Natural variability of macro-zooplankton and larval fishes off the Kimberley, north-western Australia: Preliminary findings

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Abstract

During the austral autumn, spatial (regional cross-shelf) and temporal (tidal cycle and spring-neap cycle) variability of macro-zooplankton and larval fishes off the Kimberley coast were examined in conjunction with the physical oceanography. Though surface waters were isothermal across the study area, strong stratification was evident and warm, high salinity surface waters overlaid a cooler, less saline water mass. There was no evidence of frontal features over the shelf or at the shelf break. Variability of macro-zooplankton, particularly krill and larval fishes, was defined by significant cross-shelf structuring in relation to isobath; higher concentrations were recorded for coastal waters, compared to shelf and oceanic waters. *Pseudeuphausia latifrons* was the dominant krill species in shelf waters, whereas the more speciose oceanic assemblages were dominated by species of the genus *Stylocheiron*. The greater diversity and concentrations of larvae of neritic teleost families for assemblages at the 50 m isobath distinguished coastal waters from those further offshore and within the more turbid waters of King Sound. Assemblages in proximity to the Lacepede Islands were also taxonomically distinct. The occurrence of larvae of commercially valuable teleost fishes, such as the Lutjanidae, Serranidae and Scombridae, in the study region is an important consideration for environmental and fisheries management. This study provides a baseline which can be used to evaluate anthropogenic disturbance to the Kimberley pelagic ecosystem.

Keywords: Macro-zooplankton, larval fishes, euphausiids, assemblages, oceanography

Introduction

The Kimberley has one of the least studied marine pelagic ecosystems off Australia and, in particular, the zooplankton is poorly known. Existing zooplankton studies for the region comprise those from Scott Reef (McKinnon *et al*. 2003) and the southern north-west shelf (NWS) (Wilson *et al*. 2003a; 2003b). A recent review of larval fish studies off Western Australia highlighted the absence of published work for the Kimberley region (Beckley *et al*. 2009) though an early study by Young *et al*. (1986) was completed off the southern NWS.

Game *et al*. (2009) noted the increasing exposure of pelagic ecosystems to anthropogenic disturbances which have the potential for significant negative impacts. Zooplankton is integral in marine food webs (Richardson 2008), for example, as a food source for baleen whales (Rennie *et al*. 2009) and whale sharks (Wilson & Newbound 2001, Jarman & Wilson 2004). The planktonic larval stage is crucial for reproductive success of many marine organisms including those with conservation significance such as corals and fishes which also have high economic value. Thus, there is an urgent need to understand the pelagic ecosystem of the Kimberley by establishing the composition and natural variability of

the zooplankton component and the key physical processes which drive this variability.

Planktonic communities are strongly influenced by physical oceanography at a range of spatial and temporal scales. In continental shelf systems around the world, physical processes, such as internal waves, tidal mixing, localised upwelling and wind-driven currents influence the distribution of water masses and their associated zooplankton (*e.g.* Botsford *et al*. 1994, Bradbury & Snellgrove 2001, McKinnon *et al*. 2003, Mackas & Coyle 2005).

Circulation of waters off the NWS, including the Kimberley, is understood to be a complex interaction between tides, wind and regional forcing by large-scale currents at the shelf break (Brink *et al*. 2007, Condie & Andrewartha 2008). The strongest influence upon circulation is by barotropic tides which are semi-diurnal and characterised by a large spring tidal range of >10 m (Holloway 1983; Cresswell & Badcock 2000; Condie & Andrewartha 2008). Tidal forcing induces an instantaneous response upon circulation and transport (Condie & Andrewartha 2008) and the influence upon zooplankton may be evident at temporal scales of hours (tidal cycle) to weeks (spring-neap cycle). Longer term transport over the inner and mid-shelf of the Kimberley is mostly controlled by wind-driven Ekman transport and there is a seasonal reversal in transport resulting from the change from the summer monsoon to winter
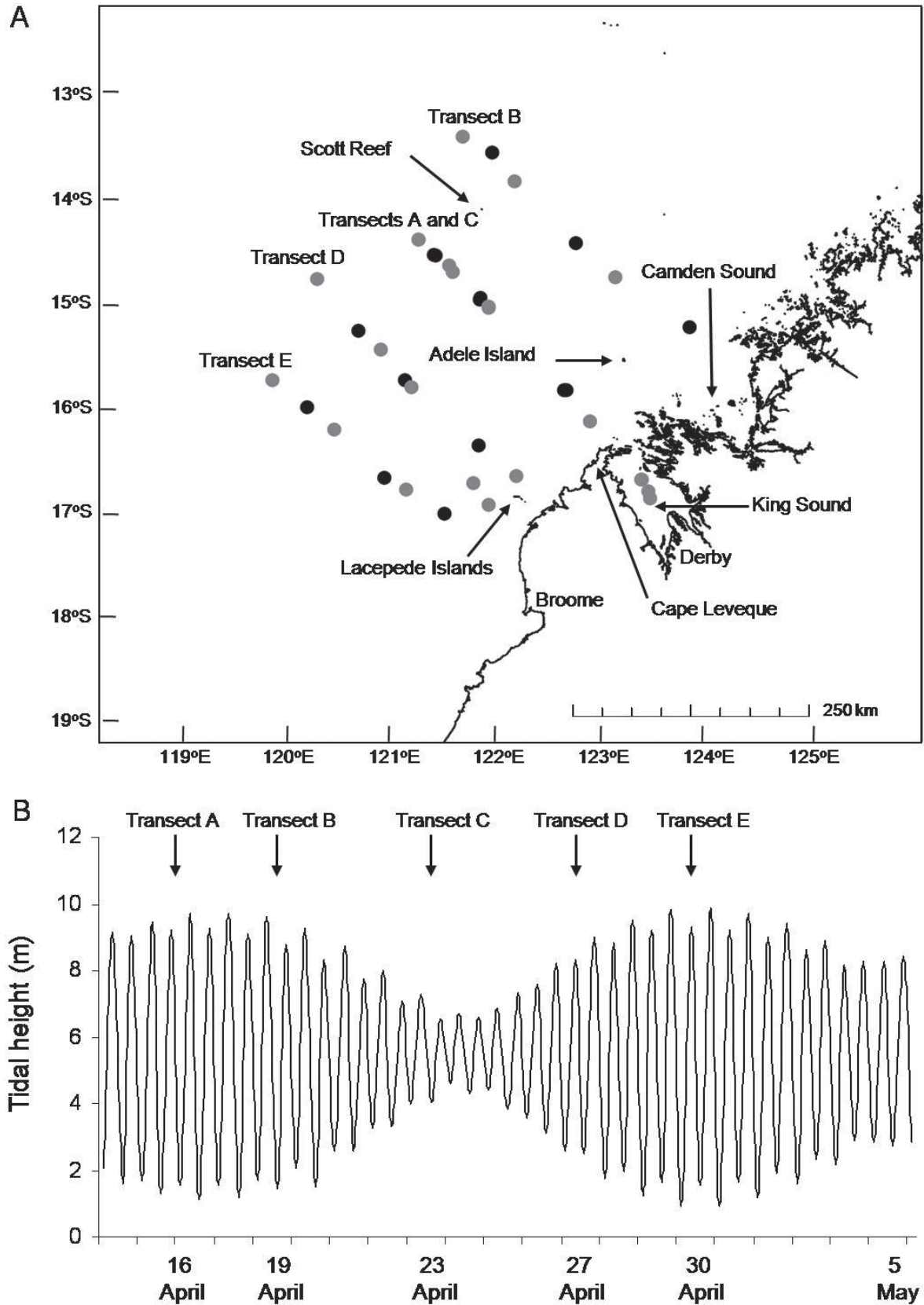
Figure 1. A) The survey area showing the location of sampling stations occupied off the Kimberley coast, north-western Australia, in April 2010. The grey-shaded circles represent stations that were occupied for 2 hours while the black-shaded circles represent sampling stations that were occupied for 12 hours over a full tidal cycle. Note: A and C represent the same transect that was surveyed during the spring (transect A) and neap (transect C) tides. B) Tidal height data for Broome corresponding with the sampling period and indicating when each transect was sampled.

south-easterly trade winds (Condie & Andrewartha 2008).

The water column of the NWS is strongly stratified in summer, characterised by a shallow mixed layer (~20 m) resulting from intense solar heating of surface and near-surface waters (Church & Craig 1998) while waters are generally well mixed during winter (Holloway & Nye 1985). Coupled with steep bathymetry and very large tidal amplitudes, the interaction of these features is known to result in the generation of strong internal waves at the shelf break (Van Gastel *et al*. 2009). It is likely that these will exert strong influence upon plankton occupying the shelf waters off the Kimberley.

This study presents the preliminary findings on the natural variability of macro-zooplankton and larval fishes in shelf and offshore waters of the Kimberley. It was conducted as part of a multidisciplinary investigation of physical forcing of productivity on the Kimberley shelf. The aim is to contribute baseline information on the zooplankton component of the pelagic ecosystem of the Kimberley.

Methods

This study was conducted from the Marine National Facility R.V. *Southern Surveyor* (voyage 03/2010) in the austral autumn over a period of 3.5 weeks (14 April to 5 May 2010). Five cross-shelf transects off the Kimberley coast which included waters in proximity to the offshore atoll, Scott Reef, were surveyed (Fig. 1). Six sampling stations were located along each transect at the 50 m (coastal), 100 m (inner shelf), 200m (mid shelf), 500 m (outer shelf) and 1000 m and 2000 m (oceanic) isobaths. Transect lines A and C extended into King Sound adding a coastal embayment endpoint to the cross-shelf gradient. Sampling in proximity to the Lacepede Islands provided a shoreward extension of transect D. The research voyage encompassed a spring-neap cycle and transect A was sampled (14 April; new moon) during the spring tide and repeated a week later (transect C, 21 April; first quarter moon) to coincide with the neap tide (Fig.1).

Sampling at the 2000 m, 500 m and 100 m stations and within King Sound and in proximity to the Lacepede Islands took approximately 2 hours and involved a single CTD cast and replicate plankton tows using a bongo net. To ascertain if there was net change in zooplankton between subsequent tides, the 1000 m, 200 m and 50 m stations were sampled at the start and end of a 12 hour period. The physical oceanography was examined using repeated CTD casts at approximately hourly intervals at these stations. Further, a 24 hour study was completed at a single shelf location during which the influence of tidal cycle on zooplankton was examined in detail (to be reported elsewhere).

Conductivity-temperature-depth-oxygen (CTD-O$_2$) measurements were performed using a Seabird SBE 19+ instrument which was equipped with dual temperature and conductivity sensors and a Chelsea TGI fluorometer. Casts were to 1000 m depth, or to ~10 m above the bottom in shallower water. These data were used to examine water masses and other physical features such as fronts which may have been present during the time of sampling.

Continuous underway measurement of the horizontal velocity along the ship's track was obtained using a vessel-mounted RDI 75 kHz Ocean Surveyor Acoustic Doppler Current Profiler (ADCP) (Teledyne RD Instruments). The instrument was set to record from just below the surface to a maximum water column depth of 300 m and data were averaged in 8 m depth bins.

Replicated depth-integrated bongo net samples (100 μm and 355 μm meshes, mouth area 0.196 m^2, diameter 0.6 m) were obtained by towing the nets obliquely to the surface from a maximum depth of 150 m (or from 10 m off the bottom in shallow water) at a ship's speed of 2 knots for 15 minutes. A mechanical General Oceanics flow meter was positioned centrally in each of the nets and they were linked electronically to a CSIRO-developed interface from which the tow profile could be monitored and the volume of seawater filtered quantified. The samples from all stations were preserved in 5% formaldehyde. For examination of macro-zooplankton, particularly krill and larval fishes, only data from the 355 μm net are presented here.

The bio-volume, expressed as the settled volume (ml / m^3 filtered seawater), of macro-zooplankton from each 355 μm bongo net sample was determined using the standard method of George and White (1985). Settled volumes of plankton were measured (to nearest 1 ml) by pouring the samples into graduated cylinders and allowing the material to settle for 24 hrs. If necessary, detritus (pieces of macro algae) and large organisms (*e.g.* jellyfish) were removed prior to establishing the settled volume.

Plankton samples were sorted with the aid of a dissecting microscope. Larval fishes, squid and lobster phyllosoma were removed for later identification and the zooplankton assemblages were described in terms of their composition, i.e. major taxonomic groups. Numerical abundance of euphausiids was established using the sub-sampling method of Gibbons (1999) and counts were standardised to the number per m^3 of filtered seawater. Adult and juvenile stages were identified to species level using relevant literature (Baker *et al*. 1990; Gibbons 1999; Ritz *et al*. 2003).

The counts of larval fishes were standardized to number of larvae per m^3 of filtered seawater. Larval fishes were identified to family level using relevant literature (*e.g.* Moser & Ahlstrom 1970, Moser 1984, Olivar & Beckley 1997, Neira *et al*. 1998, Olivar & Fortuño 1991, Leis & Carson-Ewart 2000, Richards 2006).

Uni- and multivariate techniques were applied using the statistical software package SPSS 14.0 to examine spatial and temporal trends in the bio-volume of macro-zooplankton and the concentrations of larval fishes. Spatial factors included transect and isobath while temporal factors included spring and neap tides, subsequent tides and day versus night (diel). Prior to analysis, the bio-volume of macro-zooplankton and concentrations of larval fishes were log$_{(10)}$ transformed. For all ANOVA tests Levene's test for homogeneity of variances was applied; where non-homogeneity existed in the data set, *post hoc* testing using the Games-Howell test, which assumes unequal variances, was used for pair-wise comparisons. Analyses were approached iteratively using a three-way ANOVA design to identify
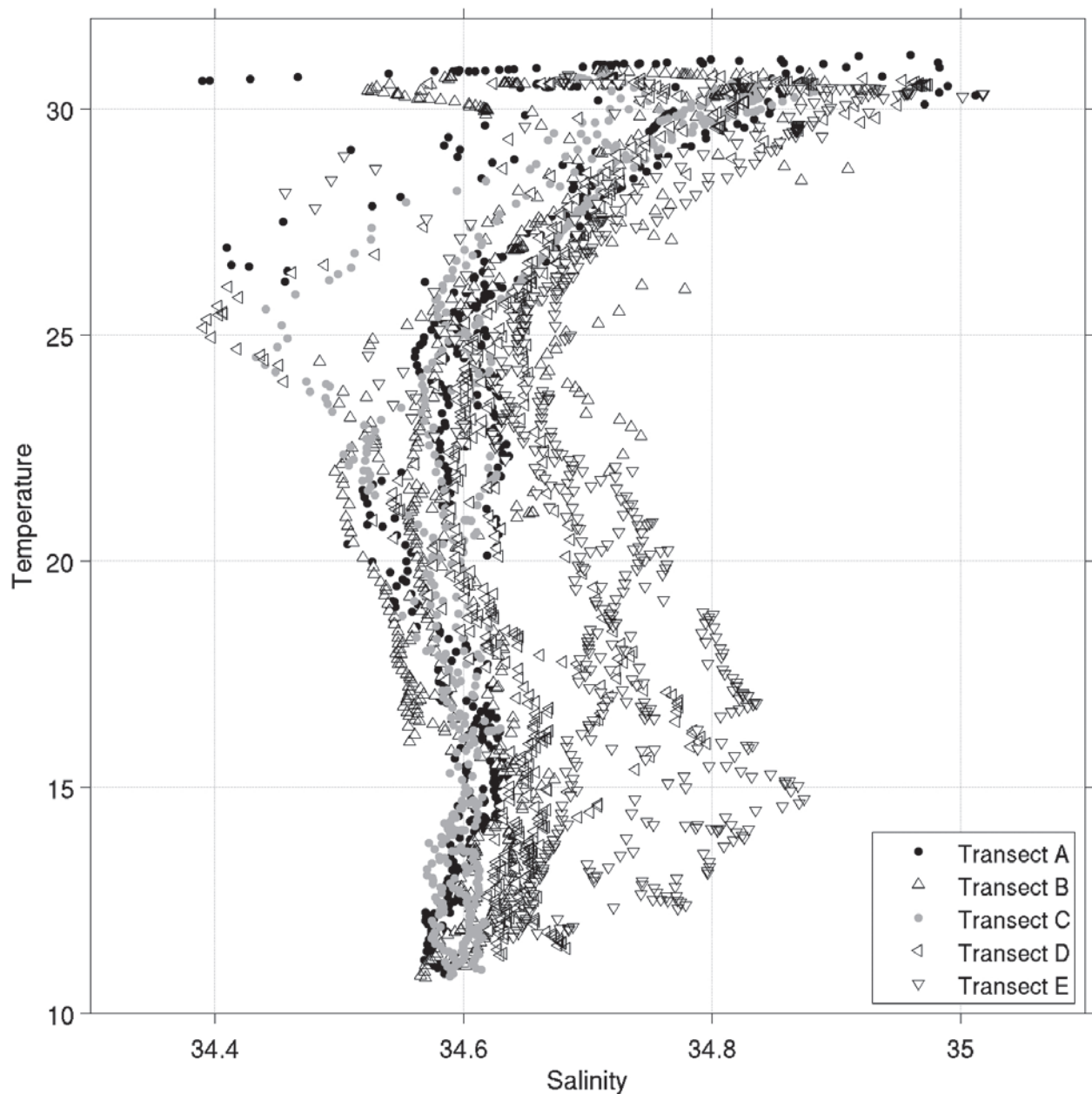
Figure 2. Temperature-salinity profiles of the upper 300 m of the water column measured over all transects off the Kimberley coast.

the factor(s) most responsible for the observed patterns. This analysis used only those samples collected at 12 hr sampling stations.

Subsequently, a one-way ANOVA was used to resolve significant differences in relation to isobath using all samples from all 2 hr and 12 hr sampling stations, including stations within King Sound and in proximity to the Lacepede Islands. Differences between spring and neap tides were examined using a two-way ANOVA (transect and isobath) for samples collected at transects A (spring tide) and C (neap tide).

Analysis of larval fish assemblage structure was undertaken using the PRIMER-6 software package (Clarke & Warwick 2005). Prior to analysis, the concentrations of larval fishes were $\log_{(x+1)}$ transformed to

reduce the weighting of dominant families and a Bray-Curtis resemblance matrix was constructed. The spatial structure of larval fish assemblages was examined using multi-dimensional scaling ordination (MDS) with samples classified according to isobath. Hypothesis testing in relation to larval fish assemblages was done iteratively and commenced using a three-factor PERMANOVA design (Anderson *et al.* 2005) applying the same format as described above. Significant results were examined *post hoc* using the analysis of similarity (ANOSIM) routine to determine where the significant differences existed. The similarity percentage routine (SIMPER) routine was applied to identify the taxa most responsible for delineation between the different larval fish assemblages.

Results

Oceanography

Temperature-salinity (T-S) profiles of the upper 300 m of the water column for shelf and offshore waters revealed two distinct water masses; high temperature (>30°C) and high salinity (>34.7 psu) surface water overlaid upon cooler, lower salinity water (Fig. 2). The T-S profile indicated that there was little spatial variability, i.e. between transects, in these properties during the sampling period. Cross-shelf sections of T and S are illustrated for transect B which extended into coastal waters at the entrance to Camden Sound. This showed that, vertically, the upper water column (to ~60 m depth) was strongly isothermal (Fig. 3A). The warm, high salinity water mass was present from the shelf break (~200 m) to the inner shelf but there was some evidence of lower salinity coastal water (Fig. 3B). The salinity of
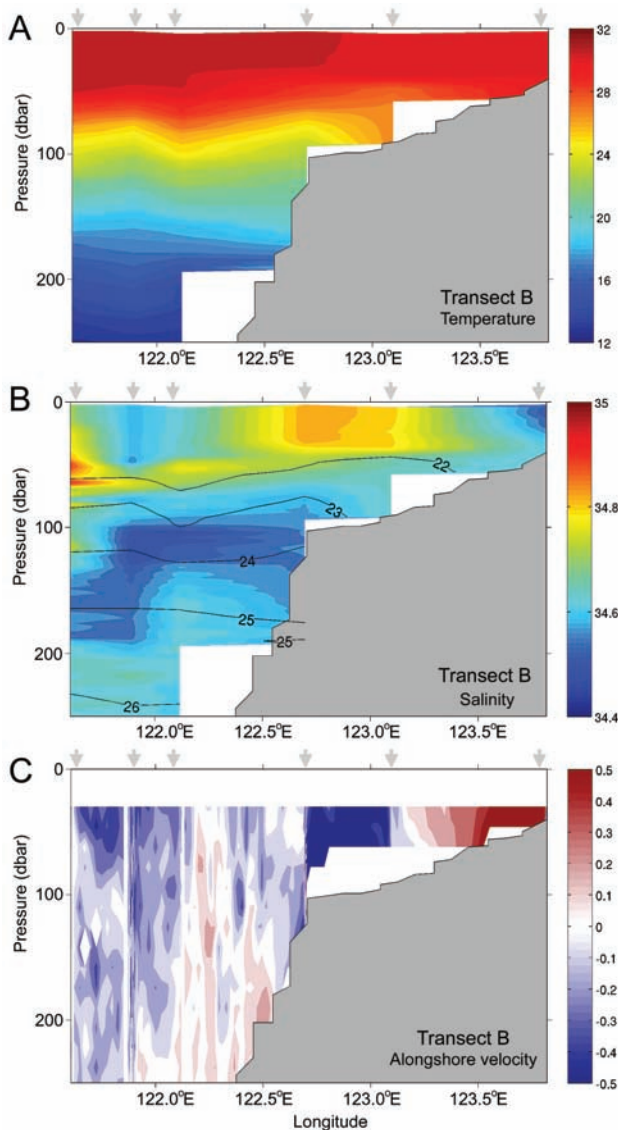
shelf water was higher by 0.3 psu, but up to 0.6°C cooler, compared with waters occupying the same depths further offshore and this may represent evaporative cooling over the broad shallow shelf. There appeared to be no obvious frontal features over the shelf or at the shelf break. Current velocities were strongest in the alongshore direction (Fig. 3C) and were, on average, 0.1–0.2m s^{-1} greater than in the cross-shelf direction. Over a tidal cycle, i.e. between subsequent low tides, there was an apparent shift from a stratified water column at low tide to one that was well mixed around mid to high tide as illustrated by an inner shelf station along transect C (Fig. 4).

Macro-zooplankton

The mean bio-volume of macro-zooplankton (settled volume ml / m^3) showed a decreasing trend from coastal to oceanic waters although there was some spatial variability (Fig. 5). Mean bio-volume of zooplankton was highest at the 50 m isobath (1.52 ml / m^3) and decreased offshore (<0.4 ml / m^3) (Fig. 6A). In proximity to the Lacepede Islands, mean zooplankton bio-volume was higher (0.89 ml / m^3) than in King Sound (0.33 ml / m^3).

A three-factor ANOVA revealed this cross-shelf pattern to be significant in relation to isobath and transect ($p < 0.001$) but inspection of the F-ratios indicated that

Figure 3. A) Temperature, B) salinity (density in contours) and C) alongshore velocity (blue denotes south-westward flow and red north-eastward flow) along transect B. Arrows denote CTD cast locations.
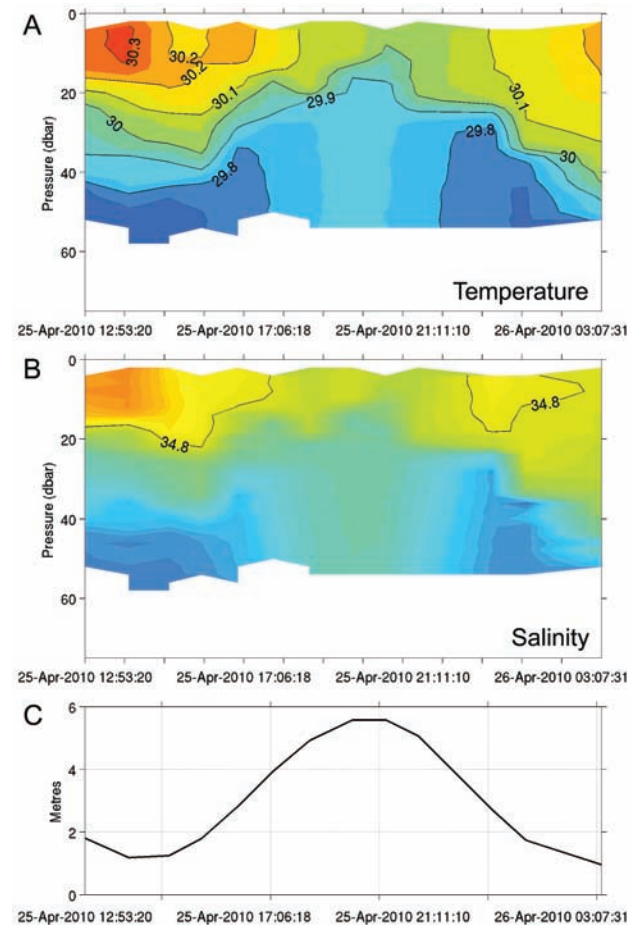

Figure 4. A) Temperature and B) salinity profiles sampled at ~50 m depth along transect C over a 12 hour tidal cycle. C) Tidal height at Adele Island, just north of the transect.

Table 1

Results of three-factor ANOVA which examined differences in the bio-volume of macro-zooplankton (ml settled volume / m^3) in relation to the factors isobath, transect and diel variation for samples collected in shelf and oceanic waters off the Kimberley coast, north-western Australia, April 2010.

Factors	df	MS	F	p
Isobath	2	12.3	215.6	<0.001
Transect	4	0.53	9.5	<0.001
Diel	1	0.01	0.3	0.6
Isobath x Transect	8	0.42	7.3	<0.001
Isobath x Diel	2	0.1	1.8	0.18
Transect x Diel	4	0.13	2.2	0.09
Isobath x Transect x Diel	7	0.13	2.2	0.06
Residual	29			
Total	58			

isobath exerted the strongest influence (F-ratio two orders of magnitude greater than the other main effects and interactions; Table 1). One-way ANOVA showed that cross-shelf structuring was defined largely by the significantly higher (p<0.001) bio-volume at the 50 m isobath (as well as in proximity to the Lacepede islands, p<0.01) when compared with stations further offshore and within King Sound. Three-way ANOVA identified the influence of subsequent tides to be confounded by diel variation, although neither was significant. Two-way ANOVA showed a significant difference overall in the mean bio-volume of macro-zooplankton between spring and neap tides (p <0.001). Significantly higher bio-volume corresponding with the neap tide was only recorded for the 50 m, 100 m and 200 m isobaths (Fig. 7A).

Within macro-zooplankton assemblages, copepods and euphausiids were ubiquitous across the study area though chaetognaths and sergestid shrimps (*Lucifer* spp.) were often abundant at mid and inner shelf stations. Larval cephalopods and lobster phyllosoma were recorded at both shelf and oceanic stations and the larval and post-larval stages of decapod crustaceans (mostly crab zoea), echinoderms (crinoid pluteus larvae and post-larval ophiuroids), gastropods and polychaetes were also conspicuous components of the Kimberley macro-zooplankton.

Concentrations of euphausiids (largely comprised of larval stages) were highest (6.9 / m^3) at the 50 m isobath but were not recorded in coastal waters in the vicinity of the Lacepede Islands (Fig 6B). Very low concentrations (<0.1 / m^3) of larval and adult stage euphausiids were recorded within King Sound. *Pseudeuphausia latifrons* was the most abundant euphausiid overall and dominated euphausiid assemblages in shelf waters while oceanic stations were dominated by species of the genus *Stylocheiron* (in particular, *S. carinatum*) and *Euphausia* species.

Larval fishes

Mean concentrations of larval fishes (number / m^3 seawater) for depth-integrated bongo samples (range: 0.06 – 3.2 larvae / m^3) revealed a decreasing trend from coastal to oceanic waters (Fig. 8) and significant

structuring in relation to isobath, transect and diel variation (Table 2). F-ratios showed that isobath exerted the strongest influence upon the observed pattern. As described for macro-zooplankton, the influence of subsequent tides was confounded by diel variation.

One-way ANOVA indicated that cross-shelf structuring was driven by the significantly higher concentrations of larval fishes inshore at the 50 m isobath (1.36 larvae / m^3; p<0.001) and in proximity to the Lacepede Islands (1.5 larvae / m^3; p<0.01) compared to stations further offshore and within King Sound (Fig. 6C). Instances where the concentrations of larval fishes in plankton samples were <0.1 larvae / m^3, of which there were two, were associated with the presence of large jellyfish or an observably higher abundance of other planktonic predators such as chaetognaths. There was no significant difference (p = 0.27) in the concentrations of larval fishes between spring and neap tides (Fig. 7B).

Depth-integrated bongo sampling collected 6,513 larval fishes representing 110 teleost families and, across all transect stations, there was a high diversity of teleost families (range: 35 – 57 families: Fig. 6D). In general, the number of neritic families (n = 90 families) declined offshore whereas the number of oceanic meso-pelagic families decreased towards the coast. Samples from both King Sound and the Lacepede Islands contained only the larvae of neritic families and were considerably lower in diversity (14 and 22 families, respectively).

The percentage contributions of larval fishes by family for assemblages representing each isobath revealed taxonomic differences with distance offshore (Table 3). Coastal and reef-dwelling families were most abundant over the shelf and included the Gobiidae (gobies), ptereleotrine Microdesmidae (dartfishes), Lutjanidae (snappers and fusiliers), Pomacentridae (damselfishes), epinepheline Serranidae (groupers and coral trouts), Labridae (wrasses), Mullidae (goatfishes) and Scaridae (parrotfishes).

At the shelf break and offshore, there was a greater abundance of larvae of pelagic families such as the Gempylidae and Scombridae (tunas: *Katsuwonus pelamis*, *Auxis* and *Thunnus* species and mackerels: *Rastrelliger*

Table 2

Results of three-factor ANOVA which examined differences in the concentrations of larval fishes (number / m^3) in relation to the factors isobath, transect and diel variation for samples collected in shelf and oceanic waters off the Kimberley coast, north-western Australia, April 2010.

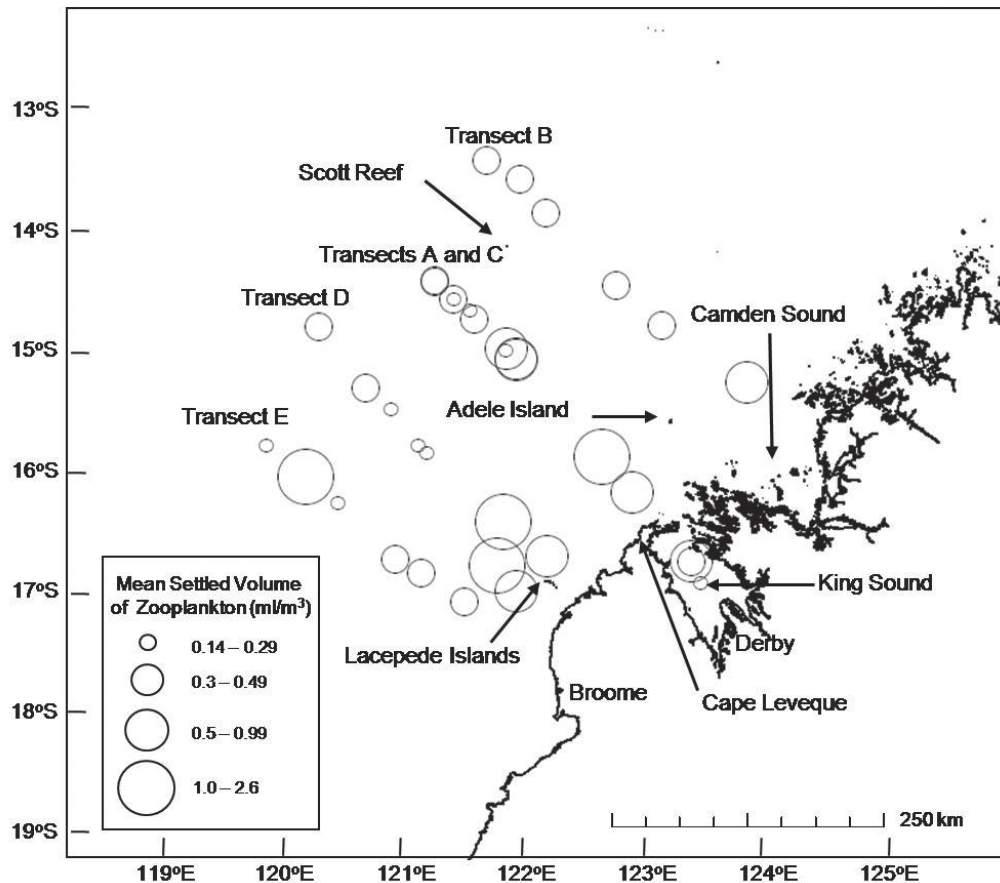| Factors	df	MS	F	p
Isobath	2	13.9	80	<0.001
Transect	4	0.7	4.1	0.01
Diel	1	1.7	9.6	0.004
Isobath x Transect	8	0.08	0.47	0.8
Isobath x Diel	2	0.04	0.21	0.8
Transect x Diel	4	1.3	7.6	<0.001
Isobath x Transect x Diel	7	0.28	1.6	0.2
Residual	29			
Total	58			

Figure 5. Mean bio-volume of macro-zooplankton (ml / m³) sampled using a 355 μm mesh bongo net in shelf and oceanic waters off the Kimberley coast, north-western Australia, April 2010.

and *Scomberomorus* species). Myctophidae larvae were the most abundant of the meso-pelagic families and were ubiquitously distributed in oceanic and shelf waters. These larvae accounted for >35% of all larvae in assemblages at the outer shelf (200 m) and offshore but were less abundant toward the coast. In contrast, Bregmacerotidae (pelagic codlets) declined in their contribution with distance offshore. Leptocephalus larvae, in particular those of the neritic Congridae (conger eels), were a conspicuous component of the oceanic assemblage.

Multi-dimensional scaling ordination of larval fish assemblages showed clear spatial separation which defined a gradient from coastal to oceanic waters. Assemblages in coastal waters (50 m isobath), including those in proximity to the Lacepede islands, were clearly separated from assemblages at the mid and outer shelf (100 m and 200 m), shelf break (500 m) and oceanic (1000 m and 2000 m) stations (Fig. 9). The King Sound assemblage was also distinct from all other assemblages and was characterised by low diversity.

There was significant structuring of larval fish assemblages in relation to transect, isobath and diel variation as well as significant interaction between each of these terms (Table 4). Isobath exerted the strongest influence upon the observed structure as indicated by the higher value for the components of variation.

Cross-shelf structuring of larval fish assemblages was defined by the strongly significant difference between the 50 m assemblage compared to all other assemblages (Appendix 1: ANOSIM R >0.8 for all pair-wise isobath comparisons). The larval fish assemblage characterising the Lacepede Islands was also significantly different from all other assemblages. The main distinction between these two assemblages (50 m and Lacepede Islands) and those further offshore was the higher abundance of neritic larvae, particularly Bregmacerotidae, Engraulidae, Gobiidae and Nemipteridae which were generally absent further offshore, as well as fewer Myctophidae over the inner shelf. The Lacepede Island assemblage was delineated from that occurring at the 50 m isobath by the complete absence of myctophid larvae. The larval fish assemblage which characterised King Sound was also significantly different (R >0.7, p = 0.001) from all other assemblages based on the low abundance of larvae of a few neritic families. Mid and outer shelf (100 m and 200 m) assemblages were significantly different from oceanic assemblages (R >0.2, p = 0.001) and were defined largely by differing concentrations of the ubiquitously distributed Myctophidae larvae and larvae of some neritic families. Two-way ANOVA revealed an overall significant difference in larval fish assemblages between spring and neap tides (R = 0.5, p = 0.001), however pair-wise comparisons using one-way ANOSIM could not be conducted due to insufficient replication.
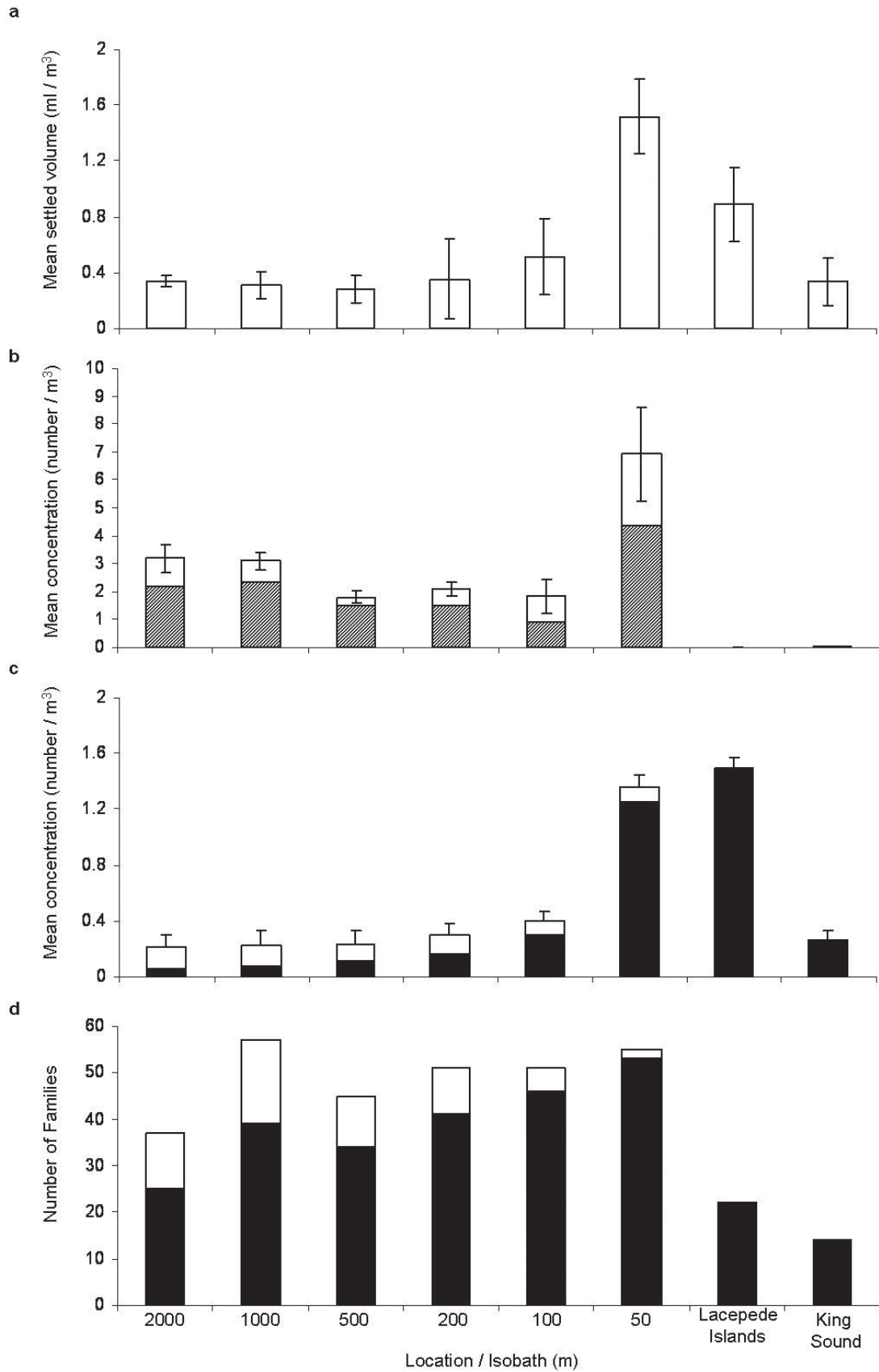
Figure 6. A) The mean bio-volume (ml / m^3 seawater) of macro-zooplankton, B) mean concentrations (number / m^3 seawater) of euphausiids, C) mean concentrations of larval fishes and D) total number of families of larval fishes from depth-integrated bongo samples for shelf and oceanic waters off the Kimberley, north-western Australia in April 2010. The standard errors are given for the total mean values of concentrations.
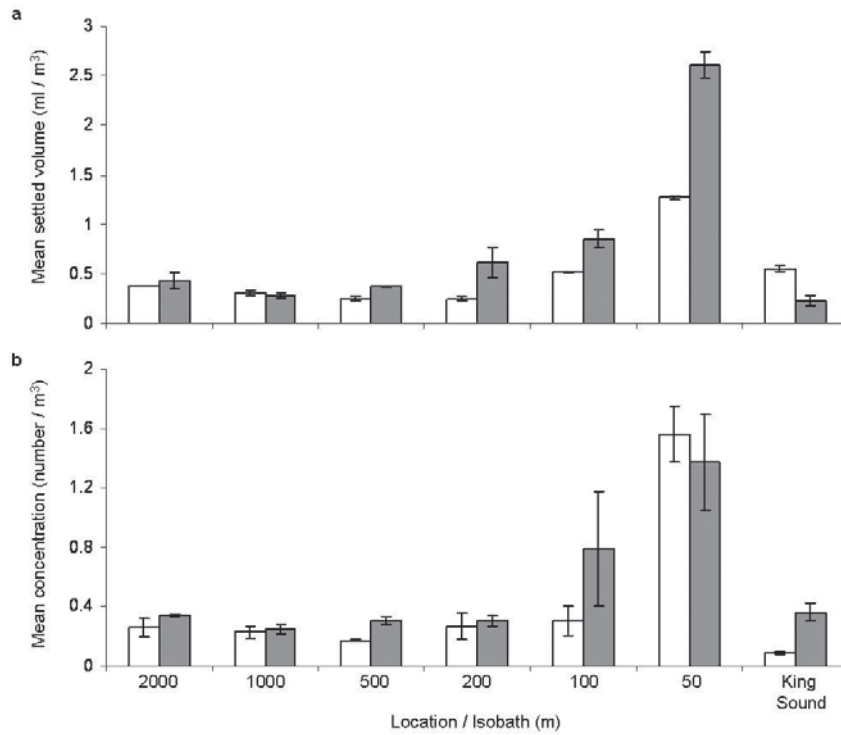
Figure 7. Comparison of A) the mean bio-volume (ml / m³ seawater) of macro-zooplankton and B) the mean concentration (number / m³ seawater) of larval fishes between spring (transect A) (white bars) and neap (transect C) (shaded bars) tides for depth-integrated bongo samples from shelf and oceanic waters off the Kimberley coast, north-western Australia in April 2010. The standard error is given for all mean values.
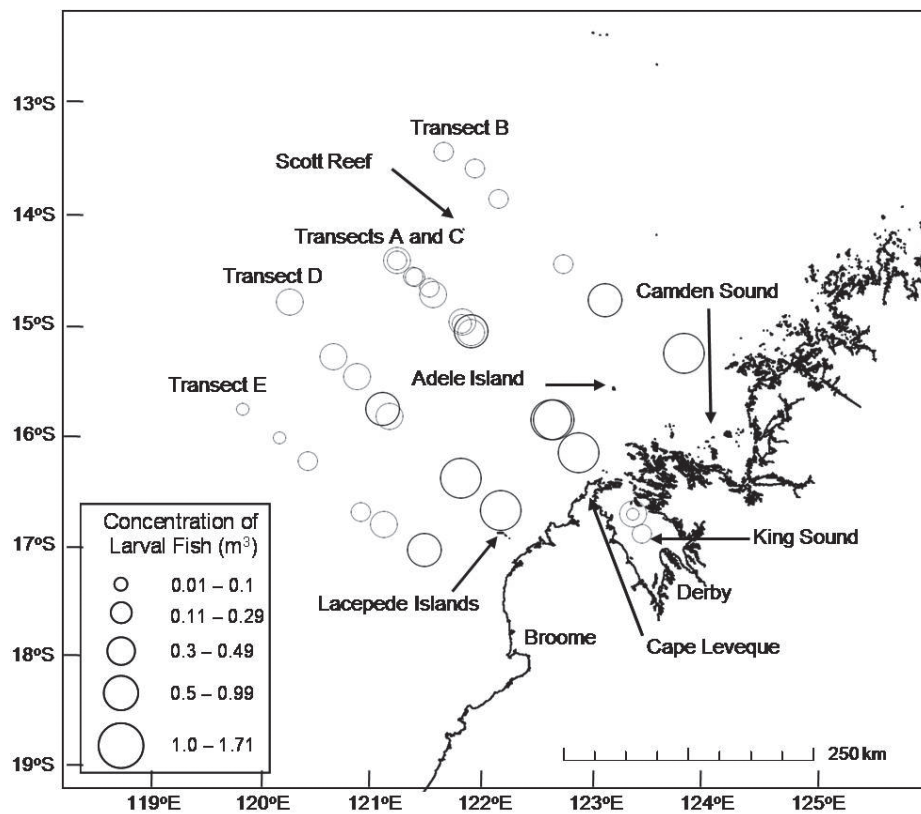

Figure 8. Mean concentration of larval fishes (number / m³) sampled using a 355 μm mesh bongo net in shelf and oceanic waters off the Kimberley coast, north-western Australia, April 2010.

Table 3

Mean percentage composition by family for larval fish assemblages across the respective isobaths off the Kimberley coast, north-western Australia. Note: only the ten most abundant families by mean concentration are shown for each isobath and spaces do not indicate absence. The superscript indicates the oceanic meso-pelagic families.

Family	Sampling Location (%)							
	2000m	1000m	500m	200m	100m	50m	Lacepede Islands	King Sound
Apogonidae					3.3	5.2	3.3	6.4
Bregmacerotidae		9.3	14.6	15.3	17.4	25.7		
Callionymidae						2.8	1.1	
Carangidae					3.6	1.9		1.5
Champsodontidae		2.4	3.1	5.3	7.9			
Congridae	2.8	2.8	6.8					
Engraulidae						15.9	49.3	
Gempylidae	2.6	2.5	2.0					
Gobiidae				2.9	6.6	15.2	32.8	27.3
Gonostomatidae°	8.4	8.7	4.6	2.2				
Labridae	6.1	1.9	3.1					1.1
Lutjanidae				3.9	3.2			
Microdesmidae				2.7				
Melanostomiidae°	1.8							
Monacanthidae						2.4	2.1	
Mugilidae								3.9
Mullidae					4.7	2.2		
Myctophidae°	42.0	40.4	38.5	35.9	20.1	8.1		
Nemipteridae						4.6	4.4	3.6
Paralepididae°				5.5	3.3			
Pempheridae								1.7
Phosychthyidae°	6.7	6.0	2.1					
Pinguipedidae							2.3	
Scaridae			1.5					
Sciaenidae								18.9
Scombridae	2.2	2.0		3.6				
Scopelarchidae°	4.7							
Scorpaenidae			2.3					
Sillaginidae								15.5
Sparidae								16.4
Sternoptychidae°	2.8	3.1						
Synodontidae					2.8	3.5		
Other neritic taxa	14.7	13.4	17.9	17.3	24.4	15.8	4.6	3.7
Other meso-pelagic taxa	5.2	7.6	3.4	2.4	1.8	0.1		

Discussion

The upper water column off the Kimberley coast in the austral autumn was strongly isothermal across the study area with warm, high salinity waters extending to ~60 m depth (SST >30°). A second, deeper water mass was cooler and less saline. Temperatures of the upper water column reported by Brink *et al.* (2007) for the region west of the Kimberley were several degrees cooler but they sampled in the austral winter. The TS signature of the deeper water mass was similar for the two studies. For coastal waters off the Dampier Archipelago to the south of the Kimberley, Pearce *et al.* (2003) reported similar high water temperatures in summer and autumn.

As in the current study, Brink *et al.* (2007) found no evidence of frontal features over the shelf or at the shelf break. However, Belkin *et al.* (2009) noted the seasonal evolution of regional frontal patterns over the NWS due to periodic upwelling (Holloway *et al.* 1981). In summer, numerous small-scale fronts develop which, as the season progresses, coalesce to form large-scale (hundreds of kilometres long) coherent filaments which are temporally persistent (weeks to months).

Table 4

Results of three-factor PERMANOVA which examined structuring of larval fish assemblages in relation to the factors isobath, transect and diel variation for samples collected in shelf and oceanic waters off the Kimberley coast, north-western Australia, April 2010.

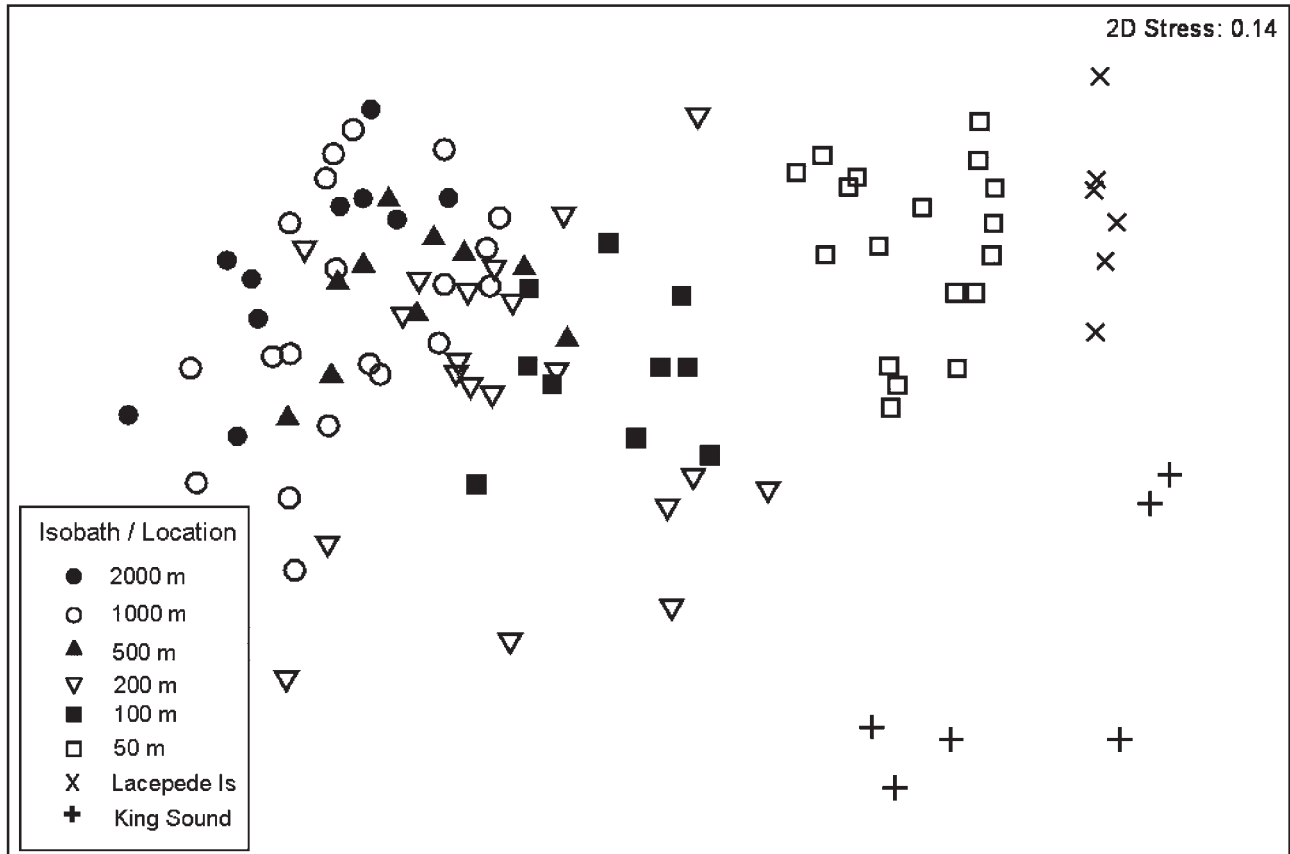| Factors	df	Mean Square	Components of Variation	Pseudo-F	p
Transect	4	3970	15.9	3.9	<0.001
Isobath	2	30322	39.1	30.1	<0.001
Diel	1	5720	12.8	5.7	<0.001
Transect x Isobath	8	3756	26.8	3.7	<0.001
Transect x Diel	4	2096	14	2.1	0.002
Isobath x Diel	2	2440	12.6	2.4	0.002
Transect x Isobath x Diel	7	1591	17.1	1.6	0.009
Residual	29	1007	31.7		
Total	57				

Figure 9. Multi-dimensional scaling (MDS) representation of the structuring of larval fish assemblages for all depth-integrated bongo samples in oceanic waters and over the shelf (including in proximity to the Lacepede Islands and in King Sound) off the Kimberley coast, north-western Australia, April 2010. Samples are coded by isobath.

Tropical continental shelves are characterised with turbid, low-density plumes associated with river discharge and these can form strong density fronts in coastal waters. These are known to influence the distribution and ecology of planktonic organisms (Grimes and Finucane 1991, Thorrold & McKinnon 1995, Grimes & Kingsford 1996). Although north-western Australia experiences significant rainfall (>1000 mm) during the summer monsoon, during 2010, there was atypical lower rainfall (BoM 2010) and, consequently, there was no evidence of turbidity fronts.

Continental shelf waters of the region are understood to experience a high degree of current variability in response to semi-diurnal tides and offshore forcing by regional currents at the shelf break (Holloway & Nye 1985, Holloway 1995). The horizontal velocity field indicated that alongshore advection, which attained velocities of up to 0.5 m s^{-1}, was generally greater than advection in the cross-shelf direction, particularly over the shelf. This is consistent with an earlier study of Holloway (1983) which showed that tidal velocities shift from cross-shelf at the shelf break and become predominantly along-shelf nearer the coast.

As illustrated by a station located in coastal waters, there was a breakdown of stratification corresponding with the high tide (vertical mixing) although the water column rapidly returned to stratified conditions on the

ebbing tide. Although strong temperature stratification of shelf waters persists over summer and autumn on the NWS (Van Gastel *et al.* 2009), vertical mixing is expected to periodically re-distribute planktonic biota and other properties of the water column.

Spatially, there was significant cross-shelf structuring of zooplankton bio-volume in relation to isobath. The biomass of zooplankton over tropical continental shelves is generally greatest in coastal waters (*e.g.* Nair *et al.* 1981, Wilson *et al.* 2003a, Munk *et al.* 2004) and associated with higher phytoplankton biomass (Wilson *et al.* 2003a, Lamb & Peterson 2005, Stenseth *et al.* 2006). The pattern of higher zooplankton bio-volume, including higher concentrations of larval euphausiids, in coastal waters off the Kimberley corresponded with the high chlorophyll *a* concentration (Thompson & Bonham this issue). Offshore, the correlation between phytoplankton and zooplankton biomass is known to be generally weaker due to the influence of physical processes which introduce strong variability to the distribution of planktonic biomass (Gibbons & Hutchings 1996).

Besides the common macro-zooplankton taxa such as copepods, euphausiids and chaetognaths, the diversity of zooplankton of the Kimberley during this study was enhanced by the occurrence of the pelagic larval stages of a number of benthic invertebrates. Off the southern NWS, Wilson *et al.* (2003a) described similar zooplankton

assemblages although the greater abundance of amphipods and cumaceans they reported may be related to their use of light traps for sampling. Although benthic marine invertebrates have widely contrasting reproductive strategies, the occurrence of their larvae indicates that spawning of some taxa occurs in the austral autumn. This is an important consideration when assessing the potential impacts of anthropogenic disturbance to the pelagic ocean in the Kimberley region.

The concentration of larval-stage euphausiids infers recent production and, as the larval duration is only a few days in warm water (Iguchi & Ikeda 1994), could support higher trophic levels, particularly plankton-feeding megafauna. In terms of species composition there was a clear cross-shelf pattern; coastal and inner shelf waters (50 m and 100 m isobaths, respectively) were dominated by *P. latifrons* and krill assemblages were much less speciose compared to those of outer shelf and oceanic waters that were dominated by larvae of the genus *Stylocheiron*. A similar study off the southern NWS also described the dominance of *P. latifrons* on the shelf (Wilson *et al.* 2003b). In general though, this study has only reported broad taxonomic groups for macro-zooplankton assemblages and it is possible that further spatial and temporal trends will be elucidated from a detailed analysis of their taxonomic composition and abundance.

Overall, the larval fish composition described for shelf and offshore waters off the Kimberley coast was consistent with that described by Young *et al.* (1996) for the southern NWS, and other tropical waters such as the Great Barrier Reef (Leis 1993) and the Andaman Sea (Munk *et al.* 2004). Depth-integrated larval fish assemblages displayed significant cross-shelf structuring in relation to isobath and, as with other studies (*e.g.* Harris *et al.* 2001, Gray & Miskiewicz 2000, Muhling *et al.* 2008), the coastal assemblage was the most distinct and had a higher diversity of neritic taxa. Notably, the occurrence of larvae of commercially valuable teleost fishes, such as the Lutjanidae, Serranidae and Scombridae, throughout the study region in autumn is an important consideration for environmental and fisheries management. Similarly, the prevalence of larvae of meso-pelagic oceanic Myctophidae warrants investigation of their biogeography and trophic significance in the eastern Indian Ocean (*e.g.* Kawamura 1994).

In general, the cross-shelf larval distributions of larvae of neritic and oceanic meso-pelagic fish taxa, is indicative of their dispersal by advective processes. However, we note that, in this study, the offshore occurrence of larvae of reef-dwelling fishes may have been sourced from the nearby Scott and Seringapatam Reefs which are located at the shelf break. Further, the less diverse larval fish assemblages of the Lacepede Islands and King Sound were distinct from the 50 m isobath assemblage suggesting less exchange between these unique locations and shelf waters. The restricted distribution of larval engraulids in coastal waters during this study is also suggestive of limited cross-shelf exchange as these larvae preferentially distribute themselves in near-surface waters making them susceptible to offshore wind-driven Ekman transport (Muhling & Beckley 2007). However, light winds prevailed for the duration of the Kimberley voyage which did not favour this type of advective transport.

In the absence of frontal structures the observed cross-shelf distributions of macro-zooplankton and larval fishes could be related to other physical and / or biological processes (*e.g.* spawning areas) operating at a range of spatial and temporal scales which were not resolved in this study. For instance, the depth-integrated bongo tows (to 150 m depth) sampled both the shallow and deeper water masses occurring in the study region. They are also insensitive to small-scale vertical patchiness such as the association of zooplankton with the deep chlorophyll maximum (Cullen 1982). Depth-stratified sampling will be required to resolve such effects and may also elucidate diel influences which accounted for a small amount of the variability in the data. It is also probable that differences exist over the tidal cycle (i.e. between high and low tides) which analysis of additional data from the 24 hour sampling station should resolve.

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Appendix 1

One-way ANOSIM and SIMPER analyses between larval fish assemblages classified according to the factor of isobath. The species listed are those which contributed highest and most consistently to the differences between assemblages. The letter given in superscript (x for columns, y for rows) refers to the assemblage in which the given family was more abundant. Avg. Dissim. = average dissimilarity between stations.

	King Sound	Lacepede Is.	50 m	100 m	200 m	500 m	1000 m	2000 m
King Sound	Avg. Dissim. 72% Gobiidae							
Lacepede Is.	R = 0.7, p = 0.002 Engraulidae^y Gobiidae^y	Avg. Dissim. 40% Gobiidae Engraulidae Apogonidae						
50 m	R = 0.9, p = 0.002 Bregmacerotidae^y Gobiidae^y Sparidae^y	R = 0.4, p = 0.002 Engraulidae^y Bregmacerotidae^y Gobiidae^x	Avg. Dissim. 54% Engraulidae Bregmacerotidae Gobiidae Nemipteridae Apogonidae					
100 m	R = 0.9, p = 0.001 Myctophidae^y Bregmacerotidae^y Gobiidae^x Sparidae^x	R = 1.0, p = 0.001 Engraulidae^y Gobiidae^x Myctophidae^y Bregmacerotidae^y	R = 0.8, p = 0.001 Bregmacerotidae^x Engraulidae^y Gobiidae^y	Avg. Dissim. 55% Bregmacerotidae Myctophidae				
200 m	R = 0.9, p = 0.001 Myctophidae^y Gobiidae^x Bregmacerotidae^y Sparidae^x	R = 1.0, p = 0.001 Engraulidae^x Gobiidae^x Myctophidae^y	R = 0.8, p = 0.001 Bregmacerotidae^x Engraulidae^y Gobiidae^x		Avg. Dissim. 64% Myctophidae Bregmacerotidae Champsodontidae Paralepididae			
500 m	R = 1.0, p = 0.001 Myctophidae^y Gobiidae^x Sillaginidae^x Sparidae^x	R = 1.0, p = 0.001 Engraulidae^x Gobiidae^x Myctophidae^y	R = 1.0, p = 0.001 Bregmacerotidae^x Engraulidae^x Gobiidae^x	R = 0.5, p = 0.001 Bregmacerotidae^x Myctophidae^y Champsodontidae^x Gobiidae^x		Avg. Dissim. 55% Myctophidae Bregmacerotidae		
1000 m	R = 1.0, p = 0.001 Myctophidae^y Gobiidae^x Sillaginidae^x Sparidae^x Apogonidae^x	R = 1.0, p = 0.001 Engraulidae^x Gobiidae^x Myctophidae^y	R = 0.1, p = 0.001 Bregmacerotidae^x Engraulidae^y Gobiidae^x Myctophidae^x Nemipteridae^x	R = 0.5, p = 0.001 Bregmacerotidae^x Myctophidae Champsodontidae^x Gobiidae^x	R = 0.2, p = 0.001 Myctophidae^x Bregmacerotidae^x Champsodontidae^x		Avg. Dissim. 60% Myctophidae Gonostomatidae	
2000 m	R = 0.1, p = 0.001 Myctophidae^y Gobiidae^x Sparidae^x	R = 1.0, p = 0.001 Engraulidae^x Gobiidae^x Myctophidae^y Nemipteridae^x	R = 1.0, p = 0.001 Bregmacerotidae^x Engraulidae^x Gobiidae^x Myctophidae^x Nemipteridae^x	R = 0.8, p = 0.001 Bregmacerotidae^x Myctophidae^x Champsodontidae^x Gobiidae^x	R = 0.3, p = 0.003 Myctophidae^x Bregmacerotidae^x	R = 0.2, p = 0.01 Myctophidae^x Gonostomatidae^y		Avg. Dissim. 57% Myctophidae Phosychthyidae Gonostomatidae