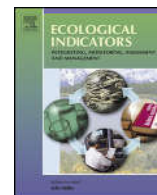




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Case Study

Macrobenthic–mud relations strengthen the foundation for benthic index development: A case study from shallow, temperate New Zealand estuaries

Ben P. Robertson^{a,b,*}, Jonathan P.A. Gardner^{a,c,d}, Candida Savage^{b,e}^a School of Biological Sciences, Victoria University of Wellington, Wellington 6140, New Zealand^b Department of Marine Science, University of Otago, Dunedin, New Zealand^c Key Laboratory of Freshwater Animal Breeding, Ministry of Agriculture, College of Fisheries, Huazhong Agricultural University, Wuhan 430070, PR China^d Freshwater Aquaculture Collaborative Innovation Center of Hubei Province, Wuhan 430070, PR China^e School of Biological Sciences, University of Cape Town, Cape Town, South Africa

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ABSTRACT

Globally the input of sediment to coastal systems, in particular to estuaries, is predicted to increase due to anthropogenic activities. Sediment mud content is a powerful driver of ecologically important, macrobenthic taxa in estuarine intertidal flats. Accordingly, forecasting species responses to increased sedimentation is fundamental for effective ecosystem management, particularly for productive, geologically young, and sand-dominated estuaries that characterise many countries, including New Zealand (NZ). Modelling studies have highlighted the non-linear, highly variable responses of taxa to mud concentration. However, existing taxon-specific models have not adequately accounted for the full mud gradient, the influence of potentially confounding variables (e.g. organic enrichment, heavy metal concentrations), or regional differences in species responses. Furthermore, such models are often based on qualitative expert consensus of the membership of taxa in ecological groups that characterise their sensitivity to mud content. In this study, data from 25 unmodified to highly disturbed, shallow NZ estuaries, were used to develop an ecologically relevant model to relate the responses of 39 taxa to sediment mud content for use in the intertidal flats of shallow, temperate estuaries. Preliminary analyses indicated that sediment mud content was the dominant driver of macroinvertebrate community composition among sites, total organic carbon was of secondary importance and heavy metals did not explain significant variation in composition. Regression analysis revealed a significant linear relationship between sediment mud and total organic carbon content, which permitted subsequent analyses to be based on mud content alone. Generalised additive models were used to develop taxon-specific models that, according to *k*-fold cross validation, accurately predicted both probability of presence (up to 79% deviance explained) and maximum density (up to 96% deviance explained) along the sediment mud gradient (0.1–92.3%). Estimates of “optimal mud range” and “distribution mud range” were quantitatively-derived for each taxon and used to categorise taxa into one of five ecological groups (identical to those used in existing biotic indices), based on their individual sensitivities to increasing mud content. By removing expert consensus from the grouping process, the classification methods established herein provide strong support for the use of quantitative indices for the assessment and management of estuarine condition in response to increasing sediment mud content. The findings indicate that NZ estuarine sediments (2–25% mud) support a more diverse and abundant macroinvertebrate assemblage and exhibit low organic enrichment (<1% total organic carbon) compared to estuaries with >25% mud content.

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1. Introduction

Changes in land-use and coastal development have increased rates of sediment inputs to estuaries (Thrush et al., 2004) and are expected to increase still further in many parts of the world (Halpern et al., 2008). The elevated delivery to and retention of terrigenous mud (<63 µm particle diameter) in estuarine systems

* Corresponding author at: Department of Marine Science, University of Otago, 310 Castle Street, Dunedin, New Zealand. Tel.: +64 3 4797496; fax: +64 3 4798336.
E-mail address: ben.robertson@postgrad.otago.ac.nz (B.P. Robertson).

can impair feeding, behavioural responses, larval recruitment, and trophic interactions in coastal food-webs (Norkko et al., 2002; Ellis et al., 2002; Cummings et al., 2003; Duarte et al., 2005; Jones et al., 2011; Vasconcelos et al., 2011). Consequently, quantitative models to forecast changes in macrobenthic community composition in relation to increasing mud content are important tools for estuarine monitoring and assessment programmes worldwide, including The European Water Framework Directive (WFD of the European Union 2000), New Zealand's National Estuarine Environmental Assessment and Monitoring Protocol (EMP; Robertson et al., 2002), and the United States Environmental Protection Agency National Estuary Programme (US EPA, 2009). Such information is particularly important in the context of shallow, intertidal, short water residence time (i.e. <1 day) estuaries (SSRTEs), which are vulnerable to sedimentation owing to the large area of intertidal habitat available for mud deposition and the subsequent enhancement of macroalgal blooms that affect estuaries in many countries, including New Zealand (NZ). To date, models of macrobenthic species-specific changes in abundance have established functionally variable, non-linear responses of taxa to increasing mud content (Norkko et al., 2002; Ysebaert et al., 2002; Thrush et al., 2003; Anderson, 2008; Sakamaki and Nishimura, 2009; Pratt et al., 2014). However, most taxon-specific models do not adequately account for the full mud gradient (with data often dominated by mud content <40%), for the influence of other potentially confounding variables (e.g. organic enrichment, heavy metal concentrations), or for regional differences in species responses. Accordingly, there is an urgent need for quantitative macrobenthic–mud response models that are conditioned on multi-estuary data, which represent a broad spatial scale (i.e. applicable at a national rather than regional level), comprehensive mud gradient, and more taxa with varying sensitivity across the full mud gradient.

An important, yet frequently overlooked, application of macrobenthic–mud models is their ability to inform various biotic indices that are commonly used to assess estuarine benthic condition (see review in Borja et al., 2012). These indices are based on the seminal research of Gray (1974), which focussed on animal–sediment relationships to describe habitat preferences of biological assemblages. These relationships were further developed to describe groups of taxa according to their different pollution tolerances (e.g. Pearson and Rosenberg, 1978; Borja et al., 2000). Despite their cost-effectiveness and apparent global application, such indices lack a strong quantitative foundation. For example, the widely used AZTI-Tecnalia marine biotic index (AMBI; Borja et al., 2000) and the more recent traits based index (TBI; Rodil et al., 2013), rely largely on qualitative expert consensus to categorise taxa into “ecological groups” (EGs), based on taxon-specific sensitivities to an increasing organic enrichment and heavy metal or mud gradient, respectively. Keeley et al. (2012) highlighted the subjective nature of expert consensus and sought to combine it with quantitative modelling approaches to assign individual taxa to EGs. However, like much of the AMBI list containing >6500 taxa, Keeley et al. (2012) assigned EGs on the basis of organic enrichment stress (i.e. specifically beneath subtidal finfish farms). Quantitative species-specific models that have focussed on sedimentation stress include the probability of occurrence and mean density (based on Generalised Linear Models; GLMs) (Ysebaert et al., 2002; Thrush et al., 2003; Sakamaki and Nishimura, 2009), and canonical analysis and quantile regression splines approach (Anderson, 2008). In the latter approach, models characterised change in assemblages using the maximum density (i.e. 95th percentile of the abundance distribution) of select species along an increasing mud gradient and allowed estimation of an optimum mud value (i.e. preferred mud content) for certain taxa. However, these models, and associated information (i.e. optimum mud values), are yet to be used to

strengthen the foundation of biotic indices such as the AMBI and TBI.

The primary objective of the present study was to develop quantitative models of macrobenthic–mud relations in shallow, temperate estuaries to improve understanding of species-specific responses to increased sedimentation. Secondly, these models of ecologically relevant “ranges” (Holt, 2003) were then used to categorise taxa into EGs, rather than relying on expert consensus. Analyses were first undertaken to distinguish the mud content gradient from other environmental gradients that are known to co-vary with mud and hence synergistically influence macrofaunal assemblages. Following this, building on the approaches of Thrush et al. (2003) and Anderson (2008), we employed a two-step procedure that utilised generalised additive models (GAMs – a flexible class of a generalised linear model based on backfitting with linear smoothers; Wood and Augustin, 2002) to predict the distributions and maximum densities of 39 common macrobenthic taxa along a mud gradient. The present dataset, based on 135 intertidal sites in 25 SSRTEs distributed throughout NZ and spanning ~12° of latitude, effectively expands the regional scale, mud gradient range and the number of taxa modelled in earlier studies. Then, using GAMs, an “optimum” (i.e. preferred mud range) and “distribution” (i.e. the mud range over which a given taxa was present) mud range was derived for each taxon. These two quantitative estimates then informed membership of taxa into one of five mud-specific EGs (groupings identical to those listed in the AMBI, representing 0.1–92.3% mud content), thereby strengthening the foundation and applicability of quantitative indices for the assessment and management of estuarine condition in response to increasing sediment muddiness. It is envisaged these EG classification methodologies are globally applicable (i.e. to SSRTEs outside NZ), and also could be used to group taxa in freshwater or terrestrial systems. However, since species occurrences and species-specific responses to increasing sediment mud content likely vary on a global scale, the models developed herein should be locally validated *a priori* before being applied to a new country. Overall, this study provides new information fundamental to improving current conservation and management standards that aim to safeguard the environmental integrity of temperate SSRTEs.

2. Materials and methods

2.1. Study locations and sampling protocol

This study focusses on the spatial (not temporal) variability in macroinvertebrate taxa among locations. In total, 135 locations in 25 estuaries, encompassing most of NZ (Fig. 1), were selected based on the criteria outlined in the National Estuary Monitoring Protocol (NEMP) (Robertson et al., 2002). The tidal rivers, lagoons, harbours and deltas surveyed represent a range of common estuary types (Table 1), with most characterised by relatively short water residence times (<1 day) and dominated by intertidal habitat (>90%, except the Firth of Thames, a large coastal embayment, which was added because it is characterised by 85 km² of intertidal habitat available for mud deposition); properties common to estuaries worldwide (e.g. Nicastro and Bishop, 2013; Sutula et al., 2014). The number of sampling locations within each estuary was allocated proportionately to each estuary's size and extent of intertidal mud and sandflat habitat. Large estuaries (≥30 km²) were generally allocated more locations (maximum of 6), while small estuaries (≤10 km²) were allocated fewer locations (e.g. 2). Sampling locations were chosen and the sampling protocol itself was carried out in accordance with the National Estuary Monitoring Protocol (NEMP) (Robertson et al., 2002). All sampling was conducted during the southern hemisphere summer (January to March) over a 13 year

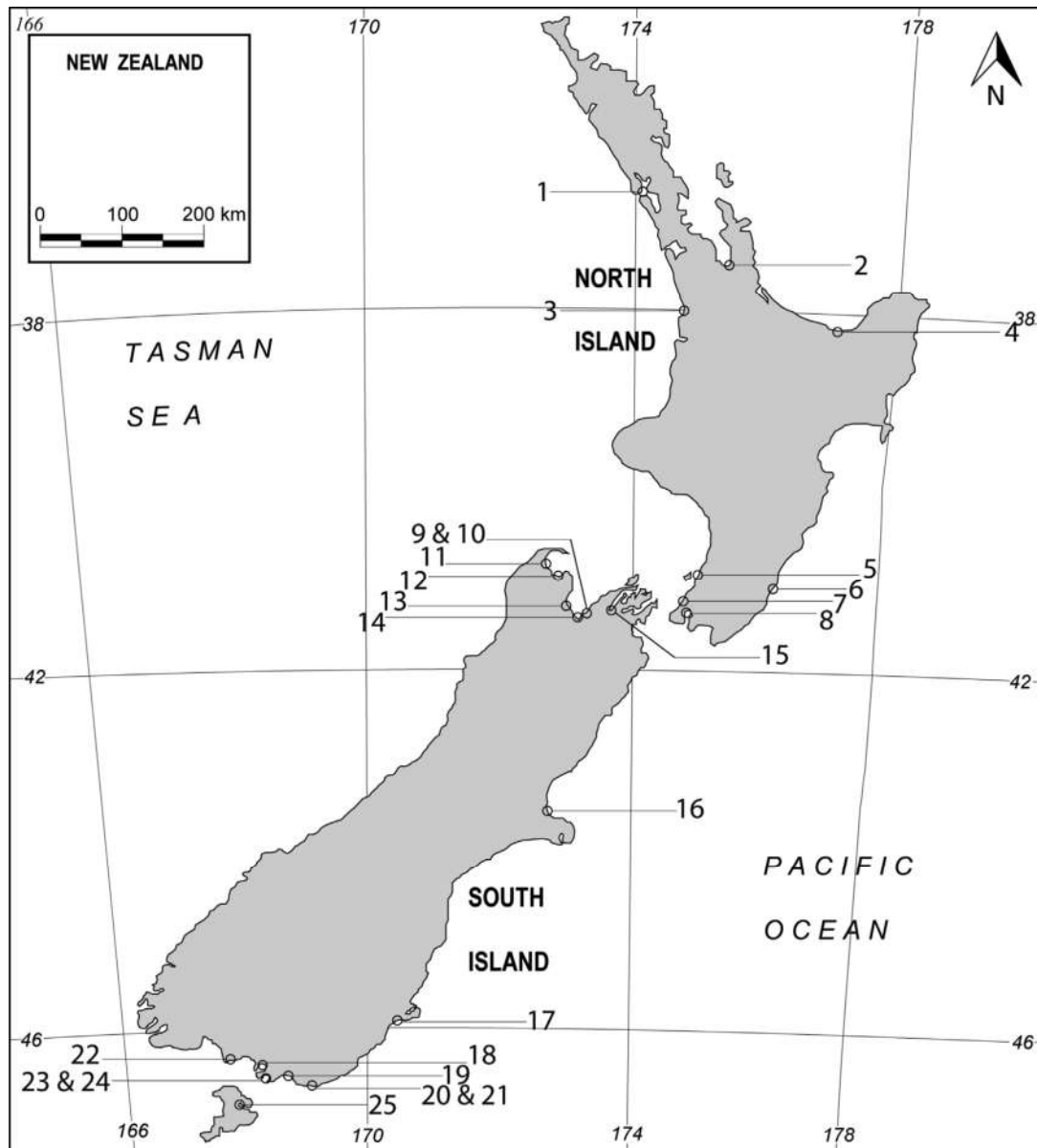


Fig. 1. Geographic locations of the 25 estuaries sampled throughout New Zealand. Refer to [Table 1](#) for number codes per location and for physical details corresponding to each estuary.

period (2001–2013). By targeting regions that represent the dominant habitat type of an NZ estuary (i.e. non-vegetated intertidal flats within mid to low tidal elevations), rather than subjectively selecting sites to encompass a full range of environmental conditions, the present data set provides an ecologically robust representation of NZ's SSRTes.

At each site, an area of 20×8 m for TRM estuaries, and 60×30 m for all other estuaries, was divided into a grid with twelve 'plots' of equal size. Within ten of the sampling plots, a random position was defined using random number tables and the following sampling undertaken.

From each location, apart from sampling in 2001–2005 which was conducted at a per plot level in 8 of the 25 estuary sites, three samples (two samples representing a composite from four plots, and one from two plots) of the top 20 mm of sediment (each approx. 250 g) were collected and subsequently analysed for: (1) grain size distribution (% mud, sand, gravel) using wet sieving and gravimetric calculations; (2) total organic carbon (TOC)

via catalytic combustion, separation, thermal conductivity detector (Elementary Analyser); and (3) heavy metal contaminants (total recoverable Cd, Cr, Cu, Ni, Pb and Zn) using nitric/hydrochloric acid digestion, ICP-MS (low level) USEPA 200.2. Composite sampling was considered robust as these samples were obtained by combining four individual samples taken from the same within-location plots as those sampled during plot-level sampling. Plot-level data were then averaged to reflect the composite-level situation. The specific metals analysed were selected because they provide a good indication of the potential for toxicity in urban estuaries ([Williamson and Morrissey, 2000](#)). Analyses were based on whole sample fractions, and were compared with the Australian and NZ Guidelines for Fresh and Marine Water Quality ([ANZECC, 2000](#)). We accounted for the potential negative influence of the measured heavy metals on fauna by excluding data from all locations where heavy metal concentrations exceeded biotoxicity criteria (refer to [Appendix A](#) for heavy metals data and associated biotoxicity criteria for each estuary).

Table 1
General features of the estuaries, harbours and embayments sampled. Abbreviations: 'Estuary type', TL = tidal lagoon, CE = coastal embayment, TRM = tidal river mouth, TRD = tidal river/delta, IB = island barrier (modified from Hume et al., 2007 to account for estuaries with significant delta areas, e.g. Freshwater); and for 'Dominant land use', P = pasture, NFS = native forest/scrub, EFS = exotic forest/scrub, Urb = urban (NIWA's Catchment Land Use for Environmental Sustainability model – CLUES 10.1).

Number code	Estuary	Region	No. of locations/sampling events ^a	Latitude	Estuary type	Estuary area (km ²)	Intertidal area (km ²)	Catchment area (km ²)	Dominant land use	Spring tidal range (m)
1	Kaipara (Otamatea Arm)	Northland	3, 1	36°18' S	TL	17	6.8	614	P	2.4
2	Firth of Thames	Waikato	5, 1	37°04' S	CE	721	85	4194	P/NFS/EFS	2.9
3	Raglan Harbour	Waikato	5, 2	37°45' S	TL	31	13.2	532	P/NFS/EFS	2.9
4	Ohiwa	Bay of Plenty	4, 1	38°00' S	TL	27	18.9	186	NFS/P	1.7
5	Waikanae	Wellington	1, 3	40°52' S	TRM	0.3	0.06	149	NFS/P	1.2
6	Whareama	Wellington	2, 3	41°00' S	TRM	1.1	0.1	531	P/NFS/EFS	1.3
7	Porirua Harbour	Wellington	2, 3	41°06' S	TL	8.2	2.8	171	P/NFS	1.0
8	Hutt River	Wellington	2, 3	41°14' S	TRM	0.3	0.1	635	NFS/P	1.1
9	Nelson Haven	Tasman	3, 1	41°13' S	TL	15	8.9	129	NFS/ENS/Urb	3.6
10	Delaware	Tasman	3, 1	41°09' S	TL	3.5	3.3	93	NFS/ENS/P	3.5
11	Aorere (Ruataniwha)	Tasman	3, 1	40°39' S	TRD	8.6	7.3	711	NFS	3.6
12	Motupipi	Tasman	2, 1	40°50' S	TL	1.7	1.6	41	NFS/P	3.6
13	Moutere Inlet/Delta	Tasman	2, 3	41°09' S	TL (IB)	7.6	7.2	182	EFS/P	3.6
14	Waimea	Tasman	4, 4	41°17' S	TL (IB)	33	29.5	913	NFS/EFS/P	3.6
15	Havelock	Marlborough	2, 2	41°16' S	TRM	8	1.6	1200	NFS/P	2.2
16	Avon Heathcote	Canterbury	3, 1	43°32' S	TL	7	6	188	Urb/P	1.8
17	Kaikorai	Otago	1, 1	45°55' S	TL	1.5	1.3	55	P/Urb	1.7
18	New River	Southland	6, 7	46°28' S	TL	46	34.1	4314	P	2.2
19	Fortrose	Southland	2, 4	46°34' S	TL	5	2.1	5520	P	2.1
20	Waikawa	Southland	2, 4	46°37' S	TL	7	5.7	237	NFS/P	2.0
21	Haldane	Southland	2, 5	46°38' S	TL	2	1.9	70	NFS/P	2.0
22	Jacobs River	Southland	5, 7	46°20' S	TL	7.2	5.6	1527	P	1.9
23	Awarua	Southland	2, 1	46°34' S	TL	27	21.3	50	NFS/P	2.0
24	Bluff	Southland	2, 1	46°33' S	TL	28	14.3	40	NFS/P	1.9
25	Freshwater	Stewart Island	2, 4	46°54' S	TRD	8.1	6.2	320	NFS	1.9

^a Indicates the number of locations and sampling events (at all locations) within each estuary site over the 13 year period (2001–2013).

Macrofaunal communities were sampled from each of the 10–12 plots using a 130 mm diameter (area = 0.0133 m²) core manually driven 150 mm into the sediment. Samples were sieved on a 0.5 mm mesh and retained fauna were preserved in 95% isopropyl alcohol/seawater solution. Macrofauna were identified to the highest possible taxonomic resolution and counted. In total, 96,803 individuals belonging to 208 macrofaunal taxa were recorded from the 135 sampling locations. To enable comparative analyses with the sediment characteristics, macrofaunal abundances were averaged relative to their corresponding sediment samples.

2.2. Preliminary distinction of sediment mud content from other environmental gradients

Initially, we distinguished the sediment mud gradient (0.1–92.3%; see Fig. 2 for cumulative frequency distribution) from the TOC gradient (0.08–3.8%) (Fig. 3) and sediment heavy metal concentrations (i.e. all heavy metals data combined on a single PCA axis generated in PRIMER v6), as the most powerful environmental gradient explaining patterns in the macroinvertebrate assemblage structure (all 208 taxa) among the locations sampled. The analysis utilised the BIOENV routine within the BEST function of PRIMER v6 (Clarke and Gorley, 2006), with the macrofaunal community based on Bray–Curtis dissimilarities of square-root transformed taxa abundance data, and the environmental gradient(s) based on Euclidean distance matrices. It revealed that the sediment mud gradient alone accounted for most of the variation

in macrobenthic assemblages among sampling locations (Spearman correlation = 0.31). When combined with the TOC gradient, the correlation decreased (Spearman correlation = 0.27). However, linear regression analysis indicated that the two gradients were strongly correlated ($R^2 = 0.71$; $P = 0.001$). The sediment heavy metal

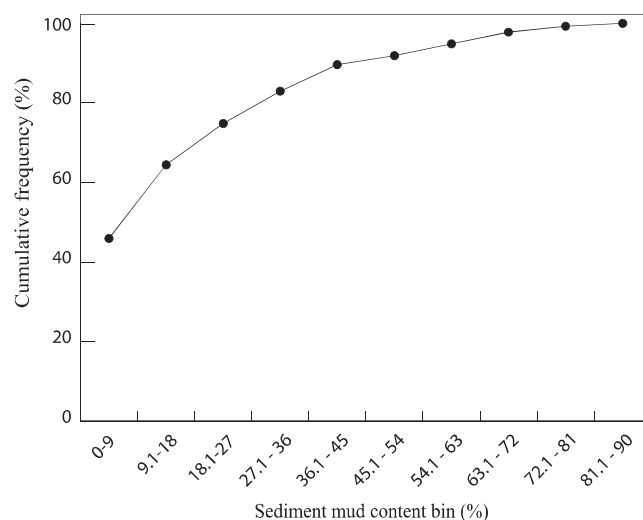


Fig. 2. Cumulative frequency plot showing the distribution of location-specific observations (%) within each mud concentration bin used to generate species-specific models.

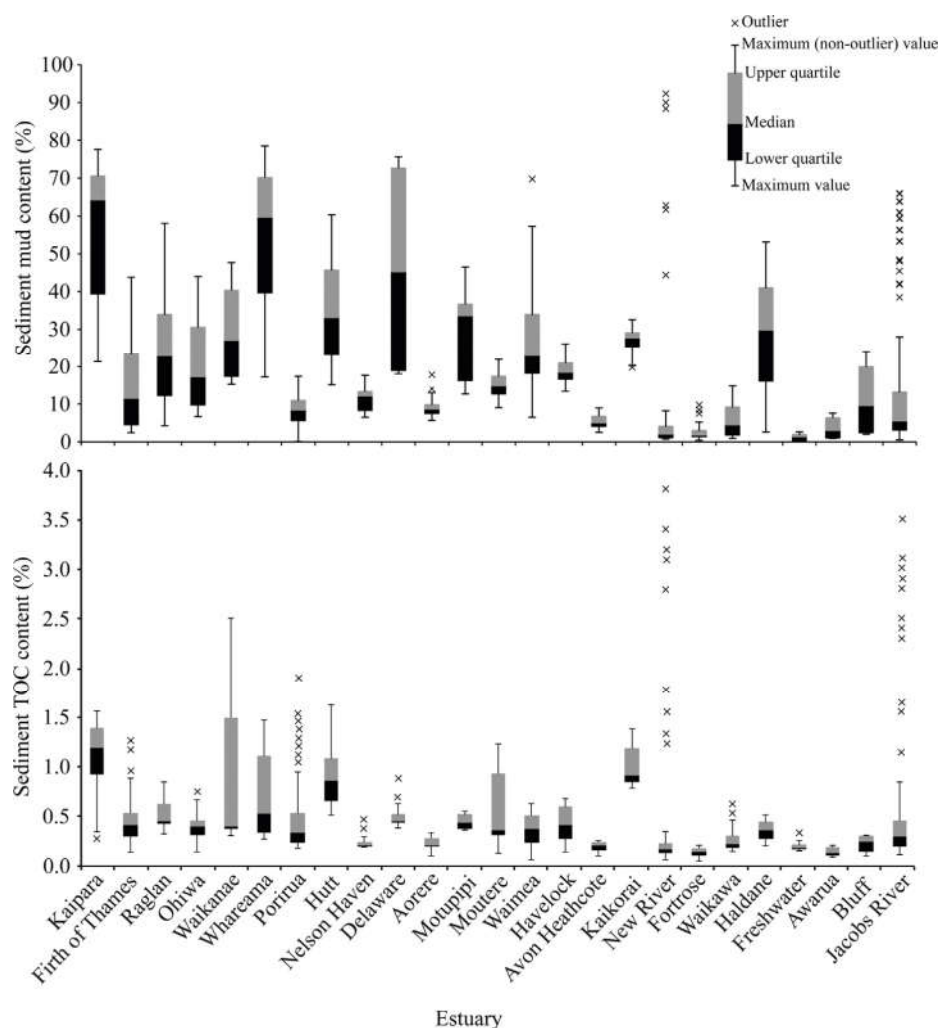


Fig. 3. Box plot showing the sediment mud (above) and total organic carbon (below) content ranges of the 25 NZ estuaries sampled.

gradient also showed a strong correlation with the mud gradient ($R^2 = 0.78$; $P = 0.001$), but was not distinguished with mud and TOC as a powerful macrofaunal explanatory factor, according to the BIOENV analysis. Overall, these results highlight the collinearity between the gradients of the three environmental gradients, and therefore support the development of taxon-specific models based on relations with the sediment mud gradient exclusively, since this was the best predictor. In addition, ANOSIM analysis revealed no significant (Global R: 0.14; $P > 0.05$) effect of region (i.e. region as defined in column 3 of Table 1) on the macroinvertebrate assemblages among estuary sites.

2.3. Modelling taxon-specific responses to sediment mud content

Generalised additive models (GAMs) were used to investigate the effects of sediment mud content on macroinvertebrate distributions and abundances. GAMs can be used to explore nonlinear relationships between dependent and explanatory variables, fitting non-parametric smoothers, and also permit implementation of several statistical distributions (Guisan et al., 2002). Of the 208 taxa recorded, taxa were considered for modelling if they were present at more than 10 of the 135 locations and in numbers greater than 2 individuals per core. This generated a dataset containing 96 taxa from which to develop models. Taxon-specific responses to increasing sediment mud content were modelled as a

function of their (1) probability of presence, conditioned on binary (macrofaunal presence/absence) data following a binomial distribution; and (2) associated density maxima, conditioned on the upper quartile of presence-only values following a gamma (link function = log) distribution, with 'sediment mud content' considered the main effect and 'estuary' a random effect in each model. For both model types, k (smoothing term) was selected based on both the deviance explained and visual assessment of model fit against the raw data, which ensured an ecologically realistic model fit. For models predicting taxon-specific density maxima, sediment mud content data were split into 10 equal bins, and the upper quartile of each taxon's abundance in each bin was determined, meaning that n varied considerably among taxa (i.e. 12–279). The upper quartile was modelled so as to account for the ecological 'ceiling factor' concept outlined in Thomson et al. (1996). For both model types, Bonferroni correction was employed to account for multiple testing and considered significant only for those taxa for which $P < 0.05/96 = 0.0005$. However, because this correction is known to be conservative (Carmel et al., 2013), the raw P -values (i.e. $P < 0.05$) were also documented. Preliminary assessment of the 96 models (based on model deviance and the statistical significance of the mud gradient as a reliable explanatory variable) resulted in the reporting of 39 (71,138 individuals) taxon-specific models. These 39 taxa represent a range of phyla, life-histories and functional groups that are common to the intertidal regions of NZ's estuaries

Table 2
General information on the 39 taxa selected for modelling in relation to sediment mud content. For taxonomic level, S = species, G = genus, F = family, O = order, C = class, P = phylum.

Taxa	Feeding type	Faunal group	Phylum	Taxonomic level
<i>Anthozoa</i> sp. 1	Surface predator	Anthozoa	Cnidaria	S
<i>Anthopleura aureoradiata</i>	Surface predator	Anthozoa	Cnidaria	S
<i>Edwardsia</i> sp.	Subsurface deposit-feeder	Anthozoa	Cnidaria	S
<i>Nemertea</i>	Surface predator	Nemertea	Nemertea	P
<i>Aglaophamus</i> spp.	Surface predator	Polychaete	Annelida	G
<i>Aonides</i> spp.	Surface deposit-feeder	Polychaete	Annelida	G
<i>Boccardia syrtis</i>	Surface deposit-feeder	Polychaete	Annelida	S
<i>Capitella</i> spp.	Subsurface deposit-feeder	Polychaete	Annelida	G
<i>Maldanidae</i>	Subsurface deposit-feeder	Polychaete	Annelida	F
<i>Microspio maori</i>	Subsurface deposit-feeder	Polychaete	Annelida	S
<i>Nereidae</i>	Surface deposit-feeder	Polychaete	Annelida	F
<i>Orbinia papillosa</i>	Subsurface deposit-feeder	Polychaete	Annelida	S
<i>Prionospio</i> spp.	Surface deposit-feeder	Polychaete	Annelida	G
<i>Sabellidae</i>	Surface suspension-feeder	Polychaete	Annelida	F
<i>Scolecoides</i> spp.	Surface deposit-feeder	Polychaete	Annelida	G
<i>Scoloplos cylindricus</i>	Subsurface deposit-feeder	Polychaete	Annelida	S
<i>Amphibola crenata</i>	Surface deposit-feeder	Gastropoda	Mollusca	S
<i>Cominella glandiformis</i>	Surface predator	Gastropoda	Mollusca	S
<i>Haminoea zelandiae</i>	Surface predator	Gastropoda	Mollusca	S
<i>Notoacmea helmsi</i>	Surface grazer	Gastropoda	Mollusca	S
<i>Potamopyrgus</i> spp.	Surface deposit-feeder	Gastropoda	Mollusca	G
<i>Zeacumantus lutulentus</i>	Subsurface deposit-feeder	Gastropoda	Mollusca	S
<i>Austrovenus stutchburyi</i>	Surface suspension-feeder	Bivalvia	Mollusca	S
<i>Cyclomactra ovata</i>	Surface suspension-feeder	Bivalvia	Mollusca	S
<i>Macomona liliana</i>	Surface deposit-feeder	Bivalvia	Mollusca	S
<i>Nucula</i> spp.	Surface deposit-feeder	Bivalvia	Mollusca	G
<i>Paphies australis</i>	Surface suspension-feeder	Bivalvia	Mollusca	S
<i>Amphipoda</i> spp. ^a	Surface deposit-feeder	Amphipoda	Arthropoda	G
<i>Amphipoda</i> sp. 1	Surface deposit-feeder	Amphipoda	Arthropoda	S
<i>Amphipoda</i> sp. 2	Surface deposit-feeder	Amphipoda	Arthropoda	S
<i>Austrominius modestus</i>	Surface suspension-feeder	Maxillopoda	Arthropoda	S
<i>Colurostylis lemurum</i>	Surface grazer	Cumacean	Arthropoda	S
<i>Cumacea</i>	Surface deposit-feeder	Cumacea	Arthropoda	O
<i>Exosphaeroma</i> spp.	Surface scavenger	Isopoda	Arthropoda	G
<i>Helice crassa</i>	Surface scavenger	Decapoda	Arthropoda	S
<i>Macrophthalmus hirtipes</i>	Surface scavenger	Decapoda	Arthropoda	S
<i>Ostracoda</i>	Surface scavenger	Ostracoda	Arthropoda	C
<i>Paracorphium excavatum</i>	Subsurface deposit-feeder	Amphipoda	Arthropoda	S
<i>Tanaid</i> spp.	Surface scavenger	Tanaidacea	Arthropoda	G

^a *Amphipoda* spp. does not include abundance data from *Amphipoda* sp. 1 or *Amphipoda* sp. 2.

(Table 2). All GAMs were generated in R (3.0.1 GUI 1.61 Snow Leopard build 6492) using the mgcv package (<http://cran.r-project.org/web/packages/mgcv/index.html>).

The predictive performances (i.e. accuracy) of taxon-specific models were evaluated by *k*-fold cross validation using the CVgam() function of the R package, gamclass (<http://cran.r-project.org/web/packages/gamclass/index.html>). This approach generates two estimates; first, a scale parameter (GAMscale) estimate based on the complete data, and second, an estimate of mean squared error scale parameter from cross-validation (CV-mse-GAM), and hence gives an unbiased estimate of accuracy. For a model to have a good predictive capacity, the mean square estimate will be slightly larger than the scale estimate, if the model assumptions (i.e. iid data) hold.

2.4. Classification of taxa into ecological groups

Initially, 'optimum' and 'distribution' ranges were calculated for each modelled taxon as a function of the sediment mud gradient (Fig. 4). The optimum was defined as the mud content ranges over which taxa exhibit their maximum density, and was estimated using the density maxima models. To achieve this, a cutoff point was set at the upper 40% of the raw (non-zero) abundance data, because this value provided a balance between mud content with low abundance (i.e. suboptimal conditions) and mud fractions with high abundance (i.e. highly preferred conditions) for all modelled taxa. Distribution range was defined as the mud concentration

range over which at least one individual occurred, and was obtained using raw abundance data.

To assign individual taxa to EGs (e.g. see Borja et al., 2000; Keeley et al., 2012), these ranges (based on their corresponding

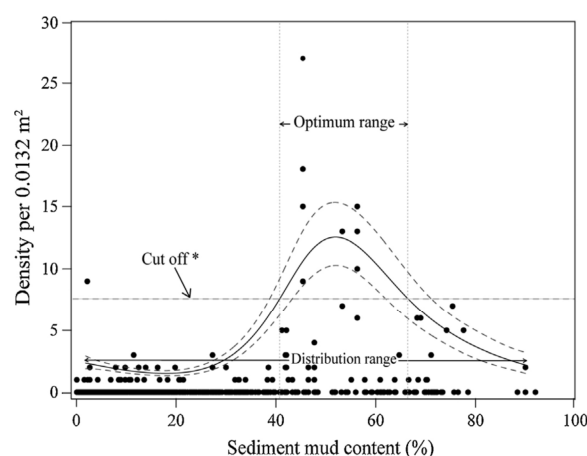


Fig. 4. Conceptualised estimation of an optimal and distribution mud range for a given taxon. The GAM shown is conditioned on the upper quartile of the presence only data (including 95% CI). Cut off * represents the taxon density at which the lower 60% meets the upper 40% of the raw (non-zero) abundance distribution, with the intersecting vertical grey lines indicating the taxon's optimum mud range. Raw abundance data overlaid, including zero values.

Table 3
Optimum and distribution mud subcategories used to assign (mud-specific) EGs to individual taxa.

Subcategory integer	Optimum mud range (%)	Distribution mud range (%)	Ecological group (EG)	Qualitative ecological interpretation
1	0–10	<40	I	Taxa highly sensitive to mud; present under predominantly sandy conditions
2	10–30	<60	II	Taxa sensitive to mud, but with an affinity for relatively low mud concentrations
3	Range >40 mud percentage units	<80	III	Taxa insensitive to mud; present at various mud concentrations
4	30–50	<90	IV	Taxa with an affinity for mud, but unable to tolerate elevated mud concentrations
5	50–100	<100	V	Taxa highly tolerant of mud with a strong affinity for elevated mud concentrations

subcategory integers; Table 3) were combined, then averaged, and any non-integers rounded either up or down towards the optimum subcategory integer. For example, a taxon exhibiting an optimum and distribution mud range of 12–18% (Optimum subcategory = 2) and 1–18% (distribution subcategory = 1), respectively, would be assigned to EG = II (based on $2 + 1/2 = 1.5$, and 1.5 rounded towards the optimum = 2), reflecting a taxon that is relatively sensitive to increasing mud content. The benefit to this approach was that it considered both the preferred mud range and the total mud range over which a given taxon was found, rather than considering only a single value along the mud gradient (e.g. Keeley et al., 2012), or only the distribution mud range (e.g. Norkko et al., 2002), both of which are likely less ecologically robust with respect to assigning EGs to taxa. Appendix B provides information on the remaining 57 taxa not selected for modelling, including optimal and distribution mud ranges, and assigned EGs, estimated by visual interpretation of their associated raw abundance data.

3. Results

3.1. Taxon-specific responses to sediment mud content

GAMs predicting taxon probability of presence over the mud gradient explained between 17.1% and 79.1% of the deviance of the binary data distributions. Predictive accuracy was high for all modelled taxa distributions (i.e. slight margin between GAMscale and *k*-fold MSE estimates), and sediment mud content was shown to be a significant predictor of species-specific presence and maximum density (Table 4). The GAMs developed for individual taxa exhibited seven broad functional forms, with no taxa responding monotonically (Fig. 5). Of these, positive response curves were generated for multiple taxa including *Scolecopides* spp., *Exosphaeroma* spp., *Potamopyrgus* sp., and negative response curves for *A. crenata*, *C. ovata* and *M. maori* in relation to increasing sediment mud content (see 'Functional response' numbers 4, 5 (negative) and 7 (positive) in Table 4 for taxa showing similar responses). Numerous taxa including *Nucula* spp., *Prionospio* spp., *Amphipoda* sp. 2, *M. hirtipes*, *Aonides* spp., *B. syrtis* and *M. liliana* exhibited Gaussian responses, indicating the highest probability of presence at intermediate mud concentrations (see 'Functional response' numbers 1, 2, 3 and 6 in Table 4 for taxa showing similar responses). It is important to note the differences in the magnitude of responses among taxa with respect to their probability of presence. For example, although the response curves for *M. liliana* and *Nucula* spp. exhibited similar functional forms, with the highest likelihood of presence between 5% and 25% mud content, *M. liliana* is ~25% more likely to be observed than *Nucula* spp. over this sediment mud range throughout the sampled estuaries.

GAMs constructed in order to predict density maxima along the mud gradient explained between 25.9% and 96.5% of the deviance in the abundance distribution, and for all models sediment mud content was a significant predictor (Table 4). Predictive accuracy was

relatively high (i.e. slight margin between GAMscale and *k*-fold MSE estimates) for most modelled taxa, but was reduced for *Anthozoa* sp. 1, *Taniad* sp. and *Austrominius modestus*, reflecting the low sample sizes of these taxa. Nevertheless, these responses, similar to the functional response of the models predicting probability of presence, varied considerably as a function of sediment mud content, and reflected seven broad functional response groups (Fig. 6). Of these, a positive response (*Exosphaeroma* spp.), a negative response (*A. modestus*; see 'Functional response' 5 in Table 4 for taxa showing similar responses) and Gaussian relationships (*B. syrtis*, *A. crenata*, *C. ovata*, *M. hirtipes*, *Prionospio* spp., *Scolecopides* spp., *M. liliana*, *Microspio maori*, *Nucula* spp., *Aonides* spp., *Potamopyrgus* spp. and *Amphipoda* sp.) were all recorded (Table 4). Notably, for taxa that exhibited a Gaussian response, which was the majority, there was substantial variation in the sediment mud content at which taxa exhibited their associated maximum densities. For example, both *Aonides* spp. and *Nucula* spp. occurred at greater densities in low mud content, whereas *Scolecopides* spp. and *Potamopyrgus* spp. showed preference for intermediate mud concentrations.

3.2. Assigning taxon-specific ecological groups (EGs)

Ecological group (EG) membership was derived for each taxon based on the optima and distribution range values for mud content calculated from the density maxima models (Table 5). Among the 39 taxa modelled, considerable variation existed in the extent of optimum mud range estimates (i.e. the width of the mud range) and also the upper limit of these ranges. For instance, 11 (28.6%) and 9 (23.8%) taxa revealed relatively narrow optimum ranges of <10 and <20 mud percentage units, respectively. In the former group, these were *Taniad* spp., *M. maori*, *Aonides* spp., Sabellidae, Cumacea, *H. zelandiae*, Maldanidae, *Z. lutulentus*, *Amphipoda* spp., *Amphipoda* spp. 2, and *Exosphaeroma* spp., of which 3 taxa appeared to be limited to mud concentrations <10%, 5 to concentrations <20%, 1 to a concentration <40%, and only 2 taxa exhibited an affinity for mud concentrations >60%. For the latter 9 taxa (23.8%), *O. papillosa*, *C. lemurum*, *S. cylindriker*, Ostracoda, *A. modestus*, *N. helmsi* appeared to be limited to mud concentrations <20%, *Anthozoa* sp. 1, *Nucula* spp. to concentrations <30%, and *A. aureoradiata* limited to sediment mud concentrations <50%. Most other taxa reflected wider ranges in mud optima; the ranges for 35.7% of taxa were <40 mud units and <70 mud units for the final 12% of taxa. Overall, the optimum ranges for 11 (28.2%) and 14 (35.9%) of the 39 modelled taxa were limited to mud concentrations <30% (i.e. EG = I and II, respectively), and the remaining 6 (15.4%) and 4 (10.2%) taxa were limited to mud concentrations <60% (i.e. EG = III or IV, respectively), and 4 (10.2%) to mud concentrations <95% (i.e. EG = V).

The taxon-specific optimum mud ranges and the optimum mud content values estimated in the present study were concordant with 80% of the corresponding taxa in Anderson (2008). By contrast, only 20% of the peak abundances estimated by Thrush et al. (2003) fell between the present optimum ranges for corresponding

Table 4
Summary of GAMs predicting probability of presence (conditioned on binary data, $n = 1403$), and maximum density (conditioned on the upper quartile of presence only values) for 39 macroinvertebrate taxa. For both model types, 'Sediment mud content' was considered the main effect and 'Estuary' a random effect. 'Deviance explained (%)' indicates the proportion of the variation explained by sediment mud content, and 'Mud significance (p)' reflects the significance of the effect of the sediment mud gradient. Numbers 1 to 7 under 'Functional response' correspond to the functional response of taxa numbered as in Figs. 5 and 6 (e.g. *Anthozoa* sp. 1 exhibits a similar functional response to *Boccardia syrtis*). Model 'accuracy' is reflected by differences between GAM scale and 10-fold MSE estimates, with a relative slight difference indicative of high accuracy.

Taxa	Probability of occurrence			Maximum density			n (k-folds) ^a
	Functional response	Deviance explained (%)	Mud significance (p)	GAM scale	10-fold MSE	Deviance explained (%)	
<i>Anthopleura aureoradiata</i>	1	56.6	0.005*	0.1302	0.1304	85.3	73
<i>Capitella</i> spp.	1	48.4	0.012*	0.1820	0.1835	78.7	99
<i>Scoloplos cylindricifer</i>	1	44.6	0.029*	0.1001	0.1002	62.7	45
<i>Cominella glandiformis</i>	1	17.1	0.005	0.1339	0.1347	45.5	77
<i>Nucula</i> spp.	1	59.5	3.43e-13**	0.1433	0.1443	84.7	84
<i>Colurostylis lemurum</i>	1	49.8	4.85e-08**	0.0672	0.0673	88.2	35
<i>Ostracoda</i>	1	54.2	6.34e-07**	0.0457	0.0457	88.4	28
<i>Nemertea</i>	2	20.2	1.87e-06**	0.2361	0.2386	25.9	247
<i>Nereidae</i>	2	45.6	0.013*	0.1861	0.1863	70.3	130
<i>Prionospio</i> spp.	2	52.7	0.012*	0.2142	0.2152	60.7	131
<i>Austrovenus stutchburyi</i>	2	38.3	0.001*	0.1888	0.1896	72.2	279
<i>Macomona liliana</i>	2	48.6	1.06e-15**	0.1949	0.1952	59.5	173
<i>Maldanidae</i>	3	57.0	0.021*	0.0465	0.0467	65.5	29
<i>Amphipoda</i> sp. 2	3	49.7	3.23e-09**	0.0378	0.0383	94.7	23
<i>Edwardsia</i> sp.	4	43.7	<2e-16**	0.1657	0.1665	43.4	112
<i>Microspio maori</i>	4	49.3	1.17e-11**	0.1417	0.1419	64.3	88
<i>Paphies australis</i>	4	40.6	<2e-16**	0.1510	0.1515	48.8	100
<i>Amphipoda</i> spp.	4	39.5	0.022*	0.2137	0.2140	70.2	142
<i>Cumacea</i>	4	51.0	0.001*	0.1330	0.1330	46.4	80
<i>Amphibola crenata</i>	5	29.4	0.002*	0.1300	0.1307	43.6	95
<i>Cyclomacra ovata</i>	5	31.6	0.014*	0.0374	0.0377	72.0	23
<i>Austrominius modestus</i>	5	36.9	0.002*	0.0144	0.0419	79.5	20 (6-fold) ^b
<i>Anthozoa</i> sp. 1	6	62.6	0.001*	0.0227	0.0228	83.5	12 (4-fold) ^b
<i>Aglaophamus</i> spp.	6	41.1	9.65e-07**	0.1254	0.1255	29.9	99
<i>Boccardia syrtis</i>	6	51.1	5.41e-12**	0.0867	0.0868	58.3	46
<i>Orbinia papillosa</i>	6	38.2	1.07e-09**	0.1337	0.1337	53.0	76
<i>Sabellidae</i>	6	46.8	0.001*	0.0403	0.0404	87.4	19 (5-fold) ^b
<i>Haminocera zelandiae</i>	6	58.7	0.045*	0.0193	0.0551	34.2	30
<i>Notoacmea helmsi</i>	6	40.2	0.024*	0.1234	0.1235	53.8	63
<i>Zeacumantus lutulentus</i>	6	41.2	0.012*	0.0422	0.0425	71.8	44
<i>Tanaid</i> spp.	6	68.0	3.01e-05**	0.0310	0.0312	64.3	16 (5-fold) ^b
<i>Potamopyrgus</i> spp.	7	47.1	2.97e-07**	0.1687	0.1696	66.8	81
<i>Amphipoda</i> sp. 1	7	41.4	1.22e-05**	0.1208	0.1219	64.0	57
<i>Helice crassa</i>	7	35.1	0.001*	0.0551	0.0561	72.5	46
<i>Paracarophium excavatum</i>	-	79.1	4.90e-07**	0.1227	0.1232	83.8	61
<i>Aonides</i> spp.	-	50.6	<2e-16**	0.1694	0.1695	90.8	102
<i>Scolecoplepides</i> spp.	-	35.9	0.006*	0.2191	0.2197	76.8	186
<i>Exosphaeroma</i> spp.	-	51.0	9.67e-07**	0.0546	0.0550	86.1	31
<i>Macrophthalmus hirtipes</i>	-	27.6	<2e-16**	0.1480	0.1487	77.5	117

^a n (k-folds) indicates the number of (upper quartile) samples used to condition the density models (n), as well as the number of folds used for model cross validation when n was too small to achieve 10-folds.

^b low model accuracy compared to those of species for which 10-fold cross validation was possible.

* Significance ($P < 0.05$).

** Bonferroni corrected significance ($P < 0.0005$).

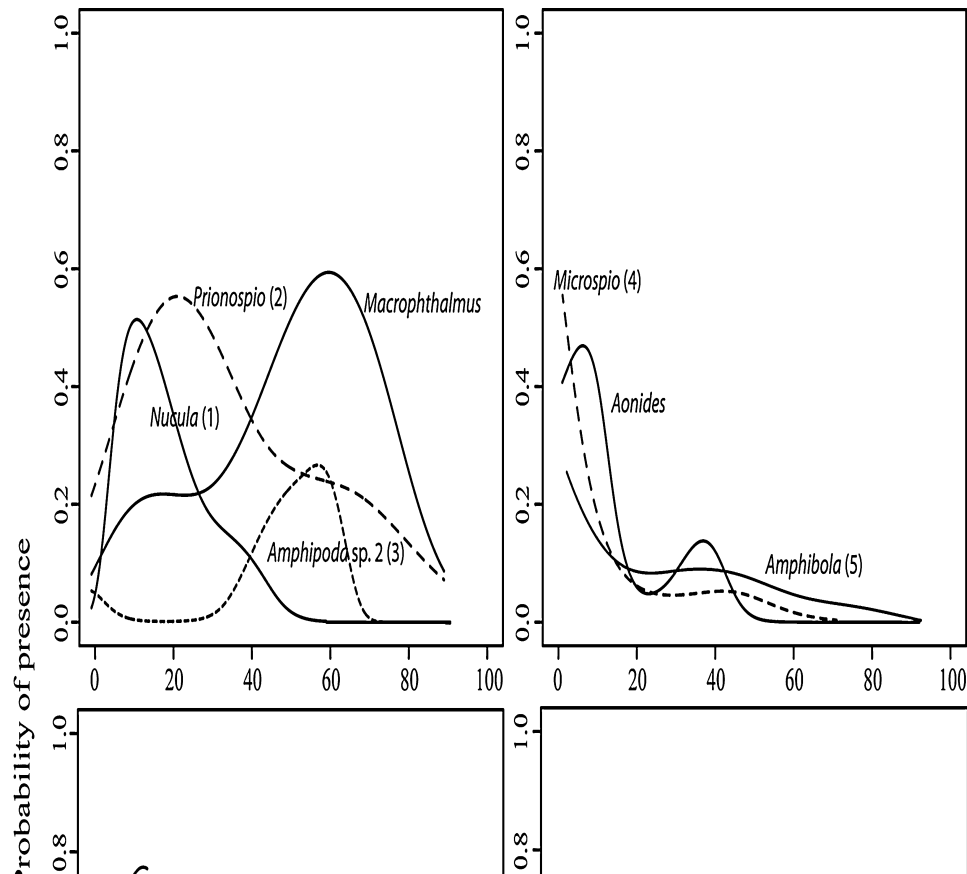


Fig. 5. GAMs predicting probability of presence for 15 macroinvertebrate taxa from 25 NZ estuaries in relation to sediment mud content. These taxa (full scientific names in Table 3) were selected as their functional response curves represent the full range of responses of all taxa. Numbers associated with particular taxa correspond to the functional response of certain taxa in Table 4. Taxa without numbers are those that exhibit unique responses.

taxa. In the latter case, discrepancies were apparent for 7 individual taxa (*S. cylindrifera*, *Aonides* spp., *B. syrtis*, *A. stutchburyi*, *Nucula* spp., *A. aureoradiata*, *H. crassa*). All of these taxa (except *A. aureoradiata*) occurred at lower mud concentrations in the Thrush et al. (2003) study (0–10%). Further comparison between the present optimum mud ranges and those characterised in Anderson (2008) also reveals differences among taxa. In the present study, *A. aureoradiata* exhibited a preference for intermediate (23.8–43.8%) mud concentrations, whereas Anderson (2008) reported that it occurred at lower (4%) concentrations of mud. By contrast, there was better agreement for *M. hirtipes*, which, in the present study, preferred elevated (44.1–68.5%) mud concentrations, while Anderson (2008) reported that it showed an optimum of 41.2% mud. Most of the taxa correspondence occurred at the species level (66.6% average between both previous studies), while 33.3% were at the genus level.

4. Discussion

Enhanced sedimentation rates and, in particular, increased muddiness (fine sediments <63 μm), can significantly alter estuarine ecosystem structure and function (Gacia and Duarte, 2001; Lohrer et al., 2004; Jones et al., 2011). Quantitative models that predict the presence and optimal density of macrobenthic taxa across a gradient of mud content provide valuable information to forecast species sensitivities to changes in sediment grain size. Using such models and data from 135 locations within 25 SSRTEs across New Zealand encompassing 0.1–92.3% sediment mud content, this study showed that (1) macrobenthic diversity and abundance was

greatest at low mud content; (2) highly accurate mud sensitivity models could be developed for 39 taxa; (3) associated species-specific ecological groupings based on mud sensitivity could be identified; and (4) the species-specific ecological groupings could be used to strengthen biotic indices and resource management decisions.

4.1. Taxon-specific responses to sediment mud content

4.1.1. Macrobenthic diversity and abundance greatest at low mud content

The sediment mud fraction was the dominant predictor of macrobenthic species composition, with more diverse and abundant macrobenthic communities occurring in sediments with low to intermediate mud concentrations (<25–30%). Below this threshold, a large proportion of taxa reflected relatively narrow optimal density ranges (<10%), thereby highlighting the vulnerability of estuarine macrofauna to inputs of fine sediment beyond natural levels. The results indicate that New Zealand SSRTE sediments with low to intermediate mud concentrations (2–25%) are more likely to contain diverse and abundant macrobenthic assemblages compared to areas where mud content exceeds 30%. This reflects the various direct and indirect effects of fine sediment deposition on benthic fauna (reviewed in Thrush et al., 2004). For example, models for the very sensitive, suspension-feeding sabellid fanworm polychaetes and the barnacle *A. modestus* exhibited optimal mud ranges <10% and <15% mud content respectively, whereas the upper limit of mud tolerance for the large-bodied suspension-feeding bivalves *Paphies australis* and *Austrovenus stutchburyi* was <40% and

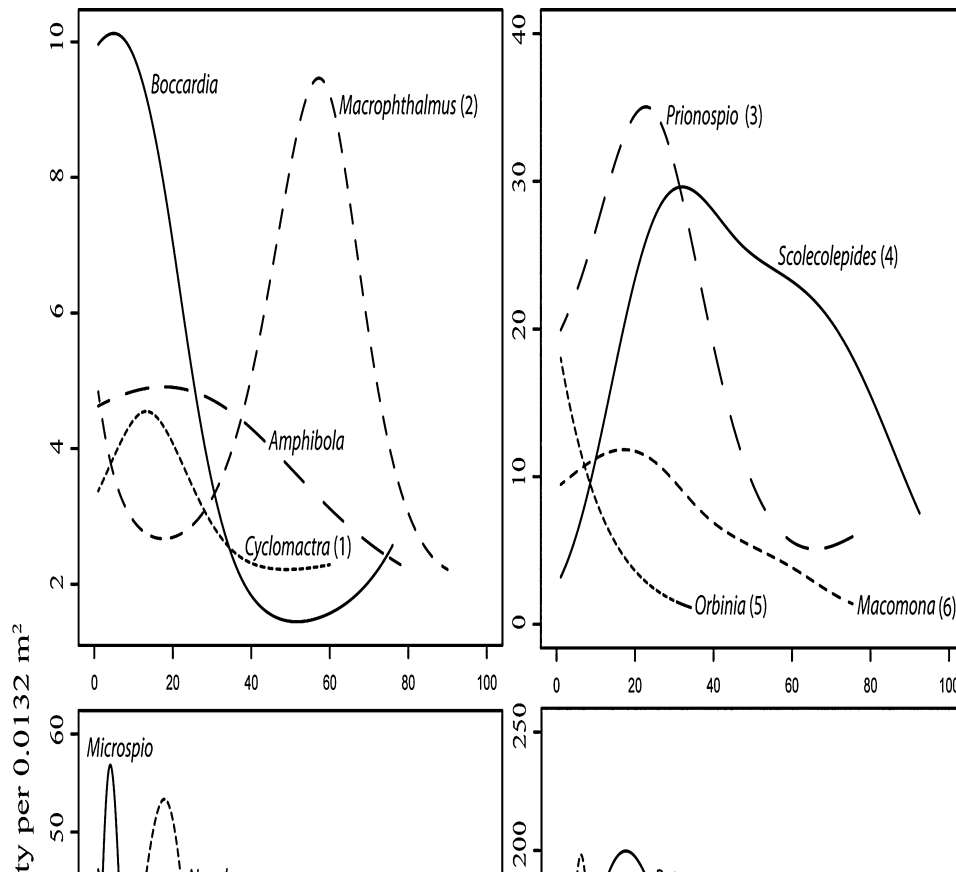


Fig. 6. GAMs reflecting maximum densities for 15 macroinvertebrate taxa from 25 NZ estuaries relative to sediment mud content. These taxa (full scientific names in Table 3) were selected as their functional response curves represent the full range of responses of all taxa. Numbers associated with particular taxa correspond to the functional response of taxa in Table 4. Taxa without numbers are those that exhibit unique responses. Models were conditioned on the upper quartile of presence only data.

<50%, respectively. By contrast, Anderson (2008) showed optimal mud content of 3.4% for *P. australis* and 11.3% for *A. stutchburyi*. This discrepancy is likely due to the varying upper limit of the mud gradient sampled between the two studies (i.e. Anderson (2008) measured up to ~40% mud, whereas the current study included sites with 92% mud); but nevertheless highlights the preference of the two taxa for relatively low mud content habitats. Since large suspension-feeding bivalves are key species that influence nutrient cycling and productivity in sediment habitats (Lohrer et al., 2004; Thrush et al., 2006) and positively influence functional diversity of associated macrofaunal communities (Savage et al., 2012), any direct negative effects of sedimentation on these species may lead to detrimental changes in estuarine ecosystem functioning (Thrush et al., 2006; Barbier et al., 2011).

4.1.2. High number of taxa modelled

According to the models, which had powerful predictive capacity (i.e. high accuracy for most taxa), sediment mud content generally explained high proportions of the deviance in distribution and maximum density of 39 common estuarine invertebrate taxa. This result supports the findings of Thrush et al. (2003), Anderson (2008) and Sakamaki and Nishimura (2009), and in turn highlights the importance of sediment mud content as a reliable predictor of the distribution and abundance of NZ estuarine macrofauna. Other studies, which have been limited to a narrower mud range (e.g. Mediterranean estuaries with mud content ~75%; Puente and Diaz, 2008), have not identified sediment mud content as the single best predictor of macrobenthic distribution, while some studies highlight factors such as tidal range, salinity and biomass of seagrass

as reliable predictors of macrobenthic assemblages (Edgar et al., 1999). Differences in tidal range can also have a strong affect on sediment mud content (Deloffre et al., 2007).

This study also showed that, while multiple taxa exhibited similar functional response curves for both optima and distribution models, models predicting the probability of presence of taxa generally exhibited a less constrained relationship with increasing sediment mud content compared to those predicting maximum density (e.g. see *Nucula* spp., *Prionospio* spp., *Scolecolepides* spp. and *Exosphaeroma* spp. in Figs. 4 and 5). This trend was likely due to macroinvertebrates occurring over a wide variety of estuarine habitat types (Edgar et al., 1999; Yozzo and Osgood, 2012; Barnes, 2013), whereas maximum densities tend to be reached only under restricted environmental conditions, otherwise known as the 'ceiling factor' concept (Thomson et al., 1996). Accordingly, the present results indicate that response curves based on taxon-specific maximum densities (i.e. conditioned on upper quartile data) are more sensitive and, hence, more robust in informing ecological group (EG) membership, relative to species presence per se (e.g. Leonardsson et al., 2015) and/or presence/absence data.

4.2. Assigning taxon-specific Ecological Groups (EGs)

The model outputs allowed classification of each of the 39 invertebrate taxa into one of five mud-specific EGs, based on the 'optimum mud range' and a 'distribution mud range' calculated from the maximum density plots and raw data, respectively. The functional response curves of the majority of macrofaunal taxa were in general agreement with Norkko et al. (2002), although

Table 5

Optimum and distribution percentage mud ranges and corresponding final mud-specific ecological group (EG) classification for 39 macroinvertebrate taxa. Optimum range indicates the percentage mud range over which taxa exhibit their highest abundances. Distribution range indicates the mud content range where at least one individual occurs. For Final EGs, I = highly sensitive; II = sensitive; III = widely tolerant; IV = relatively positive response; V = highly positive response to increasing sediment mud fraction.

Taxon	Optimum mud range (%)	Extent of optimum range (mud units)	Upper limit of optimum mud range (%)	Distribution mud range (%)	Anderson (2008) Optimum mud content (%) ^b	Thrush et al. (2003) Peak abundance mud content (%) ^c	Norkko et al. (2002) EG ^d	EG (this study)
<i>Tanaid</i> spp.	0.1–6.1	0–10	<10	0.1–35			II	I
<i>Orbinia papillosa</i>	0.1–14	0–20	<15	0.1–41.2			II	I
<i>Colurostylis lemurum</i>	0.8–11.6	0–20	<15	0.8–58	3.4 (3.4, 3.4)		II	I
<i>Microspio maori</i>	1.2–7.5	0–10	<10	0.7–56			–	I
Cumacea	1.6–10.2	0–10	<15	0.5–53			–	I
<i>Scoloplos cylindriifer</i>	2–16.1	0–20	<20	0.1–39.3		0	II	I
<i>Haminoea zelandiae</i>	2.5–12.3	0–10	<15	0.1–31			–	I
<i>Aonides</i> spp.	2.6–10.1	0–10	<15	0.6–45.6	7.9 (3.3, 16.1)	0	I	I
Ostracoda	3–15.9	0–20	<20	2–43.0			–	I
Sabellidae	3.5–10	0–10	<10	1.7–36.5			–	I
Maldanidae	5–13.2	0–10	<15	5.7–47.8			–	I
<i>Austrominius modestus</i>	0.1–11.4	0–20	<15	0.1–70.1			–	II
<i>Aglaophamus</i> spp.	0.9–24.5	0–30	<30	0.7–60.9			–	II
<i>Notoacmea helmsi</i>	1–19.5	0–20	<20	0.1–71.5			I	II
<i>Boccardia syrtis</i>	1–22.4	0–30	<30	0.8–76.5		~25	II	II
<i>Cyclomactra ovata</i>	1–26.1	0–30	<30	0.8–60.4			–	II
<i>Macomona liliana</i>	1–38.6	0–40	<40	0.1–75.4	16.6 (10.2, 26.4)	~18	II	II
<i>Paphies australis</i>	1–39.8	0–40	<40	0.1–75.7	3.4 (3.3, 4.5)		I	II
<i>Prionospio</i> spp.	2.9–38	0–40	<40	0.1–73.1			–	II
Anthozoa sp. 1	6.8–22.5	0–20	<30	7.9–51.7			–	II
<i>Austrovenus stutchburyi</i>	6.8–44.9	0–40	<50	0.1–80	11.3 (7.7, 14.8)	0	II	II
<i>Zeacumantus lutulentus</i>	7–17.1	0–10	<20	6.5–46			–	II
<i>Edwardsia</i> sp.	7–33.3	0–30	<40	0.1–71.1			–	II
<i>Nucula</i> spp.	8.8–25.1	0–20	<30	1–55.1	11.7 (10.0, 14.1)	0	II	II
<i>Amphipoda</i> spp.	8.9–37.5	0–10	<40	0.4–73.4			–	II
Nereidae	14–59.5	0–40	<60	0.9–77.6			IV	III
<i>Anthopleura aureoradiata</i>	23.8–43.8	0–20	<50	0.1–55		0	II	III
Nemertea	0.1–61.3	0–70	<70	0.1–75.4	1.0 (0.0, 10)		III	III
<i>Amphibola crenata</i>	1–53.1	0–60	<60	0.1–78.5			–	III
<i>Potamopyrgus</i> spp.	4.1–35.4	0–40	<40	0.5–92			–	III
<i>Cominella glandiformis</i>	5–75.0	0–70	<80	0.1–75.7			I	III
<i>Amphipoda</i> sp. 2	50.5–60.9	0–10	<70	0.1–65.9			–	IV
<i>Paracorophium excavatum</i>	12.6–54.8	0–50	<60	0.1–92			V	IV
<i>Scolecoplepides</i> spp.	15.1–75.5	0–60	<80	0.5–92			V	IV
<i>Capitella</i> spp.	20.7–55.3	0–40	<60	0.1–92			–	IV
<i>Helice crassa</i> ^a	38.9–70	0–30	<70	0.1–90	28 (3.4, 41.2)	~20	V	V
<i>Amphipoda</i> sp. 1 ^a	43.3–82	0–40	<90	0.1–92	41.2 (28.5, 41.8)		–	V
<i>Macrophthalmus hirtipes</i> ^a	44.1–68.5	0–30	<70	0.1–90			III	V
<i>Exosphaeroma</i> spp. ^a	84.8–92	0–10	<95	1–92.0	41.2 (28.5, 41.8)	88	–	V

Maximum density models and raw presence only values were used to extract values for taxa optimum and distribution ranges, respectively.

^a As most taxa were intolerant of mud content beyond ~40%, those which exhibited optimum ranges beyond ~40% were considered highly tolerant (i.e. EG = 5) of elevated mud concentrations.

^b Estimated optimum percentage mud (and 95% confidence interval) for taxa, based on abundance data collected from 7 upper North Island (NZ) estuaries (Anderson, 2008).

^c Percentage mud at which taxa exhibited peak densities (estimated visually) in 19 upper North Island (NZ) estuaries (Thrush et al., 2003).

^d Mud-specific ecological group classifications, based on taxa distributions in 1 upper North Island (NZ) estuary (Norkko et al., 2002).

mud-specific EGs ranked some taxa (only marginally) differently. For instance, the current study suggests that the numerically dominant polychaete *Aonides* spp., which exhibited optimum and distribution mud ranges between 2.6–10.1% and 0.6–45.6% respectively, is a taxon that is 'sensitive' to increasing sediment mud content, rather than the 'highly sensitive' rating it received in Norkko et al. (2002). Similarly, discrepancies in the EG classifications were apparent for some taxa that represent diverse feeding types (e.g. *Notoacmea helmsi*, *Paphies australis*, *Anthopleura aureoradiata*, Nereidae, *Cominella glandiformis*, *Paracorophium excavatum*, *Scolecoplepides* spp. and *Helice crassa*). These discrepancies likely arise for two reasons. Firstly, EG classifications developed in Norkko et al. (2002) were based on data from a single estuary located in the upper North Island, New Zealand, whereas the present study was based on a dataset representing a substantially larger spatial scale and variety of estuary types. Secondly, to provide additional flexibility for fitting curves to nonlinear relationships between macrofauna and mud content, the present study utilised GAMs,

while both Norkko et al. (2002) and Thrush et al. (2003) used General Linear Models (GLMs). GAMs were selected in this study for their capacity to more accurately represent animal–environment relations (Guisan et al., 2002).

According to Borja et al., 2012 and Rodil et al. (2013), macrofaunal–environment relations can be predicted based on groupings of lesser taxonomic resolution, such as faunal group and feeding type. Borja et al. (2012) suggest that high mud content sediments are typically characterised by detritus and deposit-feeding taxa. In the current study, however, few clear macroinvertebrate–mud relations follow a clear trend for feeding guilds. For example, of the four common surface deposit-feeding polychaetes (*Aonides* spp., *Boccardia syrtis*, *Prionospio* spp. and *Scolecoplepides* spp.), *Aonides* spp. was the most sensitive to increasing sediment mud content, while *Scolecoplepides* spp. was the most tolerant, with no predictable relationship in sensitivity for this feeding type. Apart from the three suspension-feeding bivalves (*Paphies australis*, *Austrovenus stutchburyi* and *Cyclomactra ovata*),

which all reflected an affinity to low mud conditions (EG=II), the lack of a uniform response at the faunal group or feeding type level in this research has implications for benthic indices or monitoring protocols that aim to assess the health of estuarine habitat based on low taxonomic resolution data.

4.2.1. Strengthening biotic indices and resource management

The development of highly accurate sensitivity information for a key estuarine indicator means that the foundation on which biotic indices such as the AMBI (Borja et al., 2000) and TBI (Rodil et al., 2013) are developed, can be strengthened by the use of quantitative models, rather than the frequently-used expert consensus approach, to assign individual taxa to EGs (e.g. Keeley et al., 2012.).

In terms of resource management, the mud-specific EG classifications developed herein are particularly important for SSRTes for two main reasons. Firstly, given that most NZ estuaries are dominated by sandy sediments, a legacy of the short period since the country was covered with native forest, the provision of mud-specific EGs for individual taxa that predominantly prefer sand is vital if sound management decisions are to be made. Without these comprehensive classifications, assessment of the ecological impact of sedimentation on NZ SSRTes would rely heavily on international groups for taxa that may not relate to local conditions. For example, the AMBI enrichment rating (Borja et al., 2000) for the spionid *Aonides* spp. is EG = III (enrichment tolerant) whereas the findings of this research place it in EG = I (mud and organic enrichment intolerant). Another example is the mobile crab, *Helice crassa*, where the AMBI enrichment rating and the Norrko et al. (2002) rating is EG = II (sensitive to muddy/organically enriched sediments), whereas this research places it in EG = V (highly tolerant of mud and organic enrichment). Because macrobenthic assemblages are considered good indicators of ecosystem health given their strong link with sediments, potential errors in the assignment of appropriate ratings to NZ taxa will invariably lead to faulty assessment of estuary condition.

Secondly, as alluded to above, the findings include two of the key environmental factors that could be contributing to the macrobenthic response, sediment particle size (often viewed as the primary controlling factor; Dauer et al., 2000) and total organic carbon (often viewed as the primary screening-level indicator of eutrophication; Hyland et al., 2005; Magni et al., 2009; Sutula et al., 2014). The results are particularly useful for management, in that they provide ecological groupings not just for muddiness but also, because of the strong correlation between the two variables, for increasing organic enrichment. Incorporation of these groupings into an estuary biotic index for mud and organic enrichment would provide regional authorities with both a means to rapidly assess current estuary condition and a screening tool to predict the likely ecological condition based on low cost monitoring of physico-chemical parameters. The strong need for such tools that aid in interpretation of state of the environment monitoring is supported, for example, by the recent move by NZ regional authorities to fund the

development of an estuary trophic assessment toolbox that includes the influences of mud and organic enrichment on biological communities (New Zealand EnviroLink Tools Project). Such tools are also being developed in other countries (e.g. California, USA; Sutula, 2011)

5. Conclusion

Inputs of mud (beyond natural levels) to estuarine intertidal flats have adverse implications for macrofaunal assemblages and associated ecosystem health. Consequently, robust tools to predict future ecological state along a gradient of sediment mud content, among other gradients (e.g. organic enrichment), are needed to enable informed ecosystem-level management. In this study, preliminary multivariate analyses confirmed that sediment mud content is a powerful predictor of macrobenthic taxa among the 25 NZ estuaries assessed. At the individual taxon level, the models of probability of presence and the maximum density for the 39 taxa assessed revealed a variety of functional response curves. These ranged from taxa that were negatively affected by increasing sediment mud content, through those which preferred intermediate mud concentrations, to a few taxa that showed a preference for elevated levels of mud. From these modelled relationships, 39 species were successfully classified into EGs, including a number of ecologically important macrobenthic taxa with narrow optimum mud ranges. In categorising taxa into groups, expert consensus was successfully eliminated, replaced by quantitative, less subjective methods, thereby strengthening the foundation of biotic indices such as AMBI and others that presently rely on expert opinion for species-specific EG classification. Overall, the findings indicate that NZ estuarine sites with 2–25% mud content support a diverse and abundant macroinvertebrate assemblage and low organic enrichment (<1% total organic carbon) compared to systems characterised by >25% mud. Such findings clearly support the future development of sedimentation guidelines for estuaries to address ongoing increases in mud content, in terms of both vertical and areal extent.

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Appendix A.

Estuary-level mean heavy metal concentrations (± 95 CI) from the 25 New Zealand estuaries sampled. NA indicates heavy metal(s) data not available for analysis.

Estuary	Cadmium (mg/kg dw)	Chromium (mg/kg dw)	Copper (mg/kg dw)	Nickel (mg/kg dw)	Lead (mg/kg dw)	Zinc (mg/kg dw)
Kaipara (Otamatea Arm)	0.96 (± 0.06)	27.50 (± 3.60)	14.54 (± 0.96)	10.91 (± 0.92)	19.83 (± 4.26)	86.90 (± 16.28)
Firth of Thames	NA	NA	NA	NA	NA	NA
Raglan Harbour	NA	NA	NA	NA	NA	NA
Ohiwa	<0.20 (NA)	7.44 (± 0.62)	4.00 (± 0.39)	3.90 (± 0.35)	5.32 (± 0.74)	27.69 (± 2.19)
Waikanae	0.04 (± 0.003)	12.77 (± 0.55)	7.38 (± 0.40)	10.19 (± 0.38)	10.14 (± 0.31)	44.80 (± 1.38)
Whareama	0.04 (± 0.002)	9.08 (± 0.32)	7.29 (± 0.49)	9.21 (± 0.38)	6.76 (± 0.28)	39.70 (± 1.81)
Porirua Harbour	0.03 (± 0.001)	8.00 (± 0.58)	3.81 (± 0.22)	5.76 (± 0.42)	6.55 (± 0.33)	39.13 (± 2.55)
Hutt River	0.05 (± 0.003)	14.34 (± 0.30)	9.46 (± 0.25)	11.93 (± 0.20)	16.74 (± 0.39)	67.53 (± 1.60)
Nelson Haven ^b	<0.10 (NA)	22.16 (± 0.98)	5.44 (± 0.32)	23.84 (± 1.17)	3.82 (± 0.12)	24.52 (± 0.96)
Delaware	<0.10 (NA)	43.07 (± 1.25)	11.00 (± 1.20)	17.20 (± 1.11)	3.82 (± 0.57)	44.07 (± 5.03)
Aorere (Ruatanuiwha)	0.20 (± 0.03)	24.02 (± 1.34)	7.08 (± 0.51)	13.69 (± 0.57)	6.09 (± 0.79)	37.50 (± 1.02)
Motupipi	0.03 (± 0.01)	35.00 (± 3.87)	7.72 (± 0.87)	22.30 (± 2.68)	5.09 (± 0.52)	35.90 (± 3.72)
Moutere Inlet/Delta ^b	0.02 (± 0.001)	32.53 (± 0.98)	6.62 (± 0.21)	71.82 (± 3.34)	4.47 (± 0.16)	29.51 (± 1.20)
Waimea ^b	0.17 (± 0.04)	54.13 (± 2.87)	8.98 (± 0.30)	73.71 (± 2.07)	6.93 (± 0.33)	37.19 (± 1.10)
Havelock	0.19 (± 0.06)	43.82 (± 5.78)	10.28 (± 0.44)	27.82 (± 3.35)	5.32 (± 0.35)	39.02 (± 2.76)
Avon Heathcote	<0.20 (NA)	15.63 (± 0.55)	3.19 (± 0.13)	6.60 (± 0.20)	6.33 (± 0.52)	38.23 (± 1.49)
Kaikorai	<0.20 (NA)	48.42 (± 0.95)	16.75 (± 0.69)	15.58 (± 0.61)	45.25 (± 1.16)	184.17 (± 6.13)
New River	0.26 (± 0.05)	13.60 (± 1.20)	6.42 (± 0.83)	8.38 (± 1.11)	4.96 (± 0.53)	35.59 (± 4.03)
Fortrose	0.54 (± 0.15)	4.93 (± 0.32)	2.08 (± 0.11)	3.25 (± 0.57)	2.40 (± 0.16)	24.62 (± 3.71)
Waikawa	<0.20 (NA)	7.41 (± 0.38)	2.45 (± 0.18)	4.41 (± 0.25)	1.59 (± 0.09)	11.78 (± 0.96)
Haldane	<0.20 (NA)	8.72 (± 0.74)	4.37 (± 0.44)	6.21 (± 0.55)	2.26 (± 0.16)	23.44 (± 2.11)
Jacobs River	0.28 (± 0.05)	11.11 (± 0.66)	14.67 (± 1.38)	7.85 (± 0.65)	4.54 (± 0.42)	41.69 (± 3.12)
Awarua	<0.10 (NA)	5.28 (± 1.36)	1.49 (± 0.39)	3.26 (± 0.59)	1.19 (± 0.27)	12.37 (± 4.09)
Bluff	<0.10 (NA)	9.94 (± 1.69)	3.25 (± 0.58)	5.65 (± 1.19)	1.59 (± 0.22)	13.30 (± 4.61)
Freshwater	<0.10 (NA)	3.28 (± 0.14)	1.44 (± 0.04)	2.75 (± 0.08)	0.68 (± 0.02)	6.51 (± 0.20)
ISQG-Low trigger limit ^a	1.5	80	65	21	50	200
ISQG-High trigger limit ^a	10	370	270	52	220	410

^a ANZECC (2000) trigger limits.

^b Geologically nickel and chromium enriched catchment (Robinson et al., 1996; Rattenbury et al., 1998).

Appendix B.

Optimum and distribution mud % ranges and mud-specific EG classifications for the 57 taxa that were not considered for modelling. Both the optimum and distribution ranges were estimated through visual interpretation of the raw macroinvertebrate abundance data.

Taxa	Optimum mud range (%)	Distribution mud range (%)	Ecological group (EG)
<i>Abarenicola affinis</i>	5–10	5–10	I
Hesionidae	0–10	0–20	I
<i>Hemipodus simplex</i>	0–10	0–10	I
<i>Platynereis australis</i>	5–15	2–15	I
<i>Polynoidae</i> sp.	5–15	5–15	I
<i>Scolecopsis</i> sp.	0–10	0–25	I
<i>Sphaerodoropsis</i> sp.	1–5	0–6	I
<i>Spirobranchus cariniferus</i>	10–15	10–15	I
<i>Eatoniella olivacea</i>	5–15	5–15	I
<i>Micrelenchus tenebrosus</i>	0.1–20	0.1–40	I
<i>Xymene plebeius</i>	5.2–12.2	5–15	I
<i>Zeacumantus subcarinatus</i>	5–20	2–35	I
<i>Soletellina</i> sp.	1–15	0–25	I
<i>Amphipoda</i> sp. 3	5–10	4–25	I
<i>Callianassa filholi</i>	1–25	1–25	I
<i>Isocladus</i> sp. 1	0.5–5	0.5–15	I
Mysidacea	0–5	0–60	I
<i>Paravireia pistus</i>	0–5	0–5	I
<i>Trochodonta dendyi</i>	0.1–15	0.1–15	I
Turbellaria	0–10	0–55	II
Nematoda	2–12	0–60	II
Sipuncula	2–30	2–42	II
Ampharetidae	5–15	5–15	II
<i>Aricidea</i> sp.	2–35	2–60	II
<i>Armandia maculata</i>	5–20	2–45	II
<i>Axiiothella serrata</i>	0–15	0–15	II
<i>Boccardia</i> sp.	0–20	0–70	II
Dorvilleidae	10–20	0–18	II

Glyceridae	10–15	0–95	II
<i>Goniada</i> sp.	1–30	1–30	II
<i>Macroclymenella stewartensis</i>	5–15	1–44	II
<i>Owenia petersenae</i>	5–40	0–40	II
<i>Perinereis vallata</i>	0–20	0–72	II
Phyllodocidae	0–40	0–40	II
Syllidae	1–56	1–56	II
<i>Diloma subrostrata</i>	0–20	0–75	II
<i>Amphipoda</i> sp. 4	0.1–35	0.1–35	II
Copepoda	0.7–5	0.7–77	II
<i>Natantia</i> sp. 1	5–10	0–75	II
Phoxocephalidae	5–20	0.1–55	II
Spheromatidae	0.6–20	0.6–55	II
<i>Diptera</i> sp.	10–20	5–80	II
<i>Ceratonereis</i> sp. 1	35–80	35–80	III
Cirratulidae	2–55	1–70	III
<i>Heteromastus filiformis</i>	0–70	0–70	III
<i>Magelona</i> sp.	25–45	1–60	III
<i>Nicon aestuariensis</i>	15–55	0–90	III
Paraonidae	2–80	0–80	III
<i>Pectinaria australis</i>	0–55	0–75	III
<i>Perinereis camiguinoides</i>	2–70	2–70	III
<i>Polydora</i> sp.	2–78	2–78	III
<i>Spionidae</i> sp. 1	3–80	0–80	III
Oligochaeta	0–80	0–80	III
<i>Theora lubrica</i>	15–45	10–60	III
<i>Haliscarcinus</i> sp.	0.1–65	0.1–75	III
<i>Arthritica bifurca</i>	1–90	0.1–92	IV
<i>Amphipoda</i> sp. 7	37–92	2–92	IV

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