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Distribution of *Jasus* spp. (Decapoda: Palinuridae) phyllosomas in southern waters: implications for larval recruitment

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ABSTRACT: We sampled the distribution of mid- and late-stage (= advanced) *Jasus* group *'lalandii'* rock lobster phyllosomas at 28 approximately equidistant stations across ~16 000 km of ocean between the west coast of Africa and the west coast of New Zealand to determine whether the larvae were mostly associated with the patchy allopatric distribution of the adults or were widespread. The *Jasus* phyllosomas (n = 210) occurred in greatest abundance in the general vicinity of adults. Nucleotide-sequencing and restriction-fragment length polymorphism (RFLP) techniques were used to identify 93 of these larvae from 18 stations to species level. Most of the larvae caught were *J. lalandii* and *J. edwardsii*, and a few were probably *J. paulensis*. Most of these larvae were taken near (within a few hundred kilometres) their respective adult habitat off southern Africa, Australia and New Zealand, and Amsterdam Island. The exceptions were small numbers of *J. lalandii* larvae in the southwest Indian Ocean as far east as Amsterdam Island, adjacent to the *J. paulensis* habitat, and *J. edwardsii* larvae across the south Tasman Sea. A single larva off southwest Africa could not be identified to any known *Jasus* species and may indicate the presence in the genus of an as yet undiscovered species or subspecies. No *J. caveorum*, *J. frontalis*, or *J. verreauxi* (and probably no *J. tristani*) were found. Our results suggest that *Jasus* spp. larvae which subsequently recruit to benthic populations use behavioural strategies and/or physical mechanisms to avoid being carried too far away from their parental ground. However, a proportion of larvae, small yet possibly not insignificant, occurs great distances from where adults of the species are known. These larvae are unlikely to recruit to benthic populations, but their occurrence invites further consideration of how *Jasus* spp. maintain allopatric populations.

KEY WORDS: Palinurid · *Jasus* · Phyllosoma larvae · Larval recruitment · South Atlantic Ocean · Indian Ocean · Tasman Sea

INTRODUCTION

The rock (spiny) lobsters *Jasus* spp. (Decapoda: Palinuridae) live in coastal waters and on nearshore and offshore seamounts in mid-south latitudes of the South Atlantic, Indian, and South Pacific Oceans and of the Tasman Sea. Many *Jasus* spp. fisheries are commercially, recreationally, and traditionally valuable. Understanding larval recruitment processes and, in particular, knowing larval sources will greatly assist sound management of these fisheries. Sampling larvae to test hypotheses concerning recruitment processes is difficult because of the large ocean distances involved and the size of vessel required; more papers, therefore, speculate on larval distributions than provide actual data on larval occurrence. There is a need for improved global understanding of larval-drift patterns and recruitment mechanisms in this genus through the sampling of planktonic distributions.

Jasus spp. separate into the *'verreauxi'* group, containing only *J. verreauxi*, and the *'lalandii'* group containing all other species (Holthuis & Sivertsen 1967). The *'lalandii'* group comprised only *J. lalandii* until Holthuis (1963) recognised that there were separate species, based on adult morphology and colour. The group was subdivided by Holthuis & Sivertsen into the

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'lalandii' subgroup (*J. lalandii* off southern Africa, *J. edwardsii* in New Zealand, and *J. novaehollandiae* in Australia) and the *'frontalis'* subgroup (*J. frontalis* off Chile, *J. tristani* in the South Atlantic Ocean, and *J. paulensis* in the south Indian Ocean). George & Kensler (1970) extended the list of external characters used by Holthuis & Sivertsen to distinguish species in the *'lalandii'* group, and provided support for the subgroups. The morphology of *J. caveorum*, a species recently described from the east South Pacific Ocean, suggests its inclusion in the *'frontalis'* subgroup (Webber & Booth 1995).

DNA analyses support the existence of the *'verreauxi'* and *'lalandii'* groups and the distinction in the *'lalandii'* group between the species *Jasus edwardsii*, *J. lalandii*, *J. tristani*, *J. frontalis*, *J. paulensis* and *J. caveorum*, but not between *J. edwardsii* and *J. novaehollandiae* (Brasher et al. 1992, Ovenden et al. 1992, 1997). *J. edwardsii* and *J. novaehollandiae* have since been synonomized. DNA studies have not supported subdivision of the *'lalandii'* group into subgroups *'lalandii'* and *'frontalis'* (Ovenden et al. 1997), so the morphological and colour distinctions between these groups appear to be of less evolutionary significance than previously thought. No hybrids are known.

Benthic distribution of *Jasus* spp.

Jasus group *'lalandii'* species are known mainly from depths of <200 m in southern temperate waters (Holthuis 1991), around large land-masses and islands and on seamounts. New populations, including a new species, have been discovered as seamounts have been fished for the first time (e.g. Webber & Booth 1988, 1995). There is no sympatry in *Jasus* spp. except in Australasia between *J. verreauxi* and *J. edwardsii* over part of the range of *J. edwardsii*.

Jasus tristani occurs at the Tristan da Cunha Archipelago and Gough Island and on the Vema Seamount (see Fig. 3) (Holthuis & Sivertsen 1967, Heydorn 1969). Annual landings are generally about 400 t (FAO statistics), with the Vema Seamount now fished only occasionally after large catches in the 1960s. *J. lalandii* lives on the west and southwest coasts of southern Africa between 23° S and 28° E, the main fishery being between 25 and 34° S (Pollock 1986). Annual commercial landings are presently around 4500 t (FAO statistics). *J. paulensis* lives in the Indian Ocean around St. Paul and Amsterdam Islands and on seamounts over a wide area to the northeast of these islands (see Fig. 3) (Webber & Booth 1988, Holthuis 1991). It is also present on seamounts south of Madagascar (Webber & Booth 1988), and is occasionally seen at Kerguelen Island (de la Rue 1954, in Holthuis 1991). Annual catches from the main fishery, at St. Paul and Amsterdam Islands, are 300 to 600 t (M. Barbarin, Armement Sapmer pers. comm.). *J. edwardsii* forms the basis of important fisheries in Australia (Brown & Phillips 1994) and New Zealand (Booth & Breen 1994). In Australia, the species occurs south from Geraldton in the west, along the south coast and around Tasmania, and as far north as Coffs Harbour on the east coast; annual commercial landings are about 4900 t, most coming from South Australia and Tasmania (Brown & Phillips 1994). New Zealand commercial landings are around 2700 t yr^{-1} (National Institute of Water and Atmospheric Research [NIWA], data). The species occurs from the Three Kings Islands in the north to the Auckland Islands in the south, and east to the Chatham Islands (Kensler 1967), but the main fishery is along the east, south, and southwest coasts of the mainland (Booth & Breen 1994). *J. edwardsii* is also present on seamounts in the Tasman Sea (Booth et al. 1990). *J. caveorum* occurs in the east South Pacific Ocean on the Foundation Seamount Chain (Webber & Booth 1995). Since its discovery in 1995, at least 20 t have been taken. *J. frontalis* is known only from the Juan Fernandez Archipelago and Islas Desventuradas in the east South Pacific Ocean (Arana 1987, Holthuis 1991). Annual landings are about 40 t.

A rock lobster best fitting the description of the *Jasus 'lalandii'* group was taken in quantity (tonnes) in the early 1960s on South Pacific Ocean seamounts southeast of the Foundation Seamount Chain, near 40° S, 100° W (B. Blocker, South Pacific International Ltd, pers. comm.). No specimens are available, and recent fishing expeditions to this general area have failed to relocate these lobsters (authors' unpubl. data).

Jasus verreauxi (the *'verreauxi'* group) forms small commercial fisheries in northern New Zealand and southeast Australia (Booth 1986, Booth & Breen 1994, Brown & Phillips 1994). All developmental stages, including the phyllosoma larvae (McWilliam & Phillips 1987, Kittaka et al. 1997), are distinguishable morphologically from the *'lalandii'* group species.

Breeding and development of the *Jasus 'lalandii'* group

Jasus edwardsii and *J. lalandii* are the best-studied species. The following account is primarily based on these 2 species, but also draws on scattered reports of the reproductive biology of the other *Jasus* spp. The *Jasus 'lalandii'* group breed in the austral winter (Grua 1963, Holthuis & Sivertsen 1967, Silas 1967, Heydorn 1969, Street 1969, Winstanley 1977, Roscoe 1979, Arana et al. 1985, Pollock 1986, Holthuis 1991, Webber & Booth 1995). Fecundity is high (tens of thousands to

hundreds of thousands of eggs; Annala 1991). Females spawn in autumn (April to May), and eggs hatch in spring to summer (September to January). Early phyllosomas are rapidly transported offshore into oceanic waters. The larval life lasts many months, in nature at least 12 mo (Pollock 1986, Booth 1994), although larvae can be cultured to metamorphosis in about 10 mo (Kittaka 1988, Kittaka et al. 1988). Settlement is often highest during winter (Holthuis & Sivertsen 1967, Lewis 1977, Pollock 1986, Booth 1994, Gardner et al. 1998); together with the hatching times and minimum larval development period this points to a larval life of ~18 mo. However, settlement is often also high in summer, and indeed can occur at any time of the year, so a larval life of >18 mo is also possible (see Booth [1994] for further discussion). This extended larval life may come about through delayed metamorphosis to the puerulus stage and/or by mark-time moulting (Gore 1985, Phillips & McWilliam 1986, Pollock 1990a, Booth 1994, Booth & Phillips 1994). Claims that the *Jasus 'lalandii'* group larvae are morphologically distinguishable (Miller 1985, Phillips & McWilliam 1986, McWilliam & Phillips 1987) are unverified.

Patterns of larval recruitment in *Jasus* spp.

Jasus spp. are typical shallow-water rock lobsters (Booth & Phillips 1994) that spend months as phyllosoma larvae in waters tens to hundreds of kilometres from shore (Gurney 1936, Lazarus 1967, Lesser 1978, Pollock & Goosen 1983, Pollock 1986, 1990b, 1991, Booth & Stewart 1992, Booth 1994, Pollock et al. 1995, Booth et al. 1998). The lobsters return to shore as transparent postlarvae (pueruli) after metamorphosing near the shelf break (near the 1000 m contour). Phyllosomas appear suited to passive drift, and in culture horizontal swimming is weak (Kittaka 1994). This, together with their long period offshore, means that currents are likely to be important in the transport of larvae (Booth & Phillips 1994). Indeed, the strength of the east-directed currents in southern temperate waters and in the Southern Ocean (e.g. Shannon et al. 1973), together with the duration of the larval stage, mean that theoretically *Jasus* spp. larvae could disperse over large tracts of the southern hemisphere (Phillips & McWilliam 1986, Pollock 1990a). However, it is increasingly apparent that most currents are far more complex than a simple flow between 2 points, and that eddying and recirculation are common to them. Such eddies may be crucial to palinurid larval recruitment, preventing at least some larvae from being carried too far from the parental ground, and providing a means of shoreward transport (Phillips 1981, Lee et al. 1994, Polovina & Moffitt 1995, Chiswell & Roemmich 1998). Indeed, Chiswell & Booth (1999) showed that the distribution of mid-stage *J. edwardsii* larvae off the east coast of New Zealand was correlated with dynamic height in a large offshore eddy.

There are 2 main alternative hypotheses for the mechanisms of larval recruitment in rock lobsters. The first is that the long-lived phyllosomas remain near the adult grounds through evolved behaviours (e.g. changing vertical distribution to effect different horizontal distributions), or through local physical processes (e.g. presence of counter currents). This hypothesis was referred to as a 'closed' recruitment pattern by Menzies & Kerrigan (1979), an example being *Panulirus cygnus* off Western Australia (Phillips 1981). The second hypothesis is that the phyllosomas are dispersed widely—the 'open' recruitment pattern, sensu Menzies & Kerrigan (1979). For *Jasus* spp., open recruitment patterns might include those in which larvae are haphazardly dispersed over large distances in the Southern Ocean (Silas 1967), transported around ocean basins (Pollock 1990a, Pollock & Melville-Smith 1993), or carried across seas or large sections of ocean (Silas 1967, Williamson 1967, Heydorn 1969, Stander et al. 1969, Winstanley 1970, Lutjeharms & Heydorn 1981a,b, Phillips & McWilliam 1986, Booth et al. 1990). However, there could also be variation in larval recruitment mechanism throughout a species' range and over time. While for a particular species at any particular time one hypothesis may best define the recruitment mechanism for the majority of its larvae, most larvae may be part of an alternative mechanism at other times.

It could be argued that the limited information on the distributions of larval *Jasus* spp. are consistent with either hypothesis. On the one hand, *Jasus 'lalandii'* group larvae have been taken over wide areas of the southeast South Atlantic, central south Indian, and eastern South Pacific oceans and the south Tasman Sea. They were taken in large numbers (tens to hundreds per tow) from near the coast of southern Africa, and 3000 km westward, to near the Tristan da Cunha Archipelago (Pollock & Goosen 1983, Pollock 1986, 1991, Pollock et al. 1995). Larval numbers were much lower west of these islands, but sampling did not take place west of 15° W and any northern or southern boundary to this area of high larval abundance was not defined. More often, numbers of phyllosomas per station have been small (<10) (Gurney 1936, Silas 1967, Baez 1973, Booth et al. 1990).

On the other hand, more contained larval distributions exist. Advanced phyllosomas of the *Jasus 'lalandii'* group (Stages 5 to 11, presumably *J. edwardsii*) were taken in large numbers (hundreds per tow) up to 1300 km off the east coast of the North Island of New Zealand (Booth et al. 1998), beyond which area num-

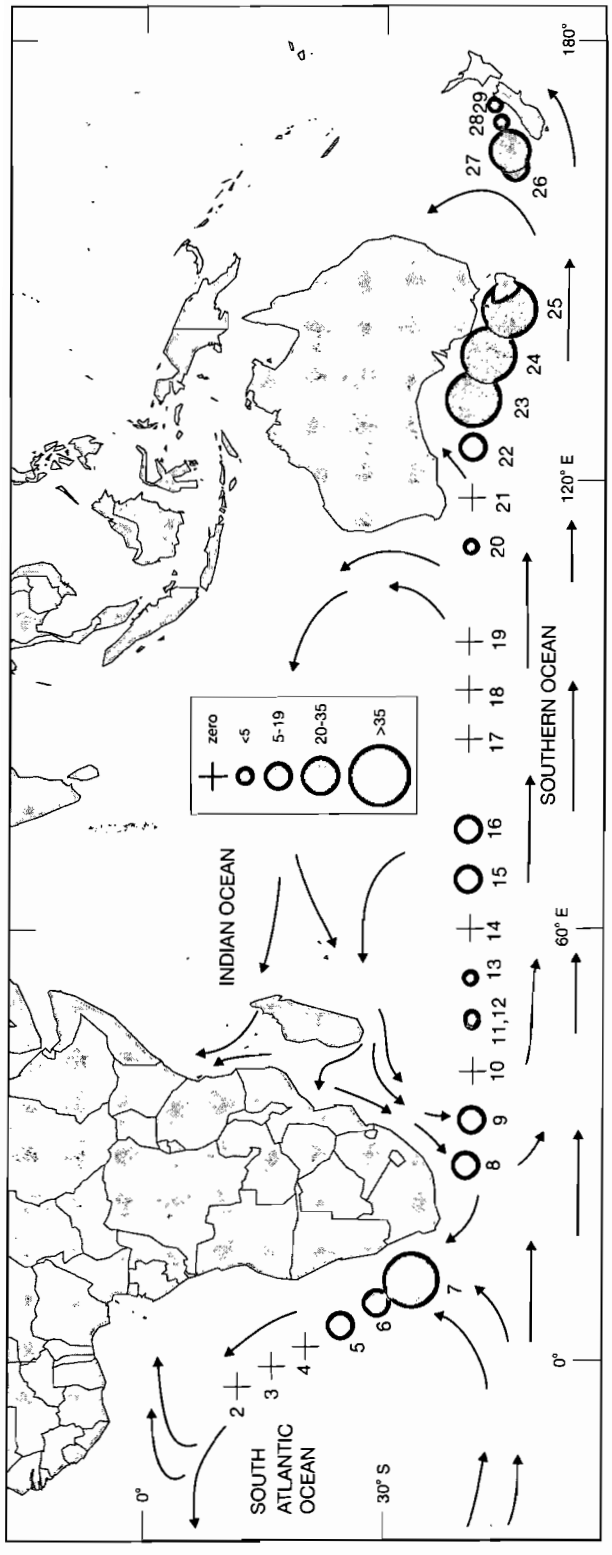

Fig. 1. *Jasus* group *'lalandii'* larvae collected in June/July 1991 (standardised to 60 min tow). Sizes of filled circles are proportional to sizes of larval catch (all larvae were Stage 5 or beyond). + = no larvae; numbers = station numbers; generalised flow pattern (arrows) after Shannon et al. (1973)

bers fell markedly. This larval pool appears to have clear boundaries (Booth & Stewart 1992, Booth 1994), the offshore boundary being the prominent Louisville Ridge, which rises to near the surface from 4000 m. Within this area, eddy recirculation seems to be important in larval retention (Chiswell & Roemmich 1998, Chiswell & Booth 1999).

Our hypotheses and data source

The delivery voyage of RV 'Tangaroa' from Norway to New Zealand in June/July 1991 provided an opportunity to test the hypothesis that advanced *Jasus 'lalandii'* group larvae are most abundant near (tens to hundreds of kilometres) the adult grounds, and that they become increasingly sparse with distance downstream in the oceanic flow. Discovery of late-stage larvae in high numbers throughout an ocean basin or predominantly well away from the adult grounds would be evidence against this hypothesis. The voyage passed through or by areas occupied by 4 of the 6 species of the *'lalandii'* group of *Jasus*: *J. tristani*, *J. lalandii*, *J. paulensis*, and *J. edwardsii* (see Fig. 3). With the breeding seasons and larval development periods described earlier, advanced larvae of all *Jasus* spp. were expected in the southern waters in June to July, as found in earlier studies. Not only did we expect total numbers of *Jasus* spp. larvae to be highest near the adults, but also, using genetic analyses to allow identification to species level, we expected that the larval distribution of a species would broadly match the adult distribution. Further, we expected that the size of the larval catch of a species would broadly reflect the relative size of its commercial catch in the fishery: *J. edwardsii* and *J. lalandii* larvae should therefore be much more abundant overall than the larvae of other *Jasus* species. Here we report the results of the 'Tangaroa' sampling, and the implications of the results in understanding large-scale larval recruitment patterns in *Jasus* spp.

METHODS

Plankton. This was sampled at 28 approximately equidistant stations across ~16 000 km of ocean once the RV 'Tangaroa' reached 11° S in the South Atlantic Ocean. The transect route and sampling (Fig. 1) reflected the known distribution of adults along coasts and on seamounts, the need to comply with national ocean jurisdictions, maintaining direct passage, a port call (Hobart), and sea condi-

tions. Jurisdiction issues meant that most sampling was conducted at least 200 nautical miles (370 km) from shore. Heavy sea conditions resulted in missing strategic stations off Cape of Good Hope, near Amsterdam Island, and out of Hobart. The net was a 65 m long, Engel, fine-meshed midwater trawl towed at a headline depth of 30 m. The mouth of the net was ~60 m^2. The mesh size (12 mm) resulted in the capture of mid- (Stages 5 to 7) and late- (Stages 8 to 11) stages of *Jasus* spp. larvae. One 20 to 60 min tow was made each night, as weather permitted, starting about 2 h after sunset. Towing speed was the slowest possible, ~2 to 3 knots (3.7 to 5.6 km h^{-1}).

Fresh phyllosomas were stored in 70% ethanol for DNA and morphometric analyses; others were stored in buffered formalin for morphometric measurements. Only fresh larvae removed from the net after each station tow were attributed to that station.

Phyllosomas of *Jasus* spp. were distinguished from other phyllosomas primarily through the shape of the cephalon, the size of the cephalon relative to the abdomen, and the shape and length of the antennae (see Lazarus 1967 and Lesser 1978 for details of the full larval development). Advanced *'lalandii'* group larvae are readily distinguishable from *J. verreauxi*, since only the latter have setose exopods on the 5th pereiopods and on the 3rd maxillipeds (McWilliam & Phillips 1987, Kittaka et al. 1997). The phyllosomas were staged according to Lesser's (1978) key for *J. edwardsii*, irrespective of species, or based on size. Total length (TL) is the distance between the base of the eyestalks and the posterior margin of the telson. The larvae are deposited at the Museum of New Zealand Te Papa Tongarewa, Wellington.

Genetic analyses of larvae. Of the *Jasus* spp. phyllosomas collected, 93 were chosen for mtDNA analysis to give a wide geographic coverage of the transect. Genomic DNA was isolated from a portion of a single, ethanol-preserved leg or small amount of cephalon or abdomen from each phyllosoma using CTAB (hexadecyltrimethylammonium bromide) and Proteinase K (Doyle & Doyle 1987), and resuspended in 50 µl of sterile water. Of this DNA, 2 µl was used as a template for the polymerase chain reaction (PCR) to amplify a fragment of the mitochondrial cytochrome-c oxidase subunit gene I (COI), ~700 base pairs in length, using the primers LCO1490 (5' GGTCAACAAATCATAAAGATATTGG 3') and HCO2198 (5' TAAACTTCAGGGTGACCAAAAAATCA 3') of Folmer et al. (1994). The reaction conditions were the same as in Folmer et al., except that the total volume of the PCR was 25 µl, the final MgCl concentration was 1.75 mM, and 0.5 µl of each primer (10 mM) was used. The cycling conditions were 1 cycle at 95°C for 4 min, 60°C for 45 s, and 72°C for 2 min; followed by 35 cycles of 95°C for 30 s, 40°C for 1 min, and 72°C for 1 min, with a final extension at 72°C for 5 min. DNA from the PCR was visualized with UV light after standard submarine gel electrophoresis, using 1.5% agarose (Promega) and TBE buffer, and staining with ethidium bromide.

The PCR product from 29 randomly chosen larvae was cycle-sequenced using dye-terminator chemistry and an ABI autosequencer with the LCO primer. The nucleotide-sequence obtained was confirmed from the opposite DNA strand of a subset of 9 of these larvae using the HCO primer. Phylogenetic analysis of 540 base pairs of sequence data from larvae and adults from Ovenden et al. (1997) was performed using the neighbour-joining method on Kimura 2-parameter distances with 500 bootstrapped replicates. Larvae were identified to species according to their common membership of a monophyletic clade with an adult of known species on the neighbour-joining tree.

The number and location of *Hae* III (GGCC) and *Nla* III (CATG) restriction sites in 29 sequenced larvae were determined using the software MacDNAsis Pro (Version 1.0). These sites were also identified in corresponding nucleotide-sequence from 3 adult *Jasus edwardsii*, and 1 adult each of *J. lalandii*, *J. tristani*, *J. paulensis*, *J. frontalis*, and *J. caveorum* from the study of Ovenden et al. (1997), and were found to be diagnostic for species. The presence of restriction sites in sequenced larvae was confirmed by digestion, electrophoresis, and visualization of restriction fragments. All remaining larvae were digested with the 2 restriction enzymes and fragments visualized, and identifications were performed to species level. The Genbank accession numbers for the adult *Jasus* sequence data are AF192866 to 83.

Morphology of larvae. Larvae identified to species from mtDNA were examined using light and scanning electron microscopy to search for distinguishing external features.

RESULTS

Samples obtained

We caught ~400 phyllosomas, of which 210 were, through their morphology, *Jasus 'lalandii'* group at mid- and late-stages of development (Table 1, which also gives the numbers of larvae per station standardised for a 60 min tow). None was *J. verreauxi*. Although sampling began 1300 km further north in the South Atlantic Ocean, at 11° S, it was not until 23° S that phyllosomas of *Jasus* spp. were first encountered. Thereafter they were taken at several stations all the way to New Zealand, but usually in the general vicinity (within a few hundred kilometres) of *Jasus* adults. The greatest abundances of *Jasus* spp. larvae were

Table 1. Catch of palinurid phyllosomas at Stns 2–29 shown in Fig. 1. Counts are for *Jasus 'lalandii'* group, except for column *'Panulirus* stdised' (1 *Jasus* sp. puerulus was also caught at Stn 17). Stn 1 was calibration station. Stage: development based on Lesser (1978) and larval size; *Jasus* stdised: total catch of *Jasus* spp. larvae standardised to 60 min tow; *Jasus* DNA: number of larvae from sample of *Jasus* spp. larvae determined to species level using mtDNA; *lal*: *J. lalandii*; *paul/trist*: *J. paulensis* or *J. tristani*; *edw*: *J. edwardsii*; ?: unknown *Jasus* sp.; *Panulirus* stdised: catch of *Panulirus* spp. larvae (mainly *P. versicolor* and *P. longipes longipes*) standardised to 60 min tow; blank: no larvae of that stage or species caught

Stn	Stage							*Jasus* total	*Jasus* stdised	*Jasus* DNA	*Jasus* species	*Panulirus* stdised
	5	6	7	8	9	10	11					
2												
3												
4												
5				2	1			3	6	2	*lal*	
6		2	1	1				4	5	3	*lal*	5
7	4	14	11	41	7	1		78	104	24	*lal* + 1?	33
8		1	1	2	2		1	7	9	6	*lal*	4
9		1	1	1		2		5	13	3	*lal*	73
10												
11				1	1			2	4	1	*lal*	32
12					1	1		2	2	1	*lal*	24
13							1	1	2	1	*lal*	
14												
15				3				3	6	2	*paul/tris*	
16						6		6	12	5	*paul/tris* + 1 *lal*	
17												
18												
19												
20				1				1	2			
21												
22				4	1			5	10	4	*edw*	
23			1	16	3		12	32	87	8	*edw*	
24	1	3	3	7				14	35	10	*edw*	
25		3	6	12	1			22	63	8	*edw*	
26		1	1	8	1			11	16	7	*edw*	
27		1	4	4	2			11	21	6	*edw*	
28	1			1				2	3	2	*edw*	
29				1				1	2			
Total	6	26	29	105	20	10	14	210	402	93		171

near the west and south coasts of South Africa, off eastern parts of southern Australia, and in the eastern Tasman Sea. The other phyllosomas caught belonged to *Panulirus* spp. (Table 1) and scyllarid species.

Genetic identification of *Jasus* larvae

A total of 4 *Hae* III and 4 *Nla* III sites were found in the sequence data of 36 larvae of unknown species, and of the adult *Jasus* spp. that had been sequenced. Combinations of these sites identified 8 *Hae* III and 5 *Nla* III morphs, making 13 species-specific haplotypes in all (Table 2). These haplotypes were assigned to species-specific groups by the phylogenetic analysis of sequenced larvae and adults (Fig. 2). The only clade of larval and adult sequences which grouped together on <95% of bootstrap replicates was *J. lalandii* (Fig. 2). The lower bootstrap value on this clade may reflect the higher intraspecific diversity for this species (0.0183 ± 0.0066) compared with that of *J. edwardsii* (0.0138 ± 0.0081) and, possibly, of *J. tristani*/*J. paulensis* (0.0172 ± 0.0073), although bootstrap values are also sensitive to the presence of unresolved regions of sequence data across all individuals in a tree.

The single haplotype described for *Jasus paulensis* and *J. tristani* (Haplotype DC, Table 2) confirms their close phylogenetic relationship, which had previously been noted by Ovenden et al. (1997). We could not conclusively distinguish these 2 species. Larvae identified to this clade were assumed to be *J. paulensis* because of their close proximity to the *J. paulensis* adults and their distance from *J. tristani* adults. No larvae were *J. caveorum*. Haplotype designations from RFLP analysis of those larvae not sequenced identified a further 30 *J. lalandii*, 31 *J. edwardsii*, and 3 *J. tristani*/*J. paulensis*.

One larva from Stn 7 (Haplotype CD, Table 2, sequenced with both primers) was not part of any spe-

Table 2. *Jasus* spp. *Hae* III and *Nla* III restriction-site presence and absence of 13 mitochondrial haplotypes, and numbers of each that were found in a sample of larvae and adults from which sequence or RFLP data were obtained. Restriction sites numbered from beginning of sequence obtained with LCO1490 primer. n = sample size

n (seq)	n (RFLP)	*Hae* III morph	*Nla* III morph	*Hae* III 188	*Hae* III 200	*Hae* III 344	*Hae* III 404	*Nla* III 199	*Nla* III 336	*Nla* III 436	*Nla* III 466
J. edwardsii											
13	28	C	B	0	0	0	0	1	1	1	0
3	0	C	F	0	0	0	0	1	1	0	0
1	0	H	B	0	0	1	0	1	1	1	0
J. lalandii											
4	28	A	A	0	1	0	0	1	0	0	0
2	2	A	D	1	1	0	0	1	0	1	0
2	1	A	E	1	0	0	0	1	0	0	1
1	0	B	A	0	1	0	1	1	0	0	0
2	0	G	A	1	1	1	0	1	0	0	0
1	0	G	E	1	1	1	0	1	0	0	1
J. tristani/J. paulensis											
5	3	D	C	1	0	1	0	0	0	1	0
Unknown											
1	0	C	D	0	0	0	0	1	0	1	0
J. caveorum											
1	0	F	D	0	1	0	0	1	0	1	0
J. frontalis											
1	0	E	B	1	0	0	0	1	1	1	0

cies-specific monophyletic clade (Fig. 2). The average Kimura 2-parameter distance between this larva and each of 3 other species (*Jasus edwardsii*, *J. frontalis*, and *J. paulensis*) was similar to the pairwise distance among the 3 known species (Table 3).

Morphological identification of *Jasus* spp. larvae

The only morphological distinctions possible were those which identified larvae to *Jasus 'lalandii'* group (i.e., the larvae were not *J. verreauxi*). No external features were found enabling us to distinguish to species those phyllosomas identified to species using DNA.

Overall distribution of *Jasus 'lalandii'* group larvae

All *Jasus 'lalandii'* group larvae were found near places at which benthic populations of *Jasus 'lalandii'* group are known, with the exception of moderate numbers at 2 stations off southeast South Africa (Stns 8 and 9; Fig. 1).

All phyllosomas were mid- or late-stage (Table 1; least-developed were Stage 5), with little hint of more advanced larval development with increased distance from the benthic population. The mesh size of the trawl does not routinely retain larvae earlier than Stage 5 (Booth 1994), but earlier larvae were not expected,

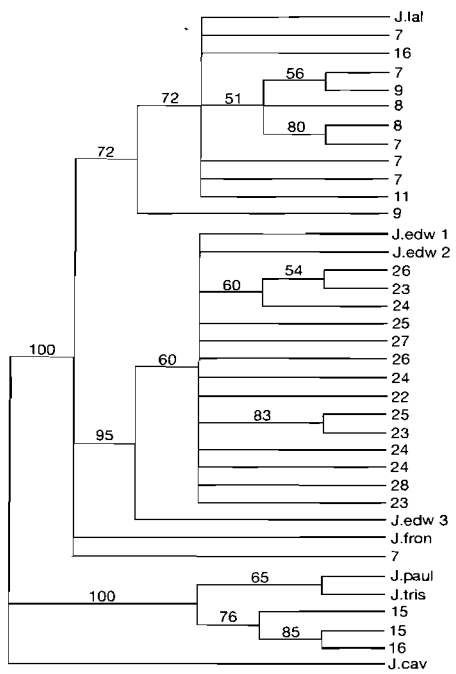

Fig. 2. *Jasus* spp. Bootstrapped neighbour-joining cladogram describing relationships between 29 larvae and 7 adults drawn from partial-sequence data of COI mitochondrial gene. Numbers on right = station numbers; numbers on bars = bootstrap probabilities (as %) based on 500 resamplings; J.lal = *J. lalandii*, J.edw = *J. edwardsii*, J.fron = *J. frontalis*, J.paul = *J. paulensis*, J.tris = *J. tristani*, J.cav = *J. caveorum*. In addition, a single unknown larva was caught at Stn 7

Table 3. *Jasus* spp. Mean (above diagonal) and standard deviations (below diagonal) of pairwise Kimura 2-parameter distances between 4 species (adults and larvae) and a single larva of unknown specific designation (Specimen No. 7.15). na: not applicable

	J. lalandii (1)	*J. edwardsii* (2)	*J. tristani*/ *J. paulensis* (3)	*J. frontalis* (4)	Unknown larva (5)
1		0.0425	0.0824	0.0478	0.0340
2	0.0060		0.0843	0.0442	0.0383
3	0.0097	0.0098		0.0840	0.0879
4	0.0059	0.0029	0.0089		0.0463
5	0.0045	0.0037	0.0098	na	

given the months of hatching. For the east South Atlantic, larvae were mainly Stages 6 to 8 which, based on a spring spawning, would have been ~8 mo old. Phyllosomas from the southwest Indian Ocean included a larger proportion of later stages (Stages 9 to 11), with those at Stn 16, near Amsterdam Island, all being penultimate and including both *Jasus lalandii* and *J. paulensis*. Larvae off southern Australia and across the Tasman Sea were almost all Stages 6 to 9. The notable exception was the catch of 12 large (38 to 43 mm TL), final-stage phyllosomas together with 20 earlier larvae at Stn 23, south of Streaky Bay in South Australia; these probably represented 2 different annual cohorts.

Distribution of *Jasus 'lalandii'* group larvae by species

When sequence and RFLP data were combined, making it possible to designate 93 larvae to species, it was found that the *Jasus* phyllosomas usually occurred near to known benthic populations of that particular species (Fig. 3); *J. lalandii* larvae were taken off the west coast of southern Africa, *J. paulensis* in the vicinity of seamounts and islands in the central south Indian Ocean, and *J. edwardsii* across eastern parts of southern Australia, in the south Tasman Sea, and off New Zealand. Again, the notable exception was *J. lalandii* larvae in waters of the southwest Indian Ocean. No larvae attributable to *J. frontalis* or *J. caveorum* were caught.

DISCUSSION

Until now, our appreciation of larval recruitment mechanisms in *Jasus* spp. has generally been speculative, or based on sampling from too narrow geographical limits or too small volumes of water for firm conclusions to be drawn. The transect sampled in this study is the first in which it has been possible on a large scale (thousands of kilometres of ocean), using a large net that filters large quantities (hundreds of thousands of cubic metres) of water, to address hypotheses concerning the larval distribution of *Jasus* spp. and the dispersal of larvae of various species in relation to the distribution of the adults. We were interested to discover if the numbers of advanced *Jasus* spp. larvae were highest in the general vicinity of the adults, and then declined markedly with distance, which would suggest a geographically small-scale recruitment mechanism. An alternative result, with larvae widespread and more or less evenly distributed along the various portions of the transect, such as through the South Atlantic Ocean, might point to recruitment mechanisms that function over scales at least the size of ocean basins.

Distribution of larvae

Phyllosomas of the *Jasus 'lalandii'* group, considered in total, occurred in greatest abundance in the general vicinity (within a few hundred kilometres) of where *Jasus 'lalandii'* group adults are known to exist, except in the southwest Indian Ocean, where unexpectedly high numbers were caught. Highest concentrations of larvae were near the west and south coasts of South Africa, off southern Australia, and in the Tasman Sea, broadly coincident with the areas of most abundant adults. *Jasus* spp. phyllosomas were also taken in small numbers in the south central Indian Ocean, an area in which small populations of *Jasus* adults exist.

The hypothesis of geographically small-scale larval-retention mechanisms is supported at the species level also, most larvae identified to species being geographically closely associated with their respective adults. For the abundant species, *Jasus lalandii* and *J. edwardsii*, the advanced larvae never occurred upstream of the adults in the prevailing oceanic flow. For *J. lalandii* in the southeast South Atlantic Ocean equatorward flow of the Benguela Upwelling System (Shillington 1998), larval numbers fell dramatically downstream (north) of the main area of the adults, and larvae were not caught north of 23° S. There was no suggestion of relatively constant larval numbers with

distance north from the adults; instead, numbers declined with distance from the adult population. All *J. edwardsii* phyllosomas were caught within the geographic range of the adults of that species; phyllosomas were first encountered off the Great Australian Bight, and larvae were taken from there to the end of the transect off Cook Strait, New Zealand. Much of this region is influenced by the east-directed West Wind Drift (see Shannon et al. 1973).

For *Jasus lalandii* in the southwest Indian Ocean, however, there was more distant downstream (eastward) drift, with larvae taken in small to moderate numbers in the south Indian Ocean as far east as Stn 16 (73° E, halfway to Australia), including areas over or near seamounts containing benthic populations of *J. paulensis*. It is likely that these larvae were transported east from the southern South African breeding grounds in the Agulhas Return Current and/or further south, the West Wind Drift of the Southern Ocean (e.g. see Chapman 1988, Lutjeharms et al. 1988, Collette & Parin 1991). Lazarus (1967) also found *Jasus 'lalandii'* group larvae east of the benthic populations, the larvae being present right out to his easternmost transect near 22° E.

Although it was not possible to determine the species of all *Jasus* larvae caught, the results point firmly to species supporting the largest commercial fisheries, *J. lalandii* and *J. edwardsii*, being the most abundant larvae. The few larvae caught that were attributed to *J. paulensis/J. tristani* were only from stations adjacent to St. Paul and Amsterdam Islands, where total larval catches were, at best, moderate.

Just under 90% of all larvae caught were at Stages 5 to 9, similar to the situation often seen off the east coast of the North Island of New Zealand in winter (Lesser 1978, Booth 1994); the larvae probably came from the previous (1990) spring-spawning. There were only 2 stations (Stns 16 and 23, in the central south Indian Ocean and south of South Australia, respectively) which yielded significant catches of final stages; these larvae probably came from the 1989 spawning. The data are therefore consistent with recruitment mechanisms based primarily on annual cycles of larvae, not on larvae a year or more older.

Our results suggest that larvae that will eventually recruit to benthic populations of their respective species generally use behavioural strategies and/or physical mechanisms to avoid being carried too far from the parental ground. Were more-widespread dispersal taking place, on the scale of ocean basins, then relatively constant larval numbers, or a much more gradual decline in larval numbers with increasing distance from the adults, and proportionately fewer mid-stage larvae would be expected. (If larvae were transported further afield before recruiting, only early and very late stages would be expected in any quantity near

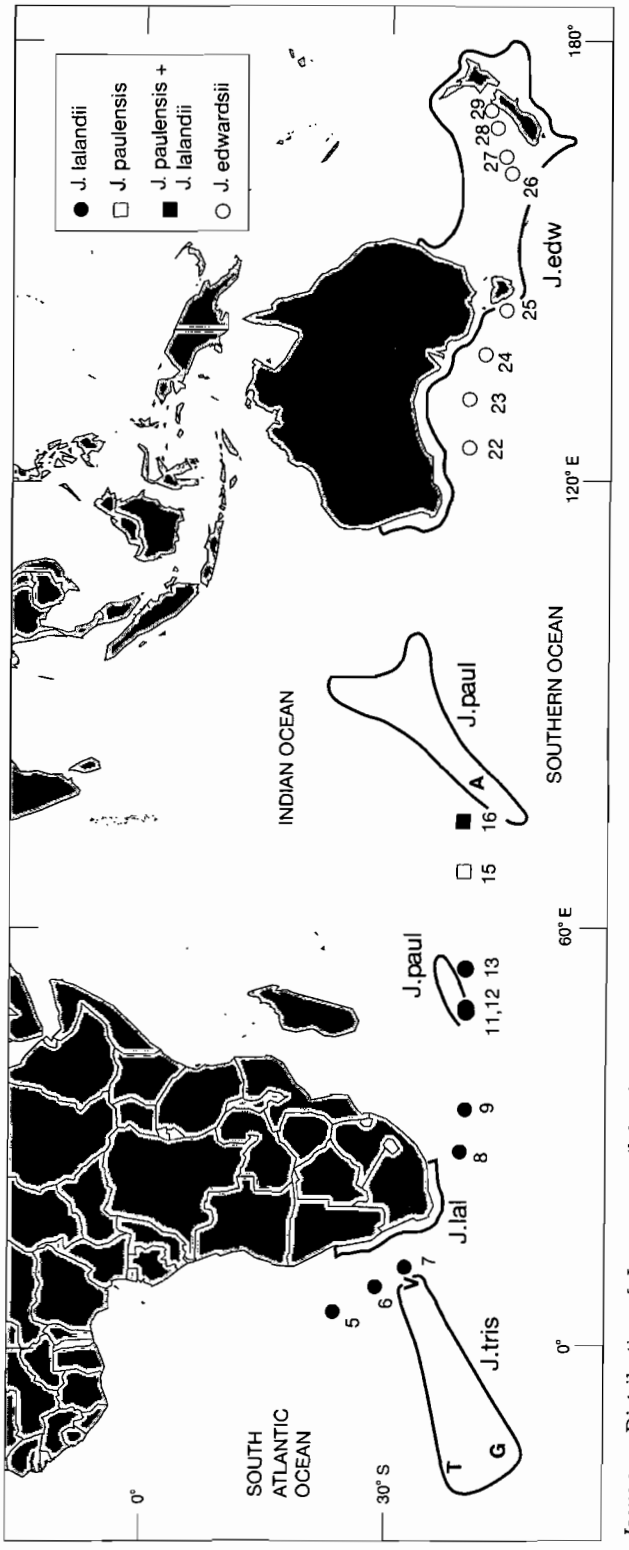

Fig. 3. *Jasus* spp. Distribution of *Jasus* group *'lalandii'* larvae identified genetically from the 210 larvae collected in June/July 1991 (see Table 1), and benthic occurrence of *Jasus* group *'lalandii'* based on references given in text and in Webber & Booth (1988). In addition, a single unknown *Jasus* larva was caught at Stn 7. Numbers = station numbers; V = Vema Seamount; T = Tristan da Cunha; G = Gough Island; A = Amsterdam and St. Paul Islands

adult grounds in winter.) Also, southern oceans would not generally be species-specific for adults and larvae. The recruitment mechanism for *Jasus lalandii* appears to have a latitudinal extent in the South Atlantic about the same as the benthic range of the species itself. The first 3 stations sampled off southern Africa (11 to 19° S), which were north of the range of benthic populations of *J. lalandii* (Pollock 1986), yielded no *Jasus* larvae. The following 3 stations, within the range of benthic *J. lalandii* (23° S and south), contained *Jasus* spp. larvae. Mid-stage larvae were particularly well represented, as was also reported for this region in winter by Lazarus (1967) and Pollock (1986). Our sampling could not address the east–west distribution of phyllosomas, but the lack of *J. tristani* larvae is consistent with a larval-recruitment mechanism being centred further west than our transect for that species. For *J. edwardsii* off southern Australia, the east–west distribution of the larvae matches that of the main benthic populations; large numbers of larvae were found only in eastern parts, coincident with the main benthic populations (Brown & Phillips 1994). Previous sampling off the east coast of the North Island of New Zealand (Booth et al. 1998) found larvae largely confined to a 1300 km wide pool, with a north–south distribution coinciding with the areas of high coastal postlarval settlement and recruited fishery.

An alternative explanation of our results, which is not testable with the present data, is that larvae disperse widely, but that much higher proportions of those close to the adults survive. To test this hypothesis, genetic analyses of early- and late-stage larvae would reveal the relationship between larval age and distance from the adults' grounds.

Although our results are from a single transect of unreplicated samples, and therefore may not necessarily represent the full picture at the time of sampling, nor indeed the usual picture, they are, for the South Atlantic section at least, consistent with the only other equivalent sampling—that of the Discovery Committee, reported by Gurney (1936).

The extensive plankton surveys of the Discovery Committee during the 1920s to 1950s included the South Atlantic Ocean; the sampling was undertaken to extend the knowledge of the southern marine environment. Phyllosomas from the 1925 to 1935 expeditions (station data in Discovery Reports, Volumes 1, 4, 21, and 22: Anonymous 1929, 1932, 1942, 1943) were described by Gurney (1936). Fig. 4 shows the position of all Gurney's stations in the South Atlantic Ocean which contained phyllosomas (palinurid or scyllarid); those containing *Jasus 'lalandii'* group larvae are highlighted. Also shown are the station positions for which Gurney did not report larvae. We have not been able to confirm that all phyllosomas from all samples were extracted and reported but other authors (e.g. Saisho 1966) appear to have proceeded as if this were so, and Gurney (1936, p. 423) himself states that no *Jasus* spp. larvae were taken west of near Tristan da Cunha. *Jasus* larvae occurred only off southern Africa, most commonly between 30 and 40° S. There was no evidence for entrainment of larvae via the Benguela Upwelling System into the more northern or western parts of the South Atlantic Gyre. The pattern emerging, which is consistent with data of Lazarus (1967), Pollock & Goosen (1983), Pollock (1986, 1991), Pollock et al. (1995), and the present study, is that there is a wedge of *Jasus* spp. larvae confined almost entirely to the southeast South Atlantic Ocean, with no larvae at all taken much further west than near Tristan da Cunha. This region of highest abundance of *Jasus* spp. larvae includes an area of very complex and dynamic hydrology. The low catches or absence of phyllosomas in the west South Atlantic is not surprising, given the paucity in abundance and species of scyllarids and palinurids on the east coast of South America compared with other areas such as those which border the west Indian Ocean (Holthuis 1991).

Our conclusion from these results is that, in general, *Jasus* spp. larvae that will eventually recruit to benthic populations remain near the adults, even though, as they develop, they may be transported tens or hundred of kilometres from shore. Larvae which do not remain so close to the adults are transported to an unknown fate, such as the *J. lalandii* which drift east into the south Indian Ocean. The exception seems to be those *J. edwardsii* transported the 2000 km from Australia to New Zealand.

Comparisons with other species

The only other data set extensive enough for comparison is that for *Panulirus cygnus* off Western Australia, where a moderately broad pool (perhaps 1500 km east–west) of larvae is indicated, with a north–south range about the same as that of the benthic population (Phillips 1981). This pattern is similar to that suggested for another west-coast population, *Jasus lalandii* in the South Atlantic Ocean (present data), for *J. edwardsii* off southern Australia and New Zealand (present data), and for *J. edwardsii* off the east coast of the North Island of New Zealand (Booth et al. 1998).

The *Panulirus* spp. larvae caught in the present study (Table 1) provide useful comparisons with the *Jasus* spp. data. Benthic *Panulirus* spp. do not occur on the west coast of southern Africa, yet *Panulirus* spp. larvae were taken at Stns 6 and 7 in moderate numbers (compared with *Jasus* spp.). Pollock (1991) and Pollock

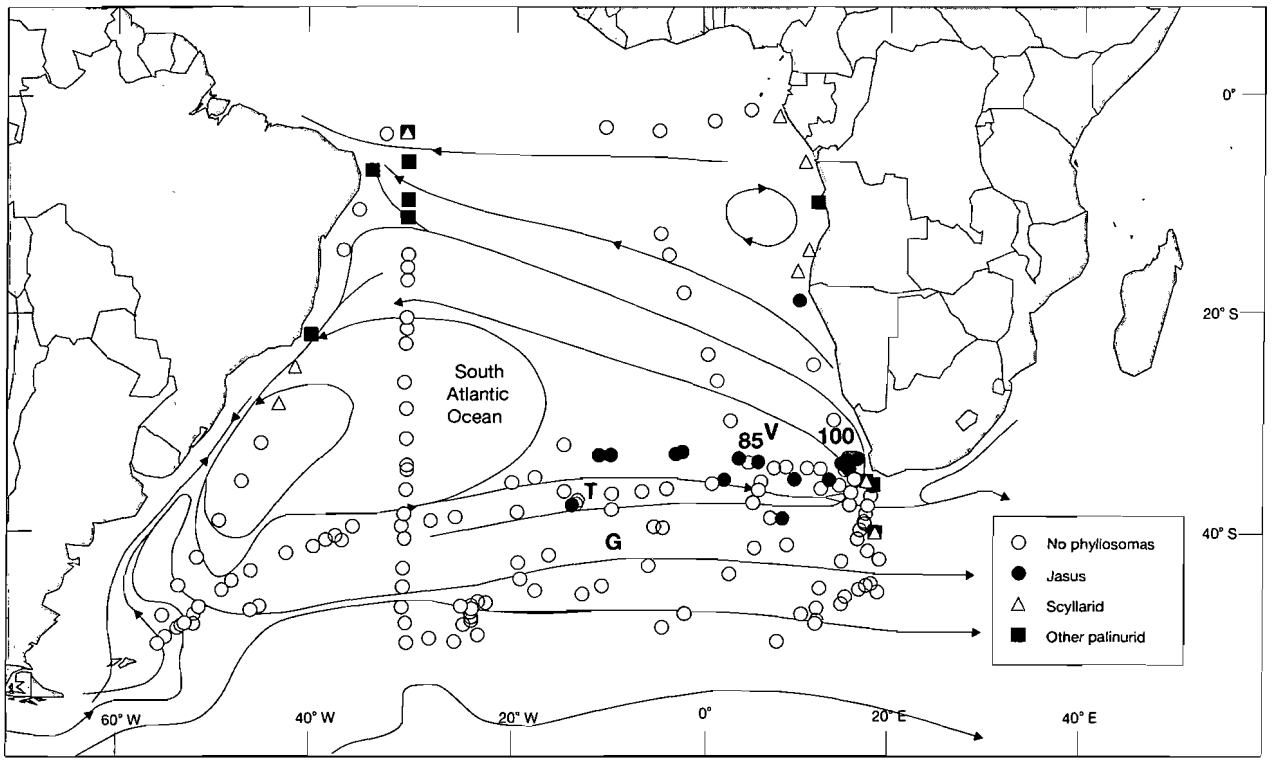

Fig. 4. Details of phyllosoma sampling reported by Gurney (1936). Map shows positions of all stations in Atlantic Ocean between Equator and 50° S from which fine-meshed net samples taken in upper 150 m of the ocean and at least ~100 km from shore contained phyllosoma larvae (palinurid or scyllarid) (from Discovery Committee 1925–1935 expeditions) (filled symbols). (●) stations with *Jasus 'lalandii'* group larvae, all had 1 to 3 advanced larvae, except Stns 85 and 100, which contained 21 and 11 advanced larvae, respectively; (○) all other stations between Equator and 50° S, which (presumably) did not contain phyllosomas; arrows show upper ocean currents and gyres (after Peterson & Stramma 1991). V = Vema Seamount; T = Tristan da Cunha; G = Gough Island

et al. (1995) also reported *Panulirus* larvae off the west coast, and cited this as evidence for the already well known transport of water from the southwest Indian Ocean into the east South Atlantic (Chapman 1988, Shillington 1998). Again, this seems to be an example of long-distance transport of larvae which does not lead to subsequent recruitment to benthic populations.

Several *Panulirus* species live on the southeast coast of southern Africa and further north (Berry 1971), so catches of *Panulirus* spp. larvae at stations in the southwest Indian Ocean, in numbers exceeding those of *Jasus* spp., were not surprising, and had been reported previously by Berry (1974). These phyllosomas were probably transported in the same flow as that carrying the *J. lalandii* larvae. *Panulirus* spp. phyllosomas were not, however, caught beyond Stn 12, while *J. lalandii* larvae were taken a further 2500 km east. One possible explanation is that, while *J. lalandii* larvae die at sea, *Panulirus* spp. larvae use some behavioural and physical opportunities to recruit back to benthic populations, possibly in a return flow associated with the South Madagascar Ridge (see Pollock 1989, Loder et al. 1998). Another possibility is that the tropical *Panulirus* spp. larvae die sooner in the cool water.

Implications of our results

Our conclusion that larval-recruitment mechanisms of *Jasus* spp. are of much more modest geographic scale than the size of ocean basins has some bearing on *Jasus* spp. resource-management because, intuitively, the smaller the scale of the larval recruitment system, the greater the chance that larval recruitment is derived from local spawnings and the possibility of there being a stock–recruit relationship. However, the long larval period and the extent of the offshore transport still make any persistent stock/recruit tie unlikely beyond that of no larvae where there is no stock. Our data also are consistent with Australia being a source of larval recruitment for New Zealand, although Australia is probably a much less important larval source than the New Zealand breeding stock itself, except possibly for the west and southwest of New Zealand (Booth et al. 1990). Although our study does not pro-

vide any direct information on the geographic scale of the recruitment mechanism for *J. frontalis* or *J. caveorum*, the restricted distribution and low abundance of the adults of those species favour confined mechanisms. Further support for this lies in the fact that although geographically by far the closest of all *Jasus* spp., these 2 species are only distantly related genetically (Ovenden et al. 1997).

When appropriate settlement cues are not available to competent larvae (Crisp 1974), some crustaceans can continue to moult without further morphological development (Gore 1985). *Jasus* spp. larvae appear to have this ability before metamorphosing to the puerulus stage. For example, Booth (1994) followed larval cohorts in the plankton and examined settlement peaks, and found that *J. edwardsii* larvae reach the final stage in 12 mo but can remain in the plankton up to 24 mo before metamorphosing. Furthermore, they can be cultured to settlement in just 10 mo (Kittaka et al. 1988, Kittaka 1994). Prolonged larval life gives the opportunity for more extensive dispersal of larvae than would be the case if larvae progressed directly to metamorphosis, as discussed by Pollock (1990a). The several large Stage 10 and 11 phyllosomas captured during our study may represent an example of delayed metamorphosis, since their size and development were much greater than those of the other larvae in the catches. However, the proportion of such larvae was small (<10%). One possible adaptive advantage of such an extended but variable larval life, which does not appear to lead to new or distant colonization, is that settlement can take place over many months of the year.

There are still several important unresolved issues. Genetic drift in isolated populations can be prevented by the successful recruitment of, on average, only 1 immigrant per generation (Hartl 1981), so how do *Jasus 'lalandii'* group species remain allopatric, given the extended development and wide dispersal potential of some larvae? In particular, how does the South African population of *J. lalandii*, only 1000 km east of the Vema Seamount population of *J. tristani* and in the same general north-flowing arm of the South Atlantic Gyre, remain distinct? And why does *J. lalandii* not occur on the seamounts in the southwest Indian Ocean and in the vicinity of St. Paul and Amsterdam Islands—areas both occupied by *J. paulensis*? Any mixing of species has important implications for management where, for example, phyllosoma, puerulus, juvenile, or pre-recruit abundance is measured for stock assessment, forecasting, and management: it would be reassuring to know that all lobsters belonged to the local target species. Possible explanations for failure of immigrants to reach adulthood include: (1) no appropriate cue for metamorphosis, (2) no appropriate cue for settlement, (3) pueruli settle but do not survive the early juvenile phase, and (4) juveniles survive, but do not mature sexually. Fulfilment of the first 2 possible explanations would be very difficult to test, but there are possible indications of them: phyllosomas of *Panulirus longipes femoristriga* are found near the coast of Hawaii, but adults of this species have not been reported from Hawaii (Phillips & McWilliam 1986); in the present study, *Panulirus* spp. larvae were taken off west South Africa. Genetic analyses of puerulus collections would address the 3rd possibility, e.g. *P. cygnus* pueruli have been taken on collectors in areas of Western Australia well north of the area where the adults of this species are found (Phillips & McWilliam 1986). The 4th possibility could be addressed through field sampling: key morphological and colour differences exist between several of the *Jasus* species (George & Kensler 1970). Because there are no reports of mixed species populations of *Jasus*, nor of wild-caught *Jasus* hybrids, any developmental blocks probably occur early in life.

The terms 'open' and 'closed' have been used to describe palinurid recruitment patterns (Menzies & Kerrigan 1979), but we question their usefulness for *Jasus* spp. and possibly for other palinurid genera. The feature which distinguishes the larval recruitment patterns of particular *Jasus* species is the geographic extent of the pattern, not how open-ended it is. For example, for *J. lalandii* in the South Atlantic, it is important to know whether the larvae are confined to southeast parts, or whether they can be found over the entire ocean basin (sensu Pollock 1990a).

Because of the limited ability of early- and mid-stage phyllosomas to swim horizontally, the position at which the larvae are captured can provide insight into current flows and directions—even though larval behaviours may reduce the extent of any such transport. Our results point to the following main currents: (1) some westward then northward flow from the southwest Indian Ocean into the southeast South Atlantic; (2) in the opposite direction, some eastward flow from the South Atlantic Ocean into the southwest Indian Ocean; (3) an eastward flow across the south Tasman Sea.

The capture of the unidentified *Jasus* larva off southern Africa suggests the presence of at least 1 more species in this genus. The larva appeared to share a polyphyletic origin with *J. edwardsii* and *J. frontalis* (Fig. 2), suggesting that it may be an as yet undiscovered species or outlying population of *Jasus* as opposed to a species, known or unknown, from another rock lobster genus. Although unexpected, its occurrence is consistent with the recent discovery of *J. caveorum*, the first new species of *Jasus* reported for more than 100 yr. This discovery arose when new areas in the vast South Pacific Ocean were fished for the first time (Webber & Booth 1995). However, although the

phylogenetic analysis (Fig. 2) and the pairwise nucleotide-distances (Table 3) suggest that the unknown larva may belong to a new *Jasus* species, the intraspecific lineage (Fig. 2) and sequence diversity of *J. lalandii* and *J. edwardsii* are, at least, considerable. Further analysis of either more individuals from each species, or more sequence data from existing individuals, may uncover existing diversity which may encompass that of the unknown larva. Similarly, further sequence data from larvae identified by the RFLP method may reveal diversity undetected by the 2 restriction enzymes used here.

CONCLUSIONS

Our results are based on the first extensive survey of palinurid larval distributions using large nets in southern oceans where the larvae have been identified to species level. They indicate that most *Jasus* spp. larvae that recruit to benthic populations employ behavioural strategies and/or physical processes (not yet understood) to avoid being carried too far (more than hundreds of kilometres) from the parental grounds. If widespread circulation in ocean basins were taking place, more widespread occurrence of larvae would be expected, and late-stage larvae would have been more strongly represented in our samples, at least off west Africa. Our results for *Jasus* spp., together with those already available for *Panulirus cygnus*, question the likelihood of larval recruitment mechanisms on an ocean-basin scale for any palinurid (see Pollock 1989, 1990a). Our results, together with those of Lee et al. (1994) and Chiswell & Booth (1999), show how localised recruitment mechanisms can be; however, a small, but perhaps not insignificant, percentage of *Jasus* spp. larvae are carried great distances. We conclude (as did Pollock 1990a) that there must then be some block to the establishment and breeding of the species in these distant waters, but our work sheds no further light on this.

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LITERATURE CITED

Annala JH (1991) Factors influencing fecundity and population egg production of *Jasus* species. In: Wenner A, Kuris A (eds) Crustacean egg production. AA Balkema, Rotterdam, p 301–315

Anonymous (1929) Station list 1925–1927. Discov Rep 1:3–140

Anonymous (1932) Station list 1929–1931. Discov Rep 4:3–230

Anonymous (1942) Station list 1931–1933. Discov Rep 21:2–226

Anonymous (1943) Station list 1933–1935. Discov Rep 22:3–196

Arana P (1987) Historical perspective and projections of the fisheries activity in the Archipelago of Juan Fernandez, Chile. In: Castilla JC (ed) Islas oceanicas Chilenas: conocimiento cientifico y necesidades de investigaciones. Ediciones Universidad Catolica de Chile, Santiago, p 319–353

Arana P, Dupre E, Gaete V (1985) Ciclo reproductivo, talla de primera madurez sexual y fecundidad de la langosta de Juan Fernandez (*Jasus frontalis*). In: Arana Espina P (ed) Investigaciones marinas en el Archipielago de Juan Fernandez. Escuela de Ciencias del Mar, Facultad de Recursos Naturales, Universidad Catolica de Valparaiso, Valparaiso, p 187–211

Baez P (1973) Larvas phyllosoma del Pacifico sur Oriental (Crustacea, Macrura, Scyllaridea). Rev Biol Mar Valparaiso 15:115–130

Berry PF (1971) The spiny lobsters (Palinuridae) of the east coast of southern Africa: distribution and ecological notes. Investl Rep Oceanogr Res Inst, Durban 27:1–23

Berry PF (1974) Palinurid and scyllarid lobster larvae of the Natal coast, South Africa. Investl Rep Oceanogr Res Inst, Durban 34:1–44

Booth JD (1986) Recruitment of packhorse rock lobster *Jasus verreauxi* in New Zealand. Can J Fish Aquat Sci 43: 2212–2220

Booth JD (1994) *Jasus edwardsii* larval recruitment off the east coast of New Zealand. Crustaceana 66:295–317

Booth JD, Breen PA (1994) The New Zealand fishery for *Jasus edwardsii* and *J. verreauxi*. In: Phillips BF, Cobb JS, Kittaka J (eds) Spiny lobster management. Blackwell Scientific Publications, Oxford, p 64–75

Booth JD, Phillips BF (1994) Early life history of spiny lobster. Crustaceana 66:271–294

Booth JD, Stewart RA (1992) Distribution of phyllosoma larvae of the red rock lobster *Jasus edwardsii* off the east coast of New Zealand in relation to the oceanography. In: Hancock DA (ed) Australian Society for Fish Biology Workshop Larval Biology. Australian Government Publishing Service, Canberra, p 138–148 (Bureau of Rural Resources Proceedings No. 15)

Booth JD, Street RJ, Smith PJ (1990) Systematic status of the rock lobsters *Jasus edwardsii* from New Zealand and *J. novaehollandiae* from Australia. NZ J Mar Freshw Res 24: 239–249

Booth JD, Forman JS, Stotter DR (1998) Abundance of early life history stages of the red rock lobster, *Jasus edwardsii*, with management implications. NZ Fish Assessment Res Doc 98/10:(Ministery of Fisheries Wellington) 1–130

Brasher DJ, Ovenden JR, White RWG (1992) Mitochondrial DNA variation and phylogenetic relationships of *Jasus* spp. (Decapoda: Palinuridae). J Zool 227:1–16

Brown RS, Phillips BF (1994) The current status of Australia's rock lobster fisheries. In: Phillips BF, Cobb JS, Kittaka J (eds) Spiny lobster management. Blackwell Scientific Publications, Oxford, p 33–63

Chapman P (1988) On the occurrence of oxygen-depleted water south of Africa and its implications for Agulhas–Atlantic mixing. S Afr J Mar Sci 7:267–294

Chiswell SM, Booth JD (1999) Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. Mar Ecol Prog Ser 183:227–240

Chiswell SM, Roemmich D (1998) The East Cape Current and two eddies: a mechanism for larval retention? NZ J Mar Freshw Res 32:385–397

Collette BB, Parin NV (1991) Shallow-water fishes of Walters Shoals, Madagascar Ridge. Bull Mar Sci 48:1–22

Crisp DJ (1974) Energy relations of marine invertebrate larvae. Thalassia Jugosl 10:103–120

Doyle JJ, Doyle JL (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochem Bull 19:11–15

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molec Mar Biol Biotechnol 3:294–299

Gardner C, Cawthorn A, Gibson I, Frusher S, Kennedy RB, Pearn RM (1998) Review of the southern rock lobster *Jasus edwardsii* puerulus monitoring program: 1991–1997. Tech Rep Dep Prim Ind Fish Mar Res Div 52:1–51

George RW, Kensler CB (1970) Recognition of marine spiny lobsters of the *Jasus lalandii* group (Crustacea: Decapoda: Palinuridae). NZ J Mar Freshw Res 4:292-311

Gore RH (1985) Molting and growth in decapod larvae. In: Schram FR (ed) Crustacean issues, Vol 2. AA Balkema, Rotterdam, p 1–66

Grua P (1963) Maturité, cycle sexuel, soies ovigères des langoustes Australes femelles *Jasus paulensis* Heller 1863—étude statistique. Comité national français des recherches antarctiques 4:1–35

Gurney R (1936) Larvae of decapod crustacea. Discov Rep 12: 379–440

Hartl DL (1981) A primer of population genetics. Sinauer Associates, Sunderland, MA

Heydorn AEF (1969) The South Atlantic rock lobster *Jasus tristani* at Vema Seamount, Gough Island and Tristan da Cunha. Investl Rep Div Sea Fish Repub S Afr 73:1–20

Holthuis LB (1963) Preliminary descriptions of some new species of Palinuridea (Crustacea, Decapoda, Macrura Reptantia). Proc K Ned Akad Wet 66:54–60

Holthuis LB (1991) Marine lobsters of the world: an annotated and illustrated catalogue of species of interest to fisheries known to date. FAO Fish Synopsis 125(13):1–292 (FAO Species Catal No. 13)

Holthuis LB, Sivertsen E (1967) The Crustacea Decapoda, Mysidacea and Cirripedia of the Tristan da Cunha Archipelago with a revision of the 'frontalis' subgroup of the genus *Jasus*. Results Norw Sci Exped Tristan da Cunha 1937–1938 52:1–55

Kensler CB (1967) The distribution of spiny lobsters in New Zealand waters (Crustacea: Decapoda: Palinuridae). NZ J Mar Freshw Res 1:412-420

Kittaka J (1988) Culture of the palinurid *Jasus lalandii* from egg stage to puerulus. Nippon Suisan Gakkaishi 54:87–93

Kittaka J (1994) Culture of phyllosomas of spiny lobster and its application to studies of larval recruitment and aquaculture. Crustaceana 66:258–270

Kittaka J, Iwai M, Yoshimura M (1988) Culture of a hybrid of spiny lobster genus *Jasus* from egg stage to puerulus. Nippon Suisan Gakkaishi 54:413–17

Kittaka J, Ono K, Booth JD (1997) Complete development of the green rock lobster, *Jasus verreauxi* from egg to juvenile. Bull Mar Sci 61:57–71

Lazarus BI (1967) The occurrence of phyllosomata off the Cape with particular reference to *Jasus lalandii*. Investl Rep Div Sea Fish Repub S Afr 63:1–38

Lee TN, Clarke ME, Williams E, Szmant AF, Berger T (1994) Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. Bull Mar Sci 54:621–646

Lesser JHR (1978) Phyllosoma larvae of *Jasus edwardsii* (Hutton) (Crustacea: Decapoda: Palinuridae) and their distribution off the east coast of the North Island, New Zealand. NZ J Mar Freshw Res 12:357-370

Lewis RK (1977) Rock lobster puerulus settlement in the south east. SAFIC 13:9–11

Loder JW, Boicourt WC, Simpson JH (1998) Western ocean boundary shelves. Coastal segment (W). In: Robinson AR, Brink KH (eds) The sea, Vol 11. John Wiley & Sons, New York, p 3–27

Lutjeharms JRE, Heydorn AEF (1981a) The rock-lobster *Jasus tristani* on Vema Seamount: drifting buoys suggest a possible recruiting mechanism. Deep-Sea Res 28A:631–636

Lutjeharms JRE, Heydorn AEF (1981b) Recruitment of rock lobster on Vema Seamount from the islands of Tristan da Cunha. Deep-Sea Res 28A:1237

Lutjeharms JRE, Shannon LV, Beekman LJ (1988) On the surface drift of the Southern Ocean. J Mar Res 46:267–279

McWilliam PS, Phillips BF (1987) Distinguishing the phyllosoma larvae of rock lobster species of the genus *Jasus* (Decapoda, Palinuridae) in the waters of Australia and New Zealand. Crustaceana 52:1–24

Menzies RA, Kerrigan JM (1979) Implications of spiny lobster recruitment patterns of the Caribbean—a biochemical genetic approach. Proc Gulf Caribb Fish Inst 31:164–178

Miller DGM (1985) A late phyllosoma larva of *Jasus tristani* Holthuis (Decapoda, Palinuridea). Crustaceana 50:1–6

Ovenden JR, Brasher DJ, White RWG (1992) Mitochondrial DNA analyses of the red rock lobster *Jasus edwardsii* supports an apparent absence of population subdivision throughout Australasia. Mar Biol 112:319–326

Ovenden JR, Booth JD, Smolenski AJ (1997) Mitochondrial DNA phylogeny of red and green rock lobsters (genus *Jasus*). Mar Freshw Res 48:1131–1136

Peterson RG, Stramma L (1991) Upper-level circulation in the South Atlantic Ocean. Prog Oceanogr 26:1–73

Phillips BF (1981) The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr Mar Biol Annu Rev 19:11–39

Phillips BF, McWilliam PS (1986) The pelagic phase of spiny lobster development. Can J Fish Aquat Sci 43: 2153–2163

Pollock DE (1986) Review of the fishery for and biology of the cape rock lobster *Jasus lalandii* with notes on larval recruitment. Can J Fish Aquat Sci 43:2107-2117

Pollock DE (1989) Spiny lobsters. In: Payne AIL, Crawford RJM (eds) Oceans of life off southern Africa. Vlaeberg, Cape Town, p 70–80

Pollock DE (1990a) Palaeoceanography and speciation in the spiny lobster genus *Jasus*. Bull Mar Sci 46:387–405

Pollock DE (1990b) Spiny lobster survey at Tristan da Cunha. Lobster Newsl 3(1):4

Pollock DE (1991) Spiny lobsters at Tristan da Cunha, South Atlantic: inter-island variations in growth and population structure. S Afr J Mar Sci 10:1–12

Pollock DE, Bailey G, van der Byl P (1995) Phyllosoma larvae in the south-east Atlantic: a case for long-distance dispersal. Lobster Newsl 8(1):6–7

Pollock DE, Goosen PC (1983) Phyllosoma larvae survey for west coast rock lobsters. S Afr J Sci 79:144

Pollock DE, Melville-Smith R (1993) Decapod life histories and reproductive dynamics in relation to oceanography off southern Africa. S Afr J Mar Sci 13:205–212

Polovina JJ, Moffitt RB (1995) Spatial and temporal distribution of the phyllosoma of the spiny lobster, *Panulirus marginatus*, in the northwestern Hawaiian Islands. Bull Mar Sci 56:406–417

Roscoe MJ (1979) Biology and exploitation of the rock lobster *Jasus tristani* at the Tristan da Cunha Islands, South Atlantic, 1949–1976. Investl Rep Sea Fish Brch S Afr 118:1–47

Saisho T (1966) Studies on the phyllosoma larvae with reference to the oceanographical conditions. Mem Fac Fish Kagoshima Univ 15:177–239

Shannon LV, Stander GH, Campbell JA (1973) Oceanic circulation deduced from plastic drift cards. Investl Rep Sea Fish Brch S Afr 108:1–31

Shillington FA (1998) The Benguela Upwelling System off southwestern Africa. Coastal segment (16,E). In: Robinson AR, Brink KH (eds) The sea, Vol 11. John Wiley & Sons, New York, p 583–604

Silas EG (1967) On the taxonomy, biology and fishery of the spiny lobster *Jasus lalandei frontalis* (H. Milne-Edwards) from St. Paul and New Amsterdam Islands in the southern Indian Ocean, with an annotated bibliography on species of the genus *Jasus* Parker. In: Proceedings of the Symposium on Crustacea—Part IV. Marine Biological Association of India, Bangalore Press, Bangalore, p 1466–1520

Stander GH, Shannon LV, Campbell JA (1969) Average velocities of some ocean currents as deduced from the recovery of plastic drift cards. J Mar Sci 27:293–300

Street RJ (1969) The New Zealand crayfish *Jasus edwardsii* (Hutton 1875). Fish Tech Rep NZ Mar Dep 30:1–31

Webber WR, Booth JD (1988) *Projasus parkeri* (Stebbing, 1902) (Crustacea, Decapoda, Palinuridae) in New Zealand and description of a *Projasus* puerulus from Australia. Natl Mus N Z Rec 3:81–92

Webber WR, Booth JD (1995) A new species of *Jasus* (Crustacea: Decapoda: Palinuridae) from the eastern South Pacific Ocean. NZ J Mar Freshw Res 29:613–622

Williamson DI (1967) Some recent advances and outstanding problems in the study of larval crustacea. In: Proceedings of the Symposium on Crustacea—Part II. Marine Biological Association of India, Bangalore Press, Bangalore, p 815–823

Winstanley RH (1970) Rock lobster larvae in the Tasman Sea. Tasm Fish Res 4(1):11–12

Winstanley RH (1977) Biology of the southern rock lobster. In: The Victorian southern rock lobster fishery Seminar. Fisheries and Wildlife Division, Ministry for Conservation, Victoria, p 1–6

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