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Characterising shelter preferences in captive juvenile *Jasus edwardsii* (Palinuridae)

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Abstract Any attempt to enhance rock lobster production by increasing survival after settlement, or by ongrowing or outplanting young juveniles, requires knowledge of the shelter preferences of young juveniles. For juvenile *Jasus edwardsii* in the wild these are not well known. Information available suggests that juveniles up to c. 35 mm carapace length (CL) occupy shelters that generally conform closely to their body dimensions but that larger juveniles use shelters of more variable dimension, often much larger than their body size. We investigated mainly physical factors important in shelter choice by 15–59 mm CL (c. 2–24-month-old juveniles) in laboratory tank experiments. In overnight tests, all sizes of juvenile lobster chose to occupy holes (shelters with sides) over open horizontal gaps. Preference for open horizontal gaps versus horizontal crevices (where the height reduces from a maximum at the mouth to zero at the opposite end) was much less clear-cut; choice varied according to lobster size. For the number of entrances into holes, there was evidence for an ontogenetic shift in preference, small lobsters preferring two openings over one, whereas those >30 mm CL (c. 9 months old) preferred one over two. For lobsters <40 mm CL, the hole size and gap size preferences revealed were generally consistent with the field evidence for *J. edwardsii* in that there was a close and proportional relationship between lobster size and shelter size; what differed was that the open gaps chosen in the tanks by the smallest lobsters (15–19 mm CL) were larger than the holes used in the tank experiments and 30–50% larger than those reportedly used in the field. For lobsters >40 mm CL, the holes and gaps chosen in the tanks were generally larger and more variable in size, as in the field.

Keywords palinurid; rock lobster; *Jasus edwardsii*; juvenile; habitat preference; enhancement

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INTRODUCTION

The red (spiny) rock lobster *Jasus edwardsii* (Hutton, 1875) (family Palinuridae) is an important commercial and recreational seafood in Australasia, the New Zealand wild stocks of which are fully exploited (Sullivan & O'Brien 2002). Potential means of increasing production include: (1) catching or culturing pueruli or juveniles to later ongrow or outplant; and (2) increasing juvenile survival and abundance in the wild by moderating the impact of any survival bottlenecks in the early benthic life history. Knowing the form of shelter preferred by young juvenile lobsters can facilitate these. The focus of this work was juveniles 15–59 mm carapace length (CL) (c. 2–24 months post-settlement).

Little is known of the ecology of juvenile palinurids (Herrnkind et al. 1994), mainly because their cryptic colour and behaviour mean that they are difficult to locate and study. For shallow-water palinurids, including *J. edwardsii*, most settlement appears to take place inshore, in waters a few metres deep. It is common for the juveniles first to be asocial, and then to become communal at c. 1 year of age (Lipcius & Eggleston 2000). The evidence for *J. edwardsii* is that first instar juveniles are not attracted to conspecifics (Butler et al. 1999; Booth 2001) and, based mainly on tank studies, they remain asocial and mainly solitary until they reach c. 35 cm CL (c. 1 year) (Butler et al. 1999; Frusher et al. 1999). However, the field evidence concerning gregariousness is not unequivocal. In probably the most comprehensive field observation of shelter occupancy by young *J. edwardsii*, Edmunds (1995) found that most small juveniles (<35 mm CL) were solitary, yet MacDiarmid (1994) reported that only 15–16% of juveniles <30 mm CL in the field resided solitarily. Cohabitation with conspecifics is widespread for lobsters >35 mm CL (MacDiarmid 1994; Edmunds 1995).

There is little field information on the characteristics of shelters used by young juveniles of any palinurid, including *J. edwardsii*, compared with that available for late juveniles and adults. Virtually all 15–60 mm CL *J. edwardsii* in both New Zealand and Australia have been found on hard substrates in shelters with low levels of ambient light and into which the lobsters can withdraw (Lewis 1977; Gabites 1990; Booth & Forman 1995; Edmunds 1995; Frusher et al. 1999; NIWA divers). The smaller lobsters have been most commonly reported to occupy holes not much larger than themselves (Lewis 1977; Edmunds 1995; Frusher et al. 1999). For example, pholad (bivalve) holes containing first instar juveniles (mainly 12–15 mm CL) in Port Gisborne, on the south-east coast of the North Island of New Zealand, averaged 17.5 mm diameter (SD 4.38 mm), holes available being 6–26 mm in diameter (Booth & Forman 1995). Broadly consistent with this, catch rates of pueruli and first instar juveniles combined were significantly lower when the crevice openings of the crevice collector (Booth & Tarring 1986) used to monitor levels of *J. edwardsii* settlement in Australasia were smaller (12 mm high) or larger (60 mm high) than the standard 25 mm (Booth & Forman 1995). Edmunds (1995) found that juveniles up to 35 mm CL displayed a strong relationship between shelter size and body size, the lobsters occupying shelters that generally conformed to their body dimensions and the holes used being relatively deep compared with the width or height of the entrance. Typically a 17 mm CL juvenile occupied a hole with an opening c. 25 mm high, a 25 mm CL juvenile a hole c. 45 mm high, and a 35 mm CL lobster a 55 mm high hole.

For juveniles larger than 35 mm CL, Edmunds (1995) found that the dimensions of the shelters occupied were more variable, the lobsters often being present in shelters much larger than their body size, and usually with more than one opening to the rear or sides. The shelters were often quite expansive, such as open ledges and boulder junctions. Edmunds (1995) found that 40 mm CL juveniles used shelters averaging c. 70 mm in height; 50 mm CL juveniles used 100 mm high shelters; and 60 mm CL juveniles used 130 mm high shelters. Gabites (1990) also found that larger juveniles occupied a wide range of shelter sizes, the lobsters most often dwelling in wide, horizontal shelters with a roof. Although most shelters had only one opening, fewer lobsters than expected were found in those shelters than in ones with two or more openings. Consistent with these observations, NIWA divers report juveniles frequently occupying crevices such as those that exist among small boulders and between stones and the sea floor, and also flat, more or less horizontal spaces, such as those that occur beneath large flat boulders that are not sitting flush with the sea floor.

In all such field observations it is not possible to separate choice of shelter from occupancy patterns that result from other factors, including predation pressure—something which is possible in laboratory experiments. In tank studies, first instar *J. edwardsii* juveniles preferred conditioned refuges over those unconditioned, horizontal apertures over vertical ones, and rough surfaces over smooth (Booth 2001). The preferred number of openings (entrances) for first instar juveniles was unclear, although field experiments using pipes open at both ends or one end suggested that there was either no preference or possibly preference for one opening (A. Jeffs & S. Hooker, NIWA pers. comm.). There have been no similar tank studies of shelter choice for larger juvenile *J. edwardsii*.

These observations of shelter choice/occupancy for *J. edwardsii* seem to be generally consistent with those available for other palinurids. Species being solitary and occupying body-scaled shelter as newly settled juveniles and becoming gregarious and occupying much larger holes when reaching c. 1 year of age include *Panulirus argus* (Marx & Herrnkind 1985), *P. japonicus* (Chen et al. 1987; Yoshimura & Yamakawa 1988; Norman et al. 1994; Yoshimura et al. 1994), *P. cygnus* (Jernakoff 1990), and *P. ornatus* (Dennis et al. 1997).

In this study we investigated mainly the physical features of the shelters chosen and occupied by *J. edwardsii* juvenile lobsters up to c. 60 mm CL in tank experiments. The features of the basic experimental units, concrete blocks, were purposely constrained by the commercial product readily available—these are more likely to be used in any attempt to improve lobster survival in field enhancement initiatives and in ongrowing facilities than custom-made structures. We were particularly interested in changes, including any ontogenetic, in shelter choice regarding hole size and shape, and in the number of openings (entrances).

METHODS

Source and size of experimental animals

Lobsters were collected within or near Port Gisborne, New Zealand (38°41′S, 178°02′E) and the experiments conducted in sea-water tanks set up in a live lobster holding plant in Gisborne. Lobsters were grouped into the following size categories (or composites thereof) for study: 15–19, 20–29, 30–39, 40–49, and 50–59 mm CL juveniles. The very small juveniles (15–24 mm CL, c. 2–6 months old) were taken mainly on crevice collectors. Larger juveniles (c. 6–24 months old and 25–59 mm CL) were caught by hand by divers. (*J. edwardsii* is rarely taken smaller than 70 mm CL in traps—see Gardner et al. 2001.) The lobsters were held for up to 8 days (but usually less than 5 days) without feeding as they were used in the experiments—which were conducted about monthly over the course of more than 1 year—and then returned into the wild near to where they had been captured. Because lobsters had to be obtained afresh each month, there was little control possible over the numbers available for each size group, which were sometimes very variable.

Experimental procedures

Tank experiments in still but aerated sea water were used to determine the occupancy by the juvenile lobsters of particular shelter types. Tanks were stocked to a level approaching the realistic maximum when the lobster and tank sizes were considered. Overall sample numbers for each experiment were increased through replication, but in the analyses of results, replicates were combined. Simultaneous field and tank approaches in shelter testing, where any differences in shelter occupation observed would be at least in part a result of predator pressure, would have been preferable but were not possible. The difficulty in locating sufficient small juveniles in the field, and the logistics and experimental implications of restraining them in the study sites so they could be repeatedly censused, meant that only tank experiments took place. These tank experiments allowed shelter choice to be expressed in a predation- and predator-free environment. Because *J. edwardsii* are active at night and take cover during the day, it was assumed that overnight was a reasonable interval for any choice of refuge to be established. Lobsters were released into the centre of the tank in the early evening and their positions noted, without disturbance, early the next morning. Usually, any individual lobster was used only once for any particular experiment. Although they were held for several days in any one session of experiments, we assumed they retained their instinctual predator-avoiding behaviour and hence all their natural preferences for shelter characteristics.

For most experiments, the tanks used were round, flat-bottomed, just under 1 m in diameter, and filled with sea water to a height of c. 15 cm. However, in tests of open horizontal gap height preferences (see later), particularly for lobsters >40 mm CL, a larger tank was necessary; this was 58 × 115 cm, filled to c. 20 cm with sea water. The facilities and tanks available meant that no more than one pair of options (e.g., one pair of hole sizes) could be tested at any one time in any one tank. The numbers of lobsters in the tank that became associated with a shelter type after being left undisturbed overnight was interpreted to be a measure of how much the lobster was attracted to or preferred that shelter type.

For many of the experiments we used commercial, hollow construction blocks (Firth Industries Ltd, P.O. Box 30 102, Lower Hutt, New Zealand) of two types: 10.01 (39 cm long × 19 cm wide × 9 cm high, with three equally spaced 9.5 cm long × 3.8 cm high holes through the width) and 15.01 (39 × 19 × 14 cm, with two 13.0 × 8.2 cm holes through the width). Concrete blocks such as these are useful because they are rough textured and so readily accumulate biofilm, they are standard in size and form, readily available and inexpensive, they can be built into a myriad of forms, and they are dense, durable, and resilient in sea water. Smaller holes were required for the small lobsters; these were created by inserting lengths of 18 mm (4 pieces), 25 mm (3), or 32 mm (2) internal diameter alcathene pipe into each hole in the 10.01 blocks. No blocks were available with hole sizes intermediate between those of the 10.01 and 15.01 blocks, nor were inserts placed in the 15.01 blocks. In all experiments, the blocks were placed so that the holes were horizontal.

Level of conditioning

The level of conditioning (seasoning) of shelters can strongly influence invertebrate occupancy. Conditioning here means the development of a biofilm layer and, when conditioned for long enough, the growth of larger items, both invertebrate and plant. Levels of conditioning tested by lobster size group ranged from none to 12 months for blocks that contained what was estimated to be about the optimal hole size for that size group of lobster (25 mm diam. inserts for 15–19 mm and 20–29 mm CL lobsters, 10.01 bricks without inserts for larger lobsters), but with any large growth scraped off. Blocks with their alcathene pipes in place were conditioned by being immersed within Port Gisborne, from which the water for the experiments was also drawn. For all size groups tested (15–19, 20–29, 30–49, and 50–59 mm CL), the occupancy preference order was 12 months conditioned = 3.5 months conditioned = 2.5 months conditioned > 1 month conditioned > well soaked > new. The results showed that several months of conditioning was preferred so all shelter choice experiments used materials that had been conditioned in Port Gisborne for at least 3 months.

Shelter choice experiments

Different shelter shapes were compared for each lobster size group: (1) horizontal holes (a more-or-less round space with firm walls in which the depth far exceeds the diameter); (2) horizontal open gaps (a flat space where the firm floor and roof are parallel and there are no sides); and (3) horizontal closed crevices (a flat space with firm floor and roof but no sides and where the height reduces from a maximum at the mouth to zero at the opposite end). We assumed that lobsters up to at least 40 mm CL (a little over 1 year) were asocial and therefore acted independently—that the presence of one lobster in the tank did not influence the search for and occupancy of a refuge by another lobster. Previous work (e.g., Edmunds 1995; Butler et al. 1999) suggested that such an assumption would not necessarily hold for juveniles between 1 and 2 years (c. 40 and 60 mm CL), but many of the experiments used shelters in which only one animal could fit and so to that extent lobsters would have behaved independently. Ideally, so as to account for any lack of independence in shelter choice and for any chemical cue that might have remained within previously occupied shelters, every experiment would have been conducted with a single lobster and previously unoccupied (but nevertheless conditioned) blocks—something not logistically possible. The holes tested were those provided by the blocks, with lengths of alcathene pipe inserted for the smaller lobsters—all well conditioned—as described above. The gaps and crevices were created by using well-conditioned sheets of 5 mm thick cement sheet supported above the tank floor by thin spacers. When occupancy of gaps was compared with that of holes, the cement sheets had about the same surface area as the block (39 × 19 cm). Gap and crevice occupancy was tested using these same sheets for most of the experiments involving small lobsters, but using 40 × 40 cm sheets for others and for the larger lobsters.

When comparing hole size preferences, hole sizes thought appropriate to the size class of the lobster were tested first, and then the range broadened, lobster numbers being kept appropriate to the lobster and tank sizes. (A similar approach was taken when determining open gap size choice.) Also, there were always enough holes of each of the two hole sizes being compared to house all lobsters, and usually there were equal numbers of holes of each of the two sizes. The exception was for small lobsters when the number of the smaller holes exceeded that of the larger ones. Results in which the lobsters mostly occupied the hole size that was more numerous must be treated with caution; conversely, where the hole size chosen was the one least abundant, the result was particularly compelling.

The preference for number of openings (entrances) into horizontal holes was determined for each size group of lobster, with equal numbers of holes with one or two openings being available. For example, three 10.01 bricks were used in a tank, two of which had their holes blocked at one end whereas in the third brick the holes were unblocked.

Statistical analyses

The null hypothesis was that there was no difference in level of association of the lobsters with the different options being tested, so the counts would be the same. For the experiments investigating hole versus crevice and crevice versus open gap preferences, the preferred number of openings, and for the hole size and open gap size experiments where there was the choice of only two refuge sizes, the chi-square test for goodness of fit of the observed numbers of animals to the expected number was used.

For the hole size and open gap size experiments where there were three or more choices tested, the data were analysed using a Bradley-Terry model (Bradley & Terry 1952; Agresti 1990).

$$P(\text{hole } i \text{ preferred to hole } j) = \gamma_i / (\gamma_i + \gamma_j)$$

where γ_i is a positive-valued parameter associated with hole *i*—a measure of the "desirability" of hole *i*. Thus the odds of hole *i* being selected over hole *j* are γ_i/γ_j.

The model was implemented in R version 1.81 (R Development Core Team 2003), which uses an alternative parameterisation:

$$\text{logit}[P(\text{hole } i \text{ preferred to hole } j)] = \lambda_i - \lambda_j$$

where $\lambda_i = \log \gamma_i$ for all *i*, and the parameters λ are estimated by maximum likelihood.

Analyses were carried out separately for each different size group of lobsters for ease of implementation and interpretation. For each size group, the theoretical probability of a particular hole size being selected, given a choice of all possible hole sizes, was obtained by examining each preference parameter against all others:

$P_{select} = \gamma_i / \Sigma_i \gamma_i$ for all hole sizes *i*.

RESULTS

Hole versus open gap

Where occupancy of more-or-less round holes was compared with open gaps, all size groups used the holes more than the gaps (Table 1). In all but one size group, the difference was significant; for 30–39 mm CL juveniles, it was nearly so at $P = 0.067$.

Open gap versus crevice

When an open gap was tested against a crevice, only the larger lobsters showed any preference: 30–39 mm CL lobsters preferred gaps and those 40–49 mm CL preferred crevices (Table 2).

Hole size

Juveniles up to 39 mm CL (c. 1 year) generally preferred small holes. The holes most used by 15–19 mm CL lobsters were 25 mm diameter, 38 mm diameter for 20–29 mm lobsters, and 38/82 mm for 30–39 mm CL lobsters (Tables 3–5). The larger lobsters (40–59 mm CL) preferred much larger holes (82 mm, Table 6), but size preferences were not further narrowed down.

Open gaps

Juveniles 15–19 mm CL occupied comparatively large (32 and 38 mm high) gaps (Tables 7–9). The results for larger juveniles were more similar to those found for hole use: 20–29 mm CL juveniles preferred 38 and 32 mm holes; 30–39 (38 and 82 mm); 40–49 (82 and 100 mm); and 50–59 mm (100 mm).

Number of entrances

When testing the preferred number of openings, one versus two, and using holes near the optimal size for each size group, there was a change in choice with size. There was preference (compelling but not

Table 1 Use by juvenile *Jasus edwardsii* lobsters of holes versus open gaps. (d.f. = 1 for each size group; CL, carapace length; *N*, number of lobsters; χ^2, chi-squared; *P*, p value; NS, not significant.)

Size group (mm CL)	Aperture size (mm)	*N*	χ^2	*P*	Choice and significance
15–19	25	24	24.00	<0.001	Hole $P < 0.001$
	32	24	6.00	0.014	Hole $P < 0.05$
20–29	38	20	20.00	<0.001	Hole $P < 0.001$
30–39	38	30	3.33	0.067	Hole NS
40–49	38	12	5.33	0.021	Hole $P < 0.05$
50–59	80	12	12.00	<0.001	Hole $P < 0.001$

Table 2 Use by juvenile *Jasus edwardsii* lobsters of open gaps versus crevices. Gap and crevice dimensions in mm. (d.f. = 1 for each size group; CL, carapace length; *N*, number of lobsters; χ^2, chi-squared; *P*, p value; NS, not significant.)

Size group (mm CL)	Gap height	Crevice opening height	*N*	χ^2	*P*	Choice and significance
15–19	32	40	39	2.08	0.150	Crevice NS
20–29	38	50	24	0.17	0.683	Gap NS
30–39	38	50	14	10.29	0.001	Gap $P < 0.001$
40–49	38	50	26	9.85	0.002	Crevice $P < 0.01$

Table 3 Experiments undertaken to quantify hole size (diameter) preference in juvenile *Jasus edwardsii* lobsters, 15–39 mm carapace length, in three size groups. (*N*, number of lobsters.)

Size group	Hole sizes (mm)	*N*	Size group	Hole sizes (mm)	*N*
15–19	18 versus 25	51	20–29	25 versus 32	22
	18 versus 32	18		25 versus 38	18
	18 versus 38	18		25 versus 82	16
	25 versus 32	19		32 versus 38	20
	25 versus 38	20		32 versus 82	31
	32 versus 38	20		38 versus 82	19
			30–39	32 versus 38	23
				32 versus 82	18
				38 versus 82	46

Table 4 Parameter estimates for 15–39 mm carapace length (CL) lobsters, in three size groups, using holes of different diameter (in mm, indicated by the λ subscript). Lobster size groups in mm CL. (SE, standard error.)

		Desirability			
Size group		Estimate	SE	*z* value	*P*
15–19	λ_{18}	0	–	–	–
	λ_{25}	1.8108	0.2855	6.344	< 0.001
	λ_{32}	1.1275	0.3522	3.202	0.001
	λ_{38}	–0.2675	0.3566	–0.750	0.453
20–29	λ_{25}	0	–	–	–
	λ_{32}	2.0401	0.4444	4.591	< 0.001
	λ_{38}	2.9990	0.5330	5.627	< 0.001
	λ_{82}	0.6151	0.4188	1.469	0.142
30–39	λ_{32}	0	–	–	–
	λ_{38}	1.5034	0.4152	3.621	< 0.001
	λ_{82}	1.3129	0.4211	3.118	0.002

Table 5 Overall selection probabilities (P_{select}) and pairwise significance tests (*P*) for hole use by juvenile *Jasus edwardsii* lobsters, 15–39 mm carapace length, in three size groups. Hole sizes (mm diam.) are presented in order of highest selection probability to lowest. *P* values refer to adjacent pairings.

Size group	Overall hole size selection probability (P_{select})	Significance tests of overall hole sizes with adjacent categories (*P*)
15–19	25(0.558) > 32(0.282) > 18(0.091) > 38(0.070)	25 (0.051) > 32(0.001) > 18(<0.001) > 38
20–29	38(0.656) > 32(0.251) > 82(0.060) > 25(0.033)	38(0.022) > 32(<0.001) > 82(0.142) > 25
30–39	38(0.488) > 82(0.403) > 32 (0.109)	38(0.492) > 82(0.002) > 32

Table 6 Use of holes by juvenile *Jasus edwardsii* lobsters, 40–59 mm carapace length, in two size groups. (d.f. = 1 for each size group; *N*, number of lobsters; χ^2, chi-squared; NS, not significant.)

Size group	Hole sizes tested (mm)	*N*	χ^2	*P*	Choice and significance
40–49	38 versus 82	17	0.53	0.467	82 > 38 NS
50–59	38 versus 82	12	8.33	0.004	82 > 38 *P* < 0.01

Table 7 Experiments undertaken to quantify open horizontal gap size preferences by juvenile *Jasus edwardsii* lobsters, 15–59 mm carapace length, in five size groups. (*N*, number of lobsters.)

Size group	Gap heights (mm)	*N*	Size group	Gap heights (mm)	*N*
15–19	18 versus 32	67	30–39	32 versus 38	10
	25 versus 32	75		32 versus 80	12
	32 versus 38	44		32 versus 100	6
	32 versus 45	9		38 versus 80	6
	32 versus 52	15		38 versus 100	6
	32 versus 59	15		80 versus 100	6
	38 versus 45	36	40–49	32 versus 38	8
	38 versus 52	17		38 versus 80	8
	38 versus 59	15		38 versus 100	15
	45 versus 52	36		38 versus 120	15
	45 versus 59	15		80 versus 100	8
	52 versus 59	19		80 versus 120	15
20–29	25 versus 32	6		100 versus 120	7
	32 versus 38	44	50–59	60 versus 80	8
	32 versus 50	17		60 versus 100	10
	32 versus 60	10		60 versus 120	19
	32 versus 80	10		80 versus 100	8
	38 versus 50	17		80 versus 120	10
	38 versus 60	12		100 versus 120	10
	38 versus 80	12			
	50 versus 60	16			
	50 versus 80	10			
	60 versus 80	12			

Table 8 Parameter estimates for 15–59 mm carapace length *Jasus edwardsii* lobsters, in five size groups using open horizontal gaps of different height (in mm, indicated by the λ subscript). Lobster size groups in mm. (SE, standard error.)

		Desirability			
Size group		Estimate	SE	*z* value	*P*
15–19	λ_{18}	0	–	–	–
	λ_{25}	0.1504	0.3581	0.420	0.674
	λ_{32}	0.7841	0.2634	2.977	0.003
	λ_{38}	0.7638	0.3711	2.058	0.040
	λ_{45}	0.2457	0.4183	0.587	0.557
	λ_{52}	–0.7423	0.4394	–1.689	0.091
	λ_{59}	–1.6325	0.5072	–3.218	0.001
20–29	λ_{32}	0	–	–	–
	λ_{38}	0.4122	0.2624	1.571	0.116
	λ_{50}	–0.7638	0.3328	–2.295	0.022
	λ_{60}	–0.3537	0.3552	–0.996	0.319
	λ_{80}	–0.8465	0.3801	–2.227	0.026
30–39	λ_{32}	0	–	–	–
	λ_{38}	0.45304	0.49291	0.919	0.358
	λ_{80}	0.28659	0.46587	0.615	0.538
	λ_{100}	0.02162	0.5442	0.040	0.968
40–49	λ_{32}	0	–	–	–
	λ_{38}	1.0986	0.8165	1.346	0.179
	λ_{80}	2.2887	0.9987	2.292	0.022
	λ_{100}	1.5181	0.9352	1.623	0.105
	λ_{120}	–0.8839	1.0335	–0.855	0.392
50–59	λ_{60}	0	–	–	–
	λ_{80}	0.2974	0.4917	0.605	0.545
	λ_{100}	1.9684	0.5985	3.289	0.001
	λ_{120}	0.2401	0.3964	0.606	0.545

Table 9 Overall selection probabilities (P_{select}) and pairwise significance tests (P) for open horizontal gap use by juvenile *Jasus edwardsii* lobsters, 15–59 mm carapace length, in five size groups. Gap sizes (mm) are presented in order of highest selection probability to lowest. P values refer to adjacent pairings.

Size group	Overall gap height selection probability (P_{select})	Significance tests of overall gap size with adjacent categories (P)
15–19	32(0.259) > 38(0.254) > 45(0.151) > 25(0.138) > 18(0.118) > 52(0.056) > 59(0.023)	32(0.938) > 38(0.058) > 45(0.814) > 25(0.674) > 18(0.091) > 52(0.019) > 59
20–29	38(0.368) > 32(0.244) > 60(0.171) > 50(0.113) > 80(0.104)	38(0.116) > 32(0.319) > 60(0.244) > 50(0.830) > 80
30–39	38(0.319) > 80(0.270) > 100(0.207) > 32(0.203) > 25(0)	38(0.754) > 80(0.634) > 100(0.968) > 32(*) > 25
40–49	80(0.524) > 100(0.242) > 38(0.159) > 32(0.053) > 120(0.022)	80(0.178) > 100(0.358) > 38(0.178) > 32(0.392) > 120
50–59	100(0.664) > 80(0.125) > 120(0.118) > 60(0.093)	100(0.007) > 80(0.904) > 120(0.545) > 60

*There was one trial where lobsters were offered a choice between 32 and 25 mm gaps. Always the 32 mm gap was chosen, which precluded the inclusion of the 25 mm data in the statistical analyses. The 25 mm gap was subjectively placed at the bottom of the preference listing.

Table 10 Use by juvenile *Jasus edwardsii* lobsters of refuges (blocks) with one or two openings. (d.f. = 1 for each size group; CL, carapace length; N, number of lobsters; χ^2, chi-squared; NS, not significant.)

Size group (mm CL)	N	χ^2	P	Choice and significance
15–19	55	3.07	0.080	2 > 1 NS
20–29	48	0	1.00	1 = 2
30–49	27	1.81	0.178	1 > 2 NS
50–59	20	9.80	0.002	1 > 2 $P < 0.01$

significant) for two holes by 15–19 mm CL lobsters (almost significant at $P = 0.080$), to no detectable preference for those 20–29 mm CL, to one opening preferred by all the larger lobsters (Table 10).

DISCUSSION

The results from these experiments indicate that for all sizes of lobster, 15–59 mm CL, horizontal holes are preferred over open horizontal gaps. For 15–19 mm CL lobsters, the optimal hole diameter of those tested was 25 mm and two openings were preferred; the optimum gap height was larger, 32/38 mm. For 20–29 mm CL lobsters, the optimal hole diameter of those tested was 38 mm with either one or two openings; the optimum gap height was 38 mm. For 30–39 mm CL lobsters, the optimal hole diameter of those tested was large, in the range 38–82 mm, and one opening was preferred; the optimum gap height was also 38–82 mm. For 40–49 mm CL lobsters, the optimal hole diameter of those tested was 82 mm, and one opening was preferred; the optimum gap was 82/100 mm. For 50–59 mm CL lobsters, the optimal hole diameter between those tested was 82 mm and one opening was preferred; the optimum gap height was 100 mm. Although all holes <38 mm diameter were of alcathene, and all those ≥38 mm were of brick, all surfaces were well conditioned with natural marine growth and at least to that extent were similar.

The difficulty in locating sufficient juveniles for experiments to be conducted *in situ* in the wild, and other logistic constraints, meant that the investigations were confined to captive lobsters. The choices of shelter size by each of the different size groups found in the tanks are generally consistent with records from the field except that the smallest lobsters (15–19 mm CL) generally chose much larger gaps (but not holes) than expected. For example, Edmunds (1995) found 17 mm CL lobsters in holes c. 25 mm high, but we found them choosing much larger gaps (32 and 38 mm high).

As discussed by Edmunds (1995), for lobsters <35 mm CL small holes closely fitting the body size of the lobster provide a high degree of protection from both predators and environmental forces. The close association of the lobster's size and hole dimensions is likely to restrict the entry of larger predators and enable the lobster to wedge itself in the hole to resist extraction and displacement. In contrast, the relatively spacious shelters frequently inhabited by >35 lobsters mm CL provide access for larger predators and provide fewer opportunities for wedging. However, these shelters frequently provide more opportunities for escape through additional openings or the enlarged opening, and for cohabitation with conspecifics which may facilitate protection through communal defence behaviour, increased prey vigilance, and concealment among conspecifics (Edmunds 1995). It is possible that the unexpectedly large open gaps selected by the 15–19 mm CL lobsters in the tank experiments above reflected some such joint defence behavioural choice elicited among these juveniles when placed in the most unnatural situation of having many small conspecifics in close proximity. The absence of direct predatory pressure may also have contributed, although because the lobsters were held for short periods (only a few days) it is not expected they had acclimatised to the conditions.

The choice of holes over gaps by all lobster size groups may indicate that holes are likely to be more effective than crevices in the construction of puerulus collectors. Indeed holes can be equally or even more effectual for *J. edwardsii* (A. Jeffs & S. Hooker, NIWA pers. comm.), but holes often fill with marine growth and silt and so are more difficult to maintain in a standard sampling condition than are crevices.

The preference exhibited toward the number of openings (entrances) in hole shelters (two for the smallest lobsters, with evidence for an ontogenetic shift in preference to one for the larger ones) was unexpected. In nature, the solitary and cryptic smaller lobsters (Butler et al. 1999) are most often observed in simple, single-opening holes such as pholad shafts; yet in the tanks, holes with two openings were chosen over those with one. One explanation might be that, although two openings are preferred—perhaps because of the additional escape route available—small holes with two openings are rare in nature. For the larger size groups of experimental lobsters, holes with one opening were used significantly more often than those with two, which is also at odds with the field observations for *J. edwardsii* summarised earlier. Again, part of the explanation may lie in there being few large holes with only one opening, the larger recesses more likely being crevices than holes.

Reservations associated with these laboratory studies include: (1) the small size of the tanks (see Rodriguez et al. 1993 for discussion of the implications of experimental scale); (2) most of the experiments were in static water that did not reflect the physical and chemical complexity of the natural benthic environment; (3) the lobsters may not have behaved naturally because they were contained, perceiving greater and more prolonged threat than in the wild; (4) any density-dependence of association was not addressed, although tank numbers were generally low; and (5) some results were inconclusive because of the necessarily low numbers of animals used. Nevertheless, laboratory experiments, in which certain components of the environment are controlled for, are well established and widely used in behavioural studies. They have potential to discern the effects of predator and prey pressure on habitation patterns in the field because these can be specifically excluded. When tank results are consistent with field observations, the conclusions are particularly compelling.

Recommendations for the design of ongrowing tanks and of artificial reefs aimed at enhancing juvenile survival in the wild can be made from this work. For all juvenile size groups up to at least 60 mm CL, but ignoring any practical issues associated with ongrowing such as tank cleaning and removal of excess food, and the economic need to maintain high lobster densities, horizontal holes should be provided over open horizontal gaps. The holes should have two openings for the smallest size groups but only one opening for the larger ones, and the shelters provided should have been conditioned for several months. Presumably provision of shelters with the optimal characteristics indicated by these experiments can result in less stressed lobsters that are more likely to thrive.

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