THE ADAPTIVE VALUE OF AGGREGATION AMONG JUVENILE CARIBBEAN SPINY LOBSTER: AN EVALUATION USING INDIVIDUAL-BASED MODELING

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ABSTRACT

Ontogenetic changes in gregariousness by pre-reproductive animals, like that observed in juvenile Caribbean spiny lobsters (*Panulirus argus*), may be adaptive and reflect size-specific changes in the effectiveness of aggregation in promoting survival. Alternatively, aggregation may simply result from changes in the distribution or availability of suitable habitat structure, or from other behaviors that enhance survival. There are currently two hypotheses explaining the potential benefits of gregarious behavior in juvenile spiny lobsters, both of which focus on increasing survivorship by reducing predation pressure: the group benefit hypothesis and the guide hypothesis. The group benefit hypothesis argues that aggregations of juvenile lobsters reduce individual susceptibility to predators because groups are better able to fend off attackers or benefit by dilution of risk. The guide hypothesis suggests that aggregation is a consequence of shelter seeking behavior, in which individuals searching for shelter follow conspecific odors, thus reducing the time they spend in the open exposed to higher predation rates. The guide mechanism should be most effective in areas of low shelter density. We used an individual-based, spatially-explicit model describing recruitment of juvenile spiny lobster in the Florida Keys to compare behavioral models incorporating a guide effect and group benefit under conditions of high and low shelter densities. We found that the guide effect significantly enhanced survival only under the most extreme circumstances where shelter was scarce, the risk of predation highest, and the effective distance of the guide effect strongest. In contrast, small increases in direct group benefit led to significantly higher population abundances under a wide range of conditions.

INTRODUCTION

Social aggregation is a widespread phenomenon among animals, with well-known examples from such divergent groups as birds, mammals, and crustaceans. The resources around which animals typically aggregate are food and mates (Wilson, 1975), and gregariousness potentially has many benefits, although these may be counter-balanced by concomitant costs (Wilson, 1975). The benefits associated with grouping are related to resource exploitation (Alexander, 1974; Wilson, 1975), environmental modification (Seeley and Heinrich, 1981), or predation.

Foraging efficiency can be enhanced by information exchange within social groups, such as the waggle dance of honeybees, or by group effort in overwhelming or finding prey (Pitcher et al., 1982). The formation of social groups to promote mating success is widely known, and includes behaviors such as lekking in some birds and mammals (Beehler and Foster, 1988; Appolonio et al., 1992) and mate guarding in many types of animals, including crabs (Komdeur et al., 1999). Examples of aggregation for the purpose of environmental modification include huddling to improve thermoregulatory efficiency (Hill, 1983) and movement in formations to reduce drag, as seen in the V-formations of the Canada Goose (Badgerow, 1988) and single-file queues of spiny lobster (Bill and Herrnkind, 1976). Among the potential costs of social aggregation are increased intraspecific competition and increased rates of disease transmission (Greenfell and Dobson, 1995; Hess, 1996).

Aggregation may also reduce the risk of predation. Mutual vigilance results in earlier detection of predators or reduced vigilant times for individuals in groups (Powell, 1974; LaGory, 1987; Pulliam, 1973). Group defense, such as mobbing by flocks of birds (Robinson, 1985) and the formation of defensive rosettes by adult spiny lobsters (Herrnkind, 1980), is another example of the benefits of aggregation for survival. In its most simple form, an individual's probability of mortality may also decline when in a group due to the dilution of risk (Calvert et al., 1979; Foster and Treherne, 1991).

The ecological forces driving social aggregation are not static and may vary with environmental conditions, e.g., predator or prey density, and with the developmental stage of the individual, resulting in changes in social behavior over the lifetime of an organism. For instance, gregarious use of shelters by juvenile and adult spiny lobster (Palinuridae) has been reported in many species including *Panulirus argus* (Berrill, 1975; Davis, 1977), *P. interruptus* (Nevitt et al., 2000; Zimmer-Faust et al., 1985), *P. ornatus* (Trendall and Bell, 1989), and *Jasus lalandii* (reviewed by Atema and Cobb, 1980) among others. At least two palinurid species, *P. argus* and *J. edwardsii*, are solitary as early benthic juveniles, then become gregarious as they grow larger (Eggleston and Lipcius, 1992; MacDiarmid, 1994; Childress, 1995; Childress and Herrnkind, 1996; Butler et al., 1997; Butler et al., 1999). Perhaps the best information on ontogenetic shifts in aggregative behavior exists for the Caribbean spiny lobster, *P. argus*.

Caribbean spiny lobsters have a complex life history featuring marked ontogenetic shifts in habitat use and social behavior. Adult *P. argus* are highly gregarious, and benefit from cooperative group defense (Herrnkind, 1980), but spiny lobsters are not social during their earliest life stages. Larvae and postlarvae are asocial, even after the postlarvae settle and metamorphose to the early benthic juvenile stage,

which also remain solitary for three to five months within clumps of macroalgae within coastal nursery habitats (Marx and Herrnkind, 1985; Herrnkind and Butler, 1986; Childress and Herrnkind, 1996). Early benthic juvenile *P. argus* are cryptically colored and asocial, presumably adaptations arising in response to the higher mortality rates experienced by small aggregations than by those that remain solitary (Childress and Herrnkind, 1996; Butler et al., 1997). Yet, upon reaching approximately 15 mm carapace length (CL), individuals gradually shift to residency within crevice shelters, e.g., sponges, complex octocorals, solution holes, etc., and within these shelters they often share space with conspecifics (Berrill, 1975; Forcucci et al., 1994; Childress and Herrnkind, 1996; Herrnkind et al., 1997). As juvenile spiny lobsters grow, their preferences for specific types of crevice shelters changes (Butler et al., in press). Although the survival rates of juvenile *P. argus* dwelling in different habitats, e.g., seagrass, hard bottom, coral reefs, mangroves, differ significantly (Herrnkind and Butler, 1986; Eggleston et al., 1990; Smith and Herrnkind, 1992; Acosta and Butler, 1997), there are no detectable differences in their survival when residing in different types of shelter, e.g., sponges, holes, artificial shelters (Glaholt, 1990; Childress, 1995).

The presence of conspecific odor influences the choice of shelter by large juveniles (> 25 mm CL) (Childress, 1995; Ratchford and Eggleston, 1998) and adults (Nevitt et al., 2000). For large, pre-reproductive juvenile lobsters, gregariousness appears to enhance recruitment to the adult population by reducing their risk of predation (Eggleston and Lipcius, 1992; Mintz et al., 1994). However, experiments using tethering have failed to detect a significant effect on mortality for groups of like-size juvenile *P. argus* (Childress and Herrnkind, 2001). Similar experiments have demonstrated that groups of juvenile southern rock lobster, *Jasus edwardsii*, experience lower mortality once they reach about 25 mm CL (Butler et al., 1999). However, *P. argus* and *J. edwardsii* occupy very different habitats and although *J. edwardsii* does not appear to be shelter-limited (Kensler, 1967; Booth, 1979; Butler et al., 1999; MacDiarmid, 1991, 1994), *P. argus* juveniles often are (Butler and Herrnkind, 1997; Herrnkind et al., 1997). It is therefore likely that the forces driving their common social ontogeny are also different.

An alternate hypothesis to the group benefit argument for aggregation is the guide effect (Childress, 1995; Childress and Herrnkind, 1997). This hypothesis suggests that aggregation is a by-product of the attraction to the odors of conspecifics, and it probably evolved as a means by which individual lobsters could locate shelters more quickly. Individuals benefit by reducing the amount of time they spend searching for shelter, and thus their risk of predation when they are in the open and most vulnerable. A distinguishing aspect of the guide hypothesis is that aggregation need not directly confer any selective advantage. Instead, aggregation is viewed as a by-product of an efficient means of locating appropriate shelters quickly. Using macrocosms supplied with a single shelter, Childress and Herrnkind (2001) found that the searching time for naïve individuals could be reduced by as much as 66% when conspecifics are present in the shelter. However, any resulting effect on mortality has not been estimated. In addition, the degree to

which lobsters may depend on chemosensory guidance to locate shelter in nature is unclear, as they have several additional means of navigation. Adult lobsters retain spatial memory and can navigate using landmarks and hydrodynamic cues (Nevitt et al., 1995). Lohmann et al. (1995) demonstrated that adult and juvenile lobsters also can navigate using Earth's geomagnetic field. Thus, it seems likely that the guide effect would be of the most benefit to lobsters moving either into unfamiliar territory or into areas where shelter is scarce. It is important to recognize that the group benefit and guide mechanisms are not mutually exclusive and might operate simultaneously in real populations. However, adequate tests of the relative advantages afforded by both mechanisms and their potential population level effects have yet to be conducted, due in part to the difficulty of monitoring such a mobile marine organism on a large scale.

In this study, we attempted to evaluate the sensitivity of recruitment to the subadult population, i.e., lobsters over 50 mm CL, using an individual-based, spatially-explicit model of the juvenile lobster population of the Florida Keys. We explicitly and independently incorporated both the group benefit and guide effect mechanisms in the model and tested the effects of different levels of group benefit (direct reduction of the probability of mortality) and guide effect (reduction of search times) on recruitment at different shelter densities. To further explore the sensitivity of both behavioral models, we also examined the effect of local spatial memory, i.e., "knowledge" of the location of local shelters, on the effectiveness of the guide effect. We predicted that the guide effect would be more important in simulations with low shelter density and long search-time windows. We also predicted that the existence of local spatial memory would diminish the importance of the guide effect and that the effectiveness of group benefit would be independent of shelter density.

METHODS

The model we used was a modification of one previously developed to explore the effects of habitat disturbance (Butler et al., 2005) and spatial variation in postlarval supply (Butler et al., 2001) on recruitment of postlarval *P. argus* to 50 mm carapace length (CL), the size at which juvenile lobsters begin to interact with the fishery. Detailed descriptions of the model are presented in Butler (1994), Butler et al. (2001), and Butler et al. (2005). In this paper, we briefly describe the model's general structure, then provide a detailed description of the elements that were altered for these simulations, specifically shelter selection and its influence on mortality. Appendix A contains a summary of the range of conditions that we explored in our simulations comparing the relative benefits of the group effect and the guide effect.

Physical Structure of the Model

The model was spatially explicit, consisting of 245 habitat cells (each ~ 12 km²) in a 7 × 35 grid, constituting a map of the nearshore habitat around the Florida Keys and included the majority of the primary nursery habitat for *P. argus* in South Florida (Herrnkind et al., 1997). Based on visual surveys of the dominant habitat type at more than 300 sites throughout the region (Herrnkind et al., 1997), each model cell was designated as being either seagrass or hard-bottom habitat according to the geographic location it represented. Within hard-bottom cells, the abundance of each of five types of crevice shelter, i.e., loggerhead sponges, other sponges, solution holes, octocoral-sponge complexes, and other structures—mainly corals, was specified in terms of a lobster carrying capacity. Individual shelters within cells were not modeled explicitly. Instead, the number of shelters of a particular type in each cell was multiplied by the mean number of lobsters

that usually reside in shelters of that type to arrive at a weighted lobster carrying capacity for each shelter type in each hard-bottom cell.

In the simulations described here, static arrays of shelter capacities were used, based on data from habitat surveys made by divers at 128 hard-bottom sites throughout the Florida Keys (see Herrnkind et al., 1997). The densities of shelters observed in the field were used as the "high shelter density" treatment level to define the geographically corresponding hard-bottom habitat cell in the model. For hard-bottom cells that did not have corresponding field sites, the shelter densities of the closest field site were used. Nothing is known about shelter limitation in algae or seagrass beds, so the capacity of these habitats was assumed to be unlimited. Other physical features specified in the model included the timing of the new moon, which affected postlarval supply, and temperature, which affects lobster growth rates and changed seasonally from 17.8°C to 31.5°C.

Life History Elements

Superimposed on this spatial landscape was an individual-based model of juvenile *P. argus* recruitment to 50 mm carapace length (CL). Individuals were removed from the model once they attain this size because at about 50 mm CL, juveniles begin to interact with adults, enter traps, and are impacted by the fishery (Lyons and Hunt, 1991). Each of the process routines were modeled on a daily time step for each individual in the population, except for settlement, which occurred once every lunar cycle on the night of the new moon. Nearly all processes were probabilistic and, whenever possible, the functions describing the probability of a particular event were obtained by fitting curvilinear functions to empirical data (Tablecurve Ver.1.12 software, Jandel Scientific Co.).

The model included subroutines simulating postlarval settlement, shelter selection, mortality, growth, and movement among spatial cells. Within each of these subroutines, individuals were processed in random order. The model produced output every fifth time step (day) and included nearly a dozen different types of data, those most relevant for these simulations being: 1) the number of lobsters recruiting to the > 50 mm CL size class, and 2) the mean search time and number of lobsters searching for shelter.

Postlarval Settlement.—Each new moon, the program generated a cohort of new postlarvae whose abundance fluctuated each month in accord with historical data from 1993-2003 (Acosta et al., 1997; Tom Matthews, Florida Marine Research Institute, Marathon, FL unpublished data). New postlarvae were distributed randomly across the 245 spatial cells, with approximately 80% settling in hard-bottom cells and 20% in seagrass cells (Herrnkind and Butler 1986). To initially populate the model, it ran for two simulated years (26 lunar months) prior to the period of interest, and used the long-term mean postlarval supply for each month during this spin-up period. Preliminary runs of the model using monthly-averaged postlarval supply demonstrated that the abundance of large juveniles (> 50 mm CL), stabilized after 18 months, hence, our conservative choice of a two-year initialization period.

Growth.—New settlers were randomly assigned a size between 5.0 and 7.0 mm CL. Individual lobster growth was then modeled as a discontinuous process using empirically determined probability distributions to specify molt increments and intermolt intervals, which varied as a function of size, time-since-last molt, and temperature (Hunt and Lyons, 1986). There is no evidence that growth of *P. argus* in nature is density-dependent (Butler and Herrnkind, 2000), so it was modeled as a density-independent process with no food resource limitation.

Movement Among Cells.—Movement of lobsters among habitat cells was random in direction and its probability depended upon individual size and shelter availability in the current cell. No movement was permitted across the northern or southern edges of the model domain, which mimics the real system where habitat, salinity, and depth limit the availability of nursery habitat in those directions. Movement across the east and west boundaries was "wrapped", so that lobsters exiting the eastern edge of the model re-entered at the corresponding cell on the western edge. This was a convenient means of approximating movement of lobsters to and from the area beyond the modeled region.

Due to the prohibitive expense of simulating every individual lobster in the Florida Keys, conservatively estimated in the billions each year (Butler et al., 2005), the model used smaller areas, approximately 1000 m^2, to represent the dynamics of searching and shelter selection within each 12 km^2 habitat cell. This choice of scale has an additional advantage in that all of the empirical work on which this model was based was carried out on sites of similar size, ranging from 30 m × 30 m to 50 m × 50 m (see Butler

et al., 2005). Movements in and out of such small areas are not equivalent to movement among habitat cells, but clearly must be proportional. Thus, to determine an appropriate factor with which to scale movement among 12 km^2 habitat cells, we assumed that small juveniles were unlikely to traverse an area larger than one local area (~ 1000 m^2) in one day. Thus, the exchange of individuals among adjacent habitat cells would logically involve only those lobsters along the periphery of each habitat cell, the width of this periphery being the same as that of a simulated local area (~ 0.0316 km). We assumed that movement is non-directional, so approximately one quarter of the lobsters calculated by the model to leave the periphery of one cell would enter an adjacent habitat cell during one daily time step.

Shelter Selection.—The shelter selection routine determined how long each lobster spent searching for shelter and the type of shelter in which it resided for the diurnal portion of the 24 hour time step. Shelter choice depends on lobster size and our model included these dynamics as described in our introduction. For example, lobsters < 15 mm CL resided in macroalgae or seagrass and did not move from these shelter types or among spatial cells. Between 15 and 20 mm CL, lobsters were in a transitional state, and those in hard-bottom areas resided either in the algae or in crevice shelters, depending on their size and the availability of shelter (these are hereafter referred to as transitional individuals). Above 20 mm CL, lobsters resided only in crevice shelters if available. If appropriate dens were unavailable, lobsters of the sizes modeled took shelter around less protective structures that the model treated as the protective equivalent of seagrass. In nature, juvenile lobsters are rarely observed in the open during the day, unless disturbed (Herrnkind and Butler, 1986; Butler, unpublished data). The maximum density of lobster shelters in hard-bottom sites in the Florida Keys is estimated to range from 8 to 708 den spaces per 1000 m^2 (Herrnkind et al., 1997), and this range was used in the model as the "high shelter density" treatment. We also ran simulations with "medium shelter density" and "low shelter density", arbitrarily set at 50% and 33% (respectively) of that estimated in field surveys. The shelter selection procedure only affected lobsters that were in hard bottom cells and those large enough to leave the algae, including randomly selected transitional individuals. Lobsters in seagrass cells were assumed to remain within the cover of seagrass while sheltering and while foraging.

Each simulated 24-hour period, all crevice shelters were emptied, and the occupants were placed in the open to simulate nocturnal foraging activity. The amount of time each individual spent in the open depended on its size and on the amount of time required for it to return to shelter. Transitional individuals (15-25 mm CL) were assumed to forage for only one-third of the night (3.3 hours) since they are known to stay within a meter or two of their shelters while foraging (Andree, 1981; Schratwieser, 1999), whereas larger lobsters (> 25 mm CL) used the entire night. On returning from foraging, lobsters seeking shelter were assumed to have made their shelter selection prior to sunrise, which closely mimics observed behavior in the field and sets a limit on the amount of time available for searching, which we refer to as the search window.

Earlier versions of the model used a two-hour search window, simulating the crepuscular return of lobsters to shelters because this is the period when adults return to shelter after foraging (Cox et al., 1997). Since the actual behavior and timing of juvenile lobsters returning from foraging is not known, but clearly would affect our results, our simulations included different search window lengths, from two to four hours. Lobsters in seagrass habitat and those residing in algae had no search time. For lobsters seeking crevice shelters in hard bottom cells, we compared six behavioral models that differed in whether their search was random or guided by the presence of conspecifics, and in the level of local knowledge that the lobsters were assumed to have.

Our most basic model of shelter selection combined a random search and no spatial memory so that every lobster using post-algal crevice shelters performed an unguided search based on random selection of potential shelters. Starting with a randomly chosen individual, the program attempted to place each lobster in a shelter according to its size-specific shelter preferences, described in detail by Butler et al. (2005). If any shelters of the type the focal lobster most preferred were available in the local area, then the lobster was placed in that shelter type. Otherwise, the program attempted to place it in its next-most preferred shelter type, and so on. If no shelters were available of any of the types that the lobster is known to use, then it was not placed in a shelter. If the lobster was successfully placed in a shelter, its search time was then calculated as described below.

Simulating the Unguided Search for Shelters.—The function describing the expected search time for unguided lobsters was based on repeated random selection of a shelter from among all of the shelters in the local area of the types the lobster is known to use, with replacement, until an unoccupied shelter was found. Mathematically, the probability of selecting an available shelter in a single trial, P, is equal to the number of unoccupied shelters, U, divided by the total number of shelters from which the individual could choose, C, or $P = UC^{-1}$. If Y is a random variable denoting the number of the trial in a series of trials on which the first available shelter is found, then Y is distributed geometrically, and the expected value of Y, the mean number of trials needed to find an unoccupied shelter, is P^{-1} or $U^{-1}C$ (Hogg and Craig, 1995).

The average amount of time spent searching any given arrangement of shelters is proportional to the number of trials needed to find an unoccupied shelter. We assumed that the time required for each trial varies inversely proportional to shelter density, such that each trial requires a fraction of the available search time equal to C^{-1}. This abstraction was necessitated by the lack of internal structure in our habitat cells, but we believe that it was a reasonable assumption, since increasing shelter density necessarily decreases the average distances among shelters, thus traveling time between them. The proportion of crepuscular time spent searching for shelter, t, was calculated as the product of the expected number of trials and the proportion of time for a single trial, so $t = (U^{-1}C)(C^{-1}) = U^{-1}$. Given that x represents the order of an individual in a series of lobsters that are searching the same set of shelters, e.g., $x = 1$ denotes the first lobster to search; $x = 2$ denotes the second lobster to search, etc., then $U^{-1} = (C - x + 1)^{-1}$, and the proportion of the search window used by each individual is given by the function $f(x) = (C - x + 1)^{-1}$, for $x \in 1, 2, 3, \ldots, C$. The proportion of the search window length spent searching was set to 1 if no shelters were available. We refer to this as the geometric search model. Representative curves are presented in Fig. 1, showing the search times for lobsters in habitat cells with different shelter capacities.

Simulating the Guide Effect Search for Shelter.—We chose to use a piecewise function to model the Guide effect. The function increased linearly from zero to its maximum effect at a critical proportion of shelters occupied, then declined linearly to zero at 100% occupancy. In deciding on the form of the Guide effect function, we assumed that there is no guide effect when no lobsters are in the shelters within a cell. This discounts the possibility of an effect by residual odors in previously used shelters. Even if this assumption is violated, the potential effect is small compared to effects on subsequent lobsters simply because the search time for the first lobster is expected to be short even without guidance. It is also possible that there is a threshold of shelter occupancy below which the chemical signal is too weak to elicit a response. Preliminary runs of the program indicated that the guided search might have very little effect on recruitment; therefore, to improve the likelihood of detecting an effect, the threshold shelter occupancy for all of our runs was zero. At the other extreme, when all of the shelters are occupied, the guide effect cannot provide an advantage, so the search consumes all of the available crepuscular search time. Between these two extremes, the most likely shape of the Guide effect function is unclear and unspecified by any existing empirical data or theoretical predictions.

The strength of response to the chemical signal appears to be dependent on the cumulative mass of lobsters in the shelter (Ratchford and Eggleston, 1998), so the guide effect should increase as more lobsters occupy shelters and groups form. Beyond this generalization, we reasoned as follows. We use the term "den" to signify a discrete object in which or under which lobsters shelter, such as a single sponge or solution hole. In addition to the number of dens in an area, the number of lobsters that can cohabit each den (ignoring lobster size for simplicity) determines the lobster carrying capacity for the habitat. At some point, enough shelters are occupied that it becomes increasingly likely that searching lobsters will be drawn to dens that are full, reducing the effectiveness of the guide effect. The guide effect must therefore reach a maximum when some critical proportion of shelters is occupied, then decline to zero effect when all shelters are occupied. In our model, the threshold value, maximum effect, and critical proportion of shelters occupied were user-supplied values.

To calculate the actual search time for any given lobster, the guide effect function value was subtracted from the geometric search time, and the result of this was multiplied by the length of the search window in hours, with the additional constraint that the resulting search time could not be less than zero. Preliminary runs of the model with various parameter values indicated that it produced very little effect on search time unless the critical occupancy proportion was set above 0.6. For our final runs, we chose to set

this value at 0.8, and varied the effect strength to achieve the desired reduction in mean search times. Figure 1 shows representative search time curves for the unguided search and for the guided search at different shelter densities, and the parameterizations of the guided search model used in our simulations. In particular, Fig. 1B and D show that the guided search model is capable of reducing search times to zero for most lobsters searching for shelter, and did so at our "high" level. Clearly, the unguided search model leaves little room for improving search times at higher shelter densities, whereas larger differences between the unguided and guided search times are produced at lower shelter capacities.

The Effect of Local Knowledge.—Our unguided search model required all lobsters using crevice shelters to search for shelter every day. Given that lobsters retain spatial memory and are able to navigate by other means, this is an unrealistic scenario that would be expected to produce higher mortality rates as lobsters are more exposed to predators during their search. On the other hand, this provides the best circumstance for a mechanism that reduces search time, like the guide effect, to enhance survivorship. To provide a more realistic test of the guide effect, we developed two variations of the model that did not require every lobster to search randomly, simulating the effect of spatial memory. The more extreme model treated only those lobsters that moved to a different habitat cell as naïve. All others in the cell were assumed to be familiar with their local surroundings and had no need to search for shelter. The second variation treated all lobsters that would have moved out of their current 1000 m² local area as naïve. Note that under the assumption that lobsters do not cross more than one 1000 m² area in a 24-hour period, the more extreme model is roughly equivalent to allowing the lobsters knowledge of the areas immediately adjacent to their current location, whereas the second variation restricts knowledge to the current local area.

Mortality and Group Benefit.—The daily probability of mortality was calculated as the sum of nighttime and daytime mortalities. The probability of mortality at night, i.e., while in the open and foraging solitarily, was size-specific, whereas the daytime probability of mortality was both size- and shelter-dependent. These functions were obtained by fitting curvilinear functions to empirical data from earlier tethering experiments (Smith and Herrnkind, 1992) using the least squares method. The hourly probabilities of mortality, P, for lobsters of a given size, S, were as follows:

$P_O = 0.373/[24 \times (0.305 + S)]$ for lobsters in the open;
$P_S = 0.15/[24 \times (S - 0.409)]$ for transitional lobsters in macroalgae and lobsters in postalgal shelters; and
$P_G = 0.228/[24 \times (S - 0.766)]$ for lobsters in seagrass (see Fig. 3 in Butler et al., 2005, and the detailed description provided therein).

In addition, the diurnal portion of the daily probability of mortality for lobsters in crevice shelters was reduced by multiplying the probability of mortality by a fractional factor depending on the size of the group of lobsters sharing the focal individual's den, simulating a group benefit effect. This factor was defined by a straight linear function with no effect at a group size of one lobster, and increasing continuously with group size thereafter with a user-defined slope. The general equation for the group benefit factor, B_G, was:

$$B_G = 1 - \{0.5/[(M_{50} - 1) \times (N - 1)]\}$$

where M_{50} was the group size at which the hourly mortality rate was reduced by 50%, and N was the size of the group containing the focal lobster. Group size was dependent on shelter type (Butler et al., 2005) and we used the empirical distribution of group sizes for each shelter type (Fig. 2) observed at 21 sites located throughout the Florida Keys (M. Butler, unpublished data).

Simulations

To investigate the independent and potentially interactive effects of: a) the time lobsters have to search for shelter, b) shelter density, c) strength of attraction to conspecifics, and d) effectiveness of grouping in reducing the risk of mortality, we ran simulations in a $2 \times 3 \times 3 \times 3$ crossed design (summarized in Appendix A). We used two search window intervals, 2 and 3 hours. We included three levels of shelter density (low, medium, and high), where the high level used the shelter densities measured at field sites and the medium and low shelter density levels were set at 50% and 33% (respectively) of the densities estimated in field surveys. We also used three levels of guide strength (unguided, low, and high) where the low and high treatment levels used values of 0.8 and 1.293, respectively. These levels were chosen based on preliminary runs, which indicated that the resulting

High Shelter Density
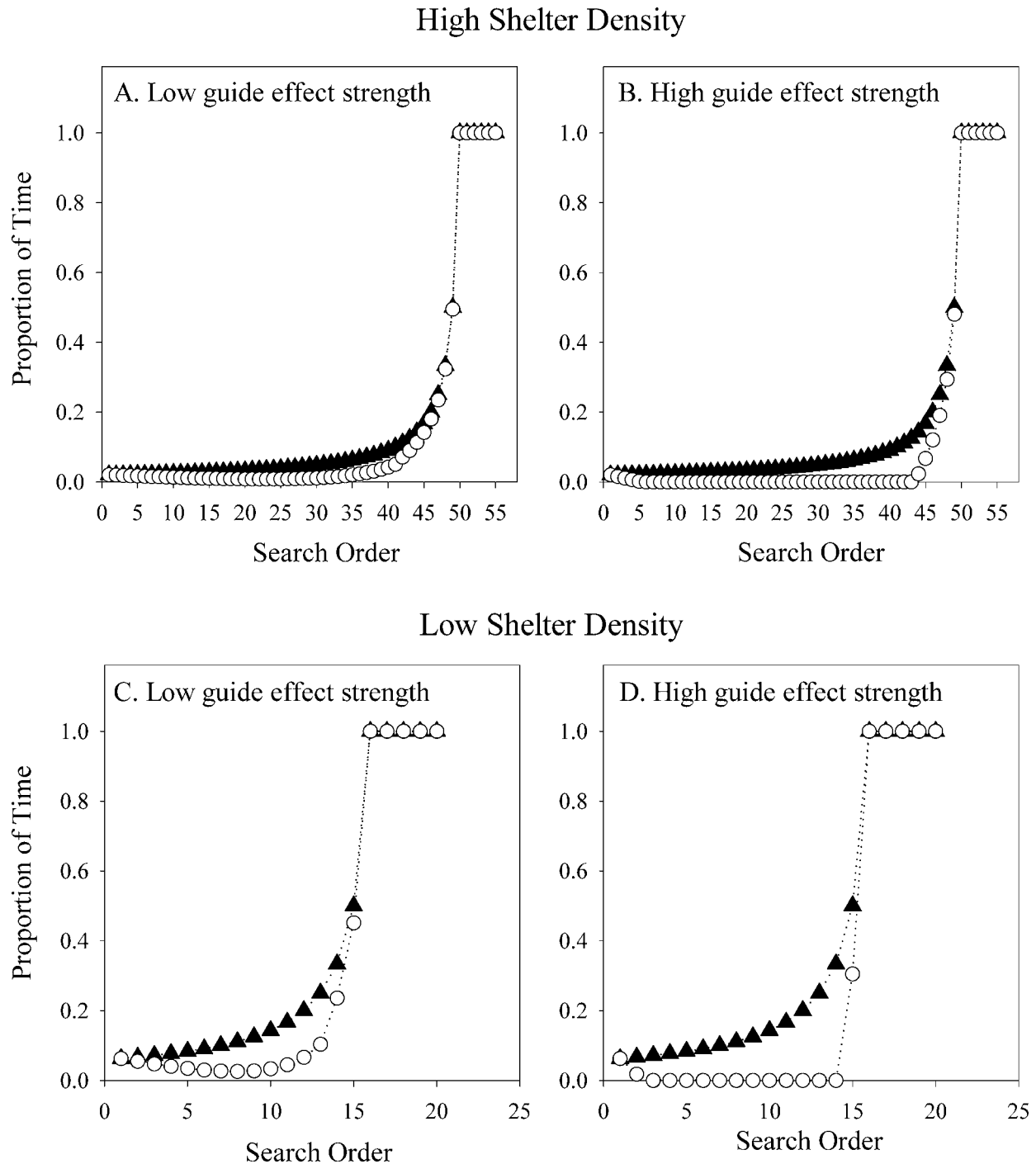

Low Shelter Density

Fig. 1.   Calculated search time curves. These examples show the resulting proportion of the time available to search for shelters that simulated lobsters used with an unguided search model (solid triangles) and a search guided by conspecific odor cues (open circles) in a cell with 50 shelters (charts A and B), and a cell that has 15 shelters (charts C and D). Search time proportions generated by the guided model in Charts A and C are the result of the low guide strength level. The guided searches in Charts B and D used the high guide strength. Search order is the sequence of searches from the first lobster to search to the last.

functions would reduce search times by approximately 50% for the low treatment level and 65% for the high. Three levels of group benefit strength were also simulated, labeled: none, low, and high. At the low group benefit level, lobsters within groups of 30 individuals would be expected to experience 50% of the hourly mortality rate of solitary lobsters; at the high level, groups of six lobsters would experience the same 50% reduction in hourly mortality. Based on preliminary results, five independent replicates of each combination of the four factors were required to detect a 5% difference in recruitment with a power of 0.8 at the $\alpha = 0.05$ significance

level. All runs simulated a ten year time period, from 1993 to 2003. As in previous simulations, we used the number of lobsters that attained 50 mm CL in the model as our measure of recruitment success.

To explore the effects of spatial memory and potential interactions with the guide effect and different search window lengths, we used a $2 \times 3 \times 3$ factorial design (summarized in Appendix A). The spatial memory models used in these simulations were the local memory model, which treated all lobsters leaving their 1000 m^2 area as naïve in the subsequent search, and the regional memory model, which only treated those lobsters leaving the
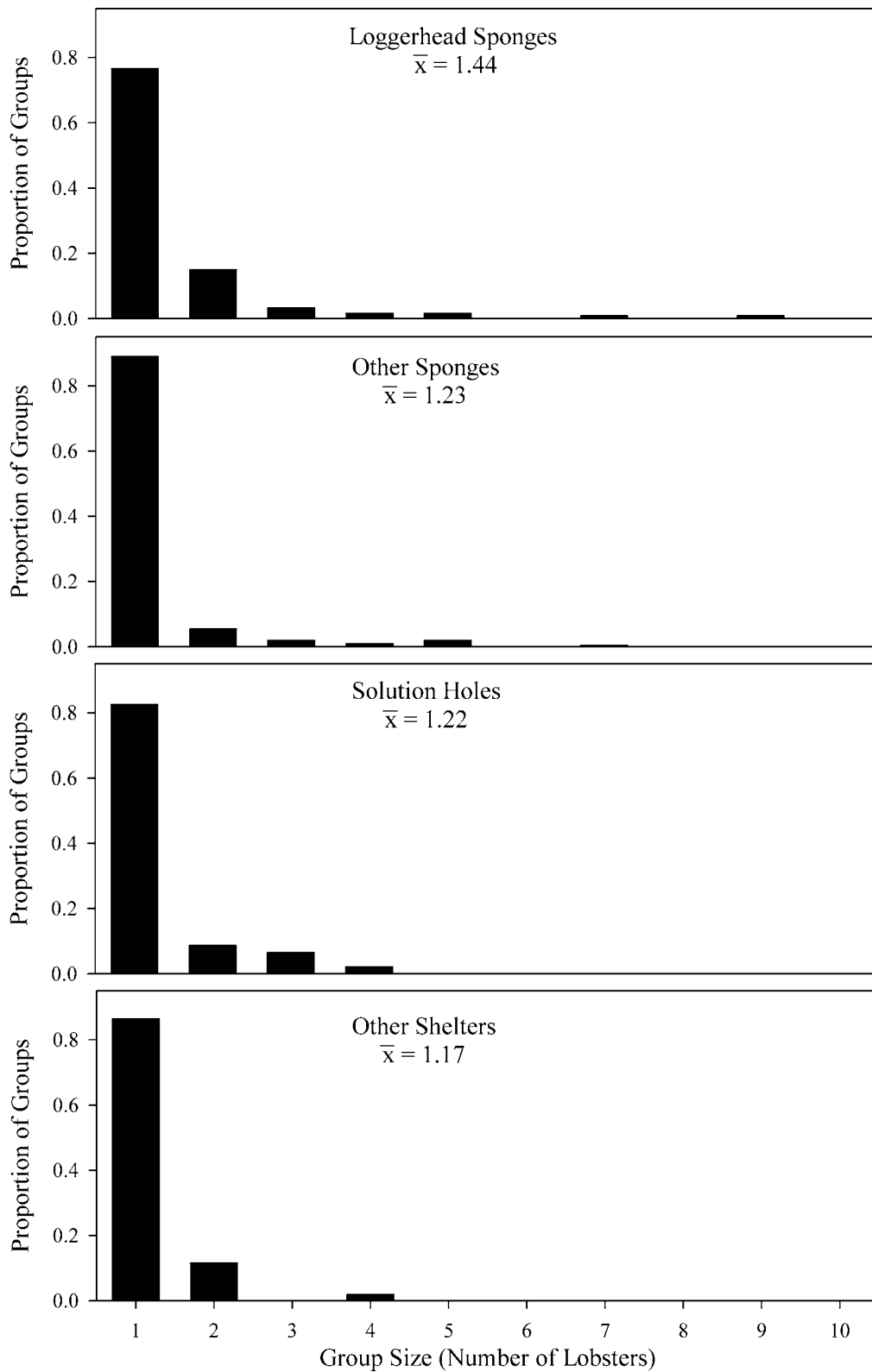
Fig. 2.   Distributions of group sizes for juvenile lobsters in different hard-bottom shelter types. Group sizes were surveyed at 21 0.1 ha sites throughout the Florida Keys, USA (Butler, unpublished data). Note that one shelter type used in the model, octocoral complexes, is not included in this figure because only solitary lobsters were observed taking shelter under them.
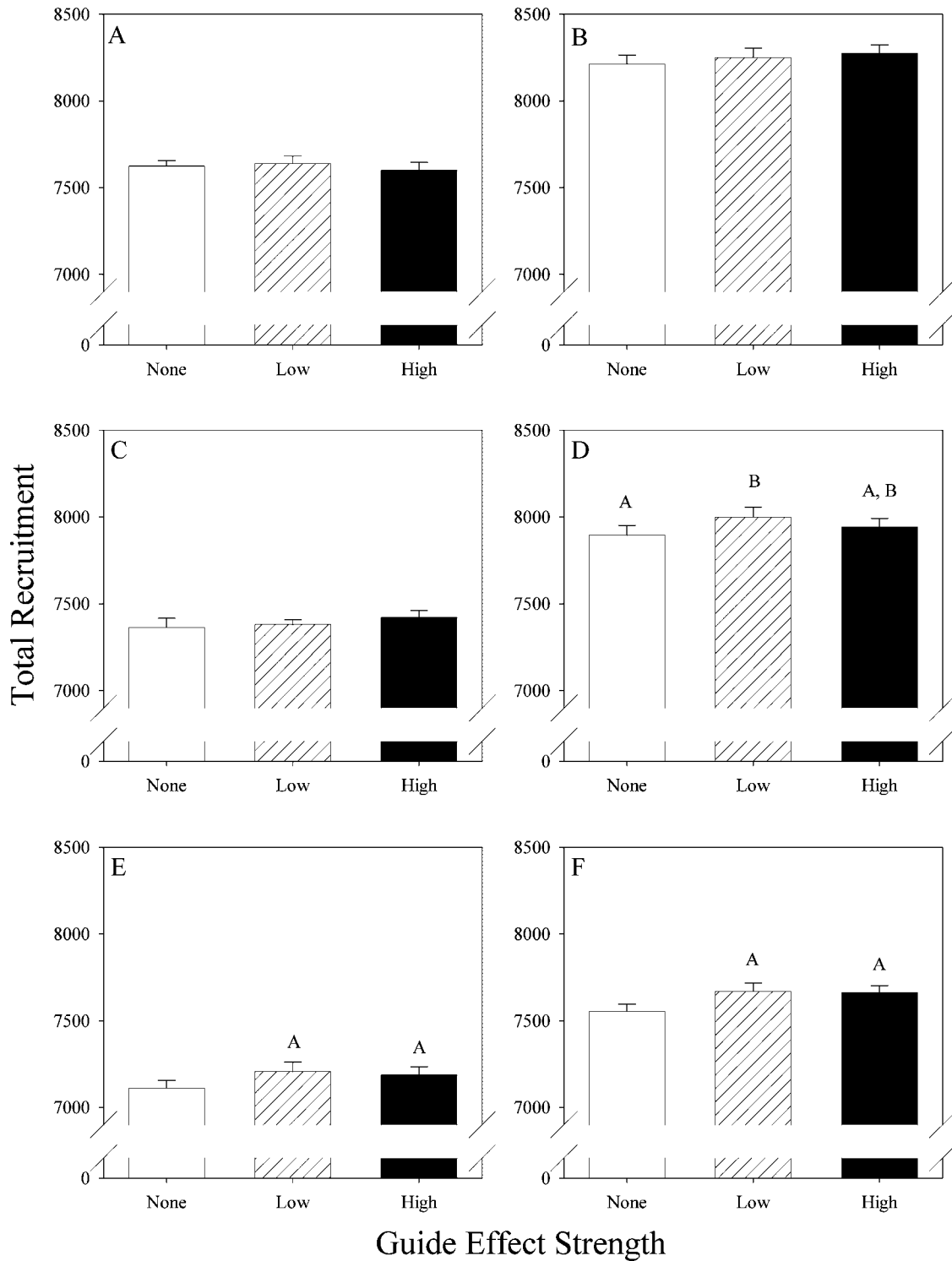
Fig. 3. Number of lobsters recruiting to 50 mm CL resulting from simulations incorporating three levels of guide effect strength at three shelter densities designated as high (A, B), medium (C, D), and low (E, F), and search window lengths of 2 hours (A, C, and E) and 3 hours (B, D, and F). Within each graph, groups that were significantly different from each other at the $\alpha = 0.05$ level are identified with different letters. With all lobsters required to search for shelter every day, the guided search failed to significantly enhance recruitment at high shelter densities. At 50% of the realistic shelter density, the guide effect significantly enhanced recruitment only when the search window was increased from two hours to three. At the lowest shelter density, the guide effect significantly enhanced recruitment regardless of search window length.

12 km^2 habitat cell as naïve. Because of the way we scaled movement among 12 km^2 cells, the regional memory model does not assume that the lobsters have knowledge of the entire cell. Rather it simulates knowledge only of the current 1000 m^2 area and the 1000 m^2 areas immediately

adjacent to it. We used the same three levels of guide effect strength (none, low, and high) as in the previous set of simulations. We also used three search window intervals (2, 3, and 4 hours). The four-hour search window simulations were added after we determined that there was no significant

Table 1. Analysis of variance examining the independent and interactive effects of shelter density, search window length, guide effect strength, and group benefit strength on the rank-transformed number of simulated lobsters recruiting to 50 mm carapace length.

Source	d.f.	Mean square	F	P
Shelter density (SH)	2	233,042.008	549.626	< 0.001
Search window (SW)	1	833,111.126	1964.880	< 0.001
Guide strength (G)	2	3855.769	9.094	< 0.001
Group benefit (D)	2	99,151.244	233.847	< 0.001
SH * SW	2	4544.056	10.717	< 0.001
SH * G	4	1020.711	2.407	0.050
SH * D	4	693.890	1.637	0.166
SW * G	2	864.684	2.039	0.133
SW * D	2	1570.915	3.705	0.026
G * D	4	167.039	0.394	0.813
SH * SW * G	4	672.415	1.586	0.179
SH * SW * D	4	1846.150	4.354	0.002
SH * G * D	8	393.418	0.928	0.494
SW * G * D	4	607.906	1.434	0.224
SH * SW * G * D	8	785.379	1.852	0.069
Error	216	424.001		
Total	269			

Table 2. Analysis of variance examining the effects of guide effect strength, given different levels of spatial memory, on the recruitment of simulated lobsters to 50 mm CL. The spatial memory models tested assumed either that: (a) only migrants from one habitat cell to another were naïve with respect to shelter location or (b) that all lobsters moving within habitat cells were naïve. Three levels of guide strength (none, low, and high), and three search window lengths (2, 3, and 4 hours) were tested. Numbers of recruits were rank-transformed.

Source	d.f.	Mean square	F	P
Spatial Memory (Memory)	1	511.433	0.848	0.358
Search Window (SW)	2	592,704.000	982.412	<0.001
Guide Effect Strength (G)	2	386.574	0.641	0.528
Memory * SW	2	918.504	1.522	0.2203
Memory * G	2	418.816	0.694	0.501
SW * G	4	447.574	0.742	0.564
Memory * SW * G	4	291.441	0.483	0.748
Error	234	603.315		
Total	251			

effect of guide effect strength given the two- and three-hour treatment levels. To enhance the likelihood of detecting significant differences due to the guide effect, all of these simulations were carried out at the low shelter density. Fourteen independent replicates of each treatment combination were generated.

The simulation program was written in Fortran 90 using Microsoft Fortran Powerstation, and run on a Pentium 4 (3.2 GHz)-based microcomputer. The results were analyzed using SPSS version 9.0 for Microsoft Windows. All ANOVA models were analyzed using the GLM procedure. The assumptions underlying ANOVA were tested using the Shapiro-Wilk Test to evaluate normality and Levene's Test to evaluate homogeneity of variances. Our design resulted in 270 independent computer runs for our main comparisons, consisting of five replicates of each of 54 treatment combination simulations.

RESULTS

Simulations in Which Lobsters Search Randomly for Shelter

We used a four-way ANOVA to identify the effects of search window length, shelter density, guide effect strength, and group benefit strength on recruitment success, i.e., total number of lobsters surviving to 50 mm CL. The raw data from the model did not meet the assumptions of normality or homoscedasticity, and no transformation was found that improved the fit of the data; therefore, the statistical analyses were performed on rank transformed data, and the results are summarized in Table 2. We found a significant three-way interaction among shelter density, search window length, and group benefit strength ($F_{4,216} = 4.354$, $P = 0.002$). There was also a significant two-way interaction between shelter density and guide effect strength ($F_{4,216} = 2.407$, $P = 0.050$). In addition, the four-way interaction term was marginally non-significant ($F_{8,216} = 1.852$, $P = 0.069$). Multiple comparisons among all treatment combinations using the REGW F-test showed a general trend of increasing recruitment with increasing shelter density and increasing search window length, but was otherwise uninformative. However, our intent in manipulating shelter density and search window length was not to determine whether these factors could affect recruitment success, but rather to determine whether some combination of levels of these

factors could be found at which the guide effect or group benefit significantly enhanced recruitment. Therefore, we separately analyzed the model output using the REGWF-test for each of the six combinations of levels of these factors, clearly revealing the nature of the interactions. Figures 3-5 summarize these results.

At high shelter densities, the guide effect did not significantly enhance recruitment; nor was there a detectable effect at medium shelter densities when lobsters were restricted to a two-hour search window (Fig. 3A-C). However, the guide effect did result in higher recruitment given the three-hour search window. The low guide effect strength simulation resulted in a statistically significant increase in recruitment of 1.3%, but the result of the high guide strength level was not significantly different from this or from the unguided model (Fig. 3D). The average increase in recruitment due to the guide effect with a three-hour search window was a 0.9%. At low shelter densities, both the low and high levels of guide effect strength had similar effects, resulting in a 1.2% increase in recruitment when restricted to a two-hour search window, and a 1.4% increase with a three-hour search window (Fig. 3E, F). These modest changes in recruitment occurred despite the rather large impact of the guide effect on search time for shelter. On average, the low guide effect strength reduced search times for lobsters that found crevice shelters by 53%, and the highest guide effect level reduced search times by 63% (Fig. 4).

In contrast, there was only one circumstance in which group benefit failed to significantly enhance recruitment: at the lowest level of benefit, the lowest shelter density, and the shortest search window (Fig. 5E). At every other combination of shelter density and search window, both high and low group benefit strength significantly enhanced recruitment (Fig. 5A-D, F). The significant increases in recruitment ranged from 0.6% to 1.3% for the low group benefit level, and from 3.6% to 5.1% for the high group benefit level.

Simulations Incorporating Spatial Memory by Lobsters

To compare guide effect models that included simulation of spatial memory, we used a three-way factorial ANOVA
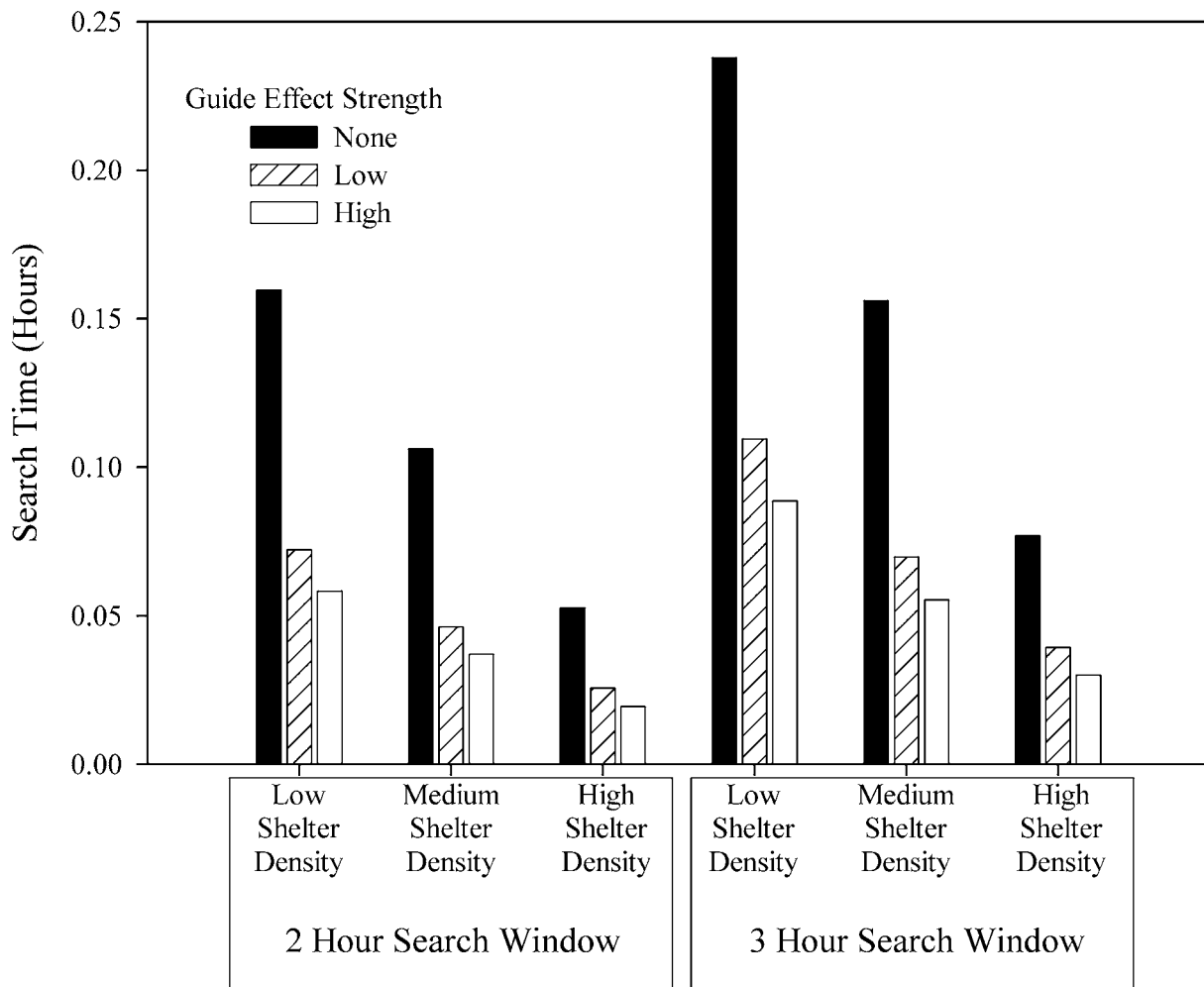
Fig. 4. Mean search times for all lobsters searching for and finding hard-bottom crevice shelters in simulations using three levels of guide strength (a measure of the effectiveness of conspecific cues in reducing search time), at three different shelter densities and two search window lengths. Search times of lobsters under the low level of guide strength were, on average, 53% lower than those of lobsters that did not respond to conspecific cues. Search times for lobsters at the high level of guide strength were 63% lower than those that were unguided.

(spatial memory model, search window length, and guide effect strength) to detect significant differences in recruitment success of lobsters to 50 mm CL. The data did not meet the assumptions of the ANOVA, and no transformation was found that improved their fit; therefore, the analysis was performed using rank-transformed data. The results of this analysis are summarized in Table 2. There were no significant interactions among the factors. There were also no significant differences in recruitment due to the different spatial memory models ($F_{1,234} = 0.848$, $P = 0.358$), though there was a significant increase in recruitment with increasing search window length ($F_{2,234} = 982.412$, $P < 0.001$). In contrast to the simulations that did not include spatial memory, there was no significant effect of guide strength, even when the search window was increased to four hours ($F_{2,234} = 0.641$, $P = 0.528$). In the case of the regional memory model, in which only lobsters leaving a 12 km^2 habitat cell were classified as naïve, only about 0.03% of the lobsters using crevice shelters in hard-bottom habitat were required to search for shelter each day. When all lobsters leaving a 1000 m^2 arena were considered

naïve (the local memory model), approximately 5% of that population was required to search each day. This suggests that, if lobsters retain spatial memory of the surrounding habitat, the effectiveness of the guide effect is nil because few individuals need to search for shelter using conspecific odors.

DISCUSSION

Two hypotheses have been suggested to account for gregariousness of juvenile Caribbean spiny lobsters. The traditional view holds that aggregation directly enhances survivorship either by cooperative group benefit or dilution of risk (Eggleston and Lipcius, 1992; Mintz et al., 1994). The alternative hypothesis posits the intriguing idea that formation of groups may be without any benefit of its own, but rather is a side-effect of the mechanism by which shelter is located (Childress, 1995; Childress and Herrnkind, 1997). In this alternative view, survivorship of solitary lobsters in shelters does not differ from those within groups that are sheltered. The only benefit gained is to reduce the amount of time that lobsters must spend in the open searching for
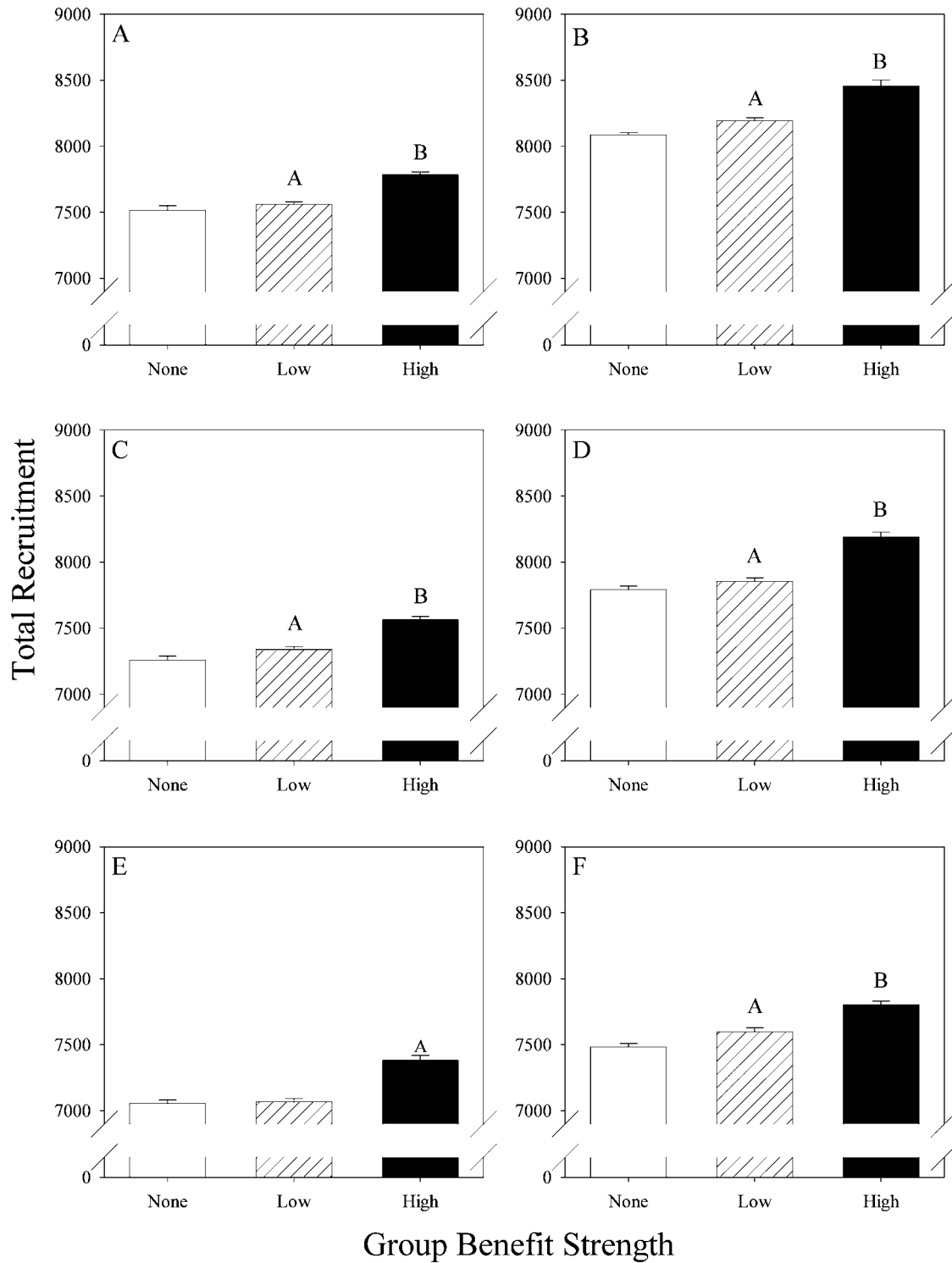
Fig. 5. Number of lobsters recruiting to 50 mm CL comparing the effects of three group benefit levels at three shelter densities, designated as high (A, B), medium (C, D), and low (E, F), and search window lengths of 2 hours (A, C, and E) and 3 hours (B, D, and F). Within each graph, groups that were significantly different from each other at the $\alpha = 0.05$ level are identified with different letters. At the highest level tested, group benefit resulted in significantly greater recruitment at every combination of shelter density and search window length. At the low level of group benefit strength, recruitment was significantly enhanced for every combination, except for the lowest shelter density and shortest search window.

shelter at the conclusion of each night's foraging, and thus their risk of mortality from predators during this period each day. Manipulative field experiments have been employed to attempt to directly measure the effect of aggregation on

mortality rates, but equivalent tests on the indirect effect of altered search behavior on mortality rates are difficult and have not been attempted. Therefore, we tested these alternative hypotheses using a model capable of simulating

differences in shelter density and juvenile lobster behavior to determine their likely effects on recruitment at a spatial scale unapproachable in the field. Our simulation results suggest that the guide effect alone is inadequate to explain social aggregation of juvenile *P. argus*. These results are contingent on two primary assumptions: 1) the guide effect only alters the search for shelter during the crepuscular period following noctural foraging, and 2) actual shelter densities are similar to or at most 77% lower than the density of large structures measured in field surveys the Florida Keys.

Spiny lobsters are clearly attracted to each other at the ages we modeled. Tests of this attraction have been conducted in small arenas, small (~ 8 m diameter) and large (20 m by 40 m) mesocosms and Y-mazes (Eggleston and Lipcius, 1992; Childress and Herrnkind, 1996; Butler et al., 1997; Ratchford and Eggleston, 1998, 2000; Childress and Herrnkind, 2001), and in controlled studies in the field (Zimmer-Faust et al., 1985; Nevitt et al., 2000). In these studies, individual lobsters find, then reside in, shelters with conspecifics (or their odors) more often or more quickly than those without. Yet, other mechanisms beside social cues can also direct lobsters back to shelter after an evening of foraging in the open. For example, adult and large juvenile *P. argus* retain spatial memory and have a homing ability (reviewed by Herrnkind, 1980) that may be based on hydrodynamic cues (Nevitt et al., 1995) and magnetic orientation (Lohmann et al., 1995; Boles and Lohmann, 2003). Although there is no doubt that post-algal juvenile and adult spiny lobsters are attracted to one another, the question is what, if any, selective advantage does aggregation confer?

Our primary set of simulations manipulated shelter density and three aspects of lobster behavior: the maximum amount of time spent searching for shelter, the effectiveness of following conspecific odor cues in reducing search time, and the effectiveness of aggregation in directly reducing mortality. We began with shelter densities similar to those measured in the field and a search window length similar to that of adult *P. argus*. We reasoned that the guide effect would be more important under conditions of lower shelter density and longer search windows. Therefore, we progressively reduced overall shelter density in the model and increased the search window length until a significant guide effect was detected. We parameterized the guided search model with values that were intended to approach the effect on search times measured by Childress and Herrnkind (2001) in mesocosm studies. In that study, the presence of conspecifics reduced search time by 66% on average. Our modeling of the guide effect achieved similar reductions in search times. In simulations that did not include local spatial memory, the guide effect resulted in search times that were 53%-63% lower than those of the unguided model depending on the hypothesized strength of the guide strength that we employed.

However, the guide effect only enhanced recruitment, i.e., survival to 50 mm CL in our model by $\sim 1\%$. It did so only when shelter density was set at 50%-67% of the density of shelters measured in the field, and only when the daily search window period took 3-4 h. Although juvenile *P. argus* are not particularly choosy about what constitutes

shelter (Childress and Hunt, 2002), it is not obvious how lobsters perceive shelter quality and therefore how much the density of large structures on a site differs from the true availability of shelters. This is why we varied shelter density in our simulations. We believe that it is unlikely that juvenile lobsters spend 3 to 4 hours each night searching for shelter. However, the nightly duration of the search period and the relative risks of predation that they face during this period relative to other times of the day is crucial to the guide effect hypothesis and thus should be determined empirically at a sufficiently fine scale to permit confident model parameterization. Our modeling results suggest that if the guide effect is to have relevancy for survival under modern conditions, i.e., current levels of predation and shelter abundance, then the search window length must be long, the probability of mortality during the crepuscular period high, and shelters scarce.

Moreover, when we incorporated the more realistic condition that lobsters retain each day an awareness of the location of nearby shelters, we found that the number of lobsters benefiting from the guide effect was insufficient to affect recruitment success regardless of the search period or shelter density. Nighttime field observations of juvenile *P. argus*, ranging in size from 25 to 45 mm CL, suggest that most do not move more than a few meters from their shelters while foraging (Andree, 1981; Schratwieser, 1999; Butler and Dolan, unpublished data,). If so, then it is unlikely that the guidance of conspecific odors would be required for them to relocate shelter. The guide effect is likely to be more effective when large juveniles, e.g., > 45 mm CL, roam more widely into previously unexplored areas. We do not doubt that such events occur, but what fraction of the juvenile population engages in long-distance movements each night is unknown.

In contrast with the guide effect, the group benefit directly modifies the probability that a lobster is killed. Thus, an increase in recruitment is not surprising if the simulated effect of group benefit is sufficiently large. In our simulations, both the low and high group benefit treatment levels significantly enhanced recruitment, and did so by decreasing daytime mortality of lobsters in shelters by only 0.6% to 5.1%, respectively. Recent field- and laboratory-based studies of *P. argus* have failed to find significant differences in mortality for juvenile lobsters sheltering alone or in groups of smaller individuals. Yet, one of the most comprehensive studies of *P. argus* juvenile survivorship, estimated using tethering, would only have been able to detect differences in survivorship among treatments of greater than 25% assuming a desired power of 0.8 (Childress and Herrnkind, 2001). Our results indicate that a much larger sampling effort would be required (on the order of several hundred individuals per treatment) to detect differences in mortality similar to even the lowest level at which our model predicts that grouping would accrue significant benefits. Clearly more precise estimates of natural mortality are needed to properly evaluate the potential benefit of aggregation.

Both the guide effect and group benefit hypotheses suggest that lobsters should be highly aggregated, though for different reasons. It is therefore noteworthy that field observations of juvenile *P. argus* vary greatly in the fre-

quency with which individuals share dens. Anywhere from 20% to 50% of the individuals observed in field studies shelter alone, and most groups consist of only two or three lobsters per den (Marx and Herrnkind, 1985; Forcucci et al., 1994; Childress, 1995; Butler and Herrnkind, 1997; Childress and Herrnkind, 1997). One explanation for these observations is that conspecific odor cues may not always be detectable, particularly in turbulent flow caused by currents (Zimmer-Faust et al., 1995; Finelli et al., 1999). However, the existence of so many solitary or small groups of lobsters also depends on the scale on which aggregation is measured. Several lobsters may each reside alone in their respective dens and are thus solitary on a scale of a single hard-bottom structure. Yet, lobsters attracted to one another may aggregate at scales of several meters if the dens are small and scattered a few meters apart. In fact, the great majority of the structures available to juvenile lobster in Florida's nurseries is small and can shelter only one or a few individuals at one time. The largest aggregations of juvenile lobsters are predictably found under the occasional large rock outcropping or coral head.

It has been argued that this pattern of aggregation would favor the guide effect hypothesis, because no formulation of group defense considers such dispersed aggregations (Childress, 1995). Although it is true that simple attraction of wandering lobsters by conspecifics cues to shelters that are already full would create loose aggregations if adjacent dens a meter or two away were available, but this is not the guide effect. Rather, this pattern stems from attraction to conspecific chemical cues, which is the precursor condition to both the guide effect and the group benefit effect. For this to be evidence of the guide effect requires demonstration that search time and probability of mortality for these loosely aggregated individuals was somehow lower. With respect to the group benefit effect, late arriving lobsters would not benefit from group defense in such a loose aggregation, but it is possible that the dilution effect on predation risk could operate on this scale.

We believe that shelter selection is probably a reflection of the interplay of several factors including: shelter availability, shelter scaling to lobster size, conspecific density, chemotaxis, and predator density (Eggleston et al., 1997; Eggleston and Lipcius, 1992; Eggleston et al., 1990). Shelter choice involves trade-offs, the solutions of which might be examined in a framework similar to optimal foraging models. For example, a lobster may chance upon an unoccupied den while following an odor cue to a more distant, occupied den. It must then decide whether staying alone in this shelter carries a higher risk than the exposure associated with continuing on to the occupied shelter. The decision may depend on the strength of the odor signal, the physical characteristics of the potential den, and the proximity of predators. If predation pressure is high, more weight might be given to being sheltered. Clearly, this process is highly dependent on local conditions and could give rise to the various observations mentioned. Flexibility in social behavior may indeed be important in highly variable local ecological circumstances.

In summary, we have used an individual-based spatially-explicit model to look at the impact of different forms of social behavior and habitat structure on the survival, and thus recruitment, of juvenile spiny lobsters at a scale and resolution not generally possible in behavioral models. In this application, we incorporated specific behavioral mechanisms that have been proposed to explain the observed distributions of aggregations of Caribbean spiny lobster. Our results suggest that the population-level consequence of a direct group benefit, as measured by the number of recruits surviving to the sub-adult stage, may be substantial. The benefit of grouping, e.g., group defense, dilution, and vigilance, appears to outweigh that of the guide effect, given current shelter densities, risks of predation, and the state of our knowledge regarding the search for shelter by lobsters. Our results do not discount the benefit of conspecific attraction based on odor cues as a mechanism to locate appropriate shelters, but the benefits of this behavior appear to be those associated with aggregation. As with any modeling exercise, we are unable to definitively state that only one mechanism is operating in the real system. Unfortunately, the available empirical data that can be brought to bear on this issue are insufficient for direct parameterization of all of the important factors in the model. Final resolution of this matter may require more robust field tests of these two hypotheses explaining the evolution of aggregation in palinurid lobsters.

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APPENDIX A

Each of the following tables summarizes the key objectives of each set of simulations and lists the factors that were tested in a completely crossed design, i.e., every combination of levels shown for a set of simulations were tested. Below the tables, we define the levels of each factor.

Definitions

Search Type

unguided: lobsters searched randomly for shelter, with no guidance from conspecific cues.

low guide strength: the maximum reduction of the proportion of time available to search for shelter that lobsters spent searching was 0.8, but the proportion of time spent searching could not be less than zero. This resulted in a mean reduction of the proportion of available time spent searching of approximately 53%.

high guide strength: the maximum reduction of the proportion of time available to search for shelter that lobsters spent searching was 1.293, but the proportion of time spent searching could not be less than zero. This

Simulation Set 1

Objective: Examine the relative benefit of reducing search time vs. aggregation on the recruitment success of juvenile Caribbean spiny lobsters for different search window lengths and shelter densities.

Search type	Spatial memory model	Group benefit level	Search window length	Shelter density level
Unguided	None	None	2 hours	Low
Low Guide Strength		Low	3 hours	Medium
High Guide Strength		High		High

Simulation Set 2

Objective: Examine the importance of the guide effect on lobster recruitment with different degrees of lobster spatial memory and different search window lengths.

Search type	Spatial memory model	Group benefit level	Search window length	Shelter density level
Low Guide Strength	None	None	2 hours	Low
High Guide Strength	Local		3 hours	
	Regional		4 hours	

resulted in a mean reduction of the proportion of available time spent searching of approximately 63%.

Spatial Memory

none: all lobsters using crevice shelters searched for shelter every day.

local: only lobsters leaving the 1000 m^2 area in which they resided were required to search for shelter.

regional: only lobsters leaving the 12 km^2 habitat cell in which they resided were required to search for shelter.

Group Benefit Level

none: daytime mortality rates for lobsters in crevice shelters were not reduced by group size.

low: daytime mortality rates for lobsters in crevice shelters were reduced by a linear function of group size, which reached a 50% reduction at a group size of six lobsters.

high: daytime mortality rates for lobsters in crevice shelters were reduced by a linear function of group size, which reached a 50% reduction at a group size of 29 lobsters.

Shelter Density

high: the density of each shelter type in each cell was set at the density measured at the corresponding field site (Butler et al., 2005).

medium: the density of each shelter type in each cell was set to 50% of the density measured at the corresponding field site.

low: the density of each shelter type in each cell was set to 33% of the density measured at the corresponding field site.