

A conceptual surrogacy framework to evaluate the habitat potential of submarine canyons

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Abstract

The seascape of the vast Australian continental margin is characterised by numerous submarine canyons that represent an equally broad range of geomorphic and oceanographic heterogeneity. Theoretically, this heterogeneity translates into habitats that may vary widely in their ecological characteristics. Here we describe the methodology to develop a framework to broadly derive estimates of habitat potential for pelagic and epibenthic species (including demersal fishes), and benthic infauna in all of Australia's known submarine canyons. Our analysis shows that the high geomorphic and oceanographic diversity of Australian submarine canyons creates a multitude of potential habitat types. In general, it appears that canyons may be particularly important habitats for benthic species. Canyons that incise the shelf tend to score higher in habitat potential than those confined to the slope. Canyons with particularly high habitat potential are located mainly offshore of the Great Barrier Reef and the NSW coast, on the eastern margin of Tasmania and Bass Strait, and on the southern Australian margin. Many of these canyons have complex bottom topography, are likely to have high primary and secondary production, and have less intense disturbance to sediment. The framework presented here can be applied – once refined and comprehensively validated with ecological data - to help managers make informed conservation decisions, especially for high value canyons.

Key-words: habitat diversity, fauna environmental association, niches, continental margin, predictions; spatial planning

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1 Introduction

Although submarine canyons occupy only ~2.5% of the global seafloor area (Harris et al. 2014), they are important geomorphic features, mainly because they are conventionally regarded as hotspots of marine biodiversity (De Leo et al. 2010; Vetter et al. 2010). Many canyons have complex topography and heterogeneous substrate types, including exposed rocks and various sediment types (De Leo et al. 2012; Hargrave et al. 2004; Kenchington et al. 2014; Schlacher et al. 2007). The complex topography of canyons can result in equally complex hydrodynamics (Allen et al. 2001; Carter and Gregg 2002; Kampf 2007; Klinck 1996), leading to multifaceted transport processes of sediment, nutrients, and biological particles (Canals et al. 2006; de Stigter et al. 2007; Jordi et al. 2005; Martin et al. 2011; Puig et al. 2013; Zuniga et al. 2009). For example, elevated nutrient levels in the water column and sediment have been reported from several canyons (Garcia et al. 2008; Kiriakoulakis et al. 2011; Palanques et al. 2005; Tesi et al. 2010; van Oevelen et al. 2011). This increased level of nutrients, often in the vicinity of canyon heads and the upper reaches, can lead to strong primary and secondary production associated with canyons (Cartes et al. 2010; Skliris and Djenidi 2006; Vetter 1994; Vetter et al. 2010).

This study proposes a conceptual surrogacy framework to evaluate the habitat potential of submarine canyons, using Australia as an example. Submarine canyons are distributed along all margins of Australia, with over 700 mapped to date (Heap and Harris 2008; Huang et al. 2014). A proportion of Australian submarine canyons that incise into the continental shelf and are located in relatively shallow waters are under increasing anthropogenic stress such as bottom trawling and activities associated with oil and gas resources (Harris and Whiteway 2011). Australian submarine canyons are regarded as a special class of seabed geomorphic feature with relatively high surrogacy potential for predicting marine biodiversity (Harris 2007; Harris et al. 2008). Many individual canyons and canyon clusters have subsequently been recognised as *Key Ecological Features* (KEFs) (Commonwealth of Australia 2013a) and/or have been included in the national network of Marine Protected Areas (Commonwealth of Australia 2013b). In many instances, this protection status is based on expert opinions or surrogacy inferences for biological and ecological properties that are not yet validated and do not distinguish between individual canyons on the basis of their habitat potential to support enhanced biodiversity (Williams et al. 2009) – the lack of robust surrogacy models makes them potentially unsuitable and stresses the need to develop ecologically more meaningful models to better inform both conservation and fisheries management across the Australian marine estate (see also Althaus et al. 2017; Schlacher et al. 2014).

To better chart Australia's submarine canyons, Huang et al. (2014) have updated the maps of Heap and Harris (2008), and used a broader range of metrics to describe the geophysical characteristics of these submarine canyons and derive a classification of canyons based on those characteristics. A

conclusion from both Williams et al. (2009) and Huang et al. (2014) is that Australian submarine canyons are quite variable in their physical characteristics. What has not been previously assessed is how variability in physical characteristics translates into habitat potential with distinct attributes relevant to marine fauna - this forms the chief question tested in this paper.

This study evaluates the natural habitat potential of Australia's submarine canyons from the aspect of their broad physical and biochemical environments; thus, aspects of anthropogenic pressure such as fishing activities and offshore oil and gas developments on canyon habitats are not considered, here. Habitat potential, in this study, is defined as the likelihood of appropriate habitat for selected marine species or communities. We use a surrogacy approach for the assessment of habitat potential, largely for the reason that there are few biological datasets that provide the necessary detail and spatial coverage. Abiotic surrogates can be used to score potential ecological habitat conditions or biodiversity values when direct measurements of these are not available (Huang et al. 2011; Zacharias and Roff 2000). For the Australian continental margin, there are a substantial number of marine environmental datasets available (e.g., Huang et al. 2010, 2013), making a surrogacy-based approach to score submarine canyon habitat potential a feasible option.

Kostylev (2012) proposed using a "habitat template" based on the axes of "disturbance" and "scope for growth" (or productivity) for habitat mapping. It is well recognised that productivity and disturbance are two determinants of species diversity (Kadmon and Benjamini 2006; Kondoh 2001; Paterson et al. 2011; Worm et al. 2002). In addition, habitat heterogeneity has also been considered as an important environmental driver of species diversity (Levin et al. 2001; McClain and Barry 2010). It has been shown that habitat heterogeneity usually has a positive relationship with species diversity; while, for productivity and disturbance, the relationships may often be unimodal (Kadmon and Benjamini 2006; Kondoh 2001; Levin et al. 2001; Worm et al. 2002). Fundamentally, surrogacy makes critical assumptions about the relationship between measured abiotic environmental variables and the predicted biological features of interest (McArthur et al., 2010). Hence, it must be recognised that there can be appreciable uncertainty about predictions, because ecological relationships may be untested, key abiotic variables may be missing, spatial and temporal scales between biotic and abiotic variables may be incomparable or inappropriate, and/or interactions between predictor and response variables may be unknown. Accordingly, the starting point for our study was to review environmental variables that are likely to influence the habitat potential for fauna in submarine canyons and explicitly describe the mechanisms and assumptions underlying our surrogacy models.

2 Review of Canyon Habitat Variables

We identify three classes of habitat variables: habitat heterogeneity; productivity, and disturbance to form the principal axes in a conceptual framework for an assessment of the habitat potential of Australian submarine canyons. Individual environmental variables that structure canyon habitats are grouped under one of these three classes.

2.1 Habitat Heterogeneity

Variability in the physical attributes of submarine canyons can be described in terms of canyon shape and size, topography, and substrate type (Table 1). Previous canyon studies have indicated positive relationships between the diversity and abundance of canyon fauna and metrics of topographic complexity such as slope, vertical relief, canyon incision depth and canyon transverse profile (Brodeur 2001; De Leo et al. 2014; Gili et al. 2000; Schlacher et al. 2007; Yoklavich et al. 2000).

Modelling studies also suggest that longer, narrower, and deeper canyons tend to generate stronger upwelling fluxes and downward transport capacity (Allen and Hickey 2010; Klinck 1996; Wahlin 2002). In one study, canyon length has been found to have a positive relationship with species richness of benthic macrofauna (De Leo et al. 2014). Limited evidence also suggests cetaceans may be more likely to be associated with larger canyons (Moors-Murphy 2014). In addition, substrate heterogeneity and topographic complexity are believed to create concentrating and aggregating processes that can result in increased prey abundance and foraging efficiency for cetaceans (Greene et al. 1988; Moors-Murphy 2014).

The number of different substrate types has been shown to be positively related to the abundance and diversity of epibenthic species and demersal fish communities in canyons (e.g., De Leo et al. 2012; Kenchington et al. 2004). Hard substrates (e.g. exposed rocks, boulders) provide attachment sites for corals and other megabenthos, with some fish species showing positive associations with these features (De Leo et al. 2012; De Mol et al. 2011; Hargrave et al. 2004; Yoklavich et al. 2000). Acoustic backscatter data, as a proxy of substrate types, have been shown to be correlated with the diversity of macrofauna and megafauna on the seafloor of canyons (De Leo et al. 2014; Schlacher et al. 2007). With regard to meiofauna and macrofauna, diversity can be higher in areas of more mixed sediment grain size (Leduc et al. 2014; Levin et al. 2001). In some instances, other sediment properties (e.g. proportion of sand or mud) can be useful as a surrogate for benthic fauna distribution (Bianchelli et al. 2010; Currie and Sorokin 2014; De Leo et al. 2012; Louzao et al. 2010; Paterson et al. 2011).

2.2 Productivity

The productivity status of a submarine canyon can be assessed through direct measurement of variables including particulate organic matter, chlorophyll-*a*, and inorganic nutrients. The flux of organic matter in particular can be positively correlated with a range of benthic and pelagic species in canyons (Bosley et al. 2004; De Leo et al. 2012; De Leo et al. 2014; Gili et al. 2000; Kiriakoulakis et al. 2011; Levin et al. 2001; Tesi et al. 2010; Vetter and Dayton 1998; Vetter and Dayton 1999). Chlorophyll-*a* concentrations, as an index of the standing stock of phytoplankton, can also have a positive or unimodal relationship with the abundance and diversity of canyon fauna (Currie et al. 2012; Leduc et al. 2014; Palanques et al. 2005). In addition, concentrations of inorganic nutrients (e.g. nitrate, phosphate) have been shown to have a positive relationship with the productivity of phytoplankton in canyons (Guerreiro et al. 2014; Mendes et al. 2011). Moreover, although the relationship between productivity and oxygen is complex, De Leo et al. (2012) and Levin et al. (2001) suggest a generally positive relationship between benthic diversity and oxygen levels of the bottom water.

Sediments in a few canyons have been found to be enriched in organic matter and chlorophyll-*a* compared with adjacent slope sediments (Garcia et al. 2008; Kiriakoulakis et al. 2011; Leduc et al. 2014), suggesting that benthic meiofauna and macrofauna may benefit from enhanced food resources inside canyons (Bianchelli et al. 2010; Paterson et al. 2011; van Oevelen et al. 2011; but see Cunha et al. 2011). For example, Leduc et al. (2004) and Patterson et al. (2011) both found that higher chlorophyll-*a* concentrations in canyon sediments led to higher abundance and biomass of benthic meiofauna and macrofauna species. In addition, other sediment nutrient indicators such as nitrogen can also be positively related to higher abundance and biomass of benthic macrofauna species (Cunha et al. 2011; Paterson et al. 2011). The concentration of sediment organic matter has also been shown to influence the community structure and biomass of epibenthic species in canyons (Currie and Sorokin 2014; Kenchington et al. 2014).

Canyons can influence water movement for example by funnelling offshore deep water up onto the slope. Upwelling, which often occurs in canyons (Allen and Hickey 2010; Currie et al. 2012; Jordi et al. 2005; Klinck 1996), is an important mechanism for bringing bottom nutrients to near the surface (Bosley et al. 2004). It has been shown that canyon upwelling enhances the abundance of phytoplankton, zooplankton and fish (Genin 2004; Skliris and Djenidi 2006), and possibly also the local abundance of cetaceans as a result (Moors-Murphy 2014). Topographically complex canyons can induce greater vertical mixing that can both advect deeper nutrient-rich waters into the euphotic zone and enhance the down-canyon transport of organic matter (Tesi et al. 2010). In addition, strong bottom currents near the canyon floor are likely to resuspend sediments and transport suspended particles laterally, resulting in increased organic matter levels in the water column (Garcia et al. 2008), a process that could benefit suspension feeders (De Mol et al. 2011; Hargrave et al. 2004; Rowe 1971).

Distance from canyon to the source of material flux could index the amount of nutrients and organic matter reaching a canyon (Vetter and Dayton 1998; Vetter and Dayton 1999). Indeed, such measures (e.g., distance to shore) have been shown to have a negative relationship with benthic macrofauna and megafauna abundance and diversity (De Leo et al. 2014; Hargrave et al. 2004; McClain and Barry 2010). Finer sediments (e.g., mud) often have higher organic matter content than coarser sediments (Currie and Sorokin 2014; Currie et al. 2012; Rowe et al. 1982); as a result, finer sediment may support higher benthic macrofauna biomass (Rowe et al. 1982).

2.3 Disturbance

Natural disturbance in canyon systems can occur from several processes. Near-bottom currents can move and resuspend sediments, and sediment mass movement and deposition can strongly influence habitat stability and species populations (McClain and Schlacher 2015). In the Nazaré, Setúbal and Cascais canyons along the Iberian Margin, Paterson et al. (2011) used several complementary statistics of current speed and sediment deposition (e.g. maximum, range) to estimate physical disturbance, finding that, in combination with productivity, they were significant drivers of polychaete assemblages. The relationships between these disturbance variables and polychaete abundance and diversity are, however, not well understood, likely due to the complex interactions between the disturbance and productivity variables (Kadmon and Benjamini 2006; Kondoh 2001). Levin et al. (2001), however proposed a unimodal diversity pattern for current flow and biotic disturbance, regarding deep-sea macrofauna. They also suggest that the relationship between catastrophic disturbance such as sediment mass movement and deep-sea macrofauna diversity is negative (Levin et al. 2001).

3 Materials and Methods

3.1 Environmental Variables

Based on our synthesis of published relationships between environmental variables and canyon biodiversity, and on data availability for the Australian margin, we chose 22 environmental variables (Table 1) as surrogates to very broadly derive estimates of possible habitat potential for 753 Australian submarine canyons; of these, 713 are situated on the main continental margin (Huang et al. 2014) and 40 in Australian external territories (Norfolk Island and Cocos Islands) (Figure 1). The details for the generation of these 22 environmental variables are provided in the supplementary section of the paper.

Briefly, ten variables were used to score spatial heterogeneity, ten to score productivity, and two to score disturbance. The analysis is restricted to the upper reaches of canyons because it is along this

part of a canyon where environmental gradients are likely to change most rapidly and where the potential for habitat heterogeneity is greatest (de Stigter et al. 2007; Gardner 1989; Koho et al. 2007; Schlacher et al. 2007; Tesi et al. 2010; Trincardi et al. 2007; van Oevelen et al. 2011; Zuniga et al. 2009). It is also the area where anthropogenic pressure is likely to be concentrated. We define the upper reach as the canyon section where water depth is shallower than the canyon mid-point, in turn defined as the depth at the canyon head plus half of the total depth range of the canyon.

3.2 Habitat Potential Assessment Methods

The canyon habitat potential was assessed for three faunal groups: a) pelagic species (e.g. fishes, marine mammals, cephalopods); b) epibenthic species (including suspension feeders such as larger corals, sponges, crinoids, and associated demersal fishes), and; c) infauna (including meiofauna and smaller macrofauna; e.g. worms, smaller crustaceans). For each canyon, the assessment comprised three sequential steps:

- 1.) calculating the '*habitat potential score*' for each environmental variable based on the most plausible relationship between the environmental predictor and a biological / ecological response;
- 2.) averaging across variable scores (equally weighted) within each class of attributes or habitat variables (e.g. habitat heterogeneity, productivity and disturbance) to derive '*attribute scores*'; and
- 3.) averaging these attribute scores (equally weighted) to derive an overall '*index of habitat potential*' for the canyon.

3.2.1 Calculating canyon habitat potential scores for individual environmental variables

Two aspects were determined in the first step: i) the environment-biology relationship, either positive, negative, or unimodal (only applied to some sub-variables), and ii) the thresholds that define the mathematical scoring functions. The relationships were determined based on the ecological knowledge obtained from our review of canyon habitat variables (described below; also see section 2). For a positive relationship, the scoring function (S) was defined as:

$$S = \begin{cases} 1, V > T1 \\ \frac{V-T2}{T1-T2}, T2 < V < T1 \\ 0, V < T2 \end{cases} \quad (1)$$

Where V is the variable value from a canyon, T1 and T2 are the upper and lower thresholds for the habitat variable, respectively. Similarly, for a negative relationship, the scoring function (S) was defined as:

$$S = \begin{cases} 1, V < T2 \\ \frac{V-T1}{T2-T1}, T2 < V < T1 \\ 0, V > T1 \end{cases} \quad (2)$$

For some habitat variables, suitable thresholds values were determined based on the reasons explicitly stated below. For the remaining habitat variables, we used the variable statistics of mean and standard deviation (s.d.) to determine the appropriate thresholds. In these cases, $T1 \approx \text{mean} + 2 \text{ s.d.}$; and $T2$ was determined as $T2 \approx \text{min}$. The statistics of min, mean and s.d. were obtained from the variable values of all 753 canyons (Table S1). Instead of using maximum as the upper threshold, we assume that when the variable value reaches its mean plus two standard deviations we are likely to see either the plateauing or equilibrium state in terms of the environment-biology relationship.

The canyon habitat variables considered here were scored using the threshold functions listed in Table S1, based on their hypothesized relationships to habitat potential described below.

Volume (*V_m*) - Volume is a function of canyon width and depth along the upper reach. Because larger volumes have a higher probability to contain more habitat types (e.g. where a canyon incises into varied geological substrata), we hypothesize a positive relationship between *V_m* and habitat heterogeneity and, therefore, habitat potential (e.g., De Leo et al. 2012; Kenchington et al. 2014).

Number of branches (*NoB*) - A larger number of branches are likely to contain more habitat types, for the same reasons as above. Thus, the relationship between *NoB* and habitat potential is hypothesized to be positive (e.g., De Leo et al. 2012; Kenchington et al. 2014).

Head incision (*HI*) – The depth range of a canyon head incision is positively related to a canyon's topographic complexity and volume. Thus, the relationship between *HI* and habitat potential is also hypothesized to be positive (e.g., Gili et al. 2000).

Standard deviation of depth (*StdD*) - The standard deviation of the water depths at all locations within a canyon upper reach indicates the size and topographic complexity of the canyon upper reach. Thus, the relationship between *StdD* and habitat potential is hypothesized to be positive (e.g., Moors-Murphy 2014).

Rugosity (*Rg*) - Bottom rugosity also indicates topographic complexity. Thus, the relationship between *Rg* and habitat potential is hypothesized to be positive (e.g., Moors-Murphy 2014)

Average gradient (*AG*) - Gradient of the canyon floor/walls potentially indicates topographic complexity. Thus, the relationship between *AG* and habitat potential is postulated to be weakly positive (e.g., De Leo et al. 2014; Gili et al. 2000; Schlacher et al. 2007).

Standard deviation of gradient (*StdG*) - The standard deviation of the slope gradient at all locations within a canyon upper reach also indicates topographic complexity. Thus, the relationship between *StdG* and habitat potential is hypothesized to be positive (e.g., De Leo et al. 2014).

Percentage of gradient > 15° (*pG15*) – Percentage of canyon floor/walls greater than 15° can be used to indicate topographic complexity. The variable may also be a proxy of proportion of hard substrates because hard substrates are often associated with steeper slope. Thus, the relationship between *pG15* and habitat potential is hypothesized to be positive (De Leo et al. 2012; De Mol et al. 2011; Hargrave et al. 2004; Yoklavich et al. 2000).

Percentage of hard substrates (*pHard*) - Hard substrates can provide preferred attachment sites for epibenthic macrofauna. Thus, the relationship between *pHard* and habitat potential is hypothesized to be positive (De Leo et al. 2012; De Mol et al. 2011; Hargrave et al. 2004; Yoklavich et al. 2000).

Average sediment particle diversity (*ASPD*) - Sediment particle diversity indicates heterogeneity of sediment types on the seafloor. A smaller *ASPD* value corresponds to a more diverse sediment particle composition (Supplementary Materials). Therefore we hypothesized a negative relationship between *ASPD* and habitat potential (Leduc et al. 2014; Levin et al. 2001). In addition, T1 and T2 were calculated as the theoretical maximum ($\text{std}(100,0,0)=47$) and minimum ($\text{std}(33.3,33.3,33.3)=0$), respectively.

Distance to shelf break (*DtSB*) - Distance of the canyon head to the shelf break is used as a proxy for the potential input of detritus and other organic materials from terrestrial sources (rivers) and continental shelf waters. Thus, the variable *DtSB* was hypothesized to have a negative relationship with habitat potential based on the assumption that the greater the distance from the shelf break the lower the potential for nutrients to be supplied to the canyon head (e.g., De Leo et al. 2014; Hargrave et al. 2004).

Surface upwelling (*surUp*) - In the southern hemisphere, surface upwelling is more likely to occur when the coast is to the right of the surface current, while down-welling occurs when the coast is to the left of the surface current (Klinck 1996). Thus in the Australian context, the East Australian Current favours upwelling, while the Leeuwin Current favours down-welling. Comparing a canyon's foot to head direction with the most frequent surface current directions, we were able to evaluate whether a canyon is favourable to upwelling or down-welling and thus infer the likelihood of surface upwelling. Table S2 lists the rules that assign habitat potential scores according to the canyon's foot to head directions, the most frequent surface current directions and the 2nd most frequent surface current directions. For all other situations, the canyons were assigned a score of 0, indicating down-welling. This process was applied to all four seasons (sub-variables, Supplementary Materials) to obtain *surUp_{au-S}*, *surUp_{wi-S}*, *surUp_{sp-S}* and *surUp_{su-S}*. Variable *surUp* was then calculated as:

$$\text{surUp} = \text{surUp}_{\text{au-S}} + \text{surUp}_{\text{wi-S}} + \text{surUp}_{\text{sp-S}} + \text{surUp}_{\text{su-S}} \quad (3)$$

It was hypothesized that *surUp* has a positive relationship with habitat potential on the basis that upwelling promotes nutrient flux to a canyon (e.g., Genin 2004; Moors-Murphy 2014; Skliris and Djenidi 2006).

Euphotic depth upwelling (*eupUp*) – The euphotic zone not only receives enough light for photosynthesis to occur, but also has strong vertical mixing that promotes nutrient exchange in the water column. Upwelling to the euphotic zone is thus hypothesized to be positively related to habitat potential (e.g., Genin 2004; Moors-Murphy 2014; Skliris and Djenidi 2006). Two aspects determine the influence of variable *eupUp*: upwelling intensity and upwelling frequency. Based on Kunze et al. (2002) we considered an upward water motion an upwelling event if its vertical velocity reached at least 10m/day which translates into *w* (vertical velocity) of 0.000116 m/s. We used the following function to calculate an upwelling intensity score:

$$Up_{I_S} = \begin{cases} 0, & I < 0.000116 \\ \frac{0.5 \times (I + 0.000057)}{0.000173}, & 0.000289 < I \leq 0.000116 \\ 1, & I \geq 0.000289 \end{cases} \quad (4)$$

Where *I* is the intensity; and a velocity of 0.000289m/s equals 25m/day.

The upwelling score was then calculated as:

$$Up_S = \min(Up_{I_S}, F) \quad (5)$$

Where *F* is the upwelling frequency and $\min()$ is the minimum function.

The above equations were applied to all four seasons (sub-variables, Supplementary Materials) to obtain *eupUp_{au-S}*, *eupUp_{wi-S}*, *eupUp_{sp-S}* and *eupUp_{su-S}*. Variable *eupUp* was then calculated as:

$$eupUp = eupUp_{au-S} + eupUp_{wi-S} + eupUp_{sp-S} + eupUp_{su-S} \quad (6)$$

It was hypothesized that *eupUp* has a positive relationship with habitat potential following the same logic as used for surface upwelling (e.g., Genin 2004; Moors-Murphy 2014; Skliris and Djenidi 2006).

Mixed layer depth upwelling (*mldUp*) - The ocean mixed layer has strong vertical mixing. Upwelling to the mixed layer can thus be assumed to be positively related to habitat potential (e.g., Genin 2004; Moors-Murphy 2014; Skliris and Djenidi 2006). The same process and equations (4-6) as above were used to calculate *mldUp_{au-S}*, *mldUp_{wi-S}*, *mldUp_{sp-S}*, *mldUp_{su-S}* and *mldUp*. It was also hypothesized that *mldUp* has a positive relationship with habitat potential (e.g., Genin 2004; Moors-Murphy 2014; Skliris and Djenidi 2006).

Bottom dissolved oxygen (*O2*) - Bottom water oxygen is likely to have a positive relationship with benthic diversity (e.g., De Leo et al. 2012; Levin et al. 2001). T1 and T2 were determined as 4.0 and 1.12 ml/l, respectively (Best et al. 2007).

Chlorophyll-*a* (*Chla*) - Surface chlorophyll-*a* is a commonly used indicator of ocean primary productivity. In the Australian context of mostly oligotrophic ocean conditions (Poloczanska et al. 2007) the relationship between chlorophyll-*a* concentrations and habitat potential is likely to be positive (e.g., Currie et al. 2012). In other words, the positive relationship follows the ascending part of the unimodal relationship (Levin et al. 2001). Therefore, equation 1 was applied to all four seasons to obtain *Chla_{au-S}*, *Chla_{wi-S}*, *Chla_{sp-S}* and *Chla_{su-S}*, where T1 and T2 were determined as 1.0 and 0.1 mg/m³ (Antoine et al. 1996). The variable *Chla* was then calculated as:

$$Chla = Chla_{au-S} + Chla_{wi-S} + Chla_{sp-S} + Chla_{su-S} \quad (8)$$

It was hypothesized that *Chla* has a positive relationship with habitat potential (e.g., Currie et al. 2012).

Particulate organic carbon (POC) – Surface particulate organic carbon flux is one of the most important indicators of surface-water nutrient status. Again, in Australia, its relationship with habitat potential is positive. Therefore, equation 1 was applied to all four seasons to obtain POC_{au-S} , POC_{wi-S} , POC_{sp-S} and POC_{su-S} , where T1 and T2 were determined as 150 and 20 mg/m³ (Stramski et al. 2008). Variable POC was then calculated as:

$$POC = POC_{au-S} + POC_{wi-S} + POC_{sp-S} + POC_{su-S} \quad (9)$$

It was hypothesized that *POC* has a positive relationship with habitat potential of pelagic species (e.g., Bosley et al. 2004; De Leo et al. 2012; De Leo et al. 2014; Gili et al. 2000; Kiriakoulakis et al. 2011; Levin et al. 2001; Tesi et al. 2010).

Bottom particulate organic carbon (bPOC) - Similar to *POC*, bottom particulate organic matter is an important indicator of bottom-water nutrient status. Again, in Australia, its relationship with habitat potential is positive. Therefore, equation 1 was applied to all four seasons to obtain $bPOC_{au-S}$, $bPOC_{wi-S}$, $bPOC_{sp-S}$ and $bPOC_{su-S}$, where T1 and T2 were determined as half of those for *POC*: 75 and 10 mg/m³. Variable *bPOC* was then calculated as:

$$bPOC = bPOC_{au-S} + bPOC_{wi-S} + bPOC_{sp-S} + bPOC_{su-S} \quad (10)$$

It was hypothesized that *bPOC* has a positive relationship with habitat potential of benthic species (e.g., Bosley et al. 2004; De Leo et al. 2012; De Leo et al. 2014; Gili et al. 2000; Kiriakoulakis et al. 2011; Levin et al. 2001; Tesi et al. 2010).

Percentage of Mud (pMud) - Fine (muddy) sediments typically have high organic matter content (Currie and Sorokin 2014; Currie et al. 2012; Rowe et al. 1982). Thus, we hypothesized that the variable *pMud* has a positive relationship with habitat potential (e.g., Rowe et al. 1982). Gravel content in sediment has little organic matter. For sediment consisting only of mud and sand, it is classified as 'mud' when the sand to mud ratio is less than 1/9 and 'sand' when the sand to mud ratio is greater than 9 (Folk, 1974). This translates into T1 of 90% and T2 of 10%.

Average bottom current speed (ABCS) - Bottom currents can enhance food availability in the bottom water by re-suspending sediments and transporting particles laterally (Garcia et al. 2008). The averaged bottom current speed is thus hypothesized to have a positive relationship with habitat potential. Therefore, equation 1 was applied to all four seasons (sub-variables, Supplementary Materials) of *ABCS* to obtain $ABCS_{au-S}$, $ABCS_{wi-S}$, $ABCS_{sp-S}$ and $ABCS_{su-S}$, where T1 was determined as 0.2 m/s which is strong enough to resuspend fine sediment (Clifton and Dingler 1984) and T2 was determined as 0. Finally, variable *ABCS* was calculated as:

$$ABCS = ABCS_{au-S} + ABCS_{wi-S} + ABCS_{sp-S} + ABCS_{su-S} \quad (7)$$

It was hypothesized that *ABCS* has a positive relationship with habitat potential (e.g., De Mol et al. 2011; Hargrave et al. 2004; Rowe 1971).

Maximum bottom current speed (*maxBCS*) – Fast bottom currents can move and re-suspend sediments. Thus, the maximum and the range of bottom current speeds have been used to represent the potential disturbance to benthic infauna (Paterson et al. 2011). Here we hypothesized that maximum bottom current speed has a unimodal relationship with habitat potential for infauna (Levin et al. 2001). Four threshold values (0, 0.2, 0.3 and 0.5 m/s) were used to represent this unimodal relationship in the following scoring function:

$$maxBCS_S = \begin{cases} \frac{maxBCS}{0.2}, & maxBCS < 0.2 \\ 1, & 0.2 \leq maxBCS \leq 0.3 \\ \frac{(0.5-maxBCS)}{0.2}, & 0.3 < maxBCS \leq 0.5 \\ 0, & maxBCS > 0.5 \end{cases} \quad (11)$$

This equation was applied to all four seasons to obtain $maxBCS_{au_S}$, $maxBCS_{wi_S}$, $maxBCS_{sp_S}$ and $maxBCS_{su_S}$. Variable *maxBCS* was then calculated as:

$$maxBCS = maxBCS_{au_S} + maxBCS_{wi_S} + maxBCS_{sp_S} + maxBCS_{su_S} \quad (12)$$

It was determined that *maxBCS* has a positive relationship with habitat potential after the unimodal relationship has been taken into account for individual seasons.

Range of bottom current speed (*rangeBCS*) - Similar to *maxBCS*, we determined that the range of bottom current speed follows the unimodal relationship with habitat potential. Four thresholds were used to determine the unimodal relationship: 0, 0.15, 0.25 and 0.4 m/s, respectively. The scoring function is:

$$rangeBCS_S = \begin{cases} \frac{rangeBCS}{0.15}, & rangeBCS < 0.15 \\ 1, & 0.15 \leq rangeBCS \leq 0.25 \\ \frac{(0.4-rangeBCS)}{0.15}, & 0.25 < rangeBCS \leq 0.4 \\ 0, & rangeBCS > 0.4 \end{cases} \quad (13)$$

This equation was applied to all four seasons to obtain $rangeBCS_{au_S}$, $rangeBCS_{wi_S}$, $rangeBCS_{sp_S}$ and $rangeBCS_{su_S}$. Variable *rangeBCS* was then calculated as:

$$rangeBCS = rangeBCS_{au_S} + rangeBCS_{wi_S} + rangeBCS_{sp_S} + rangeBCS_{su_S} \quad (14)$$

It was hypothesized that *rangeBCS* has a positive relationship with habitat potential after the unimodal relationship has been taken into account for individual seasons.

3.2.2 Assessment of potential habitat for pelagic species

We used ten variables to index potential habitat for pelagic species, weighting each variable equally (Table 1).

Cetaceans have been shown to occur in greater number near and above larger canyons (Moors-Murphy 2014), and according to Gili et al. (2000), canyon incision depth and slope are positively

associated with greater hydromedusan diversity. In addition, concentrating and aggregating processes that can increase the abundance of the pelagic species would likely occur in areas of complex topography such as canyon walls that have a steeper slope (Moors-Murphy 2014). Therefore, we selected four heterogeneity metrics (*Vm*, *HI*, *AG* and *StdG*), to calculate the attribute score of habitat heterogeneity for pelagic species (Table 1). The scoring function was defined as:

$$Hp_S = mean(Vm_S, HI_S, AG_S, StdG_S) \quad (20)$$

Elevated levels of organic matter and inorganic nutrients in the water column of canyons can result from stronger shelf-slope exchanges and upwelling from deeper water (Allen et al. 2001; Jordi et al. 2005), leading at some sites to higher rates of primary production and increased pelagic species diversity and abundance (e.g., Bosley et al. 2004; Genin 2004; Gili et al. 2000; Guerreiro et al. 2014; Mendes et al. 2011). Thus, six metrics describing nutrient status, inputs, and primary productivity were selected to calculate the attribute score of productivity (*sensu lato*; Table 1). The scoring function was defined as:

$$Pp_S = mean(DtSB_S, surUp_S, eupUp_S, mldUp_S, Chla_S, POC_S) \quad (21)$$

We did not have environmental variables to assess the disturbance to the habitats of pelagic species. Accordingly, the habitat potential index for pelagic species was calculated as:

$$P_S = mean(Hp_S, Pp_S) \quad (22)$$

3.2.3 Assessment of potential habitat for epibenthic species

We used 13 habitat variables to index habitat potential for epibenthic species including suspension feeders and demersal fishes (Table 1); as was the case for pelagic species, each variable contributed equally.

Nine variables capturing complementary facets of canyon habitat heterogeneity (e.g. substrate heterogeneity, topographic complexity, canyon shape and size) were included to calculate the attribute score of habitat heterogeneity as follows:

$$He_S = mean(Vm_S, NoB_S, HI_S, StdD_S, Rg_S, pG15_S, AG_S, StdG_S, pHard_S) \quad (23)$$

In terms of the attribute score of productivity (*sensu lato*), we selected four variables likely to be of relevance for epibenthic species (Table 1): (i) Distance to shelf break (*DtSB*) is used as a proxy for particulate nutrients that could sink to the bottom (Cartes et al. 2010); (ii) The variable *bPOC* is used to estimate the quantity of organic matter in the bottom water (De Leo et al. 2012); (iii) *O2* is used to indicate oxygen availability in the bottom water (De Leo et al. 2012) and; (iv) Average bottom current (*ABCS*) is used as an indicator of potential to transport organic matter and nutrients to the suitable habitats of epibenthic suspension feeders and demersal fish species (De Mol et al. 2011; Hargrave et al. 2004). The scoring function is:

$$Pe_S = mean(DtSB_S, ABCS_S, O2_S, bPOC_S) \quad (24)$$

Again, we did not have environmental variables to assess the disturbance to the habitats of epibenthic communities. The habitat potential index for epibenthic species was calculated as:

$$E_S = mean(Hmg_S, Pmg_S) \quad (26)$$

3.2.4 Assessment of potential habitat for benthic infaunal species

We used nine variables to index habitat condition for benthic infaunal species, encompassing smaller macrobenthos and meiobenthos, commonly associated with unconsolidated sedimentary seafloor (Table 1).

We selected three variables to calculate the attribute score of habitat heterogeneity for infauna species (Table 1): i) variable *ASPD* indicates sediment heterogeneity which has been shown to affect benthic infaunal diversity and abundance (Leduc et al. 2014; Levin et al. 2001); ii) slope, and; (iii) standard deviation of slope, have also been related to benthic macrofauna abundance and diversity (De Leo et al. 2014). The scoring function is:

$$Hi_S = mean(AG_S, StdG_S, ASPD_S) \quad (27)$$

In terms of productivity, four variables were selected to calculate the attribute score (Table 1). Variables *DtSB*, *bPOC* and *O2* affect not only epibenthic species but also benthic macrofauna species (De Leo et al. 2014; Levin et al. 2001). The variable *pMud* can be used as a proxy of sediment organic matter (Rowe et al. 1982). The scoring function is:

$$Pi_S = mean(DtSB_S, O2_S, bPOC_S, pMud_S) \quad (28)$$

The attribute score of disturbance for infauna species was calculated by two variables (Table 1): (i) maximum bottom current, and; (ii) range of bottom current. These were chosen because strong bottom currents can alter sedimentary habitats by increasing sediment instability (Paterson et al. 2011). The scoring function is:

$$Di_S = mean(maxBCS_S, rangeBCS_S) \quad (29)$$

The habitat potential index for infauna species was calculated as:

$$I_S = mean(Hmc_S, Pmc_S, Dmc_S) \quad (30)$$

3.2.5 Classification of canyon habitat potential

We used an objective approach to classify the overall habitat potential of the 753 canyons based on similarity of the three index values (pelagic index score (P_S), epibenthic index score (E_S) and infauna index score (I_S)). The flexible beta clustering technique (Belbin et al. 1992) with Euclidean distance metric was used for the classification, complemented by Non-metric multidimensional scaling (NMDS) ordination.

3.2.6 Validation

We used an underwater video dataset (MarLIN 2014) for a preliminary biological validation of the habitat potential scores (Kloser et al. 2017). Data on the occurrence of dominant epifauna types in one second video frames was available for transects from 14 canyons located in the southern margins (Figure 1). We used five epifauna types commonly found in Australian canyons: bryozoans, sponges, soft corals, crinoids, and other visible sessile fauna. In addition, we also used the trophic guild 'suspension feeders', which includes all of the above taxonomic groups, in this preliminary validation.

The validation was carried out by calculating both Pearson product-moment correlation coefficients and Spearman's rank correlation coefficients between the proportions of the image frames and the habitat potential scores for the epibenthic communities and testing the significance of these correlations. We also generated scatter plots between the individual epifauna types and the habitat potential scores of epibenthic species to help interpret their relationships.

4 Results and Discussion

4.1 Canyon habitat potential index values

Scores for the habitat potential of Australian submarine canyons are wide ranging across all three biological assessment classes (pelagic, epibenthic and infauna; Table 2). The lowest index scores are for a small number of slope-confined canyons that range from 0.06 for pelagic species to 0.15 for infauna species. Peak scores of ~0.8 were assigned variously across all biological groups for both slope-confined and shelf-incising canyons. This spread of index values is shown in frequency histograms for each biological group (Figure 2). Thus, the index scores for pelagic species indicate a

near-normal distribution, slightly skewed towards lower scores. The index scores for epibenthic species skew toward higher scores, with the index scores for infauna further skewed towards higher scores. Among the two main canyon types (shelf-incising ($n=95$) and slope-confined ($n=658$)), the mean index scores for each assessment class were significantly higher for shelf-incising canyons ($F > 90.03$; $p < 0.001$; Figure 3).

These results indicate the wide range of canyon physical forms and environmental conditions that influence canyon biodiversity, particularly at the continental scale. These results also indicate that Australian submarine canyons may offer particularly high habitat potential for the benthic species (Table 2; Figure 2). This is not surprising given that submarine canyons are abrupt seabed geomorphic features that are able to offer heterogeneous habitats for various benthic species (e.g., Cunha et al. 2011; De Mol et al. 2011; Paterson et al. 2011; Vetter et al. 2010). It is also not surprising to find that the shelf-incising canyons have higher habitat potential than the slope-confined canyons. This is because the shelf-incising canyons are likely to provide more heterogeneous habitats, due to their larger size and more complex shape (Huang et al. 2014), which may lead to favourable concentrating and aggregating processes (Greene et al. 1988; Moors-Murphy 2014). They are also likely to offer higher productivity due to their stronger interaction with major ocean boundary currents and higher likelihood to receive nutrient inputs from coastal and continental shelf waters (e.g., Vetter and Dayton 1998; Vetter and Dayton 1999).

4.2 Distribution of canyons with good habitat potential

The spatial distributions of canyon habitat potential index values are shown in Figures S1-S3. Canyons with good habitat potential are particularly of interest for marine biodiversity management and conservation. In this study, we suggest that a canyon offers good habitat potential for marine species if it has a habitat potential index value greater than or equal to 0.7. Selecting a uniform threshold instead of three for the three habitat assessment categories puts them on the same base. The habitat score of 0.7 was considered an appropriate threshold in this study because:

- it approaches the higher end of the resultant habitat scores (Table 2), and
- it is the highest value of the upper 95% confidence intervals obtained from the objective classification process (section 3.2.5) (Figure 5a; section 4.3).

Among the 753 Australian submarine canyons, 135 of them offer good habitat potential for at least one of the three marine species categories: pelagic species ($n=13$), epibenthic species ($n=36$) and infauna species ($n=124$). Most of these good potential canyons are located along the eastern margin; some of them are located along the southern margin (Figure 4a). There are two common features for these 135 canyons that boost their productivity for pelagic and benthic species. First, they either intersect or are very close to the shelf break ($DtSB_S=0.97\pm 0.09$). This provides them greater potential to receive materials flux and nutrient inputs from land and shelf water (e.g., De Leo et al. 2014; Hargrave et al. 2004; Vetter and Dayton 1998; Vetter and Dayton 1999) that are the food sources of a

variety of marine pelagic and benthic species. The other is that these canyons have abundant oxygen supply in the bottom water ($O2_S=0.97\pm 0.05$), which is beneficial for benthic communities (e.g., De Leo et al. 2012; Levin et al. 2001).

The 13 canyons that offer good habitat potential for pelagic species are mostly located offshore of Eden (Figure 4c) and the east coast of Tasmania (Figure 4d). They have high chlorophyll-a concentrations in the surface water ($Chla_S=0.91\pm 0.2$) and strong upwelling potential ($eupUP_S=0.95\pm 0.12$), provide a productive environment for pelagic species ($Pp_S=0.84\pm 0.06$) (Bosley et al. 2004). They also have fairly complex topography, with steep slopes and heterogeneous substrates ($StdD_S=0.85\pm 0.2$; $pG15_S=0.93\pm 0.1$; $AG_S=0.93\pm 0.1$), which would likely generate favourable concentrating and aggregating processes for the benefit of pelagic species (Greene et al. 1988; Moors-Murphy 2014).

The canyons that offer good habitat potential for epibenthic species are located offshore of the Great Barrier Reef (n=7; Figure 4b), the coast of southern Queensland and New South Wales (n=16; Figure 4c), the south-east coast of Tasmania (n=4; Figure 4d), the Murray canyon group (n=4; South of Adelaide; Figure 4d) and the Albany canyon group (n=5; Figure 4e). Among them, the canyons on the eastern margin of Australia have relatively high benthic productivity ($Pe_S=0.85\pm 0.07$). They often have strong enough bottom current conditions ($ABCS_S=0.76\pm 0.2$) that can deliver food particles to epibenthic species (De Mol et al. 2011; Garcia et al. 2008; Hargrave et al. 2004). Some canyons (e.g., those along the south-east coast of Tasmania) also have very high particulate organic carbon concentrations in the bottom water ($bPOC_S=0.99\pm 0.02$). Most of these 27 canyons are also fairly complex in bottom topography and shape ($HI_S=0.71\pm 0.1$; $StdD_S=0.72\pm 0.27$; $pG15_S=0.90\pm 0.11$; $AG_S=0.86\pm 0.1$). The nine canyons in the Murray and Albany groups have moderately high habitat heterogeneity for epibenthic species ($He_S=0.70\pm 0.06$), due to complex topography, variable shape and large size ($NoB_S=0.77\pm 0.18$; $StdD_S=0.99\pm 0.02$; $StdG_S=0.87\pm 0.07$; $AG_S=0.78\pm 0.12$).

The canyons that offer good habitat potential for infauna species are distributed along the eastern and southern margins of Australia (Figures 4b-e). These canyons have intermediate disturbance regime that favours the diversity of infauna species ($Di_S=0.87\pm 0.08$) (Levin et al. 2001), provided by intermediate bottom current speed. Many of these canyons, especially those in the Murray and Albany groups, have relatively complex bottom topography that can be beneficial for infauna species ($StdG_S=0.87\pm 0.03$; $AG_S=0.79\pm 0.09$) (De Leo et al. 2014). Many of them are also moderately high in productivity ($Pi_S=0.73\pm 0.06$). For example, there are 37 such canyons along the coast of Tasmania (Figure 4d) that have very high bottom particulate organic carbon concentrations ($bPOC_S=0.96\pm 0.06$).

Few canyons offer good habitat potential for all three categories of marine species (pelagic, epibenthic and infauna), with only five identified here. One is located offshore of the border between New South Wales and Queensland; three are located off Eden; the other is located off the south-east coast of Tasmania (Figures 4c&d). These canyons are fairly complex in topography ($pG15_S=0.93\pm0.12$; $AG_S=0.92\pm0.12$; $StdD_S=0.78\pm0.32$; $HI_S=0.76\pm0.06$; $StdG_S=0.70\pm0.15$) so that they are able to provide heterogeneous habitats for a variety of marine species. They also provide potentially highly productive environment for marine species. They are located in areas with strong upwelling potential ($eupUp_S=0.92\pm0.18$; $mldUp_S=0.74\pm0.28$) that can bring bottom nutrients to near the surface (Bosley et al. 2004). Indeed, these areas are under the influence of frequent upwelling driven by the East Australian Current and favourable wind, especially in the areas off Eden and Coffs Harbour (Commonwealth of Australia, 2013a; Oke and Middleton 2000; Roughan and Middleton 2004). In addition, these canyons have also relatively high chlorophyll-*a* and particulate organic carbon concentrations in the surface water, and oxygen supply and particulate organic carbon concentrations in the bottom water ($Chla_S=0.82\pm0.33$; $POC_S=0.74\pm0.18$; $O2_S=0.97\pm0.02$; $bPOC_S=0.70\pm0.19$). The disturbance to the sediment of these canyons is close to intermediate, which is fairly favourable for infauna species ($Di_S=0.81\pm0.09$).

Nationally, 24 canyons distributed along the eastern and southern margins offer good habitat potential for two of the categories (epibenthic and infauna communities) (Figures 4b&c&d&e). These canyons are quite productive for benthic communities ($Pe_S=0.85\pm0.08$; $Pi_S=0.73\pm0.03$). They have favourable bottom current conditions that can deliver food particles to epibenthic species (De Mol et al. 2011; Garcia et al. 2008; Hargrave et al. 2004) and generate intermediate sediment disturbance that is often associated with higher infauna diversity (Levin et al. 2001) ($ABCS_S=0.80\pm0.18$; $maxBCS_S=0.84\pm0.12$; $rangeBCS_S=0.82\pm0.10$). Many of these canyons are also fair complex in topography ($pG15_S=0.83\pm0.14$; $AG_S=0.83\pm0.09$; $StdD_S=0.74\pm0.27$) that provides heterogeneous habitats for benthic communities. Another canyon, located off the north-east coast of Tasmania, offers good habitat potential for both pelagic and infauna communities (Figure 4d). This canyon provides a productive environment for pelagic species with high surface chlorophyll-*a* and particulate organic carbon concentrations and strong upwelling potential ($Chla_S=0.98$; $POC_S=0.91$; $surUp_S=0.78$; $mldUp_S=1.0$; $eupUp_S=0.75$), and for infauna species with high oxygen supply and particulate organic carbon concentrations in the bottom water ($O2_S=0.99$; $bPOC_S=0.80$). This canyon also has a degree of topographic complexity ($StdG_S=0.87$; $AG_S=0.89$) that is favourable for pelagic and infauna species (Moors-Murphy 2014; De Leo et al. 2014). It also has relatively favourable sediment disturbance environment for infauna species ($Di_S=0.73$). Another three canyons located off the Eden coast (Figure 4c) offer good habitat potential for both pelagic and epibenthic communities. These canyons provide productive environment for pelagic species with high Chlorophyll-*a* and moderately high particulate organic carbon concentrations in surface water and potentially strong upwelling to euphotic layer

($Chla_S=0.95\pm 0.04$; $POC_S=0.73\pm 0.02$; $eupUp_S=1.0$). These canyons also have fairly complex topography ($StdD_S=0.92\pm 0.13$; $pG15_S=0.91\pm 0.15$; $AG_S=0.92\pm 0.14$; $HI_S=0.74\pm 0.11$; $StdG_S=0.74\pm 0.03$) that provides heterogeneous habitats.

4.3 Classification of canyon habitat potential

The overall canyon habitat potential classification resulted in four distinct groups of canyons, which we term: 'high' (n=161; $P_S=0.58\pm 0.07$; $E_S=0.64\pm 0.07$; $I_S=0.70\pm 0.06$), 'high-medium' (n=317; $P_S=0.42\pm 0.06$; $E_S=0.53\pm 0.06$; $I_S=0.58\pm 0.09$), 'medium-low' (n=175; $P_S=0.28\pm 0.05$; $E_S=0.36\pm 0.05$; $I_S=0.44\pm 0.05$) and 'low' (n=100; $P_S=0.18\pm 0.04$; $E_S=0.25\pm 0.04$; $I_S=0.34\pm 0.05$). The NMDS ordination plot indeed confirms that the four classes are well-separated (Figure 5a). The class separations are statistically significant based on the 95% confidence intervals (Figure 5a). The spatial distribution of these habitat potential classes is shown in Figure S4.

Figure 5b shows the distribution of the canyons that were assigned with the 'high' habitat potential class. With one exception, these canyons are located along the eastern and southern margins, similar to the spatial pattern of the 135 canyons that offer good habitat potential (Figure 4a). The most notable clustering regions include the Great Barrier Reef region, the margin off New South Wales coast, the margin off Tasmania coast, the Murray canyon group and the Albany canyon group (Figure 5b). Overall, these canyons with the 'high' habitat potential class have relatively heterogeneous habitats because of their complex bottom topography ($HI_S=0.62\pm 0.21$; $StdD_S=0.60\pm 0.28$; $pG15_S=0.68\pm 0.24$; $AG_S=0.72\pm 0.18$; $StdG_S=0.63\pm 0.20$). They are also relatively productive due to their proximity to the shelf break ($DtSB_S=0.96\pm 0.09$), abundant oxygen supply and moderately high particulate organic carbon concentrations in the bottom water ($O2_S=0.96\pm 0.05$; $bPOC_S=0.66\pm 0.23$), and moderately high primary productivity in the surface water ($Chla_S=0.60\pm 0.34$; $POC_S=0.70\pm 0.21$). In addition, the disturbance regime within these canyons is relatively favourable ($Di_S=0.73\pm 0.19$) for infauna species.

4.4 Validation

The Pearson and Spearman correlation coefficients between the proportions of the image frames and the habitat potential scores of epibenthic communities from the 14 validation canyons are shown in Table 3. The corresponding scatter plots are displayed in Figure 6. The epifauna types of bryozoan, crinoids and sponges do not have significant correlations with the habitat scores of epibenthic species. The proportions of soft corals have a positive and significantly high correlation ($p < 0.01$) with the habitat heterogeneity scores for epibenthic species (He_S) (Table 3; Figure 6). The scatter plot indicates that soft corals are less likely to be present when the He_S score is smaller than 0.5; after this threshold, the occurrence of soft corals increases in more spatially heterogeneous canyons (Figure 6).

These five heterogeneous canyons are much larger in size ($Vm_S=0.94\pm 0.15$), have multiple branches ($NoB_S=0.89\pm 0.24$), provide much more complex topography ($StdD_S=1.0$; $Rg_S=0.22\pm 0.09$; $pG15_S=0.55\pm 0.15$; $AG_S=0.64\pm 0.14$; $StdG_S=0.81\pm 0.13$), and offer greater availability of hard substrates ($pHard_S=0.54\pm 0.16$) than the remaining nine canyons ($Vm_S=0.08\pm 0.17$; $NoB_S=0.22\pm 0.18$; $StdD_S=0.60\pm 0.32$; $Rg_S=0.06\pm 0.02$; $pG15_S=0.23\pm 0.11$; $AG_S=0.38\pm 0.08$; $StdG_S=0.47\pm 0.12$; $pHard_S=0.46\pm 0.19$).

The correlation test also reveals a positive and significant correlation ($p < 0.01$) between the proportions of soft corals and the final habitat potential index values for epibenthic species (E_S) (Table 4; Figure 6). In addition, according to the correlation test, the proportions of other visible sessile fauna and the trophic guild 'suspension feeders' have significantly positive correlations with the productivity scores of epibenthic species (Pe_S) (Table 3; Figure 6), likely determined by bottom current that is able to deliver food particles to the sessile suspension feeders (De Mol et al. 2011; Hargrave et al. 2004).

5 Summary and Conclusion

This study confirms that Australian submarine canyons offer variable habitat potential due to their diversity in geomorphic and oceanographic characteristics. Although canyons along the eastern margin are generally smaller in size than those along the southern and western margins (Huang et al. 2014), many of these canyons are fairly complex in topography which is a major determining factor for habitat heterogeneity. Importantly, the canyons along the eastern margin are much more productive than the southern and western margins for two main reasons. Firstly, they have higher primary productivity measured by chlorophyll-*a* and particulate organic carbon concentrations, likely due to the narrower continental shelf that enhances higher terrigenous inputs. Secondly, interaction of these canyons with the upwelling favourable East Australia Current would bring nutrients from deeper waters to the mixing layer and euphotic depths, aided by frequent wind-driven upwelling events, the nutrients could even reach the surface water (Commonwealth of Australia, 2013a; Klinck 1996; Oke and Middleton 2000; Roughan and Middleton 2004). In addition, the bottom current conditions are more favourable on this margin than on other margins, which can deliver food particles to epibenthic megafauna (De Mol et al. 2011; Hargrave et al. 2004) and generate intermediate sediment disturbance environment for infauna (Levin et al. 2001). As a result, most of the canyons that were identified as having potentially good habitat are located along this margin (Figures 4&5). The other two notable findings are that:

- shelf-incising canyons are able to offer higher habitat potential than slope-confined canyons (Table 2; Figure 3), and

- canyons offer higher habitat potential for infauna species than for epibenthic species and for pelagic species (Table 2).

The partial validation for the canyon habitat potential assessment based on a limited number of canyons that have available biological data is mixed. Encouragingly, we did find a significant and positive correlation between epibenthic habitat potential and the proportions of soft corals and other visible sessile fauna (Table 3; Figure 6). However, we did not find positive correlations between the epibenthic habitat potential and the proportions of the three remaining epibenthic fauna types (Table 3; Figure 6).

We acknowledge that this canyon habitat potential assessment has some limitations. Firstly, due to the lack of data, we could not use some potentially important habitat variables. For example, sediment biogeochemical properties are important to the evaluation of the habitat productivity for benthic infauna species. Some important aspects of the habitat disturbance factor such as sediment mass movement and cascading events also could not be evaluated (Levin et al. 2001). Another important limitation is the data quality. Many data used in this study are potentially too coarse in spatial resolution to adequately assess the canyon habitat characteristics. The majority of the data layers used were the outputs of interpolation, prediction and modelling studies. As a result, there are potentially substantial uncertainties associated with them. In addition, the simple habitat potential assessment method implemented in this study may need to be improved in any future assessment, for example by assigning weights to individual variables and habitat condition factors.

There are a number of possible management and research implications arising from the scoring presented here. The results of the canyon habitat potential assessment may be used to establish conservation and management priorities. In general, monitoring of canyon condition could be focused on the eastern Australian margin, and to a lesser degree the southern margin. In particular, the five "super" canyons on the eastern margin that offer good habitat potential for a variety of pelagic and benthic communities should receive high management priority. Other canyon groups such as those off the coast of south-eastern Tasmania, Murray canyons and Albany canyons could also receive management attention. We have little understanding of the ecosystems of these canyons with good habitat potential and/or being classified as 'high' habitat class. Multi-disciplinary surveys and studies can be designed and conducted to collect baseline environmental and biological information, and to investigate the interactions among key ecological processes such as upwelling, sediment fluxes and hydrodynamics, nutrient cycling and the coupling of benthic and pelagic systems in and around these canyons. In addition, additional data collection and modelling at broader scales would alleviate the above-mentioned data availability and quality issues and thus contribute to expanded knowledge of Australian submarine canyons and their effective management.

In conclusion, we find that the high geomorphic and oceanographic diversity of Australian submarine canyons creates a multitude of potential habitat types for marine species and assemblages associated with these systems. We presented a framework that describes a methodology to derive estimates of potential habitat potential for the pelagic, epibenthic and infauna species. Geographic patterns, when analysed for the entire continental margin of Australia, indicate that canyons with particularly high potential habitat are located mainly offshore of the Great Barrier Reef the NSW coast, and the eastern margin of Tasmania and Bass Strait, and within the Albany and Murray groups. Many of these canyons tend to offer relatively heterogeneous habitats because of their complex bottom topography, provide productive environment benefited from their closeness to the shelf break to receive terrestrial inputs and the oceanographic processes that likely enhance primary productivity, and have relatively favourable sediment disturbance environment. The framework detailed here can be relevant and serve as guide – once refined and validated with more comprehensive ecological data - in a management and conservation context to identify canyons (or groups of canyons) that are likely to represent high-value habitats along vast continental margins of the world where marine planning decisions may require spatial prioritization decisions.

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Figure Captions

Figure 1: The spatial distribution of the Australian submarine canyons. The stars indicate the locations of the 14 validation canyons.

Figure 2: Histograms of the canyon habitat potential index scores; a) P_S (habitat potential index score for pelagic species); b) E_S (habitat potential index score for epibenthic species); c) I_S (habitat potential index score for infauna species).

Figure 3: The habitat potential index scores comparing shelf-incising canyons and slope-confined canyons. The error bars show 95% confidence intervals. P_S (habitat potential index score for pelagic species); E_S (habitat potential index score for epibenthic species); I_S (habitat potential index score for infauna species).

Figure 4: The spatial distribution of canyons with good habitat potential; a) overall pattern with blue points indicate the canyons with good habitat potential ($n=135$); b) Great Barrier Reef region; c) margin off the coast of southern Queensland and New South Wales; d) margin off the coast of Victoria, Tasmania and South Australia; e) margin off the west and south-west of Western Australia.

Figure 5: Classification of canyon habitat potential; a) NMDS (non-metric multidimensional scaling) plot showing the separations of the four canyon classes; the values on the plot are 95% confidence intervals of the corresponding habitat potential index values; b) the spatial distribution of the canyons with the 'high' class (blue points; $n=161$).

Figure 6: The scatter plots for the 14 validated canyons; The black solid line shows the linear fit. The red solid line shows the polynomial fit. The corresponding R^2 values for the fits are also shown. He_S (habitat heterogeneity score for epibenthic species); Pe_S (productivity score for epibenthic species); E_S (habitat potential index score for epibenthic species).

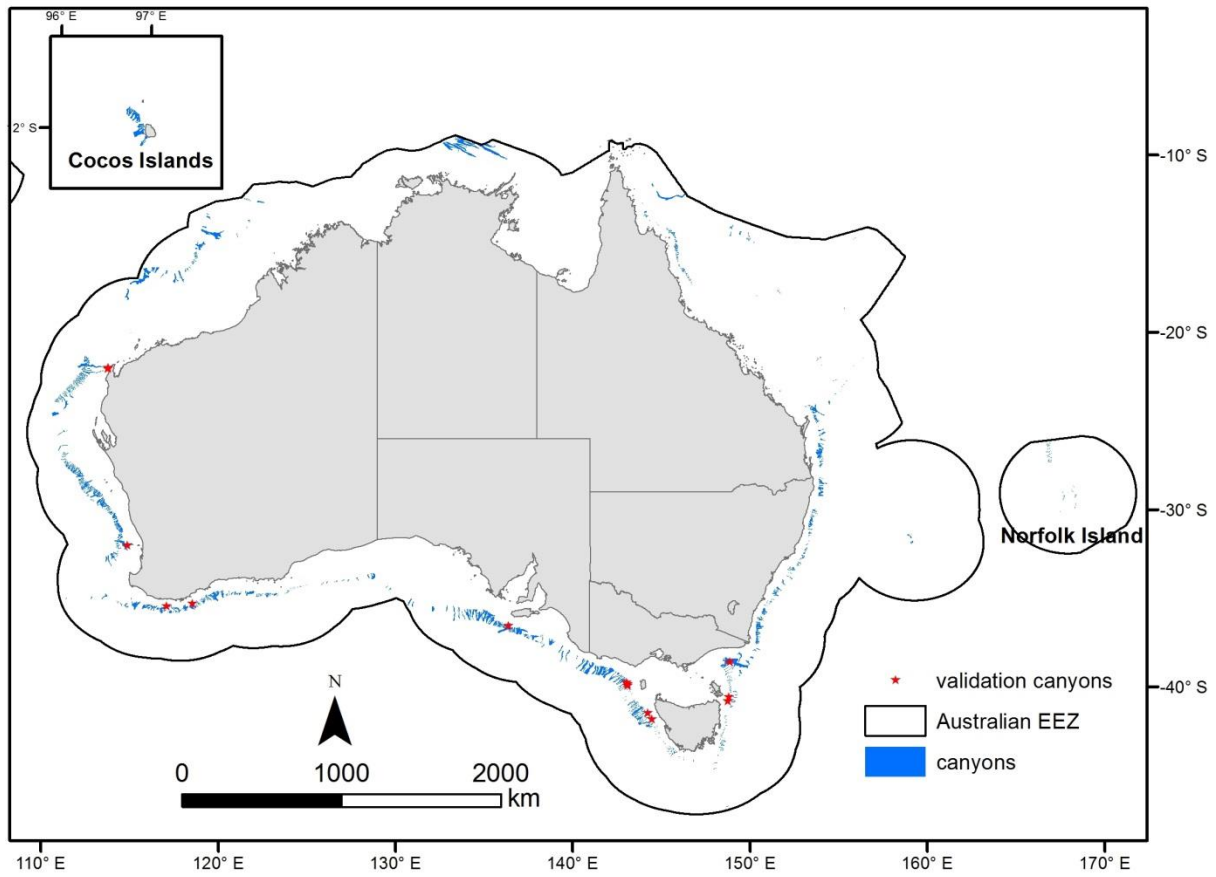


Figure 1: The spatial distribution of the Australian submarine canyons. The stars indicate the locations of the 14 validation canyons.

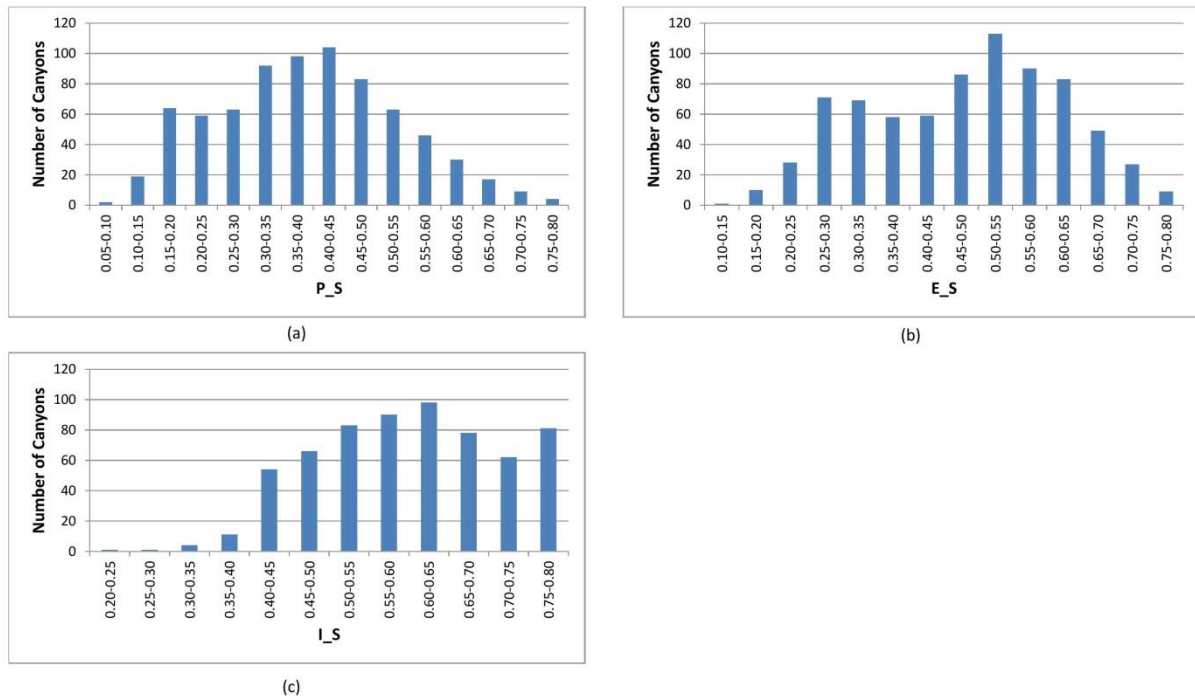


Figure 2 Histograms of the canyon habitat potential index scores; a) P_S (habitat potential index score for pelagic species); b) E_S (habitat potential index score for epibenthic species); c) I_S (habitat potential index score for infauna species).

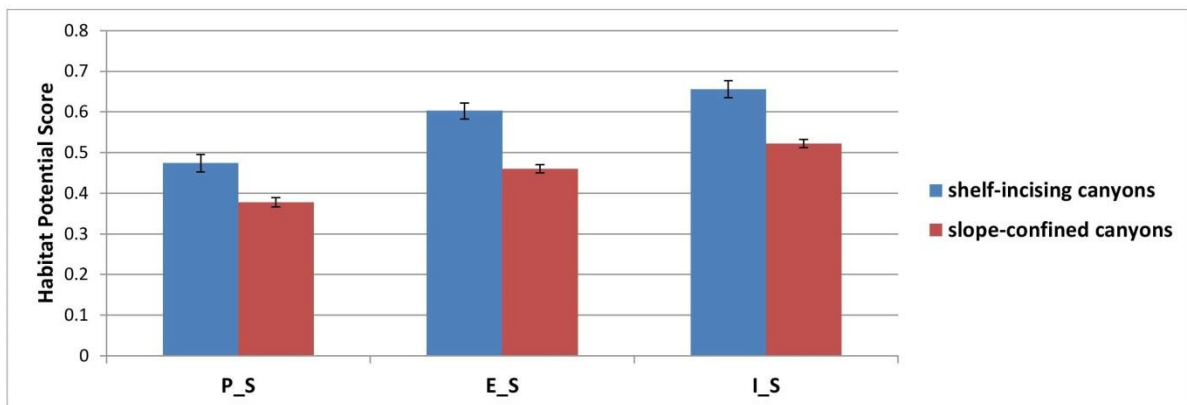


Figure 3: The habitat potential index scores comparing shelf-incising canyons and slope-confined canyons. The error bars show 95% confidence intervals. P_S (habitat potential index score for pelagic species); E_S (habitat potential index score for epibenthic species); I_S (habitat potential index score for infauna species).

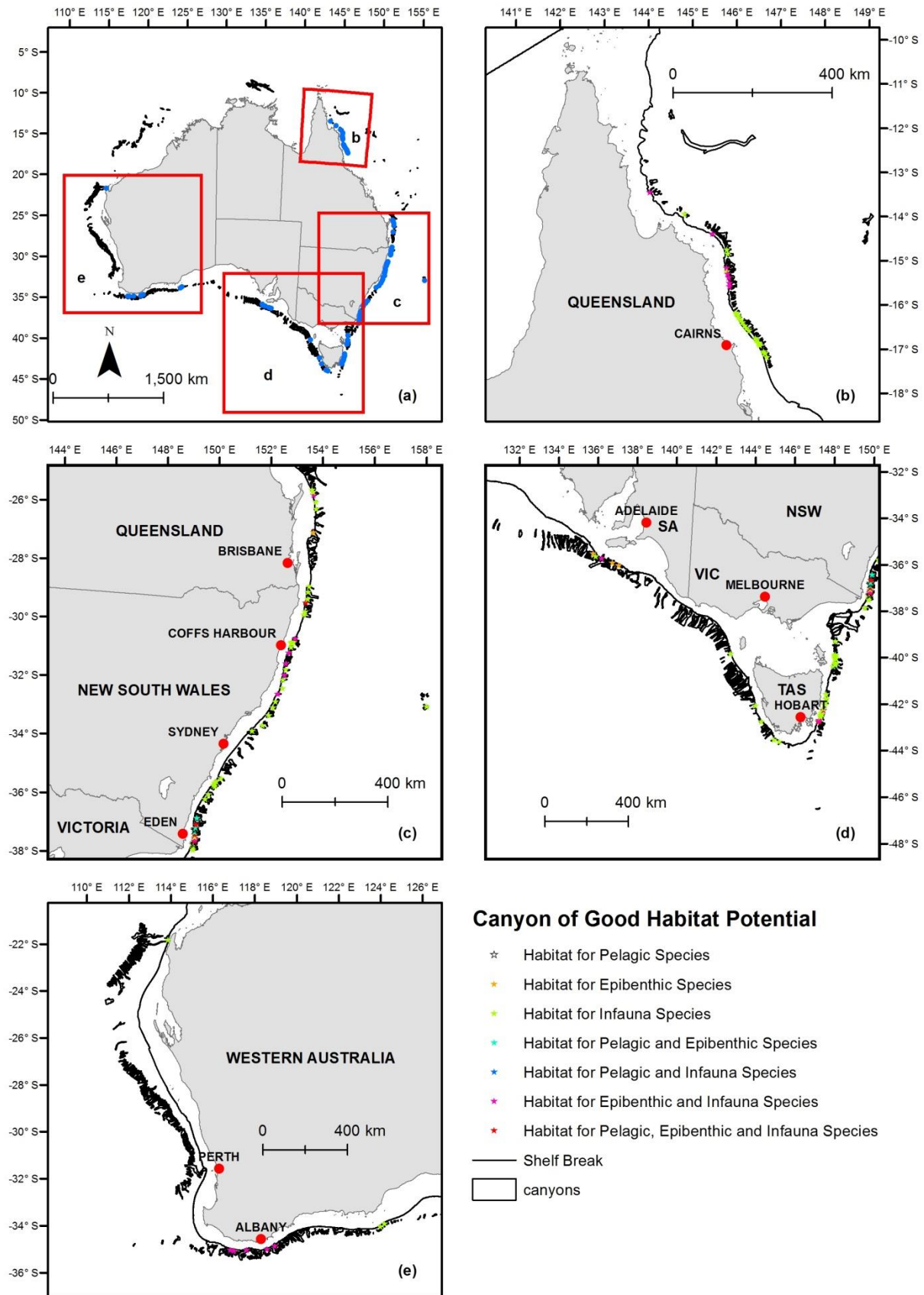


Figure 4: The spatial distribution of canyons with good habitat potential; a) overall pattern with red points indicate the canyons with good habitat potential (n=135); b) Great Barrier Reef region; c) margin off the coast of southern

Queensland and New South Wales; d) margin off the coast of Victoria, Tasmania and South Australia; e) margin off the west and south-west of Western Australia.

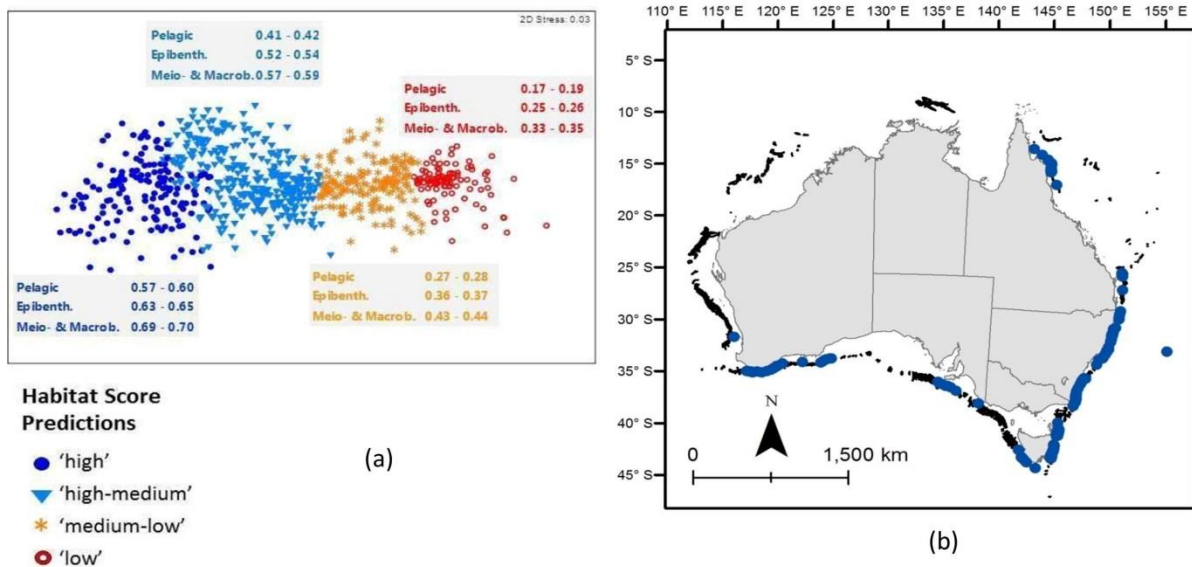


Figure 5: Classification of canyon habitat potential; a) NMDS (non-metric multidimensional scaling) plot showing the separations of the four canyon classes; the values on the plot are 95% confidence intervals of the corresponding habitat potential index values; b) the spatial distribution of the canyons with the 'high' class (red points; n=161).

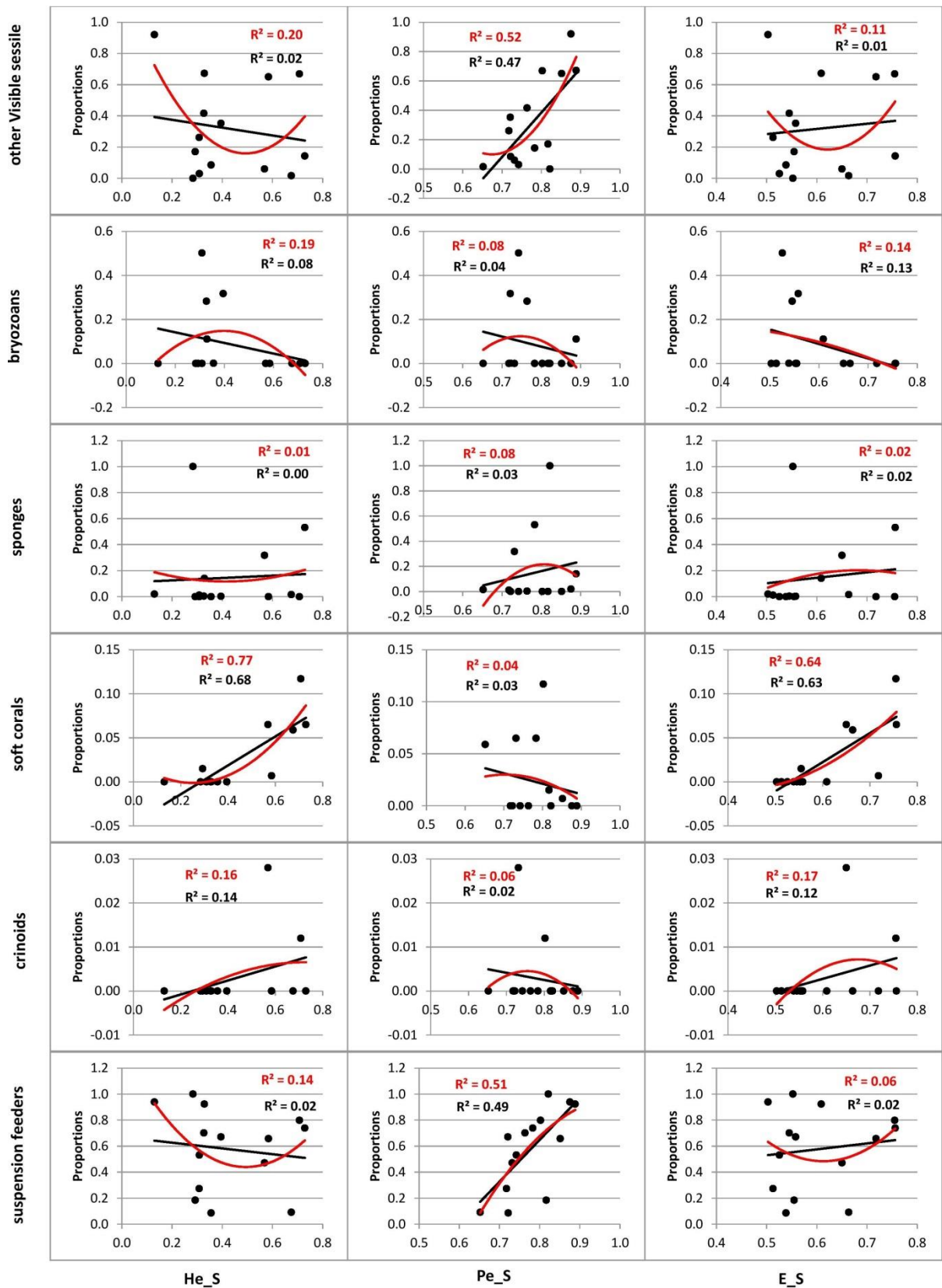


Figure 6: The scatter plots for the 14 validated canyons; The black solid line shows the linear fit. The red solid line shows the polynomial fit. The corresponding R^2 values for the fits are also shown. He_S (habitat heterogeneity score for epibenthic species); Pe_S (productivity score for epibenthic species); E_S (habitat potential index score for epibenthic species).

Table 1: Habitat variables chosen for the assessment of pelagic habitats, epi benthic suspension feeders and demersal fish habitats, and benthic infauna (macrofauna and meiofauna) habitats

Attribute	Variable Code	Variable Name	Dataset Source*	Pelagic	Epibenthic	Infauna
Heterogeneity	Vm	Volume	NC	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	
	NoB	Number of branches	NC		<input checked="" type="checkbox"/>	
	HI	Head Incision	NC	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	
	StdD	Standard deviation of water depth	NC	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	
	Rg	Rugosity	NC		<input checked="" type="checkbox"/>	
	pG15	Percentage of gradient > 15°	NC		<input checked="" type="checkbox"/>	
	AG	Average gradient	NC	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
	StdG	Standard deviation of gradient	NC		<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
	pHard	Percentage of hard substrates	NB		<input checked="" type="checkbox"/>	
	ASPD	Average Sediment particle diversity	NS			<input checked="" type="checkbox"/>
Productivity	DtSB	Distance to shelf break	NC	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
	surUp	Surface upwelling	BR/NC	<input checked="" type="checkbox"/>		
	eupUp	Euphotic depth upwelling	BR	<input checked="" type="checkbox"/>		
	mldUp	Mixed layer depth upwelling	BR	<input checked="" type="checkbox"/>		
	ABCS	Average bottom current speed	BR		<input checked="" type="checkbox"/>	
	O2	Bottom Dissolved Oxygen	CA		<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
	Chla	Chlorophyll a	MO	<input checked="" type="checkbox"/>		
	POC	Particulate organic carbon	MO	<input checked="" type="checkbox"/>		
	bPOC	Bottom particulate organic carbon	MO/NC		<input checked="" type="checkbox"/>	<input checked="" type="checkbox"/>
	pMud	Percentage of Mud	NS			<input checked="" type="checkbox"/>
Disturbance	maxBCS	Maximum bottom current speed	BR			<input checked="" type="checkbox"/>
	rangeBCS	Range of bottom current speed	BR			<input checked="" type="checkbox"/>

Note: NC=National Canyon Dataset, NB=National Backscatter Dataset, NS=National Sediment Dataset, BR=Bran3.5 Dataset, CA=CARS 2006 Dataset, MO=MODIS Dataset, HC=Historical Cyclone Dataset

Table 2: Statistics of the canyon habitat potential assessment shown for all canyons and separate for shelf incising canyons (n=95) and slope-confined canyons (n=658).

		min	max	mean	s.d.
Pelagic species (P_S)	All	0.06	0.78	0.39	0.14
	Shelf-incising canyons	0.17	0.70	0.47	0.11
	Slope-confined canyons	0.06	0.78	0.38	0.14
Epibenthic species (E_S)	All	0.12	0.79	0.48	0.14
	Shelf-incising canyons	0.34	0.78	0.60	0.10
	Slope-confined canyons	0.12	0.79	0.46	0.14
Infauna species (I_S)	All	0.15	0.80	0.54	0.14
	Shelf-incising canyons	0.33	0.80	0.66	0.10
	Slope-confined canyons	0.15	0.80	0.52	0.13

Note: s.d.: standard deviation

Table 3: Pearson and Spearman Correlation Coefficients for the 14 validated canyons

	Bryozoan		Sponges		Soft corals		Crinoids		Other visible sessile fauna		Suspension feeders	
	r	rho	r	rho	r	rho	r	rho	r	rho	r	rho
He_S	-0.28	-0.11	0.06	-0.07	0.82 ^{**}	0.75 ^{**}	0.38	0.41	-0.16	-0.03	-0.13	-0.17
Pe_S	-0.19	-0.16	0.18	0.13	-0.18	-0.12	-0.14	-0.22	0.69 ^{**}	0.52 [*]	0.70 ^{**}	0.70 ^{**}
E_S	-0.37	-0.32	0.13	0.10	0.79 ^{**}	0.82 ^{**}	0.34	0.38	0.10	0	0.13	-0.08

Note: two-star superscript indicates significant at the confidence level of 99%; one-star superscript indicates significant at the confidence level of 95%