



Influence of climate on Pelorus Sound mussel aquaculture yields: predictive models and underlying mechanisms

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ABSTRACT: Multiple regression models were used to predict aquaculture production in Pelorus Sound, a 50 km long estuary supporting 68% of New Zealand's greenshell mussel *Perna canaliculus* aquaculture industry (worth NZ\$204 million per annum). Mussel meat yield was modelled using both biological predictors, including seston (indexed by particulate nitrogen, PN), phytoplankton and nutrients collected over 9 yr (July 1997 to November 2005) by the mussel industry, and physical, climatic predictors, including Southern Oscillation Index (SOI), along-shelf winds, sea surface temperature (SST) and Pelorus River flow, held in New Zealand national databases. Yield was best predicted using biological predictors collected locally at the farms inside the sound, but it was also predictable using only physical predictors collected distant from the farming region. Seston (mussel food) was also predictable using the physical predictors. Optimal predictor sets for yield and seston differed between summer and winter half-years. In summer, deep water (which enters the sound through the estuarine circulation) at the sound entrance was nitrate (NO_3^-)-rich during upwelling conditions (negative SOI, NNW wind stress and cool SST). The increased NO_3^- levels, in turn, triggered increased PN within the sound. In the winter half-year, PN was unrelated to upwelling and NO_3^- effects at the entrance and was instead related to river flow. Remotely-sensed SST data showed that in summer, upwelling affected the entrance waters of the sound under negative SOI and upwelling-favourable wind stress, patterns which dissipated in winter. Overall, these results show that time series of physical drivers can be useful for explaining production variation of farmed bivalves and indicate the prospects for using data routinely collected in national databases for predicting mussel yield.

KEY WORDS: Bivalve · Prediction · ENSO · Upwelling · River flow · Estuaries · Phytoplankton · Seston

INTRODUCTION

Predicting the biological yield of aquaculture is important to the industry carrying out the farming. Planning stocking rates on the basis of predicted growing conditions, or predicting the longevity or return periods of poor growing conditions, requires

understanding of the drivers of secondary production of the aquaculture system. Mussel aquaculture relies on suspended seston supply for its nutrition (Figueiras et al. 2002), so it can be expected that variability in seston supply will affect farming success. Seston, in turn, is formed via primary production and is composed of living and detrital material (Verity 2002b),

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so it is reasonable to expect that environmental drivers of primary production will have flow-on effects on seston abundance and bivalve aquaculture performance (Nixon & Buckley 2002). Such linkages mean that if predictive models and understanding of the drivers of seston abundance can be developed, plausible models for predicting mussel yield may follow.

In spite of the importance of developing such predictive capability, relationships between environmental variation and bivalve aquaculture yield have rarely been demonstrated (Kremer et al. 2000). The teleconnections of large-scale climatic drivers, for example between basin-scale El Niño Southern Oscillation (ENSO) dynamics (McPhaden et al. 2006) and local atmospheric and oceanic effects, can be subtle. The way they combine to drive conditions conducive to primary and secondary production within coastal marine ecosystems can be complex and variable (e.g. Monbet 1992, Cloern 2001, Bar-

bosa et al. 2010, Friedland et al. 2012). Overall, processes must be observed across wide time and space scales, to understand their relationships. Large sets of appropriate environmental data (atmospheric, hydrometric and oceanic) are needed, along with aquaculture production information, set against a background of local ecosystem understanding (e.g. Alvarez-Salgado et al. 2008, Barbosa et al. 2010). Such requirements appear to have made predictive models of bivalve aquaculture yield relatively rare.

In considering mussel production in Pelorus Sound, New Zealand (Fig. 1), Zeldis et al. (2008) examined correlations among physical, chemical and biological variables and variation in mussel aquaculture yield. This large estuary supports ca. 68% of the NZ\$204 million per annum, 75 000 t fresh weight, national production of New Zealand greenshell *Perna canaliculus* mussels, which are grown on hundreds of individual farms throughout its main channel,

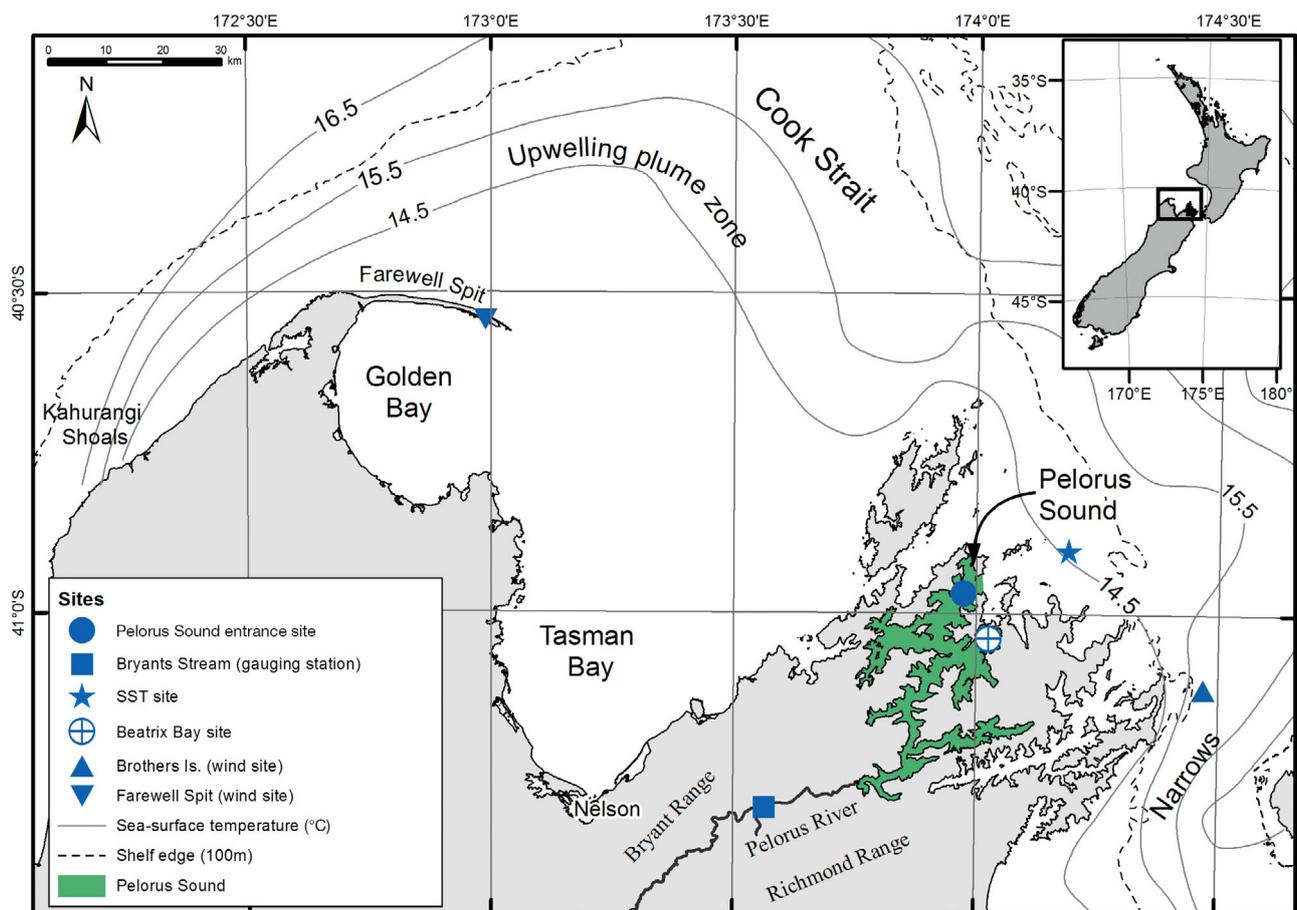


Fig. 1. Central New Zealand: northern South Island (rectangle), including Pelorus Sound (green). Isotherms in Cook Strait show location of upwelling-affected waters in western Cook Strait (from ship survey data collected in summer [January–February] 1980, summarized by Harris 1990). Also shown are western Cook Strait continental shelf (100 m isobath), sampling sites in Pelorus Sound (Beatrix Bay) and at Pelorus entrance, the location of sea surface temperature (SST) data collection, the Brothers Island and Farewell Spit wind gauging stations and the Pelorus River (Bryant's Stream) river flow gauging station

side-arms and embayments (New Zealand Marine Farming Association: www.nzmf.co.nz/industryinfo.asp). Starting in early 1999, farm production in the sound declined by ca. 25% (measured in terms of per capita meat yield), followed by recovery through 2002, resulting in substantial economic impacts and distortions within the industry (Hayden et al. 2000). Similar fluctuations have been observed again in more recent, anecdotal accounts (2007–2008: S. Preece in Marlborough Express of 6 May 2008). Major environmental and economic incentives thus underscored the need to understand the drivers of mussel production in Pelorus Sound.

In disentangling the drivers of mussel yield in this ecosystem, Zeldis et al. (2008) showed that overgrazing by mussels (i.e. top-down effects: Prins et al. 1998, Ogilvie et al. 2000, Møhlenberg et al. 2007, Huang et al. 2008) could not explain the 1999–2002 yield minimum. Instead, bottom-up effects of oceanic and river nitrogen (N) supply were proposed as drivers of the variation in mussel yield, consistent with other studies demonstrating relationships of marine secondary production with N supply (reviewed by Nixon & Buckley 2002). Zeldis et al. (2008) correlated the yields with physical environmental variables (e.g. ENSO, sea surface temperature [SST], along-shelf wind stress and river flow) and chemical and biological variables (e.g. nitrate [NO_3^-], phytoplankton and particulate nitrogen [PN], as a proxy for seston). However, the relationships were not quantified within a predictive model, nor were the underlying biophysical mechanisms of NO_3^- and sestonic food supply in Pelorus Sound well understood.

Here, we present new analyses which quantify the relationships of drivers of mussel yield and seston in the sound, using multiple regression models which include effects of physical 'distal' variables (i.e. those measured distant from the farming region), and more 'local' chemical and biological variables measured in the farming region within the sound. Specifically, the models were used to test 3 hypotheses: (1) that variations in mussel yield can be predicted using observed variations in the large-scale, distal physical variables; (2) that variations in mussel yield can be better predicted from observed variations in local chemical and biological conditions than from large-scale, distal physical conditions; and (3) that the seston food supply for mussels can be successfully predicted using distal variables.

We then explain the predictions of the regression models with investigations of the underlying mechanisms of Pelorus Sound seston and mussel yield variation. Nitrate data collected at the entrance to

the sound where it joins Cook Strait (Fig. 1) were analysed to describe relationships of seston abundance within the sound with 'new' NO_3^- fluxes from Cook Strait and from the Pelorus River. At larger scales, we examined teleconnections of macro-scale forcing with mesoscale upwelling dynamics affecting NO_3^- supply at the sound entrance, using spatial correlations of SST, wind and Southern Oscillation Index (SOI) data, to describe linkages of central New Zealand oceanography with seston biomass variation within the sound. Via our 3 hypotheses, a key question we answer is whether seston abundance and aquaculture yield within Pelorus Sound can be predicted using only the distal physical variables which are routinely available in national databases, or if it is necessary to use local chemical or biological data collected within the farming region.

MATERIALS AND METHODS

Environmental setting

Pelorus Sound is a relatively deep (40 m average), narrow, highly indented drowned valley estuary about 56 km long at the north end of New Zealand's South Island (Fig. 1). Riverine input, dominated by the Pelorus River, and estuarine exchanges with Cook Strait both affect the dynamics of the sound (Bradford et al. 1987, Gibbs et al. 1992, Dupra 2000) with seasonally varying influence (Zeldis et al. 2008). Pelorus River flow rates average 18 and 22 $\text{m}^3 \text{s}^{-1}$ and NO_3^- concentrations average 140 and 170 mg N m^{-3} in summer and winter, respectively (Shearer 1989), such that winter river NO_3^- loads are twice those of summer. River inputs also affect vertical density stratification in the sound, influencing interactions between light and nutrient environments of phytoplankton (Gibbs & Vant 1997, Strayer et al. 2008, Barbosa et al. 2010).

Oceanic effects on the sound are also seasonal. The sound entrance is affected by upwelled waters advected there from the Kahurangi Shoals upwelling zone at the western approaches of the Strait (Harris 1990; our Fig. 1). The upwelling is driven by winds from the west (Harris 1990, Shirtcliffe et al. 1990) and is potentially enhanced during El Niño summers, when the negative SOI state correlates with westerly winds over New Zealand (Gordon 1986, Mullan 1998). This correlation weakens in spring/autumn and disappears completely in winter, when negative SOI correlates with winds from the SW and S, respectively (Gordon 1986, B. Mullan pers. comm.).

Data sources and analyses

SOI data (based on Tahiti and Darwin air pressures) were obtained from January 1979 to May 2009 (Australian Bureau of Meteorology, www.bom.gov.au/climate). Wind velocities were obtained from Brothers Island (Agent 4395) adjacent to Pelorus Sound entrance and at Farewell Spit (Agent 3798; Fig. 1) in NW Cook Strait for the same period (NIWA National Climate Centre). The continental shelf edge adjacent to Brothers Island has an approximate NNW–SSE orientation (330° – 150° ; Fig. 1), so along-shelf (v) components of the winds were calculated with the wind bearings rotated to orient them with the local bathymetry, by resolving the wind vector along -30° (v positive toward 330°). Wind stress was calculated as in Sharples & Greig (1998). Note that in the convention applied here, negative values correspond to wind stress blowing from the NNW and positive values indicate stress blowing from the SSE. Wind stresses at Farewell Spit were extracted on the W–E (270° – 90°) bearing corresponding to the orientation of the shelf occurring at that location (Fig. 1), with wind stress toward 90° being negative and toward 270° positive. Major and minor wind axes were calculated by the methods of Preisendorfer & Mobley (1988) to describe the mean wind variability at the 2 locations. Monthly mean SST was obtained using AVHRR satellite radiometer data (NIWA SST Archive, NSA: Uddstrom & Oien 1999) over the greater Cook Strait region for January 1993 to May 2009 at 5 km^2 resolution. Monthly averaged sea-surface wind stress anomalies (Brothers Island or Farewell Spit) and SOI were correlated with SST at each 5 km^2 pixel location over the greater Cook Strait region from January 1993 (start of the NSA archive) to May 2009. To monitor temperatures specifically at the entrance to the sound, averaged data from a 3-by-3 pixel array centred on 40.90°S , 174.19°E , were used (Fig. 1). Pelorus River flows gauged at Bryant's Stream (Fig. 1) were obtained from the NIWA Climate Centre from January 1979 to May 2009 and were analysed using the methods of McKerchar (2002).

Samples collected weekly for assessing chemical (NO_3^- ; ammonium, NH_4^+ ; PN; and particulate carbon, PC) and biological (chlorophyll a , chl a ; and diatom and dinoflagellate taxon carbon) variables were obtained from Marlborough Shellfish Quality Programme (MSQP) monitoring and analysed as described by Zeldis et al. (2008). Total microphytoplankton carbon biomass was calculated as the sum of these taxa and accounted for an average of 71% of total phytoplankton carbon (Safi & Gibbs 2003).

These variates were obtained in Beatrix Bay (mid-Pelorus Sound; Fig. 1) for the period July 1997 to May 2009. Data on per capita meat yield of mussels were obtained from Sealord Shellfisheries for 11 378 mussel farm long-lines harvested in Pelorus Sound from July 1997 until November 2005 (the end of their data availability). Upon harvest, a sample of 20 mussels from each line was weighed whole, then cooked, shelled and the meat re-weighed, on board the harvesting vessel. Weekly-collected NO_3^- and PN samples from the MSQP station at the entrance to the sound (Fig. 1) were obtained at 40 m depth for the period February 2002 to May 2009 (the start and end dates of their collection period) using a Van Dorn closing bottle and analysed according to Zeldis et al. (2008).

Monthly anomalies of SST, wind stress, river flow, chemical and biological variates and mussel yield were obtained by calculating the mean for each variate for every month in its respective time series, and then subtracting from it the mean for each month over the entire time series.

Regression modelling and correlations

Based on prior knowledge, the seasonality of environmental drivers of the sound (see 'Environmental setting', above) we split the data for our regression models and correlations into 2 sets, representing summer (October through March) and winter (April through September) half-years, with 50 and 48 monthly observations in each, respectively. Table 1 defines the variables used and describes the models used to test our 3 hypotheses. We applied lags of 1 mo between measurement times of biological and physical anomalies to account for the timescale of Pelorus Sound water mass turnover (ca. 20 d; Heath 1976, Dupra 2000) and phytoplankton growth responses (ca. 1 to 2 wk; Chang et al. 2003). Mussel yield anomalies were lagged by 1 mo with respect to biological anomalies and by 2 mo with respect to physical anomalies to account for the response of mussel yield to variable food supply and its physical forcing, respectively (Ren & Ross 2005). Data from July 1997 to September 2005 (the time span of the mussel yield data coincident with the lagged physical data) were used in the regression modelling.

The aims of our modelling were to assess links between local and distal predictor variables (see 'Introduction') and the response variables mussel yield and PN (index of seston), where local variables were chemical and biological data derived from

Table 1. (a) Regression model parameter definitions and (b) model descriptions for predictions of anomalies of mussel yield and particulate nitrogen (PN) concentrations in winter and summer half-years

(a)			
Variable name	Variable definition		Unit
SOI	Southern Oscillation Index		–
Wind	Along-shelf wind-stress anomaly (positive from SSE)		Pa
SST	Sea surface temperature anomaly		°C
Flow	Pelorus River flow anomaly		m ⁻³ s ⁻¹
Nit	Nitrate concentration anomaly		mg N m ⁻³
PN	Particulate nitrogen concentration anomaly		mg N m ⁻³
Chl	Chlorophyll anomaly		mg m ⁻³
Diat	Diatom carbon anomaly		mg C m ⁻³
Phy C	Total microphytoplankton carbon anomaly		mg C m ⁻³
Yield	Average yield of mussels in Pelorus Sound anomaly		%
(b)			
Model type	Predictand	Predictors	Model description
Distal	Yield	SOI, Wind, SST, Flow	Predicts yield as a function of physical ('distal') drivers
Local	Yield	PN, Diat, Nit, Chl, Phy C	Predicts yield as a function of chemical and biological ('local') drivers
Distal	PN	SOI, Wind, SST, Flow	Predicts PN as a function of physical ('distal') drivers
Mean	Yield, PN	Na	Predicts the mean of the observed yields or PN

water samples collected proximal to the mussel farms (in mid-Pelorus Sound at Beatrix Bay) and distal variables were physical data observed remote from the farming locations which were routinely available from national meteorological, hydrometric and remote sensing databases. The predictor variables (Table 1a) for each of these models were chosen specifically to test our 3 hypotheses (Table 1b). In order to nullify the effect of co-variation within the predictor sets, we did not include dissolved inorganic nitrogen (DIN), PC or dinoflagellate C anomalies as predictors in our models because they were highly correlated (Pearson correlation coefficients >0.7) with NO₃⁻, PN and phytoplankton C anomalies, respectively. Ciliates are filtered by *Perna canaliculus* (Zeldis et al. 2004) and were enumerated in the MSQP data. However, their N-specific variation was only 4 to 5% of PN variation in summer and winter, respectively (data not shown) and so was not considered in the regression modelling.

All models were fitted to the data using linear regression and included 2-way interactions between all predictors. Standard forwards and backwards stepwise linear regression was applied to each model to identify the minimal adequate model from all possible terms included in each model. Therefore, not all available terms (Table 1b) were necessarily included in each model. The Akaike information criterion (AIC; Akaike 1973) was used to apply a penalised log likelihood method to evaluate the trade-off between degrees of freedom and fit of the model as explana-

tory parameters were added or removed (Crawley 2002). As selecting terms on the basis of AIC alone has been shown to be somewhat liberal in its choice of terms, a value of $k = 4$ was used for the multiple of the number of degrees of freedom used for the penalty in the stepwise procedure (Venables & Ripley 2002). Mean models, in which each predicted value is the mean of all observed values (Table 1b), were devised to provide null explanation models, for comparisons with our regression models. All model analyses were performed using 'R' software (R Development Core Team 2012).

A jackknife cross-validation procedure (Efron 1982) was used to provide an independent test of each regression model. This cross-validation procedure was applied by leaving out all data associated with each observation and then predicting the left-out observation using all remaining observations. For each model of each response in each season, scatterplots of observed against jackknife predicted values were plotted and overlaid with a linear regression with observed values on the y -axis as recommended by Piñeiro et al. (2008). We also calculated the root-mean-square-deviance (RMSD):

$$\text{RMSD} = \sqrt{\left(\frac{\sum_{i=1}^n (Y_{\text{obs}} - Y_{\text{pred}})^2}{n} \right)} \quad (1)$$

where Y_{obs} and Y_{pred} are the observed and predicted yield, respectively, and n is the number of observations. RMSD represents a measure of the overall dif-

ference between observed and estimated yield and PN anomalies for each model. We then tested for significant differences between mean absolute error calculated from each of our jackknifed models in comparison to the appropriate Mean model using analysis of variance (ANOVA). This allowed testing of the null hypothesis that errors for each model were not significantly different to the corresponding mean model. When assessing the significance of these ANOVAs, we relaxed the conventional alpha value of 0.05 to 0.1. There were several reasons for this relaxation: (1) the observed data were a small subsample of the true population and therefore have associated uncertainties; (2) there are unquantified uncertainties associated with the observed values due to measurement errors as well as the predicted values due to prediction errors; (3) we used a jackknife procedure to provide a more stringent test than would have been the case had fitted values been used; and (4) our models are designed to aid the mussel industry based on balance of probabilities; we therefore accepted an increased probability of rejecting the null hypothesis when it was in fact true (increased Type I errors).

Pearson correlations between physical anomalies (SOI, wind and SST) were made using data from January 1993 to May 2009 (197 values) and between physical anomalies and NO_3^- and PN collected at the sound entrance from February 2002 to May 2009 (88 values), both split nearly equally between half-years. Parametric analysis was used, as Shapiro-Wilks tests showed normal variate distributions. No time lags were applied to the NO_3^- anomalies in this analysis because the Pelorus Sound entrance is close to Cook Strait where the wind and SST anomalies were measured.

RESULTS

Regression modelling of mussel yield and seston biomass

The stepwise reduction procedure provided particular formulations that minimised AIC and therefore represented the best trade-off between model complexity and explanatory power for both the distal and local predictors in both summer and winter. The minimally adequate distal and local models revealed several significant predictors (Table 2). Probability (based on RMSDs) that mean absolute errors calculated from jackknifed distal model predictions of yield were the same as those from the mean model

Table 2. Multiple regression models predicting mussel yield anomalies within Pelorus Sound as functions of distal and local predictors for the summer half-year and the winter half-year ($n = 50$ mo for each half-year). Note that positive wind stress is from the SSE, and negative wind stress is from the NNW. Variables as in Table 1. *** $p < 0.001$, ** $p \geq 0.001$ to < 0.01 , * $p \geq 0.01$ to 0.10

Predictor	Coefficient	SE	<i>t</i>	<i>p</i>
Distal: yield in summer				
Constant	-0.331	0.954	-0.347	0.731
SOI	-0.198	0.086	-2.294	0.027*
Wind	-23.035	9.876	-2.333	0.025*
Flow	0.002	0.051	0.046	0.963
SOI: Wind	1.399	0.698	2.005	0.051*
Wind: Flow	-0.908	0.389	-2.332	0.025*
Distal: yield in winter				
Constant	1.837	1.318	1.394	0.170
SST	-9.693	2.747	-3.528	0.001***
Flow	0.195	0.075	2.586	0.013*
Local: yield in summer				
Constant	0.800	0.809	0.989	0.328
PN	0.174	0.041	4.273	0.000***
Diat	0.224	0.050	4.471	0.000***
Local: yield in winter				
Constant	1.508	1.090	1.383	0.173
PN	0.381	0.066	5.763	0.000***

was $p = 0.077$, and that from the analogous local model was $p = 0.003$. This was evidence to support our first hypothesis that variations in monthly mussel yield can be predicted using observed variations in large-scale, physical drivers. Comparison of time series, scatterplots and regression statistics of observed values against jackknife-predicted yield anomalies indicated that the distal models explained less variation in yield than the local models (Fig. 2a–f). This was evidence to support our second hypothesis that variations in monthly mussel yield can be better predicted from observed variations in local biological conditions than from observed variations in large-scale physical drivers.

Each model showed seasonal structures of the drivers. In summer, the optimal distal model predictors of increased yields were negative SOI, NW wind stress and interactions among SOI, wind stress and river flow, and optimal local model predictors were increased PN and diatoms. In winter, the optimal distal model predictors of increased yields were cool SST and increased river flow, and the optimal local model predictor was increased PN. Given the seasonal division of the drivers of mussel yield and the importance of PN (our index of seston, or mussel food) in predict-

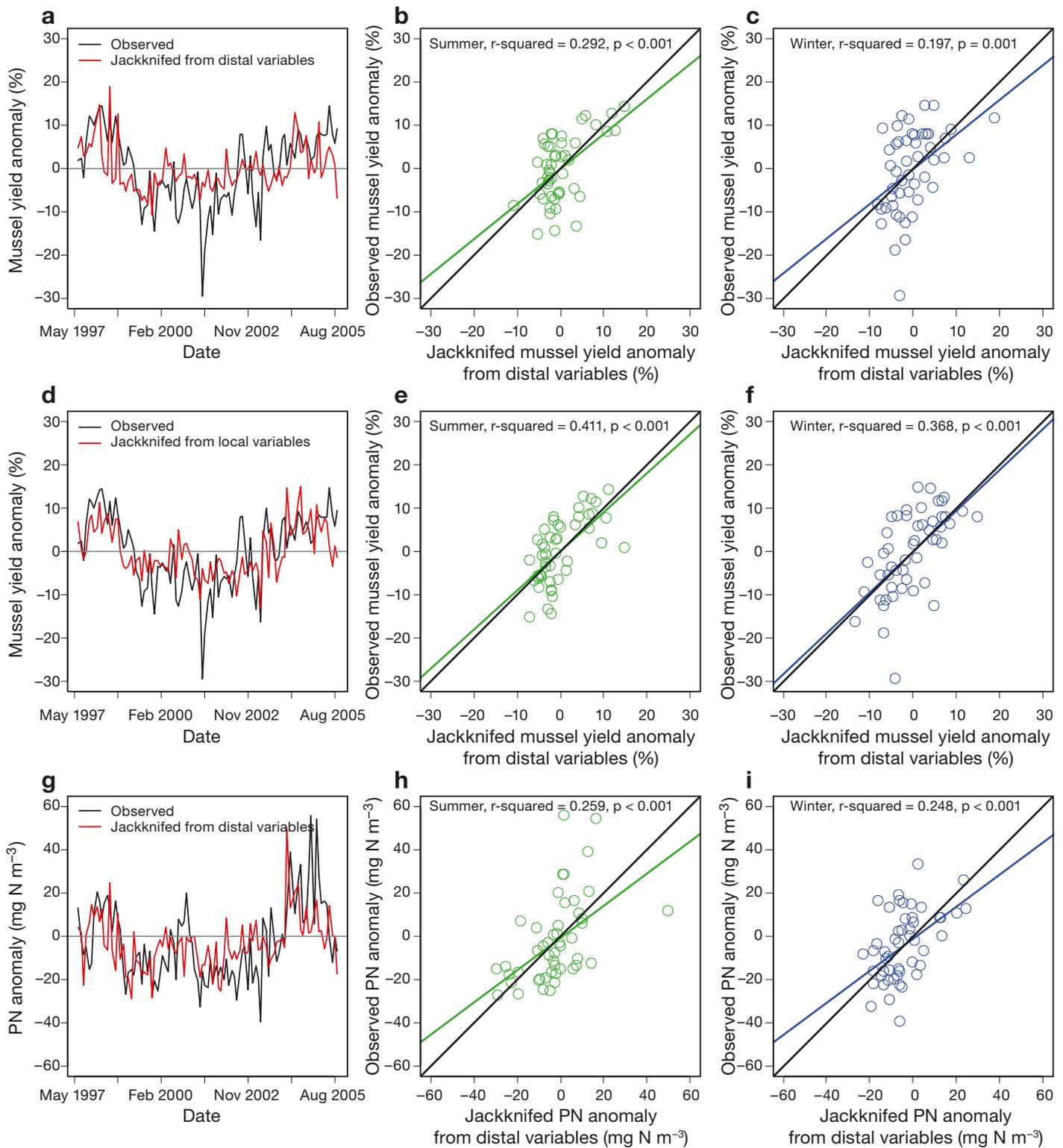


Fig. 2. (a) Time series of monthly mussel yield anomalies (as % of absolute value of yield) predicted by distal physical predictors (calculated using coefficients in Table 2), plotted with observed yield anomalies. (b, c) Jackknife-predicted values in summer (green) and winter (blue), with fitted linear regression lines; black line is $x = y$. (d–f) Same as above but for yields predicted using local chemical and biological predictors. (e–g) Same as above but for particulate nitrogen (PN) anomalies predicted by distal physical predictors

ing mussel yield (Table 2), it was not surprising that the distal model of PN also showed seasonal division of its drivers (Table 3). The set of distal predictors of increased PN in summer included NW wind stress, cool SST, increased river flow and an interaction of SST and river flow. The predictors of increased PN in winter were cool SST, increased river flow and an interaction of SOI and wind stress. Overall, the predictors reproduced the time series of observed PN (Fig. 2g–i), and there was a probability of 0.078 that the mean absolute errors calculated from jackknifed distal model predictions of PN were the same as those from the mean model. This was evidence to support our third hypothesis that the sestonic food supply for mussels can be successfully predicted using distal variables.

While the predictions suggested that distal and local variables were significant drivers of variation of mussel yield and their sestonic food (PN) in the sound, the mechanisms by which they could do so were not explained. This is the subject of the following sections.

Correlations between NO_3^- dynamics outside and inside Pelorus Sound

In the summer half-year, anomalies of NO_3^- measured at 40 m depth in the entrance to the sound (Fig. 1) correlated negatively with anomalies of SOI, SST and along-shelf wind stress (Table 4), such that

Table 3. Multiple regression models predicting particulate nitrogen (PN) anomalies within Pelorus Sound (Beatrix Bay) as a function of distal predictors for the summer half-year ($n = 50$ months) and winter half-year ($n = 48$ months). Note that positive wind stress is from the SSE, and negative wind stress is from the NNW. Variables as in Table 1. *** $p < 0.001$, ** $p \geq 0.001$ to < 0.01 , * $p \geq 0.01$ to 0.10

Coefficient	Estimate	SE	<i>t</i>	<i>p</i>
Distal: PN in summer				
Constant	2.917	2.730	1.069	0.291
Wind	-47.274	24.242	-1.950	0.058*
SST	-15.718	5.526	-2.844	0.007**
Flow	0.457	0.215	2.125	0.039*
SST: Flow	-0.888	0.410	-2.163	0.036*
Distal: PN in winter				
Constant	0.437	2.343	0.187	0.853
SOI	0.115	0.228	0.503	0.618
Wind	32.681	32.673	1.000	0.323
SST	-19.611	4.804	-4.082	0.000***
Flow	0.470	0.155	3.032	0.004**
SOI: Wind	6.337	2.856	2.219	0.032*

NO_3^- increased under conditions of El Niño, cool SST and increased wind stress from the NNW. In the winter half-year, NO_3^- at 40 m depth at the sound entrance was not correlated with SOI or wind stress, but increased under cool SST. Nitrate at 40 m was positively correlated with PN sampled within the sound (in Beatrix Bay) in the summer half-year (Fig. 3a) but not in winter (Fig. 3b). We found no significant relationship between anomalies of PN at 40 m in the entrance waters and PN within the sound, in either summer ($p = 0.27$, $n = 38$) or winter ($p = 0.80$, $n = 37$; data not shown).

Concentrations of NO_3^- at 40 m in the sound entrance and PN within the sound diverged in the winters of 2005 and 2007 (arrows in Fig. 3c), when entrance NO_3^- concentration was high and within-sound PN was low. These were the 2 driest winters in the entire 30 yr record of flow measurements on the Pelorus River (see annotated river flows in Fig. 3c). Cases when entrance NO_3^- was low and within-sound PN was high occurred in the winters of 2004 and 2008, when above-average river flows occurred. These patterns were consistent with the significant relationships of river flow with PN in the multiple regression modelling (Table 3) in winter.

Our regression modelling and correlations thus showed that in summer there were significant relationships between upwelling-related physical variables measured outside the sound, on mussel yield (Table 2), PN in the sound (Table 3), and NO_3^- concentration in the oceanic end-member waters of the

Table 4. Correlations of the Southern Oscillation Index (SOI), anomalies of along-shelf wind stress at Brothers Island and Farewell Spit, sea surface temperature (SST) at Pelorus Sound entrance and NO_3^- measured in Pelorus Sound entrance at 40 m depth (Fig. 1) for summer and winter half-years. For Brothers Island winds, positive (negative) wind stress is from the SSE (NNW); for Farewell Spit winds, positive (negative) wind stress is from the E (W). Pearson product-moment coefficients are shown; ** $p < 0.01$, * $p = 0.01$ to 0.05

Parameter	Wind, Brothers	SST	NO_3^-
Summer			
SOI	0.25*	0.34**	-0.39**
Wind, Brothers	-	0.25*	-0.46**
Wind, Farewell	0.71**	0.54**	-0.33*
SST	-	-	-0.44**
Winter			
SOI	0.03	0.35**	-0.17
Wind, Brothers	-	-0.07	-0.15
Wind, Farewell	0.49**	0.11	-0.08
SST	-	-	-0.56**

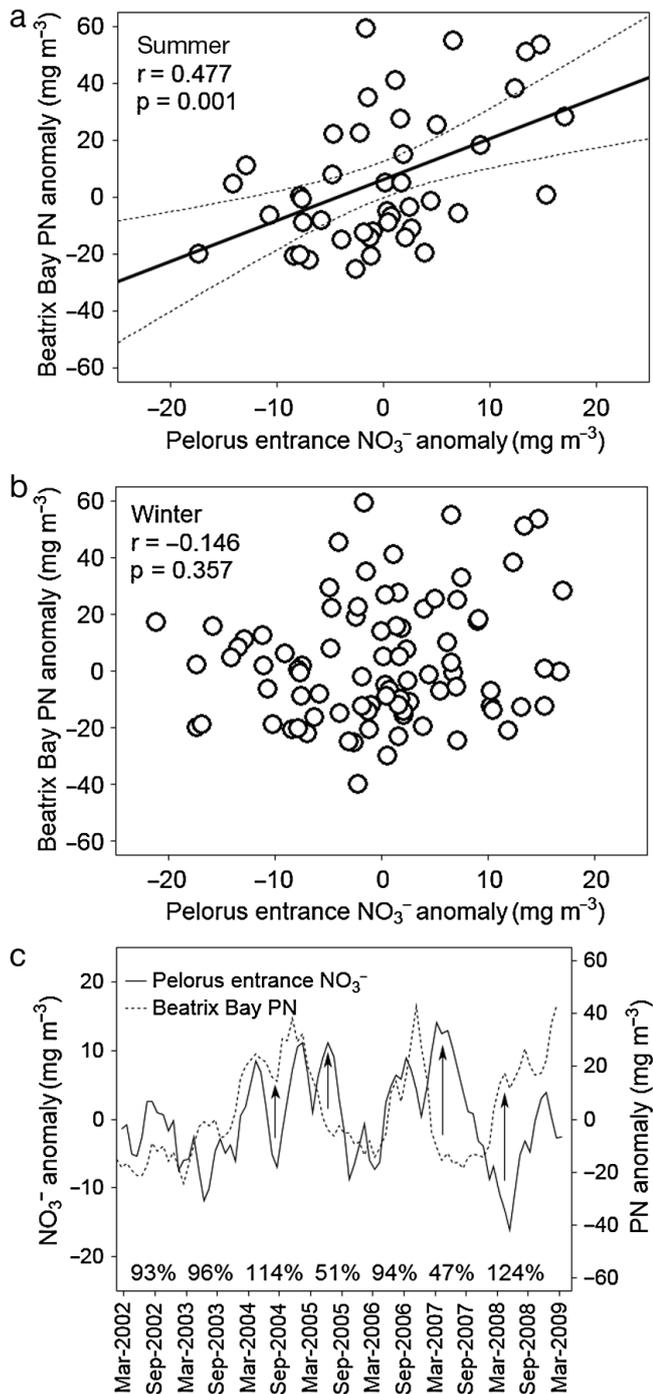


Fig. 3. Nitrate anomalies at Pelorus Sound entrance at 40 m depth plotted against particulate nitrogen (PN) anomalies within the sound (Beatrix Bay) in (a) the summer half-year (with least-squares fit, 95% confidence interval) and (b) the winter half-year, respectively. (c) Nitrate anomalies at the sound entrance at 40 m depth (solid line) and PN anomalies sampled within the sound (dashed line) over 2002 to 2009. Arrows indicate periods of divergence of the NO₃⁻ and PN time series (see 'Results'). Percentages are winter half-year mean river flows, as percentages of mean winter flows over the whole 30 yr Pelorus River flow record

sound (Table 4), but that these relationships disappeared in winter. We next use wind stress, SOI and spatially-resolved remotely-sensed SST time series to explain these relationships.

Spatial correlations in Cook Strait

At Brothers Island adjacent to the entrance of Pelorus Sound (Fig. 1), winds are most often oriented in NNW and SSE directions (Fig. 4a), while at Farewell Spit at the western approaches to Cook Strait they are most often oriented closer to due west and east (Fig. 4b). Both orientations are close to parallel with shelf bathymetry at their respective locations (Fig. 1). Correlations of monthly anomalies of wind stresses at Brothers Island with SST over the region in the summer half-year (Fig. 5a) showed a zone of highest positive correlation near Kahurangi Shoals (Fig. 1) west of Farewell Spit, such that increased stress from the NNW (i.e. negative) had a strong association with cool water at that location. The zone of relatively high correlation ($r = 0.45$ to 0.25) extended into western Cook Strait, and included the sound entrance (consistent with the positive summer wind–SST correlation [$r = 0.25$] at the entrance; Table 4). In the winter half-year (Fig. 5b), the wind–SST correlation at the upwelling zone dissipated and much lower correlations occurred over the entire region (consistent with the non-significant winter wind–SST correlation [$r = -0.07$] at the sound entrance; Table 4).

For winds measured at Farewell Spit, the correlations with Cook Strait SST in summer were high ($r = 0.60$) at Kahurangi Shoals (Fig. 5c), such that westerly (negative) wind stress was strongly associated with cool water. The high-correlation zone ($r = 0.60$ to 0.50) extended throughout the western strait including all of Golden and Tasman Bays and the entrance waters of Pelorus Sound (Table 4). As for Brothers Island winds, in winter the correlation weakened considerably, halving in the Kahurangi Shoals area (Fig. 5d) and western strait and essentially disappearing throughout the rest of the strait including the sound entrance.

In summary, westerly wind stress measured at Farewell Spit was well correlated with cool water at the entrance of Pelorus Sound, in summer. These winds were steered toward the SSE nearer the sound entrance where they correlated with entrance SST. In winter, these upwelling-related patterns of correlation were absent or muted.

Similar to the summer spatial correlations of wind stress and SST, the summer spatial correlation of SOI

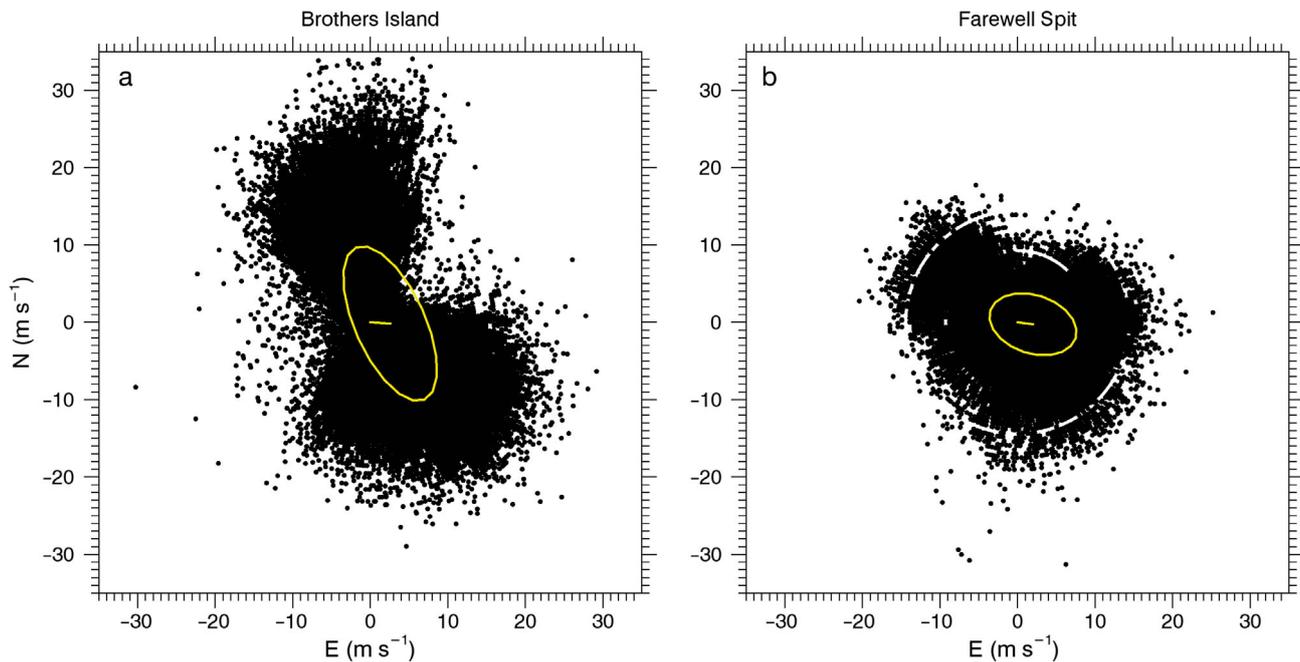


Fig. 4. Wind velocities (eastings, northings) for (a) Brothers Island from 1983 to 2009 and (b) Farewell Spit from 1986 to 2009. The yellow ellipse in each plot represents the variability in the vector data. A straight yellow line joins the centre of the ellipse (the mean value) with the origin. The major/minor axes of the ellipse represent the directions of largest/smallest variability

with SST (Fig. 5e) showed a zone of high correlation at Kahurangi Shoals. This zone trended into the western Cook Strait in a formation which intercepted the Pelorus Sound entrance area with correlation $r = 0.35$ to 0.40 (Fig. 5e, Table 4). This pattern was set against a background of lower correlation ($r = 0.25$ to 0.30) over the wider region, outside the upwelling zone. In winter (Fig. 5f), the SOI–SST correlation within the upwelling zone downstream of Kahurangi Shoals weakened significantly ($r = 0.10$), relative to its surrounding waters and also with respect to its summer value.

DISCUSSION

Effectiveness of local and distal predictors of mussel yield and seston

Zeldis et al. (2008) proposed that mussel yield in the largest mussel producing region in New Zealand (Pelorus Sound) could be predicted using environmental variables. Our present results confirmed this, but extended those findings to show that, perhaps unsurprisingly, the chemical and biological predictors collected locally to the mussel farming region within the sound were better predictors than physical predictors collected distally to the farming region. The local predictors are closely tied to the food sup-

ply for bivalve aquaculture: diatom carbon and most significantly, PN, as an index of particulate organic matter, or seston. This indicated that investments in monitoring of local chemical and biological conditions could produce the most accurate predictive models of yield.

The regression modelling identified minimal adequate models which represented the best trade-off between degrees of freedom and fit of the model. For the local predictors, this was quite exclusive, with relatively few predictors found to optimise the fit. The modelling excluded chl *a* and phytoplankton cell carbon but consistently optimised on PN, indicating its more consistent influence on mussel yield variation than the phytoplankton indices. This finding was likely due to the fact that PN (as an index of seston) in Pelorus Sound was composed of quite low proportions of living material (~16%, indexed by phytoplankton cell carbon: Zeldis et al. 2008). Most suspended biomass was not in living cells, similar to Skidaway River Estuary, USA, where most suspended biomass was detrital (Verity 2002b). Zeldis et al. (2008) proposed that variable living:dead proportions and variable phytoplankton taxonomic proportions in the seston could have lowered the correlation of living cellular components of seston with mussel yield, while not greatly affecting the variability of seston overall. It was proposed that the combination of heterotrophic and autotrophic cycling within the

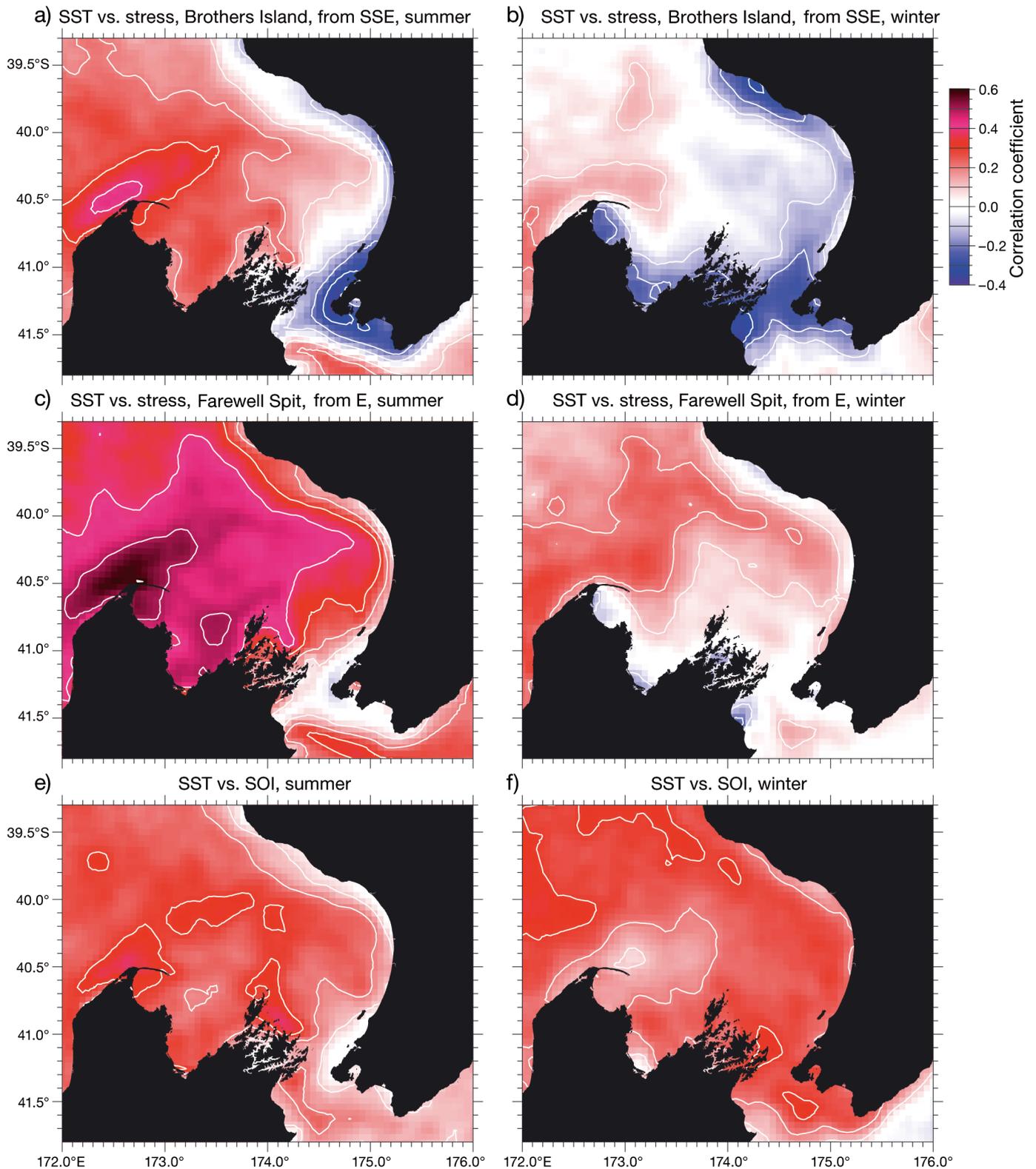


Fig. 5. (a,b) Spatial correlations of Cook Strait sea surface temperature (SST) and wind stress at Brothers Island in (a) summer and (b) winter half-years (positive stress is from SSE: 150°). (c,d) Spatial correlations between Cook Strait SST and wind stress measured at Farewell Spit in (c) summer and (d) winter half-years (positive stress is from E: 90°). These results show that in summer, winds with components from the E (W) correlate with warm (cold) waters, in the western Cook Strait. (e,f) Spatial correlations between Cook Strait SST and SOI in (e) summer and (f) winter half-years. These results show that in summer, La Niña conditions correlate with warm waters, and El Niño conditions correlate with cold waters, in western Cook Strait

seston stabilises its variability, lessening short-term, 'boom–bust' cycles which characterise the living phytoplankton cell (autotrophic) components of estuarine plankton, a point also made by Boynton et al. (1982) and Verity (2002b).

Our regression models showed that mussel yield and PN were also predictable using only physical variables collected distally to the farming region (albeit with somewhat reduced precision relative to the local predictors). Similar to the local models, the distal models were also quite exclusive in the selection of predictors. For models of summer yield, this excluded SST (Table 2a), which, while significantly correlated with yield (Pearson product moment correlation $r = 0.29$; not shown), was less strongly correlated with yield than were SOI ($r = 0.45$) or wind stress ($r = 0.47$), which were included in the model. Correlation among these predictors (Table 4) may also have been a reason for exclusion of SST in this case.

The physical data represented by the distal predictors are routinely collected in New Zealand within national environmental monitoring programmes and databases. Unlike the collection of 'in water' chemical and biological samples, their collection does not incur expense and effort by individual stakeholders (in this case, aquaculture companies), yet we have shown that such data can be used to predict mussel aquaculture yield. Similar monitoring capabilities are available in other countries with bivalve aquaculture industries, suggesting that they could be similarly applied if relationships among physical drivers and aquaculture yield can be derived and understood mechanistically.

Mechanisms of oceanic NO_3^- supply to Pelorus Sound entrance

In the summer half-year, negative SOI, increased wind stress from the west, cooler SST and increased NO_3^- at 40 m depth in the Pelorus Sound entrance indicated that upwelling affected sound entrance waters. These physical conditions correlated with enhanced seston (PN) and mussel yield in summer, inside the sound. A mechanism for this is discussed here. Northwesterly winds at Brothers Island and westerly winds at Farewell Spit both correlated with cool SST off the sound entrance (Fig. 5a,c) in summer. The Farewell Spit wind station is close to Kahurangi Shoals, where westerly winds (blowing from 270° toward 90°) are close to the ideal (along-shelf) direction favourable for upwelling (Bradford et al. 1986, Harris 1990, Shirtcliffe et al. 1990). There is evidence that

the Kahurangi Shoals upwelling is the main source of SST variation at the Pelorus entrance, rather than upwelling more local to the Pelorus entrance. Water upwelled at Kahurangi Shoals is typically advected into the strait and driven southeast toward the Pelorus Sound entrance, under the prevailing west-to-east residual flow caused by the mean dynamic height difference through Cook Strait (Chiswell 2000). This was identified by Harris (1990) and described as an 'eddy street' which forms at Kahurangi Shoals and is swept eastward through the strait.

The coherent pattern in the summer SOI–SST correlation (Fig. 5e) also indicated upwelling at Kahurangi, reflecting the correlation of negative SOI and westerlies in summer in central New Zealand (Gordon 1986, Mullan 1998: see 'Environmental setting'). Bradford et al. (1986) showed that in summer, upwelling episodes at Kahurangi Shoals periodically injected NO_3^- -rich slope waters into the shelf water column, which had been depleted of NO_3^- by phytoplankton during the summer growth season. These enriched water masses drift eastward through Cook Strait and create horizontal NO_3^- maxima at the Pelorus Sound entrance, correlated with episodes of upwelling-favourable winds (Table 4).

In winter, relationships of westerlies and SST at the Pelorus Sound entrance were absent (Fig. 5b,d). At this time, the continental shelf water column in NW Cook Strait is nearly completely vertically mixed (Harris 1990), such that local upwelling-favourable winds exert little influence on surface water composition, including its heat content. However, we showed that SOI and SST were correlated in winter (Fig. 5f, Table 4). SOI is related to SST variation over the wider New Zealand Exclusive Economic Zone, thought to be driven during negative SOI by cooler southerlies, with net heat loss from the upper ocean (Mullan 1998), and with net heat gain during positive SOI, as warmer northeasterlies cover the region. Thus, in summer, the localised zone of higher correlation within and downstream of Kahurangi Shoals arose from upwelling, driven by SOI-correlated winds, which augmented the wide-area background cooling and warming from SOI-correlated air–sea exchange. In winter, the wide-area SOI-correlated air–sea exchange appeared to be the main source of SST variability.

The winter mixing of deep and surface shelf waters in Cook Strait minimises vertical variation in nutrient concentrations (Harris 1990, Gibbs et al. 1992), resulting in non-significant relationships of NO_3^- at the sound entrance with upwelling-favourable winds. In winter the only significant correlation for NO_3^- was

with SST. Potential (albeit conjectural) mechanisms for this are that cool SST allows build-up of mixed layer NO_3^- , caused by slowed primary production and NO_3^- uptake (Eppley 1972, Bouman et al. 2005) or that increased winter southerlies cause deepened winter mixed layers and more NO_3^- entrainment. Irrespective, this winter oceanic NO_3^- variation did not correlate with winter variation in seston (PN) within the sound, unlike in summer.

Forcing of seston biomass and mussel aquaculture yield within Pelorus Sound

We next describe the oceanic and riverine forcing of seston concentration and mussel yield within the sound. The sampling at the sound entrance at 40 m depth detected 'new' NO_3^- available for estuarine transport into the sound (Gibbs et al. 1992) from Cook Strait. These NO_3^- anomalies were correlated with PN anomalies within the sound, but only in summer. No relationship was found between PN in the deep entrance waters with PN in the sound. Thus, it appeared that oceanic NO_3^- loading was underpinning PN formation within the sound, rather than direct PN loading from the ocean, in the summer half-year. These findings elucidated the mechanism driving the correlations between PN in the sound with upwelling-favourable winds and cool SST at the sound entrance found by Zeldis et al. (2008).

In the winter half-year, the numerous instances when the relation between NO_3^- at the sound entrance and PN within the sound strongly diverged and when PN instead correlated with river flow variation were strong evidence of the dominant effects of river flow on seston production in winter. This probably operated through the twin effects of freshwater inputs on nutrient supply and stratification, which alleviated co-limitation by nutrient and light levels (Mann & Lazier 1991, Cloern 1999) by simultaneously adding riverine NO_3^- and maintaining cells in the upper water column (Gibbs & Vant 1997). Although the multiple regression models identified river flow as a significant predictor of PN in both summer and winter, its influence in summer was unlikely to be as large as in winter, because NO_3^- loading rate was only about half that of winter.

It is primary production of organic matter which underlies PN formation in estuaries, fuelled by DIN supply and driven by combined autotrophic and heterotrophic cycling (Eppley et al. 1977, Verity 2002b). In Pelorus Sound over 9 yr there was an approximately 40 mg m^{-3} range in PN concentration from a

maximum in 1998 to a minimum from 2001 to 2003, followed by recovery (Fig. 2g), relative to an absolute mean concentration of PN of about 50 mg m^{-3} over that period (Zeldis et al. 2008). The sampling within the sound and at the sound entrance, combined with remotely sensed SST and hydrometric data, has provided plausible mechanisms for the findings of the regression modelling: that NO_3^- loading was underpinning PN formation within the sound, but that it was driven differently in summer (from Cook Strait) than in winter (from Pelorus River). Our regression modelling showed that the PN variation was strongly related to mussel yield in Pelorus Sound, as it is in other aquaculture regions (Figueiras et al. 2002, Strohmeier et al. 2005).

Previous studies have successfully modelled relationships of climatic variation and estuarine phytoplankton or seston biomass (e.g. Peterson et al. 1985, Lehman 1992, Verity 2002a, Møhlenberg et al. 2007), while other studies have demonstrated relationships between bivalve aquaculture yield and variation in its primary food supply (Armstrong 1982, Figueiras et al. 2002). However, in few cases have models of climatic drivers of phytoplankton or seston biomass been extended to consider the flow-on effects on yield of farmed bivalves. Figueiras et al. (2002) showed that upwelling/downwelling dynamics adjacent to the Galician Rías affected phytoplankton biomass and seston quality, which were shown by Fernández-Reiriez et al. (1996) to drive mussel growth rates. Blanton et al. (1987) had previously shown that upwelling indices (along-shelf winds) off Galicia were linked to mussel condition index, through the linkages with seston. This set of studies, along with ours in Pelorus Sound, are, to our knowledge, the only ones which have demonstrated linkages from climatic variation in physical forcing to formation of seston biomass, through to bivalve aquaculture yield.

CONCLUSIONS

With the addition of multiple regression modeling and new ocean and remote sensing time series, the present study has elucidated propositions made in earlier work (Zeldis et al. 2008) about forcing of Pelorus Sound bivalve aquaculture yield. It has described the ENSO teleconnection with mesoscale upwelling and its relationship with water mass composition and the nutrient supply to the Pelorus Sound entrance. The previously proposed summer–winter separation of nutrient drivers (oceanic in summer, riverine in winter) is robust: summer upwelling af-

fects variation in the NO_3^- inventory at the sound entrance, but this relationship breaks down in winter; there is connectivity between the NO_3^- inventory at the sound entrance and seston (PN) concentration within the sound (but only in summer); and winter variations of seston concentration in the sound are explained by fluctuations in winter river flow. Overall, these results show that time series of biological, chemical and physical drivers can be useful for explaining nutrient loading and seston concentrations in estuaries and that ultimately they can explain variation in secondary production (Nixon & Buckley 2002), in this case, of farmed bivalves. This outcome signifies the important role of climatic forcing in underpinning the food supply and yield of Pelorus Sound mussel aquaculture.

The multiple regression modelling showed that, while the best predictions included the locally collected chemical and biological information, it was also possible to make useful predictions solely from information contained in national databases of physical data, to explain why current growing conditions may be better or worse than average. This raises the potential for gaining information on lead time in terms of predicting growing conditions, and also on the potential longevity of good or bad conditions, once they take hold. Refinement of these predictions will depend on better understanding of periodicity in climatic patterns. Numeric ocean and estuarine models would be worthwhile objectives for future work, to further our understanding of underlying processes. Finally, further work incorporating new time series of mussel yield information is required to refine these predictions for the benefit of the Pelorus Sound mussel industry.

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