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Using optimised otolith sectioning to determine the age, growth and age at sexual maturity of the herbivorous fish *Kyphosus bigibbus*: with a comparison to using scales

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Abstract. Determining the population parameters of herbivorous fishes facilitates our understanding of their overall effects on ecosystems. However, this has not been successful with species such as *Kyphosus bigibbus* that are difficult to age using otoliths. In this study, we estimated the age, growth and age at sexual maturity of *K. bigibbus* off the west coast of Kyushu, Japan, using fish scales and otoliths. Scales were found unreliable because they caused underestimation of the age of fish older than 5 years, whereas otoliths were reliable when used with our improved otolith-sectioning methodology. The maximum age and fork length were 46 years and 574 mm for females and 32 years and 506 mm for males. According to the von Bertalanffy growth curves, females became slightly larger than males, and both sexes showed nearly asymptotic fork lengths after 10 years. The age at 50% sexual maturity for females and males was 3.2 and 1.9 years respectively, which is extremely early considering their maximum age. The year-class composition of *K. bigibbus* suggests that its recruitment may have increased rapidly since 1999, following noticeable losses of kelp forests in this region. Our findings will contribute to the understanding of algal forest ecosystems and advancement of fish ageing studies.

Additional keywords: algal deforestation, *isoyake*, Kyphosidae, life history.

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Introduction

Algal forests, particularly kelp forests, are important biogenic habitats in temperate ecosystems (Teagle *et al.* 2017), providing immense ecological, social and economic benefits (Smale *et al.* 2013; Bennett *et al.* 2016; Blamey and Bolton 2018). Although algal forests are declining globally, there is a high degree of geographic variation caused by variations in local stressors, such as harvesting, trampling, habitat modification, eutrophication and overgrazing (Mineur *et al.* 2015; Krumhansl *et al.* 2016). Overgrazing of temperate macroalgae is usually caused by sea urchins (Steneck *et al.* 2002). However, there has recently been an increasing interest in overgrazing by herbivorous fishes (Vergés *et al.* 2014*a*). For example, in the Mediterranean Sea, the range expansion of tropical rabbitfishes that first entered the basin via the Suez Canal has caused considerable damage to algal forests (Vergés *et al.* 2014*b*). Moreover, Gianni *et al.* (2017) suggested that a Mediterranean native herbivorous fish (*Sarpa salpa*) presents a potential threat to algal forests because its abundance may have increased recently. On the west coast of Australia, an extreme marine heat wave in 2011 caused extensive losses of algal forests and a concurrent increase in tropical herbivorous fishes, which are now suppressing the recovery of algal forests (Smale and Wernberg 2013; Wernberg *et al.* 2013, 2016). Furthermore, on the east coast of Australia, algal forests have gradually declined, whereas there has been a concurrent increase in tropical herbivorous fishes (Basford *et al.* 2016; Vergés *et al.* 2016). In these areas of algal deforestation on both sides of Australia, feeding assays have identified *Kyphosus bigibbus* as a major consumer of kelp (Bennett *et al.* 2015; Vergés *et al.* 2016).

There has been increasing concern over the ongoing leaf structure loss of kelp species on the west coast of Kyushu, Japan, caused by overgrazing by herbivorous fishes, which was first detected in the autumn of 1998 (Kiriyama *et al.* 1999; Kiyomoto *et al.* 2000). Observations of feeding behaviour and the bite marks of several fish species on algae indicated that *Siganus fuscescens*, *Calotomus japonicus* and *Kyphosus* spp. are responsible for this phenomenon (Kiriyama *et al.* 2001). Subsequent surveys showed that four *Kyphosus* species are distributed in this region, with *K. bigibbus* being the most abundant (Yamaguchi 2010). Yamaguchi (2010) suggested that herbivorous fishes' greater activity and consumption of newly germinated large brown algae in winter was a response to current global warming-associated increases in winter

seawater temperatures, and that it may be changing the balance of algal forest ecosystems.

Areas of algal deforestation (termed '*isoyake*') exist in most of Japan's coastal prefectures, with overgrazing by herbivorous fishes representing a potential cause of algal deforestation in southern Japan (Fisheries Agency 2015). Accordingly, a countermeasure currently recommended by the Japanese government to control algal deforestation involves the culling of herbivorous fishes (Fisheries Agency 2015). Within this framework, researchers have attempted to catch schooling *K. bigibbus* near breakwater structures using gill-nets (Kuwahara 2015). However, the biological and ecological properties of herbivorous fishes are not yet fully understood. Thus, it remains unclear whether culling is an effective strategy to prevent algal deforestation.

K. bigibbus is widely distributed in the subtropical and temperate regions of the Indian, Pacific and Atlantic oceans (Knudsen and Clements 2013, 2016). This species is an obligate herbivore, with a diet consisting predominantly of brown algae (Clements and Choat 1997; Clements and Zemke-White 2008; Yatsuya *et al.* 2015). In the Ningaloo Reef, Australia, *K. bigibbus* is one of the main consumers of macroalgae, with feeding rates being highest when individuals of this species form part of monospecific groups (Michael *et al.* 2013). There are both resident and nomadic individuals of this species (Pillans *et al.* 2017). The movement patterns of resident individuals demonstrate high fidelity to particular patch reefs and large home ranges, leading to large-scale landscape changes in the form of areas largely devoid of macroalgae (termed 'halos') around patch reefs (Downie *et al.* 2013; Pillans *et al.* 2017). On the west coast of Kyushu, Japan, *K. bigibbus* migrates diurnally, and its activity declines markedly when the seawater temperature decreases to ~17°C (Yamaguchi *et al.* 2006; Yamaguchi 2010). The spawning and maturation patterns of this species have been elucidated only in populations inhabiting this region. Spawning occurs from June to October (with activity peaking in June–July), and the fork length (FL) at 50% sexual maturity is 360 and 284 mm for females and males respectively (Yamaguchi *et al.* 2011). Inoue *et al.* (2006) estimated the age and growth of *K. bigibbus* in this region, reporting a maximum age of 13 years; these authors used fish scales for age determination because otoliths were small, irregularly shaped and their opaque zones were not clearly visible on otolith sections. However, many studies have demonstrated that age estimation using fish scales can result in serious underestimation for some species (e.g. Beamish and Chilton 1982; Gray *et al.* 2012; Baudouin *et al.* 2016). Therefore, *K. bigibbus* age and growth need to be estimated using more accurate age determination methods.

The aim of this study was to compare the use of fish scales and otolith sections (prepared using an improved methodology) to evaluate the efficacy of the methods based on these two structures to determine the age, growth rate and age at sexual maturity of *K. bigibbus*. The findings obtained here are expected to provide baseline knowledge on the population dynamics of this species. We believe that this will facilitate future studies on how the culling of *K. bigibbus* will affect algal forests, allowing appropriate measures to be implemented in order to protect algal forest ecosystems and the herbivorous fishes that use them.

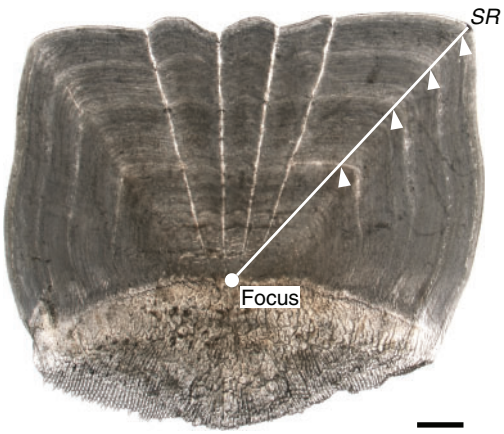

Fig. 1. Scale from a 4-year-old male *Kyphosus bigibbus* (384-mm fork length). Arrowheads indicate the outer edges of opaque zones. The scale radius (SR) is the distance from the focus to the distal margin of the dorsal side in the anterior field. Scale bar: 1 mm.

Materials and methods

Fish collection and measurements

Between May 2004 and February 2009, 388 specimens of *K. bigibbus* were collected at depths ranging from ~3 to 25 m off the Nagasaki Peninsula, Japan, using set and gill-nets. Detailed information about the study site has been previously presented (Kume *et al.* 2010). In addition, five juvenile *K. bigibbus* specimens found near drifting algae were collected from the same area in August 2007. In the laboratory, the FL (mm) and bodyweight (BW; g) of fish were measured. Individuals were classified as female, male or unsexed based on macroscopic examination of the gonads, which were dissected. Length–weight relationships for females and males (unsexed fish were included in both sexes for the analyses) were analysed by fitting the allometric function:

$$BW = aFL^b$$

Parameters a and b were estimated using a non-linear least-squares procedure with the 'Solver' function in MS Excel (Microsoft, Redmond, WA, USA). To compare the length–weight relationships between females and males, analysis of covariance (ANCOVA) was performed on the log-transformed dataset. This, and all other ANCOVA tests, were performed using BellCurve (Social Survey Research Information, Tokyo, Japan) for MS Excel.

Preparation of scales

For each fish, the third scale below the scales of the lateral line scale that was the 20th from the posterior end of the lateral line was removed. The scales were washed with 0.5% KOH solution, observed under a light transmission microscope (SMZ1000; Nikon, Tokyo, Japan; magnification 8×) and photographed using a digital camera (DS-Fi1; Nikon) mounted on the microscope. An alternating pattern of translucent and opaque zones in the scales was observed (Fig. 1). If the scale was a regenerated scale, characterised by an opaque focus (Lou 1992), the data

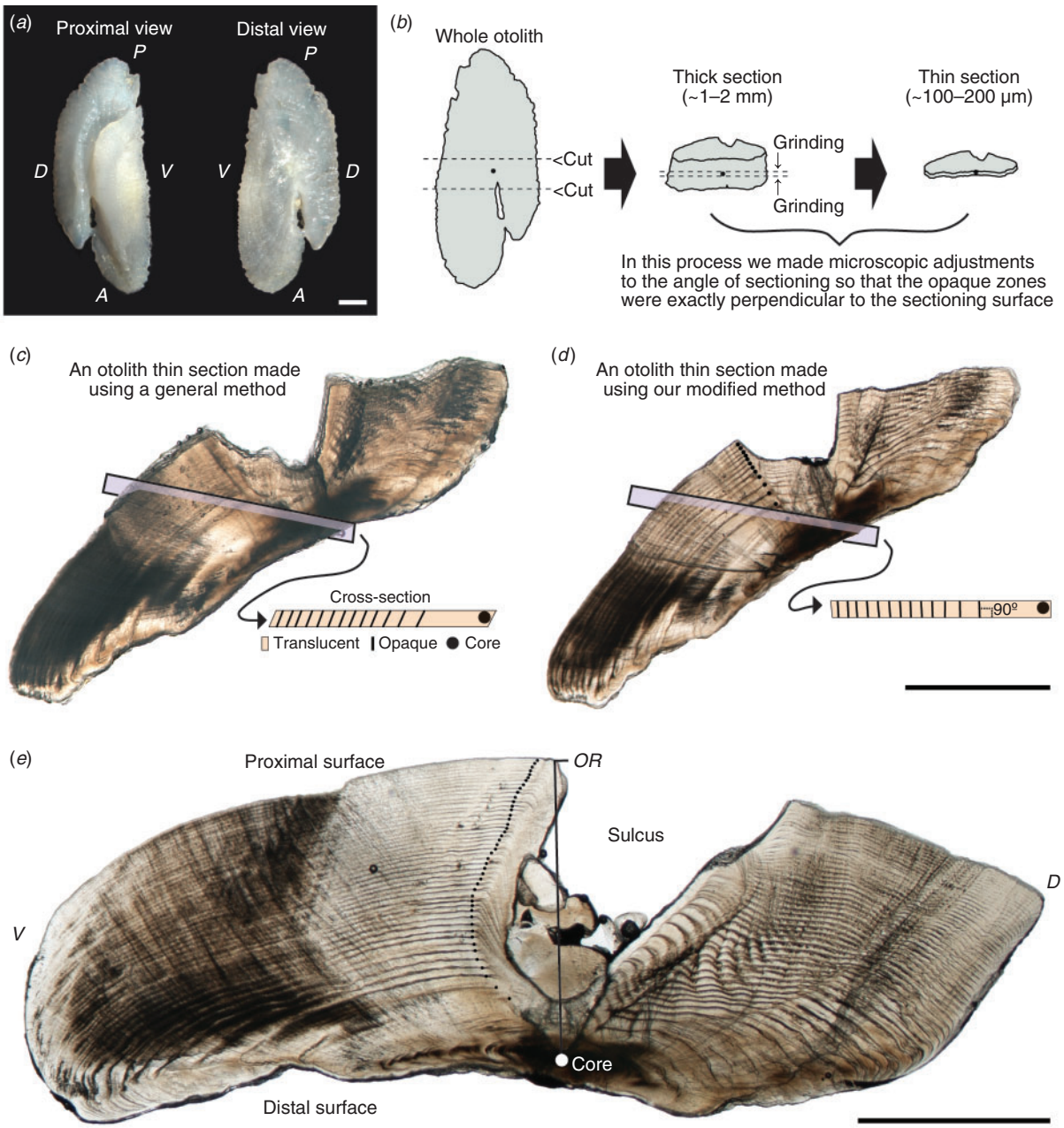

Fig. 2. Preparation of otolith sections from *Kyphosus bigibbus*. (*a*) Whole right sagittal otolith from a 6-year-old male (406-mm fork length, FL). (*b*) Illustrations showing sectioning steps. (*c*) Left and (*d*) right otolith section from a 13-year-old female (539 mm FL). The opaque zones were not perpendicular to the sectioning surface in the left section (*c*), whereas they were exactly perpendicular to the sectioning surface in the right section (*d*). (*e*) Right otolith section from a 46-year-old female (544 mm FL). The otolith radius (OR) is the distance from the core to the edge of the ventral lobe next to the sulcus. The black points indicate opaque zones. P, posterior; A, anterior; D, dorsal; V, ventral. Scale bars: 1 mm.

were excluded. Scale readings were undertaken using digital images. The scale radius (SR; mm) was measured from the focus to the distal margin of the dorsal side in the anterior field (Fig. 1). The relationship between FL and SR was calculated using MS Excel, and ANCOVA was performed to test the significance of differences between sexes (unsexed fish data were included in the dataset of both sexes).

Preparation of otolith sections

Sagittal otoliths were removed from the fish, cleaned and stored dry (Fig. 2*a*). A vertical mark was drawn across the core of each otolith with a well-sharpened pencil under the microscope (SMZ1000; Nikon) and each otolith was then embedded in acrylic resin. To obtain otolith sections in which opaque zones were exactly perpendicular to the sectioning surface, we

followed a two-step otolith sectioning procedure (Fig. 2*b*). First, each embedded otolith was cut along the vertical pencil mark with a diamond disc saw to obtain transverse thick sections (~1–2 mm) containing the core. This step was needed because we could not know the slope of opaque zones in the otolith unless we observed the sectioned otoliths under the microscope. Second, both sides of the transverse thick sections were ground using 80- to 4000-grit waterproof sandpaper, making microadjustments to the angle of sectioning with frequent observations under the microscope until the sections were ~100–200 μm thick with an exposed core. This step was very important because the clarity of opaque zones in otolith sections was closely dependent on the perpendicularity of the opaque zones. Comparisons between the left and right otolith sections of the same specimen are shown in Fig. 2*c*, *d*. Because the left section (Fig. 2*c*) was produced using a general method (i.e. through macroscopic adjustments to the angle of sectioning), the opaque zones were not perpendicular to the sectioning surface, and thus are not clearly visible. By contrast, the right section (Fig. 2*d*), which was produced by using the modified method proposed herein, has clearly visible opaque zones, exactly perpendicular to the sectioning surface. The resulting thin sections were immersed in 100% glycerol, observed under a transmitted light microscope (SMZ1000; Nikon; magnification 20–40×) and photographed using a digital camera (DS-Fi1; Nikon) mounted on the microscope. An alternating pattern of translucent and opaque zones surrounding a central opaque region was observed in otolith sections (Fig. 2*d*, *e*). Otolith readings were performed using digital images. The otolith radius (OR; mm) was measured from the core to the edge of the ventral lobe next to the sulcus (Fig. 2*e*). The relationship between FL and OR was calculated using MS Excel, and ANCOVA was performed on the log-transformed dataset to test the significance of differences between the sexes (unsexed fish data were included in the dataset of both sexes).

Validation of ageing methods

To determine the periodicity of opaque zone formation, edge and marginal increment analyses were performed. Edge analysis was based on the method described by Yamaguchi *et al.* (2004), and it was performed to examine monthly changes in the percentage occurrence of structures with an opaque margin. Marginal increment analysis, based on that described by Coulson *et al.* (2009), was used to examine monthly trends in the marginal increment of the structures (i.e. the distance between the outer edge of the outermost opaque zone and the structure periphery). The marginal increment was expressed as the proportion of the distance between the outer edges of the two outermost opaque zones, and differences among months were compared using the Kruskal–Wallis test in BellCurve (Social Survey Research Information).

Precision and bias

The number of opaque zones for each scale and otolith was counted three times by the same person, without knowledge of fish length or previous counts. If the resulting counts were the same on two or more readings, that value was recorded as the number of opaque zones. If the counts differed in all three readings, the specimen was deemed illegible. The average percentage error (APE) and CV were calculated using the three counts, and the precisions of the scale and otolith opaque zone observations were compared (Beamish and Fournier 1981; Chang 1982). Campana (2001) suggested that acceptable levels of APE and CV are less than 5.5 and 7.6% respectively. In addition, an age-bias plot was used to investigate systematic variations in the scale and otolith opaque zone counts (Campana *et al.* 1995).

Growth curves

Following the method of Fowler and Short (1998), each fish was assigned an age in months based on the number of opaque zones in its age structure and taking into account its date of capture, an 'average' birth date (approximate mid-point of the spawning period) of 1 August (Yamaguchi *et al.* 2011) and a time of year at which the opaque zones were formed. Length-at-age data for females and males were fitted to the von Bertalanffy growth function (VBGF) using a non-linear least-squares procedure with the 'Solver' function in MS Excel. The VBGF was calculated as follows:

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)}\right]$$

where L_t is the FL at age t, L_∞ is the theoretical asymptotic length, k is the growth rate coefficient and t_0 is the theoretical time at zero length. To improve the fit of VBGF at young ages, juveniles were added to the length-at-age data as an age-0 group; small, unsexed fish were included in the datasets of both sexes. A likelihood ratio test (Kimura 1980) was used on these datasets to determine whether growth curves differed by sex, following Paul and Horn (2009).

Age at sexual maturity

Considering the individuals (females: $n = 53$; males: $n = 41$) collected in the spawning season for which maturity was determined by histological examination of the gonads based on Yamaguchi *et al.* (2011), the percentage of mature individuals in each age class was fitted to the following logistic model:

$$Y = \left[1 + e^{(aX+b)}\right]^{-1}$$

where Y is the proportion of mature individuals at age X, and a and b are empirical parameters estimated using a non-linear least-squares procedure. The age at 50% sexual maturity (A_{50}) for each sex was calculated using the following equation:

$$A_{50} = -ba^{-1}$$

Results

Length–weight relationship

Of the 393 fish that were collected, 190 were female (169–574 mm FL, 131.0–4391.4 g BW), 189 were male (214–506 mm FL, 256.6–3306.4 g BW) and 14 were unsexed

(43–238 mm FL, 1.4–333.0 g BW). The relationships between FL and BW for females and males were not significantly different (ANCOVA on log-transformed data: $F = 3.46$; d.f. = 1, 405; $P = 0.064$). Therefore, the relationship between FL and BW for combined sexes (Fig. 3) was estimated as follows:

$$BW = 3.35 \times 10^{-5} FL^{2.95}$$

where $r^2 = 0.98$.

Growth of scales and otoliths

Nine of the 388 scales collected had regenerated and were therefore excluded from the analyses. The relationship between FL and SR for females and males (Fig. 4*a*) was significantly different (ANCOVA: $F = 4.24$; d.f. = 1, 386; $P < 0.05$) and was expressed using the following linear equations:

$$FL = 51.8SR + 5.19$$

for females, where $r^2 = 0.92$; and

$$FL = 54.4SR - 8.38$$

for males, where $r^2 = 0.93$.

However, the relationship between FL and OR for females and males (Fig. 4*b*) was not significantly different (ANCOVA on log-transformed data: $F = 0.581$; d.f. = 1, 395; $P = 0.45$) and was better expressed for combined sexes using the following logarithmic (rather than linear) equation:

$$FL = 308 \ln(OR) + 497$$

where $r^2 = 0.81$.

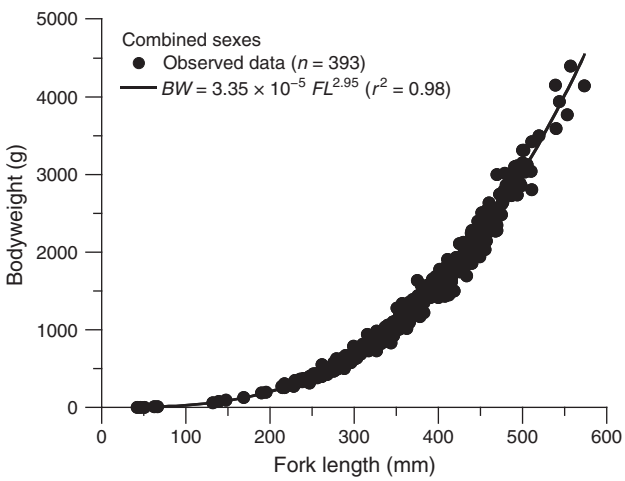

Fig. 3. Length–weight relationships for female and male *Kyphosus bigibbus*. BW, bodyweight; FL, fork length.

Validation of ageing methods

Among the 379 scales examined (excluding the 9 regenerated scales), 340 (89.7%) had legible opaque zones. In comparison, all 388 otoliths examined had legible opaque zones. The scale edge analysis indicated that the monthly proportion of specimens with opaque margins fluctuated throughout the year, regardless of month and season (Fig. 5*a*). Similarly, although the mean monthly marginal increments on the scales were significantly different (Kruskal–Wallis test: $\chi^2 = 50.7$; d.f. = 11; $P < 0.001$), they fluctuated throughout the year (Fig. 5*c*). However, the edge analysis of otoliths showed that opaque margins appeared only on the otoliths of specimens caught in May, June and July (Fig. 5*b*). The mean monthly marginal increments of otoliths were significantly different (Kruskal–Wallis test: $\chi^2 = 120$; d.f. = 11; $P < 0.001$). Specifically, mean monthly increments were high between December and June, and then declined sharply from June until

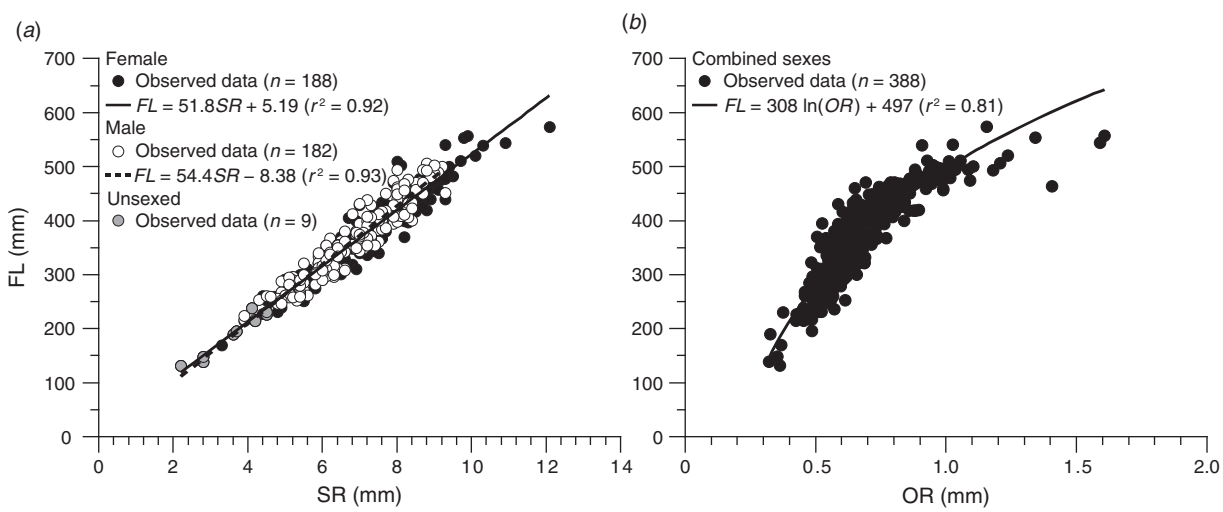

Fig. 4. Relationships between fork length (FL) and (*a*) scale radius (SR) and (*b*) otolith radius (OR).

August (Fig. 5*d*). Thus, even though a clear periodicity of opaque zone formation could not be detected in the scales, a clear periodicity was detected in the otoliths, confirming that the opaque zones become delineated from the edge of the otolith between June and August.

Precision and bias

Analysis of opaque zone count precision showed that, for scales, the APE was 9.7% and the CV was 12.8%. However, for otoliths, the APE was 0.2% and the CV was 0.3%, indicating considerably higher reading precision. In the present study, 0–12 and 1–46 zones were recorded in *K. bigibbus* scales and otoliths respectively. Comparison of opaque zone counts between scales and otoliths of the same fish specimens indicated that the percentage agreement of opaque zone counts between the structures decreased with increasing age, and was 0% for fish older than 8 years (Table 1). The occurrence of systematic variation in counts between scales and otoliths was evaluated using an age-bias plot (Fig. 6). The opaque zone counts for samples with one to five zones generally showed a close correlation, and there was a linear relationship for these samples. Beyond five opaque zones, the difference became larger and the data exhibited a non-linear relationship, with the scales invariably underestimating the age of the specimen. The greatest difference in a fish specimen was 34 zones.

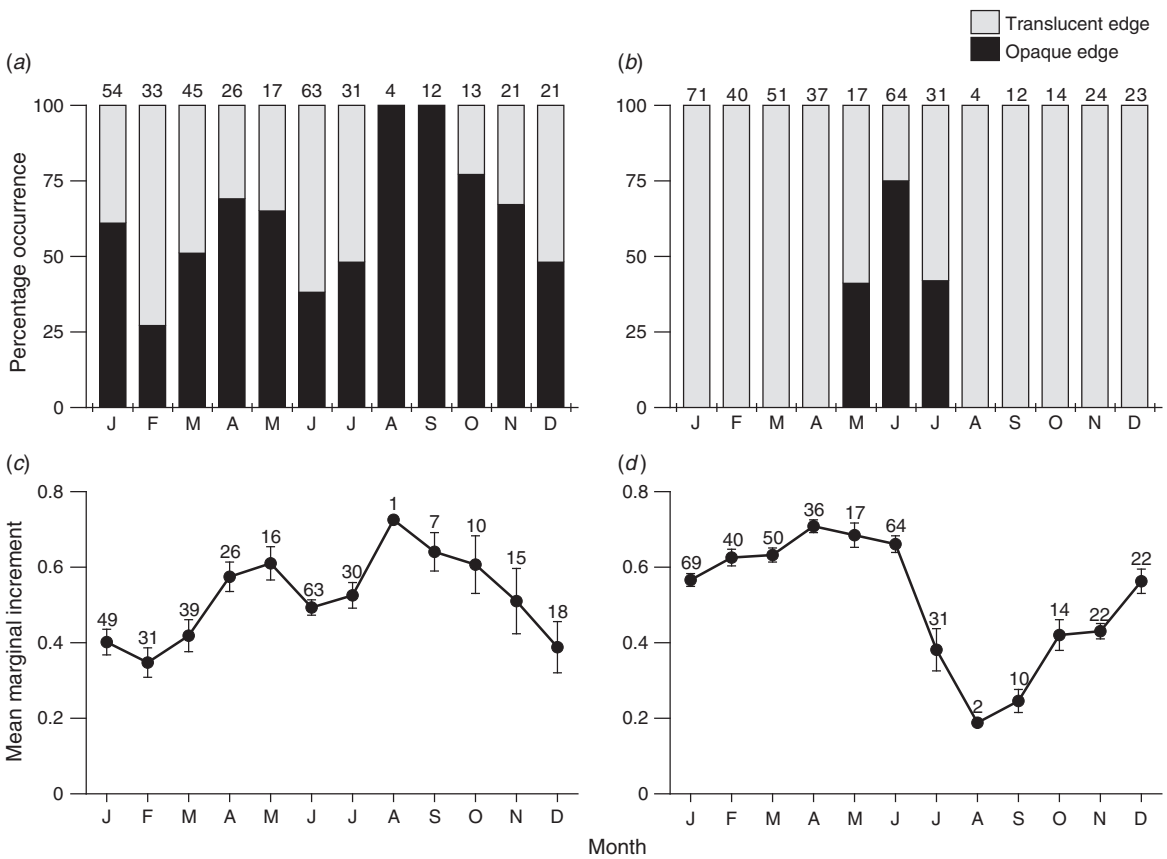

Fig. 5. (*a*, *b*) Monthly percentage occurrence of translucent and opaque margins on scales (*a*) and otoliths (*b*) of *Kyphosus bigibbus*. (*c*, *d*) Changes in the mean monthly marginal increment (±1 s.e.m.) on scales (*c*) and otoliths (*d*) of *K. bigibbus*. Numbers above columns and symbols indicate sample sizes.

Table 1. Agreement of opaque zone counts between scales and otoliths in terms of otolith opaque zone group

	Otolith opaque zone group							
	1	2	3	4	5	6	7	8–46
Number of specimens	11	58	75	78	40	25	27	65
Number of specimens in agreement with scale opaque zone counts	6	29	28	29	10	2	6	0
Agreement (%)	55	50	37	37	25	8	22	0

Growth curves

Because the opaque zones in the otoliths were validated as annuli, age estimations were performed based on these otoliths.

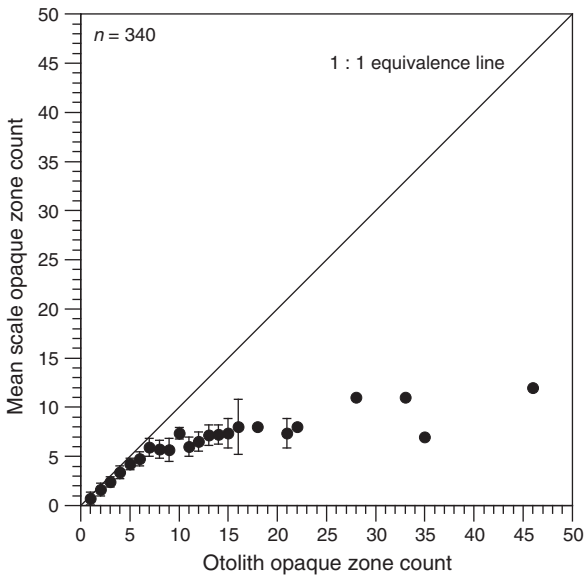

Fig. 6. Age-bias plot comparing opaque zone counts on scales and otoliths of *Kyphosus bigibbus*. Each error bar represents the standard deviation around the mean scale opaque zone count for all fish whose otoliths were assigned a given count.

The length-at-age data fitted the VBGF for each sex (Fig. 7), which was calculated as follows for females:

$$L_t = 512\left[1 - e^{-0.26(t+0.46)}\right]$$

where $r^2 = 0.94$; and for males:

$$L_t = 484\left[1 - e^{-0.28(t+0.47)}\right]$$

where $r^2 = 0.95$.

The likelihood ratio test indicated that the VBGF was significantly different between sexes ($\chi^2 = 22.8$; d.f. $= 3$; $P < 0.001$). The VBGFs showed that females became slightly larger than males as they became older, and that females and males reached 95% of L_∞ at 11 and 10 years of age respectively. The observed maximum age for females and males was 46 years (544 mm FL) and 32 years (463 mm FL) respectively.

Age at sexual maturity

Based on the estimated ages determined from the otoliths, the percentage of mature females in the 2-, 3- and 4-year age classes was 0, 42 and 78% respectively, with all females reaching maturity after 5 years (Fig. 8*a*). By contrast, 64% of males reached maturity at 2 years of age and all males reached maturity after 3 years (Fig. 8*b*). The age at 50% sexual maturity was 3.2 years for females and 1.9 years for males.

Year-class strength

The number of samples differed across the 6-year sampling period. However, the lifespan of *K. bigibbus* spans multiple

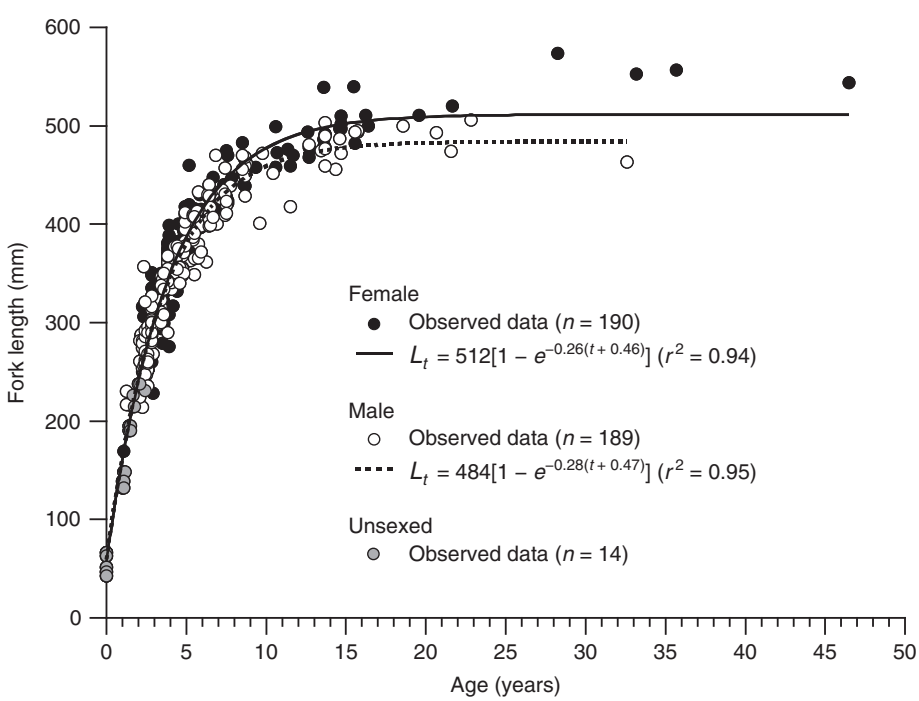

Fig. 7. von Bertalanffy growth curves fitted to the lengths-at-age of female and male *Kyphosus bigibbus*. L_t, fork length at age t.

decades. Thus, there was virtually no sampling bias for year-class strength. The oldest specimen was born in 1962, with a few individuals being born between 1962 and 1998. However, there was a rapid increase in the number of individuals born from 1999 onwards (Fig. 9).

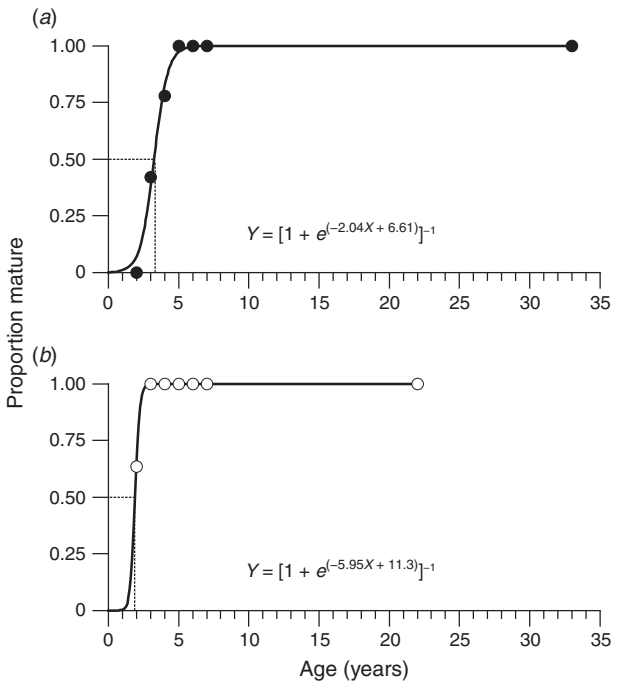

Fig. 8. Proportion of mature (*a*) female and (*b*) male *Kyphosus bigibbus*, in sequential 1-year age classes, caught during the spawning period. *Y*, proportion of mature individuals at age *X*.

Discussion

Our comparison of the opaque zones of scales and otoliths of *K. bigibbus* and their validity as age-determining structures showed that scales should be used with caution. Because the opaque zones were not clearly visible in the scales, there were many errors in reading the number of zones. In particular, the identification of opaque zones in scales was difficult in marginal areas. This may be why a clear periodicity could not be detected in scale opaque zone formation with edge and marginal increment analyses, which depend on the visibility of zones in the marginal areas of structures. Because the opaque zone counts for samples with one to five zones generally showed close correlation between scales and otoliths, the opaque zones in scales may also be formed annually. For samples with more than five zones, the opaque zone counts on scales were lower than those in otoliths, as described by Beamish and McFarlane (1987). Because scale growth is proportional to somatic growth (Fig. 4*a*), slower somatic growth coincides with a decreased scale growth rate. Therefore, the pattern of newly formed opaque zones in the scales of specimens that exhibit slower growth rates would be extremely dense and virtually unreadable.

In comparison, opaque zones were clearly visible in the otoliths, even in marginal areas. Therefore, a clear periodicity could be detected in otolith opaque zone formation. Moreover, otolith growth continued towards the proximal side after somatic growth began to plateau (Fig. 4*b*). Thus, sectioned otoliths could be used to determine the age of older specimens, as described by Beamish (1979). In the present study, we initially believed that we would have difficulty observing opaque zones in otolith sections (Fig. 2*c*). However, by carefully making microscopic adjustments to the section angle, we were able to prepare otolith sections in which the opaque zones could be read clearly in virtually all instances (Fig. 2*d*, *e*). To read zones in otolith sections clearly, researchers have used various techniques, such

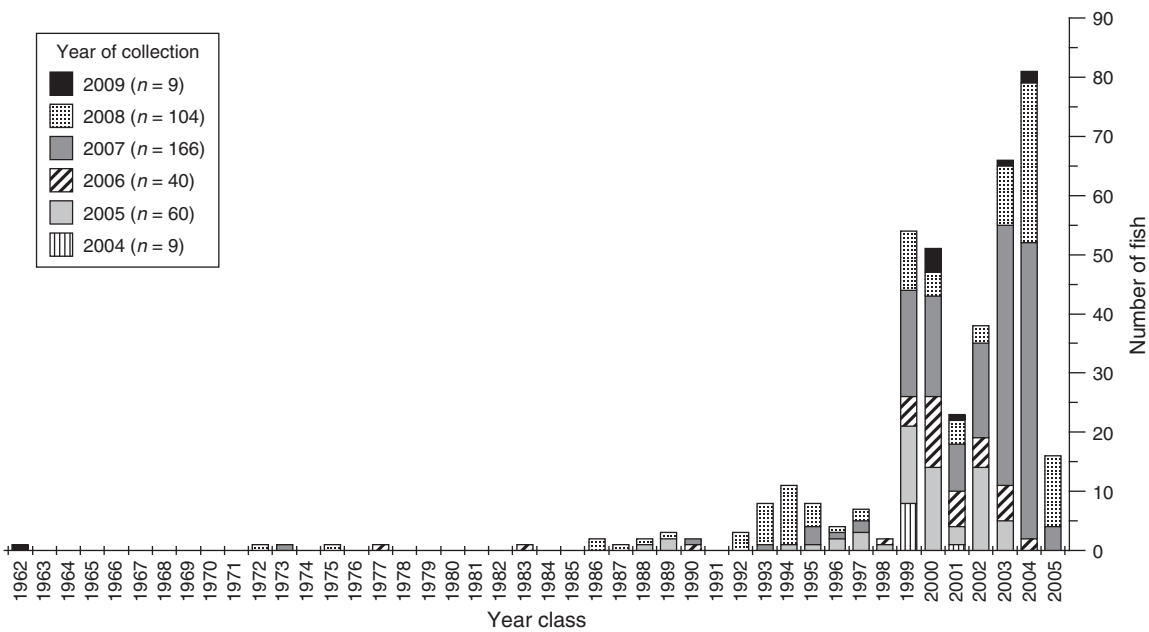

Fig. 9. Number of *Kyphosus bigibbus* in each year class collected between 2004 and 2009.

as burning (Christensen 1964; Power 1978; Francis 1981), staining (Albrechtsen 1968; Richter and McDermott 1990; Arneri *et al.* 2001), thin sectioning (Beamish 1979; Anderson *et al.* 1992; Wakefield *et al.* 2017) and image enhancement techniques (Estep *et al.* 1995; Dwyer *et al.* 2003; Campana *et al.* 2016). Moreover, the clarity of zones in otolith sections is affected by various factors, such as section thickness (Chilton and Beamish 1982; Peres and Haimovici 2004), cutting orientation (e.g. perpendicular to the anterior posterior axis or sulcus acusticus; Beamish 1979; Wakefield *et al.* 2017) and observation methods (e.g. using transmitted or reflected light; Morales-Nin and Panfili 2002; VanderKooy 2009). Differences in shape, size and composition of otoliths among species require species-specific modifications to otolith section preparation (VanderKooy 2009). Here, we found that the clarity of opaque zones in otolith sections of *K. bigibbus* was closely dependent on the perpendicularity of the opaque zones. VanderKooy (2009) introduced an observation technique for an otolith section that was not cut absolutely perpendicular to the core: by tilting a microscope slide so that the opaque zones were perpendicular to the observation plane, it was possible to correct the double images of the opaque zones. We also used this observation technique to improve opaque zone clarity in *K. bigibbus* otolith sections. However, this technique alone could not ensure the accurate perpendicularity of opaque zones. Therefore, to ensure that opaque zones were exactly perpendicular to the sectioning surface, we had to adjust the angle of sectioning by careful hand grinding with frequent observation under the microscope while transforming a thick section into a thin section. Although this is a time-consuming procedure, preparing otoliths using the described techniques may also enhance the precision of age determination for other fish species.

Based on otolith sections, the maximum ages of *K. bigibbus* females and males were determined to be 46 and 32 years respectively. Off South Africa, the maximum age of *Neoscorpis lithophilus*, also within Kyphosidae (Knudsen and Clements 2016), was 10 years (Mann *et al.* 2002). Moreover, among the Scorpididae, which is the most closely related family to Kyphosidae (Knudsen and Clements 2016), the maximum age of *Scorpis lineolata* off eastern Australia was 54 years (Stewart and Hughes 2005) and that of *Scorpis aequipinnis* off western Australia was 68 years (Coulson *et al.* 2012). The maximum age of *Labracoglossa argenteiventris* and *Medialuna californiensis*, also members of Scorpididae, off central Japan and southern California respectively was 8 years for both (Watari *et al.* 2005; Bredvik *et al.* 2011). Although the factors contributing to these lifespan differences are not entirely clear, they illustrate that the lifespan of *K. bigibbus* is relatively long compared with that of closely related species.

Froese and Binohlan (2000) have developed an empirical relationship between longevity and age at maturity based on the data for over 400 fish species. Coulson *et al.* (2012) compared the relationships between A_{50} and maximum age for *S. aequipinnis* and *S. lineolata* with that of other fishes using the equation of Froese and Binohlan (2000) and showed that the A_{50} of 14.1 and 16.1 years for female and male *S. aequipinnis* respectively was typical for species with similar longevity, whereas the A_{50} of 2.5 years for *S. lineolata* would be far more typical of a species with a much shorter life cycle. Based on the equation of Froese and Binohlan (2000), and using the maximum ages obtained for female and male *K. bigibbus* specimens, we predicted an A_{50} for female and male *K. bigibbus* of 14.7 and 10.2 years respectively; these values are higher than the actual A_{50} estimated in our study (3.2 and 1.9 years for females and males respectively). Therefore, the ages at sexual maturity for *K. bigibbus* are relatively low compared with those of other species with similar longevity.

Early maturation and considerable longevity are indicative of a potentially long reproductive lifespan and thus long-term population recruitment. Several fishes inhabiting shallow reef habitats have similar life history strategies, with long-term population recruitment (e.g. Stewart and Hughes 2005; Ewing *et al.* 2007; Andrews *et al.* 2016). This strategy reduces the risk of a population collapsing during long periods of environmental conditions that are unfavourable for successful recruitment (Leaman and Beamish 1984). Therefore, species with this life history strategy have often been considered to have evolved to compensate for uncertainty in reproductive success in any given year, and often exhibit highly variable year-class strength in their populations (Longhurst 2002; Walsh *et al.* 2010; Stewart 2011). In addition, Coulson *et al.* (2010) suggested that, under certain circumstances, far greater mortality of smaller and younger individuals and constraints on the growth of adults may play major roles in selecting for early maturity and a long life.

On the west coast of Kyushu, Japan, three herbivorous fishes (i.e. *K. bigibbus*, *Siganus fuscescens* and *C. japonicus*) are considered to have a critical effect on algal forests (Kiriyama *et al.* 2001; Yamaguchi 2010). Among these three herbivorous fishes, the maximum age and standard length of 46 years and 506 mm recorded for *K. bigibbus* in this study greatly exceeded the 13 years and 357 mm for *S. fuscescens* (Katayama *et al.* 2009) and the 8 years and 384 mm for *C. japonicus* (Kume *et al.* 2010; G. Kume, unpubl. data). Furthermore, *K. bigibbus* is an obligate herbivore, unlike the other two species (Yamaguchi *et al.* 2010). Therefore, at the individual level, *K. bigibbus* could have a more significant effect on algal forests than either *S. fuscescens* or *C. japonicus*.

Our results suggest that *K. bigibbus* recruitment may have increased rapidly since 1999. There has been extensive loss of kelp forests in the study area resulting from overgrazing by herbivorous fishes since the autumn of 1998 (Kiriyama *et al.* 1999), with recent increases in seawater temperatures being cited as a potential factor contributing to this phenomenon (Kiriyama 2009; Yamaguchi 2010). In the coastal waters of Meshima, Nagasaki Prefecture, which is near the study area, mean annual sea water temperature increased by ~0.9°C from 1955 to 2003, and has remained high since 1998, with a peak record of 22.6°C (Kiriyama 2009). High seawater temperatures may decrease winter mortality of *K. bigibbus*, leading to an increase in the number of overwintering individuals that are able to spawn the following season (Figueira and Booth 2010). Beck *et al.* (2017) indicated that temperate macroalgal patches may strongly inhibit the recruitment of many tropical reef fish species, primarily planktivores and herbivores. The noticeable losses of kelp forests in 1998 may have facilitated the rapid increase in *K. bigibbus* recruitment since 1999. Thus, it is important to elucidate the early life history strategies of this species to address these issues.

In tropical regions, reducing exploitation of herbivores is considered to lead to protection of coral reefs, because herbivores contribute to the maintenance of coral reefs by removing macroalgal species (Bellwood *et al.* 2004; Hughes *et al.* 2007; Mumby and Harborne 2010). *K. bigibbus* also plays a major role in the removal of macroalgae, as reported in Ningaloo Reef, Australia (Michael *et al.* 2013). The feeding activity of herbivorous fishes could also contribute towards sustaining communities associated with temperate algal forests. For example, their feeding activity causes the detachment and drifting of portions of *Sargassum* species, which constitute an essential nursery ground for larval or juvenile fishes (Yamaguchi 2008). This process results in some kelp matter sinking to the seabed, providing a food source for abalone and turban shells (Noda 2006). Furthermore, Ruz *et al.* (2018) suggested that kelp consumption by the herbivorous fish *Aplodactylus punctatus* may positively affect kelp populations by facilitating the transport of kelp zoospores. Therefore, the loss of herbivorous fishes could adversely affect algal forest ecosystems. In Japan, the government has recommended culling herbivores to preserve algal forests (Fisheries Agency 2015). However, regarding herbivorous fishes as harmful organisms and culling them indiscriminately could lead to ecosystem destruction (Yamaguchi 2006).

We expand on the findings of existing studies on the behavioural and reproductive ecology and feeding habits of *K. bigibbus* (Yamaguchi *et al.* 2006, 2011; Yamaguchi 2010) by clarifying several life history traits for this species. However, details of the early life history, population dynamics and population structure of *K. bigibbus* remain unclear. In conclusion, before implementing any culling strategy as a means to preserve algal forests, we must first establish the biological and ecological characteristics of herbivorous fishes, including *K. bigibbus*, and determine how they contribute to each ecosystem.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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