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Larval dispersal dampens population fluctuation and shapes the interspecific spatial distribution patterns of rocky intertidal gastropods

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Abstract

Many marine benthic invertebrates pass through a planktonic larval stage whereas others spend their entire lifetimes in benthic habitats. Recent studies indicate that non-planktonic species show relatively greater fine-scale patchiness than do planktonic species, but the underlying mechanisms remain unknown. One hypothesis for such a difference is that larval dispersal enhances the connectivity of populations and buffers population fluctuations and reduces local extinction risk, consequently increasing patch occupancy rate and decreasing spatial patchiness. If this mechanism does indeed play a significant role, then the distribution of non-planktonic species should be more aggregated—both temporally and spatially—than the distribution of species with a planktonic larval stage. To test this prediction, we compared (1) both the spatial and the temporal abundance–occupancy relationships and (2) both the spatial and the temporal mean–variance relationships of population size across species of rocky intertidal gastropods with differing dispersive traits from the Pacific coast of Japan. We found that, compared to planktonic species, non-planktonic species exhibited (1) a smaller occupancy rate for any given level of mean population size and (2) greater variations in population size, both spatially and temporally. This suggests that the macroecological patterns observed in this study (i.e., the abundance–occupancy relationships and mean–variance relationships of population size across species) were shaped by the effect of larval dispersal dampening population fluctuation, which works over both space and time. While it has been widely assumed that larval dispersal enhances population fluctuations, larval dispersal may in fact enhance the connectivity of populations and buffer population fluctuations and reduce local extinction risks.

1. Introduction

Many marine benthic invertebrates pass through a planktonic larval stage after hatching, whereas others completely lack any planktonic dispersal stage and spend their entire lifetimes in benthic habitats (Thorson 1946, 1950, Strathmann 1985, Bhaud 1993). Such variation in developmental mode is commonly found in the early life histories of many taxa of marine invertebrates, regardless of habitat type (Thorson 1946, 1950, Amio 1963). Furthermore, such variation is sometimes found among closely related species living in the same habitat (Amio 1963, Adachi and Wada 1998, Furota et al. 2002). Such contrast in developmental mode raises questions about the ecological consequences of the life histories of these forms. This is because dispersal is a crucial process in many marine benthic populations, and is hypothesized to be a process underlying the interspecific variation of both abundances and distributions (Foggo et al. 2007). A credible relationship between developmental modes and distribution was initially reported from benthic marine invertebrates in the second half of the last century; macroecologists discovered that, for gastropods, planktonic-dispersing species have a greater geographic range than non-planktonic species (Hansen 1978a, 1978b, Jablonski and Lutz 1983, Scheltema 1989, Bhaud 1993). More recently, however, Lester et al. (2007) analyzed extensive data from marine taxa and demonstrated that dispersal ability is of little value in predicting geographic range size, indicating that although dispersal can be an important process moderating species' distribution, other processes are more responsible for interspecific variation of range size.

Recently several studies have indicated links between the developmental mode of marine benthic invertebrates and their spatial distribution patterns at a finer spatial scale within their geographical ranges. For example, Johnson et al. (2001) found that, for intertidal molluscs, species without a floating larval stage showed relatively greater fine-scale patchiness than species with a larval dispersal stage. Similarly, Foggo et al. (2007) reported that, for echinoderms, the y-intercept of the fitted line of the abundance–occupancy relationship plotted for species with a floating larval stage was higher than that for non-planktonic species; i.e., for any given level of mean population size, planktonic-dispersing species tended to exhibit a greater regional occupancy rate than did non-planktonic species. Such an interspecific distribution pattern has often been explained as a direct consequence of the contrasting difference in dispersal scales. That is, more distant dispersal should result in less aggregated distribution at the local scale (Foggo et al. 2007) because it weakens the influence of the spatial heterogeneity of adult distribution on the juvenile distribution pattern (Uriz et al. 1998, Reed et al. 2000). Another explanation, but one which is not mutually exclusive with the previous explanation, is that larval dispersal enhances the connectivity of populations and buffers population fluctuations and reduces local extinction risk (Emlet 1995, Eckert 2003, Frost et al. 2004), consequently increasing patch occupancy rate and decreasing spatial patchiness (Foggo et al. 2007). If the latter mechanism plays a significant role, then the distribution of non-planktonic species should be more aggregated temporally as well as spatially than that of planktonic-dispersing species. That is, the former should show a smaller occupancy rate and greater variation in population size for any given level of mean population size, both spatially and temporally, than do the latter. However,

these predictions have not been examined previously; as far as we know, only one study has demonstrated that larval dispersal dampened population fluctuation of marine benthos (Eckert 2003).

To test these hypotheses, we compared and contrasted the slopes, fits, and y-intercept of the fitted line of (1) both spatial and temporal abundance–occupancy relationships and (2) both spatial and temporal mean–variance relationships of population size (Taylor’s power law) across species with differing dispersive traits. We simultaneously applied these two regression analyses to the data because this may enable us to draw more valid conclusions about the effect of larval dispersal on distribution patterns, since the abundance–occupancy relationship and the mean–variance relationship of population size respectively focus on different criteria of aggregation under similar levels of mean abundance: the proportion of occupied sites or variation of abundance.

Four developmental modes are commonly found for marine gastropods: planktotrophic development (feeding larvae), lecithotrophic development (non-feeding larvae), direct development (larvae hatch as benthic juveniles), and ovoviviparity (Thorson 1950). In the first and second of these, the larvae pass through a planktonic life stage after hatching (planktonic development), whereas the others completely lack a planktonic dispersal larval stage (non-planktonic development). In this research, we compared spatiotemporal patterns in distribution between species with planktonic development and species with non-planktonic development, because pelagic larval duration may not be reliably different between species with planktotrophic development and species with lecithotrophic development across broad geographic and taxonomic scales (Mercier et al. 2013).

2. Material & Methods

2.1. Sites and samples

A hierarchical nested sampling design (Noda 2004) was used for the layout of each study site (Table A1; Fig. 1). Five rocky shores were chosen for the census of intertidal gastropods at each of six regions (Eastern Hokkaido, Southern Hokkaido, Rikuchu, Boso, Nanki, and Osumi) along the Pacific coast of Japan between latitudes 31°N and 43°N, with the intervals between neighboring regions ranging from 263 to 513 km (mean \pm SD: 404.9 \pm 107.3 km). Within each region, we chose five shores at intervals of 2.7 to 17 km (mean \pm SD: 8.2 \pm 4.3 km) along the coastline. Within each shore, we established five 5000-cm² census plots on steep rock walls in semi-exposed locations at intervals of 3.1 to 378 m (mean \pm SD: 37.3 \pm 48.9 m). The angles of the rock walls in the plots varied between 41° and 103° (mean \pm SD: 71.6 \pm 15.8°) from horizontal (0°). Although the slopes varied across sites, most of the census sites (all plots except three) had slopes of between 50° and 100°, which were neither moderate nor overhanging slopes. Each plot was 50 cm wide by 100 cm high, and the mean tidal level corresponded to the vertical midpoint of the plot. Detailed descriptions of the study sites and biogeographic features of the area can be found in previous works (Okuda et al. 2004, Nakaoka et al. 2006). We counted and identified all gastropod species in our census plots in July or August (summer) from 2004 to 2010. From 2007 on, we were unable to survey several plots because they were damaged by storms or buried by sediments (Table A1).

To analyze spatial distribution patterns, we first obtained the following quantities for each species, region, and year: proportion of occupied plots (the number of occupied plots divided by the number of observed plots; Table A1), mean density of individuals per occupied plot in each year (sum of the number of individuals in each plot divided by the number of occupied plots), and the spatial mean and variance of population size (mean and variance of the number of individuals calculated over all observed plots). We then averaged these quantities over all years for each species and region, and finally obtained (1) average proportion of occupied plots, (2) average density of individuals per occupied plot, (3) average spatial mean of population size, and (4) average spatial variance of population size. The first two of these variables were used for analysis of the spatial abundance–occupancy relationship, while the last two variables were used for analysis of the spatial mean–variance relationship of population size.

To analyze temporal distribution patterns, we first obtained the following quantities for each species and plot: proportion of years in which that species occupied the plot (the number of years that the plot was occupied divided by the number of years the plot was observed; Table A1), mean density of the plot in occupied years (sum of the number of individuals in each year divided by the number of occupied years), and the temporal mean and variance of population size (mean and variance of the number of individuals calculated over observed years). We then averaged these quantities over plots in the same region for each species and region, and finally obtained (1) average proportion of occupied years, (2) average density of a plot in occupied years, (3) average temporal mean of population size, and (4) average temporal variance of population size. The first two of these variables were used for analysis of the temporal abundance–occupancy relationship, while the last two variables were used for analysis of the temporal mean–variance relationship of population size.

2.2. Species

Developmental modes were taken from Habe (1956), Amio (1963), Ohgaki (1997), Yamamoto (1997), Furota et al. (2002), Kanamori et al. (2004), Kuramochi (2005), Maeda and Doi (2006), and personal communications from molluscan researchers Dr. Naoya Abe, Dr. Roberto Lombardo, and Dr. Naotomo Ohta. To preclude the influence of fisheries, such as harvesting and production and release of seedlings, for further analyses we used species with known developmental modes but with the exclusion of two commercial species, *Turbo cornutus* and *Haliotis diversicolor aquatilis* (Table A2).

2.3. Analysis

In our intertidal gastropod dataset (Table A2), 43 out of the 59 planktonic development species belonged in two mono-developmental clades, i.e. Patellogastropoda and Vetigastropoda. Therefore to reduce phylogenetic effect on spatial and temporal population characteristics which is not related to mode of development, following analyses were performed for (1) all taxa and (2) taxa excluding 43 taxa belonging in Patellogastropoda and Vetigastropoda

2.3.1. Abundance–occupancy relationship

We assumed that the abundance–occupancy relationship can be expressed by the model of Hanski and Gyllenberg (1997), in which the logit of occupancy linearly correlates with the log of density. To examine the effect of developmental mode on spatial and temporal abundance–occupancy relationships, we used linear mixed effect models where the logit-transformed averaged proportion of occupied plots (or of occupied years) of each species in every region was treated as the response variable. As predictor variables, we considered developmental mode, log of averaged density in plots (or in years) in which occupancy was recorded for each species in every region, and an interaction term between these two factors as fixed effects, as well as region- and species-specific random intercepts. In one region (Eastern Hokkaido), we had to exclude *Littorina sitkana* from these analyses, because the averaged proportion of occupied plots (and of occupied years) was 1, and therefore we could not obtain logit-transformed values.

2.3.2. Mean–variance relationship of population size

To examine the effect of developmental mode on spatial and temporal mean–variance relationships, we used linear mixed effect models where the log of averaged variance of population size per total number of plots (or per total number of years) of each species in every region was treated as the response variable. As predictor variables, we considered developmental mode, log of averaged mean of population size per total number of plots (or per total number of years) of each species in every region, and an interaction term between these two factors as fixed effects, as well as region- and species-specific random intercepts.

All statistical analyses were executed with R 3.0.2 (R Development Core Team 2013; available at www.R-project.org). Linear mixed effects models were fitted with the lmer function in the lmerTest package (Kuznetsova et al. 2014).

3. Results

3.1. Rocky intertidal gastropod fauna

Our dataset contained 359,897 individuals belonging to 72 taxa. We categorized these into the two dispersal modes: 15 were non-planktonic species and 59 were species with planktonic dispersal (Table A2). Among the 15 non-planktonic species, 2 species were ovoviviparous. Planktonic species included 43 lecithotrophic and 16 planktotrophic taxa.

3.2. Abundance–occupancy relationship

Spatial and temporal relationships were quantitatively resembled to each other. For cases of all taxa comparison, the results of linear mixed models showed that the log of density and the interaction term between developmental mode and the log of density were significant predictors of both spatial and temporal occupancies (Tables 1, 2). For cases of comparison with taxa excluding Patellogastropoda and Vetigastropoda, the log of density and developmental mode were significant predictors of spatial occupancy, while the former was not a significant predictor of temporal occupancy (Tables 1, 2). In all cases, for any given level of mean population density, regional occupancy rate was greater for

planktonic-dispersing species than for non-planktonic species (Figs. 2, 3), demonstrating that the former species exhibited less aggregated distribution than did the latter species.

3.3. Mean–variance relationship of population size

As with the abundance–occupancy relationship, the spatial and temporal mean–variance relationships of population size mirrored each other. For cases of all taxa comparison, the results of linear mixed models showed that the log of mean population size, developmental mode and the interaction term between developmental mode and the log of mean population size were significant predictors of both spatial and temporal variances of population size (Tables 3, 4). For cases of comparison with taxa excluding Patellogastropoda and Vetigastropoda, the log of mean population size and developmental mode were significant predictors of both spatial and temporal variances of population size (Tables 3, 4). In all cases, for any given level of mean population size, non-planktonic species exhibited greater variance than planktonic species (Figs. 4, 5), demonstrating that the former species exhibited more aggregated distribution than did the latter species.

4. Discussion

4.1. Spatial patterns

Our results show that non-planktonic species exhibit a more aggregated distribution than do species with planktonic dispersal at a local scale. Similar patterns have been reported with respect to various other habitats and taxa. Using a dataset of 362 subtidal benthic invertebrates, including polychaetes, crustaceans, molluscs, and echinoderms occurring across 446 grid squares of 1 km² around the British Isles, Foggo et al. (2007) found that the y-intercept of the abundance–occupancy relationship was greater for planktonic-dispersing organisms than for non-planktonic organisms irrespective of taxon. Johnson et al. (2001) also reported that non-planktonic species showed relatively greater fine-scale patchiness than planktonic species for intertidal molluscs on the coast of the Isle of Man. Thus it can be concluded that non-planktonic species tend to exhibit a more aggregated distribution at a local scale than do planktonic dispersal species for marine benthos. However, several studies based on comparisons among higher taxonomic groups, such as phyla or classes, failed to find any influence of larval dispersal on the abundance–occupancy relationship (Foggo et al. 2003, Frost et al. 2004). In those cases, it is inevitable that the observed abundance–occupancy relationships will be influenced by many confounding factors such as breadth of resources, habitat selection capabilities, and vital rates (Gaston et al. 1997). Furthermore, the form of abundance–occupancy relationship is often strongly influenced by phylogeny (Gaston et al. 1997), differing considerably among higher taxa (Webb et al. 2009).

4.2. Temporal patterns

While larval supply can influence the population dynamics of marine benthos (Yoshioka 1982, Caffey 1985, Connell 1985, Gaines and Roughgarden 1985, Gaines et al. 1985, Roughgarden et al. 1985, Minchinton and Scheibling 1991, Gaines and Bertness 1992), very little is known about the relationship between developmental mode and population dynamics (review by Olafsson et al. 1994,

Eckert 2003). Until recently, it had been widely assumed that the floating larval stage increases the amplitude of population fluctuations (Thorson 1950, Levinton 1982, Strathmann 1985, Roughgarden et al. 1988). Thorson (1946, 1950) compared five sympatric bivalves and suggested that species with a long larval planktonic period exhibited greater population fluctuations and higher temporal variation in recruitment than did other species with short or no planktonic period. Underwood and Fairweather (1989) suggested that species with long planktonic periods would undergo large population fluctuations because of two mechanisms. First, their high fecundity combined with variation in planktonic mortality would cause great fluctuations in settlement. Second, as a result of planktonic mortality, variation in the floating period would change the number of surviving larvae that settle. However, there appears to be no credible evidence that floating species exhibit greater population fluctuation than non-planktonic species. In contrast, recent works based on analysis of data that can be considered more reliable from the aspect of quality and quantity showed patterns opposite to the widely accepted view (Eckert 2003). Eckert (2003) analyzed a dataset consisting of a diverse group of intertidal and subtidal benthos and found that non-planktonic species exhibited greater population fluctuation than planktonic species. Similarly, the present study, based on analysis of data collected from 135 sites along the Pacific coast of Japan, showed that for rocky intertidal gastropods, non-planktonic species exhibited greater population fluctuation than planktonic species. Thus, it can be concluded that larval dispersal may dampen population fluctuations in a manner similar to the effect of dispersal on population dynamics of terrestrial organisms (den Boer 1968, Vance 1980, Hanski 1991, Hastings 1991, Doebeli 1995).

4.3. Underlying mechanisms of observed patterns

Our results show that, compared to planktonic species, non-planktonic species exhibit (1) a smaller occupancy rate for any given level of mean population size and (2) greater variations in population size, both spatially and temporally. These findings suggest that a dampening effect of larval dispersal on population fluctuation may work over both space and time (Eckert 2003). Recent theoretical works (Hanski 2000, Watkinson et al. 2003, Freckleton et al. 2005) demonstrate that dispersal enhances the connectivity of populations and buffers population fluctuations and reduces local extinction risks, consequently increasing patch occupancy rate and decreasing spatial patchiness at the metapopulation level. This mechanism may be a major explanation for why, for various taxa of marine benthos from various habitats, non-planktonic species exhibit a more aggregated distribution at a local scale than do planktonic dispersal species (Reed et al. 2000, Johnson et al. 2001, Foggo et al. 2007). Indeed, analysis of fossil shells demonstrates that the extinction probability is lower for species with a floating larval stage than it is for species without a floating larval stage (Jablonski and Lutz 1983, Jablonski 1986, Valentine and Jablonski 1986). Such a difference is also partially due to the effect of larval dispersal on population connectivity and local extinction risks.

4.4. Conclusions

This study shows that, for rocky intertidal gastropods from the Pacific coast of Japan, compared to planktonic species, non-planktonic species exhibited (1) a smaller occupancy rate for any given level

of mean population size and (2) greater variations in population size, both spatially and temporally. This finding strongly suggests that the observed macroecological patterns, i.e., the abundance–occupancy relationship and the mean–variance relationship of population size across species, were shaped by the effect of larval dispersal dampening population fluctuation, which works over both space and time (Eckert 2003). Although it had been widely assumed that larval dispersal enhanced population fluctuations, larval dispersal may in fact enhance the connectivity of populations and buffer population fluctuations and reduce local extinction risks.

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Figures

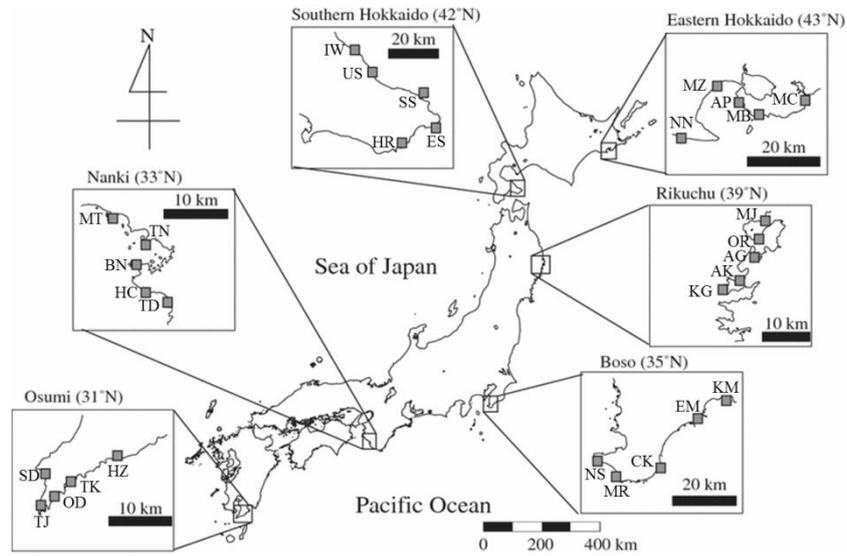


Fig. 1. Study site locations. Five rocky shores (filled squares) were chosen for the census of intertidal gastropods in each of six regions (Eastern Hokkaido, Southern Hokkaido, Rikuchu, Boso, Nanki, and Osumi) along the Pacific coast of Japan between latitudes 31°N and 43°N. See Table 1 for abbreviations of shores.

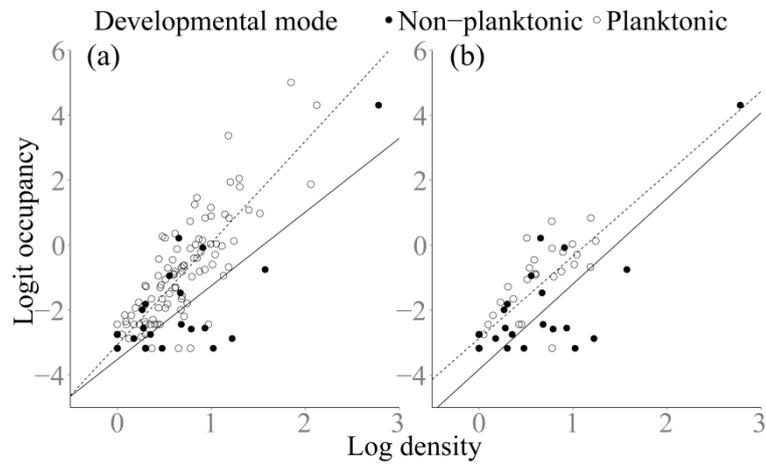


Fig. 2. Spatial abundance–occupancy relationship for rocky intertidal gastropods for all taxa (a) and taxa excluding Patellogastropoda and Vestigastropoda (b) sampled from six regions along the Pacific coast of Japan between latitudes 31°N and 43°N. Each point represents a different species and region ($n = 142$) and the lines were fitted based on the results of a linear mixed effect model (Table 3). The occupancy of a species in each region is the mean value of the proportions of occupied plots (number of occupied plots per 25 plots) from different years; density is the mean value of the mean density (individuals per 0.5-m² plot) in plots from different years in which occupancy was recorded.

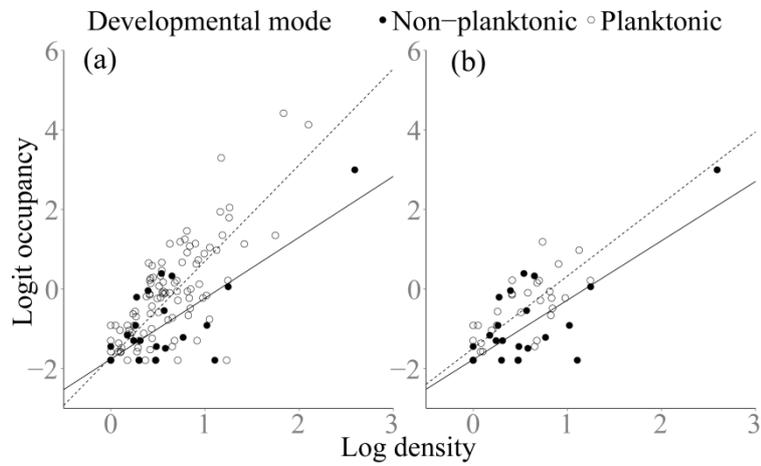


Fig. 3. Temporal abundance–occupancy relationship for rocky intertidal gastropods for all taxa (a) and taxa excluding Patellogastropoda and Vestigastropoda (b) sampled from six regions along the Pacific coast of Japan between latitudes 31°N and 43°N. Each point represents a different species and region ($n = 150$) and the lines were fitted based on the results of a linear mixed effect model (Table 4). The occupancy of a species in each region is a mean value of the proportions of occupied years (number of occupied years per 7 years) from different plots; density is the mean value of the mean density (individuals per 0.5-m² plot) in plots in which occupancy was recorded.

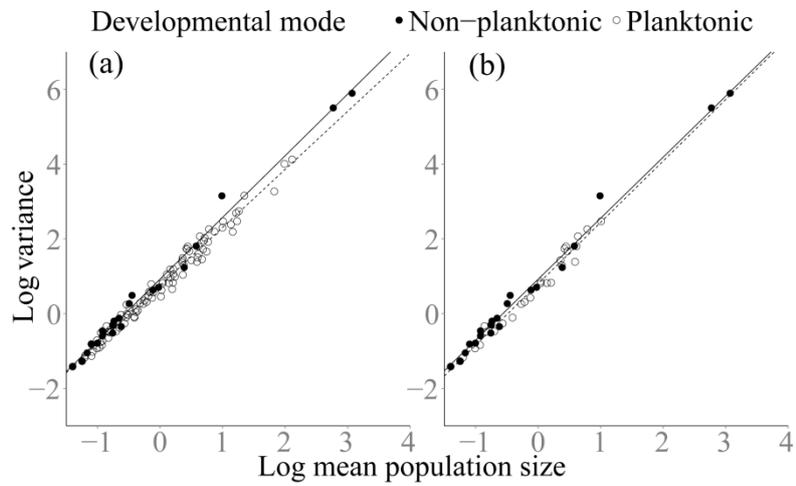


Fig. 4. Spatial mean–variance relationship of population density (Taylor’s power law) for rocky intertidal gastropods for all taxa (a) and taxa excluding Patellogastropoda and Vestigastropoda (b) sampled from six regions along the Pacific coast of Japan between latitudes 31°N and 43°N. Each point represents a different species and region ($n = 143$) and the lines were fitted based on the results of a linear mixed effect model (Table 5). The mean (or the variance) of a population size of a species in each region is the mean value of mean (or variance) of population size (individuals per 0.5-m² plot) per all 25 plots from different years.

Tables

Table 1. Results of a linear mixed effect model examining the spatial abundance–occupancy relationship across species for all taxa (a) and taxa excluding Patellogastropoda and Vestigastropoda (b) with differing dispersive traits for rocky intertidal gastropods from the Pacific coast of Japan. Logit-transformed averaged proportion of occupied plots of each species in every region was treated as the response variable. As predictor variables, we considered the developmental mode and log of averaged density in plots in which occupancy was recorded for each species in every region, and an interaction term between these two factors as fixed effects, as well as region- and species-specific random intercepts. See text for detailed explanation of variables.

	All taxa				Taxa excluding Patellogastropoda and Vestigastropoda			
	Estimate	Std.Error	t value	P(> t)	Estimate	Std.Error	t value	P(> t)
Intercept	-3.5228	0.3011	-11.701	<0.001	-3.8289	0.3290	-11.640	<0.001
Log density	2.2684	0.3301	6.871	<0.001	2.6322	0.3338	7.885	<0.001
Developmental mode (values of Planktonic for that of Non-planktonic)	0.4534	0.3294	1.376	0.172	0.9541	0.4283	2.228	0.033
Log density × Developmental mode	0.8639	0.3747	2.305	0.023	-0.0984	0.4178	-0.235	0.815

Table 2. Results of a linear mixed effect model examining the temporal abundance–occupancy relationship across species for all taxa (a) and taxa excluding Patellogastropoda and Vestigastropoda (b) with differing dispersive traits for rocky intertidal gastropods from the Pacific coast of Japan. Logit-transformed averaged proportion of occupied years for each species in every region was treated as the response variable. As predictor variables, we considered developmental mode and log of averaged density in years in which occupancy was recorded for each species in every region, and an interaction term between these two factors as fixed effects, as well as region- and species-specific random intercepts. See text for detailed explanation of variables.

	All taxa				Taxa excluding Patellogastropoda and Vestigastropoda			
	Estimate	Std.Error	t value	P(> t)	Estimate	Std.Error	t value	P(> t)
Intercept	-1.76414	0.23198	-7.605	<0.001	-1.7731	0.2095	-8.464	<0.001
Log density	1.53087	0.28943	5.289	<0.001	1.4920	0.2395	6.230	<0.001
Developmental mode (values of Planktonic for that of Non-planktonic)	0.04634	0.24968	0.186	0.853	0.2837	0.2484	1.142	0.262
Log density × Developmental mode	0.88572	0.32848	2.696	0.008	0.3213	0.3496	0.919	0.362

Table 3. Results of a linear mixed effect model examining the spatial mean–variance relationship of population size across species for all taxa (a) and taxa excluding Patellogastropoda and Vestigastropoda (b) with differing dispersive traits for rocky intertidal gastropods from the Pacific coast of Japan. Log of averaged variance of population size per total number of plots for each species in every region was treated as the response variable. As predictor variables, we considered developmental mode, log of averaged mean of population size per total number of plots for each species in every region, and an interaction term between these two factors, as fixed effects, as well as region- and species-specific random intercepts. See text for detailed explanation of variables.

	All taxa				Taxa excluding Patellogastropoda and Vestigastropoda			
	Estimate	Std.Error	t value	P(> t)	Estimate	Std.Error	t value	P(> t)
Intercept	0.92270	0.03587	25.723	<0.001	0.91963	0.04171	22.046	<0.001
Log mean population size	1.64854	0.02972	55.470	<0.001	1.63133	0.03417	47.738	<0.001
Developmental mode (values of Planktonic for that of Non-planktonic)	-0.17406	0.03952	-4.405	<0.001	-0.12343	0.05723	-2.157	0.044
Log mean population size × Developmental mode	-0.09603	0.03410	-2.816	0.006	0.01058	0.04865	0.218	0.829

Table 4. Results of a linear mixed effect model examining the temporal mean–variance relationship of population size across species for all taxa (a) and taxa excluding Patellogastropoda and Vestigastropoda (b) with differing dispersive traits for rocky intertidal gastropods from the Pacific coast of Japan. Log of averaged variance of population size per number of years for each species in every region was treated as the response variable. As predictor variables, we considered developmental mode, log of averaged mean of population size per total number of years for each species in every region, and an interaction term between these two factors as fixed effects, as well as region- and species-specific random intercepts. See text for detailed explanation of variables.

	All taxa				Taxa excluding Patellogastropoda and Vestigastropoda			
	Estimate	Std.Error	t value	P(> t)	Estimate	Std.Error	t value	P(> t)
Intercept	0.47571	0.03481	13.667	<0.001	0.47662	0.03653	13.047	<0.001
Log mean population size	1.61562	0.03507	46.068	<0.001	1.61887	0.03584	45.172	<0.001
Developmental mode (values of Planktonic for that of Non-planktonic)	-0.14813	0.03566	-4.154	<0.001	-0.11103	0.04599	-2.414	0.024
Log mean population size × Developmental mode	-0.18157	0.04119	-4.408	<0.001	-0.06516	0.06246	-1.043	0.301

Supplementary material

Table A1. Number of plots in each region over the 7 years of the census. From 2007 on, several of the plots could not be surveyed because they were damaged by storms or buried by sediment.

Region	Census period : spatial analysis	Shore (abbreviations)	Number of plots						
			2004	2005	2006	2007	2008	2009	2010
Eastern Hokkaido	Summer 2004 to Summer 2009	Mochirippu (MC)	5	5	5	5	5	5	4
		Mabiro (MB)	5	5	5	5	5	5	5
		Aikappu (AP)	5	5	5	5	5	5	5
		Monshizu (MZ)	5	5	5	5	5	5	5
		Nikomanai (NN)	5	5	5	5	5	5	5
		Total	25	25	25	25	25	25	24
Southern Hokkaido	Summer 2004 to Summer 2006	Iwato (IW)	5	5	5	5	4	5	4
		Usujiri (US)	5	5	5	5	5	5	5
		Shishibana (SS)	5	5	5	2	2	2	2
		Esan (ES)	5	5	5	2	2	2	2
		Hiura (HR)	5	5	5	5	5	5	5
		Total	25	25	25	19	18	19	18
Rikuchu	Summer 2004 to Summer 2006	Myojin (MJ)	5	5	5	5	5	5	5
		Oura (OR)	5	5	5	5	5	5	5
		Aragami (AG)	5	5	5	5	5	5	5
		Akahama (AK)	5	5	5	4	4	3	3
		Katagishi (KG)	5	5	5	5	0	5	5
		Total	25	25	25	24	19	23	23
Boso	Summer 2004 to Summer 2010	Kominato (KM)	5	5	5	5	5	5	5
		Emi (EM)	5	5	5	5	5	5	5
		Chikura (CK)	5	5	5	5	5	5	5
		Mera (MR)	5	5	5	5	5	5	5
		Nishikawana (NS)	5	5	5	5	5	5	5
		Total	25	25	25	25	25	25	25
Nanki	Summer 2004 to Summer 2010	Hacchoiso (HC)	5	5	5	5	5	5	5
		Bansho (BN)	5	5	5	5	5	5	5
		Tenjinsaki (TN)	5	5	5	5	5	5	5
		Metsuura (MT)	5	5	5	5	5	5	5
		Tomida (TD)	5	5	5	5	5	5	5
		Total	25	25	25	25	25	25	25
Osumi	Summer 2004 to Summer 2010	Henzuka (HZ)	5	5	5	5	5	5	5
		Takenoura (TK)	5	5	5	5	5	5	5
		Odomari (OD)	5	5	5	5	5	5	5
		Tajiri (TJ)	5	5	5	5	5	5	5
		Shimadomari (SD)	5	5	5	5	5	5	5
		Total	25	25	25	25	25	25	25

Table A2. Developmental mode and feeding habits of rocky intertidal gastropods collected from six regions (Eastern Hokkaido, Southern Hokkaido, Rikuchu, Boso, Nanki, and Osumi) along the Pacific coast of Japan between latitudes 31°N and 43°N during summer 2004 to summer 2010.

	Species	Developmental mode
PROSOBRANCHIA		
Patellogastropoda		
Nacellidae		
	<i>Cellana toreuma</i> (Reeve, 1854)	Planktonic ^a
	<i>Cellana nigrolineata</i> (Reeve, 1839)	Planktonic ^a
	<i>Cellana grata</i> (Gould, 1859)	Planktonic ^a
Lottiidae		
	<i>Niveotectura pallida</i> (Gould, 1859)	Planktonic ^a
	<i>Patelloida saccharina form lanx</i> (Reeve, 1855)	Planktonic ^a
	<i>Patelloida pygmaea</i> (Dunker, 1860)	Planktonic ^a
	<i>Lottia cassis</i> (Eschscholtz, 1833)	Planktonic ^a
	<i>Lottia sp.</i>	Planktonic ^a
	<i>Lottia dorsuosa</i> (Gould, 1859)	Planktonic ^a
	<i>Lottia langfordi</i> (Habe, 1944)	Planktonic ^a
	<i>Lottia kogamogai</i> Sasaki & Okutani, 1994	Planktonic ^a
	<i>Lottia tenuisculpta</i> Sasaki & Okutani, 1994	Planktonic ^a
	<i>Lottia lindbergi</i> Sasaki & Okutani, 1994	Planktonic ^a
	<i>Nipponacmea schrenckii</i> (Lischke, 1868)	Planktonic ^a
	<i>Nipponacmea fuscoviridis</i> (Teramachi, 1949)	Planktonic ^a
	<i>Nipponacmea concinna</i> (Lischke, 1870)	Planktonic ^a
	<i>Nipponacmea nigrans</i> (Kira, 1961)	Planktonic ^a
	<i>Nipponacmea habei</i> Sasaki & Okutani, 1994	Planktonic ^a
	<i>Tectura emydia</i> (Dall, 1914)	Planktonic ^a
Vetigastropoda		
Haliotidae		
	<i>Haliotis diversicolor aquatilis</i> Reeve, 1846	Planktonic ^a
Fissurellidae		
	<i>Montfortula picta</i> (Dunker, 1860)	Planktonic ^a
Trochidae		
	<i>Chlorostoma lischkei</i> Tapparone-Canefri, 1874	Planktonic ^a
	<i>Chlorostoma xanthostigma</i> A. Adams, 1853	Planktonic ^a
	<i>Omphalius rusticus</i> (Gmelin, 1791)	Planktonic ^a
	<i>Omphalius nigerrimus</i> (Gmelin, 1791)	Planktonic ^a
	<i>Margarites helicinus pilsbryi</i> (Kuroda & Habe, 1952)	Planktonic ^a
	<i>Monodonta labio form confusa</i> Tapparone-Canefri, 1874	Planktonic ^a
	<i>Monodonta neritodes</i> (Philippi, 1849)	Planktonic ^a
	<i>Monodonta perplkexa perplexa</i> Pilsbry, 1889	Planktonic ^a
	<i>Diloma suavis</i> (Philippi, 1849)	Planktonic ^a
	<i>Cantharidus japonicus</i> (A. Adams, 1853)	Planktonic ^a
	<i>Cantharidus callichroa</i> (Philippi, 1849)	Planktonic ^a
	<i>Cantharidus jessoensis</i> (Scherenck, 1863)	Planktonic ^a
	<i>Roya eximia</i> (Nevill, 1869)	Planktonic ^a
	<i>Calliostoma unicum</i> (Dunker, 1860)	Planktonic ^a
	<i>Calliostoma multiliratum</i> (Sowerby II, 1875)	Planktonic ^a
	<i>Lirularia iridescens</i> (Scherenck, 1863)	Planktonic ^a
	<i>Conotalopia mustelina</i> (Gould, 1861)	Planktonic ^a
Turbinidae		
	<i>Homalopoma nocturnum</i> (Gould, 1861)	Planktonic ^a
	<i>Homalopoma amussitatum</i> (Gould, 1861)	Planktonic ^a
	<i>Turbo cornutus</i> Lightfoot, 1786	Planktonic ^a
	<i>Turbo stenogyrus</i> Fischer, 1873	Planktonic ^a
	<i>Turbo cornatus coreensis</i> (Récluz, 1853)	Planktonic ^a

Table A2. Continued

	Species	Developmental mode
Neritimorpha		
Neritidae		
	<i>Nerita albicilla</i> Linnaeus, 1758	Planktonic ^a
	<i>Nerita japonica</i> Dunker, 1860	Non-planktonic ^a
Discopoda		
Cerithiidae		
	<i>Rhinoclavis kochi</i> (Philippi, 1848)	Planktonic ^a
	<i>Ittibittium parcum</i> (Gould, 1861)	Non-planktonic ^b
Planaxidae		
	<i>Planaxis sulcatus</i> (Born, 1778)	Non-planktonic ^c
Batillariidae		
	<i>Batillaria multiformis</i> (Lischke, 1869)	Planktonic ^d
	<i>Batillaria cumingii</i> (Crosse, 1862)	Non-planktonic ^d
Littorinidae		
	<i>Lacuna uchidai</i> (Habe, 1953)	Non-planktonic ^e
	<i>Lacuna decorata</i> (A.Adams, 1861)	Planktonic ^e
	<i>Peasiella habei</i> Reid & Mak, 1998	Planktonic ^f
	<i>Littoraria scabra</i> (Linnaeus, 1758)	Non-planktonic ^f
	<i>Nodilittorina radiata</i> (Souleyet in Eydoux & Souleyet, 1852)	Planktonic ^a
	<i>Nodilittorina trochoides</i> (Gray, 1839)	Planktonic ^f
	<i>Littorina brevicula</i> (Philippi, 1844)	Planktonic ^a
	<i>Littorina sitkana</i> (Philippi, 1846)	Non-planktonic ^a
Neogastropoda		
Muricidae		
	<i>Ergalatax contractus</i> (Reeve, 1846)	Planktonic ^a
	<i>Muricodrupa fusca</i> (Küster, 1862)	Non-planktonic ^g
	<i>Ceratostoma inornatus</i> (Récluz, 1851)	Non-planktonic ^a
	<i>Nucella lima</i> (Gmelin, 1791)	Non-planktonic ^a
	<i>Marula musiva</i> (Kiener, 1834)	Planktonic ^h
	<i>Thais bronni</i> (Dunker, 1860)	Planktonic ^a
	<i>Thais clavigera</i> (Küster, 1860)	Planktonic ^a
Nassariidae		
	<i>Niotha livescens</i> (Philippi, 1849)	Planktonic ^a
	<i>Reticunassa fratercula</i> (Dunker, 1860)	Non-planktonic ⁱ
Buccinidae		
	<i>Neptunea arthritica</i> (Bernardi, 1857)	Non-planktonic ^j
	<i>Japeuthria ferrea</i> (Reeve, 1847)	Non-planktonic ^k
	<i>Japeuthria cingulata</i> (Reeve, 1847)	Non-planktonic ^k
	<i>Buccinum chishimanum</i> Pilsbry, 1904	Non-planktonic ^j
PULMONATA		
Basommatophora		
Siphonariidae		
	<i>Siphonaria sirius</i> Pilsbry, 1894	Planktonic ^a
	<i>Siphonaria japonica</i> (Donovan, 1824)	Planktonic ^a
	<i>Siphonaria acmaeoides</i> Pilsbry, 1894	Planktonic ^a

^a Amio (1963).

^b Kuramochi (2005).

^c Ohgaki (1997).

^d Furota et al. (2002).

^e Kanamori et al. (2004).

^f Habe (1956).

^g Yamamoto (1997).

^h Abe naoya personal communication.

ⁱ Roberto Lombardo personal communication.

^j Maeda & Doi (2006).

^k Ohta Naotomo personal communication.

