

Fish response to expanding tropical *Sargassum* beds on the temperate coasts of Japan

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ABSTRACT: The invasion of tropical *Sargassum* species and extinction of temperate *Sargassum* species on the temperate coasts of several countries is associated with global warming. However, little is known about how these shifts in habitat-forming species impact local ecosystems and fisheries. To better understand the effects of tropical *Sargassum* colonization on temperate coastal fishes, we investigated differences in the habitat use patterns of fishes in temperate and tropical *Sargassum* species beds over 2 seasons on the temperate coast of Japan. The tropical *Sargassum* species were characterized by lower thallus height and a shorter vegetative period compared with temperate species; the thalli of the former were absent during autumn and winter. Peak of recruitment of juvenile fishes matched the biomass peak of both algae from late spring to early summer. Moreover, assemblage structures and food habits of fishes as well as the density of commonly consumed invertebrates did not differ significantly between the temperate and tropical algal beds during these seasons, suggesting that the habitat function (living/refuge space and foraging availability) of tropical algae was similar to that of temperate algae for most fishes. However, although most fishes displayed low specificity to host algae, some species, including important fishery species, recruited only during the middle of winter, when tropical algae were unavailable. This suggests that declining temperate algae may negatively affect some fish populations and fisheries within the next few decades.

KEY WORDS: Fish · Global warming · Invasion · *Sargassum* · Temperate coast

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INTRODUCTION

Over the past 25 yr, the tropical belt has expanded by 2° to 5° latitude (Fu et al. 2006, Seidel et al. 2008). The edges of the tropical belt are the outer boundaries of the subtropical dry zones, and their poleward shift could lead to fundamental shifts in marine ecosystems, brought about by changes in water temperature and related organism invasions and extinctions (Walther et al. 2002, Harley et al. 2006, Cheung et al. 2009). However, it is not clear how global warming is disrupting marine biodiversity and ecosystems or what the impact may be on commercial fisheries

around tropical-temperate boundaries (Cheung et al. 2010, Hoegh-Guldberg & Bruno 2010, Wernberg et al. 2011a).

In general, the distributions of marine organisms tend to extend poleward as the global ocean warms, with the result that high latitude regions experience a high frequency of invasion and an overall increase in species richness (Cheung et al. 2009). Moreover, the combined effects of species invasions and changing environments associated with rising water temperatures can cause the extinction of native species (Harley et al. 2006). One of the clearest and most profound effects of climate change on the world's oceans

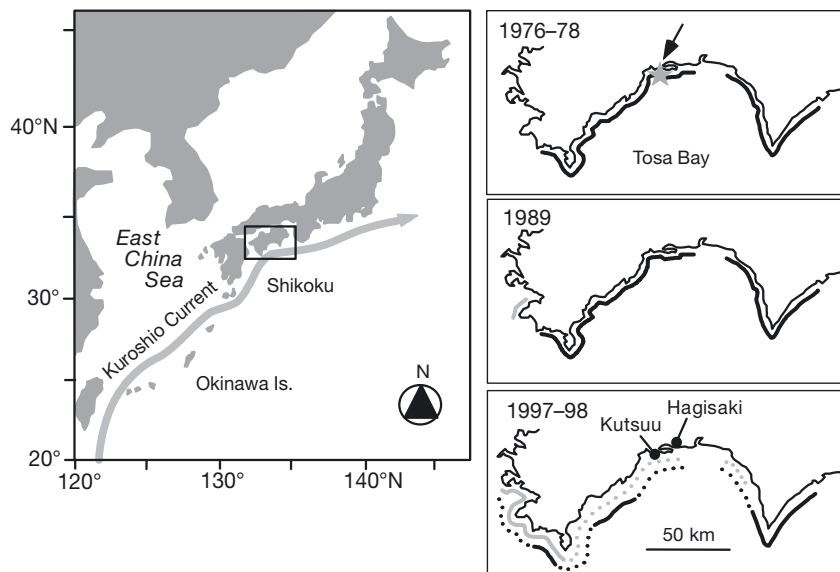


Fig. 1. Tosa Bay in western Japan and the study sites Kutsuu and Hagsaki. Panels on the right show the distribution of temperate (black) and tropical (gray) *Sargassum* species along the coast of Tosa Bay during the late 1970s, 1980s, and 1990s (modified from Hiraoka et al. 2005). Continuous lines indicate rich vegetation and dotted lines indicate patchy vegetation. (★) Monthly seawater temperature sampling station of Kochi Prefectural Fisheries Experimental Station (see Fig. 2b)

is its impact on habitat-forming species (Hoegh-Guldberg & Bruno 2010). For example, warming ocean temperatures are driving a major contraction in the distribution of kelp forests (Steneck et al. 2002) and coral reefs (Carpenter et al. 2008). Invasion and extinction of habitat-forming species alter local species diversity and community structure; relatively little is known about how such species turnover affects ecological functions and services. However, there is evidence that recent global climate change is driving a rapid poleward range expansion of tropical marine organisms, particularly in areas near poleward flowing ocean currents (e.g. western Japan and eastern Australia) (Yamano et al. 2011, Johnson et al. 2011).

The Kuroshio Current is a western boundary current of the subtropical ocean gyre in the North Pacific and one of the strongest ocean currents in the world. The current begins off the east of the Philippines and flows north-eastward to the Pacific side of Japan. Tosa Bay is located in western Japan, and it is strongly affected by the offshore Kuroshio Current (Fig. 1). The bay belongs to the temperate geographical division, but the surface seawater temperature (SST) offshore, beyond the bay, is higher than average for temperate zones, and rose by about $+1.26^{\circ}\text{C}$ between 1902 and 2010 (Fig. 2a), a rate of warming

twice the world average of $+0.51^{\circ}\text{C}$ (Japan Meteorological Agency 2010). In particular, SST of coastal areas has increased rapidly during winter months (January–March) over the past 30 yr (Fig. 2b). In response to these increases in SST, temperate coastal habitat-forming species have been replaced by tropical ones. In the 1970s, temperate *Sargassum* species dominated the coastal area of Tosa Bay (Fig. 1). In the 1980s, temperate *Sargassum* species still dominated the bay, but some beds declined in the eastern region (Fig. 1). During this period, tropical *Sargassum* species began to colonize the western region, possibly because western waters, strongly affected by the Kuroshio Current, are the warmest areas of Tosa Bay. The tropical *Sargassum* species expanded throughout Tosa Bay and some temperate species beds became sparse or disappeared during the late 1990s (Fig. 1), when the lowest winter water temperature rose by approxi-

mately 2°C compared with that in the 1980s (Fig. 2b). Although biological factors are possible causes for changes in the algal flora of this region (e.g. herbivorous animals prefer native algae compared with invasive algae) (Monteiro et al. 2009), the increase in SST is one of the most plausible causes (Hiraoka et al. 2005).

Communities of temperate *Sargassum* species, which is the main habitat-forming species on temperate rocky reefs along with kelps, are used as nursery habitats and feeding grounds by various fishes and invertebrates, including those that are important to fisheries (Taylor & Cole 1994, Kamimura & Shoji 2009). However, the tropical *Sargassum* species found on the temperate coasts are characterized by a lower thallus height and a shorter vegetation period (mainly spring and summer seasons) compared with temperate species (almost year-round vegetation) (Nagai et al. 2011), suggesting that the shift from temperate to tropical *Sargassum* may negatively affect algal fish assemblages. The decline and quantitative changes in macroalgal species (e.g. *Sargassum* and kelp) associated with increasing SST is a growing concern on the temperate coasts of several countries, and the impact on coastal ecosystems and the fisheries that rely on these species is a serious

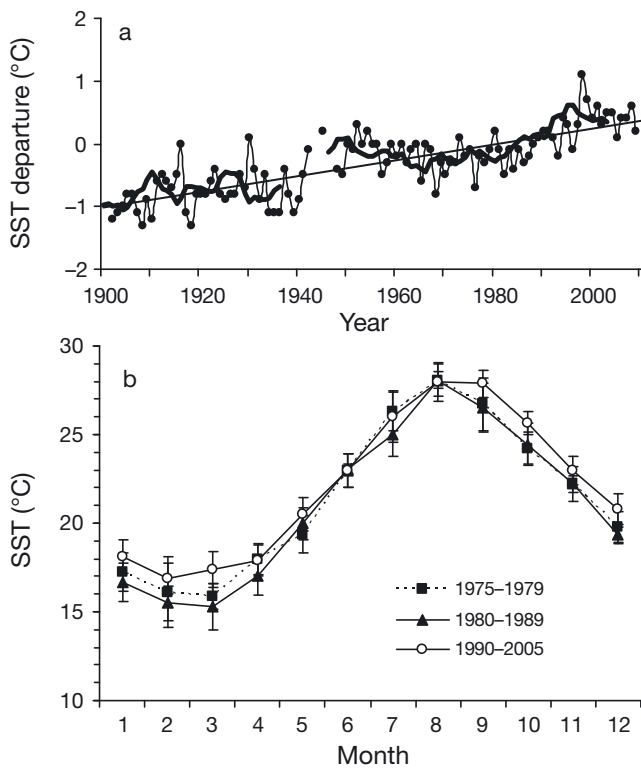


Fig. 2. (a) Time series plot of annual averaged surface seawater temperature (SST) offshore, beyond Tosa Bay (data source: Japan Meteorological Agency) and (●) anomalies from the 1971 to 2000 mean for the period from 1902 to 2009. The bold line shows the 5 yr running mean, and the straight line indicates the long-term linear trend ($y = 0.0126x - 1.0244$). Data source: Japan Meteorological Agency. (b) Monthly average SST (\pm SD) in the coastal area of Tosa Bay (data source: Kochi Prefectural Fisheries Experimental Station, see Fig. 1) during the 1970s, 1980s, and the period 1990–2005

concern worldwide (Lima et al. 2007, Wernberg et al. 2011a,b). For example, the kelp *Ecklonia cava* population in the middle Tosa Bay almost disappeared during the late 1990s with increasing SST and the catch of the kelp-associated abalone in this region has declined dramatically (Serisawa et al. 2004).

To better understand the effects of tropical algae colonization on temperate coastal fishes, we investigated differences in the habitat use patterns of fishes in temperate and tropical *Sargassum* species beds over 2 seasons in Tosa Bay. The following questions were addressed: (1) How do the seasonal patterns of coverage and the height of algae differ between the temperate and tropical *Sargassum* beds? (2) How do the seasonal patterns of fish assemblage structures differ in temperate and tropical *Sargassum* beds? (3) Do the feeding habits of fishes and densities of commonly consumed invertebrates differ in temperate and tropical *Sargassum* beds?

MATERIALS AND METHODS

Study sites

This study was conducted at Kutsuu ($33^{\circ}23'N$, $133^{\circ}20'E$) and Hagsaki ($33^{\circ}26'N$, $133^{\circ}27'E$) in central Tosa Bay, western Japan (Fig. 1). Each site is protected from coastal waves by an offshore concrete breakwater, and both temperate and tropical *Sargassum* beds were present in shallow rocky bottom areas. The distance between the 2 sites is approximately 12 km across the Yokonami Peninsula.

The temperate alga *Sargassum yamamotoi* has long been widespread on shallow rocky reefs (0.5 to 2.5 m depth) in Kutsuu. *S. yamamotoi* beds in the study period covered an area of ca. 2200 m². The tropical brown alga *S. assimile* has been present at Kutsuu since the late 1980s (Hiraoka et al. 2005), and it now forms dense beds on rocks, that covered ca. 1350 m² in the study period. *S. assimile* beds were located at a depth of ca. 2 to 4 m and 20 m away from the nearest *S. yamamotoi* beds. Other brown algae such as *S. ilicifolium* (tropical) and *S. hemiphylum* (temperate) were present in patches around *S. assimile* beds.

In Hagsaki, the temperate species *Sargassum patens* has long been dominant in the shallow water area (0.5 to 2.5 m). *S. patens* beds in the study period covered ca. 1450 m². The tropical alga *S. carpophyllum* has been present at Hagsaki since around 2002 (Haraguchi et al. 2006). It now forms dense beds on rocky stones, and covered ca. 2300 m² in the study period. These were located at a depth of 1 to 4 m and 20 m away from the nearest *S. patens* beds. Other brown algae including *S. ilicifolium* and *S. alternatopinnatum* (both tropical species) occurred sparsely between and around *S. patens* and *S. carpophyllum* beds.

Temporal variation in seawater temperature (at 5 m depth) was monitored every hour from January 2009 to December 2010 using the data loggers deployed at each site. The coldest water temperature was approximately 16°C at Kutsuu and 15°C at Hagsaki in February (winter), whereas the highest water temperature was approximately 29°C from late August to early September (summer) at each site during 2009 and 2010 (Fig. 3). Seasonal patterns of water temperature were similar at the 2 sites; however, the water temperature at Hagsaki was marginally lower than that at Kutsuu from October to March. Salinity was similar at each site during fine weather (ca. 34 to 35). The underwater visibility at Hagsaki was marginally lower (<10 m) than that at Kutsuu (10 to 15 m), and

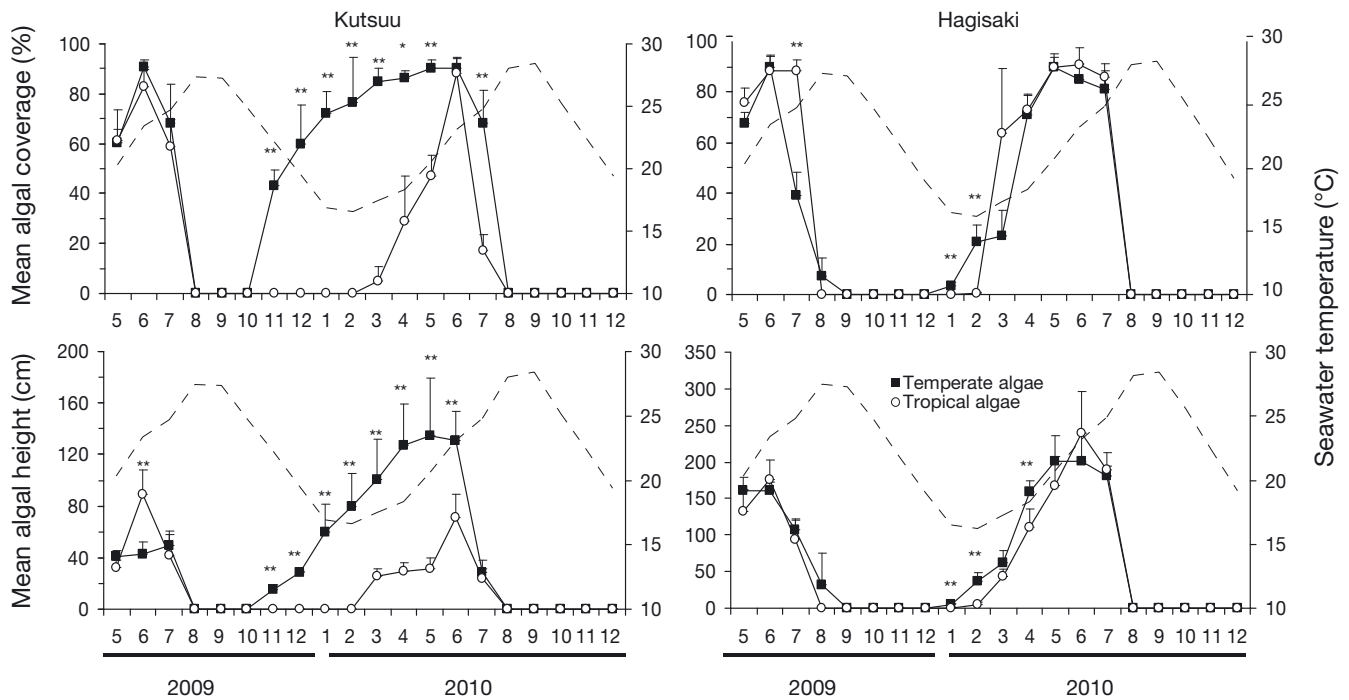


Fig. 3. Mean algal coverage and height (+SD) of (■) temperate and (○) tropical *Sargassum* during each month from May 2009 to December 2010 at Kutsuu and Hagusaki. The dashed line indicates the monthly average seawater temperature (5 m depth) at each site. * $p < 0.05$ and ** $p < 0.01$ between tropical and temperate algae by t -test with Bonferroni-corrected alpha value

the value of the former decreased temporarily after heavy rain due to discharge from the Niyodo River, located 3 km to the east of the Hagusaki site.

Temporal patterns of algae and fish

Fish assemblages in temperate and tropical *Sargassum* beds were assessed every month at each site by visual census from May 2009 to December 2010. In each census, five 20×1 m belt transects, separated from each other by at least 10 m, were established at random in each bed, and all fishes within the transect area were counted. Individual fishes were visually identified to species based on Nakabo (2002) and their total length estimated in size classes of 1 cm (roving fishes) and 0.5 cm (resident fishes). To determine the percent coverage of focal algae species (*Sargassum yamamotoi* and *S. assimile* in Kutsuu; *S. patens* and *S. carpophyllum* in Hagusaki) on each transect, all algae within the entire area of each transect (20 m^2) were identified to the species level, while their surface area was measured approximately using a scaled rope after the fish census. The thallus height of focal algal species was expressed as the mean length of 10 thalli randomly selected from within each transect. Other algal species (e.g. *S. ilici-*

folium) were excluded from the analysis because of their low coverage. Each census was performed between 09:00 and 15:00 h, with each transect being censused once.

A 2-sample t -test with Bonferroni-corrected alpha value was used to evaluate any difference in algal coverage and height between algal types (temperate algae vs. tropical algae) each month. Before the analyses, all data were transformed to arcsin square root (x) for algal coverage and $\log(x + 1)$ for algal height.

Species richness and density of fishes censused in the beds were compared between algal types and sampling time using a mixed-model 2-way analysis of variance (ANOVA). In this analysis, algal type was considered a fixed factor and sampling time a random factor. Before the analyses, all data were transformed to $\log(x + 1)$ to improve the homogeneity of variances as required by Levene's test. All of the statistical analyses were conducted using SPSS 12.0J.

The degree of similarity of fish assemblages in temperate and tropical algal beds during each month at each site was calculated using the Bray-Curtis similarity coefficient based on the number of individuals of each species. Prior to the analysis, the abundance data were fourth-root transformed to normalize distributions and stabilize variances, as recommended

by Clarke (1993). The resultant similarity matrix was subjected to a 2-way mixed model permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) with algal type as a fix factor and sampling month as a random factor. The similarity of fish assemblages in temperate and tropical algal beds each month were represented graphically using non-metric multidimensional scaling (MDS). The ordinations were performed using data averaged over the 5 samples within each bed every month to simplify the presentation and make habitat groupings clearer. PERMANOVA and MDS were performed using the PRIMER (v6) computer package.

Feeding habits of fishes

To elucidate differences in the diet composition of dominant fishes in tropical and temperate beds, a gut content analysis was conducted. Fishes were collected from the tropical and temperate algal beds (>20 m away from fish census area) at the 2 sites using a gill net and a screen net during June and July in 2009 and 2010. Immediately after fish collection, concentrated formalin was injected into the body cavity of each specimen, and the fish was then preserved in 10% formalin. In the laboratory, the standard lengths (SL) of all specimens were measured to the nearest 0.1 mm.

During the study period, 11 dominant species belonging to 4 feeding groups (benthivores, herbivores, detritivores, and omnivores) were collected. At least 3 individuals of each species from each bed type were required for analysis; 3 species (*Petroscirtes breviceps*, *Prionurus scalprum*, and *Pomacentrus coelestis*) from Hagsaki were excluded from the analysis because they did not meet this criterion. Food items in the gut contents of each fish specimen were identified to the lowest possible taxon. The percentage volume of each food item in the diet was visually estimated from a 1 × 1 mm grid slide under a binocular microscope as follows: gut contents were squashed to a uniform depth of 1 mm and the area taken up by each item measured. The area of each item was then divided by the total area covered by the gut contents in order to calculate the percentage volume of that item in the diet. Food resource use was expressed as the mean percentage composition of each item by volume, which was calculated by dividing the sum total of the individual volumetric percentages for the item by the number of specimens examined. Specimens with empty guts were excluded from the analysis

The diet differences of tropical and temperate beds were examined for each feeding group. The Mann-Whitney *U*-test was used to test for differences in the percentage volume of major food items (contributing >5% of total volume) in the 2 bed types. Individuals collected during 2009 and 2010 were pooled for each species in the analysis because the diet composition did not differ in the 2 years. Similar body size individuals were used for analysis to avoid the possibility of ontogenetic food preference.

Density of invertebrates commonly consumed by fishes

To elucidate any differences in the density of commonly consumed invertebrates in tropical and temperate beds, epifaunal invertebrates were collected during June 2009. Specimens were collected using a hand-closing net (net mesh 0.1 mm, net length 75 cm, mouth opening 50 × 50 cm) covering 2500 cm² of the seafloor; a 10 cm long × 3 cm diameter polyvinyl chloride (PVC) pipe was attached to the end of the net. The net was carefully positioned in the algal beds by a diver so as to completely enclose the *Sargassum* without disturbing the epifaunal components. The net mouth was then closed, and the *Sargassum* was cut at the base. Visually, no epifauna were lost during this sampling procedure. In the laboratory, the *Sargassum* was washed in the net using sand-filtered seawater to remove the invertebrates, which were collected through the PVC pipe at the net end and preserved in 5% buffered formalin. The wet weight of algae was measured for each replicate. Five replicate samples were randomly collected (at least 10 m apart) from temperate and tropical algal beds in each station.

A 2-sample *t*-test with Bonferroni-corrected alpha value was used to compare the densities of important food items (ind. kg⁻¹ algal weight) in tropical and temperate algal beds. Prior to these analyses, all data were log (*x* + 1)-transformed to produce homogeneous variances.

RESULTS

Algal height and coverage

From November 2009 to February 2010 (late autumn and winter), only temperate *Sargassum* covered the shallow reefs and no tropical *Sargassum* (or other algae) were vegetative at either site. *Sar-*

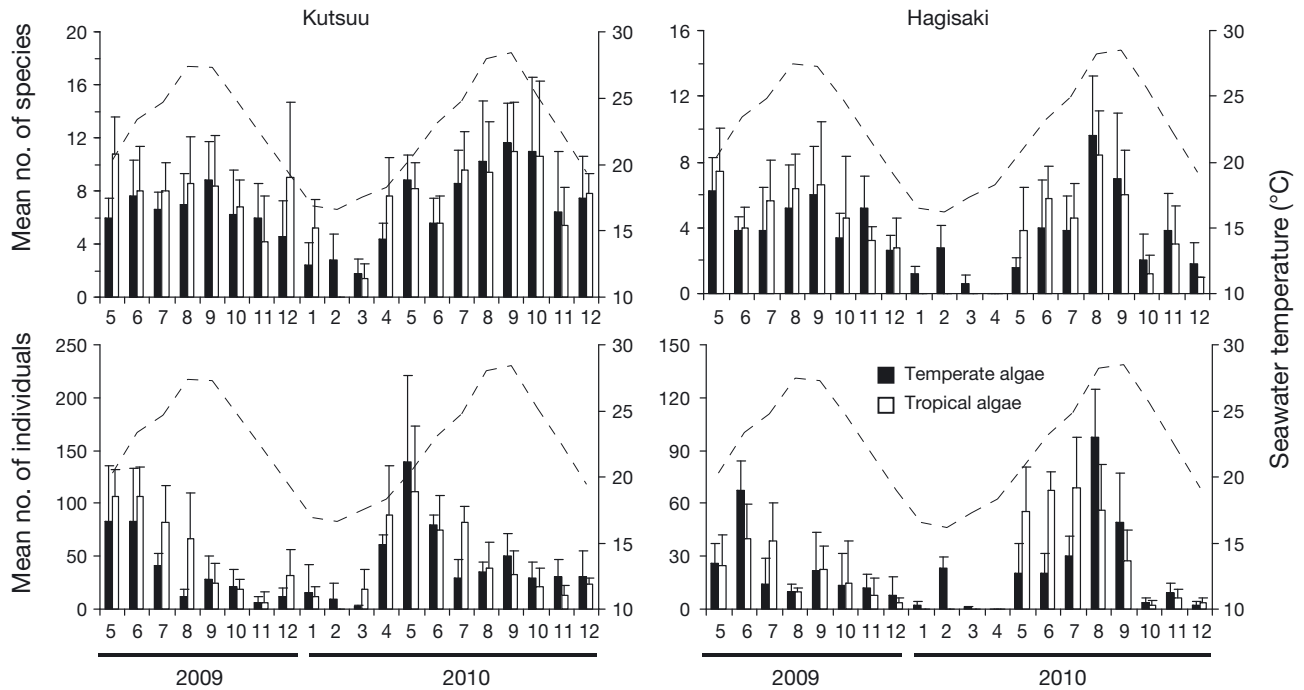


Fig. 4. Mean numbers (+SD) of fish species and individual fishes per transect (1×20 m, $n = 5$) in temperate and tropical *Sargassum* beds during each month from May 2009 to December 2010 at Kutsuu and Hagusaki. The dashed line indicates the monthly average seawater temperature (5 m depth) at each site

gassum yamamotoi started to grow in Kutsuu from November, whereas *S. patens* started to grow in Hagusaki from January (Fig. 3). Tropical algae started to grow from March at each site as the water temperature began to increase. From May to July, most of the temperate and tropical algae matured and the coverage of both algae exceeded 60% at each site. The thalli of temperate and tropical algae lost their blades, fronds, and receptacles after the reproductive season of both algal types from May to late July. During September and October, only holdfasts with small pieces of vegetative material attached remained, and the rocks were coated with turf algae at each site. Although the temperate and tropical algae had a similar biomass peak during May to July during both years, the temperate algae in Kutsuu (*S. yamamotoi*) exhibited a difference in growth onset between years (unusually, there was almost no vegetation during November and December in 2010).

The pattern of the temporal change in algal height was parallel to that in coverage, with the thalli being highest in June and July (Fig. 3). Temperate algae were significantly taller than tropical algae for most months (t -test, $p < 0.05$ for Bonferroni-corrected alpha value), and were often exposed during low tides.

Fish assemblage structure

During the study period, 84 species were recorded from 37 families in the temperate and tropical algal beds at Kutsuu (Table S1 in the supplement at www.int-res.com/articles/suppl/m464p209.pdf). Of these, 53 species were found in both algal beds, 12 were observed only in the temperate bed, and 19 were observed only in the tropical bed. In total, 60 species belonging to 34 families were found in the 2 Hagusaki beds (Table S2). Of these, 37 species were found in both beds, 12 were found only in the temperate bed, and another 11 species were found only in the tropical bed. No fish species were specific to temperate beds at both sites, or to tropical beds at both sites.

There were no significant differences in species numbers and individual numbers between the temperate and tropical algal beds during the study period at Kutsuu (2-way ANOVA: $F_{1,160} = 0.15$, $p = 0.70$ for species numbers; $F_{1,160} = 0.42$, $p = 0.52$ for individual numbers) or at Hagusaki (2-way ANOVA: $F_{1,160} = 0.81$, $p = 0.38$ for species numbers; $F_{1,160} = 0.39$, $p = 0.54$ for individual numbers). However, we found significant seasonal changes in these numbers at both Kutsuu (2-way ANOVA: $F_{19,160} = 5.7$, $p < 0.001$ for species numbers; $F_{19,160} = 7.1$, $p < 0.001$ for individual numbers) and Hagusaki (2-way ANOVA:

$F_{19,160} = 9.0$, $p < 0.001$ for species numbers; $F_{19,160} = 6.7$, $p < 0.001$ for individual numbers) (Fig. 4). At each site, the seasonal pattern of species numbers roughly paralleled that of the seawater temperature, with higher numbers during May to September and lower numbers during January to March (Fig. 4). The seasonal increase in individual numbers was similar to that of species numbers, as many fish juveniles began to be recruited to each bed from April to May, but with a faster drop-off after their seasonal peak. Overall, the seasonal patterns of individuals roughly paralleled that of the algal coverage at each site, i.e. with high numbers recorded May to July when the algal vegetation peaked, followed by a decline after August when the algae started to disappear. Although coverage of both temperate and tropical algae was close to zero from August to September, the species number was high at each site during these months, due to occurrence of generalist habitat species (i.e. species that occur in a variety of habitats such as sandy bottoms). In February, fishes were only observed in the temperate bed at each site.

Although most fish species were found in both algal beds at each site, the densities of some species differed between the temperate and tropical beds during some seasons. During spring (May–June), a higher density of *Girella punctata* juveniles was observed in the temperate bed compared with that in the tropical bed at each site (Tables S1 & S2), and this trend was significant at Hagsaki (Mann-Whitney U -test, $p = 0.05$ during both months). From late autumn to the middle of winter (December–February), when the tropical algae thalli were not present, *Stethojulis interrupta* was abundant in the temperate beds at each site. Moreover, *Scombrops boops* and *Chaenogobius gulosus* juveniles began recruiting to the temperate beds during February.

MDS of the similarities of fish assemblages in the 2 beds at Kutsuu during each month indicated a clear grouping of assemblages between seasons rather than algal types with a similarity level of 35 and 43%, respectively (Fig. 5). In terms of algal similarity, there were no clear groupings of assemblages in the spring and summer groups (May–August) or in the autumn group (September–December). On the other hand,

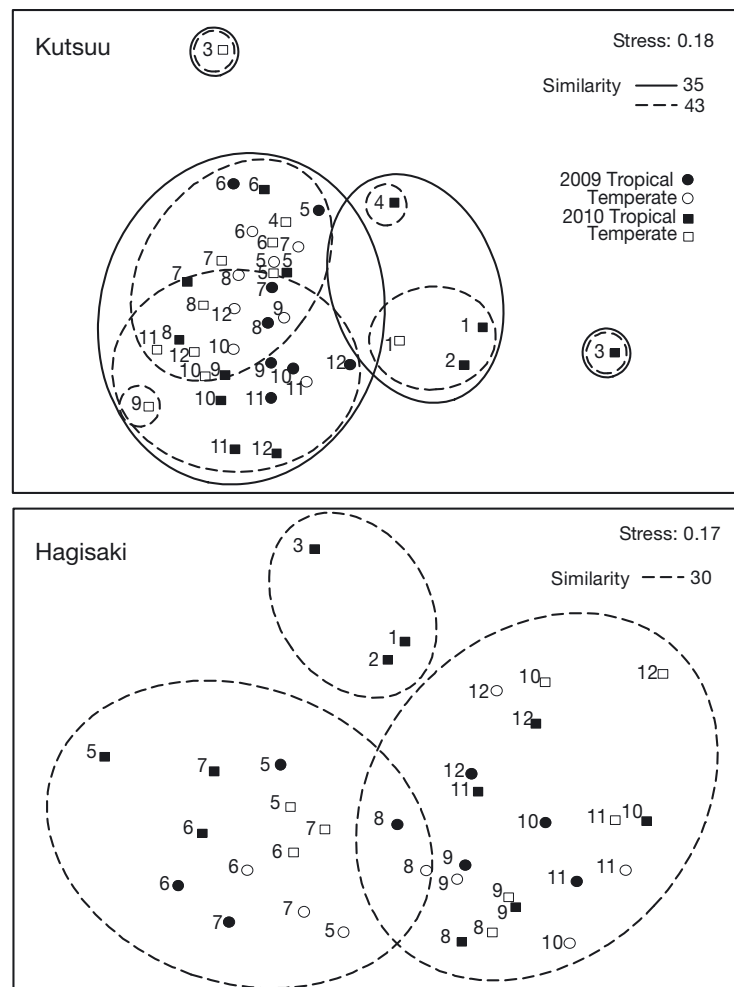


Fig. 5. Multidimensional scaling (MDS) of the similarity of fish assemblages in temperate and tropical *Sargassum* beds during each month from May 2009 to December 2010 at Kutsuu and Hagsaki. Open symbols indicate fish assemblages in temperate *Sargassum* beds, while solid symbols indicate those in tropical *Sargassum* beds. Numbers indicate the month in 2009 (circles) and 2010 (squares)

low similarity was observed between the 2 beds from February to April. Two-way PERMANOVA detected a significant difference between sampling months (Pseudo- $F = 5.1$, $p < 0.01$) and algal types (Pseudo- $F = 9.1$, $p < 0.01$), indicating that algal types were separated from each other during winter and early spring. At Hagsaki, the fish assemblages were largely divided into 3 major seasonal groups with a 30% similarity level, i.e. the January–March group (only temperate algae present), May–July group (vegetation peak period), and August–December group (no vegetation period) (Fig. 5). There were no clear differences between the fish assemblages in the 2 beds during August to December, whereas marginal separation was observed during May to July. Two-way

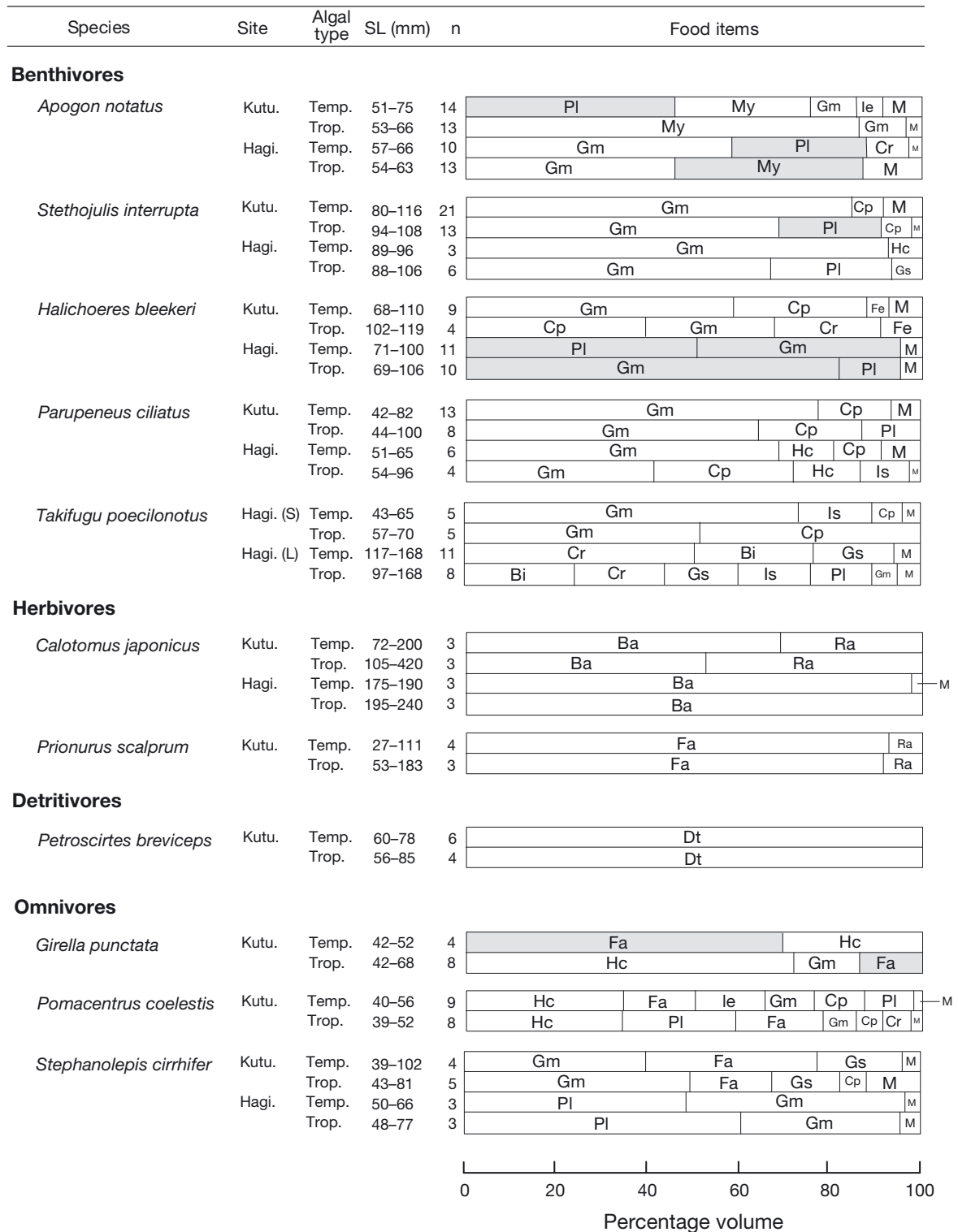


Fig. 6. Mean percentage volume of food items (%V) for each fish species sampled at Kutsuu (Kutu.) and Hagiisaki (Hagi.) in temperate (temp.) and tropical (trop.) algal beds. For each fish species, the range of standard length (SL) and number of fish (n) examined containing food are shown. For *T. poecilonotus*, individuals were grouped as small (S, <70 mm SL) or large (L, >100 mm SL). Gray portions indicate significant differences ($p < 0.05$, Mann-Whitney U test) in the %V of the food items between the 2 bed types at each site. Food items: harpacticoid copepods (Hc), gammaridean amphipods (Gm), corophiid amphipod (Cp), mysids (My), isopods (Is), shrimps (Sh), crabs (Cr), errant polychaetes (PI), gastropods (Gs), bivalves (Bi), detritus (Dt), filamentous algae (Fa), red algal fronds (Ra), brown algal fronds (Ba), invertebrate eggs (Ie), fish eggs (Fe). M: items composing less than 5% of the gut content volume of each species

PERMANOVA detected significant a difference between months (Pseudo- $F = 5.7$, $p < 0.01$) and a marginally significant difference between algal types (PERMANOVA: Pseudo- $F = 2.0$, $p = 0.05$).

Feeding habits of fishes

No significant diet difference was observed between the temperate and tropical algal beds at each site for benthivores, herbivores, detritivores, and omnivores (Fig. 6). *Calotomus japonicus* fed on both types of *Sargassum* at each site.

Density of the invertebrates commonly consumed by fishes

Important food items for benthivores and omnivores such as gammaridean amphipods, corophiid amphipods, harpacticoid copepods, and polychaetes were abundant in both temperate and tropical algal beds (Fig. 7). Most food items did not display clear density difference patterns between the 2 algal types at each site.

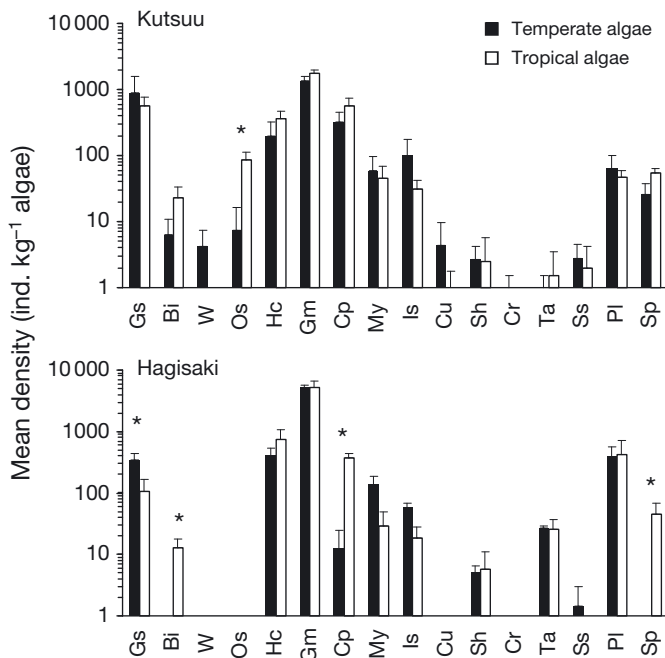


Fig. 7. Mean densities (+SD) of 16 types of invertebrates in algae (ind. kg⁻¹) in temperate and tropical *Sargassum* beds at Kutsuu and Hagsaki. *Significant difference ($p < 0.05$, t -test with Bonferroni-corrected alpha value) in density between the 2 bed types at each site. W: water mites; Os: ostracods; Cu: cumaceans; Ta: tanaids; Ss: sea spiders; Sp: sedentary polychaetes. For other abbreviations, see Fig. 6

DISCUSSION

Fish responses to tropical *Sargassum* invasion

Climatically driven changes in the composition of habitat-forming species are generally expected to have important community- and ecosystem-level consequences (Duffy 2003, Harley et al. 2006). The impact of a tropical algal invasion on the native assemblages of temperate fishes depends on the host plant specificity of fish species and the similarities between temperate and tropical algae. Although the seasonal vegetation pattern differed between tropical and temperate *Sargassum* species in Tosa Bay, the thalli of the former being unavailable during the autumn and winter seasons, the high level recruitment of juvenile fishes occurred during the biomass peak of both algae from late spring to early summer (May–July). The high availability of an algal nursery habitat during the recruitment season is important for most fish populations because mortality rates during the benthic life stages of marine fishes are generally the highest in the youngest and smallest classes (Shulman & Ogden 1987, Dahlgren & Eggleston 2001). Moreover, fish assemblages were not clearly different between the temperate and tropical algal beds during these seasons, suggesting that the habitat function (living/refuge space and foraging availability) of tropical algae was similar to that of temperate algae for most fish species in this region. Indeed, food habits of benthivorous and omnivorous fishes did not differ significantly between the temperate and tropical algal beds and this phenomenon was most likely due to the abundance of commonly consumed invertebrates in both types of bed. Such a low specificity of the epifaunal invertebrates in the host macroalgae has also been found in native and human-induced invasive macroalgae ecosystems, since the general finding is that native and invasive algae share a similar highly complex thallus morphology, as well as epifauna that use epiphytes as food resources rather than the macroalga itself (Viejo 1999, Wernberg et al. 2004, Buschbaum et al. 2006). Tropical seaweeds are hypothesized to possess stronger chemical defenses against herbivory than temperate seaweeds due to the perceived increase in grazing intensity at lower latitudes (Bolser & Hay 1996), suggesting that tropical *Sargassum* invasion could negatively affect temperate herbivorous fishes. Although the small sample size limits the robustness of the conclusions, this hypothesis is not supported by the results of the present study, since we found no differences in the density and food habits of herbivo-

rous fishes between the temperate and tropical algal beds at each site.

Despite the low host-algal specificity of most fishes, some fish species were missing from the tropical algal bed or temperate algal bed at each site. However, no fish species were specific to a bed type at both sites and the low density of each individual species (<0.8 individuals per 20 m², except for *Chaenogobius gulosus*) limited the inference strength of our results. On the other hand, the abundance of several species differed between the temperate and tropical algal beds during the winter and early spring, when the algal coverage and/or the height of the temperate species were much higher than for the tropical species. For example, juveniles of *Girella punctata*, which is a popular angling species in Japan, were often observed in the canopy of temperate algae around the sea surface during May. The feeding habits of *G. punctata* did not differ between the temperate and tropical beds, so algal height may determine host-algal selection by these juveniles. *Scombrops boops* is an important fishery species in Japan, which recruited to temperate algal beds during February, when only temperate algae were available. This phenomenon suggests that temperate algae provide an important juvenile habitat for *S. boops* during the winter. We do not consider that this conclusion is significantly undermined by the lack of replicate winter data in our study, since temperate *Sargassum* vegetation has widely been reported in the bay (e.g. Ohno et al. 1990) during the winter and the spawning season of *S. boops* is from October to March (Mochizuki 1984); thus the phenomenon may well be similar each year. Indeed, temperate *Sargassum* species were observed at both sites during February 2011 (Y. Nakamura pers. obs.). A similar phenomenon was observed for other species in the Seto Inland Sea, northern Shikoku, where the important fishery species *Sebastes cheni* juveniles settled into *Sargassum filicinum* beds from late February to March, where they remained until May during the peak of algal vegetation (Kamimura & Shoji 2009).

Since the geographic expansion of tropical *Sargassum* in Tosa Bay during the 1980s, tropical species have become established permanent members of the algal community in the low intertidal and upper subtidal zones in rocky environments. Despite their successful dispersal and increasing densities, tropical *Sargassum* algae have not entirely replaced indigenous temperate *Sargassum*, and at present, there is no evidence that the tropical algal invasion has had negative effects on the habitat for temperate fishes. However, although no clear evidence has emerged to

date (including this study) that the new *Sargassum* species are having a negative impacts on fisheries in the region, our findings must be interpreted with caution because we lack appropriate historical baseline fish data for the last 30 yr (Pauly 1995, Lotze & Worm 2009). Therefore, we cannot exclude the possibility that tropical macroalgal invasions are having detrimental long-term effects on the native commercial and noncommercial fishes.

Future of fish–macroalgal associations under global warming

Just 30 yr of warmer temperatures at the end of the twentieth century have affected the phenology of organisms, range and distribution of species, and composition of communities (Walther et al. 2002). The rate of warming of the Earth's climate from 1976 to 2000 was greater than at any other time during the last 1000 yr (IPCC 2007). Dramatic increases in SST and tropical organisms have been observed in Tosa Bay during the last 30 yr. An important question is whether this trend will continue in the future. Climate projections suggest that air temperature around Tosa Bay will be +2.5 to 3.0°C higher in 2090–2099 compared with 1980–1999 (under the middle of the road AIB scenario; IPCC 2007), indicating that SST is also very likely to increase in the next 100 yr.

The velocity of Kuroshio current increases with global warming (Sakamoto et al. 2005), which will push warm waters and tropical organisms further north. Warming temperatures can facilitate the establishment and spread of accidentally introduced species (Stachowicz et al. 2002). Therefore, if the water temperature continues to increase, the number of tropical macroalgal species may gradually increase in Tosa Bay. An increase in tropical species may impact native temperate species via competition for space (White & Shurin 2011). Although this remains uncertain, the recent expansion of tropical *Sargassum* species and decline in temperate *Sargassum* species in the bay suggests that tropical algae will be a prominent component of Japanese temperate coasts in the future. Indeed, an expansion of tropical macroalgal (*Sargassum*) species with increasing SST has been observed in several temperate coastal regions in western Japan (Aratake et al. 2007) and eastern Australia (Wernberg et al. 2011b). The increased SST may prolong the vegetative and reproductive period of tropical *Sargassum* species but shorten the vegetative period or lead to the extinction of some temperate *Sargassum* species, because

most of the latter are not tolerant of high temperatures (above 27 to 30°C) (Haraguchi et al. 2005). A prolonged vegetative period of tropical *Sargassum* species with an increasing SST may allow most fish species to use the latter as an alternative habitat to temperate *Sargassum* beds, which may stabilize their populations. In Amami-Oshima Island (28° N, 129° E) in the subtropical–temperate boundary zone, for example, tropical *Sargassum* species vegetate through the whole year, but a growth peak is observed during the spring and summer seasons (with thallus heights of 40 to 90 cm between April and September and 20 cm during the late autumn and winter seasons) (Ikari et al. 2010). The SST during winter season in Amami-Oshima Island is 2 to 3°C higher than in Tosa Bay, but the SST of Tosa Bay at the end of the 21st century is expected to be similar to the current SST of Amami-Oshima Island. Therefore, the most likely scenario within the next few decades is a continuous decline of temperate *Sargassum* on Japanese temperate coasts and the increasing domination of tropical *Sargassum*, but with the latter only vegetating during the spring and summer seasons. Thus, some fish populations could decline if the fish recruitment and algal vegetative period do not coincide, since juveniles would not have access to the shelter and food resources afforded by algal beds, especially during the winter season. However, fish are mobile and could shift their spawning season or distribution area in response to changes in water temperature. Thus, there may be shifts in the fish recruitment season as well as invasions and local extinctions of some fish species. For example, juvenile black rockfish *Sebastes cheni* recruit to macroalgal beds during the late winter-early spring, and they might spawn later if the ambient water temperature increased (Shoji et al. 2011). Holbrook et al. (1997) found a significant increase in southern-ranging species and a decrease in northern-ranging species with increasing SST in fish communities in kelp habitat off California between 1974 and 1993. Because dependence on algal habitat is different among invasive fish species, further research on algal–fish association scenarios under global warming should take account of this dependence, as well as possible shifts in the spawning season in response to increasing seawater temperature.

Overall, the present study emphasizes that most fish species can use tropical *Sargassum* as an alternative habitat to temperate *Sargassum*, but the gradual increase in SST will shorten the overall vegetative period of coastal algae and this may have a negative impact on local fish populations and fisheries. Sim-

plistic models of relationships between temperature and biota are not ideal for predicting future biological changes because the spatiotemporal patterns of temperature and subsequent biological responses are often not straightforward (Duffy 2003, Hsieh et al. 2005). However, we consider that the results presented in this paper help to elucidate the potential sensitivity of temperate algal ecosystems and related fisheries to climate change. The study provides inputs for the development of adaptation policies to minimize the effects of global change in marine ecosystems on coastal ecosystem services.

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