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 'verreauxii' group, containing only *J. verreauxii*, 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
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 Saperpers 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 south-east 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).


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; Annale 1991). Females
spawn in autumn (April to May), and eggs hatch in
spring to summer (September to January). Early phyl-
losomas 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 (Kit-
taka 1988, Kittaka et al. 1988). Settlement is often
highest during winter (Holthuis & Silvertsen 1967,
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 sum-
mer, 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 molting (Gore
1994, Booth & Phillips 1994). Claims that the Jasus
'lalandii' group larvae are morphologically distin-
guishable (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 phyllo-
soma 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 trans-
parent 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 in-
creasingly apparent that most currents are far more
complex than a simple flow between 2 points, and that
diffusion 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,

Indeed, Chiswell & Booth (1999) showed that the dis-
tribution of mid-stage J. edwardsii larvae off the east
cost 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 hori-
Zontal distributions), or through local physical pro-
ces (e.g. presence of counter currents). This hypoth-
esis was referred to as a 'closed' recruitment pattern by
Menzies & Kerrigan (1979), an example being Pan-
ulirus cygnus off Western Australia (Phillips 1981). The
second hypothesis is that the phyllosomas are dis-
persed widely—the 'open' recruitment pattern, sensu
Menzies & Kerrigan (1979). For Jasus spp., open
recruitment patterns might include those in which lar-
vae 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
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 hun-
dreds 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 sta-
ton have been small (<10) (Gurney 1936, Silas 1967,

On the other hand, more contained larval distribu-
tions exist. Advanced phyllosomas of the Jasus 'la-
landii' 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-

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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-
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. 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' GGTCAACAAATCATAAA-GACCAAAAAATCA 3') of Folmer et al. (1994). 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.

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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

<table>
<thead>
<tr>
<th>Morphotype</th>
<th>n (seq)</th>
<th>n (RFLP)</th>
<th>Hae III</th>
<th>Nla III</th>
</tr>
</thead>
<tbody>
<tr>
<td>J. edwardsii</td>
<td>13</td>
<td>28</td>
<td>C</td>
<td>B</td>
</tr>
<tr>
<td>J. lalandii</td>
<td>4</td>
<td>28</td>
<td>A</td>
<td>A</td>
</tr>
<tr>
<td>J. tristani/J. paulensis</td>
<td>3</td>
<td>28</td>
<td>D</td>
<td>C</td>
</tr>
</tbody>
</table>

J. 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).

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.
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

<table>
<thead>
<tr>
<th></th>
<th>J. lalandii (1)</th>
<th>J. edwardsii (2)</th>
<th>J. tristani/</th>
<th>J. frontalis (4)</th>
<th>Unknown larva (5)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>J. paulensis (3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.0425</td>
<td>0.0824</td>
<td>0.0478</td>
<td>0.0340</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.0060</td>
<td>0.0843</td>
<td>0.0442</td>
<td>0.0383</td>
<td></td>
</tr>
<tr>
<td>3</td>
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<td>0.0879</td>
<td></td>
</tr>
<tr>
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<td>0.0029</td>
<td>0.0089</td>
<td>0.0463</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0.0045</td>
<td>0.0037</td>
<td>0.0098</td>
<td>na</td>
<td></td>
</tr>
</tbody>
</table>

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. Phylosomas 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 phylosomas 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 phylosomas 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.
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 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
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 hundreds 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 distinctly 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 & Kessler 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 was 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


Booth JD, Lovendy: Larval distribution of Jasus spp.

Pollock DE (1990b) Spiny lobster survey at Tristan da Cunha. Lobster News 3(1):4
Booth & Ovenden: Larval distribution of Jasus spp.

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


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