



Influence of Environmental Factors on Nutritional Condition of Spiny Lobster *Panulirus argus* (Decapoda: Palinuridae)

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Received: 4 October 2022 / Revised: 17 March 2023 / Accepted: 20 March 2023
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Abstract

Environmental influence on lobster's physiology is a topic little addressed around the world. We determined the impact of biotic (food availability) and abiotic (temperature, salinity, and dissolved oxygen) environmental factors on nutritional condition of *Panulirus argus* (Latreille, 1804) from the Caibarien fishing region, Cuba. Eleven sites were sampled from 2010 to 2015, during dry and rainy seasons. Blood Refractive Index (BRI) and Kcl (total weight/carapace length) were used as nutritional condition indicators. Benthic food availability index (BFAI) was also determined. BRI and Kcl were both correlated with BFAI and varied significantly among sites and years. Salinity showed interannual differences, with lowest value in 2013. BFAI gradually increased between 2010 and 2015. Generalized Additive Model (GAM) for Kcl was 84.8% deviance explained ($R^2=77.6\%$), showing an environmental important influence on lobster's nutritional condition. "Site", dissolved oxygen, and BFAI had significant impacts on Kcl. GAM for BRI was 34.6% deviance explained ($R^2=25.3\%$), only salinity significantly impacted lobster's blood parameters. Environmental influence in lobster's nutritional condition was multifactorial and included biotic and abiotic variables. Food availability makes vary BRI and Kcl, nevertheless, they are both sensitive in different way to environmental factors and should have different interpretation.

Keywords Dissolved oxygen · Food availability impact · Natural habitat · Temperature

Introduction

The environmental influence on physiology of the spiny lobster *Panulirus argus* (Latreille 1804), in the natural habitat, is a topic little addressed around the world and not previously studied in Cuba, where coastal zones and marine ecosystems have been greatly impacted by natural and anthropogenic disturbances (González-Díaz 2015;

Mouso-Batista et al. 2019). Caibarien fishing region, in the central sector of the Sabana-Camagüey Archipelago (SCA), is considered the most anthropized area of Cuba (Baisre 1985; Lopeztegui-Castillo et al. 2021b), therefore biological communities are susceptible to several factors. The deterioration of benthic communities in this region may imply low water quality (García-García et al. 2008; Montalvo-Estévez et al. 2008; Álamo et al. 2013), and a decreased food availability, affecting the abundance, distribution, and physiology of lobsters.

Tourism development in the SCA has generated conflicts of interest and different levels of stress in the underwater platform and the keys, which adding to the effects of climate change have decreased biodiversity (Alcolado et al. 1999, 2007). Among natural environmental factors affecting this region extreme meteorological events like hurricanes have been mentioned (Fernández-Vila and Chirino-Núñez 1993; Betanzos-Vega et al. 2013). The SCA has been impacted directly or indirectly by 14 intensive hurricanes between 2001 and 2016, although the greatest and most recent impact was caused by Hurricane Irma, in September 2017

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(Fonseca-Rivera et al. 2020; Mitrani-Arenal et al. 2020; Lopeztegui-Castillo et al. 2021b).

Among the anthropogenic factors with the greatest influence, organic pollution, and eutrophication due to agriculture and the lack of waste treatment have been reported (Alcolado et al. 1999; Montalvo-Estévez et al. 2013, 2014). The destructive effect of trawl nets, the damming of rivers, and the construction of hotels and causeways have been also mentioned (Alcolado et al. 2007; Martínez-Daranas 2007). The naturally limited circulation of marine water and the high rate of evaporation, mainly in summer, adding to the scarcity of fresh water sources, give rise to high salinity values (Fernández-Vila and Chirino-Núñez 1993; Betanzos-Vega et al. 2013). This effect is intensified by the shallow depth (Betanzos-Vega et al. 2010, 2015).

Although some studies in this region have addressed aspects on relating environmental factors with abundance and distribution of marine species (Alcolado et al. 1998, 2007; Martínez-Daranas et al. 2021), the impact of the environmental stress on physiology of benthic organisms, is practically unknown. No environmental factors in the SCA have been related to lobster's nutritional condition, which is understood as the extent to which organisms have accumulated reserves to allow normal physiological function and growth (Moore et al. 2000).

Currently, several methods used to determine the nutritional condition of crustaceans provide evidence that standardization is needed to make results comparable among the increasing number of studies (Lopeztegui-Castillo 2021). The advantages and disadvantages of inexpensive and wide-ranging indices which could be applied in the field are discussed with respect to the blood refractive index (BRI) and the effectiveness of the Kcl index (total weight/carapace length relationship), remarking their importance as exposers of the actual lobster's nutritional condition (Lorenzon et al. 2011; Lopeztegui-Castillo 2021). Also, a decreased nutritional condition could cause declining immunological response and reproduction problems, both unfavorable effects for resources with a high commercial value. Understanding these aspects could help to clarify the effects of food availability and the variation of abiotic factors on the physiology and behavior of the lobster at any impacted region. This study aimed to determine the impact of biotic (food availability) and abiotic (temperature, salinity, and dissolved oxygen) environmental factors on the nutritional condition of spiny lobster *Panulirus argus* (Latreille 1804) from the Caibarien fishing region.

Materials and Methods

Study area and Sampling site's Location

The SCA extends for 465 km from the central (Punta Hicacos) to the east (Bahía Nuevitas) of the northern coast of Cuba. It is an area of 10,118 km², including 2,517 keys (60% of Cuban keys), with a total area of 3,400 km², and constitutes a natural barrier between oceanic and inner water, which 3 m average depth (Alcolado et al. 2007). In the Caibarien, central sector of the SCA, eleven sampling sites were established on soft bottom seagrasses, both near the platform edge and in inner waters. Average distance between adjacent sites was 12 km (Fig. 1).

Recently, an incipient recovery for zoobenthic community has been reported in a few places associated with local management measures (Lopeztegui-Castillo et al. 2021b). However, seagrasses and other marine ecosystems continue to be under considerable environmental stress, mainly due to coastal pollution, causeways, and the impact of bottom trawling nets (Martínez-Daranas et al. 2021).

Benthic food Availability Index

Food availability was estimated considering the relevance of benthic mollusks in the trophic spectrum of *P. argus* (Espinoza et al. 1990; Herrera et al. 1991; Lopeztegui-Castillo et al. 2021a; Martínez-Coello et al. 2015, 2022a, b). It was an index based on the assessment of the alive, shelled mollusks community from the soft bottom's benthos. Mollusks communities were sampled by dragging sediments with 4 mm mesh size of the dragged collector. Benthic Food Availability Index methodology, proposed by Lopeztegui-Castillo et al. (2021a), was used:

$$BFAI = \log_{10}(|\sqrt{S * D * B}|)$$

Where S: shell mollusk species number; D (ind/m²): shell mollusk density; B (g/m²): shell mollusk biomass.

Nutritional Condition Indices

Lobsters came from commercial catches and were captured in artificial shelters (casita), the same shelters used by the commercial fishery. Only lobsters having all appendages and without external signs of reproduction, molting or diseases were considered (Cruz et al. 1990; Cruz 2002). Immediately after lobsters were captured, hemolymph was extracted from the pericardial sinus using disposable 3 ml syringes. Lobsters were then sexed, measured, and weighed. Lobster's total body wet weight was measured with a technical scale (± 0.1 g). Carapace length was measured with

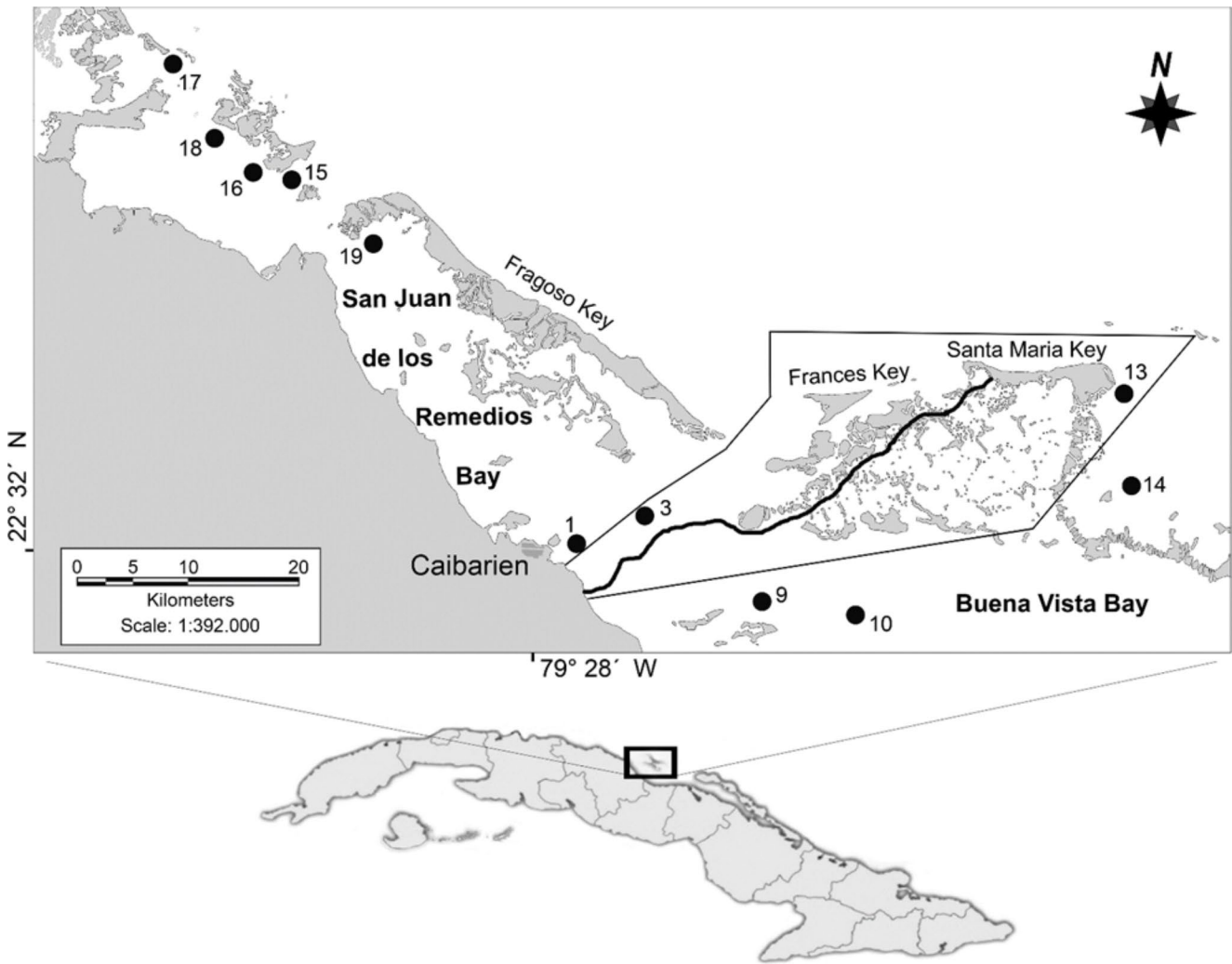


Fig. 1 Location of the study zone and the 11 sampling sites in lobster fishing area from Caibarien region, at a central sector of Sabana-Camagüey Archipelago

Vernier caliper (± 0.1 mm). The morphometric nutritional index $Kcl = \text{total weight} / \text{carapace length}$, and the analytic BRI (Blood Refractive Index) were determined. A hand-held Fisher Brix (0–50%) refractometer was used in natural environmental conditions for BRI measurements, following Lopeztegui-Castillo and Capetillo-Piñar (2021).

Temporal Analysis

Food availability (BFAI), nutritional condition indices (Kcl and BRI), and the abiotic variables (temperature, salinity, and dissolved oxygen), were determined one month during dry season (from November to April) and one month during rainy season (from May to October), during 2010, 2011, 2013 and 2015. Sites 1, 3, 9 and 10 were sampled from 2010 to 2015, remaining sites were sampled only in 2015.

Data Analysis

Shapiro-Wilks's test was used to corroborate non-normal distribution premises in analyzed variables, so non-parametric tests were applied. Abiotic variables (temperature, salinity, and dissolved oxygen) and food availability were compared among sites and years using the Kruskal-Wallis multiple comparison test by ranges. Paired comparisons (between dry and rainy seasons) were evaluated by using a Mann-Whitney U test. Variations in nutritional indices and environmental variables, as well as the relationship between them, were analyzed between 2010 and 2015.

Environmental variables correlated to nutritional condition morphophysiological indices were food availability (BFAI), temperature ($^{\circ}\text{C}$), salinity (‰), and dissolved oxygen (mg/L). The abiotic factors were measured by multiparameter Hanna HI-9828 probe, at the dredged sites around.

Lobsters for nutritional condition determination were caught no more than 4 km surrounded such dredged sites. The influence of environmental variables (predictor or independent variables) on nutritional condition indices (response or dependent variables) was quantified by Generalized Additive Models (GAM), applying a Gamma distribution with a logarithmic link function. Spearman correlation coefficient between nutritional indices and environmental variables was also calculated.

GAMs allow analysis of independent variables with non-linear effects on a dependent variable (Venables and Ripley 2004). Sites were also considered as a random component ("Site"). The appropriate additive model was chosen by visualizing the residuals graph and considering the Akaike Information Criteria (AICc) (Burnham and Anderson 2002). GAMs were run in R 4.1.0 free software platform (R Core Team 2021), using *mgcv* packages (Wood 2017) for adjusting the model and *MuMIn* (Barton 2020) to estimate AICc. When Shapiro-Wilk test identified that the

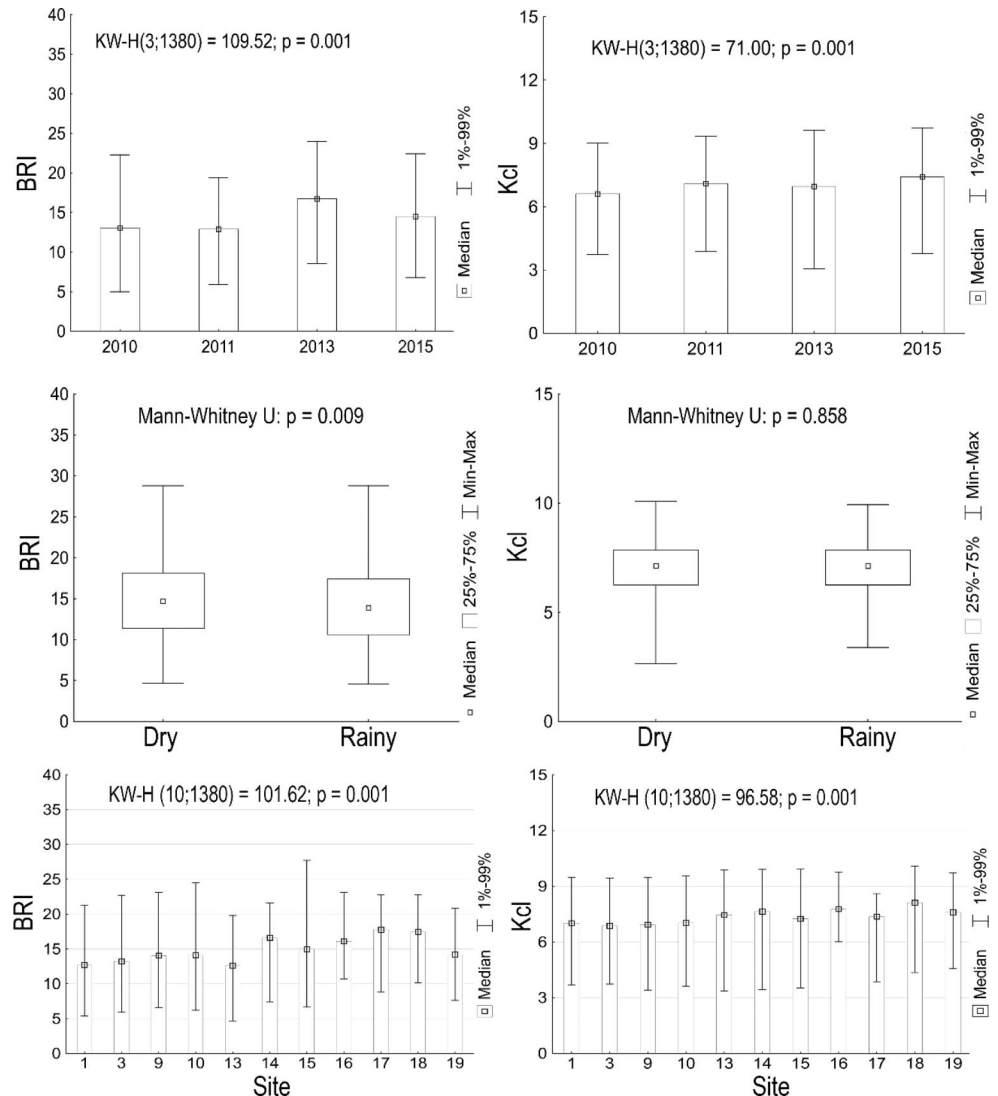
normality assumption was not met, spatio-temporal variations of the nutritional condition indices and the environmental variables were established by applying a multiple Kruskal-Wallis by ranks test.

Results

Both BRI and Kcl nutritional condition indices varied significantly from 2010 to 2015, although no trend was observed. During the dry season, lobster nutritional condition was higher than during the rainy season, however, significant differences ($p < 0.05$) were detected only for BRI. Variations among sites were significant for BRI and Kcl, usually showing higher values at sites (13–19) located near the platform edge (Fig. 2).

Comparison of the annual mean values of abiotic variables and food availability showed significant variation for salinity, with its lowest value in 2013 but without a defined

Fig. 2 Spatio-temporal variation on lobster's nutritional condition indices, in the fishing region of Caibarien, Cuba



trend among years. Food availability gradually increased between 2010 and 2015, although significant differences were established only between this last year and the previous ones. Temperature was significantly higher during the rainy season while salinity average value was the lowest. Dissolved oxygen and food availability did not show differences between seasons (Fig. 3).

Spearman's rank correlation coefficient showed a positive but low magnitude and no statistically significant relationship between BRI and Kcl. Temperature and salinity did not show association with either of the two nutritional condition indices, however, food availability had a significant positive correlation with both nutritional indices. Dissolved oxygen was significantly correlated only with BRI (Table 1).

Food availability was the only environmental variable whose spatial variation was significant, showing higher values at sites sampled in 2015 (Fig. 4).

There was not collinearity among any variables. Akaike information criterion showed a fittest model including "site" as a random component. Generalized Additive Model for Kcl was 84.8% deviance explained, with an adjusted $R^2 = 77.6\%$. The variables "site" ($F = 2.838$; $p = 0.001^{**}$), DO ($F = 4.054$; $p = 0.005^{**}$), and BFAI ($F = 17.934$; $p < 0.001^{***}$) had a significant impact on Kcl index. Generalized Additive Model for BRI was 34.6% deviance explained, with an adjusted $R^2 = 25.3\%$. Only the salinity significantly impacted on BRI index ($F = 3.243$; $p = 0.0385^*$) (Fig. 5).

Discussion

Environmental stress in the fishing region of Caibarien, possibly imposes generalized conditions of deterioration that homogeneously reduce the resilience of marine ecosystems and evenly affect biological communities. Changes on benthic communities' distribution, benthic organisms' abundance decreases, and seagrasses disturbances, have been reported as deterioration signs at all SCA regions (Martínez-Daranas 2007; Martínez-Daranas et al. 2021; Lopeztegui-Castillo et al. 2021b). These changes to benthic communities could imply a decrease of food availability for lobster (Lopeztegui-Castillo et al. 2021a), resulting in unfavorable variations in lobster's nutritional condition indices, which could be detected differently by each index based on its methodological characteristics (Oliver and MacDiarmid 2001; Lopeztegui-Castillo 2021). The energy supplied by each food category could also have an important influence (Díaz-Iglesias et al. 2001; Perera et al. 2003a, b).

Coastal pollution, causeways which limit water circulation and induce habitat fragmentation, and intensive fishing with bottom trawl nets, have been identified among the anthropogenic factors with the greatest impact on SCA,

also accentuated by natural factors such as high intensity and more frequent hurricanes (Baisre 1985; Alcolado et al. 2007; Martínez-Daranas et al. 2021). Although multiple environmental factors impacting Caibarien's biotic communities have been reported, present results showed that not all of them have a significant influence on lobster's nutritional condition. Therefore, it is suggested that the magnitude and multifactorial nature of environmental stress can modify the impact that each stressor introduces on an organisms' physiology and behavior. Each new factor that is added to the synergy modifies the magnitude in which the others influence and causes changes to organisms, that modify the way in which they respond to the influence of the previous factors. From this perspective, other factors such as turbidity, the levels of night lighting associated with the lunar cycle, the abundance of predators, and the degree of primary production, could be affecting lobster's nutritional condition, therefore these parameters should be considered in future studies.

Differences among sites corroborated that lobster's nutritional condition was usually lesser at inner sites, where environmental impact is greater and food availability is limited. Those sites were typically near the Cuban coastline, receiving industrial wastewater without treatment and other solid wastes (Montalvo-Estévez et al. 2008, 2013, 2014). Sites at the platform edge, where circulating water, food availability and benthic communities are usually favorable (Alcolado et al. 1998; Lopeztegui-Castillo et al. 2021a, b; Martínez-Daranas et al. 2021), showed the higher values of nutritional condition indices. Consequently, lobsters at these edge sites could have higher growth rate and sizes, according to Buesa (1987), González-Sansón et al. (1991), Briones-Fourzán and Lozano-Alvarez (2001), and Lozano-Alvarez et al. (2002). Also, ontogeny life cycle naturally determines larger lobsters' movements to deeper waters at the edge sites (Cruz et al. 1986). Some fishing aspect like fishing effort and the number and type of traps and artificial shelter used, could also influence nutritional condition (Baisre 2004; Morales et al. 2013; Butler et al. 2022).

Spatial variation on BRI and Kcl indices suggest a different environmental impact even at a small scale (among sites). Consequently, it could be inferred that factors significantly affecting lobster's nutritional condition should vary significantly among sites. The anthropic influence (Baisre 1985, 2004; Cobas et al. 2015; Martínez-Daranas et al. 2021), hurricane incidence (Puga et al. 2013), variation of hydroclimatic and oceanographic characteristics (Betanzos-Vega et al. 2011, 2013, 2019), and different levels of eutrophication and coastal pollution (García-García et al. 2008; Montalvo-Estévez et al. 2008, 2013, 2014; Álamo et al. 2013), could have determined spatial differences in food availability, salinity, dissolved oxygen, and other factor not

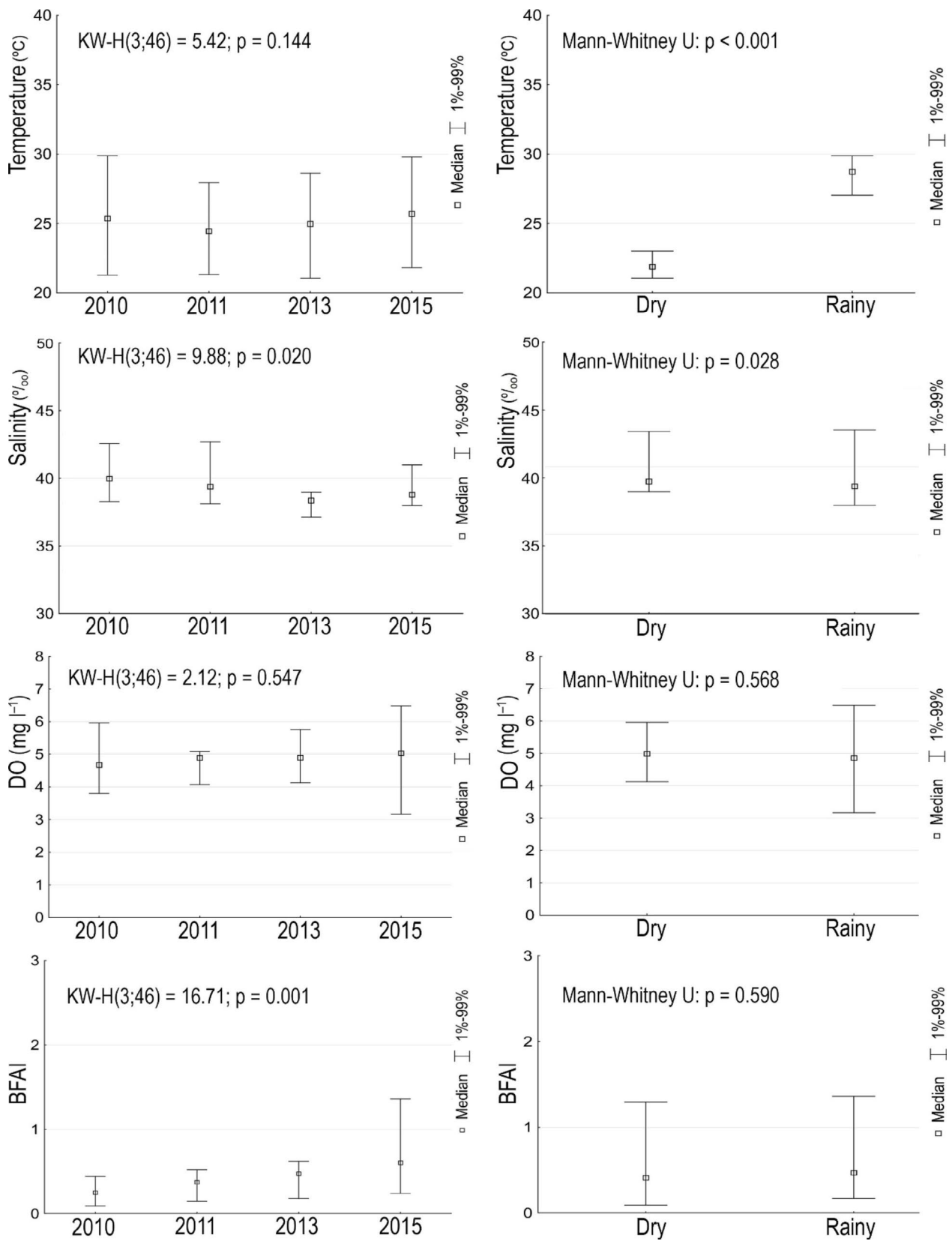


Fig. 3 Variation of the environmental variables among years and between the dry and rainy season, in the fishing region of Caibarien, Cuba. BFAI: Benthic Food Availability Index; DO: dissolved oxygen

Table 1 Spearman correlation coefficient quantifying association between nutritional condition indices, and between those indices and each environmental variable registered in the fishing region of Caibarien, Cuba. Kcl: morphometric index of nutritional condition; BRI: Blood Refractive Index; BFAI: Benthic Food Availability Index; DO: dissolved oxygen; *: significance

	$R_{\text{Spearman}}; p < 0.05$	
	BRI	Kcl
Temperature ($^{\circ}$ C)	-0.2062	0.1977
Salinity ($^{\circ}$ / $_{00}$)	-0.2694	-0.1226
DO (mg/L)	0.4389*	0.2459
BFAI	0.3374*	0.5513*
BRI	-	0.1749

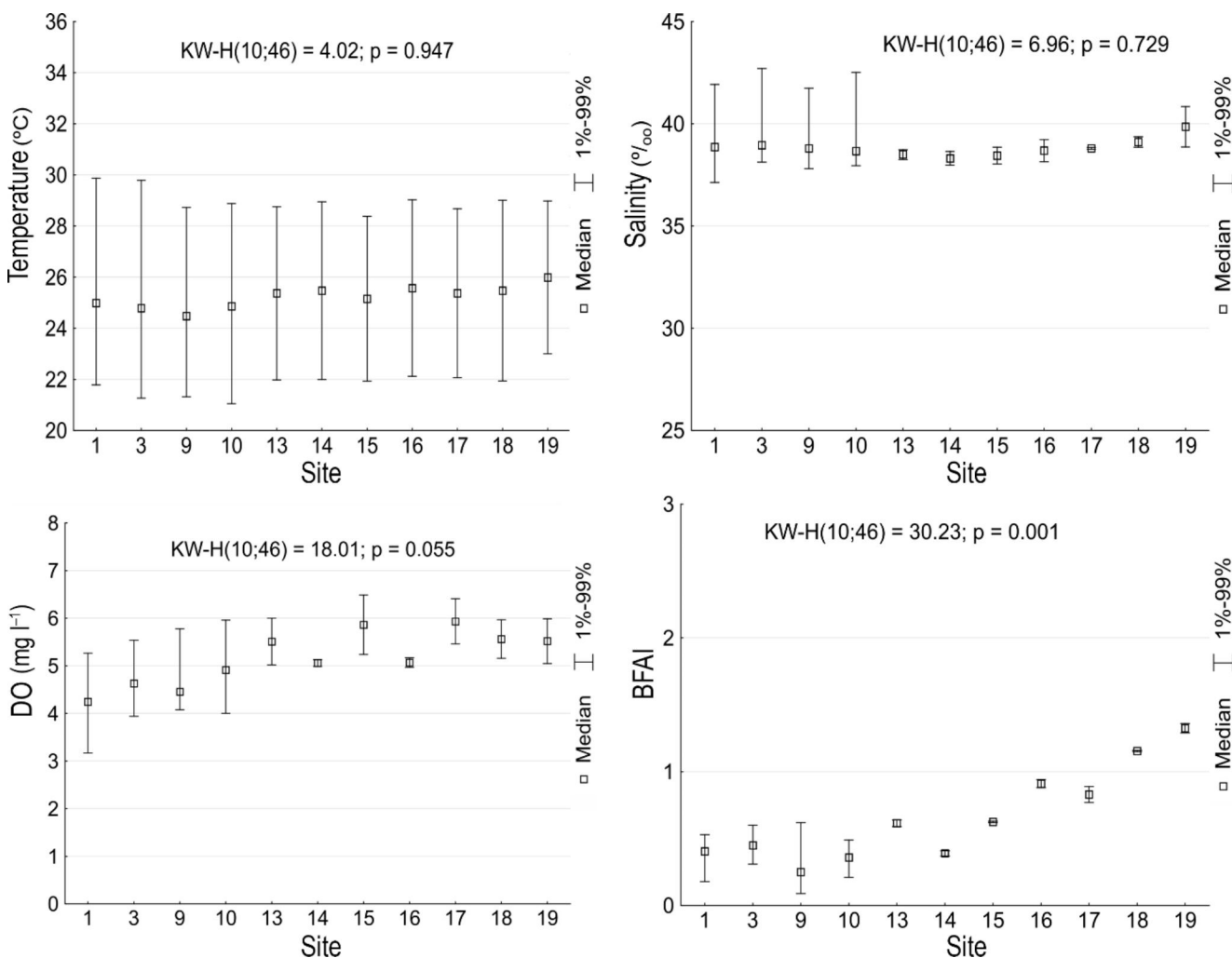


Fig. 4 Spatial variation of the environmental variables, as an average for 2010–2015 period, in the fishing region of Caibarien, Cuba. BFAI: Benthic Food Availability Index; DO: dissolved oxygen

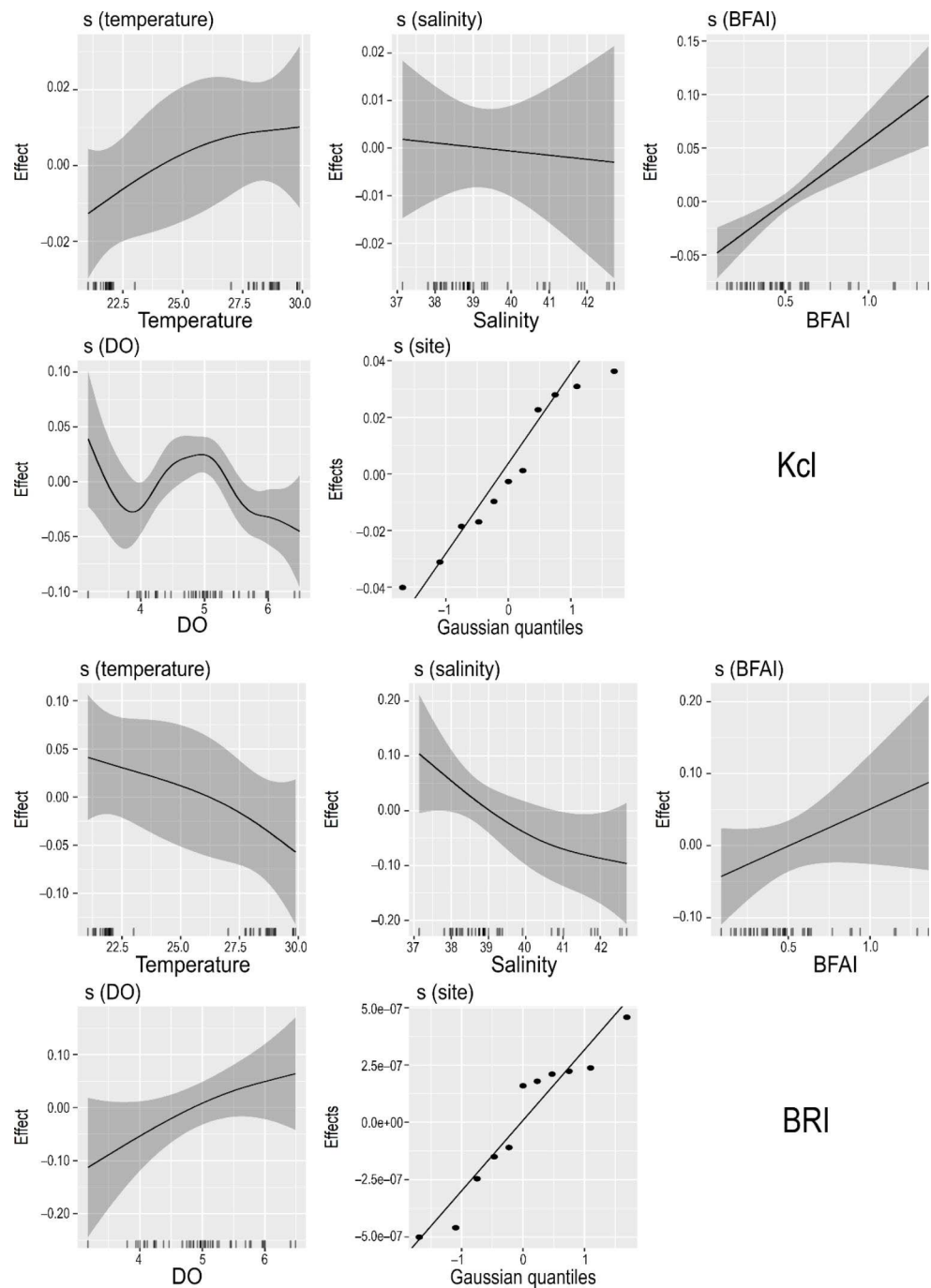
measured but potentially having the possibility to significantly impact lobster’s nutritional condition.

The high salinity values obtained are already characteristic of this region and its negative effect on biological communities has been well documented (Alcolado et al. 2007; Montalvo-Estévez et al. 2008; Betanzos-Vega et al. 2010, 2011, 2013). The temperature did not show significant difference among years, but a slightly increasing trend

was observed between 2011 and 2015. This would be due

to global warming (Fonseca-Rivera et al. 2021), but local effects conditioned by shallow depth and limited water circulation could be also influencing such increasing trend. Neither on spatial scale (among sites) the temperature varied significantly. Consequently, variation in nutritional condition indices could not be attributed to temperature but to other environmental factors.

Fig. 5 Generalized additive model quantifying the impact of environmental variables on lobster's morphometric (Kcl) and analytical (BRI) nutritional condition indices, in the fishing region of Caibarien, Cuba. BFAI: Benthic Food Availability Index; DO: dissolved oxygen



Being one of these other factors, the food availability showed a significant association (Spearman correlation coefficient) with both indices of nutritional condition. However, the Generalized Additive Model, which links the interaction of several factors, detected a significant impact of BFAI only on Kcl. Based on the results of this multivariate statistics tool, the environmental factors that affect BRI and Kcl indices are totally different in this region. BRI was significantly affected only by salinity variations, while Kcl was

significantly affected by food availability, dissolved oxygen, and sites variations.

Sites with highest food availability values were those at the platform edge. At these sites, the greater exchange with oceanic waters and the remoteness of polluting sources favors a better development of the benthic community (Lopeztegui-Castillo et al. 2021b; Martínez-Daranas et al. 2021). Nevertheless, inner sites values are better examples of the deteriorated habitat conditions reported at all SCA (Alcolado et al. 2007; Montalvo-Estévez et al. 2008;

Betanzos-Vega et al. 2011, 2013, 2015; Lopeztegui-Castillo et al. 2021b; Martínez-Daranas et al. 2021). Excluding edge sites result in 19% decreased food availability (BFAI=0.36), which corroborate the advanced environmental deterioration reported in the SCA inner waters.

Dissolved oxygen did not show significant differences between the dry and rainy seasons, although temperature was higher during the rainy season. Usually, increasing temperatures imply a dissolved oxygen decline, but phytoplankton blooms at the end of the rainy season make increase dissolved oxygen levels in Cuban semi-enclosed waters (Moreira et al. 2007, 2014; Seisdedo-Losa et al. 2021). Also, nutrient enrichment, which have typically been higher at this region, favor phytoplankton blooms which increase dissolved oxygen levels (Álamo et al. 2013; Bustamante-López et al. 2016; Seisdedo-Losa et al. 2021).

Salinity variations cause important physiological changes mostly related to the osmotic regulation processes and consequently energy reserves consumption (Ramaglia et al. 2018; Strefezza et al. 2019), therefore they could affect lobster's nutritional condition. High salinities found in Caibarien present a persistent multifactorial origin (platform shallow depth and natural narrowness, drought processes, river damming, and causeways construction) and could contribute to explain physiological variations, like a declined nutritional condition, in lobsters. Negative effects of drought processes on fishes and other marine organisms, associated with decreases in circulation, flow, and renewal of the waters, has been reported in coastal zones of Cuba (Barcia et al. 2019). Although some authors have valued higher ranges (Zhang et al. 2016), several studies in crustaceans propose that variations between 3 and 5 units of salinity could induce metabolic changes and modify organisms' responses to temperature and pH variations (Speare et al. 1996; Cardoso-Mohedano et al. 2018; Ramaglia et al. 2018; Strefezza et al. 2019). The average salinity value reported for other fishing regions of Cuba, like the gulf of Batabanó, is more than 3 salinity units lower than obtained in the present study for Caibarien (Betanzos-Vega et al. 2019).

Each environmental factor could affect lobster's physiology and behavior, but the impact depends on synergistic action with other stressors that also determine habitat quality (Wang et al. 2016; Gutzler and Butler 2017; Lopeztegui-Castillo 2021). Increased temperature can cause nutritional deficiency if insufficient food, but if the diet is adequate, it causes an increase in metabolic activity and in the rate of consumption and conversion of the food, without consequences on the nutritional condition (Wang et al. 2016; Fitzgibbon et al. 2017). Similarly, variations in salinity cause different effects depending on its association with other factors like water acidification or turbidity (Ramaglia et al. 2018; Strefezza et al. 2019), but they are better tolerated

when organisms are well fed (Zhang et al. 2016). Due to these aspects, the multifactorial nature of the environmental influence on the nutritional condition makes possible that certain factors, such as variations in salinity or food availability, have a different effect at each analyzed region.

Hemolymph protein concentration is directly proportional to the biomass of the hepatopancreas (Wang and McGaw 2014; Gutzler and Butler 2017). Thus, it is possible that low winter temperatures, concomitant with decreases in metabolic activity, could induce a greater accumulation of energy reserve substances. Corroborating, lobster nutritional condition was greater during the dry season, which means that this season is better for live lobster commercialization or for when lobsters must be submitted to long-term stresses. Consequently, a better lobster's physiology, which could mean better condition to withstand adverse environmental factors and to avoid diseases incidence, is expected during dry season. Also, decreased nutritional condition could cause a reduction of reproductive potential for lobsters. Lobsters with deficient nutritional condition are susceptible to diseases and could produce a smaller number of eggs or/and eggs with a lesser viability or fertility (Briones-Fourzán et al. 2009; Atherley et al. 2021). These reductions could cause a decrease of recruitment and lobster population abundance and fishery harvest (Baisre 2000a, b).

Acknowledgements This study was supported by the Fisheries Research Center of Cuba and by the fishermen and managers of Caibarien (EPICAI fishery industry). ALC and YOE also appreciate the CONACyT financial supporting for doctoral studies. LAAC is grateful for the support received through COFAA and EDI from the Instituto Politécnico Nacional.

Authors' Contributions A.L.C. designed the study and wrote de main manuscript text. Y.O.E. carried out statistical analysis and graphic illustration. L.A.A.C. final revision and edition.

Funding Not applicable.

Data Availability The datasets generated and analyzed during the current study are available from the first author upon reasonable request.

Declarations

Ethical Approval The data were collected based on the commercial lobster fishing and did not require any additional permits from the authorities. Lobsters were not exposed to any additional harm.

Competing interests There is no conflict of interest.

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