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Metapopulation dynamics of *Tigriopus brevicornis* (Harpacticoida) in intertidal rock pools

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ABSTRACT: Rock pools above the level of mean high tide are frequently occupied by harpacticoid copepods of the genus *Tigriopus*. The network of populations in separate pools can be viewed as a metapopulation. However, in a dynamic environment subject to rainfall, tidal flushing and wave wash, there may be no particular structure to rock pool populations. Time series samples from pools at different levels on the shore were used to test for the presence of separate local population dynamics of *T. brevicornis* (Müller). Sample counts taken from the same pool 2 d apart showed autocorrelation in pools from the upper and middle of the range occupied by *T. brevicornis*. However, the dynamics of different pools were not strongly correlated. For counts of copepodites and adults, the degree of coupling between pools was a function of distance. The height of high tide affected counts in pools. Copepodite and adult numbers fell in pools at the lower end of the species range during spring tides. In comparison, there were spring-tide-associated increases in copepodite and adult numbers in pools above the mean height of high tide. Persistence of populations on the shore may therefore be aided by upshore movement of copepodites and adults during spring tides. Multivariate analysis of stage structure in pools suggested that pools acted as individual systems over a period of 31 d. The results indicate a degree of local population dynamics in separate pools, but the inferred metapopulation structure does not follow the classical model, since extinction events were rare in pools above the mean high tide level.

KEY WORDS: Metapopulation · Rock pool · Spatial structure · Tidal · Dynamics

INTRODUCTION

Intertidal pools represent an attractive system for studying the spatial structure of populations, as individual pools are discrete and easily sampled. Each seperate rock pool may contain a local population of any particular species. When considering a group of local populations within some larger area, it is common to refer to such an assemblage as a 'metapopulation' (Hanski & Simberloff 1997). The spatial element added to population dynamics by considering metapopulations may have fundamental consequences for species conservation and evolution (Kareiva 1990, Hanski & Gilpin 1997). Perhaps the best known example is that extinction at a single site is not permanent, as recolonisation is possible from elsewhere in the metapopulation (Levins 1969). Various authors have studied aspects of metapopulation biology using brackish or freshwater rock pools containing *Daphnia* spp. or beetles (Hanski & Ranta 1983, Bengtsson 1993, Bengtsson & Ebert 1998, Svensson 1999). However, the presence of a spatial structure to population density does not necessarily imply that metapopulation dynamics are important. If dispersal between pools is too high, each individual may pass through several pools within a lifetime and the habitat will no longer effectively be subdivided into local populations (Harrison & Taylor 1997). Hence, the first aim of any description of the spatial and temporal population dynamics of a species should be to estimate the interdependence of local populations. A second point relevant to intertidal sys-

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tems is that pool height on the shore reflects the degree of tidal flushing. Submergence of pools during high tides may affect local population sizes due to increases in washout and predation (Dethier 1980).

Rock pool harpacticoids such as *Tigriopus* spp. are found worldwide, and have been widely used in studies of population genetics (Dybdahl 1994, Burton 1997, Burton et al. 1999), physiology, and biochemical assays (Shaw et al. 1997, McAllen et al. 1998, Forget et al. 1999, McAllen et al. 1999). Species distributions do not necessarily overlap, and the identity of copepods used in different studies therefore varies. North American research has generally focused on *T. californicus* (Baker), which inhabits rock pools along the Pacific coast. *T. japonicus* Mori is found in the western Pacific. There has been some confusion of the taxonomy of European species. Earlier works tend to cite *T. fulvus* (Fischer) as the occupant of North Atlantic pools. However, the currently accepted position is that *T. fulvus* is found in the Mediterranean and Madeira, being replaced by *T. brevicornis* (Müller) on the Atlantic coasts to the north (Bozic 1960, Huys et al. 1996). Species from the Southern Hemisphere are less clearly described and may currently be thought of as members of a *T. angulatus* 'complex' (Davenport et al. 1997). Despite differences in the taxonomic identity of copepods used, studies of *Tigriopus* spp. tend to reach similar conclusions. *Tigriopus* spp. are conspicuous occupants of pools at and above the high water mark (Fraser 1936a,b, Igarashi 1959, Dethier 1980, Powlik 1999). Differences in life history tend to be slight (Fraser 1936a). *Tigriopus* spp. can tolerate broad ranges of salinities and temperatures (Damgaard & Davenport 1994), although the limits of thermal tolerances tend to be species-specific (Davenport et al. 1997). *T. californicus* and *T. brevicornis* possess a dormancy response which appears to aid survival, particularly in the face of extreme salinities and temporary loss of pool water by evaporation (Fraser 1936a, Ranade 1957, Powlik & Lewis 1996). *T. californicus* has several feeding appendages that facilitate an omnivorous diet including detritus, faecal pellets, protists, diatoms and small crustaceans (Lewis et al. 1998). The dietary versatility of *Tigriopus* spp. is further demonstrated by the range of food stocks on which cultures have been maintained (Fraser 1936a, Powlik et al. 1997).

Although studies of *Tigriopus* spp. appear frequently in the literature, field surveys of populations are relatively rare (Powlik 1999). Such surveys generally summarise data on average population sizes by season and pool height on shore with little attention paid to more detailed spatial and temporal patterns of population dynamics. A relative lack of detailed field data is also evident in metapopulation ecology as a whole: there is a general bias towards theoretical investigations (Kareiva 1990, Nee et al. 1997, Hanski 1999). Existing case studies of metapopulations usually concern terrestrial or freshwater species (e.g. Hanski 1994, Sjögren Gulve 1994, Thomas et al. 1998; but see Pfister 1998 for an intertidal example). *Tigriopus* spp. in rock pools appears to represent a good model system for addressing empirical aspects of metapopulation dynamics in a marine system. This study uses repeated sampling of *T. brevicornis* from pools to examine 2 questions: (1) Are populations of copepods in separate pools part of a metapopulation or just samples from a single shore-wide population mixed during high tides? (2) How does the height of pools on the shore affect local population dynamics?

METHODS

Field surveys. A transect 5 m wide and perpendicular to the shoreline was haphazardly selected at Port St. Mary in the Isle of Man (4° 44′ W, 54° 4′ N). This transect extended just beyond the range of levels encompassed by high water neaps and high water springs (7.3 to 9.4 m above chart datum). The shore at Port St. Mary is formed by a gently sloping platform of limestone with a rise of 1 m for 16 m of shoreward travel (see Southward 1953 for a general description of the area). Pool locations within the transect were mapped and related to height above chart datum using records of the high tide mark on a number of calm days. Tidal levels are given with reference to chart datum at Liverpool, the relevant port used for predictions in the available tide tables. Chart datum at Liverpool is estimated to be 0.2 m above the height of the lowest astronomical tide. The tidal range at Port St. Mary is approximately 4.2 m during neaps and 8.4 m at springs. The sample transect contained 88 pools with depths ranging from 1.5 to 21.5 cm and areas of between 0.04 and 2.1 m^2.

A 125 ml wide-mouth polypropylene bottle was used to take samples from pools. Bottles could be instantaneously filled with the minimum of disturbance to benthic cells and detritus by placing them horizontally onto the bottom of pools. In contrast to the results of Powlik (1998a), sampling with a bottle was an effective method of capturing nauplii (the difference may be due to the larger bottle size used by Powlik). Individuals of *Tigriopus brevicornis* were identified to life history stage (Nauplius Stages I–V, Copepodid Stages I–V, and adults identified to sex) following Fraser (1936a) using an inverted microscope after overnight settlement of fixed 10, 25 or 100 ml sub-samples. Use of a standard cylindrical plankton chamber ensured accurate sub-sample volumes. The size of chamber used depended on the number of copepods counted, with larger chambers used for recounts of samples where individuals were rare or absent. All counts were subsequently converted to numbers ml^{-1}.

The distribution of *Tigriopus brevicornis* population sizes within the mapped pools was surveyed on December 4, 1997 and July 22, 1998. A time series was collected from pools in July and August 1998 to look more closely at temporal patterns of abundance. Sampling was stratified by dividing the transect into top, middle and bottom sections. Three pools were selected at random (using dice throws) from those avialable in each section. Sampled pools were at a height of between 7.34 to 7.36 m above chart datum in the bottom section, 8.46 to 8.6 m in the middle section, and 9.43 to 9.53 m above chart datum on the upper shore. For simplicity, these groups of pools are referred to hereafter as lower, mid and upper shore pools respectively. However, the group labels are for convenience rather than accuracy: pools described as lower shore were actually at the level of neap high tides. Time series samples were taken every 2 d for a period of 31 d, with all samples taken at the time of daytime low water. This time series allows an assessment of the role of changes in tidal flushing as it spans 2 spring-neap tidal cycles. The sampling period approximates 1 generation time for *T. brevicornis* (given as between 31 and 60 d by Fraser [1936a] and Harris [1973]). Temperature and salinity conditions in the rock pools were measured at the same time as sample collection using a WTW multiline P4 meter fitted with temperature and conductivity probes.

Comparisons of stage structure. The abundance of different life history stages can be used as a marker for the degree of mixing between pools. If the pools are mixed when covered by high tides, the abundances of different life stages in different pools will be similar. However, behavioural responses to high tide, such as swimming down and holding onto the substratum or the presence of chemical cues (Bozic 1975), may facilitate pool fidelity. Such pool fidelity may lead to the formation of separate local populations. There are 2 alternative patterns of local population structure. The specific features of each pool (such as depth or flushing rate: Metaxas & Scheibling 1993) may influence the resident local population, leading to different stage structures in separate pools over extended periods of time. Conversely, local populations of copepods may be unaffected by the individual nature of the pools that they inhabit. If this is the case, local populations may have a similar structure even if there is no mixing of individuals between pools. Multivariate methods based on the similarity between samples can be used to test for patterns in the population structures of different pools. If population structures are more similar within a time series from the same pool than between separate pools, this implies that pool fidelity results in a metapopulation with separate populations influenced by the local conditions in each pool. The null hypothesis is that repeated samples from the same pool are no more similar than samples from separate pools. Accepting the null hypothesis implies either extensive mixing between pools or separate pool populations insensitive to the local conditions. Similarities between the population structure in separate samples were calculated using the Bray-Curtis coefficient, S_{il}:

$$S_{il} = 100\left(1 - \frac{\sum_{j=1}^{n} |y_{ij} - y_{lj}|}{\sum_{j=1}^{n} (y_{ij} + y_{lj})}\right) \qquad (1)$$

where y_{ij} and y_{lj} are the counts for life history stage j in samples i and l respectively, and n is the total number of life history stages (12, including nauplii, copepodites and adults of both sexes). If samples have identical numbers of the different life history stages, then the Bray-Curtis coefficient is equal to 100. Conversely, the Bray-Curtis coefficient is 0 when a pair of samples have no life history stages in common. Differences in stage structure between pools were examined using the ANOSIM subroutine of the PRIMER package (Clarke & Warwick 1994). The ANOSIM procedure compares the similarity within predefined groups of samples to the average similarity between the groups of samples. A test statistic is generated to suggest whether the groups are consistent (samples are more similar within the predefined groups than between groups) in a manner analogous to univariate ANOVA. An ANOSIM test statistic of 1 is generated when all replicates within groups are more similar to each other than any replicates from different sites. In comparison, a test statistic near 0 suggests that samples within groups are no more alike than samples selected at random from different groups. The significance of the ANOSIM test statistic can be assessed using a randomisation test. Samples are randomly assigned to the predefined groups to indicate whether the measured value of the test statistic could have arisen by chance alone. For the analysis in this paper, the predefined groups are the 9 separate time series from individual pools. A significant ANOSIM test implies that different pools retained distinctly different stage structures throughout the period of the time series. Data were not transformed before multivariate analysis. Alternative analyses with log- and square-root transformed data had no effect on the conclusions, indicating that the multivariate analyses were not influenced by skewed count data.

Time series analyses. Temporal patterns in nauplii, copepodite and adult counts from individual pools were also analysed using several different correlation analyses. Autocorrelation refers to dependence between points within a time series (Chatfield 1996). This dependence is estimated by calculating the correlation coefficient between all possible pairs of x_i and x_{i+n}, where x_i is a point in the data series and x_{i+n} is a point n time steps away from x_i. For example the autocorrelation calculated from a plot of all possible pairs of counts from adjacent sampling dates (15 points) indicates the dependence between samples taken 2 d apart from the same pool. Positive correlation coefficients indicate that samples with relatively high counts are likely to be followed by high counts in the next sample (and conversely, low counts are likely to be followed by low counts). If the correlation coefficient is 0, then the value of a count on any one occasion is, on average, independent of the count in the preceding sample. Pool fidelity by copepods should result in positive autocorrelation coefficients, whereas complete mixing is expected to reduce the degree of autocorrelation in time series. As an alternative, however, complete mixing may lead to temporal autocorrelation if the entire shore acts as 1 population. Examining the relationships between time series in different pools as a function of the distance between the pools tested this hypothesis. The similarity between time series in different pools can be measured using inter-pool correlations of x_i against y_i; where x_i and y_i are counts at time i from separate pools (16 points for each comparison between separate pools). If the shore acts as a single population, then inter-pool correlations should be positive and unrelated to the distance between pairs of pools. With every possible comparison made among different pools within and between shore levels, there are 36 different inter-pool correlations. Unfortunately, the slope in plots of inter-pool correlations against distance between pools cannot be assessed with standard parametric techniques, as individual pools are used more than once. Repeated use of individual pools means that points are not strictly independent (Ranta et al. 1995). Hence, the significance of relationships between the distance between pools and the degree of coupling was assessed using the Mantel test (Sokal & Rohlf 1995). The Mantel test generates a large number of correlation coefficients using random permutations of one of the data sets. The significance of the measured correlation coefficient can then be judged by counting the fraction of randomly generated coefficients that equal or exceed the measured value.

Spring tides will flush high shore pools and increase the immersion period of lower shore pools. The effects of these changes in flushing were assessed using correlations between pool counts and the height of high water on the shore on the day samples were taken. Time series were differenced ($x_{i+1} - x_i$) to remove the problems associated with autocorrelated data and to eliminate long-term trends (Chatfield 1996). All correlations used nonparametric methods (Spearman's coefficient) as the counts were not expected to conform to the assumptions of parametric methods. Data used in subsequent analyses of variance were tested for homogeneity using Cochran's test (Underwood 1997). If analysis of variance suggested significant differences between treatments, pairs of treatments were examined for significant differences using the Student-Newman-Keuls (SNK) procedure (Underwood 1997).

RESULTS

Counts of *Tigriopus brevicornis* in December and July were of comparable size (Fig. 1). Nauplii and copepods occupied a wider range of pool heights in the summer survey. Other species of crustaceans were found in pools, including copepods such as *Harpacti-*

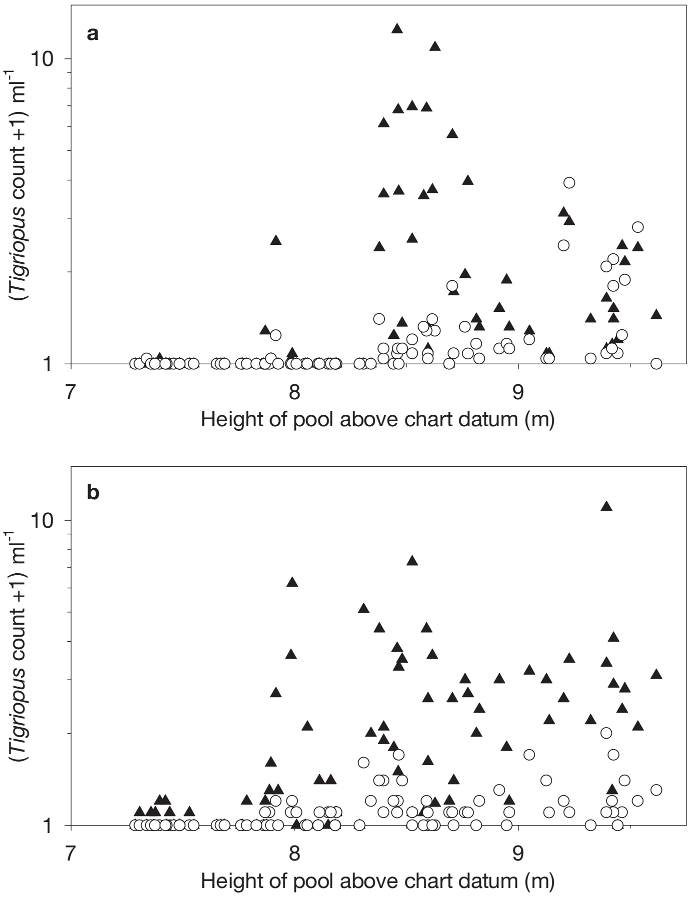

Fig. 1. *Tigriopus brevicornis.* Counts in pools during (a) December and (b) July. (○) Counts of nauplii; (▲) counts of copepodites and adults

cus spp. and ostracods. However, these species were only occasionally recorded, never in high numbers, and were restricted to pools at the seaward end of the transect. Sessile pool occupants included barnacles in all pools below 8 m, mussels in the lowest pool, red algal turfs below 8.2 m, and green algae (generally *Enteromorhpa* spp.) in most pools. The percentage cover of green algae increased with increasing shore height ($r_s = 0.635$, n = 88, $p < 0.001$). When covariation with pool height was controlled, the variation in green algal cover was not significantly associated with residual pattern in counts of nauplii or copepods. Time series from individual pools demonstrated considerable temporal variation in salinity and temperature (Fig. 2). Sharp rises in salinity in the middle and upper shore pools were associated with neap tides. The falls

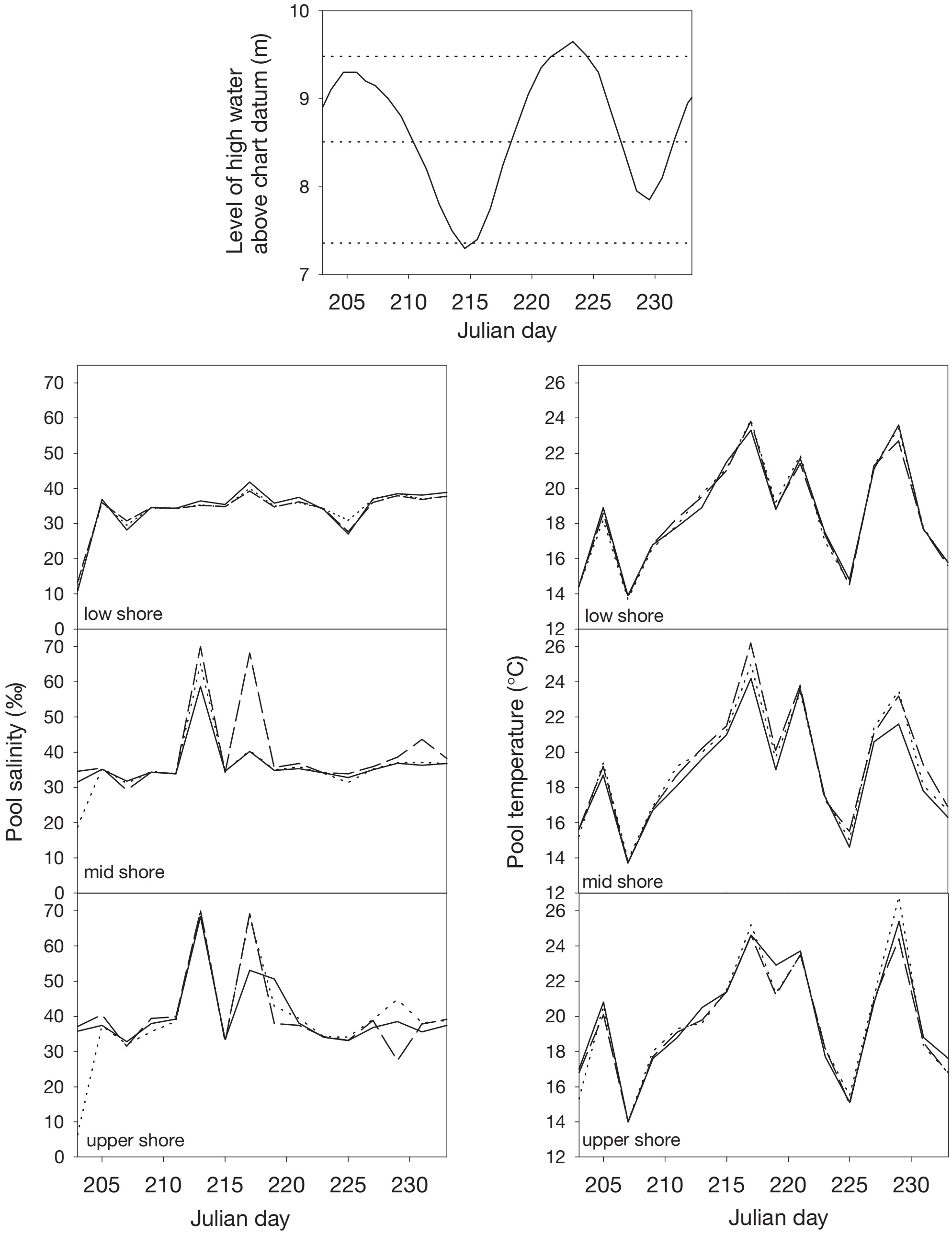

Fig. 2. Physical conditions in separate pools during the 31 daytime series. Julian day indicates days after January 1. Dotted lines on the graph of high water levels are the average heights of the lower, mid and upper shore pools used for the time series. The high water levels shown are the average daily heights of high tide predicted by tide tables and hence do not include effects of breaking waves

in salinity between Days 213 and 215 were associated with a rainstorm. Time series of nauplii, copepodites and adults were variable, but there were no clear long-term trends (all nonparametric correlations between counts and Julian day were not significant at an overall α level of 0.05, following a Bonferroni correction for multiple hypothesis testing). In upper and mid shore pools, there was little evidence for extinction and recolonisation events; *T. brevicornis* was always present. In contrast, there were 8 'extinction' events (all life history stages absent in at least 1 count) in time series from lower shore pools. It is difficult to conclude that *T. brevicornis* was entirely absent, but its absence from samples certainly indicates very low average abundances.

Comparisons between pool populations

Analyses of time series from separate pools using Bray-Curtis similarity coefficients suggested that pools retained distinctively different population structures throughout the 31 d sampling period (ANOSIM analysis of 9 separate groups, test statistic value = 0.363, $p < 0.001$). The value of the test statistic was not exceeded in 20 000 randomisations of the data, suggesting that the results are unlikely to have arisen by chance alone. Differences between pools were not solely due to differences in the average abundance of time series. If the data were standardised to produce proportions of each life history stage within each sample, differences between pools were retained (ANOSIM test statistic value = 0.248, $p < 0.001$).

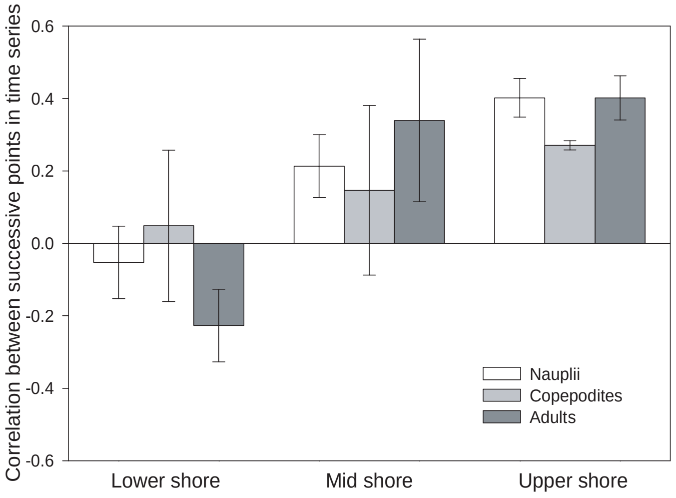

Fig 3. *Tigriopus brevicornis*. Autocorrelations within time series at different heights on the shore. Positive values indicate relationship between the counts in successive sample from the same pool. Error bars are ± SE

Comparison of temporally adjacent points in the time series of counts revealed significant differences in the extent of autocorrelation (Table 1, Fig. 3). Mid and upper shore pools had significantly stronger autocorrelations than lower shore pools (SNK tests, $p < 0.05$). There was no significant interaction with grouped life history stage. If the autocorrelation analysis was extended to pairs of counts 4 d instead of 2 d apart, no significant patterns were detected and correlation coefficients were not significantly different from 0.

The strength of inter-pool correlations appeared to decrease as a function of the distance between pools, with Mantel tests indicating significantly negative slopes for copepodites and adults (Fig. 4). Inter-pool correlations were generally weak. Over 90% of calculated coefficients were below the critical value for $p < 0.05$ (0.497).

Tidal effects on pool populations

The height of high tide influenced counts from pools with a significant interaction between life history stage and level of pools on the shore (Table 2, Fig. 5). The average correlations between nauplii counts and the height of high water were not affected by pool level (SNK tests, $p > 0.05$). In comparison, the average correlations between tidal height and both copepodite and adult counts were negative in lower shore pools but positive in mid shore pools (SNK tests, $p < 0.05$). Cross-correlations of adult abundance with tidal height were also significantly different when comparing lower and upper shore pools (SNK test, $p < 0.05$). The changes in abundances do not reflect changes in pool volume due to evaporation or freshwater inflow. Loss of pool water to evaporation during neap tides increased salinity, but these losses were not reflected by increased copepod counts. Salinity readings can be used to adjust the counts from pools to correct for changes in pool volume. However, applying such a correction did not alter

Table 1. *Tigriopus brevicornis*. Results of analysis of variance on correlations (r_s) between adjacent points within time series. Cochran's test implies that variances were homogenous ($C = 0.299$, not significant). Individual counts in pools were divided into 3 life history groups: nauplii (Stages I to V), copepodites (Stages I to V) and adults. ns: non-significant results

Source of variation	df	MS	*F*	p-value
Shore level	2	0.4511	7.40	<0.01
Life history group	2	0.0023	0.04	ns
Level × group interaction	4	0.0510	0.84	ns
Residual	18	0.0609		

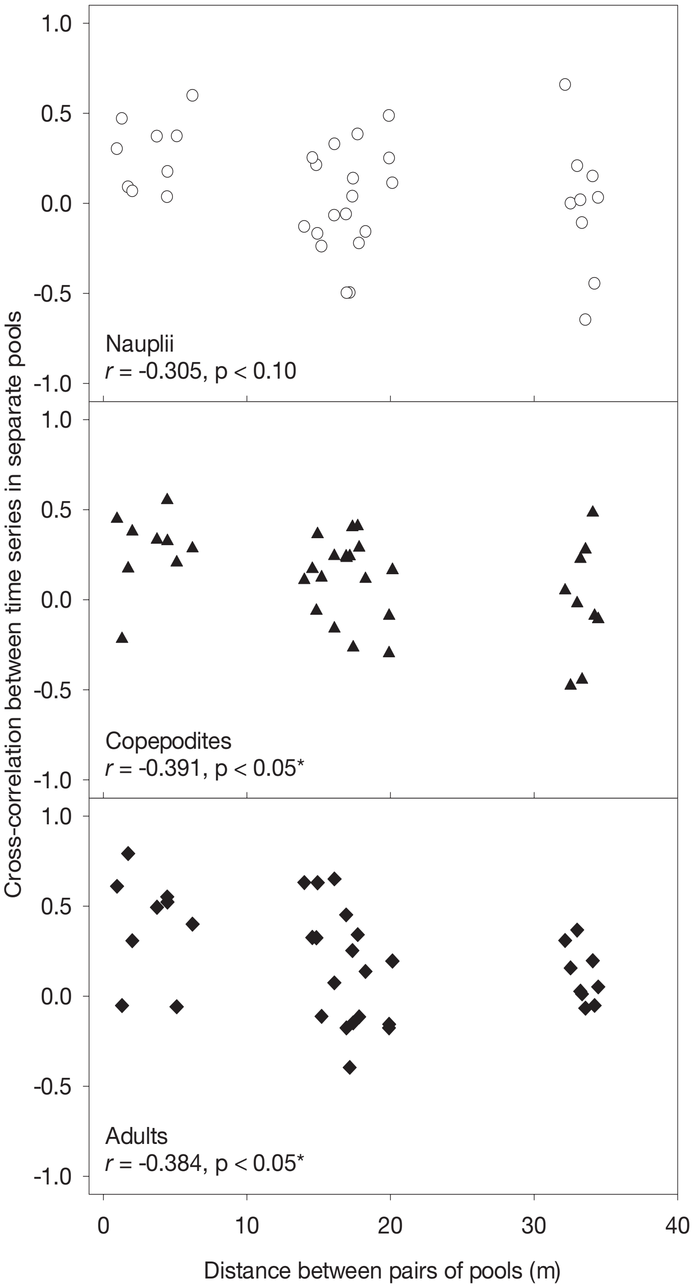

Fig. 4. *Tigriopus brevicornis*. Cross-correlations between all possible pairwise combinations of pools. Correlation coefficients were tested for significance using Mantel tests

the conclusions from the analysis of variance (in fact, the F ratio of the interaction term increased slightly from 3.68 to 4.82).

The height of high tide was a better predictor of copepod counts than salinity or temperature within pools. The average correlations between counts and the physical variables of salinity and temperature were less than 0.1 and not significantly different from 0.

DISCUSSION

The results from time series data clearly indicate a metapopulation structure for *Tigriopus brevicornis.* The alternative hypothesis that individual rock pools contain a random sample from a shore-wide population can be rejected as, over a timescale approximating the generation time for *T. brevicornis*, pools maintained distinct local population stage structures. Abundances were positively autocorrelated within time series from upper and mid shore pools, indicating a degree of population stability even in the presence of occasional tidal flooding of pools. The importance of local population processes was further emphasised by the weak correlations between time series from different pools. Combinations of chance historical effects and the characteristics of individual pools, such as volume and depth, would appear to generate a degree of local population dynamics in each pool (Metaxas & Scheibling 1993, 1994). The decay of inter-pool correlation coefficients with distance for copepodite and adult counts, however, suggests that pools are not totally independent: dispersal or similar environmental conditions can partially link the dynamics of pools over short distances.

The lower shore pools, close to the level of high water neaps, were strongly affected by increased tidal flushing in comparison to pools higher on the shore. Populations were unpredictable, with no significant autocorrelations in time series. There were zero counts in time series from lower shore pools, implying densities of <0.01 *Tigriopus brevicornis* ml^{-1}, and possibly indicating extinction events. Cross-correlations of counts with the height of high tide suggested an interesting interaction between life history group and height of pools on the shore. Counts of nauplii were not affected by spring tides. In comparison, copepodites and, particularly, adults were negatively correlated with spring tides in lower shore pools but positively correlated with spring tides in mid and upper shore

Table 2. *Tigriopus brevicornis*. Results of analysis of variance on cross-correlations between counts in time series and the height of high tide. Variances were considered to be homogenous (Cochran's test, $C = 0.282$, not significant). Three life history groups were used in the analysis: nauplii (Stages I to V), copepodites (Stages I to V) and adults. ns: non-significant results

Source of variation	df	MS	*F*	p-value
Shore level	2	0.3434	13.34	<0.001
Life history group	2	0.0587	2.28	ns
Level × group interaction	4	0.0948	3.68	<0.05
Residual	18	0.0257		

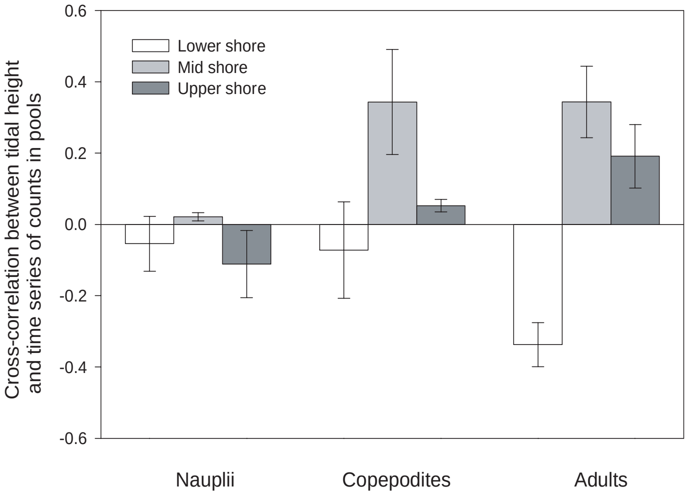

Fig. 5. *Tigriopus brevicornis*. Relationships between counts of different life history groups and height of high water on the day the samples were taken. Error bars are ± SE

pools. Hence, at the same time that copepodites and adult densities were decreasing in lower shore pools, their abundances were increasing in mid and upper shore pools. *Tigriopus* spp. are not considered to be planktonic, an observation supported by the persistent genetic differences between populations on separate rock outcrops (Burton 1997). Therefore, the most likely source for spring tide increases in populations in mid and upper shore pools is upshore migration of a proportion of the copepodites and adults which leave lower shore pools. It is interesting that the mid shore pools appear to have stronger cross-correlations with tidal height than the upper shore pools. This may reflect the fact that, in comparison to the mid shore, upper shore pools were only linked to the rest of the shore by occasional high tides and wave wash. Igarashi (1959) presented data for *T. japonicus* that are consistent with the hypothesis of upshore migration on spring tides; there were spring tide associated increases in the proportion of adults and copepodites in pools below the splash zone. Other crustaceans are known to follow a rising tide (Lawrie et al. 1999), and such a mechanism could cause the patterns shown and thus increase the persistence of individuals on the shore. Nauplii, which do not show any evidence for upshore migration, are considered to have a less developed swimming ability when compared to other life history stages (Powlik et al. 1997). *Tigriopus* spp. populations are thought to have relatively lower abundances of nauplii than pelagic copepods (Harris 1973, Powlik 1998b). It has been suggested that the relatively low nauplii numbers may reflect cannibalism (Powlik 1998b); however, selective retention of copepodites and adults represents an alternative mechanism for relatively low nauplii numbers in *Tigriopus* spp. populations.

Despite the evidence for a spatial population structure, *Tigriopus brevicornis* cannot be described as a classical metapopulation: persisting due to a balance between local extinction and colonisation processes. For upper and mid shore pools there were no extinctions observed in the 31 daytime series and, with 1 exception, all 42 pools between 8.38 and 9.62 m above chart datum were occupied in both summer and winter surveys. A similar situation has been reported for San Juan Island, Washington, by Dethier (1980): *T. californicus* was almost always present in pools between the heights of mean and maximum high water. Powlik (1998b, 1999) also found *T. californicus* to be characteristic of pools just above the level of average high water, although he recorded higher extinction levels. Dybdahl (1994) reported high extinction levels in pools (approx. 35 %); however, many of the pools surveyed in his study were splash pools, at or above the level of the spring high tides. Despite recording extinction events, Dybdahl concluded, from genetic evidence, that *T. californicus* was not persisting as a classical metapopulation. Powlik & Lewis (1996) suggest that Dybdahl may have underestimated the desiccation resistance of *T. californicus*, leading to misidentification of extinction events. The refuge value of sediment and green algae (*Enteromorpha* spp.) in upper shore pools may also have been underestimated previously (McAllen 1999). It is, however, clear from the separate studies of *Tigriopus* spp. that local populations are highly persistent in pools above mean high water.

The heterogeneity in conditions associated with the height of pools on the shore may enhance the persistence of *Tigriopus* spp. (Burton 1997). High shore and splash pools can provide refuges from both predation (Dethier 1980) and from washout during exceptionally high tides and storms. Conversely, lower shore pools may act as refuges during calm dry spells when upper shore pools dry out. The upshore movement of individuals from lower shore pools on spring tides could act as a means of replenishing or recolonising dried out pools. Lower shore pools also ensure that washout of individuals does not necessarily mean permanent loss from upper shore populations; there is always the possibility of re-supply of at least a few individuals on spring tides. Genetic evidence supports this dynamic view of *Tigriopus* spp. movement on the shore: all pools contained the same allele frequencies 8 mo after introducing novel alleles to 4 pools on an outcrop (Burton & Swisher 1984). The importance of dispersal between pools at different shore heights could be tested by comparing population dynamics on continuous shores, such as Port St. Mary, with shores that contain natural or artificial discontinuities, which act as barriers to dispersal. Recovery after a drought or storm should be more rapid on continuous shores than on discontinuous shores.

Other species also appear to benefit from spatial heterogeneity in resources. Beetles can survive drought periods by transferring to refuge pools (Svensson 1999), and checkerspot butterflies benefit from heterogeneity in food plant resources associated with different microclimates (Weiss et al. 1988). Such results suggest that, for species occupying patch networks, conservation efforts should be broadened to encompass sites beyond those that appear optimal at any one time.

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