DRAFT MANUSCRIPT

Detecting trends in the tropical or temperate dominance of fish assemblages using multivariate models and indicator regions

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Abstract

1. Oceanic warming is projected to result in the 'tropicalization' of fish assemblages, as species shift towards the poles. Detecting when these assemblage shifts occur will provide important context for the management of fisheries and marine ecosystems.

2. Southwestern Australia has been shown to have a diverse and yet very stable marine ecosystem. The sea surface temperature gradient along the coast has a consistent influence on the turnover of the fish assemblage. This provides an ideal situation to test methods for detecting change in fish assemblages, due to changing temperature regimes.

3. We used spatial data, along a temperature gradient, to model the regional turnover in fish assemblage composition. For this regional model to be useful for longterm monitoring, within region temporal variation should be non-significant compared to any between region variations.

4. We compared monitoring data from three of the ten regions (up to 6 years) to the model of assemblage turnover, to test the within and between region variation.

5. Although different temporal trends were observed for each of the three regions the between location variation for each was found to be small.

6. ***Synthesis and applications*** This study demonstrates a cost-efficient method of detecting assemblage shifts across regions. The consistent trends between locations within regions suggest that the regional model of assemblage turnover will be sensitive to detecting overall regional trends. Temporal replication and correlations between changes observed in temperature and fish assemblages will provide further demonstrations of this method.

INTRODUCTION

- Patterns of temperature driven range shifts for demersal fish species have been observed across latitudinal (Perry et al. 2005) and depth gradients (Dulvy et al. 2008). Recent studies have projected that increasing ocean temperatures will result in an overall 'tropicalization' of demersal fish assemblages, as species shift their ranges towards the poles (W. W. L. Cheung unpublished data). In particular locations, this will result in change in the relative abundance of certain species and local extinction and invasion events.

- Long-term monitoring has been recognised to be useful for understanding ecological variation and processes (Bernstein and Zalinski 1983). However, monitoring studies vary between those that have spatially extensive sampling with the aim of providing information on average changes in populations or factors across areas (Tapp et al. 1993, Meire et al. 1994, Ysebaert and Herman 2002, Anderson 2008); and those that are restricted to few sentinel sites, often with a high degree of within-site and time replication (Greenstreet and Hall 1996, Hewitt and Thrush 2007). This study demonstrates how both these approaches can be combined in a cost-efficient approach to detecting changes in fish assemblage composition at particular locations relative to a regional model of assemblage turnover.

- At regional scales, effective marine management requires documentation of ecosystem status and changes to that status at a variety of scales. However, both modelling (Fulton et al. 2004) and empirical studies (Blanchard et al. 2008) of long term data have found that spatial heterogeneity of system dynamics can act to hide long term patterns (Hewitt and Thrush 2007). Therefore, for a monitoring approach (turnover of fish assemblage) to provide useful information the level of variation within regions would need to be significantly less than variation between regions.

- Southwestern Australia has been shown to have a diverse and yet very stable marine ecosystem. The sea surface temperature gradient along the coast has a consistent influence on the turnover of the fish assemblage. This provides an ideal situation to test methods for detecting change in fish assemblages, due to changing temperature regimes (Langlois submitted). It has been predicted that under a 'business-as-usual' climate change scenario (W. W. L. Cheung unpublished data) endemic species such as the Baldchin groper *Choerodon rubescens* and Breaksea cod *Epinephelides armatus* will shift their centre of distributions southward by 271-616 km by 2060. The rates of species range change, and local extinction and invasion events, have not been predicted to be uniform along the coast of southwestern Australia. In particular, the southwest Capes region has been predicted to experience a much faster rate of warming and change in the fish assemblage than central parts of the coast such as the Houtman-Abrolhos Islands.

- Constrained multivariate models have been shown to be useful for modelling turn over in assemblages and characterising multiple species response to environmental gradients (Anderson 2008). This study aims to construct a multivariate model of the turnover in the fish assemblage, attributed to temperature, along the coast of southwestern Australia. This model will then be used asses the between and within regional variation in the fish assemblage, attributed to the temperature model.

METHODS

Sampling locations

The 12 locations sampled in southwestern Australia extend from the Houtman Abrolhos Islands, off the central west coast, to Middle Island, in the Recherche Archipelago near the Great Southern Bight (Fig. 1). The Abrolhos Islands have an average winter sea surface temperature of 19.9 ^{o}C and are located in a biogeographical overlap zone between temperate and tropical fish. The hard reef assemblage of the area is dominated by corals, but often mixed with beds of the temperate kelp *Ecklonia radiata* (Watson et al. 2007). Conversely, average winter temperature at Middle Island is around 16.3 ^{o}C (see Table 1), and the region is characterised by extensive kelp beds and a much more temperate demersal fish assemblage (Hutchins and Swainston 2003).

From the 12 locations sampled, demersal fish data from a total of 252 sites were used in the analyses (Table 1). These sites only contained samples that were collected over, or adjacent to, hard reef habitats in water depths of 30-70 meters. To integrate fine-scale spatial variation within sites (100s meters), all analyses were based on the averages calculated for each site, from between three to six replicate samples.

In addition to this regional baseline, monitoring of the fish assemblages has been conducted at multiple locations within three regions. Three locations at the Houtman-Abrolhos Islands have been monitored annually (Wallabi, Pelsaert and Easter Island groups) from 2004 to 2010. Two locations have been monitored around Perth for three years (2007, 2008 and 2010) and two locations have been sampled around the Southwest Capes from 2006 to 2010 (Cape Naturaliste and Injidup).

To construct the regional baseline, monthly average winter sea surface temperatures were obtained from MODIS-AQUA at 4 km resolution for the period from 2004 until 2007. The closest pixel available was never further than 5 km from initial data point for longitude and 12 km for latitude. Studies of water temperature driven range extension events, have found that winter temperatures are a good descriptor of the recruitment and survival of marine assemblages (Ling and Johnson 2009, Portner et al. 2010). Vertical stratification on the southwestern Australian continental shelf is generally small (Pearce and Feng 2007), and empirical studies have found good concordance between the average near-bottom temperature gradient and satellite-derived surface measurements (Smale and Wernberg 2009).

Sampling methods

To obtain this large-scale data set, it was necessary to choose a standardised sampling method that would obtain a broad sample of the fish assemblage. Baited remote underwater stereo-video (stereo BRUV) was chosen as this method samples a representative suite of trophic groups (Watson et al. 2007). This method has been shown to be comparable to, and in some cases more efficient and cost effective than, diver-based census methods and is not limited by depth (Langlois et al. 2010). Stereo BRUV will however, only provides a relative estimate of the density of taxa as the distance of attraction will be different between species (Harvey et al. 2007). Stereo BRUV has also been shown to be less susceptible to inter observer variability than traditional diver-based visual census methods; it therefore provides useful method for estimating the relative abundance of species over large spatial gradients and multiple comparable studies.

Stereo BRUV systems were comprised of two SONY HC 15E video cameras mounted 0.7 m apart on a base bar inwardly converged at 8 degrees to gain an optimized field of view with visibility of 7 m distance. A synchronising diode and bait basket was positioned in front of the cameras. Each system was deployed by boat and left to film on the sea floor for a period of one hour. With multiple systems in use, a single stereo BRUV could be deployed at one position, followed by one at a second position and so on, maximising sampling efficiency. Previous research in temperate regions has found that >36 minutes is required to obtain measures of the majority of fish species, and that 60 minutes is advisable to include targeted fish species (Watson et al. 2007). Systems were baited with 800 grams of pilchards (*Sardinops sagax)* in a plastic-coated wire mesh basket, suspended 1.2 m in front of the two cameras. The pilchards were crushed to maximise dispersal of the fish oil. Adjacent replicate stereo BRUV deployments were separated by at least 250 m to avoid overlap of bait plumes and reduce the likelihood of fish moving between stereo BRUV stations within the comparable sites across the 12 locations sampled (see Table 2 for details).

Stereo BRUV samples were analysed through a custom database (BRUVS1.5.mdb©, Australian Institute of Marine Science 2006). This database enabled us to manage data collected from the field operations and tape readings, capture the timing of events and reference images of the seafloor and fish in the field of view. For stereo BRUV we recorded the maximum number of any one species seen at one time during the recording (MaxN; Priede et al. 1994). Estimates of MaxN are considered to be a conservative measure of abundance, particularly in areas where fish occur in high-densities (Harvey et al. 2007).

To ensure a standardized sampling unit, the program PhotoMeasure (www.seagis.com.au) was then used to estimate the range of all fish within the field of view from stereo-video images at the time of MaxN. All abundance estimates of each fish species were limited to within a maximum distance of six meters from the cameras resulting in a sample unit area of 37 m^2.

Data analysis

Multivariate analyses

Overall patterns of variation in the community sampled at all of the locations were visualised with metric multidimensional scaling (mMDS). To specifically model changes in the assemblage correlated with changes in winter temperature, canonical correlation of principal coordinates was used (CAP, Anderson and Willis 2003). This method searches the gradient of choice out, even in the presence of potentially high variation in other directions of the data cloud that might be due to other factors. CAP uses principal coordinates (PCO, Gower, 1966) from the resemblance matrix, and a check on over parameterisation is needed (i.e., to avoid including too many axes and finding spurious relationships). This was achieved by choosing the number of PCO axes (m) that minimised a leave-one-out residual sum of squares (Anderson and Robinson 2003). All multivariate analyses were based on modified Gower (log base 10) similarity measure and done using the PERMANOVA+ add-on package for PRIMER v6 (Anderson et al. 2008).

To investigate if the fish community was changing in a particular ‘direction’ relative to the regional model, centroids for each year of monitoring data from the two locations sampled in the Capes region (Westera et al. 2008) was calculated simultaneously with the baseline data before fitting the working regional model. Monitoring data from the Capes region was projected into the wSST gradient model using the “new sample” function in the CAP routine in PERMANOVA+. The trajectory of the monitoring data was projected onto the canonical axis of the wSST gradient model to see whether its temporal change coincided with predicted changes that would occur from increase wSST. This canonical axis for the site along the wSST gradient was plotted through time and examined for trends.

Analysis of covariance was used to examine the level of variation in the fish assemblage between and within regions through time, relative to the canonical model.

RESULTS

Regional turnover in the fish assemblage with temperature

Across the 12 location sampled for the regional baseline, 26 870 individual fish from 208 taxa were observed. The mMDS ordination (Fig 2a) indicates a consistent pattern of change in the assemblage from the cool temperate locations sampled to the warmer sub-tropical locations. Canonical analysis of the assemblage found a strong correlation with winter temperature (using m = 6 principal coordinate axes) of δ^2 = 0.982 (Fig. 2b), indicating that the fish assemblages changes in a predictable way along the temperature gradient.

Temporal turnover in the fish assemblage with temperature

Temporal change in the fish assemblage through time, relative to the canonical model for temeprature, showed regional trends but little within region variation (Fig. 3, Table 2). At the Houtman-Abrolhos Islands, the fish assemblage composition appeared to be relatively stable over the 6 years of monitoring. The northern and adjacent Wallabi and Easter Island groups appeared to be more similar that the southern Pelsaert group but were not significantly different. In contrast, the trajectory of the Perth region suggests that over the three sampling times over 4 years there has been a shift in the assemblage towards a more tropical assemblage composition. Again, there was very little variation amongst the two locations sampled in the Perth region. A stronger trend of increasingly more tropical assemblage composition is apparent at the two locations sampled around the southwestern Capes, except for the last sampling point, the only sampling time during winter, that suggested an opposite trend. Both the locations sampled at the Capes appeared to have very similar canonical trajectories.

DISCUSSION

- Based on a multivariate canonical model describing the turnover in the fish assemblage along a gradient in sea surface temperature, this study has found that within region temporal variation is less than between region variation.
- Although the monitoring data used in this study covers only a short period (maximum of six years) there a patterns on change in the assemblage consistent with predictions based on ocean warming projections (W. W. L. Cheung unpublished data). The seven years of monitoring data from the Houtman-Abrolhos Islands suggest no particular trend of the fish assemblage becoming either more temperate or tropical species dominated. Whilst the three and six year of monitoring data collected from the Perth and Capes regions suggest a gradual trend of increasingly dominance of tropical species. All except for the last time of sampling used from the Capes region, which was the only sample collected during winter. However, it must be noted that these trends have only been observed over a very short time-scale of at maximum 6 years, which is much less than the temporal scale of short term variation in regional ocean climate.
- However, the finding of very small levels of with region (between location) variation in any changes in the composition of the fish assemblage suggests that the method presented here will be very sensitive to detecting any long term changes in the fish assemblages within the monitored region relative to the regional model.
- The regional model used in this study is based on the turnover in the entire fish assemblage along the observed gradient in winter sea surface temperature along the southwestern Australian coast. Observation of seasonal variation in the temporal trend of change in the composition of the fish assemblages could be explained by tropical species being more active during summer and less active during winter (Portner et al. 2010). Which may be particularly evident when using the baited remote underwater stereo-video systems used in the current study, given the observed relationship between water temperature and response of various fish species to bait (Stoner et al. 2006).

- The old, climatically buffered, oligotrophic seascape of southwestern Australia has provided an ideal situation to test the models used in this study, due to the lack of confounding spatial and temporal variables and relatively homogenous environment (Langlois submitted). However, despite the relatively consistent temperature gradient along the coast it is interesting to note that different trends have been observed between the monitored regions. has a consistent influence on the turnover of the fish assemblage. This provides an ideal situation to test methods for detecting change in fish assemblages, due to changing temperature regimes. Further investigations on these pattern, once more monitoring data has been collected, should investigate patterns between actual trends in sea surface temperature and the trends detected in this study.

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Table 1. The number of samples and sites collected at each location along the coast of southwestern Australia. All samples were collected from, or adjacent to, hard reef habitats in water 30-70 meters deep. Average winter sea surface temperature (wSST) were obtained from MODIS-AQUA at a 4 km resolution.

Location	wSST(^{o}C)	# Sites	# Samples
Abrolhos	19.91	14	69
Jurien west	19.41	17	62
Jurien east	19.25	20	73
Two Rocks	18.93	18	151
Perth north	18.34	16	58
Perth south	18.44	16	57
Capes	17.63	39	105
Injidup	17.53	17	59
Broke	17.31	38	145
Albany	17.06	16	60
Point Anne	16.72	10	36
Middle Island	16.33	31	110
Total		252	98

Table 2. Results of three factor analysis of covariance examining the between region and between location variation with time. Significant effects are shown in bold.

Source	df	MS	F	*P*
Time	1	1.977	120.8	**0.001**
Region	1	0.161	433.56	**0.001**
Location (Region)	3	3.872	3.911	0.161
Res	48	4.752	9.901	
Total	53	0.187		

Figure 1. Map of southwestern Australia showing the position of the 12 sampling locations: Ab, Abrolhos Islands; JW, Jurien West; JE, Jurien East; TR, Two Rocks; PN, Perth North; PS, Perth South; CN, Cape Naturaliste; In, Injidup; Br, Broke; Al, Albany; PA, Point Anne; MI, Middle Island. Average isotherms (˚C) from 2005-2007 are shown, indicating the influence of the Leeuwin current.

Figure 2. (a) Unconstrained metric MDS ordination and (b) constrained canonical correlation (CAP) of the fish assemblage (208 taxa) with average winter sea surface temperature (wSST) (with n = 3-6 replicates pooled). The CAP also reports the squared canonical correlation coefficient (δ^2). All analyses were based on modifed Gower log 10 dissimilarities, and the CAP used m = 6 principal coordinates. Error bars are $\pm$ 1 SE on the canonical axis.

Figure 3. Temporal fish assemblage data from the three indicator regions projected through the canonical model of turnover in the fish assemblage with existing temperature gradient along the coast of southwestern Australia. Error bars are $\pm$ 1 SE.

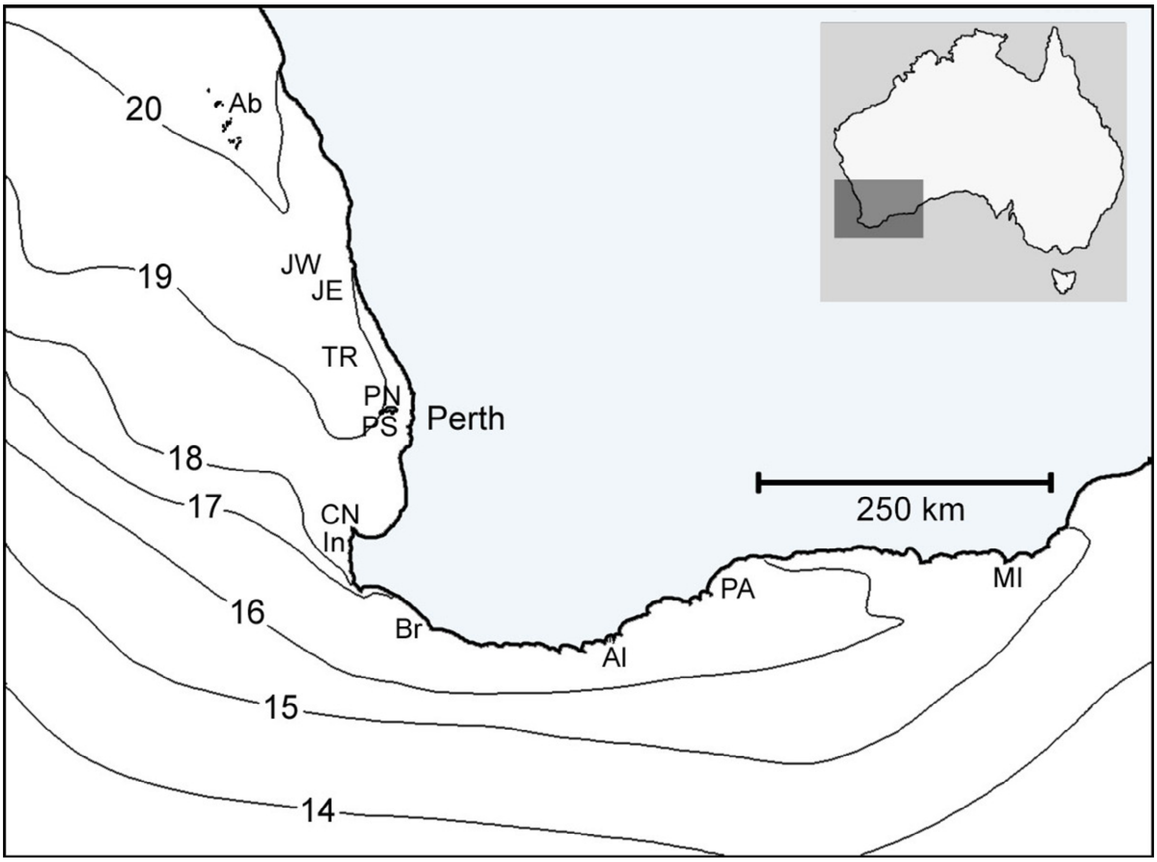


Figure 1

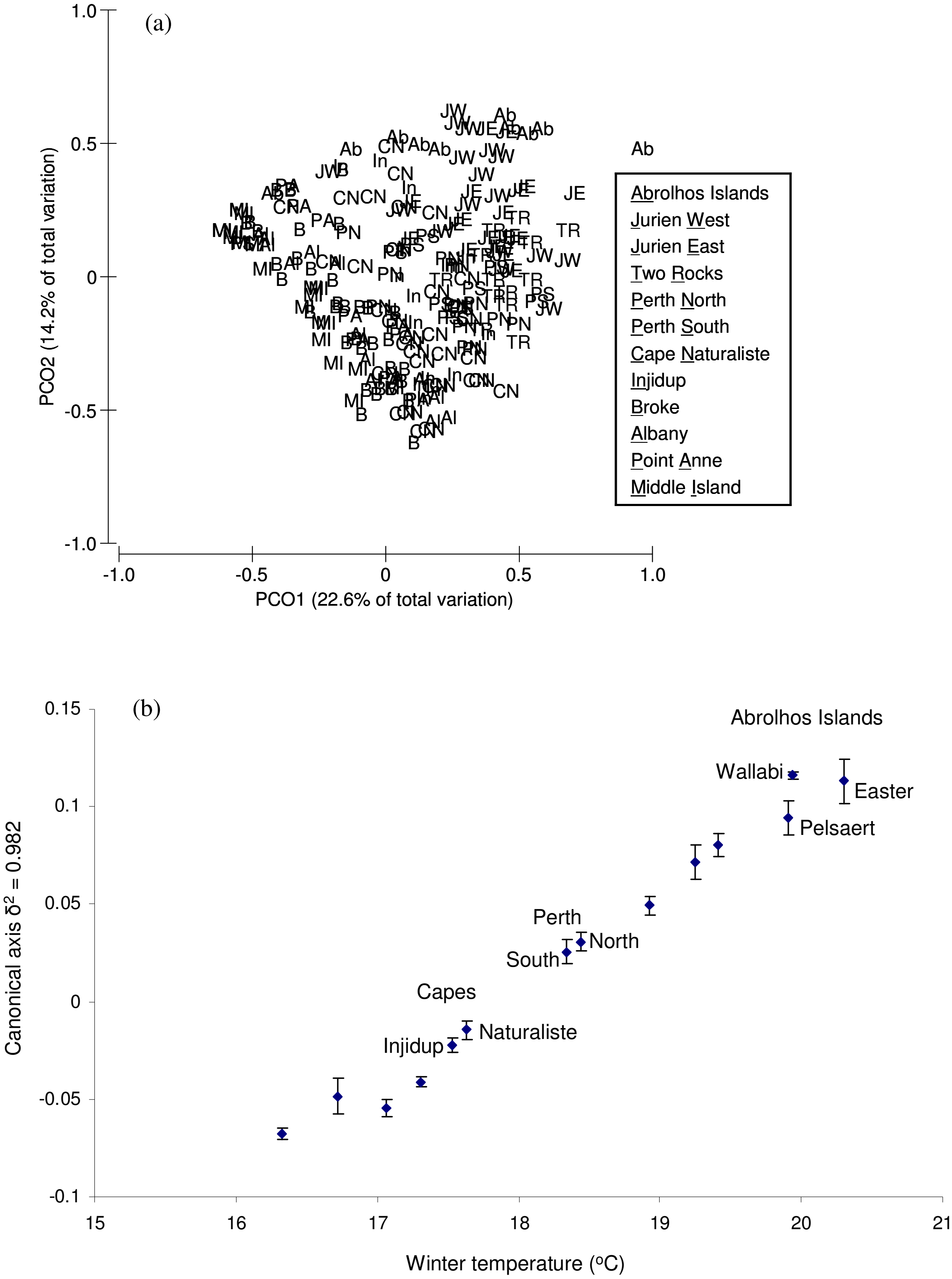
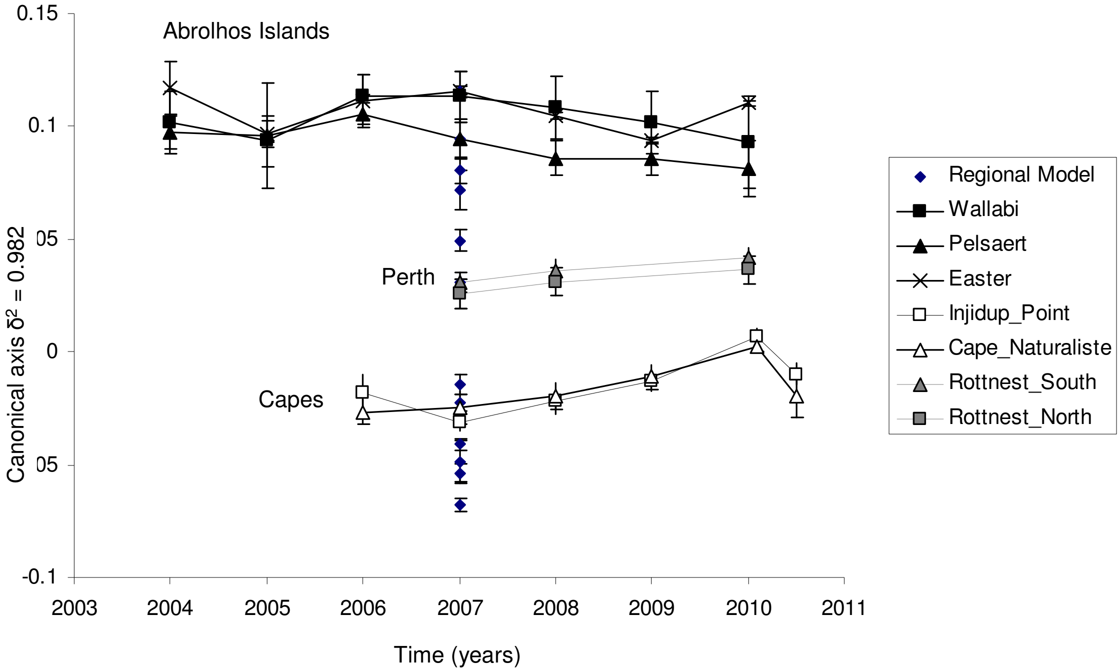

(a)
PCO2 (14.2% of total variation)
PCO1 (22.6% of total variation)
1.0
0.5
0
-0.5
-1.0
Abrolhos Islands
Jurien West
Jurien East
Two Rocks
Perth North
Perth South
Cape Naturaliste
Injidup
Broke
Albany
Point Anne
Middle Island
(b)
Canonical axis δ^2 = 0.982
Winter temperature (°C)
0.15
0.1
0.05
0
-0.05
-0.1
15
16
17
18
19
20
21
Abrolhos Islands
Wallabi
Easter
Pelsaert
Perth
North
South
Capes
Naturaliste
Injidup

Figure 2



Abrolhos Islands
Perth
Capes
Canonical axis δ² = 0.982
0.15
0.1
05
0
05
-0.1
2003
2004
2005
2006
2007
2008
2009
2010
2011
Time (years)
Regional Model
Wallabi
Pelsaert
Easter
Injidup_Point
Cape_Naturaliste
Rottnest_South
Rottnest_North

Figure 3