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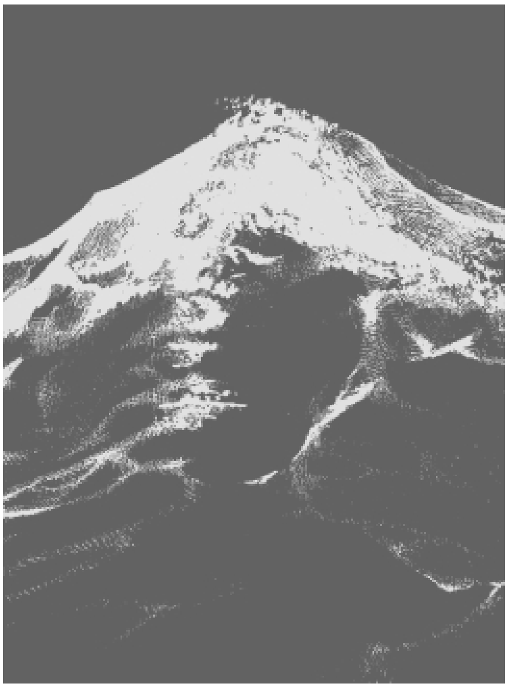

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Fecundity dynamics of female spiny lobster (*Panulirus argus*) in a south Florida fishery and Dry Tortugas National Park lobster sanctuary

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Abstract. Using diver surveys, we compared the size structure, fecundity, and reproductive season of spiny lobsters (*Panulirus argus*) in the Dry Tortugas National Park lobster sanctuary with those of spiny lobsters in the south Florida fishery. The number of lobsters of both sexes larger than the legal size limit declined sharply in the fishery but not in the sanctuary. Clutch sizes were larger in the Dry Tortugas sanctuary, averaging 0.8 million, than in the fishery, averaging 0.3 million. The reproductive season was shorter and more intense in the sanctuary than in the fishery. In addition, lobsters in the sanctuary begin producing eggs at a larger size and produce more eggs per gram of body mass than lobsters in the fishery. Peak egg production occurs earlier in larger lobsters than in small ones. Establishing a fundamental reason for the differences between lobster reproduction in the sanctuary and that in the fishery is not possible until the chronological age of lobsters can be determined, but one hypothesis consistent with these differences is that, if lobsters reproduce at a certain chronological age, then sublethal fishery practices may account for slower growth for some lobsters resulting in some smaller but older reproductively active lobsters.

Introduction

The spiny lobster (*Panulirus argus*) population in south Florida, USA, is extensively harvested by both commercial and recreational fishers. During the 1990s, total commercial landings have been approximately six million pounds per year, and recreational landings two million pounds per year (Harper 1995; Sharp *et al.* in press). The management of the spiny lobster fishery includes a minimum size limit (76 mm CL [carapace length]), a closed season (from April 1 to August 6), prohibition of the harvest of egg-bearing lobsters, daily recreational bag limits, and a commercial trap-reduction program that reduced the number of traps in the water from approximately 704 thousand to 530 thousand between 1993 and 2001.

Spiny lobster reproductive activity in south Florida occurs along the reef tract from the Dry Tortugas through Key Largo, principally between the months of February and August (Davis 1974; Gregory *et al.* 1982; Lyons *et al.* 1981) (Fig. 1). Within this area, two populations of lobsters (one unexploited and one exploited) were sampled during the breeding season (March through October) from 1996 to 1998. The unexploited breeding population is located in a 190-km^2 sanctuary that was established in 1973 in the Dry Tortugas National Park. Because the maximum life span of the spiny lobster is on the order of 20 years, we assume this lobster population has become 'unexploited–stable' (*i.e.*, all changes that would occur between the exploited and

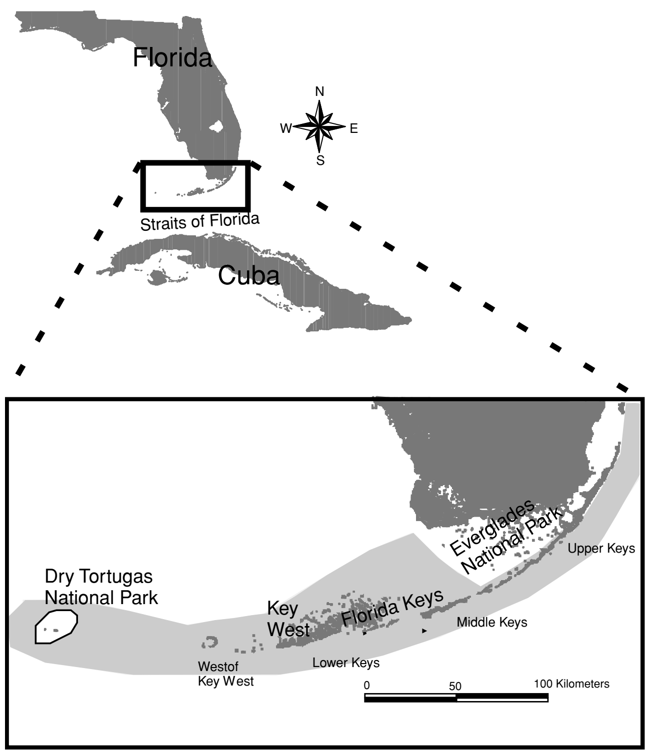

Fig. 1. Location of the Florida Keys lobster fishery (shaded area) and the Dry Tortugas National Park lobster sanctuary.

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unexploited state have taken place). The exploited breeding population is located along the Florida Keys reef tract from Key Largo to Marquesas Key (Fig. 1).

The purpose of this study was to compare the fecundity dynamics of spiny lobsters in the Florida Keys fishery and in the Dry Tortugas sanctuary. Specifically, we compared the sizes of lobsters producing eggs and the times of year during which eggs are produced, the percentage of lobster biomass expended for egg production as a function of size, and the onset of egg production as a function of size.

Methods

Field methods

From 1996 to 1998, divers conducted spiny lobster population surveys along the reef tract from the upper Florida Keys to the Dry Tortugas (Fig. 1). The Dry Tortugas and four areas of the Florida Keys reef tract were surveyed from March to September at six-week intervals ($n = 6$). Three surveys were conducted within each area: deep survey (>15 m), fore reef (ocean side of the reef crest), and back reef (landward side of the reef crest). Two sets of dives of these surveys were conducted in the Dry Tortugas. A survey consisted of a one-hour search. For better standardization of effort, time spent handling lobsters was not counted as part of the search time. Full one-hour searches were not always possible during the deeper dives. For abundance estimates, these dives were standardized to one hour.

Lobsters were captured and returned to the boat, where information about sex and reproductive status was recorded. Egg masses, when present, were shaved from the pleopods and brought to the laboratory for analysis.

Laboratory methods

Three subsamples of eggs were separated from each egg mass and counted. Each subsample and the entire egg mass were weighed (wet weight) to the nearest 0.0001 g. The estimated egg count for the entire mass was equal to the count of the subsample times the total egg mass weight divided by the subsample weight (see Cox and Bertelsen 1997).

Analyses

The egg-production season (percentage of egg bearers by size class and month) was fitted to a 3D surface by means of a normal smoothing kernel (Simonoff 1996). We used ordinary least-squares linear regression of the percentage of egg bearers on size class to evaluate the onset of egg production.

A fecundity-to-lobster-mass (number of eggs per gram of body mass) by carapace-length equation was produced from the ratio of the fecundity-to-carapace-length equation from Cox and Bertelsen (1997) and a mass-to-carapace-length equation (Florida Marine Research Institute, unpubl. data). This equation was used to examine size distributions of egg bearers in terms of eggs per gram of body mass from the Dry Tortugas sanctuary and the Florida Keys fishery.

Results

We conducted 288 dive surveys and logged observations of more than 3600 lobsters. Lobsters were found at depths ranging from near the surface to 28 m. Sizes ranged from 15 to 184 mm CL. The size distribution of lobsters for both sexes in the fishery showed a sharp decline in numbers above the legal size (76 mm CL), whereas in the Dry Tortugas, neither female nor male lobsters began to decline in number until well above the legal size (Fig. 2).

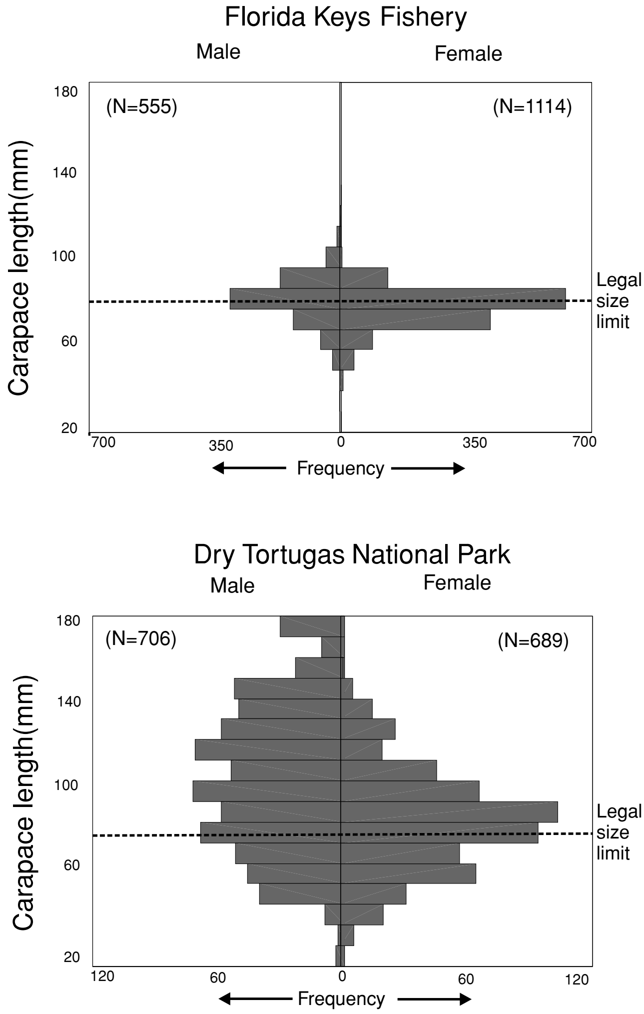

Fig. 2. Size distributions of male and female lobsters in the fishery and Dry Tortugas National Park.

We estimated the number of eggs in 404 egg clutches collected during the surveys. Egg counts ranged over two orders of magnitude; the largest egg count was from the Dry Tortugas (1.95 million eggs) and the smallest from the area west of Key West (0.03 million eggs). The overall distribution of egg clutch sizes in the Dry Tortugas was much larger than that in the fishery (Fig. 3*a*). Mean clutch size was significantly larger in the Dry Tortugas than in the Florida Keys fishery (t-test; $\alpha < 0.001$), presumably because the overall size of reproductively active female lobsters was larger in the Dry Tortugas and because the minimum size of lobsters beginning to produce eggs was 57 mm CL in the fishery and 70 mm CL in the sanctuary (Fig. 3*b*).

Egg-bearing lobsters were found over a greater portion of the year in the fishery than in the Dry Tortugas. The earliest we observed lobsters bearing eggs was April 15 in the Dry Tortugas and March 14 in the fishery, whereas the latest we

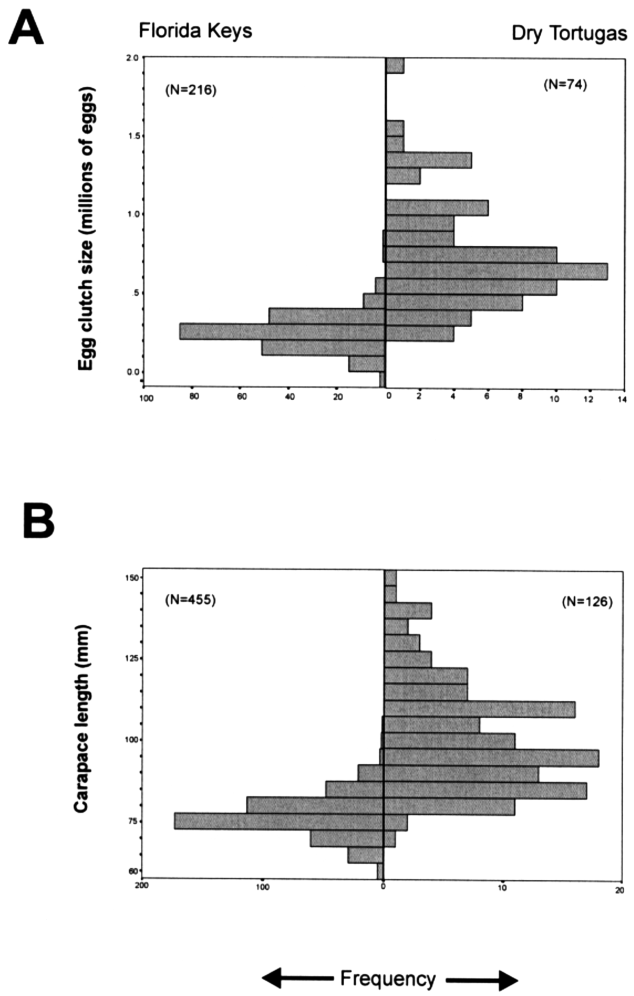

Fig. 3. (*A*) Size–frequency distribution of egg clutch size in the Dry Tortugas population and Keys fishery and (*B*) size–frequency distribution of egg bearers in the Dry Tortugas population and Keys fishery.

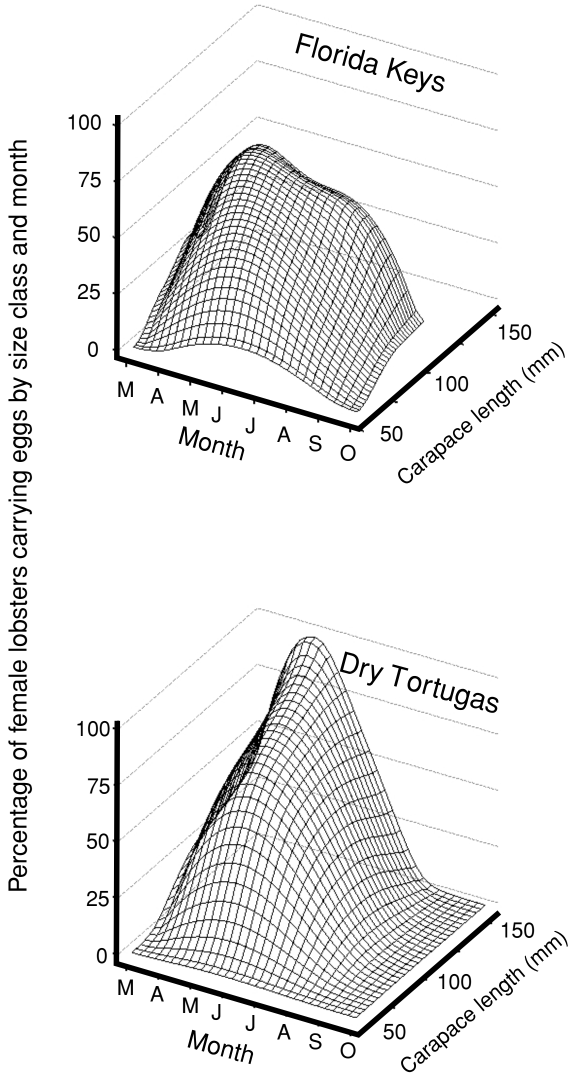

Fig. 4. Smoothed response surface showing the percentage of egg bearers by time and size, for the Dry Tortugas lobster population and Florida Keys fishery. The smoothed response surface was generated with a normal smoothing kernel.

observed lobsters bearing eggs was August 14 in the Dry Tortugas and October 22 in the fishery. By calculating the percentage of egg-bearing lobsters by size class and time of year, and then developing a smooth-surface plot of percentage of egg bearers by time and size, we found that the breeding season in the Dry Tortugas is not only shorter but more concentrated than that in the fishery (Fig. 4): nearly 100% of larger-sized lobsters were bearing eggs at the breeding season's peak in the Dry Tortugas. From the surface plots (Fig. 4), we estimated the peak egg-bearing time for different-sized egg-bearing lobsters. Egg bearers larger than 90 mm CL were almost exclusively found in the Dry Tortugas, and their peak egg-bearing time occurred in mid-May. Egg bearers ranging from 80 to 90 mm CL were found in both the Dry Tortugas and Florida Keys fishery, and their peak egg-bearing time occurred in late May in both areas. Egg bearers smaller than 80 mm CL were found nearly exclusively in the fishery, and their peak egg-bearing time was in early June.

The onset of egg bearing in lobster populations has been expressed with various parameters, such as minimum size of egg bearers, mean size of egg bearers, and the percentage of egg bearers by size class. The minimum size of egg-bearers we observed was 57 mm CL in the fishery and 70 mm CL in the Dry Tortugas. The 3D surface charts (Fig. 4), which interpolate the percentages of egg bearers by time and size, suggested the presence of smaller egg bearers than we

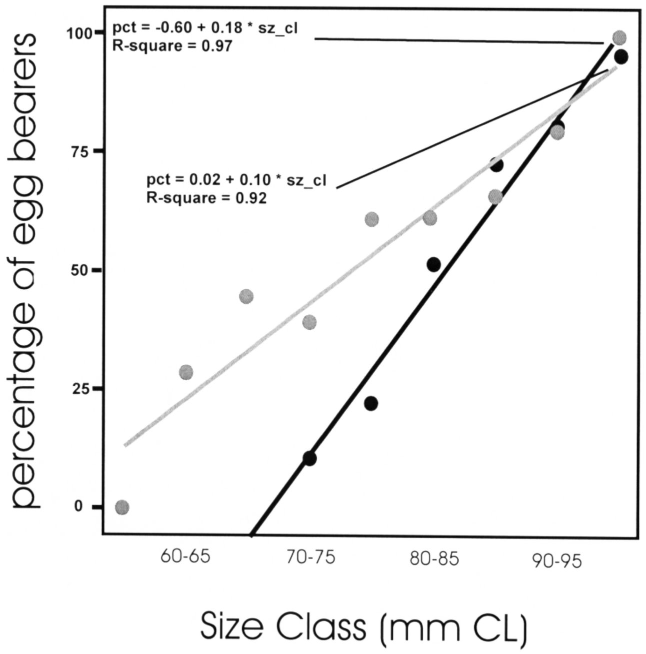

Fig. 5. The onset of egg bearing in the Florida Keys fishery (light circles) and Dry Tortugas (dark circles) lobsters. Shown is the percentage of egg-bearing lobsters during the peak reproductive season (April–June) by size class in both regions, from the minimum size at which eggs are present to the first size class in which more than 90% are egg bearing. The least-squares linear regressions for the two regions are statistically significantly different ($\alpha = 0.005$).

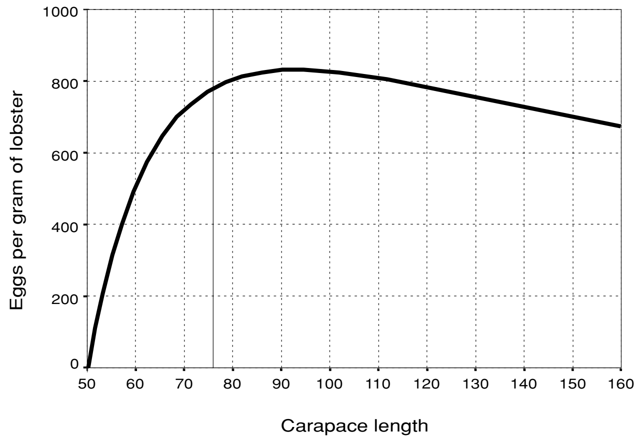

Fig. 6. The estimated reproductive effort (RE) in number of eggs produced per gram of lobster body mass by carapace length. See text for details of curve generation.

observed, but this suggestion was probably an artifact of the smoothing process. The mean size of egg-bearers was 77 mm CL in the fishery and 101 mm CL in the Dry Tortugas. The size of lobsters at the onset of egg production was examined as a function of the percentages of egg bearers in different size classes, from the first size class bearing eggs through the size class with the highest percentage of egg bearers. For these determinations, we used observations from between the months of April and June, when peak egg production occurred. In the fishery, egg bearers appeared in low percentages starting with the 60–65 mm CL size class, increased to near 100% by the 95–100 mm CL size class, and remained near 100% through the largest size class (105–110 mm CL) found in the fishery. In the Dry Tortugas, egg bearers appeared in the 70–75 mm CL size class, increased to near 100% in the 95–100 mm CL size class, and remained near 100% through the 150–155 mm CL size class. The Dry Tortugas sanctuary and the Florida Keys fishery differed significantly ($\alpha = 0.005$) in the onset of egg production, which was a linear function of size for the two areas and occurred over a narrower size range in the Dry Tortugas than in the fishery (Fig. 5).

Although a gonadal somatic index calculation was not possible because we did not measure the mass of each egg bearer, a measure of reproductive efficiency in units of eggs per gram of body mass by carapace length can be estimated from the relationship between egg clutch size and carapace length (Cox and Bertelsen 1997) (Eq. 1) and a morphometric equation that estimates biomass from carapace length (Florida Marine Research Institute, unpubl. data) (Eq. 2).

$$\text{Egg count} = -231{,}212 + 91.88\ CL_{mm}^{2} \quad (1)$$

where CL_{mm} is carapace length in millimetres.

$$Mass_{g} = 0.00184 * CL_{mm}^{2.82} \quad (2)$$

where $Mass_g$ is mass in grams and CL_{mm} is carapace length in millimetres. Dividing Eq. 1 by Eq. 2 gives an expression for the reproductive effort (RE) in eggs per gram of body mass for a given carapace length (Eq. 3).

$$RE_{\text{eggs per gram of body mass}} = -1.26*10^{8}*CL^{-2.828} + 4.99*10^{4}*CL^{-0.828} \quad (3)$$

This equation predicts a maximum reproductive effort of 830 eggs per gram of body mass by lobsters between 90 and 95 mm CL (Fig. 6). For lobsters smaller than 80 mm CL, the predicted number of eggs per gram of body mass falls to 500 eggs per gram at 60 mm CL and zero eggs per gram at 50 mm CL. For lobsters larger that 95 mm CL, the equation predicts a slow decline in reproductive effort to 700 eggs per gram of body mass at 150 mm CL. The relationship between eggs per gram of lobster and carapace length was plotted against the size distribution of egg bearers in the Florida Keys fishery and Dry Tortugas sanctuary (Fig. 7). The size range at which lobsters exceed 800 eggs per gram of body mass (80 to 110 mm CL) is approximately the same as the

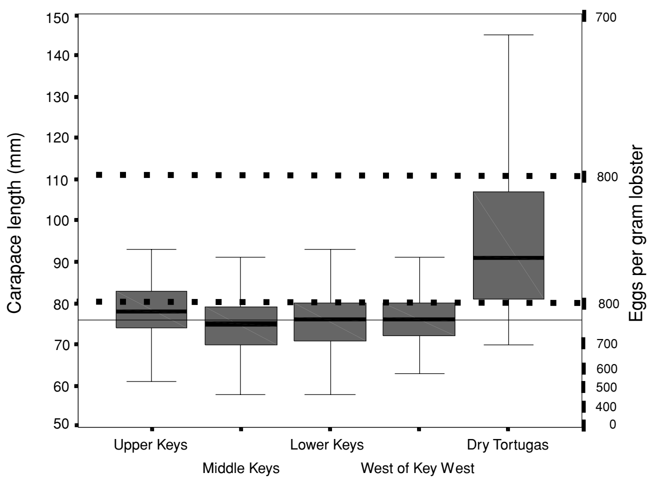

Fig. 7. Box-plot distribution of the sizes of egg-bearing lobsters by region (exploited = Upper, Middle, Lower Keys, and West of Key West; unexpoited = Dry Tortugas). The second y-axis represents the reproductive efficiency (REs) in eggs per gram of lobster body mass. The two dotted lines represent the upper and lower sizes at which lobsters exceed 800 eggs per gram of body mass.

interquartile range (the box in the box plot) of egg-bearing lobsters in the Dry Tortugas sanctuary. Nearly all egg bearers within the interquartile range in the Florida Keys fishery produce eggs at a rate below 800 eggs per gram of body mass.

Discussion

Because the size distribution of egg bearers in the Dry Tortugas coincides with the predicted maximum in reproductive effort (Fig. 7), and because the breeding season is short and includes a greater percentage of the female population as egg bearers at the peak (Fig. 4) in the Dry Tortugas, the fecundity dynamics of this population seem to be better than those in the Florida Keys fishery. We are left with a question, however: Why do lobsters less than 70 mm CL produce eggs in the fishery but very few lobsters less than 80 mm CL and none less than 70 mm CL produce eggs in the Tortugas sanctuary (Fig. 5)? The proximate answer to this question is that, in heavily fished populations, reproduction at a smaller size constitutes a common 'compensatory response'. 'Smaller' also generally implies 'younger', and although size and age must be correlated to some degree in spiny lobsters, no currently available method permits estimation of the age of any given lobster captured in the field. The fundamental answer to the question asked above is difficult to determine without age information, but commonly expressed hypotheses are (1) genetic selection or pressure on the exploited population (2) food availability (quantity and/or quality) (3) chemical or behavioural inhibition of smaller lobsters by larger lobsters, and (4) differentially slower growth rates in some individuals in the exploited population.

The genetics-based natural-selection scenario postulates that, in a heavily fished population, individuals are likely on average to reproduce at an earlier age (and therefore smaller size) and to have smaller clutches because those that do not (Fig. 6) are more likely to be harvested. In the unexploited population, which has a much smaller risk of mortality, growing into the optimal size before reproduction (i.e., >80 mm CL; Fig. 6) would result in production of more offspring. Over time, selection pressure would reduce the age of reproductive maturity in the fishery. For south Florida spiny lobsters, genetic responses seem unlikely because of the long-range (nine-month planktonic) dispersal of larvae, which would eliminate the possibility of local selection pressure. Because pan-Caribbean genetic studies have not found any regional genetic markers in spiny lobsters (Silberman *et al.* 1994), it is highly doubtful that the Dry Tortugas and Florida Keys populations differ genetically.

Differences in food availability between the fishery and the sanctuary also seem unlikely, but this conjecture cannot currently be proven. Although food availability can alter size and age at which of the onset of egg production occurs in small laboratory-reared crustaceans, no consistent pattern emerges in the relationship of size, age, and food availability to egg production (Wenner *et al.* 1985). If food were limiting, one response might be the production of a smaller clutch. Although the Florida Keys and Dry Tortugas show little overlap in the sizes of egg-bearing females, where this small overlap occurs, the numbers of eggs produced do not appear to differ. In addition, when the egg-clutch-size-to-carapace-length data were separated for the Dry Tortugas sanctuary and the Florida Keys fishery, the resulting predictive curves were nearly indistinguishable (see Bertelsen and Cox 2001).

The only evidence from the present study for inhibition of maturity of smaller females by larger females, by means of behavioural or chemical cues, is the presence of small egg-bearing female lobsters and the absence of large female lobsters in the Florida Keys fishery. Also, small female lobsters do not bear eggs in the Dry Tortugas sanctuary, where large female lobsters are present. One inconclusive observation from our study that does not support a chemical or behavioural cue is that the time of the peak in egg production (late May) was the same for the egg bearers in the 85–95 mm CL size class in the Dry Tortugas sanctuary, where very large (100–150 mm CL) egg bearers were present, and for the egg bearers in that same size class in the Florida Keys fishery, where very large egg bearers are absent. One might argue that, if inhibitory factors were present in the sanctuary, those 85–95 mm CL lobsters in the fishery might advance their breeding time, the timing of reproduction by different-sized lobsters may be determined solely by water-temperature changes (see Lipcius and Herrnkind 1987). As for behavioural inhibition, we did not observe any aggression (such as the 'pecking-order aggression' seen in some fishes) between different-sized females during the breeding season, during either diving or operation of a remotely operated vehicle. If a behavioural cue is given by larger lobsters trying to inhibit egg production in smaller lobsters, it is probably subtle. Male-to-male aggression on the other hand, was observed during both diving and operation of the remotely operated vehicle. Any chemicals released as cues would be rapidly diluted in the 2- to 5-knot currents we regularly encountered in the Dry Tortugas, Tortugas Banks, and west of Key West. If chemicals are released as cues, localized upstream populations within the Dry Tortugas region would probably receive far fewer of these cues than downstream populations would. Perhaps one way that chemicals could inhibit egg production in smaller lobsters is through cumulative exposure over time. This hypothesis could perhaps be tested by means of reciprocal transplants of various sized female lobsters and by experimental exposure of different-sized female lobsters to each other in tanks within a laboratory.

Another hypothesis is that some individuals in the fished population grow more slowly and that the smaller egg producers are as old as any other egg producer in the population. This explanation is consistent with the differences in the fecundity dynamics presented here. The underlying assumptions are that female lobsters begin egg production at a particular chronological age and that stochastic fishery-related events slow growth among some individuals in the fished population. This hypothesis predicts a greater variance in age within any given size class of lobster in the Florida Keys fishery than in the Dry Tortugas sanctuary. This hypothesis also predicts that, although egg production will commence at a smaller size in the fishery, some size will exist at which all individuals, whether in the fishery and in the sanctuary, are old enough to produce eggs (see, e.g., Fig. 4). Although the first prediction is not yet testable (because we have no way to calculate the age of lobsters), the relationship between the percentages of egg bearers by size class supports the second prediction.

Slower growth rates for some individuals within the fished population could be induced by sublethal injuries, such as breakage of legs and antennae, that occur during handling by recreational and commercial fishers. Sublegal lobsters are routinely placed into traps to serve as attractants for other lobsters. Some of these animals die, and others are released or escape after a period of starvation (see Davis 1981; Brown and Caputi 1985; Hunt and Lyons 1986; Hunt *et al*. 1986). Estimates of the percentage of external injury to lobsters in fished areas range from 40% (Davis 1981) to 10% (Lyons *et al*. 1981). The metabolic costs to lobsters due to starvation during confinement are not known. We propose that, because of reduced growth rates brought about by injury or confinement, small egg bearers are older than those in the same size class not producing eggs. The difference between the fishery and the sanctuary in the minimum size of egg bearers is an indicator of the degree of sublethal injury that is experienced by lobsters in the fishery. Conversely, if a fishery is managed to reduce or avoid sublethal injury, lobsters should grow at a rate closer to optimum, and females should begin producing eggs nearer to their reproductively optimum size.

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