Predictability of cockle (*Austrovenus stutchburyi*) population trends in New Zealand's northern North Island

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ABSTRACT

Population monitoring programmes are used to gain knowledge about system functioning or about the response of a system's state to management measures. The current study provided an assessment of comprehensive monitoring data of intertidal bivalve populations in northern New Zealand. In this region, a number of bivalve species are targeted in recreational and customary fisheries, including cockles (*Austrovenus stutchburyi*) that are one of the main target species. To monitor the sustainability of cockle populations, regular population surveys have been conducted since the 1990s at different northern New Zealand sites, although the sampling frequency has varied greatly across sites. Furthermore, a general lack of fishing data for the target populations prevents a systematic assessment of management measures and population trends within a fishery assessment framework. In view of these shortcomings, the current study provided a systematic phenomenological assessment of the survey data to make general recommendations about the effectiveness of management and for guiding prioritisation and design for future surveys. The assessment was based on a Bayesian state-space model that simultaneously analysed monitoring data from 21 incomplete survey time-series between 1999–2000 and 2014–15. The model showed that the predictability of estimated large-size cockle densities was highly site-specific. Across all sites, the predictability of density trends could be used to guide the prioritisation of sites to be included in the survey, or to adjust the sampling frequency at individual sites. Based on the current analysis, existing management measures in the form of fishery closures at some of the sites appear to be effective in allowing recovery of depleted cockle populations. Only those sites that had management measures in place showed an increase in large cockle densities. In the absence of fishing data, adaptive management and targeted intervention could be used to further assess the efficacy of management measures.

Keywords: shellfish populations, population monitoring, state space models, marine reserves

INTRODUCTION

Population monitoring programmes are usually implemented for a combination of scientific and management purposes: scientific monitoring aims to learn about the system functioning, whereas monitoring for management aims to learn about the system state and its response to management (Lyons et al., 2008; Yoccoz, Nichols, and Boulinier, 2001). Regardless of the specific purpose, any monitoring is ideally set up with clear objectives, which, in turn, determine the types of data to collect, as well as other aspects of the sampling design, such as sampling frequency and intensity (Yoccoz, Nichols, and Boulinier, 2001). In both types of monitoring, the data can be used to distinguish competing hypotheses of how the system functions. Furthermore, within an adaptive management process, the feedback between management action and system response is used to establish better management and improve the monitoring (Lyons et al., 2008).

While clear objectives can facilitate the establishment of well-defined monitoring programmes, many monitoring programmes are set up as "blanket surveillance" programmes that lack clear objectives or reflect *a priori* ignorance about the system (Nichols and Williams, 2006), making it impossible to set priorities. When there is a lack of data at the outset, the monitoring is often carried out to provide first information about a system state and its functioning, which can (and should) then lead to improved monitoring in the future within an adaptive management cycle.

Learning about system properties from surveillance monitoring is thus a requirement for improv-

ing knowledge of the system and future monitoring in systems that are data- and knowledge-poor. At the same time, inferring system properties retrospectively from surveys not purposefully designed for a particular analysis introduces a range of pitfalls (Nichols, 1999; Nichols and Williams, 2006; Walters, 1997). Such data are often incomplete and may not have the properties needed to test particular system properties (Nichols and Williams, 2006). Even where adaptive management and associated monitoring aim to improve system understanding and management, learning about system properties can be challenging, when data are not collected with a particular hypothesis and analysis in mind. Furthermore, a number of processes influence populations and introduce complex temporal and spatial patterns (Bjornstad and Grenfell, 2001). For this reason, data need to be embedded in a framework that incorporates these sources of uncertainty (Barker and Sauer, 1992; Calder et al., 2003; Nichols, 1999).

Coastal and estuarine systems present unique challenges in this respect, concentrating the ecological complexity of the land-sea interface, where dynamics acting on relatively short timescales, such as weather patterns and hydrodynamic regimes interact with patterns acting over longer timescales, such as long-term coastal erosion and ocean acidification at ocean-basin scales. Furthermore, human population density and activity are often concentrated on coasts, adding an increasingly important dimension of socio-economic complexity to coastal ecological systems.

This study focused on intertidal bivalves in northern New Zealand, where their populations are found in this realm of socio-ecological importance and complexity: species such as cockle (tuangi, or littleneck clam, *Austrovenus stutchburyi*) and pipi (*Paphies australis*) are valued species in recreational and customary fisheries throughout New Zealand, and treasured as traditional Māori food (kai moana) (Hartill, Morrison, and Cryer, 2005; Hauraki Mori Trust Board, 2003). Both species are found in a range of sheltered and semi-enclosed marine habitats such as embayments, estuaries, and harbours, where they frequently form high-density patches and extensive beds within intertidal sediments, with population densities exceeding 1000 individuals per square metre (Hooker, 1995; Morton and Miller, 1973).

These bivalve populations are influenced by biological variability and ecological complexity, making their science-based management difficult. For example, the distribution of intertidal bivalves is fragmented into populations (or sub-populations) at individual beaches or estuaries, with unknown levels of fishing at each site. As bivalve population dynamics can be driven by a host of factors (see Hartill, Morrison, and Cryer, 2005, for a discussion of these factors), complete monitoring to identify these factors and to elucidate their role and relative importance at each site is challenging at best, and generally involves substantial data collection. This difficulty was highlighted in a recent assessment of non-commercial fishing of bivalve populations in northern New Zealand (Hartill, Morrison, and Cryer, 2005). Although there was a clear sign of fishing impact at the study sites, even sites that were in relative close proximity differed greatly in their dynamics. This finding led the authors to conclude that better data on fishing pressure would not necessarily provide certainty about sustainable fishing levels at individual sites (Hartill, Morrison, and Cryer, 2005).

In northern New Zealand, cockle and pipi populations are monitored in a survey programme (henceforth "AKI surveys", in keeping with the official acronym for Auckland intertidal bivalve surveys), that is commissioned by the Ministry for Primary Industries (MPI). Within this monitoring programme, a subset of (usually 12) northern North Island beaches and estuaries is sampled most years (i.e., the survey did not take place in some years). The main objective of the survey series has generally been to provide abundance and density estimates of both bivalve species at the selected sites, and to compare these estimates with those from previous surveys (e.g., Berkenbusch and Neubauer, 2015). To date, there has been no clearly formulated scientific rationale that informs which sites are surveyed each year, and the survey effort is often directed to sites that receive public attention. As result, sampling is irregular at all sites, with some sites more intermittently surveyed than others. In addition, several sites have only been surveyed once as this initial sampling revealed low numbers of individuals, and a lack of infaunal bivalve populations. In addition to the AKI surveys, cockle populations at some of the sites are included in an annual community shellfish monitoring programme, coordinated by the Hauraki Gulf Forum (Ross and Tyler, 2012).

In view of the ecological complexity associated with coastal systems, and the difficulty to determine population dynamics at individual sites, the data from the AKI survey series are not ideally suited for identifying system behaviour. In the absence of a more mechanistic understanding of population dynamics at individual sites, forms of adaptive management can provide insights into overall coherence of population dynamics, and the importance of fishing and fishing controls for individual sites.

Adaptive management incorporates management measures within an experimental framework (i.e., by randomised assignment of management units to a particular treatment). Within this framework, the effectiveness of management can be assessed through comparative analysis of the outcomes under different treatments (Walters, 1997; Walters, 2007). Recent AKI surveys documented a noticeable decline in the density and abundance of large-size cockle ($\geq$30 mm shell length) (e.g., Berkenbusch and Neubauer, 2015). Based on data showing low or declining population trends at a number of sites, management measures were put in place, including permanent and seasonal closures to allow recovery of adult cockle populations.

These closures have generally been in response to public demand, following a perceived decline and high fishing pressure, with data from recent surveys used to support these closures. Owing to the limited knowledge of factors determining local population dynamics, these fishing regulations are largely an intuitive, and possibly inadequate management tool (Hartill, Morrison, and Cryer, 2005). For example, when significant habitat degradation (i.e., erosion and changes in sediment properties) causes the decline or disappearance of bivalve populations (e.g., as implicated at Waikawau Beach, Coromandel Peninsula; Berkenbusch and Neubauer, 2015), fisheries closures would be ineffective in reversing the population declines. Nevertheless, given that specific management action only targeted what can be considered a random subset of sites with declining populations, these closures have potential to provide information about the expected effectiveness of closures for managing cockle populations.

In this study, we assessed the value of the historical dataset provided by the AKI surveys (and also additional data from the Hauraki Gulf Forum community bivalve monitoring programme) for supporting adaptive management and improvements to the survey design. For this assessment, we used a hierarchical Bayesian state-space model to simultaneously analyse monitoring data from 21 incomplete intertidal bivalve survey time-series from northern North Island, New Zealand. The overall aims of this analysis of the datasets were to i) investigate local predictability of trends to make recommendations that can be used to adjust the sampling frequency; ii) investigate geographical coherence of population dynamics to identify sites that might respond similarly to management; and iii) provide a preliminary review of effects of closures at some of the sites. Combined, these analyses formed the basis of general recommendations for prioritisation of annual sampling effort and general future improvements of the monitoring programme.

METHODS

Northern North Island shellfish survey field methods

The northern North Island shellfish monitoring programme is a series of bivalve surveys that were initiated in 1992 (Morrison et al., 2009). With some changes in the species included in the initials surveys, the overall emphasis of the monitoring programme has been on cockles that are one of the main target species for non-commercial fisheries, and their populations are restricted to intertidal areas. In contrast, pipi populations frequently extend into subtidal areas that are inaccessible to the intertidal surveys, so that monitoring data may only provide incomplete population information and not robust population trends. For this reason, the current study only focused on cockle populations.

Sampling for the monitoring programme involves a subset of (usually 12) northern North Island sites most years, selected from a set of sites throughout a number of regions, including Hauraki Gulf (regional code HAGU), Manukau Harbour (MANU), Coromandel Peninsula (CORO), Bay of Plenty (BPLE), Eastern Northland (ENLD) and Waikato's west coast (WKTO; see Figure 1 and Appendix A for a list of all sites).

Since 1996, the AKI surveys have been based on the same general sampling protocol (Morrison, Pawley, and Browne, 1999; Pawley, 2012). The protocol involved the combination of a systematic design and a two-phase stratified random design (Pawley and Ford, 2007). The stratification accounted for spatial variation along and down the shore. The number of sampling points was chosen to provide estimates of cockle abundance with a coefficient of variation (CV) of less than 20%.

The intertidal sampling uses a pair of benthic cores (15 cm diameter each) that combined sampled a surface area of 0.035 m^2 (to 15 cm depth; see, for example, (Morrison, Pawley, and Browne, 1999; Pawley, 2012)). The sampling depth encompassed the maximum burrowing depths of the infaunal bivalves concerned, which reside in the top 10 cm of the sediment (i.e., 1–3 cm for cockles, (Hewitt and Cummings, 2013); and 8–10 cm for pipi; (Morton and Miller, 1973)).
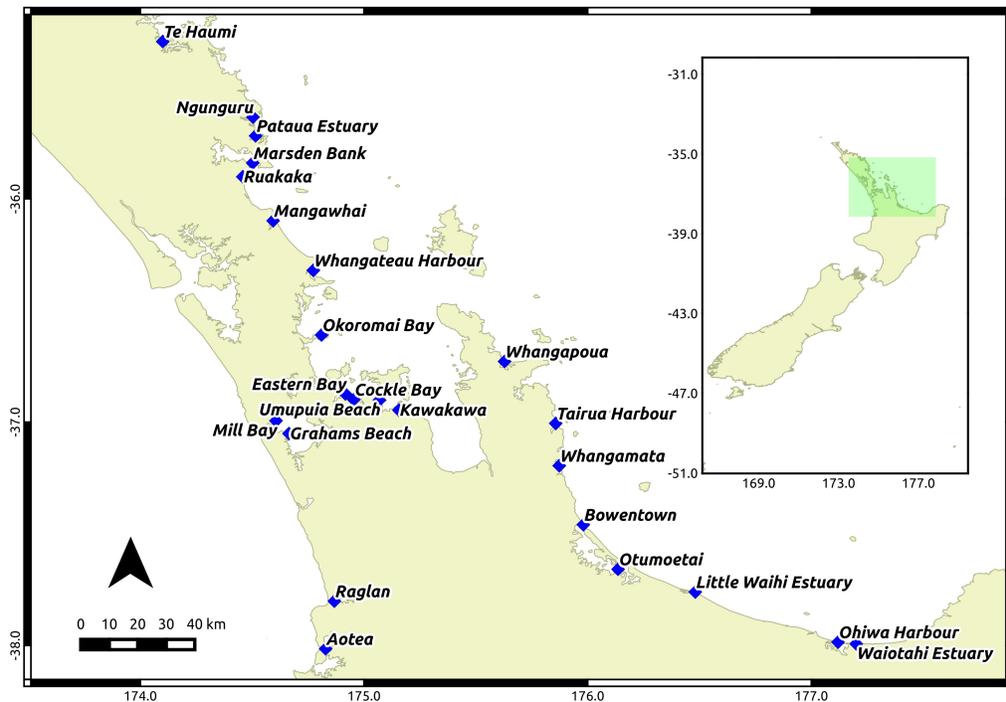
Figure 1. Map of all sites included in the current analysis of bivalve monitoring surveys in northern New Zealand.

Hauraki Gulf Forum community shellfish monitoring

In addition to the AKI survey data, the current study included data from the Hauraki Gulf Forum community shellfish monitoring programme to investigate similarity in trends at sites where both monitoring programmes are conducted (see further information about these data in Appendix B).

Data preparation

The present study focused on cockle population densities over time for the period between 1999–2000 and 2014–15. As current management measures involve seasonal or permanent closures at some of the sites in response to perceived trends, a particular focus was on large-size cockles ($\geq$30 mm shell length), which are considered to be primarily targeted and, therefore, most directly impacted by the fishing.

Raw data from all surveys to date were extracted from the MPI beach survey database, for survey dates between the 1999–00 and 2014–15 fishing years (the New Zealand fishing year is between 1 October and 31 September). These data were summarised into estimates of density according to the standard methodology for these surveys. Specifically, for each sampling point, the two cores within each grid cell were considered as a single sampling unit. The local density (individuals per m^2) was then calculated as the weighted average density over all strata, and the associated standard error was calculated (Pawley, 2012). This estimate was obtained for all cockle sizes, as well as for each of two size classes: sub-recruits (i.e., $\leq$12 mm shell length) and large cockles (i.e., considered to be the main target group of fishing; $\geq$30 mm).

As survey strata were not always consistent among all surveys at any one site, survey strata for all surveys and years were manually assessed for consistency. For each site, heuristic rules were then applied to obtain comparable values among surveys. Where strata were inconsistent, the first option was to delete inconsistent strata. For some surveys, however, all strata were inconsistent. For these surveys, all strata were kept if the overall size of the survey strata did not change, thus assuming that strata covered similar geographical areas. If this was not assured, the site was deleted from the present analysis for lack of comparability through time.

Data analysis

Estimates of cockle densities over time at each site were analysed using Bayesian time-series models. This chosen modelling framework accounts for the lack of information about fishing or demographic parameters of these bivalve populations. Furthermore, no single survey time series was complete (i.e., no site was surveyed each year) and many sites had been surveyed less than three times overall. The latter sites were not included in the current analysis, as time series with less than three time points generally provide little to no information about system dynamics. For this reason, only sites with at least three surveys were included here (Figure 1). Moreover, only sites where at least one estimate for large-size cockle densities exceeded 10 cockle per m^2 were included, in an attempt to *a priori* exclude sites that appear to be unsuitable for these animals.

Time-series model

We employed a Bayesian state-space framework to fill in the time series and jointly model time series across all sites. This framework has the advantage that it can easily deal with missing values in the survey time series, and in a hierarchical (random-effects) setup, information about system dynamics can be shared amongst individual sites (e.g., Clark and Bjornstad, 2004; Thorson and Minto, 2015). The modelling focused on the dynamics of large- size cockle ($\geq$30 mm shell length) densities; however, for comparative purposes, the model was also run for pre-recruit cockle densities and overall densities (see section below). In the state-space framework, estimated cockle densities from surveys were treated as observations with known error, which we assumed follow a truncated normal distribution. The model for the estimated density $z_{i,y}$ from survey i in year y with variance $\varepsilon_{i,y}^2$ can thus be written as:

$$z_{i,y} \sim TN(d_{i,y}, \varepsilon_{i,y}^2, 0),$$

where TN is the truncated normal distribution, and the third parameter is the lower truncation limit.

The process equation models the true underlying density dynamics (those of d_i). The density is assumed to follow a mean-reverting auto-regressive process. This assumption means that in the absence of any observations, the time series will revert to the long term mean of the time series. While clearly not realistic, we do not have knowledge of population dynamics and removals that would allow us to make more realistic predictions away from data. Specifically, we assumed that the true mean density $d_{i,y}$ in survey i and year y is gamma distributed, with mean $v_{i,y}$ and variance $v_{i,y}/\tau_i$, where

$$d_{i,y} \sim G(v_{i,y} * \tau_i, \tau_i) \tag{1}$$

$$v_{i,y} = \mu_i + \rho_i(d_{i,y-1} - \mu_i) \tag{2}$$

$$= \rho_i d_{i,y-1} + (1 - \rho_i)\mu_i \tag{3}$$

$$\tau_i \sim G(\alpha, \alpha) \tag{4}$$

$$\rho_i \sim B(\delta, 1) \tag{5}$$

In this formulation, the second line illustrates the mean reversion property of the process. The variable ρ_i is the auto-regressive parameter, and τ_i is a scalar that gives the mean relative to the mean square deviation (i.e., analogous to the inverse of the CV). Both τ and the auto-regressive parameter ρ are formulated as random draws from a population-level distribution over all sites. This formulation allows information on auto-regressive properties and volatility of the time series to propagate from data-rich beaches to data-deficient beaches. The hyper-prior for τ is vague with $\alpha = G(10^{-4}, 10^{-4})$ and the prior for ρ is chosen such that extreme values are unlikely, specifically δ $G(1,1)$ (an illustration of realisations of ρ and τ under these priors is shown in Appendix C Figure C1).

Time-series models have a well known starting value problem, and this problem is especially prevalent when no observation is available for the first time point, as was the case for some of the sites analysed here. In practice, this limitation means that the prior for $d_{i,1}$ is difficult to specify, namely $v_{i,1}$ is not defined by Equation 3. The *a priori* expectation according to Equation 3 is that $v_{i,1} = \mu_i$ (i.e., as autocorrelation tends to zero), and it thus seemed reasonable to set the prior mean to μ_i, together with a reasonably large variance to accommodate the possibility that $v_{i,1}$ may in reality not be close to μ_i. In addition, however, when the time series is weakly stationary (i.e., $\rho_i \approx 1$), or a survey time series has large gaps, there may be little information contained in the data about μ_i and hence v_i in regions away from the data. This was the case for early (unsampled) years of the HGF data, as well as some time series in the AKI data (vis the large sampling gap at Eastern Beach in Figure 2). To avoid unreasonable

estimates away from the data, the prior distribution for μ_i were therefore adjusted to approximately reflect observed values, with a larger variance so as not to give too much weight to the prior. This approach meant a $G(0.5, 0.001)$ prior distribution for μ_i was used for total, recruit and HGF cockle densities, and a $G(0.1, 0.001)$ prior distribution for μ_i was used for large-size cockle densities.

The model was estimated using Markov Chain Monte Carlo (MCMC), implemented in the Gibbs sampling software JAGS (Plummer, 2013) and run from R (R Core Team, 2015) using the `R2jags` and `rjags` packages. The model code is given in Appendix D. All models were run with three independent chains starting from different stating values, and were for 100 000 iterations, after discarding 10 000 iterations as burn-in. Convergence was assessed visually and using Gelman-Rubin diagnostics.

Both the auto-regressive parameter and CV will determine the predictability of local trends. For this reason, we used $\rho_i \tau_i$ as a measure of predictability (the predictability index), which can be used to rank beaches in terms of the estimated predictability.

Investigating trend coherence

We used a posterior cross-correlation based approach to investigating coherence (similarity) of estimated cockle density dynamics. First, we investigated similarity of dynamics among large-size cockle densities at all sites by estimating the time-series cross-correlation $\gamma_{i,j}$ between sites i and j as a functional of the posterior distribution of the true density dynamics for all combinations of sites. This investigation resulted in a matrix of cross-correlations among sites for each MCMC sample:

$$\gamma_{i,j}^s = \frac{\sum_y (d_{i,y}^s - \bar{d}_i^s)(d_{j,y}^s - \bar{d}_j^s)}{\sigma_{d_i}^s \sigma_{d_i}^s}, \tag{6}$$

for sample s of the MCMC. We then used posterior summaries $\hat{\gamma}_{i,j}$ (namely, the posterior mean, and the posterior probability of the cross correlation being positive) as measures of coherence.

In order to better visualise similarity in dynamics, we transformed the resulting posterior summary of cross-correlation into a distance using $d_{i,j} = (1 - \hat{\gamma}_{i,j})/2$. We then performed hierarchical clustering (using the complete linkage setting in the R's default `hclust` function) on the distance $d_{i,j}$. We then used the order of the resulting clustering to re-order and visualise the matrix of $\hat{\gamma}_{i,j}$. Colouring the clustering dendrogram by region provided information about regional coherence in cockle density trends.

As a second question, we sought to investigate whether densities of sub-recruits at sites were correlated with the density of large-size cockles in subsequent years. For this question, we independently estimated time series for large-size cockles and sub-recruits, and calculated their cross-correlation with a time lag of two or three years.

Are beach closures associated with recovery?

The basic model outlined above can be slightly modified to investigate weather closures at beaches are correlated with increasing large-size densities at those sites. To this end, we wrote the process model in terms of growth rates in density, dropping the mean reveerting porperty as this property was found to make it difficult to explicitly investigate closures. The porcess model to investigate closures was therefore:

$$v_{i,y} = r_{i,y} \times d_{i,y-1}, \tag{7}$$

and express the growth rate in terms of an overall mean trend m and a closure effect

$$log(r_{i,y}) = m_i + \beta_i I_{i,y-1}, \tag{8}$$

where $beta_i$ is the beach specific closure effect and $I_{i,y-1}$ is an indicator variable indicating whether the the beach had been closed in year $y-1$ (i.e., we expect closure effect to be present from th year following a closure). The prior for both β_i and m_i was specified hierarchically; the mean was given a vague N(0,1000) prior and a population variance was estimated from gamma prior; $G(0.001, 0.001)$.

Extending the model to include HGF data

To include the Hauraki Gulf Forum data, we used the same stat-space model (Equation 3), with the assumption that at sites which have been surveyed for both programmes, the data reflect the same underlying trend, but with a site specific offset ω_i that is estimated within the model. Specifically, the model

for the estimated density from the HGF data, $z_{i,y}^{HGF}$, from survey i in year y was formulated as:

$$z_{i,y}^{HGF} \sim TN(d_{i,y} + \omega_i, \varepsilon_{i,y}^{HGF}, 0)$$
$$\omega_i \sim N(\eta, \xi)$$

The ω_i are thus estimated hierarchically, such that there is thought to be a distribution of offsets centered on the mean offset η. Note that we assumed that offsets were due to methodological differences, such that at beaches with multile HGF sites, we estiamted a single mean trend for the HGF data.
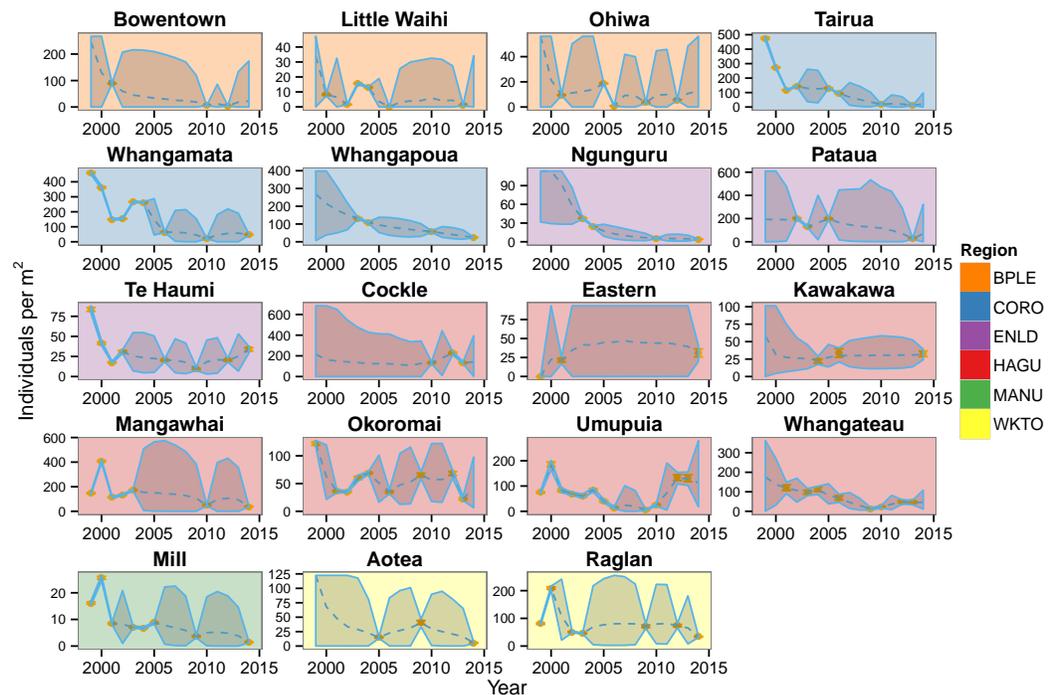
RESULTS

Predictability of local trends

Figure 2. Estimated trends (dashed lines) of large-size ($\geq$30 mm shell length) cockle densities (per m^2) at all sites, using a Bayesian auto-regressive model. Points and intervals show individual survey estimates and their associated standard deviations. Colours indicate regions - BPLE: Bay of Plenty, CORO: Coromandel Peninsula, ENLD: Eastern Northland, HAGU: Hauraki Gulf, MANU: Manukau Harbour, WKTO: Waikato.

Our state-space model generally seemed to follow population trends well (Figure 2), but the predictability of estimated large-size cockle population density dynamics was highly site-specific (Table 1). Uncertainty increased rapidly away from survey estimates, depending on autocorrelation relative to volatility at each site. The posterior distribution for the auto-regressive parameter ρ_i was highly variable among sites (Table 1, Appendix C Figure C2), resulting in a wide predictive distribution for the autocorrelation parameter, albeit slightly skewed towards high autocorrelation (i.e., skewed towards 1; Appendix C Figure C3). Distributions of ρ_i for sites on Coromandel Peninsula were generally high and relatively certain, with most of the density located at $\geq$0.65, reflecting smooth trends and low year-to-year variability. Conversely, other sites such as Ohiwa Harbour and Okoromai Bay had low estimated autocorrelation coefficients, reflecting variability around a quasi-stationary mean density. Sites with relatively few surveys overall (e.g., Aotea Harbour) or with few surveys in successive years (e.g., Kawakawa

Table 1. Posterior median autocorrelation ρ and scaled variance (Var$_s$) and posterior percentiles (5th, 50th and 95th percentile) for the predictability index (PI) for all analysed sites, estimated from the Bayesian time-series model. Larger values for auto-correlation and the predictability index suggest higher predictable cockle densities year-to-year, while a larger variance suggests more volatile time-series. The regions were BPLE: Bay of Plenty, CORO: Coromandel Peninsula, ENLD: Eastern Northland, HAGU: Hauraki Gulf, MANU: Manukau Harbour, WKTO: Waikato.

Beach	Region	ρ	$Var_{i_{sc}}$	PI		
				5%	50%	95%
Bowentown	BPLE	0.54	1.77	0.01	0.39	1.46
Little Waihi	BPLE	0.40	12.60	0.01	0.11	0.29
Ohiwa	BPLE	0.22	9.82	0.00	0.06	0.22
Tairua	CORO	0.65	19.55	0.07	0.15	0.24
Whangamata	CORO	0.67	39.27	0.04	0.11	0.17
Whangapoua	CORO	0.84	1.77	0.12	0.63	1.35
Ngunguru	ENLD	0.62	0.49	0.27	0.88	1.83
Pataua	ENLD	0.66	41.02	0.01	0.09	0.27
Te Haumi	ENLD	0.33	4.41	0.02	0.16	0.33
Cockle	HAGU	0.52	33.80	0.01	0.07	0.22
Eastern	HAGU	0.44	11.70	0.01	0.11	0.44
Kawakawa	HAGU	0.51	1.01	0.03	0.43	1.70
Mangawhai	HAGU	0.43	86.64	0.00	0.04	0.10
Okoromai	HAGU	0.26	9.12	0.01	0.08	0.24
Umupuia	HAGU	0.73	32.23	0.04	0.12	0.21
Whangateau	HAGU	0.79	8.50	0.08	0.27	0.47
Mill	MANU	0.59	3.52	0.06	0.31	0.59
Aotea	WKTO	0.48	10.33	0.01	0.13	0.44
Raglan	WKTO	0.40	31.10	0.01	0.07	0.17

Bay West) had broader distributions for ρ_i, with little information provided by the posterior predictive distribution.

Similarly, the variance (scaled to the mean) showed considerable variability, even within individual regions (Table 1, Appendix C Figure C4). The posterior distributions for τ_i were generally more peaked, with high variability estimated for Mangawhai and Whangamata harbours. For both these sites, density estimates fluctuated strongly during initial surveys, followed by a period of relative stability. Nevertheless, the initial fluctuation introduced relatively high uncertainty about true densities between survey data points.

The predictability index, which uses $\rho_i\tau_i$ as a measure of predictability, showed strong patterns within regions (Figure 3), mirroring differences in time-series variability and autocorrelation. Sites with smoothly declining trends, such as Whangapoua Harbour on Coromandel Peninsula and Ngunguru Estuary in eastern Northland, had the highest and most certain predictability indices, with a posterior mode at approximately 1. Other sites with smooth trends or stable populations but a small number of surveys, such as Kawakawa Bay West), had posterior predictability modes near 1. Nevertheless, the posterior distributions at these sites also showed substantially more uncertainty, owing to the lower sample size. Pre-recruit density time-series, estimated independently from large-size densities (Figure 4), seemed to provide little information about large-size densities two to three years ahead (Figure 5). Many of the distributions of cross-correlations showed overlap or were close to zero. Only Umupuia Beach showed a relatively strong correlation between pre-recruit and large-size densities. Nevertheless, there was a noticeable trend of negative cross-correlations for beaches with declining trends for large-size cockle (e.g., Whangamata, Whangapoua and Tairua harbours), and estimated trends of pre-recruits at these beaches were generally positive (Figure 4).

Similarity and regional coherence of trends

Posterior cross-correlation among sites showed only limited regional coherence. There were three generally well-defined sub-trees in the dendrogram defined by the dynamic clustering (Figure 6, Appendix
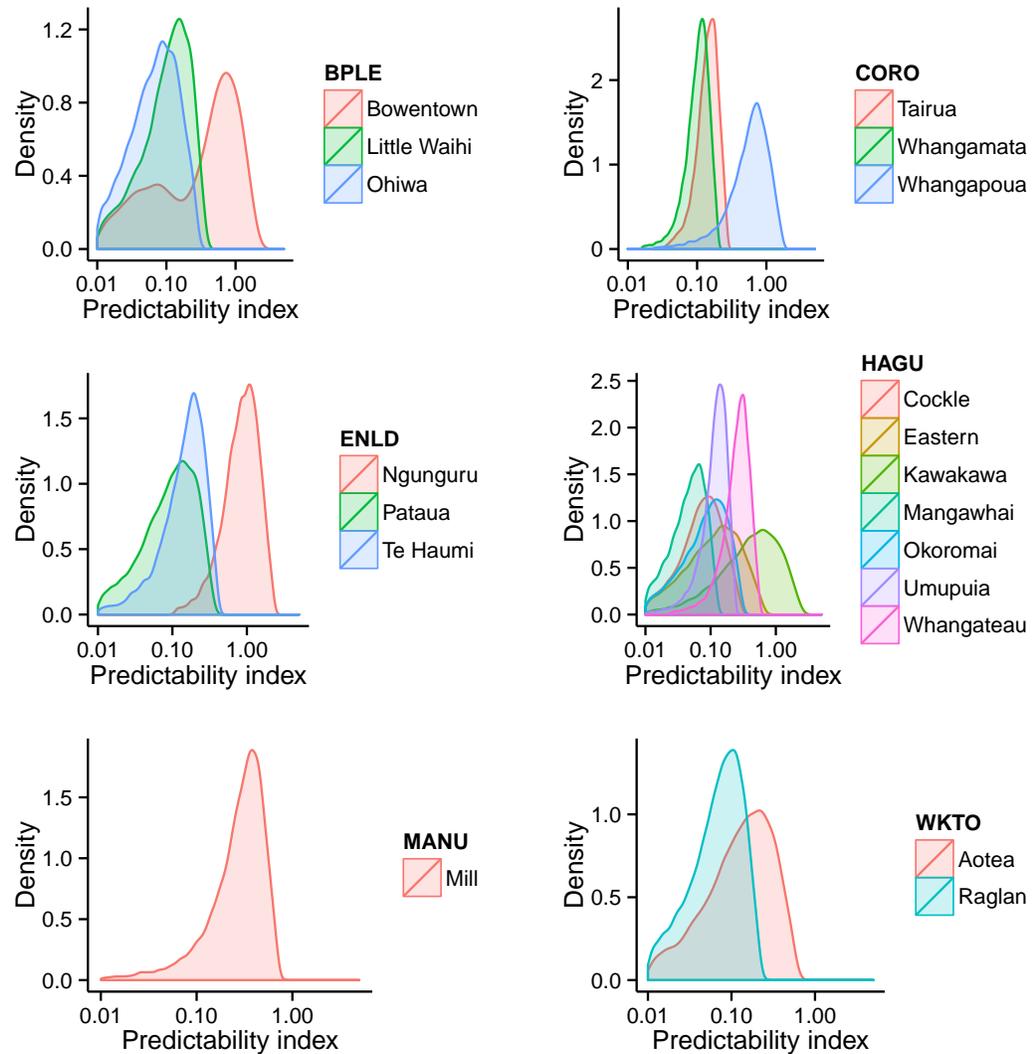
Figure 3. Posterior density estimates for the predictability index at each site. A larger value for predictability index suggests higher predictable cockle densities year-to-year. Abbreviations indicate regions, including BPLE: Bay of Plenty, CORO: Coromandel Peninsula, ENLD: Eastern Northland, HAGU: Hauraki Gulf, MANU: Manukau Harbour, WKTO: Waikato.

C Figure C5). Nevertheless, only one cluster was clearly dominated by a single region. This cluster was defined along the lines of sites with increasing trends and flat trends (Kawakawa Bay West, Eastern Beach and Cockle Bay), whereas the other clusters were defined along sites with trends ranging from declining to stable.

The clearest regional clusters were found in the most similar regions of the two main clusters. Three of the five most strongly related sites (Whangapoua, Tairua and Whangamata harbours) were in the Coromandel Peninsula region, all showing strong but smooth declines in large-size cockle densities. The three sites with the most distinct increases in cockle densities (Eastern Beach, Cockle Bay, and Kawakawa Bay West) were in the Hauraki Gulf region.

Are beach closures associated with recovery?

Closures were associated with a clear positive change in the trend estimate at all sites (Figure 7, Table 2). This change resulted in a high likelihood (81-86%), where the posterior distribution peaked near a growth rate of one. Posterior mean estiamtes of growth rates were between 17% at Eastern Beach and 24% at
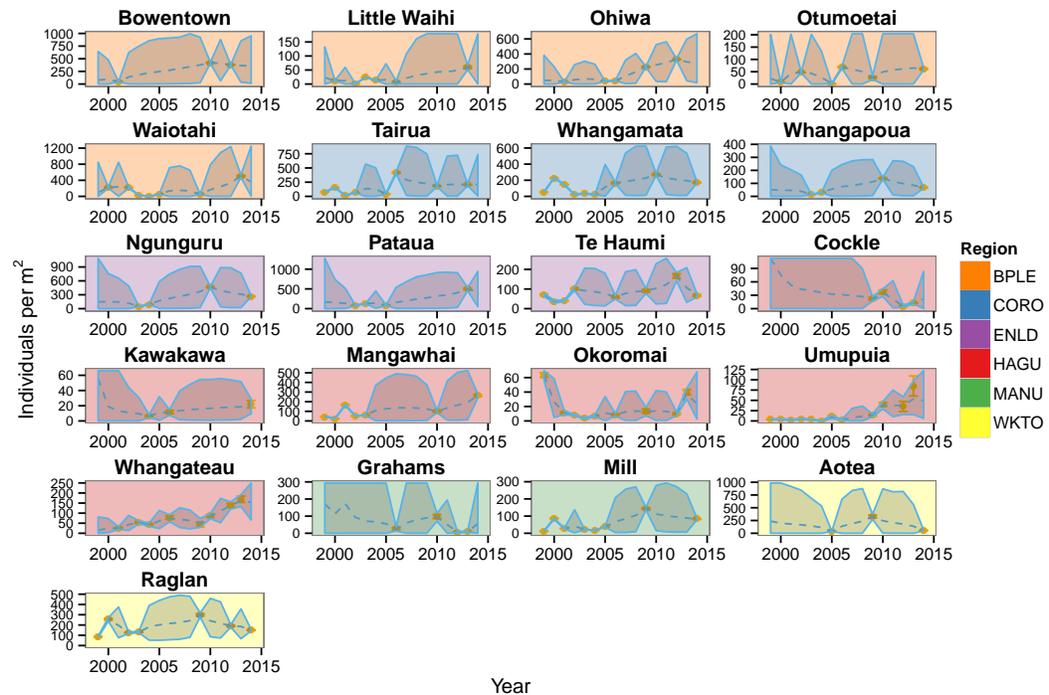
Figure 4. Estimated trends (dashed lines) of pre-recruit size (i.e., ≤15 mm shell length) cockle densities (per m^2) at all beaches, using a Bayesian auto-regressive model. Points and intervals show individual survey estimates and their associated standard deviations. Colours indicate regions - BPLE: Bay of Plenty, CORO: Coromandel Peninsula, ENLD: Eastern Northland, HAGU: Hauraki Gulf, MANU: Manukau Harbour, WKTO: Waikato.

Whangateau Harbour, as opposed to negative estimated growth rates of 6% to 9% declines per year prior to closures.

Adding Hauraki Gulf Forum data

Adding HGF data to AKI survey data in the model changed estiamtes away from survey years (Figure 8). In Kawakawa Bay, estimates of trends between 2006 and 2014 AKI surveys from the combined dataset suggest a substantial increase in large Cockle densities followed by a strong decline. In Cockle Bay, estimates from combined data suggest a decline prior to AKI surveys, followed by an increase since 2008. In Whangateau Harbour, the addition of HGF data pulled the estimates prior to 2009 towards higher values, suggesting that the over-all decline between 2005 and 2010 followed a strong peak in large-size densities in 2005, rather than being a continuous decline as suggested by the AKI data alone. In Whangapoua Harbour, the HGF data supported the linear decline inferred from the AKI data alone. Estimated trends from remaining HGF survey sites are shown in Appendix C Figure C6.

DISCUSSION

The aim of this study was to jointly analyse data from all northern North Island intertidal bivalve populations to make recommendations for improving the current monitoring design and guide prioritisation and design for future surveys. Using hierarchical modelling allowed the analysis of data from a large set of surveys across sites. The current study provides a first integrated view across all past surveys, and allowed a more complete analysis of local and regional trends. Notably, we provide evidence that beach closures are very likely to produce population recoveries.

Our investigation of predictability of cockle density trends across all sites can be used to prioritise sites, or to adjust the sampling frequency at individual sites relative to their predictability. Low predictability for Mangawhai Harbour, for instance, would suggest an increase in sampling effort to increase
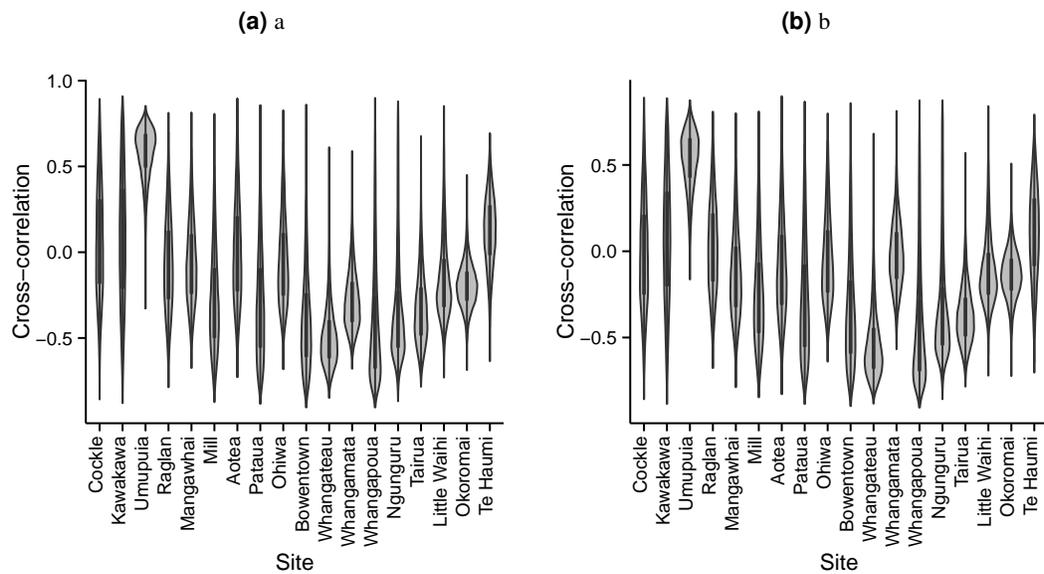
Figure 5. Posterior distributions for empirical cross-correlation estimates for time series of pre-recruits (i.e., ≤15 mm shell length) and large-size cockle (≥30 mm shell length) at the monitoring sites for which models for both large-size and pre-recruit-size were run, with a lag of (a) two years and (b) three years. The violin plot summarises the distribution, with the width of the violin proportional to the posterior density at a given parameter value (i.e., the most likely parameter value is found at the widest point of the violin).

certainty about the status of the cockle population at this site. In contrast, based on high predictability, sampling at Whangapoua Harbour and Ngunguru Estuary could be deemed adequate.

In spite of the Bayesian model inferring high predictability at some sites, the modelling suggested that for the majority of sites, uncertainty about populations was substantial whenever gaps of more than one year existed between surveys. Furthermore, the cross-correlation analysis suggested that pre-recruit densities provide little predictive information about future recruits to the large-size class. It is, therefore, unlikely that these uncertainties in large-size cockle densities can be reduced by considering the full length-frequency distribution. Inversely, contrasting trends in large and pre-recruit size densities at many sites with declining large-size densities point to density dependent mechanisms, with limits to recruitment at high densities. However, even high densities in pre-recruits do not seem translate into increased numbers of large cockle after two to three years. This may be due to harvest pressure being high enough to remove individuals that grow beyond a certain size, but other causes of mortality may be important, such as increased natural mortality in sediments that are suitable for pre-recruit sized cockle but not for large cockle.

Some caution is needed when applying time-series estimates to practical management. In particular, the smoothest and most predictable trends in the dataset are all downward trends towards low values of large-size cockle densities. It would seem advisable to monitor these sites more closely, even if management action has been taken to revert downwards trends. Furthermore, the present model generally assumed that the parameters driving dynamics at each site, namely the auto-correlation and volatility, do not change through time. This assumption means that past sudden fluctuation (e.g., catastrophic events) will influence estimates at sites where they were present. Conversely, this assumption may lead to over-optimistic estimates of predictability at sites where such events have not occurred over the course of the monitoring programme. As it is not possible to implement specific monitoring for these rare events (e.g., Nichols and Williams, 2006), they are generally noticed as they occur at a site (e.g., by members of the public), which may lead to a survey at an affected site.

While our model analysis revealed limited regional coherence in trends of large-size cockle densities, all three sites on Coromandel Peninsula (Tairua, Whangamata, and Whangapoua harbours) had very similar declining trends. They were also among the four sites with the most similarity in population
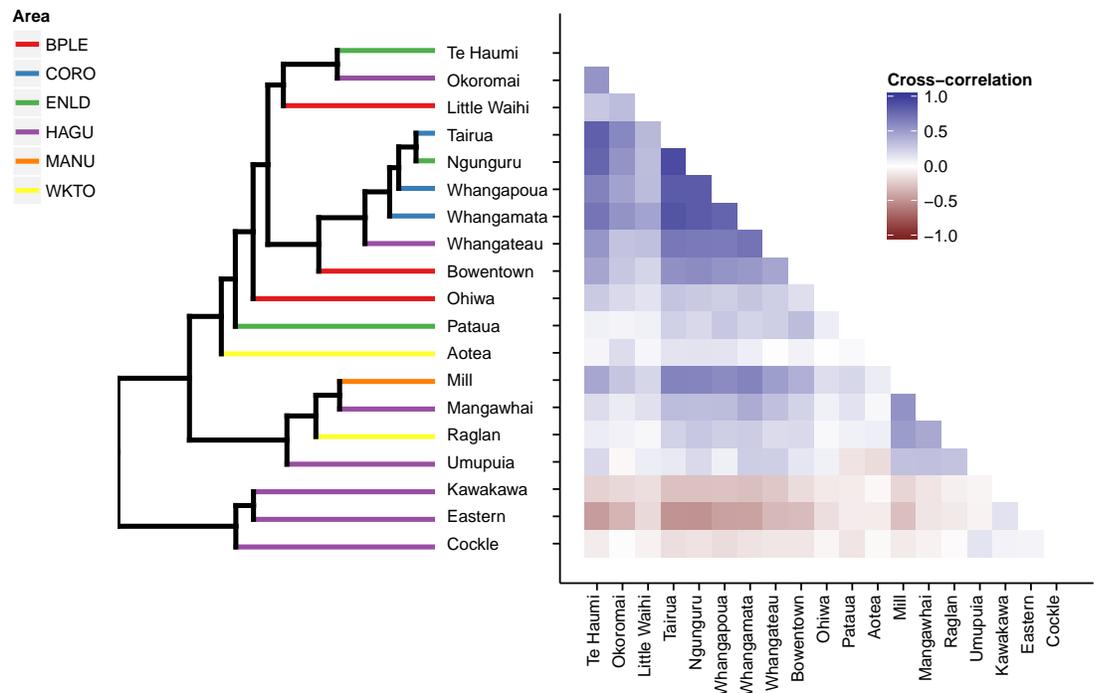
Figure 6. Posterior mean cross-correlation among estimated cockle density time-series at all sites. The tree is based on hierarchical (complete linkage) clustering of cross-correlations (transformed to distance using $d_{i,j} = (1 - \gamma_{i,j})/2$), with branch colours representing regions (BPLE: Bay of Plenty, CORO: Coromandel Peninsula, ENLD: Eastern Northland, HAGU: Hauraki Gulf, MANU: Manukau Harbour, WKTO: Waikato). Cross-correlation Values further from zero indicate stronger correlations (either positive, or negative) and shorter branches indicate sites with higher similarity of dynamics.

dynamics, such that, from a management perspective, it would seem feasible to only survey one of the three Coromandel Peninsula sites per year. However, it remains unclear whether the declines were caused by the same factors at all three sites, such as continued fishing pressure or other environmental factors. As noted above, such downward trends should probably monitored more closely. Thus, instead of lower monitoring effort, surveys at these sites could provide an opportunity to explicitly integrate learning about system functioning into the monitoring objective (e.g., Nichols and Williams, 2006). This could be achieved in an adaptive monitoring framework, in which management actions are taken deliberately to learn about system responses to management. By applying a management measure to one or more sites that have similar characteristics, comparison between sites with and without management measures provides potential to gain insight into responses to management actions.

Contrasting management measures are already present among sites situated in Hauraki Gulf. Specifically, Eastern Beach has been closed to shellfish collection since 1993, whereas Cockle Bay has had a seasonal closure over summer since 2008. Both Eastern Beach and Cockle Bay showed a marked increase in large cockle densities since management measures were implemented, although densities at the former site have changed little between 2002–03 and 2014–15, and there remains considerable uncertainty about the population trajectory between these surveys. Another Hauraki Gulf site, Umupuia Beach (half-way between Cockle Bay and Kawakaway Bay West) showed a general decline in large cockle densities that was followed by an increase after the closure of the site in 2010, although this trend was not significantly positive due to uncertainty associated with recent surveys. Similarly, a more northern Hauraki Gulf site, Whangateau Harbour, showed an increase in densities since the fishery closure in 2010, following a prolonged decline in abundance at this site (including a mass mortality event in 2009). It, therefore, seems that the existing management of fishing pressure has a strong effect, producing desired recoveries in bivalve densities.
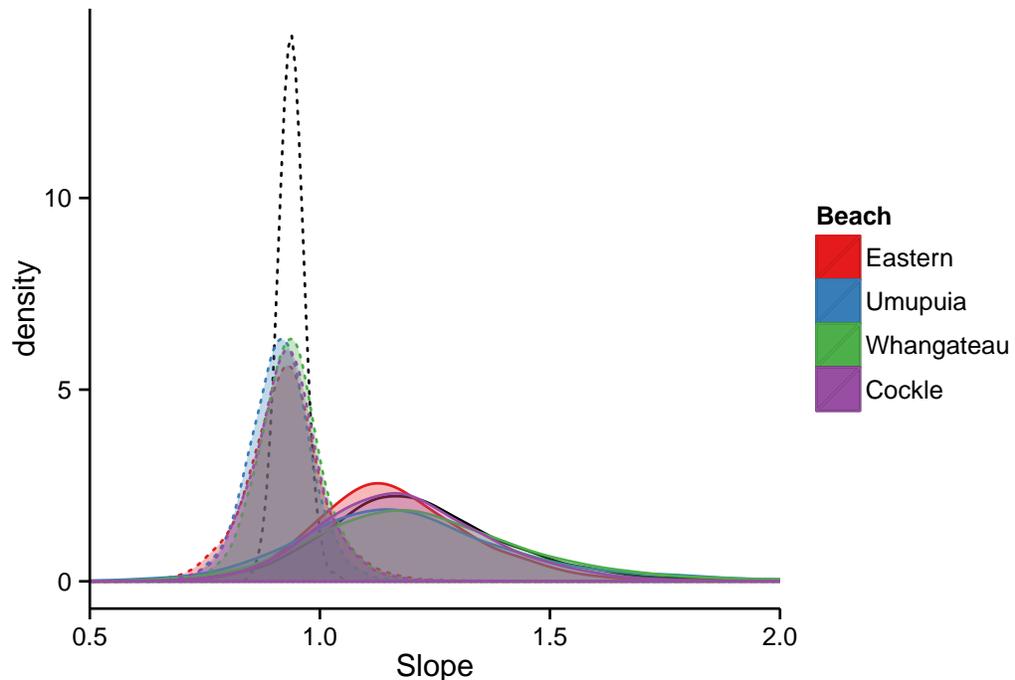
Figure 7. Posterior distributions for the closure effect, showing the estimated yearly change in density pre-closure (dashed lines), and post close (solid lines) for each of four beaches. The estimate of the mean trend across beaches pre- and post closure from the hierarchical formulation is given for comparison (black line).

Population recoveries under closures are perhaps not surprising, given that observed levels of recreational and customary fishing have been shown to strongly impact local cockle populations (Hartill, Morrison, and Cryer, 2005). Nevertheless, at one the sites that have not been closed in this region, Okoromai Bay, cockle densities were relatively stable across the surveys despite a lack of specific management measures. In Kawakawa Bay West, integrated modelling of AKI and HGF data suggested an increase in large cockle densities, followed by a marked decline in recent years. Only the third site, Mangawhai Harbour, showed a continuous decline in the densities of large-size cockles. These findings highlight that factors other than fishing influence exploited populations.

To gain a more mechanistic understanding of population dynamics and to disentangle the effects of fishing from natural variability, it would be necessary to substantially increase the monitoring effort. While this kind of monitoring aimed at understanding system dynamics is standard in commercial fisheries, where catch and effort data, and fishery-independent surveys form the basis for stock assessments, this level of data collection is unlikely to be feasible for these localised, low value, non-commercial fisheries (Hartill, Morrison, and Cryer, 2005). Furthermore, given the difficulty of collecting adequate data on recreational and customary fishing levels, a more complete and mechanistic understanding of population dynamics will likely remain elusive for these bivalve populations. Even comprehensive data collections of some of the bivalve populations included here have been shown to provide insufficient certainty about fishing impacts and sustainable yields (Hartill, Morrison, and Cryer, 2005).

In the absence of data on fishing pressure, adaptive management and targeted management intervention, such as temporary site closures or size limits, can be used to improve knowledge of the efficacy of management measures. This kind of management approach also helps to elucidate the importance of fishing relative to other factors that determine cockle populations, such as habitat characteristics. Paired with improvements to the monitoring programme, such as the inclusion of broad-scale sediment assessments in recent surveys (e.g., Berkenbusch and Neubauer, 2015), adaptive management provides an opportunity to build a level of understanding of factors that determine the observed cockle population

Table 2. Posterior summaries for estimated growth rates pre- and post- closure at beaches with closures. The summaries comprise the posterior mean, the standard deviation (sd) of the posterior distribution and the probability that the growth rate at beach i is positive, i.e., $P(r_i > 0)$.

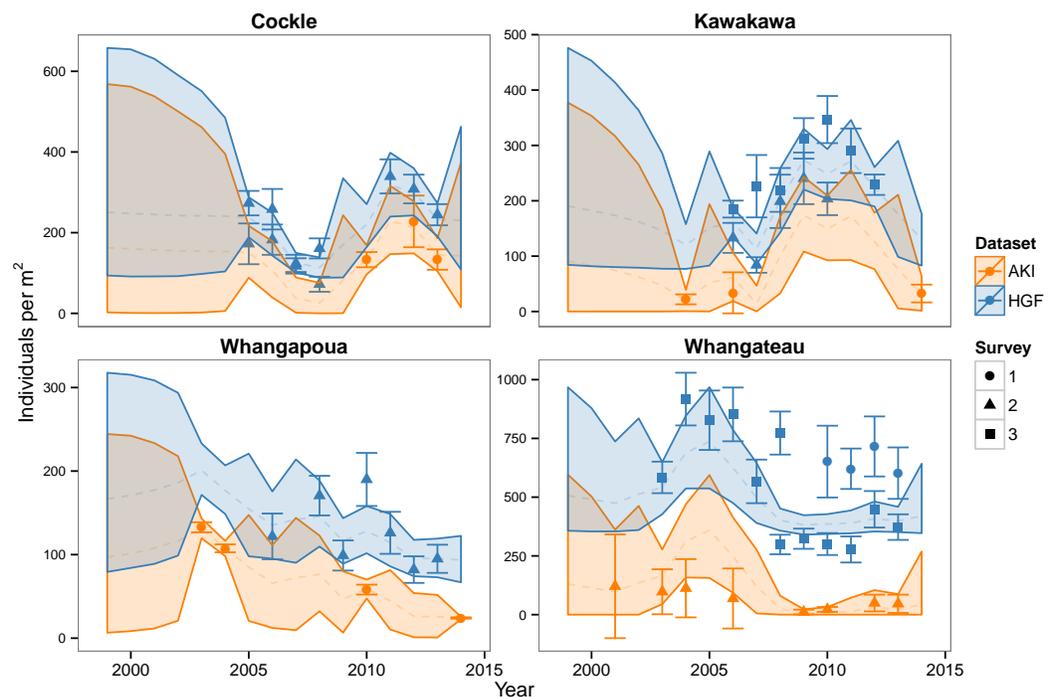| Beach	Closure year	Mean		sd		$P(r_i > 0)$	
		Pre-closure	Post-closure	Pre-closure	Post-closure	Pre-closure	Post-closure
Population trend		0.94	1.22	0.03	0.21	0.02	0.88
Eastern	1993	0.92	1.17	0.09	0.17	0.15	0.85
Umupuia	2008	0.91	1.21	0.07	0.28	0.09	0.81
Whangateau	2010	0.94	1.24	0.07	0.27	0.16	0.85
Cockle	2008	0.93	1.19	0.08	0.18	0.14	0.86

Figure 8. Estimated trends (dashed lines) of total cockle densities (per m²) at sites surveyed by both the Auckland Intertidal Surveys and the Hauraki Gulf Forum community shellfish monitoring programme (colours indicate survey programme), using a Bayesian auto-regressive model. Points and intervals show individual survey estimates and their associated standard deviations. The point shapes differ to differentiate when multiple sites were surveyed at a single beach with the HGF monitoring programme. The underlying trend was assumed to be identical between surveys series at any beach, but offset by a constant between survey series.

dynamics across the northern New Zealand sites.

ACKNOWLEDGEMENTS

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