Estuarine, Coastal and Shelf Science xxx (2014) 1–10

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Drifting algae and fish: Implications of tropical *Sargassum* invasion due to ocean warming in western Japan

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A R T I C L E I N F O

Article history:
Received 22 December 2013
Accepted 25 May 2014
Available online xxx

Keywords:
drifting algae
fish
global warming
Sargassum
Tosa Bay

A B S T R A C T

Evidence is accumulating that the invasion and extinction of habitat-forming seaweed species alters coastal community structure and ecological services, but their effects on the pelagic environment have been largely ignored. Thus, we examined the seasonal occurrence patterns of indigenous temperate and invasive tropical drifting algae and associated fish species every month for 2 years (2009–2011) in western Japan (Tosa Bay), where a rapid shift from temperate to tropical *Sargassum* species has been occurring in the coastal area since the late 1980s due to rising seawater temperatures. Of the 19 *Sargassum* species (31.6%) in drifting algae, we found that six were tropical species, whereas a study in the early 1980s found only one tropical species among 12 species (8.3%), thereby suggesting an increase in the proportion of tropical *Sargassum* species in drifting algae during the last 30 years. Drifting temperate algae were abundantly present from late winter to summer, whereas tropical algal clumps occurred primarily during summer. In the warm season, fish assemblages did not differ significantly between drifting temperate and tropical algae, suggesting the low host–algal specificity of most fishes. We also found that yellowtail juveniles frequently aggregated with drifting temperate algae from late winter to spring when drifting tropical algae were unavailable. Local fishermen collect these juveniles for use as aquaculture seed stock; therefore, the occurrence of drifting temperate algae in early spring is important for local fisheries. These results suggest that the further extinction of temperate *Sargassum* spp. may have negative impacts on the pelagic ecosystem and associated regional fisheries.

1. Introduction

Globally, increasing evidence suggests that the geographic distributions of marine organisms are undergoing rapid geographic changes, which are associated with an increasingly warm climate (Harley et al., 2006; Hoegh-Guldberg and Bruno, 2010; Feary et al., 2013). The increased incidence of natural populations with range expansions and contractions during warm or cool periods has been demonstrated widely among habitat-forming corals and seaweeds (Lima et al., 2007; Greenstein and Pandolfi, 2008; Yamano et al., 2011; Wernberg et al., 2011). Seaweeds are ecologically important primary producers and ecosystem engineers, which play central roles in cold-temperate waters (Steneck et al., 2002). However, recent studies have found that the invasion and extinction of seaweed species (kelps and fucoids) caused by long-term and episodic climate changes have altered the local species diversity and community structure, which has negative impacts on ecological functions and services (Harley et al., 2012; Wernberg et al., 2013).

Western Japan has experienced substantial ocean warming over the last century, which may be attributable to the recent warming of the Kuroshio Current (Wu et al., 2012), and it is a global hotspot for biological change as organisms respond to the warming of coastal waters (Yamano et al., 2011; Tanaka et al., 2012; Nakamura et al., 2013). Tosa Bay is located in western Japan and is affected strongly by the offshore Kuroshio Current (Fig. 1a). The geographical division of the bay is temperate, but the surface seawater temperature (SST) of coastal areas has increased rapidly during the winter months over the past 30 years (Fig. 1b). Together with these increases in the SST, the abundance of tropical macroalgae *Sargassum* (Fucales) species has increased substantially, whereas

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http://dx.doi.org/10.1016/j.ecss.2014.05.018
0272-7714/

Please cite this article in press as: Yamasaki, M., et al., Drifting algae and fish: Implications of tropical *Sargassum* invasion due to ocean warming in western Japan, Estuarine, Coastal and Shelf Science (2014), http://dx.doi.org/10.1016/j.ecss.2014.05.018

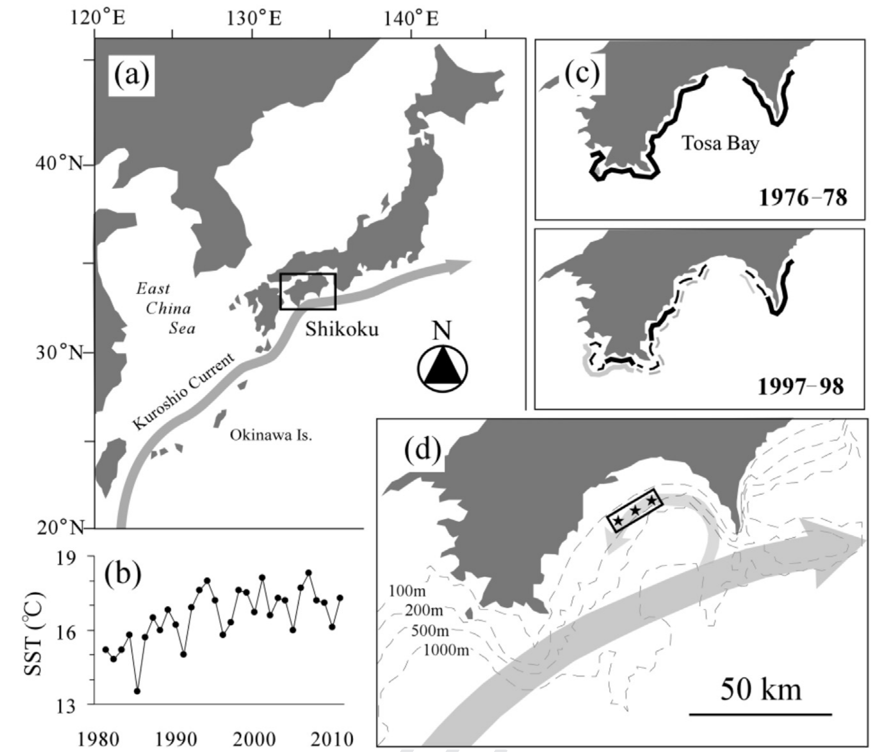

Fig. 1. (a) Map of the study site, showing the location of Tosa Bay. (b) Trends in surface seawater temperature (SST) in the coldest month (February) at the coastal area of central Tosa Bay from 1981 to 2011. (c) Distribution of temperate *Sargassum* species (black) and tropical *Sargassum* species (gray) along the coast of Tosa Bay during the late 1970s and 1990s. The continuous line indicates rich vegetation and the dotted line indicates patchy vegetation for each *Sargassum* species. The distribution map was modified from that reported by Hiraoka et al. (2005). (d) The box indicates the area sampled for drifting algae; (★): monthly SST sampling stations of Kochi Prefectural Fisheries Experimental Station within the present study area. The thick arrow represents the main axis of the Kuroshio Current and the anticlockwise thin arrow shows the major surface current inflow into Tosa Bay (Kuroda et al., 2008).

temperate *Sargassum* species have decreased significantly (Tanaka et al., 2012). In the 1970s, temperate *Sargassum* species dominated the coastal area of Tosa Bay (Fig. 1c). However, in the late 1980s, temperate *Sargassum* species still dominated the bay, but tropical *Sargassum* species began to colonize the western region, possibly because the western waters were strongly affected by the Kuroshio Current, and they were the warmest areas of Tosa Bay. In the 1990s, the tropical *Sargassum* species expanded throughout Tosa Bay and some temperate species beds became sparse or disappeared (Fig. 1d). Human-induced events associated with coastal development, such as increase in artificial hard structures and sedimentation, are possible causes for the decline and shift in habitat-forming macroalgal species (Thompson et al., 2002), but the phenomenon seen in Tosa Bay has often been observed in long-established harbors and pristine rocky reefs; thus, an increase in the SST is thought to be one of the most plausible causes for the shift from temperate to tropical *Sargassum* spp. (Tanaka et al., 2012).

The tropical *Sargassum* spp. found in Japanese temperate reefs exhibit annual characteristics in terms of their life cycles (a short vegetation period, primarily in the spring and summer seasons), which contrast greatly with the perennial characteristics of most temperate species (almost year-round vegetation) (Nagai et al., 2011). Therefore, it is expected that the shorter vegetation periods caused by algal species shifts may have negative effects on fish populations that rely on coastal algal beds. In Tosa Bay, for example, Terazono et al. (2012) found that juveniles of the important fishery species *Scombrops boops* only recruited to temperate *Sargassum* beds during the middle of winter when tropical *Sargassum* were unavailable. *Sargassum* that have been broken or detached by strong waves often drift on the surface of offshore areas, and many fish juveniles, including important fishery species (e.g., family Carangidae), are attracted to the drifting algae for shelter and food (Kingsford and Choat, 1985; Safran and Omori, 1990; Kingsford, 1992, 1993; Dempster and Kingsford, 2004). Large numbers of drifting *Sargassum* are observed in Tosa Bay; therefore, it is expected that the algal species shift in coastal areas may affect the seasonal occurrence patterns of drifting algae and associated fish. Moreover, we may also expect that possible changes in the seasonal occurrence patterns of drifting algae may affect local and regional fisheries because yellowtail (*Seriola quinqueradiata*) juveniles are frequently associated with drifting algae in the bay and local fishermen collect these juveniles during the spring season for use as aquaculture seed stock (Uehara et al., 2006). Yellowtail capture occurs mostly in western Japan and the Republic of Korea, where farming has developed rapidly during the 1970s and 1980s. Furthermore, the annual production of farm-raised yellowtail is now three times greater than that of the fishing catch in Japan (Nakada, 2008).

Evidence is accumulating that invasions and extinctions of habitat-forming seaweed species alter the coastal community structure, ecological functions, and services (Serisawa et al., 2004; Harley et al., 2012; Terazono et al., 2012; Wernberg et al., 2013; Voerman et al., 2013), but their effects on the pelagic environment have been largely ignored. This study aimed to determine the importance of tropical and temperate *Sargassum* spp. in determining the structure of the fish communities associated with drifting algae. We hypothesized that fish assemblages would not

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