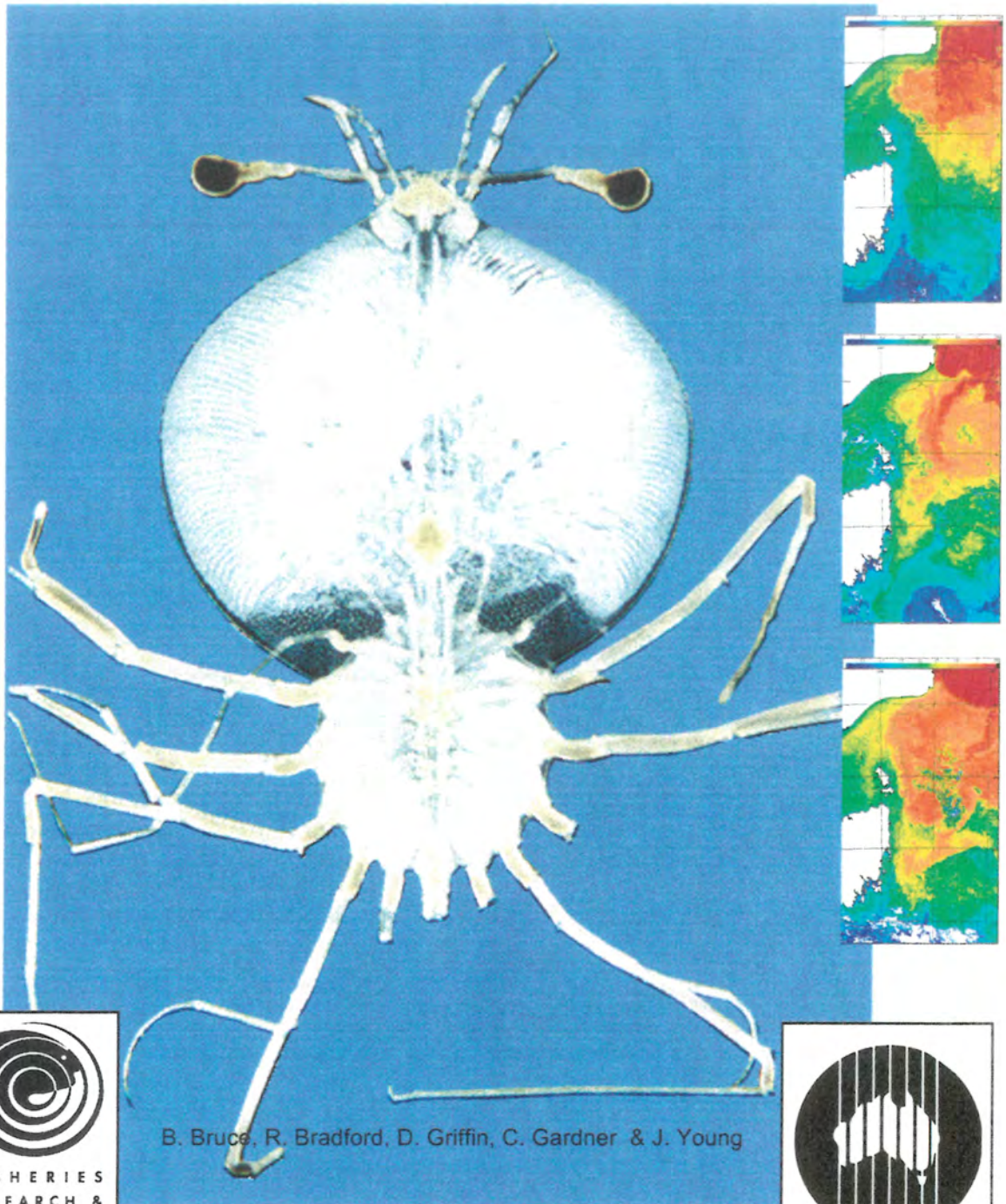
A synthesis of existing data on larval rock lobster distribution in southern Australia

Project 96/107



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Final Report to FRDC

FISHERIES RESEARCH & DEVELOPMENT CORPORATION

CSIRO

A SYNTHESIS OF EXISTING DATA ON LARVAL ROCK LOBSTER DISTRIBUTION IN SOUTHERN AUSTRALIA

Final Report to the Fisheries Research and Development Corporation

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B. Bruce, R. Bradford, D. Griffin, C. Gardner and J. Young

CSIRO Marine Laboratories Hobart

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1. Non-technical Summary

The southern rock lobster fishery is worth over $100 million annually. It is considered to be fully exploited and catch rates are declining in some regions (eg north-east Tasmania and Victoria). Current management practices divide the fishery into seven functionally independent zones and assume that populations within each zone contribute only to local recruitment. However, southern rock lobster larvae are long-lived and have been found considerable distances (100's of kilometres) from shore in areas of southern Australia dominated by west to east current flows. This suggests ample opportunity for long distance transport of larvae between management zones. Recruitment within a management zone may thus not be restricted to larvae produced solely within that zone, but may depend on what happens in either adjacent or distant zones. There are large variations in egg production throughout the range of the fishery (and in some cases between areas in the same management zone). It is thus possible that egg production in certain regions is more important in sustaining the fishery than that from others.

The implications of geographically variable egg production, the extent of larval dispersal, factors influencing settlement of puerulus and the effects on these of environmental variability are issues in which managers, researchers and the industry have long shared an interest. These issues have important ramifications for the long-term management of the fishery. In addition, using the level of puerulus settlement to monitor the health of the fishery; collecting newly settled puerulus from the wild for aquaculture; culturing southern rock lobster larvae from eggs and the question of whether reproductive output from southern rock lobster in marine reserves may contribute to local recruitment, have further increased the demand for information about early life history stages and the factors influencing their growth, survival, transport and settlement.

This study examined the larval biology and ecology of the southern rock lobster based on approximately 3000 archived plankton and mid-water trawl samples held, principally, by CSIRO, Tasmanian Aquaculture and Fisheries Institute (TAFI – formerly DPIF, Tas), and the Marine and Freshwater Research Institute (MAFRI). Additional samples were provided by the National Institute of Water and Atmosphere (NIWA, New Zealand) and some samples were opportunistically collected during the project to fill in areas where there was a lack of archived samples. The combined sample set covered the major geographic range of the fishery. Details of larval growth, duration and distribution were combined with concurrently collected hydrographic data and satellite based observations to examine possible larval transport mechanisms, connectivity between management zones and physical factors that may influence the supply of larvae on a regional basis.

Southern rock lobster have a similar early life history strategy to that reported for other rock lobsters. Larvae develop through a series of 11 flattened leaf-like stages (phyllosoma) before finally

transforming into a non-feeding swimming stage that resembles the juvenile (puerulus). Phyllosoma of southern rock lobster were collected throughout the region, except within Bass Strait. Phyllosoma were found to the limit of sampling in most regions and up to 550km from the coast. Abundances of phyllosoma were similar to that reported for other rock lobster species elsewhere. The highest abundances were recorded in Tasmanian waters. Early (stages I – IV) stage larvae were primarily collected from shelf waters; mid (stages V – VIII) and late (stages VIIIA – XI) larvae were found offshore, or in the vicinity of the shelf break. Early stage larvae were collected in Spring and Summer; mid stage larvae in Autumn; mid and late stage larvae in Winter. Larvae were primarily confined to the upper 100 m of the water column and were commonly found at the surface. There was some evidence of larvae vertically migrating into the surface waters at night, although the pattern was less marked than reported for other rock lobster species. Southern rock lobster phyllosoma were sometimes collected at the surface during the day, although most daytime captures were either late afternoon or early morning.

Southern Rock lobster phyllosoma were primarily found within a limited temperature-salinity (T/S) range when compared to the total data set. The T/S signature of this "phyllosoma water" (12.2-15.0 °C; 34.70-35.08 ppt) corresponded to water of the Subtropical Front (STF), a major convergence zone separating the cool Sub-Antarctic Water (SAW) from warmer waters of tropical origin (eg the East Australian Current or the Leeuwin Current).

We estimated a mean total larval duration of 17-18 months, with puerulus first appearing 15-16 months after hatching. Given these estimates and the timing of major settlement peaks in eastern Tasmanian waters, we suggest that the first major settlement of southern rock lobster, after hatching in Spring-Summer, is during the following summer, 13-17 months later. We suspect that some phyllosoma do not settle at that time but remain competent to do so, and continue to settle through the following winter up to some 20-24 months after hatching. This model accounts for the two cohorts of larvae observed in plankton samples at most times of the year and helps explain why puerulus may settle at most times of the year.

We used satellite-based observations of circulation processes (eg. altimetry, sea surface temperature – SST and satellite tracked drifters) combined with broad-scale animation techniques to look at transport processes in southern Australia that were of a scale relevant to the early life history of southern rock lobster. We specifically concentrated on circulation processes within the Subtropical Front where the majority of larvae occurred. Satellite tracked drifters released around Tasmania showed a remarkable tendency to remain within several hundred kilometres of the coast for periods up to 19 months and several returned to, or near to, shelf waters after lengthy periods offshore. Interestingly, drifter paths suggest that advection need not always follow a west to east pattern but some reverse flows also occur. In a couple of notable cases, drifters returned to the same site of deployment after periods in excess of 12 months offshore. While it is doubtful that phyllosoma behave the same as a satellite tracked drifter, this does suggest that there are mechanisms that could limit the loss of southern rock lobster larvae to a

generalised west to east flow. We propose that the larvae contributing to successful settlement may be those that are not lost in the west to east flow but are those that are able to take advantage of these regional retention mechanisms. The spatial scale of these mechanisms may dictate which areas in southern Australia have linked settlement patterns.

Southern rock lobster phyllosoma were restricted to waters south of north-east mainland Tasmania (the northern limit of the STF) and it is thus doubtful that significant settlement occurs north of Flinders Island. This distribution also suggests that puerulus may not reliably settle at Flinders Island each year and that larval supply (and thus presumeably settlement) may be dependant on the behaviour of the STF. This is supported by evidence of either low-level, or complete settlement failure in this area in various years. Thus, settlement at Flinders Island may not reliably indicate trends in adult stock but rather the supply of larvae via large-scale physical oceanographic phenomena.

The seasonal cycle of the STF and East Australian Current may, in part, account for the bimodal pattern of settlement observed off the east coast of Tasmania. The STF moves north and south on a seasonal basis and its position coincides with the timing of peak settlement periods along that coast. There is also some evidence that inter-annual variability in the seasonal movement of the STF and East Australian Current water may influence overall settlement patterns off eastern Tasmania.

Results of the project demonstrate the utility of larval data, the value of archiving previously collected samples and the advantages of combining biological and physical data sets over scales relevant to the early life history of target species. The data visualization and animation techniques used provide a way of examining broad-scale factors that may influence settlement patterns and larval transport processes.

2. Background

The southern rock lobster (*Jasus edwardsii*) is an Australasian species that supports some of the most valuable fisheries in both southern Australia and New Zealand. The commercial catch of southern rock lobster (SRL) in Australian waters is worth in excess of $100 million dollars annually. The majority of the catch is taken in South Australia, Victoria and Tasmania. The SRL fishery is considered to be fully exploited throughout the Australian region with catch rates declining in some areas (eg north-eastern Tasmania and Victoria).

The Australian fishery is divided into seven functionally independent management units (Western Australia, Tasmania, New South Wales, and two each in South Australia and Victoria), each of which assume SRL populations within their zone only contribute to local recruitment. Genetic homogeneity throughout the distribution of *J. edwardsii* suggests that there is some mixing between zones which has been attributed to larval dispersal (Ovenden & Brasher 1994). However, migration rates as low as one individual in one thousand per generation are sufficient to maintain genetic homogeneity between populations (Lewontin 1974 as in Scheltema 1986). Therefore, it has not been resolved whether there are several biologically independent breeding populations or whether there are important, discrete sources of larvae that supply and maintain recruitment to the various regions of the fishery.

3. Need

The need to understand more about the early life history of SRL is summed up by the following questions that have been commonly posed by industry, researchers and managers:

- To what extent are populations (or management zones) connected via larval transport?
- Where do recruits come from?
- Does what happen in one management zone (eg over fishing) influence another?
- Are some areas of the fishery more important for generating recruits than others?
- Can the regional, annual and inter-annual signals detected by puerulus settlement monitoring programs be interpreted so as to give a picture of the health of the fishery and eventually be incorporated into management strategies and catch predictions with the same success as achieved for western rock lobster?

Egg production varies markedly across the range of the SRL fishery. For example, egg production is less than 15% of the virgin biomass in the north west of Tasmania and nearly 100% in the south of Tasmania (Kennedy et al. 1994). It is thus possible that egg production in some areas is more important in sustaining the fishery than egg production from others. A key unknown within the SRL fishery is whether management zones are self-recruiting or depend on larvae from outside their own boundaries. The dominant current regimes across much of the distribution of the fishery are from west to east. However, it is not known whether western populations are important source localities for recruitment throughout the east and hence deserving of special management considerations. Nor is it known if there

are specific oceanographic processes that retain larvae within different regions and facilitate recruitment to some populations.

Understanding the links between management zones through spawning production, larval dispersal and recruitment, and the role played by environmental variability, are important for the long-term sustainability and optimal management of the SRL fishery in southern Australia.

Since the implementation of this project, a further need for information on the larval stages of SRL and interpreting patterns of puerulus settlement has been generated by the developing interest in phyllosoma culture and both the harvesting and on-growing of puerulus. Questions posed by aquaculture relate to what conditions phyllosoma grow and survive best in the wild; what characterises good and bad growth and comparing the condition of wild caught to reared larvae as an initial bench mark for aquaculture progress.

Concerns over the effects of puerulus collection for aquaculture has further highlighted issues directly related to the questions posed above including the source of settlers, why settlement patterns vary on a regional and inter-annual basis, and the regional implications of puerulus harvesting.

4. Objectives

The specific objectives of this project were to:

- Map the distribution of SRL in southern Australia from existing plankton samples
- Hind-cast interannual, depth-dependent, ocean circulation and hydrography during the period of larval availability
- Determine possible larval transport mechanisms and their implications for the connectivity of management zones in the SRL fishery
- Examine the relationship between offshore ocean climate, distribution of phyllosoma and settlement of puerulus off eastern Tasmania

A parallel objective was to identify the most significant weakness in our understanding of larval transport processes and determine the most appropriate directions for future work.

In response to the increasing demand for information about SRL larvae from aquaculture, we added the further objectives of describing the temperature and salinity conditions in which larvae are found in the wild and an analysis of the growth patterns of phyllosoma.

5. Overall Methods

5.1 Scope and Rationale of Project

The primary basis for the project has been the analysis of archived plankton and mid-water trawl samples that were collected across broad areas of southern Australian coastal and offshore waters over

the last ten years. These samples had been collected during a series of research cruises designed primarily to sample other taxa including mid-water fishes, general zooplankton, larval fish, fish eggs, krill and phytoplankton. Studies from which samples were examined included those previously funded by FRDC as well as studies funded by CSIRO and cooperating institutions. This approach has had both significant advantages and disadvantages.

Prior to this study, very little data was available on the distribution of SRL larvae in southern Australia thus any targeted sampling would have first required an exploratory field program. The re-analysis of the existing samples represented a considerable saving over instigating a field program from scratch. This was particularly emphasized by the broad spatial and temporal coverage provided by the samples. Rock lobsters have widely spread and long lived larvae that occur primarily in offshore waters. It is thus important to match sampling to scales relevant to this aspect of their life history. The estimated cost of ship-time alone to recollect the samples available to the project was estimated at $3.6 million. It was obviously neither practical nor economically viable to pursue a new field program of this magnitude. The analysis of existing samples presented a considerable cost and time saving over establishing a field program to repeat the sampling effort that was available to us.

Despite these benefits, working with samples collected for other purposes also presented some difficulties. Samples were not initially collected with phyllosoma or puerulus in mind and thus the original sampling strategies may not always have maximised the chances of detecting their presence or matched the optimal scale required for resolving specific questions (eg vertical distribution). Samples spanned a ten-year period and, although it was possible to compare some areas on an interannual and seasonal basis, the overall data set on distribution represents a composite image with a resultant decrease in temporal resolution. This is, however, an inevitable consequence of the scale of distribution in rock lobster larvae. Many samples had been previously sorted for other taxa (either in lab or rough sorted and processed at sea) and it is thus possible that some phyllosoma may have been inadvertently discarded or lost during this process. Finally, some samples had been poorly curated after they were initially sorted. This resulted in some phyllosoma being in poor condition or placed in fixatives that were inappropriate for some techniques (eg genetics). As a result, our analyses have been largely exploratory to seek and interpret data relevant to the issues identified in Section 3 (Need).

5.2 Sources of data (collaborating institutions)

Zooplankton and micronekton samples archived at CSIRO and TAFI formed the majority of the data set. Some data on SRL larval distribution in offshore waters of southern Australia was also obtained from NIWA (Dr John Booth). Where possible, we also obtained additional material via opportunistic sampling during CSIRO cruises within the study area during the course of the project (GAB, offshore western Tasmania). Finally, sorted phyllosoma were provided by MAFRI from one of their cruises in Bass Strait. The sources of samples are listed in Table 1.

Puerulus settlement data for Tasmanian waters was supplied by TAFI.

Table 1 Sources of samples

Cruise	Vessel	Institution	Year	Area	Original sampling target
CH189	Challenger	DPIF (Tas)*	1989	EC Tasmania	Jack mackerel larvae
CH190	Challenger	DPIF (Tas)	1989	EC Tasmania	Jack mackerel larvae
CH193	Challenger	DPIF (Tas)	1989	EC Tasmania	Jack mackerel larvae
CH197	Challenger	DPIF (Tas)	1989	EC Tasmania	Jack mackerel larvae
CH198	Challenger	DPIF (Tas)	1989	EC Tasmania	Jack mackerel larvae
CH215	Challenger	DPIF (Tas)	1989	EC Tasmania	Jack mackerel larvae
CH217	Challenger	DPIF (Tas)	1989	EC Tasmania	Jack mackerel larvae
CH218	Challenger	DPIF (Tas)	1990	EC Tasmania	Jack mackerel larvae
CH219	Challenger	DPIF (Tas)	1990	EC Tasmania	Jack mackerel larvae
CH221	Challenger	DPIF (Tas)	1990	EC Tasmania	Jack mackerel larvae
CH222	Challenger	DPIF (Tas)	1990	EC Tasmania	Jack mackerel larvae
CH224	Challenger	DPIF (Tas)	1990	EC Tasmania	Jack mackerel larvae
CH225	Challenger	DPIF (Tas)	1990	EC Tasmania	Jack mackerel larvae
CH226	Challenger	DPIF (Tas)	1990	EC Tasmania	Jack mackerel larvae
CH249	Challenger	DPIF (Tas)	1991	EC Tasmania	Jack mackerel larvae
CH250	Challenger	DPIF (Tas)	1991	EC Tasmania	Jack mackerel larvae
CH254	Challenger	DPIF (Tas)	1991	EC Tasmania	Jack mackerel larvae
CH256	Challenger	DPIF (Tas)	1991	EC Tasmania	Jack mackerel larvae
CH258	Challenger	DPIF (Tas)	1991	EC Tasmania	Jack mackerel larvae
CH321	Challenger	DPIF (Tas)	1993	EC Tasmania	unknown
CH1997a	Challenger	DPIF (Tas)	1993	EC Tasmania	Puerulus
DR01/94	Dell Richie	CSIRO	1994	EC Tasmania	Orange roughy eggs
DR02/94	Dell Richie	CSIRO	1994	EC Tasmania	Orange roughy eggs
DR03/94	Dell Richie	CSIRO	1994	EC Tasmania	Orange roughy eggs
DR01/95	Dell Richie	CSIRO	1995	EC Tasmania	Orange roughy eggs
DR02/95	Dell Richie	CSIRO	1995	EC Tasmania	Orange roughy eggs
DR1/92	Dell Richie	CSIRO	1992	WC Tasmania	Blue grenadier eggs
DR2/92	Dell Richie	CSIRO	1992	WC Tasmania	Blue grenadier eggs
DR3/92	Dell Richie	CSIRO	1992	WC Tasmania	Blue grenadier eggs
DR4/92	Dell Richie	CSIRO	1992	WC Tasmania	Blue grenadier eggs
FR12/89	Franklin	CSIRO	1997	EC Tasmania	Phyllosoma
FR2/97	Franklin	MAFRI	1997	Bass Strait	Larval fish
FR3/97	Franklin	CSIRO	1997	Tas waters	Opportunistic: larval fish+phyllosoma
FR10/97	Feranklin	CSIRO	1997	Tas waters	Opportunistic: larval fish+phyllosoma
KR1	Scottsman	CSIRO	1990	EC Tasmania	Krill
KR2	Scottsman	CSIRO	1990	EC Tasmania	Krill

Cruise	Vessel	Institution	Year	Area	Original sampling target
KR3	Scottsman	CSIRO	1990	EC Tasmania	Krill
KR4	Scottsman	CSIRO	1990	EC Tasmania	Krill
KR5	Scottsman	CSIRO	1990	EC Tasmania	Krill
KR6	Scottsman	CSIRO	1990	EC Tasmania	Krill
KR7	Scottsman	CSIRO	1990	EC Tasmania	Krill
KR8	Scottsman	CSIRO	1990	EC Tasmania	Krill
KR9	Scottsman	CSIRO	1990	EC Tasmania	Krill
KR10	Scottsman	CSIRO	1990	EC Tasmania	Krill
SS2/91	S. Surveyor	CSIRO	1991	Tas waters	Zooplankton
SS1/92	S. Surveyor	CSIRO	1992	Offshore Tas	Zooplankton+nekton
SS2/92	S. Surveyor	CSIRO	1992	Tas waters	Zooplankton
SS3/92	S. Surveyor	CSIRO	1992	Tas waters	Zooplankton
SS4/92	S. Surveyor	CSIRO	1992	Tas waters	Zooplankton
SS4/93	S. Surveyor	CSIRO	1993	Offshore Tas	Zooplankton
SS5/93	S. Surveyor	CSIRO	1993	NSW, Vic + Tas	Larval fish + zooplankton
SSTL/93	S. Surveyor	CSIRO	1993	NSW, Vic + Tas	Larval fish
SS2/94	S. Surveyor	CSIRO	1994	NSW, Vic + Tas	Larval fish, zooplankton, nekton
SS3/94	S. Surveyor	CSIRO	1994	Offshore Tas	Zooplankton + nekton
SS11/95	S. Surveyor	CSIRO	1995	Tas+Sthn Ocean	Opportunistic: larval fish+phyllosoma
SS3/96	S. Surveyor	CSIRO	1996	NSW, Vic + Tas	Zooplankton
SS1/98	S. Surveyor	CSIRO	1998	Tas + SA	Opportunistic: larval fish+phyllosoma
TangDC	Tangaroa	NIWA	1991	Southern Aust	Phyllosoma

* Now TAFI (Tasmanian Aquaculture and Fisheries Institute)

5.3 Sample Coverage

5.3.1 Geographic

The available samples covered a wide area of southern and south-eastern Australia (Figure 1). A total of 2,843 samples were examined during the study. These represented about 2500 stations and were taken from 1989–1998. Samples were collected using a variety of net systems (see descriptions below). In some cases, different systems were towed at the same station or multiple samples were taken with the same gear. Bongo and surface net collections made up about 50% of all the samples, while collections using the depth stratified net systems (EZ and MIDOC) accounted for roughly 35% of the total number of samples (Table 2). Sample coverage was not evenly spread throughout the study area. Nearly 70% of the samples came from the Tasmanian region. The remaining samples came from: South Australia (9.7%), Victoria (8.2%) and southern New South Wales (13.5%). Sample coverage off the east coast of Tasmania was the most comprehensive (61% of the total), covering both shelf and offshore waters over multiple years (Figure 2).

Table 2: Summary of stations occupied by region and net type for all samples sorted from archives and from opportunistic cruises.

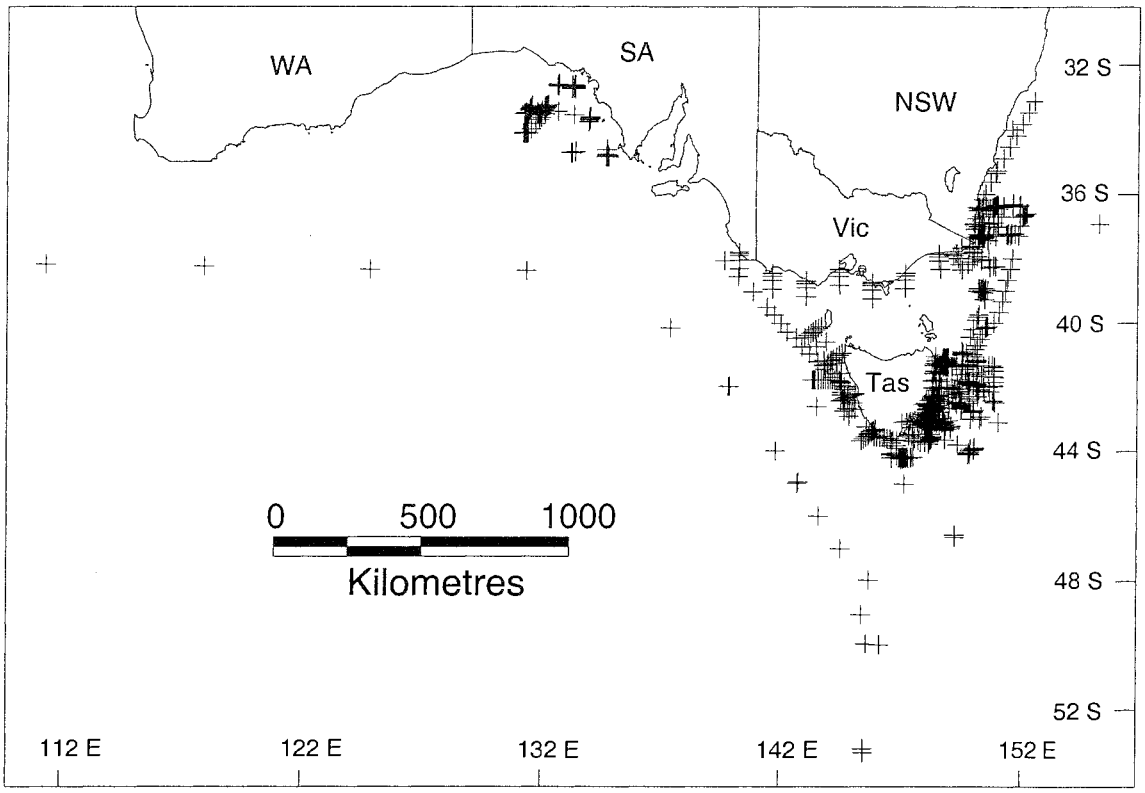


Figure 1. The location of samples analysed

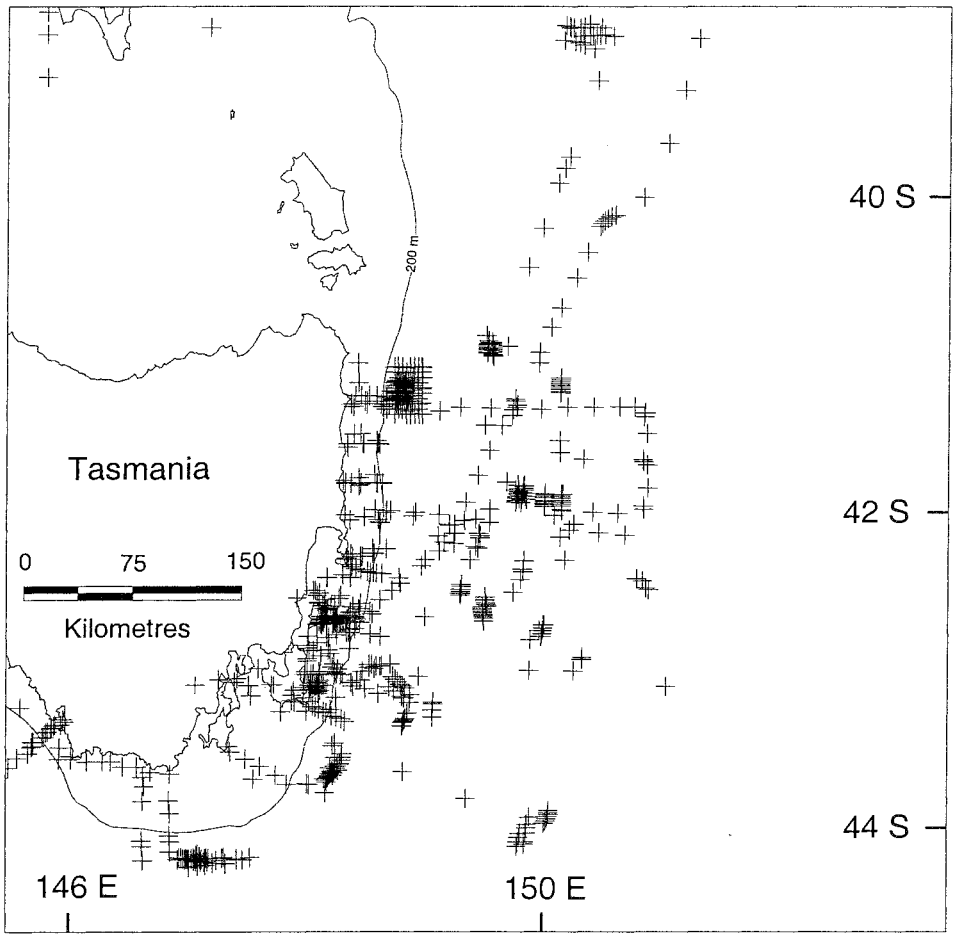


Figure 2. Sample distribution off eastern Tasmania. Line denotes 200 m contour.

Region	Number of samples from each net type							Total
	EZ	Bongo	MIDOC	Ring	Surface	Vertical hauls	Unident. net type	
East Coast Tasmania	328	344	279	65	453	249	24	1742
West Coast Tasmania	12	10	9	–	116	–	12	159
Southern Tasmania	40	–	1	–	5	–		46
South Australia	14	77	91	–	95	–		277
Victoria	81	49	26	–	78	–		234
New South Wales	–	123	68	–	194	–		385
Total # Samples	**475**	**603**	**474**	**65**	**941**	**249**	**36**	**2843**

5.3.2 Annual

Samples were available from every year between 1989 and 1998. However, the distribution of sampling effort was not even between years (Figure 3, Table 3). Sampling effort ranged from 22 samples in 1995 (0.8% of the total number of samples sorted) to 736 samples in 1992 (25.9% of the total number of samples sorted).

Table 3: Summary of the number of samples sorted by year.

Year	# Samples	% of Total	Year	# Samples	% of Total
1989	70	2.5	1994	340	12.0
1990	251	8.8	1995	22	0.8
1991	68	2.4	1996	371	13.0
1992	736	25.9	1997	234	8.2
1993	459	16.2	1998	290	10.2

5.3.3 Seasonal

Sampling effort was similarly variable between seasons. Spring was the least sampled period; Winter was the period of best coverage (Table 4)

Table 4: Summary of samples sorted by season
(Sum.= 1 Dec-28/9 Feb; Aut.= 1 Mar-31 May; Win.=1 Jun-31 Aug; Spr.= 1Sep-30 Nov)

Season	# Samples	% of Total
Summer	1039	36.6
Autumn	590	20.7
Winter	1137	40.0
Spring	77	2.7

5.4 Net Systems:

Five net systems (surface, ring, EZ, MIDOC, and bongo) were routinely used to collect samples throughout the study region. Samples were also examined from a sixth net (vertical haul) used in a series of fish egg surveys (orange roughy and blue grenadier) off the east and west coasts of Tasmania. Three sampling strategies (surface, depth stratified and vertically integrated) were used depending on the gear and the objectives of the original survey. In some cases (eg bongo and ring nets), the same net type was used for different tow strategies. Towing protocols and net construction differed between systems and each is described below.

5.4.1 Surface sampling

Surface net

The surface net consisted of a square frame with a mouth area of $1m^2$. The net was made of 1000μm nylon mesh (Nytal 20 GG) with a mesh porosity of 58 percent. Volume filtered was measured using a General Oceanics (GO) mechanical flowmeter fitted inside the mouth of the net. The surface net was usually deployed from either CSIRO's RV *Franklin* or RV *Southern Surveyor*. The net was towed beside the vessel from a davit rigged amidships and was usually deployed concurrently with other net systems towed astern or on departing a hydrographic (CTD) station. The net in all cases was towed at a ship's speed of between 2.5 and 3.5 knots for 10–15 minutes.

Ring net

The ring net was equivalent to one side of a 70cm bongo net with a net mouth area of $0.38m^2$. The net was made of 500μm nylon mesh (Nytal 38 GG) with a mesh porosity of 49.5 percent. Volume filtered was again measured with a GO mechanical flowmeter fitted to the mouth of the net. The net was towed beside the vessel at a speed of 2.5 - 3.5 knots for 10–20 minutes in a similar manner to the surface net.

Bongo net

The bongo net consisted of two 70 cm diameter nets (mouth area = $0.38m^2$) with a mesh size of either 1000μm or 500μm (depending on the original study) and was towed from a central pivoting point. Volume filtered by the bongo net was calculated from a GO mechanical flowmeter fitted inside the mouth of one of the nets. The bongo system was fitted with a depressor and towed beside the vessel at a speed of 2.5 - 3.5 knots for 10–20 minutes in a similar manner to the surface net.

5.4.2 Depth stratified sampling

EZ (BIONESS) net

The EZ net was used to sample discrete depth strata for macrozooplankton. The EZ net consisted of a towed frame, with a mouth opening of $1m^2$, fitted with up to 10 nets of 335μm mesh (Nytal 52 GG; mesh porosity = 46%). Each net could be opened and closed from an onboard control system with communication between ship and net via a conducting tow cable. The tow cable also relayed real-time

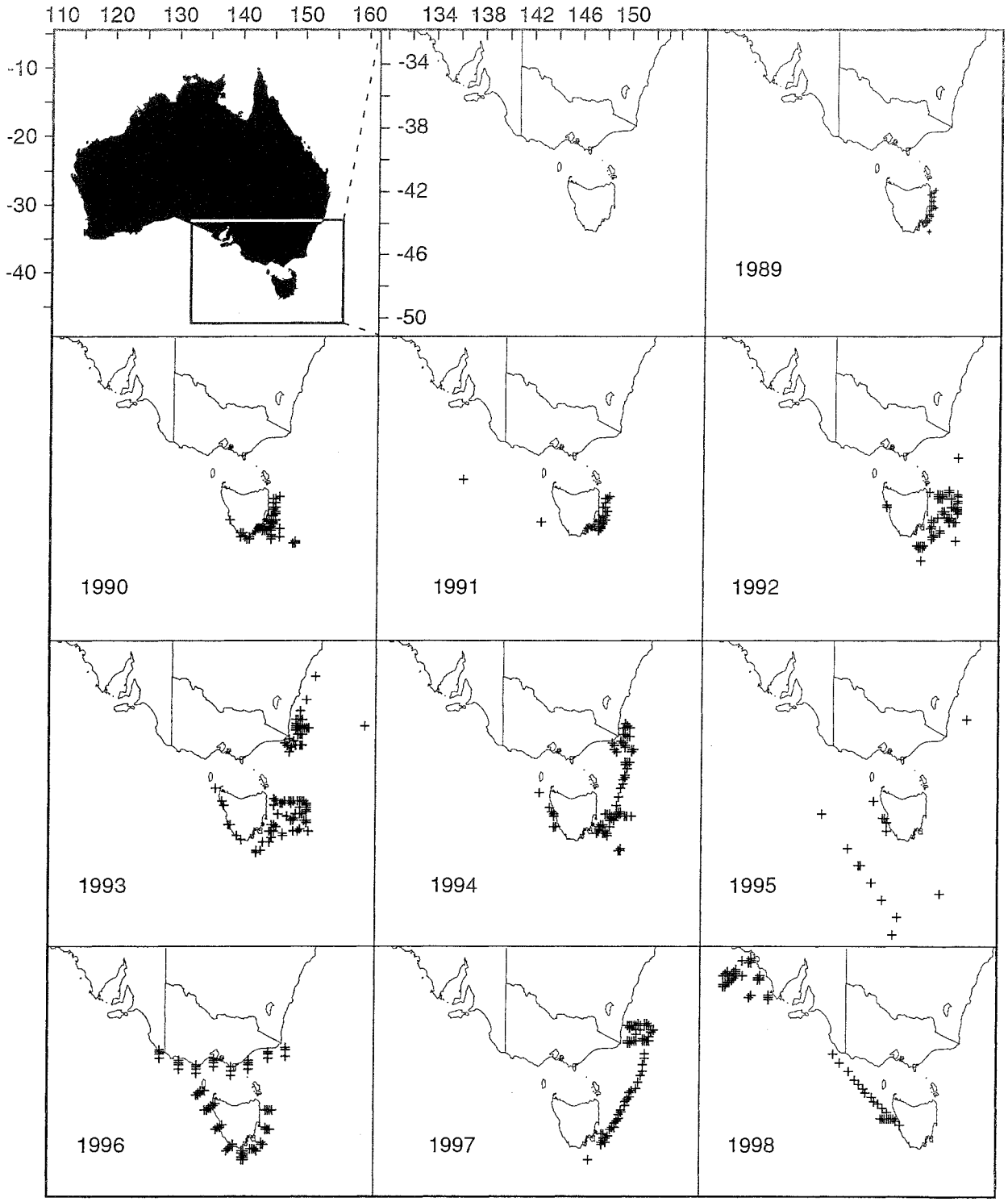


Figure 3: Sample coverage by year.

information to the vessel from sensors on the frame that provided net depth, rate of descent/ascent, elapsed fishing time and volume filtered. The system was towed from the stern of the vessel at a speed of about 3 knots. A typical tow profile consisted of an oblique tow from the surface to the maximum depth, followed by sampling through discrete strata back to the surface. The maximum depth sampled and the resolution of depth strata varied according to water depth, and in some cases, the original target species. A typical tow off the shelf consisted of an oblique set from the surface to 400m over a 40-minute period; followed by 10-20 minute hauls from 400–300m, 300–200m, 200–100m and 100m to the surface. In some cases, this tow strategy varied - some tows were at set depths (eg 400 m) for 10 mins and on some cruises, sampling depths ranged in 100 strata down to 800 m.

MIDOC net

The MIDOC net consisted of a multiple opening/closing codend system (Pearcy *et al.* 1977) fitted to a standard midwater pelagic trawl net (International Young Gadoid Pelagic Trawl – IYGPT). The codend system was capable of carrying six nets of 500μm (Nytal 38 GG; mesh porosity = 49.5%) each able to be individually opened and closed. A mechanical preset timer fitted to the frame of the codend triggered the opening/closing mechanism. The total depth sampled and the resolution of depth strata varied according to water depth. A typical tow would involve an oblique tow from the surface to depth, followed by sampling at discrete depths back to the surface. A typical tow off the shelf usually consisted of an oblique set from the surface to 400m over a 30 to 40-minute period; followed by 15 to 20 minute hauls from 400–300m, 300–200m, 200–100m, and 100m to the surface. A Scanmar trawl sensor system was used to monitor net geometry, door spread, headline height, height of the gear above the bottom, and depth below the surface. The volume filtered by the MIDOC net was estimated using the formula:

$V = S \cdot d \cdot A$, where

S is ship's speed ($m \cdot s^{-1}$), d is duration of tow (s), and A is mouth area (m^2).

5.4.3 Vertically integrated sampling

Bongo net

A second bongo net was usually deployed astern of the vessel when towing a bongo net at the surface. Tows were oblique (no opening/closing mechanism was used) to within 10m of the seafloor over the shelf or to a maximum of 200m off the shelf. Tows varied in their duration according to the maximum depth sampled. The net system was towed using a conducting tow cable from the stern of the ship at a speed between 2.5 to 3.5 knots. Sensors fitted to the frame of the bongo net relayed depth, descent/ ascent rate, temperature and elapsed fishing time in real-time to a control room on-board the vessel. Volume filtered was measured by an electronic General Oceanics flowmeter attached inside the mouth of the net.

Vertical haul net

Additional vertically integrated macrozooplankton samples were available that were collected using a vertical haul net (mouth area = $2m^2$, mesh size = 500μm). The vertical haul net was deployed closed to within 10m of the seafloor or to a maximum depth of 1000m off the shelf, then opened and hauled vertically to the surface at a constant rate. Volume filtered by the vertical haul net was calculated from a GO mechanical flowmeter attached to the frame of the net.

Ring net

A series of oblique tows were made off eastern Tasmania (Maria Island) in 1990 to a maximum of 40m depth using a ring net. The ring net was comparable to one side of the 70cm bongo net (mouth area = $0.38m^2$, mesh size = 500μm). Volume filtered by the ring net was calculated from a GO mechanical flowmeter that was attached to the mouth of the net.

5.5 Sample Processing

5.5.1 At sea

Both the initial sample processing and the fixatives used at sea varied between net systems and according to the needs and objectives of the original sampling exercise.

Samples from the ring net (surface and oblique) and vertical haul were generally fixed in 10% formaldehyde in seawater buffered with sodium acetate. Surface net samples were either fixed in formaldehyde (as above) or ethanol. One net from each bongo tow was generally fixed in ethanol; the other in 10% formaldehyde in seawater buffered with sodium tetraborate. MIDOC and EZ tows were usually fixed in 10% formaldehyde in seawater.

In some cases samples had been roughly sorted into major taxa on board the vessel. This was generally the case for MIDOC and EZ net tows. In these cases it is possible that some phyllosoma may have been lost or overlooked as they were not the target of the original sampling. Where sampling occurred during the course of this project, phyllosoma were rough sorted from samples on-board the vessel and transferred immediately to ethanol to allow for genetic identification.

Many samples originally fixed in formaldehyde had been transferred to 70% ethanol at some time prior to the present study.

5.5.2 Laboratory

In the laboratory, samples were sorted under a low-powered Maggilamp and any phyllosoma were removed and placed in either 70% ethanol (for specimens taken from formaldehyde fixed samples) or

95% ethanol (for specimens from ethanol fixed samples). No samples were split for the present study, however, many of the archived samples had previously been split. In all such cases every effort was made to retrieve and resort all fractions of the split sample. Where all the fractions were not available the number of phyllosoma in the whole sample was estimated using the formula:

$$N*2^{\wedge(ns)},$$

where N = number of phyllosoma and ns = the number of splits.

5.6 Physical oceanographic data sets

The physical oceanography for each cruise was described from a series of Conductivity-Temperature-Depth probe (CTD) casts that recorded depth, temperature, salinity, and a variety of other parameters. The depth of casts varied according to the primary purpose of each cruise, however, in general casts were made to within 10m of the seafloor or to a maximum of 1000m. The oceanographic data was also used to ground-truth archived AVHRR (Advanced Very High Resolution Radiometer) satellite images of sea surface temperature, dating back to 1990. Satellite images were processed further, first to reduce the effects of cloud cover for each particular cruise, and secondly, to provide images used in visual models (animations) of variations in sea surface temperature (SST) over the period of available samples.

Physical oceanographic data sets (primarily temperature salinity, and SST) were also extracted from the CSIRO data archive for the period 1990-1998. These data sets were combined with satellite altimeter data and paths of satellite tracked surface drifters to examine mesoscale circulation patterns of relevance to the transport of rock lobster larvae.

Further details of the physical oceanographic data sets available to the project and the analyses made are described in Section 6.6: Physical Oceanographic Analyses

5.7 Identification of phyllosoma

Phyllosoma were identified, primarily through morphological analysis, by comparing specimens to published descriptions of larvae (see below). While this presented little problem for identification to genus, the identification of spiny lobster larvae to species continues to be problematic due to their morphological similarity (Booth and Phillips 1994). Phyllosoma of the two Australasian *Jasus* species, *Jasus verreauxi* (green or eastern rock lobster) and *J. edwardsii* (southern rock lobster) were readily distinguished by the development in the former of a biramous fifth pereiopod by stage IV (McWilliam and Phillips 1987) and were thus separated in our samples. *J. verreauxii* hatch their larvae in northern NSW, some 1500 km from our main sampling region and it is unlikely that earlier stage larvae were present in our samples. With the exception of *J. verreauxi* and *J. edwardsii*, rock lobsters of the *Jasus* genus have allopatric (non-overlapping) distributions. In most cases, researchers have previously

assumed that any *Jasus* phyllosoma caught within their limit of sampling (generally < 500 km from shore) were of the locally occurring species. This is probably quite reasonable as the adult distributions of the different *Jasus* species are generally separated by many thousands of kilometres. However, some *Jasus* phyllosoma have been found in excess of 1500 km from shore and this as well as their lengthy, pelagic larval duration has lead to hypotheses of cross or circum-ocean basin transport. Booth and Grimes (1991), reporting on a sampling exercise from the west coast of Africa, across the Indian Ocean and south Tasman Sea to the west coast of New Zealand, found that *Jasus* phyllosoma were generally captured within 1000 km of the location of their adult populations. For the purpose of this study, we have largely assumed that the non-*verrauxi Jasus* larvae captured in our sampling were *J. edwardsii*. However, we note that phyllosoma identified (using genetic techniques) as *Jasus lalandi* (the South African *Jasus* species) were reported by Booth and Grimes (1991) in the Australasian sector, despite them not being recorded here as either juveniles or adults. It is thus possible that some *J. lalandii* larvae may also be present in our samples. Following the genetic approach to identification as used by Ovenden and Booth (*submitted*) will greatly assist in clarifying the overlap in distribution of phyllosoma of different *Jasus* species.

Phyllosoma were fixed in ethanol in all the opportunistic sampling during this project for such purposes and although some work was initiated on genetic identification in this project, we did not pursue it further than a preliminary phase in-lieu of the publication of methods for identifying *Jasus* phyllosoma by Ovenden and Booth (*submitted*). We have, however, reported on our preliminary analyses in the section 5.7.2 below.

5.7.1 Morphological

Phyllosoma were identified to genus using the keys of Lesser (1974, 1978), Phillips *et al.* (1981), and McWilliam & Phillips (1987). *Jasus* phyllosoma were further identified to species, where possible, and then staged using the classification of Lesser (1978) (for stages I-IV) and as modified by Booth (1994) for stages V-XI (Table 5).

Table 5: The stage classification for mid and late stage *Jasus edwardsii* phyllosoma. (Modification of Lesser's (1978) classification by Booth (1994).

Stage	Uropods	Pleopods	Others
XI	with many lateral spines	appendix internal fully developed	fully developed gills full segmentation over abdomen
XA	prominent lateral spine trace of other spines	developing appendix internal	bud-like gills full segmentation over abdomen
X	traces of lateral spines	bud-like appendix internal	dorsal and ventral segmentation

IX	cleavage complete (2/3 cleft of total length)	1/3–2/3 cleft (cleavage complete at 2/3 total length)	slight dorsal and ventral segmentation
VIIIA	1/2–2/3 cleft	1/4–1/3 cleft	slight ventral segmentation
VIII	1/4–1/2 cleft	elongated buds, either un-cleft or <1/4 cleft	no visible segmentation
VII	slight cleft (<1/4)	raised ridges	
VI	buds uncleft	low ridges	
V	buds	absent	

5.7.2 Genetic Analysis

We initiated some preliminary genetic analyses on tissue from adult *J. edwardsii* in order to establish the basis for the identification of ethanol and DMSO fixed larvae. Dr Jenny Ovenden (QDPI) subsequently provided her protocol for DNA extraction and PCR amplification that she had used to identify *Jasus* larvae (Ovenden and Booth *submitted*), however, time constraints prevented us from further pursuing this technique. Our preliminary analyses are presented below for completeness.

DNA Extraction

Fresh tissue samples from adult *Jasus edwardsii* were collected from specimens held in the aquaculture facility at TAFI and immediately put on ice. Aliquotes of each sample were preserved in either ethanol, Dimethyl sulfoxide (DMSO), or frozen at -80°C. DNA was isolated from fresh, frozen, ethanol, and DMSO treated tissue following the protocol of Doyle and Doyle (1987) (see Table 6) and resuspended in 200µl double distilled water (ddH_2O).

Table 6: Protocol for DNA extraction (modified from Doyle and Doyle 1987)

1. Immerse sample tissue in 200µl of 2x CTAB.
2. With a plastic mortar, grind the tissue then add a further 500µl of 2x CTAB.
3. Add 5µl of proteinase K (20 mg/ml solution).
4. Vortex briefly then incubate at 65°C for 20 minutes before grinding for a second time. Continue the incubation for a further 40 minutes.
5. Following incubation, add 600µl chloroform-isoamyl (24:1), mix well and centrifuge for 15 minutes at room temperature.
6. Pipette off the supernatant to a new tube and add 600µl of phenol-chloroform-isoamyl (25:24:1); shake lightly and centifuge for 3 minutes at room temperature.
7. Perform a final extraction in 600µl of chloroform-isoamyl and centrifuge for 20 seconds at room temperature.
8. Pipette the supernatant into 600µl cold (-20°C) isopropanol and mix gently.
9. Let sit for at least one hour in at 4°C; then centrifuge for 30 minutes at 4°C.
10. Pipette off the supernatant and add 1ml 70% cold (-20°C) ethanol. Mix gently then centrifuge for 5

minutes at 4°C. Repeat once to clean up all the salts.

11. Dry the pellet in a vacuum centrifuge for 25 minutes or until the sample is dry.
12. Resuspend the pellet in 200µl of ddH_2O.

The products of the DNA extraction were visualised under UV light following standard submarine gel electrophoresis, using 1.5% agarose stained with ethidium bromide,

Polymerase Chain Reaction (PCR) Amplification

Ten to twenty microlitres of the DNA extract were used as a template for PCR amplification of the cytochrome *c* oxidase subunit I gene. DNA template extracted from bigeye tuna (BET) was used as a control in all PCR amplifications. DNA template dilutions of 1:10 and 1:50 were used in the initial PCR amplifications; expanded to no dilution, 1:5, 1:10, 1:50, and 1:100 in the final amplifications. Initial PCR amplifications followed the protocol of Folmer *et al.* (1994) and then were repeated using the protocol of Ovenden and Booth (*submitted*). Their protocol differed slightly in both the reaction mix and cycling conditions used. The amplification primers used (see Folmer *et al.* 1994) were:

LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and
HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3')

The DNA product was visualised on a 1.5% agarose gel, stained with ethidium bromide, under UV light.

5.7.3 Results of genetic analyses

DNA Isolation

DNA was isolated from 10 preserved tissue samples of adult *Jasus edwardsii*. Ethanol and DMSO preservation of the tissue samples did not affect the amount of DNA extracted, with approximately equivalent amounts of template extracted from each preservative (Figure 4).

Polymerase Chain Reaction (PCR) Amplification

Initial amplifications of DNA were positive using the 16S primer, but negative for the *COI* primer. We were subsequently able to produce a faint positive result for *COI* using the procedures of Ovenden and Booth (*submitted*) with a 1:10 dilution of template derived from DMSO preserved tissue (Figure 5).

The optimal dilution rate for the DNA template was examined in a further PCR amplification. A range of template dilutions from 'no dilution' to 1:100, from both ethanol and DMSO preserved tissue, was again trialed using the protocols of Ovenden and Booth (*submitted*). Template using the 16S primer was amplified from all dilutions except 1:100; template using the *COI* primer was amplified only from the undiluted, 1:5, and 1:10 dilutions (Figure 6).

DNA Sequencing

The products of the PCR amplifications were pooled (same animal, same preservative, same primer) and sequenced. We were able to sequence the pooled product from the 16S primer and the control but, we were unable to successfully obtain a sequence from the pooled product of the *COI* primer.

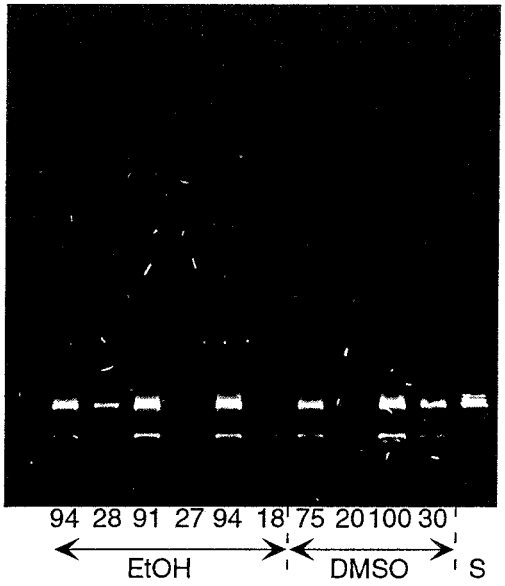


Figure 4: Agarose gel of DNA extraction products from 10 adult *Jasus edwardsii* (S = lambda hindi standard ladder; number refers to the weight (in g) of raw tissue used in the extraction; EtOH = ethanol preserved tissue; DMSO = dimethyl sulfoxide preservation).

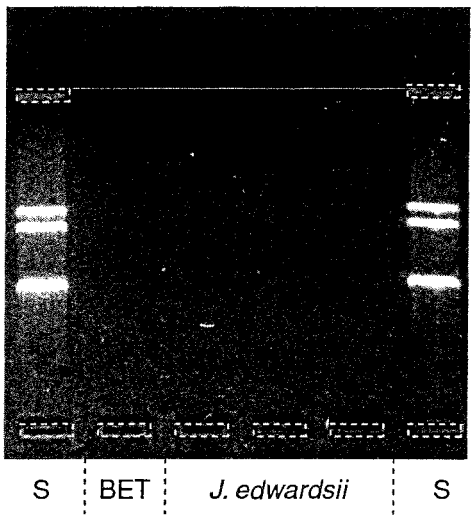


Figure 5: Agarose gel of PCR products from *Jasus edwardsii* and *Thunnus obesus* (bigeye tuna) (S = PBR322 standard ladder; BET = bigeye tuna control; faint PCR bands and the wells have been highlighted by open boxes).

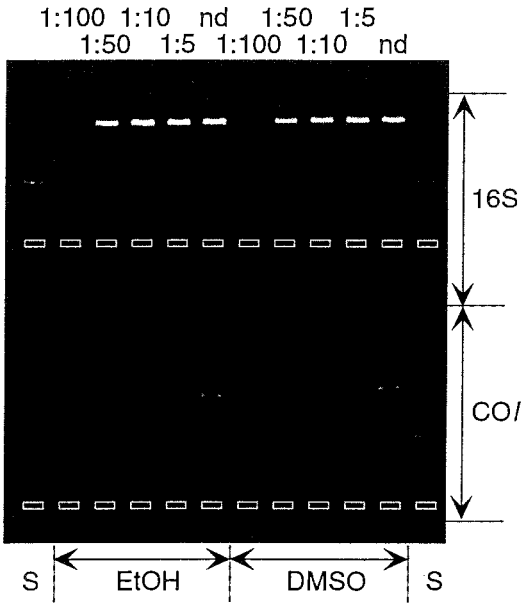


Figure 6: Agarose gel of PCR (expanded dilution range test) products from *Jasus edwardsii* (S = PBR322 standard ladder, open boxes denote the position of the wells; EtOH = ethanol preservation; DMSO = dimethyl sulfoxide preservation; dilution ratio denoted along the top (nd = no dilution); primer is denoted along the right side).

5.7.4 Discussion of genetic analyses

DNA Isolation

The difficulty in sequencing DNA from the COI primer runs prevented us from applying the genetic technique to the identification of phyllosoma. We were able to successfully isolate DNA from tissue that had been preserved in either ethanol or in DMSO, however, we were unable to amplify enough of the template to sequence the DNA. We suspect that our initial protocol of resuspending the pellet in 200µl of ddH_2O was too great a dilution of the DNA to amplify in a single PCR. Ovenden and Booth. (*submitted*) used only 50µl of ddH_2O to resuspend DNA pellets from phyllosoma tissue and we will subsequently follow this recommendation in future analyses.

Despite not pursuing the genetic approach for confirming the identification of phyllosoma in this study, the technique offers a valuable tool for clarifying the distribution of phyllosoma in areas where larvae of more than one species may overlap. We concur with Cobb (1997) that, where possible, phyllosoma should be fixed in alcohol for genetic confirmation of their identification in future and we have archived material for this purpose.

6. Project Results

6.1 Geographic distribution of phyllosoma

6.1.1 Introduction

The distribution of phyllosoma was examined by combining data from all net tows. Descriptions of nets and tow protocols are provided in Section 5.4. Abundances of phyllosoma were converted to numbers per 1000 m^3 for all nets. While this conversion to a standardised abundance is convenient for presenting the spatial data, there are some problems in doing so as net systems varied in their filtration efficiency and in their effectiveness in capturing phyllosoma (see section 5.1 *Scope and rationale of project*). These differences were difficult to quantify and were ignored for the analysis of distribution. Thus abundances can only be regarded as indicative in some samples (particularly from the MIDOC net system).

Tasmanian waters were the most intensively sampled and provided the best spatial and temporal coverage. Thus we first briefly present and discuss regional analyses based on the entire data set and then concentrate on analyses within Tasmanian waters.

Data Presentation: For both simplicity and due to the low numbers of larvae recorded in some stages, *Jasus edwardsii* phyllosoma were grouped into three developmental periods: early (stages I–IV), mid (stages V–VIII) and late (stages VIIIA–XI) stages. The data were plotted using the GIS program MapInfo.

6.1.2 Results

Phyllosoma of all species were collected across the range of sampling from the head of the Great Australian Bight to mid New South Wales (Figure 7). *Jasus edwardsii* phyllosoma were recorded primarily in Tasmanian coastal and offshore waters, no doubt partially reflecting the intensive sampling effort in this region, and in offshore waters south of the GAB. *Jasus edwardsii* phyllosoma were absent from Bass Strait, which was dominated by phyllosoma of scyllarid species. No samples were available along approximately 500 km of coastline between the Eyre Peninsula and Port Macdonnell in South Australia, thus our understanding of the distribution of phyllosoma is incomplete for this area.

Jasus edwardsii phyllosoma almost exclusively dominated shelf and offshore waters of western and southern Tasmania. Whereas high abundances of both *J. edwardsii* and other phyllosoma (again primarily scyllarids) were recorded from shelf and offshore waters of eastern Tasmania.

Jasus edwardsii phyllosoma were almost entirely restricted to waters south of 40^0 30"S (just south of Flinders Island) in the western Tasman Sea. Scyllarid phyllosoma dominated samples to the north of this latitude in eastern Victoria and southern NSW.

Jasus edwardsii phyllosoma were captured offshore to the limit of sampling in waters east and west of Tasmania (to approximately 220 and 150 km offshore respectfully) and south of the GAB (to 550 km). However, *J. edwardsii* phyllosoma were almost entirely restricted to within 70 km of the south coast of Tasmania despite sampling stations extending to over 700 km from shore in this region.

Stage distribution – Jasus edwardsii

Early stage *J. edwardsii* phyllosoma were almost exclusively found in shelf waters and were most abundant off eastern and southern Tasmania (Figures 7 and 8). Very few early stage phyllosoma were taken seaward of the shelf break except off the west coast of Tasmania where some were recorded up to 100 km offshore in March 1998. Mid and late stage phyllosoma were found almost exclusively seaward of the shelf break and were widely distributed to the limit of sampling in most regions. Mid stage larvae were the most abundant stage category recorded in offshore waters.

Jasus verreauxi phyllosoma

Phyllosoma of *Jasus verreauxi* were recorded in low numbers at three stations off south eastern NSW and two stations off eastern Tasmania (Figure 9). Nearly all *J. verreauxi* phyllosoma were captured in February 1994 and were within a strong southward flowing plume of the East Australian Current that extended down the eastern Tasmanian coast. The exception was a single phyllosoma collected in winter 1992 off north-eastern Tasmania.

Seasonal distribution

Both *Jasus edwardsii* and non-*Jasus* phyllosoma were recorded in all seasons (Figures 10 and 11) in southern Australian waters. Several regions were poorly sampled during some seasons (eg GAB and Bass Strait) thus we are unable to determine the full range of seasonal distribution for waters other than Tasmania. The spatially most extensively sampled season was Summer. *Jasus edwardsii* phyllosoma

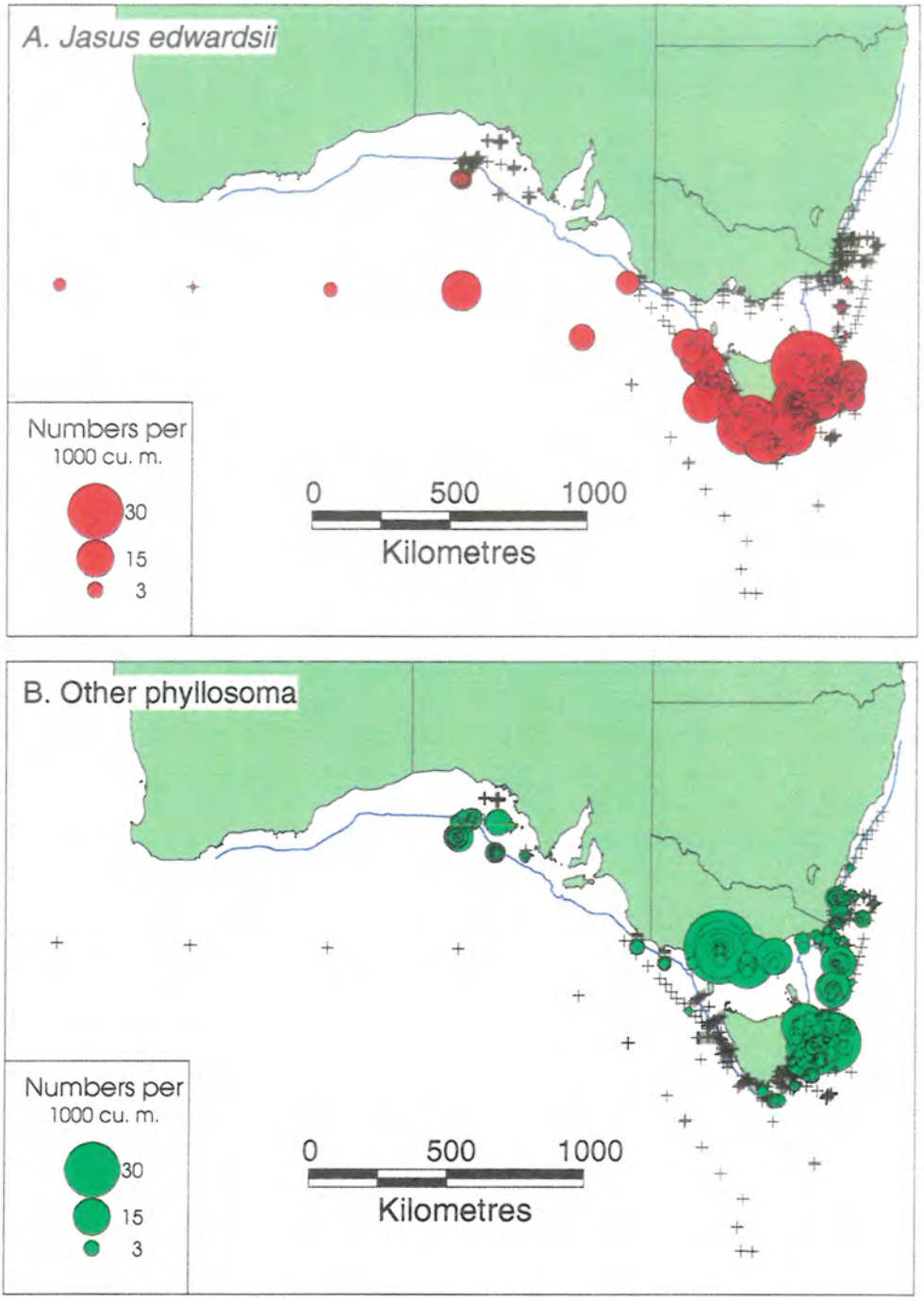


Figure 7: Distribution of phyllosoma in southern Australia

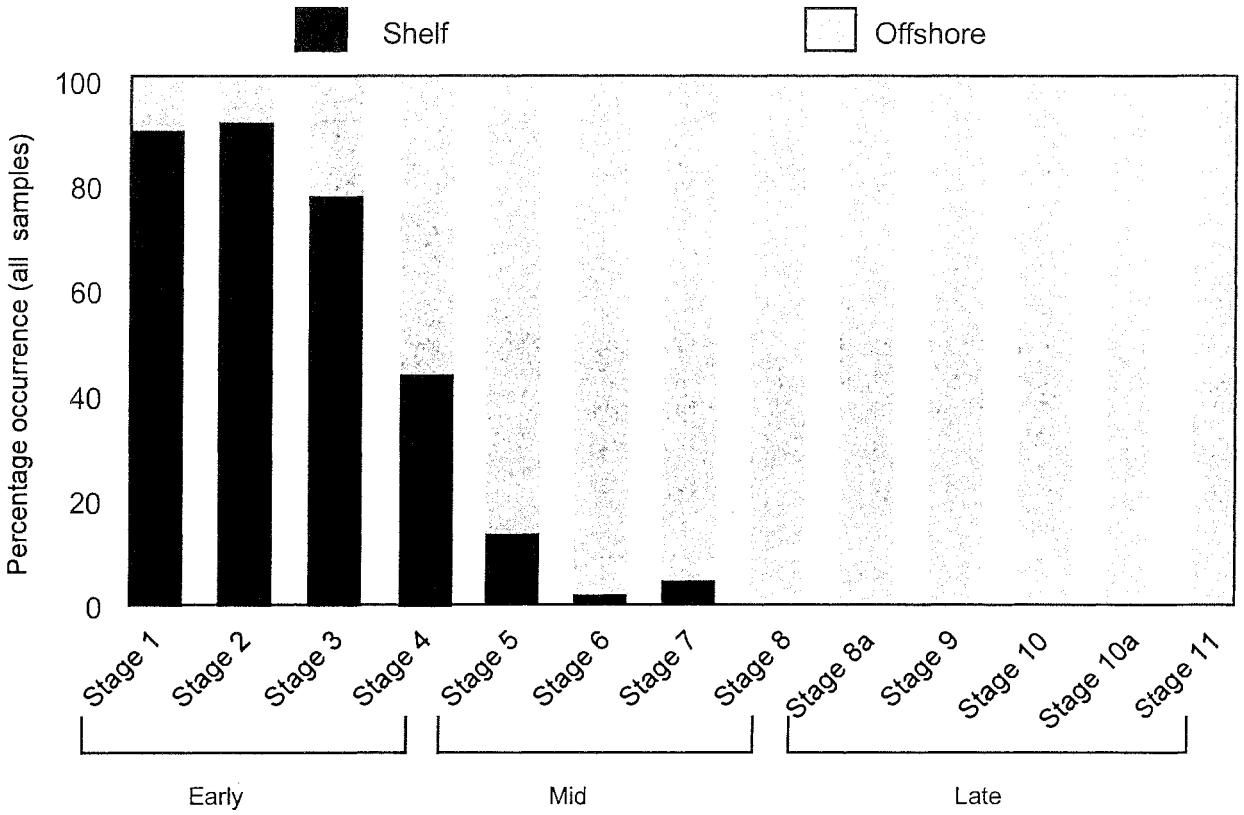


Figure 8: Combined onshelf/offshelf distribution of *J. edwardsii* phyllosoma by stage

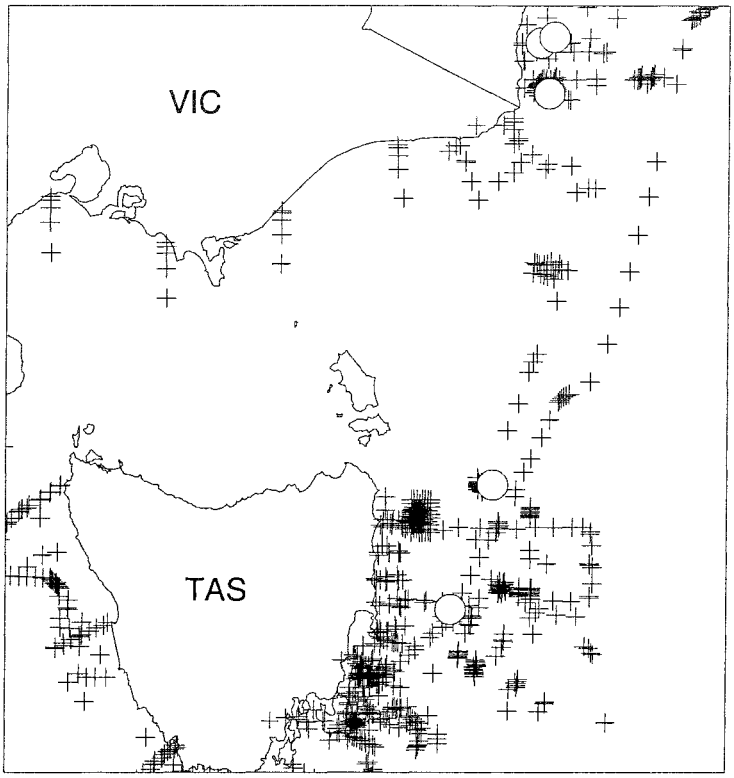


Figure 9: Distribution of J. verreauxi phyllosoma

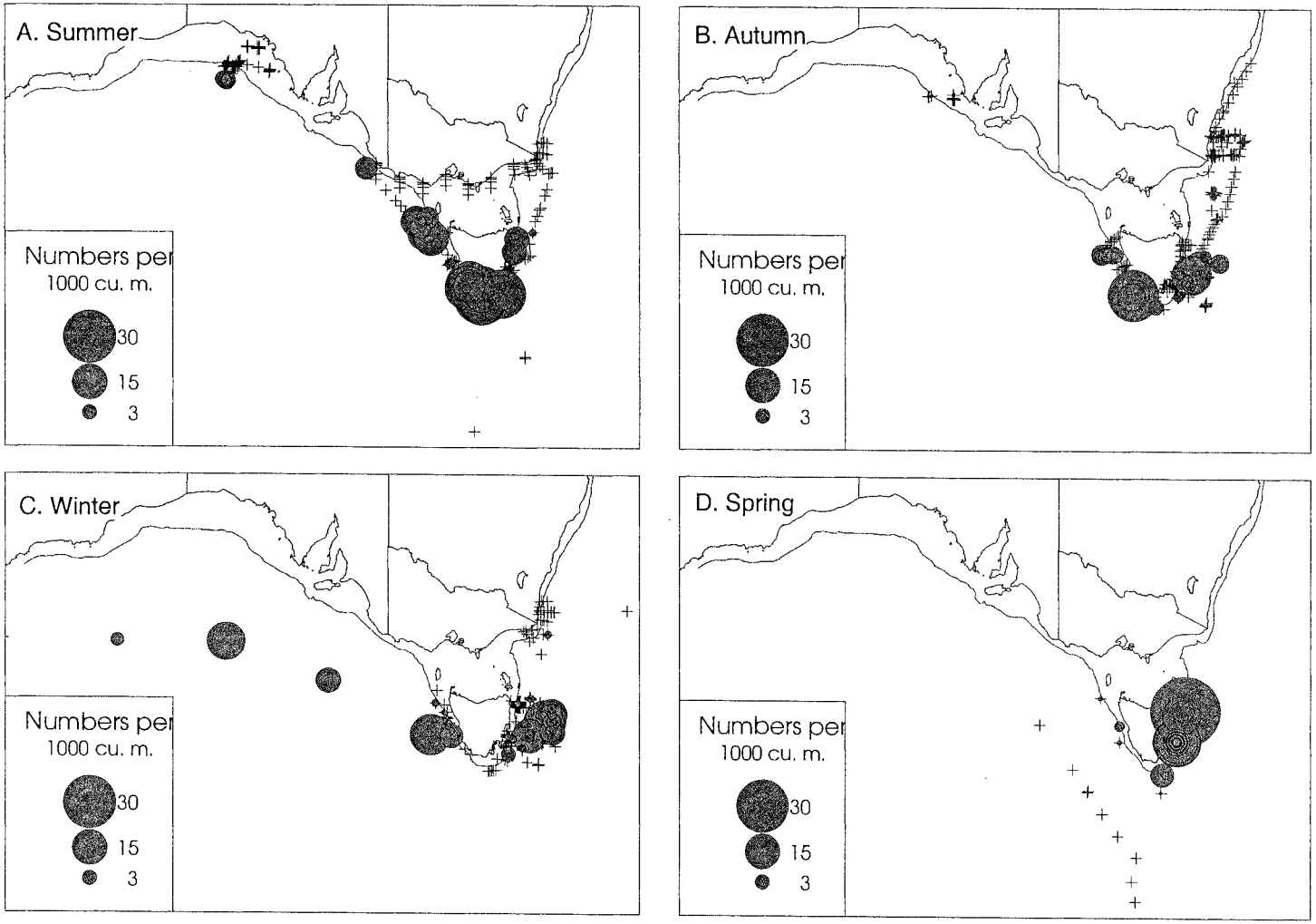


Figure 10: Seasonal distribution of Jasus edwardsii phyllosoma in southern Australia

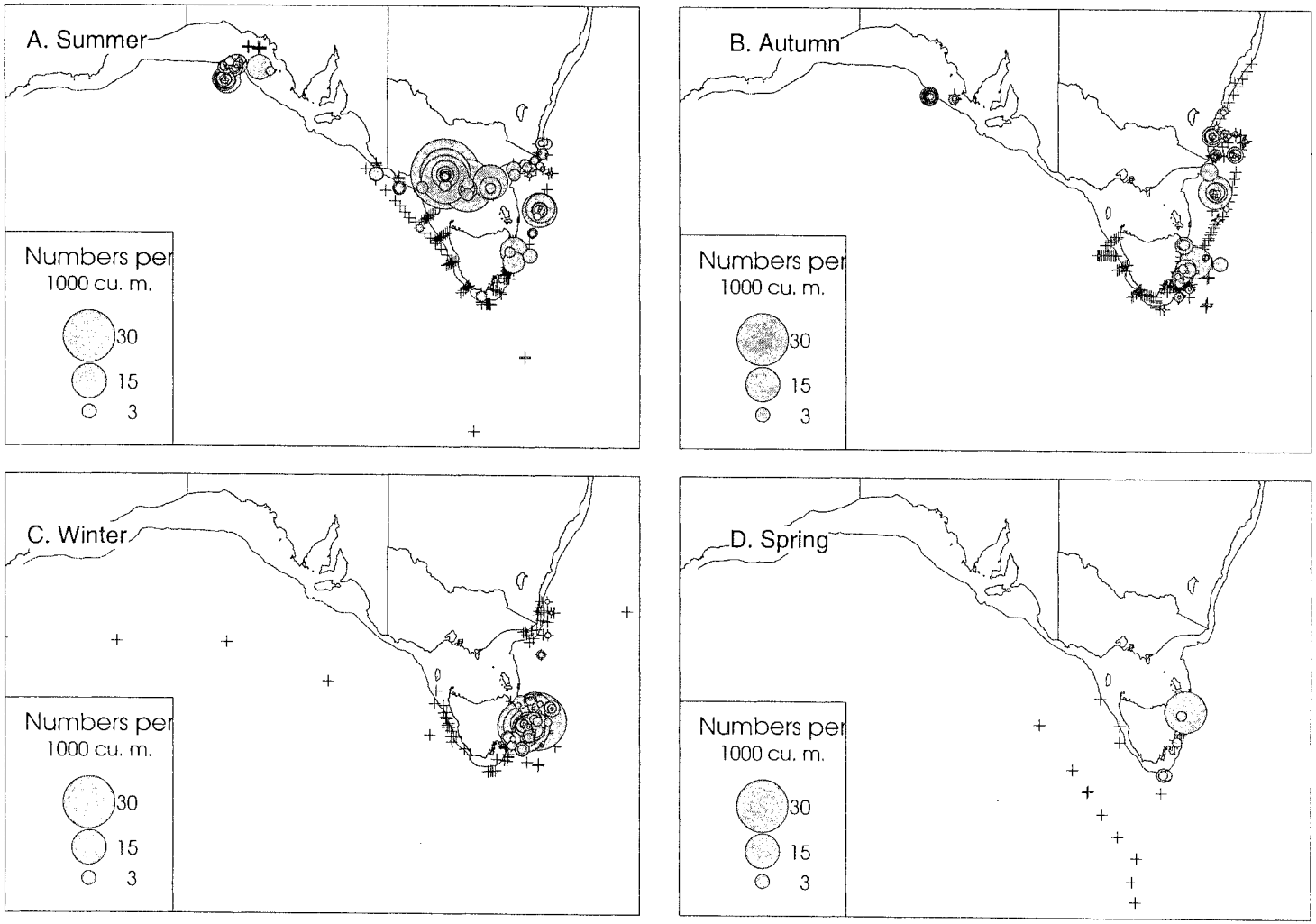


Figure 11: Seasonal distribution of other (non-Jasus) phyllosoma in southern Australia

were recorded across the range of sampling during Summer with the exception of Bass Strait. *Jasus edwardsii* phyllosoma were present in offshore waters of South Australia during Summer but were not recorded over adjacent shelf waters despite intensive effort with both surface and subsurface sampling gear.

Tasmanian waters

Sampling in Tasmanian waters presented a more detailed view of seasonal distribution. *Jasus edwardsii* phyllosoma were found throughout Tasmanian waters during Summer (Figure 12). Early stage phyllosoma dominated samples, particularly in the southern region and were the only stage collected in shelf waters. Mid and late stage phyllosoma were only present in the samples seaward of the shelf break off the north-east and north-west coasts. Relatively few offshore samples were available for the Summer period and thus the offshore extent of the distribution of phyllosoma was not well defined.

Jasus edwardsii phyllosoma were recorded almost exclusively from offshore waters in Autumn (Figure 13) and were dominated by mid and late stages particularly in the east and south. Early stage phyllosoma were present in a series of samples taken offshore from Sandy Cape in the north-west. These samples were taken in early March 1998 and thus were only just outside of the Summer period.

Mid and late stage *J. edwardsii* phyllosoma were recorded in Winter samples particularly in the extensively sampled offshore region of the east coast (Figure 14). No early stage phyllosoma were recorded from winter samples.

The Spring sample coverage was poor throughout the Tasmanian region; however, *J. edwardsii* larvae were found in the majority of samples collected at that time of year (Figure 15). Early stage phyllosoma dominated and most were recorded from shelf waters on the east coast. Very few offshore samples were available for the Spring period and thus the offshore distribution of phyllosoma was not well defined.

Distribution of pueruli

Jasus edwardsii pueruli were only rarely present in our samples. Small numbers were recorded in samples taken in Autumn off the west coast of Tasmania and in winter off the east coast of Tasmania. *J.edwardsii* pueruli were taken in either surface net tows or EZ tows that sampled through the surface layer and all were taken at night. They were recorded in waters with surface temperatures of 15.5-15.77 ^{0}C. All *J. edwardsii* pueruli were taken seaward of the continental shelf at distances varying from 8-53 km from the shelf break.

Small numbers of pueruli that were morhorplogically similar to *J. edwardsii* were also caught off south eastern NSW in Autumn 1996. We were unable to confirm the identity of these pueruli, however their capture to the north of regions where *J. edwardsii* phyllosoma and pueruli were predominantly caught and their location in EAC water of 20.75-21.18^{0}C suggest that they may have been J. *verreauxi*.

6.1.4 Discussion

The general features of the distribution of *Jasus edwardsii* phyllosoma in southern Australia were similar to that reported by other researchers for panulirid early life history stages. Early stage *J. edwardsii* phyllosoma dominated shelf waters while mid and late stages were found almost exclusively offshore to the limit of sampling in most areas. Similar distributions have been reported for *Panulirus* species by Rimmer and Phillips (1979), Yeung and Mcgowan (1991), and Polovina and Mitchum (1992) and for *Jasus* species by Pollock (1986) and Booth (1994) – see review by Booth and Phillips (1994).

Phyllosoma are generally sparsely distributed and, with the exception of large catches of early stages around the periods of hatching, abundances are low relative to other zooplankters (Booth and Phillips 1994). The abundances of *J. edwardsii* phyllosoma recorded in our samples (up to 167/1000 m^3 in shelf waters and up to 33/1000 m^3 in offshore waters) were similar to that reported for phyllosoma in studies elsewhere, although the use of nets in other studies where volume filtered was not easily calculated, limits the ability to compare with our data. Phillips and Pearce (1997) reported abundances of *Panulirus cygnus* phyllosoma off the West Australian coast of up to 94/1000 m^3. Yeung and McGowan (1991) reported abundances of *Panulirus* phyllosoma of up to 47/1000 m^3 off Florida. Lesser (1978) reported early stage *Jasus edwardsii* phyllosoma in abundances of up to 300/1000 m^3 off the coast of New Zealand although average abundances of all stages were considerably less (0.9 – 9.94/1000 m^3 depending on tow type).

The timing of occurrence of early stage phyllosoma was consistent with a single, annual (though protracted) period of larval release during Spring and Summer. The highest abundances of early stage phyllosoma were recorded during the reported peak hatching times in Spring, similar to that reported for *Jasus lalandii* in South Africa (Pollock 1986) and for *J. edwardsii* in New Zealand (Booth 1994).

The offshore limit of distribution for *J. edwardsii* phyllosoma in southern Australian waters was not resolved from the samples available to us, but confirmed that substantial numbers of phyllosoma may be found at distances of up to 550 km from shore. Pollock (1986) reported *J. lalandii* phyllosoma up to 460 km off the Atlantic coast of South Africa and *J. edwardsii* phyllosoma have been recorded in samples spanning the South Tasman Sea between Australia and New Zealand and up to 1500 km to the east of New Zealand (Booth and Phillips 1994, Booth and Grimes 1991). The relatively limited offshore extent of phyllosoma to the south of Tasmania (up to 70 km), despite sampling up to 700 km from shore may be a result of the sampling methods. Several of these southern stations were only sampled during the day using a surface net. Daytime surface net captures of *J. edwardsii* phyllosoma were significantly lower (and in many cases - zero) than those recorded at night due to vertical migration (see section 6.2 Vertical distribution) and this result may thus not fully reflect the southern limit of distribution of *J. edwardsii* phyllosoma.

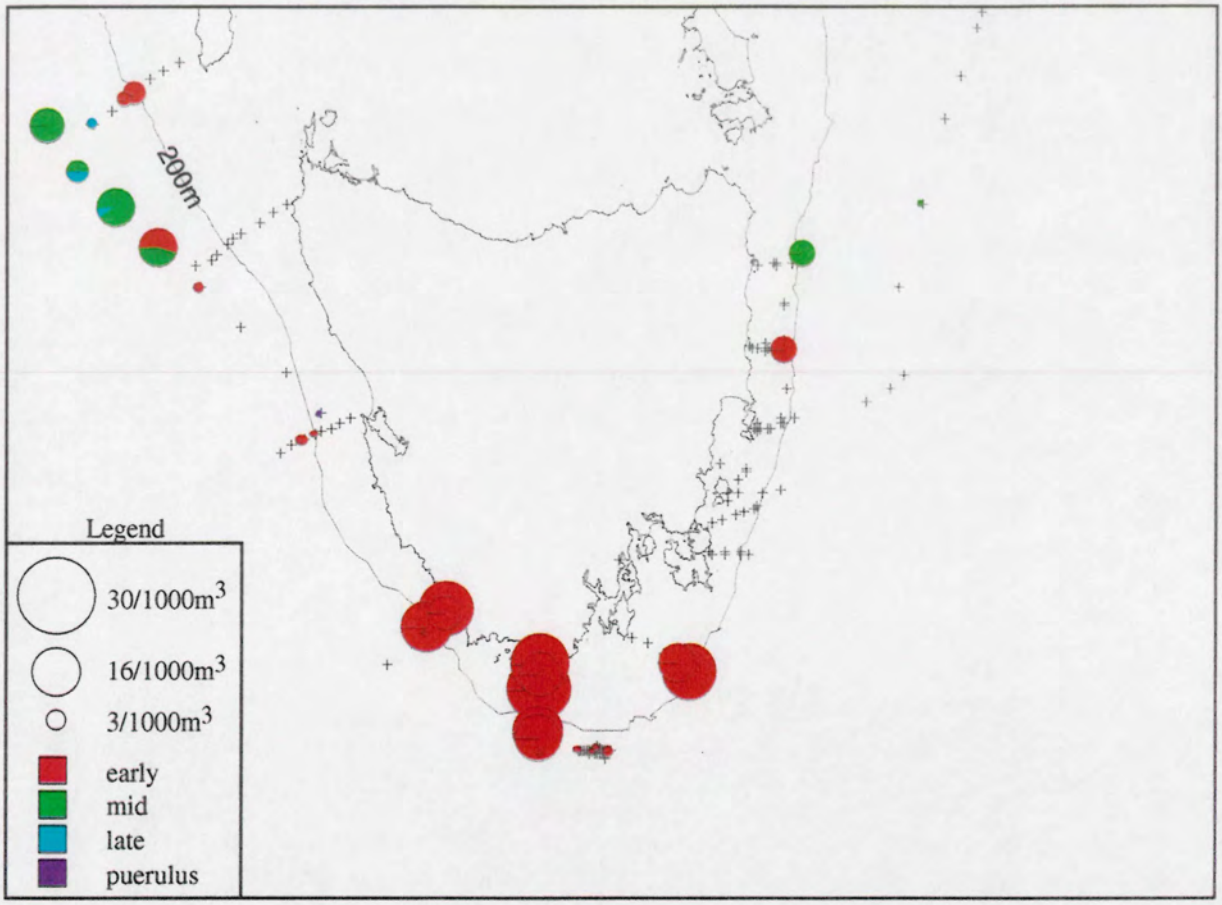


Figure 12: Summer distribution of *Jasus edwardsii* phyllosoma in Tasmanian waters.

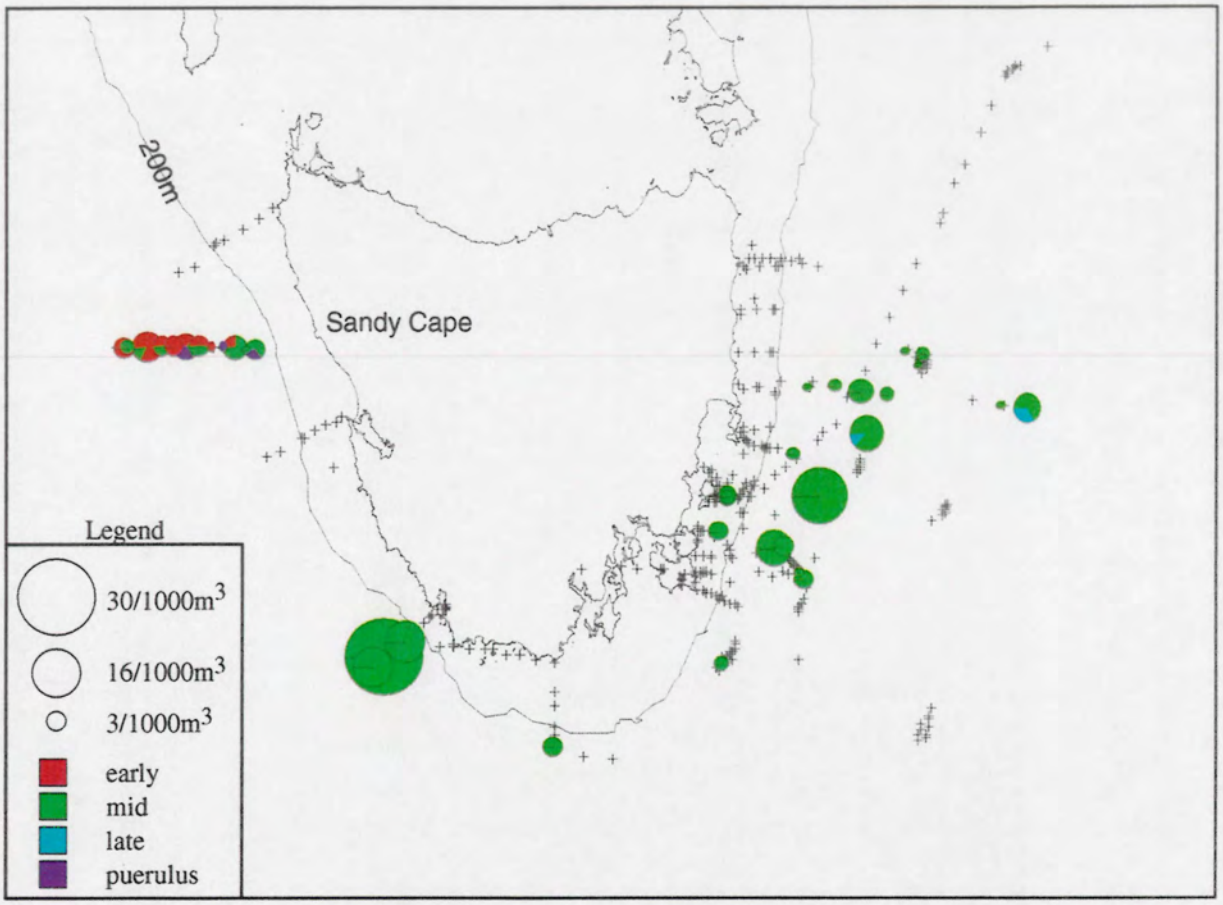


Figure 13: Autumn distribution of *Jasus edwardsii* phyllosoma in Tasmanian waters.

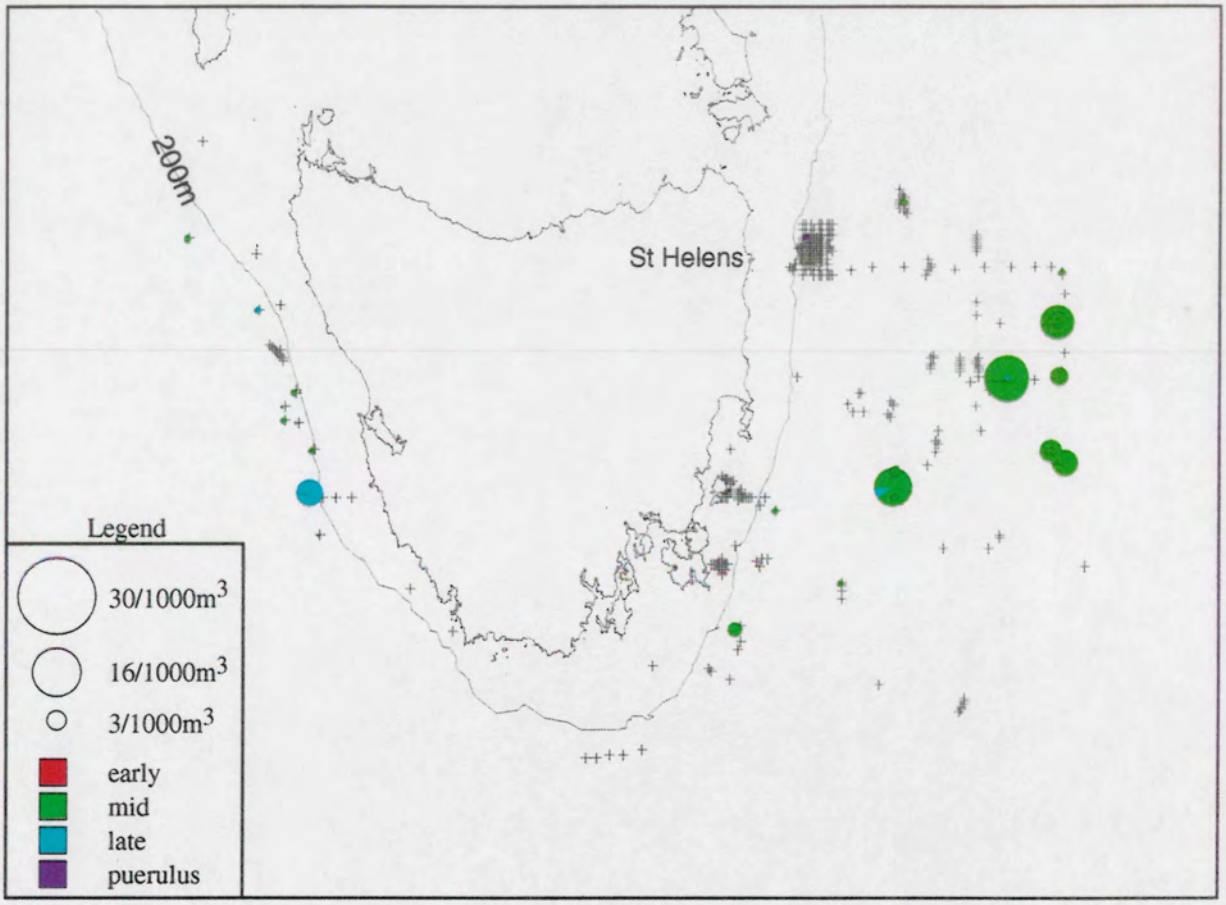


Figure 14: Winter distribution of *Jasus edwardsii* phyllosoma in Tasmanian waters.

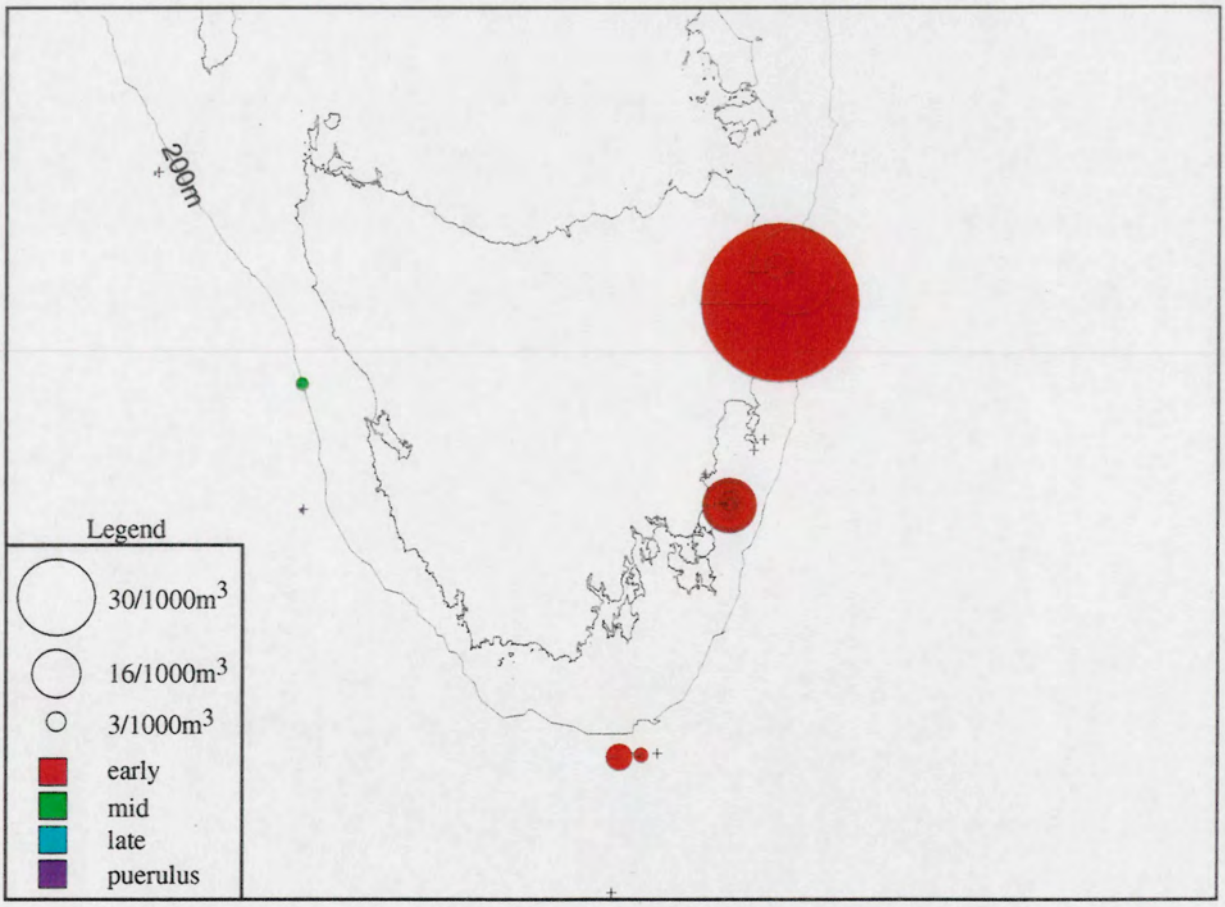


Figure 15: Spring distribution of *Jasus edwardsii* phyllosoma in Tasmanian waters.

Jasus edwardsii phyllosoma were widespread in all southern Australian waters with the exception of Bass Strait and in the Tasman Sea to the north of the Tasmanian mainland. The absence of mid and late stage *J. edwardsii* phyllosoma in the broad shelf region of Bass Strait is not unexpected given the propensity for these stages to occur offshore. However, the lack of early stage phyllosoma in Bass Strait was surprising given the distribution of reproductively active adults in the region. Given that the known peak in hatching occurs in Spring and our Bass Strait samples were taken during Summer, the lack of early stage larvae is most likely due to the available samples not coinciding with the availability of early stage phyllosoma prior to their advection from these waters. Early stage phyllosoma were, however, recorded from all other areas that were sampled in Summer.

The discontinuity in the distribution of *Jasus edwardsii* phyllosoma in east coast waters to the north of mainland Tasmania corresponds to the northern limit of the Subtropical Front (STF). The implications of this are discussed in detail in Section 6.6.4. A similar discontinuity in the distribution of *J. edwardsii* phyllosoma, though latitudinally reversed, has been reported off eastern New Zealand by Booth and Stewart (1992). They reported that phyllosoma were widely distributed off the east coast of the North Island but almost absent from waters south of the Southland Current off the east coast of the South Island. This distribution of phyllosoma coincided with the overall pattern of settlement on the New Zealand coast. Settlement was much higher on the east coast of the North Island where late stage phyllosma were more abundant offshore. Booth and Stewart (1992) and Booth (1994) have suggested that the regional oceanography off the east coast of New Zealand and specifically, the presence of re-circulation cells off the North Island that could retain phyllosoma verses their absence off the South Island, play a major role in larval supply and hence settlement. We suggest that the northern limit of *J.edwardsii* phyllosma observed off north east Tasmania similarly restricts the majority of settlement to areas south of this region and thus places Flinders Island at the northern extreme of regular settlement. The implications of this are discussed further in Section 6.6.4.

Puerulus

Jasus edwardsii

The low numbers of pueruli recorded in our samples is consistent with the observations of other researchers (see Booth and Phillips 1994, and references therein). Pueruli are believed to be widely but sparsely distributed and thus difficult to catch in reasonable numbers (Phillips *et al.* (1978). Booth (1994) caught *J. edwardsii* pueruli almost exclusively at night and generally over the shelf or the continental slope. Our pueruli were similarly caught at night and close to shelf and slope waters. The shelf break region is believed to be where metamorphosis from late stage phyllosoma to puerulus occurs (Booth and Phillips 1994 and references therein). Our data, although consistent with this hypothesis, are insufficient to shed further information on this process in *J. edwardsii.*

Jasus verreauxi

The occurrence of small numbers of *J. verreauxi* phyllosoma off eastern Tasmania is consistent with observations of low level settlement of this species in Tasmanian waters (Frusher *et al.* 1997). There

are no reproductive populations of *J. verreauxi* in either Tasmanian or Victorian waters and puerulus settling in Tasmanian waters were presumed by Frusher *et al.* (1997) to have originated from the known spawning grounds off northern NSW and transported southwards by the EAC. The location of most of the *J. verreauxi* phyllosoma in the EAC plume off eastern Tasmania supports this current as the mechanism of transport into Tasmanian waters although McWilliam and Phillips (1983), surprisingly, did not report capturing any *J. verreauxi* phyllosoma either inside or outside eddies of the EAC along the central and south coasts of NSW. Two pueruli tentatively identified as *J. verreauxi* were recorded in EAC water off southern NSW.

6.2 Vertical Distribution

6.2.1 Introduction

Diurnal vertical migrations are well documented in zooplankton and micronekton communities and play an important role in the transport of zooplankton and phyllosoma (Booth and Phillips 1994). Larvae of several species of rock lobster are known to migrate vertically through the water column on a diel basis. The best documented example is for *Panulirus cygnus* where Rimmer and Phillips (1979) demonstrated the role of vertical migration in larval transport to and from offshore waters. The data is less detailed for some other species (eg *Panulirus interruptus* – see Johnson 1971) although several studies have indicated that *P. interruptus* phyllosoma are more prevalent in surface waters at night than during the day (Chittleborough and Thomas 1969). Pollock (1986) indicated that *Jasus lalandii* undergo a diurnal migration from depths not exceeding 300m during the day to the surface 100m during the hours of darkness. Booth (1994) reported that *Jasus edwardsii* underwent diurnal migrations at least as extensive as that seen in other palinurid species.

Understanding the vertical distribution of phyllosoma is an important prerequisite for understanding and modelling transport processes and hence the linkages between regions of southern Australia. We report herein, the first data on the vertical distribution of *Jasus edwardsii* in southern Australian waters.

6.2.2 Methods

Discrete depth samples obtained from the MIDOC, EZ and surface net systems were used to examine the diel vertical distribution of phyllosoma in southern Australian waters. Section 5.4 provides details of tows and tow protocols. Further details of tow protocols are provided in Young *et al.* (1996).

Data Analysis: All data were standardised to the number of larvae per 1000 m^3 and comparisons of the vertical distribution of phyllosoma were made separately for each net system. Due to the low overall numbers of larvae, data were combined from all samples and seasons rather than comparing individual site series. This introduced a considerable limitation to the analyses and thus the results are only indicative of overall trends and cannot be further analysed with respect to concurrently collected physical data series at any one site or area. Samples were assigned to day or night based on the sunrise-

sunset times on the day and at the position (latitude/longitude) of sampling. Sunrise-sunset times were established using the US Navy web site:

http://aa.usno.navy.mil/AA/data/docs/RS_OneDay.html#formb

The number of samples available from day series was considerably lower than for night series for both the EZ and MIDOC thus day and night data series were also analysed separately for these net systems. The vertical distribution of all phyllosoma were compared first (all species combined) followed by analyses for *Jasus edwardsii*. The MIDOC data were log-transformed as this gave the most even distribution of residuals. Comparisons between depths were made using the ANOVA function of SYSTAT, with significant differences investigated using a Tukey post hoc comparison (Zar 1984). The overall number of larvae recorded from EZ sample series was too low to warrant a full statistical comparison and thus results have only been described and have not been further analysed.

The abundance of larvae recorded by the surface net was compared between combined day and night series. Abundances in surface net tows were markedly higher than for the other two net systems and the number of samples available from day and night tow series were both more numerous and more similar in number (sampling effort). Due to marked departures from normality for surface data sets and the large heterogeneity of variances between day and night abundances, comparisons were made using the non-parametric Mann-Whitney U-Test with ties in ranking resolved by mid-ranks (Zar 1984). Phyllosoma are often characterised by a patchy distribution (Booth and Phillips 1994) and thus, not unexpectedly, many surface net samples (both day and night) contained no phyllosoma. For this reason, only positive tows (ie those that contained larvae) were compared. This obviously reduced *n* and hence the power of the test (Leis 1991). The significance of all analyses was assessed at the P=0.05 level.

6.3.3 Results

MIDOC Net:

A total of 252 MIDOC samples (day n=20; night n=232) were available to the study. Sampling sites were primarily located off eastern Tasmania and south-eastern NSW with a small number of sites off the south and west Tasmanian coasts (Figure 16). Sampling sites were all located seaward of the continental shelf to a maximum distance of approximately 220 km from shore.

Phyllosoma (all species combined) were widely distributed throughout the range of the sampling sites (Figure 16). *Jasus edwardsii* phyllosoma were primarily recorded in samples south of 40 ^{0}S (Flinders Island) and were less commonly encountered than phyllosoma of other species. *Jasus edwardsii* phyllosoma were located in only three MIDOC samples taken north of 40 ^{0}S (in depth strata of 0-100 m, 100-200 m and 300-400 m). Non-*Jasus* phyllosoma (primarily scyllarids) were present at sites throughout the sampling range but tended to be most common in samples off southern NSW.

Phyllosoma (all species combined) were recorded in all except the 200-300 m depth stratum during the day, however, there were no significant differences in abundance between strata (ANOVA: n = 20; df = 3; F-ratio = 0.52; p = 0.67; Figure 17). Only *J. edwardsii* phyllosoma were present in the upper most

(0-100 m) stratum during the day. Both *J edwardsii* and unidentified scyllarid phyllosoma were also present in samples from the 300-400 m stratum. The abundance of *J. edwardsii* phyllosoma tended to be higher in the 0-100 m stratum, however differences were not significant (ANOVA: n = 20; df = 3; F-ratio = 0.87; p = 0.48). *Jasus verreauxii* phyllosoma were found in a single net tow in a 100-200m stratum off eastern Tasmania (Figure 16a).

There was a significant difference in the vertical distribution of all phyllosoma at night (ANOVA: n = 232; df = 3; F-ratio = 6.39; p = 0.00) with abundances generally exceeding the daytime series for all strata (Figure 17). The abundance of phyllosoma in the 0-100m stratum was significantly greater than all other strata (Tukey post hoc test, p = 0.00 for all comparisons). Catches at night were dominated by phyllosoma of scyllarid species with *Jasus edwardsii* accounted for only about 20% of the catch when present.

There was also a significant difference in the night-time depth distribution of *J. edwardsii* phyllosoma (ANOVA: n = 232; df = 3; F-ratio = 4.68; p = 0.00). A Tukey post hoc test indicated that the abundance of *J. edwardsii* phyllosoma was significantly greater in the 0–100m stratum when compared to any of the other three strata (Table 7). However, abundances of *J. edwardsii* phyllosoma were generally similar to those found during the day.

Too few *J. edwardsii* larvae were collected to adequately investigate stage distribution by depth.

Table 7: Results of a Tukey post hoc test to determine where the difference was in the depth distribution of *Jasus edwardsii* phyllosoma and *Scyllarus* spp. phyllosoma.

Species	Comparison	$\lvert \log \overline{X}_2 - \log \overline{X}_1 \rvert$	p
Jasus edwardsii	100–0m > 200–100m	0.002	0.01
J. edwardsii	100–0m > 300–200m	0.002	0.00
J. edwardsii	100–0m > 400–300m	0.002	0.04
Scyllarus spp.	100–0m > 200–100m	0.008	0.01
Scyllarus spp.	100–0m > 300–200m	0.007	0.02
Scyllarus spp.	100–0m > 400–300m	0.008	0.00

EZ Net:

A total of 235 EZ samples (day n=38; night n=197) were available to the study. Sampling sites were located off eastern and southern Tasmania (Figure 18). Sampling sites were all located seaward of the continental shelf to a maximum distance of approximately 215 km from shore.

Phyllosoma (all species combined) were widely distributed across the range of sampling sites (Figure 18). *J. edwardsii* phyllosoma were most commonly recorded off southern Tasmania and accounted for

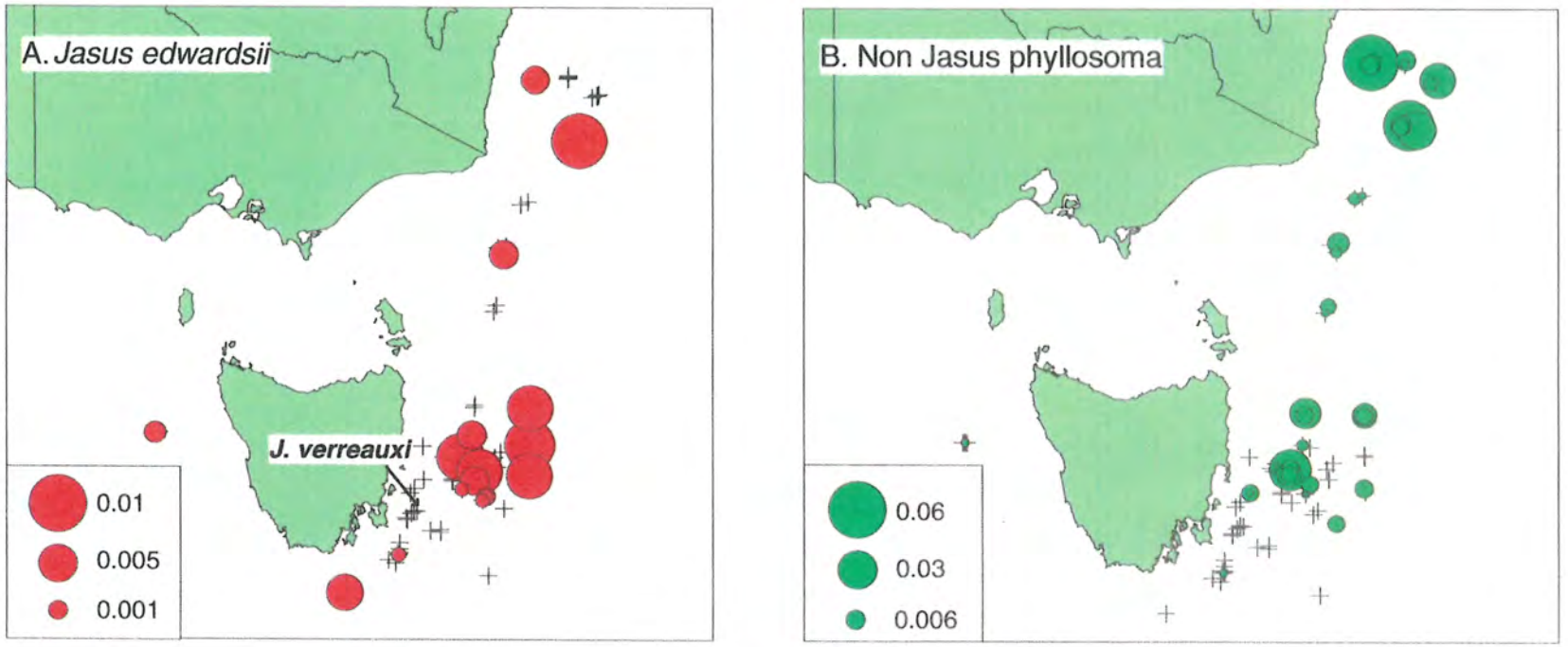


Figure 16: Distribution of MIDOC samples. Scale = numbers of phyllosoma per 1000 cu. m. volume filtered.

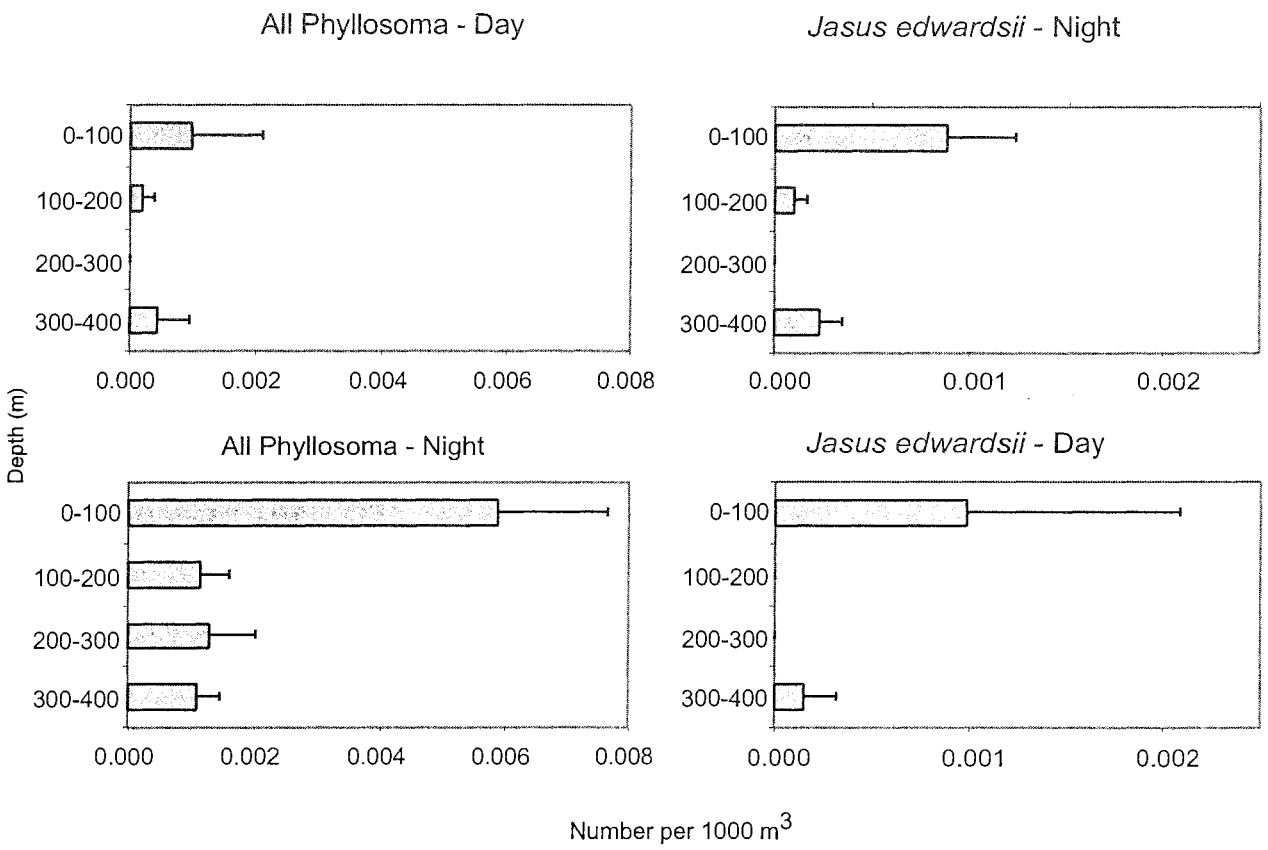


Figure 17: Vertical distribution of phyllosoma - MIDOC data. Bars give standard error.

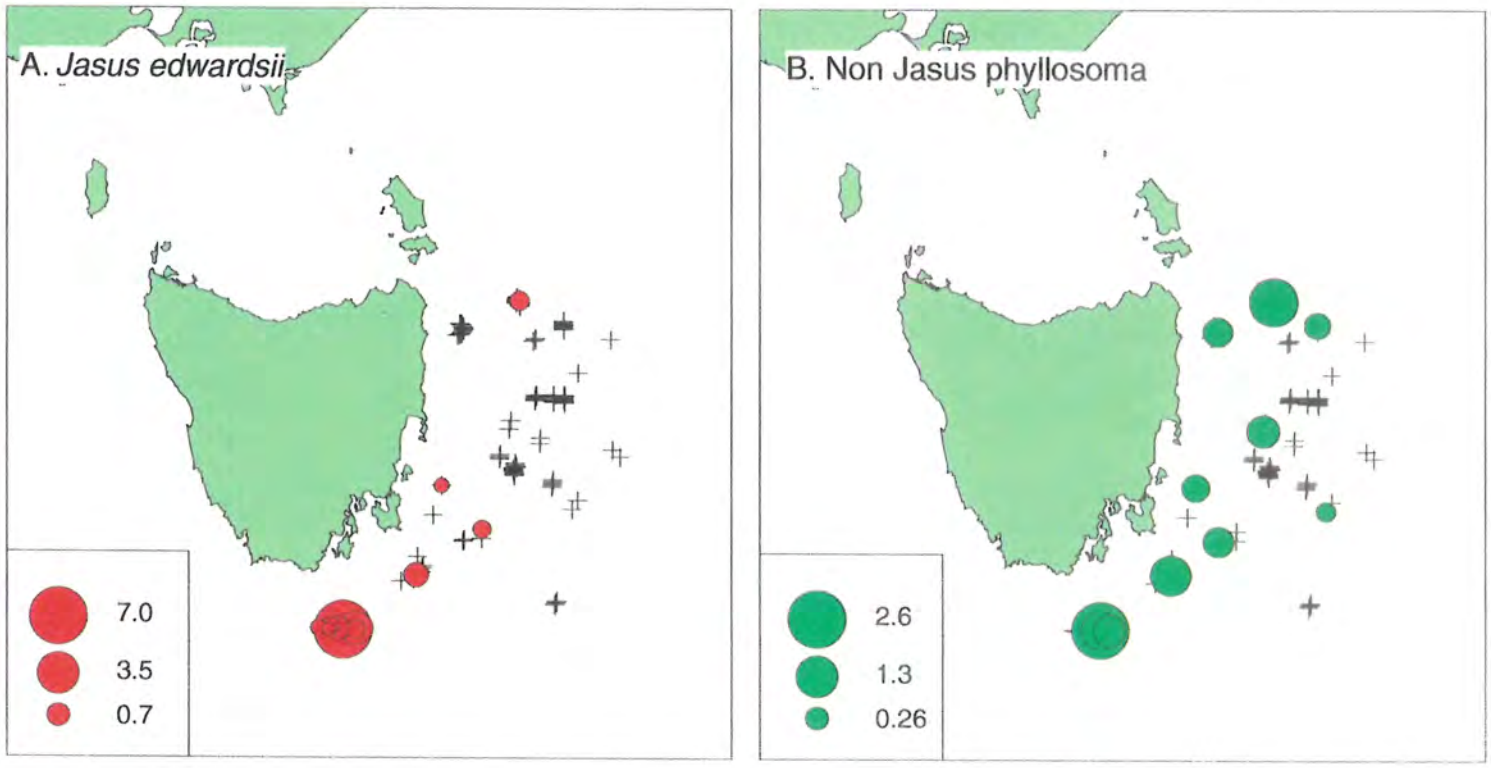


Figure 18: Distribution of EZ net samples. Scale = numbers of phyllosoma per 1000 cu. m. volume filtered.

53% of the phyllosoma recorded. Non-*Jasus* phyllosoma (primarily scyllarids) were distributed relatively evenly throughout the range of sites sampled.

Phyllosoma (all species combined) were most commonly encountered in the upper two depth strata (0-100 m and 100-200 m) during both day and night sample series (Figure 19). *J. edwardsii* phyllosoma were similarly most commonly encountered in the upper two depth strata during both day and night series (Figure 19). *J. edwardsii* phyllosoma were also recorded from a depth of 500-600 m during a night sample off southern Tasmania.

Surface net

A total of 917 surface net samples (day n=406; night n=511) were available to the study (Figure 20). Sampling sites were widely distributed between the eastern GAB and south eastern NSW with the majority of sites located in Tasmanian waters (Figure 21). Sampling sites included a considerable number of both shelf and offshore samples out to a maximum distance of 720 km from shore.

Phyllosoma (all species combined) were widely distributed but were primarily recorded off the west, south and east coasts of Tasmania, no doubt reflecting the higher sampling effort in those regions (Figure 21). *Jasus edwardsii* phyllosoma were located off South Australia in the eastern GAB and just west of the Victorian border as well as around the west, south and east coasts of Tasmania, in both shelf and offshore waters (Figure 21). *Jasus edwardsii* phyllosoma were absent from surface tows taken in Bass Strait. Despite extensive sampling between north eastern Tasmania and south eastern NSW, *J. edwardsii* phyllosoma were rarely encountered and almost entirely restricted to samples taken south of 41^0S off eastern Tasmanian. Non- *Jasus* phyllosoma (primarily scyllarids) were recorded in the eastern GAB region of South Australia, through Bass Strait and throughout the eastern sampling region between south eastern NSW and south eastern Tasmania.

Jasus edwardsii phyllosoma were present in 5.7% of surface tows taken during the day (abundances ranging from 0.77-17.62 larvae/1000 m^3) and 13.7% of surface tows taken at night (abundances ranging from 0.87-33.93 larvae/1000 m^3). Night-time abundances were significantly higher than those during the day in tows that were positive for *J. edwardsii* phyllosoma (Mann Whitney U test, p= 0.0017) and larvae were captured in at least some tows during every hour sampled during the night. This suggests that some level of movement out of the surface layer was occurring during the day. This movement was obviously not absolute given the presence of *J. edwardsii* phyllosoma in some daytime surface samples. However, no *J edwardsii* phyllosoma were recorded at the surface between 0800 and 1300, and the highest daytime catches were in samples taken prior to 0800 and after 1600 (Figure 22).

Combined Depth Distribution

Presence absence data were combined from all three net systems to summarise the overall sampling effort and vertical distribution patterns for *Jasus edwardsii* phyllosoma (Figure 23). The data reflect the

large number of samples that were collected at the surface over the 24hr period, with a lower number of samples collected during daylight hours from the subsurface depth strata. In summary, phyllosoma were concentrated at the surface and within the upper 100 m during the night. However, they were also be recorded at night to depths of 500-600 m. *Jasus edwardsii* phyllosoma were less commonly encountered during the day but when recorded they were also primarily present at the surface and within the upper 100 m.

6.3.4 Discussion

The overall number of larvae recorded in samples available for the analysis of vertical distribution was very low and many samples contained no phyllosoma at all. This markedly reduced the power of our analyses and thus vertical distribution is still a major source of uncertainty in our understanding of the ecology and behaviour of *Jasus edwardsii* larvae. The reasons for the low abundances of larvae in our vertical sample series are probably due to a number of factors (see also Section 5.1 *Scope and rationale of project*). Phyllosoma numbers offshore can vary widely (Booth and Phillips 1994) and they are generally patchily distributed (Rimmer 1980, Phillips *et al.* 1981). Thus it is perhaps not surprising that some tows contained few or no larvae. Phyllosoma are relatively uncommon in most areas compared to other zooplankters. (see also section on distribution in general).

There are few previous reports of abundances of phyllosoma in offshore waters of southern Australia with which to compare our data. J. Booth (NIWA, pers. comm.) sampled at six stations 140-550 km from shore across southern Australia in winter 1995 using a fine mesh midwater trawl (mouth area 55-61 m^2). Samples were taken at 30m depth. Based on the reported mouth area of the net, tow speed and duration and assuming 100% filtration/capture efficiency, captures of *Jasus* phyllosoma ranged from 0.39 – 19.15 larvae per 1000 m^3 (mean = 8.35) Our surface tows (0.77 – 33.93 larvae per 1000 m^3) indicated comparable abundances but our MIDOC and EZ captures were orders of magnitude below these values. Both MIDOC and EZ samples had been previously rough sorted on-board the vessel and had their macro-zooplankton removed and stored. Most samples had also been re-examined in the laboratory. Both exercises may have resulted in the inadvertent loss of some phyllosoma and thus reduced the number available for our analyses. The mesh size of the MIDOC net was also not conducive to retaining all phyllosoma that entered the mouth area.

Other contributing factors to the low numbers of phyllosoma in samples from the opening closing net systems were the initial sampling design and the subsequent handling of samples both at sea and in the laboratory prior to being examined for this project. The original sampling strategies were not designed with phyllosoma in mind and thus the vertical scale of sampling was not always conducive to maximising either the number of larvae captured or resolving specific details of vertical migration. Most strata sampled with the EZ and MIDOC nets were 100 m thick and the duration of tows within each stratum was restricted to 20 minutes or less. Thus the amount of time spent sampling any specific

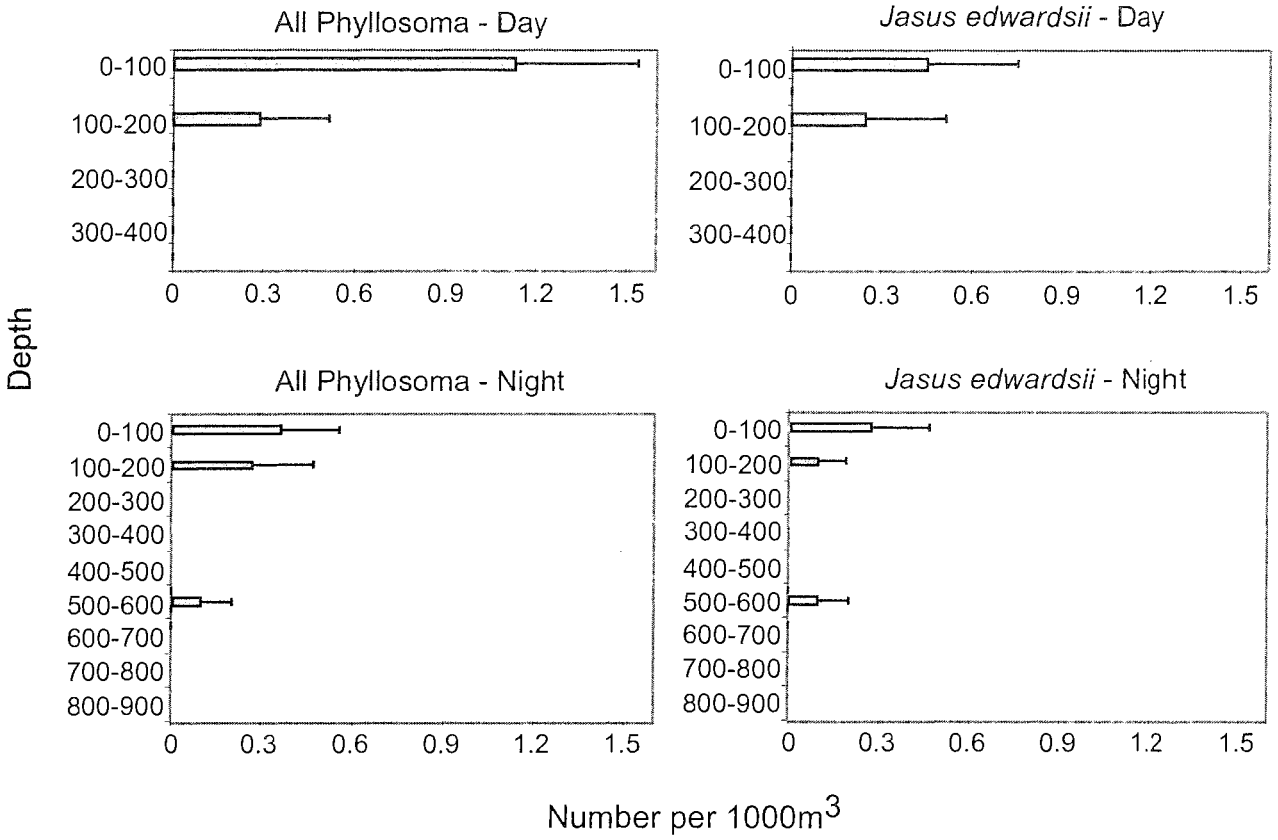


Figure 19: Vertical distribution of phyllosoma (EZ data). Bars give standard error.

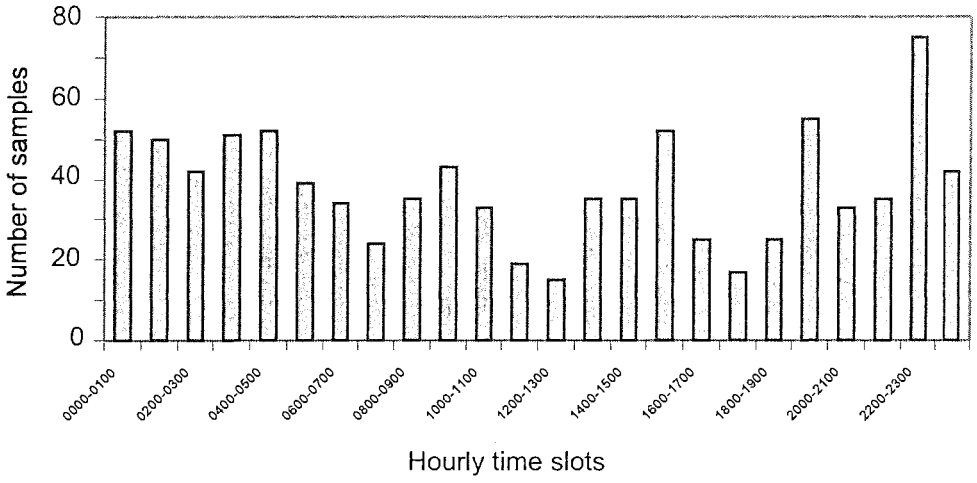


Figure 20: Surface sampling effort (all years combined)

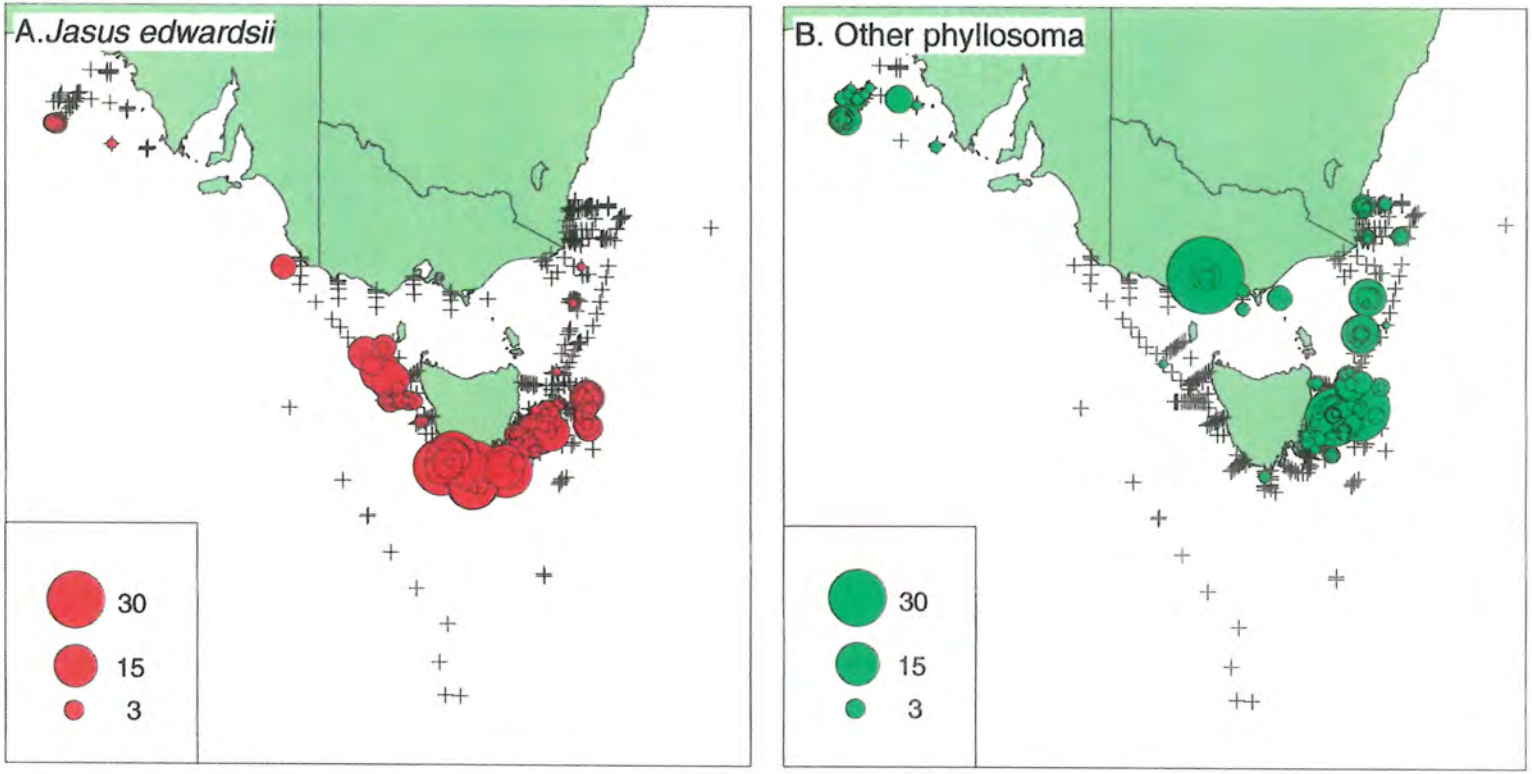


Figure 21: Distribution of surface samples. Scale = numbers of phyllosoma per 1000 cu. m. volume filtered.

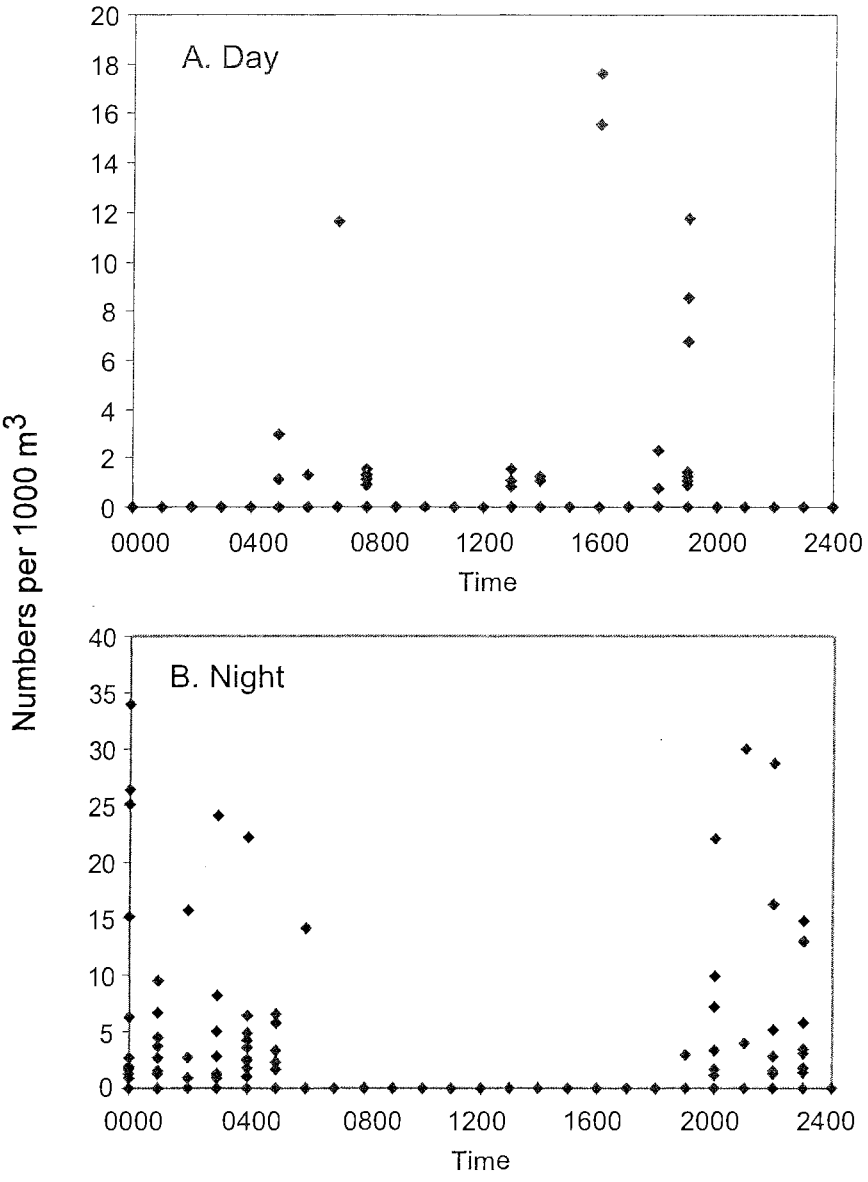


Figure 22: Day and night surface net captures of *Jasus edwardsii* phyllosoma

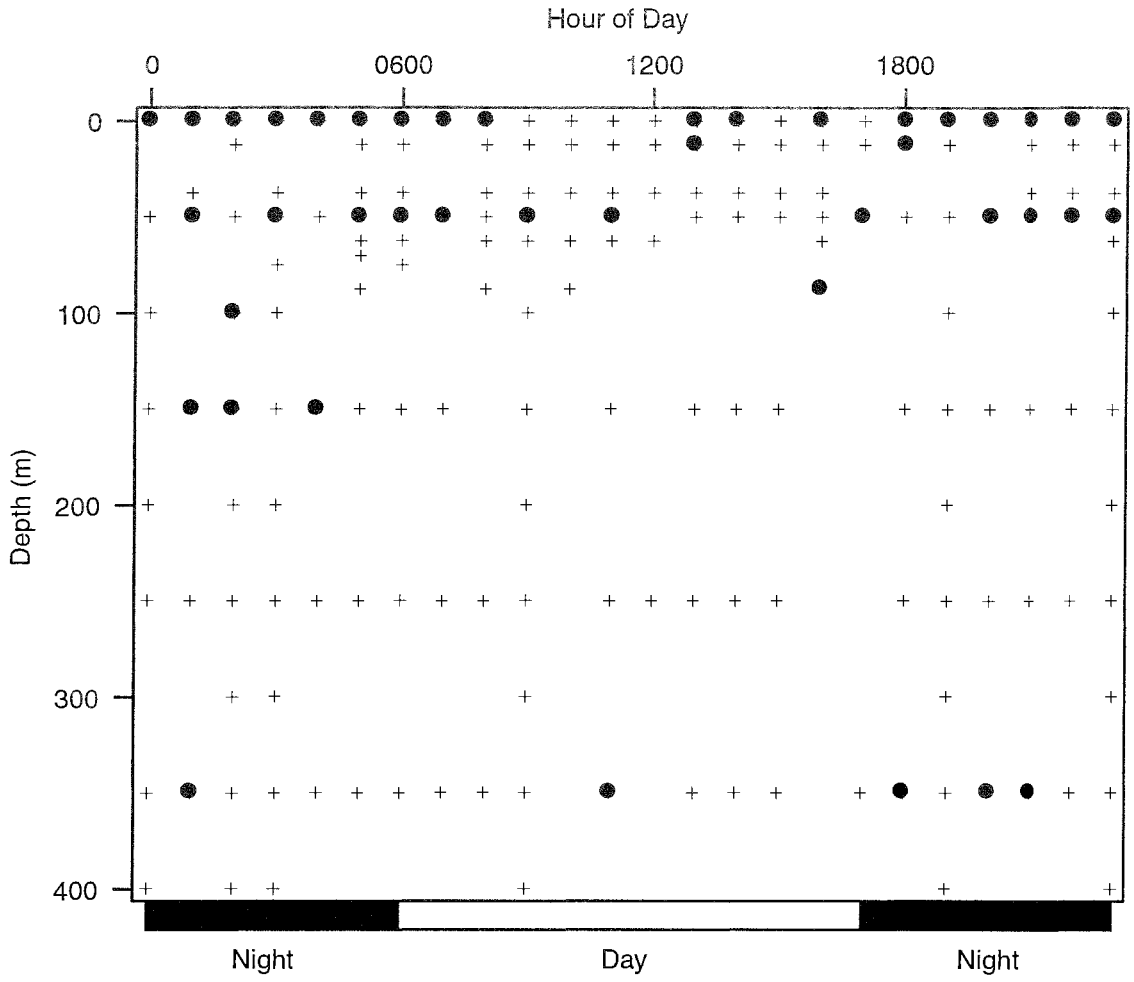


Figure 23: Presence/absence data for *Jasus edwardsii* phyllosoma collected using the EZ, MIDOC, and surface net systems (Crosses = absent; filled circles = present).

depth within a tow was quite low. Most phyllosoma have been reported from the upper 150 m (Booth and Phillips 1994) and their diel changes in depth have been elucidated by sampling strata of a much finer vertical scale than was available to us. Rimmer and Phillips (1979) for example, sampled four strata between the surface and 100 m during the day and the surface and 160-240 m at night in their extensive study of the diel vertical distribution of *Panulirus cygnus* phyllosoma off Western Australia. Yeung and McGowan (1991) sampled depth strata of 25 m thick in their work on phyllosoma off Florida.

The coarse scale of the sampling strata combined with the low numbers of phyllosoma caught may account for the lack of significant differences in the vertical distribuion of *J. edwardsii* phyllosoma between day and night series in our samples. This would particularly be the case if the main extent of vertical migration was less than the scale of the sampled strata.

Despite these inadequacies with the vertical sample series, the results support the observations of Booth (1994) and Pollock (1986) that *Jasus* larvae are widely distributed within the upper 100-200 of the water column and that there is some movement away from the surface waters during the day. Pollock (1986) reported that *Jasus lalandii* phyllosoma were almost exclusively found in the upper 100m at night and descended to depths no greater than 300 m during the day. Booth (1994) found *J. edwardsii* larvae in the upper 200 m at night (most commonly 0-30 m) and from 30 – 310 m during the day. Booth (1994) also reported, from a separate series of tows, that abundances of *J. edwardsii* phyllosoma increased at both 30 and 100m during the night and decreased at both depths during the day. The results of both Pollock's and Booth's studies, however, were based on only a very limited number of tows and small numbers of phyllosoma. Thus our overall understanding of the diel vertical distribution in *Jasus* phyllosoma still must be regarded as some what rudimentary. At least some phyllosoma from samples in our MIDOC and the fine mesh midwater trawls used by Pollock and Booth may not have come from the strata sampled. Rimmer (1980) and R. Pitcher, CSIRO Marine Research, Cleveland (pers. comm.) noted a propensity for phyllosoma to be caught up within the mesh ahead of the cod end of some net systems. Phyllosoma caught in the mesh during multi-strata tows may be washed through into the catch of a separate stratum thus biasing some tow results. This was less problematic for the EZ net series where separate nets (rather than just the cod-end) open and close. The deepest recorded *J. edwardsii* phyllosoma caught in our EZ net series was taken in the 500-600 depth strata. Thus we believe that *J. edwardsii* phylloama must at least occasionally reach these depths.

Data from our surface net series gives the strongest indication of diel vertical migration in *Jasus edwardsii* phyllosoma. Larvae were most abundant at the surface during night although some were caught during the day. Most day captures were either prior to 0800 or after 1600. These captures were generally within 1 hour of sunrise or sunset for the position and date sampled and thus may reflect phyllosoma that had recently entered the surface layer (prior to darkness) or those about to retreat to

deeper depths during the day. Even so, some *J. edwardsii* phyllosoma were captured between 1300 and 1500 and this suggests that not all move to deeper depths during the day.

Stage specific differences in diel vertical behaviour were identified by Rimmer and Phillips (1979) as being crucial to the offshore transport and onshore return of *Panulirus cygnus* phyllosoma off Western Australia. Our data were not sufficient to establish if *J. edwardsii* phyllosoma have any stage specific patterns in diel vertical behaviour. Booth (1994) reported finding no evidence for such differences in vertical distribution between stages of *J. edwardsii* phyllosoma off New Zealand.

6.4 Larval Duration

6.4.1 Introduction

Spiny lobsters have among the longest larval durations of any crustaceans (Pollock 1995). This protracted larval duration, combined with their offshore distribution, offers considerable opportunity for widespread dispersal of larvae. Phyllosoma of the *Jasus* group are believed to have some of the longest larval durations of the spiny lobsters with estimates ranging from 12 to >30 months (Booth 1994, Pollock 1986).

Understanding the duration of this stage is a basic prerequisite for interpreting larval distribution, transport processes, recruitment dynamics, linkages to physical oceanography and modelling dispersal.

Unlike larval fin-fish, where otoliths provide a tool for estimating larval age, phyllosoma have no comparable hard parts that store information on growth. Estimates of larval duration of phyllosoma have been based on the period between hatching and settlement of puerulus, and the seasonal progression of stages captured via plankton sampling (Booth 1994, Pollock 1986, Lesser 1978, Chittleborough and Thomas 1969).

We have followed these techniques and, for comparison, we have also applied a growth rate derived from cultured phyllosoma to estimate larval duration of wild caught phyllosoma.

6.4.2 Methods

Larval duration

Three methods were explored to provide estimates of larval duration.

1. Occurrence of stages

The occurrence of stages was plotted by their Julian day of capture for the combined data set. This provided information on the range of stages at any one time during the year. Two cohorts of larvae

were present in the combined annual plot. These cohorts were separated and replotted using Julian day 280 (the first day when large numbers of Stage I phyllosoma were recorded in the data set) as day 1. Total larval duration was first estimated based on the number of days from this date (linear days) to the appearance of puerulus in the data set and second, by calculating the time to puerulus from an equation fitted to the data.

2. Occurrence of stage I to observed puerulus settlement

Larval duration was also estimated based on the time between the occurrence of stage I phyllosoma in our data set and known seasonal peaks in puerulus settlement for Tasmania (from data supplied by TAFI).

3. Growth rate data from aquaculture

The total length of all wild caught *Jasus edwardsii* phyllosoma was measured using a Wild M5A binocular microscope fitted with an eye-piece graticule (Figure 24). Although the growth of phyllosoma occurs by way of moulting, and thus is not a continuous length function, for the purpose of estimating stage duration we calculated an incremental growth rate from known size at age data for cultured *J. edwardsii* phyllosoma (Tong *et al.* 1997) using the equation:

$$\sum_{i=1}^{n}((\overline{X}_2 - \overline{X}_1)/IP)/n$$

where n = number of stages and IP = the mean intermoult period for phyllosoma kept at 18°C and fed 8 brine shrimp per day (d). This growth rate was then used to estimate the total age in days of wild caught phyllosoma based first, on the sum of stage durations calculated from the mean total length observed for each stage, and second from the exponential growth function derived from the same data set. A duration of 19 d was used for the duration of the puerulus stage based on Kittaka (1990). This value was within the range estimated by Booth and Stewart (1993) for *J. edwardsii* puerulus in the field.

6.4.3 Results

Larval Duration

1. Occurrence of stages

The distribution of stage by Julian day indicated that there were at least two cohorts of phyllosoma present in plankton samples at any one time of year (Figure 25). Stage I phyllosoma were present over a protracted period from day 253 (early September) to day 42 (mid February) with a peak around early-mid October. Large numbers of stage I phyllosoma were first recorded on day 280 (early October). Phyllosoma followed a steady developmental progression with stages I-III dominant during Spring and

Summer, and stages V-VIII dominant in Winter. Stage X-XI phyllosoma were present over most of the year. Puerulus were recorded in late Summer, Autumn and Winter.

The total age of puerulus in the data set, after converting Julian day to linear day, ranged from 512 d – 683 d (16.8-22.5 months). There was a significant linear relationship between stage and linear day (Julian day 280 = 1; ANOVA n=679, F-ratio=4585.902, p=<<<0.001; Figure 26). The regression of stage on linear day provided an estimate of 535 d (17.6 months) to reach puerulus. However residuals were strongly negative for ages greater than approximately 500 d indicating that the linear relationship underestimated age after this point.

2. Appearance of stage 1 to observed puerulus settlement

Stage I phyllosoma were present from early September to mid February but were most abundant during October and November. The timing and magnitude of puerulus settlement in Tasmanian waters varies by region however the dominant patterns are for summer (December-January) and winter/spring settlement (August-September) peaks over a low level of settlement throughout most of the year (Gardner *et al.* 1999). If settlement occurs during the first winter, after hatching in spring, then this suggests a minimum age to puerulus of 9-12 months for the winter period and 13-17 months for the subsequent summer period. However, settlement in under 12 months is not supported by the presence of two cohorts of phyllosoma in samples, nor by the above analysis of stage by linear day. If we assume that the first settlement of puerulus does not occur until the following summer, then the ages of puerulus during settlement peaks would be 13-17 months (summer) and 20-24 months for the subsequent winter. The combined average age of settling puerulus would be 18.5 months. These latter age estimates are consistent with those based on linear day.

3. Growth rate data from aquaculture

Size at stage

There was a considerable overlap in the total length of wild caught *J. edwardsii* phyllosoma of different stages (Table 8).

Table 8: Total length at stage for wild caught phyllosoma

Stage	Mean total length	Standard deviation	range	n
I	2.05	0.07	1.85-2.29	150
II	2.95	0.15	2.44-3.28	108
III	3.87	0.57	2.6-4.8	95
IV	6.12	1.12	4.2-8.1	29
V	9.59	2.49	6.79-19.33	51
VI	12.17	1.70	8.18-15.75	53

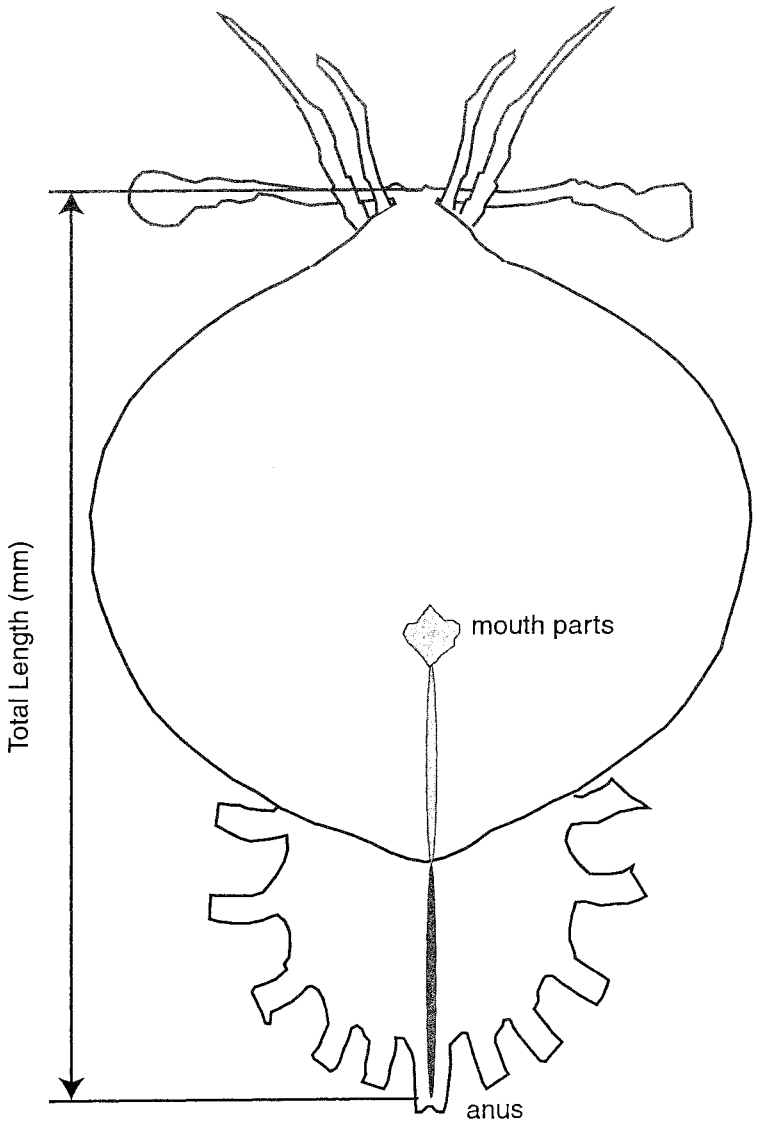


Figure 24: Method for the measurement of total length in *Jasus edwardsii* phyllosoma.

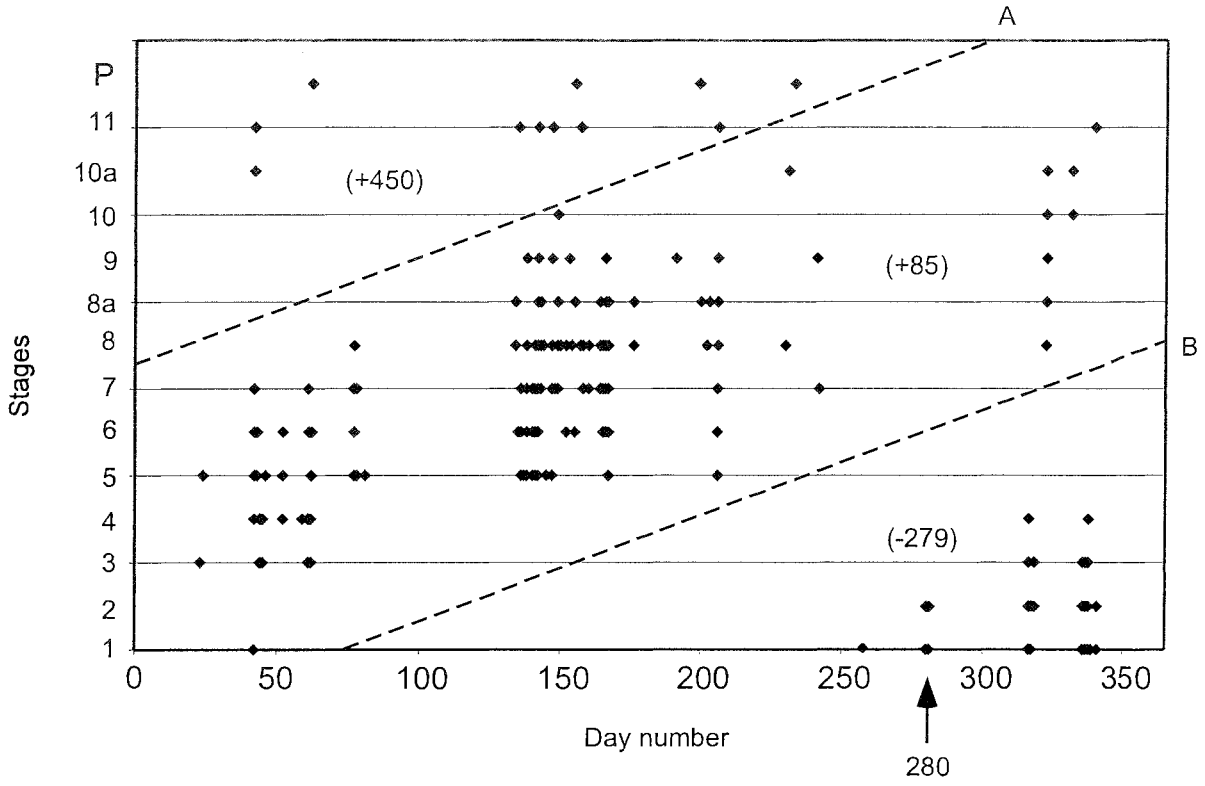


Figure 25: Annual occurrence of phyllosoma stages for J. edwardsii. Lines A + B separate stage cohorts. Numbers in parentheses denote number days added/subtracted to Julian day number of capture to estimate total total age in days (linear day) based on day 280 as birth-date.

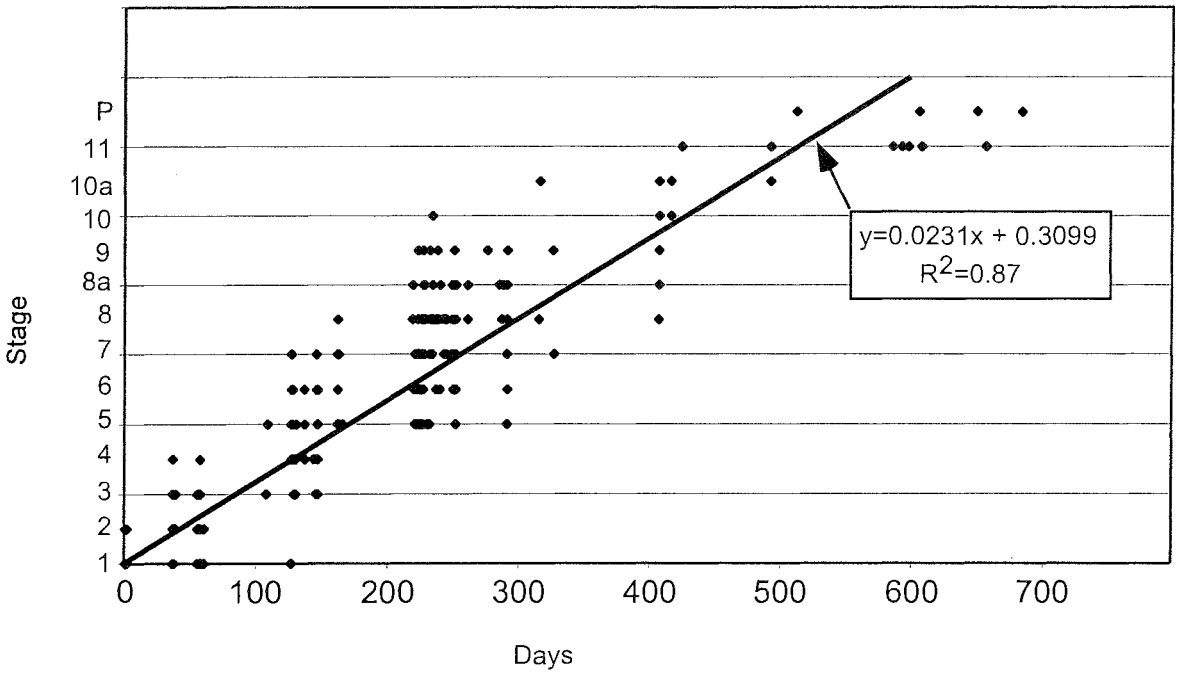


Figure 26: Regression of stage versus linear day for *J. edwardsii* phyllosoma

VII	15.46	1.30	12.5-18.83	60
VIII	18.77	2.15	13.5-24.0	57
VIIIa	21.23	2.13	18.25-24.67	11
IX	25.86	1.51	22.67-28.25	10
X	29.75	1.53	28.67-30.83	2
IXa	36.10	2.02	33.5-38.33	4
XI	36.57	1.61	34.00-39.33	12

Mid stage phyllosoma were the most variable in total length. Stage V phyllosoma varied by over 12 mm in length (6.79-19.33) between individual specimens, although 50 out of the 51 measured were between 6.79 and 13.13 mm in length.

There was a significant, non-linear relationship between size (total length) and stage in wild caught *J. edwardsii* phyllosoma (total length = $1.5554 \times 10^{0.3188stage}$ R^2=0.97) (Figure 27).

A growth rate of 0.084 mm d^{-1} was derived from Tong *et al.* (1997) for cultured *J. edwardsii* phyllosoma. When applied to the mean total length at stage for wild caught phyllosoma, this growth rate provided estimates of stage duration ranging from 5.5 –103.8 d and a total larval duration of 545 d (14.9 months) (Table 9). When applied to the size at stage derived from the above growth equation, the growth rate provided estimates of stage duration ranging from 9.6 –122.5 d and a total larval duration of 636 d (20.9 months) (Table LG1).

Table 9: Estimates of stage duration and total larval duration for wild caught phyllosoma based on a growth rate of 0.084 mm d^{-1} derived from Tong *et al.* (1997).

	Age estimate (days)	
Stage	Using mean size at stage for wild caught phyllosoma	Using size from derived growth eqn *Length* = $1.5554 \times 10^{0.3188stage}$ R^2=0.97
1	24.4	25.5
2	10.7	9.6
3	10.9	13.2
4	26.9	18.1
5	41.3	24.9
6	30.7	34.2
7	39.1	47.1
8	39.5	64.8
8A	29.2	41.0
9	55.1	48.1
10	18.2	122.5

10A	103.8	77.6
11	5.5	91
Puerulus*	19	19
Total duration days	454.3 d	636.6
(months)	(14.9 mo)	(20.9 mo)

*From Kittaka 1990

Larval Growth Rate

The total length of *J. edwardsii* phyllosoma with each developmental stage did not differ with the time of year when they were collected (Figure 28). Similarly, there was no relationship between size within a stage and either region or salinity (Figure 29). There were no clear trends within the data on size versus temperature, with most plots showing a relatively random distribution of points with the exception of stages VI and XI (Figure 30). In both of these stages there was a non-significant trend for larger phyllosoma to have been collected from warmer water.

6.4.4 Discussion

Our data support the observations of Booth (1994) and Lesser (1978) that *Jasus edwardsii* have a pelagic larval duration in excess of 12 months and a mean larval duration of approximately 18 months. Our estimated range for total larval duration of 13-24 months suggests considerable plasticity in larval development times and are also consistent with the minimum estimates of Pollock (1986) for *J. lalandii* phyllosoma off South Africa.

Despite the inherent differences between conditions in the field and laboratory culture, the estimates of larval duration derived from laboratory growth rate data were remarkably consistent with the other methods used.

We observed a similar, wide range in sizes within stages as that reported by for *J. edwardsii* phyllosoma by Booth (1994) with the exception of very late stages (eg. XI) where our total range was considerably less (5.33 mm vs 20 mm). Only a relatively small number of stage XI phyllosoma were measured compared to Booth's data set and this may account for the differences observed. The wide range in size within stages has been cited as possible evidence for mark-time moulting where phyllosoma moult and increase in size without developing into the next stage (Booth 1994, Gore 1985). Booth (1994) also suggested that size differences within a stage may reflect growth, moulting or temperature effects associated with different sources of larvae. Thus size of larvae may be a possible proxy for region of origin and perhaps useful for examining mixing between geographic regions.

Our data, combined with settlement data from TAFI suggests the following model for larval development and subsequent settlement (Figure 31). Larvae hatch in spring and early summer and develop over the following 12 months with phyllosoma first reaching competency to settle some 13-16

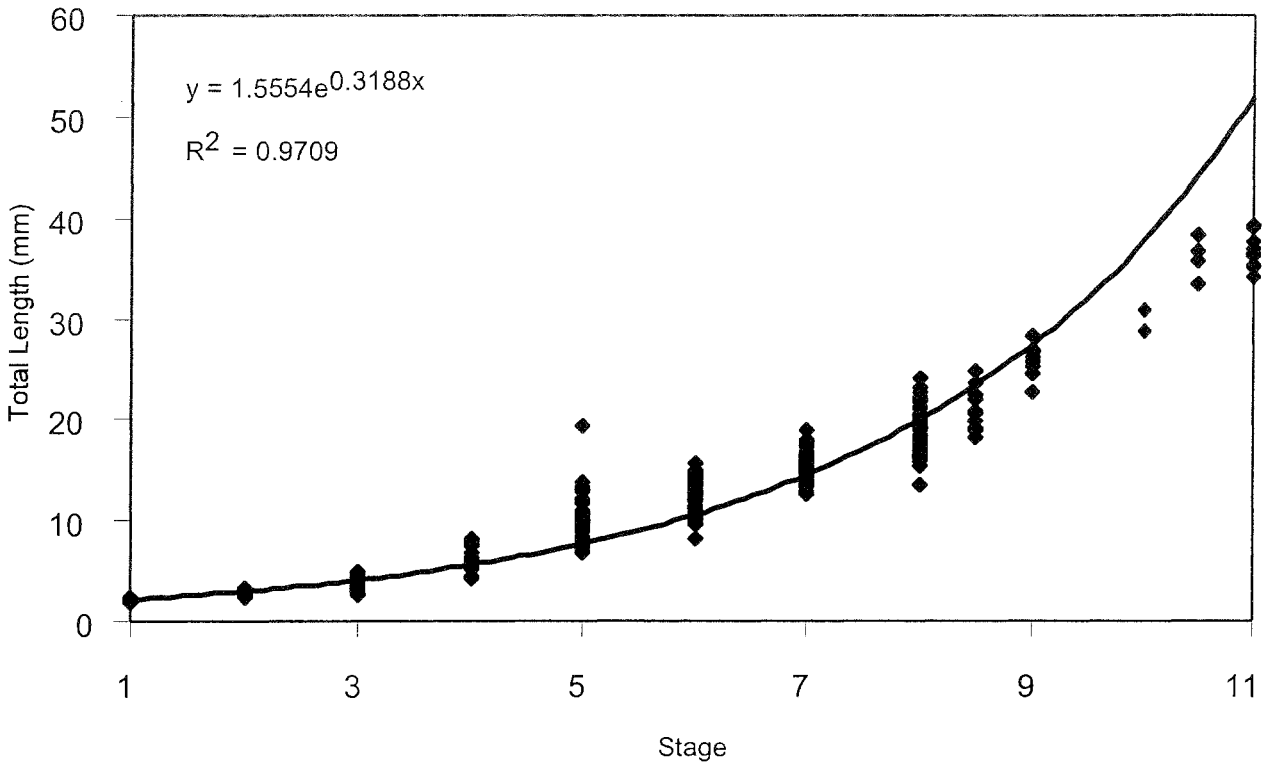


Figure 27: Length versus stage for wild caught *J. edwardsii* phyllosoma.

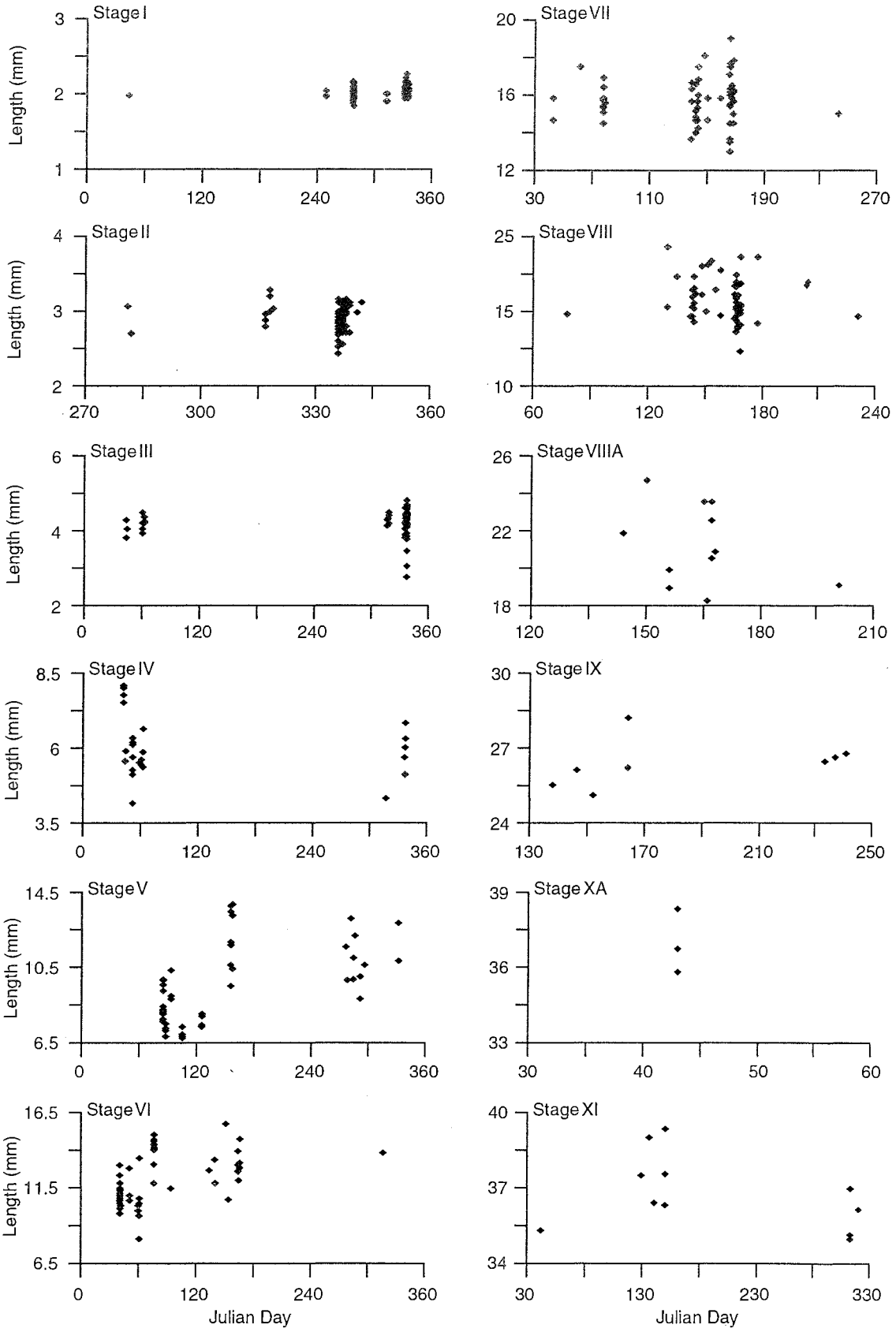


Figure 28: Distribution of total length (mm) of *Jasus edwardsii* phyllosoma against Julian day by developmental stage.

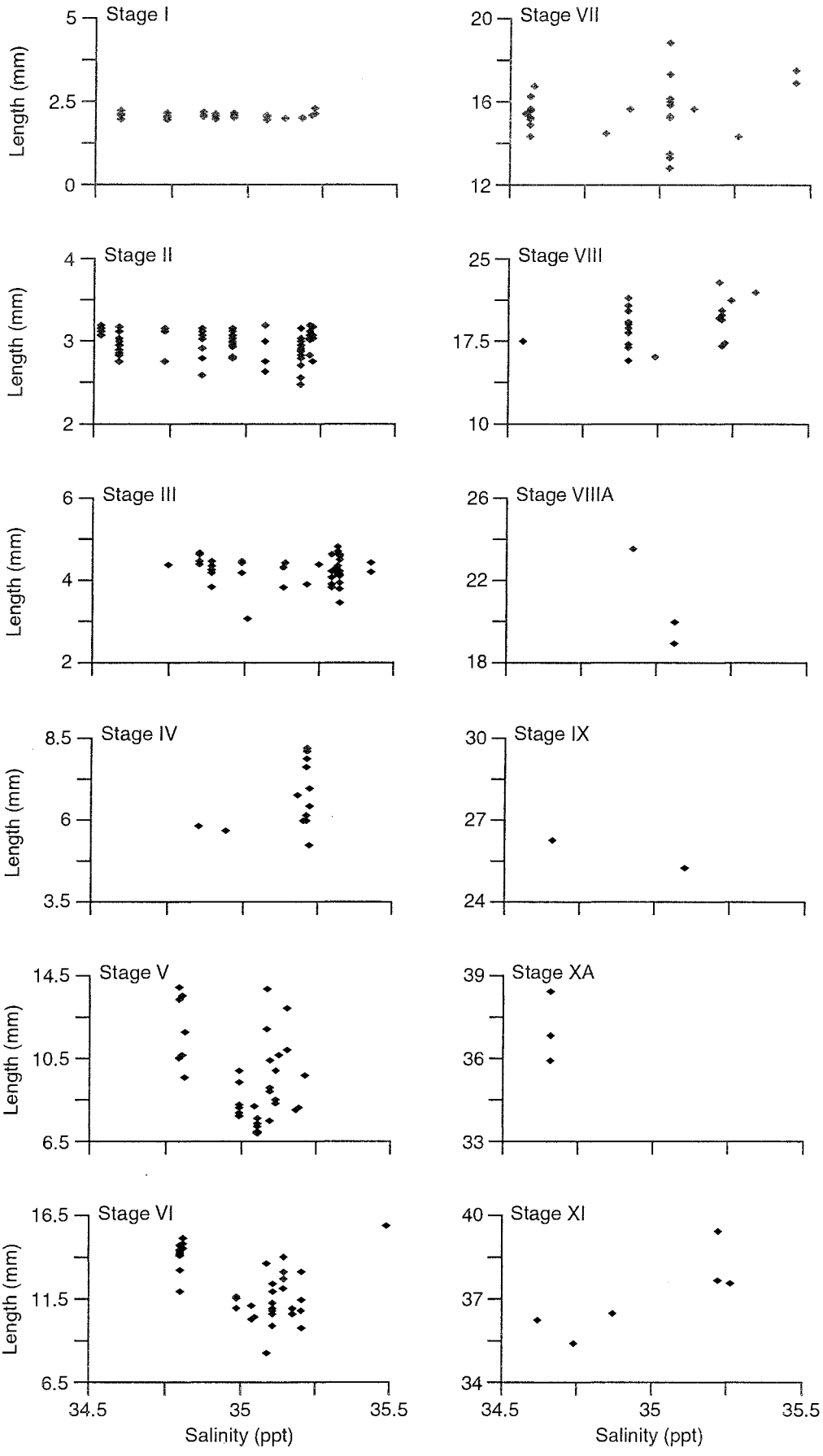


Figure 29: Distribution of total length (mm) of *Jasus edwardsii* phyllosoma against surface salinity (ppt) by developmental stage.

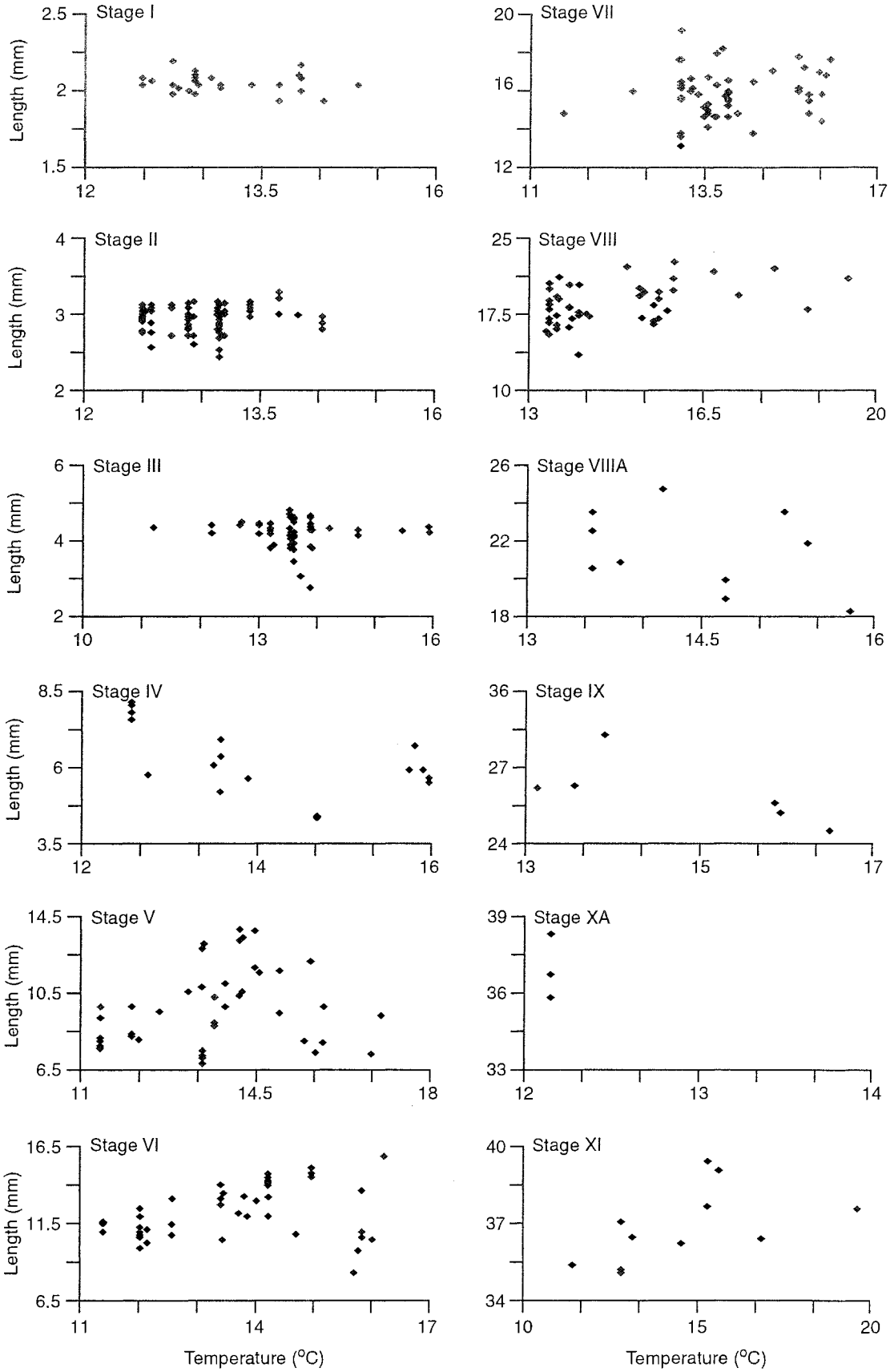


Figure 30: Distribution of total length (mm) of *Jasus edwardsii* phyllosoma against temperature (°C) by developmental stage.

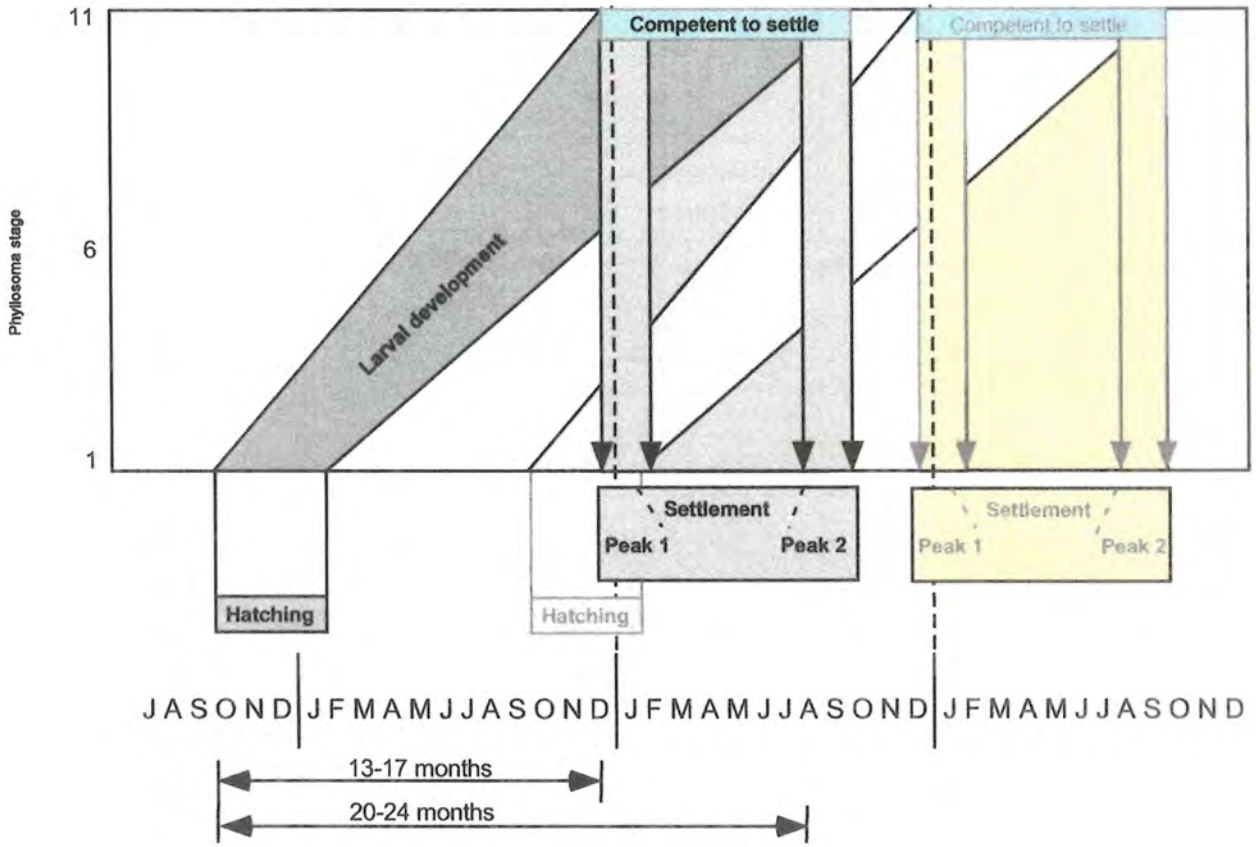


Figure 31: Early life history model (hatching to settlement) for *Jasus edwardsii* in southern Australia

months later. Variable growth rates combined with both the protracted period of hatching and a possible extended period of competency to metamorphose and settle, extend the window of settlement into the following year with puerulus settlement extending to at least 20-24 months after the period of hatching. This model adequately explains the existence of two cohorts of phyllosoma in any 12 month period (contained within the vertical dotted lines of Figure 31), records of late stage phyllosoma at most times of the year and settlement over most periods of the year. The model does not explain, however, the bimodal peaks in puerulus settlement observed at several Tasmanian sites and similarly observed in other parts of southern Australia and New Zealand (Kennedy *et al.* 1994, Booth 1994, Gardner *et al.* 1998, J. Prescott SARDI pers. comm.). This topic will also be further explored in Section 6.6.4 - Oceanographic links, larval distribution and settlement processes.

6.5 Regional comparison of phyllosoma size

Several researchers have suggested the value of assessing growth characteristics as a possible tool in identifying the origin of larvae. The premiss is based on that a least some component of size and growth reflect the environmental conditions (eg temperature or food availability) that a larva has been subjected to. These conditions can vary between regions and thus variability in growth may be used as a proxy for regional environmental conditions. The growth trajectories of larval fish from otolith microstructure analyses have been found to be significantly different between regions in southern Australia and have aided in interpreting regions where juveniles of mixed origin occur (eg Bruce *et al. in press*). Booth (1994) suggested that a least some of the variability in size within stages of *J. edwardsii* phyllosoma stages observed off New Zealand may be the result of mixing of larvae from different sources. We compared the sizes of *J. edwardsii* phyllosoma on a regional basis to see if there was evidence of regional differences in larval size.

6.5.1 Methods

Two regions (eastern and western Tasmania) were selected based on their differences in broad scale physical oceanography (see below). The dividing line between east and west was arbitrarily set at Cape Bruny on the southern tip of Bruny Island. This had some premiss as the easterly flow of the Zeehan Current often departs from the coast at approximately this point shifting water south and offshore (particularly during the summer-autumn period when EAC derived water dominates the east coast of Tasmania). Insufficient numbers of phyllosoma, spanning all stages, were available for a complete comparison with other regions although sufficient stage IV and V phyllosoma were available from South Australia to enable a comparison between Tasmania and that region. Total lengths of phyllosoma (see Section 6.4.2) were log-transformed and compared by ANOVA between regions.

6.5.2 Results and discussion

There was a significant difference in size at stage between eastern and western Tasmania (ANOVA n=530, r^2=0.969; F=4.324; p=0.038). However, there was also a significant interaction between the factors stage and region (F=12.056; p=0.001) indicating that size at stage relationships did not follow a

standard pattern between regions. Overall sample sizes were small for some stages and thus it is possible that this biased results for certain comparisons.

There was no significant difference in the size of stage IV phyllosoma between South Australian and Tasmania (ANOVA n=28; F=2.712, p=0.112). However, stage V phyllosoma from South Australia were significantly smaller than from Tasmania (ANOVA n=48; F=14.927; p=0.000). Only summer samples were available for South Australian waters whereas stage V phyllosoma from Tasmania included summer, autumn and early winter specimens. Stage V *J. edwardsii* phyllosoma may progress through several instars of increasing size (Kittaka *et al.* 1988). Thus, size comparisons may have been confounded by the time (= season) of collection. This was supported by analysis of size versus season for stage V phyllosoma within the entire data set. Stage V phyllosoma were significantly different in size between seasons with size increasing from summer to winter (summer mean=8.087 mm, SE=0.328; autumn mean 10.723 mm, SE=0.343; winter mean 11.833 mm, SE 1.136; all comparisons $p<0.01$). When confined to summer collections only, Stage V phyllosoma from South Australia were still significantly smaller than stage V from Tasmanian waters (ANOVA n=23; F=27.030; p=0.000).

Water temperature was significantly higher in South Australian waters (mean SA 17.3 °C; mean Tas 12.62 °C) for the summer sampling periods. The smaller sizes of stage V phyllosoma from South Australia are consistent with data from laboratory studies on the effects of temperature on phyllosoma growth. The sizes of *J. edwardsii* phyllosoma were significantly smaller at higher rearing temperatures in experiments conduced at NIWA, NZ (G. Moss, personal communication). *Jasus edwardsii* phyllosoma that fell within the size range of South Australian Stage 5 phyllosoma were recorded from the west coast of Tasmania in early Autumn and off the east coast of Tasmania in Summer. The Autumn, west coast captures were within a region of the Zeehan Current that, from SST images, linked directly to South Australian waters and thus it is possible that these phyllosoma may have originated from the latter region. At this stage, however, this can only be considered as circumstantial.

6.6 Physical oceanographic analyses

6.6.1 Physical oceanography of southern Australia

The physical oceanography of various regions of southern Australia has been recently reviewed by Cresswell (*in press*), Bax and Williams (1999), Church and Craig (1998) and Rintoul *et al.* (1997) and we refer readers to these works rather than presenting an additional review here. We have drawn upon these reviews to assist in the interpretation of our data and analyses. Briefly, southern Australia and, in particular the south eastern region, is an oceanographically complex area where numerous currents and major water masses meet and interact. The boundary between waters originating from tropical regions of Australia and those from the Southern Ocean is commonly referred to as the Subtropical Front (STF). The STF extends as a major zone of convection throughout the region at a latitude of approximately 40°S. Currents from the Western Australian seaboard (Leeuwin Current) and from the

eastern seaboard (East Australia Current - EAC) form the basis of the northern boundary of the STF. The eastern seaboard (NSW – eastern Tasmania) is a dynamic region with strong currents associated with eddies and filaments generated by the EAC which extend (summer) and retreat (winter) along the east coast of Tasmania on a seasonal basis. The Tasmanian region is complicated further by a southward flowing current (Zeehan Current) along the outer continental shelf of the west coast (Baines *et al.* 1983). Peak flows of the Zeehan Current occur in winter when it can reach around southern Tasmanian and up the east coast to at least Schouten Island (Cresswell *in press*). The EAC dominates the east coast of Tasmania in summer – often extending several hundred kilometres south of the island, entraining the Zeehan Current in the process and producing offshore flows from the shelf south of Bruny Island (Cresswell 1998).

The western region of southern Australia is similarly dynamic with meanders and strong currents associated with the extension of the Leeuwin Current into the western region of the Great Australian Bight (GAB) (Church and Craig 1998). However, the region between the western GAB and southern Tasmania has comparatively weaker currents (with the exception of some seasonally variable flow regimes on the shelf). Currents in this region follow a generalised west to east flow, however, there are often several areas of weak westerly flow and weak transient eddies in offshore regions (Church and Craig 1998, G. Cresswell pers. comm., this study). Weak westerly flows also occur to the south of Tasmania. There is considerable inter-annual variability in the positions of the frontal boundaries and in the strengths of the various currents throughout southern Australia (Cresswell *in press*).

The STF was identified as playing an important role in the distribution of *J. edwardsii* phyllosoma during this study and many of the analyses concentrate on this feature.

6.6.2 Methods

Several physical oceanographic data sets were available for analyses.

CTD casts and physical oceanographic data archive

CTD (Conductivity, temperature, depth) casts were routinely collected at most net sampling stations that were taken on CSIRO cruises. In most cases, several other parameters (including dissolved oxygen, fluorescence, nitrate, phosphate, silicates) were also available from CTD casts. The CTD data from cruises where net tows were taken, as well as all other cruises where CTD casts were made, are archived by CSIRO and were used to describe the distribution of water mass properties across southern Australia (Figure 32). Temperature and salinity (T/S) are useful parameters that can be used to describe the source region(s) of a water mass. A T/S plot was constructed using all available data from net sampling stations across southern Australia. The abundance of *J. edwardsii* phyllosoma was then plotted for each station, as an overlay, to examine their distribution relative to all water masses sampled and identify T/S bounds for their distribution. The overall distribution of water with these T/S properties (referred to herein as 'phyllosoma water') was then assessed based on the complete CSIRO data archive.

Satellite tracked sea surface drifters

The trajectories of satellite tracked sea surface drifters released in south eastern Australia between 1991 and 1998 were used to examine detailed circulation patterns and provide insights into possible larval transport processes. In most cases, drifters were released in waters over the continental shelf. Drifters are described, in detail, by Cresswell (*in press*). Briefly, they consisted of a cylindrical surface unit (0.6m in length and 0.2 m diameter) with a 0.5 m whip antennae. Units were manufactured by Moonraker Technology Pty. Ltd., Hobart. The surface unit was attached to a drogue set at a depth of 15 m. Position fixes, to better than 1 km, were provided from NOAA satellites carrying the CLS-Argos system.

Sea surface temperature images and data

We accessed similar data sets to those described by Bax and Williams (1999), although over different time periods, and over a wider geographic range. Briefly, CSIRO Marine Research processes one kilometre resolution NOAA-12 AVHRR (Advanced Very high Resolution Radiometer) data to generate composite images of sea surface temperature (see Walker and Wilkin 1998 for further details). Two primary SST products were examined.

(a) Five kilometre resolution, 10 day composite images were used to examine the broad scale physical oceanographic features of south eastern Australia from 1988-1997. Images are available at http://www.dmr.au/~griffin/OISST. We used these data to examine the broad-scale physical oceanographic features of the region bracketing the period over which we had samples, as well as examining the relationship between offshore ocean climate and the settlement of *J. edwardsii* puerulus in Tasmanian waters. The latitudinal position where the 14.5-15 degree isotherm contacted the shelf edge off the south eastern Australian coast was estimated from a composite SST image (mid-month) for each month between December 1990 and December 1997. The 14.5-15 degree isotherm was selected as a proxy for the location of the northern boundary of the STF. Waters south and north of the 15 degree isotherm were identified from satellite images as being of STF and EAC origin respectively. We assumed that the period between the northward passage of the 14.5-15 degree isotherm and its subsequent southward return, marked the period of exposure to waters of STF origin at any one site on the adjacent coast. The seasonal position of the 14.5-15 degree isotherm, the period of exposure to STF water and the monthly index of puerulus settlement (the latter from data supplied by TAFI) were then plotted for the Bicheno and Flinders Is sites.

(b) Time series of averaged sea surface temperatures were also calculated from archived SST images over a boxed area off Bicheno (eastern Tasmania) as a second analysis of the seasonal passage of the 15 degree isotherm past this site and again compared to puerulus settlement data.

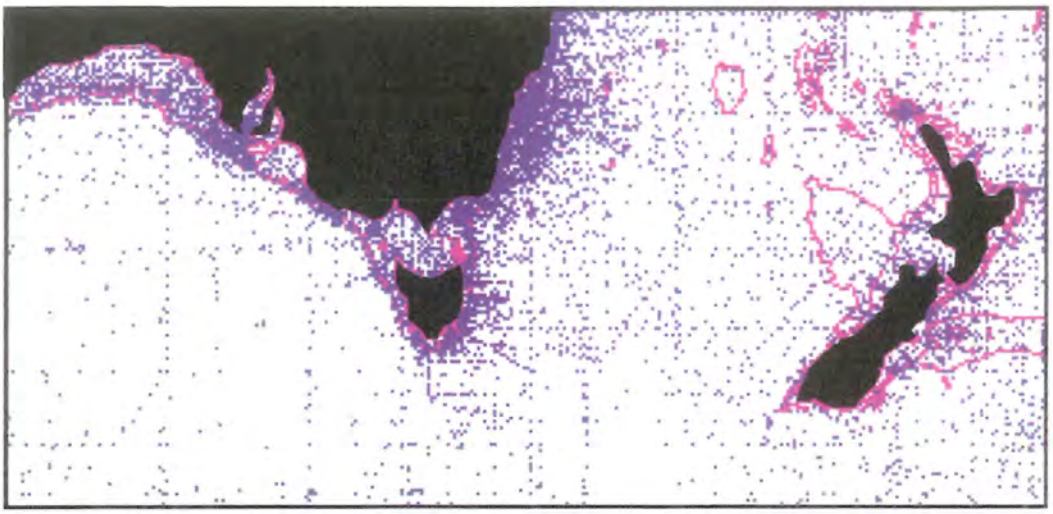


Figure 32: Location of all hydrographic sampling sites (CSIRO data archive)

Animations

Broad-scale circulation features across southern Australia were examined using animations of SST, altimeter data and satellite tracked surface drifters. Puerulus settlement data for sites monitored in Tasmania were also added to animations in a first cut attempt to examine settlement with respect to regional circulation features. Animations are stored as 'fli' files on the accompanying CD.

6.6.3 Results

Temperature-salinity plots

Jasus edwardsii phyllosoma were primarily found within a limited temperature-salinity (T/S) range when compared to the total data set. The T/S signature of this "phyllosoma water" was 12.2-15.0 °C; 34.70-35.08 ppt (Figure 33). Two occurrences of early stage *J. edwardsii* phyllosoma in waters of anomalously low salinity were excluded from the description of "phyllosoma water". These specific samples came from shelf waters of western Tasmania in an area heavily influenced by freshwater run-off.

The distribution of waters matching this T/S signature described the position of the STF (Figure 34). This "phyllosoma water" formed a continuous band extending throughout waters of southern Australia between approximately 37 °S and 45 °S west of Tasmania and a similar band, though more tightly clustered, across the Tasman Sea to New Zealand between 42 °S and 45 °S. The T/S signature of waters where pueruli were located was similarly plotted. *Jasus vereauxii* pueruli were located in EAC derived water, whereas *J. edwardsii* pueruli where located in waters matching the signature of the northern boundary of the STF and shelf waters of western, southern and eastern Tasmania (Figure 34).

Satellite-tracked Drifters

The overall movement of drifters released in Tasmanian waters followed the generalised west to east flow pattern described for these latitudes (Rintoul *et al.* 1997), with drifters eventually meandering across the south Tasman Sea towards New Zealand (see Cresswell, *in press*, for further details). Drifters followed an essentially zonal path at the expected latitude of the STF in offshore waters to the east of Tasmania (Figure 35). There appeared to be little exchange of drifters across the STF boundary into waters of more northern origin. The pattern of drifter movement was, however, considerably more complex within 500 km of the Tasmanian coast (Figure 35). Drifters remained within 500 km of the Tasmanian coast for periods ranging up to 19 months before moving eastwards across the south Tasman Sea. During these periods drifters moved in a complex series of both clockwise and anticlockwise circulations, with the most common areas of 'eddying' occurring off the south east coast and the south west to central west coast. Drifters were, at times, entrained into the southward flowing Zeehan current that transported them from the west coast to the central east coast during winter. Drifters entrained into the Zeehan current during summer were transported offshore in the vicinity of South-East Cape presumably as a result of interaction between the Zeehan Current and the EAC. Drifters often moved in a westerly direction in offshore waters, particularly to the south and west of

Tasmania. Several drifters either returned to or close to their point of release after periods of 11-19 months circulating in offshore waters. The movement of drifters was generally restricted to waters south of 41° 30" S on both the east and west coasts of Tasmania and corresponded to movements within the broad STF zone. However, some drifters made occasional excursions northward to 39°S-40°S – roughly the level of Flinders and King Islands during winter and early spring.

These features are most easily seen in the animation on the accompanying CD.

SST and puerulus settlement data

The seasonal changes and interplay between the various water masses in south eastern Australia, as described by various authors, were observed in all years of the SST data set (Figure 36). The latitudinal position of the 14.5-15 degree isotherm shifted north and south along the south eastern Australian coast between approximately 45°S and 36°S on a seasonal basis, with the northern and southern extremes reached in about August and March respectively. There was some variation between years in the both the timing and duration of exposure to STF water at both the Bicheno and Flinders Island sites.

Bicheno

Puerulus settlement peaks at Bicheno coincided to the period of exposure to STF water in all cases except February 1995 (Figure 37) There was also some low level settlement recorded at most times of the year except for the autumn months of 1991, 1992 and 1993. Settlement within the period of exposure to STF water was, however, highly variable. Similarly, the magnitude of settlement was variable from year to year and there was no obvious relationship between the magnitude of settlement and the position of the 14.5-15 degree isotherm. Interestingly, settlement peaks commonly occurred around the timing that the 14.5-15 degree isotherm passed northwards and southwards, leading to two annual settlement peaks in 1991, 1992 and 1993. The 14.5-15 degree isotherm fluctuated off Bicheno in 1994 and that year recorded three settlement peaks. Settlement was highest in 1995 and occurred in three peaks (February, August-September and November). The main peak occurred in August-September, well within the period of exposure to STF water. The second main peak occurred in November and marked the southward passage of the 14.5-15 degree isotherm. Single settlement peaks were recorded in both1996 and 1997. The period of exposure to STF water in 1997 was the shortest for any year observed during the data set.

The settlement of puerulus was plotted against time averaged sea surface temperatures calculated from a boxed area adjacent to the shelf, east of Bicheno (Figure 38). Settlement on the adjacent coast occurred over a wide range of temperatures from 11.8 °C – 20.6 °C. Peak settlement events coincided with water temperatures of less than 15 °C.

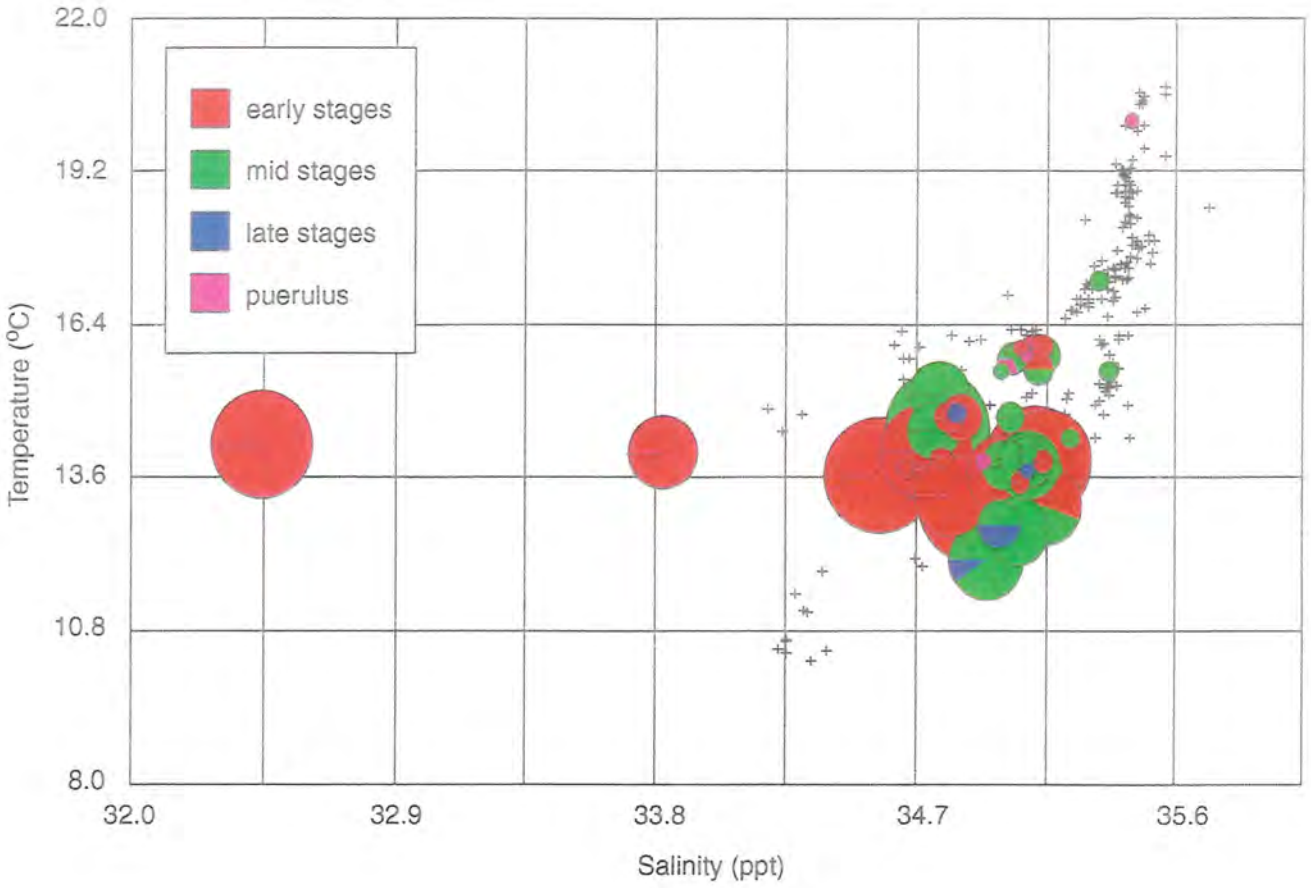


Figure 33: Temperature/salinity characteristics of *Jasus edwardsii* larval distribution.

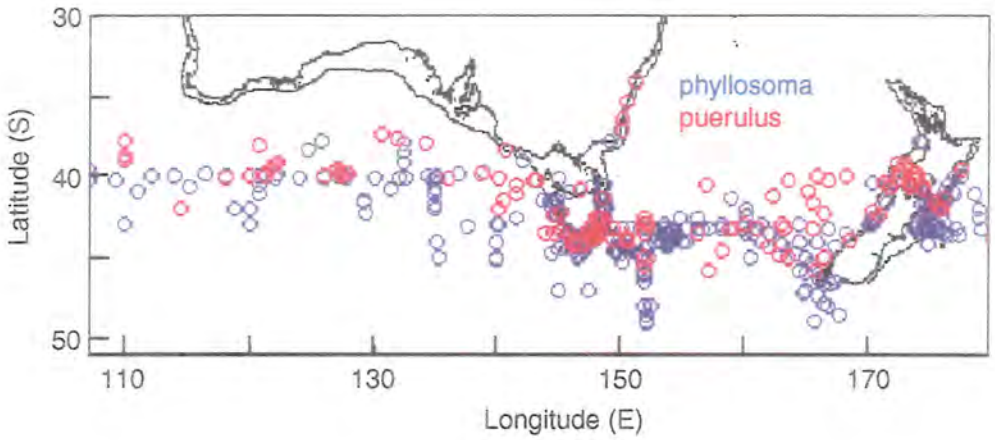


Figure 34: Position of waters within the temperature and salinity range in which the majority of *Jasus edwardsii* phyllosoma and puerulus were collected.

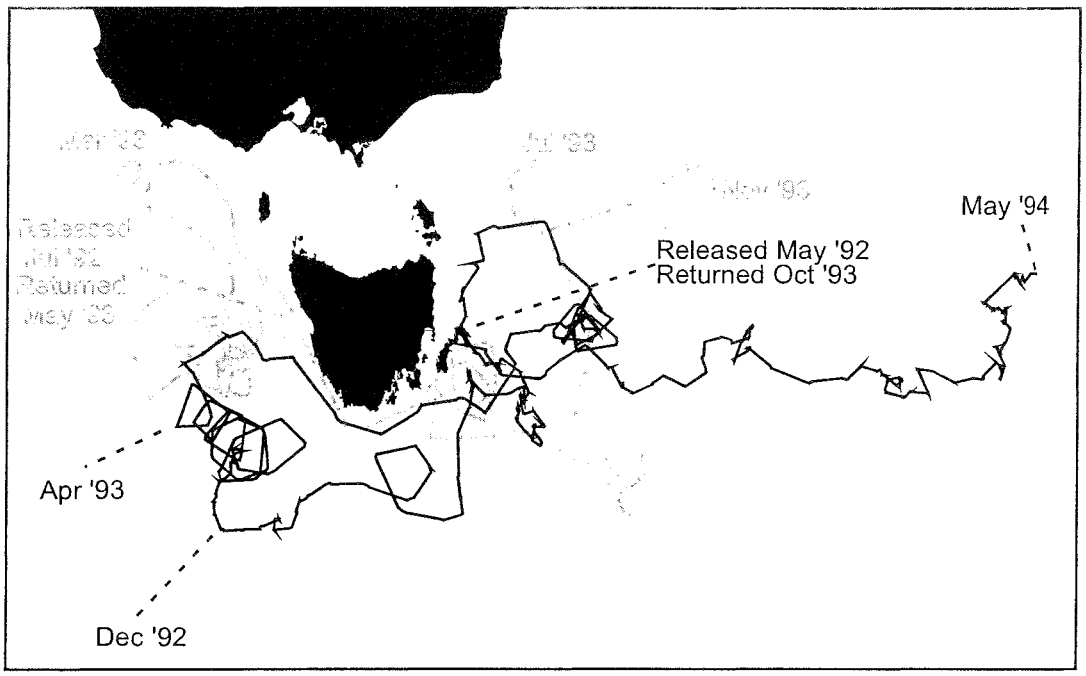


Figure 35: Paths of two satellite tracked surface drifters released in Tasmanian coastal waters

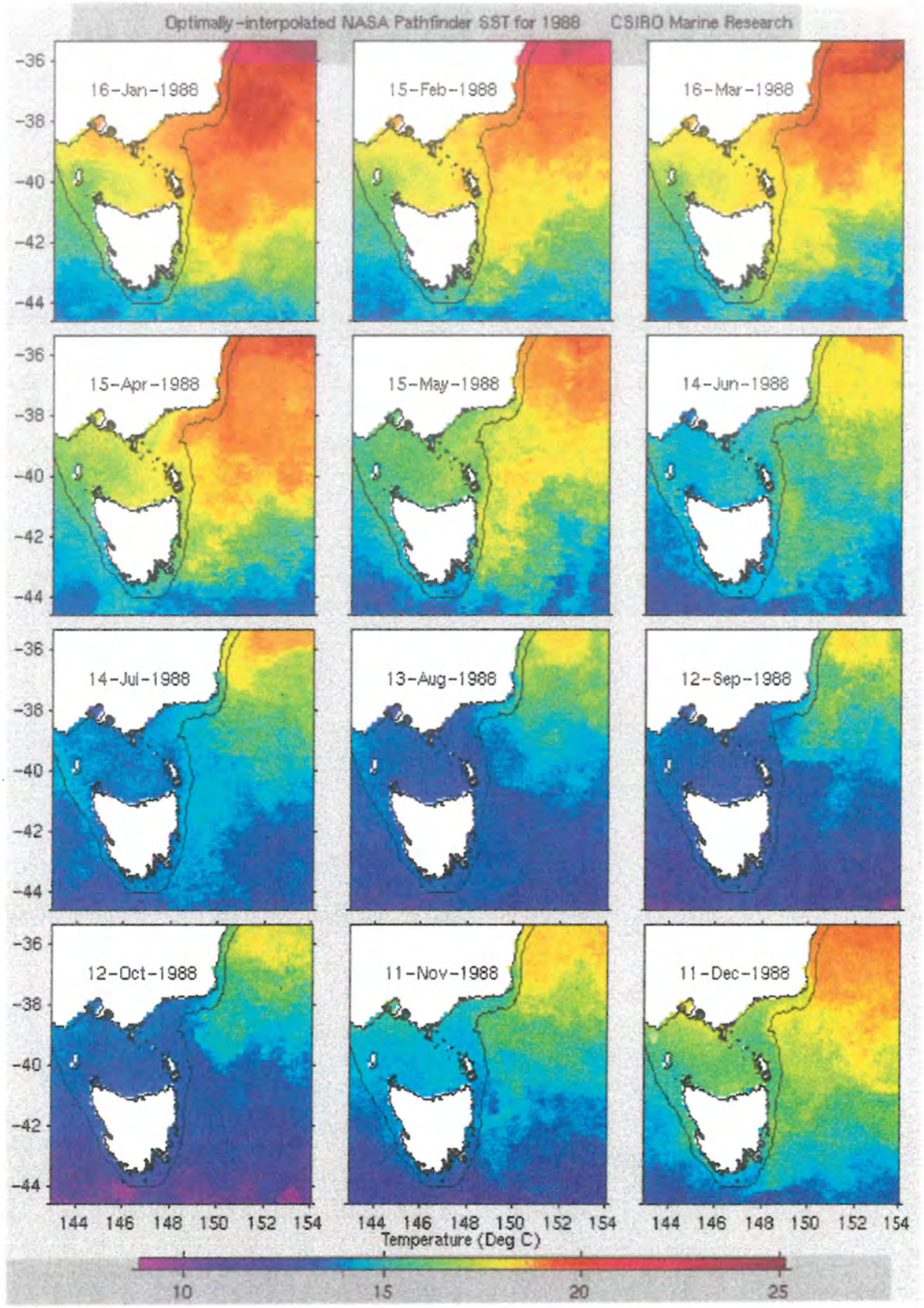
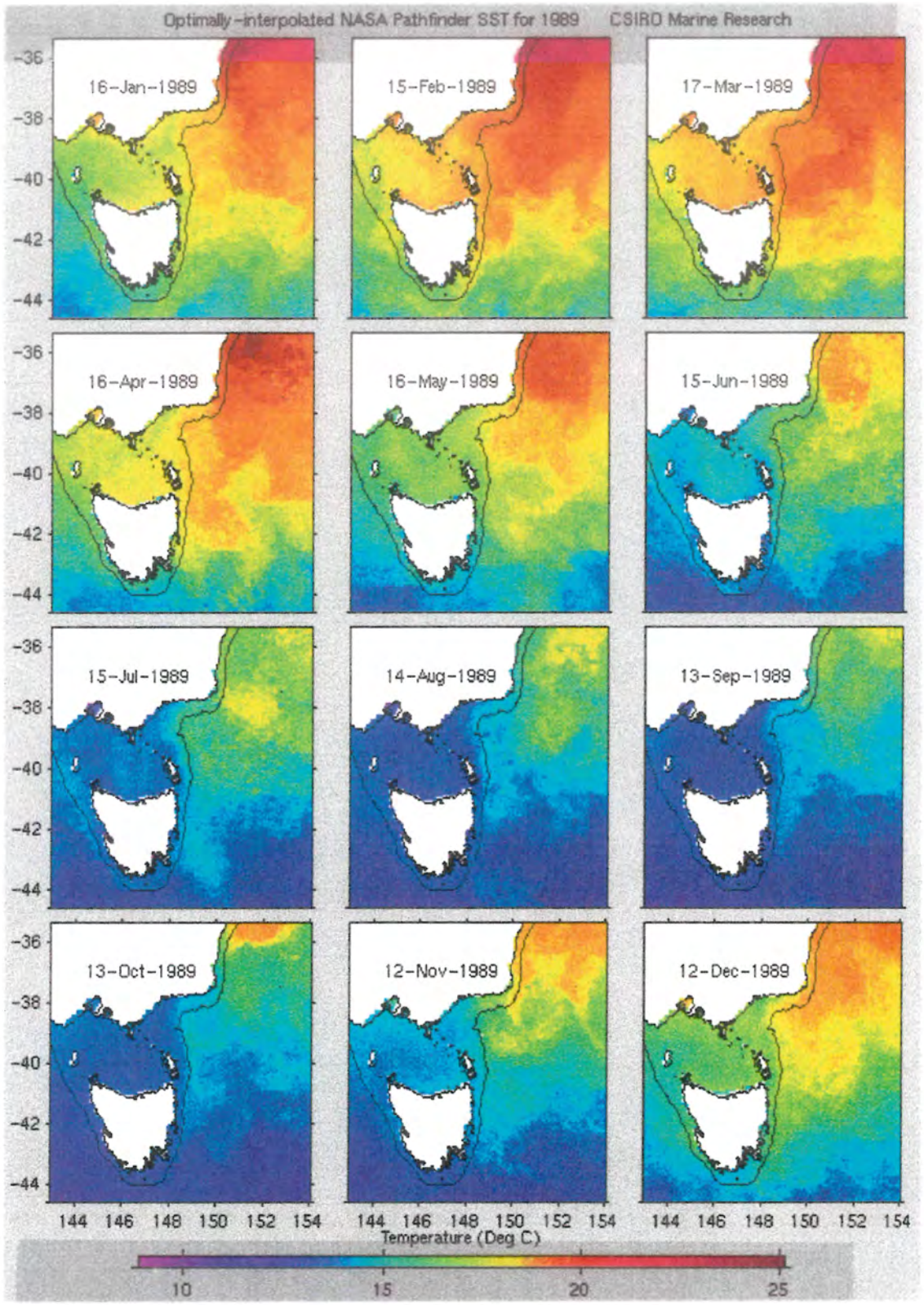


Figure 36: Monthly AVHRR images of sea surface temperature for SE Australia, 1988-1997.



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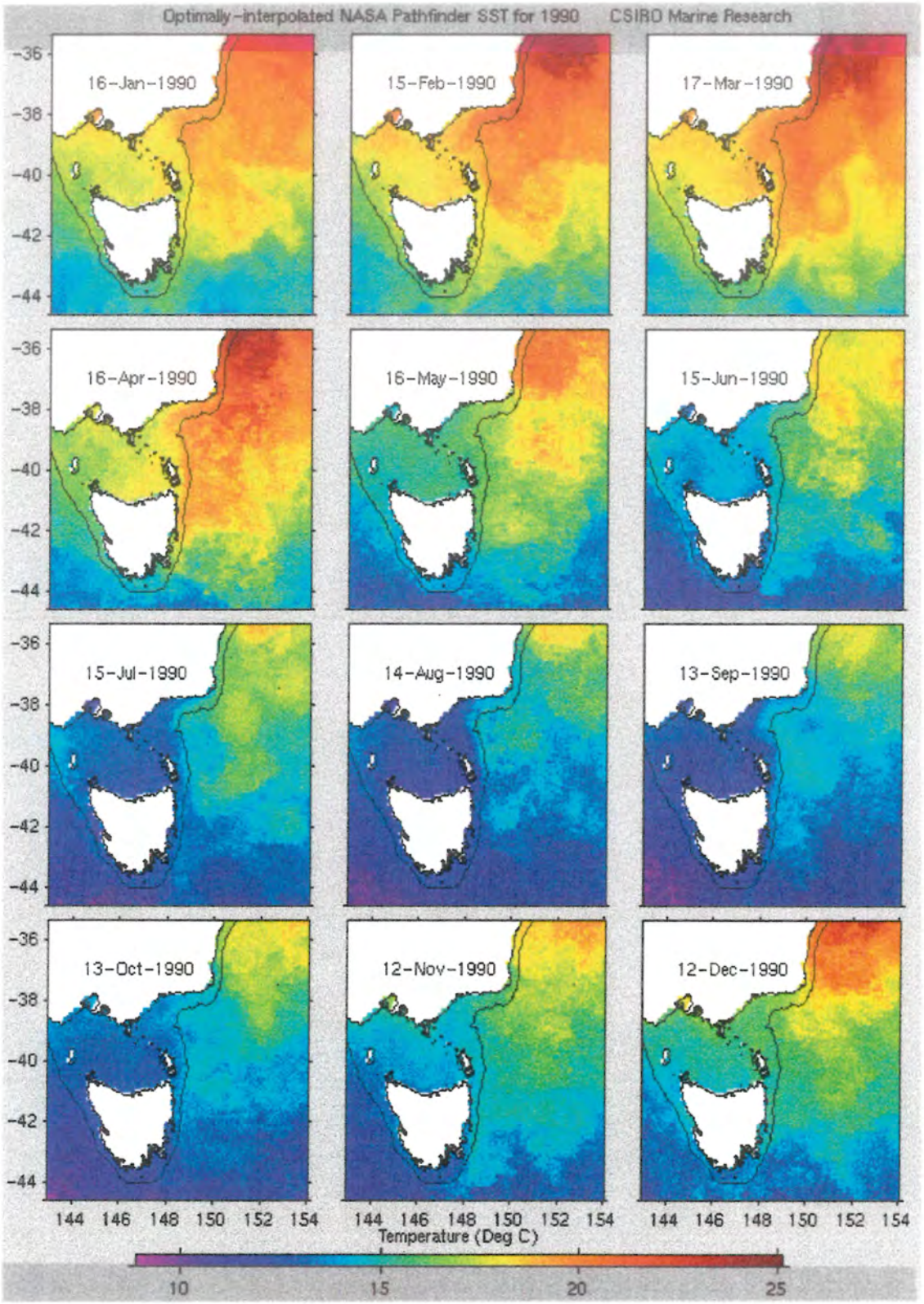

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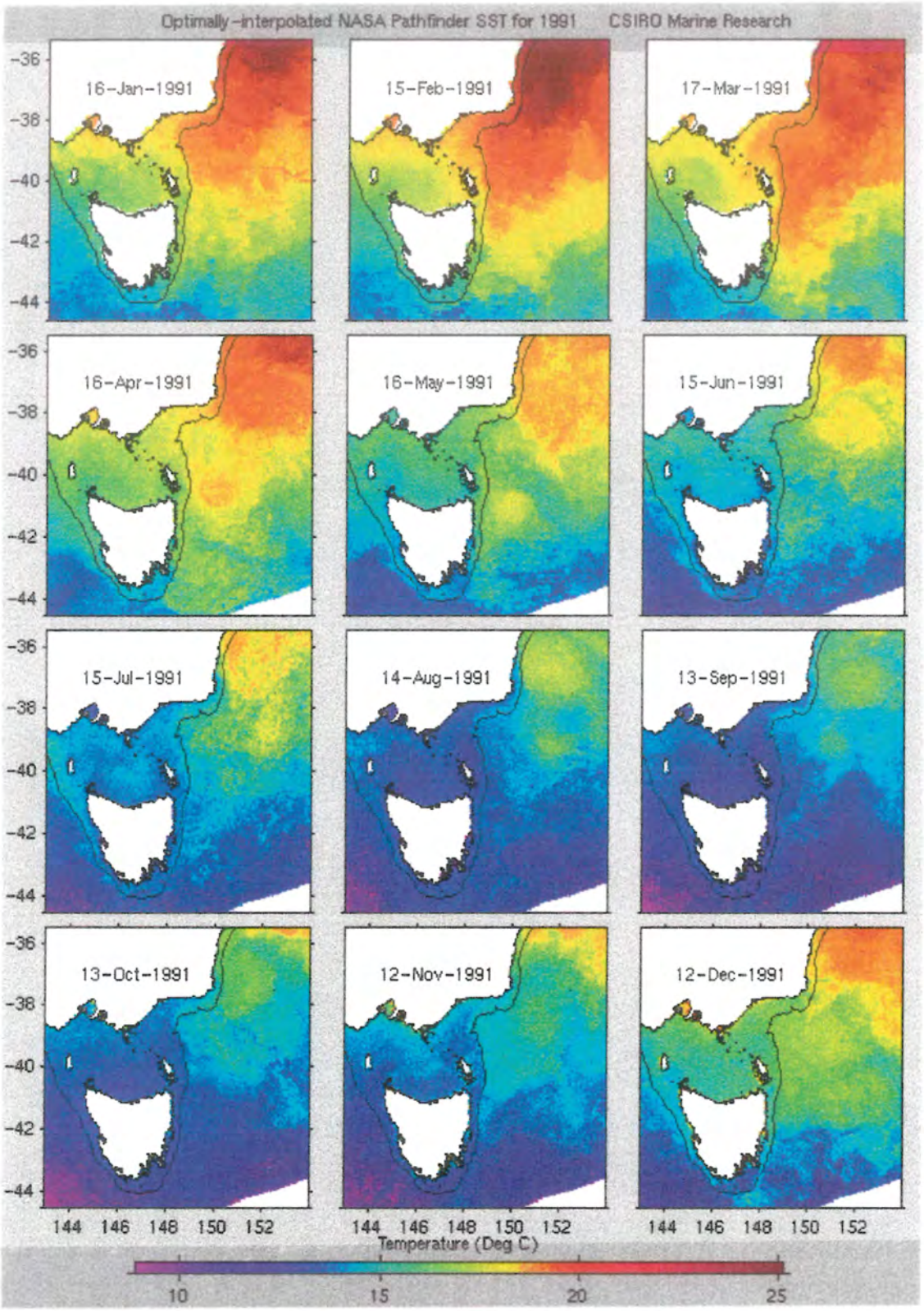

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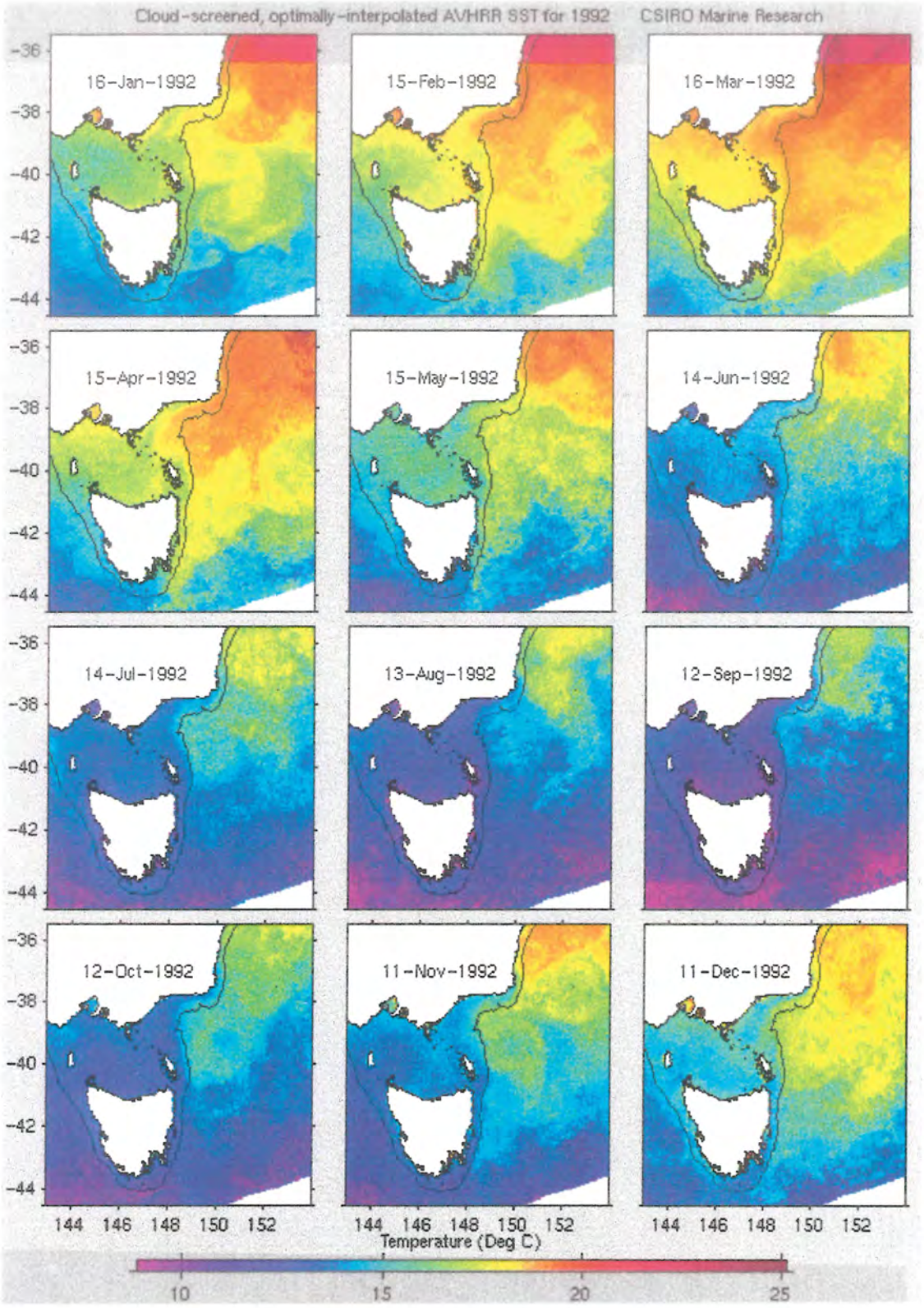

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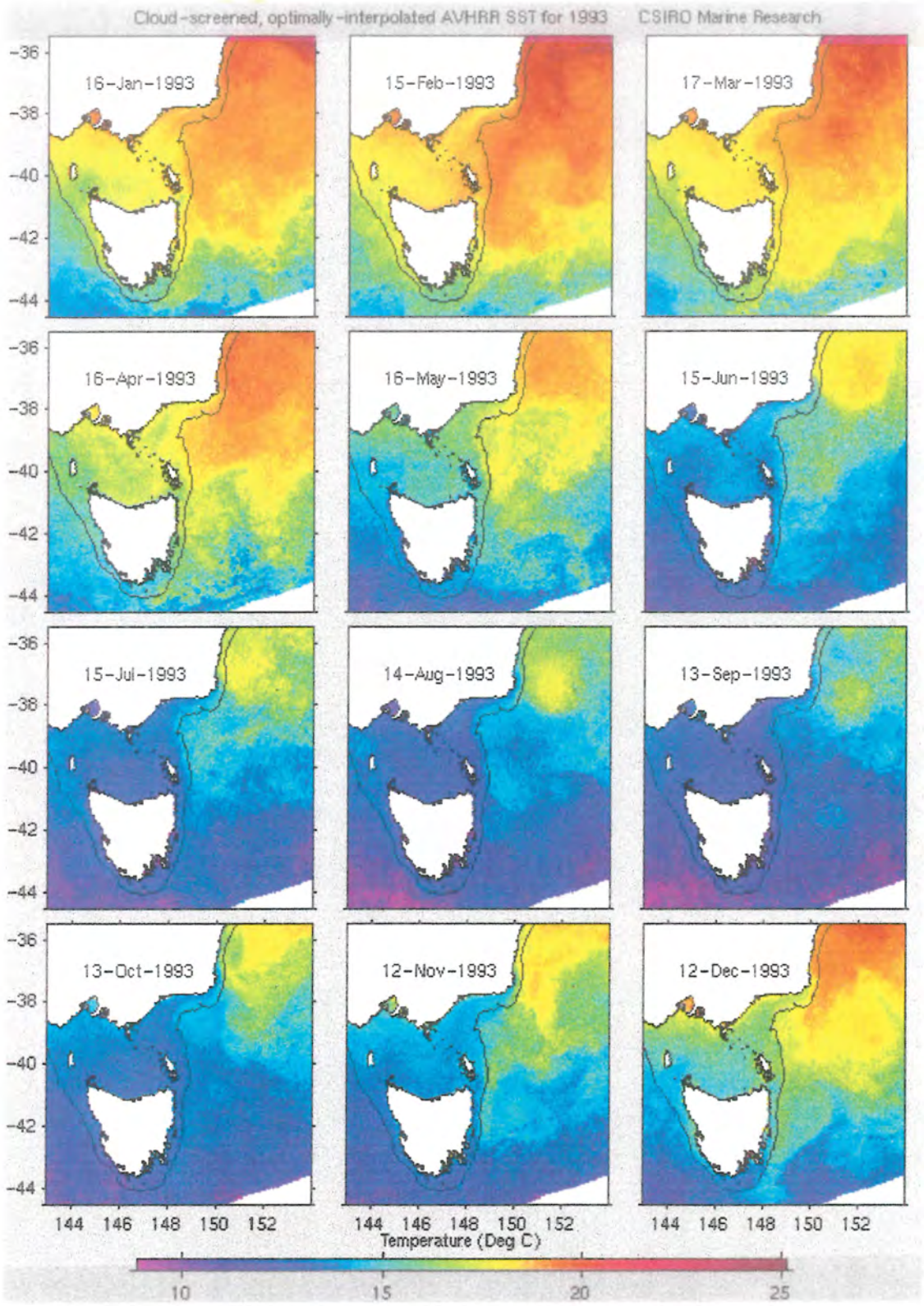

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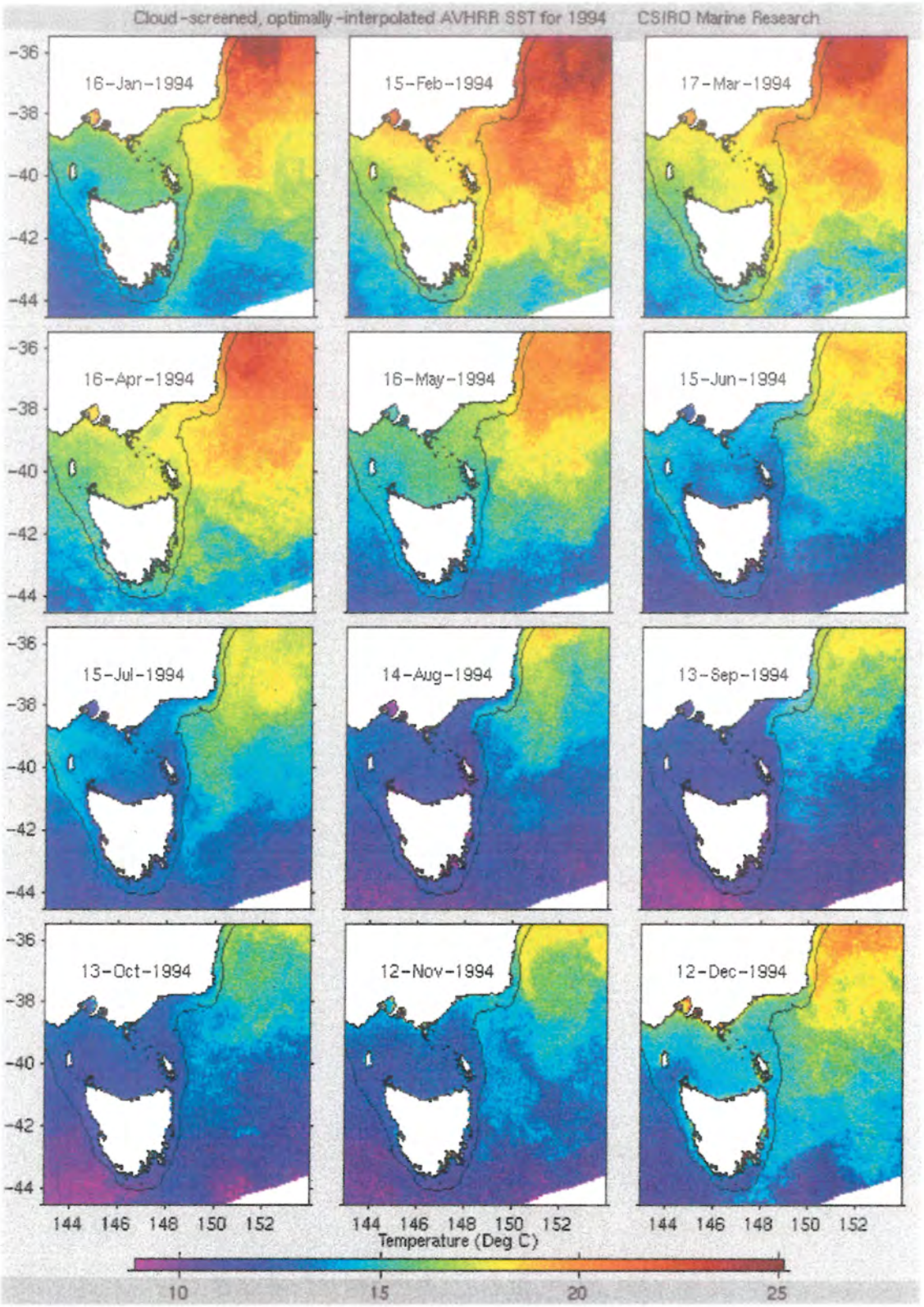

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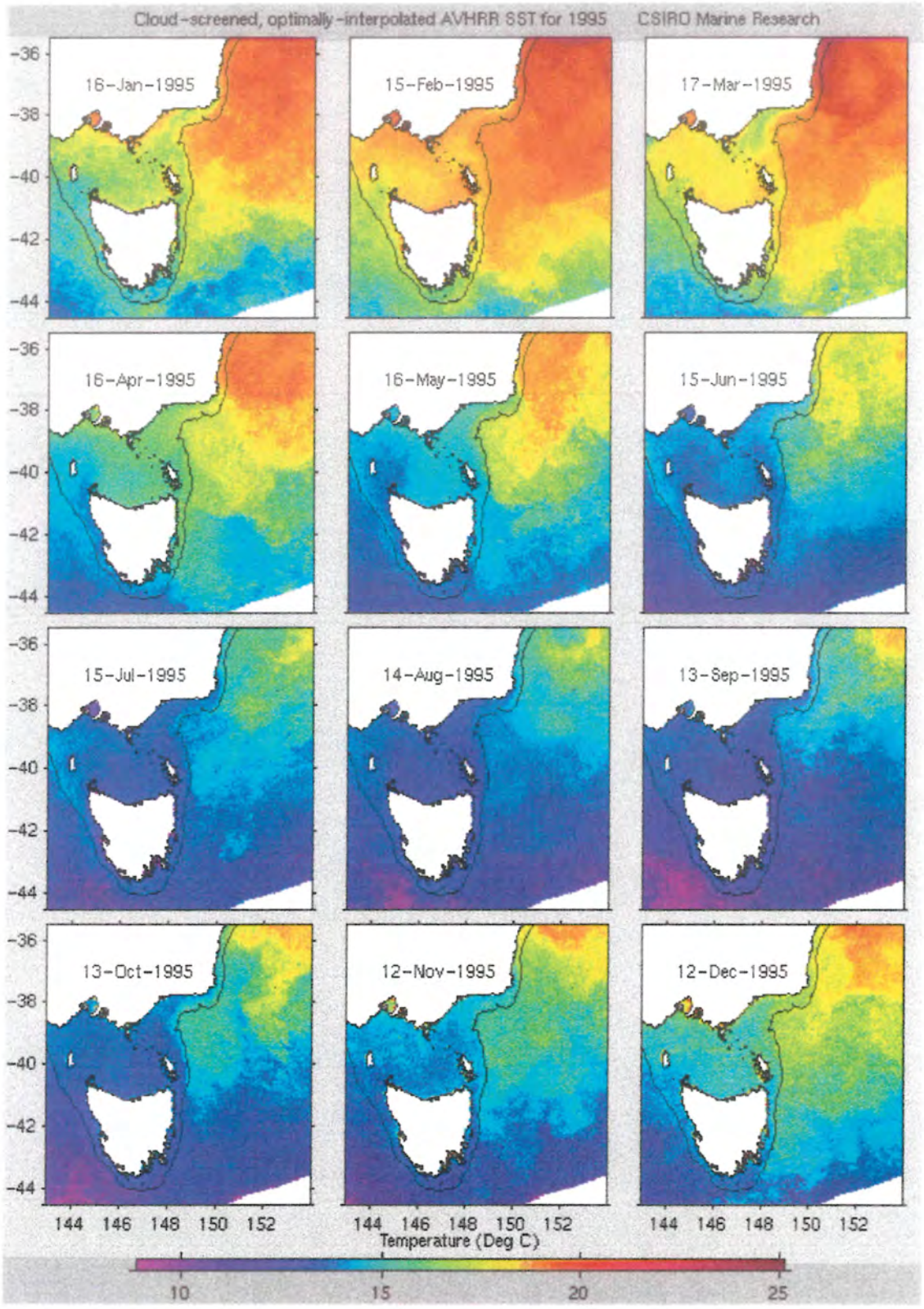

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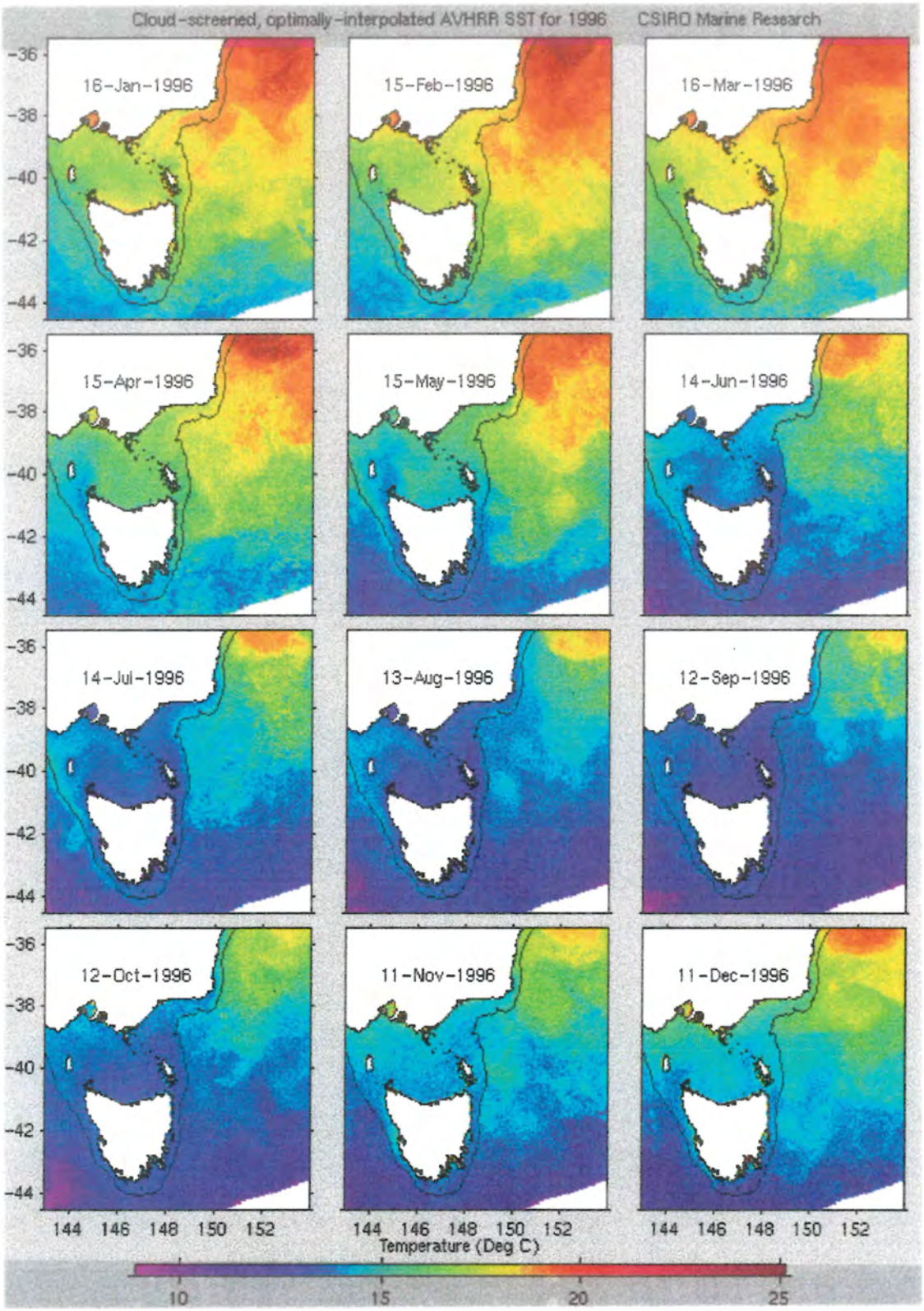

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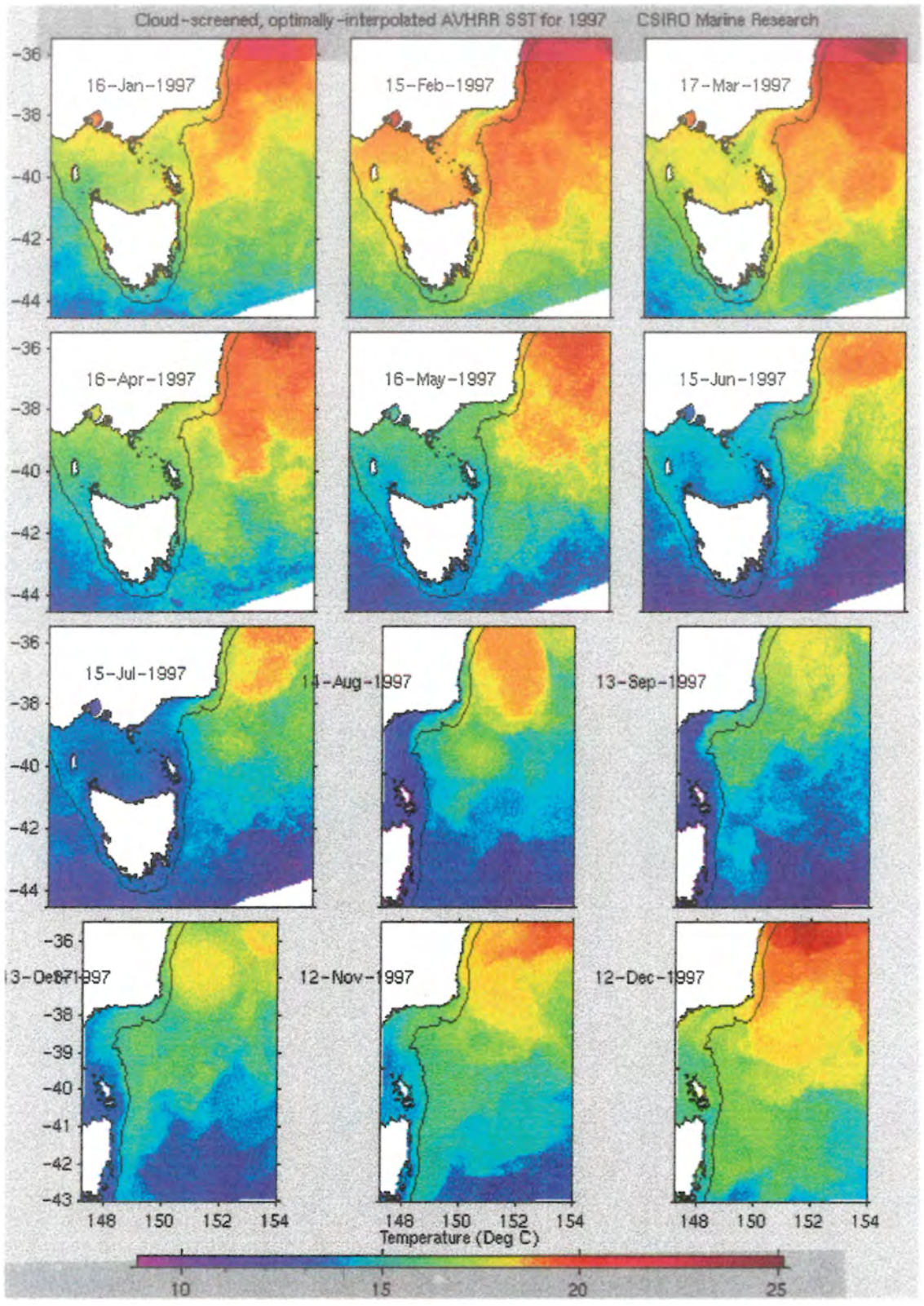


Figure 36: continued

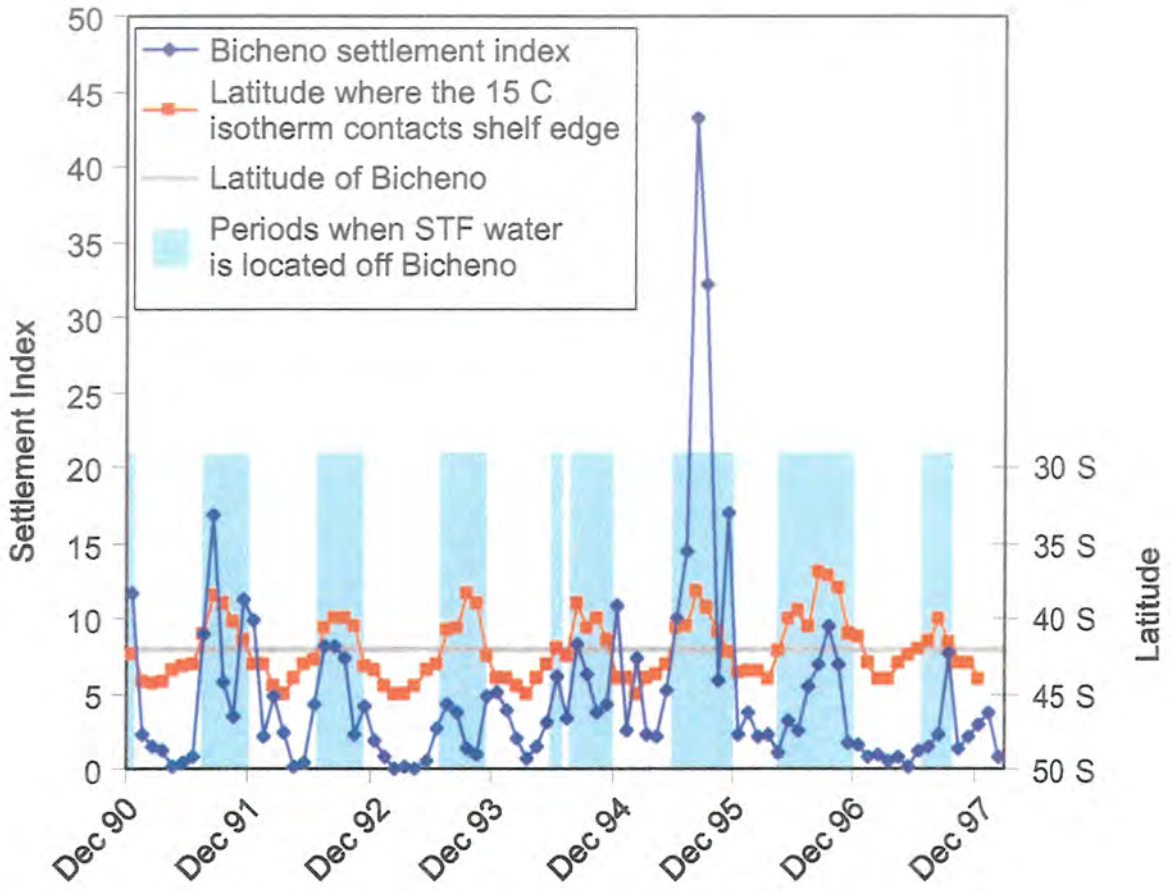
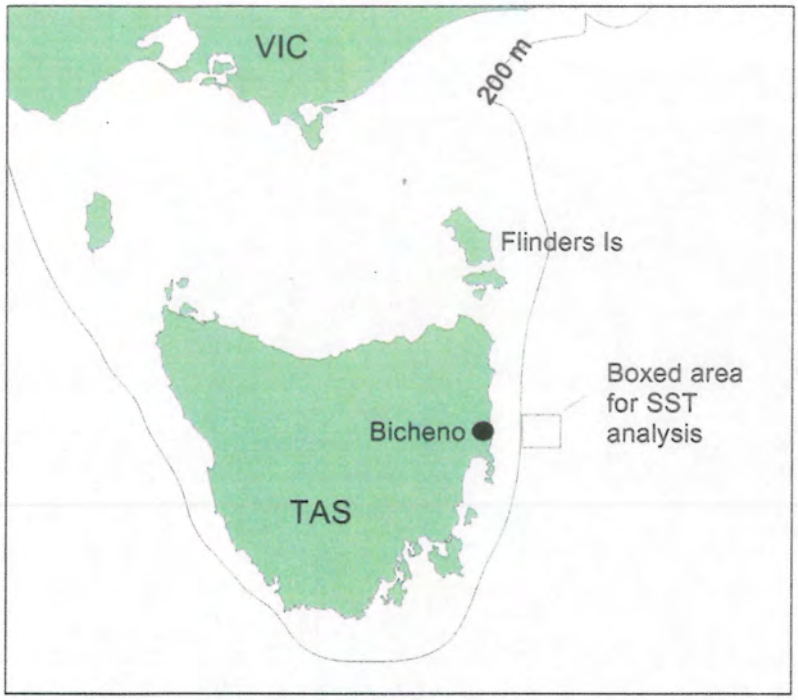


Figure 37: Puerulus settlement at Bicheno and the offshore position of the STF



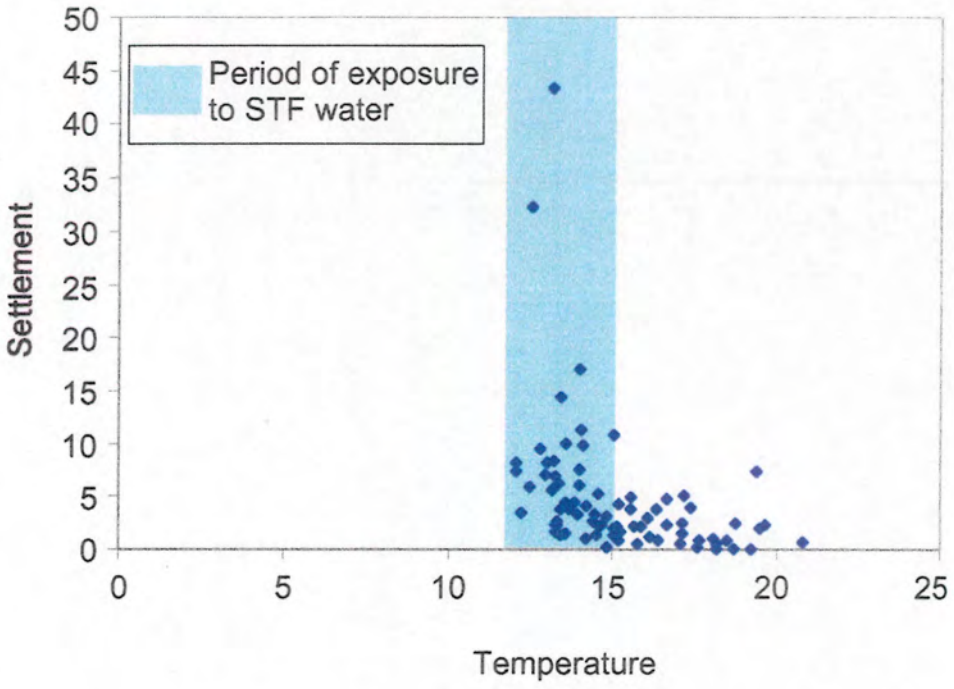


Figure 38: The relationship between puerulus settlement at Bicheno and offshore temperature

Flinders Island

Settlement data was only available from the Flinders Island site from January 1996 and thus the time period for comparison to STF events was short. However, settlement similarly corresponded to the passage of STF water marked by the 14.5-15 degree isotherm (Figure 39). The periods of exposure to STF water were shorter than the corresponding periods further south at Bicheno, particularly in 1997 when the 14.5-15 degree isotherm was only recorded off Flinders Island in July. This corresponded to the timing of peak settlement in 1997. The inter-annual magnitude of settlement at Flinders Island closely followed the northward extent of the 14.5-15 degree isotherm (and subsequent duration of exposure of the site to STF water), with 1996 having over double the settlement recorded in 1997. Two years of data, however, are obviously insufficient to test the significance of this observation.

6.6.4 Discussion

Oceanographic links, larval distribution and settlement processes

The temperature/salinity data and the spatial distribution of phyllosoma (see Section 6.1) both suggest that *Jasus edwardsii* phyllosoma are primarily found within waters of the STF. Interestingly, the distribution of "phyllosoma water" (= STF), based on our data, also marks the distribution of *J. edwardsii* phyllosoma in New Zealand waters reported by Booth (1994) (see Figure 34) and in particular, the presence of larvae off the east coast of the North Island and their almost total absence off the east coast of the South Island.

Circulation processes within the STF also suggest that this water mass may play a major role in not only structuring the distribution of phyllosoma but also in the supply of larvae for settlement. The STF is described by a generalised east to west flow in southern Australia. However, satellite tracked surface drifters released around Tasmania and entering waters of the STF, show a remarkable propensity to remain within several hundred kilometres of the coast for periods up to 19 months and several returned to, or near to, shelf waters after lengthy periods offshore. Interestingly, drifter paths suggest that advection need not always follow a west to east pattern but some reverse flows also occur – particularly in waters some 300-500 km seaward of the shelf break. In a couple of notable cases, drifters returned to the same site of deployment after periods in excess of 12 months offshore. While it is doubtful that phyllosoma behave the same as a satellite tracked drifter, this does suggest that there are mechanisms that could limit the advective loss of *J. edwardsii* larvae to a generalised west to east flow. Animations off SST, altimeter data and estimated surface current vectors across southern Australia also suggest a complex series of transient circulation cells that offer opportunities for localised retention of particles. These animations also show west to east transport in the vicinity of the continental shelf and reverse flows offshore (see accompanying CD). A combination of frequent, small scale meandering of the west to east flow near shelf waters, interaction between currents such as the Zeehan current and the EAC (off southern Tasmania) and local wind stress, results in offshore transport into the convergent STF zone. We propose that the *J. edwardsii* phyllosoma contributing to successful settlement in southern Australia, may be those that are not lost in the west to east flow but are those that are able to take

advantage of water parcels that become isolated from the generalised zonal flow. The actual processes that may restrict the advective loss of some larvae are difficult to determine without further knowledge of the diel vertical behaviour of *J. edwardsii* phyllosoma. However, the behaviour of satellite tracked surface drifters suggests that a complicated stage-specific depth behaviour, as reported for the western rock lobster by Rimmer and Phillips (1979) may not be required to return *J. edwardsii* from offshore waters to the vicinity of the shelf in southern Australia.

The early life history model proposed for *Jasus edwardsii* in Section 6.4 predicts the protracted nature of puerulus settlement observed in southern Australia but fails to account for the timing of settlement within that protracted window. Puerulus settlement on the east coast of Tasmania is often (but not exclusively) marked by a pattern of bimodal annual settlement with the exception of Flinders Island (Kennedy *et al.* 1994, Gardner *et al.* 1998). Our data suggests a link between the timing of settlement and the presence of STF water off the coast in east coast Tasmanian waters. The STF moves north and south on a seasonal basis and puerulus settlement largely corresponded to the availability of STF water off the shelf at both Bicheno and Flinders Island. In several cases, the timing of peak settlement occurred close to the timing of the passage of the northern boundary of the STF passed the puerulus monitoring site. However, settlement data is collected on a monthly basis and the resultant lack of temporal resolution restricts the ability to further assess this relationship. In addition, our identification of STF water based on the 14.5-15 degree isotherm can only be regarded as approximate and this, no doubt, further introduces some level of variability in the relationship between the northern boundary of the STF and the timing of puerulus settlement.

The timing of settlement at Flinders Island, although data only covers two complete years, suggests a strong STF link and it will be of interest to follow the timing of settlement at this site in future. Flinders Island is at the northern limit of seasonal movement of the 14.5-15 degree isotherm and is often only exposed to STF water for a limited period. Settlement at Flinders Island is unimodal (Kennedy *et al.* 1994 , Gardner *et al.* 1998) and occurred during the single period when STF water was present off the coast in 1996 and 1997. This suggests that Flinders Island lies at the northern-most limit for *J. edwardsii* settlement. Kennedy *et al.* (1994) reported that the Flinders Island region of the fishery was subject to recruitment failure and noted that catch rates and spawning biomass had declined significantly in the region. We suggest that interannual variability in settlement in this area more reflects the movement of the STF rather than the health of the fishery at this site. This suggests that the long term stability of the fishery at Flinders Island is dependent on the level of larval supply.

Reasons for the interannual variability in the magnitude of puerulus settlement in Tasmanian waters were beyond the scope of this project to investigate. Larval supply via links to STF water are unlikely to be the only factor and settlement will probably depend on various processes during the protracted larval phase, the behaviour of puerulus and processes influencing onshore/offshore transport as similarly suggested for other rock lobster species (see review by Booth and Phillips 1994).

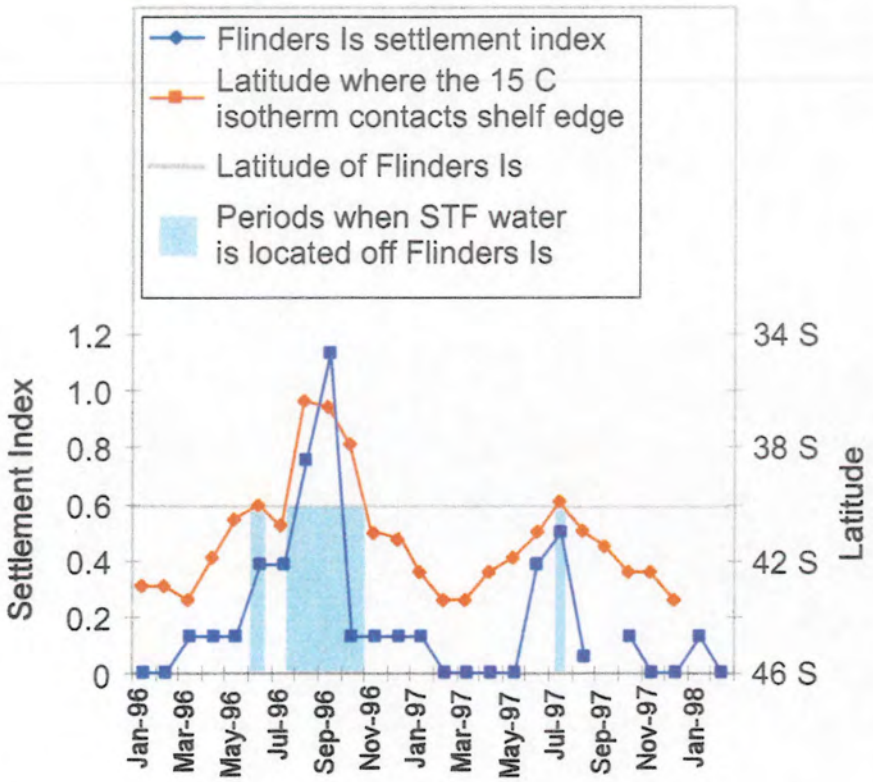


Figure 39: Puerulus settlement at Flinders Island and the offshore position of the STF

Bimodal settlement patterns in *Jasus edwardsii* have been reported for other regions in both Australia and New Zealand (Booth 1994, J. Prescott SARDI pers. comm.). However, we currently have insufficient data to suggest possible causes for these patterns.

Larval transport processes and regional connectivity of populations

The protracted larval duration and widespread distribution of *J. edwardsii* phyllosoma in offshore waters of southern Australia, and across the Tasman Sea between Australia and New Zealand, appear to offer considerable opportunities for transport between Australian management zones and between Australian and New Zealand waters. The genetic homogeneity across this range supports at least some transport of phyllosoma between regions (Ovenden and Brasher 1994). The difficulty is interpreting the overall extent to which this occurs and whether there is sufficient exchange between some (or all) areas so as to have implications for regional management of the fishery. It is possible that genetic homogeneity is maintained by a few successful expatriates that are insignificant for the purpose of management.

The generalised west to east flow of ocean currents in southern Australia (and specifically within the STF) suggests that transport of larvae should generally be from western to eastern regions of the fishery. If such transport is a dominant feature of *Jasus edwardsii* early life history, we would expect a compensatory movement of later life history stages back to the west to avoid a gradual easterly displacement of the population. Such contranatant movements occur in the green rock lobster (*J. verreauxi*) in both eastern Australia and New Zealand (Booth 1994). Another implication of a dominant downstream dispersal of larvae and a subsequent contranatant movement is that we would expect spawning in *J. edwardsii* to be largely limited to western populations. Neither contranatant movements nor geographically limited spawning areas appear to be the case in *J. edwardsii,* so some other compensatory mechanism must be operating to minimise the effects of west to east dispersal during the larval stage.

We believe that a west to east transport of larvae is far too simplified given the complex circulation processes of southern Australia and particularly those within the STF which, based on the distribution of larvae, appears to play an important role in the distribution of phyllosoma. Compared to the eastern and western seaboards of Australia, current speeds are significantly lower off South Australia, Victoria and western Tasmania. Despite these lower velocities, there is still considerable complexity in circulation processes across the GAB and around Tasmania. Moreover, there appears to be considerable opportunities for phyllosoma to become isolated from the average west to east flow field and for periods matching the pelagic duration of *J. edwardsii* larvae (see above section on Oceanographic links, larval distribution and settlement processes).

The advection of some *Jasus edwardsii* phyllosoma between management zones in southern Australia would appear to be inevitable and would account for the genetic homogeneity reported by Ovenden and Brasher (1994). Similarly, the low level occurrence of *J. edwardsii* phyllosoma across the Tasman Sea suggests that a proportion of southern Australia phyllosoma rejoin the generalised west to east flow and

may be transported into New Zealand waters thus resulting in a genetic link between Australian and New Zealand populations. The trajectories of satellite tracked drifters suggests that this transport is similarly associated with circulation features of the STF and can occur on time scales within the estimated duration of the larval stage Cresswell (*in press*). Drifters followed a more zonal pattern of movement once in excess of 500 km east of Tasmania as opposed to the complex recirculation observed in waters less than 500 km from Tasmania. We thus consider it unlikely that larvae found in excess of this 500 km zone would contribute to recruitment back to southern Australian fisheries.

These features of rock lobster early life history and larval transport may be more widespread than just for southern Australia. Recirculation features occurring over similar scales (ie within 500 km of the coast) have been reported for several other regions where researchers have studied rock lobster larvae and have been linked to distribution as well as regional transport and settlement processes (eg Polovina et al, Phillips.... Booth 1994) and the trajectories of satellite tracked surface drifters have been matched with possible transport pathways (Lutjeharms and Heydorn 1981, Polovina and Mitchum 1992). Rock lobster larvae of many different species have been found considerable distances (> 1000 km) from shore and in some cases in considerable abundance (see Booth and Phillips 1994, and Booth 1994 for examples). This has led to speculation that local larval production may contribute to considerable offshore pools of larvae that may circulate over wide scales (eg ocean basins) before returning to settle to their natal populations (Pollock 1986, Booth 1994). We propose that such offshore occurrences of phyllosoma generally represent larvae that have been lost to their natal populations and are of little significance to the dynamics and management of their natal rock populations. The importance of such offshore distributions probably lies in their evolutionary significance by contributing to intermittent gene flow between distant populations or in establishing/replenishing expatriate populations that may lead to subsequent speciation. This may explain the widespread distribution of the closely related '*Jasus lalandii*' group (of which *J. edwardsii* is a member) throughout Southern Hemisphere waters in latitudes approximately corresponding to the STF.

Jasus verreauxi similarly occurs in both Australia (eastern sea board) and New Zealand (primarily around the North Island). However, unlike *Jasus edwardsii*, Australian and New Zealand populations of *J. verreauxi* are reported to be genetically distinct (Ovenden and Brasher 1994). Australian *Jasus verreauxi* migrate to grounds off northern NSW to release larvae and we have located *J. verreauxi* phyllosma in EAC water as far south as eastern Tasmania, some 1500 km distant from the breeding ground. It is also clear that *J. verreauxi* settle in Tasmania – occasionally in quite reasonable numbers (Gardner *et al. in press*). The NSW breeding ground of *J. verreauxi* is to the north of where the EAC separates from the coast and where some of the EAC feeds into the Tasman Front which extends across the Tasman Sea to northern New Zealand. Satellite tracked surface drifters released into the EAC confirm a link between the two regions that has similarities to that observed between Tasmanian and southern New Zealand (G. Cresswell CSIRO Marine Research pers. comm.). The distances between Australia and New Zealand in these two regions are similar (1500-1700 km in the south and 1800-1900 km in the north). Thus, on the outset, there appears to be no physical oceanographic reason why

Australian and New Zealand populations of *J. verreauxi* should be genetically isolated. *Jasus verreauxi* is reported to have a much shorter (and perhaps less plastic) pelagic larval duration than *Jasus edwardsii* (8-12 months for *J. verreauxi* (Kittaka *et al.* 1997); 13-24 months for *J. edwardsii* – this study). Transport times between northern NSW and northern New Zealand may be too long for the successful settlement of Australian *J. verrreauxi* in New Zealand.

6.7 Gear Comparisons

6.7.1 Introduction

The large number of samples available to us, collected from a range of net systems, provided the opportunity to examine which net system might best be employed should future sampling be required. The net systems covered the range of samplers that have been commonly used in other studies of the distribution of phyllosoma.

6.7.2 Methods

Comparisons of the catch rates of phyllosoma between net systems were made using the ANOVA function of Systat. Abundance data were standardised to number per 1000m^3 of water filtered; then log-transformed for all analyses, as this gave the most even distribution of residuals. Where a significant difference was identified by ANOVA, a Tukey post hoc test was used to resolve where that differences lay.

6.7.3 Results

Between Net Comparisons – All Phyllosoma:

Overall, there was a significant (ANOVA: N = 2763; F-ratio = 22.12; p = 0.00) difference in the abundance of phyllosoma collected by the various net systems with no significant difference (ANOVA: N = 2763; F-ratio = 0.21; p = 0.64) in abundance between day and night. However, there was a significant interaction (ANOVA: N = 2763; F-ratio = 17.96; p = 0.00) between the factors 'time of day' and 'net type' when comparing between net types. For this reason, comparisons between net systems were made separately for day and night.

During the day, there was considerable variability in the effectiveness of the net systems (Figure 40). In general, the EZ and ring nets collected significantly more phyllosoma than either the MIDOC, vertical haul, or bongo nets; the ring net also collected significantly more phyllosoma than the surface net (Table 10). The vertical haul net was the least efficient of all the nets, apart from the IYGPT, at collecting phyllosoma during the day.

During the night, the most effective net system for collecting phyllosoma was the surface net (Figure 40). The abundance of phyllosoma in surface net samples was significantly greater than that from all other nets except the ring net (Table 10). In addition, the bongo net collected significantly more phyllosoma than the MIDOC net.

Table 10: Tukey post hoc results by day and night of between net comparisons on the efficiency of nets to collect phyllosoma.

Time of Day	Comparison	MSE	df	p
Day	Vertical < Bongo	0.36	1344	0.02
	Vertical < BIONESS	0.36	1344	0.00
	Vertical < Ring	0.36	1344	0.02
	Vertical < Surface	0.36	1344	0.00
	IYGPT < BIONESS	0.36	1344	0.02
	IYGPT < Ring	0.36	1344	0.00
	Bongo < BIONESS	0.36	1344	0.04
	Bongo < Ring	0.36	1344	0.00
	Surface < Ring	0.36	1344	0.00
Night	Surface > Bongo	0.51	1407	0.02
	Surface > BIONESS	0.51	1407	0.00
	Surface > IYGPT	0.51	1407	0.00
	Surface > Vertical	0.51	1407	0.00
	Bongo > IYGPT	0.51	1407	0.03

Between Net Comparisons – Jasus edwardsii:

Overall, there was a significant (ANOVA: N = 2763; F-ratio = 16.76; p = 0.00) difference between the abundance of *Jasus edwardsii* phyllosoma collected by the various net systems (Figure 41), with no significant (ANOVA: N = 2763; F-ratio = 1.09; p = 0.30) difference between day and night catches. However there was a significant (ANOVA: N = 2763; F-ratio = 7.75; p = 0.00) interaction between the factors 'time of day' and 'net type'. Due to the interaction, comparisons between net types were analysed separately by day and night.

During the day there was a significant (ANOVA: N = 1350; F-ratio = 16.29; p = 0.00) difference in the efficiency of nets to collect *J. edwardsii* phyllosoma. The ring net collected significantly more phyllosoma than any of the other nets (Tukey: MSE = 0.17; df = 1344; p = 0.00, for all comparisons). Despite this, there was very little difference between the efficiency of the other nets to collect *J. edwardsii* during the day (Figure 42).

At night, there was, again, a significant (ANOVA: N = 1413; F-ratio = 20.14; p = 0.00) difference in the efficiency of nets to collect *J. edwardsii.* In contrast to the daytime collections, the surface net collected significantly (Tukey: MSE = 0.28; df = 1407; p = 0.00, for all comparisons) more *J. edwardsii* than any of the other nets except the ring net (Figure 42). Collections with the ring net did not differ from those of any of the net systems.

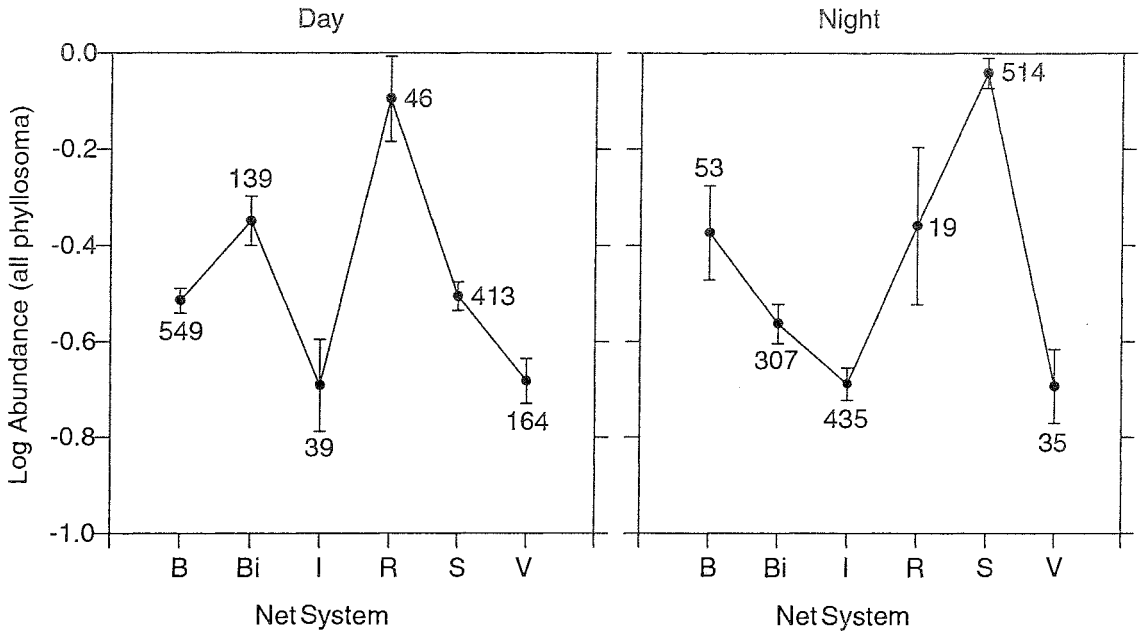


Figure 40: Comparison between net systems of the mean square means (± 1SE) of the log-transformed abundance of all phyllosoma combined (B = bongo net, Bi = BIONESS net, I = IYGPT [MIDOC] net, R = ring net, S = surface net, V = vertical haul net; number refers to number of samples sorted).

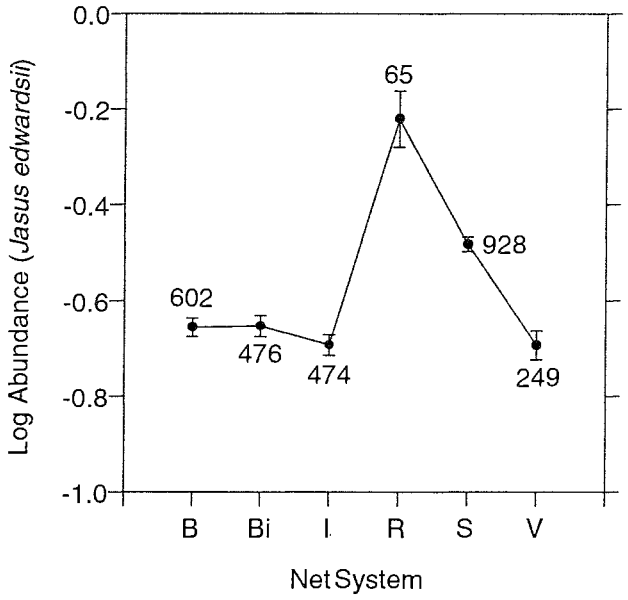


Figure 41: Comparison between net systems of the least square means (± 1 SE) of the log-transformed abundance of *Jasus edwardsii* phyllosoma - day and night samples combined (B = bongo net, Bi = BIONESS net, I = IYGPT [MIDOC] net, R = ring net, S = surface net, V = vertical haul net; number refers to number of samples sorted).

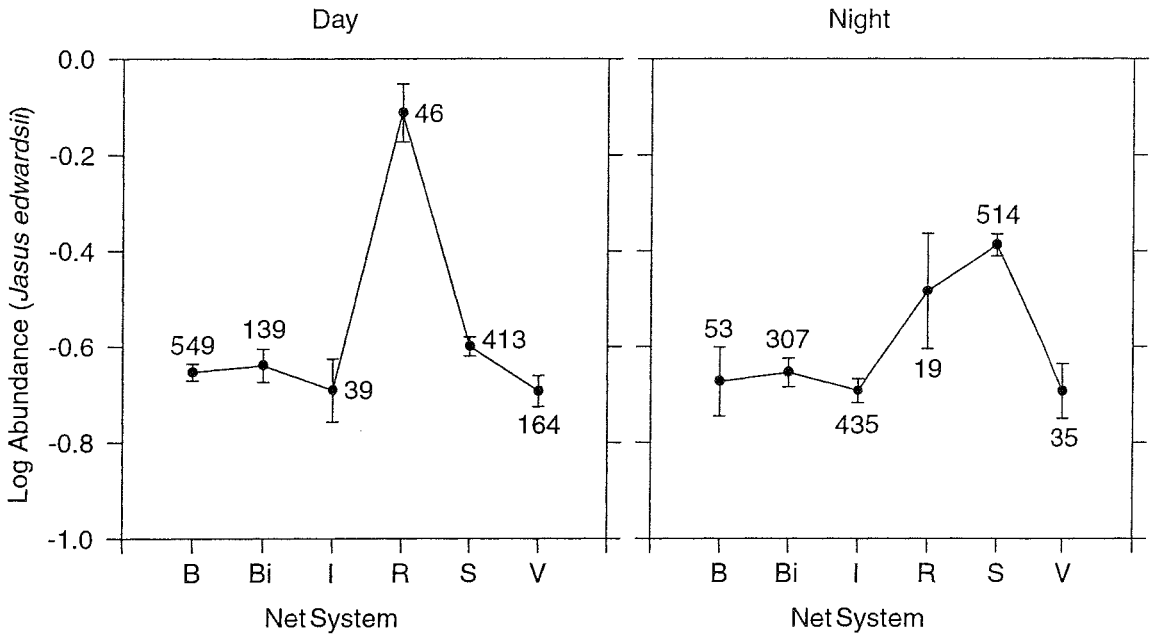


Figure 42: Comparison between net systems of the least square means (± 1 SE) of the log-transformed abundance of *Jasus edwardsii* phyllosoma (B = bongo net, Bi = BIONESS net, I = IYGPT [MIDOC] net, R = ring net, S = surface net, V = vertical haul net; number refers to number of samples sorted).

6.7.4 Discussion

The original rationale for comparing catches of phyllosoma between different net types was to assess which nets might best be used in future should further sampling of phyllosoma be required. However, the comparison of catches between nets was confounded by a number of factors and the results are generally difficult to interpret. First, each system had a different mesh size (335μm - 1000μm in the cases of the Bongo, EZ, ring and surface nets) and in the case of the MIDOC, mesh size was variable along the length of the net. The MIDOC net routinely missed collecting the early stages of the phyllosoma due to its larger mesh sizes. Second, not all nets were used in the same location and third, not all nets were used at the same time of year. Location and time of year are important factors when comparing abundance both within and between net systems. For example only the bongo, surface and ring nets were used on the shelf during the Spring when large numbers of early stage phyllosoma were present. The EZ net, with a similar mesh size was only used in offshore waters where phyllosoma are more widely dispersed and thus less abundant in catches.

The overall decision as to which net type to use in future sampling will be dependent on the questions asked and the areas sampled. Sampling on the shelf for early stage phyllosoma can be effectively done using relatively small fine mesh nets (eg ring and bongo). The slightly larger EZ net may be used effectively in both shelf and offshore waters, however abundances in our EZ samples were extremely low – far lower than that reported for phyllosoma in other areas using a similar system (for further details see Section 6.2 – Vertical Distribution). The large midwater trawl with a fine mesh liner (FMMWT) used by Booth in various studies off New Zealand, is effective at sampling large volumes of water and collecting large numbers of phyllosoma. This is an important consideration as one of the main limiting factors in studies of the distribution of phyllosoma is the low numbers caught in most studies. The FMMWT does have its disadvantages in that it can be difficult to operate in moderate to rough seas (common in southern Australia); it is difficult to estimate the volume filtered and hence quantify the catches between tows and phyllosoma tend to hook up in meshes in advance of the cod end and may contaminate subsequent tows. This latter point is worth considering when such a system is used in conjunction with an opening and closing cod-end system to examine vertical distribution (R. Pitcher, CSIRO Marine Research, Cleveland, pers. comm.). Nevertheless, the success with which the system has been used in studies in New Zealand suggest that future sampling in southern Australian waters should consider using a similar system.

One of the most informative and 'value for money' net systems was the surface net, particularly when deployed at night. The surface net was highly portable, collected large numbers of phyllosoma (at night), could be simply deployed from a wide range of vessels and could be deployed when fishing other types of gear. The surface net could only provide information on overall distribution and apart from detecting movement in or out of the surface layer, provided little information on vertical migration.

7. Benefits

The results of the project provide the first analysis of larval processes and the potential for regional connectivity of rock lobster stocks in southern Australia. Results of the project will be of direct benefit to researchers and managers who are seeking to monitor the status of the southern rock lobster via puerulus settlement programs. Settlement in southern Australia is complicated by the region's diverse oceanography and its role in larval survival and larval supply. These features must be taken into account when interpreting the results of puerulus monitoring programs. Results from the project also provide timely benefits to the developing efforts in the culture of southern rock lobster by providing hitherto unknown details of larval duration and growth as well as the conditions in which phyllosoma are commonly found in the wild. The project has also highlighted the benefits of archiving samples, the utility of drawing together biological and physical oceanographic data, the future potential for high resolution oceanographic models and visual animation techniques for interpreting and communicating complex spatial data sets.

8. Further Development

The project has highlighted the value of archiving plankton samples, even when they have been collected with other taxa in mind. The samples analysed in this project, and those collected since in other parts of southern Australia, also contain significant numbers of fin-fish larvae and are a valuable source of data on the early life history of a large number of fin-fish species. These larvae will be the subject of a further FRDC project. We recommend that plankton samples collected in future – particularly as part of FRDC projects – be suitably archived for analyses of other components

We have only been able to examine the regional connectivity of southern rock lobster stocks in a preliminary manor. The most significant shortfalls in the data are the lack of detailed vertical distribution and behaviour data and the availability of complex oceanographic models with sufficient skill to track the transport of larval " particles". The recent development of 3-dimensional non-linear hydrodynamic model for southern Australian shelf and offshore waters has proved valuable in plotting the trajectories of fin-fish larvae (eg Bruce *et al.* submitted) and offers considerable future scope for investigations of larval transport off southern Australia in general. Similarly more recent developments in the analysis of satellite based altimeter data offers scope for the synoptic analysis of surface currents. An example of such analyses is presented as an animation of sea surface height, surface current vectors and SST on the accompanying CD. Further information is however required on the vertical distribution of phyllosoma to make best use of these developing models.

We have found the use of animation techniques and invaluable tool in both understanding and presenting complex spatial data sets and presentations of these animations have been well received by both industry and fellow researchers during the project. Development of these animation techniques and their application to other forms of fisheries data is an obvious future direction.

Our analyses have emphasised the complexity of processes driving larval transport and their relationship to puerulus settlement but the benefits in a multi-disciplinary approach to their interpretation. We would strongly recommend retaining the puerulus monitoring program for southern rock lobster in southern Australia. However, it is clear that the interpretation of puerulus settlement data must take into consideration the offshore ocean climate and how interannual variability in currents may impact the timing and magnitude of settlement on a regional basis.

There appears to be considerable future scope for collecting information that will be of use to the culture of phyllosoma from wild caught larvae. Growth rates for wild larvae are useful benchmarks for comparison of the success of cultured phyllosoma. We have also had preliminary discussions with other researchers regarding the analysis of lipid content of wild phyllosoma- again as a benchmark to compare the development of cultured phyllosoma.

9. Conclusion

Southern rock lobster (*Jasus edwardsii*) phyllosoma follow a similar early life history strategy to that reported for other rock lobsters. Early stage larvae were found predominantly in shelf waters; middle and late stage larvae were found offshore (sometimes hundreds of kilometres) and the few puerulus collected were generally in the vicinity of the shelf break. Early stage larvae were generally found in Spring and Summer; mid and late stages in Winter and puerulus in Autumn and Winter. Interestingly, there was little evidence of a complicated, stage specific, pattern of vertical distribution. Larvae were primarily confined to the upper 100 m and were commonly at the surface, particularly at night.

Jasus edwardsii phyllosoma were primarily found within a limited temperature-salinity (T/S) range when compared to the total data set. The T/S signature of this "phyllosoma water" (12.2-15.0 °C; 34.70-35.08 ppt) corresponded to water of the Subtropical Front (STF), a major convergence zone separating the cool Sub-Antarctic Water (SAW) from warmer waters of tropical origin. SRL puerulus were located in water with a T/S signature matching the northern boundary of the STF and characteristic of shelf waters around Tasmania.

Both stage and total larval duration were examined based on the time of year when different stages were caught. At any one time of year, there were two cohorts of larvae, thus supporting a larval duration in excess of one year. Early stage larvae were present from September to January indicating a protracted period of larval release. We estimated a mean total larval duration of 17-18 months and we suggest that the first major settlement after a spring-summer hatching is during the following summer (15-16 months later). The subsequent winter settlement is the second peak and occurs some 22-23 months after hatching.

Circulation patterns within the STF provided possible clues regarding the transport processes of *J. edwardsii* phyllosoma. Satellite tracked drifters released around Tasmania showed a remarkable propensity to remain within several hundred kilometres of the coast for periods up to 19 months and several returned to, or near to, shelf waters after lengthy periods offshore. Interestingly, drifter paths suggest that advection need not always follow a west to east pattern but some reverse flows also occur. In a couple of notable cases, drifters returned to the same site of deployment after periods in excess of 12 months offshore. While it is doubtful that phyllosoma behave the same as a satellite tracked drifter, this does suggest that there are mechanisms that could limit the advective loss of *J. edwardsii* larvae to a generalised west to east flow. We propose that the larvae contributing to successful settlement may be those that are not lost in the west to east flow but are those that are able to take advantage of these regional retention mechanisms. The spatial scale of these mechanisms may dictate which areas in southern Australia have linked settlement patterns. The trajectories of some drifters also suggested a link between southern Tasmanian and New Zealand populations of *J. edwardsii*.

Our data suggests a link between the timing of settlement and the presence of STF water off the coast of eastern Tasmania. The STF moves north and south on a seasonal basis and puerulus settlement largely corresponded to the availability of STF water off the shelf at both Bicheno and Flinders Island.

Results of the project demonstrate the utility of larval data, the value of archiving previously collected samples and the advantages of combining biological and physical data sets over scales relevant to the early life history of target species. The data visualization and animation techniques used, provide a way of examining broad-scale factors that may influence settlement patterns and larval transport processes.

10. Acknowledgments

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11. Appendix 1: Intellectual Property

No commercial intellectual property arose form this work.

12. Appendix 2: Staff

Name	Barry Bruce		
Position	Principal Investigator		
Organisation	CSIRO		
Unit	Division of Marine Research		
Postal Address	GPO Box 1538		
	Hobart		
	Tasmania 7001		
Telephone	(03) 6232 5413	Facsimile	(03) 6232 5486

Name	Russell Bradford		
Position	Zooplankton Biologist		
Organisation	CSIRO		
Unit	Division of Marine Research		
Postal Address	As Above		
Telephone	(03) 6232 5200	Facsimile	(03) 6232 5000

Name	David Griffin		
Position	Physical Oceanographer		
Organisation	CSIRO		
Unit	Division of Marine Research		
Postal Address	As Above		
Telephone	(03) 6232 5244	Facsimile	(03) 6232 5000

Name	Jock Young		
Position	Zooplankton Ecology		
Organisation	CSIRO		
Unit	Division of Marine Research		
Postal Address	As Above		
Telephone	(03) 6232 5360	Facsimile	(03) 6232 5000

Name	Stuart Frusher
Position	Research Scientist
Organisation	Tasmanian Aquaculture and Fisheries Institute
Unit	Taroona
Postal address	Taroona Research laboratories
	Crayfish Point
	Taroona TAS 7053