The following supplement accompanies the article

Stability in marine fish communities

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SUPPLEMENT

Text S1

Gompertz population model

The parameters in the B and C matrices represent potential interactions between functional groups or between an external driver and a functional group. All interactions were allowed to occur if the data supported the parameter. Model selection was conducted by iteratively fitting every possible combination of the *B*-matrix and selecting the model with the lowest AICc (Ives et al. 2003; Viscido and Holmes, 2010; Holmes and Ward 2012). The most reduced model possible would contain only density-dependent terms (diagonal of the B-matrix) while the full model had an estimated parameter for every interaction possible in the B-matrix. Parameters were estimated for the complete matrix of external drivers (*C*-matrix) in every model fit due to computing constraints. A single survey would require over a million runs to work through every combination of the *B* and *C* matrices, which was simply not feasible.

The state space framework allowed the incorporation of both measurement error and process error enabling better quantification of the true information within the trawl survey data sets. The process error variance (*Q*) was estimated within the model as an unconstrained variance-covariance matrix. The measurement error variance (*R*) was not estimated, but was calculated from the standard errors for each trawl survey and input into the model. The standard errors derived from the survey design represent only part of the measurement error in the system (Pennington 1985, 1995; Krause et al. 2002). We doubled the calculated measurement errors for each functional group to account for additional error. The model did not converge in 6 ecosystems when the measurement error was doubled and had to be reduced (North Sea, Celtic Sea, Irish Sea, Northern Gulf of St. Lawrence, Whale Rock and Fox Island). Standard errors were not available for every trawl survey. The standard errors from the Celtic Sea were used for the Irish Sea. The 2 bodies of water are adjacent and both are surveyed by CEFAS. The South African West Coast survey was fit with the standard errors from the New Zealand Chatham Rise survey. Both sample in deep water, have high diversity and are near the Southern Ocean. The initial biomass of each functional group was fixed as the observed biomass in the first year and was not estimated. The models were fit with maximum likelihood using a Kalman Filter (Holmes and Ward, 2012).

Two levels of environmental proxies were used as potential external drivers to capture different time scales within the Gompertz population model. Annual change was captured with variations in sea surface temperature (SST). We used the Extended Reconstruction Sea Surface Temperatures (NOAA ERSST V3 data) provided by NOAA/OAR/ESRL PSD, which runs through 2008 for most surveys (Smith et al. 2007; Xue et al. 2003) and 2 other data sources for the Alaskan surveys which extended to 2011. The Eastern Bering Sea SST was from Bering Sea mooring data (station M2) from NOAA's Fisheries-Oceanography Coordinated Investigations (FOCI) Program available at the Bering Sea Climate Website (BSCW, 2011) and the Gulf of Alaska SST was from another SST data source at

NOAA/OAR/ESRL PSD (Kalnay et al. 1996). The Alaskan SST data sets matched the NOAA ERSST V3 data, but had SST for the additional years. The North Atlantic Oscillation (NAO) (Hurrell and Deser, 2009; NCAR, 2011), Pacific Decadal Oscillation (PDO) (JISAO, 2011) and the Southern Oscillation Index (SOI) (NWS, 2011) were included to capture semi-decadal to decadal time scale changes in the respective basins.

The aggregate exploitation time series did not completely overlap with the trawl-survey time-series for all areas in all years. In 4 of the surveys the exploitation rate was one year short of the trawl-survey time-series. The southern Grand Banks trawl survey (3NO) was missing the exploitation from 1952-1958 and the Pierre Bank survey (3Ps) was missing years 1951-1959, 1961, 1966, 1971, and 1975. All missing years were filled in with the value the year prior, the first year available or the mean of the years before and after (Worm et al. 2009). The fishing mortality of walleye pollock, the largest fishery in the United States, was a large component of the exploitation rate for the Eastern Bering Sea. The fishing mortality rate for walleye pollock alone was used for the years 2009-2011 in the Eastern Bering Sea in order to extend the time series. In a similar manner, the fishing mortality for the largest fishery in New Zealand, hoki, was used to extend the time for the New Zealand Chatham Rise over the period 2009-2011.

Eigenvalue analysis

Stability analysis from the results of the Gompertz population model was performed by comparing the variance of the stationary distribution of each interaction matrix (B matrix in the linear, multispecies Gompertz model) with the variance of the process error (unaccounted for environmental variability) (Ives et al. 2003). The variance of the stationary distribution ($\tilde{v}_\infty$) is the variance of the process error (Ψ^2) along the eigenvector corresponding to the eigenvalue (λ).

$$\tilde{v}_\infty = \frac{\Psi^2}{(1-\lambda^2)} \tag{S1}$$

If the magnitude of the dominant eigenvalue is less than or equal to one ($|\lambda| \leq 1$), under steady state conditions, the system is considered stable - the biomass of each functional group will move toward its stationary distribution. The smaller the magnitude of λ the closer the variance of the stationary distribution is to the variance of the process error and the more stable the system will be (Ives et al. 2003). Biomass trends of the observed data that are not stable are interpreted as being driven by external factors such as the environment or fishing.

Eigenvalue stability analysis was conducted on simulated B-matrices to determine the effect of different levels of interactions on overall stability. Two levels of (off diagonal) interaction terms (weak, strong) with zero, 2, 4 or 6 terms were nested within 4 levels of (diagonal) density-dependent terms (low, moderate, high, mixed). In the Gompertz population model the density-dependence term is (*b*-1) so high levels of density dependence equate to low values along the diagonal. The high level of density dependence was set at 0.1, moderate was 0.5, low was 0.9 and mixed was 0.1, 0.5, 0.9. Weak interactions ranged from -0.3 to 0.3 and were randomly drawn from a uniform distribution. Strong interactions ranged from -0.9 to -0.6 and 0.6 to 0.9 and were randomly drawn from a uniform distribution. Zero, 2, 4 or 6 interaction terms were included for each simulated *B*-matrix and were placed at random in the off-diagonal of the matrix. Each combination of synthetic *B*-matrices was simulated 1000 times to get the 5th, 50th and 95th quantiles.

$$\begin{bmatrix} 0.1 & 0 & -0.12 \\ 0.24 & 0.1 & 0 \\ 0 & 0 & 0.1 \end{bmatrix}$$

The simulated matrix above represents a system with high density dependence (0.1 in the diagonal) and 2 randomly placed weak interactions drawn from a uniform distribution.

$$\begin{bmatrix} 0.1 & 0.71 & 0 \\ 0.63 & 0.5 & 0 \\ 0.84 & -0.89 & 0.9 \end{bmatrix}$$

The second example represents a system with mixed density dependence (0.1, 0.5, 0.9 in the diagonal) and 4 randomly placed strong interactions drawn from a uniform distribution.

Fishing pressure index

The catch divided by biomass ($\frac{C}{B}$) is a common metric to calculate exploitation in a given area. The RAM legacy database (Ricard et al. 2011) provided the data to go beyond this simple fraction removed method. The use of the U_{msy} value incorporates the life-history of the taxa involved and standardizes across ecosystems making them directly comparable. The $\frac{C}{B}$ method takes no account of the productivity of the system or the individual stocks making it difficult to compare across ecosystems.

The fishing pressure index is limited by the assessments available; however in most cases the assessments cover the dominant stocks in an area and constitute the bulk of the catch. In the Canadian ecosystems only 2 or 3 assessments were available. These 2 or 3 stocks however, made up almost all the catch and the fishing pressure index with only these few assessments were similar or more informative than the standard $\frac{C}{B}$ method. We divided the NAFO catch data by the total survey biomass to get an estimate of exploitation in each of the Canadian ecosystems by the $\frac{C}{B}$ method. The $\frac{C}{B}$ method was then compared to the the fishing pressure index (Fig. S5). The 2 methods are quite similar, particularly for St. Pierre Bank and the Northern and Southern Gulf of St. Lawrence. The overall trends are similar for the Scotian Shelf and Southern Grand Banks, but do differ. The $\frac{C}{B}$ method suggests that exploitation was very high in early 1970s on the Scotian Shelf and then dropped substantially for the rest of the time series. The FPI indicates that exploitation was high throughout most of the time series and only declined in the 1990s. On the Southern Grand Banks the 2 indices are similar through the 1980s, but the $\frac{C}{B}$ method does not capture the large increase in exploitation in the late 1980s - early 1990s just before the collapse of cod and the ban on fishing. While both methods have value, the Fishing Pressure Index provided more information on the history of exploitation in each ecosystem (Fig. S4).

Gompertz model results

The Gompertz state-space model fit the observed data well (Figs. S6 & S7). Vector autoregressive models within a state-space framework attempt to fit the true state of the observed time-series. They account for the measurement and process error in the data and pull out the overall trends. The predicted results typically track closely with the observed time-series.

Community metrics

Community metrics are a function of the underlying ecosystem processes as well as the length of time over which the data are collected. The longer the sampling period, the greater the chance that more rare species will be collected, increasing diversity and the higher the probability that the abundance of organisms will change potentially leading to higher variance and lower stability. We examined the 4 community metrics (TSI, evenness, variance-ratio test and synchrony) for each ecosystem in relation to the length of the sampling period, the length of the available trawl survey (Table S2 & Fig. S10).

Linear regressions indicated that none of the community metrics exhibit a significant relationship with the length of the trawl survey at $\alpha = 0.05$. Simpson's Evenness was close, however 2 of the surveys did not follow the trend. Overall there was not a systematic trend suggesting that the length of the sampling period influenced the value of the community metrics. The community metrics varied across ecosystems as a function of the taxa and interactions within that ecosystem.

A number of studies have found that ecosystems with greater diversity exhibit greater stability (Tilman 1996; Tilman et al. 2006). The more species there are in the environment, the finer the functional roles are divided and the greater the chance that a particular species will be tolerant or even thrive under alternative conditions. The ecosystem will be more stable because there are more species resulting in a wider diversity of occupied niches which can compensate for those that are impacted by a perturbation or disturbance. Compensation is often measured as the negative covariance among a group of species (Gonzalez and Loreau 2009). Alternatively, stability may be a function of the dominant species which structure the ecosystem (Sasaki and Lauenroth 2011). We examined the stability of the marine ecosystems with the Temporal Stability Index (TSI) (Lehman and Tilman 2000) and compared it with measures of diversity, compensation (variance-ratio test, Loreau and Mazancourt (2008) synchrony) and dominance (evenness). The goal was to determine if these community metrics could provide understanding to ecosystem level processes in marine communities. The community metrics were regressed against the TSI (Fig. S10).

There was a weak, borderline significant relationship between the TSI and diversity as stated in the results section and no relationship between the TSI and the other indices. The community metrics did not elucidate any overall patterns in the ecosystem dynamics. The stable systems did not exhibit asynchronous trends in biomass or negative covariance suggesting compensation. The stable systems showed weak trends with diversity and no trend with evenness (dominant taxa). Part of the reason for the lack of relationships in these data when they have been found previously, in other ecosystems, may be due to an incorrect application of the simple metrics. The majority of the community metrics utilize standard deviation, variance and covariance to calculate their value. These methods work well when the same technique is used to collect the data; however the trawl survey data were collected by numerous different institutions with different gear and methodology which incorporate different levels of measurement error into the observations. Without accounting for the varying levels and types of error in the data it may not be possible to compare across ecosystems. The linear, multispecies Gompertz population model explicitly accounted for the process and measurement errors and thus provided a more complex, but better suited tool to examine these particular data sets.

Table S1: Trawl surveys

Survey	Location	Institution
Grand Banks	NAFO divisions 3NO	DFO Newfoundland
St Pierre Bank	NAFO divisions 3PS	DFO Newfoundland
N. St Lawrence	Northern Gulf of St Lawrence	DFO Quebec
S. St Lawrence	Southern Gulf of St Lawrence	DFO Southern Gulf of St Lawrence
Scotian Shelf	Scotian Shelf and Bay of Fundy	DFO Maritimes
Gulf of Maine	Gulf of Maine	Northeast Fisheries Science Center
GSO-Fox Island	Narragansett Bay, Fox Island	University of Rhode Island, Graduate School of Oceanography
GSO-Whale Rock	Narragansett Bay, Whale Rock	University of Rhode Island, Graduate School of Oceanography
Georges Bank	Georges Bank	Northeast Fisheries Science Center
Mid-Atlantic	Mid-Atlantic Bight	Northeast Fisheries Science Center
North Sea	International Bottom Trawl Survey quarter 1	International Council for the Exploration of the Sea
Irish Sea	Irish Sea 4m Beam Trawl survey	Centre for Environment, Fisheries and Aquaculture Science
Celtic Sea	English Celtic Sea Portuguese High Headline Trawl survey	Centre for Environment, Fisheries and Aquaculture Science
South Africa-WC	South Africa, West Coast	Marine and Coastal Management
NZ-Chatham Rise	Chatham Rise	National Institute of Water & Atmospheric Research
Gulf of Alaska	Gulf of Alaska	Alaska Fisheries Science Center
GoA Small Mesh	Gulf of Alaska small mesh shrimp survey	Alaskan Department of Fish and Game
Aleutian Islands	Aleutian Islands	Alaska Fisheries Science Center
E. Bering Sea	Eastern Bering Sea shelf	Alaska Fisheries Science Center

Table S2: The output of the linear regression between the community metrics and the length of the trawl surveys.

	Estimate	SE	t-value	p-value
β_0	59.8702	31.7490	1.89	0.0765
TSI	1.1718	0.8827	1.33	0.2019
β_0	0.0449	0.0790	0.57	0.5767
Evenness	0.0045	0.0022	2.06	0.0555
β_0	1.2108	0.1898	6.38	< 0.0001
V-R test	0.0002	0.0056	0.03	0.9771
β_0	0.5181	0.0881	5.88	< 0.0001
Synchrony	0.0004	0.0026	0.14	0.8921

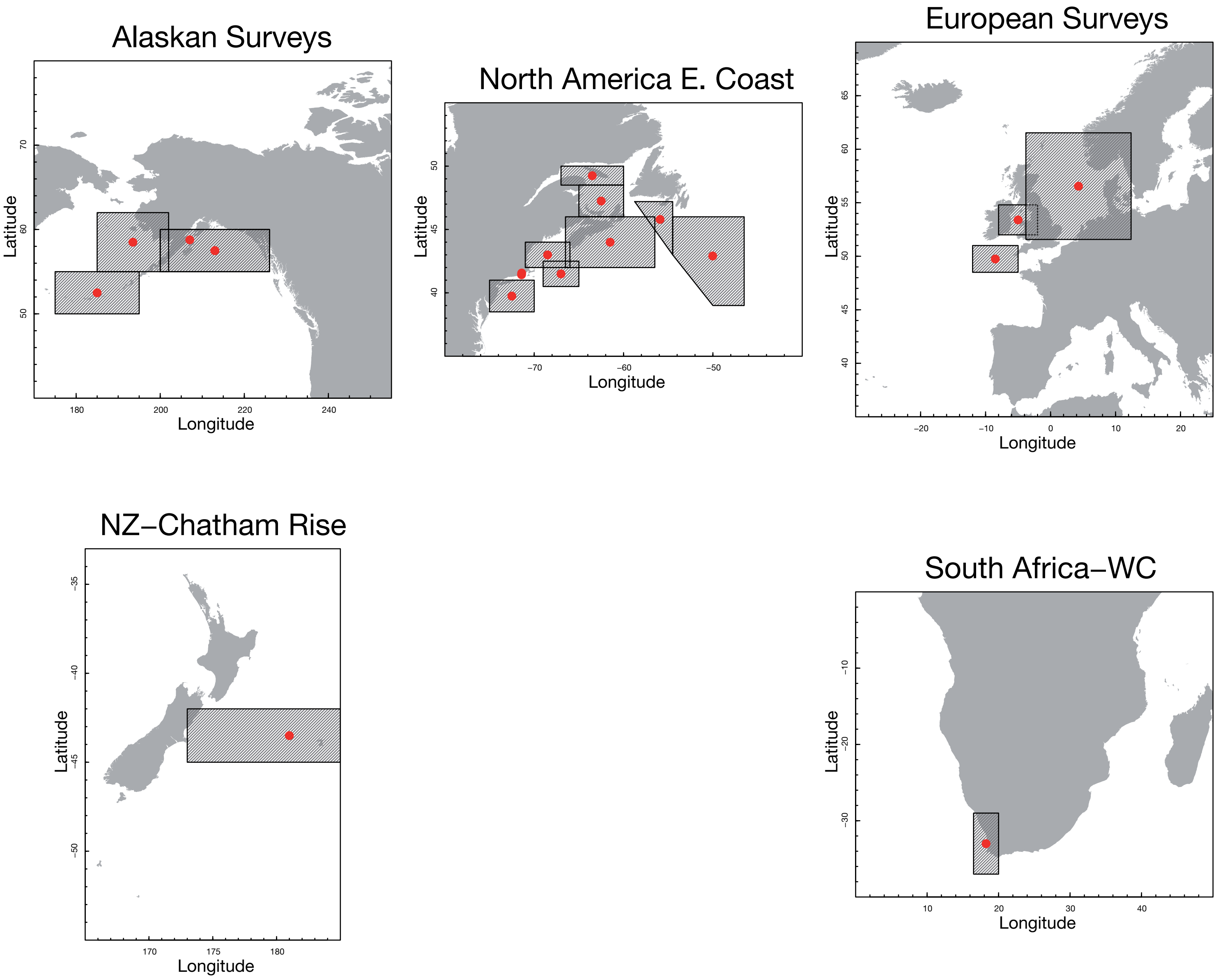

Fig. S1. The approximate location of each fisheries independent trawl survey.

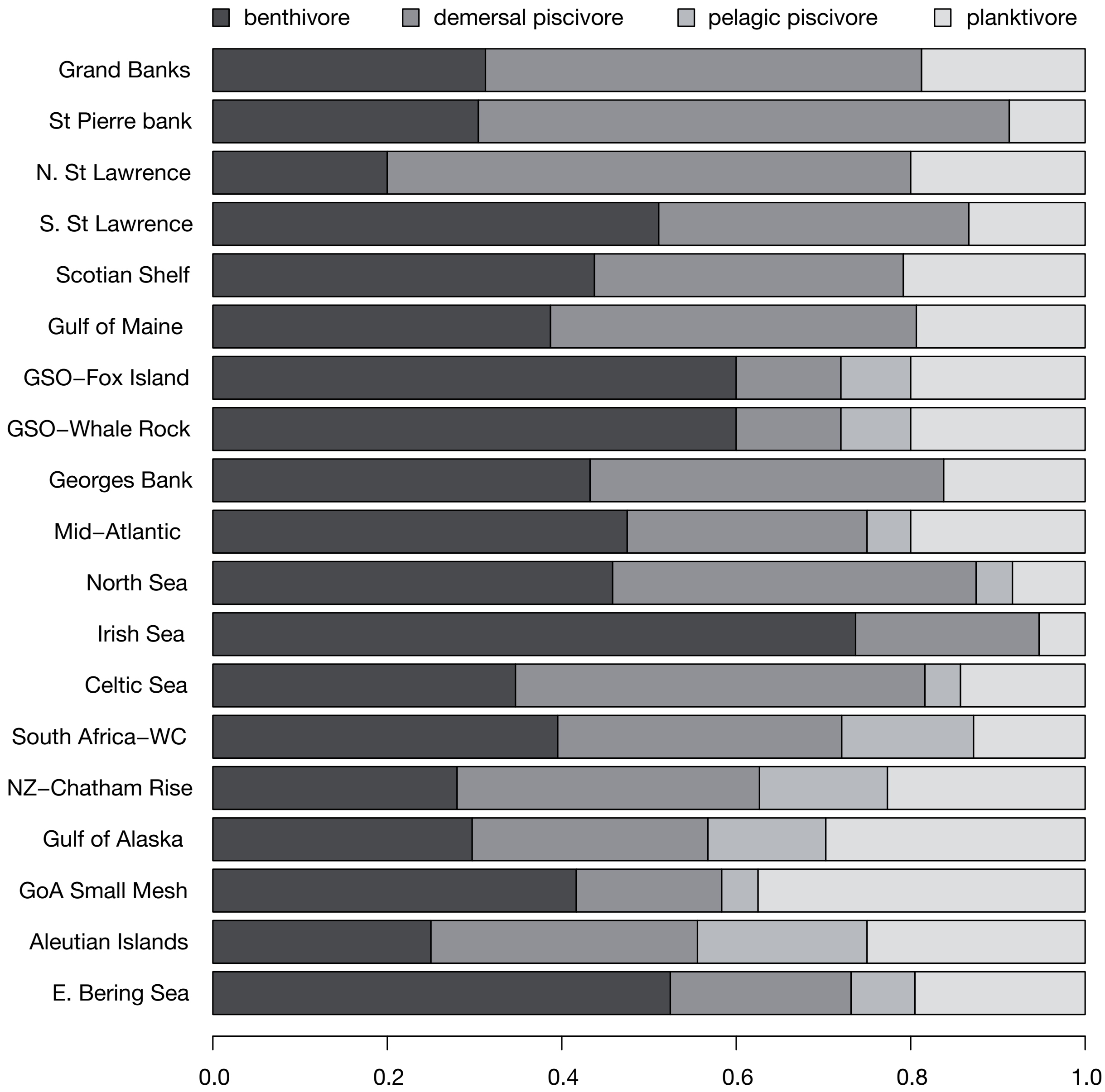

Fig. S2. The proportion of the number of taxa in each functional group.

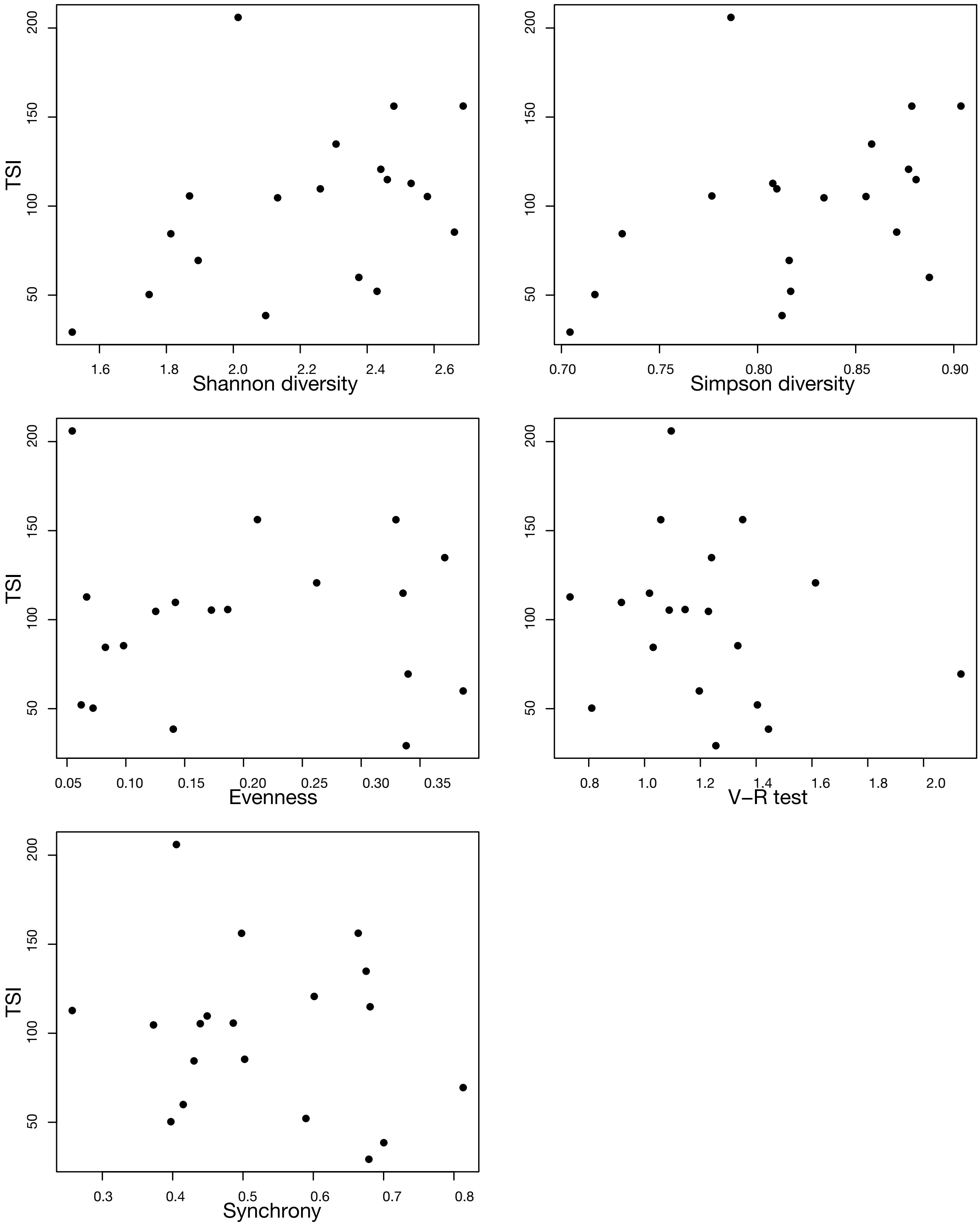

Fig. S3. Temporal Stability Index (TSI) and measures of diversity, evenness and compensation.

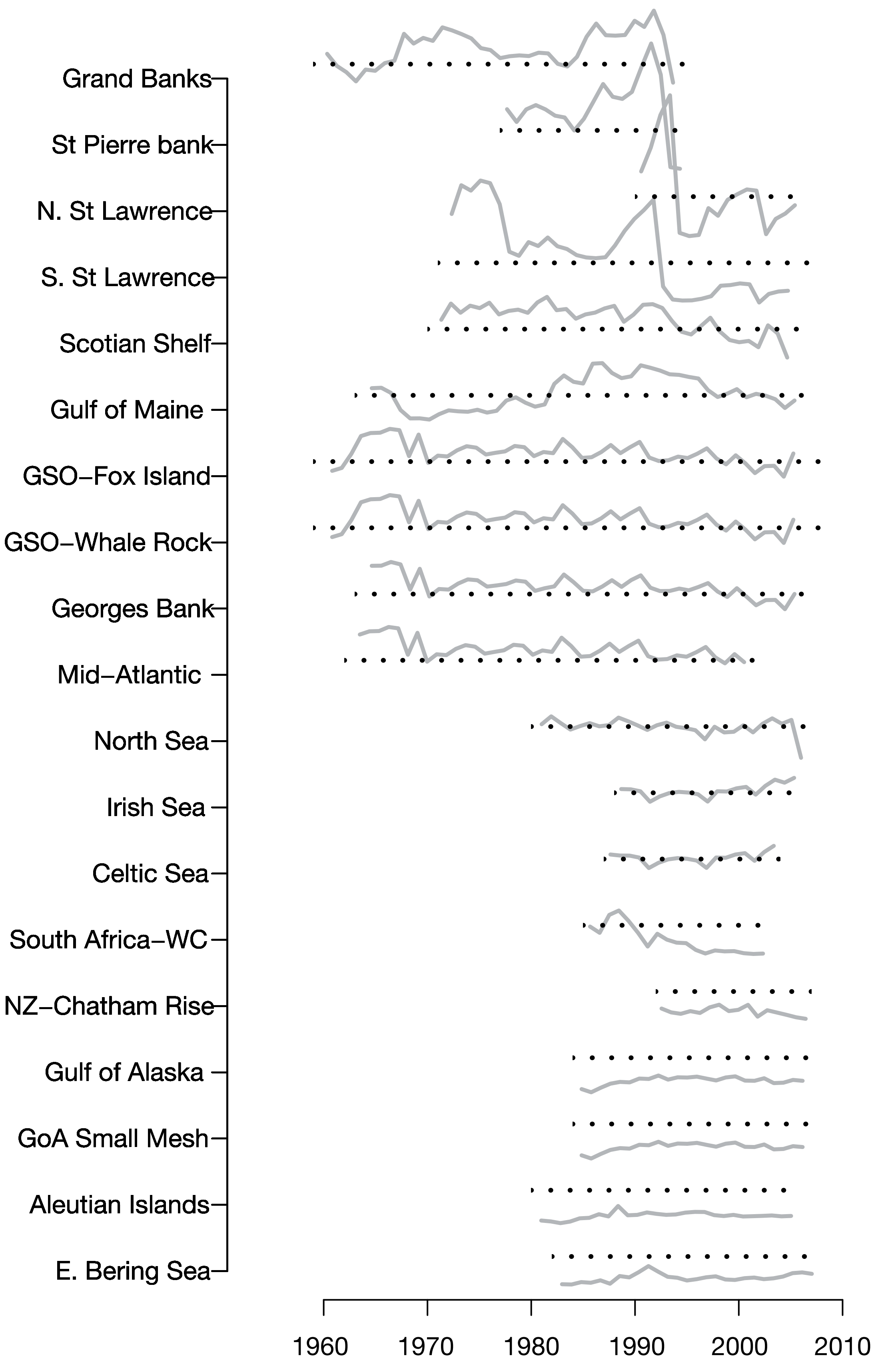

Fig. S4. The standardized mean fishing pressure index (FPI_t) (grey line) for each survey over the time series based on stock assessments. The length of the FPI_t matches the length of the survey data. The dotted line represents the community level reference point (U_{msy}). Different numbers of assessments were used due to availability.

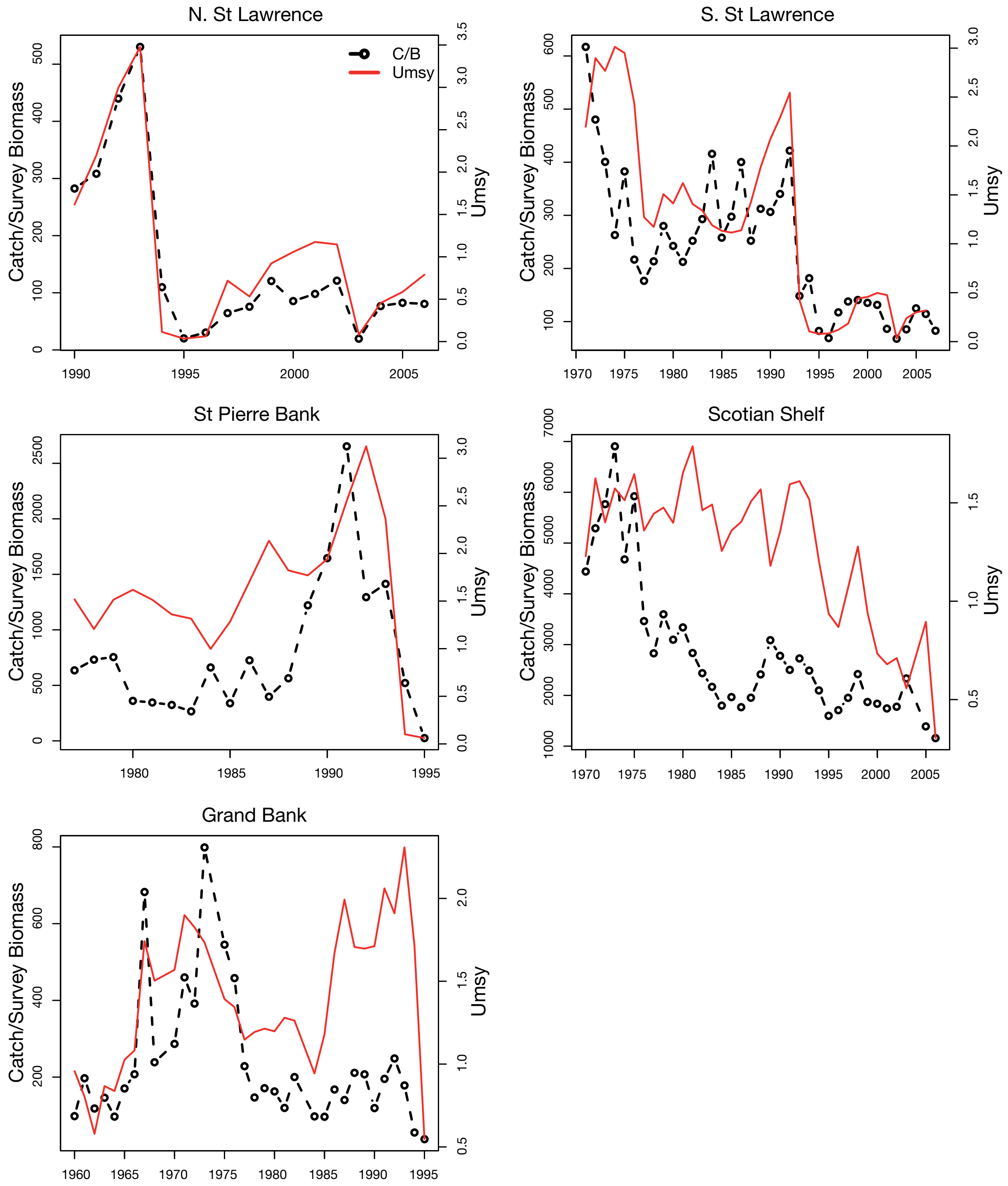

Fig. S5. Comparison between the Fishing Pressure Index exploitation method and the catch over the survey biomass method for the Canadian stocks.

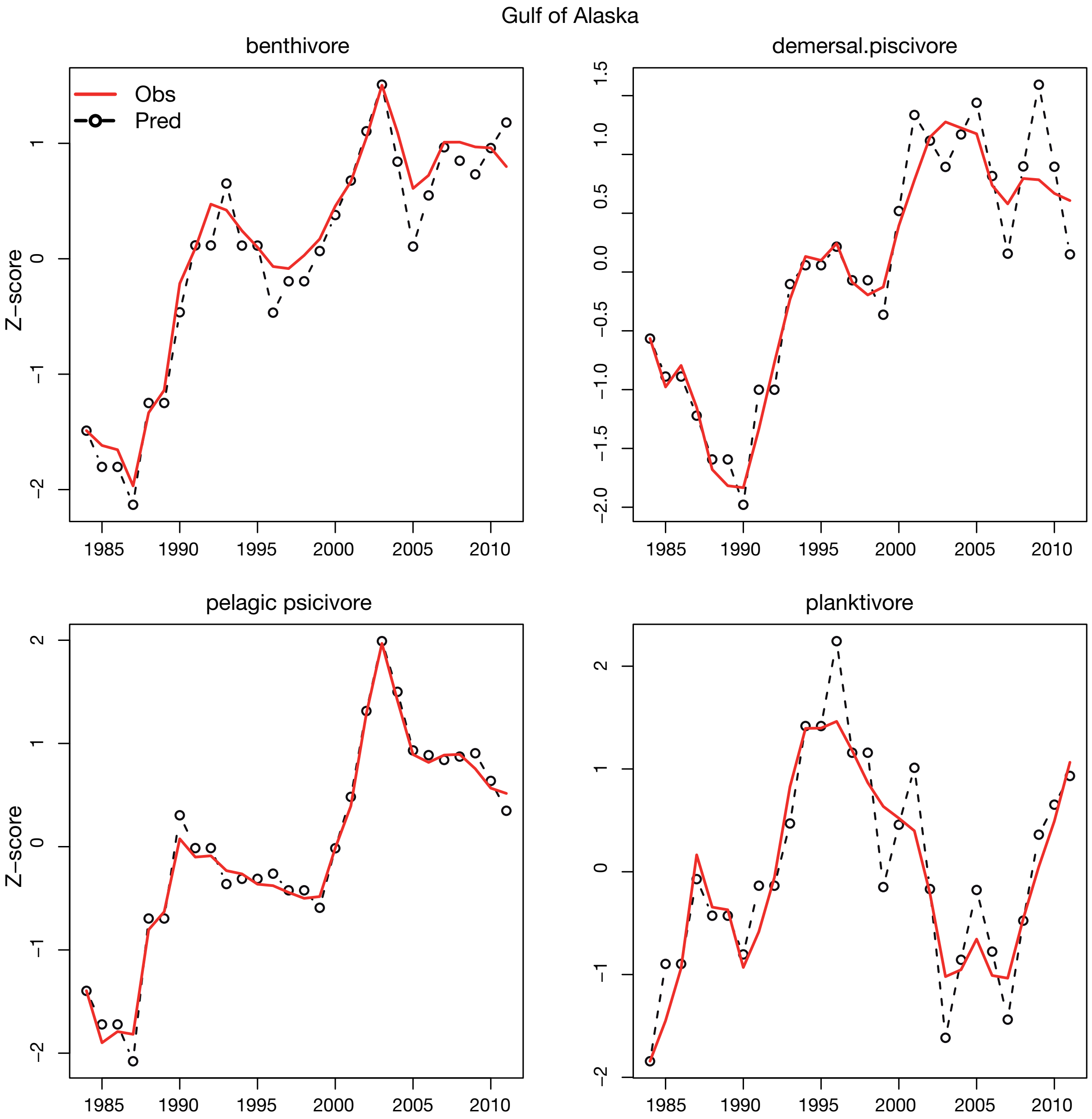

Fig. S6. The *Z*-scored, observed, functional group biomass and the predicted biomass from the linear, multispeciees Gompertz population model for the Gulf of Alaska trawl survey.

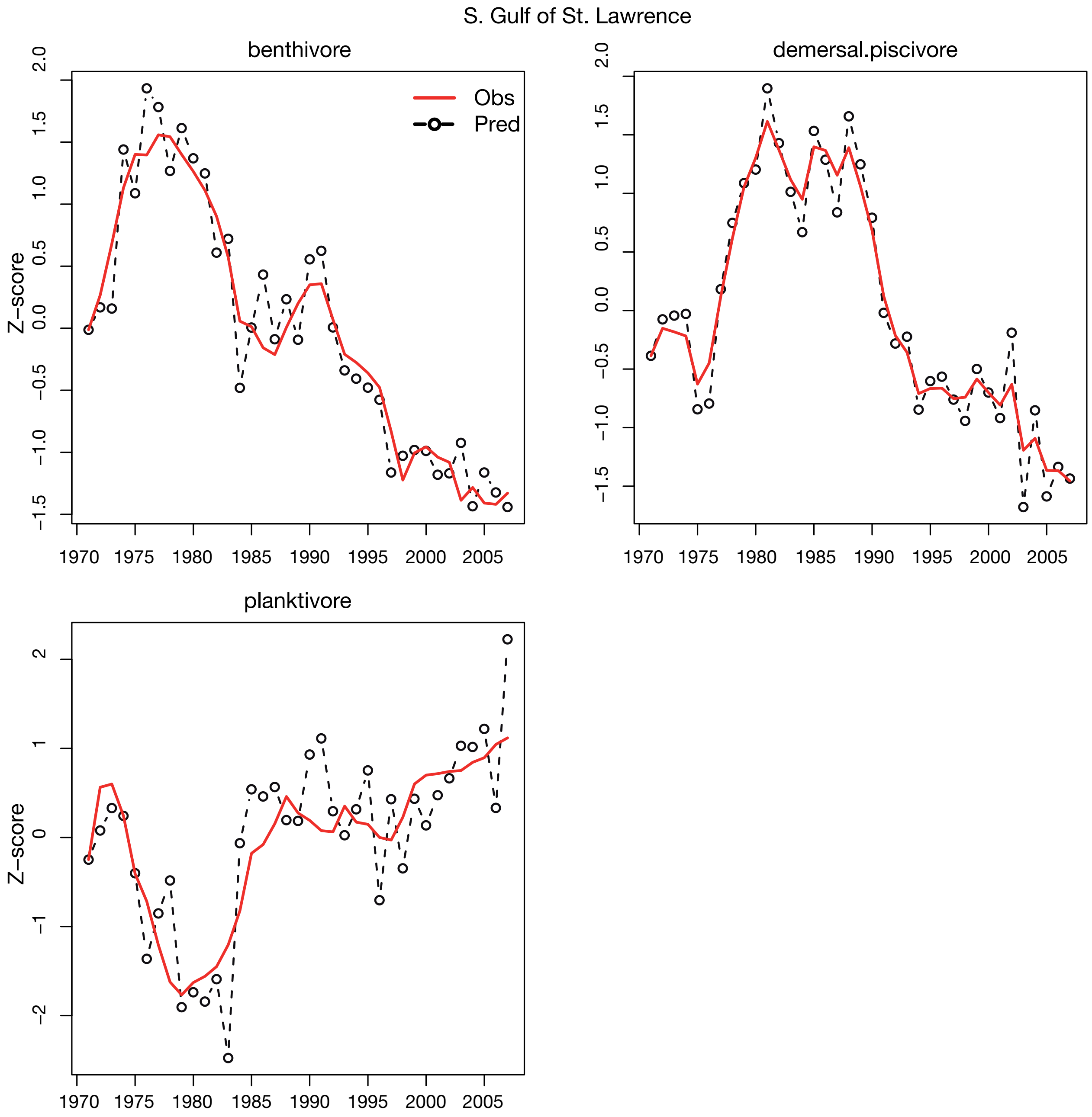

Fig. S7. The *Z*-scored, observed, functional group biomass and the predicted biomass from the linear, multispeciees Gompertz population model for the Southern Gulf of St. Lawrence trawl survey.

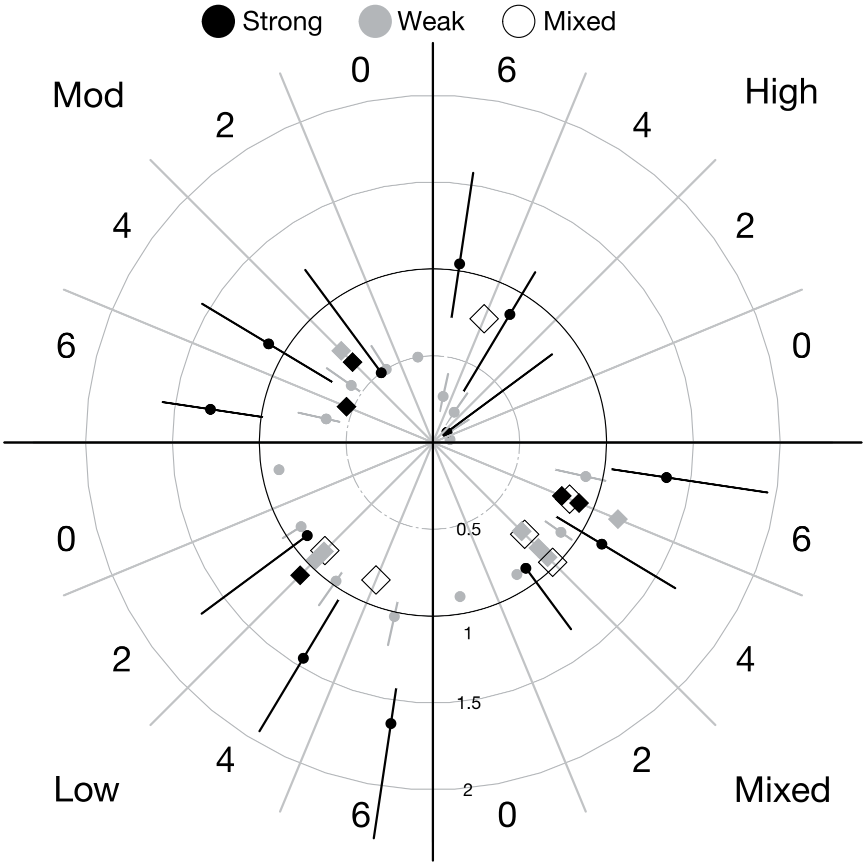

Fig. S8. The median eigenvalues of the 1000 simulated systems (circles) and the real systems (squares). The unit circle is divided into 4 quadrants based on the level of density dependence (diagonal of the *B*-matrix). The shading represents the strength of the interactions (off-diagonal of the *B*-matrix). The bar is the 5th and 95th quantile of the 1000 simulations. The subdivisions within the quadrant are the number of interactions from zero to 6. The eigenvalues from the real systems (squares) largely fell into the low or mixed level of density dependence and were close to one. The eigenvalue for the high density-dependent system without interactions is very close to zero and is difficult to see. Systems with high to moderate levels of density dependence and weak interactions are always stable under steady state conditions.

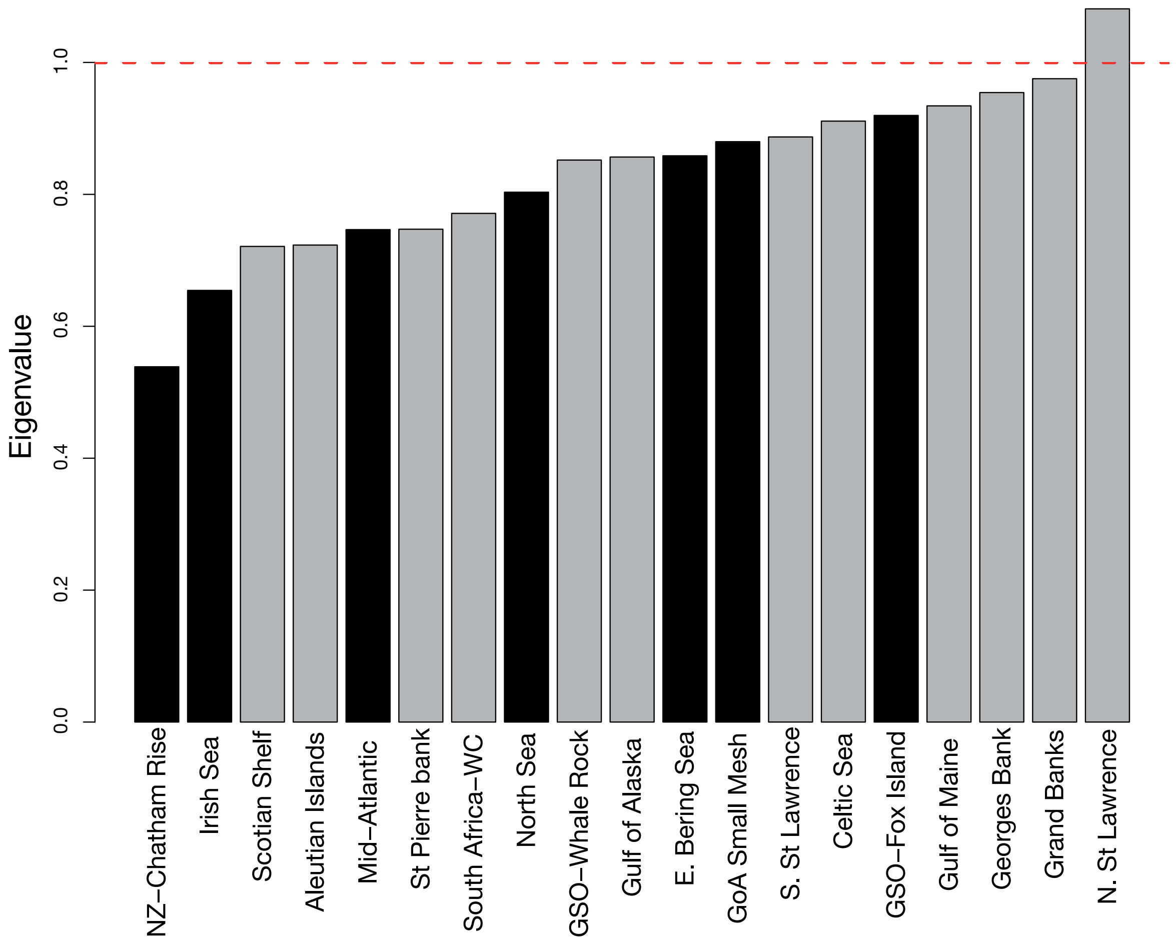

Fig. S9. The dominant eigenvalue of the interaction matrix for each survey. A value below one indicates that the system will go to equilibrium under steady state conditions. Values closer to zero indicate more stable systems that can better resist perturbations.

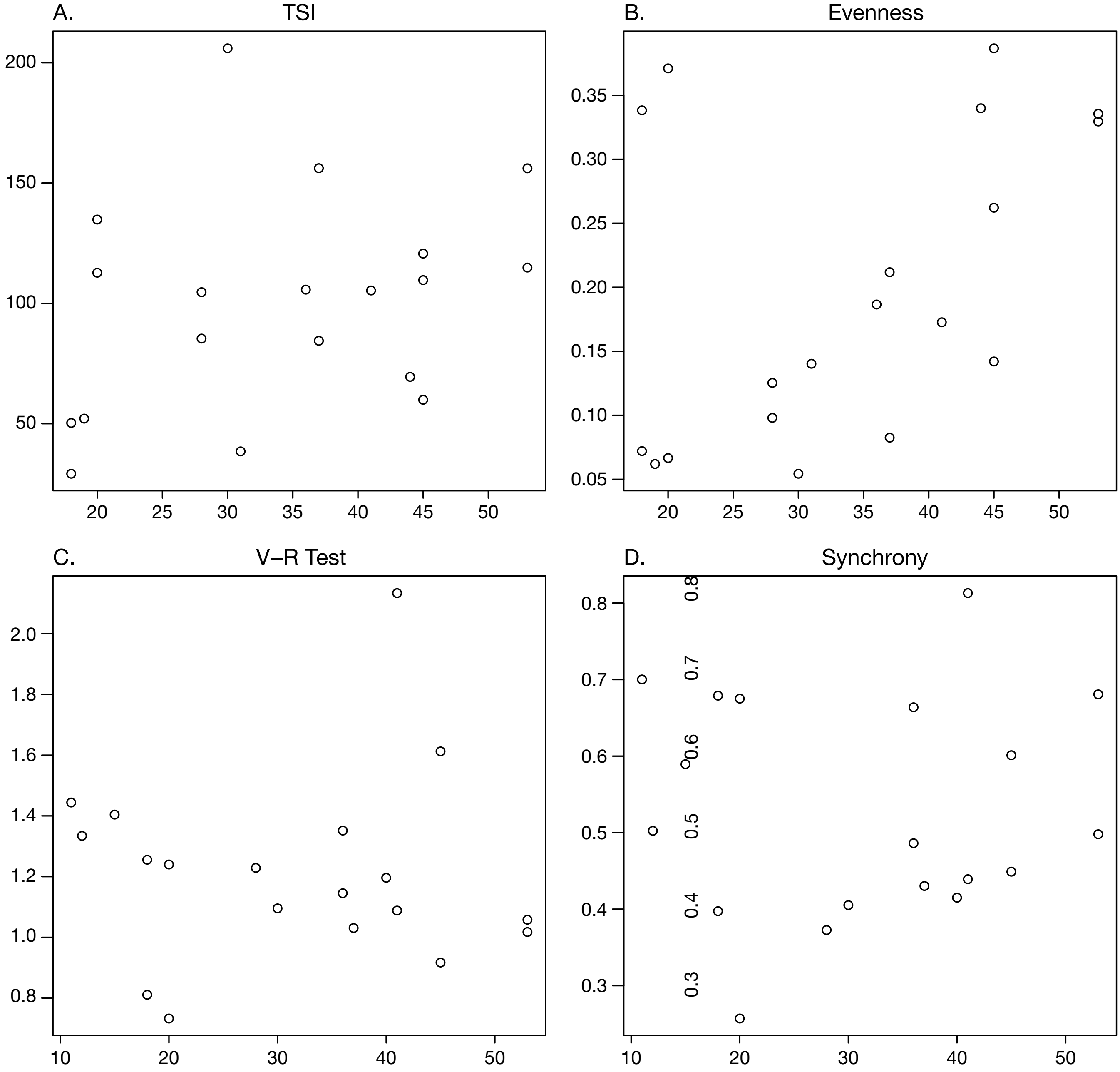

Fig. S10. The relationship between the length of each trawl survey and the associated community metric.

LITERATURE CITED

BSCW (2011) Bering Climate: Sea surface temperature. www.beringclimate.noaa.gov/data/index.php

Gonzalez A, Loreau M (2009) The causes and consequences of compensatory dynamics in ecological communities. Annu Rev Ecol Evol Syst 40:393–414

Holmes E, Ward E (2012) Analysis of multivariate time-series using the MARSS package R-cran, version 2.8

Hurrell J, Deser C (2009) North Atlantic climate variability: the role of the North Atlantic Oscillation. J Mar Syst 78:28–41

Ives A, Dennis B, Cottingham K, Carpenter S (2003) Estimating community stability and ecological interactions from time series data. Ecol Monogr 73:301–330

JISAO (2011) Joint Institute for the Study of the Atmosphere and Ocean at the University of Washington: Pacific Decadal Oscillation. www.jisao.washington.edu/pdo/PDO.latest

Kalnay E, Kanamitsu M, Kistler R, Collins W and others (1996) The NMC/NCAR 40-Year Reanalysis Project. Bull Am Meteorol Soc 77:437–471

Krause AE, Hayes DB, Bence JR, Madenjian CP, Stedman RM (2002) Measurement error associated with surveys of fish abundance in Lake Michigan. J Gt Lakes Res 28:44–51

Lehman C, Tilman D (2000) Biodiversity, stability and productivity in competitive communities. Am Nat 156:534–552

Loreau M, Mazancourt C (2008) Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. Am Nat 172:E48–E66

NCAR (2011) Climate data guide: North Atlantic Oscillation. http://climatedataguide.ucar.edu/guidance/hurrell-north-atlantic-oscillation-nao-index-station-based

NWS (2011) NOAA Climate Prediction Center: Southern Oscillation Index. www.cpc.ncep.noaa.gov/data/indices/soi

Pennington M (1985) Estimating the relative abundance of fish from a series of trawl surveys. Biometrics 41:197–202

Pennington M (1995) Measuring the effect of changes in catchability on the variation of marine survey abundance indices. Fish Res 23:301–310

Ricard D, Minto C, Jensen O, Baum J (2011) Evaluating the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. Fish Fish 13:380–398

Sasaki T, Lauenroth W (2011) Dominant species, rather than diversity, regulates temporal stability of plant communities. Oecologia 166:761–768

Smith T, Reynolds R, Peterson T, Lawrimore J 2007. Improvements to NOAA's Historical Merged Land-Ocean Surface Temperature Analysis (1880–2006). http://www.ncdc.noaa.gov/ersst/

Tilman D (1996) Biodiversity: population versus ecosystem stability. Ecology 77:350–363

Tilman D, Reich P, Knops J (2006) Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632

Viscido S, Holmes E (2010) Statistical modelling of communities and ecosystems using the lamda software tool. Environ Model Softw 25:1905–1908

Worm B, Hilborn R, Baum J, Branch T and others (2009) Rebuilding global fisheries. Science 325: 578–585

Xue Y, Smith T, Reynolds R (2003) Interdecadal changes of 30-yr SST normals during 1871–2000. J Clim 16:1601–1612