UNIVERSIDADE ESTRADUAL DE SANTA CRUZ

PROGRAMA DE PÓS-GRADUAÇÃO ECOLOGIA E CONSERVACAO DA BIODIVERSIDADE

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CAUSALITY POWER AND AUTONOMY IN ECOLOGY: INTEGRATION OF ENVIRONMENTAL INFORMATION IN THE 'LOBSTER HOLOBIONT'

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Tese apresentada ao Programa de Pós-Graduação Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, como requisito parcial à obtenção do título de Doutor em Ecologia da Conservação.

Orientado: Prof. Dr. Leandro Loguercio

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UNIVERSIDADE ESTRADUAL DE SANTA CRUZ

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Dedico a:

A toda mi familia y amigos que me apoyaron desde un principio, en especial a mi esposa Mónica y mis hijos Valeria y Santiago. A mis padres Rosalba y José del Carmen, mi hermano Rubén y las tías Flor Angela y Berta, quienes en mi ausencia estuvieron muy pendientes de mi familia. Igualmente, a mi querida Dora, cuyo hermoso recuerdo, mantiene un especial lugar en mi corazón.

De la vida no quiero mucho.
Quiero apenas saber que intenté todo lo que quise,
tuve todo lo que pude,
amé lo que valía la pena y
perdí apenas lo que, nunca fue mío.

Pablo Neruda

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ABSTRAC

The survival and persistence of Biological Systems (BSs) depends, in part, on their composition and structural dynamics, as well as on their functional capacity to integrate and transfer information. From the hologenomic point of view, and through a systematic review, we approached the current knowledge about the structural characteristics of the community of bacterial microsymbionts of lobsters. Apparently, at least part of these bacterial communities is an integral part of the lobster's body, being closely associated with the identity and condition of the host. This panorama allowed us to include a hologenomic view in studies aimed at the conservation and management of this organism, a recognized fishing resource. Such a complex condition of this system allowed us to maintain the idea of the impact that the environment can have on BSs, but, at the same time, it opened the door to explore the possibility of the existence of a 'power of cause' that the BSs probably have on the environment. From this condition, we found a thinking system little explored in ecology, i.e., the 'complex thinking'. In this system, the role of ‘information’ is addressed and how its flux allows us to deepen our knowledge on particular characteristics of BSs, such as emerging properties and their possible relationships with ecological issues. As a consequence of this perspective, and after an extensive review and study of the literature on the topic, we sought to bring to light the potential of BSs 'autonomy' as a causal power, capable of interfering and interacting with the environment, making both intricately responsible for ecological patterns and processes. From this view, the ability of BSs to ‘integrate information’ emerges as an emerging property, highlighting the ‘power to choose’ as an important guiding variable in ecological processes. Consequence of this exercise and in search of evidence in this direction, we explored the existing literature, together with empirical observational data, on the post-larval settlement of lobsters by assessing the incidence of 'unusual' events in the incorporation of new information to BSs, as well as the relevance of these events in the autonomy and potential of persistence of these organisms. Taken together, this thesis demonstrates the viability of complex thinking in ecology and conservation d opens lines of research that are intended to be explored in this universe of lobsters and in the conservation of biodiversity and biological resources.

Keyword*: *Complexly thinking, Lobster holobiont, Post-larval, Settlement, Information Integration, Common and Rare Event.

RESUMO

A sobrevivência e persistência dos Sistemas Biologicos (BSs) dependem, em parte, de sua composição e dinâmica estrutural, bem como de sua capacidade funcional de integrar e transferir informações. A partir do ponto de vista hologenômico, e mediante revisão sistemática, abordamos o conhecimento corrente sobre as características estruturais da comunidade de microssimbiontes bacterianos das lagostas. Aparentemente, ao menos parte dessas comunidades bacterianas são parte integrante do corpo da lagosta, estando intimamente associadas à identidade e condição do hospedeiro. Este panorama nos permite incluir uma visão hologenômica em estudos voltados para a conservação e manejo deste organismo, um reconhecido recurso pesqueiro. Essa condição complexa deste sistema nos permitiu manter a ideia do impacto que o ambiente pode ter nos BSs, mas, ao mesmo tempo, abriu a porta para explorar a possibilidade de 'poder de causa' que os BSs provavelmente têm sobre o meio ambiente. A partir dessa condição, encontramos um sistema de pensamento pouco explorado em ecologia, i.e., o 'pensamento complexo'. Neste sistema aborda-se o papel da 'informação' e como seu fluxo nos permite aprofundar características particulares dos BSs, como propriedades emergentes e as possíveis relações com questões ecológicas. Como conseqüência dessa perspectiva, e após uma extensa revisão e estudo de literatura sobre o tema, buscou-se trazer à luz o potencial da 'autonomia' dos BSs como poder causal, capaz de interferir e interagir com o ambiente, tornando ambos intrincadamente responsáveis pelos padrões e processos ecológicos. A partir dessa visão, a capacidade dos BSs para 'integrar informações' surge como propriedade emergente, destacando o 'poder de escolher' como importante variável diretora de processos ecológicos. Consequência deste ensaio e em busca de evidências nessa direção, exploramos a literatura existente, juntamente com dados empíricos observacionais, sobre o assentamento pós-larval de lagostas avaliando a incidência de eventos ‘não-usuais’ na incorporação de novas informações aos BSs, bem como a relevância desses eventos na autonomia e potencial de persistência desses organismos. Tomada em conjunto, a tese demonstra a viabilidade do pensamento complexo em ecologia e conservação, e abre linhas de pesquisa que pretendem ser exploradas nesse universo das lagostas e da conservação da biodiversidade e dos recursos biológicos.

Palavras chave: ***Pensamento Complexo, Holobionte lagosta, Pos-larval, Assentamento, Integração da Informação, Eventos comuns e inusuais.***

RESUMEN

La sobrevivencia y persistencia de los Sistemas Biológicos (BSs) depende, en parte, de su composición y dinámica estructural, así como de su habilidad para integrar y transferir información. Desde una perspectiva hologenómica y mediante una revisión sistemática abordamos las características estructurales de la comunidad micro simbionte de las langostas. Al parecer estas comunidades bacterianas hacen parte integral del cuerpo de las langostas y se asocian con la identidad y condición del hospedero. Panorama que permite incluir una visión hologenómica a los estudios enfocados a la conservación y manejo de este organismo. Esta condición de sistema complejo, nos permitió mantener la idea sobre, el impacto que tiene el entorno sobre los SB. Pero a la vez, abrió la puerta para explorar el poder causal que tienen los SB sobre el entorno. Al explorar esta posible condición, nos topamos con líneas de pensamiento poco exploradas como el “pensamiento complejo” y una cantidad de información que nos permitieron profundizar sobre particularidades propias de los SBs como las propiedades emergentes y su posible relación con asuntos ecológicos. Consecuencia de esta perspectiva y tras una extensa revisión sobre este panorama, se realizó un ensayo que intentó colocar sobre la mesa, el poder autónomo de los SBs como poder causal, capaz de interferir el poder causal del entorno, ambas responsables de los patrones o procesos ecológicos. Desde esta visión, la información y la capacidad de los sistemas biológicos para integrarla, cobran gran relevancia, y se destaca la autonomía como direccionador de procesos ecológicos. Consecuencia de este ensayo y en procura de evidencias, exploramos con base a la literatura existente sobre el asentamiento postlarval de las langostas y con datos empíricos, la incidencia de los eventos raros en la incorporación de nueva información a los SBs y la relevancia que estos eventos en la autonomía y el potencial de persistencia. En conjunto, esta tesis demuestra la viabilidad del pensamiento complejo en ecología y conservación, y abre líneas de investigación que pretender ser exploradas en ese universo de las langostas, y de la conservación de la biodiversidad de los sistemas biológicos.

Palabras Claves: Pensamiento Complejo, Holobionte Langosta, Post-larva, Asentamiento, Integración de la Información, Eventos comunes y raros.

INTRODUCTION

Adaptation and persistence, as ecological phenomena, can be challenged within the current paradigms if we observe and assess them from the standpoint of *information flux*, and link that with the concept of the ‘living’ as a complex system. In this sense, the power of connections that Biological Systems (BSs) have with themselves (structural parts and functions) and with the environment, can have consequences in their ability to adapt and evolve. In other words, such a connectivity and the flux of information can be thought as parts of a process that confers the ability to BSs to ‘reduce uncertainty’ in relation to their immediate environment. This view establishes that the relationship between a BS's abilities to ‘internalize’, ‘manipulate’ and ‘generate’ information will increase its potential for persistence. It has been already put forward that BSs are not born with all the necessary information to persist, so that effectiveness in such ‘decision making’ processes seems to be a crucial “life or death” issue. Recently, some authors have suggested that the emergent property of a system to be able to ‘integrate information’ can generate, as a consequence, a certain degree of *autonomy* to such system. In this sense, a BS can be seen and evaluated as holding an ‘interpretative capacity’ of its immediate environment, which could be viewed as an ability to ‘make choices’.

Among the various paradigms with validity in ecology, the view of the environment as the causal power of phenomena, being the major factor responsible for selective processes has been predominant thus far. From this perspective, the flow of matter, energy and information between the environment and the BSs induces us to finding functional patterns and correlations, with the final cause (predictive models) for the phenomena being the effects (characteristics and variation) of the environment, i.e., although the BSs do influence the environment, it is the BSs that ultimately *react* to the environment. From this, it is the variability of the environment what mainly shapes the observable ecology patterns. From two major thinking systems in science (analytical and systemic), the already demonstrated correlations and cause-effect relationships between environmental and systems variables provide a robust support for that perspective, which has allowed the generation of an array of theories related to, for instance, adaptation, natural selection, biodiversity, loss of it, ecosystem instability, succession, niche theory, etc.. It is important to note that, from the *behavior* of a BS (at various distinct scales), issues such as diversity or adaptive capacity have also been addressed and explained. Nevertheless, individual or collective behaviors end up being viewed as 'subject to' the environment, independently of it being modified or not by the systems. As Lalana mentions, "*Organisms exert some influence on their evolution*."; however, it is the modified environment what ultimately influences the selective pressures. As Carl Sagan said, "*the selection is imposed from outside*".

Keeping this perspective in mind, there is a trend in ecology to correlate the emergent property of a system to 'integrate information' (i.e., the ability of 'cognition') with the environment, suggesting that it arises *in response to environmental challenges*. That is, new environmental conditions or environmental variability favors the emergence of 'cognition' (with variable intensities and characteristics, depending on the BS in play). These variant conditions require the development of new behaviors or strategies that allow the systems to 'solving problems', which are issues observed and considered, for example, in birds. Our claim has been that, for the last centuries, all 'responsibility' for these cognitive processes has been left to the environment, disregarding the possibility that an autonomous, 'deliberative' capacity of a BS (allowing 'options to be taken'), could interact and interfere with the final 'causal power' of the environment. Hence, in the present study, I am proposing the incorporation of a third thinking system in the science of ecology and conservation: the *complex thinking*. Under this, the 'cognition', as an emergent character/condition manifested by a system in different forms and intensities, may directly interfere in the end points of interactive processes with the environment. Despite that the causal power the environment has on BSs is undeniable*,* I propose, as an alternative and complementary view, that the power of cause that the environment exerts on BSs *changes over time* and, at the same time, *is not the same for all the different BSs,* being dependent on the *type of information* that a BS integrates, at a particular time. Our aim is having a more complete ability to devise predictive models that can lead to better informed decisions on management and conservation strategies.

These approaches challenge the search for new theories and, of course, the search for new evidence that will allow us to clarify a variety of important issues related to this context. Questions such as how *autonomy* is possible; how does it develop; how it is selected; in what level it is presented; what is its potential as ‘power of cause’ in the systems or in the environment, what is its impact on adaptation or persistence, what are evidence of events or environmental conditions that allow increasing or restricting autonomy, can all be addressed and investigated.

From this third system of thought, I expect an interference with theories in ecology and conservation, and so, with the predictive power on ecological processes and observable patterns. From its evolutionary nature, the ‘cognitive ability’ should not be seen as something exclusive to the human species; it can be seen as a complex biological property evolving in multiple ways in different living systems. Although *information* as a quantifiable variable (see glossary) is a relatively abstract term, complex thinking leads to the view that BSs, in addition to ‘manipulate’, can also generate and introduce *information* to the environment, thereby increasing its complexity. In the theoretical approach of this thesis, I rely on ideas such that BSs can ‘design’ their immediate environment with some degree of ‘intentionality’, taken as something that bears a ‘power of cause’ that interferes with the environment, thereby further promoting their adaptation and persistence. An ability that is based on the composition and structural potential, along with functional capacity, and is the result of internalization, integration, processing and generation of *information*. It is such a complex process of generation and flow of information in the systems within the environment that I suspect are partly responsible for an array of observable ecological patterns, which include a variety of emerging behaviors, such as cooperation, competition, symbiosis, mutualism, etc. Cognitive abilities of BSs are certainly delimited by environmental facts related to, for instance, the avaliability of resources and space, metabolic issues, thermodynamics, predation, climate, etc., with all of them embedded in conditions of ‘monotonous’ (frequent) and ‘unusual’ (rare) events that end up modulating the ‘environmental information’ available to the systems.

Supported by the view of authors such as Haan, Maldonado, Tononi, Vedral, among others, I embrace the idea of a ‘complexly thinking’ on natural (and anthropic-derived) selective processes that lead to a better interpretation of the environment as a whole, including their BS components. That is to say: cognition of BSs helps reducing ‘uncertainty’ around them and, by doing so, not only do the most numerous persist, so does the most ‘intelligent’, i.e., the one who predicts best. This thesis explores this idea from the perspective of thinking in a complex way, as described by Morin. Lobsters (Crustacea: Decapoda) are used in this work as a model organism, due to the familiarity I have with this taxonomic group.

Throughout its evolutionary history, the lobsters have persisted in the last three mass extinctions and is currently under an atypical experience, without any background (Anthropocene and anthropic-derived causes of the potential sixth mass extinction on Earth). This group of crustaceans are experiencing multiple and simultaneous unusual events in their immediate surroundings, at a fairly rapid pace. Under these circumstances, I was first caught by the interesting alternative view of lobsters as hosts of complex microbial communities, whose interactions in many ways and levels have brought to light the Hologenomic Theory of Evolution by Zilber-Rosenberg and Rosenberg, a view that raised our understanding of complex interactive systems to a further level of matter, energy and information exchange. Yet under a classical systemic thinking approach, a primary emergent property of ‘holobiontness’ is explored in chapter 1. Being stimulated by these possibilities and knowledge (which led to study and readings on network and information theories), I was then directed towards complex systems and the alternative ‘complex way of thinking’ as an interesting, complementary scientific thinking system. In chapter 2 (and in the glossary), I develop a series of basic, fundamental concepts required to understand the characteristics and consequences of the ‘thinking complexly’ about BSs and the environment; I also start proposing to apply these views, thoughts and methods to ecological issues related to conservation of biodiversity and biological resources. Finally, in chapter 3, I have merged the complex way of thinking to the lobsters *milieu*, by exploring previously collected data on post-larval settlements under this new thinking system. This philosophical process provided alternative and interesting explanations for the empirical data available, as well as left a series of questions as open avenues of future research.

GLOSSARY AND ACRONYMS

Autonomous: Not controlled by others or by outside forces. Independent. Act independently. Effect in itself.

Biological system (**BS**): A complex system capable of perceiving, integrating, storing and generating information. In this study, the observer is a synonym. The BS in this approach can be the individual, the population or their lineage. That is, a biological system extends from its evolutionary history as a population, to the current individual.

Certainty: Clear knowledge about something.

Choices: an act or instance of selection, an alternative. Governed by subjectivity. It can be individual or collective.

Challenge: Difficult or dangerous situation that a complex system faces.

Cognition: The mental process including aspects such as perception and integrating of information. That which in a BS comes to be known are claimed to be individual instances of subjective, conscious experience.

Disturbance: Temporary change in environmental conditions, which causes a change in the structure of a system. (e.g., fires, floods, storms, meteorite fall). Anthropogenic disturbances are deliberate actions to modify the environment.

Dysbiosis: Is a term for a microbial imbalance or maladaptation on, an impaired microbiota.

Decision: The act of taking one option. In an estimate of the situation, with information about the immediate environment.

Death: Cessation or death is a state of total permanent disinformation between its parts (as a whole) and its Immediate Environment (IE) in an BS. This prolonged inability destabilizes and disintegrates the system. It makes it diffuse, unrecognizable, formless.

Deliberate: Voluntarily and intentionally.

Environment Immediately (EI): It is the biotic and abiotic environment of a BS, including all the information that has been selected and because it is sensitive to it.

Evolution: Is change in the heritable characteristics of biological populations over successive generations.

Endosymbiotic: Is any organism that lives within the body or cells of another organism most often, though not always, in a mutualistic relationship.

Exosymbiotic: It is any organism that lives outside and in permanent contact with the body of a host, but not always, in a mutualistic relationship.

Emerging: Attributes that arise from the interaction of the parts of a complex system. They cannot be identified in the properties of the components that form it. Able to affect BS itself.

Experienced: Having had experience in an activity or life in general: a highly experienced traveler. Skilled or knowledgeable as the result of active participation or practice.

Experience: Ability acquired by having done, lived or felt.

Fitness: The proper condition of a BS that allows you to perform any physical action possible. It relies on the genotype of the BS and the information of its immediate environment.

Fundamental: serving as a basis supporting existence or determining essential structure or function.

Hologenome: It is a theory related to evolution. recasts the individual animal or plant (and other multicellular organisms) as a community or a "holobiont" – the host plus all of its symbiotic microbes. Consequently, the collective genomes of the holobiont form a "hologenome". Holobionts and hologenomes are structural entities.

Holobiont: Is an assemblage of a host and the many other species living in or around it, which together form a discrete ecological unit.

Homeostasis: A state of equilibrium, as in a BS, maintained by self-regulating processes.

Homeorhesis: "flow - cycle", is a concept encompassing dynamical systems which return to a periodic trajectory.

Intentionality: Deliberate action, supported by the information that contains or integrates the BS.

Information: Taking the living (BS) as a limit, we can understand information as a unit capable of altering the state of uncertainty proper to the system about its immediate environment. The change that this unit can generate depends on the sensitivity (state and condition of the BS), which adopts or arises after an evolutionary process. The information generates the matrix of an observer, that is, it builds a place and time where matter and energy are manifested. The information progressively reduces the entropy within the BS and at the same time increase into the IE, making it more complex.

Live: In terms of information, the system becomes alive when it internalizes the environment, begins to "travel" (time / space) and memorize. Evidence, integrates and generates information.

Microbiome: Ecological communities of commensal, symbiotic and pathogenic microorganisms. Synonymous of **microbiome, microbiota.**

Monotonous: Tediously repetitious or lacking in variety.

Nestedness: It's a representation or hierarchical pattern of species composition among fragments of landscapes. Nesting occurs when species found in smaller fragments constitute subsets of those in larger biota. "one structure nested".

Ontogenetic: The developmental history of an organism within its own lifetime, synonymous of ontogenic.

Observer: A complex system capable of carrying out measurements that allows obtaining information from the environment.

Pathogens: describe an infectious microorganism, can which produce disease.

Post-larval: Stage or stages in the development of an animal following the larval stage, especially those in which some larval characteristics are retained, before the animal attains fully adult form (used especially of fishes and marine invertebrates). In lobsters, the post-larval state is called pueruli (plural) or puerulus (singular).

persistence: the act of persisting; continued effort for the existence. In ecology, the persistence of a species depends in part on a minimum viable number, capable of reproducing.

Problem: Assumption that needs a solution, depends on the observer.

Symbiotic: Is any type of close and long-term biological interaction between two different biological organisms, be it mutualistic, commensality, or parasitic.

Structure: A structure is an arrangement and organization of interrelated elements in a material object or syste.

Stochastic: Pertaining to a process involving a randomly determined sequence of observations each of which is considered as a sample of one element from a probability distribution.

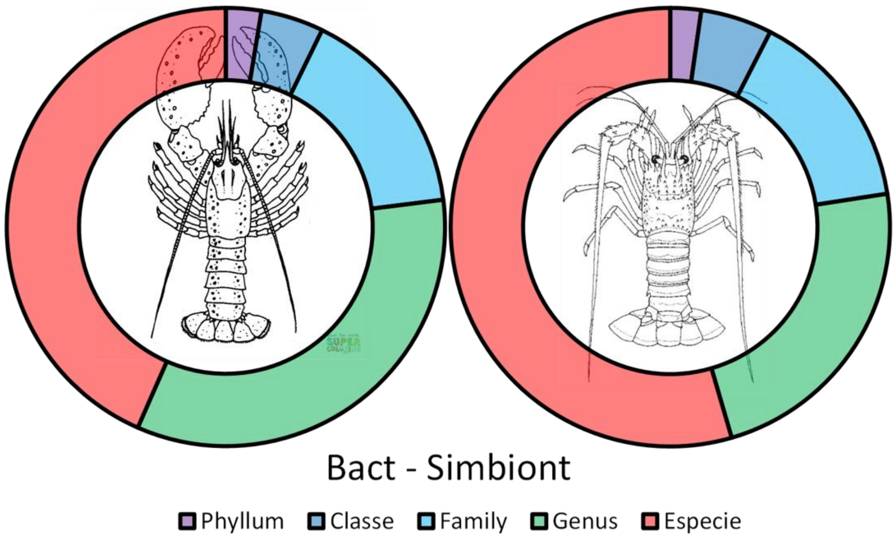
Subjectivity: Dependent on the BS who thinks or feels it. It is an individual and autonomous character, (The feeling of being "me").

Subjective: Relating to the way of thinking or feeling and not the object itself.

Uncertainty: Is a situation that involves imperfect and/or unknown information. Therefore, it is dependent on the identity and condition of the BS. Difficulty measuring, lack of information.

CHAPER I

A HOLOGENOMIC VIEW ON LOBSTERS: MICROBIOME CHARACTERISTICS AND CONSEQUENCES IN ECOLOGY AND CONSERVATION



ABSTRACT

Recently, there has been a greater interest in understanding how higher organisms relate with their symbiotic microbial communities and how this relationship affects behavior, health and adaptation of the host. In the efforts to address the management of lobster resources, little has been discussed about how these relationships can influence the ability or response capacity of lobsters to face environmental challenges. Through a systematic analytical review, the present study aimed at characterizing the current understanding, trends and gaps concerning symbiotic microbiota associated with lobster, as well as their consequences on the ecology and conservation of this resource. This study focused on associated bacterial communities present during the ontogenetic development and in different tissues of lobsters of the Palinuridae, Scyllaridae and Nephropidae families. The results indicated that most of the studies focus on the exoskeleton of juveniles and adults of a single lobster species, *Homarus americanus*, with much less attention given to the other species. In general, until now, there are 17 bacterial phyla and about 262 genera (most belonging to the phyla Proteobacteria and Bacteriodetes) that have been isolated in natural and/or laboratory-reared populations. Such proportion among taxonomic levels is maintained regardless of the family, ontogenetic state or lobster’s tissue. The classes α-Proteobacteria, γ-Proteobacteria, and Flavobacteria are the richest in bacterial genera, according to the studies addressed. By means of taxonomic levels relationships, bacterial symbiont communities related to the identity and health condition of the host were compared. Results showed a wide collection of microorganisms that appear to be an integral part of the lobster body, but also suggest effects of the host health conditions in the structure of the associated bacterial communities. This information allowed us to expand, from a hologenomic perspective, our understanding of the dynamics of this resource and discuss conservation aspects for the holobiont-lobster unit.

INTRODUCTION

The critical role of microbes for terrestrial and aquatic environments on Earth is based on their diversity, abundance and functional protagonism on an array of biogeochemical processes; these generate countless substances of intra or extracellular characteristics that are distributed in an immense variety of ways, within and among ecosystems (Kirchman 2008, Ovreas & Curtis 2011, Cunha et al. 2010). As simple example of this importance, microorganisms have the unique ability to fix atmospheric nitrogen (N_2) and make it usable in the reduced form (NH_3) for the construction of proteins, or for photosynthetic processes, which are the basis of oceans' food net (Gonzales et al. 2008; Voss et al. 2013). Estimated average densities of bacteria in the ocean can reach 500,000 cells / cm^3 in photic zones, about 100,000 cells / cm^3 in the aphotic zones, and around 1.000.000 cells / cm^3 in upwelling systems (Gonzales et al. 2008). Molecular techniques have been unravelling a great gap on the knowledge about the true bacterial diversity that exists on the planet (Youssef et al, 2015; Schulz et al. 2017). Other relevant issues are related to the ability of bacteria to rapidly and frequently exchange genetic information, which allows the expression of a great variety of distinct responses to countless environmental challenges, and in short periods of time, leading to a remarkable adaptability repertoire (Gonzales et al, 2008; Logue et al. 2015). Improving our understanding of the intricate, though knowledgeable structural and functional interaction of microbiotas with virtually all hosts and ecosystems on Earth have been claimed as an urgent action to help coping with climate changes (Cavicchioli et al, 2019).

Throughout the last century and thus far, many studies have been carried out on symbiotic microorganisms present in lobsters, highlighting the scarce presence of parasites and pathogens comparatively with other marine organisms (Shield 2011). This symbiont community, which has been mostly linked to diseases and infections, is composed of a diverse group of animals, chromista fungi, protozoa, viruses, and bacteria. Studies related to associated bacteria can be referenced from the 1930s, indicating their infectious role in lobsters (Hess 1937;

Snieszko & Taylor 1947). However, symbiotic bacteria are part of the adaptive or evolutionary processes of eukaryotes, a subject already put forward for almost a century (Williams 1927; Haag 2018). In relation to the microbial ecology, it is important to highlight the microbial assemblages and their relationship with the health or illness of the hosts (Meres et al.,2012). Shade and Handelsman (2012) emphasize the importance in identifying a 'core microbiome', or the P-symbionts (Moya et al. 2008), since it can help to define host fitness and predict responses of this community to disturbances. The dynamics of such interaction among microbiota, marine host-life forms and an array of environmental factors has been realized as crucial for the final health outcome of the hosts (Moya et al, 2008; Burn et al, 2016); this is so much so, that surveillance of marine diseases through ocean temperature monitoring have been recently advanced (Maynard et al, 2016).

The evidences of these host-symbionts links are such that Zilber-Rosenberg and Rosenberg (2008) have proposed the 'hologenomic theory of evolution' that seeks to explain adaptive and evolutionary processes through a unit called 'holobiont'. Such a conceptual framework might help to understand in more detail, for example, redistribution of species, capacity of resilience in face of climate change, or emergence of novel diseases within marine populations (Magris et al. 2014; Groner et al. 2016). However, Moran and Sloan (2015), argue that organisms can have intimate and ancient associations with micro-symbionts, but this does not imply co-evolutionary processes, so it is only under specific circumstances that the selection unit is at a holobiont level. This debate has been coming along with better clarification of concepts and their proper usage, as well as with new conciliatory views concerning structure and functions of the halobiont 'whole' (Theis et al. 2016; Catania et al. 2017; Haag 2018). When dealing with comparisons among holobionts (subjected or not to whatever treatment of interest), there are two major (micro)ecological parameters that can be assessed, to provide a view on the variation of the host-associated microbiome: (i) the composition and (ii) richness of microbial taxa. These are two ways of addressing one of the four generalizations of the hologenomic theory of evolution, i.e. that variation in the hologenome can occur through amplification/reduction as well as through changes in composition of the host-associated microbes (Zilber-Rosenberg and Rosenberg, 2008).

Molecular methods have evidenced the vast microbial community present in marine environments and the important support they provide in biogeochemical processes (Pedrós-Aliós 2006; Massana 2011). These methods have been allowing us (i) to learn more about characteristics of bacterial communities present in higher organisms, (ii) to concatenate these symbiotic relationships with condition of the host within their environment, and (iii) to determine the consequences of this host-symbiont relationship in the adaptation, plasticity, ecology and evolution of eukaryotic hosts.

In crustacean decapods, particularly for lobsters, the basic support for its management in natural environments and development of alternative production systems is the knowledge of their life cycle, physiology, health and aspects related to its ecology. To date, knowledge on how bacterial community can influence the fitness of lobsters is still in its infancy. This paper presents a systematic review on what has been investigated and unveiled about structural characteristics of symbiotic bacterial communities of lobsters, addressing taxonomic and diversity aspects of both the lobster and bacterial species under interactive modes of living. A novel method to compare groups pairwisely ased on proportions of distinct taxonomic levels is proposed and presented. We sought to understand a possible effect of these communities on the ecology and conservation of this marine resource, as well as to highlight the trends and gaps of the investigations carried out to date in this theme. Important aspects and questions for future required research has been discussed.

METHODS

Literature-review strategy

With the Publish or Perish tool (Harzing, 2007), scientific articles that contained 'lobster(s)' and 'crustaceans' in the title, and 'bacteria', 'OTUs', ‘Microbiome’, and ‘Holobiont’ in the whole text (not necessarily all together), a total of 753 primary-studies articles were retrieved (through Google Scholar); our research database was assembled with publication whose dates ranged from the 1960s to December 2018. Furthermore, 20 reviews associated with symbionts causing disease in lobsters were also found; for this study, only the 10 available online were used to provide a succinct description of the symbionts (Sm1). Thus, the present study also includes reviews, which have focused on endo- and exosymbiotic bacteria of lobsters; they were added to those 753 articles in our database. The inclusion and exclusion criteria of this first selection are specified in Sm2. The database reflects the taxonomy and presence of bacteria in the different defined items, e.g. species of lobster, healthy or sick, stage of development, tissue, habitat. Thus, 56 documents were selected (Sm3).

Our analysis was limited to bacterial communities present in different ontogenic stages, organs and structures, fitness, and life condition of lobsters belonging to the Palinuridae, Scyllaridae and Nephropidae families. These aspects were used to assemble our study’s groups. To contextualize our study, a synthesis was made by linking previous studies to articles related to the hologenomic theory of evolution, published since the year 2000; from this year until 2008, we defined the articles we assessed as being related to such theory based on the type of their information and interpretation presented, since this theory/concepts were specifically launched only after 2008. The species names, lineage and general characteristics of the bacteria found were reviewed from the following databases: World Register of Marine Species (WoRWS) (http://www.marinespecies.org/index.php); Taxonomy browser of the National Center for Biotechnology Information (NCBI) (https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi), and List of Prokaryotic names with Standing in Nomenclature (LPSN)(http://www.bacterio.net).

Analysis of the information and data

An assessment and description of the trends found in the studies related to the lobsters' microbiomes were performed. This description was based on the relative number of studies within each of our study groups, which were discriminated based on the isolation and identification methods, source tissues for the bacterial isolations, fitness and life condition of the lobsters. Using a "Word cloud"-like online tool (https://www.nubedepalabras.es/), we created a graphic based on the frequency of keywords occurring in the articles. The descriptive statistics on the retrieved literature database were recorded and worked out in MS Excel^{TM} spreadsheets (Sm4).

Through the information processing in our local database of selected articles, we identified possible confounding factors among the studies that might cause noise in the classification of the data collected and in the interpretation of the results. In addition, we proposed a specific methodology to investigate the relationship among the microbial taxa levels associated to the study groups here defined, which were addressed in a pairwise manner (see below). In order to address these issues, the following definitions were considered:

1. The richness index (S) was estimated for each of the bacterial taxonomic levels as being the total number of Species (Ssp), or Genera (Sgen), or Families (Sfam), or Classes (Scla), or Phyla (Sphy); this index provided comparative values for variability of the symbiotic community for any contrasting groups ('A' and 'B'), according to the taxonomic level considered. In addition, any two contrasting groups can be also compared in a normalized manner by finding the proportions of each taxonomic level within the sum of all levels. The study groups were defined and compared in a pairwise manner as follows: endo- *vs* exo-symbionts ('End' *vs* 'Exo'); wild *vs* laboratory-controlled conditions ('W' *vs* 'L'); healthy *vs* diseased ('H' *vs* 'D'); Gram-positive *vs* Gram-negative ('G+' *vs* 'G– '); and Nephropidae *vs* Palinuridae lobster families (N *vs* P).

2. For these contrasting groups, we estimated the similarity index of Jaccard (*J*) for each taxonomic level of the isolated bacteria described in our local

database. For instance, taking the *genus* taxonomic level into consideration, the estimate of the corresponding Jaccard's similarity index between two contrasting groups 'A' and 'B' followed the equation [1]:

[1]

$$\boldsymbol{J(G) = \frac{SG_C}{SG_A + SG_B - SG_C}}$$

where Sg_C is the richness index for common genera between the two groups A and B, Sg_A is the richness index for genera of group A, and Sg_B is the richness index for genera of group B. Considering the contrasting groups we established above, the only pair that could not be assessed through the *J* similarity index is the pair Gram-positive / -negative, since there is no bacteria that can be of both types simultaneously (the Sg_C factor in the formula above).

Since the similarity estimates for the contrasting groups (for each lobster family) were based on their richness values (of discrete, countable and independent nature), these *J* values were pairwisely compared statistically through chi-square/G-test analyses with correction of Yates when recommended due to low frequencies (Ayres et al, 2007; McDonald, 2014); richness data were set on a 2 x 2 contingency tables, testing for the null hypothesis of independence between the two categorical variables, i.e. 'contrasting study categories' (see above) and 'sharing taxa' ('common' vs 'unique' to each study group, for each taxonomic level). The statistical significance threshold was set at a probability of 10% ($P < 0.1$). The analyses were performed using the open-access statistical software 'BioEstat 5.0' (Ayres et al., 2007).

3. Finally, we proposed an alternative method to search for possible relationships between 'bacterial community structures' and the 'host condition'. The method is based on the richness index (S) of the different taxonomic levels (see above) and is aimed at providing a comparison strategy based on a normalization procedure, in order to reduce the inherent noise of compiling data from distinct studies (i.e., different model organisms, research methods, timeframe, scientific questions addressed, biases, etc.). For the scope of this study, this method was

named as ‘Comparison based on Taxa Proportions’, or ‘CTP’, and it was applied in a pairwise manner to the lobsters’ microbiomes in the various study groups (see item ‘1.’ above). As a first step, we estimated the relationships (proportions) between two contiguous taxonomic levels in a decreasing hierarchical taxa series (with increasing values per taxa level), i.e. ‘Phylum/Class’, ‘Class/Family’, ‘Family/Genus’ and ‘Genus/Species’. Such a pairwise relationship (PR) between two contiguous taxonomic levels was estimated as shown by the next equation.

[2]

$$\boldsymbol{PRI} = \frac{\boldsymbol{S_{HTL}}}{\boldsymbol{S_{LTL}}}$$

Where S is the richness indexes (see item 1 above), with the *Htl* label indicating the immediate higher taxonomic level in relation to the immediate lower one, indicated by the *Ltl* label; the ‘*i* ' label of PR is a generic description for the contiguous taxonomic levels relationships, e.g. PRphy/cla relates phyla (higher) to class (lower) levels, PRcla/fam relates class (higher) to family (lower), and so on. After the PRs are calculated for each series (study group). The PR values ranged from 0 to 1, so that when the value is closer to the unity, the diversification (i.e. the S index) is similar between two contiguous taxonomic levels. Contrarywise, when PR approaches ‘zero’, the S index of the lower taxonomic level tends to be very high, indicating a greater diversity than the immediate previous (higher) taxonomic level.

As shown in the Results section, from this methodological perspective, we were able to assess intrinsic properties of each bacterial community from its taxonomic composition, and compare all categories in a normalized manner. These results are accompanied by a series of linear and ring-type colored graphs for the study groups, in which each colored section corresponds to an S index. Taking into account the results obtained with the analysis of similarity between contrasting groups, the ‘Ho’ hypothesis that there is a positive relationship between the proportional PR series and the health status of the host was proposed.

RESULTS

General trends of the studies

Based on the series of studies selected by applying our search protocol (Sm2), an overview of the research on the association of lobsters and bacterial communities is presented (Fig. 1). The first investigations in the beginning of the century have isolated chitinolytic bacteria present in the exoskeleton of *Homarus americanus* wild (Hess, 1937) and those that were later associated with population declines of this species on the coasts of the State of Main (USA)(Snieszko and Taylor, 1947). Subsequently, in the first review articles published in the 1970s, bacteria belonging to the classes Bacilli, Cyanophyceae and Γ–Proteobacteria were reported as being present in juveniles and larvae of lobsters reared in the laboratory (Steenbergen and Schapiro 1974, Fisher et al., 1978). Since then, reviews on these aspects of the association between lobsters and bacteria appeared more frequently (Fig. 1a); also, as seen from the word cloud, the link between bacteria and diseases (Fig. 1a) stood out in the entire series of reviews until 2013. Despite being a group of lobsters with a complete technical package related to their cultivation and manipulation in the laboratory (Lavalli and Spanier 2007), the scarce information in the scientific literature related to bacteria present in the lobster family Scyllaridae is remarkable. Only a small group of eukaryotic parasites from the Cestodes, Cyclophores and Cirripedios groups have been reported for this lobster family (Shields et al 2006, Shield 2011).

We found a not very extensive literature that describes the bacterial communities present in sick and healthy lobsters (Sm3). From an ontogenic perspective, the highest percentage of studies focused on adults (49%), followed by larvae (24%). Only one article focused its research on post-larvae states (Fig. 1b). In relation to the type of tissue under study, the exoskeleton (28%), hemolymph (20%) and digestive system (16%) were the most frequent. On the other hand, 49% of the studies focused on wild lobsters, 22% in laboratory conditions and 0.02% in semi-controlled systems (culture) (Sm6). In general, we found that the vast majority of research covers only three (7%) of the 43 species reported for the Nephropidae family, 15 (32%) of the 47 species reported for the Palinuridae family, and none in the Scillaridae. This bias of research focus towards the three species of the Nephropidae family can be seen from the fact that 53% of all the selected studies have focused on them (Sm6). In relation to the methods of isolation and identification, we observed three main methods: classical culture-dependent, molecular culture-independent, and electron microscopy. Approximately 60% of the investigations have isolated bacteria by the culture-dependent techniques, and 31%

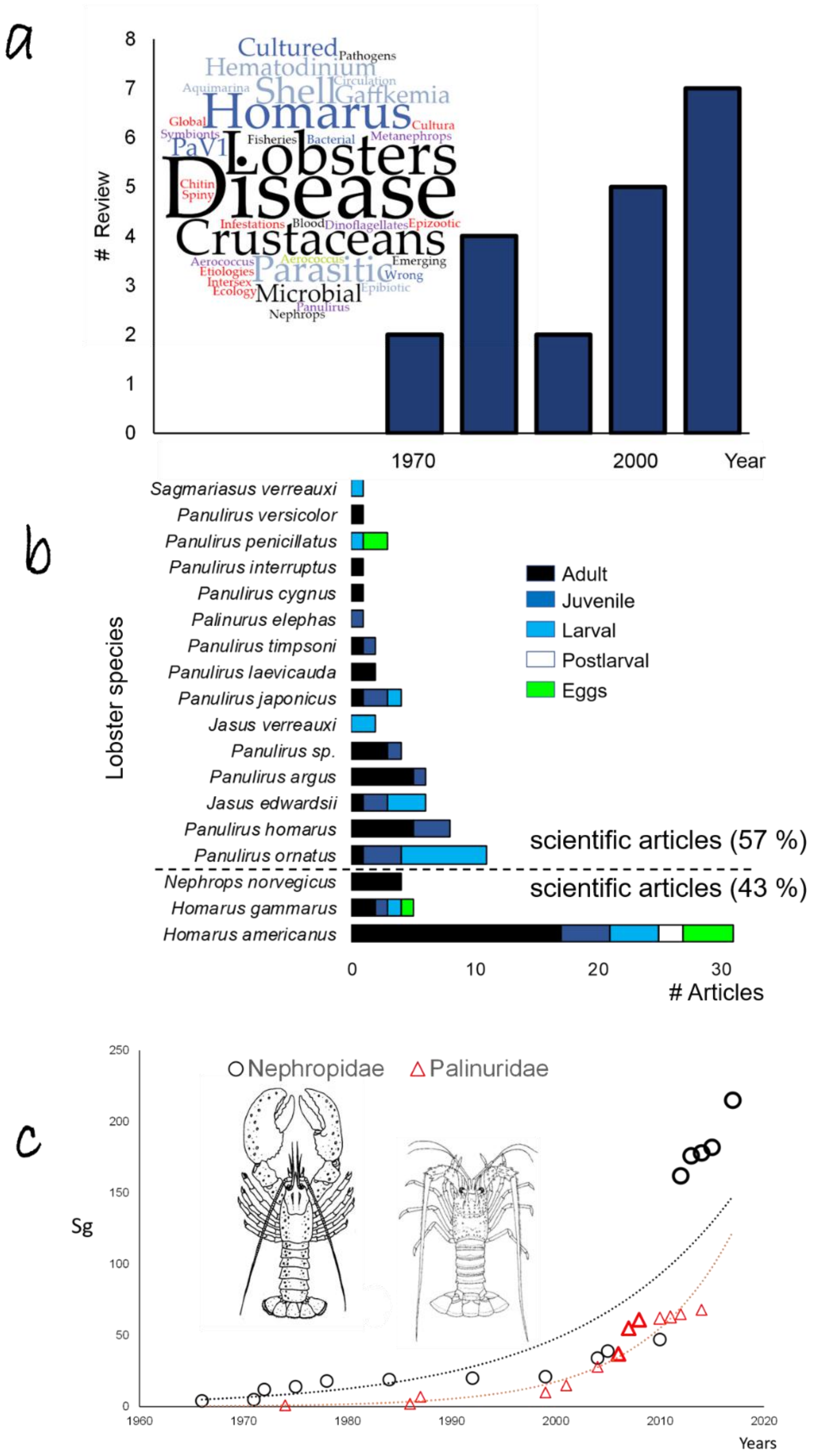


Figure 1: Scientific literature status on lobster research. (a): "word cloud" with the frequency of keywords included in the titles of reviews, and their publication frequency in the last 48 years (see References Tx.SM1). (b): Frequency distribution of research that has focused on 18 species of lobster from the families Palinuridae (above dotted line) and Nephropidae (below dotted line) (c): Accumulation curve of bacterial genera of Nephropidea and Palinuridae families reported in the investigations carried out from the 1960's until Dic/2017. Thin-line markers in the graph indicate culture-dependent methods for isolation and

identification of bacteria, whereas thick-line markers indicate culture-independent methods.

by the molecular non-culturing methods (Sm6), with these being most recently employed. It is important to note that techniques involving classical microbiology use specific culture media for some groups of bacteria. From the 1930s to the end of the last century, few species of symbiotic bacteria were isolated and cultured from lobsters (Fig. 1c). Due to the increased use of culture-independent techniques, mainly after the 2000s, the records of taxonomic genera of these prokaryotes in lobsters have increased exponentially (Fig. 1c). So far, around 400 species of bacteria have been isolated/identified, including new candidates and still unclassified species located in the phyla Proteobacteria, Bacteriodetes, Actinobacteria, Chloroflexi, Firmicutes, Planctomycetes and Tenericutes (Sm5).

Structural characteristics of the bacterial community

Contrasting conditions and similarity levels

The whole set of bacteria isolated/identified in the selected literature for the two lobster's families was divided into exo- and endosymbionts, and compared in terms of (i) 'richness' of genera within bacterial taxonomic classes and (ii) Jaccard's similarity indexes of four bacterial taxonomic levels (Fig 2). A total of 17 bacterial phyla, comprising 38 classes, 116 families and 262 genera, have been isolated from the two lobster families. The greatest richness was observed in the α- and Γ-Proteobacteria classes (53% of all genera), followed by Flavobacteria, β-Proteobacteria, Bacilli, Actinobacteria and Mollicutes, which comprised 29% of the genera; the remaining 18% of genera were found distributed in 25 classes (Fig. 2a). As a whole, the genera richness of the exo-symbiont microbiome was about four times greater than that of the endo-symbionts. For the lobster's Palinuridae family, the *Vibrio*, *Bacillus*, *Photobacterium* and *Pseudoalteromonas* genera showed the highest specific richness indexes, while for Nephropidae, the *Vibrio*, *Mycoplasma*, *Micrococus* and *Pseudoalteromonas* genera showed the highest indexes (Sm7). Considering the different taxonomic levels observed in the communities of exo- *vs* endo-symbiont of the two lobster families (Fig. 2b), it was possible to observe a higher structural similarity within the Palinuridae family, which was significantly higher than that observed within the Nephropidae family, for all taxa compared, except ‘phyllum’ (Fig. 2b). Interestingly, the two lobster’s families showed mostly the same pattern of Jaccard’s similarity indexes between exo- and endo-symbionts across the four taxonomic levels, although for the Nephropidae, the *J* value for classes and phyla were the highest and almost the same, whereas for Palinuridae, only the value for classes was the highest (Fig. 2b).

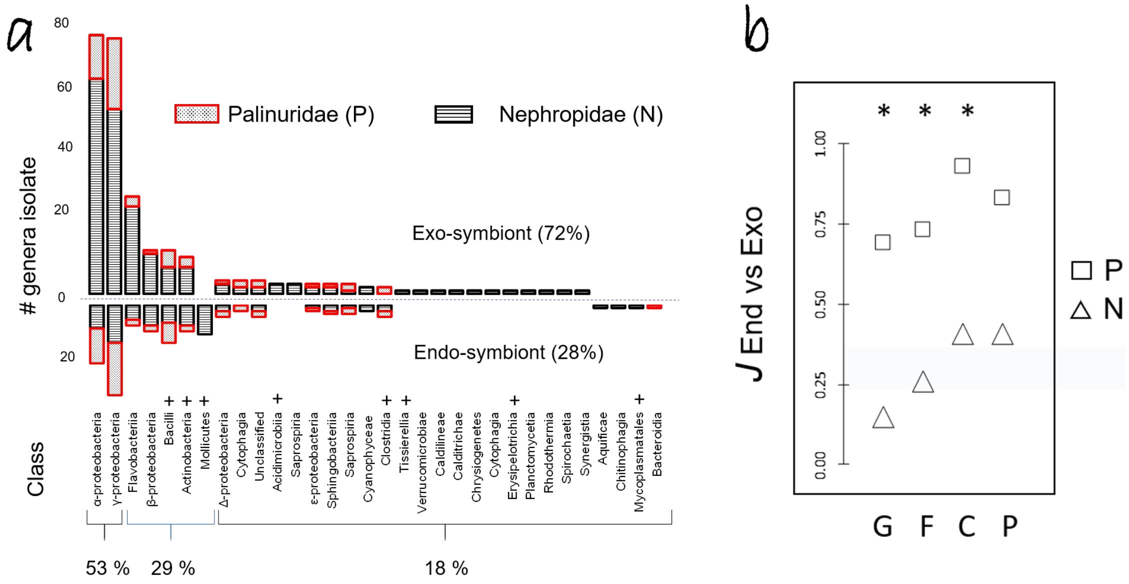


Figure 2: Identified bacterial communities reported for the lobster´s families Nephropidae (N) and Palinuridae (P). (a): Ranking of genera richness of isolated bacteria according to the taxonomic classes. Gram-positive bacteria are indicated by a plus sign (+) above the corresponding classes. (b): Similarity of Jaccard to different taxonomic levels (G: genera; F: family; C: Classe; P: Phyla) between Exo and Endo-symbiont communities of lobsters.

The similarity *J* indexes of the bacterial communities between contrasting conditions are summarized in Fig. 3, with statistical significance assessed by pairwise chi-square/G tests on 2 x 2 contingency tables, involving the frequency of common and unique taxa (see Methods). Not unexpectedly, the similarity for the bacterial communities’ structures between the two lobster families (N *vs* P) is very low for the taxonomic levels in general, at around ~25% (Fig. 3). Moreover, as also seen in for the Exo- *vs* Endo-symbionts comparison (Fig. 2b), due to the decreasing counts per taxon, the *J* values tend to increase with higher taxonomic levels for the two lobster families (i.e. from genus to family, and from family to class), although similarity at the phylum level was lower than at the class level (Fig.

3a); such pattern was noticed for all study groups assessed pairwisely, with a remarkable exception for the similarity between diseased and healthy individuals (D *vs* H) for the Palinuridae family (Fig. 3b). Palinuridae and Nephropidae appeared to be significantly different from each other only for the ’genus’ and ‘family’ taxa levels, considering the D *vs* H similarity (Fig. 3b), and for the ‘genus’ in terms of similarity between wild- and lab-reared (W *vs* L) lobsters (Fig. 3d). Interestingly, at the taxonomic level of ‘class’ only, the similarity between the two lobsters’ families was significantly higher for diseased (D) than for healthy (H) lobsters (Fig. 3a). Taken together, these results showed that, despite a tendency of increasing similarities at higher taxonomic levels (Figs. 2b and 3), no particular taxonomic level stood up as being able to detect statistical differences for all the pairwise comparisons tested, although ‘genus’ tended to be the best for this purposes (Figs. 2b, 3b and 3d).

When comparing groups of different membrane-compounds binding affinities (i.e. Gram-positive and -negative bacteria), the same overall trend of increasing *J* values with higher taxonomic levels, i.e. with less overall taxa counts, was observed (Fig. 4). For Nephropidae, the highest similarity between H and D groups was seen for the ‘class’ level for ‘G–‘ bacteria, and for ‘phylum’ for ‘G+’ bacteria; the low H *vs* D similarity at ‘genus’ and ‘family’ for both Gram types were almost identical (Fig. 4a). For Palinuridae, ‘G–‘ bacteria were more similar between H and D groups at the ‘genus’ and ‘family’ levels, ‘G+‘ bacteri0a were more similar at ‘class’ level, and both Gram types were identical at ‘phyllum’ level. Overall, however, in terms of common and unique richness between healthy and diseased lobsters in both families, these results showed that the bacterial membrane physical structure (G+ or G–) was not able to statistically discriminate the health status in any of the bacterial taxonomic levels.

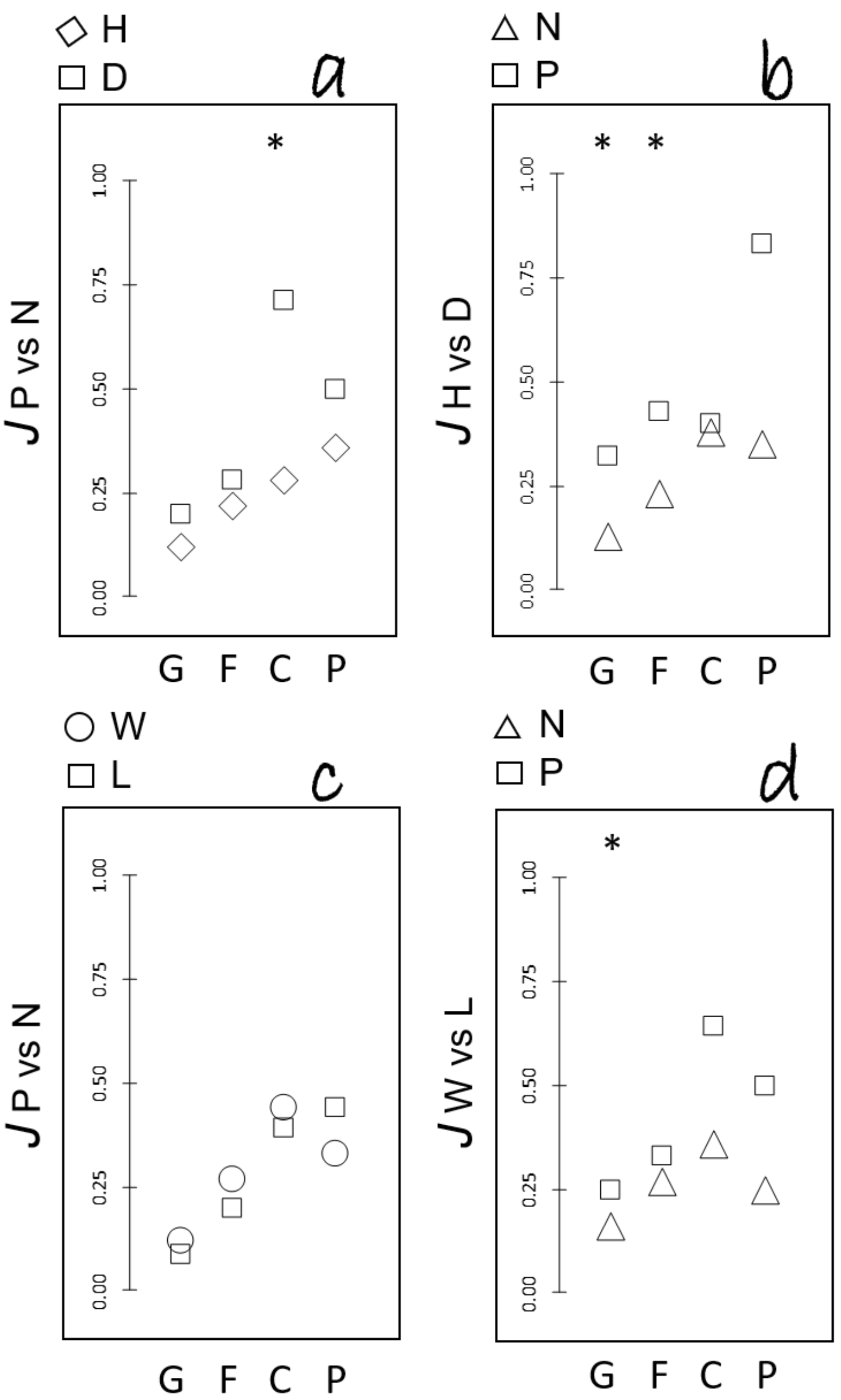


Figure 3: Similarity (JI) of the bacterial community present in the lobster in contrast categories. Similarity in the four taxonomic levels taken as a reference (G: genera, F: family, C: Classe, P: Phyla). Comparison between the Nephropidae and Palinuridae families concerning the state of fitness (Health vs disease) (a), and concerning their environment (Wild vs Laboratory) (c). Comparison of environmental conditions concerning identity (b, d). (*): significant difference.

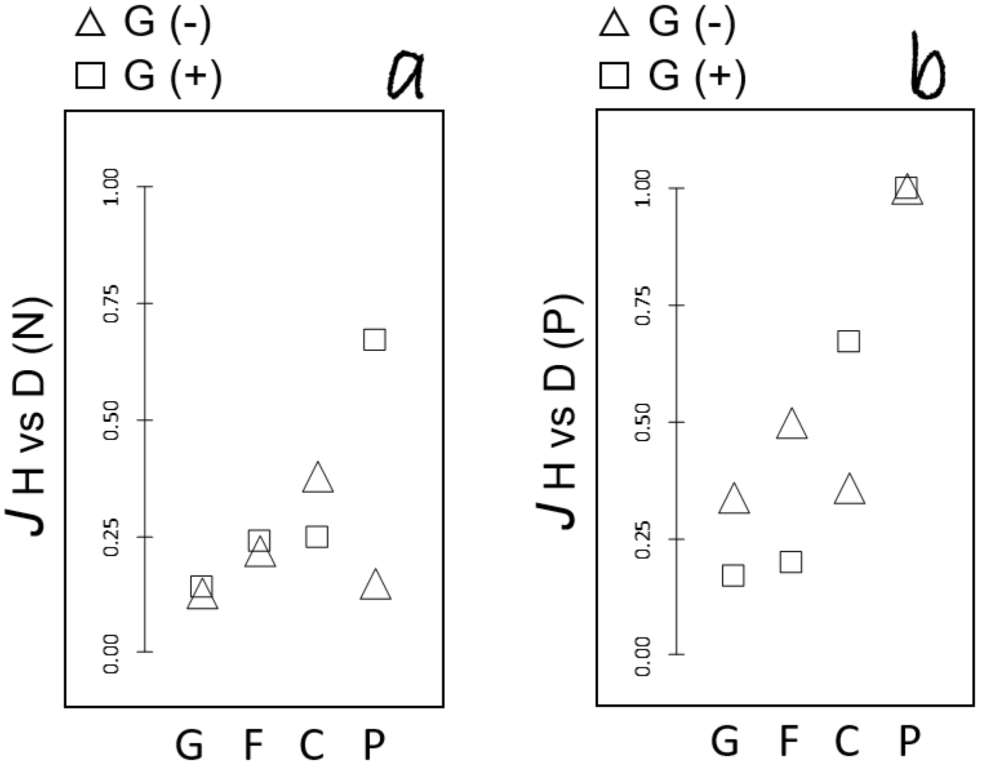


Figure 4:Structure of the bacterial community Gram (-) and Gram (+) present in lobster disease and health this tow family´s lobster. Similarity index (JI) in the four taxonomic levels taken as a reference. (a): Palinuridae. (b): Nophropidae.

Bacterial presence/richness in ontogenic stages and tissues of lobsters

With regards to the ontogenic development of lobsters, most of the bacterial isolations reported in the literature have been obtained from adults, juveniles and larvae (Fig. 5), employing a variety of isolation and identification methods in different lobster sources (Sm8). In general, the results are highlighting the scarce amount of studies in bacterial isolation from eggs and post-larvae (Fig. 5c). The Bacilli, β- and Γ-Proteobacteria classes showed the highest richness values in bacterial genera, with the latter class being the only one present in all ontogenic stages of Nephropidae (Fig. 5a). In Palinuridae, an overall lower richness of bacterial classes were observed, in the same three most abundant ontogenic stages studied in Nephropidae (Fig. 5b), with an opposed pattern, however, in relation to Nephropidae, i.e. higher number of genera observed in larvae than in adults and juveniles (Fig. 5c). Despite that a ‘nested’ structure could be noticed overall for Nephropidae, with most bacterial classes persisting up to later stages after being incorporated at earlier stages, some classes otherwise showed an oscillatory pattern along the lobster development, as they appeared and disappeared as the ontogenic stages progresses (Fig. 5a; see Discussion). Moreover, an interesting inverse qualitative pattern was observed for Palinuridae, in which fewer bacterial classes were apparently retained from the larval stage onwards (Fig. 5b).

When considering the bacteria isolated from different target tissues of lobsters, the greatest richness of bacterial genera isolated has been seen from the exoskeleton (Fig. 5f) as the preferred studied tissue for exo-symbionts, which represent ~3/4 of the isolated bacteria (Fig. 2a); for the endo-symbionts, the digestive system (gut) was the one with highest richness of bacterial genera (Fig. 5f). Considering both lobster families, the Γ-Proteobacteria and Bacilli classes appeared as being the most ubiquitous (Fig. 5d). It is possible to observe here a rather rich and somewhat nested structure. Where the most complex communities, structurally speaking, are associated with the areas of greatest contact with the environment and diminish, in rich, in the organs or internal system. However, in the Palinuridae family (5e) the nested structure is not evident.

Bacterial taxonomic series in lobsters’ families

Comparing the RP between sick and healthy within each lobster family, according to the bacterial staining characteristics (G +, G -) of the isolated lobster community, let's look at the following (Fig. 6): At the level of (G / Sp), three (75%) of the four cases analyzed show significant differences. At the level of (F / C) only one (25%) of the four cases showed differences. For the highest levels (C / F, P / C) the differences were insignificant. Only the group of G- between healthy and sick in the Palinuridae family does not show significant differences at any level (Fig. 6a).

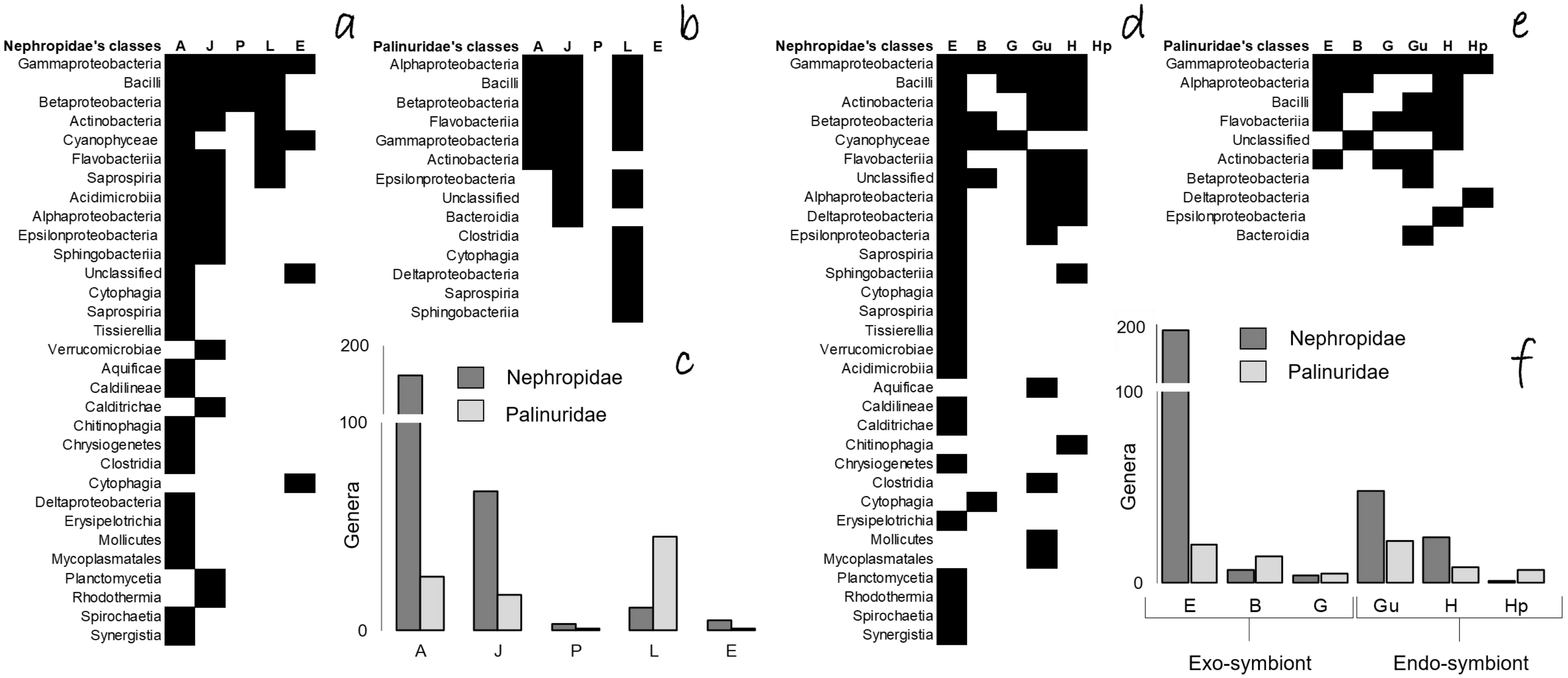


Figure 5: Assessment of records in the scientific literature concerning bacterial identification in lobster's ontogenetic stages and tissues. (a, b, d, e): Presence - absence of classes of bacteria, in the ontogenetic development and tissues, in the two lobster families. (c): Richness of isolated genera in the different developmental stages of lobsters. A: Adult, J: Juvenile, P: Post-larval, L: Larval, E: Egg. (f): Richness of genera isolated from the different tissues of the families Palinuridae and Nephropidae E: Exoskeleton, B: Biofilm: portion of the body's surface, G: Gills, Gu: Gut, H: Hemolymph, Hp: Hepatopancreas.

When observing the proportional series (Fig. 6b) in the ring graphs, a “harmonic” behavior is evident among the healthy lobsters of the Nephropidae family. That is, the two series (G + vs G-) tend to the same proportional distribution. Distribution, somewhat similar, when observing the healthy Palinuridae Family. In contrast, in sick lobsters of the Palinuridae family, that harmony in the proportional distribution is lost, the loss of harmony being less evident in the Nephropidae family.

In general, the condition of the host can be characterized, partially, by the loss or not of these proportional relationships between their bacterial communities. This loss may be associated with dysbiosis that characterizes sick lobsters.

These models show, in a certain way, the past and the present of the relations between the microbiome and the host. Allowing to observe, at the level of bacterial taxa, the persistence, flow or loss of bacterial lineages.

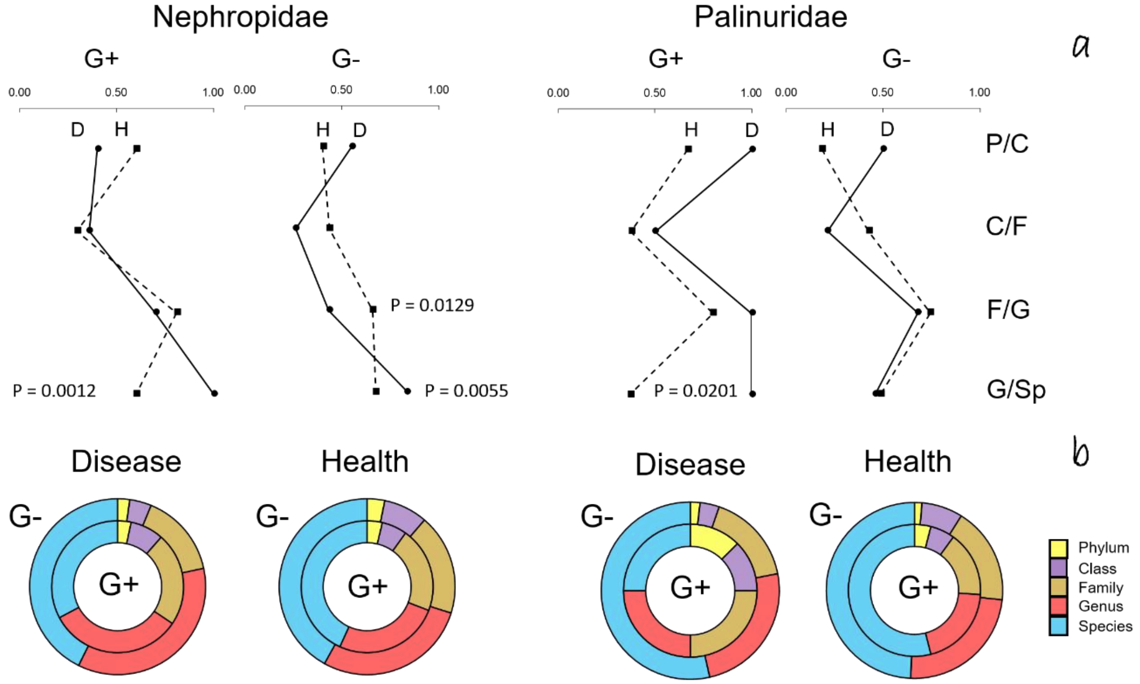


Figure 6:Comparison between lobster condition (G + vs G-) and (Health vs Disease) for each lobster family. PR behavior between consecutive taxonomic pairs and statistical differences detected (P = value) with the model to compare proportions (a). Ring diagrams with the proportional sequences of G + and G- bacteria between lobsters of the same family and different fitness (b).

DISCUSSION

Overview of trends in studies on lobsters and microbiota

While there is information on bacteria isolated from the entire ontogenic cycle of lobsters, research reflects a strong emphasis on diseases present in some of these stages and only on lobsters of commercial interest. Unfortunately, such a panorama generates only a partial understanding of the microbiome and its relationship, say for example, with adaptive processes. However, these investigations have allowed characterizing the effects of these diseases on natural populations and developing strategies that have allowed the development of these crustaceans in the aquaculture industry (Ooi et al., 2017a; Ooi et al., 2017b).

Considering the last 80 years of research involving lobsters and their related microbes, we observe a trend of search on species of commercial interest, especially those affected by some type of disease. The studies analyzed here essentially focus on adult populations of *H. americanus*, with the remaining research distributed in different ontogenic stages of other lobster species. This panorama indicated a not unexpected tendency of seeking solutions for problems of productivity (fishing and aquaculture), which has consequently led to a biased understanding of the microsymbionts in lobsters. Little information is available in early stages of development for most lobsters, despite this being an essential aspect for managing this resource. Therefore, there is a need to broaden objectives and approaches of the research on lobsters' bacterial communities, so that we can better address their involvement and implications in ecological and conservation issues.

In terms of composition and dynamics of the structure of bacterial taxa (Figures 1-3, and supplementary material), the existence of patterns that are related to particular host conditions is suggested. However, the biases caused by the trends and methods in the investigations, relate the particular conditions of the host and its associated bacteria incompletely. The general pattern observed in the analyzes of similarity and proportional series could suggest the existence of a structural relationship with the condition or identity of the host. Under this scale of study and perspective, a "holobion vision" can be applied (Catania et al., 2017).

Aspects concerning adaptation

We suggest that the differences observed (Fig. 2 – 6) between two contrasting conditions (e.g. two families of lobster, or sick and healthy animals), with regard to a finer structure of the respective bacterial communities, are simply a reflection of a continuous process of adaptation to ever changing environmental conditions. As pointed out in various reports (e.g. Rosenberg et al. 2009; Douglas and Werren 2016; Theis et al. 2016, Catania et al. 2017), both stochastic (horizontal transfers) and selection-driven (vertical transfers) modes of bacterial association to hosts can interfere in final responsive.

About 350 m.y. ago, the Nephropidea and Palinuridae families have diverged and occupied contrasting niches; as a result, the lobster claw has persisted in cold- or deep-water environments, while spiny lobsters in warm, shallow water (Lavery et al. 2014; Bracken-Grissom et al. 2014, Davis et al. 2015). Therefore, their homeostatic conditions and the characteristics of their life cycles have been adjusted to these environmental conditions (Phillips et al. 2006). Following such an adaptive/evolutionary reasoning, it is plausible to suggest that the structure of the lobsters' associated bacterial community is the reflection of the host-microbes interaction dynamics characteristic of lobsters. In this sense, one can view the final phenotypes of hosts (lobsters) as the consequence of a direct connection with microorganisms, in which they act both as sources and results of environmental variation, i.e microbial species and populations work simultaneously as effectors of changes in the host's internal environment, and receptors of host's responsive physiology to them and to the external environment. Within the framework of the hologenomic theory (Theis et al. 2016), but incorporating the idea of functional integration (either based on the etiological or systemic concepts of function – Catania et al., 2017), we suggest that the similar taxonomic-levels proportions found in all conditions assessed (Fig. 1 - 5) might reflect a lobster-specific ecoevolutionary dynamics of host-microbes interaction, i.e. a fulfillment of a proposed 'holobiont' concept (Theis et al. 2016), at least in this scale of analysis.

Accepting the criticism that not always a (or every) 'host-specific microbe' relationship falls within the holobiont/hologenome original concept (Moran & Sloan 2015; Douglas & Werren 2016), an understanding of the analytical scale and degree of functional integration can help in defining the level of 'holobiontness' that can be attributed to a given symbiotic association (Catania et al. 2017). There is evidence of the existence of particular bacteria that allow adaptation and survival of some marine organisms under particular environmental conditions. For instance, (i) marine sponges whose symbiotic bacterial communities are linked to phenotypic plasticity in the face of environmental changes (Webster & Thomas 2016); (ii) the algae Caulerpa taxifolia obtains its power of invasion and adaptation from its microbial symbionts (Arnaud-Haond et al. 2017); (iii) in some bivalve mollusks, symbionts help them to metabolize hydrocarbons and thus to persist in deep areas (Raggi et al. 2013; Desriac et al. 2013), a condition also observed in the deep-water shrimp *Rimicaris exoculata* (Cowart et al. 2017). Raising to a next scale, the Coral Probiotic Hypothesis (Reshef et al. 2006), and so, the hologenomic theory of evolution (Zilber-Rosenberg & Rosenberg 2008) have arisen from the observation that, in some corals, the possible existence of a dynamic relationship between host, symbiotic microorganisms and environmental conditions could explain the observed emergence through time of an advantageous selection-driven, disease-resistant coral phenotype. The 'holobiont' view was proposed as a consequence of an evidence-based (Koren & Rosenberg 2006; Ainsworth et al. 2008) indication that exchange of microorganisms could be an ecoevolutionary strategy of coral host to adapt to abiotic and biotic changes in the surrounding environment (Reshef et al. 2006). Specificity has also been observed towards symbionts and their importance in coral homeostasis considering environmental changes (Grajales & Sánchez 2016; Peixoto et al. 2017).

In the case of lobsters, a similar perspective could be noticed in the reports. Studies have shown that local conditions such as food supplies or physical-chemical properties can alter the population structure of the bacteria present in the digestive tract (Meziti et al. 2010; Sang & Fotedar 2010; Ooi et al. 2017a) or in the hemolymph (Ooi et al. 2017b).

The overall ‘nested’ pattern of bacterial classes’ richness observed in the Nephropidae family (Fig. 5a) suggests a tendency of incorporation and persistence of bacterial lineages and so, functions. This bacterial progression in the ontogenic development of lobsters, which might be reasonably expected, due to a higher body volume and capacity of adults to hold bacterial loads, or as a result of a journey throughout different environments throughout its ontogenetic development.

Interestingly, the data also suggest that, for Palinuridae, there appeared to be a reverse trend of decreasing the richness of bacterial classes as the ontogenic development progress (Fig. 5b). Nevertheless, since the present work is a comprehensive analytical compilation of studies from the literature, with expected heterogeneity and biases in terms of isolation and identification methods and lobster sources (Sm6 and Sm8), extreme care must be exercised in the interpretation of these results. Further controlled studies of bacterial isolation following the ontogenic stages of the same lobster individuals (experimental models) are certainly required to provide more conclusive information on this issue.

According to Agrawal (2001), effects of environmental variations can be alleviated by phenotypic plasticity, a characteristic that affects the interaction of the organism with other community members and with the new habitat. This trait can occur in all stages of life, improving the individual’s ability to adapt (Marshall et al. 2010, Sanford & Kelly 2011). Such capacity can obviously be greatly improved with the help of microsymbionts. As pointed out by Reshef et al. (2006), changes in associated microbial composition would allow hosts to adapt more rapidly to changes in the environment (Fig. 3C, 5). Hence, whether this aspect falls within the scope of a possible ‘evolutionary response’ (Zilber-Rosenberg & Rosenberg 2008; Rosenberg et al. 2009), or otherwise helps explain the occurrence of ‘phenotypic plasticity’ remains as a matter of conceptual debate.

Aspects related to health

The research suggest, that the changes in the living conditions can generate modifications in the associated microbial communities of the host. If these changes are drastic, it can generate a loss of the best homeostatic condition of the host-microbiota system. That is, stress factors, can lead, for example, to the appearance of diseases (Ainsworth et al., 2008). In this context, Groner et al. (2016) highlight the importance of designing mechanisms that allow an early diagnosis of changes in the homeostasis of marine organisms and, therefore, promote changes in management plans in a timely and appropriate manner.

In general, some of the lobster diseases are associated with bacteria that proliferate externally or internally, being able to affect different organs and functions in any ontogenic stage (Shield 2011). Given these conditions, crustaceans and especially lobsters, have a series of strategies to mitigate the progress of diseases, for example. Whit activating of the prophenoloxidase system (ProPO) (Sritunyalucksana & Soderhall 2000), whit the presence of antimicrobial peptides in the exoskeleton (Brisbin et al. 2015), or behavioral actions that help avoiding infection from other diseased individuals (Butler IV et al. 2015; Candia-Zulbarán et al. 2015). Due to these strategies, lobsters are regarded as very efficient in their defense system. Unfortunately, the weakening of some of these mechanisms is evident due to significant and sustained changes in the environment, as well as pollution and overexploitation (Tlusty et al. 2008; Byrne 2011; Shield 2011; Meres et al. 2012; Stentiford 2012; Cornwall & Eddy 2014; Samuelsen et al. 2014; Briones-Fourzán & Lozano-Álvarez 2015; Oliveira et al. 2015; Maynard et al. 2016; Groner et al. 2016). For instance, the advance of epizootic shell diseases (ESD) in lobsters have been linked to high temperatures (Glenn & Pugh 2006) or diet (Quinn et al. 2012). Hernroth et al. (2015) observed that changes in environmental abiotic factors, such as pH or oxygen deficiencies can increase the susceptibility of *N. novegicus* to bacterial diseases, and Waller et al. (2016) noted the problems that high CO_2 levels can cause to larvae of *H. americanus*.

Lobsters have bacterial communities that normally exist in their carapace, so that an undesired change in these communities, called ‘dysbiosis’, has been indicated as being related to ESD (Harper & Talbot 1984; Chistoserdov et al. 2012; Meres et al. 2012; Feinman et al. 2017). Bell et al. (2012) highlight that this associated bacterial structure changes as the disease develops, so that they can become pathogenic over time, a condition that has been described in *P. argus* (Porter et al. 2001). An interesting finding is that similar communities were described between samples, regardless of the place of isolation or homeostasis level of the animals (Quinn et al. 2013b). However, some of these bacteria can have different consequences to the host, depending on where they are in the body (Fisher et al. 1978). Not every host-bacteria relationship is linked to diseases; for example, Harper & Talbot (1984) have highlighted the benefits of bacteria in the viability of claw lobsters’ eggs, due to their controlling effects on fungi. Goulden et al. (2012), on the other hand, highlighted the ability of natural communities of symbiotic bacteria present in *Panulirus ornatus* larvae to control pathogens. [For complementary information and further details on the etiology of emerging diseases in lobsters, and their contributing factors, see; Behringer et al. (2011); Shields 2013; Whitten et al. 2014; Middlemiss et al. (2015); Briones-Furzán et al. (2015); Pérez-Campos et al. (2016); Simpsom et al. (2017); Feinman et al. (2017)].

In addition to the above, it has been observed that physiological/ontogenic processes such as ecdysis can also display alteration in the bacterial community present in the digestive tract of *N. norvegicus*, with the dominance of chitinolytic bacteria being favored (Meziti et al. 2012; 2010). Taken together, all these aspects suggest that environmental and physiological challenges to which the host is exposed can be mitigated or controlled more efficiently by the nature and intensity of the interactions with the microsymbiont community.

Bacterial predominant taxonomic lineages can be called generalists, since their representatives are widely distributed in the host (Fig. 5). This perspective suggests the existence of a bacterial community with a long history associated with lobster. For example, the bacteria of the Thiotrichaceae family, of the 107 reported, is the only one that reports representatives present throughout the ontogenetic cycle of claw lobsters.

In general, we can suggest that the structure (richness, proportional relationship, persistence - absence) and its dynamics (patterns) can define a "central microbiome" that is probably more closely related to the host's identity, the homeostatic state, or to the conditions of the surrounding environment. Therefore, it is important to open a space for a deeper understanding of functional issues.

Future research on the lobster microbiome could clarify possible links and mechanisms "host-microbiome-environment". In addition, a deeper understanding of the factors that drive the composition and persistence of the bacterial communities associated with lobsters, will have a direct impact on the definition of strategies for the management of this resource.

Ecological and conservation implications

The clearest ecological consequences observed in these investigations are related to changes in the distribution and abundance of populations, due to the loss of individuals for bacterial diseases.

Few investigations correlated, the communities of microsymbionts with the adaptability of lobsters. For example, Goulden et al, (2012) relate the food supply with the variation of the intestinal microbiome in lobster larvae. Kumar et al. (2010) the micro-symbiotes and the promotion of growth. Others already show more specific relationships such as the microbiome present in eggs and the ability to defend against pathogens Harper and Talbot (1984).

It is observed that lobsters have a wide collection of microorganisms that are part of their integrity. A condition that grants to the lobsters a series of "genetic tools" that collaborate in several processes, among them the adaptive, which reinforces its persistence or performance. This allows us to expand the frontiers by proposing strategies aimed at improving our knowledge in relation to this association. In this way improve the management of this resource, seeing the lobsters as a set called holobiont.

These host-symbiont relationships may have implications for the persistence capacity of a population or meta-population. It may be that the ontogenetic features of the host allow a continuous exchange of bacterial communities, between distant host populations. In the case of lobsters, this exchange, via larval connectivity, can be one of the mechanisms that potentialize their adaptation to environmental conditions.

Concerning it, there are some questions, for example.

What ecological consequence is generated by the exchange of microorganisms among the lobster populations, and how do they influence the capacity of persistence or resilience, before environmental variations?

Does the structural of lobster holobiont, permanently conform to different conditions of the environment in which it develops (e.g., throughout ontogeneticc development) and allows you to solve multiple local problems?

The complicated structural dynamics of the lobster holobiont, are a characteristic of a generalist BS, with high potential to persist and low-risk extinction?

CONCLUSIONS

In general, research focuses on some species of lobsters of commercial interest, with the most studied bacterial communities associated with the exoskeleton. There is a complex group of bacterial symbionts composed of 17 Phylum, which was isolated from different species of lobster, ontogenetic states, tissues, and homeostatic conditions. Regardless of the identity or condition of the lobster, the classes of α and Γ - proteobacteria cover the greatest richness of genera.

The structure observed between the different bacterial taxonomic levels were useful to associate them with the condition and identity of the host. In this case, the PR can be associated with the host's health status, accepting the Ho initially assumed. However, caution should be exercised with these results due to the biases detected.

The large collection of microorganisms, which persist or alternate throughout the ontogenetic development of lobsters, or that are observed in the different tissues or organs of lobsters. Stresses the importance of possible functional relationships that bacteria have with the integrity of lobsters.

The genetic complexity that a holobiont like lobster shows today is possibly associated with its long life history, which covers a wide spatial and temporal range. This taxonomic group has survived three mass extinctions and faces a fourth. It is possible to think that the weakening in the persistence of this type of “generalist” organism is an indicator of the scope of an unexpected set of events experienced by biological systems.

The close host-micro-symbiote relationship is evident, therefore, research approaches can be more useful, from a hologenomic perspective and thus improve the understanding of this host-microbiome relationship. A perspective that includes ecological processes at multiple temporal and spatial scales.

This study, shows, the great need to deepen the research on the micro-symbiote community and the implications that this has on the ability of persistence of lobsters. Observed this relationship as an ability to interpret the environment and solve problems.

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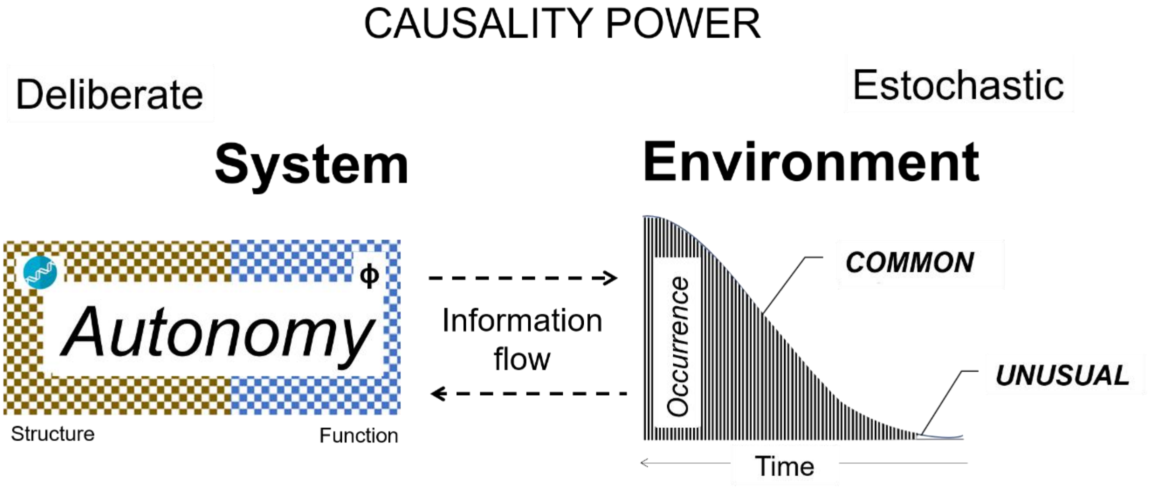
CHAPER II

THINKING COMPLEXLY IN ECOLOGY: INFORMATION INTEGRATION AND RARE EVENTS



HIGHLIGHTS

Thinking about complexity and thinking in a complex way are two different complementary perspectives in ecology.

The biological systems are specialized in internalizing information from the surroundings, resulting in reduction of the ‘uncertainties’ of its interaction with the immediate environment.

The integration of information in the system appears as an emergent property that tends to decrease the risk of extinction.

Rare events help to guide information internalization and are fundamental in the ‘learning’ processing of the systems.

ABSTRAC

The causal forces that affects behavior, diversity and persistence of biological systems is invariably sought in the environment, with its characteristic elements, components and patterns of change. The correlations and predictive models found so far under this approach are those that have been driving decision-making processes in defining better conservation strategies. The environment has been seen as the major factor responsible for the ecological processes, and so, what and where we have to research and act to achieve meaningful biological conservation. From the complexity thinking we develop here an array of ideas that show, from another perspective, how biological systems themselves may directly influence the functioning and outcomes of ecological processes, consequently affecting how we can, or should, develop our conservation actions. Those ideas are based on the force of a possible emergent property of biological systems that would allow them to incorporate/integrate new ‘information’ from the particularities and the dynamics of the environment. In this circumstances, it may be that ‘unusual’ or ‘rare’ events in the immediate (perceivable) environment provide new information to be incorporated and integrated into a biological system, which might turn them into a more adaptive mode. We attempted to build on this view as being able to provide an alternative framework which may help explain characteristic features of biological systems, in terms of adaptation and potential to persist. From this perspective, the causes of known ecological patterns, such as abundance, dispersion, distribution, etc., is discussed as being associated with this emerging property of complex biological system, going beyond the view of the environment as the sole source of causal forces for ecosystemic processes. By framing this article around the persistence and stability of biological systems, we took a brief tour on 'systemic thinking' and 'thinking in complexity' on various aspects of ecology. As a consequence of these views and methods, we highlight that integration of information (in different forms, scales and intensities) appears as an emerging force that can give 'power of choice' to biological systems, which may actively modify the net results of environmental variation. The view of this approach as complementary to the current classic view of matter and energy as underlying forces to ecological processes is discussed.

Keywords: System, environment, emergent property, integrated information, rare event, autonomy.

INTRODUCTORY VIEWS AND QUESTIONS

One of the recent challenges at human thinking has been the inclusion of a vision in 'complexity', a term that has been incorporated into ecological language as a descriptor of a set of elements and processes that occur simultaneously in a biological system (e.g., Lenton & Oijen, 2002; Mesjasz, 2016; Watanabe et al., 2018), Barnes et al. (2018). However, Morin (1993) says that thinking about complexity implies a detachment from a single line of thought, as well as an integration of multiple theories, which generate a cognitive challenge for an observer. According to Maldonado (2015), thinking about complexity is a task in which innovation, criticism, creativity and suspicion are necessary; he proposes the focus of studies should not be directed to 'objects', but rather to 'problems'. In this sense, the major issue is to learn how to perceive that not all problems are complex, and those that are, require an approach that employs different methodological tools (Maldonado 2016). According to Cilliers (2007), it is possible that such an approach would impact more the interpretation of the results than the scientific method itself.

In recent years, research in computing (Zotos et al. 2015), education (Swanson & Widmwe, 2018), human security (Masys, 2018), politics (Maldonado, 2018a) and health (Aristizábal et al. 2019) have been assessed from the perspective of complexity; however, such an approach has been recent in relation to ecological problems (e.g., https://www.journals.elsevier.com/ecological-complexity). In ecology, the environment is generally the focus of attention as the main source of causative factors, that is, variables such as abundance, distribution, connectivity, persistence, divergence, diversity, etc., are triggered by, and addressed as a result of environment action. Recently, approaches considering 'autonomy' of the systems, which is a concept related to their ability to internalize the variability of the environment and generate a 'decision power', have already been addressed (Schuck-Paim et al. 2008; Sol, 2009; Sol et al. 2010; Sih 2013; Fristoe et al. 2017; Sayol et al. 2016; Ashton et al. 2018; Sayol et al. 2018). However, the environment remains viewed as the main source of causes of such property.

In general, environmental challenges, new environmental conditions or environmental variability, all demand from a biological system the development of new behaviors or strategies that allow it to 'solve' problems, i.e., variability in the environment generates conditions that drive 'decision-making' as an emergent property of the biological system. Under this view, it is pertinent to ask whether the collective and individual histories of 'members' of a system can relate with acquired capacities of the system of being both (i) less 'surprised' in a 'well-known' environment and (ii) properly responsive in highly variable environments with unexpected conditions. Answering such question highlights the importance and impact of the so called 'rare events' on biological systems. This topic in general has been addressed in Ecology in network theory (Réka et al. 2000; Lindley et al. 2014), mass extinctions (Petchey & Gaston 2002; Bond & Grasby 2017; Bartlett et al. 2018; Sahney & Benton 2018; Currie 2018), adaptive radiation (Nielsen et al. 1998; Schilthuizen et al. 2001; Schilthuizen et al. 2004; Seehausen, 2004) and succession (Turner et al. 1998).

According to several authors (Tononi 2008; Balduzzi & Tononi, 2008; Edlund et al. 2011) Barrett 2014), any complex system, by its very nature, can 'incorporate/integrate information' ('I.I.') from the environment, as well as generate new information to this same environment. This allows them, in a certain way and to some degree, to detach from the stochasticity of the environment, so being more or less 'autonomous'. Under this view, emerging or intrinsic properties of a biological system can interfere with ecological events (e.g., Haan, 2006). Such an approach has been recently incorporated to innovative scientific investigations, by including 'cognition' as a system's element that arises due to environmental interference and communication, which has been called 'cognitive ecology' (Sol, 2009).

Henceforth, it is worth asking: can the ability to 'I.I.', as an intrinsic value of any given 'living' system in its own scales and proportions, has the power of interfering in the organization and persistence of itself on the planet? Furthermore, to the extent that living things internalize the environment and, thereby, progresses towards 'autonomy' in different levels, can they deliberately affect the physical environment next to them, and so, contribute non-randomly to its variation? Considering that the available information is dispersed on these issues (e.g., Maturana & Valera (1973); Llinas (2008)), in this review, we sought to identify and assess a variety of contexts and subjects that could allow us to advance the discussion on the 'complex thinking' in Ecology. From the standpoint of some perspectives and questions that we consider relevant for ecological processes, our approach attempted to provide alternative explanatory panoramas that could aid in the development of environmental conservation and management strategies.

REVIEW METHOD

In order to generate a context in the complex ecology and to answer the questions posed, we conducted a panoramic review as defined by Guirao (2015). From some ecological theories, we explored the causal relationships between the environment and the biological systems (BS) from properties such as stability and persistence. Emerging properties of systems such as the integration of information (I.I.; Tononi, 2008), as well as rare events and their impact on BS were incorporated into the assessment. Relevant traits capable of triggering and guiding the BS and that have not yet been taken into account in ecological contexts were also considered.

To generate this theoretical approach, we did a search for information using key-words such as Complex, System, Ecosystem, Ecology, Network, Think, Evolution, Rare event, Change, Adaptive, Biodiversity, Community, Species, Conservation, Information, Environment, Learning, Persistence, Stability, Connectivity, Autonomy, and Integration of information. The search strategy was delimited by 80 scientific journals, 69% of which corresponded to the field of biology (Fig. 7). Finally, 120 documents were selected, which we considered as the most relevant to help us build the conceptual framework we propose to address the questions posed.

The gathering and processing of information was supported by the free access *Publish or Perish* version 6.2 software (Harzing, 2007). This present review was developed from a framework in complexity as described by E. Morin (1993), and developed into four main sub-sections, as described next.

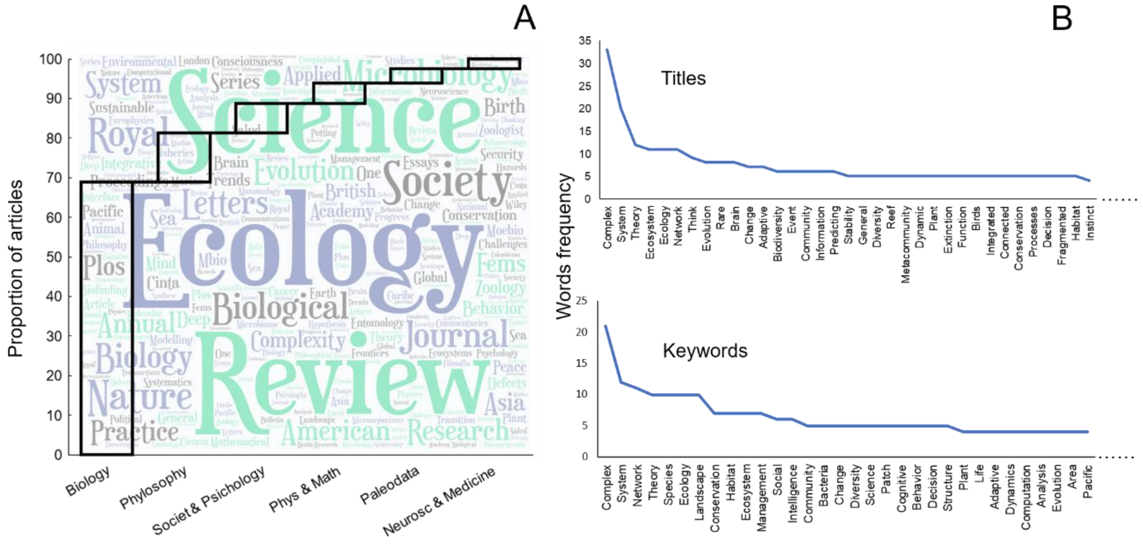


Figure 7: Graphical summary of the characteristics of the selected publications. A: Proportion of articles by field of study, word cloud of scientific journals. B: Frequency of words in title and keywords of the selected publications.

COMPLICATED *VS*. COMPLEX SYSTEMS – AN ECOLOGICAL VIEW

The efforts to understand the 'nature of Nature' as expressed by Morin is long-standing and include an extensive list of study objectives in Ecology. From a systemic-thinking point of view, these efforts have included ideas covering systems' organization and their potential to persist and evolve; as a result, a variety of ecological theories applied to conservation have arisen. In this section, we explored the change of view from a merely 'complicated' system to a more sophisticated and intricate 'complex' system. In short, the former concept deals with a system composed of a large number of elements so diverse and intricately connected in multiple ways, that it is hardly understood how it works, and which depends on external inputs to function (e.g., a computer: when it is unplugged, it stops functioning); on the other hand, a 'complex' system display the same properties as in the previous one, but in which the whole structural and functional *self-maintained dynamics* allows the appearance of 'emergent properties', such as in the biological systems (e.g., a butterfly).

The General Theory of Systems proposes a series of principles that describe the organization and interaction of related elements, which together generate a system’s behavior (Bertalanffy, 1976). Those principles are based on the integrated observation of phenomena in their structural and interactive wholeness, which is so applied to provide a particular view of a BS. The line of thought adopted by Lotka (1922) highlights that the relationships among beings, structures and interactions of the various elements in the system are considered on a mere mechanic plane. The use of terms such as ‘efficiency’, ‘network’, ‘complexity’ and ‘dynamics’ have introduced new perspectives to explain events in biology and ecology. For instance, Bertalanffy's work (1976) is based on systemic thinking that has incorporated a variety of theories, thereby developing an interdisciplinary approach; this author emphasizes that "*this thinking is relevant insofar as reductionism becomes important*". In studying the nature of BSs, Bertalanffy describes ‘closed’ and ‘open’ systems, based on a view from the thermodynamic laws: the first is isolated, whereas the second exchanges matter and energy permanently with the environment, thereby keeping a continuous departure from balance. Nevertheless, in his view, the systems tend to a final state of ‘homeostasis’, establishing a point of non-conflict with the environment. Said in a different manner, the environment pushes, guides and defines, being the final cause of a BS functioning. An example of this is seen in the models proposed by Lotka-Volterra (Wilson et al., 2006). In general, BSs are characterized by presenting a hierarchical order in their structure and function, whose exchange of matter and energy makes them dynamic, progressive and irreversible. From the perspective of Arnold & Osorio (1998), the dimensions of a study could rather depart from an internal view of the system itself (its parts and their relationships, and its borders). That is, they delimit the BS according to their origin and direct relation to the environment, and includes an extensive list of concepts that guide a systemic language required to address the questions.

In the middle of the last century, (Waddington 1959) focused on the biological units and called this perspective and view as ‘Systems Biology’, where terms such as epigenetics, genetic assimilation and ‘homeorhesis’, among others, were incorporated to the terminology used. From a holistic perspective as defined by Freeman (2005), have incorporated the computation, cybernetics and self -

organization theories, and proposed different models to describe BSs. At present, the development of the 'omics' supports these models, which have had a great impact, for example, on health (Byrne 2010), as well as on an array of other fields of knowledge (Ventura et al., 20157; Oliveira & Piña, 2015; Vayssier-Taussat et al., 2014) In general, though, a mechanistic vision of the BS yet predominates, where the 'living' trait can be explained solely upon mathematical grounds (Siekmann 2018).

In ecology, the theory of systems complex has explained, in part, the dynamics of the biodiversity, and the functioning and resilience of systems as well (e.g., Levin, 1998; 2000). Terms and concepts such as 'chaotic dynamics', 'unpredictability', 'regularities', 'self-organization' have been applied to studies on evolution and the possibility of 'multiple stable states' in the environments has been suggested as an alternative and complementary view (e.g., Lenton & Oijen, (2002); Leibold et al. 2004; Gross (2008); Kininmonth et al. 2010; Langenheder et al. 2016; Watanabe et al. (2018); Barnes et al. (2018). Nevertheless, descriptions have tended to rely on the approach of viewing a BS as many parts interacting simultaneously, which end up making it difficult to understand and explain the whole; therefore, due to this, the studies tend yet to focus only on the parts, and so, only indirectly inferring on the whole. From this perspective, we could say that the global analytical approach, in most studies, comes from a view of the system as being 'complicated' and not as being 'complex' (Allen et al., 2018). Thinking about the complexity of a 'living' thing must go beyond a 'simpler', reductionist-like description of a BS by its constituent parts as belonging to highly 'complicated' systems that are causally correlated with highly 'complicated' environments. The intention of thinking on complexity requires one to detach him/herself from a single line of thoughts and be able to make a better integration and interpretation of the phenomena that occur within and around the 'living' entity. As already mentioned, E. Morin has been one of the precursors and defenders of this viewpoint and study strategy (Ramirez 1995).

From this complexity standpoint, 'cognition' appears as an emergent trait, which results from the ability that a BS display of 'integrating information'

(I.I.)(Anderson, 1972; Haan, 2006; Tononi, 2008; Gignoux et al., 2017). This trait, ultimately, allows a system to boost and generate new features for the 'living', with consequences to the surrounding environment. From R. Rosen (Bertalanffy 1976), and recently, from Cárdenas et al. 2017, it is suggested that the 'skills' of BSs are supported by emerging particularities. Thus, the approach of viewing the 'living thing' as a 'machine' that respond to environmental cues only mechanically would be insufficient and/or incomplete.

In the context of emergent properties, '*information*' takes a fundamental role and can be described from two perspectives. In one, matter and energy underlie the information, which is embedded in the philosophical line of the materialistic monism. In this case, information is linked to, and dependent from, for example, genetic material or communities' structure and environmental variability (Ben-Jacob, 2009). In the second perspective, we can base our approach on the ideas of Bertalanffy, who suggested that *information can also occur in the absence of matter or energy* (1976). This interpretation, on its hand, fits the philosophical line of dualism (Maldonado 2018b), where information is the fundamental unit of reality and is independent and prior to the matter and energy (Vedral, 2011).

From our perspective, these two views on information can be complementary and coexist at the same time in a system, an approach already made by Salthe (2005). In organisms, this duality can be evidenced during their ontogenic development, where the structural complexity and the progression towards 'independence' increase with time. Another example can be observed in mutualistic/symbiotic relationships at the holobiont level (Theis et al, 2016; Catania et al, 2017), where we believe that higher organisms progressively incorporate greater structural and functional complexity into the system, as well as a greater capacity to integrate information from various sources, and so, increase its power of 'decision' (Fig. 8). This translates into higher levels of *autonomy*, that is making some 'choices' within the framework of their physical/functional abilities.

BIODIVERSITY, STABILITY AND PERSISTENCE

Frequently, and under a contingent view, in ecology we seek to understand how the dispersion and concentration of matter and energy influences the built, loss, and organization of biodiversity, and how it persists. At the end of the 1960s', Odum (1969) suggested that within an ecosystem, the trophic network essentially describes the way in which energy and matter flow within it. Modulated by the succession, this dynamic brings a play between variety and equity to the ecosystem, whose oscillation progressively tends to stability. He suggested that these units tend to be as large and diverse as possible. He also compared the senescence of an organism with the conditions of an ecosystem, providing an apparently paradoxal view: while an organism would tend to degrade and die when facing disturbances to its own stability, it is precisely those disturbances what prevent the collapse and maintain a 'dynamically stable' state in the whole ecosystem. This would depend on the intensity and regularity of the given disturbances (e.g., significant variations in water level or fire in certain spots). A similar position that tries to explain how the environment affects biodiversity is the hypothesis of 'intermediate disturbances' (Connell 1978), which is a subject in current debate (Fox 2013; Sheil & Burslemm 2013).

From another perspective, 'stability' has been correlated with the way in which the elements that make up the system are connected, i.e., a network structure that is molded by the environment. As an example, May (1972) suggests that ecological systems that are too rich in strong connections are more prone to instability. In other words, *strong* interactions in *few* species and *weak* interactions in *many* species could be a particularity present on stable systems. In addition, it is suggested that such an organization generates patterns that regulate the average interaction forces, thereby supporting the stability of the system. Complicated-type of interactions of processes present in ecological succession at different scales, in different environments and in the biology of organisms were also highlighted. In summary, the structure and stability of the BSs depend on the particularities of the environment, which persistently direct the system to the homeostasis; since this underlying concept relates to the idea that a given 'end state' can be reached from many different ways/manners, Bertalanffy defines it as '*equifinality*' (1976).

On the other hand, Holling (1973) argues that ecosystems' structure and function can be correlated with the probability of extinction of its elements, which he called 'persistence'; that is, the presence of fewer elements (individuals/species) in an ecosystem would lead to a lower probability of this ecosystem to persist. Holling argued that, under variable climatic conditions, wide fluctuations in the structure of a population can be observed, but not enough to extinguish it, i.e., the degree of plasticity in the organization of a BS is selected by the variation of the environment (e.g., an unstable population displaying wide fluctuations and being highly resilient shows a high organizational plasticity in its structure, as opposed to a lower plasticity under less variation in the environment). Structures such as meta-populations (Hanski 1998; Grilli et al. 2015) or meta-communities (Wilson 1992; Leibold et al. 2004) are examples of high organizational plasticity. Interestingly, Zilber-Rosemberg and Rosemberg (2008) brought such a view of plasticity to the holobionts as one generalization for their 'hologenomic theory of evolution'; in other words, this view independs from the observational scale of analysis (e.g., Arita 2005; Hawoong & Barabási, 2000). In short, a higher variability of the environment can favor the persistence of a BS at population/community level; however, from the individual systems' standpoint (at the organism level), disturbances or environmental stresses can alter their own internal/physiological organizational plasticity, which can lead to unbalances, and so, diminish persistence of the individuals/species (McCann, 2000).

From the theoretical framework of these authors, the stability of a BS and its persistence (either at organism or at population/community levels) depend on the variability and types and frequency of disturbances in the system's environment, which alter the *connectivity* of the systems internally (e.g., organisms and its parts, communities and its parts, etc). In comprehensive terms, we could say that a variable environment together with environmentally-led stresses select systems whose parts, structure and function belong to a *free-scale network*, as described by Hawoong & Barabási (2000)(see above), despite the inexorable existence of those scales affecting BS at different levels (e.g., atomic, molecular, cellular, multicellular/organismal, community, etc. scales). Such an idea fits nicely to the above description by May (1972) about strong *vs* week connections in the systems' parts and their relation to instability and, by the same token, to the debate on the usefulness of the holobiont/hologenome theory (e.g., see Theis et al, 2016; Catania et al, 2017). Thus, the variability of the environment and its disturbances can be grouped together as *part of a sistem's history* that reflects its organizational plasticity. However, at certain conditions, a system can become another system. To achieve this 'breaking point', Scheffer & Carpenter (2003) suggest that gradual changes in structure and function must occur and move to an alternate state, "without warning" (something similar was also described by Levin, 1998; 2000; Cadotte et al. 2011; for visual description, see https://www.youtube.com/watch?v=oczrY39QcTM). Based on aspects of the theory that states that chaos can occur from ordered patterns, Scheffer & Carpenter (2003) suggest the following scenario in the dynamics of a system: first, a system can behave in several ways, but remain identifiable as single one; i.e., it expresses itself as *alternative stable states*, which can be explained from the viewpoint of the 'attractor' models of Lorenz (1976). Suddenly, a particular change of a certain type and given magnitude in a single variable can totally alter the systems' expression/states to such a point that it becomes another system, with expression of very new different states that completely changes the initial attractor variables relationships (**REFs**). In this line of thoughts, some authors (Sugihara et al. 2012; Zhang et al. 2015; Moore 2018); Yan & Zhang 2018) use nonlinear models to detect causalities in complex ecosystems and predict in what circumstances these changes may occur.

Another relevant issue in the *stability* and *persistence* of a BS comes from the idea of *variability/complexity of its parts*. Barbier et al. (2018) highlight that the mechanisms that shape the diversity, functionality and stability of a system are related to complex individual behaviors. Communities would stabilize as a result of collective dynamic patterns based upon individual stochastic behaviors. A lot more complementary information that allows us to understand more deeply the stability and persistence of BS is currently available, of which we refer to some recent studies related to networks (Jiang et al., 2017; Valverde et al., 2017; Zamborain-Mason et al., 2017), connectivity (Terml et al., 2007; Treml & kool, 2017), fragmentation (Fahrig 2017; Fletcher et al., 2018; Fahrig et a,. 2019), anthropic activity (Evans et al., 2016), climate change and management (Tujo et al 2017; Brodie et al., 2016). In general, these studies have focused on the variability of the environment measured from the frequency, intensity and duration of events, which establish the stochastic framework in which the system's view is developed. Also, the extension and local impact of these events on a BS can generate alternative states of structure and function, such as those observable in different scale: tropical forest succession processes (Norden et al. 2015; Arroyo-Rodríguez et al. 2017), deep communities (Smith & Hessler 1987; Marcus et al. 2009; Sylvan, et al. 2012), reef systems (Done, 1999; Wilson et al. 2006) or microbial biofilm formation (O'Toole 2000; Stoodley 2002; Lawes et al. 2016).

From our perception and understanding of these theories and studies, we can advance the following: a high organizational plasticity is a particular feature of highly persistent BSs, and the view of the environment acting on shaping and directing these features can provide predictions and explanations from several standpoints. To us, at the end, the stability and persistence of a system can be correlated with the *instability* and *disorder* of its parts, which together generate observable patterns. The more complex is the structure of a system, the greater is the disorder it will be possible to observe, at least in a superficial manner; in other words, 'complexity' enhances the organizational plasticity of a BS. In ecology, yet the current and most employed theoretical framework shapes the hypotheses based on that the environment underpins *stability* and *persistence* of a BS, which can be more simply described from a mechanic view. The tendency of the system's parts towards stability is taken as a progressive and finalistic process called *homeostasis*. Under this view, the causal forces are sought and found repeatedly in the *perturbations* and *variability* of the environment, to which the organisms tend to respond mechanically. We claim that the degree of *autonomy* (or *independence*) that a BS has in relation to its surrounding environment is a relevant force, capable of triggering and shaping ecological processes. Therefore, further knowledge can emerge from such a complementary view, and so, it should also be taken into account in ecological investigations.

COMMON VS RARE (UNUSUAL) EVENTS

When thinking about homeostasis, we may be observing only part of a complicated dynamic, where the *homeorhesis* would be the rule. Historical environmental patterns, with their characteristic disturbances and environmental variability, would shape the systems, such that the occurrence of *rare events* would allow a BS to incorporate new information, whose processing would potentiate its stability and capacity to persist in the environment. Here, we call *rare* (or *unusual*) *events* as new conditions that had never happened before, and that are characterized by unexpected phenomena with high impact on the systems (Maldonado 2019). From our perspective, we propose that a rare event (RE) is not part of the history of events that have occurred in or around a system, or that the system has not had previous experience of said event; hence, REs are a fundamental part of the dynamics of the BSs. In this context, we emphasize that, in recent years, issues such as chaos, fluctuations, attractors, non-linearity, and bifurcations have been increasingly incorporated into the ecological language.

In ecology, an ‘event’ is an observable phenomenon, both in the environment (e.g., winters, glaciations, droughts, warming or anoxia of the oceans, continental displacement, earthquakes, volcanism, etc.) and in the BS itself (e.g., germination, flowering, reproduction, migration, settlement, etc.). The events associated with the environment have categories based upon their magnitude and can be *dangerous*, *disastrous* or *catastrophic*, all with consequences in evolutionary processes, such as natural selection (Begon et al., 2006). In this sense, these events can be associated with disturbances that have a greater or lesser impact on a BS, depending on their type (e.g., fires,landslides), extent, intensity and frequency.

Maldonado (2016) describes the events in relation only to the detection frequency by the BS. Thus, the '*common events*' (CEs) are repetitive or cyclic (e.g., day-night, lunar periods, hurricane periods), whereas the REs are those that has not been detected (or "felt") by the BS (e.g., an emerging disease; see below). Depending on this particularity, then the events can have a greater or lesser impact. With this approach, we can understand that common and rare events ultimately build the '*immediate environment*' (IE) of any BS. Under this view, CEs and REs can be understood as events that induce a BS to "*elaborate"* on its IE and "*interpret"* it at its "*convenience"*. A BS would perceive its IE continuously and simultaneously as a set of facts or variables (e.g., temperature, salinity, luminosity, pressure, concentration levels of some substance, etc.); the detection of non-significant variations on those variables is internalized by a BS to providing a feel of the time frames within events (e.g., autumn season, ocean tides, moon phases, seawater upwellings, etc.), whereas significant variations in those variables allow a BS to perceive a *temporal sequence* (cycles) of events (e.g., all seasons of the year, seasonal dynamics of ocean currents, year-round management stages of modern crops, etc.). We intuit that the temporal sequences of events allow a BS to update its predictive abilities. This idea is based on nonlinear models such as those of Lorenz (1976) whose projections generate what Lorenz called '*strange attractors*'".

Returning to Maldonado (2016), the *frequency* of events' registration by a BS help characterizing the variability of its IE. It is worth highlighting as a conceptual framework that a BS is sensitive only to information types that are somehow associated to which they have been selected for, e.g., detection of magnetic fields in lobsters or turtles (Boles & Lohmann, 2003; Lohmann et al., 2007); electric fields in sharks (Fields et al., 2007), or different sound frequencies or electromagnetic waves in bats or insects (Redgwell et al., 2009; Klocke et al., 2011), etc.). So, the common or rare events are dependent on the condition and identity of the BS. In this sense, Maldonado (2016; 2018) proposes that the information that a BS perceives can be of two different forms: monotonous or unusual.

An information can be ‘***monotonous***’ when events are best predicted by a BS, that is, the frequency of new information is reduced as a BS develops, which thus increase its predictive power (Fig. 1). In this case, information patterns in the IE are identified by the BS as being *known* or *repetitive* (e.g., variations in the night light intensity on Earth’s surface caused by the lunar phases), make it *easier* to better solve problems related to those events (e.g., evade predators, find food resources, find a new home or areas of growth, reproduce, etc.). The more *common* is an event, the more *monotonous* is the information it offers; as a consequence, such type of information in little improves the predictive ability of the BS, so that with few more details, a BS can more easily and quickly predict the more likely future events of its IE. Therefore, we intuit that a system incorporates the mechanisms that allow it to “feel” that an information of the IE is monotonous (and so, allow it to react more promptly) through the evolutionary force of *natural selection*. Said in a different manner, expression of survival instincts, for example (Jung, 1919; Sun & Wilson, 2013; Blumberg, 2017), would reflect evolutionary accumulation of monotonous information to a point that the physiological responses to given stimuli (driven by selection) become inherently mechanical (and so, automatic, quick and fast). Epigenetics (Villota-Salazar et al., 2016), as well as hologenomics (Borderstein and Theis, 2015), would bring other examples of mechanisms expressed by BSs to interpret their surroundings as a result of “feeling” certain information from the IE. Gould & Marler (1987) suggest that organisms are prepared to *learn* more easily certain things than others, and that they are limited by the information they receive, store and use. However, Jung (1919) have already suggested that the origin of *instincts* could not be explained only by genetic inheritance; it must be *learned* at some point, which is an idea that could be applicable to any system capable of integrating information. Blumberg (2017) suggests that instinct is a behavior that develops individually under the guidance of typical experiences of the species". This would happen in ecological contexts, so that the instincts would be not only genetically programmed or determined, but also that they would arise (or improve?) in each generation, through a cascade of physical stimuli and biological influence that generate information to be incorporated. In other words, the evolutionarily acquired mechanisms must be triggered by IE and, from there, information is incorporated, leading to automatic responsive behaviors.

Alternatively, an information can be '***unusual***' (or rare) when a particular event with one or more variables with values *not previously registered* is perceived by a BS. The unusual or (RE) is supposed to be totally new information from the IE, for which the BS *feels* it for the first time at some point in its ontogenic development. As in monotonous information, caution should be taken when talking about a BS, because as we define it (see glossary), such system can be an individual or its lineage/population, and it is from this scale perspective that an event must be realized as being rare or not. Therefore, considering any event, it will be unusual, depending on whether it occurs for the first time for an individual or for a population/community. The unusual information from the IE can trigger mechanisms that would allow a BS to then react mechanically, given appropriate time to incorporate information in its lineage (above we associated it with instinct). In other words, a RE may initially be unusual for an individual, but as it is repeated (either from an individual or from a lineage perspective), it will become *more common*, and so, it will allow its incorporation to the prediction ability of the BS. It is relevant to state that, due to the ontogenic nature, young individuals experience more REs than adults in their individual life span. If we describe a BS as a lineage, then a RE will be one that had not been "*experienced*" until that moment; hence, there is no background that could allow an adequate reaction from the system, making it a problem or situation that must be resolved in a novel, different manner. Thus, the impact of a RE will depend on the phylogenetic or ontogenetic development, and on the frequency that such an event happens for an individual, population or lineage, and is registered by it. (e.g., alterations to the environment due to meteorite fall, increase in CO_2 levels, decreases in oxygen levels in the oceans, or anthropic activity). Maldonado (2016) suggests that "highly unlikely events have a greater impact than those that occur regularly," thus, REs can profoundly "surprise" a BS. We understood that BSs become "experts" in reacting to common events (i.e., a lower frequency of REs) and, therefore, tend to abound under these “facilitated” conditions; on the other hand, they tend to be more restricted where predictability is more difficult, as determined by a higher frequency of REs. Exposure to common and rare events maintains and incorporates new information to the BS, so that (sub)populations subject to a higher frequency of REs would incorporate information to a degree that they will increase the chances to persist under inappropriate conditions that bear potential for species extinction. From this view, Balmford (1996) and Betts et al. (2019) propose that *extinction filters* tend to leave relatively more resistant species in a given area.

Maldonado describes the above circumstances as the “ability of systems to be less surprised”. From this, we intuit that the power of a BS to “decide” how to solve something under the rare conditions can play a fundamental role in its functional outcomes (e.g., changes in the diet by changes of environment, which implies changes in the structure and function of the bacterial community present in the digestive tract of a host). The information is very relevant, and although it is a rather abstract term, it is currently taken into consideration from two philosophical lines of thoughts, Monism and Dualism (see Glossary and section # 3 above). From a similar perspective, we can view information based on ‘classical’ (Shannon 1948) or ‘quantic’ (Shumacher 1995) standpoints, with the former being predominant in shaping observations on ecology and life itself (e.g., diversity, composition, abundance, thermodynamics, genomics, etc.) (Smith 2000). From the quantic-type information, some relationships with BSs have already been studied (e.g., photosynthesis or magnetic fields; Arndt et al., 2009; Kolli et al., 2012).

Adami (2012) incorporates the *theory of information* to the process of evolution itself and emphasizes that the greater the capacity to predict the environmental settings, the greater the functional abilities of the BS. From an alternative, not human-centered view, this can be a measure of a system’s *intelligence*. Maldonado (2018) states that ‘adaptation’ and ‘learning’ are required for persistence of a system, such that ‘proper decisions’ *based on experience* is a matter of life or death. As just mentioned, the ability of a BS not to be ‘surprised’ will depend on how complexly it is organized, and consequently, ‘how informed it is’. In this context, the temporal and/or spatial scale in which events are perceived and recorded by a BS is relevant for their definition. A true BS's sensitivity to the events is fundamental, as this is the first step for the influx of information, which further allows recognition, prediction and adaptation of the BS to the IE, under different levels of interactive complexity. As a corollary of this idea, the 'niche construction' theory highlights that "organisms exert some influence on their own evolution" (Lalana 2015).

EMERGING PROPERTIES OF SYSTEMS

Information is essential in generating *emergent properties* of a system. Tononi (2008) in his 'manifesto' develops on how the emergent property of 'cognition' in a system is possible and how to quantitatively measure it, associating it with the system's ability to integrate information (I.I.). From this view, the causal sources of ecological patterns are also related to the ability of BSs to internalize information and 'making choices' (Haan, 2006; Tononi, 2008). In fact, I.I./cognition can be an evolutionary characteristic that generates degrees of *independence* between the system and the environment, in the sense that not all functions, actions and activities of a BS exclusively result from 'mechanic' reactions to environmental stimuli. It is yet difficult to quantify and predict the emerging states of a system, although this idea was already proposed half a century ago (Anderson, 1972). The capacity of I.I. and its possible relationship with adaptive processes, persistence and even with diversification processes should be also considered in ecological studies. Tononi (2008) and Maldonado (2014; 2018b) pay close attention to information processing, as they treat information as a fundamental entity that can generate changes in structure and function of a system. These authors suggest that as life manifests itself, 'uncertainty' of a BS with regards to 'what to expect' from the IE is reduced; on this idea, the capacity of a system of I.I. is related to an array of intangible properties, such as 'making decisions', 'intentionality', 'risk calculation', 'mental experiments', 'solving problems', ‘proposing destinations’, ‘selecting’, ‘grouping’, ‘ordering’, etc., can be all sources of change, adaptation and, consequently, stability and persistence of BSs.

From this perspective. *We suggest that the evolutionary or ontogenetic development of BSs can transit from chaos to regularity, from environment-dependency to autonomy, from stochasticity to finalistic actions. A schematic view is presented (Fig. 8) where, for example, the ontogenic development of crustaceans, or the evolution of hominids, or bacterial succession processes conform to this approach. Biologically, the information allows a system to make better predictions about the environment, that is, generate greater autonomy; the selective process leads to a ‘better’ interpretation of the environment.*

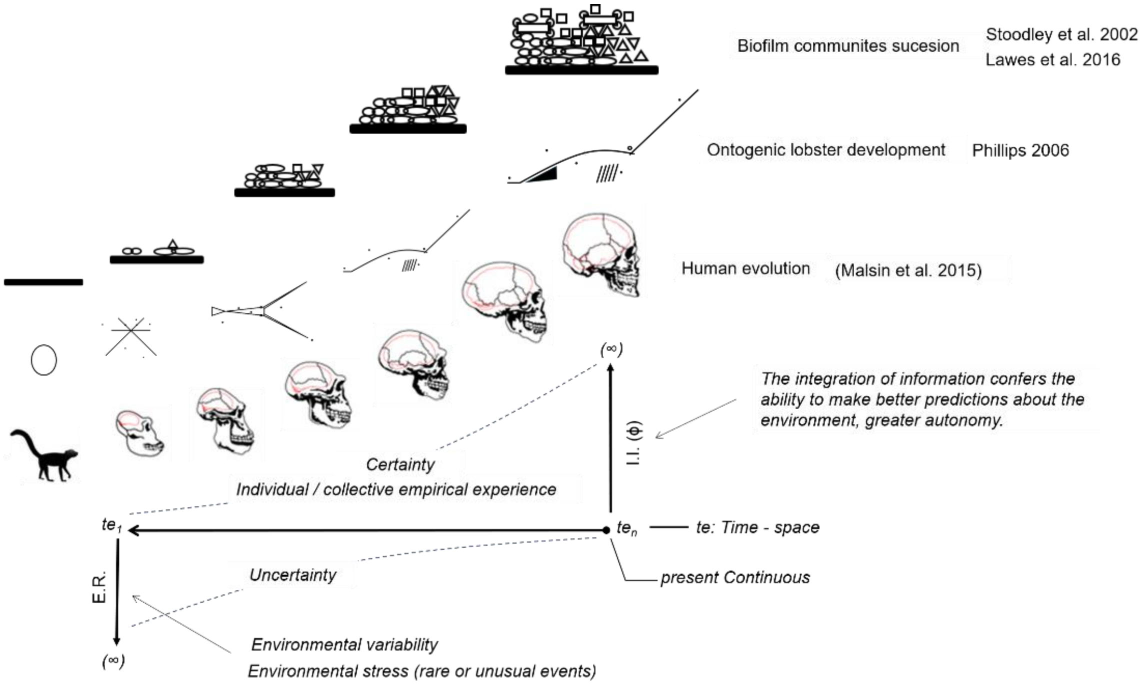


Figure 8: Graphical scheme that hypothetically represents the progression of complexity in biological systems. The integration of information by a system would increase its ‘autonomy’, improve the quality and scope of its prediction power, and decrease uncertainty regarding its IE. ‘Cognition’ appears as the ability to integrate information (ϕ); Rare events (E.R.) would be related to stressing conditions of the environment to the system.

Analogous to Tononi's theory, a ‘holobiont’ (from the hologenomic theory of evolution mentioned above – Zilber-Rosenberg & Rosenberg, 2008; Rosenberg & Zilber-Rosenberg 2009) can be thought of as a *network* that ‘manipulates’ information. The holobiont as the evolutionary unit is taken as a set of interacting elements (microorganisms and host cells, with their genetic material, biochemistries and physiologies) whose connection and dynamics can be causally correlated (e.g., Pita et al, 2018; Cregger et al. 2018; Ugarelli et al. 2017). In other words, it is a whole set of genes whose expression leads to interactive cells within the host and with the environment, thus allowing the holobiontic organism to operate in both the mechanical and cognitive forms, at different levels and intensities. The holobiont as a BS fits to the Tononi's view of I.I. that allows the system to 'choosing', 'grouping', etc., which help reducing the system 'uncertainty' about the IE. Persistence of a BS of holobiontic-type would depend on its ability to integrate information, and so, generate cognition. Thus, the amplified magnitude of connections under this hologenomic view would provide a larger array of new and more information that would increase the system's ability to cope with the environment.

Systems that do not process information or do not solve problems properly would be more likely to become extinct (Maldonado 2014; 2016, 2017, 2018b). From its evolutionary nature, the 'cognitive reality' is not exclusive to the human species, and has been evolving in multiple ways in different living systems (Ben-Jacob 2009; Trevaguas 2005; Calvo 2016; Owen et al. 2016). This view of systems bearing the emergent property of cognition can also be extended to groups and social organizations in biology, such as bees and ants colonies, metapopulations, and *quorum sensing* type of communication (e.g. Alexander 1974; Water & Fewell, 2012, Zamborain-Mason et al, 2017; Franks et al., 2003; Conradt & Roper, 2005). To us, I.I./cognition is a biological property that comes from the dynamics between matter, energy, and information, which allows, among other things, the 'planning of a destination'. The quality and scope of this prediction depend on the individual and/or collective complexity of a BS (Fig. 9). An environment would become more complex as a result of BSs being able to 'memorize' the IE conditions, to 'project' a future, to create 'purpose', all in a progressive dynamics that reduce 'uncertainty' to the system; this view strengthen the impact of autonomy as a causal agent to phenomena. There are other studies, however, which do consider 'decision making’ processes as required to solve environmental ‘challenges’ for BSs, but that leave causality as only dependent from the environment (e.g., Sol et al. 2005; 2010; Sayol et al. 2018). Tononi (2008) has proposed a variable ‘phi’ (ϕ) to *quantify* the emergent property of cognition; as seen from Fig. 9

We suggest that the I.I. can be synthesized in biological systems in different ways, covering a whole spectrum that can go between a hyperconnected collective organization of less individual complexity (Procaryotes), to an organization with greater individual complexity (Eucaryotes).

From this point of view, decisions would have a fundamental role in the organization of the ‘living’, and its reality can be adjusted to some principles suggested by Aliev et al. (2015), which can be applied to an ecosystem context as follows: BSs realities depend upon (i) possible ‘options’ that the environment offers, (ii) sensitivity of the system to the IE, (iii) ability of the system to take some of those options, (iv) ‘risk calculation’, processing and I.I., which depend on the ‘experience’ of the system, and (v) a certain degree of ‘opportunity’ related to the stochasticity of the environment.

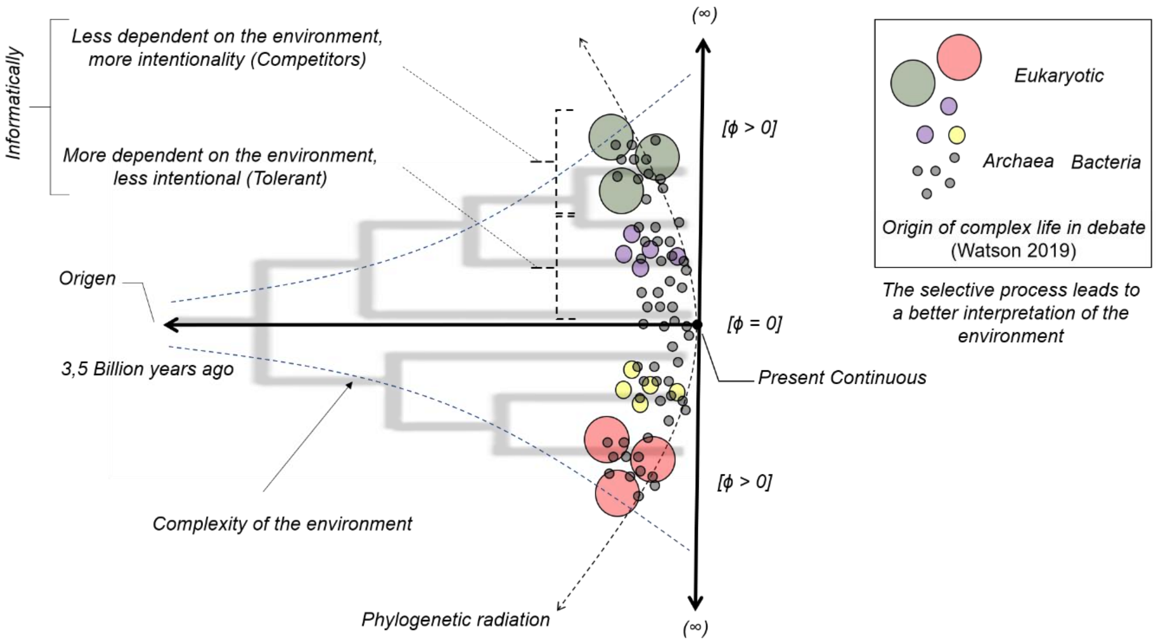


Figure 9: Progression in the environment's complexity. This graphical scheme is representing the hypothetical progression of the flow and incorporation of new information by BSs. The emergent property of 'cognition' is represented by 'phi' (ϕ), which can be expressed in BSs in different ways, covering a wide spectrum that goes from hyperconnected collective organizations, with less complex individuals and a greater dependence on environment (e.g., Archeae, Bacteria), to an organization with greater complexity of its individuals each with greater autonomy (Eukariotic).

CONCLUSIONS AND OUTLOOK FOR BIOLOGICAL CONSERVATION

In general, the observations, experiments and theoretical approaches in ecology have allowed us to model and, to a certain degree, predict the behavior of ecosystems in the face of events such as fragmentation, climate change or other anthropogenic effects. Although other theories, such as networks, graphs, self-organization, hierarchies, chaos, non-linearity, etc., are currently being incorporated into the analyses of ecological issues, the analytical perspective in ecology is yet mostly fitted into a systemic view, with description of the systems based on the 'complication' concept; this is supported basically from the materialistic 'monism', where matter and energy are the underlying principles governing the information flow. Only recently, as described by Morin (1993), the idea of 'complex systems' have been explored in ecological questions.

Generally, most theories in ecology explain the causal relationships between the environment and its pertaining systems under particular conditions, e.g., 'island theory', 'edge effect', 'metapopulations', 'niche theory', 'neutral, succession', etc. More recently, novel disciplines such as *cognitive ecology* have been breaking through in the attempt to explain this emergent property of BSs of incorporating and integrating information (I.I.) based on the variability of/changes in the 'perceivable' (immediately surrounding) environment. Considering that such an emergent property, to certain degrees, generates 'intentionality' and 'independence' from the environmental stochasticity, it is likely that ecological properties such as distribution, connectivity or abundance can be markedly affected by such property. From this perspective, we suggest that the different capacities of BSs to I.I. influence the direction of ecological processes as much as it does the environment. Systems having a greater ability to be 'less surprised' would have lower risks of extinction, thereby improving persistence to populations or communities. The approach of recognizing ‘intentionalities’ in the ‘living’ provide a further and alternative analystical perspective, which can be studied on an array of different systems and scales (i.e., microbial, individual, population, lineage, community, holobiont, colony, etc.). The challenge, though, is to ask relevant questions and design appropriate methods for this approach.

We think that *stability* cannot refer to only a fraction of what happens in the system or in the environment; this concept should be seen as a result of a full and global dynamics involving both parts, which, in turn, would allow increasing and save information by the BSs. The concept of *homeorhesis* (more than homeostasis) has the power of broaden the possibility of more comprehensive descriptive models for ecosystems, by viewing *construction* and *destruction* as inseparable and fundamental parts of any systems’ lifespan. Perhaps, conservation strategies should not be looking only at one, or few conditions that a system can manifest at a given moment; it may be more effective to allow a blending of ‘matter’, ‘energy’, ‘information’ and ‘time’ in the elaboration of more robust predictive models, something that I.I./cognition appears to offer. , Depending on the particularities of the events and the systems, information will tend to increase and accumulate, as opposed to the classical Lavoisier’s view on the energy conservation of the universe. For example, lineages of greater geological/phylogenetic age, less young individual organisms, or those with wider ranges of dispersion will tend to be *less surprised* by the environment. It is reasonable to suspect that global events of greater impact potential, such as the ocean’s anoxia, acidification and warming , will more likely select those beings that have already experienced closely similar events, these being the ones with a greater opportunity to persist. Likewise, depending on their particularities, REs can allow incorporation (and so, integration) of new information about the environment into the system, making it more *autonomous*.

Under this view, interesting possibilities can be advanced in the case of a metapopulation structure. While some populations can persist in *monotonous* environments (with lower environmental variability), others strive in less monotonous, more variable environments, such as those characteristic of the. limits (borders) of their physical distribution. This situation would lead to different challenges and behaviors among the populations, which may reflect in ecological particularities such as species abundance. From the view of complex thinking here discussed, we can suggest that those populations located in the physical distribution limits, facing greater environmental challenges, could internalize and integrate information differently from those in more monotonous environments, granting them an important value, from the informative point of view. In turn, due to their likely lower abundance due to the limiting conditions, they would be more vulnerable populations in a limited timeframe. Hence, this would imply a necessity of their inclusion in the conservation efforts. We speculate that this whole structure and dynamics would allow a greater capacity to metapopulations to face REs and persist, thereby being the ‘unit’ of conservation to be considered.

Keeping the environment as less variable as possible has been the spearhead of most conservationists, with the decision to guarantee species persistence being largely based on preserving most stable environments and avoiding short-term changes. From what is discussed above, we claim that monotonous environments, i.e. ’environments whose variability is *known* by the systems’ may not be a full guarantee of their persistence, as the environment can ‘surprise’ them, and so, lead to their extintion. The ‘nature of Nature’ may be telling us that, in order for BSs to persist, it might be better to be ‘prepared’ to the changes to allow appropriate adjustments, rather than simply maintaining what is there and avoiding ‘facing the inevitable’.

Complex systems such as the BSs can be thought and explained mechanically, as it would be simple ‘complicated’ systems. Such an approach has been widely applied, for instance, in functional genetics and ecology, so that the ‘living’ is seen in the predictive models essentially as a reactive being in relation to its immediate environment (in various different scales). However, in doing this way, the emergent properties (which can generate *autonomy*, which indeed turn predictive models into challenging issues) are frequently not considered. Actually, the ‘complicated’ and ‘complex’ terms and concepts end up being mixed up and treated (unconsciously?) as synonyms, so that the systems are said to be *complex*, but are treated, in fact, as *complicated* ones. Our study approach humbly aims to complement what has been the scientific-based views that has supported ecology and conservation, the causal relationships between phenomena and their repercussions and consequences. Despite being challenging, an approach based on ‘complex thinking’ is necessary, and has the undeniable potential of broadening the scope and allow better decisions on conservation strategies.

From this whole perspective, we leave some questions we believe should be more explored in the *milieu* of biological conservation:

- Is it possible to correlate the level of autonomy reached by the systems, with the architecture and dynamics of their immediate environment?
- Does the ‘capacity for decision’ (as a result of cognition), together with rare (unusual) events in the environment, have the potential to trigger and drive diversification?
- Is the ability to integrate information capable of generate a certain degree of independence of a biological system to its immediate environment, and at what levels?
- Do higher structural complexity in BS correlate with more complex ‘decision abilities'?
- Evolutionarily, highly complex systems can be causative sources of environmental variation?
- How do we measure (or represent) the system’s ‘decisions’?
- Is there a relationship between the ‘ability to diversify’ a lineage and ‘what is learned’ by that lineage?
- Would the development of the emergent property of 'cognition' in a system be a result of only contingency or also of its previously set 'intentionalities' ?
- Does the ‘intention’, in its respective scales, proportions and levels of cognitive expression, influence the organization and persistence of the ‘living’ in an ecosystem?

- Is the dynamics in the organization of the biological systems and the environments able to describe the biosynthesis of information in the space-time?

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CHAPER III

COMPLEX THINKING: UNUSUAL AND COMMON EVENTS AND THEIR IMPACT ON POSTLARVAL SETTLEMENT OF SPINY LOBSTER ***Panulirus argus***

Post larval lobster

ABSTRACT

Generally, the centralized distribution of information describes the normal behavior of nature (e.g. a dominant average value), and the unlikely or rare, is taken as a simply extreme condition in the distribution of that information. It is in that context that the dominant becomes fundamental. There are few references in ecology, which literally address the issue of rare events. It is generally investigated indirectly and covers (e.g. from rare species due to their abundance or form of defense, to heavy rains in desert areas). Thus, the rare is treated as something extraordinary with some impact on the normal conditions of the environment or the system. This approach guides the way of managing, as it is believed that places or moments where it is best represented should be conserved (e.g. abundance, breeding seasons, breeding areas, etc.). From the complexity, the rare or unlikely takes on great importance, since it is assumed that it has a fundamental link in the functioning of the systems. We believe it, is these events that incorporate new information into biological systems and make them less vulnerable. From a historical perspective supported by information published on the postlarval settlement of *Panulirus argus* and with data collected during three on-site sampling campaigns. We describe and analyze common events and possible rare events that are influencing the development of this crustacean at the postlarval level. Since the systematic review, it is not easy to differentiate a common event from a rare one. Although none of the articles explicitly mentions it, there is a general idea that limits centrality as a common condition and its extremes as a descriptor of the unusual. However, for us the common is subject to the cyclicity or frequency in which an event occurs and as such in organisms such as lobster, the rare is difficult to detect. There is a lack of exploratory effort on this idea and the possible impacts that rare events can bring to the early stages of development. Finally, with the empirical information, we defend the importance of sink sites due to the unusual conditions that postlarvae face to survive. The relevance is in the possible increase of the potential of this species, to be less surprised by its immediate

environment. We suggest that in generalist species (broad-spectrum distribution) rare events may be better observed in peripheral populations.

INTRODUCTION

One of the recent areas of interest that has been addressing the ‘thinking complexly’, is the study of ‘rare’ events (REs), which in our case, will be related to the ‘functioning’ of a biological system (BS) on ecological contexts (e.g., persistence, distribution, abundance, etc.). Studies in other areas of investigation (e.g., car accidents, Theofilatos, 2016; philosophy, Maldonado, 2016; or computational models, Lindley, 2014) have been explicitly related to REs. In ecological research, REs as such have not been very much studied; Sebens (1985) have described REs in intertidal populations favored by the massive and unexpected death of predators; Cho et al. (2017) do the same when describing moments of synchronous flowering. In general, an RE is approached as a particular behavior or as simply something exceptional in the developmental timeframe of a given BS, so that ecologists tend to observe the ‘unusual’ indirectly, such as in atypical environments of lakes with extreme pH that limit life to extremophilic bacteria, or in rainfalls in desert areas (Begon et al., 2006); in species invasion (Gray et al., 2005; Tobin 2018), or in environmental changes due to the anthropic action (Díaz, et al., 2003; Gove et al., 2019). They also observe *rarity* in BSs themselves, for instance, in the selection of polymorphic rare alleles (Trotter & Spencer 2007; Otto et al., 2008), in rare species due to their particularities in defense (McClintock et al., 1994, 2001) or in their occurrence (Gray & Elliot 2009; Gray 2005), or else, in diseases and pandemics (Begon et al., 2006).

From the perspective we wish to develop, we propose that *new information* might be likely incorporated by BSs by means of REs. The *accumulation* and *variation* of information would generate changes in both the BSs and their ‘immediate environment’ (IE). As a consequence, a BS can express more *autonomy* (chapter 2), such that its potential for adaptation and persistence increases. Therefore, it is the rise of such an emergent property in a BS that would provide its ability to 'interpret' and 'predict' the environment (Haan, 2006); in other words, we are proposing that unusual events are fundamental in help reducing the 'uncertainty' of a BS with regards to its IE, thereby reducing the risks of a BS 'to be surprised'. Overall, these circumstances would increase the potential of a BS to react towards its better adaptation and persistence, an effect that depends on a BS identity (e.g., organism, population, community, etc.) and condition (e.g., health state, ontogenic stage, etc.).

In a biological context, we have found recent literature that highlights how fundamental is 'information' in the life strategy of a BS. Hodin et al. (2017) describe the ability of invertebrate larvae to simultaneously and hierarchically 'integrate information' (I.I., chapter 2) with different arrangements, during their ontogenic development. This perspective allows us to think on the ability/power of a BS to manipulate information and determine its destination, not as a simple and early state of a *passive* development. In other taxonomic groups, such as bacteria (Fucua et al., 1994; Abisado et al., 2018), insects with social organization, such as ants and bees (Vissher 2007), and even at tissues' level (Chen et a., 2015), the information integration (I.I.) by the system leads to the ability of 'choosing' by some of its members, which can therefore affect the whole group. This particularity has been known as *quorum sensing* (QS), being a mechanism that allows a 'collective decision' to be taken. It operates with a minimum number of interacting individuals (a *threshold*) and, according to Franks et al. (2003) and Conradt & Roper (2005), such a threshold depends on the environmental conditions (under stressful conditions, this threshold appears to be lower). Other studies have been explaining the ability of a system to 'make choices' from the *theory of networks* (Waters & Fewell, 2012) and associate it with the emergent property of 'cognition' displayed by a complex system (Tononi, 2008); the human being cognition would be merely the most largely developed of such property through evolution of BSs on Earth.

There is a very complex ontogenic development process possible to be observed/addressed in decapod crustaceans; hence, for this reason, we took a species of lobster as a study model in our case, to further develop ideas related to ‘complex thinking’. The lobster’s species *Panulirus argus* (Palinuridae family) presents a planktonic phase that lasts between 7 and 18 months. During this period, it changes in size and develops new appendices and modifications, which have been described as being associated with the ability to drift, swim and *detect information* as well (Montgomery et al., 2006; Goldstein et al., 2008); it can also emit sounds (Fornshell & Tesei 2017). Once at its last larval stage, the developing lobster experiences *metamorphosis*, thus acquiring an intermediate form between the planktonic and the benthonic, which is a developmental phase (*pueruli*) that remains for a few days and ‘makes every possible effort’ to approach coastal areas (Kough et al., 2014). Its ‘abilities’ of detecting multiple physico-chemical signals (Phillips & Macmillan, 1987; Jeffs & Montgomery 2005; Espinosa-Magaña et al., 2018), and of emitting sounds (Meyer-Rochow & Penrose, 1974), as well as their structural and physiological capacity for swimming (Calinski & Lyons 1983; Baez et al., 2018) persist under these circumstances. This thereby allows pueruli to ‘intentionally’ head towards the coast (Hodin et al, 2017). According to Cowen et al. (2007), if there were a *purely passive behavior* in the pueruli, their probability of arriving at the coast would be markedly reduced. Periods and areas with consistently higher levels of the settlement have been observed in various parts of the Greater Caribbean and, to date, studies have indirectly highlighted that this effort is individual and gradual. No publication, however, has suggested any joint action that helps in the postlarval settlement process.

In this study, from the perspective of ‘complex thinking’ involving common and rare events, as well as I.I (Tononi, 2008), we addressed results of the postlarval settlement process of *P. argus* under a different theoretical framework. The data were obtained from direct *on site* campaigns, involving different depths and seasons for the larvae and post-larvae collection, with appropriate descriptive statistical processing. From two sources of information, we attempted to highlight the impact that these events can have on this early development phase, describing possible ecological consequences and how these views and perspectives can affect the approach of devising better management strategies for effective conservation of this resource.

METHOD

Information sources

We use two sources of information: the first is related to empirical studies published by this (Jaimes et al., 2016) and other authors, with which we seek to identify the *common* and *rare* events that have been affecting the post larval settlement (Sm9). The second source is a series of empirical data (this study) obtained during three sampling campaigns, where post larval settlement in the Colombian Caribbean Coast was evaluated. Data that were obtained between 2002 and 2010 (Jaimes et al., 2016) (Sm10).

Source 1: Systematic Review of related literature.

Initially, articles were searched on the web using the “publish or perish” tool (V.6). The selection criteria are observed in Table 1. In total, 609 documents were collected in the first phase. This list was passed through a second filter and finally, 57 articles related to the *P. argus* species were selected (Sm11). The treatment of this information (organization, filters, elimination of repeated, graphics design) was carried out in the Excel program. The word cloud was generated with the free access program, available on the site https://www.wordclouds.com/

Table 1: Inclusion and exclusion criteria of the selected articles for the systematic review.

Inclusion	All article with the keywords “puerulus”, “postlarval”, “postlarvae”, “settlement”, “pueruli”, “puerulos” and the “lobster”, within the general text of the document.
Exclusion	Articles that focus on fauna associated with collectors Articles that focus on methods for post-larval collection Articles that focus on genus Puerulus Other crustacean or ontogenic development Articles not available on the internet Book chapters, News letrer, Reports, thesis, workshop, citations.

We characterized the *common* and *rare* events that have been reported directly or indirectly so far, based on the following criterion: if an event (or fact) was reported at least twice in the timeframe of the publications, it will be considered as 'common'; for instance, if the consistent record of post-larval settlement in all lunar faces was described in more than one of the studies assessed, then the settlement becomes a 'common' event throughout the lunar month (e.g. Briones-Furzan & Gutiérrez-Carbonell 1992; Gordon & Vasques 2005). In these cases, the intensity in which an event has happened during the settlement was not taken into account. We also systematized how these events could be related to the maximum and minimum values recorded in the post larval settlement, as well as pondered its consequences in the management/protection of this organism.

Source 2: Post larval settlement (empirical information)

Data were collected from three campaigns carried out on the Colombian Atlantic coast as follows: campaign 'A', between the years 2002 – 2004 (Jaimes et al., 2016; Appendix); 'B', between 2006 – 2007; and 'C', between 2009 – 2010 (Sm 11). These campaigns were originally designed to characterize the temporal space behavior of the postlarval settlement, for management purposes.

The method of collection and monitoring during the campaign A, as well as the conditions and characteristics of each sampling station, are specified in Jaimes et al. (2016)(see Appendix). A series of 20 submerged collectors type GuSi (Gutiérrez et al., 1992) were installed and distributed in 5 stations along 14 km in the coastal zone of the Magdalena Department, Colombia (Fig. 10). Unlike most studies, the collectors were located in depths between 10 and 11 m (Fig. 11), in two geomorphologically different areas. The sampling frequency was monthly, occurring at the 'first quarter' of the lunar phases; the personnel, equipment, and tools were necessary for the installation and revision of the submerged collectors.. The process in the collection method is illustrated in Fig. 12.

In the campaigns B and C, the sampling effort was made at the station with the most consistent time pattern and the highest settlement previously observed in the campaign A. Complementing the procedures in campaign A, new types of collectors were included and a new spatial arrangement was implemented in the water column (Fig. 11), with the objective of assessing in more details the effects of depth and horizontal extension on the postlarval settlement. An area of approximately 300 m^2 was covered in the water column (Fig 11). This effort in sampling was similar to the campaign A and is explained in Fig 12. The database used in this section is shown in Sm11.

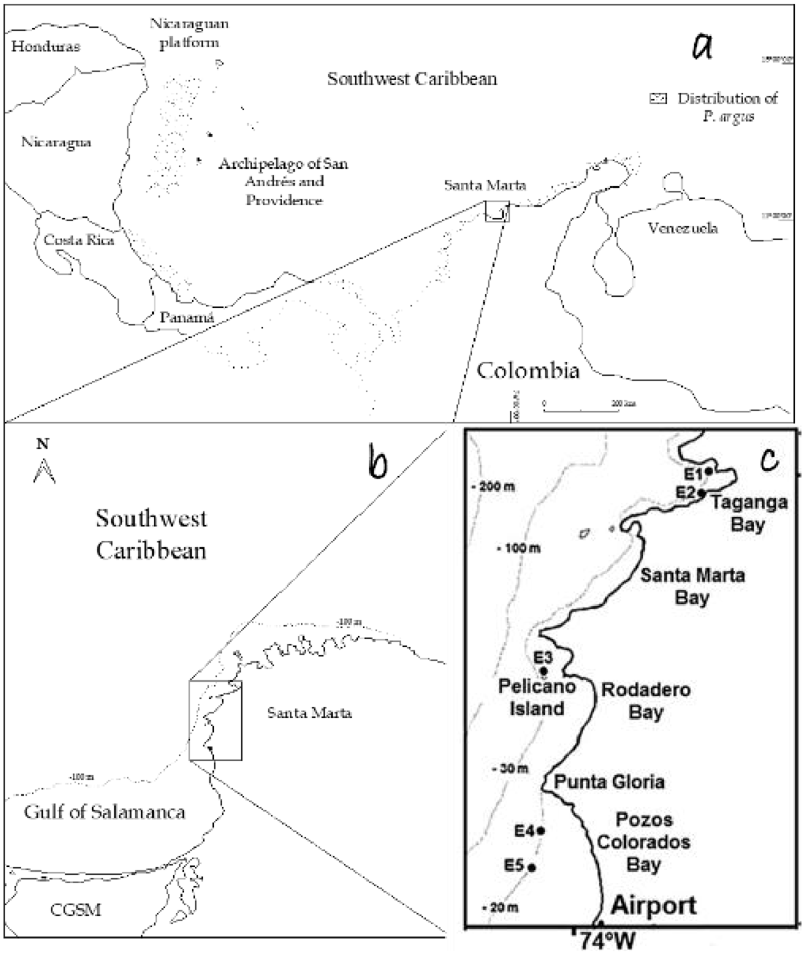

Figure 10: Description of the collection area for the post-larval settlements. Santa Marta Region (StM) in the Colombian Caribbean (a, b). Sampling area and distribution of sampling stations ‘En’ (c).

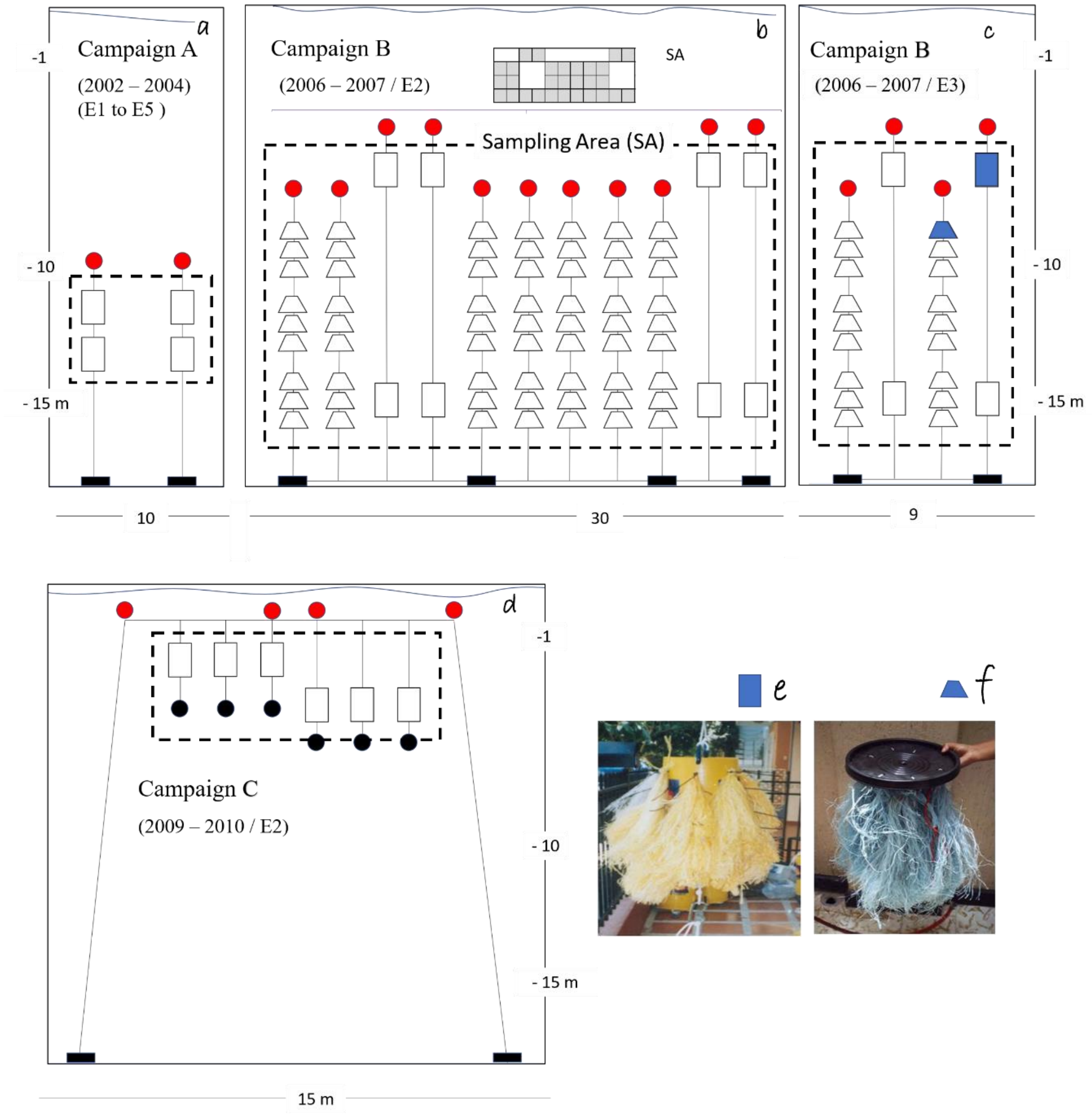

Figure 11: Experimental design of the sampling stations. The spatial arrangement of the submerged collectors during the three sampling campaigns is shown from a – d. The depths of the corresponding stations are shown on far left and right columns and the horizontal lengths of the collecting stations are shown at the bottom of the schemes. The dotted line delimits the effective sampling area, which is represented in a small grid on top of the scheme, with the position of each collector shown in gray (only B-E2). The red circles represent the buoys and the black circles and rectangles, the ballasts. This representation is not on scale. Type of collectors used: 'GuSi' type (e) and 'Column' type (f).

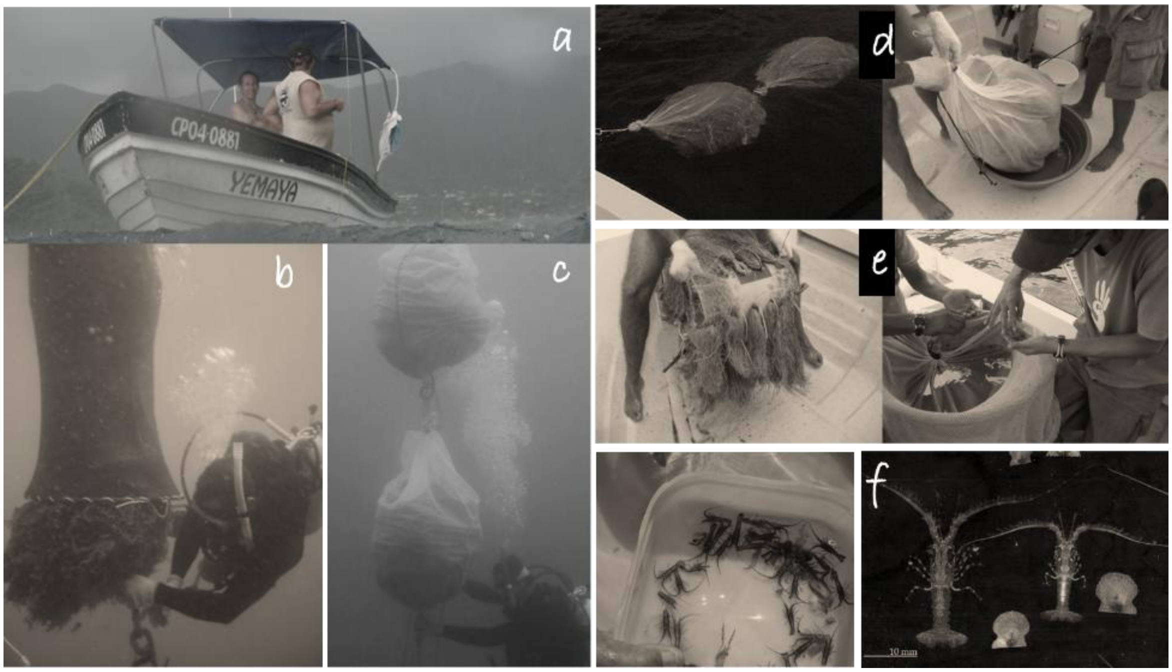

Figure 12: Pictures describing the collection method/procedures. Displacement to the sampling area and procedure for the removal and installation of the collectors underwater (a, b, c). Review of the collectors on deck, separation, and identification of the captured post-larvae (d, e, f).

Data analysis

A cluster similarity analysis was used to determine possible differences between the five sampling stations. In this case, we use the data from campaign A, together with the value of the slope of the sea floor platform, which was estimated on the 30-m deep isobath. The results are accompanied by a graphical representation in Bubble-plot of the density per square meter (m^2) of post-larvae. Initially, we estimated the capture densities per m^2 with the capture values (number of post-larvae captured per collector = Ip). This estimate was based on the average value of the collector coverage area (0.7 m^2).

We made a graphic comparison with Matrix-plot and Box-plot, in order to show possible differences in catches by collectors and locations within the sampling area in campaigns B and C. We assessed these results with a one-way ANOVA between the estimated catch values per m^2. For these analyses, the free software PAST v. 2.17c was used. For a temporal representation of the data, we use a scatter plot, using months or angle of declination of the earth as a predictor variable, and the post-larval density (P/m^2) as the dependent variable.

RESULTS

From our systematic review procedure, several reviews and book chapters were found, which describe how the post-larval settlement (PLS) occurs in Palinuridae (Fig. 13). Together, they generate a fairly detailed picture of this process; the last review was published by Stanley et al. (2015) and book chapters by Felder et al. (2017). Within the framework of the currently published and available literature, we will emphasizing the most common or unusual events reported on the *Panulirus argus* species, and whether they seem important for the adaptive capacity of this lobster species.

In general, about the ‘puerulus’ phase, there is an extensive literature from the beginning of the last century (Fig. 13). To date, research has been conducted on 33 species belonging to three Lobster Families, i.e., Palinuridae (27), Nephropidae (3), and Scyllaridae (2), all of them showing commercial interest. We included the Nephropidae and Scyllaridae families in these results, despite they have not presented post-larvae with the morphological characteristics of pueruli. The Palinuridae family covers 77% of the published work and particularly the species *Panulirus argus* 36% (Fig. 13). About 24% of the publications could not be fully obtained online.

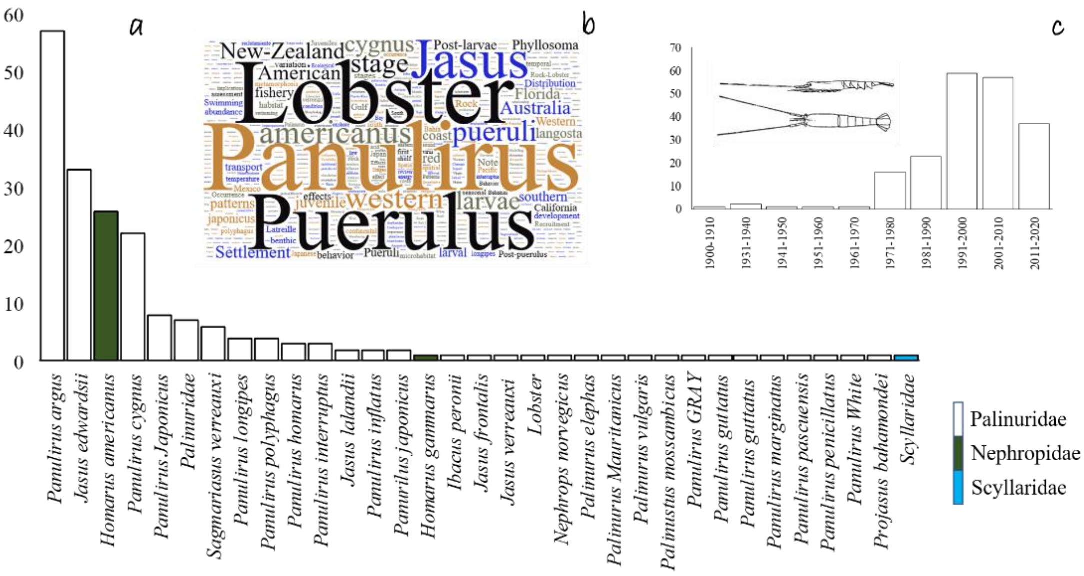

Figure 13: Metric characteristics of the systematic review's selected articles. (a) Distribution of publications by species of study. (b) Word cloud made with the titles of 268 published articles related to the post-larval phase of lobsters of commercial interest. (c) Historical progression of studies on this theme.

The various studies related to post-larval *P. argus* show different approaches and views related to PLS. Many of them correlate large-scale or astronomical oceanographic conditions with characteristics at the seascape level (Eggleston et al., 1998; Aguilar et al., 1999; Dahlgren & Staine et al., 2007; Golddtein & Buttler 2009, Jaimes et al., 2016). Physiological or genetic functioning of post-larvae related to PLS have also been characterized (Silberman et al., 1994; Limbourn et al., 2008; Fitzgibbon et al., 2014). With regards to the productive sector, authors have focused on techniques and methods to help predicting fishing efforts and the development of alternative strategies for production (e.g. Butler IV & Herrnkind 1992; Cruz et al., 2006; Davis et al., 2007). Finally, some studies have highlighted structural and functional peculiarities of pueruli, which have allowed a better explanation for the settlement process (Calinsky & Lyons 1983; Briones-Furzan 1994; Briones-Furzan et al., 2008; Ehrhardt & Fitchett 2010). In general, all these studies were justified from the commercial importance given to this organism; strategies that seek, at least to maintain the current volumes of capture have been the core of these studies. Nevertheless, fishery data (FAO, 2018) show a general decline in traditional fishing areas regarding the lobster resource.

The 'common' and the 'unusual' in post-larval settlement

It is at the outer edge of the continental shelf that the metamorphosis of phyllosoma to puerulus occurs, and it is suggested that it would be activated by some environmental signals, such as salinity, temperature or sound (Phillips & McWilliam 1987). It has also been suggested that, due to the *lecithotrophic* condition (see glossary) of pueruli, which do not feed during the period of post-larval settlement (PLS), the metamorphosis could be triggered by high, sufficient levels of internal energy reserves of the previous larval stage (Phillips & McWilliam 2008). The PLS in *P. argus* has been described as a short-term transitional process (7 to 14 days) that occurs between the last planktonic phase of puerulus (right after a metamorphosis) and the early youth, benthic stage (e.g., Igarashi 2010; Heatwole et al., 1991; Butler IV et al., 2001) (SM_13,14). The function of the puerulus stage is to go to shallow areas near the coast (e.g., Wolfe & Felgenhauer 1991; Herrnkind & Butler 1986; Cruz et al., 2007), with about its first 3- or 4-days of swimming as the time to overcome the extension of the continental shelf (e.g., Calinski & Lyons 1983; Bannerot et al., 1991). The variation in the duration of this stage has been correlated with the temperature, which would influence the swimming capacity and/or distance traveled by the post-larvae, with consequences in their dispersion or suitable substrate finding, according to time of the year (e.g., Herrnkind et al., 1994). It is generally assumed that the effort to reach coastal areas is individual.

In general, the studies correlate the maximum and minimum times and/or individual numbers in the PLS with three basic aspects: 1) the density-dependence to the parental population (e.g., place, times and number of adults) and to survival, dispersion and larval retention (e.g., Briones-Furzan et al., 2008; Ehrhardt & Fitchett 2010); 2) environment-dependency related to ocean-atmospheric, astronomical events, structural and physico-chemical conditions of the seascape, or inter-specific interactions (e.g., Ward 1989; Max 1986; Cruz et al., 1991, Gordon & Vasques 2006; Dahlgren & Staine 2007; Jaimes et al., 2016); and 3) intrinsic characteristics related to genetic structure, physiology and behavior (e.g., Calinski

& Lyons 1883; Goldtein & Butler IV 2009; Lecchini et al., 2010; Baeza et al., 2018). The combination of these three aspects determines the particularities in the settlement levels in the entire distribution area of this crustacean throughout the year.

It can be observed from various studies a clear searching intention of finding patterns and generating predictive models supported essentially on the environmental conditions, settings and variation (e.g., Cruz et al., 1991; Gonzales & Wehrtmann 2011). The light intensity (e.g., Briones-Furzan 1992; Gordon & Vasques 2006, Gonzales & Wehrtimann 2011) and the extent and position of the ocean eddies on large and small scales (e.g., Briones-Furzan et al., 2008; Gordon & Vasques 2006) are two main factors that have been persistently related to maximums and minimums in the settlement. There is also another group of variables that have been used to partially explain the variations in the settlement at sea level, such as the structure and dynamics of benthos, physico-chemical properties or predation levels (e.g., Quinn & Kojis 1997, 2003; Meggs 2006; Jaimes et al., 2016). Maximum settlements are observed more frequently in (i) the summer season, depending on the hemisphere; (ii) on nights with a new moon (low light); and (iii) at the surface level of water, approximately at 1.0 atmosphere of pressure. They are also linked to complex benthic structures such as seagrass, macroalgae or mangrove areas, as well as to preferences caused by the multiple physico-chemical signals that the post-larva detects. However, the PLS is also observed, though in lower levels, under contrasting conditions to these described above, i.e., the post-larvae can also enter the coastal areas at daylight hours, in other lunar phases, at up to 4.0 atmospheres of pressure (depths of 30 m), in other seasons of the year, and in areas with structurally fairly simpler bottoms (e.g., mud or sand). These reports are consistent in every area of study, which allows us to associate them with 'common' situations. Null records of settlements are associated with the limits of post-larval survival; for instance, it is well known from experimentation that post-larvae die at temperatures below 20ºC or above 30ºC (Litle jr 1977; Field & Butler IV 1994), as well as under salinities other than 35 ppm.

Similarly, no PLS has been observed in the vicinity or mouths of rivers (Goldtein & Butler VI 2009).

All these data have helped to generate models describing ecological patterns and predicting possible futures. From the perspective we wish to advance, though, that knowledge seems insufficient to answering/explain questions that arise from 'complex thinking': (i) how do post-larvae acquire the ability to 'understand' the immediate environment? (ii) What is their potential to respond to extraordinary events? (iii) How vulnerable will they be under those circumstances?

From an adaptive perspective, and following the current paradigms, it has been suggested that the high dispersion of lobster larvae and their subsequent arrival at the coast is the result of the dynamics in the coastal environment structure (e.g., seagrass beds can modify their distribution depending on time and intensity of hurricanes, or macroalgae meadows may vary in their distribution and abundance, depending on the season of the year) (e.g., Herrnkind & Butler IV 1986). The dispersed characteristic of post-larvae arrival increases the probability of them finding a suitable substrate which is heterogeneous and dynamic. The scientific literature has reported that it is possible to detect post-larval settlements in a very wide environmental range, covering almost any region on the continental shelf of the American Atlantic, with the limits associated with temperature and salinity. As mentioned above, some authors treat 'unusual' events as changes in the dominant mean values (e.g., temperatures of "unusual summers" as the determinant factor of decreases in settlement levels) (Littel jr 1997; Briones-Furzan et al., 2008).

More recent studies have indeed highlighted the 'autonomous capacity' of larvae and post-larvae as a characteristic that supposedly helps increasing the arrival success in suitable areas, that is, the settlement would not be a random phenomenon, but actually caused by an 'intention' in doing it; some authors (Phillips & Mcmillan 1987; Butler et al., 2009; Lecchini et al., 2010) suggest that *self-recruitment* (see glossary) is common and dependent on such an ability. Only passive displacements reduce connectivity and would decrease PLS probabilities, as we have already mentioned. The issue of the ‘common’ *vs* the ‘unusual’ in the settlement processes is not treated under the complex thinking framework in any study, beyond the investigations on the attempt to correlate environmental conditions with the observed patterns that favor or not the settlement mechanism/process. It is not discussed whether is the environmental conditions or the BSs themselves that are relevant or not in the potential to persist or in the adaptive capacity of this crustacean. Generally, PLS is explained indirectly as a consequence of the strength of selective forces.

Management and conservation

In terms of management of this organism as a resource, the search for regions that show the highest survival rates of juveniles and adults stands out, as the fishing industry depends on it. As we mentioned, the capacity of larvae and post-larvae to take an option has only recently started to be addressed. However, this latter development in the interpretation of the facts has not yet changed the views on ‘intentionality’ in the management of the lobster resource. There is still a widespread idea that areas with greater survival of juveniles and adults are the most suitable for their protection. This idea is supported by studies such as those of Lipcius et al. (1997), which classify places for conservation, depending on the supply of larvae and post-larvae arrival. In brief, regions/places where there is a high emigration of larvae due to a high number of breeding adults are called ‘source’ areas, whereas those places showing high post-larvae immigration, but with high mortality of juveniles and adults, are called ‘sink’ areas. Such a view implies that the design of Marine Protected Areas (MPAs) should be based on ‘source’ areas and connectivity, a trend that marks the direction of future studies and the destination of the greatest research effort towards conservation. From a classical evolutionary view, we can say that, for generations, the stochastic actions of the environment have selected those who have made this transition better, permanently adjusting the adaptive capacity of this lineage. That is why it is generally assumed that, where there are more juveniles or adults, they should be protected. As we mentioned earlier, this may be an incomplete view under the perspective we bring forward here.

Other ecological approaches propose possible MPAs based on the connectivity and persistence of the *metapopulation* structure and its relationship with the distribution or abundance of juveniles and/or adults. From a systemic thinking standpoint, these approaches have allowed a detailed knowledge on the behavior of this ontogenic phase in relation to the environment. However, a better understanding is yet needed on whether this process is maintained as such, or if it has been changed, in relation to how it functions. It is important to mention that no publication has reported investigation on whether there are ecological advantages for lobster in being a generalist, nor on the importance of it being an organism that explores so diverse environments throughout its ontogenetic development. There is no study on the possible effects of ‘unusual’ events on its potential ‘power’ to persist.

Post-larval settlement in Santa Marta, Colombia period (2002 - 2010)

Campaign A

The dependence of PLS levels in the Santa Marta (StM) region on large-scale environmental conditions, such as the Panama-Colombia eddy, or on local conditions, such as transparency and salinity, was described by Jaimes et al. (2016). Similar relationships were found in other regions of the Greater Caribbean and the Coasts of Brazil. However, the high PLS rates observed, when compared to those reported in the Greater Caribbean (SM-4), were not discussed. We believe that the numerous post-larval (PL) entries into the coastal zone observed from these data, which were not yet reported in the literature, may be related to an ‘inner-dependent’ issue.

It was previously suggested that the slope of sea floor might better explain the differences in settlement rates between stations, and so, possibly the high catch values in the region. However, the slope of the platform could only partially explain the differences between the five collection stations. According to the cluster analysis, stations E1 and E2, and E4 and E5, formed two groups clearly defined by their similarities in the slope value and settlement rates. However, the results from E3 departed from this pattern, as it presented a high slope (32.4%), but showed relatively low catches (21 PL . m^{-2} . month^{-1}) (Fig. 14). The data published in Jaimes et al. (2016) account for only two groups (E1, E2) and (E3, E4, E5) which shared similar physico-chemical conditions.

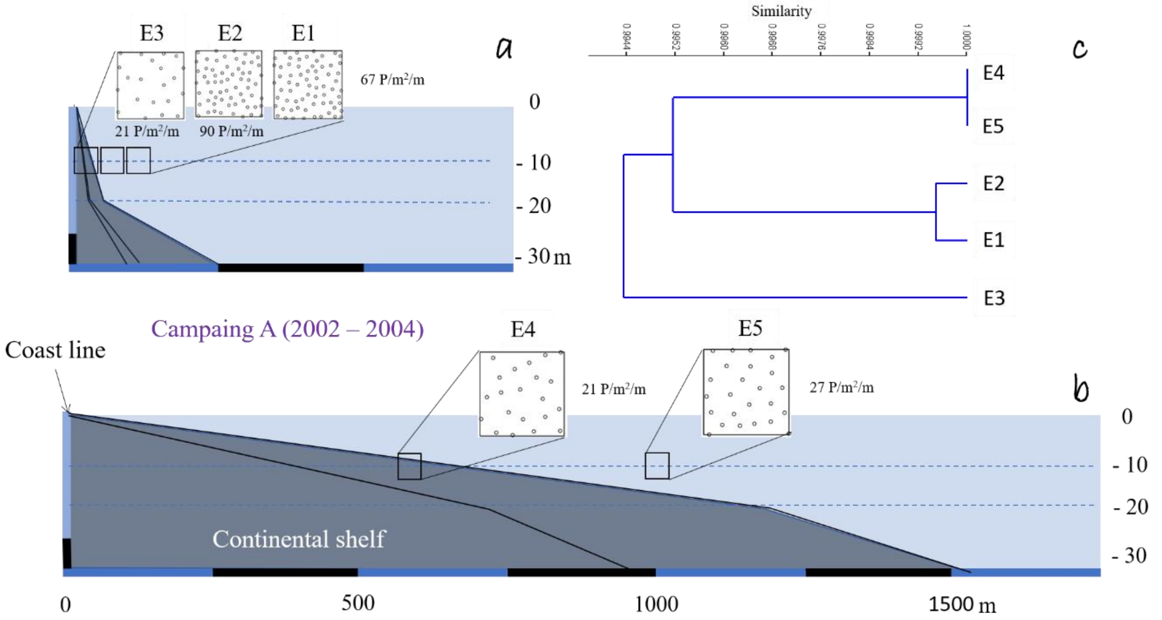

Figure 14:Graphical representation of the profiles on the continental shelf (slope) and post-larval settlement. Average values of the density of post-larvae (PL) trapped in the five sampling stations during campaign A. (a) E1, E2, E3, (b) E4, E5. (c) Cluster similarity analysis between the five stations, taking into account densities of capture, slopes, and extension of the platform. Data was expressed as average values of post-larvae (PL) per m2, per month.

From these results, we could suggest that conditions above or below a certain slope value of the platform might discourage post-larval settlement. However, E2 and E3 have similar slopes but their settlement rates were significantly different. It is possible that the slope might be one interfering factor that affects capture densities, but which could not explain alone the differences between nearby locations, or the high values reported for the region. For 16 months and at a depth between 10-11 m, a total of 8860 PL was captured, with an estimated average of 51 PL.m-^{2}.month^{-1} for the region. The E2 reached an average of 90 PL.m-^{2}.month^{-1} and the E3, E4, each with 21 PL.m^{-2}.month^{-1} (Fig. 14). As mentioned earlier, the high values obtained in this campaign were consistent with those from other regions of the Greater Caribbean. The seasonal behavior of the post-larval settlement and its possible links with nearby adult populations are discussed in Jaimes et al. (2016).

Campaign B

It was observed that consistently high catches of post-larvae were equally possible between depths of 4.5 and 15 m. In total, 10042 PL were collected in an effective area of 170.1 m^2 (E2 + E3), with an average value of 59 PL.m-^{2}.month^{-1}.

During this campaign, no significant differences were observed between capture values within the sampled area, neither by depth, nor horizontally, nor by type of collector. A tendency to catch a greater number of post-larvae as the collector deepens was noticed. (Fig. 15).

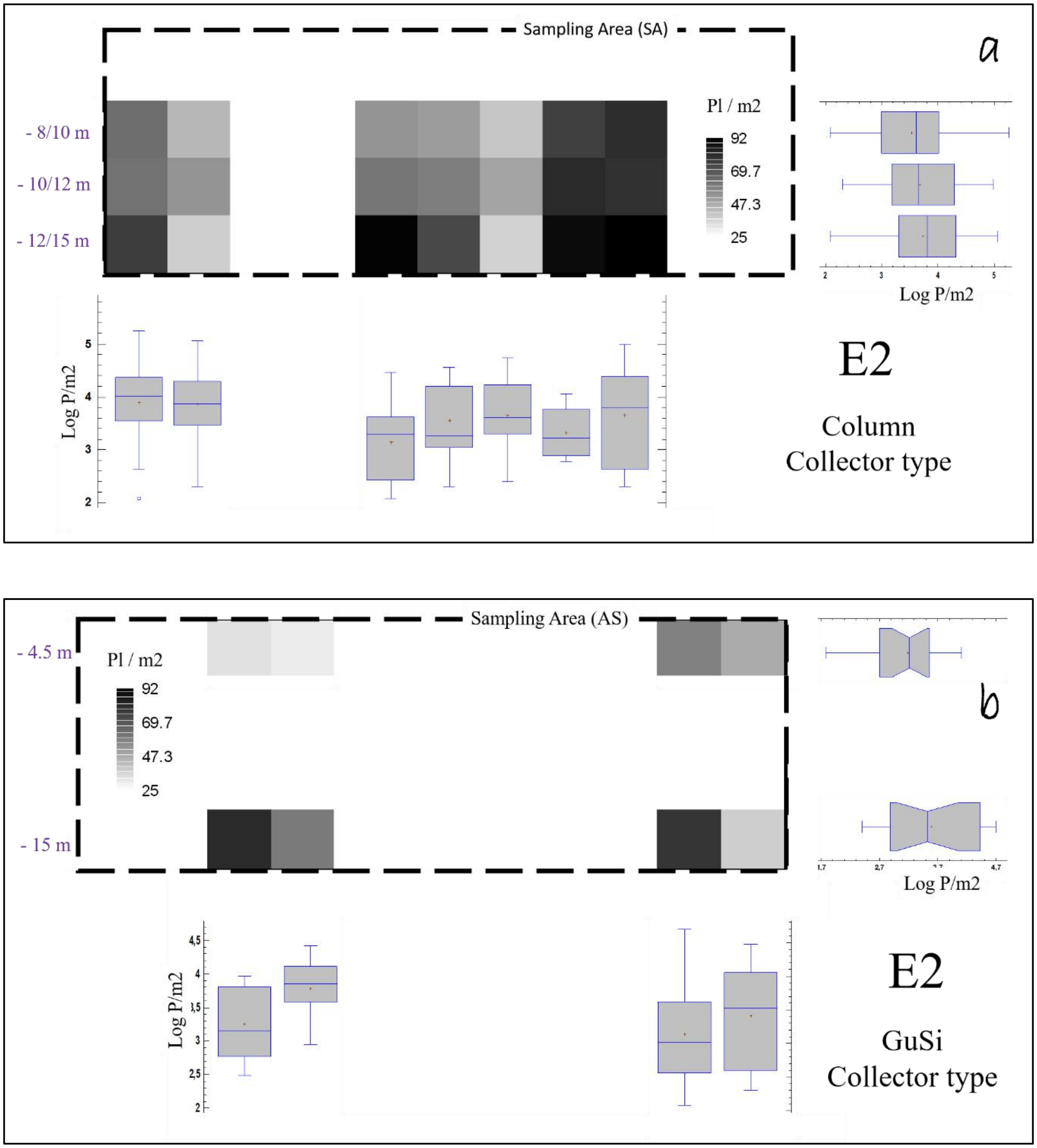

Figure 15:Post-larval settlement trends in E2 (PL . m^{-2}) during campaign B. The grayscale generated with Matrix Plot analysis shows the average density and trend of settlements in the sampling area. Boxplot analyses between collectors of the same type, which were compared horizontally and vertically, show that in no case the disposition of the collector has significantly affected the capture. (a) E2 column collectors, (b) E2 GuSi collectors.

Having a horizontal extension of approximately 30 m (300 m^2), the E2 station collected a total of 8731 PL in an effective capture area of 135.8 m^2 for 10 months. The maximum estimated value was observed in April, at a depth of 15 m, and the minimum (5 PL.m^{-2}) in November, at a depth of 4.5 m. An average of post-larvae capture of 63 PL.m^{-2}.month^{-1} was estimated (Fig. 16).

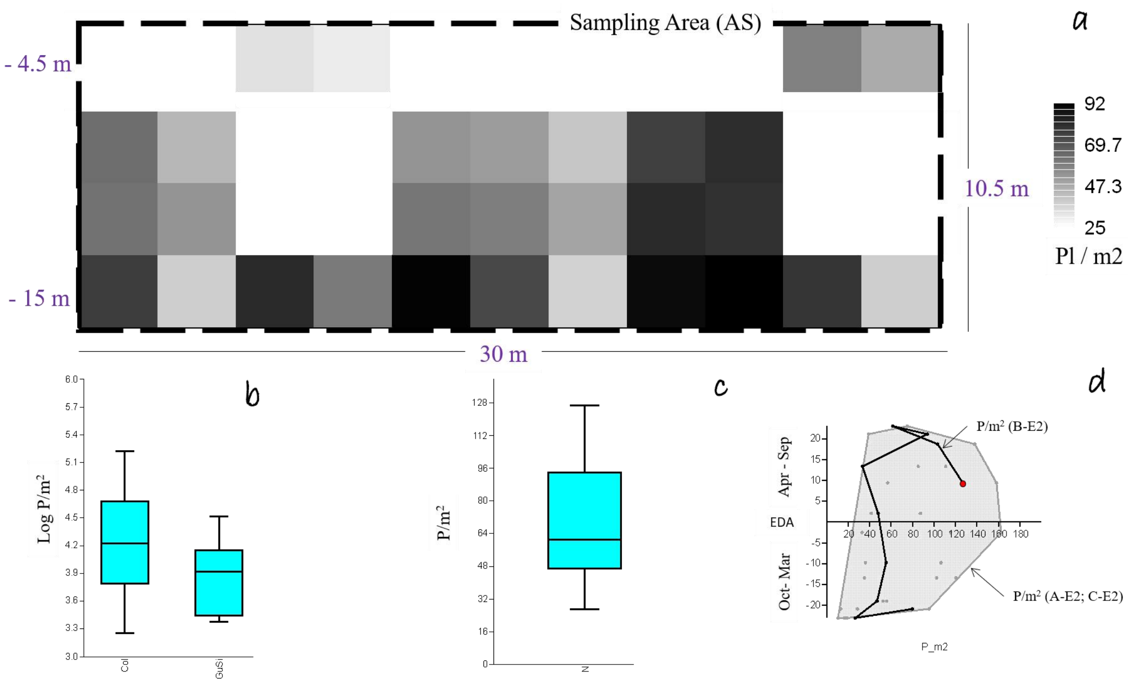

Figure 16:The density of settlement (PL . m^{-2}) in E2, during campaign B. The grayscale generated with Matrix-plot analysis (a) represents, in each of the coloured squares, the average density captured by the collector. The capture trend was observed within the sampling area. In relation to the Matrix-plot, the depths of the collectors are indicated on the left, the vertical distance of the SA on the right, and the horizontal distance of the SA at the base. The type of collector did not significantly affect the capture of pueruli (b), estimating an average value of 63 PL.m^{-2}.month^{-1} (c). The scatter plot between the 'earth decline angle' (EDA) and the capture densities (CD) (d) shows the trajectory of the settlements of the B-E2 campaign (black line), with the red dot marking the date when the collection campaign has started; using the 'Convex hull' option in the PAST software, a gray polygon was generated, with the extreme values being the correlations between the EDA vs CD variables of the A-E2, C-E2 campaigns.

Consistently high catches were also observed in E3, with a total of 1311 PL collected in an effective capture area of 22.6 m^2 for 6 months. The maximum estimated value was 179 PL.m^{-2}, at a 15-m deep site in November, and the minimum was 8 PL.m^{-2} at a depth of 4.5 m in July. The average catch in this campaign was 39 PL.m^{-2}.month^{-1}.

The spatial pattern observed in E3 was more dispersed, without differences between collectors and depth. The temporal variation in this campaign showed a trend similar to campaign A, that is, the highest values were generally achieved between April and September.

Campaign C

During this period, in E2, at a shallow depth of 1 – 3 m, a total of 1467 PL were captured in an effective area of 35 m^2, over 9 months, with an average of 42 PL.m^{-2}.month^{-1}. Like the previous campaigns, the maximum counts were recorded between April and September, with the catches consistently staying at high levels (Fig. 17).

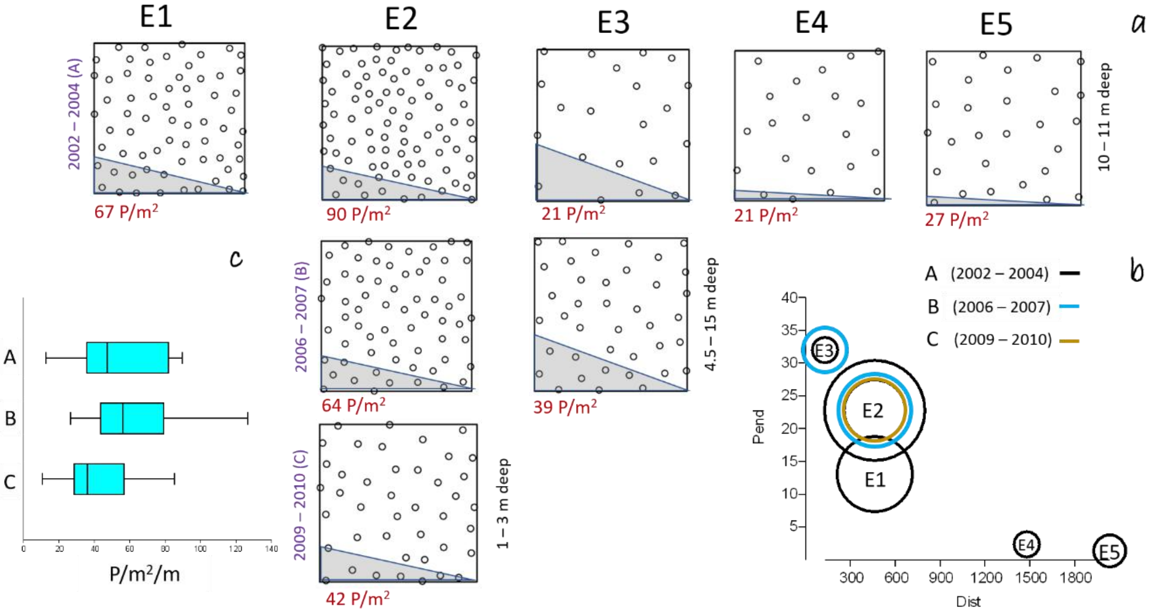

Figure 17:Graphical representation of the average capture value per m2 (squares) of post-larvae (white dots) in the StM region between the years 2002-2010. The relative slope of the platform is represented in gray located at the base of each square. The set of squares represents the average value of the capture density in the sampled stations, depending on the campaign; Campaign A: E1 to E5, Campaign B: E2 and E3, Campaign C: E2 (a). Bubble plot relating the slope of the continental shelf (vertical axis), the distance reached between the coastline and the 30-m isobath (horizontal axis) and average capture density at each station and in each sampling campaign (area and color of the circle) (b). Box-plot comparing the average capture densities of the three campaigns (c).

Taken together, the results of the three PL collection campaigns during the study period of 2002 – 2010 in the StM region showed that there was a massive post-larvae entry in that area, with significant differences between some nearby conditions caused by different seascape (e.g., slope of the platform, variations in the physico-chemical conditions, and the structure of the benthos – Jaimes et al., 2016). Such a massive entry of post-larvae, and the poor survival of juveniles and adults due to a scarcely suitable habitat, makes this a *sink* area. Temporary records show a unimodal trend, with significant fluctuations throughout the year, a general condition that coincides cyclically with the EDA period (Jaimes et al., 2016).

DISCUSSION

The 'unusual' and the 'common' in the environment

We consider that it is necessary to briefly describe some key events that have marked the historical development of the spiny lobster, aiming at clarifying about the ideas of common or unusual events as influencing its development. The movements of the planet and its position about the plane of the ecliptic (e.g. rotation, translation or declination angle), as well as the periodical influence of the moon that orbits the planet, are involved in determining the cyclicality of large-scale events. Thus, the variability in the light intensity, the effect of the moon's gravity, and the variation in the surface temperature of the planet, ultimately assemble the framework that structures the general climate of the planet. The seasons, ocean currents, hurricanes, tides or the direction and intensity of the winds are explained from there. Cyclical events, even those whose periods cover several years such as the 'El Niño' Southern Oscillation event (ENSO).

On the other hand, plate tectonics is a force whose dynamics have been structurally diversifying and influencing the origin, spatial arrangement, and geomorphology of the continents. The volcanism and earthquakes are dependent on it. In this case, the cyclicity of events in plate tectonics occurs in the sense of grouping and de-grouping the large plates' fragments, which give rise to, for example, the 'supercontinents'. Such a cyclicity can also be observed for example in the magnetic inversion of the planet. The conjugation of events like these, permanently generate and modify the multiplicity of landscapes and their climatic conditions on smaller, regional/local scales, which take part of the stochastic course of the living on the planet. The inclusion of BSs in this dynamics turns the environment even more diversified, thereby turning the underlying environmental cyclicality a lot more complex. The BSs enter the scene between 3,000 to 4,000 million years ago (m.y.a.) and, under that cyclicity and as new systems on Earth, were initially very much environment-dependent. The Eukaryotes are evidenced by about 1,500 m.y.a. (Zhu et al., 2016), time for adjustments and beginning of the process of mechanical ‘understanding’ of that environment. Another 900 m.y. pass to the first BS with neuronal tissue arise (Moroz 2015), what can be considered a ‘substantial improvement’ in the possibility to ‘feel’ the environment. This suggests that the ability of a BS to internalize information from its immediate environment (IE) and, at the same time, increase its complexity, seems a relatively slow process in its beginnings, marked by cyclical events that provide *information* to the systems. Since to date, evolutionary history has experienced five mass extinctions, we can think on it as a ‘common event’ in the largest possible scale of BSs on Earth; what would not be common (the ‘unusual’) is the *origin* of some of these events (Bond & Grasby 2017), e.g., the origin of the currently undergoing, anthropic-derived sixth mass extinction.

Lobsters arose about 350 m.y.a (Tsang et al., 2008; Wolfe et al., 2018), on the eve of the Pangea formation, which also agrees with the Devonian extinction. To date, the evolutionary trajectory of lobsters has experienced three mass extinctions and now is facing a fourth. Today, the families Nophropidae, Palinuridae and Scyllaridae together have 161 species reported and their ontogenic developments cover a wide variety of environments on the planet (Holthuis, 1981; Phillips, 2006). These particularities, plus the environmental conditions in which lobsters strive, suggest them as BSs that may possess a higher capacity to be ‘less surprised’, i.e., they would be more ‘experts’ and, as such, would display a higher capacity to persist. The success of an early developmental stage that is quite complex and widely distributed geographically may well be a consequence of a deep ‘knowledge’ that lobsters may have accumulated throughout evolution about their IE. Said in a different manner, this would be that complexity, cognition and I.I. expressed in ontogenetic development can be a characteristic of BSs that has overcome multiple rare events throughout its (evolutionary) history. This idea fits well with studies of Balmford (1996) and Betts et al. (2019), who talk about *environmental filters* and their impact on the more likely persistence of organisms that descend from those that had 'experienced' exposition to harsher environments. Currently, like all the BSs of the planet, lobsters are facing a novel mass extinction; here comes the ability of a BS to 'solve problems' of their IE, which would be supported by the history of the underlying cyclical events. Such an idea finds further support in the work of Lalana (2015) and Adami (2012).

The 'unusual' and the 'common' in the post-larval settlement

The postlarval settlement (PLS) of this crustacean occurs permanently and simultaneously over a wide area of the continental shelf of the American Atlantic, between 32.30 N and 23.30 S, which includes islands separated from the continent by approximately 1400 km, e.g., Florida to Bermuda (Hateley & Sleeter 1993, Willian 1986). If we consider this current feature together with the evolutionary history briefly mentioned above, it is reasonable to ponder that lobsters have been building and adjusting what we call a *metapopulation*; such a condition relies on the connectivity and its probability (Koug 2014, Riveiro 2017; Lisel et al., 2018), which would be translated in *complex thinking* as the 'accumulated ability' to 'communicate' and exchange information between the members of the component populations. Therefore, we could say that modifications in the direction of ocean and air currents, changes in temperature, structure dynamics and morphology of the benthos, or even the hurricanes, all may have been contributing a great deal to a variety of conditions against which the lobsters have been exposed to, which, in turn, would potentiate their persistence capacity. We intuit that these organisms, having such an 'extensive experience', may bear a greater capacity (expressed in multiple forms) of *reacting* to unusual events (e.g., their higher capacity to face emerging diseases such as that caused by PaV1 virus, whose survival ability as a populational system can consist in the 'collective detection' of affected individuals, followed by their collective 'rejection' (Butler, 2008; Lozano-Álvarez et al., 2008). Such an intrinsic condition of the species would be of great value, as it would not be easy to 'surprise' it with rare events of great magnitude. It is very important to mention, however, that bearing more of such an emerging property does not mean that the species is ‘extinction-proof’; we want to simply imply that, in their case, there might exist a relatively greater ‘persistence power’, supported by an acquired higher ability to manipulate (internalize and integrate), generate and share *information*.

When we refer to the concept/idea of *information* in complex thinking (see Chapter 2), it is important to highlight that it would not only be related to the potential that BS has in its genetic constitution and/or physiological plasticity, or other types of traits recently investigated (e.g., epigenetics, hologenomics); we are also referring to that *information* that can generate ‘subjectivity’ (*cognition*), that is, that emerging property of being able to ‘make choices’. In the context of scientific research currently available for lobsters, with the data published so far, we acknowledge that it has been difficult to detect unusual events during PLS. Those that describe contrasting conditions such as captures of pueruli at depths of more than 20 m (Heatwole et al., 1991), maybe events that occasionally happen, and so, are not that rare. We base this argument on the fact that settlement in these periods or conditions has been consistently occurring, not being therefore an unusual matter. Under these circumstances, rare events could let us be able to capture pueruli in waters of very low salinity or with temperatures below 20^{o}C, which would indicate they have been exposed to such out-of-limits, never-faced conditions. The wide variety of conditions under which PLS can be observed can reflect a large number of ‘choice’ possibilities at the time of settlement. Hodin et al. (2017) described it as the ability to simultaneously and hierarchically integrate information, with different arrangements, which would allow the pueruli to recognize and reach settlement areas. Hinojosa et al. (2016) suggest that same environmental conditions may, or may not, favor settlement in different regions, a panorama that would highlight the great *plasticity* in recognizing signals and ‘taking options’ among moments that the lobster BS ‘feels’ all the time.

Pueruli of other palinurids have been captured at a distance from the coastline, between 20 and 200 km. These distances may well exceed the range of some possible signals coming from the coast (e.g., sounds go up to 40 km;

chemical signals, can reach up to approximately 50 km, etc.). On the other hand, other possible signals such as the reflection of the moon or daylight, or the magnetism are not affected by the distance to the coast. Thus, pueruli may have 'learned' to process a mixture of signals for their guidance (Jeff et al., 2001; 2005), an idea that fits well to the proposal of Hodin et al (2017) mentioned above. Another score to this view can come from the rationale on characteristics of the larval stage; initially, it was assumed that lobster larvae were passively dispersed through ocean currents, i.e., they did *not* have an *active* role in their dispersion and retention to their place of origin (Olvera & Ordoñez 1988), thereby limiting the phenomenon of *self-recruitment*. However, at the beginning of the century, it became clearer that self-recruitment could be a norm (Cowen et al., 2007). Butler IV et al. (2011) observed that, in most cases, dispersions failed to exceed 400 km away from the place of origin, thereby favoring self-recruitment. Bruce et al. (2007) observed that when distances greater than 1000 km were exceeded, the probability of return to any place on the original coast was significantly reduced. Therefore, the retention, importation and exportation of early stages of development are frequent mechanisms, each of which having possible advantages for the meta-population. Thus, local populations are maintained and information is imported and exported. In addition, it appears that there is a potential for the meta-population to explore new areas, as it has been shown by the presence of this species in the African continent, i.e., places about 2,650 km (Brazil - Canary Islands) and 4,350 km (Brazil - Porto Novo) apart from each other (Marchal 1967, Freitas & Castro 2005).

All these particularities can account for such a supposed ability achieved by this species that allows its members to explore new environments, thereby expanding its distribution, and so, reducing 'uncertainties' about their IE. In general, we can say that, frequently, the two mechanisms of dispersion and retention are fundamental parts of common behavior, which would make this species a BS with a relatively higher potential for persistence, despite the changes currently ongoing and expected to come for the marine environment.

The massive post-larval settlement

A common condition that usually occurs in the PLS is the gradual and individual entry that increases in a period of low night light. It has been estimated that, in a lunar month, 65% of the pueruli captured in the collectors correspond to the period between a ‘waning quarter’ and a ‘new moon’, and 25% of them enter the collecting stations between a new moon and a rising moon (Jaimes 2000); in other words, 90% of pueruli enter within a period not exceeding 15 days, matching to descriptions done by Littel Jr et al. (1997), Quinn & Kijos (1997), Gonzales & Wehrtmann, (2011). On the other hand, experimental and observational data show an *active swim* during only the first three days of the puerulus phase. It has also been observed that pueruli swim linearly with a relatively constant speed (7-10 cm/sec) and can hardly evade objects (Calinsk & Lyons, 1983, Butler & Herrnkind 1991, Goldtein & Butler IV 2009). These conditions suggest that the entry of post-larvae (i) can occur during a not so extensive time period and, as observed in the three collecting campaigns presented above, (ii) they can do so in large numbers in relatively small areas.

Hence, it is possible that such a massive recruitment event might not be so extraordinary, as a supposed result of a combination of rare conditions. Alternatively, it is possible to think that in areas such as those of Puerto Morelos in Mexico (Briones-Fourzán et al., 2008), this event occurs because it has certain similarities with the areas studied in the Colombian Caribbean, which, in this case, can be related to environmental contexts such as geomorphology and oceanographic conditions. We believe that these massive arrival have not been detected in other places simply because it is assumed by the scientific community dealing with lobsters (an assumption most likely due to the interpretation of the results obtained from the sampling designs frequently employed) that the common thing to expect is that pueruli arrive progressively during a lunar month, on an individual basis, and that this behavior is dependent on the light intensity and/or other factors at the sea landscape level. In this sense, a different interpretation for these results (Figs. 5 and 8) can be here advanced. In other studies, a massive entry of post-larvae for other crustaceans has already been reported: in a relatively short period of 3 days, the entry of around 1000 post-larvae per m^2 has been estimated, which reach the coast and seek inland shelter (Hartnoll & Clark 2006). For lobster juveniles, a progressive *gregarious social behavior* has been noticed during growth, which was claimed as a possibility that allows an improvement of defenses against predators. Mass migrations are common in adult lobster populations and it seems to be initiated by a 'consensus'. Herrnkind & Mclean (1971) and Herrnkind & Kanciruk (1977) call it a *migratory restlessness* (or "zugunruhe"), caused by the increase in sociality among individuals, which is an apparently density-dependent issue. It has also been shown that this behavior correlates with some physico-chemical variables. Taken all these data/information together, a very likely explanation for such type of social/gregarious behavior is the phenomenon of *quorum sensing*: without mentioning 'complex thinking', this has been described as a 'strategy' based on signals (information?) detectable when the number of 'communicating individuals' reach a threshold, which allows the organisms to *take a collective decision*. Besides lobsters, other examples of *quorum sensing* have been already described in insects (e.g., Vissher, 2007), other species of a social nature, such as migratory birds (e.g. Conradt & Roper 2005), and in bacteria (Facua et al., 1994; Abisado et al., 2018).

The QS phenomenon is supported by the communication capacity among the population members. For instance, there is plenty of evidence for the ability of the post-larvae of this crustacean, and even of various other marine invertebrates, to generate a wide range of sounds (Coquereau et al., 2016a), as well as sensorial capacities for physico-chemical signals (Nishida, 2002). In adults of some palinurid and homarid species, that communicative capacity has been registered, but its ecological relevance is unknown; in general, they are frequently associated with improvement of defense, or feeding capacities. In studies such as those of Edmonds et al. (2016), noise pollution have been described as harmful to crustaceans, as they can interfere with communication behavior and physiology. Our results corroborated that post-larval entry may occur at relatively high densities, in a relatively short times, and over a relatively small horizontal extent. Further hypothesis-driven research are certainly warranted to in-depth address the possibility of QS ability being present at the time of post-larval settlement in this lobster species.

Reducing uncertainty

Assuming, at this point, a certain *capacity of choice* by the post-larvae as an emerging property derived from I.I. (Tononi, 2008), their settlement in a wide variety of marine landscapes and under various environmental circumstances gain a further layer of understanding. From such perspective, it appears not so unexpected that a large number of post-larvae arrive with sustained intensity over time in a place that offers little advantage for their survival. Indeed, the StM region is characterized by the absence of largely-extended seascapes of phanerogams or macroalgae, lack of mangrove, little representation of coral structures, with the sea floor mostly composed of sand or mud, with a platform that is not very extensive (Rojas et al., 1994; Invemar, 2005; Rubio-Polanía & Trujillo-Arcila, 2013). The bottomline would be that recognizing and reaching proper settlement areas as described by Hodin et al., (2018) is an expected feature of lobsters as BSs, but that same ability to I.I. from the environment can lead to different *choices* with *unusual* consequences. From the classical analytical/systemic view, the ‘unfortunate’ massive arrival of post-larvae to places like this would result in a high mortality rate. From a current conservation standpoint, the StM region would present the condition of a *sink* (Lipcius et al., 1997), being marked as an irrelevant place, due to its consequent low impact on the abundance or distribution of juveniles and adults, with little relevance for the persistence of this species.

The massive post-larval arrival here reported can be treated jointly with previous data by Jaimes et al. (2005), who recorded small numbers of surviving juveniles and adults in the StM region. Focusing on the idea of probability of survivors that can reach the adult, reproductive stage, another perspective can be put forward. We intuit that these survivor individuals (originated from a large population of arriving post-larvae) may give an account of developmental circumstances that are quite limited in resources, space, protection, mobility, etc., which are ‘problems’ that are to be faced all the time on that type of environment. That is, it would not be the same type of information processing to reach conditions where the risk of death is lower (e.g., coastal areas with diverse and abundant seascapes with a broad representation of seagrass or macroalgae) in relation to reaching conditions where the risk of death is higher (e.g., structurally simple coastal areas such as those composed of soft bottoms). Catches of juveniles and adults in sandy bottoms (Jaimes et al., 2005) indicate the crossing of these individuals through places where they are quite vulnerable; therefore, the likelihood of running into rare events may be higher in areas like these, which are information likely to be ‘stored’ to allow ‘reduction of uncertainty’ by the BS about the IE. We suggest that the massive entry of post-larvae to those extreme conditions propitiate a particular process of selection at the meta-population level, as mentioned above. Hence, under this point of view of ‘preserving previous experiences’ by the BSs, marginal areas should also be considered for protective actions, in an integrative manner with those source/biodiversity rich ones. The importance of *sink* places like these would be supported by the idea that the so called ‘peripheral populations’ in those areas would increase the likelihood of running into rare events, and so, incorporating new information into the BS. From this perspective, the idea of monotonous and unusual information (Chapter 2) can be better observed in meta-population organizations such as this.

What should we preserve?

About management strategies, efforts generally do not focus on peripheral populations, which are characterized, in this study, by having few juveniles or adults dispersed due to settings-dependent conditions that limit their survival. Due to these marginal areas being considered irrelevant, with impact on fisheries being negligible, such a perspective tends to result in the eligibility of research projects, which, in general, rely on the most common conditions, or on finding out how adverse conditions affect an ‘ideal’ condition. It is assumed within the management plans that areas with greater environmental stability, i.e., with no significant variations in physical, chemical, structural or functional conditions, are the most suitable for maintaining a species, population or community. In fact, under stable conditions, BSs generally evidence in the wide distribution, abundance or reproducibility. Similarly, at the community level, high diversity is associated with these conditions, a perspective that has led to the protection of these areas. However, recently isolated areas are beginning to be defended by highlighting their contribution to biodiversity (Wintle et al., 2019), but not yet because of their extreme condition value within the environmental variability and contribution with new information to BSs.

Connectivity between populations is very important and genetic studies have highlighted the importance of the link between populations (gene flow) via larval dispersion (Truelove et al., 2014) and its application to the design of MPAs. However, these links are highlighted only on source populations, or where they are better represented, or with less risk of local extinction. It is assumed that areas where populations are more representative are the most suitable for preservation because they will ensure greater persistence of BSs. A contradictory issue in this case is that it is assumed that the exchange of information is essential, but the focus remain only on the most 'common', dismissing the rare or unusual. It is true, though, that in organisms of wide distribution (the *generalists*, as in the case of lobsters), it is more difficult to detect unusual events in the PLS process. However, we suspect that it may be more likely to detect the 'unusual' more easily in peripheral populations. We can argue that anthropic actions (depending on the type and frequency) can generate unusual events and, as such, can act as 'filters' for BSs with greater potential to manipulate information.

There is still a lot of empirical and theoretical work that allows us to better defend the idea of rare events as important ones for the generation of the *ability to persist*, from a BS standpoint. We see it important to open lines of research that offer us a broader picture of issues in BSs such as the 'power of choice' and the ability of 'not to be surprised'. From a complex thinking framework, we assume the position that BSs by nature tend to 'reduce their uncertainty' about their IE, with the incorporation of mechanisms that allow ‘manipulating information’ by the BS can be more frequently generated in peripheral populations.

CONCLUSIONS

Global cyclic events have allowed BSs such as lobsters to have a better ‘perception’ of the environment. Common or repetitive events (e.g., lunar cycles, seasons of the year, etc.) and unexpected events (e.g., the origin of mass extinctions) may have allowed them to enhance their persistence through the emerging property of I.I. (i.e., ‘cognition’). For 350 m.y.a., lobsters have been *internalizing the dynamics* of their IE and constantly updating their intrinsic *predictive models*. Their complex ontogenic development may be a reflection of these emerging properties and mechanisms.

On the other hand, the loss of cyclicity in environmental events can be represented by, for example, (i) the sustained and increasing introduction of chemical and toxic substances into the marine environment, (ii) the excessive release of CO_2 by fossil combustion into the atmosphere, and in general, by any human activity of a non-cyclical nature, such as (iii) agricultural production, (iv) extraction of parental populations with great reproductive potential, (v) loss of breeding areas for youth population, etc. These are possibly generating a greater and intense sequence of rare events, with significant modification of the IE variables related to BSs. The *new information* that a BS can incorporate, as we are addressing them, come from those unusual events. In long-standing evolutionary stories, as in the case of lobster, unusual events are difficult to identify. Thus, the effort to investigate a progressive weakening of a *generalist* BS would be better of focusing on *peripheral populations*. We believe that permanent local extinctions of peripheral populations, and consequently the *loss of information exchange with other populations*, may have the power to weaken the meta-population. From the points of view of *information* and the *ability of reducing uncertainty*, that idea is suggests that the supporting stands that sustain the BSs adaptability and persistence would be lost. If more facts are found that further demonstrate the importance of these peripheral populations for the persistence of the meta-population, then the protection of these areas might be included as also a priority.

Particularly in the PLS, the great *plasticity* in the 'choice of places' to continue developing may be considered as an indication of a significant capacity to interpret the IE. However, the results obtained of a massive entry of post-larvae to coastal areas so apparently inappropriate, as well as the possible mechanisms that cause them and their possible consequences in the persistence of this crustacean, require more detailed studies to clarify several related issues.

The ontogenic cycle of this organism and its evolutionary history make it a proper study model. It can help us understand how a living system through atypical experiences may be able to adapt to different environments. Although there is an important effort to understand the sensorial abilities and capacities of these organisms affecting their behavior, other ecological matters such as their distribution, connectivity, persistence, ontogenetic development and diversification, are yet of limited knowledge.

The unusual events and their perception in permanent and immediate operation are the framework that allow I.I. by a BS and updates on their intrinsic *predictive models*. Although the *matter* and *energy* in limited space-time generate the physical framework where BSs can develop, adapt and persist, it is the *information* and its flux within BSs, and between them and their IE, that generates *choices* (subjectivity), a force that would also has the 'power of cause' in varying environments.

The 'common' and the 'rare' are complementary and simultaneous; it may be more comprehensive to observe the BSs not only from dominant condition, as this may be transient. It will likely be more advantageous to observed them as a whole, as fractionation is not appropriate in complex thinking.

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SUPLEMENTARY MATERIAL

CHAPER I

Sm 1: Symbionts (bacteria are not included) and lobster species (Palinuridae, Nophrophidae and Scyllaridae families) reported in the review studies conducted between the 70s and the year 2014, (Fisher 1977; Fisher et al., 1978; Johoson 1983; Stewart 1984; Fisher 1988; Getchell 1989; Abraham et al., 1996; Martin & Hose 1999; Evans et al., 2000; Stentiford & Shields 2005; Shields et al., 2006; Vogan et al., 2008; Stentiford & Neil 2011; Shield 2011; Behringer et al., 2011; Behringer et al., 2012; Small et al., 2012; Shields 2013; Tietjen 2014).

Host

Paniluridae	*Panulirus argus*
	Panulirus cygnus
	Panulirus interruptus
	Panulirus japonicus
	Panulirus longipes
	Panulirus ornatus
	Panulirus penicillatus
	Panulirus polyphagus
	Panulirus versicolor
	Panulirus vulgaris
	Jasus verreauxi
	Jasus edwardsii
	Palinurus elephas
Nephrophidae	*Homarus americanus*
	Homarus gammarus
	Homarus vulgaris
	Metanephrops andamanicus
	Metanephrops boschmai
	Metanephrops challengeri
	Metanephrops japonicus
	Metanephrops sagamiensis
	Metanephrops sibogae
	Metanephrops sinensis
	Metanephrops velutinus
	Nephrops norvegicus
Scyllaridae	*Thenus orientalis*
	Scyllarides spp.

Symbiotns

Kingdom	Grupo	# sp.
Animalia	Cestoda	1
	Helminths	1
	Poliqueta	1
	Cicloforo	2
	Nematode	2
	Isopod	3
	Nemertes	3
	Amphipods	4
	Trematoda and other worm	4
	Cirripedio	6
	Copepods	10
Chromista	Alveolata	1
	Bacillariophyta	1
	Other phototropics	4
	Oomycetes	5
	Ciliophora	10
Fungi	Deuteromycetes	1
	Opisthokonta	1
	Ascomycota	2
	Microsporidia	2
	Other fungi	2
Protozoa	Amoebozoa	2
	Bacillariophyta	1
	Other Protozoa	4
Viruses	PaV1 / WSSV	2

Sm 2: Terms of inclusion and exclusion with which articles related to the bacterial communities present in lobsters were selected.

Inclusion	Title	Species related to the families Palinuridae, Scillaridae and Nephropidae, or ontogenic stages and tissues of lobsters.
	Methods	Investigation wiht any method, isolate and identify bacteria from any lobster tissue or fluid. Investigation wiht live lobsters.
	Other documents	Three chapters focused on diseases and pathogens present in lobsters and two articles in Spanish.
Exclusion	*Reports, thesis, news, projects, conferences, posters, dissertation, books, book chapters, working meeting, citations, workshop. *Other symbionts (viruses, protozoa, fungi, etc.) *Experiments where bacteria are inoculated and correlated with physiological or behavioral reactions *Antibacterial treatments (vaccines, pressure, temperature, etc.) * Except for those articles that partially inform the origin of isolated bacteria (e.g. Zha et al., 2018), with limited access to supplementary material (e.g. Zha et al., 2019), infectious post-capture conditions (e.g. Ridgway et al., 2007), have higher bacterial levels or unclear data (e.g. Ooi et al., 2017).	

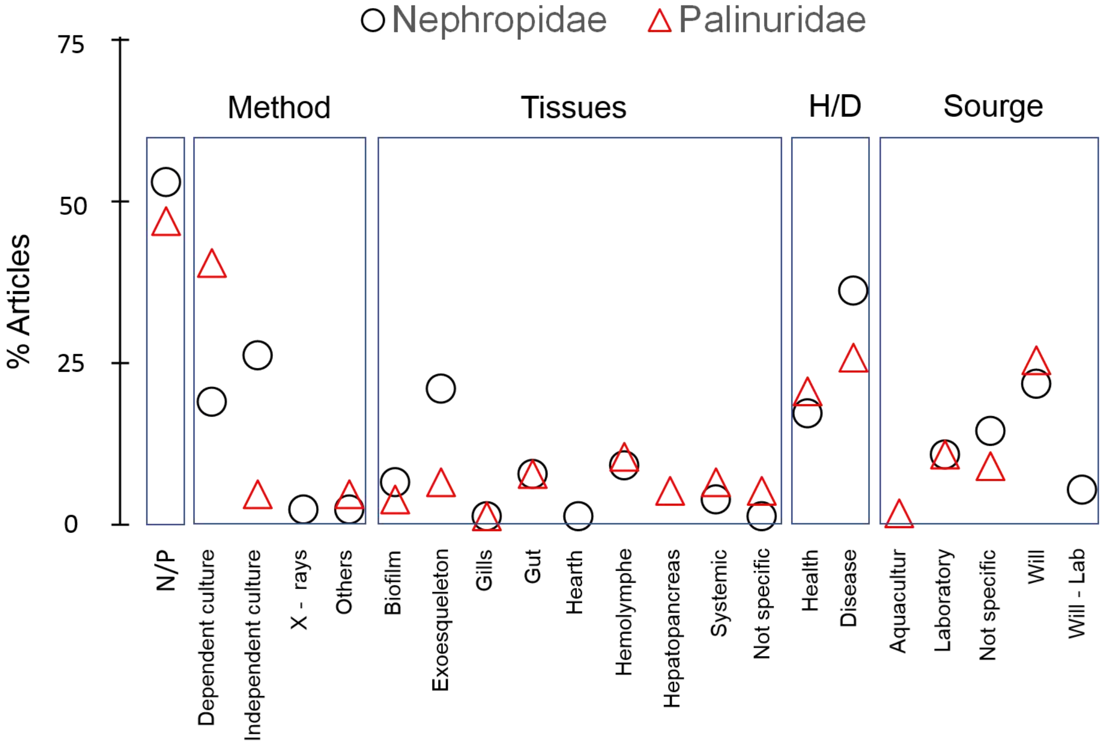
Sm 3: Bibliographic references used for the characterization of the bacterial structure present in the families Nephropidae and Palinuridae.

Sm 4: Data-base. The table in Excel that relates the characteristics of the lobsters (identity and condition) with the species of bacteria isolated from different tissues and ontogenetic states of the lobsters. Includes reference and year of publication.

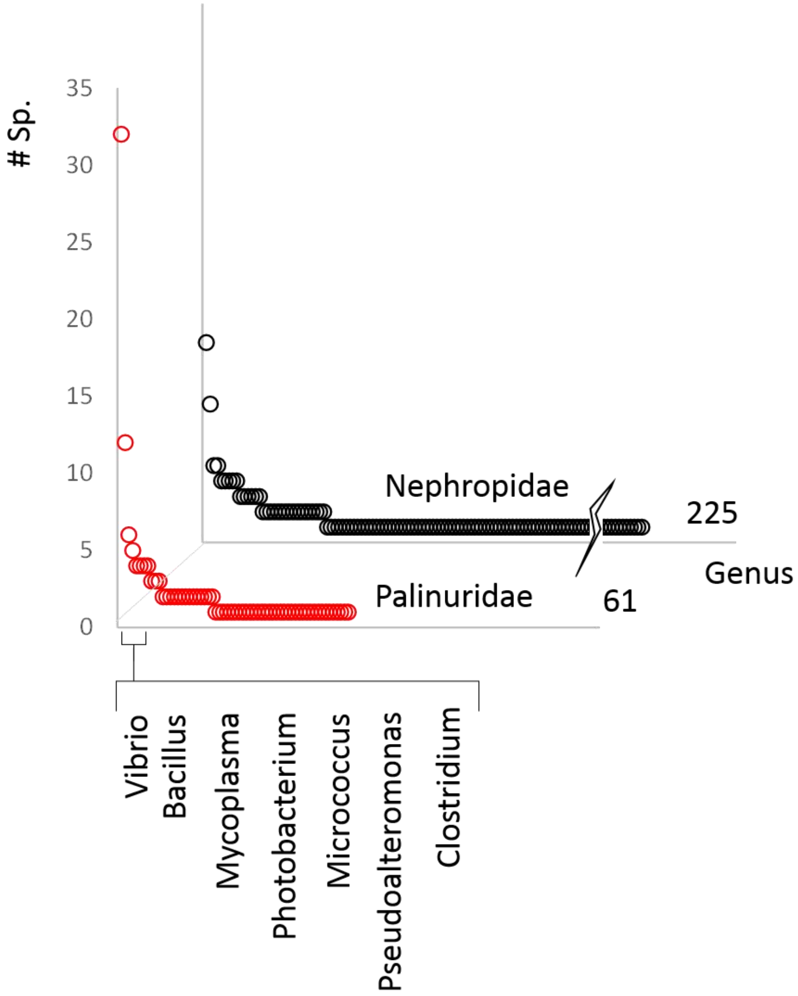
Phylla	Classe	Family	Genera	Specie
Proteobacteria	Gammaproteobacteria	Shewanellaceae	*Shewanella*	
		Thiotrichaceae	*Leucothrix*	
		Pseudoalteromonadaceae	*Pseudoalteromonas*	
		Pseudomonadaceae	*Pseudomonas*	
		Aeromonadaceae	Unclassified	
		Alteromonadaceae		
		Cardiobacteriaceae		
		Enterobacteriaceae		
		Vibrionaceae		
	Alphaproteobacteria	Cohaesibacteraceae		
		Hyphomicrobiaceae		
		Rhodobacteraceae		
	Deltaproteobacteria	Nannocystaceae		
	Epsilonproteobacteria	Flavobacteriaceae		
FCB group (Bacteriodetes)	Flavobacteriia	Flavobacteriaceae		
		Unclassified		
	Bacteroidia	Bacteroidaceae		
	Sphingobacteriia			
Actinobacteria	Acidimicrobiia	Acidimicrobineae		
		Corynebacterineae		
Chloroflexi	Caldilineae	Caldilineaceae		
Firmicutes	Bacilli	Pasteuriaceae		
		Bacillaceae		
Tenericutes	Mollicutes			
Planctomycetes				

Sm 5: Minimum taxonomic levels, where unclassified specimens are recorded.

Figures Material supplementary



Sm 6: Percentage of research articles done in lobsters of the families Nephropidae (N) and Palinuridae (P) by category. the terms described in the x-axis belong to those used in the articles which were part of this revision.



Sm 7: The richness of genera of bacteria present in the two lobster families. It highlights only the first seven bacterial genera.

Sm 8: The table in Excel that relates the isolation and identification technique, Dependent culture (Dc) or Independent culture (DId). Include references.

CHAPER III

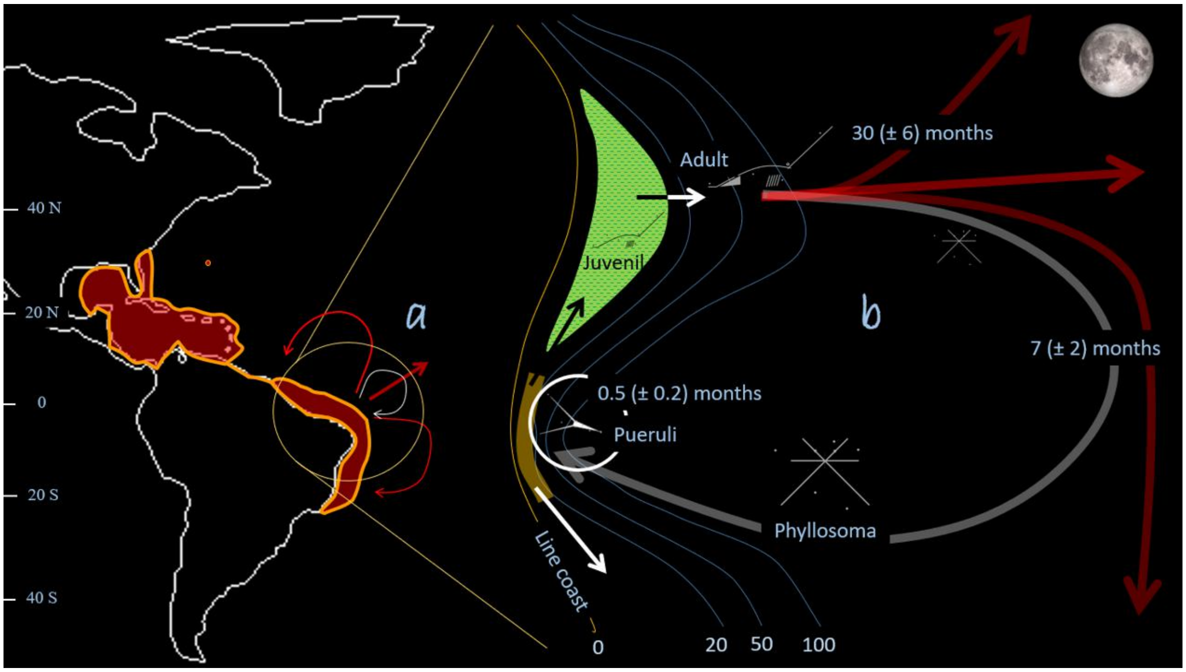
Sm 9: Excel table showing all the selected publications taking into account the selection and exclusion criteria. The table allows, through filters, to select the types of documents that want to be included. (e.g., all articles that investigate pueruli or puerulos of Panuliris argus). References are included.

Inclusion	All article with the keywords “puerulus”, “postlarval”, “postlarvae”, “settlement”, “pueruli”, “puerulos” and the “lobster”, within the general text of the document.
Exclusion	Articles that focus on fauna associated with collectors Articles that focus on methods for post-larval collection Articles that focus on genus Puerulus Other crustacean or ontogenic development Articles not available on the internet Book chapters, News letrer, Reports, thesis, workshop, citations.

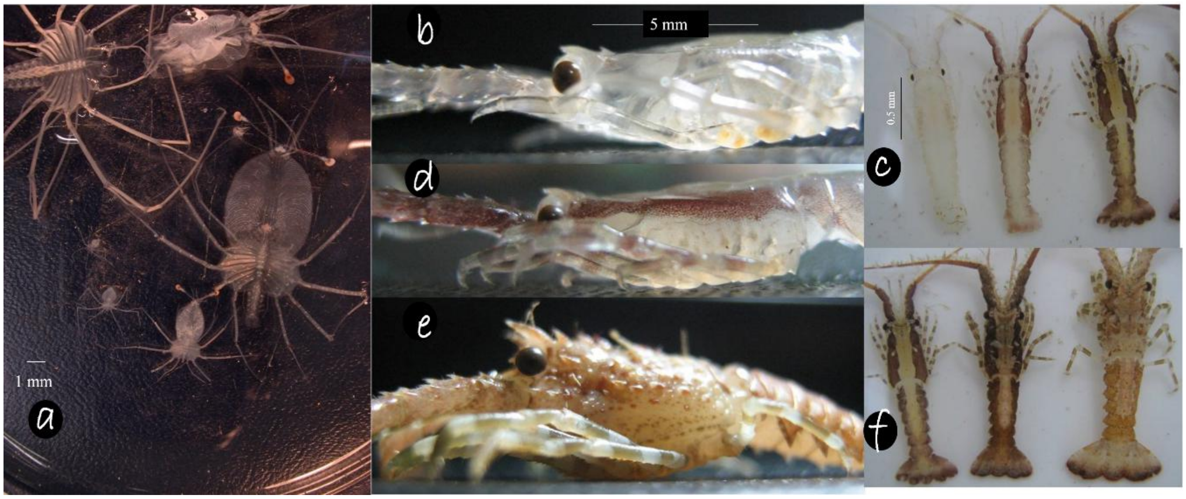
Sm 10: Terms of inclusion and exclusion with which articles related to the postlarval settlement in *Panulirus argus* were selected.

Sm 11Bibliographic references used for the characterization of the rare and common events observed during the post-larval settlement in *Panulirus argus*

Sm 12: Data-base. The table in Excel. Data collected from the settlement in the region of Santa Marta Colombia. It relates to time (2002 - 2010), locations, pending of shelf, and post-larvae density per square meter.



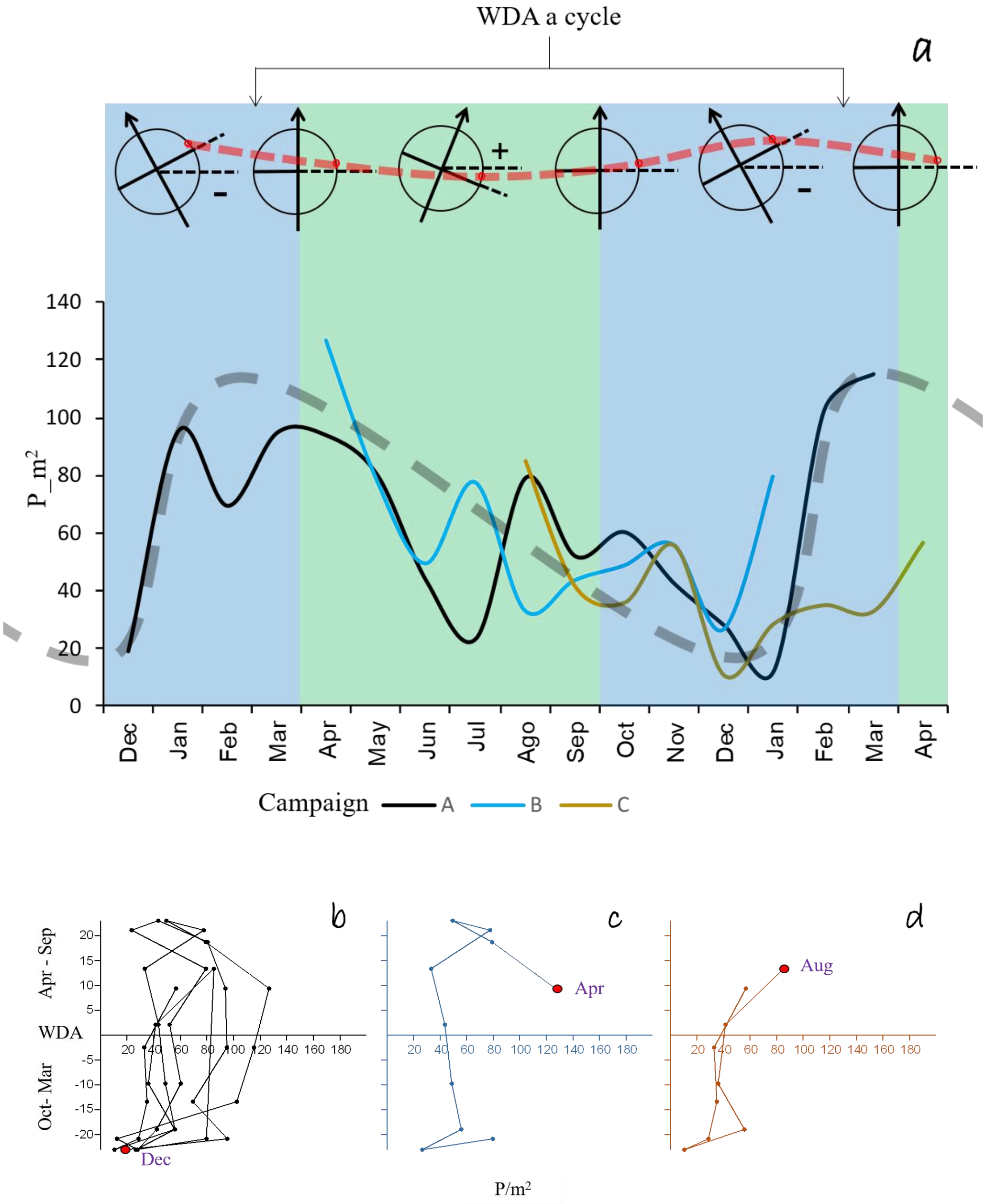
Sm 13:Diagram of the area of distribution in the American continent and general scheme of the life cycle of P. argus. (a) Representation of possible movements of the larvae depending on the oceanographic conditions and place of birth. White arrow, self-recruitment. Red arrows, possible dispersion directions. (b) Stages of ontogenetic development, residence times and areas where it occurs. The moonlight reflection marks the possible displacements (vertical or horizontal) observed throughout the development of the lobster (negative phototropism). In the white circle the pueruli phase.



Sm 14:Larvae and postlarval of Palinuridae. (a) Phillosomas of P. gracilis. (b) Pueruli in its transparent phase, a moment that can last about three days from the metamorphosis (phyllosoma - pueruli), has an active directed swim. (d) the pigmented phase of the pueruli, its swimming activity decreases, it can last between four or five days. (c) Puerulus in its pigmentation process between 8 to 10 days. (e, f) Post-puerulus or early juvenile phase, morphologically similar to adults. Photos: Juan C. Jaimes M.

Localidad	Ip	Profundidad	Referencia
Bermudas (USA)	1.5		Ward, 1989
Cayos de la Florida (USA)	5.4	1,5 - 3 m	Little y Milano, 1980
Matias (Cuba)	18.8	1 m	Cruz, 2000
Hicacos (Cuba)	26.3	1- 3 m	Cruz, 2000
Cantiles (Cuba)	9.2	1- 3 m	Cruz, 2000
Bocas de alonso (Cuba)	1.2	1- 3 m	Cruz, 2000
Bahía Ascención (México)	1,5 - 5,51	1 - 2,5 m	Briones *et al*., 2000
Puerto Morelos (México)	9,8 - 28,0	1 - 2,5 m	Briones *et al*., 2000
St. Thomas, Islas Virgenes (USA)	1.09		Kojis *et al.* , 2003
St. Thomas, Islas Virgenes (USA)	0.07		Gordon y Vasques, 2006
Antigua	9.3		Bannerot *et al*., 1992
Jamaica	3		Young, 1991
Isla de Providencia (Colombia)	7.1	5 - 7 m	Jaimes, 2000
Puerto Rico	11.8		Monterrrosa, 1992
Parque Tayrona, Santa Marta (Colombia)	8.38	4 - 20 m	Cordoba, 1997
Fortaleza, (Brasil)	1.32	4 - 6 m	Conceicao *et al*., 1996
Bahia de Taganga Expuesto (Colombia)	63	10 - 11 m	Jaimes et al., 2016
Bahia de Taganga Protegido (Colombia)	47	10 - 11 m	Jaimes et al., 2016
Isla Pelícano (El Rodadero) (Colombia)	19	10 - 11 m	Jaimes et al., 2016
Punta Gloria (Colombia)	14	10 - 11 m	Jaimes et al., 2016
Pozos Colorados (Colombia)	15	10 - 11 m	Jaimes et al., 2016

Sm 15:Settlement values recorded in some regions of the Greater Caribbean



Sm 16:Temporal variation of settlement density (DS) in E2, during the three campaigns. (a) Linear representation of maximums and minimums in the DS. A World Decline Angle (WDA) cycle is represented at the top, the red dotted line marks the oscillation of the study region along a WDA cycle. The gray dotted line marks the trend of the DS along a WDA cycle. (b) The trajectory of the DS observed in campaign A. (C) Trajectory of the DS observed in campaign B. (d) Trajectory of the DS observed in campaign C. the red dot marks the beginning (month) of the season.