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学位論文題目	Temporal and spatial variability in early life history events of *Sebastes inermis* in Sendai Bay, northern Japan.（仙台湾におけるメバルの初期生活史の時空間的変動）
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論 文 内 容 要 旨

INTRODUCTION

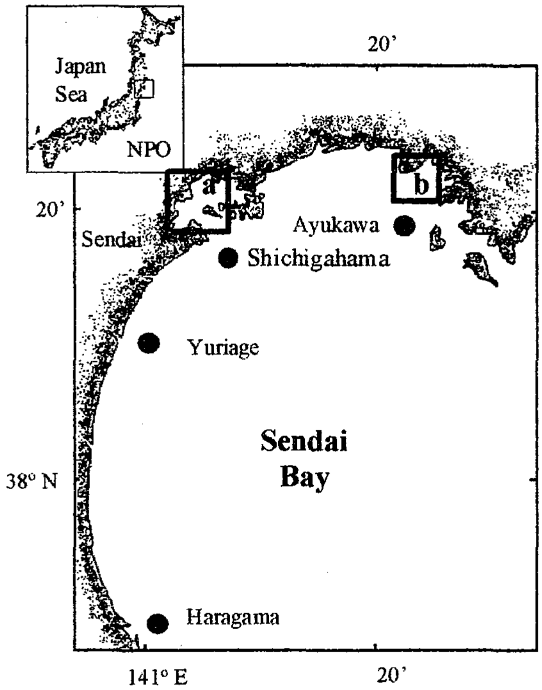

Fig. 1 Map of Sendai Bay, Miyagi, northern Japan, showing the locations at which adult female (filled circles) and YOY (rectangle) *S. inermis* were collected. a) Matsushima-*Zostera marina* bed and b) Kitsunesaki- *Sargassum* bed s.

Young-of-the-year (YOY) of Some *Sebastes* migrate into nearshore areas (e.g. seagrass beds, *Sargassum* beds, or kelp canopy habitats) as larvae or juveniles after completing their planktonic stage offshore. The black rockfish *S. inermis,* a commercially important species from southern Hokkaido to Kyusyu in Japan and in southern Korea (Kido 1984), is one of the rockfishes that occupy temporarily nearshore nursery grounds. *S. inermis* extrudes their larvae in winter months in rocky areas, and, after a planktonic stage, transforming juveniles move into *Zostera* or *Sargassum* beds during the spring season. As juveniles increase in size and as the biomass in the nursery grounds become unfavorable, they move to deeper habitats. However, on this life cycle there are questions unresolved yet. Do larvae and/or young juveniles move actively or passively into the nearshore zone? How do they synchronize the migration with the timing of settlement? What role might the planktonic duration play in this adaptive strategy? Do YOY discriminate between *Zostera* and *Sargassum* beds? What is the contribution of each nursery ground to sustaining the adult population? These aspects are mandatory to understand the relationship between the life stage and the population dynamics of the adult stock. In order to disclose these questions I used information from field collections, analysis of the macrostructure, microstructure and microchemistry of otoliths of YOY *S. inermis* settled in *Zostera* and *Sargassum* beds in a northwest coast of Sendai Bay (Fig. 1). The goal was to examine the following 4 aspects of the early life history of this rockfish.

1.- Spatio-temporal distribution of extrusion of *S. inermis* in Sendai Bay

Because the extrusion season can affect the dynamics of settlement of juveniles into nearshore nursery grounds, I examine here the spatio-temporal distribution of extrusion in four sites from south to north along Sendai Bay: Haragama, Yuriage, Shichigahama and Ayukawa (Fig.1). To perform this research, 941 females were caught by angling and gill nets from October 2000 to March 2001. The total length, total weight, and ovary weight as well as GSI were recorded. In parallel, age determination was focused to determine the age structure of the sapwners in each location. For all fish collected year rings of sagittae were counted. In addition ovaries of females were classified in 4 morphological stage: a) ripe b) fertilized, c) eyed, and d) spent ovaries. Both mean GSIs and ovary weight showed that extrusion season of *S. inermis* ranged from late December to early March. In addition, frequency of occurrence of development stages showed that the extrusion season shifted in both temporal and spatial scales, beginning and finishing earlier in southern locations than in northern ones (Fig.2.I). Such a variation in reproductive traits within a small spatial scale of kilometers as in *S. inermis* has not been reported for any other rockfish species to date. In addition, older and bigger female *S. inermis* tended to start their extrusion earlier than younger and/or smaller females and the shift appeared to be gradual (Fig. 2.II). This declination in age and body size progressed gradually from the beginning to the end of the extrusion season in all locations, with plots for Ayukawa showing the significantly lower age and size. These findings are relevant for fishery management of this species.

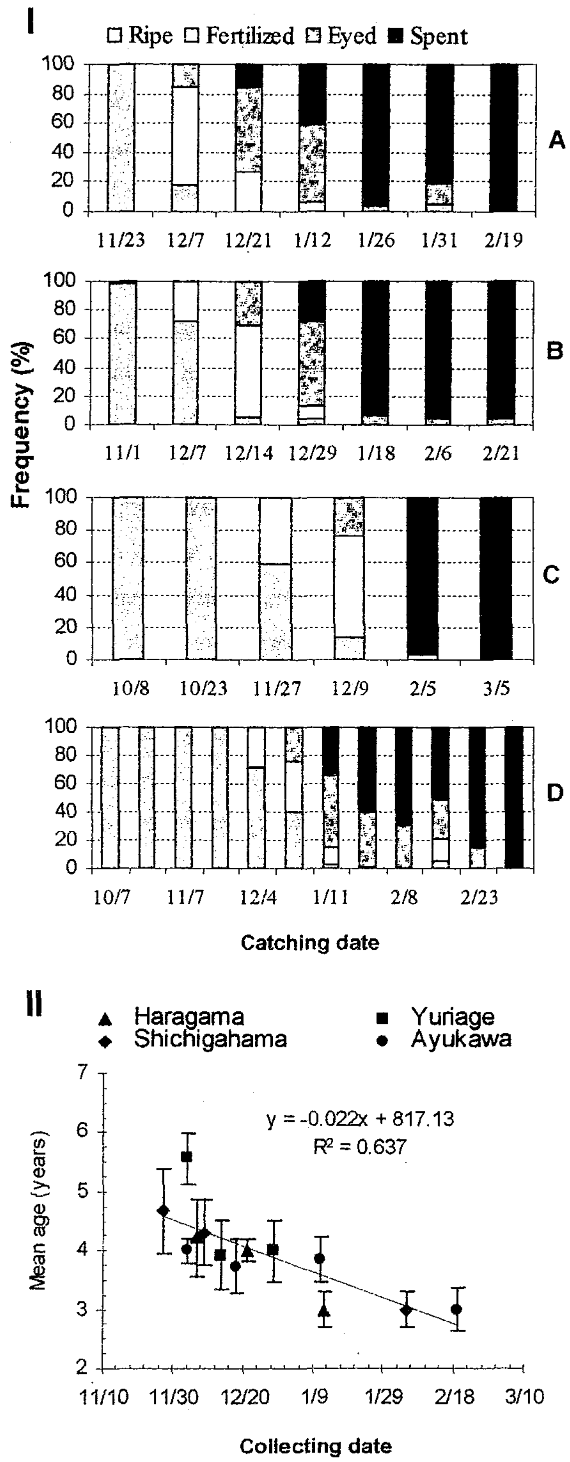

Fig.2.(I) Percentage of occurrence of four development stages of ovaries in female *S. inermis* collected from October 2000 to March 2001 in four locations in Sendai Bay: Haragama (A), Yuriage (B), Shichigahama (C), and Ayukawa (D). **II)** Change in age structure of female *S. inermis* with fertilized ovaries as reproductive season progressed in Sendai Bay. Each plot represents a single collection date in a given site. Vertical bars denote the standard deviation.

2.- Otolith microstructure (OM) of the black rockfish, *Sebastes inermis*

In addition to age and growth, fish otoliths may also record life history events such as metamorphosis, settlement, and migration. In this section I focused to analyze in detail the OM of juvenile *S. inermis* collected in Matsushima-*Zostera marina* bed to disclose the early life history events recorded on them, and to validate extrusion check and the daily periodicity of the increment deposition. YOY *S. inermis* were collected in a *Zostera marina* bed in Matsushima Bay from March to November in 1998 and 1999. The extrusion check was validated upon examining newly extruded reared larvae. Tetracycline treatments and a thermal marking experiment showed that the otolith increments were produced daily. Four zones were observed (Fig. 3): a clear central zone (CZ), which evolved a clear extrusion check (EC), after which a planktonic zone (PZ) was deposited (Fig. 3A). PZ extends from EC to a clear transition check (TCh) (Fig. 3 B&C). This check marks the boundary between the PZ and the following layer, the post-settlement zone (PSZ). PZ zone appears to constitute the planktonic period for this species. Increment widths after TCh (i.e. during the PSZ) were clearly broader than those in the PZ. The PSZ seemed to be formed by the shift of environmental conditions with the immigration into seagrass belts. To the border of otolith appeared the hyaline zone (HZ, Fig. 3D), visible only in bigger juveniles. It is a translucent growth zone with increments narrower and less resolvable than those of the outer boundary of the PZ. This layer extended over the remaining period of juveniles in the seagrass beds (from summer to autumn), and gradually the resolution of the increments decreased. This research has shown that the planktonic duration and post settlement period can be distinguished to study the patterns of settlement of this species into nearshore nursery grounds.

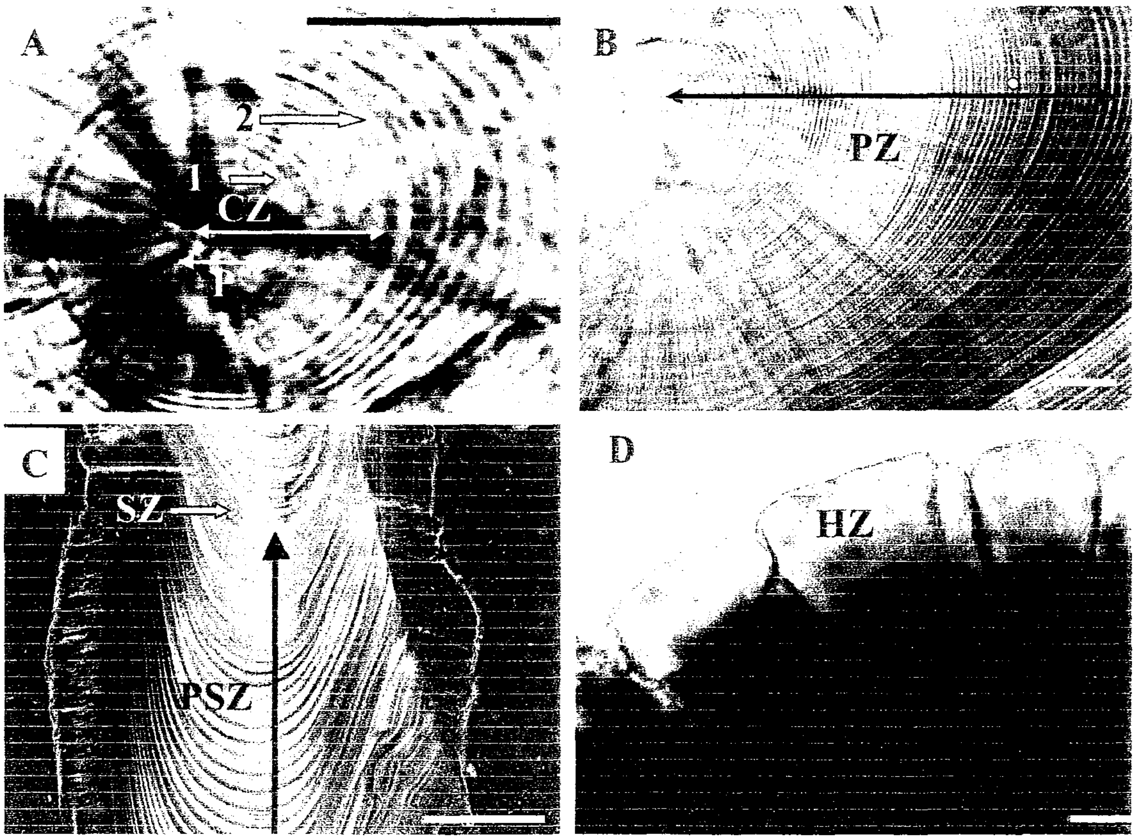

Fig.3 Light microscopic image of the sagittae of post-settled juveniles *S. inermis* in nearshore nursery grounds (A) CZ:central zone; (B) PZ: planktonic zone; (C) SZ: settlement zone; PSZ: post-settlement zone. (D) HZ: hyaline zone. A, C, D: sagittal planes; B: frontal plane. Scale bar= 30 μm.

3.- Patterns of settlement of juvenile *S. inermis* into *Zostera* and *Sargassum* beds in Sendai Bay

In this study I examined the temporal pattern of extrusion, planktonic period, growth rates (GR) of individual YOY during their planktonic period, as well as the temporal patterns of settlement of YOY *S. inermis* collected from 1998 to 2001 in Matsushima-*Zostera* and Kitsunesaki-*Sargassum* beds. Otolith analyses were used to estimate temporal patterns of settlement. YOY arrived in distinctive groups from early April to middle May (Fig. 4 A). Settlement groups occurred around new and full moon phases (in spring tides) almost all years in Matsushima-Zostera bed, except for 1998, in which YOY arrived around third-quarter moon phases (in neap tides). The synchronism to the new and full moons was also observed for those YOY settling into Kitsunesaki *Sargassum* bed. I then analyzed timing of parturition, planktonic duration and growth rate during the planktonic stage, as well as the size at settlement. Parturition dates also occurred around the new and full moon (Fig. 4B), and were distributed mainly from early January to late February in almost years and habitats. In addition, YOY extruded earlier first appeared in the beds and vice versa. Planktonic periods ranged widely among settlement groups, years and habitats (from about 50 to 115 days). GRs of individual YOY ranged from 0.1 to 0.3 mm/d, following a similar trend among settlement groups, years and between habitats (Fig. 5), although settlers with longer planktonic period had the lower planktonic growth rates (Fig. 6.I). There were interannual differences in planktonic growth rates, particularly in first 3 week of the larval life (Fig. 6.II). Surface water temperature during the planktonic period followed a parabolic tendency from early January to late April, with coolest temperature on February and March (Fig. 6.III).

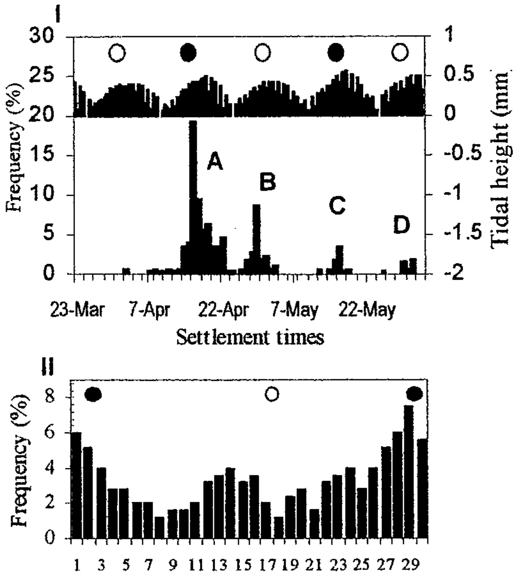

Fig. 4 Temporal patterns of settlement (I) and birth dates (II) of *S. inermis* in Matsushima-*Zostera* bed in 1999, which was also the most common pattern observed. Filled and open circles denote new moon and full moon. Maximal tidal heights are plotted for each day.

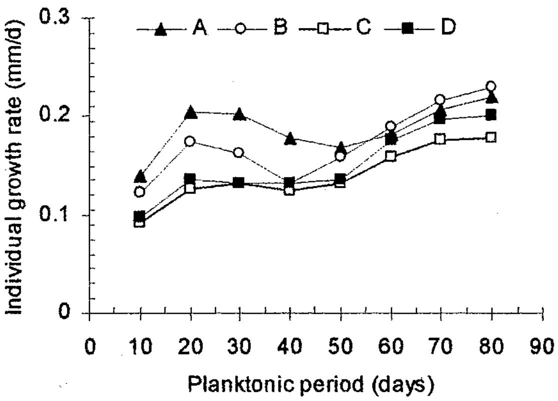

Fig.5 Changes in 10 day-average of growth rates of individual YOY *S. inermis* during their planktonic period in offshore waters before settling in Matsushima-*Zostera* bed in 1999. Capital letters denote settlement groups illustrated in the Fig. 4.

The general trend was a consistent pattern in the size at settlement around 20 mm TL between habitats and among settlement groups (Fig. 6.IV).

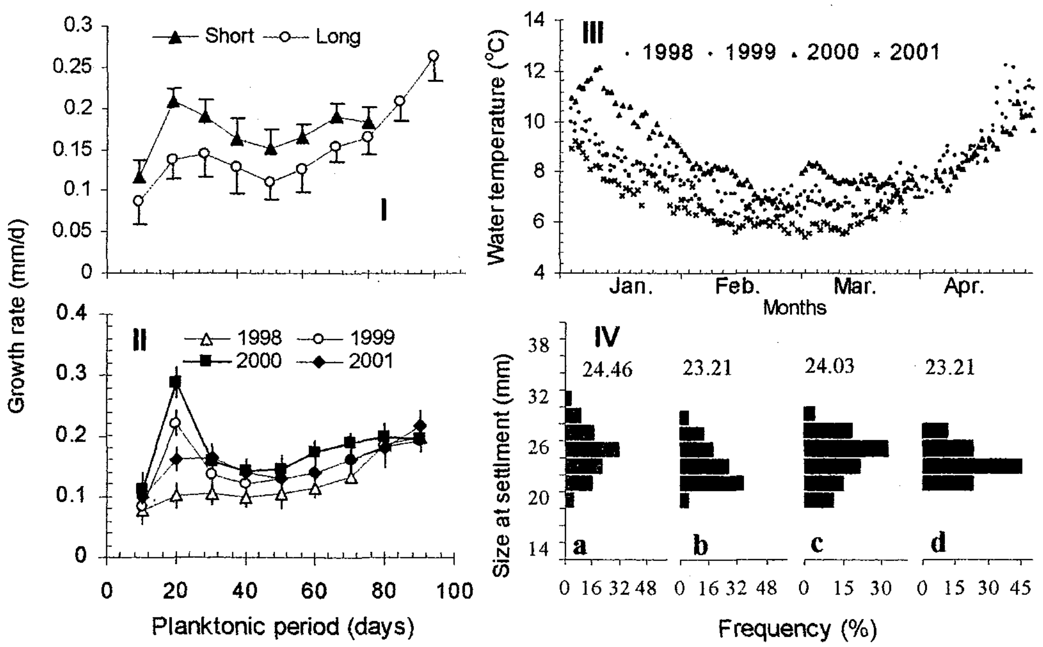

Fig. 6 A 10 day-average of individual growth rates for YOY *S. inermis* having shorter and longer planktonic periods (**I**). Interannual comparison of growth rate during planktonic periods (**II**). Plots of daily water temperature from 1998 to 2001 in Tashiro Island, Sendai Bay, northern Japan (**III**). Size at settlement of YOY in Matsushima-*Zostera* bed in 1999; letters denote settlement groups and numerals in the graph denote mean values (**IV**).

4.- Life history traits of YOY *S. inermis* during the post-settlement period in *Zostera* and *Sargassum* beds in Sendai Bay.

Young-of-the-year (YOY) *Sebastes inermis* uses seagrass beds as a temporary nursery ground after completing the planktonic stage in offshore waters. In this study, I examined the seasonal changes in abundance and the early life history traits of YOY *S. inermis* in a *Zostera marina* bed in Matsushima Bay. I analyzed the daily growth increment of otoliths to estimate birth dates 1998, 1999, 2000 and 2001-year classes. In addition, I addressed on the seasonal variability in growth rates after settlement in *Zostera* and *Sargassum* beds. The results obtained showed the following main traits in almost years: CPUE of YOY in Matsushima decreased sharply in summer months (Fig. 7. III) synchronizing with the maximum values of water temperature (Fig. 7.I) and the lowest values of leaf length of *Z. marina* (Fig. 7.II). There were inter-annual fluctuations in the magnitude of settlement into seagrass bed. Composition of birth dates in Matsushima-Zostera bed ranged from Late December to early March, but the range varied among years. Growth rates ranged from 0.4 to-0.8 mm/d after settlement in both habitats, and settled groups followed a same growth trajectory regardless arriving time (Fig. 7.IV). Settlers that were extruded earlier first appeared in the *Zostera* bed, and they were the first to leave, whereas those YOY extruded later tended to stay longer in *Zostera* belt.

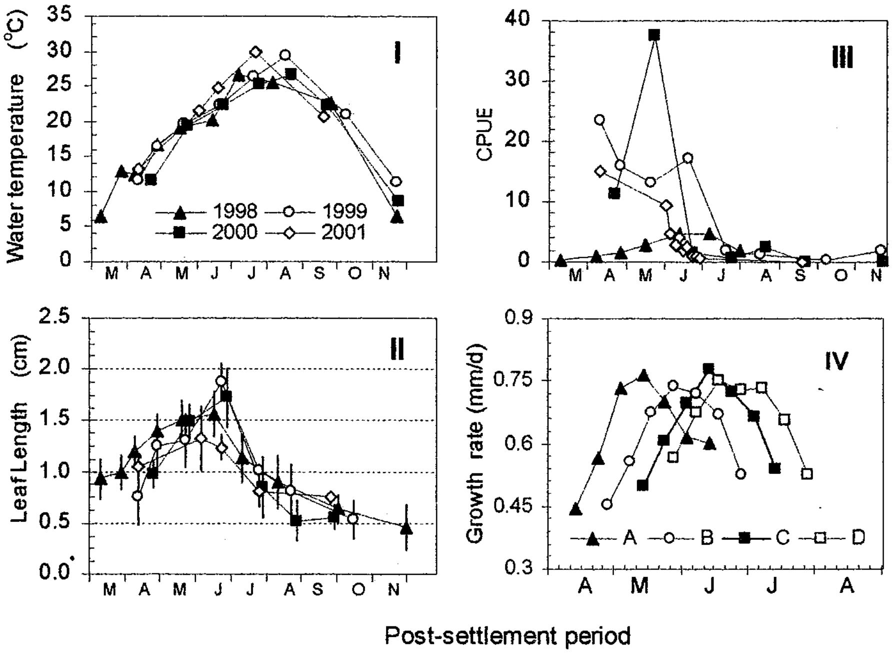

Fig. 7 Seasonal fluctuation in water temperature (I), mean maximum leaf length of *Zostera marina* (II), mean CPUE of YOY *S. inermis* (III), and post-settlement growth rate of individual YOY in each arriving group (capital letters) (IV

5.- Contribution of Matsushima-*Zostera* bed to sustaining the adult population of *S. inermis*.

Knowledge on the contribution of YOY fishes growing in *Zostera* nursery grounds to the adult population is mandatory for fisheries management. The goals of this research were: to evaluate 2 new techniques for classifying YOY *S. inermis* into *Zostera* and *Sargassum* beds, based on the microchemistry of otoliths (using high resolution inductively coupled plasma mass spectrometry (HR-ICPMS), and measurements of the otolith kernel (the macroscopic nucleus area of otolith of adult fish). Juvenile *S. inermis* from Matsushima-*Zostera* and *Sargassum* beds were distinguished with high accuracy using both the trace elements

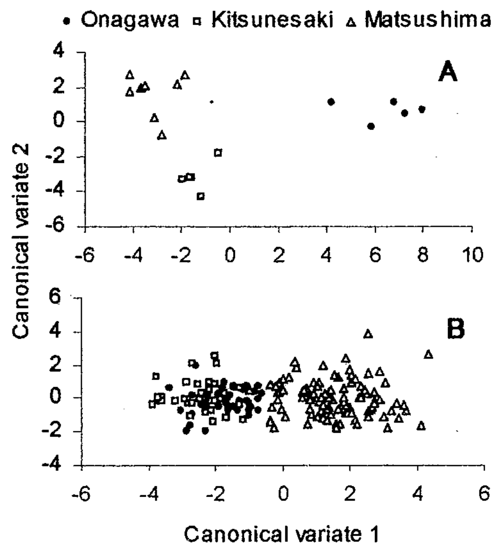

Fig. 8 Plots of the first 2 canonical discriminant functions for the trace elemental composition (A) kernel measurements (B) of otoliths from YOY *S. inermis* collected in *Zostera* (Matsushima) and *Sargassum* beds (Onagawa and Kitsunesaki) in summer of 2001.

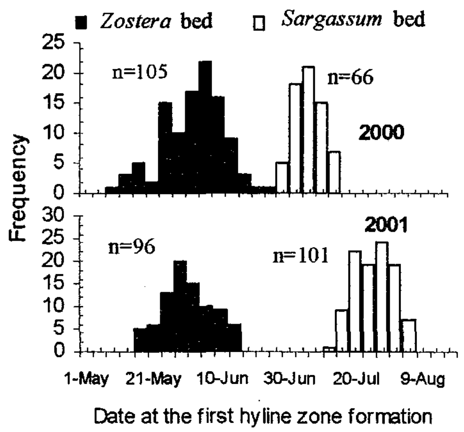

Fig. 9 Date at formation of the first hyaline zone estimated by otolith microstructure analysis for YOY *S. inermis* collected in Matsushima-*Zostera* and *Sargassum* beds in summer of 1999 and 2001

(TE=Li, Mn, Ni, Cu, Zn, and Ba, Fig. 8A) and the kernel measurements (KM=width & length, Fig. 8B). These findings suggest that TE and KM can be used as natural tags of YOY growing in nearshore nursery grounds. In particular, the width and length of the otolith kernel allowed to perform discriminant algorithms to classify the adult fish with unknown past life, and revealed that over 50% of adult fishes collected in various sites were those which grew in Matsushima-*Zostera marina* bed. The propriety of KMs as a natural tag was based upon the fact that the first hyaline zone in otolith of YOY *S. inermis* were formed at a relatively fixed time in Matsushima-*Zostera* and Kitsunesaki-*Sargassum* beds each year, although significantly later in the *Sargassum* bed than in the *Zostera* area (Fig. 9).

DISCUSSION AND CONCLUSIONS

Otolith analyzes as underlined here demonstrated to be a powerful and accurate tool to disclose the early life history events of the black rockfish *S. inermis*, i.e. the extrusion, planktonic period, settlement patterns, and post-settlement period in *Zostera* and *Sargassum* beds, as well as to estimate the contribution of Matsushima-*Zostera* bed to the adult population.

Extrusion, planktonic period and temporal patterns of settlement

Results support that the timing of extrusion and settlement seem to be triggered by a similar environmental signal (moon phase) to maximize settlement. Older females with a higher reproductive potential spawned first in sites closer to Matsushima-*Zostera* bed (the preferred habitat in view of its high contribution to the adult population), whereas the younger one spawned later in sites closer to *Sargassum* bed. Hence, these findings suggest that there is an adaptive strategy developed for this species to synchronize maximal reproductive potential with successful use of its nearshore nursery habitats. Settlement of *S. inermis* occurred in temporally separated patches, independent of age, and was hence under active behavioral control. Settlers arrived mainly at new and full moon phases suggesting that settlers used the spring tidal currents to move shoreward actively and faster. Synchronism to first and third quarter moon phases seemed to be exceptional and governed by unknown mechanisms. Settlers arrived at a consistent size, and its optimization seemed to be linked to the planktonic growth rates, which ranged from 0.1 to 0.25 mm/d. These values are lower in comparison with other non-winter sapwners of

Sebastes. Despite this, it appears that the adaptive selection of timing of extrusion in winter months is advantageous when settlement occurs in pulses and at a consistent body size, because a variable planktonic period does not affect largely to the settlement size when growth rate is low.

Post-settlement period

Growth rates ranged from 0.4 to 0.8 mm/d after settlement in both habitats, and settled groups followed a same growth trajectory regardless the arriving time. This fact supports that settlement at temporally separated groups seemed to be an adaptive response to optimize the use of shallow nursery habitats in which the high water temperature in summer may be critical for bigger YOY than for smaller ones. The existence of optimal temperatures for growth not only suggest why YOY *S. inermis* need to recruit at pulses to optimize growth during a season of increasing water temperature, but also that the higher temperatures in summer contribute to the progressive migration of YOY from the *Zostera* bed. In consequence, YOY arriving in later groups do not need to migrate from the bed because they still have not attained the size at which the high water temperature may become a limiting factor. These findings are the first field evidences supporting the hypothesis of Love et al (1991) that ontogenetic movements of juvenile rockfishes from nursery areas into deeper water is attributed to ontogenetic changes in temperature preference, rather than lack of suitable preys or habitats.

Contribution of nursery grounds to the adult population

Juvenile *S. inermis* from Matsushima-*Zostera* and *Sargassum* beds were distinguished with high accuracy using kernel measurements of otoliths. The discriminant function generated revealed that the relative percentage of adults that grew in Matsushima-*Zostera marina* beds were over 50% The high contributions of YOY that grew in Matsushima-*Zostera* not only suggest that this habitat is crucial for this species, but also suggest that settlement magnitude into *Zostera* bed is an indicator of year class strength. Hence, it is possible to predict the relative abundance of a cohort of adult *S. inermis*, while it is in its first year of life. In consequence, it might be possible to test the hypothesis that growth and survival during the larval period might be directly related. The figure 10 shows settlement magnitude as an indicator of year class strength in the fours years studied. Growth rate during the early larval stage and settlement magnitude were significantly correlated, which supports the hypothesis of enhanced survival in fast growing fish.

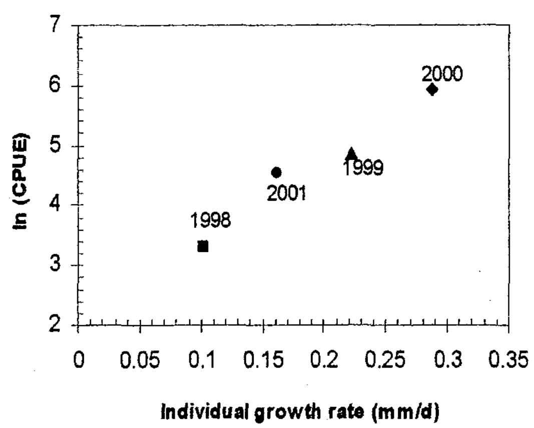

Fig. 10 Fitted regression (r^2=0.96) between the mean growth rate (mm/d) at the 3 week of the larval life and the abundance of YOY *S. inermis* collected in mid-May in Matsushima-*Zostera* bed. The regression support the hypothesis that a more rapid growth rate result in an enhanced survival.

論文審査結果要旨

メバル（*Sebastes inermis*）は北海道から九州までの浅海岩礁域に棲息する卵胎生の漁獲対象種で，外洋の岩礁域で産まれた後，外洋に面した岩礁域の褐藻ホンダワラ群落（ガラモ場）や内湾の維管束植物のアマモ群落（アマモ場）で，初春から盛夏にかけて，そこを保育場として生活を送ることが知られており，古くから数多くの研究が行われてきた。しかし，保育場への移入・回遊や着底個体数の変動機構，それらの場所における成長，減耗や移出機構といった個体群変動を解明する上で鍵となる事項についての研究は殆ど行われてこなかった。この研究ではそれらのことを耳石の微細構造の解析により追求した。

著者は最初に，仙台湾南部から北部までの4カ所における産仔期の時間的変動を雌親魚の調査により明らかにしている。産仔は12月下旬から3月初旬の間に起こり，南ほど，また高齢で大型の個体ほど早かった。

次に，発育に伴う生態的変化が耳石の成長軸（時間軸）に沿った微細構造の変化として捉えられるか否かを解析した。まず，中心帯の外側に見られるマークが産仔マークであること，その外側の微細輪紋が日周輪であることを産仔直後の仔魚の耳石の観察と耳石にマーキングした仔魚の飼育により確認した。また，アマモ場に出現し始める体長，孵化後経過日数，日単位での成長履歴，生態的変化に関する情報から，浮遊・遊泳生活期，着底生活への移行期，着底後の生活期を示す微細構造が存在することを明らかにし，この成果に基づいて以下の事柄を明らかにした。

まず，4月上旬から5月中旬までの期間に沿岸に近づいた仔魚は明瞭に識別できる幾つかの群として，月周期に同調し，大潮を利用して保育場に移動し，着底することを明らかにした。さらに，産仔は主に1月上旬から2月下旬の期間に満・新月に同調して起こること，早く産まれた群ほど早い時期に着底するが，着底するまでの浮遊・遊泳期の長さは大きく変動し，産仔期，産仔場との関係で長い浮遊・遊泳期を持つ仔魚ほどその間の成長速度が低いことを明らかにした。これらのことにより，満・新月に同調した産仔による効率的移送システムと浮遊・遊泳期の成長変動が至適体長での着底を可能ならしめる機構として機能している可能性を示した。

着底後の各個体の日成長履歴と各加入群の保育場からの逸出過程を解析した結果，稚魚がアマモの枯死による食物条件の悪化により保育場を離れるのではなく，個々の加入群はある一定の体長に達すると，成長に伴う至適温度の低下により随時保育場を離れること，このこととパルス状に保育場に加入する加入の仕方がアマモ場での種内競争を緩和している可能性があることを示した。

最後に，内湾のアマモ場，外海のガラモ場での稚魚に耳石の構造，微量金属に有意な違いがあることを示し，産卵親魚の耳石を用いて内湾アマモ場育ちの親魚の割合を求め，仙台湾の親魚の約50％が松島湾のアマモ場育ちであることを示し，保育場としての重要性を具体的数値として示した。

これら知見はメバルの初期生活史，特に保育場への加人，移出機構と内湾アマモ場の親魚個体群への貢献度の高さを初めて異体的に示したものであり，審査員一同，博士の学位を授与するのに充分に値するものと判断した。