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**Ontogenetic changes in social aggregation in New Zealand rock lobsters**

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## Abstract

Ontogenetic changes in the behavior, spatial distribution, or habitat use of a species are presumably adaptations to ecological forces that differ in their effect on various life stages. The New Zealand rock lobster (*Jasus edwardsii*) is one of several species of spiny lobster that exhibits dramatic ontogenetic shifts in sociality and spatial distribution, and we tested whether such changes are adaptive. We first surveyed several natural populations of *J. edwardsii* to unequivocally document size-specific differences in aggregation. In the laboratory, we tested the responsiveness of various sizes of lobster to different conspecific cues (e.g., chemical scent) that might promote aggregation of certain sized lobsters. Finally, we tethered lobsters of different sizes alone and in groups to test whether the effect of size-specific differences in aggregation on mortality sufficiently explain ontogenetic changes in aggregation.

Our results offer compelling evidence that juvenile *J. edwardsii* undergo an ontogenetic change in sociality that alters their spatial distribution and enhances their survival. Our field surveys show that juvenile *J. edwardsii* are solitary when small and then become social and aggregate as they grow larger. We then demonstrate, using laboratory experiments, that there is a size-specific increase in the response of juvenile *J. edwardsii* to the chemical cues of larger conspecifics that accounts for these ontogenetic changes in aggregation. Finally, our tethering results confirm that this change in social condition is selectively advantageous: aggregation does not increase the survival of small lobsters, but larger lobsters survive better in groups. Thus, in this study we demonstrate the linkage between ontogenetic changes in the spatial distribution of a species, the behavioral process that creates the pattern, and the selective advantage conferred by these developmental changes.

## Introduction

Social aggregation is widespread among marine animals. It occurs in mammals and fish of many kinds (Pitcher 1986), and in a diversity of invertebrate groups including: squid, krill, molluscs, (Catterall and Poiner 1983, Stoner and Ray 1993), decapod crustaceans (Atema and Cobb 1980, among others), and others (Ritz 1994). Social aggregations develop because of mutual attraction among conspecifics and the evolution of cooperative group behavior that enhances individual defense, foraging, movement, or reproduction (Wilson 1975). Social groups differ from other aggregations that arise indirectly in response to patchy resources. For example, where settlement on limited substrates or foraging on concentrated patches of food results in clusters of animals. Social aggregation can be beneficial because it can increase vigilance and group defense against predators, reduce the *per capita* probability of mortality from predation, and may improve detection of food resources (see reviews by Bertram 1978, Pitcher et al. 1982, Pulliam and Caraco 1984, Lima and Dill 1990). However, the benefits of aggregation may be counter-balanced by increases in intraspecific competition for food resources (Milinski and Parker 1991), or by increased mortality caused by predators that also forage in groups and thus locate clumped prey more easily (Major 1978, Hamner 1984). Aggregation can also be non-adaptive for cryptic or camouflaged animals (Harvey and Greenwood 1978, Owen 1980, Dukas and Clark 1995, Butler et al 1997). Moreover, the ecological conditions favoring social aggregation are not static and vary with changes in predator density, resource (food or habitat) availability, and individual size or developmental stage (i.e., ontogeny; Wilson 1975, Trivers 1985).

Ontogenetic changes in social aggregation often take one of two forms. Social aggregations are common during its early life stages when individuals are small, vulnerable, and

1 inexperienced. Aggregation often diminishes among subadults, but can reappear at adulthood  
2 for reproductive purposes. Less common are species that are solitary as juveniles and  
3 aggregated as pre-reproductive adolescents or subadults. This type of ontogenetic behavioral  
4 pattern can develop, for example, where aggregation by defenseless juveniles increases their  
5 detection by predators and thus their probability of mortality (Tinbergen et al. 1967, Dukas and  
6 Clark 1995, Butler et al. 1997). Cryptic behavior and camouflage coloration is beneficial to  
7 juveniles under these conditions. Spiny lobsters (Crustacea; Palinuridae) are one group of  
8 marine organisms that exhibits this pattern; most species appear to be solitary when young and  
9 then aggregate as they grow larger (Herrnkind et al. 1994, Lipcius and Cobb 1994, Phillips and  
10 Booth 1994).

11 Spiny lobsters have complex life cycles involving several ontogenetic stages and habitats.  
12 Their larvae are typically planktonic for 6 - 18 months and then metamorphose into a non-  
13 feeding puerulus postlarval stage lasting several weeks. Postlarvae swim and are advected  
14 nearshore where they settle in shallow, architecturally complex habitats (Herrnkind et al. 1994).  
15 There are no data that discern whether spiny lobster larvae or postlarvae actively aggregate or  
16 are social, although postlarvae periodically settle in dense aggregations in natural habitats  
17 (Jernakoff 1990, Booth 1979, Booth and Phillips 1994, Norman et al. 1994) and on artificial  
18 collectors (Phillips and Booth 1994). Newly settled early benthic juvenile (EBJ; = postpuerulus;  
19 see Lavalli and Lawton 1996) lobsters live in holes or dense vegetation, are solitary, and at least  
20 one species (Caribbean spiny lobster, *Panulirus argus*) is asocial at this stage (Herrnkind et al.  
21 1994, Childress and Herrnkind 1996). As they grow, lobsters inhabit increasingly larger crevices  
22 through adulthood, which for some species results in a marked shift in their choice of habitat and  
23 pattern of aggregation (Berrill 1975, Cobb 1981, Herrnkind and Butler 1986, Trendall and Bell

1 1989, Herrnkind and Lipcius 1989, Glaholt 1990, Eggleston and Lipcius 1992). Yet, no study  
2 has linked these ontogenetic changes in aggregation with the proximate processes that promote  
3 them or has offered evidence that such changes enhance survival or fecundity.

4 Findings from several unrelated studies suggest that there are distinct ontogenetic  
5 differences in aggregation of *Jasus edwardsii*, the New Zealand rock or spiny lobster. All stages  
6 are found in rocky habitats; juveniles and adults tend to aggregate in particular dens  
7 (MacDiarmid et al. 1991, MacDiarmid 1991, 1994), whereas EBJ occupy small shelters  
8 individually (Kensler 1966, Booth 1979, 1991, Booth and Bowring 1988). This increase in the  
9 patchiness of lobsters with size may be due to: (i) ontogenetic changes in behavior that enhance  
10 social aggregation of larger lobsters, (ii) differential mortality of lobsters among shelter locations  
11 that creates patches of survivors, or (iii) differences in the spatial distribution of crevices of  
12 different sizes. If the first hypothesis is true and *J. edwardsii* actively congregate as juveniles  
13 and adults, then they must have some means of locating one another. Chemical (odor) detection  
14 is a likely mechanism. It is used by the adults and subadults of other species, notably *P.*  
15 *interruptus* (Zimmer-Faust et al. 1985, Zimmer-Faust and Spanier 1987) and *P. argus* (Childress  
16 and Herrnkind 1996). It is not known whether *J. edwardsii* responds to chemical cues, or if the  
17 use of chemical cues varies among the life stages of this or any species of lobster.

18 Thus, in this study we sought to: (i) determine whether the aggregation of *J. edwardsii*  
19 varies among ontogenetic stages, (ii) investigate behavioral mechanisms that might create  
20 changes in aggregation, and (iii) examine the potential selective value of ontogenetic changes in  
21 aggregation. We first characterized the natural spatial distribution of non-reproductive lobsters  
22 of three natural ontogenetic stages: EBJ (< 20 mm carapace length; CL), juveniles (20-40 mm  
23 CL), and subadults (40-85 mm CL). In the laboratory, we then determined if chemical cues play

1 a role in establishing the spatial patterns we observed in the field. Finally, we evaluated whether  
2 aggregations of different ontogenetic stages in natural dens, alters their affects mortality and thus  
3 has adaptive significance under present ecological conditions. Our results offer compelling  
4 evidence that juvenile *J. edwardsii* undergo an ontogenetic change in sociality that alters their  
5 spatial distribution and enhances their survival.

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## Methods and Materials

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### Ontogenetic Changes in the Spatial Distribution of Natural Populations

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To document ontogenetic changes in the spatial distribution of *J. edwardsii*, we first conducted two separate observational studies. In the first study, we documented the degree of aggregation of various size classes of lobsters (EBJ, juveniles, adolescents) on a single occasion in natural habitats at several sites along the east coast of New Zealand (Fig. 1). To better assess the aggregation patterns of EBJ, which were not well represented in our large-scale sampling, we conducted a second study where we focused our sampling effort at a single location (Gisborne Harbor) and recorded the distribution of EBJ there repeatedly over many months. This sampling protocol also allowed us to examine whether temporal changes in postlarval settlement density altered the subsequent spatial distribution of postlarvae and EBJ that had recently settled.

*Large-scale Observations of Lobster Distributions:* We determined the spatial distribution of lobsters of all sizes on shallow (1 - 15 m) rock reefs at four locales spread along approximately 1000 km of New Zealand's eastern coastline on both the North and South Islands. From north to south, those locales were: 1) the Cape Rodney-to-Okakari Point Marine Reserve on the northeast coast of the North island at Leigh (Leigh), 2) the south coast of the North Island

1 near Wellington Harbor (Wellington), 3) the Kaikoura Peninsula on the northeast coast of the  
2 South Island (Kaikoura), and 4) Otago Harbor on the southeast coast of the South Island (Otago;  
3 Fig. 1).

4 Two sites 100 - 500 m apart were surveyed at each locality. At each site, five replicate  
5 50 m x 10 m (500 m<sup>2</sup>) quadrats were demarcated by divers using tape measures. These large  
6 quadrats were in turn subdivided into ten 5 m x 5 m (25 m<sup>2</sup>) quadrats. Divers then searched  
7 within each of the 25 m<sup>2</sup> quadrats for lobsters dwelling in the crevices within the rock reef. We  
8 recorded the number, size (to nearest 5 mm), and sex of all lobsters observed in each group.  
9 Thus, the abundance and pattern of aggregation of lobsters of all sizes were collected from a  
10 total of 800 25 m<sup>2</sup> quadrats from four locales scattered along the east coast of New Zealand.

11 These data were partitioned into three data sets to allow us to describe separately the  
12 size-specific distribution of EBJ, juveniles, and adolescent lobsters. Data collected from the 25  
13 m<sup>2</sup> quadrats were used to describe the distribution of lobsters in crevices because they were most  
14 likely to yield the information we desired on small-scale aggregation patterns. However, since  
15 these data were obtained from adjoining 25 m<sup>2</sup> quadrats created from the subdivision of 500 m<sup>2</sup>  
16 quadrats, data collected from the small quadrats may not be independent, even if the larger  
17 quadrats were. Therefore, we present only descriptive plots of the frequency with which lobsters  
18 of different sizes aggregate (see Hurlbert 1984, Heffner et al. 1996). We did not attempt to use  
19 inferential statistics or spatial indices intended for analysis of randomly collected data.  
20 Nonetheless, these plots are useful for examining whether lobsters of different sizes tend to  
21 dwell solitarily in crevices or coinhabit crevices with conspecifics.

22 *Lobster Distribution and Settlement at Gisborne Harbor:* Because small EBJ lobsters  
23 were underrepresented in our large-scale surveys, we used another data set to more thoroughly

1 investigate their spatial dispersion. We sampled pueruli and EBJ that were dwelling in holes on  
2 vertical rock faces beneath the No. 7 Wharf at Gisborne Harbor on the east coast of the North  
3 Island of New Zealand (Fig. 1). The Gisborne Wharf is approximately 200 m long and beneath  
4 it lies a vertical rock wall about 2 m high from its top edge (defined by the mean low tide) to its  
5 bottom edge where it meets the gently sloped, silty bottom. Concrete pilings that support the  
6 wharf are set into the wall at approximately 3 m intervals, thus forming about 60 discrete rock  
7 faces that are approximately 6 m<sup>2</sup> in area and separated by the 0.5 m wide concrete pilings.

8         There is little algal growth on the rock wall because the wharf shades it, but it is covered  
9 by encrusting sponges, ascidians, and tunicates. Importantly, the wall is also peppered with  
10 innumerable small holes excavated by pholad molluscs. It is in these holes that postlarvae settle  
11 and EBJ reside. The dimensions of the holes on the Gisborne Wharf wall resemble those used  
12 by newly-settled *Panulirus japonicus* EBJ in Japan (Norman et al. 1994). We estimate that  
13 within our sampling quadrats unoccupied holes were at least an order of magnitude more  
14 numerous than holes occupied by lobsters. They were so abundant that they were unlikely to  
15 have influenced the distribution of lobsters at even the smallest spatial scale that we measured  
16 (10 cm x 10 cm).

17         We collected two separate sets of distributional data on pueruli and EBJ: (1) a long-term,  
18 large spatial scale survey and (2) a short-term, small spatial scale survey. Our long-term data  
19 set included 29 monthly surveys (April - November 1993; March - December 1994; January -  
20 December 1995; January, March, and April 1996) of at least 9 and up to 25 separate rock faces  
21 out of the 60 available. During each survey, a diver carefully scanned each 6 m<sup>2</sup> rock face and  
22 recorded the number of lobsters found dwelling in holes. Each rock face is a natural sampling  
23 unit of nearly equal size, so we computed estimates of lobster density (mean  $\pm$  1 sd) and spatial

1 dispersion. We used the Standardized Morisita's Index to describe spatial dispersion because  
2 this index is unbiased by density or sample size (Myers 1978). This index ranges from + 1.0 to -  
3 1.0. A random distribution yields a value of 0, positive values indicate a clumped or patchy  
4 distribution, whereas uniform patterns produce a negative value.

5 Commensurate with these long-term surveys, we also monitored the monthly settlement  
6 of pueruli into five crevice collectors (Booth and Tarring 1986, Phillips and Booth 1994)  
7 deployed under the wharf on the bottom in front of the rock wall. These data allowed us to  
8 compare the correlation between the number of postlarvae settling in collectors and the  
9 subsequent spatial distribution of settled pueruli and EBJ (using Morisita's Standardized Index,  
10 described above) in holes on the rock face.

11 Our short-term data set covered the period from March - December 1995 (10 mos.). In  
12 these surveys, the position of each puerulus or EBJ on ten of the rock faces was recorded in more  
13 detail. To do this, we established a permanent reference rope line near the top of the ten rock  
14 faces and then used a 0.5 m x 0.5 m (0.25 m<sup>2</sup>) PVC quadrat, divided by string into 10 cm x 10  
15 cm subplots, to record the number of lobsters that divers observed in each 0.01 m<sup>2</sup> portion of the  
16 rock faces. We surveyed the top meter of each rock face in this manner. To document daily  
17 patterns of lobster residency within holes on a rock face, we marked the position of each  
18 puerulus or EBJ with individually numbered nail tags driven into the rock near the occupied  
19 hole. We also tagged a subsample of the lobsters we found with color-coded wire antennae tags,  
20 or by clipping the tips of their antennae. We did so without removing the lobsters from their  
21 holes to minimize disturbance to the lobsters. We then resurveyed these ten rock faces for the  
22 next 2 - 3 days and noted any changes in the occupancy of holes by lobsters. The results of these

1 surveys (see Results) confirm that our procedures did not disturb lobsters enough to drive them  
2 from their shelters, and hence alter their distribution.

3         The design of our short-term surveys permitted us to examine the distribution of pueruli  
4 and EBJ dwelling in holes at several spatial scales. Since our 0.25 m<sup>2</sup> sampling quadrats were  
5 laid end to end across the ten rock faces and were subdivided into twenty five 0.01 m<sup>2</sup>  
6 subquadrats, they essentially constitute a series of ten 0.01 m wide belt transects (or string of  
7 adjacent quadrats) stretching across the rock faces. We used these data from the first day of each  
8 monthly sampling and Hill's Two Term Local Quadrat Variance Method (TTLQV; Hill 1973) to  
9 examine the pattern of dispersion across several spatial scales. The TTLQV method yields  
10 estimates of variance using increasingly larger quadrats along a transect, in our case, for  
11 quadrats, from 0.01 m<sup>2</sup> to 1 m<sup>2</sup>. Variances are typically plotted against quadrat size and  
12 pronounced peaks in the variance indicate clumping at the corresponding quadrat size. Thus,  
13 differences in spatial dispersion can be evaluated simultaneously at several scales, which is not  
14 possible when random quadrats are used.

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#### 16 Laboratory Tests of Aggregation Cues

17         *Experimental Trials:* We used a set of laboratory experiments to address two related  
18 questions: (1) does aggregative behavior vary among ontogenetic stages (e.g., EBJ, juvenile,  
19 adolescent) and (2) if aggregation occurs, do chemical cues - as opposed to visual or auditory  
20 cues - play a role in the processes? To answer these questions, individual lobsters of one of the  
21 three ontogenetic groups were permitted to choose among three alternative shelters: (i) a shelter  
22 with no specific lobster cues (shelter treatment), (ii) a shelter supplied with water from a head  
23 tank containing similar sized conspecifics (shelter + chemical cue treatment), or (iii) a shelter

1 containing two lobsters of a similar size as the test lobster, but isolated from the rest of the  
2 experimental arena by a transparent plastic barrier (shelter + decoys treatment). To control for  
3 treatment artifacts, every shelter was physically identical and each received water flow from a  
4 separate head tank. The “shelter” and “shelter + decoys” treatments received sea water without  
5 conspecific cues. Forty-eight replicates were run on postpueruli and 24 replicates each on  
6 juvenile and subadult lobsters. All lobsters were used only once in the study.

7         Our experiments were carried out from April - June 1995 in a large wet laboratory at the  
8 National Institute for Water and Atmospheric Research in Wellington, New Zealand . Water  
9 temperature during this period ranged from 12 ° - 15° C and the photoperiod in the laboratory  
10 was set at 12 L: 12 D. The experiments were conducted in four round plastic experimental tanks  
11 or “arenas” (1.6 m diameter x 0.5 m tall) fitted with separate flow-through seawater systems  
12 (Fig. 2). Each arena received filtered seawater through water lines connected to three separate  
13 head tanks (20 cm x 33 cm x 55 cm), which in turn received seawater from the main laboratory  
14 flow-through system. Three water lines entered each experimental arena and were attached to  
15 one of three separate lobster shelters (Fig. 2). The water flow into each shelter was 0.2 l/min.,  
16 for a combined flow rate of 0.6 liter/min. into each arena. In one head tank we held captive  
17 lobsters of a certain size to serve as the source of our chemical cue treatment. For trials with  
18 EBJ, juveniles, and subadults, we placed 12, 6, and 3 (respectively) similar-sized individuals into  
19 the head tank that dispensed the chemical effluent. We placed more juveniles than subadults in  
20 the head tanks to keep the biomass in the head tanks similar among treatments. We used as  
21 many EBJ in the head tanks as was logistically feasible, but this was far fewer than what would  
22 be necessary to equal the lobster biomass in the juvenile and subadult treatments. However,  
23 preliminary trials (see *Testing of Artifacts*) revealed that our experiments with EBJ would be

1 unaffected by this difference, since EBJ are unresponsive to water conditioned by other lobsters,  
2 regardless of the biomass used to create the chemical signal.

3 Three shelters, separated by about 120 cm, were positioned uniformly along the edge of  
4 each experimental arena. The size of the shelter we used in each experiment differed depending  
5 on the size of the lobsters we were testing. Two bricks (235 mm x 74mm x 94 mm) each with  
6 ten holes (22 mm dia.), and stacked one upon the other, served as shelter suitable for occupation  
7 by EBJ. Two stacked concrete partition blocks (392 mm x 192 mm x 141 mm) with oblong  
8 holes (80 mm high x 130 mm wide) served as a shelter in tests with the two larger lobster size  
9 classes (juveniles and adolescents).

10 In all experiments, regardless of the shelter type, a large transparent plastic bag (0.1 mm  
11 thick) filled with seawater and open to the atmosphere at the top, enclosed the top shelter block,.  
12 When an individual shelter was to receive lobsters to serve as “decoys” in the experiment, the  
13 lobsters were placed in these plastic bags. These live lobster decoys could enter and exit holes in  
14 the top shelter block or brick. They therefore presented a visual and, perhaps, auditory cue for  
15 experimental lobsters, but they were physically isolated and could transmit no chemical cue  
16 outside the bag. A plastic bag enveloped the top of each shelter in all the arenas, to control for  
17 any potential bias created by the presence of the plastic bag. The bags were periodically checked  
18 for leaks, but none occurred.

19 *Testing for Artifacts:* To test for possible artifacts caused by differences in the biomass  
20 or size of lobsters used in the head tanks to supply the chemical effluent in our formal tests, we  
21 ran three more experiments. In the first set of tests (“Biomass Effect” trial), the biomass of the  
22 EBJ in the head tank creating the chemical signal for the EBJ trials was increased by an order of  
23 magnitude (from ca. 15 g in the formal trials to ca. 125 g) in 20 replicate runs. If EBJ responded

1 differently in this test than in the formal trial, then biomass probably plays a role in the detection  
2 of chemical cues by small lobsters and may confound our results.

3 For the second bias test (“Subadult Cue” trial), six subadult lobsters (40 - 70 mm CL; ca.  
4 450 g) were placed in the head tank that dispensed the chemical cue and tested with EBJ as the  
5 focal animals; 35 replicates were completed. If EBJ responded differently in this test compared  
6 with the formal tests or the Biomass Effect test, then we would suspect that later ontogenetic  
7 stages produce a chemical signal that earlier stages can detect but do not themselves produce.

8 The third bias test (“EBJ Cue” trial) is essentially the reverse of the Subadult Cue trial.  
9 In this case, 125 g of EBJ were placed in the head tanks to provide a chemical cue and subadult  
10 lobsters were tested in the experiment. We ran 25 replicates of this experiment. If subadults  
11 respond to EBJ cues as well as others, then aggregation results from a response to some chemical  
12 signal common to all lobster stages, not just those produced by large lobsters. Alternatively, if  
13 subadults do not respond to the EBJ signal but do respond to cues from larger lobsters, then their  
14 response is specific to cues released by similar-sized conspecifics.

15 These laboratory data were analyzed using log-linear goodness of fit tests (G statistic)  
16 run separately for each lobster size class, since the shelter size and source of the chemical cues  
17 tested differed slightly among the experiments for each size class. Whether we were analyzing  
18 data for EBJ, juveniles, or adolescents the critical test was whether the frequency of shelter  
19 occupancy differed significantly among the shelter only, shelter + chemical cue, or shelter +  
20 decoys treatments.

21

22 Field Tests of Aggregation and Den Type Effects on Mortality

1           The chief objective of this field experiment was to evaluate whether aggregation in or  
2 occupancy of specific dens affects the relative rate of mortality of juvenile lobsters of different  
3 sizes. We tethered individual lobsters belonging to one of three ontogenetic stages in natural  
4 habitats under one of three experimental conditions: (1) single lobster tethered in an unoccupied  
5 natural shelter that had been recently occupied (i.e., a known lobster den; “Single-Unoccupied”  
6 treatment), (2) three lobsters of similar size tethered together in a natural crevice that was not  
7 known to have been occupied by lobsters (“Triple-Unoccupied” treatment), and (3) a single  
8 lobster tethered in an occupied natural shelter together with a group (3 – 6) of similar sized  
9 naturally aggregated lobsters (“Single-Occupied” treatment).

10           If aggregation reduces mortality, then we expected that more of the focal lobsters would  
11 be killed in the Single-Unoccupied treatment than in the Triple-Unoccupied treatment. If  
12 specific crevices are chosen by lobsters as dens because they afford better shelter from predators,  
13 then we predicted that mortality would be lower in the Single-Occupied treatment (where a  
14 single lobster is tethered in an existing den amidst other aggregated lobsters) as compared with  
15 the Triple-Unoccupied treatment.

16           *Experimental Trials:* Our experiments were conducted at two distant locations on the  
17 North Island of New Zealand: the first at Inner Table Top Reef in the Cape Rodney-to-Okakari  
18 Point Marine Reserve near Leigh, about 90 km north of Auckland (April - May 1995) and the  
19 second 560 km further south at Point Gordon on the Miramar Peninsula in Wellington Harbor  
20 (May 1995 - February 1996). Early benthic-stage juvenile lobsters were tethered at both the  
21 Leigh and Wellington sites; juvenile and adolescent lobsters were tethered only at the  
22 Wellington site. There was no significant difference in the mortality rate of EBJ within

1 treatments among sites ( $\chi^2 = 0.61$ ,  $df = 1$ ,  $P = 0.44$ ), so we do not distinguish results among sites  
2 in our final analyses.

3 Early benthic-stage juveniles were collected from crevice collectors, held in the  
4 laboratory for 1 month or less, and then tethered to bricks with a 25 cm long strand of 1.8 kg (4  
5 lb) test monofilament. Early benthic stage juveniles typically dwell in small holes and so they  
6 were tethered to bricks so that they could withdraw into one of ten 1 cm x 10 cm deep holes in  
7 each brick. They were fastened to the monofilament by forming a loop in the line, which was  
8 tightened around the cephalothorax between the third and fourth pairs of legs, and also glued  
9 (cyanoacrylate gel glue) to the dorsal surface of the cephalothorax. The other end of the line  
10 was tied through a hole in the brick. Early benthic-stage juveniles assigned to the two solitary  
11 lobster treatments were tied to one of the center holes in the bricks, two additional EBJ were tied  
12 to two of the outer holes in the bricks to create the triple lobster treatment.

13 Juvenile and adolescent lobsters were collected by divers and generally held in the  
14 laboratory for < 1 mo, although one group was held in captivity for nearly a year. Mortality rates  
15 for these two groups were nearly identical (22% versus 30% after 48 hrs), so we did not  
16 differentiate among them in our final analysis. These larger lobsters were also tethered singly or  
17 in groups of three to bricks, but unlike the EBJ, the juveniles and adolescents could not withdraw  
18 inside the brick holes. The brick simply anchored the lobsters in place in the desired natural  
19 crevice. We also used heavier 5.4 kg (12 lb) test and longer (50 cm) monofilament tethers for  
20 juvenile and adolescent lobsters.

21 Tethered lobsters were held for a few hours or overnight in the laboratory to check for  
22 initial mortality or escapes and then outplanted at 5 - 10 m depth into natural crevices on rocky  
23 reefs. We mapped the position of each tether location so that we could easily relocate them.

1 Small lobsters are generally killed faster than large lobsters, so the duration of each tethering  
2 trial varied with lobster size to ensure a measurable response. We revisited each EBJ tethering  
3 location after 12 and 24 hrs, each juvenile lobster tethering location after 24 and 48 hrs, and each  
4 adolescent tethering location after 48 and 96 hrs and recorded the condition of each tethered  
5 lobster.

6 We used log-linear model analysis (G-statistic with William's correction factor) to  
7 determine whether mortality (presence or absence of a tethered individual) differed significantly  
8 among the three treatment conditions. The tethering experiments conducted on the three  
9 different ontogenetic stages of lobsters differed in duration and in the way that the brick was  
10 used; either as a shelter (EBJ) or simply as a tethering post (juveniles and subadults). Because of  
11 the inherent differences in these experimental procedures, these data sets were analyzed  
12 separately for each ontogenetic stage of lobsters. The key statistical comparisons are among  
13 treatments (single-unoccupied, single-occupied, triple-unoccupied) within an ontogenetic  
14 grouping. When we analyzed the data we included only data for one observation period per size  
15 class: 24 hrs for postpueruli, 24 hrs for juveniles, and 96 hrs for subadults. These time periods  
16 were chosen because they best satisfied the cell size assumptions of the log-linear tests, and thus  
17 maximized the validity of the statistical results. Furthermore, when lobsters are tethered together  
18 in groups, the results for more than one individual can be recorded, but data from only one  
19 individual should be analyzed to preserve independence among replicates. We chose *a priori* to  
20 use only the data from the lobsters tethered in the center of each group in our analyses.

21 *Testing for Artifacts:* We also conducted two experiments to test for possible bias in our  
22 tethering results (Peterson and Black 1994). Most of the lobsters we used in these experiments  
23 were collected in the field and tethered within a few days, but some of the subadult lobsters had

1 been held in the laboratory for a few months before being tethered. Therefore, our first test of  
2 possible tethering bias was to determine whether holding lobsters in the laboratory for a few  
3 months affected their relative rate of survival. Subadult lobsters held in the laboratory for at  
4 least a month were tethered in dens with other naturally occurring lobsters. The results of these  
5 tethering trials were compared with results for lobsters that were tethered immediately after  
6 capture in the field; both sets of lobsters were exposed to the same treatment condition (i.e.,  
7 Single - Occupied” treatment). The results for these two groups were nearly identical: 70% of  
8 the laboratory-held lobsters and 78% of the field-caught lobsters survived tethering for 96 hrs.

9       The second test of bias was designed to determine if escapes from the tethers varied  
10 among sizes or differed when lobsters were tethered alone or in groups of three. We observed  
11 lobsters tethered alone and in groups of three and recorded the frequency of escape of EBJ and  
12 subadult lobsters in the laboratory for 24 and 96 hrs (respectively) to document escape rates from  
13 tethers. None of the EBJ escaped. The escape rates for subadults that were triple-tethered,  
14 however, was unexpectedly high at nearly 25% versus < 5% for single-tethered subadult  
15 lobsters. Fortunately, this bias does not alter interpretation of our main results because in the  
16 field, we had the highest survival or retention (see Results) of lobsters in the treatment where  
17 lobsters were tethered in triplicate, thus our data are conservatively biased.

18

19

## **Results**

### Ontogenetic Changes in the Spatial Distribution of Natural Populations

20  
21       *Large-scale Observations of Lobster Distributions:* Our surveys of lobster aggregation  
22 patterns in 25 m<sup>2</sup> quadrats at four locales scattered along the east coast of New Zealand revealed  
23 a distinctive difference in the pattern of aggregation between EBJ and both juvenile and subadult

1 lobsters (Fig. 3). Early benthic stage juvenile lobsters were most often found alone or in small  
2 groups of < 4 individuals. In contrast, juveniles and subadults were often found in groups and  
3 most often in large groups exceeding 10 individuals (Fig. 3).

4 *Lobster Distribution and Settlement at Gisborne Harbor:* Up to 13 *J. edwardsii* EBJ were  
5 found dwelling in holes on a single 6 m<sup>2</sup> rock face (a density of 2.2 m<sup>2</sup> ) along the rock wall in  
6 Gisborne Harbor, but their average density over the 29 month period was only 0.17 m<sup>2</sup>, or about  
7 1 EBJ per rock face. During the 29 month period, we observed 595 pueruli and EBJ, and during  
8 the last 10 months of that time we tagged a subsample of 42 EBJ and noted the subsequent  
9 positions of tagged individuals on the rock wall for two days after tagging. Most (77%) of the  
10 tagged EBJ were observed again during the next two days and most of those (77 - 81%) had not  
11 moved from their original den. The few EBJ that had moved were found close by, typically less  
12 than 20 cm away (mean = 13 cm), although one individual moved to a new den 2 m away  
13 overnight.

14 Our long term (29 month) surveys describing the spatial distribution of EBJ *J. edwardsii*  
15 indicate that the lobsters were distributed randomly within holes on a rock wall in Gisborne  
16 Harbor. The distribution of EBJ yielded a Standardized Morisita's index between - 0.5 and 0.5  
17 on 21 of 29 monthly surveys (Fig. 4), indicating that the distribution of EBJ was usually random.  
18 On the eight occasions when the index exceeded 0.5, the values clustered very near this  
19 minimum significance value. A chi-square test (with Yates correction) of this distribution of  
20 significant and non-significant index values ( $\chi^2 = 2.15$ ,  $df = 1$ ,  $P = 0.1428$ ,  $1-\beta = 0.29$ ) showed  
21 that eight occurrences of a significant index value in 29 instances is not significantly different  
22 from random expectations.

1 A weak positive correlation ( $r = 0.41$ ;  $df = 29$ ;  $P = 0.03$ ) existed between monthly postlarval  
2 settlement density on artificial collectors and the Standardized Morisita's index describing  
3 clumping of EBJ on the rock wall (Fig. 4). This indicates that EBJ become more aggregated at  
4 the scale of a rock face ( $6 \text{ m}^2$ ) when settlement is highest, but as noted above, the EBJ were  
5 never highly aggregated even when their densities were at their maximum.

6 Using the more detailed surveys conducted during the last 10 months of the study and Hill's  
7 TTLQV method, we again found no evidence that *J. edwardsii* EBJ aggregate at scales ranging  
8 from  $2 \text{ m}^2$  to  $20 \text{ m}^2$  (Fig. 5). Interpretation of peaks in the variance plots produced using Hill's  
9 method are admittedly subjective. But evidence for clumping is usually limited to sharp peaks  
10 quite distinct from the mean variance (Ludwig and Reynolds 1988). The variance peaks in the  
11 TTLQV plot we produced were low and poorly defined across the spatial scales we examined,  
12 thus indicating a random distribution. We tried to investigate aggregation at even smaller spatial  
13 scales, down to  $0.2 \text{ m}^2$ , but EBJ occurred so infrequently at scales  $< 2 \text{ m}^2$ , that the analysis could  
14 not be run.

#### 15 Laboratory Tests of Aggregation Cues

16 In our laboratory tests of aggregation cues, we discovered that subadults aggregate using  
17 chemical cues released by similar-sized individuals, whereas lobsters at earlier ontogenetic  
18 stages do not. *Jasus edwardsii* EBJ and juveniles responded similarly to our three experimental  
19 treatments (Fig. 6). Early benthic stage juveniles ( $n = 48$ ;  $G = 1.87$ ;  $df = 2$ ;  $P = 0.39$ ) and  
20 juveniles ( $n = 24$ ;  $G = 2.10$ ;  $df = 2$ ;  $P = 0.35$ ) did not seek shelters with live decoys or respond to  
21 potential chemical cues from similar-sized conspecifics. In contrast, subadult *J. edwardsii* were  
22 attracted to shelters supplied with water conditioned by either similar-sized conspecifics ( $G =$   
23  $13.16$ ;  $df = 2$ ;  $P = 0.001$ ; Fig. 6) or EBJ ( $G = 14.48$ ,  $df = 2$ ,  $P = .001$ ).

1           The lack of a response by EBJ to the chemical effluent treatment is not due to a low  
2 biomass of EBJ in the head tank dispensing the effluent. When we boosted the biomass of  
3 pueruli in the head tank by an order of magnitude to approximate the biomass in the juvenile and  
4 subadult trials, the result was unchanged. Early benthic stage juveniles still chose shelters  
5 without regard to the experimental treatment ( $n = 35$ ;  $G = 0.20$ ;  $df = 2$ ;  $P = 0.90$ ). Similarly,  
6 EBJ did not respond to the same chemical cues to which the subadult lobsters reacted so  
7 strongly. Early benthic stage juveniles were just as apt to dwell in control shelters, shelters with  
8 decoys, and in shelters where dispensed water was from head tanks holding subadult lobsters ( $n$   
9  $= 19$ ;  $G = 0.33$ ;  $df = 2$ ;  $P = 0.85$ ).

#### 11 Field Tests of Aggregation and Den Type Effects on Mortality

12           The relative mortality of tethered *J. edwardsii* varied with individual size and tethering  
13 treatment, and aggregation among the adolescent tethered lobsters improved the focal  
14 individual's chance of survival. Solitary EBJ survived just as well (26% alive after 24 hrs) as  
15 those that were aggregated (24% alive after 24 hrs; Fig. 7). However, EBJ tethered singly in a  
16 crevice already occupied by larger lobsters survived better (52% alive after 24 hrs) than EBJ  
17 tethered alone or in groups of three in an unoccupied crevice ( $G = 6.025$ ,  $P = 0.05$ ,  $df = 2$ ; Fig.  
18 5). Juvenile lobsters survived equally well in all three treatments ( $G = 3.40$ ;  $P = 0.18$ ;  $df = 2$ ;  
19 Fig. 7). Only subadult lobsters gained an appreciable survival advantage when they were  
20 aggregated ( $G = 7.18$ ;  $P = 0.03$ ;  $df = 2$ ; Fig. 7). The survival of subadult lobsters more than  
21 doubled when they were tethered with other subadults, whether they were in an occupied den  
22 with naturally occurring lobsters or in an unoccupied den with tethered lobsters.

## 23 **Discussion**

1  
2 *Ontogenetic Patterns of Aggregation*  
3

4           Changing habitat requirement and associated changes in the local ecological conditions  
5 experienced by a species' different developmental stages may select for ontogenetic changes in  
6 aggregation, sometimes creating situations where juveniles are solitary and adults are  
7 aggregated. For example, the small-scale spatial distributions of planktonic larvae are often an  
8 unpredictable consequence of physical dynamics in the water column. Following the planktonic  
9 period, specific settlement requirements and the distribution of suitable habitat patches results in  
10 aggregations of settlers. Some invertebrates even settle aggregatively in response to the  
11 chemical cues of kin (Keough 1984, Connel 1985). Thereafter, differences in postsettlement  
12 growth and survival among settlement sites can further concentrate older individuals into  
13 discrete clumps. On rocky shores, for example, crevices shield animals from the crush of waves,  
14 resulting in aggregations of bivalves, gastropods, and barnacles. Patches are created on a  
15 smaller scale where ever small holes or depressions on rocky substrates offer species such as  
16 bryozoans, barnacles, or crabs refugia from fish predators (Keough and Downes 1984, Eggleston  
17 and Armstrong 1995, Butler and Herrnkind 1997). Yet, this type of aggregation, dictated by the  
18 distribution of habitat and so common among marine benthic invertebrates, is not a consequence  
19 of ontogenetic changes in social behavior like that observed in spiny lobsters.

20           The early life history of shallow-water spiny lobster has now been sufficiently well  
21 studied that a consistent ontogenetic pattern in social behavior is emerging. Spiny lobster  
22 postlarvae appear to settle randomly within suitable natural habitats and they are often sparsely  
23 distributed (Herrnkind and Butler 1994, Field and Butler 1994), as are the early benthic stage  
24 juveniles that dwell solitarily in crevices or vegetation (e.g., *P. argus*: Marx and Herrnkind 1985,  
25 Herrnkind and Butler 1986, 1994, Butler et al. 1997; *P. cygnus*: Jernakoff 1990; *P. japonicus*:

1 Yoshimura and Yamakawa 1988, Norman et al. 1994; *P. interruptus*: Serfling and Ford 1975;  
2 and others). As they grow larger, the juveniles become increasingly social and aggregate in  
3 dens. In Caribbean spiny lobsters, the size at which juveniles change behavior corresponds with  
4 a shift in habitat use and depends on whether larger conspecifics are nearby (Childress and  
5 Herrnkind 1996). The gregarious subadults and adults of most species reside in different  
6 habitats than EBJ (e.g., *P. argus*, *P. cygnus*), or in larger den structures within the same habitat  
7 (e.g., *J. edwardsii*). The adults and subadults of a few species are known to be attracted by  
8 chemical cues released by conspecifics (*P. interruptus*: Zimmer-Faust et al. 1985, Zimmer-Faust  
9 and Spanier 1987 ; *P. argus*: Childress and Herrnkind 1996).

10 This study indicates that aggregation occurs primarily among larger lobsters because the  
11 response to chemicals released by conspecifics does not develop until adolescence. We found  
12 that EBJ and juveniles do not respond to chemical effluents produced by larger, subadult  
13 lobsters. In contrast, subadults exhibit a striking aggregative response to chemical cues  
14 produced by other lobsters. We also provide new evidence that the resultant aggregation of  
15 adolescent lobsters confers on participants an ecological advantage - better protection from  
16 predators - that is not available to smaller, earlier life stages. Aggregation is beneficial for  
17 subadult and adult lobsters (Eggleston and Lipcius 1992 and this study), but small juvenile  
18 lobsters, even groups of them, are ineffective in defending themselves against predators. Their  
19 best defense is to reduce encounter rates with potential predators and they do so by limiting their  
20 movement and being cryptic (Butler et al. 1997).

21 Our tethering results also suggest that EBJ *J. edwardsii* may survive better if they were to  
22 dwell in dens with groups of large conspecifics, who presumably fend off potential predators.  
23 However, this result may be more of an experimental curiosity than an ecologically significant

1 finding. In nature, the various spiny lobster life stages often live in different habitats or seek  
2 different sized dens, so cohabitation by various ontogenetic stages is often not a possibility.

3

4

### 5 *Ecological Processes Promoting Aggregation*

6 Our tethering results do not support the hypothesis that lobster aggregations occur in  
7 specific dens that offer extraordinary protection from predators. The key test of this hypothesis  
8 is a comparison of the results where single lobsters were tethered in existing dens alongside  
9 several resident lobsters (Single-Occupied treatment) versus the situation where three lobsters  
10 were tethered together in a crevice that was previously unoccupied (Triple-Unoccupied  
11 treatment). The results did not differ significantly between these two treatments for any of the  
12 lobster size classes we tested. Therefore, differential survival among potential den sites does not  
13 explain the observed patchy distribution of lobsters. This result still begs the question of why  
14 certain dens are occupied more often than others (Herrnkind et al. 1975, MacDiarmid 1994). A  
15 den's proximity to food, migration routes, or sources of settlers are plausible explanations for  
16 unusually high residency in some dens.

17 The residual "scent" of lobsters that recently occupied the den would also be an attractant  
18 to other lobsters and offers another explanation for the more persistent use of some dens. In  
19 some regions, such as the Hawaiian islands (Parrish and Polovina 1994) and the Florida Keys  
20 (Butler and Herrnkind 1997, Herrnkind et al. 1997), suitable dens for large lobsters are scarce.  
21 Under those circumstances, there may be competition for limited dens, or there could be  
22 cooperative use of them (Eggleston et al. 1990, Sharp et al. 1998) if the dens are large enough to  
23 permit multiple occupants. It has been suggested that the evolution of social aggregation of *P.*

1 *argus* and their use of chemical cues for locating conspecifics may have developed as a means to  
2 locate suitably-sized crevices where crevices are sparse and patchily distributed (Childress and  
3 Herrnkind 1996). *Panulirus argus* makes nightly forays far from their dens to feed in adjacent  
4 seagrass and rubble habitats, so chemical cues emanating from den sites occupied by  
5 conspecifics may serve as a beacon that guides individuals to a den more quickly, thus reducing  
6 unnecessary exposure to predators.

7         But the conditions typically experienced by *J. edwardsii* may be different. Potential den  
8 sites appear to be much more abundant among the rocky reefs skirting the New Zealand  
9 shoreline. Juvenile *J. edwardsii* also do not engage in the same nightly long-distance foraging  
10 migrations across open habitat as the tropical *P. argus*. Instead, *J. edwardsii* eat the abundant  
11 prey concentrated on the high-biomass temperate reefs surrounding their dens. These  
12 observations, and our experimental results, suggest that the response of juvenile *J. edwardsii* to  
13 the chemical signals of conspecifics may have evolved as a behavior to concentrate individuals  
14 in defensive pods, rather than as a means to locate shelter from afar, as is the case for the  
15 Caribbean spiny lobster. This may be a particularly effective strategy for *J. edwardsii*, which is  
16 morphologically more robust and more aggressive than its Caribbean counterpart.

17         Both of these hypotheses concerning the evolution of social communication in spiny  
18 lobsters and its adaptive significance have theoretical support, although the development of  
19 chemical signals for the purpose of group defense may offer a more rapid evolutionary  
20 trajectory. Theoretical studies of social selection and the evolution of animal signals indicate  
21 that behavioral responsiveness to conspecific signals is subject to runaway selection (Tanaka  
22 1996). These theories are typically tendered as explanations for interspecific aggressive  
23 interactions, but the necessary conditions are applicable to the chemical signaling and social

1 aggregation scenario that occurs in spiny lobsters. Theory suggests that the evolution of social  
2 behavior converges most rapidly on a single genetic equilibrium when receivers benefit from the  
3 signal and when the signal provides reliable information about the signaler (Tanaka 1996). In  
4 the case of *J. edwardsii*, both the individuals that release the chemical cue (signalers) and those  
5 that are attracted to it (receivers) benefit from the social aggregation that the signal promotes,  
6 because mortality is lower when lobsters form groups.

7         Changes in the propensity of spiny lobsters to aggregate as they age is but one of many  
8 ontogenetic shifts that occur as these animals grow from the EBJ stage to adulthood. Their  
9 choice of shelters and even habitats change as they grow. Their coloration changes, usually  
10 rendering them more cryptic in their new habitat (Butler et al. 1997). Their activity patterns and  
11 rates of movement also change as they age (Childress and Herrnkind 1994), and their diet is  
12 altered, perhaps reflecting the lobster's change in habitat use and morphology (Herrnkind et al.  
13 1988, Wolfe and Felgenhauer 1991). For species with complex life cycles, this suite of dramatic,  
14 interrelated ontogenetic changes reflects what must be a profound shift in the character of the  
15 environment and selective pressures that affect the success of various developmental stages as  
16 individuals approach maturity.

17

18

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## Figure Legends

**Figure 1:** Location of sites along the coast of New Zealand where lobster surveys and tethering experiments were conducted.

**Figure 2:** Diagram of the laboratory set-up designed to test for an aggregative response by a single lobster in one of three ontogenetic stages (EBJ, juveniles, subadults) released into an experimental tank with three shelters offering either: (1) shelter (Shelter treatment), 2) shelter plus the chemical scent of conspecifics (Shelter + Chemical Cue treatment) or 3) shelter plus the visual or auditory cues produced by conspecific decoys enclosed in a plastic bag (Shelter + Decoy treatment). Four of these experimental arenas were constructed and ran simultaneously.

**Figure 3:** Three frequency distributions describing the percentage of lobsters of three ontogenetic stages that were observed in different group sizes within 800 25 m<sup>2</sup> quadrats sampled at four locations along the New Zealand east coast.

**Figure 4:** The relationship between the mean monthly settlement of postlarvae and EBJ on collectors in Gisborne Harbor (x axis) and the degree of clumping (Morisita's Standardized Index; y axis) by newly settled pueruli and EBJ during 29 monthly surveys. Months when Morisita's Standardized Index exceeded  $\pm 0.5$  (indicated by hatched lines in the graph) indicate that the distribution of settlers was significantly different from random. The results of a correlation analysis testing whether settlement magnitude was significantly correlated with settler distribution are also shown.

**Figure 5:** The results of short-term surveys examining the spatial distribution of postlarvae and EBJ dwelling in holes on a rock face in Gisborne Harbor. On the y-axis, is a variance estimate determined using Hill's Two Term Local Quadrat Variance Method, which permits examination of the pattern of dispersion of settlers across spatial scales ranging from 2 m<sup>2</sup> to 20 m<sup>2</sup> (x-axis). Pronounced peaks in the values, which would indicate clumping of settlers at the corresponding quadrat size, are not present indicating a random distribution of lobsters. The Index of Dispersion (I) and Green's Index of Dispersion were also calculated for each sample month and the ranges of those values over the 10 month period are also shown.

**Figure 6:** Results of the laboratory study that show the percentage of lobsters in each of three ontogenetic stages that chose one of three possible shelter treatments: 1) shelter alone (Shelter treatment), 2) shelter with lobster decoys, but no chemical cues (Shelter + Decoy treatment), or 3) shelter supplied with the chemical scent of conspecifics (Shelter + Chemical Cue treatment).

**Figure 7:** The relative survival (percent survival ) of individual lobsters in one of three ontogenetic stages tethered in the field in one of three treatment conditions: 1) a single individual tethered alone in an unoccupied crevice (Single-Unoccupied treatment), 2) a single individual tethered in a crevice already occupied by other lobsters (Single-Occupied treatment), and 3) three individuals tethered together in an unoccupied crevice (Triple-Unoccupied). The results of the log-linear tests are shown in each panel.