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Using multi-species surplus production models to estimate ecosystem-level maximum sustainable yields

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Abstract

We used time series of biomass and catches for the major commercial groundfish stocks in the Eastern Bering Sea/Aleutian Islands region and in the Gulf of Alaska to compute annual surplus production for 1977–2004. Annual surplus production and average annual biomass were aggregated across stocks within each region to examine the relationship between total surplus production and total aggregated biomass. We fit two surplus production models (Graham-Schaefer and Pella-Tomlinson) to the observed relationships to estimate maximum multi-species surplus production (equivalent to maximum sustainable yield) of the groundfish complexes in these ecosystems. Maximum multi-species surplus production was estimated to be approximately 2.5×10^6 t in the Bering Sea/Aleutian Islands and 330×10^3 t in the Gulf of Alaska. These point estimates were smaller than the sum of single-species MSY proxies from recent stock assessments, and estimates for the Gulf of Alaska were much smaller than earlier estimates that were used to specify optimum yield ranges for the Gulf of Alaska groundfish complex. Therefore, optimum yield ranges for the Gulf of Alaska may need to be re-assessed to reflect more recent conditions.

We further estimated the effects of environmental variability on annual surplus production using correlations and generalized surplus production models with environmental covariates. Results suggest that surplus production in the Bering Sea may be lower during conditions associated with the positive phase of the Pacific Decadal Oscillation, which is characterized by warmer temperatures, reduced ice, and reduced wind mixing over the shelf. Similarly, surplus production on the Gulf of Alaska shelf was lower during years with warm bottom temperatures coupled with low salinities in late winter. If maximum multi-species surplus production varies as a result of environmental variability, optimum yield ranges for the groundfish complexes in these ecosystems should take such fluctuations into account.

Keywords: Graham-Schaefer model; Pella-Tomlinson model; Productivity; Ecosystem-based fisheries management; Bering Sea; Gulf of Alaska

1. Introduction

An ecosystem-based approach to fisheries management has become a key goal of national and international institutions. In the United States, two recent ocean commissions have advocated ecosystem-based approaches and the Sustainable Fisheries Act mandates the establishment of an advisory panel "to develop recommendations to expand the application of ecosystem principles in fishery conservation and management activities". A key objective of any ecosystem approach is maintaining the productivity of fish communities, as well as harvests from those communities, within a desired range. To achieve this objective the North Pacific Fishery Management Council has defined maximum sustainable yield (MSY) and optimum yield (OY) ranges for the groundfish complexes of the Eastern Bering Sea/Aleutian Islands region (BSAI) and for the Gulf of Alaska (GoA). Total removals from both groundfish complexes are required by statute to remain within these ranges, which therefore provide a powerful tool to help prevent ecosystem overfishing.

Estimates of system-wide MSY may be obtained by summing single-species MSYs or by estimating a multi-species MSY using multi-species or ecosystem models. Historical estimates of aggregate MSY for the Gulf of Alaska and Bering Sea were based on proxies such as allowable biological catches estimated from stock assessments done in the mid-1980s and summed across all managed stocks (NPFMC, 2005a,b). Early ecosystem models suggested that aggregate MSY may provide a conservative estimate of sustainable yields for the BSAI groundfish complex (Laevastu et al., 1982). However, multi-species models (e.g. Collie and Gislason, 2001), ecosystem models (Walters

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et al., 2005), and general ecosystem principles suggest that the sum of single-species MSYs can be a poor proxy for the MSY of a multi-species complex because of ecological interactions and fishing impacts. For highly complex, multi-species systems we generally do not know whether compensatory or depensatory responses to fishing will prevail and whether system-level yields will be lower or higher than those predicted from single-species assessments (Walters et al., 2005).

Because of the unknown effects of complex interactions, alternative approaches are required to estimate the maximum sustainable yield of the BSAI and GoA groundfish communities. A variety of multi-species and ecosystem models are available for exploratory analyses and to obtain multi-species reference points (Hollowed et al., 2000). Several such models have recently been fit to ecosystems of the Northeast Pacific (Trites et al., 1999; Livingston and Jurado-Molina, 2000; Aydin et al., 2002), but have not been used to obtain estimates of ecosystem-level MSY or other reference points because of a lack of clear definitions of system-level MSY and because estimates are fraught with large uncertainties. Here we use a simple empirical approach that treats the multi-species complex of each region as though it were a single stock and estimates parameters through the use of surplus production models of the Graham-Schaefer and Pella-Tomlinson type (Quinn and Deriso, 1999). These models relate aggregate measures of annual surplus production (the amount of production available to be fished in a given year without changing the biomass of the stock) to total current biomass and provide empirical estimates of the maximum yield that can be taken on a sustainable basis from the BSAI and GoA groundfish complexes. We refer to these estimates as maximum multi-species surplus production (MMSP) and consider them to be estimates of ecosystem-level MSY, given that all of the major commercial stocks were included in the analysis. The use of production models as a supplement to stock-recruitment modelling and as a standard component of the stock assessment process was recently advocated by MacCall (2002) and Jacobson et al. (2002). Aggregating data across stocks reduces the extreme variability often observed in single-species models (Ralston and Polovina, 1982) and implicitly accounts for some of the multi-species constraints on total biomass and surplus production.

The primary goal of our study was to obtain empirical estimates of maximum multi-species surplus production for the BSAI and GoA groundfish complexes and to provide an approach to set reasonable upper limit for total removals from each system based on these estimates and their uncertainty. Because productivity of individual stocks may vary in response to climate variability we further examined the effects of environmental variability on MMSP.

2. Material and methods

The only data requirements for surplus production models with known biomass (or biomass that is assumed to be known)

Table 1
Stocks and stock groups used in analysis by species and region (BSAI, Bering Sea and/or Aleutian Islands, GoA, Gulf of Alaska), age at recruitment to the assessed stock, average biomass from 1977 to 2005, and average annual catches from 1977 to 2004

Scientific name	Common name	Region	Age	B (10^3 t)	C (10^3 t)
Atheresthes stomias	Arrowtooth flounder	BSAI	1+	600	13
		GoA	3+	1414	12.2
Hippoglossoides elassodon	Flathead sole	BSAI	3+	709	12
		GoA	3+	269	1.5
Reinhardtius hippoglossoides	Greenland turbot	BSAI	1+	204	18
Hippoglossus stenolepis[a]	Pacific halibut	GoA	6+	335	18
Limanda aspera	Yellowfin sole	BSAI	2+	2149	122
Lepidopsetta sp.	Rock sole	BSAI	2+	1103	38
Pleuronectes quadrituberculatus	Alaska plaice	BSAI	3+	1304	16
Glyptocephalus zachirus	Rex sole	GoA	3+	84	2.3
Microstomus pacificus	Dover sole	GoA	3+	142	1.8
Theragra chalcogramma	Walleye pollock	BSAI	3+	9419	1171
		GoA	3+	1683	111
Gadus macrocephalus	Pacific cod	BSAI	3+	1134	159
		GoA	3+	452	47
Pleurogrammus monopterygius	Atka mackerel	BSAI	3+	432	42
Anoplopoma fimbria[b]	Sablefish	GoA	4+	284	20
Sebastes alutus	Pacific ocean perch	BSAI	3+	276	9.0
		GoA	6+	158	9.2
Sebastes polyspinis	Northern rockfish	BSAI	3+	177	2.4
		GoA	6+	111	2.9
Sebastes variabilis	Dusky rockfish	GoA	4+	48	1.9
Sebastes aleutianus	Rougheye rockfish	GoA	3+	36	0.9

Notes: (a) Includes IPHC regulatory areas 2B, 2C and 3A; (b) includes Bering Sea, Aleutian Islands, and Gulf of Alaska with the majority of the stock occurring in the Gulf of Alaska.

are time series of catch and biomass. Estimates of beginning of year biomass and total catches for all major groundfish stocks in the BSAI and GoA (Table 1) were obtained from recent stock assessments (NPFMC, 2005c,d, Steven Hare, International Pacific Halibut Commission, pers. comm.). Annual surplus production (ASP) was calculated for each stock as:

$$\mathrm{ASP}_{j,t} = B_{j,t+1} - B_{j,t} + \delta_j C_{j,t}$$

where $B_{j,t}$ is the estimated "adult" biomass of stock j at the beginning of year t, $C_{j,t}$ the catch of stock j during year t, and δ_j is a stock-specific correction factor that accounts for growth and mortality that would have taken place between the time the catch was taken and the beginning of year $t+1$. This factor can be important for some stocks (Jacobson et al., 2001), but was close to one for a number of demersal stocks examined by Jacobson et al. (2002). For this analysis, we assumed $\delta_j = 1$ for each stock, which is equivalent to assuming that all catches are taken at the end of the year or that mortality and growth are balanced between the time the catch is taken and the beginning of the following year. The "adult" biomass included all fishes of age x and older with x ranging from 1 to 6 (most often $x = 3$, Table 1). Total annual surplus production ($\mathrm{ASP_t}$) and total beginning-of-year biomass (B_t) for an entire groundfish complex were estimated by summing across all stocks within the BSAI and GoA, respectively. The average annual biomass $\bar{B}_\mathrm{t}$ that produced $\mathrm{ASP_t}$ was computed as $\bar{B}_\mathrm{t} = (B_\mathrm{t} + B_\mathrm{t+1})/2$. To examine the relationship between total surplus production and average annual biomass we plotted $\mathrm{ASP_t}$ against $\bar{B}_\mathrm{t}$ and fit a Graham-Schaefer model (GS) and a Pella-Tomlinson model (PT) to the data (Fig. 1) (Quinn and Deriso, 1999). While there is no theory to suggest that a surplus production model for a composite of stocks would have the same form as those used for single stocks, we interpret model parameters as multi-species equivalents of the single-species case. Total aggregated unfished biomass (B_∞), maximum multi-species surplus production (MMSP), the corresponding aggregated biomass at which MMSP is achieved (B_m), and uncertainty in these quantities were estimated from these models. In the two-parameter GS model, B_m is not estimated because MMSP is assumed to occur at $B_\mathrm{m} = B_\infty/2$ (Fig. 1), a rather restrictive and unrealistic assumption. Therefore, we also fit the three-parameter PT model, which allows maximum production to occur at any biomass level, to examine how robust the estimates of maximum multi-species surplus production (MMSP) are to the form of the model.

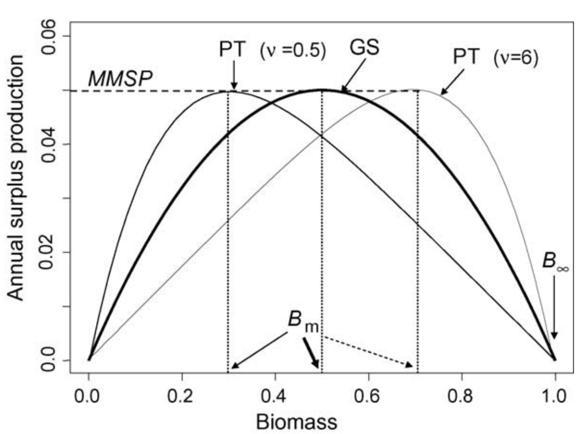

Fig. 1. Alternative surplus-production–biomass relationships based on Graham-Schaefer model (GS, heavy line), and Pella-Tomlinson models (PT) for two values of parameter ν. Parameters of interest to management include maximum surplus production (MMSP), biomass at which maximum surplus production occurs (B_m), and unfished biomass (B_∞).

Fitting the surplus production–biomass relationship is straightforward if biomass is assumed to be known without error. Although this assumption is unrealistic, it would be difficult to develop a statistical methodology that would allow for such errors in the models examined here. Therefore, we ignored errors in biomass, as is common practice in stock-recruitment modelling. Assuming an additive error structure for annual surplus production, the estimating equations take the form of a multiple linear regression for the Graham-Schaefer model and a non-linear regression for the Pella-Tomlinson model (Quinn and Deriso, 1999):

$$\text{Graham-Schaefer}: \quad \mathrm{ASP_t} = \alpha \times \bar{B}_\mathrm{t} + \beta \times \bar{B}_\mathrm{t}^2 + \varepsilon_\mathrm{t}$$

$$\text{Pella-Tomlinson}: \quad \mathrm{ASP_t} = \alpha \times \bar{B}_\mathrm{t} + \beta \times \bar{B}_\mathrm{t}^\nu + \varepsilon_\mathrm{t}$$

where α, β, and ν are model parameters and ε_t are model residuals that are assumed to be normally distributed. After examining the distribution of these residuals the additive error structure was judged to be appropriate for both the GoA and BSAI. However, moderate to strong serial correlation was evident in the residuals for the Gulf of Alaska. Therefore, we fit models for the Gulf of Alaska with and without allowing for first-order autocorrelation ($\varepsilon_\mathrm{t} = \phi\varepsilon_{\mathrm{t}-1} + \omega_\mathrm{t}$, where $\omega\ N(0, \sigma_\omega^2)$). Note that for the purpose of estimating MMSP we view these models as simply providing a reasonable statistical description of the data and we include observation errors as the only source of uncertainty, but no process errors.

Parameter estimates and their full posterior distribution were obtained in a Bayesian framework using Markov Chain Monte Carlo methods as implemented in WinBUGS (Spiegelhalter et al., 1995). Models were directly parameterized in terms of B_∞ and MMSP (Quinn and Deriso, 1999) and parameters were constrained to fall within reasonable bounds. Specifically, B_∞ was constrained using a censored normal prior probability with a mean equal to the maximum observed value of $\bar{B}_\mathrm{t}$, a very large variance, a lower bound equal to the mean of the observed biomass values, and no upper bound. However, to obtain realistic estimates for the Gulf of Alaska groundfish complex, we further used an upper bound equal to twice the maximum observed biomass. For the PT model, we initially constrained the biomass at which maximum surplus production occurs (B_m, Fig. 1) to fall within the range from $0.2B_\infty$ to approximately $0.8\ B_\infty$ by using a uniform prior probability for ν ($0.35 < \nu < 12.3$). Maximum surplus production MMSP was constrained to be positive using a censored normal prior probability with a mean equal to the maximum observed $\mathrm{ASP_t}$, a very large variance, a lower bound of zero, and no upper bound. Model runs with different prior distributions were conducted to test the sensitivity of parameter estimates to these prior probability specifications, particularly

Table 2
Correlations (r) between environmental indices (running averages of the previous three years) from the Bering Sea and Gulf of Alaska and two production indices, annual surplus production (ASP_t) and residuals from a Graham-Schaefer surplus production model (ε_t), and probability P that correlation is different from zero based on t-test

Variable	ASP_t		ε_t	
	r	P-value	r	P-value
Gulf of Alaska				
Kodiak air T[a]	0.101	0.708	−0.056	0.835
SST summer[b]	−0.106	0.656	−0.112	0.638
SST winter[b]	−0.226	0.382	−0.224	0.388
GAK1 SST[c]	−0.054	0.827	−0.080	0.745
GAK 1 Bottom T[c]	**−0.531**	**0.051**	**−0.533**	**0.061**
GAK1 surface salinity[c]	**0.513**	**0.088**	**0.511**	**0.090**
Discharge[d]	−0.152	0.620	−0.175	0.566
Wind mixing[e]	0.129	0.633	0.132	0.626
Upwelling (60°N)[f]	0.229	0.412	0.225	0.420
El Nino (SOI)[g]	0.278	0.335	0.260	0.369
PDO[h]	−0.399	0.199	−0.396	0.202
Bering Sea				
St. Paul air T[a]	0.131	0.592	0.067	0.785
SST summer[b]	−0.097	0.659	−0.113	0.607
SST winter[b]	−0.203	0.330	−0.208	0.308
Bottom T[i]	0.019	0.937	−0.059	0.805
Ice extent[j]	−0.079	0.735	−0.041	0.859
Ice retreat[j]	−0.141	0.543	−0.085	0.716
Cold pool[k]	−0.141	0.564	−0.058	0.813
Wind mixing[l]	0.340	0.155	0.331	0.154
Bloom date[m]	**−0.397**	**0.074**	−0.336	0.127
Entrainment[m]	0.035	0.865	0.090	0.648
El Nino (SOI)[g]	0.073	0.747	−0.003	0.988
Arctic Oscillation[n]	0.074	0.730	0.111	0.591
PDO[h]	**−0.425**	**0.055**	**−0.362**	**0.098**

Correlations significant at 90% confidence level are highlighted. Data description and sources.

[a] Annual air temperature index for Kodiak airport and St. Paul Island based on data provided by the Western Regional Climate Center (http://www.wrcc.dri.edu/summary/climsmak.html).

[b] Summer (May–September) and winter (previous October–March) sea-surface temperature anomalies averaged over 57–59°N, 149–151°W (GoA) and 57–59°N, 163–171°W (Bering Sea) provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA (http://www.cdc.noaa.gov/).

[c] Estimated annual sea-surface (0–20 m) temperature anomalies, annual bottom (200–250 m) temperature anomalies, and January–May surface salinity anomalies at station GAK 1 (59°50.7′N 149°28.0′W), based on data provided by Tom Weingartner, Institute of Marine Sciences, University of Alaska, Fairbanks, AK and the Exon Valdez Oil-Spill Trustee Council, Anchorage, Alaska, USA.

[d] Total estimated annual freshwater discharge into the Gulf of Alaska, provided by Tom Royer, Center for Coastal Physical Oceanography, Old Dominion University, Norfolk, Virginia, USA.

[e] Summer (May–September) average magnitude of winds at Middleton Island, provided by Seth Danielson, Institute of Marine Sciences, University of Alaska, Fairbanks, Alaska, USA.

[f] Cumulative sum of positive daily upwelling indices, May through September, based on data provided by the Pacific Fisheries Environmental Laboratory, NOAA, Pacific Grove, California, USA (http://www.pfeg.noaa.gov/index.html).

[g] Southern Oscillation Index (standardized Tahiti minus standardized Darwin sea level pressure) averaged over 12 months (previous May to April) based on NCEP/NCAR reanalysis data provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA (http://www.cdc.noaa.gov/cdc/reanalysis/).

[h] Winter (November–March) average Pacific Decadal Oscillation index (Mantua et al., 1997) provided by the Joint Institute for the Study of the Atmosphere and Oceans, University of Washington, Seattle, Washington (http://tao.atmos.washington.edu/pdo/).

[i] Index of average bottom temperature on the eastern Bering Sea shelf during summer, adjusted for data of sampling (Mueter et al., 2006), based on bottom trawl survey data (provided by Alaska Fisheries Science Center, NMFS, NOAA, Seattle, Washington).

[j] Average percentage of NMFS survey area covered by ice, January–May, and week of year during which average ice concentration on the Southeast Bering Sea shelf decreases to less than 20%. Indices are based on digital ice charts from the Arctic Climatology Project, National Ice Center (http://www.natice.noaa.gov), modified from Palmer (2003).

[k] Average spatial extent of the pool of cold water remaining on the Southeast Bering Sea shelf in summer, based on NMFS trawl survey data and adjusted for date of sampling (Mueter et al., 2006).

[l] Summer (May–September) average of daily wind mixing ($m^3\ s^{-3}$) at 57°N, 164°W (Nicholas Bond, PMEL, NOAA, pers. comm.).

[m] Estimated onset of (non-ice-related) spring bloom on middle Bering Sea shelf at 57°N, 164°W and July–August entrainment of nutrient-rich deep water into surface layer, based on one-dimensional mixed-layer depth model developed by Carol Ladd, Pacific Marine Environmental Laboratory, NOAA, Seattle, Washington.

[n] Arctic Oscillation index average for (previous) December through March, based on NCEP reanalysis data, provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado, USA (http://www.cdc.noaa.gov/cdc/reanalysis/).

the effects of censoring on estimates of MMSP and B_m in the PT model.

In addition to modelling surplus production as a function of biomass, we examined relationships between production and regional environmental indices to test whether productivity varies in response to environmental fluctuations. Annual surplus production is the sum of new recruitment and growth less natural mortality (deaths) in a given year, where recruitment to the "assessed stock" occurs at ages ranging from 1 to 6 years, depending on the species (Table 1). Recruitment and growth of recruits is affected by environmental conditions during pre-recruit stages (prior to year *t*), whereas annual growth of already recruited individuals is primarily affected by conditions during year *t*. To capture potential environmental effects on growth and recruitment during both pre-recruit and adult stages we examined correlations between surplus production in a given year and regional or large-scale environmental indices averaged over the previous 3 years (Table 2). We chose to use three-year averages a priori because recruitment in most stock assessments occurs at age 3, therefore the moving average reflects environmental conditions from the early juvenile stage to the present for new recruits. Other time lags were examined but are not reported here to minimize the chances of identifying spurious correlations. Both ASP_t and residuals from the GS model (ε_t) were used in the correlation analysis. Variables that were significantly ($P < 0.1$) correlated with these indices based on a simple *t*-test (Zar, 1999) were considered for further modelling.

Potential covariates identified in the correlation analysis were incorporated in generalized versions of the Graham-Schaefer and Pella-Tomlinson surplus production models. Environmental effects were initially modelled as either additive or multiplicative effects on the logistic growth parameter *r* or on carrying capacity *K* in the familiar logistic formulation of the Graham-Schaefer model (e.g. Quinn and Deriso, 1999):

$$\mathrm{ASP} = r \times B \times \left(\frac{1 - B}{K}\right)$$

In this formulation, *r* is directly proportional to maximum surplus production (MMSP), and *K* is identical to the unfished biomass (B_∞). Preliminary model comparisons among the different ways of including effects of environmental variability on surplus production suggested that multiplicative effects on the growth parameter *r* generally resulted in the best fit based on the Akaike Information Criterion (not shown). Therefore, we present only results for a model that incorporates multiplicative effects on *r*:

$$\mathrm{ASP_t} = r \times \mathrm{e}^{\delta \cdot X_t} \times \bar{B}_t \times \left(\frac{1 - \bar{B}_t}{K}\right) + \varepsilon_t$$

where X_t represents an environmental index that was standardized to have mean 0 and standard deviation 1. Thus, parameter *r* reflects the intrinsic growth rate under average environmental conditions ($X_t = 0$). Maximum surplus production under these conditions is $\mathrm{MMSP} = rK/4$. The Pella-Tomlinson model can be formulated similarly in terms of productivity and carrying capacity:

$$\mathrm{ASP} = r \times B \times \left(1 - \left(\frac{B}{K}\right)^{\nu - 1}\right)$$

Environmental effects were incorporated in the PT model analogously to the generalized GS model above and all parameters and their full posterior distributions were obtained through Bayesian estimation.

3. Results

3.1. Trends in total biomass and surplus production

The total combined groundfish biomass of BSAI stocks included in our analysis (Table 1) increased from an estimated 8.5×10^6 t in 1977 to more than 20×10^6 t in 1987 and has fluctuated between 15 and 22×10^6 t since then (Fig. 2). Total groundfish biomass in the GoA increased from 4×10^6 t in 1978 to 6.5×10^6 t in 1982, before decreasing again to 5×10^6 t in 1985. Estimated biomass has remained relatively constant since then. Groundfish biomass was dominated by walleye pollock (*Theragra chalcogramma*) in the Bering Sea and by walleye pollock and arrowtooth flounder (*Atherestes stomias*) in the Gulf of Alaska (Fig. 3). Interannual fluctuations in total biomass in the Bering Sea were largely driven by variability in pollock biomass (Fig. 3a). A long-term decreasing trend in walleye pollock biomass in the GoA was compensated by an increase in arrowtooth flounder (Fig. 3b). Trends in biomass of these two species were strongly negatively correlated ($r = -0.85$). Stocks

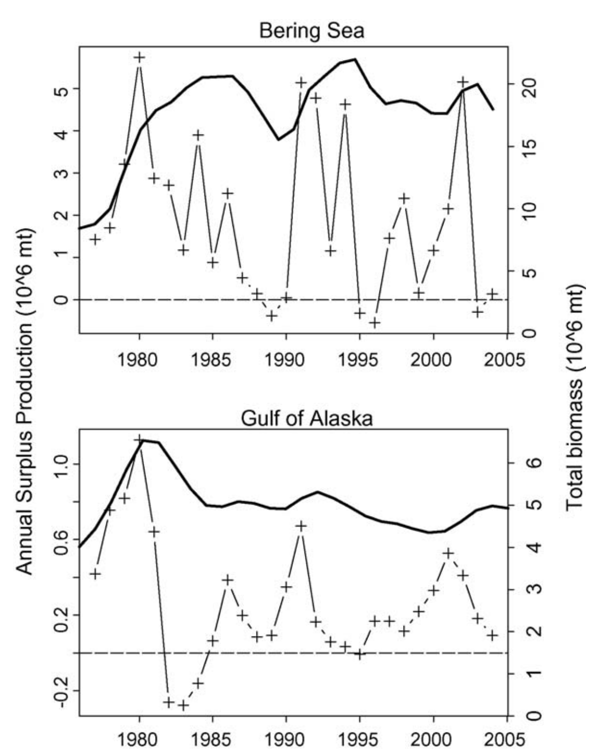

Fig. 2. Time series of total biomass summed across major species in the Bering Sea and Gulf of Alaska based on 2005 stock assessments (heavy lines) and estimated annual surplus production (thin line with '+' symbol).

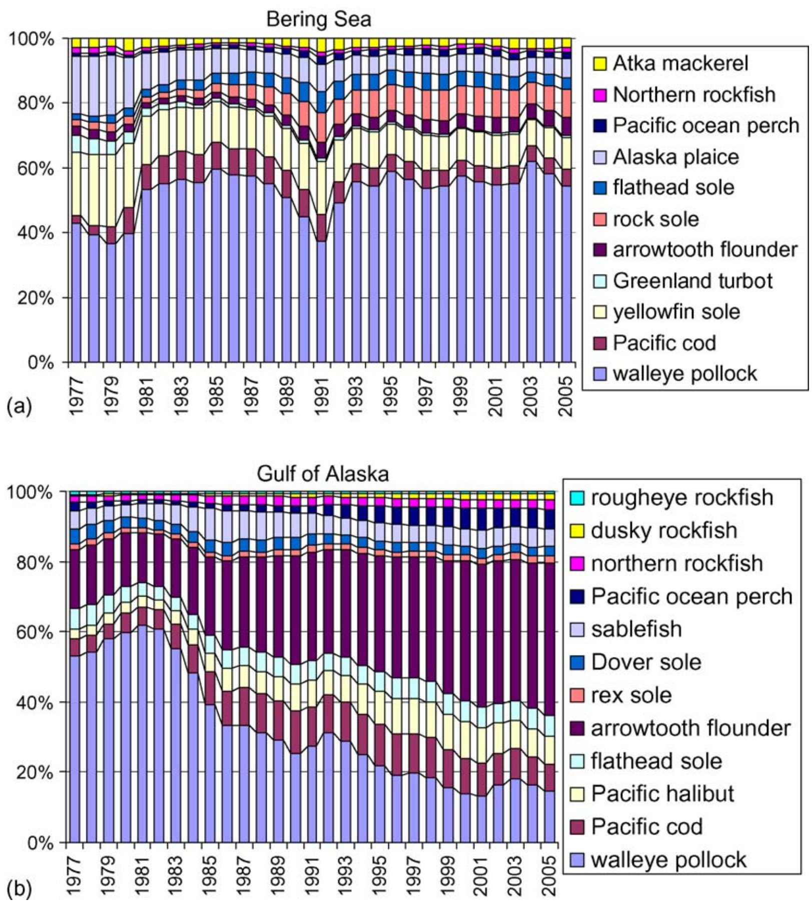

Fig. 3. Relative species composition of the commercially harvested component of the groundfish community by year from 1977 to 2005 in the Bering Sea/Aleutian Islands and in the Gulf of Alaska.

included in this analysis comprise, on average, 93% of the total groundfish catch per unit effort (CPUE, excluding invertebrates) in summer bottom trawl surveys on the Eastern Bering Sea shelf (1982–2004, Mueter, unpubl. data) and over 99% of total commercial landings, excluding invertebrates, in the BSAI region between 1977 and 2004 (NPFMC, 2005c). The GoA stocks included in our analysis comprised, on average, 83% and 68% of the groundfish CPUE in bottom trawl surveys in the western (west of 149°W) and eastern GoA, respectively, and over 90% of total annual groundfish landings (excluding invertebrates) from the GoA (NPFMC, 2005d). These percentages were relatively stable for the years for which data are available and we assume that trends in the major commercial species reflect trends in the total groundfish community. Pelagic species such as herring or sandlance were not included in our analyses due to the lack of available biomass estimates. While no estimates are available for most small pelagics, the estimated biomass of the most commonly encountered species, Pacific herring (*Clupea pallasi*), is only a very small fraction of the groundfish biomass (<2%; NPFMC, 2005c).

Total annual surplus production fluctuated greatly from year to year, averaging 1.9×10^6 t in the BSAI region and 260×10^3 t in the GoA between 1977 and 2004. Surplus production was, on average, 12% of the estimated mid-year biomass in the BSAI, but only 5.4% of the estimated biomass in the GoA. In the BSAI, ASP_t decreased throughout the 1980s, increased sharply from 1990 to 1991 as a result of a strong year class of walleye pollock, and has fluctuated widely with a decreasing trend since then (Fig. 2). Overall, there was a long-term (1977–2004) decreasing trend in ASP_t of 52×10^3 t per year in the BSAI region, but the trend was not significant (Test for linear trend: $t = -1.18$, $P = 0.248$). In the GoA, surplus production decreased sharply from 1980 to 1982, was negative for several years due to a sharp decline in total biomass, and has remained relatively stable around 215×10^3 t since 1985.

3.2. Surplus production–biomass relationships

Surplus production–biomass relationships for individual stocks are shown in Fig. 4 and display remarkable similarities among species. The most striking feature, evident in most stocks, was a clock-wise trajectory characterized by a period of relatively low biomass and relatively high or increasing surplus production from the late 1970s into the early to mid 1980s. This high surplus production resulted in increasing biomass trends for most stocks through at least the mid 1980s or early 1990s. As biomass reached high levels, surplus production tended to decrease (often to negative ASP values) and was low for most stocks in the late 1980s and/or throughout the 1990s. This reduced surplus production in turn resulted in decreasing

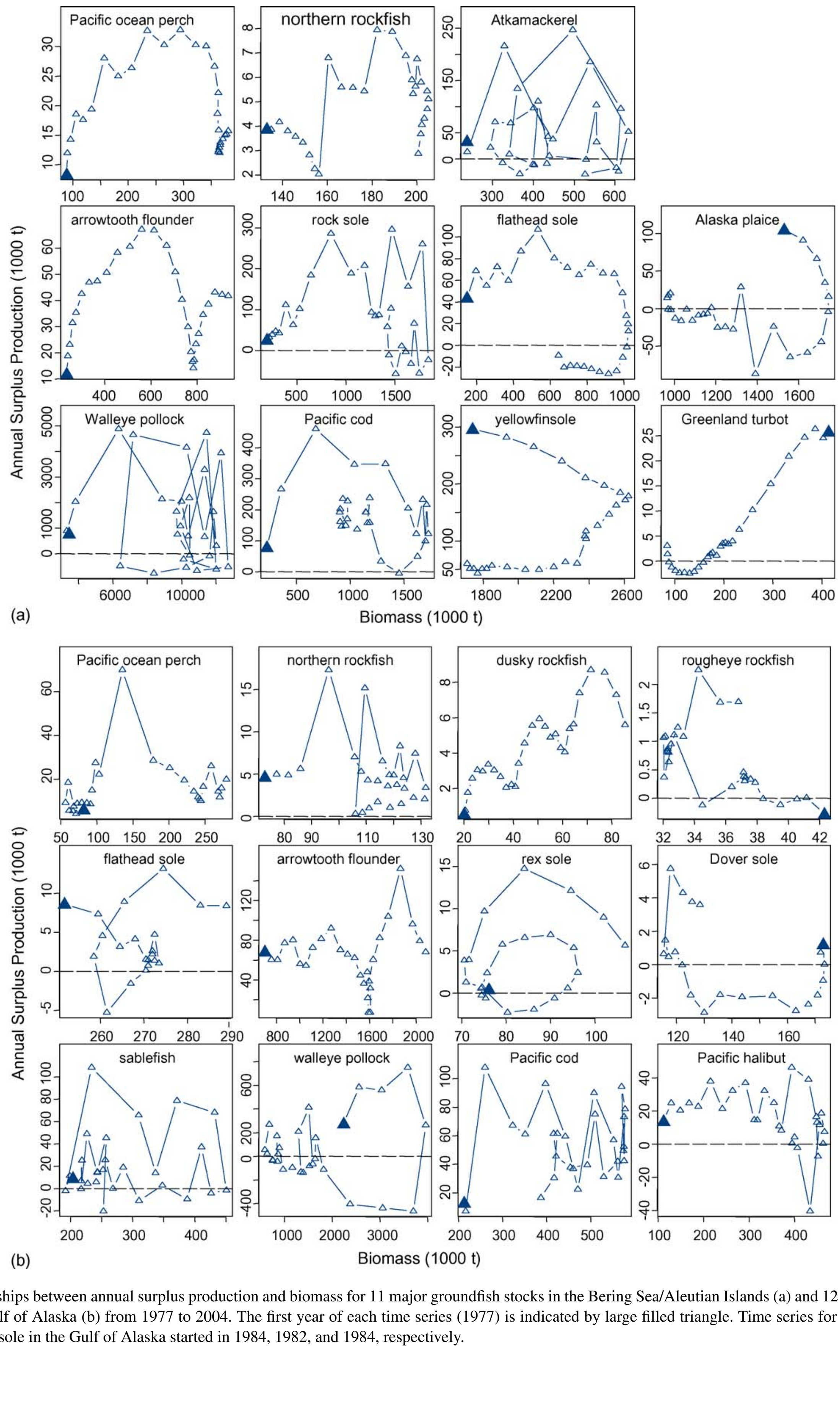

Fig. 4. Relationships between annual surplus production and biomass for 11 major groundfish stocks in the Bering Sea/Aleutian Islands (a) and 12 major groundfish stocks in the Gulf of Alaska (b) from 1977 to 2004. The first year of each time series (1977) is indicated by large filled triangle. Time series for flathead sole, rex sole, and Dover sole in the Gulf of Alaska started in 1984, 1982, and 1984, respectively.

biomass levels throughout the 1990s for many stocks. In spite of lower biomass, production did not increase in most cases as would be expected under the surplus production model with constant productivity and carrying capacity. These patterns are likely to result from fluctuations in productivity and/or carrying capacity, in addition to density-dependent responses to fishing.

After aggregating biomass across stocks, there was relatively little contrast in total biomass between 1977 and 2004 and only limited evidence for a dome-shaped relationship between surplus production and biomass, particularly in the GoA (Fig. 5). Model fits suggest that biomass in recent decades was well above the biomass that produces MSY and may have been near 75% of unfished biomass for most of the past 2 decades. However, both unfished biomass (B_∞) and B_m were very poorly estimated in most cases (Table 3; Fig. 5) and may be much higher or lower than the point estimates. In contrast, estimates of MMSP, the parameter of primary interest in this study, were generally less variable and provide useful approximations for the maximum yield that can be harvested sustainably from the groundfish complexes of the BSAI and GoA. Estimates for the GoA differed between the two models and had large credibility intervals (CI, the Bayesian equivalent of a confidence interval based on the posterior probability distribution of a given parameter of interest) (Table 3; Fig. 5). The large CIs were due to the small contrast in total biomass during the period of study. Estimates for MMSP correspond to a value of B_m that is outside the range of the observed data, therefore it was very sensitive to the form of the model and to the prior distributions on B_m and B_∞.

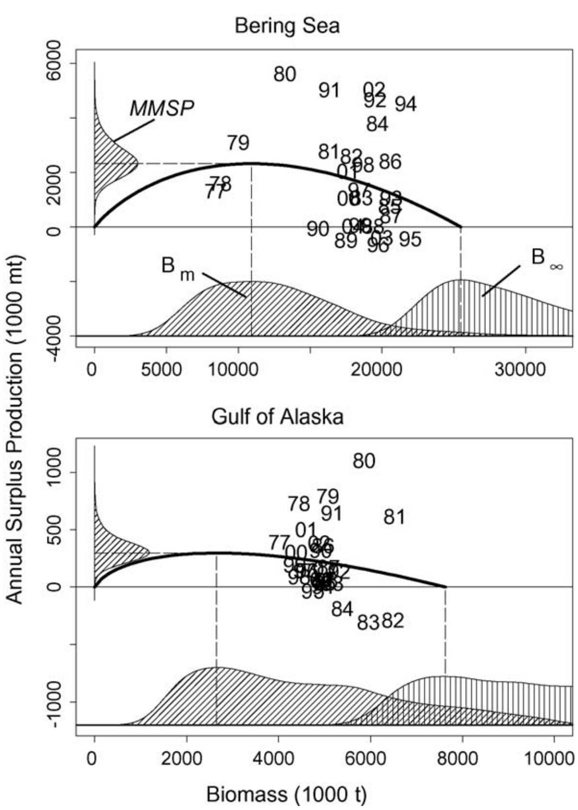

Fig. 5. Relationships between annual surplus production and total biomass for the Bering Sea and Gulf of Alaska groundfish complexes. Model fits corresponding to the mode of the posterior distributions of parameters of the Pella-Tomlinson surplus production model are indicated by solid lines. Full posterior probability distributions for three parameters of interest are indicated along the *x*-axis (unfished biomass, B_∞, and biomass corresponding to peak production, B_m) and along the *y*-axis (maximum multi-species surplus production MMSP).

Table 3
Parameter estimates with 95% credibility intervals for two surplus production models fit to the total annual surplus production–total biomass relationships of the groundfish complexes in the Bering Sea/Aleutian Islands and in the Gulf of Alaska

	Graham-Schaefer			Pella-Tomlinson		
	Mean	Median	95% CI	Mean	Median	95% CI
Eastern Bering Sea/Aleutian Islands						
B_∞ (10^6 t)	38.7	32.7	22.5–85.3	29.1	28.0	22.0–42.4
B_m (10^6 t)	19.4	16.4	11.2–42.7	12.7	12.0	5.86–24.7
MMSP (10^6 t)	2.28	2.23	1.34–3.49	2.47	2.41	1.42–3.90
σ (10^6 t)	1.97	1.94	1.51–2.61	1.96	1.94	1.50–2.59
Gulf of Alaska						
B_∞ (10^6 t)	9.56	9.52	6.22–12.9	9.45	9.31	6.26–12.9
B_m (10^6 t)	4.78	4.76	3.11–6.45	4.54	4.17	1.59–9.24
MMSP (10^3 t)	286	283	146–445	332	316	161–598
σ (10^3 t)	335	330	256–445	336	330	259–446

Posterior distributions for each parameter were obtained via MCMC in a Bayesian model formulation and are summarized below. 95% Credibility intervals (CI) are based on the 2.5th and 97.5th percentile of the posterior distribution. Parameter σ denotes standard deviation of the residuals. These models included no environmental effects or auto-correlation.

Maximum multi-species surplus production in the BSAI was estimated to be approximately 2.47×10^6 t based on the Pella-Tomlinson model, with a 95% credibility interval ranging from 1.42 to 3.90×10^6 t (Table 3). The biomass at which MMSP occurs was poorly estimated with a mean of 12.7×10^6 t. The model suggested that B_m is much less than half of B_∞ (Fig. 5) and B_m was often close to its lower limit imposed by the prior constraint $0.2B_\infty < B_m$ (Fig. 5). If the constraint on the lower limit was relaxed, the estimate of B_m decreased and the estimate of MMSP increased. For example, using the constraint $0.1B_\infty < B_m < 0.9B_\infty$ resulted in mean estimates for B_m and MMSP of 11.7×10^6 and 2.59×10^6 t, respectively. Lacking data at lower levels of total biomass, B_m cannot be estimated with any confidence because it requires extrapolation outside the range of observed values. Estimates of MMSP for the GoA were more variable with point estimates of 286 and 332×10^3 t for the GS and PT models, respectively (Table 3). There was significant autocorrelation in the residuals for the Gulf of Alaska models, but no obvious trend over time. However, models that included autocorrelation did not converge and we only show results for models without autocorrelation. This implies that our credibility intervals underestimate the true uncertainty about the parameter estimates.

We compared our estimates of long-term MMSP to the sum of single-species MSYs from recent stock assessments (Table 4). Both quantities provide an estimate of multi-species MSY. Because MSY and the corresponding fishing mortality F_{MSY} are estimated for very few stocks, we used a proxy for MSY based on F_{ABC}, the fishing mortality corresponding to the maximum allowable biological catches (ABCs), for stocks that had no estimates. The proxy was calculated by summing annual deter-

Table 4
Sum of single-species allowable biological catches (ABCs) across stocks included in our analysis by region and year, based on recent stock assessments

Year	BSAI (10^3 t)	GoA (10^3 t)
2002	3119	415
2003	3227	438
2004	3592	538
2005	2929	497
2006	2896	455
Average	3152	469

Average ABCs over several years were taken to be a proxy for MSY. No separate ABCs were estimated for dusky rockfish, rougheye rockfish, and rex sole in 2002–2004. These were set equal to the 2005/2006 average.

minations of single-species ABCs across all included stocks by region for each year from 2002 to 2006, and averaging across years (for details on estimating ABCs, see NPFMC, 2005a). This procedure was followed because it is consistent with the way MSY and OY ranges were estimated historically. The resulting sum of single-species ABCs for the stocks included in our analysis was 3.15×10^6 t in the BSAI and 469×10^3 t in the GoA, considerably larger than our point estimates of MMSP. No estimate of uncertainty for this sum was available but it fell well within the 95% credibility intervals of our estimates for MMSP (Table 3). An alternative estimate of multi-species MSY may be obtained by summing single-species overfishing limits (OFLs) across stocks. The OFL for a stock corresponds to MSY where known and to a proxy otherwise (NPFMC, 2005a) and is always larger than the ABC. Therefore, the difference between MMSP and the sum of single-species MSY is likely to be larger than indicated in Table 4.

3.3. Environmental effects on surplus production

Correlations between surplus production (either ASP_t or residuals from the Graham-Schaefer model) and environmental indices were typically small (<0.5) and rarely significant (Table 2). Most of the environmental indices were specific to the Gulf of Alaska or to the Bering Sea, with the exception of two large-scale variables that may affect both systems (Southern Oscillation Index and Pacific Decadal Oscillation). Regional variables included measures of air temperature, water temperature (both surface and bottom), and wind mixing for both regions. Several indices describing winter ice conditions were included for the analysis of Bering Sea surplus production because sea ice is a major driver of marine productivity in the eastern Bering Sea (Niebauer et al., 1995; Hunt et al., 2002). Similarly, freshwater discharge and surface salinities were examined in the GoA because freshwater is a major driver of the Alaska Coastal Current, which impacts productivity on the GoA shelf (Royer et al., 2001).

In the BSAI we found significant negative correlations between the PDO index and surplus production (ASP_t or GS residuals, ε_t) (Fig. 6). The Pacific Decadal Oscillation in its positive phase is associated with warm air and sea-surface temperatures, reduced ice cover, an early ice retreat, and reduced winds over the shelf. However, none of these variables were significantly correlated with surplus production. We included the PDO in a generalized surplus production model to estimate its potential (multiplicative) effect on MMSP. In the GoA, relationships between ASP_t and both annual bottom temperatures and winter/spring (January–May) surface salinities at station GAK 1 were significant at the 90% level (Table 2; Fig. 6). Because estimates of surface salinity were not available for all years and were well correlated with bottom temperatures ($r = -0.49$), we incorporated only bottom temperatures in the generalized surplus production model.

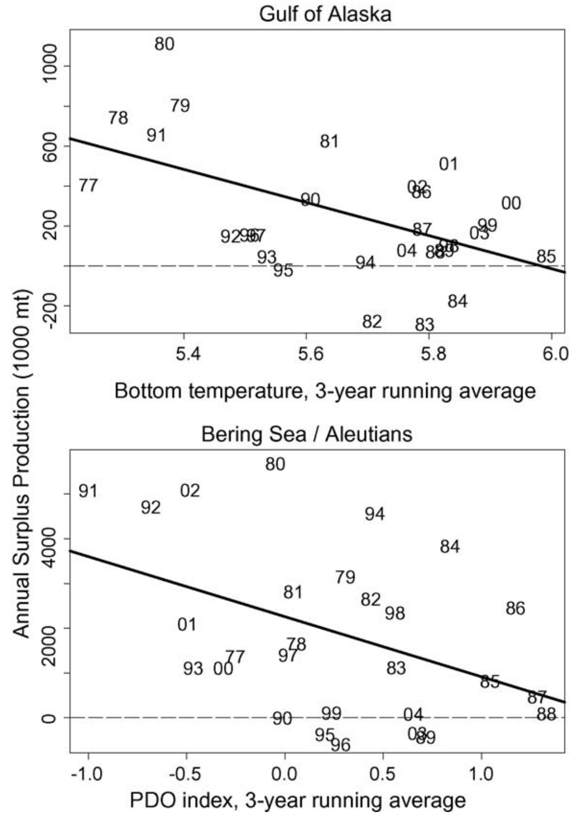

Fig. 6. Relationships between total annual surplus production and annual average bottom temperature on the shelf (Gulf of Alaska) and the Pacific Decadal Oscillation index (Bering Sea). Linear trends are significant at the 95% significance level.

The generalized Pella-Tomlinson model for the BSAI groundfish complex suggested an apparent negative effect of the PDO on maximum surplus production that was significantly different from zero ($\delta = -0.48$, 95% CI: -0.91 to -0.08). Estimates of the parameters B_∞ (30.4×10^6 t), B_m (14.2×10^6 t), and MMSP (1.99×10^6 t) were similar to those from models without the covariate (Table 3), but had somewhat wider credibility intervals. However, uncertainty about MMSP (95% CI: 1.04–3.19×10^6 t) did not increase compared to the original PT model that had no environmental variables (Table 3). For the GoA groundfish complex, the generalized PT model incorporating a multiplicative effect of GAK 1 bottom temperatures on productivity (as measured by the intrinsic growth rate r) suggested that maximum surplus production in the GoA decreased significantly with bottom temperature ($\delta = -0.63$, 95% CI: -1.30 to -0.12). The estimated effect implies a nearly two-fold increase in MMSP (95% CI: 1.1–3.7) of the GoA groundfish complex for a decrease in bottom temperature corresponding to one standard deviation (approximately 0.2 °C).

4. Discussion

The aggregate approach described here provided reasonable empirical estimates of maximum surplus production for the groundfish complexes of the Bering Sea and Gulf of Alaska by integrating the effects of historical patterns in species composition and abundance into overall estimates of productivity and carrying capacity. These estimates provide a reference point, MMSP, that can be viewed as the ecosystem equivalent of single-species MSYs. However, any reference point based on simple aggregated models should be interpreted with caution. In addition to ignoring variability in fish growth, recruitment, natural mortality, and age structure, as in single-species production models, aggregate production models also fail to account for differences in productivity among species. Maybe for this reason few studies have aggregated biomass across species (e.g. Ralston and Polovina, 1982). Although we aggregated across all of the major commercial groundfish species, we could not include other important components of the ecosystem such as invertebrates or forage species which may serve both as prey for and compete with groundfishes. Therefore, our conclusions apply only to the commercially exploited groundfish community and assume no major trends in the other components, an assumption that should be evaluated separately. In spite of these shortcomings, we suggest that our estimates of multi-species MSY are more appropriate than the sum of single-species MSYs and provide an alternative approach to setting limits on overall removals from an exploited species complex.

Improved ways to set limits on total removals from a given ecosystem are needed if such limits are going to be used as part of an ecosystem-based approach to management. In the past, OY ranges, which provide both lower and upper limits on total removals (with the expectation that catches will be at least as high as the lower limit), were obtained by arbitrarily reducing the sum of single-species MSY proxies to account for ecosystem considerations as well as for model and estimation uncertainties. The resulting OY ranges as specified in the Fisheries Management Plans for the BSAI and GoA groundfish fisheries are $1.4–2 \times 10^6$ t in the BSAI and $140–800 \times 10^3$ t in the GoA (NPFMC, 2005a,b). The 2×10^6 t upper limit in the Bering Sea has served as an effective constraint on removals from the BSAI ecosystem since 1981 and has been cited as an example of incorporating ecosystem considerations into fisheries management (Witherell et al., 2000). In contrast, catches in the GoA have been well below the upper limit since the inception of OY ranges. This reflects both lower exploitation rates in the GoA compared to the Bering Sea and, as suggested by our results, an unrealistically high value for the upper OY limit as currently specified (800×10^3 mt compared to our best MMSP estimate of 332×10^3 mt).

To establish more objective upper limits for total removals (i.e. for the upper limit of the OY range), we propose a simple approach based on estimates of maximum multi-species surplus production. Under a risk-neutral approach the upper catch limit would be set equal to the best point estimate of MMSP to ensure that total yield (Y) does not exceed MMSP more than 50% of the time (assuming no implementation error). However, to be precautionary, a more risk-averse approach that limits the chances that total yield exceeds MMSP to a fixed probability $P^* < 0.5$ such that $\Pr(Y > \text{MMSP}) < P^*$ could be adopted (Prager et al., 2003). The choice of P^* depends on the degree of risk-aversion desired. For example, using a risk-averse value of $P^* = 0.2$ and posterior distributions of MMSP from our Bayesian analysis of the PT model (Table 3), this approach produces upper catch limits of 1.96×10^6 t for the BSAI and 246×10^3 t for the GoA (i.e. under this model the probability that actual catches up to these limits exceed MMSP for the species complex is 20% or less). Although the choice of P^* is as arbitrary as a proportional reduction in MSY (or MMSP) to obtain OY, this approach accounts for uncertainty in the estimate of MMSP. For $P^* = 0.2$ the upper OY limit for the BSAI region is close to the current cap of 2×10^6 t of groundfish. Therefore, $P^* = 0.2$ approximately reflects the current degree of risk aversion that is implied by the OY range specified in the Fisheries Management Plan for BSAI groundfish. If the same degree of risk aversion is applied to the GoA, the estimated cap for GoA groundfish catches (246×10^3 t) is much lower than the current limit of 800×10^3 t and was exceeded by the actual catches (only considering those species that were included in the analysis) in 22 of the past 30 years. However, current biomass is considerably higher than our point estimate of B_m (approximately 75% of the estimated unfished biomass, Fig. 5), implying that average historic levels of removals have been less than the MMSP. Based on our results, the current limit of 800×10^3 t has a very high chance of exceeding MMSP (with over 99% probability, see Fig. 7), suggesting a need to adjust the limit downward. Note however that our MMSP estimate does not include the catches of all species in the BSAI and GoA fisheries (99% and 90% of total catches, respectively).

The outlined approach provided reasonable estimates of maximum multi-species surplus production for the Gulf of Alaska and Bering Sea and offers a pragmatic approach to setting upper limits for total removals from these multi-species groundfish complexes. Our estimates of MMSP or system-wide MSY were generally smaller than recent estimates of the sum of single-species MSYs (or MSY proxies) across the included species (Table 4). This suggests that multi-species considerations, at least in these ecosystems, may require more conservative upper limits for total yield than the sum of single-species MSYs. However, the sum of single-species MSYs were well within 80% credibility limits of our estimates of MMSP and at present it is not clear which estimates provide better proxies for system-level MSY.

Our results further suggest that fixed OY ranges may not be appropriate because of slow changes in average productivity. The historical, fixed optimum yield ranges were established in part to encompass observed variability in allowable biological catches, which were believed to reflect biological productivity of the groundfish complex, and in part to allow for a profitable fishery operating in a relatively stable management environment. However, there is increasing recognition that biological produc-

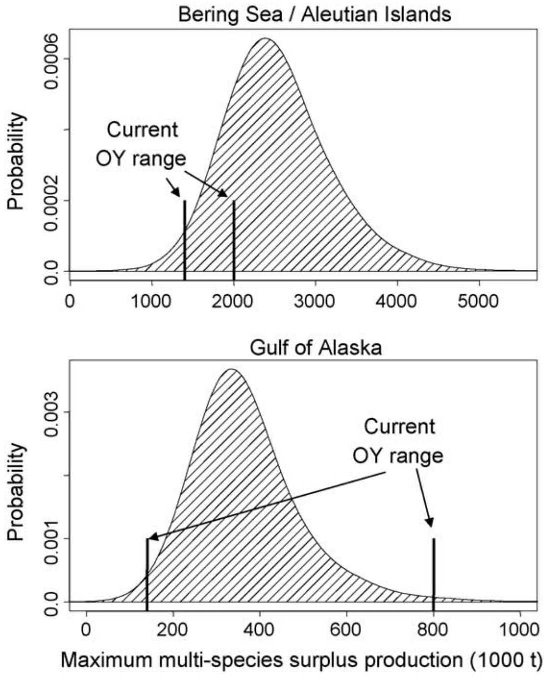

Fig. 7. Posterior distribution of Bayesian estimates of maximum surplus production for the groundfish complexes in the Bering Sea and Gulf of Alaska based on a Pella-Tomlinson model fit to aggregated data. Estimates were expanded to the entire groundfish complex (including target species not included in the analysis and non-target fish species) based on the ratio of the total catch of species included in our analysis to total recorded groundfish catches, averaged over the last 5 years (2000–2004). Vertical lines indicate current optimum yield (OY) ranges as specified in fisheries management plans.

tivity of the GoA and BSAI groundfish communities may change in response to environmental regime shifts (e.g. Conners et al., 2002; Wilderbuer et al., 2002). Such variability in overall productivity is supported by our findings that variability in surplus production for the BSAI and GoA groundfish complexes was significantly related to environmental variability. This raises the question whether system-level MSY/OY ranges should consist of fixed ranges or should be allowed to vary with changes in productivity over time.

We discuss several options for specifying total allowable removals from a multi-species complex in a fluctuating environment. First, MSY and OY ranges could be set sufficiently conservative to account for periods of low productivity. This essentially reflects the current policy of specifying a fixed OY range. Drawbacks include the potential for unsustainable harvests during periods of low productivity (i.e. if system-level productivity is reduced below the upper OY limit, while single-species considerations may suggest allowable catches near the upper end of the OY range) and foregone catches during periods of high productivity. Second, system-wide MSY levels could be reviewed and adjusted periodically, or even annually, to reflect changing environmental conditions. However, such adjustments require a better understanding of the critical time scales of environmental variability and their effects on productivity. Currently, it is not clear whether the observed relationships are primarily a consequence of interannual variability or decadal-scale (regime-like) variability in productivity. Regime-like dynamics have been shown to dominate the total production of salmon populations in the Northeast Pacific (Hare and Francis, 1995) and recent evidence supports similar regime shifts in the productivity of groundfish communities in the mid-1970s (Conners et al., 2002) and in the late 1980s (Wilderbuer et al., 2002). Our ability to detect, let alone predict, such regime changes in a timely manner is limited at present. Third, system-level yields could be based on a "constant F"-type approach similar to the harvest control rules that are widely used to specify allowable catches for individual stocks. However, there is no accepted definition of fishing mortality at a multi-species level, thus it is unclear at present how to implement such an approach. Clearly, there is much room for additional research to develop acceptable ecosystem-level reference points.

We found a large discrepancy between the current OY limits for the GoA groundfish complex and our estimate of maximum multi-species surplus production (Fig. 7). Historical MSY and OY ranges were derived from single-species estimates based on data available in the mid-1980s, when MSY of arrowtooth flounder alone was estimated to be over 500×10^3 t. More recent estimates of arrowtooth flounder MSY were on the order of $150–220 \times 10^3$ t (NPFMC, 2005b). Alternatively, our estimates of MMSP may be too low because of the very limited contrast in total biomass between 1977 and 2004. Overall exploitation rates for the groundfish complex in the Gulf of Alaska (3.5–7%) over this period have generally been much lower than in the Bering Sea and total biomass has remained remarkably stable. Therefore, estimates of surplus production at reduced levels of total biomass, corresponding to higher exploitation rates, are lacking. This lack of contrast requires extrapolation outside the region of observed biomasses to obtain estimates of maximum surplus production. Such extrapolation is highly uncertain and may underestimate the true surplus production if biomass were reduced below recent levels. Current harvest rates in the GoA are low because of the minimal exploitation of arrowtooth flounder (<1%), which account for approximately 50% of the biomass of commercial groundfish in the GoA. Increased exploitation of arrowtooth flounder and a corresponding decrease in total biomass could provide the necessary contrast to obtain improved estimates of total MSY in the multi-species fishery. Until better estimates of multi-species MSY become available, we suggest that the existing upper OY limit for the Gulf of Alaska be reduced to better reflect the estimated maximum multi-species surplus production.

Our analysis reflects conditions during the period examined and may have been influenced by changes in management and in the environment at the beginning of the study period. The common pattern of clock-wise surplus production–biomass trajectories (Fig. 4) needs to be interpreted in the context of such changes. Peak removals from the groundfish complexes occurred in the late 1960s in the GoA and early 1970s in the BSAI (NPFMC, 2005a,b) and may have resulted in the low biomass levels of some species in 1977. The passage of the Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA) in 1976 led to the phasing out of foreign fisheries and a reduction in the catches of a number of species such as

Pacific Ocean perch and sablefish. However, any changes resulting from the changes in management are confounded with and cannot easily be separated from concurrent changes in the North Pacific climate, which underwent a pronounced regime shift around 1976/77. It appears likely that the regime shift resulted in an increase in productivity (growth parameter r or carrying capacity K) that was reflected in strong recruitment of a number of groundfish stocks in the late 1970s (e.g. Hollowed et al., 2001) and may explain the widespread increase in biomass during the late 1970s/early 1980s (Fig. 4). The view that environmental effects were responsible for the observed increases in biomass after 1976 is supported by the case of Greenland turbot, which provide a striking counter-example to the other species (Fig. 4a). Unlike most species, Greenland turbot had a high biomass in 1977 in spite of a long history of exploitation. Greenland turbot biomass has decreased since 1977 in spite of much reduced exploitation rates (NPFMC, 2005a), which is more consistent with environmental effects on productivity than effects from fishing.

These observations, results from our environmental models, and other studies suggest that overall groundfish productivity in the Bering Sea and Gulf of Alaska varies in response to environmental fluctuations. The relationships in Fig. 6 appear to reflect reduced growth and/or reduced recruitment during warm years, contrary to previous observations that groundfish recruitment tends to be enhanced during warm years (Hollowed and Wooster, 1995). In particular, a strong decreasing trend in surplus production of non-pollock groundfish species in the Bering Sea (not shown) appears to result from both reduced recruitment (Wilderbuer et al., 2002) and reduced growth (Palmer, 2003) of flatfishes during the 1990s. The reduced spatial extent and earlier retreat of sea ice from the Eastern Bering Sea during warm years may decrease the supply of primary production to the benthic community through mechanisms described by Hunt et al. (2002), reducing the growth of those species that primarily consume benthic prey (Palmer, 2003). In the Gulf of Alaska, reduced surplus production was associated with warm bottom temperatures and low surface salinities in late winter and spring. Salinity on the Gulf of Alaska shelf is positively correlated with nutrient concentrations and we speculate that the observed relationship was the result of reduced water column productivity associated with low nutrient concentrations, which may limit the amount of new growth of groundfish species. However, at this point, the estimated effects of environmental variability on surplus production are highly uncertain and potentially spurious because of the relatively large number of variables examined.

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