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*Coastal Ecosystems*, 2014, vol 1, 1-13



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## Abstract

A population of the asari (Manila) clam, *Ruditapes philippinarum*, on the Nakatsu tidal flat, Japan, has collapsed in recent decades. Our previous study reported high clam mortality from post-settlement until fishable size (30 mm shell length) on this flat. Although the reasons are unclear, a recent increase in warm-water predators, portunid crabs, and the longheaded eagle ray may have contributed to the high mortality. In this study, we prepared netting treatment plots and observed clam mortality and growth under these. We were unable to prepare a no-net control plot, so the results were compared with those of previous studies on this flat, to assess the netting effect. *R. philippinarum* spat (11.6 mm shell length) were released in 49-m<sup>2</sup> plots (1500 individuals m<sup>-2</sup>) and were covered with nets attached to floats. Size after 10 months (final shell length 26.3–30.4 mm) was similar to that in previous netting experiments and comparable to that in a eutrophic area, suggesting that food availability was not the limiting factor. Clam survival (24–41% after 10 months) and final biomass density (1.9–3.7 kg m<sup>-2</sup>) were higher than those from no net situations in previous studies. Although still uncertain, predation by snails that invaded the nets might have contributed to the mortality reported here. These results suggest that predation may be a significant cause of clam mortality that has suppressed the *R. philippinarum* population in this flat to levels lower than its carrying capacity.

**Keywords:** global warming; predator exclusion netting; top-down control; clam culture

## Introduction

Bivalve populations have declined worldwide, for reasons that differ among systems. Complex factors, including overfishing, disease, habitat loss, competition from invasive species, global warming, and trophic cascades, have been associated with these declines (Beukema & Dekker 2005;

Fegley *et al.* 2009; Laing, Walker & Areal 2006; Mann & Powell 2007; Marsden & Adkins 2010; Myers *et al.* 2007; Troost 2010; Wilberg *et al.* 2011). Appropriate methods for restoring decimated bivalve populations cannot be identified until the underlying causes are understood.

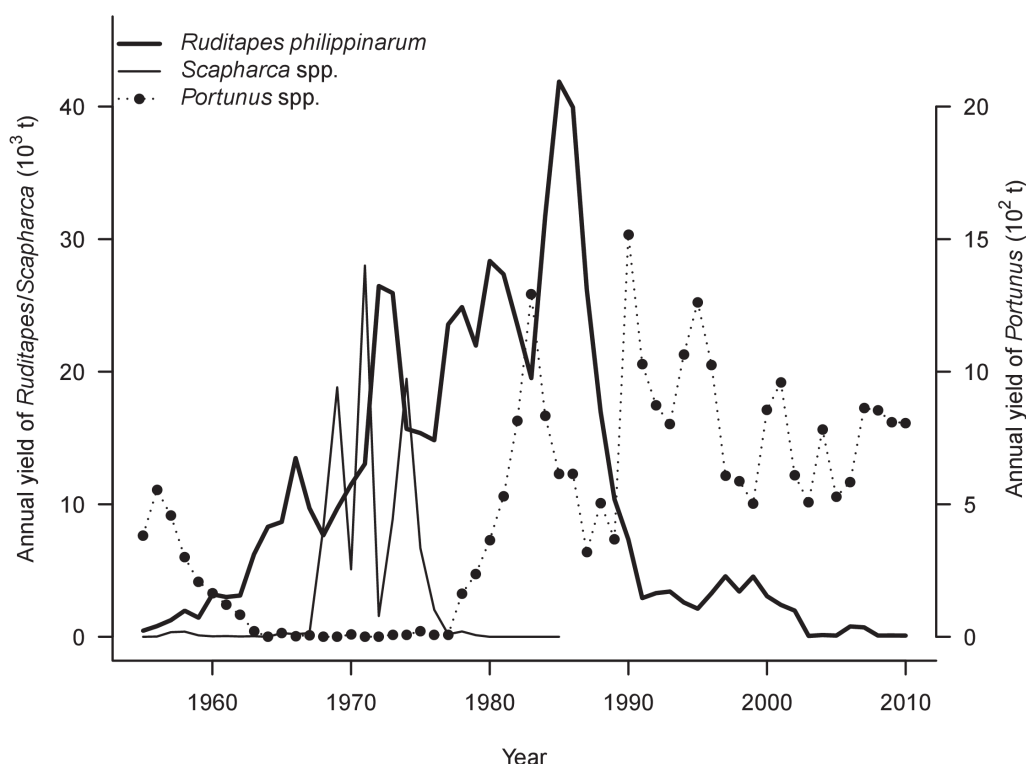
An example of population decline in bivalves can be seen in the asari (Manila) clam, *Ruditapes philippinarum*

(Adams & Reeve, 1850), in Japan. This species is native to the Pacific coast of Asia, where it primarily inhabits estuarine tidal flats. *R. philippinarum* has also been introduced into coastal habitats globally (Goulletquer 1997) and is known as one of the world's most commercially important aquaculture species (Statistics and Information Service of the Fisheries and Aquaculture Department 2012). In contrast to its proliferation in areas in which it is not native, the *R. philippinarum* population in Japan has declined in recent decades (Tamaki *et al.* 2008; Toba *et al.* 2007). There has been a remarkable decline in the Nakatsu tidal flat in the Suo-nada Sea (western Seto Inland Sea, Japan), where >25000 t were harvested at its maximum in the 1980s; the harvest declined to <500 t by the 2000s (Ministry of Agriculture, Forestry and Fisheries, Japan 2012). High post-settlement mortality rates (0–15% survival  $y^{-1}$ ) before fishable size (30-mm shell length) observed in wild *R. philippinarum* populations are thought to underlie the recent population decline in the Nakatsu tidal flat (Tezuka *et al.* 2012).

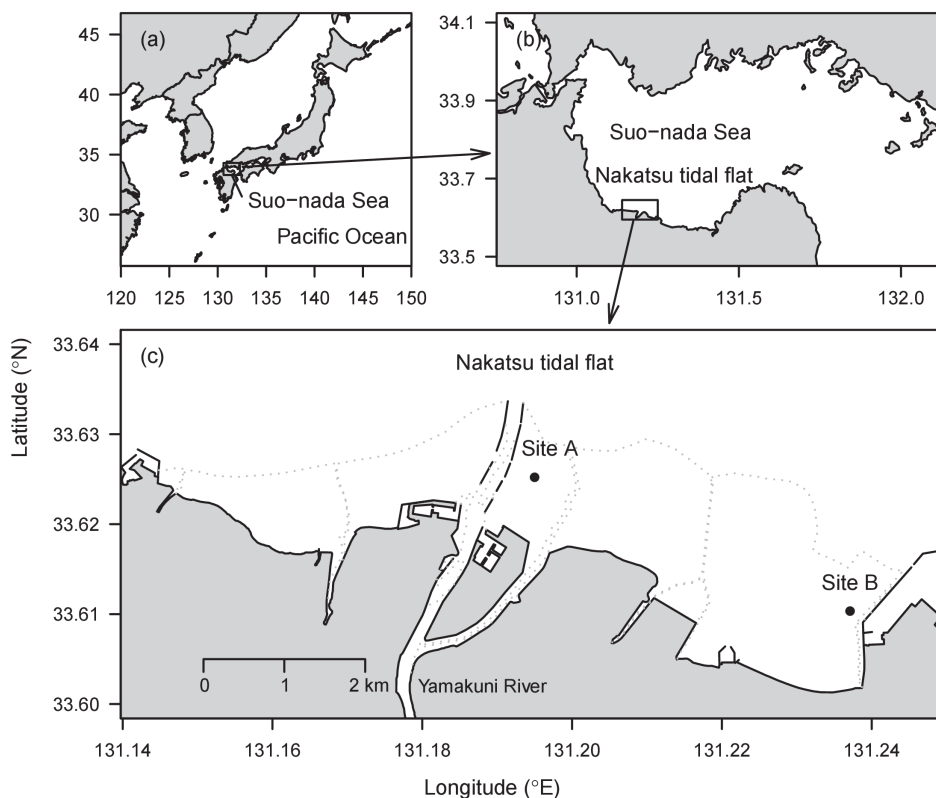
Although the cause of the high mortality remains unclear, a recent increase in warm-water predators,

including gazami crabs (*Portunus trituberculatus* Miers and *Portunus pelagicus* Linnaeus) and the longheaded eagle ray (*Aetobatus flagellum* Bloch & Schneider), may be a contributing factor. Fishery statistics show an increase in gazami crab production and a decrease in *R. philippinarum* production since the late 1970s (Fig. 1). Although statistics for the longheaded eagle ray are not available, this species is also thought to have had a severe impact on clam populations in this region, especially since the 2000s (Fukuda & Zenitani 2010; Shigeta 2008; Shigeta & Usuki 2012; Yamaguchi, Kawahara & Ito 2005).

In this study, we prepared netting treatment plots, which were expected to exclude the swimming predators mentioned, to observe clam mortality and growth under netting treatments on the Nakatsu tidal flat. However, we were unable to prepare a no net control plot. Therefore, we compared our results with those of no net situations in previous studies, which reported very low clam survival, to see the effect of netting. Although our results were limited, this information will be potentially valuable in understanding the cause of the clam population decline and for future clam culture trials on this flat.



**Figure 1:** Annual yield of clams *Ruditapes philippinarum* and *Scapharca* spp., and the gazami crabs (*Portunus* spp.) in the Suo-nada Sea from 1955 to 2010. There is no post-1985 data for *Scapharca* spp.



**Figure 2:** Maps of the experimental sites. (a) The location of the Suo-nada Sea (Seto Inland Sea) in Japan; (b) the location of the Nakatsu tidal flat, Suo-nada Sea; and (c) the experimental sites.

## Materials and methods

### Study site and experimental setting

The netting treatment plots were set at two sites (sites A and B) on the Nakatsu tidal flat, Suo-nada Sea, Seto Inland Sea, Japan (Fig. 2). The range in annual water temperature was 6–32 °C and the salinity 20–33 (personal observations using a continuous TS meter; Compact-CTW, JFE Advantech Co., Ltd., Hyogo, Japan, 2008–2009). The mean spring tidal range was 2.88 m. The relative height of both sites from the nearly lowest low water level (NLLWL) was +1.2 m, which was –0.8 m below the mean sea level of +2.0 m. Site A was a sand flat (median grain size 0.44 mm, silt-clay 0.65%) with no vegetation, while site B had finer substrates (median grain size 0.19 mm, silt-clay 1.5%) covered by Japanese eelgrass (*Zostera japonica* Ascherson & Graebner). Five samples collected with a 0.04 m<sup>2</sup> quadrat and a 2 mm mesh sieve revealed no *R. philippinarum* and no predatory species at either site at the beginning of the experiment in June 2011.

Two 49 m<sup>2</sup> plots were established at each site, and hatchery-reared *R. philippinarum* spat (1 year old, mean shell length = 11.6 mm) were introduced in the plots (1500 individuals m<sup>-2</sup>) by spreading over the sediment surface on June 1–2, 2011, during low tide (Fig. 3). Clam spat density (1500 individuals m<sup>-2</sup>) followed that of previous studies conducted on this flat, 570–2000 individuals m<sup>-2</sup> (Table 1). One of the two plots at each site was then covered with a fine (5 mm mesh) multifilament polyethylene net and the other plot with a coarse (9 mm mesh) monofilament polyethylene net. Nine sets of floats (500 mL PET plastic bottles) tied with string to sandbags were placed under each net to keep the nets floating approximately 10–20 cm above the sediment when submerged at high tide. To prevent the nets from being dislodged by waves and water currents, a stainless-steel chain (5 mm diameter) was tied to the bottom edge of each net as a weight. Additionally, the edges of the nets were buried approximately 10 cm into the sediment, to prevent predators from invading the nets, and fixed with spiral tacks at 1.75 m intervals from each corner. Sandbags were then placed on the periphery of the nets between the tacks to help prevent dislodging.





**Figure 3:** Initial establishment of the clam culture experiment in June 2011 (a–d), and the plot at the end of the experiment in April 2012 (e). (a) Establishment of the 49-m<sup>2</sup> plot, (b) spreading clam spat into the plot, (c) covering the plot with the net, and (d) the net at high tide (floating above the sediment).

We could not set the control, no-net plot because of insufficient clam spat numbers. However, previous studies observed very low clam survival on this flat when unprotected. Ito & Ogawa (1999) reported very low clam survival when the clam spat was seeded without a net, < 3% survival after 3 months, during 1994–1995 on this flat. More recently, Tezuka *et al.* (2012) observed low clam survival rates, 0–15%  $y^{-1}$  in the wild unprotected clam population during 2005–2008. Although we could not set the control plot, we compared our results (with net) with those of the previous studies (without net) on this flat.

#### Clam sampling

At 1, 3, 6, and 10 months after the beginning of the experiment (early June 2011), six samples were randomly taken from each plot using a 0.04 m<sup>2</sup> quadrat and a 2-mm mesh sieve (total area = 0.24 m<sup>2</sup>). On the following day, the numbers of *R. philippinarum* in each sample were counted and shell lengths were measured with a caliper (Super Caliper CD67-S20PM; Mitutoyo Co., Ltd., Kawasaki, Japan) to the nearest 0.01 mm. The number of predators in each sample was counted and their maximum body length was measured. Clam biomass (wet weight with shell) was estimated using the relationship between shell length (SL, mm) and wet weight (WW, g) given by Solidoro *et al.* (2000):  $WW = 0.00026 SL^3$ .

#### Statistical analysis

*R. philippinarum* survival and growth observed in this study

were compared with those from other studies (Table 1). For comparison, growth rates were calculated as follows,

$$\text{Growth rate (mm } y^{-1}) = (SL_2 - SL_1) / t \quad (1)$$

where  $SL_1$  = initial shell length,  $SL_2$  = final shell length, and  $t$  = experimental duration in years. Similarly, survival rate was calculated as follows,

$$\text{Survival rate (\% } y^{-1}) = \exp(\ln S / t) \times 100 \quad (2)$$

where  $S$  is the final survival defined as  $S$  = final clam density / initial clam density. One-way analysis of variance (ANOVA) and post-hoc Tukey HSD multiple comparisons were used to compare the differences in growth and survival rates among this and other studies according to the type of protection used (Table 1). The clam survival rates were arcsine-transformed to improve the normality and homogeneity of variance before being compared.

Differences in *R. philippinarum* growth and survival rates between sites A and B ( $n = 2$ ) and between the fine and coarse-mesh nets ( $n = 2$ ) in this study were assessed by two-way ANOVA without interaction effects. Differences in predator density between sites and between mesh sizes were analyzed by two-way ANOVA for the combined data from all sampling dates (1, 3, 6, and 10 months). The predator density data were log-transformed to improve the normality and homogeneity of variance. However, it should be noted that we did not set enough replicates to show the difference between sites and between mesh sizes, and thus these should be examined further. All analyses were performed in the R Language and Environment for Statistical Computing (R Development Core Team 2013).

## Results

We found that the PET bottles pierced through and broke the coarse nets at sites A and B, because of heavy barnacle settlement onto those bottles. These nets were unable to float at the sampling sites after 3 and 6 months, respectively. The barnacles were removed and the holes mended during sampling. Barnacle settlement onto the PET bottles was also observed in the fine-mesh plots but these nets were not severely damaged. The differences in damage were likely to result from the multifilament (fine) vs. monofilament (coarse) nature of the nets. Additionally, we found that one part (approximately 1.5 m wide) of the coarse net at site B was torn off after 6 months. This damage was probably caused by strong waves and currents generated by storms in early autumn. The uncovered part of the net was reburied during sampling.

*Ruditapes philippinarum* shell length increased from

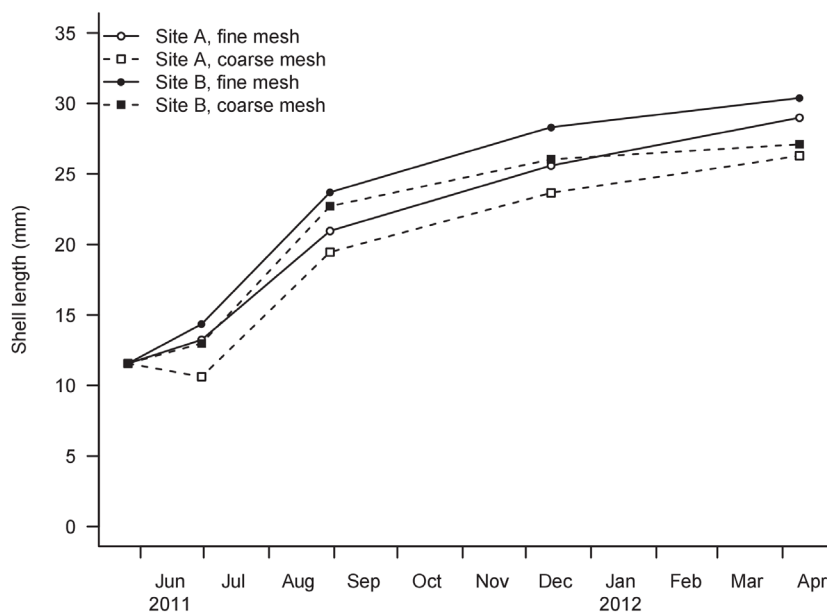
11.6 mm in June 2011 to 26.3–30.4 mm (mean = 28.2 mm) at the end of the experiment in April 2012 (Fig. 4). Our growth rates had a range of 17.6–22.6 mm  $y^{-1}$  (Table 1). These rates were similar to those from recent caging experiments from 2006 to 2010, which had a range of 20.2–25.0 mm  $y^{-1}$  (Tukey HSD,  $P = 0.23$ ), and those from netting experiments that had a range of 19.3–20.2 mm  $y^{-1}$  (Tukey HSD,  $P = 0.99$ ). However, the growth rates in this study were significantly higher than those from no net wild populations from 2005 to 2007, which had a range of 13.3–15.9 mm  $y^{-1}$  (Tukey HSD,  $P = 0.01$ ). It should be noted that these growth rates were obtained from different conditions, i.e., year, initial density, and site in the same flat, and thus we cannot distinguish which factor caused the differences in growth. There was no significant difference in growth rates between sites (two-way ANOVA,  $P = 0.16$ ), but there was a slight difference (two-way ANOVA,  $P = 0.06$ ) in growth rates according to mesh size.

Clam density remained >1100 individuals m<sup>-2</sup> (approximately > 70% of the initial density) until the end

**Table 1.** Data on *Ruditapes philippinarum* mortality and growth on the Nakatsu tidal flat. Sources are: (1) Ito & Ogawa (1999), (2) Tezuka et al. (2012), (3) Hayashi et al. (2008), (4) Hirakawa et al. (2010), and (5) Katano et al. (2010).

| Type of protection (mesh size) used | Period            | Initial density<br>(ind m <sup>-2</sup> ) | Final survival<br>(%) | Survival rate<br>(% y <sup>-1</sup> ) | Initial SL<br>(mm) | Final SL<br>(mm) | Growth rate<br>(mm y <sup>-1</sup> ) | Source     |
|-------------------------------------|-------------------|-------------------------------------------|-----------------------|---------------------------------------|--------------------|------------------|--------------------------------------|------------|
| net (3.5 mm × 5 mm)                 | 1994–1995         | 2000                                      | 12.3                  | 12.3                                  | 5.8                | 26.0             | 20.2                                 | (1)        |
| net (3.5 mm × 5 mm)                 | 1994–1995 (9 mo)  | 2000                                      | 16.3                  | 8.9                                   | 6.5                | 21.0             | 19.3                                 | (1)        |
| no net                              | 1994–1995 (9 mo)  | 2000                                      | 3                     | 0.9                                   | 6.5                | NA               | NA                                   | (1)        |
| no net (wild population)            | 2005–2006         | 13100                                     | 0.8                   | 0.8                                   | 7.86               | 21.8             | 13.9                                 | (2)        |
| no net (wild population)            | 2005–2006         | 2140                                      | 1.1                   | 1.1                                   | 11.5               | 25.6             | 14.1                                 | (2)        |
| no net (wild population)            | 2006–2007         | 5250                                      | 14.5                  | 14.5                                  | 5.3                | 18.6             | 13.3                                 | (2)        |
| no net (wild population)            | 2006–2007         | 3990                                      | 9.4                   | 9.4                                   | 2.6                | 18.5             | 15.9                                 | (2)        |
| net (9 mm)                          | 2006–2007         | 2000                                      | 0.6                   | 0.6                                   | 10.2               | 22.4             | (12.2)                               | (3)        |
| cage (12 mm × 6 mm, plastic)        | 2006–2007         | 570                                       | 64.4                  | 64.4                                  | 10.2               | 30.4             | 20.2                                 | (3)        |
| net (9 mm)                          | 2008 (3 mo)       | 2000                                      | 0.3                   | 0.0                                   | 10.1               | NA               | NA                                   | (4)        |
| cage (4 mm, stain-less steel)       | 2008–2009         | 2000                                      | 31.7                  | 31.7                                  | 10.1               | 32.0             | 21.9                                 | (4)        |
| net on gravel bottom (9 mm)         | 2009–2010 (13 mo) | 2000                                      | 37.0                  | 39.9                                  | 10.8               | 30.9             | 18.6                                 | (5)        |
| cage (4–9 mm, stainless steel)      | 2009–2010 (10 mo) | 2000                                      | 35.0                  | 28.4                                  | 9.5                | 30.3             | 25.0                                 | (5)        |
| cage (4–9 mm, net)                  | 2009–2010 (10 mo) | 2000                                      | 29.0                  | 22.6                                  | 9.5                | 30.0             | 24.6                                 | (5)        |
| net with floats (4 mm, site A)      | 2011–2012 (10 mo) | 1500                                      | 34.7                  | 28.1                                  | 11.6               | 29.0             | 20.9                                 | This study |
| net with floats (9 mm, site A)      | 2011–2012 (10 mo) | 1500                                      | 40.6                  | 33.9                                  | 11.6               | 26.3             | 17.6                                 | This study |
| net with floats (4 mm, site B)      | 2011–2012 (10 mo) | 1500                                      | 33.1                  | 26.5                                  | 11.6               | 30.4             | 22.6                                 | This study |
| net with floats (9 mm, site B)      | 2011–2012 (10 mo) | 1500                                      | 24.2                  | 18.2                                  | 11.6               | 27.1             | 18.6                                 | This study |

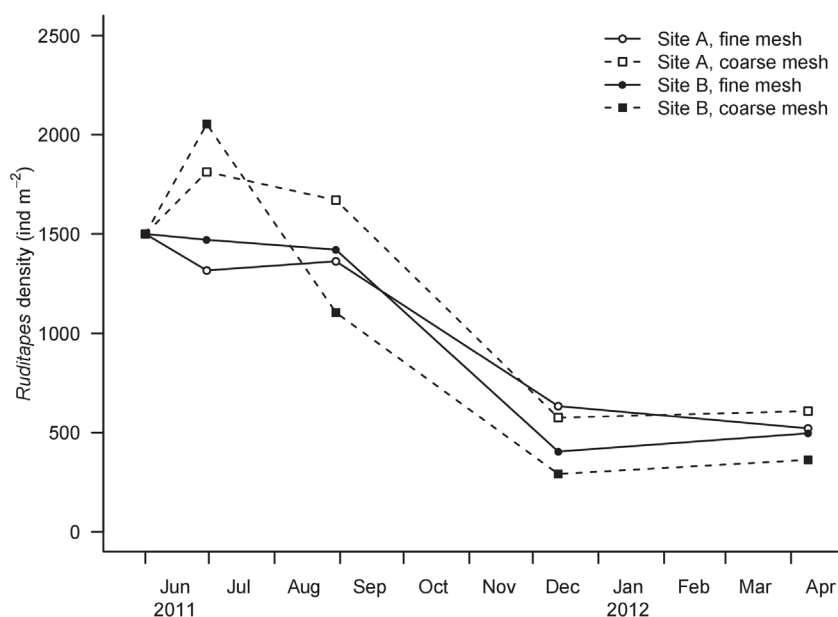




**Figure 4:** Mean shell length of *Ruditapes philippinarum* in experimental plots from June 2011 to April 2012.

of August (after 3 months) (Fig. 5). However, the density decreased from August to December and remained constant during winter; by the end of the experiment, density varied from 360 to 610 (mean = 500) individuals  $m^{-2}$ . In total, 24–41% (mean = 33%) of the initial *R. philippinarum* population survived to April 2012. Survival rates in the present study were 18.2–33.9%  $y^{-1}$  (Table 1). These values were significantly higher than those from (i) no net conditions

in 1994–1995 and (ii) wild populations from 2005 to 2007, which ranged 0.9–14.5%  $y^{-1}$  (Tukey HSD,  $P = 0.03$ ). Our rates were also significantly higher than those from previous netting experiments in which the nets were set directly onto the sand flats, which had a range of 0–12.3%  $y^{-1}$  (Tukey HSD,  $P = 0.04$ ). On the other hand, the observed survival rates were not significantly different from those in the caging experiments carried out during 2006–2010, i.e. 22.6–64.4%



**Figure 5:** Mean density of *Ruditapes philippinarum* in experimental plots from June 2011 to April 2012.



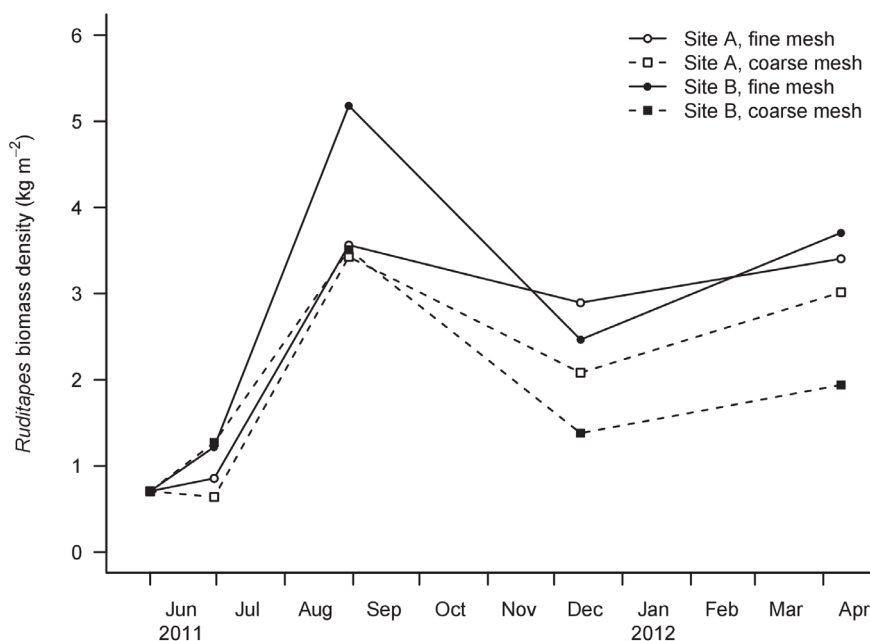
$y^{-1}$  (Tukey HSD,  $P = 0.86$ ). There was no significant difference in survivorship between sites (two-way ANOVA,  $P = 0.44$ ) or mesh sizes (two-way ANOVA,  $P = 0.87$ ).

Biomass density increased rapidly from its initial value of  $0.7 \text{ kg m}^{-2}$  and peaked at the end of August ( $3.4\text{--}5.2 \text{ kg m}^{-2}$ ), but decreased during autumn (Fig. 6). The final density range was  $1.9\text{--}3.7 \text{ kg m}^{-2}$  (mean =  $3.0 \text{ kg m}^{-2}$ ). At the end of the trial, clam biomass density was not significantly different between either the sites (two-way ANOVA,  $P = 0.67$ ) or the fine and coarse meshes (two-way ANOVA,  $P = 0.36$ ).

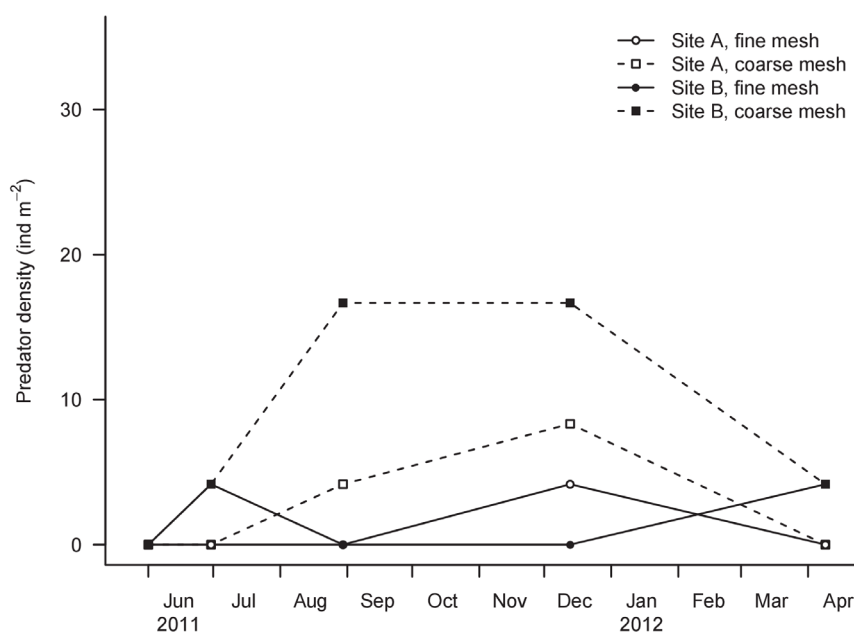
Although we did not find any predators at the beginning, predators invaded all of the plots during the experiment (Fig. 7). Predatory moon snails (*Glossaulax didyma* Röding) and the veined rapa whelk (*Rapana venosa* Valenciennes) were identified (Fig. 8); *Glossaulax didyma* and *R. venosa* comprised approximately 75% and 25% of the predator density, respectively. The mean shell diameter (height) was  $29.8 \pm 5.1 \text{ mm}$  for the moon snail and  $45.5 \pm 16.2 \text{ mm}$  for the rapa whelk. For all sampling dates combined, predator density was significantly higher at site B than at site A (two-way ANOVA,  $P < 0.05$ ) and significantly higher in the coarse than in the fine mesh (two-way ANOVA,  $P < 0.05$ ). Mean predator density (all sampling dates) was highest in the coarse-mesh plot at site B ( $10.4 \text{ individuals m}^{-2}$ ) and lowest in the fine-mesh plot at site A ( $1.0 \text{ individuals m}^{-2}$ ).

## Discussion

The *R. philippinarum* growth rate observed in this study was similar to that of other caging and netting experiments on this flat. It was also comparable to the values reported from Tokyo Bay, Japan, a known eutrophic area in which wild *R. philippinarum* spat (10 mm) grew to 30 mm in 1 year (Toba *et al.* 2007). Other researchers have reported slower growth rates for this species. On the French coast, von Bertalanffy growth-function parameters obtained for *R. philippinarum* were  $K = 0.72 \text{ y}^{-1}$  and  $L_{\infty} = 41.1 \text{ mm}$  (Dang *et al.* 2010), which correspond to 11.6-mm spat reaching 26.7 mm in one year. Ohba (1959) reported that 10-mm wild *R. philippinarum* spat grew to 20 mm in 1 year in the Seto Inland Sea, Japan. The higher growth rate reported here was unexpected as reduced phytoplankton abundances were observed in the study area. It has been reported that the mean surface Chl-*a* concentration around the flat decreased by about 25% from approximately  $4 \mu\text{g L}^{-1}$  in the 1980s to  $3 \mu\text{g L}^{-1}$  in the 1990s (Fisheries Research Agency 2005). Although it has been suggested that the recent decrease in phytoplankton abundance is one of the causes of *R. philippinarum* population decline in other regions of Japan (Tamaki *et al.* 2008), our results suggest that the abundance of food



**Figure 6:** Mean biomass density of *Ruditapes philippinarum* in experimental plots from June 2011 to April 2012.



**Figure 7:** Mean predator density in experimental plots from June 2011 to April 2012. Predator density is shown as the sum of the moon snail, *Glossaulax didyma*, and the veined rapa whelk, *Rapana venosa*. The moon snail was more abundant (75%) than the rapa whelk (25%).

resources did not inhibit clam growth during our experiment.

However, growth rates exhibit spatio-temporal variation and are affected by numerous factors. Indeed, the *R. philippinarum* growth rate in this study was faster than that previously reported for the wild clam population on this tidal flat; during 2005–2007, 2.62–11.5 mm wild clam spat grew to 18.5–25.6 mm (Table 1) (Tezuka *et al.* 2012). This difference might be due to selective predation on larger clams in the wild population. In similar vein, the hard clam, *Mercenaria mercenaria*, exhibited higher growth rates in the absence of predators (Nakaoka 2000).

Variation in growth rates may also result from differences in food supply and clam density. The mean surface Chl-*a* concentration during our experiment was approximately 25% higher than typical levels (Hara & Namimatsu 2012), while initial clam density (1500 individuals m<sup>-2</sup>) was lower than previously reported values (2140–13100 individuals m<sup>-2</sup>, Tezuka *et al.* 2012). These data suggest that the faster clam growth observed here might be a result of greater-than-average food availability and lower clam density.

The faster growth might also be attributed to the presence of netting. Increased deposition of food particles due to reduced water currents might have resulted in faster clam growth under the net (Peterson, Summerson & Duncan 1984). Microphytobenthos, an important food source for *R. philippinarum* (Dang *et al.* 2009), is generally more abundant in silty areas than in exposed sand (de Jong & de Jonge 1995), and therefore might be abundant under the nets. Slightly higher growth in the fine-mesh plot observed in this

study might have been due to an increased deposition of food particles and abundant microphytobenthos in the fine mesh. The effects of annual variation in growth, density, and netting growth require further investigation.

Clam survival rates recorded here (18.2–33.9% y<sup>-1</sup>) were higher than the values obtained under no-net conditions in previous studies (0–15% y<sup>-1</sup>) and the final biomass (1.9–3.7 kg m<sup>-2</sup>) was also higher than that reported for the natural clam population on this flat (<1.5 kg m<sup>-2</sup> biomass at 30 mm in shell length, Tezuka *et al.* 2012). Our survival data were comparable to those of previous caging experiments in this flat, in which 31.7–35% of 9.5–10.1 mm clam spat survived after 10–12 months under a 1-m<sup>2</sup> stainless-steel and net cage (Table 1) (Hirakawa, Hayashi & Egashira 2010; Katano, Egashira & Tsuru 2010).

Netting or caging has been suggested as an effective means of improving clam survival on the Nakatsu tidal flat. Higher survival under netting or caging would primarily result from predator exclusion and increased sediment stability (i.e., a lower probability of being washed out of the sediment during the stormy season from late autumn to early spring). Survival was higher when netting was used with floats, as in this study, rather than directly on the ground. Much lower survivorship, 0–12.3% y<sup>-1</sup>, was reported when nets were placed directly on the ground in this flat (Table 1) (Hayashi, Hirakawa & Nakagawa 2008; Hirakawa, Hayashi & Egashira 2010). It has been reported that raising the net a few centimeters above the sediment surface results in higher survivorship (Spencer, Edwards & Millican 1992). The use of floats with netting provides a low-cost substitute for caging



**Figure 8:** Predators observed in the study site. (a) *Rapana venosa*, and (b-d) *Glossaulax didyma*. Scale bars are 1 cm.

and is expected to result in higher survivorship than netting directly on the ground.

However, clam spat survival during this experiment was still low (24.2–40.6% survival after 10 month) compared with other studies; e.g., Cigarria & Fernández (2000) reported approximately 35–65% survival after 1 year when protected with plastic netting. Although the causes of this mortality are unclear, predation may be responsible. Given that predatory snails consume 0.5 clams per day (Rodrigues 1986, Savini & Occhipinti-Ambrogi 2006) and the snail densities of 1–10 individuals  $m^{-2}$  seen in this study, snails could have consumed 100–1000 individuals  $m^{-2}$  over 7 months (winter was excluded from this calculation). Thus, predation might have been important, particularly in the highest density plot (coarse net at site B).

Disease is also a potential cause of mortality. Although we did not focus on diseases in our experiment, a high prevalence of *Perkinsus* spp. was observed on the Nakatsu tidal flat (Hamaguchi, Sasaki & Usuki 2002), which can potentially kill clam spat (Waki *et al.* 2012). Hypoxia may also be a cause of mortality in early autumn (Senjyu *et al.* 2001), although we did not observe it during our experiment. Further study is required to determine the causes of mortality other than predation.

The effect of predation would have increased during

the *R. philippinarum* population decline on the Nakatsu tidal flat. Fishery statistics show that production in the asari and sarubo (ark) clam (*Scapharca* spp.) fisheries increased during the 1960s and 1970s, while gazami crab (*Portunus* spp.) production declined to almost zero (Fig. 1). The statistics suggest that these clam populations increased to reach the maximum carrying capacity when predation pressure was alleviated. A recent increase in the gazami crab population may maintain clam populations at lower levels. In addition to the gazami crab increase, predation by the longheaded eagle ray would have had a severe effect on clam populations in this region since its frequent appearance after the 2000s (Fukuda & Zenitani 2010; Shigeta 2008; Yamaguchi, Kawahara & Ito 2005). Fishery statistics for this species are not available; however, it has been estimated that >5000 longheaded eagle rays (>50 t cumulative weight) inhabited the Nakatsu tidal flat during summer 2007 and 2008 (Fukuda & Zenitani 2010).

The increase in mean winter seawater temperature in this region (approximately 1°C from 1973–1987 to 1988–2002) (Fisheries Research Agency 2005), might have contributed to an increase in warm-water predators such as the gazami crab and the longheaded eagle ray. The decrease in the gazami crab observed during the 1960s and 1970s might have been the result of colder water



temperatures or hypoxic conditions caused by eutrophication (Ariyama & Secor 2010; Hines *et al.* 2010).

Predatory gastropods (*Glossaulax didyma* and *Rapana venosa*) that invaded our experimental plots may be a significant cause of clam mortality in the study area, despite their relatively lower consumption rates compared with predatory crabs and eagle rays (Eggleston, Lipcius & Hines 1992; Rodrigues 1986; Sato, Chiba & Hasegawa 2012; Savini & Occhipinti-Ambrogi 2006; Usuki, Sakiyama & Yamasaki 2012). Furthermore, predation by ducks (*Anas acta* Linnaeus) may also be an important factor of clam mortality in winter on this flat. It seems likely that the *R. philippinarum* population in the Nakatsu tidal flat is under top-down control by predation and is suppressed to a lower level than its carrying capacity.

Clam culture is considered feasible on the Nakatsu tidal flat with adequate predation prevention, despite recent environmental changes. However, some improvements to our method, particularly for increasing clam survival, will be required for commercial clam culture on this flat. Given that 10-mm clam spat grew to 30 mm (7 g) and 30% survival

after 1 year at an initial density of 1500 individuals m<sup>-2</sup>, we could produce approximately 3 kg m<sup>-2</sup>. This corresponds to 2000 JPY m<sup>-2</sup> if clam prices are 650 JPY kg<sup>-1</sup>. The costs for the clam spat and the netting should not exceed this amount. However, this may be difficult if the cost of artificially reared clam spat was >1000 JPY for the 1500 clams and the cost of the netting was >1000 JPY m<sup>-2</sup>. Using wild clam spat, if available, may be cheaper. Additionally, spatio-temporal variation in the growth rate and the cause of mortality should be investigated in more detail.

## Acknowledgments

We thank Y. Shima, H. Yamasaki, K. Sakiyama, M. Ishida, A. Iwamoto, and A. Ito for help with fieldwork. This study was financially supported in part by the Fisheries Agency of Japan.

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Published: 18 December 2014

## ••• Editor's note •••

Despite the lack of no-net controls and replications, our reviewers and the Editor believe that the paper contains potentially useful information on a commercially important bivalve species, *Ruditapes philippinarum*.