



Using realized thermal niche to validate thermal preferences from laboratory studies. How do they stand?

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ARTICLE INFO

Keywords:

Thermal preferences
Realized thermal niche
Niche conservatism
Local adaptation
Crustacean
Fish
Octopus maya

ABSTRACT

Temperature is recognised as the main factor controlling the species fitness and performance. Naturally, the thermal preferences (TP) of aquatic organisms obtained in controlled conditions have been used to relate physiological performance with field data since they are a good proxy to the fundamental niche. Literature suggests that dispersal capabilities, biological interactions, acclimatisation, adaptation, among others might play a role in species distribution; thus, in reality, species are usually occupying a realized thermal niche (RTN). Therefore, this study was designed to inquire into the following questions: Are the TP of tropical aquatic ectotherms found in laboratory conditions similar to their RTN? Can TP be validated with occurrences in the wild? To answer these questions, this study compared the TP obtained from previously published works with the RTN of the crabs *Callinectes similis* and *C. sapidus*, the fishes *Centropomus undecimalis* and *Ocyurus chrysurus*, the lobster *Panulirus argus*, and the octopus *Octopus maya* obtained from occurrences from 1693 documents. When RTN values were tested against the TPs obtained in laboratory, no significant differences were found for fish species ($P > 0.05$); in contrast, differences for the benthic invertebrates were reported ($P < 0.05$). At least two factors could have been affecting these results: differences in the average tolerances between geographically distinct populations (local adaptation) and the dispersal capabilities that might have been forcing a differentiation between populations. If, as proposed, fishes can actively follow thermal optimum, their response to warming scenarios could be faster than benthic organisms. If our hypothesis is true, the uncertainty of climate change could be reduced when the local adaptation is taking into consideration.

1. Introduction

Temperature has been established as the governing rate factor of biochemical reactions in ectothermic organisms regulating the physiological and behavioural functions (Angilletta, 2009). Cellular and physiological functions, such as metabolism, development, growth,

movement, and reproduction are dependent on temperature, which provokes effects at organismal, population, community, and ecosystem levels (Angilletta, 2009) and make temperature an influencing factor through the rate at which an organism can perform an ecologically relevant activity (Grigaltchik et al., 2012; Huey and Stevenson, 1979; Pörtner et al., 2017). Considering that the foraging theory predicts that

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<https://doi.org/10.1016/j.ecolind.2020.106741>

Received 30 October 2019; Received in revised form 13 July 2020; Accepted 17 July 2020

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animals select areas where their growth rates can eventually be maximised (Stephens and Krebs, 1986), it is often assumed that ectothermic animals tend to inhabit areas within their suitable temperature range (Hughes and Grand, 2000; Sunday et al., 2012). This hypothesis has been used to conceptually validate thermal preference (TP) results of aquatic vertebrates and invertebrates in controlled conditions in an attempt to obtain information about how the thermal changes occurring in nature modulate their preferences (Noyola et al., 2015).

Indeed, evidence points out temperature as an important factor that regulates spatio-temporal changes to species distributions (Poloczanska et al., 2016, 2013). For example, laboratory studies have predicted that warming anomalies could lead the cephalopod species, *Octopus maya* to migrate from west to east during a El Niño year when octopus catches increased in the eastern region of the continental shelf (Ángeles-González et al., 2017).

Although such interpretation is useful, reasonable doubts emerge related to the viability of validating laboratory studies by field data. For instance, Huff et al., (2005) showed that a group of trouts (*Oncorhynchus mykiss*) tended to select temperatures that comparable to those of maximum growth, which in theory should be close to the natural thermal niche of the species. However, they also observed that thermal niches of the wild populations of this fish species varied by ecoregion. Similarly, Beitinger and Fitzpatrick (1979), noted that studies of optimal temperature for growth reported differences between sample sites for the largemouth bass; nonetheless, laboratory studies showed final preference despite their different geographic origin of the studies (Huff et al., 2005).

Regardless of those mixed results, plenty of meta studies have shown the importance of temperature as the factor governing population and community structures (Bradie and Leung, 2016; Sunday et al., 2012) and even being associated to ongoing changes in distribution and phenology (Poloczanska et al., 2016, 2013). Although laboratory data have been used to make proposals about how thermal changes affect organism distribution, few studies have tried to directly relate physiological performance with field data (Beitinger and Fitzpatrick, 1979; Deacon et al., 1987; Ferguson, 1958; Gift, 1977; Huff et al., 2005; Payne et al., 2016). Studies have suggested that the information generated in laboratory can be a good proxy to the fundamental niche (Hutchinson, 1957; Kearney and Porter, 2009; Kearney et al., 2010), in other words, the non-interactive environment that contains the ecological conditions in which a species can thrive (Hutchinson, 1978). The fundamental niche is a unifying concept that has provided insight into the causes of species distribution and abundance (Anderson and Martínez-Meyer, 2004; Martin et al., 2016; Martínez-Meyer, 2005; Martínez-Meyer et al., 2013). Thus, from a thermal point of view, understanding climate change effects on species should require analyses of both of the thermal physiological traits in the laboratory and fundamental niche of the species in their range of distribution (Bennett et al., 2018).

Indeed, other authors have suggested that laboratory data might be a better method to assess the impact of global warming in comparison to merely statistical techniques as they can reconstruct the fundamental niche more accurately, reducing the uncertainty that the purely statistical models have (Kearney and Porter, 2009; Peterson et al., 2015).

However, while the laboratory data could accurately represent the biological requirements that maximise fitness in the geographic space, they can potentially fail to represent species distribution. What could be provoking such mismatches? Evidence has shown that distribution cannot always be linked only to TP; dispersal capabilities (locomotion capabilities, currents), biological factors (intra- and interspecific competition) (Soberón and Peterson, 2005), acclimatisation (phenotypically), adaptation (genetically) (Angilletta, 2009), photoperiod, circadian rhythms, stresses, infections or chemicals could be affecting thermal selection (Reynolds, 1977). Thus species are in reality occupying a realized niche, a subset of the fundamental niche (Peterson et al., 2011; Soberón and Nakamura, 2009; Soberón and Peterson, 2005).

This inability to reflect real species occupied distribution somewhat mirrors the mismatches observed in the validation of laboratory with field data. Under an ideal scenario, the combination of field data with laboratory data would be highly desirable for accurate environmental impact assessments (Gift, 1977) and should coincide; however, if mismatches between the data exist, potential troubles for prediction emerges. Conversely, if the laboratory and field data are similar, inferences or mechanistical and statistical predictions may have a greater accuracy (Barve et al., 2011; Hijmans and Graham, 2006; Kearney and Porter, 2009; Peterson et al., 2011; Saupe et al., 2012; Soberón and Nakamura, 2009; Soberón and Peterson, 2005).

The lack of information and mixed results from the few previous works published allowed us to raise a couple of questions. Are the TP of tropical aquatic ectotherms found in laboratory similar to their realized thermal niche (RTN) found in field data? Can we validate TP with occurrences in the wild?

Perhaps a comparison between field data and physiological studies could allow us to generate an axiom of why such differences or matches exist (Hijmans and Graham, 2006); indeed, such ideas are currently being developed as a result of the concern of climate change impact in the biological system (Payne et al., 2016), though as mentioned, works are quite scarce (Murchie et al., 2011).

Thus, hypotheses can be developed according of the results obtained. For instance, if differences are found, a process of local adaptation could have been occurring, which is something to be expected between populations exposed to different environmental conditions (Araújo et al., 2013; Gibert et al., 2001). Another possibility is that dispersal restrictions could limit choosing suitable environments (competition, locomotion, absence of refuges, etc.) (Berg et al., 2010; Saupe et al., 2012; Soberón and Nakamura, 2009; Soberón and Peterson, 2005). Therefore, when predicting the impact of global warming, species with this type of characteristic may show a higher uncertainty; thus, careful interpretation must be done when analysing this species.

Conversely, if no differences were found, a process of niche conservatism, that is, the inclination of species to retain their niches over time (Martínez-Meyer and Peterson, 2006; Peterson et al., 1999; Peterson, 2011) because their thermoregulatory behavior (Angilletta et al., 2002a; Buckley et al., 2015; Huey et al., 2003) could be present, thus, the data obtained from laboratory and field could be good indicators of the vulnerability of the species studied. Moreover, according to Huff et al. (2005), the coupling of laboratory findings with field observations can potentially resolve the thermal requirements of targeted species. To test these hypotheses, data obtained in laboratory conditions, previously published (Noyola et al., 2015; Rodríguez-Fuentes et al., 2017; Tremblay et al., 2017), was used for analysis and comparison besides the natural distribution ranges of the crabs *Callinectes similis* and *C. sapidus*, the fish *Centropomus undecimalis*, and *Ocyurus chrysurus*, the lobster *Panulirus argus*, and the octopus *O. maya*. This information could help to obtain information that potentially reduce the uncertainty related with the interpretation of the future impact of global warming in the species studied, which is especially important nowadays since climate change represents one of the greatest challenges that mankind may face (Vinagre et al., 2016).

2. Materials and methods

2.1. Occurrence records

Occurrence records were obtained from literature review from June 2017 to June 2018 from published articles, books, posters, technical reports and theses for juveniles and adults of six marine species of commercial importance in the Gulf of Mexico: crabs *C. sapidus* and *C. similis*, common snook *C. undecimalis*, red Mexican four-eyed octopus *O. maya*, spiny lobster *P. argus* and yellowtail snapper *O. chrysurus*. The scientific names of these species were used as a search term on the

web search engine Google scholar; occurrences were recorded if sampling points or the names of the localities were reported. Although articles published in the 1900s were used, the main documents in this study were published after 2000 and until 2019. Any work related with zooplanktonic larval stages was ignored.

Occurrences were georeferenced with Google Earth and then extracted in decimals to a .csv with the library “rgdal” (Bivand et al., 2019) from the programming language R (R Core team, 2019). Furthermore, to visually explore species distribution, the databases were mapped using libraries *maps* (Becker et al., 2018b), *sp* (Pebesma and Bivand, 2018), *mapproj* (McIlroy, 2018), *mapdata* (Becker et al., 2018a), *mapplots* (Gerritsen, 2018) and *rgeos* (Bivand and Rundel, 2019). Collected references were added as [Supplementary material](#).

2.2. Environmental data

World environmental layers for mean surface and bottom temperature (from 2000 to 2014) at minimum depths were obtained from Bio-Oracle at a resolution of 5 arcmin (<http://www.bio-oracle.org/> - for details see Assis et al. (2018)). Bottom layers were used for the invertebrates *C. sapidus*, *C. similis*, *O. maya* and *P. argus*, and surface layers were considered for the fish *C. undecimalis* and *O. chrysurus* surface layers.

2.3. Spatial occurrences and extraction of environment data

The occurrences identified from the literature review were superimposed on the environmental layers to extract the pixel value with the library *raster* (Hijmans, 2019) from R (R Core Team, 2019); this methodology gave us an approximation to a RTN. However, before the extraction of the data, spatial filtering was done to reduce the overrepresentation of environmental data of highly sampled sites (Boria et al., 2014), thus, we only used one occurrence by pixel to characterize the RTN.

2.4. Laboratory data

Preferred temperatures were previously published by Noyola et al. (2015, 2013), and Rodríguez-Fuentes et al. (2017). For this purpose, they used juveniles for the fishes (*O. chrysurus*, *C. undecimalis*), and juveniles and adults for octopus (*O. maya*), juveniles of lobster (*P. argus*), and adult crabs (*C. sapidus* and *C. similis*). Fish and octopus' specimens were obtained from aquaculture facilities where juveniles are frequently produced from captive broodstock. That facilities are in Universidad Nacional Autónoma de México, Faculty of Sciences at Sisal, Yucatán, México. Lobsters were obtained from wild populations close to Isla Mujeres (Quintana Roo, México) while crab species (unpublished data for *C. sapidus*) were obtained from wild populations in the coastal zone off Sisal Harbor.

Briefly, all the animals were acclimated for three weeks at constant temperatures of 18, 22, 26 and 30 °C (except for *O. chrysurus* whose survival at 18 °C was < 5%, so the lower acclimation temperature for this species was 20 °C). Animals were kept in containers at a density of 20 organisms per container with re-circulated, filtered and UV sterilised seawater (Noyola et al., 2015). The volume of the tanks was adjusted according to the type of organism. Fish (8 cm total length), and mollusks (3 to 6 cm length of the shell) juveniles were maintained in 60 L tanks at a density of 20 animals per tank. The octopus were individualized in 500 ml chambers, which were placed in 3-m² tanks thermally controlled. Crab species (6 to 7 cm wide of the carapace) were maintained individualized in 6-L tanks, connected to a re-circulatory seawater system thermally controlled (see details in Noyola et al., 2015). Juvenile lobsters (3.6 cm carapace length) were maintained in 60-L tanks at a density of eight lobsters per tank. Details of thermal control and maintenance of experimental organisms are in Noyola et al. (2015) and Rodríguez-Fuentes et al. (2017). To determine

the TP an acute method was used. In this method, the acclimated animals were exposed to a horizontal temperature gradient for 120 min until they selected a preferred temperature (Reynolds and Casterlin, 1979). Fish species were tested in groups of three animals each time (N = 5 groups of three animals of each species by acclimation temperature), while the rest of the species were individually tested (N = 15 data per species and acclimation temperature).

A control experiment was performed to evaluate the distribution of animals of each species in the tube used to form the horizontal gradient. Control groups of animals of each species (N = 5 groups of three fish of each species and acclimation temperature and 15 data per species and acclimation temperature of the rest of the tested species) was placed in the horizontal gradient with the seawater at each acclimation temperature. This control group allowed determining that the final location was indeed due to temperature selection. More details of the procedures are in Noyola et al. (2015) and Rodríguez-Fuentes et al. (2017).

2.5. Exploration and statistical analyses of the data

Normality assumption was evaluated with a Shapiro-Walk test using temperature values extracted from the occurrences (RTN) and TP from laboratory data (Fish species: N = 5 data per species and acclimation temperature; molluscs, crustaceans, and octopus species: 15 data per acclimation temperature). Data tended to non-normality ($P < 0.05$), therefore, the RTN and TP were reported as median, quantiles and range. The occurrence records and laboratory data (were expressed in boxplots. Furthermore, a Mann-Whitney *U* test was done to compare statistical differences between the TP and RTN. All the statistical analyses and plots were performed using R (R Core Team, 2019).

3. Results

3.1. Occurrence records

Of the total documents reviewed (1693), this study obtained 7059 occurrence records of the species studied along their distribution range. Of the total documents reviewed, 574 references and 2102 records, and 128 references and 376 records belonged to *C. sapidus* and *C. similis*, respectively. For the fish *C. undecimalis*, 233 references were reviewed obtaining 836 records while for *O. chrysurus* 369 references were reviewed and 982 records were obtained. For *O. maya*, 62 references recording 1621 occurrences along its distribution range were analysed. For the lobster *P. argus*, 327 references were reviewed obtaining 1142 occurrence records. The collected references were dated from 1900 to the present. However, most of the occurrences belonged to works from the year ~2000 onwards (see [Supplementary material](#)).

3.2. Distribution, realized thermal niche (RTN) and laboratory thermal preference (TP)

With the exception of *O. maya*, an endemic octopus of the Yucatan Peninsula, Mexico, other species were recorded along the Atlantic Ocean. Most occurrences of the fishes *C. undecimalis*, *O. chrysurus* and the crustacean *P. argus* and *C. similis* were mainly restricted to western Atlantic in tropical and subtropical latitudes. However, *C. similis* was reported only in North America while the lobster *P. argus* had a few records in Cape Verde and the Ivory Coast in western Africa. In contrast, the blue crab *C. sapidus* was recorded from tropical to temperate waters even in the Mediterranean and Baltic seas where it is considered an invasive species (Fig. 1).

Ranges of RTN widely differed among species; some of these species are from cold to warm environments while others are restricted only to warmer temperatures. The transcontinental *C. sapidus* was reported in a wide range of temperatures, from those as cold as 8.5 °C to warm waters of 28.7 °C with a median value of ~21 °C. The lesser blue crab *C. similis*, and the common snook *C. undecimalis* had also been reported in

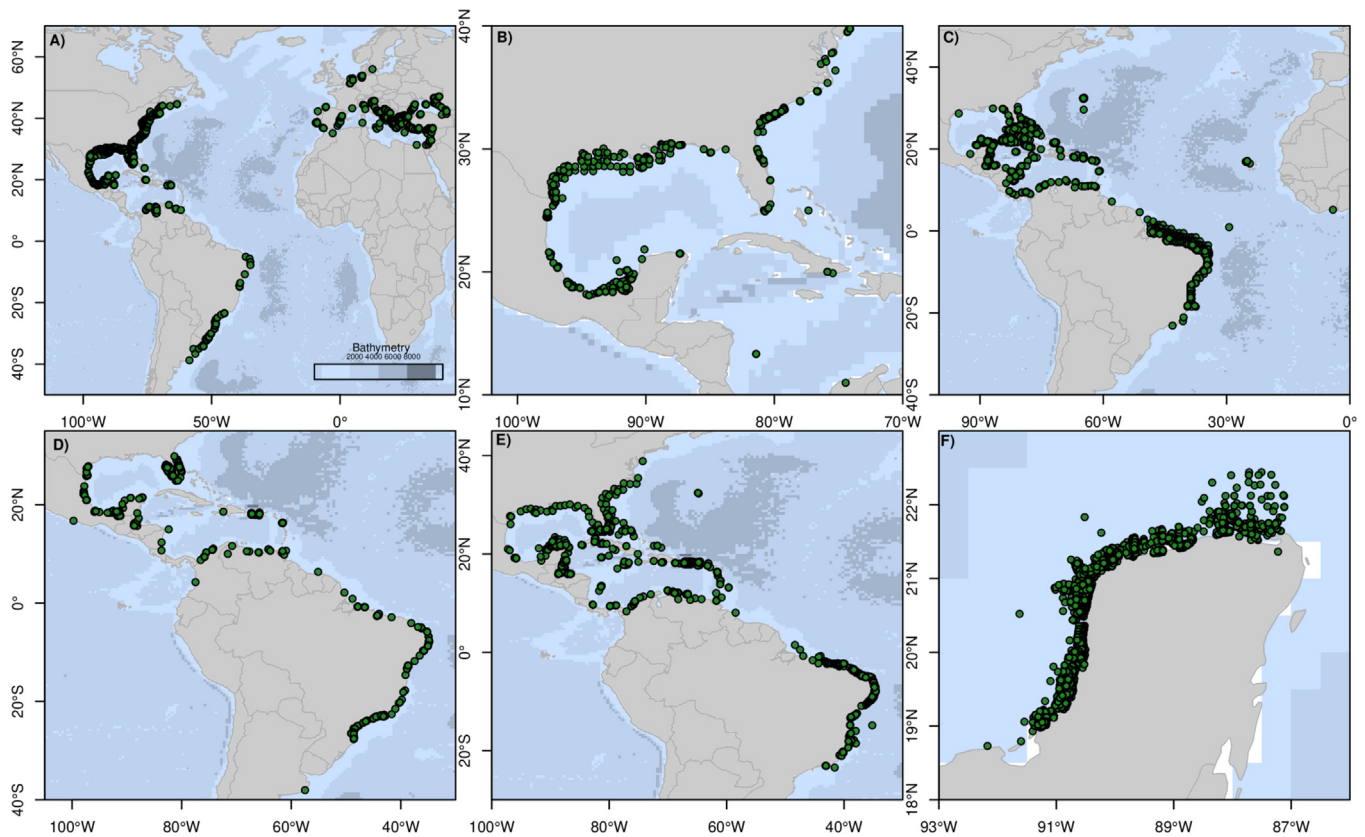


Fig. 1. Geographical occurrences of *Callinectes sapidus* (a), *C. similis* (b), *Panulirus argus* (c), *Centropomus undecimalis* (d), *Ocyurus chrysurus* (e), and *Octopus maya* (f) obtained from the review of 1693 documents.

Table 1

Descriptive statistics and range of realized thermal niche for the six marine species studied. Preferred temperatures obtained in laboratory are from. Additionally, *P* values from Mann-Whitney test between realized thermal niche (RTN) (°C) of natural populations and Thermal Preferences (TP) in acclimated animals in laboratory are shown.

		Temperature (°C)					
		Quartile					
	Species	Min	Lower	Median	Upper	Max	P value
Juveniles and adults	<i>C. sapidus</i> Nature	8.5	16.4	21.4	24.1	28.7	< 0.001
Adults	<i>C. sapidus</i> Laboratory	21.3	27.6	30.1	32.4	36.6	
Adults and juveniles	<i>C. similis</i> Nature	20.7	23.8	24.4	26.6	28.0	< 0.001
Adults	<i>C. similis</i> Labobratory	18.0	20.8	23.3	24.8	30.3	
Adults and juveniles	<i>P. argus</i> Nature	24.7	26.5	27.4	27.9	28.9	< 0.001
Adults and juveniles	<i>P. argus</i> Laboratory	25.1	30.0	32.0	34.4	39.0	
Adults and juveniles	<i>C. undecimalis</i> Nature	21.4	24.5	26.0	27.5	29.6	0.48
Juveniles	<i>C. undecimalis</i> Laboratory	24.2	24.8	25.4	27.5	29.5	
Adults and juveniles	<i>O. chrysurus</i> Nature	25.2	26.7	27.5	27.9	28.8	0.18
Juveniles	<i>O. chrysurus</i> Laboratory	22.6	25.1	26.5	28.4	31.7	
Adults and juveniles	<i>O. maya</i> Nature	25.0	26.3	26.6	27.2	27.5	< 0.001
Adults and juveniles	<i>O. maya</i> Laboratory	12.3	20.0	22.1	25.7	31.1	

relatively cold water (20.7 and 21 °C respectively). Conversely, the octopus *O. maya*, a species with a small distribution area, and *O. chrysurus* were restricted to high temperatures within the ranges of RTN from 25 to 27 °C. For most of these species the median RTN was reported around ~25 and 27 °C. The notable exception was the species *C. similis*, a tropical-temperate species whose RTN reported was ~24 °C. We must highlight the restricted range of temperatures explored by the octopus (Fig. 1, Table 1).

When RTN values were tested against the data of the TP obtained in laboratory, no significant differences were found for *C. undecimalis* and *O. chrysurus* ($P > 0.05$). In contrast, statistical differences were

observed between RTN and TP of *C. sapidus* whose TP values were ~9 °C higher than RTN ($P < 0.0001$; Table 1). Moreover, for *P. argus* and *C. similis*, TP resulted 5 and 1 °C higher than RTN, respectively while for *O. maya*, TP was ~4 °C lower than RTN (Table 1; $P < 0.05$) (Fig. 2).

4. Discussion

4.1. Thermoregulatory behaviour, niche conservatism and local adaptation

The results obtained showed that while the nektonic species of *C.*

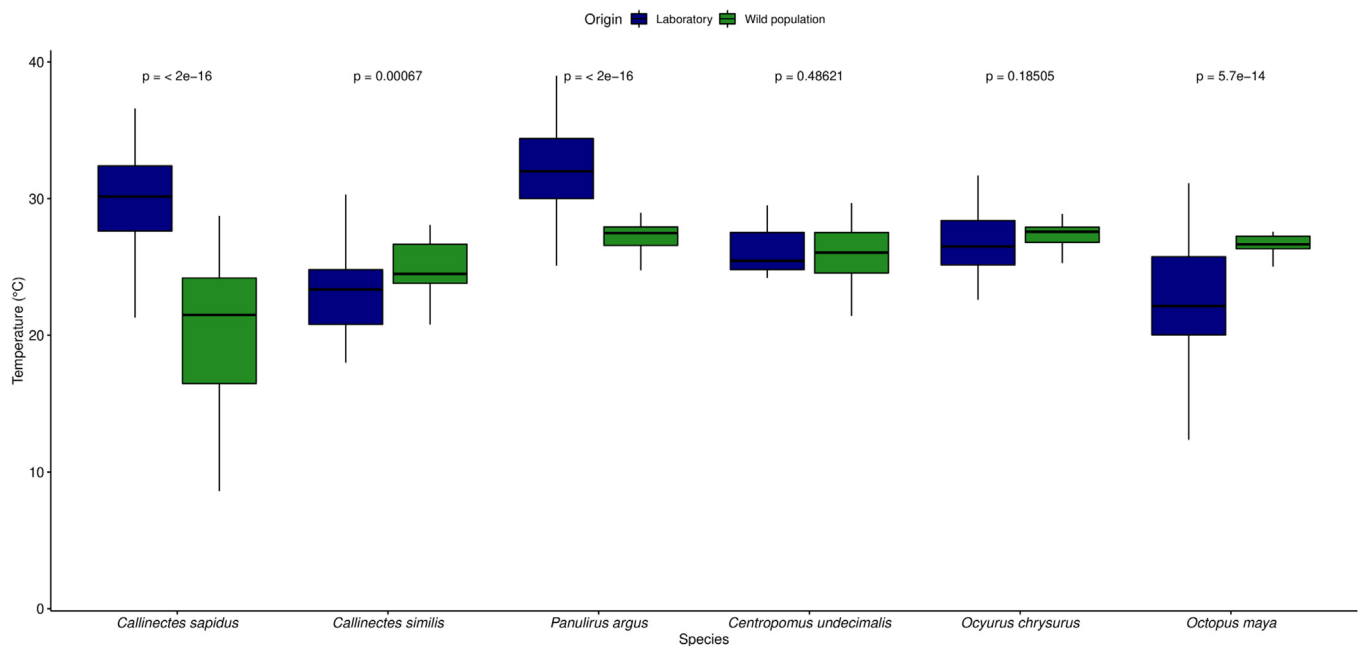


Fig. 2. Realized Thermal Niche (RTN) (red) and Thermal Preferences (TP) in laboratory conditions (blue) of six species. Boxplot indicates median (dark line and number above the whisker); upper and lower quartile (box); and range (bars).

undecimalis and *O. chrysurus* had similar preferred thermal ranges in wild populations and laboratory conditions, *C. similis*, *C. sapidus*, *P. argus* and *O. maya* did not. At least two factors could have been affecting the thermal behaviour of animals: (i) geographic variation in temperature tolerance and/or differences in the individual average tolerances between geographically distinct populations and (ii) dispersal capabilities that might have been forcing a differentiation or conservation of the niche.

The results allowed us to hypothesise that the superior swimming ability of fishes have allowed them self-directed movement to areas where they can maximise their fitness (Pörtner and Farrell, 2008). Assuming that a stimulus does not produce a physiological shock, thermoregulatory behaviour might reduce exposure to these negative conditions allowing them to escape (Magnuson et al., 1979), thus, eliminating or reducing the probability of adaptive responses (Buckley et al., 2015; Eliosa-León et al., 2010; Huey et al., 2003; Olla et al., 1980) leading to niche conservatism (Holt and Barfield, 2001) and an increase in specialisation (Wiens et al., 2010). Moreover, predatory species, such as *C. undecimalis* and *O. chrysurus* tend to show higher dispersal rates thanks to their larger body size, home range, spatial resource use and thermal plasticity (Holt, 1996; Noyola et al., 2015).

The results of thermal preferences obtained in this study agrees with Payne et al. (2016) who found evidence that the aerobic scope for tropical and temperate fish species reflected the environmental tolerance across latitudes, supporting the hypothesis that the aerobic scope is a process that controls the distribution of marine species (Pörtner et al., 2017; Pörtner and Farrell, 2008). Indeed, Pörtner and Knust (2007), had found previously that the aerobic scope could satisfactorily explain field data findings, explaining ecological patterns, such as abundance. In this sense, Paschke et al. (2018) demonstrated that *C. undecimalis* and *O. chrysurus* had a higher aerobic scope than more sedentary fish (clown fish), suggesting that those species have enough energy to satisfy the energetic requirements related with thermoregulatory processes.

Conversely, organisms with lower locomotion capabilities might fail to detect suitable habitats, so natural selection should favour traits that allow adaptation (Holt, 1996; Holt and Gaines, 1992) in which temporal phenomena, such as hurricanes and gradient in temperature due to bathymetry could be creating a process of “soft allopatry” generating

divergence in niche (Pyron et al., 2015).

If, as in most populations, tolerances reflect habitat temperatures and latitudinal distribution (Kuo and Sanford, 2009; Sorte et al., 2011; Sunday et al., 2012), this study may hypothesise that higher TP recorded by the decapods *C. sapidus* and *P. argus* than for the fish species *C. undecimalis* and *O. chrysurus* were the result of local adaptation by species living in different thermal regimes. Indeed, the tropical zone of the Yucatan Peninsula where TP were obtained is characterised by high temperatures.

In Chesapeake Bay, a thermal range from 15 to 19 °C was observed for *C. sapidus* maximal survival while a range from 19 to 22 °C was identified to obtain high quality spawns (Bembe et al., 2017). Similarly, the sub-tropical population of *P. argus* showed optimum temperature for survival and growth at 23.6 ± 0.2 °C, 6.4 °C lower than the preferred temperatures (30 °C) from Florida population (Reynolds and Casterlin, 1979). In comparison, crabs and lobsters from the Yucatan peninsula showed preferred thermal ranges from 26.2–33.4 °C and 25–39 °C (Noyola et al., 2015; Rodríguez-Fuentes et al., 2017) respectively, in laboratory conditions demonstrating that tropical populations have maximum performance at higher thermal regimes. The lesser blue crab *C. similis* followed a different pattern being a species with affinity to colder waters (RTN of 24.2 °C and TP of 23.3 °C). Indeed, field works made in the Yucatán Peninsula continental shelf have shown that spawners aggregate during the winter season while juveniles reared in elevated temperatures exhibited decreased intermolt and growth per molt (Celis-Sánchez et al., 2014).

This process of thermal adaptation along a broad spectrum of climates (Narum et al., 2013) provides species with environmental resilience. For example, Alaniz-Rodriguez et al. (2017) showed that pelagic larval dispersal allowed *C. sapidus* gene to flow southward to northward direction, suggesting that in warming scenarios low latitudes could be “rescue” populations helping more sensitive populations to cope with a climate-driven extinction (Diniz-Filho et al., 2019; Sorte et al., 2011).

Though the larval phase allows benthic organisms broad-scale movements, they are dependent on currents for their displacement (Cowen and Sponaugle, 2009; Pineda et al., 2007). Furthermore, the planktonic phase is vulnerable due to their narrow thermal windows (Pörtner and Farrell, 2008); additionally, the need to settle is a risky event with high levels of mortality (e.g., Hunt and Scheibling, 1997), so

connectivity between populations due larval dispersal may not always be as strong as generally assumed (Weersing and Toonen, 2009). Thus, it is unlikely that benthic organisms could easily access to settlements that maximise their fitness. As an example, the literature review denoted an absence of occurrences of *P. argus* in eastern Mexico (Cruz et al., 2001). Evidence indicated that a lack of offshore gyres existed, which constraint larvae long enough to settle a population (Briones-Fourzán et al., 2008; Ehrhardt et al., 2011). In this sense, lower densities of *P. argus* in eastern Mexico could have been due to incapacity of the larvae to reach and settle and not because of inability of adult animals to survive.

Laboratory studies of *O. maya* have demonstrated that an interval from 18 to 27 °C is optimum for growth and survival (Noyola et al., 2013) and 22 to 26 °C for reproduction (Caamal-Monsreal et al., 2016; Juárez et al., 2015, 2018; López-Galindo et al., 2019; Sanchez-García et al., 2017), which have been validated via field data (Ángeles-González et al., 2017; Juárez et al., 2018). However, in this study, higher and narrower RTN were observed than TP, suggesting that other forces were affecting the thermal behaviour in the continental shelf of Yucatan. Avendaño et al. (2019) reported that the small-scale fisheries focus their catch efforts of *O. maya* in shallow waters (< 30 m) while the fishing effort of *O. vulgaris* occurs in deeper waters of > 30 m; thus, the narrow RTN observed could be linked to competition of *O. vulgaris* that restricts the number of refuges and preys available for *O. maya*. Furthermore, differences between TP and RTN could also be explained via mobility capacity and environmental barriers. For instance, *O. maya* distribution is restricted due to discharges of the Grijalva-Usumacinta River in Campeche, Mexico because this river system has modified soil substrate and generated dilution and loading of organic matter (Rabalais, 2004) affecting negatively octopus populations (Sobrinho et al., 2002). Additionally, this species lacks a larval phase, which decreases the potential to expand its distribution (Villanueva et al., 1995).

The evolution of thermal sensitivity in ectothermic organisms and TP relates body temperature with the environment (Angilletta et al., 2002b). This relationship is no coincidence, as the environment has selected organisms that have acquired the capacity to select temperatures in which their performance is maximal.

Understanding the scopes of thermal selectivity in wild populations is of the uttermost importance as the prospects of adaptation or niche conservatism have important implication in predicting the effects of climate change on species re-distributions. If, as predicted, fish can actively follow certain thermal regimes, their response to climate change could be faster than that of benthic organisms (Poloczanska et al., 2016, 2013). In this sense, our results showed that widely distributed species may exhibit niche conservatism (Kalkvik et al., 2012) if their locomotion capabilities allow it. If our hypothesis is true, the uncertainty of the direction of the impacts of climate change will be reduced in most of the species studied. For instance, fish species might migrate faster to thermal favourable environments than benthic species. In contrast, adaptation may play a greater role in benthic species.

4.2. Laboratory and field data as estimators of thermal preferences

The objective of any environmental indicator is to accurately measure the fundamental niche of a species. In this sense, laboratory data is grounded in physicochemical principles providing a mechanistic understanding of species distribution (Kearney et al., 2010). These analyses usually require laborious experiments and/or calculations, and thus are not readily applicable to large numbers of species (Peterson et al., 2015); however, when available data exist, they are pointed out as good indicators useful to estimate potential distribution change under non-analogous scenarios (Kearney et al., 2010; Peterson et al., 2015). Regardless of these recommendations, the estimations obtained from a single population may not always be precise enough since the ponderation of a few locally adapted units may underestimate the full potential of the niche (Peterson et al., 2015). Indeed, the results in this

study suggest that the TP of the benthic species used in the analyses were for the most part tropical-adapted populations; thus, if predictions of marine resources were done with such data, the results would be less than satisfactory, specially if they were extrapolated to other regions or times.

Conversely, the use of occurrences across the geographic space provides a quicker test of niche tolerance (Peterson et al., 2015). However, occurrences may also fail to accurately predict the thermal niche breadth, because the presence of a species depends not only on the abiotic environment but also on complex biotic, dispersal and adaptation processes that could conduct to partitioning the niche (Soberón and Peterson, 2005). In such circumstances and as was observed in laboratory studies, that information could conduct to misinterpretation about the prediction of the effects of the warming in the distribution of aquatic species (Peterson et al., 2015). In light of these mixed results, if the objective of a research study is to inquire about the potential effects of climate change or any environmental anomaly in species distribution, a correct modelling unit should be selected. For example, in this study the TP obtained in the laboratory for *C. sapidus* should be used only for predictions in tropical populations. Similarly, if the objective is to build a realized niche, perhaps the models should be built according to relevant occurrences to a locally adapted population.

4.3. Caveats and future work

Although the hypotheses proposed in this study are interesting, important caveats must be considered while interpreting the results. The most important shortcoming of this research could be related to the difficulty of accurately assigning a temperature value to each occurrence. In reality occurrences are geographically static while environmental temperature has an important temporal variation. Many studies have failed to give precise data about the sites of sampling the organisms (see Supplementary material). Furthermore, even if the studies have reported exact dates, it is unlikely to have access to environmental data for each work, specially before the year 2000.

In this sense, this study assumes that occurrences are in equilibrium with the environment, which could reduce the interpretive capacity of its results. In hindsight it would be a greater weakness for species that inhabit sub-tropical and temperate environments as the blue crab *C. sapidus*. Moreover, marine species experience differences in temperature preferences during their ontogenetic development, which can be important in defining species distribution (Robinson et al., 2011). This effect was reduced by not considering works related to larval phases, but a separation was not possible for juveniles and adults since many publications report both stages; thus, the results in this study consist of a composite of thermal preferences under at least two phases of the life cycle of this species.

In addition, the effect that other environmental variables could have in the species distribution was not considered. For instance, temperature preferences can covariate with salinity since both environmental variables modify the physiological response of organisms (Hernández et al., 2006; Re et al., 2012; Re et al., 2005). This variable is especially important to consider since three of the species studied (*C. sapidus*, *C. similis* and *C. undecimalis*) can be found in estuarine ecosystems and the approach used in our study did not account for such differences. Regardless of this drawback, the occurrences obtained in this study were mainly from marine populations so the effect of such changes were unlikely to greatly affect our results.

Considering the drawbacks previously mentioned, and with the objective to further test our hypotheses, future studies in depth should be performed. For instance, our efforts could be directed to tropical marine species that do not experience such high thermal variations. Additionally, the idea of more species needs to be assessed because an extensive literature review, such as this one may not be time efficient; occurrences can be obtained from online repositories, such as the Global Biodiversity Information Facility (<https://www.gbif.org/>) and

the Ocean Biogeographic Information System (<https://obis.org/>). In a similar manner, efforts to concentrate physiological thermal tolerances data exist, such as GlobTherm (Bennett et al., 2018) that may help us find the literature available for physiological experiments. If our ideas stand the tests, the uncertainty of how fish and benthic species may react would decrease because physiological and occurrence data would be a better indicator of thermal tolerance for fish species than for benthic species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study is the result of a Graduate Studies doctoral degree thesis at Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (UNAM); the authors are grateful to UNAM and to the Consejo Nacional de Ciencia y Tecnología (CONACYT) for the scholarship funding the development of this research. Most of the data for *Octopus maya* used in this study were obtained from the projects funded by CONACYT: 154400x and 237057. This study was also partially financed by PAPIIT program-UNAM to CR (PAPIIT IN204019). The authors are also grateful to Aura Buenfil-Ávila; Otilio Avendaño and Torrejón-Magallanes who helped collecting the occurrence data and reviewing them; Diana Fischer for editorial services in English.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106741>.

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