

Seasonality in the strength and spatial scale of processes determining intertidal barnacle population growth

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Summary

1. Population growth rate is determined by both density-dependent and density-independent processes. In the temperate zone, the strength and spatial scale of these processes are likely to differ seasonally, but such differences have rarely been quantitatively examined.

2. Coverage, the area occupied by organisms, is a measure of resource use in sessile marine populations. Population models used for density-based studies should be able to characterize effectively fluctuations in coverage, but few have tried to apply such models to sessile populations.

3. We observed coverage of the intertidal barnacle *Chthamalus challenger* at 20 plots on four shores along the Pacific coast of Japan over 8 years. We then fitted a population model that incorporated both a density-dependent process (strength of density dependence) and density-independent processes (intrinsic growth rate and stochastic fluctuation at different spatial scales) to these data to analyse the seasonal variation of these processes and answer the following two questions: (i) How do the effects of density-dependent and density-independent processes on population growth vary seasonally? (ii) At what spatial scale, regional (tens of kilometres), shore (hundreds of metres), or rock (tens of centimetres), does density-independent stochastic fluctuation most strongly affect population size changes?

4. Barnacle population size tended to decrease in summer, when population dynamics were characterized by a relatively lower intrinsic growth rate, weaker density dependence and stronger stochastic fluctuation. In contrast, population size tended to increase in winter, reflecting a higher intrinsic growth rate, strong density dependence and weak stochastic fluctuation.

5. In summer, population growth rate was strongly affected by regional-scale stochastic fluctuation, whereas in winter it was affected more by rock-scale stochastic fluctuation, suggesting that populations were strongly affected by regional-scale processes in summer but not in winter.

6. These results indicate that seasonally variable density-dependent and density-independent processes determine the population dynamics of *C. challenger*. Therefore, to understand fluctuation patterns of populations of this species, seasonality should be taken into account. Moreover, this study demonstrates that population models commonly used for density-based studies are also applicable to coverage-based population studies.

Key-words: cover, density dependence, intertidal rocky shore, population synchrony, recruitment, seasonal variability, state-space model, thermal stress

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Introduction

A central goal of population studies is to understand how population dynamics are determined by density-dependent and density-independent processes (Royama 1992; Turchin 1999, 2003). Density dependence, that is, the functional relationship between the per capita rate of population change and population density (Turchin 2003), can result from resource competition (Royama 1992; Rodenhouse *et al.* 2003; Sillett, Rodenhouse & Holmes 2004), predation (Gaines & Roughgarden 1985; Hixon & Carr 1997), or site-dependent regulation due to interactions between heterogeneity of habitat quality and habitat selection by individuals (Rodenhouse, Sherry & Holmes 1997; McPeck *et al.* 2001; Rodenhouse *et al.* 2003). Density-independent processes, such as climate (Forchhammer *et al.* 1998; Lima & Jaksic 1998; Sæther *et al.* 2008; Tyler, Forchhammer & Øritsland 2008), habitat heterogeneity (Wang *et al.* 2006) and food availability (Saitoh *et al.* 2008), can operate at different spatiotemporal scales. Density-independent processes can affect population dynamics directly (Forchhammer *et al.* 1998; Sæther *et al.* 2008), or indirectly by altering density-dependent processes (Wang *et al.* 2006), or both (Saitoh *et al.* 2008; Tyler, Forchhammer & Øritsland 2008).

Two aspects of the spatiotemporal variation of density-dependent and density-independent processes are not well understood: (i) their seasonal variation and the effect of that variation on population change and (ii) the spatial scales at which the various processes operate. Except in the tropical zone, seasonal variation of environmental factors and processes is common in both terrestrial and shallow-marine systems. Therefore, it is likely that population dynamics of organisms in such habitats is determined by seasonally different density-dependent and density-independent processes. However, the seasonality of these processes has been studied in only a few taxa, such as voles (Turchin & Ostfeld 1997; Hansen, Stenseth & Henttonen 1999; Saitoh *et al.* 2003; Stenseth *et al.* 2003). Examination of the spatial scale of population synchrony should provide insight into large-scale processes, such as climate fluctuation and dispersal of individuals, which can impact spatially distinct populations simultaneously at spatial scales corresponding to those of the responsible processes (Bjørnstad, Ims & Lambin 1999; Koenig 1999).

In the case of sessile marine organisms such as corals, mussels, barnacles, ascidians and algae, population size is often recorded as coverage, the area occupied by the organisms, because individuals compete for space, which thus functions as a resource (Menge 2000; Tanner, Hughes & Connell 2009). Coverage is determined by the density and body size of individuals (Roughgarden, Iwasa & Baxter 1985), and changes in coverage are thus affected by recruitment, body growth and mortality of individuals (Roughgarden, Iwasa & Baxter 1985; Petraitis 1995). Coverage changes are likely to be 'coverage-dependent' because recruitment density (Gaines & Roughgarden 1985;

Navarrete & Castilla 1990; Connell, Hughes & Wallace 1997; Dunstan & Johnson 1998; Kent, Hawkins & Doncaster 2003) and post-recruitment growth and mortality (Bertness & Grosholz 1985; Gaines & Roughgarden 1985; Bertness 1989; Reed 1990; Sanford *et al.* 1994; Dunstan & Johnson 1998) are often negatively correlated with coverage. Therefore, coverage fluctuations should be well described by density-dependent population models, which are commonly used in density-based studies. Although coverage data are readily available for sessile marine species (e.g. Sutherland 1990; Burrows, Moore & James 2002; Tanner, Hughes & Connell 2009), coverage fluctuations have rarely been analysed with density-dependent population models (but see Tanner, Hughes & Connell 2009). In this study, we use 'density-dependent' and 'density-independent' to mean 'coverage-dependent' and 'coverage-independent', respectively (Tanner, Hughes & Connell 2009).

During their early life stage, planktonic larvae of intertidal barnacles disperse for several weeks and then settle on substrata. Their settlement rate and post-settlement growth and survival rates can be affected by both density-dependent and density-independent processes. Pre-emption of settlement space by adults often reduces the settlement rate of larvae (Raimondi 1990; Sutherland 1990; Kent, Hawkins & Doncaster 2003), and intraspecific competition often reduces survival rate of adults (Connell 1961; Bertness 1989; Sanford *et al.* 1994; Menge 2000), suggesting that the population dynamics of these barnacles is density-dependent. Their settlement, growth and survival rates also vary seasonally (Raimondi 1990; Sanford *et al.* 1994; Miyamoto, Noda & Nakao 1999) and spatially, depending on oceanographic processes (Pineda 1991; Sanford & Menge 2001; Pineda, Hare & Sponaugle 2007), hydrodynamic conditions (Sanford *et al.* 1994; Leonard *et al.* 1998; Sanford & Menge 2001; Larsson & Jonsson 2006) and local thermal conditions (Bertness 1989; Bertness *et al.* 1991; Sanford *et al.* 1994; Noda *et al.* 2000). Also, their population growth rates are sometimes synchronized over large spatial scales (e.g. Dye 1998; Burrows, Moore & James 2002).

The acorn barnacle *Chthamalus challengerii* Hoek is the dominant sessile animal in the mid to high intertidal zone along the shores of northern Japan (Nakaoka *et al.* 2006). From 2002 to 2009, we conducted a survey of 20 permanent plots on four shores along the Pacific coast of northern Japan. To examine how the population dynamics of *C. challengerii* reflects interactions between density-dependent and density-independent processes, we statistically modelled coverage data of this species, which we characterized by several parameters such as strength of density dependence, intrinsic growth rate and stochastic fluctuation at different spatial scales. We addressed the following two questions: (i) How do the effects of density-dependent and density-independent processes on population growth vary seasonally? (ii) At what spatial scales do density-independent stochastic fluctuations strongly affect population changes?

Materials and methods

CENSUS DESIGN

We used a hierarchical sampling design (Noda 2004b) to examine spatial patterns of *C. challenger* population dynamics. We chose four shores (Myojin, 39°28' N, 142°00' E; Aragami, 39°24' N, 141°58' E; Akahama, 39°21' N, 141°56' E; and Katagishi, 39°20' N, 141°54' E) situated between 2.6 and 7.9 km apart along the Pacific coast of northern Japan (Fig. 1). Within each shore, we haphazardly established five 5000-cm² census plots on the rock walls in semi-exposed locations, with distances between neighbouring plots ranging from 7.8 to 209 m (mean \pm SD, 59.2 \pm 70.3 m). Each plot was 50 cm wide by 100 cm high (this vertical dimension was chosen to approximately correspond to the vertical range of *C. challenger* distribution in this region; Kado 2003), and the mean tidal level corresponded to the vertical midpoint. The midpoints and corners of all plots were permanently marked by insertion of plastic or stainless steel anchors into the rock. We defined three spatial scales corresponding to the three hierarchical levels of the census design: regional scale, corresponding to the entire study area (i.e. tens of kilometres); shore scale, within a single shore (hundreds of metres); and rock scale, a single census plot (tens of centimetres).

Coverage of *C. challenger* was measured at each plot twice a year, in April or May (spring) and in October or November (autumn), from autumn 2002 to spring 2009, except spring 2008. All measurements were made at low tide. The coverage of the entire plot was estimated by a point sampling method in which the occurrence of *C. challenger* at 200 points on a grid with 5-cm intervals in both vertical and horizontal directions was recorded. *C. challenger* was rare (temporal average coverage < 4%) in two plots at Aragami and in one at Akahama; therefore, these three plots were excluded from analysis. We defined the period between the spring and autumn censuses as summer and that between the autumn and spring censuses as winter.

In the study region, phytoplankton blooms occur during winter, peaking between February and April (Furuya, Takahashi & Iizumi 1993). The low spring tide occurs during the day from late March to early September and during the night from late September to early March (Japan Meteorological Agency, <http://www.data.kishou.go.jp/db/tide/suisan/>). Recruitment of *C. challenger* occurs mainly between May and November (R. Kado, pers. comm.). Predators of

barnacles such as whelks and starfish were rarely found at any of the plots throughout the census period (Fukaya *et al.*, data not shown).

DATA ANALYSIS

Statistical modelling of population dynamics

We applied a state-space model, composed of a process model representing the underlying population dynamics and a data model incorporating observation error. This model is able to separate process error in the population dynamics from observation error, and it can accommodate missing data (Clark & Bjornstad 2004; Clark 2007). In the process model, the population growth rate of *C. challenger* was decomposed into several density-dependent or density-independent components. The density-dependent component included in the model was the strength of the density dependence (the change in the population growth rate in relation to the population size). The density-independent components were the intrinsic growth rate (the temporally averaged density-independent growth rate) and the density-independent stochastic fluctuations of growth rate at regional, shore and rock scales. The process model comprised three levels, each modelled using a different equation, representing the rock, shore and regional levels. Population dynamics of *C. challenger* in each plot was modelled at the rock level; spatial variability in intrinsic growth rate and the strength of density dependence within each shore were modelled at the shore level; and the spatial variation in intrinsic growth rate and strength of density dependence among shores were modelled at the regional level. In the data model, frequency of *C. challenger* in each plot was assumed to follow a binomial distribution.

Data model. Given population size (cm² coverage) $A_{t,j,i}$ at plot i on shore j and census date t , the observed number of points occupied by *C. challenger* in plot i on shore j at census date t , $y_{t,j,i}$, was assumed to follow a binomial distribution (BIN) in which the occurrence probability is the proportional coverage of the *C. challenger* population, that is, $A_{t,j,i}$ divided by 5000 (= the total plot area in cm²), and the number of trials is equal to the number of census points (i.e. 200):

$$y_{t,j,i} \sim \text{BIN}(200, A_{t,j,i}/5000). \quad \text{eqn 1}$$

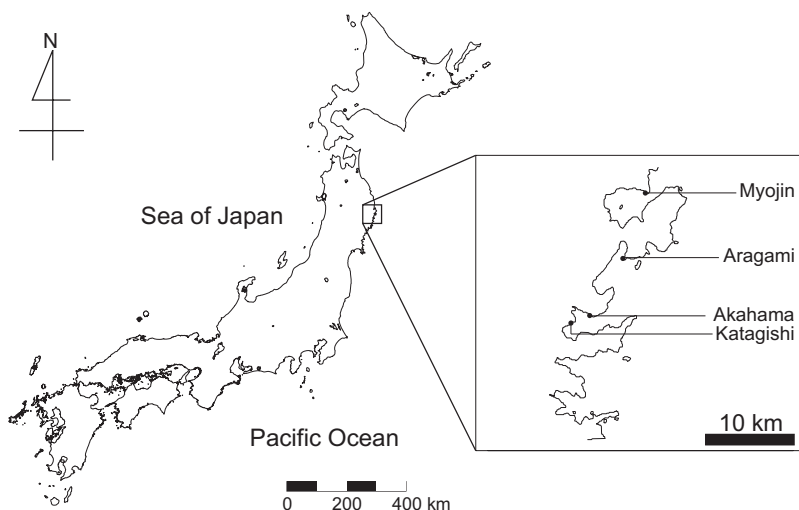


Fig. 1. Study site locations. Four shores (solid circles) were chosen along the Pacific coast of northern Japan.

Process model. The Gompertz population model (Royama 1992; Turchin 2003), which does not include any time-lag, was applied at the rock level, because at this level the population growth rate was linearly related to the logarithm of population size (Fukaya, unpublished results). The log of population size is described as follows:

$$\ln(A_{t,j,i}) = r_{s,j,i} + (1 - \alpha_{s,j,i}) \ln(A_{t-1,j,i}) + \theta_{t-1} + \omega_{t-1,j} + \varepsilon_{t-1,j,i} \quad \text{eqn 2a}$$

$$\theta_t \sim N(0, \sigma_{\text{region } s}^2) \quad \text{eqn 2b}$$

$$\omega_{t,j} \sim N(0, \sigma_{\text{shore } s}^2) \quad \text{eqn 2c}$$

$$\varepsilon_{t,j,i} \sim N(0, \sigma_{\text{rock } s}^2), \quad \text{eqn 2d}$$

where $r_{s,j,i}$ and $\alpha_{s,j,i}$ are respectively the intrinsic growth rate and strength of density dependence in plot i on shore j in season s , corresponding to the period between census date $t - 1$ and t (i.e. summer or winter). θ_{t-1} , $\omega_{t-1,j}$ and $\varepsilon_{t-1,j,i}$ represent the normally distributed (N), density-independent stochastic fluctuations of growth rate between time $t - 1$ and t at the regional, shore and rock scale, respectively, centred around the mean model $[r_{s,j,i} + (1 - \alpha_{s,j,i}) \ln(A_{t-1,j,i})]$. The terms $\sigma_{\text{region } s}^2$, $\sigma_{\text{shore } s}^2$ and $\sigma_{\text{rock } s}^2$ represent the variances of θ_t , $\omega_{t,j}$ and $\varepsilon_{t,j,i}$, respectively, in season s . At the shore level, the intrinsic growth rate and strength of density dependence on shore j were assumed to have a multivariate normal distribution (MN):

$$\begin{pmatrix} r_{s,j,i} \\ \alpha_{s,j,i} \end{pmatrix} \sim \text{MN} \left(\begin{pmatrix} \gamma_{s,j}^{(r)} \\ \gamma_{s,j}^{(\alpha)} \end{pmatrix}, \Sigma_{\text{shore}} \right) \quad \text{eqn 3a}$$

$$\Sigma_{\text{shore}} = \begin{pmatrix} \text{Var}(r) & \text{Cov}(r, \alpha) \\ \text{Cov}(r, \alpha) & \text{Var}(\alpha) \end{pmatrix}, \quad \text{eqn 3b}$$

where $\gamma_{s,j}^{(r)}$ and $\gamma_{s,j}^{(\alpha)}$ denote the average of $r_{s,j,i}$ and $\alpha_{s,j,i}$, respectively, in season s on shore j , and Σ_{shore} denotes the covariance matrix of $r_{s,j,i}$ and $\alpha_{s,j,i}$. $\text{Var}(r)$ and $\text{Var}(\alpha)$ denote the variance of $r_{s,j,i}$ and $\alpha_{s,j,i}$, respectively, and $\text{Cov}(r, \alpha)$ denotes the covariance of $r_{s,j,i}$ and $\alpha_{s,j,i}$ within each shore.

In the regional-level equation, shore averages of intrinsic growth rate $[\gamma_{s,j}^{(r)}]$ and strength of density dependence $[\gamma_{s,j}^{(\alpha)}]$ were assumed to have a multivariate normal distribution:

$$\begin{pmatrix} \gamma_{s,j}^{(r)} \\ \gamma_{s,j}^{(\alpha)} \end{pmatrix} \sim \text{MN} \left(\begin{pmatrix} \mu_s^{(r)} \\ \mu_s^{(\alpha)} \end{pmatrix}, \Sigma_{\text{region}} \right) \quad \text{eqn 4a}$$

$$\Sigma_{\text{region}} = \begin{pmatrix} \text{Var}(\gamma^{(r)}) & \text{Cov}(\gamma^{(r)}, \gamma^{(\alpha)}) \\ \text{Cov}(\gamma^{(r)}, \gamma^{(\alpha)}) & \text{Var}(\gamma^{(\alpha)}) \end{pmatrix}, \quad \text{eqn 4b}$$

where $\mu_s^{(r)}$ and $\mu_s^{(\alpha)}$ respectively denote the regional average of intrinsic growth rate and strength of density dependence in season s . Σ_{region} denotes the covariance matrix of $\gamma_{s,j}^{(r)}$ and $\gamma_{s,j}^{(\alpha)}$. $\text{Var}(\gamma^{(r)})$ and $\text{Var}(\gamma^{(\alpha)})$ denote the variance of $\gamma_{s,j}^{(r)}$ and $\gamma_{s,j}^{(\alpha)}$, respectively, and $\text{Cov}(\gamma^{(r)}, \gamma^{(\alpha)})$ denotes the covariance of $\gamma_{s,j}^{(r)}$ and $\gamma_{s,j}^{(\alpha)}$.

Regional averages were modelled as follows:

$$\mu_{\text{winter}}^{(r)} = \mu_{\text{summer}}^{(r)} + \delta^{(r)} \quad \text{eqn 5a}$$

$$\mu_{\text{winter}}^{(\alpha)} = \mu_{\text{summer}}^{(\alpha)} + \delta^{(\alpha)}, \quad \text{eqn 5b}$$

where $\delta^{(r)}$ and $\delta^{(\alpha)}$ represent the seasonal differences in the regional average of intrinsic growth rate and strength of density dependence, respectively.

Shore and regional averages of seasonal population growth rate, correlation between r and α at each spatial scale, sum total of stochastic variance ($\sigma_{\text{total } s}^2$) and its seasonal difference, and relative strength of stochastic fluctuation at each spatial scale were also examined. Expressions of these parameters are shown in Appendix S1.

Parameter estimation and posterior assessment of model fit

We used independent and uninformative prior distributions for the parameters. Priors for $\sigma_{\text{region } s}^2$, $\sigma_{\text{shore } s}^2$ and $\sigma_{\text{rock } s}^2$ in eqn (1) were specified as the uniform distribution (U), $U(0, 100)$. Priors for Σ_{shore} and Σ_{region} in eqns (3) and (4) were specified as the inverse Wishart distribution (IW), $IW(\mathbf{R}, 2)$ where \mathbf{R} is a diagonal matrix in which all diagonal elements are 0.000001. Priors for μ and δ in eqn (5) were specified as the normal distribution (N), $N(0, 1\ 000\ 000)$.

The model was fitted to the data by the Markov chain Monte Carlo (MCMC) method in WinBUGS (Spiegelhalter *et al.* 2003). To confirm independence of the posterior probability on initial values, three independent iterations were executed. Estimates were obtained from 1 000 000 iterations after a burn-in of 10 000 iterations, thinning at intervals of 1000. The Bugs code of the model is given in Appendix S2.

Convergence of the posterior distribution was assessed by an autocorrelation function of each parameter and the R -statistic (Gelman *et al.* 2004). Goodness-of-fit was evaluated by posterior predictive assessment using the chi-squared discrepancy (Gelman, Meng & Stern 1996; Gelman *et al.* 2004).

Results

The posterior distribution adequately converged. Autocorrelation of the posterior sample of almost all parameters was significant only within five adjacent samples, except for several parameters related to intrinsic growth rate and density dependence in summer; autocorrelation of these parameters was significant within 10–30 adjacent samples. For all model parameters, the R -statistic was < 1.2 . The chi-squared discrepancy was not significant ($P = 0.328$), indicating that the model was consistent with the observed data.

Temporal fluctuations in coverage at the four shores are shown in Fig. 2, and the distributions of the estimated population growth rate in each plot $[\log(A_{t,j,i}) - \log(A_{t-1,j,i})]$ are shown in Fig. 3a. Populations of *C. challenger* tended to decrease in summer and to increase in winter: the shore and regional averages of the growth rate were significantly negative in summer but positive in winter (Fig. 3b,c).

The effects of density-dependent and density-independent processes on the population growth rate also differed seasonally. The regional average of the intrinsic growth rate was 2.147 in summer and 4.794 in winter, and the 95% credible interval of seasonal difference did not include zero (Fig. 4a), indicating that intrinsic growth rate was significantly lower in summer than in winter. The regional average of strength of density dependence was 0.378 in summer, but 0.723 in winter, indicating that density dependence was weaker in summer than in winter, although the lower end of the 95% credible interval of seasonal difference was slightly less than zero (Fig. 4b). Regional-scale and shore-scale correlation

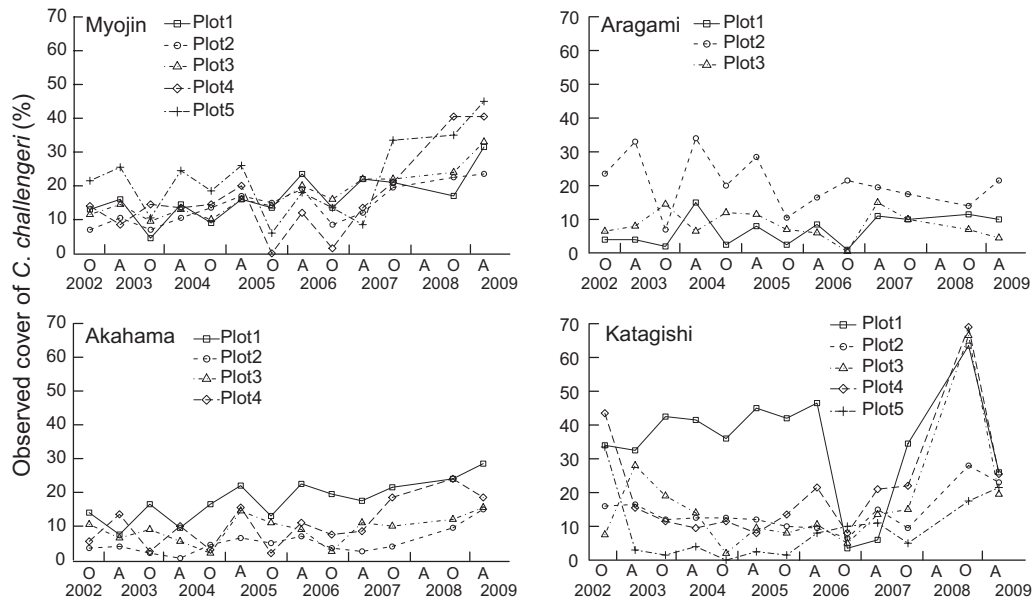


Fig. 2. Temporal fluctuations in coverage of *Chthamalus challengerii* in each plot at (a) Myojin, (b) Aragami, (c) Akahama and (d) Katagishi. For each shore, different symbols are used for different plots. Censuses were conducted twice a year, April or May (A) and October or November (O). Data from two plots at Aragami and one plot at Akahama were excluded because of low frequency of *C. challengerii* in those plots (see Census design).

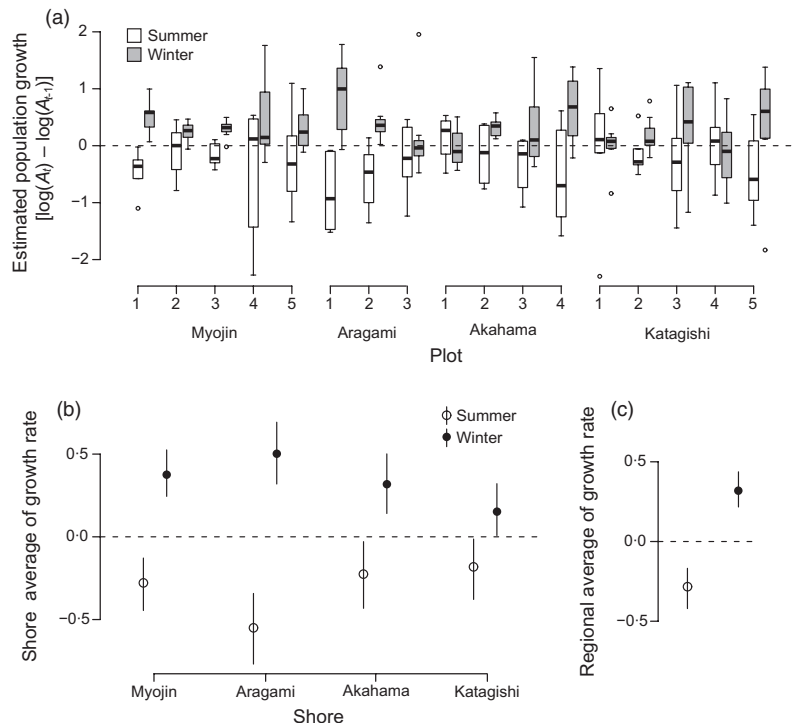


Fig. 3. (a) Distribution of seasonal population growth rate of *Chthamalus challengerii* in each plot. Population growth was estimated as the posterior median of $\log(A_t) - \log(A_{t-1})$. Box-and-whisker plots show the median (horizontal bold line inside the box), interquartile range (box), range (whiskers) and outliers (circles). Data from two plots at Aragami and one plot at Akahama were excluded because of low frequency of *C. challengerii* in those plots (see Census design). (b) Shore average of seasonal growth rate. (c) Regional average of seasonal growth rate. In (b) and (c), open and solid circles show the posterior medians, and the bar represents the 95% credible interval of the posterior distribution.

coefficients were 0.230 and 0.257, respectively, suggesting that intrinsic growth rate and strength of density dependence were positively correlated, although these estimates include

large uncertainty (i.e. broad credible intervals) (Table 1). Total variance of the stochastic fluctuation was 0.827 in summer and 0.207 in winter, and the 95% credible interval of

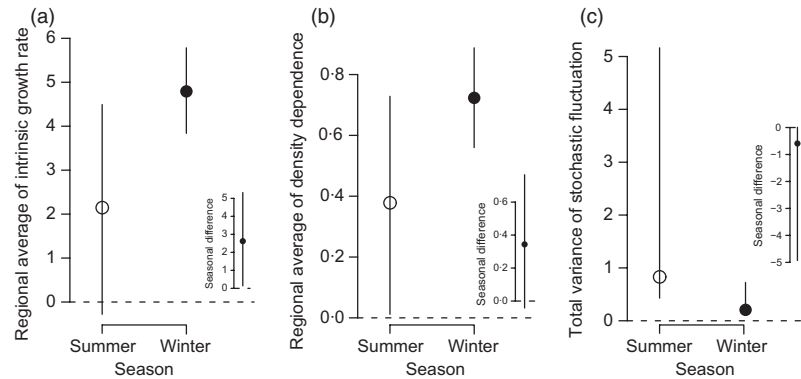


Fig. 4. (a) Regional average of intrinsic growth rate [$\mu^{(r)}_s$] and its seasonal difference [$\delta^{(r)}$]. (b) Regional average of strength of density dependence [$\mu^{(\alpha)}_s$] and its seasonal difference [$\delta^{(\alpha)}$]. (c) Total variance of stochastic fluctuation ($\sigma^2_{\text{total } s}$) and its seasonal difference ($\sigma^2_{\text{total winter}} - \sigma^2_{\text{total summer}}$). Open and solid circles represent posterior medians and bars represent the 95% credible interval of the posterior distribution.

Table 1. Posterior distributions of some examined parameters (excluding those shown in figures). Values at each plot of intrinsic growth rate and strength of density dependence ($r_{s,j,i}$ and $\alpha_{s,j,i}$), and stochastic fluctuation at shore and rock scale ($\omega_{t,j}$, $e_{t,j,i}$) are omitted. Bold values and values in brackets are the posterior median and the 95% credible interval, respectively

Parameters	Season	
	Summer	Winter
Intrinsic growth rate (r)		
Regional-scale spatial variance*	0.009 [0.002, 0.229]	
Shore-scale spatial variance*	0.009 [0.002, 0.449]	
Strength of density dependence (α)		
Regional-scale spatial variance*	0.003 [0.001, 0.015]	
Shore-scale spatial variance*	0.003 [0.001, 0.013]	
Spatial correlation of r and α		
Regional-scale covariance*	0.001 [-0.004, 0.042]	
Shore-scale covariance*	0.001 [-0.002, 0.071]	
Regional-scale correlation coefficient*	0.230 [-0.659, 0.910]	
Shore-scale correlation coefficient*	0.257 [-0.554, 0.921]	
Variance of stochastic fluctuation		
Regional scale	0.389 [0.065, 0.470]	0.036 [0.001, 0.528]
Shore scale	0.029 [0.001, 0.171]	0.033 [0.002, 0.127]
Rock scale	0.364 [0.238, 0.552]	0.121 [0.075, 0.190]

*Parameter values assumed to be identical in both seasons.

the seasonal difference did not include zero (Fig. 4c), indicating that the effect of stochastic variations was significantly stronger in summer than in winter. The larger total variance of stochastic fluctuation in summer was due to increases in regional-scale and rock-scale variance. Regional-scale variance in summer (0.389) was 11 times that in winter (0.036), and rock-scale variance in summer (0.364) was three times that in winter (0.121); however, seasonal variation in shore-scale variance was small (Table 1).

Spatial scale of influential density-independent fluctuation also differed seasonally (Fig. 5). Rock-scale fluctuation was relatively influential in both seasons; in particular, it was the most important scale of stochastic fluctuation in winter. Shore-scale fluctuation was not important in either season. Relative strength of regional-scale fluctuation was seasonally variable: it was large and the most influential scale of stochastic fluctuation in summer, whereas it was much less

important in winter. This result indicates that population dynamics in summer was strongly influenced by regional-scale stochasticity whereas rock-scale fluctuation was more important in winter. Estimated regional stochastic fluctuation (θ_r) is shown in Fig. 6. As suggested by the seasonal difference in variance of regional fluctuation (Table 1), θ_r tended to be more variable in summer than in winter. In the summers of 2005 and 2006, populations of *C. challenger* decreased regionally, whereas they increased regionally in the summers of 2007 and 2008.

Discussion

Our results highlight several aspects of the spatiotemporal variation of density-dependent and density-independent processes in *C. challenger* population dynamics. Population dynamics was determined differently, depending on the sea-

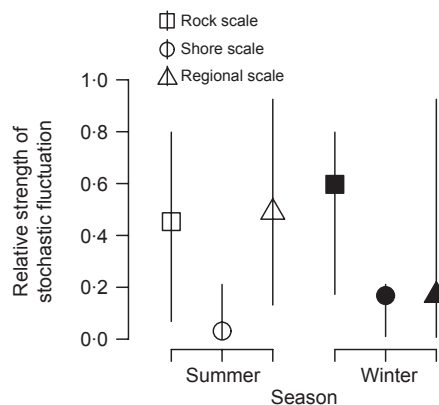


Fig. 5. Seasonal variation in the relative strength of stochastic fluctuation at each spatial scale. Posterior medians of the relative strength at rock scale, shore scale and regional scale are represented as squares, circles and triangles, respectively. Bars represent the 95% credible interval of the posterior distribution.

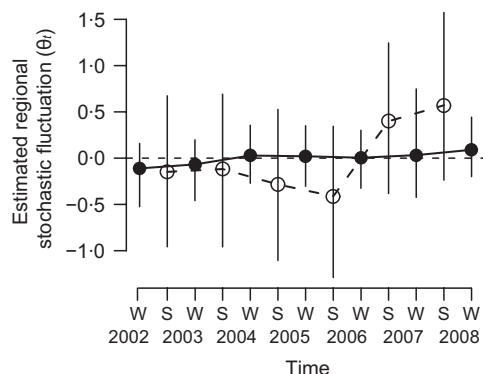


Fig. 6. Time series of estimated regional fluctuation (θ_t). Black circles and solid line represent the posterior median of the regional fluctuation in winter. Open circles and broken line represent the posterior median of the regional fluctuation in summer. Bars represent the 95% credible interval of the posterior distribution.

son. In summer, when coverage decreased, population growth rate reflected a lower intrinsic growth rate, weaker density dependence and large stochastic fluctuation. In winter, when coverage increased, population growth rate reflected a higher intrinsic growth rate, stronger density dependence and small stochastic variation. Spatial scale of influential density-independent fluctuation also differed seasonally. The most influential stochastic fluctuation was at the regional scale in summer but at the rock scale in winter. These results suggest that seasonally different density-dependent and density-independent processes determine the population dynamics of *C. challenger*.

Seasonal variation in strength of density dependence may result from two, not mutually exclusive, mechanisms. First, density dependence may vary seasonally because its strength depends on intrinsic growth rate. In sessile marine populations, increases in recruitment intensity and body growth rate can lead to direct contact between individuals,

thus inducing density-dependent mortality (Connell 1961; Roughgarden, Iwasa & Baxter 1985; Bertness 1989; Sanford *et al.* 1994; Dunstan & Johnson 1998). Thus, a higher intrinsic growth rate can result in strong density dependence in sessile populations. Our results indicated that strength of density dependence and intrinsic growth rate were positively correlated both seasonally and spatially, which supports the inference that strength of density dependence is a function of intrinsic growth rate. Secondly, facilitative (inversely density-dependent) interaction is likely to weaken density dependence in summer. It is known that when thermal and desiccation stress is high, aggregation of individual barnacles can increase survivorship by reducing thermal and desiccation stress (Lively & Raimondi 1987; Bertness 1989).

Seasonal variation in intrinsic growth rate might result from seasonal differences in body growth and survival rates. Lower body growth and survival rates caused by strong thermal stress in summer may lead to a lower intrinsic growth rate in that season. Heat and desiccation stress decrease barnacle body growth and survival rates (e.g. Lively & Raimondi 1987; Bertness 1989; Sanford *et al.* 1994). In our study area, daily maximum temperature on rock surfaces at mean tidal level from July to September sometimes exceeds 40 °C (Fukaya *et al.*, data not shown). In the barnacle *Semibalanus balanoides* Linnaeus, a New England species with a midtidal zone habitat, this temperature is the maximum at which survival is possible (Bertness 1989). Mortality in our study area is therefore probably high in summer, causing the observed decreasing tendency of the population, even though recruitment occurs mainly in this season. In winter, the observed higher intrinsic growth rate may be due to higher body growth and survival rates in that season. In this region, phytoplankton blooms occur from February to April (Furuya, Takahashi & Iizumi 1993), suggesting that food availability for *C. challenger* is enhanced during those months (Bertness *et al.* 1991; Sanford & Menge 2001). Higher population growth rate in winter suggests body growth processes dominates in this season.

Population synchrony is caused by the dispersal of conspecific individuals and of interacting species such as predators, and by spatially correlated environmental forcing, that is, the Moran effect (Bjørnstad, Ims & Lambin 1999; Koenig 1999). Dispersal of barnacle larvae is often synchronized (Noda 2004a; Lagos *et al.* 2007), and the spatial scale of synchronization can be tens or hundreds of kilometres (Lagos *et al.* 2007; Broitman *et al.* 2008; Navarrete, Broitman & Menge 2008). Thus, synchronized recruitment is likely to cause synchronization of barnacle population growth (Dye 1998; Burrows, Moore & James 2002). However, in the case of *C. challenger* in this region, dispersal is probably not the cause of synchrony; rather, environmental forcing is more likely to cause regional fluctuation. In Appendix S3, we show scatter plots of estimated regional fluctuation (θ_t) in summer in relation to recruitment intensity, which was measured as coverage of recruits in a cleared plot next to each census plot. Estimates of θ_t and the regional average recruitment intensity in summer were not correlated ($r = 0.36$, $P = 0.557$;

Fig. S3a). By contrast, θ_t was negatively correlated with average maximum air temperature in June ($r = -0.91$, $P = 0.01$; Fig. S3b), recorded by the Automated Meteorological Data Acquisition System (AMeDAS) of the Japan Meteorological Agency in the study region (at Yamada, 39°27' N, 141°57' E, and at Kamaishi, 39°16' N, 141°53' E). Given that summer is the season of decreasing coverage, it is likely that regional synchrony was caused by synchronized mortality induced by strong thermal stress experienced at low tide (Lively & Raimondi 1987; Bertness 1989; Sanford *et al.* 1994). Predators of barnacles such as whelks and starfish were probably not the cause of the synchrony because they were rarely found at any plot during the census period (Fukaya *et al.*, data not shown).

Because marine benthic populations tend to be open, recruitment processes are often more important than post-recruitment processes for determination of population structure and dynamics. Population dynamics is mainly determined by fluctuation of recruitment intensity when recruitment is limited, whereas density-dependent processes determine local population abundance when recruitment is sufficient (Gaines & Roughgarden 1985; Caley *et al.* 1996; Menge 2000). In the case of barnacle populations, several studies have reported the importance of recruitment variability (e.g. Gaines & Roughgarden 1985; Roughgarden, Iwasa & Baxter 1985; Sutherland 1990; Noda 2004a; Navarrete, Broitman & Menge 2008), and patterns of the *C. challenger* distribution in southern Hokkaido, 300 km north of the study region, are also determined by recruitment (Miyamoto, Noda & Nakao 1999). Our results suggest, however, that coverage of *C. challenger* in the study region was mainly determined by post-recruitment processes throughout the year. In summer, the main recruitment season, population growth rate and intrinsic growth rate were lower than in winter despite the potential supply of new individuals. In addition, population growth rate was correlated with thermal stress rather than with recruitment intensity (Appendix S3), suggesting the potential importance of desiccation-induced mortality of adults in this season. In winter, population fluctuation was density-dependent, suggesting that recruitment is not limited in these populations and that density-dependent growth or mortality, or both, controls population growth in this season.

Examining effects of seasonal and scale-related variation in density-dependent and density-independent processes is important for understanding and predicting population dynamics. In this study, we revealed prominent seasonal variation in strength and spatial scales of density-dependent and density-independent processes, by using seasonal hierarchical sampling and a statistical approach in which seasonal and spatial scale-dependent variation of population growth was estimated with sampling error taken into account. Although we focused on population dynamics of a sessile organism, for which population size was measured by coverage, similar sampling and analytical approaches are effective for studies of mobile animals where population size is measured by density.

Conclusions

Because recruitment (Raimondi 1990; Sutherland 1990; Kent, Hawkins & Doncaster 2003), growth (Wetthey 1983; Roughgarden, Iwasa & Baxter 1985; Bertness, Gaines & Yeh 1998) and survival rates (Connell 1961; Bertness 1989; Sanford *et al.* 1994; Menge 2000) often depend on coverage, fluctuations of marine sessile species coverage are likely in general to be related to coverage itself. However, few studies have tested this hypothesis. Our study demonstrated that changes in coverage can be successfully quantified by applying a density-dependent population model in which population dynamics are characterized by intrinsic growth rate, strength of density dependence and density-independent stochastic fluctuation at multiple spatial scales. This result suggests that analysis of a coverage time-series data set of a sessile marine population under different conditions can provide new insight into the processes and mechanisms underlying population fluctuation. For example, under sufficient recruitment, density-dependent mortality should strongly influence population fluctuations (Gaines & Roughgarden 1985; Roughgarden, Iwasa & Baxter 1985; Bertness 1989; Bertness, Gaines & Yeh 1998), but environmental stochasticity should remain important for population dynamics, as reported in this study. On the other hand, in recruitment-limited populations, density-dependent mortality does not occur but the population growth of such populations can still be density-dependent as long as recruitment depends on density (Caley *et al.* 1996), a phenomenon that has been frequently observed (Gaines & Roughgarden 1985; Navarrete & Castilla 1990; Reed 1990; Connell, Hughes & Wallace 1997; Dunstan & Johnson 1998; Kent, Hawkins & Doncaster 2003). Thus, in a recruitment-limited population, coverage change should be determined mostly by stochastic components, but density-dependent components should also be important reflecting density-dependent recruitment. Applying density-dependent population models to coverage time-series data will provide tests of these predictions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Summary of parameters calculated from the posterior probabilities of the model parameters.

Appendix S2. BUGS code of fitted model.

Appendix S3. Correlations between regional stochasticity (θ_i) in summer and recruitment intensity, and between regional stochasticity and air temperature.

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