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Contribution to the Supplement: '*Lobsters in a Changing Climate*'

Original Article

Mate choice in temperate and tropical spiny lobsters with contrasting reproductive systems

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Sperm limitation of reproductive success is common in decapod crustaceans, favouring mating systems in which females compete for large males of high reproductive value. We investigated these phenomena in two species of spiny lobsters—one temperate, one tropical—with contrasting reproductive systems: the Southern Rock Lobster (*Jasus edwardsii*) and the Caribbean Spiny Lobster (*Panulirus argus*). We hypothesized that female mate selection should be more pronounced in the temperate *J. edwardsii* than in the tropical *P. argus* because *J. edwardsii* matures later, has a shorter mating season, and produces just one clutch of eggs per year that benefit from significant maternal investment of resources. As hypothesized, experiments conducted in large mesocosms revealed that female *J. edwardsii* cohabited with large males more often than expected by chance during their receptive period, but not at other times. Large male *J. edwardsii* cohabited in dens with the largest unmated females, whereas small males exhibited no mate size preference. In contrast, the proportion of female and male *P. argus* that co-occupied dens with the opposite sex was no more than expected by chance. Cohabitation patterns in the wild supported these laboratory findings for both species. Our results demonstrate the tight connection between contrasting reproductive strategies and the specificity of mate choice in spiny lobsters that are consistent with predictions based on environmental seasonality in temperate vs. tropical ecosystems.

Keywords: *Jasus*, mate choice, *Panulirus*, reproduction, spiny lobsters.

Introduction

Latitudinal gradients in animal life history characteristics, such as the trade-off in maternal investment in egg mass vs. numbers of eggs (i.e. clutch size), are deeply rooted in evolutionary biology theory (MacArthur and Wilson, 1967; Pianka, 1970; Reznick *et al.*, 2002). These differences are paraphrased by the classic *r*-selected vs. *K*-selected life history dichotomy: species that evolved at lower latitudes display *r*-selected life history attributes (e.g. many offspring at low "cost" to the parent, thus: high fecundity, early maturity, low parental investment, etc.) and those that evolved at higher latitudes tend to be *K*-selected (e.g. fewer and better provisioned offspring: lower fecundity, late maturity, large parental investment, etc.). Empirical evidence from a variety of taxa, including marine fish (Vila-Gispert *et al.*, 2002; Foster and Vincent, 2004) and crustaceans (Anger *et al.*, 2002; Sarma *et al.*, 2005), is consistent with this theory. Latitudinal differences in life history theory are also relevant to applied fields such as fishery management, that to be effective must adopt different management regulations where latitudinal gradients in life history exist (Fromentin and Fonteneau, 2001).

Spiny lobsters (Decapoda; Palinuridae) are good models for exploring the implications of latitudinal differences in the evolution of reproductive life history characteristics such as mate choice and competition and the potential effects of, or implications for, human exploitation of those populations. Spiny lobsters have a global distribution, their patterns of reproduction vary latitudinally, their reproductive systems are finely tuned with very low sperm:egg ratios, and their size-dependent breeding systems are sensitive to changes caused by overfishing (Lipcius *et al.*, 1983; Lipcius, 1985; DeMartini *et al.*, 1993; MacDiarmid and Butler, 1999; Kelly *et al.*, 2000; Melville-Smith and de Lestang, 2006; Butler *et al.*, 2011). We investigated latitudinal effects on mating systems in two species of spiny lobsters with contrasting reproductive systems: a temperate species—the Southern Rock Lobster (*Jasus edwardsii*) from New Zealand and south Australia; and a tropical species—the Caribbean Spiny Lobster (*Panulirus argus*).

We hypothesized that mate selection should be stronger in *J. edwardsii* than in *P. argus* for at least two reasons: *J. edwardsii* has fewer lifetime mating opportunities and the consequences of a missed mating opportunity are severe. Female *J. edwardsii* breed only once per year after a pre-mating molt and during a 3–5 month autumn mating season repeated over an average of 7 years (Pollock, 1991). So a single mating opportunity represents ~5–15% of the average lifetime matings for *J. edwardsii*. In contrast, female *P. argus* mate and spawn up to three times per year depending on their size (Lyons *et al.*, 1981; Maxwell *et al.*, 2009) and do so over a prolonged breeding season (6–12 months depending on latitude) and for anywhere from 5 to 30 years (Pollock, 1997; Bertelesen and Mathews, 2001; Ehrhardt, 2008; Maxwell *et al.*, 2009). So a single mating constitutes as little as 1.5% of all matings by a long-lived female *P. argus*. Moreover, the fecundity of female *J. edwardsii* drops 10% each day that mating is delayed once a female becomes receptive and, if no mate is found, absorption of the egg mass scars the ovaries resulting in up to a 40% drop in fecundity the following mating season (MacDiarmid and Sainte-Marie, 2006). In contrast, if female *P. argus* do not find a mate, they simply extrude the unused egg mass (Butler *et al.*, 2011). In short, the reproductive cost of not acquiring a mate for female *J. edwardsii* (the temperate species) is far greater than that for *P. argus*.

The same temperate–tropical differences that give rise to disparate female reproductive patterns and mate selection also influence the choice of mates by male lobsters. Large male spiny lobster should preferentially choose and compete for large competent females with whom to mate, given their greater egg production, and this preference should be more strongly exhibited by male *J. edwardsii*. In both *J. edwardsii* and *P. argus*, female fecundity is size dependent with the largest females producing 9–19 times the number of eggs per clutch of the smallest mature females (MacDiarmid and Sainte-Marie, 2006). However, the short breeding season of *J. edwardsii* in temperate climates and limited mating opportunities with females that mate only once per year should result in stronger male–male competition for mates in *J. edwardsii* than for *P. argus*.

Yet, these highly evolved differences in the reproductive biology of tropical and temperate species may be similarly affected by overfishing. In intact populations within MPAs where large males are still present, spiny lobsters exhibit lek-style mating systems in which large males defend specific dens or groups of dens from other males and females travel among these males and their territories (MacDiarmid, 1994; Bertelsen and Cox, 2001; Bertelsen and Matthews, 2001; Robertson and Butler, 2012). However, this lek-style mating system breaks down in heavily fished spiny lobster populations where large lobsters, especially large males, are absent and smaller individuals tend not to establish or defend mating territories (MacDiarmid, 1994; Bertelsen and Cox, 2001; Bertelsen and Matthews, 2001).

Here, we describe how we first compared the reproductive biology of these two species of spiny lobster whose life histories are indicative of temperate and tropical species. We then conducted a series of female and male mate choice experiments in large, outdoor mesocosms and compared those findings with field observations of mating and den co-occupancy. As predicted by life history theory, we hypothesized that (i) preference for larger mates would be strongest by females, larger individuals, and in *J. edwardsii* compared with *P. argus,* and (ii) male–male competition would also be most intense among large males, particularly *J. edwardsii.*

Methods

Southern rock lobster mesocosm experiments

Mature male and pre-molt female *J. edwardsii* were obtained from the Chatham Islands and near Wellington, New Zealand, and transferred to a flow-through seawater system (Figure 1). Only *J. edwardsii* of a size whereby all are certain to be mature (>90 mm CL) were included in our experiments. Lobsters were measured (carapace length; CL), individually marked with colour-coded antennae tags, and distributed among six 1.8 m diameter × 0.6 m deep concrete holding tanks. Sexes were held separately until the start of the experiments. The lobsters in each holding tank had continuous access to live blue mussels (*Mytilus galloprovincialis*) for food and were shaded from sunlight.

Experiment 1: mate choice by female J. edwardsii

The choice of a mate by small (99–108 mm CL) and large (127–153 mm CL) mature female *J. edwardsii* were tested at four different phases of the mating cycle: pre-molt, early post-molt, late post-molt, and egg-bearing. The designation of reproductive stages that we tested for *J. edwardsii* are related to a specific pre-mating molt that females undergo each year before the breeding season. To define these stages for each female, we calculated the expected day of mating from a function incorporating molt-mate interval, day of molting, and female size (MacDiarmid, 1989b). We then used this information to subdivide the period between molting and mating into two phases: early post-molt and late post-molt.

The experiment was conducted in two large outdoor tanks measuring 7 × 5 and 2 m deep (~75 000 l) and covered by a plastic mesh screen that reduced the ambient light level by 75%. In each corner, a shelter was constructed from two hollow concrete building blocks supporting a 500 × 500 mm concrete paving slab. Shelters were large enough to simultaneously house a large male and a large female. One shelter was left empty, but in the other three shelters we tethered either a large mature male (~180 mm CL), a small mature male (~100 mm CL), or a female of the same size and reproductive stage as the test female. Lobsters were tethered to their shelter by a 0.5 m length of 40 kg test-strength monofilament fishing line. The line was attached to the lobster via a swivel on a plastic cable tie fastened around the cephalothorax between the second and third walking legs. This fit snugly between the legs and allowed normal locomotor activity. Tethering is more commonly used as a means to compare relative rates of predation on marine animals under differing conditions, and its utility and problems have been thoroughly debated (Peterson and Black, 1994; Aronson and Heck, 1995; Aronson *et al.*, 2001). We used it simply to constrain an individual lobster near a particular den. Perhaps doing so may result in some behavioural artefact, but we know of no method to constrain a specific sized lobster within a specific shelter that would have been less obtrusive. The length of the tether and lack of any obstructions in each den minimized the potential for tangling of the tether that might alter lobster behaviour. Otherwise, lobsters

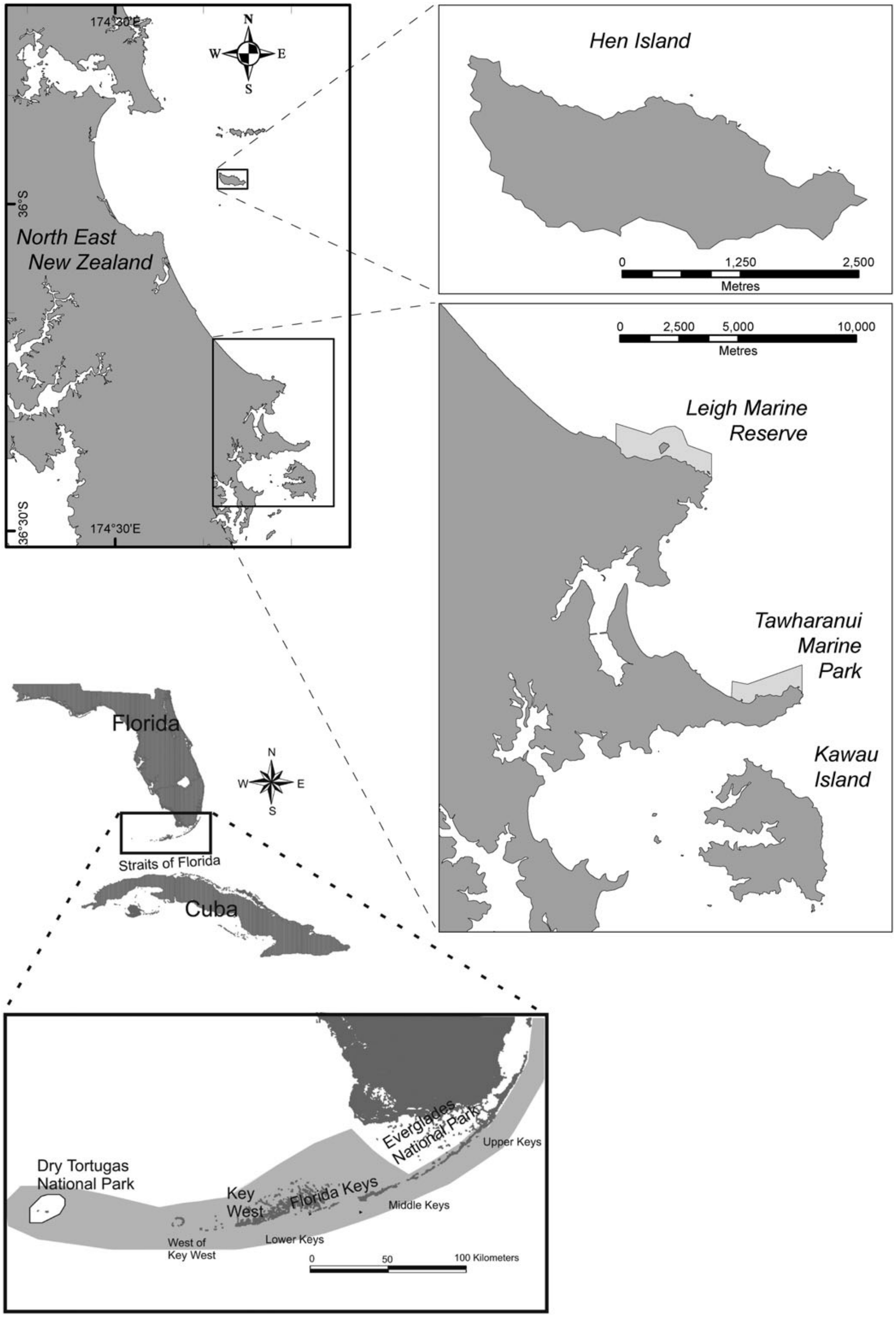

Figure 1. Field study sites in northeast New Zealand and Florida, USA.

appeared to behave normally and remained sheltered within each den during the day.

The test female was liberated in the centre of the test tank and her position in the tank recorded 24 h later, after which she was removed. To eliminate any bias in shelter choice due to the uneven distribution of natural light penetration or water circulation, the positions of the shelters and tethered lobsters were rotated around the tanks among replicates. Both experimental tanks ran simultaneously until 20 or more females had been tested for each combination of size and molt stage. The choice of the test females among the different shelters was analysed using a log-linear goodness-of-fit test with an even distribution of females among shelters as the expected outcome if shelter choice was random.

Experiment 2: mate choice by male J. edwardsii

The same tanks, shelters, tethering arrangements, and experimental protocols were used as in Experiment 1. However, in this case, females of four different sizes (<99, 100–119, 120–139, and >140 mm CL) were tethered singly in each shelter. Two sets of replicates were run with either pre-molt or post-molt unmated females tethered to shelters. In both cases, a single small (99–112 mm CL) or large (178–185 mm CL) mature male was liberated in the centre of the test tank and its position in the tank recorded 24 h later. Both experimental tanks ran simultaneously until 20 or more males of each size had been tested for the two female molt phases. The choice of the test males among the different shelters was tested using log-linear goodness-of-fit tests with an even distribution of males among shelters as the expected outcome if shelter choice was random.

Caribbean spiny lobster mesocosm experiments

Mature male and female *P. argus* were obtained from reef environments in the Florida Keys and the Dry Tortugus National Sanctuary (USA) by divers (Figure 1). Lobsters were transported to the Keys Marine Laboratory (Long Key, FL, USA) where they were measured (CL), individually marked with colour-coded antennae tags, and transferred to four outdoor flow-through holding tanks (2 m diameter × 1 m depth). Sexes were held separately until the start of the experiments. The lobsters in each holding tank were provided shelter and were fed frozen shrimp and squid daily. Only *P. argus* of a size whereby all are certain to be mature (>80 mm CL) were included in our experiments.

Experiment 3: mate choice by female P. argus

This experiment was run outdoor in two large (~15 m long by 7 m wide by 1.5 m deep), oblong concrete channels supplied with flow-through seawater. Four shelters as described in Experiment 1 were placed equidistant around the perimeter of each channel. Four alternative shelter conditions were established for this experiment. To three of the shelters, we tethered either a large mature male (>120 mm CL), a small mature male (<100 mm CL), or a female the same size and reproductive condition as the test female. The fourth shelter was left empty. Lobsters were tethered as described for Experiment 1. Each morning, a test female was liberated in the centre of the test channel and her position in the tank recorded 24 h later after which she was removed. We first tested the shelter (i.e. mate) choice of unmated small (<90 mm CL) and large (>100 mm CL) females during the reproductive season, and to contrast these patterns with shelter choice at other times of year, we repeated the test during the non-reproductive season ($n = 19–63$ lobsters per experimental condition; mean = 37). Female choice of the available den partners was analysed using log-linear goodness-of-fit tests. Four separate analyses were run comparing mate choice by small and large females during the reproductive season and during the non-reproductive season; an even distribution of females among the four shelter conditions was considered the expected outcome if shelter choice was random.

Experiment 4: mate choice by male P. argus

To investigate mate choice by male *P. argus*, we used a similar experimental protocol as that described in Experiment 3. However, in this case, a single small (80–100 mm CL) or large (>120 mm CL) male lobster (as opposed to a female lobster as in Experiment 3) was released in each mesocosm to choose among four different shelter conditions: a small female (<90 mm CL) tethered in a den, a large female (>100 mm CL) tethered in a den, an equivalent size male tethered to a den, or an empty den. We ran these trials for small ($n = 26$) and large ($n = 36$) males during the reproductive season and, as for the female tests described above, repeated the test during the non-reproductive season ($n = 12–57$ for small and large males, respectively). Again, log-linear goodness-of-fit tests were used to assess non-random shelter associations for small and large males during the reproductive and non-reproductive periods.

Field studies

We examined patterns of male and female dispersion and courting activity in wild populations of *J. edwardsii* and *P. argus* in unfished marine reserves and nearby fished areas. For *J. edwardsii,* we studied four adjacent populations—two protected (Leigh Marine Reserve and Tawharanui Marine Park) and two fished (eastern side of Kawau Island and northwest Hen Island)—in northeast New Zealand (Figure 1). At each of these localities, the abundance, size frequency, sex ratio, and courting activity of lobsters was estimated during the peak of mating in June 1995. At each locality, divers observed lobsters during daylight hours at four sites, two shallow (1–10 m) and two deep (11–20 m), situated within areas of crevice and boulder habitat in which *J. edwardsii* are primarily found. At each site, we searched for lobsters within five haphazardly placed 50 × 10 m transects. Lobsters were counted, their sex determined, and their size estimated using established visual techniques (see MacDiarmid, 1989a, 1991). Lobsters in each den were recorded separately. Courting activity was defined by lobsters engaged in "frontal approach" behaviour, which is unique to pre-copulatory courtship in spiny lobsters (Lipcius *et al*., 1983; Lipcius and Herrnkind, 1985; MacDiarmid and Kittaka, 2000). Before the surveys, 2 days were spent training divers to reliably estimate CL to within ±5 mm over the whole size range (20–200 mm CL). The same three divers were used throughout the survey.

Fished populations of *P. argus* in four areas of the Florida Keys (Carysfort Reef in the northeast to Marquesas Rocks in the west) and a protected population in the Dry Tortugus National Marine Sanctuary (USA) were also studied *in situ* by divers (Figure 1). Every 6 weeks from March to September in 1996 and 1997, two back-reef (landward side of reef crest, 1–6 m), two fore-reef (seaward of the reef crest, 1–10 m), and two deep-reef (>15 m) sites were chosen for study within each of the regions in the Florida Keys and at the Dry Tortugus. At each site, divers searched for lobsters for two 30 min periods; the time needed to capture each lobster with a hand net was not included in the search period. All lobsters captured from each den were held in separate mesh bags for later processing aboard a research vessel. If a lobster evaded capture, we noted its sex (if known) and estimated its CL. We also noted whether lobsters were dwelling alone or cohabiting with other individuals in a den. For each captured lobster, we determined its CL and sex. The presence and condition (i.e. fresh, used, single, multiple) of spermatophores on females was also noted. Lobsters were released unharmed after processing.

To determine whether male *P. argus* patterns of cohabitation were influenced by male–male competition, we used computer simulations to determine if the difference in size of the two largest males in dens was significantly different from that produced when we randomly resampled the data to repopulate the dens. The data were blocked by site (Tortugas, Upper Keys, Lower Keys), year, and month; the number of dens, and den occupants were held constant in the simulations. Dens were then repopulated using the lobsters captured within the site–month–year blocks and the difference in size between the largest and second largest males in each den was calculated. These results were then compared with the original field data. If there was little difference between the randomized and observed datasets, we concluded that observed pattern was due to other factors (e.g. population structure and den availability) other than interactions among males.

Results

Southern rock lobster mesocosm experiments

Experiment 1: mate choice by female J. edwardsii

Before molting, neither large nor small mature female *J. edwardsii* showed any particular preference when given a choice of four shelters that were either empty or contained a single tethered mature female, small mature male, or large mature male (Figure 2). However, soon after molting the majority of the large (72%), and many small (46%) females chose to cohabit with a large male ($G = 31.3$, d.f. = 3, $p < 0.001$and $G = 17.4$, d.f. = 3, $p < 0.001$, respectively; Figure 2). This preference by large and small females for shelters containing the largest male increased to 78 and 71%, respectively, during the 25–35 days between molting and mating (Figure 2). After mating had taken place and females were brooding eggs, both large and small females showed a tendency to cohabit with other females, though only in larger females was this statistically significant ($G = 15.6$, d.f. = 3, $p = 0.0014$; Figure 2). Never did females prefer to shelter in any particular corner of the test tanks (i.e. there was no tank position bias).

Experiment 2: mate choice by male J. edwardsii

Large mature males showed no tendency to shelter with pre-molt females of any particular size ($G = 0.40$, d.f. = 3, $p = 0.940$; Figure 3). However, they showed an increasing preference for cohabitation with large, unmated post-molt females. This preference rose steadily from 12% cohabiting with the smallest females to 42% cohabiting with the largest females (Figure 3). When all four female size classes were included in the analysis, the trend was non-significant ($G = 5.35$, d.f. = 3, $p = 0.148$). However, pooling of the results for the two largest and two smallest female size classes indicated there was a significant tendency for large males to shelter with females larger than 120 mm CL ($G = 3.95$, d.f. = 1, $p = 0.0470$). Small mature males showed no tendency to shelter with any size of pre-molt ($G = 4.50$, d.f. = 3, $p = 0.210$) or post-molt ($G = 1.31$, d.f. = 3, $p = 0.724$) mature female (Figure 3). Never did males prefer to shelter in any particular corner of the test tanks.

Caribbean spiny lobster mesocosm experiments

Experiment 3: mate choice by female P. argus

In the non-mating season, large female *P. argus* preferentially sheltered in empty shelters or with other females, whereas small females showed no shelter preference (Figure 4). During the reproductive season, the proportion of both large and small mature females that denned with mature males was significantly higher (51–52%; Figure 4) than in the non-mating season (19–40%; large females: $G = 20.05$, d.f. = 3, $p < 0.001$; small females: $G = 16.63$, d.f. = 3, $p < 0.001$). However, the distribution of females among the four den types during the reproductive season was no different from expected by chance alone (Figure 4). These results suggest that female *P. argus* actively avoid male-occupied dens most of the year, but this relaxes during the reproductive season when females freely associate with males with no particular preference for male size.

Experiment 4: mate choice by male P. argus

In the non-mating season, the greatest proportion of large mature male *P. argus* denned alone, although this was not statistically significant (Figure 5); small males also showed no den preference (Figure 5). During the reproductive season, the proportion of small and large mature male *P. argus* that denned with mature females was significantly higher (51–55%) than at other times of year (33–34%; large males: $G = 10.94$, d.f. = 3, $p = 0.012$; small males: $G = 30.61$, d.f. = 3, $p << 0.001$). The distribution of males among the four den types during the breeding season, however, was no different from expected by chance alone (Figure 5). These results suggest that male *P. argus*, especially large individuals, are solitary in dens most of the year but freely associate with females during the reproductive season with no clear preference for females of any size.

Field studies

Jasus edwardsii

We observed 44 courting male and female *J. edwardsii* at the four field sites in New Zealand, although most (91%) of these were observed in the two MPAs. Most males (95%) were larger than the females they were courting. In only two cases was the male the same size as the female and never at any locality was the male smaller than the female he courted. There was a marginally significant, positive relationship between the size of courting pairs in the Leigh Marine Reserve ($r^2_{\text{adj}} = 0.086$, $F_{1,37} = 4.46$, $p = 0.042$) but no relationship among the size of courting pairs within the Tawharanui Marine Park ($r^2_{\text{adj}} = 0.055$, $F_{1,15} = 1.87$, $p = 0.192$).

At both localities, the dispersion of courting among male size classes was significantly different from expected by the relative abundance of mature male size classes (Leigh $\chi^2 = 69.15$, d.f. = 11, $p << 0.001$; Tawharanui $\chi^2 = 72.48$, d.f. = 10, $p << 0.001$). In both marine reserves, courting was exclusively undertaken by large mature males: courting males were all ≥130 mm CL at the Leigh Marine Reserve and ≥120 mm CL at the Tawharanui Marine Park (Figure 6). Although smaller (90–120 mm CL) individuals comprised 42 and 50% of the mature male populations at Leigh and Tawharanui, respectively, none was observed courting. Too few courting pairs were observed at fished localities to determine the mating success of different sized males.

The dispersion of mature post-molt, but as yet still unmated, female *J. edwardsii* among dens containing a large male differed with female size on reefs within the Leigh Marine Reserve (Table 1).

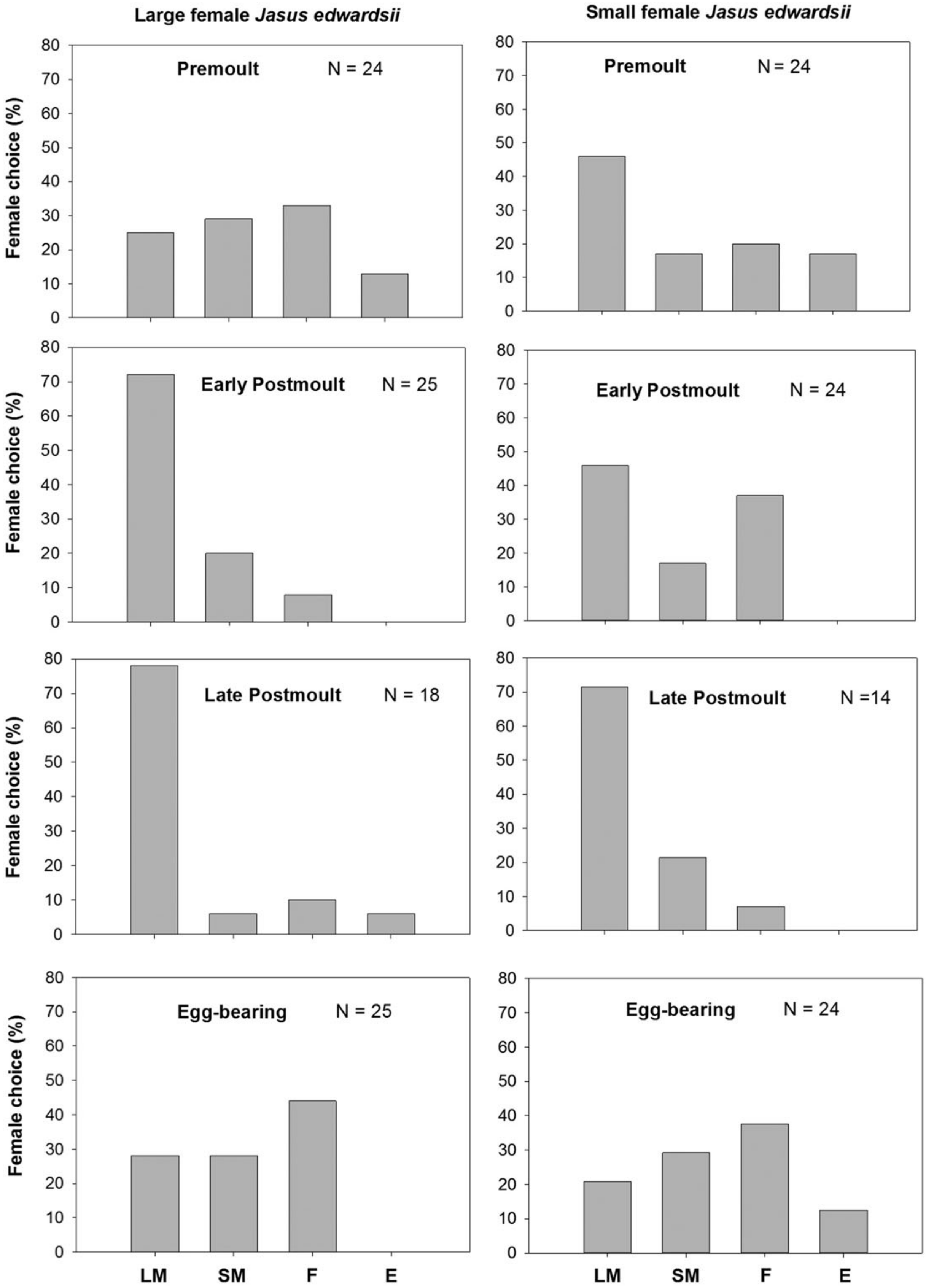

Figure 2. *Jasus edwardsii.* Patterns of cohabitation of paired (a) small and (b) large mature females. Expected frequencies are based on independent female choice from Experiment 1. Random frequencies are those that would occur if females neither choose large males nor competed for them.

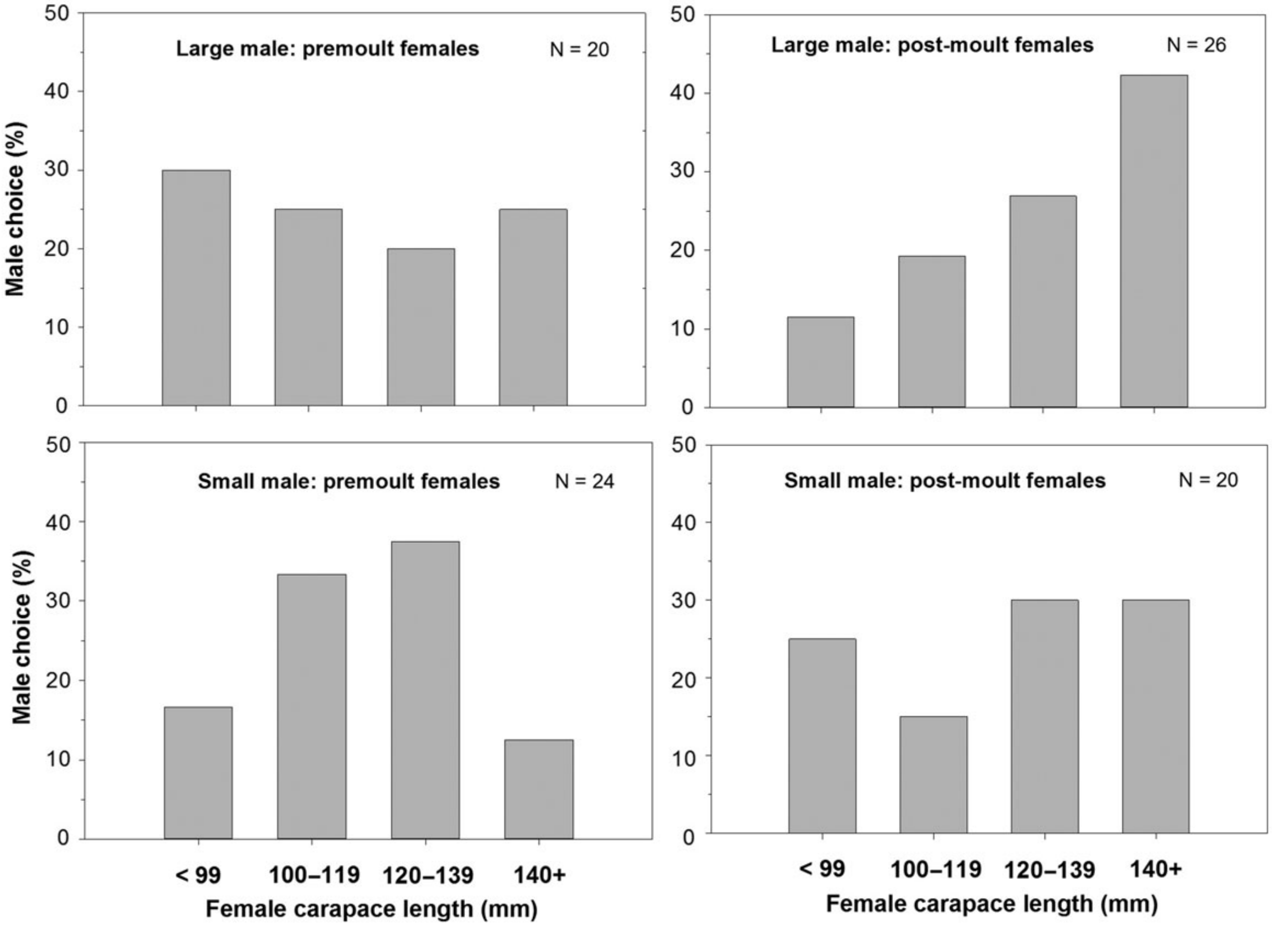

Figure 3. *Jasus edwardsii.* Shelter choices by (a and b) large mature males and (c and d) small mature males when dens contained one of four size classes of tethered pre-molt or post-molt mature females.

The proportion of small ($<$120 mm CL), post-molt females sheltering alone, or cohabiting in groups with a large male was no different from that expected under a random model of dispersion ($\chi^2 = 0.609$, d.f. $= 3$, $p = 0.894$). Large post-molt females, in comparison, were significantly dispersed among more males (i.e. fewer male dens had no females), were much more frequently alone with large males, and occurred less often in groups with a large male than expected ($\chi^2 = 18.45$, d.f. $= 4$, $p = 0.001$).

Panulirus argus

We observed no courtship among *P. argus* in the field, probably because most courting activity in this species takes place during crepuscular periods (Lipcius and Herrnkind, 1985) and at night (Bertelsen and Horn, 2000), whereas our fieldwork was conducted during the day. Instead, as a proxy, we used the incidence of females with new spermatophores cohabiting with a single mature male to indicate the likely size of mating pairs. Although often males were larger than the females, in some instances, they were smaller, especially at the Dry Tortugas. There was no relationship among the size of females with new spermatophores or the male cohabiting with them at either the Florida Keys ($r^2_{\text{adj}} = 0.083, F_{1,19} = 2.86$, $p = 0.110$) or the Dry Tortugus Sanctuary ($r^2_{\text{adj}} = -0.068$, $F_{1,6} = 0.552$, $p = 0.485$). There was no evidence of females bearing multiple spermatophores.

The frequency of cohabitation of male *P. argus* with like-sized males reflects the intensity of male–male competition for females and it varies with male size. At the Dry Tortugus Sanctuary, mating activity is most intense in February and March and peaks again in June when some females mate again to fertilize a second clutch (Bertelsen and Cox, 2001). Large males ($>$101 mm CL) were never observed together in dens during the first intense phase of mating, but male–male cohabitation briefly increased in May before dropping again in June/July (Figure 7a–c) when some females mate again. A similar pattern was observed for smaller mature males except that they began cohabitating earlier in the year.

In the fished Florida Keys population, males $>$101 mm CL were too rarely observed to determine patterns of cohabitation. There the reproductive season starts in late March/April and lasts until September without the pronounced peaks in mating activity evident at the Dry Tortugus (Bertelsen and Cox, 2001). This is also reflected in the patterns of mature male cohabitation, which was less pronounced than at the Dry Tortugas Sanctuary (Figure 7d and e).

Competition among male *P. argus* of different sizes is also apparent at the Dry Tortugus Sanctuary when the size of the two largest males in a den is compared at different times of the year. This analysis excludes those dens in which males were solitary and is thus a conservative measure of the degree to which large males will tolerate the presence of other males in a den during the peak of mating in

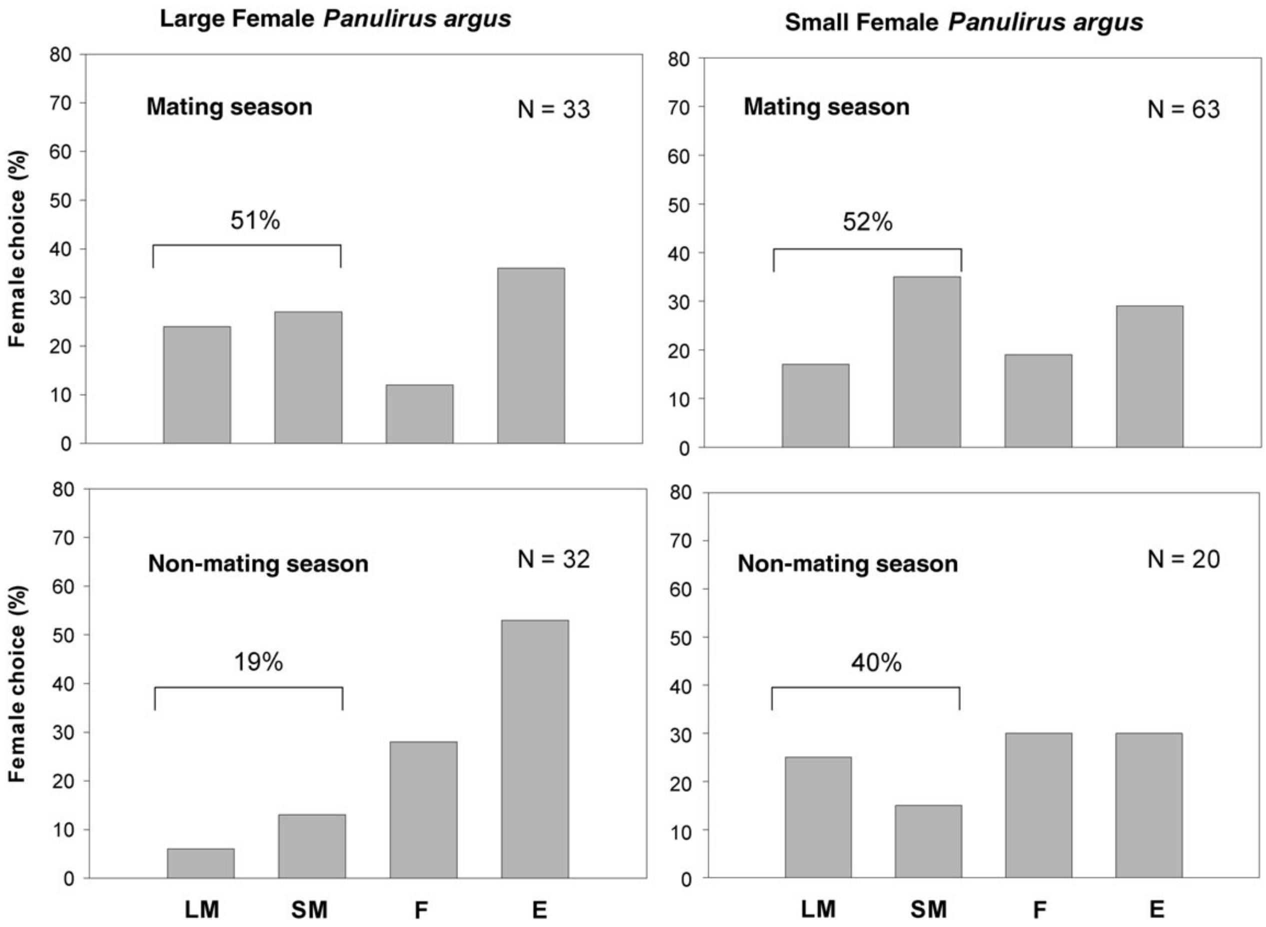

Figure 4. *Panulirus argus.* Shelter choice by large and small mature females during the mating (top panels) and non-mating (bottom panels) seasons.

February–March. At this time of year, cohabiting males differ by ~60 mm in CL, which equates to a fivefold difference in body weight. This difference in body size among cohabiting males decreased sharply after the mating period. In the fished Florida Keys population, large males were rare and the difference in size of the two largest males in a den was lower than found at the Dry Tortugus and did not show the same sharp peak.

To determine the extent that these patterns of male association were influenced by the availability of different sized males in the population, we randomly repopulated the dens in computer simulations. These results show that at the Dry Tortugus Sanctuary, the observed difference in the size of cohabiting males early in the year, especially if the den contained a large male, was much larger than expected due to chance alone. In the fished Florida Keys population where large males were rare, the distribution of males among dens was not different from that explained by random association.

Discussion

We documented differences in the mating systems of two species of spiny lobster that are consistent with, and presumably linked to, the evolution of drastically different reproductive characteristics representative of temperate and tropical species. The results of our mesocosm experiments and field observations revealed that mate selection in the temperate species (*J. edwardsii*) is more precise than in its tropical dwelling counterpart (*P. argus*), especially among larger individuals. Large female *J. edwardsii* preferentially cohabited with large males during the mating season and *vice versa* (Figures 2 and 3). This contrasts with the behaviour of both sexes outside of the mating season (e.g. before the female pre-mating molt and once egg-bearing) when they exhibited no preference for cohabitation with large individuals of the opposite sex. In contrast, female and male *P. argus* did not discriminate among mating partners of different sizes, although females cohabited with males more frequently during the mating season (Figures 4 and 5). These species-specific differences in mate size preferences revealed in mesocosm mate choice experiments were also borne out in field observations of mate choice (Figures 6 and 7). Our findings are in keeping with evolutionary theory because in *J. edwardsii*, the variance in mate quality is higher and the cost of poor mate choice greater, especially for larger females. More specifically, there are greater rewards for *J. edwardsii* than for *P. argus* to mate with a larger partner who can provide more and larger eggs resulting in more robust larvae, or more sperm for males (Annala and Bycroft, 1987; MacDiarmid and Butler, 1999; Butler *et al.*, 2015). The consequences of not locating a suitable mate are also dire for *J. edwardsii* females, because unmated females incur long-term ovarian damage and thus a significant reduction in annual and lifetime egg production (Pollock, 1991; MacDiarmid and Butler, 1999; MacDiarmid *et al.*, 1999).

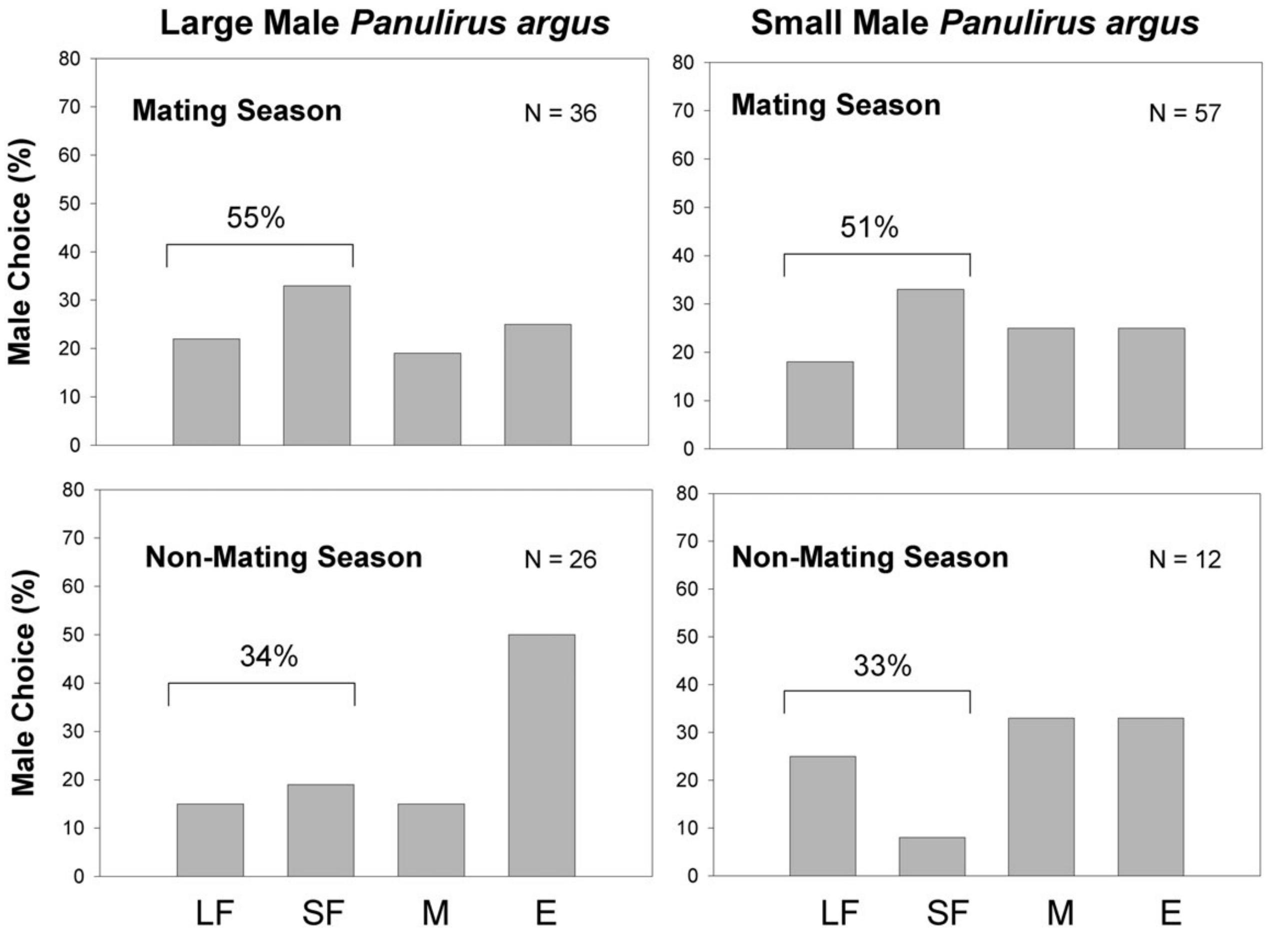

Figure 5. *Panulirus argus.* Shelter choice by large and small mature males during the mating (top panels) and non-mating (bottom panels) seasons.

The differences that we observed in mate selectivity by females were expected because of the differing reproductive strategies of the lobsters. The number of egg clutches a female produces on average each year and over her lifetime, and the consequences of not finding a suitable mate, differ markedly between these species, whose reproductive dynamics are representative of the two predominate evolutionary courses that the palinurids have taken.

For females of the temperate species, *J. edwardsii,* there is only one annual opportunity to breed (MacDiarmid, 1989b) over an average reproductive life of 7 years (Pollock, 1991). Therefore, on average each mating constitutes 100% of a female's annual matings and 14% of her lifetime matings. In addition, because the spermatophore is short-lived, mating must take place within a relatively narrow 1–2 day window coinciding with peak egg fertility, otherwise the proportion of the clutch able to be successfully fertilized decreases substantially (MacDiarmid *et al.*, 1999; MacDiarmid and Kittaka, 2000). Unmated females do not extrude unfertilized eggs, which typically for larger females (>125 mm CL) results in severe damage to her ovaries that greatly diminishes her reproductive output in future years (MacDiarmid *et al.*, 1999). Thus, there is strong selective pressure on female *J. edwardsii* with ripening ovaries to first locate potential mates and then to choose a male likely to have sufficient sperm to fertilize all of her eggs in a single mating timed to coincide with her peak fertility.

The strong selective pressures that have presumably driven the evolution of a precise system for selection of males by female *J. edwardsii* are absent for the tropical species, *P. argus*. Female *P. argus* become reproductive in 1.5–2 years post-settlement and remain reproductively active throughout their lifetime, which is unknown but may approach 30 years. Each mating season for *P. argus* is several months long and large females produce two to three clutches a year (Bertelsen and Cox, 2001). In addition, female *P. argus* can mate up to 28 days before extruding eggs, which allows females time to locate a more appropriate male if the first male is judged too small to provide enough sperm. Finally, if no mate is located, then female *P. argus* simply release unfertilized eggs with no long-term consequences on future matings.

Female mate choice is well described among crabs (Christy, 1987; Kendall and Wolcott, 1999; Sainte-Marie *et al.*, 1999) and in the clawed lobsters, *Homarus americanus* (Atema, 1986; Gosselin *et al.*, 2003) and *Homarus gammarus* (Debuse *et al.*, 1999, 2003), but in few other decapod crustaceans. However, it is likely to evolve in any species where there is high variance in male quality coupled with a method for females to distinguish among these males. Laboratory experiments using female *J. edwardsii* suggest that although a chemosensory mechanism is important, visual and possibly tactile cues also play a role in mate choice (Raethke *et al.*, 2004).

An alternative explanation for the patterns of association between post-molt female *J. edwardsii* and large males is that the males provide a measure of protection during the vulnerable soft-shell phase after molting, as occurs in *H. americanus* (Atema, 1986; Gosselin *et al.*, 2003). The evidence, however, is counter to this interpretation. First, if the protection hypothesis is true, then smaller post-molt females would be more likely to seek shelter with a male for protection after molting. Moreover, the association would decrease rapidly after molting as the female's new shell hardened. In fact, the patterns were opposite, which suggests that the association between post-molt females and large males is not associated with protection after molting. Post-molt protection of females by males is also irrelevant in *P. argus* as mature males and females molt well before the beginning of the reproduction season (Lyons *et al.*, 1981).

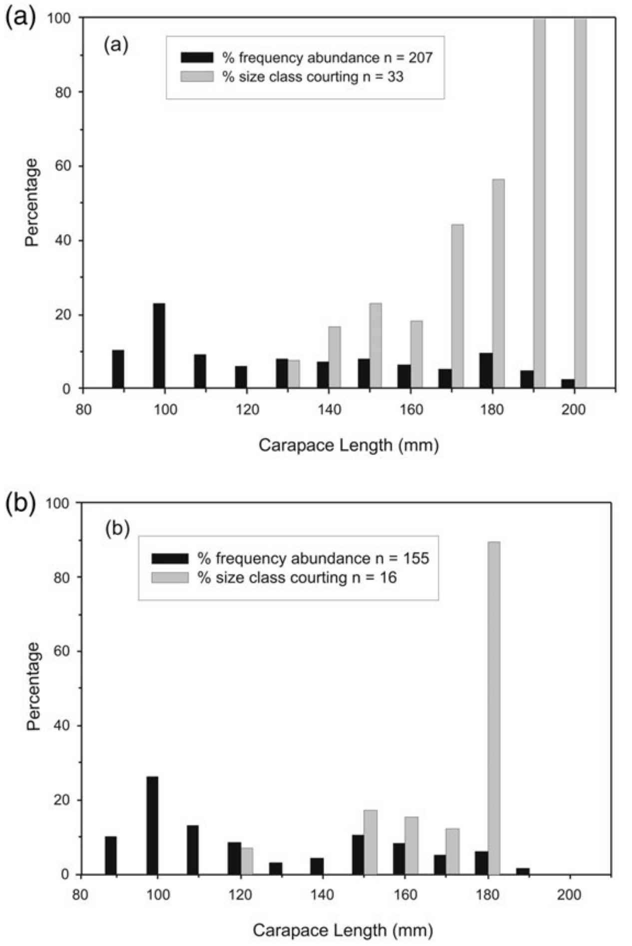

Figure 6. *Jasus edwardsii*. The frequency of mature males in 10 mm size classes and the proportion of each size class observed engaged in courting activities at (a) Leigh Marine Reserve and (b) Tawharanui Marine Park.

Table 1. *Jasus edwardsii*: expected and observed frequencies (%) of cohabitation with large mature males for two size classes of late post-molt unmated females in the Leigh Marine Reserve during the peak of mating in June 1995. Frequencies expected based on independent or random female association were calculated from a Poisson model.

	Female size class			
	<120 mm CL		**≥120 mm CL**	
Number of females in male den	**Expected (%)**	**Observed (%)**	**Expected (%)**	**Observed (%)**
0	42.81	41.86	25.5	17.07
1	36.8	34.88	34.93	51.22
2	15.83	18.6	23.93	21.95
3	4.54	4.65	10.88	2.44
4+	–	–	4.77	7.32
Mean # of females per den	0.86	0.86	1.37	1.37

The preference by large male *J. edwardsii* to cohabit with large females and the absence of any such relationship in *P. argus* suggests that this is linked to the increase in egg quality with female size in female *J. edwardsii* as has been found in other species (Kraak and Bakker, 1998). Although there is no relationship between female size and egg size in *P. argus* (Butler *et al.*, 2015), large female *P. argus* share with female *J. edwardsii* the desirable attribute of high egg production. Still, we found no evidence that male *P. argus* preferentially choose to den with or mate mostly with larger females (MacDiarmid and Butler, 1999). This makes sense when males can match the size of the ejaculate with the size of the female and thus the number of eggs available to fertilize. There is little advantage to mate with a large female in these circumstances except the additional costs of having to locate and court several times with successive small females to fertilize the equivalent number of eggs that a large female produces. These costs may be low if the mating season is long and the probability of a male mating on any specific day is low.

Theory suggests that when both males and females exercise mate choice, it gives rise to assortative mating with high-quality females mating with high-quality males and a decline in this correlation over the course of the mating season (Johnstone, 1997). We found little field evidence for size assortative pairing of courting *J. edwardsii* or *P. argus;* neither has it been documented in *P. guttatus* (Robertson and Butler, 2012), which cohabits coral reefs with *P. argus* in the Caribbean. However, two factors not yet included in reproductive models may play an important role in determining mating patterns. First, male–male competition when large males are present prevents smaller mature males from participating in reproduction (MacDiarmid, 1989a), thereby limiting the size range of males available for females to choose among. Second, the choice by large male *J. edwardsii* for large females observed in our laboratory experiments was much less intense than that of large females for large males (43 vs. 78%) and small males exhibited no preference at all. Thus, in *J. edwardsii*, the size association of males and post-molt females is dominated by the preference by all sizes of post-molt females for large males. In contrast, male and female *P. argus* do not appear to discriminate among size classes of the opposite sex during the reproductive period.

In both species, competition among males is a major element in the mating system. This is reflected in the frequency with which large males segregate during the peak of the mating season. In *J. edwardsii* as few as 5% of large males (>140 mm CL) cohabit in dens at this time of year (MacDiarmid, 1994) and no large mature male *P. argus* (>101 mm CL) den with other like-sized males at the Dry Tortugus Sanctuary during the peak of mating. Smaller male *P. argus* are therefore relegated to suboptimal habitats where reproductively active females are scarce. At Looe Key in the Florida Keys, for example, most reproductive activity is on the fore reef where female:male sex ratios are ∼4:1 during the reproductive season (Hunt *et al.*, 1991), whereas in nearby habitats, sex ratios are near 1:1 and reproductive activity is nil. Male–male competition in areas where large males are common prevents small male *J. edwardsii* from participating in reproduction (MacDiarmid, 1989a, this study).

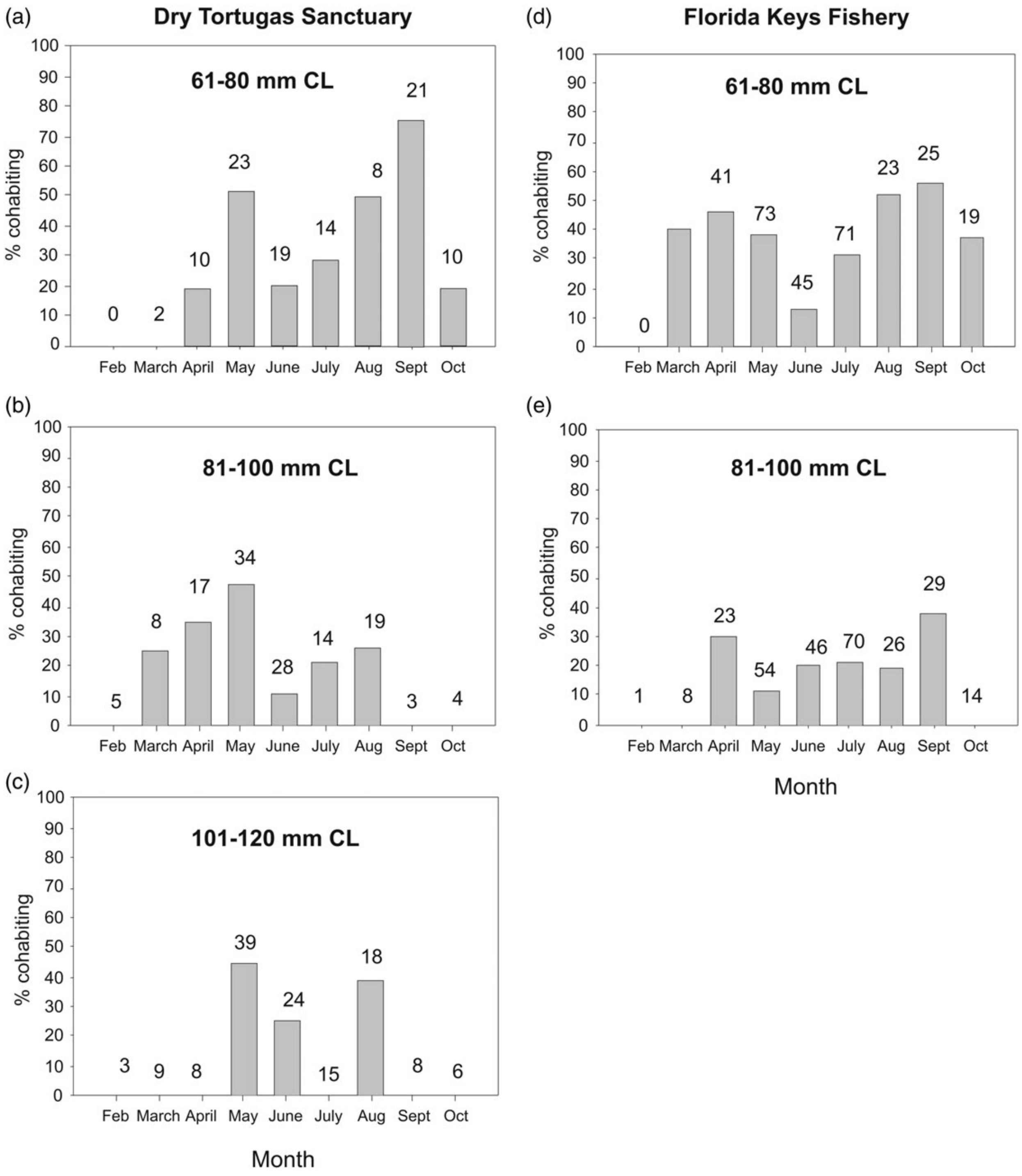

Figure 7. *Panulirus argus.* Cohabitation patterns of three sizes of mature males from (a – c) the Dry Tortugus Sanctuary and (d and e) the fished Florida Keys. The number of males sampled is shown above each bar.

Larger males cohabit with many mature females (MacDiarmid, 1994), a greater proportion engage in courting activity, usually do not move far from their den, and rarely shift among dens on consecutive days (MacDiarmid *et al.*, 1991). Small mature male *J. edwardsii*, in contrast, often share shelters (up to 60% at peak of mating; MacDiarmid, 1994), cohabit with no or few mature females, are excluded from courting activities, move greater distances at night than large males, frequently shift shelters on consecutive days, and have low levels of fidelity on a reef (MacDiarmid *et al.*, 1991; MacDiarmid, 1994; Kelly and MacDiarmid, 2003). However, some smaller mature males are tolerated in the dens of large males.

The patterns of mate selection and competition in *J. edwardsii* and *P. argus* that we found depend on variance in mate quality and the cost of mating. These patterns are likely to be common across a range of temperate and tropical decapods. In species—typically temperate—that have only one brood per year (many crabs, all temperate clawed and spiny lobsters) or mate only once in their lifetime and rely on stored sperm supplies thereafter (e.g. snow crabs, blue crabs; Kendall and Wolcott, 1999; Rondeau and Sainte-Marie, 2001; Sainte-Marie *et al.*, 2002; Sainte-Marie, 2007), the cost of mating with an inadequate male is high. Consequently, the evolutionary pressure for females to develop mate selection and perhaps competition strategies is likely to be intense. In contrast, in species—often tropical—that mate and brood many times per year or can sequester sperm from many males, the cost of mating with a single male with insufficient sperm is much lower and the selection for mate choice and competition strategies is also much reduced (Sato *et al.*, 2005).

Many decapods are exploited commercially and males in particular are sometimes heavily fished (Carver *et al.*, 2005; Sato and Goshima, 2006, 2007; Sato *et al.*, 2010). Even with similar levels of male and female exploitation, male size is reduced disproportionately by fishing because males grow much larger than females (MacDiarmid and Sainte-Marie, 2006). For high-value commercially fished species like spiny lobsters whose populations worldwide are almost universally considered fully or overexploited, there are few situations where natural mating dynamics remain intact (Rowe and Hutchings, 2003; Fenberg and Roy, 2008). In rare cases, there are spiny lobster species whose natural abundance or size render them unacceptable candidates for widespread commercial fishing (e.g. *P. guttatus*), providing the opportunity to study natural mating systems (Robertson and Butler, 2009). Yet for most species of spiny lobster, only in large and well enforced, unfished marine reserves do there exist populations whose abundance, size composition, and sex ratio are unaltered by humans and thus their mating dynamics a true reflection of the species evolutionary past (Jack and Wing, 2010). Without those vestiges of unspoiled natural populations, our understanding of lobster biology goes wanting and the consequent management of exploited populations is flawed being based on targets whose foundation are "natural baselines" that are unknown or shift (Heino *et al.*, 2013). For example, it is a common misconception among fishers and managers of *P. argus* that spawning stocks and mating activities occur in deeper waters >20 m. This is true in heavily exploited lobster populations where the preponderance of large lobsters are relegated to deeper waters where fishing intensity is less—but this is a *consequence* of fishing, and not the natural system. In large, effectively enforced MPAs like the Dry Tortugas nearly all of the mating activity occurs in shallow water <8 m where large, mature lobsters roam freely. The extirpation of large male and female lobsters through overfishing of spiny lobsters worldwide has often dramatically changed mating systems that evolved based on size-specific male–female relationships. The mating systems of overfished lobster populations now persist as a scramble competition for mates among barely mature individuals that mate at most once before capture by fishers. Overfishing is a strong selective force indeed that can greatly alter the reproductive biology of species with strong consequences for population sustainability (Coltman *et al.* 2003; Garcia *et al.*, 2012; Kuparinen and Hutchings, 2012). Thus, studies like ours that reveal the true mating behaviour of marine species not only offer insight into the factors shaping the evolution and maintenance of animal breeding systems, they remind us of the potential effects of fishing on reproductive dynamics and population sustainability.

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