Application of macroecological theory to predict effects of climate change on global fisheries potential

William W. L. Cheung*, Chris Close, Vicky Lam, Reg Watson, Daniel Pauly

Sea Around Us Project, Fisheries Centre, The University of British Columbia, 2202 Main Mall, Vancouver,
British Columbia V6T 1Z4, Canada

ABSTRACT: Global changes are shaping the ecology and biogeography of marine species and their fisheries. Macroecology theory, which deals with large scale relationships between ecology and biogeography, can be used to develop models to predict the effects of global changes on marine species that in turn affect their fisheries. First, based on theories linking trophic energetics and allometric scaling of metabolism, we developed a theoretical model that relates maximum catch potential from a species to its trophic level, geographic range, and mean primary production within the species' exploited range. Then, using this theoretical model and data from 1000 species of exploited marine fishes and invertebrates, we analyzed the empirical relationship between species' approximated maximum catch potential, their ecology, and biogeography variables. Additional variables are included in the empirical model to correct for biases resulting from the uncertainty inherent in the original catch data. The empirical model has high explanatory power and agrees with theoretical expectations. In the future, this empirical model can be combined with a bioclimate envelope model to predict the socio-economic impacts of climate change on global marine fisheries. Such potential application is illustrated here with an example pertaining to the small yellow croaker *Larimichthys polyactis* (Sciaenidae) from the East China Sea.

KEY WORDS: Macroecology · Climate change · Fisheries · Catch

INTRODUCTION

Theory and empirical evidence indicate that global climate change is a factor increasingly affecting the ecosystems of terrestrial and marine biomes (e.g. Cramer et al. 2001, Hughes et al. 2003, Parmesan & Yohe 2003). However, far less research is conducted on ocean impacts (e.g. through fisheries) than on terrestrial systems. Environmental conditions in the ocean — such as acidity, ocean currents, and productivity — are likely to change (Hobday et al. 2006), and global mean air temperature is predicted to increase at a rate of around 0.2°C per decade during this century (IPCC 2007). Climate warming may lead to a contraction of the highly productive marginal sea ice biome and an increase in global primary production in the ocean of 0.7 to 8.1%, with large regional variations (Sarmiento et al. 2004). These would have significant impacts on marine ecosystems and on human society, which depends on fish for food and income (Walther et al. 2002).

Macroecology, trophic energetics, and metabolic scaling provide theories that are particularly applicable to predict the effects of global changes on marine fisheries potential. Macroecology studies the relationship between organisms and their environment, including patterns of abundance, distribution, and diversity of species at large spatial and temporal scales (Brown 1995, Gaston & Blackburn 2000, Blackburn & Gaston 2003). Specifically, empirical and comparative studies in macroecology of terrestrial and aquatic organisms reveal consistent relationships between abundance and other ecological, physiological, and

environmental attributes such as distribution and body size (Gaston et al. 1997). For example, abundance between species is positively related to distribution size in animal assemblages (Hanski 1982, Brown 1984, Gaston & Blackburn 2000). Moreover, abundance is determined by metabolic scaling and trophic energetics (flow and storage of energy in the ecosystem) of the organisms (Jennings & Mackinson 2003). For example, the metabolic rate of an organism is related to body mass by an allometric relationship (Kleiber 1932). Body mass is also related to an animal's life history and trophic ecology (Charnov 1993, Gaston & Blackburn 2000, Woodward et al. 2005, Jennings et al. 2007). In addition, the energy requirement of a population (partly determined by the average metabolic rate of the individuals) and its trophic ecology are related to population abundance (Damuth 1981, Gaston & Blackburn 2000, Blackburn & Gaston 2003, Jennings & Mackinson 2003, Brown et al. 2004, Jennings et al. 2007). Some of these attributes (e.g. distribution range) are sensitive to climate change (Brown 1995, Roessig et al. 2004). Given that fisheries productivity is a function of abundance, species' geographic ranges, life histories, and ecology, it is possible to predict first-order effects of climate change on fisheries productivity by predicting changes in these variables.

Studying the application of macroecological theory to predict climate change effects at a global scale is made possible by the availability of global databases of biology and fisheries. For example, FishBase (www.fishbase.org) provides fundamental life history information (e.g. maximum body length, trophic level) of all extant species of marine fishes. The databases compiled by the Sea Around Us Project (www.seaaroundus.org) consist of predicted distribution ranges and spatially explicit catch data (expressed in 30' latitude × 30' longitude grid cells) of over 1300 commercially exploited fish and invertebrate taxa. At the time of writing, 1000 of these were at the species level and were used here. The above databases can be used to develop empirical relationships to predict catch potential of exploited marine species from simple life history and biogeography attributes.

In this study, we aimed to apply macroecology theory to develop an empirical model to determine catch potential of commercially exploited fishes and invertebrates from their life history, ecology, and biogeography. Here, catch potential is defined as the maximum annual catch when a species is fully exploited, averaged over several years. The life history and biogeography attributes, including trophic level, range size, and primary productivity, were obtained from the Sea Around Us Project database and FishBase (see URLs above, which also provide details on data sources).

Based on the developed empirical relationship, we discuss the potential effects of climate change on catch potential of exploited fishes and invertebrates.

MATERIALS AND METHODS

Theoretical model. The metabolic rate of an organism scales almost universally with body size. This relationship can be described by an allometric equation (Kleiber 1932):

$$I = c \times W^b \qquad (1)$$

where I is whole-organism metabolic rate, W is body mass, c is a normalization constant independent of body size, and b is the allometric exponent. The exponent b can be approximated as 0.75 for all species (e.g. Kleiber 1932, West et al. 1997, 1999, Gillooly et al. 2001).

Assuming that total energy required to support metabolism (E) is proportional to whole-organism metabolic rate I, total energy required to support a population of N individuals at equilibrium carrying capacity can be obtained from:

$$E = N \times c' \times W^b \qquad (2)$$

where c' is a constant.

The energy available (E) for a specific population of animals at trophic level λ in an ecosystem can be calculated from:

$$E = \gamma \times P \times TE^{\lambda-1} \qquad (3)$$

where P is total primary production, TE is the transfer efficiency, and γ is the proportion of energy at trophic level λ that is utilized by the population (e.g. Ware 2000). Therefore, under equilibrium conditions, the total energy required to support the population can be estimated by combining Eqs. (2) & (3):

$$N \times c' \times W^b = \gamma \times P \times TE^{\lambda-1} \qquad (4)$$

Biomass at carrying capacity (B_∞) can be calculated from equilibrium abundance at carrying capacity (N) and average individual body mass (W):

$$B_\infty = N \times W \qquad (5)$$

Substituting Eq. (5) into Eq. (4):

$$c' \times B_\infty \times W^{b-1} = \gamma \times P \times TE^{\lambda-1} \qquad (6)$$

Maximum sustainable yield (MSY) is defined as the highest average theoretical equilibrium catch that can be continuously taken from a stock under average environmental conditions (Hilborn & Walters 1992). Based on a simple logistic population growth function and under equilibrium conditions, MSY can be defined as:

$$\text{MSY} = \frac{B_\infty \times r}{4} \qquad (7)$$

where r is the intrinsic rate of population increase and B_∞ is the biomass at carrying capacity (Schaefer 1954, Sparre & Venema 1992). Rearranging Eq. (7) to express B_∞ in terms of MSY and r:

$$B_\infty = \frac{4 \times \text{MSY}}{r} \qquad (8)$$

Substituting Eq. (8) into Eq. (6):

$$\frac{4 \times c' \times \text{MSY} \times W^{(b-1)}}{r} = \gamma \times P \times TE^{\lambda-1} \qquad (9)$$

Furthermore, W scales negatively and allometrically with intrinsic rate of population increase (r) (Fenchel 1974):

$$r = d \times W^h \qquad (10)$$

where d and h are constants. Thus,

$$\frac{4 \times c' \times \text{MSY} \times W^{(b-1)}}{d \times W^h} = \gamma \times P \times TE^{\lambda-1} \qquad (11)$$

The values of the scaling exponents b and h are approximately 0.75 and −0.25, respectively (Fenchel 1974, Jennings et al. 2007). Therefore, W can be eliminated from the equation:

$$\frac{4 \times c'}{d} \times \text{MSY} = \gamma \times P \times TE^{\lambda-1} \qquad (12)$$

Taking logarithmic transformation at both sides, and rearranging terms,

$$\log \text{MSY} = \log P + (\lambda-1) \times \log TE + \log \gamma - \log \frac{4 \times c'}{d} \qquad (13)$$

However, in many cases, only a fraction of the entire geographic range of a species is exploited. Assuming that the exploited range encompasses unit stocks, primary production from the exploited range (P') is considered in calculating the average MSY. MSY from the exploited range, or MSY', can be calculated from:

$$\log \text{MSY}' = \log(P') + (\lambda-1) \times \log TE + \log \gamma - \log \frac{4 \times c'}{d} \qquad (14)$$

Furthermore, as average TE is generally around 0.10 in marine ecosystems (Pauly & Christensen 1995), it is negative on a logarithmic scale and approximately constant between species and trophic levels. Therefore,

$$\log \text{MSY}' = \log P' - a \times \lambda + \log \gamma + g \qquad (15)$$

where a and g are constants.

Developing an empirical relationship. Using empirical data from commercially exploited fishes and invertebrates, we developed an empirical relationship to predict average maximum catch from a species. We used a generalized linear model (GLM; Venables & Ripley 1999) to develop an empirical relationship between observed average maximum catch, primary production, geographic range, and species' ecology. The empirical equation was based on the theoretical relationship developed in Eq. (15):

$$\log_{10} \text{MSY}' = m + c_1 \times \log_{10} P' + c_2 \times \lambda + \varepsilon \qquad (16)$$

where m is the intercept and c1 and c2 are coefficients of the regression model, respectively, and ε is an error term. Since the proportion of primary production available at a trophic level that is used by a population (γ) is not available and difficult to estimate for most marine species, we assumed it to be a random variable incorporated in the intercept and error terms. As maximum catch potential is positively related to primary productivity, we hypothesized that the values of c_1 should be positive. Moreover, since TE is always smaller than unity, and its logarithmic form is incorporated in the coefficient of λ, c_2 should be negative.

The average maximum annual catch from a species was calculated from catch time-series data. Global catches of 1000 species of fishes and invertebrates from 1950 to 2003 were obtained from the Sea Around Us Project (www.seaaroundus.org). The catch data, compiled from statistics produced by the United Nations Food and Agriculture Organization (FAO) and other sources, were spatially disaggregated onto a 30' latitude × 30' longitude grid map of the world ocean (Watson et al. 2004). For each of the 1000 species, we calculated the average maximum annual catch, a proxy of MSY', from the mean of the 5 highest annual catches across the time series. Alternatively, the highest annual catch from the catch time series was used to test the sensitivity of our analysis to the method for estimating MSY'.

For species with a relatively short history of exploitation, the highest annual catch averaged over 5 yr may not depict the maximum catch potential, as the population may be underexploited. Thus, the estimated average maximum annual catch may be an underestimation of the true maximum catch potential. Therefore, we calculated the number of years with catch data (CT) by species and introduced it as an additional variable to correct for such bias. We hypothesized that if exploitation history is longer (thus yielding longer catch time-series), the average maximum annual catch would approach the true maximum catch potential, i.e.

$$\text{Average maximum annual catch} \times CT \rightarrow \text{MSY}' \qquad (17)$$

We also attempted to correct for the possibility of underestimation of catches resulting from taxonomic aggregation in the catch records. In catch statistics,

catches were often reported in aggregated taxonomic groups at genus, family, or higher taxonomic levels. For instance, catches of small yellow croaker may be reported as *Larimichthys* sp. or sciaenids. Thus, catches of small yellow croaker might be underestimated. To correct for such bias, we also calculated the catch from genera and families that originated from the same exploited range of the corresponding species. To be consistent with the maximum catch estimation, for each species we calculated the average value from the 5 years when the highest catches were recorded. We hypothesized that catches reported as higher taxonomic aggregates (genera and families) are approximately proportional to the degree of misreporting (and thus underestimation) of the species' catch. Catch at higher taxonomic aggregates (HTC) was included in the multiple regression model. Therefore, the model becomes:

$$\log_{10}\text{MSY}' = m + c_1 \times \log_{10} P' + c_2 \times \lambda + c_3 \times \log_{10}\text{CT} + c_4 \times \log_{10}\text{HTC} + \varepsilon \tag{18}$$

For each species, P' in Eq. (18) was calculated from total primary production in the species' exploited range:

$$P' = \sum_{i=1}^{n} P_i \times A_i \tag{19}$$

where P_i is the annual primary production per unit area (g C m^{-2}) of a spatial cell i in a 30′ latitude × 30′ longitude grid map of the world ocean; A_i is the area of the spatial cell i; and n is the total number of spatial cells where the species' catch was recorded. Estimates of ocean primary production included production from phytoplankton only, i.e. production from seagrasses or benthic micro- and macro-algae was not accounted for. The estimates were based on a model (Platt & Sathyendranath 1988) that estimates depth-integrated primary production from the chlorophyll pigment concentration obtained from the SeaWiFS satellite (http://seawifs.gsfc.nasa.gov/SEAWIFS.html) and photosynthetically active radiation (e.g. Bouvet et al. 2002). The estimated primary production, which pertains to the period from October 1997 to September 1998, was then interpolated for small areas without coverage to provide estimates that covered the entire world ocean on a 30′ latitude × 30′ longitude grid (Lai 2004).

We attempted to correct for a statistical bias in estimating total primary production from the exploited range of the species (P'). The estimated species' area of occupancy generally increases with the scale of the spatial grid with an allometric relationship (Kunin 1998):

$$A_S = h \times S^{k}$$
$$\text{or} \tag{20}$$
$$\log A_S = \log h + k \log S$$

where A_S is the estimated area of occupancy at spatial resolution S, and h and k are constants. The exponent k depends on a species' range size, as species with a restricted and aggregated range tend to have a smaller scaling exponent k than wide-ranging species with scattered distributions (Fig. 1). Thus, when an average scaling exponent k is applied to all studied species, as in the case of our analysis, the true area of occupancy of the species is likely to be overestimated for species with a wide geographic range (larger value of k) and underestimated for species with a restricted range (Fig. 1). Since the total annual primary production available for the species (P') is a function of the true area of occupancy, the bias resulting from the scale-area relationship should be corrected. Thus, species' geographic range size calculated at the 30′ × 30′ spatial scale (A) was included in Eq. (18) to correct for such biases:

$$\log_{10}\text{MSY}' = m + c_1 \times \log_{10} P' + c_2 \times \lambda + c_3 \times \log_{10}\text{CT} + c_4 \times \log_{10}\text{HTC} + c_5 \times \log_{10} A + \varepsilon \tag{21}$$

where c_5 is a constant with a sign expected to be negative.

Predicted geographic ranges for the 1000 fishes and invertebrates were obtained from the Sea Around Us Project. Geographic ranges of the species were predicted from boundaries and preferences of latitudinal range, depth range, habitats, and published occurrence range (see Close et al. 2006 for details), and used to calculate the total area of occurrence. Moreover, based on the spatially-explicit catch data, we calculated the total area where the geographic range of a species was exploited, i.e. had a non-zero catch (A_e). Trophic levels,
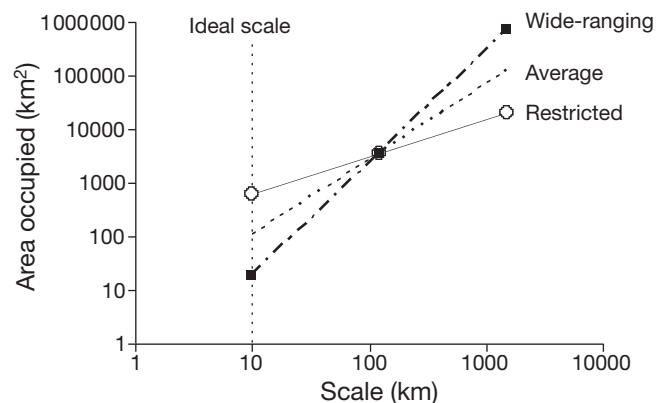

Fig. 1. Hypothetical relationships between the scale of the spatial grid and estimated area of occupancy of species with wide geographic ranges (broken line, filled squares), restricted ranges (solid line, open circles), and the average from the above 2 (dotted line; adapted from Kunin 1998). The vertical broken line represents the ideal scale in which the estimated area of occupancy is close to the true value. At the ideal scale, the estimated area of occupancy from the average line underestimates the true occupancy area of species with restricted ranges and overestimates that for wide-ranging species

also taken from the Sea Around Us Project's database, were based on FishBase (www. fishbase.org) for fishes, and on SeaLifebase (www. sealifebase.org) and other sources for invertebrates. Trophic level may vary between different populations of a species because of differences in local food webs, but, at the scale of our analysis (global), we used the cross-population average trophic level of the species. This approximation contributes to the overall variance of the empirical model.

We ran the GLM model specified in Eq. (21) in the statistical program *R*. We assumed a Gaussian distribution error (ε) in the GLM. The validity of this assumption was tested by examining the residuals from the regression analysis. We examined the normality assumption of the model with the Shapiro-Wilk test and tested for existence of outliers with Cook's distances test (Cook & Weisberg 1982). Moreover, we tested for any unexpected non-linearity in the variables by conducting Alternating Conditional Expectations analysis (Breiman & Friedman 1985). We used the acepack package of *R* to run the analysis. Finally, using current and climate-shifted distributions of the small yellow croaker *Larmichthys polyactis* (Sciaenidae) predicted by an existing dynamic bioclimate envelope model (see Cheung et al. 2008 for details) as an example, we illustrated the application of our model in assessing the impact of climate change on global fisheries. In the case study of the small yellow croaker, the focus is on the application of the empirical model in predicting impacts of climate change on fisheries given some predictions of distribution shift of a species. The validity of the predicted distribution shift is dealt with elsewhere (see Cheung et al. 2008).

RESULTS

Predicting maximum annual catch

The average maximum annual catch of the 1000 species of fishes and invertebrates were significantly affected by annual primary production in the species' exploited range, trophic level, geographic range, and the number of years of records in the catch time-series (Table 1). Levels of significance for the above terms were high ($p < 0.01$). The full model was significant at the 99% confidence level and explained over 70% of the variation in the average maximum annual catches of the species (Fig. 2). The significance of the terms in the GLM was not affected when a subset of the data (i.e. including species with CT ≥ 5 yr only, N = 878 species) was used (Fig. 2). Annual primary production (P'), trophic level (λ), geographic range (A), number of years of records (CT), and the catch from higher taxo-

Table 1. Test statistics of the full GLM as specified in Eq. (21). P': annual primary production from exploited range; λ: trophic level; CT: number of years with catch data; HTC: catch from higher taxonomic groups; A: geographic range

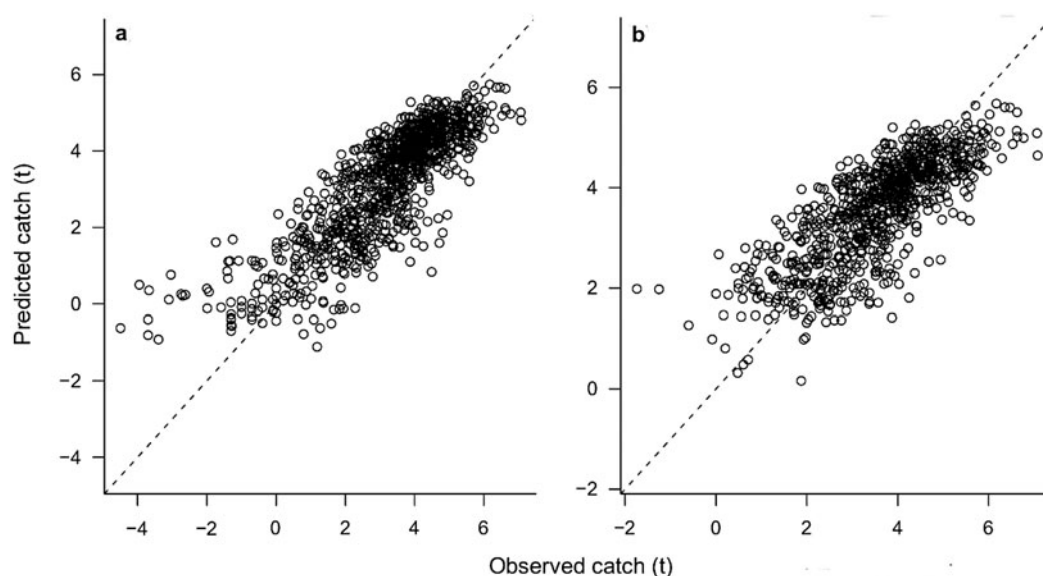| Terms	Estimate	SE	t	p
Intercept	−2.881	0.299	−9.638	< 0.001
$\log_{10}(P')$	0.826	0.051	16.158	≪ 0.001
λ	−0.152	0.046	−3.301	< 0.001
$\log_{10}(CT)$	1.887	0.076	24.892	≪ 0.001
$\log_{10}(HTC)$	0.112	0.022	5.089	< 0.001
$\log_{10}(A)$	−0.505	0.055	−9.269	< 0.001

Fig. 2. Relationship between predicted mean values from the multiple regression and the observed average maximum annual catch (log-transformed) using (a) full dataset (N = 1000, R^2 = 0.703, p < 0.001) and (b) subset of data with number of years with catch data (CT) × 5 (N = 878, R^2 = 0.606, p < 0.001)

nomic groups (HTC) remained highly significant (p < 0.001). Moreover, the explanatory power of the model remained strong ($R^2 = 0.67$) when alternative estimates of MSY′ were used. The coefficients of the factors varied only by an average of about 5.8%.

The effects of the model terms generally agreed with the theoretical model developed in this paper (Eq. 15; Table 1). The effect of total annual primary production from the exploited range was positive, whereas the effects of trophic level and geographic range were negative. Moreover, the number of years of exploitation was effective in correcting for the underestimation of average maximum potential catch in species with short catch time-series. The empirical model resulting from the full dataset (N = 1000) to predict maximum catch potential is:

$$\log_{10} \text{MSY}' = -2.881 + 0.826 \times \log_{10} P' -$$
$$0.505 \times \log_{10}(A) - 0.152_{10} \times \lambda + 1.887 \times \log_{10} \text{CT} +$$
$$0.112 \times \log_{10} \text{HTC}' + \varepsilon \tag{22}$$

The assumptions of multiple regression analysis (homogenous variance and normality) were generally met. Residuals from the regression of the full dataset (N = 1000) were not correlated with the mean fitted values of the model, i.e. the slope of the regression between the 2 variables was not significantly different from 0 (p > 0.05, Fig. 3). This indicated that the variance of the model was homogenous. A Shapiro-Wilk test showed that the distribution of the residuals was significantly different from normal (Shapiro-Wilk test, p < 0.05); the residuals appeared S-shaped on a normal-quartile plot (Fig. 3). Conversely, when species with <5 yr of catch records were excluded from the analysis (resulting N = 878), the distribution of the residuals became approximately normally distributed (Shapiro-Wilk test, p = 0.025), while their variances remained homogenous. Furthermore, the residuals from the subset of data generally fell on a straight line in a normal-quartile plot. Thus, the deviation from normality in the full dataset resulted mainly from the highly uncertain data points. In addition, based on Cook's distance test, we did not identify any significant outliers from the model.

We did not find any unexpected nonlinearity in the relationship between maximum annual catches and the independent variables (Fig. 4). The transfor-

mations of the independent variables resulting from the Alternating Conditional Expectations analysis were approximately log-linear for annual primary production from exploited range (P'), geographic range (A), number of years with catch record (CT), and catches from higher taxa. The estimated transformation for trophic level (TL) was approximately linear. These agree with the transformations that we employed in the regression model (Eq. 21).

Maximum annual catch and climate change

Given the predicted current and climate-shifted distributions of the small yellow croaker, its catches would likely shift northward, although the total predicted annual catch would remain relatively unchanged. The predicted current relative distribution of small yellow croaker centered at approximately 31.25° N (Fig. 5a). Under a hypothetical 2.5°C increase in average global ocean temperature, the dynamic bioclimate envelope model described by Cheung et al. (2008) predicted a northward shift in both the centroid and north-south range limits of its distribution. Simultaneously, if the ecology of the small yel-
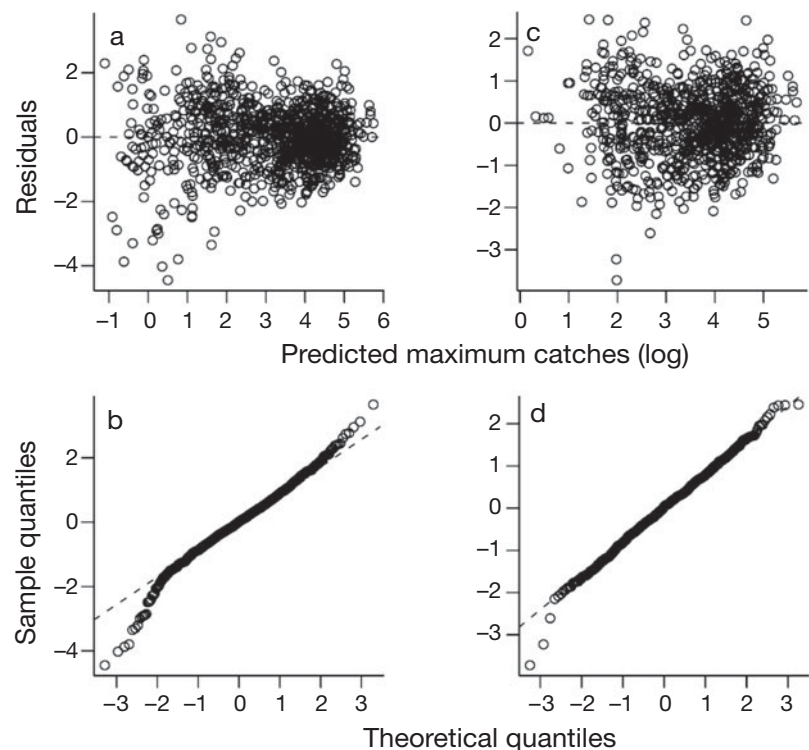

Fig. 3. Diagnostic plots for the regression analysis. (a,c) Residuals from the regression against the mean fitted value, and (b,d) normal quartile plot. Full dataset (N = 1000) was used in (a) and (b) while a subset of data was used in (c) and (d). Dashed lines are the best-fitting relationship between (a,c) the residuals and the filtered values and (b,d) the variables in the vertical and horizontal axis of each plot. Note different scales on axes
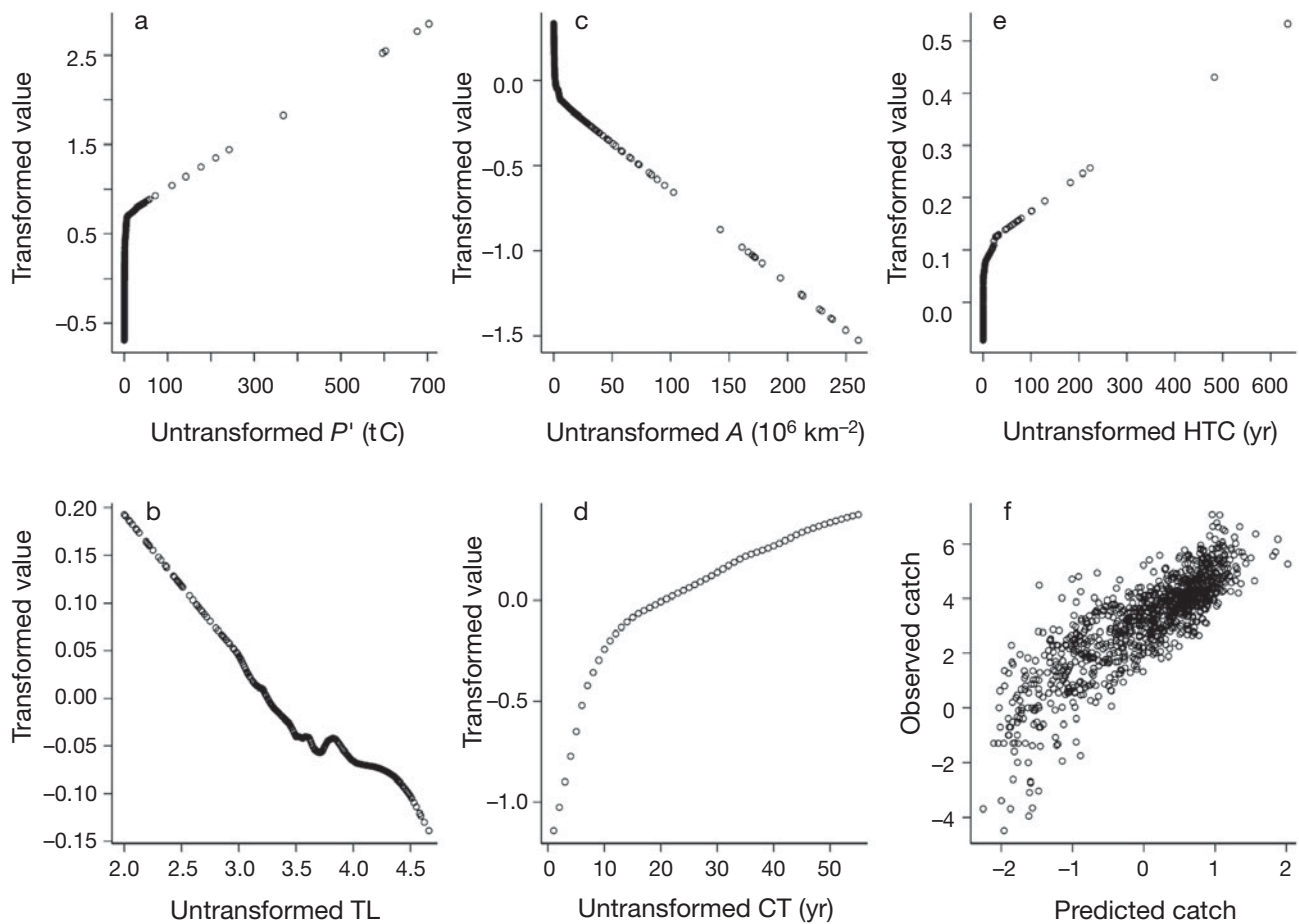
Fig. 4. Optimal transformation of the independent variables identified from the Alternating Conditional Expectations analysis: (a) annual primary production from exploited range (*P'*), (b) trophic level (TL), (c) geographic range (*A*), (d) number of years with catch records (CT), (e) catch from higher taxonomic groups (HTC), and (f) observed maximum annual catch against predicted values from the multiple regression of these transformed variables

low croaker remained the same, its area of occurrence was predicted to increase from 770 000 km^2 to 1 221 000 km^2. Assuming that primary production remained constant at the current level, total primary production within the distribution range of small yellow croaker increased by 40.1%. Using the empirical relationship we developed (Eq. 21), the predicted maximum catch potential of small yellow croaker did not change significantly (p > 0.05) from the current level under the hypothetical ocean warming scenario. However, the relative distribution of the catch potential decreased largely near the southern limits of the current distribution range, i.e. off Taiwan and the Ryukyu and Diaoyutai Islands, but increased near the northern range limits, i.e.

North and South Korea and Japan (main islands; Table 2). The catch potential off mainland China decreased slightly. Areas with the highest absolute increase in catch potential were Japan (main islands) and North Korea.

Table 2. Predicted distribution of relative catch potential by areas of Exclusive Economic Zones

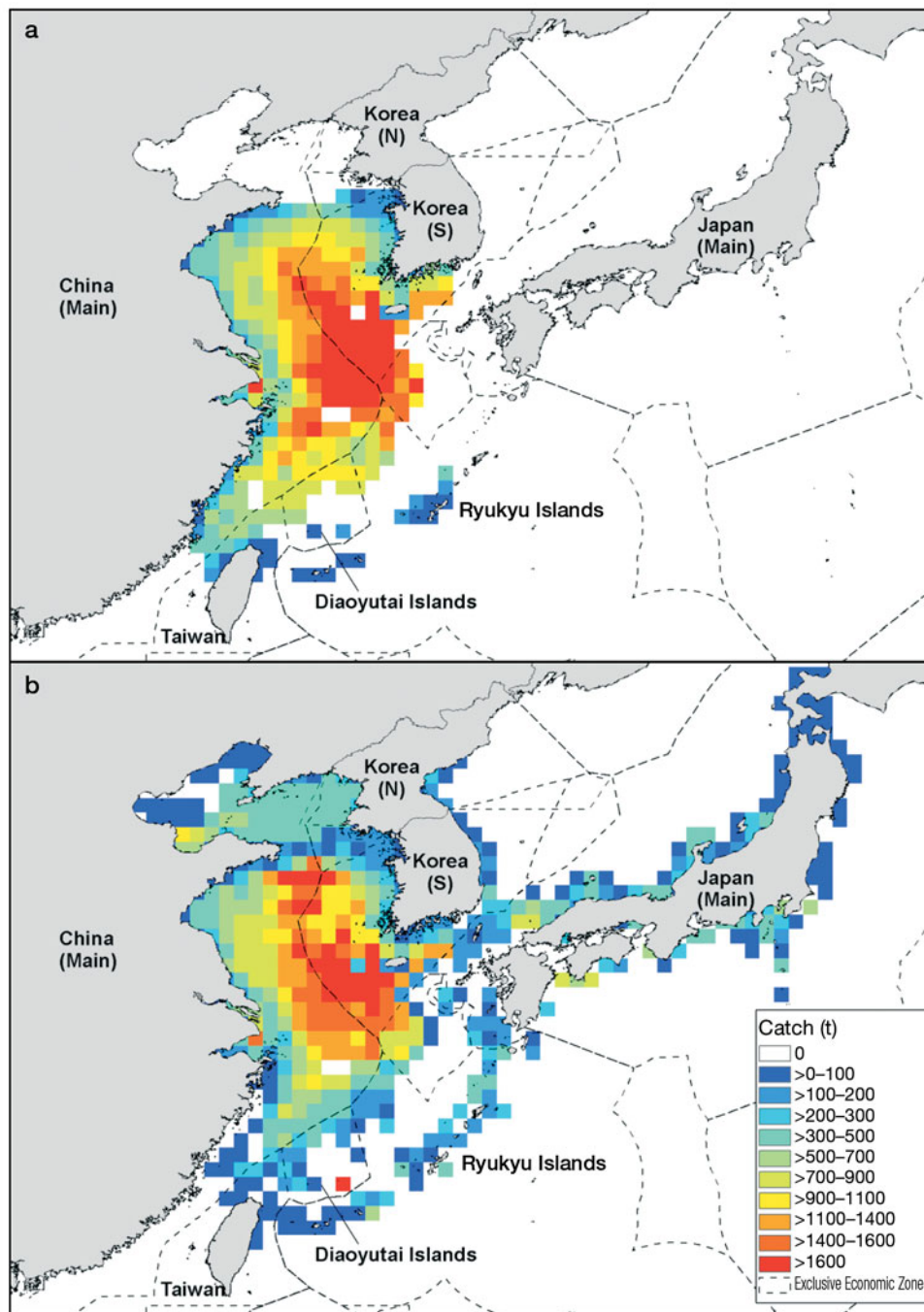| Exclusive Economic Zone by area	Predicted relative catch potential (%)		Relative change in catch potential (%)
	Current (2000s)	Climate-shifted	
Japan (main islands)	0.3	7.6	2433.3
North Korea	0.8	4.5	462.5
South Korea	26.5	33.3	25.7
China (mainland)	51.6	44.4	−14.0
Ryukyu & Diaoyutai Islands (Japan)	14.1	8.4	−40.4
Taiwan	6.8	1.8	−73.5

Fig. 5. *Larimichthys polyactis* (Sciaenidae). (a) Current (early 2000s) and (b) climate-shifted distributions of the small yellow croaker. The current distribution was generated from the method described by Close et al. (2006). The climate-shifted distribution was predicted by a dynamic bioclimate envelope model described by Cheung et al. (2008), under a hypothetical increase in average global ocean temperature of 2.5°C. Boundaries of Exclusive Economic Zones are delineated by the dashed lines

DISCUSSION

This study demonstrates that maximum catch potential for marine fishes or invertebrates can be reasonably predicted at a global scale. The empirical relationship between catch potential and biogeographic and ecological attributes was developed from a wide range of taxonomic groups (from krill to tuna) and species with very different life history and ecology (small to large-bodied, herbivores to top predators). Given the high uncertainty of the original data (catch, geographic range, and trophic levels), the explanatory power

of the statistical model was unexpectedly high. Moreover, the empirical model was supported by and agreed with a theoretical model developed from well-established hypotheses concerning trophic energetics (e.g. Ware 2000) and allometric scaling of metabolism (e.g. Brown et al. 2004).

An important application of the empirical relationship developed in this study is to predict the impacts of climate change on the catch potential of world fisheries. If ocean temperature and ocean circulation continue to change in the future as anticipated (IPCC 2007), species' geographic ranges and the mean primary production available for the species are likely to change (Roessig et al. 2004, Sarmiento et al. 2004, Hobday et al. 2006). Empirical evidence shows that geographic ranges of marine species have shifted toward cooler waters as ocean temperature increased (e.g. Perry et al. 2005). The empirical model developed here, which includes both primary productivity and species' geographic range as independent variables, can be used to quantitatively predict the effects of such changes on the catch potential of fish and invertebrate species. This can be largely facilitated by the use of global dynamic bioclimate envelope models to predict the changes in relative distribution and geographic range of marine fishes and invertebrates under scenarios of future changes in ocean conditions (e.g. temperature, currents) obtained from climate models (Cheung et al. 2008). Such application of the empirical model was illustrated here with the case of the small yellow croaker. Thus, combining the empirical model with the dynamic bioclimate envelope model provides a powerful tool to assess climate change impacts on catch, and thus the socio-economics of marine fisheries globally and in different parts of the world. This can potentially improve the estimations of the global cost of climate change (Stern 2006).

The high variance between the observed average maximum annual catch and the model predictions is partly a result of the approximation involved in representing trophic dynamics. Although the explanatory power of the model is reasonably high, the uncertainty associated with the predicted maximum annual catch covers about 1 order of magnitude. This can be partly explained by the difficulties in predicting the differential utilization of energy between species within a trophic level, i.e. the variable γ in Eq. (15) (Jennings et al. 2007). In this analysis, a mean trophic level across life history stages was assumed for each species. However, trophic levels change during ontogeny (Pauly et al. 2001), and thus a single value of trophic level may not capture the full range of trophic levels that an organism can occupy in an ecosystem (Jennings et al. 2002, Jennings & Mackinson 2003). This can confound the analysis of allometric scaling of trophic dynamics (Jennings & Mackinson 2003, Maxwell & Jennings 2006).

Empirical studies of allometric relationships in macro-ecology (e.g. abundance-body size relationship) have reported inconsistent values of scaling exponents (e.g. Blackburn & Gaston 1997, Belgrano et al. 2002). Alternative values of the scaling exponent may exist in some taxa (e.g. Clark & Johnston 1999, Glazier 2005, van der Meer 2006, White et al. 2007) or life stages (Pauly 1981). Since our empirical model was derived from such allometric relationships, the uncertainty in scaling exponents may have contributed to the variance of our model. In contrast, if the scaling exponent in Eq. (1) deviates from 0.75, i.e. the value that we employed in our analysis, log-transformed body size (W) will have an effect on the maximum catch potential of a species (Eq. 12). Since $\log(W)$ is closely correlated with trophic level, deviation from our assumed value for the scaling exponent would have been partly accounted for by the coefficient of the trophic level term in the empirical model. Thus, the uncertainty in the value of the scaling exponent should not affect the validity of our empirical model. In addition, previous studies suggested the use of individual body size-based analysis that may potentially improve the representation of trophic dynamics and analysis of allometric relationships (e.g. Jennings et al. 2007). However, at the scale of this study (global), data for such size-based analysis were not available. Thus, we used the best available species-based data to identify a suitable empirical relationship.

Other sources of uncertainty in the model include the approximations involved in estimating the maximum catch potential and geographic range of species. Maximum catch potential was approximated by the average maximum recorded catch in the catch time-series. The catch time-series data originated from fisheries statistics compiled by the FAO, which may not represent the total extractions from the sea. FAO fisheries statistics rely largely on countries' voluntary reports of their annual fisheries catches, which may not be accurate (see Watson & Pauly 2001, Zeller et al. 2007). Catches that were not landed (discards), low-value bycatch, and catches from illegal, unregulated, or unreported (IUU) fisheries were poorly recorded (Pauly et al. 2002). Moreover, observed maximum catch is affected by changes in fishing effort (Hilborn & Walters 1992). The latter depends largely on changes in fisheries regulations, market prices of catch, cost of fishing, and subsidies. Conversely, the low sensitivity of the model parameters to alternative estimates of maximum catch potential suggests that the use of the average maximum recorded catch of a species is a rough, but robust, approximation of the maximum catch potential.

Another source of uncertainty is the predicted geographic range. In this study, the coarse resolution of

the spatial database and the large number of species limited us to use predicted area of occurrence (Close et al. 2006) as a proxy to calculate geographic range. However, as occurrence area may include areas that the species does not inhabit, area of occupancy identified from spatial data at a fine scale, i.e. the area where a species actually occurs, is a better measure to represent the geographic range and habitat usage of a species (Gaston & Blackburn 2000). If finer-scale data are available, allometric relationships can be developed to extrapolate area of occupancy at a fine spatial scale (Kunin 1998, Kunin et al. 2000). In this analysis, we attempted to correct for the bias resulting from the difference in allometric relationships between species with different spatial distribution patterns. However, the underlying allometric relationships for each species remained unknown. In the future, finer scale occupancy data will be collated and combined with the coarser scale occurrence data to investigate how the 'scale-area' allometric relationship can be used to improve the predictions of maximum catch potential.

The variance of the empirical model may have small effects on the prediction of changes in catch potential under scenarios of climate change. Errors resulting from the inconsistency in allometric scaling exponents and from the methods used for estimating maximum catch potential and geographic range should remain similar when ocean conditions change. Thus, predictions of relative change in maximum catch potential of species, given scenarios of future primary production and geographic range, should be robust to such model uncertainties. Alternatively, as species composition and trophic ecology in an area changes, the partitioning of energy between species within a trophic level (represented by the term γ in Eq. 15) may also change. Such changes are not currently captured by our model. Improved understanding of the mechanism that determines energy partitioning between species within a trophic level may improve the representation of such effects in the regression model. Also, use of trophodynamic ecosystem models such as Ecopath with Ecosim (Pauly et al. 2000, Christensen & Walters 2004) can provide additional information to evaluate large-scale effects of climate change on the marine ecosystem.

In conclusion, the empirical model developed in this study is the first attempt to derive a model suitable for estimating marine catch potential by species at a global scale. The model is representative of a wide range of marine fishes and invertebrates and has a surprisingly high explanatory power. Although inherent uncertainty in the original data and model parameters result in high variance in the predicted maximum catch potential, predicted relative changes in catch potential under climate change-induced changes in biogeography should be robust to handle the uncer-

tainties. In the future we will combine this empirical model with a bioclimate envelope model for marine fishes and invertebrates to predict the socio-economic impacts of climate change on marine fisheries.

LITERATURE CITED

Belgrano A, Allen AP, Enquist BJ, Gillooly JF (2002) Allometric scaling of maximum population density: a common rule for marine phytoplankton and terrestrial plants. Ecol Lett 5:611–613

Blackburn TK, Gaston KJ (1997) A critical assessment of the form of the inter-specific relationship between abundance and body size in animals. J Anim Ecol 66:233–249

Blackburn TM, Gaston KJ (eds) (2003) Macroecology. Blackwell, Oxford

Bouvet M, Hoepffner N, Dowell MD (2002) Parameterization of a spectral solar irradiance model for the global ocean using multiple satellite sensors. J Geophys Res 107(C12): 3215. doi:10.1029/2001JC001126

Breiman L, Friedman JH (1985) Estimating optimal transformations for multiple regression and correlation. J Am Stat Assoc 80:580–598

Brown JH (1984) On the relationship between abundance and distribution of species. Am Nat 124:255–279

Brown JH (1995) Macroecology. The University of Chicago Press, Chicago, IL

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85: 1771–1789

Charnov EL (1993) Life history invariants. Oxford University Press, Oxford

Cheung WWL, Lam V, Pauly D (2008) Dynamic bioclimate envelope model to predict climate-induced changes in distributions of marine fishes and invertebrates. In: Cheung WWL, Pauly D, Lam V (eds) Modelling present and climate-shifted distributions of marine fishes and invertebrates. Fisheries Centre Research Reports 16(3), Fisheries Centre, University of British Columbia, Vancouver, p 5–50

Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecol Model 172:109–139

Clarke A, Johnston NM (1999) Scaling of metabolic with body mass and temperature in teleost fish. J Anim Ecol 68: 893–905

Close C, Cheung WWL, Hodgson S, Lam V, Watson R, Pauly D (2006) Distribution ranges of commercial fishes and invertebrates. In: Palomares MLD, Stergiou KI, Pauly D (eds) Fishes in databases and ecosystems. Fisheries Centre Research Reports 14 (4), Fisheries Centre, University of British Columbia, Vancouver, p 27–37

Cook RD, Weisberg S (1982) Residuals and influence in regression. Chapman & Hall, London

Cramer W, Bondeau A, Woodward FI, Prentice IC and others (2001) Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Global Change Biol 7: 357–373

Damuth J (1981) Population density and body size in mammals. Nature 290:699–700

Fenchel T (1974) Intrinsic rate of natural increase: the relationship with body size. Oecologia 14:317–326

Gaston KJ, Blackburn TM (2000) Pattern and process in macroecology. Blackwell Science, Oxford

Gaston KJ, Blackburn TM, Lawton JH (1997) Interspecific abundance-range size relationships: an appraisal of mechanisms. J Anim Ecol 66:579–601

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. Science 293:2248–2251

Glazier DS (2005) Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. Biol Rev Camb Philos Soc 80:611–662

Hanski I (1982) Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38:210–221

Hilborn R, Walters CJ (1992) Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman & Hall, New York

Hobday AJ, Okey TA, Poloczanska ES, Kunz TJ, Richardson AJ (eds) (2006) Impacts of climate change on Australian marine life. Part C. Literature review. Report to the Australian Greenhouse Office (September 2006), Canberra

Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts and the resilience of coral reefs. Science 301:929–933

IPCC (Intergovernmental Panel on Climate Change) (2007) Summary for policymakers. In: Solomon S, Qin D, Manning M, Chen Z and others (eds) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, p 1–18

Jennings S, Mackinson S (2003) Abundance-body mass relationships in size-structured food webs. Ecol Lett 6: 971–974

Jennings S, Warr KJ, Mackinson S (2002) Use of size-based production and stable isotope analysis to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. Mar Ecol Prog Ser 240:11–20

Jennings S, De Oliveira JAA, Warr KJ (2007) Measurement of body size and abundance in tests of macroecological and food web theory. J Anim Ecol 76:72–82

Kleiber M (1932) Body size and metabolism. Hilgardia 6: 315–332

Kunin WE (1998) Extrapolating species abundance across spatial scales. Science 281:1513–1515

Kunin WE, Hartley S, Lennon JJ (2000) Scaling down: on the challenge of estimating abundance from occurrence patterns. Am Nat 156:560–566

Lai S (2004) Primary production. 'Sea Around Us' Project, Fisheries Centre, the University of British Columbia Vancouver. Available at: www.seaaroundus.org/doc/saup_manual. htm#3 (Accessed 27 July 2007)

Maxwell TAD, Jennings S (2006) Predicting abundance-body size relationships in functional and taxonomic subsets of food webs. Oecologia 150:282–290

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pauly D (1981) The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Ber Dtsch Wiss Komm Meeresforsch 28:251–282

Pauly D, Christensen V (1995) Primary production required to sustain global fisheries. Nature 374:255–257

Pauly D, Christensen V, Walters C (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J Mar Sci 57:697–706

Pauly D, Palomares ML, Froese R, Sa-a P, Vakily M, Preikshot D, Wallace S (2001) Fishing down Canadian aquatic food webs. Can J Fish Aquat Sci 58:51–62

Pauly D, Christensen V, Guénette S, Pitcher TJ and others (2002) Towards sustainability in world fisheries. Nature 418:689–695

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Nature 308:1912–1915

Platt T, Sathyendranath S (1988) Oceanic primary production: estimation by remote sensing at local and regional scales. Science 241:1613–1620

Roessig JM, Woodley CM, Cech JJ, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. Rev Fish Biol Fish 14:251–275

Sarmiento JL, Slater R, Barber R, Bopp L and others (2004) Response of ocean ecosystems to climate warming. Global Biogeochem Cycles 18:GB3003, doi:10.1029/2003 GB002134

Schaefer M (1954) Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Bull I-ATTC 1:27–56

Sparre P, Venema SC (1992) Introduction to tropical fish stock assessment. Part 1. Manual. FAO Fisheries Technical Paper 306, FAO, Rome

Stern N (2006) The economics of climate change: the Stern review. Cambridge University Press, Cambridge

van der Meer J (2006) Metabolic theories in ecology. Trends Ecol Evol 21:136–140

Venables WN, Ripley BD (1999) Modern applied statistics. Springer, New York

Walther GR, Post E, Convey P, Menzel A and others (2002) Ecological responses to recent climate change. Nature 416:389–395

Ware DM (2000) Aquatic ecosystems: properties and models. In: Harrison PJ, Parsons TR (eds) Fisheries oceanography: an integrative approach to fisheries ecology and management. Blackwell Science, Oxford, p 161–194

Watson R, Pauly D (2001) Systematic distortions in world fisheries catch trends. Nature 414:534–536

Watson R, Kitchingman A, Gelchu A, Pauly D (2004) Mapping global fisheries: sharpening our focus. Fish Fish 5:168–177

West GB, Brown JH, Enquist BJ (1997) A general model for the origin of allometric scaling laws in biology. Science 276:122–126

West GB, Brown JH, Enquist BJ (1999) The fourth dimension of life: fractal geometry and allometric scaling of organisms. Science 284:1677–1679

White CR, Cassey P, Blackburn TM (2007) Allometric exponents do not support a universal metabolic allometry. Ecology 88:315–323

Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH (2005) Body size in ecological networks. Trends Ecol Evol 20:402–409

Zeller D, Booth S, Davis G, Pauly D (2007) Re-estimation of small-scale for U.S. flag-associated islands in the western Pacific: the last 50 years. Fish Bull (Wash DC) 105: 266–277