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Title

Patterns and processes of population dynamics with fluctuating habitat size: a case study of a marine copepod inhabiting tide pools

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Abstract

The logistic model is a fundamental population model often used as the basis for analyzing wildlife population dynamics. In the classic logistic model, however, population dynamics may be difficult to characterize if habitat size is temporally variable because population density can vary at a constant abundance, which results in variable strength of density-dependent feedback for a given population size. To incorporate habitat size variability, we developed a general population model in which changes in population abundance, density, and habitat size are taken into account. From this model, we deduced several predictions for patterns and processes of population dynamics: (1) patterns of fluctuation in population abundance and density can diverge, with respect of their correlation and relative variability; and (2) along with density dependence, habitat size fluctuation can affect population growth with a time lag because changes in habitat size result in changes in population density. In order to test these predictions, we applied our model to population dynamics data of 36 populations of *Tigriopus japonicus*, a marine copepod inhabiting tide pools of variable sizes caused by weather processes. As expected, we found a significant difference in the fluctuation patterns of population abundance and density of *T. japonicus* populations with respect to the correlation between abundance and density and their relative variability, which correlates positively with the variability of habitat

size. In addition, we found direct and lagged-indirect effects of weather processes on population growth, which were associated with density dependence and impose regulatory forces on local and regional population dynamics. These results illustrate how changes in habitat size can have an impact on patterns and processes of wildlife population dynamics. We suggest that without knowledge of habitat size fluctuation, measures of population size and its variability as well as inferences about the processes of population dynamics may be misleading.

Introduction

Population dynamics are determined by both density-dependent processes, such as competition and predation, and density-independent processes, such as environmental fluctuation and physical disturbance (Royama 1992, Turchin 2003). Recent advances in population ecology include the elucidation of processes that determine wildlife population growth in a wide range of taxa. These advances were achieved by means of a statistical approach in which logistic growth models were used for testing the structure of density-dependent regulation (e.g., Turchin 1990, Sibly et al. 2005, Brook and Bradshaw 2006), estimating the effects of density-dependent and density-independent processes on population growth rate (e.g., Forchhammer et al. 1998, Sæther et al. 2008, Rotella et al. 2009), and quantifying spatiotemporal variations in patterns and processes of population dynamics (e.g., Williams et al. 2003, Liebhold et al. 2006, Saitoh et al. 2008, Fukaya et al. 2010).

The logistic growth model is the simplest and most fundamental population model that can generate different types of population fluctuation depending on model parameters (Royama 1992, May and McLean 2007). The general form of an ecologically feasible and discrete version of the logistic model can be represented as:

$$N_t = N_{t-1} \exp[f(N_{t-1}, N_{t-2}, \dots, U_{t-1}, U_{t-2}, \dots, \varepsilon_{t-1})], \quad (1)$$

where N_t represents population size at observation time t and $f(\cdot)$ is a function of preceding population size $N_{t-1}, N_{t-2}, \dots$ and density-independent extrinsic factors $U_{t-1}, U_{t-2}, \dots$ determining average per capita population growth rate, including unknown exogenous influences modeled as the random variable ε_{t-1} (Royama 1992, Turchin 2003).

In previous studies, both population abundance (i.e., the number of individuals; Forchhammer et al. 1998, Saitoh et al. 2008, Rotella et al. 2009) and density (i.e., the number of individuals per unit area or volume; Turchin 1990, Williams et al. 2003, Liebhold et al. 2006) were used for N_t in the logistic growth model (N_t can also be referred to as population size; Sæther et al. 2008, Grøtan et al. 2009). This fact implies the assumption of a stable relationship between population abundance and density. As population abundance and density were considered to represent an identical fluctuation pattern, they were both used to represent population size and the strength of density-dependent feedback in the same way. If the habitat size of a population varies with time, however, the coherence between abundance and density is no longer possible because at a constant abundance, the population density will vary with changes in habitat size (Note: This is not related to the sampling process, with researchers changing the size of a sampling area, but is a real biological process experienced by

organisms.) This implies that in a bounded habitat, changes in habitat size may result in variable strength of density-dependent feedback for a given population size (Sutherland 1996, Debinski and Holt 2000). Changes in habitat size can be widely observed in both terrestrial and aquatic environments. For example, the volumes of rock pools and ponds are often variable due to changes in the balance of influx and outflow or evaporation. Areas of forest, grassland, and seagrass beds can also vary due to both anthropogenic activities and natural fluctuations. However, few studies have incorporated habitat size variability in the framework of logistic population models.

Here, we expand the logistic model so as to account for changes in habitat size and explicitly describe changes in population abundance and density separately. Letting H_t represent habitat size at time t , changes in habitat size can be described as follows:

$$H_t = g(H_{t-1}, H_{t-2}, \dots, U_{t-1}, U_{t-2}, \dots, \omega_{t-1}), \quad (2a)$$

where $g(\cdot)$ is an arbitrarily defined function determining habitat size at time t . Habitat size may depend on preceding habitat size $H_{t-1}, H_{t-2}, \dots$ (i.e., an autoregressive process) and extrinsic factors $U_{t-1}, U_{t-2}, \dots$, under the influence of stochastic error ω_{t-1} . By defining population density as the number of individuals per unit habitat size, a general discrete logistic growth model of

varying habitat size, where N_t and D_t are population abundance and population density at time t , respectively, is formulated as follows:

$$N_t = N_{t-1} \exp[f(D_{t-1}, D_{t-2}, \dots, U_{t-1}, U_{t-2}, \dots, \varepsilon_{t-1})] \quad (2b)$$

$$D_t = N_t / H_t \quad (2c)$$

where $f(\cdot)$ is a function determining per capita population growth as in Eqn (1). Per capita population growth rate is assumed to depend on population density rather than population abundance because, in general, biological processes affecting the demographic rate of individuals, such as competition, will become more severe as population density increases (Sutherland 1996, Berryman 2004). Some of the extrinsic factors U may affect either changes in habitat size, population growth, or both. Equations (2b) and (2c) can be described in linear form by taking the logarithms:

$$\log N_t = \log N_{t-1} + f(D_{t-1}, D_{t-2}, \dots, U_{t-1}, U_{t-2}, \dots, \varepsilon_{t-1}) \quad (3a)$$

$$\log D_t = \log N_t - \log H_t. \quad (3b)$$

Some general predictions for the patterns and processes of population dynamics with

temporally varying habitat size can be deduced from Eqns (2) and (3). First, fluctuation patterns of population abundance and density should diverge due to changes in habitat size. We expect that variability in habitat size generally decreases the correlation between trajectories of abundance and density and increases the variability of population density relative to population abundance. Details of this feature are described in Appendix A1. Second, along with density dependence, habitat size fluctuation should affect population growth with a time lag because changes in habitat size result in changes in population density. It is also possible that some of the extrinsic factors $\mathbf{U}$ (see Eqns [2a] and [2b]) affect both population abundance and changes in habitat size simultaneously, resulting in direct and lagged-indirect effects of the factors on population growth. Our model predicts more complex density-dependent structure than classic logistic models (Fig. 1).

These predictions indicate that changes in habitat size can strongly affect patterns and processes of population dynamics in collaboration with density dependence. To demonstrate the influence of habitat size fluctuation on wildlife population dynamics, we applied our model to populations of the marine copepod *Tigriopus japonicus*, which inhabits supralittoral tide pools in Far East Asia. Along with the short generation time of *Tigriopus*, this species is ideal for testing the effect of habitat size variability on population dynamics because its habitat size (i.e., water volume within a tide pool) is temporally variable due to weather processes. The

objectives of this study were to estimate the predicted divergence in the fluctuation of density and abundance of *T. japonicus* populations, and to estimate the effect of density-dependent feedback and density-independent weather processes on the species' population growth. We developed a Bayesian state-space model in which the dynamics of population abundance, population density, and water volume in tide pools were described, while accounting for observation error of these variables. We show that habitat size variability can significantly affect patterns of *T. japonicus* population trajectories. We also found that along with negative density feedback, weather processes determining changes in water volume of tide pools can have both direct and lagged-indirect impacts on population growth that drive local and regional population dynamics of this species. We conclude that without knowledge of habitat size fluctuation, measures of population size and its variability, as well as estimation of density-dependent regulation mechanisms, may be misleading.

Materials and Methods

Tigriopus japonicus and its habitat

Tigriopus japonicus is a marine copepod inhabiting supralittoral tide pools along coasts of Far East Asia (Ki et al. 2009). The life cycle of *T. japonicus* is short; it reaches adulthood 8 to 24 days after hatching, depending on water temperature, via six stages of nauplius and five stages of copepodite (individuals mature at the sixth copepodite stage; Igarashi, 1963, Itô, 1970, Koga, 1970). Adult females repeatedly produce brood sacs, including 20 to 50 eggs in a clutch, at intervals of several days (Koga 1970). *Tigriopus* spp. are known to have density-dependent interactions, such as cannibalism (Lazzaretto and Salvato 1992, Gallucci and Ólafsson 2007) and maternal inhibition of hatching (Kahan et al. 1988). Potential predators in lower sea-level habitat are fish and sea anemone (Dethier 1980), but these predators did not appear in the tide pools we observed. Previous studies reported that wave action causes dislodgement of individuals from tide pool habitat, resulting in the rapid reduction of population density (Tokioaka and Suzuki 1939, Igarashi 1959, Dethier 1980, Burton and Swisher 1984). Although *Tigriopus* spp. lack desiccation-resistant dormancy stages (Hanaoka 1940, Dybdahl 1994), individuals can withstand desiccation by using the moisture of rock crevices, gravel, sediment, or algae when a tide pool is dry, and the population can recover after the pool is refilled with

water (Tokioka and Suzuki 1939, Dybdahl 1994, Powlik and Lewis 1996, McAllen 1999). The facts that tide pools within a rock reef are connected to each other by the movement of individuals (Burton and Swisher 1984, Dybdahl 1994) and that rock reef populations separated by ocean or sandy beach are genetically differentiated (Burton et al. 1979, Burton and Feldman 1981) suggest that *Tigriopus* populations persist as a metapopulation consisting of a number of tide pools within a rock reef (Dybdahl 1994, Johnson 2001). Most movement of individuals between tide pools occurs when pools are connected by streams of water for a brief period after rain or wave action (Burton et al. 1979, Dybdahl 1994).

A single tide pool is a distinctly bounded habitat. Its size can be defined as the water volume contained within the pool (Igarashi 1959, Powlik 1998, Johnson 2001). Water volume within tide pools in the supralittoral zone is temporally variable because of weather processes; the water volume can decrease due to evaporation during periods of fine weather and can increase because of water and seawater inflow during rainy and windy weather (Tokioka and Suzuki 1939, Igarashi 1959).

Data collection

We conducted field censuses in 36 tide pools in the supralittoral zone (1.2 to 7.2 m above mean tide level) on an exposed rock reef in southern Hokkaido (41°43'N, 141°03'E) from 6 May to 7

July 2003. We sampled water from each tide pool to estimate the density of *T. japonicus* and measured water depth to calculate water volume at 2-day intervals (i.e., 32 observations were conducted during the census period). We conducted fieldwork from 07:00 to 12:00 h. To examine the effects of weather processes on population growth and changes in habitat size, we also collected wave intensity and precipitation data.

Density of *T. japonicus*: At each tide pool, we collected three 20-mL samples of water, including *T. japonicus* individuals, using a pipette. When the water volume of a tide pool was low, we reduced the amount of water sampled to 10 or 5 ml or sometimes we sampled no water. We fixed samples in 5% formalin, and counted the number of individuals of *T. japonicus* in the laboratory using a binocular microscope. We did not conduct sampling when access to a tide pool was difficult because of bad weather conditions (e.g., storms). Consequently, 6.31% of potential data were not available.

Water volume of tide pools: At each census, we measured the depth of each tide pool at a fixed point. At the end of our field survey, we investigated the relationship between depth and water volume at each tide pool by draining off the water from the pool and then adding a known amount of water. By using linear interpolation and extrapolation, we obtained a volume

estimate for every 1-mm depth at each tide pool. We did not conduct measurement of depth when a tide pool was not accessible because of bad weather conditions or when a pool was too shallow to measure depth. Consequently, 3.70% of potential water volume data were not available. For data that were lacking due to low water volume, we complemented the data with random variables drawn from a uniform distribution with an interval of zero and estimated the water volume at 1-mm depth for each tide pool. We confirmed that our result was robust to stochastic fluctuation of the complemented data. Note that in the following analysis, the effects of wave intensity on changes in abundance and water volume might be underestimated, less precise, or both due to a lack of data associated with stormy weather.

Wave intensity: We measured the strength of wave pressure at 13 fixed points within the census shoreline using a maximum velocity recorder (Bell and Denny 1994) during each census interval (i.e., 2 days). Because these measurements did not provide wave intensity at each tide pool, we calculated the scaled average wave intensity, a reef-scale variable indicating the relative intensity of wave action for each census interval, and used it in subsequent analyses.

We calculated the scaled average wave intensity for each census interval as $W_t = \frac{x_t}{\max(x_t)}$,

where x_t is the mean scaled wave pressure, $x_t = \frac{\sum_{k=1}^{13} w_{kt}}{\max_k(w_{kt})}$, where w_{kt} and $\max_k(w_{kt})$

represent the observed wave pressure at fixed measurement point k at census interval $t-1$ and t and the maximum wave pressure observed at point k , respectively.

Precipitation: We obtained data for precipitation during each census interval from the database of the Automated Meteorological Data Acquisition System of the Japan Meteorological Agency (<http://www.data.jma.go.jp/obd/stats/etrn/index.php>). We used data from Toitomari ($41^{\circ}43'N$, $141^{\circ}00'E$), an observation station located about 4 km from the census shore. Considering the time of day when the maximum precipitation per hour was observed, we summed the daily precipitation to obtain the amount of precipitation for each census interval. We calculated scaled precipitation for each census interval by dividing data by the maximum precipitation, and this scaled precipitation was used for subsequent analysis.

Statistical modeling

We analyzed data within the framework of state-space modeling (Clark 2007, Royle and Dorazio 2008, Link and Barker 2010), which is composed of two submodels, a process model representing the underlying dynamics of unobserved state variables and a data model describing the sampling process of data. By taking observation error into account, this approach enabled us to obtain less biased estimates of dynamic parameters and to

accommodate missing data in the analysis (Clark and Bjørnstad 2004, Freckleton et al. 2006).

We developed a hierarchically structured state-space model with a process model representing the dynamics of population abundance of *T. japonicus* and water volume at each tide pool and a data model representing the observation process of population density and water volume.

We adopted a fully Bayesian approach to fit the model to the data because the Bayesian paradigm is ideal for fitting state-space models that contain many latent variables (Clark and Bjørnstad 2004, Clark 2007, Royle and Dorazio 2008). The Bayesian approach is also advantageous for ecological studies because it enables the acquisition of a posterior distribution of derived parameters (i.e., parameters that are a function of estimated parameters), which can often provide various ecological insights (Royle and Dorazio 2008, Link and Barker 2010).

Here, we describe the essential part of our data model and process model. Full descriptions of the model and parameter estimation are supplied in appendix A2 and A3.

Data model: The number of *T. japonicus* individuals in a sample was assumed to be generated by an overdispersed Poisson process. The number of individuals in the j th sample collected at tide pool i on census date t , n_{tij} , was assumed to follow a Poisson distribution with an intensity of λ_{tij} :

$$n_{tij} \sim \text{Po}(\lambda_{tij}), \quad (4)$$

where λ_{tij} is assumed to follow a normal distribution:

$$\log \lambda_{tij} \sim N(\log D_{ti} + \log v_{\text{sample } ti}, \sigma_{\text{obsn}}^2). \quad (5)$$

Here D_{ti} is the unobserved population density (individuals/L) and $v_{\text{sample } ti}$ is the amount of water sampled (L) at tide pool i on census date t , and σ_{obsn}^2 is a parameter determining the overdispersion of Poisson processes. Note that the average of the normal distribution

$\log D_{ti} + \log v_{\text{sample } ti}$ corresponds to $\log(D_{ti} \times v_{\text{sample } ti})$, which represents the expected number of individuals in the sample.

The water volume data were assumed to have a log-normal error. That is, the logarithm of the water volume observed at tide pool i on census date t , v_{ti} , was assumed to follow a normal distribution:

$$\log v_{ti} \sim N(\log H_{ti}, \sigma_{\text{obsv}}^2), \quad (6)$$

where H_{ti} is the unobserved water volume (L) of tide pool i on census date t and σ_{obsv}^2 is the

variance of the observation error.

Process model: We considered wave intensity and precipitation as determinants of population growth and changes in water volume. We also included population density in the model of population growth. With N_{ti} , H_{ti} and D_{ti} representing population abundance (individuals), water volume (L) and population density (individuals/L) at tide pool i on census date t , respectively, and W_{t-1} and P_{t-1} are scaled average wave intensity and scaled precipitation observed between census dates $t-1$ and t , the dynamics of N_{ti} and H_{ti} were described as follows:

$$\log N_{ti} = \log N_{t-1i} + \alpha_{0i} + \alpha_{1i} \log D_{t-1i} + \alpha_{2i} W_{t-1} + \alpha_{3i} P_{t-1} + \omega_{Nt-1i} + \varepsilon_{Nt-1i} \quad (7a)$$

$$\log H_{ti} = \log H_{t-1i} + \beta_{0i} + \beta_{1i} W_{t-1} + \beta_{2i} P_{t-1} + \omega_{Ht-1i} + \varepsilon_{Ht-1i} \quad (7b)$$

$$(\omega_{Nt-1}, \omega_{Ht-1})' \sim \text{MN}[(0,0)', \Sigma_{\omega}] \quad (7c)$$

$$(\varepsilon_{Nt-1i}, \varepsilon_{Ht-1i})' \sim \text{MN}[(0,0)', \Sigma_{\varepsilon}], \quad (7d)$$

where α_{0i} , α_{1i} , α_{2i} , and α_{3i} represent intrinsic growth rate, the strength of density dependence, and the effects of wave intensity and precipitation, respectively, on population growth at tide pool i ; β_{0i} , β_{1i} , and β_{2i} represent average volume change when there were no waves or precipitation and the effects of wave intensity and precipitation on volume change, respectively,

at tide pool i ; ω_{Nt-1} and ω_{Ht-1} represent stochastic fluctuation in population abundance and water volume, respectively, which simultaneously affects all tide pools; ε_{Nt-1i} and ε_{Ht-1i} represent stochastic fluctuation in population abundance and water volume, respectively, which affects each tide pool independently; and Σ_{ω} and Σ_{ε} represent the covariance matrix of ω and ε , respectively. Note that although the equation for population abundance (Eqn [7a]) is similar to a log-linear Gompertz population model (Royama 1992, Turchin 2003), it is not the same because population abundance and density are explicitly separated.

We specified population density at tide pool i on census date t , D_{ti} , by dividing population abundance, N_{ti} , by water volume, H_{ti} . The logarithmic form was represented as follows:

$$\log D_{ti} = \log N_{ti} - \log H_{ti}. \quad (8)$$

Derived parameters: As derived parameters, we obtained the logarithm of changes in population abundance ($\Delta \log N_{ti}$), population density ($\Delta \log D_{ti}$), and water volume ($\Delta \log H_{ti}$) for each time and pool. We also calculated the variance of population abundance ($\text{Var}[\log N]$), density ($\text{Var}[\log D]$), and water volume ($\text{Var}[\log H]$); the lag-0 cross-correlation between the logarithm of population abundance and the logarithm of population density ($\text{Cor}[\log N, \log D]$);

and the scaled variability of population density relative to abundance ($\text{Var}[\log D]/\text{Var}[\log N]$) at each tide pool. The equations used to calculate these variables are available in Appendix A2. Data, latent variables, and derived parameters involved in the model are summarized in Appendix A3.

Parameter estimation and assessment of model adequacy: We fitted the model to data by the Markov chain Monte Carlo method in WinBUGS (Lunn et al. 2000). We specified vague priors to parameters and hyperparameters. To confirm the independence of the posterior probability on initial values, we executed three independent iterations. We obtained estimates from 1,500,000 iterations after a burn-in of 100,000 iterations, thinning at intervals of 500. The BUGS code of the fitted model and a R script of sample data is provided in Appendix A4 and A5.

We evaluated the goodness-of-fit of the model by posterior predictive assessment using a χ^2 discrepancy quantity defined as $T(\mathbf{y}, \boldsymbol{\theta}) = \sum_i \frac{[y_i - E(y_i | \boldsymbol{\theta})]^2}{\text{var}(y_i | \boldsymbol{\theta})}$, where y_i represents the univariate responses and $\mathbf{y}$ represents their vector, and $\boldsymbol{\theta}$ is the model parameter (Gelman et al. 2004a). We calculated the posterior predictive p-value as $p = \Pr[T(\mathbf{y}^{\text{rep}}, \boldsymbol{\theta}) \geq T(\mathbf{y}, \boldsymbol{\theta}) | \mathbf{y}]$, where $\mathbf{y}^{\text{rep}}$ is a vector of the posterior predictive value of the data.

In order to examine the assumption of our population model that population growth

depends on population density rather than abundance, we fit another model in which the classical logistic assumption was adopted (i.e., $\log D_{t-1i}$ in Eqn [7a] was replaced with $\log N_{t-1i}$, while all other elements were kept the same as in the original model). Between these two models, we compared the square of the correlation coefficient (R^2) between population growth and density or abundance calculated for each tide pool to assess if the strength of the association with population growth varies between density and abundance. Parameter estimates were also compared between the two models.

Results

Effects of habitat size variability on patterns of population abundance and density

Fig. 2 shows the estimates of population abundance and population density of *T. japonicus* and water volume. In some tide pools, population abundance and density showed similar fluctuation patterns (Fig. 2A), while patterns in the fluctuation of population abundance and density were extremely different in some tide pools due to the fluctuation of water volume (Fig. 2B). In the tide pool where the abundance–density correlation was the lowest (Fig. 2B), we observed stationary fluctuation in population abundance, whereas population density showed a different fluctuation pattern, with several peaks characterized by a gradual increase and rapid decline, reflecting changes in water volume. Population trajectories observed at several other tide pools are provided in Appendix A6. Generally, trajectories of abundance and density differed to some degree due to changes in water volume, although there were some differences in this tendency among tide pools (Appendix A6).

Divergence in patterns of population abundance and density was related to the variability of habitat size. There was a significant negative correlation between the correlation coefficient of population abundance versus density ($\text{Cor}[\log N, \log D]$) and the variance of water volume ($\text{Var}[\log H]$) (Fig. 3A). The correlation coefficient between abundance and

density ($\text{Cor}[\log N, \log D]$) varied among tide pools, with a range of 0.25 to 0.96 (posterior median; Fig. 3A). On the other hand, there was a significant positive correlation between scaled variance of population density relative to abundance ($\text{Var}[\log D]/\text{Var}[\log N]$) and variance of water volume ($\text{Var}[\log H]$). The variability of population density was higher than that of population abundance (i.e., $\text{Var}[\log D]/\text{Var}[\log N] > 1$) in all of the observed tide pool populations, where the fluctuation in population density was amplified at a maximum of 16.2 (posterior median) times larger than that of population abundance (Fig. 3B).

Processes determining changes in population abundance and water volume

Changes in abundance were characterized by negative density dependence as well as negative effects of wave intensity and precipitation (Table 1). On the other hand, changes in water volume were determined by positive effects of wave intensity and precipitation (Table 1). Credible intervals of the effects of wave intensity on abundance and water volume, however, included zero, suggesting that uncertainty remains for the effects of wave intensity. These estimates of regional averages reflected changes in abundance and water volume at each tide pool (Fig. 4).

Fig. 5 shows the distributions of changes in population abundance, water volume, and population density estimated for the 36 tide pools. Changes in population abundance, density,

and habitat size were synchronized among tide pools due to weather processes. As suggested by the estimates of parameters determining population growth and water volume change, population abundance (Fig. 5A) and water volume (Fig. 5B) tended to change synchronously when there was an increase in precipitation or wave intensity (Fig. 5D). Weather-induced reductions in population abundance and increases in water volume resulted in substantial reductions in population density (Fig. 5C, note that the magnitude of density change is larger than that of changes in abundance and water volume). For the fluctuations in abundance, we often observed synchronous increases (Fig. 5, white triangles) subsequent to a synchronous decrease (Fig. 5, black triangles).

Adequacy of the model

The goodness of fit evaluated by χ^2 discrepancy suggested that our model tended to overfit the data of water volume ($p = 0.98$), but it was consistent with the data of population density ($p = 0.86$). Fig. 6 shows the relationships between population growth rate and population density, which corresponds to the assumption of our model, or between population growth and abundance, which corresponds to the assumption of classical logistic models, estimated at a tide pool population of *T. japonicus*. We found a virtually linear relationship between population growth and population density (Fig. 6A) but a less distinct relationship between

population growth and population abundance (Fig. 6B). Overall, population density explained more variation in population growth (40%, on average) than did population abundance (35%, on average; Fig. 6C). For some parameters determining population growth (α_0 , α_1 , and α_2), we also found that estimates were systematically higher or lower in the model including the classical logistic assumption, than those in the original model (Appendix A7). We rarely found nonlinear relationships between the logarithm of population growth and the logarithms of population density or abundance.

Discussion

We found a significant difference in the fluctuation patterns of population abundance and density of *T. japonicus* populations. A mathematical analysis of Eqn (3b) reveals that divergence between the trajectories of abundance and density depends on the extent of habitat size variability and cross-covariance between abundance and habitat size (Appendix A1). Although cross-covariance between abundance and habitat size has opposite effects on the two properties of abundance–density divergence, an increase in habitat size variability causes both a decrease in the cross-correlation between the trajectories of abundance and density and an increase in the variability of density (Appendix A1). Therefore, we generally expect that fluctuations in population abundance and density diverge as habitat size variability increases (details of the effects of habitat size variability on the abundance–density divergence are provided in Appendix A1). We suggest that estimating population size and its variability in wildlife populations with variable habitat size should be done cautiously because observed population density may not accurately reflect population abundance. For example, most previous studies of *Tigriopus* populations estimated population size by measuring population density (e.g., Igarashi 1959, Powlik 1998, Johnson 2001), but these results may not reflect true population size, particularly in tide pools where the water volume is highly variable (e.g., tide

pools at high sea level or sheltered tide pools). Our model predicts that without taking habitat variability into account, measures of population size and population variability may be misleading.

When population growth depends on population density, factors determining habitat size are expected to affect population growth by changing population density (Fig. 1B). In the present *T. japonicus* populations, weather processes (i.e., rainfall and wave action, with some uncertainty in the latter; Table 1) play an important role in regulation of local and regional population dynamics. We found a negative effect of population density on population growth and a positive effect of precipitation and wave strength on changes in habitat size (Table 1, Fig. 4), which indicates that weather processes indirectly affect population growth of *T. japonicus* with a time lag by reducing population density. In addition to the effect of weather processes on habitat size, we also found that they had a negative impact on population growth (Table 1, Fig. 4). This means that weather processes can significantly reduce population density by simultaneously reducing population abundance and increasing habitat size, which may lead to a substantial relaxation of intraspecific interactions and result in greater subsequent population growth. Synchronous increases in population abundance were often observed after a synchronous decrease caused by weather processes (Fig. 5), suggesting that indirect and delayed regulation induced by weather processes and density dependence actually drive local

and regional populations of *T. japonicus*.

In addition to the influence on the estimation of population size and its variability, changes in habitat size can also have significant impacts on inferences on the density-dependent structure of population growth. The classic logistic model implicitly assumes that population growth rate is a function of population abundance, because without changes in habitat size abundance also represents population density (Royama 1992, Turchin 2003). In contrast, we considered the case where divergence can exist between population abundance and density and assumed that population growth is a function of density rather than abundance because biological processes determining demographic rate of individuals, such as competition or cannibalism, are thought to become stronger as population density increases (Sutherland 1996, Berryman 2004). We examined the validity of our assumption and confirmed that variation in population growth was better explained by density than abundance (Fig. 6). In addition, in the model with the classical logistic assumption we found that estimates for some parameters that determine changes in abundance were systematically different from those in our original model (Appendix A7). These results suggest that if classical logistic models are fitted to a population system with varying habitat size, the estimation of model parameters may be biased, which would consequently result in incorrect inferences about the processes of population dynamics.

Models of population dynamics incorporating habitat size variability can also be interpreted as classic logistic models with temporally varying parameters. For example, our statistical model for *T. japonicus* populations turns out to be a log-linear Gompertz population model, a population model frequently used in empirical studies (Forchhammer et al. 1998, Williams et al. 2003, Liebhold et al. 2006, Sæther et al. 2008, Rotella et al. 2009, Fukaya et al. 2010), in which habitat size is included as a determinant of the intrinsic growth rate and strength of density dependence. Letting H_t and $\mathbf{U}_t$ be habitat size and a vector of density-independent factors at time t , respectively, the model developed in this study can be rewritten as follows:

$$\log N_t = \log N_{t-1} + \alpha_0 + \alpha_1 \log D_{t-1} + f(\mathbf{U}_{t-1}) \quad (9a)$$

$$\log D_t = \log N_t - \log H_t. \quad (9b)$$

Here we have omitted the subscripts for tide pool i for simplicity. By substituting Eqn (9b) into Eqn (9a) and replacing subscript t with $t-1$ in (9b), we obtain:

$$\log N_t - \log N_{t-1} = (\alpha_0 - \alpha_1 \log H_{t-1}) \left(1 - \frac{-\alpha_1}{\alpha_0 - \alpha_1 \log H_{t-1}} \log N_{t-1} \right) + f(\mathbf{U}_{t-1}), \quad (10)$$

which we can interpret as a log-linear Gompertz model with temporally varying intrinsic growth rate $r_{t-1} = (\alpha_0 - \alpha_1 \log H_{t-1})$ and carrying capacity $K_{t-1} = -r_{t-1}/\alpha_1$ depending on the logarithm of habitat size H_{t-1} . A change in habitat size ($\Delta \log H_t$) induces changes in intrinsic growth rate and carrying capacity equal to $-\alpha_1 \Delta \log H_t$ and $\Delta \log H_t$, respectively (Fig. 7A). For the *T. japonicus* population, because α_1 was estimated to be significantly negative (Table 1, Fig. 4B), an increase in habitat size should increase both the intrinsic growth rate and carrying capacity simultaneously and thus population growth at a particular population size is expected to increase (Fig. 7A). This prediction is consistent with the observed pattern of population growth (Fig. 5). It is unclear, however, why an increase in habitat size resulted in an increase in the intrinsic growth rate of this species. It is possible that an inflow of rain or seawater affects not only the population density but also environmental conditions of a pool that may affect the intrinsic growth rate, such as salinity, water temperature, and oxygen concentration (e.g., Tokioka and Suzuki 1939, Hanaoka 1940, Igarashi 1959). Further research is required to clarify the mechanisms underlying changes in the intrinsic growth rate associated with habitat size fluctuation.

In the case of a nonlinear Ricker-type functional form (Turchin 2003), which is also often used in empirical population studies (Turchin 1990, Brook and Bradshaw 2006, Saitoh et al. 2008), a qualitatively similar interpretation is possible. With a Ricker-type form, changes in

population abundance and density are described as follows:

$$\log N_t = \log N_{t-1} + \alpha_0 + \alpha_1 D_{t-1} + f(\mathbf{U}_{t-1}) \quad (11a)$$

$$D_t = N_t / H_t. \quad (11b)$$

By substituting Eqn (11b) into Eqn (11a) and replacing subscript t with $t-1$ in (11b), we obtain:

$$\log N_t - \log N_{t-1} = \alpha_0 \left(1 - \frac{-\alpha_1}{\alpha_0 H_{t-1}} N_{t-1} \right) + f(\mathbf{U}_{t-1}), \quad (12)$$

which we can interpret as a Ricker model with a fixed intrinsic growth rate $r = \alpha_0$ and temporally varying carrying capacity $K_{t-1} = -(\alpha_0/\alpha_1)H_{t-1}$ depending on habitat size H_{t-1} . A change in habitat size (ΔH_t) induces a change in carrying capacity equal to $-(\alpha_0/\alpha_1)\Delta H_t$ (Fig. 7B). Although in the Ricker model habitat size only affects the carrying capacity and does not affect the intrinsic growth rate, an increase in habitat size results in an increase in population growth at a particular population size, as in the Gompertz model (Fig. 7B).

The effect of habitat size variability on density-dependent population dynamics was considered by Sutherland (1996), who developed a model that predicts the consequences of habitat loss for migratory species that utilize wintering habitat and breeding habitat in different

seasons. This model, predicting different consequences between loss or gain of wintering habitat and that of breeding habitat, is widely applicable to many migratory species such as birds (Sutherland 1996). Compared to the model of Sutherland (1996), our model seems to provide a somewhat different framework. First, migration of organisms is not necessarily assumed in our model. This model will, however, also be applied to migratory species who utilize habitats of different size at different times by interpreting migration as an event of habitat size change. Second, our model involves factors determining changes in habitat size, which enables us to elucidate complex processes of population dynamics (Fig. 1). Finally, in contrast to Sutherland's model, which predicts changes in equilibrium population size for a given habitat change, our model predicts population growth rate at a given time by accommodating changes in habitat size and population abundance. Because of this feature, our model can still be applicable even if the temporal scale of habitat size variability is short enough to prevent a population from reaching its equilibrium size.

Logistic models incorporating changes in habitat size can be widely applied to populations in both terrestrial and aquatic ecosystems in which habitat size is bounded and varies due to environmental factors or anthropogenic activities. Animals facing anthropogenic habitat change may be a case that our model fits well. Debinski and Holt (2000) reported that crowding of individuals of bird, small mammal, and insect species can be observed in small

fragmented habitat patches, whereas such high density can be relaxed in subsequent years.

Such crowding caused by habitat destruction and subsequent decline in population density may be well captured by our modified logistic model. Our model may also be applicable to marine invertebrates and fish populations that depend on seagrass beds or coral reefs, the areas of which can vary due to their intrinsic dynamics and extrinsic drivers including climate, epidemics, and human activity (Roberts and Hawkins 1999). As shown in this study, our model can be applied to animal populations in rock pools. Incorporating factors that determine habitat size variability into logistic models will improve our understanding of population dynamics under variable environments, as well as our ability to predict the future of populations facing human-induced environmental changes.

Several extensions of our framework are possible in future work. For example, the effects of population abundance or density on habitat size can be considered. This would be the case when modification or destruction of habitat is caused by the inhabiting organisms, for example, the loss of vegetation caused by activities of herbivores, such as nutria and snow geese (Kerbes et al. 1990, Ford and Grace 1998). In addition, by expanding the definition of population density, our framework can be used in more general situations. Berryman (2004) suggested that “a model for the process of population regulation should be based on ... the ratio of population size to its limiting factor” (see also Berryman 1999). By replacing habitat

size with the amount of a limiting resource, our model becomes the kind of population model that Berryman (2004) proposed. The explicit separation of changes in population abundance and density will provide a more general framework for understanding the patterns and processes of wildlife population dynamics under fluctuating environments.

Conclusions

By applying a hierarchically structured population model that incorporates changes in habitat size, our analysis of *T. japonicus* populations confirms predictions deduced from a general population model with varying habitat size. We found a significant difference in the fluctuation patterns of population abundance and density of *T. japonicus* populations with respect to the correlation between abundance and density and their relative variability. In addition, we found direct and lagged-indirect effects of weather processes on population growth, which were associated with density dependence and impose regulatory forces on local and regional population dynamics. These results illustrate how changes in habitat size can have an impact on patterns and processes of wildlife population dynamics. Our results also indicate that without knowledge of habitat size fluctuation, measures of population size and its variability and estimates of density-dependent regulation mechanisms may be misleading.

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References

- Bell, E. C. and Denny, M. W. 1994. Quantifying “wave exposure”: a simple device for recording maximum velocity and results of its use at several field sites. – J. Exp. Mar. Biol. Ecol. 181: 9–29.
- Berryman, A. A. 1999. Principles of population dynamics and their application. - Stanley Thornes.
- Berryman, A. A. 2004. Limiting factors and population regulation. - Oikos 105: 667-670.
- Brook, B. W. and Bradshaw, C. J. A. 2006. Strength of evidence for density dependence in abundance time series of 1198 species. - Ecology 87: 1445-1451.
- Burton, R. S. and Feldman, M. W. 1981. Population genetics of *Tigriopus californicus* II. Differentiation among neighboring populations. - Evolution 35: 1192-1205.
- Burton, R. S. and Swisher, S. G. 1984. Population structure of the intertidal copepod *Tigriopus californicus* as revealed by field manipulation of allele frequencies. - Oecologia (Berlin) 65: 108-111.
- Burton, R. S. et al. 1979. Population genetics of *Tigriopus californicus* (Copepoda: Harpacticoida): I. Population structure along the Central California coast. – Mar. Ecol. Prog. Ser. 1: 29-39.

- Clark, J. S. 2007. Models for ecological data: an introduction. - Princeton Univ. Press.
- Clark, J. S. and Bjørnstad, O. N. 2004. Population time series: process variability, observation errors, missing values, lags, and hidden states. - Ecology 85: 3140-3150.
- Debinski, D. M. and Holt, R. D. 2000. A survey and overview of habitat fragmentation experiments. – Conserv. Biol. 14: 342-355.
- Dethier, M. N. 1980. Tidepools as refuges: predation and the limits of the Harpacticoid copepod *Tigriopus californicus*. – J. Exp. Mar. Biol. Ecol. 42: 99-111.
- Dybdahl, M. F. 1994. Extinction, recolonization, and the genetic structure of tidepool copepod populations. – Evol. Ecol. 8: 113-124.
- Forchhammer, M. C. et al. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. – Proc. R. Soc. B 265: 341-350.
- Ford, M. A. and Grace, J. B. 1998. Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. – J. Ecol. 86: 974-982.
- Freckleton, R. P. et al. 2006. Census error and the detection of density dependence. – J. Anim. Ecol. 75: 837-851.
- Fukaya, K. et al. 2010. Seasonality in the strength and spatial scale of processes determining intertidal barnacle population growth. – J. Anim. Ecol. 79: 1270-1279.

- Gallucci, F. and Ólafsson, E. 2007. Cannibalistic behaviour of rock-pool copepods: an experimental approach for space, food and kinship. – J. Exp. Mar. Biol. Ecol. 342: 325-331.
- Gelman, A. et al. 2004. Model checking and improvement. - In: Bayesian Data Analysis. Second Edi. Chapman & Hall, pp. 157-196.
- Grøtan, V. et al. 2009. Spatial and temporal variation in the relative contribution of density dependence, climate variation and migration to fluctuations in the size of great tit populations. – J. Anim. Ecol. 78: 447-459.
- Hanaoka, T. 1940. Reproduction and metamorphosis of two species of Harpacticoid Copepoda. - Suisan Gakkwai Ho (Proceedings of the Scientific Fisheries Association) 8: 32-44. [In Japanese]
- Igarashi, S. 1959. On the relationship between the environmental conditions of tide pool and the *Tigriopus* population. - Bulletin of the Marine Biological Station of Asamushi 9: 167-171.
- Igarashi, S. 1963. Developmental cycle of *Tigriopus japonicus* Mori. - Science Report of the Tohoku University. Series 4, Biology 29: 59-72.
- Itô, T. 1970. The biology of a harpacticoid copepod, *Tigriopus japonicus* Mori. - Journal of the Faculty of Science, Hokkaido University, Series 6, Zoology 17: 474-500.

- Johnson, M. P. 2001. Metapopulation dynamics of *Tigriopus brevicornis* (Harpacticoida) in intertidal rock pools. – Mar. Ecol. Prog. Ser. 211: 215-224.
- Kahan, D. et al. 1988. Maternal inhibition of hatching at high population densities in *Tigriopus japonicus* (Copepoda, Crustacea). – Biol. Bull. 174: 139-144.
- Kerbes, R. H. et al. 1990. Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. – J. Applied Ecol. 27: 242-258.
- Ki, J. S. et al. 2009. Phylogeography of the copepod *Tigriopus japonicus* along the Northwest Pacific rim. – J. Plankton Res. 31: 209-221.
- Koga, F. 1970. On the life history of *Tigriopus japonicus* Mori (Copepoda). - Journal of the Oceanographical Society of Japan 26: 11-21. [In Japanese with English abstract]
- Lazzaretto, I. and Salvato, B. 1992. Cannibalistic behaviour in the harpacticoid copepod *Tigriopus fulvus*. – Mar. Biol. 113: 579-582.
- Liebhold, A. M. et al. 2006. Geographic variation in density-dependent dynamics impacts the synchronizing effect of dispersal and regional stochasticity. – Popul. Ecol. 48: 131-138.
- Link, W. A. and Barker, R. J. 2010. Bayesian inference: with ecological applications. - Academic Press.
- Lunn, D. J. et al. 2000. WinBUGS-a Bayesian modelling framework: concepts, structure, and extensibility. – Stat. Comput. 10: 325-337.

- May, R. M. and McLean, A. R. 2007. Theoretical Ecology. Third Edi. - Oxford Univ. Press.
- McAllen, R. 1999. *Enteromorpha intestinalis*-a refuge for the supralittoral rockpool harpacticoid copepod *Tigriopus brevicornis*. – J. Mar. Biol. Assoc. UK. 79: 1125-1126.
- Powlik, J. J. 1998. Seasonal abundance and population flux of *Tigriopus californicus* (Copepoda : Harpacticoida) in Barkley Sound, British Columbia. – J. Mar. Biol. Assoc. UK. 78: 467-481.
- Powlik, J. J. and Lewis, A. G. 1996. Desiccation resistance in *Tigriopus californicus* (Copepoda, Harpacticoida). – Estuar. Coast. Shelf S. 43: 521-532.
- Roberts, C. M. and Hawkins, J. P. 1999. Extinction risk in the sea. – Trends. Ecol. Evol. 14: 241-246.
- Rotella, J. J. et al. 2009. An evaluation of density-dependent and density-independent influences on population growth rates in Weddell seals. - Ecology 90: 975-984.
- Royama, T. 1992. Analytical population dynamics. - Chapman & Hall.
- Royle, J. A. and Dorazio, R. M. 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. - Academic Press.
- Saitoh, T. et al. 2008. Effects of acorn abundance on density dependence in a Japanese wood mouse (*Apodemus speciosus*) population. – Popul. Ecol. 50: 159-167.
- Sibly, R. M. et al. 2005. On the regulation of populations of mammals, birds, fish, and insects. -

Science 309: 607-10.

Sutherland, W. J. 1996. Predicting the consequences of habitat loss for migratory populations.

– Proc. R. Soc. B 263: 1325-1327.

Sæther, B.-E. et al. 2008. Geographical gradients in the population dynamics of North

American prairie ducks. – J. Anim. Ecol. 77: 869-882.

Tokioka, T. and Suzuki, T. 1939. The observation of a Copepoda living in a tide pool, *Tigriopus*

japonicus Mori. - Seitaigaku Kenkyu (Ecological Review) 5: 152-159. [In Japanese]

Turchin, P. 1990. Rarity of density dependence or population regulation with lags. - Nature

344: 660-663.

Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. - Princeton

Univ. Press.

Williams, C. K. et al. 2003. Population dynamics across geographical ranges: time-series

analyses of three small game species. - Ecology 84: 2654-2667.

Supplementary material (Appendix o20515 at <www.oikosoffice.lu.se/appendix>). Appendix

A1-6.

Table

Table 1. Posterior distributions of the regional averages of parameters determining changes in population abundance and water volume

Parameter	Posterior median [†]	95% credible interval
Population abundance		
Intrinsic growth rate (μ_{α_0})	2.15	(1.59, 2.77)
Density dependence (μ_{α_1})	-0.26	(-0.36, -0.17)
Effect of wave intensity (μ_{α_2})	-0.54	(-1.27, 0.20)
Effect of precipitation (μ_{α_3})	-0.83	(-1.51, -0.15)
Water volume		
Intercept (μ_{β_0})	-0.19	(-0.44, 0.07)
Effect of wave intensity (μ_{β_1})	0.36	(-0.30, 1.02)
Effect of precipitation (μ_{β_2})	1.03	(0.38, 1.68)

[†]A bold posterior median indicates that zero is not included within the 95% credible interval.

Figures and Figure legends

Fig. 1. (A) Structure of density-dependent population growth in classical logistic models. A perfect correlation between population abundance and density (i.e., no temporal variation in habitat size) is implicitly assumed. (B) Structure of density-dependent population growth in the logistic model incorporating habitat size variability. Population density is specified by population abundance and habitat size, which enables changes in habitat size to contribute to population growth with a time lag in collaboration with density dependence.

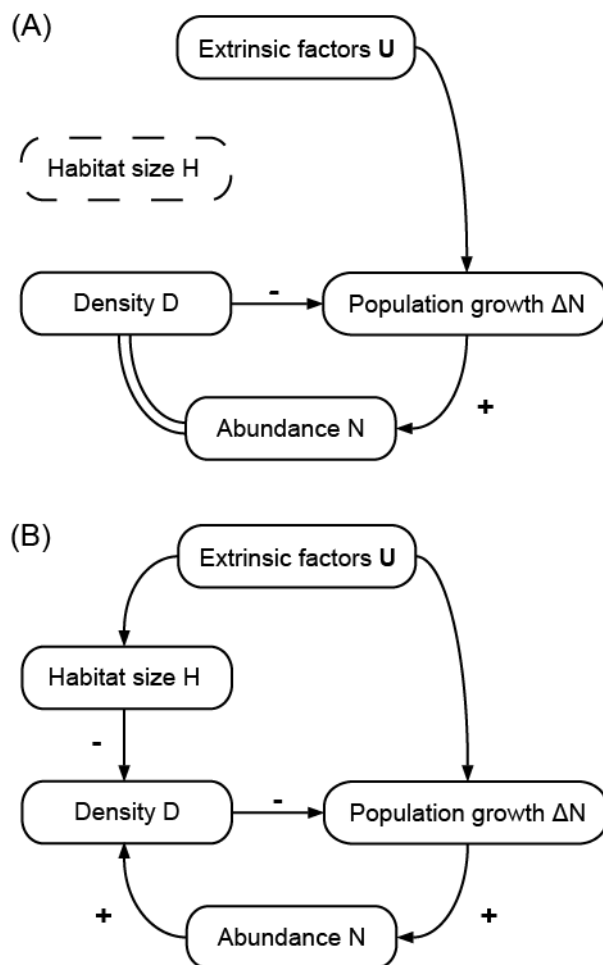


Fig. 2. Fluctuations of population abundance (individuals) and density (individuals/L) of *Tigriopus japonicus* and water volume (L) in the tide pool with the highest abundance–density correlation (A: correlation coefficient = 0.96) and the tide pool with the lowest abundance–density correlation (B: correlation coefficient = 0.25). Open circles, solid lines and shaded gray represent observed values, posterior medians, and 95% credible intervals, respectively. Scaled wave intensity and scaled precipitation are shown in the lowest row of each figure.

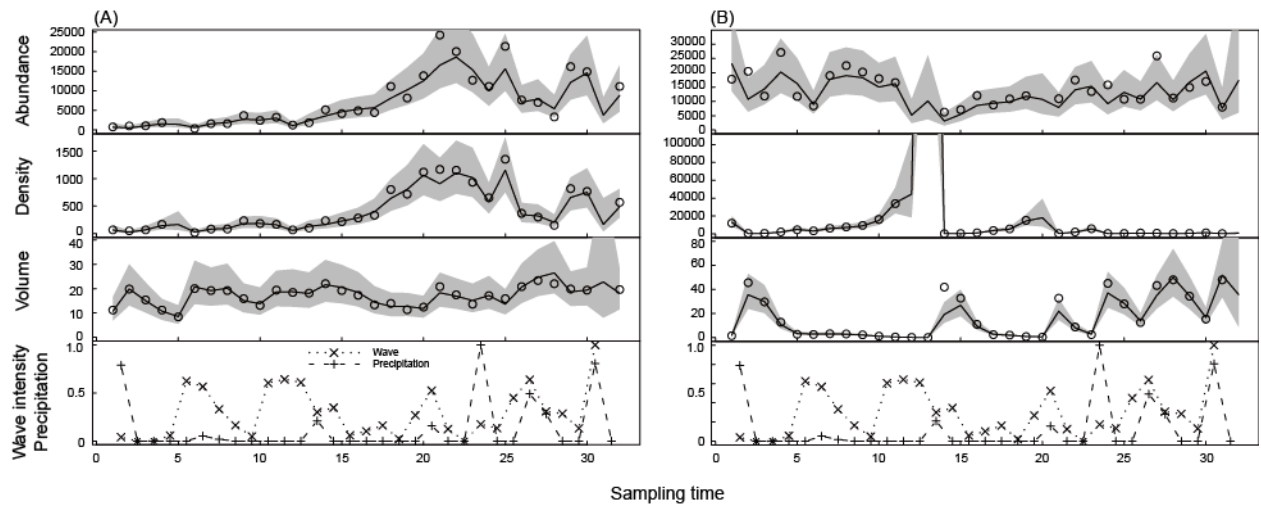


Fig. 3. Relationships between (A) variance of water volume ($\text{Var}[\log H]$) and correlation coefficient of $\log N_{ti}$ and $\log D_{ti}$ ($\text{Cor}[\log N, \log D]$) and (B) variance of water volume and scaled variance of population density relative to abundance ($\text{Var}[\log D]/\text{Var}[\log N]$). The posterior distribution of the correlation coefficient between the two variables is also shown for each plot. Open circles and bars represent posterior medians and 95% credible intervals, respectively. Dashed horizontal lines represent $\text{Cor}(\log N, \log D) = 0$ for (A) and $\text{Var}(\log D)/\text{Var}(\log N) = 0$ for (B).

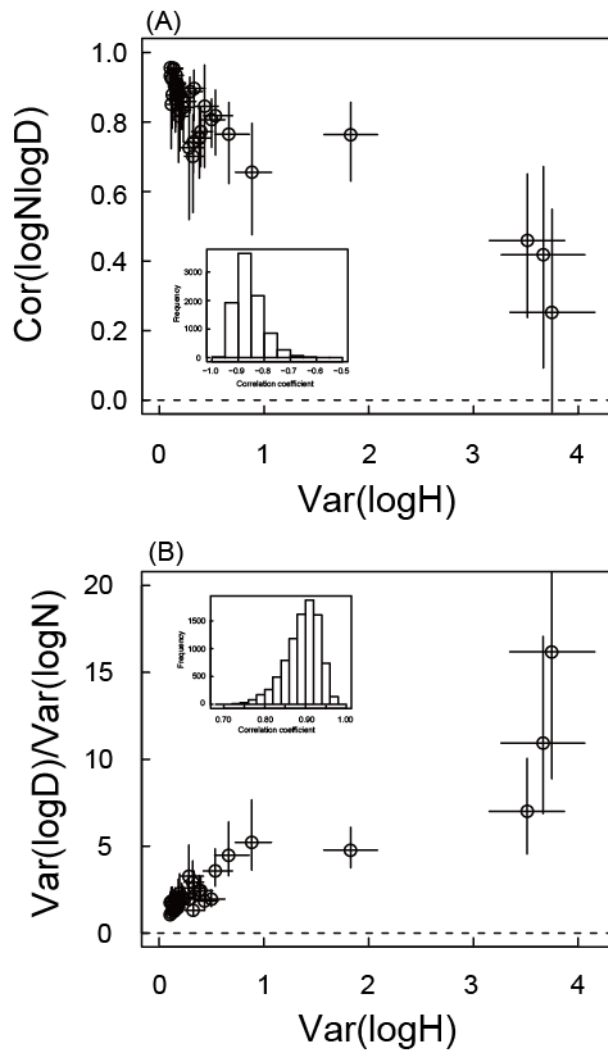


Fig. 4. Histograms of the posterior median of parameters determining changes in population

abundance (α_{0i} , α_{1i} , α_{2i} , and α_{3i}) and water volume (β_{0i} , β_{1i} , and β_{2i}) estimated at 36 tide pools.

Shaded bins indicate negative ranges.

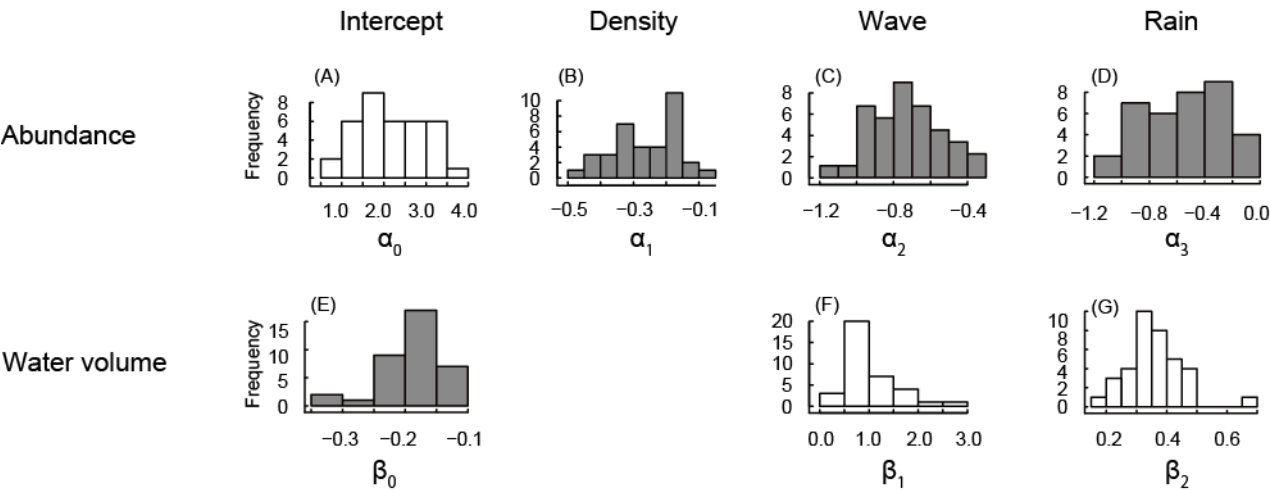


Fig. 5. Tukey box plots of the posterior median of changes in (A) population abundance ($\Delta \log N_{ti} = \log N_{t+1i} - \log N_{ti}$), (B) water volume ($\Delta \log H_{ti} = \log H_{t+1i} - \log H_{ti}$), and (C) population density ($\Delta \log D_{ti} = \log D_{t+1i} - \log D_{ti}$) estimated at 36 tide pools for each census date. Synchronous decreases and increases of abundance are marked with triangles atop the figure, indicating below-zero maximum (synchronous decrease; black) and above-zero minimum (synchronous increase; white). Scaled wave intensity and scaled precipitation are also shown, as in Fig. 2.

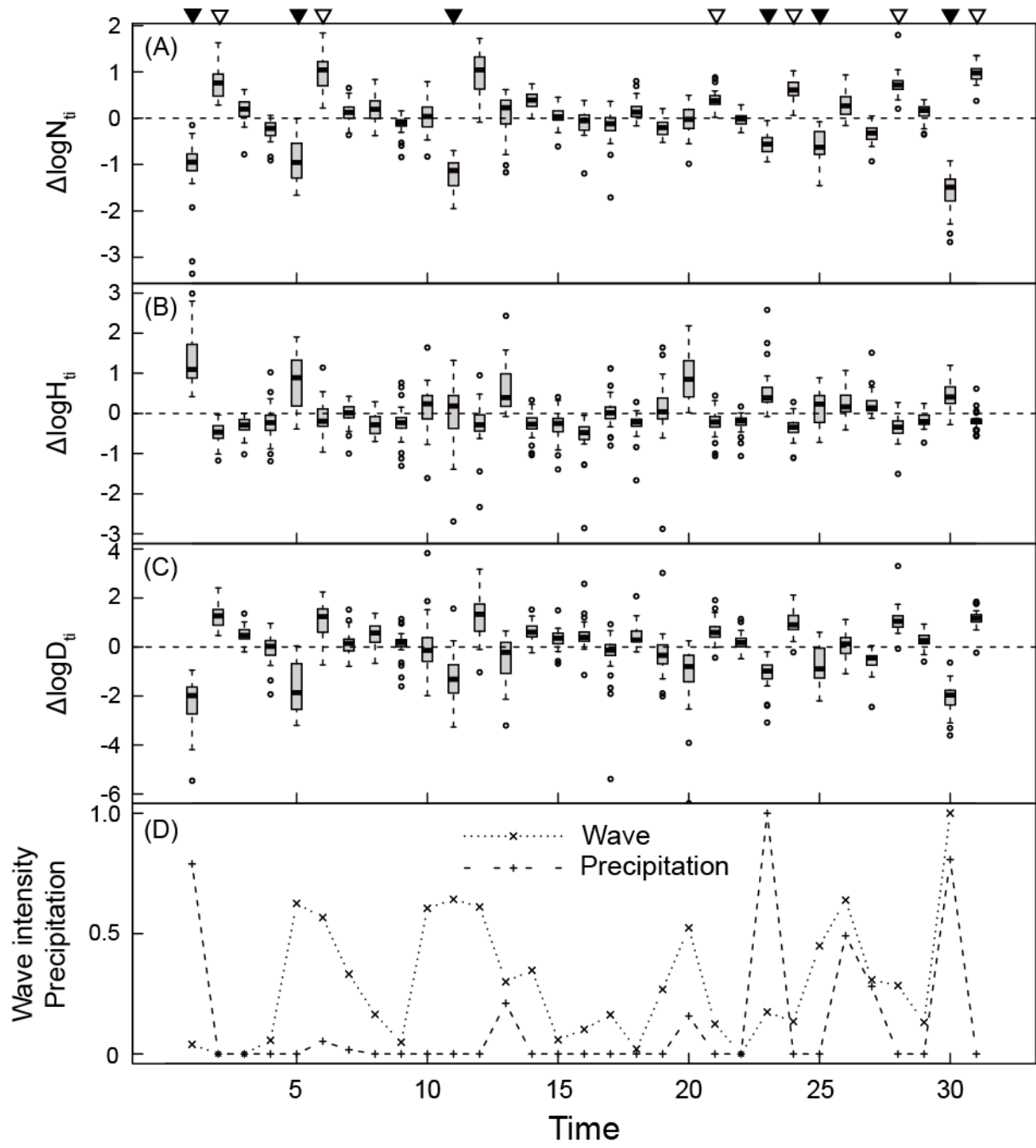


Fig. 6. An example of relationships between (A) posterior medians of the logarithm of population growth ($\Delta \log N_t = \log N_{t+1} - \log N_t$) and posterior medians of the logarithm of population density ($\log D_{t-1}$) estimated in our original model and (B) posterior medians of the logarithm of population growth and posterior medians of the logarithm of population abundance ($\log N_{t-1}$) estimated in another model with classical logistic assumption. (C) Tukey box plot of posterior medians of the square of the correlation coefficient (R^2) between $\Delta \log N_t$ and $\log D_{t-1}$ or $\log N_{t-1}$ estimated at 36 tide pools. Model “logD” indicates the modified logistic model in which the population growth rate was assumed to be a function of log population density, whereas model “logN” indicates the classical logistic model in which the population growth rate was assumed to be a function of log population abundance.

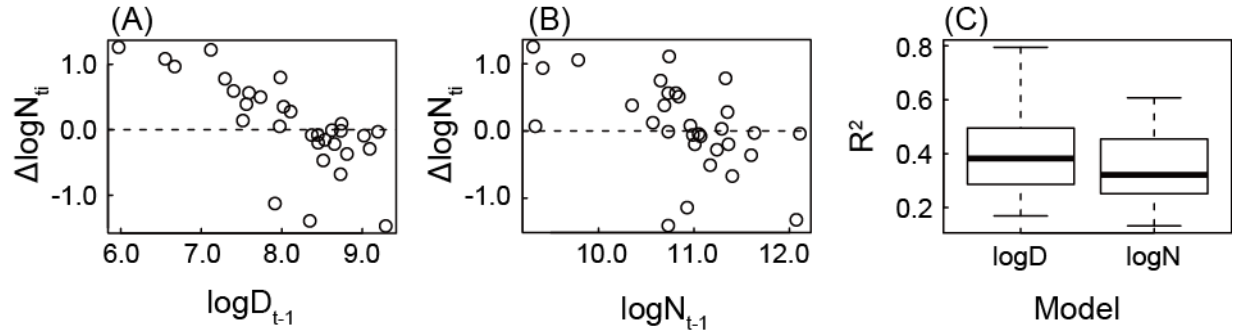
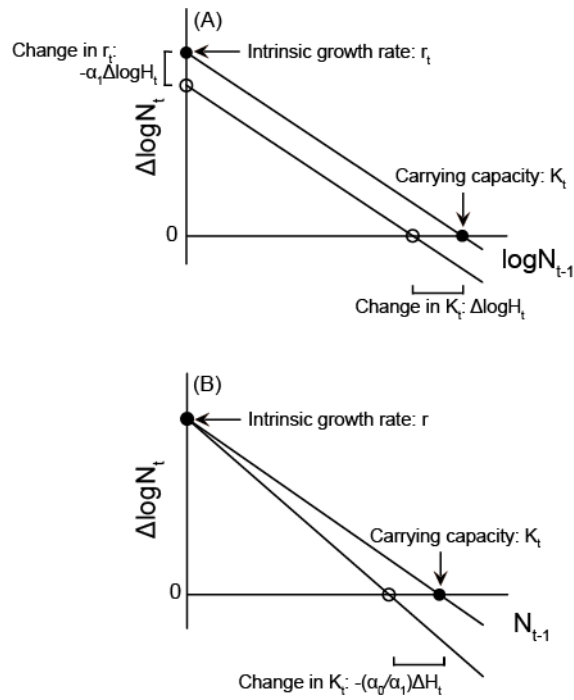


Fig. 7. Effects of changes in habitat size ($\Delta \log H_t = \log H_{t+1} - \log H_t$ or $\Delta H_t = H_{t+1} - H_t$) on intrinsic growth rate (r) and carrying capacity (K) in the Gompertz population model (A) and in the Ricker population model (B). White and black circles represent intrinsic growth rate and carrying capacity under low and high water volume, respectively.



Appendix A1

Let log of population density at time t , $\log D_t$, be defined by two random variables with finite variances, log of population abundance $\log N_t$ and log of habitat size $\log H_t$, as follows:

$$\log D_t = \log N_t - \log H_t. \quad (\text{A1-1})$$

Because $\log D_t$ is a random variable comprised of two additive random variables, the mean and variance of $\log D_t$ and the lag-0 cross-covariance and cross-correlation between $\log N_t$ and $\log D_t$ can be represented as a function of the mean, variance, and lag-0 cross-covariance of $\log N_t$ and $\log H_t$, respectively.

Mean of $\log D_t$

$$E(\log D) = E(\log N) - E(\log H). \quad (\text{A1-2})$$

Variance of $\log D_t$

$$\text{Var}(\log D) = \text{Var}(\log N) + \text{Var}(\log H) - 2\text{Cov}(\log N, \log H), \quad (\text{A1-3a})$$

which is equal to

$$\frac{\text{Var}(\log D)}{\text{Var}(\log N)} = 1 + \frac{[\text{Var}(\log H) - 2\text{Cov}(\log N, \log H)]}{\text{Var}(\log N)}. \quad (\text{A1-3b})$$

Lag-0 cross-covariance between $\log N_t$ and $\log D_t$

$$\text{Cov}(\log N, \log D) = \text{Var}(\log N) - \text{Cov}(\log N, \log H). \quad (\text{A1-4})$$

Lag-0 cross-correlation between $\log N_t$ and $\log D_t$

$$\begin{aligned} \text{Cor}(\log N, \log D) &= \frac{\text{Cov}(\log N, \log D)}{\text{Var}(\log N)^{1/2} \text{Var}(\log D)^{1/2}} \\ &= \frac{\text{Var}(\log N) - \text{Cov}(\log N, \log H)}{\text{Var}(\log N)^{1/2} [\text{Var}(\log N) + \text{Var}(\log H) - 2\text{Cov}(\log N, \log H)]^{1/2}}. \end{aligned} \quad (\text{A1-5})$$

Implications for patterns of population dynamics

These results indicate that the divergence between trajectories of abundance and density, with

respect to the correlation between them ($\text{Cor}[\log N, \log D]$: Eqn [A1-5]) and the variability of density relative to abundance ($\text{Var}[\log D]/\text{Var}[\log N]$: Eqn [A1-3b]), depends on the extent of habitat size variability ($\text{Var}[\log H]$) and lag-0 cross-covariance between abundance and habitat size ($\text{Cov}[\log N, \log H]$). Generally, an increase in $\text{Var}(\log H)$ causes both a decrease in $\text{Cor}(\log N, \log D)$ and an increase in $\text{Var}(\log D)/\text{Var}(\log N)$, whereas $\text{Cov}(\log N, \log H)$ has opposite effects on them.

Correlation between trajectories of abundance and density: Eqn (A1-5) suggests that

- (1) When the implicit assumption of the classical logistic model, invariability of habitat size (i.e., $\text{Var}[\log H] = 0$ and hence $\text{Cov}[\log N, \log H] = 0$) holds, fluctuations in abundance and density are perfectly correlated (i.e., $\text{Cor}[\log N, \log D] = 1$).
- (2) Because the variance of habitat size ($\text{Var}[\log H]$) increases the denominator in Eqn (A1-5), it decreases the lag-0 cross-correlation between log abundance and density.
- (3) The lag-0 cross-correlation between log abundance and density is positive when $\text{Cov}(\log N, \log H) < \text{Var}(\log N)$, but it is negative when $\text{Cov}(\log N, \log H) > \text{Var}(\log N)$. Negative cross-correlation can be realized only when variability in habitat size is larger than that in abundance (i.e., $\text{Var}[\log H] > \text{Var}[\log N]$) because

the Cauchy-Schwartz inequality,

$$\text{Cov}(\log N, \log H) \leq \text{Var}(\log N)^{1/2} \text{Var}(\log H)^{1/2}, \quad (\text{A1-6})$$

indicates that $\text{Cov}(\log N, \log H) < \text{Var}(\log N)$ is invariably true when $\text{Var}(\log H) < \text{Var}(\log N)$ because $\text{Var}(\log N)^{1/2} \text{Var}(\log H)^{1/2} < \text{Var}(\log N)$.

Variability of population density relative to population abundance: Eqn (A1-3b) suggests that

- (1) When the implicit assumption of the classical logistic model, invariability of habitat size (i.e., $\text{Var}[\log H] = 0$, and hence $\text{Cov}[\log N, \log H] = 0$), holds, the amplitude of density fluctuation is the same as that of abundance fluctuation (i.e., $\text{Var}[\log D]/\text{Var}[\log N] = 1$).
- (2) Because variance of habitat size ($\text{Var}[\log H]$) increases the numerator of the second term of the right side of Eqn (A1-3b), it increases the variability of density relative to abundance.
- (3) The variability of density is larger than that of abundance (i.e., $\text{Var}[\log D]/\text{Var}[\log N] > 1$) when $\text{Cov}(\log N, \log H) < \text{Var}(\log H)/2$ but it is smaller

(i.e., $\text{Var}[\log D]/\text{Var}[\log N] < 1$) when $\text{Cov}(\log N, \log H) > \text{Var}(\log H)/2$. The latter case can be realized only when variability in abundance is larger than one-quarter that of habitat size (i.e., $\text{Var}[\log N] > \text{Var}[\log H]/4$) because the Cauchy-Schwartz inequality (Eqn [A1-6]) indicates that $\text{Cov}(\log N, \log H) < \text{Var}(\log H)/2$ is invariably true when $\text{Var}(\log N) < \text{Var}(\log H)/4$ because $\text{Var}(\log N)^{1/2}\text{Var}(\log H)^{1/2} < \text{Var}(\log H)/2$.

Appendix A2

We analyzed data within the framework of state-space modeling (Clark 2007, Royle and Dorazio 2008, Link and Barker 2010), which is composed of two submodels, a process model representing the underlying dynamics of unobserved state variables and a data model describing the sampling process of data. By taking observation error into account, this approach enabled us to obtain less biased estimates of dynamic parameters and to accommodate missing data in the analysis (Clark and Bjørnstad 2004, Freckleton et al. 2006). We developed a hierarchically structured state-space model with a process model representing the dynamics of population abundance of *T. japonicus* and water volume at each tide pool and a data model representing the observation process of population density and water volume.

A fully Bayesian approach was adopted to fit the model to the data because the Bayesian paradigm is ideal for fitting state-space models that contain many latent variables (Clark and Bjørnstad 2004, Clark 2007, Royle and Dorazio 2008). The Bayesian approach is also advantageous for ecological studies because it enables the acquisition of a posterior distribution of derived parameters (i.e., parameters that are a function of estimated parameters), which can often provide various ecological insights (Royle and Dorazio 2008, Link and Barker 2010).

Data, latent variables, and derived parameters involved in the model are summarized in Appendix A3.

Data model: The number of *T. japonicus* individuals in a sample was assumed to be generated by an overdispersed Poisson process. The number of individuals in the j th sample collected at tide pool i on census date t , n_{tij} , was assumed to follow a Poisson distribution with an intensity of λ_{tij} :

$$n_{tij} \sim \text{Po}(\lambda_{tij}), \quad (\text{A2-1})$$

where λ_{tij} is assumed to follow a normal distribution:

$$\log \lambda_{tij} \sim N(\log D_{ti} + \log v_{\text{sample } ti}, \sigma_{\text{obsn}}^2). \quad (\text{A2-2})$$

Here D_{ti} is the unobserved population density (individuals/L) and $v_{\text{sample } ti}$ is the amount of water sampled (L) at tide pool i on census date t , and σ_{obsn}^2 is a parameter determining the overdispersion of Poisson processes. Note that the average of the normal distribution

$\log D_{ti} + \log v_{\text{sample } ti}$ corresponds to $\log(D_{ti} \times v_{\text{sample } ti})$, which represents the expected number

of individuals in the sample.

The water volume data were assumed to have a log-normal error. That is, the logarithm of the water volume observed at tide pool i on census date t , v_{ti} , was assumed to follow a normal distribution:

$$\log v_{ti} \sim N(\log H_{ti}, \sigma_{\text{obsv}}^2), \quad (\text{A2-3})$$

where H_{ti} is the unobserved water volume (L) of tide pool i on census date t and σ_{obsv}^2 is the variance of the observation error.

Process model: Wave intensity and precipitation were considered as determinants of population growth and changes in water volume. Population density was also included in the model of population growth. With N_{ti} representing population abundance (individuals) and D_{ti} population density (individuals/L) at tide pool i on census date t and W_{t-1} is scaled average wave intensity and P_{t-1} is scaled precipitation observed between census dates $t-1$ and t , the dynamics of N_{ti} and H_{ti} were described as follows:

$$\log N_{ti} = \log N_{t-1i} + \alpha_{0i} + \alpha_{1i} \log D_{t-1i} + \alpha_{2i} W_{t-1} + \alpha_{3i} P_{t-1} + \omega_{Nt-1} + \varepsilon_{Nt-1i} \quad (\text{A2-4a})$$

$$\log H_{ti} = \log H_{t-1i} + \beta_{0i} + \beta_{1i} W_{t-1} + \beta_{2i} P_{t-1} + \omega_{Ht-1} + \varepsilon_{Ht-1i} \quad (\text{A2-4b})$$

$$(\omega_{Nt-1}, \omega_{Ht-1})' \sim \text{MN}((0,0)', \Sigma_{\omega}) \quad (\text{A2-4c})$$

$$(\varepsilon_{Nt-1i}, \varepsilon_{Ht-1i})' \sim \text{MN}((0,0)', \Sigma_{\varepsilon}), \quad (\text{A2-4d})$$

where α_{0i} , α_{1i} , α_{2i} , and α_{3i} represent intrinsic growth rate, the strength of density dependence, and the effects of wave intensity and precipitation, respectively, on population growth at tide pool i ; β_{0i} , β_{1i} , and β_{2i} represent average volume change when there were no waves or precipitation and the effects of wave intensity and precipitation on volume change, respectively, at tide pool i ; ω_{Nt-1} and ω_{Ht-1} represent stochastic fluctuation in population abundance and water volume, respectively, which simultaneously affects all tide pools; ε_{Nt-1i} and ε_{Ht-1i} represent stochastic fluctuation in population abundance and water volume, respectively, which affects each tide pool independently; and Σ_{ω} and Σ_{ε} represent the covariance matrix of ω and ε , respectively. Note that although the equation for population abundance (Eqn [A2-4a]) is similar to a log-linear Gompertz population model (Royama 1992, Turchin 2003), it is not the same because population abundance and density are explicitly separated.

The parameters determining changes in population abundance and water volume should differ among tide pools, depending on the environmental conditions, topography, and spatial location of each tide pool. To incorporate such spatial heterogeneity, we specified different

parameter values for each tide pool. Spatial variation in parameters determining changes in population abundance and water volume were assumed to follow multinormal distributions:

$$(\alpha_{0i}, \alpha_{1i}, \alpha_{2i}, \alpha_{3i})' \sim \text{MN}((\mu_{\alpha_0}, \mu_{\alpha_1}, \mu_{\alpha_2}, \mu_{\alpha_3})', \Sigma_{\alpha}) \quad (\text{A2-5a})$$

$$(\beta_{0i}, \beta_{1i}, \beta_{2i})' \sim \text{MN}((\mu_{\beta_0}, \mu_{\beta_1}, \mu_{\beta_2})', \Sigma_{\beta}), \quad (\text{A2-5b})$$

where μ_{α_0} , μ_{α_1} , μ_{α_2} , μ_{α_3} , μ_{β_0} , μ_{β_1} , and μ_{β_2} are the regional average of α_{0i} , α_{1i} , α_{2i} , α_{3i} , β_{0i} , β_{1i} , and β_{2i} , respectively, and Σ_{α} and Σ_{β} are the covariance matrices of $(\alpha_{0i}, \alpha_{1i}, \alpha_{2i}, \alpha_{3i})'$ and $(\beta_{0i}, \beta_{1i}, \beta_{2i})'$, respectively.

Population density at tide pool i on census date t (individuals/L), D_{ti} , was specified by dividing population abundance, N_{ti} (individuals), by water volume, H_{ti} (L). The logarithmic form was represented as follows:

$$\log D_{ti} = \log N_{ti} - \log H_{ti}. \quad (\text{A2-6})$$

Derived parameters: As derived parameters, we obtained the logarithm of changes in population abundance ($\Delta \log N_{ti}$), population density ($\Delta \log D_{ti}$), and water volume ($\Delta \log H_{ti}$) for each time and pool. We also calculated the variance of population abundance ($\text{Var}[\log N]$),

density ($\text{Var}[\log D]$), and water volume ($\text{Var}[\log H]$); the lag-0 cross-correlation between the logarithm of population abundance and the logarithm of population density ($\text{Cor}[\log N, \log D]$); and the scaled variability of population density relative to abundance ($\text{Var}[\log D]/\text{Var}[\log N]$) at each tide pool.

Letting X_{ti} be a latent variable in the model (i.e., population abundance, N ; population density, D ; and water volume, H), the logarithm of changes in variable X_{ti} ($\Delta \log X_{ti}$) for time t at tide pool i is calculated as follows:

$$\Delta \log X_{ti} = \log X_{t+1i} - \log X_{ti}. \quad (\text{A2-7})$$

Letting T as the length of time-series, the variance of $\log X_t$ at a tide pool is calculated as follows:

$$\text{Var}(\log X) = \frac{1}{T} \sum_{t=1}^T \{\log X_t - E(\log X)\}^2, \quad (\text{A2-8})$$

where $E(\log X)$ is the empirical mean of $\log X_t$ time series (Cressie and Wikle 2011).

The correlation between log population abundance and density at a tide pool is calculated by the zero-order cross correlation function, as follows (Cressie and Wikle 2011):

$$\text{Cor}(\log N, \log D) = \frac{\frac{1}{T} \sum_{t=1}^T \{\log N_t - E(\log N)\} \{\log D_t - E(\log D)\}}{\text{Var}(\log N)^{1/2} \text{Var}(\log D)^{1/2}}. \quad (\text{A2-9})$$

The scaled variance of population density relative to the variance of population abundance at a tide pool is calculated by dividing $\text{Var}(\log D)$ by $\text{Var}(\log N)$.

Parameter estimation and assessment of model adequacy: The model was fitted to the data by the Markov chain Monte Carlo method in WinBUGS (Lunn et al. 2000). Vague priors were specified to parameters and hyperparameters as follows: uniform prior $[U(0, 10,000)]$ was specified for σ_{obsn} and σ_{obsv} ; normal prior $[N(0, 100^2)]$ was specified for μ_{α_0} , μ_{α_1} , μ_{α_2} , μ_{α_3} , μ_{β_0} , μ_{β_1} , and μ_{β_2} ; inverse-Wishart prior was specified for Σ_{α} $[IW(\text{diag}(1, 4), 4)]$, Σ_{β} $[IW(\text{diag}(1, 3), 3)]$, and Σ_{ω} and Σ_{ϵ} $[IW(\text{diag}(1, 2), 2)]$, where $\text{diag}(x, n)$ indicates an $n \times n$ diagonal matrix with diagonal elements x . To confirm the independence of the posterior probability on initial values, three independent iterations were executed. Estimates were obtained from 1,500,000 iterations after a burn-in of 100,000 iterations, thinning at intervals of 500 in order to save memory. The BUGS code of the fitted model and a R script of sample data is provided in Appendix A4 and A5.

Convergence of posterior was monitored with the Gelman–Rubin diagnostic ($\hat{R}$).

Gelman et al. (2004a) suggested that convergence will be acceptable if $\hat{R}$ were below 1.1 for all parameters of interest. In our model, although the value of $\hat{R}$ was about 1.14 for four nuisance parameters ($\log\lambda_{tij}$), it was lower than 1.03 for all other parameters, indicating that our posterior can be treated as a sample from the target distribution.

The goodness-of-fit of the model was evaluated by posterior predictive assessment using a χ^2 discrepancy quantity defined as $T(\mathbf{y}, \boldsymbol{\theta}) = \sum_i \frac{[y_i - E(y_i | \boldsymbol{\theta})]^2}{\text{var}(y_i | \boldsymbol{\theta})}$, where y_i represents the univariate responses and $\mathbf{y}$ represents their vector, and $\boldsymbol{\theta}$ is the model parameter (Gelman et al. 2004b). The posterior predictive p-value was calculated as $p = \Pr[T(\mathbf{y}^{\text{rep}}, \boldsymbol{\theta}) \geq T(\mathbf{y}, \boldsymbol{\theta}) | \mathbf{y}]$, where $\mathbf{y}^{\text{rep}}$ is a vector of the posterior predictive value of the data.

In Bayesian inference the choice of prior matters for the estimation of variance for random effects, particularly in cases where the number of units is small or group-level variance is close to zero (Lambert et al. 2005, Gelman 2006). For example, studies have suggested that group-level variance may not be appropriately estimated when the number of units is less than five (Lambert et al. 2005, Gelman 2006) or when the group-level variance is less than 0.001 (Lambert et al. 2005). However, this was not the case for our results. The number of examined tide pools in our study was larger than 30, so we could expect the number of units for random effects to have been sufficient to estimate group-level variance appropriately (Lambert et al.

2005). In addition, our posterior estimates for group-level variance were generally larger than the order of two decimal places. In fact, despite having tested several different priors, our primary results reported here were consistent with regard to choice of priors (Fukaya et al. results not shown).

References

Clark, J. S. 2007. Models for ecological data: an introduction. - Princeton University Press.

Clark, J. S. and Bjørnstad, O. N. 2004. Population time series: process variability, observation errors, missing values, lags, and hidden states. - Ecology 85: 3140-3150.

Cressie, N. and Wikle, C. K. 2011. Statistics for spatio-temporal data. - Wiley.

Freckleton, R. P. et al. 2006. Census error and the detection of density dependence. – J. Animal Ecol. 75: 837-851.

Gelman, A. 2006. Prior distributions for variance parameters in hierarchical models. - Bayesian Analysis 1: 515-533.

Gelman, A. et al. 2004a. Posterior simulation. - In: Bayesian Data Analysis. Second Edi. Chapman & Hall, pp. 283-310.

Gelman, A. et al. 2004b. Model checking and improvement. - In: Bayesian Data Analysis.

Second Ed. Chapman & Hall, pp. 157-196.

Lambert, P. C. et al. 2005. How vague is vague? A simulation study of the impact of the use of

vague prior distributions in MCMC using WinBUGS. - Statistics in Medicine 24:

2401-2428.

Link, W. A. and Barker, R. J. 2010. Bayesian inference: with ecological applications. -

Academic Press.

Lunn, D. J. et al. 2000. WinBUGS-a Bayesian modelling framework: concepts, structure, and

extensibility. - Statistics and Computing 10: 325-337.

Royama, T. 1992. Analytical population dynamics. - Chapman & Hall.

Royle, J. A. and Dorazio, R. M. 2008. Hierarchical modeling and inference in ecology: the

analysis of data from populations, metapopulations and communities. - Academic Press.

Turchin, P. 2003. Complex population dynamics: a theoretical/empirical synthesis. - Princeton

University Press.

Appendix A3

Table A3-1. Data, latent variables and derived parameters involved in the model.

Variable	Description
Data	
n_{tij}	Number of individuals in the j th sample collected at tide pool i on census date t
V_{ti}	Water volume observed at tide pool i on census date t
$V_{\text{sample } ti}$	Amount of water sampled at tide pool i on census date t
W_t	Scaled average wave intensity observed between census dates t and $t+1$
P_t	Scaled precipitation observed between census dates t and $t+1$
Unobserved latent variables	
N_{ti}	Population abundance at tide pool i on census date t

D_{ti} Population density at tide pool i on census date t

H_{ti} Water volume of tide pool i on census date t

Parameters and hyperparameters

λ_{tij} Intensity of Poisson process for n_{tij}

σ_{obsn}^2 Variance of λ_{tij}

σ_{obsv}^2 Observation variance of v_{ti}

$\alpha_{0i}, \alpha_{1i}, \alpha_{2i}, \alpha_{3i}$ Parameters determining population growth of tide pool i

$\beta_{0i}, \beta_{1i}, \beta_{2i}$ Parameters determining change in water volume of tide pool i

$\mu_{\alpha_0}, \mu_{\alpha_1}, \mu_{\alpha_2}, \mu_{\alpha_3}, \mu_{\beta_0}, \mu_{\beta_1}, \mu_{\beta_2}$ Regional averages of $\alpha_{0i}, \alpha_{1i}, \alpha_{2i}, \alpha_{3i}, \beta_{0i}, \beta_{1i}$ and β_{2i}

$\Sigma_{\alpha}, \Sigma_{\beta}$ Covariance matrix of α and β values

ω_{Nt}, ω_{Ht} Stochastic fluctuation of population abundance and water volume between census dates t and t+1, which simultaneously affects all tide pools

$\varepsilon_{Nti}, \varepsilon_{Hti}$ Stochastic fluctuation of population abundance and water volume between census dates t and t+1, which affects each tide pool independently

$$\Sigma_{\omega}, \Sigma_{\varepsilon}$$

Covariance matrix of ω and ε values

Derived parameters

$$\Delta \log N_{ti}$$

Log of change in population abundance between census dates t and $t+1$ at tide pool i

$$\Delta \log D_{ti}$$

Log of change in population density between census dates t and $t+1$ at tide pool i

$$\Delta \log H_{ti}$$

Log of change in water volume between census dates t and $t+1$ at tide pool i

$$\text{Var}(\log N)$$

Temporal variance of population abundance (calculated for each tide pool)

$$\text{Var}(\log D)$$

Temporal variance of population density (calculated for each tide pool)

$$\text{Var}(\log H)$$

Temporal variance of water volume (calculated for each tide pool)

$$\text{Cor}(\log N, \log D)$$

Correlation coefficient between the logarithm of population abundance and logarithm of population density (calculated for each tide pool)

$\text{Var}(\log D)/\text{Var}(\log N)$

Scaled variability of population density relative to
abundance (calculated for each tide pool)

Appendix A4

```
model{

  ### Data model #####

  ## Observation of population density

  for (i in 1:N.pool) { # For each tide pool

    for (t in 1:N.time) { # For each observation

      for (k in 1:3) { # No of individuals in each sample

        cnt[t, i, k] ~ dpois(lambda[t, i, k])

        log(lambda[t, i, k]) <- max(-15, min(log.lambda[t,

          i, k], 15))

        log.lambda[t, i, k] ~ dnorm(m.log.lambda[t, i],

          prec.obs[1])

      }

      ## Expected number of individuals is D[inds/L] * v.samp[L]

      m.log.lambda[t, i] <- log.D[t, i] + log.v.samp[t, i]

      ## Observation of volume
```

```

log.v[t, i] ~ dnorm(log.N.H[t, i, 2], prec.obs[2])

}

}

### End of Data model #####

### Process model #####

for (i in 1:N.pool) { # For each tide pool

  for (j in 1:2) { # For abundance and volume (t = 1)

    log.N.H[1, i, j] ~ dnorm(0.0, 0.0001)

  }

  ## density (t = 1)

  log.D[1, i] <- log.N.H[1, i, 1] - log.N.H[1, i, 2]

}

for (t in 2:N.time) { # For each observation (t > 1)

  for (i in 1:N.pool) { # For each tide pool

    log.N.H[t, i, 1:2] ~ dmnorm(M.log.N.H[t, i, ], Prec.N.H[, ])

```

```

## abundance (t > 2)

M.log.N.H[t, i, 1] <- (log.N.H[t - 1, i, 1] + alpha[i, 1] +
alpha[i, 2] * log.D[t - 1, i] + alpha[i, 3] * wave[t - 1] + alpha[i, 4] * precipitation
[t - 1] + omega[t - 1, 1])

## volume (t > 2)

M.log.N.H[t, i, 2] <- (log.N.H[t - 1, i, 2] + beta[i, 1] + beta[i,
2] * wave[t - 1] + beta[i, 3] * precipitation [t - 1] + omega[t - 1, 2])

## density (t > 2)

log.D[t, i] <- log.N.H[t, i, 1] - log.N.H[t, i, 2]

}

## regional fluctuation of abundance and volume

omega[t - 1, 1:2] ~ dmnorm(Zero[], Prec.omega[, ])

}

```



```

### Parameters ###

## Observation variance

for (k in 1:2) { # For density and volume

    prec.obs[k] <- pow(sigma.obs[k], -2)

    sigma.obs[k] ~ dunif(0, 10000)

}

## Deterministic component of abundance change

for (i in 1:N.pool) { # 1:Intrinsic growth rate, 2:Density dependence,
3:Effect of wave, 4:Effect of precipitation

    alpha[i, 1:4] ~ dmnorm(Mean.alpha[, ], Prec.alpha[, ])

}

for (j in 1:4) {# Regional averages of alpha

    Mean.alpha[j] ~ dnorm(0.0, 0.0001)

}

Prec.alpha[1:4, 1:4] ~ dwish(R1[, ], 4) # Spatial variance of alpha

```

```

## Deterministic component of volume change

for (i in 1:N.pool) {# 1:Intercept, 2: Effect of wave, 3:Effect of
precipitation

    beta[i, 1:3] ~ dnorm(Mean.beta[, ], Prec.beta[, ])

}

for (j in 1:3) {# Regional averages of beta

    Mean.beta[j] ~ dnorm(0.0, 0.0001)

}

Prec.beta[1:3, 1:3] ~ dwish(R2[, ], 3) # Spatial variance of beta

## Process error

Prec.N.H[1:2, 1:2] ~ dwish(R3[, ], 2) # Local-scale fluctuation

Prec.omega[1:2, 1:2] ~ dwish(R3[, ], 2) # Regional-scale fluctuation

### End of Process model #####

```

```
## Complementing missing values for wave

wave[31] ~ dunif(0, 1)

}
```

Notes: `N.time` and `N.pool` are number of temporal and spatial replicates respectively. `Zero` is a vector of length 2 composed of 0. `R1`, `R2`, and `R3` are four-, three-, and two-dimensional square matrices, respectively, of which diagonal elements are set to 1.

Appendix A5

```
# Specify data
```

```
N.time <- 32
```

```
N.pool <- 5
```

```
cnt <- array(c(100, 7, 11, 42, 77, 45, 118, 185, 307, 225, 167, NA, NA, 7, 2, 14,
47, 44, 56, NA, 6, 24, 56, 9, 4, 12, 10, 6, 8, 20, 5, NA, 37, 7, 16, 43,
14, 50, 35, 58, 91, 137, 232, 304, 657, 7, 10, 30, 147, 121, 147, 23, 15, 32, 70, 4,
79, 11, 11, 6, 29, 22, 3, NA, 124, 9, 24, 25, 30, 18, 21, 62, 74, 20, 87, 18,
26, 60, 8, 14, 28, 57, 41, 38, 13, 33, 44, 15, 4, 25, 10, 4, 12, 9, 6, NA,
55, 5, 40, 61, 121, 12, 35, 22, 71, 74, 43, 5, 21, 27, 65, 43, 70, 55, 64, 36,
18, 28, 47, 12, 35, 11, 41, 18, 41, 35, NA, 45, 1, 0, 4, 6, NA, 0, 1, 2,
1, 5, 4, 2, 1, 4, 7, 6, 9, 20, 9, 23, 20, 20, 23, 19, 30, 8, 7, 1, 6,
15, NA, 12, 115, 9, 7, 42, 71, 105, 169, 137, 137, 396, 176, NA, NA, 2, 7, 25, 42,
51, 57, NA, 6, 33, 71, 5, 9, 8, 10, 4, 8, 31, 1, NA, 45, 4, 15, 61, 41, 37,
50, 43, 70, 140, 94, 180, 178, 14, 42, 88, 75, 211, 100, 89, 29, 4, 13, 4, 2, 43,
37, 11, 29, 38, 4, NA, 42, 8, 14, 32, 16, 22, 34, 36, 13, 66, 32, 19, 21, 18,
19, 22, 63, 29, 66, 42, 11, 32, 19, 20, 6, 27, 11, 17, 3, 4, 5, NA, 137, 8,
```

```

21, 70, 90, 2, 30, 7, 34, 53, 25, 0, 25, 20, 90, 90, 78, 63, 91, 26, 10, 41,

39, 12, 40, 12, 26, 14, 47, 72, NA, 59, 1, 2, 0, 2, NA, 1, 1, 2, 3, 3, 2,

0, 1, 2, 5, 4, 5, 15, 19, 18, 31, 23, 17, 15, 24, 1, 6, 5, 28, 14, NA, 12, 140,

11, 6, 43, 116, 50, 84, 139, 118, 341, 164, NA, NA, 0, 4, 27, 20, 68, 112, NA, 8,

62, 41, 7, 10, 32, 16, 4, 10, 16, 4, NA, 30, 2, 10, 35, 15, 19, 28, 55, 72,

62, 112, 288, 429, 18, 31, 78, 84, 151, 41, 74, 26, 38, 33, 14, 26, 27, 17, 1, 4,

49, 8, NA, 13, 7, 11, 20, 20, 8, 30, 3, 34, 16, 16, 17, 34, 10, 9, 42, 42,

29, 42, 64, 12, 20, 28, 37, 29, 5, 11, 11, 2, 6, 8, NA, 70, 10, 21, 46, 135,

4, 25, 30, 73, 43, 35, 2, 23, 22, 98, 72, 77, 65, 86, 38, 29, 30, 41, 22, 62,

3, 34, 31, 34, 67, NA, 34, 2, 1, 0, 2, NA, 0, 3, 1, 10, 3, 4, 2, 4, 8,

1, 7, 6, 13, 15, 26, 19, 26, 16, 5, 27, 13, 5, 3, 15, 17, NA, 10), dim = c(N.time,

N.pool, 3))

log.v <- matrix(c(0.4054651, 3.8199077, 3.3877744, 2.5494452, 0.9820785,

0.9282193, 1.1216776, 1.0750024, 0.7701082, 0.1133287, -0.7133499, -2.0402208,

-5.7946911, 3.7345696, 3.4904285, 2.3915113, 0.8754687, 0.6931472,

-0.2231436, -0.9675840, 3.4904285, 2.1747517, 0.8754687, 3.8082168, 3.3322045,

2.5176965, 3.7658405, 3.8712010, 3.5380566, 2.7212954, 3.8712010, NA,

1.7227666, 3.0349530, 2.3674361, 2.1041342, 1.8764069, 1.6863990, 2.2894999,

```

2.2894999, 2.0668628, 1.7917595, 1.3686394, 0.9001613, 0.1133287, 2.7972813,
 2.2752139, 1.9459101, 1.4816045, 1.2119410, 0.7466879, -0.3147107, 2.3674361,
 2.1041342, 1.8764069, 2.8136107, 2.2617631, 1.9919755, 2.5336968, 3.2268440,
 2.4680995, 2.1162555, 3.3786109, NA, 4.6051702, 5.0751738, 4.9052748,
 4.7874917, 4.5849675, 4.4998097, 4.6496654, 4.6921732, 4.6921732, 4.6321042,
 4.4810798, 4.3781441, 4.3583741, 5.0470315, 4.9296421, 4.8415853, 4.5217886,
 4.6582369, 4.3702071, 4.3583741, 4.9416424, 4.7004804, 4.9052748, 4.9052748,
 4.9296421, 4.8415853, 4.9175693, 5.0470315, 5.0398057, 5.0325925, 5.0751738,
 NA, 1.2809338, 2.2049723, 1.8357764, 1.6863990, 1.2237754, 2.1126345, 1.9740810,
 1.9740810, 1.7917595, 1.4255151, 1.9459101, 2.1894164, 2.0541237, 2.1894164,
 1.9169226, 1.9169226, 1.6292405, 1.5107219, 1.3029128, 2.2192035, 1.8357764,
 1.9169226, 1.8131947, 2.1598688, 1.9740810, 2.0014800, 2.1126345, 2.3795461,
 1.8870696, 2.0281482, NA, 2.0281482, 2.4159138, 2.9856819, 2.7317667, 2.4159138,
 2.1282317, 2.9957323, 2.9549103, 2.9549103, 2.7625384, 2.5741378, 2.9652731,
 2.9123507, 2.8975680, 3.0910425, 2.9549103, 2.8495498, 2.5862591, 2.6297282,
 2.4300984, 2.5176965, 3.0349530, 2.8587664, 2.6100698, 2.8402474, 2.7625384,
 3.0349530, 3.1497401, 3.0910425, 2.9856819, 2.9652731, NA, 2.9755296),
 N.time, N.pool)

[illegible]

```

-3.912023, -3.912023, -4.000000, -3.912023, -3.912023, -3.912023, -3.912023,
-3.912023, -4.000000, -3.912023, -3.912023, -3.912023, -3.912023, -3.912023,
-3.912023, -3.912023, -3.912023, -3.912023, -3.912023, -3.912023, -3.912023,
-3.912023, -3.912023, -3.912023, -3.912023, -3.912023, -3.912023, -3.912023,
-3.912023, -3.912023, -3.912023, -3.912023, -3.912023, -3.912023, -4.000000,
-3.912023), N.time, N.pool)

```

```

precipitation <- c(0.78947368, 0.00000000, 0.00000000, 0.00000000, 0.00000000,
0.05263158, 0.01754386, 0.00000000, 0.00000000, 0.00000000, 0.00000000,
0.00000000, 0.21052632, 0.00000000, 0.00000000, 0.00000000, 0.00000000,
0.00000000, 0.00000000, 0.15789474, 0.00000000, 0.00000000, 1.00000000,
0.00000000, 0.00000000, 0.49122807, 0.28070175, 0.00000000, 0.00000000,
0.80701754, 0.00000000, NA)

```

```

wave <- c(0.03993886, 0.00000000, 0.00000000, 0.05631555, 0.62504154, 0.56643980,
0.33192423, 0.16418128, 0.04847837, 0.60481497, 0.64231158, 0.61046082,
0.29998710, 0.34766102, 0.05922753, 0.10221290, 0.16249540, 0.02028816,
0.26796455, 0.52373666, 0.12465345, 0.00000000, 0.17394329, 0.13466182,
0.44905628, 0.63913615, 0.30745595, 0.28429158, 0.13167998, 1.00000000, NA,
NA)

```



```

# Label each dimension of data

dimnames(cnt) <- list(sprintf("time%s", 1:N.time), sprintf("pool%s", 1:N.pool),
NULL)

dimnames(log.v) <- dimnames(log.v.samp) <- list(sprintf("time%s", 1:N.time),
sprintf("pool%s", 1:N.pool))

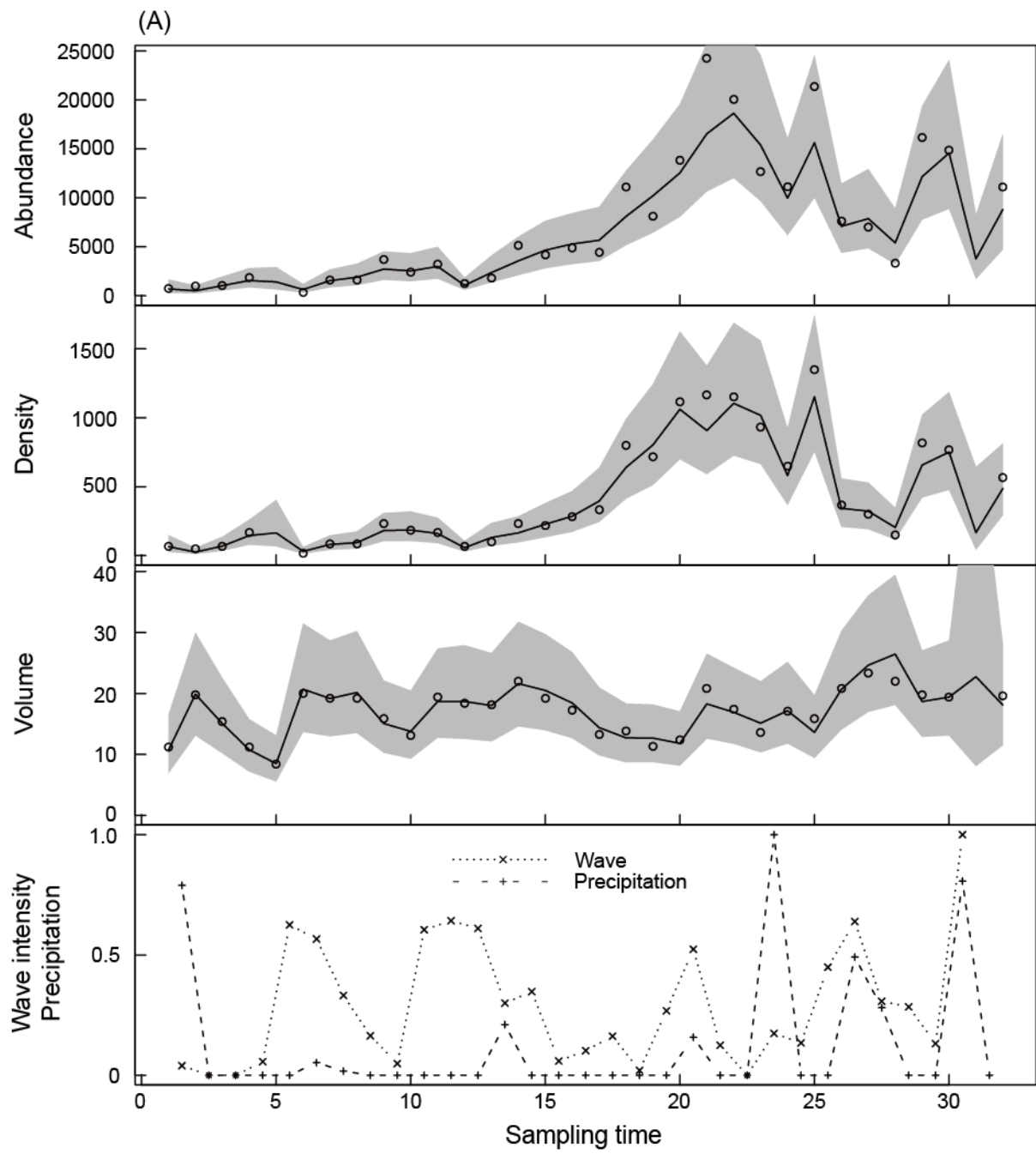
names(precipitation) <- names(wave) <- sprintf("time%s", 1:N.time)

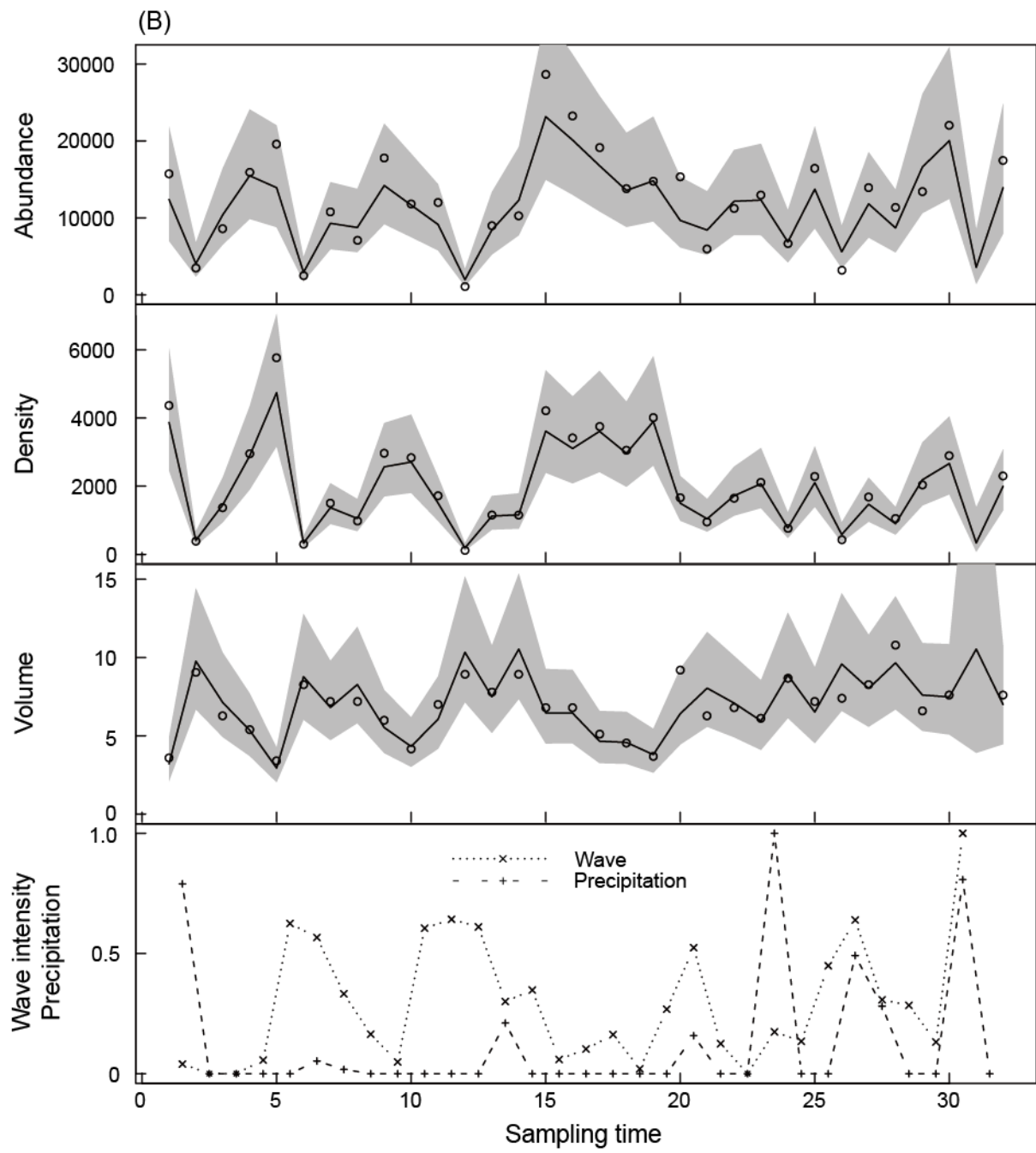
```

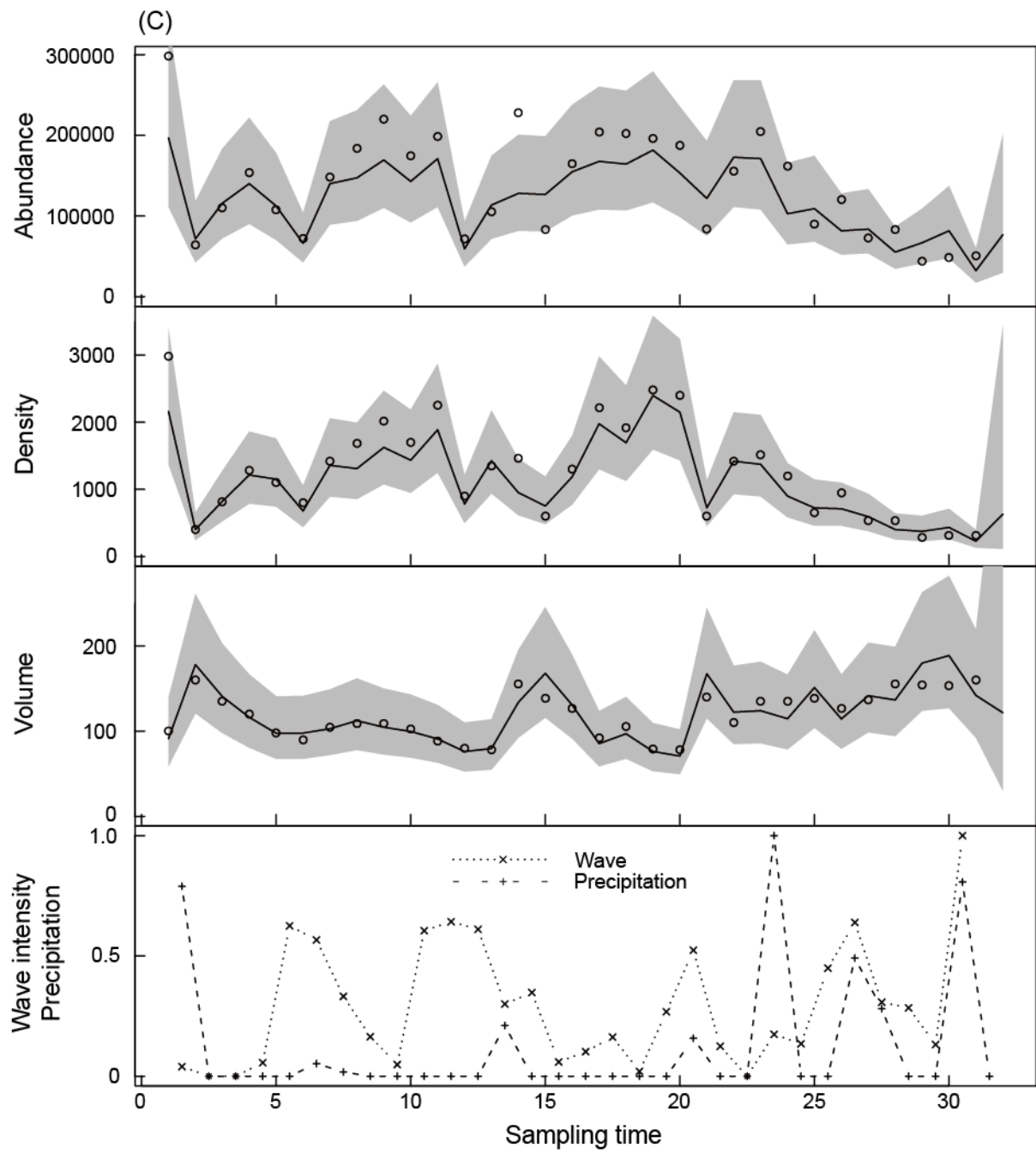
Note: Sample data provided here correspond to those of five tide pools which we showed population trajectories in Appendix A6. Note that posterior with this sample data may be different from our results because data used for parameter inference is not same although it is subset of complete data we used.

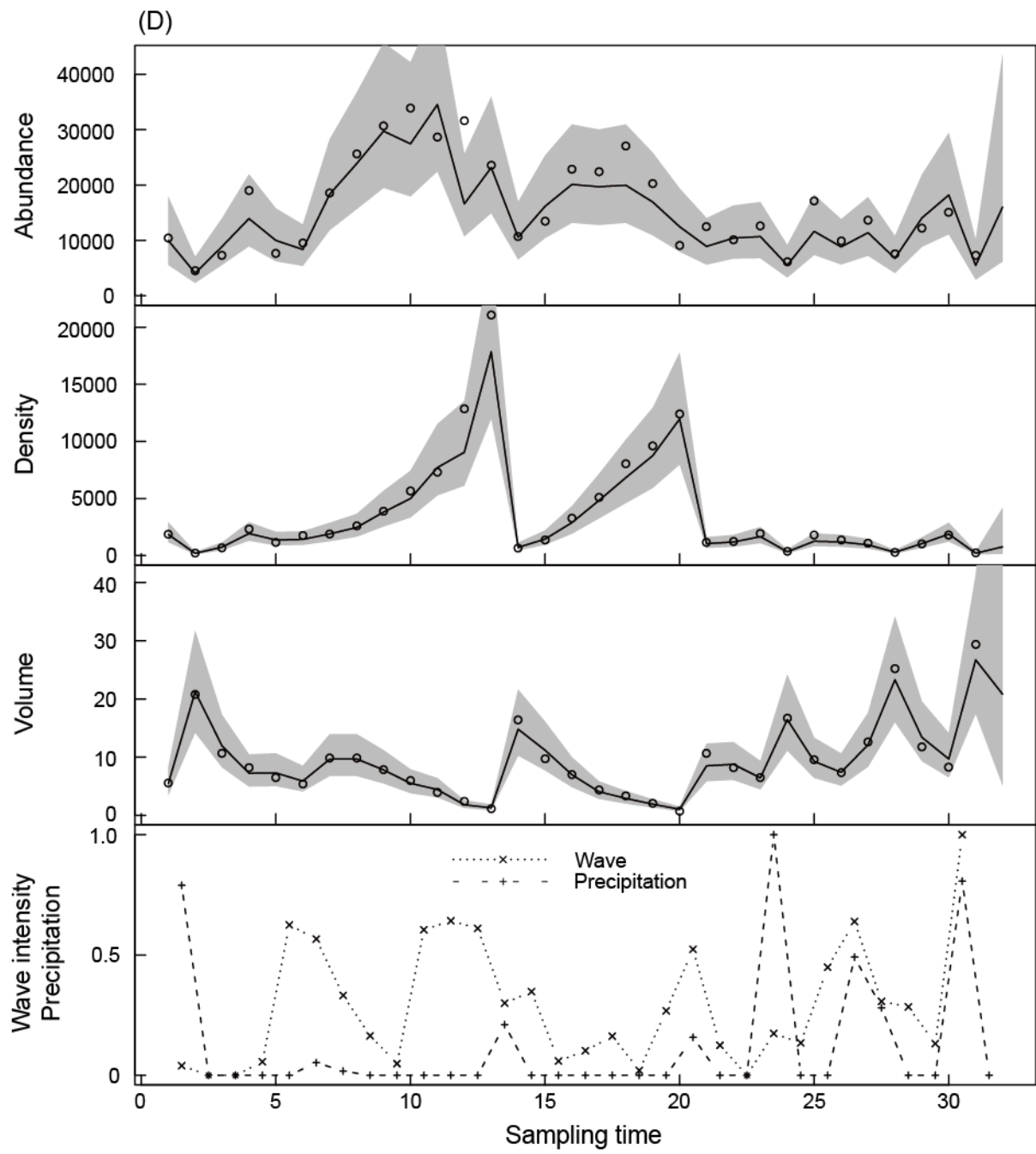
Appendix A6

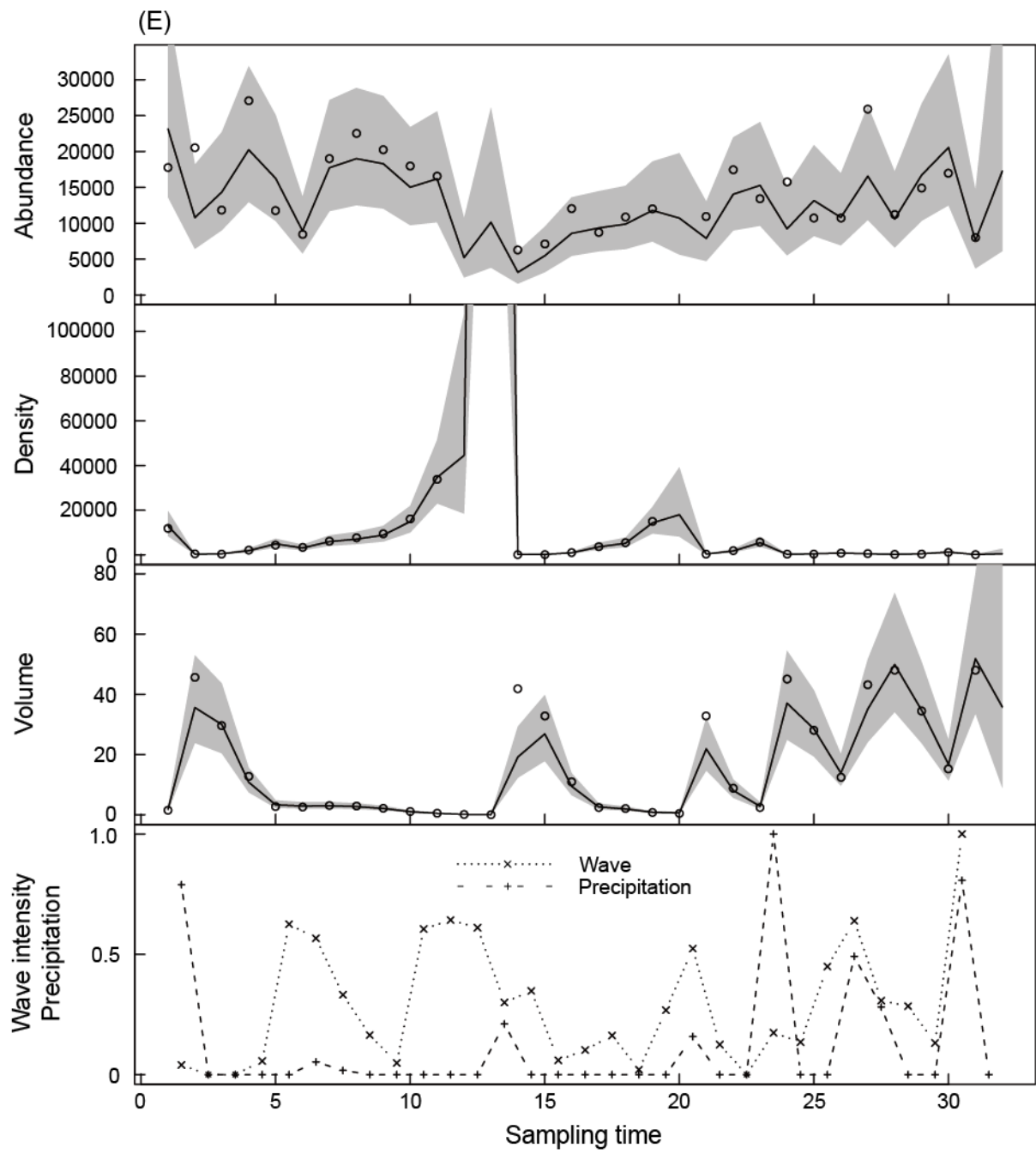
Fig. A6-1. Fluctuations of population abundance (individuals) and density (individuals/L) of *Tigriopus japonicus* and water volume (L) in the tide pool with the highest abundance–density correlation (A, correlation coefficient = 0.96), medium-high correlation (B, correlation coefficient = 0.90), medium correlation (C, correlation coefficient = 0.85), medium-low correlation (D, correlation coefficient = 0.76), and the lowest correlation (E, correlation coefficient = 0.25). Open circles, solid lines, and shaded gray represent observed values, posterior medians, and 95% credible intervals, respectively. Scaled wave intensity and scaled precipitation are shown in the lowest row of each figure. Data of these tide pools are provided in Appendix A5.











Appendix A7

Fig. A7-1. Posterior median of parameters determining changes in population abundance (α_{0i} , α_{1i} , α_{2i} , and α_{3i}) and water volume (β_{0i} , β_{1i} , and β_{2i}) estimated at 36 tide pools. Model “logD” indicates the modified logistic model in which population growth rate was assumed to be a function of log population density, whereas model “logN” indicates the classical logistic model in which population growth rate was assumed to be a function of log population abundance.

