean spiny lobster *Panulirus argus* for successive developmental stages sampled across the shelf and off the eastern Yucatan Peninsula, Mexico. Final-stage larvae accumulate considerable lipid reserves (26 ± 2.8% SD of dry weight), mostly saturated FAs (65.4 ± 2.1% of total FAs). Proportions of the FAs 14:0, 15:0, and 16:1n-7 tended to decrease from final larvae to settled juveniles, consistent with their use as a key energy source, although the dominant energy sources in all developmental stages were 16:0 and 18:0. In contrast, the percentages of 20:4n-6 (arachidonic acid) and 20:5n-3 (eicosapentaenoic acid) tended to increase with development, consistent with being conserved. Bacterial and flagellate FA markers dominated in final-stage larvae, indicating a microbial loop foodweb as the source of lipid reserves. Such foodwebs are characteristic of the oligotrophic waters in which the larvae of both sub-tropical and temperate spiny lobsters species are also found. Similarities in the accumulation and use of FAs between the tropical *P. argus* and spiny lobsters from cooler regions of the world suggest that their extended larval period is a means of acquiring sufficient energy reserves whilst feeding in oligotrophic oceanic waters.

KEY WORDS: Fatty acid profile · Fatty acid trophic markers · Lipid energy reserves · Microbial loop · Foodweb · Tropical spiny lobsters

1. INTRODUCTION

Spiny lobsters (Decapoda: Achelata: Palinuridae) possess some of the longest planktonic larval durations among marine organisms, lasting from 4 to 22 mo, depending on the species (Phillips et al. 2006a). Their larvae, known as phyllosomata (singular: phyllosoma), are planktotrophic and develop through numerous stages in offshore, oceanic waters. Phyllosomata are highly transparent and have a dorso-ventrally flattened body that differs markedly from that of the reptant benthic phase of the life cycle, which mostly occupies habitats in shallow coastal waters. The final phyllosoma stage metamorphoses into a post-larva (sensu Booth & Phillips 1994) or decapodid (sensu Anger 2001) known as puerulus, which is morphologically more similar to the adult but possesses well developed swimming musculature and appendages, and remains completely transparent (Wells et al. 2001). The puerulus swims actively from the point of metamorphosis in

*Corresponding author: briones@cmarl.unam.mx

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ORIGINAL PAPER

Untangling the effects of size, habitat and invertebrate biodiversity on parasite prevalence in the Caribbean spiny lobster

Charlotte E. Davies[1,2] · Patricia Briones-Fourzán[1] · Enrique Lozano-Álvarez[1]

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Abstract

The spiny lobster *Panulirus argus* is an important benthic mesopredator and a major fishing resource across the Wider Caribbean region. This species is host to the pathogenic virus PaV1 and metacercariae of *Cymatocarpus solearis*, a digenean trematode whose first intermediate host remains unknown. Previous studies found that the probability of infection with PaV1 was higher in juvenile lobsters and in densely vegetated habitats (suggesting that marine vegetation can be an environmental reservoir for PaV1), whereas the probability of infection with *C. solearis* was higher for larger lobsters and in poorly vegetated habitats. To increase insight into the role of habitat and body size in the ecology of lobster diseases, the presence of both *C. solearis* and PaV1 in *P. argus* was investigated across three contrasting zones in Bahía de la Ascensión, Mexico (19°35′27″N, 87°38′06″W): reef, lagoon and shallow habitat. Additionally, habitat complexity, cover of benthic components, and macroinvertebrate biodiversity were characterized in each zone. Consistent with previous studies, probability of infection with PaV1 (both at a clinical and infective level) decreased with increasing lobster size and was highest in the seagrass-rich lagoon, supporting the idea that marine vegetation could be an environmental reservoir for PaV1. In contrast, the probability of infection with *C. solearis* increased significantly with lobster size but did not vary with zone, suggesting no relationship with benthic substrate type. However, based on results of macroinvertebrate diversity, the gastropods *Cerithium litteratum* and *Tegula fasciata* are put forward as potential candidates for the first intermediate hosts of *C. solearis.*

Introduction

In the changing climate, marine diseases are thought to be on the rise (Ward and Lafferty 2004; Lafferty and Hofmann 2016). Anthropogenic factors associated with climate change, pollution and invasive species have all been research targets for understanding marine disease dynamics (Harvell et al. 2002, 2004). However, ecosystem health as a whole can be encompassed by a range of categories, from anthropogenic disturbances to ecological factors such as species richness and diversity as well as disease (Lafferty and Gerber 2002; McCallum et al. 2005; Aburto-Oropeza et al. 2015).

In the Wider Caribbean region, the spiny lobster *Panulirus argus* is an important benthic mesopredator and a major fishing resource, with annual landings of over 27,000 tons in the past 10 years (FishStatJ 2019). This species, however, can be infected with PaV1 (*Panulirus argus* virus 1), the first known naturally occurring virus of a lobster, as well as a range of macroparasites, bacteria, and fungi (see Shields 2011 for review). *Panulirus argus* virus 1 was first discovered as the causative agent of an emergent disease affecting *P. argus* in Florida Bay, USA in 1999 by Shields and Behringer (2004). It has since been found throughout the Caribbean (Moss et al. 2013). *Panulirus argus* virus 1 has been mainly reported in juvenile lobsters (Behringer et al. 2006) and is highly pathogenic. Laboratory trials have shown that PaV1 is mainly transmitted through contact

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✉ Charlotte E. Davies
CEDavies72@gmail.com

[1] Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Universidad Nacional Autónoma de México, 77580 Puerto Morelos, Quintana Roo, Mexico

[2] Present Address: Department of Biosciences, College of Science, Swansea University, Singleton Park, Swansea, Wales SA2 8PP, UK

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Short Communication

Occurrence of *Panulirus meripurpuratus* and *Panulirus laevicauda* (Decapoda: Achelata: Palinuridae) in Bahía de la Ascensión, México

Patricia Briones-Fourzán[1], Cecilia Barradas-Ortiz[1], Fernando Negrete-Soto[1] Iris Segura-García[2] & Enrique Lozano-Álvarez[1]
[1]Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología Universidad Nacional Autónoma de México, Puerto Morelos, México
[2]Smithsonian Marine Station, Smithsonian Institution, Fort Pierce, FL, USA
Corresponding author: Patricia Briones-Fourzán (briones@cmarl.unam.mx)

ABSTRACT. The Caribbean spiny lobster *Panulirus argus* (Latreille, 1804), previously considered to range from North Carolina, USA, to Rio de Janeiro, Brazil, and throughout the wider Caribbean region, was recently divided into two species based on morphology and coloration: *Panulirus meripurpuratus* Giraldes & Smyth, 2016 in Brazil, and *P. argus* north of the Amazon-Orinoco River plume. Here we report on the presence of two individuals of *P. meripurpuratus* and four of *Panulirus laevicauda* (Latreille, 1804), another species typical of Brazil, in Bahía de la Ascensión, Mexico. This bay is located in the area where the Caribbean current - the main route by which South Atlantic water can reach this coast after entering the Caribbean basin through the Lesser Antillean passages - impinges the Mexican Caribbean coast before turning north to give rise to the Yucatan Current. The potential for larval retention is increased in this area, potentially explaining the episodic occurrence of Brazilian spiny lobster species in Bahía de la Ascensión.

Keywords: Palinuridae; spiny lobsters; connectivity; dispersal; Caribbean Current; Mexican Caribbean

Spiny lobsters (Crustacea: Decapoda: Achelata: Palinuridae) are marine megacrustaceans that constitute valuable fishing resources and play important roles as mesopredators in all tropical and subtropical ecosystems in which they dwell (Phillips *et al*., 2013).

Until recently, the spiny lobster genus *Panulirus* was thought to be represented by four species in the western Atlantic region. *Panulirus laevicauda*, occurring from Florida to Brazil but present only in sufficient numbers to support a long-term fishery in Brazil, *Panulirus echinatus*, confined to the northeast of Brazil and the mid-Atlantic islands, *P. guttatus*, an obligate reef-dweller mainly distributed in the wider Caribbean region north from Florida to Venezuela-Surinam, and *P. argus*, presumably with the broadest latitudinal range, from Bermuda and North Carolina, USA, to Rio de Janeiro, Brazil (Holthuis, 1991). Since the late 1990s, however, several studies argued for the splitting of *P. argus* into two distinct subspecies or species based on genetic evidence (*e.g*., Sarver *et al.*, 1998, 2000; Naro-Maciel *et al*., 2011; Tourinho *et al*., 2012). *Panulirus argus westonii*, a provisional name proposed by Sarver *et al.* (1998) for the Brazilian subspecies, remained a *nomen nudum* (Chan, 2010; WoRMS, 2018a). More recently, Giraldes & Smyth (2016) divided *P. argus* into two separate species based on morphology and patterns of coloration: *P. argus* north of the Amazon-Orinoco River plume, and *Panulirus meripurpuratus* in Brazil. This new species has been recognized (WoRMS, 2018b).

Bahía de la Ascensión is a large, shallow bay located on the eastern margin of the Yucatan Peninsula, Caribbean coast of Mexico, where an important fishery for *P. argus* is based on the extensive use of "casitas" (Briones-Fourzán *et al.*, 2000). Casitas are large, low-lying artificial shelters that can harbor multiple lobsters and are deployed on seagrass, sandy or hard bottoms within the bay (Briones-Fourzán *et al.*, 2000). *Panulirus guttatus* occurs on the coral reefs along the mouth of the bay, but this obligate reef-dweller does not

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Nutritional and immunological evaluation of juvenile spiny lobsters *Panulirus argus* (Latreille, 1804) (Decapoda: Achelata: Palinuridae) naturally infected with the PaV1 virus

Nancy Herrera-Salvatierra[1], Cristina Pascual-Jiménez[2], Juan Pablo Huchin-Mian[3], Enrique Lozano-Álvarez[4], Jorge Montero-Muñoz[1], Patricia Briones-Fourzán[4] and Rossanna Rodríguez-Canul[1]

[1]*Departamento de Recursos del Mar, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Unidad Mérida, Km. 6 Antigua Carretera a Progreso, CORDEMEX, Mérida, Yucatán, Mexico. Cp. 97310;*
[2]*Universidad Nacional Autónoma de México, Facultad de Ciencias, Unidad Académica Sisal, Puerto de Abrigo s/n, Sisal, Yucatán, 97355 Mexico;*
[3]*Department of Biology, Division of Natural and Exact Sciences, University of Guanajuato. Noria Alta s/n, Guanajuato, 36050 Mexico; and*
[4]*Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Puerto Morelos, Quintana Roo, 77580 Mexico*

Correspondence: R.Rodriguez-Canul; e-mail: rossanna.rodriguez@cinvestav.mx

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ABSTRACT

Panulirus argus virus 1 (PaV1) causes a long-lasting and systemic infection in the spiny lobster *Panulirus argus* (Latreille, 1804). Immunological, physiological, and nutritional indicators in the hemolymph and hepatopancreas were studied to investigate the effect of PaV1 on the spiny lobster. This included chymotrypsin, trypsin, glucosidase, cholesterol, acylglycerides, proteins, glycogen, hemagglutination, prophenoloxidase (proPO), phenoloxidase (PO), total hemocyte counts (THC), and hemocyte subpopulations. Spiny lobsters were sorted into uninfected, lightly, moderately, and severely infected groups based on the number of Cowdry Type A viral inclusions detected in their connective tissues. The results showed that the digestive enzymes chymotrypsin ($P < 0.001$), trypsin ($P < 0.001$), and glucosidase ($P < 0.001$) significantly decreased in the hepatopancreas as severity of PaV1 infection increased, denoting a loss of digestive efficiency. Cholesterol ($P < 0.001$), acylglycerids ($P < 0.001$), and protein ($P < 0.101$) values decreased in the hepatopancreas but increased in hemolymph. Glycogen from hepatopancreas decreased in moderately and severely infected lobsters. THC and the sub-populations of hyaline and semi-granular cells, as well as hemagglutination, were lower in the infected group than the uninfected group, but granular cells increased in the severely infected group. The proPO and PO enzymes had a 1:1 ratio in uninfected lobsters, but this balance disappeared in PaV1-infected lobsters, which showed an increase in proPO and a decrease in PO. Results from this study showed that the depletion of immunological, physiological, and nutritional indicators in lobsters infected with PaV1 included the deficiency of digestive efficiency, reduction of nutritional status, and decline in energy reserves.

Key Words: blood metabolites, digestive enzymes, fisheries, immunology, prophenoloxidase

INTRODUCTION

The Caribbean spiny lobster *P. argus* (Latreille, 1804) supports an economically valuable fishery throughout the Caribbean (Ehrhardt *et al.*, 2011). This species is currently affected by the pathogenic virus *Panulirus argus* Virus 1 (PaV1) (Shields & Behringer, 2004; Huchin-Mian *et al.*, 2008). PaV1 is a double stranded DNA virus that is icosahedral in shape (mean size ± SD 182 ± 9 nm). The virus is still unclassified but shares characteristics of the families Herpesviridae and Iridoviridae (Shields & Behringer, 2004). PaV1 was first detected in juvenile *P. argus* from the Florida Keys, USA (Shields & Behringer, 2004) but the virus has been reported throughout most of the Caribbean Sea (Huchin-Mian *et al.*, 2008;

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Coral Reef Degradation Differentially Alters Feeding Ecology of Co-occurring Congeneric Spiny Lobsters

Patricia Briones-Fourzán[1], Lorenzo Álvarez-Filip[1], Cecilia Barradas-Ortíz[1], Piedad S. Morillo-Velarde[1†], Fernando Negrete-Soto[1], Iris Segura-García[2], Alberto Sánchez-González[3] and Enrique Lozano-Álvarez[1]*

[1] Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Mexico, [2] Smithsonian Marine Station, Smithsonian Institution, Fort Pierce, FL, United States, [3] Laboratorio de Espectrometría de Masas, Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, La Paz, Mexico

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Rochelle Diane Seitz, William & Mary's Virginia Institute of Marine Science, College of William & Mary, United States

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***Correspondence:**
Patricia Briones-Fourzán
briones@cmarl.unam.mx

†Present address:
Piedad S. Morillo-Velarde, CONACYT–Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Veracruz, Mexico

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Caribbean coral reefs are undergoing massive degradation, with local increases of macroalgae and reduction of architectural complexity associated with loss of reef-building corals. We explored whether reef degradation affects the feeding ecology of two co-occurring spiny lobsters: *Panulirus guttatus*, which is an obligate reef-dweller, and *Panulirus argus*, which uses various benthic habitats including coral reefs. We collected lobsters of both species from the back-reef zones of two large reefs similar in length (∼1.5 km) but differing widely in level of degradation, at the Puerto Morelos Reef National Park (Mexico). We measured the carapace length (CL) and weight (W) of lobsters, estimated three condition indices (hepatosomatic index, HI; blood refractive index, BRI; and W/CL ratio), and analyzed their stomach contents and stable isotope values (δ^{15}N and δ^{13}C). All lobsters tested negative for the presence of the virus PaV1, which can affect nutritional condition. Stomach contents yielded 72 animal taxa, mainly mollusks and crustaceans, with an average of 35 taxa per species per reef, but with much overlap. In *P. guttatus*, CL, HI, BRI, and W/CL did not vary with reef, but mean isotopic values did. The isotopic niche of *P. guttatus* showed little overlap between reefs, reflecting differences in local carbon sources and underlining the habitat specialization of *P. guttatus*, which exhibited a higher trophic position on the more degraded reef. Overall, the trophic position of *P. guttatus* was higher than that of *P. argus.* In *P. argus*, none of the variables differed between reefs and the isotopic niche was wide and with great overlap between reefs, reflecting the broader foraging ranges of *P. argus* compared to *P. guttatus*. Additional isotopic values from 16 *P. argus* caught at a depth of 25 m in the fore reef suggest that these larger lobsters forage over different habitats and have a higher trophic position than their smaller conspecifics and congeners from the back reef. The feeding ecology of *P. argus* appears to be less influenced by coral reef degradation than that of *P. guttatus*, but our results suggest a buffering effect of omnivory against habitat degradation for both lobster species.

Keywords: Caribbean sea, habitat degradation, nutritional condition, omnivory, *Panulirus argus*, *Panulirus guttatus*, stable isotope analyses, stomach contents

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Confirming validity measures of visual assessment of PaV1 infection in Caribbean spiny lobsters

Rebeca I. Candia-Zulbarán[1,2], Patricia Briones-Fourzán[2,*], Enrique Lozano-Álvarez[2]

[1]Universidad Nacional Autónoma de México, Programa de Posgrado en Ciencias del Mar y Limnología, Ciudad Universitaria, Ciudad de México, 04510, Mexico

[2]Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Puerto Morelos, Quintana Roo, 77580, Mexico

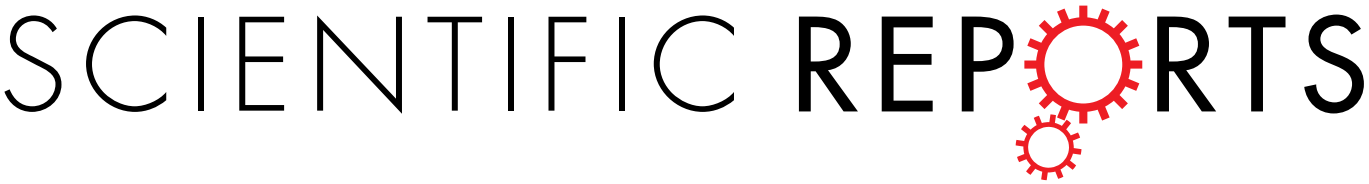
ABSTRACT: *Panulirus argus* virus 1 (PaV1) affects wild populations of Caribbean spiny lobsters. PaV1 can be lethal but shows predilection for juvenile lobsters. Because *P. argus* is one of the most valuable fisheries around the wider Caribbean region, monitoring disease prevalence in local populations is desirable. Diseased lobsters are easily recognized by their milky hemolymph, but this sign only becomes evident in advanced stages of infection. Other methods have been developed to detect PaV1, but are less practical for long-term monitoring of patterns of infection in populations. A previous study estimated the validity measures (sensitivity and specificity) of detection of PaV1 infection by observed clinical signs against endpoint PCR assays, using a representative sample of lobsters comprising mainly subadults and adults from a commercial fishing area. In the present study, these validity measures were estimated in a similar manner for a different population comprising mainly juveniles from a protected nursery area. We obtained virtually the same sensitivity and specificity values (0.48 and 1, respectively) for observed clinical signs as in the previous study (0.51 and 1, respectively), confirming the validity of applying a simple 2× correction factor to monitor the patterns of PaV1 infection over time based on more easily conducted visual assessments of a representative sample of the population.

KEY WORDS: *Panulirus argus* virus 1 · Sensitivity · Specificity · Diagnostic tests · Clinical signs · PCR · Crustacean

1. INTRODUCTION

The Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) (Crustacea: Decapoda: Achelata: Palinuridae) is a valuable fishing resource for 26 countries in the wider Caribbean region (FAO 2018). After a protracted pelagic larval phase, postlarvae of *P. argus* settle in seagrass habitats and marine vegetation of reef lagoons and shallow bays. The small juvenile lobsters (~6–50 mm carapace length, CL) remain in these habitats for several months, until the large juveniles, or subadults (~50–80 mm CL), migrate to coral reefs, which are inhabited by adults (~80–200 mm CL). *P. argus* is affected by the pathogenic virus *Panulirus argus* virus 1 (PaV1). Since its discovery in Florida (USA) in 1999 (Shields & Behringer 2004), PaV1 has been detected in many other Caribbean countries (Moss et al. 2013). PaV1, which can be lethal, shows predilection for juvenile lobsters. Macroscopic (clinical) signs of PaV1 infection are a milky hemolymph that fails to clot and a reddish discoloration over the carapace (Shields & Behringer 2004, Lozano-Álvarez et al. 2008). However, these signs do not become evident until the infection is in a rather advanced stage (Cruz Quintana et al. 2011). Therefore, an unknown proportion of individuals in a given population could be subclinically infected at any given time. To understand the potential effects of PaV1 on populations of *P. argus*, it would be desirable to monitor prevalence levels in local lobster populations over time.

*Corresponding author: briones@cmarl.unam.mx



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Habitat degradation alters trophic pathways but not food chain length on shallow Caribbean coral reefs

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Piedad S. Morillo-Velarde[1,3], Patricia Briones-Fourzán[1], Lorenzo Álvarez-Filip[1], Sergio Aguíñiga-García[2], Alberto Sánchez-González[2] & Enrique Lozano-Álvarez[1]

Habitat degradation can affect trophic ecology by differentially affecting specialist and generalist species, and the number and type of interspecific relationships. However, the effects of habitat degradation on the trophic ecology of coral reefs have received limited attention. We compared the trophic structure and food chain length between two shallow Caribbean coral reefs similar in size and close to each other: one dominated by live coral and the other by macroalgae (i.e., degraded). We subjected samples of basal carbon sources (particulate organic matter and algae) and the same 48 species of consumers (invertebrates and fishes) from both reefs to stable isotope analyses, and determined the trophic position of consumers and relative importance of various carbon sources for herbivores, omnivores, and carnivores. We found that both reefs had similar food chain length and trophic structure, but different trophic pathways. On the coral-dominated reef, turf algae and epiphytes were the most important carbon source for all consumer categories, whereas on the degraded reef, particulate organic matter was a major carbon source for carnivores. Our results suggest that the trophic structure of the communities associated with these reefs is robust enough to adjust to conditions of degradation.

One of most evident effects of habitat loss and degradation in terrestrial and aquatic ecosystems is a decline in the diversity of ecological communities via changes on species abundance and richness[1,2]. However, habitat degradation can modify the number of species interactions, potentially altering the trophic ecology[3,4]. For example, in a forest subjected to selective logging in Borneo, species of ground-feeding and understorey-feeding birds had significantly higher trophic positions than they had in a non-logged forest[5]. In Moorea, the stable isotopic signatures of marine carbon sources and consumers differed significantly between two bays as a result of different levels of anthropogenic activities causing differences in mean annual river flow to each bay[6].

Life history traits may also determine the response of species to habitat degradation, with specialist species generally being more affected than generalist species[7,8]. For example, butterfly species with a narrow feeding niche and low levels of mobility and reproduction were most strongly affected by habitat loss across a wide range of habitats in America and Europe[9]. Also, among bird species, long-lived, large, non-migratory, forest specialists were less likely to occur and less abundant in more intensively man-used habitats than were short-lived, small, migratory, habitat generalists[10].

Coral reefs are the most biologically diverse ecosystems in tropical waters and provide important ecosystem services to millions of people around the world[11]. However, coral reefs are being widely affected by a combination of global and local stressors, including climate change-induced coral bleaching, diseases, overfishing, and eutrophication[12]. Habitat degradation on coral reefs is mainly manifested as declines in the abundance of reef-building corals and their replacement by macroalgae or other organisms[13–15]. Coral reef degradation is already affecting community structure by changing diversity and abundance of species[16,17] as well as ecosystem functioning and services[18,19]. The removal of particular species (e.g., by overfishing) and the addition or increase in abundance of others may fundamentally change ecological feedbacks, resulting in a transition of the ecosystem

[1]Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, Mexico. [2]Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, La Paz, Baja California Sur, Mexico. [3]Present address: CONACYT–Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Boca del Río, Veracruz, Mexico. Correspondence and requests for materials should be addressed to E.L.-Á. (email: elozano@cmarl.unam.mx)

Diversity and abundance of conspicuous macrocrustaceans on coral reefs differing in level of degradation

Roberto González-Gómez[1,2], Patricia Briones-Fourzán[1], Lorenzo Álvarez-Filip[1] and Enrique Lozano-Álvarez[1]

[1] Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, Mexico

[2] Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mexico, Ciudad de México, Mexico

ABSTRACT

Coral reefs sustain abundant and diverse macrocrustaceans that perform multiple ecological roles, but coral reefs are undergoing massive degradation that may be driving changes in the species composition and abundance of reef-associated macrocrustaceans. To provide insight into this issue, we used non-destructive visual census techniques to compare the diversity and abundance of conspicuous macrocrustaceans (i.e., those >1 cm and visible without disturbance) between two shallow Caribbean coral reefs similar in size (~1.5 km in length) and close to each other, but one ("Limones") characterized by extensive stands of the branching coral *Acropora palmata*, and the other ("Bonanza") dominated by macroalgae and relic coral skeletons and rubble (i.e., degraded). We also assessed the structural complexity of each reef and the percent cover of various benthic community components. Given the type of growth of *A. palmata*, we expected to find a greater structural complexity, a higher cover of live coral, and a lower cover of macroalgae on Limones, and hence a more diverse and abundant macrocrustacean community on this reef compared with Bonanza. Overall, we identified 63 macrocrustacean species (61 Decapoda and two Stomatopoda). Contrary to our expectations, structural complexity did not differ significantly between the back-reef zones of these reefs but varied more broadly on Limones, and the diversity and abundance of macrocrustaceans were higher on Bonanza than on Limones despite live coral cover being higher on Limones and macroalgal cover higher on Bonanza. However, the use of various types of microhabitats by macrocrustaceans differed substantially between reefs. On both reefs, the dominant species were the clinging crab *Mithraculus coryphe* and the hermit crab *Calcinus tibicen*, but the former was more abundant on Bonanza and the latter on Limones. *M. coryphe* occupied a diverse array of microhabitats but mostly coral rubble and relic skeletons, whereas *C. tibicen* was often, but not always, found associated with colonies of *Millepora* spp. A small commensal crab of *A. palmata*, *Domecia acanthophora*, was far more abundant on Limones, emerging as the main discriminant species between reefs. Our results suggest that local diversity and abundance of reef-associated macrocrustaceans are partially modulated by habitat degradation, the diversity of microhabitat types, and the establishment of different commensal associations rather than by structural complexity alone.

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Corresponding author
Patricia Briones-Fourzán,
briones@cmarl.unam.mx

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Morphometric relationships and seasonal variation in size, weight, and a condition index of post-settlement stages of the Caribbean spiny lobster

Rogelio Martínez-Calderón[1,2], Enrique Lozano-Álvarez[1] and Patricia Briones-Fourzán[1]

[1] Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, Mexico

[2] Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

ABSTRACT

Spiny lobsters have a protracted pelagic, oceanic larval phase. The final larval stage metamorphoses into a non-feeding postlarva (puerulus) that actively swims towards the coast to settle in shallow habitats and does not resume feeding until after the molt into the first-stage juvenile. Therefore, the body dimensions and nutritional condition of both settled pueruli and first juveniles are likely to vary over time, potentially playing a crucial role in the recruitment to the benthic population. We compared carapace length (CL), height (CH), and width (CW); total length (TL), and body weight (W) between pueruli and first juveniles of the Caribbean spiny lobster, *Panulirus argus*, as well as morphometric relationships between both developmental stages. Except for CL, all other dimensions were larger in first juveniles, but more markedly CH and W. The slopes of the CH vs CL, CW vs CL, and W vs CL regressions differed significantly between stages, and all log-transformed relationships showed isometry in both stages, except for the CH vs CL relationship, which showed positive allometry. These results reflect a morphological change from the flatter, more streamlined body of the puerulus, to the heavier, more cylindrical body of the juvenile. We also analyzed seasonal variations in CL, W, the W/CL index (a morphometric condition index), and a modified W/CL index (i.e. after controlling for a significant effect of CL) of both stages using individuals monthly collected over 12 consecutive seasons (Autumn 2010–Summer 2013). In both stages, all three variables exhibited significant seasonal variation. For pueruli, the modified W/CL index differed from average in only two seasons, winter 2011 (higher) and summer 2013 (lower), but showed great within-season variation (larger coefficients of variation, CV), potentially reflecting variability in nutritional condition of larvae prior to metamorphosis and in the distances swum by individual pueruli to the settlement habitats. For first juveniles, the modified W/CL index was higher than average in winter and spring 2011, and lower in autumn 2011 and winter 2012, but showed less within season variation (smaller CVs), suggesting a combination of carry-over effects of puerulus condition and effects of local conditions (e.g., food availability and predation risk). These findings warrant further investigation into factors potentially decoupling settlement from recruitment processes.

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Corresponding author
Patricia Briones-Fourzán,
briones@cmarl.unam.mx

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research paper

Energy cost of the onshore transport of postlarvae of the Caribbean spiny lobster, *Panulirus argus*

[1] *Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Mexico.*

[2] *Institute of Marine Science & School of Biological Sciences, University of Auckland, Auckland, New Zealand.*

***** *Corresponding author email: <briones@cmarl.unam.mx>.*

Alí F Espinosa-Magaña [1]
Patricia Briones-Fourzán [1]*
Andrew Jeffs [2]
Enrique Lozano-Álvarez [1]

ABSTRACT.—Recent studies suggest that energy reserves play a crucial role in the recruitment of postlarval spiny lobsters. After a protracted pelagic larval phase that develops in oceanic waters, the final stage phyllosoma larva metamorphoses into a non-feeding postlarva (puerulus) that actively swims shoreward to settle in shallow coastal habitats and does not resume feeding until after the molt into juvenile. We examined the content of total protein (TP), total lipid (TL), and lipid classes in five developmental stages of the spiny lobster, *Panulirus argus* (Latreille, 1804), involved in the transition from pelagic to benthic life: final stage phyllosomata, nektonic pueruli, transparent benthic pueruli (newly settled), pigmented pueruli, and first-instar juveniles; collected in autumn 2012 and spring 2013. TL decreased progressively with development, from 26% of dry weight in phyllosomata to 7% in juveniles in autumn (a 73% decrease), and from 25% to 6% in spring (a 76% decrease). In all stages, phospholipid accounted for approximately 80%–87% of TL. TP was higher in all three pueruli substages than in phyllosomata and juveniles. Although season did not significantly affect either TL or TP content, the decline in TL between final phyllosomata and nektonic pueruli was greater in autumn, suggesting a greater energy cost of metamorphosis at warmer temperatures, whereas the decline in TL between nektonic and transparent benthic pueruli was more marked in spring, when the Yucatán Current is stronger, potentially increasing the energy cost of shoreward swimming. These findings may partially explain the interannual seasonal settlement patterns observed in this species.

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Spiny lobsters (Crustacea: Decapoda: Achelata: Palinuridae) constitute important fisheries wherever they occur and are usually among the most abundant invertebrate mesopredators in the habitats where they dwell (Lipcius and Eggleston 2000). The life cycle of spiny lobsters is one of the longest and most complex within crustaceans. It consists of a planktonic larval phase of up to 12 stages (the phyllosomata; singular: phyllosoma) with a duration of many months; a nektonic postlarval phase

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research paper

Avoiding disease vs avoiding predation: testing the trade-off in *Panulirus argus*

Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Puerto Morelos, Quintana Roo, CP 77580, Mexico.

** Corresponding author email: <elozano@cmarl.unam.mx>.*

***Enrique Lozano-Álvarez** **
Leslie N Cid-González
Rebeca I Candia-Zulbarán
Fernando Negrete-Soto
Cecilia Barradas-Ortiz
Patricia Briones-Fourzán

ABSTRACT.— Caribbean spiny lobsters, *Panulirus argus* (Latreille, 1804), usually avoid sheltering with conspecifics exhibiting the PaV1 viral disease, yet commonly cohabit with them in large, low-lying artificial shelters called "casitas" that are deployed in shelter-poor habitats in certain fisheries. We tested two hypotheses proposed to explain this finding: (A) that in shelter-poor habitats, healthy lobsters make a trade-off between avoiding disease and avoiding predation; and (B) that the large size of casitas allows segregation between healthy and diseased lobsters. We conducted eight experiments in seawater tanks fitted with two casitas, one empty and one harboring either a healthy or a diseased tethered lobster ("resident"), or both harboring a healthy or a diseased resident. We then introduced six healthy, free-ranging lobsters (FR-lobsters) into each tank (three replicates per experiment) and recorded their location after approximately 40 hrs. Experiments were conducted with and without a predatory triggerfish. Without predators, FR-lobsters used empty casitas and those harboring healthy residents, but avoided casitas harboring diseased residents, preferring to remain in the open. With a predator present, FR-lobsters used empty casitas and those harboring healthy but also diseased residents, suggesting that disease avoidance depends to some degree on availability of alternate shelter and immediacy of predation risk. In larger casitas deployed in a reef lagoon, co-occurrence of wild diseased and healthy lobsters was relatively high, but the probability of finding diseased lobsters segregated from healthy lobsters decreased with increasing number of lobsters. Overall, the results support both hypotheses, reflecting the complex but flexible behavior of *P. argus* under different ecological contexts.

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Resistance to starvation of first-stage juveniles of the Caribbean spiny lobster

Alí Espinosa-Magaña[1,2], Enrique Lozano-Álvarez[2] and Patricia Briones-Fourzán[2]

[1] Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Ciudad de México, México

[2] Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, México

ABSTRACT

The non-feeding postlarva (puerulus) of spiny lobsters actively swims from the open ocean to the coastal habitats where it settles and molts to the first-stage juvenile (JI). Because pueruli use much of their energy reserves swimming and preparing for the post-settlement molt, the survival of JIs presumably depends on resuming feeding as soon as possible. To test this hypothesis, the resistance to starvation of JIs of the Caribbean spiny lobster, *Panulirus argus*, was evaluated by measuring their point-of-no-return (PNR, minimum time of initial starvation preventing recovery after later feeding) and point-of-reserve-saturation (PRS, minimum time of initial feeding allowing for food-independent development through the rest of the molting cycle) in a warm and a cold season. Each experiment consisted of eight groups: a continuously fed control (FC) group, a continuously starved control (SC) group, and six groups subjected to differential periods of either initial starvation and subsequent feeding (PNR experiments) or initial feeding and subsequent starvation (PSR experiments). No JIs molted under continuous absence of food (SC). In both PNR experiments (temperature in warm season: 29.79 ± 0.07 °C, mean ± 95% CI; in cold season: 25.63 ± 0.12 °C) mortality increased sharply after 9 d of initial starvation and intermolt periods increased with period of initial starvation, but were longer in the cold season. The PNR_{50} was longer in the warm season (12.1 ± 1.2 d, mean ± 95% CI) than in the cold season (9.5 ± 2.1 d). In PRS experiments (temperature in warm season: 29.54 ± 0.07 °C; in cold season: 26.20 ± 0.12 °C), JIs that molted did so near the end of the feeding period; all JIs initially fed for up to 6 d succumbed, and no JIs molted after 13 d of starvation despite having fed previously. The PRS_{50} did not differ between the cold (13.1 ± 0.7 d) and warm seasons (12.1 ± 1.1 d). JIs of *P. argus* exhibit a remarkable resistance to starvation considering that the previous non-feeding, energy-demanding puerulus phase lasts for ~3 weeks. However, JIs appear to have a relatively higher degree of dependence on food to complete development to JII during the cold season than during the warm season. Therefore, JIs of *P. argus* would appear to be more resistant to starvation during the warm season.

Subjects Developmental Biology, Ecology, Marine Biology

Keywords Decapoda, Palinuridae, Point-of-no-return, Point-of-reserve-saturation, *Panulirus argus*, First-stage juveniles

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Corresponding author
Alí Espinosa-Magaña,
disarm22@hotmail.com

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Does reef architectural complexity influence resource availability for a large reef-dwelling invertebrate?

Enrique Lozano-Álvarez[a,*], Nelia Luviano-Aparicio[a], Fernando Negrete-Soto[a], Cecilia Barradas-Ortiz[a], Sergio Aguíñiga-García[b], Piedad S. Morillo-Velarde[a,1], Lorenzo Álvarez-Filip[a], Patricia Briones-Fourzán[a]

[a] Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Prol. Av. Niños Héroes s/n, Puerto Morelos, Quintana Roo 77580, Mexico
[b] Laboratorio de Espectrometría de Masas, Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, Apdo. Postal 592, La Paz, Baja California Sur 23096, Mexico

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ABSTRACT

In coral reefs, loss of architectural complexity and its associated habitat degradation is expected to affect reef specialists in particular due to changes in resource availability. We explored whether these features could potentially affect populations of a large invertebrate, the spotted spiny lobster *Panulirus guttatus*, which is an obligate Caribbean coral reef-dweller with a limited home range. We selected two separate large coral reef patches in Puerto Morelos (Mexico) that differed significantly in structural complexity and level of degradation, as assessed via the rugosity index, habitat assessment score, and percent cover of various benthic components. On each reef, we estimated density of *P. guttatus* and sampled lobsters to analyze their stomach contents, three different condition indices, and stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) in muscle. Lobster density did not vary with reef, suggesting that available crevices in the less complex patch still provided adequate refuge to these lobsters. Lobsters consumed many food types, dominated by mollusks and crustaceans, but proportionally more crustaceans (herbivore crabs) in the less complex patch, which had more calcareous macroalgae and algal turf. Lobsters from both reefs had a similar condition (all three indices) and mean $\delta^{15}N$, suggesting a similar quality of diet between reefs related to their opportunistic feeding, but differed in mean $\delta^{13}C$ values, reflecting the different carbon sources between reefs and providing indirect evidence of individuals of *P. guttatus* foraging exclusively over their home reef. Overall, we found no apparent effects of architectural complexity, at least to the degree observed in our less complex patch, on density, condition, or trophic level of *P. guttatus*.

1. Introduction

Habitat architecture can greatly influence the abundance and diversity by providing more niches and ways of exploiting environmental resources (Bruno and Bertness, 2001). In Caribbean coral reefs, architectural complexity depends on the presence of key reef-building, morphologically-complex corals such as *Acropora* and *Orbicella* species, which have suffered rapid geographical declines from diseases and other factors associated with anthropogenic activities, resulting in loss of architectural complexity (Álvarez-Filip et al., 2009, 2011). In addition to coral decline, habitat degradation is evident in reefs with local increases of macroalgae (Bruno et al., 2009; Nelson et al., 2016; Suchley et al., 2016).

Habitat degradation is expected to result in loss of species richness and abundance of reef fishes, particularly reef specialists (i.e., fishes that live exclusively in coral reefs) (Munday, 2004; Álvarez-Filip et al., 2011, 2015). This would be consistent with a greater vulnerability of specialists to disturbances (e.g. McKinney, 1997). However, predictions for invertebrate taxa are less clear, as different studies have obtained contrasting results (see Graham and Nash, 2013). For example, in Indonesia, Fuchs (2013) observed that more complex reef habitats had greater abundance and diversity of echinoderms, ascidians and mollusks, and Fabricius et al. (2014) found that loss of architectural complexity was associated with a decrease in many macroinvertebrate groups, especially predation-prone mobile taxa, including crustaceans. By contrast, Idjadi and Edmunds (2006) reported a positive relation between coral traits and diversity, but not abundance, of reef-associated invertebrates, with topographic complexity accounting for a great

* Corresponding author.
E-mail address: elozano@cmarl.unam.mx (E. Lozano-Álvarez).
[1] Current address: CONACYT – Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana, Hidalgo 617, Col. Río Jamapa, Boca del Río, Veracruz 94290, Mexico.

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Variability in prevalence of *Cymatocarpus solearis* (Trematoda, Brachycoeliidae) in Caribbean spiny lobsters *Panulirus argus* (Decapoda: Palinuridae) from Bahía de la Ascensión (Mexico)

Patricia Briones-Fourzán *, Rubén Muñoz de Cote-Hernández, Enrique Lozano-Álvarez

Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Prol. Av. Niños Héroes s/n, Puerto Morelos, Quintana Roo 77580, Mexico

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ABSTRACT

Cymatocarpus solearis, a brachycoeliid trematode that parasitizes sea turtles, uses spiny lobsters *Panulirus argus* as second intermediate hosts. We examined variability in infection by *C. solearis* in Bahía de la Ascensión, Mexico, a tropical bay with a highly productive fishery for *P. argus* that is based on the extensive use of casitas (large artificial shelters), which can harbor multiple juveniles and adults of this gregarious lobster species. We sampled 3956 lobsters from 466 casitas distributed over three bay zones within two closed seasons and one fishing season. In these lobsters (9.5–115.2 mm carapace length, CL), the average infection prevalence was 11.7% but the probability of infection increased significantly with size. Prevalence varied with season but was consistently higher in one zone than in the other two zones. Infection with *C. solearis* was negatively related with clinical infection with *Panulirus argus* Virus 1 (PaV1). We also sampled 405 lobsters from the commercial catch obtained throughout the bay at the onset of the fishing season. In these relatively larger lobsters (70.3–168.0 mm CL), average prevalence of *C. solearis* was higher (23.5%) but was not affected by lobster size or sex. Encysted metacercariae occurred in both abdominal and cephalothoracic muscles. The effects of *C. solearis* on phenotypic traits of *P. argus* that may potentially impact the host population dynamics and fisheries remain to be investigated.

1. Introduction

Spiny lobsters (Decapoda: Achelata: Palinuridae) constitute major fishing resources wherever they occur (Phillips, 2000); therefore, knowledge on the parasites and diseases that afflict them is important. The Caribbean spiny lobster *Panulirus argus* has relatively few known parasites (Shields, 2011), two of which have been reported in Bahía de la Ascensión (Mexico): the digenetic trematode *Cymatocarpus solearis* (=*C. undulatus*) (Plagiorchiida: Xiphidiata: Brachycoeliidae) which uses *P. argus* as a second intermediate host (Gómez del Prado et al., 2003), and the unclassified virus *Panulirus argus* Virus 1 (PaV1), which appears to be specific for *P. argus* (Shields and Behringer, 2004). To our knowledge, prevalence levels of *C. solearis* have only been estimated in the population of *P. argus* in the Gulf of Batabanó, Cuba (Cruz-Quintana, 2012). In contrast, prevalence levels of PaV1 and potential risk factors have been more widely assessed in populations of *P. argus* (reviewed in Behringer et al., 2011; Huchin-Mian et al., 2013), probably because PaV1 poses a more immediate risk as it can be lethal to juvenile lobsters.

P. argus sustains important fisheries throughout the wider Caribbean region, where it is caught with many types of fishing methods. In Bahía de la Ascensión, a large bay located in the eastern coast of the Yucatán peninsula, the fishery for *P. argus* depends on the extensive use of "casitas". Casitas are rectangular, low-lying artificial shelters that mimic large crevices and can harbor multiple lobsters over a broad size range (Lozano-Álvarez et al., 1991). Gregariousness in *P. argus* is mediated by conspecific chemical cues that guide shelter-seeking individuals to shelters harboring conspecifics, thus reducing their exposure to predators (Childress and Herrnkind, 2001). Moreover, lobsters sharing a shelter use their spiny antennae jointly to fend off approaching predators (Herrnkind et al., 2001). By promoting gregariousness, casitas

* Corresponding author.
E-mail address: briones@cmarl.unam.mx (P. Briones-Fourzán).

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coral reef paper

Dietary partitioning between sympatric species of spiny lobster in a coral reef system

Iris Segura-García [1, 2 *]
Patricia Briones-Fourzán [1]
Simon de Lestang [3]
Enrique Lozano-Álvarez [1]

[1] *Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Domicilio Conocido, Puerto Morelos, Quintana Roo, 77580 Mexico.*

[2] *Present address: Smithsonian Marine Station at Fort Pierce, 701 Seaway Dr, Fort Pierce, Florida 34949.*

[3] *Western Australian Fisheries and Marine Research Laboratories, PO Box 20, North Beach, Western Australia, 6025 Australia.*

[*] *Corresponding author email: <irissegurag@gmail.com>, Telephone: +1(772) 462-0999, Fax: +1(772) 461-8154.*

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ABSTRACT.—Throughout the Wider Caribbean Region, the spotted spiny lobster, *Panulirus guttatus* (Latreille, 1804), dwells and forages exclusively in coral reef habitat after post-larval settlement, whereas its sympatric species, the Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804), undergoes ontogenetic habitat shifts, with smaller individuals dwelling in reef lagoon habitats and larger individuals dwelling in reef habitats, but exhibiting broad foraging ranges. Stomach content, and carbon and nitrogen stable isotopes analyses were used to examine dietary partitioning between co-occurring *P. guttatus* and reef-dwelling *P. argus* in a coral reef system off Mexico. Both species fed on a wide variety of invertebrates, but mollusks contributed more to the diet of *P. guttatus* and crustaceans to the diet of *P. argus*. The two species had different ranges of isotopic composition and each filled a unique trophic position within the local food web. A Bayesian mixing model revealed a distinct contribution of different food sources to the diet of these lobsters. Reef herbivores were the primary food source for *P. argus* and an important food source for *P. guttatus*, but the latter also consumed more carnivores, resulting in a higher trophic position relative to *P. argus*. The isotopic niche space, delineated by means of bivariate ellipses, exhibited no overlap between species, and *P. argus* exhibited a significantly larger niche area than *P. guttatus*. These results suggest that, in addition to a differential use of habitat resources, a differential use of food resources facilitates the local coexistence of these two congeners.

Competition occurs when two or more species use the same resource that is in limited supply, and has been considered an important evolutionary force leading to niche separation or specialization (Pianka 1978). Basic principles of niche theory suggest that complete niche overlap between sympatric species is evolutionarily impossible (Gause 1934, Hardin 1960); therefore, to coexist, species must differ in some way (i.e., reduced niche overlap) (Chesson 2000). Differential use of vital resources (e.g., food or habitat) may facilitate the local coexistence of ecologically-similar or closely-related species (Kneitel and Chase 2004, Lozano-Álvarez et al. 2007).

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Contribution to the Supplement: '*Lobsters in a Changing Climate*'

Original Article

Aggressive behaviour of spotted spiny lobsters (*Panulirus guttatus*) in different social contexts: the influence of sex, size, and missing limbs

Patricia Briones-Fourzán*, Roberto Domínguez-Gallegos, and Enrique Lozano-Álvarez

Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo 77580, Mexico

**Corresponding author: tel: +52 998 8710009; fax: +52 998 8710138; e-mail: briones@cmarl.unam.mx*

Briones-Fourzán, P., Domínguez-Gallegos, R., and Lozano-Álvarez, E. Aggressive behaviour of spotted spiny lobsters (*Panulirus guttatus*) in different social contexts: the influence of sex, size, and missing limbs. – ICES Journal of Marine Science, 72: i155 – i163.

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Panulirus guttatus is a sedentary spiny lobster that exhibits cryptic behaviour and a low degree of gregariousness. Because these lobsters are obligate coral reef-dwellers and avoid sandy expanses, they are potentially distributed in relatively small, discrete populations with variable social contexts, which can strongly influence the expression of aggression. The present study examined the relative importance of sex, size, and the number of missing limbs in the shelter-related aggressive behaviour of replicated groups of four lobsters that differed in social context (i.e. same-sex and mixed-sex groups). Each group was held in a seawater tank with a single artificial cave-like shelter. The interior of the cave was video-recorded for 72 h and the number of aggressions performed by each individual was quantified in a 10-min segment of video per hour. Most aggressions were related to occupancy of the shelter inner space and tended to end when individuals were sufficiently spaced out. In general, per-capita rates of aggression were higher at night and size was an important predictor of aggressiveness among individuals of the same sex. Males were substantially more aggressive than females, but the number of missing limbs significantly impacted the degree of aggressiveness in males. In mixed-sex groups, fewer aggressions occurred when the largest individual was a male than when it was a female, suggesting that it may take longer for smaller males to assert themselves. Our results provide insights into some potential consequences of increase in fishing pressure and loss of habitat complexity in Caribbean reefs for the social behaviour and population dynamics of these lobsters.

Keywords: aggression, agonistic interactions, Caribbean coral reefs, social behaviour, social context, spiny lobsters.

Introduction

In many animal systems, aggressive behaviour is an important component of agonistic and social behaviour that includes actual attacks or any threats of attack (Huber and Kravitz, 2010). Although aggression and dominance are not necessarily correlated (Hand, 1986; Drews, 1993), large crustacean males are typically more aggressive and tend to dominate smaller conspecifics, often monopolizing resources such as food, mates, or shelter (Lee and Fielder, 1983; Thorpe *et al.*, 1994; Edsman and Jonsson, 1996; Beattie *et al.*, 2012). In clawed decapods (e.g. crabs, crayfish, and clawed lobsters), the claws constitute potentially deadly weapons and hence agonistic interactions involve ritualized displays that serve as tests of strength rather than actual attacks (Neil, 1985; Huber and Kravitz, 1995; Davis and Huber, 2007). In contrast, in the clawless spiny lobsters (Decapoda: Achelata: Palinuridae), ritualized threat behaviours have not evolved and agonistic behaviour can involve a great deal of contact and struggle, but is less likely to result in injury or death (Atema and Cobb, 1980; Cobb, 1981).

Spiny lobsters are large, nocturnally active crustaceans that depend on available structured shelter to hide from predators. Spiny lobsters exhibit gregarious sheltering, a behaviour mediated by conspecific chemical communication (Childress, 2007). Although the degree of gregariousness varies with species, even in highly gregarious species individuals can behave aggressively towards conspecifics attempting to share shelters and may form dominance hierarchies

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Contribution to the Supplement: '*Lobsters in a Changing Climate*'

Original Article

Caribbean spiny lobsters equally avoid dead and clinically PaV1-infected conspecifics

Rebeca I. Candia-Zulbarán[1,2]*, Patricia Briones-Fourzán[2], Enrique Lozano-Álvarez[2], Cecilia Barradas-Ortiz[2], and Fernando Negrete-Soto[2]

[1]*Universidad Nacional Autónoma de México, Posgrado en Ciencias del Mar y Limnología, Ciudad Universitaria, México DF, Mexico*
[2]*Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Puerto Morelos, Quintana Roo, Mexico*

**Corresponding author: tel: +52 998 8710009; e-mail: daarani@yahoo.com.mx*

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Social behaviour in Caribbean spiny lobsters (*Panulirus argus*) is mediated by conspecific chemical cues. These lobsters can be attracted to shelters emanating chemical cues from conspecifics but tend to avoid shelters emanating chemical cues from injured conspecifics, dead conspecifics, and conspecifics with visible signs of a potentially lethal disease caused by the pathogenic *Panulirus argus* virus 1 (PaV1). However, previous studies have not controlled for the presence of PaV1 (i.e. subclinical infection) in grossly "healthy" lobsters, although visible signs of disease do not appear until several weeks after infection. We conducted a controlled experiment using a set of 2 m-long Y-mazes to examine and contrast the response of *P. argus* lobsters to shelters emanating chemical cues from conspecifics in four different conditions: uninfected, subclinically PaV1-infected (i.e. infected but not diseased), clinically PaV1-infected (i.e. infected and diseased), and dead. Using polymerase chain reaction, we tested for PaV1 in all grossly healthy lobsters and used exclusively uninfected lobsters in intermolt as focal lobsters. Focal lobsters similarly avoided shelters emanating chemical cues from clinically infected (80% avoidance) and from dead conspecifics (85% avoidance), but their response to chemical cues from uninfected and from subclinically infected conspecifics did not differ significantly from random. These results indicate that PaV1-diseased lobsters produce chemical cues that are as repellent to conspecifics as are chemicals emanating from dead conspecifics, and that subclinically infected lobsters either do not emit the repellent chemicals or they do so at sub-threshold levels. However, the nature of the repellent chemicals and whether they originate from the pathogen or the host remains to be determined.

Keywords: avoidance behaviour, chemical cues, disease, *Panulirus argus*, *Panulirus argus* virus 1.

Introduction

The Caribbean spiny lobster, *Panulirus argus* (Latreille, 1804) is one of the most valuable fishing resources in the Western Central Atlantic and constitutes by itself over 50% of the world catch of spiny lobsters (Phillips *et al.*, 2013). *Panulirus argus* has a complex life cycle and undergoes several habitats shifts during its benthic life. The post-larvae settle in vegetated habitats where the small juveniles remain for a few months and exhibit asocial behaviour. However, larger juveniles eventually shift from the vegetation to occupying structured crevice-type shelters, a habitat shift that coincides with a change from asocial to social behaviour (Childress and Herrnkind, 2001a, b). The most ubiquitous example of sociality in *P. argus* and other spiny lobsters is gregarious sheltering, which is mediated by intraspecific chemical cues released in the urine (Ratchford and Eggleston, 1998; Horner *et al.*, 2006, 2008). For an individual seeking shelter, following conspecific scents into a den both reduces its time of exposure and allows it to assess the quality of the den (Nevitt *et al.*, 2000; Childress and Herrnkind, 2001a), while congregating in dens can increase per capita survival through either a "dilution effect" or "group defense behavior" (Eggleston *et al.*, 1990; Childress and Herrnkind, 2001a, b; Briones-Fourzán *et al.*, 2007). However, gregariousness is not generated by chemical attraction *per se* unless the benefits of aggregation outweigh the costs (Loehle, 1995; Childress, 2007). Benefits of

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Introduction to the Supplement: '*Lobsters in a Changing Climate*'

Introduction

Lobsters: ocean icons in changing times

Patricia Briones-Fourzán* and Enrique Lozano-Álvarez

Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales Puerto Morelos, Universidad Nacional Autónoma de México, Quintana Roo, México

**Corresponding author: tel: + 52 998 8710009; e-mail: briones@cmarl.unam.mx*

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The 10th International Conference and Workshop on Lobster Biology and Management was held in Cancún, Mexico, in May 2014. The papers included in this supplementary issue of the *ICES Journal of Marine Science* are a sample of the multidisciplinary nature of the conference and provide new knowledge of the biology, ecology, fisheries, and management and aquaculture of clawed, spiny, and slipper lobsters. The emphasis of the conference was climate change and its consequences for lobster biology, population dynamics, ecology, and fisheries. As noted in several papers, climate change is already affecting different lobster species by altering growth rates, sizes at maturity, the timing of reproductive processes, duration of larval development, and the timing and levels of settlement; by affecting key benthic habitat-forming species in settlement habitats; by increasing the risk of disease and impacting the behavioural ecology of lobsters, and by changing the spatial distribution of the stocks and, hence, affecting catches and the territorial behaviour of fishers. Other issues addressed at the conference included aquaculture and enhancement—the holy grails of lobster management—sustainable management strategies, and a fascinating review of the use of lobsters through human history. In addition to their economic importance, lobsters continue to provide valuable information to understand different marine environments in a changing climate.

Keywords: biology, clawed lobsters, climate change, fisheries, management, slipper lobsters, spiny lobsters.

Introduction

Marine lobsters are a diverse group of large, abundant, long-lived, crustaceans that inhabit a wide range of habitats. Lobsters are highly valued and sustain some of the most profitable fisheries in all tropical, subtropical, and temperate-cool waters of the world. In 2012, worldwide landings of marine lobsters were ~294 000 metric tons (mt) with a value of around US $2800 million, with an additional 2000 mt produced through aquaculture (FAO, 2014). Chan (2010) recognized 248 lobster species in 55 genera and 6 families from 4 infraorders; however, most commercially important species are members of the families Nephropidae (clawed lobsters and scampi), Palinuridae (spiny or rock lobsters), and Scyllaridae (slipper lobsters).

Apart from their economic importance, lobsters play key roles in the maintenance of healthy and diverse marine ecosystems, given their generally high local abundances and trophic position as benthic consumers. Lobsters exhibit different types of lifestyles and reproductive strategies—even within the same genus—and display complex behaviours, yet are relatively easy to keep in the laboratory and to use in controlled experiments. Thus, lobsters provide valuable information to understand different marine environments in a changing world and constitute useful subjects, and even model organisms, for many types of biological and ecological studies (Cobb, 2006).

The International Conference and Workshop on Lobster Biology and Management

In January 1977, a group of 34 scientists from six countries met in Perth, Australia, to discuss issues on lobster ecology and physiology. Over time, the scope widened and the meeting became the "International Conference and Workshop on Lobster Biology and Management" (or ICWL for short). The aims of the ICWL are to review recent advances in the study of all aspects of the biology, ecology, fisheries, and aquaculture of clawed, spiny, and slipper lobsters; to identify gaps in current knowledge and future research priorities, and to encourage collaborative studies for future research. Established and new generations of lobster scientists, academics, students, managers, and industry representatives attend the ICWLs to exchange knowledge and mingle in a friendly atmosphere. After Perth, subsequent ICWLs were held in Saint Andrews, Canada

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Genetic analysis reveals temporal population structure in Caribbean spiny lobster (*Panulirus argus*) within marine protected areas in Mexico

Nathan K. Truelove [a,b,*], Kim Ley-Cooper [c], Iris Segura-García [b,d], Patricia Briones-Fourzán [d], Enrique Lozano-Álvarez [d], Bruce F. Phillips [c], Stephen J. Box [b], Richard F. Preziosi [a]

[a] Faculty of Life Sciences, The University of Manchester, Manchester M13 9PT, UK
[b] Smithsonian Museum of Natural History, Smithsonian Marine Station, Fort Pierce, FL 34949, USA
[c] Department of Environment and Agriculture, Curtin University, Bentley, WA, Australia
[d] Instituto de Ciencias del Mar y Limnologiía, Unidad Académica Puerto Morelos, Universidad Nacional Autoínoma de México, PO Box 1152, Cancuín 77500, Mexico

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ABSTRACT

Management efforts for improving the sustainability of the Caribbean spiny lobster (*Panulirus argus*) fishery require knowledge of population connectivity. The aim of this study is to investigate population connectivity of *P. argus* at two levels: (1) spatially between two marine protected areas (MPAs) in the Caribbean coast of Mexico, and (2) temporally within MPAs; by genotyping discrete size classes lobsters using microsatellite markers. No evidence of population differentiation between lobster populations from Banco Chinchorro and Sian Ka'an MPAs was found ($P = 0.139$). In contrast significant levels of population differentiation among discrete size classes of lobsters was found ($F_{ST} = 0.0054$; $P = 0.0052$). Temporal variation among the genotypes of new larval recruits may explain these results. Future research will be required to directly test the genotypes of new larval recruits in Banco Chinchorro and Sian Ka'an MPAs to confirm this hypothesis.

1. Introduction

The Caribbean spiny lobster, *Panulirus argus* is widely distributed in the Caribbean and Western Atlantic from North Carolina to Rio de Janeiro Brazil (Diniz et al., 2005). This species of spiny lobster is one of the most economically valuable fished single species in the Caribbean (Butler et al., 2011; Ley-Cooper et al., 2013). Despite management and conservation efforts to sustain the *P. argus* fisheries, commercial landings have been in decline since the 1990s (Ehrhardt et al., 2010). Management efforts for improving the sustainability of the *P. argus* fishery requires knowledge of population connectivity among Caribbean nations (Kough et al., 2013). Several studies have used a variety of genetic methods to assess population connectivity in *P. argus* (Sarver et al., 1998; Silberman et al., 1994; Naro-Maciel et al., 2011; Tourinho et al., 2012). Phylogenetic analyses based on mitochondrial (mtDNA) and nuclear sequence markers suggest that Caribbean and Brazilian spiny lobster populations originally attributed to *P. argus* belong to different species (Tourinho et al., 2012). There have been no reports of structuring among subpopulation in the Brazilian subspecies. However, recent studies of population structuring among Caribbean subpopulations using mtDNA markers have provided conflicting results. Diniz et al. (2005) suggested that northern Caribbean subpopulations might be distinct from southern populations, yet Naro-Maciel et al. (2011) found no evidence of genetic differentiation among subpopulations in Puerto Rico, Bahamas, and Florida. Polymorphic microsatellite markers (msatDNA) are widely considered more powerful for resolving population structure than mtDNA markers, particularly at small spatial scales (Hellberg, 2009; Lukoschek et al., 2008). For example, preliminary results of spiny lobster genetic differentiation in Belize based on msatDNA suggested that subregional population structure may exist among marine protected areas (MPAs) in the Mesoamerican region (Truelove et al., 2012).

MPAs in the Mesoamerican Barrier Reef System (MBRS) often focus on locally based management such as preserving important

* Corresponding author at: Smithsonian Museum of Natural History, Smithsonian Marine Station, Fort Pierce, FL 34949, United States. Tel.: +1 7724620993.
E-mail address: trueloven@gmail.com (N.K. Truelove).

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DISEASES OF AQUATIC ORGANISMS
Dis Aquat Org

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NOTE

Panulirus argus virus 1 detected in oceanic postlarvae of Caribbean spiny lobster: implications for disease dispersal

Enrique Lozano-Álvarez[1,*], Patricia Briones-Fourzán[1], Juan Pablo Huchin-Mian[2], Iris Segura-García[1], Juan Pablo Ek-Huchim[2], Mónica Améndola-Pimenta[2], Rossanna Rodríguez-Canul[2]

[1]Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Puerto Morelos, Quintana Roo, 77580 México
[2]Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional-Unidad Mérida, Yucatán, 97310 México

ABSTRACT: *Panulirus argus* virus 1 (PaV1), a pathogenic virus that specifically attacks Caribbean spiny lobsters *Panulirus argus*, was recently detected in newly settled postlarvae of *P. argus*. As PaV1 appears not to be vertically transmitted, infected postlarvae likely acquire PaV1 from the water, but whether this can occur in oceanic waters where the planktonic larvae (phyllosomata) metamorphose into nektonic postlarvae remains unknown. Late-stage phyllosomata and postlarvae of *P. argus* were collected at distances of 2 to 100 km from the Caribbean coast of Mexico in 2 oceanographic cruises. Most postlarvae were caught in the upper meter of water, usually along with masses of floating *Sargassum* algae. A PaV1-PCR assay was used to test 169 phyllosomata (stages VI–X) and 239 postlarvae. All phyllosomata tested negative, but 2 postlarvae, 1 from each cruise, tested positive for PaV1. These postlarvae were collected at 55 and 48 km offshore over depths of 850 and 1800 m, respectively, suggesting that postlarvae can acquire PaV1 in offshore waters. We hypothesize that floating *Sargassum* may be an environmental reservoir for PaV1. The PaV1 allele (460 pb) found in an infected postlarva was more closely related to PaV1 alleles found in lobsters from Puerto Rico than in lobsters from any other location (including Mexico), suggesting high gene flow and long-distance dispersal of PaV1, consistent with previous studies of high genetic connectivity across the Caribbean.

KEY WORDS: PaV1 · Disease connectivity · *Panulirus argus* · PCR assays · Puerulus · Viral disease · *Sargassum*

INTRODUCTION

Panulirus argus virus 1 (PaV1) is a pathogen that specifically attacks Caribbean spiny lobsters *Panulirus argus*, a major fishing resource throughout the wider Caribbean region. The life cycle of *P. argus* includes a long (5 to 9 mo) planktonic larval phase that comprises 10 stages ('phyllosomata') followed by metamorphosis into a swimming, non-feeding postlarva ('puerulus') (Goldstein et al. 2008). Metamorphosis occurs in offshore, oceanic waters beyond the shelf break (Phillips & McWilliam 2009), from where postlarvae actively swim across the continental shelf to settle in coastal shallow habitats of benthic

*Corresponding author: elozano@cmarl.unam.mx

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Addressing environmental considerations for Marine Stewardship Council certification: A case study using lobsters

Lynda M. Bellchambers [a,*], Bruce F. Phillips [b], Mónica Pérez-Ramírez [c], Enrique Lozano-Álvarez [d], Kim Ley-Cooper [b,e], Armando Vega-Velazquez [f]

[a] Marine Ecology and Monitoring Section (MEMs), Western Australian Fisheries and Marine Research Laboratories, Department of Fisheries, Government of Western Australia,, PO Box 20, North Beach, WA 6920, Australia
[b] Department of Environment and Agriculture, School of Science, Curtin University, GPO Box U1987, Perth, WA 6845, Australia
[c] Department of Hydrobiology, Universidad Autónoma Metropolitana (UAM), Av. San Rafael Atlixco 186, Col. Vicentina, Mexico City 09340, Mexico
[d] Unidad Académica de Sistemas Arrecifales (Puerto Morelos), Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, PO Box 190. Cancun QR 77500, Mexico
[e] Colectividad RAZONATURA A.C. Av. Cozumel esq. Calle 28, Condominios Magic Paradise, depto. B4, Col. Centro, Playa del Carmen, Quintana Roo 77710, Mexico
[f] Instituto Nacional de la Pesca/Centro Regional de Investigación Pesquera-La Paz, Km # 1, Carretera a Pichilingue, La Paz, B. C. S., 23020, Mexico

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ABSTRACT

This paper uses the Western Australian rock lobster, the first fishery certified by MSC, as a case study to discuss some of the environmental issues encountered in MSC's Principle 2 and the strategies implemented to address them. Experience with the certification of Western Australian rock lobster has highlighted the importance of; comprehensive documentation of current and historical information, monitoring and research, a transparent process of risk identification and the value of an independent advisory group to review risks and guide research directions.A comparison of other certified lobster fisheries worldwide revealed that third party certification consistently identified specific environmental issues, indicating that the strategies implemented to support the ongoing certification of the Western Australian rock lobster fishery may be relevant to other fisheries.

1. Introduction

In recent years there has been concern over the sustainability of global fish stocks [1–3] and the impact of fishing on the marine environment [4,5]. While many fisheries around the world are being fished and managed sustainably the increased profile of stock sustainability and the potential impacts of fishing practices on the environment has led to an increased awareness of environmental issues by the general public and conservation groups [6–10].

Coupled with the rise in public awareness is the progression towards a more holistic approach to fisheries management in the form of Ecosystem Based Fisheries Management (EBFM). EBFM considers the cumulative impacts on the environment of all fisheries-related activities operating in an area while also taking into account social, economic and external factors (i.e. climate change and other non-fishing related activities) [11–13]. In Australia, the Environment Protection Biodiversity and Conservation (EPBC) Act and Ecologically Sustainable Development (ESD) Commonwealth requirements for export fisheries have meant that many fisheries have incorporated ecological risk assessments into their management strategies for some time. However, in some cases the implementation of EBFM has meant a significant increase in the information required [14]. In other countries, such as Mexico sustainability principals have been incorporated into legislation through a decree in "Ley de Pesca y Acuacultura Sustentatable" or through the consideration of different sustainability initiatives such as the FAO International guidelines for securing sustainable small scale fisheries [15]. However, the practical implementation of these principles in many cases lags behind the original intention of the guidelines or legislation. Regardless, these processes have undoubtedly led to an unprecedented need and pressure to examine the sustainability of fishing practices, particularly in relation to habitats and ecosystems. Growing awareness of sustainable fishing practices has led to an increase in consumer demand for sustainably-sourced seafood products [16–18] with a number of international retailers, such as Aldi, Carrefour, Tesco, Sainsbury's and Wal-Mart, and more recently Australian retailers (Woolworths and Coles) selling and promoting eco-labelled seafood products.

* Corresponding author. Tel.: +61 08 9203 0175.
E-mail address: Lynda.Bellchambers@fish.wa.gov.au (L.M. Bellchambers).

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An unfished area enhances a spiny lobster, *Panulirus argus,* fishery: implications for management and conservation within a Biosphere Reserve in the Mexican Caribbean

K. LEY-COOPER

Department of Environment and Agriculture, Curtin University, Perth, WA, Australia

S. DE LESTANG

Department of Fisheries, Western Australian Fisheries and Marine Research Laboratories, North beach, WA, Australia

B. F. PHILLIPS

Department of Environment and Agriculture, Curtin University, Perth, WA, Australia

E. LOZANO-ÁLVAREZ

Unidad Académica de Sistemas Arrecifales (Puerto Morelos), Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Mexico

Abstract The Caribbean spiny lobster, *Panulirus argus,* Latreille, is the main source of income for the communities in the Sian Ka'an Biosphere Reserve Mexico. The fishery has recently been certified as sustainable by the Marine Stewardship Council provided that further stock assessment is carried out. A total of 379 lobsters were tagged in an unfished area offshore from the Bahía del Espíritu Santo fishing grounds to assess whether lobsters remained within these areas and were thus fully protected. The lobsters recaptured in the shallow area (5.3%) were sufficient to develop a multistate mark recapture model, which takes into account fishing and natural mortality, tag reporting rate and tag loss. This estimated that between 15 and 20% of all adult lobsters dwelling in the unfished area moved into the fishery and were subjected to exploitation. This study suggests that the offshore unfished area provides protection to the majority of the stock in this area while adding to and maintaining fishing yields within the inshore commercial fishery.

KEYWORDS: community based conservation, coral reef, fisheries, population dynamics.

Introduction

Marine protected areas (MPAs) are often defined as no take zones where fishing is prohibited. As part of the conservation efforts to sustain exploited species such as lobsters, MPAs are designed to preserve important habitats that serve as shelter, foraging grounds or movement corridors, as well as protecting the breeding stocks and increasing the fishery yield of the target species (Acosta 1999; Goñi *et al.* 2010). In Biosphere Reserves like Sian Ka'an (SK-BR see map rectangular insert Fig. 1), where fishing is allowed but access is restricted and operations only occur within areas of less than 20 m depth (MRAG-Americas 2012; Ley-Cooper *et al.* 2013),

Correspondence: Kim Ley-Cooper, Department of Environment and Agriculture, Curtin University, GPO Box U1987, Perth, Western Australia, 6845, Australia (e-mail: kim.ley@postgrad.curtin.edu.au)

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ORIGINAL ARTICLE

Estimates of exploitation rates of the spiny lobster fishery for *Panulirus argus* from tagging within the Bahía Espíritu Santo 'Sian Ka'an' Biosphere Reserve, Mexican Caribbean

KIM LEY-COOPER[1]*, SIMON DE LESTANG[2], BRUCE F. PHILLIPS[1] & ENRIQUE LOZANO-ÁLVAREZ[3]

[1]*Department of Environment and Agriculture, Curtin University, Western Australia, Australia,* [2]*Department of Fisheries, Western Australia, Australia, and* [3]*Reef Systems Unit at Puerto Morelos, Institute of Marine Sciences and Limnology, National Autonomous University of Mexico, Mexico*

Abstract

The Caribbean spiny lobster (*Panulirus argus*) fishery is currently being assessed for a certification process. It is the main economic activity within the Biosphere Reserve of Sian Ka'an-Mexico (SK), which is a marine-protected area where restricted access fishing is allowed. In this study, commercial catch rates were examined, and lobsters over a wide size range were tagged throughout the 2010/2011 fishing season, to assess fishing mortality rates and movement patterns in Bahía Espíritu Santo-SK. Lobster tag recovery data were aggregated into 2-week periods and analysed using a modified Brownie model that was parameterized to account for lobster tag-reporting, and the lobster tag-retention rates. This allowed the estimation of instantaneous rates of natural and fishing mortality, considering catchability and fishing effort. Independent aquaria trials were conducted to better estimate lobster tag retention, tagging-induced mortality and interviews with fishermen were conducted to better estimate lobster tag reporting. Based mainly on legal-sized juveniles with fast growth rates found in casitas, the stock is subject to fishing to a maximum depth of 20 m, because of the prohibition of SCUBA diving and the use of other fishing gear. The Brownie model indicated that exploitation rates within this bay area were high, >0.94. Changes in catch per unit of effort and catchability throughout the season explain how the 'casita/campo' system allows for a seasonal replenishment of juveniles and adults, which has kept the landings relatively stable for the past decade.

Key words: *Lobster fishery,* Panulirus argus, *tagging, marine protected areas, exploitation rates*

Introduction

The Caribbean spiny lobster *Panulirus argus* (Latreille, 1804) is widely distributed from the southern USA to Brazil and throughout the Caribbean (Butler et al. 2011). This species is the most valuable resource fished within the Mexican Caribbean, but there is still a lack of knowledge regarding the basic mechanisms and processes that determine the dynamics of the local populations, which are part of the Caribbean's meta-population. Historically, spiny lobster fisheries have supported important commercial fisheries along the Caribbean, but increased fishing pressure has reduced lobster abundance, and currently most fisheries are being depleted (Ehrhardt et al. 2010).

This study was based in Bahía Espiritu Santo, which is located on the central coast of the State of Quintana Roo, in the Mexican Caribbean (Figure 1). It is a shallow bay with an area of approximately 300 km^2 (Sosa-Cordero et al. 1999) with very similar habitat characteristics and oceanographic conditions to Bahía de la Ascensión (Lozano-Álvarez & Negrete-Soto 1991; Sosa-Cordero et al. 1998) which is to the north. Bahía de la Ascensión has been more thoroughly studied (see review by Briones-Fourzán et al. 2000, Sosa-Cordero et al. 2008). Both bays are within the Sian Ka'an Biosphere Reserve (SK), which is a protected area where the fishery is currently co-managed by federal government authorities such as the National Commission for Protected

*Correspondence: Kim Ley-Cooper, Aquatic Science Research Unit, Curtin University, Brodie Hall Building, 1 Turner Avenue, Technology Park, Bentley, Western Australia 6102, Australia. E-mail: kim.ley@postgrad.curtin.edu.au

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ORIGINAL ARTICLE

Increased reproductive opportunity: a potential benefit of seasonal aggregation for a little-gregarious and highly sedentary spiny lobster

PATRICIA BRIONES-FOURZÁN*, ERIKA MAGALLÓN-GAYÓN & ENRIQUE LOZANO-ÁLVAREZ

Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, México

Abstract

The spiny lobster *Panulirus guttatus* is a highly sedentary, obligate reef-dweller that exhibits a low degree of gregariousness yet reproduces year-round. Previous laboratory studies revealed that these lobsters were significantly attracted to scents released by conspecifics during a 'high reproductive activity' period (HRA, ~60% of ovigerous females on average) but not during a 'low reproductive activity' period (LRA, ~20%), suggesting that becoming more closely distributed at the right time may increase reproductive opportunities for these lobsters. We tested this hypothesis in the field. We marked all crevices harbouring *P. guttatus* lobsters ('dens') on two isolated coral reef patches over six consecutive sampling periods (three during an LRA and three during the ensuing HRA) and recorded the number, sex and size of lobsters in each den. Dens marked at a given time were considered as harbouring zero lobsters at previous times. For each site, a model selection based on parameters of the negative binomial distribution showed that m (mean lobsters/den) varied little over time but that k (dispersion parameter) decreased across the LRA and remained low (indicating a more clumped distribution) across the HRA. These trends in aggregation were further confirmed by values of Lloyd's 'patchiness', supporting the hypothesis that seasonal aggregation increases reproductive opportunities for *P. guttatus*. However, the tendency to aggregate appeared to be modulated by density and mean size of lobsters, which differed with site. These findings have potential implications for exploited *P. guttatus* populations and invite further study of the complex behaviours that characterize sedentary lobsters.

Key words: *Gregariousness, negative binomial distribution, reproductive opportunity, spiny lobsters, social behaviour*

Introduction

The spatial distribution of a population provides valuable information on how individuals use a particular habitat. In nature, many populations show some degree of clumping or aggregation, with more samples containing few or no individuals than samples containing a high number of individuals (Fisher 1941; Bliss & Fisher 1953; Lloyd 1967). However, factors such as food preferences, anti-predator defence, mating opportunities, or rapid changes in numbers of individuals influence the patterns of population distribution (Andrewartha & Birch 1954; Krebs 1999; Chapple 2003). In mobile animals, these patterns are further influenced by the extent of movements and by social behaviour, which involves any kind of interaction – hence communication – between conspecific individuals, and the consequences of these interactions (Lloyd 1967; Davis 1994). Among other things, social interactions include aggression, competition, vigilance, gregariousness, migrations, courtship and copulation (Andrewartha & Birch 1954; Brown 1975; Atema & Cobb 1980; Chapple 2003). Given the potential tradeoffs between the costs and benefits of alternative strategies (e.g. to aggregate or not) at any given time, the distribution of a population is likely to change in time (Helms Cahan et al. 2002; McArdle & Anderson 2004).

Spiny lobsters (family Palinuridae) are large, nocturnal benthic crustaceans that depend on available structured shelter for diurnal protection. The younger juveniles of spiny lobsters are generally asocial and tend to remain widely dispersed, but the older juveniles and adults of many species exhibit

*Correspondence: Patricia Briones-Fourzán, Unidad Académica de Sistemas Arrecifales, ICML-UNAM, P.O. Box 1152, Cancún, Q.R. 77500 México. E-mail: briones@cmarl.unam.mx

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Panulirus argus virus 1 (PaV1) infection prevalence and risk factors in a Mexican lobster fishery employing casitas

Juan Pablo Huchin-Mian[1,*], Rossanna Rodríguez-Canul[1], Patricia Briones-Fourzán[2], Enrique Lozano-Álvarez[2]

[1]Laboratorio de Inmunología y Biología Molecular, Centro de Investigación y de Estudios Avanzados–Unidad Mérida, Instituto Politécnico Nacional, Mérida, Yucatán 97310, Mexico

[2]Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo 77580, Mexico

ABSTRACT: In Bahía de la Ascensión in Mexico, the Caribbean spiny lobster *Panulirus argus* fishery is based on extensive use of artificial shelters (casitas) that can harbor both juveniles and adults of this highly gregarious species. There is concern that the use of casitas might increase contact transmission of *Panulirus argus* virus 1 (PaV1). However, a previous study found no evidence for lobster crowding within casitas influencing the prevalence of clinical PaV1 disease, although differences in clinical prevalence were noted between different bay environments. To investigate this more closely, 683 lobsters were sampled from casitas in 2 zones in this bay (Vigía Chico, a shallow low-vegetation zone, and Punta Allen, a deeper dense-vegetation zone) previously found to have the lowest and highest prevalence, respectively, of observed clinical signs. When hemolymph collected from these lobsters was tested by PCR, the prevalence of PaV1 infection was found to be significantly lower in Vigía Chico relative to Punta Allen irrespective of season or the size, sex, or presence of shell injuries on lobsters. Among 714 large commercial-catch lobsters collected throughout the bay, the prevalence of infection was low irrespective of year or sex. For all lobsters tested, the sensitivity (0.510) at which PaV1 infection was detected by observed clinical signs was about half that determined by PCR, but the specificity of clinical signs was absolute (1), indicating that a simple 2× correction factor can be used to accurately estimate PaV1 infection prevalence based on more easily conducted visual assessments of lobsters.

KEY WORDS: PaV1 · *Panulirus argus* · Commercial catch · Prevalence of infection · Artificial shelters · Sensitivity and specificity · Bahía de la Ascensión · Caribbean · Mexico

INTRODUCTION

The Caribbean spiny lobster *Panulirus argus* is the only known host of *Panulirus argus* virus 1 (PaV1) (Shields & Behringer 2004). PaV1 has been detected in *P. argus* from numerous countries in the northwest Caribbean (Butler et al. 2008, Huchin-Mian et al. 2008, 2009, Cruz Quintana et al. 2011, Moss et al. 2013), where this species sustains important fisheries industries (Seijo 2007, Ehrhardt et al. 2010). Although PaV1 primarily impacts smaller juveniles (Shields 2011), *P. argus* of all sizes can become infected (Huchin-Mian et al. 2009, Behringer et al. 2012). Experimentally, PaV1 can be transmitted via ingestion of diseased tissue, water exposure over distances of a few meters, and especially by physical contact between diseased and naive lobsters (Butler et al. 2008). While some lobsters develop acute dis-

*Email: jpablo.huchin@gmail.com