

## Using age to evaluate reproduction in Caribbean spiny lobster, *Panulirus argus*, in the Florida Keys and Dry Tortugas, United States

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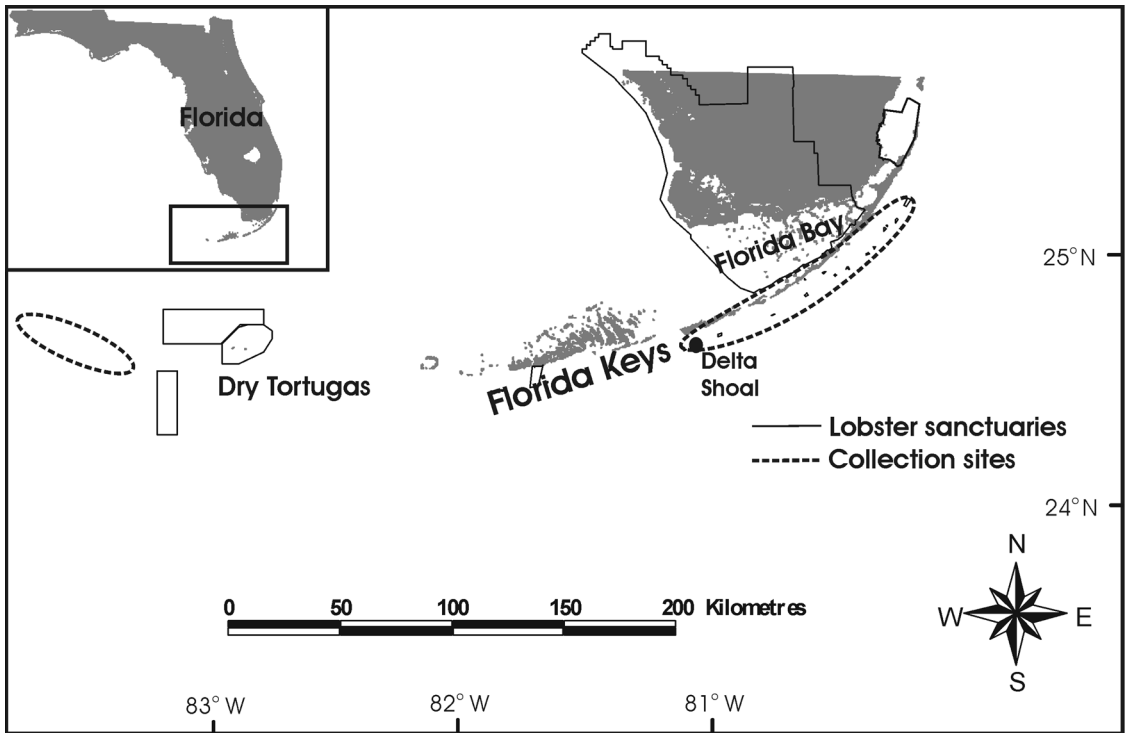
**Abstract** For many species of lobsters, size at sexual maturity varies across spatially separated populations. This is so for two populations of Caribbean spiny lobster, *Panulirus argus*, in southern Florida, where females from open-fishing areas around the Dry Tortugas mature at a larger size than females from open-fishing areas in the Florida Keys. Variations in onset of maturity between populations of lobsters have been attributed to different environmental conditions, lobster density, and/or fishing pressure. We used age as estimated by histologically expressed neurolipofuscin to examine differences in size at maturity in *P. argus*. Neurolipofuscin content measured in known-age, laboratory-reared animals in a previous study was used to estimate age in wild-caught *P. argus*. We show that lobsters from the Florida Keys are significantly smaller than lobsters of the same age from the Dry Tortugas. This difference in growth rates between lobsters from the two locations likely explains the differences in size at onset of maturation. High rates

of injury from fishery practices in the Florida Keys and differential predation on slow-growing lobsters in the Dry Tortugas may account for these differences in growth rates. Additionally, we compared the ages of reproductive females collected from breeding grounds of the Florida Keys to same-sized non-reproductive females from an area in the Florida Keys where there was no evidence of breeding. We found that females possessing eggs early in the breeding season were significantly older than females that bore eggs later in the breeding season or that did not produce eggs. Older females also produced more clutches of eggs. Our research indicates that reproduction is related to age in *P. argus*. The intense fishery and the methods used to fish lobsters are the most likely causes of the reduction in spiny lobster population size structure and size at maturity.

**Keywords** maturity; growth; neurolipofuscin, fishery

### INTRODUCTION

Disparity in size at maturity between different populations has been observed in many lobster species throughout the world, including rock lobster, *Jasus edwardsii*, off southeastern Australia (Hobday & Ryan 1997); western rock lobster, *Panulirus longipes cygnus*, off southwestern Australia (Chittleborough 1976); spiny lobster, *P. homarus*, in the Arabian Sea off the coast of the Sultanate of Oman (Mohan 1997); spiny lobster, *Palinurus elephas*, in the western Mediterranean Sea (Goñi et al. 2003); European lobster, *Homarus gammarus*, off Scotland, United Kingdom (Lizárraga-Cubedo et al. 2003); and American lobster, *Homarus americanus*, off New England, United States (Little & Watson 2005). These disparities in size at maturity are generally attributed to differing environmental conditions (i.e., temperature, food availability) (Mohan 1997; Little & Watson 2005), lobster density (Chittleborough 1976), and/or fishing pressure (Mohan 1997; Goñi et al. 2003; Lizárraga-Cubedo et al. 2003).



**Fig. 1** Location of study sites in the Florida Keys and Dry Tortugas, United States. Spiny lobster, *Panulirus argus*, collection sites are areas circled with dashed lines. Lobster sanctuaries are outlined with solid lines.

Differences in size structure and size at maturity are also evident in two populations of Caribbean spiny lobster, *P. argus* (Latrielle, 1804), in southern Florida, United States. These areas of interest are the open-fishing areas of the Florida Keys and the open-fishing areas around the Dry Tortugas, a group of islands located 113 km west of the Florida Keys, where fishing pressure is less intense than in the easily accessed Florida Keys (Fig. 1). Length-frequency distributions of lobsters show that lobsters from fishing grounds around the Dry Tortugas are significantly larger than lobsters from the Florida Keys fishery (Bertelsen et al. 2004). Female spiny lobsters in the Florida Keys with carapace lengths (CLs) as small as 57 mm have been observed carrying eggs, whereas no female less than 70 mm CL from the Dry Tortugas has been observed with eggs (Bertelsen & Matthews 2001). Bertelsen & Matthews (2001) offer several hypotheses for the size-at-maturity differential between the two populations. We explored their hypothesis that different growth rates between the two populations have resulted in female lobsters from the Florida Keys reaching maturation (defined

as when 50% females are ovigerous) at a smaller size than female lobsters from the Dry Tortugas, resulting in smaller reproductive females from the Florida Keys that are the same age as any of the egg-producers from the Dry Tortugas. Although other studies have demonstrated varying sizes at maturation in spatially separated lobsters, none have used age (as estimated by neurolipofuscin) to explain why female lobsters mature at different sizes in two locations.

Age in crustaceans can be estimated by histologically determining the lipofuscin content in the central nervous system (Wahle et al. 1996; Belchier et al. 1998; Sheehy et al. 1998; Bluhm & Brey 2001; Sheehy & Bannister 2002). Lipofuscin accumulates in cells as a result of their normal metabolism (Terman & Brunk 2004). Since lipofuscin accumulates in a predictable way, it is an accurate biomarker for physiological age in arthropods (Fonseca et al. 2005), so it can be an important tool for population ecologists and fishery biologists (Sheehy et al. 1998; Sheehy & Bannister 2002). Maxwell et al. (2007) found that neurolipofuscin accumulation in *P.*

*argus* steadily increased as lobsters aged but varied seasonally in laboratory-grown, known-age lobsters. In the current study, we used the neurolipofuscin-age relationship developed from known-age lobsters raised at water temperatures similar to those in the Florida Keys (Maxwell et al. 2007) to estimate age in wild-caught lobsters. Most of the individual variation in neurolipofuscin concentration is explained by either chronological age or temperature (Sheehy & Bannister 2002), so data for known-age laboratory animals should provide a reliable standard for age determinations of field animals.

The purpose of this study was to examine if sexual maturity is related to age in *P. argus*. To address this question, we first explored why size at maturity differed between lobsters from the Florida Keys and Dry Tortugas by comparing their estimated ages to determine if animals from the Florida Keys were older, and thus presumably growing more slowly, than similar-sized animals from the Dry Tortugas. Second, we compared the estimated ages of reproductive females collected from breeding grounds of the Florida Keys to similar-sized non-reproductive females from an area in the Florida Keys where there has been no evidence of breeding (Lyons et al. 1981; Davis & Dodrill 1989). (We were unable to collect egg-bearing lobsters from the Dry Tortugas.) Third, we assessed the timing of reproduction and the number of clutches of eggs relative to estimated age in these groups of lobsters from the Florida Keys.

## MATERIALS AND METHODS

### Collection of age and size data

For neurolipofuscin-sampling, 145 lobsters between 40 and 147 mm CL were collected from commercial lobster traps at different locations in the Florida Keys in January and February 2001, and 99 lobsters between 80 and 179 mm CL were collected from fishing grounds around the Dry Tortugas in February 2002. Although we attempted to collect about 10 animals per 10-mm size class, we collected fewer animals from the larger size classes because large animals were rare, especially in the Florida Keys (Table 1). In addition, sublegal-sized animals (<76 mm CL) were rarely caught in traps in the Dry Tortugas, so we had no animals <80 mm CL from Dry Tortugas. We randomly selected one eyestalk for age determination from each lobster from the Florida Keys, and we collected both eyestalks from lobsters from the Dry Tortugas, of which one was randomly selected.

Data collected by observers in the fishery were used to develop size-frequency distributions of male and female lobsters caught in traps in the Florida Keys and Dry Tortugas (fishery observer methods are described in Matthews 2001). Although data from observers were collected throughout the fishing season (August to March) each year between 1993 and 2001, only 5573 lobsters (2413 male and 3160 female) caught and measured in January and February 2001 in the Florida Keys

**Table 1** Mean ( $\pm$  SD) estimated age of female and male *Panulirus argus* from the Dry Tortugas and Florida Keys (United States) for each 10 mm carapace length (CL) size class.

Size class (mm CL)	Dry Tortugas				Florida Keys			
	Females		Males		Females		Males	
	<i>n</i>	Age (yr)	<i>n</i>	Age (yr)	<i>n</i>	Age (yr)	<i>n</i>	Age (yr)
40.0–49.9					4	0.82 $\pm$ 0.20	9	1.05 $\pm$ 0.27
50.0–59.9					14	1.33 $\pm$ 0.54	11	1.16 $\pm$ 0.34
60.0–69.9					11	1.07 $\pm$ 0.27	11	1.14 $\pm$ 0.38
70.0–79.9					8	1.34 $\pm$ 0.24	8	1.33 $\pm$ 0.52
80.0–89.9	9	1.29 $\pm$ 0.33	4	1.02 $\pm$ 0.22	10	1.56 $\pm$ 0.64	11	1.41 $\pm$ 0.38
90.0–99.9	6	1.11 $\pm$ 0.19	6	1.49 $\pm$ 0.55	14	2.19 $\pm$ 1.02	9	2.06 $\pm$ 0.71
100.0–109.9	5	1.42 $\pm$ 0.82	5	1.68 $\pm$ 0.45	4	2.28 $\pm$ 1.07	10	2.19 $\pm$ 0.81
110.0–119.9	7	1.84 $\pm$ 1.15	8	1.49 $\pm$ 0.48	3	2.18 $\pm$ 0.11	8	2.29 $\pm$ 0.77
120.0–129.9	6	2.48 $\pm$ 0.48	5	1.82 $\pm$ 0.48				
130.0–139.9	6	2.63 $\pm$ 0.67	5	1.75 $\pm$ 0.26				
140.0–149.9	4	3.71 $\pm$ 1.58	5	2.40 $\pm$ 0.88				
150.0–159.9	3	2.71 $\pm$ 1.17	8	3.16 $\pm$ 0.97				
160.0–169.9			2	3.39 $\pm$ 0.30				
170.0–179.9			5	2.85 $\pm$ 1.07				

were used to create the size-frequency distribution. This period corresponded with sampling of lobsters for neurolipofuscin content. The only winter fishery observations in the open-fishing area near the Dry Tortugas included 1067 lobsters (445 male and 622 female) observed in January, February, and March 1995.

### Laboratory observations of reproduction at age

Early in the breeding season in mid-April of 2005, we collected from 2 locations 3 groups of 8–10 female lobsters for a total of 27 similar-sized females (between 65 and 82 mm CL). Lobsters were caught on SCUBA with tickle stick and net. The first group, 8 ovigerous females, was collected from Delta Shoal (Fig. 1). Delta Shoal and other barrier reefs offshore from the Florida Keys are typical breeding areas for *P. argus* (Lyons et al. 1981). The second group, 9 females, was also collected from Delta Shoal and appeared to be immature at the start of the breeding season (defined as lacking eggs, enlarged ovaries, or spermatophores). The third group, 10 females, was collected from Florida Bay and the bridges connecting the islands of the Florida Keys where, historically, there have been no ovigerous females (Lyons et al. 1981; Davis & Dodrill 1989).

Lobsters were transported to the Florida Fish and Wildlife Conservation Commission (FWC) laboratory, in Marathon, Florida, and placed in flow-through water systems that provided sea water from Florida Bay. Four or five females from each group were housed in 1500-litre circular aquaria that measured 1.6 m wide by 0.8 m deep. The remaining females pooled from all 3 groups were housed together in a 9500 litre aquarium that was 3.6 m wide by 1.0 m deep. We supplied females with large male lobsters; each tank had 1 male that was at least 102 mm CL and a second male that was at least 82 mm CL. The larger tank had a third large male. Each animal had a unique colour-coded antenna tag so that we could monitor growth and reproductive condition. Lobsters were caught approximately every 10 days for retagging, measuring (to the nearest 0.1 mm CL), and evaluating reproductive condition. In mid-September 2005, after no signs of reproduction had been observed for 6 weeks, we sampled one randomly selected eyestalk from each animal for neurolipofuscin.

### Estimating age in wild-caught animals

Eyestalk tissue was processed and sectioned, and neurolipofuscin was identified, imaged, and analysed

according to the methods described in Maxwell et al. (2007). We estimated age of animals collected in the Florida Keys and Dry Tortugas by applying the linear regression describing neurolipofuscin accumulation in known-age lobsters raised at FWC (Maxwell et al. 2007). There was no difference in the neurolipofuscin accumulation rates of males and females of known age, so the same regression was applied to both sexes. We verified the rate of neurolipofuscin accumulation indicated by the linear regression with modal analyses on neurolipofuscin-concentration distributions of wild-caught lobsters from Florida (Matthews et al. 2009, this issue).

### Statistical tests

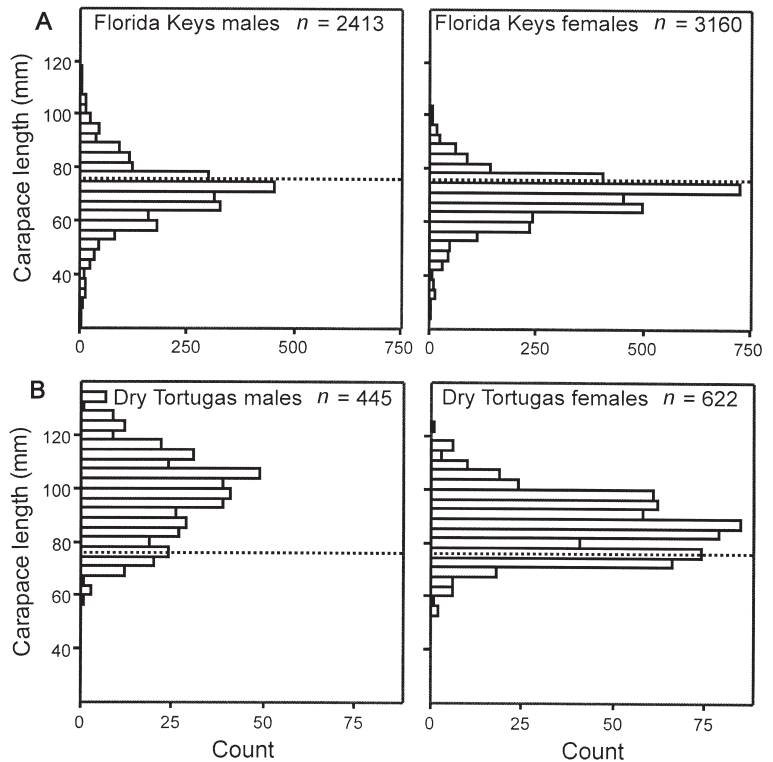
If data met the requirements, we used parametric tests (*t* tests and ANOVA); if not, we used non-parametric tests (Mann-Whitney and Kruskal-Wallis). We used an analysis of covariance (ANCOVA) to determine the effects of sex, size and origin on age of spiny lobster from the Florida Keys and Dry Tortugas. We completed a custom model univariate analysis of variance and found no significant interactions between independent variables, so we applied a full factorial one-way ANCOVA with size as a covariate. We used an independent samples *t* test to compare the ages of same-sized (80–120 mm CL) lobsters from the Florida Keys and Dry Tortugas. Mann-Whitney tests were used to compare size-frequency data and size of lobsters older than 2 years collected from the Florida Keys and Dry Tortugas for age analysis. A Kruskal-Wallis test was used to compare initial size of lobsters in the experiments comparing age of reproductive and non-reproductive females in the Florida Keys. We used a one-way analysis of variance (ANOVA) to compare age, growth, and number of egg clutches in the experiments comparing age of reproductive and non-reproductive females in the Florida Keys. Where significant, differences within categories were compared using a multi-comparison LSD test. All tests were conducted according to Sokal & Rohlf (1987) with an  $\alpha$  level of 0.05.

## RESULTS

### Age and growth of lobsters

The size-frequency data gathered by examining lobsters caught in traps in the Florida Keys and Dry Tortugas showed that lobsters from Dry Tortugas were considerably larger (Mann-Whitney test,  $U = 599985.5$ ,  $P < 0.001$ ) than lobsters from Florida Keys (Fig. 2). Similarly, there was only some overlap

**Fig. 2** Length-frequency distributions for male and female *Panulirus argus* captured in traps from **A**, Florida Keys (January and February 2001) and **B**, Dry Tortugas (January, February, and March 1995). Reference line denotes the minimum legal size for lobsters in Florida.

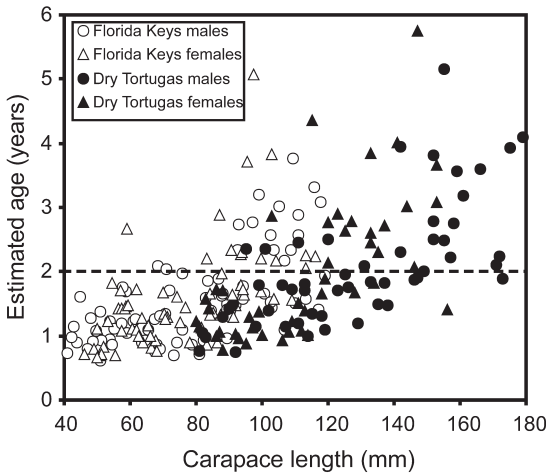


**Table 2** ANCOVA table for analysis to determine the effects of sex, size, and origin on age of *Panulirus argus* from traps in the Florida Keys and Dry Tortugas. Size (carapace length) was the covariate, and sex and origin (Florida Keys or Dry Tortugas) were fixed factors.

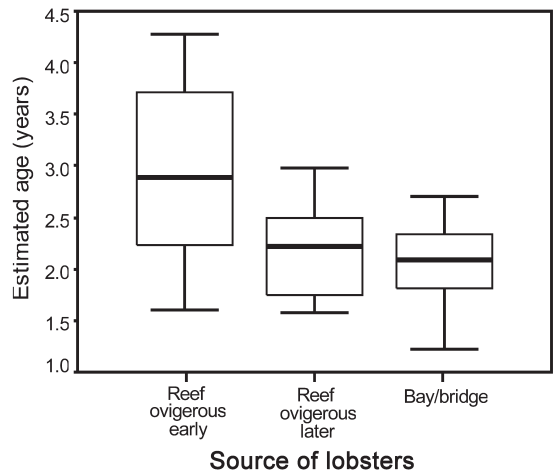
Effect	SS	d.f.	MS	F	P
Size	72.74	1	72.74	181.0	<0.001
Sex	1.97	1	72.76	181.06	<0.05
Origin	9.63	1	9.63	23.97	<0.001
Sex × Origin	0.75	1	0.74	1.86	<0.05
Error	96.01	239	0.40		

in size between lobsters caught in the Florida Keys and Dry Tortugas for neurolipofuscin sampling (Table 1). Comparing size versus estimated age showed the differences in size at age between spiny lobsters in the Florida Keys and Dry Tortugas (Fig. 3). Spiny lobsters from the Dry Tortugas ( $n = 39$ ) older than 2 years were considerably larger than lobsters from the Florida Keys ( $n = 30$ ) of the same age ( $U = 57.5$ ,  $P < 0.001$ ) (Fig. 3). Adjusting for size, ANCOVA showed that there was a significant difference in age between males and females and a significant difference in age between lobsters

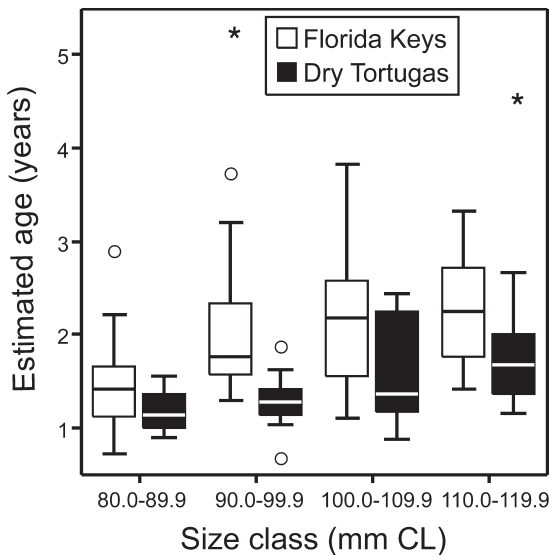
from the Florida Keys and Dry Tortugas, but no significant interaction between sex and origin (Table 2). Because lobsters smaller than 80 mm CL were absent from the Dry Tortugas sample and lobsters larger than 120 mm CL were absent from the sample from Florida Keys, we focused on animals of 80–120 mm CL to test for age differences of similar-sized lobsters (Fig. 4). Animals from the Florida Keys ( $n = 69$ ) were, on average, older than their same-sized counterparts in the Dry Tortugas ( $n = 53$ ) ( $t$  test, d.f. = 120,  $t = 3.573$ ,  $P < 0.001$ ) and had more variance in age (Fig. 4, Table 1).



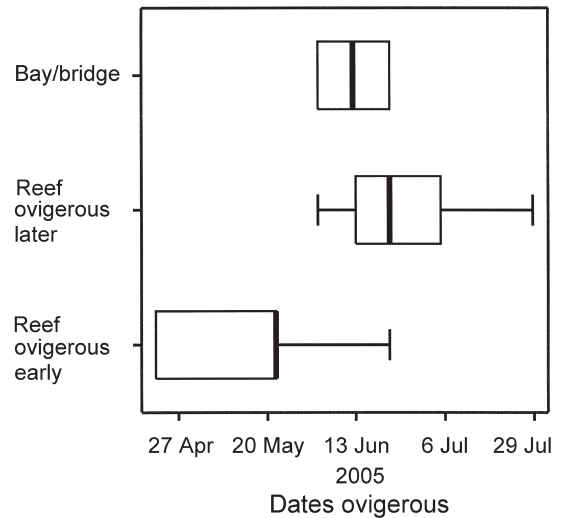
**Fig. 3** Age (as estimated by neurolipofuscin content) of *Panulirus argus* captured in traps in the Florida Keys (January and February 2001) and Dry Tortugas (February 2002). Lobsters older than 2 years are delineated by the dotted line.



**Fig. 5** Boxplot of estimated ages of 3 groups of female *Panulirus argus* ( $n = 8$  per group). Reef ovigerous early and reef ovigerous later collected from Delta Shoal; bay/bridge females that did not breed collected from Florida Bay and the bridges connecting the islands of the Florida Keys. (Central line denotes median; whiskers show lowest and highest values (excluding outliers).)



**Fig. 4** Boxplot of estimated ages of similar-sized (80–120 mm carapace length, CL) *Panulirus argus* from the Florida Keys and Dry Tortugas. Central line denotes median, whiskers show lowest and highest values (excluding outliers). (Open circles denote outliers, asterisks denote extremes.)



**Fig. 6** Timing of reproduction of 3 groups of ovigerous female *Panulirus argus*. Reef ovigerous early ( $n = 8$ ) and reef ovigerous later ( $n = 8$ ) collected from Delta Shoal; bay/bridge ( $n = 2$ ) collected from Florida Bay and the bridges connecting the islands of the the Florida Keys. (Central line denotes median; whiskers show lowest and highest values (excluding outliers).)

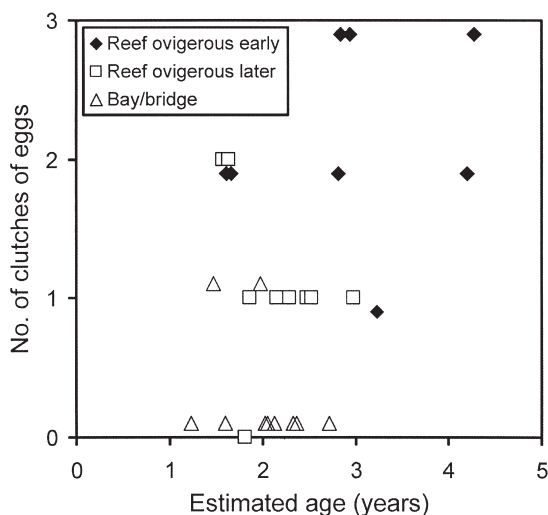
### Age and maturity

In the experiments comparing age of reproductive and non-reproductive females in the Florida Keys, we first confirmed that groups were the same size as per the experimental design (Kruskal-Wallis test,  $\chi^2 = 5.853$ , d.f. = 2,  $P > 0.05$ ). Of the 9 female lobsters from the reef that showed no signs of maturation at the time of collection, 8 became ovigerous later in the season (referred to as “reef ovigerous later”). Females collected from the reef that were reproductive at the onset of the experiment (“reef ovigerous early”) were significantly older than the 8 non-reproductive females collected from non-breeding grounds (“bay and bridges”) and the 8 females collected from the reef that were reproductive later in the breeding season (ANOVA, d.f. = 2,  $F = 3.887$ ,  $P < 0.05$ ) (Fig. 5). (One female collected from the reef that did not become ovigerous (age = 1.5 years) and two females collected from the bay and bridges that did become ovigerous (ages 1.2 and 1.7 years) were excluded from analysis because we were trying to compare age of reproductive animals collected from the breeding grounds and non-reproductive animals collected from the non-breeding grounds.) There were also differences in growth rate between female lobsters collected at the reef and those collected at the bay and bridges. On average, females collected from the non-breeding grounds grew more during the study (10.8 mm CL) than both groups of females collected from the reef (6.4 mm CL for reef ovigerous early and 5.6 mm CL for reef ovigerous later) (ANOVA, d.f. = 2,  $F = 4.064$ ,  $P < 0.05$ ).

There were differences between groups in the time during which females were ovigerous and in the number of clutches of eggs. Older females that were ovigerous early also finished breeding earlier than younger females that became ovigerous later (Fig. 6). Lobsters collected from the reef that were reproductive at the onset of the experiment produced more clutches of eggs than animals that were ovigerous later in the breeding season (ANOVA, d.f. = 2,  $F = 24.728$ ,  $P < 0.001$ ) (Fig. 7). Two females collected from the non-breeding grounds each produced one clutch of eggs.

### DISCUSSION

The size-frequency data of trap-caught lobsters show that lobsters from the Dry Tortugas were considerably larger than lobsters from the Florida Keys. Even though there were 6 years between size-frequency data collections, this trend has been



**Fig. 7** Relationship between estimated age and number of clutches of eggs in *Panulirus argus* collected in the Florida Keys. Reef ovigerous early ( $n = 8$ ) and reef ovigerous later ( $n = 9$ ) collected from Delta Shoal; bay/bridge ( $n = 10$ ) collected from Florida Bay and the bridges connecting the islands of the Florida Keys.

evident since the 1970s when researchers first started surveying lobsters in the Dry Tortugas and Florida Keys (Davis 1975; Bertelsen et al. 2004). Our results from the neurolipofuscin analyses show that spiny lobsters from the Dry Tortugas reached larger sizes at younger ages than those from the Florida Keys, demonstrating a faster growth rate. There was little overlap in the size ranges of lobsters older than 2 years in the Florida Keys and Dry Tortugas, and to be the same age at these different sizes, lobsters must have grown at different rates at the two locations. Previous studies indicated that the size of lobsters at 50% maturity from the Dry Tortugas was considerably larger than that of lobsters from the Florida Keys (Davis 1975; Bertelsen & Matthews 2001). Our data suggest that lobsters of different sizes at onset of maturity in the Dry Tortugas and Florida Keys are likely the same age. We hypothesize that the difference in size at which *P. argus* mature is probably owing to differences in the growth rates between the two populations, even though they share a common age at maturity.

There are a number of possible reasons for the difference in growth rate between the two populations. Factors that could influence growth include water temperature, food availability, population density, population genetics, predation

pressure, and fishing pressure (Chittleborough 1976; Mohan 1997; Bertelsen & Matthews 2001; Goñi et al. 2003; Lizárraga-Cubedo et al. 2003; Little & Watson 2005). Food availability and temperature differences do not seem to be likely explanations why lobsters from the Florida Keys and Dry Tortugas have different growth rates. Studies of prey abundance in the Florida Keys suggest that food abundance is not limited and that prey items are not depleted if lobster density is locally increased (Nizinski 2007). Differences in temperature are an unlikely factor affecting growth because there was little difference in sea surface temperatures (average temperature did not vary more than 1°C), recorded by NOAA data buoys in the Florida Keys and Dry Tortugas (<http://www.ndbc.noaa.gov/Maps/Florida.shtml>), and the two areas are at the same latitude. In addition, more deep-water lobster habitat exists in the Dry Tortugas (FMRI et al. 2000), which should coincide with colder bottom temperatures and slower growth rates, but lobsters in the Dry Tortugas were growing faster, not slower than their Florida Keys counterparts. Population density, which varies across the Dry Tortugas and Florida Keys (Bertelsen et al. 2004), could potentially cause differential growth. However, it would be difficult to assess the effects of population density in the Florida Keys and Dry Tortugas, because of the temporal variation owing to high catch rates during the open fishing season and the spatial variation caused by marine protected areas (Bertelsen et al. 2004; Cox & Hunt 2005).

Genetic differences in the Florida Keys and Dry Tortugas populations are doubtful considering that *P. argus* has 5- to 9-month-long planktonic phyllosoma stages, which should adequately mix the populations (Lyons 1980; Goldstein et al. 2006). In addition, Silberman et al. (1994) found no regional genetic markers during a pan-Caribbean study of *P. argus* mitochondrial DNA. The only potentially genetically different lobster population is in Brazil (Sarver et al. 1998). Therefore, we do not believe that the smaller size at maturity of spiny lobsters in the Florida Keys is an inherited trait given the homogeneity of *P. argus* mitochondrial DNA and the probable long distances travelled during the larval stages.

A possible explanation for the different growth rates between animals in the Florida Keys and Dry Tortugas is a difference in predation pressure between the two locations. The greater abundance of large fish predators (e.g., red grouper, *Epinephelus morio*, and black grouper, *Mycteroperca bonaci*) in the Dry Tortugas relative to the number in the highly exploited Florida Keys (Schmidt et al. 1999; Ault et

al. 2002, 2005) may result in size-dependent mortality of slower-growing lobsters in the Dry Tortugas and select for fast-growing lobsters. Lobsters growing quickly may attain a size refuge and be more likely to survive. Animals growing at a slower rate may be more likely to be preyed upon by the large groupers and other lobster predators (Childress & Jury 2006) that are abundant in the Dry Tortugas (Schmidt et al. 1999; Ault et al. 2002, 2005).

We believe that the most significant factors affecting growth rates in the Florida Keys and Dry Tortugas are the differences in fishing methods and fishing pressure. The abundant sublegal-sized lobsters and absence of large lobsters in the Florida Keys, evident in the size-frequency distributions, illustrate this point. The intense commercial and recreational fisheries have a tremendous influence on the lobster populations (Lyons & Kennedy 1981; Hunt & Lyons 1986; Hunt et al. 1986; Matthews 2001; Eggleston et al. 2003; Parsons & Eggleston 2005). The use of live under-sized lobsters as bait in the trap-based commercial fishery and sublethal injuries associated with the intense diver-based recreational and commercial fisheries in the Florida Keys likely reduce growth rate, because lobsters generally do not feed when they are confined in traps (Lyons & Kennedy 1981; Hunt et al. 1986; Matthews 2001) and injured lobsters must allocate energy, otherwise used for growth, for regenerating limbs that have been lost (Davis & Dodrill 1980; Lyons & Kennedy 1981). Because the Dry Tortugas are distant (>110 km) from the closest port, fishing pressure is less intense than in the more accessible Florida Keys. Thus, there is limited recreational and commercial diving for lobsters in the Dry Tortugas (Davis 1977); the fishery is primarily trap-based (E. Little, NOAA pers. comm. 2008). The relatively short supply of small lobsters in the fished areas around the Dry Tortugas also precludes the practice of baiting traps with sublegal-sized lobsters. So, growth rates may appear enhanced in the Dry Tortugas because of the limited fishing pressure, short supply of bait lobsters, and the loss of slower-growing lobsters owing to size-dependent predation, and growth rates may be reduced in the Florida Keys owing to injuries and confinement. Highly variable growth rates for lobsters in the Florida Keys (compared with similar sized animals from Dry Tortugas) are consistent with the hypothesis that some lobsters are injured and have slow growth rates, whereas others have managed to avoid traps and recreational fishers and have growth rates more consistent with lobsters from the laboratory (Maxwell et al. 2007) and the Dry Tortugas.

The general paucity of older lobsters in both the Florida Keys and Dry Tortugas is likely owing to the fishing pressure at both locations (Muller et al. 1997). Even though there are fewer traps, less use of sublegal-sized lobster for bait, and few commercial or recreational lobster divers in the Dry Tortugas, fishing pressure still appears to be sufficiently high to reduce the prevalence of older animals (Matthews et al. 2009, this issue).

In the laboratory, we evaluated the relationship between age and reproduction in different groups of lobsters from the Florida Keys. We showed that animals bearing eggs early in the breeding season were older than same-sized animals that bore eggs later in the season or those that were immature. Those collected from the breeding grounds that bore eggs later in the season also produced fewer clutches, so we assumed that they became mature during the course of the breeding season. The two females collected from the non-breeding grounds that produced a single clutch of eggs also likely matured during the course of the experiment. These results support our hypothesis that reproduction is primarily age-based, but the study also indicated that some young lobsters in the Florida Keys reproduce at their first opportunity, which may be late in the usual reproductive season. This late-season mating appears to extend the “normal” March to June reproductive season (based on observations from Dry Tortugas National Park, where there is a large marine reserve and probably the least disturbed population of lobsters in Florida) to March–September in the Florida Keys (Bertelsen & Matthews 2001). The late breeding that occurs in the Florida Keys is probably a result of the fishing methods and the intensity of the fishery, but the mechanism by which this protracted breeding season happens is unclear. The implications for supplying larvae to the greater Caribbean lobster population late in the season are unknown.

Although the initial size of females collected from breeding grounds and nonbreeding grounds did not differ, growth rates did. Females collected from the non-breeding grounds grew faster than females collected from the reef because ovigerous animals generally do not moult until after they finish mating for the year, to retain their developing eggs (Quackenbush 1994).

Large female spiny lobsters are capable of carrying considerably more eggs than smaller females. The maximum reproductive effort of 830 eggs per g body mass by lobsters is between 90 and 95 mm CL (Bertelsen & Matthews 2001), but fewer female lobsters attained this size in the Florida Keys compared with Dry Tortugas. Maturing at optimal size, as lobsters

do in the more undisturbed environment of the Dry Tortugas, improves reproductive output (Bertelsen & Matthews 2001); total reproductive output is also greater in older females because they tend to produce more clutches of eggs than newly mature females.

Our study indicates that the fishery has an impact on the size structure and fecundity of Caribbean spiny lobster. We believe that the practice of using sublegal-sized lobsters as bait and that injuries caused by handling small lobsters in the Florida Keys reduce the growth rate of lobsters so that they mature at a smaller size. The fishery may also affect the timing of the reproductive season (Bertelsen & Matthews 2001). Total harvest of spiny lobster in the Caribbean appears to have peaked and subsequently declined in the past 5 years (Ehrhardt 2005). Although there has not been a decline in the supply of pueruli to the Florida Keys (FWC unpubl. data), timing of larval supply may be important to the local production of lobsters (Butler et al. 2001). Egg production of lobsters living in the Florida Keys is a fraction of the egg production in an undisturbed population (Lyons et al. 1981, Bertelsen et al. 2004), and it seems unlikely that the Caribbean-wide lobster population could maintain itself if the Florida Key's level of fishing pressure occurred throughout the population.

#### ACKNOWLEDGMENTS

Grant no. NA17FF2871 from the Marine Fisheries Initiative Program (MARFIN) of the National Oceanic and Atmospheric Administration (NOAA) and grant no. 1998-0249-005 from the National Fish and Wildlife Foundation supported Kerry Maxwell's Master of Science degree and this research. We thank Cathleen Drilling, Jennifer Fortier, Paul Harrison, John Hunt, Paul Mages, Joshua Moore, Valentine Nduku, Vivian Ngo-Vu, Manfred Schmidt, Stopher Slade, Grant Stoecklin, and Marie Tellier for their technical assistance; commercial fishers Rick LaFlair, Gary Nichols, Ernie Piton, and Pete Worthington for allowing us to collect tissue samples aboard their vessels; and Gabriel Delgado, Matthew Grober, Cindy Lewis, Judy Leiby, Adrianna Zito, and two anonymous reviewers, for their comments and editing.

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