

# Spatio-temporal variation in fish condition is not consistently explained by density, temperature, or season for California Current groundfishes

James T. Thorson

Fisheries Resource and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112, USA

**ABSTRACT:** Condition (the relationship between individual weight and length) has been researched in fisheries science for over 100 yr and is claimed to be an integrated measure of physiological status for fishes. Spatial or temporal variation in condition can contribute to otherwise unexplained variation in the relationship between spawning biomass and recruitment. Individual condition is also included in age-structured population models, which use weight at age to convert population estimates between numbers and biomass. However, no study has analyzed spatial and temporal variation in condition for multiple marine species. Here I apply recent improvements in spatial modeling to analyze coastwide variation in condition for 28 groundfishes in the California Current. I show that, on average, 22% of individual-level variation in condition can be explained via persistent (constant over time) and annually varying spatial differences in condition, and condition for many species varies 10 to 20% spatially and among years. While population density, bottom temperature, and calendar date are parsimonious descriptors of condition in several species, the sign of these coefficients varies, and their magnitude is small relative to the magnitude of residual spatial and temporal variation. Additionally, annually varying spatial differences have nearly twice the magnitude of persistent spatial differences in condition. I therefore conclude that dynamic habitat conditions contribute a substantial portion of variation in individual condition for these groundfishes. Spatial and temporal variation in condition will be important for population models that convert between numbers, fishery catch, and population biomass, and may also clarify unexplained variability in productivity for marine fishes.

**KEY WORDS:** Relative condition factor · Spatial analysis · Weight at length · Northeast Pacific groundfish · State-dependent life history theory · Fish growth · Density dependence · Gaussian random fields

—Resale or republication not permitted without written consent of the publisher—

## INTRODUCTION

Fish condition can be broadly defined as the relationship between fish length and weight (Le Cren 1951) and has been studied and written about for over a century (Nash et al. 2006). Individual condition has historically been used in fisheries and wildlife sciences to infer whether environmental conditions are favorable or unfavorable for a given population (Owen & Cook 1977, Boxrucker 1987). Typically, decreased condition is interpreted to indi-

cate that a population, its competitors, or its predators have elevated densities such that feeding rates for the population are depressed (Boxrucker 1987, Pardoe et al. 2008).

Ecological theory and empirical evidence suggests that plump individuals (those that have greater weight for a given length) are likely to have accumulated greater energy reserves and thus be more capable of reproductive investment and therefore more fit (Glazier 2000, Jørgensen et al. 2006, Morgan et al. 2010). Given this greater reproductive invest-

ment, information about individual condition may explain variation in the relationship between spawning stock biomass and subsequent juvenile production ('recruitment'). Individual condition also influences the rate at which sexually mature fishes skip spawning in particular years (Burton 1994, Rideout et al. 2005). The relationship between spawning biomass and recruitment is famously variable (Hjort 1926, Cushing 1990, Thorson et al. 2014), and any information that helps to improve understanding of reproductive potential or predictions of recruitment could be helpful for management of exploited fisheries (Haltuch & Punt 2011, Morgan et al. 2011).

Fishes generally have allometric growth, e.g. a linear regression of the logarithm of weight against the logarithm of length will have a slope different (and often greater) than 3 (Froese et al. 2014). This implies that fish species often gain weight faster than would result if the relative shape and tissue density of a given individual were maintained while increasing its size (Nash et al. 2006). Recommended measures of individual condition (e.g. Le Cren's relative condition factor, and relative weight) account for allometric growth and define individual condition via residuals around the expected allometric weight-length relationship, where methods differ in how residuals are specifically defined, estimated, and reported (Blackwell et al. 2000).

The relationship between weight and length for a population of fishes will depend upon many factors, including fish behavior, life history strategy, tactical responses to the environment (e.g. phenotypic plasticity), and multispecies interactions (Rochet 2000, Shelton et al. 2013). This complicates any simple interpretation of fish condition (Copeland et al. 2008). Condition is known to vary seasonally as food availability, temperature, and diversion of energy towards gonadal tissue for spawning influence the relative size and density of different body tissues (Le Cren 1951, Cada et al. 1987, Pope & Willis 1996, Lambert & Dutil 1997a, Pardoe et al. 2008, Vainikka et al. 2009). Laboratory studies have also documented that Atlantic cod *Gadus morhua* and smallmouth bass *Micropterus dolomieu* have increased probability of starvation when individual condition drops below a particular level, where this starvation threshold may in some cases depend upon age and temperature, among other factors (Shuter et al. 1989, Lambert & Dutil 1997b).

Researchers have previously claimed that condition is an 'integrated measure of physiological status for fish populations' (Murphy et al. 1990). Spatial and temporal variation in condition is routinely docu-

mented by US state agencies and used to inform the stocking rates and management of freshwater fishes (Blackwell et al. 2000). Average condition is also routinely described for marine fishes (e.g. Moutopoulos & Stergiou 2002), although descriptive analyses of marine fishes often do not include spatial or temporal variation in condition. Individual condition has been studied for some well-studied marine species, particularly in the North Atlantic, including for Greenland halibut (Junquera et al. 1999), and Atlantic cod *Gadus morhua* near Iceland (Pardoe et al. 2008, Pardoe & Marteinsdóttir 2009) and near Newfoundland, Canada (Morgan et al. 2010). Feeding rates and individual condition have also been studied in anadromous species, where the decision to transition from freshwater to marine stages may be informed by individual energy storage (Thorpe et al. 1998, Beakes et al. 2010). Spatial and temporal variation in fish condition has not been generally compared among multiple species of marine fishes, and this perhaps contributes to the smaller role in marine ecology for analysis of changes in condition. The absence of comparative research regarding spatial variation in condition for marine fishes is important, given that changes in individual condition could cause unexplained variation in recruitment (Marshall & Frank 1999), e.g. by causing variation in productivity that may have contributed to the collapse of Atlantic cod near Newfoundland (Lambert & Dutil 1997b).

I therefore provide the first comparison of spatial and temporal variation in condition for multiple marine species. I specifically use 9 yr of data from the California Current (US West coast, offshore from Oregon, Washington, and California) for 28 groundfish species. These species have previously been used as a reference set for testing spatial models of population densities, so spatially varying estimates of population density are available over the entire range for each species. Bottom temperature, date, and location is also available for all samples, as well as the sex, length, and weight for each sampled individual. I seek to determine (1) whether spatial and temporal variation can explain a substantial portion of observed variation in fish condition; (2) whether species density, bottom temperature, or calendar date explains spatial variation and/or fish condition for individual species; and (3) whether any of these variables have a consistent effect across species, or within groups of species with similar habitat or phylogeny. I consider a variable to have a consistent effect on these species (or a group of species that have similar habitat, phylogeny, or depth) if the variable is identified as being a parsimonious descriptor of spa-

tial and temporal variation (using model selection tools) for many of these species, and additionally if the direction of the effect is generally either positive or negative for the species for which it is selected.

## METHODS

Average weight is often assumed in fisheries research to vary allometrically with length as:

$$w = \alpha L^\beta \quad (1)$$

where  $w$  is weight,  $L$  is length,  $\beta$  is the allometric coefficient ( $\beta = 3$  implies isometric growth), and  $\alpha$  is the condition coefficient. This allometric relationship in some cases is modified to allow  $\alpha$  and  $\beta$  to vary between males and females (e.g. Vainikka et al. 2009), given that females of sexually dimorphic species will generally allocate energy differently between growth, risk avoidance, and reproductive investment than males. Individual fishes often have persistent differences in growth rates and activity levels so, when fitting this model to data, researchers commonly assume that individual weights vary log-normally around the average relationship:

$$\log(w_i) = \alpha_0 + \alpha_s S(i) + \log(L_i) [\beta_0 + \beta_s S(i)] + \varepsilon_i \quad (2)$$

$$\varepsilon_i \sim N(0, \sigma_w^2)$$

where  $w_i$  and  $L_i$  are weight and length for the  $i$ -th individual with available data,  $\alpha_0$  is the average female condition,  $\alpha_s$  is the male offset for condition,  $S(i)$  is the sex for individual  $i$  (0 = female; 1 = male; 0.5 = unknown),  $\beta_0$  is the average female allometry,  $\beta_s$  is the male offset for allometry,  $\varepsilon_i$  is residual variation, and  $\sigma_w$  is the standard deviation (in log-space) for residual variation. Eq. (2) incorporates data from males and females in one single model. Some studies have instead treated data for males and female individuals in separate models, which would be identical to Eq. (2), except that modelling each sex separately also assumes that  $\sigma_w^2$  varies between sexes (Eq. 2 assumes an identical  $\sigma_w^2$ ). I have instead modeled differences between males and females explicitly, because I subsequently introduce additional variance parameters and coefficients representing the effect of measured covariates. Preliminary analysis indicated that estimating all spatial, temporal, and covariate effects separately for each sex leads to poor model performance (i.e. nonconvergence in some cases), and Eq. (2) provides a more parsimonious treatment that still estimates systematic differences in individual condition between males and females.

I seek to include spatial variation in individual condition using information for measured covariates (i.e. population density, bottom temperature, and calendar date) as well as residual variation that is spatially correlated. The latter can arise when a habitat variable drives variation in a process (i.e. individual condition), but this variable is not directly measured (Thorson & Minto in press). I therefore partition variability into 4 components: temporal (changes in individual condition throughout the population's range in a given year), spatial (areas with increased condition for all years), spatio-temporal (areas with increased condition in a particular year), and individual (residual variation in condition for each individual fish) variation. This partitioning has previously been advocated as a method for summarizing and synthesizing information about ecological indicators like individual condition (Larsen et al. 2001), and as a first analysis step when there are multiple hypothesized drivers of observed variation (Gelman 2005, Thorson & Minto in press).

I specifically use Gaussian random fields to account for spatially-correlated residual variation:

$$\log(w_i) = \alpha_0 + \alpha_s S(i) + A_{J(i)} + E_{J(i), T(i)} + d_{T(i)} + \sum_{k=1}^{n_k} \gamma_k \mathbf{X}_{i,k} + \log(L_i) [\beta_0 + \beta_s S(i)] + \varepsilon_i \quad (3)$$

$$\varepsilon_i \sim N(0, \sigma_w^2)$$

where  $\mathbf{X}$  is a matrix of  $n_k$  measured covariates,  $\gamma_k$  is the effect of the  $k$ -th covariate,  $d_{T(i)}$  represents temporal variation (constant across space in a given year) in the year  $T(i)$ , and the values of the random fields are  $A_{J(i)}$  representing spatial variation (constant for all years) at location  $J(i)$  associated with sample  $i$  (this notation is explained in more detail in the 'Model estimation' section below), and  $E_{J(i), T(i)}$  representing spatio-temporal variation (which varies for each year) at location  $J(i)$  for year  $T(i)$ . This spatial model for individual condition implies the assumption that the allometric scaling coefficients  $\beta_0$  and  $\beta_s$  are constant spatially, and attributes any spatial variation to condition rather than differences in the allometric relationship between weight and length.

Using Eqs. (2 & 3), Le Cren's (1951) relative condition factor can be calculated as:

$$\log(CF_i) = \log\left(\frac{w_i}{\bar{w}_i}\right) \quad (4)$$

where  $CF_i$  is condition factor for individual  $i$  relative to a standard weight  $\bar{w}$  calculated using the length of this individual (Blackwell et al. 2000, Pardoe et al. 2008). This equation identifies areas when individual weight is greater or less than the average weight for

a fish of a given size. Given the assumption that  $\bar{w}$  is calculated as the average weight at age over all years and locations (i.e.  $\bar{w}$  is calculated as the left-hand side of the nonspatial model in Eq. 2) and predicted weight ( $w_i$ ) is calculated using spatial, temporal, and spatio-temporal variability (i.e. using Eq. 3), the relative condition factor can be calculated as:

$$\begin{aligned} \log(CF_i) &= \log(w_i) - \log(\bar{w}_i) \\ &= A_{J(i)} + E_{J(i),T(i)} + d_{T(i)} + \sum_{k=1}^{n_k} \gamma_k \mathbf{X}_{i,k} \end{aligned} \quad (5)$$

### Model estimation

Temporal variation ( $d$ ) in relative condition factor is estimated as a random effect:

$$d_t \sim \text{Normal}(0, \sigma_d^2) \quad (6a)$$

where  $\sigma_d^2$  is the variance among years in relative condition factor that is explained by a year effect. Spatial variation ( $A$ ) and spatio-temporal variation ( $E_t$ ) are estimated as Gaussian random fields (GRFs):

$$\begin{aligned} A &\sim \text{GRF}(0, \Sigma_A) \\ E_t &\sim \text{GRF}(0, \Sigma_E) \text{ for all } t \end{aligned} \quad (6b)$$

where  $\Sigma_A$  and  $\Sigma_E$  are the spatial covariances for these random fields:

$$\Sigma_A(s, s') = \sigma_A^2 \cdot \text{Matérn}(|\mathbf{H}(s - s')|) \quad (7)$$

where  $s$  and  $s'$  are 2 spatial locations,  $\sigma_A^2$  is the marginal variance of random field  $A$ , and  $\text{Matérn}(|\mathbf{H}(s - s')|)$  is the Matérn distance function, which calculates the correlation between samples at locations  $s$  and  $s'$  given their distance  $|s - s'|$  after a linear transformation  $\mathbf{H}$  which accounts for geometric anisotropy (for further details see Thorson et al. 2015a). GRFs are a convenient statistical approach for implementing a 2-dimensional smoother for a response variable (in this case, individual condition) over spatial dimensions. Geometric anisotropy is included to account for the fact that locations might be less correlated when moving in one direction (i.e. inshore–offshore) than another (i.e. along the coast). GRFs are also preferable to other typical smoothers (e.g. a spline in a generalized additive model) because a GRF will revert to its expected value (e.g.  $A$  and  $B$  will revert to zero) in areas with little data.

For computational reasons, I use a predictive modeling framework where I approximate random fields  $A$  and  $E$  as being piecewise constant (Thorson et al. 2015a). This approximation requires specifying the desired number of knots ( $n_j$ ) where any location  $s(i)$  for sample  $i$  will have a value for random field  $A$

equal to the value of  $A$  at the nearest knot  $J(i)$  (and  $E$  is approximated similarly). Given  $n_j$ , the location of each knot is determined using a  $k$ -means algorithm applied to the location for all available sample locations. This implies that the density of knots is proportional to the sampling intensity of the survey design used to obtain the available data. In the following, I use  $n_j = 1000$ , while confirming that results are qualitatively similar when increasing the number.

Fixed-effect parameters are estimated by maximizing the marginal likelihood when integrating across the probability of random effects. Nonlinear optimization is accomplished in the R statistical platform (R Core Development Team 2013), and the marginal likelihood (i.e. integrating across  $A$  and  $E$ ) is calculated using the Laplace approximation as implemented by Template Model Builder (Kristensen et al. 2014). The probability of random fields is approximated using the stochastic partial differential equation approach (Lindgren et al. 2011), as explained in detail in Thorson et al. (2015b). The code is publicly available on my website ([https://github.com/James-Thorson/spatial\\_condition\\_factor](https://github.com/James-Thorson/spatial_condition_factor)) for those who are interested in replicating this analysis in other regions or for other species.

### Available data

I apply this spatial model for relative condition factor to data for 28 groundfish species off the US West Coast. These species have been used previously as a reference set when testing spatial and index-standardization tools and include all 'data-rich' assessed stocks in the region as well as additional populations which have sufficient data for estimating a delta-generalized linear mixed model (Thorson & Ward 2013, 2014). These species vary in phylogeny and life history, and include flatfishes, rockfishes, roundfishes, and a chondrythian (Pacific dogfish). All species are all either demersal or exhibit both demersal and pelagic behaviors (J. Cope pers. comm. 2014). To facilitate comparison among species, I have divided all 28 species among the following groups (see Table 1): shallow shelf rockfishes, deep shelf rockfishes, slope rockfishes, nearshore flatfishes, shelf flatfishes, slope flatfishes, elasmobranchs, and roundfishes (Cope et al. 2011, Anonymous 2013). Many of these 28 species have experienced large directional trends in abundance over time (e.g. Pacific hake, see Thorson & Ward 2014 for plots), and all have spatial variation in densities. I hypothesize that bottom temperature will have a strong impact on individual con-

dition for these fishes, given that ambient temperature has been documented previously to influence the weight at age for demersal fishes in natural settings (Brander 1995). However, temperature may also influence the spatial distribution for a population, potentially causing a confounding of temperature and density in explaining spatial variation in growth rates (Michalsen et al. 1998). I also hypothesize that nearshore and shelf species may have a different magnitude of temporal and spatial variation than slope species, because the demersal environment off the continental shelf is likely to vary less from year to year than habitats that are on the continental shelf or nearshore.

I analyze all observations of length and weight from 2003 to 2011 from the Northwest Fisheries Science Center shelf-slope bottom trawl survey (Bradburn et al. 2011), after excluding tows that were deemed unsatisfactory by the sampling team (e.g. did not achieve the area swept that was specified in the sampling design). Collections from this bottom trawl survey range from May 17 to October 8 of each year, with most samples conducted during May/June and August/September (Bradburn et al. 2011). This survey follows a stratified-random sampling protocol, and hence allows for inference at a population-wide spatial scale. The design covers an area of ~130000 km<sup>2</sup>, and excludes areas in southern California that are designated as cowcod conservation areas and hence prohibit bottom trawling gear. The stratified design has 6 sampling strata, generated as a 3 × 2 cross of 3 depth categories and 2 latitudinal categories. The design has approximately uniform sampling intensity (0.4 to 0.7 tows per 1000 ha) throughout its sampling domain, with the exception of deep areas south of Point Conception in southern California (with ~0.1 tows per 1000 ha).

### Covariates and model selection

I explore the ability of 3 covariates to explain spatial variation in individual condition. Each covariate corresponds to a hypothesized driver of spatial variation in condition, and is likely to explain at least some variation. I therefore use the Akaike's information criterion (AIC; Akaike 1974) and seek to evaluate the strength of evidence that different covariates have substantial explanatory power (Burnham & Anderson 2002). In particular I include the following:

(1) Population densities: Population density is estimated for every predictive knot by a geostatistical delta-generalized linear mixed model (delta-GLMM)

using a zero-inflated negative binomial distribution, applied to catch rates (in numbers) from the same data set. The delta-GLMM is similar to that described in Thorson et al. (2015a), but instead analyzes catch rates expressed in numbers rather than weight (i.e. estimated densities are expressed as numbers-per-unit-area). Population densities may be either negatively associated with condition whenever increased density leads to decreased prey densities and hence decreased feeding, or positively associated with condition whenever individuals select habitats that are conducive to increased condition.

(2) Bottom temperatures: Bottom temperature measurements are available for every sampling occasion and are appropriate as a measure of ambient temperature for these 28 species, which have either demersal or mixed demersal and pelagic habitat usage (see Table 1 for listing). Elevated water temperature is associated with increased metabolic rate, and greater metabolic rate can lead to either decreased condition if food is not available to offset increased metabolism, or increased condition if higher activity levels lead to greater food acquisition (Cada et al. 1987, Shelton et al. 2013). Even when individuals can feed to satiation, changes in ambient temperature will affect food conversion efficiency and thus will likely impact individual condition (Björnsson et al. 2001).

(3) Calendar date: The calendar date (e.g. February 15 = 46, etc.) is available for every sampling occasion, and is included to account for seasonal trends in condition. Seasonal variation in condition is well-documented for many populations (Le Cren 1951, Cada et al. 1987), although the timing and shape of variation will depend upon seasonal variation in food availability, water temperature, and spawning behaviors (among other processes).

Each of these covariates is standardized to have a mean of zero and a variance of 1 prior to inclusion in the model. This implies that  $\gamma\mathbf{X}$  (the covariate times its coefficient) has a standard deviation of  $\gamma$ , such that coefficients can be interpreted via comparison with the standard deviation of spatial, temporal and spatio-temporal variation, as well as that of residual variation.

## RESULTS

I show estimated spatio-temporal variation in relative condition factor for English sole as a first example (Fig. 1), estimated using the spatial model that includes AIC-selected covariates. This illustrates that nearshore habitats south of Point Conception in

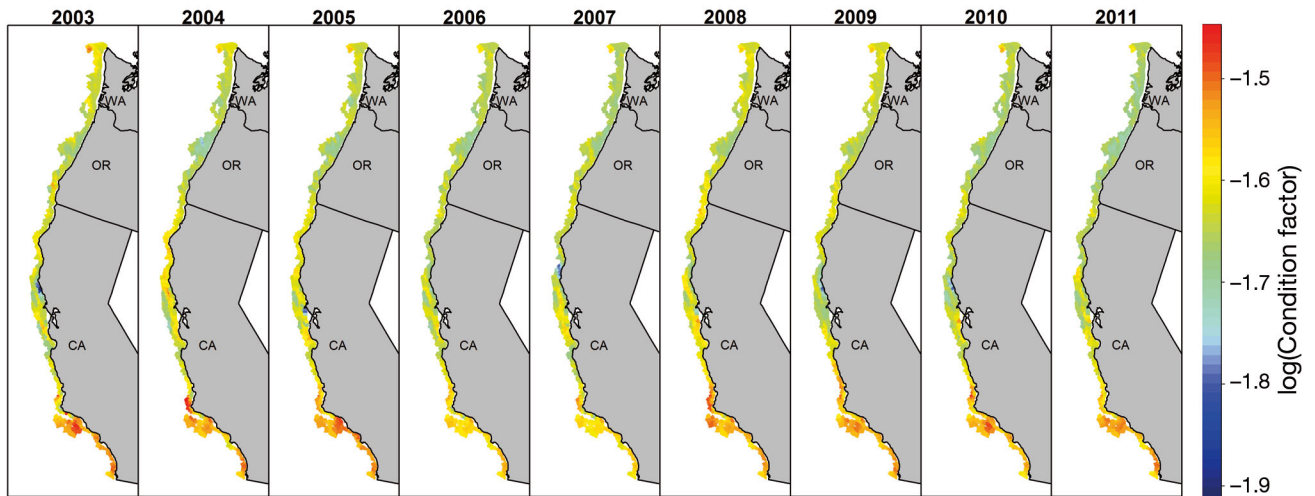


Fig. 1. Spatial variation in the logarithm of condition factor (CF) for the Akaike's information criterion (AIC)-selected model for English sole (a 0.1 difference in the logarithm corresponds to a ~10% difference in weight at length), when plotting CF estimates for areas within the population's central range (the minimum set of cells that constitutes 99% of total abundance on average across years)

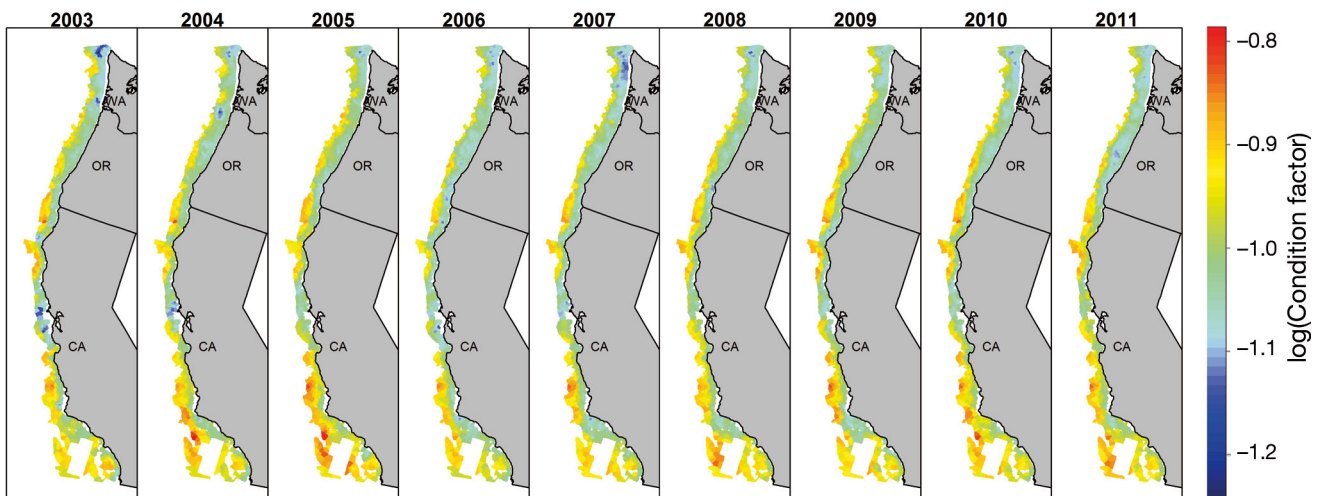


Fig. 2. Spatial variation in the logarithm of condition factor for the Akaike's information criterion (AIC)-selected model for Dover sole. See Fig. 1 caption for description

southern California have condition ~20% greater than average condition off Oregon and southern Washington, and that southern California condition is particularly elevated in 2003–2005. An illustration of relative condition factor for Dover sole (Fig. 2) provides a contrasting example, where nearshore habitats coastwide have condition 10 to 25% lower than offshore habitats. In this case, increased condition offshore could be explained either by plumper individuals moving offshore, or by offshore habitats being conducive to increased energy storage and hence increased condition.

Model selection shows that several species have a substantial improvement in model fit from including

bottom temperature, date, and population densities. For example, sablefish has a very substantial improvement in model fit from including date and, to a lesser extent, bottom temperature ( $\Delta\text{AIC} = 320.7$  relative to a model with neither variable; Table 1). Inspection of maps representing spatial variation in condition factor for sablefish (not shown) indicate almost no visible difference between models with and without covariates. The improvement in fit therefore arises from a decrease in magnitude of the residual spatial and spatio-temporal variance (spatial:  $\sigma_A$  decreases from 0.030 to 0.019; spatio-temporal:  $\sigma_E$  decreases from 0.042 to 0.037). This small decrease in magnitude for residual spatial and spatio-temporal

Table 1. Species used in this analysis and model selection results using the Akaike's information criterion applied to the maximum marginal likelihood for each model. Habitat: demersal (D) or mixed demersal and pelagic (M). Group: shallow-shelf rockfish (SS-R), deep-shelf rockfish (DS-R), slope rockfish (SL-R), nearshore flatfish (NS-F), shelf flatfish (SH-F), slope flatfish (SL-F), elasmobranch (Elas), or roundfish (RF). Models are abbreviated using a 3-digit code representing the presence (1) or absence (0) of temperature/density/date covariates, e.g. model 011 does not include temperature but does include density and date. Parentheses: no. of species with selected model

Common	Species name		Group	Habitat	Akaike's information criterion							
	Scientific				000(7)	001(1)	010(2)	011(5)	100(4)	101(4)	110(3)	111(2)
<b>Flatfishes</b>												
Sanddab	<i>Citharichthys sordidus</i>		NS-F	D	3.2	1.2	5.1	3.2	0.0	0.1	2.0	2.1
Petrale	<i>Eopsetta jordani</i>		SH-F	D	404.8	21.2	385.1	0.0	378.5	22.1	343.2	0.0
Dover sole	<i>Microstomus pacificus</i>		SL-F	D	278.3	106.2	257.8	86.3	211.3	23.1	187.5	0.0
Arrowtooth	<i>Atheresthes stomias</i>		SL-F	D	356.4	9.1	356.4	0.0	350.1	10.0	349.5	1.0
English sole	<i>Parophrys vetulus</i>		SL-F	D	248.4	0.9	250.3	2.9	241.9	0.0	243.6	1.8
<b>Rockfishes</b>												
Greenspotted	<i>Sebastes chlorostictus</i>		SS-R	D	0.0	2.0	1.8	8.3	1.9	3.9	3.4	5.4
Yellowtail	<i>S. flavidus</i>		SS-R	M	16.6	3.7	18.4	5.6	13.9	0.0	15.5	1.4
Chilipepper	<i>S. goodei</i>		SS-R	M	8.5	11.3	7.0	7.8	4.5	5.6	0.0	1.5
Canary	<i>S. pinniger</i>		SS-R	M	10.9	10.6	12.8	12.5	0.0	1.5	2.0	3.4
Yelloweye	<i>S. ruberrimus</i>		SS-R	D	0.0	0.9	3.5	5.8	1.1	1.8	5.1	3.7
Halfbanded	<i>S. semicinctus</i>		SS-R	D	6.3	1.7	5.9	0.0	7.2	2.9	6.5	0.9
Darkblotched	<i>S. crameri</i>		DS-R	D	36.8	20.3	21.0	0.0	38.4	19.0	22.9	0.9
Greenstriped	<i>S. elongatus</i>		DS-R	D	1.2	2.0	0.0	1.4	2.6	3.8	2.0	3.4
Widow	<i>S. entomelas</i>		DS-R	D	9.5	2.8	10.7	3.8	9.2	0.0	9.9	6.1
Rosethorn	<i>S. helvomaculatus</i>		DS-R	D	12.4	12.9	14.2	8.7	0.0	2.3	0.2	1.3
Shortbelly	<i>S. jordani</i>		DS-R	M	0.0	1.8	2.0	4.7	1.7	3.5	3.7	5.5
Cowcod	<i>S. levis</i>		DS-R	D	2.1	0.6	1.9	0.0	4.0	2.6	3.2	2.0
Bocaccio	<i>S. paucispinis</i>		DS-R	M	0.2	1.3	0.0	1.2	2.0	3.0	2.0	3.1
Sharpchin	<i>S. zacentrus</i>		DS-R	D	0.0	1.7	0.8	2.2	1.6	3.2	2.7	3.9
Shortspine thornyhead	<i>Sebastolobus alascanus</i>		SL-R	D	76.5	78.4	18.1	19.1	45.3	47.3	0.0	1.6
Rougheye	<i>S. aleutianus</i>		SL-R	D	4.1	6.1	5.3	7.2	0.0	1.8	1.3	3.2
Pacific Ocean perch	<i>S. alutus</i>		SL-R	M	4.3	6.3	1.7	3.6	3.1	6.7	0.0	2.0
Longspine thornyhead	<i>Sebastolobus altivelis</i>		SL-R	D	0.0	1.1	1.9	3.1	1.8	3.0	3.8	5.0
Aurora	<i>S. aurora</i>		SL-R	D	0.0	1.4	1.4	2.7	2.0	3.3	3.4	4.7
Redbanded	<i>S. babcocki</i>		SL-R	D	0.0	1.3	1.8	3.2	0.8	2.6	2.8	4.5
<b>Other</b>												
Sablefish	<i>Anoplopoma fimbria</i>		RF	M	320.7	91.2	315.7	83.4	246.9	0.0	248.0	0.2
Hake	<i>Merluccius productus</i>		RF	M	93.1	8.3	94.1	10.2	82.7	0.8	75.6	0.0
Dogfish	<i>Squalus acanthias</i>		Elas	M	21.2	0.0	23.2	1.0	21.0	1.7	22.8	2.8

variation indicates that, even given selected covariates, there is considerable spatial variation that is not captured by our set of potential covariates. Other species that show a substantial improvement from including covariates (in terms of  $\Delta AIC$ ) include most flatfishes (petrale, dover, arrowtooth, and English sole), shortspine thornyhead, and Pacific hake. These species share in common the fact that they are observed in a large proportion of sampling occasions, so it is not surprising that including covariates leads to a greater improvement in model fit than species with relatively little information.

Model selection indicates considerable variation regarding which covariates provide a parsimonious fit to available length-weight data for each of the 28 groundfish species (Table 1). Seven species have a

model without covariates selected by AIC, and all 7 are rockfishes. Date is selected for 12/28 species, temperature is selected for 13/28, and density for 12/28, and no single combination of covariates appears to have the greatest fit (with the greatest number of species selected for the model without covariates). The sign of estimated covariates varies among species, with date being positive in 10/12 cases, temperature positive in 7/13, and density positive in 6/12 cases (Table 2). I therefore conclude that no one covariate has a consistent effect for these species, either in terms of being selected for a large number of species, or in terms of having a similar (positive or negative) effect across species.

Further examination shows that the nonspatial model (which accounts for sex-specific differences in

Table 2. Summaries of model fit for the AIC-selected model for each individual species (see Table 1 for best fit for each species), including SD of residual variation for spatial and nonspatial models of relative condition factor, the relative magnitude of spatial and spatio-temporal variation, and the magnitude of coefficients for each covariate (the absolute value of these coefficients is approximately comparable to the SD of spatial and spatio-temporal variation). See Table 1 for definitions of groups and habitats.  $T$  = temperature

Species	Group	Habitat	Variance explained		Spatial variance components			Covariates		
			Nonspatial residual SD	Proportion of variance explained	Spatial ( $\sigma_A$ )	Spatio-temporal ( $\sigma_E$ )	Temporal ( $\sigma_D$ )	Bottom $T$	Density	Date
<b>Flatfishes</b>										
Sanddab	NS-F	D	0.177	0.195	0.079	0.198	0.023	0.013	–	–
Petrale	SH-F	D	0.109	0.239	0.026	0.053	0.012	–	–0.034	0.045
Arrowtooth	SL-F	D	0.127	0.290	0.052	0.046	0.010	–0.032	–0.015	0.029
Dover sole	SL-F	D	0.107	0.240	0.031	0.083	0.011	–	0.023	0.047
English sole	SL-F	D	0.129	0.305	0.182	0.145	0.009	0.008	–	0.044
<b>Rockfishes</b>										
Greenspotted	SS-R	D	0.143	0.194	0.160	0.233	0.007	–	–	–
Yellowtail	SS-R	M	0.075	0.212	0.000	0.141	0.015	–0.017	–	0.017
Chilipepper	SS-R	M	0.151	0.205	0.000	0.124	0.008	–0.019	0.020	–
Ca-ry	SS-R	M	0.095	0.200	0.105	0.157	0.013	–0.035	–	–
Yelloweye	SS-R	D	0.105	0.092	0.063	0.000	0.004	–	–	–
Halfbanded	SS-R	D	0.250	0.233	0.045	0.182	0.017	–	0.027	–0.032
Darkblotched	DS-R	D	0.126	0.236	0.000	0.081	0.009	–	0.029	0.018
Greenstriped	DS-R	D	0.150	0.214	0.055	0.103	0.017	–	0.012	–
Widow	DS-R	D	0.079	0.249	0.099	0.129	0.000	0.015	–	0.022
Rosethorn	DS-R	D	0.148	0.231	0.392	0.273	0.018	0.040	–	–
Shortbelly	DS-R	M	0.244	0.332	0.122	0.411	0.013	–	–	–
Cowcod	DS-R	D	0.183	0.402	0.252	0.483	0.000	–	–0.051	–0.035
Bocaccio	DS-R	M	0.114	0.199	0.000	0.112	0.000	–	–0.016	–
Sharpchin	DS-R	D	0.133	0.297	0.093	0.088	0.019	–	–	–
Shortspine thornyhead	SL-R	D	0.142	0.185	0.046	0.061	0.008	–0.012	–0.039	–
Rougeye	SL-R	D	0.108	0.197	0.040	0.030	0.021	0.043	–	–
Pacific Ocean perch	SL-R	M	0.109	0.315	0.030	0.126	0.000	0.029	0.021	–
Longspine thornyhead	SL-R	D	0.198	0.122	0.038	0.077	0.017	–	–	–
Aurora	SL-R	D	0.124	0.196	0.037	0.053	0.008	–	–	–
Redbanded	SL-R	D	0.145	0.216	0.001	0.079	0.012	–	–	–
<b>Other</b>										
Sablefish	RF	M	0.109	0.150	0.019	0.037	0.007	–0.018	–	0.028
Hake	RF	M	0.156	0.238	0.000	0.087	0.016	0.014	–0.008	0.034
Dogfish	Elas	M	0.120	0.205	0.023	0.073	0.023	–	–	0.015

condition and allometry) has average coefficient of variation of 13.8% (range: 7.5 to 25.0%) among the 28 groundfish species (Table 2 and Fig. 3). This represents individual-level variability, and hence includes the combined impact of measurement errors and rounding for weights measured at sea, individual variation in growth trajectory and energy storage, gonadal development, etc. The spatio-temporal model explains on average 22.0% (6.6 to 40.1%) of this variance via smooth spatial and temporal variation in relative condition factor. Flatfishes generally have a greater proportion of the variance in relative condition factor explained by spatial and temporal variation than rockfishes. This may indicate that flatfishes have greater plasticity in relative condition than do the rockfishes in this study, or it may reflect the fact that

the flatfishes in this study generally have greater information to inform spatial modelling in general (as also indicated by the large  $\Delta$ AIC values for flatfishes in Table 1 relative to those for rockfishes). Species explaining a large proportion of variance generally have larger marginal standard deviation for spatial variation (e.g. cowcod:  $\sigma_A = 0.25$ ,  $\sigma_E = 0.48$ ), and spatial variation is on average smaller in magnitude (average  $\sigma_A$ : 0.07; Table 2 and Fig. 4) than spatio-temporal variation (average  $\sigma_E$ : 0.13). Temporal variation is generally the smallest component of variation in all species (average  $\sigma_D$ : 0.01), and inspection of annual residuals indicate no trends across species or species-groups. Given that covariates are standardized to have a variance of 1, the coefficient of covariates (i.e.  $\gamma$ ) can be compared directly with the standard deviation of spa-



tial and spatio-temporal variation. This reveals that measured covariates generally have a small magnitude relative to residual variation.

## DISCUSSION

In this study, I have shown that there is considerable spatial and temporal variation in relative condition factor for 28 marine groundfishes in the California Current. On average for these species, spatial, temporal, and spatio-temporal variation account for ~20% of total variation among individuals observed in the survey. In general, spatio-temporal variation has a larger magnitude than spatial variation for these species, and the magnitude of temporal variation generally approaches zero. I therefore conclude that dynamic habitat conditions (i.e. local environmental conditions that change over time) are associated with a substantial fraction of individual-level variation in relative condition.

Spatial variation in individual condition as identified in this study could have important implications for population dynamics and stock assessment models for marine fishes. A 20% change in weight at length between different segments of a population (e.g. as observed here for English sole) would mean that a reported quantity of fishery catch (commonly expressed in units weight) consists of 20% more/less individuals in one population segment than another. Variation in growth (measured as length at age) has received increased attention in stock assessment for marine fishes and invertebrates (Punt et al. 2013, Taylor & Methot 2013, Thorson & Minte-Vera in press), but variation in condition is not generally included in stock assessment models (Methot & Wetzel 2013). Similarly, a 20% increase in spawning biomass for a given number of individuals could contribute to significant increases in reproductive output for an age-structured population (Fitzhugh et al. 2012, Shelton et al. 2012). This increase may be greater than proportional (i.e. >20% increase in reproductive output given a 20% increase in condition) if increased individual condition leads to a decrease in the proportion of individuals that skip spawning (Rideout et al. 2005). The potential implications of spatial variation in individual condition on stock assessment models can be explored using decision analysis (e.g. management strategy evaluation; Sainsbury et al. 2000). However, decision analysis is best conducted after plausible states of nature (e.g. spatial variation in condition) have been estimated by studies such as this (Punt 2008).

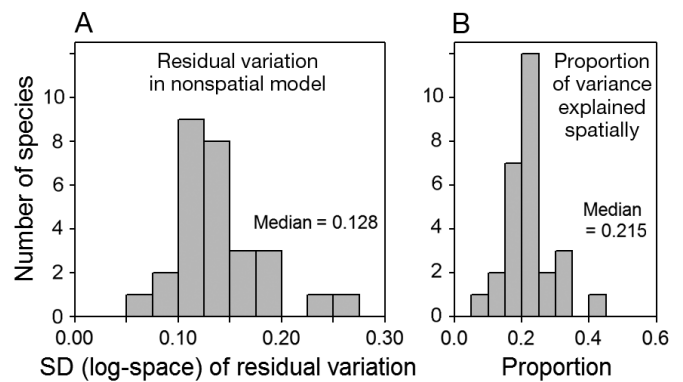


Fig. 3. Model fit for each of 28 groundfishes. (A) Residual variation in nonspatial model (see Table 2: 4th column); (B) proportion of variance that is explained using a model with spatial, temporal, and spatio-temporal variation in condition factor (Table 2: 5th column). Median values are listed in each plot

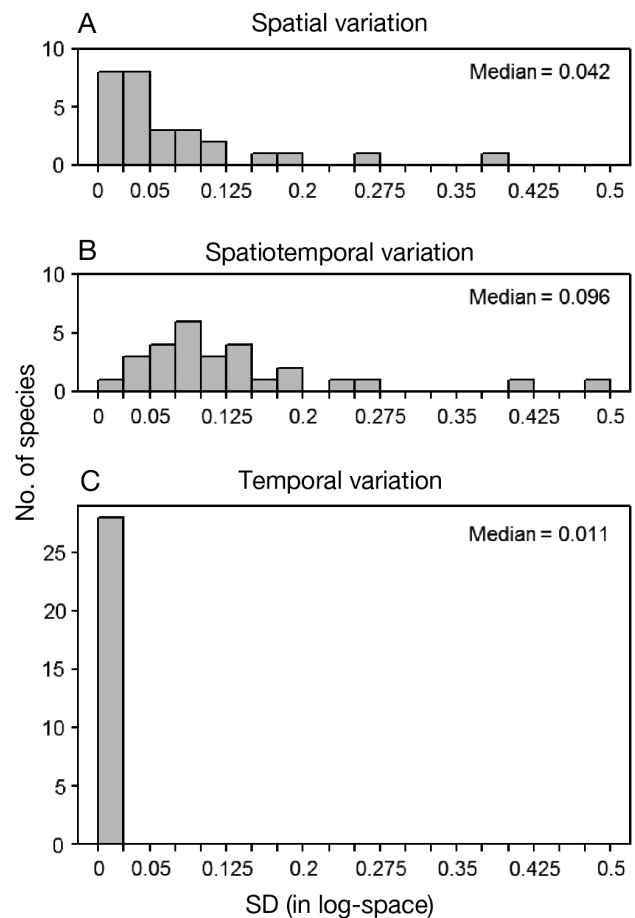


Fig. 4. Magnitude (A) of spatial (see Table 2: 6th column), (B) spatio-temporal (Table 2: 7th column) and (C) temporal variation (Table 2: 8th column) in the spatial model for condition factor for each of 28 groundfishes. Median values are listed in each plot

While models including calendar date, population density, and bottom temperature are parsimonious for many of these groundfishes, these covariates have a small magnitude relative to the magnitude of spatial and spatio-temporal variation, and no covariate has a consistent effect across these 28 fishes (either in terms of being parsimonious for the majority of species, or in terms of having a consistent positive or negative sign of the estimated coefficient). I therefore conclude that much of the spatial and spatio-temporal variation in condition remains unexplained by bottom temperature, date, and population densities. I hypothesize that estimated spatial and temporal variation could be caused by multispecies interactions (e.g. competition with other species with similar feeding habits) that must be modeled in a species-specific manner, or correlated with other measures of oceanographic conditions (e.g. surface temperature as an index of upwelling strength; Barth et al. 2007). However, testing the impact of competitors will require additional life history research, given that a list of likely competitors is not available for each species in this data set. I therefore suggest that future research use existing trophic and diet information to identify which species are competitors, and explore density of competitors as a potential covariate.

Individual condition (the relationship between weight and length) is one component of the larger study of individual growth. Growth arises from a complex process that includes reproductive strategy and plastic responses to an individual's environment (tactics; Rochet 2000). In particular, growth involves optimizing allocation of energy between activity, survival, reproductive output, and investment in future reproduction (Jørgensen et al. 2006, Beakes et al. 2010, Charnov et al. 2013), as well as the behavioral trade-off between energy acquisition and feeding success (Shelton et al. 2013). Growth (the relationship between weight, length, and age) could be jointly modeled in a spatio-temporal framework, and a joint analysis would help elucidate whether spatial variation in condition (the weight-at-length relationship) is associated with similar spatial variation in growth (i.e. the length-at-age relationship).

In this study, I therefore seek to initiate a larger investigation into spatial and spatio-temporal variation in growth of marine fishes. Towards this end, I have made the spatial modelling code available publicly (see 'Methods' section), which can be used to replicate this analysis in other oceanographic regions or for additional species. Spatial variation in condition has implications for state-dependent life history theory, where increased condition may contribute to

variation observed in the relationship between spawning potential and subsequent recruitment. This relationship is highly variable (Thorson et al. 2014), although some of the variation may be explainable via age-structured processes (Shelton et al. 2012) or by including additional details regarding parental condition (Lambert & Dutil 1997b, Marshall & Frank 1999, Morgan et al. 2011). In particular, variation in individual condition may contribute to observed variation in spawning frequency for fishes that either skip spawning in some years (Rideout et al. 2005, Jørgensen et al. 2006), or spawn multiple times in a single year (Fitzhugh et al. 2012). Therefore, spatial analysis of variation in growth (length at age) and condition (weight at length) may prove important in quantifying the impact of fishing on fish populations.

However, I agree with previous authors in concluding that the interpretation of individual condition is complicated and fraught (Le Cren 1951, Copeland et al. 2008). In particular, ambient temperature, density, and calendar date can each be argued *a priori* to have a potentially positive or negative impact on individual condition, depending upon the environmental conditions and behavioral responses of the population. Conversely, an observed pattern in individual condition can be attributed to many possible mechanisms. I therefore argue that observational analysis of spatial variation in condition must be complemented by detailed analysis at other scales, for example using small-scale observation of individual behaviors in wild or controlled conditions, before putative mechanisms can be evaluated definitively (Thorson et al. 2015c).

Finally, this study illustrates the increasing feasibility of spatial analysis of fish demographics due to new computational and statistical tools (Lindgren et al. 2011, Kristensen et al. 2014). Spatial models can be used to infer habitat preferences (Shelton et al. 2014), density dependence (Thorson et al. 2015b), and species interactions (Ovaskainen et al. 2010). Spatial models can also be estimated with increasing demographic detail, where individual-level processes (growth, survival, and maturity) can be estimated as varying over large spatial scales. I predict that spatial models will continue to grow in importance for descriptive analyses such as this, e.g. because proper detection of density dependence requires accounting for spatial variation in population densities (Ray & Hastings 1996, Michalsen et al. 1998, Thorson et al. 2015b). Improvements in spatial analysis methods will likely offer new insights into long-standing questions in fisheries science, such as variation in individual condition (Le Cren 1951).

**Acknowledgements.** I thank the FRAM survey team for their ongoing efforts in providing an amazing, synoptic survey of fish density and condition for the US West Coast. I also thank in particular J. Cope, who contributed substantially to the categorization and interpretation of results for individual species, and who is always extremely generous with his time. T. Hay, B. Horness, and A. Hicks helped me to access and interpret the survey data; J. Wallace computed the sampling intensity of the bottom trawl survey design analysed here; O. Shelton provided ongoing discussions of spatial modeling and fish growth; and N. Tolomieri and 2 anonymous reviewers provided comments on an earlier draft. Finally, I thank H. Skaug and K. Kristensen for making possible the new spatial approach to the analysis of long-standing questions in fisheries science.

#### LITERATURE CITED

- Akaike H (1974) New look at statistical-model identification. *IEEE Trans Automat Contr* 19:716–723
- Anonymous (2013) April 2013 Briefing Book. Pacific Fisheries Management Council, Portland, OR
- Barth JA, Menge BA, Lubchenco J, Chan F and others (2007) Delayed upwelling alters nearshore coastal ocean ecosystems in the northern California current. *Proc Natl Acad Sci USA* 104:3719–3724
- Beakes MP, Satterthwaite WH, Collins EM, Swank DR and others (2010) Smolt transformation in two California steelhead populations: effects of temporal variability in growth. *Trans Am Fish Soc* 139:1263–1275
- Björnsson B, Steinarsson A, Oddgeirsson M (2001) Optimal temperature for growth and feed conversion of immature cod (*Gadus morhua* L.). *ICES J Mar Sci* 58:29–38
- Blackwell BG, Brown ML, Willis DW (2000) Relative weight (Wr) status and current use in fisheries assessment and management. *Rev Fish Sci* 8:1–44
- Boxrucker J (1987) Largemouth bass influence on size structure of crappie populations in small Oklahoma impoundments. *N Am J Fish Manag* 7:273–278
- Bradburn MJ, Keller AA, Horness BH (2011) The 2003 to 2008 US West Coast bottom trawl surveys of groundfish resources off Washington, Oregon, and California: estimates of distribution, abundance, length, and age composition. US Dep Commer, NOAA-NMFS, Northwest Fisheries Science Center, Seattle, WA
- Brander KM (1995) The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). *ICES J Mar Sci* 52:1–10
- Burnham KP, Anderson D (2002) Model selection and multi-model inference, 2nd edn. Springer, New York, NY
- Burton MPM (1994) A critical period for nutritional control of early gametogenesis in female winter flounder, *Pleuronectes americanus* (Pisces: Teleostei). *J Zool (Lond)* 233:405–415
- Cada GF, Loar JM, Sale MJ (1987) Evidence of food limitation of rainbow and brown trout in southern Appalachian soft-water streams. *Trans Am Fish Soc* 116:692–702
- Charnov EL, Gislason H, Pope JG (2013) Evolutionary assembly rules for fish life histories. *Fish Fish* 14:213–224
- Cope JM, DeVore J, Dick EJ, Ames K and others (2011) An approach to defining stock complexes for US West Coast groundfishes using vulnerabilities and ecological distributions. *N Am J Fish Manag* 31:589–604
- Copeland T, Murphy BR, Ney JJ (2008) Interpretation of relative weight in three populations of wild bluegills: a cautionary tale. *N Am J Fish Manag* 28:368–377
- Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv Mar Biol* 26:249–293
- Fitzhugh GR, Shertzer KW, Kellison GT, Wyanski DM (2012) Review of size- and age-dependence in batch spawning: implications for stock assessment of fish species exhibiting indeterminate fecundity. *Fish Bull* 110:413–425
- Froese R, Thorson JT, Reyes RB (2014) A Bayesian approach for estimating length–weight relationships in fishes. *J Appl Ichthyology* 30:78–85
- Gelman A (2005) Analysis of variance—why it is more important than ever. *Ann Stat* 33:1–53
- Glazier DS (2000) Is fatter fitter? Body storage and reproduction in ten populations of the freshwater amphipod *Gammarus minus*. *Oecologia* 122:335–345
- Haltuch MA, Punt AE (2011) The promises and pitfalls of including decadal-scale climate forcing of recruitment in groundfish stock assessment. *Can J Fish Aquat Sci* 68:912–926
- Hjort J (1926) Fluctuations in the year classes of important food fishes. *ICES J Mar Sci* 1:5–38
- Jørgensen C, Ernande B, Fiksen Ø, Dieckmann U (2006) The logic of skipped spawning in fish. *Can J Fish Aquat Sci* 63:200–211
- Junquera S, Roman E, Paz X, Ramilo G (1999) Changes in Greenland halibut growth, condition and fecundity in the Northwest Atlantic (Flemish Pass, Flemish Cap and southern Grand Bank). *J Northwest Atl Fish Sci* 25:17–28
- Kristensen K, Thygesen UH, Andersen KH, Beyer JE (2014) Estimating spatio-temporal dynamics of size-structured populations. *Can J Fish Aquat Sci* 71:326–336
- Lambert Y, Dutil JD (1997a) Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? *Can J Fish Aquat Sci* 54:104–112
- Lambert Y, Dutil JD (1997b) Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. *Can J Fish Aquat Sci* 54:2388–2400
- Larsen DP, Kincaid TM, Jacobs SE, Urquhart NS (2001) Designs for evaluating local and regional scale trends. *Bioscience* 51:1069–1078
- Le Cren ED (1951) The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *J Anim Ecol* 20:201–219
- Lindgren F, Rue H, Lindström J (2011) An explicit link between Gaussian fields and Gaussian Markov random fields: the stochastic partial differential equation approach. *J R Stat Soc Series B Stat Methodol* 73:423–498
- Marshall CT, Frank KT (1999) The effect of interannual variation in growth and condition on haddock recruitment. *Can J Fish Aquat Sci* 56:347–355
- Methot RD, Wetzel CR (2013) Stock synthesis: a biological and statistical framework for fish stock assessment and fishery management. *Fish Res* 142:86–99
- Michalsen K, Ottersen G, Nakken O (1998) Growth of North-east Arctic cod (*Gadus morhua* L.) in relation to ambient temperature. *ICES J Mar Sci* 55:863–877
- Morgan MJ, Rideout RM, Colbourne EB (2010) Impact of environmental temperature on Atlantic cod *Gadus morhua* energy allocation to growth, condition and reproduction. *Mar Ecol Prog Ser* 404:185–195
- Morgan MJ, Perez-Rodriguez A, Saborido-Rey F, Marshall CT (2011) Does increased information about reproduc-

- tive potential result in better prediction of recruitment? Can J Fish Aquat Sci 68:1361–1368
- Moutopoulos DK, Stergiou KI (2002) Length–weight and length–length relationships of fish species from the Aegean Sea (Greece). J Appl Ichthyology 18:200–203
- Murphy BR, Brown ML, Springer TA (1990) Evaluation of the relative weight (Wr) index, with new applications to walleye. N Am J Fish Manag 10:85–97
- Nash RD, Valencia AH, Geffen AJ (2006) The origin of Fulton's condition factor—setting the record straight. Fisheries (Bethesda, Md) 31:236–238
- Ovaskainen O, Hottola J, Siitonen J (2010) Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. Ecology 91: 2514–2521
- Owen M, Cook WA (1977) Variations in body weight, wing length and condition of mallard *Anas platyrhynchos platyrhynchos* and their relationship to environmental changes. J Zool 183:377–395
- Pardoe H, Marteinsdóttir G (2009) Contrasting trends in two condition indices: bathymetric and spatial variation in autumn condition of Icelandic cod *Gadus morhua*. J Fish Biol 75:282–289
- Pardoe H, Thórdarson G, Marteinsdóttir G (2008) Spatial and temporal trends in condition of Atlantic cod *Gadus morhua* on the Icelandic shelf. Mar Ecol Prog Ser 362: 261–277
- Pope KL, Willis DW (1996) Seasonal influences on freshwater fisheries sampling data. Rev Fish Sci 4:57–73
- Punt AE (2008) Refocusing stock assessment in support of policy evaluation. In: Tsukamoto K, Kawamura T, Takeuchi T, Beard TD, Kaiser MJ (eds) Fisheries for global welfare and environment. TerraPub, Tokyo, p 139–152
- Punt AE, Huang T, Maunder MN (2013) Review of integrated size-structured models for stock assessment of hard-to-age crustacean and mollusc species. ICES J Mar Sci 70:16–33
- R Core Development Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ray C, Hastings A (1996) Density dependence: Are we searching at the wrong spatial scale? J Anim Ecol 65: 556–566
- Rideout RM, Rose GA, Burton MP (2005) Skipped spawning in female iteroparous fishes. Fish Fish 6:50–72
- Rochet MJ (2000) A comparative approach to life-history strategies and tactics among four orders of teleost fish. ICES J Mar Sci 57:228–239
- Sainsbury KJ, Punt AE, Smith AD (2000) Design of operational management strategies for achieving fishery ecosystem objectives. ICES J Mar Sci 57:731–741
- Shelton AO, Munch SB, Keith D, Mangel M (2012) Maternal age, fecundity, egg quality, and recruitment: linking stock structure to recruitment using an age-structured Ricker model. Can J Fish Aquat Sci 69:1631–1641
- Shelton AO, Satterthwaite WH, Beakes MP, Munch SB, Sogard SM, Mangel M (2013) Separating intrinsic and environmental contributions to growth and their population consequences. Am Nat 181:799–814
- Shelton AO, Thorson JT, Ward EJ, Feist BE (2014) Spatial semiparametric models improve estimates of species abundance and distribution. Can J Fish Aquat Sci 71: 1655–1666
- Shuter BJ, Ihssen PE, Wales DL, Snucins EJ (1989) The effects of temperature, pH and water hardness on winter starvation of young-of-the-year smallmouth bass, *Micropterus dolomieu* Lacepede. J Fish Biol 35:765–780
- Taylor IG, Methot RD (2013) Hiding or dead? A computationally efficient model of selective fisheries mortality. Fish Res 142:75–85
- Thorpe JE, Mangel M, Metcalfe NB, Huntingford FA (1998) Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evol Ecol 12:581–599
- Thorson JT, Minte-Vera C (in press) Relative magnitude of cohort, age, and year effects on size at age of exploited marine fishes. Fish Res
- Thorson JT, Minto C (in press) Mixed effects: a unifying framework for modelling in aquatic ecology. ICES J Mar Sci, doi:10.1093/icesjms/fsu213
- Thorson JT, Ward E (2013) Accounting for space-time interactions in index standardization models. Fish Res 147: 426–433
- Thorson JT, Ward EJ (2014) Accounting for vessel effects when standardizing catch rates from cooperative surveys. Fish Res 155:168–176
- Thorson JT, Jensen OP, Zipkin EF (2014) How variable is recruitment for exploited marine fishes? A hierarchical model for testing life history theory. Can J Fish Aquat Sci 71:973–983
- Thorson JT, Shelton AO, Ward EJ, Skaug H (2015a) Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES J Mar Sci, doi:10.1093/icesjms/fsu243
- Thorson JT, Skaug H, Kristensen K, Shelton AO, Ward EJ, Harms J, Benante J (2015b) The importance of spatial models for estimating the strength of density dependence. Ecology, doi:10.1890/14-0739.1
- Thorson JT, Cope J, Kleisner K, Shelton A, Samhuri J, Ward E (2015c) Giants' shoulders 15 years later: lessons, challenges, and guidelines in fisheries meta-analysis. Fish Fish 16:342–361
- Vainikka A, Mollet F, Casini M, Gaardmark A (2009) Spatial variation in growth, condition and maturation reaction norms of the Baltic herring *Clupea harengus membras*. Mar Ecol Prog Ser 383:285–294

Editorial responsibility: Romuald Lipcius,  
Gloucester Point, Virginia, USA

Submitted: October 7, 2014; Accepted: January 12, 2015  
Proofs received from author(s): March 31, 2015