Potential effects of elevated temperature on seasonal movements in slipper lobsters, Scyllarides latus (Latreille, 1803), in the eastern Mediterranean

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Potential effects of elevated temperature on seasonal movements in slipper lobster, *Scyllarides latus* (Latreille, 1803), in the eastern Mediterranean

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Abstract

Temperature serves a predominant motivator for movement and activity over a wide range of mobile marine ectotherms. Water temperature modulates the movements of many lobster species, which can vary widely over spatial and temporal scales. Providing insight into the thermal preferences (and refuges) that some lobsters seek remains a key tenet to our understanding of the behavioral ecology of these animals. The Mediterranean slipper lobster (*Scyllarides latus*) shows seasonal movements throughout most of its range and is subject to a changing thermal environment. We examined the seasonal movements of *S. latus* within a small marine reserve (Rosh Hanikra Marine Reserve, RHR) off the coast of Israel and tested the hypothesis that *S. latus* engage in increased movements when subjected to temperatures outside their preferred range. We conducted a field survey in the RHR and tagged lobsters (n = 81, carapace length, CL_{avg} = 88.7 ± 4.6) to investigate their activity during their putative summer movement. In the lab, we exposed a separate set of lobsters (n = 10, CL_{avg} = 83.1 ± 6.1) to the same thermal profiles as in the field and assayed their locomotion using activity wheels. Field results revealed that lobsters tagged in shallow waters moved to deeper, cooler waters (~ 30 m) over the course of 2 - 2.5 months, traveling an average distance of 3.4 km (range = 1 - 5 km). Our lab results showed that *S. latus* are more active at higher temperatures during dawn hours, but revealed that warming water temperatures elicited markedly longer movements over a similar timeframe. Combined, these findings suggest that increasing water temperatures in the eastern Mediterranean (Levant) may affect lobster movements and could alter seasonal patterns of distribution as well.

Keywords: *Scyllarides latus*; slipper lobster; movement ecology; thermal threshold; Levant basin.

Introduction

Mobile marine ectotherms are highly influenced by changes in temperature and respond in many cases through movements or changes in activity. Highly mobile crustaceans like lobsters have the capacity to engage in daily, seasonal, and migratory excursions on a variety of temporal and spatial scales (reviewed in Bauer, 2018). Water temperature has a significant and pervasive factor on the movement and distribution of lobsters due to their preference to some temperatures, and avoidance of others (Herrnkind, 1980; Lawton & Lavalli, 1995; Childress & Jury, 2008). Related studies of both clawed (nephropid) and spiny (palinurid) lobsters, particularly commercially important species, have greatly enhanced our understanding of lobster movements, their patterns and processes and, as a result, have driven important fishery-related assessments for lobsters, including those in the Mediterranean (Follesa *et al.*, 2008; Phillips *et al.*, 2013; Colloca *et al.*, 2017; Catanese *et al.*, 2018; Alborés *et al.*, 2019; Cau *et al.*, 2019).

By comparison, movement studies in a third major group of lobsters, scyllarids (slipper lobsters), are far less studied due to their cryptic behaviors and diminutive status as a worldwide fishery (Spanier & Lavalli, 2007; 2013). Nonetheless, some scyllarid species (~30/89) comprise targeted fisheries or bycatch from shrimping, or are part of an increasing artisanal fishery (DeMartini & Williams, 2001; Pessani & Mura, 2007; Spanier & Lavalli, 2007; de Almeida Duarte *et al*., 2010; Giraldes *et al*., 2015). Empirical evidence suggests that the exploitation of some slipper lobster species has been steadily increasing (Spanier & Lavalli, 2013; de Almeida Duarte *et al*., 2014) and merits continued investigations of their life-cycle processes including their growth, movement, and behavior.

The Mediterranean slipper lobster, *Scyllarides latus*, (Latreille, 1803) represents a commercially- and ecolog-

482

Medit. Mar. Sci., 21/2 2020, 482-492

ically important species throughout its range. Like other scyllarids, *S. latus* are highly mobile, can attain large sizes, and inhabit a range of depths (4-100 m) in the Mediterranean Sea and eastern Atlantic Ocean from Portugal south to Gambia, the Azores, and Cape Verde (Martins, 1985; Spanier & Lavalli, 1998). As with many scyllarid lobsters, there remain gaps in the knowledge of natural history, behavior, reproduction, and development of *S. latus* to the extent that it is currently considered a data deficient species under the IUCN Red List (Butler *et al*., 2011) due to the lack of useful information relevant to managing this species as a fishery.

In the Levantine basin of the Eastern Mediterranean, adult *S. latus* are most frequently found on hard substrata and rocky outcroppings in coastal waters where they shelter during the day on the ceilings of highly recessed and dimly lit caves or crevices (Spanier *et al*., 1993; Barshaw & Spanier, 1994). With respect to activity and movement, these lobsters show strong nocturnal and crepuscular behavior entrained by an endogenous circadian rhythm (Spanier *et al*., 1993; Goldstein *et al*., 2015). Typically, the number of *S. latus* in these shallow waters decreases toward the end of the summer and fall when they are rare or completely absent in nearshore habitats (Spanier *et al*., 1988; Spanier & Lavalli, 1998).

A long-term study by Spanier *et al.* (1988) suggested that *S. latus* move to deeper, cooler waters to avoid the high and perhaps unfavorable, late summer and early fall water temperatures of the shallower and warmer Levant basin. That study's hypothesis was evaluated by collecting and tagging lobsters that were released on an artificial reef (20 m depth), and monitored over three consecutive years. Results indicated that lobster numbers peaked in the spring months (the reproductive season) but subsequently decreased toward mid-summer and were rare by late fall. These results correlated well with temperature (warm temperatures had few lobsters, and vice-versa; see Figure 3 in Spanier *et al*., 1988) but did not identify a temperature value that served as a threshold for inducing movement to other thermal refuges. Therefore, a primary goal of the present study was to address how temperature (and specifically thermal thresholds) influence seasonal movements for *S. latus* in the Levant basin.

Through its effect on water temperature, climate change is predicted to influence both temporal and spatial shifts in lobster populations (Caputi *et al*., 2013; Boavida-Portugal *et al*., 2018). Factors in a changing ocean climate (e.g. temperature, salinity, carbonate chemistry) can subsequently shift the patterns of distribution of lobsters in some areas and potentially modulate many aspects of their life-history including the timing of molt and reproductive maturation, among others (Waddy & Aiken, 1995; Caputi et *al*., 2013; Jury & Watson, 2013; Goldstein & Watson, 2015).

Although we have a better understanding of the temperature-movement paradigm for both clawed (e.g. Jury & Watson, 2013) and spiny (e.g. Kanciruk & Herrnkind, 1978) lobster groups, there is disproportionately less known of this connection with slipper lobsters. Thus, the other goal of our work was to experimentally elicit

incrementally warmer thermal conditions for *S. latus* to determine what thermal 'trigger' might motivate these animals to move and, to what extent. This information has value not only to our particular study area (a small marine reserve in the eastern Mediterranean), but also serves to provide empirical data that potentially allow us to predict how changes in ocean climate may alter movement patterns in this species on smaller scales. To address these goals, we first confirmed the shallow-to-deeper water movements in *S. latus* between summer and fall using a mark-recapture pilot study. We then complimented this field-based study in the laboratory to evaluate an overall index of lobster activity (running wheels) to assay their movements using a temperature range matching that in the field.

Materials and Methods

Field study site

The Rosh Hanikra National Marine Nature Reserve (herein, RHR) is located ~ 5 km north of the city of Nahariyya on the northern Israeli coast and borders Lebanon on its northern boundary at Rosh Hanikra (33°03′00″N; 35°06′00″E, Figure 1, also see Becker & Lavee, 2009). Since 1968, the RHR has been overseen and managed by the Israel Nature and Park Authority and comprises an area 5 km (north-south) by 15 km (east-west). Like many shallow inshore systems in northern Israel, subtidal ben-
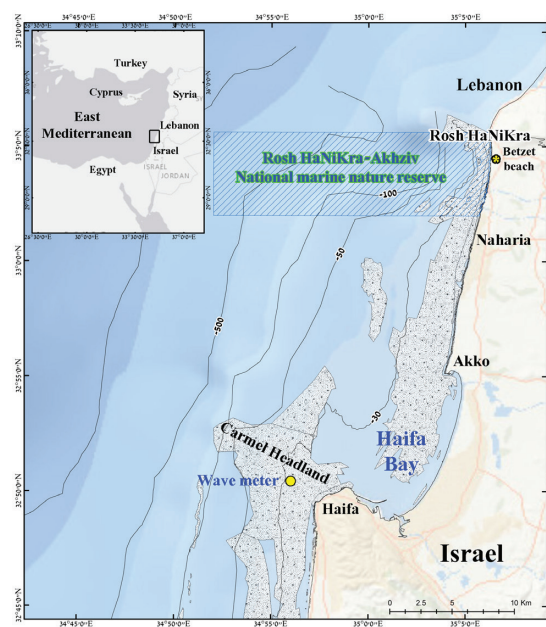

Fig. 1: Field study location in the Eastern Mediterranean Sea. The Rosh Hanikra Marine Reserve (RHR) in the northern part of the Israeli coast bordering Lebanon on its northern boundary at Rosh Hanikra. The RHR comprises an area 5 km in length (North-South) by 2 km width (East-West) covering a total of 10 km². (Figure adapted from Spanier *et al*., 2017).

Medit. Mar. Sci., 21/2, 2020, 482-492

483

thic habitats are characterized by hard complex substrata (i.e. cemented aeolian sandstone, locally termed Kurkar) that commonly include submerged ridges, caves, crevices, rocky outcroppings, and solution holes (Eytam & Ben-Avraham, 1992). These features support shelters for slipper lobsters where they are commonly found aggregating in groups during the day (Spanier *et al.*, 1993). Previous research (Spanier *et al.*, 1988) in this study area have substantiated the proclivity of *S. latus* to reside in such places and this is where we focused our survey and tagging efforts.

Field tagging study

All lobsters were collected by SCUBA divers in the spring of 2013 in shallow waters (15-20 m) of the RHR, ~ 1 - 2 km west from the Betzet beach area (Fig. 1). Animals were placed in catch bags and brought to the surface where they were processed for tagging onboard a small research vessel. All lobsters were inspected for injuries and measured to the nearest 1 mm carapace length (CL) using standard dial calipers. Each lobster was fitted with a flexible T-bar anchor tag (FD series, Floy Tag & Mfg. Inc., Seattle, WA) that was inserted into the musculature at the base of the dorsal carapace (between the third and fourth abdominal segments) with a Mark III tagging gun. Previous studies have tested the efficacy (i.e. tag retention and mortality) of this tag type and its placement in both lab and field studies with good success (Spanier & Barshaw, 1993; Bianchini *et al*., 2001; Follesa *et al.*, 2008; 2011). Each tag contained a unique ID number and contact information to report recaptured animals. Informational flyers were posted at a nearby local dive shop and at fishing harbors in the area to inform fishers and recreational divers of the details of this study.

A total of 81 lobsters (carapace length; CL_{avg} = 88.7 ± 4.6 mm, 50 males, 31 females, two of which were ovigerous) were caught over the period of March-April 2013, tagged, and released in the same areas where they were collected. It is worthwhile to note that although these tagging numbers are relatively low compared with other studies, it is very challenging to find ample numbers of *S. latus* for such work, and we recognize this limitation. Tagged lobsters were released in clusters in three separate areas at depths of 10 - 15 m and all tagged lobsters were released using a weighted volitional cage (plastic mesh cage with two escape vents) lowered to the bottom in the release area, similarly to Goldstein & Watson (2015). A total of four temperature loggers (HOBO Pendant logger, model UA-002-64, Onset Computer Co., Bourne, MA) were installed in the study area: two at the release locations (10-12 m depth), and two at deeper locations (25 m) ~ 2 - 3 km from the release site. We also had one other temperature logger inside the recesses of a cave where slipper lobsters were collected (12 - 15 m depth). All loggers were retrieved and downloaded at regular intervals.

We conducted monthly SCUBA surveys (May-October) throughout the tagging area and in deeper waters using both visual and transect surveys designed after Clark

et al. (2015) to obtain relative lobster abundance and to standardize our approach. Briefly, divers collected lobsters present along each of four 30 m transects (4 - 5 m wide) in each of the cardinal directions at three distinct sites. In addition, caves and solution holes were checked at each survey, and we enlisted the help of recreational divers to assist in these survey efforts. Artisanal fishermen were contacted and volunteered to fish in some of our survey areas, but tended to set their nets in deeper waters (> 20 m) and reported tagged lobster captures when they occurred. For all lobsters recaptured (or sighted) through diving or fishing efforts, we noted the depth and location for each animal. We also estimated the longest distance traveled for those lobsters using the 'distance measuring' tool in ArcGIS v.10.4.1 (ESRI, Redlands, CA). We compiled all recapture locations to produce a geo-referenced map to examine dispersal patterns during the course of the study but particularly at two distinct intervals, end of summer and fall.

Laboratory activity assays

Animal preparation

We conducted these assays in 2014 so that we could model our temperature regimes after our field study. For this assay, slipper lobsters (n = 10) were collected in one of two ways: (1) by SCUBA divers (n = 7) from just outside the RHR at depths similar to the field study collection sites or; (2) purchased fresh and live at a local fish market (n = 3); again to help supplement low catch rates from the field. All animals were transported by coolers to the University of Haifa Marine Laboratory for all subsequent work. *S. latus* were kept in individual holding aquaria (50 L/each) with filtered seawater collected from a similar location, and fitted with both biological and mechanical filtration systems, aeration, and acclimated to the approximate temperature that corresponded to field conditions in late winter/early spring temperatures (Fig. 2). New seawater (set to the same temperature as each tank) was exchanged for each holding tank every 2 - 3 days. All lobsters were held at lighting regimes (12:12 h., light: dark) produced by full-spectrum lights (Ikea Sparsam model 1230, 7 W, 45 lm W^{-1}) at an intensity of 1850 ± 0.64 lux. Lobsters were fed twice weekly a combination of fresh mussels and limpets.

Experimental setup

In an effort to assess overall activity measured by distance moved, we conducted a series of activity assays using two 'running wheels'; running wheel assemblies were designed after Chabot *et al*. (2004) for horseshoe crabs (*Limulus polyphemus*). Briefly, each wheel was constructed from the bottom half of a 19 L plastic utility bucket that was cut in half horizontally. Both halves were connected using a small PVC rod (axel) and the wheel was perforated with small holes to allow the flow of wa-
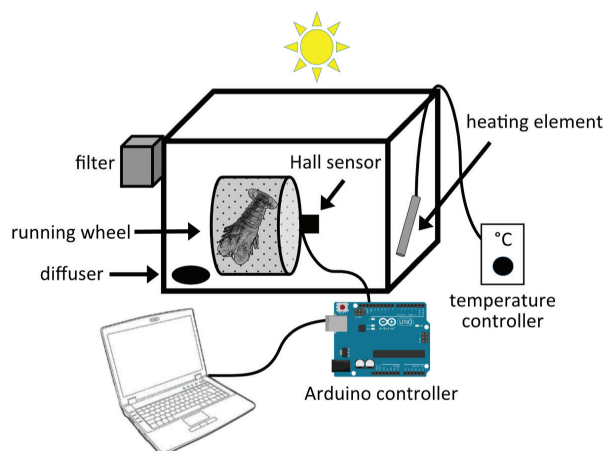
484

Medit. Mar. Sci., 21/2 2020, 482-492

Fig. 2: Running wheel assemblies for examining activity with temperature (see methods for full details). The wheel is affixed to a PVC A-frame and placed at the bottom of a 50 L aquarium tank. Seawater was maintained using a small power filter and water could be incrementally heated with the addition of a submersible heater. To obtain data, a small magnet was mounted on the inside of the wheel along with a Hall effect sensor that was connected to a microcontroller and recorded data to a laptop computer.

ter as it turned. The wheel was affixed to a PVC A-frame stand that was weighted to allow it to stand at the bottom of each of two replicate 50 L aquaria tanks (Fig. 2). Seawater was circulated throughout the 50 L aquarium tank using a small power filter (Aqueon 10, Franklin, WI) and seawater could be incrementally heated with the addition of a submersible 500 W titanium heater (FinnexTH500+, Rhinelander, WI) coupled to a digital thermostat controller (model Nema type 4X, Aqualogic Inc., San Diego, CA).

Running wheel assays

A single lobster was placed in each running wheel apparatus (two in total) and allowed to acclimate for four hours during the day when their activity is negligible (Spanier & Lavalli, 1998; Goldstein *et al*., 2015); lighting conditions mimicked those in the holding tanks. Conceptually, as each animal engaged in horizontal movement (i.e. walking), the wheel turned and rotations were enumerated (Fig. 2) to determine an index of activity. To accomplish this, we fastened a small magnet to a position on the inside of the wheel while also mounting an analog transducer (Hall effect sensor, model ACS712, 66-185 mV/A output sensitivity Sparkfun, Niwot, CO) to the outside running wheel frame which, when in close alignment to the magnet, responded in the form of an output voltage (switch). The Hall sensor was integrated with a microcontroller board (Arduino Uno-3, Adafruit Industries, New York, NY) that logged voltage data to a MacBook Pro laptop (Apple Inc., Cuppertino, CA) via a serial interface and coding algorithm written in an Arduinio 'Sketch' interface (see: https://github.com/arduino).

Thus, as an animal began its movement inside the running wheel, one rotation corresponded to an event as logged by our sensor configuration. In this case, a single

rotation was calculated as $(2\pi*r)$ or 0.82 m. A total of 10 lobsters (CL_{avg} = 88.7 ± 4.6 mm, 6 males and 4 females) were tested in our running wheels. At the outset of each trial, we started each individual lobster at a temperature of 20°C (lower end) for a 24 h period, after which we incrementally increased temperatures 1°C for each subsequent 24 h period for a total trial period of nine consecutive days (28°C, higher end); each lobster was allowed to walk freely within each wheel. Lobsters were not fed during each trial but water was exchanged (as described for the holding tanks) in the early morning during documented periods of inactivity (see Goldstein *et al*., 2015). In all trials, we first quantified the number of wheel rotations and compared these with each temperature value along our thermal gradient from 20 - 28°C. Secondly, we compared the overall activity for each of these lobsters over 24 h by calculating the percentage of time active (wheel rotations) vs. the percentage of time inactive (no wheel rotations) between two treatments (20°C vs. 28°C) over five designated time periods [1) 0:00-4:00; 2) 5:00-7:00; 3) 8:00-14:00; 4) 15:00-19:00; and 5) 20:00-23:00]. These time periods were selected as they correspond to diel activity patterns for *S. latus* in a complementary study (Goldstein *et al*., 2015).

Statistical analyses

We utilized a repeated measures ANOVA design (under standard parametric statistical assumptions) to compare the index of activity at these two temperatures and regression analysis to compare movement along with increasing temperatures. We also set up two types of controls in this study to help us validate if lobsters simply changed walking patterns with time at a constant temperature (control-1) or if our data were the result of increasing temperature (i.e. temperature that caused the

index of activity to change; control-2). In control-1 we tested a total of four lobsters (CL_{avg} = 86.2 ± 3.3 mm, 2 males and 2 females) that were subjected to a constant temperature (20°C) over the same nine-day trial period as the experimental lobsters (20° - 28°C); in control-2 we subjected an additional four lobsters (CL_{avg} = 85.1 ± 2.2 mm, 2 males and 2 females) to changes in low temperature (20 - 22°C) and high-temperature (26 - 28°C). Lobsters in both controls were used in the same running wheel apparatus setup and acclimated similarly as the experimental animals. All data were analyzed using JMP v. 13.0.0 (SAS Institute, Cary, NC) statistical software and means are reported as ±sem.

Results

Temperature data

In-situ seawater temperatures (HOBO temperature loggers) for two separate (but comparative) time series are given in Figure 3. Over the March-November period, bottom seawater temperatures averaged 23.8 ± 1.3°C for 1984-1986 (data from Spanier *et al.*, 1988) and 25.1 ± 1.4°C for 2010-2013. A measureable increase in temperature (+10.4% for 1984-1986 and +19% for 2010-2013) began in late spring (May) and continued through the summer, peaking in August. These seasonal increases in bottom temperature were always higher for the period 2010-2013 than for 1984-1986 (Fig. 3). Additionally, temperatures, from the two cave structures we monitored, were slightly cooler (average = 24.2 ± 0.8°C) but not different from the 2010-2013 time series (t-test, t_{15} = 0.46, p = 0.61).

Field study

A total of 11 separate lobsters were recaptured, 9 by SCUBA and 2 by trammel net, 13.6% recaptured) during surveys in July at an average seawater temperature of 28.8°C corresponding to depths ranging from 5-35 m (average = 20 m, Fig. 4). Temperatures were confirmed by divers or fishermen who sampled the water at depth using a HOBO temperature logger for a total of 15 min. A total of three lobsters were recaptured (all by SCUBA, 6.2% recaptured) during surveys in September at an average seawater temperature of 28.6°C corresponding to depths of 15-55 m (average = 25 m, Fig. 4). Over the course of the study a total of three lobsters were recaptured twice. Lobsters dispersed generally in a south or west direction from their original point of tag and release; one lobster remained at the tagging location for the duration of the study (verified by SCUBA). The longest distance traveled by lobsters that were captured in July (n = 11) ranged from 0.1 - 3.9 km compared with distances traveled by lobsters (n = 5) that were captured in September and ranged from 2.1 - 3.9 km. Although we did not find differences between male and female lobster movements, one of our tagged ovigerous females moved the furthest which warrants further investgation with more animals in the future (Fig. 4).

Laboratory study

In general, there was a positive association between the index of activity and increasing seawater temperatures for all lobsters tested (n = 10) in this assay (Pearson's correlation, r^2_{adj} = 0.78, $F_{1,35}$ = 62.38, p < 0.001, Fig. 5); there were also no differences (p = 0.89) between males and females with respect to movement in these tri-
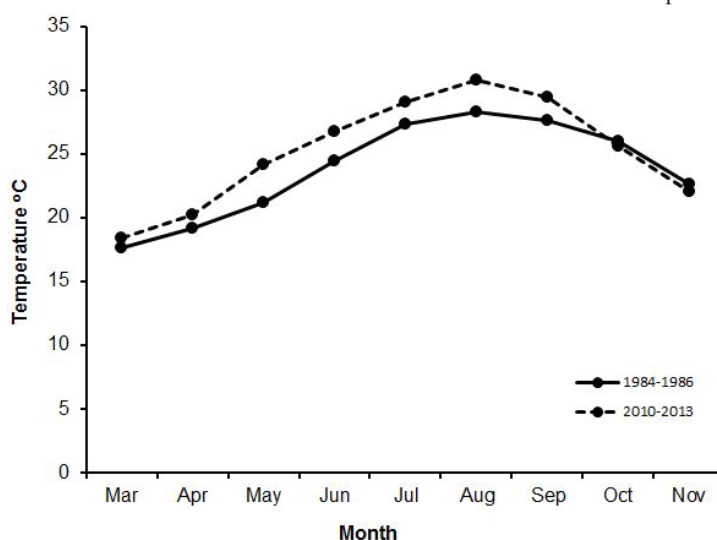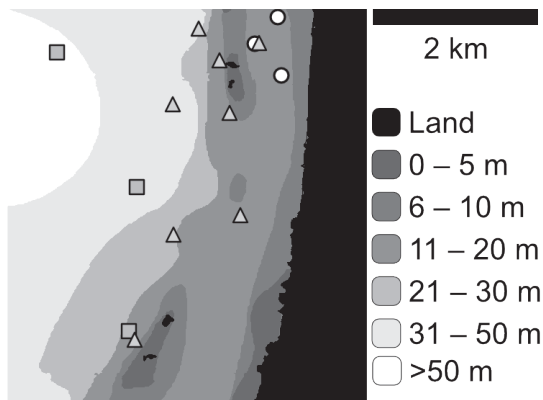

Fig. 3: Monthly temperature averages (± sem) compiled over three field seasons for 1984-1986 (reference data from Spanier *et al.*, 1988, closed circles) and 2010-2013 (this study, open circles) for representative inshore locations using oceanographic data and *In-situ* temperature (HOBO) loggers, respectively. From March-November, bottom seawater temperatures averaged 23.8 ± 1.3°C for 1984-1986 and 25.1 ± 1.4°C for 2010-2013.

486

Medit. Mar. Sci., 21/2 2020, 482-492

Fig. 4: Initial collection and release locations (~~black~~ circles) for lobsters (n = 81,) in the RHR between March-April, 2013. The majority of tagged lobsters (n = 63) were released using volitional cages; the remaining lobsters (n = 18) were released by SCUBA divers in the same areas; recapture locations in July (n = 11, triangles) and September (n = 3, squares).

als. Temperatures > 24°C resulted in linear movements that were markedly different from those < 24°C (Table 1). Furthermore, there was no significant difference in lobsters (n = 3) and their index of activity at a constant (20°C) temperature (control-1, r^2_{adj} = 0.087, $F_{4,12}$ = 0.033, p = 0.860) nor was there a difference in the index of activity at either the low or high ranges of temperature change (control-2, r^2_{adj} = 0.042, p = 0.61 (low); r^2_{adj} = 0.029, p = 0.74 (high). When evaluating lobsters over their diel period of activity at two disparate temperatures (20°C vs. 28°C), activity appeared to be comparable across all time periods; however, we did find a difference with respect to early morning time periods of 5:00-7:00 AM (RMANO-VA, $F_{1,7}$, p = 0.032, Tukey HSD, p < 0.01, Fig. 6).
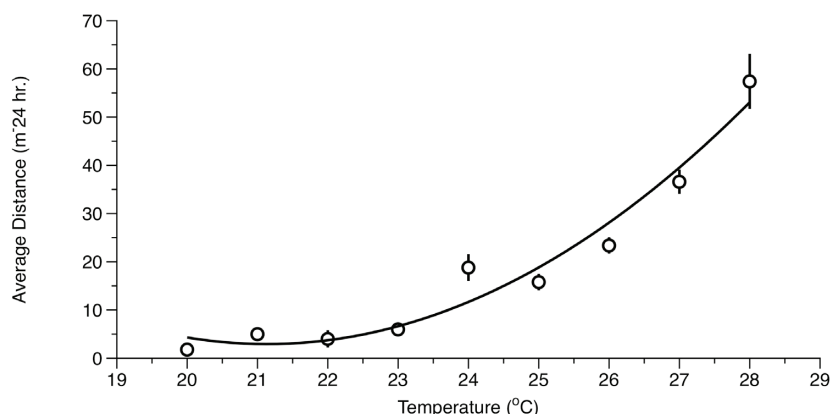
Discussion

Despite patterns of decadal variability, the Mediterranean Sea remains one of the most vulnerable bodies of water in the world (Adloff *et al*., 2015; Mariotti *et al*., 2015; Schroeder *et al*., 2016; Lionello & Scarascia, 2018). Due to a host of factors including habitat loss, eutrophication, pollution, overexploitation, the establishment of alien species, and the rise in overall sea-surface temperature, the Mediterranean, including the Levant basin (our study area), is considered a hot spot for climate change (Turley, 1999; Galil, 2007; 2009; Coll *et al*., 2010; Edelist *et al*., 2012). Considering the importance of lobsters (*S. latus*) in the eastern Mediterranean, as a commercially important species, and the role that they play as a sentinel for climate change, we were interested in following patterns of seasonal movement under contrasting thermal regimes for Mediterranean slipper lobster.

Our results suggest that lobsters tagged in shallow waters (15 - 20 m) of the Levant basin move into deeper, cooler waters during the winter season as already shown by Spanier *et al*. (1988). However, we were also able to pair these movements in the field with a laboratory assay at temperatures that represented *in-situ* conditions to examine the activity of these animals over elevated seawater temperature events, albeit over a shorter time frame. The shallow-to-deep seasonal movements by *S. latus* occur even in disparate portions of their range. For example, DaFranca & Paes-DaFranca (1961) studied the movements of *S. latus* in the Cape Verde islands and reported catches of lobsters in spring to late summer in shallow waters, however they did not sample for lobsters over the winter months. In the Azores Islands, in the western Mediterranean, Martins (1985) investigated *S. latus* caught during local commercial fishing operations and found that lobsters moved from shallow (5-20 m) into deeper (70-75 m) waters in the fall making directed movements back to shallow waters in the spring. More recently, a study in the Balearic Islands suggests

Fig. 5: Relationship between the distance lobsters traveled with increasing seawater temperatures (Pearson's correlation, r^2_{adj} = 0.78, $F_{1,35}$ = 62.38, p < 0.001) with model (second-order polynomial) model as:
Activity = -66.38+3.02*Temp+0.53*(Temp-23.89)². Temperatures > 24°C resulted in movements that were markedly different than those <24°C. However, activitiy levels were not different with temperature except for dawn hours (see Fig. 6). Values given ± sem (see Table 1).

Medit. Mar. Sci., 21/2, 2020, 482-492

487

Table 1. Distances moved by lobsters (n= 10) in the running wheels (see Fig. 2) in association with temperature. Average linear distances moved are given in m 24^{-hr} ± sem.

Temp. °C	Avg. Dist. (m/24hrs)
20	1.8 ± 0.4
21	5.0 ± 0.5
22	4.0 ± 0.4
23	6.0 ± 0.9
24	18.8 ± 2.8
25	15.8 ± 1.7
26	23.4 ± 1.7
27	36.6 ± 2.5
28	57.4 ± 5.7

that *S. latus* remain in deeper waters year-round, hibernating in caves where the temperature stays warmer during the winter months (Díaz *et al*., 2017). Other tagging campaigns with slipper lobsters (reviewed in Spanier & Lavalli, 2007) report a variety of seasonal horizontal migrations that include waters around Sicily, the Galapagos Islands, the Florida Keys, and Western Australia. Although many of these studies involved large, programmatic efforts and many more tagged animals than the present study, the patterns that were discerned (e.g. seasonal movements to deeper, cooler waters), including recapture rates (range: ~ 6-14%) were comparable with our study's findings from the field. Having the ability to describe fine-scale movements in slipper lobsters using acoustic telemetry, as has been done in other lobsters (e.g. Moland *et al*., 2011; Bertelsen, 2013; Goldstein & Watson, 2015) as well as in a recent pilot acoustic telemetry study of *S. latus* in the RHR (Miller, 2019; Alexandri *et al*., 2020), would provide a valuable and much needed tool for a more comprehensive understanding of the spatio-temporal requirements for *S. latus*. To-date, only one published study using slipper lobsters (*S. latus*) attempted

to use acoustic tagging to evaluate tag retention and molting of animals held in cages in the Azores (Schmiing & Afonso, 2009). Clearly, more work is needed to study this underrepresented group of lobsters and their associated movement ecology.

The motivations for such lobster movements have been less clear, although some examples point to environmental thresholds (i.e. temperature, turbidity) as a trigger initiating such movement events. Very few studies have been able to show conclusively that water temperature is the only parameter tied to lobster movements. For example, Kanciruk & Herrnkind (1978) reported that temperature decreases coupled with high wave action and increased turbidity correlate well with mass movements of Caribbean spiny lobster (*Panulirus argus)* to offshore waters in the Bahamas. Goldstein & Watson (2015) documented a similar pattern for clawed lobsters (*Homarus americanus*) in the southern Gulf of Maine in the fall when water temperatures appear to reach a critical lower thermal threshold initiating the seasonal movements of lobsters into deeper waters. Even more recently, Spanier *et al*. (2017) showed that intense winter storms might actually be the cause of *S. latus* strandings (on beaches) as was the case in the winter of 2016. We do know that, in general, water temperature (both absolute values and rates of change) has a pervasive influence on many aspects of lobster life histories (in many species) including modulating growth and reproductive maturity, as well as in synchronizing the molt cycle (Spanier & Lavalli, 1998; Waddy & Aiken, 1995; Hearn *et al*., 2007). Other ecophysiological factors (e.g. dissolved oxygen, pH, turbidity) may also be at play and also work to influence movement as well and could be incorporated into future high-resolution tracking studies.

The movement of lobsters to deeper, cooler waters, along with their propensity to increase their activity in response to elevated seawater temperatures (Spanier *et al*., 1988; the present study), supports a general paradigm that *S. latus,* as well as other lobsters, avoid ele-
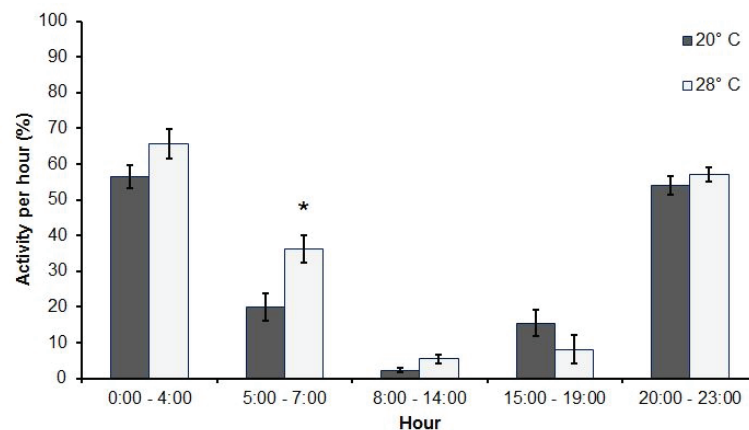

Fig. 6: Average activity per hour over a 24 hr. period for lobsters (n = 8) at two different temperatures, 20°C (spring) and 28°C (summer) over five distinct times of day in the running wheel apparatus (see Fig. 2 for details). Activity appeared to be comparable across all periods but not different across temperature values. however, we did find a difference with respect to our early morning time frame (ANOVA, $F_{1,7}$, p = 0.032, Tukey HSD, p < 0.01) of 5:00-7:00 AM.

vated temperatures that typically manifest themselves at certain times of the year (Spanier *et al*., 1988, Childress & Jury, 2008; Jury & Watson, 2013; the present study). In the Levant basin of the Mediterranean, these unfavorable temperatures may exceed 30°C at times (Fig. 3), and may be implicated in molting complications (Spanier & Barshaw, 1993) and possibly other physiological challenges (e.g. respiration, feeding, acid-base balance, Spanier & Lavalli, 2007). In some cases, *S. latus* held in the laboratory for prolonged periods of time (> 2 months) at water temperatures exceeding 27°C, experienced high levels of mortality (Spanier & Barshaw, 1993; Spanier & Goldstein, pers obs). Physical conditions in the eastern Mediterranean have changed dramatically over the last two decades (Rilov & Treves, 2010; Marba *et al*., 2015) and data support the trend that sea surface temperature in the Levantine basin has increased by ~ 1-2°C over the last 20 years (Edelist *et al*., 2012; Fig. 3). Longer-term oceanographic data in this geographic area further corroborates this change as Gertman *et al*. (2013) and Ozer *et al*. (2017) report increases of the Levantine surface water temperature (0.1°C/year) over the last 33 years averaging 24-25°C in the mid-1980s compared with 26-27°C in 2010-2015. Just as pivotal, both minimum (winter) and maximum (summer) water temperatures are also increasing, which may facilitate not only the persistence of invasive species (Rilov & Treves, 2010), but also the challenges that native fauna such as lobsters (and other decapods) would encounter. This includes synchronizing important biological processes and cuing to environmental triggers like temperature thresholds, which modulate both their daily and seasonal activities.

Collectively then, these rapid rates of increase may be particularly problematic to species (even highly mobile ones) such as lobsters. In the present study, the option for individual lobsters to move sooner (i.e. leave shallow areas to move to deeper ones) and move further (Fig. 5) may have implications for some life-history events such as the timing associated with egg development and hatching location in ovigerous females. While a marine reserve like RHR may help support these animals with sufficient physical habitat, resources, and protection from fisheries, it may not necessarily serve as an adequate thermal refuge. This and other environmental criteria (e.g. pH, dissolved oxygen, salinity) should be considered in the selection and design of future reserves or marine protected areas (MPAs), especially in shallow, coastal locations that may not support seasonal movements for slipper lobsters (DiNardo & Moffitt, 2007; Hearn *et al.*, 2007). In studies that have examined lobsters in reserves (Childress, 1997) the following common features emerge with respect to MPAs: 1) the need for reserves to be large enough to support the range of movements that lobsters exhibit (Kelly & MacDiarmid, 2003); 2) protecting sufficient critical habitats (e.g. fore reef) that are important to lobster life-histories (Bertelsen, 2013); and 3) the inclusion of deep habitat to support cooler, wintertime temperatures during seasonal movements (Moland *et al*., 2011). In the context of MPA conservation and management, it is difficult to ascertain the full extent to which our tagged lob-

sters utilized the RHR, especially given the small number of animals that we were able to tag due to logistical challenges (see Goñi *et al.*, 2006; Follesca *et al.* 2008, 2011). However, applying the maximum rate of lobster activity at the highest temperature (28°C) obtained from our laboratory based simulations, lobsters showed movements of ~ 50 m over a 24 hr period (Fig. 5, Table 1). If we extend this theoretical value over the putative 2.0 - 2.5 month time-frame when these lobsters typically undergo seasonal movements (Spanier *et al*., 1988), this equates to ~ 3-4 km which makes it possible for some lobsters to reside within the confines of the RHR. However, these are indeed theoretical values obtained in laboratory-based assays and may not translate accurately to values *in-situ*. Therefore, whether or not *S. latus* stay or leave the RHR, having access to a thermal refuge during times when shallow, inshore temperatures are elevated should be a consideration in RHR planning. Twice over the course of this study, we dropped a temperature logger from our research vessel and recorded temperatures at 50-60 m depths in the range of 23-24°C. Thus, the deeper habitats that are within the reach of freely moving lobsters may be integral to helping these animals orchestrate aspects of their life-history (e.g. egg incubation) that require cooler temperatures for a finite period of time. This has certainly been the case in clawed lobster (*Homarus americanus*, Waddy & Aiken, 1995) and laboratory-based assays with *S. latus* could help further expand on these potential physiological requirements.

Quite a few populations of slipper lobsters have been depleted, some even to the point of becoming rare in parts of their range. *S. latus* was declared a marine species in need of protection in the western Mediterranean (Spanier, 1991; Butler *et al*., 2011) and a moratorium on slipper lobster harvesting in Sardinia was declared between 2000-2003 (Pessani & Mura, 2007). In 2005, *S. latus* was declared a protected marine species by the Israel Nature and Park Authority (Miller, 2019), however more management is needed to protect and foster sustainable harvesting of this species (Spanier & Lavalli, 2007). Due to overfishing of spiny lobsters, fishermen are more inclined to shift their efforts to slipper lobster (e.g. Polovina, 2005; Hearn *et al*., 2007); this has been reflected in world markets and is becoming increasingly concerning. Therefore, improving the biological database for such species allows fisheries managers to make better decisions for continued sustainability and buffer against the intense fishing effort and habitat degradation that plagues the unique Mediterranean basin.

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References

Adloff, F., Somot, S., Sevault, F., Jorda, G., Aznar, R. *et al.*, 2015. Mediterranean Sea response to climate change in an ensemble of twenty first century scenarios. *Climate Dynamics*, 45, 2775-2802.

Alexandri, T., Miller, E., Spanier, E., Diamant, R., 2020. Tracking the slipper lobster using acoustic tagging: Testbed description. *IEEE Journal of Ocean Engineering*, 45, 577-585.

Alborés, I., García-Soler, C., Fernández, L., 2019. Reproductive biology of the slipper lobster Scyllarus arctus in Galicia (NW Spain): Implications for fisheries management. Fisheries research, 212, 1-11.

Barshaw, D.E., Spanier, E., 1994. The undiscovered lobster: A first look at the social behavior of the Mediterranean slipper lobster, Scyllarides latus (Decapoda, Scyllaridae). Crustaceana, 67, 187-197.

Bauer, R., 2018. Life cycle and seasonal migrations. p. 203-229. In: Life histories -- The natural history of the crustacean, Welbon, G.A., Thiel, M. (Eds). Oxford University Press, London.

Becker, N., Lavee, D., 2009. Commercial development and conservation values: The case of Rosh Haniqra Marine Reserve in Israel. Journal of Infrastructure Development, 1, 93-217.

Bertelsen, R.D., 2013. Characterizing daily movements, nomadic movements, and reproductive migrations of Panulirus argus around the Western Sambo ecological reserve (Florida, USA) using acoustic telemetry. Fisheries Research, 144, 91-102.

Bianchini, M.L., Bono, G., Ragonese, S., 2001. Long-term recaptures and growth of slipper lobsters, *Scyllarides latus*, in the Strait of Sicily (Mediterranean Sea). *Crustaceana,* 74, 673-680.

Boavida-Portugal, J., Rosa, R., Calado, R., Pinto, M., Boavida-Portugal, I. *et al.*, 2018. Climate change impacts on the distribution of coastal lobsters. *Marine Biology*, 165, 186.

Butler, M., MacDiarmid, A., Cockcroft, A., 2011. *Scyllarides latus*. *The IUCN Red List of Threatened Species* 2011: e.T169983A6698918. http://dx.doi.org/10.2305/IUCN.UK.2011-1.RLTS.T169983A6698918.en. (Accessed 15 December 2019).

Caputi, N., de Lestang, S., Frusher, S., Wahle, R.A., 2013. The impact of climate change on exploited lobster stocks. p. 129-168. In: *Lobsters: biology, management, aquaculture, and fisheries 2nd Edition*. Phillips, B.F. (Ed) John Wiley & Sons, Ltd, Oxford.

Catanese, G., Hinz, H., del Mar Gil, M., Palmer, M., Breen, M. *et al.*, 2018. Comparing the catch composition, profitability and discard survival from different trammel net designs targeting common spiny lobster (Palinurus elephas) in a Mediterranean fishery. PeerJ, 6, e4707.

Cau, A., Bellodi, A., Cannas, R., Fois, M., Guidetti, P. et al., 2019. European spiny lobster recovery from overfishing enhanced through active restocking in fully protected areas. Scientific reports, 9, 1-11.

Chabot, C.C., Kent, J., Watson, W.H .III., 2004. Circatidal and circadian rhythms of locomotion in Limulus polyphemus. Biological Bulletin, 207, 72-75.

Childress, M.J. 1997. Marine reserves and their effects on lobster populations: report from a workshop. *Marine and Freshwater Research*, 48, 1111-1114.

Childress, M.J., Jury, S.H., 2008. Behaviour. p. 78-112. In: *Lobsters: Biology, management, aquaculture, and fisheries*. Phillips, B.F. (Ed). Blackwell Publishing, Oxford.

Clark, A.S., Jury, S.H., Goldstein, J.S., Langley, T.G., Watson, W.H. III., 2015. A comparison of American lobster size structure and abundance using standard and ventless traps. *Fisheries Research*, 167, 243-251.

Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasra, F., *et al.*, 2010. The biodiversity of the Mediterranean Sea: Estimates, patterns, and threats. *PLos ONE*, 5, e11842, 1-36.

Colloca, F., Scarcella, G., Libralato, S., 2017. Recent trends and impacts of fisheries exploitation on Mediterranean stocks and ecosystems. *Frontiers in Marine Science*, 4, 244.

DaFranca, P., Paes-Da Franca, M.L., 1961. Nova contribuicao para o conhecimento da lagostas do arquipelago de Cabo Verde. *Notas mimeografadas do Centro Biologia Piscatoria*, 19, 1-17.

DeMartini, E.E., Williams, H.A., 2001. Fecundity and egg size of *Scyllarides squammosus* (Decapoda: Scyllaridae) at Maro Reef, Northwestern Hawaiian Islands. *Journal Crustacean Biology*. 21, 891-896.

Díaz, D., Hereu, B., Aspillaga, E., Muñoz, A., Bartumeus, F. et al., 2017. Hibernation of the slipper lobster Scyllarides latus in the western Mediterranean. Presented at the 11th International Lobster Biology and Management Workshop., 4-7 June 2017. Portland, Maine USA.

DiNardo, G.T., Moffitt, R.B., 2007. The Northwestern Hawaiian island lobster fishery: A targeted slipper lobster fishery. p. 243-262. In: *The biology and fisheries of the slipper lobster. Crustacean Issues 17*. Lavalli, K.L., Spanier, E. (Eds). CRC Press, New York.

de Almeida Duarte, L.F., Severino-Rodrigues, E., Gasalla, M.A., 2010. Slipper lobster (Crustacea, Decapoda, Scyllaridae) fisheries off the southeastern coast of Brazil: I. exploitation patterns between 23°00′ and 29°65′S. *Fisheries Research*, 102, 141-151.

de Almeida Duarte, L.F., Rodrigues, E.S., Pinheiro, M.A.A., Gasalla, M.S., 2014. Slipper lobsters (Scyllaridae) off the southeastern coast of Brazil: relative growth, population structure, and reproductive biology. *Fisheries Research*, 113, 55-68.

490

Medit. Mar. Sci., 21/2 2020, 482-492

Edelist, D., Golani, D., Rilov, G., Spanier, E., 2012. The invasive venomous striped eel catfish *Plotosus lineatus* in the Levant: possible mechanisms facilitating its rapid invasional success. *Marine Biology*, 159, 283-290.

Eytam, Y., Ben-Avraham, Z., 1992. Morphology and sediments of the inner shelf off northern Israel. Israel Journal of Earth Sciences, 41, 27-44.

Follesa, M.C., Cuccu, D., Cannas, R., Cabiddu, S., Murenu, M. *et al.,* 2008. Effects of protection on spiny lobster abundance and size (*Palinurus elephas* Fabr. 1787) in a Central Western Mediterranean Area. *Hydrobiologia,* 606, 63-68.

Follesa, M.C., Cannas, R., Cau, A., Cuccu, D., Gastoni, A. *et al.,* 2011. Spillover effects of a Mediterranean marine protected area on the European spiny lobster *Palinurus elephas* resource. *Aquatic Conservation Marine Freshwater Ecosystem,* 21, 564-572.

Galil, B.S., 2007. Seeing Red: Alien species along the Mediterranean coast of Israel. *Aquatic Invasions*, 2, 281-312.

Galil, B.S., 2009. Taking stock: Inventory of alien species in the Mediterranean Sea. *Biological Invasions*, 11, 359-372.

Gertman, I., Goldman, R., Ozer, T., Zodiatis, G., 2013. Interannual changes in the thermohaline structure of the Southeastern Mediterranean. *Rapp Comm int Mer Médit*, 40, 211.

Giraldes, B.W., Silva, A.Z., Correa, F.M., Smyth, D.M., 2015 Artisinal fishing of spiny lobsters with gillnets – A significant anthropic impact on tropical reef ecosystem. Global Ecology and Conservation, 4, 572-580.

Goldstein, J.S., Watson, W.H. III., 2015. Seasonal movements of American lobsters in southern Gulf of Maine coastal waters: Patterns, environmental triggers, and implications for larval release. Marine Ecology Progress Series, 524, 197-211.

Goldstein, J.S., Dubofsky, E.A., Spanier, E., 2015. Into a rhythm: diel activity patterns and behaviour in Mediterranean slipper lobsters, Scyllarides latus. ICES Journal of Marine Science, 72(i), 147-154.

Goñi, R., Quetglas, A., Reñones, O., 2006. Spillover of spiny lobsters Palinurus elephas from a marine reserve to an adjoining fishery. Marine Ecology Progress Series, 308, 207-219.

Hearn, A., Toral-Granda, V., Martinez, C., Reck, G., 2007. Biology and fishery of the Galapagos slipper lobster. p. 287-308. In: *The biology and fisheries of the slipper lobster. Crustacean Issues 17*. Lavalli, K.L., Spanier, E. (Eds). CRC Press, New York.

Herrnkind, W.F., 1980. Spiny lobsters: patterns of movement. p. 349-407. In: The biology and management of lobsters, vol. 1. Physiology and Behavior. Cobb, J.S., Phillips, B.F. (Eds). Academic Press, New York.

Kanciruk, P., Herrnkind, W., 1978. Mass migration of spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): behavior and environmental correlates. *Bulletin of Marine Science*, 28, 601-623.

Kelly, S., MacDiarmid, A.B., 2003. Movement patterns of mature spiny lobsters, *Jasus edwardsii*, from a marine reserve. *New Zealand Journal of Marine and Freshwater Research*, 37, 149-158.

Jury, S.H., Watson, W.H. III., 2013. Seasonal and sexual differences in the thermal preferences and movements of American lobsters. *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 1650-1657.

Lawton, P., Lavalli, K.L., 1995. Postlarval, juvenile, adolescent, and adult ecology. p. 47-81. In: *Biology of the lobster Homarus americanus*. Factor, J.R. (Ed) Academic Press, San Diego.

Lionello, P., Scarascia, L., 2018. The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change*, 18, 1481-1493.

Marba, N., Jorda, G., Agusti, S., Girard, C., Duarte, C.M., 2015. Footprints of climate change on Mediterranean Sea biota. *Frontiers in Marine Science*, 2, 56.

Mariotti, A., Pan, Y., Zeng, N., Alessandri, A., 2015. Long-term climate change in the Mediterranean region in the midst of decadal variability. *Climate Dynamics*, 44, 1437−1456.

Martins, H.R., 1985. Biological studies of the exploited stick of the Mediterranean locust lobster *Scyllarides latus* (Latreille, 1803) (Decapoda: Scyllaridae) in the Azores. *Journal Crustacean Biology*, 5, 294-305.

Miller, E., 2019. Do marine nature reserves enhance the conservation of the Mediterranean Slipper lobster (Scyllarides latus)? MSc Thesis. University of Haifa, Israel, 66 p.

Moland, E., Olsen, E.M., Knutsen, H., Knutsen, J.A., Enersen, S.E. *et al*., 2011. Activity patterns of wild European lobster *Homarus gammarus* in coastal marine reserves: implications for future reserve design. *Marine Ecology Progress Series*, 429, 197-207.

Ozer, T., Gertman, I., Kress, N., Silverman, J., Herut, B., 2017. Interannual thermohaline (1979-2014) and nutrient (2002-2014) dynamics in the Levantine surface and intermediate water masses, SE Mediterranean Sea. *Global Planet Change*, 151, 60-67.

Pessani, D., Mura, M., 2007. The biology of the Mediterranean Scyllarids. p. 264-286. In: *The biology and fisheries of the slipper lobster. Crustacean Issues 17*. Lavalli, K.L., Spanier, E. (Eds). CRC Press, New York.

Polovina, J.J. 2005. Climate variation, regime shift, and implication for sustainable fisheries. *Bulletin of Marine Science*, 76, 233-244.

Phillips, B.F., Wahle, R.A., Ward, T.J., 2013. Lobsters as part of marine ecosystems – A Review. p. 1-35. In: *Lobsters: biology, management, aquaculture, and fisheries 2nd Edition*. Phillips, B.F. (Ed). John Wiley & Sons, Ltd, Oxford.

Rilov, G., Treves, C., 2010. Climate change effects on marine ecological communities. p. 51-68. In: Seaweeds and their role in globally changing environments. Alvaro, I., Einav, R., Seckbach, J. (Eds). Springer, Amsterdam.

Schmiing, M., Afonso, P., 2009. Acoustic tag retention of the Mediterranean slipper lobster *Scyllarides latus* (Latreille, 1802) in the Azores Arquipélago. *Life and Marine Sciences*, 26, 37-43.

Schroeder, K., Chiggiato, J., Bryden, H.L., Borghini, M., Ismail, S.B., 2016. Abrupt climate shift in the Western Mediterranean Sea. *Scientific Reports*, 11 (6), 23009.

Spanier, E., Tom, M., Pisanty, S., Almog, G., 1988. Seasonality and shelter selection by the slipper lobster *Scyllarides latus* in the southeastern Mediterranean. *Marine Ecology Progress Series*, 42, 247-255.

Spanier, E., 1991. Artificial reefs to insure protection of the adult Mediterranean slipper lobster, *Scyllarides latus* (Latreille, 1803). p. 179-185. In: *Les Espéces Marines á Protéger en Méditerranée*. Boudouresque, C.F., Avon, M.,

Medit. Mar. Sci., 21/2, 2020, 482-492

491

Gravez, V. (Eds). GIS Posidonia, Marseille.

Spanier, E., Barshaw, D.E., 1993. Tag retention in the Mediterranean slipper lobster. Israel Journal Zoology, 39, 29-33.

Spanier, E., Lavalli, K.L. 1998. Natural history of *Scyllarides latus* (Crustacea Decapoda): A review of the contemporary biological knowledge of the Mediterranean slipper lobster. *Journal of Natural History*, 32, 1769-1786.

Spanier, E., Lavalli, K.L., 2007. Slipper lobster fisheries: Present status and future perspectives. P. 377-391. In: *The biology and fisheries of the slipper lobster. Crustacean Issues 17*. Lavalli, K.L., Spanier, E. (Eds). CRC Press, New York.

Spanier, E., Lavalli, K.L. 2013. Commercial Scyllarids. p. 414-466. In: *Lobsters: biology, management, aquaculture, and fisheries 2nd Edition*. Phillips, B.F. (Ed) John Wiley & Sons, Ltd, Oxford.

Spanier, E., Almog-Shtayer, G., Fiedler, U., 1993. The Mediterranean slipper lobster Scyllarides latus the known and the unknown. BIOS, 1 (1), 49-58.

Spanier, E., Miller, E., Zviely, D., 2017. Winter stranding of Mediterranean slipper lobsters, Scyllarides latus. Regional Studies in Marine Science, 14, 126-131.

Turley, C.M., 1999. The changing Mediterranean Sea – A sensitive ecosystem? *Progress in Oceanography*, 44, 387-400.

Waddy, S.L., Aiken, D.E., 1995. Temperature regulation of reproduction in female American lobsters, *Homarus americanus. ICES Marine Science Symposium*, 199, 54-60.

492

Medit. Mar. Sci., 21/2 2020, 482-492