

國立臺灣大學理學院海洋研究所

博士論文

Institute of Oceanography

College of Science

National Taiwan University

Doctoral Dissertation



氣候與漁撈效應對魚群空間分布與體長結構之影響

Climate and fishing effects on the distribution and size
structure of exploited fish populations

杜貞儀

Chen-Yi Tu

指導教授：謝志豪 博士

Advisor: Chih-hao Hsieh, Ph.D.

中華民國 107 年 6 月

June, 2018

致謝

在海洋所待了比我預期還要長的時間，這大概是海洋界變化最劇烈的十年：盼望許久總算下水的新船、還有成立海洋事務專責機關。而我自己的求學階段，也到了該告一段落的時候。最要感謝的，莫過於指導教授謝志豪老師，一直以來都願意放手讓我去作，實在看不下去才出手。以及同樣在老師剛回來的第一年進實驗室的俊偉和珮綺，是分屬不同學程、同在 403 研究室努力的夥伴，也在今年一起畢業了。

長期以來我不斷打擾同所的三木健老師和王慧瑜老師，非常感謝他們這些年來在理論生態學、漁業生物學、資源管理以及寫作的指點；以及曾於日本海水產研究所任職，現於中國海洋大學任教的田永軍博士，讓我有機會參與日本海底拖網漁業研究，這也構成第二章的主要內容。其他三位口試委員，丘臺生老師、黃向文老師以及黃文彬老師，都分別對論文初稿的缺失和不足提出許多寶貴建議。

實驗室的助理、學長姐和學弟妹在這些日子以來幫了許多忙。我收集整理了第三章分析用的資料，但初步分析出自匡庭；第四章的北海底拖調查資料分析，政喻的碩士論文也用了同一份資料的其中一部分，我們對資料結構和分析結果有過不少討論。另外還要感謝佑青多年來在行政上的協助，曉沛學姊的時相討論，以及 422 研究室的梵絃、怡君、小咪、Ester、思綸、小胖、403 研究室的政翰、柏如、宜芳、宗佑、琬萱、穎婕、沂潔。並且要特別感謝遠在日本福岡的九州大學、同樣在研究上努力的吳馥宇（水母）學姊，時常以各種補給物資互相支援。以及滔滔夥伴庭君和依璇多年的支持和合作，使我在博士班後半的日子裡，得到許多難得可貴的經驗。

最後，我要感謝我的父母和弟弟，他們總是容忍我常常不在家、截止日期前的健忘、丟三落四、左耳進右耳出，讓我得以任性的做著自己想做的事。

摘要



氣候與漁撈活動對於魚的影響是近年研究的焦點。雖然全球尺度的統合分析顯示，對溫度升高的反應有著分布往極區移動的趨勢，然而不同物種間的反應仍有許多變異。而漁撈族群的體長結構同時受氣候與捕撈行為影響，但兩者究竟各佔多少比例，亦屬未知。更重要的是，魚群分布與體長結構間可能有相互關係，這是由於魚類隨個體發育而有棲地移轉的現象。因此，為了更全面的了解氣候變遷以及捕撈活動對魚群的影響，需要能同時涵蓋分布與體長結構的分析框架。

本研究中，我採用三種研究角度來切入氣候與漁撈活動對魚群分布與體長結構的影響。在第一章中將簡要介紹現象以及研究背景，而第二章則以日本海底拖漁業為例，研究不同生活史特徵魚群的分布與豐度，如何反應年間與年代際間的環境變動，結果顯示暖化對於日本海內體型較大的物種有負面影響。第三章關注魚群體長結構，以變異分離法來拆解氣候與漁撈的協同效應對體長的影響。結果顯示漁撈能解釋絕大多數魚群的體長變異，而受到漁撈壓力波動較大的魚群，其體長結構對溫度的反應也更大。這顯示，漁撈活動可能會讓魚群對環境變動更為敏感。第四章則檢視魚群於不同生活史階段的空間分布變化如何受氣候因素（如溫度）影響。結果發現，成魚階段因溫度變化而分布移動較稚魚階段快，而成魚與稚魚往同方向移動的物種，通常其成魚與稚魚階段的空間分布有較大重疊，可能表示該物種的成魚與稚魚的棲位相近，因此對溫度變化有類似的反應。

總結本研究的結果，空間分布與體長結構確實在魚群對氣候以及捕撈活動的反應有一定關聯，因此必須同時檢視兩者才能對魚群的反應有較全面的了解。這些結果應能對氣候變遷下的生態系漁業管理提供有助益的訊息。

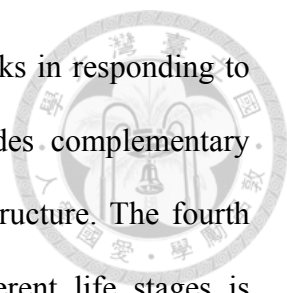
關鍵字：氣候變遷、空間分布、體長結構、漁撈效應、生活史特徵

Abstract



Climate and fishing effect on the exploited populations is an important research topic. Although the global meta-analysis indicates a general pattern of poleward distributional shifts in response to rising temperatures, the specific responses have varied among species. The size structure of exploited populations is simultaneously affected by both climate and fishing, but what determines the relative contribution of the two remains unknown. More importantly, the dynamics of distribution and size structure of exploited populations may be interwoven because of the ontogenetic habitat shift of fish. Therefore, a framework to incorporate these two demographic aspects is urgently needed to gain the whole picture for understanding exploitation population's response to climate and fishing effect.

In my thesis, I use three different approaches to investigate climate and fishing effects on the distribution and size structure of the exploited fish populations. The first chapter describes the general phenomenon and set the research scene. The second chapter describes how fish with different life history traits respond differently at interannual and decadal scales of climate change, using the bottom trawl fishery in the Japan Sea as an example. The results indicate that the distributional changes of species in response to decadal climate variability are best explained by asymptotic length, which indicates that warming has greater negative effects on larger fishes in the Japan Sea. The third chapter focuses on the size structure of exploited fish population, with emphasis on applying variation partitioning to disentangle the synergetic effect of climate and fishing. The results show that fishing has the most prominent effect on the size structure of exploited stocks. In addition, the fish stocks experienced higher variability in fishing displayed a greater response to temperature in their size structure,



suggesting that fishing may elevate the sensitivity of exploited stocks in responding to environmental effects. The variation partitioning approach provides complementary information to univariate size-based indicators in analyzing size structure. The fourth chapter examines how the change in spatial distribution at different life stages is affected by climate change in exploited fish populations. I found adult stage generally move faster as response to temperature change than juvenile stages. Also, the species whose adults and juveniles move toward the same direction are more likely to have more overlapping in distribution among the two life stages, indicating that adults and juveniles of given species occupying similar niches are more likely to have similar response.

Overall, this study concludes that size structure and distribution are related in the response of the exploited population to climate and fishing effects. It would be necessary to examine both for a better understanding the responses of exploited populations. These results may provide useful information for ecosystem-based fisheries management in light of climate change.

Keywords: climate change, spatial distribution, size structure, fishing effect, life history traits

Table of Content



Chapter 1 Introduction	1
Chapter 2 Climate effect on species distribution: case study in Japan Sea	6
Introduction	6
Material and methods	7
Result	12
Discussion	13
Conclusion	16
Chapter 3 Fishing and temperature effects on the size structure of exploited fish stocks.....	25
Introduction	25
Material and methods	30
Results and Discussion	35
Conclusion	37
Chapter 4 Stage dependency in species distribution as response to climate change	47
Introduction	47
Material and method	49
Result	51
Discussion	52
Conclusion	54
Chapter 5 Conclusion	62
References.....	64
Appendices	75
I. Fishing effort of Japan Sea single trawl fisheries, 1972-2002	75
II. Data source, map in variation partitioning analysis.....	77

List of Figures

- Figure 2-1 An example map in 1972 showing the spatial distribution of CPUE (kg/haul) for Pacific cod (*Gadus macrocephalus*) calculated from the Japan Sea Offshore Bottom Trawl dataset during spawning season.22
- Figure 2-2 Annual anomalies time series of the environmental variables. The vertical dash lines indicate the duration of cold (1977/78-1988/89) period based on PDO and NPI (Hare and Mantua, 2002). The trend lines (dash line) and correlation coefficients are shown in the time series when a significant long-term trend ($P<0.05$) exists.23
- Figure 2-3 Summaries of the movement from the cold to the warm period ($\Delta domain$). The y-axis denotes the unit of velocity for the arrow vectors in the vertical direction, with $1^\circ \approx 111.2$ km. The significant distributional shifts passed the randomization test (see text) were shown in black line.24
- Figure 3-1 Boxplot shows the variation of size structure explained by the fishing, temperature, and interactive effect. Results of ANOVA indicate that the fraction of variation explained by fishing is significantly higher than the temperature ($P=0.019$) and interactive effect ($P<0.001$), but fraction of variation explained by temperature is not significantly different from interaction ($P=0.344$).42
- Figure 3-2 Boxplot shows the variation of size structure explained by the fishing, temperature, and interactive effect grouped by areas. Fraction of variation explained by fishing is significantly different from both temperature ($P=0.005$) and interaction ($P<0.001$) in West US.43
- Figure 3-3 Boxplot shows the variation of size structure explained by the fishing, temperature, and interactive effect grouped by the habitat of species. Particularly, fraction of variation explained by fishing is significantly different from both temperature ($P=0.0014$) and interaction ($P<0.001$) for demersal species.44
- Figure 3-4 Explained variation by temperature in relation to the mean and CV of mortality ratio or temperature. The line is the best-fitted regression line based on the linear mixed effect model with each fishing/temperature index as fixed effect and habitat as random effect. The solid line indicates the significant result (d).45

Figure 3-5 Comparison of P values of (a) fishing and (b) temperature effect estimated from the variation partitioning approach versus univariate SBIs. The diagonal line represents the 1:1 line. Results of binomial test indicate that variation partitioning is more efficient in rejecting the null hypothesis (p -value is smaller) than the univariate SBIs in detecting temperature effects (Probability of success=0.63, $P=0.003$) and marginally in fishing effects (Probability of success=0.56, $P=0.10$)

.....46

Figure 4-1 An example map showing of centroid changes through time (1991Q1-2014Q3) for adult (red) and juvenile (blue) stages using Atlantic cod. ..57

Figure 4-2 Box plot summarizing moving speed (absolute value of b_1 in latitude $\sim b_1 * \text{temperature} + b_0$) as response of temperature for the adult and juvenile stages. Only the species found a significant relationship with temperature were included. The Mann-Whitney U test indicates significant difference ($P=0.036$) between two stages.58

Figure 4-3 Box plot of summarizing moving speed (absolute value of b_1 in latitude $\sim b_1 * \text{temperature} + b_0$) as response of temperature for the different catch type and biogeographic groups. Only the species at given stage found a significant relationship with temperature were included. The Mann-Whitney U test indicates no significant difference between two catch types in adult stage (a) and biogeographic groups (b).59

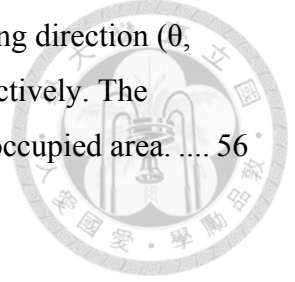
Figure 4-4 Feather plots for each species show the how moving direction of centroid varies through time. The red arrows denote adult stage, while the blue arrows denote juvenile stage.60

Figure 4-5 Relationship between ratio of overlapped area and correlation of moving direction between adult and juvenile stages. Species with high proportion of overlapped area are more likely to move in the same direction ($R^2=0.46$).61

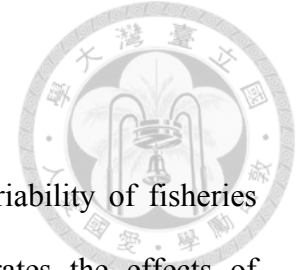
List of Tables

Table 2-1 Life history traits (age at maturation A_m and asymptotic length L_{inf}) and geographical affinity of the target species in the Japan Sea single-trawl fisheries (Tian <i>et al.</i> , 2011). The asymptotic lengths are mostly compiled from Ogata (1980) with some exceptions (see note).....	17
Table 2-2 Correlation matrix of environmental variables	18
Table 2-3 Results of regression analyses investigating the effects of interannual changes in environmental variables on median latitude and longitude and boundary (minimum latitude/ longitude for cold water species and maximum latitude/ longitude for warm water species, respectively). The decadal changes between two domains (cold-warm) are also shown here.	19
Table 2-4 Results of logistic regression ($\text{logit}(y) \sim \beta_0 + \beta_1 x$) investigating effects of geographical affinity and life history traits (x) on species' response (y) to climate variations at interannual (latitude and longitude are shown separately in (a) Distribution) and decadal scale. The AIC intercept (β_0), and regression coefficient (β_1) values with significance in the Rao's score test ($P < 0.05$) are in bold font. ..	20
Table 2-5 Average abundance (kg/haul) in the cold and warm period and results of regression analyses linking the environmental variables with abundances.....	21
Table 3-1 Data regions and periods for the 28 commercial stocks. The abbreviation in the bracket indicates the location of stock: AI, Aleutian Islands; EBS, East Bering Sea; GOA, Gulf of Alaska.	39
Table 3-2 Results of variation partitioning showing the relative contribution of fishing, temperature, and their interactive effect to the total variation (in term of adjusted R^2 value) for each of the 28 stocks	40
Table 3-3 Results of univariate linear regression analysis on % variation explained by fishing or temperature versus each life history trait, mean mortality ratio (meanF_M), CV of mortality ratio (cvF_M)), mean temperature (meanTemp), and CV of temperature (cvTemp)	41
Table 4-1 Species used in analysis. The trophic level and biogeography is from Yang (1982) and the juvenile length is obtain from ICES FishMap.....	55

Table 4-2 Regression coefficient on latitudinal shift of centroid to temperature in two stages (b_{adult} and b_{juvenile}) and the correlation coefficient of moving direction (θ , angle) between adult and juvenile stages for each species, respectively. The overlap ratio is the ratio of overlapped area divided by the full-occupied area. 56



Chapter 1 Introduction



Climate and fishing are two major driving forces for the variability of fisheries resources (Perry et al. 2005). Accumulating evidence demonstrates the effects of climate on the spatial distribution, abundance, size structure and phenology of populations (Stenseth et al. 2002, Parmesan and Yohe 2003, Ottersen et al. 2010, Walther 2010, Doney et al. 2012, Cheung et al. 2013b). Interestingly, recent meta-analyses indicated that the rates of the observed shifts in the distribution and phenology of marine species are comparable to or greater than those of terrestrial systems, which may be due to an area of high velocity (movement of isotherm over year) extending across broader regions in the ocean than land (Burrows et al. 2011) or the greater dispersal facilitated by circulation in the marine environment (Poloczanska et al. 2013).

For fishes, climate effect on spatial distributions of fishes is well documented (Perry et al. 2005, Dulvy et al. 2008, Hsieh et al. 2008a, Mueter and Litzow 2008, Hsieh et al. 2009b, Nye et al. 2009, Engelhard et al. 2011, Keller et al. 2013, Pinsky et al. 2013, Bell et al. 2015). These changes of spatial distribution are not random, as the abundance-occupancy relationship described by meta-population theory and the density-dependent habitat selection (DDHS). Based on DDHS, species may occupy the distinctive patches or optimal habitat first (MacCall 1990). Hence, climate-induced reorganization of communities may have ecosystem consequences that could cause changes in fisheries production (MacNeil et al. 2010, Hollowed et al. 2013). Such relationship between abundance and spatial distribution also imply that change in spatial distribution may further impact the population abundance and eventually persistence

(Hsieh et al. 2010a).

In addition to distribution, climate effects on size structure of population (Daufresne et al. 2009a) also receive much attention. Warming can cause size structure shrink toward smaller size (Cheung et al. 2013a). This may be due to the metabolism at individual levels (Gillooly et al. 2001a), which increases growth rate and causes earlier maturation at population level (Neuheimer and Grønkjær 2012). Besides metabolic mechanism, warming may indirectly affect the population structure through the recruitment process that increases the proportion of juvenile in the whole populations (Sundby 2000).

Furthermore, the responses of species to climate variability can vary greatly (Chen et al. 2011), even within the same ecosystem (Hsieh et al. 2005, Perry et al. 2005, Tian et al. 2008, Hsieh et al. 2009a, Nye et al. 2009). Some studies link the species response with life history traits. In the North Sea study, species with a short life span and small body size were more likely to shift poleward as a result of warming (Perry et al. 2005). However, some studies suggest that the distributional response depends on the biogeography of each species; for example, the southern and northern fish stocks of the continental shelf of Northeast U.S. have exhibited contrasting responses to recent warming (Nye et al. 2009).

However, climate and fishing effect can interweave with each other that become difficult to separate. Some evidences suggest fishing may increase the sensitivity of exploited populations to climate variability (Hsieh et al. 2006a). Fishing is a process of size-selective removal of larger individuals, which may truncates the population structure toward smaller size. There are three consequences at the population levels that may due to fishing: change of the size structure that reduces the buffering capacity of the population (Hsieh et al. 2006a); reduced spatial homogeneity in exploited species

(Hsieh et al. 2008b) or removal of spatial-subunits that results in increasing overall population sensitivity to climate fluctuation at interannual to multi-decadal scales (Ottersen et al. 2006); and alteration of life-history traits (de Roos et al. 2006). Although a growing number of studies have tried to investigate the synergetic effect of climate and fishing, the relative contribution of changing species spatial distribution and size structure remains poorly understood.

It is also known that species spatial distribution and size structure are not two independent characteristics. Individuals at different life stages may migrate into different habitats, or part of the habitats, is often referred as ontogenetic habitat migration. This provides multiple possible ways for climate to affect individual species as they grow and mature (Rijnsdorp et al. 2009, Petitgas et al. 2013). Although previous studies suggest ontogenetic migration of marine species is common (Wilbur 1980, Gibson et al. 2002, Kotwicki et al. 2005, Hoff 2008), many of the studies focused on specific habitat (Dahlgren and Eggleston 2000) and only limited studies focused on exploited species (Barbeaux and Hollowed 2018).

To investigate climate and fishing effects on the distribution and size structure of the exploited fish populations, a more complex, thorough approach is necessary. In this thesis, I try to investigate the effects from three different approaches: climate effect on spatial distribution of species with different life history traits; climate and fishing effects on size structure of exploited species; and climate effect on the distribution of exploited and unexploited species at different life stages. The second chapter describes how fish with different life history traits respond at interannual and decadal scales of climate change, using the bottom trawl fishery in the Japan Sea as a case study. The results indicate that the distributional changes of species in response to decadal climate variability are best explained by asymptotic length, indicating that warming has greater

negative effects on larger fishes in the Japan Sea.

The third chapter focuses on the size structure of exploited fish population, with emphasis on applying variation partitioning to disentangle the synergetic effect of climate and fishing. By applying the variation partitioning to the size structure data, the results show that fishing has the most prominent effect on the size structure of exploited stocks. In addition, the fish stocks experienced higher variability in fishing have a greater response to temperature in their size structure. This may suggest that fishing may elevate the sensitivity of exploited stocks in responding to environmental effects. This variation partitioning approach, which provides complementary information to univariate SBIs in analyzing size structure, may provide insight for ecosystem-based fisheries management

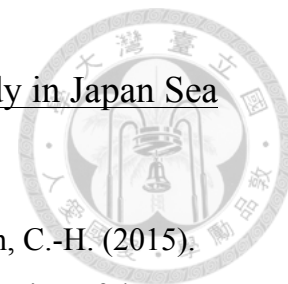
In the fourth chapter, I examine how the change in species distribution at different life stages is affected by climate change in exploited fish populations. I used International Bottom Trawl Survey at North Sea as an example and divided each species into two subgroups based on their size: juvenile and adult. I found adult stage generally move faster as response to temperature change than juvenile stages. Also, the species whose adults and juveniles move toward the same direction are more likely to have more overlapping in distribution among the two life stages, indicating that adults and juveniles of given species occupying similar niches are more likely to have similar response. The results may have further implications for studies on population level responses, namely that ontogenetic differences should be taken into consideration when assessing the impacts.

Overall, this study concludes that size structure and distribution are both important for understanding the responses of exploited populations to climate and fishing effects. These results may provide useful information for ecosystem-based fisheries

management in light of climate change.



Chapter 2 Climate effect on species distribution: case study in Japan Sea



(This chapter is originally published as: Tu, C.-Y., Tian, Y., & Hsieh, C.-H. (2015). Effects of climate on temporal variation in the abundance and distribution of the demersal fish assemblage in the Tsushima Warm Current region of the Japan Sea. *Fisheries Oceanography*, 24(2), 177–189. <http://doi.org/10.1111/fog.12101>.)

Introduction

To demonstrate the climate effect on species distributional response, I looked into the demersal fish assemblage of the Tsushima current region of Japan Sea. The data we analyzed comprised the catches and efforts of the Japanese single-trawling fishery, which were derived from the Japan Sea Offshore Bottom Trawl fisheries dataset (JSOBT). Because of the wide-coverage and the target species vary in their geographical affinities and life history traits (Table 2-1), the single trawling data may provide a unique opportunity to examine how the biological characteristics of species influence their response to climate variability.

Previous studies of the ecosystem response to climate variability in the Japan Sea found possible relationships between climate and biological populations (see the summary in Chiba et al. (2008)). The Japan Sea is a semi-enclosed sea, thus the seasonal and interannual variations in its hydrography are presumably affected by basin-scale climatological events (Naganuma 2000, Watanabe et al. 2003). The 1976/77 shift in the plankton biomass in the Japan Sea ecosystem coincided with the Pacific Decadal Oscillation (Chiba and Saino 2002, Chiba et al. 2005). This change to a lower trophic level might have been transferred to upper trophic levels because the

abundances of fishes also exhibited similar decadal variability. A more recent study found that different pattern of abundance fluctuated between the cold- and warm-water species during the regime shift in the late 1980s (Tian et al. 2011), which indicates the importance of the geographical affinity of fishes in response to environmental forcing. However, most of these studies only focused on changes in abundance. Thus, the climate-driven changes in the geographical distributions of the biological population at interannual and decadal scales are unclear. The geographical distributions of some demersal species appear to reflect the decadal variability in climate (Tian et al. 2008), but no systematic studies have investigated the distributional responses of demersal species at interannual and decadal scales. In addition, the relationships of these responses to the ecological and life history traits of demersal species remain elusive.

In this chapter, I assessed the environmental variability in the Tsushima Current region of the Japan Sea based on local- and basin-scale environmental indicators. I also investigated whether the changes in distribution and abundance were significant at interannual (1972–2002) and decadal scales [between the cold (1977–1988) and warm (1989–2002) periods]. Finally, I determined how well the geographic affinity and life history traits could explain the sensitivity of the responses of species. I anticipated that this approach based on using two temporal scales to assess changes in geographical distribution and abundance would elucidate how demersal fishes have responded to environmental variation in the Japan Sea ecosystem.

Material and methods

Fisheries data

To examine the effects of climate on the abundances and distributions of demersal species, I studied 19 species from the fisheries targets that underwent single trawling

during 1972-2002 based on the JSOBT dataset (Misu 1974, Tian et al. 2008, Tian et al. 2011). For further analysis on life history effect and data consistency, I excluded species recorded as a group and the data in offshore area owing to the limited species and discontinuous records in space and time. To generate the distribution map for each month for each species, I summed up the catch and effort in each fishing area (the smallest unit in record is 10' x 10' grid) and calculated the catches per unit effort (CPUE) by dividing the total catches by the total efforts (number of hauls) in the grid. In following analysis, I only consider the spawning season of each species because climate variability acting at the ocean surface is more likely to affect demersal species during their spawning (Minami and Tanaka 1992, Rijnsdorp et al. 2009). I used the spatial data averaged across the spawning period to produce the annual map.

For the indices of spatial distribution to each species, I calculated CPUE-weighted median latitude and longitude as the distribution center for each species using annual CPUE map, and a time series for the distribution center for each species was obtained. In addition, the southern and northern boundaries were calculated as the minimum and maximum latitudes, respectively, where a species occurred on the annual CPUE map. Similarly, the eastern and western boundaries were calculated as the maximum and minimum longitudes, respectively.

Environmental variables

To understand the effects of climate on the Japan Sea ecosystem, I examined local- and basin-scale climate indicators. The local-scale indicator was the 50-meter depth water temperature (wt50m) in the Tsushima Current region. The basin-scale climate indices comprised the Pacific Decadal Oscillation (PDO; Mantua and Hare (2002)), Arctic Oscillation (AO, Thompson and Wallace (1998)), North Pacific Index (NPI,

Trenberth and Hurrell (1994)) and Asian Monsoon Index (MOI, (Hanawa et al. 1988, Watanabe et al. 2003)). In the analysis of the environmental data, I only used the quarterly data that corresponded to the fishery data.

The correlation analysis between the local- and basin-scale climate indicators detected a complex interaction between atmospheric forcing and local water temperature (Fig. 2-2, Table 2-2).

Analysis of environmental effects on the demersal species

To understand the effects of climate on the demersal species, I analyzed the shifts in distribution and abundance separately at both interannual and decadal scales, I used the analytical framework reported by Hsieh et al. (2009b), and outlines of the procedures are given as follows. I defined the cold (1977–1988) and warm (1989–2002) periods based on previous studies of the decadal variability in the Japan Sea ecosystem (Chiba and Saino 2002, Chiba et al. 2005, Tian et al. 2008). In the decadal analyses, I excluded data obtained before 1976 because previous studies (Chiba and Saino 2002, Chiba et al. 2005, Tian et al. 2008) suggest that a decadal shift occurred in 1976/77. In addition, the data period (1972–1976) was too short to make quantitative comparisons. Thus, I focused on the decadal event. The temperature anomalies suggested that a minor warming may have occurred prior to 1976, but it is likely to have been part of fluctuations on a shorter time scale in the Japan Sea rather than a decadal event (Kato et al. 2006).

To examine the distributional response at the interannual scale, I performed regression analysis of the environmental variables and distribution center (median latitude/longitude) for each species. I also investigated 1-year and 3-year time-lagged values that represented the delayed environmental effects, which have been observed in

fish species in the North Sea (Perry et al. 2005) and southern California region (Hsieh et al. 2008a). To account for the serial dependency of the time series in regression analyses, I calculated the regression coefficient using the estimated generalized least square (EGLS) method and computed the bootstrapped (1000 times) 95% confidence limits for the hypothesis test (Ives and Zhu 2006). In addition, I examined the boundary of the distribution relative to the environmental variables. I only examined the minimum latitude (5th percentiles) as the southern boundary for cold water species and the maximum latitude (95th percentiles) as the northern boundary for warm water species, respectively, because the Japan Sea is near the southern most limit for most of the cold water species and the northernmost limit for warm water species. In addition, the dynamics at the range boundaries (latitudinal and elevation in terrestrial ecosystem) are expected to be more sensitive to climate variability (Parmesan and Yohe 2003). For the longitudinal boundary, both the minimum and maximum longitudes (with the same calculation as in latitudinal boundaries) were used in analysis. I included abundance in the analysis and examined the partial correlations between the distribution center (or boundary) and environmental variables if a species' distribution center (or boundary) was significantly correlated with abundance ($P < 0.05$), because the geographical extent of marine populations may be correlated with their population size (MacCall 1990, Hsieh et al. 2010a). The aim was to separate the possibility that the distributional shift was caused solely by expansion/constriction due to changes in population size. However, our results were qualitatively the same when abundance was not included as a covariate. For the time series regression analyses, I set the significance level at 5%, without correcting for multiple tests. My analyses aimed to explore potential climate effects, but various climate indices are correlated (Table 2) thus different tests should not be considered to be independent.

At the decadal scale, to examine the change in the geographical distribution of each taxon from the cold to warm period, I estimated the centroid for each period based on the time series of the distribution centers (the median latitude and longitude were considered simultaneously) by 50% convex-hull peeling (Zani et al. 1998), where all of the distribution centers were weighted equally. This method is robust to the bias caused by potential outliers. I then tracked the movement direction and magnitude of each species from the cold to warm period to determine the decadal variation in the distribution centers. Finally, I used an ANOVA-like randomization test (Hsieh et al. 2008a) to examine whether the shift in centroids between the cold and warm periods was statistically significant for each species.

I then considered whether differences in geographic affinity and life history traits existed between geographically shifting and non-shifting species. I defined the “geographically shifting species” as those species that exhibited significant distributional shifts at interannual or decadal scales (changes in their distributional domain from the cold to the warm period). For the interannual scale, I analyzed the latitudinal and longitudinal shifts separately. The “geographical affinity” was defined as the cold or warm water group (see Table 2-1) based on studies of a species’ biogeography (Nishimura 1968). The life history traits comprised age at maturation (A_m) and asymptotic length (L_{inf}) because these traits were available for all of the species examined. Univariate and multivariate logistic regressions (the latter with stepwise forward selection based on AIC) were used to determine factors that are able to classify the different responses (shift or non-shift) in geographical distributions. The goodness-of-fit was evaluated by AIC, and then Rao's score test (Rao 1948) was used to test whether the value of regression coefficient is significant. Rao test is asymptotically equivalent to the likelihood ratio and Wald test, but it is known to be useful for testing

the improvement of model fit if variables that are currently omitted are added to the model. Therefore, Rao test is often recommended for identifying variable in stepwise forward selection.



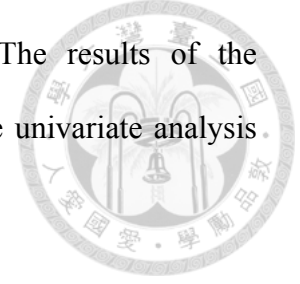
Result

The interannual variations in the distribution centers of the demersal species were largely related to environmental variables (Table 2-3). The median latitude and longitude were correlated with environmental variables for more than half of the species, and a limited number of species exhibited distributional shifts only in their boundaries. The rate of latitudinal shift (center) ranged from -54 to 44 km/°C with an overall average of 5.110 ± 6.617 (standard error) km/°C. Similarly, the longitudinal shift (center) ranged from -45 to 52 km/°C with an overall average of 6.281 ± 6.565 (standard error) km/°C.

Approximately 68% of the species exhibited a significant distributional shift from the cold to the warm period at the decadal scale (Table 2-3), but the movement direction varied among species (Figure 3). Four species in the cold water group exhibited significant poleward shifts, particularly *Gadus macrocephalus*, *Theragra chalcogramma*, and *Squalus acanthias* (Figure 2-3). However, these poleward shifts did not prevail in warm water species. The most significant poleward shift occurred in *Glossaodon semifasciatus*, whereas *Paralichthys olivaceus*, *Pagrus major*, and *Evynnis japonica* exhibited significant equatorward shifts among the warm water species (Figure 2-3b).

The results of the logistic regression showed that none of the variables we examined (life history traits and geographical affinity) could classify the different distributional responses (shifting v.s. nonshifting) among the species at the interannual

scale (Table 2-4a). At decadal scale, the L_{inf} was significant ($P = 0.042$) for classifying the distributional responses among the species (Table 2-4a). The results of the multivariate logistic regression were quantitatively the same as the univariate analysis results; thus, only the latter are shown.



Discussion

In this study, I examined the changes in the geographical distribution of the demersal fish assemblage in the Japan Sea and found significant effects of climate. The responses in the distribution in terms of latitudinal and longitudinal shifts at the interannual scale were found in both the cold water and warm water groups. The configuration of the narrow continental shelf in the Japan Sea runs from the northeast to the southwest (Figure 2-1), which may suggest that the overall trend in the along-shore movement is related to environmental variability. However, the rate of distributional shift in the Japan Sea was smaller than that found in a previous study (Poloczanska et al. 2013) and it exhibited a high variance. This also suggests that the universal poleward shift detected by a global-scale meta-analysis might not hold at the regional scale (see Perry et al. (2005)). One may argue that a deepening of the vertical distribution is a more universal response to warming than a latitudinal shift for demersal fishes (Dulvy et al., 2008); however, the demersal fishes surveyed during the warming period did not reveal evidence of deepening in the Japan Sea (Kawamura 2009).

The distributional shifts at the decadal scale also exhibited along-shore movement, but the scales varied among different species (Figure 2-3). In contrast to a previous study (Perry et al., 2005), I found that species with a large body size (L_{inf}) were more likely to respond by changing their distribution (Table 2-4). It is unclear why I reached the opposite conclusion, but Morita et al. (2010) provided a possible explanation. Using

a simple bioenergetic model, they showed that the optimal temperature for growth decreases with increasing body size, which indicates that species with large body sizes may be more vulnerable to warming. It is also possible that fishing may affect the species distributional response to climate change. The large species in the Japan Sea, such as *G. macrocephalus*, *S. acanthias*, and *P. olivaceus*, are important targets of fisheries, thus these large species may experience a higher rate of exploitation than other species. These effects of fishing on the spatial distribution of marine fish were also found in the California Current region, where the exploited species were more sensitive to warming (Hsieh et al. 2008a).

I observed variations in the distributional shift among species at both interannual and decadal scales. It is possible that the different physiological requirement of species or even multiple stocks within one species may have restricted their distribution. In the Japan Sea, *Arctoscopus japonicus* and *P. olivaceus* are known to comprise two separate stocks. For *A. japonicus*, the recent catch statistics for all fisheries combined suggest that the northern stock has been depleted since 1980 (Fujiwara et al. 2009) whereas the southern stock remains relatively stable (Matsukura et al. 2014). Similarly, the northern stock of *P. olivaceus* was listed as unsustainable in a recent stock assessment report (Uehara et al. 2014) whereas the southern stock was listed as sustainable (Nakagawa et al. 2014). This north–south difference may explain the southeastward movement of *P. olivaceus*, as shown in Figure 3. In addition to the presence of multiple stocks of certain species in the Japan Sea, other fisheries such as small-scale trawling in the coastal area of Kyoto Prefecture also target the single-trawling species. This multi-fisheries scenario may generate regional differences among species and stocks. These regional differences could also indicate differences in the responses to climate or fishing.

In addition, several other processes can generate various responses in the

distributional shift among species (Chen et al. 2011, Hollowed et al. 2013). In addition to environmental factors and primary production, which are often linked with the recruitment success (e.g., Beaugrand et al. (2003a)), species interactions (e.g. competition and predation) may also play roles in mediating the response to climate change. For flatfish, the competition for habitat can affect the success of recruitment during the post-larval stages. Some studies indicate that the quantity of available habitat is crucial for juvenile settlement and it also affects recruitment (Gibson 1994, van der Veer et al. 2000). Thus, interspecific density dependence (Hixon and Jones 2005) may become important when suitable habitats are limited. For demersal species in the Japan Sea, predation or cannibalism by adult individuals may also contribute to the mortality during the juvenile stages and affect recruitment (Minami 1986, Tominaga and Nashida 1991). In these conditions, climate is not the only driving force that affects the distributions of species. It would be interesting to investigate how these biotic processes mediate the distributional responses of species to climate variability.

The use of a CPUE map to infer the distributions of species may be one of the limitations of our analyses. The fishing effort distribution for single trawl fisheries remained consistent in space and time (see Appendix I), but it is widely known that the fleet dynamics and fishermen-related factors can also affect the CPUE pattern (Branch et al. 2006). It might be possible to examine the fleet dynamics to approximate the behavior of fishermen as a Levy flight process, which is a stochastic process that is used commonly to study the foraging behavior of predators (Viswanathan et al. 1996). It is often assumed that price is the key factor that affects the behavior of fishermen, but a case study in North Sea fisheries found that the behavior of fishermen was only marginally correlated with the fish price and fishing effort (Marchal et al. 2007). A recent review also suggests that the economic factor is not the only driver of fleet

dynamics (van Putten et al. 2012). Although I neglected the influence of fleet dynamics on the fishing effort and CPUE in the present study, this issue may be addressed in future studies.



Conclusion

In this study, I provide quantitative evidence of shifts in the distributions and abundances of the demersal fish assemblage in the Japan Sea in response to climate variation. The decadal variations in distributions were explained largely by the asymptotic length, which may suggest that warming has greater negative effects on larger fishes, thereby indicating the possible effects of fishing activities. Not every kind of responses can be classified by life history traits or geographical affinity in our study. Thus, my findings support previous studies, which showed that life history traits or geographical affinity alone, are not sufficient for interpreting the responses of species to climate variation (Hsieh et al. 2008a, Hsieh et al. 2009b). Furthermore, it would be difficult to project the responses of species to future climate change based on any single factor. More studies of the interactions among species and the biological nonlinear amplification of environmental effects will be necessary to obtain a better understanding of the effects of climate on marine ecosystems.

Table 2-1 Life history traits (age at maturation A_m and asymptotic length L_{inf}) and geographical affinity of the target species in the Japan Sea single-trawl fisheries (Tian *et al.*, 2011). The asymptotic lengths are mostly compiled from Ogata (1980) with some exceptions (see note).

No.	Species	Common Name	Affinity	Depth (m)	A_m	L_{inf} (cm)	Spawning season
1	<i>Gadus macrocephalus</i>	Pacific cod	Cold water	200-300	4	91.3	Jan-Mar
2	<i>Theragra chalcogramma</i>	Walleye pollock	Cold water	100-500	3	56.1	Dec-Mar
3	<i>Pleurogrammus azonus</i>	Arabasque greenling	Cold water	<200	2	43.5	Sep-Nov
4	<i>Arctoscopus japonicus</i>	Japanese sandfish	Cold water	300-500	2	27.8	Dec-Mar
5	<i>Squalus acanthias</i>	Piked dogfish	Cold water	150-180	10	124.0 ^{*1}	Feb-May
6	<i>Glyptocephalus stelleri</i>	Witch flounder	Cold water	200-300	2	58.9	Jan-Apr
7	<i>Hippoglossoides dubius</i>	Flathead flounder	Cold water	150-500	5	55.8	Feb-Apr
8	<i>Pleuronectes herzensteini</i>	Brown sole	Cold water	30-130	2	28.2	Feb-May
9	<i>Microstomus achne</i> ^{*2}	Slime flounder	Cold water	50-400	3	71.5 ^{*1}	Feb-Apr
10	<i>Hippoglossoides pinetorum</i>	Pointhead flounder	Warm water	150-190	2	37.0	Jan-Mar
11	<i>Eopsetta grigorjewi</i>	Shotted halibut	Warm water	<140	2	40.8	Feb-Mar
12	<i>Tanakius kitaharai</i>	Willow flounder	Warm water	80-150	2	28.0	Dec-Jan ^{*3}
13	<i>Glossanodon semifasciatus</i>	Deepsea smelt	Warm water	<200	1	25.5 ^{*1}	Jan-Sep
14	<i>Paralichthys olivaceus</i>	Bastard halibut	Warm water	<150	2	80.7	Mar-Jul
15	<i>Pagrus major</i>	Silver seabream	Warm water	<100	3	54.4	Apr-Jul
16	<i>Eynnys japonica</i>	Crimson seabream	Warm water	30-130	2	34.0 ^{*1}	Jul-Sep
17	<i>Dentex tumifrons</i>	Deepsea snapper	Warm water	<200	2	41.5 ^{*1}	Sep-Nov ^{*4}
18	<i>Lepidotrigla microptera</i>	Redwing searobin	Warm water	70-140	1	30 ^{*5,6}	Feb-Jun
19	<i>Trichiurus japonicus</i>	Largehead hairtail	Warm water	20-140	1	65.8 ^{*1}	Apr-Oct

*1 FishBase (Froese and Pauly 2013)

*2 It is the main species of "other cold water flounders" (Pleuronectidae spp.) group from JSOBT dataset as in Tian *et al.* (2011)

*3 Narimatsu *et al.* (2007)

*4 Also spawn during March-May, but the peak of CPUE is in September-November.

*5 Use maximum length to represent asymptotic length because L_{inf} is unavailable.

*6 Fujioka *et al.* (1990)

Table 2-2 Correlation matrix of environmental variables

	wt50m	PDO	NPI	AO
PDO	-0.3673*			
NPI	0.2702	-0.6613*		
AO	-0.1052	0.2027	0.0627	
MOI	-0.3022	0.1078	-0.4732*	-0.0757

* Indicates a significant correlation ($P < 0.05$).

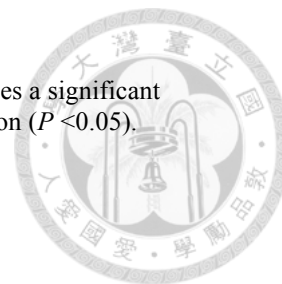


Table 2-3 Results of regression analyses investigating the effects of interannual changes in environmental variables on median latitude and longitude and boundary (minimum latitude/ longitude for cold water species and maximum latitude/ longitude for warm water species, respectively). The decadal changes between two domains (cold-warm) are also shown here.

Species	Median latitude	Latitudinal boundary	Median longitude	Longitudinal boundary	Shift in domain
<i>Gadus macrocephalus</i>	+wt50m(1)		+wt50m(1)		+
<i>Theragra chalcogramma</i>	+MOI		+wt50m +AO(0, 1)		+
<i>Pleurogrammus azonus</i>					+
<i>Arctoscopus japonicus</i>	+MOI(3)		+wt50m(3) +MOI(3)	+PDO(3)	
<i>Squalus acanthias</i>	+wt50m +AO +MOI	+wt50m (0, 1)	+wt50m +AO		+
<i>Glyptocephalus stelleri</i>	+wt50m		+AO(3)		+
<i>Hippoglossoides dubius</i>					
<i>Pleuronectes herzensteini</i>					
<i>Microstomus achne</i>	+wt50m +PDO		+wt50m -PDO		+
<i>Hippoglossoides pinetorum</i>		+PDO(1)†			+
<i>Eopsetta grigorjewi</i>			+wt50m(1)		
<i>Tanakius kitaharai</i>			+NPI(1)	+PDO(0, 1)† +AO(0, 1) † +NPI(1) † +MOI(1) †	
<i>Glossanodon semifasciatus</i>					+
<i>Paralichthys olivaceus</i>	+NPI(1) +AO(1)		+wt50m(1) +AO(1) +MOI(3)		+
<i>Pagrus major</i>	+wt50m(0, 1)		+NPI(3)		+
<i>Evynnis japonica</i>					+
<i>Dentex tumifrons</i>	+NPI(1) +AO(1)		+PDO(3) +NPI(3) +AO(3)		+
<i>Lepidotrigla microptera</i>	+NPI(0, 3) +MOI(3)		+wt50m(1) +NPI(3)		
<i>Trichiurus japonicus</i>					+

A +/- sign along with the environmental variable represents significant positive/negative correlation ($P < 0.05$). The number in the bracket indicates the lag-year with a significant correlation. For the analyses concerning boundary, "†" indicates a significant correlation in maximum boundary and the other unmarked variables indicates a significant correlation in minimum boundary.

For the decadal shift ("shift in domain"), "+" represents a significant ($P < 0.05$) shift from the cold (1977-1988) to the warm (1989-2002) period.

Table 2-4 Results of logistic regression ($\text{logit}(y) \sim \beta_0 + \beta_1 x$) investigating effects of geographical affinity and life history traits (x) on species' response (y) to climate variations at interannual (latitude and longitude are shown separately in (a) Distribution) and decadal scale. The AIC intercept (β_0), and regression coefficient (β_1) values with significance in the Rao's score test ($P < 0.05$) are in bold font.

(a) Distribution

		AIC	β_0	β_1	Rao	P
Latitude	Affinity	25.752	1.658	-0.405	0.148	0.701
	A _m	25.745	0.728	0.117	0.141	0.708
	L _{inf}	25.234	0.076	0.019	0.596	0.440
Longitude	Affinity	10.279	-16.410	18.487	1.173	0.279
	A _m	11.636	1.999	0.394	0.127	0.722
	L _{inf}	9.444	-5.682	0.259	0.977	0.323
Decadal	Affinity	27.675	0.539	0.154	0.024	0.876
	A _m	27.385	0.359	0.162	0.277	0.599
	L _{inf}	21.372	-3.079	0.088	4.144	0.042

(b) Abundance

		AIC	β_0	β_1	Rao	P
Interannual	Affinity	27.675	30.102	30.113	2.555	0.110
	A _m	-1.540	0.102	0.008	0.184	0.668
	L _{inf}	0.110	0.668	0.677	0.174	0.677
Decadal	Affinity	25.465	25.888	25.846	0.434	0.510
	A _m	0.693	0.030	-0.005	0.012	0.912
	L _{inf}	0.510	0.912	0.813	0.056	0.813

Table 2-5 Average abundance (kg/haul) in the cold and warm period and results of regression analyses linking the environmental variables with abundances.

Species	Cold period (1977-1988)	Warm period (1989-2002)	Regression analysis
<i>Gadus macrocephalus</i>	13.752	11.686	+AO(3)
<i>Theragra chalcogramma</i>	17.372	15.196	+NPI
<i>Pleurogrammus azonus</i>	70.654	62.121	
<i>Arctoscopus japonicus</i>	26.731	8.220	
<i>Squalus acanthias</i>	36.199	18.206	
<i>Glyptocephalus stelleri</i>	10.533	4.900	+AO(1)
<i>Hippoglossoides dubius</i>	21.807	8.073	+wt50m(1)
<i>Pleuronectes herzensteini</i>	1.962	0.748	+MOI
<i>Microstomus achne</i>	4.069	2.325	+NPI
<i>Hippoglossoides pinetorum</i>	19.580	15.085	+PDO(1)
<i>Eopsetta grigorjewi</i>	0.893	0.249	+NPI(1) +PDO(3)
<i>Tanakius kitaharai</i>	1.122	0.495	
<i>Glossanodon semifasciatus</i>	34.112	24.779	
<i>Paralichthys olivaceus</i>	1.965	0.962	
<i>Pagrus major</i>	0.624	1.134	+NPI
<i>Evynnis japonica</i>	0.744	2.240	
<i>Dentex tumifrons</i>	0.849	1.299	
<i>Lepidotrigla microptera</i>	0.732	0.477	
<i>Trichiurus japonicus</i>	1.426	0.247	

Bold indicates a significant difference ($P < 0.05$) of abundance between the cold and warm period. The significant positive/negative correlation ($P < 0.05$) is indicated by a +/- sign along with the environmental variable for the regression analysis. The number in the bracket indicates the lagged year with a significant correlation.

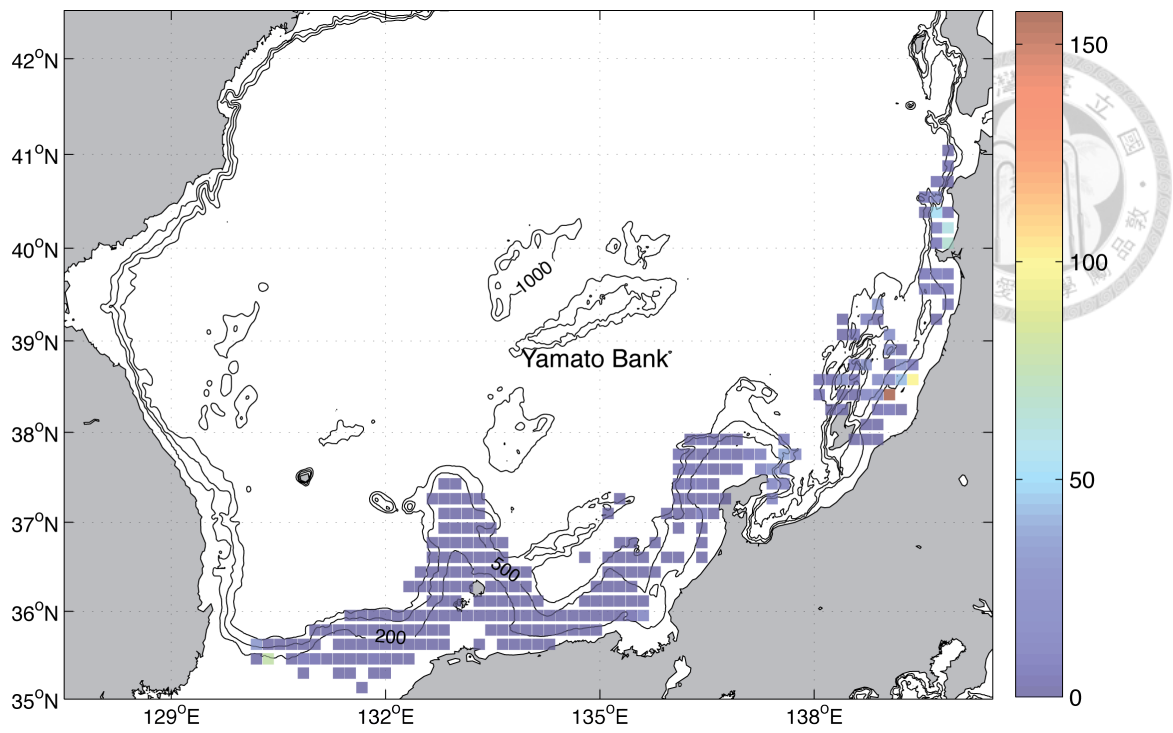


Figure 2-1 An example map in 1972 showing the spatial distribution of CPUE (kg/haul) for Pacific cod (*Gadus macrocephalus*) calculated from the Japan Sea Offshore Bottom Trawl dataset during spawning season.

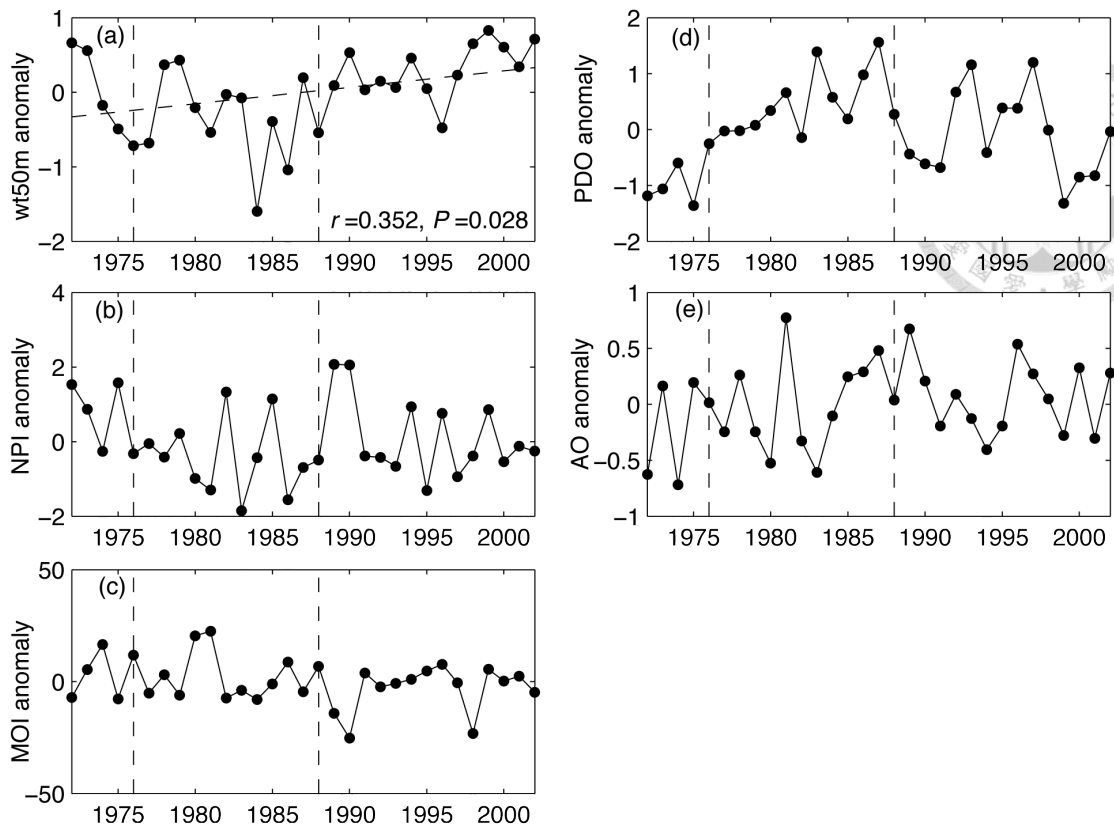


Figure 2-2 Annual anomalies time series of the environmental variables. The vertical dash lines indicate the duration of cold (1977/78-1988/89) period based on PDO and NPI (Hare and Mantua, 2002). The trend lines (dash line) and correlation coefficients are shown in the time series when a significant long-term trend ($P < 0.05$) exists.

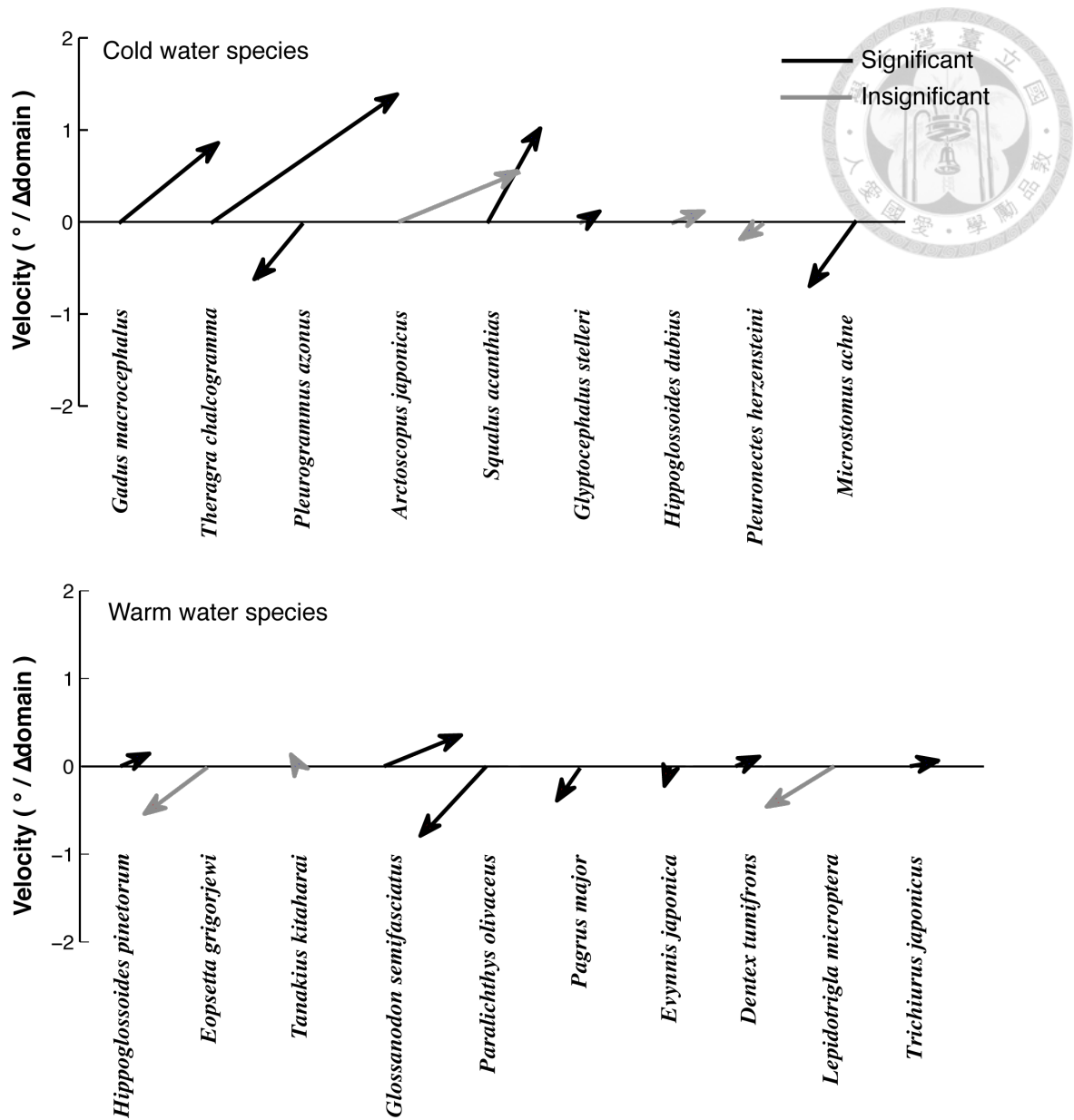


Figure 2-3 Summaries of the movement from the cold to the warm period (Δ domain). The y-axis denotes the unit of velocity for the arrow vectors in the vertical direction, with $1^\circ \approx 111.2$ km. The significant distributional shifts passed the randomization test (see text) were shown in black line.

Chapter 3 Fishing and temperature effects on the size structure of exploited fish stocks



Introduction

Size structure plays an important role in maintaining reproductive potential and stability of fish population. For example, larger individuals tend to produce more and better eggs (Hsieh et al. 2010b, Hixon et al. 2014) and have a longer spawning season (Berkeley and Houde 1978, Lambert 1987, Hutchings and Myers 1993, Sogard et al. 2008); small and large individuals may spawn at different sites (Trippel et al. 1997, Lawson and Rose 2000, Vandeperre and Methven 2007). Such bet-hedging strategies provide resilience capacity for populations to sustain under unfavorable conditions (Hsieh et al. 2010b, Ripa et al. 2010, Schindler et al. 2010). Hence, investigating the change of size structure may provide insight of how resilient a fish population can be.

Several external forcings may alter the size structure of a fish population. The most well-known examples are fishing and temperature. Fishing represents size-selective removal of larger individuals that can truncate the size structure of a fish population (Barnett et al. , Bianchi et al. 2000, Berkeley et al. 2004, Ginter et al. 2015), which in turn may cause recruitment failure (Ottersen et al. 2006), reduce the reproductive outputs (Scott et al. 2006), and increase variability of fish populations (Hsieh et al. 2006b, Anderson et al. 2008, Rouyer et al. 2012). It may also lead to evolutionary consequences (Heino et al. 2015); for example, the genetic differences found in the populations of Atlantic cod (*Gadus morhua*) from Iceland is due to difference in depth-associated fishing mortality (Jakobsdóttir et al. 2011). As such, balanced

exploitation (Law et al. 2012) and harvest-slot-limit (Gwinn et al. 2015) have been proposed to prevent fishing-induced size truncation.

Apart from fishing, increasing sea water temperature caused by global warming may also lead to shrinking size structure of marine fish populations (Daufresne et al. 2009b, Cheung et al. 2013a). Elevated ambient water temperature directly influences fish metabolism at individual level (Gillooly et al. 2001a), which increases growth rate and causes earlier maturation at population level (Neuheimer and GrønkJær 2012). Also, temperature may indirectly influence the recruitment processes through trophic transfer (Sundby 2000) and thus change the size structure. Based on the match/mismatch hypothesis, the larvae survivorship relates to the match between the timing of larval feeding and the food production (Cushing 1990). For example, rising temperature since mid-1980s has modified the plankton ecosystem and reduced the survival of young cod in the North Sea (Beaugrand et al. 2003b). While the fishing and temperature effects have been well documented, their relative contributions on the size structure of fish populations remain poorly understood. This is a critical issue particularly for exploited stocks, because overfishing has been shown to enhance the sensitivity of fish abundance and distribution to climate (Hsieh et al. 2008b, Hidalgo et al. 2011, Rouyer et al. 2014); nevertheless, whether such synergistic effect also occurs in size structure remains relatively unexplored.

Previous studies on quantifying fishing or temperature effects on the size structure of fish populations have been focused on univariate size-based indicators (SBI). Some studies used the upper 95-percentile of the length frequency (L_{95}) to test fishing effect (Rochet et al. 2010, Brunel and Piet 2013), while the other used length class diversity to investigate the stability of population through time (Marteinsdottir and Thorarinsson 1998). Recently, European Commission Marine Strategy Framework Directive required

regional (or local) fishery reports to provide the information of basic SBIs (e.g. the mean length) in order to improve the management and maintain the sustainable development (Farmer 2012). However, it remains unclear whether these univariate SBIs could represent the entire size structure and the status of a population. It has been suggested that no single SBI can represent an effective overall indicator for external forces (Shin et al. 2005). Also, SBIs need to be selected carefully based on their implications. For example, L_{95} can only reflect the variety of large fish in fish population. The analysis with the North Sea cod, herring and plaice found L_{95} failed to reveal the effects of external forces on fish population, as it was rather insensitive in responding to fishing mortality (Brunel and Piet 2013).

To overcome the limitation of existing SBIs, it needs an alternative approach to (1) analyze complete information of size structure and (2) examine how external forces affect the size structure. Here, I employed the variation partitioning approach to conduct a size structure-based analysis that examines the variation of size class composition in response to external forcings. Variation partitioning can be best understood as a method for extending multivariate regression. In multivariate regression ($y \sim x$), y represents a univariate response vector and x represents multiple predictors, x_1 , x_2 , etc. (each is a vector) and possibly their interactions; the contribution of each predictor variable (x_i) can be evaluated by partial R-square. Whereas in variation partitioning ($Y \sim X$), Y represents a multivariate matrix and X represents multiple predictors, X_1 , X_2 , etc. (each is a matrix); the contribution of each predictor matrix (X_i) and their interaction is also evaluated by partial R-square (Peres-Neto et al. 2006). Variation partitioning is commonly used in community ecology to examine the relationship between species composition (Y matrix) and various sets of explaining variables (e.g. 2 or 3 predictor matrices) (Peres-Neto et al. 2006). This method has also been extend to analyze

temporal and space-time variation of community composition data (Griffith and Peres-Neto 2006). Here, I borrow this concept to analyze temporal variation of size composition data in responding to fishing, temperature, and the interaction, with the simplification that fishing and temperature is just a vector. Specifically, for a given fish population, I apply the variation partitioning to quantify how the temporal variation of their size composition responds to fishing, temperature and their interaction (see Methods). The explained fraction of variation (partial R-square) by each factor then allows us comparing their relative contribution in affecting length composition through time.

Next, I perform a cross-stock meta-analysis linking the relative contribution of fishing or temperature (the output of variation partitioning as explained fraction of variation) to the life history traits of fishes, as well as long-term mean and variability of fishing or temperature (see Methods). This meta-analysis aims to examine which factor can explain the relative contribution of fishing, temperature and their interaction across stocks. This meta-analysis is motivated by the fact that life history traits are associated with the size structure of population (De Roos et al. 2003). I hypothesize that the large, slow growth, and late-matured species is more likely to be impacted by fishing in their size structure because size-selective removal (i.e. size truncation) may be more severe in these species (Rouyer et al. 2011) and their recovery will take longer time (Jennings et al. 1999, De Roos et al. 2003). I also hypothesize that small species is more vulnerable to temperature effects, because smaller species are more sensitive to temperature changes due to the constraints from metabolic allometries (Gillooly et al. 2001b).

Furthermore, I expect that fishing and temperature might exhibit interactive effects via multiple ways (Perry et al. 2010, Planque et al. 2010). For example, the long-term

fishing effect, such as long-term mean and variability of mortality ratio (fishing mortality divided by natural mortality, F/M) may affect the relative contribution of temperature in explaining temporal variation of size structure. Here, I standardize fishing mortality by natural mortality in order to have a fair cross-stock comparison. Motivated by previous studies showing that fishing elevated sensitivity of exploited stocks to environmental changes (Hsieh et al. 2006b, Anderson et al. 2008, Rouyer et al. 2011), I hypothesize that the fish stocks experienced higher fishing pressure is more responsive to temperature effect in their size structure. I also hypothesize that habitat conditions, including mean and variability of temperature, affect the relative contribution of fishing effect. For instance, Wang *et al* (Wang et al. 2014) found that temperature affects the cod's life history trait, making the cod population more vulnerable to fishing.

My objectives are, first, to apply variation partitioning to quantify how the variation of size structure responded to fishing, temperature and the interactive effects for 28 exploited stocks (Table 1) living in a wide range of habitats, including the west coast of US, Alaska, and North Sea (Figure S1). Secondly, I linked the fraction of explained variation by fishing (or temperature) to life history traits (including von Bertalanffy growth rate (K), length infinity (L_{inf}), age at maturation (A_{50}), length at maturation (L_{50})), as well as long-term mean and variability of fishing and habitat temperature conditions. Finally, to demonstrate the efficacy of our approach, I compared the performance of variation partitioning approach with the traditional univariate SBIs analyses. This comparison is straightforward, as both the univariate SBIs analysis and variation partitioning are computed using similar linear modeling of variance/covariance, with the difference only in the response variable- the response variable is a vector (y) in the univariate SBIs analysis whereas the response variable is a

matrix (Y) in the variation partitioning; two methods have the same explaining variables (i.e. fishing and temperature).



Material and methods

Size structure data of commercial stocks

I collected length frequency data from 28 exploited stocks, which contain temporal coverage over 20 years and annual fishing mortalities (or exploitation rates) estimated by stock assessment are available (Table 3-1, Table S1). These stocks came from 3 regions in the northern hemisphere (Figure S1): (1) the west coast of US (West US), which is part of Northeast Pacific; (2) Alaska, which separates into 3 fishing areas- Aleutian Islands (AI), Gulf of Alaska (GOA), and Bering Sea; and (3) North Sea. Collectively, these 28 stocks in 3 regions were well studied, spanning distinct distribution of size structure, with a wide range of life-history traits and habitats, and therefore are representative of a compilation of global-scale fish stocks (Table S2).

I primarily use length frequency from the fisheries-independent surveys for each stock. These are the length frequency per size range of the given year as arranged in the stock assessment report. For Alaska region, the survey data includes bottom trawl survey in Aleutian Island (AI), East Bering Sea shelf (EBS) and Gulf of Alaska (GOA). For the North Sea, I compiled the length frequency of ICES International Bottom Trawl Survey in the North Sea (NS-IBTS). I used the 1st quarter (Q1) in NS-IBTS for consistency because there was only annual Q1 survey prior to 1991. For the west coast of US, I used fisheries-dependent length compositions instead of bottom trawl survey because the data from fishery-independent surveys during 1980-1990 were limited.

Fishing and natural mortality

To quantify the fishing effect, I used time series of annual fishing mortality from the stock assessment reports (Supplementary Table S3-1). I focus on the single fishery whenever possible to minimize the uncertainty in fishing selectivity due to changing gears. I noted that analyses in the west coast of US use exploitation rate instead of fishing mortality in stock assessment. To make a fair comparison for meta-analysis, I transformed the exploitation rate into fishing mortality through the relationship between mortality and survival rate in fisheries (Ricker 1975). Here I first assume that these fisheries are type II fishery, in which the fishing and nature mortality operate concurrently. The exploitation rate (μ), fishing mortality (F), natural mortality (M), instantaneous total mortality rate (Z) and actual total mortality (A) have following relationships:

$$\mu = F \cdot A / Z \quad (1)$$

$$Z = F + M \quad (2)$$

$$A = 1 - e^{-(F+M)} \quad (3)$$

the equation (1) can also be written as:

$$\mu = F \cdot (1 - e^{-(F+M)}) / (F + M)$$

With the known exploitation rate and natural mortality, this equation can be solved numerically and yields the fishing mortality. The natural mortality here is mostly compiled from the value of preferred model in the stock assessment reports (Supplementary Table S3-1, Table S3-2).

Temperature

In analysis, I primarily used empirical measurements of temperature along with the trawl surveys (see Supplementary Figure S3-2). The North Sea (53-59°N, 3°W-10°E) near-bottom temperature is the station observations of hydrochemical measurements

from ICES Oceanographic database (<http://ocean.ices.dk/HydChem/HydChem.aspx>) at Q1 (January-February), with coverage of almost entire North Sea. For the Alaska region, Aleutian Islands, East Bering Sea and Gulf of Alaska, the bottom trawl surveys provide bottom temperature measurements (data available at website of NOAA Alaska Fisheries Science Center, https://www.afsc.noaa.gov/RACE/groundfish/survey_data/data.htm). I took average for all the stations that the species occurred. Although many demersal species examined here have a pelagic phase at larval-juvenile stages and some species (e.g. Atlantic cod) forage on the whole water column, the preliminary analysis on surface (see Figure S3) and bottom temperature suggests that they are highly correlated (AI: 0.92, EBS: 0.72, GOA: 0.67, North Sea: 0.76). This suggests even the water is stratified, the interannual variability is very similar in temperate-sub arctic ocean. Therefore, I used only the bottom temperature collected in trawl survey for these 4 areas in our analysis. For the west coast of US, I used the sea surface temperature from NCEP/NCAR Re-analysis monthly mean (data available at website of NOAA Earth System Research Laboratory <http://www.esrl.noaa.gov/psd/data/timeseries/>) and then took aerial average (31.4-48.6°N and 54.4-56.3°W) to represent the entire region.

Variation partitioning to quantify fishing and temperature effect on size structure

To determine how much of the temporal variation in size structure is explained by fishing and temperature effect, variation partitioning (*aka.* redundancy analysis) was used to decompose the total variation of length composition of each stock through years. The response variable here is the matrix of size composition data through time. The explanatory variables were time series of annual fishing mortality and temperature. The unbiased estimation of adjusted R^2 (accounting for sample size effect) provides a test with correct Type I error rate and good power for redundancy analysis (Peres-Neto et al.

2006). I reported the adjusted R^2 for the pure effect of fishing, temperature and their interaction. Next, I perform permutation test (1000 times) to evaluate the significance of each fraction. Although the significance test cannot be done for the interactive component (Peres-Neto et al. 2006), I still report the interactive component for the sake of comparison.

To incorporate the lag effect of temperature, I additionally used 1 year- and 3 year-lag temperature as explanatory variables in variation partitioning. For the stocks in Alaska, sampling interval is 2- or 3-year, and thus I only considered 2 or 3-year lag. I did not investigate lagged effect of fishing; I assumed that fishing instantaneously affects adult population while temperature may affect the size structure through influencing the future recruitment at early life stages (e.g. egg and early larvae). Because variation partitioning does not estimate log-likelihood in the procedure, the best model is selected according to the largest effective size (highest total adjusted R^2 (see Table 2)). The fraction of variation explained by fishing and temperature from the best model was used in further analyses.

Variables affecting the relative contribution of fishing and temperature effect

To investigate what determines the relative contribution of fishing and temperature across stocks, I considered the following variables (see Supplementary Table S3-2): (1) life history traits: von Bertalanffy growth rate (K), length-at-infinity (L_{inf}), age at maturation (A_{50}) and length at maturation (L_{50}); (2) indices of fishing effect: long-term mean and variability of mortality ratio (i.e. fishing mortality/natural mortality, F/M); and (3) indices of temperature effect: long-term mean and variability of temperature. I used the mortality ratio (F/M) to reflect the fishing strength among different stocks. Because fisheries management usually sets optimal fishing mortality (F_{opt}) proportional

to natural mortality (M) (Walters and Martell 2002), here I defined mortality ratio as fishing mortality normalized by natural mortality (F/M). When comparing multiple stocks with different natural mortalities, the mortality ratio can better reflect the impact of fishing pressure for cross-stock analyses.

To examine whether life history traits, long-term mean and variability of fishing and temperature have influenced the relative contribution of fishing and temperature effect, I first used simple univariate regression analysis to test each variable above. I then build a linear mixed effect model (LMM) with the same variable as fixed effect and habitat as random effect to check if the observed pattern remains.

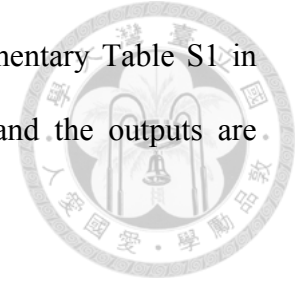
Comparing the performance of univariate SBIs to variation partitioning

To demonstrate the efficiency of variation partitioning, I compared the P value of explained fraction in the variation partitioning to the P value in regression with univariate SBIs. The univariate SBIs considered in the analysis were: 95% percentile of length class (L_{95}), mean length, Shannon diversity, Pielou's evenness index, and skewness. After calculating the univariate SBIs, each SBI was fitted to a regression model where $SBI \sim temperature + fishing + temperature*fishing$. If the P value of variation partitioning were lower than that of multilinear regression, it would suggest that variation partitioning is more efficient than univariate SBIs in terms of rejecting the null hypothesis.

Computation and data availability

All computation was done with R version 3.3.3. Variation partitioning was carried out using R package *vegan* (Oksanen et al. 2017). The linear mixed effect model was done with R package *lme4* (Bates et al. 2015). Further model testing and model

diagnostics were done with R package lmerTest (Kuznetsova et al. 2017). The original data (except few stocks via personal communications, see supplementary Table S1 in appendices for details), the R scripts to carry out all analyses, and the outputs are available at: <https://zenodo.org/record/1211120>.



Results and Discussion

My results of variation partitioning showed that the variance of size structure could be appreciably explained by fishing (on average of 10.9%), which is significantly higher than that of temperature and interaction ($P=0.019$ and $P=0.00023$ in ANOVA with paired t-test) (Figure 3-1). Specifically, 12 out of 28 stocks were significantly affected by fishing while 7 stocks were significantly associated with temperature (Table 3-2); whereas, the interactive effect is small in most of stocks (Table 3-2).

I also found difference in fishing and temperature effect among regions (Figure 3-2) and habitat types (Figure 3-3). Fraction of variation explained by fishing is significantly different from temperature ($P=0.005$) and interaction ($P<0.001$) in the west US. Both fishing and temperature effects are not significantly different from interaction in Alaska ($P=0.74$ and $P=0.73$) and North Sea ($P=0.27$ and $P=1$) (Figure 3-2). Among habitat types, fishing effect on size structure was significantly different from both temperature and interaction for demersal species ($P=0.0014$ and $P<0.001$ ANOVA with paired t-test) (Figure 3-3).

I employed the variation partition approach to analyze the time-series data of size structure of exploited stocks and found that fishing effect on size structure prevails (Table 3-2). Such commensurate result goes with the study that analyzed the stock biomass of 28 stocks in the Northeast Atlantic (Rouyer et al. 2014); that is, in a large-scale, fishing is the most critical factor. My analyses echo the increasing concern

over effects of fishing on size structure of exploited stocks (Blanchard et al. 2005, Planque et al. 2010, Cheung et al. 2013a, Ginter et al. 2015).

I note however, many of these studies applied univariate size-based indicators (SBIs) as proxies for the change of fish size structure. My approach incorporates the full size structure information in the analysis without assuming distribution of size data. Comparison between variation partitioning and univariate SBIs suggests that variation partitioning is more efficient in rejecting the null hypothesis (p-value is smaller) than the univariate SBIs (Figure 3-5), particularly in detecting temperature effects (Probability of success=0.63, $P=0.003$) although only marginally in fishing (Probability of success=0.56, $P=0.10$). In other words, variation partitioning can be a useful complementary method to investigate the external forcings on size structure of fish populations, in addition to univariate SBIs.

My multi-stock meta-analytical framework also allows us to investigate how life history traits, and long-term mean and variability of fishing and temperature influence on the explained variation of size structure responding to fishing or temperature. The stocks experienced higher fishing variability (CV of mortality ratio) is more responsive to temperature effect in their size structure (Table 3-3, Figure 3-4d, $P=0.038$). This supports my hypothesis that fishing elevates the sensitivity of exploited stocks in responding to environmental changes.

Surprisingly, I found none of the life history traits is able to explain the fishing and temperature effect (Figure S4, S6). Also, the total adjusted R^2 (Table 3-2) suggests that fishing plus temperature explained at most 44% of variation among 28 stocks. There may be other factors associated with body size, such as oxygen limitation of thermal tolerance (Pörtner and Knust 2007), affect the response to fishing/temperature effect in the size structure.

Through the application of variation partitioning, I had expected the efficacy to identify interactive effect of fishing and temperature on the size structure. However unexpectedly, my results indicate that the interaction effect is very weak (Figure 3-1). This finding may superficially be interpreted as evidence for lack-of interaction of fishing and temperature on size structure because fishing effects have dominated. However, I caution the interpretation of this finding, as variation partitioning is a linear variance decomposition method, which cannot account for nonlinear interactions.

While I demonstrate the efficacy of our size-structure based, meta-analytical framework to examine fishing and temperature effects on size composition of exploited stocks, I shall point out some caveats in our study. First, fishery-dependent data may lose some information due to the discard of small-size individuals. Second, there were fewer pelagic species than demersal and benthic species in our dataset, which might cause biased interpretation. Third, I assume an instantaneous response or a fixed lag in order to relate changes in size structure to changes in temperature, and I cannot provide detailed information concerning size class-specific response. This may be an important concern, because, for example, a warm year may lead to a strong year class and therefore affect the size structure of this year (Daufresne et al. 2009b, Pekcan-Hekim et al. 2011, Heikinheimo et al. 2014), whereas the effect of temperature on the asymptotic body size may occur for several years.

Conclusion

I introduced the size-structure based approach relying on variation partitioning to quantify fishing and temperature effects on size composition of exploited fish stocks, instead of focusing on univariate size-based indicators. Through our multi-stock meta-analytical framework, I found fishing explained most of the variation (Figure 3-1),

but difference existed between different regions (Figure 3-2) and habitats (Figure 3-3). I acknowledge that our analytical method still assumes linear responses of size structure to external forcings (as all univariate SBIs analyses do), because the nonlinear response forms remain unknown. Nevertheless, our analytical framework is a step toward better quantification of fishing and temperature effects on the size structure of exploited stock in the context of life history theory. The information gained here may be useful for ecosystem-based approaches to fisheries.

Table 3-1 Data regions and periods for the 28 commercial stocks. The abbreviation in the bracket indicates the location of stock: AI, Aleutian Islands; EBS, East Bering Sea; GOA, Gulf of Alaska.

Area	Species	Common Name	Data period	Data length
West US	<i>Atheresthes stomias</i>	Arrowtooth flounder	1986-2006	20
West US	<i>Sebastes goodie</i>	Chilipepper rockfish	1978-2006	28
West US	<i>Sebastes crameri</i>	Dark blotched rockfish	1977-2008	31
West US	<i>Microstomus pacificus</i>	Dover Sole	1966-2004	38
West US	<i>Parophrys vetulus</i>	English Sole	1965-2008	43
West US	<i>Ophiodon elongatus</i>	Lingcod	1965-2008	43
West US	<i>Sebastolobus altivelis</i>	Longspine thornyhead	1981-2003	22
West US	<i>Eopsetta jordani</i>	Petrale sole	1966-2008	42
West US	<i>Sardinops sagax</i>	Sardine	1981-2008	27
West US	<i>Sebastes diploproa</i>	Splitnose rockfish	1978-2008	30
West US	<i>Sebastes ruberrimus</i>	Yelloweye rockfish	1978-2007	29
Alaska (AI)	<i>Gadus chalcogramma</i>	Walleye pollock	1983-2006	9
Alaska (GOA)	<i>Gadus chalcogramma</i>	Walleye pollock	1984-2009	24
Alaska (EBS)	<i>Hippoglossoides elassodon</i>	Flathead sole	1982-2010	28
Alaska (GOA)	<i>Hippoglossoides elassodon</i>	Flathead sole	1984-2009	11
Alaska (EBS)	<i>Gadus macrocephalus</i>	Pacific cod	1982-2009	27
Alaska (GOA)	<i>Gadus macrocephalus</i>	Pacific cod	1984-2009	11
Alaska (GOA)	<i>Glyptocephalus zachirus</i>	Rex sole	1978-2007	11
North Sea	<i>Gadus morhua</i>	Cod	1977-2014	37
North Sea	<i>Melanogrammus aeglefinus</i>	Haddock	1977-2014	37
North Sea	<i>Clupea harengus</i>	Herring	1977-2014	38
North Sea	<i>Scomber scombrus</i>	Mackerel	1980-2014	34
North Sea	<i>Trisopterus esmarkii</i>	Norway pout	1984-2014	30
North Sea	<i>Pleuronectes platessa</i>	Plaice	1977-2014	37
North Sea	<i>Pollachius virens</i>	Saithe	1977-2014	37
North Sea	<i>Solea solea</i>	Sole	1977-2014	37
North Sea	<i>Sprattus sprattus</i>	Sprat	1977-2014	37
North Sea	<i>Merlangius merlangius</i>	Whiting	1990-2014	24

Table 3-2 Results of variation partitioning showing the relative contribution of fishing, temperature, and their interactive effect to the total variation (in term of adjusted R² value) for each of the 28 stocks.

Area	Species	Fishing	Interaction	Temp.	Total adjR ²
West US	<i>Atheresthes stomias</i>	0.211	0.000	0.070	0.262‡
West US	<i>Sebastes goodie</i>	0.176	0.000	0.000	0.173
West US	<i>Sebastes crameri</i>	0.012	0.000	0.030	0.029‡
West US	<i>Microstomus pacificus</i>	0.038	0.001	0.094	0.134
West US	<i>Parophrys vetulus</i>	0.000	0.005	0.021	0.009§
West US	<i>Ophiodon elongatus</i>	0.214	0.000	0.058	0.253‡
West US	<i>Sebastolobus altivelis</i>	0.391	0.000	0.006	0.392‡
West US	<i>Eopsetta jordani</i>	0.093	0.000	0.005	0.093
West US	<i>Sardinops sagax</i>	0.033	0.000	0.035	0.057§
West US	<i>Sebastes diploproa</i>	0.122	0.000	0.015	0.110
West US	<i>Sebastes ruberrimus</i>	0.312	0.045	0.040	0.398§
Alaska (AI)	<i>Gadus chalcogramma</i>	0.000	0.000	0.368	0.266
Alaska (GOA)	<i>Gadus chalcogramma</i>	0.000	0.042	0.000	0.000
Alaska (EBS)	<i>Hippoglossoides elassodon</i>	0.000	0.000	0.064	0.025‡
Alaska (GOA)	<i>Hippoglossoides elassodon</i>	0.134	0.000	0.000	0.109§
Alaska (EBS)	<i>Gadus macrocephalus</i>	0.071	0.000	0.034	0.104§
Alaska (GOA)	<i>Gadus macrocephalus</i>	0.003	0.022	0.000	0.000
Alaska (GOA)	<i>Glyptocephalus zachirus</i>	0.312	0.000	0.059	0.226
North Sea	<i>Gadus morhua</i>	0.067	0.078	0.094	0.239§
North Sea	<i>Melanogrammus aeglefinus</i>	0.139	0.000	0.011	0.116‡
North Sea	<i>Clupea harengus</i>	0.003	0.009	0.001	0.013§
North Sea	<i>Scomber scombrus</i>	0.000	0.011	0.000	0.000
North Sea	<i>Trisopterus esmarkii</i>	0.000	0.000	0.001	0.000
North Sea	<i>Pleuronectes platessa</i>	0.292	0.112	0.037	0.440
North Sea	<i>Pollachius virens</i>	0.027	0.042	0.037	0.106
North Sea	<i>Solea solea</i>	0.000	0.012	0.072	0.078‡
North Sea	<i>Sprattus sprattus</i>	0.025	0.000	0.102	0.108
North Sea	<i>Merlangius merlangius</i>	0.372	0.000	0.001	0.351§

* indicates $P < 0.05$; ** indicates $P < 0.01$; § indicates maximum adjusted R² at 1-year lag;

‡ indicates maximum adjusted R² at 3-year lag.

Table 3-3 Results of univariate linear regression analysis on % variation explained by fishing or temperature versus each life history trait, mean mortality ratio (meanF_M), CV of mortality ratio (cvF_M), mean temperature (meanTemp), and CV of temperature (cvTemp).

		A ₅₀	L ₅₀	L _{inf}	K	meanF_M	cvF_M	meanTemp	cvTemp
Fishing	coeff.	0.014	-0.001	0.000	-0.089	-0.004	0.075	0.009	-0.022
	P value	0.125	0.622	0.596	0.509	0.840	0.511	0.163	0.459
Temperature	coeff.	0.000	0.001	0.000	0.040	0.004	0.122	-0.003	-0.017
	P value	0.975	0.523	0.927	0.599	0.673	0.048	0.343	0.308

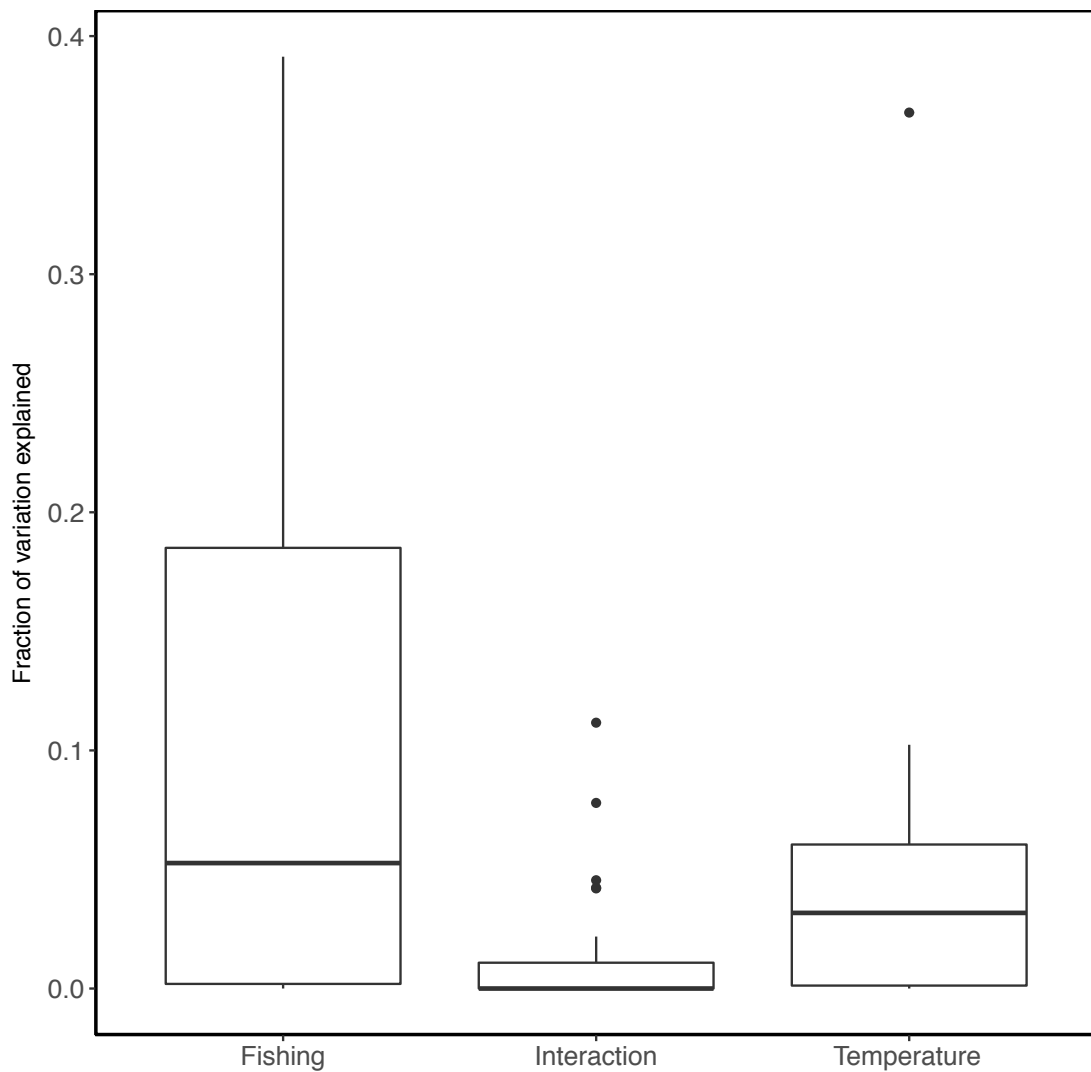


Figure 3-1 Boxplot shows the variation of size structure explained by the fishing, temperature, and interactive effect. Results of ANOVA indicate that the fraction of variation explained by fishing is significantly higher than the temperature ($P=0.019$) and interactive effect ($P<0.001$), but fraction of variation explained by temperature is not significantly different from interaction ($P=0.344$).

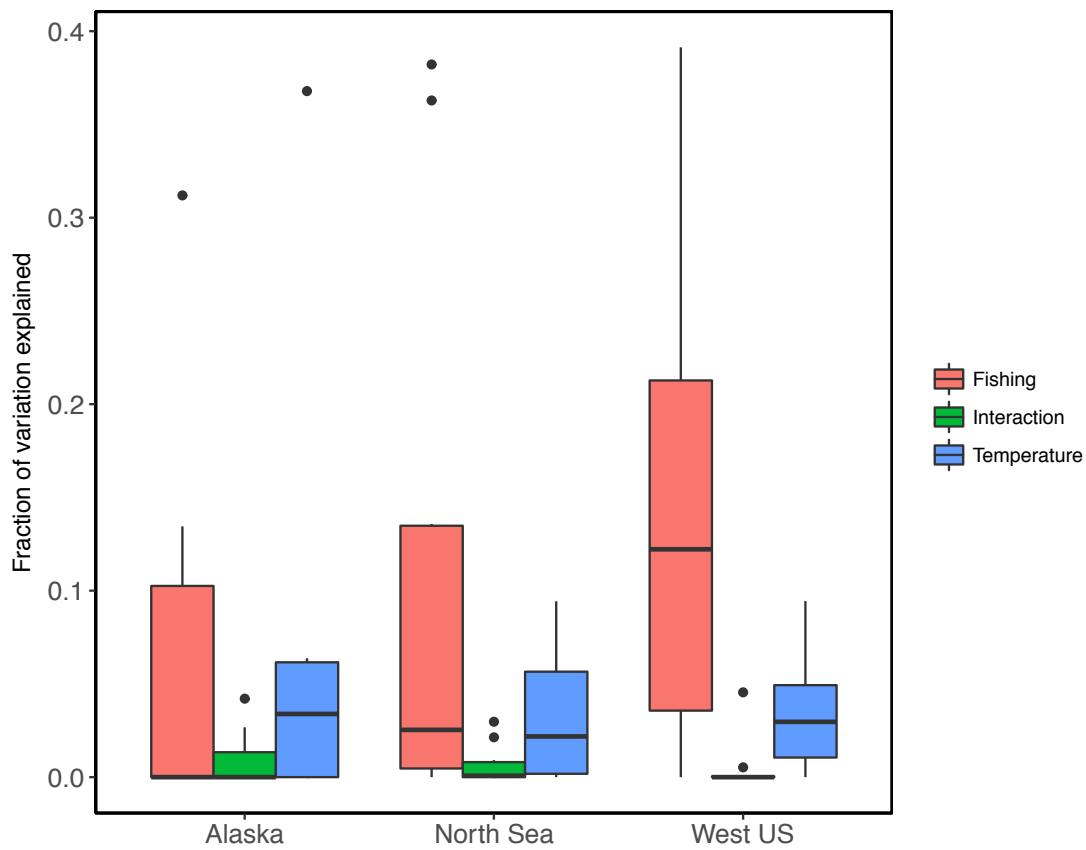


Figure 3-2 Boxplot shows the variation of size structure explained by the fishing, temperature, and interactive effect grouped by areas. Fraction of variation explained by fishing is significantly different from both temperature ($P= 0.005$) and interaction ($P<0.001$) in West US.

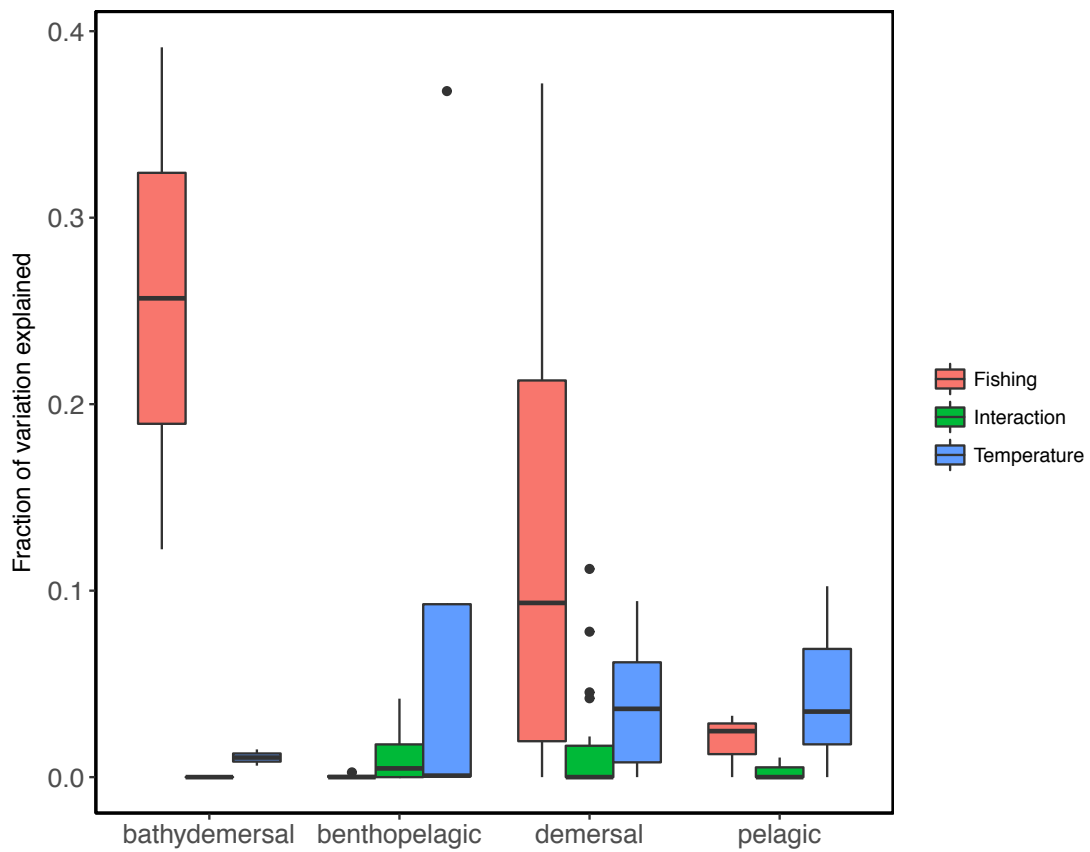


Figure 3-3 Boxplot shows the variation of size structure explained by the fishing, temperature, and interactive effect grouped by the habitat of species. Particularly, fraction of variation explained by fishing is significantly different from both temperature ($P=0.0014$) and interaction ($P<0.001$) for demersal species.

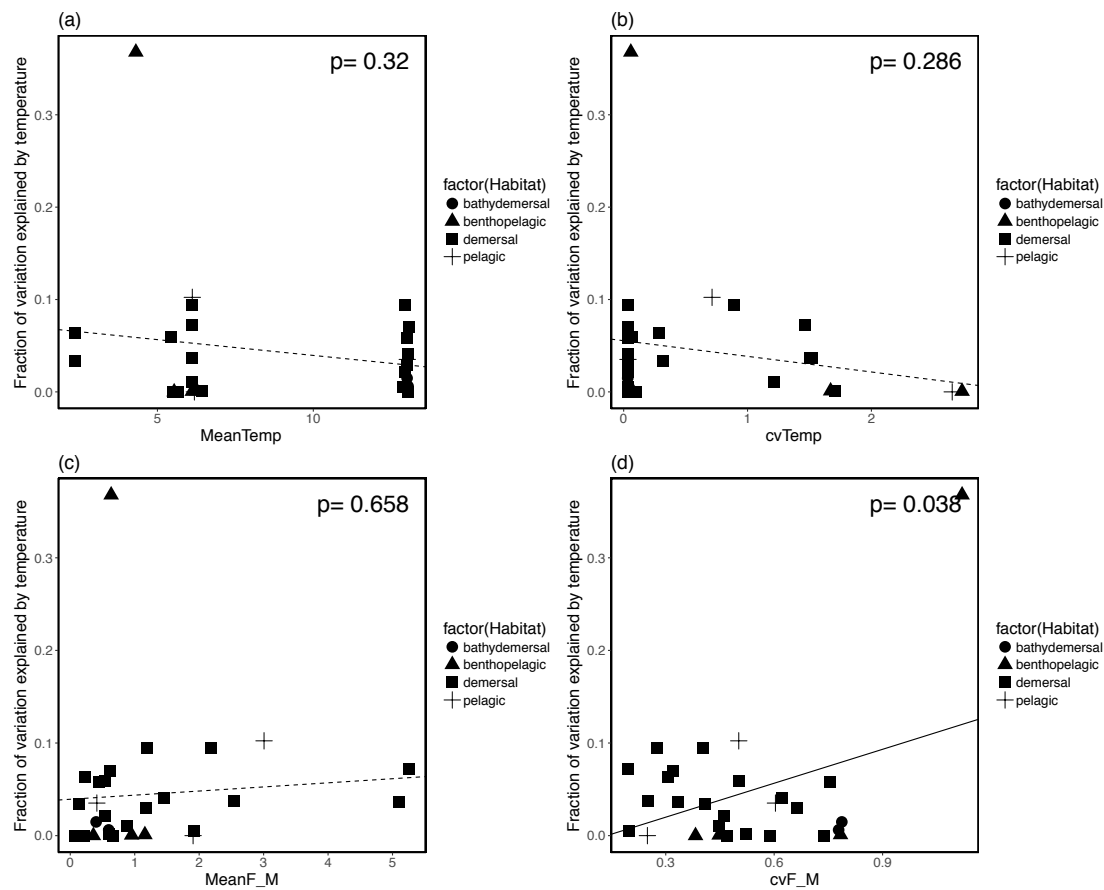


Figure 3-4 Explained variation by temperature in relation to the mean and CV of mortality ratio or temperature. The line is the best-fitted regression line based on the linear mixed effect model with each fishing/temperature index as fixed effect and habitat as random effect. The solid line indicates the significant result (d).

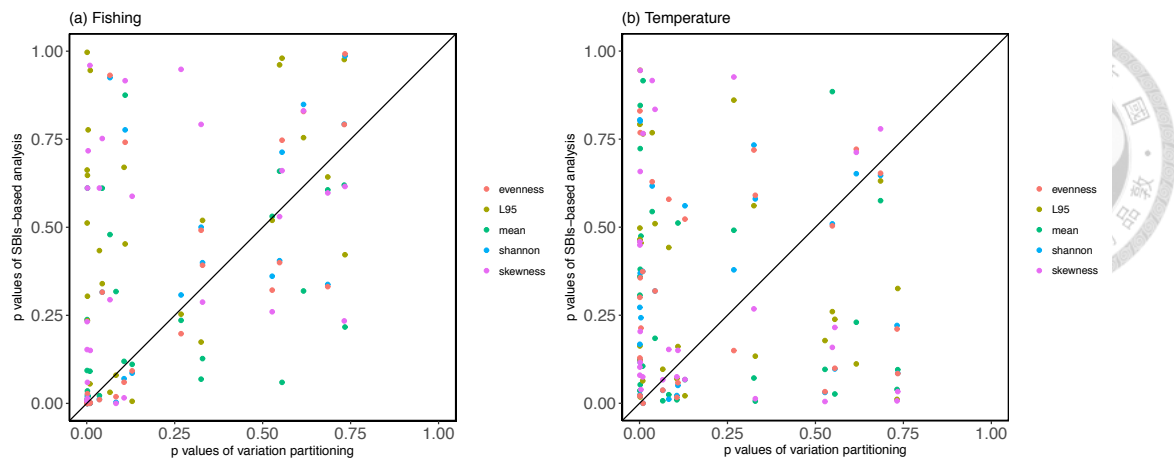
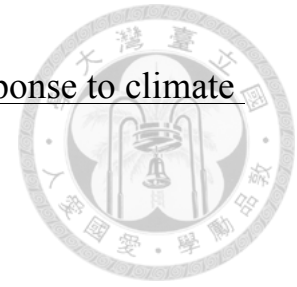


Figure 3-5 Comparison of P values of (a) fishing and (b) temperature effect estimated from the variation partitioning approach versus univariate SBIs. The diagonal line represents the 1:1 line. Results of binomial test indicate that variation partitioning is more efficient in rejecting the null hypothesis (p -value is smaller) than the univariate SBIs in detecting temperature effects (Probability of success=0.63, $P=0.003$) and marginally in fishing effects (Probability of success=0.56, $P=0.10$)

Chapter 4 Stage dependency in species distribution as response to climate change



Introduction

Distributional changes for marine population have been documented by many studies (Parmesan and Yohe 2003, Walther 2010). Meta-analysis at global scale suggests that pole-ward shifting prevails, but response may vary at different scale (Chen et al., 2011). It has also been suggested that species may respond to local temperature (Pinsky et al. 2013). Still the other studies try to link the distributional response to exploitation status, biogeography or life history trait. In California region, exploited species are more sensitive to climate change (Hsieh et al. 2008b) and the responses vary between oceanic and coastal species. It was found in North Sea that small, short-life span species are more likely to shift poleward (Perry et al., 2005), but the case study in Japan Sea found the opposite (Tu et al. 2015). These studies reveal a complex picture for the species distributional response to climate change.

However, previous studies often treated population as a whole or focused only on the adult stage. These studies overlooked the fact that age/size structure is one of the important biological processes that bear great influence on how the population spatial structure responds to environmental process. For example, individuals of different age/size may inhabit different areas due to age/size specific habitat and mobile capabilities. This phenomenon, often refer as ontogenetic migration, receives relatively less attention until recently (Barbeaux and Hollowed 2018). Previous studies suggest ontogenetic migration of marine species is common (Wilbur 1980, Gibson et al. 2002,

Kotwicki et al. 2005, Hoff 2008, Petitgas et al. 2013); however, studies designed to decipher whether ontogeny could affect population response to climate remain scarce.

Diverse life histories within a marine ecosystem present multiple avenues for climate to impact individual species as they grow and mature (Rijnsdorp et al. 2009, Petitgas et al. 2013). Evaluating effects of climate variability at different life stages across multiple species could help identify which species are sensitive to changes in the environment and whether consistent chokepoints exist for species with similar strategies.

In this study, I aim to investigate how fish at different life stages are affected by climate change in their spatial distribution with contrast between target and bycatch species. Specifically, I test the following hypothesis about difference between adult and juvenile stages in response to climate change. First, I hypothesize that adults are more responsive to environmental changes by moving faster than juveniles, considering that mobility is proportional to the body size (Strona et al. 2012). I will also examine whether the catch status and biogeography affect the pattern of responses, as the difference among the biogeography groups were found in abundance (Engelhard et al., 2011). Secondly, I examine whether adults and juveniles exhibit similar response to changing temperature in their moving direction. I expect to find that adults and juveniles are more likely to move in the same direction if the species has greater overlapped spawning and nursery ground. High overlapping ground suggests that both stages occupy similar niche in the system and thus should exhibit similar response to climate. Results from this study may help us understand whether and how adults and juveniles respond differently to climate change, providing new insights for ecosystem-based fisheries management.

Material and method

Fish size and distribution data

Fish size and distribution data was collected until 2017 in the North Sea during the International Bottom Trawl Survey (IBTS), obtained from the DATRAS database operated by the International Council for the Exploration of the Sea (ICES). IBTS surveys were carried out at least two hauls per ICES statistical rectangles of 1° latitude \times 0.5° longitude per quarter of the year, which provided a good coverage for entire North Sea. Survey was conducted in both 1st and 3rd quarter after 1991. Since many species start to settle at nursery ground on the 3rd quarter (Nicolas et al. 2014), only data after 1991 were used in the analysis. I used the catch rate per length class per subarea to study the distribution of each species.

Since the IBTS targets at demersal fish, I included only demersal/benthopelagic species that were caught at a minimum of 10 subareas in each quarter and year. The selected species consisted of both target and by-catch species, in which the target species generally have a higher trophic level than by-catch species (Table 4-1). I used the juvenile length threshold found in the literatures was used to separate the adults and juveniles.

For the environmental factors, I used the near-bottom temperature of the respective quarters at North Sea (53°N – 59°N , 3°W – 10°E) to represent the climate effect in the North Sea. The data come from the station observations of hydrochemical measurements from the ICES Oceanographic database (<http://ocean.ices.dk/HydChem/HydChem.aspx>), with coverage of almost the entire North Sea.

Temperature effect on distribution

To analyze the temperature effect on distribution, I calculated the

abundance-weighted mean latitude and longitude for both the adult and juvenile stages in each year for each species. An example of cod is shown in Figure 1. This is the centroid of the distribution that will be used for further analysis.

To understand how adult and juvenile stages respond to temperature, I separated the analysis into two parts. First, I performed regression analysis between the latitude of centroid and temperature by generalized least squared method with correlation structure of AR(2) process to account for the serial correlation in the time series for quarterly records (only Q1 and Q3). The regression coefficient b_1 ($^{\circ}\text{latitude}/^{\circ}\text{C}$) in $\text{latitude} \sim b_1 * \text{temperature} + b_0$ from the generalized least squared method represents the moving velocity with respect to the temperature. For summarizing the result, I took the absolute value of b_1 to turn the velocity into speed for comparing among different catch status and biogeography groups.

Secondly, I compared the moving direction of adult and juvenile stages. To obtain the direction from movement of centroid, I converted the time series of centroid into vector by taking first-difference. The time series were further transformed into the polar coordinate, which transformed the vector into two components: angle (θ) and strength (ρ). I took the angle component as the direction of movement for further analysis.

I then performed correlation analysis between angle component of adult and juvenile. If significant correlation exists in the moving direction between the two stages, I further investigated whether it is related to the distributional overlap between adult and juvenile habitats (spawning and nursery grounds). Here, I assume that if the adult and juvenile moves in the same direction, the adult and juvenile may have greater overlap in their distribution because two life stages occupy similar niche. To quantify the overlap between adult and juvenile, I first calculate total number of subarea occupied by either adult or juvenile in given quarter and year (full area). Then I calculate the total number

of subarea occupied by both adult and juvenile. The ratio of overlapped area to full area, which is the total number of overlapped subarea divided by the full area, is used to represent the habitats overlap in cross-species comparison. By taking the ratio, I can account for the difference between habitat sizes among species. I use the annual average value of occupancy ratio to represent the general condition for a given species.

Result

My result shows 5 species are sensitive to temperature in the latitudinal shift adult stages, namely cod, haddock, hake, Norway pout and grey gurnard (Table 4-2). Among them, cod, haddock and grey gurnard are also sensitive to temperature at juvenile stage. These species have coherent response in adult and juvenile stages as the signs of regression coefficient are the same.

Generally, the adult moves faster than juvenile in the latitudinal shift (Figure 4-2). The Mann-Whitney U test indicates significant difference ($P=0.036$) between two stages. Since no bycatch species shows significant latitudinal shifts with temperature in juvenile stage, I only compare difference between the adult stage of target and bycatch species. Though adults of target species tend to move faster than bycatch, it also has larger variation and shows no significant difference to bycatch species ($P=0.20$ in Mann-Whitney U test, Figure 4-3(a)). In addition, no significant difference is found between biogeography groups ($P=0.79$ in Mann-Whitney U test, Figure 4-2(b)).

The direct comparison of moving direction shows large variation among species in the feather plot (Figure 4-3). For example, the adult and juvenile moved to different direction through time in cod. On the contrary, the adult and juvenile are heading toward the same direction in grey gurnard. The correlation of moving direction between adult and juvenile suggests only hake, saithe, grey gurnard and long rough dab move in

the same direction (Table 4-2). Also, the species that adult and juvenile move in the same direction are more likely to have more overlapping in distribution among two life stages (Figure 4-5).



Discussion

My analysis found about half of the species examined show significant latitudinal shift with temperature in adult stages, while about less than 1/3 in juvenile stages (Table 4-2). In addition, adult generally moves faster than juvenile stages among species with significant latitudinal shift due to temperature (Figure 4-2). Some of the species' latitudinal shifts in response to temperature are consistent with previous study (Perry et al. 2005), which also found cod, grey gurnard and Norway pout significantly correlated with temperature.

However, the same study didn't found significant relationship between temperature and latitudinal shift in hake and haddock as seen only at adult stage in my analysis (Table 4-2). This suggests that stage-specific response, which was neglected in the previous study, actually plays an important role in certain species. But why hake and haddock show significant response only at adult stage is unclear. This may need further investigation. Even so, the general pattern supports my hypothesis that the difference in distributional response to temperature is related to the difference in body size between life stages (Figure 4-3).

In addition, the difference between adult and juvenile is not significant among catch status and biogeographic groups (Figure 4-4). Although the sample size is relatively small, it reaches different conclusion with previous study combining both adult and juvenile but focus on abundance from the same NS-IBTS survey data (Engelhard et al. 2011). The study examines both abundance and distribution of

demersal species in Japan Sea not only found difference between abundance and distributional response, but also found ecological and life history traits can only partially explain the response (Tu et al. 2015). Recent study on species distribution in Gulf of Maine found that none of the ecological traits examined can explain the distributional response due to temperature (Schuetz et al. 2018). The complex pattern of climate sensitivity in species response may due to behavioral (Woods et al. 2015), physiological flexibility (Kearney et al. 2012, Dillon et al. 2016) or rapid adaptation (Bradshaw and Holzapfel 2006, Visser 2008, Hoffmann and Sgrò 2011). This may be a possible direction to design empirical studies for clarification.

Interestingly, I found species that adult and juvenile move in the same direction (Table 4-2) are more likely to have overlapped distribution for these two stages (Figure 4-5). Such high overlapping in distribution may indicates that that adult and juveniles of given species actually occupied similar niches. Therefore, the given species are more likely to have similar response. For the two species that adult and juvenile move in separate direction, hake is generally known as a widely distributed species in Northeast Atlantic (ICES, 2006) which indicates that it may be able to occupy a wider niche than other species in North Sea. Therefore, a low overlapped area ratio (0.329) and negative correlation in moving direction (-0.084) between adult and juvenile stage is not surprising. But little is known about the biology of saithe, except the fact that it is a semi-pelagic species most abundant in the northern part of North Sea (ICES, 2006). It is possible that saithe is also a widely distributed species, with recapture was found at Iceland and Norwegian coast in previous study (Armannsson et al., 2007).

Finally, the result from this study shows the ontogenetic difference and overlap in distribution may provide some management insights for reducing discards. North Sea flatfish trawl fisheries has long been known for the high discard rate. Several discard

reduction measures such as increasing mesh size and imposing a minimum landing size have been imposed in early 2000, but these only promoted use of unselective trawls while the poor enforcement of the quota system has exacerbated discard quantities. (Catchpole et al, 2005). Both grey gurnard and long rough dab found significant correlation between adult and juvenile stage in moving direction (Table 4-2) are already bycatch species (Table 4-1). Grey gurnard even has a discard rate ranged between 72% and 89% of the total catch between 2012 to 2015 (ICES, 2016). In light of climate change, both adult and juvenile are possible to shift in distribution for these species. A proper spatial management procedure such as closure of fishing area needs to reflect the change in distribution so that it can reach the goal of discards reduction.

Conclusion

In this study, I found adult stage generally move faster as response to temperature change than juvenile stages. But overall no significant difference was found between the different biogeographic groups. Also, the species that adult and juvenile move toward the same direction are more likely to have more overlapping in distribution among the two life stages. This may indicate that adult and juvenile of given species actually occupies similar niches and therefore more likely to have similar response. The results from this study highlight the importance to take ontogenetic distribution shift into consideration when discussing the effect of climate change to fish species.

Table 4-1 Species used in analysis. The trophic level and biogeography is from Yang (1982) and the juvenile length is obtained from the ICES FishMap.

Species	Common name	Biogeography	Catch status	Trophic level	Juvenile (cm)
<i>Gadus morhua</i>	Cod	Boreal	Target	4.4	69.7
<i>Melanogrammus aeglefinus</i>	Haddock	Boreal	Target	4.1	30
<i>Merlangius merlangus</i>	Whiting	Lusitanian	Target	4.4	20
<i>Merluccius merluccius</i>	European hake	Lusitanian	Target	4.4	20
<i>Trisopterus esmarkii</i>	Norway pout	Boreal	Target	3.2	15
<i>Pleuronectes platessa</i>	European plaice	Boreal	Target	3.3	25
<i>Pollachius virens</i>	Saithe	Boreal	Target	4.4	20
<i>Eutrigla gurnardus</i>	Grey gurnard	Lusitanian	Bycatch	3.6	23
<i>Hippoglossoides platessoides</i>	Long rough dab	Boreal	Bycatch	3.7	14
<i>Limanda limanda</i>	Dab	Boreal	Bycatch	3.3	25
<i>Microstomus kitt</i>	Lemon sole	Boreal	Bycatch	3.3	27

Table 4-2 Regression coefficient linking latitudinal shift of centroid to temperature in the two stages (b_{adult} and b_{juvenile}) and the correlation coefficient of moving direction (θ , angle) between adult and juvenile stages for each species, respectively. The overlap ratio is the ratio of overlapped area divided by the full-occupied area.

(*denotes for $P < 0.05$, ** denotes for $P < 0.01$, *** denotes for $P < 0.001$)

Species	b_{adult}	b_{juvenile}	Corr_{θ}	Overlap ratio
Cod	0.264***	0.060**	0.268	0.406
Haddock	-0.114***	-0.076***	0.164	0.840
Hake	0.082**	-0.013	-0.084*	0.329
Whiting	-0.012	0.080	0.288	0.888
Norway pout	-0.139***	-0.077***	0.248	0.740
Plaice	-0.013	0.015	0.534	0.701
Saithe	0.001	0.037	-0.098*	0.059
Dab	-0.037	-0.009	0.586	0.661
Grey gurnard	0.091***	0.014	0.600*	0.815
Lemon sole	0.002	-0.053	0.077	0.592
Long rough dab	0.015	-0.025	0.523*	0.866

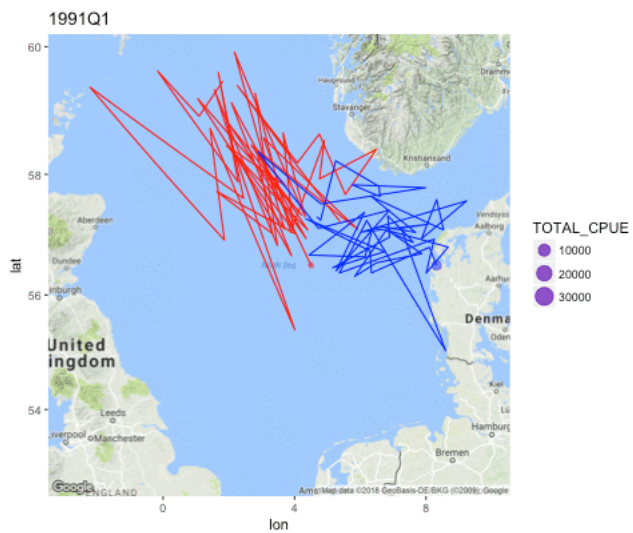


Figure 4-1 An example map showing of centroid changes through time (1991Q1-2014Q3) for adult (red) and juvenile (blue) stages using Atlantic cod.

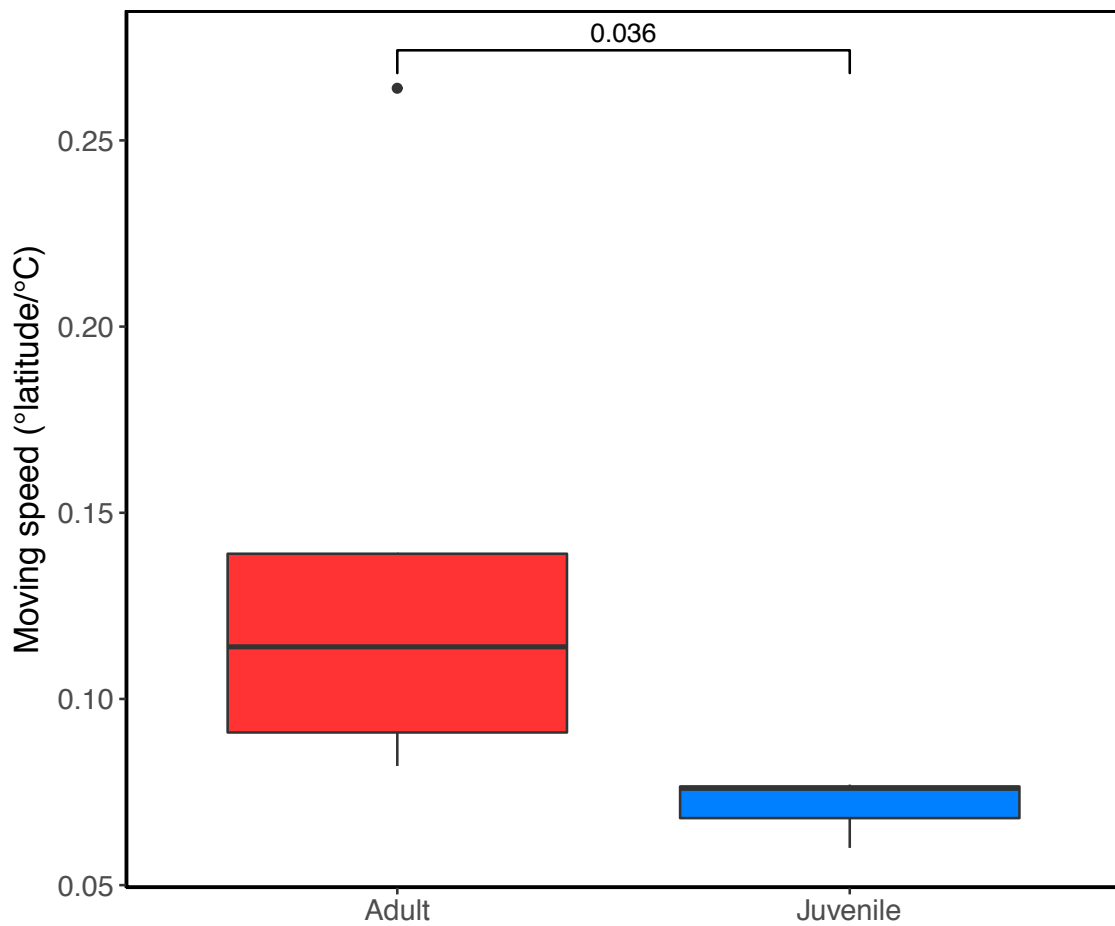


Figure 4-2 Box plot summarizing moving speed (absolute value of b_1 in latitude $\sim b_1 \times \text{temperature} + b_0$) as response of temperature for the adult and juvenile stages. Only the species found a significant relationship with temperature were included. The Mann-Whitney U test indicates significant difference ($P=0.036$) between two stages.

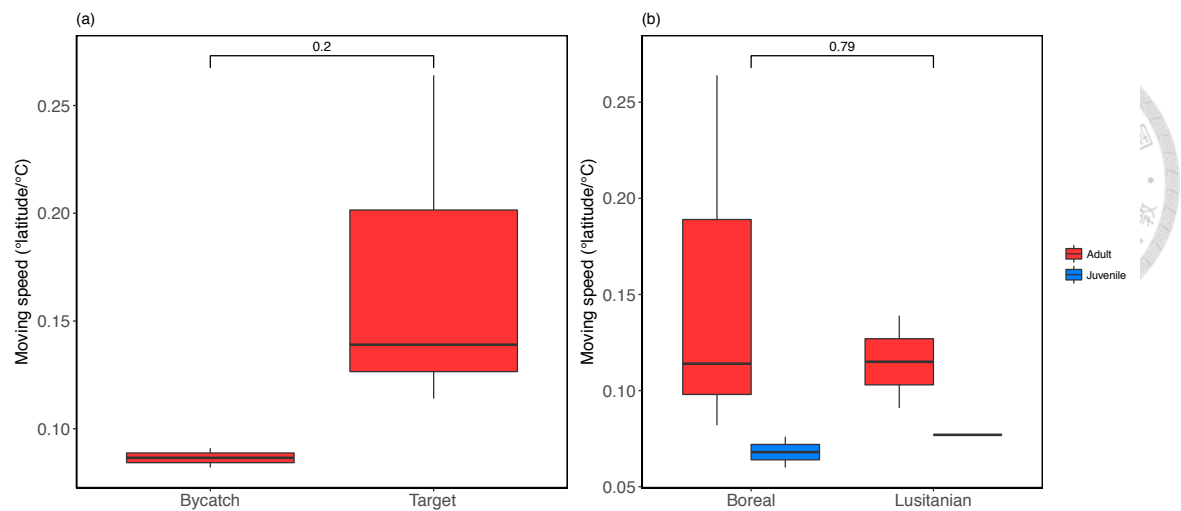


Figure 4-3 Box plot of summarizing moving speed (absolute value of b_1 in latitude $\sim b_1 * \text{temperature} + b_0$) as response of temperature for the different catch type and biogeographic groups. Only the species at given stage found a significant relationship with temperature were included. The Mann-Whitney U test indicates no significant difference between two catch types in adult stage (a) and biogeographic groups (b).

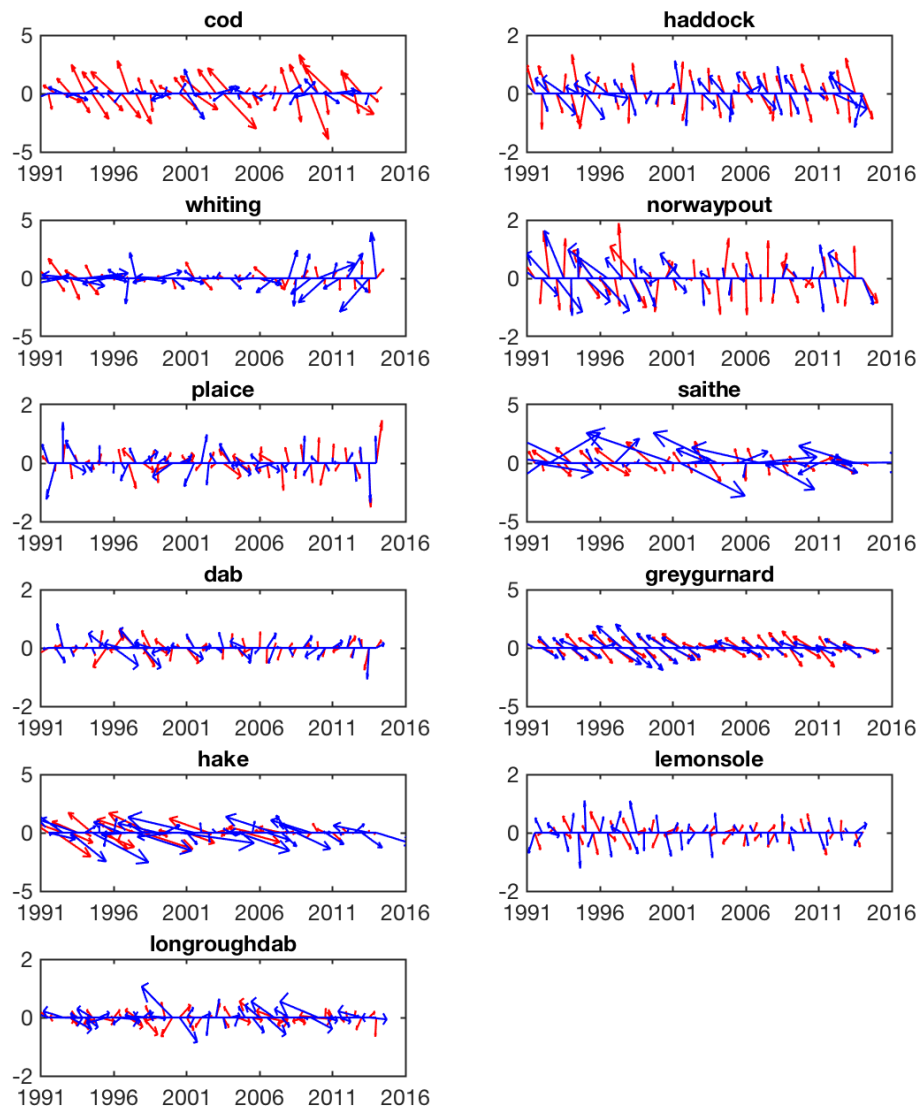


Figure 4-4 Feather plots for each species show the how moving direction of centroid varies through time. The red arrows denote adult stage, while the blue arrows denote juvenile stage.

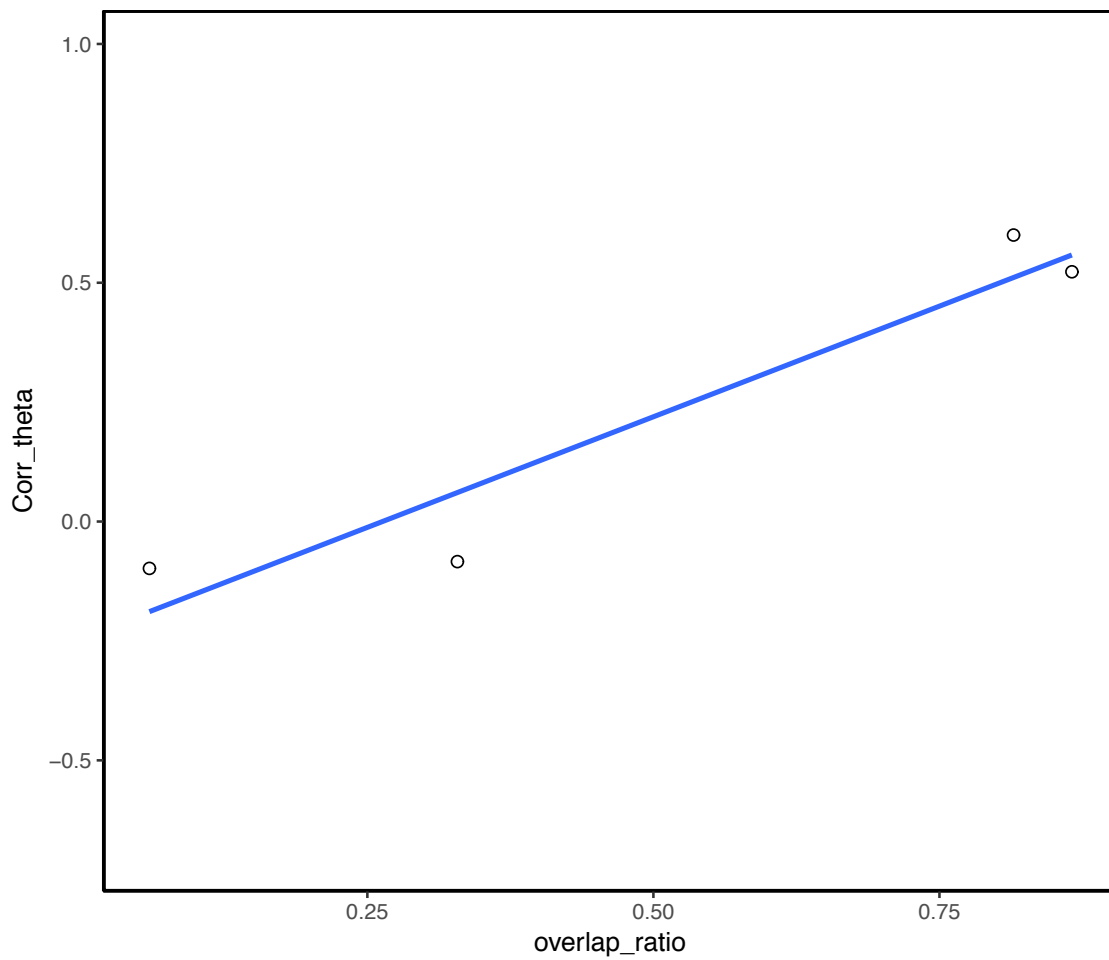
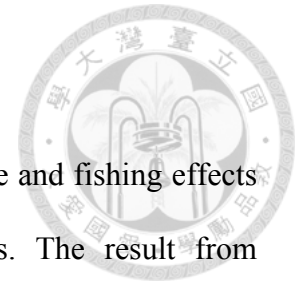


Figure 4-5 Relationship between ratio of overlapped area and correlation of moving direction between adult and juvenile stages. Species with high proportion of overlapped area are more likely to move in the same direction ($R^2=0.87$).

Chapter 5 Conclusion



In this thesis, I used three approaches to investigate the climate and fishing effects on distribution and size structure of exploited fish populations. The result from examining the distributional and abundance shift due to climate indicates that warming has greater negative effects on larger fishes in the Japan Sea. In addition, analyzing the entire size structure by variation partitioning to separate the fishing and temperature effect indicates that fishing explains most of the variations. Furthermore, analyzing the distribution shift shows adult stage generally moves faster as response to temperature change than juvenile stages. Also, the species whose adults and juveniles move toward the same direction are more likely to have more overlapping in distribution among the two life stages, indicating that adults and juveniles of given species occupying similar niches are more likely to have similar response. This may suggest ontogenetic difference should also be taken into consideration when assessing the impact of climate change.

Besides the results, there are several methodological remarks may be useful in the fisheries management. First, a clear theme emerges from the three chapters is the importance of body size for understanding the response of exploited populations to fishing and temperature. Population size structures and size-based life history traits can be easily linked with underlying mechanism. Some of the analytical method developed in this study, such as variation partitioning, may have potential to provide complimentary information for management.

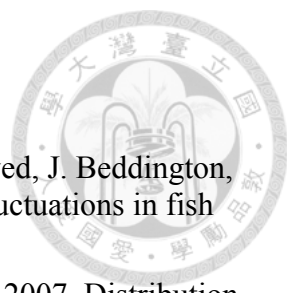
Another information that may have potential in management purpose is using mortality ratio for cross-stock comparison. Although natural mortality is very difficult to estimate, it actually includes the biological process such as species competition.

Current management scheme usually sets fishing mortality at certain spawning stock biomass (F_{SSB}) as management target. I found several stocks with fishing mortality much higher than their natural mortality, which may be a warning sign that the fishing intensity is too high even though it can maintain F_{SSB} .

Finally, the ontogenetic distribution shifts need to be taken into consideration for spatial management. There is difference in response to temperature between adults and juveniles. Species that has overlapped distribution between adults and juveniles not only occupy the same niche, but also are more likely to have higher discard rate with undesirable or uneconomical body size. To reduce the discard rate, seasonal or partial closure for such overlapped area may be necessary. Here I only used annual averages in the analysis; however, the overlap area may change through different quarters and years. Such management procedure may be needed for consistently review with incorporating the realtime survey data to reflect the change.

To sum up, advances in both method and continuing data collection are needed achieve the goal of integrated ecosystem assessment- quantitative evaluation and synthesis of information on physical, chemical, ecological and human processes that provide the scientific understanding to deliver advice on societal trade-off between different policy options. Size and distribution are two important characteristics of exploited fish populations that should be part of the evaluation in the ecosystem assessment. For an ecosystem under multiple stressor including warming and fishing, understanding the possible relationship between stressor, population and the ecosystem will always be the first step toward ecosystem-based management.

References

- 
- Anderson, C. N. K., C. H. Hsieh, S. A. Sandin, R. Hewitt, A. Hollowed, J. Beddington, R. M. May, and G. Sugihara. 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* **452**:835-839.
- Armannsson, H., S. T. Jonsson, J. D. Neilson, and G. Marteinsdottir. 2007. Distribution and migration of saithe (*Pollachius virens*) around Iceland inferred from mark-recapture studies. *ICES Journal of Marine Science* **64**:1006-1016.
- Barbeaux, S. J., and A. B. Hollowed. 2018. Ontogeny matters: Climate variability and effects on fish distribution in the eastern Bering Sea. *Fisheries Oceanography* **27**:1-15.
- Barnett, L. A. K., T. A. Branch, R. A. Ranasinghe, and T. E. Essington. Old-Growth Fishes Become Scarce under Fishing. *Current Biology*.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. 2015 **67**:48.
- Beaugrand, G., K. M. Brander, J. Alistair Lindley, S. Souissi, and P. C. Reid. 2003a. Plankton effect on cod recruitment in the North Sea. *Nature* **426**:661-664.
- Beaugrand, G., K. M. Brander, J. A. Lindley, S. Souissi, and P. C. Reid. 2003b. Plankton effect on cod recruitment in the North Sea. *Nature* **426**:661.
- Bell, R. J., D. E. Richardson, J. A. Hare, P. D. Lynch, and P. S. Fratantoni. 2015. Disentangling the effects of climate, abundance and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. *ICES Journal of Marine Science* **72**:1311-1322.
- Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* **29**:23-32.
- Berkeley, S. A., and E. D. Houde. 1978. Biology of two exploited species of halfbeaks, *Hemiramphus brasiliensis* and *H. balao* from southeast Florida. *Bulletin of Marine Science* **28**:624-644.
- Bianchi, G., H. Gislason, K. Graham, L. Hill, X. Jin, K. Koranteng, S. Manickchand-Heileman, I. Payá, K. Sainsbury, F. Sanchez, and K. Zwanenburg. 2000. Impact of fishing on size composition and diversity of demersal fish communities. *ICES Journal of Marine Science* **57**:558-571.
- Blanchard, J. L., N. K. Dulvy, S. Jennings, J. R. Ellis, J. K. Pinnegar, A. Tidd, and L. T. Kell. 2005. Do climate and fishing influence size-based indicators of Celtic Sea fish community structure? *ICES Journal of Marine Science* **62**:405-411.
- Bradshaw, W. E., and C. M. Holzapfel. 2006. Evolutionary Response to Rapid Climate Change. *Science* **312**:1477.
- Branch, T. A., R. Hilborn, A. C. Haynie, G. Fay, L. Flynn, J. Griffiths, K. N. Marshall, J. K. Randall, J. M. Scheuerell, E. J. Ward, and M. Young. 2006. Fleet dynamics and fishermen behavior : lessons for fisheries managers. *Canadian Journal of Fisheries and Aquatic Sciences* **1668**:1647-1668.

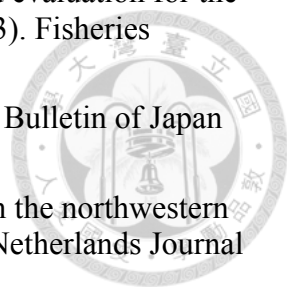
- Brunel, T., and G. J. Piet. 2013. Is age structure a relevant criterion for the health of fish stocks? *ICES Journal of Marine Science* **70**:270-283.
- Burrows, M. T., D. S. Schoeman, L. B. Buckley, P. Moore, E. S. Poloczanska, K. M. Brander, C. Brown, J. F. Bruno, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, W. Kiessling, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. B. Schwing, W. J. Sydeman, and A. J. Richardson. 2011. The pace of shifting climate in marine and terrestrial ecosystems. *Science (New York, N.Y.)* **334**:652-655.
- Catchpole, T. L., C. L. J. Frid, and T. S. Gray. 2005. Discards in North Sea fisheries: causes, consequences and solutions. *Marine Policy* **29**:421-430.
- Chen, I. C., J. K. Hill, R. Ohlemüller, D. B. Roy, and C. D. Thomas. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science (New York, N.Y.)* **333**:1024-1026.
- Cheung, W. W. L., J. L. Sarmiento, J. Dunne, T. L. Frolicher, V. W. Y. Lam, M. L. Deng Palomares, R. Watson, and D. Pauly. 2013a. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Clim. Change* **3**:254-258.
- Cheung, W. W. L., J. L. Sarmiento, J. Dunne, T. L. Frölicher, V. W. Y. Lam, M. L. Deng Palomares, R. Watson, and D. Pauly. 2013b. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change* **3**:254-258.
- Chiba, S., M. N. Aita, K. Tadokoro, T. Saino, H. Sugisaki, and K. Nakata. 2008. From climate regime shifts to lower-trophic level phenology: Synthesis of recent progress in retrospective studies of the western North Pacific. *Progress In Oceanography* **77**:112-126.
- Chiba, S., Y. Hirota, S. Hasegawa, and T. Saino. 2005. North – south contrasts in decadal scale variations in lower trophic-level ecosystems in the Japan Sea. *Fisheries Oceanography* **14**:401-412.
- Chiba, S., and T. Saino. 2002. Interdecadal change in the upper water column environment and spring diatom community structure in the Japan Sea: an early summer hypothesis. *Marine Ecology Progress Series* **231**:23-35.
- Cushing, D. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Pages 249-293 *Advances in marine biology*. Elsevier.
- Dahlgren, P. C., and B. D. Eggleston. 2000. Ecological process underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* **81**:2227-2240.
- Daufresne, M., K. Lengfellner, and U. Sommer. 2009a. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences* **106**:12788-12793.
- Daufresne, M., K. Lengfellner, and U. Sommer. 2009b. Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences of USA* **106**:12788-12793.

- de Roos, A. M., D. S. Boukal, and L. Persson. 2006. Evolutionary regime shifts in age and size at maturation of exploited fish stocks. *Proceedings of the Royal Society B: Biological Sciences* **273**:1873-1880.
- De Roos, A. M., L. Persson, and E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecology Letters* **6**:473-487.
- Dillon, M. E., H. A. Woods, G. Wang, S. B. Fey, D. A. Vasseur, R. S. Telemeco, K. Marshall, and S. Pincebourde. 2016. Life in the Frequency Domain: the Biological Impacts of Changes in Climate Variability at Multiple Time Scales. *Integrative and Comparative Biology* **56**:14-30.
- Doney, S. C., M. Ruckelshaus, J. Emmett Duffy, J. P. Barry, F. Chan, C. A. English, H. M. Galindo, J. M. Grebmeier, A. B. Hollowed, N. Knowlton, J. Polovina, N. N. Rabalais, W. J. Sydeman, and L. D. Talley. 2012. Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science* **4**:11-37.
- Dulvy, N. K., S. I. Rogers, S. Jennings, V. Stelzenmiller, S. R. Dye, and H. R. Skjoldal. 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* **45**:1029-1039.
- Engelhard, G. H., J. R. Ellis, M. R. Payne, R. ter Hofstede, and J. K. Pinnegar. 2011. Ecotypes as a concept for exploring responses to climate change in fish assemblages. *ICES Journal of Marine Science* **68**:580-591.
- Farmer, A. M., editor. 2012. *Manual of European Environmental Policy*. Routledge, London.
- Frank, K. T., B. Petrie, W. C. Leggett, and D. G. Boyce. 2018. Exploitation drives an ontogenetic-like deepening in marine fish. *Proceedings of the National Academy of Sciences* **115**:6422.
- Froese, R., and D. Pauly. 2013. FishBase.
- Fujioka, T., T. Takahashi, T. Maeda, T. Nakatani, and H. Matsushima. 1990. Annual life cycle and distribution of adult gurnard *Lepidotrigla microptera* in Mutsu Bay, Aomori Prefecture. *Nippon Suisan Gakkaishi* **56**:1553-1560.
- Fujiwara, K., T. Hirose, T. Miyajima, and A. Yamasaki. 2009. Miniaturization of the mature size of female *Hippoglossoides dubius* off Kyoto Prefecture. *Nippon Suisan Gakkaishi* **75**:704-706.
- Gibson, R., L. Robb, H. Wennhage, and M. Burrows. 2002. Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. *Marine Ecology Progress Series* **229**:233-244.
- Gibson, R. N. 1994. Impact of habitat quality and quantity on the recruitment of juvenile flatfishes. *Netherlands Journal of Sea Research* **32**:191-206.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001a. Effects of size and temperature on metabolic rate. *Science* **293**:2248-2251.
- Gillooly, J. F., J. H. Brown, G. B. West, V. M. Savage, and E. L. Charnov. 2001b. Effects of Size and Temperature on Metabolic Rate. *Science* **293**:2248.

- Ginter, K., A. Kangur, P. Kangur, and K. Kangur. 2015. Consequences of size-selective harvesting and changing climate on the pikeperch *Sander lucioperca* in two large shallow north temperate lakes. *Fisheries Research* **165**:63-70.
- González-Irusta, J. M., and P. J. Wright. 2016. Spawning grounds of Atlantic cod (*Gadus morhua*) in the North Sea. *ICES Journal of Marine Science* **73**:304-315.
- Griffith, D. A., and P. R. Peres-Neto. 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* **87**:2603-2613.
- Gwinn, D. C., M. S. Allen, F. D. Johnston, P. Brown, C. R. Todd, and R. Arlinghaus. 2015. Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish and Fisheries* **16**:259-281.
- Hanawa, K., T. Watanabe, N. Iwasaka, T. Suga, and Y. Toba. 1988. Surface thermal conditions in the western North Pacific. *Journal of Meteorological Society of Japan* **66**:445-456.
- Heikinheimo, O., Z. Pekcan-Hekim, and J. Raitaniemi. 2014. Spawning stock–recruitment relationship in pikeperch *Sander lucioperca* (L.) in the Baltic Sea, with temperature as an environmental effect. *Fisheries Research* **155**:1-9.
- Heino, M., B. Díaz Pauli, and U. Dieckmann. 2015. Fisheries-induced evolution. *Annual Review of Ecology, Evolution, and Systematics* **46**:461-480.
- Hidalgo, M., T. Rouyer, J. C. Molinero, E. Massut, J. Moranta, B. Guijarro, and N. C. Stenseth. 2011. Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series* **426**:1-12.
- Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* **71**:2171-2185.
- Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* **86**:2847-2859.
- Hoff, G. R. 2008. A nursery site of the Alaska skate (*Bathyraja parmifera*) in the eastern Bering Sea. *Fishery Bulletin* **106**:233-244.
- Hoffmann, A. A., and C. M. Sgrò. 2011. Climate change and evolutionary adaptation. *Nature* **470**:7335: 479.
- Hollowed, A. B., M. Barange, R. J. Beamish, K. Brander, K. Cochrane, K. Drinkwater, M. G. G. Foreman, J. a. Hare, J. Holt, S. i. Ito, S. Kim, J. R. King, H. Loeng, B. R. MacKenzie, F. J. Mueter, T. a. Okey, M. a. Peck, V. I. Radchenko, J. C. Rice, M. J. Schirripa, A. Yatsu, and Y. Yamanaka. 2013. Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science* **70**:1023-1037.
- Hsieh, C. H., 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., H. J. Kim, W. Watson, E. Di Lorenzo, and G. Sugihara. 2009a. Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. *Global Change Biology* **15**:2137-2152.
- Hsieh, C. H., C. S. Reiss, R. P. P. Hewitt, G. Sugihara, and S. C. Reiss. 2008a. Spatial analysis shows fishing enhances the climatic sensitivity of marine fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **65**:947-961.
- Hsieh, C. H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006a. Fishing elevates variability in the abundance of exploited species. *Nature* **443**:859-862.
- Hsieh, C. H., A. Yamauchi, T. Nakazawa, and W.-F. Wang. 2010a. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences* **72**:165-178.
- Hsieh, C. H., C. S. Chen, T. S. Chiu, K. T. Lee, F. J. Shieh, J. Y. Pan, and M. A. Lee. 2009b. Time series analyses reveal transient relationships between abundance of larval anchovy and environmental variables in the coastal waters southwest of Taiwan. *Fisheries Oceanography* **18**:102-117.
- Hsieh, C. H., C. S. Reiss, J. R. Hunter, J. R. Beddington, R. M. May, and G. Sugihara. 2006b. Fishing elevates variability in the abundance of exploited species. *Nature* **443**:859-862.
- Hsieh, C. H., S. C. Reiss, R. P. Hewitt, and G. Sugihara. 2008b. Spatial analysis shows 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. 2010b. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences* **72**:165-178.
- Hufnagl, M., M. a. Peck, R. D. M. Nash, T. Pohlmann, and A. D. Rijnsdorp. 2013. Changes in potential North Sea spawning grounds of plaice (*Pleuronectes platessa* L.) based on early life stage connectivity to nursery habitats. *Journal of Sea Research* **84**:26-39.
- Hutchings, J. A., and R. A. Myers. 1993. Effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2468-2474.
- Ives, A. R., and J. Zhu. 2006. Statistics for correlated data: phylogenies, space, and time. *Ecological Applications* **16**:20-32.
- Jakobsdóttir, K. B., H. Pardoe, Á. Magnússon, H. Björnsson, C. Pampoulie, D. E. Ruzzante, and G. Marteinsdóttir. 2011. Historical changes in genotypic frequencies at the Pantophysin locus in Atlantic cod (*Gadus morhua*) in Icelandic waters: evidence of fisheries-induced selection? *Evolutionary Applications* **4**:562-573.
- Jennings, S., S. P. R. Greenstreet, and J. D. Reynolds. 1999. Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology* **68**:617-627.
- Katoh, O., N. Nakagawa, S. Matsui, H. Yamada, and T. Watanabe. 2006. Long-term fluctuations of water temperature in the Japan Sea and the Tsushima Strait

- shown by data from prefectural observations along the coastal and offshore measurement lines. *Bulletin of Coastal Oceanography* **44**:19-24.
- Kawamura, S. 2009. The relationship between distribution of demersal fish and bottom environmental factors in the coastal waters of Northern Niigata Prefecture. *Bulletin of Niigata Prefecture Fisheries Marine Research Institute* **2**:3-14.
- Kearney, M. R., A. Matzelle, and B. Helmuth. 2012. Biomechanics meets the ecological niche: the importance of temporal data resolution." *Journal of Experimental Biology* **215**.6: 922-933.
- Keller, A. a., M. J. Bradburn, and V. H. Simon. 2013. Shifts in condition and distribution of eastern North Pacific flatfish along the U.S. west coast (2003–2010). *Deep Sea Research Part I: Oceanographic Research Papers* **77**:23-35.
- Kotwicki, S., T. W. Buckley, T. Honkalehto, and G. Walters. 2005. Variation in the distribution of walleye pollock (*Theragra chalcogramma*) with temperature and implications for seasonal migration. *Fishery Bulletin* **103**:574-587.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest Package: Tests in Linear Mixed Effects Models. 2017 **82**:26.
- Lambert, T. C. 1987. Duration and intensity of spawning in herring *Clupea harengus* as related to the age structure of the mature population. *Marine Ecology Progress Series*:209-220.
- Law, R., M. J. Plank, and J. Kolding. 2012. On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES Journal of Marine Science* **69**:602-614.
- Lawson, G. L., and G. A. Rose. 2000. Small-scale spatial and temporal patterns in spawning of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:1011-1024.
- Lough, R. G., P. C. Valentine, D. C. Potter, P. J. Auditore, G. R. Bolz, J. D. Neilson, and R. I. Perry. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. *Marine Ecology Progress Series*:1-12.
- MacCall, A. D. 1990. Dynamic geography of marine fish populations. Washington Sea Grant Program, Seattle.
- MacNeil, M. A., N. a. J. Graham, J. E. Cinner, N. K. Dulvy, P. a. Loring, S. Jennings, N. V. C. Polunin, A. T. Fisk, and T. R. McClanahan. 2010. Transitional states in marine fisheries: adapting to predicted global change. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365**:3753-3763.
- Mantua, N. J., and S. R. Hare. 2002. The Pacific Decadal Oscillation. *Journal of Oceanography* **58**:35-44.
- Marchal, P., J.-J. Poos, and F. Quirijns. 2007. Linkage between fishers' foraging, market and fish stocks density: Examples from some North Sea fisheries. *Fisheries Research* **83**:33-43.
- Marteinsdottir, G., and K. Thorarinsson. 1998. Improving the stock & recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1372-1377.

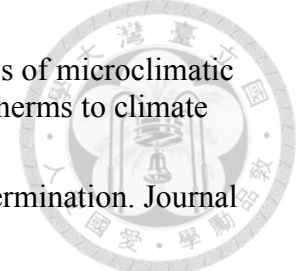
- 
- Matsukura, R., K. Fujihara, and T. Goto. 2014. Stock assessment and evaluation for the northern stock Japanese sandfish in the Japan Sea (fiscal 2013). Fisheries Agency and Fisheries Research Agency of Japan, Tokyo.
- Minami, T. 1986. Predation on the young flatfishes in the Japan Sea. Bulletin of Japan Sea Regional Fisheries Research Laboratory **36**:39-47.
- Minami, T., and M. Tanaka. 1992. Life history cycles in flatfish from the northwestern Pacific, with particular reference to their early life histories. Netherlands Journal of Sea Research **29**:35-48.
- Misu, H. 1974. Demersal fisheries resources in Tsushima Warm Current region. Pages 91-110 in J. S. o. F. Science, editor. Kouseisha-Kouseikaku.
- Morita, K., M.-a. Fukuwaka, N. Tanimata, and O. Yamamura. 2010. Size-dependent thermal preferences in a pelagic fish. Oikos **119**:1265-1272.
- Mueter, F. J., and M. A. Litzow. 2008. Sea Ice Retreat Alters the Biogeography of the Bering Sea Continental Shelf. Ecological Applications **18**:309-320.
- Naganuma, K. 2000. The Sea of Japan as the natural environment of marine organism. Bulletin of Japan Sea Regional Fisheries Research Laboratory **50**:1-42.
- Nakagawa, M., K. Suzuki, and T. Yoshida. 2014. Stock assessment and evaluation for the stock of Bastard halibut in the Southern Japan Sea and East China Sea (fiscal 2013). Fisheries Agency and Fisheries Research Agency of Japan, Tokyo.
- Narimatsu, Y., A. Yamanobe, and M. Takahashi. 2007. Reproductive cycle, age, and body size at maturity and fecundity of female willowy flounder *Tanakius kitaharai*. Fisheries Science **73**:55-62.
- Neuheimer, A. B., and P. Grønkjær. 2012. Climate effects on size-at-age: Growth in warming waters compensates for earlier maturity in an exploited marine fish. Global Change Biology **18**:1812-1822.
- Nicolas, D., S. Rochette, M. Llope, and P. Licandro. 2014. Spatio-Temporal Variability of the North Sea Cod Recruitment in Relation to Temperature and Zooplankton. PLOS ONE **9**:e88447.
- Nishimura, S. 1968. The zoogeographical aspects of the Japan Sea, Part IV. Publication of Seto Marine Biology Lab **15**:329-352.
- Nye, J. A., J. S. Link, J. A. Hare, and W. J. Overholtz. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. Marine Ecology Progress Series **393**:111-129.
- Oksanen, J., F. G. Blachent, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2017. vegan: Community Ecology Package. R package version 2.4-3.
- Ottersen, G., D. O. Hjermann, and N. C. Stenseth. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. Fisheries Oceanography **15**:230-243.
- Ottersen, G., S. Kim, G. Huse, J. J. Polovina, and N. C. Stenseth. 2010. Major pathways by which climate may force marine fish populations. Journal of Marine Systems **79**:343-360.

- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37-42.
- Pekcan-Hekim, Z., L. Urho, H. Auvinen, O. Heikinheimo, J. Lappalainen, J. Raitaniemi, and P. Söderkultalahti. 2011. Climate warming and pikeperch year-class catches in the Baltic Sea. *Ambio* **40**:447-456.
- Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology* **87**:2614-2625.
- Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. *Science* **308**:1912-1915.
- Perry, R. I., P. Cury, K. Brander, S. Jennings, C. Mollmann, and B. Planque. 2010. Sensitivity of marine systems to climate and fishing: Concepts, issues and management responses. *Journal of Marine Systems* **79**:427-435.
- Petitgas, P., A. D. Rijnsdorp, M. Dickey-Collas, G. H. Engelhard, M. A. Peck, J. K. Pinnegar, K. Drinkwater, M. Huret, and R. D. Nash. 2013. Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography* **22**:121-139.
- Pinsky, M. L., B. Worm, M. J. Fogarty, J. L. Sarmiento, and S. A. Levin. 2013. Marine taxa track local climate velocities. *Science (New York, N.Y.)* **341**:1239-1242.
- Planque, B., J.-M. Fromentin, P. Cury, K. F. Drinkwater, S. Jennings, R. I. Perry, and S. Kifani. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems* **79**:403-417.
- Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. Schwing, S. A. Thompson, and A. J. Richardson. 2013. Global imprint of climate change on marine life. *Nature Climate Change*:1-7.
- Pörtner, H. O., and R. Knust. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**:95-97.
- Rao, C. R. 1948. Large sample tests of statistical hypotheses concerning several parameters with applications to problems of estimation. *Mathematical Proceedings of the Cambridge Philosophical Society* **44**:50-50.
- Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* **191**:382.
- Rijnsdorp, A. D., M. A. Peck, G. H. Engelhard, C. Mollmann, and J. K. Pinnegar. 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science* **66**:1570-1583.
- Ripa, J., H. Olofsson, and N. Jonzon. 2010. What is bet-hedging, really? *Proceedings of the Royal Society B: Biological Sciences* **277**:1153-1154.
- Rochet, M.-J., V. M. Trenkel, A. Carpentier, F. Coppin, L. G. d. Sola, J.-P. L'Éaut'É, J.-C. Mah'É, P. Maiorano, A. Mannini, M. Murenu, G. Piet, C.-Y. Politou, B. Reale, M.-T. Spedicato, G. Tserpes, and J. A. Bertrand. 2010. Do changes in environmental and fishing pressures impact marine communities? An empirical assessment. *Journal of Applied Ecology* **47**:741-750.

- Rouyer, T., J.-M. Fromentin, M. Hidalgo, and N. C. Stenseth. 2014. Combined effects of exploitation and temperature on fish stocks in the Northeast Atlantic. *ICES Journal of Marine Science* **71**:1554-1562.
- Rouyer, T., G. Ottersen, J. M. Durant, M. Hidalgo, D. Ø. Hjermann, J. Persson, L. C. Stige, and N. C. Stenseth. 2011. Shifting dynamic forces in fish stock fluctuations triggered by age truncation? *Global Change Biology* **17**:3046-3057.
- 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.
- Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* **465**:609-612.
- Schuetz, J. G., K. E. Mills, A. J. Allyn, K. Stamieszkin, A. Le Bris, and A. Pershing, J. 2018. Complex patterns of temperature sensitivity, not ecological traits, dictate diverse species responses to climate change. *Ecography* **0**.
- Scott, B. E., G. Marteinsdottir, G. A. Begg, P. J. Wright, and O. S. Kjesbu. 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecological Modelling* **191**:383-415.
- Shin, Y.-J., M.-J. Rochet, S. Jennings, J. G. Field, and H. Gislason. 2005. Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of Marine Science* **62**:384-396.
- Sogard, S. M., S. A. Berkeley, and R. Fisher. 2008. Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. *Marine Ecology Progress Series* **360**:227-236.
- Stenseth, N. C., A. Myserud, G. Ottersen, J. W. Hurrell, K. S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* **297**:1292-1296.
- Strona, G., P. Galli, S. Montano, D. Seveso, and S. Fattorini. 2012. Global-scale relationships between colonization ability and range size in marine and freshwater fish. *PLOS ONE* **7**:e49465.
- Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia* **85**:277-298.
- Thompson, D. W. J., and J. M. Wallace. 1998. The Arctic Oscillation signature in the wintertime geopotential height and temperature fields. *Geophysical Research Letters* **25**:1297-1300.
- Tian, Y., H. Kidokoro, and T. Fujino. 2011. Interannual-decadal variability of demersal fish assemblages in the Tsushima Warm Current region of the Japan Sea: Impacts of climate regime shifts and trawl fisheries with implications for ecosystem-based management. *Fisheries Research* **112**:140-153.
- Tian, Y., H. Kidokoro, T. Watanabe, and N. Iguchi. 2008. The late 1980s regime shift in the ecosystem of Tsushima warm current in the Japan/East Sea: Evidence from historical data and possible mechanisms. *Progress In Oceanography* **77**:127-145.

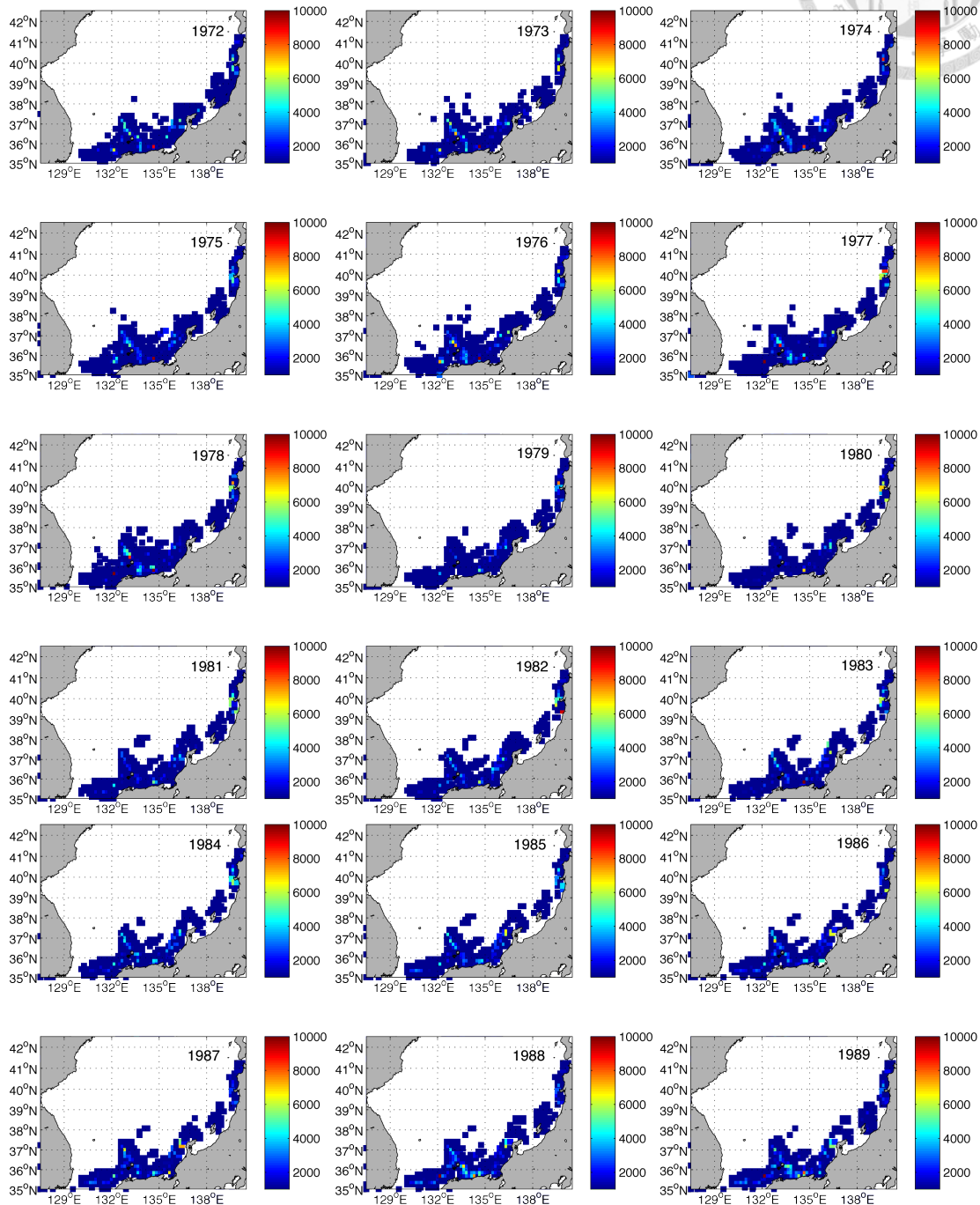
- Tominaga, O., and K. Nashida. 1991. Interspecific relationship between Brown sole and other demersal fishes in the coastal waters of Northern Niigata Prefecture. *Bulletin of Japan Sea Regional Fisheries Research Laboratory* **41**:11-26.
- Trenberth, K. E., and J. W. Hurrell. 1994. Decadal atmosphere-ocean variations in the Pacific. *Climate Dynamics* **9**:303-319.
- Trippel, E. A., O. S. Kjesbu, and P. Solemdal. 1997. Effects of adult age and size structure on reproductive output in marine fishes. Pages 31-62 in R. C. Chambers and E. A. Trippel, editors. *Early Life History and Recruitment in Fish Populations*. Springer Netherlands, Dordrecht.
- Tu, C.-Y., Y. Tian, and C.-H. Hsieh. 2015. Effects of climate on temporal variation in the abundance and distribution of the demersal fish assemblage in the Tsushima Warm Current region of the Japan Sea. *Fisheries Oceanography* **24**:177-189.
- Uehara, S., T. Iseki, and Y. Yagi. 2014. Stock assessment and evaluation for the northern-central stock of Bastard halibut in the Japan Sea (fiscal 2013). Fisheries Agency and Fisheries Research Agency of Japan, Tokyo, Japan.
- van der Veer, H. W., R. Berghahn, J. M. Miller, and A. D. Rijnsdorp. 2000. Recruitment in flatfish, with special emphasis on North Atlantic species: Progress made by the Flatfish Symposia. *ICES Journal of Marine Science* **57**:202-215.
- van Putten, I. E., S. Kulmala, O. Thébaud, N. Dowling, K. G. Hamon, T. Hutton, and S. Pascoe. 2012. Theories and behavioural drivers underlying fleet dynamics models. *Fish and Fisheries* **13**:216-235.
- Vandeperre, F., and D. A. Methven. 2007. Do bigger fish arrive and spawn at the spawning grounds before smaller fish: Cod (*Gadus morhua*) predation on beach spawning capelin (*Mallotus villosus*) from coastal Newfoundland. *Estuarine, Coastal and Shelf Science* **71**:391-400.
- Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society of London B: Biological Sciences* **275**:1635: 649-659.
- Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley. 1996. Lévy flight search patterns of wandering albatrosses. *Nature* **381**:413-415.
- Walters, C., and S. J. Martell. 2002. Stock assessment needs for sustainable fisheries management. *Bulletin of Marine Science* **70**:629-638.
- Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **365**:2019-2024.
- Wang, H. Y., L. W. Botsford, J. W. White, M. J. Fogarty, F. Juanes, A. Hastings, M. D. Holland, and K. Brander. 2014. Effects of temperature on life history set the sensitivity to fishing in Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* **514**:217-229.
- Watanabe, Y. W., M. Wakita, and N. Maeda. 2003. Synchronous bidecadal periodic changes of oxygen, phosphate and temperature between the Japan Sea deep water and the North Pacific intermediate water. *Geophysical Research Letters* **30**:10-13.

- Wilbur, H. M. 1980. Complex life cycles. *Annual Review of Ecology and Systematics* **11**:67-93.
- Woods, H. Arthur, M. E. Dillon, and S. Pincebourde. 2015. The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *Journal of Thermal Biology* **54**: 86-97.
- Yang, J. 1982. The dominant fish fauna in the North Sea and its determination. *Journal of Fish Biology* **20**:635-643.
- Zani, S., M. Riani, A. Corbellini, I. Statistica, U. Parma, and V. Kennedy. 1998. Robust bivariate boxplots and multiple outlier detection. *Computational Statistics & Data Analysis* **28**:257-270.

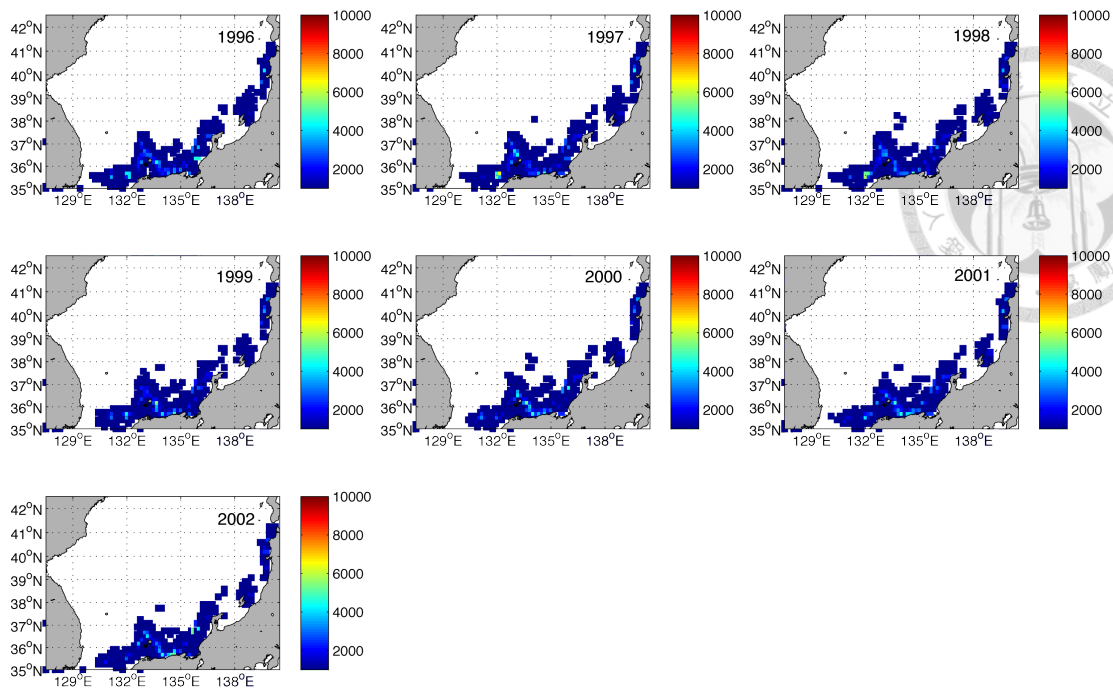


Appendices

I. Fishing effort of Japan Sea single trawl fisheries, 1972-2002



Supplementary Figure S2-1 Annual fishing effort distribution of the Japan Sea single trawling, 1972-1989



Supplementary Figure S2-2. Annual fishing effort distribution of the Japan Sea single trawling, 1990-2002




II. Data source, map in variation partitioning analysis

Supplementary Table S3-1. Data source for size structure, fishing mortality, and life history traits of each stock. For Alaska, the abbreviation in the bracket indicates the locations of stock used as a management unit: AI, Aleutian Island; GOA, Gulf of Alaska; BSAI, Bering Sea and Aleutian Islands

Species	Common Name	Length composition	Fishing mortality/Exploitation	A50	L50	Linf	K	M
<i>Atheresthes stomias</i>	Arrowtooth flounder*	From PacFIN database for fillet fishery ¹	Exploitation rate ¹	1	1	1	1	1
<i>Sebastes goodie</i>	Chilipepper rockfish	Trawl fishery ²	Exploitation rate ²	3	3	3	3	2
<i>Sebastes crameri</i>	Dark blotched rockfish	Fisheries observation ⁴	Exploitation rate ⁴	5	5	6	6	4
<i>Microstomus pacificus</i>	Dover Sole	Fishery in northern and southern region combined ⁷	Exploitation rate ⁷	8	8	8	8	7
<i>Parophrys vetulus</i>	English Sole	Fishery from the north (N=42) region ⁹	Exploitation rate ⁹	10	10	11	9	9
<i>Ophiodon elongatus</i>	Lingcod	Fishery observation at north ¹²	Exploitation rate ¹²	13	13	11	11	12
<i>Sebastolobus altivelis</i>	Longspine thornyhead	Coast-wide length composition from the commercial landings in California (CA) ¹⁴	Exploitation rate ¹⁴	14	14	14	14	14
<i>Eopsetta jordani</i>	Petrale sole	Fishery length observation ¹⁵	Exploitation rate ¹⁵	16	16	15	15	15
<i>Sardinops sagax</i>	Sardine*	Fishery length observations at north ¹⁷	Exploitation rate ¹⁷	17	17	17	17	17

<i>Sebastes diploproa</i>	Splitnose rockfish	California (CA) domestic trawl fishery observation ¹⁸	Exploitation rate ¹⁸	19	19	5	5	18
<i>Sebastes ruberrimus</i>	Yelloweye rockfish	Length composition at port and observer ²⁰	Exploitation rate ²⁰	21	21	20	20	20
<i>Gadus chalcogramma</i>	Walleye pollock (AI)*	AI triennial survey ²²	Exploitation rate ²³	23	24	23	23	23
<i>Gadus chalcogramma</i>	Walleye pollock (GOA)	Shelikof Strait surveys in 1981-2010 ²⁵	Exploitation rate ²⁶	26	26	27	27	26
<i>Hippoglossoides elassodon</i>	Flathead sole (EBS)*	EBS survey size composition ²⁸	Fishing mortality estimates from selected (base) model ²⁸	28	28	28	28	28
<i>Hippoglossoides elassodon</i>	Flathead sole (GOA)*	GOA triennial survey size composition ²⁹	Fishing mortality from the preferred (Alternative 1) model ²⁹	30	30	30	30	29
<i>Gadus macrocephalus</i>	Pacific cod (EBS)	Length frequencies for post 1981 EBS trawl survey ³¹	Estimates of fishing mortality rates by Model B1 ³¹	24	24	32	32	31
<i>Gadus macrocephalus</i>	Pacific cod (GOA)	Length frequencies for sub27 (cm) + 2plus (cm) trawl survey by length bin 1984-2009 ³³	Estimates of fishing mortality rates by Model B1 ³³	34	34	34	34	33
<i>Glyptocephalus zachirus</i>	Rex sole (GOA)	GOA triennial survey size composition ³⁵	Fishing pressure from final model estimates ³⁵	36	36	36	36	35
<i>Gadus morhua</i>	Cod	NS-IBTS ³⁷	Fishing pressure of age 2-4 ³⁸	39	39	39	39	40
<i>Melanogrammus aeglefinus</i>	Haddock	NS-IBTS ³⁷	Fishing pressure of age 2-4 ⁴¹	39	39	39	39	40
<i>Clupea harengus</i>	Herring	NS-IBTS ³⁷	Fishing pressure of age 2-6 ⁴²	43	43	44	44	45

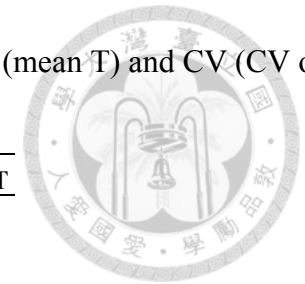




<i>Scomber scombrus</i>	Mackerel	NS-IBTS ³⁷	Fishing pressure of age 4-8 ⁴⁶	47	47	39	39	48
<i>Trisopterus esmarkii</i>	Norway pout	NS-IBTS ³⁷	Fishing pressure of age 1-2 ⁴⁹	39	39	39	39	50
<i>Pleuronectes platessa</i>	Plaice	NS-IBTS ³⁷	Fishing mortality of age 2-6 ⁵¹	39	39	39	39	40
<i>Pollachius virens</i>	Saithe	NS-IBTS ³⁷	Fishing pressure of age 4-7 ⁵²	39	39	39	39	40
<i>Solea solea</i>	Sole	NS-IBTS ³⁷	Fishing mortality of age 2-6 ⁵³	54	54	54	54	40
<i>Sprattus sprattus</i>	Sprat	NS-IBTS ³⁷	Fishing pressure of age 1-2 ⁵⁵	11	11	56	56	45
<i>Merlangius merlangius</i>	Whiting	NS-IBTS ³⁷	Fishing pressure of age 2-6 ⁵⁷	39	39	39	39	58

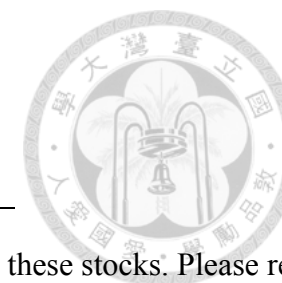
*Female and male has different age at maturation (A_{50}), length at maturation (L_{50}), L_{inf} and K . We only use female in the analysis.

Supplementary Table S3-2 Life history traits, natural mortality (M), mean of mortality ratio (meanF_M), temperature (mean T) and CV (CV of F_M, CV of T) for the analyzed species/stocks.



Species	Habitat	Linf	K	A50	L50	M	Mean F	M	Mean T	CV of F	M	CV of T
<i>Atheresthes stomias</i>	demersal	72.26	0.17	4.00	37.30	0.166	0.618	13.079	0.321	0.033		
<i>Sebastes goodie</i>	demersal	56.60	0.20	3.00	26.00	0.16	0.664	13.046	0.588	0.031		
<i>Sebastes crameri</i>	demersal	39.18	0.09	4.00	27.00	0.07	1.171	13.008	0.662	0.033		
<i>Microstomus pacificus</i>	demersal	47.40	0.09	7.00	31.10	0.09	1.198	12.927	0.402	0.034		
<i>Parophrys vetulus</i>	demersal	57.00	0.30	4.00	23.00	0.26	0.542	12.937	0.461	0.032		
<i>Ophiodon elongatus</i>	demersal	104.00	0.20	3.80	55.70	0.18	0.444	12.997	0.755	0.032		
<i>Sebastolobus altivelis</i>	bathydemersal	31.20	0.06	11.00	17.80	0.06	0.596	13.040	0.778	0.034		
<i>Eopsetta jordani</i>	demersal	56.24	0.14	5.15	33.10	0.2	1.923	12.892	0.199	0.031		
<i>Sardinops sagax</i>	pelagic	30.00	0.91	1.25	16.00	0.4	0.413	13.014	0.603	0.035		
<i>Sebastes diploproa</i>	bathydemersal	34.18	0.13	7.00	19.00	0.048	0.401	13.009	0.787	0.033		
<i>Sebastes ruberrimus</i>	demersal	62.38	0.49	11.60	38.78	0.047	1.457	13.036	0.623	0.031		
<i>Gadus chalcogramma</i> (AI)	benthopelagic	58.69	0.34	4.50	39.00	0.2	0.634	4.308	1.120	0.058		
<i>Gadus chalcogramma</i> (GOA)	benthopelagic	57.70	0.32	4.90	43.00	0.3	0.358	5.537	0.382	0.077		
<i>Hippoglossoides elassodon</i> (EBS)	demersal	44.60	0.10	8.70	24.00	0.2	0.222	2.367	0.305	0.282		
<i>Hippoglossoides elassodon</i> (GOA)	demersal	48.86	0.16	8.74	33.30	0.2	0.069	5.486	0.469	0.095		
<i>Gadus macrocephalus</i> (EBS)	demersal	104.30	0.22	5.80	67.00	0.34	0.134	2.347	0.409	0.314		
<i>Gadus macrocephalus</i> (GOA)	demersal	156.72	0.08	4.30	50.00	0.38	0.206	5.660	0.738	0.102		
<i>Glyptocephalus zachirus</i> (GOA)	demersal	41.82	0.39	5.10	35.20	0.17	0.539	5.432	0.504	0.071		
<i>Gadus morhua</i>	demersal	123.10	0.23	3.80	69.70	*	2.179	6.118	0.276	0.893		
<i>Melanogrammus aeglefinus</i>	demersal	68.30	0.19	2.50	33.50	*	0.873	6.118	0.447	1.210		
<i>Clupea harengus</i>	benthopelagic	33.60	0.33	3.00	25.30	*	0.952	6.118	0.448	2.732		
<i>Scomber scombrus</i>	pelagic	39.90	0.36	1.50	25.00	0.15	1.906	6.185	0.249	2.652		
<i>Trisopterus esmarkii</i>	benthopelagic	23.00	0.52	2.30	19.00	*	1.158	6.263	0.784	1.671		
<i>Pleuronectes platessa</i>	demersal	54.50	0.11	2.50	26.60	0.1	5.105	6.118	0.334	1.506		

<i>Pollachius virens</i>	demersal	177.10	0.07	4.60	55.40	0.2	2.533	6.118	0.250	1.517
<i>Solea solea</i>	demersal	45.30	0.36	4.00	28.90	0.1	5.261	6.118	0.194	1.461
<i>Sprattus sprattus</i>	pelagic	15.00	0.50	2.00	11.50	*	3.007	6.118	0.502	0.714
<i>Merlangius merlangius</i>	demersal	42.40	0.32	1.50	20.20	*	0.597	6.416	0.522	1.703



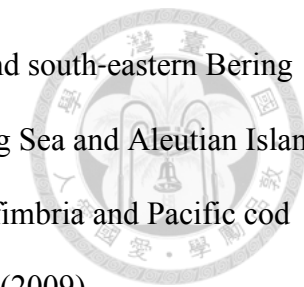
* The estimates of natural mortality were under continuous revising for management purpose during the data period for these stocks. Please refer to original reference (see supplementary Table S2-1) or dataset compiled by me (<https://zenodo.org/record/1210792>) for details.

Sources

- 1 Kaplan, I. C. & Helser, T. E. Stock assessment of the arrowtooth flounder (*Atheresthes stomias*) population off the west coast of the United States in 2007. (Pacific Fishery Management Council, 2007).
- 2 Field, J. C. Status of the Chilipepper rockfish, *Sebastes goodei*, in 2007. (2007).
- 3 Wilkins, M. E. Size composition, age composition, and growth of chilipepper, *Sebastes goodei*, and bocaccio, *S. paucispinis*, from the 1977 rockfish survey. *Mar. Fish. Rev.* **42**, 48-53 (1980).
- 4 Wallace, J. R. & Hamel, O. S. Status and future prospects for the darkblotched rockfish resource in waters off Washington, Oregon, and California as updated in 2009. 97220-91384 (2009).
- 5 Echeverria, T. W. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. *Fishery Bulletin* **85** (1987).
- 6 Archibald, C., Leaman, B., Station, P. B. & Shaw, W. *Growth and mortality estimates of rockfishes (Scorpaenidae) from BC coastal waters, 1977-1979*. (Nanaimo, BC: Government of Canada, Fisheries and Oceans, 1981).
- 7 Sampson, D. B. The status of Dover sole off the US West Coast in 2005. *Pacific Fisheries Management Council, Portland, OR* (2005).
- 8 Hunter, J. R., Butler, J. L., Kimbrell, C. & Lynn, E. A. Bathymetric patterns in size, age, sexual maturity, water content, and caloric density of Dover sole, *Microstomus pacificus*. *CalCOFI Reports* **31**, 132-144 (1990).
- 9 Stewart, I. J. Updated US English sole stock assessment: Status of the resource in 2007. (2007).
- 10 Sampson, D. B. & Al-Jufaily, S. Geographic variation in the maturity and growth schedules of English sole along the US west coast. *Journal of Fish Biology* **54**, 1-17 (1999).
- 11 Froese, R. & Pauly, D. *FishBase*, <<http://www.fishbase.org/>> (2016).
- 12 Hamel, O. S., Sethi, S. A. & Wadsworth, T. F. Status and future prospects for lingcod in waters off Washington, Oregon, and California as assessed in 2009. 565-626 (2009).



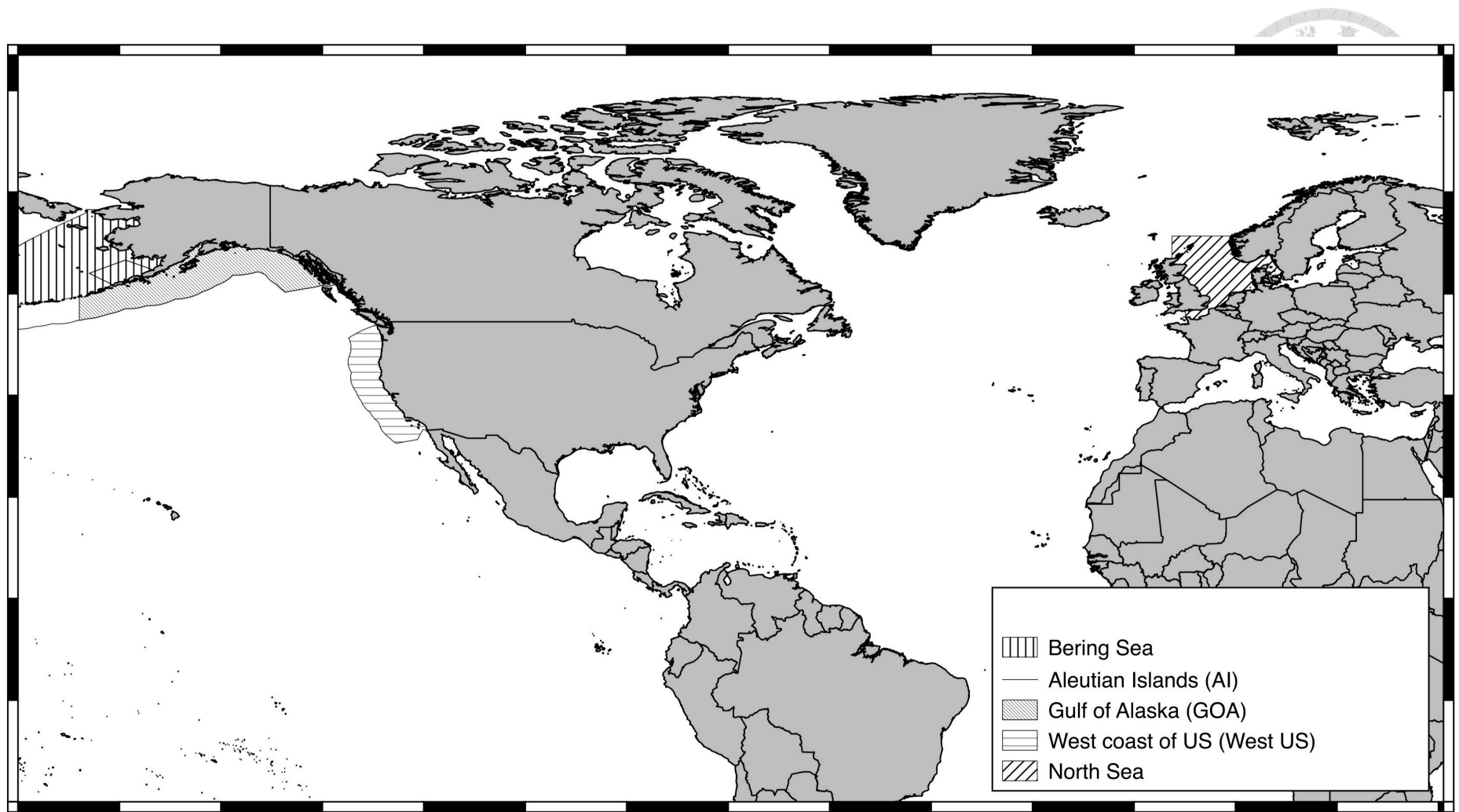
- 13 Silberberg, K. R., Laidig, T. E., Adams, P. B. & Albin, D. Analysis of maturity in lingcod, *Ophiodon elongatus*. *California Fish and Game* **87**, 139-152 (2001).
- 14 Fay, G. Stock assessment and status of longspine thornyhead (*Sebastolobus altivelis*) off California, Oregon and Washington in 2005. *Pacific Fisheries Management Council, Portland, OR* (2005).
- 15 Haltuch, M. A. & Hicks, A. Status of the US petrale sole resource in 2008. (2009).
- 16 Hannah, R. W., Parker, S. J. & Fruh, E. L. Length and age at maturity of female petrale sole (*Eopsetta jordani*) determined from samples collected prior to spawning aggregation. *Fishery Bulletin* **100**, 711-719 (2002).
- 17 Hill, K. T. *et al.* Assessment of the Pacific sardine resource in 2007 for US management in 2008. (2007).
- 18 Gertseva, V. V., Cope, J. M. & Pearson, D. E. Status of the US splitnose rockfish (*Sebastes diploproa*) resource in 2009. (Northwest Fisheries Science Center, NOAA Fisheries, 2009).
- 19 Boehlert, G. & Kappenman, R. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the northeast Pacific Ocean. *Mar. Ecol. Prog. Ser* **3**, 1-10 (1980).
- 20 Stewart, I. J., Wallace, J. R. & McGilliard, C. Status of the US yelloweye rockfish resource in 2009. (2009).
- 21 Hannah, R. W., Blume, M. T. & Thompson, J. E. *Length and age at maturity of female yelloweye rockfish (Sebastes rubberimus) and cabezon (Scorpaenichthys marmoratus) from Oregon waters based on histological evaluation of maturity.* (Oregon Department of Fish and Wildlife, Marine Resources Program, 2009).
- 22 Personal communication from Steve Barbeaux, research fishery scientist at Alaska Fisheries Science Center. Email: steve.barbeaux@noaa.gov
- 23 Barbeaux, S., Ianelli, J., Gaichas, S. & Wilkins, M. A: Assessment of the Pollock stock in the Aleutian Islands. (2009).
- 24 Witherell, D. Groundfish of the Bering Sea and Aleutian Islands area: species profiles 2001. *North Pacific Fishery Management Council, Anchorage, AK* **99501** (2000).
- 25 Personal communication from Martin Dorn, research fishery scientist at Alaska Fisheries Science Center. Email: Martin.Dorn@noaa.gov
- 26 Dorn, M. *et al.* Assessment of walleye pollock in the Gulf of Alaska. *Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska*, 53-156 (2010).
- 27 Megrey, B. A. Population dynamics and management of walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska, 1976–1986. *Fisheries Research* **11**, 321-354, doi:[http://dx.doi.org/10.1016/0165-7836\(91\)90008-4](http://dx.doi.org/10.1016/0165-7836(91)90008-4) (1991).
- 28 Stockhausen, W. T., Nichol, D. & Palsson, W. Assessment of the flathead sole stock in the Bering Sea and Aleutian Islands. (2012).
- 29 Stockhausen, W. T., Wilkins, M. E. & Martin, M. H. 8. Assessment of the Flathead Sole Stock in the Gulf of Alaska. 681-742 (North Pacific Fishery Management Council, Anchorage, AK, 2009).



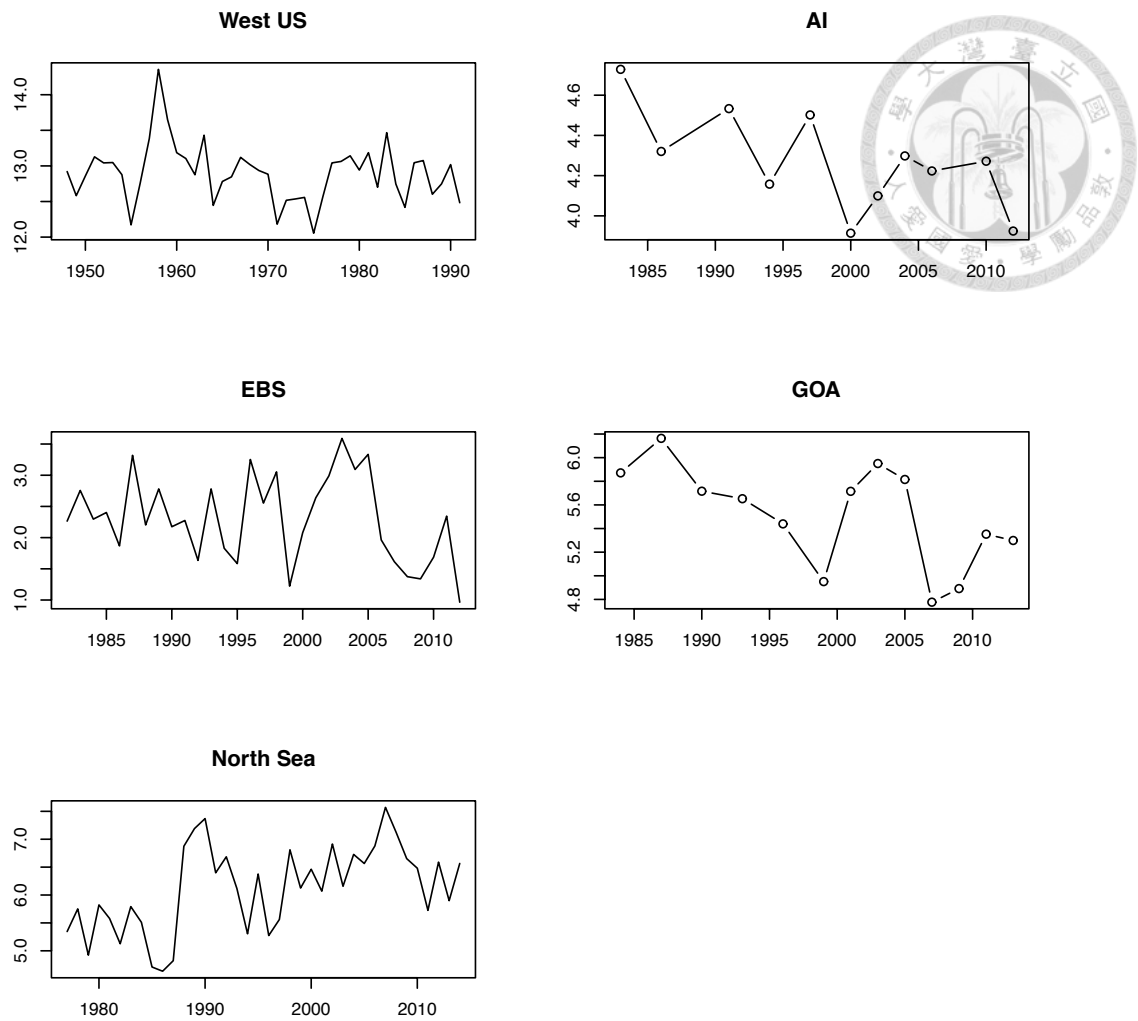
- 30 Stark, J. W. A comparison of the maturation and growth of female flathead sole in the central Gulf of Alaska and south-eastern Bering Sea. *Journal of fish biology* **64**, 876-889 (2004).
- 31 Thompson, G. G., Ianelli, J. & Lauth, R. R. Chapter 2: Assessment of the Pacific cod stock in the eastern Bering Sea and Aleutian Islands area. 235-440 (2009).
- 32 Kimura, D., Shimada, A. & Lowe, S. Estimating von Bertalanffy growth parameters of sablefish *Anoplopoma fimbria* and Pacific cod *Gadus macrocephalus* using tag-recapture data. *Fishery Bulletin* **91**, 271-280 (1993).
- 33 Thompson, G. G., Ianelli, J. & Wilkins, M. Assessment of the Pacific cod stock in the Gulf of Alaska. 165-352 (2009).
- 34 Stark, J. W. Geographic and seasonal variations in maturation and growth of female Pacific cod (*Gadus macrocephalus*) in the Gulf of Alaska and Bering Sea. *Fishery Bulletin* **105**, 396-407 (2007).
- 35 Stockhausen, W. T., Wilkins, M. E. & Martin, M. H. 6. Assessment of the Rex Sole Stock in the Gulf of Alaska. 629-690 (North Pacific Fishery Management Council, Anchorage, AK, 2009).
- 36 Abookire, A. A. Reproductive biology, spawning season, and growth of female rex sole (*Glyptocephalus zachirus*) in the Gulf of Alaska. *Fishery Bulletin* **104**, 350-359 (2006).
- 37 ICES. *North Sea International Bottom Trawl Survey (1977-2014)*, <<http://datras.ices.dk>> (
- 38 ICES. *Cod (*Gadus morhua*) in Subarea IV and Divisions VIIId and IIIa West (North Sea, Eastern English Channel, Skagerrak)* <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=8052>> (2016).
- 39 Jennings, S., Reynolds, J. D. & Mills, S. C. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **265**, 333-339, doi:10.1098/rspb.1998.0300 (1998).
- 40 ICES. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). 19pp (Hamburg, Germany, 2017).
- 41 ICES. *Haddock in Subarea IV and Divisions IIIa West and VIa (North Sea, Skagerrak and West of Scotland)* <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=8068>> (2016).
- 42 ICES. *Herring in Subarea IV and Divisions IIIa and VIIId (North Sea autumn spawners)* <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=7689>> (2016).
- 43 ICES. ICES FishMap Species fact sheets- Herring (*Clupea harengus*). (2006).
- 44 Kienzle, M. Estimation of the Parameters of von Bertalanffy Growth Function for the Main Commercial Species of the North Sea estimation of the parameters of von Bertalanffy growth function for the main commercial species of the North Sea. (2005).
- 45 ICES. Report of the Herring Assessment Working Group for the Area South of 62°N (HAWG). 867 (ICES HQ, Copenhagen, Denmark, 2016).



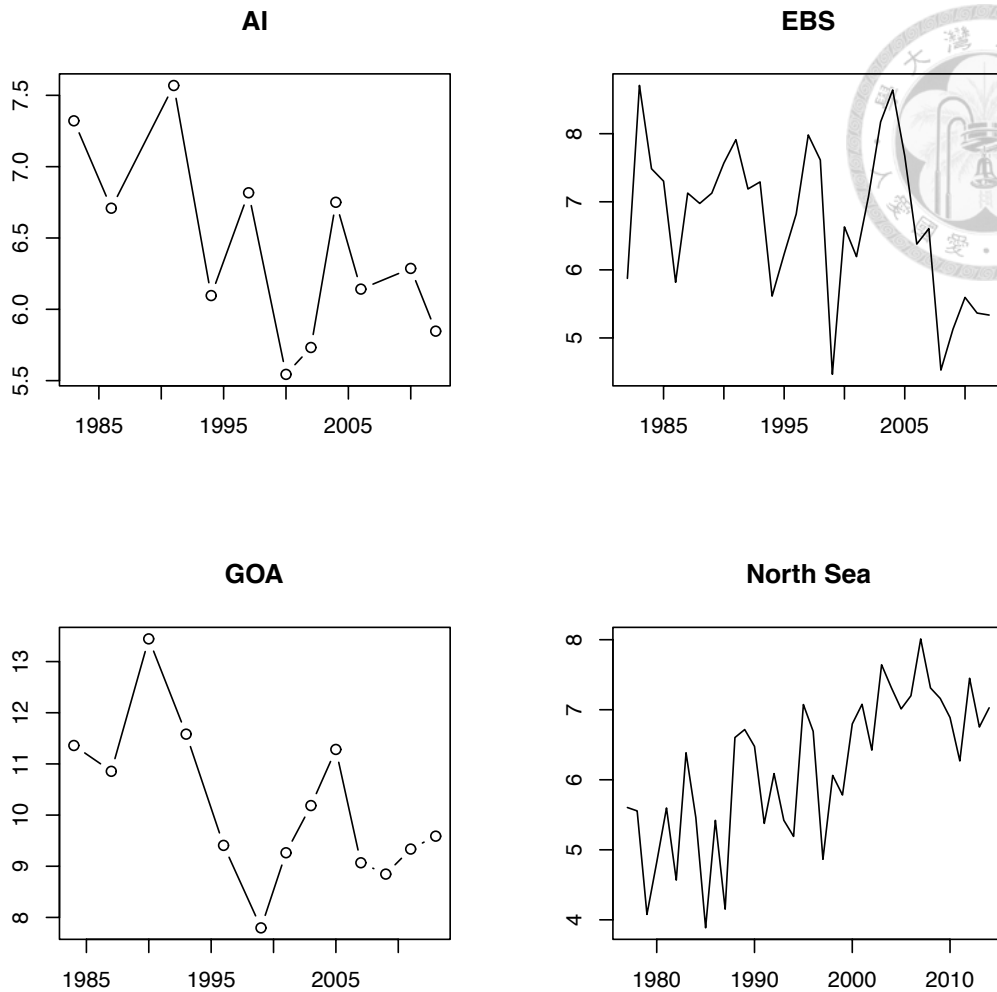
- 46 ICES. *Mackerel in the Northeast Atlantic (combined Southern, Western and North Sea spawning components)* <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=8120>> (2016).
- 47 ICES. ICES FishMap Species fact sheets- Mackerel (*Scomber scombrus*). (2006).
- 48 ICES. Report of the Working Group on Widely Distributed Stocks (WGWIDE). 500 (ICES HQ, Copenhagen, Denmark, 2016).
- 49 ICES. *Norway Pout in Subarea IV (North Sea) and IIIa (Skagerrak - Kattegat) - Autumn assessment* <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=7998>> (2016).
- 50 ICES. Report of the Benchmark Workshop on Norway Pout (*Trisopterus esmarkii*) in Subarea 4 and Division 3a (North Sea, Skagerrak, and Kattegat). 69 (Copenhagen, Denmark, 2017).
- 51 ICES. *Plaice Subarea IV (North Sea)* <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=7445>> (2016).
- 52 ICES. *Saithe in Subarea IV (North Sea) Division IIIa West (Skagerrak) and Subarea VI (West of Scotland and Rockall)*, <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=8066>> (2016).
- 53 ICES. *Sole in Subarea IV (North Sea)*, <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=7722>> (2016).
- 54 de Veen, J. F. On changes in some biological parameters in the North Sea sole (*Solea solea* L.). *ICES Journal of Marine Science* **37**, 60-90, doi:10.1093/icesjms/37.1.60 (1976).
- 55 ICES. *Sprat in Subarea IV (North Sea)* <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=7181>> (2016).
- 56 Froese, R. & Sampang, A. Potential indicators and reference points for good environmental status of commercially exploited marine fishes and invertebrates in the German EEZ. (2013).
- 57 ICES. *Whiting Subarea IV (North Sea) and Division VIIId (Eastern Channel)* <<http://standardgraphs.ices.dk/ViewCharts.aspx?key=7483>> (2016).
- 58 ICES. Report of the Inter-Benchmark Protocol for Whiting in the North Sea (IBP Whiting). 119 (By correspondence, 2016).



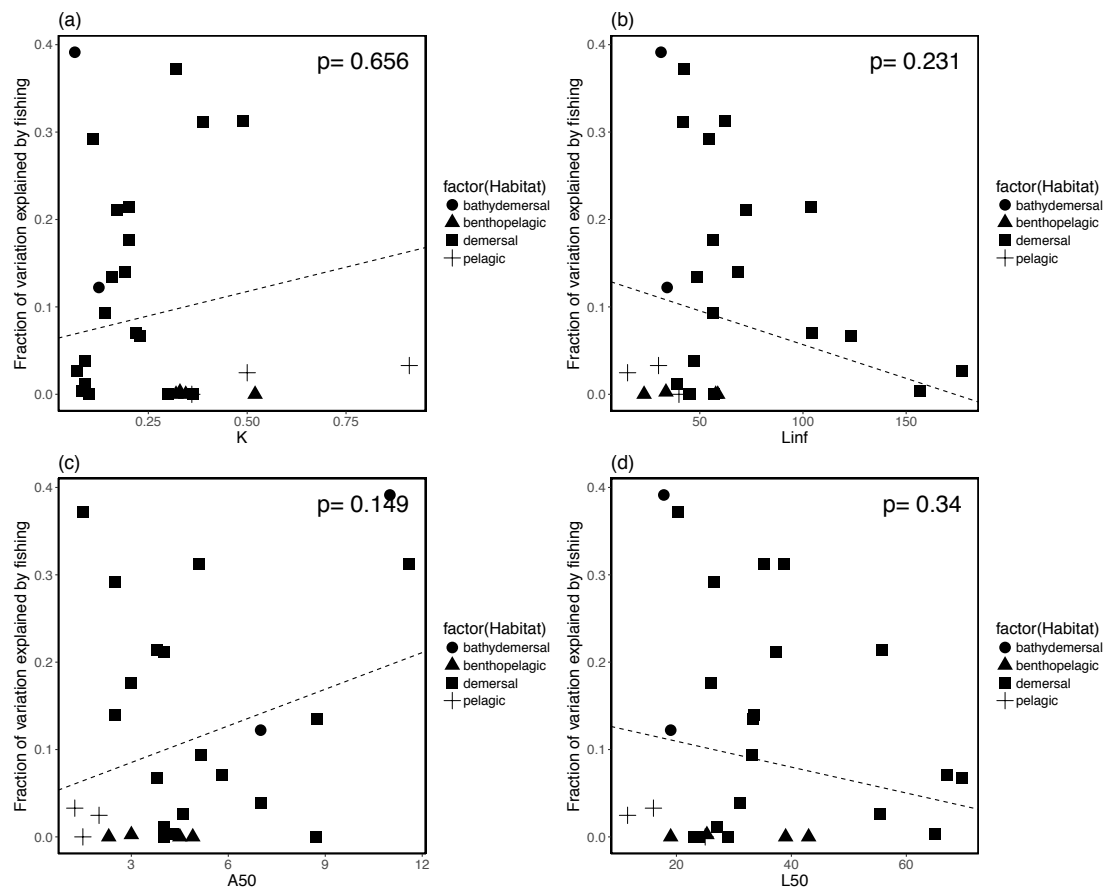
Supplementary Figure S3-1. Fishing areas defined in the analysis. This map is generated with QGIS 2.18.13 “Las Palmas” on Mac OS X (Available online at <http://www.kyngchaos.com/software/qgis>)



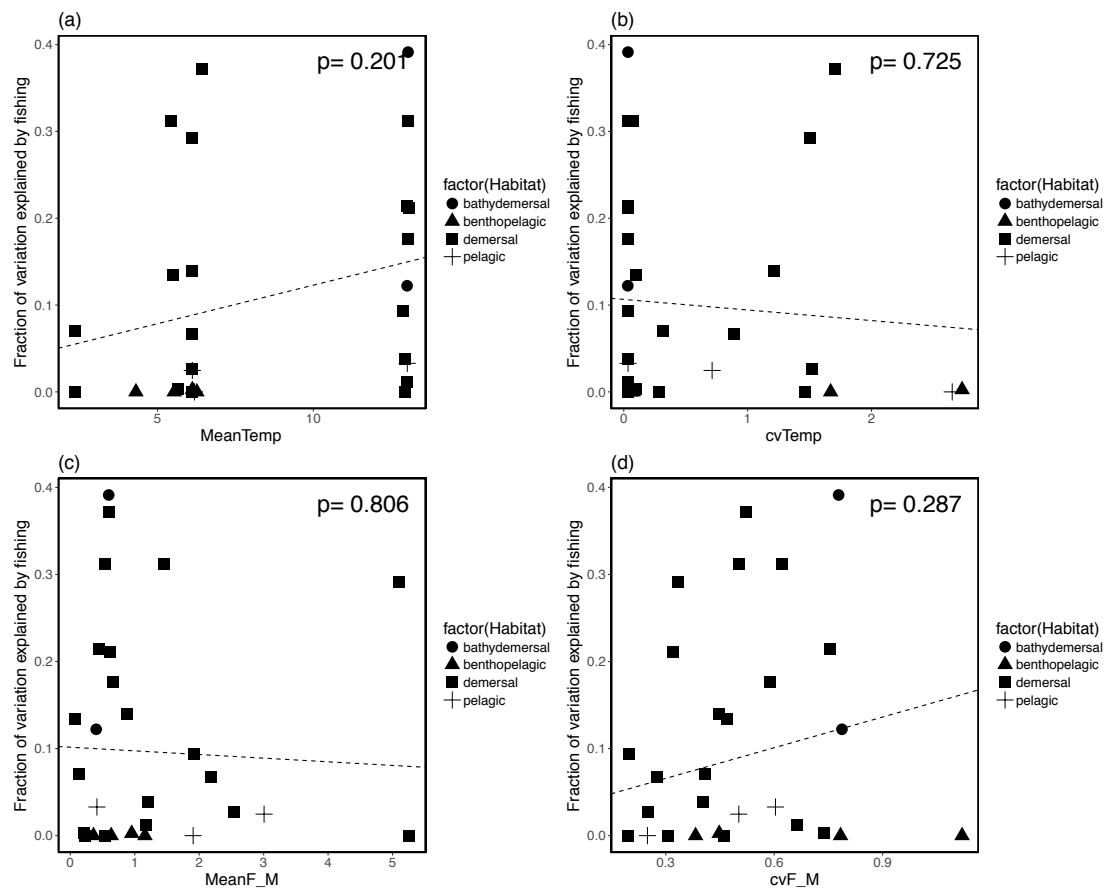
Supplementary Figure S3-2. Time series of temperature used in the analysis. For the west coast of US, we used the average sea surface temperature. For other regions, we used the average of bottom temperature from the trawl survey. The dots in AI and GOA represent the sampling years.



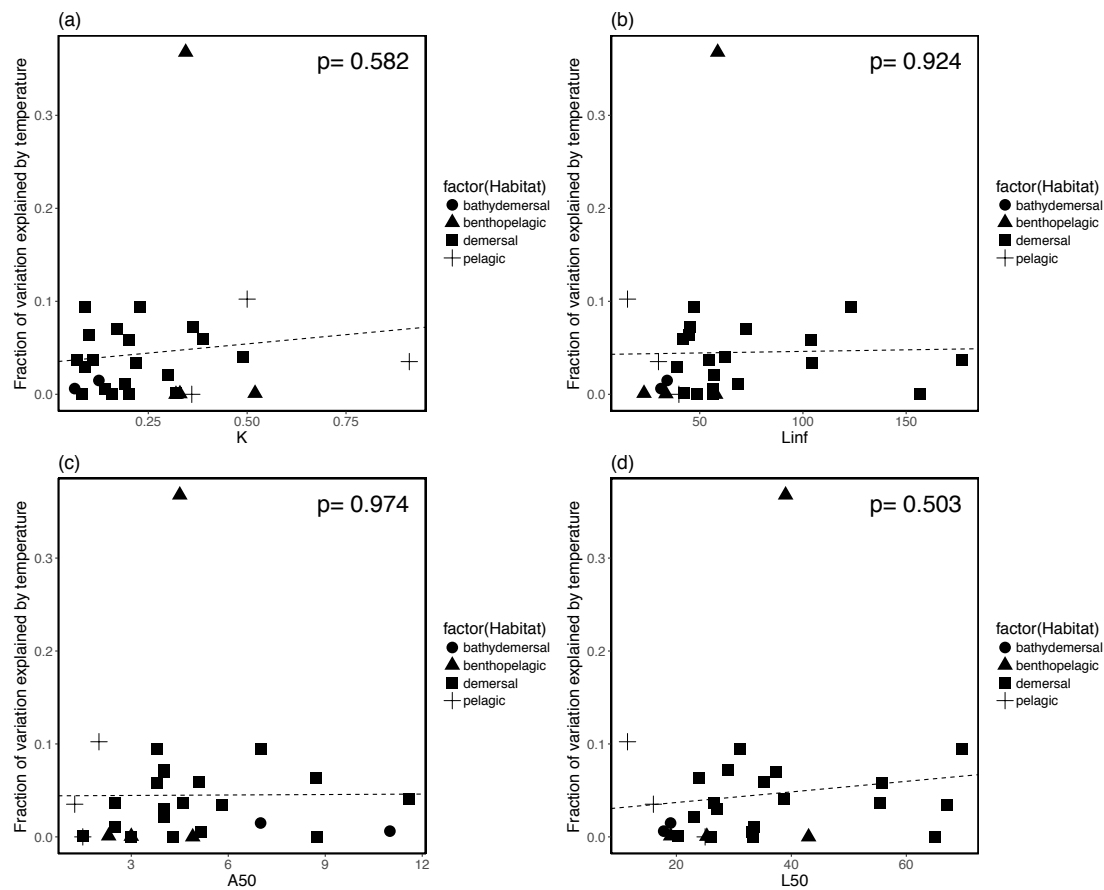
Supplementary Figure S3-3. Time series of surface temperature measurements in AI, EBS, GOA and North Sea. Surface temperature of AI, EBS and GOA were measured during bottom trawl survey. The North Sea surface temperature is all data collected at depths of <10m from reduced CTD, bottle, underway/pump and mooring data in Marsden Square no. 216 (North Sea) via <http://ocean.ices.dk/data/surface/surface.htm>. The dots in AI and GOA represent the sampling years.



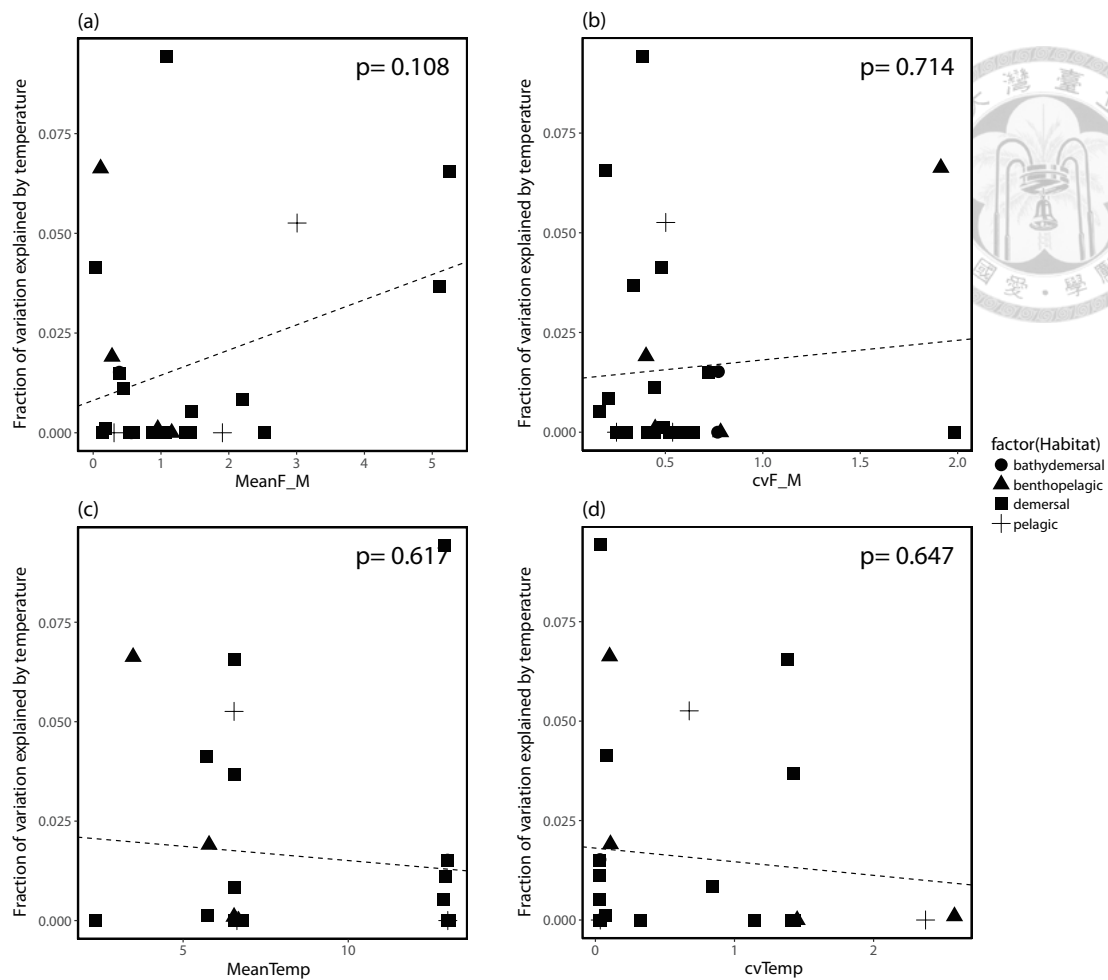
Supplementary Figure S3-4. Explained variation by fishing in relation to the life history traits. The dash line is the best- fitted regression line based on LMM.



Supplementary Figure S3-5. Explained variation by fishing in relation to the mean and CV of mortality ratio or CV of temperature. The dash line is the best-fitted regression line based on LMM.



Supplementary Figure S3-6. Explained variation by temperature in relation to life history traits. The dash line is the best-fitted regression line based on LMM.



Supplementary Figure S3-7. Explained variation by fishing in relation to the mean and CV of mortality ratio or CV of temperature. The dash line is the best-fitted regression line based on LMM.