Relative importance of local biotic and environmental factors versus regional factors in driving macrobenthic species richness in intertidal areas

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ABSTRACT: Species richness depends on both regional and local factors, including regional species pools and habitat type. We compared diversity, scaling from α (site species richness) to β (heterogeneity in species richness) and γ (location species richness), at 6 different intertidal habitat types within 8 coastal locations in the New Zealand North Island. Physical variables at each location (the harbour total area to high water, tidal prism and % intertidal) and habitat variables (comprising habitat fragmentation indices and number and size of patches) were correlated with the diversity measures, evaluating the importance of local variables against regional species pools. Results showed that differences in diversity indices within locations were greater than between locations, and that generally habitats with structuring fauna (cockles, seagrass, tubeworms) held higher diversity than purely sedimentary habitats (mud and sand). In all habitats except mud, local variables had significant interaction with diversity; patch size had a positive effect for all diversity measures, and fragmentation indices had negative effects. The intertidal extent also negatively affected diversity, especially regional species richness. These findings underline the importance of minimising habitat loss and fragmentation for the conservation of marine soft sediments.

KEY WORDS: Diversity measures · Habitats · Macroinfauna · New Zealand · Soft bottoms

INTRODUCTION

In a generalised framework of marine ecosystem degradation (Thrush & Dayton 2002), research is needed to underpin conservation efforts. Major recent management initiatives are centered on the concepts of protection of important habitats (e.g. essential fish habitats, Benaka 1998) and biogeographical zones (Turpie 2000). Bioregionalisation schemes are generally considered at large scales (from hundreds to thousands of kilometres), whereas the influence of habitats is generally considered at small scales (up to hundreds of metres) (Witman et al. 2004). The interaction of factors operating at these 2 scales is likely to be crucial for the determination of appropriate conservation strategies. For example, species richness is controlled both by local factors, including habitat variables, and the regional species pool. The extent to which biotic

habitats and sediment type can override other local factors (e.g. flow patterns, landscape structure, anthropogenic factors) and broad-scale constraints imposed by the regional species pool is largely unknown.

Many studies demonstrate strong regional gradients in diversity in marine systems (e.g. Sanders 1968, Ellingsen & Gray 2002). 'Regional scale' can be considered as any area larger than the sampling scale; however, it has frequently been considered to be on the order of hundreds to thousands of kilometres (Witman et al. 2004). The strong effect of regional patterns of species richness on local diversity has been demonstrated by estimation of species accumulation curves over increasing numbers of areas (Ugland et al. 2003) and the incorporation of geographic ranges into species–area relationships (Ney-Nifle & Mangel 2000). The effects of the regional species pools on local diversity are likely to be a consequence of a number of

factors, both biotic and environmental. Regional species pools and the dispersion capacity of organisms (Ellingsen & Gray 2002, Klimek et al. 2008) will interact with environmental characteristics, such as grain size, organic content (Etter & Grassle 1992, Gray 2002), oceanographic conditions or environmental stress (Witman et al. 2004).

In many marine systems, specific habitats (e.g. tropical coral reefs, kelp beds, seagrass meadows, seamounts) have particular importance for biodiversity, increasing environmental heterogeneity and complexity, and thus providing refuge for organisms (Thrush & Dayton 2002). Habitat heterogeneity and habitat diversity have been demonstrated to have strong effects on estimates of biodiversity (Connor & McCoy 1979, Ellingsen 2002). Ellingsen & Gray (2002) demonstrated that habitat heterogeneity increased the slope of the relationship between area and species accumulation, such that predictions of biodiversity made without taking habitat heterogeneity into account were underestimates. The total species curve for increasing number of areas (Ugland 2003) has been adapted by Thrush et al. (2006) for increasing numbers of habitats, and again demonstrated increased predictions of biodiversity. Therefore, a greater variety of habitats, however defined, would hold higher species richness than a single habitat, even if the single habitat is considered to be a high species diversity habitat such as seagrass.

The role of key species in providing structured habitats in soft-sediments is sometimes ignored, but increasingly the role of reef-forming species in providing 3-dimensional complexity and stabilising the seafloor is seen as an important driver of biodiversity (Hewitt et al. 2005, Thrush et al. 2006b). However, this is dependent on the scale of the biogenic habitat, which must be sufficiently large to have a positive effect on diversity (Hewitt et al. 2005). Reef-forming species modify the nutrient flow, increasing the nutrient exchange between the benthos and the boundary layer, boost microphyte production by releasing nutrients, and give protection from predators (Gray 2002). The role of species that bioturbate the sediment, such as large burrowing species (Lohrer et al. 2004, Solan et al. 2004), is more variable. While such species can also modify nutrient flows and increase microphyte production, their movement can destabilise the seafloor and disturb infauna (Widdicombe et al. 2000, Norkko et al. 2006), potentially decreasing diversity (Lohrer et al. 2008).

Nevertheless, despite the importance of estimating diversity and avoiding the loss of species, there are few between-habitat comparisons of marine biodiversity, especially across multiple locations. Estuaries and coasts are systems of strong physical gradients and communities in these areas are considered to be driven by environmental forcing (Thrush et al. 2004). As a result,

variability in diversity–habitat relationships due to the interaction between environmental variables and the regional species pool could be high. We analyse macrobenthic diversity patterns across intertidal soft-sediment habitats at 8 locations in the New Zealand Auckland region (North Island), investigating the relative effects of regional species pools, habitat types and local environmental factors. Habitat is defined by its predominant features that create structural complexity or by other geological features like grain size (Airoldi & Beck 2007). Six habitat types were defined either by sediment type (i.e. mud, sand) or by the presence of a key species that was common enough across the locations to be used, with patches ranging in size from 5 m^2 to 1 km^2. The key species included bioturbators and species providing biogenic structure. Specifically, we raised the following 3 questions. (1) Is there a difference in macrobenthic diversity between habitats defined by sedimentary features and those defined by key infaunal species? (2) Are regional species pools the dominant force in driving differences between habitat–diversity relationships across locations? (3) Is the local environment (local physical variables and habitat patch characteristics) important? These questions were answered using biodiversity defined as α (average species richness within habitat), γ (total species richness for a habitat within a location) and β (within-habitat heterogeneity). The results for α, γ and β were compared to determine whether scale dependency in biodiversity occurred.

METHODS

Sample areas. Data on intertidal soft-sediment benthic macrofauna (originally obtained for various New Zealand environmental agencies) was available for 8 estuaries: southern Kaipara Harbour, Tamaki Strait (TamakiS), Whitford Embayment, Karepiro Bay, Kawau Bay, Tamaki Estuary (TamakiE), Mahurangi Harbour and the inner Waitemata Harbour (Fig. 1). All of these estuarine systems (hereafter called locations) are within 100 km of each other, although Kaipara opens to the Tasman Sea, while the others open to the Pacific Ocean. The locations range in size from 440 to 4.6 km^2 and also in the degree to which they are intertidal, although all include multiple tidal creeks and wave-exposed sand-flats.

Physical data was available for each location (see www.naturalhazards.net.nz/tools/nzcoast/coastal), some of which is summarized in Table 1: the harbour total area to high water, the percentage of intertidal area (% intertidal) and the tidal prism. Other physical factors could also affect diversity, such as currents or turbidity; however these data were not available and tidal prism is considered a good surrogate for currents in estuaries (T. H. Humes pers. comm.).

The majority of the sampling had been conducted in order to map benthic habitats and communities within each estuary. Thus, habitat descriptions were available for each site and the number and sizes of different habitats could be calculated. Based on these descriptions, 6 dominant habitat types were identified for analysis: seagrass meadows (*Zostera mulleri*), tube worm beds (most frequently *Boccardia syrtis*, but also the maldanids *Macroclymenella stewartensis* and *Asychis* sp.), adult cockle beds (*Austrovenus stutchburyi*; individuals defined as adults when shell length >20 mm), adult wedge shell beds (*Macomona liliana*; adult shell length >20 mm [hereafter: *Macomona*]), unvegetated mudflats (>20% mud content) and unvegetated fine sand flats (>80% fines). A number of other habitats were recorded but either only occurred infrequently in a location or only occurred in a few of the locations; therefore these habitats were not included in the study. All of the selected habitats occurred in the 8 locations except seagrass, which did not appear at Karepiro, Waitemata and Whitford. Sedimentary habitats were considered to be the unvegetated
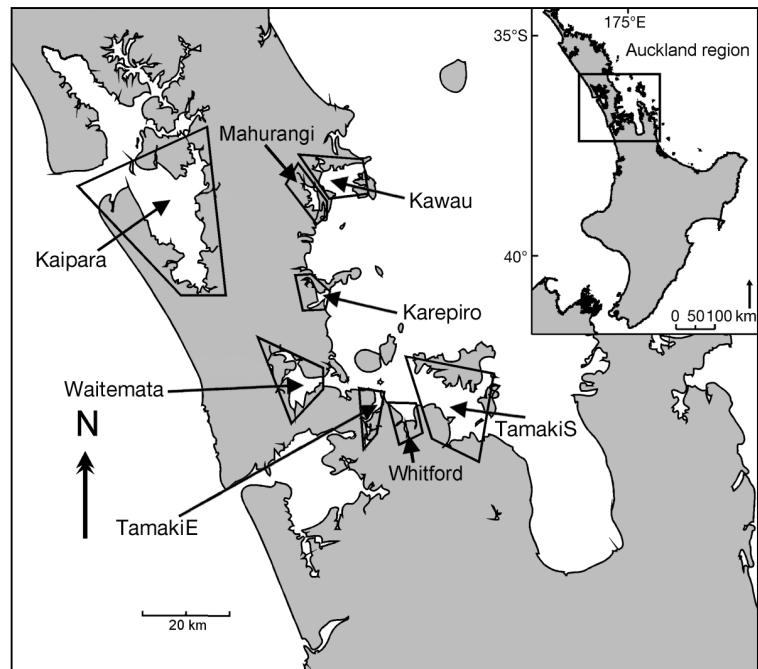

Fig. 1. Study area with the 8 locations: southern Kaipara Harbour, Kawau Bay, Mahurangi Harbour, Karepiro Bay, inner Waitemata Harbour, Tamaki Estuary (TamakiE), Whitford Embayment and Tamaki Strait (TamakiS). Note that southern Kaipara Harbour opens to the Tasman Sea, all others open to the Pacific Ocean

Table 1. Summary of estuarine and habitat patch characteristics in each location. Splitting index values in the upper section of the table are for each (whole) location, the splitting index values in the lowest section of the table are for each habitat within a location. na = data not available

	Kaipara	Karepiro	Kawau	Mahurangi	TamakiE	TamakiS	Waitemata	Whitford
Area to high water (km^2)	440	4.6	121.5	24.6	11.7	310	79.8	14.4
% intertidal area	41.9	49	7.3	51.2	40	8.1	36.2	81.5
Tidal prism (km^3)	1.615	na	na	0.044	0.037	na	0.177	0.018
Simpson index	0.25	0.22	0.23	0.67	0.26	0.33	0.49	0.35
Splitting index	0.05	0.04	0.03	0.03	0.07	0.08	0.02	0.110
Number of patches								
Cockle	6	12	12	6	3	7	10	4
Macomona	11	6	3	3	1	6	7	6
Mud	6	12	10	14	8	6	21	8
Sand	13	7	12	4	4	15	16	6
Seagrass	10	na	2	3	1	3	na	na
Tubeworm	7	2	8	2	5	6	10	4
Average patch size (km^2)								
Cockle	1.67	0.03	0.17	0.12	0.03	0.19	0.10	0.25
Macomona	2.12	0.11	0.13	0.16	0.25	0.18	0.18	0.09
Mud	2.27	0.05	0.22	0.64	0.21	1.07	0.86	0.62
Sand	3.12	0.08	0.14	0.13	0.31	0.53	0.36	0.66
Seagrass	7.75	na	0.34	0.05	0.45	0.01	na	na
Tubeworm	3.95	0.16	0.06	0.08	0.18	0.23	0.12	0.09
Splitting index								
Cockle	0.01	0.02	0.07	0.01	0.001	0.01	0.01	0.01
Macomona	0.01	0.07	0.01	0.01	0.01	0.01	0.01	0.01
Mud	0.01	0.06	0.09	0.66	0.13	0.12	0.44	0.21
Sand	0.04	0.05	0.05	0.01	0.07	0.19	0.04	0.13
Seagrass	0.16	na	0.01	0.001	0.01	0.001	na	na
Tubeworm	0.02	0.02	0.01	0.001	0.04	0.01	0.01	0.001

mud and sand flats; cockle beds, tube worm beds and seagrass meadows represented biogenic structured habitats; and *A. stutchburyi* and *M. liliana* are both bioturbators and thus represented bioturbated habitats.

The distances between locations were determined by GIS and were measured as the shortest distance along the coastline between estuary mouths or embayment boundaries.

Sampling. Although the sampling at the 8 locations was conducted for various purposes and in different years (between 1999 and 2006) and months (in summer, between November and February), a 13 cm diameter/15 cm deep corer was used in every instance. Different mesh sizes (either 1 or 0.5 mm) were used among the studies, but both sizes were used in 4 of the studies, enabling data correction for inter-study calibration. Species found only on 0.5 mm mesh sieves were removed from the data sets and counts were converted to presence/absence.

Between 3 and 9 sites were available for each habitat type within each location. For all but the largest of seagrass meadows, sites were located in different patches of a habitat. The number of core samples collected at a site varied from 3 to 12; however, 3 samples were randomly chosen at those sites with more samples to avoid an unbalanced design. Data from the 3 samples per site were pooled in order to obtain a minimum sample size and the sites within each habitat were considered as replicates. In all studies, the benthic macrofauna had been identified in the same laboratory to the same taxonomic level (generally species) and counted.

Diversity calculations. *Alpha diversity*: The species richness at each site (*S*) was calculated with PRIMER (Clarke & Warwick 1994), and was used to determined average species richness for each habitat at each location.

Gamma diversity: The total species richness at the habitat scale was determined by prediction as it is highly dependent on the number of samples and patches sampled. To calculate this, species accumulation curves were derived for each habitat within each location using the Mao Tau estimation available in Estimate S (Colwell 2001) and a best-fit curve (generally a semi-log or log-log function) was obtained. Although few species accumulation curves reached an asymptote, the species richness predicted to be obtained with 100 samples was selected as the γ species richness value, given that the degree of separation between curves was more-or-less established by 100 samples. Below this point some of the accumulation curves cross, with the result that within each location the habitat holding the highest γ might be different to the habitat holding the highest α (e.g. Mahurangi in Fig. 2).

Beta diversity: The heterogeneity of species richness occurring within each habitat (β) was calculated as the difference between γ and α diversity indices, i.e. $\beta = \gamma - \alpha$

(Lande 1996, Crist et al. 2003). This definition, rather than γ/α (Whittaker 1960), was used as more accurately representing within-site heterogeneity (Vellend 2001).

Local vs. regional factors controlling diversity indices. Initially we were interested in whether there were any consistent differences between the diversity of habitats defined by structuring organisms and those defined solely by sedimentary features. A 2-way ANOVA (SPSS v.17) was used to detect differences in α diversity between habitats as fixed factor (6 levels, each habitat included as a different level of the factor habitat) and locations as random factor (8 levels corresponding to locations) and the significance of the interaction term of both factors. A Bonferroni post-hoc test was done for pairwise comparisons between habitat types. For γ and β diversity (which had no within-habitat replication) Friedman's rank test was used to test whether the relative ranking in diversity between habitats was similar across locations.

Next we were interested in the importance of regional species pools estimated as differences in diversity between distant locations. We considered that we had 2 distinct regional species pools; the east coast (Pacific Ocean) and the west coast (Tasman Sea) of New Zealand. The analysis showed whether there was a consistent difference between Kaipara, the only west coast location, and the remaining east coast locations. We also thought that there might be a gradual change in the available species along the 70 km distance between the most northern and southern locations on the east coast. To determine whether east coast locations closest to one another were more similar in their estimates of diversity than those further apart, we used Pearson correlations (with α = 0.05).

Finally, multiple regression was used to identify which, if any, of the environmental variables best predicted the observed pattern in diversity indices across locations. Some of the variables included in the analysis were the same for each habitat type within location, and comprised those based on estuarine areal information (i.e. area to high water, % intertidal, tidal prism) and estimates of heterogeneity or fragmentation (i.e. Simpson's diversity index and the splitting index, the latter defined as the sum across all habitats of individual patches divided by the total area of the habitat, a_{ij}/A_j squared). Variables that differed for each habitat type were number of patches, average patch size and an index of habitat division (p_i, calculated as the splitting index before summing across habitats).

Multiple regressions were constructed as generalized linear models with interactions between dependent variables and non-linearity of responses considered and included as necessary. The appropriate error structure was determined using visual inspection of half-normal plots of residuals and plots of residuals versus predicted
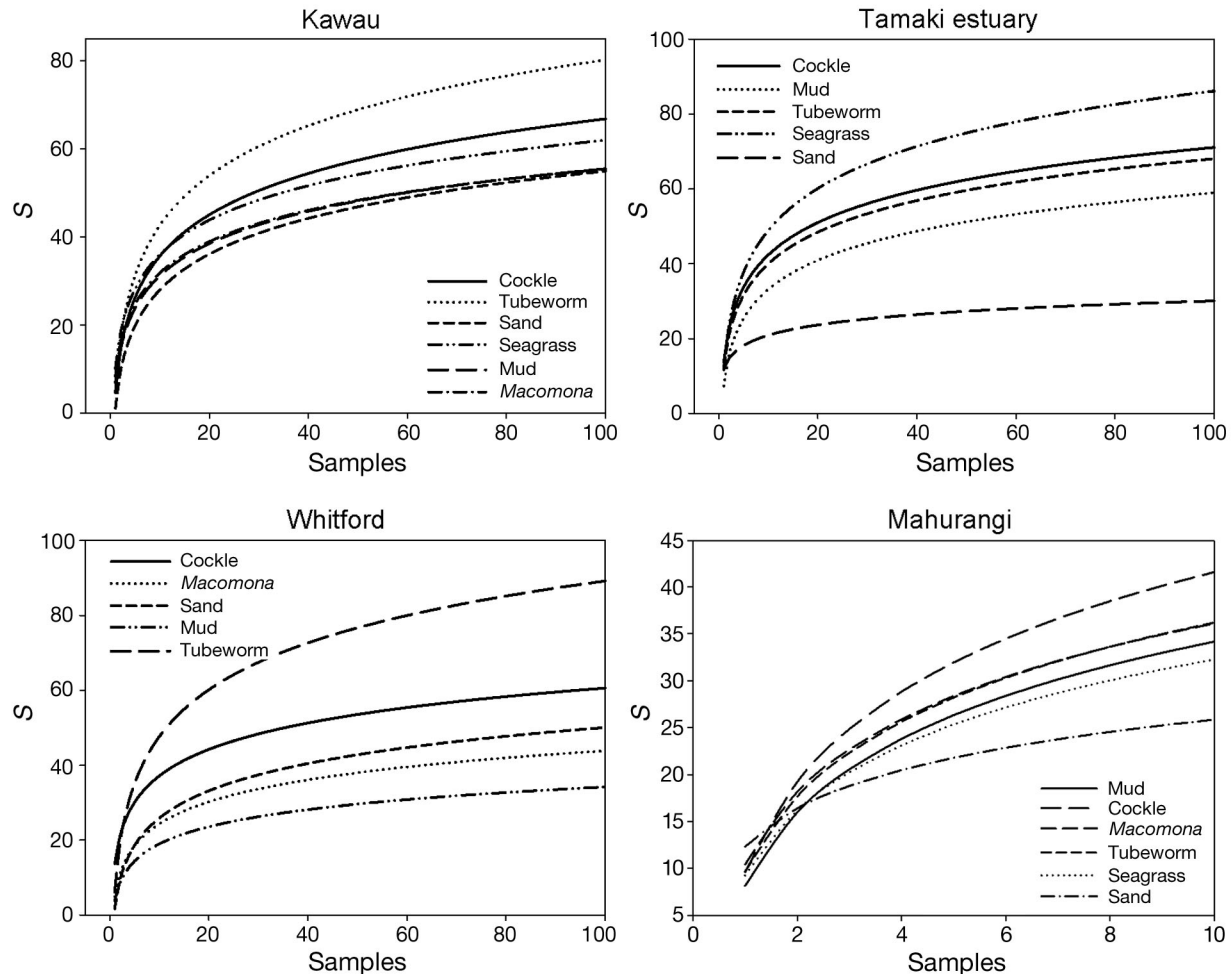
Fig. 2. Species accumulation curves (S = no. of species) at 100 samples per habitat. Results shown for Kawau, Tamaki estuary, Whitford and Mahurangi locations. Results for Mahurangi show the first section of the curves where the ranking in habitat diversity changes. Only 1 *Macomona* site was sampled at TamakiE, therefore this curve is omitted (estimation of curve too imprecise)

values. If overdispersion was indicated for Poisson error structures (Pearson chi-squared/df > 3), quasi-likelihood estimation was used. Backwards selection with an exit value of p = 0.15 was used to produce the most parsimonious model, defined using Akaike's Information Criteria (results of which were coincident with R^2 statistics). Co-linearity diagnostics were examined (Belsley et al. 1980) to ensure that highly correlated environmental variables were not included in the final model.

RESULTS

Diversity indices: α, γ and β

The 2-way ANOVA on α diversity (Table 2) showed significant differences among habitats, with a significant interaction with location, indicating that differences among habitats depended on the location (Table 3). The Bonferroni test determined a non-signif-

icant pairwise comparison for cockle vs. seagrass, *Macomona* vs. tubeworm and mud vs. sand. Nevertheless, no common pattern of differences between habitats was found across locations. Generally, habitats designated by fauna (i.e. cockle, seagrass, tubeworm and *Macomona*) held higher species richness than mud and sand habitats, with the exception of Mahurangi where diversity was similar across habitats (Table 2). Importantly, α diversity in Kaipara (open to the Tasman Sea) showed no consistent differences to the other locations, which open to the Pacific Ocean.

The comparison of γ diversity at the different habitats across locations showed a clearer pattern than α diversity, with generally higher diversity in the communities with habitat-structuring fauna (cockle, tubeworm and seagrass), and lower diversity in mud and sand habitats (Table 2). However, the Friedman rank test (Table 3) detected some significant differences in γ diversity across habitats. Kaipara again showed no significant differences to the other locations.

Table 2. α, γ and β diversity measures found in each location. γ at *Macomona* habitat in Tamaki estuary was not estimated due to the small sample size (1 site sampled)

	Location	Cockle	*Macomona*	Mud	Sand	Seagrass	Tubeworm
α diversity							
Kaipara	14.71	15.00	14.33	11.00	9.21	21.33	17.29
Karepiro	14.05	18.75	10.00	12.20	12.00	–	10.00
Kawau	14.26	15.56	16.00	13.25	10.13	20.50	14.00
Mahurangi	18.90	21.78	18.00	18.10	19.00	18.67	15.50
TamakiE	16.76	24.00	21.00	14.73	11.33	25.33	19.60
TamakiS	14.32	14.50	15.25	14.33	10.91	16.00	18.83
Waitemata	11.24	19.50	22.00	8.68	10.77	–	12.40
Whitford	14.40	21.67	11.33	8.25	9.80	–	20.00
γ diversity							
Kaipara	–	72.7	70.4	55.6	58.6	118.5	86.1
Karepiro	–	69.1	45	43.1	50	–	29.4
Kawau	–	66.7	55.4	55.4	54.9	61.9	80.1
Mahurangi	–	73.5	61.7	60.1	39.4	55.2	62.7
TamakiE	–	71.1	–	75.1	63.2	93.4	86.4
TamakiS	–	57.3	56.2	58.2	56.4	56.5	65.8
Waitemata	–	65.2	58.2	52.2	52.2	–	63.9
Whitford	–	60.6	43.9	34.2	50.1	–	89.2
β diversity							
Kaipara	–	57.7	56.07	44.6	49.39	97.17	68.81
Karepiro	–	50.35	35.00	30.90	38.00	–	19.40
Kawau	–	51.14	39.40	42.15	44.78	41.40	66.10
Mahurangi	–	51.72	43.70	42.00	20.40	36.53	47.20
TamakiE	–	47.08	–	60.36	51.92	68.11	66.84
TamakiS	–	42.80	40.95	43.87	45.49	40.50	46.97
Waitemata	–	45.70	36.20	43.52	42.43	–	51.50
Whitford	–	38.93	32.57	25.95	40.30	–	69.20

In general, β diversity showed the same pattern as γ diversity (Table 2), with the highest values at the habitats with structuring fauna (cockle, seagrass and tubeworm) and the lowest values in the purely sedimentary habitats of mud and sand (but occasionally in *Macomona* and seagrass). The Friedman rank test detected significant differences in β diversity across habitats (Table 3). The β diversity represented as a percentage of γ generally showed high percentages (Fig. 3), with all habitats having between 70 and 80%, with a few exceptions: 50% in sand habitat at Mahurangi, 15% in mud and 40% in *Macomona* habitats at Waitemata.

Table 3. Statistical tests for differences in diversity indices between habitats. ANOVA test for γ diversity (*F*-statistic) and Friedman's rank test for γ and β indices (chi-squared). *Significant at p = 0.05

	df	*F*/chi-squared	p
Alpha			
Location	7	1.85	0.096
Habitat	5	8.24	<0.001*
Location × Habitat	32	1.69	0.014*
Gamma	5	14.53	0.012*
Beta	5	12.93	0.024*

Relationship between diversity indices and distances between locations

Fig. 4 shows the total α, γ and β habitat diversities in each habitat plotted against the east coast locations arranged by increasing distance along the coastline. This visually demonstrates that differences between diversity indices at the locations are not related to the shortest distance along the coastline between adjacent locations. The Pearson correlation of distances between locations and α, β and γ diversities was not significant (p = 0.05).

Relationship between diversity and environmental variables

Some strong consistencies were observed in the variables that regression analysis selected as important predictors of diversity (Table 4). Patch size was frequently important, and diversity was always predicted to increase with increased patch size. Number of patches in a location was less frequently important, but diversity was always predicted to decrease as number of patches increased. The estuarine areal information was also important, always in a negative relationship,
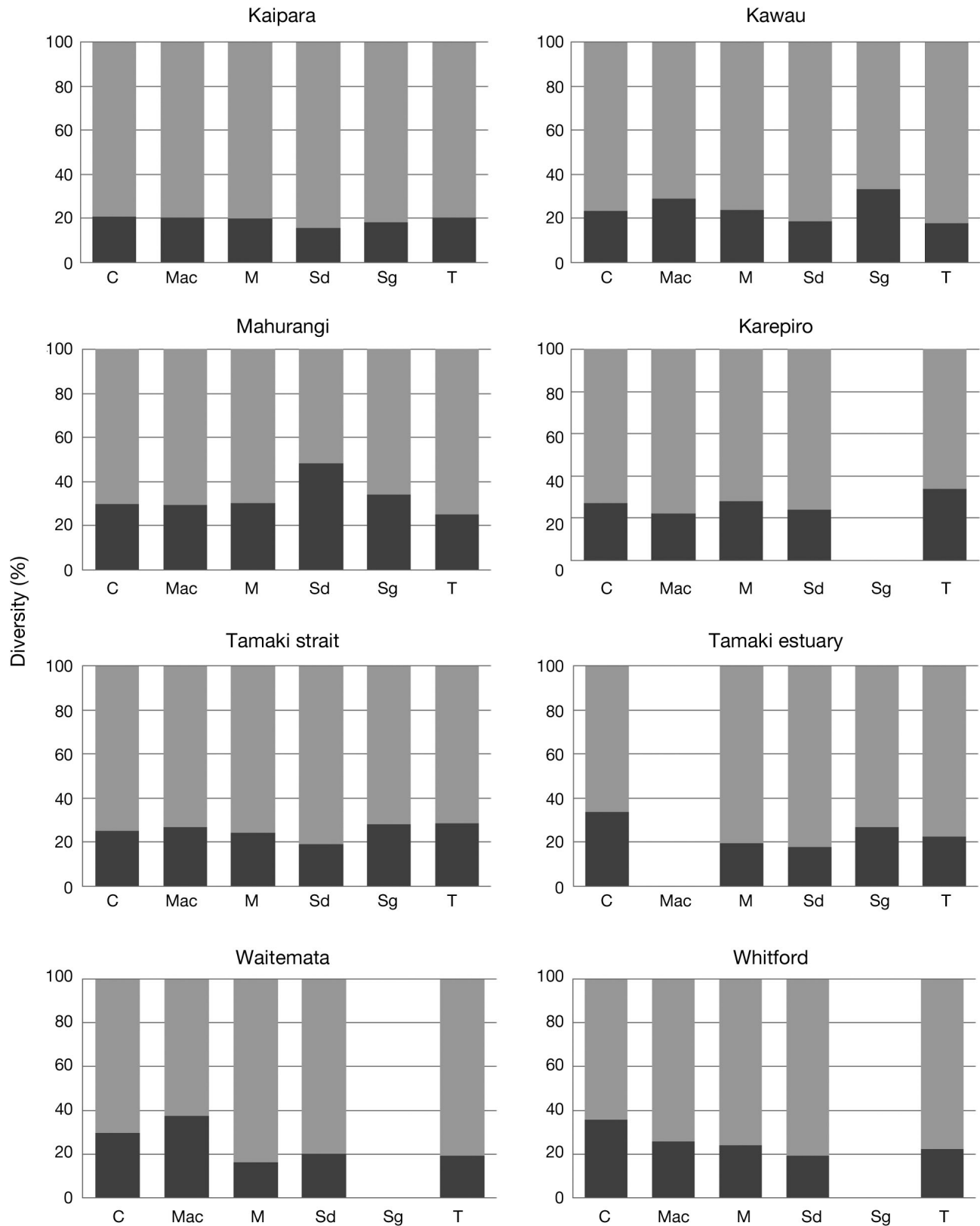
Fig. 3. β (light grey) and α (dark grey) diversity indices as a percentage of γ diversity. C: cockle, Mac: *Macomona*, M: mud, Sd: sand, Sg: seagrass, T: tubeworm
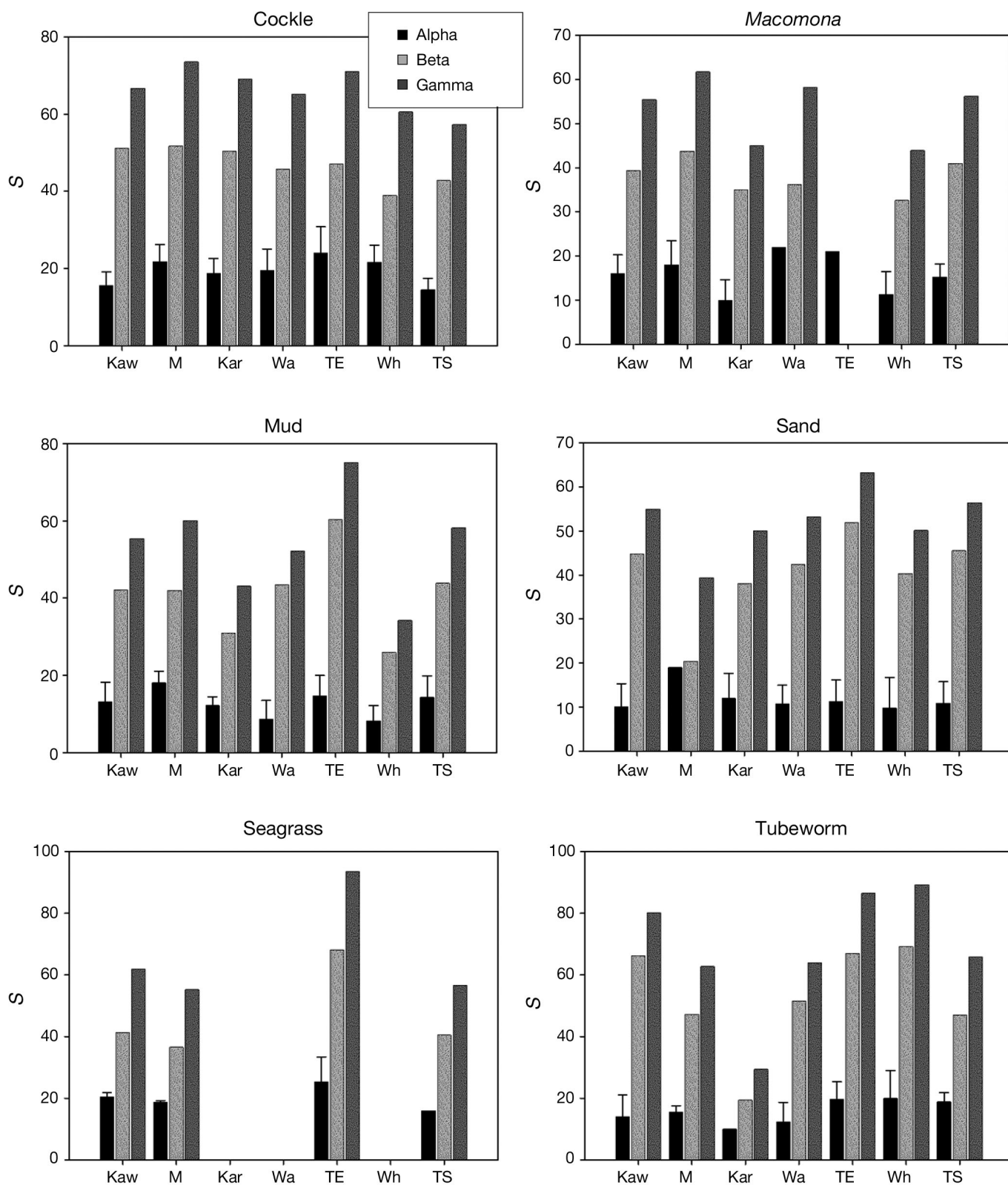
Fig. 4. α, β and γ diversities (*S* = no. of species) at each habitat plotted against east coast locations arranged by increasing distance from Kawau. Kawau (Kaw)–Mahurangi (M) 6 km (nearest edges), M–Karepiro (Kar) 31 km, Kar–Waitemata (Wa) 21 km, Wa–Tamaki Estuary (TE) 6.2 km, TE–Whitford (Wh) 6.8 km, Wh-Tamaki Strait (TS) <1 km (the kilometre values are distances between adjacent locations)

Table 4. Multiple regression analysis summary. Habitats in which diversity shows a positive or negative significant relation with the independent variables (Co: cockle, M: *Macomona*, Sg: seagrass, Sd: sand, Tb: tubeworm)

	Alpha	Gamma	Beta
Positive effects			
Patch size	Ma, Tb, Sg	Co, Ma, Sd, Tb, Sg	Co, Ma, Tb, Sg
Simpson's index	Sd		
Splitting index	Tb		
Negative effects			
No. patches	Co, Sg		Ma
Simpson's index		Sd	Sd
Splitting index	Ma		
Habitat division	Tb	Ma, Tb	Tb
Area to high water	Co	Co, Sd	Co
% intertidal		Co, Sd	Co
Tidal prism	Ma	Ma, Tb	Tb

and the actual measure of the estuarine area varied (area to high water, tidal prism, % of intertidal area). Indices directly representing fragmentation were also important, either at the location or habitat scale; those at the habitat scale always predicted a negative influence on diversity. Habitat fragmentation indices at the location scale were more variable. Habitat fragmentation was predicted to have a positive effect on species richness at 2 locations, for the rest it was predicted to have a negative effect. Variance explained by the models varies from 44 to 83 (Table 5) for all but the mud habitat; for this habitat no significant predictors were observed.

DISCUSSION

Differences in the effect of habitat types on α, β and γ macrobenthic diversity measures were not consistent across locations. However a general pattern emerged, with habitats with structuring fauna (cockle, tubeworm and seagrass) holding higher diversity than mud and sand habitats that lacked dominant habitat-defining species. The habitats dominated by the bioturbator *Macomona liliana* showed variable results. Although a similar pattern was generally observed for α, β and γ, in some locations some of the species accumulation curves crossed, shifting (between α and γ) the order of habitats holding the higher diversities (Fig. 2). Several variables were well correlated with the diversity measures, with patch size generally having a positive effect on diversity, and number of patches, habitat fragmentation indices, and estimates of area location having negative effects.

One of our most interesting findings was that the ranking of the effect of habitats on biodiversity was not consistent across locations. This was surprising as sea-grass is internationally considered to be a habitat with high biodiversity. New Zealand seagrass is, however, different to many of the seagrass habitats found in other countries. It comprises one species only (*Zostera mulleri*), that has relatively short blades (~15 cm long) and a sparse growth form, especially in the intertidal (Turner et al. 1996). Published New Zealand studies on the effect of seagrass on infaunal biodiversity show variable results. While some studies observe higher species richness in seagrass than other habitats (Henriques 1980, Alfaro 2006), a study conducted in multiple locations in 3 different months found variable results (Turner et al. 1999).

However, some common patterns were observed. Mud and sand habitats represent the homogeneous sedimentary seabed that generally holds lower diversity than those areas with a high density of habitat formers (Gray 2002, Thrush et al. 2006b). In this study, cockles, tubeworms and seagrass beds increased 3-dimensional complexity and these habitats were more likely to have higher average numbers of species (α diversity) than the other habitats. Cockle and tubeworm mat habitats were also more likely to have higher total numbers of species (γ diversity) living in the sediment around them. Cockles and tubeworms are also likely to increase sediment deposition, including organic matter which may benefit deposit feeders (Berkenbusch & Rowden 2007, Hewitt & Norkko 2007), and to stabilise the sediment (Widdows et al. 1998). Cockles, however, are also bioturbators, destabilising the sediment surface, which is often expected to have a negative effect on α biodiversity (Lohrer et al. 2008). The habitat based on the other bioturbator (*Macomona liliana*) in this study was associated with lower diversity. *M. liliana* feeds on the surface sedimentary layer, thus decreasing sediment stability and affecting sediment oxygenation and nutrient fluxes (Thrush et al. 2006b), effects which have been demonstrated to have a negative effect on a number of species (Thrush et al. 1992).

Regional species pools did not seem to be important for controlling the relationship between a habitat and its biodiversity, and differences in species richness of habitats between locations were not significant. This is in contrast to many studies that demonstrate variability in diversity at a regional scale related to latitudinal gradients and depth (Poore & Wilson 1993, Gray 2001). However, the scale of the study might be too limited (within the order of 10 to 100 km) to detect a regional gradient.

Table 5. Multiple regression summary, including model parameters and identifying variables that contribute to differences in diversity indices at each habitat type. Estimate = parameter slope estimate. A to high W = area to high water

Habitat	Diversity	R^2	Variables	df	F	p	Estimate
Cockle	Alpha	0.79	Model	2	30.66	0.0016	
			Error	5			
			Intercept	1	23.04	<0.0001	25.25
			No. patches	1	−4.40	0.007	−0.55
			A to high w	1	−6.68	0.001	−0.02
	Gamma	0.45	Model	3	2.74	0.177	
			Error	4			
			Intercept	1	12.83	<0.001	78.12
			% intertidal	1	−1.81	0.144	−0.21
			A to high W	1	−2.62	0.058	−0.08
			Patch size	1	2.81	0.048	22.26
	Beta	0.56	Model	3	4.06	0.104	
			Error	4			
			Intercept	1	11.10	<0.001	59.29
			Patch size	1	3.10	0.036	21.52
			% intertidal	1	−2.52	0.065	−0.26
			A to high W	1	−2.36	0.077	−0.06
Macomona	Alpha	0.64	Model	3	5.25	0.071	
			Error	4			
			Intercept	1	0.46	0.667	4.22
			Splitting index	1	−2.50	0.066	−74.7
			Tidal prism	1	−2.22	0.090	−0.12
			Patch size	1	2.03	0.112	15.37
	Gamma	0.76	Model	3	39.52	0.006	
			Error	3			
			Intercept	1	−1.47	0.237	−17.21
			Tidal prism	1	−4.82	0.017	−0.39
			Patch size	1	6.08	0.008	68.23
			Habitat division	1	−3.02	0.056	−127.08
	Beta	0.76	Model	2	68.87	<0.001	
			Error	4			
			Intercept	1	10.27	<0.001	20.02
			Patch size	1	9.89	<0.001	22.82
			No. patches	1	−3.93	0.017	−1.55
Sand	Alpha	0.44	Model	1	11.84	0.013	
			Error	6			
			Intercept	1	3.10	0.021	5.73
			Simpson	1	3.44	0.014	16.61
	Gamma	0.83	Model	4	7.71	0.063	
			Error	3			
			Intercept	1	8.05	0.004	52.58
			Simpson	1	−3.22	0.048	−28.56
			Patch size	1	2.72	0.072	16.17
			% intertidal	1	−2.51	0.087	−0.23
			A to high W	1	−2.16	0.119	−0.04
	Beta	0.53	Model	1	16.00	0.007	
			Error	6			
			Intercept	1	11.69	<0.001	60.78
			Simpson	1	−4.00	0.007	−54.25
Tubeworm	Alpha	0.85	Model	3	15.37	0.012	
			Error	4			
			Intercept	1	6.67	0.003	10.29
			Patch size	1	2.42	0.073	2.21
			Habitat division	1	−6.40	0.003	−453.2
			Splitting index	1	4.75	0.009	81.80
	Gamma	0.74	Model	3	7.90	0.037	
			Error	4			
			Intercept	1	12.82	<0.001	85.56
			Habitat division	1	−4.53	0.010	−2467.6
			Patch size	1	2.26	0.087	51.69
			Tidal prism	1	−2.02	0.113	−1.02

Table 5 (continued)

Habitat	Diversity	R^2	Variables	df	F	p	Estimate
	Beta	0.69	Model	3	6.34	0.053	
			Error	4			
			Intercept	1	10.52	<0.001	66.62
			Habitat division	1	−4.00	0.016	−2067.1
			Patch size	1	1.91	0.129	41.52
			Tidal prism	1	−1.69	0.166	−0.81
Seagrass	Alpha	0.83	Model	2	10.27	0.088	
			Error	2			
			Intercept	1	16.04	0.004	26.53
			No. patches	1	−4.42	0.047	−3.17
			Patch size	1	4.52	0.045	3.42
	Gamma	0.62	Model	1	11.47	0.043	
			Error	3			
			Intercept	1	4.03	0.027	45.72
			Patch size	1	3.39	0.043	23.05
	Beta	0.58	Model	1	9.62	0.053	
			Error	3			
			Intercept	1	2.51	0.087	28.24
			Patch size	1	3.10	0.053	20.93

In the absence of strong effects of regional species pools, local factors such as hydrodynamics, patch size, habitat fragmentation and anthropogenic activities are the most likely factors affecting how much biodiversity a specific habitat holds. We consistently found variables relating to local habitat fragmentation to negatively affect diversity in both the *Macomona* and tubeworm habitats. We also found the number of patches to have a negative effect on average species richness in cockle and seagrass habitats. Patch size had a generally positive effect on diversity in all habitats (except mud), probably through some interaction between hydrodynamics and a more stable community with higher patch area. The habitat fragmentation variables seem not to affect the species richness at the mud habitat, possibly because in many areas of New Zealand this habitat is increasing. Interestingly, the intertidal area was also generally important, with increasing intertidal area associated with decreasing diversity in most habitats. A plausible explanation is that the size of the intertidal may be related to the current flow and degree of wave activity, with lower species richness in wave-exposed areas (Gray 2002). Conversely, packing could be interacting with sampling design. Large shallow intertidal areas would allow species to pack less densely. As sampling takes place at a specific location along the intertidal slope gradient (mid-tide line and just below) less species would be collected. This would have serious implications for sampling estuary diversity as it would constrain assumptions about the relation between area sampled and species encountered.

The amount of variation in habitat diversity explained by local factors was generally good (45 to 85%), although there are many other factors that would likely increase explanatory power. For example, specific information on hydrodynamics, rather than the simplistic flushing rates that we used, could be expected to reveal the impact of both waves and currents on local biodiversity, since these would control the dispersal of organisms across beds of tubeworms and seagrass, and erosion in all habitats (Aller 1989, Turner et al. 1997). Anthropogenic factors, such as pollution and terrigenous sedimentation, are also likely to be important (Thrush et al. 2004), as may be density or biomass of the key species.

While γ diversity for each habitat across locations showed a similar pattern to the α diversity index, species accumulation curves for the different habitats in a location often crossed one another, thus ranking average species richness by habitat would not give the same result as ranking by γ diversity. This was particularly obvious for the seagrass habitat in Kawau which had high average species richness but low heterogeneity between sites, resulting in lower γ diversity than expected. This result highlights the importance of measuring diversity at a regional scale, and suggests that species richness calculated from point samples has the potential to mislead conservationists. Generally, β diversity was around 70 to 80% of γ diversity, representing more than half of the regional species diversity. This is actually an underestimation of the problem as our species accumulation curves did not reach an asymptote. Moreover, increasing the spatial scale at which diversity was measured (α to γ) did not result in local factors becoming less important. We still did not observe strong differences between locations that could be related to dispersal or oceanographic variables, as we anticipated from other studies (e.g. Turner

et al. 1997). Instead, patch size and habitat fragmentation were important at α and γ scales.

Species richness is often used in conservation planning to identify habitats with high diversity, for protection. However, habitat size and connectivity needs to be considered (Saura & Pascual-Horta 2007). This study underlines the importance of habitat fragmentation as having negative effects on diversity (particularly in cockle, *Macomona* and seagrass habitats), and the size of habitat patches having positive effects at all diversity scales and within all habitats. Marine soft sediments worldwide are being homogenised by anthropogenic activities that remove sediment structures and sessile fauna that increase the complexity of the seabed (Thrush et al. 2006b). The decrease of species richness, scaling from α to γ, linked with habitat fragmentation observed at the 8 locations, highlights the importance of reducing habitat fragmentation and maintaining connectivity patterns between habitats for marine ecosystem conservation.

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