Predictive models of small fish presence and abundance in northern New Zealand harbours

Malcolm P. Francis [a,*], Mark A. Morrison [b], John Leathwick [c], Cameron Walsh [b], Crispin Middleton [b]

[a] National Institute of Water and Atmospheric Research Ltd, Private Bag 14901, Wellington, New Zealand
[b] National Institute of Water and Atmospheric Research Ltd, PO Box 109695, Auckland, New Zealand
[c] National Institute of Water and Atmospheric Research Ltd, PO Box 11115, Hamilton, New Zealand

Abstract

A broad-scale, small-fish survey was carried out in northern New Zealand inshore waters using beach seines. The survey covered 30 estuaries spanning ca 1000 km of coastline and three degrees of latitude. Correspondence analysis and cluster analysis were used to identify assemblages, and Generalized Additive Models (GAMs) were used to model the abundance and occurrence of individual species. We aimed to assess the utility of these models for making predictions. The results were mixed. Descriptive models of fish abundance performed well for four out of 12 species; for most other species, and species richness, the models described the data well but performed poorly to moderately under cross validation. Predictive models of fish abundance usually performed worse than descriptive models, but appeared reasonable for four species. Presence–absence models performed better overall than abundance models: descriptive models showed good performance for all 12 species, and predictive models performed well for eight species. For an independent data set, the models successfully predicted occurrence for five species. Water clarity, salinity and the amount of freshwater inflow were important predictor variables. Despite the limitations of our GAMs, they should be useful for planning intensive process-based research, and for guiding the management of human activities that impinge on coastal marine environments.
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1. Introduction

Estuaries and shallow, sheltered coastal embayments play a central role as nursery grounds for many inshore fish species (Gillanders, 1997; Kneib, 1997; Beck et al., 2001; Morrison et al., 2002; Heck et al., 2003). Numerous studies have been conducted at varying spatial and temporal scales to determine what species occur in such habitats, and in what quantity (Laegdsgaard and Johnson, 1995; Ronnback et al., 1999; Lazzari et al., 2003; Hindell and Jenkins, 2004). These studies have provided a basis for designing and executing intensive process-based studies, including experimental manipulations, and the testing of predictions. Despite this large body of work, the spatial scale of most studies has been relatively limited, and there are large gaps in our understanding of the spatial structuring of fish nurseries over a scale of 10s to 1000s of kilometres, including latitudinal effects (but see Vieira and Musick, 1993; Edgar et al., 1999). Reasons for this include the complex field logistics and high costs of such work, divisions across state and legislative boundaries in and among some countries (with associated geographic funding constraints), and a strong individual researcher focus on fine scale process-orientated studies. While the

* Corresponding author.
  E-mail address: m.francis@niwa.co.nz (M.P. Francis).

ultimate goal of ecological science is to understand what processes produce the observed species and assemblage patterns, without an appropriate description of distributional patterns, our ability to conduct such studies is severely hampered (Underwood et al., 2000).

Broad-scale ecological surveys are fundamental for the development of large-scale descriptive and predictive models of fish presence and abundance. Within such a quantitative framework, a wide range of management activities can be more effectively executed, including the placement of Marine Protected Area networks (Conover et al., 2000), spatial zoning of different permitted fishing activities (Rice and Cooper, 2003), controls on land-based activities to reduce sediment run-off and pollutant contamination (Delvalls et al., 1998), and regulating recreational use of the coastal environment (Coleman et al., 2004). More intensive, process-based research can then be targeted at those elements considered essential (or representative, unique, rare), and the findings of such work scaled up to the overall framework (Zacharias et al., 1998; McCormick et al., 2000).

With the wide adoption of Geographic Information Systems (GIS), the intensive use of spatial data is now tractable. In both terrestrial (e.g., Kulakowski et al., 2004) and freshwater (Toepfer et al., 2000; Wyatt, 2003) ecosystems, GIS are now important tools for research and management. The use of these tools in estuarine and coastal ecosystems is less advanced but is expanding rapidly (Eastwood et al., 2001, 2003; Jones et al., 2002).

In this study, we carried out a broad-scale, small-fish survey in northern New Zealand inshore waters. Estuarine fish habitat work in New Zealand has been minimal and geographically limited. Currently, there is no broad-scale information on the location and importance of fish nurseries, or on which fish species are dependent on estuaries. Even the initial settlement and recruitment areas of the most valuable inshore finfish species (the sparid *Pagrus auratus*) were largely unknown until very recently. In this paper, we present the results of a survey of 30 estuaries spanning ca 1000 km of coastline and three degrees of latitude. We develop statistical models of fish presence and abundance, and assess the predictive ability of these models. Our ultimate aim is to predict the presence and/or abundance of fish species in unsampled estuaries as a basis for intensive ecological research at smaller spatial scales, and for management purposes. This study is the first in a series which will eventually cover the full 1600 km latitudinal range of New Zealand's 350 estuaries.

2. Materials and methods

2.1. 25-Harbour survey

Twenty-five estuaries and coastal bays around the northern North Island of New Zealand were surveyed by beach seine between 20 January and 30 March 2001 (Fig. 1, Table 1). Hereafter we refer to these estuaries and bays as 'harbours', for consistency with the official names of most of them. The 25 harbours ranged in size from the large Kaipara Harbour (a 743-km^2 drowned valley composed of several major sub-estuaries) and Firth of Thames (a 729-km^2 coastal embayment) to several small tidal lagoons less than 10 km^2 in area. The amount of fresh water flowing into these harbours also varies dramatically, from high at Port Waikato, which is the mouth of the Waikato River, the largest river in North Island (31,300,000 m^3 mean inflow over a 12.4-h tidal cycle) to minimal in Mangemangeroa Estuary (17,100 m^3). Harbours having a wide variety of physical characteristics, and covering the full geographic range of both west and east coasts of northern North Island, were chosen for this study in order to encompass the maximum possible contrast in fish habitat and therefore abundance.

2.2. 6-Harbour survey

Two years after the 25-harbour survey, in 6—18 February 2003, Kaipara Harbour was re-surveyed and five new harbours were surveyed for the first time (Fig. 1, Table 1). A total of 43 stations were sampled. This was done to test predictions developed from models of fish abundance and presence generated from the data collected during the 25-harbour survey. Both surveys used the same sampling techniques.

2.3. Sampling design and procedure

Sampling was conducted during daylight hours, within 2.5 h of low tide. Previous work has shown that sampling this way produces the highest estimates of fish species richness, and of relative abundance for most species (Morrison et al., 2002). For a few species, night sampling produces higher abundance estimates, but logistic and safety constraints did not permit night sampling.

Sampling stations in each harbour were arranged along anticipated environmental gradients, from the brackish upper reaches to the harbour mouth. Eight stations could be sampled comfortably over a single low tide, so this was set as the target minimum per harbour. Occasionally this target was not achieved, with only 5—7 stations being sampled (Table 1). Large harbours were allocated additional (up to 40) stations in order to sample all habitats adequately. The exception was the large Firth of Thames which for logistical reasons had the fewest stations (five). Small harbours were sampled by one team of two people in one day, whereas the largest harbours required two teams of two working for 2—3 days. Station positions were determined using a Global Positioning System.
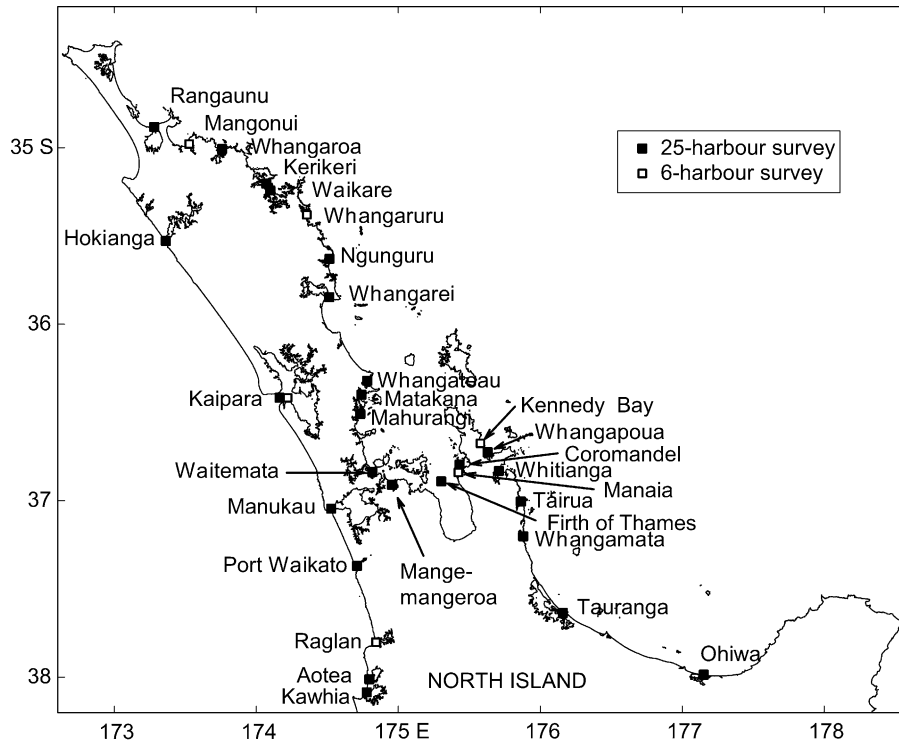
Fig. 1. Map of northern North Island of New Zealand showing harbours sampled in 25-harbour survey (January–March 2001) and 6-harbour survey (February 2003). Symbols indicate harbour mouths, and not actual sampling locations.

Fish were sampled using beach seine nets constructed of braided knotless nylon. Nets were 11-m wide and 2.3-m high, with 9-mm mesh and 4-m long codend. Attached to each end of the net were 5-m bridles and 15-m sweeps (combined distance 20 m), the sweep end being the point from which the net was hauled. When fishing, a sweep/bridle angle of ca 25–35° produced a net mouth width of ca 9 m, which was thought to be most effective for fish retention.

Our aim was to sample from and including the channel adjacent to the tidal flats, upon and across part of the tidal flat. At stations that could be comfortably waded (<1.2 m deep), nets were deployed manually, parallel to the shoreline, from a 3.5-m-long, shallow-draft, inflatable boat, and then hauled to the shore by two people. For deeper stations, a grapnel anchor with a short length of chain was attached to one of the sweeps, and deployed from the boat onto the shore. The boat reversed offshore to the full length of the sweep, turned at right angles down-current to set the net parallel to the shoreline, and then drove back into the shoreline setting the second sweep. The two sweeps were then hauled in the same manner as for the manually deployed sets.

Hauling speed was constant at a slow walking pace. Very soft mud occasionally 'bogged' the net, requiring that it be pursed, and the mud manually sieved through the mesh. The groundrope weight ensured direct contact with the seabed throughout the tow, even when the water depth exceeded the net's 2.3-m drop. In these circumstances, it was estimated that the net fished the bottom 1.0–1.2 m of the water column.

Tow length could not be standardised, because of the highly variable seabed slope, variation in the state of the tide, and the need to haul the net on to the shore in order to retrieve the catch. At extreme low tide, the beach seine may have sampled only the subtidal channel and a small amount of the adjacent tidal flat, whereas a large amount of the tidal flat may have been included in stations conducted 2.5 h before or after low tide. The distance towed varied from 10 to 220 m (mean 41 m, std dev. 31 m). The estimated mean swept area was 369 m^2, but ranged from 90 to 1980 m^2.

Catches were retrieved from the net, bagged, labelled, stored on ice in the field, and frozen on return to suitable facilities. Subsequently, samples were thawed in the laboratory, sorted to species, counted, and measured to the millimetre below fork or total length (depending on the tail shape of the species). For catches of more than 200 fish per species, a random sub-sample was measured. Catch rates (numbers of fish per kilometre towed) were calculated and treated as estimates of relative abundance. Depth at the start of the tow, and the distance towed, could affect the efficiency of the net and therefore the catch rate. We accounted for such variability by including these variables as predictors in our models (see below).

Table 1
Type and area of the harbours surveyed, number of beach seine stations conducted in each harbour, and number of fish species caught (excluding species caught at fewer than 2% of stations overall). Harbours are arranged from south-west to south-east (see Fig. 1) within the two surveys (25-harbour and 6-harbour)

Harbour	Harbour type	Area (km^2)	Number of stations	Number of species
25-Harbour survey				
Kawhia	Tidal lagoon	67.6	8	12
Aotea	Tidal lagoon	31.9	8	14
Port Waikato	Drowned valley	18.2	8	6
Manukau	Drowned valley	365.6	30	15
Kaipara	Drowned valley	743.1	40	18
Hokianga	Drowned valley	106.5	16	18
Rangaunu	Drowned valley	101.7	8	14
Whangaroa	Drowned valley	25.4	8	14
Kerikeri	Drowned valley	35.8	8	11
Waikare	Drowned valley	52.1	6	11
Ngunguru	Tidal lagoon	5.1	8	10
Whangarei	Drowned valley	103.6	16	14
Whangateau	Tidal lagoon	7.5	8	10
Matakana	Tidal lagoon	4.2	8	14
Mahurangi	Drowned valley	24.6	8	13
Waitemata	Drowned valley	79.8	32	14
Mangemangeroa	Coastal embayment	0.6	8	9
Firth of Thames	Coastal embayment	729.1	5	7
Coromandel	Coastal embayment	25.4	8	13
Whangapoua	Tidal lagoon	13.0	8	14
Whitianga	Tidal lagoon	15.5	8	16
Tairua	Tidal lagoon	6.0	8	12
Whangamata	Tidal lagoon	4.4	8	14
Tauranga	Drowned valley	200.4	24	17
Ohiwa	Tidal lagoon	26.8	8	16
6-Harbour survey				
Raglan	Tidal lagoon	31.9	8	15
Kaipara	Drowned valley	743.1	7	14
Mangonui	Tidal lagoon	8.7	8	15
Whangaruru	Drowned valley	11.7	8	13
Manaia	Tidal lagoon	6.3	6	11
Kennedy Bay	Drowned valley	4.9	6	9

Beach seines are most effective at sampling small fishes, and poor at retaining larger animals because of escapement around the sides or over the top of the net. Inspection of the length-frequency distributions of the fishes caught showed that few fish longer than 250 mm were caught (39 fish in the 25-harbour survey). We therefore omitted fish 250 mm or longer, except for large sand flounder (*Rhombosolea plebeia*) and yellow-belly flounder (*Rhombosolea leporina*) which are probably well sampled by the net. We also omitted all short-finned eels (*Anguilla australis*) as they are rarely retained by the net because of their shape and behaviour (only 17 were caught, three of them shorter than 250 mm).

2.4. Site physical variables

At each station, a number of site physical variables were recorded (Table 2). Substratum composition was classified subjectively into four classes (from soft mud to sand) and surface sediment samples were collected and archived for analysis at a later date. The presence of vegetation (mangroves, *Avicennia marina* var. *australasica*, and seagrass, *Zostera muelleri*) at or near each sampling station was also recorded.

The depth at the start of each tow was measured using a weighted tape measure. Depths ranged between 0.2 and 1.0 m for shallow gradient sets and between 1.0 and 6.0 m for deeper channel sets. Water samples were collected and frozen for salinity measurements on return to the laboratory using a TPS WP-84 handheld meter. Salinity measurements were not available for 21 stations (7%) spread across four different harbours. Water clarity was measured with a 200-mm Secchi disk, and temperature was measured with a TPS WP-82 handheld meter.

The distance of each station from the harbour mouth was determined in a GIS from the latitude and longitude

Table 2
Predictor variables used in GAMs. The levels of each categorical variable are shown in square brackets

Variable type	Variable name	Description
Harbour	*Harbour*	Harbour
Site location	*Latitude*	Latitude (°S)
	Coast	Coast of North Island [east, west]
Site physical	*Substratum*	Sediment type at station [soft mud, firm mud, sandy mud, sand]
	Vegetation	Aquatic vegetation at or near station [none, mangroves nearby, seagrass nearby, seagrass present at station]
	Depth	Depth at start of tow (m)
	Salinity	Salinity at start of tow
	Clarity	Water clarity at start of tow measured by Secchi disk (m)
	Temperature	Water temperature at start of tow (°C)
	Distpercent	Distance of station between mouth and upper end of harbour (%)
	Towdist	Distance towed by beach seine (m)
	Time	Time of day
Harbour physical	*Type*	Harbour type [coastal embayment, drowned valley, tidal lagoon]
	Tideflow	Ratio of spring tidal prism to total estuary volume
	Riverflow	Ratio of river inflow to total estuary volume
	Complexity	Shoreline complexity index
	Area	Harbour surface area at spring high tide (m^2)
	Tiderange	Mean M2 tide range (mm)
	Catchtemp	Annual mean terrestrial catchment temperature (°C)

of both locations, and expressed as a percentage of the distance between the mouth and the upper reaches of the harbour. The distance covered by each beach seine tow was estimated by eye, and the time of day was recorded.

2.5. Data analyses

2.5.1. Fish assemblages

Two complementary but fundamentally different multivariate approaches were used to identify fish assemblages: ordination and clustering. Similar results from the two techniques would provide confidence that any identified species assemblages were robust. We used correspondence analysis (CA), implemented by the CORRESP procedure in SAS, for ordination (Greenacre, 1984; Ter Braak and Prentice, 1988). CA is equivalent to a weighted principal components analysis of χ^2 transformed data. The transformation converts the abundance data into χ^2 distances among species (Legendre and Legendre, 1983; Digby and Kempton, 1987), and the weighting increases the influence of stations containing larger numbers of fish. Since our aim was to identify species assemblages, we interpreted only the species ordination, and not the station ordination. Rare species, defined as those occurring in fewer than 5% of the stations, were eliminated from the data set before analysis to prevent them having an undue influence on the results (Gauch, 1982).

Ward's minimum variance cluster analysis (WCA; an agglomerative hierarchical method) was also applied to the same suite of species using the CLUSTER procedure in SAS. The abundance data were χ^2 transformed by dividing each element of the species by stations matrix by the row (species) total and the square root of the column (stations) total, and weighted by the row total (total abundance of a species) before analysis so that the clustering was performed in the same space as that used for the CA.

2.5.2. Predictor variables

Nineteen predictor variables were developed for use in Generalized Additive Models (GAMs, Hastie and Tibshirani, 1990). These variables fall into two main types – those describing the spatial location of the sampling stations, and those describing the physical environment. Each of these two main types is further subdivided into two subtypes (Table 2).

Spatial location variables may add predictive power by acting as surrogates for one or more unknown environmental variables, or variables that cannot be measured easily. They can also potentially capture genuine geographic effects, such as proximity to favourable habitat features such as spawning sites, or where juvenile dispersal is aided by particular habitat combinations. However, spatial variables offer limited insight into the possible causal factors influencing the distribution and abundance of fishes. We applied GAMs with and without spatial location variables in order to assess their descriptive and predictive utility.

The first spatial subtype consists of the variable *Harbour*, which has a separate level (and therefore model coefficient) for each harbour. This variable therefore captures spatial variability at the medium scale. The second spatial subtype consists of the variables *Latitude* and *Coast*, which allow for large-scale geographic variation with latitude, and between the east and west coasts of North Island.

Variables describing the physical environment fall into two subtypes – those that are specific to individual sampling stations (site physical variables), and those that apply to an entire harbour or its catchment (harbour physical variables).

Site physical variables were described above (see also Table 2). The percentage distance of each station from the harbour mouth (*Distpercent*) is strictly a location variable, but it may act as a surrogate for one or more physical variables that vary along an estuarine gradient. In doing so, it integrates across the full range of short-term temporal variation (especially over a tidal cycle) thereby providing a measure of the average, gradient-dependent, physical conditions experienced by fish at each site. Some of the other site physical variables (e.g., *Salinity*, *Clarity*, *Temperature*) were measured only at the time of sampling (daytime low tide), and do not reflect the range of conditions experienced by fish. The depth at the start of each beach seine tow (*Depth*), the distance towed (*Towdist*), and the time of day (*Time*) are 'nuisance' variables that may affect the catch rates of fishes, and need to be allowed for when modelling abundance.

Harbour physical variables were selected from a larger set of variables compiled for a physical classification of New Zealand estuaries (Hume et al., 2003; T. M. Hume, NIWA, Hamilton, pers. comm.). This data set contains numerous measured and derived variables describing harbour physical properties and dimensions, oceanic and terrestrial forcing, wind and waves, and terrestrial catchment properties (e.g., hydrology, geology, vegetation, temperature). A subset of 33 potential predictor variables was selected, based on an a priori consideration of the factors most likely to affect fish abundance. This subset was then reduced to the final subset of seven variables (Table 2) by eliminating one of each pair of highly correlated variables ($|r| > 0.9$), and variables with missing values.

2.5.3. Descriptive and predictive models

Using the 25-harbour data set, GAMs were developed that related species abundance to physical variables for the 12 most frequently caught fish species (Table 3). Similar GAMs were developed for species

Table 3
Frequency of occurrence and numbers of fish caught at 305 beach seine stations during the 25-harbour survey, arranged in descending order of frequency of occurrence. Only species caught at more than 2% of the stations are included. The species group column summarises the principal life style (D, demersal; P, schooling pelagic) and habitat (C, open coastal waters; F, freshwater; H, harbours, estuaries and sheltered bays) of each species, and the life stages sampled in this study (A, adults and juveniles; J, juveniles only)

Common name	Scientific name	Family	Code	Species group	Frequency	Number
Yellow-eyed mullet	*Aldrichetta forsteri*	Mugilidae	AFO	P, H, J	275	30,151
Exquisite goby	*Favonigobius exquisitus*	Gobiidae	FEX	D, H, A	211	11,962
Sand flounder	*Rhombosolea plebeia*	Pleuronectidae	RPL	D, H, J	190	1663
Speckled sole	*Peltorhamphus latus*	Pleuronectidae	PLA	D, H, A	186	3120
Anchovy	*Engraulis australis*	Engraulidae	EAU	P, H, J	111	8968
Yellow-belly flounder	*Rhombosolea leporina*	Pleuronectidae	RLE	D, H, J	100	821
Sand goby	*Favonigobius lentiginosus*	Gobiidae	FLE	D, H, A	93	2538
Smelt	*Retropinna retropinna*	Retropinnidae	RRE	P, F, A	85	6847
Estuarine triplefin	*Grahamina nigripenne*	Tripterygiidae	GNI	D, H, A	81	2837
Spotty	*Notolabrus celidotus*	Labridae	NCE	D, C, A	70	239
Snapper	*Pagrus auratus*	Sparidae	PAU	D, C, J	48	248
Grey mullet	*Mugil cephalus*	Mugilidae	MCE	P, H, J	45	272
Mottled triplefin	*Grahamina capito*	Tripterygiidae	GCA	D, H, A	39	225
Trevally	*Pseudocaranx dentex*	Carangidae	PDE	D/P, C, J	30	83
Parore	*Girella tricuspidata*	Girellidae	GTR	D, C, J	25	298
Garfish	*Hyporhamphus ihi*	Hemiramphidae	HIH	P, H, J	24	429
Red gurnard	*Chelidonichthys kumu*	Triglidae	CKU	D, C, J	19	34
Spotted stargazer	*Genyagnus monopterygius*	Uranoscopidae	GMO	D, H, J	15	18
Estuarine stargazer	*Leptoscopus macropygus*	Leptoscopidae	LMA	D, H, J	14	54
Jack mackerel	*Trachurus novaezelandiae*	Carangidae	TNO	P, C, J	13	33
Kahawai	*Arripis trutta*	Arripidae	ATR	P, C, J	11	23

richness, defined as the number of fish species caught at each station after excluding species that were caught in fewer than 2% of stations across the entire survey area (see Table 3 for the full list of 21 species). Rare species are either not a normal component of the fish fauna in the harbours surveyed, or not usually vulnerable to the beach seine sampling method.

The response variable used in the initial GAMs was relative abundance (catch in numbers per kilometre) for each species, or species richness. For a number of fish species, the predictive power of these models was low, so further models were applied to presence–absence data to determine whether it was easier to predict fish occurrence than abundance.

A series of GAMs was fitted to each response variable (Table 4). Our approach was to explore the effect of adding and deleting variable types, in an attempt to develop models with practical predictive ability. Three descriptive models were developed. Model 1 (*Harbour-Site*) included *Harbour* and all the site physical variables as predictor variables. This represents a minimal model that allows each harbour to have its own mean relative abundance, or probability of occurrence, and incorporates a basic suite of environmental variables measured at the sampling station. Model 2 (*Site-Location*) goes a step further by using specific information about a site's geographic location (*Latitude*, *Coast*) in place of *Harbour*, thus allowing the detection of more general geographic patterns of abundance or occurrence. Model 3 (*Environment*) uses both site and harbour physical

variables but no variables describing geographic location. This model therefore attempts to describe the occurrence or abundance of a fish species, or species richness, using only measurable features of the physical and chemical environment.

Two predictive models were then developed. Model 4 (*Prediction*) incorporates only predictor variables that are readily available for harbours and sampling sites throughout northern North Island; consequently this model enables prediction for harbours or sites that have not been sampled previously. Most site physical variables are not available for new sites without conducting a dedicated field sampling programme, so they cannot be used for prediction. However, *Distpercent* is included in

Table 4
Type and number of predictor variables used in five GAM models. Response variables were fish species abundance or presence–absence, and species richness. See Table 2 for a list and description of variables

Model	Name	Variables in model			
		Harbour	Site location	Site physical	Harbour physical
1	Harbour-Site	1		9	
2	Site-Location		2	9	
3	Environment			9	7
4	Prediction		2	1[a]	7
5	Prediction-Habitat		2	3[b]	7

[a] Distpercent.
[b] Substratum, Vegetation, Distpercent.

this model because it can be determined easily from a chart of the harbour once sampling stations have been selected. Model 5 (*Prediction-Habitat*) goes a step further by adding two habitat descriptors, *Substratum* and *Vegetation*, as predictor variables. Although these variables are not usually available in advance, they may be determined with minimal field sampling effort and may add significant predictive power compared with Model 4.

GAMs were fitted in Splus statistical software (Chambers and Hastie, 1993) using the Generalized Regression Analysis and Spatial Prediction (GRASP) suite of programs (Lehmann et al., 2002a, 2002b). GAMs are non-parametric extensions of Generalized Linear Models (GLMs) that allow non-linear (smooth) response surfaces to be fitted using a range of different error structures (e.g., binomial, Poisson, see Hastie and Tibshirani, 1990).

For relative abundance data and species richness, we used a quasi-Poisson model with a log-link function, and for presence–absence data we used a quasi-binomial model with a logit-link function. Quasi likelihood models do not specify the error structure a priori, but allow it to be determined from the variance function. This enables the estimation of the dispersion parameter, which may differ dramatically from the default value of one assumed in non-quasi models. Models were fitted to the data in a stepwise backwards fashion to select significant predictors. Starting models incorporated continuous variables smoothed with four degrees of freedom; the significance of including the smoothed variable, or of including a simpler linear form (with one degree of freedom) instead, was tested using an analysis of variance. A probability level of 0.01 was used for these tests to limit the inclusion of spurious variables in the model. Interaction terms were not included in the models because a large number of main effect variables were offered to each model and processing times were already significant. Further details of the model fitting procedure are provided by Lehmann et al. (2002a, 2002b).

Variable selection in a model may depend on the order in which predictor variables are offered to it; this occurs when two or more variables can substitute for each other in a model, producing similar overall fits. We offered variables to the models in the order shown in Table 2.

Salinity measurements were missing for some stations in the 25-harbour survey, so models were initially fitted to a reduced data set of 284 stations for which salinity data were available. If *Salinity* was selected as a significant variable, the final model was based on this reduced set; if *Salinity* was non-significant, it was dropped from the suite of variables offered to the model, and the model was re-fitted using the full data set of 305 stations.

2.5.4. Model validation

The validity of the GAMs was tested in several ways using GRASP routines. For models fitted to abundance data, we compared the values predicted for each station with the observed values using the correlation coefficient as a measure of model performance. We also used 10-fold cross validation, in which 90% of the data were used to predict the abundance of fish in the remaining 10% of stations; this process was carried out 10 times using randomly selected data subsets (without replacement) until the abundance of fish at all stations had been predicted. The correlation coefficient between observed and predicted values was again used as a measure of model performance. For presence–absence models, we used the area under the Receiver Operating Characteristic (ROC) curve (Fielding and Bell, 1997) in place of correlation coefficients to test performance.

The above validation methods suffer from non-independence of the data sets used to develop and validate the GAMs. To overcome this problem, we used the 6-harbour data set, containing data collected in the same way but two years later, to test the models developed from the 25-harbour data set. For all stations in the six harbours, we predicted probability of occurrence using the relevant 25-harbour presence–absence models based on the full data set for each species. Five of the six harbours had not been sampled in the 25-harbour survey, and therefore provide a strong test of the generality of the model predictions. The ROC statistic was used as a measure of model performance. An additional performance measure, the percentage of samples correctly classified by the model, was also calculated. For this purpose, we assumed that a predicted probability of occurrence greater than or equal to 0.5 represented a predicted presence. Unfortunately, the two-year time lag between the 25-harbour and 6-harbour surveys means that the between-survey validation may be confounded by temporal effects, particularly inter-annual variation in year class strength. The results of the between-survey validation might therefore underestimate true within-year model performance.

3. Results

3.1. Catch composition and large-scale distribution patterns

In the 25-harbour survey, 71,211 fish from 34 species were caught at 305 stations. Twenty-one species were caught in more than 2% of the stations, but only four species (*Aldrichetta forsteri*, *Favonigobius exquisitus*, *Rhombosolea plebeia*, *Peltorhamphus latus*) were caught in more than half of the stations (Table 3, Fig. 2a). *Aldrichetta forsteri*, a schooling mullet, was by far the most abundant species, occurring in 90% of all stations
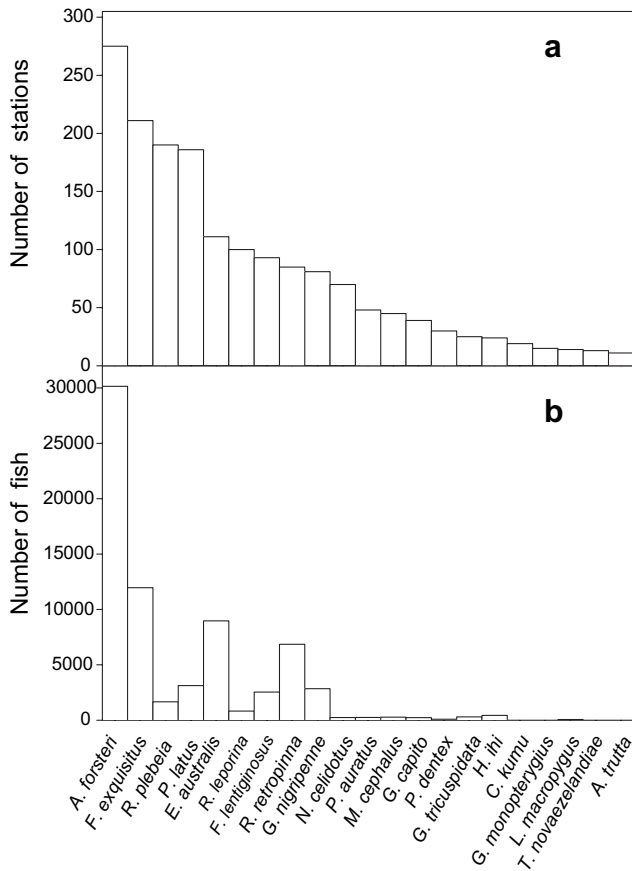
Fig. 2. Frequency (a) and total abundance (b) of fish species caught by beach seine at 305 stations in 25 harbours. Only species occurring in more than 2% of stations are shown.

and comprising 42% of the catch by number. The seven most abundant species (*A. forsteri*, *F. exquisitus*, *Engraulis australis*, *Retropinna retropinna*, *P. latus*, *Grahamina nigripenne*, *Favonigobius lentiginosus*) made up 93% of the total catch by number (Table 3, Fig. 2b). A long tail of 12 rarer species occurred occasionally to relatively often (in 4–23% of stations) but were only caught in small numbers (Fig. 2a, b).

The number of species caught in each harbour varied threefold (range 6–18; Table 1), but because of differences among harbours in the number of stations sampled, and in a wide range of other factors, raw species richness is not very informative. The species caught fall into a range of behavioural life styles (demersal, schooling pelagic), principal habitat types (freshwater, sheltered inshore waters, open coastal waters), and life stages sampled (small species for which both adults and juveniles were sampled, large species for which only juveniles were sampled) (Table 3). Thirteen of the 21 species (62%) occur mainly in sheltered inshore waters, and are regarded as residents of the sites surveyed in this study. However, some of these species (notably *Rhombosolea plebeia*, *Mugil cephalus*) also occur along open coasts, and spawn at sea. Seven

species (33%) occur mainly in open coastal waters, and are either transient members of the harbour fauna, or use harbours as nursery grounds (sensu Beck et al., 2001). One species (*Retropinna retropinna*; 5%) occurs mainly in freshwater. Thirteen of the 21 species (62%) were caught mainly as juveniles, but for most of these, gear selectivity is likely to be the main reason; i.e. large individuals were able to avoid the net. Only five species that are vulnerable to beach seines seem to use these harbours mainly as nurseries before migrating to the open coast (*Pagrus auratus*, *Pseudocaranx dentex*, *Girella tricuspidata*, *Chelidonichthys kumu*, *Arripis trutta*); however all these species except *G. tricuspidata* also occur along open coasts as juveniles. A number of other species use the harbours both as nurseries, and as adult habitat.

Aldrichetta forsteri occurred in all 25 harbours and was abundant everywhere (Fig. 3). The three flatfish species (*Peltorhamphus latus*, *Rhombosolea plebeia*, *Rhombosolea leporina*) were also common in most harbours, with no clear, large-scale abundance patterns. However, large-scale spatial variation was observed for many other species. *Mugil cephalus* and *Chelidonichthys kumu* occurred exclusively or mainly in west coast harbours (Fig. 4), whereas *Grahamina nigripenne*, *Favonigobius lentiginosus*, *Girella tricuspidata*, *Leptoscopus macropygus*, and *Notolabrus celidotus* occurred exclusively or mainly in east coast harbours (Fig. 5). *Favonigobius exquisitus* was widespread, but was much more abundant in Kaipara Harbour than elsewhere. *Retropinna retropinna* was also widespread, but most (92%) of the catch by number came from two harbours, Port Waikato and Ngunguru.

3.2. Fish assemblages

Seventeen species occurred in more than 5% of the stations. A preliminary CA on these species was dominated by *Hyporhamphus ihi*, which was an outlier on five of the first six CA axes. Although this species was caught at 24 stations, 41% of the catch came from just one station. We therefore omitted *H. ihi*, and carried out a CA and WCA on the remaining 16 species.

The first two CA axes explained 33.9% of the variation in the data, and the first five axes explained 72.4%. At a 6-cluster level, most species grouped into two distinct assemblages, but four species remained unassociated with any others (Fig. 6):

Assemblage 1 – *Favonigobius exquisitus*, *Rhombosolea plebeia*, *Peltorhamphus latus*, *Rhombosolea leporina*, *Mugil cephalus*, *Grahamina capito*, *Chelidonichthys kumu*
Assemblage 2 – *Aldrichetta forsteri*, *Notolabrus celidotus*, *Pagrus auratus*, *Pseudocaranx dentex*, *Girella tricuspidata*
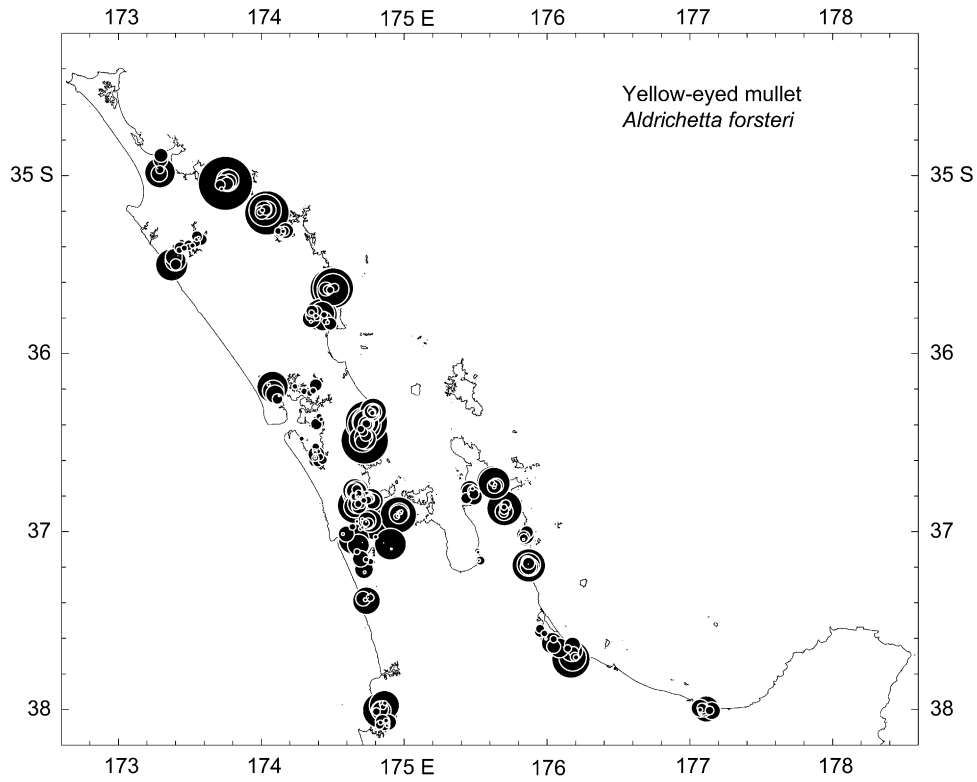
Fig. 3. Catch rate of yellow-eyed mullet (*Aldrichetta forsteri*) in 25-harbour beach seine survey. Circle area is proportional to catch rate (maximum circle size = 37,000 fish per km towed).
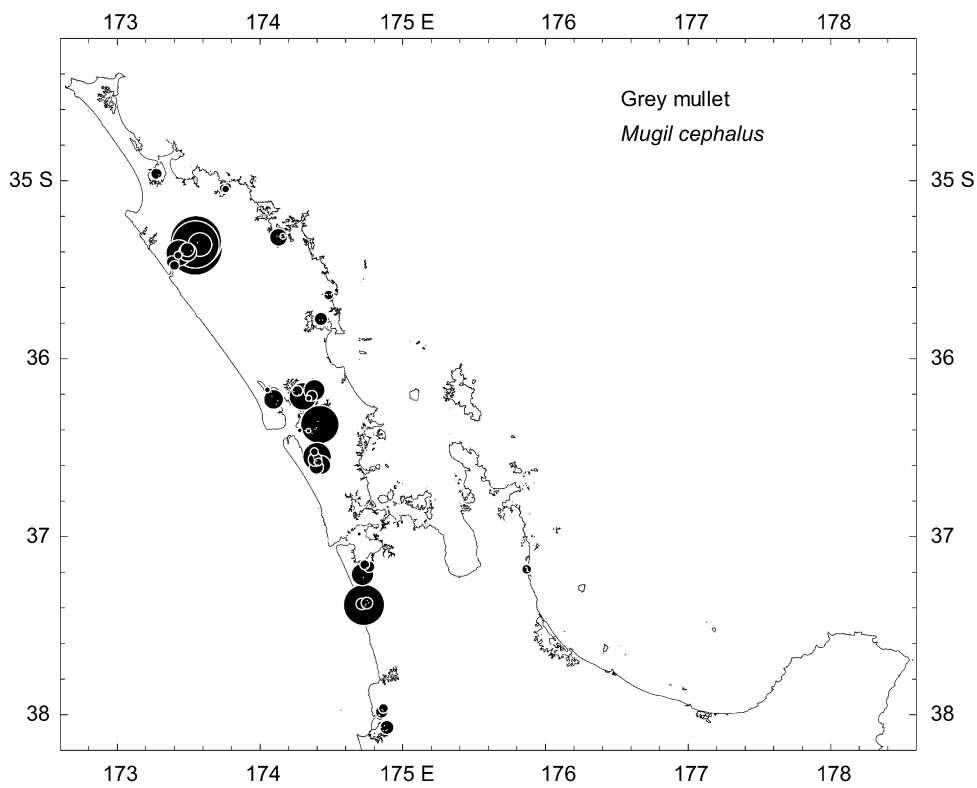

Fig. 4. Catch rate of grey mullet (*Mugil cephalus*) in 25-harbour beach seine survey. Circle area is proportional to catch rate (maximum circle size = 1450 fish per km towed).
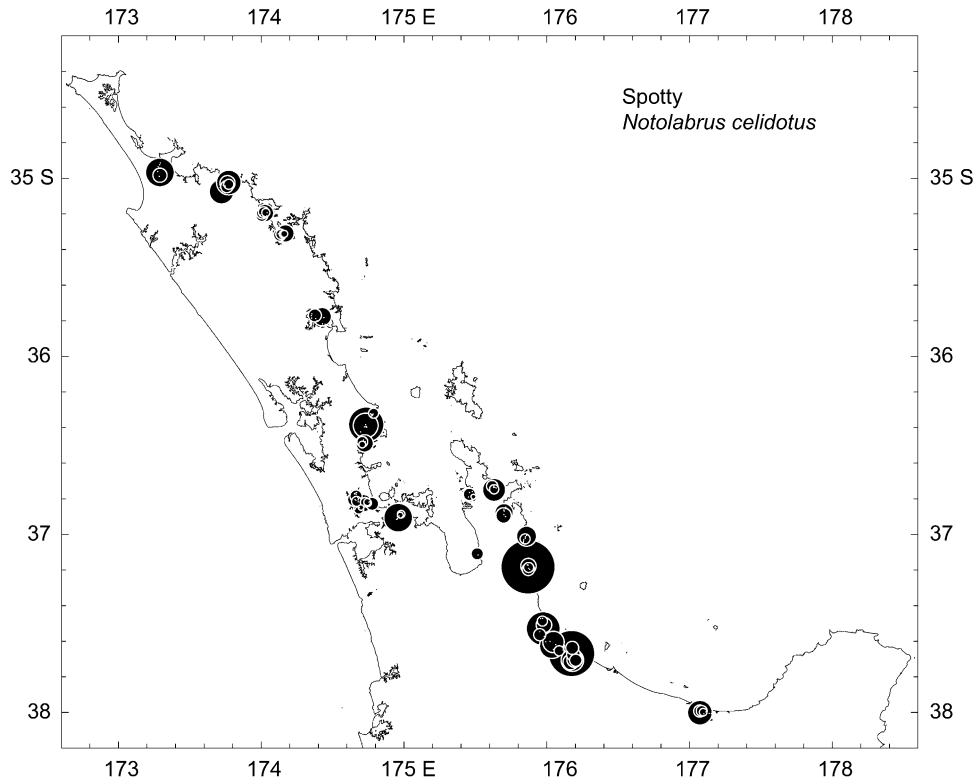
Fig. 5. Catch rate of spotty (*Notolabrus celidotus*) in 25-harbour beach seine survey. Circle area is proportional to catch rate (maximum circle size = 950 fish per km towed).

Unassociated species − *Engraulis australis*, *Favonigobius lentiginosus*, *Retropinna retropinna*, *Grahamina nigripenne*

Reducing the number of clusters resulted in *Grahamina nigripenne* merging with Assemblage 1 (5 clusters), and *Favonigobius lentiginosus* merging with Assemblage 2 (4 clusters). However, these two species were strongly separated from the other species in the respective assemblages on the fourth CA axis (not shown), so the 6-cluster solution appears most plausible.

3.3. Descriptive and predictive models

Fig. 7 shows two measures of the performance of GAM descriptive Models 1−3 fitted to abundance data for 12 fish species and species richness. The *X*-axis shows the performance of each best-fit model when fitted to all available data, and the *Y*-axis shows the performance when tested by 10-fold cross validation. A high score on both axes indicates that a model describes the available data well, and that a model based on a 90% subset of the data provides reasonable predictions (i.e. it is relatively robust).

For most species, and for species richness, the three different descriptive models were similar in performance − the 'performance polygon' for each species was

usually small (Fig. 7). However, there was some fine-scale pattern in the results: Model 1 usually performed best (nine out of 13 models) when applied to all data. Under cross validation, Model 1 was generally best for species that were well predicted by the models, whereas Model 3 was generally best for species that were not as well predicted. This indicates that, even for species whose abundance was predicted best by our models, one or more important, harbour-specific variables was missing from the suite offered to the models; i.e. when *Harbour* was not included in the model, the other variables offered to Models 2 and 3 were not able to compensate, and overall model performance dropped. *Retropinna retropinna* was a good example: most of the catch of this species came from just two harbours, a feature that was captured well by the inclusion of *Harbour* in Model 1; however, Models 2 and 3 did not perform as well for this species.

Model performance varied widely among species. Good model performance was observed for *Retropinna retropinna*, *Grahamina nigripenne*, *Favonigobius exquisitus*, and *Favonigobius lentiginosus*. Two species (*Rhombosolea plebeia*, *Aldrichetta forsteri*) were poorly described by the models. For the remaining species (*Rhombosolea leporina*, *Mugil cephalus*, *Peltorhamphus latus*, *Pagrus auratus*, *Notolabrus celidotus*, *Engraulis australis*), an apparently good descriptive model performed poorly under cross validation, suggesting
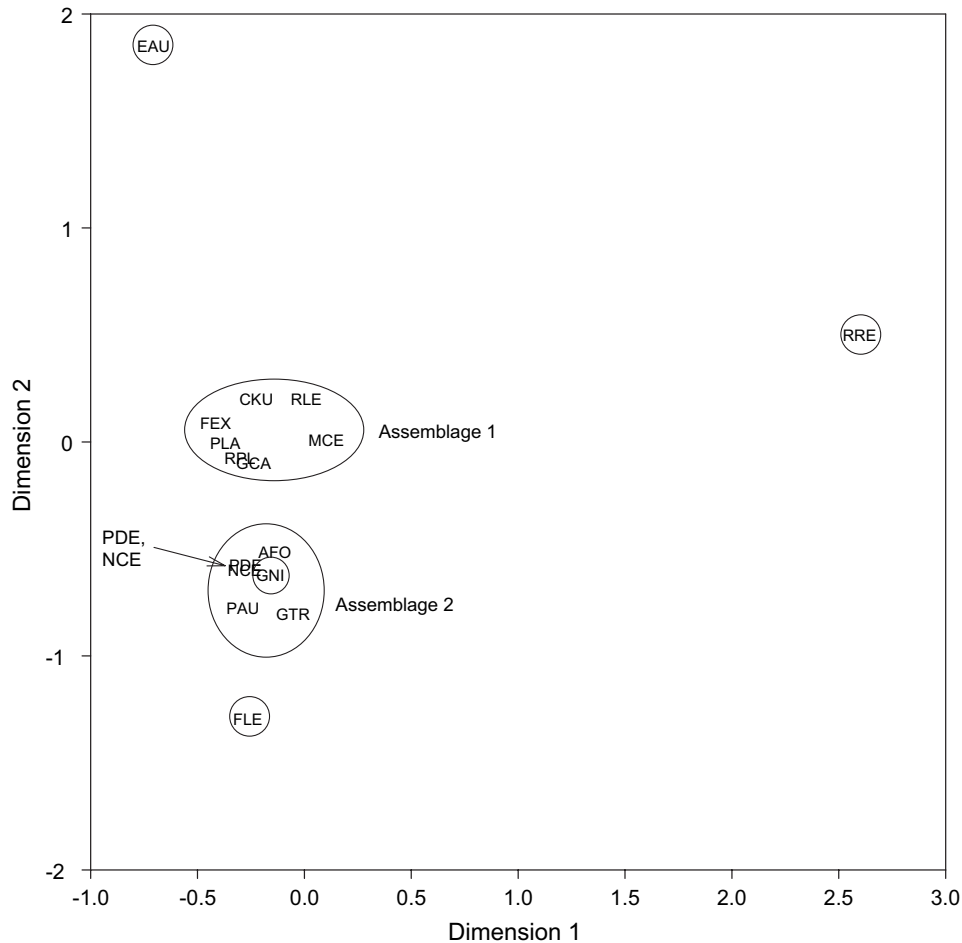
Fig. 6. Correspondence analysis ordination of 16 fish species, with two assemblages and four unassociated species identified by Ward's cluster analysis indicated by ovals and circles. Three-letter species codes are shown in Table 3.

significant over-fitting to the data. Inspection of the correlation plots indicated that this was usually because each data set had only a few stations with high catch rates, and they strongly influenced which predictor variables were included in the model. When these influential stations were not selected in the 90% sub-samples used for cross validation, the models were unable to predict these high values, confirming that the model was over-fitted to these rare high catch-rate stations. Species richness was moderately well described by all models, and performed reasonably under cross validation.

Model 3 (*Environment*) generally performed well under cross validation, relative to other descriptive models, and we summarise the variables selected for each species and species richness in Table 5. *Clarity* was selected 11 out of the maximum possible 13 times (12 species plus species richness), and *Salinity* was selected eight times. The variables selected most frequently were (in descending order) *Clarity* > *Salinity* > *Distpercent* = *Time* = *Tiderange* > *Substratum* = *Depth* = *Riverflow*. All variables offered to the model were selected at least three

times. The variables most frequently selected as one of the three most important variables in the model were *Clarity* = *Riverflow* > *Salinity* > *Towdist*. Overall, *Clarity*, *Salinity*, and *Riverflow* appear to be the most useful of the variables available to this study for describing the abundance of harbour fish species.

For Model 3, the relationships among species abundance (or richness) and each predictor variable are shown in Table 5. The relationships varied from simple linear patterns (positive or negative) to more complex unimodal or bimodal trends. Bimodal patterns are difficult to interpret for most environmental variables; for example, it is not clear why *Peltorhamphus latus* would have high abundance at both low and high temperatures, with low abundance at intermediate temperatures. Interactions among variables, or among species, may be important. One hypothesis worth exploring further is that the abundance of a predator or competitor peaks at intermediate values of the variable, thus reducing the population abundance of its prey to a level below that which can be physically supported by the environment. Bimodal patterns
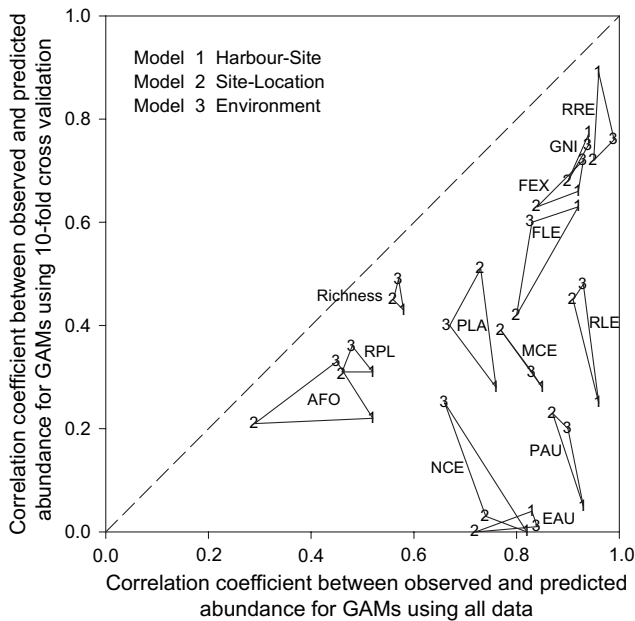
Fig. 7. Performance of three descriptive models of abundance for 12 fish species and species richness for the 25-harbour data set. The dashed line is the 1:1 line of equivalence. Numerals indicate model numbers, and solid lines link models for the same species. Three-letter species codes are shown in Table 3.

occurred only once in a 'top three' variable, so another possible explanation is that they may be spurious.

Conversely, bimodal relationships occurred three times in the variable *Time*, and these may represent real patterns. It is plausible that some species have higher catchability in the morning and evening, perhaps because low light levels make net avoidance difficult (e.g., the schooling pelagics *Engraulis australis* and *Retropinna retropinna*), or because they may burrow into the sediment during the middle of the day (e.g., the demersal flounder *Rhombosolea leporina*).

Predictive Models 4 and 5 were identical for five species (*Aldrichetta forsteri*, *Engraulis australis*, *Mugil cephalus*, *Notolabrus celidotus*, *Pagrus auratus*). For two species (*Grahamina nigripenne*, *Rhombosolea plebeia*), Model 5 performed slightly better than Model 4 based on the correlation coefficient, but slightly worse under cross validation. For the remaining five species (*Favonigobius exquisitus*, *Favonigobius lentiginosus*, *Peltorhamphus latus*, *Rhombosolea leporina*, *Retropinna retropinna*) and species richness, Model 5 performed better than Model 4, sometimes substantially so, under both performance criteria. Thus the inclusion of the habitat variables *Substratum* and *Vegetation* improved the predictive models for some species but not others.

Predictive models generally performed worse than descriptive models. Fig. 8 compares Model 3 (*Environment*) with Model 5 (*Prediction-Habitat*). This degraded performance results from the restricted subset of predictor variables available for the predictive models.

Prediction models provided good fits to the data ($r > 0.75$) for four species (*Retropinna retropinna*, *Grahamina nigripenne*, *Favonigobius exquisitus*, *Rhombosolea leporina*), and cross validation performance for these species was moderate ($r = 0.41–0.61$). Model 5 performance for species richness was also reduced compared with Model 3.

Descriptive and predictive models were developed using presence–absence data to determine whether we were more successful in predicting occurrence than abundance. ROC statistics, used here as performance measures for presence–absence models, must be substantially greater than 0.5 to indicate a performance better than could be expected by chance. For Model 3, ROC statistics exceeded 0.75 for models fitted to the full data, and 0.70 for cross validation, for all species (Fig. 9). This performance degraded substantially for some species in predictive Model 5, but our ability to predict species occurrence was high (ROC > 0.75 on both axes) for eight of the 12 species (*Favonigobius lentiginosus*, *Notolabrus celidotus*, *Mugil cephalus*, *Engraulis australis*, *Grahamina nigripenne*, *Favonigobius exquisitus*, *Rhombosolea leporina*, *Retropinna retropinna*).

Predictive Model 5 developed from the presence–absence data from the 25-harbour survey was then used to predict the occurrence of each fish species at the 43 stations sampled during the 6-harbour survey (Fig. 10). Occurrence was well predicted for five of the same eight species (*Notolabrus celidotus*, *Grahamina nigripenne*, *Favonigobius exquisitus*, *Rhombosolea leporina*, *Retropinna retropinna*) (ROC > 0.70; percentage of samples correctly classified > 70%). For *Mugil cephalus*, 81% of samples were correctly classified, but the ROC was less than 0.5. Our predictions for *Engraulis australis*, *Favonigobius lentiginosus*, *Rhombosolea plebeia*, *Pagrus auratus* and *Peltorhamphus latus* were mediocre to poor. The occurrence of *Aldrichetta forsteri* was correctly classified in most (98%) of the stations, but this was a result of the nearly universal occurrence of this species; a similar success rate could be achieved by simply predicting its presence at all stations (Fielding and Bell, 1997). The ROC for *A. forsteri* was low, indicating that this statistic is of little use in comparing observed and predicted values for species having very high (or very low) prevalence.

4. Discussion

This study examined the performance of GAMs in describing and predicting the abundance or presence of a suite of 12 estuarine fishes and species richness. We focused on the broad picture (multiple harbours across a spatial scale of 1000 km, and multiple species) in order to assess the overall utility of this approach for making predictions. The results were mixed. Descriptive models

Table 5
Variables selected in GAM *Environment* Model 3 showing the nature of the relationship between each continuous variable, or the level of each categorical variable, and fish abundance or species richness

Variable	Levels	FEX	RPL	PLA	RLE	MCE	AFO	NCE	PAU	EAU	FLE	RRE	GNI	Richness	Times selected	Times in top three
Assemblage		1	1	1	1	1	2	2	2	U	U	U	U			
Substratum	Soft mud	+		+	+					−			+	0	6	1
	Firm mud	+		−	+					0		+	+		6	1
	Sandy mud	+		0	+					+		+	+		6	1
	Sand	−		0	−					0		−	−		6	1
Vegetation	None	0			0	0		0	0						5	1
	Mangroves nearby	−			0	+		0	−						5	1
	Seagrass nearby	−			−	0		0	0						5	1
	Seagrass present	+			0	+		+	+						5	1
Depth							+		+	+	−	∪	+	+	6	3
Salinity		+			−	−	+	+	+	+		−			8	5
Clarity		−	−	−	−			∪	+	−	+	−	−	−	11	6
Temperature		−	+	∪		+					−				5	2
Distpercent		+			+	+		+	∩	∪				+	7	0
Towdist		−		−				−				−	−		5	4
Time		−			∪	−			∩	∪		∪	−		7	2
Type	Coastal bay	+				0	−						−		4	2
	Drowned valley	−				0	+						+		4	2
	Tidal lagoon	+				+	−						−		4	2
Tideflow			∩			−				∪		∩			4	2
Riverflow			−	−						−		?	−	−	6	6
Complexity		+	+	+							−				4	1
Area							−	−		−			−		4	2
Tiderange		−				+		−	?		−		∪	−	7	2
Catchtemp					?	+						+			3	0

Species are arranged by descending frequency of occurrence within assemblages (U indicates an unassociated species). Blank cells indicate non-significant variables. Shading indicates the three variables (and their associated levels) contributing most to each model. Also shown (last two columns) are the number of times each variable was selected in the best-fit model, and the number of times it was selected in the top three variables. −, negative; +, positive; 0, intermediate; ∩, unimodal with intermediate optimum; ∪, bimodal with low and high optima; ?, indeterminate. Three-letter species codes are shown in Table 3.

of fish abundance performed well for four out of 12 species; for most other species, and species richness, the models described the data well but performed poorly to moderately under cross validation. The latter problem may in part be a result of the small sample sizes, because some models were strongly influenced by a small number of stations with high species abundance, and also the absence of other potential predictors. Predictive models of fish abundance usually performed worse than descriptive models, but appeared reasonable for four species. The reduced performance of predictive models is partly attributable to the smaller number of variables included (Model 5, mean = 3.9 variables, $N = 13$) compared with descriptive models (Model 3, mean = 7.1 variables, $N = 13$).

Presence–absence models performed better overall than abundance models: descriptive models showed good performance for all 12 species, and predictive models performed well for eight of the 12 species. Furthermore, predictions made for an independent data set (collected two years later than the data used for model development) successfully predicted occurrence for five species. A sixth species (*Aldrichetta forsteri*) occurred in nearly all samples in this part of New Zealand, so the occurrence models were effectively redundant.

Our overall conclusion is that GAMs were successful in describing and predicting the occurrence of most species, and moderately successful in predicting their abundance. This is encouraging, considering that our models suffer from a number of limitations, and have the potential to be significantly improved. Better models could be built with better environmental data. Our models were offered a limited set of environmental variables, some of which were point measurements that did not account for tidal, diel, or seasonal variation. Our harbour physical variables were informative at the medium spatial scale only; i.e. they were useful for discriminating among harbours, but not among stations within harbours. For some species at least, information on the physical habitat (substratum and vegetation) significantly improved model performance; in fact for some species, predictions from Model 4 were of little practical use, suggesting that resources devoted to an initial habitat survey, in order to provide the information required to fit Model 5 GAMs, would greatly increase the chances of obtaining useful predictions.
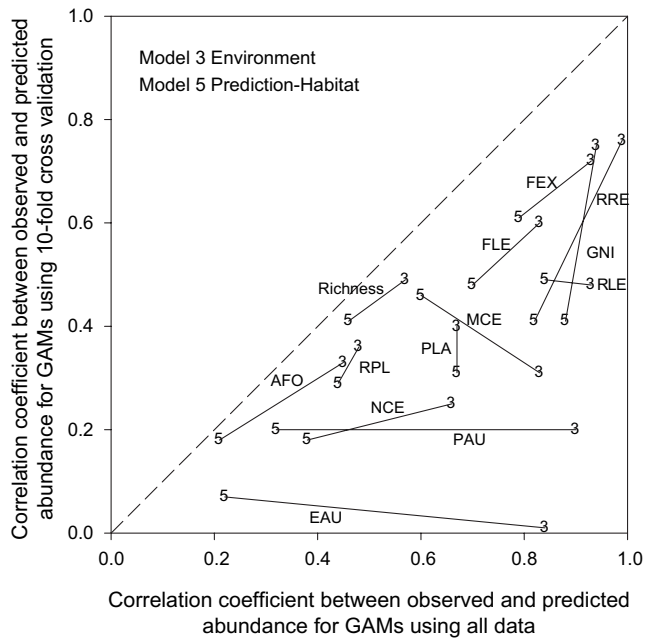
Fig. 8. Performance of a predictive model (Model 5) compared with a descriptive model (Model 3) for the abundance of 12 fish species and species richness for the 25-harbour data set. The dashed line is the 1:1 line of equivalence. Numerals indicate model numbers, and solid lines link models for the same species. Three-letter species codes are shown in Table 3.
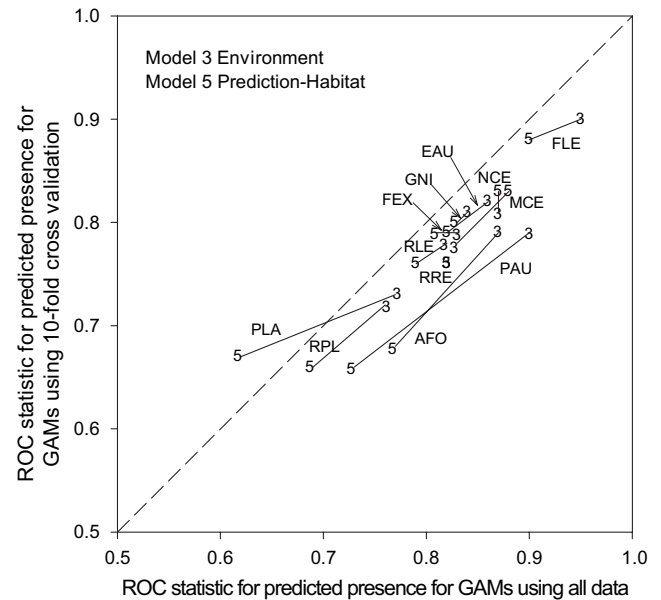

Fig. 9. Performance of a predictive model (Model 5) compared with a descriptive model (Model 3) for the presence of 12 fish species for the 25-harbour data set. The dashed line is the 1:1 line of equivalence. Numerals indicate model numbers, and solid lines link models for the same species. Three-letter species codes are shown in Table 3. Models 3 and 5 were identical for *Retropinna retropinna* (RRE).

Future model development requires environmental variables that describe both the average conditions experienced by fish, and the spatial and temporal variability in those conditions. Attrill (2002) has shown that salinity variation, rather than salinity per se, is a better predictor of invertebrate species diversity in estuaries. Such variables are likely to be more powerful in predicting abundance and occurrence than were the point measurements available in this study, and surrogate variables such as *Distpercent*. Better predictions may also be possible for harbours for which hydrodynamic models exist (e.g., Manukau Harbour: Bell et al., 1998), but few are available in New Zealand. Remotely sensed environmental data (e.g., water colour, temperature, turbidity) are now becoming available at sufficiently fine resolution (2 km or less) to provide synoptic summaries for the habitats of estuarine fishes. Such data are potentially powerful predictors for some of the larger harbours in our study.

Our models also have temporal and spatial limitations. They were based on samples collected in summer, when fish abundance is highest for many species (authors' unpublished data). The applicability of the models to other seasons needs to be tested. Furthermore, our models are limited to harbours in the northern North Island of New Zealand. Harbours further south experience different conditions, notably temperature, that are known to affect the occurrence and abundance of shallow water reef fishes around New

Zealand (Francis, 1996). Thus our models are not necessarily applicable outside the region surveyed.

The independent, 6-harbour validation test spanned two years, so it was not a test of within-season performance. The test was applied only to presence–absence data; the predictive ability of models among years might be expected to be worse for abundance data because of likely variation in year class strength (most fish sampled by beach seine were from the 0+ and 1+ age classes). Year class abundance in estuaries varies as a result of both pre-settlement and post-settlement processes (e.g., Petrik et al., 1999; Potter et al., 2001; Neuman and Able, 2003; Smith and Sinerchia, 2004). Few studies have so far investigated the inter-annual stability of fish-habitat relationships, leading to suggestions that "efforts to quantify essential fish habitat will be limited in their effectiveness until inter-annual variability can be assessed" (Able, 1999). But prediction across years is necessary (unless the resources exist to conduct within-year sampling whenever research or management questions need to be addressed), so the performance of our predictive models for the 6-harbour data set may be a more realistic reflection of their practical utility.

Beach seine nets are inherently selective. The main sampling biases result from the escapement of very small fish through the meshes, and the escapement of large fish around or over the net. Our models clearly apply only to the part of the fauna that is both vulnerable to capture by beach seines, and available in the area sampled;
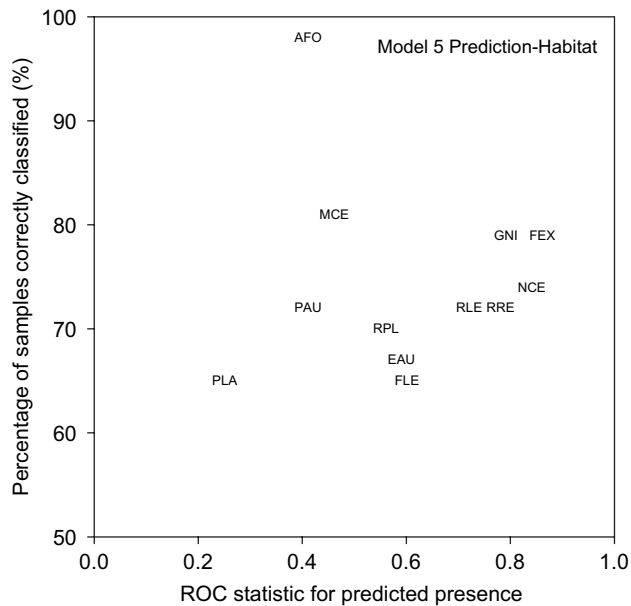
Fig. 10. Performance of a predictive model (Model 5) for the presence of 12 fish species for the 6-harbour data set as measured by the ROC statistic, and the percentage of samples that were correctly classified (assuming that a threshold probability greater than or equal to 0.5 represents a predicted presence). Three-letter species codes are shown in Table 3.

i.e. small or juvenile fishes that have limited avoidance behaviour, and which inhabit intertidal flats and the upper subtidal fringe of shallow harbours. The poor performance of models for some species may be attributable to their low vulnerability or availability to the nets. For example, *Pagrus auratus* mainly inhabits deeper channels and the central parts of harbours that were not sampled in this study (authors' unpublished data), suggesting that beach seine samples are not appropriate for monitoring and modelling their abundance. Similarly, *Engraulis australis* is a schooling pelagic species that may be more abundant in central harbour waters than around the fringes.

Water clarity, salinity and the amount of freshwater inflow were important variables in describing and predicting the abundance and occurrence of fishes. This is not surprising, given that these variables reflect some of the major physical processes that occur in estuaries, and have been shown to affect fish and macro-invertebrate species richness, abundance and biomass in other estuaries (Thiel et al., 1995; Marshall and Elliott, 1998; Wagner and Austin, 1999; Whitfield, 1999; Ysebaert et al., 2002; Martino and Able, 2003; Maes et al., 2004). Other variables were also important, and inspection of the relationships between each variable (or each level in the case of categorical variables) and species abundance revealed that the GAMs were generally interpretable and plausible.

The fish assemblages identified by CA and WCA were generally consistent with the results of the Model 3

GAMs (Table 5). Of the five Assemblage 1 species for which GAMs were developed, four showed a negative relationship with *Clarity* (they were more abundant at low clarity stations), and three showed a positive relationship with *Distpercent*, *Complexity*, and one or more of the mud levels of *Substratum*. These results suggest that Assemblage 1 species are associated mainly with the muddy, turbid, upper reaches of harbours that have a complex coastline. Of the three Assemblage 2 species for which GAMs were developed, all showed a positive relationship with *Salinity*, and two showed a positive relationship with *Depth* and the 'seagrass present' level of *Vegetation*. Assemblage 1 species apparently prefer higher salinity waters, seagrass beds, and deeper water (either channels adjacent to the tidal flats or surface waters away from the shore).

The assemblage composition also reflects larger scale biogeographic factors. Four of the seven Assemblage 1 species (*Favonigobius exquisitus*, *Mugil cephalus*, *Grahamina capito*, *Chelidonichthys kumu*) were most abundant in harbours on the west coast of North Island (the remaining three species occurred in similar numbers on both coasts). Conversely, three of the five Assemblage 2 species (*Notolabrus celidotus*, *Pagrus auratus*, *Girella tricuspidata*) were most abundant on the east coast (the remaining two occurred in similar numbers on both coasts). Similar large-scale patterns are apparent in western and north-eastern Atlantic estuaries (Vieira and Musick, 1993; Elliott and Dewailly, 1995).

Despite the limitations of our data and models, we believe they will be useful within the northern North Island for planning intensive process-based research, and for guiding the management of human activities that impinge on coastal marine environments. Detailed results of the GAMs for individual species will be reported elsewhere. Furthermore, we have recently sampled harbours in the south-eastern South Island and Stewart Island of New Zealand using the same methods, and are currently extending our modelling to those areas.

Our approach has widespread applicability elsewhere, and our results lead to several recommendations that may assist other researchers. We identified patterns in estuarine fish abundance over a large spatial scale that has rarely been achieved previously (but see Vieira and Musick, 1993; Edgar et al., 1999). Failure to survey a sufficiently large spatial scale may result in predictive models that do not account for major regional variability. It may also result in the omission of important predictor variables from the models, or conversely, the inclusion of unimportant variables, thus limiting their utility. The use of GAMs to identify predictive environmental variables is uncommon in marine studies but should become routine in the future. Many of the relationships between fish abundance and environmental variables in our study were non-linear,

indicating that GLMs, which have traditionally been used for this kind of analysis, could provide a poor fit to the data, and erroneous predictions. We have shown that presence–absence models performed better than abundance models, so researchers and managers need to be aware of the trade-off between achieving precise but potentially inaccurate predictions (abundance models) and achieving less informative but more accurate predictions (presence–absence models). Variation in year class strength must be considered if models developed in one year are used to predict fish abundance or presence in another. Information on sediment and vegetation characteristics of the fish habitat can significantly enhance the predictive capability for some species, and is probably worth collecting despite the additional expense.

Acknowledgements

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