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Seasonal variation in horizontal and vertical structure of larval fish assemblages off south-western Australia, with implications for larval transport.

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Abstract

The coastal ocean off south-western Australia is characterised by the southward-flowing Leeuwin Current, which suppresses the upwelling typically associated with other eastern boundary currents in the southern hemisphere. This results in a unique environment for the transport and survival of planktonic fish larvae. The horizontal and vertical structure of larval fish assemblages off south-western Australia was investigated during winter (August 2003) and summer (January 2004), and related to these unusual regional oceanographic and biological processes. Larval fish were sampled along a four station transect running from the inner continental shelf to offshore waters, using depth-integrated bongo net tows, and depth-stratified EZ net tows. The distribution of taxa across the shelf and offshore was strongly influenced by the current regime at the time of sampling. Larval fish assemblage structure reflected the distinctive oceanographic conditions found during each season, and vertical depth distributions of larvae affected their horizontal location. Continental shelf samples were dominated by larvae of pelagic fishes, such as clupeiform species (e.g., *Sardinops sagax*), while offshore assemblages were characterised by larvae of oceanic families, such as Myctophidae and Phosichthyidae. The winter cruise (August 2003) was completed during a time of strong, southerly Leeuwin Current flow, while the northward-flowing Capes Current, in combination with surface offshore Ekman transport, predominated during summer. The vertical depth preferences of larvae were particularly influential in affecting their horizontal position; especially so for surface-dwelling larval fishes found during summer. This study represents the first documentation of the vertical structure of ichthyoplankton assemblages in the oligotrophic waters off south-western Australia.

Introduction

Physical oceanographic processes are highly influential in regulating the distribution of pelagic fish eggs and larvae, and influence distribution on a variety of scales, ranging from a few metres to thousands of kilometres (Bruce *et al.*, 2001). The distribution of some taxa can be related to specific oceanographic features, such as ocean currents, eddies and jets, with variations in such features having implications for larval fish survival and recruitment (Doyle *et al.*, 1993). Some coasts are also characterised by the presence of upwelling or downwelling features, which affect both the dispersal of larvae, and the concentration of prey items available to them (Rodriguez *et al.*, 1999; Santos *et al.*, 2004). Smaller scale processes, such as the formation of coastal and tidal fronts, may also be important (Kingsford *et al.*, 1991; Grioche and Koubbi, 1997; Sanvicente-Anorve *et al.*, 2000). Some fish species in areas with strongly seasonal oceanographic features have been found to adapt their spawning times and locations to take advantage of favourable transport mechanisms for their larvae, and to avoid times where disadvantageous mechanisms, such as strong offshore Ekman transport, prevail (Parrish *et al.*, 1981; Hutchings *et al.*, 2002). The structure of the larval fish assemblage within a region will therefore be influenced by the seasonal patterns of spawning by different species, and the presence and strength of the oceanographic processes with which spawning times coincide.

The ability of larval fishes to survive the pelagic phase, and return to a suitable habitat for their adult life, may be dependent on their ability to regulate their dispersal or retention (Heath, 1992; Urho, 1999; Cowen, 2002). As the strength and flow direction of many currents differ with respect to depth through the water column, the ability of a larva to vertically position itself is also a mechanism by which a favourable horizontal position may be achieved or maintained (Heath, 1992). However, larvae of different species often differ in their response to the physical environment, and in their depth distributions. As a result, larvae of some species may utilise transport processes that others do not (Leis, 1982; Gray, 1996; Cowen *et al.*, 2003). Larval fish may position themselves vertically in the water column to align themselves with a particular physical or biological feature, such as the thermocline, or the chlorophyll maximum layer (Ahlstrom, 1959; Kendall and Naplin, 1981; Matsuura *et al.*, 1993; Groenkjaer and Wieland, 1997). Additionally, the selection of depth ranges by larvae may change with growth, with many species shown to change behaviours as they age (Leis, 1982, 1991; Smith, 2000). As larvae develop fins, and increasingly effective swimming abilities, they possess the potential for significant horizontal, as well as vertical, movements. Therefore, while larval fish assemblages may be well-aligned to oceanographic boundaries on a regional scale, fine-scale processes and larval fish behaviour are

also potentially important in structuring assemblages on a more local scale: the scale at which most larval fish sampling is carried out (hundreds of metres).

Oceanographic conditions off temperate south-western Australia are unique. Unlike other eastern boundary currents, which flow equatorward, and promote upwelling, the Leeuwin Current off south-western Australia flows poleward, suppressing large-scale upwelling (Pearce, 1991) (Fig. 1). The Leeuwin Current is driven by an alongshore height gradient, as a result of the interconnection between the Pacific and Indian Oceans through the Indonesian Archipelago (Godfrey and Ridgway, 1985), which overwhelms the opposing equatorward wind stress. The current is characterised by the southward penetration of comparatively warm, low salinity water along the continental shelf break to the southern-most point of Western Australia, where the current rounds Cape Leeuwin and flows eastward across the Great Australian Bight (Cresswell, 1991; Ridgway and Condie, 2004). The flow of the Leeuwin Current is at a maximum in the austral autumn and winter, when southerly wind stress is weakest. In the austral summer, when southerly wind stress is at a maximum, the Leeuwin Current is located farther offshore, and is greatly weakened, and localized upwelling may occur south of Cape Naturaliste. Under the influence of southerly winds, this feature may extend northward as a narrow, cooler stream of water inshore of the weakened Leeuwin Current. This inshore flow is the Capes Current (Gersbach *et al.*, 1999; Pearce and Pattiaratchi, 1999).

Despite the potential influence of south-western Australian oceanography on the transport and survival of larval fishes, little is known about such interactions. Most published work on the region has been restricted to studies of estuaries and the nearshore environment (e.g., Gaughan *et al.*, 1990; Neira and Potter, 1992), with the exception of a description of larval fish assemblages in conjunction with oceanographic data, from a three year biological oceanography project (Muhling *et al.*, in press).

Results from the two cruises described here aimed to compare the vertical and horizontal structure of larval fish assemblages between summer and winter sampling cruises, and to relate larval fish assemblage patterns to regional oceanographic processes. It was hypothesized that the larval fish assemblage structure would mirror the distinctive oceanographic conditions found during each season, and that vertical depth distributions of larvae would affect their horizontal transport. Taxon-specific differences in vertical distribution were examined for both seasons, and implications for the resultant dispersal or retention of larvae are discussed.

Method

Sampling

Two nine day cruises aboard the *RV Southern Surveyor* were undertaken off south-western Australia in August 2003 (winter), and January 2004 (summer). A four-station transect was occupied, with stations located at 40m depth (Station B: inner shelf), 100m (Station C: outer shelf), 300m (Station D: shelf break) and 1000m (Station E: offshore) (Fig. 1). Temperature, salinity and chlorophyll-*a* data were obtained from CTD casts taken from each station over the cruise periods, with zooplankton and primary productivity samples also collected (Koslow *et al.*, 2006).

Depth stratified plankton samples were taken with an opening and closing EZ net, fitted with 10 nets of 335 μm mesh (mouth area 1.0m^2). A flowmeter positioned in front of the net was used to calculate the volume of seawater sampled by each net during each tow. EZ nets were used to sample depth strata as shown in Table I. The net was towed at a ship speed of approximately 2 knots, with sampling taking place during both day and night. Replicated, oblique bongo net tows, fitted with 355 μm mesh (mouth area 0.196m^2), were taken at the same sampling stations (B to E) during the day only, towed to 150m depth, or just above the bottom in shallower water (Table II). Ranges of volumes sampled were 270 - 2524m^3 per net in the EZ net (largely dependent on stratum depth), and 116 - 398m^3 in the bongo nets. Plankton samples from both nets were fixed in 10% buffered formaldehyde immediately after collection.

Larval fish were removed from plankton samples with the aid of a dissecting microscope. Where samples contained a very large amount of plankton, they were split using a Folsom splitter, and half the sample was sorted (shown in italics in Table II). These sub-samples were considered to be sufficiently representative of the whole sample as they had high larval fish abundances, and low species diversities. Abundances from these samples were multiplied by two to obtain an estimate of larval fish density per m^3 of seawater sampled. Larval fishes were preserved in 70% ethanol after sorting, and identified to family, and species where possible, using relevant literature (e.g., Leis and Carson-Ewart, 2000; Neira *et al.*, 1998). Numbers of larval fish per m^3 of sampled seawater were determined using the flowmeters fitted to both net types, with mean densities and standard errors calculated for replicated tows. Larval fish densities from bongo nets were then converted to number per m^2 , using the depth of the net sample.

Data analyses

Sea-surface temperature (SST) data were acquired from the Western Australian Satellite Technology and Applications Consortium (WASTAC), and the images were processed by CSIRO Marine Research at Floreat, Western Australia.

Temperature and chlorophyll-*a* profiles across the transect for each cruise were constructed using CTD casts taken between plankton sampling stations, in order to improve spatial resolution. The position of the thermocline was defined as the zone of greatest change in temperature with depth through the water column. Chlorophyll-*a* biomass was derived from fluorescence data from CTD casts, using a regression equation determined after consideration of data from three years of sampling in the area (Koslow *et al.*, 2006).

Current profiles with depth were obtained for January 2004 only, from a hull mounted Acoustic Doppler Current Profiler (ADCP) (150KHz narrow band, RD Instruments). East-west, and north-south component data were taken for the duration of the cruise, and later averaged into 20-minute profiles. By subtracting the east-west and north-south components of the ship's speed from the relative components measured by the ADCP, absolute east-west and north-south current components were calculated through the water column. Profiles were extracted for each of the four sampling stations, with data binned every 8m. The shallowest mean depth extracted was 16.8m.

Larval fish abundances were compared between seasons, and between sampling zones using the replicated bongo net tows. For these analyses, data from stations B and C were combined as "shelf" data, while data from stations D and E were combined to give "offshore" data, as too few samples were obtained to compare larval fish between each station within each cruise. This pooling of stations was validated using analysis of similarity (ANOSIM) testing in the Primer-6 software package (Clarke, 1993). The Mann-Whitney test, in SPSS 14.0, was used for all tests for differences in mean larval fish abundances between seasons, or between sampling zones within seasons. Profiles were used to display the depth-stratified EZ net larval fish density values. Larval fish abundance profiles from EZ net data comparing seasons examined night data only, as no day-time tows were taken for stations B and E in summer, due to equipment failure. Vertical distributions of the six most abundant taxa were examined and compared using EZ net data only (no. m⁻³), and horizontal distributions were compared using both bongo net and EZ net data (no. m⁻²). The standard lengths of larval clupeids from EZ net samples were also recorded to enable comparisons of summer and winter distributions.

Differences between larval fish assemblages from between seasons, and between shelf and offshore station groupings within each season, were investigated using ANOSIM, in Primer-6 (Clarke, 1993). To decrease the weighting of dominant species, larval fish abundances were log transformed [$\log(x+1)$] prior to analysis. Relationships between assemblages from different seasons and stations were displayed using Multi-Dimensional Scaling (MDS) ordination. Assemblages collected between tow types (bongo nets and EZ nets) were also tested using ANOSIM, as were differences between day and night samples from the EZ net, to validate the combining of these samples for later assemblage analyses.

The similarity percentage routine SIMPER was applied to the data to identify taxa characteristic of the assemblages from each zone (shelf or offshore) of each season (summer or winter), and also those taxa responsible for distinguishing between assemblages. Taxa that distinguished assemblages from the same zone, between summer and winter samples, were also identified. Characteristic and distinguishing taxa were defined as those for which the ratio between the contribution of the taxa to the average dissimilarity within or between groups to the standard deviation was greatest (Clarke, 1993). Day and night samples from bongo and EZ net samples were combined for these analyses, with EZ net samples integrated to the same sampling depth as the bongo nets.

Results

Oceanographic conditions

Satellite SST images from the August 2003 and January 2004 cruises were typical of the expected oceanographic patterns at these times of year. During the August 2003 cruise, the warm, southward-flowing Leeuwin Current was the dominant feature, covering stations B, C and D across the transect (Fig. 2). However, station E was west of the outer edge of the Leeuwin Current, in the cooler Sub-Tropical Surface Water (STSW hereafter). During the January 2004 cruise, temperature differentiation across the transect was weaker than in winter (Fig. 2). Stations C, D and E were located within water of Leeuwin Current origin. Station B was located in water of a similar temperature to the other stations, but may have been influenced by a weak upwelling wake that resulted from the cooler Capes Current flowing northwards past Rottnest Island.

During the winter cruise, the Leeuwin Current was clearly evident as a mass of warm, low salinity water situated against the shelf break (Fig. 2). A halocline within the current was located at around 70m depth. The water mass inshore of the Leeuwin Current was relatively cool (17-18°C). In the summer profile, there was less distinction with temperature and salinity across the transect, and the Leeuwin Current, although present over the outer shelf and slope, was shallower than in winter.

There was also some evidence of offshore water upwelling onto the shelf in summer. The thermocline was not strong in either season (Fig. 2), but was deeper in summer than in winter. Chlorophyll-*a* biomass profiles showed that chlorophyll concentrations were higher across the shelf in winter, and that the chlorophyll maximum within the water column tended to be at a shallower depth than in summer, and more clearly defined, especially at its deepest limit (Fig. 2). In summer, there was a deeper, more diffuse chlorophyll maximum layer, at around 100m depth, with a slight increase near the surface at the shelf break.

January 2004 ADCP data supported the results from satellite and CTD data. Currents at station B were flowing to the north-west at 0.1 to 0.2 m/s (Fig. 3). Current profiles from station C showed changes in the current profile with depth. At the top of the water column, the currents were flowing in a north-westerly direction, similar to station B, but with a stronger westerly component (0.35 m/s). However, this current weakened, and reversed, with depth through the water column, approaching zero between 60 and 70 m depth, and then flowing weakly to the south-east near the bottom (0.12 m/s). Station D also showed a westerly current component at shallower depths, with current speeds peaking at around 112m water depth (0.42 m/s). Below 160m depth, the current reversed, and flowed weakly eastwards. The north-south component at station D was very weak above 120 m depth, below which it flowed strongly southwards, with speeds peaking at 190m depth (0.32 m/s). The current at station E flowed in a south-westerly direction above 170 m depth, below which it flowed in a north-westerly direction.

Taxonomic composition and abundances of larval fish assemblages.

In total, 5713 larval fishes were identified from all plankton samples taken: 4657 from the EZ net tows (1726 from winter and 2931 from summer), and 1056 from the bongo net tows (425 from winter and 631 from summer). Larvae from 59 teleost families, and 107 identifiable taxa were recorded. The winter shelf and offshore samples both contained a total of 52 taxa, with the summer shelf samples containing 55 taxa, and the summer offshore samples 46 taxa. There were pronounced differences in dominant taxa between summer and winter samples (Table II). Some taxa, such as *Apogonops anomalous*, *Etrumeus teres* and *Diaphus* 'slender' spp. were much more abundant in summer, whereas Clinidae sp. 1, *Scopelopsis multipunctatus* and *Cyclothone* spp. were more abundant in winter. Other taxa, such as *Diogenichthys atlanticus* and *Vinciguerria* spp., were abundant at both sampling times.

When mean larval fish abundances from bongo net tows were compared between seasons, lower abundances of larvae were caught in winter than in summer ($P = 0.006$) (Fig. 4). There was no

significant difference between mean larval fish abundances on the shelf between summer and winter ($P = 0.40$). There were, however, significantly greater mean larval fish abundances offshore (stations D and E) in summer than in winter ($P = 0.03$). Within seasons, there was no significant difference between larval fish abundance on the shelf vs. offshore during winter ($P = 0.60$), or summer ($P = 0.20$).

During winter, the shelf station assemblages were dominated numerically by *Sardinops sagax*, which comprised 35% of all larvae caught. Larvae of *S. multipunctatus* (10%), *Lampanyctus* spp. (5%) and *Cyclothone* spp. (5%) were the next most abundant taxa. The winter offshore assemblage was dominated by larvae from the oceanic families Myctophidae, Gonostomatidae, Paralepididae, Sternoptychidae and Phosichthyidae, with 85% of larvae caught belonging to these families. *Scopelopsis multipunctatus* (17%) was the most abundant species, with *Cyclothone* spp. (16%) and *D. atlanticus* (7%) also common.

As with the winter shelf assemblage, the summer shelf assemblage was dominated by larvae from the Clupeiformes, with *S. sagax* (31%) and *E. teres* (21%) the most abundant. *Engraulis australis* larvae were also present in summer, but at much lower abundances (2%). Larvae from the Carangidae (16%) and Labridae (7%) were also common in summer shelf samples. As with the winter offshore assemblage, the summer offshore group was dominated by oceanic larvae from the Myctophidae, Gonostomatidae, Paralepididae, Sternoptychidae and Phosichthyidae, with 87% of larvae in summer offshore samples belonging to these families. Larvae of *Diaphus* 'slender' spp. were the most abundant (46%), with larvae of *Vinciguerria* spp. (9%) and *Lampanyctus* spp. (6%) also common.

Horizontal structure of larval fish assemblages.

Analysis of similarity (ANOSIM) tests between samples taken from EZ nets, with data combined to 150m depth (total larval fish caught between 0-150m depth, divided by total volume sampled 0-150m), and bongo net samples revealed no difference between larval fish assemblages between the two net types, during either season (winter: $R = 0.06$, summer: $R = -0.06$). There was also no difference between the integrated EZ net data between day and night tows ($R = -0.14$). The two sample groups were therefore combined to provide greater replication when examining differences in assemblages between seasons, and across the sampling transect within seasons. Multi-dimensional scaling ordination of all samples showed a gradation from inner shelf (station B) to offshore (station E samples), as well as a clear distinction between winter and summer samples (Fig. 5).

Using the combined dataset, larval fish assemblages between the winter and summer cruises, from all sampling stations, were significantly distinct ($R = 0.20$). When shelf samples only were examined, there was also a significant difference between seasons ($R = 0.20$), however, the distinction between seasons was much stronger when only offshore samples were considered ($R = 0.75$). Within summer cruise samples, shelf larval fish assemblages were strongly distinct from offshore assemblages ($R = 0.97$). This distinction was also present during winter, but was much weaker ($R = 0.37$). These differences, and the results of the SIMPER analysis below, were considered to justify the pooling of data into shelf and offshore zones.

Larval fish assemblages from the shelf in summer were best distinguished from those in winter by greater abundances of Carangidae spp. and Labridae sp. 1 (Table III). The main distinction between summer and winter offshore assemblages was the dominance of *Diaphus* 'slender' spp. in summer, as well as the higher abundances of *D. atlanticus* in winter. Within each cruise, summer shelf samples were distinguished from summer offshore larval fish assemblages by greater abundances of *Diaphus* 'slender' spp. and *D. atlanticus* offshore, and greater abundances of Carangidae spp. on the shelf (Table III). Winter shelf assemblages contained higher abundances of *S. sagax* and Monacanthidae larvae than offshore assemblages, although these taxa were less reliable indicators than those in the previous comparisons, as shown by the lower SIMPER test statistic values (Table III). This reflected the weaker distinction between shelf and offshore assemblages in winter than in summer.

Larval *S. sagax* were found commonly on both cruises, with higher abundances on the shelf than offshore ($P=0.01$) (Fig. 6). In winter, *S. sagax* larvae were found primarily at station B, with low abundances of larvae at stations C and D, while in summer, larvae were found farther offshore. A similar pattern was observed for the larvae of another clupeid, *E. teres* (Fig. 6). Larvae of this species were also found farther offshore during summer. In summer, the lengths of *S. sagax* larvae increased with increasing distance from shore, with larvae from station B significantly smaller than at stations C to E ($P<0.001$) (Fig. 8). This trend was not apparent in winter. *Etrumeus teres* larvae from station B were also significantly smaller than those at stations C to E in summer ($P = 0.03$), but the difference was weaker and less obvious than for *S. sagax* (Fig. 8).

In contrast, larvae of the most abundant myctophid species, *Diaphus* 'slender' spp., were found across the outer shelf and offshore regions on both cruises, with higher abundances offshore than on the shelf ($P=0.03$) (Fig. 6). These larvae were much more abundant in summer ($P = 0.02$). Larvae of

Vinciguerria spp. were found across the outer shelf and offshore on both cruises, however, they were most abundant at stations D and E in summer, and at stations C and D in winter (Fig. 6). There was no significant difference between mean abundances of *Vinciguerria* spp. between shelf and offshore stations, reflecting their tendency to be found further inshore than *Diaphus* 'slender' spp. ($P=0.70$).

Vertical distributions of common larval fish taxa.

Comparison of the vertical structure of larval fish densities between winter and summer showed that in both seasons, most larval fishes (>90%) were found in the upper 100m of the water column, across the sampled transect (Fig. 7). Larval fish densities also tended to be highest in the shallowest depth strata, with the exception of station C in summer. Most larval fish (~93%) were found above the thermocline.

Larvae of some coastal and shelf taxa, such as tripterygiids and *S. sagax*, showed a more offshore distribution in summer than in winter (Fig. 6). In contrast, larvae of coastal taxa with larvae that tended to avoid the surface layer, such as the Gobiidae (Leis, 1991; Olivar and Sabates, 1997), were not distributed farther from shore in summer than in winter (Fig. 6).

Sardinops sagax larvae were primarily collected in the upper 75m of the water column on both cruises (Fig. 6), and no evidence of diel vertical migration was evident on the vertical scales sampled (Fig. 9). There was also no evidence of differing vertical distribution between different size classes (Fig. 9). *Etrumeus teres* showed a similar depth distribution to *S. sagax*, although it was found in higher densities in the two deeper strata in summer at station C (Fig. 6). The highest densities, at station C between 30 and 55m depth, corresponded to the base of the north-westerly flowing mixed layer (Fig. 3). *Diaphus* 'slender' spp. were found throughout the water column at the two offshore stations, but were most abundant in the upper 60-70m (Fig. 6). A broader depth distribution of *Diaphus* 'slender' spp. larvae at station D in summer corresponded to a deeper thermocline and halocline at this station. Larvae of *Vinciguerria* spp. were similarly distributed to *Diaphus* 'slender' spp., also being more abundant in surface strata (Fig. 6). Tripterygiid larvae were found predominantly in the surface depth strata on both cruises, but were more abundant in summer. In contrast, gobiid larvae avoided the surface depth stratum, especially in summer (Fig. 6), and were largely located in areas of weak, south-easterly current flow (Fig. 3).

Discussion

Larval fish assemblage structure and oceanographic processes.

The oceanographic conditions encountered during the two cruises studied were representative of typical winter and summer regimes for the area (Muhling *et al.*, in press; Pearce *et al.*, 2006; Pearce and Pattiaratchi, 1999), and the distinctions found here between winter and summer larval fish assemblages are likely to be representative of general seasonal differences.

The larvae collected were from fishes which occupy a wide variety of adult habitats. These included coastal and shelf reef taxa (gobiids, monacanthids, pempherids), sandy bottom and seagrass associated taxa (callionymids), pelagic species (*S. sagax*, *E. teres*, *Scomber australasicus*), tropical vagrants (*Chromis* sp. 1) and oceanic taxa (*Scopelopsis multipunctatus*, *Vinciguerria* spp. and other myctophid larvae) (Neira *et al.*, 1998; Hutchins and Thompson, 2001).

Assemblages were largely distinct between seasons, between depth strata, and between shelf and offshore sampling stations. Seasonal differences were likely due to the contrasting oceanographic conditions present during summer and winter, to which adult fish have presumably adapted their spawning times and locations.

Larval fish transport is strongly influenced by water mass structure and movement (Olivar and Beckley, 1994; Grothues and Cowen, 1999; Hare *et al.*, 2001). However, where current strength and direction is not uniform with depth, the vertical distributions of larval fishes will influence their transport and retention (Leis, 1982, 1991; Olivar and Sabates, 1997). The vertical structure of currents in many regions changes seasonally, with processes such as offshore Ekman transport stronger at certain times of year (Bailey, 1981; Doyle *et al.*, 1993). Oceanography off south-western Australia is also highly seasonal, however, the influence of vertical distributions of larval fishes in this region on transport and retention has not been studied previously.

Winter oceanographic conditions off south-western Australia are characterised by strong southwards flow of the warm Leeuwin Current, and the close proximity of this current to the coast (Pearce and Pattiaratchi, 1999). Transport mechanisms during winter are dominated by along-shore processes, resulting from both wind-driven transport, and the strong Leeuwin Current; cross-shelf transport processes are comparatively much weaker, and generally result only from meanders and jets of the Leeuwin Current (Cresswell, 1991; Pearce *et al.*, 2006). The winter larval fish assemblage on the shelf and slope was therefore composed largely of Clupeidae larvae, which were found shorewards of the main body of the Leeuwin Current, and oceanic larval fishes associated

with shoreward intrusions of the Leeuwin Current. The offshore station E was situated outside the outer boundary of the Leeuwin Current, resulting in a very low abundance, low diversity assemblage of oceanic species. Larval fish assemblages reflected the high oceanographic connectivity across the shelf and offshore in winter, with assemblages not differentiated as strongly between shelf and offshore samples as in summer.

Conditions during summer were distinct from those during winter, with the Leeuwin Current weaker, and farther from shore. Oceanic larvae, such as those from the Myctophidae, were found in high abundances at stations D and E in summer, especially near the surface. While these stations were located in water of Leeuwin Current origin, ADCP data indicated that the flow of the current was much weaker than in winter, possibly reducing larval fish advection from the region. A small eddy feature appeared to be situated over stations D and E during the January cruise (Alan Pearce, CSIRO, pers. comm., 2005), therefore it is also possible that this feature in some way retained or concentrated these larvae around the area sampled.

Studies from other coastal oceans have also found seasonal differences in larval fish assemblages related to seasonal oceanographic changes, including changes in current fields with depth (e.g., Doyle et al., 1993; Olivar and Sabates, 1997). Larval fish assemblages in the study region have previously been found to correlate closely to water mass structure (Muhling *et al.*, in press). Data presented in this study show stations subject to strong alongshore transport throughout the water column in winter tended to support a distinctive larval fish assemblage. In contrast, the weaker alongshore processes in summer led to greater vertical delineation of assemblages, and the northwards flow of the Capes Current, inshore of the Leeuwin current, decreased the spatial connectivity across the shelf. However, this effect was partially offset by the presence of surface, offshore Ekman transport, caused by strong southerly wind events characteristic of south-western Australia during summer (Gersbach *et al.*, 1999), which was clearly evident from the ADCP data. Westward currents were present in the mixed layer at all stations sampled in January. This resulted in larvae of some coastal and shelf species being more widely distributed across the shelf, and being found farther offshore, in summer than in winter.

This was especially the case for larvae with a more neustonic distribution, as the westerly component of the current at stations C and D weakened with depth. Larvae of taxa that tended to avoid the surface waters, such as the Gobiidae (Leis, 1991; Gray, 1993), showed more similar horizontal distributions between the two seasons. Surface neuston net samples from the same cruises discussed here also showed that larvae and small juveniles from families such as the

Carangidae, Clupeidae, Monacanthidae and Tripterygiidae were distributed much farther offshore in summer than in winter (Chisholm, 2004). This effect of vertical distribution on horizontal transport has also been found previously in other coastal oceans, including off north-west America (Bailey, 1981), and south-eastern Australia (Smith, 2000). Off southern Africa, Olivar et al. (1998) have shown that shorewards intrusions of the Agulhas Current resulted in the transport of oceanic fish larvae onto the shelf, and that offshore wind events in the Benguela Current ecosystem resulted in offshore transport of coastal fish larvae. Hickford and Schiel (2003) also found the larvae of reef fish off the east coast of New Zealand, including tripterygiids, to be dispersed farther from shore than would be expected, given their demersal eggs.

Vertical structure of larval fish assemblages.

Depth distribution of larval fishes may be affected by the position and strength of physical features (Ahlstrom, 1959, Kendall and Naplin, 1981). The broad depth strata sampled in this study did not allow fine-scale vertical distribution of larval fish to be established. However, some taxa were still shown to be potentially aligning themselves to physical gradients. Conditions during both cruises were not strongly stratified, especially on the shelf, due to a storm before the winter cruise, and strong southerly seabreezes before the summer cruise (Koslow *et al.*, 2006). Larvae of some taxa, such as *S. sagax*, and *Diaphus* 'slender' spp., were mostly found above the thermocline. In addition, *Diaphus* 'slender' spp. were found to be distributed deeper in the water column at station D than station E in summer, corresponding to a deeper mixed layer at station D. Tripterygiid larvae were generally neustonic, but showed a broader depth distribution closer to shore: a pattern also found by Hickford and Schiel (2003).

Larval fishes may actively position themselves at depths of maximum prey item abundance, often co-incident with the chlorophyll maximum layer (Matsuura *et al.*, 1993; Groenkjaer and Wieland, 1997). The chlorophyll-*a* profiles across the transect were very different between the two seasons studied. Inshore and shelf chlorophyll-*a* concentrations were much higher in winter than in summer, and there was a deep chlorophyll maximum layer present in summer, as is usually the case off south-western Australia (Hanson *et al.*, 2005; Lourey *et al.*, 2006). However, larval fish were not found to be aligning themselves to the chlorophyll maximum layer on either cruise. Instead, taxon-specific patterns of vertical distribution were dominant.

In conclusion, it was found that the initial hypothesis, that the distinctive oceanographic conditions found between summer and winter would be reflected in the larval fish assemblage, was supported. The distribution of larvae across the shelf and offshore appeared to be strongly influenced by the

current regime at the time of sampling. The vertical depth preferences of larvae also appeared to be influential in affecting their horizontal position, especially with respect to surface-dwelling larval fishes.

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Table and Figure Legends

Fig. 1: Schematic diagram showing the study area off south-western Australia, including the Two Rocks transect, and the approximate location and direction of flow of the Leeuwin Current off the coast of Western Australia.

Fig. 2: Sea surface temperature images of the Leeuwin Current derived from the Advanced Very High Resolution Radiometer (AVHRR) Band 4 on the NOAA-16 and -17 satellites. The black line is the 200 m isobath, approximating the continental shelf break. The study transect, and sampled stations, are shown. Images courtesy of WASTAC. CTD-derived profiles of temperature, and chlorophyll-*a* biomass across the sampled transect are also shown for August 2003 and January 2004. Data and interpolation courtesy N. Mortimer and SRFME project.

Fig. 3: ADCP data for January 2004: A) West-east component, B) South-North component. 20 minute-averaged data are shown every 8m for stations B (40m) C (100m), D (300m) and E (1000m). Available data are shown for the depth of the water column at each station, except for station E, where only the top 300m is shown.

Fig. 4: Larval fish abundances from day-time replicated bongo net samples from stations B (40m) to E (1000m): August 2003 and January 2004. Black bars denote winter samples, white bars denote summer samples. Standard errors are shown.

Fig. 5: Multi-dimensional scaling ordination of bongo net, and EZ net (integrated to 150m depth) samples from stations B (40m) C (100m), D (300m) and E (1000m) from August 2003 and January 2004.

Fig. 6: Densities of larval *Sardinops sagax*, *Etrumeus teres*, *Diaphus* 'slender' spp., *Vinciguerria* spp., Tripterygiidae spp. and Gobiidae spp. (per 1000m³) across the sampled transect from shelf to offshore waters, night samples only. Densities are plotted for each depth bracket, for August and January cruises. All night depth brackets described in Table I are shown.

Fig. 7: Total densities of larval fish (per 1000m³) across the sampled transect from shelf to offshore waters in August 2003 and January 2004 (night EZ data only). Densities are plotted for each depth bracket, and the approximate upper and lower boundaries of the thermocline are shown. All depths described in Table I were sampled.

Fig. 8: Length frequency distributions of *Sardinops sagax* (top) and *Etrumeus teres* (bottom) between summer and winter cruises, at stations B (40m) C (100m), D (300m) and E (1000m).

Fig. 9: Vertical distribution between day and night (top) and length frequency with depth (bottom) of *Sardinops sagax* larvae collected in August 2003, at stations B (40m) and C (100m). Note different scales between stations.

Table I: Depth strata sampled by the EZ net on the Two Rocks transect: winter vs. summer. Samples where only half the sample was sorted, due to a very high volume of plankton, are indicated in italics.

Table II: Abundances (number/m²) of all larval fish species collected at stations B to E in the EZ nets only, winter and summer. Note: no daytime samples were taken at stations B and E in summer, due to equipment failure. Rank abundances of the twenty most common species are shown.

Table III: Results of similarity percentage (SIMPER) comparison between larval fish assemblages, to find taxa that best distinguish between shelf and offshore assemblages, during summer and winter. The ratio between the contribution of each species to the average dissimilarity between sample groups to the standard deviation is shown in parentheses, with greater values denoting a better distinguishing species (Clarke, 1993).

Table I:

Station	EZ net depths sampled in August 2003 (winter).	EZ net depths sampled in January 2004 (summer).	Bongo net samples taken: August 2003 and January 2004.
B (40m)	0-10m, 10-20m, 20-30m (day) 0-8m, 8-20m, 20-30m (night)	No deployment during the day 0-9m, 9-20m, 20-30m (night)	Two replicated tows to just above the bottom (day).
C (100m)	0-25m, 25-50m, 50-75m (day) 0-25m, 25-50m, 50-75m (night)	0-30m, 30-65m, 65-85m (day) 0-30m, 30-55m, 55-80m (night)	Two replicated tows to just above the bottom (day).
D (300m)	0-30m, 30-70m, 70-120m (day) 0-30m, 30-70m, 70-120m, 120-230m (night)	0-30m, 30-80m, 80-120m, 120-150m, 150-200m (day) 0-30m, 30-80m, 80-120m, 120-150m, 150-200m (night)	Two replicated tows to 150m depth (day).
E (1000m)	0-30m, 30-80m, 80-150m (day) 0-30m, 30-70m, 70-150m (night)	No deployment during the day 0-30m, 30-65m, 65-90m, 90-150m, 150-300m (night)	Two replicated tows to 150m depth (day).

Table II:

Family	Species	Winter				Summer				Rank of abundance
		Stn B #/m ²	Stn C #/m ²	Stn D #/m ²	Stn E #/m ²	Stn B #/m ²	Stn C #/m ²	Stn D #/m ²	Stn E #/m ²	
Eel leptocephalii	Eel leptocephalii			0.12	0.15					
Clupeidae	<i>Etrumeus teres</i>	0.18	0.86	1.12		0.72	20.94	1.64	0.25	3
	<i>Sardinops sagax</i>	16.45	3.80	4.25		9.34	21.94	3.91	2.29	2
	<i>Spratelloides robustus</i>	0.04								
	Clupeiformes spp.		0.55				0.85	1.23		
Engraulidae	<i>Engraulis australis</i>		0.06	0.10		0.21	1.63	1.31	1.75	13
Gonostomatidae	<i>Cyclothone</i> spp.		2.77	7.13	2.96		0.12	1.00	0.52	8
	Gonostomatidae other				0.04		0.06			
Stomiidae	Stomiidae sp. 1		0.14							
Chauliodontidae	<i>Chauliodus sloani</i>		0.37	0.97	0.10					
Idiacanthidae	<i>Idiacanthus anstroptomus</i>			0.08	0.04					
Sternoptychidae	<i>Argyropelecus</i> spp.				0.07					
	Sternoptychidae other								0.20	
Phosichthyidae	<i>Vinciguerria</i> spp.		2.36	3.94	0.28		0.46	7.90	4.70	4
	<i>Pollichthys</i> sp. 1				0.14					
Scopelarchidae	<i>Scopelarchus</i> sp. 1		0.73	0.17						
Paralepididae	Paralepididae spp.			0.25				0.63	0.90	
Evermannellidae	<i>Evermannella</i> sp.							0.06		
Notosudidae	Notosudidae sp. 1		0.11	0.21	0.18					
Myctophidae	<i>Benthosema suborbitale</i>		0.09	1.35				0.06		
	<i>Ceratoscopelus warmingii</i>						0.04			
	<i>Centrobranchus</i> sp. 1			0.09	0.05					
	<i>Diaphus</i> 'slender' spp.		2.64	2.11	0.15		0.39	25.35	36.94	1
	<i>Diaphus</i> stubby spp.							0.31		
	<i>Diogenichthys atlanticus</i>		0.76	3.77	0.89		0.06	3.94	2.81	9
	<i>Hygophum</i> spp.		0.26	1.93	1.15		0.04	0.13		19
	<i>Lampadena</i> spp.			0.43			0.31	1.91	6.05	11
	<i>Lampanyctodes</i> sp.				0.09					
	<i>Lampanyctus</i> spp.		3.10	3.05	0.31		0.20	6.18	2.37	7
	<i>Lobianchia dofleini</i>		0.09	0.12					0.13	
	<i>Lobianchia gemellari</i>			0.82						
	<i>Myctophum asperum</i>							2.09	3.03	12
	<i>Myctophum phengodes</i>		0.15	0.30	0.05		0.05	0.15		
	<i>Notoscopelus resplendens</i>		0.20	0.96	0.11			0.06	0.33	
	<i>Notolynchnus valdiviae</i>							0.05		
	<i>Scopelopsis multipunctatus</i>		5.93	8.16	2.59					6
	<i>Symbolophorus</i> spp.		0.41	0.10				0.37		
Gadiformes	Gadiformes spp.			0.10						
Bregmacerotidae	<i>Bregmaceros</i> sp.		0.37	1.01				0.31		
Moridae	Moridae spp.	0.18	0.39	0.89		0.08	0.30			
Ceratiidae	Ceratoidea sp. 1			0.17						
Trachichthyidae	Trachichthyidae sp. 1	0.09								
Melamphaeidae	Melamphidae spp.			0.04				0.07		
Syngnathidae	Syngnathidae sp. 1			0.17		0.10				
	Syngnathidae sp. 2	0.06								
Scorpaenidae	Scorpaenidae sp. 1		0.68	0.91	0.97				0.49	20
	Scorpaenidae sp. 2			0.17			0.57		0.13	
	Scorpaenidae sp. 3	0.02				0.10				
	Scorpaenidae sp. 4							0.31		
Acropomatidae	<i>Apogonops anomalous</i>						3.58	0.79	0.39	14
Platycephalidae	Platycephalidae sp. 1					0.02	0.27			
	Platycephalidae sp. 2					0.10				
Callanthidae	<i>Callanthius</i> sp. 1		0.26							
Serranidae	Serranidae sp. 1		0.77			0.07				
Plesiopidae	<i>Paraplesiops</i> sp. 1		0.07							

Percichthyidae	<i>Howella</i> sp. 1				0.04		0.06			
Terapontidae	Terapontidae sp. 1					0.21	0.42			
Apogonidae	Apogonidae sp. 1	0.02								
Dinolestidae	<i>Dinolestes lewini</i>	0.17						0.10	0.12	
Nemipteridae	<i>Nemipterus</i> sp. 1						0.21			
Mullidae	Mullidae sp. 1		0.09				0.57	1.45	1.43	18
Sillaginidae	<i>Sillago</i> spp.		0.17			0.14				
Carangidae	Carangidae spp.	0.12	0.06			1.48	14.35	0.70	0.04	5
	<i>Pseudocaranx</i> spp.						0.21			
	<i>Seriola</i> sp. 1								0.04	
	<i>Trachurus novazelandiae</i>								0.94	
Pempheridae	Pempheridae spp.	0.07				0.26	0.85			
Chaetodontidae	Chaetodontidae sp. 1				0.04					
Pomacentridae	<i>Chromis</i> sp. 1						0.04	0.46	2.01	
	<i>Amphrioption</i> sp. 1		0.06				0.06	0.06	0.04	
	Pomacentridae sp. 1						0.21			
	Pomacentridae sp. 2						0.24	0.12	0.08	
Labridae	Labridae sp. 1	1.95	0.28	0.63		0.58	6.19	0.05	0.47	10
	Labridae sp. 2					0.08				
	Labridae sp. 3								0.24	
	Labridae sp. 4						0.21			
	Labridae sp. 5			0.12		0.04	0.40	0.06		
	Labridae sp. 6				0.08					
Chiasmodontidae	<i>Kali macrura</i>		0.09	0.43						
Creedidae	<i>Creedia haswellii</i>	0.74	1.01				0.74			
Leptoscopidae	Leptoscopidae sp. 1	0.49		0.33						
Percophidae	<i>Enigmapercis reducta</i>					0.02	0.51		0.09	
Blenniidae	<i>Parablennius postoculomaculatus</i>	0.10				0.52				
Tripterygiidae	Tripterygiidae sp. 1	0.09	0.14			0.54	0.25	0.35	0.04	
Clinidae	Clinidae sp. 1	0.68	0.31							
Odacidae	Odacidae sp. 1	1.04				0.20	0.52			
Pinguipedidae	<i>Parapercis</i> spp.	0.10	0.07							
Gonorhynchidae	<i>Gonorhynchus greyii</i>				0.04					
Gobiesocidae	<i>Alabes</i> sp. 1	0.27				0.04	0.42			
	Gobiesocidae sp. 1	0.07	0.12			0.03				
	Gobiesocidae sp. 2						0.27			
Callionymidae	Callionymidae sp. 1	0.60	0.40	0.09			2.43	0.06		16
Gobiidae	<i>Afurcogobius suppositus</i>					0.29	1.76			
	Gobiidae sp. 2					0.10	0.80			
	Gobiidae sp. 3	0.44	0.20	1.80			0.19	0.64	0.29	17
Scombridae	<i>Scomber australasicus</i>						0.46	1.43	0.69	
	Scombridae sp. 1	0.02								
Nomeidae	<i>Psenes whiteleggii</i>				0.03					
Pleuronectiformes	Pleuronectiformes spp.	0.20		0.74		0.08	0.24	0.17	0.04	
Paralychthidae	Paralychthidae sp. 1						0.06			
Monacanthidae	Monacanthidae spp.	0.89	0.39	0.66		0.24	0.66	0.17		
Unidentified	Unidentified sp. 1	0.80	0.99	1.76			0.27			15

Table III:

SIMPER comparison	Distinguishing taxa
Summer shelf vs. winter shelf	Carangidae spp.: More in summer. (1.8) Labridae sp. 1: More in summer. (1.4)
Summer offshore vs. winter offshore	<i>Diaphus</i> 'slender' spp.: More in summer (2.6) <i>Diogenichthys atlanticus</i> : More in winter (1.7)
Summer shelf vs. summer offshore	<i>Diaphus</i> 'slender' spp.: More offshore (2.1) Carangidae spp.: More on shelf (1.9) <i>D. atlanticus</i> : More offshore (1.6)
Winter shelf vs. winter offshore	<i>Sardinops sagax</i> : More on shelf (1.0) Monacanthidae: More on shelf (0.90)

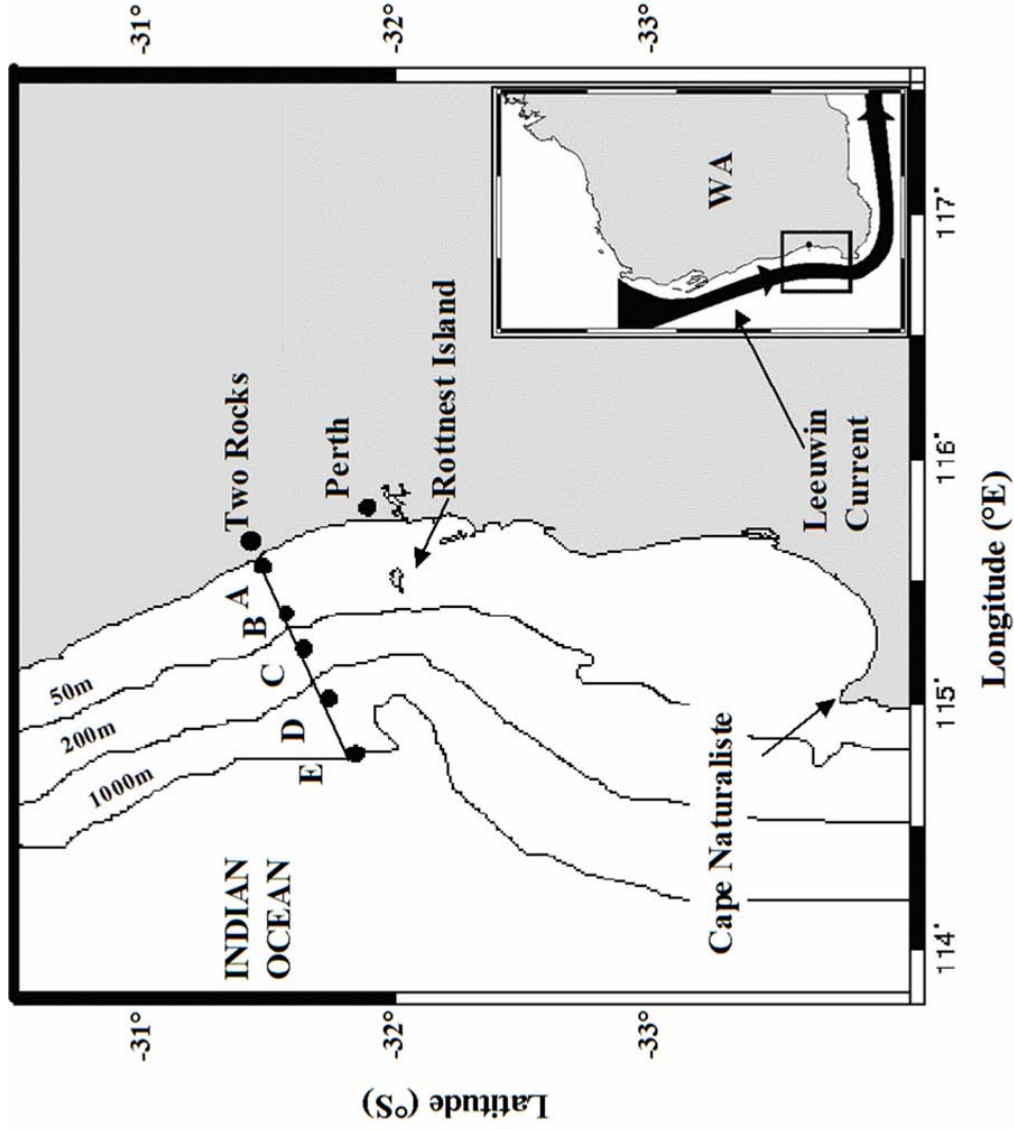


Figure 1

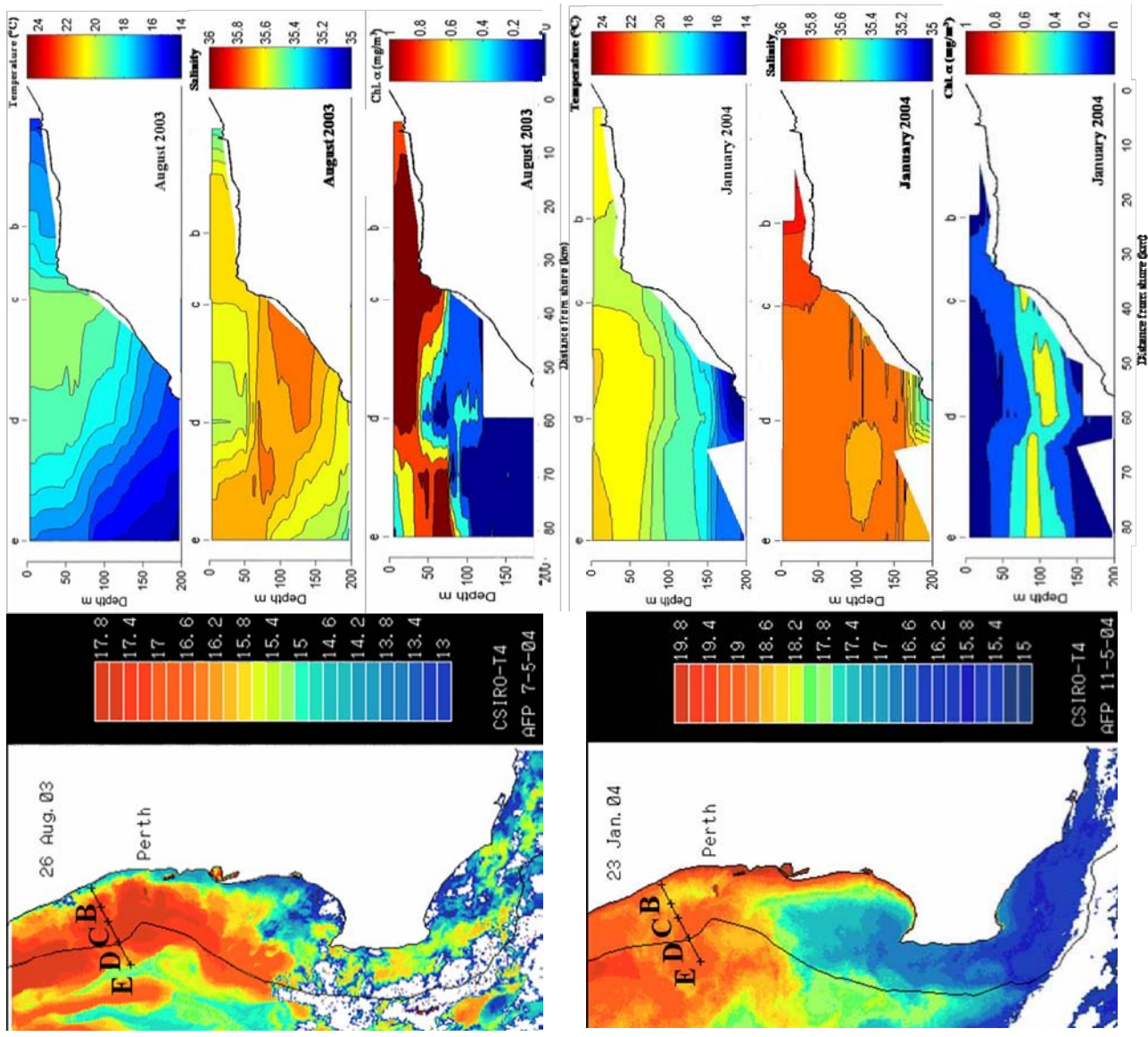


Figure 2

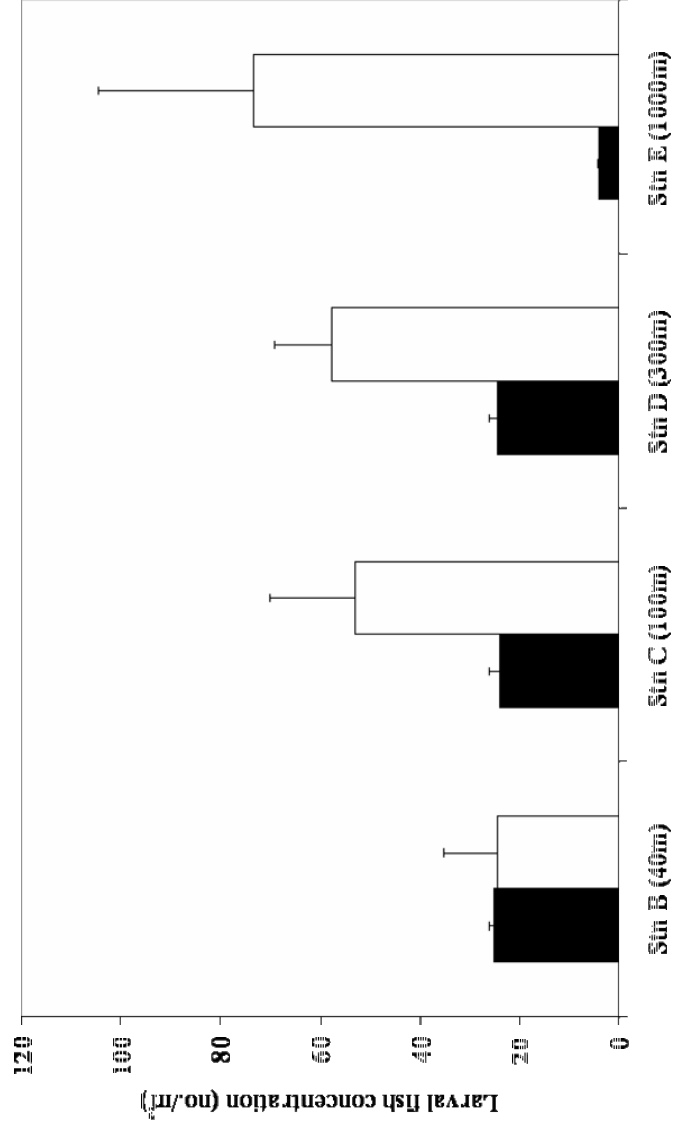


Figure 3

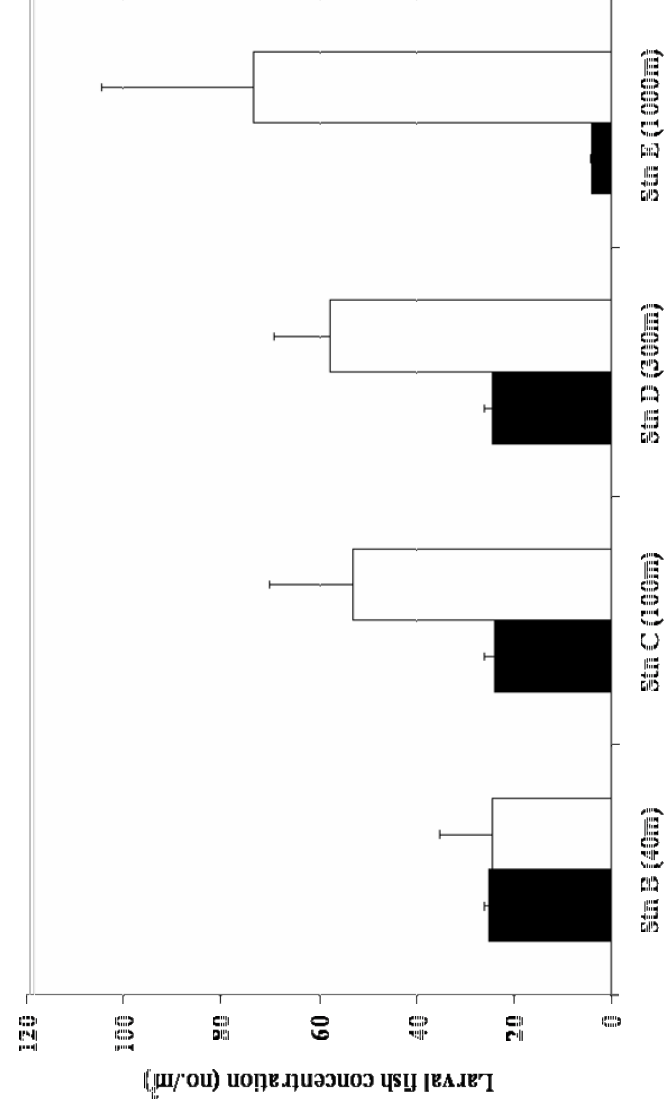


Figure 4

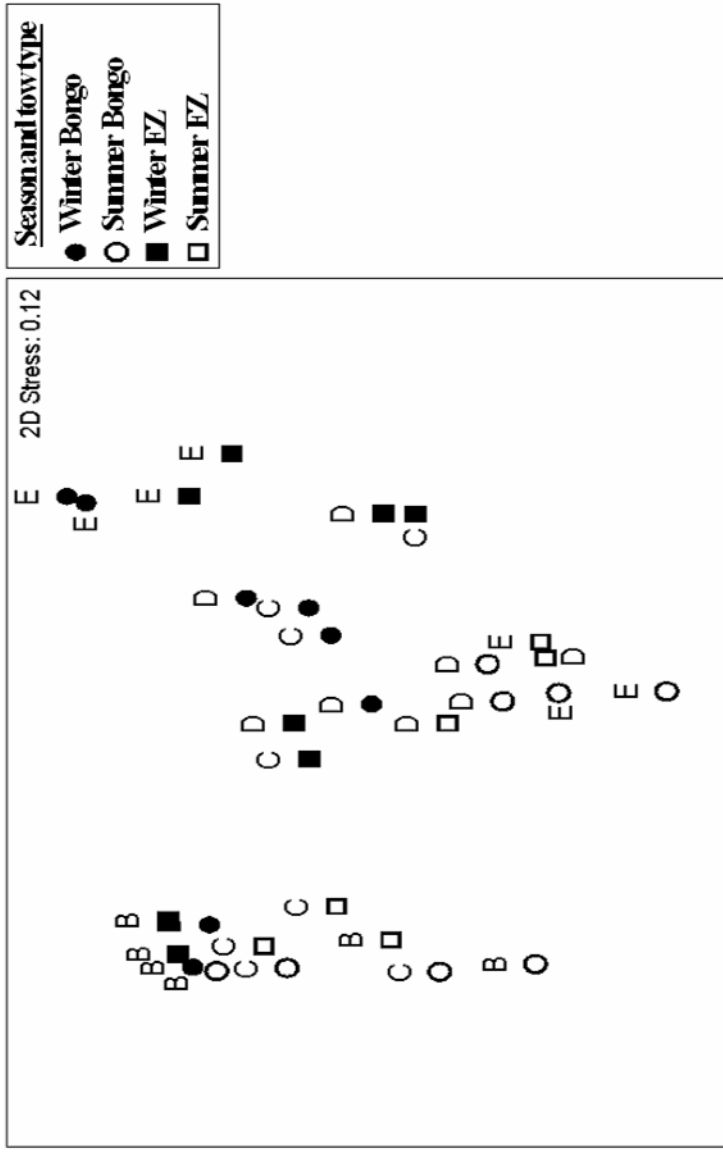
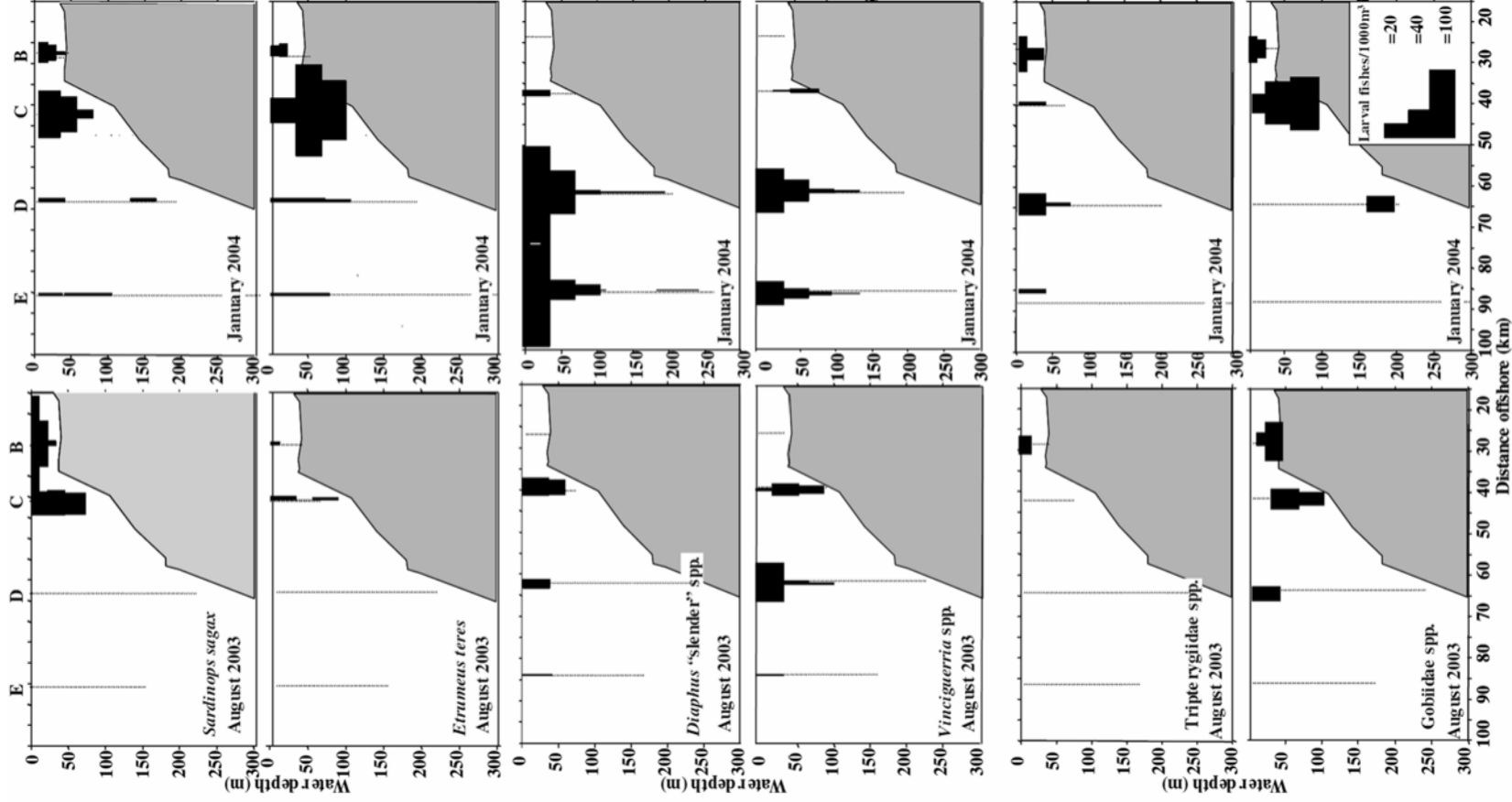
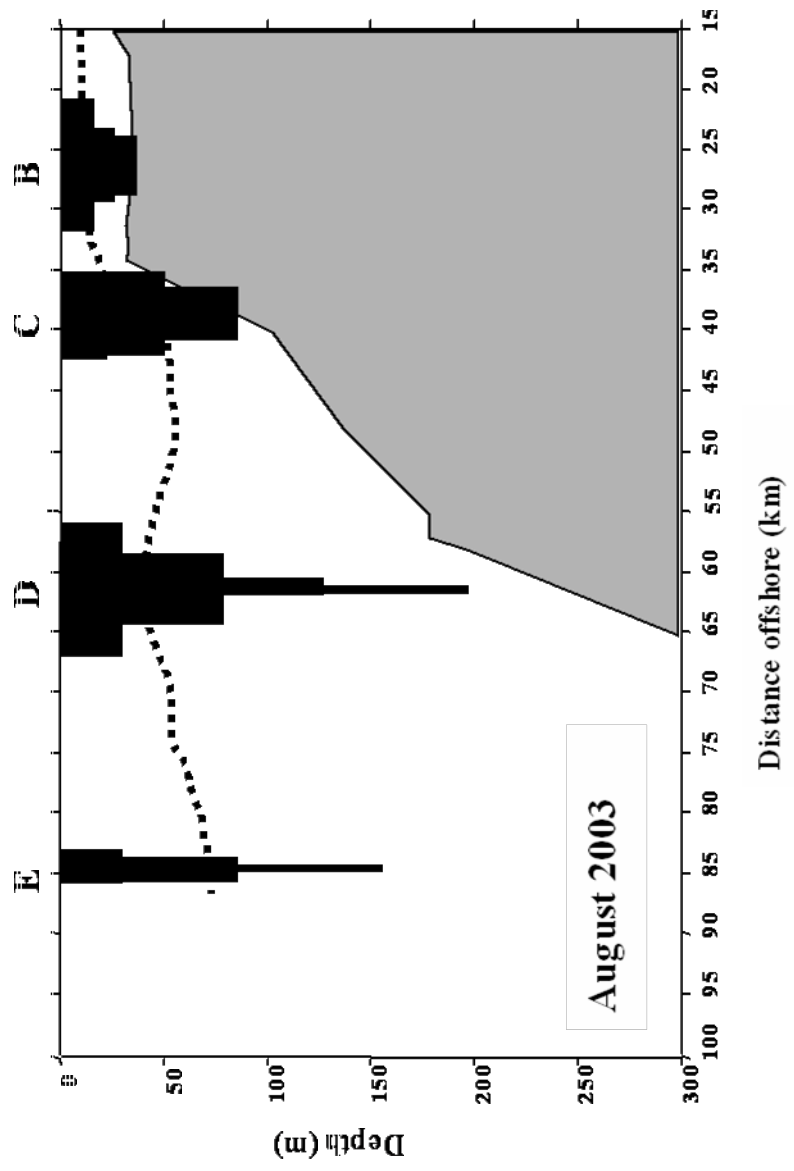


Figure 5





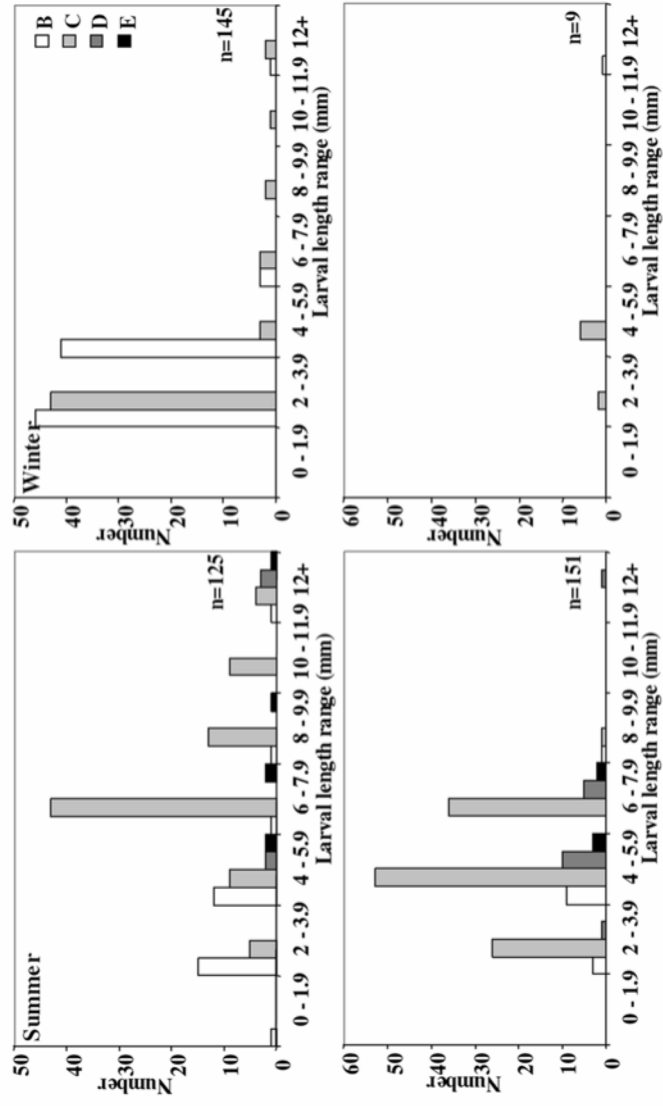


Figure 8

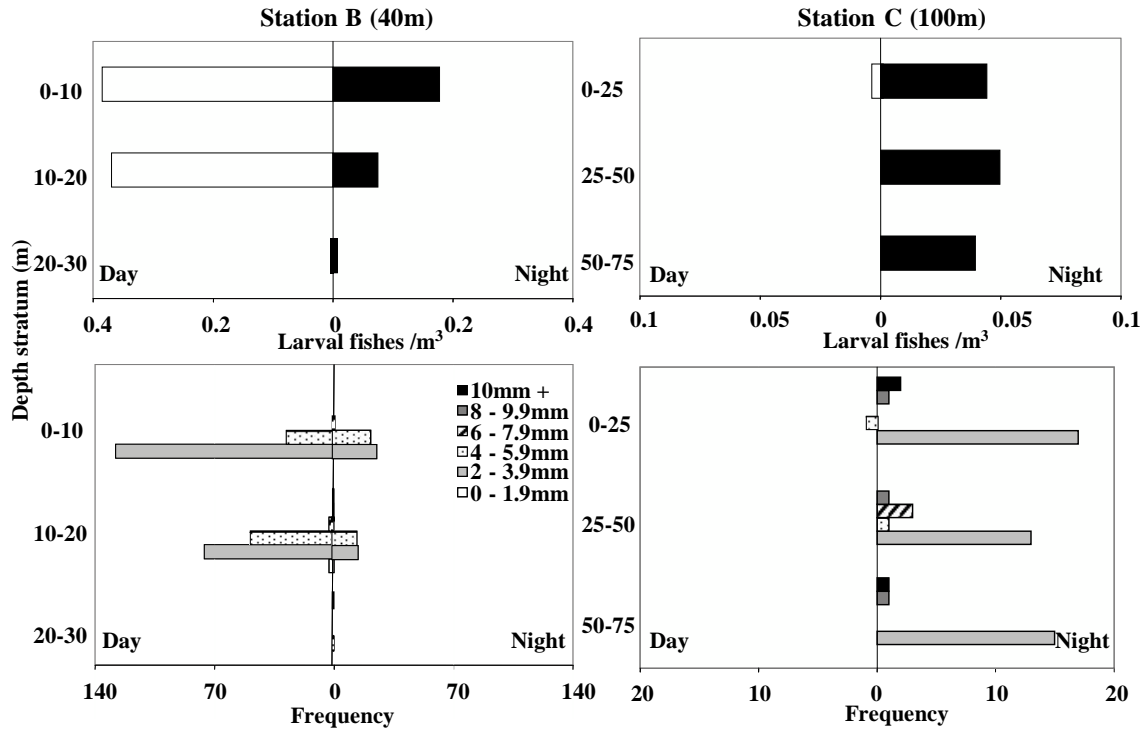


Figure 9