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Substrate size mediates thermal stress in the rocky intertidal

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Abstract. Variation in physical factors, such as slope, orientation, and wind exposure, shapes thermal conditions. Variation in substrate size is common in many habitats, but its thermal consequences for organisms are not well characterized. Larger substrates should remain more thermally stable and act as thermal refuges for associated organisms during short, thermally stressful periods such as midday temperature peaks or tidal exposure. In observations and a transplant and thermal integration experiment, we found that larger rock substrates stayed cooler and facilitated greater survival of the barnacle *Semibalanus balanoides* in the high intertidal relative to small substrates during the hot summer months in southern New England, USA. However, in thermally benign northern New England, rock substrate size had no effect on barnacle distributions, indicating that the thermal effects of substrate size are mediated by regional climate.

Key words: abiotic factors; barnacle; climate change; heterogeneity; Narragansett Bay, Rhode Island, USA; Semibalanus balanoides; *temperature thermal refuge*

INTRODUCTION

The thermal suitability of a habitat is of primary importance for organisms' physiology, survival, and distribution (Orton 1920, Huey 1991). Environmental temperatures that exceed organisms' optimum and critical thermal limits have sublethal and lethal effects that structure communities (Southward 1958, Somero 2002). Although on large spatial scales (100s to 1000s of kilometers) thermal stress corresponds to latitudinal and climate gradients (Somero 2005), on smaller scales thermal stress varies greatly within landscapes. Heterogeneity in physical factors, such as wind and wave exposure, slope, shade, or soil moisture, directly affects heat transfer and the temperatures of organisms (Helmuth 1998, Holtmeier and Broll 2005, Helmuth et al. 2006*a*).

Substrate size is an additional and often-overlooked aspect of environmental heterogeneity that has important thermal effects and can affect species distributions. Snakes, for example, take advantage of substrate-size temperature effects to stay within a preferred temperature range by retreating to sites underneath medium-size rocks that neither overheat during the day nor become too cool during the night (Huey et al. 1989).

Massive substrates warm more slowly (Holman 1968) and may, thereby, provide refuge for thermally stressed organisms during warm spells of limited duration. Bertness (1989) found that barnacles on larger boulder substrates avoided the extreme high temperatures of smaller cobble substrates, and, consequently, survival was greater on boulders. In free-standing species, body size has a similar effect to that of substrate size for small, sessile organisms such as barnacles coupled to their substrates (Denny and Harley 2006). Stevenson (1985) found that the body temperature of more massive free-standing ectotherms deviates more from ambient air temperature and exhibits smaller daily temperature fluctuations than that of smaller ectotherms. Accordingly, we expect sessile residents on larger substrates to experience lower temperature extremes and greater temperature stability than conspecifics on smaller substrates.

Understanding how thermal conditions are influenced by environmental heterogeneity informs predictions of the biological effects of altered temperature regimes, which has emerged as an important issue in the face of climate change. In the midst of rapidly rising air temperatures (1.1°–6.4°C increase predicted this century; IPCC 2007), scientists and managers seek to understand climate change's biological effects, which will include increases in thermal stress for some species. For example, several recent studies have predicted high risk among tropical (Deutsch et al. 2008, Kearney et al. 2009) and montane (Bernardo and Spotila 2006) ectotherms because modeled air temperatures will exceed their critical thermal maxima. Species that can thermoregulate by accessing cold spots, such as in shade or belowground, are predicted to fare better (Kearney et al. 2009). For organisms living close to their thermal limits, the availability of physically benign areas that provide refuge from thermal stress will be of key importance to their survival of more frequent and intense warm spells (Helmuth et al. 2005, Kareiva et al. 2008).

Marine invertebrates in the high rocky intertidal, subject to physically stressful aerial conditions during

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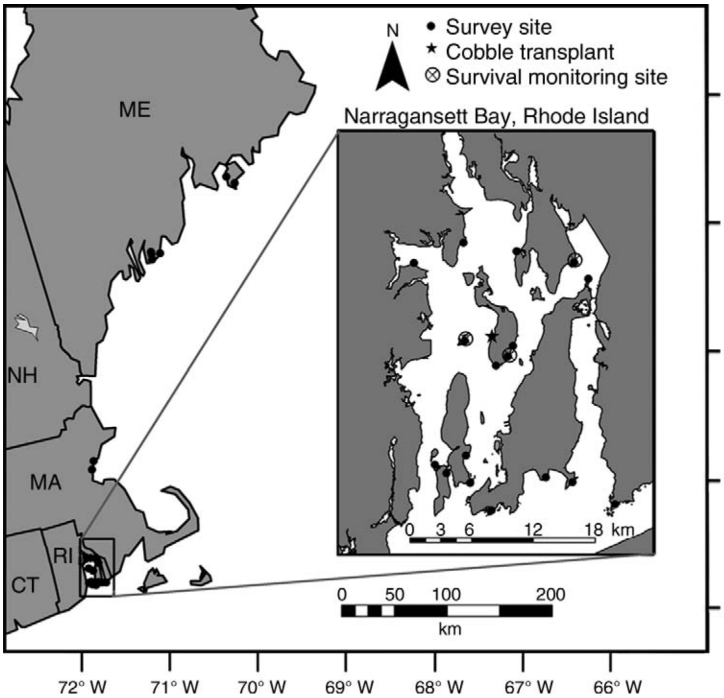

FIG. 1. Map of New England study sites. Inset: Narragansett Bay, Rhode Island, USA.

tidal exposure, live close to their thermal limits (Somero 2002, 2005). Due to its thermal sensitivity, many have described the rocky intertidal community as a sentinel of the biological effects of climate change (Southward et al. 1995, Bertness et al. 1999, Sagarin et al. 1999, Helmuth et al. 2006*b*). In particular, barnacles, which occupy the highest, most physically stressful elevations in the intertidal (Southward 1958), are model organisms for studying thermal stress and have been observed to be affected by substrate size variation in the past (Bertness 1989). In this paper we present observational and experimental evidence that heterogeneity in substrate size, by mediating thermal stress, affects the survival and distribution of the barnacle *Semibalanus balanoides*. Furthermore, in surveys across a regional latitudinal climate gradient, we find that substrate size effects on *S. balanoides* vary predictably with latitude.

METHODS

Study organism and location

We examined how the thermal environment and survival and distribution of *Semibalanus balanoides* vary across three size classes of rock substrate (bedrock, boulders, and cobbles) in the New England region of the United States. S. balanoides has commonly been chosen for studies of thermal tolerance (e.g, Foster 1969, Wethey 1983, 1984, Bertness 1989, Bertness et al. 1999) for its fast-growing, abundant, and sessile adult stage. In addition, its body temperature mimics the substrate temperature within 1°C (Bertness 1989), and its upper elevational limit is set by lethal thermal stress in southern New England (Wethey 1983, 1984, Bertness 1989, Wethey 2002). *S. balanoides* is also a preferred prey species and habitat engineer that facilitates mussel settlement (Menge 1976, Petraitis 1990). The median lethal temperature (LT50) for *S. balanoides* is 44.3°C in short exposure in a warm water bath (Foster 1969), but may be lower in aerial exposure. Davenport and Davenport (2005) found a median lethal temperature in air of 34.9°C for a Scottish population of *S. balanoides*. At our warmest New England sites in Narragansett Bay, Rhode Island (USA), substrate temperatures easily exceed 50°C on a hot summer day (Bertness 1989).

Survivorship across substrate size

We made detailed observations of barnacle mortality on three size classes of rocks at two Narragansett Bay sites, Haffenreffer and Hope Island (Fig. 1). Rock size classes followed geological grain size classification (cobble, 64–256 mm; boulder, >256 mm; and bedrock, continuous with belowground substrate [Prothero and Schwab 2004]). We followed barnacle survival through time within 15×15 cm marked plots on cobble, boulder, and bedrock surfaces at three intertidal elevations, low (0.23 m above mean lower low water (MLLW), middle (0.46 m above MLLW), and high (0.69 m above MLLW) ($N = 3$–6 plots/substrate class/level/site, depending on substrate availability). This elevation gradient spanned much of the barnacle zone; at Haffenreffer, no barnacles were present in May 2008 on cobbles above 0.46 m elevation. For reference, tidal range in Narragansett Bay is 1.25 m. To facilitate comparisons between loose and stationary rocks and to prevent mortality due

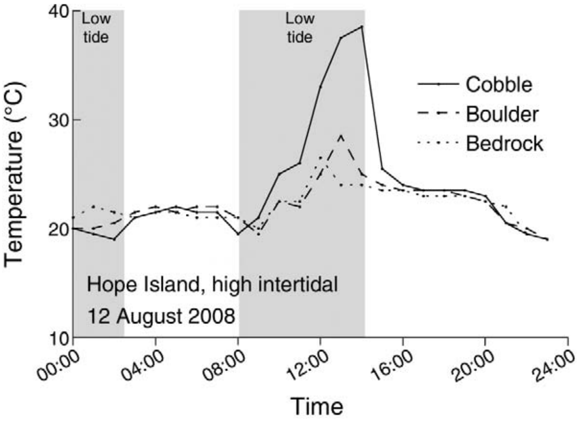

FIG. 2. A representative temperature profile of substrate classes during 24 hours that included a midday low tide (12 August 2008). Gray shading indicates periods of aerial exposure, based on verified tide data (*available online*: ⟨http://tidesandcurrents.noaa.gov/⟩).

to rolling (Sousa 1979), we stabilized cobble substrates with two rebar posts and 2.54 cm Aquamesh (Riverdale Mills, Northbridge, Massachusetts, USA).

Plots were established at the beginning of June 2008 and photographed monthly through September 2008, when individuals were presumed to survive to reproduce in the fall. To measure density and survival through time, we counted juvenile barnacles in a 45-cm^2 subsection of each photo in ImageJ (Rasband 2008). We calculated survivorship at each time point as density scaled by maximum density within each record. Rock temperatures were monitored at one-hour intervals in August with iButton dataloggers ($N = 2$ dataloggers/substrate/level/site; Thermochron DS1921G model, resolution ±0.5°C; Maxim/Dallas Semiconductor Corporation, Dallas, Texas, USA) affixed to the rock surface with marine epoxy (Carboline Company, St. Louis, Missouri, USA). In field tests, iButton temperature records were an adequate, albeit imperfect, proxy for barnacle temperatures ($R^2 = 0.85$, see Appendix: Fig. A1). From iButton data, we calculated the maximum daily temperature of each substrate.

We tested for differences in final density and survival across sites, substrate classes, and tidal elevations with a three-way factorial ANOVA in JMP statistical software (SAS Institute 2003). When factors were significant, we tested for differences between treatment combinations with Tukey's hsd post hoc tests. Prior to analyses, we logarithmic-transformed density data and angular-transformed percentage survival data to approximate normal distributions.

Experimental manipulation of substrate size

To directly examine the relationship between substrate size and temperature, we experimentally manipulated substrate size with a thermal integration treatment of transplanted cobbles. We transplanted cobbles evenly covered in juvenile barnacles from a cobble beach to adjacent bedrock in early May 2008 at Old Maid's Cove in Narragansett Bay (Fig. 1). Transplanted cobbles were bolted to bedrock at low, middle, and high intertidal heights and randomly assigned one of two thermal-integration treatments: embedded in concrete, a material that transfers heat similarly to rock and buffered cobbles' thermal regimes ("buffered"), or isolated from the bedrock by a mesh spacer to prevent heat conduction from the underlying bedrock ("isolated") ($N = 8$ replicates/treatment/level).

Cobbles were photographed every three weeks through August 2008 to monitor barnacle survival during the summer months (see note, Appendix: *Additional methods*). Densities, survival, and rock temperatures ($N = 3$ iButtons/treatment/level) were measured as above. We used an angular transformation for percentage survival data. We used repeated-measures ANOVA (in JMP) to test for the effects of intertidal height, thermal treatment, their interaction, and time on barnacle survival.

Substrate size effects across a regional climate gradient

As heat stress primarily impacts high-intertidal survival, we used the upper reach of barnacle survival as an index of heat-induced mortality. In September and October 2008, after the heat stress of the summer had subsided, we surveyed the maximum elevation of barnacles at 27 sites in five New England subregions (Fig. 1; Appendix: Table A1) on cobble, boulder, and bedrock substrates to examine how regional variation in climate modifies the thermal effects of substrate size and shapes barnacle distributions. See Appendix: Additional methods for survey methods.

To explain the effects of rock substrate type, region, and their interaction on the maximum elevation of barnacles, we constructed a linear mixed-effects model in R statistical software with package nlme (Pinheiro et al. 2008), using the maximum-likelihood method. Prior to analysis, the maximum elevation as a percentage of the tidal range was transformed using an angular transformation for percentage data. Site was treated as a random effect in the model.

RESULTS

Survivorship across substrate size

Cobble surfaces reached higher daytime temperatures than the surfaces of boulders or bedrock (Fig. 2; Appendix: Fig. A2). Mean August temperatures of larger substrates were marginally cooler than those of smaller cobbles (0° to 0.9°C cooler, depending on site and elevation). Daily maximum temperatures were 2.3° to 6.6°C cooler. Notably, substrate surface temperatures of cobbles exceeded 44°C, a lethal threshold for *S. balanoides,* whereas larger substrates did not (Appendix: Fig. A2).

During summer 2008, barnacle survival in Narragansett Bay (Rhode Island, USA) was affected by rock

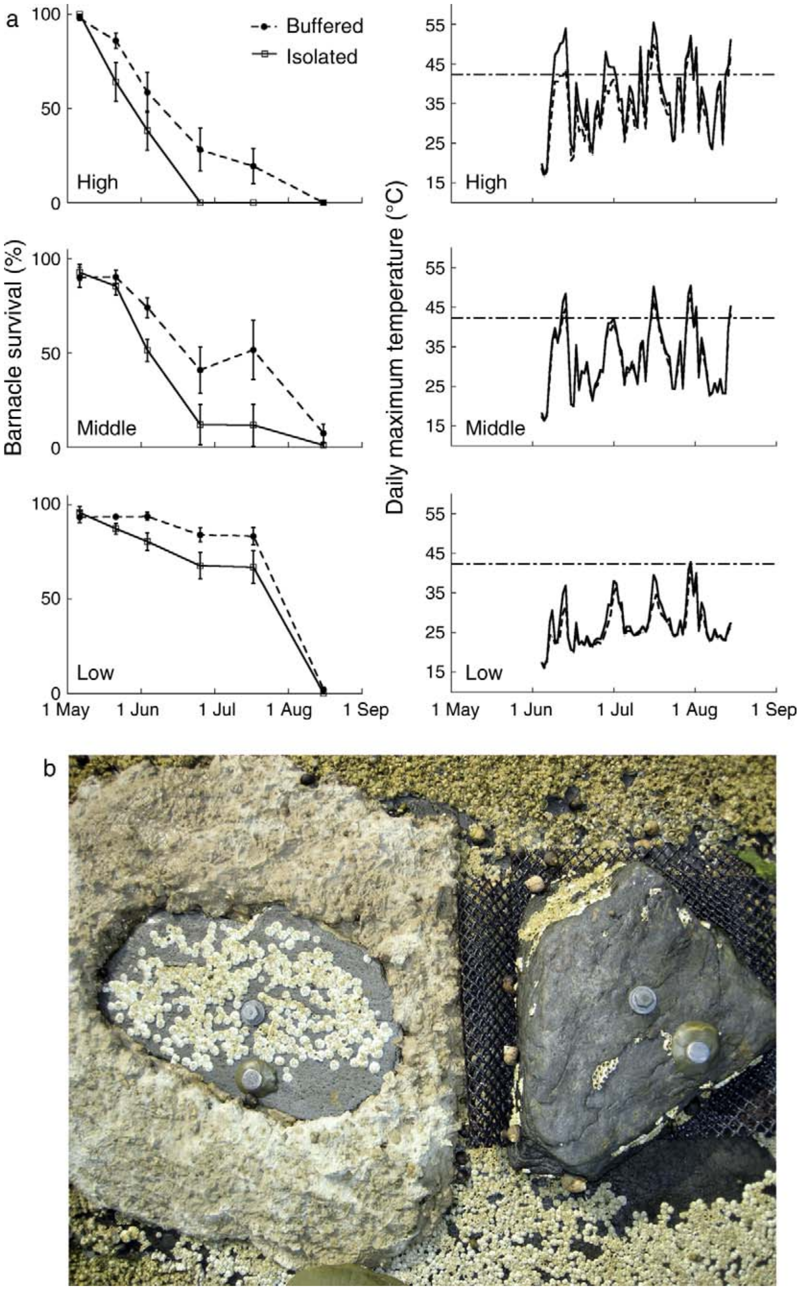

FIG. 3. (a) Percent survival of barnacles (left panels) and substrate temperature (right panels) in an experimental manipulation of substrate size at three tidal elevations. "Buffered" cobbles were embedded in concrete to be thermally joined to the underlying bedrock. "Isolated" cobbles were isolated from underlying bedrock by a mesh spacer. $N = 8$ cobbles per treatment per elevation. The dot-dashed line in temperature graphs indicates 44°C, a lethal temperature for *Semibalanus balanoides*. (b) Photo showing high intertidal buffered (left) and isolated (right) cobbles on 25 June 2008, halfway through the experiment. Initially, barnacle densities were equal on all cobbles.

size, tidal elevation, and site (three-way interaction; Appendix: Fig. A3 and Table A2). At both sites, barnacles survived higher in the intertidal on larger substrates than on cobbles (Appendix: Fig. A3 and Table A2). On boulder and bedrock substrates only, barnacle mortality was greater in the lower intertidal, although not significantly so (Appendix: Fig. A3 and Table A2). We frequently observed whelks, *Nucella lapillus*, and seastars, *Asterias forbesi*, on large substrates at lower elevations. At Hope Island, all barnacles on cobbles in the high intertidal died, while on larger substrates 24–34% of high intertidal barnacles survived the summer heat (Appendix: Fig. A3 and Table A2).

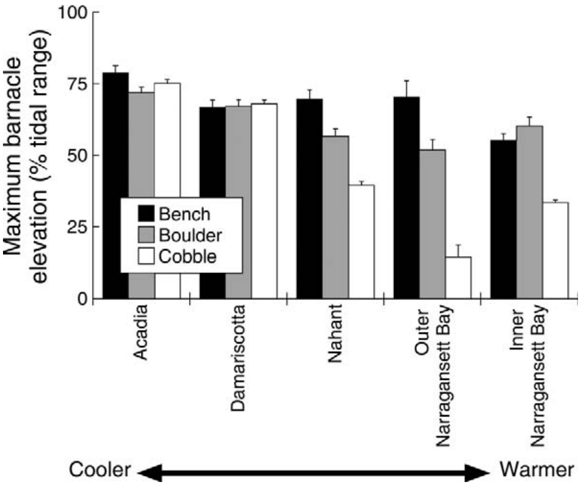

FIG. 4. Maximum barnacle elevation for different substrate size classes across five subregions within New England that span a climate gradient. Data are means + SE.

Experimental manipulation of substrate size

Experimentally increasing substrate size by thermally integrating cobbles to a bedrock bench reduced the mean daily maximum substrate temperature by 3.1°C (±0.3°C) and delayed 100% barnacle mortality by seven weeks in the high intertidal (Fig. 3). Early in the summer, thermal buffering reduced daily maximum temperatures of transplanted cobbles by over 8°C for several days, which reduced barnacle exposure to lethal temperatures (Fig. 3). High-intertidal barnacles died earlier in the summer than those in the low intertidal (time × elevation effect, Appendix: Table A3). At all elevations, thermal buffering extended barnacle survival time (time × treatment effect, Appendix: Table A3).

Barnacle mortality on transplanted cobbles was nearly complete (>90%) in all treatments by the end of the experiment. However, maximum survival occurred on thermally buffered cobbles in the mid-intertidal, where 7% of barnacles survived (Fig. 3).

Substrate size effects across a regional climate gradient

Across a regional latitudinal climate gradient, the extent of the barnacle zone reached higher in more thermally benign northern habitats (region effect, $F_{4,\,23} = 4.53$, $P = 0.0076$; Fig. 4). Within cooler northern subregions, substrate size did not affect the distribution of barnacles, whereas in more thermally stressful southern subregions, substrate size was a strong determinant of the maximum elevation occupied by *S. balanoides* (substrate size × region effect, $F_{8,\,250} = 12.83$, $P < 0.0001$; substrate size effect, $F_{2,\,250} = 79.60$, $P < 0.0001$; Fig. 4).

DISCUSSION

Evidence from observations, field experiments, and surveys across a climate gradient supports the hypothesis that substrate size mediates thermal stress for sessile residents such as barnacles and affects their survival and distribution. In thermally stressful Rhode Island, barnacles survived higher in the intertidal on larger substrates (Appendix: Fig. A3 and Table A2), because, as predicted, larger substrates were more thermally stable and less frequently exceeded the critical maximum temperature of S. balanoides (Fig. 2; Appendix: Fig. A2).

At a regional scale, barnacle distributions are a function of local substrate size acting within large-scale climate variation. Substrate size had large effects on the maximum elevation of barnacles in thermally stressful southern New England; barnacles lived twice as high on bedrock as on cobbles in Massachusetts and Rhode Island subregions (Fig. 4). In cooler northern New England, however, substrate size did not affect barnacle occupancy.

Substrate size caused occasional differences in surface temperatures of >6°C in Narragansett Bay. In addition to affecting barnacle survival and distribution (Poloczanska et al. 2008), a temperature difference of this magnitude can alter the direction of intra- (Bertness 1989, Bertness et al. 1999) and interspecific interactions (Leonard 2000) in the rocky intertidal. It is remarkable that the thermal effects of substrate size are rarely considered in rocky intertidal ecology, where substrate size varies greatly and also affects disturbance frequency (Sousa 1979).

Other abiotic mechanisms, such as slope and orientation (Harley 2008), wave exposure (Harley and Helmuth 2003), timing of tidal exposure (Mislan et al. 2009), and wind and fog (Helmuth et al. 2006*a*), additionally and interactively shape local thermal conditions in the intertidal. We surmise that substrate size can have as large as or larger effects than these factors because we were able to detect a strong signal of substrate size in temperature and barnacle mortality patterns where factors such as slope and orientation varied (K. B. Gedan, unpublished data).

Identifying and protecting thermal refuges for adaptation to climate change

We have identified large rock substrates as a physical refuge from thermal stress for intertidal invertebrates, particularly species that are physically coupled to their substrate. Refuges from environmental stress increase ecosystem resilience by maintaining a population to replenish disturbed or stressed populations, and they are important for the short-term preservation of ecological communities during periods of environmental change (Crowder and Figueira 2006). Identification of thermal refuges can inform reserve design and conservation planning for adaptation to climate change (Hoffman 2003, Kareiva et al. 2008, McLeod et al. 2009).

Thermal refuges identified by relationships between physical factors and populations can be incorporated into climate-change planning at a local scale, which is often where conservation and management decisions are made (Leslie 2005). For example, coral-conservation practitioners have recommended protecting thermally stable reef locations, such as those in shade, upwelling zones, or high current flow, where corals are less likely to bleach (McLeod et al. 2009). An alternate, but related, management approach is to protect heterogeneity, thereby incorporating many different refuge types (Kareiva et al. 2008, McLeod et al. 2009).

Once a refuge is identified, mapping its distribution can help target locations for conservation. In Rhode Island, we have found that bedrock thermal refuges are unevenly distributed: exposed bedrock is common along the open coast, but rare inside Narragansett Bay (Appendix: Fig. A4), a distribution that is likely common in drowned-river-valley-type estuaries. The thermally stressful climate of the inner bay relative to the open coast (Bertness et al. 1999) compounds the need for thermal refuges where they are rare. This highlights the value of large substrates to act as thermal-stress refuges in rocky intertidal communities within Narragansett Bay.

The conservation strategy of protecting thermal-stress refuges is critical for organisms living at their thermal limits, such as rocky intertidal species, desert lizards, tropical ectotherms, or reef corals (Somero 2005, Deutsch et al. 2008, Kearney et al. 2009, McLeod et al. 2009), to adapt to climate change. In thermally stressful locations, the persistence and adaptation of vulnerable assemblages may depend upon the availability of thermal refuges.

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APPENDIX

Additional methods plus four figures and three tables presenting statistical summaries, site information, and supporting data, including field verification of the correlation between rock and barnacle body temperatures, daily maximum temperature, and barnacle density and survival at Haffenreffer and Hope Island sites, and the geographic distribution of bedrock and cobble substrates in Narragansett Bay, Rhode Island (*Ecological Archives* E092-050-A1).