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Biology of Herbivorous Fish in the Coastal Areas of Western Japan

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Abstract—Seaweed beds in Japanese coastal waters have significantly declined in recent years and feeding by herbivorous fish has been identified as one of the potential causes of this decline. In the western coastal areas of Kyushu, seaweed consumption by fish species such as the mottled spinefoot (*Siganus fuscescens*), sea chubs (*Kyphosus* spp.), and the Japanese parrotfish (*Calotomus japonicus*) has become a matter of concern. Our research group has been investigating the biology of herbivorous fish in the coastal waters around western Kyushu and Okinawa. This paper presents some of the results of our work with a focus on the biology of herbivorous fish, including their distribution, age, growth, sexual maturity, sex change, feeding, behavioral ecology, and population structure. Investigation of the stomach contents of herbivorous fish revealed that *Kyphosus bigibbus* fed mainly on the seaweed sargassum throughout the year. In contrast, other fish supplemented their diet of seaweed with amphipods and other organisms. Experiments to determine food preference were performed on captive *K. bigibbus*, and their results supported the results of the stomach content analysis. Both experiments showed that the fish selectively fed on *Sargassum fusiforme* and *Undaria pinnatifida*. Herbivorous fish off the west coast of Kyushu were tracked using a biotelemetry technique, which indicated that the fish inhabited seaweed beds during the daytime. The activity of *S. fuscescens* and *K. bigibbus* markedly declined when the water temperature decreased to approximately 20°C and 17°C, respectively, but it was observed that these fish overwintered in these areas. This study demonstrates that the recent rise in winter ocean temperatures has extended the period of activity of herbivorous fish. The results contradict the hypothesis that herbivorous fish species migrate southward during colder periods.

Keywords: Isoyake, sea desertification, herbivorous fish, migration, ultrasonic telemetry methods, life history, population structure

1. INTRODUCTION

Seaweed beds in Japanese coastal waters have significantly declined in recent years and feeding by herbivorous fish has been identified as one of the potential causes of this decline. The recent increase in temperatures due to global warming is considered to have led to the northward extension of the distribution of herbivorous fish species in western Japanese coastal waters. Moreover, it has been proposed that the change in the distribution of fish populations has led to an increase in seaweed consumption

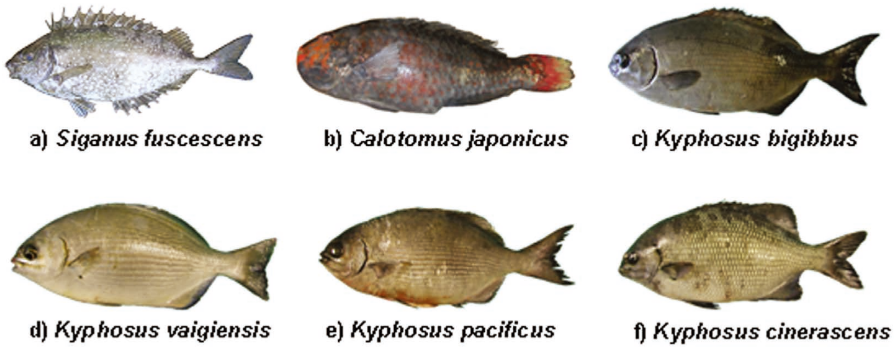

Fig. 1. Main target herbivorous fish species investigated in our study.

by these species. However, detailed information on the biology of herbivorous fish has not been obtained. The cause and effect relationships between feeding damage inflicted by herbivorous fish and "Isoyake" have not yet been elucidated. Seaweed biomass in western Japanese coastal waters seems to have decreased, and it appears that the balance between herbivorous fish populations and seaweeds has been temporarily disturbed. In the western coastal areas of Kyushu, the increase in seaweed consumption by fish species such as the mottled spinefoot (*Siganus fuscescens*), sea chubs (*Kyphosus* spp.), and the Japanese parrotfish (*Calotomus japonicus*) has become a matter of concern (Kiyomoto et al., 2000; Kiriyama et al., 2005a, b; Fig. 1).

Our research group has been studying the distribution, feeding habits, reproductive behavior, growth, migration, population structure, and other biological aspects of herbivorous fish in coastal waters, including those around western Kyushu and Okinawa.

Our findings show that *Kyphosus* spp. are very important in understanding the feeding damage inflicted on seaweed beds by herbivorous fish. *Kyphosus* spp. have not been widely studied because they are not very important from a fishery perspective. In Japan, four species belonging to the genus *Kyphosus* are found (Sakai and Nakabo, 2004), all of which are distributed in western coastal Kyushu. *Kyphosus pacificus* is a more tropical species that is usually found in Okinawa. The most abundant *Kyphosus* species is *K. bigibbus*, a relatively large sea chub that occupies the waters off the coast of Nagasaki, western Kyushu.

Since the number of these fish caught decreases as the water temperature decreases, it was unclear why extensive damage due to feeding by fish is detected in autumn and winter.

2. BEHAVIOR AND MIGRATION

We have attempted to answer the following questions in this study: Do herbivorous fish migrate from tropical areas? What is their migration range? Do they migrate to seaweed beds for feeding? Where do they migrate during winter?

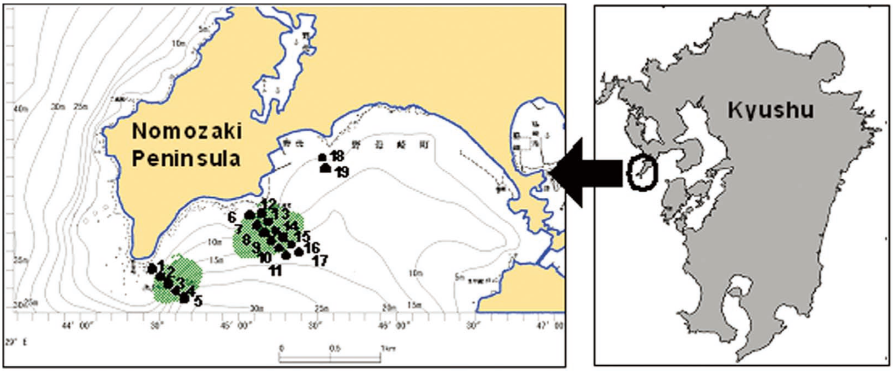

Fig. 2. Study sites in Nomozaki, Nagasaki. The circles and numbers denote the positions of the receivers.

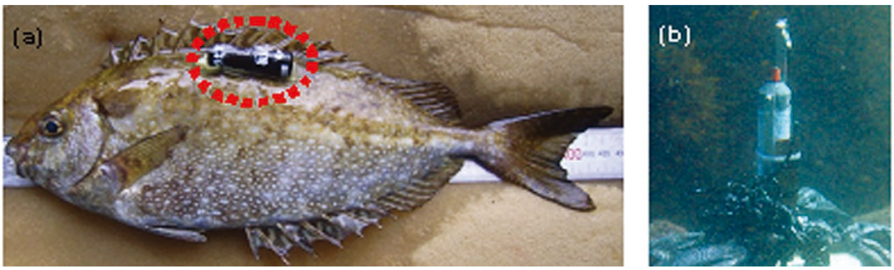

Fig. 3. *Siganus fuscescens* with transmitter attached (a) and VR2 receiver (b).

The behavior and migration of the fish were evaluated using ultrasonic telemetry methods (Yamaguchi et al., 2006). Individuals were caught using set nets and kept in tanks for several days. Their dorsal fins were tagged and they were then released. Ultrasonically tagged individuals were detected using fixed VR2 monitoring receivers (VEMCO). Transmitter signals were randomly generated at intervals of 45–75 seconds; this intermittent signal generation extended the battery life to approximately 150 days. Preliminary investigations were conducted to determine the detection range. In our study sites, the receivers accurately detected signals from the transmitters when the receivers were placed within a distance of 80 m of the transmitters. Prior to passive tracking of the fish, we tracked some individuals in the moving range of both *S. fuscescens* and *K. bigibbus* in real time. On the basis of these results and the ecological information previously acquired by our research group, we placed 19 receivers mainly on the seaweed bed in Nagasaki (Fig. 2). A total of 93 individuals (*S. fuscescens*, $n = 76$; *K. bigibbus*, $n = 11$; *K. vaigiensis*, $n = 5$; and *C. japonica*, $n = 1$) have been tracked since the first examination in November 2004 (Fig. 3).

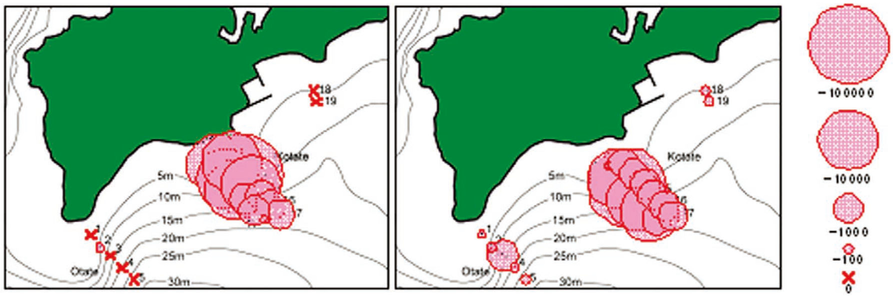

Fig. 4. Total number of signals recorded by each receiver.

Figure 4 shows the moving ranges estimated using the total number of signals detected by each receiver in 2007. For *S. fuscescens*, most signals were received from the transmitters placed in seaweed beds at Kotate (no. 6–17). Few signals were detected from the seaweed beds in Otate (no. 1–5). Further, the migration range of *K. bigibbus* was larger than that of *S. fuscescens*. The typical daily movement patterns of *S. fuscescens* and *K. bigibbus* in autumn were assessed (Yamaguchi et al., 2006). The mottled spinefoot (*S. fuscescens*) did not move at night and stayed close to the receivers placed in deep areas. It began to swim after sunrise and actively swam in the seaweed areas during the day. After sunset, it appeared to return to the same place close to the receivers in the deep areas and did not move again until the next sunrise. In contrast, no signals were detected for *K. bigibbus* from the seaweed beds in the nighttime. However, it was clear that the fish returned to the seaweed beds in the daytime via a fixed route. It appeared that at sunrise, *K. bigibbus* approached the seaweed beds from the western side of the peninsula after traveling a relatively long distance. The species returned to the west side of the peninsula again after sunset. The west side of the peninsula is a reef zone; we propose that *K. bigibbus* inhabits this zone during the night.

These typical patterns we observed changed when the water temperature decreased. Although both species inhabited the seaweed beds between December and January, they seemed to be slowly on the move. Even though the habitat had not changed much, the home ranges of the fish seemed to be somewhat deeper in winter.

The relationship between the total number of signals per day for *S. fuscescens* and *K. bigibbus* and the water temperature from November 2004 to March 2005 is shown in Fig. 5 (Yamaguchi et al., 2006). As shown in the figure, the number of signals from all *S. fuscescens* individuals markedly decreased from the beginning of December, when the water temperature was 20°C. In the case of *K. bigibbus*, the number of signals decreased from the second week of January, when the water temperature was 16–17°C. Thus, the activity of both species decreased as the water temperature fell. It is generally accepted that these herbivorous fish species migrate to southern areas during the winter; however, in this study, signals continued to be

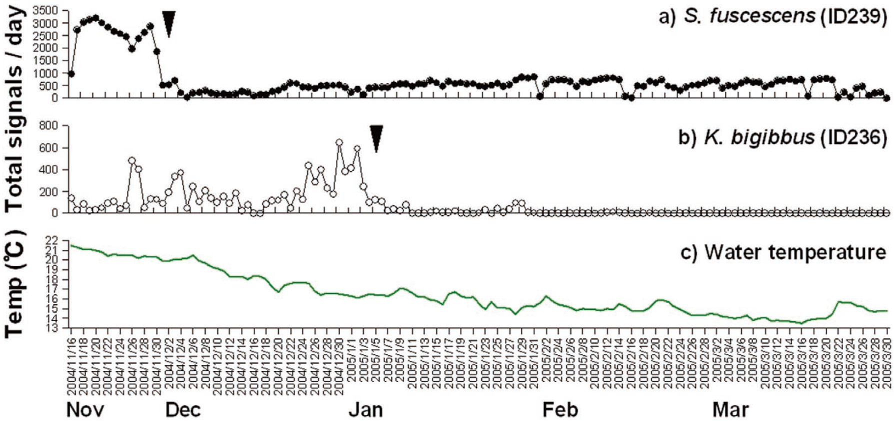

Fig. 5. Total number of signals recorded per day from November 16, 2004, to March 30, 2005, for two specimens (a, b); and changes in water temperature in the study area off Nomozaki at a depth of 7 m (c).

transmitted from the study sites during winter, but activity was decreased. This finding indicates that the fish overwinter in the same areas they live in during the warmer months and that they do not migrate. However, the decreased activity of these fish species is probably the cause of the decrease in fish catches during winter. These results, therefore, contradict the hypothesis that herbivorous fish migrate southward during winter.

The water temperature in the coastal areas of western Japan has increased by approximately 1–2°C since the mid 90s (Yamaguchi et al., 2006). Our research has demonstrated that the recent rise in winter ocean temperatures has extended the period of activity of herbivorous fish by at least 2 months, which may be the cause of the severe damage to seaweeds in recent years.

3. AGE, GROWTH, AND SEXUAL MATURITY OF *C. JAPONICUS*

The parrotfish *C. japonicus*, which belongs to the family Scaridae, is one of the few temperate species within this family (Shimada, 2000). The species is a prominent member of the reef fish communities from central Honshu to Kyushu, Japan (Kusen and Nakazono, 1991), and is an important target species for fisheries, particularly in the southern part of Japan. *Calotomus japonicus* is consequently both an ecologically and economically important fish species in the coastal areas of southern Japan.

We examined the life history of the parrotfish *C. japonicus*, using individuals collected between May 2003 and May 2008 off the Nagasaki Peninsula in northwest Kyushu, Japan-an area where this species is caught commercially, mainly as a bycatch, using set nets and gill nets (Kume et al., in press). Age determination was

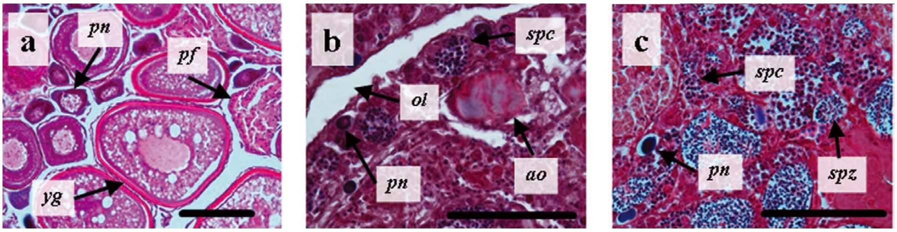

Fig. 6. Photomicrographs of sections from *Calotomus japonicus* gonads: a, Female (272 mm TL) collected in August, having postovulatory follicles in the ovary; b, Transitional individual (391 mm TL) collected in September; c, Sexually active male (390 mm TL) collected in October, having a transitional gonad. *ao*, atretic oocyte; *ol*, ovarian lumen; *yg*, oocyte at the yolk globule stage; *pf*, postovulatory follicles; *pn*, oocyte at the peri-nucleolus stage; *spc*, spermatocyte; *spz*, spermatozoa. Scale bars 100 μm

performed using scales. Marginal increment analysis revealed that growth rings were formed annually around July. Growth in both sexes was fitted to the von Bertalanffy growth function ($L_\infty = 513$, $k = 0.28$, $t_0 = 0.03$; where L_∞ is the theoretical asymptotic total length in millimeters, k is the growth rate coefficient, and t_0 is the theoretical time at zero length). The observed maximum age for both sexes was 8 years. We also characterized the reproductive biology of this species based on a gonadosomatic index and histological examination of the gonads. The spawning season extends from July to October, with peak spawning activity occurring during July and August. The fish reach sexual maturity by the second year of life. Females are assumed to be multiple spawners, since we observed specimens with postovulatory follicles in ovaries containing either yolk globule oocytes or migratory nucleus oocytes (Fig. 6a). All males had secondary testes, which were characterized by the presence of an ovarian lumen structure and sperm sinuses in the gonadal wall (Fig. 6b). This characteristic indicates that all males, irrespective of whether they were initial or terminal phase males, had undergone a sexual transition. Sex change appears to occur during the spawning season and thereafter sex-changed males are able to fertilize female eggs throughout the remainder of the current spawning season (Fig. 6c).

4. FOOD PREFERENCE

It is unclear whether all herbivorous fish consume seaweed and if they do, whether they consume seaweed selectively or non-selectively. In our research group, experiments to determine food preferences have been performed on captive adult and juvenile individuals of the *Kyphosus* spp. and *C. japonicus* that are kept in tanks (Fig. 7).

Investigation of the stomach contents of herbivorous fish revealed that *K. bigibbus* fed mainly on the seaweed sargassum throughout the year. Therefore, *K. bigibbus* appears to be specialized for feeding on seaweeds. In contrast, other fish supplemented their diet of seaweed with amphipods and other organisms. The main food consumed

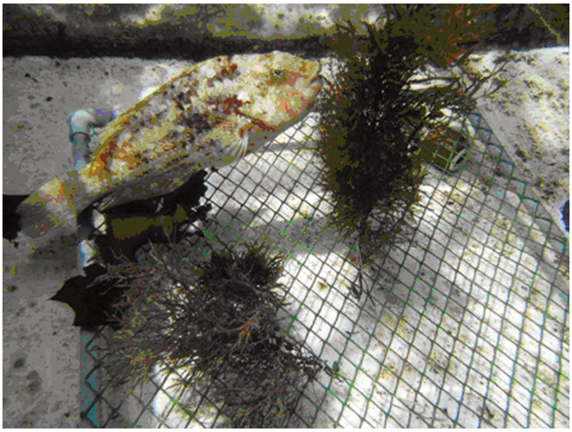

Fig. 7. Japanese parrotfish, *Calotomus japonicus*, swimming in a tank. Herbivorous fish were kept in captivity to study their feeding habits, such as selective feeding.

by *S. fuscescens* was also seaweed, constituting 85% of all food consumed, but other organisms, such as skeleton shrimps, were also found in the stomach of these fishes. Compared with *K. bigibbus* and *S. fuscescens*, *K. vaigiensis* showed a considerably varied diet. *K. vaigiensis* mainly consumed crustaceans, such as skeleton shrimps, and seems to be omnivorous rather than herbivorous.

The preference of captive *K. bigibbus* for 5 brown algae species including *Sargassum fusiforme*, *Undaria pinnatifida* and *Ecklonia kurome* was studied using multiple-choice feeding experiments. These brown algae are commonly found in the western coastal areas of Kyushu. The experiments supported the results of the stomach content analysis and showed that *K. bigibbus* selectively fed on *Sargassum fusiforme* and *Undaria pinnatifida*. *Ecklonia kurome* was the least preferred by *K. bigibbus*. *E. kurome* is an important species in the seaweed beds in Kyushu, which is severely damaged by some fish species in its natural environment (Kiriyama et al., 2001). Meanwhile, our stomach contents analysis confirmed that *E. kurome* was rarely found in the stomachs of herbivorous fish. The biomass of *S. fusiforme* and *U. pinnatifida* is low during winter; therefore, it is probable that during winter, *K. bigibbus* consumes *E. kurome*. Similar experiments are currently being conducted on other fish species.

5. POPULATION STRUCTURE OF *S. FUSCESCENS*

Our research group has been examining the population structure of *S. fuscescens* around Japan by using mitochondrial (mt) DNA sequences, in addition to geographic variations in morphological characters. Here, we focus on the genetic and morphological differences between two geographic populations of the species from Nagasaki and Okinawa Prefectures.

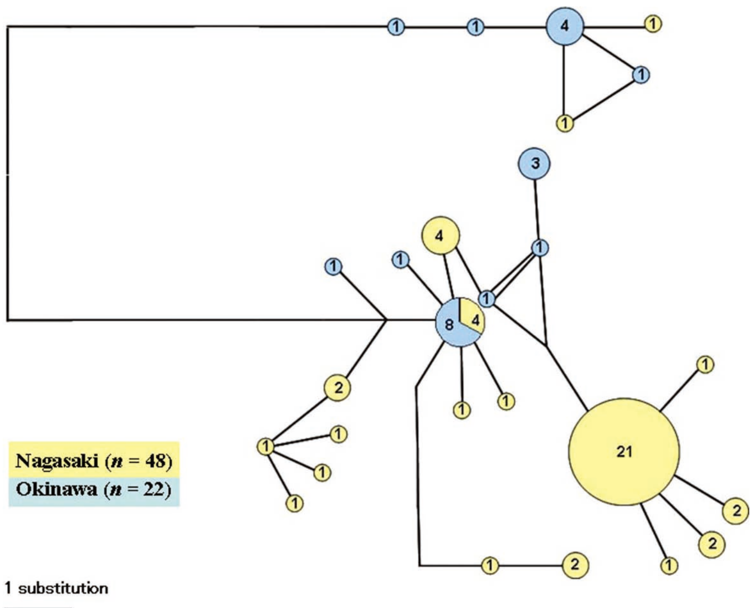

Fig. 8. Minimum spanning network tree among haplotypes of mtDNA cyt *b* gene for Nomozaki and Ishigaki populations of *Siganus fuscescens*. Each circle presents a unique haplotype; pie slices represent the fraction of two populations; the number in each slice indicates the number of individuals with a common haplotype for each population; the size of circles is proportional to the number of individuals

A total of 464 base pairs from part of the mt cytochrome (Cyt) b gene were determined from 48 specimens from Nomozaki, Nagasaki Prefecture, and 22 specimens from Ishigaki, Okinawa Prefecture. Among these base pairs, 27 haplotypes were defined, 18 of which occurred in Nomozaki and 10 in Ishigaki populations. One of the 27 haplotypes was shared between the two populations. A minimum spanning network (MSN) tree (Fig. 8) among haplotypes showed the possibility of gene flow between the two populations. However, the pair-wise fixation index (F_{ST}) between Nagasaki and Okinawa populations was 0.23, being significant ($P < 0.01$) in the permutation test by 1000 random permutations.

Vertebrae and fin rays were counted and 17 morphometric characters were measured for 184 specimens (165–275 mm in standard length (SL), mean 234.2 mm SL) from Nomozaki, and 52 specimens (171–274 mm SL, mean 203.8 mm SL) from Ishigaki. No differences were found between the two populations in terms of vertebrae or fin ray count. Linear regressions with SL as the independent variable and morphometric characters as dependent variables were estimated and assessed using analysis of covariance (ANCOVA). Significant differences [$P < 0.0029$ for an experiment-wise error rate of $P < 0.05$ after Bonferroni correction (Bonferroni,

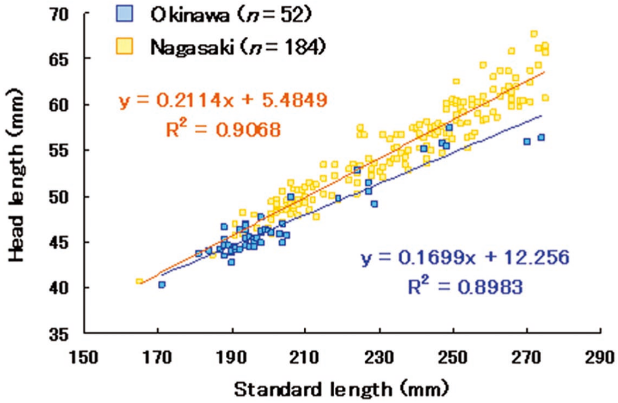

Fig. 9. Relationship between head length (mm) and standard length (mm) for *Siganus fuscescens*.

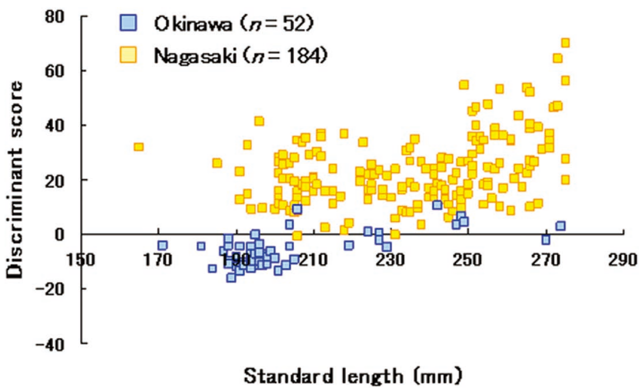

Fig.10. Plots of discriminant scores based on five morphometric characters that were significantly different between the two populations for *Siganus fuscescens*.

1936)] between the two populations were shown in the slopes of head length (Fig. 9), depth of caudal peduncle, length of caudal peduncle, distance between snout and anal fin, and length of dorsal-fin base, as well as in the intercepts of depth of caudal peduncle, length of caudal peduncle, and length of dorsal-fin base. A quadratic discriminant analysis (Fig. 10) based on these five morphometric characters yielded 95% correct assignment of specimens to locality.

The two geographic populations of *S. fuscescens* from Nomozaki and Ishigaki were thus considered to be different from each other, both morphologically and molecularly. Therefore, it is unlikely that a great number of *S. fuscescens* migrates from Okinawa Prefecture and causes the damage to seaweed beds around Nagasaki Prefecture.

6. CONCLUSION

In conclusion, we emphasize the two following points: (1) Our results regarding behavior and migration contradicted the hypothesis that herbivorous fish species migrate southward during winter, as we found that these fish do not migrate over such a long distance. Further, the results of population genetic studies indicated that the migration of *S. fuscescens* from Okinawa is insufficient to explain the damage caused to seaweed beds around Kyushu. (2) The water temperature in western coastal Japan has increased since the mid 90s. In autumn and winter especially, the water temperature has increased by approximately 1–2°C. Thus, our research demonstrates that the recent rise in winter water temperatures has extended the period of activity of herbivorous fish by at least two months. In winter, the seaweed biomass is relatively low, but the activity of these fish remains high, which may explain the severe damage to seaweed in this season.

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