

Age, Growth and Reproduction of Two Species of Scad, *Decapterus macrosoma* and *D. macarellus* in the Waters off Southern Kyushu

Tetsuro SHIRAIISHI^{1*}, Hiroshige TANAKA¹, Seiji OHSIMO¹, Hirohumi ISHIDA² and Norimasa MORINAGA²

¹ Seikai National Fisheries Research Institute, Fisheries Research Agency (Taira, Nagasaki 851–2213, Japan)

² Kagoshima Prefectural Fisheries Technology and Development Center (Ibusuki, Kagoshima 891–0315, Japan)

Abstract

Growth and reproductive characteristics of shortfin scad *Decapterus macrosoma* and mackerel scad *D. macarellus* collected in the waters off southern Kyushu were determined based on otolith readings and gonad histology, respectively. Translucent and opaque zones on sectioned otoliths were identified, and the number of opaque rings counted. Von Bertalanffy growth parameters of both species did not significantly differ between males and females, and the combined growth curves of *D. macrosoma* and *D. macarellus* were as follows: $FL_t = 346 [1 - \exp \{-0.456 (t + 0.771)\}]$ and $FL_t = 428 [1 - \exp \{-0.310 (t + 0.821)\}]$, respectively, where FL_t is fork length (mm) at age t . The spawning period was evaluated to be from May to August for *D. macrosoma* and from April to July for *D. macarellus* based on the monthly changes in the gonadosomatic index and histological observations. The fork length at 50% maturity of females was estimated as 238 mm for *D. macrosoma* and 258 mm for *D. macarellus*, and maturity age was estimated for both species as 2 years old.

Discipline: Fisheries

Additional key words: gonad histology, maturity age, otolith, spawning period

Introduction

The fishes of the family Carangidae including the genus *Decapterus* are economically important resources in tropical and subtropical waters of the world. In recent years, in relation to global warming as reported by IPCC (Intergovernmental Panel on Climate Change), the water temperature in the East China Sea and the Sea of Japan is reported to be increasing. The distribution pattern and biological characteristics such as growth and reproduction of the family Carangidae will be affected by the global warming in the future. Therefore, it is essential to clarify the biological information on these species to allow prediction and comparison of the biological characteristics with other pelagic fishes in the future. Although species of the Carangidae are used as a fishery resource in Japan, the biological characteristics have not been sufficiently investigated.

The shortfin scad *Decapterus macrosoma* and mack-

erel scad *D. macarellus* are distributed mainly in the waters off southern Japan and in the East China Sea. In the East China Sea, *D. macrosoma* distribute along the continental shelf edge area from Taiwan to the Goto Islands and in the waters off southern Kyushu, on the other hand, *D. macarellus* distribute in the coastal region from Taiwan to southern Kyushu¹¹. In the East China Sea there are six *Decapterus* species (*D. maruadsi*, *D. akaadsi*, *D. macrosoma*, *D. macarellus*, *D. tabl*, and *D. russelli*) with *D. maruadsi* and *D. macrosoma* being most abundant. The main fishery for scad (genus *Decapterus*) in the East China Sea is the large powered purse-seine fishery, and the total annual catch was more than 20,000 tons from the 1980s to 1990s. However, the annual catch amount decreased to 10,000 tons after 1998, and reached to 7,000 tons in 2006.

Previous studies on *D. macrosoma* in Japan have reported the distribution and morphological characteristics in the East China Sea¹¹, and estimated the spawning period from seasonal changes of gonadosomatic indices¹². On the other hand, for *D. macarellus* only the monthly growth

*Corresponding author: e-mail tetsuch@affrc.go.jp

Received 23 April 2009; accepted 31 August 2009.

rate based on fork length frequency data in the waters off Hachijojima¹ has been reported in Japan. However, there is no information from Japanese waters on growth using hard tissues and reproductive characteristics using histological techniques for both species.

The objective of this study is to determine age using otolith readings, and to examine sexual maturity and annual reproductive cycle using histological techniques for both species.

Materials and methods

1. Collection and measurements of samples

A total of 1,007 specimens of *D. macrosoma* obtained from August 2002 to May 2006 and 1,201 specimens of *D. macarellus* obtained from September 2002 to July 2008 in the waters off southern Kyushu were analyzed (Fig.

1). Specimens were commercially caught by large sized purse seiners and rod and line fishing, mainly off western Kagoshima Pref. for *D. macrosoma*, and off Tanegashima Island and Amami Ohshima Island for *D. macarellus*.

Specimens were measured to the nearest millimeter in fork length (*FL*) and to the nearest gram of body weight (*BW*). The gonad weight (*GW*) was measured to the nearest 0.1 g after determining the sex, and small pieces of the gonad were fixed in 10% formalin for histological observations. The gonadosomatic index (*GSI*) was calculated as $GSI = 100 \times GW / (BW - GW)$.

2. Age determination

A total of 774 specimens of *D. macrosoma* and 622 specimens of *D. macarellus* were used for age determination. Sagittal otoliths were removed, washed in freshwater and dried. The left otoliths were burned at 200°C for 30

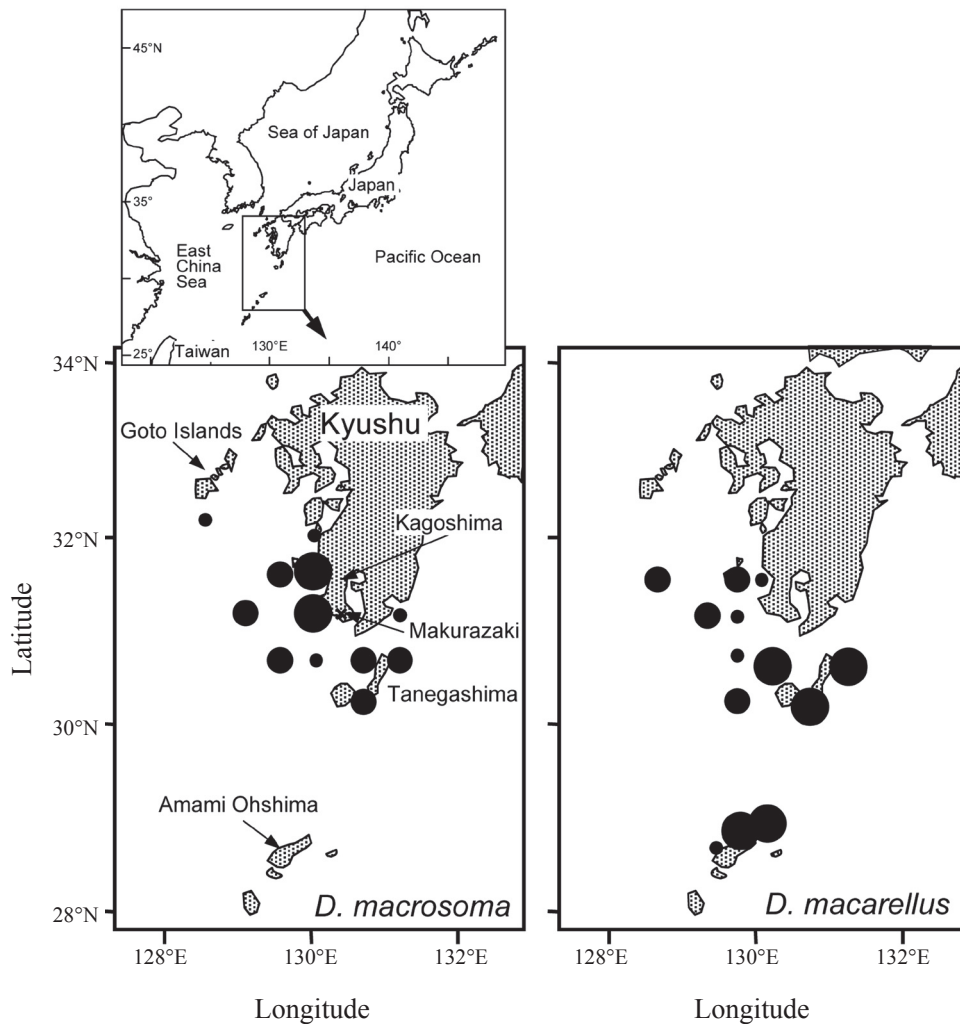


Fig. 1. The location of *D. macrosoma* and *D. macarellus* commercially caught in the waters off southern Kyushu and in the East China Sea

The size of circle indicates the number of fish caught at each site in the present study.
 ● : $0 \leq n < 50$, ● : $50 \leq n < 100$, ● : $100 \leq n$.

min in a drying oven (DO-300A, AS ONE, Osaka, Japan), embedded in resin and sectioned transversely (thickness 0.2–0.3 mm). Sectioned otoliths were observed under a digital microscope (Nikon, E-LV100D, Tokyo, Japan) with transmitted light to count the opaque rings and measure the ring radius using an otolith measurement system (ODRMS, RATOC, Tokyo, Japan). Each otolith was examined two times, with a minimum of one month between examinations, by two independent readers. If two or more examinations per otolith agreed on the number of ring marks, this number was recorded and used for the analyses. To measure the precision of age determination, the index of average percent error (*IAPE*) and the coefficient of variation (*CV*) were calculated as described in Beamish and Fournier² and Chang⁸, respectively.

The distance from the core (C) along a straight line to the inside margin of the first opaque zone was defined as the first ring radius (r_1), the sum of distance between the inside edge of each adjoining opaque zone was defined as the ring radius (r_2, r_3, \dots, r_n) and the distance from C to the otolith margin was defined as the otolith radius (R ; Fig. 2). To define the period of the formation of ring marks, we examined monthly changes in the occurrence frequency of individuals with a translucent zone on the outer margin of the otolith and in the marginal increment (*MI*). The *MI* was determined according to the equation:

$$MI = (R - r_n) / (r_n - r_{n-1})$$

where r_n is the distance from the core to the outer edge of the last annulus formed.

Age was determined for each fish on the basis of the number of ring marks (annuli) on the sectioned otolith, assuming hatch months of June for *D. macrosoma* and May for *D. macarellus*, which approximately corresponded to the middle of the spawning period (see Results). In order to describe the growth of males and females, von Bertalanffy growth equations were fitted to the observed *FL* values at age t by using nonlinear least squares regression for both sexes. The growth equation is

$$FL_t = FL_\infty [1 - \exp\{-K(t - t_0)\}]$$

where FL_t represents the fork length (mm) at age t and FL_∞ , K and t_0 represents the asymptotic fork length, the growth coefficient, and the hypothetical age at fork length equal to zero, respectively.

3. Histological observations

The fixed ovaries were dehydrated and embedded in methacrylate polymer resin (Technovit 7100, Heraeus Kulzer, Wehrheim, Germany), and 2 or 3 μm thick sections were stained using 0.5% toluidine blue solution. The stained sections were observed under an optical micro-

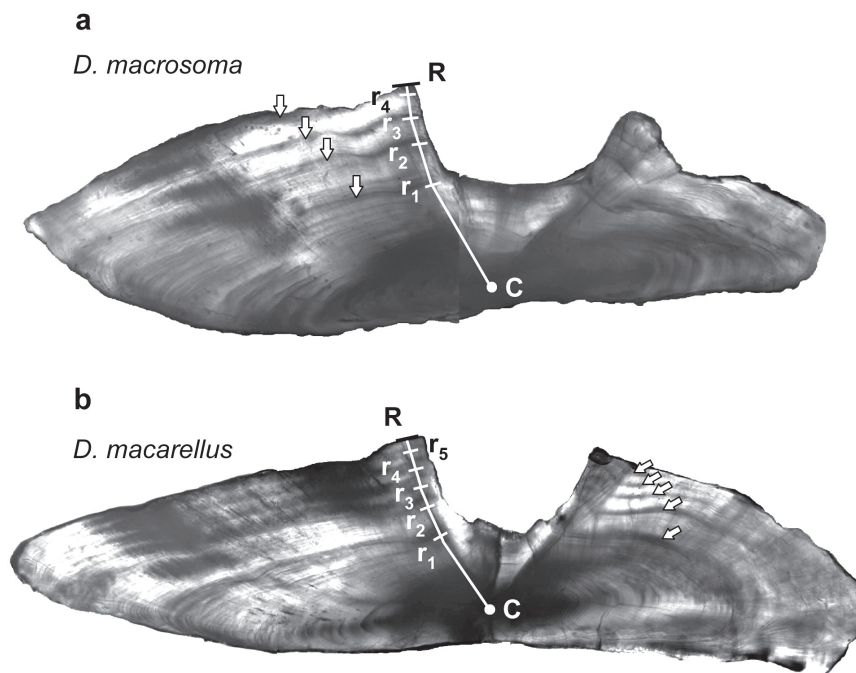


Fig. 2. Section otolith of (a) *D. macrosoma* and (b) *D. macarellus* with four and five ring marks, respectively

White arrows indicate ring marks. C: core, R: otolith radius (the sum total of the distance for each ring), r_n : ring radius of the boundary from a translucent zone to an opaque zone.

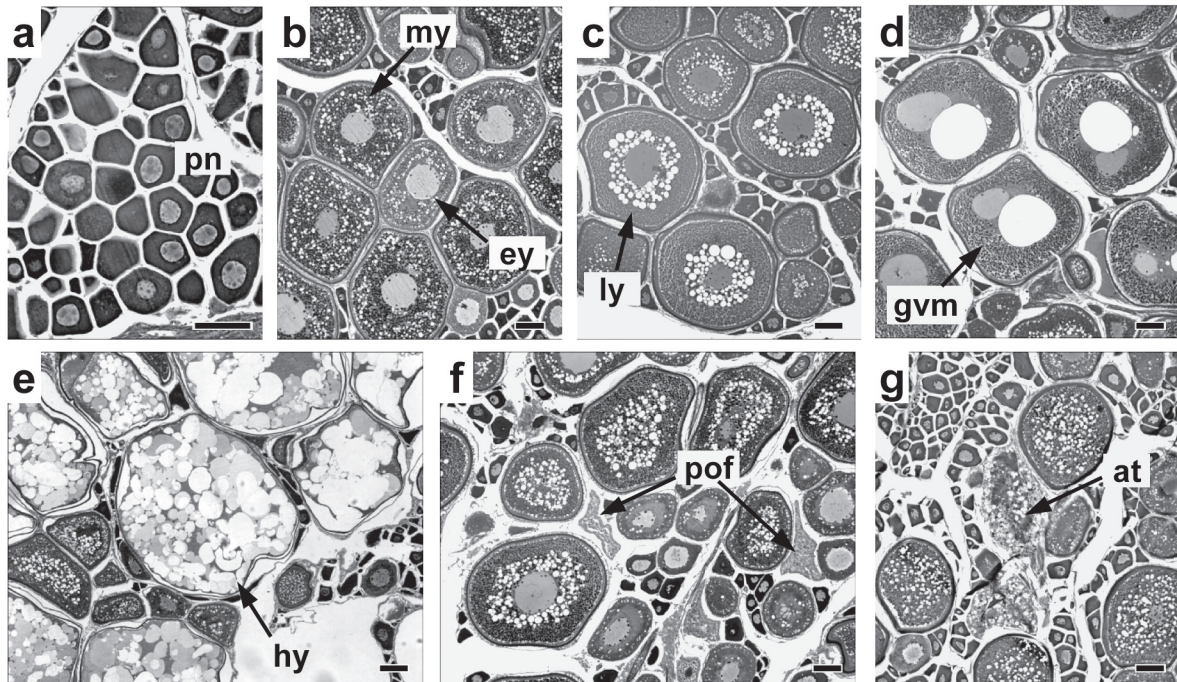


Fig. 3. Photomicrographs of ovaries at different developmental stages in *D. macrosoma*
 a: immature stage, b: developing stage, c: vitellogenic stage, d-e: mature stage, f: spawning stage, g: resting stage, at: atretic oocyte, ey: early yolk oocyte, gvm: germinal vesicle migration oocyte, hy: hydration oocyte, ly: late yolk oocyte, my: mid-yolk oocyte, pn: perinucleolus oocyte, pof: postovulatory follicle.
 Scale bar equals 100 μ m. The ovarian developmental stages of *D. macarellus* are similar to that of *D. macrosoma*.

scope and the most advanced oocyte stages were recorded. The developmental stages of oocytes were classified as perinucleolus (pn), yolk vesicle (yv), early to late yolk (ey), mid-yolk (my), late yolk (ly), germinal vesicle migration (gvm), hydration (hy), atresia (at) and the presence of postovulatory follicles (pof) recorded (Fig. 3). Totals of 244 females for *D. macrosoma* and 475 females for *D. macarellus* were examined. Only specimens larger than the minimum size at sexual maturity (see Results) were used to examine the seasonal changes of the gonad condition.

4. Sexual maturity

Size at maturity was estimated based on the examination of 209 females for *D. macrosoma* and 302 females for *D. macarellus* collected in their spawning period (see Results 4 and 5). Sexually mature females were defined as individuals with ovaries at the Vi, M or Sp stages (see Results 3). To estimate the FL at 50% maturity (L_{50}), a logistic function was fitted to the frequency of mature fish for each body size class with 10 mm interval using nonlinear least squares regression. The logistic equation was

$$Y_{FL} = 100 / [1 + \exp\{-a (FL - b)\}]$$

where Y_{FL} is the percent mature at FL, a is the slope, FL is

the fork length (mm) and b is the L_{50} .

Results

1. Growth of *D. macrosoma*

Most specimens examined from July to September had an opaque zone on the outer margin of the otolith, and the frequency with a translucent zone was high from November to January (Fig. 4a). Individuals with a new opaque zone and those without it were mixed in specimens collected from March to June (Fig. 4b), and the MI values increased gradually from July to January.

For *D. macrosoma* the rate of agreement between readers of the number of ring marks recorded was 65.6% (508 of the total of 774 specimens). The estimated maximum ages for males and females were 5 years and 4 years old, respectively. The IAPE and CV for these data were 4.04 and 5.75, respectively. The relationship between age and FL is shown in Fig. 5a. As there were no significant differences in the growth of males and females ($F = 0.52$, $p > 0.05$), then all the individuals were pooled for the estimation of the growth model. The growth model of *D. macrosoma* was estimated as follows:

$$FL_t = 346 [1 - \exp\{-0.456 (t + 0.771)\}]$$

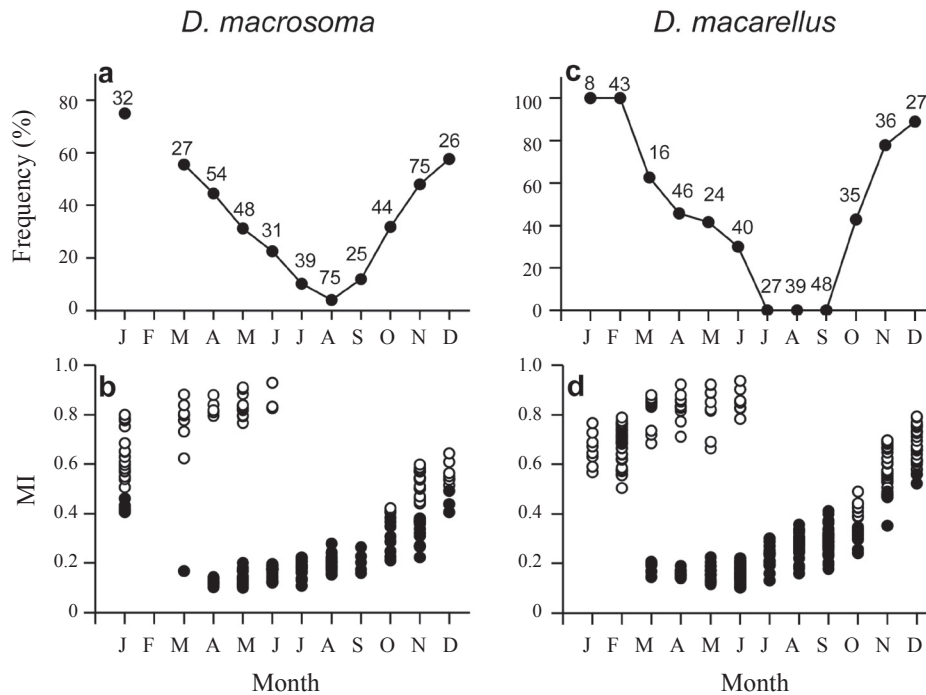


Fig. 4. Monthly changes in the frequency of appearance of a translucent zone on the outer margin of the otolith for (a) *D. macrosoma* and (c) *D. macarellus*, and in the marginal increment (MI) of the otolith for (b) *D. macrosoma* and (d) *D. macarellus*

Open and closed circles indicate the specimens with translucent and opaque zones on the outer margin, respectively. Number of fish examined each month is indicated.

2. Growth of *D. macarellus*

All specimens examined from July to September had an opaque zone on the outer margin of the otolith, and the frequency with a translucent zone was high from November to February (Fig. 4c). Individuals with a new opaque zone and those without it were mixed in specimens examined from March to June (Fig. 4d), and the MI values increased gradually from July to February.

For *D. macarellus* the rate of agreement between readers on the number of ring marks recorded was 63.5% (395 of the total of 622 specimens). The estimated maximum ages for both sexes were 8 years old. The IAPE and CV for these data were 4.20 and 5.97, respectively. The relationship between age and FL is shown in Fig. 5b. As there were no significant differences in the growth of males and females ($F = 0.78, p > 0.05$), then all the individuals were pooled for the estimation of the growth model. The growth model of *D. macarellus* was estimated as follows:

$$FL_t = 428 [1 - \exp \{-0.310 (t + 0.821)\}]$$

3. Stage of ovarian maturity

The ovaries could be divided into six stages of maturity based on the development of the most advanced oocytes and their histological characteristics.

- (1) Immature stage (Im; Fig. 3a), only previtellogenic oocytes are present, including those in the perinucleolus and yolk vesicle stages.
- (2) Developing stage (D; Fig. 3b), the most advanced oocytes are at the early yolk or mid-yolk stages.
- (3) Vitellogenic stage (Vi; Fig. 3c), the most advanced oocytes are at the late yolk stage which marks the end of vitellogenesis.
- (4) Mature stage (M; Fig. 3d, e), the most advanced oocytes are at the germinal vesicle migration or hydration stages. The degenerated old postovulatory follicles appear in some ovaries at the germinal vesicle migration.
- (5) Spawning stage (Sp; Fig. 3f), yolked oocytes and newly postovulatory follicles are present. Most postovulatory follicles disappear from the ovaries before the developing oocytes attain the germinal vesicle migration stage.
- (6) Resting stage (Re; Fig. 3g), all yolked oocytes are degenerating (atretic stage) and non-yolked oocytes are present.

4. Annual reproductive cycle of *D. macrosoma*

The mean GSI value in male *D. macrosoma* was high ($GSI > 3$) from May to July, and in female *D. macrosoma* it was high from May to August (Fig. 6a, b). The maxi-

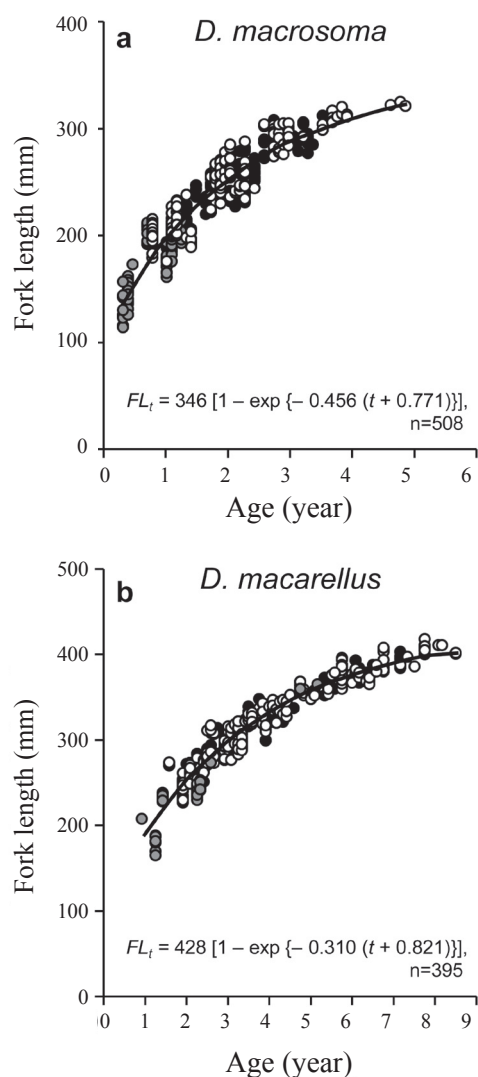


Fig. 5. Relationship between age and fork length of males (○) and females (●) for (a) *D. macrosoma* and (b) *D. macarellus*

Gray circles indicate individuals of unknown sex. Fitted curve indicates the von Bertalanffy growth curve.

imum value of the mean *GSI* for males and females was 6.1 in June and 7.3 in May, respectively. The mean *GSI* value became low in September and was under 1 from September to March.

Immature females (Im and D stages) of *D. macrosoma* were observed from September to April (Fig. 7a). Females with ovaries at the Vi stage appeared from April (approximately 27 %) to July, and all females in May exhibited the maturing condition (Vi or M stages), although specimens with ovaries at the Sp stage were not observed in May. Specimens collected in June and July had ovaries from the Vi or M stages, and females with ovaries at the Sp stage were observed. Females with ovaries at the Re stage were found from August to November.

5. Annual reproductive cycle of *D. macarellus*

The mean *GSI* value in both sexes of *D. macarellus* was high (*GSI* > 2) from April to July (Fig. 6c, d). The maximum value of the mean *GSI* for males and females was 4.1 and 3.3 in May, respectively. The mean *GSI* value decreased rapidly in August and was under 1 from October to March.

Immature ovaries (Im and D stages) of *D. macarellus* were observed in most specimens from September to March and in some specimens from April to May (Fig. 7b). Females with ovaries at the Vi, M or Sp stages appeared from April (approximately 72%) to July, and approximately 80% of females in May and June exhibited the maturing condition. Approximately 40% of females in July had ovaries at the Re stage, but females with ovaries in the maturing condition were also observed. Females with atretic ovaries were found from June to November.

6. Size of sexual maturity of *D. macrosoma*

Specimens collected from May to August (see Results 4) were used to estimate the size of sexual maturity. The minimum size at maturity of *D. macrosoma* was 232 mm *FL* based on observed specimens with mature ovaries. The logistic equation was determined as follows:

$$Y_{FL} = 100 / [1 + \exp \{-0.104 (FL - 238)\}]$$

$$(r^2 = 0.98)$$

The *L*₅₀ was found to be 238 mm and all females with *FL* ≥ 270 mm were mature (Fig. 8a). Therefore, the maturity age (*FL* = 232 mm) is estimated as 2 years old.

7. Size of sexual maturity of *D. macarellus*

Specimens collected from April to July (see Results 5) were used to estimate the size of sexual maturity. The minimum size at maturity of *D. macarellus* was 245 mm *FL* based on observed specimens with mature ovaries. The logistic equation was determined as follows:

$$Y_{FL} = 100 / [1 + \exp \{-0.087 (FL - 258)\}]$$

$$(r^2 = 0.98)$$

The *L*₅₀ was found to be 258 mm and all females with *FL* ≥ 330 mm were mature (Fig. 8b). Therefore, the maturity age (*FL* = 245 mm) is estimated as 2 years old.

Discussion

Otoliths are the hard tissues most commonly used to determine the age of fish³. The otolith annulus of fishes of the genus *Decapterus* has been used so far to estimate the age and growth of round scad *D. maruadsi* in the waters of the East China Sea off western Kyushu¹⁵. However, there

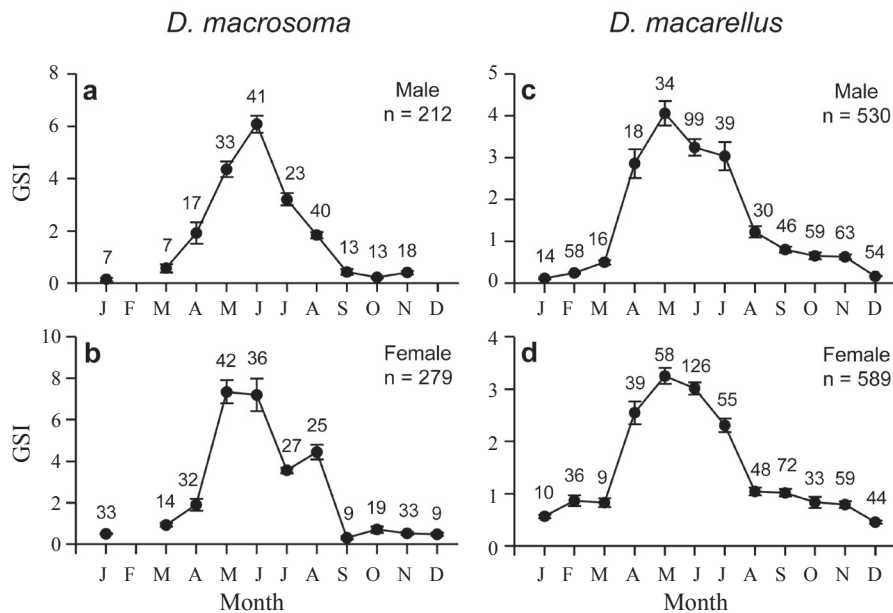


Fig. 6. Monthly changes in the mean gonadosomatic index (GSI) of mature (a) male and (b) female *D. macrosoma*, and (c) male and (d) female *D. macarellus*

Vertical bars denote the standard error. Number of fish examined each month is indicated.

are no studies for age determination using hard tissues in *D. macrosoma* and *D. macarellus*. The annulus formation season for *D. maruadsi* in the waters of the East China Sea off western Kyushu was in June which corresponds to the peak of the spawning season. The otoliths are characterized by thin opaque zones and wider translucent zones, and the opaque zone is formed from March to June in both species. These periods correspond to the spawning period of both species respectively. Therefore, it is suggested that the otoliths can be used for age determination in *D. macrosoma* and *D. macarellus*. Beamish and Fournier² suggested that *IAPE* has commonly been used to estimate variations in different readings or to estimate the reading error of different examiners. Although the rate of agreement between readers in this study was not so high (approx. 65%), the *IAPE* and *CV* values were relatively lower than those in other studies⁷ indicating the accuracy of the age determination was satisfactory.

The growth parameters, FL_{∞} and K values of *D. macrosoma* in Indonesia were estimated as 280 mm and 1.22 respectively¹⁷. The FL_{∞} and K values in Thai waters were 242 mm and 0.89 respectively⁴. The growth rate of young *D. macrosoma* in the present study is slower than that in Southeast Asian waters, but the maximum size is larger. The growth parameters of *D. macrosoma* in Indonesia waters were analyzed using length frequency data ranging from 125 to 245 mm *FL*, concentrated on 2 years old fish, and no individuals at 0 year old or more than 4 years old. Similarly, the growth parameters of *D. macrosoma*

in Thai waters were analyzed using length frequency data ranging from 135 to 225 mm *FL*, and the dominant size ranges were from 195 to 215 mm *FL* equivalent to 2-year-old individuals. In the present study, the growth parameters were estimated using otoliths of fishes that ranged from 114 to 325 mm *FL* from 0 to 5 years old, and the analysis result based on the otolith measurements of this study are considered to allow for a high degree of reliability. Therefore, we suggested that the age of *D. macrosoma* in the other waters using hard tissue will allow clearer comparisons among the areas that this species is distributed. On the other hand, there are few reports regarding age determination of *D. macarellus*, and monthly growth from fork length data has only been examined in the waters off Hachijojima, Japan¹. The size of the small fish population in the waters off Hachijojima increased by 40 mm *FL*/month from August to September, and 30 mm *FL*/month from September to November. The growth rate of young fish from August to November based on the results of this study was 17 mm *FL*/month. Therefore, it is suggested that *D. macarellus* in the waters off Hachijojima grow more rapidly than those in the waters off southern Kyushu. However, the growth rate of *D. macarellus* in the waters off Hachijojima was found from the mean values of fork length for four months (from July to October), and the reliability is low. Although study on growth of *D. macrosoma* and *D. macarellus* using hard tissue was determined in this study, it is difficult to compare the different factors affecting growth in both species, because the determina-

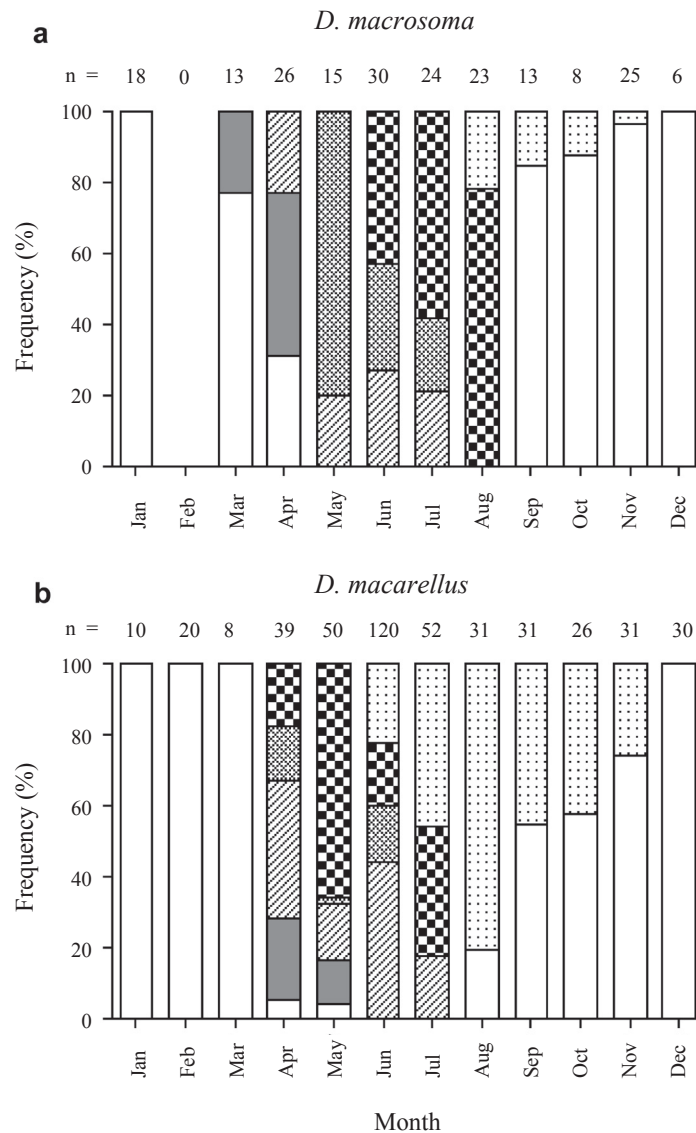


Fig. 7. Monthly changes in the frequency of occurrence of various maturity stages of ovaries of (a) *D. macrosoma* and (b) *D. macarellus*

Only specimens larger than the minimum size at sexual maturity ($FL = 232$ mm for *D. macrosoma*, $FL = 245$ mm for *D. macarellus*) were used for this analysis.

D: developing stage, Im: immature stage, M: mature stage, Re: resting stage, Sp: spawning stage, Vi: vitellogenic stage, n: number of fish examined.

□ : Im, ■ : D, ▨ : Vi, ▩ : M, ▧ : Sp, ▦ : Re.

tion methods of each study are different.

There have previously been no reports on the reproductive characteristics of *D. macrosoma* and *D. macarellus* using histological techniques. In the present study, the maturity age was estimated to be 2 years old based on results of age determination and size at maturity in both species. Our preliminary data indicated that most males larger than 226 mm *FL* for *D. macrosoma* and 230 mm *FL* for *D. macarellus* had mature stage testes during the spawning period. For both species in this study, the estimated sizes for a given age showed no significant difference between sexes, indicating that males mature and spawn at the same

age as females. Previous reported size at first maturity for female *D. macrosoma* was 177 mm *FL* in Indonesian waters¹⁷, and was 172 mm *FL* in Thailand¹⁶. These values agree with values for 1 year old, and are smaller than our estimated size of first maturity based on histological observations. There are no reports on the length at first maturity for *D. macarellus* in Japan. In Hawaii, Clarke and Privitera⁹ reported the standard length (*SL*) at first maturity of *D. macarellus* was 245 mm *SL*, and regression between standard length and fork length (*FL*) was given by the following equation; $FL = 7.23 + 1.027SL$. Therefore, the fork length at first maturity is 259 mm, and larger than

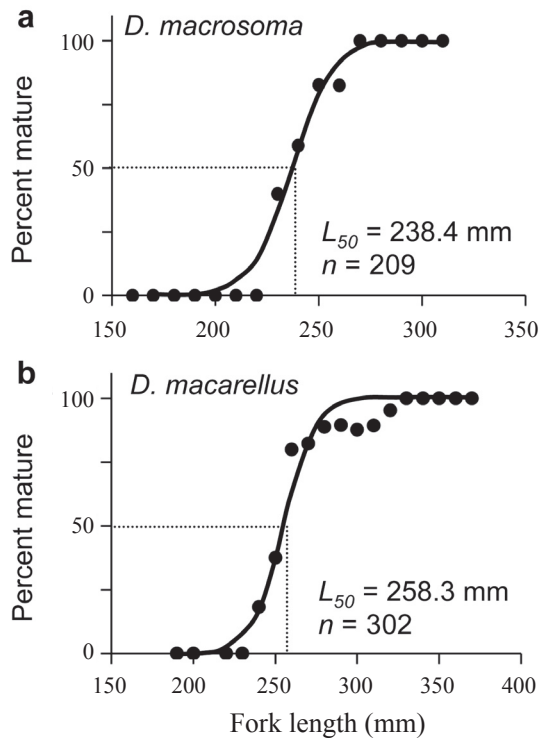


Fig. 8. Frequency distribution of mature female (a) *D. macrosoma* and (b) *D. macarellus* collected from April to August

L_{50} : 50% size at sexual maturity, n: number of fish examined.

that of our study. However, they estimated size at first maturity from the relationship between standard length and the gonad to somatic weight ratio (G/S), and did not use histological observations.

In the present study, female *D. macrosoma* and *D. macarellus* with ovaries at the mature and spawning stages appeared when the mean *GSI* was higher than 3. In the spawning stage ovary, postovulatory follicles continued to degenerate and disappear until the most advanced oocytes underwent final oocyte maturation (germinal vesicle migration or hydration stages), and the degenerated postovulatory follicles appear in some ovaries at the germinal vesicle migration, indicating that both species are multiple spawners. There is only one report on the spawning period of *D. macrosoma* in the southwestern part of the East China Sea based on monthly change of *GSI* values¹². Kishida¹² reported that the spawning period was from May to July, which approximates the results in the present study. There are no reports on the spawning period of *D. macarellus*. Our findings clearly indicate that *D. macrosoma* and *D. macarellus* have a prolonged spawning period, ranging from May to August and from April to July, respectively. In Southeast Asian waters, the spawning period for *D. macrosoma* was from February to

April based on the monthly change in *GSI* values¹⁶. This suggests that *D. macrosoma* spawn from late winter to early spring in Southeast Asian waters as against from late spring to summer in the East China Sea.

Previous studies on the genus *Decapterus* indicate that growth and reproductive characteristics differ among different habitats^{10,13,15}. However, it is not clear if these growth and reproductive differences occur due to differences in local genetic variations or environmental conditions of the habitat. There are some studies that have indicated the influence of environmental factors on biological characteristics. In the case of Atlantic cod *Gadus morhua*, growth of fishes in areas of high water temperature (low latitude regions) is faster and the size at sexual maturity is smaller than that in areas of low water temperature (high latitude regions)^{5,6}. That is, a high growth rate leads to an early start of sexual maturation. Moreover, it is suggested that variations in water temperature and trophic conditions in the winter season influence the maturation rate and spawning period of *Gadus morhua*¹⁸. In the case of jack mackerel *Trachurus japonicus*, the reproductive characteristics have changed over the long-term¹⁴, and the high fishery pressure for *T. japonicus* has led to a decrease in the spawning stock and recruitment stock biomass. In addition, it is indicated that the spawning period of *T. japonicus* in the waters off Nagasaki in recent years is earlier than that of fish from the 1950s to 1960s due to the influence of the increase of temperature of the surface layer¹⁴. Although these factors may also occur in the case of the genus *Decapterus*, at present there is insufficient data to clarify any trends. Therefore, in the future, it is necessary to monitor variations in reproductive characteristics with stock fluctuation and to further determine the growth and maturity processes before reaching 1 year old in order to understand the relationship between spawning stock and recruitment.

Additionally, the biological information provided in the present study can become an index for comparison among different sea areas. More information on the distribution, reproduction and feeding habits is needed to understand details of the life history of *D. macrosoma* and *D. macarellus*. In the future, it is important to examine the reproductive characteristics such as fecundity and spawning frequency in order to determine the mechanisms for sustaining their population at a high level.

Acknowledgments

We are grateful to the staff of Makurazaki Fishermen's Association in Kagoshima for their cooperation during the study. The present study was supported by the Fishery Agency, Government of Japan.

References

1. Anonymous (1992) Migratory fish—*Decapterus macarellus*. Publication of the Tokyo Metropolitan Fisheries Experiment Station, **366**, pp.84 [In Japanese].
2. Beamish, R. J. & Fournier, D. A. (1981) A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.*, **38**, 982–983.
3. Beamish, R.J. & McFarlane, G.A. (1987) Current trends in age determination methodology. *In* Age and growth of fish, eds. Aummersfelt, R. C. & Hall. G. E., Iowa State University Press, Iowa, 15–42.
4. Boonragsa, V. (1987) Preliminary analysis of mackerel (*Rastrelliger* and *Decapterus* spp.) resources on the west coast of Thailand. *In* Investigation on the mackerel and scad resources of the Malacca Straits BOBP/REP/39, RAS/81/051, 32–47.
5. Brander, K. M. (1994) Patterns of distribution, spawning, and growth in North Atlantic cod: the utility of inter-regional comparisons. *ICES Mar. Sci. Symp.*, **198**, 406–413.
6. Campana, S. E. et al. (1995) Spatial implications of a temperature-based growth model for Atlantic cod (*Gadus morhua*) off the eastern coast of Canada. *Can. J. Fish. Aquat. Sci.*, **52**, 2445–2456.
7. Campana, S. E. (2001) Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.*, **59**, 197–242.
8. Chang, W. Y. B. (1982) A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci.*, **39**, 1208–1210.
9. Clarke, T. A. & Privitera, L. A. (1995) Reproductive biology of two Hawaiian pelagic carangid fishes, the bigeye scad, *Selar crumenophthalmus*, and the round scad, *Decapterus macarellus*. *Bull. Mar. Sci.*, **56**, 33–47.
10. Jaiswar, A. K. Chakraborty, S. K. & Swamy, R. P. (2001) Studies on the age, growth and mortality rates of Indian scad *Decapterus russelli* (Ruppell) from Mumbai waters. *Fish. Res.*, **53**, 303–308.
11. Kishida, S. (1974) Fisheries biology of the scads (genus *Decapterus*) in the East China Sea—II. Specific distribution and annual catch. *Bull. Seikai Reg. Fish. Res. Lab.*, **45**, 1–14 [In Japanese].
12. Kishida, S. (1986) *Decapterus macrosoma*. *In* Fishes of the East China Sea and the Yellow Sea ed. Okamura, O., Seikai Regional Fisheries Research Laboratory, Nagasaki, pp.174 [In Japanese].
13. McBride, R. S. Stengard, F. J. & Mahmoudi, B. (2002) Maturation and diel reproductive periodicity of round scad (Carangidae: *Decapterus punctatus*). *Mar. Biol.*, **140**, 713–722.
14. Ohshimo, S. Yoda, M. & Hiyama, Y. (2004) Long-term changes in the reproductive characteristics of jack mackerel (*Trachurus japonicus*) in the East China Sea. *Bull. Jpn. Soc. Fish. Oceanogr.*, **68**, 245–252 [In Japanese with English summary].
15. Ohshimo, S. et al. (2006) Age, growth and reproductive characteristics of round scad *Decapterus maruadsi* in the waters off west Kyushu, the East China Sea. *Fish. Sci.*, **72**, 855–859.
16. Sutthakorn, P. & Saranakomkul, R. (1987) Biological aspects of chub mackerel and round scads on the west coast of Thailand. *In* Investigation on the mackerel and scad resources of the Malacca Straits BOBP/REP/39, RAS/81/051, 48–80.
17. Tampubolon, G. H. & Merta, I. G. S. (1987) Mackerel fisheries in the Malacca Straits. *In* Investigation on the mackerel and scad resources of the Malacca Straits BOBP/REP/39, RAS/81/051, 101–116.
18. Yoneda, M. (2006) Effects of environmental condition on growth and reproduction of Atlantic cod *Gadus morhua*. *Bull. Fish. Res. Agen. suppl.*, **4**, 31–39 [In Japanese with English summary].