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Seasonal and fishery impacts on the nutritional condition of the Caribbean spiny lobster *Panulirus argus* in Florida, USA

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ABSTRACT: The sublethal effects of fisheries (e.g. reduced nutritional condition or injuries) on the target species population are poorly understood, yet have the potential to reduce fishery efficiency and sustainability. The Caribbean spiny lobster *Panulirus argus* trap fishery in Florida (USA) uses live, sublegal-size lobsters as bait to lure other lobsters into the ~462 000 traps employed by the fishery. Long-term confinement of lobsters used as live bait causes stress, leading to the degradation of their nutritional condition or mortality; however, cumulative effects of confinement on nutritional condition throughout the fishing season and the effect on the population were unknown. We sampled sublegal- and legal-size lobsters hand-caught from a fished area (potentially affected by traps) and caught in commercial lobster traps in the fished area to determine how lobster health varies throughout the year and whether the intense recreational and commercial fisheries exhibit sublethal effects on lobster health. We compared the health of lobsters monthly for 1 yr using 2 nutritional indices (hepatopancreas dry weight and blood serum protein), and by the presence of external injuries and shell disease. Lobster blood serum protein and dry weight index varied throughout the year, peaking in late summer to early fall, dropping sharply during the winter, and rising again through the spring, likely in response to seasonal changes in environmental factors, such as water temperature. Both legal and sublegal lobsters within actively fished traps showed lower nutritional condition than lobsters from the surrounding population throughout the fishing season, suggesting that few lobsters escape traps.

KEY WORDS: Nutritional condition · Lobster health · Long-term confinement · Discard mortality

1. INTRODUCTION

The role of nutrition in animal physiology has a central theme in ecology. Accumulation of nutritional reserves is vital to growth and maturation, particularly in animals that require large reserves to cope with extended periods of nonfeeding (Urich 1994, Ciaramella et al. 2014). Arthropods, for example, require a minimum amount of stored energy to molt successfully. In crustaceans, nutritional condition is defined as the extent to which nutrient reserves (i.e. stored lipids and proteins) have accumulated to the levels required for normal physiological function and growth (Moore et al. 2000), and is generally measured as blood serum protein or a hepatopancreas-based index (e.g. Gutzler & Butler 2017). Factors that can influence nutritional condition include food availability (Barclay et al. 1983, Moore et al. 2000, Sánchez-Paz et al. 2007), seasonal changes in feeding, growth, and reproduction (Rosa & Nunes 2003),

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and water chemistry (Ocampo et al. 2003, Stoner et al. 2010, Lorenzon et al. 2011). Anthropogenic influences can also reduce nutritional reserves of crustaceans as a result of trap fishing (e.g. sublethal effects on trap discards and ghost fishing) (Stoner et al. 2010, Butler et al. 2018a,b).

Ideally, fishery practices balance maximizing catch with minimizing the unwanted effects like discard or bycatch mortality, in both target and nontarget species. To achieve greater catch rates, Caribbean spiny lobster *Panulirus argus* commercial trap fishers in Florida (USA) are permitted to bait their traps with live, sublegal-size lobsters (i.e. <76.2 mm carapace length, CL; hereafter referred to as sublegal lobsters) (Florida Administrative Code Chapter 68B-24.003, https://www.flrules.org/gateway/ruleno.asp?id=68B-24.003). Live lobsters are superior to other baits (such as cowhide, fish carcasses, and cat food) and can result in a catch per unit effort 3 times that of unbaited traps (Heatwole et al. 1988, Butler et al. 2022). Each trap is typically deployed with 2 to 5 sublegal lobsters as bait. Given the 462 000 traps used in the 2019 lobster-fishing season, at any one time upwards of 1 million sublegal lobsters will have been deployed as bait in traps (Matthews 2001). These bait lobsters can be held in traps for multiple weeks, as the traps are checked weekly during the early part of the fishing season and every few weeks by the end (Matthews 2001). This long-term confinement can compromise the health of the bait lobsters and can even result in their death (Butler et al. 2018a). This mortality is well recognized as a source of fishing discard mortality and as a reducer of future harvests (Matthews 2001, Butler et al. 2018a). Confinement-related mortality rates of sublegal lobsters in traps have been estimated to be ~10% of the total population (Hunt et al. 1986, Matthews 2001). Fishers typically do not feed bait lobsters or release them unless the lobsters are noticeably weakened.

Outside of direct mortality, many sublethal effects of long-term confinement have been identified. Lobsters caught in traps are subject to trap-related injuries, such as damaged legs or dactyls, which result when a portion of a leg protruding from a trap is severed as the trap is hauled aboard a commercial vessel (Davis 1981, Kennedy 1982). Long-term confinement has also been linked to increased prevalence of shell disease, visible as small pits or burn marks on the cuticle, blackening of the exoskeleton, and lesion melanization (Porter et al. 2001). An analysis of lobsters confined in ghost-fishing lobster traps (Butler et al. 2018b) indicated that long-term confinement resulted in the degradation of their nutritional condition. As it relates directly to the lobster fishery, degraded nutritional condition has been linked to reduced effectiveness of sublegal lobsters as bait and causes reduced catch rates (Butler et al. 2018a).

This study builds upon previous research findings from experimentally fished traps and from laboratory chemical-choice experiments to measure how the effects of long-term confinement and degradation of the health of lobsters used as bait affect the lobster population. We surveyed the health of lobsters caught in commercial traps and wild lobsters hand-caught in the same area in which those traps were fished to address the following questions: (1) Does lobster health vary throughout the year? (2) Do fishing practices diminish the health of lobsters in areas in which traps are fished? We hypothesized that the sublegal lobster population would be healthier when waters were closed to fishing (April–August) and at the beginning of the fishing season, and that the nutritional condition of the population would decline as the season progressed due to lobster confinement within and then escapement from traps. We also hypothesized that if lobsters used as bait were escaping or being released from traps, we would see a greater prevalence of shell disease and injuries within the fished area during the commercial fishing season. To our knowledge, this is the first study to examine how the nutritional condition of *P. argus* varies throughout the year, and how the trap fishery affects lobster health.

2. MATERIALS AND METHODS

2.1. Collection areas and field sampling

Sublegal lobsters and legal-size lobsters (≥76.2 mm CL, hereafter referred to as legal lobsters) were collected on 10 occasions from July 2019 through July 2020 from 2 areas (Fig. 1). Lobsters from commercial lobster traps were collected from the trap area north of Long Key Viaduct. In the fished area, divers hand-caught free-roaming lobsters. Both of these areas stood to be subject to different conditions that could influence lobster health. For example: (1) legal lobsters collected from commercial traps had been confined in the traps for an unknown period; (2) lobsters collected by hand in the fished area could have entered traps, been temporarily confined, and then escaped; could have been caught and released by recreational fishers, since the fishing area is open to commercial and recreational fisheries; or might never

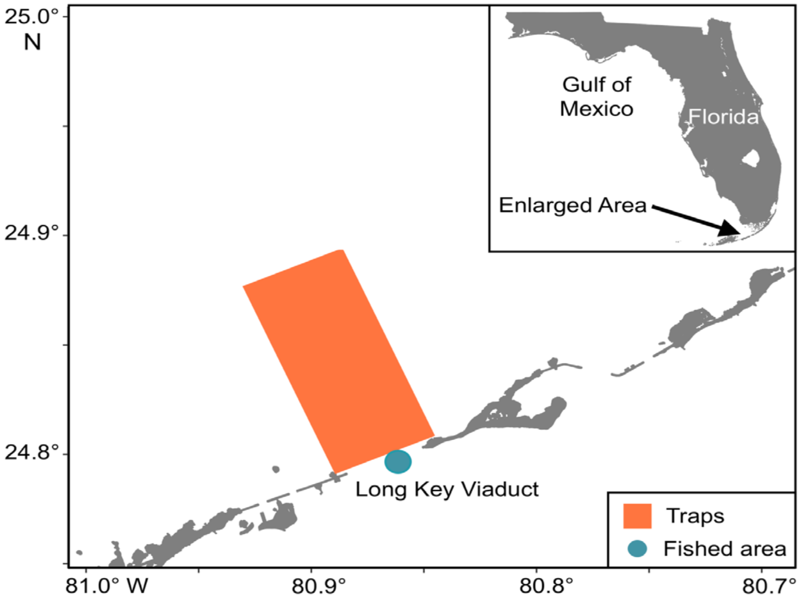

Fig. 1. Long Key in the Middle Florida Keys (USA), where lobsters were surveyed for calculation of health indices. The orange box indicates where lobsters were surveyed from commercially fished traps, the blue dot indicates where lobsters were hand-caught within the fished area near the Long Key Viaduct

have been previously caught. For simplicity, we refer to lobsters harvested from commercial traps as 'trap lobsters,' and those hand-caught from the same area in which the traps were fished as 'fished-area lobsters.' Approximately 30 sublegal (50–76.1 mm CL) and 30 legal lobsters (≥76.2 mm CL) from the fished area were collected on each sampling occasion. On commercial trap-fishing boats in the fished area, lobsters were collected and measured from 30 randomly selected traps that contained lobsters. For each trap, the total number of lobsters in the trap was recorded in addition to the metrics described Section 2.2. Empty traps were not counted; therefore, our catch rates cannot be used to determine average catch.

2.2. Lobster health metrics

All collected lobsters were surveyed for health metrics on-site immediately after they had been harvested from traps or hand-caught. Health monitoring metrics included carapace length, sex, presence of shell disease, visible signs of *Panulirus argus* Virus 1 (PaV1) infection (identified by milky hemolymph; Shields & Behringer 2004), and presence and number of external injuries (broken or missing appendages, open lesions, etc.). Thirty sublegal lobsters and 30 legal lobsters were sampled in each area in each sampling period for analysis of blood serum protein (BSP; total N = 2267). BSP refers to the amount of serum protein dissolved in the hemolymph and was determined by measuring the hemolymph refractive index. Sampling for BSP determination is not lethal and requires only ~0.1 ml of hemolymph drawn from the ventral sinus at the base of a leg with a 27-gauge, 13 mm needle and 1 ml syringe. The hemolymph refractive index was measured to the nearest 0.5 unit on a Reichert IFT40 temperature-compensated industrial refractometer. The refractive index was then converted to BSP via conversion formulae from Behringer & Butler (2006) (Table S1 in the Supplement at www.int-res.com/articles/suppl/m696p043_supp.pdf). Because molt stage affects the BSP (Smith & Dall 1982, Depledge & Bjerregaard 1989), we excluded from analysis lobsters not in intermolt (identified microscopically via a clip of a pleopod; Lyle & MacDonald 1983), leaving a total of 1192 intermolt lobsters for BSP analysis (see Supplementary Tables S2 & S3 for breakdown by area).

Of the 2267 total lobsters captured, 550 were also analyzed for determination of the hepatopancreas dry weight index (DWI; see Supplementary Tables S2 & S3 for breakdown by area). The DWI is considered a reliable indicator of nutritional condition, because the weight, which is a proxy for energy reserves, of the hepatopancreas decreases with starvation (Dall 1974, Gutzler & Butler 2017). Lobsters were euthanized within 24 h of capture, by rapid chilling on ice, Dissections were performed at the Florida Fish and Wildlife Conservation Commission South Florida Regional Laboratory in Marathon, FL, and each hepatopancreas was preserved in 95% ethanol for more than 24 h (Bryars & Geddes 2005, Gutzler et al. 2015). Hepatopancreases were dried at 60°C for 72 h, and the DWI was calculated via established formulae, one each for male and female lobsters (see Bryars & Geddes 2005 for generalized crustacean DWI formulae; see Gutzler et al. 2015 for *P. argus*-specific formulae; our Table S1). Unlike BSP, hepatopancreas DWI is not affected by molt stage; however, DWI may be correlated to animal size (see Gutzler & Butler 2017); thus, lobster weight in grams was estimated from CL based on the morphometric relationship (Matthews et al. 2003; our Table S1) and applied as a covariate in DWI analyses. Effect of sex on nutritional condition was visually evaluated via box plots (see Fig. S1) and, because we saw no difference, male and female data were pooled for analyses. We found only nonreproductive animals (i.e. had no external eggs or spermatophores) in the study area (Lyons et al. 1981); however, reproductive condition is not reported to affect hepatopancreas DWI (Herrera-Salvatierra et al. 2019).

Hepatopancreas DWI and lobster BSP are gauges of physiological condition and served as indicators of the nutritional condition of a lobster. We compared and contrasted these 2 measures for each area and each time period to estimate lobster health variability (Dall 1974, Gutzler & Butler 2017, Butler et al. 2018a,b). However, lobster health comprises more than just the 2 nutritional condition metrics that we have chosen (i.e. DWI and BSP), but also includes e.g. the presence of injuries and disease. Thus, throughout this paper we use the term 'health' when we discuss results that include BSP, DWI, and measures of injuries and disease, whereas we use the term 'nutritional condition' when we are specifically referencing BSP and/or DWI.

Generalized additive models (GAMs) were used to identify and measure the strength of relationships between lobster nutritional condition (BSP [Eq. 1a] and DWI [Eq. 1b]), capture area (i.e. trap or fished area), size classification (i.e. legal vs. sublegal), time (month), and lobster size (in mm). Lobster capture area, size classification, and their interaction were included as fixed categorical (i.e. parametric) predictors in the GAMs, whereas time and lobster size were included as semiparametric smoothed predictors. Specifically, we fit GAMs of the form:

$$\begin{aligned}\text{BSP} \sim \text{Area} \times \text{SizeClassification} + \\ s(\text{Time}) + s(\text{Size}) + \text{error}\end{aligned} \quad (1a)$$

$$\begin{aligned}\text{DWI} \sim \text{Area} \times \text{SizeClassification} + \\ s(\text{Time}) + s(\text{Size}) + \text{error}\end{aligned} \quad (1b)$$

where $s()$ parameters refer to the semiparametric smooth terms.

GAMs allow non-Gaussian error distributions, as well as nonlinear relationships between predictors and response variables by applying nonparametric smoothers to continuous predictors and additively calculating the component response (Wood & Augustin 2002). For both measures of nutritional condition, GAMs were fitted using gamma error distributions and log-link functions. Model fits were visually assessed using quantile–quantile and residuals against fitted plots. All statistical analyses were performed in R (R version 3.6.2, R Core Team 2019), using the 'tidyverse' suite of packages (Wickham et al. 2019), as well as the packages 'emmeans' (Lenth 2020) and 'mgcv' (Wood 2017), and 'gratia' (Simpson 2020).

2.3. Health monitoring and nutritional condition analysis

To explore the variability of other lobster health measures, we calculated the weighted proportions of lobsters with injuries and lobsters with shell disease for each area and sampling period for both sublegal and legal lobsters. First, lobsters were grouped by date, area, and size (either sublegal or legal). The total number of injured (L_I) or shell-diseased (L_D) lobsters for a given group was then calculated and multiplied by the mean number of animals with injuries ($\overline{L_I}$) or shell disease ($\overline{L_D}$) within each group. This product was divided by the total number of lobsters collected from a given area over all dates (L_{Area}) multiplied by the total number of lobsters collected over all areas during a given date (L_{Time}). Finally, that product was multiplied by 100 to express as a percentage the number of lobsters injured (Eq. 2a) or with shell disease (Eq. 2b):

$$\%\text{Injured} = \frac{L_I \times \overline{L_I}}{L_{Area} \times L_{Time}} \times 100 \quad (2a)$$

$$\%\text{shell diseased} = \frac{L_D \times \overline{L_D}}{L_{Area} \times L_{Time}} \times 100 \quad (2b)$$

To identify the proportion of lobsters in each area in low health, we calculated the percentage of sublegal and legal lobsters that had injuries, shell disease, or low nutritional condition (for each of the 2 indices) in each sampling period. We categorized lobsters as nutritionally compromised when DWI values were <0.5 (Gutzler & Butler 2017, Butler et al. 2018b) and when BSP values were <12 mg ml^{-1} (Behringer & Butler 2006, Gutzler & Butler 2017, Butler et al. 2018b). The percent mortality of lobsters in traps on a given date was calculated by dividing the total number of dead lobsters observed on that date by the total number of lobsters observed in the traps on that date, multiplied by 100.

GAMs were used to identify and measure the strength of relationships between the percent of lobsters with injuries and area, time (month), and lobster size class (sublegal or legal size) (Eq. 3a). The same type of GAM was used to measure the relationships between the percent of lobsters with shell disease and those variables (Eq. 3b). For both GAMs, the response variable (either percent of lobsters with injuries or percent of lobsters with shell disease) was log-transformed to meet the assumptions of the Gaussian distribution, and the models were fitted using the canonical link for the Gaussian distribution (i.e. the identity link). Models took the forms:

$$\text{Ln(proportion injured)} \sim \text{Area} + \text{SizeClass} + s(\text{Time}) + \text{error} \quad (3a)$$

$$\text{Ln(proportion diseased)} \sim \text{Area} + \text{SizeClass} + s(\text{Time}) + \text{error} \quad (3b)$$

where the *s*() parameters refer to the semi-parametric smooth terms.

Model fits were visually assessed using quantile–quantile and residual-vs.-fitted-values plots. *G*-tests for independence were used to determine whether the percentages of unhealthy animals in each area and size class differed from one another. All statistical analyses were performed in R (R Core Team 2016) using the 'tidyverse' suite of packages (Wickham et al. 2019), as well as the packages 'mgcv' (Wood 2017) and 'DescTools' (Signorell et al. 2021).

3. RESULTS

3.1. Nutritional condition

The nutritional condition (i.e. BSP and DWI) of lobsters varied throughout the year and between areas (Fig. 2). Lobsters from the fished area exhibited greater measures of nutritional condition than those from traps (Fig. 2). There were significant differences among lobsters surveyed from different areas for BSP and for DWI (Table 1, Fig. 3). Both legal and sublegal lobsters in traps had consistently lower nutritional condition throughout the fishing season; the lowest values were observed in March (Figs. 2–4). Of the trap-caught lobsters, 42.4% of sublegal lobsters and 20.7% of legal lobsters had a BSP <12 mg ml^{-1} (vs. <14% for both sizes in the fished area).

Nutritional condition (BSP and DWI) of lobsters from the fished area generally declined after the first few months of the fishing season and began to recover toward the end of the fishing season (February and March). Increases and decreases in DWI lagged 1 mo behind changes in BSP. Nutritional condition, however, did fluctuate to a degree by month sampled, as well as by lobster size (sublegal size or legal size; Fig. 2).

Throughout the survey, higher percentages of sublegal and legal lobsters in traps exhibited low BSP (<12 mg ml^{-1}) and DWI (<0.5 mg ml^{-1}) than hand-caught lobsters (for BSP, $G = 80.575$, df = 1, p <

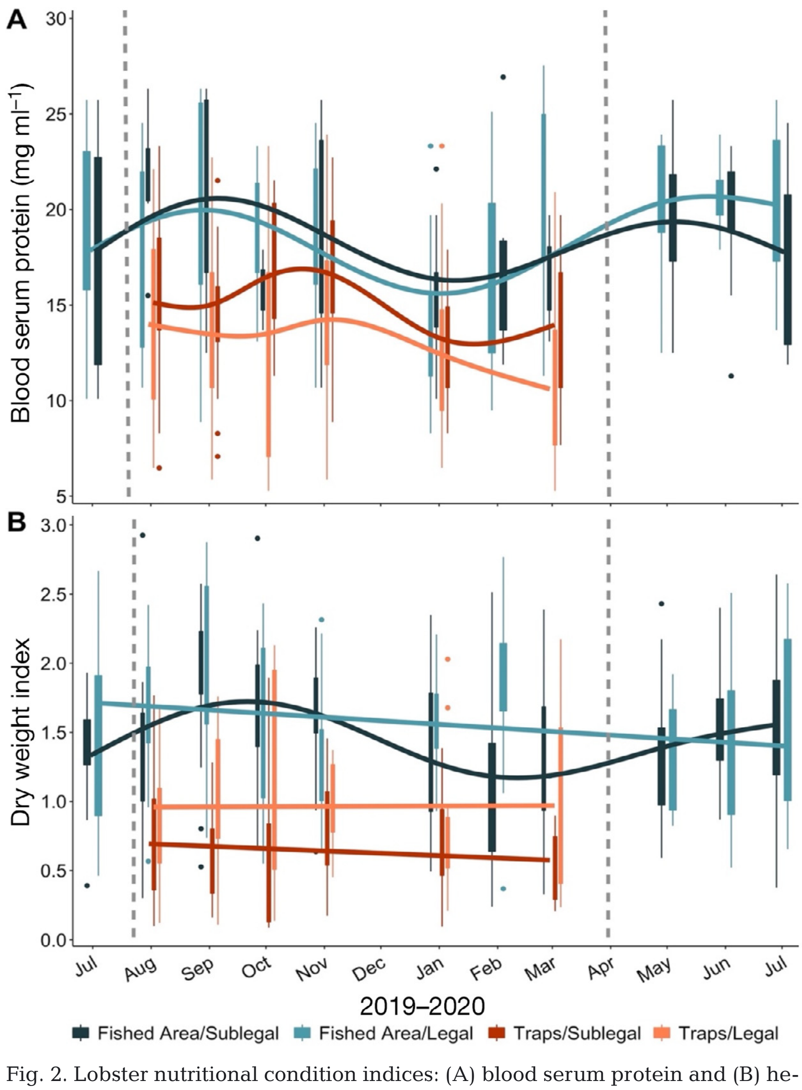

Fig. 2. Lobster nutritional condition indices: (A) blood serum protein and (B) hepatopancreas dry weight index, by area: fished area (Long Key Viaduct Bridge) and traps (traps fished north of Long Key Viaduct Bridge in Florida Bay). July 2019 sampling was done just prior to opening of the lobster fishing season; August 2019 sampling occurred just after the season opened. Vertical dashed lines represent the start (6 August) and end (31 March) of the commercial lobster fishing season. Boxes are drawn from the 25th to the 75th percentile, and whiskers are drawn from 1.5× the interquartile range (i.e. the distance between the first and third quartiles); points lying outside the whiskers are outliers. Lines are nonparametric smooths to show patterns in the time series

Table 1. Results of generalized additive models fit to blood serum protein and dry weight index data of lobsters collected throughout 2019–2020 as a function of area (fished or in traps), whether a lobster was of legal size (Yes or No), and their interaction, as well as semiparametric smooths of date and lobster size. **Bold:** significant at or less than the $\alpha = 0.05$ level

	Blood serum protein			Dry weight index		
Predictors	Estimates	CI	p	Estimates	CI	p
(Intercept)	18.76	17.96 – 19.60	**<0.001**	1.55	1.42 – 1.69	**<0.001**
Area [trap]	0.69	0.66 – 0.73	**<0.001**	0.43	0.38 – 0.48	**<0.001**
Legal [Y]	0.96	0.88 – 1.05	0.379	0.99	0.84 – 1.16	0.871
Area [trap] × Legal [Y]	1.20	1.10 – 1.30	**<0.001**	1.36	1.14 – 1.61	**<0.001**
Smooth term (Date)	632.52		**<0.001**	7.21		**0.001**
Smooth term (Size)	23.59		0.227	14.72		**0.032**
No. of observations	1192			550		
R^2	0.282			0.317		

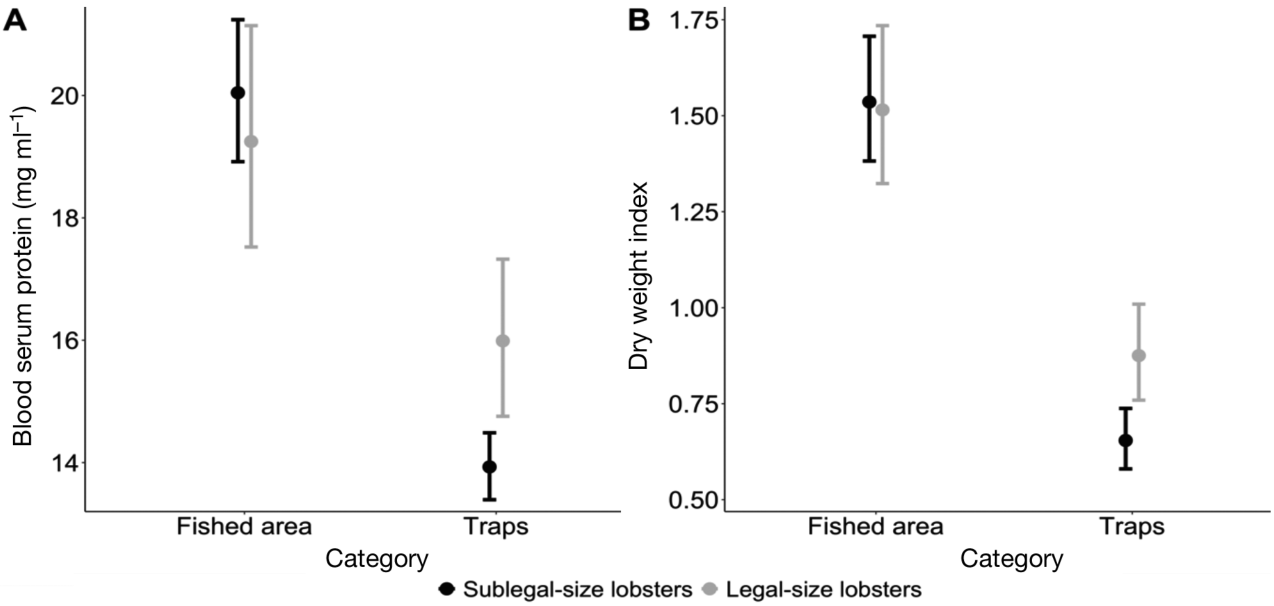

Fig. 3. Effects plots (estimated marginal means and 95% confidence intervals) based on a generalized additive regression model comparing lobster nutritional condition by 2 indices: (A) blood serum protein and (B) hepatopancreas dry weight index, by lobster size (legal size = 76.2 mm carapace length) and by area: fished area (Long Key Viaduct Bridge) and traps (traps fished north of Long Key Viaduct Bridge in Florida Bay)

0.0001; for DWI, $G = 80.041$, df = 1, $p < 0.0001$; Fig. 4). Very few lobsters in the fished area had low DWI values. The percent of lobsters with low BSP and DWI increased during the last months of the fishing season, from January through March 2020 (Fig. 4).

Mortality estimates of lobsters in traps underestimated the total number of dead lobsters in traps, given the 2 wk deployment times of the traps and that lobster carcasses in traps tend to fully decay within 3.9 d (Matthews 2001). Observations of dead lobsters in traps did, however, allow for the comparison of relative mortality between sublegal and legal lobsters between months. The percent of dead lobsters observed in traps increased from 2.6% of all legal lobsters in August to 9.4% in October (the maximum percentage observed in any month) and declined after November (7.5%) through March (0%) (Fig. 4C). Overall, 2.2% of sublegal lobsters in traps were observed dead (n = 32); 4.1% of legal lobsters (n = 10) were observed dead, but observations of dead lobsters were too few to suggest any pattern.

3.2. Prevalence of injuries and disease

Of the entire data set on injuries (2267 lobsters), 34.9% of sublegal and 29.9% of all legal lobsters in traps had injuries (most were severed legs or dactyls

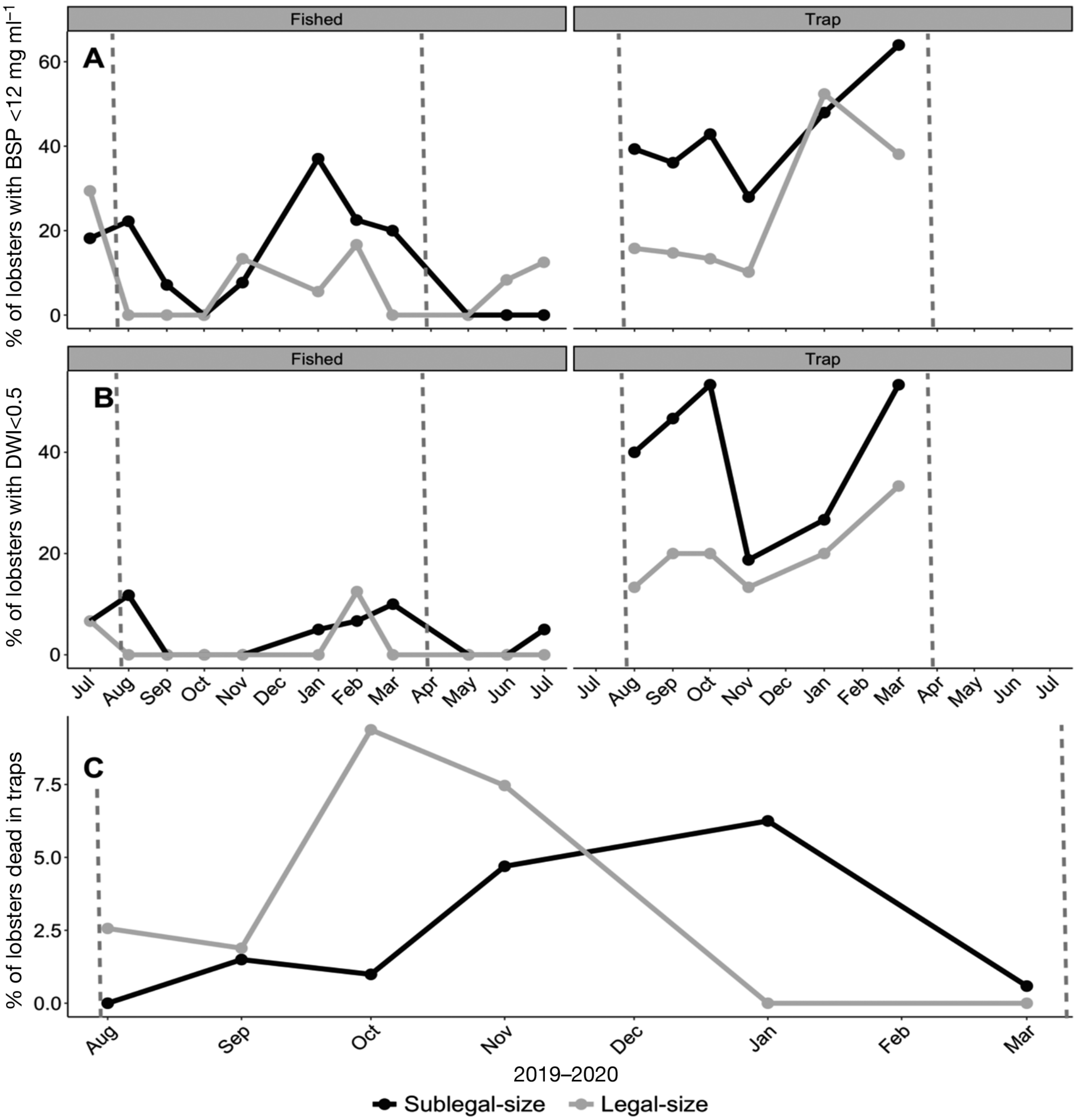

Fig. 4. Percent of sublegal-size (gray) and legal-size (black) lobsters observed with low levels of nutritional condition in (A) blood serum protein (BSP) levels <12 mg ml^{-1} and (B) hepatopancreas dry weight index (DWI) <0.5 at both areas: fished area (Long Key Viaduct Bridge) and traps (traps fished north of Long Key Viaduct Bridge in Florida Bay). Peaks of low nutritional condition in the fished area may be those lobsters that fishers released from traps as they removed traps from the water at the end of the season. (C) Percent of dead lobsters observed in traps (total of 42 dead lobsters in traps). Vertical dashed lines represent the start (6 August) and end (31 March) of the commercial lobster fishing season

caused when a trap is hauled aboard the vessel and protruding limbs are severed). Of the lobsters observed in the fished area, 19.8% of sublegal and 14% of legal lobsters had injuries (most were autotomized limbs).

The weighted percent (wt%) of lobsters with one or more injuries ranged from 4 to 14 (Table 2, Figs. 5 & 6) and was significantly higher for both sublegal and legal lobsters in traps. The prevalence of injuries in traps was lowest in August and September and

Table 2. Results of generalized additive models fit to the natural log of weighted proportions of lobsters with injuries or shell disease as a function of area (fished or in traps) and whether a lobster was of legal size (Yes or No), as well as semiparametric smooths of date. **Bold:** significant at or less than the $\alpha = 0.05$ level

Predictors	Proportion with injuries			Proportion with disease		
	Estimates	CI	p	Estimates	CI	p
(Intercept)	−0.21	−0.80 to 0.37	0.464	−0.92	−1.52 to −0.33	**0.004**
Area [trap]	2.20	1.41 to 2.98	**<0.001**	3.64	2.80 to 4.47	**<0.001**
Legal [Y]	−1.76	−2.49 to −1.03	**<0.001**	−2.69	−3.43 to −1.96	**<0.001**
Smooth term (Date)	1.00		0.636	5.43		**0.002**
No. of observations	34			34		
R^2	0.635			0.837		

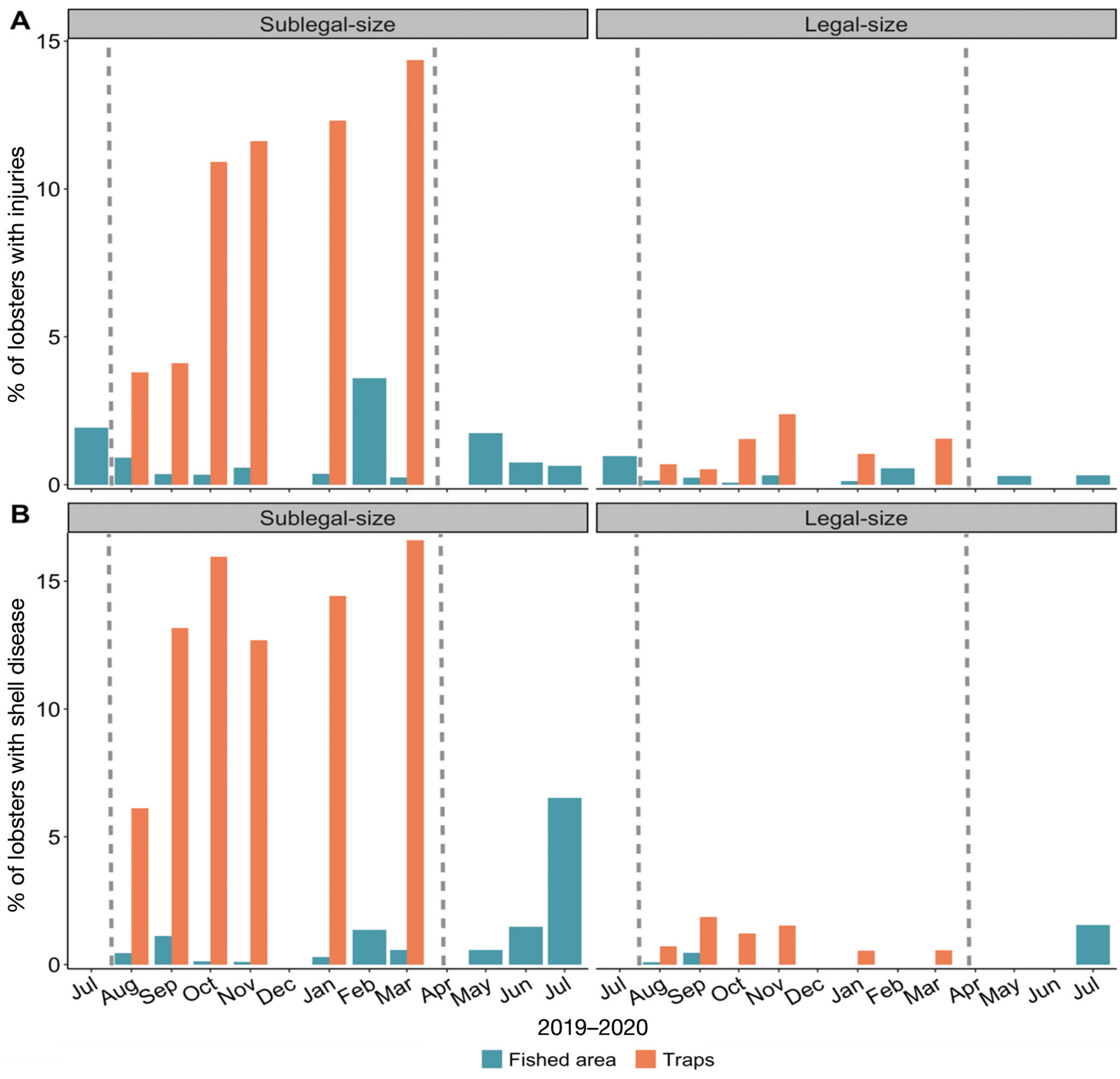

Fig. 5. Weighted percentages of lobsters with (A) injuries and (B) shell disease in the fished area (Long Key Viaduct Bridge) and traps (traps fished North of Long Key Viaduct Bridge in Florida Bay). Vertical dashed lines represent the start (6 August) and end (31 March) of the commercial lobster fishing season

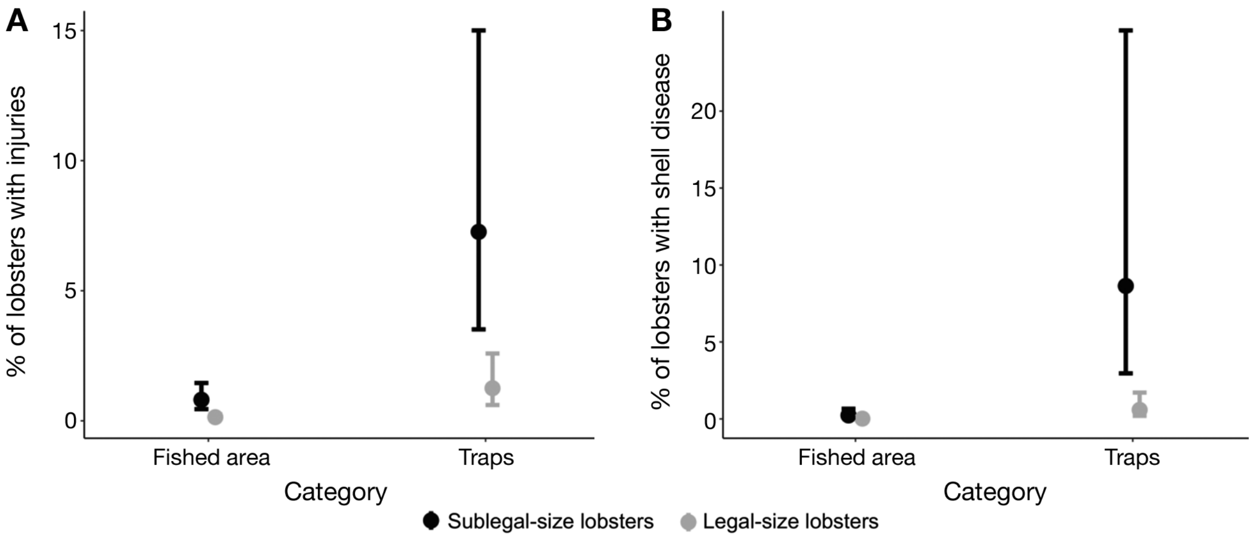

Fig. 6. Effects plots (estimated marginal means and 95% confidence intervals) of generalized additive model outputs of sublegal-size and legal-size lobsters with (A) injuries and (B) shell disease

increased from October through March. The wt% of injuries was <5 for lobsters in the fished area. The greatest weighted percentages of injuries for sublegal lobsters in the fished area occurred in July 2019 (1.14 wt%), at the start of the recreational sport lobster season, and in February 2020 (3.21 wt%), near the end of the lobster fishing season.

Shell-disease prevalence patterns were similar to injury prevalence patterns (Figs. 5 & 6). Overall, 43.1% of sublegal and 23.9% of legal lobsters in traps had shell disease, whereas 20.7% of sublegal and 10.6% of legal lobsters observed in the fished area had shell disease. Prevalence of shell disease in both sublegal and legal lobsters was consistently greater in lobsters in traps than in lobsters hand-caught in the fished area (Table 2, Figs. 5 & 6). Shell disease or injuries were also present on sublegal lobsters in the fished area, but to a lesser degree. Except for during 2 sampling periods, injuries and shell disease in the fished area was always below 2 wt%.

Three lobsters presented with visible PaV1 infection. One 36.4 mm CL male was found in the fished area in September 2019, and 2 females were brought up in commercial traps in November 2019 (55.3 and 65.8 mm CL).

4. DISCUSSION

The practice of using live sublegal lobsters as bait for the Florida spiny lobster fishery has a profound effect on the harvest capability of the fishery. The use of sublegal lobsters as bait approximately triples catch per trap (Heatwole et al. 1988); however, long-term confinement of bait lobsters results in their reduced nutritional condition, which in turn reduces their ability to attract other lobsters to the trap (Butler et al. 2018a). Also, lobsters confined longer than 2 wk have reduced health, are no longer effective bait, and are at greater risk of mortality. We found that both legal and sublegal lobsters within actively fished traps showed lower nutritional condition throughout the fishing season. Declines in lobster harvest in each month of the fishing season assuredly remains dependent on the local population, but the reduced health of lobsters available as bait likely further reduces catch efficiency.

More broadly, this study is the first, to our knowledge, to monitor the nutritional condition of spiny lobsters over the course of a year, including during the fishing season. Lobster BSP and DWI varied throughout the year, peaking in late summer to early fall, dropping sharply during the winter, and rising again through the spring. The cyclic pattern seen in the nutritional indices could be in response to seasonal changes in environmental factors, such as water temperature.

4.1. Lobster health

4.1.1. Nutritional condition

This is the first study to identify how nutritional condition of *P. argus* varies throughout the year. The peak in nutritional condition in September for lobsters in the fished area was likely a result of aboitic and biological stimuli that occur each year. The autumn migration of lobsters (Kanciruk & Herrnkind 1978) undoubtedly requires a high amount of stored energy. Lobster movement increases substantially during the fall as they prepare for migration, during which time they become active earlier in the day than usual (before sunset) and stay active much later (after sunrise), whereas the rest of the year they are active only after sunset (Kanciruk & Herrnkind 1978, Bertelsen 2013). Increased energy reserves would be required to sustain this extra activity, so this would be a natural time to reallocate nutritional stores into the hepatopancreas, perhaps to afford adequate energy stores for a long migration (for example, monarch butterflies *Danaus plexippus* increase lipid stores by nectaring on flowering plants while migrating to central Mexico and use those energy stores to overwinter and migrate back north to breed, Brower et al. 2006).

Changes in DWI lagged changes in BSP in lobsters in the fished area. BSP increased before DWI, perhaps because these nutrient storage mechanisms are mobilized at different rates, i.e. nutrients in the hemolymph are available immediately, whereas those stored in the hepatopancreas must be mobilized before their energetic reserves become available (Wen et al. 2006, Sugumar et al. 2013, Ciaramella et al. 2014). Although we noticed a 1 mo difference between BSP and DWI, this time lag could have been shorter, but would be undetectable at our sampling frequency.

Nutritional condition of legal lobsters in traps was often near or below levels known to compromise survival (Butler et al. 2018a,b). Since legal lobsters were not left in the traps longer than the 2 wk soak period, we had hypothesized that the nutritional condition of legal lobsters in traps would be similar to that of legal lobsters hand-caught in the fished area where the traps were used; yet, nutritional condition of legal lobsters in traps was consistently lower than that of legal lobsters in the fished area (Fig. 2). The health of legal lobsters in traps appears compromised even though the soak time was less than the time identified in a previous study as endangering lobster health (Butler et al. 2018b). Commercial trap fishers in Florida generally deploy traps for 1 to 2 wk soak times during the early part of the fishing season, and later increase soak time to 2–4 wk (Matthews 2001). The traps we sampled had a consistent 2 wk soak, apart from one occasion in January when the traps were in the water for 3 wk. After that longer, 3 wk soak period, 50% of legal lobsters exhibited low BSP, a greater percentage than at any other time (Fig. 4).

Nutritional condition was consistently low in 30–50% of the sublegal lobsters confined in traps, indicating that confinement in traps for more than 2 wk was long enough to significantly reduce the health of a large portion of the lobsters in traps (Figs. 2–4). This finding is consistent with our earlier work indicating significant reductions in nutritional condition after just 3 wk (Butler et al. 2018a,b). Lobsters in earlier field and laboratory experiments died when BSP fell below 10 mg ml^{-1} (Butler et al. 2018a); thus, extended soak time appears to further reduce the health of sublegal lobsters in traps. This reduction in health potentially causes sublethal effects on growth and reduced attraction to conspecifics (Butler et al. 2018a), both of which can impact survival in sublegal lobsters released from traps. Since 30–50% of sublegal lobsters in traps were near the established threshold for mortality (i.e. BSP <10 mg ml^{-1}), these health-compromised lobsters are presumed to have limited ability to escape traps (Butler et al. 2018b) or might die unseen in traps and would not rejoin the population in the fished area. Thus, only approximately half of the sublegal lobsters confined in traps might reenter the surrounding wild population.

Sublegal lobsters in the traps had the lowest nutritional condition late in the fishing season. We postulate that the declining health may be the culmination of (1) cumulative effects of multiple weeks of retention of lobsters used as bait in traps and (2) decreased ability of lobsters with compromised health to escape traps. The occurrence of the lowest average nutritional condition in March may be a result of longterm confinement, although it is not likely that those lobsters were the same as those encountered at the early part of the season. Earlier work (Butler et al. 2018b) found that mortality (at BSP < 10 mg ml^{-1}) happened after ~6 wk of trap confinement. Our observation that 30–50% of all sublegal lobsters observed in traps were near the BSP threshold associated with mortality suggests that lobsters at this advanced stage of compromised health would have been unable to escape traps and, even if they had been released, that they would likely have faced discard mortality or predation (Uhlmann & Broadhurst 2015, Butler et al. 2018b).

The greater percentage of health-compromised sublegal lobsters within the fished area late in the fishing season is not, on the surface, consistent with our findings where average health of sublegal and legal lobsters varied similarly at the same time periods. However, fishers begin removing traps from the water during the last 3 mo of the fishing season (typically over 50% of traps are removed by January; Florida Fish and Wildlife Conservation Commission unpubl. data), and so would release any sublegal bait lobsters. This may be the only time of the year when sublegal lobsters are released en masse. Twenty to 40% of sublegal lobsters within the fishing area exhibited low BSP, which might reflect the release of health-compromised bait lobsters from traps.

Our observations of the number of deaths in traps were limited to those carcasses that remained at the time a trap was pulled (i.e. only those carcasses that did not decay or were eaten). These observations were likely insufficient to estimate the degree and patterns of lobster mortality in traps because lobster carcasses decay in 3 to 4 d (Matthews 2001). These unseen lobster deaths during prolonged soak periods are a probable cause for the chronic underestimation of fishery-wide mortality rates (e.g. the Southeast Data and Assessment Review Spiny Lobster Update Review Workshop in 2010 recommended that researchers focus on providing more accurate estimates of mortality in traps so that they could be included in stock assessment models; SEDAR 2010).

4.1.2. Injuries and shell disease

We hypothesized that, if lobsters used as bait were escaping or being released from traps, we would see a greater prevalence of shell disease and injuries within the fished area during the commercial fishing season. Yet, we observed few lobsters in the fished area that had injuries consistent with those of trap lobsters, such as severed dactyls/limbs. This could indicate that few lobsters escape traps (Fig. 6). Lobsters that escaped from traps may have been undercounted using the presence of trap injuries, as limbs can be regenerated through molting. However, it is unlikely that lobsters confined in traps for even short periods would have sufficient energy reserves needed to successfully molt and regenerate limbs. This also suggests that lobsters experiencing an increased incidence of injuries, disease, and suppressed health within traps were unable to escape from traps and ultimately died.

Although injured lobsters were rarely encountered in the diver surveys, we did notice an increased injury rate during 2 sampling periods. The second-highest rate of injured sublegal lobsters, albeit only 1%, was observed in July and August 2019, just after the special recreational lobster sport season, i.e. a 2 d season during which permission to harvest lobsters is only granted to recreational fishers (Fig. 5; Sharp et al. 2005). Although some of the lobsters observed in this area might have encountered traps in the few days that the season had been open (commercial fishers began to deploy traps on 27 July in 2019), it is more likely that this spike in injuries was a result of the recreational lobster sport season that year (24–25 July). Similar instances of injuries have been reported in the Florida Keys following recreational sport seasons (Eggleston et al. 2003). The increase in prevalence of injuries in sublegal lobsters in February in the fished area may reflect bait lobsters released when many commercial fishers removed a substantial number of their traps from the water toward the end of the fishing season.

In addition to injuries, we commonly observed shell disease, manifesting as small pits or burn marks on the cuticle, blackening of the exoskeleton, or lesion melanization (Porter et al. 2001). Shell disease is prolific during warm months and wanes during cooler months (Gittens & Butler 2018). In the natural environment, molting usually rids lobsters of shell disease. In traps, however, lobsters are less likely to molt because they lack the energy that molting requires (Travis 1955, Sugumar et al. 2013) and so do not rid themselves of shell disease. This is evident in our data: in hand-caught lobsters in the fished area, shell disease and injuries were less prevalent during cooler months, yet in lobsters in traps, prevalence of shell disease remained high throughout the fishing season (Fig. 5).

4.2. Fishery harvest and lobster health

The long-term confinement of bait lobsters in traps is considered the greatest source of loss to future fishery harvest (Matthews 2001). Despite these negative impacts, fishers still have a high incentive to continue using live lobsters as bait because the use of baits can substantially improve trap catch rates in the short term (Heatwole et al. 1988). Based on Butler et al. (2018a), who showed lower catch rates in traps baited with unhealthy lobsters, the low values for lobster nutritional condition measured among all traps in this study suggests an overall diminishing of catch efficiency for the fishery. Baiting with unhealthy sublegal lobsters decreases a trap's catch and increases discard mortality. Renovation of fishing practices to proactively remove unhealthy lobsters from traps or improve the health of lobsters used as bait (e.g. by feeding or replacement of unhealthy lobsters) could achieve higher catch rates with less mortality of sublegal lobsters as bait.

The spiny lobster is typically thought to be a resilient species, yet it is vulnerable to long-term confinement. Although we expected that sublegal lobsters in traps would have reduced health, we were surprised that the health of legal lobsters in traps was also low. Another reason a change in fishing strategy would benefit fishers is that the improved health of live market lobsters would increase the fishery revenue. The highest value of this fishery relies on the sale of live lobsters to China, and the low health of legal lobsters reduces the number that are selected for the live market. Export of live lobsters is a valuable component of many lobster fisheries globally, and implications of this study extend to those live-market fisheries, as physiological stressors can result in short- and long-term changes in cardiovascular and respiratory function, energy metabolism, fluid and ionic balance, acid–base balance, and immunity (Vermeer 1987, Evans 1999, Fotedar & Evans 2011). Long-term exposure to even mild stressors can result in mortality or reduced resistance to diseases, reduced growth, and impaired reproduction (Evans 1999). The resulting impacts can reduce the grade, and thus the value, of lobsters available to these live markets (Paterson et al. 2005, Fotedar et al. 2006, Fotedar & Evans 2011).

4.3. Conclusions

This work identified fisher-induced effects on lobster health. Lobster health varied seasonally, perhaps in response to seawater temperature. Although fishing practices diminish the health of lobsters within the traps, lobsters in the surrounding environment appeared to have trap-related injuries and low nutritional condition only toward the end of the fishing season. Although we expected to observe a greater proportion of lobsters with low nutritional condition and trap-related injuries in the fishing area (from lobsters released or having escaped from traps), reduced observations of these trap-affected lobsters likely stems from a lack of lobsters escaping from traps, particularly of nutritionally deficient lobsters, which, according to our results, rarely re-enter the surrounding environment. The Florida spiny lobster trap fishery endures high mortality of sublegal lobsters to increase catch rates of legal lobsters. Increased focus on sustaining the health of sublegal lobsters within traps should not only improve catch rates and reduce fishery effort but should also result in a larger lobster population and long-term improved harvests (Butler et al. 2022).

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