Ecology, 97(5), 2016, pp. 1251–1259

Life history traits and exploitation affect the spatial mean-variance relationship in fish abundance

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Abstract. Fishing is expected to alter the spatial heterogeneity of fishes. As an effective index to quantify spatial heterogeneity, the exponent b in Taylor's power law ($V = aM^b$) measures how spatial variance (V) varies with changes in mean abundance (M) of a population, with larger b indicating higher spatial aggregation potential (i.e., more heterogeneity). Theory predicts b is related with life history traits, but empirical evidence is lacking. Using 50-yr spatiotemporal data from the California Current Ecosystem, we examined fishing and life history effects on Taylor's exponent by comparing spatial distributions of exploited and unexploited fishes living in the same environment. We found that unexploited species with smaller size and generation time exhibit larger b, supporting theoretical prediction. In contrast, this relationship in exploited species is much weaker, as the exponents of large exploited species were higher than unexploited species with similar traits. Our results suggest that fishing may increase spatial aggregation potential of a species, likely through degrading their size/age structure. Results of moving-window cross-correlation analyses on b vs. age structure indices (mean age and age evenness) for some exploited species corroborate our findings. Furthermore, through linking our findings to other fundamental ecological patterns (occupancy-abundance and size-abundance relationships), we provide theoretical arguments for the usefulness of monitoring the exponent b for management purposes. We propose that age/size-truncated species might have lower recovery rate in spatial occupancy, and the spatial variance-mass relationship of a species might be non-linear. Our findings provide theoretical basis explaining why fishery management strategy should be concerned with changes to the age and spatial structure of exploited fishes.

Key words: demographic process; size-truncation; spatial heterogeneity; Taylor's power law.

INTRODUCTION

Overfishing can induce spatial aggregation (i.e., losing spatial homogeneity) of exploited populations without causing significant changes in their abundances, likely through degrading age/size-structure (Swain and Wade 1993, Hsieh et al. 2008). Enhanced spatial aggregation (i.e., elevated spatial heterogeneity) happens in many exploited fishes and causes several deleterious effects, such as increased fluctuation in abundance and extinction of local populations (Tittensor et al. 2007, Hsieh et al. 2008, 2010, Shackell et al. 2012). Apart from fishing, several factors such as abundance, behavior, demographic traits, and the environment have been suggested also to influence the spatial heterogeneity of a population (Kearney and Porter 2009). Thus, understanding the dynamics of spatial heterogeneity in a species is important for developing informed management (Shackell et al. 2005, Hsieh et al. 2010, Ciannelli et al. 2013), and indices that can effectively summarize spatial distribution patterns are needed.

One effective way to summarize the spatial patterns of a species is using Taylor's power law, $V = aM^b$. Taylor's power law asserts that the variance (V) in population abundance is a function of mean (M) population abundance. In spatial data, the exponent b describes how spatial variance in abundance of several subpopulations changes with the mean abundance, and has commonly been used as a species-specific aggregation index: $b \approx 0$ suggests a uniform spatial distribution, $b = 1$ implies a random distribution (e.g.,, Poisson), and larger b indicates a higher degree of aggregation (Taylor 1961) (i.e., higher spatial heterogeneity) (Appendix S1, Fig. S1). Consequently, fundamental understanding of the mechanism mediating the mean-variance relationship

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Manuscript received 10 July 2015; revised 5 November 2015; accepted 2 December 2015. Corresponding Editor: D. E. Schindler.

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(indicated by Taylor's exponent *b*) is critical for monitoring changes in spatial structure for a species. In addition, Taylor's power law is suggested to have linkage with other ecological patterns, such as the occupancy-abundance (He and Gaston 2003) and size-abundance relationships (Cohen et al. 2012), potentially leading to important unification of relationships among spatial distribution, abundance, and body size in ecology. These understandings may have profound management implications to fisheries, because fishing affects not only abundance but also spatial and size distribution of a population (Hsieh et al. 2010).

Since the pioneering work by Taylor (1961), the spatial mean-variance relationship has been documented in many systems (Iwao 1968, Nestel et al. 1995, Kendal 2004, Eisler et al. 2008, Ramsayer et al. 2012). Surprisingly, empirical evidence for the mechanisms mediating Taylor's exponent is still lacking, although theoretical models have made some predictions (Taylor and Taylor 1977, Hanski 1980, Taylor 1981, Anderson et al. 1982, Yamamura 2000). Theoretically, demographics (those related to life history traits) have been shown to affect the spatial mean-variance relationship (Hanski 1980, Anderson et al. 1982, Yamamura 2000). The most well known theoretical model was proposed by Anderson et al. (1982), using stochastic Markovian population process. In this model, the authors argued that *r*-selected species have a higher *b* than *K*-selected species (as can be seen using simple mathematical argument in Appendix S2). A colony expansion model (Yamamura 2000) also showed that Taylor's exponent increases with increasing population reproduction (local growth), corroborating Anderson's hypothesis that species with *r*-selected traits have higher *b*. Noteworthy, the only previous multispecies comparative analysis (Taylor et al. 1983), however, did not agree with Anderson's theoretical prediction. This study compiled data from different surveys with various methods and environments; as such, the comparison is not adequate because Taylor's exponent is a function of environmental conditions (Perry 1988). Other existing multispecies meta-analyses did not discuss the potential influence of life history traits, and largely focused on the distribution of *b*, sampling scale, or sampling error (Hanski 1980, 1982, Taylor et al. 1983, Taylor 1986, Downing 1988, Kilpatrick and Ives 2003). Interestingly, although the effects of life history traits on Taylor's exponent have been predicted based on sound theoretical arguments (Hanski 1980, Anderson et al. 1982, Yamamura 2000), no systematic investigation with suitable empirical data has been conducted to date.

Fishing effects that exert significant impacts on life history traits (Jennings and Kaiser 1998, Hsieh et al. 2010) and spatial structure (Swain and Sinclair 1994, Hsieh et al. 2008) likely also alter the mean-variance relationship of impacted species. For example, size-selective removal may truncate the size/age structure and affect life history of exploited fishes without causing apparent abundance decline (Hsieh et al. 2006, Garcia et al. 2012). Life history traits (e.g., length, maturation age, population growth rate) have been found highly correlated to species' spatial distribution (Opdal and Jørgensen 2015). If life history traits are altered through age truncation or fishing-induced evolution (Murawski 2001, Berkeley et al. 2004, Jennings and Dulvy 2005), exploited species may become more aggregated even when the abundance was not changed, i.e., higher *b*, owing to decreased spawning ability, environmental adaptability, or migration (Jenkins et al. 2007, Hsieh et al. 2008, 2010). Furthermore, it is known that fish at different ages have different preferences for food and/or sediment characteristics, resulting in diverse habitat choices (Bohlin 1977, Marshall and Frank 1995, Stoner and Abookire 2002). Such populations with truncated age-structure may thus exhibit higher spatial heterogeneity (more aggregated spatial distribution) (Hsieh et al. 2008, Ciannelli et al. 2013). Consequently, as an aggregation indicator, Taylor's exponent (*b*) may be higher in exploited species (compared with unexploited species with similar life history traits) due to fishing.

In this study, we investigate whether life history traits and fishing influence spatial Taylor's exponent, using the 50-yr long California Cooperative Oceanic Fisheries Investigations (CalCOFI) larval fish survey dataset. Because most larvae were taken in a very early life stage of development, larvae distribution is indicative of the spatial distribution of spawners (Hsieh et al. 2006, 2008). We examined 29 fish species living in the same environment to make fair multi-species comparison in Taylor's exponent *b* in relation to species' life history traits. More importantly, we examined whether fishing drives the *b* vs. life history traits relationship of the exploited fishes to deviate from that of unexploited fishes. We tested the following hypotheses: (1) A species with *r*-selected life history traits has a larger Taylor's exponent (Anderson et al. 1982). In this work, *r*-selected life history traits are roughly defined as smaller body size and earlier maturation age. (2) An exploited species has a higher Taylor's exponent compared to unexploited species with similar life history traits, due to fishing effects.

METHODS

Data

We studied 29 coastal-neritic fish species collected in the CalCOFI larval fish surveys of 66 stations in the southern region of the California Current Ecosystem (Hsieh et al. 2005) from 1950 to 2007 (Appendix S3, Fig. S3). Because the survey frequency after 1984 is quarterly (prior to 1984, surveys were conducted on a monthly basis), we used only quarterly data throughout the sampling period to avoid the statistical bias from different sampling efforts. Among the 29 species, 16 were exploited in California, while 13 were unexploited (Hsieh et al. 2006). The life history data include maximum length, length at 50% maturation, age at 50% maturation, and trophic level for each species (Appendix S4, Table S4) (Hsieh et al. 2006). The CalCOFI fish data are available from the Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, USA (http://coastwatch.pfeg.noaa.gov/erddap/search/index.html?page=1&itemsPerPage=1000&searchFor=calcofi).

Investigation of the spatial mean-variance relationship

We investigated the spatial mean-variance relationship for each species. Note we considered only the data during the spawning period for each species (defined in Hsieh et al. 2006). We used larvae distribution as a proxy of the spatial distribution of spawners (Hsieh et al. 2006, 2008); that is, we explored the spawning distribution pattern of each species. First, for each species, we defined its principal spawning habitat. To do so, we selected the stations with at least three non-zero records in each species' spawning period from 1951 to 2007. The convex hull encompassing these stations was defined as the principal spawning habitat of that species (see example in Appendix S3, Fig. S3). As such, occasional occurrence outside the defined habitat would not be used to estimate the mean-variance relationship. Secondly, we calculated the mean and variance for the fish abundance within this area for each cruise in the spawning period. Thirdly, according to Taylor's power law, $\log(V) = \log(a) + b \times \log(M)$, we obtained the Taylor's exponent, b and intercept a (Taylor 1961), using orthogonal regression of log mean vs. log variance since both M and V contain uncertainty (Appendix S3, Fig. S2). Taylor's exponent and intercept of each species are shown in Appendix S4 (all regressions are highly significant, $P < 0.001$). Then, we carried out 1000 bootstraps to compute b for each species, in order to estimate the 95% confidence interval (with accelerated bias correction) of the bs.

We have also calculated Taylor's exponent separately for each season to account for potential seasonal variation, but found no significant difference among the values from different seasons (repeated measures ANOVA, $P = 0.19$). Therefore, we included the data for all cruises within each species' spawning period in the following analyses.

As pointed out by Engen et al. (2008), b may be positively correlated with mean abundance if the sampling unit is too small. Therefore, we first checked the relationship between b and mean abundance. We found that b shows no significant relationship with mean abundance, in both exploited ($P = 0.59$) and unexploited species ($P = 0.74$), indicating no sampling bias in our estimation of b.

Statistical analysis for the fishing and life history traits effects on Taylor's exponents

We first examined the life history traits effects on Taylor's exponents (b) by linear regression analysis. The regressions were conducted on exploited and unexploited species separately, in order to distinguish the effects from fishing. We note that, when estimating the regression slope of b vs. traits, we need to accommodate uncertainty in calculating b; that is, we considered error propagation. To achieve this, we calculated the bootstrapped slopes of regression using 1000 nonparametric bootstrapped b values from each species and estimated the 95% confidence interval of regression slope with accelerated bias correction.

Then, we used multiple linear regressions to investigate the interaction between life history traits and fishing on Taylor's exponent (in other words, we statistically tested if the regression slopes of traits vs. b were different between the exploited and unexploited groups). We tested four life history traits (T) for each of the models separately in order to investigate the robustness of the pattern. We did not carry out multivariate models that include all traits simultaneously, because the life history traits used here were correlated for the fishes (Hsieh et al. 2006) and tests for these different traits cannot be considered to be independent. Including all traits simultaneously would lead to collinearity issues in statistical analysis. We investigated the following model:

$$b = \beta_0 + \beta_1 T + \beta_2 F + \beta_3 T \times F \quad (1)$$

The exploitation status was included as a dummy variable (F) (i.e., exploited: $F = 1$; unexploited: $F = 0$). The interaction term, $T \times F$, was included in the model in order to examine whether exploitation modulates the effect of life history trait, and to test whether a difference exists between the regression slopes (b vs. T) of exploited and unexploited species. We used standardized coefficients for better comparison of the effects of predictors within and across models (Gelman 2008). Confidence intervals for the regression coefficients were calculated considering the error propagation from estimating b to the multiple linear regressions. Again, we employed the multiple linear regression analysis on each set of bootstrapped bs (1000 times) to examine how the uncertainty in b influences on estimating the coefficients of life history traits and fishing, as explained above. Other possible models which had higher AIC are shown in Appendix S3 and Table S1.

To account for the unbalanced sample size in comparing exploited vs. unexploited group, we also applied propensity score matching to select subsets from each group (exploited and unexploited) for obtaining comparable groups in testing the effect of fishing. The matched groups exhibited consistent results with the original data (Appendix S3, Fig. S2).

Our cross-species comparison is reasonable, because several studies have shown that Taylor's exponent is constant within species under the same condition (e.g., sampling scale, environment, and life stage) (Taylor et al. 1988, Nestel et al. 1995, Elliott 2004). This is in contrast with previous studies that compiled data from different surveys with various sampling methods and environments.

Furthermore, although no environmental variables were directly examined here, environmental effects were implicit in our measurement of Taylor's exponent of fish populations (Hsieh et al. 2006). We assumed that the species captured from the same ecosystem were living in the same environmental condition. Importantly, our main objective is to contrast exploited vs. unexploited species living in the same ecosystem with different life history traits.

Examining variation of Taylor's exponent vs. age structure through time for a single species

To further investigate if fishing alters the mean-variance relationship by affecting the life history traits of species, we selected four exploited species whose age structure data were available and with a sufficiently long time series (>20 yr) (Appendix S5). We used a moving-window approach to examine the cross correlation between the age structure (using mean age and age evenness as indicators) vs. Taylor's exponent for a species through time (Appendix S5).

RESULTS

Life history traits effects on Taylor's exponents

By using multi-species data in the same environment, we found that life history traits affected the exponents of the spatial Taylor's power law for fishes in the Southern California Ecosystem. When analyzing unexploited and exploited species separately: for the unexploited species, Taylor's exponents exhibited a significant negative relationship with maximum length, length at maturation, and trophic level, whereas the exploited species exhibited no significant or a positive relationship between the life history traits and Taylor's exponents (Fig. 1). The significant negative coefficients of life history traits in the results of multiple linear regressions (Fig. 2) also support that Taylor's exponent would decrease with increases in the life history traits (from *r*- to *K*-selected species).

Fishing effects on Taylor's exponents

The negative relationship between life history traits and Taylor's exponent was weaker or even become slightly positive in exploited species (Fig. 1). This pattern was confirmed by the significant interaction term of exploitation status and life history trait ($F \times T$) in the linear model (Fig. 2). The exploited species had higher Taylor's exponents than the unexploited species (after accounting for life history effects) (Fig. 2), particularly for the species having larger body size and larger size at maturation (i.e., toward *K*-selected traits). Our conclusion qualitatively held when the uncertainty of estimating b was incorporated based on bootstrap error propagation analysis (Fig. 2). In addition, the effect of life history traits and fishing still holds true when ecological traits (e.g., demersal vs. pelagic) of species were included into the multiple linear regression models (Appendix S3, Table S2).

In three of four species we examined, the cross-correlation analysis for the moving-window b and age structure indices supported our findings from the multi-species comparisons. The cross-correlation analysis demonstrated that Taylor's exponents of those species were negative correlated with mean age and age evenness (Appendix S5, Table S1 and S2). The negative correlations were found significant in the raw data of Pacific hake (*Merluccius productus*), mackerel (*Scomber japonicas*), and sardine (*Sardinops sagax*), though it was only significant when the moving window was 11 yr for Pacific hake. There was no strong statistical support, however, showing the mean age or age evenness was negatively correlated to Taylor's exponents for bocaccio (*Sebastes paucispinis*).

DISCUSSION

Life history traits effects on Taylor's exponents

Our results provided the first empirical evidence supporting Anderson's demographic model that species with *r*-selected life history traits have a higher b (Figs. 1 and 2) (Anderson et al. 1982). In addition to the theoretical argument made by Anderson et al. (1982), this pattern may arise because species with *K*-selected traits are better at buffering environmental stress than *r*-selected species in many ways. For instance, larger organisms have fewer predators (Pianka 1970), and species with larger size can tolerate wider range of food and lower quality of resources (Gordon and Illius 1996). As a result, species with *K*-selected traits are more likely to spread to different habitat types and to be more evenly distributed in space, thus exhibiting a lower b.

To the best of our knowledge, this is the first systematic comparison of Taylor exponents in relation to life history traits across species living in the same environment. Our finding of empirical relationships between Taylor's exponents vs. life history traits (Fig. 1) indicates that Taylor's power law can be explained by biological mechanisms. This goes against previous studies suggesting that Taylor's power law is subject to artifact and its parameters provide little biological meaningful information (Soberón and Loevinsohn 1987).

Fishing effects on Taylor's exponents

We suggest that the elevated Taylor's exponent b for the exploited species (Fig. 1) may be due to fishing-induced age/size-truncation effects. Age-truncation can alter demographic processes and thus increase species' spatial aggregation, and this can occur without apparent reduction in population mean abundance (Hsieh et al. 2006, Garcia et al. 2012). Note that Taylor's exponents for the exploited species exhibited a less negative relationship (i.e., flatter slope) with life history traits than

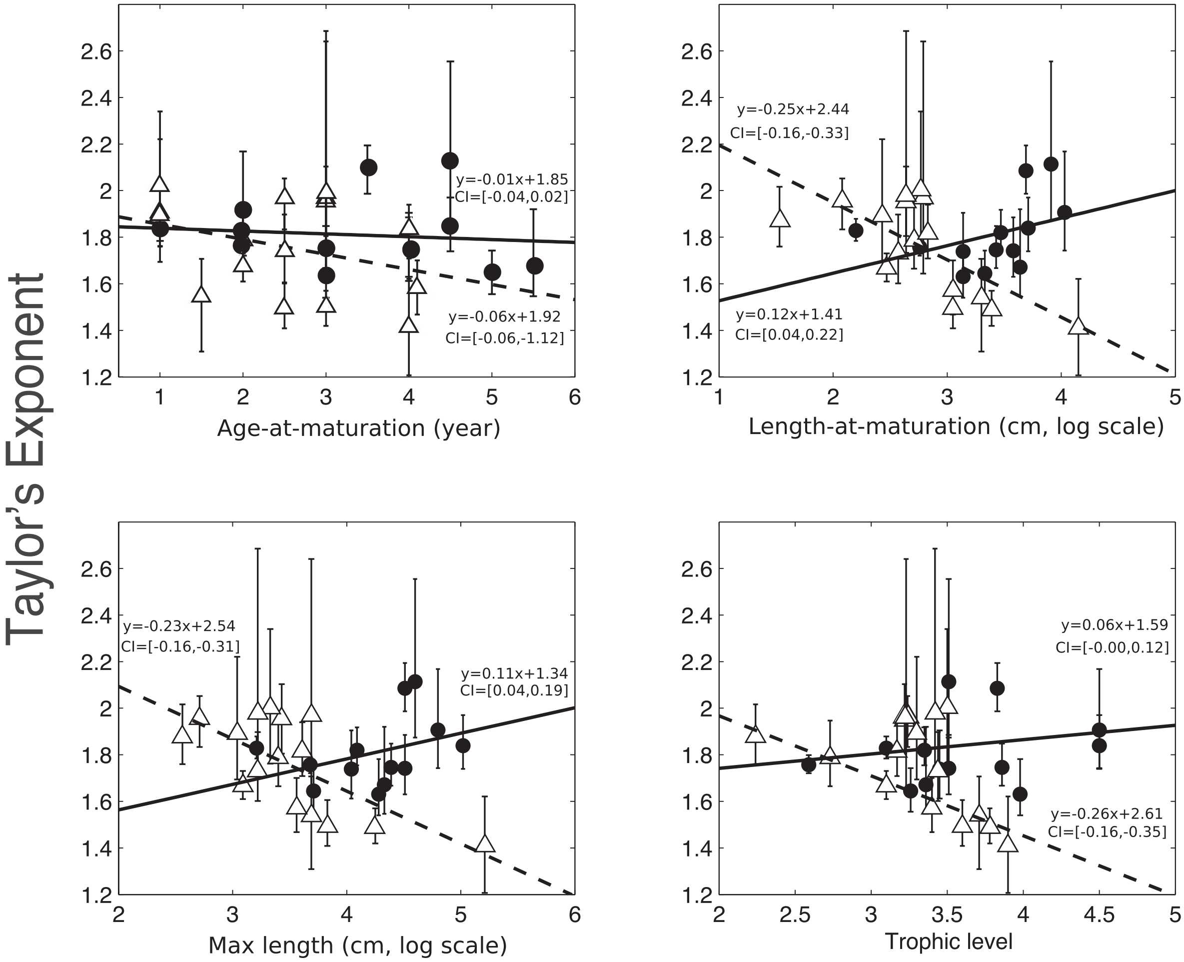

FIG. 1. The regressions of life history traits against Taylor's exponents for exploited and unexploited species. Exploited species (n = 13) are represented by filled circles and unexploited species (n = 16) by open triangles; the vertical error bar represents the 95% confidence interval (with accelerated bias correction) of the Taylor's exponent of each species estimated from nonparametric bootstraps. Results of regression analyses of Taylor's exponents vs. traits for the exploited (solid line) and unexploited (dashed line) species were shown with bootstrapped 95% confidence intervals for the slopes with incorporation of uncertainty in estimating *b*. The horizontal axes represent proxies of continuous spectrum from *r*- to *K*-selected traits. Fishing causes a change from the dashed line to the solid line.

that for the unexploited species, while their intercepts were similar (Figs 1 and 3a). If a species became more clumped because of other causes (e.g., decline in abundance) that were not related with altered life history traits, all exploited species would show a more aggregated pattern. That is, we should observe the intercept of the regression line of traits vs. Taylor's exponents to shift up without changing the slope for the exploited species (Fig. 3b); however, this is not observed in our data (Fig. 1). Therefore, we suggest that fishing may alter the traits or age/size structure of exploited species, making them behave more like *r*-selective species, in terms of higher *b*.

Although we have quantitatively examined life history traits and fishing effects on Taylor's power law, we note some additional concerns that require further study. For example, active aggregation behavior during the spawning season of some species (Coleman et al. 1996) may affect the exponent *b*. Interactions among species may also affect *b*, as a study on the temporal version of Taylor's law suggested, although a laboratory experiment did not support that this prediction can be applied to the spatial Taylor's exponent (Ramsayer et al. 2012). Nevertheless, these factors could also be influenced by fishing (Hollowed et al. 2000, Sala et al. 2001).

The moving window analysis has found negative relationship between Taylor's exponent and age-structure indices for some species (Appendix S5); however, the results were not conclusive. No significant negative correlation has been found for *b* and mean age/age evenness time series for bocaccio, and the significant negative relationship only occurred when the moving window size was 11 yr for Pacific hake. The unclear pattern might be due to the gaps in time series, small sample size for species

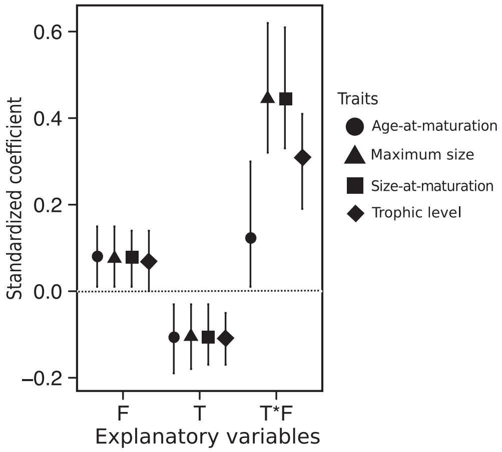

FIG. 2. Results of the multiple linear regressions relating the Taylor's exponent with each life history trait, *T*, and exploitation status (exploited or not), *F*. Standardized coefficients of each variable are presented with 95% confidence intervals (vertical bars) from bootstrap analyses incorporating uncertainty in *b*. All confidence intervals do not cross 0, indicating significant results. Model: $b = \beta_0 + \beta_1 T + \beta_2 F + \beta_3 T \times F$. The AIC for the models are −21.7, −22.6, −10.9, and −14.8 for maximum size, size-at-maturation, age-at-maturation, and trophic level, respectively.

being tested, and/or the changing environmental conditions over time (Perry 1988). In addition, lack of true baseline (data before exploitation) renders the single species analysis difficult.

Linking Taylor's exponent with the occupancy-abundance relationship

Fishing-induced elevation in *b* may have additional negative impacts on the recovery of a population's spatial coverage. To illustrate this issue, we should bear in mind that a positive correlation between abundance and geographic range often exists due to species' density-dependent habitat selection (MacCall 1989, Hsieh et al. 2010). When the population size is small, individuals tend to aggregate in their most suitable habitat; however, when the population size increases, competition intensifies and forces individuals to spread out in space (MacCall 1989). This positive relationship has been formalized into a occupancy-abundance model and coupled with Taylor's power law (He and Gaston 2003):

$$O = 1 - \varphi^{M/(1-\varphi)} \tag{2}$$

where *O* is the occupancy area (spatial coverage), *M* is the fish abundance, and $\varphi = a \times M^{b-1}$. When a population grows (i.e., *M* increases), their area coverage (*O*) also increases. According to Eq. 2, a species with a larger *b* shows a slower increasing rate of *O* when its *M* increases (Appendix S6, Fig. S1). According to our results, species with smaller body size has a larger *b* (Fig. 1); following Eq. 2, these small species will have a smaller expanding rate of *O* in respect to *M*. Interestingly, this idea can partially be supported empirically by Swain and Wade's study (Swain and Wade 1993), in which they found the distribution range expands more slowly for young fishes (presumably with smaller size) than for older fishes (presumably with larger size) when the population size increases. Moreover, in the 32-yr trawl survey data from Scotian Shelf and Bay of Fundy, Fisher and Frank (2004) show that exploited species suffering size-truncation expanded their distribution less with increasing abundance compared to their response in earlier years when their size structure was healthy. Thus, we argue that species with altered life history traits (juvenescence due to age-truncation) may also have a slower occupancy-expanding rate in respect to increasing abundance. In other words, when the abundance of an age-truncated population recovers from being overfished, their occupancy-expanding rate will be slower compared with the population whose age structure has not been damaged. Thus, fishing likely causes double jeopardy in the spatial distribution of exploited stocks: greater spatial heterogeneity and slowed spatial recovery rate.

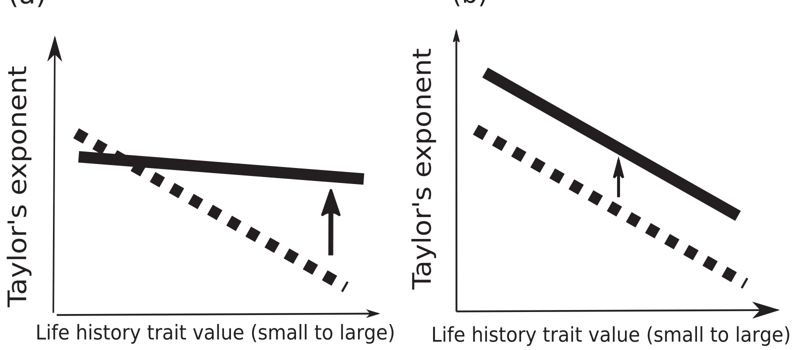

FIG. 3. Schematic demonstrating two possible scenarios of fishing affecting Taylor's exponents. (a) The slope of life history traits against *b* becomes flatter, when the species with larger traits behave more similarly as the species with smaller traits. This was observed in our Southern California data. (b) Taylor's exponents of all species shift upward, if the changes in spatial distribution are not related to life history traits.

Linking Taylor's exponent with the size-abundance relationship

The correlation between life history traits and Taylor's exponents found in our study suggests that the slope of linear logarithmic variance-mass relationship of *K*-selected species may be less negative (i.e., shallower) compared to *r*-selected species. The variance-mass allometry illustrates the relationship between spatial variance (V) of population density and average individual biomass (B) within a single species (Cohen et al. 2012):

$$\log(V)=[a+\log(u^b)]+b\times v\times\log(B) \qquad (3)$$

where a and $\log(u)$ is the intercept of Taylor's power law and single species density-mass allometry, respectively, and v is the exponent of density-mass allometry (v is typically <0). Here, the population density used by Cohen et al. (2012) is equivalent to population abundance as commonly used in the literature discussing Taylor's power law. This model shows that when the average biomass decreases in a species, V will increase through increasing mean abundance (according to density-mass allometry), which is additional to the effects of changes in b. Because our study indicates that *K*-selected species have a lower b, the negative slope $b \times v$ of Eq. 3 is supposed to be weaker for *K*-selected species, assuming v is constant across species. That is, spatial variability may be similar among different size-classes of a *K*-selected species, whereas for an *r*-selected species, the smaller size-class exhibits greater spatial variability than the larger size-class. This hypothesis needs further research, and in particular, whether v is invariant across species.

It is worth noting that, Cohen's variance-mass model implicitly assumes that changes in average biomass of a species do not affect b. In contrast, our analysis suggests that a decrease in body mass (due to size truncation) likely elevates b. Here, we propose a modified Eq. 3 to incorporate b as a function of body size (Appendix S7). With reasonable biological parameter space, we show that the negative relationship between variance and body size still exists (Appendix S7, Fig. S1). That is, even accounting for the effect of changing body size on b, spatial variance will still increase with decreasing body size. However, it should be a nonlinear rather than a linear relationship as Cohen et al. (2012) proposed (Appendix S7, Fig. S1).

Following the variance-mass model (Cohen et al. 2012), one might suspect that fishing may elevate the spatial variance simply by decreasing body size of a species, as suggested in Eq. 3. Nevertheless, the formation of Eq. 3 depends on the critical assumption of a fixed negative relationship between mean abundance vs. body size (Peters and Wassenberg 1983). For species suffering from fishing impacts, however, a reduction in body size does not necessarily imply an increase in mean abundance; that is, fishing causes the exploited population to violate the size-abundance relationship within a population. In such cases, the variance-mass model cannot explain the elevated spatial variance caused by fishing. Alternatively, the elevated spatial variance can be simply explained by Taylor's power law ($V = aM^b$). While fishing-induced age truncation increases b, the increase in V does not require reduction in mean abundance. This indeed likely happens in the incipient stage of overfishing (Swain and Sinclair 1994, Hsieh et al. 2008). As such, increasing spatial variance can be a warning signal for early stages of overfishing. Nevertheless, with intensification of fishing pressure, while b may increase, M likely decreases; under this condition, highlighting that the change in V is context dependent.

Implications for fisheries

Elevated spatial heterogeneity may make exploited species more vulnerable to environmental changes (Swain and Wade 1993, Hsieh et al. 2008), because a more homogeneous spatial distribution is a bet-hedging strategy for populations to dilute the risk of extinction (Berkeley et al. 2004, Hsieh et al. 2010, Ciannelli et al. 2013). In addition to inducing spatial heterogeneity, age truncation leads to many other undesirable consequences; for example, reduced maternal effects and larval survival (Hislop 1988, Berkeley et al. 2004), increased fluctuation in population abundance (Hsieh et al. 2006, Rouyer et al. 2012), elevated intra-specific competition (Shackell et al. 2012), and reduced dispersal ability (Shackell et al. 2012). From the viewpoint of maintaining resilient fish populations, it is important to note that populations suffering structure damages (either spatial or age/size structure) will consequently face more severe challenges to survival. Therefore, a sound fishery management strategy will be concerned with changes to the age and spatial structure of exploited fishes (Berkeley et al. 2004, Hsieh et al. 2006, 2010, Garcia et al. 2012, Ciannelli et al. 2013).

Acknowledgments

We thank Lindsay Aylesworth, Ford Ballantyne, Ethan Deyle, Chien-Chung Hsu, Takeshi Miki, Charles Perretti, Sheng-Feng Shen, Cheng-Han Tsai, Hui-Yu Wang, and Hao Ye for discussion and comments. We also thank the California Cooperative Oceanic Fisheries Investigations and Southwest Fisheries Science Center for the use of the data. This study is supported by the National Center for Theoretical Sciences, Foundation for the Advancement of Outstanding Scholarship, and Ministry of Science and Technology of Taiwan to CHH and KAKENHI (15K07219) from the Japan Society for the Promotion of Science to AY.

Literature Cited

Anderson, R. M., D. M. Gordon, M. J. Crawley, and M. P. Hassell. 1982. Variability in the abundance of animal and plant species. Nature 296:245–248.

Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29:23–32.

Bohlin, T. 1977. Habitat selection and intercohort competition of juvenile sea-trout *Salmo trutta*. Oikos 29:112–117.

Ciannelli, L., J. D. Fisher, M. Skern-Mauritzen, M. E. Hunsicker, M. Hidalgo, K. T. Frank, and K. M. Bailey. 2013. Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. Marine Ecology Progress Series 480:227–243.

Cohen, J. E., M. Xu, and W. S. F. Schuster. 2012. Allometric scaling of population variance with mean body size is predicted from Taylor's law and density-mass allometry. Proceedings of the National Academy of Sciences of the United States of America 109:15829–15834.

Coleman, F. C., C. C. Koenig, and L. A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Environmental Biology of Fishes 47:129–141.

Downing, J. A. 1986. Spatial heterogeneity: evolved behaviour or mathematical artefact? Nature 323:255–257.

Eisler, Z., I. Bartos, and J. Kertesz. 2008. Fluctuation scaling in complex systems: Taylor's law and beyond. Advances in Physics 57:89–142.

Elliott, J. M. 2004. Contrasting dynamics in two subpopulations of a leech metapopulation over 25 year-classes in a small stream. Journal of Animal Ecology 73:272–282.

Engen, S., R. Lande, and B.-E. Saether. 2008. A general model for analyzing Taylor's spatial scaling laws. Ecology 89:2612–2622.

Fisher, J. A. D., and K. T. Frank. 2004. Abundance-distribution relationships and conservation of exploited marine fishes. Marine Ecology Progress Series 279:201–213.

Garcia, S. M., et al. 2012. Reconsidering the consequences of selective fisheries. Science 335:1045–1047.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Gordon, I. J., and A. W. Illius. 1996. The nutritional ecology of African ruminants: a reinterpretation. Journal of Animal Ecology 65:18–28.

Hanski, I. 1980. Spatial patterns and movements in coprophagous beetles. Oikos 34:293–310.

Hanski, I. 1982. On patterns of temporal and spatial variation in animal populations. Annales Zoologici Fennici 19:21–37.

He, F., and K. J. Gaston. 2003. Occupancy, spatial variance, and the abundance of species. The American Naturalist 162:366–375.

Hislop, J. R. G. 1988. The influence of maternal length and age on the size and weight of the eggs and the relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. Journal of Fish Biology 32:923–930.

Hollowed, A., N. Bax, and R. Beamish. 2000. Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES Journal of Marine Science: Journal du Conseil 57:707–719.

Hsieh, C., C. Reiss, W. Watson, M. J. Allen, J. R. Hunter, R. N. Lea, R. H. Rosenblatt, P. E. Smith, and G. Sugihara. 2005. A comparison of long-term trends and variability in populations of larvae of exploited and unexploited fishes in the Southern California region: a community approach. Progress in Oceanography 67:160–185.

Hsieh, C. H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006. Fishing elevates variability in the abundance of exploited species. Nature 443:859–862.

Hsieh, C., C. S. Reiss, R. P. Hewitt, and G. Sugihara. 2008. Spatial analysis shows that fishing enhances the climatic sensitivity of marine fishes. Canadian Journal of Fisheries and Aquatic Sciences 65:947–961.

Hsieh, C. H., A. Yamauchi, T. Nakazawa, and W. F. Wang. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. Aquatic Sciences 72:165–178.

Iwao, S. 1968. A new regression method for analyzing the aggregation pattern of animal populations. Researches on Population Ecology 10:1–20.

Jenkins, D. G., et al. 2007. Does size matter for dispersal distance? Global Ecology and Biogeography 16:415–425.

Jennings, S., and N. Dulvy. 2005. Reference points and reference directions for size-based indicators of community structure. ICES Journal of Marine Science 62:397–404.

Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. Advances in Marine Biology. 34: 201–352.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–350.

Kendal, W. S. 2004. Taylor's ecological power law as a consequence of scale invariant exponential dispersion models. Ecological Complexity 1:193–209.

Kilpatrick, A. M., and A. R. Ives. 2003. Species interactions can explain Taylor's power law for ecological time series. Nature 422:65–68.

MacCall, A. D. 1989. Dynamic geography of marine fish populations. Books in recruitment fishery oceanography (USA), Washington Sea Grant Program.

Marshall, C. T., and K. T. Frank. 1995. Density-dependent habitat selection by juvenile haddock (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 52:1007–1017.

Murawski, S. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. ICES Journal of Marine Science 58:1002–1014.

Nestel, D., H. Cohen, N. Saphir, M. Klein, and Z. Mendel. 1995. Spatial distribution of scale insects: comparative study using Taylor's power law. Envrironmental Entomology 24:506–512.

Opdal, A. F., and C. Jørgensen. 2015. Long-term change in a behavioural trait: truncated spawning distribution and demography in Northeast Arctic cod. Global Change Biology 21:1521–1530.

Perry, J. N. 1988. Some models for spatial variability of animal species. Oikos 51:124–130.

Peters, R. H., and K. Wassenberg. 1983. The effect of body size on animal abundance. Oecologia 60:89–96.

Pianka, E. R. 1970. On *r*- and *K*-selection. The American Naturalist 104:592.

Ramsayer, J., S. Fellous, J. E. Cohen, and M. E. Hochberg. 2012. Taylor's Law holds in experimental bacterial populations but competition does not influence the slope. Biology Letters 8:316–319.

Rouyer, T., A. Sadykov, J. Ohlberger, and N. C. Stenseth. 2012. Does increasing mortality change the response of fish populations to environmental fluctuations? Ecology Letters 15:658–665.

Sala, E., E. Ballesteros, and R. Starr. 2001. Rapid decline of Nassau grouper spawning aggregations in Belize: fishery management and conservation needs. Fisheries 26:23–30.

Shackell, N. L., K. T. Frank, and D. W. Brickman. 2005. Range contraction may not always predict core areas: an example from marine fish. Ecological Applications 15:1440–1449.

Shackell, N. L., J. A. D. Fisher, K. T. Frank, and P. Lawton. 2012. Spatial scale of similarity as an indicator of metacommunity stability in exploited marine systems. Ecological Applications 22:336–348.

Soberón, J., and M. Loevinsohn. 1987. Patterns of variations in the numbers of animal populations and the biological foundations of Taylor's law of the mean. Oikos 48:249–252.

Stoner, A. W., and A. A. Abookire. 2002. Sediment preferences and size-specific distribution of young-of-the-year Pacific halibut in an Alaska nursery. Journal of Fish Biology 61:540–559.

Swain, D. P., and A. F. Sinclair. 1994. Fish distribution and catchability: What is the appropriate measure of distribution? Canadian Journal of Fisheries and Aquatic Sciences 51: 1046–1054.

Swain, D. P., and E. J. Wade. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 50:725–733.

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature 189:732–735.

Taylor, R. A. J. 1981. The behavioural basis of redistribution I. The delta-model concept. Journal of Animal Ecology 50:573–586.

Taylor, L. R. 1986. Synoptic dynamics, migration, and the Rothamsted insect survey. Journal of Animal Ecology 55:1–38.

Taylor, L. R., and R. A. Taylor. 1977. Aggregation, migration and population mechanics. Nature 265:415–421.

Taylor, L. R., R. A. J. Taylor, I. P. Woiwod, and J. N. Perry. 1983. Behavioral dynamics. Nature 303:801–804.

Taylor, L. R., J. N. Perry, I. P. Woiwod, and R. A. J. Taylor. 1988. Specificity of the spatial power-law exponent in ecology and agriculture. Nature 332:721–722.

Tittensor, D. P., F. Micheli, M. Nyström, and B. Worm. 2007. Human impacts on the species-area relationship in reef fish assemblages. Ecology Letters 10:760–772.

Yamamura, K. 2000. Colony expansion model for describing the spatial distribution of populations. Population Ecology 42:161–169.

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