論文の内容の要旨

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論文題目　A study on geographical characteristics of respiratory metabolism of chub mackerel (*Scomber japonicus*) and its effect on early life history based on modelling approaches （マサバ (***Scomber japonicus***) の呼吸代謝の地理的特性とモデルを用いたその初期生活史への影響に関する研究）

Chub mackerel (*Scomber japonicus*) is a small pelagic fish species widely distributed throughout the coastal areas of subtropical and temperate transition waters in the Indo-Pacific Ocean. It not only supports significant commercial fisheries especially in the northwest Pacific, but also is a common recreational target off the California coast in the northeast Pacific. In previous decades, stock biomass and landings of chub mackerel have shown large variations both in the western and eastern North Pacific, indicating a potential influence of environmental variables (e.g. sea surface temperature, prey availability and ocean currents) on the growth, recruitment and stock structure. However, since chub mackerel is a high migratory species, *in situ* data availability is limited to cover all necessary spatial distribution of chub mackerel with necessary temporal intervals. As a supplement of *in situ* data, individual-based growth-migration models are feasible tools to trace the experienced environment. Growth characteristics are possibly evaluated by a bioenergetics model, which has been applied to several small pelagic species, but no studies have developed one for investigating influences of biotic and abiotic environmental conditions on chub mackerel.

For small pelagic fishes like chub mackerel, metabolism is the primary means of energy dissipation in bioenergetic modelling and is directly related to residual energy available for growth. Therefore, understanding a species' metabolism can provide critical insight into other ecological traits and life history strategy. Although physical oceanic processes are generally well understood and can be successfully modeled, the biological processes of target organisms are less well studied and can be the primary source of uncertainty in developing an individual-based growth-migration model. Besides, species-specific ecological traits in fishes are likely to vary between populations or stocks due to differences in regional oceanic conditions. As large ocean basins have distinct east–west temperatures, even at the same latitude, habitat temperature can be significantly different due to ocean circulation. Therefore, even within the same species, geographic specificity bioenergetics parameters as well as location-specific variation in temperature and food could be shown in chub mackerel, which have oceanic-scale distributions. However, although the typical temperature range of chub mackerel is 10-27°C based on chub mackerel distributions, previous studies only measured speed dependent metabolic data at 18 and 24°C and single speed (1 *BL* s^{-1}) metabolic data at 15 and 20°C of Northeast stock, no published study has examined the oxygen consumption rate and swimming performance of Northeast stock at relatively low temperatures (i.e., below 18°C). Meanwhile, the study on metabolic performance of Northwest stock remains blank.

Therefore, this study examined whether the characteristics of respiratory metabolism of chub mackerel of different stocks are specific corresponding to the local environmental conditions. Two stocks - Northwest stock around Japan using the Kuroshio Current and the Northeast stock in the California Current system, which are distributed on opposite sides of the North Pacific at similar latitudes but where the temperature contrast is large were chosen for intraspecific comparison. For Northeast stock, this study firstly measured swimming ability and metabolic data of chub mackerel using a variable speed swim tunnel respirometer at 14°C, a relatively low temperature, using methods following those used in previous studies at higher temperatures. New data were combined with data from previous studies to estimate respiration parameters, including dependencies on temperature, growth stage (mass), and activity level (swimming speed), for a bioenergetics model and the cruising speed for a migration model. The same experiments were then conducted at 14, 18 and 24°C using wild or aquaculture chub mackerel collected from the Northwest stock. The results were compared with those of the Northeast stock under the known climatic environment each stock regularly encounters to examine potential differences in the metabolism and swimming performance between the two stocks associated with their local habitat. With estimating parameters of other terms including consumption, egestion, excretion, specific dynamic action and caloric equivalent by reviewing previous studies, a growth-migration model of Northwest stock chub mackerel was established. As an example of application, the growth-migration model was used to simulate the early life history of chub mackerel from 2002 to 2016 and the model results were calibrated with the observation data.

1. Swimming and metabolic rate measurement experiment

Swimming energetics and metabolic data from Northeast stock wild individuals [17.1-30.5 cm fork length (*FL*), 43.4-252 g, n=9] were collected at 14°C, a low temperature within the typical thermal range of this species, using two variable-speed swim-tunnel respirometry (5-L for the fish under 80 g and 30-L for the fish over 80 g; Loligo Systems, Tjele, Denmark). There was no significant relationship between U_{max}, expressed either in cm s^{-1} or $FL\ s^{-1}$, with fish mass or fork length.

For Northwest stock, 43 juvenile individuals were used, from two aquaculture sources and one wild source obtained from coastal Japan. Similarly, two variable-speed, temperature-controlled swim-tunnel respirometers (280-mL Blazka-type for small juveniles (5.5-6.5. cm, 1.7-3.4 g) and 5-L Brett-style for large juveniles (10.8-19.6 cm, 11.7-94.8g) Loligo Systems, Tjele, Denmark) were used according to the fish size. The small mackerel (5.5–6.0 cm, 1.7–3.4 g, n=13) and large wild individuals (10.8–15.8 cm, 11.7–38.2 g, n=17) were tested under the temperature of 18 and 24°C , while large aquaculture juveniles (13.8–18.6 cm, 23.0–94.8 g, n=13) were measured at 14 and 18°C . The maximum sustainable swimming speed (U_{max}) at 24°C and 14°C showed no significant relationship with fork length or mass. At 18°C, U_{max} showed a significant linear relationship with fork length (p<.05), and slope of this relationship was not significantly different than that of the Northeast stock at 18°C (ANCOVA, p=.270). Compared to Northeast stock, at a given size, U_{max} of the Northwest stock showed no significant difference at 18°C and 24°C, but was lower at 14°C.

2. Estimation of metabolism-related parameters and migration speed

The data measured by swimming and metabolic rate experiments were then combined with existing data to develop a more complete set of bioenergetic parameters for chub mackerel. Specifically, a large dataset of metabolic information for chub mackerel was compiled and applied to estimate the parameters of the respiration term used in bioenergetics modelling.

For Northeast stock, standard metabolic rate (SMR), which corresponds to metabolic rate with zero swimming speed, was estimated as SMR=$0.0103W^{-0.490}\ e^{(0.0456T)}$as a function of fish mass (W) and temperature (T). Since the aquaculture-reared fish of Northwest stock used in this study had a wider cross-sectional area at a given mass than one of the wild caught fish, a correction term of cross-sectional area at the largest girth was added to the function of SMR to eliminate the body-shape effect. As a result, SMR of Northwest stock was expressed as SM$R = 0.0290W^{-0.219}\ e^{(-21.42/T)}\ Q^{2.27}$, where Q is the ratio of cross-sectional area between aquaculture and wild. Comparing with the Northeast stock, the Northwest stock showed lower mass dependence (-0.129) and different temperature dependence ($e^{(-21.42/T)}$).

All individuals (n=76) showed a significant exponential relationship between swimming speed and size-specific oxygen consumption rate ($\dot{M}_{O2}$, mg O_2 min^{-1} kg^{-1}) except one from Northeast stock and four from Northwest stock, then used to estimate the swimming-dependence parameter d_R. The value of d_R was normally distributed and did not differ significantly between temperatures, with the expected value of 0.0235 s cm^{-1} for Northeast stock and 0.0252 s cm^{-1} for Northeast stock, respectively and the d_R of the two stocks did not differ significantly (ANOVA, p=.324). Insignificant difference of d_R between the two stocks resulted in the similar optimal swimming speed (the swimming speed with the minimum cost of transport, U_{opt}) between them. U_{opt} of Northwest stock was 39.2 cm s^{-1} (2.1–6.4 $FL\ s^{-1}$), regardless of temperature and fish mass, which was similar to 42.5 cm s^{-1} (1.5–3.0 $FL\ s^{-1}$) of the Northeast stock.

3. Growth-migration model and its application for the Northwest Pacific stock

While respiration parameters in the bioenergetic model for Northwest stock were determined by the above laboratory experiments, consumption was estimated as a function of fish mass, water temperature and prey condition using experimental and field data from eight previous studies. Other dissipation terms including egestion, specific dynamic action and excretion were defined as constant proportions of the consumption based on the estimation of a previous study.

As an application the early life history of Northwest individuals was simulated from 2002 to 2016 under satellite derived environments. The hatch day of larvae of each year in April was decided by the peak of hatch day which was estimated by otolith analysis of the fish sampled from annual scientific survey conducted by the Fisheries Research and Education Agency. The end day of simulation was decided as June 8th to be consist with the *in-situ* sampling period. Half saturation constants for consumption were adjusted to reproduce realistic growth of chub mackerel in the model comparing with that estimated from the *in-situ* sampling data. The migration was defined by a vector composition between the advection by ocean currents and predicted swimming behavior. The growth was calculated using bioenergetic model determined above. For comparison, the simulation was repeated twice under same conditions except respiration parameters once changed to those of Northeast stock (alternate experiment) to investigate the effect of specialized characteristics on respiratory metabolism.

Among over 350 thousand individuals simulated by the growth-migration model, about 130 individuals migrate into the survey area, where the compared *in situ* samples were captured, during the survey period and used for further analysis. They were clustered into 3 groups according to the daily growth rate using K-means cluster algorism. The migration routes of individuals were strongly affected by Kuroshio at first 30 days, then the fish gradually assembled to high-growth area by self-selected swimming behavior. The first group with the lowest growth rate throughout the simulation period usually had initial position where on the axis or south side of the Kuroshio, hence were transported eastward further, and experienced higher temperature but poor prey environment. The other groups which usually located at the north side of the Kuroshio axis showed relative higher growth rate. The second group, which contained second most individuals, showed the highest daily growth rate around day 28, when they had separated from Kuroshio and migrated northward to the relative high prey density area. The third group with the least individual numbers showed the highest growth rate during the first 20 days corresponding to experience relative higher temperature and extreme good prey environment, also migrated northward but a few days later than the second group. The results indicated that northward migration at early life stage could benefit the growth by reducing the energy dissipation and increasing food consumption in lower water temperature but high prey density environment. Besides, the year which contained more individuals from high-growth-rate groups (second and third) showed higher recruitment and recruitment per spawners (PRS), which supported the hypothesis that 'higher growth rate in the early stage was related to higher recruitment' indicated in the previous studies. In the alternate experiment, the individuals with metabolism characteristics of Northeast stock showed similar migration route but lower growth rate within a year, indicating the bioenergetic differences of swimming performance and metabolism of Northwest stock is specific to its local environment to maximize bioenergetic efficiency.

This study is the first study that intraspecific comparison on respiratory metabolism was conducted on small pelagic fish with basin-scale distribution. Specifically, a large dataset of metabolic information was compiled and used for developing the growth-migration model for chub mackerel. The simulation results on the early life history of chub mackerel from 2002 to 2016 verified the strong sensitivity of growth to the relative position of the Kuroshio though habitat temperature and prey density even though the satellite derived relatively coarse environmental conditions were used. The model developed in this study could be a feasible way to investigate potential mechanisms that produce strong year classes in further coupled with higher resolution environments which can represent high spatial-temporal variabilities in the Kuroshio and Kuroshio Extension areas.