

Final report to the FRDC committee on the project VMS 2Z 89-2 "Patterns of utilization of seagrass (Heterozostera) - dominated habitats as nursery areas by commercially important fish".

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Executive summary

The decline of a number of commercial fish populations in parallel with the decline of seagrass in Westernport Bay suggests a strong dependence of these species on seagrass habitat. The objective of this project was to describe and quantify patterns of utilisation of shallow -water, Heterozostera-dominated habitats of southeastern Australia, by larval and juvenile fishes of commercial significance.

Sampling of seagrassed and unvegetated habitats was undertaken over 30 months in three areas of relatively undisturbed seagrass; Swan Bay, Port Phillip Bay and Corner Inlet. A number of commercial species, including juveniles of stranger, rough and six-spined leatherjackets, and adult rock flathead, were largely restricted to seagrass habitats. Juvenile King George whiting were not always collected in seagrass but apparently utilised the enhanced food production from seagrass relative to unvegetated areas.

Juvenile flounder were collected on unvegetated habitat, however, comparison of diet and otolith rings between Swan Bay and the adjacent coast of Port Phillip Bay showed that the greater amount of seagrass detritus in Swan Bay led to higher organic content in sediments, increased prey abundances and consequent elevated feeding and growth rates. Production of juvenile flounder and other benthic feeding fishes on unvegetated habitat would therefore be increased in areas with significant seagrass detritus.

Larvae of King George whiting entered Port Phillip Bay in a late post-larval stage at an age determined from otoliths of 100 to 150 d. Spawning apparently occurred some distance to the west, and larval supply was dependent on hydrodynamics in Bass Strait and in the southern region of Port Phillip Bay. Interannual variability in recruitment of this species is probably related to interannual variability in coastal hydrodynamics.

Plankton sampling indicated that major differences in numbers of settling fish, including King George whiting, between Swan Bay and the adjacent area of Port Phillip Bay was due to habitat selection by larvae rather than larval supply. However, within habitats selected by larvae of a certain species, the number of settlers was apparently limited by the number of larvae. King George whiting post-larvae did not settle in seagrass beds exposed to strong tidal currents, but rather settled in beds where currents dissipated. Settlement did not occur further into the bay where currents were weak. This resulted in post-larvae settling in a relatively restricted area. Seagrass beds

in the settlement area, although not particularly large or dense, would be critical in providing food organisms for post-larvae.

In summary, seagrass beds were directly utilised as a habitat by juvenile commercial fish, and were also utilised indirectly as a foraging area, or through input to the detrital food chain. At least as important as the structural characteristics of the seagrass bed was the position of the bed relative to currents. By virtue of their location, some seagrass beds receive higher numbers of settling larvae. Overall, preservation of seagrass beds is extremely important to many species of commercial fish, and the value placed on individual beds will need to take into account the position of the bed relative to hydrodynamics rather than just the physical characteristics of the bed.

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1. General Introduction

A decline of over 70 % of the seagrass cover in Western Port bay occurred between 1973 and 1984 (Bulthius et al., 1984; Shepherd et al., 1989). The losses occurred predominantly from intertidal areas of Heterozostera tasmanica (Bulthius et al., 1984; Shepherd et al., 1989). Although the exact causes of this decline are not known, the major proximate cause was thought to be desiccation and/or high temperatures coupled with a fine coating of adherent mud on the leaves reducing light levels (Bulthius et al., 1984; Shepherd et al., 1989). The underlying causes of losses may have included increased turbidity and sediment deposition resulting from catchment erosion and dredging operations, increased emersion at low tide due to changes in topography and tidal hydrology, and unusually high temperatures over summer (Bulthius, 1983; Bulthius et al., 1984). Losses may have been self perpetuating; initial seagrass death may have led to mud-bank erosion, increasing suspended solids and sediment deposition in adjacent areas.

The decline in seagrass cover was paralleled by a decline of about 40 % in total commercial fish catches from Western Port bay (Fig. 1). Catches in Port Phillip Bay, excluding pilchards for which catches increased rapidly, remained relatively constant over the same period. Catch declines in Western Port bay were particularly apparent for some species, such as leatherjackets (Fig.1.1) and grass whiting (Fig. 1.2) where catches in the 1980's were at historically low levels. Although alternative explanations for the declines, such as overfishing, and changes in fishing effort or larval input, cannot be rejected, the results are suggestive of a link with seagrass decline for some species. In contrast, catches of other species such as yellow-eye mullet either showed no signs of decline, or actually increased (Fig. 1.3). King George whiting showed a more complex pattern, with a major peak in catches in the early 1970's declining to approximately pre-peak levels in the 1980's (Fig. 1.4). A similar peak was apparent for King George whiting catches in Port Phillip Bay suggesting that factors such as changes in effort, or larval input, were responsible for the peak (M. MacDonald, unpublished). Post-peak catches of King George whiting in Port Phillip Bay were approximately double that of pre-peak levels, while in Western port, pre- and post-peak levels were similar, suggesting a relatively greater decline in Western Port bay which may relate to habitat loss.

This presentation describes a three-year research project aimed at clarifying the importance of seagrass beds as settlement sites and juvenile nursery habitats for commercial fishes. Seagrass beds studied in this project were from Swan Bay, Port Phillip Bay and Corner Inlet. No major losses of seagrass occurred in these areas in the 1970's and early 80's and they therefore represent the situation in Westernport prior to seagrass loss. The objective of the project was to describe and quantify patterns of utilization of shallow-water, Heterozostera - dominated habitats in southeastern Australia, by larval and juvenile fishes of commercial significance.

Fig. 1. Annual catches of commercial finfish in Western Port bay.

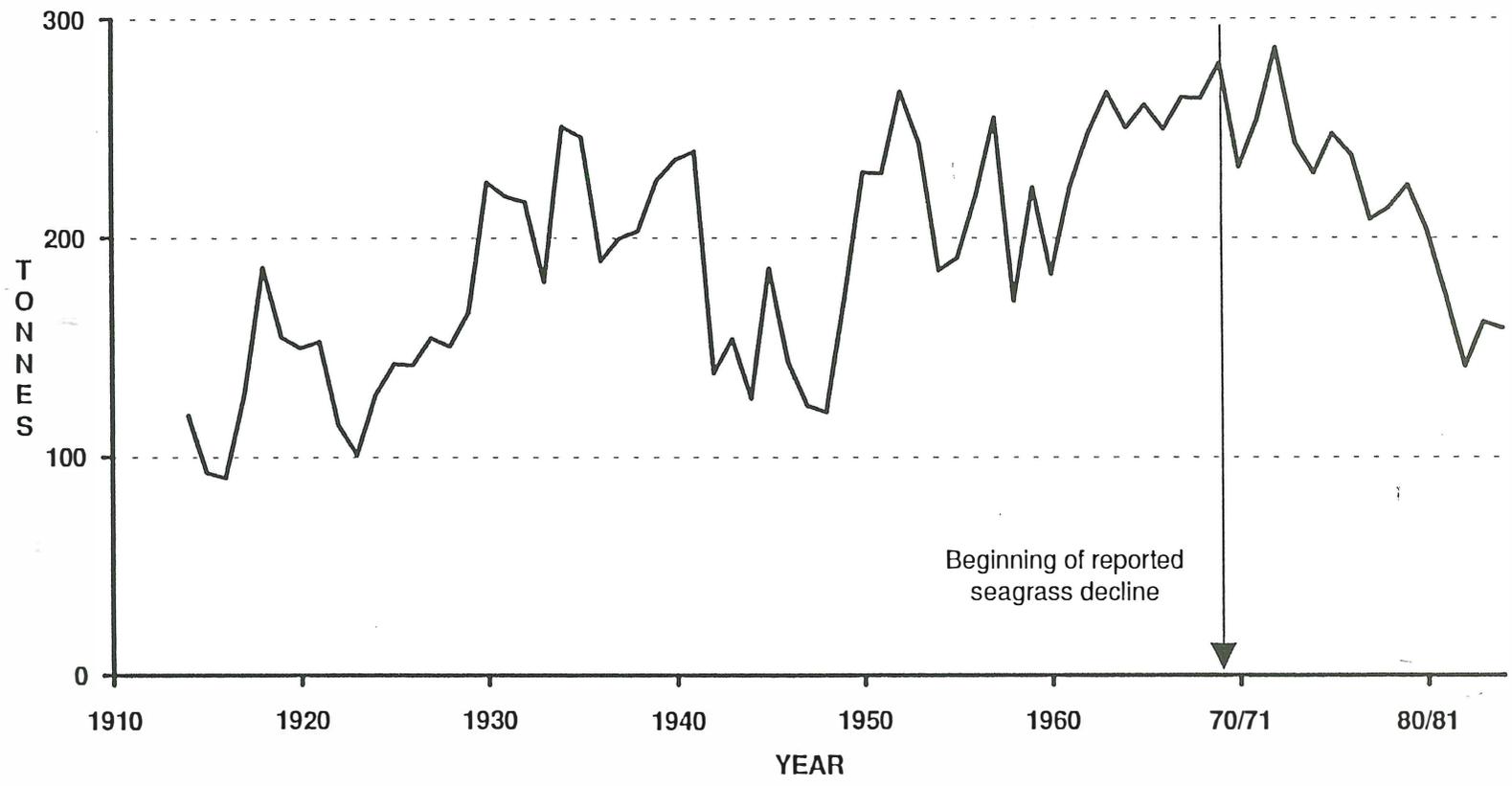


Fig. 1.1 Annual catches of leatherjackets in Western Port bay.

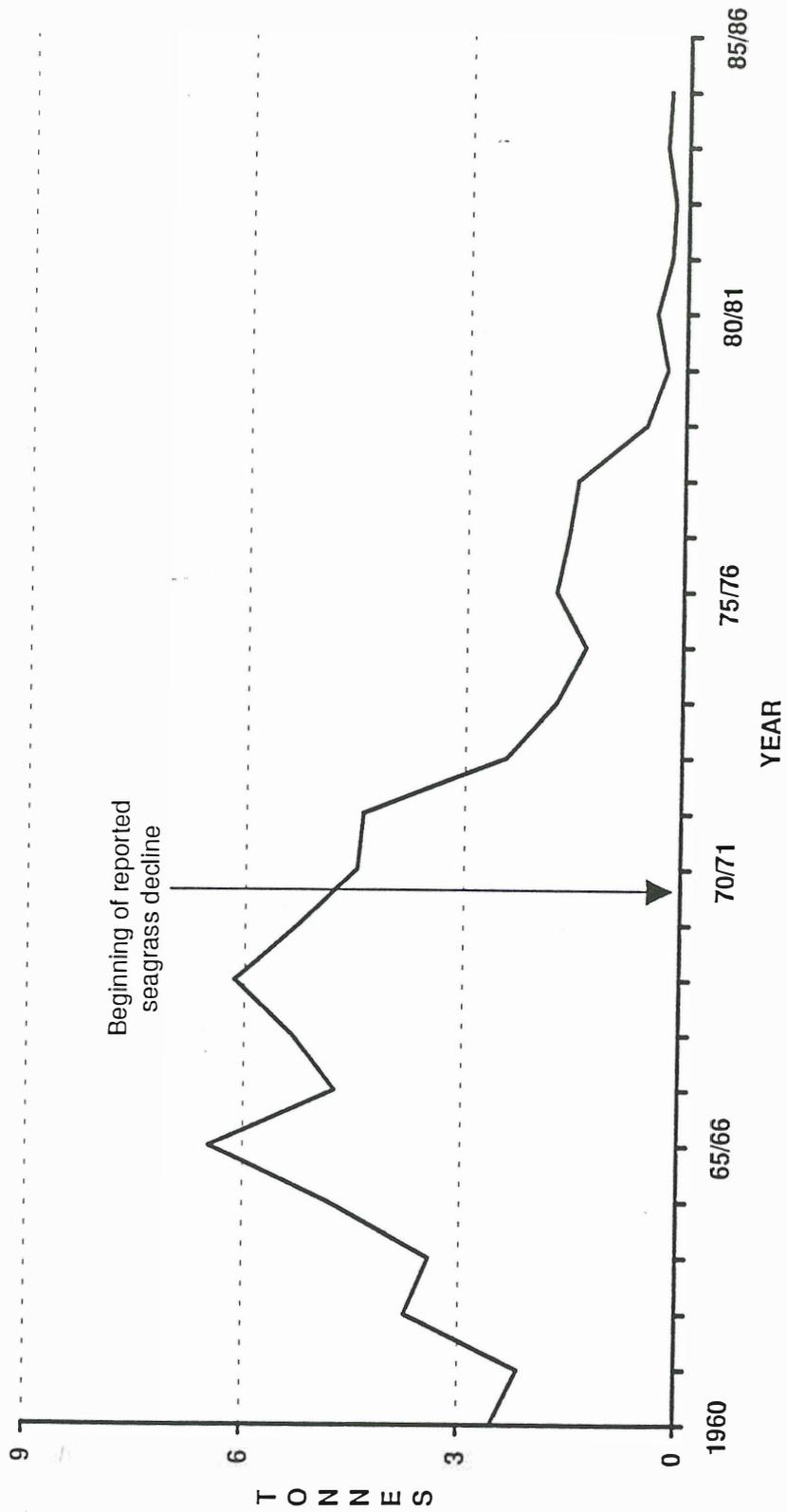


Fig. 1.2 Annual catches of grass whiting in Western Port Bay.

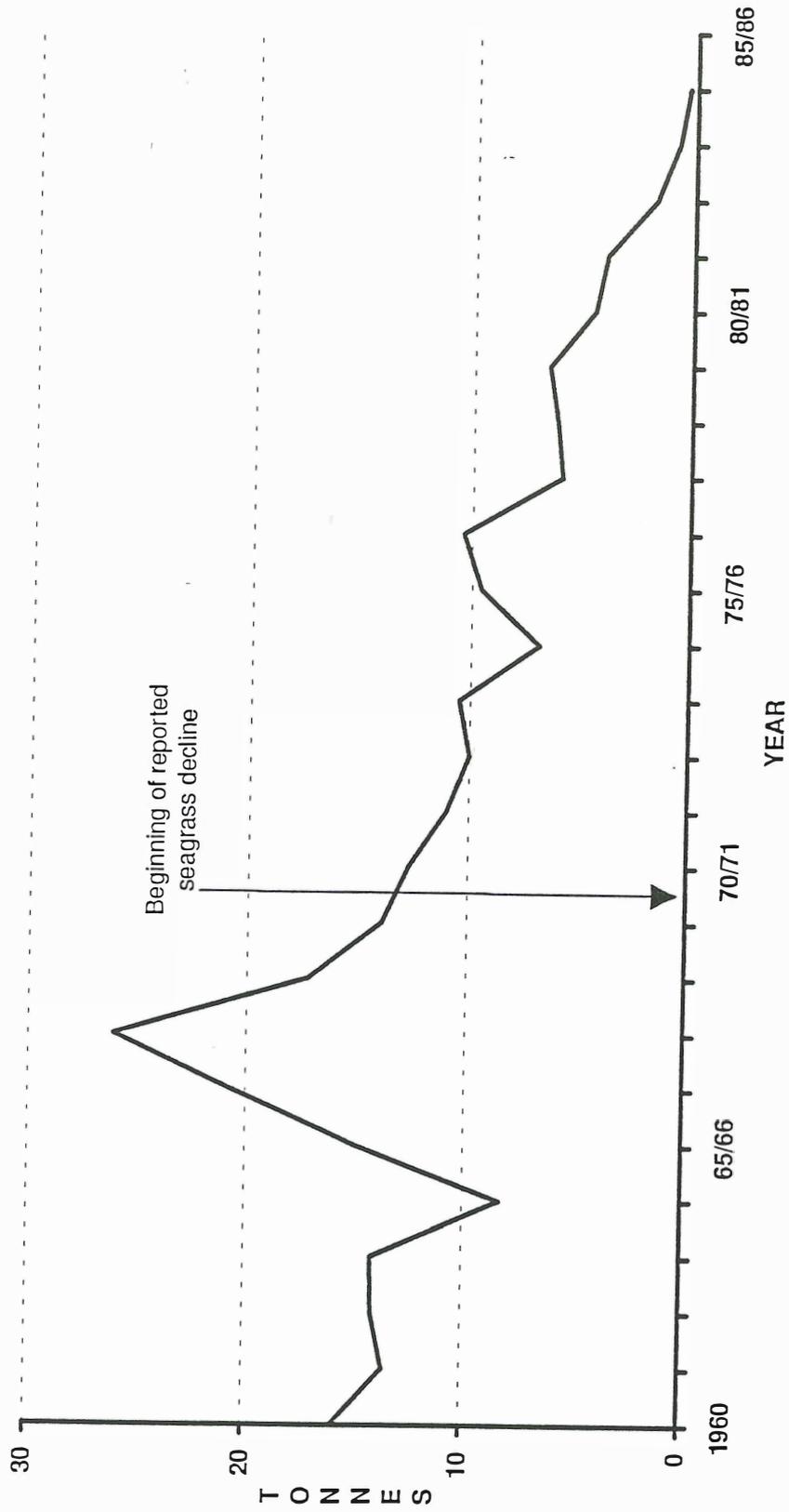


Fig. 1.3 Annual catches of yellow-eye mullet in Western Port Bay.

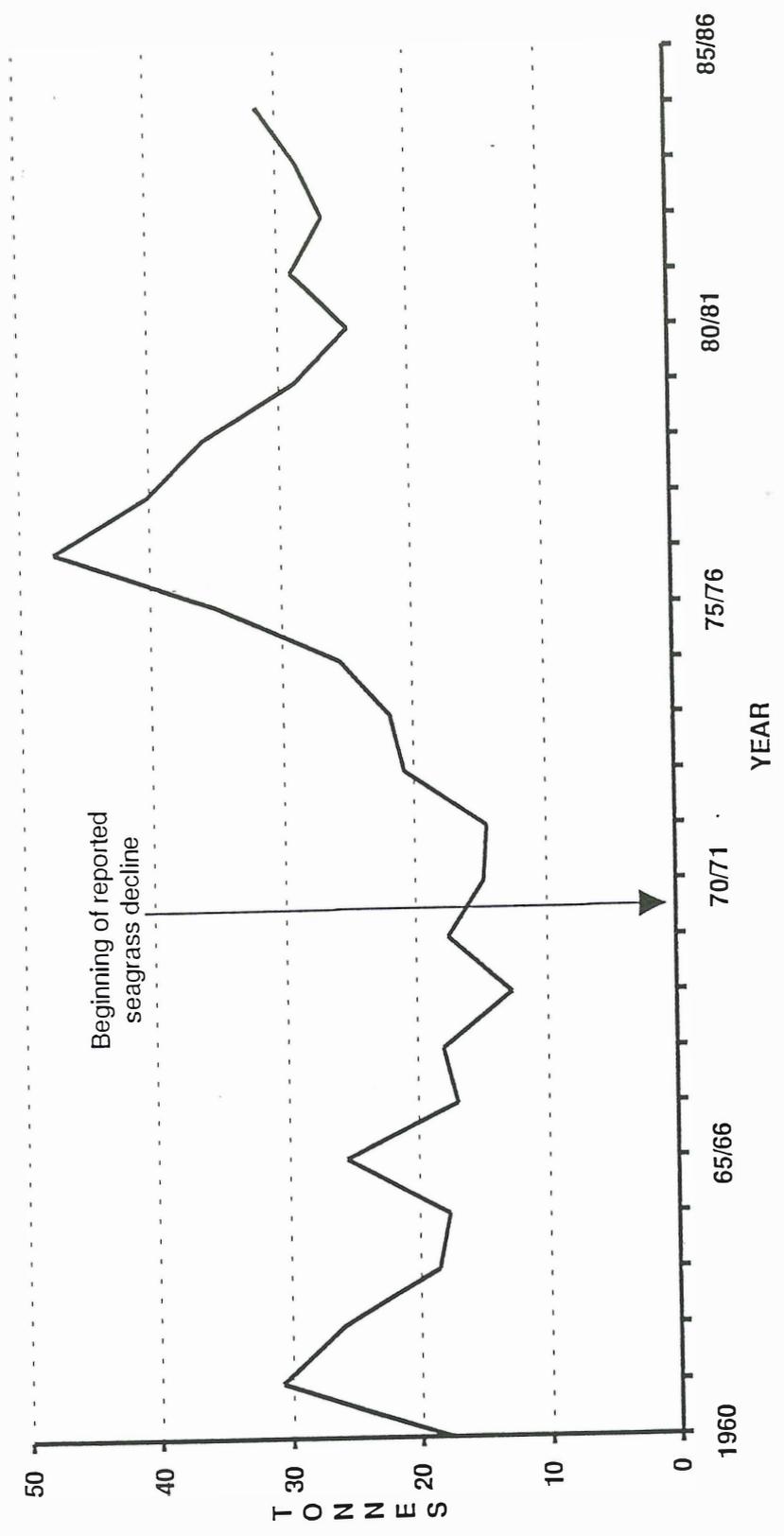
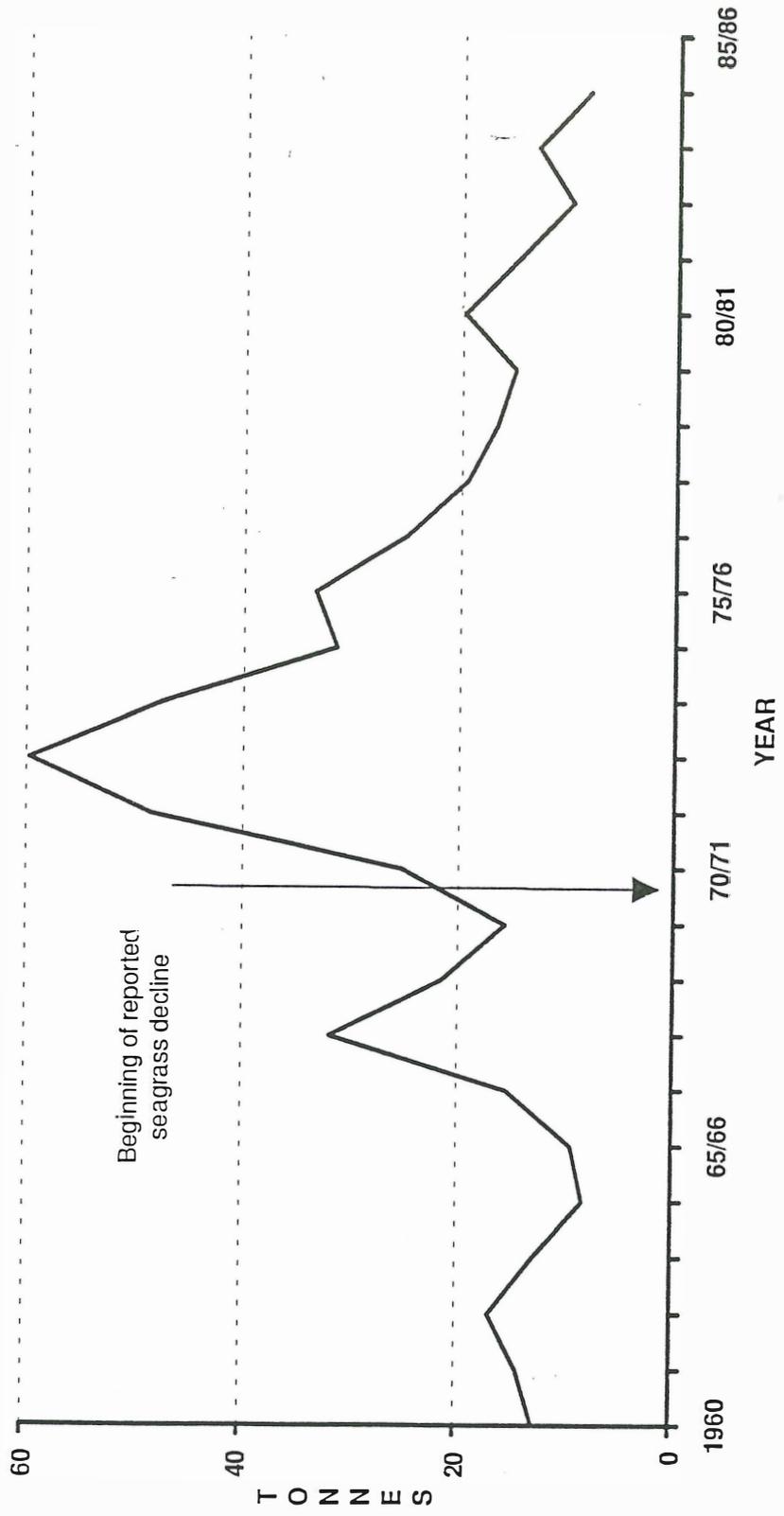


Fig.1.4 Annual catches of King George whiting in Western Port bay.



2. Distribution of juvenile fishes associated with seagrassed and unvegetated habitats

2.1 Introduction

The importance of seagrassed habitats to juvenile commercial fish can be assessed by comparison with other habitats. This may reveal species which have a direct dependence on seagrass habitat for settlement and juvenile life. Ferrell and Bell (1991) found that the seagrass Zostera contained similar numbers, but differing species of fishes compared with adjacent sand areas. Both habitats contained more species and individuals than distant sand habitats. A number of commercially important species utilised adjacent sand habitat in the juvenile stage. Humphries *et al.* (1992) found that the seagrass Ruppia supported higher abundances and biomass of juvenile fishes but a lower species diversity than bare sand areas. In general, greater species diversity and abundance of individuals has been found in seagrass compared with unvegetated habitats both overseas and in Australia (reviewed in Bell and Pollard, 1989). Species composition in seagrass includes many small species with cryptic habits, together with juveniles of larger species and some large mobile fish; in contrast, species gaining protection through schooling or camouflage were most abundant on bare substrate (Bell and Pollard, 1989). Juveniles of some commercial species in New South Wales, such as the sparids, Acanthopagrus australis and Rhabdosargus sarba, occurred most commonly on sand habitat adjacent to seagrass, but were rare on sand habitat some distance from seagrass. The aim of this section of our study was to compare the species richness and abundance of individuals in seagrass and adjacent unvegetated habitats at sites in Swan Bay, Port Phillip Bay and Corner Inlet, with emphasis on species of commercial importance. In contrast to other studies, our study concentrated on the eelgrass, Heterozostera. In general, subtidal Heterozostera habitat of southern Australia has received less attention than other seagrass habitats.

2.2 Methods

2.2.1 Study areas

It was considered that to adequately assess the importance of seagrasses as nursery areas, a comparison had to be made with non-vegetated areas. Moreover, given the high spatial variability in abundances recorded in the pilot study, multiple sampling sites in each location were necessary for conclusions from statistics to be of general relevance.

2.2.1.1 Swan Bay

Swan Bay (Fig. 2.1) is a small bay linked to Port Phillip Bay in the region of Port Phillip Heads. Swan Bay is shallow (< 3m), relatively protected from the prevailing westerly winds, and tidal currents are weak. There are large beds of subtidal eelgrass Heterozostera tasmanica together with smaller areas of intertidal eelgrass Zostera muelleri. The central region of Swan Bay tends to unvegetated sediment with large patches of drift algae, much of which is unattached but still growing. Seagrass on the adjacent coast of Port Phillip Bay consists of narrow (20 m) wide bands of Heterozostera running parallel to the shoreline. This coast is more exposed to wave action and strong tidal currents associated with Port Phillip Heads. Cover of macroalgae was very low compared with Swan Bay. Sediments in Swan Bay are fine with a relatively high organic content, in contrast, sediments on the adjacent coast of Port Phillip Bay are coarser sands with lower organic content (Shaw and Jenkins, in press, Appendix 1). The tidal range in the area was less than one metre.

Within the Swan Bay region, three sites, Queenscliff, Tin Can and North Jetty, were within the bay itself, whilst St Leonards was on the the adjacent coast of Port Phillip Bay (Fig. 2.1). Seagrass was Heterozostera tasmanica with the exception of Queenscliff which was Zostera muelleri. Seagrass at Queenscliff was approximately at the mean low-water spring (MLWS) level while at the other sites seagrass was approximately 0.5 m below MLWS. Unvegetated habitat at North Jetty and Tin Can was in the form of patches amongst seagrass and associated macroalgae.

2.2.1.2 Corner Inlet

Corner Inlet (Fig. 2.2) is a large, enclosed bay with extensive shallow (< 2 m) areas dissected by deeper channels. The tidal range is large (> 2m) and therefore currents in channels are relatively strong. There are large subtidal beds of eelgrass, Heterozostera tasmanica, and tapeweed, Posidonia australis, together with smaller areas of intertidal Zostera muelleri. Channels are generally unvegetated.

Six sites were sampled in Corner Inlet (Fig. 2.2). Seagrass at Bennison Island, Duck Point and Toora Channel was Heterozostera tasmanica whilst seagrass at Toora Beach and Canoe Point was Zostera muelleri. Both seagrass and unvegetated habitats were sampled at these sites. At a sixth site, Boat Ramp, only Heterozostera habitat was sampled, as this extensive area of seagrass had no unvegetated patches. Heterozostera

sites were subtidal at approximately 0.25 m below MLWS at Bennison Island, 0.5 m at Toora Channel and Boat Ramp, and approximately 1m below MLWS at Duck Point. Zostera sites at Canoe Point and Toora Beach were in the lower intertidal. Unvegetated areas at Bennison Island, Toora Beach and Canoe Point were approximately at the MLWS level between the Heterozostera and Zostera zones, unvegetated areas at Duck Point and Toora Channel were approximately 0.5 m below MLWS.

2.2.2 Field sampling

Pilot sampling was undertaken to determine the level of replication necessary for meaningful statistical analysis. Previous studies of fish in seagrass habitats in Victoria have concentrated on intertidal to very shallow subtidal sites. For this study it was considered desirable to sample deeper subtidal sites as well. For this purpose a modified beach seine was constructed which could be deployed from a boat in water to a depth of approximately 2 m. The net was 10 metres in length, had a 3 metre drop, and a mesh of approximately 1 mm². This mesh size allowed the collection of juvenile fishes immediately after settlement in seagrass beds. Pilot sampling indicated that a 15 m haul gave an adequate sample size but at the same time was small enough in sample area to allow specific microhabitats to be targeted. From the boat, ropes were hauled through detachable weights which stopped the net from rising from the bottom until completely retrieved. Three replicate hauls of the seine were conducted in each habitat. Fishes were preserved in 95% ethanol.

Sampling was conducted approximately monthly in Swan Bay and bimonthly in Port Phillip Bay. Sampling was begun in October 1989. In Swan Bay, both habitats were sampled at the Queenscliff site until September 1990, whilst at the Tin Can, North Jetty and St Leonards sites unvegetated habitat was sampled until the end of 1990 and seagrass habitat was sampled until the end of 1991. In Corner Inlet, both habitats were sampled at Canoe Point until August 1990 when sampling was terminated due to a loss of seagrass cover. At Toora Channel and Bennison, unvegetated habitat was sampled until December 1990 whilst seagrass was sampled until August 1991. The same sampling protocol was used at Duck Point, however, sampling in February and April was not possible due to rough sea conditions. Seagrass at Boat Ramp was also sampled until August 1991, however, sampling in unvegetated habitat was terminated after three sampling trips because unvegetated areas were overgrown with seagrass. Both habitats were sampled at Toora Beach from February 1990 until December 1990.

2.2.3 Laboratory methods

In the laboratory fishes were identified to the lowest taxonomic level possible. For important species, the standard length (from the tip of the snout to the posterior edge of the hypural plates) was measured. Where more than thirty individuals occurred in the sample a subsample of thirty was measured. A sample of King George whiting post-larvae collected from Tin Can and North Jetty in 1989 was also analysed for dietary composition. Post-larvae were placed in a drop of glycerine on a microscope slide and, while viewed under a stereo microscope, electrolytically-sharpened tungsten needles were used to tease prey items from the alimentary canal. Prey items were identified to the lowest taxonomic level possible.

2.2.4 Data Analysis

Cluster analysis was used to compare fish communities amongst site/habitat combinations. Abundances of individuals were pooled for replicates and dates. Rare (< 30 individuals) species were not included in the analysis. Dissimilarities were estimated using the Pearson correlation coefficient on log transformed and standardised data. Amalgamation was achieved using the average linkage method (Wilkinson *et al.* 1992).

Analysis of variance was conducted to estimate the significance of differences in abundance amongst sites, habitats and dates. The analysis included the three sites sampled for the entire first twelve months in Corner Inlet; Toora Channel, Bennison and Canoe Point, and the four Swan Bay sites for the equivalent sampling months. Sites were nested within the two bays; main effects were considered as fixed factors whilst site was considered a random factor. Box and residual plots were used to examine data for departures from assumptions of analysis of variance. It was necessary to log (x+1) transform the data to stabilise variances. Analyses were conducted for total fishes and for 'benthic' fishes, total fishes less the pelagic schooling atherinids and clupeoids.

2.3 Results

2.3.1 Fish community composition

2.3.1.1 Swan Bay

The community composition in seagrass habitat at North Jetty and Tin Can was dominated by the spotted pipefish, Stigmatopora argus (Table 2.1). The pattern of dominance was very similar at both sites, with other abundant species including silverfish, Leptatherina presbyteroides, Port Phillip pipefish, Vanacampus phillipi, common weedfish, Heteroclinus perspicillatus, and bridled leatherjacket, Acanthaluteres spilomelanurus. Community composition was also similar between the unvegetated habitats at these sites (Table 2.1), with dominants including spotted pipefish and Port Phillip pipefish, which were mainly associated with detached algae sometimes collected in the habitat, King George whiting, Sillaginodes punctata and girdled goby, Nesogobius sp. 1. These unvegetated habitats differed in the high abundances of silverfish at North Jetty and Castelnau's goby, Nesogobius pulchellus at Tin Can.

Dominance patterns in Heterozostera habitat at St Leonards (Table 2.1) were markedly different to the same habitat in Swan Bay. Small post-larval hardyheads (Atherinidae) were dominant in terms of numbers although their biomass contribution would have been low. In contrast to Swan Bay, wide-bodied pipefish, Stigmatopora nigra, occurred in greater numbers than spotted pipefish. Other relatively abundant species included clingfish, Parvicrepis sp. and blue sprat, Spratelloides robustus. Dominant species on unvegetated habitat at St Leonards were juveniles of the yellow-eye mullet, Aldrichetta forsteri, the greenback flounder, Rhombosolea tapirina, the long-snouted flounder, Ammotretis rostratus, and the Western Australian salmon, Arripis truttacea.

Abundance patterns at Queenscliff were also distinct from other sites (Table 2.1). Hardyheads were dominant in seagrass, however, unlike North Jetty and Tin Can, the small-mouthed hardyhead, Atherinosoma microstoma, occurred in greater numbers than silverfish. The dominant pipefish in this habitat was the hairy pipefish, Urocampus carinirostris. Also abundant relative to other habitats was the bridled goby, Arenigobius frenatus. Unvegetated habitat at Queenscliff was dominated by the long-finned goby, Favonigobius lateralis. Also common were juvenile King George whiting and greenback flounder.

2.3.1.2 Corner Inlet

The fish community on unvegetated habitats in Corner Inlet was dominated by long-finned gobies and hardyheads (Table 2.2). Wide-bodied pipefish were also relatively common, probably associated with detached macrophytes and small tufts of seagrass on the otherwise unvegetated habitat.

The species composition in seagrass habitat differed between subtidal Heterozostera sites and intertidal Zostera sites (Table 2.2). Subtidal seagrass at Bennison, Boat Ramp, Duck Point and Toora Channel was dominated by cobbler, Gymnapistes marmoratus, bridled leatherjackets, little rock whiting, Neodax balteatus, and wide bodied and spotted pipefishes. Stranger, Haletta semifasciata, were common at Boat Ramp, and Wood's siphonfish, Siphamia cephalotes, were common at Boat Ramp and Toora Channel.

In contrast to subtidal seagrass, abundant species in the intertidal seagrass at Canoe Point and Toora Beach included the blue-spotted goby, Pseudogobius olorum, the bridled goby, and the hairy pipefish (Table 2.2). Sandy sprat, Hyperlophus vittatus were abundant at Canoe Point whilst long-finned gobies were common at Toora Beach.

2.3.2 Comparison of Fish Communities amongst Sites

2.3.2.1 Cluster Analysis

Sampling sites differed more in relation to habitat type and depth rather than area of collection (Fig. 2.3). The intertidal seagrass habitats at Queenscliff, Toora Beach and Canoe Point clustered together, and were more similar to unvegetated habitats than they were to deeper, Heterozostera, habitats. This indicates that the fish community associated with the two seagrass habitats was distinctly different. Amongst Heterozostera sites, St Leonards was also distinctly different, showing greatest similarity with unvegetated sites at Tin Can and North Jetty. Unlike seagrass sites, intertidal and subtidal unvegetated habitats tended to cluster together, although Tin Can and North Jetty were quite distinct.

Table 2.1 Number of individuals and percentage contribution of each species of fish collected at sites in Swan Bay and at St Leonards.

	Nth Jetty				Tin Can				St Leonards				Queenscliff			
	Bare		Seagrass		Bare		Seagrass		Bare		Seagrass		Bare		Seagrass	
Number of samples	52		94		60		88		46		86		37		37	
Species	#	%	#	%	#	%	#	%	#	%	#	%	#	%	#	%
<i>Spratelloides robustus</i>	0		0		0		0		0		174	4.3	0		0	
<i>Engraulis australis</i>	0		0		1		0		0		0		0		0	
<i>Galaxias maculatus</i>	0		0		0		9	0.1	0		0		0		0	
<i>Pseudophycis barbata</i>	0		0		1		0		0		1		0		0	
<i>Hyporhamphus melanochir</i>	1		0		0		3		0		0		0		1	
<i>Kestratherina esox</i>	0		26	0.2	0		20	0.1	0		0		0		5	0.2
<i>Kestratherina brevirostris</i>	0		0		0		2		0		0		0		13	0.6
<i>Atherinosoma microstoma</i>	0		87	0.7	0		0		5	1.0	1		95	2.6	779	34.7
Atherinidae	229	9.4	153	1.2	203	9.1	40	0.3	12	2.5	2421	59.6	15	0.4	5	0.2
<i>Leptatherina presbyteroides</i>	289	11.8	838	6.3	2	0.1	814	5.7	1	0.2	5	0.1	0		364	16.2
<i>Stigmatopora argus</i>	479	19.6	8587	64.9	525	23.6	10261	71.8	5	1.0	175	4.3	0		3	0.1
<i>Stigmatopora nigra</i>	2	0.1	4		6	0.3	7		5	1.0	318	7.8	0		11	0.5
<i>Stigmatopora sp.</i>	1		5		0		31	0.2	0		19	0.5	0		0	
<i>Urocampus carinirostris</i>	31	1.3	123	0.9	10	0.4	47	0.3	1	0.2	2		40	1.1	598	26.6
<i>Vanacampus phillipi</i>	151	6.2	553	4.2	312	14.0	600	4.2	0		35	0.9	0		13	0.6
<i>Pugnaso curtirostris</i>	0		6		16	0.7	3		0		2		0		0	
<i>Vanacampus poecilaemus</i>	0		0		0		2		0		0		0		0	
<i>Lissocampus runa</i>	0		2		0		0		0		0		0		0	
<i>Hypsognathus rostratus</i>	1		34	0.3	0		9	0.1	1	0.2	0		0		0	
<i>Kaupus costatus</i>	0		1		0		0		0		0		0		0	
<i>Leptonotus semistriatus</i>	0		1		0		0		0		3	0.1	0		0	
<i>Gymnapistes marmoratus</i>	20	0.8	404	3.1	5	0.2	263	1.8	0		53	1.3	0		3	0.1
Scorpaenidae	1		0		0		0		0		0		0		0	
<i>Aploactisoma milesii</i>	0		0		0		0		0		1		0		0	
<i>Platycephalus laevigatus</i>	0		5		2	0.1	7		0		1		0		0	
<i>Platycephalus speculator</i>	1		0		1		0		7	1.4	0		0		0	
<i>Platycephalus bassensis</i>	15	0.6	0		4	0.2	0		0		0		0		0	
Platycephalidae	0		0		0		0		0		1		0		0	
<i>Siphamia cephalotes</i>	0		34	0.3	0		21	0.1	0		14	0.3	0		0	
<i>Vincentia conspersa</i>	0		22	0.2	0		7		0		0		0		0	
<i>Sillaginodes punctata</i>	509	20.8	67	0.5	279	12.5	78	0.5	5	1.0	46	1.1	151	4.1	36	1.6
<i>Arripis truttacea</i>	0		0		0		0		35	7.2	6	0.1	3	0.1	0	
<i>Girella zebra</i>	0		0		0		0		0		0		0		2	0.1
<i>Enoplosus armatus</i>	0		19	0.1	0		29	0.2	0		20	0.5	0		0	
<i>Dactylophora nigricans</i>	0		0		0		0		0		17	0.4	0		0	

Table 2.1 (Cont.)

Aldrichetta forsteri	0	0	6	0.3	7	228	46.9	25	0.6	64	1.7	43	1.9
Eupetrichthys angustipes	0	0	0		0	0		1		0		0	
Haletta semifasciata	4	0.2	223	1.7	2	0.1	142	1.0	0	0		0	
Neoodax balteatus	6	0.2	310	2.3	12	0.5	342	2.4	0	10	0.2	0	
Lesueurina platycephala	0	0	0		0		18	3.7	1	0		0	
Cristiceps australis	6	0.2	211	1.6	17	0.8	89	0.6	1	0.2	60	1.5	0
Heteroclinus perspicillatus	130	5.3	575	4.3	95	4.3	387	2.7	3	0.6	137	3.4	2
Heteroclinus adelaide	3	0.1	50	0.4	19	0.9	59	0.4	1	0.2	97	2.4	0
Heteroclinus tristis	0	0	0		0		0		0		0		0
Ophiclinus gabrieli	0	8	0.1	0	1	0	0	0	0	0	0	0	0
Favonigobius lateralis	160	6.5	1	82	3.7	10	0.1	10	2.1	31	0.8	3043	82.6
Nesogobius sp.1	337	13.8	18	0.1	217	9.7	3	0.6	23	0.6	91	2.5	9
Nesogobius pulchellus	19	0.8	48	0.4	353	15.8	309	2.2	0	13	0.3	0	2
Arenigobius frenatus	0	6	1	9	0.1	0	1	0	1	10	0.3	190	8.5
Tasmanogobius lastii	0	0	17	0.8	0	0	0	0	0	0	0	0	0
Callogobius mucosus	0	0	0		1	0	0	0	0	0	0	0	0
Gobiidae	0	0	8	0.4	1	0	0	0	0	0	0	0	0
Parvicrepis sp.	0	0	4	0.2	0	4	0.8	202	5.0	1	1	1	1
Foetorepus calauropomus	0	0	0		0	0	0	1	0	0	0	0	0
Ammotretis rostratus	2	0.1	1	0	0	56	11.5	3	0.1	16	0.4	0	0
Rhombosolea tapirina	21	0.9	0	2	0.1	2	71	14.6	0	143	3.9	1	1
Taratretis derwentensis	0	0	0		0	0	0	0	1	0	0	0	0
Acanthaluteres spilomelanurus	13	0.5	524	4.0	4	0.2	380	2.7	0	11	0.3	0	0
Brachaluteres jacksonianus	1	2	3	0.1	1	0	0	0	0	0	0	0	0
Meuschenia freycineti	1	223	1.7	5	0.2	272	1.9	0	23	0.6	0	0	0
Acanthaluteres vittiger	0	0	0		0	0	0	2	0	0	0	0	0
Scobinichthys granulatus	1	16	0.1	0	3	0	0	1	0	0	0	0	0
Monacanthidae	0	1	0		0	0	0	0	0	0	0	0	0
Contusus brevicaudus	2	0.1	2	0	2	14	2.9	85	2.1	4	0.1	5	0.2
Contusus richei	0	0	2	0.1	2	0	1	0	0	0	0	0	0
Tetractenos glaber	7	0.3	25	0.2	13	0.6	18	0.1	0	16	0.4	4	0.1
Diodon nichthemerus	0	6	0		5	0	3	0.1	0	0	0	0	0
Total	2443	13221	2229	14298	486	4063	3683	2246					

Table 2.2 Number of individuals and percentage contribution of each species of fish collected at sites in Corner Inlet.

Species	Bennison		Boat Ramp		Canoe Pt		Duck Pt		Toora Beach		Toora channel													
	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass	Bare	Seagrass												
	24	37	9	33	18	18	18	30	18	18	24	36												
<i>Hyperlophus vittatus</i>	0	0	0	0	17	4.6	1406	36.7	0	0	0	38	2.5	0	21	0.6								
<i>Galaxias maculatus</i>	0	0	0	0	4	1.1	0	0	0	0	0	0	0	1	0.4	0								
<i>Hyphoramphus melanochir</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.4	0								
<i>Kestratherina esox</i>	2	0.2	14	1.0	0	3	0.1	2	0.5	1	0.3	0	0	9	3.3	3	0.1							
<i>Kestratherina brevirostris</i>	0	0	27	2.0	0	0	0	0	0	0	0	0	0	0	0	0								
<i>Atherinosoma microstoma</i>	274	23.1	281	20.9	0	41	1.9	0	41	1.1	0	2	0.3	0	56	3.7	15	5.5	2	0.1				
<i>Leptatherina presbyteroides</i>	101	8.5	97	7.2	0	0	0	0	0	0	0	0	0	105	51.2	1	0.1	78	28.4	15	0.4			
Atherinidae	1	0.1	1	0.1	0	14	0.6	18	4.9	0	79	20.2	28	3.6	0	1	0.1	9	3.3	6	0.2			
<i>Hippocampus breviceps</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.4	2	0.1	0	0			
<i>Stigmatopora argus</i>	0	0	32	2.4	3	0.5	20	0.9	2	0.5	19	0.5	2	0.5	64	8.2	0	2	0.1	7	2.5	635	17.6	
<i>Stigmatopora nigra</i>	48	4.0	30	2.2	124	19.8	49	2.2	85	22.9	159	4.2	34	8.7	23	3.0	2	1.0	6	0.4	33	12.0	600	16.7
<i>Stigmatopora sp.</i>	0	0	0	0	1	0.3	1	0.3	1	0.3	1	0.3	0	0	0	0	0	0	0	0	0	0	0	
<i>Urocampus carinirostris</i>	13	1.1	100	7.4	14	2.2	22	1.0	7	1.9	373	9.7	10	2.6	11	1.4	0	0	169	11.2	0	0	29	0.8
<i>Vanacampus phillipi</i>	8	0.7	28	2.1	75	12.0	67	3.1	0	0.2	6	0.2	0	0	17	2.2	0	0	9	0.6	2	0.7	76	2.1
<i>Pugnaso curtirostris</i>	0	0	2	0.1	0	0	4	0.2	0	0	0	0	0	0	7	0.9	0	0	1	0.1	0	0	1	0
<i>Vanacampus poecilaemus</i>	0	0	20	1.5	3	0.5	12	0.6	0	0	0	0	0	7	0.9	0	0	0	0	0	0	0	16	0.4
<i>Hypselognathus rostratus</i>	0	0	1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.1
<i>Kaupus costatus</i>	2	0.2	6	0.4	0	0	0	0	1	0.3	17	0.4	0	0	0	0	0	0	9	0.6	0	0	0	0
<i>Leptoichthys fistularius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Gymnapistes marmoratus</i>	0	0	189	14.1	11	1.8	565	25.9	1	0.3	120	3.1	3	0.8	229	29.5	1	0.5	92	6.1	2	0.7	306	8.5
<i>Platycephalus laevigatus</i>	10	0.8	4	0.3	3	0.5	7	0.3	3	0.8	0	0	2	0.5	5	0.6	5	2.4	2	0.1	3	1.1	16	0.4
<i>Platycephalus speculator</i>	8	0.7	0	0	3	0.5	0	0	2	0.5	0	0	2	0.5	1	0.1	8	3.9	0	0	19	6.9	1	0
<i>Platycephalus bassensis</i>	0	0	0	0	0	0	0	0	1	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Siphamia cephalotes</i>	1	0.1	7	0.5	0	0	133	6.1	0	0	0	0	0	0	4	0.5	0	0	0	0	1	0.4	367	10.2
<i>Vincentia conspersa</i>	0	0	3	0.2	0	0	72	3.3	0	0	0	0	0	0	3	0.4	0	0	0	0	0	0	2	0.1
<i>Sillaginodes punctata</i>	29	2.4	0	0	28	4.5	0	0	1	0.3	2	0.1	10	2.6	3	0.4	0	0	0	0	2	0.7	0	0
<i>Pseudocaranx dentex</i>	0	0	0	0	1	0.2	1	0.2	24	6.5	8	0.2	0	0	0	0	0	0	0	0	0	0	17	0.5
<i>Upeneichthys sp.</i>	0	0	2	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Girella tricuspidata</i>	0	0	0	0	2	0.3	0	0	0	0	106	2.8	0	0	0	0	0	0	0	0	0	0	0	0
<i>Aldrichetta forsteri</i>	0	0	1	0.1	0	0	0	0	7	1.9	23	0.6	0	0	0	0	0	9	4.4	6	0.4	0	0	0
<i>Haletta semifasciata</i>	0	0	12	0.9	9	1.4	206	9.4	0	0	0	0	0	18	2.3	0	0	0	0	0	0	0	22	0.6
<i>Neoodax balteatus</i>	0	0	61	4.5	8	1.3	340	15.6	0	0	0	0	0	197	25.4	0	0	0	0	0	0	0	260	7.2
Odacidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Pseudaphritis urvillii</i>	0	0	0	0	0	0	5	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cristiceps australis</i>	0	0	5	0.4	1	0.2	24	1.1	0	0	0	0	0	2	0.3	0	0	0	0	0	0	0	18	0.5
<i>Heteroclinus perspicillatus</i>	4	0.3	22	1.6	22	3.5	18	0.8	0	0	5	0.1	3	0.8	19	2.4	0	0	16	1.1	1	0.4	15	0.4
<i>Heteroclinus adelaide</i>	0	0	3	0.2	2	0.3	5	0.2	0	0	0	0	0	3	0.4	0	0	0	0	0	0	0	22	0.6

Table 2.2 (Cont.)

<i>Parablennius tasmanianus</i>	0	0	0	0	0	0	0	0	0	1	0.1	0	0	0	0	0								
<i>Favonigobius lateralis</i>	570	48.0	58	4.3	184	29.3	3	0.1	104	28.0	23	0.6	212	54.2	4	0.5	45	22.0	298	19.7	64	23.3	1	
<i>Favonigobius tamarensis</i>	0		0		0		0		1	0.3	55	1.4	0		0		0		0		1	0.4	0	
<i>Nesogobius sp.1</i>	19	1.6	4	0.3	6	1.0	0		2	0.5	24	0.6	10	2.6	0		6	2.9	0		4	1.5	0	
<i>Nesogobius pulchellus</i>	8	0.7	20	1.5	0		36	1.7	0		0		6	1.5	13	1.7	0		1	0.1	0		58	1.6
<i>Arenigobius frenatus</i>	19	1.6	18	1.3	40	6.4	12	0.6	3	0.8	141	3.7	0		10	1.3	0		225	14.9	2	0.7	25	0.7
<i>Pseudogobius olorum</i>	3	0.3	111	8.3	41	6.5	11	0.5	46	12.4	1216	31.8	2	0.5	1	0.1	3	1.5	570	37.6	0		0	
<i>Tasmanogobius lastii</i>	37	3.1	0		17	2.7	3	0.1	0		0		6	1.5	0		0		0		1	0.4	6	0.2
Gobiidae	2	0.2	0		0		2	0.1	0		0		1	0.3	0		0		0		2	0.7	0	
<i>Parvicrepis sp.</i>	0		1	0.1	0		0		0		0		0		1	0.1	0		0		0		0	
<i>Ammotretis rostratus</i>	2	0.2	0		0		0		8	2.2	3	0.1	0		0		7	3.4	0		6	2.2	1	
<i>Rhombosolea tapirina</i>	14	1.2	0		0		0		21	5.7	3	0.1	1	0.3	0		13	6.3	6	0.4	6	2.2	0	
<i>Synaptura nigra</i>	0		0		0		0		1	0.3	0		0		0		0		0		0		0	
<i>Acanthaluteres spilomelanurus</i>	6	0.5	130	9.7	10	1.6	408	18.7	1	0.3	0		0		91	11.7	1	0.5	2	0.1	4	1.5	975	27.1
<i>Brachaluteres jacksonianus</i>	0		3	0.2	1	0.2	5	0.2	0		0		0		0		0		0		0		0	
<i>Meuschenia freycineti</i>	0		35	2.6	16	2.6	56	2.6	0		0		1	0.3	10	1.3	0		0		0		39	1.1
<i>Scobinichthys granulatus</i>	0		12	0.9	1	0.2	31	1.4	0		0		0		2	0.3	0		0		0		26	0.7
Monacanthidae	3	0.3	0		1	0.2	0		0		0		0		0		0		0		0		0	
<i>Contusus brevicaudus</i>	0		0		0		0		0		36	0.9	0		0		0		0		1	0.4	4	0.1
<i>Contusus richei</i>	0		0		0		0		1	0.3	12	0.3	0		0		0		0		0		2	0.1
<i>Tectractenos glaber</i>	3	0.3	3	0.2	1	0.2	1		7	1.9	29	0.8	5	1.3	1	0.1	0		5	0.3	0		7	0.2
<i>Diodon nithemerus</i>	0		2	0.1	0		3	0.1	0		0		0		0		0		0		0		0	
	1187		1345		627		2180		371		3829		391		777		205		1515		275		3601	

2.3.2.2 Analysis of Variance

Analysis of variance of total abundances and total abundance of 'benthic' fishes showed similar results (Table 2.3). A significant three-way interaction indicated that the relative abundance of fishes in seagrass and unvegetated habitats was dependent on the particular site and date examined. In general, subtidal seagrass habitats at Tin Can, North Jetty, Canoe Point and Toora Channel supported higher abundances than unvegetated habitats (Figs 2.4, 2.5). In contrast, the shallower unvegetated habitats at Queenscliff and Bennison tended to support at least as many individuals as seagrass, partially due to low absolute numbers in seagrass relative to deeper sites. Overall, abundances in both habitats were low at St Leonards with a tendency to higher numbers in seagrass on some dates.

Table 2.3 Nested analysis of variance of abundances of juvenile fishes on seagrassed and unvegetated habitats at sites in Swan Bay and Corner Inlet. ns not significant, * P<0.05, ** P<0.001.

Source	df	Total		Benthic	
		MS	F	MS	F
Date	5	2.29	2.15ns	2.28	1.80ns
Hab	1	10.43	2.67ns	10.43	2.99ns
Bay	1	0.00	0.00ns	0.00	0.00ns
Site (Bay)	5	4.11	11.29**	3.48	11.70**
Date*Bay	5	2.21	2.08ns	2.41	1.90ns
Date*Hab	5	1.44	1.09ns	1.78	1.50ns
Hab*Bay	1	0.27	0.07ns	0.27	0.08ns
Date*Hab*Bay	5	1.81	1.37ns	2.41	2.04ns
Date*Site(Bay)	25	1.06	2.93**	1.27	4.28**
Hab*Site(Bay)	5	3.91	10.74**	3.49	11.75**
Date*Hab*Site(Bay)	25	1.32	3.63**	1.18	3.98**
Residual	168	0.36		0.30	

2.3.3 Commercial species

2.3.3.1 King George whiting, Sillaginodes punctata

King George whiting in Swan Bay showed a peak in unvegetated habitats over the late spring period at Tin Can and North Jetty and a peak in February/March at Queenscliff (Fig. 2.6). Comparatively small numbers were collected from St Leonards in the late spring, predominantly in seagrass (Fig. 2.6). The late-spring peaks were associated with the influx of post-larvae of approximately 20 mm SL. Juveniles subsequently grew to a size of 80 to 100 mm over the first year (Fig. 2.7). Few King George whiting were collected in Corner Inlet (Fig. 2.8). Like Swan Bay, individuals were mainly collected from unvegetated habitats.

Diel Variation in Habitat Selection

Habitat utilisation by King George whiting post-larvae was compared between day and night in November 1989 at North Jetty (Fig. 2.9A) and October and November 1990 at Mid Jetty (Fig. 2.9B). The North Jetty station was not used in 1990 because the unvegetated area was largely colonised by seagrass. King George whiting post-larvae occurred in significantly greater abundances on unvegetated habitat both day and night in 1989 (Table 2.5) and 1990 (Table 2.6).

Table 2.5 Comparison of $\ln(x+1)$ transformed abundances of juvenile King George whiting in seagrass and unvegetated habitats between day and night at the North Jetty site, November 1989. ns not significant, * $P < 0.05$, ** $P < 0.001$

Source	df	MS	F
Habitat	1	21.895	54.096**
Day/Night	1	0.47	1.16ns
Hab * Day/Night	1	0.06	0.15ns
Residual	8	0.41	

Table 2.6 Comparison of $\ln(x+1)$ transformed abundances of juvenile King George whiting in seagrass and unvegetated habitats between day and night at the Mid Jetty site, October and November 1989. ns not significant, * $P < 0.05$, ** $P < 0.001$

Source	df	MS	F
Date	1	0.72	2.30ns
Diel	1	0.05	0.19ns
Hab	1	35.01	1.63**
Date * Diel	1	0.27	0.87ns
Date * Hab	1	2.15	6.90ns
Diel * Hab	1	3.22	0.03ns
Date * Diel * Hab	1	0.11	0.35ns
Residual	16	0.31	

Diet of King George whiting post-larvae in the smallest sizes was dominated by benthic harpacticoid copepods, and lesser proportions of planktonic crustacea (mainly calanoid copepods) and amphipods (Fig. 2.10). With growth, the proportion of harpacticoids decreased with a concomitant increase in amphipods and mysids (Fig. 2.10).

2.3.3.2 Rock whiting, Haletta semifasciata

Rock whiting were abundant at the deeper, Heterozostera sites of Swan Bay (Fig. 2.11) and were also abundant at the Boat Ramp site in Corner Inlet (Fig. 2.12). This species showed an overwhelming preference for seagrass habitat. Recruitment of this species occurred from January to March at a size of 10 to 15 mm (Fig. 2.13), which is particularly reflected by the pattern of abundance at Tin Can (Fig. 2.11). Like King George whiting, size at the end of the first year was approximately 80 to 100 mm (Fig. 2.13). Larger individuals up to 280 mm were occasionally collected (Fig. 2.13).

2.3.3.3 Six-spined leatherjacket, Meuschenia freycineti

Six-spined leatherjackets showed a similar pattern to rock whiting, with a specific preference for subtidal Heterozostera habitats of Swan Bay (Fig. 2.14) and Corner Inlet (Fig. 2.15). In this case a few individuals were also collected at St Leonards (Fig. 2.14). Settlement occurred at a size of 10 to 15 mm over an extended period through spring and summer (Fig. 2.16) which is reflected in the time-course of abundance in Swan Bay (Fig. 2.14). Larger individuals up to 250 mm were collected (Fig. 2.16).

2.3.3.4 Rough leatherjacket, Scobinichthys granulatus

This species was only collected in significant numbers in Corner Inlet (Table 2.2). Like the six-spined leatherjacket, the rough leatherjacket showed a specific preference for seagrass habitat, and highest abundances occurred at Toora Channel and Boat Ramp (Fig. 2.17). Newly settled juveniles were collected in February 1990 (Fig. 2.18). Individuals up to 160 mm SL were collected (Fig. 2.18)

2.3.3.5 Yellow-eye mullet, Aldrichetta forsteri

Yellow-eye mullet were only collected in significant numbers at the Queenscliff and St Leonards sites (Fig. 2.19). This species was collected in relatively low numbers in Corner Inlet (Table 2.2). At Queenscliff, relative abundances in the two habitats varied between sampling dates whilst at St Leonards the majority of individuals were collected on sand (Fig. 2.19). The smallest individuals, approximately 30 to 35 mm in length, were collected from February to May (Fig. 2.20). The largest individuals collected were approximately 110 mm SL (Fig. 2.20).

2.3.3.6 Western Australian salmon, Arripis truttacea

Juveniles of this species were mainly collected on unvegetated habitat at St Leonards in October and November (Fig 2.21). Individuals ranged from approximately 45 - 80 mm in standard length.

2.3.3.7 Greenback flounder, Rhombosolea tapirina and long-snouted flounder, Ammotretis rostratus.

Greenback flounder were collected in highest numbers at the Queenscliff site in the unvegetated habitat (Fig. 2.22). Settlement of this species occurred in late winter/ early spring at a size of 5 to 10 mm SL, and individuals ranged up to approximately 90 mm SL (Fig. 2.23). Juvenile long-snouted flounder were collected mainly from the unvegetated habitat at St Leonards with highest abundances in November/December (Fig. 2.24). Newly settled post-larvae of 5 to 10 mm SL were collected in August, and individuals ranged up to 115 mm SL (Fig. 2.25). These species were also collected in low numbers from Corner Inlet (Table 2.2).

2.3.3.8 Rock flathead, Platycephalus laevigatus and Castelnau's flathead, Platycephalus speculator.

Rock flathead occurred in low numbers at most sites in Corner Inlet (Fig. 2.26). This species settled over summer, and showed a change in habitat utilisation with age; newly settled individuals were collected mainly on unvegetated habitats while older juveniles and adults were only collected from seagrass (Fig. 2.27). . Castelnau's flathead also occurred in low numbers at most sites in Corner Inlet, however, this species was collected predominantly in unvegetated habitats (Fig. 2.28). These species were only rarely collected in Swan Bay (Table 2.1)

2.3.3.9 Silver trevally, Pseudocaranx dentex

Small (15 - 20 mm) juvenile silver trevally were collected at the Canoe Point and Toora Channel sites in December and February (Fig. 2.29). No clear trend in habitat utilisation was apparent.

2.3.3.10 Luderick, Girella tricuspidata

Large numbers of newly settled luderick (10 - 15 mm) were collected in Zostera habitat at the Canoe Point site in December (Table 2.2).

2.3.3.11 Sprats and anchovies, Clupeiformes, and hardyheads, Atherinidae

Catches of atherinids in the Swan Bay region were dominated by extremely high abundances of small post-larvae at St Leonards in February 1991 (Fig. 2.30). At the Queenscliff site, abundances were consistently higher in seagrass compared with unvegetated habitat (Fig. 2.30). In Corner Inlet, atherinids were collected at all sites, with highest abundances at the Bennison site (Fig. 2.31). No distinct habitat preference was apparent (Fig. 2.31).

Catches of Clupeiformes were mainly limited to high numbers of anchovy, Engraulis australis, post-larvae collected over seagrass at St Leonards in January 1990 (Table 2.1) and large numbers of sandy sprat, Hyperlophus vittatus, juveniles collected over seagrass at Canoe Point in April 1990 (Table 2.2).

2.4 Discussion

2.4.1 Community composition

It is not possible to generalise about the overall importance of seagrass relative to unvegetated habitats in southern Victoria. Some consistent trends can be drawn out; for example, fish communities associated with subtidal Heterozostera were consistent amongst sites in Swan Bay and Corner Inlet, as were communities associated with intertidal Zostera. However, there were major differences in species composition and abundance between the two habitats. It is not possible at this stage to distinguish between the effects of habitat structure and water depth in causing these differences.

There were few overall differences between bays, however, individual sites varied greatly. For example, Canoe Point was outstanding amongst intertidal seagrass sites in the high numbers of fish collected. This site was situated at a creek mouth and would have had a greater estuarine influence than other sites. The dominant species, Pseudogobius olorum is known as an estuarine species (Last *et al.*, 1983). The reduction in fish numbers at this site over time occurred concomitantly with loss of seagrass at this site.

The greater abundances of fish in unvegetated habitat relative to seagrass at Queenscliff and Bennison were due to large populations of the long-finned goby. These sites are not consistent with the traditional idea that seagrass beds support more fish than unvegetated habitats.

One extremely atypical site was at St Leonards. This Heterozostera site was very similar to other subtidal seagrass sites in Swan Bay and Corner Inlet in terms of depth and plant structure (Bird, 1990), however, abundances were much lower and species composition showed significant differences compared with other sites. This site is atypical in that it is more exposed to waves and strong tidal currents. The physical disturbance to animals may favour species adapted to turbulent environments, such as the clingfish. Moreover, this increased exposure results in lower production of benthic invertebrates (Bird, 1990), which may in turn help explain the low numbers of fish at this site.

In summary then, the relative importance of seagrass and unvegetated habitat to the diversity and abundance of fishes appears to be strongly influenced by the physical characteristics of the particular site examined.

2.4.2 Commercial species

The larval stage of a number of commercial species settled directly to deeper, subtidal Heterozostera beds, including stranger, six-spined leatherjacket and rough leatherjacket. Juveniles of these species were rarely recorded in previous Victorian studies which concentrated on shallower seagrass habitat (Robertson, 1980).

Settlement of these species occurred over the spring-summer period, coinciding with maximum seagrass growth and production of seagrass-associated invertebrates (Bird, 1990; unpublished data). These species feed on seagrass-associated biota and may live their entire life in seagrass habitat. The rock flathead showed a pattern where small juveniles often occurred on unvegetated habitat but larger individuals were only collected from seagrass, where they feed on crustaceans and fishes (Klumpp and Nichols, 1983).

The unvegetated patches amongst Heterozostera habitat in Swan Bay were the major habitat of newly settled juveniles of King George whiting. Catches of older juveniles over unvegetated intertidal habitat at Queenscliff implies a change in habitat preference with size. Robertson (1977) detected a movement of newly settled juveniles from subtidal seagrass to intertidal unvegetated habitat with growth at Crib Point, Western Port, concluding that individuals change from seagrass to unvegetated habitat because of food preference. Robertson's results showing settlement to seagrass contradicts our results for Swan Bay, however, we will show later that habitat preference in Port Phillip Bay is similar to that at Crib Point, implying that habitat preference is flexible depending on the particular environment.

It seems unlikely that King George whiting would use seagrass habitat for protection from predators. They are a schooling rather than a cryptic species, and their coloration would appear more suited to camouflage against unvegetated habitat. Habitat utilisation may therefore be related to food preferences. Although benthic harpacticoids were dominant in the diet in terms of numbers, in terms of energy input the larger amphipods and mysids would have been at least of equal importance. Harpacticoids and amphipods are generally more abundant in seagrass, whilst mysids tend to congregate at the edge of seagrass beds. Because small juveniles of King George whiting feed in mid-water (G. Jenkins pers. obs.), it is possible that individuals can maintain themselves in unvegetated patches where they receive maximum protection from camouflage, while feeding on invertebrates washed out, or associated with the edges, of seagrass beds.

In other areas it may be necessary for individuals to move over the seagrass beds to obtain sufficient food. These hypotheses are explored further in later sections. It appears, however, that juvenile King George whiting are to some extent dependent on seagrass habitat, however this is more related to food than the traditionally postulated mechanism of protection from predators.

A number of important commercial species in the juvenile stage were collected in intertidal habitats. Yellow-eye mullet showed no habitat preference at the Queenscliff site. Juvenile yellow-eye mullet feed primarily on zooplankton (Robertson, 1980; Edgar, unpublished data); therefore a lack of distinct habitat preference should not be surprising. This result may explain why yellow-eye mullet was one of the few species for which catches increased over the period of seagrass loss in Westernport Bay. Apparent preference for unvegetated habitat at St Leonards was probably more related to the fact that the unvegetated habitat was adjacent to shore, and the seagrass habitat was slightly deeper.

Juveniles of the Western Australian salmon that were collected in October and November were probably spawned between February and May of the same year in Western Australia (Robertson, 1982). The apparent preference for unvegetated habitat at St Leonards by juvenile Australian Salmon may also be related to depth. Robertson (1982) also collected juveniles of this species over largely unvegetated intertidal habitat.

Juveniles of the greenback and long-snouted flounders also utilised intertidal, unvegetated habitat. The settlement of greenback flounder at Queenscliff was examined in more detail in an honours project (May and Jenkins, 1992; Appendix 1). The lack of juvenile flounder at St Leonards compared with Queenscliff is explained by the results of another honours project. This showed that prey for the benthic feeding juvenile flounder were much more abundant on intertidal unvegetated sites in Swan Bay compared with sites on the adjacent coast of Port Phillip Bay (Shaw and Jenkins, in press; Appendix 2). This resulted in significantly increased growth rates in Swan Bay which would eventually lead to a greater production of young fish (Jenkins, Shaw and Stewart, in review; Appendix 3). Although these species preferred unvegetated habitat, elevated organic content of sediments in Swan Bay was most likely due to the accumulation and breakdown of seagrass detritus in this relatively protected environment (Shaw and Jenkins, in press; Appendix 2). It therefore seems likely that although juveniles of these species prefer unvegetated habitats, they may still depend on the seagrass-detrital food chain to provide sufficient food supplies. The same wave

exposure and tidal currents which remove organic material from unvegetated sites along the adjacent coast of Port Phillip Bay may also affect the supply of larvae to these areas. The areas of highest exposure and currents also had the least recruits (Jenkins *et al.*, in review; Appendix 3). Larval supply is unlikely to have varied greatly between the two regions (see later section), suggesting that habitat selection and/or early post-settlement mortality may have caused the observed distribution.

Canoe Point was quite different from other sites in terms of species composition and abundance, apparently related to its greater estuarine influence. In terms of commercial species, newly settled juveniles of the luderick were only collected at this site, with an apparently strong preference for seagrass. *Zostera* in estuaries of New South Wales has previously been found to be an important juvenile habitat for this species (Middleton *et al.* 1984; Ferrell and Bell, 1992). Juvenile silver trevally were also only collected from this site and nearby Toora Channel. The sandy sprat was also only collected at this site. These results suggest that further sampling of seagrass in estuarine rather than marine conditions along the Victorian coast may be warranted.

The preference for seagrass by atherinids at the Queenscliff site may relate to the fact that the small mouthed hardyhead, *Atherinosoma microstoma*, dominated at this site, whilst at other sites the silverfish, *Lentatherina presbyteroides*, were more abundant. Robertson (1980) found that small mouthed hardyheads mainly fed on seagrass epifauna whilst silverfish fed mainly on plankton in the water column.

Fig. 2.1 Location of sampling sites in Swan Bay and the adjacent coast of Port Phillip Bay, Victoria, from which juvenile fish were collected. Insets: Location of Swan Bay in Port Phillip Bay and location of Port Phillip Bay on the Australian coast.

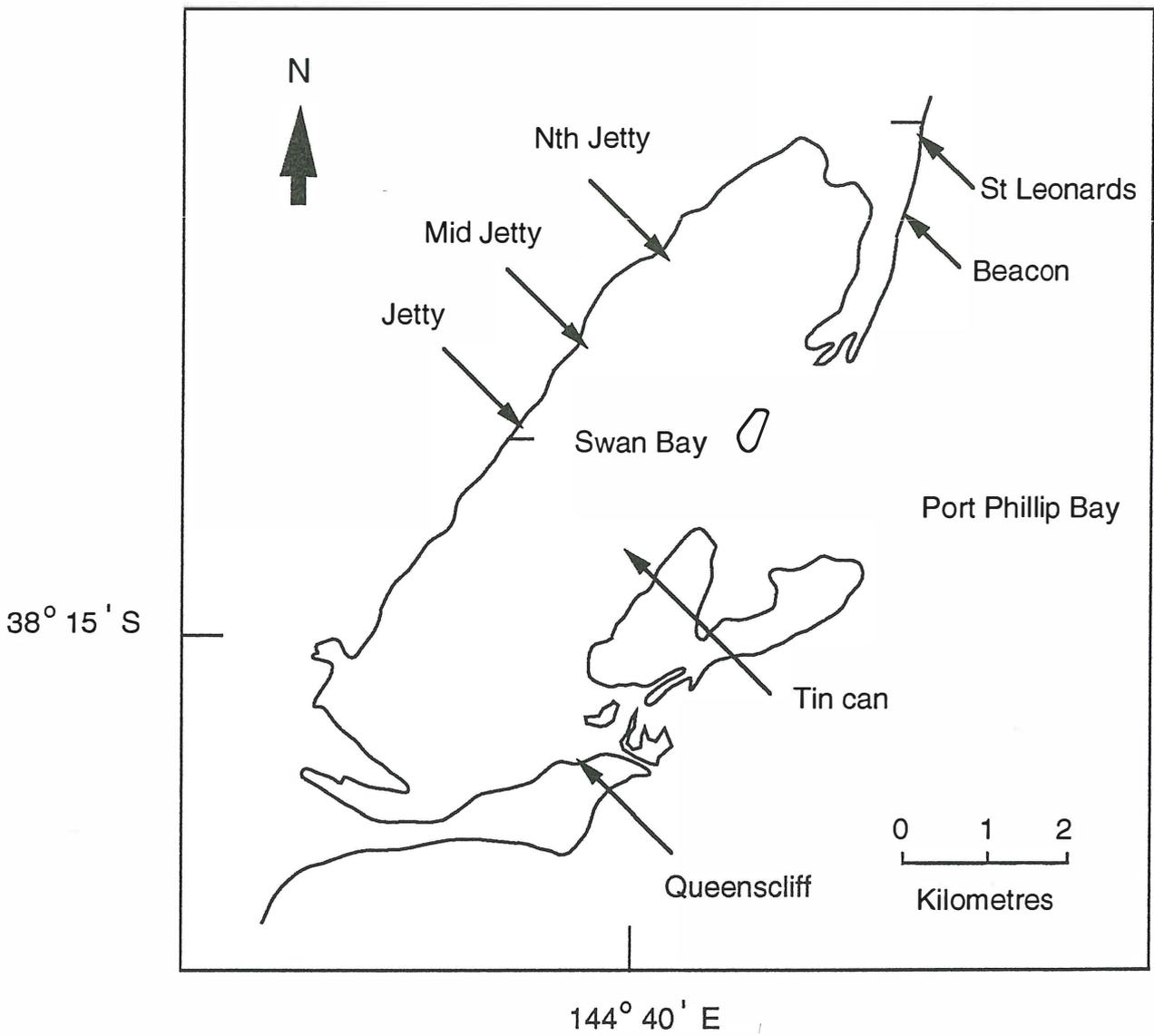
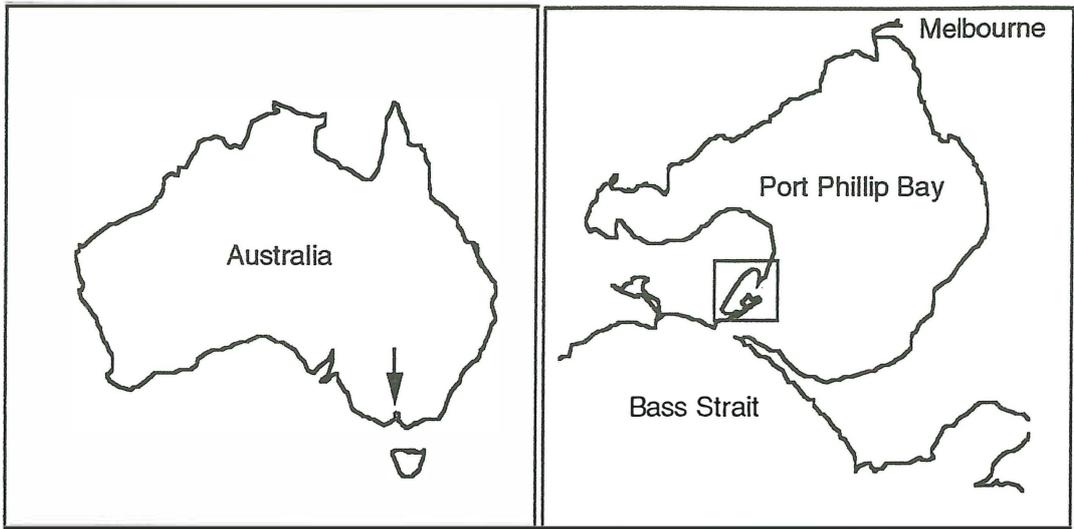


Fig. 2.2 Location of sampling sites in Corner Inlet from which juvenile fish were collected. Inset: Location of Corner Inlet on the Victorian coast.

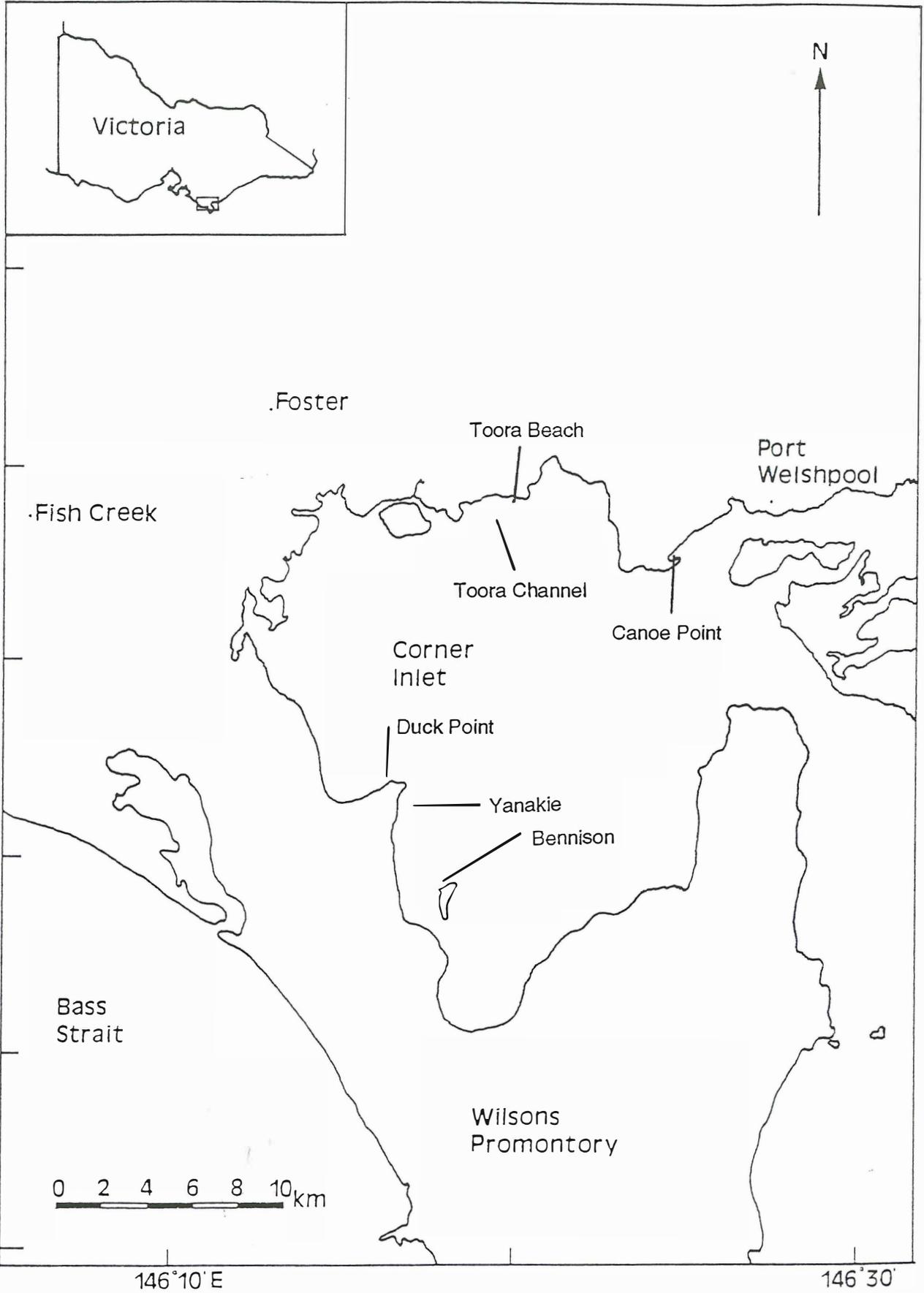


Fig. 2.3 Tree diagram showing similarities in the community composition of fishes at sites in Swan Bay and Corner Inlet. B - Unvegetated, SG - Seagrass.

Distances

0.000

2.000

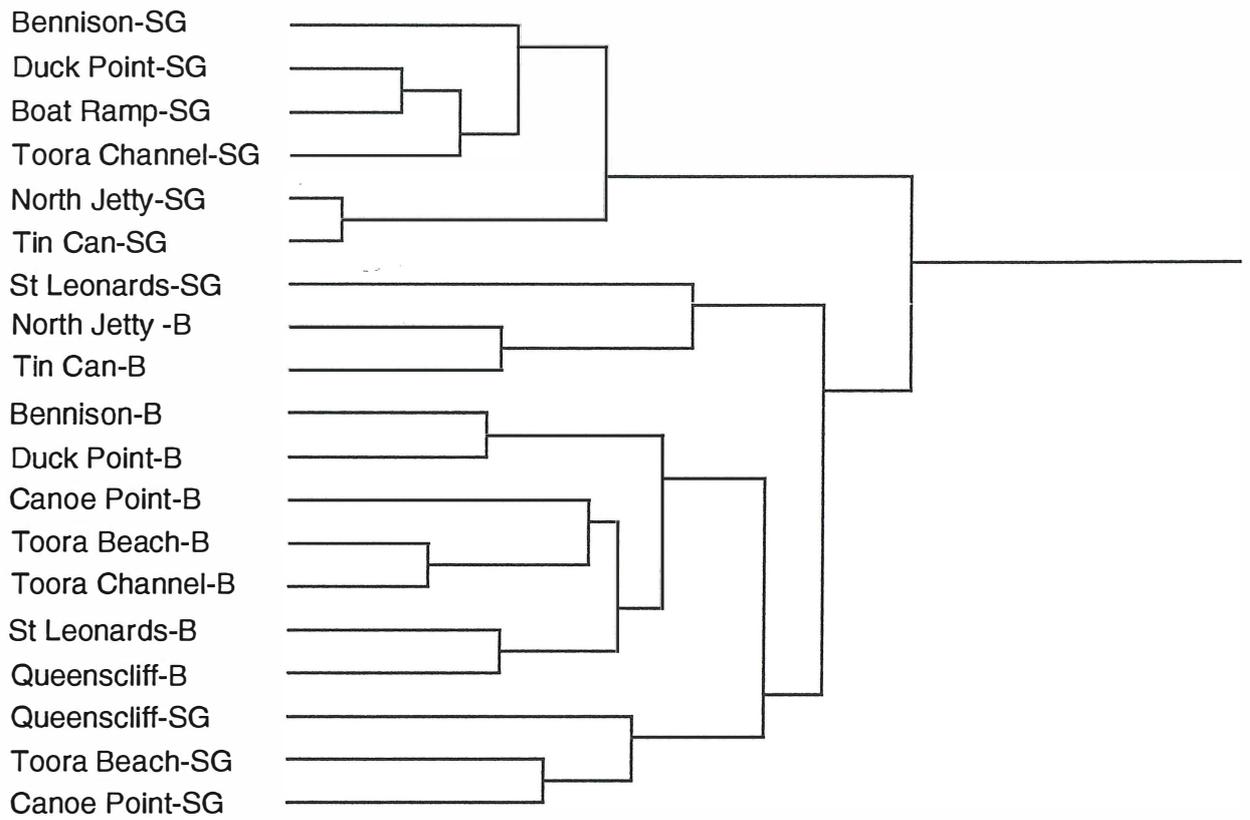


Fig. 2.4 Mean abundances of fishes collected on seagrassed and unvegetated habitats at sites in Swan Bay and Corner Inlet. Closed histograms, seagrass; open histograms, unvegetated. Error bars are standard error.

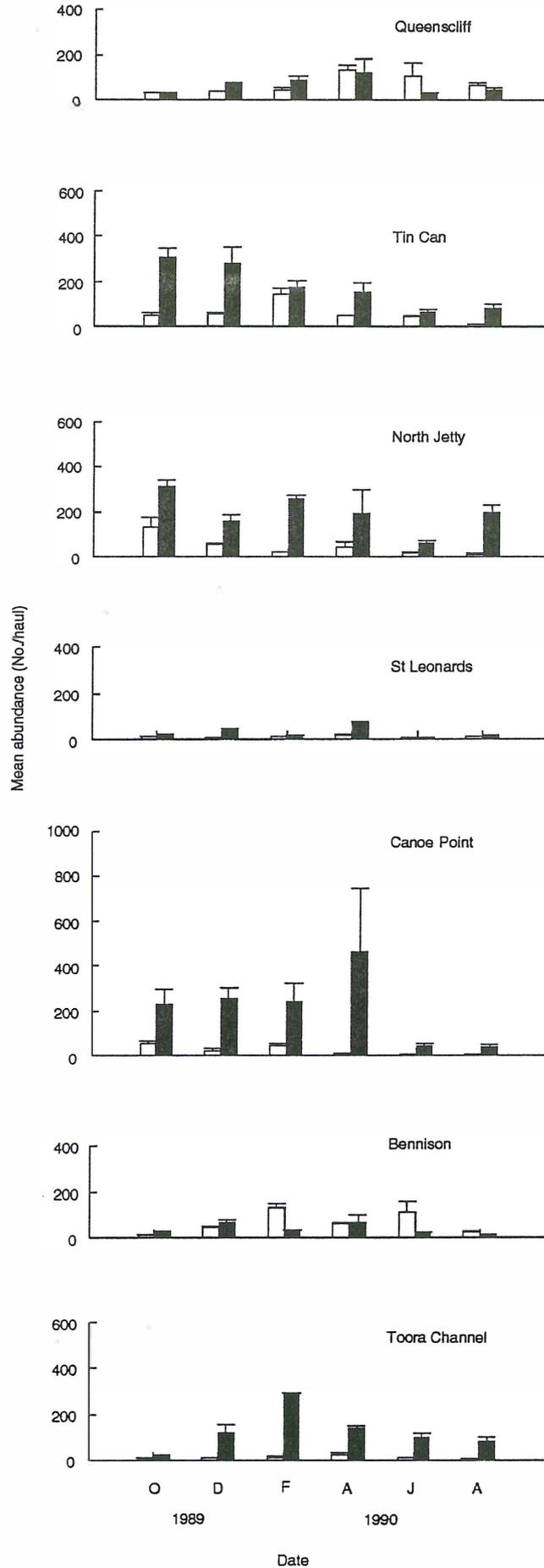


Fig. 2.5 Mean abundances of 'benthic' fishes collected on seagrassed and unvegetated habitats at sites in Swan Bay and Corner Inlet. Closed histograms, seagrass; open histograms, unvegetated. Error bars are standard error.

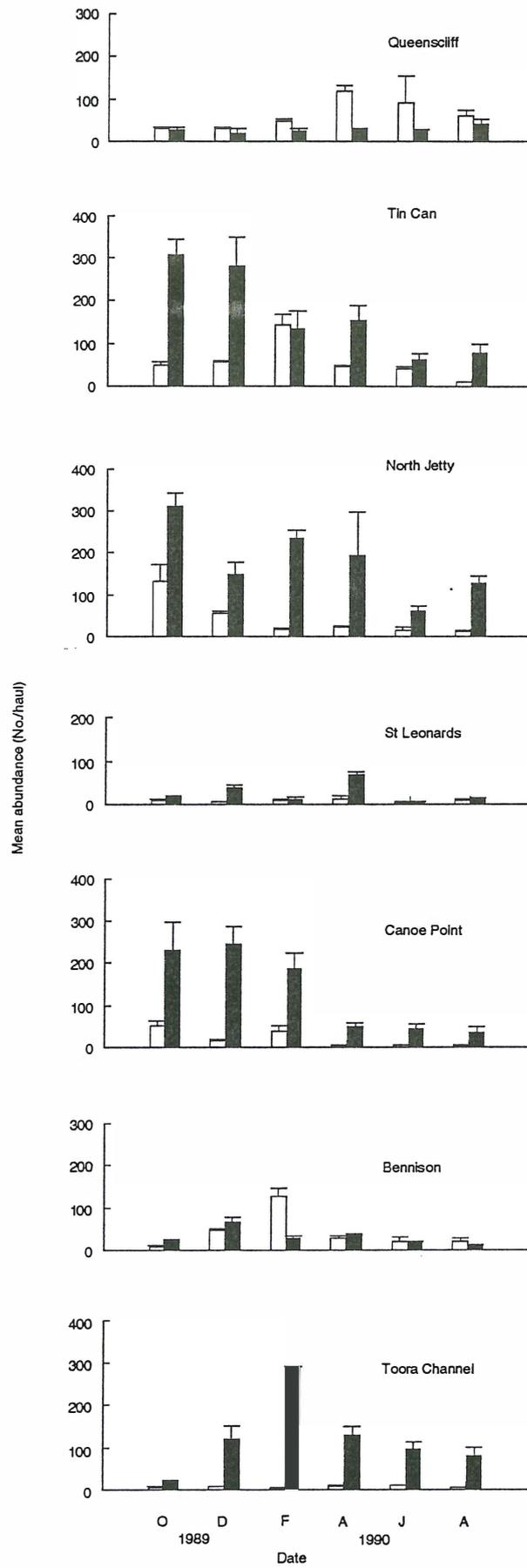


Fig. 2.6 Time-course of abundance of juvenile King George whiting in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.7 Size-frequency histograms for juvenile King George whiting in seine-net samples from Swan Bay. Open histograms, unvegetated habitat; closed histograms, seagrass habitat.

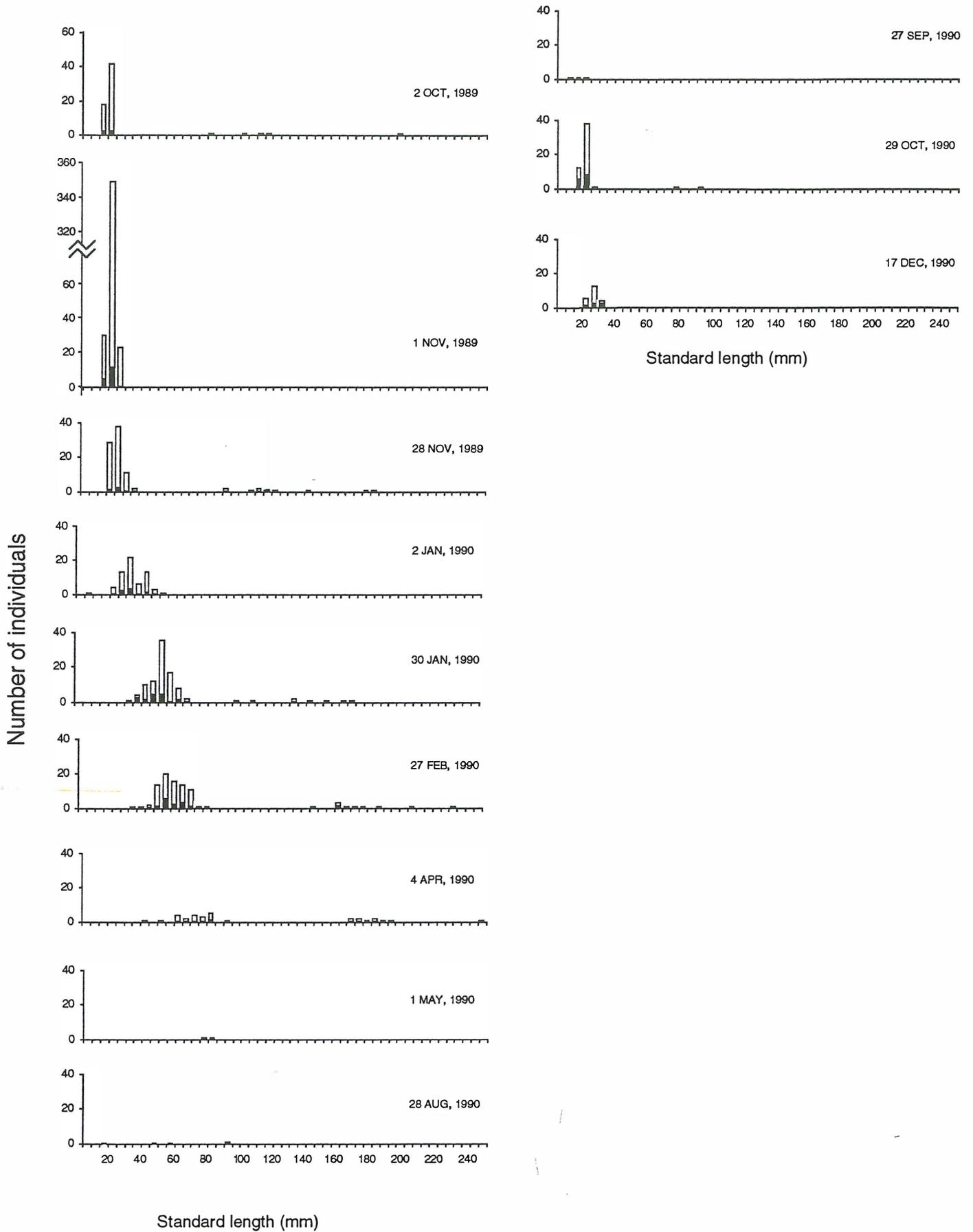


Fig. 2.8 Time-course of abundance of juvenile King George whiting in seine-net samples from Corner Inlet. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.9 Abundance of juvenile King George whiting in seagrassed and unvegetated habitat compared between day and night. A. North Jetty, October 1989. B. Mid Jetty, October and November, 1990. Open histograms, unvegetated habitat; closed histograms, seagrass habitat. Error bars are standard error.

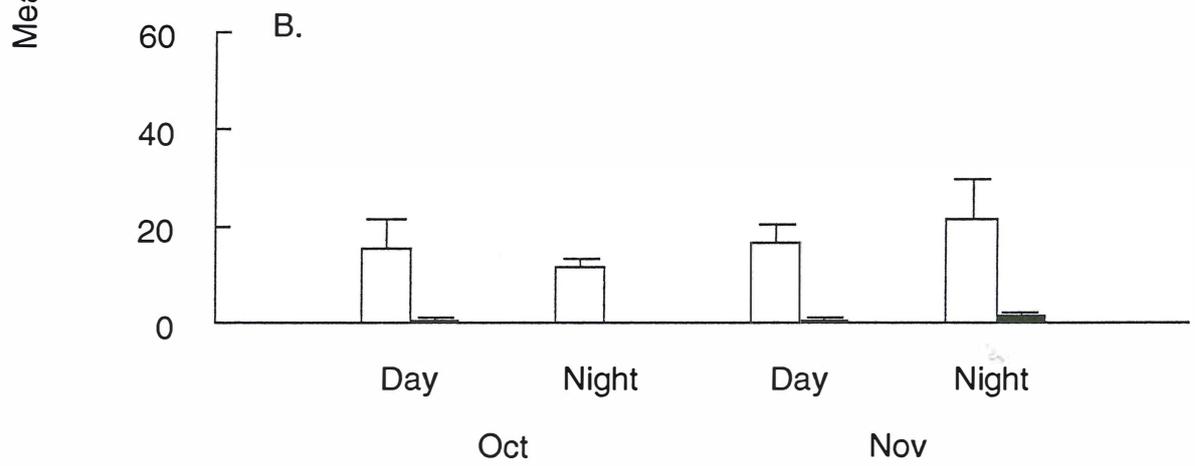
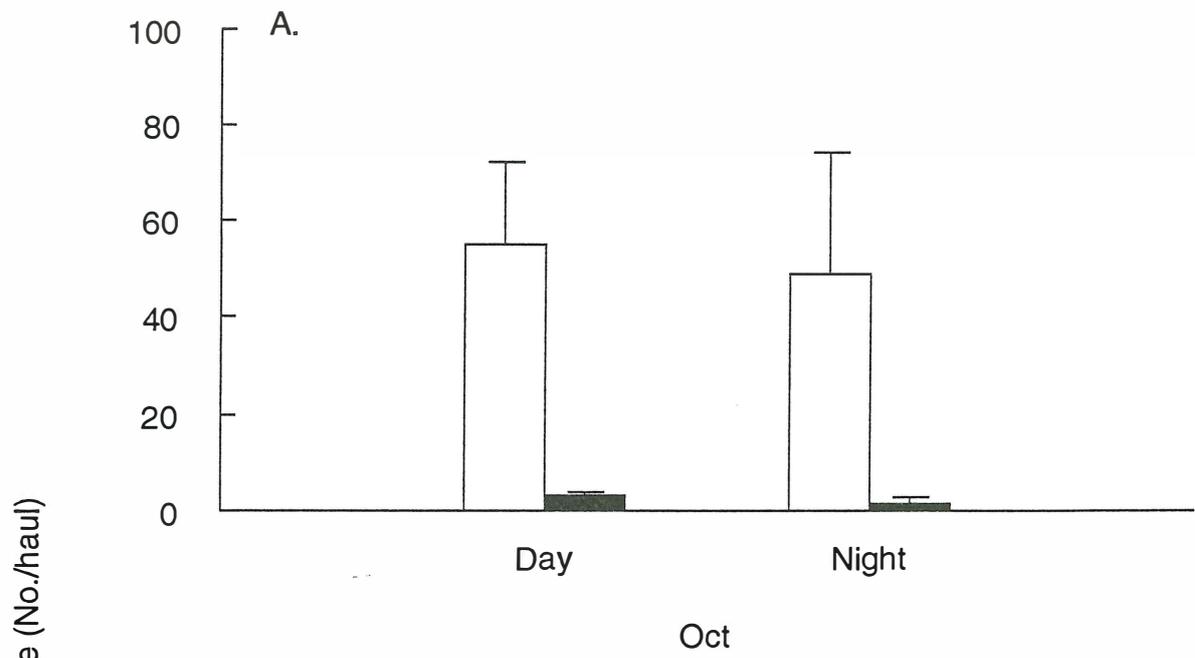


Fig. 2.10 Percentage composition of prey items in the diet of King George whiting post-larvae collected from Swan Bay, 1989.

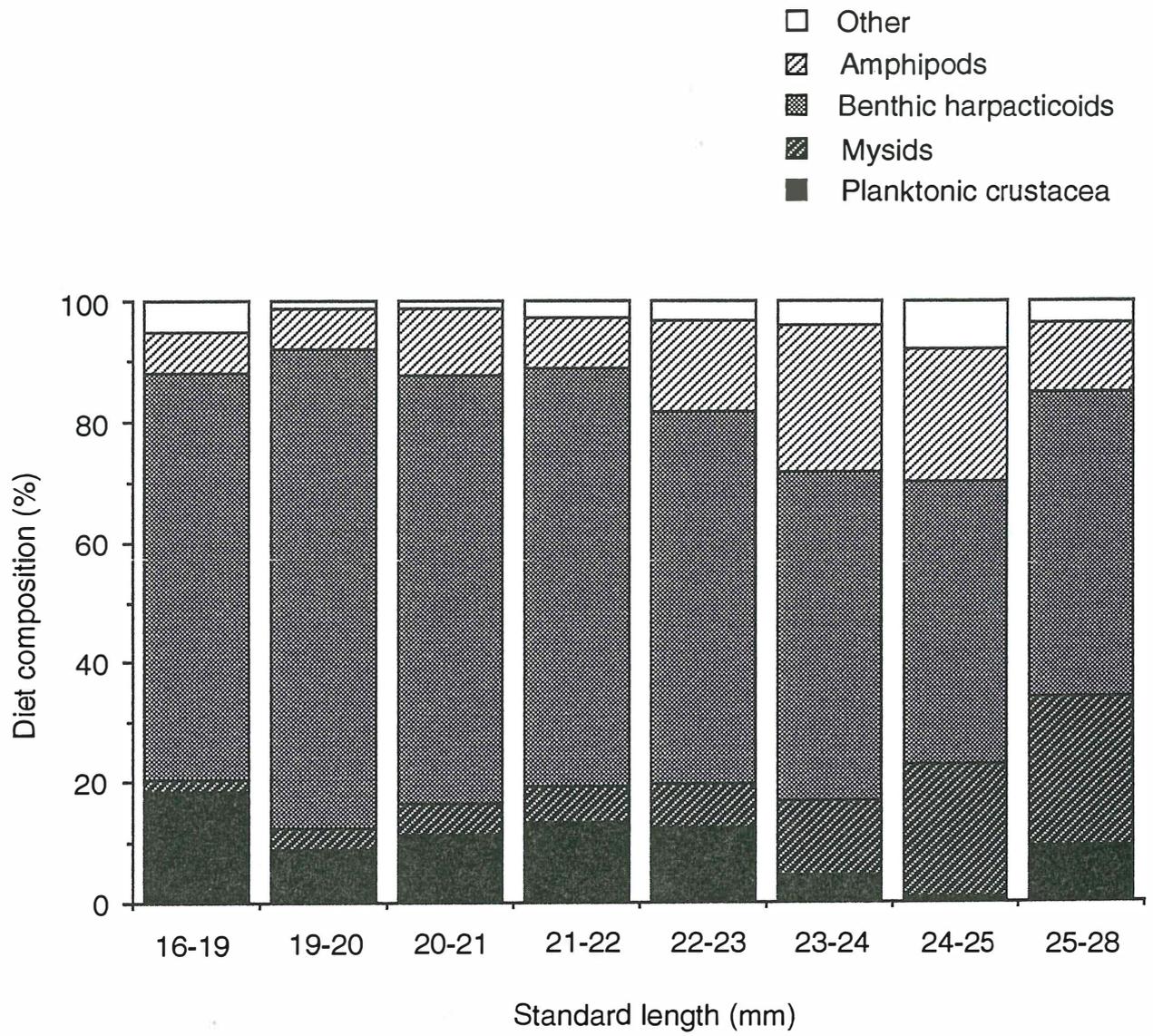


Fig. 2.11 Time-course of abundance of stranger in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.12 Time-course of abundance of stranger in seine-net samples from Corner Inlet. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.13 Size-frequency histograms for stranger in seine-net samples from Swan Bay. Open histograms, unvegetated habitat; closed histograms, seagrass habitat.

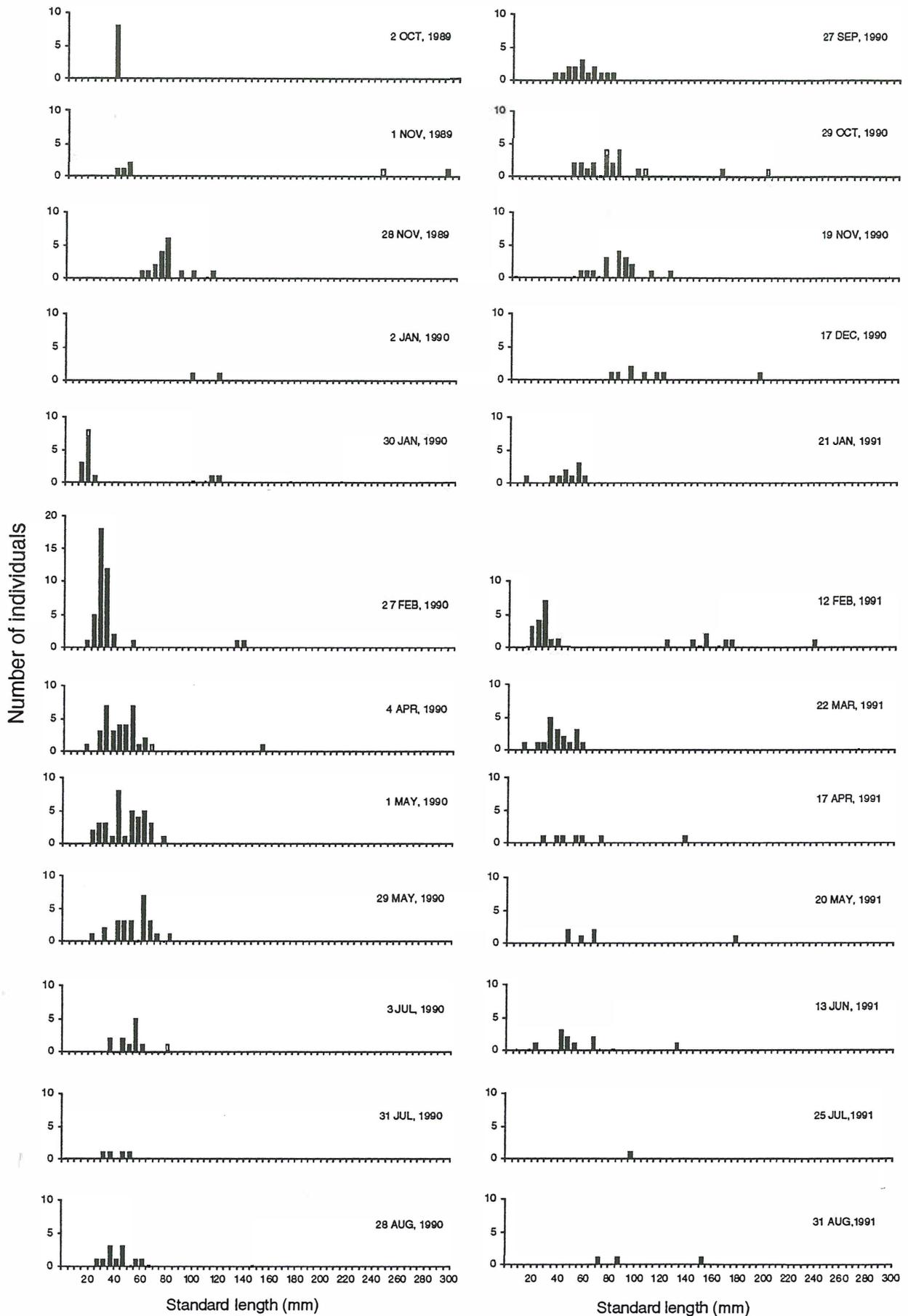


Fig. 2.14 Time-course of abundance of six-spine leatherjacket in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.15 Time-course of abundance of six-spine leatherjacket in seine-net samples from Corner Inlet. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.16 Size-frequency histograms for six-spine leatherjacket in seine-net samples from Swan Bay. Open histograms, unvegetated habitat; closed histograms, seagrass habitat.

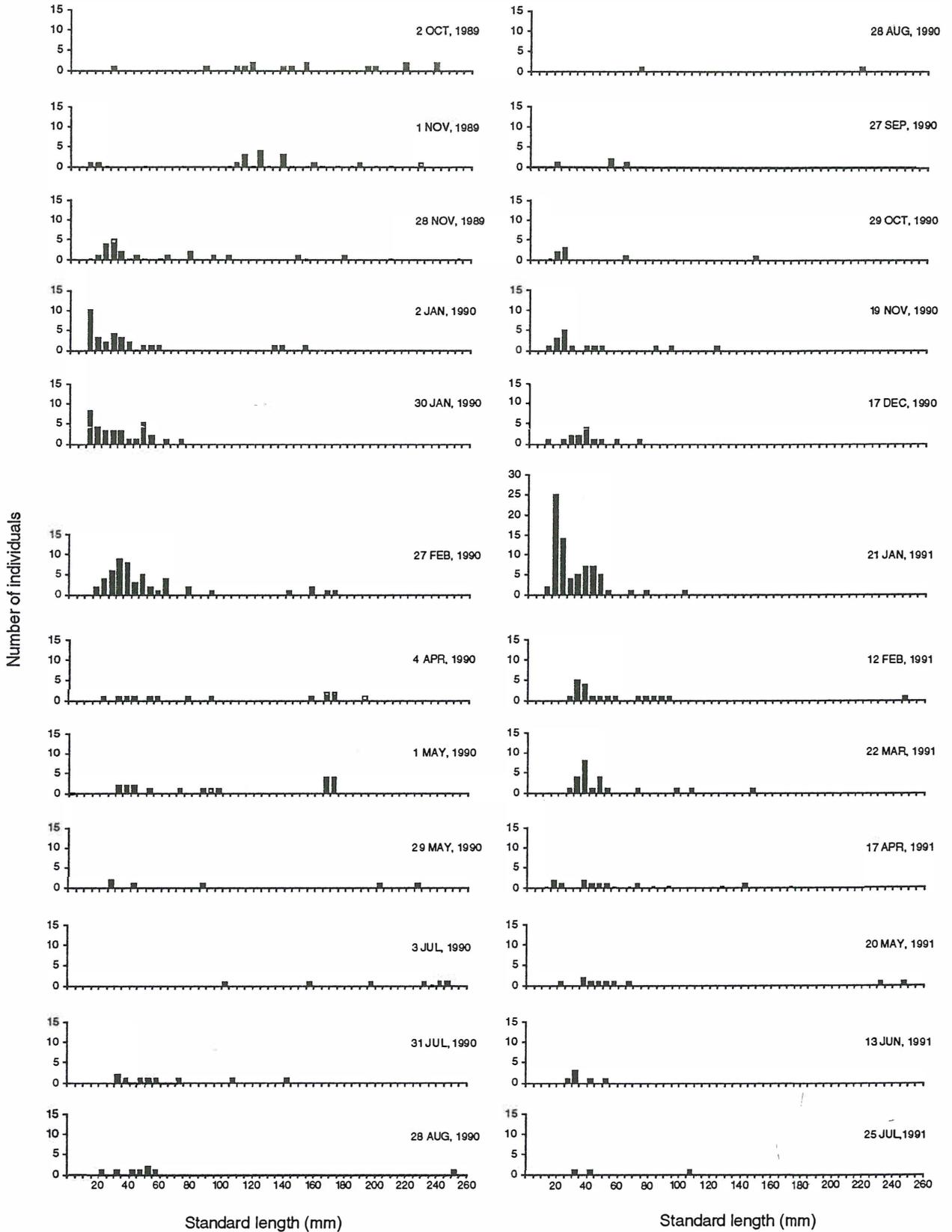


Fig. 2.17 Time-course of abundance of rough leatherjacket in seine-net samples from Corner Inlet. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.18 Size-frequency histograms for rough leatherjacket in seine-net samples from Corner Inlet. Open histograms, unvegetated habitat; closed histograms, seagrass habitat.

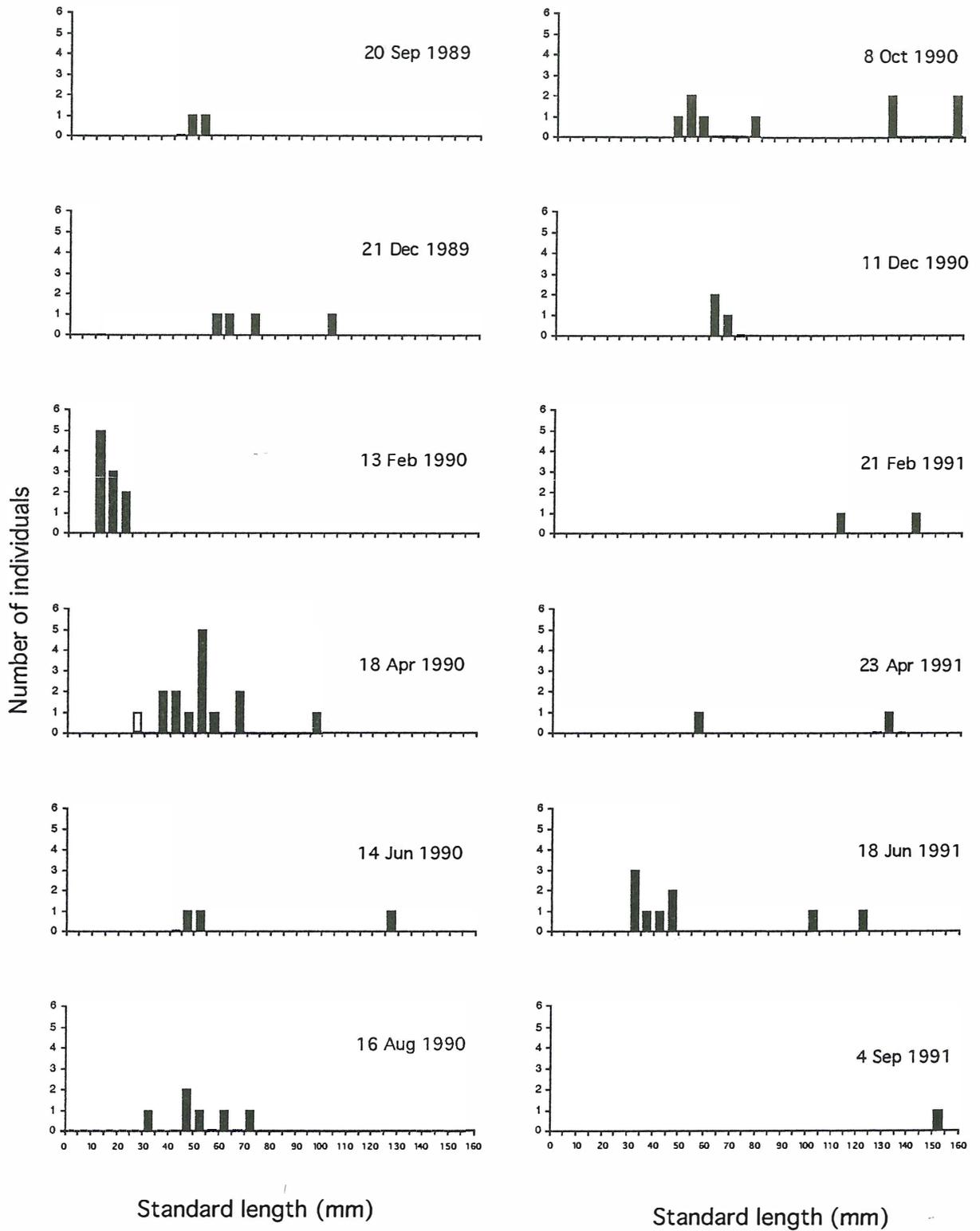


Fig. 2.19 Time-course of abundance of yellow-eye mullet in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

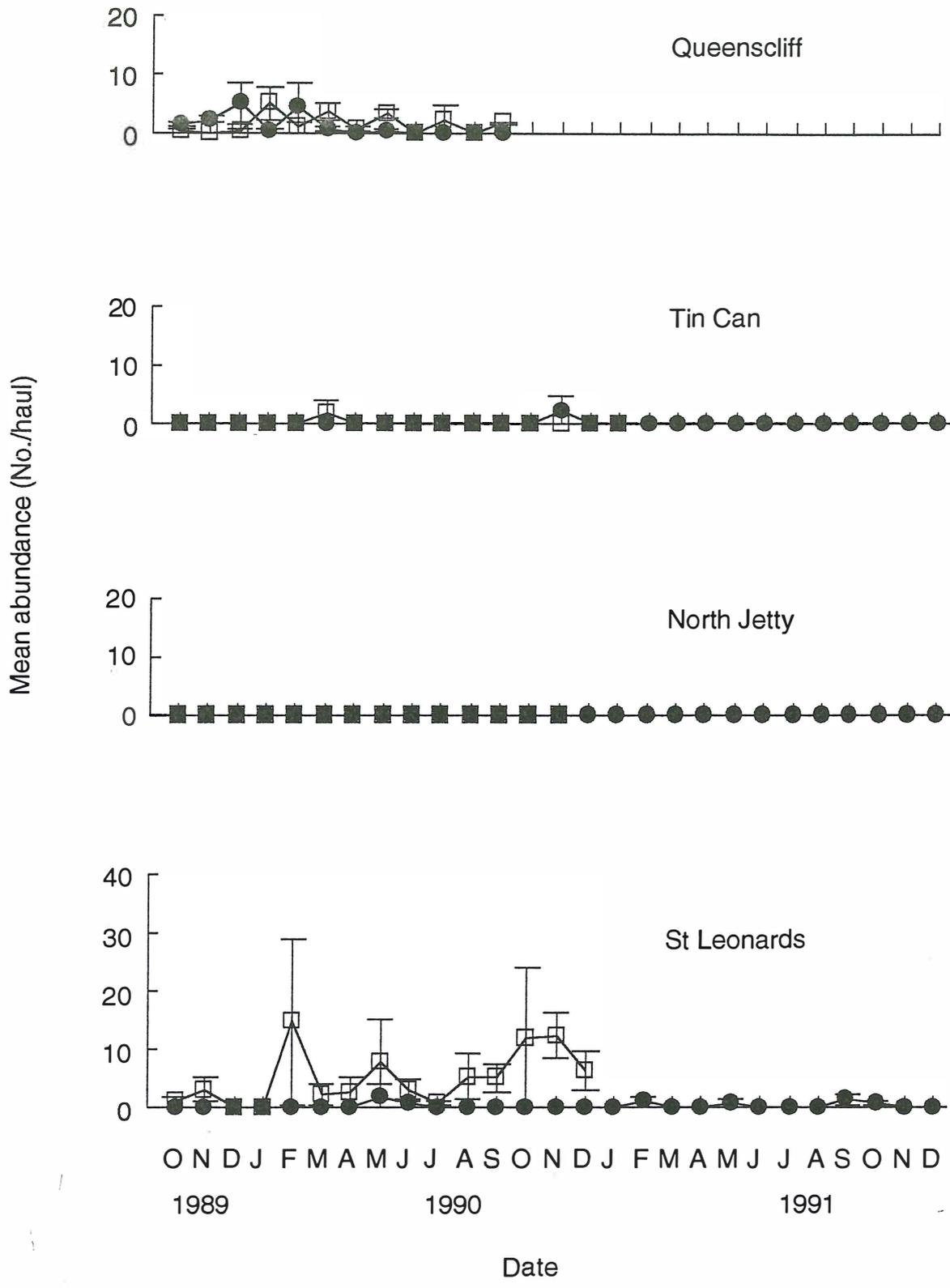


Fig. 2.20 Size-frequency histograms for yellow-eye mullet in seine-net samples from Swan Bay. Open histograms, unvegetated habitat; closed histograms, seagrass habitat.

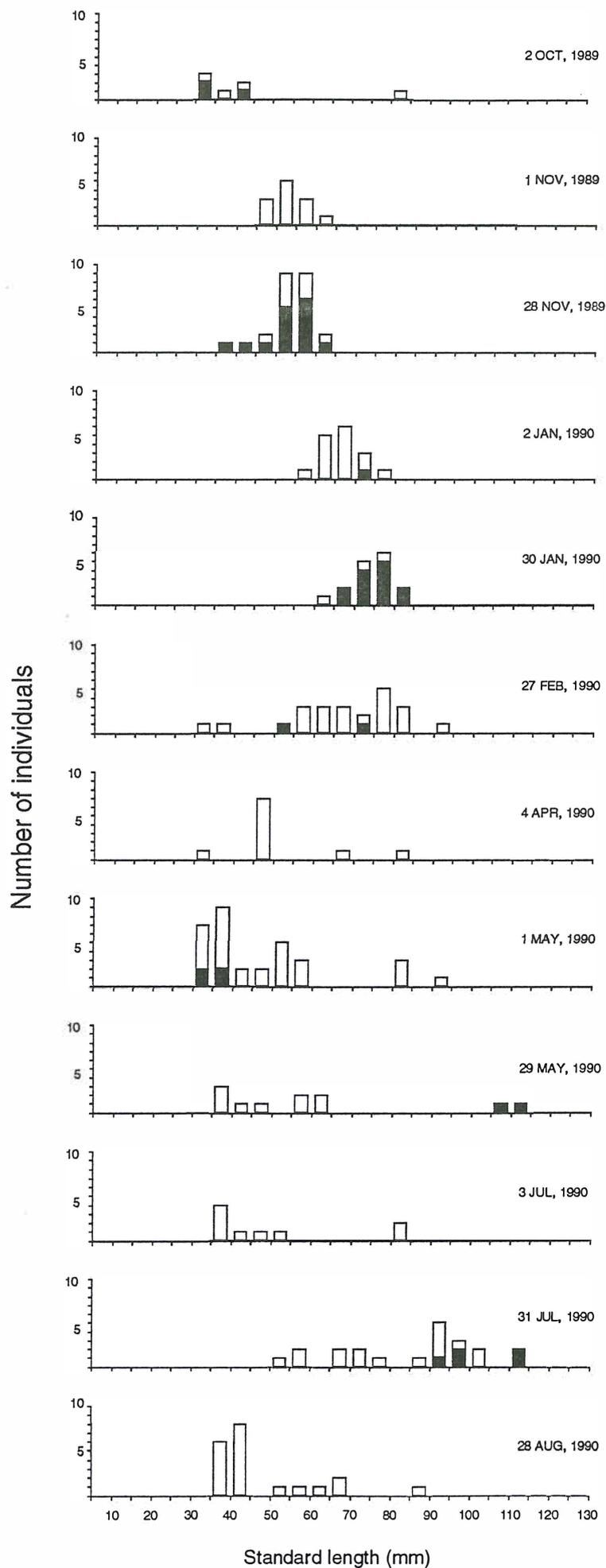


Fig. 2.21 Time-course of abundance of Western Australian salmon in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

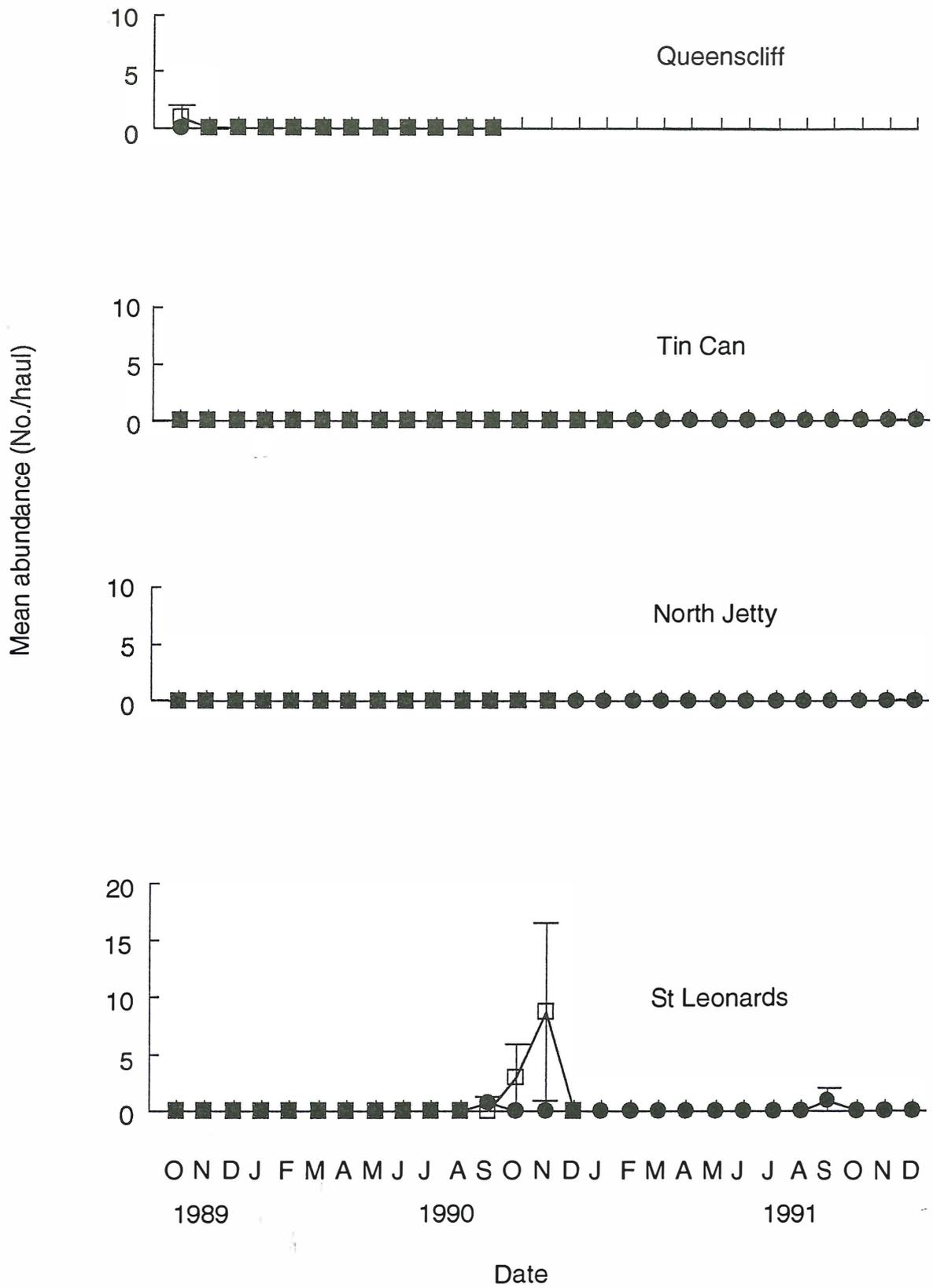


Fig. 2.22 Time-course of abundance of greenback flounder in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

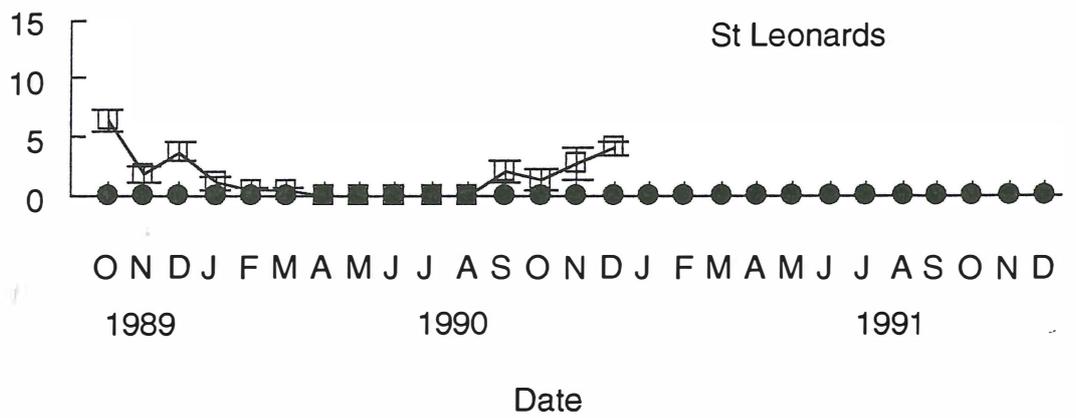
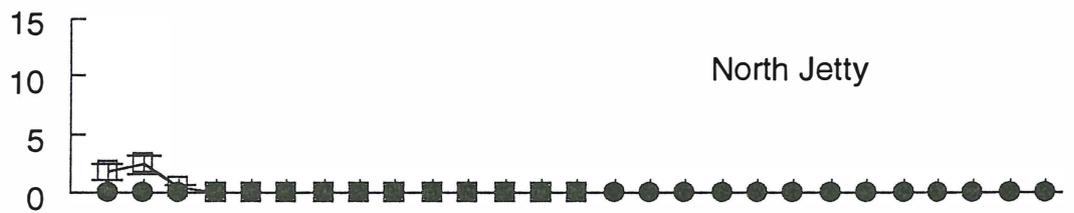
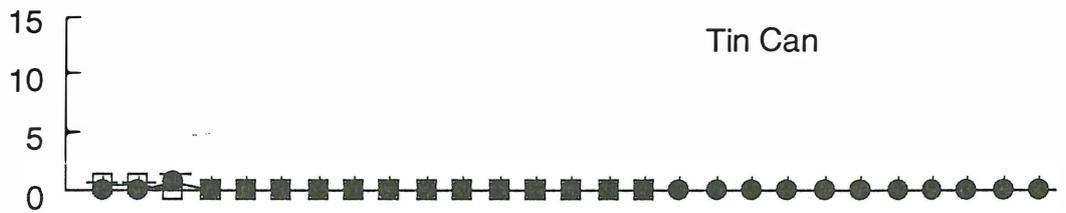
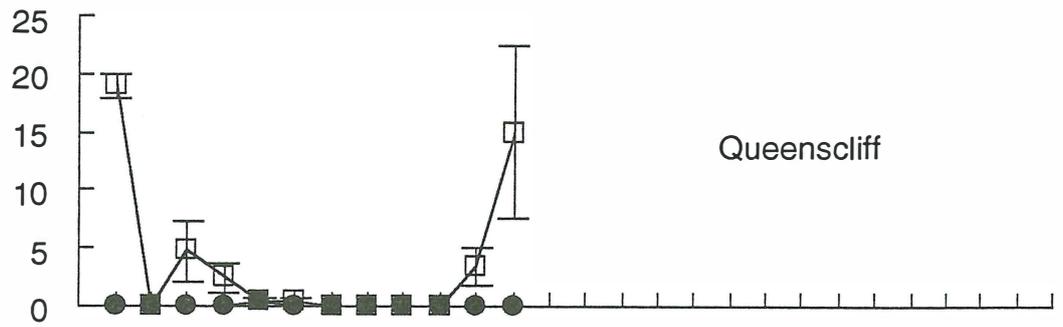


Fig. 2.23 Size-frequency histograms for greenback flounder in seine-net samples from Swan Bay. Open histograms, unvegetated habitat; closed histograms, seagrass habitat.

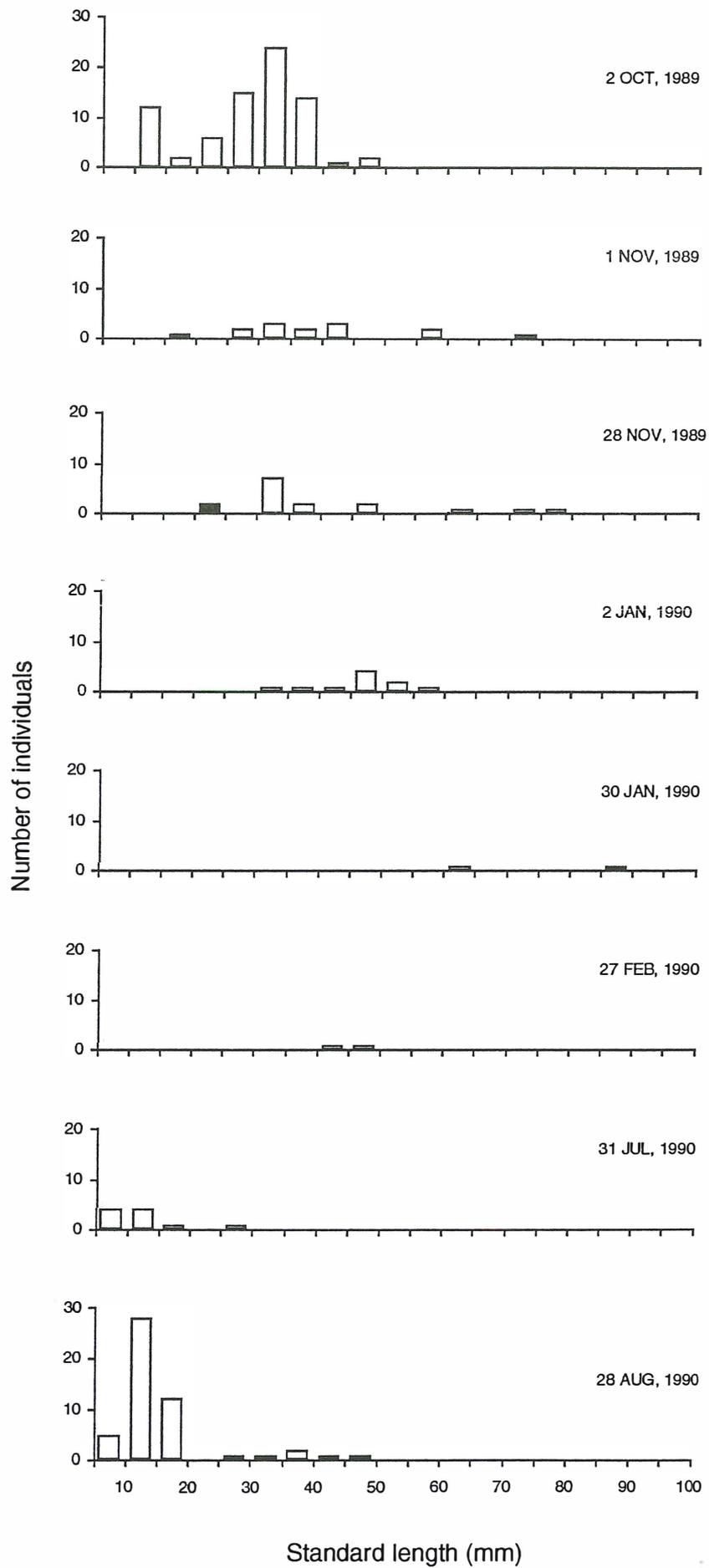


Fig. 2.24 Time-course of abundance of long-snouted flounder in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.25 Size-frequency histograms for long-snouted flounder in seine-net samples from Swan Bay. Open histograms, unvegetated habitat; closed histograms, seagrass habitat.

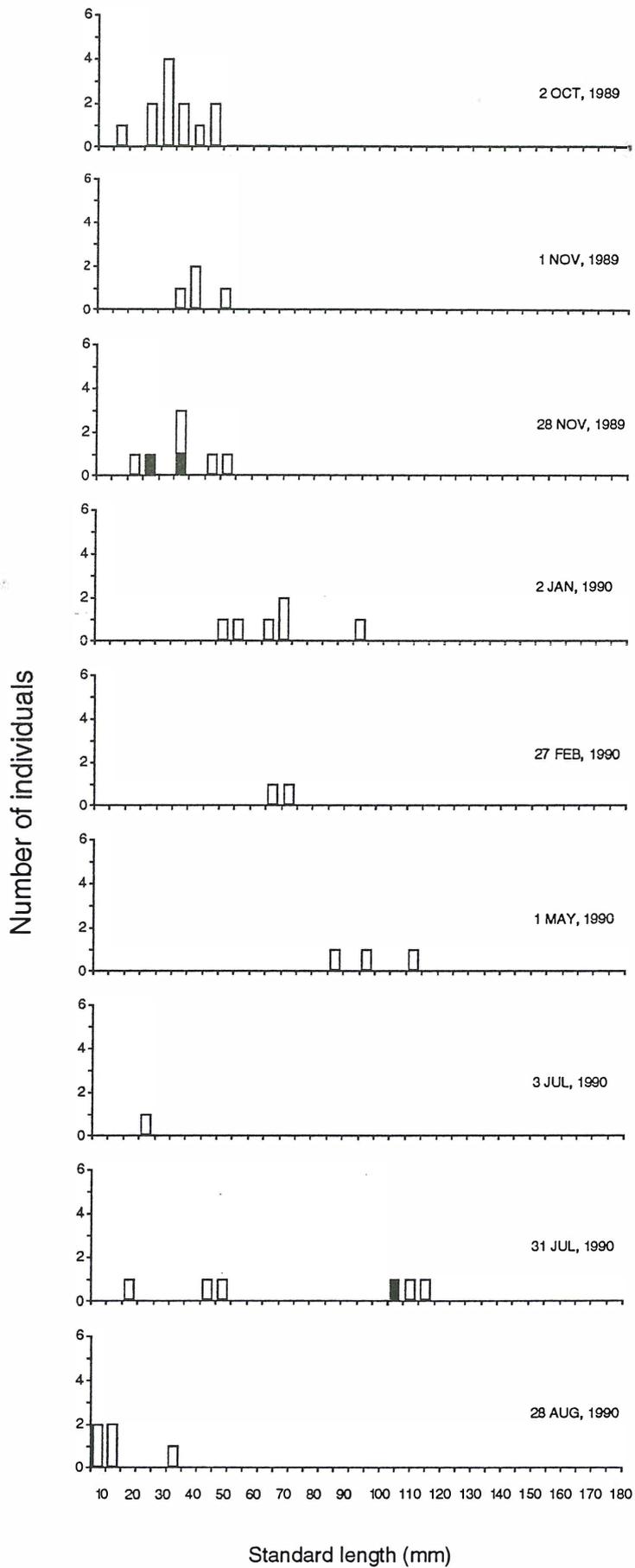


Fig. 2.26 Time-course of abundance of rock flathead in seine-net samples from Corner Inlet. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

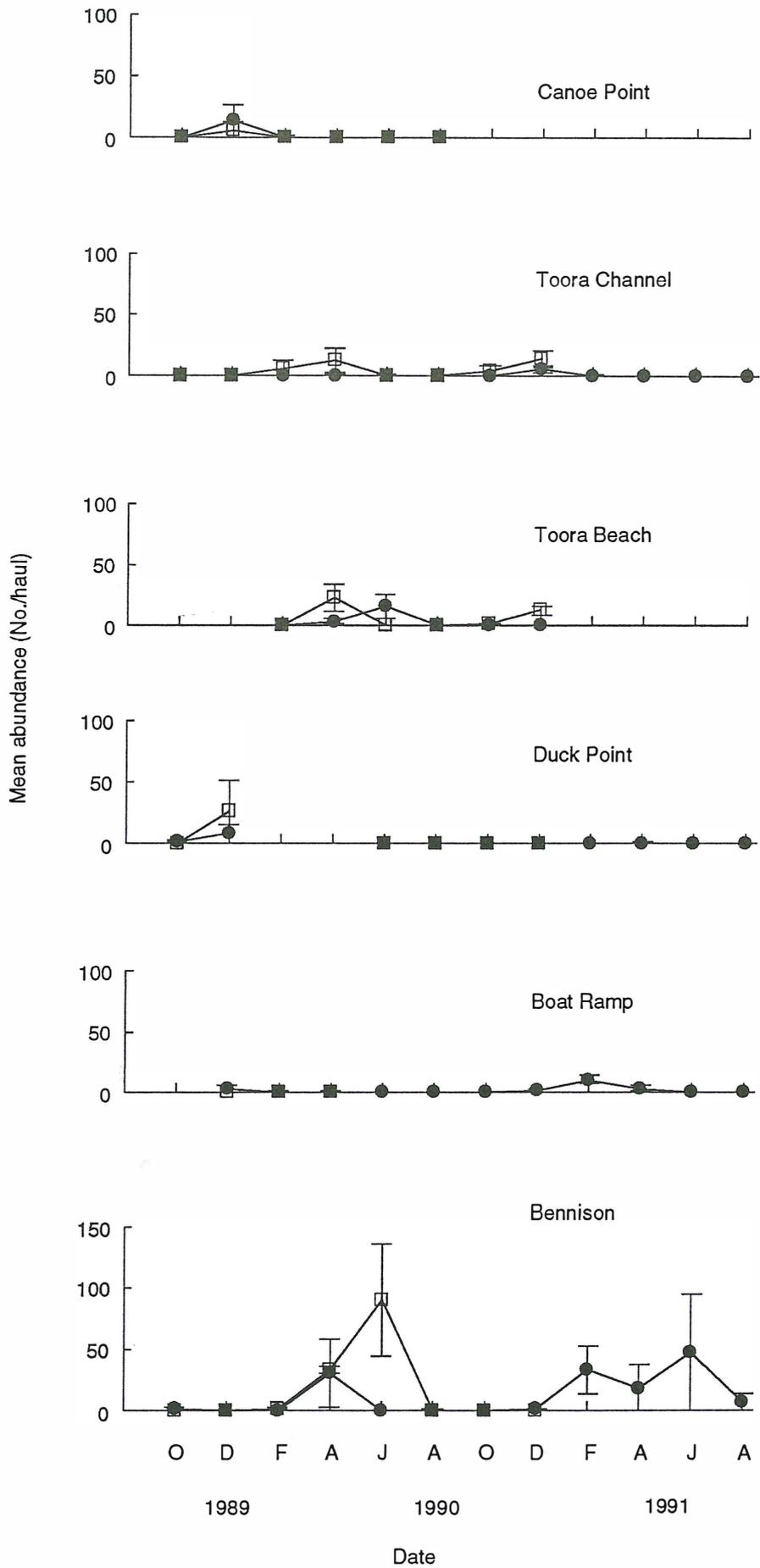
Fig. 2.27 Size-frequency histograms for rock flathead in seine-net samples from Corner Inlet. Open histograms, unvegetated habitat; closed histograms, seagrass habitat.

Fig. 2.28 Time-course of abundance of Castelnau's flathead in seine-net samples from Corner Inlet. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.29 Time-course of abundance of silver trevally in seine-net samples from Corner Inlet. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.30 Time-course of abundance of hardyheads in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 2.31 Time-course of abundance of hardyheads in seine-net samples from Corner Inlet. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.



3. The influence of larval supply on recruitment of commercial and other fishes to seagrass beds.

3.1 Introduction

Seagrass is thought to be an important habitat for fish, including many of commercial value (Bell and Pollard, 1989) and is extremely vulnerable to environmental degradation (Larkum *et al.*, 1989). The management and preservation of fishes associated with seagrass depends to some extent on the processes which structure fish communities in seagrass (Bell *et al.*, 1988). For example, if fish communities are mainly limited by the amount of cover (Heck and Orth, 1980) then beds with highest seagrass density and/or biomass should be preserved. However, if fish communities in seagrass beds are primarily limited by the availability of planktonic larvae (Bell *et al.*, 1988) then management depends on variability in recruitment. If some beds receive consistently higher recruitment than others, they should be preserved. If planktonic supply is unpredictable, then seagrass beds should be maintained in a range of sites, to maximise the chance of recruitment from stochastic input of larval patches.

Accepted theory holds that diversity and abundance of seagrass fishes is determined by amount of cover offered by seagrass as protection from predators (Heck and Orth, 1980). It follows that beds with higher biomass, density, complexity or other measure of cover will harbour a greater diversity and abundance of fishes (Orth *et al.*, 1984; Leber, 1985). Food was considered not to be a limiting factor, although this assumption has recently been called into question for macro-invertebrates in seagrass beds (Edgar, 1990).

Recently, an alternative hypothesis (Bell and Westoby, 1986) proposed that the abundance and diversity of fishes in a seagrass bed is a reflection of patchy larval input: larvae settle on the first seagrass bed they encounter, regardless of foliage characteristics. Juveniles then redistribute themselves to preferred habitats within the seagrass bed. It follows from this hypothesis that, at the scale of individual seagrass beds, the habitat complexity hypothesis will hold, however it will break down for disjunct beds at larger scales (i.e. tens of kilometres and greater) where community structure will be primarily determined by recruitment variability.

The development of theory on the structure of fish communities in seagrass beds has paralleled in many ways that relating to fish communities associated with coral reefs and rocky reef invertebrates (Doherty and Williams, 1988; Roughgarden *et al.*, 1988). In both cases the assumption was of an excess of pre-settlement larvae and that populations were limited by a resource required by adults, usually food or space. Recent intensive work has increasingly demonstrated the importance of varying larval supply in determining abundance and composition in these communities (Victor, 1986; Doherty and Williams, 1988; Roughgarden *et al.*, 1988). It follows that processes occurring in the planktonic larval phase have a major influence on the structure and dynamics of marine populations.

The relative influences of habitat quality, physical environment and larval supply on recruitment are difficult to separate in the natural situation because it is impossible to find multiple sites with identical habitat structure and physical environment. One aspect, habitat structure, can be controlled by using artificial seagrass. Previous work using artificial seagrass has given the clearest evidence yet that habitat complexity may not be the primary determinant of fish community structure in seagrass beds at spatial scales greater than individual beds. Post-settlement individuals, however, may be considerably more mobile than first suggested by Bell and Westoby (1986). Sogard (1989) found that older post-settlement fishes may migrate over relatively large areas of unvegetated bottom to colonise artificial seagrass. Such movements would modify patterns initially produced by variation in larval supply.

This section describes a sampling program aimed at evaluating the role of larval supply in determining the abundances of juvenile fishes in seagrass beds, particularly those of commercial value.

3.2 Methods

To test the generality of differences in subtidal Heterozostera communities within Swan Bay compared with St Leonards, seagrass sampling was carried out as described in the previous section, however, additional sites were sampled to investigate the effect of larval supply on population structure. An additional site, Beacon (Fig. 2.1), was sampled in Port Phillip Bay from October 1990 to February of 1991.

To investigate the importance of larval input in determining the observed patterns, plankton sampling was conducted in Swan Bay and offshore from St Leonards at approximately fortnightly intervals from late August 1990 to early January 1991. Three

replicate samples were collected at each site. The plankton net had a 0.64 m² opening square frame with a 4 m long, 1 mm mesh net attached. The net was deployed at the surface in approximately 1.5 m of water. The net was towed for approximately 10 minutes at a speed of about 1 m s⁻¹. A calibrated General Oceanics flowmeter was used to determine the volume filtered. Samples were preserved in 95% ethanol and larvae were sorted under a dissecting microscope and identified to the lowest taxonomic level possible.

The settlement of King George whiting was investigated at scales of 10's of kilometres by seining additional sites around the Bellarine Peninsula; Edwards Point (Fig. 2.1) Indented Head, Grassy Point, Point Richards, Clifton Springs and Seabrae (Fig. 3.1). Sampling was conducted in subtidal Heterozostera beds averaging 0.5 m below MLWS. Unvegetated habitats were also sampled at Grassy Point and Clifton Springs. Sampling was carried out in November and December 1990.

Seining was extended in 1991/1992 to encompass three seagrass beds at a scale of kilometres apart within five regions at a scale of 10's of kilometres apart. Sites were Point Henry, Seabrae and Grand Scenic in the Corio region; Hermsley, Bay Shore, and Clifton Springs in the Clifton Springs region; Point Richards, Calhoun and Grassy Point in the Port Arlington region; Salt Lake, St Leonards and Edwards Point in the St Leonards region (Fig. 3.1); and Tin Can, North Jetty and Swan Bay Jetty within Swan Bay (Fig. 2.1). Once again, subtidal Heterozostera beds averaging approximately 0.5 m below MLWS were sampled. Four replicates were sampled per site. Sampling was conducted in October, November, December 1991 and February 1992. Above ground biomass of seagrass was also sampled in December 1991. A 25 cm x 25 cm quadrat was used to take five replicate samples at each site. Samples were dried for 2 days at 60°C and weighed.

Plankton sampling was conducted as described for the previous year, however, in this case sampling was conducted at Grassy Point in addition to St Leonards and Swan Bay. Samples were collected approximately fortnightly from the beginning of September to the beginning of December.

Artificial seagrass units (ASUs) were constructed from 2m x 1m galvanised steel mesh. Meshes were 0.1 m x 0.1 m, providing 200 cross-points for attachment of artificial seagrass. Green polypropelene ribbon of 0.5 cm width was used to simulate Heterozostera. Eight, 90 cm lengths of ribbon were tied to each cross point, forming individual bunches with 16 leaves of approximately 40 cm length. Thus the total

density of leaves was 1600 m⁻². Meshes without leaves were used to control for possible habitat provided by the mesh.

The experiment was conducted at two locations, St Leonards and Grassy Point. Five replicate ASUs and mesh controls and areas of bare substrate were regularly interspersed providing three treatments for the habitat factor. The habitat treatments were sampled by encircling the ASUs, meshes, and equivalent areas of unvegetated substrate with a 10 m x 2 m seine net with 1 mm mesh. Pilot sampling using multiple hauls indicated that at least 80 % of the fishes in ASUs were collected in the first haul. All fishes collected were preserved in 95% ethanol.

Ontogenetic change in habitat preference of King George whiting juveniles was investigated between September 1991 and February 1992. Replicate seine net samples were taken in seagrass, Heterozostera, at North Jetty, Swan Bay Jetty and Tin Can (Fig. 2.1). In addition, subtidal unvegetated sites were sampled at Swan Bay Jetty and Tin Can, and intertidal sites with a mixture of unvegetated and sparse Zostera habitat at North Jetty and Swan Bay Jetty.

3.2.1 Data analysis

Assumptions of analysis of variance were examined using mean versus variance plots and the distribution of residuals. For nested analysis of variance of sites within bays, site was considered to be a random factor. Correlation between fish abundance and seagrass biomass was determined using the Spearman correlation coefficient. ASUs were analysed as a 2-factor ANOVA with site and habitat treatment considered as fixed factors. In all cases, transformation to $\log(x+1)$ greatly improved the homogeneity of the variances and the distribution of residuals. Significance of differences between individual means in ANOVAs were tested using Tukey's test for pairwise comparisons (Day and Quinn, 1989).

3.3 Results

3.3.1 Benthic Sampling

The total abundances in Swan Bay and Port Phillip Bay, with two sites in each bay sampled over spring - summer, were higher in Swan Bay sites on all dates except for extremely high abundances of post-larval hardyheads at St Leonards in January (Fig 3.2). Notwithstanding this, nested analysis of variance indicated significantly higher

abundances in Swan Bay (Table 3.1). Differences were much clearer when 'benthic' fishes were analysed only. Once again, Swan Bay had significantly higher abundances than Port Phillip Bay (Fig. 3.3), however in this case sites within bays were also shown to be significantly different, probably reflecting higher abundances at Tin Can relative to North Jetty (Table 3.1).

Table 3.1 Analysis of variance of fish abundances at two sites in Swan Bay and two sites on the adjacent coast of Port Phillip Bay over five sampling dates. ns not significant, * $P < 0.05$, ** $P < 0.001$

Source	df	Total		Benthic	
		MS	F	MS	F
Bay	1	39.64	25.90 *	75.42	31.55 *
Date	4	3.41	3.75 ns	0.85	2.15 ns
Site(bay)	2	1.53	3.03 ns	2.39	12.27 **
Bay * Date	4	2.55	2.81 ns	0.65	1.64 ns
Date * Site(bay)	8	0.91	1.80 ns	0.39	2.02 ns
Residual	40	0.51		0.19	

Higher abundances in Swan Bay were mainly due to high abundances of spotted pipefish (Fig. 3.4) and bridled leatherjackets (Fig 3.5), and species such as six-spined leatherjackets (Fig 2.14) and stranger (Fig 2.11) were also much more abundant in Swan Bay. Common weedfish, Heteroclinus perspicillatus occurred in only slightly lower numbers at St Leonards compared with Swan Bay (Fig 3.6) and Adelaide weedfish, Heteroclinus adelaide, occurred in similar numbers in each bay (Fig. 3.7).

Recruitment of King George whiting to the Tin Can site was lower than in the previous year. At the North Jetty site, Heterozostera had largely recolonised the previously unvegetated area. An additional site with unvegetated patches, Mid Jetty (Fig 2.1), was therefore sampled, and numbers of King George whiting post-larvae were similar to those recorded at North Jetty in the previous year. At both St Leonards and Beacon on the adjacent coast of Port Phillip Bay, numbers of King George whiting recruits were low, and individuals were only collected over seagrass habitat (Fig 3.8).

Recruitment of King George whiting around the Bellarine Peninsula showed a distinct pattern where the smallest settlers occurred in highest numbers at Grassy Point and Point Richards, with much low numbers of small post-larvae at St Leonards and

Beacon (Fig. 3.9). No post-larvae were collected at Indented Head. Significant abundances of King George whiting post-larvae were also collected at Clifton Springs and Point Henry, however, these individuals were larger than at other sites (Fig. 3.9). Adjacent unvegetated sites were also sampled at St Leonards and Clifton Springs, but no post-larvae were collected.

Total abundances of seagrass fishes over spring/summer of 1991/92 were highly variable (Fig. 3.10), with significant differences between sites within regions which varied with sampling date (Table 3.2). Overall there was no significant difference between regions (Table 3.2). 'Benthic' fishes also showed high variation between site and date (Fig 3.11), however, in this case there was a significant difference between regions (Table 3.2). The overall pattern for 'benthic' fishes changed over time. In September, before the main recruitment period commenced, abundances in all regions except Swan Bay were low (Fig. 3.11), the exception was high abundances of prickly toadfish, Contusus brevicaudus (20 - 40 mm SL), at Salt Lake. In October, abundances increased in the Port Arlington region and at Edwards Point (Fig. 3.11). Abundances tended to increase further at Port Arlington in November, as did abundances at Grand Scenic (Fig. 3.11). Patterns in October and November largely reflect the abundances of King George whiting post-larvae (Fig. 3.12). Significant numbers of King George whiting post-larvae were collected in the Port Arlington region in October and these levels were maintained in November, highest numbers were collected at Grassy Point (Fig. 3.12). High numbers at Edwards Point in October had declined dramatically by November, in contrast, abundance at Grand Scenic increased greatly from October to November (Fig. 3.12). In February, there were relatively high abundances of larvae of 'benthic' fishes at St Leonards and Edwards Point (Fig. 3.11), primarily due to recruitment of the Adelaide weedfish (Fig. 3.13). An increase in abundance at North Jetty was mainly the result of recruitment of bridled leatherjackets (3.14).

Table 3.2 Analysis of variance of fish abundances at sites nested in each of five regions around the Bellarine Peninsula over four sampling dates. ns not significant, * P<0.05, ** P<0.001

Source	df	Total		Benthic	
		MS	F	MS	F
Date	3	7.31	3.61 *	4.00	4.36 *
Region	4	7.72	3.38 ns	28.18	8.15 *
Site(region)	10	2.29	5.84 **	3.46	13.86 **
Date * Region	12	2.43	1.20 ns	1.82	1.99 ns
Date * Site(region)	30	2.02	5.17 **	0.92	3.67 **
Residual	180	0.39		0.25	

Seagrass biomass per unit area was significantly different amongst regions in December 1991 (Fig. 3.15; Table 3.3). Clifton Springs, Port Arlington and St Leonards were not significantly different from each other, biomass in Corio was significantly higher than Clifton but not significantly different from Port Arlington or St Leonards, Swan Bay had significantly higher seagrass biomass than any other region (Tukey's test, P<0.05). Overall, the total abundance of fish ($r=0.18$, P>0.5) and the total abundance of 'benthic' fishes ($r=0.33$, P>0.2) collected in November when compared amongst seagrass beds was not correlated with the biomass of seagrass per unit area of the bed (Fig 3.16).

Table 3.3 Analysis of variance of seagrass dry weight at sites nested in each of five regions around the Bellarine Peninsula sampled in December 1991. ns not significant, * P<0.05, ** P<0.001

Source	df	MS	F
Region	4	436.34	20.27**
Site(Region)	10	60.08	2.79*
Residual	60	21.52	

3.3.2 Plankton Sampling

Plankton samples over spring/summer of 1990/91 showed approximately 50 % higher numbers of fish larvae in Swan Bay compared with St Leonards (Table 3.4). This difference was mainly related to higher numbers of post-larval pipefish, *Stigmatopora* sp. (individuals could not be separated into species at this stage), and weedfish larvae (Table 3.4). Atherinid and bridled leatherjacket larvae had similar abundances at the two

Table 3.4 Mean number per 100 m⁻³ and percentage composition of fish larvae collected in plankton samples

Sampling period	September 1990 - January 1991				September 1991 - December 1991					
	St Leonards		Swan Bay		St Leonards		Swan Bay		Grassy Point	
Species	Mean	%	Mean	%	Mean	%	Mean	%	Mean	%
Stigmatopora sp.	2.21	35.40	4.27	46.72	0.64	23.33	1.60	40.15	0.54	26.30
Stigmatopora nigra	0.00	0.00	0.02	0.25	0.16	5.69	0.00	0.00	0.00	0.00
Stigmatopora argus	0.13	2.15	0.33	3.65	0.01	0.46	0.18	4.44	0.04	2.13
Hypselognathus rostratus	0.00	0.00	0.07	0.80	0.04	1.40	0.00	0.00	0.00	0.00
Vanacampus phillipi	0.01	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Clinidae	0.27	4.39	1.81	19.85	0.00	0.00	0.00	0.00	0.00	0.00
Heteroclinus perspicillatus	0.00	0.00	0.07	0.80	0.04	1.40	0.00	0.00	0.00	0.00
Gobiidae	0.40	6.46	0.11	1.23	0.12	4.44	0.01	0.34	0.00	0.00
Atherinidae	1.61	25.83	1.56	17.10	0.54	19.83	1.07	26.86	1.20	58.46
Rhombosolea tapirina	0.15	2.43	0.04	0.43	0.01	0.42	0.00	0.00	0.00	0.00
Ammotretis rostratus	0.01	0.16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Acantaluteres spilomelanurus	0.46	7.38	0.41	4.53	0.49	17.92	0.27	6.80	0.00	0.00
Meuschenia freycineti	0.26	4.20	0.09	1.03	0.07	2.56	0.30	7.50	0.08	3.92
Sillaginodes punctata	0.22	3.52	0.12	1.33	0.49	17.98	0.45	11.25	0.06	2.77
Hyporhamphus melanochir	0.08	1.28	0.07	0.75	0.00	0.00	0.00	0.00	0.00	0.00
Hippocampus breviceps	0.34	5.53	0.13	1.42	0.11	3.87	0.11	2.66	0.06	2.94
Gymnapistes marmoratus	0.06	0.93	0.00	0.00	0.02	0.83	0.00	0.00	0.00	0.00
Platycephalidae	0.01	0.15	0.01	0.11	0.00	0.00	0.00	0.00	0.08	3.65
Total	6.23		9.14		2.74		3.98		2.06	

sites and other species such as six-spined leatherjackets, King George whiting, and greenback flounder occurred in higher abundances off St Leonards than in Swan Bay (Table 3.4). Analysis of variance suggested that differences in total abundance and abundance of 'benthic' fishes between sites was dependent on the individual sampling date (Table 3.5), which is illustrated by Fig. 3.17. The pattern for King George whiting showed high variability between dates, with slightly higher abundances at St Leonards overall (Fig 3.19A).

Table 3.5 Analysis of variance of larval fish abundances in plankton samples collected in September 1990 - January 1991. ns not significant, * $P < 0.05$, ** $P < 0.001$

Source	df	Total		Benthic	
		MS	F	MS	F
Date	13	2.62	7.05 **	2.43	7.48 **
Site	1	2.55	1.04 ns	2.82	1.28 ns
Date * Site	13	2.45	6.58 **	2.20	6.78 **
Residual	56	0.37		0.32	

The highest average abundance of fish larvae in Spring 1991 occurred in Swan Bay. Abundances were approximately 50% higher than St Leonards and 100% higher than Grassy Point (Table 3.4). The difference between Swan Bay and the other sites (particularly St Leonards) was largely attributable to higher abundances of pipefish post-larvae (Table 3.4). Consistent with 1990, significant differences between the abundances of fish larvae at sites occurred, however, the relative differences varied with the date of sampling (Table 3.6, Fig. 3.18). As in 1990, pipefish and atherinid post-larvae were the dominant groups, King George whiting post-larvae were also relatively important in Swan Bay and St Leonards (Table 3.4, Fig 3.19B).

Table 3.6 Analysis of variance of larval fish abundances in plankton samples collected in September - December 1991. ns not significant, * $P < 0.05$, ** $P < 0.001$

Source	df	Total		Benthic	
		MS	F	MS	F
Date	5	1.45	4.39 *	1.10	3.62 *
Site	2	2.39	1.57 ns	3.01	3.81 ns
Date * Site	10	1.52	4.58 **	0.79	2.59 *
Residual	36	0.33		0.30	

3.3.3 Artificial seagrass

Results for total abundance of fishes showed a significant interaction between habitat type and site (Fig. 3.20, Table 3.10). This resulted from significantly higher abundances in ASUs relative to mesh and bare habitats at Grassy Point, but no significant difference among habitats at St Leonards (Tukey's test, $P < 0.05$). Abundances in ASUs at Grassy Point were significantly higher than those in ASUs at St Leonards (Tukey's test, $P < 0.05$). This difference was partly the result of migration of large numbers of pipefish to ASUs at Grassy Point (Fig 3.21). However, the result was also consistent for post-settlement King George whiting, which occurred in significantly higher numbers at Grassy Point compared with St Leonards, and in higher numbers in ASUs relative to other habitat treatments at Grassy Point (Fig. 3.22). This pattern was consistent with the pattern of recruitment of King George whiting in natural seagrass at the two sites in October (Fig. 3.12).

Table 3.7 Analysis of variance of total fish abundance in habitat treatments at St Leonards and Grassy Point. ns not significant, * $P < 0.05$, ** $P < 0.001$.

Source	df	MS	F
Site	1	8.54	49.85**
Treatment	2	1.94	11.32**
Site*treatment	2	1.21	7.06*
Residual	24	0.17	

3.3.4 Ontogenetic change in habitat preference of King George whiting

In September, very small post-larvae were mainly collected over seagrass habitat at North Jetty, in contrast with previous results for post-larvae of King George whiting in this bay. In October and November, small juveniles were mainly collected from subtidal unvegetated sites as in previous years. In February, most juvenile King George whiting were collected in intertidal habitats.

3.4 Discussion

In general, major differences in recruitment between sites could not be explained by larval supply. Species such as King George whiting, bridled leatherjacket and six-spined leatherjacket; which recruited in high abundances in Swan Bay and rarely at St

Leonards; were equally common in the plankton at both sites in 1991, and relative abundances of King George whiting post-larvae in the plankton were in direct contrast with abundances in the seagrass.

These results strongly suggest that many of the recruitment patterns observed were the result of passive physical factors or habitat selection. It is apparent that species such as King George whiting and leatherjackets cannot physically maintain themselves in seagrass beds or actively select against settling on seagrass beds in the St Leonards region. A common characteristic of species which do not settle at St Leonards is that they tend to inhabit the water column at or above the level of the seagrass (Jenkins pers. obs.). The relatively strong tidal currents and greater wave exposure may mitigate against species which do not inhabit the base of the seagrass stalks and therefore receive some protection from the currents and waves via the baffling effect of the seagrass canopy. Species which did settle at this site in reasonable numbers such as the Adelaide weedfish, wide bodied pipefish and the clingfish, *Parvicrepis* sp., tended to occur low in the seagrass canopy, and in the case of wide bodied pipefish and clingfish, were capable of attaching to seagrass to maintain position. Habitat preference is probably not this simple, for example, the Adelaide weedfish and the wide-bodied pipefish tended to occur at St Leonards, whilst their congeners, the common weedfish and the spotted pipefish, tended to be more common in sheltered habitats.

Other characteristics of the habitat may have also influenced selection. Habitat selection is apparently not related to the density of seagrass cover providing protection from predators, traditionally thought to be a major factor in determining fish numbers in seagrass beds (Heck and Orth, 1980; Orth *et al.*, 1984; Leber, 1985). Biomass of natural seagrass beds was not significantly different between the two sites, and in the case of King George whiting, the greater number of settlers at Grassy Point was consistent for artificial seagrass. Results from the artificial seagrass experiment also confirmed that this species prefers seagrass habitat in Port Phillip Bay.

A possible factor in habitat selection would be food supply. Sediment in seagrass beds in the St Leonards region has a lower organic content and correspondingly lower production of invertebrates relative to Swan Bay (Bird, 1990). This is most likely a result of wave action and currents suspending and removing detritus from the bed. Differences in production were mainly attributable to higher numbers of relatively large invertebrates in Swan Bay. The abundances (but not necessarily the types) of small prey, however, appeared to be similar in the two areas. The relative number of prey organisms in the water column which would be available to species such as King

George whiting in sheltered and exposed sites is unknown and requires further research.

A further factor not addressed in this study which could explain the observed distribution would be a higher predation rate on larvae living above the seagrass relative to other sites. There was no evidence for increased numbers of water column predators in routine seine netting at these sites, and furthermore numbers of post-larvae collected in the water column with a plankton net were relatively high, suggesting predation on these individuals was not severe.

Species which showed apparent habitat selection may have the ability to prolong larval life until a suitable habitat was found. King George whiting larvae have a long and extremely variable larval life, ranging from 90 to 150 d for post-larvae entering Swan Bay (Jenkins and May, in press; Appendix 4). Larvae apparently develop for 40 to 60 days, beyond which they change to a slow growth, competent phase, and settlement may be delayed for up to 100 d until a suitable habitat is found. Strong patterns of habitat selection in this species should therefore not be surprising. Some species of leatherjackets are also known to have an extended pelagic phase, often associated with drifting macrophytes (Kingsford and Choat, 1985). Although post-larvae of bridled and six-spined leatherjackets tended to settle at a consistent size of 10 to 12 mm, some plasticity in larval life would not be surprising.

There was evidence for the influence of larval supply on recruitment levels within preferred habitats. For example, higher numbers of pipefish, *Stigmatopora* sp. larvae in Swan Bay corresponded to very high numbers of recruits in this area. Moreover, high numbers of presettlement bridled leatherjackets in 1990 corresponded to an increased recruitment of this species to Swan Bay relative to the previous year, when most other species showed a reduced level of recruitment relative to the previous year.

Settlement patterns of King George whiting may result from a combination of habitat selection and passive patterns of physical transport. Recruitment of small post-larvae tended to be greatest in the Port Arlington region. Small post-larvae occurred in low numbers in the St Leonards region except at Edwards Point in October 1991, however, these larvae apparently did not remain in the area, or post-settlement mortality was very high, because abundances were extremely low in November. The size of King George whiting post-larvae tended to increase at sites further into the Geelong arm suggesting that post-larvae which settled in the Port Arlington area tend to migrate further into the bay after settlement. King George whiting are apparently carried into Swan Bay by tidal

currents from Bass Strait (Jenkins and Black, unpublished ms; Appendix 5). These tidal currents tend to dissipate in the Port Arlington region. It therefore seems possible that the limit of physical transport of larvae is in the Port Arlington region, precluding settlement in suitable, sheltered habitat further into the bay. As post-settlement larvae grow larger and more mobile they are able to migrate into the bay and utilise suitable habitats. Older juveniles apparently move from subtidal habitats to intertidal habitats, which is consistent with results of Robertson (1977), although Robertson attributed differences more to habitat than depth. We therefore hypothesise that larvae are transported into Port Phillip Bay by tidal currents and are subsequently unable to physically maintain themselves or actively select against habitats until the currents dissipate. Once post-larvae begin to feed and grow in the seagrass environment they are able to move deeper into the bay to suitable habitats.

4. General discussion

4.1 Importance of seagrass habitat to Fisheries

A number of commercial species appear to utilise seagrass habitat directly for shelter and food, and, as such, population fluctuations may be expected to follow fluctuations in the amount and quality of seagrass habitat. These species include stranger, rock flathead, and six-spined leatherjackets. These species do not utilise seagrass habitat as a nursery area in the traditional sense of providing shelter for juveniles only, with older individuals migrating to other habitats. There was limited evidence that *Zostera* habitat in estuarine conditions may act as a nursery in the traditional sense for luderick, as occurs in NSW estuaries. In addition to direct importance of seagrass to a number of commercial species, seagrass also provides an important habitat for prey species of pelagic commercial fishes.

Heterozostera habitat does provide a nursery habitat for King George whiting, but not in the traditional sense of providing shelter from predators, rather in the enhanced feeding conditions it apparently provides small juveniles. After a few months, whiting migrate to shallower water, moving over intertidal flats to feed. Seagrass may still influence growth of juveniles at this stage if accumulated detritus enhances food production.

Seagrass can provide enhanced feeding conditions for benthic feeding juveniles of commercial fish which do not occur in seagrass habitat. Retention of macrophyte (seagrass and algal) detritus in Swan Bay results in increased organic content of

sediments and higher production of small invertebrates. In the case of juvenile flounder this results in greatly enhanced feeding and growth rates, which would in turn lead to higher production of young fish.

Juveniles of two species, yellow-eye mullet and western Australian salmon, were previously thought to be dependent on seagrass habitat. However, our study indicates that these species tend to inhabit the shallow foreshore margin, irrespective of benthic habitat. This should not be surprising for juvenile yellow-eye mullet, which live in the water column and feed on zooplankton, and would explain the lack of correlation between catches of this species and seagrass loss.

All seagrass beds are not equal in their value to young fishes. Traditionally, the amount of cover provided by a seagrass bed was thought to be of critical importance. However, our project shows that the relationship between the position of seagrass beds and hydrodynamic patterns is of critical importance. For example, seagrass beds in the Port Arlington region of Port Phillip Bay are small and leaf cover is relatively sparse. Nevertheless, this area is a major site of settlement for King George whiting post-larvae, and would be critical in providing food when larvae transfer from planktonic to benthic food. Post-larvae do not settle in seagrass beds exposed to relatively high currents, or beds further into the bay beyond the influence of tidal currents, even if the characteristics of the beds themselves are of suitable quality in terms of cover, as demonstrated by artificial seagrass experiments. It is likely that hydrodynamic patterns in bays and estuaries and along coasts may strongly influence the importance of individual seagrass beds to commercial fishes. Worthington *et al.* (1992) have also found that certain seagrass beds accumulate greater numbers of juvenile fishes consistently, independent of habitat structure. To some extent the importance of beds may be predictable from hydrodynamic modelling.

The high variability of recruitment of King George whiting to the fishery may reflect the remote origin of larvae, and the consequent dependence of larval supply on variation in coastal hydrodynamics. Therefore, years of high recruitment probably depend on favorable hydrodynamic patterns delivering larvae and subsequent settlement in suitable seagrass areas. The lack of a direct effect of seagrass loss on King George whiting recruitment in Westernport was probably due to independent variation in larval supply, and a probable lag in population decline relative to seagrass decline because dependence is more related to food than shelter. Seagrass detritus may provide enhanced food production for juvenile whiting for some time, but not indefinitely, after the death of beds.

A number of areas of further research are suggested by the results of this project. We have hypothesised that the seagrass beds utilised by newly settled individuals of species such as King George whiting are largely determined by the position of the bed relative to hydrodynamics. Sophisticated models of the hydrodynamics of Port Phillip Bay are now available (Black *et al.* 1989), and could be used to predict settlement patterns based on prevailing climatic and oceanographic conditions. These predictions could, in turn, be compared with the actual distribution of recruits.

Another area which has received little attention by researchers is the role of seagrass habitat as a foraging area for juvenile fishes rather than simply as cover from predators. King George whiting is an example of a species for which this may be the case. Detailed studies of prey distributions and juvenile diets in seagrass and alternative habitats, together with experiments utilising artificial seagrass, could shed light on this potential link between seagrass and juvenile fish.

We speculate that King George whiting are spawning a considerable distance from their nursery areas in Port Phillip Bay. It seems possible that larvae could even be derived from South Australian stocks, which would have significant management implications. Research aimed at determining spawning areas of this important species, such as ichthyoplankton sampling in western Bass Strait, would be very valuable.

In summary, the preservation of seagrass habitat is crucial to a number of commercial species. Areas such as Swan Bay, which are relatively sheltered, have dense seagrass growth, and a strongly developed detrital food chain, should be protected from degradation. In addition, seagrass beds of lesser apparent 'quality', but which are positioned relative to hydrodynamics in such a way as to receive significant larval settlement, may also be of critical importance. Furthermore, the importance of a particular seagrass bed for settlement will depend on the species in question. In general, the question of the potential damage to commercial fisheries through degradation of seagrass beds will need to be assessed in terms of the potential of the bed to provide food and shelter, and also its spatial position in relation to hydrodynamics which will influence the number of larvae the bed accumulates.

The project has been successful when judged by the criteria proposed in the initial application.

- (a) The field program has been successfully completed.
- (b) The resultant data base has been interpreted so that clear statements can be made to industry groups and environmental managers about the value of Heterozostera habitat as a nursery for commercially-important species of fish.
- (c) Publication of results of the field research is underway.

Fig. 3.1 Location of sampling sites around the Bellarine Peninsula region of Port Phillip Bay, Victoria, from which juvenile fish were collected. Insets: Location of the Bellarine Peninsula in Port Phillip Bay and location of Port Phillip Bay on the Australian coast.

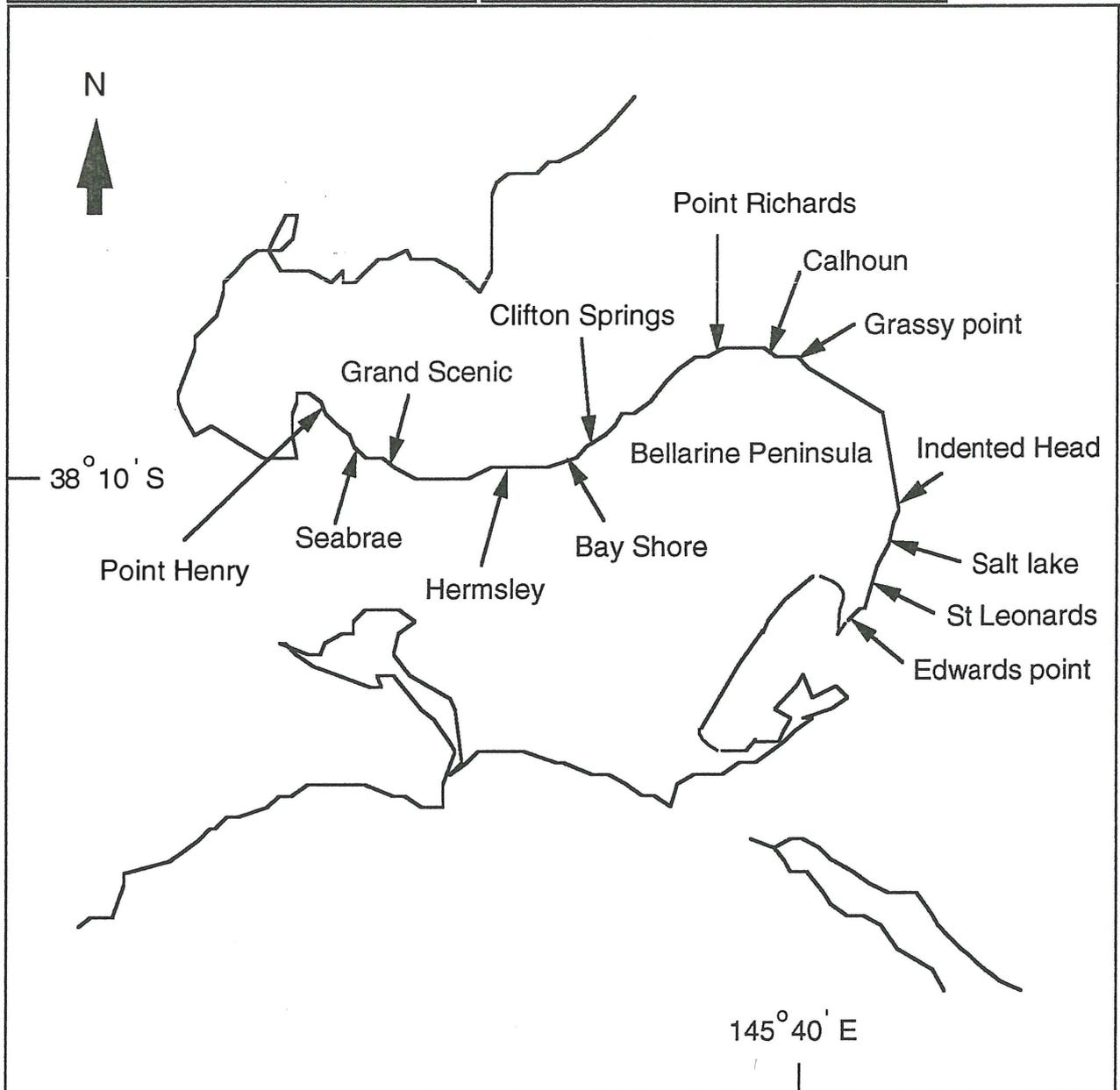
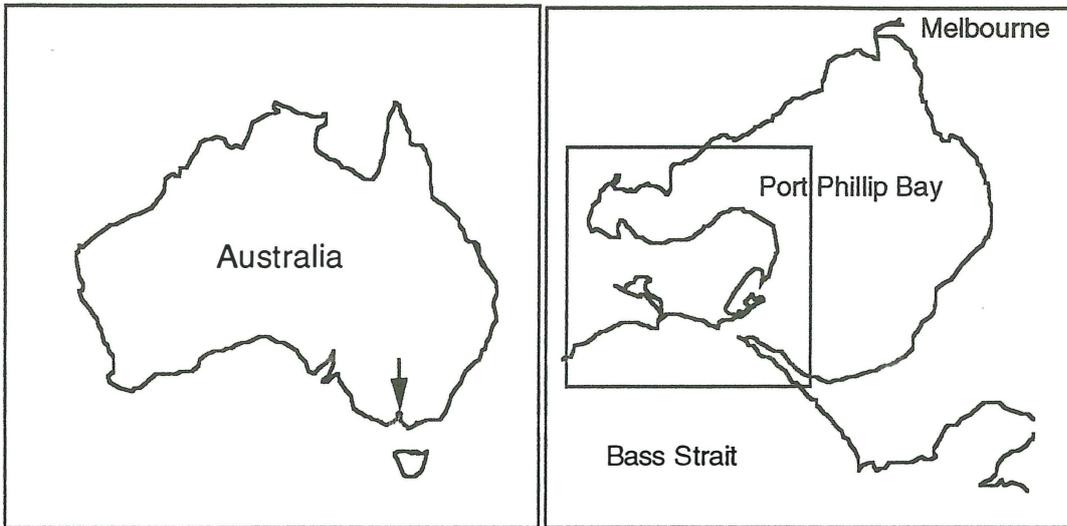


Fig. 3.2 Mean abundance of total fish at two sites in Swan Bay and two sites on the adjacent coast of Port Phillip Bay over five sampling dates. Error bars are standard error.

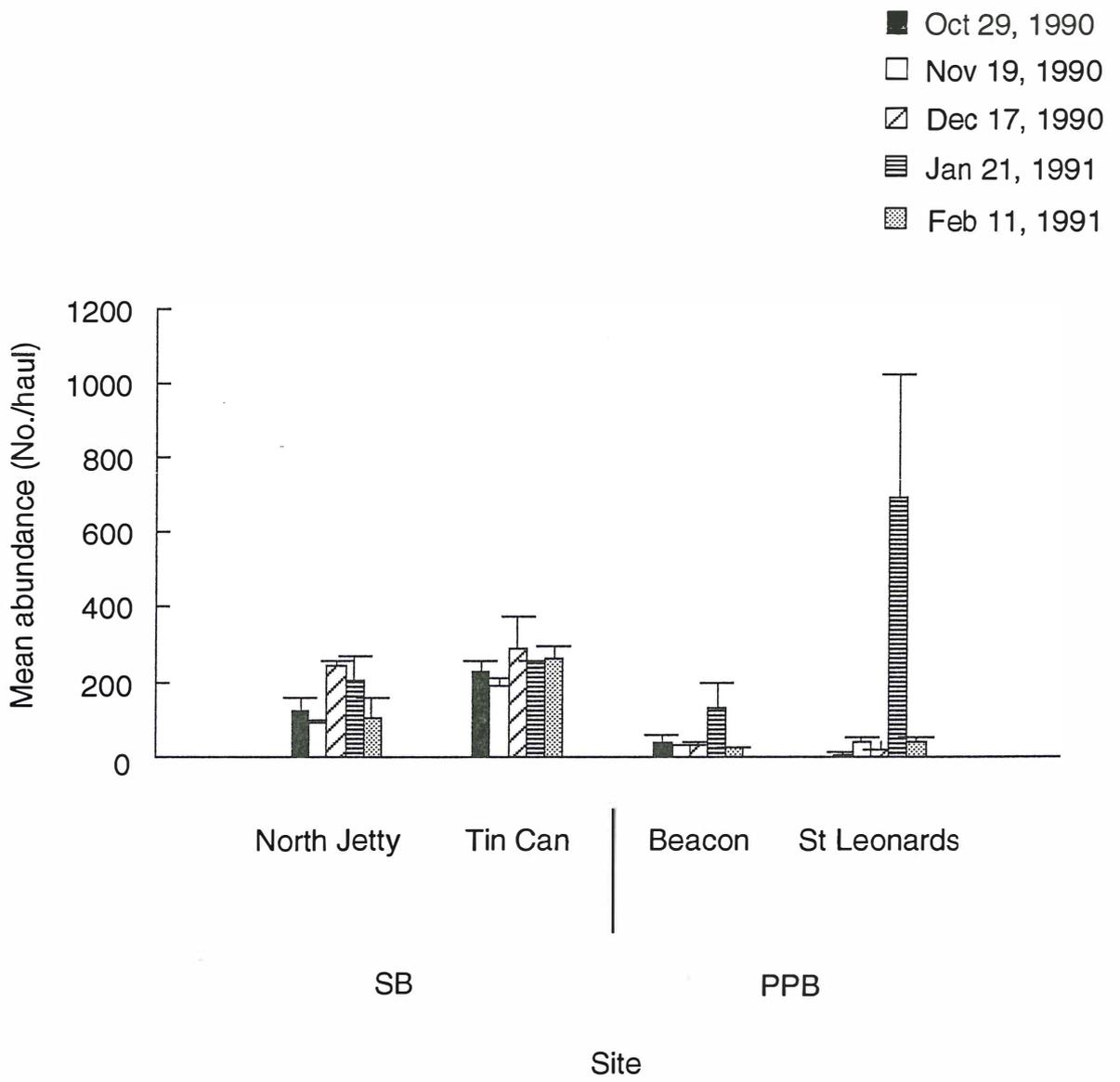


Fig. 3.3 Mean abundance of 'benthic' fish at two sites in Swan Bay and two sites on the adjacent coast of Port Phillip Bay over five sampling dates. Error bars are standard error.

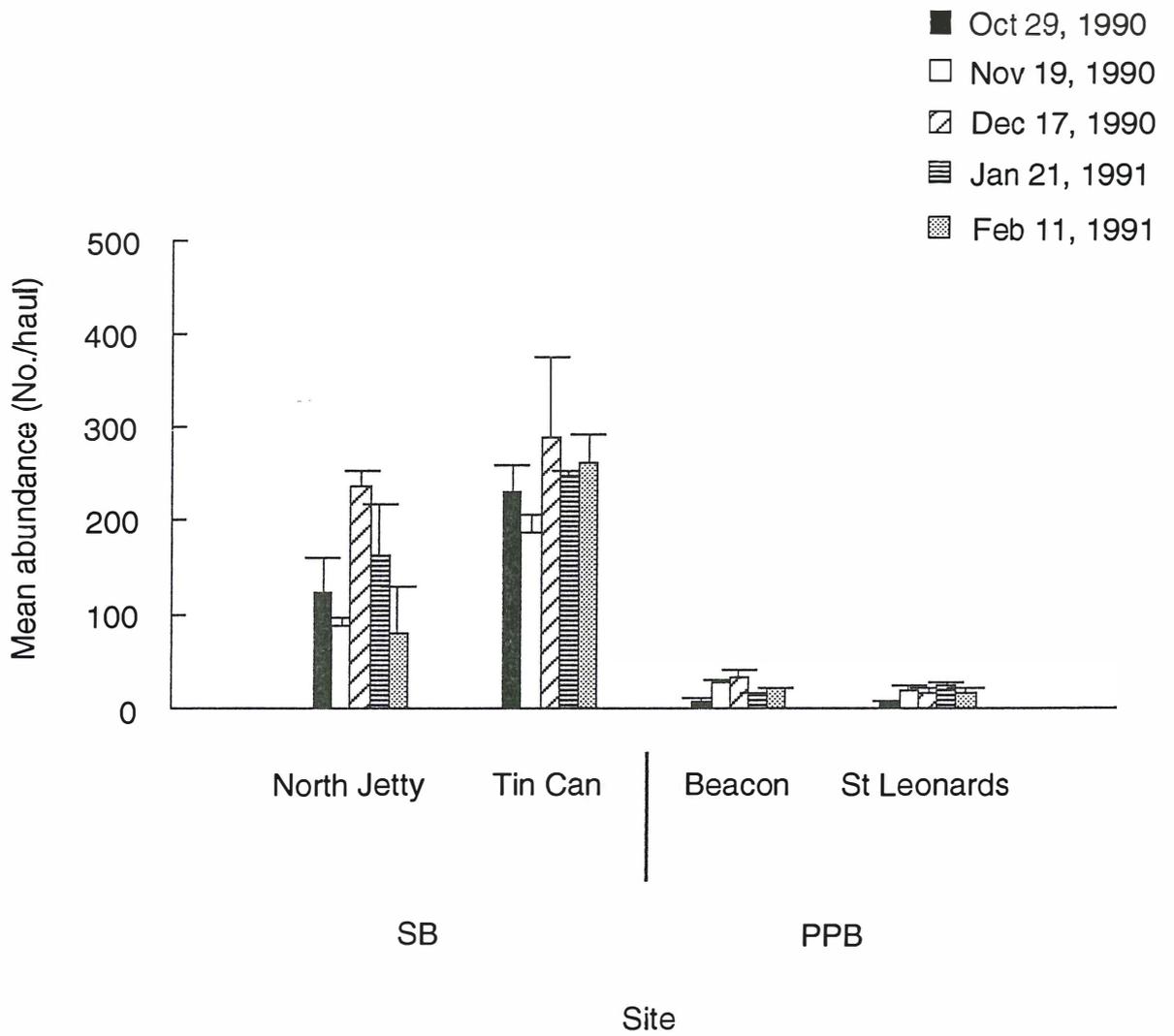


Fig. 3.4 Time-course of abundance of spotted pipefish in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 3.5 Time-course of abundance of spotted pipefish in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 3.6 Time-course of abundance of common weedfish in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 3.7 Time-course of abundance of Adelaide weedfish in seine-net samples from Swan Bay. Open squares, unvegetated habitat; closed circles, seagrass habitat. Error bars are standard error.

Fig. 3.8 Mean abundance of juvenile King George whiting on seagrassed and unvegetated habitat at sites in Swan Bay (SB) and the adjacent coast of Port Phillip Bay (PPB). StL=St Leonards, B=Beacon, TC=Tin Can, MJ=Mid Jetty. Error bars are standard error.

Fig. 3.9 Size frequency histograms for King George whiting juveniles in seine-net samples from the Bellarine Peninsula. Closed histograms, November 1990; open histograms, December 1990.

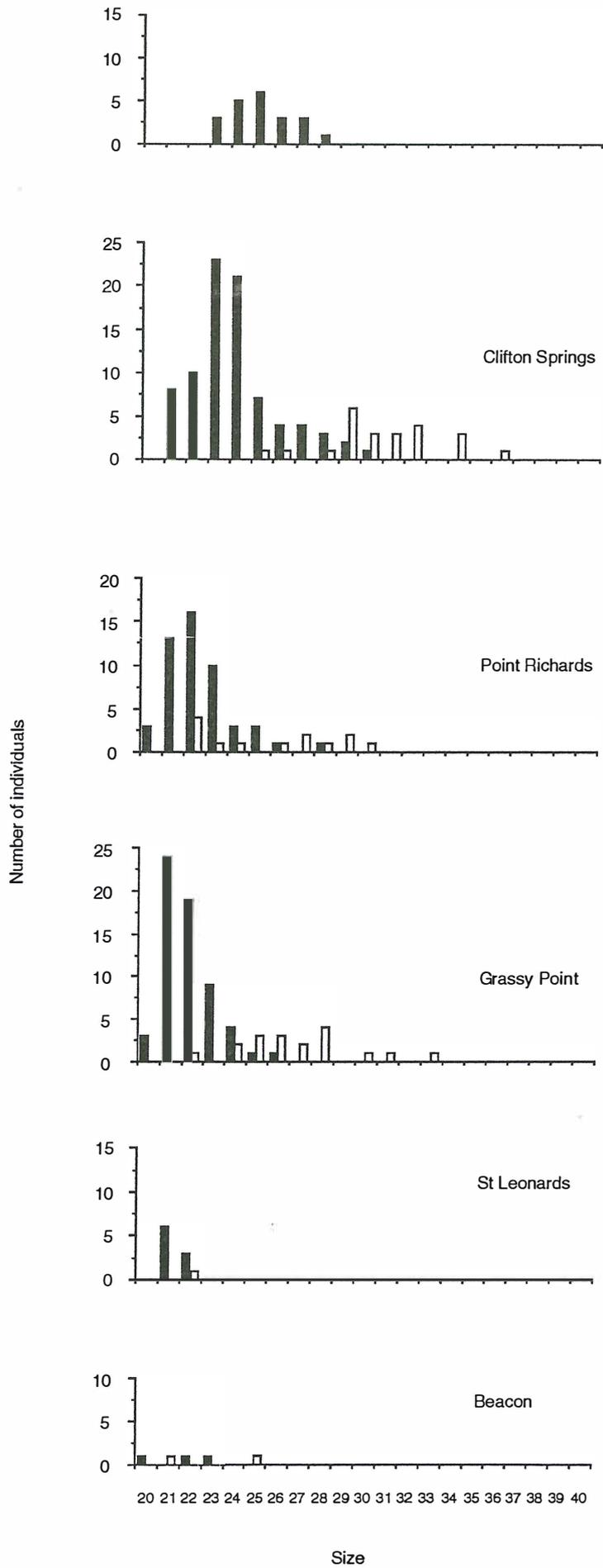


Fig. 3.10 Mean abundance of total fish in seine-net samples from sites within five regions around the Bellarine Peninsula over four sampling dates. Error bars are standard error.

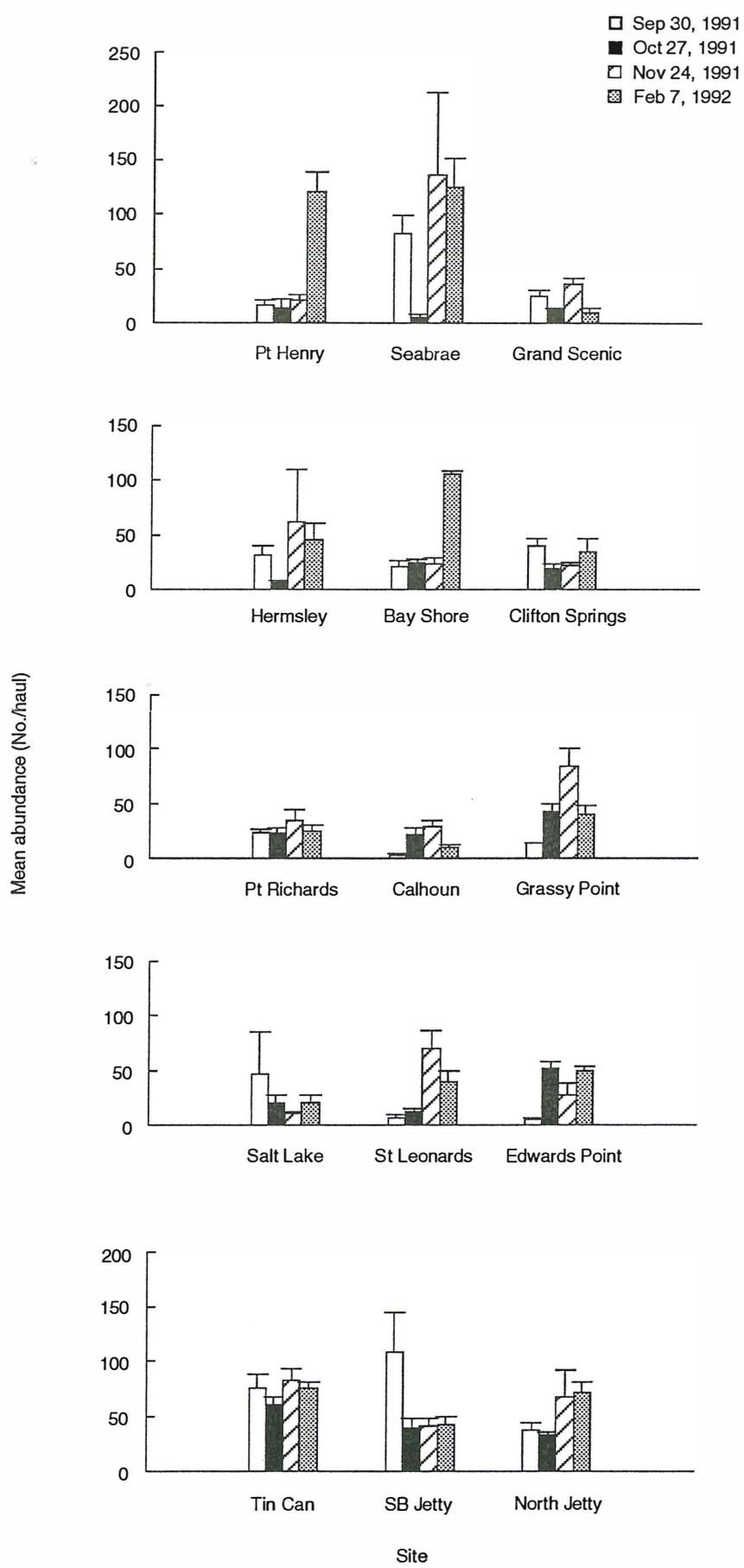


Fig. 3.11 Mean abundance of 'benthic' fish in seine-net samples from sites within five regions around the Bellarine Peninsula over four sampling dates. Error bars are standard error.

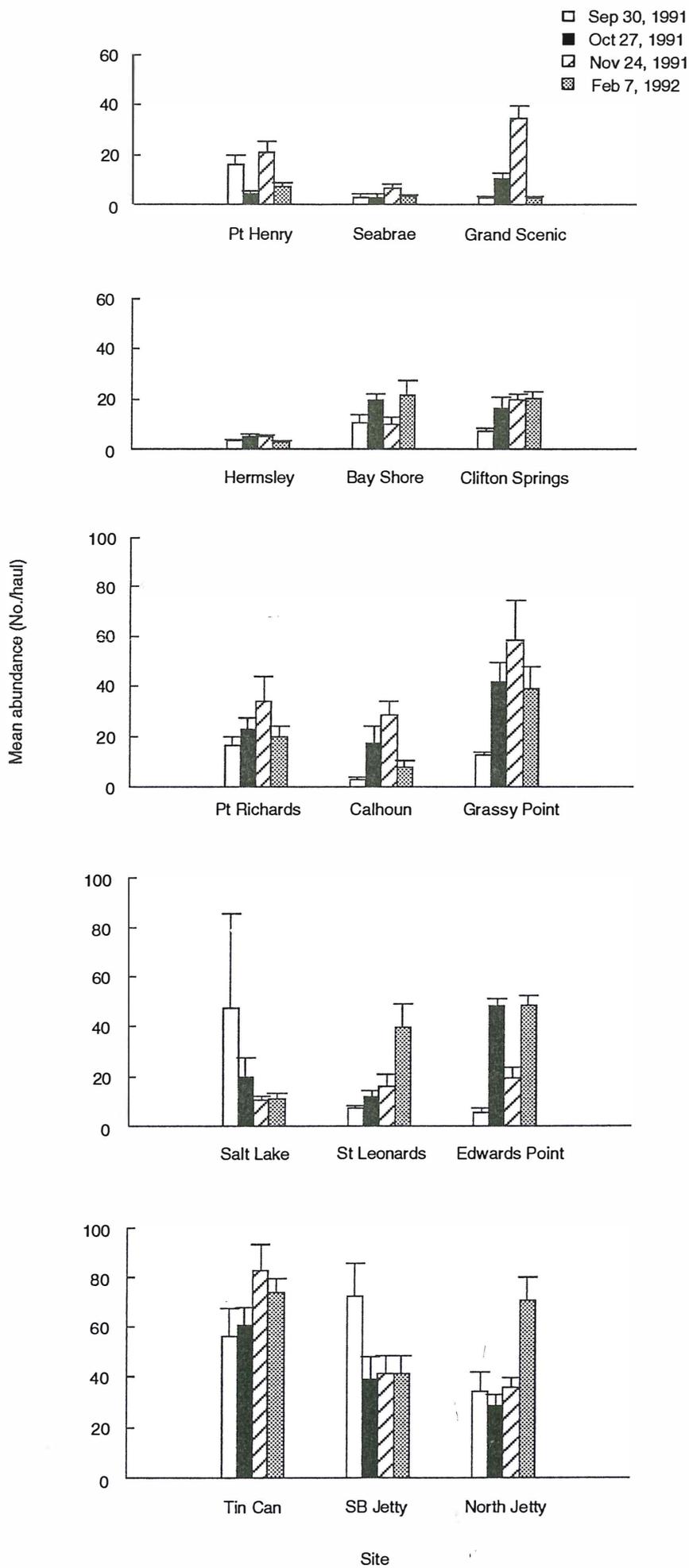


Fig. 3.12 Mean abundance of King George whiting in seine-net samples from sites within five regions around the Bellarine Peninsula over four sampling dates. Error bars are standard error.

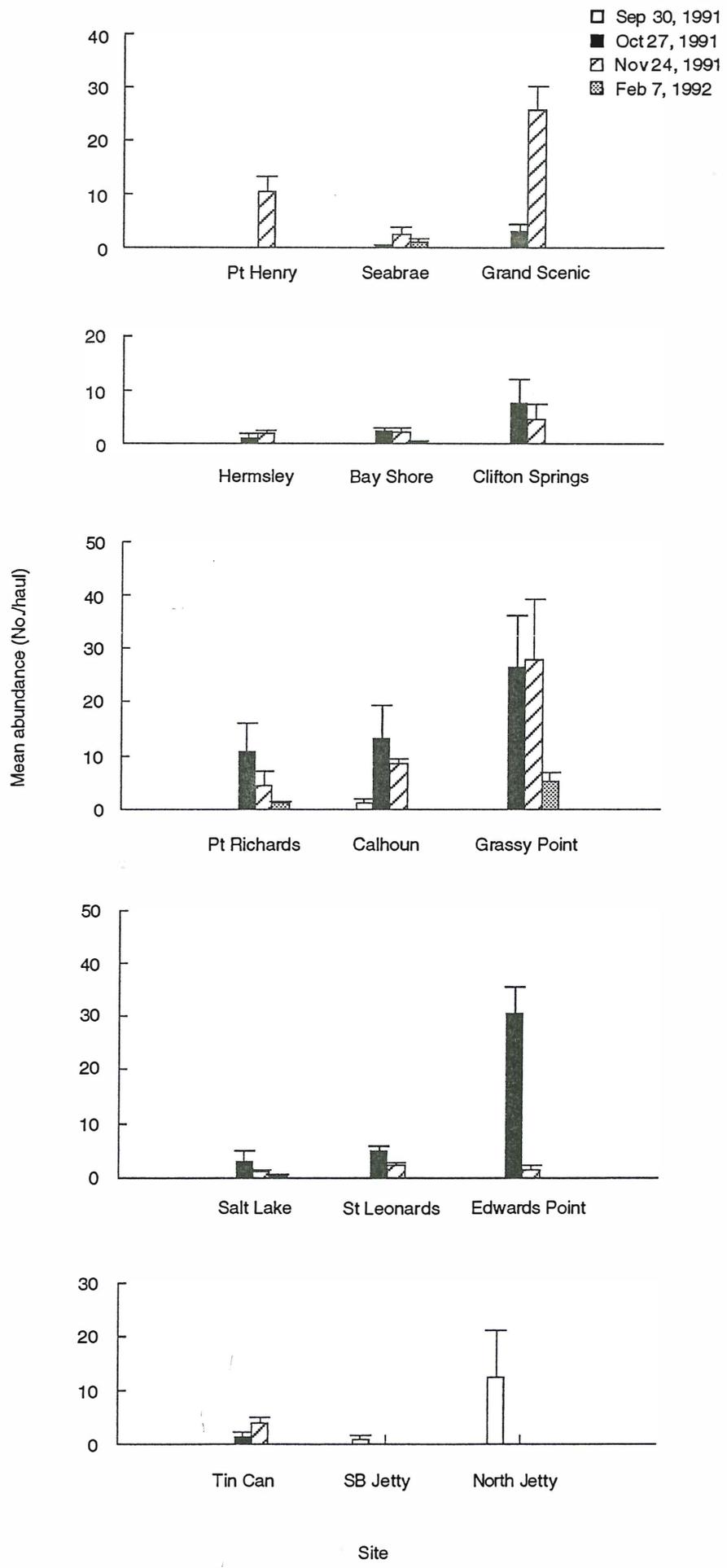


Fig. 3.13 Mean abundance of Adelaide weedfish in seine-net samples from sites within five regions around the Bellarine Peninsula over four sampling dates. Error bars are standard error.

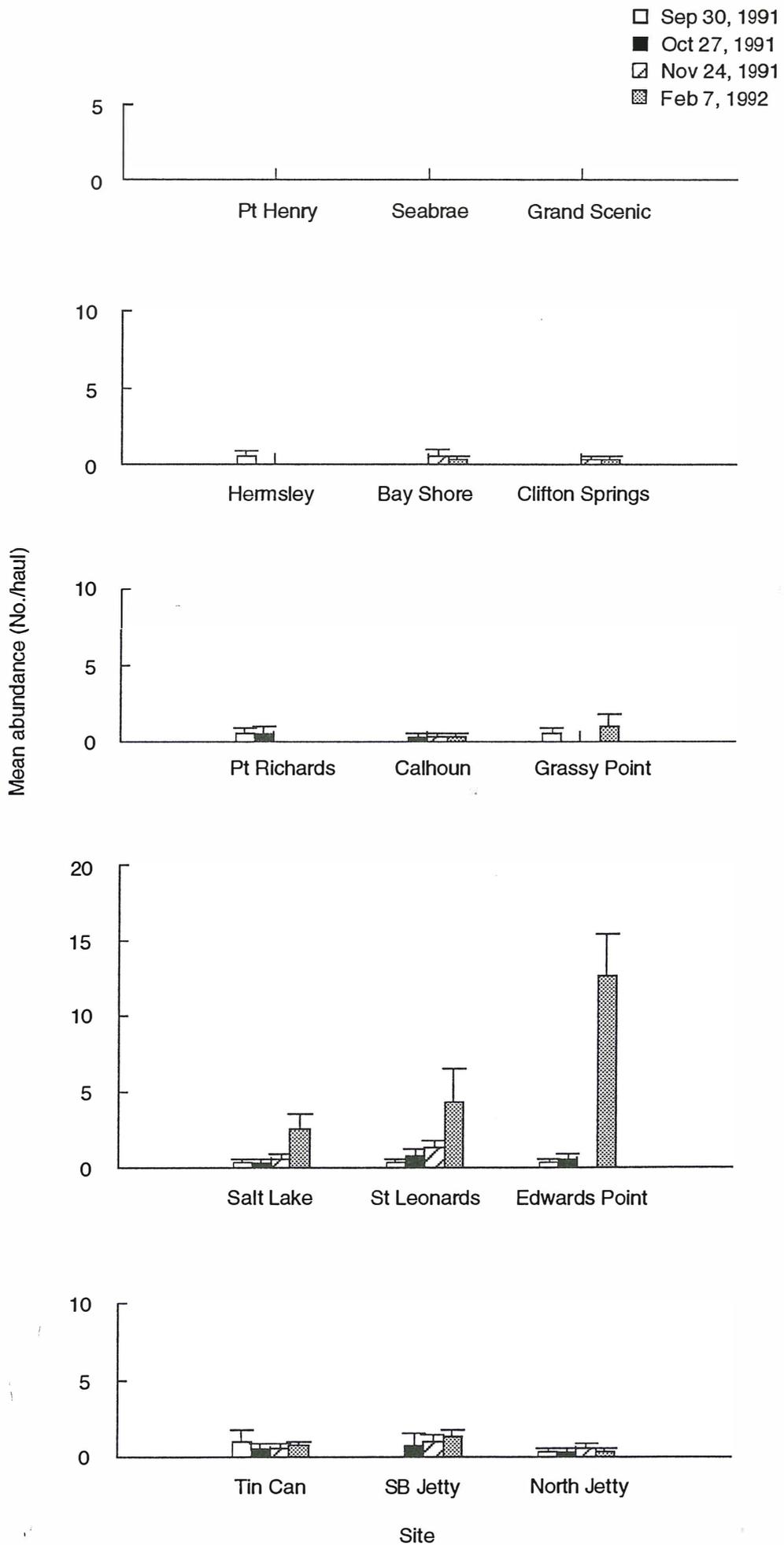


Fig. 3.14 Mean abundance of bridled leatherjackets in seine-net samples from sites within five regions around the Bellarine Peninsula over four sampling dates. Error bars are standard error.

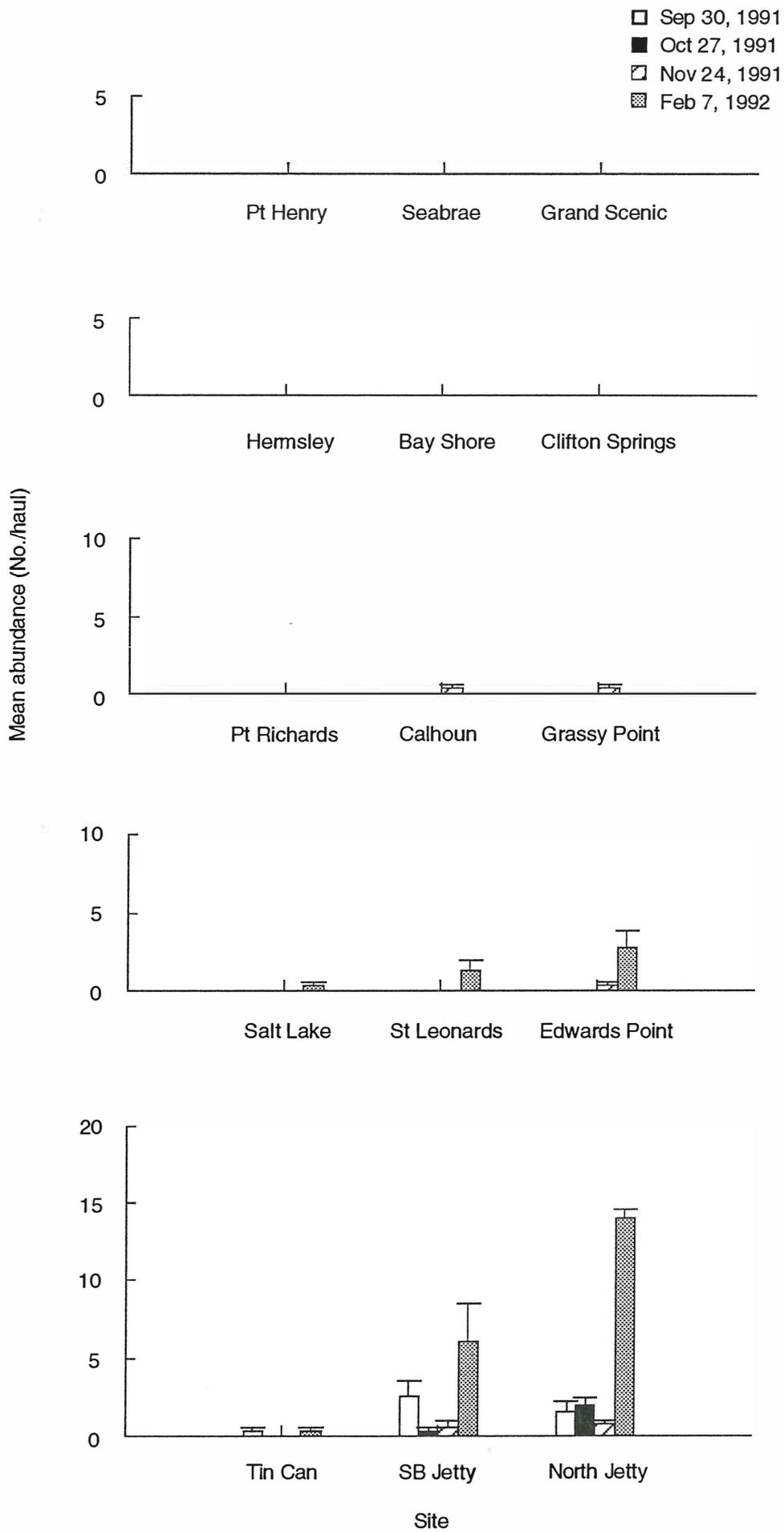


Fig. 3.15 Mean seagrass biomass from sites within five regions around the Bellarine Peninsula sampled in December 1991. PH=Point Henry, S=Seabrae, GS=Grand Scenic, H=Hermsley, BS=Bay Shore, CS=Clifton Springs, PR=Point Richards, C=Calhoun, GP=Grassy Point, SL=Salt Lake, StL=St Leonards, EP=Edwards Point, NJ=North Jetty, J=Jetty, TC=Tin Can. Error bars are standard error.

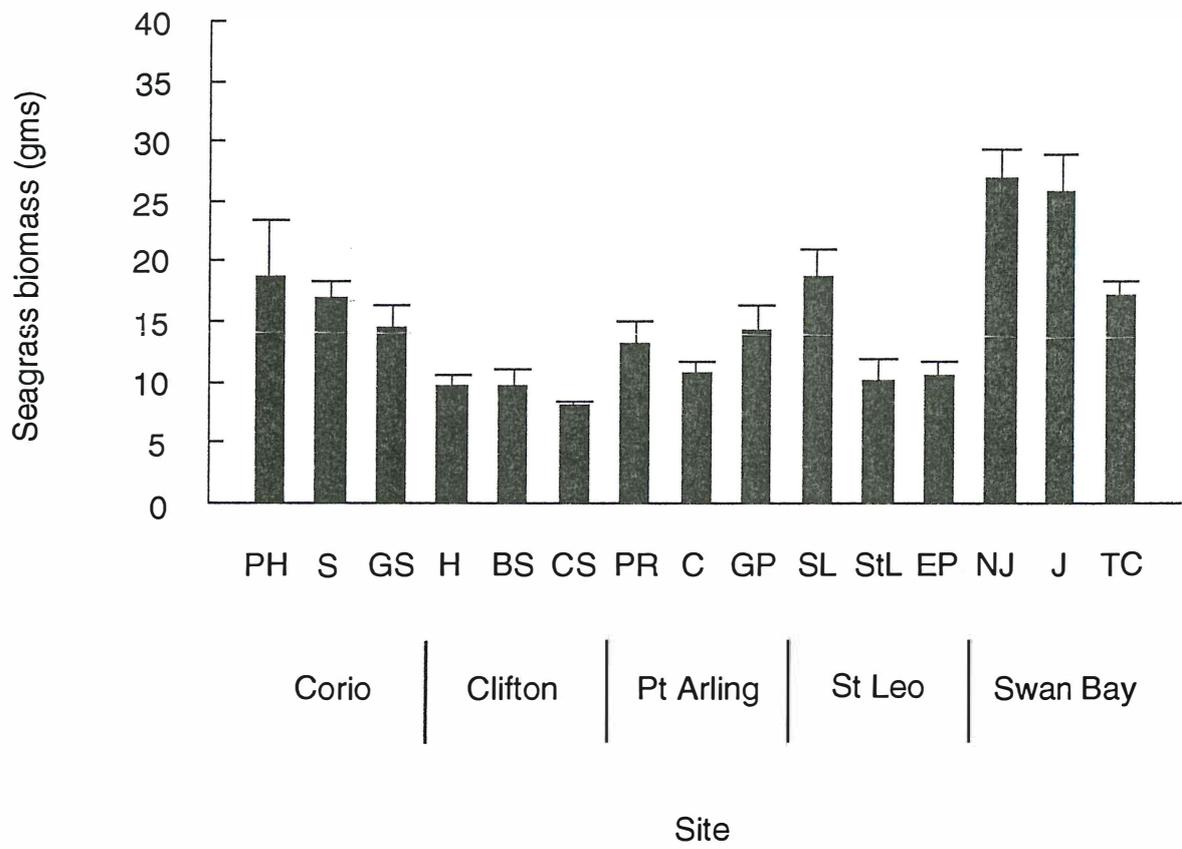


Fig. 3.16 Relationship between seagrass biomass and fish abundance at sites sampled around the Bellarine Peninsula in November/December 1991. A. Total fish, B. 'Benthic' fish.

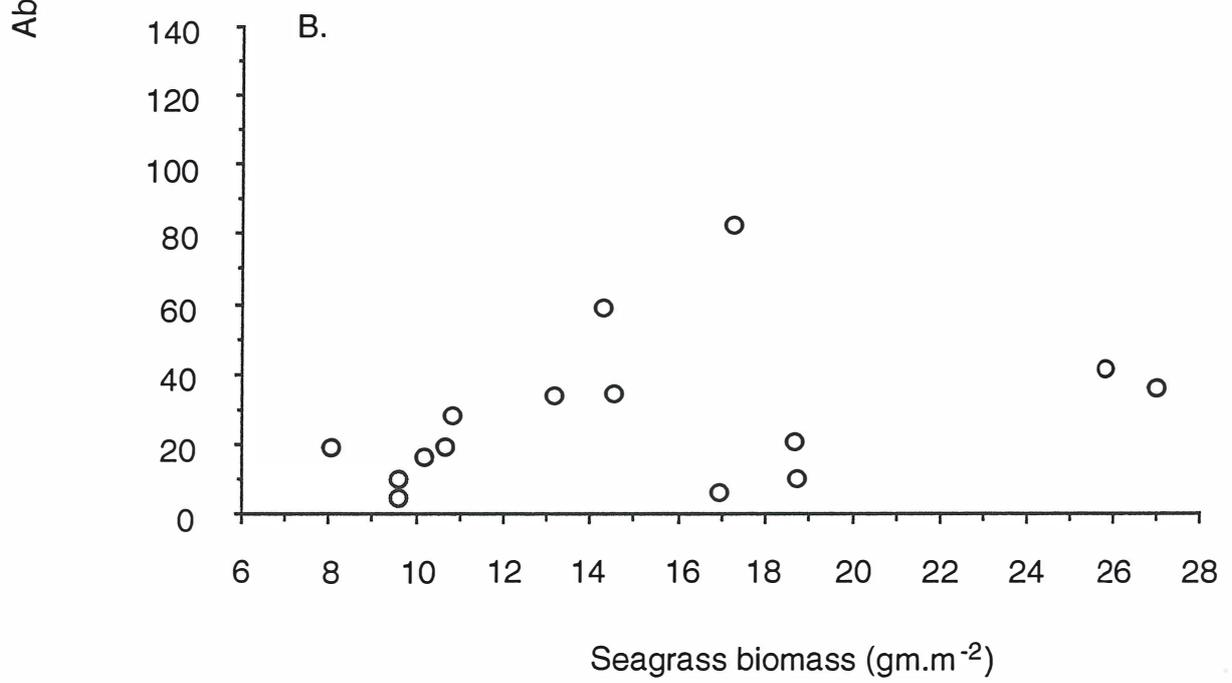
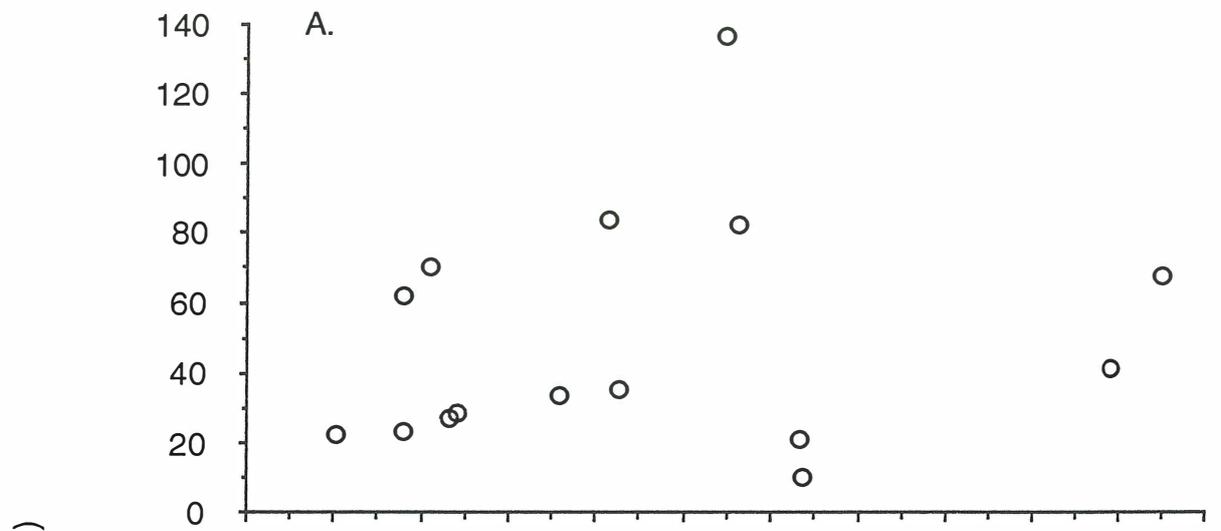


Fig. 3.17 Mean abundance of fish larvae per 100 m³ in plankton samples collected between September 1990 - January 1991. A. Total larvae, B. 'Benthic' larvae. Open squares, St Leonards; open circles, Swan Bay.

Fig. 3.18 Mean abundance of fish larvae per 100 m³ in plankton samples collected between September 1991 - December 1991. A. Total larvae, B. 'Benthic' larvae. Open squares, St Leonards; open circles, Swan Bay; closed triangles, Grassy Point.

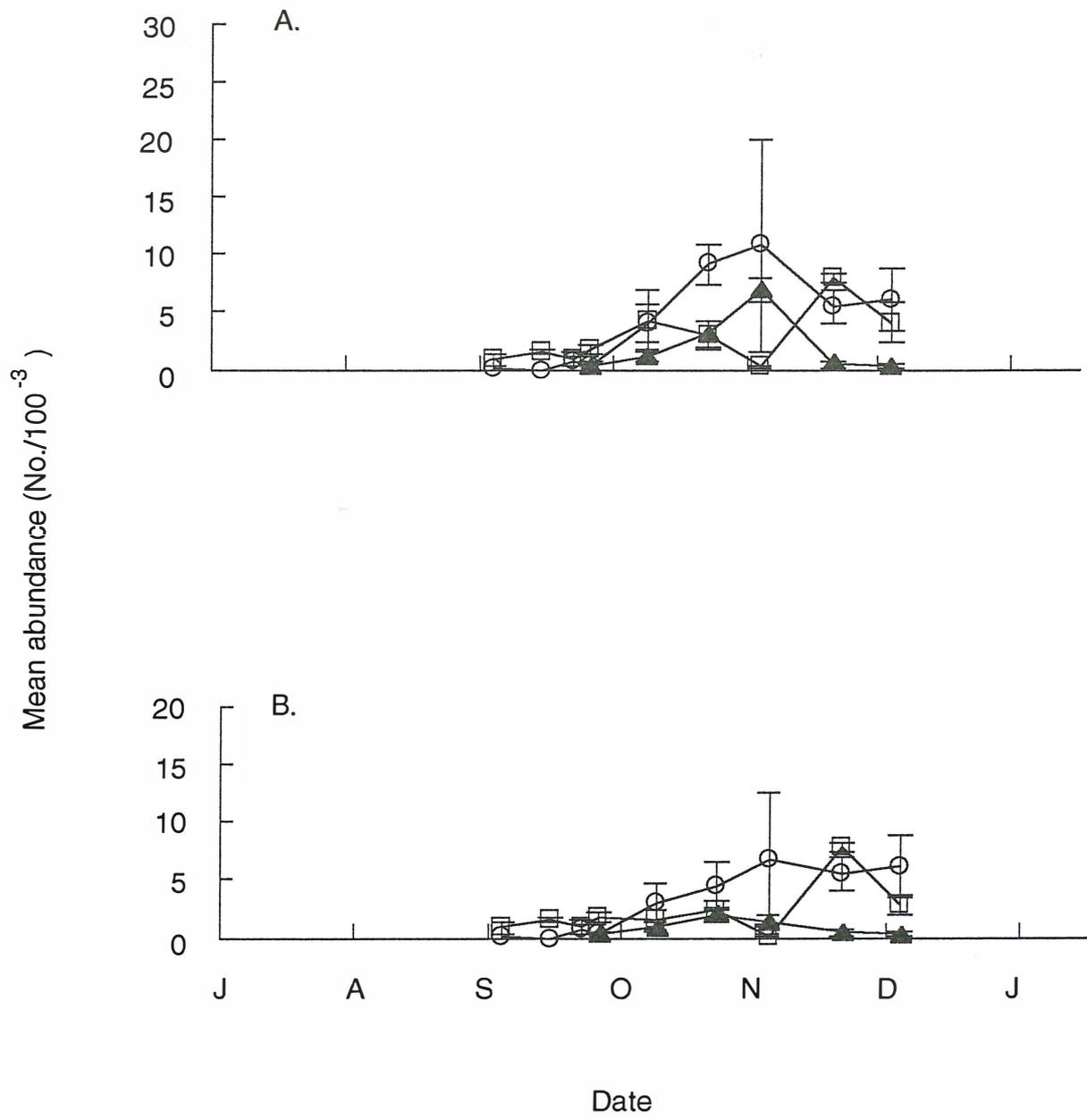


Fig. 3.19 Mean abundance of King George whiting larvae per 100 m^3 in plankton samples. A. September 1990 - January 1991, B. September 1991 - December 1991. Open squares, St Leonards; open circles, Swan Bay; closed triangles, Grassy Point.

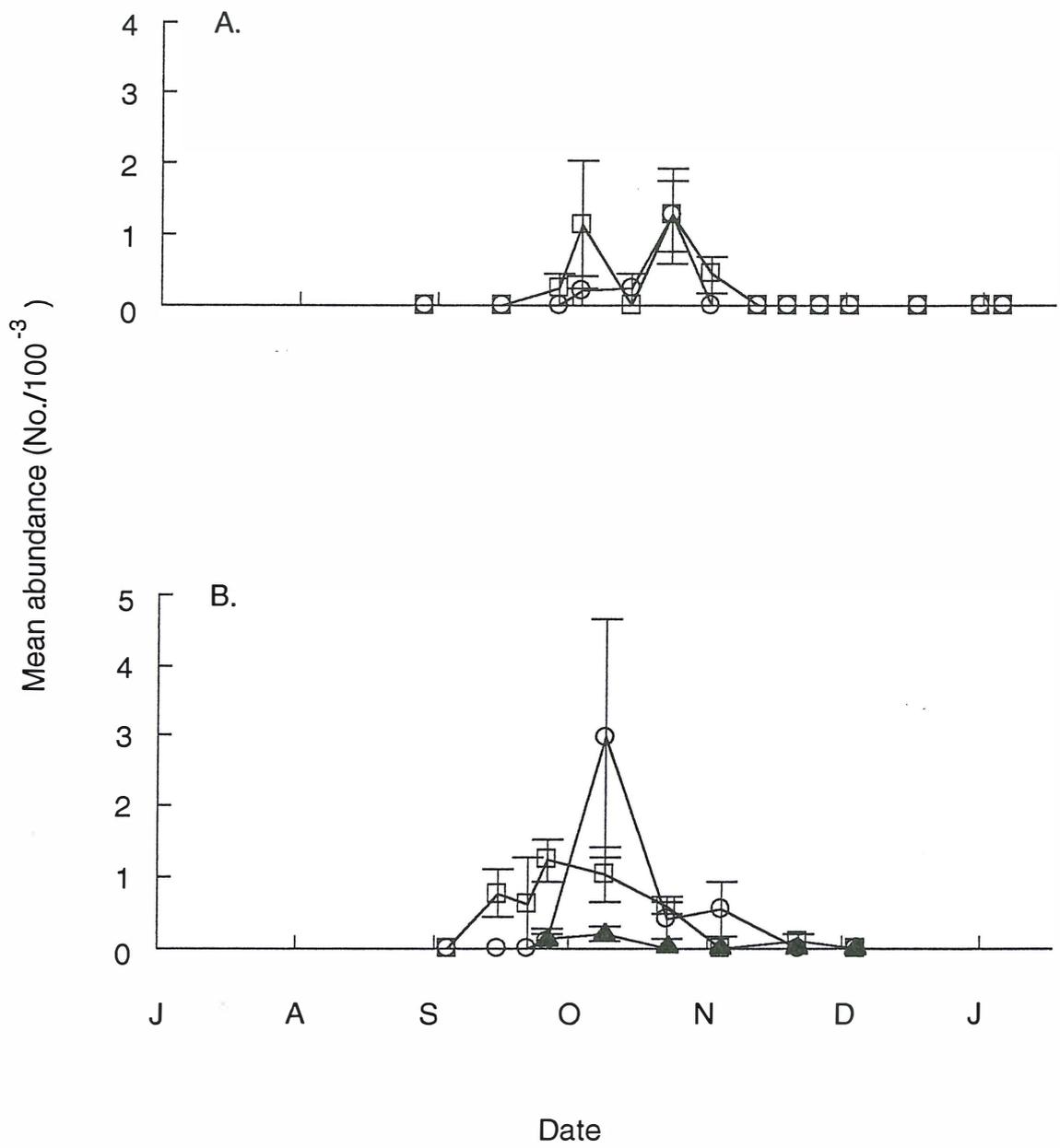


Fig. 3.20 Mean number of fish collected from artificial seagrass beds together with mesh and unvegetated controls at St Leonards and Grassy Point. Error bars are standard error.

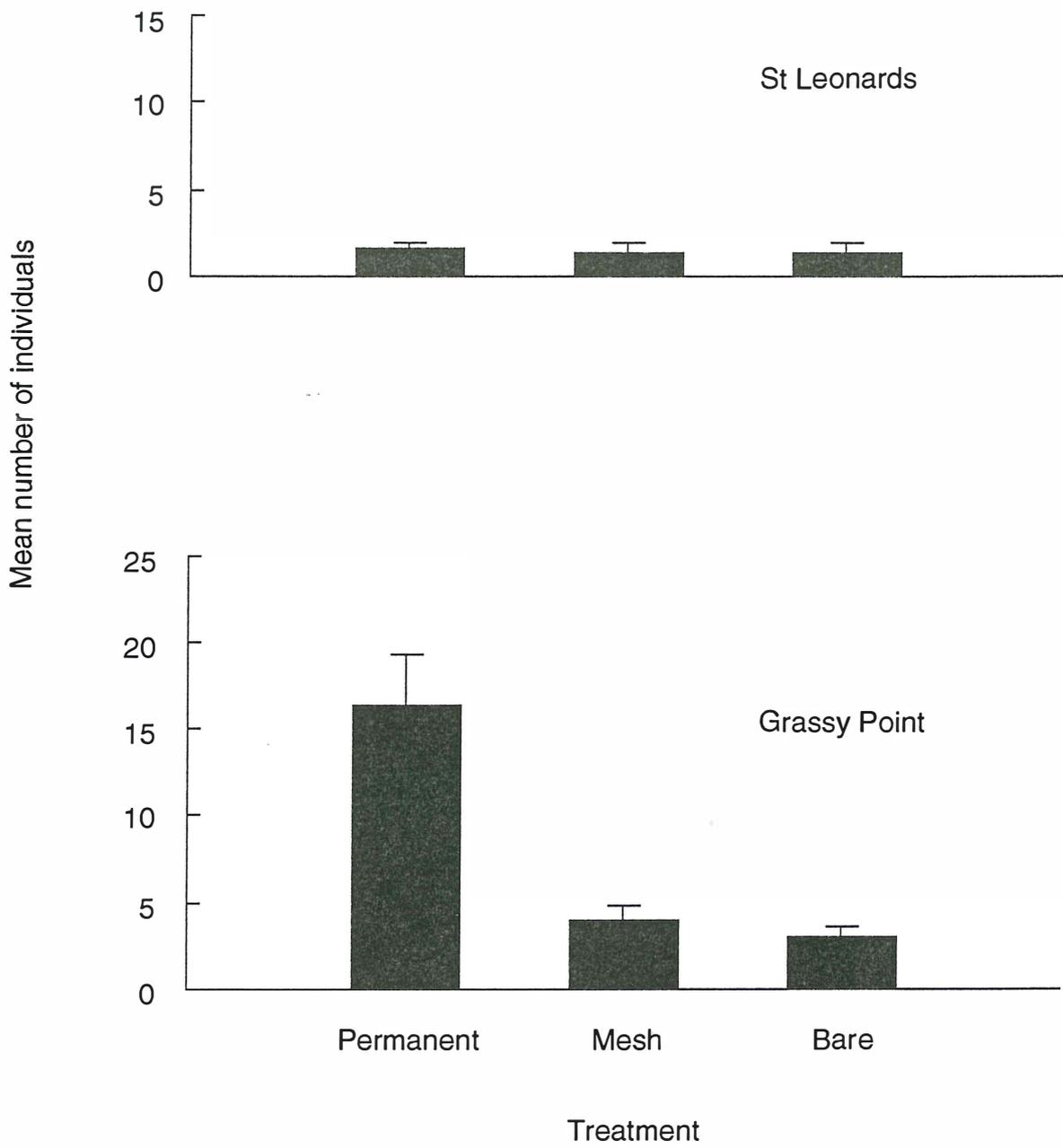


Fig. 3.21 Mean number of pipefish, Stigmatopora sp., collected from artificial seagrass beds together with mesh and unvegetated controls at St Leonards and Grassy Point. Error bars are standard error.

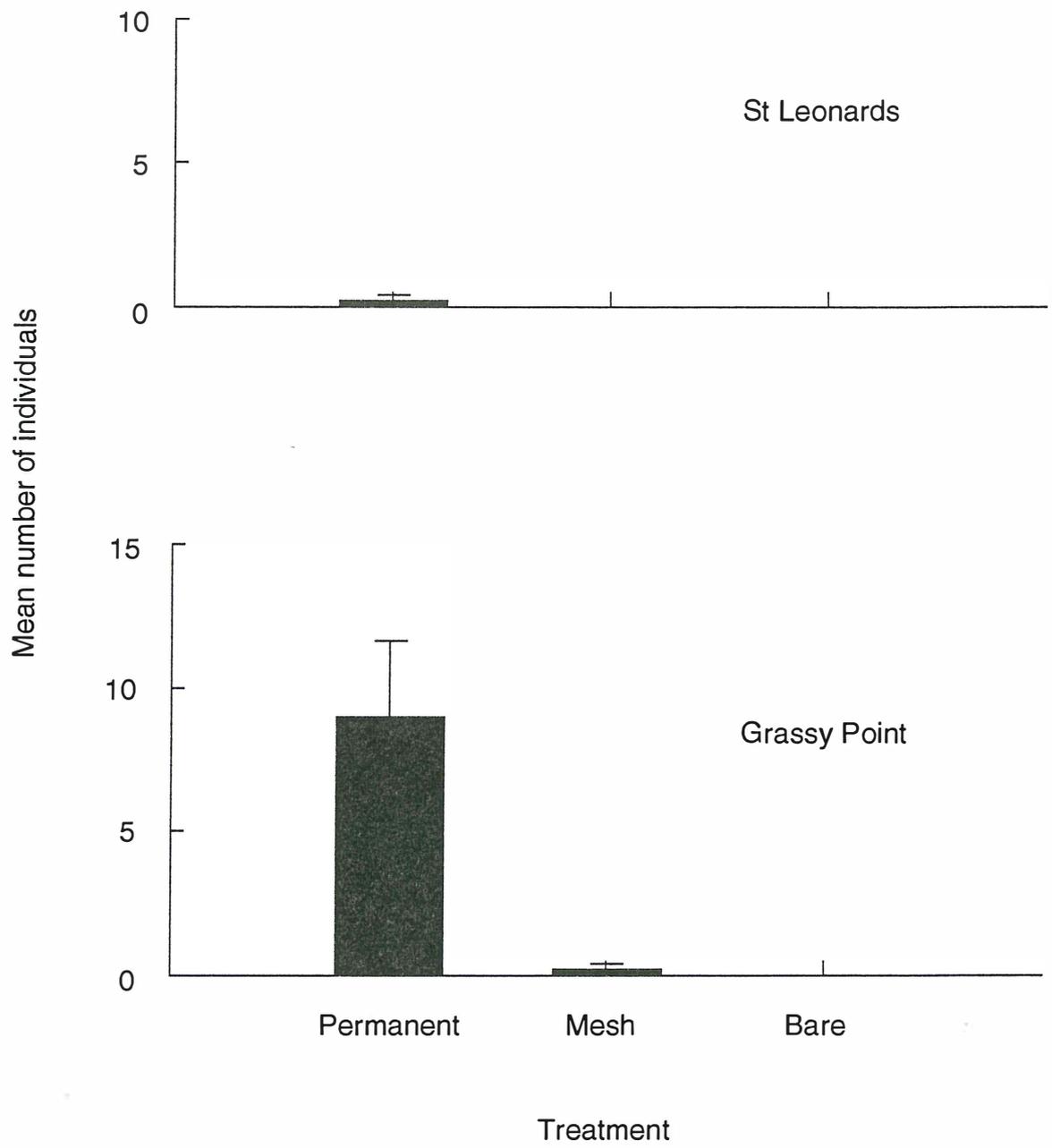


Fig. 3.22 Mean number of juvenile King George whiting collected from artificial seagrass beds together with mesh and unvegetated controls at St Leonards and Grassy Point. Error bars are standard error.

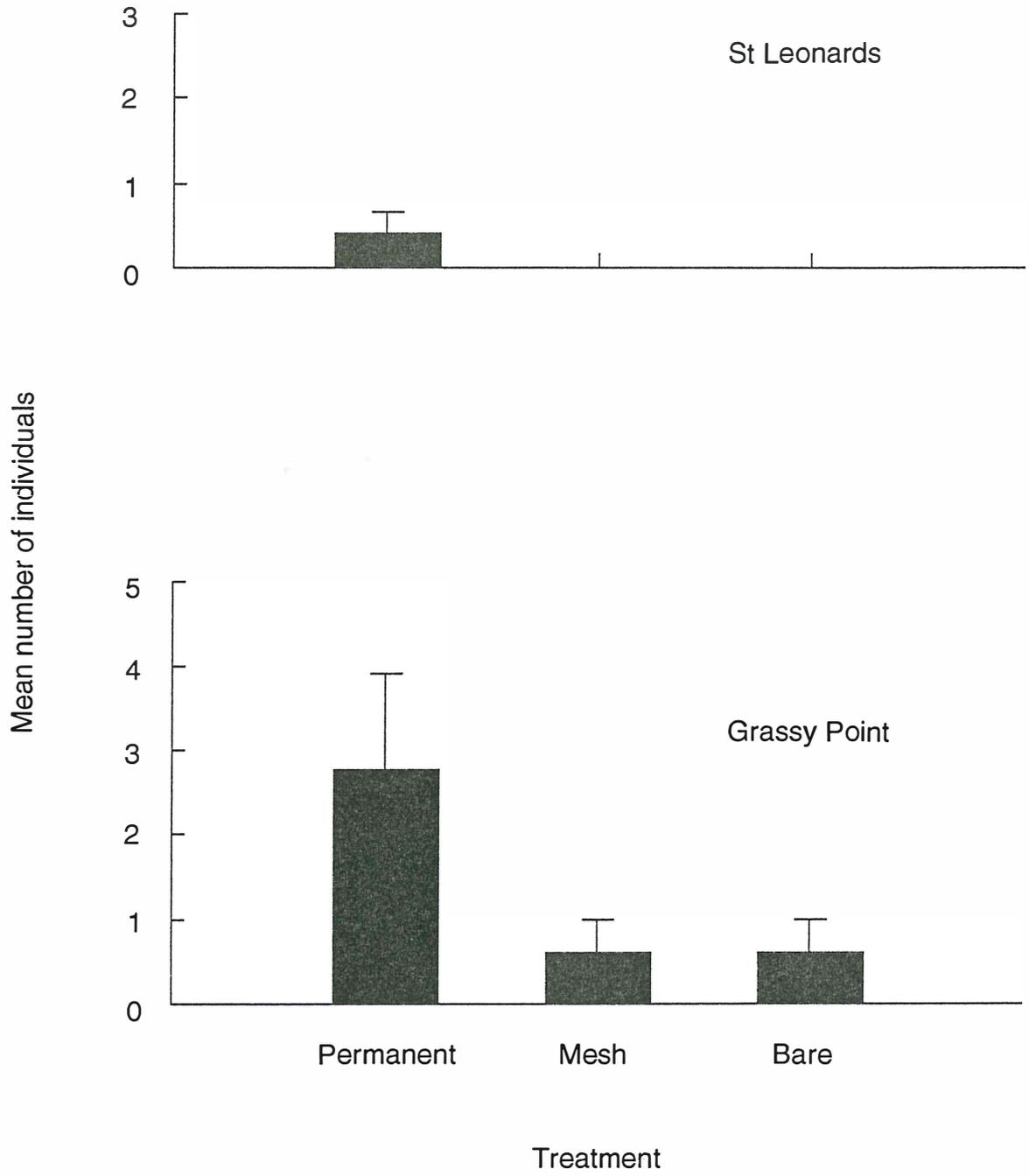
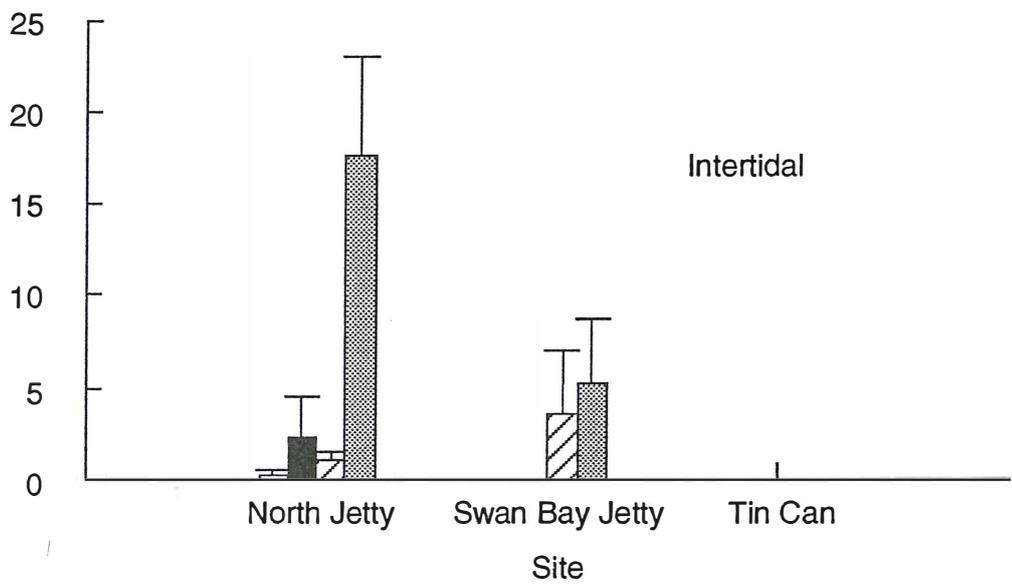
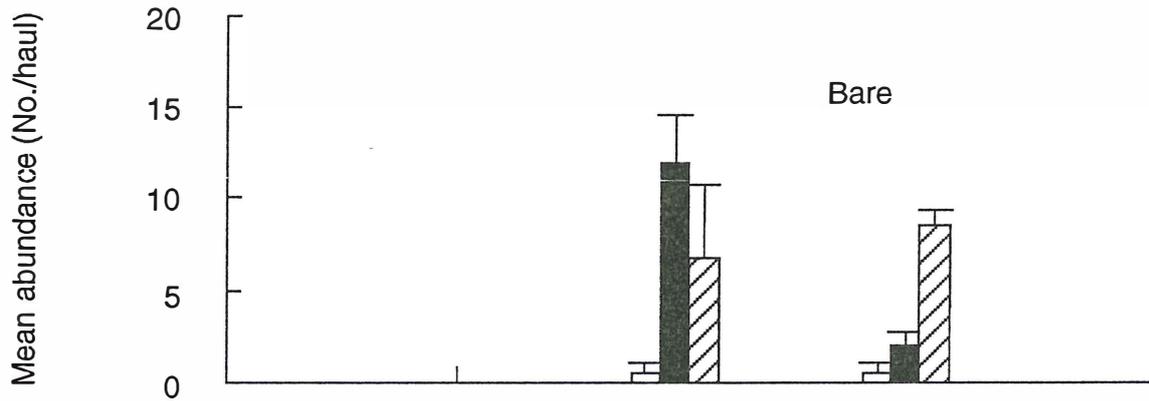


Fig. 3.23 Mean abundance of juvenile King George whiting in seine net samples from Swan Bay between September 1991 to February 1992. Error bars are standard error.



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Patterns of settlement and growth of juvenile flounder *Rhombosolea tapirina* determined from otolith microstructure

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ABSTRACT: Otolith microstructure was used to examine settlement and growth of juvenile *Rhombosolea tapirina* Günther from a site within Swan Bay, Victoria, Australia. A distinct transition zone on sagittae coincides with settlement from the pelagic larval phase to the benthic juvenile habitat. The daily settlement pattern was reconstructed using otolith increments from fish collected during and at the end of the settlement season. Settlement was continuous from July to October. However, most individuals had apparently immigrated from other settlement areas or were inaccessible to sampling for a brief period after settlement. The settlement pattern persisted over time, however, peaks were no longer evident at the end of the settlement season. The population growth rate of juvenile flounder was found to be approximately linear over the size range sampled, averaging 0.29 mm d^{-1} . A significant linear relationship between standard length and otolith radius allowed back-calculation of individual growth trajectories for a 'winter' and a 'spring' cohort. Significant differences were found in growth trajectories for each cohort; growth rate over the first 20 d post settlement for the winter cohort averaged approximately 0.17 mm d^{-1} compared to 0.23 mm d^{-1} for the spring cohort. The relationship between daily growth and air temperature was compared using cross correlation. Cross correlation functions showed a significant positive correlation at lags of 2 to 5 d for the winter cohort and a significant negative correlation at a lag of 1 d for the spring cohort. This suggests that early in the settlement season, temperature had a positive influence on metabolism, which in turn affected somatic and otolith growth rates. However, temperature apparently reached a critical level later in the season, which resulted in high temperature having a deleterious effect on metabolism, leading to a negative correlation between temperature and growth.

INTRODUCTION

For fish that have a distinct metamorphosis from a planktonic larval form to a benthic juvenile, the patterns of spawning, larval dispersal, larval mortality and habitat selection will eventually be observed in settlement patterns (Keough & Downes 1982, Doherty & Williams 1988). These patterns will be further modified by mortality in the juvenile stage. One factor in the mortality of larval and juvenile fish that may be of critical importance is growth rate. Smith (1985) suggested that the growth rates of late larval and early juvenile fish may affect the magnitude of recruitment because they determine the duration of the most vulnerable stages. Therefore, accurate estimation of growth rates of juvenile fish collected from the field,

and the evaluation of factors which may influence growth, is a necessary prerequisite to understanding mortality in juvenile fish.

Studies of growth and settlement patterns have been greatly facilitated by Panella's (1971) discovery of daily growth increments in otoliths of juvenile fish. Daily increments in otoliths have now been validated for a large number of marine and freshwater fish (Campana & Neilson 1985, Jones 1986). Because larvae and juveniles can be aged, growth rates can be determined for populations from size at age. Moreover, where there is a smooth monotonic relationship between otolith size and fish size, growth trajectories of individuals can be determined by backcalculating size from the radius to daily increments (Jenkins & Davis 1990). Furthermore, changes in increment morphology

often occur at times of ecological and physiological transitions in development (Brothers & McFarland 1981). Such a transition often occurs at the end of the larval stage, with a characteristic change in increment spacing and contrast. These 'settlement marks' allow settlement dates to be accurately determined and settlement patterns to be reconstructed.

Rhombosolea tapirina Günther is a commercially important pleuronectid in southern Australia (Hutchings & Swainston 1986). Daily periodicity of increment formation in juvenile *R. tapirina* has been validated under the assumption that stress marks on otoliths were formed due to handling and immersion in tetracycline (Stewart & Jenkins 1991). In the present study we analyse daily increments in otoliths of juvenile *R. tapirina* to determine settlement patterns and juvenile growth histories. Settlement patterns of fish collected throughout the breeding season are compared with those recorded in otoliths from fish collected at the end of the breeding season to determine if patterns were preserved in the population structure. We also construct detailed growth histories of 2 cohorts of fish settling at different times to estimate growth rates and trajectories, and to determine the effect of temperature on growth.

MATERIALS AND METHODS

Field sampling. *Rhombosolea tapirina* juveniles were collected between September and November 1989 from Swan Bay, Queenscliff (Fig. 1). Collections were made with a beach seine net (10 m × 1.5 m, mesh size 1 mm) hauled parallel and adjacent to the shore for 20 m; the net was hauled between 2 and 6 times to provide an adequate sample. Metamorphosing larvae were collected from nearby sites in Swan Bay and Port Phillip Bay (Fig. 1) on 27 September and 4 October 1990. Larvae were collected with a 0.64 m² opening, 1 mm mesh plankton net, towed at the surface for 10 min. Larvae and juveniles were immediately anaesthetized in MS 222 and then preserved in 95% ethanol. We assumed that any shrinkage in preservative was a relatively constant proportion over the size range analysed and therefore would have a minimal affect on growth rate estimates.

Otolith preparation. The standard length (SL) of specimens was determined by measuring from the snout to the caudal peduncle, to the nearest 0.1 mm, under a dissecting microscope with an ocular micrometer. Specimens were placed in a drop of water on a microscope slide and the utricular (lapilli) and saccular (sagittae) otoliths were dissected out using electrolytically-sharpened tungsten probes (or forceps, when the fish were greater than 20 mm SL). Contrast between

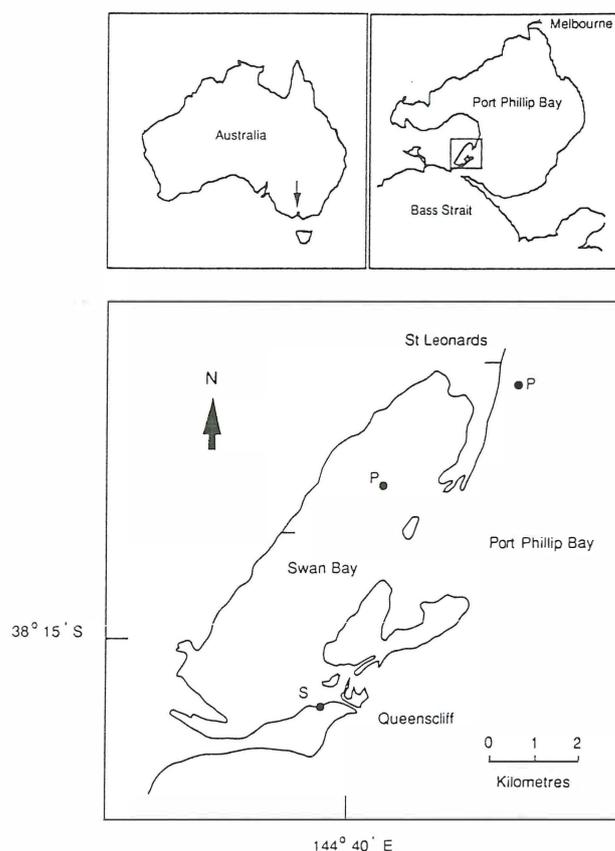


Fig. 1. Location of sampling sites in Swan Bay and Port Phillip Bay, Victoria, from which larval and juvenile flounder were collected. Insets: Location of Swan Bay in Port Phillip Bay and location of Port Phillip Bay on the Victorian coast. S: seining; P: plankton sampling

the otoliths and surrounding tissue was maximised by using a polarizing light source fitted to the stereo microscope. The otoliths were left to dry, flat side up, and then placed in immersion oil on glass slides.

Otoliths that could be read without further preparation were mounted permanently in Gurr's neutral mounting medium, with fine nylon monofilament on either side to prevent crushing by the cover slip. Otoliths that required grinding and polishing (fish greater than 18 mm SL) were cleaned with alcohol and then mounted, flat side up, in epoxy resin. Otoliths were manually ground with a succession of 600 up to 1200 grade wet and dry sandpaper until the otolith surface was reached. They were then polished with 6 µm diamond paste on a lapping machine. The lapping machine ensured that otoliths were polished on a horizontal plane.

Otolith analysis. Otolith measurements and counts were made with a compound microscope. A video camera connected to the microscope produced an image which was displayed and digitised on a Com-

modore 'Amiga' computer. Specimens were examined randomly and blindly with respect to SL. Otoliths from larvae were examined for the presence or absence of a transition zone associated with metamorphosis.

The otolith radius was measured for all fish sampled up to 40 mm, and radius to each increment was measured for 50 specimens to determine incremental widths. The radius was measured along the line of maximum otolith radius.

We attempted to count the post-settlement increments on all 4 otoliths. Post-settlement increments were defined as those deposited after the transition zone of poorly-defined increments which has previously been observed at the edge of otoliths of immediate pre-settlement flounder collected in the plankton (Jenkins 1987). A clarity value for increments was assigned in the range of 1 to 4; 1 representing low clarity and 4 representing the clearest. Only readings having a clarity of greater than 2 were accepted. When the increment count for otoliths from the same fish differed by 2 or more the data were discarded. Usable data were obtained from 94% of the fish examined, and the mean count for each fish was analysed.

All statistical analyses were the 'SYSTAT' computer programs Assumptions for parametric analyses using box plots and the distribution of

RESULTS

Otolith examination

Daily increments were clearly visible until the fish were approximately 20 mm SL. Sagittae from fish greater than 20 mm SL were ground and polished, which improved the growth increments. The number of increments counted on the sagittae were consistent with those counted on the lapilli, which were relatively small and difficult to see (Fig. 3). Widths of daily increments ranged from approximately 0.8 to 1.2 μm .

A change in the morphology of the increments was observed at approximately 60 mm SL in the sagittae (Fig. 2), and 20 mm SL in the lapilli (Fig. 3). The width of the increments

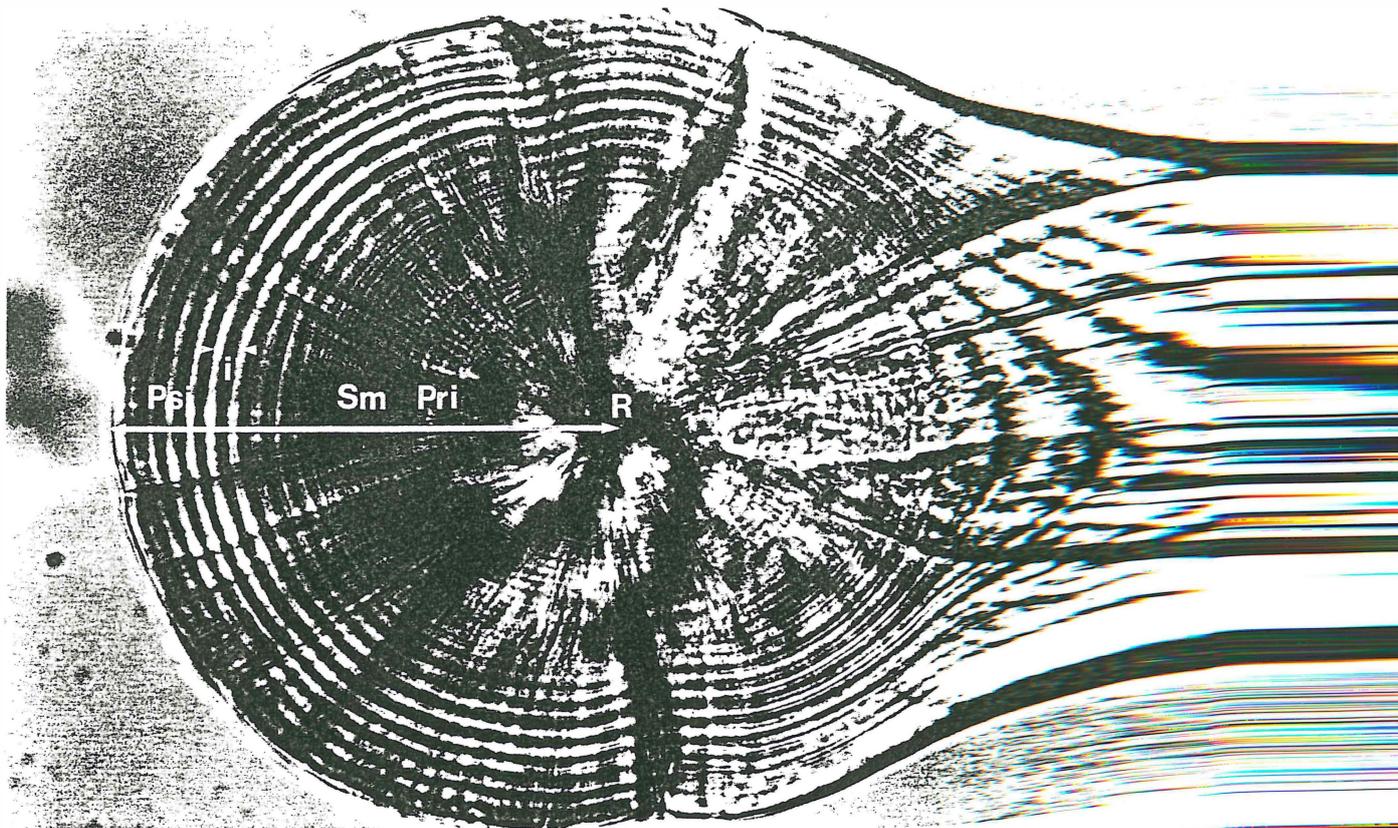


Fig. 2. *Rhombosolea tapirina*. Photomicrograph of a sagitta with 9 post settlement increments, flounder. Growth increments (i) appear as pairs of light (calcium-rich) and dark (protein-rich) bands. Psi: post settlement increments; Pri: pre settlement increments; R: radius for measurement.

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TABLE 1. Univariate repeated measures analysis of variance of temperature variation between bays with Greenhouse-Geisser conservative F-test applied. * P<0.05, ** P<0.001, ns = not significant.

Source	df	MS	F
Bay	1	3.476	39.266 *
Site	4	0.089	
Date	8	23.465	238.183 **
Bay*Date	8	0.143	1.454 ns
Error	32	0.099	

TABLE 2. Regression equations relating standard length to post-settlement increment number, and sagittal radius, for juvenile flounder from sites within Swan Bay and Port Phillip Bay. * P<0.05, ** P<0.001, ns = not significant

Site	Equation	n	R ²	F
<u>Post-settlement increment number</u>				
Port Phillip Bay				
Grassy Point	SL=0.16x+4.94	54	0.68	110.59**
Indented Head	SL=0.18x+4.58	19	0.70	40.21**
Swan Bay				
Jetty	SL=0.30x+4.34	50	0.86	288.50**
Queenscliff	SL=0.29x+4.22	48	0.73	134.84**
<u>Sagittal radius</u>				
Port Phillip Bay				
Grassy Point	SL=0.069x+0.36	46	0.81	182.13**
Indented Head	SL=0.069x+0.06	20	0.86	114.17**
Swan Bay				
Jetty	SL=0.085x-0.74	49	0.92	515.42**
Queenscliff	SL=0.080x-0.05	48	0.89	359.71**

TABLE 3. Analysis of covariance of standard length and post-settlement increment number for juvenile flounder collected in Port Phillip Bay and Swan Bay with two sites nested within each bay. PPB = Port Phillip Bay, SB = Swan Bay. * P<0.05, ** P<0.001, ns = not significant

Source	df	MS	F
Bay	1	0.787	6.089 ns
Site	2	0.129	0.142 ns
Increment no.	1	423.769	464.958 **
Bay*Increment no.	1	29.655	165.505 *
Site*Increment no.	2	0.179	0.197 ns
Error	163	0.911	

TABLE 4. Analysis of covariance of standard length and sagittal radius for juvenile flounder collected in Port Phillip Bay and Swan Bay with two sites nested within each bay. PPB = Port Phillip Bay, SB = Swan Bay. * P<0.05 , ** P<0.001, ns = not significant

Source	df	MS	F
Bay	1	0.432	2.318 ns
Site	2	0.186	0.395 ns
Radius	1	474.034	1006.752 **
Bay*Radius	1	3.846	22.314 *
Site*Radius	2	0.172	0.366 ns
Error	155	0.471	

Figure captions:

FIG. 1. Location of sampling sites in Swan Bay and Port Phillip Bay, Victoria, from which juvenile flounder were collected. Insets: Location of Swan Bay in Port Phillip Bay and location of Port Phillip Bay on the Australian coast.

FIG. 2. Time course of mean water temperature from sites in Swan Bay and Port Phillip Bay. Closed circles, Swan Bay; open circles, Port Phillip Bay. Error bars = S.D.

FIG. 3. Relationship between post-settlement increment number and size of juvenile flounder, data pooled within bays, with fitted regression lines. Open circles, Port Phillip Bay, $y=0.19x+4.94$, $R^2 = 0.76$; closed triangles, Swan Bay, $y=0.29x+4.49$, $R^2 = 0.83$.

FIG. 4. Relationship between sagittal radius and SL of juvenile flounder, data pooled within bays, with fitted regression lines. Open circle, Port Phillip Bay, $y=0.068x+0.33$, $R^2 = 0.83$; closed triangle, Swan Bay, $y=0.083x-0.48$, $R^2 = 0.91$.

Fig. 5. Settlement dates for juvenile flounder collected at two sites in Swan Bay and two sites on the adjacent coast of Port Phillip Bay.

Fig. 1

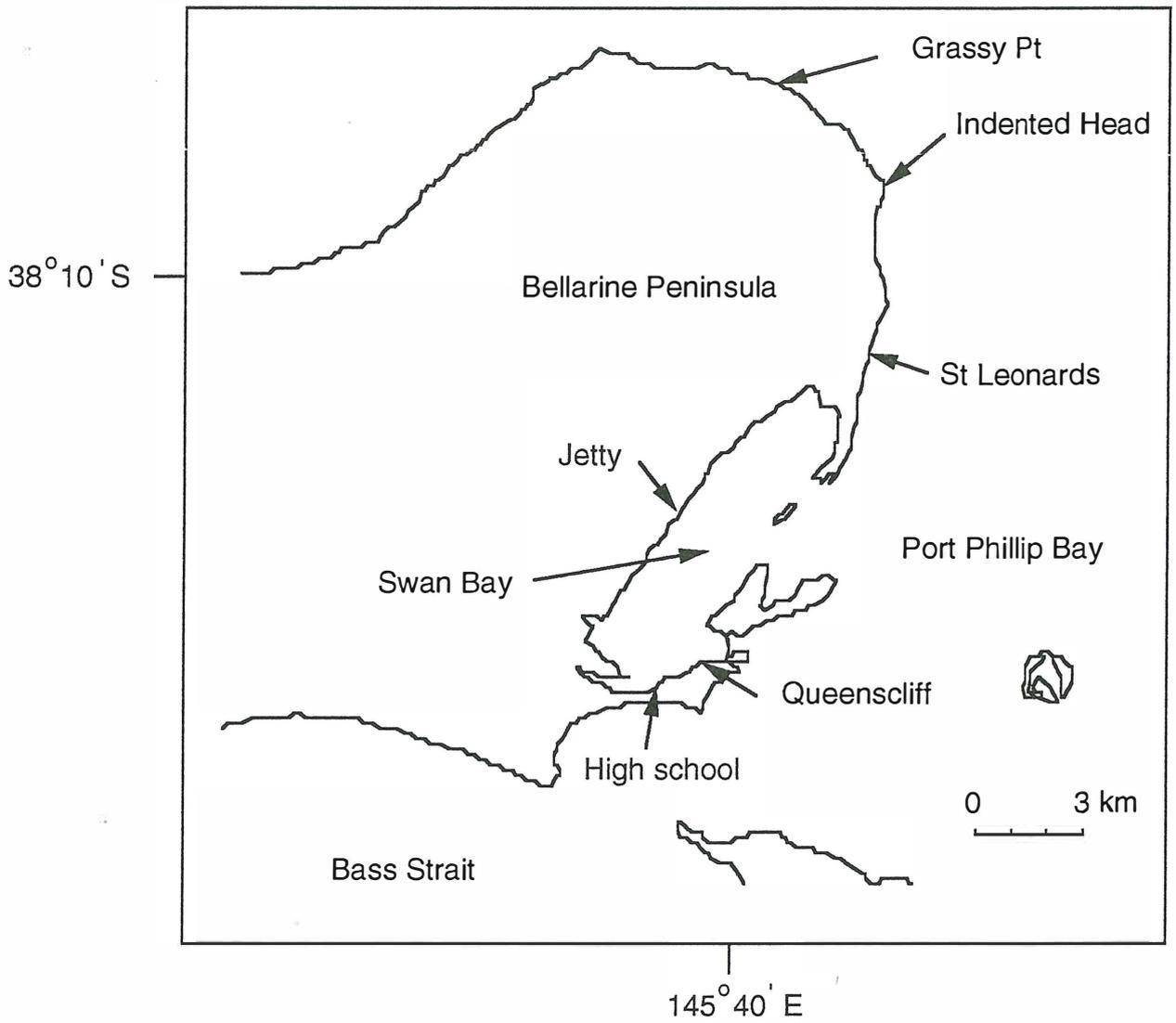
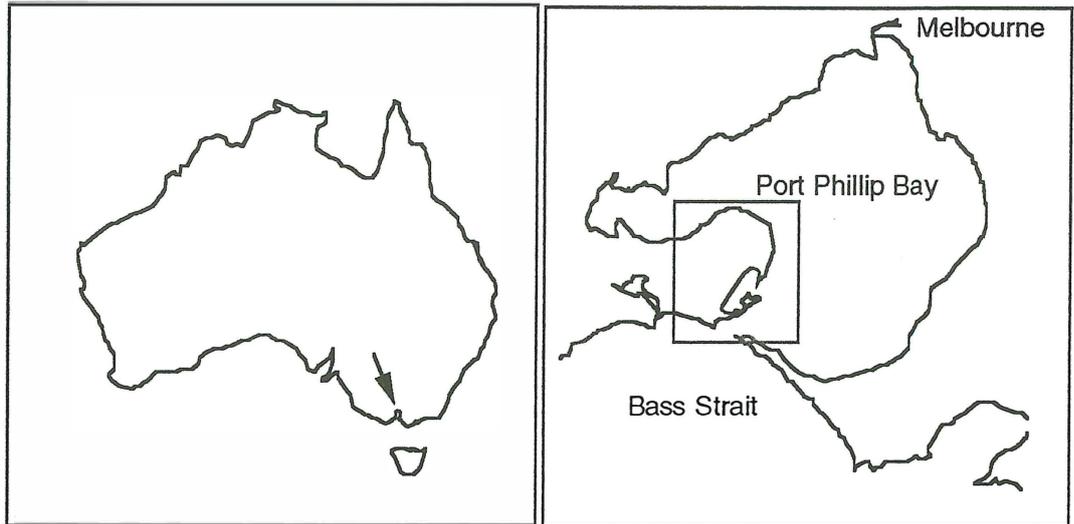


Fig. 2

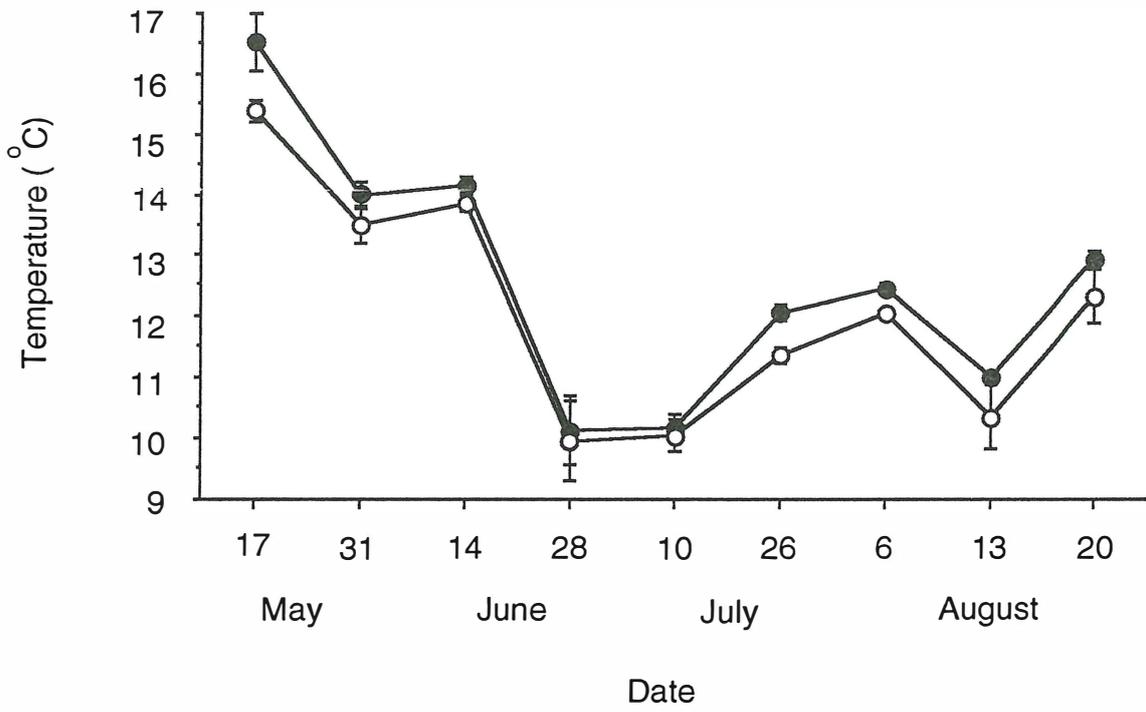


Fig. 3

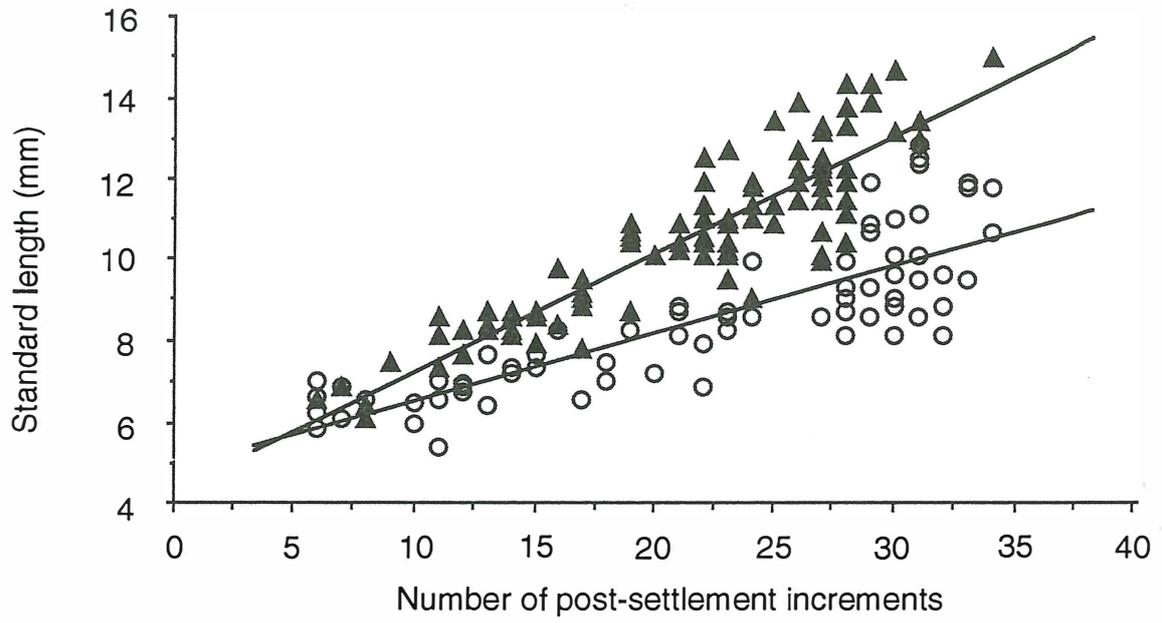
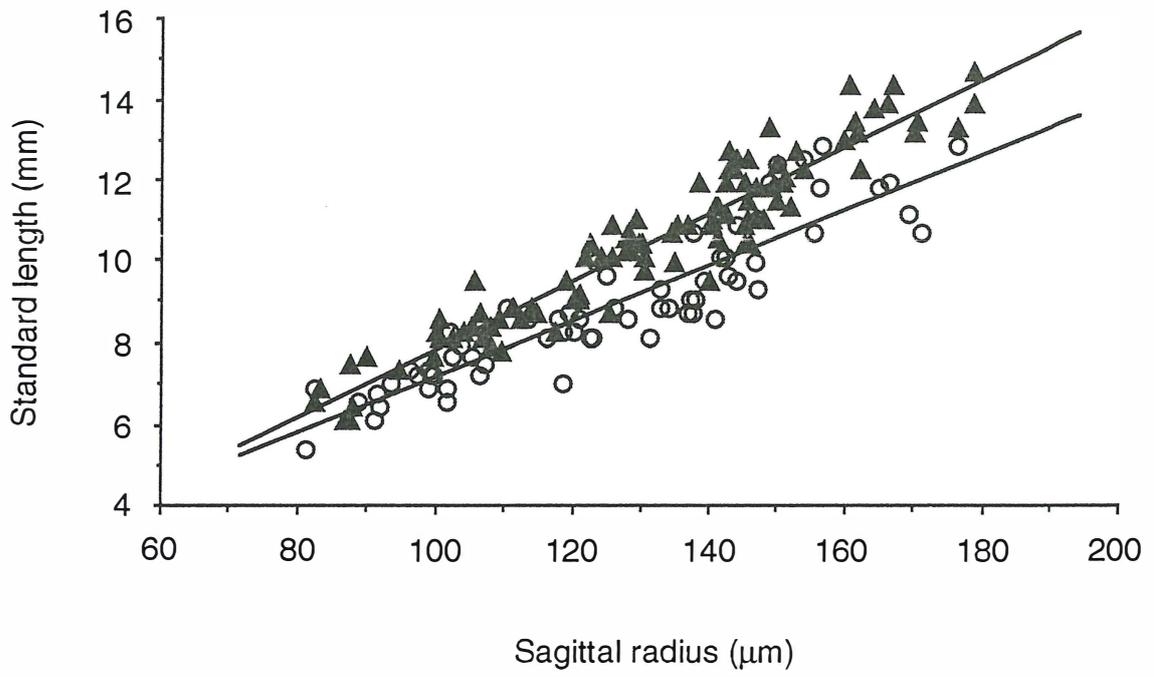
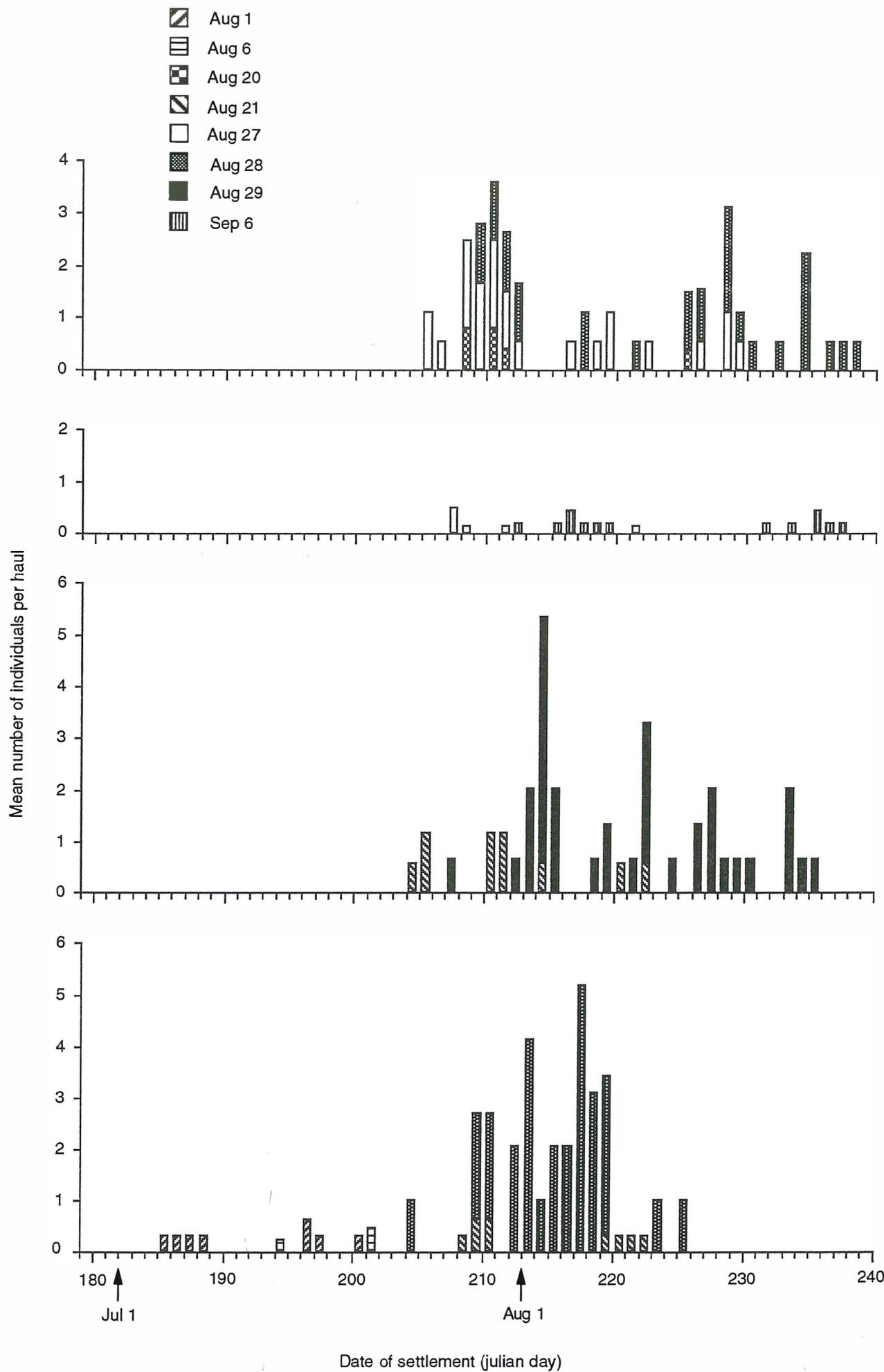


Fig. 4





VARIATION IN SETTLEMENT AND LARVAL DURATION OF KING GEORGE
WHITING, SILLAGINODES PUNCTATA (SILLAGINIDAE), IN SWAN BAY,
AUSTRALIA.

Gregory P. Jenkins and Helen M.A. May

Running head: Larval duration and settlement of King George Whiting

ABSTRACT

Otoliths were examined from late-stage larvae and juveniles of King George whiting, Sillaginodes punctata, collected from Swan Bay in Spring 1989. Increments in otoliths of larval S. punctata are known to be formed daily. A transition in the microstructure of otoliths from late-stage larvae was apparently related to environmental changes associated with entry to Port Phillip Bay. The pattern of abundance of post-larvae of S. punctata in fortnightly samples supported the contention that the transition was formed immediately prior to 'settlement' in seagrass habitats. Backcalculation to the otolith transition suggested that five cohorts had entered Swan Bay, each approximately 10 d apart, from late September to early November. Stability of this pattern for juveniles from sequential samples indicated that otolith increments continued to be formed daily in the juvenile stage. The pattern of 'settlement' was consistent for two sites within Swan Bay. The larval life of King George whiting entering Port Phillip Bay was extremely long and variable, ranging from approximately 100 to 170 days. Age at settlement was more variable than length, and growth rate at settlement was extremely slow, approximately 0.06 mm.d^{-1} . Backcalculated hatching dates ranged from April to July. Increment widths in the larval stage suggest that growth slows after approximately 45 to 75 d; beyond which individuals are in a slow growth, competent stage of 40 to 100 d. Variable larval duration and settlement is discussed in terms of early-life-history strategies and hydrodynamic processes.

There is increasing evidence that some fishes have a variable larval stage divided into precompetent and competent phases (Victor, 1986a; Cowan, 1991). 'Precompetent' refers to the developmental phase up to the point where metamorphosis and settlement is possible. 'Competent' refers to a phase where planktonic life continues although metamorphosis would be possible given suitable cues (Victor, 1986a). The competent phase is often associated with slowed growth (Victor, 1986a; Cowan, 1991). Delayed settlement and metamorphosis is well known for invertebrates in the laboratory, however, field evidence is much more limited (Pechenik, 1990). Amongst planktotrophic larvae a slow growth, competent phase apparently occurs in teleplanic larvae of some tropical gastropods (Pechenik et al., 1984; Scheltema, 1986)

Species that have the potential for delayed metamorphosis may be expected to be those that have relatively specific habitat requirements for metamorphosis and settlement (Pechenik, 1990; Cowan, 1991). Furthermore, delivery of larvae to these habitats may be dependent on specific transport and retention mechanisms (Norcross and Shaw, 1984; Cowan 1991). An extended larval life and dependence on transport and retention mechanisms to deliver larvae to specific juvenile habitats may be expected to lead to settlement variability related to variation in oceanographic processes. This variability could in turn lead to variability in recruitment to fisheries.

Daily increments in otoliths of larval and juvenile fish greatly facilitate the study of larval duration and settlement. A transition in the morphology of increments at the time of metamorphosis and settlement can be used to determine the duration of the larval phase as well as temporal and spatial patterns of settlement (Victor, 1982; Pitcher, 1988; Fowler, 1989; Cowan, 1991; May and Jenkins, 1992). Daily periodicity of increment formation in larval *S. punctata* has been confirmed using laboratory rearing experiments (B. Bruce, unpublished manuscript). In general, although the high correlation usually observed between fish size and otolith size indicates that growth will be strongly related

to increment width (Campana and Neilson, 1985), uncoupling can occur through somatic growth rate (Reznick et al., 1989; Secor and Dean, 1989) and temperature (Mosegaard et al., 1988) effects. Nevertheless, a positive, though not necessarily constant, relationship between otolith growth and somatic growth can reasonably be assumed (Cowan, 1991). This allows increment widths in the larval stage to be interpreted in terms of growth rate (Victor, 1986a; Cowan 1991).

The King George whiting, Sillaginodes punctata, is an important commercial species of southern Australia. Juveniles of this species are generally associated with seagrass habitats in sheltered bays and inlets whilst adults are found associated with deeper offshore reefs (Hutchins and Swainston, 1986). 'Post-larvae' (individuals late in the larval stage which have yet to take on juvenile characteristics such as pigmentation, formation of scales, etc.) of approximately 20 mm length were collected in Western Port Bay in September (Robertson, 1977). Post-larvae of a similar size were collected in Port Phillip Bay in September and Swan Bay in October (Jessop et al., 1986). No larvae of S. punctata, however, were collected in Port Phillip Bay over a three year period (Jenkins, 1986 a,b). In South Australia, post-larvae were collected in sheltered gulfs, however small larvae were near the mouth of Spencer Gulf and in nearshore coastal waters (Bruce, 1989; B.D. Bruce, pers. comm.). It may be hypothesised, therefore, that spawning occurs in coastal waters and larvae eventually enter sheltered gulfs and bays at a relatively large size. In this paper we use microstructure from otoliths of post-larval S. punctata from Swan Bay, Victoria, to examine variability in larval duration and settlement in this species.

METHODS AND MATERIALS

Sampling area. – Swan Bay is a sheltered, shallow (2-3 m), marine embayment adjacent to Port Phillip Bay, Victoria (Fig.1). Swan Bay has significant meadows of seagrasses; Zostera muelleri on intertidal mudbanks and Heterozostera tasmanica subtidally. There are also considerable areas of detached macroalgae (much of which is growing 'in situ') in deeper parts of the bay. The adjacent area of Port Phillip Bay is characterised by strong currents associated with tidal exchange through the narrow entrance between Port Phillip Bay and Bass Strait (Fig. 1).

Field methods. – Post-larval and juvenile S. punctata were collected from September 1989 to January 1990 at two sites, Tincan and North Jetty (Fig. 1). A seine net (10 m x 3 m x 1 mm mesh) was deployed from a boat over unvegetated patches amongst seagrass beds at a depth of approximately 1 m MLWS. The net was hauled over a distance of 15 m. Three replicate hauls, haphazardly placed and non overlapping, were made at each site. Post-larvae and juveniles were sorted from the net, anaesthetized in benzocaine, and preserved in 95% ethanol.

Laboratory methods. – For samples with more than approximately 20 post-larvae, a random subsample of 15 to 20 individuals was examined. The standard length (SL; tip of the snout to the tip of the caudal peduncle) of specimens was measured under a dissecting microscope fitted with an ocular micrometer. Specimens were placed in a drop of water on a microscope slide and the otoliths were dissected out using electrolytically-sharpened tungsten needles. Contrast between the otoliths and surrounding tissue was maximised by using a polarising light source fitted to the stereo microscope. The otoliths, which were hemispherical in shape, were left to dry, flat side up, and then placed in immersion oil on glass microscope slides.

Otolith increment counts and measurements were made with a compound microscope. A video camera connected to the microscope produced an image which was displayed and digitised on a Commodore 'Amiga' computer. Specimens were examined randomly and blindly with respect to SL. Counts and measurements were made along the longest axis of the antirostrom.

Sagittae of post-larvae generally contained clear increments from the primordium (Fig. 2A) to near the otolith edge, where increments rapidly increased in width and became confused in structure. Increments near the primordium in the lapilli were extremely narrow and could not be counted confidently with the light microscope, however, post-transition increments were discernable (Fig. 2B). We therefore used sagittae for analysis of pre-transition increments and lapilli for analysis of post-transition increments. Pre-transition increments were counted on both sagittae, and post-transition counts were counted on both lapilli, for subsamples of post larvae of S. punctata. Pre-transition increments on sagittae (n=20, Paired t = 0.501, P>0.5) and post-transition increments on lapillae (n=89, Paired t = 0.528, P>0.5) showed no significant difference and therefore subsequent counts were made on one randomly selected otolith from each pair. Post-transition increments were not clear enough to count on approximately 15 % of lapilli.

RESULTS

Post-larval *S. punctata* of approximately 16 to 22 mm SL were collected from early October to November (Fig. 3). Length-frequency distributions suggest a single cohort of post-larvae until November 28/29 when two cohorts were apparent (Fig. 3). Juveniles collected in January showed a wide range of standard lengths (Fig. 3).

The date of formation of the otolith transition was calculated under the assumption of daily-increment periodicity in the post-larval stage. Dates of otolith transition fell into distinct groups or cohorts which were consistent for the two sites and stable over time (Fig. 4). This stability over time indicates that the number of increments laid down was equal to the number of days between sampling dates, and suggests that increments formed in the post-larval/juvenile phase, like the larval phase, had a daily periodicity.

The increment transition in otoliths from smallest post-larvae collected was close to the otolith edge, suggesting that the transition formed at about the time that individuals arrived in Swan Bay. This contention was supported by the fact that the backcalculated date of transition formation corresponded well with the time-course of post-larval abundances (Fig. 5). No post-larvae were collected in mid-September which is in agreement with the fact that otolith transitions did not begin until after this date (Fig. 5). A large group of post-larvae with otolith transitions in late September were reflected in the collection of approximately 15 post-larvae per haul on October 3. Much fewer post-larvae with otolith transitions in early October were reflected by the collection of slightly fewer post-larvae collected on 16 October. Two major pulses of post-larvae with otolith transitions in mid to late October were reflected in a high abundance of post larvae collected on 2 and 3 November. Few post-larvae had otolith transitions after this date, and this was reflected in an exponential decline in post-larval and juvenile abundances after this date. From this evidence we can assume that the otolith transition is associated with ingress of post-larvae to Swan Bay. It therefore

appears that ingress occurred in five pulses over a two month period from mid September to mid November (Fig. 5). These five cohorts were separated by a period of approximately 10 to 14 d.

The growth rate of post-larvae and juveniles was assessed from the relationship between size and the number of post-transition increments (Fig. 6). A significant linear relationship for the first 50 days indicated a growth rate of 0.11 mm.d^{-1} ($n=261$, $F=284.5$, $P<0.001$). Although the sample size of older juveniles was small, there appeared to be a rapid increase in growth rate after 50 d.

Pre-transition increments could be counted without grinding or polishing on sagittae of individuals with approximately 13 or less post-transition increments (Fig. 7). Number of pre-transition increments ranged from 106 to 167. The mean number of pre-transition increments was 127.4 d (S.D.=12.0).

Standard length was regressed against total (pre + post-settlement) increment number for post-larvae with 13 or less post-settlement increments (Fig. 8). The regression was significant ($n=48$, $F=21.3$, $P<0.001$) and suggested an average growth rate in the late-larval stage of 0.06 mm.d^{-1} (Fig. 8). The unrealistically high intercept of 11.37 suggests that the growth rate must have been higher in the early larval stage. The mean total number of increments was 136.7 (S.D.=11.1) while the mean length was 20.1 (S.D.=1.2). The bias-corrected coefficient of variation (Haldane, 1955) for total number of increments ($CV=0.813$) was higher than that for length ($CV=0.058$). Coefficients of variation were compared statistically (Chambers and Leggett, 1987) using the method of Sokal and Braumann (1980) and age was found to be significantly more variable ($df=94$, Paired $t = 2.65$, $P<0.001$).

Total increment number (pre + post-settlement) was also used to hindcast the date of first increment formation for post-larvae (Fig. 9). The first increment is formed

at about the time of first feeding, approximately 4-6 d after hatching (B.D. Bruce, unpublished manuscript). Spawning occurred from approximately mid April to mid July, the majority from the beginning of May to the end of June.

Pre-transition increment widths showed a gradual increase before decreasing to a lower constant level until the post-larval stage. This trend is shown for sagittae from five randomly selected post-larvae in Figure 10. The mean number of increments to the point where increment width began to decrease was 59.4 (S.D.=7.0, range 45-74). The mean number of increments from this point to the otolith transition was 68.8 (S.D.=14.6, range 41-101). The coefficient of variation for the duration of the initial phase (C.V.=0.119) was significantly less than for the second phase (C.V.=0.212)(df=64, Paired $t = 2.978$, $P < 0.005$). The duration of the two phases was not correlated ($n=33$, $r=0.011$, $P > 0.5$).

DISCUSSION

Post-larvae of S. punctata do not undergo distinct metamorphosis and settlement where morphology and ecology change rapidly upon arrival at the juvenile habitat. There is little morphological change in post-larvae once they have arrived at the juvenile habitat (B.D. Bruce, submitted). In terms of ecology, the diet retains a large component of planktonic prey, together with seagrass-associated invertebrates (G. Jenkins, unpublished data). It is apparent then that the increase in increment width in the post-larval phase is not associated with a distinct metamorphosis (Victor, 1982; May and Jenkins, 1992). The increase in increment width would also not appear to be associated with a particular developmental stage, as it occurred over a wide range of sizes and ages. Somatic growth and otolith growth is known to be primarily influenced by temperature and food ration (Campana and Neilson, 1985). It seems likely then that arrival of post-larvae in shallow, coastal habitats is associated with increase in water temperature and/or food ration which in turn leads to an increase in somatic and otolith growth, the latter translating into increased increment width. The approximate doubling of growth rate for individuals with few post-transition increments compared with older juveniles is evidence for an increase in somatic growth upon arrival at the juvenile habitat, for which a concomitant increase in otolith growth would be expected. We hypothesise that the transition to increased increment widths is associated with entry of post-larvae to more productive and/or warmer waters of Port Phillip Bay. A similar pattern of otolith microstructure for post-larvae of S. punctata in South Australia sometimes, but not always, occurs (B. Bruce, pers. comm.). Further work is required to isolate the causes of increment width transition in post-larvae.

Length-frequency analysis suggested a single major cohort appeared in October with a possible second cohort apparent by November. This result concurs with length frequency analysis for Westernport Bay where a single cohort of approximately 20 mm appeared in September (Robertson, 1977) and for Port Phillip Bay where a cohort of

individuals of approximately 20 mm SL appeared in October (Jessop et al., 1986). Appearance of post-larvae of S. punctata of approximately 20 mm SL in Spring therefore shows interannual consistency for shallow-coastal habitats of central Victoria. In contrast, the majority of post-larvae of S. punctata in South Australia appear in shallow coastal habitats from April to September at a size of 15 to 18 mm SL, although 18 to 20 mm post-larvae have been recorded in November, a similar pattern to that observed in Victoria (Bruce, 1989).

In contrast to length-frequency analysis, otolith analysis resolved five cohorts of post-larvae of S. punctata. The lack of pattern in hatching dates and variability in larval duration indicates that temporal variation in ingress is not a result of temporal variability in spawning and a relatively fixed larval duration (Robertson et al., 1988; Hunt von Herbing and Hunte, 1991). However, the approximate 10 to 14 day period between cohorts approximates the long term cycle of low frequency oceanographic events which influence net input of water to Port Phillip Bay. Ingress of crab zoeae to estuaries appears to depend on the coincidence of patches of zoeae at the estuary mouth with an approximately 10 d cycle of coastal setup (Little and Epifanio, 1991). We hypothesise that the variability in temporal appearance of cohorts of S. punctata is also associated with cyclic positive anomalies. Analysis of temporal variation in ingress in other years in combination with hydrodynamic modelling to simulate the temporal variation in entry of passive particles to Port Phillip Bay may in the future be used to investigate this hypothesis.

Rearing experiments indicate that increment formation in sagittae of S. punctata begins at about the time of first feeding, approximately 4-6 d after fertilization (B. Bruce, unpublished data). The spawning period determined from otoliths of post-larvae of S. punctata from South Australia began slightly earlier than that determined in our study, ranging from late February to July (Bruce, 1989; B.D. Bruce, unpublished

manuscript). Unlike the present study, there was a suggestion of lunar periodicity in spawning over this period.

S. punctata has a long larval-life and appearance in juvenile habitats occurs at a relatively large size when compared with species of other groups (Brothers et al., 1983; Victor, 1986b; Wellington and Victor, 1989). The significantly greater variation in age at ingress compared with variation in length is consistent with results for flatfish and wrasse (Chambers and Leggett, 1987). The absolute variation in age at ingress is comparatively high, however the coefficient of variation is lower than recorded for flatfish and wrasse (Chambers and Leggett, 1987). In contrast the coefficient of variation in length was very similar to flatfish and wrasse (Chambers and Leggett, 1987). Growth rate of post-larvae appears to be very slow and there are indications that growth rate earlier in the larval stage must have been higher. There is a very high correlation between fish length and sagittal radius in the larval stage of S. punctata (B. Bruce, unpublished manuscript). This allows increment widths in the larval stage to be interpreted in terms of growth rate (Victor, 1986a; Cowan, 1991). Pre-transition increment widths of post-larval S. punctata from Port Phillip Bay suggest that larval growth rate increases steadily for 45 to 75 d and then decreases to a lower constant level. This pattern of increment width has also been observed in some labrids where there is a developmental phase up to a point where settlement can occur, however the pelagic phase may be extended beyond this period in a slow growth, competent phase, presumably until a suitable settlement habitat is found (Victor, 1986a; Cowen, 1991). The fact that the number of pre-transition increments in sagittae of post-larvae of S. punctata in South Australia mainly range from 60 to 80 increments (Bruce, 1989) suggests that the observed decrease in increment width signifies the onset of the competent phase. In contrast to South Australia, all post-larvae in Swan Bay had more than 100 pre-transition increments, ranging up to 170. The relatively long pre-competent phase and apparent extreme potential for extending larval life support's

Jackson and Strathmanns (1981) contention that because a species with a long pre-competent phase may be widely dispersed, a long competent phase would be necessary to increase the probability of finding a settlement site (Cowen, 1991).

We have used increment width as an index of larval growth rate in the larval stage. Variation in growth rate is known to influence the scaling between otolith growth and somatic growth. In short, otolith growth is faster (and therefore increment width is wider) relative to somatic growth in slower growing fish (Reznick et al., 1989; Secor and Dean, 1989), possibly due to a minimum deposition of calcium in the otolith (Secor and Dean, 1989). In terms of larval growth of S. punctata, the reduction in growth rate on competency may be greater than indicated by the reduction in otolith increment width (Hovencamp, 1990; Cowen, 1991). Indeed, the estimated growth rate of 0.06 mm.d⁻¹ was extremely slow compared with the usual range for marine fish larvae of 0.1 to 0.5 mm.d⁻¹ (citations in Jenkins and Davis, 1990) and compares with the rate of 0.08 mm.d⁻¹ estimated for the competent stage of larval Thalassoma bifasciatum (Victor, 1986a).

The necessity for a long competent phase would be increased where settlement sites were relatively restricted (Cowen, 1991). This would appear to be the case for S. punctata along the Victorian coast where the availability of sheltered seagrass habitats is very restricted. Cowen (1991) has also hypothesised that a longer competent period may be advantageous for larvae which depend on short duration circulation events which occur relatively infrequently. The extended competent phase allows larvae to be present when a suitable onshore circulation event occurs (Cowen, 1985). The postulated hydrodynamic control of pulsed ingress of post-larvae of S. punctata in this study is a possible example of this phenomenon.

It seems likely that in species such as S. punctata, which have a reduced-growth, competent phase, that the disadvantages of extending the larval period in which vulnerability to starvation and predation is thought to be high is more than outweighed by the advantage of increasing the probability of encountering suitable juvenile habitat. The question of why growth slows markedly at the onset of the competent stage rather than continuing at a similar rate to the precompetent phase remains open; perhaps the adaptive value of larval morphology and ecology is reduced at larger sizes (Cowen, 1991). Alternatively, perhaps the size at competency represents the most efficient for survival upon arrival to the juvenile habitat.

The only known spawning area of S. punctata is the nearshore coastal waters of South Australia (B. Bruce, unpublished manuscript), a distance of approximately 800 km from Port Phillip Bay. It seems possible, given average current speeds through Bass Strait over winter/spring period, that larvae could be transported from South Australia to Port Phillip Bay (B.D. Bruce, pers. comm.). Plankton sampling for eggs and early larvae of S. punctata off the west coast of Victoria would be necessary before spawning in Victorian waters could be discounted. The narrower range of ingress dates relative to spawning dates is somewhat surprising given the wide variation in larval duration (Victor, 1986). It is possible that if spawning occurs in western Victoria or South Australia, there may be a relatively narrow window of time when currents are capable of transporting larvae to Port Phillip Bay.

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Figure captions:

- Fig. 1 Location of sampling sites in Swan Bay, Victoria, from which post-larval and juvenile King George whiting were collected. Insets: Location of Swan Bay in Port Phillip Bay and location of Port Phillip Bay on the Australian coast.
- Fig. 2 Light micrographs of otoliths from post-larval King George whiting. (A) Sagitta, central region including primordium. (B) Lapillus, arrow indicates transition in increment width. Scale bars = 20 μm .
- Fig. 3 Length frequency distributions of post-larvae and juveniles King George whiting collected at two sites in Swan Bay from October 1989 to January 1990.
- Fig. 4 The relationship between mean abundance and date of otolith transition for post-larval and juvenile King George whiting collected at two sites in Swan Bay from October 1989 to January 1990.
- Fig. 5 The relationship between mean abundance and, (A) date of otolith transition (data in figure 4 overlaid), (B) sampling date, for post-larval and juvenile King George whiting collected at two sites in Swan Bay from October 1989 to January 1990.
- Fig. 6 Relationship between standard length of post-larval and juvenile King George whiting and the number of post-transition increments on lapilli. Linear regression equation for the first 50 post-transition increments:
 $Y=0.11X+19.22, r^2=0.51$

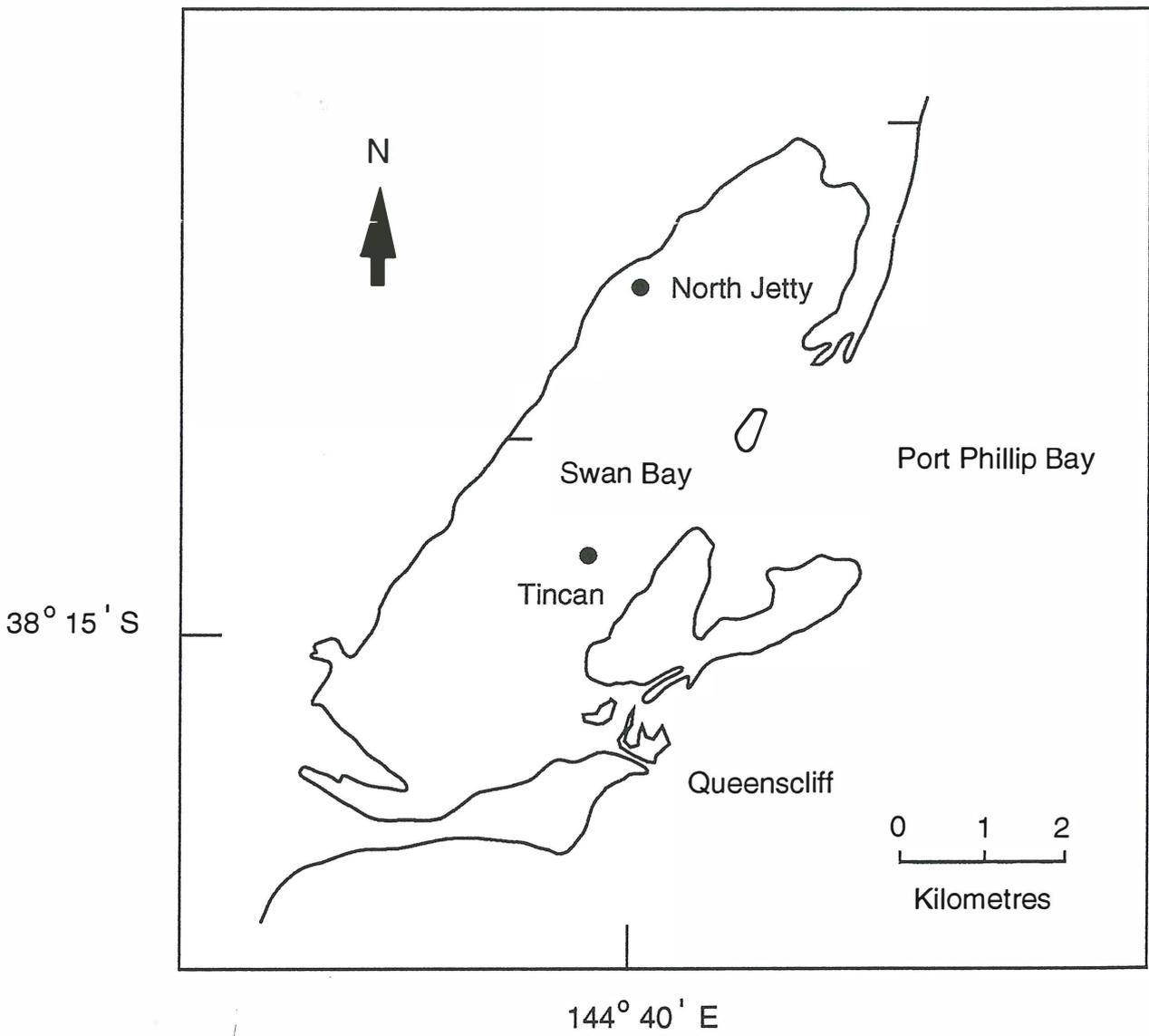
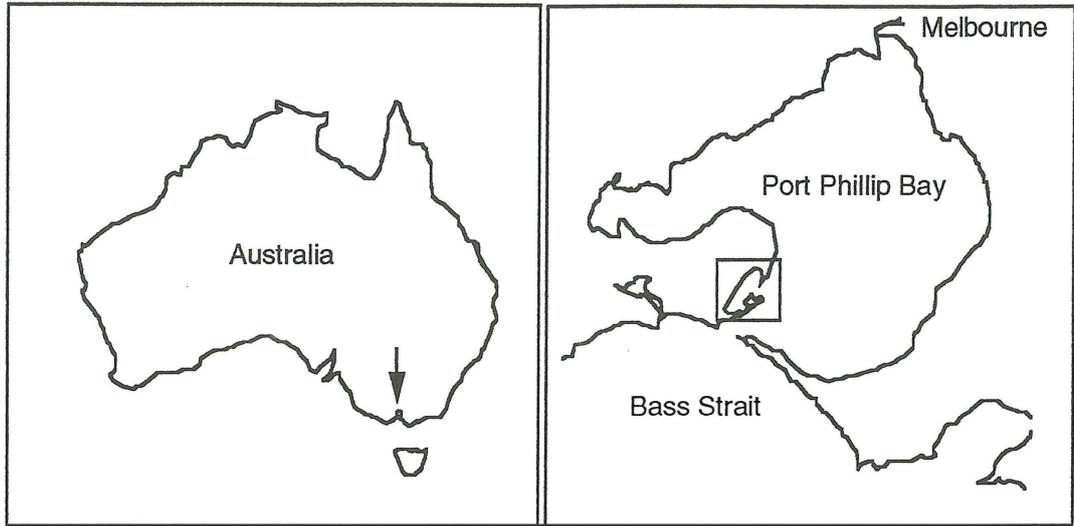
Fig. 7 Frequency distribution of the number of pre-transition increments on sagittae of post-larval King George whiting.

Fig. 8 Relationship between standard length and total increment number for post-larvae of King George whiting with 13 or less post-transition increments.

Fig. 9 Frequency distribution of the date of first increment formation for post-larvae of King George whiting with 13 or less post-transition increments.

Fig. 10 Relationship between increment width and number of pre-transition increments for five randomly selected post-larvae of King George whiting.

Fig. 1



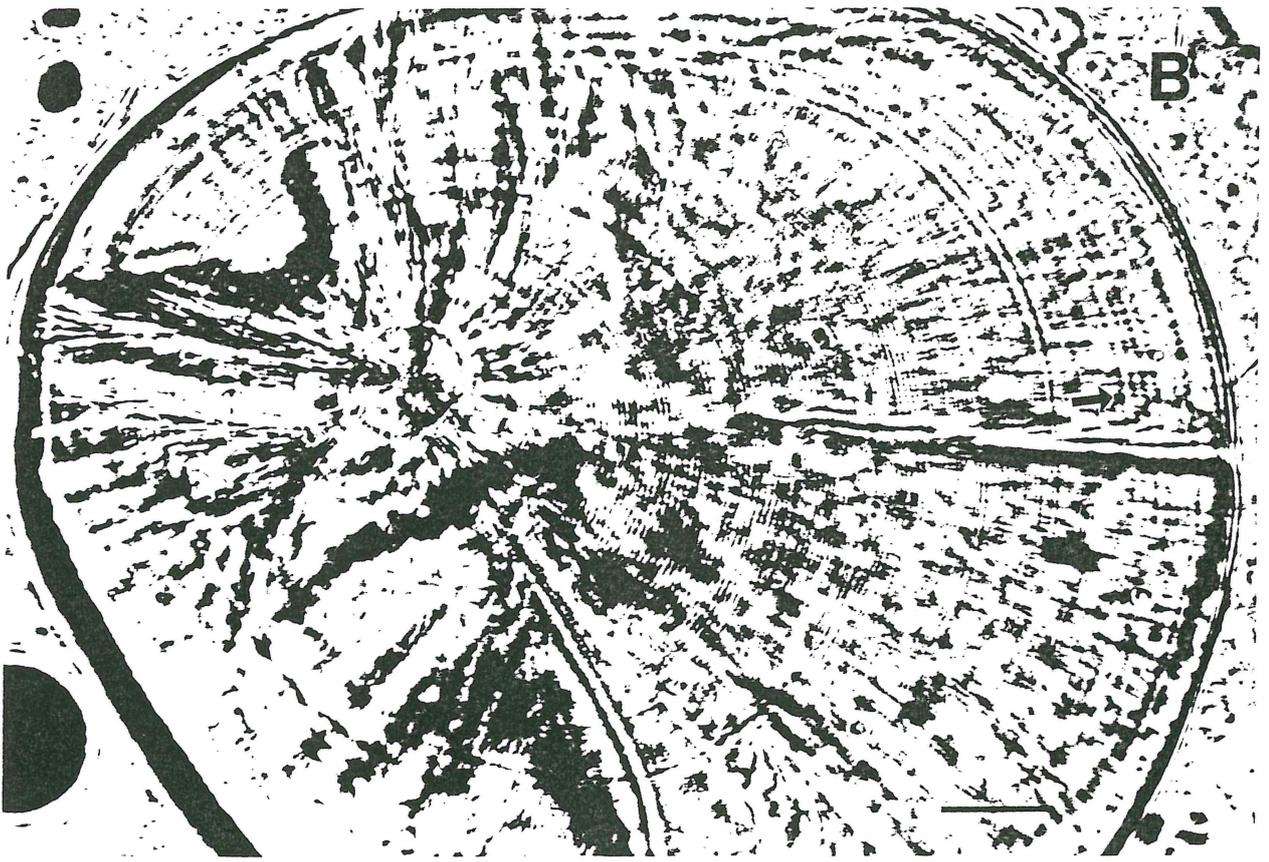
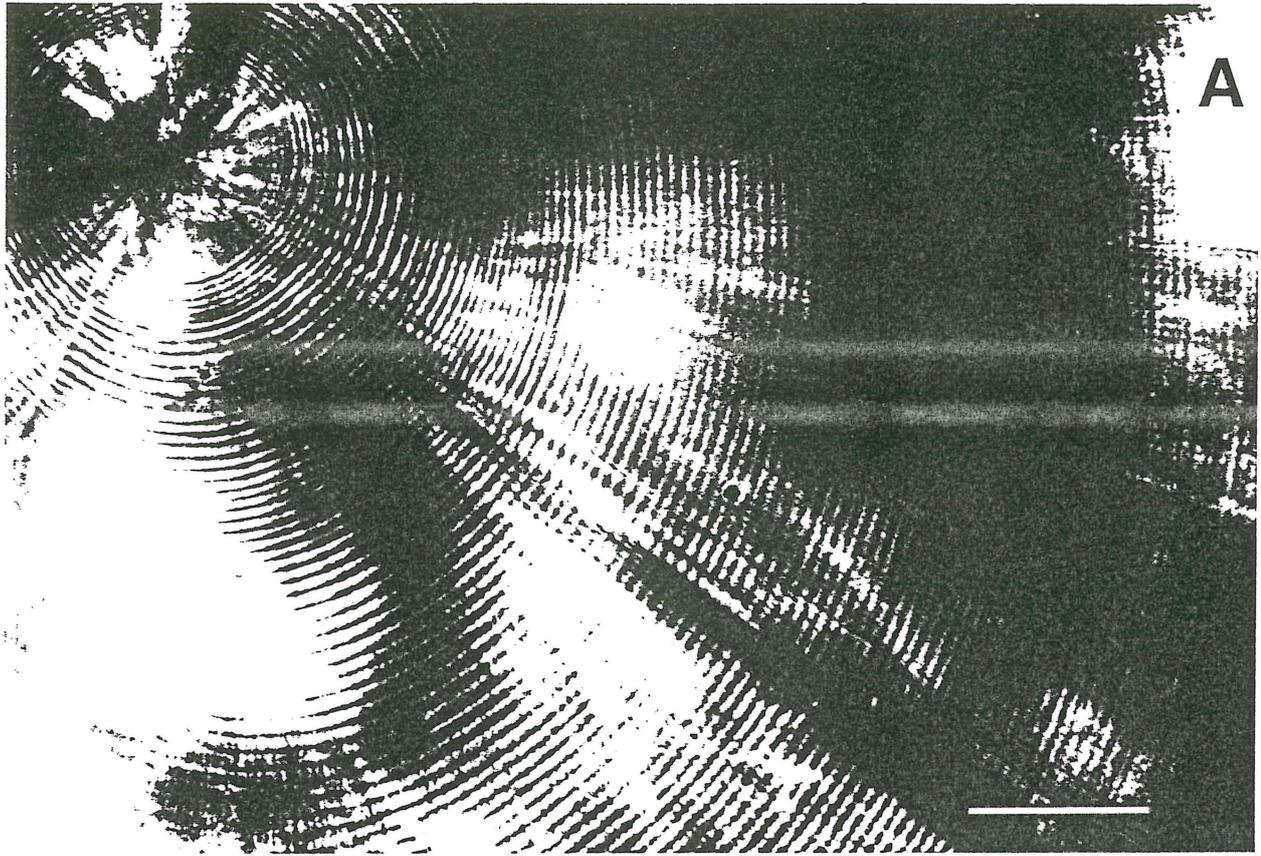


Fig. 3

■ North jetty
□ Tin can

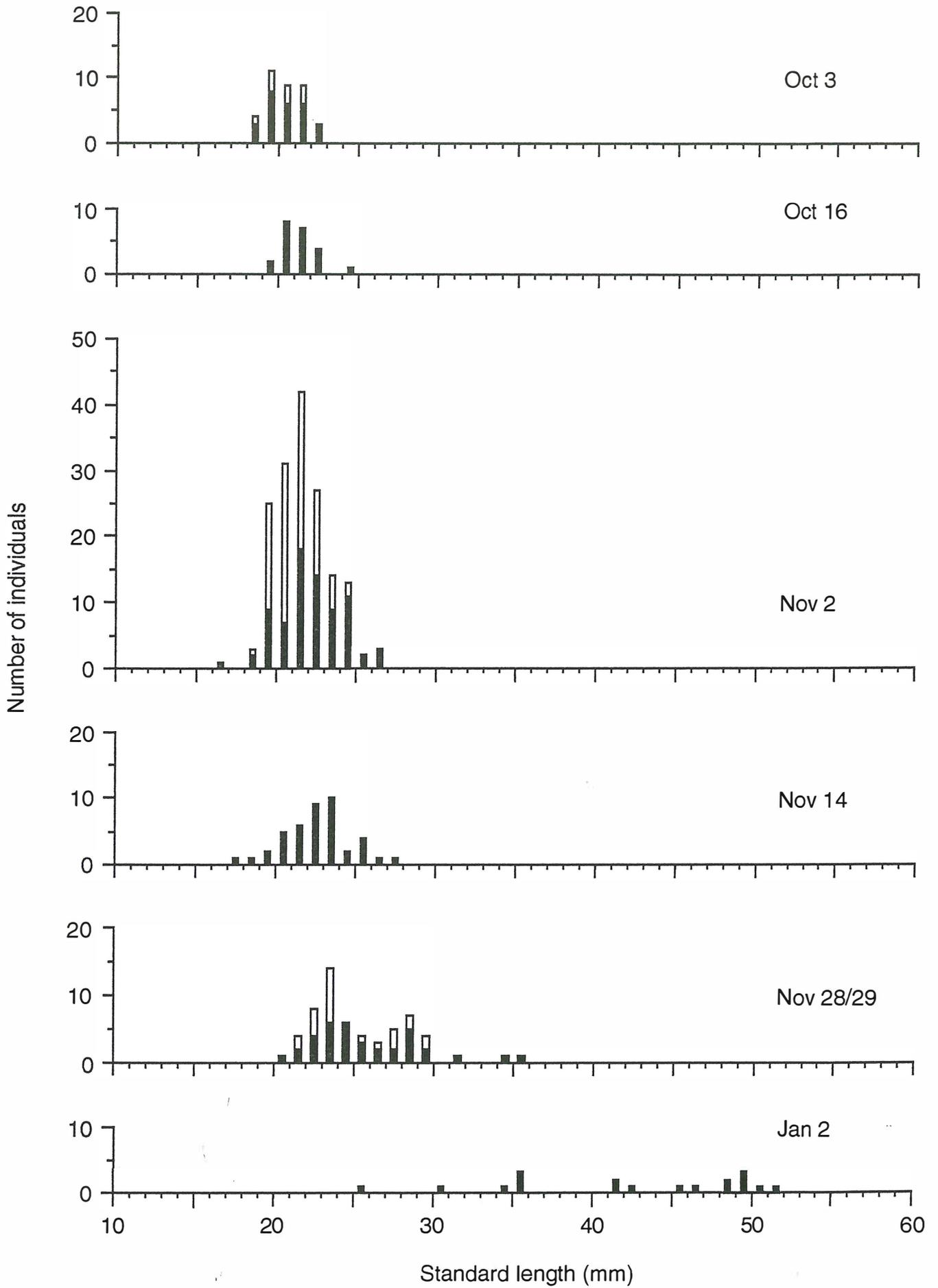


Fig. 4

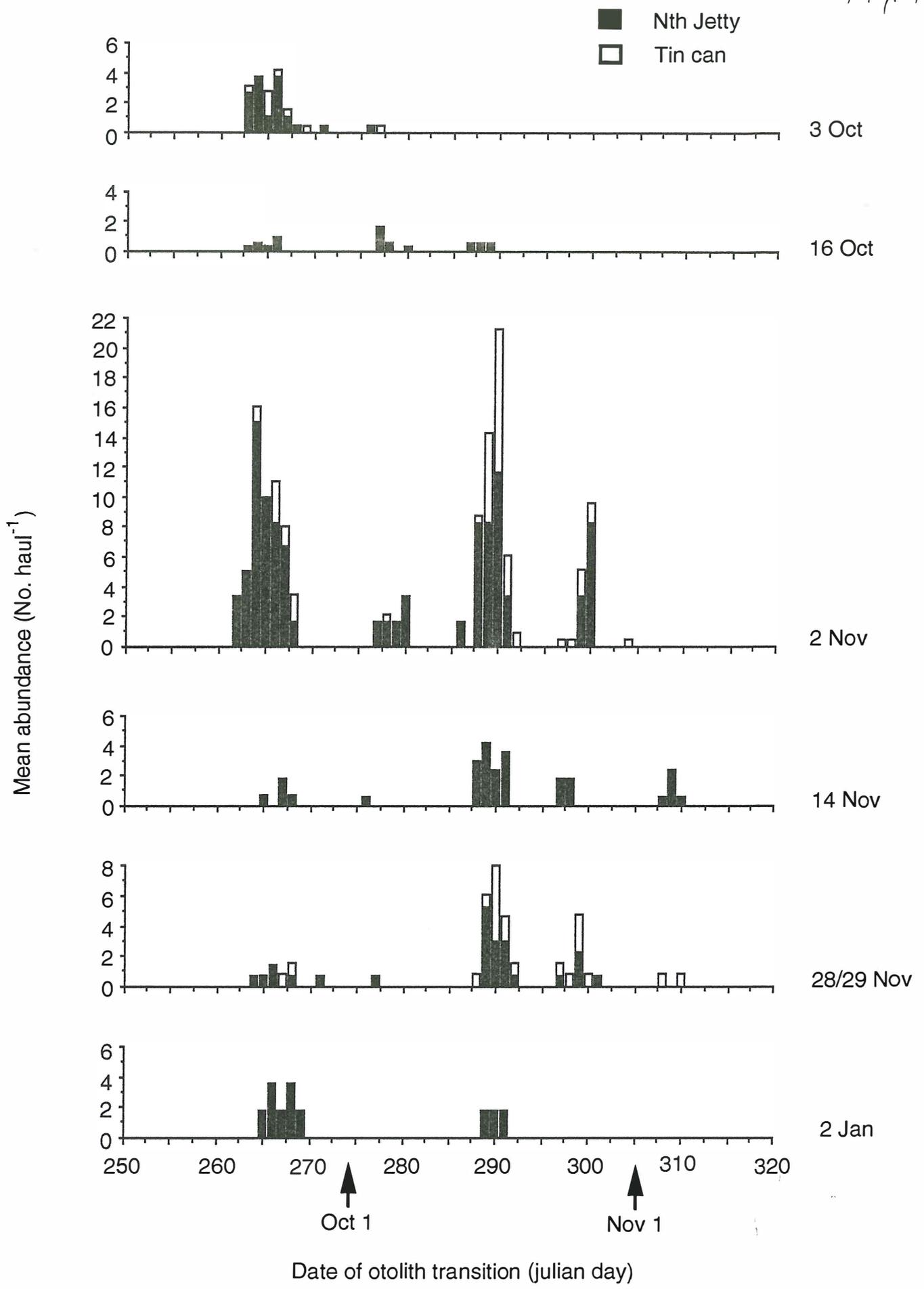


Fig. 5

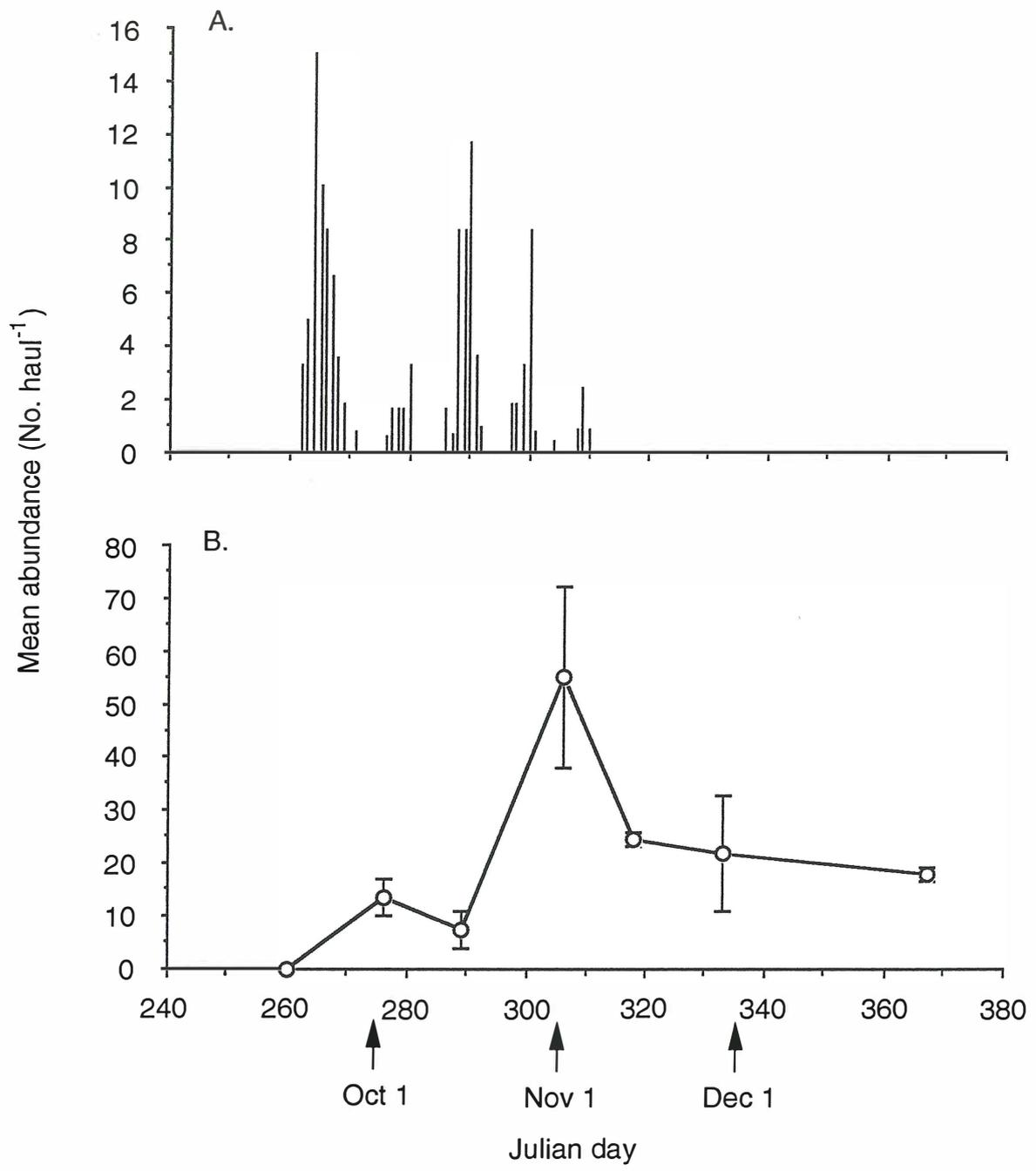


Fig. 6.

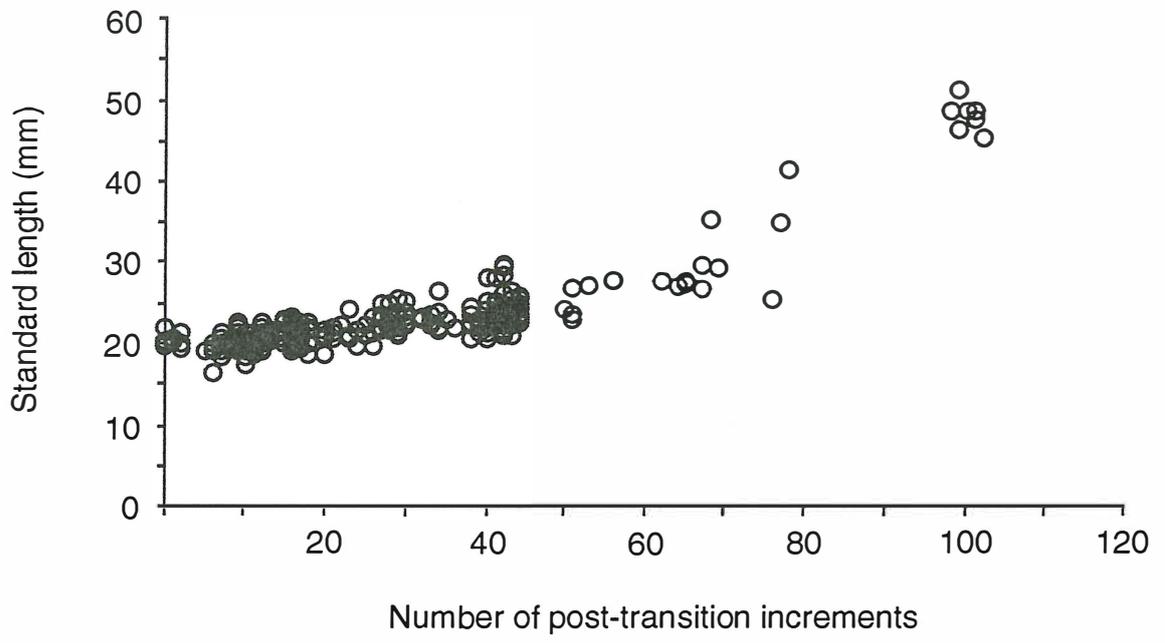


Fig. 7

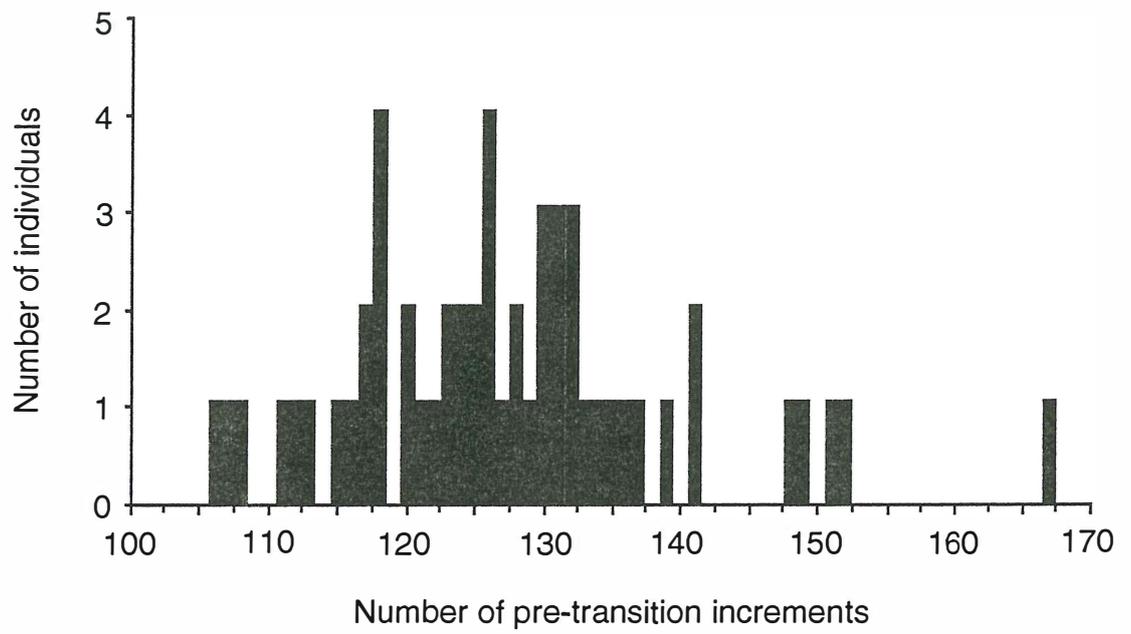


Fig. 8

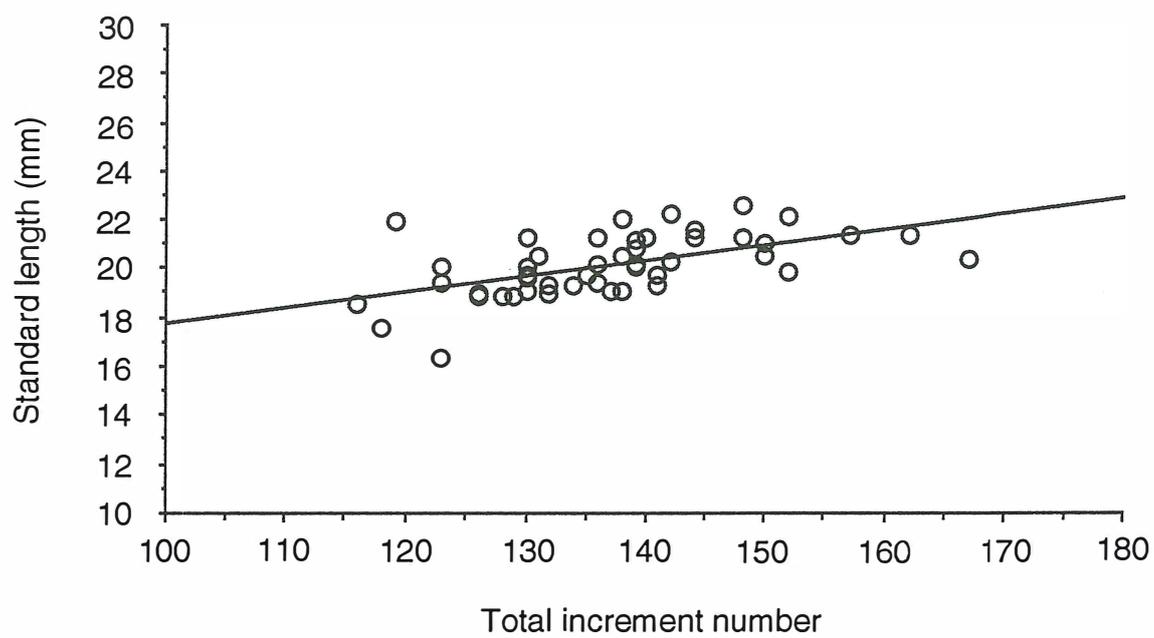


Fig. 9

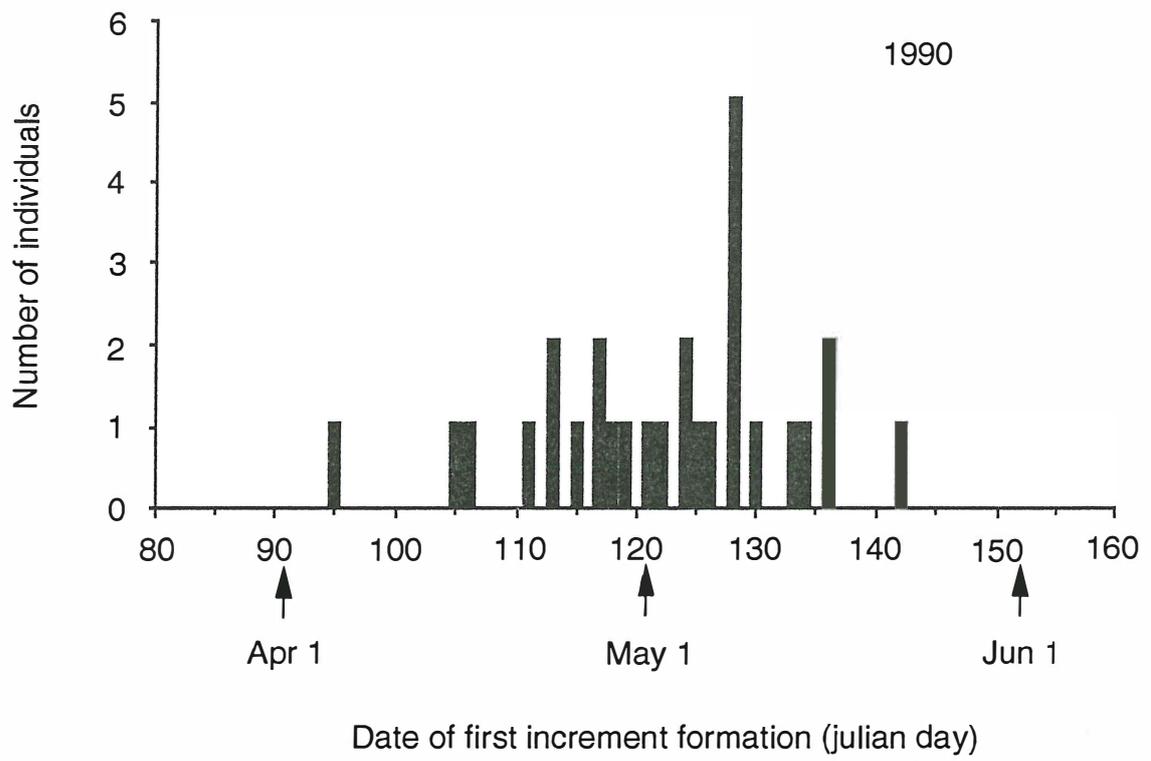
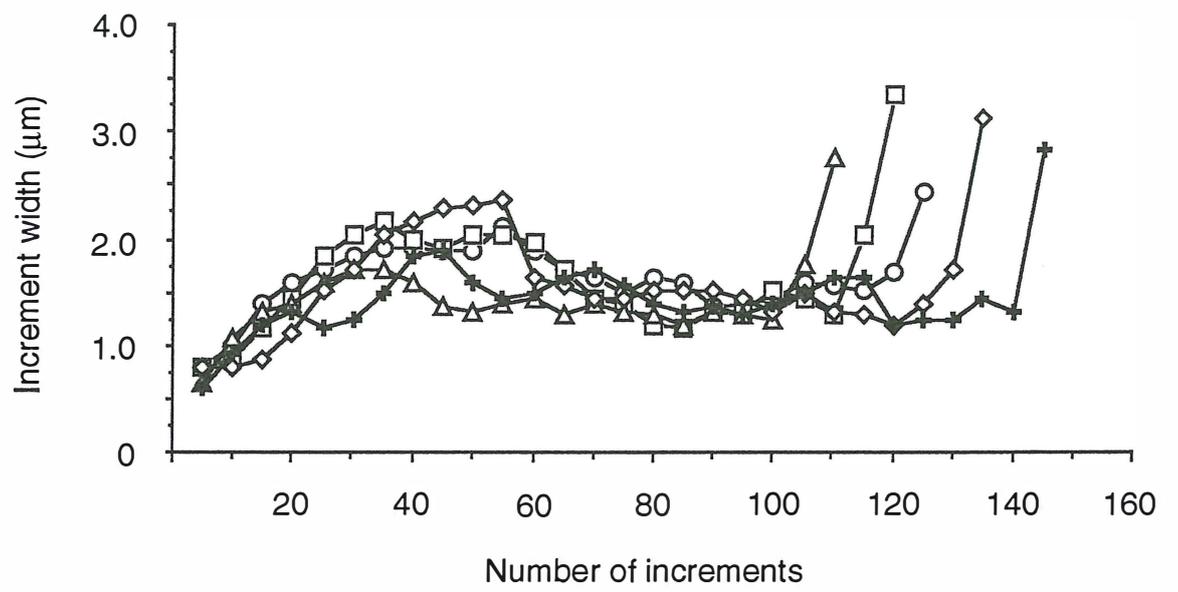


Fig. 10.



Temporal variability in settlement of a coastal fish, the King George whiting,
Sillaginodes punctata, is determined by hydrodynamic factors.

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Recent intensive work has increasingly demonstrated the importance of varying larval supply in determining the structure of marine communities (Doherty & Williams 1988, Roughgarden et al. 1988, Underwood & Fairweather 1989, Sale 1990). It follows that processes occurring in the planktonic larval phase have a major influence on the structure and dynamics of marine populations. The combination of research on small-scale coastal hydrodynamics and marine ecology is thought to be a critical area of research needed in this field (Underwood & Fairweather 1989, Sale 1990).

One approach to this research is to compare the actual distribution of recruits to the null distribution which would be predicted from models of water circulation if larvae are treated as passive particles. This approach has been used successfully to predict spatial variation in settlement of Crown of Thorns starfish (Black and Moran 1991) and abalone (McShane et al. 1988). Intra-annual variation in settlement of barnacles has been linked to variation in cross-shelf transport (Farrell et al. 1991). Large-scale spatial and inter-annual variation in recruitment of a reef fish has been linked to coastal oceanography (Cowen 1986). There is little evidence to date, however, linking small-scale spatial and short-term temporal variation in settlement of fishes to small-scale coastal oceanography. In the case of many invertebrates, correlation between settlement and coastal oceanography is not surprising as the relatively weak-swimming larvae would tend to behave as passive-particles in all but the weakest currents (Black et al. 1991, Mullineaux and Butman, 1991). However, larval fish may be expected to have greater control over movement due to larger size, a more complex behavioural repertoire, and better swimming ability. Although this assumption is often expressed, the relative importance of active and passive processes in determining the small-scale settlement patterns of fish has not been assessed using the hydrodynamic modelling/ecological sampling approach.

Ingress of the post-larvae of the King George whiting, Sillaginodes punctatus, to Port Phillip Bay and Swan Bay, Victoria, shows strong temporal variability on an

approximate ten to fourteen day cycle (Jenkins and May in press). Swan Bay is a small, shallow bay adjacent to Port Phillip Bay, a large marine embayment with a narrow entrance from Bass Strait (Fig. 1). Post-larvae of S. punctatus enter Port Phillip Bay at an advanced stage (15 - 20 mm), near the end of a long (over 100 d) and variable larval phase (Jenkins and May in press).

We have addressed the possibility that temporal variability in recruitment of Sillaginodes punctata is a passive process under the influence of variable hydrodynamics. The temporal pattern of settlement of S. punctata post-larvae to Port Phillip Bay has been determined using otolith microstructure (Jenkins and May in press).

The circulation in the bay was depicted using a comprehensive numerical hydrodynamic model of Port Phillip Bay and the adjacent ocean of Bass Strait (Black et al., 1993). The dispersal of passive "larvae" was simulated using a Lagrangian particle model (e.g. Black et al., 1990).

The hydrodynamic model solves the fluid flow equations of momentum and conservation over a spatial 1.5 km grid in 2 or 3 dimensions. The open boundary was placed 20 km south of the Bay entrance in Bass Strait which allowed the model to incorporate the ocean oscillations affecting Port Phillip Bay (Black et al., 1993).

The model boundary conditions and inputs included all of the important parameters which were wind stress, tides and low frequency sea level oscillations and major river flows. Wind-driven oscillations, barometric pressure responses and coastal-trapped waves arriving at the entrance to the bay were represented in the sea level boundary condition by using actual measurements of sea levels recording during the recruitment period.

A very high level of calibration of the Port Phillip Bay model against three years of field data has been achieved (Black et al., 1993). For example, more than 90% of the variance in the sea levels within the bay was predicted by the model. All of the forcing factors noted above were simultaneously treated in these simulations.

Although both 2- and 3-dimensional models of the bay were available, the 2-dimensional model gave a good representation of the coastal hydrodynamics of the study area. This was because dispersal in this area was controlled largely by strong tidal currents. Dispersal further into the bay is more related to wind forcing and accurate simulation may require a 3 - dimensional model (Black et al., 1993).

The dispersal stage used the velocities from the hydrodynamic model to specify the advection and a Monte Carlo random walk technique for the diffusion (Black et al., 1990). The horizontal diffusion coefficient was taken such that the random step was 10% of the advection distance. Sensitivity testing of this value showed that the general conclusions were not affected by the choice of the eddy diffusivity coefficient. The advection of particles moving with the currents was more important.

Consideration of the length of larval life and the current patterns in Bass Strait over the period of larval drift (winter, early spring) suggests that larvae entering Port Phillip Bay would have come from the west (Jenkins and May in press, Black et al., 1992). Thus, entry of particles to Port Phillip Bay and Swan Bay was simulated over the recruitment period by seeding of the model at the western Bass Strait boundary. To test the importance of this release condition, a second series of simulations was undertaken in which the particles were released in an arc in Bass Strait around the entrance to the bay, i.e. particles were assumed to arrive from all directions rather than from the west only. The second series exhibited a poor correlation with the fish recruitment data in the bay, as expected, and the results are not discussed further here. Output of the model

included temporal variability in the number of particles in model 'boxes' and the spatial distribution of particles at a bay-wide scale.

Otolith microstructure suggested that ingress to Swan Bay occurred in five pulses over a two month period from mid September to mid November (Fig. 2). These five cohorts were separated by a period of approximately 10 to 14 d. The model predictions for Swan Bay and Port Phillip Bay showed variability in the ingress of particles at approximately the same time scale as larval ingress inferred from the otolith structure (Fig 2). A gradual build-up in particle numbers was evident over the period in Port Phillip Bay, notwithstanding the cyclic flushing which occurs. In contrast, particles entering Swan Bay were not retained. The timing of input of particles to Swan Bay was similar, but not identical, to entry of particles to Port Phillip Bay as a whole (Fig. 2). The closest matching between the pattern of larval ingress and model predictions for passive particles was for Port Phillip Bay (Fig. 2). Particularly in the case of the third pulse of particle input, particle entry to Swan Bay appeared to lag particle entry to Port Phillip Bay and ingress of larvae determined from otoliths (Fig. 2).

The spatial pattern of ingress of passive particles to Port Phillip Bay predicted by the model is shown in Fig. 3. Particles entered Port Phillip Bay between three and four hundred h after the beginning of the model run. By the end of the simulation, integrated particle numbers showed that particles had penetrated approximately the southern half of Port Phillip Bay (Fig. 3).

Jenkins and May (in press) suggested that otolith microstructure was modified due to changed environmental conditions (ie food supply and temperature) upon entry of post-larvae to Port Phillip Bay and Swan Bay. Simulation results suggest that transition in otolith microstructure occurs almost immediately upon entry to Port Phillip Bay. Otolith microstructure is known to respond rapidly to environmental conditions (Maillet and Checkley 1990, Mugiya and Hirota 1991).

Inspection of data relating to wind indicated that variability in wind strength and direction occurred at a much higher frequency than variation in settlement (Fig. 4). Although settlement tended to occur over periods of increasing water level (Fig. 4), mediated by tidal variation and low frequency events, there were periods of increasing water level when ingress did not occur and the link was generally weak. In an embayment like Port Phillip Bay where wind-driven and other circulation events combine to create a complex circulation pattern, a single individual process, such as coastal upwelling or spring tides for example, will not be solely responsible for the observed recruitment.

The passage of high and low pressure systems with 7-14 day periods at these latitudes can influence particle entry to Port Phillip Bay through variation in sea level due to low-frequency oscillations at the entrance. Net inflow and outflow from the bay is approximately locked in phase with the passage of weather patterns which determine atmospheric pressure variations and the correlated wind events. Coastal-trapped waves which play an important role on this shoreline (Middleton and Viera, 1991) also have 7-14 day periods. The periods are similar those of the weather patterns but the coastal-trapped waves are not necessarily locked in phase with the prevailing weather. Each of these processes interact with the spring/neap tidal amplitude variation; the latter establishes an additional low frequency oscillation in tidal excursion and the transfer of larvae into the bay.

Within the inner bay the circulation is predominantly wind-driven. Net circulation is characterised by two counter-rotating eddies with the downwind flow occurring through the central regions of the bay and return flow around the margins (Black et al., 1993). Pulsing can be initiated at the entrance due to reversals in the longshore currents in Bass Strait. With pulsing established, the complex dynamics due to wind in the bay may further enhance the temporal variability of the recruitment events.

An alternating sequence of upwelling and downwelling at the entrance may also occur in response to changes in longshore current direction and the direct action of the wind stress on the water surface. These processes, however, are evidently not of primary importance in the case studied.

Post-larvae of S. punctatus are relatively large compared with pre-settlement larvae of most species, suggesting that they should be strong swimmers. One caveat, however, is that pre-settlement larvae are in a minimal-growth phase (Jenkins and May in press) and their metabolic and activity levels may be correspondingly low. Even if larvae can swim strongly, the relatively strong tidal-currents near Port Phillip Heads may overwhelm any behavioural effects. Behaviour may be more important further into Port Phillip Bay where lower-velocity wind-driven currents tend to dominate.

Many particles entering Port Phillip Bay tended to remain there. However, particles entering Swan Bay were only retained for a short period. Thus, behaviour does appear to play a role once post-larvae have entered Swan Bay, because individuals obviously maintain themselves in the bay whereas passive particles are rapidly displaced. Currents within Swan Bay are weak, and therefore individual post-larvae would have little trouble maintaining themselves within the bay.

A similar transport mechanism to that described here may occur with ingress of Atlantic blue crabs to Delaware Bay (Little and Epifanio 1991) and Chesapeake Bay (Goodrich et al. 1989). In these cases, influx of megalopae corresponds with periods of southward wind events and consequent positive anomalies in subtidal sea level (Little and Epifanio 1991). Like fish larvae, crab megalopae would be expected to have relatively strong swimming abilities and complex behaviour relative to many other invertebrate larvae. Intra-annual variation in barnacle recruitment in California was found to be related to the relaxation of onshore winds and consequent cessation of

coastal upwelling (Farrell et al. 1991). Unlike these studies, in our study individual climatic and oceanographic factors gave no simple indication of the underlying transport model. It was only the integration of the various factors in the modelling process which allowed the underlying transport processes to be identified.

This paper demonstrates that intra-annual variability in settlement of a coastal fish species, which would be considered a strong swimmer and behaviourally complex compared with many invertebrates, is controlled by coastal hydrodynamic processes. Active processes may be more important relative to passive transport in situations of lower current velocity. King George whiting are known to show very high variability in recruitment to the fishery in Port Phillip Bay. Our results suggest that small-scale coastal oceanography may strongly influence the interannual recruitment variability of this species. The frequency and timing of appearance of post-larvae near Port Phillip Heads in combination with hydrodynamic events allowing transport of larvae into Port Phillip and Swan Bays would influence both intra- and inter-annual variability in recruitment to this area.

Acknowledgements

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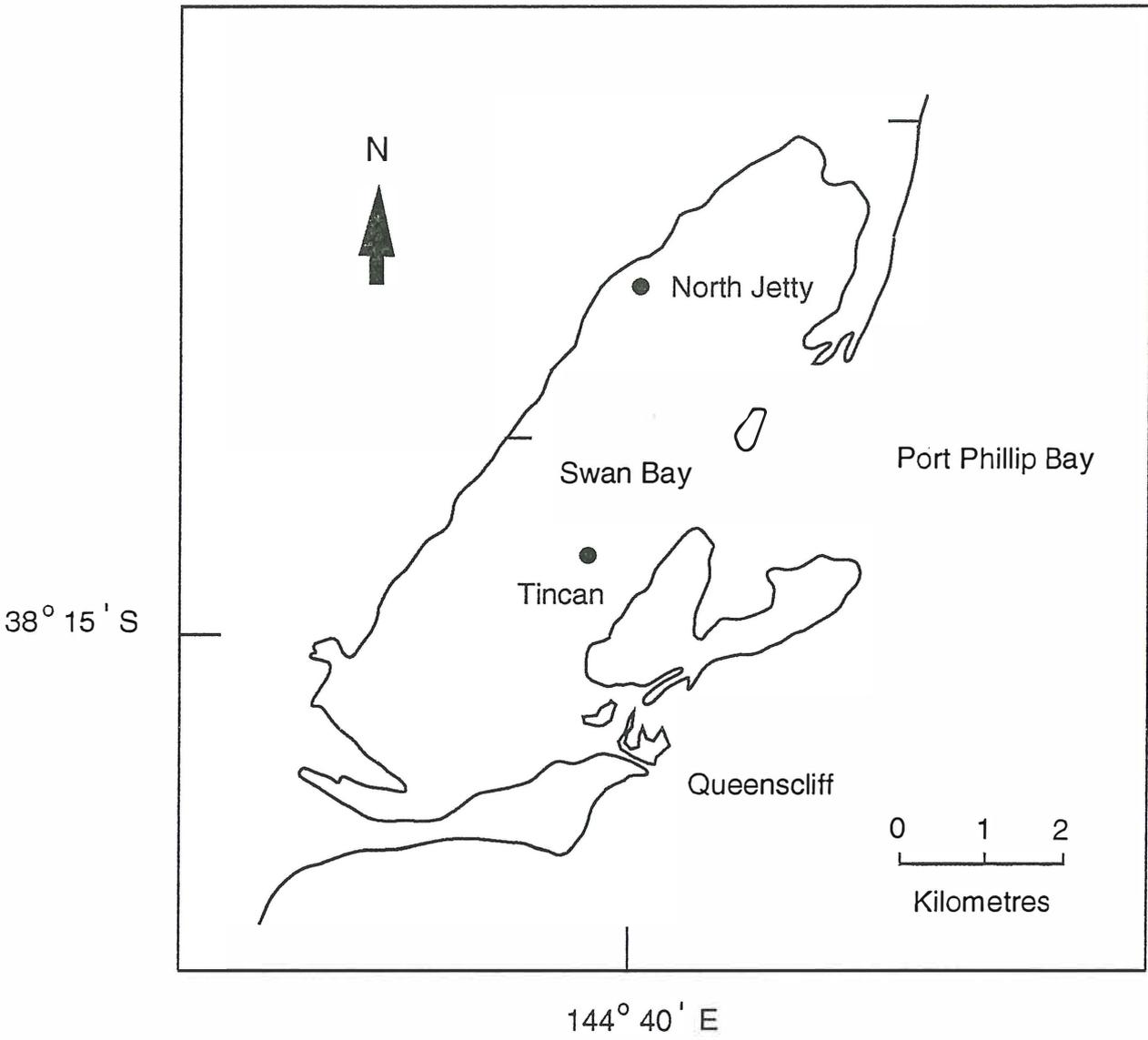
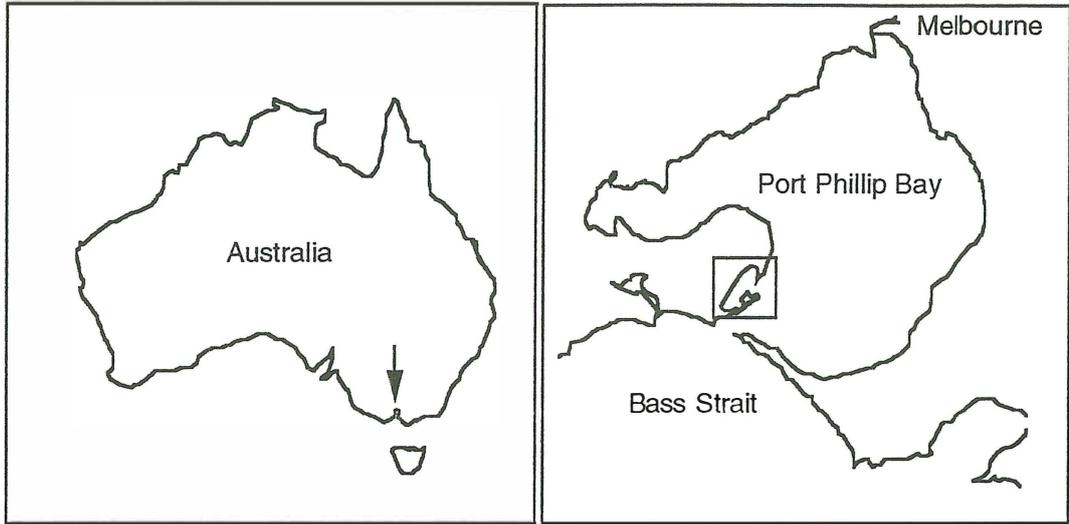
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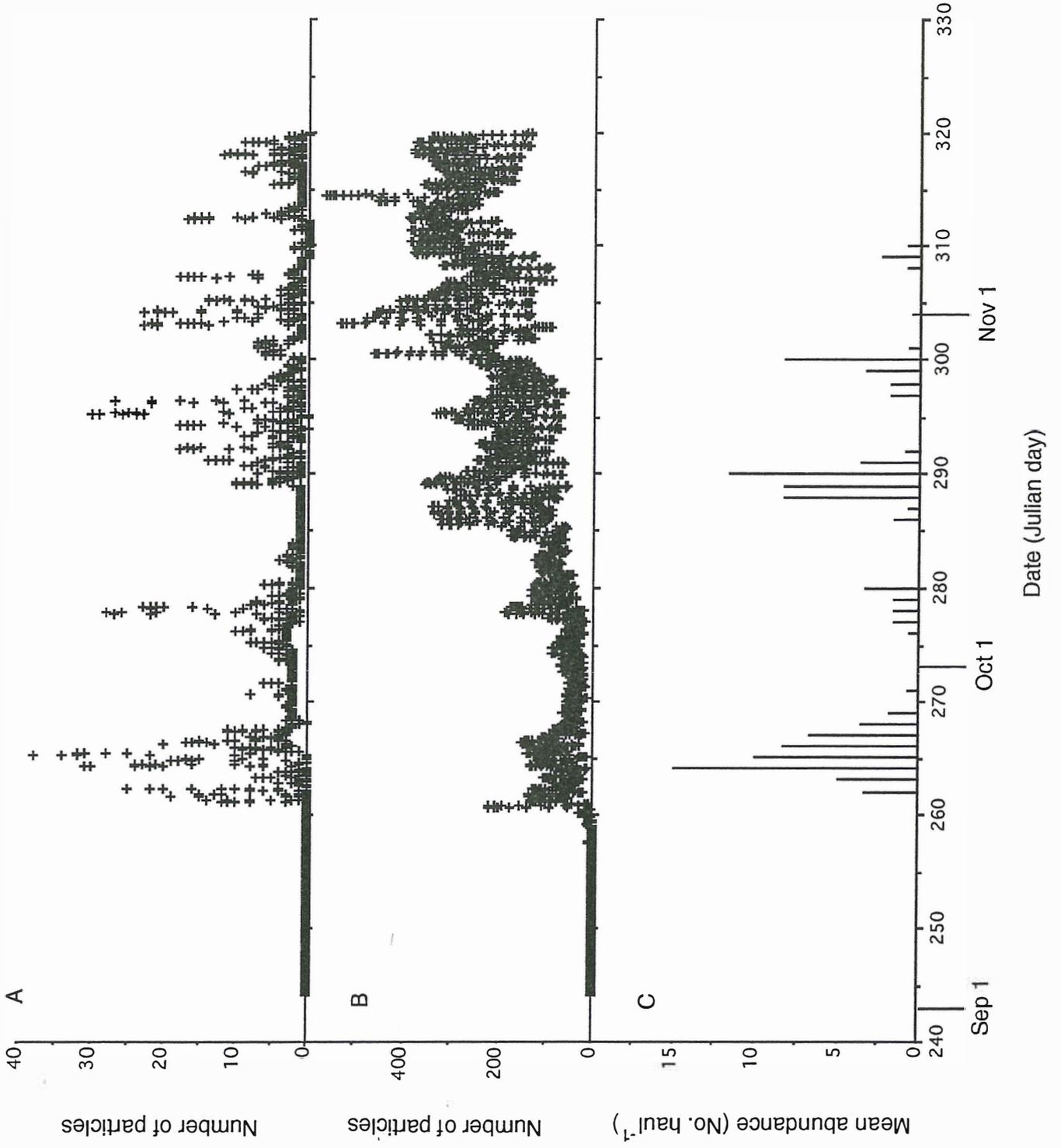
Fig. 1 Location of sampling sites in Swan Bay, Victoria, from which post-larval King George whiting were collected. Insets: Location of Swan Bay in Port Phillip Bay and location of Port Phillip Bay on the Australian coast.

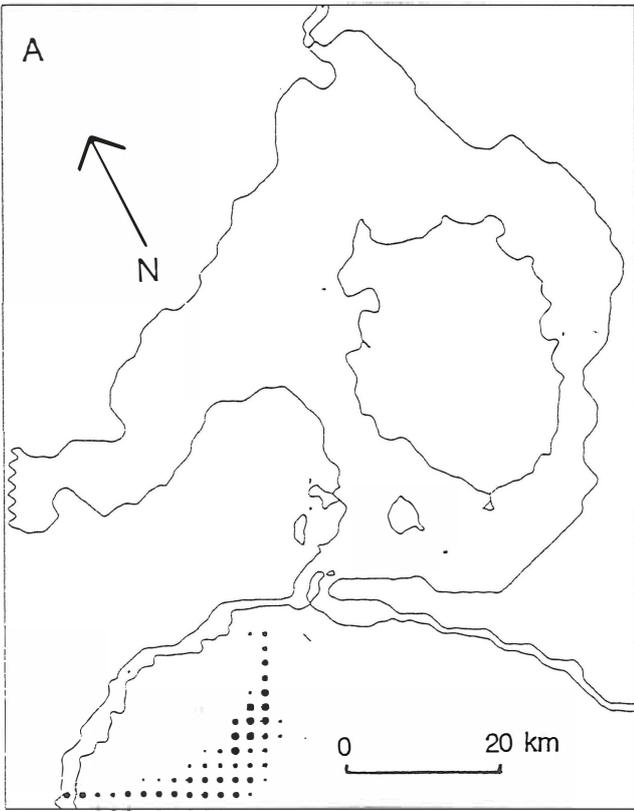
Fig. 2 Particle numbers predicted by the numerical models (A) within Swan Bay and (B) within Port Phillip Bay. C; the relationship between mean abundance and date of otolith transition for post-larval King George whiting collected at two sites in Swan Bay from October 1989 to January 1990 (Jenkins and May, in press).

Fig. 3 Model prediction of the spatial distribution of particles released from a line from the coast of Bass Strait, southwest of Port Phillip Heads, along the southern boundary of the model grid. A; instantaneous count 300 h after start (1200 h on Sep 13, 1989). B; Instantaneous count 400 h after start (1200 h on Sep 17, 1989). C; Instantaneous count 600 h after start (1200 h on Sep 26, 1989). D; integrated count 1820 h after start (2000 h on Nov 15, 1989).

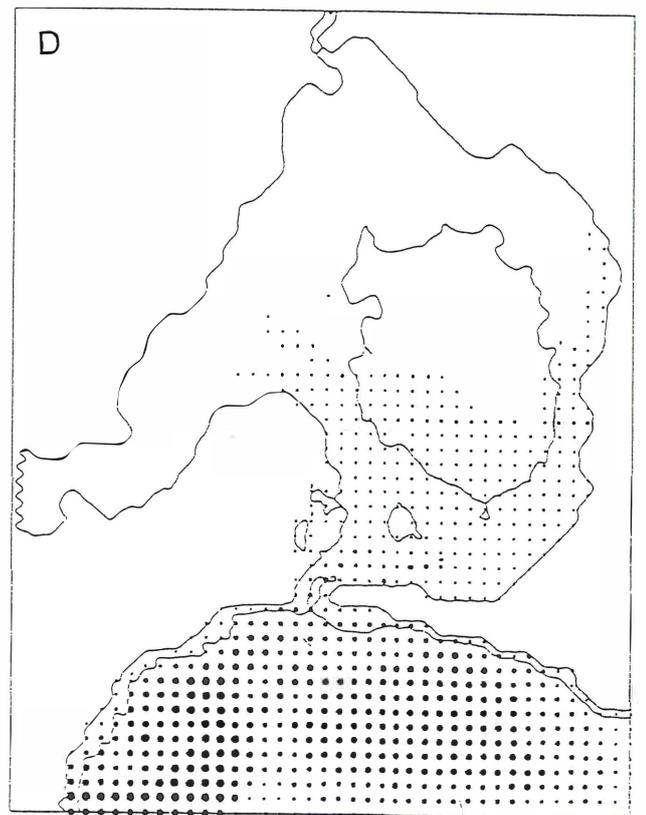
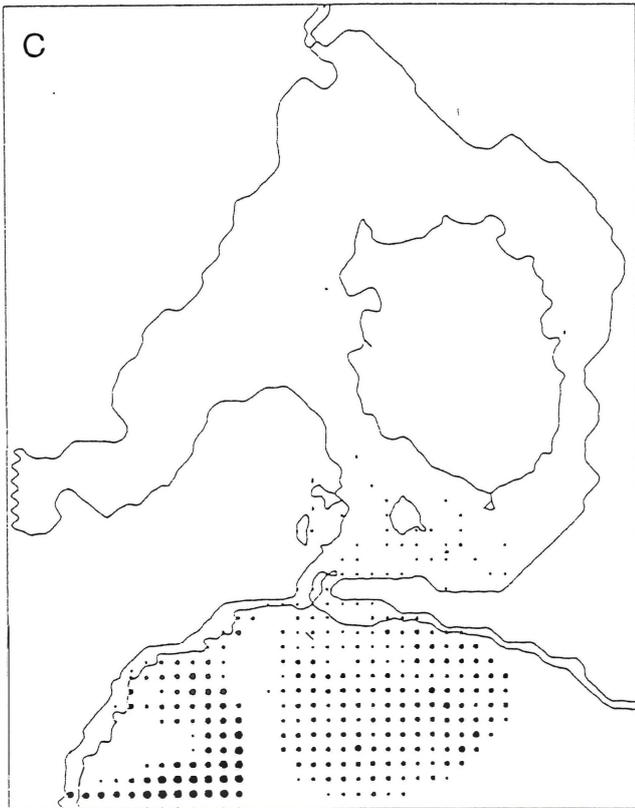
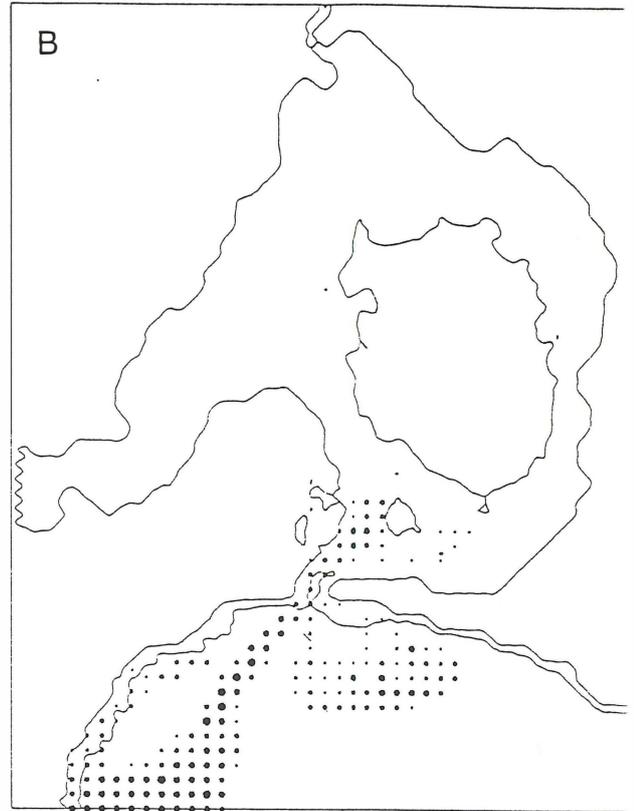
Fig. 4 A; Sea levels (metres) at the entrance to Port Phillip Bay at Point Lonsdale. B; wind speed (metres/second) at a bay site. C; wind direction ($^{\circ}$ T) . D; atmospheric pressure (hPa). E; the relationship between mean abundance and date of otolith transition for post-larval King George whiting collected at two sites in Swan Bay from October 1989 to January 1990 (Jenkins and May, in press).







0.00
 2.00
 4.00
 12.00
 36.00
 100.00



GREG JENKINS FISH SETTLEMENT. KING GEORGE WHITING
PLOTS FROM TOP ARE: (1) POINT LONSDALE MEASURED TIDES
(2&3) POINT COOK EPA WINDS, (4) MODEL RUN PPBJW2 PPB NUMBERS
(5) MEASURED NUMBERS (DATA)

