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Food-Dependent Aggregation, Mobility and Dynamics of *Ceriodaphnia dubia* and *Daphnia pulex*

by

Kim Michelle Dibble

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Food-Dependent Aggregation, Mobility and Dynamics of *Ceriodaphnia dubia* and *Daphnia pulex*" submitted by Kim Michelle Dibble in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

Models of spatially-structured predator-prey dynamics have predicted that differences in individual mobility and foraging behaviour may affect spatial distributions and consequently, population dynamics. In this thesis, I show that two freshwater cladoceran zooplankton (*Ceriodaphnia dubia* and *Daphnia pulex*) differ in swimming speed and ability to locate local regions of high-food concentration. I derive and test predictions about population-level phenomena using this information regarding differences in individual behaviour. Specifically, I predicted that under controlled laboratory conditions, *C.dubia* populations should be more spatially heterogeneous, experience smaller fluctuations in density, and have more stable dynamics in smaller environments than *D.pulex*. Experiments showed that while *C.dubia* populations were more aggregated than *D.pulex* populations, they were not more stable. *C.dubia*'s limited mobility produced fixed rather than ephemeral patches that did not alter population stability. The patchiness of the *D.pulex* populations was ephemeral and led to damped population fluctuations in large environments.

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To my mother

and

Wiggy & Gnat

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CHAPTER 1 INTRODUCTION

Natural populations display a broad range of dynamics. Some populations persist for long periods of time, with only small fluctuations in density, while others fluctuate wildly (e.g. Hassell et al. 1976, May 1976, Murdoch and McCauley 1985, Oksanen and Oksanen 1992). The densities and stability of populations are affected by many factors in the environment. However, much insight into the mechanisms governing population stability has been obtained by isolating predator-prey or consumer-resource interactions (Murdoch and Oaten 1975).

Historically, explanations regarding the stability of predator-prey populations have focused on two main ideas: the effects of density-dependent biotic factors (e.g. Murdoch and Oaten 1975, Kingsland 1985, Kuno 1987) and the effects of a spatially heterogeneous environment (e.g. Hanski and Gilpin 1991, Levin 1992). Clearly, both factors can play a part in governing predator-prey population stability.

Density-dependence in predator-prey interactions can influence dynamics by stabilizing fluctuations in density. High densities of predator or prey individuals may cause intraspecific competition (Murdoch and Oaten 1975, Kuno 1987). Competition for a limited resource, such as food or nesting sites, can reduce fecundity or survivorship and return the population to lower densities. As well, when a resource is not limiting, mutual interference can have the same effect. These forms of density-dependent regulation tend to keep populations within certain limits and promote stability. Predator-prey interactions, however, can also be destabilizing. For example, time-lags (May 1973), non-linearities in predator feeding behaviour (i.e. a type II functional response) (Rosenzweig

1971), and any tendency for density-dependent regulation to overcompensate can actually destabilize predator-prey dynamics causing population fluctuations.

Spatial heterogeneity of environment and spatially-structured interactions among individuals can have important effects on predator-prey dynamics through a variety of mechanisms. First, individuals (either prey or predators) may aggregate in regions of high food or according to environmental factors such as temperature and light. This aggregative behaviour can lead to patchy distributions of individuals that can introduce spatial density-dependence which modifies the stability of the population dynamics (Hassell and May 1974, Murdoch and Stewart-Oaten 1989). That is, spatial heterogeneity in prey and predator populations directly or indirectly modifies the density-dependent relationships, which in turn affect stability. There is much debate as to whether aggregation stabilizes or destabilizes predator-prey dynamics (Godfrey and Pacala 1992, Murdoch et al. 1992a)

Second, spatial heterogeneity may also increase the stability of predator-prey populations by dividing populations into subpopulations (collectively termed a metapopulation), which are only connected through intermittent dispersal (Hilborn 1975, Murdoch and Oaten 1975, Hastings 1990, Reeve 1990, Taylor 1990, Hanski and Gilpin 1991, Hastings 1991). Spatial barriers dividing subpopulations can take the form of geographical obstructions or merely more or less favourable foraging areas. Populations separated in space (i.e. subpopulations) are not subject to precisely the same factors and may fluctuate out of phase. This asynchrony can lead to a statistical stabilization of the population as a whole. In more extreme

cases, conditions which produce extinction in one location are unlikely to prevail in all subpopulations (Taylor 1988).

Third, refugia provided by spatial heterogeneity generally tend to stabilize the population dynamics of a predator-prey interaction. Spatial heterogeneity of the environment may create regions that are inaccessible to predators. These refugia will buffer the prey population from the full effect of predation and can increase the stability of the interaction (Maynard-Smith 1974, Tanner 1975, Mech 1977). McNair (1986) classified the conditions under which refugia are stabilizing or destabilizing.

Finally, it has recently been suggested that the limited mobility of individuals, which is related to but distinct from a behavioural response, may also be important in stabilizing population dynamics (de Roos et al. 1991, McCauley et al. 1993, Wilson et al. 1993). Individuals may form ephemeral patches, which are not dependent on an originally patchy environment, through the effect of spatially localized interactions among individuals. The size of these patches, and hence the strength of this stabilizing factor, depends in part, on individual mobility. Since, predator and prey mobility, along with features of their interaction, determines the size of "patches", the number of patches present in a finite environment or habitat will depend on the size of the environment. For example, if the habitat is small, the patch size theoretically could be larger than the habitat size. In this case, the population would be considered as a spatially homogeneous system. Increasing environment size, while holding individual mobility and qualitative features of the predator-prey interactions fixed, would increase the potential number of ephemeral,

asynchronous patches in the system and consequently increase the "stability" of the population dynamics.

To predict the population-level consequences of potential predator mobility requires consideration of behavioural responses to local prey levels and distribution. It is generally predicted that individual predators will modify their behaviour to maximize food gathering (e.g. Charnov 1976, Ramcharan and Sprules 1989). Changes in behaviour at different food levels may substantially effect predictions relating individual mobility to population dynamics. Species may be highly mobile at low food levels, in order to visit as many areas as possible, and relatively immobile at high food levels (e.g. Townsend and Hildrew 1980). Further, individuals may aggregate in high food regions (e.g. Hassell and May 1974, Jakobsen and Johnsen 1987) or avoid these regions because of toxic excretion or increases in mortality risk due to predation (e.g. Sih 1980, Holbrook and Schmitt 1988). Combinations of these behaviours may change the actual mobility of the species in different conditions and consequently change the population-level predictions. Thus, studies which attempt to make predictions about population-level phenomena based on individual mobility must also include those aspects of behaviour which influence mobility.

The main objective of my thesis is to determine if individual mobility, and behaviour which influences mobility, can cause spatial heterogeneity in predator-prey populations (distinct from externally imposed environmental heterogeneity), which in turn affects population stability. Predictions that move from individual-level phenomena to population-level consequences require experiments which examine behaviour as well as experiments which study populations. Very few

studies of this nature have been attempted (e.g Luckinbill 1974, Kareiva and Odell 1987, Lomnicki 1988, DeAngelis et al. 1992), and it is obvious that the experimental system must be selected with care. Using a freshwater zooplankton-algae system, I attempted to derive and test population-level predictions based on findings at an individual level.

Freshwater zooplankton-algal systems are ideal for examining the relationship between individual properties and population-level dynamics (McCauley et al. 1990b, Murdoch et al. 1992b). First, studies have shown that these systems are capable of producing a variety of dynamics. In particular, McCauley and Murdoch have shown that the herbivorous cladoceran *Daphnia* and their algal prey display a wide range of population dynamics that includes both stable and cyclic fluctuations (Murdoch and McCauley 1985, McCauley and Murdoch 1987, McCauley et al. 1988, McCauley and Murdoch 1990). Second, studies indicate that this range of zooplankton dynamics is internally generated via their predator-prey interaction as opposed to being externally-driven by environmental fluctuations (McCauley et al. 1988, McCauley 1993).

Third, the mechanisms underlying the population dynamics of these systems have not been satisfactorily described. Models of individual biology have been constructed for *Daphnia* based on energetics (McCauley et al. 1990a, Gurney et al. 1990) and population-level models have been synthesized (Nisbet et al. 1989, Nisbet et al. 1991, Murdoch et al. 1992a) for spatially-homogeneous systems. But at present, these models fail to account for the dynamic patterns found in natural systems (McCauley and Murdoch 1990). However, numerous studies (e.g. Cassie 1963, Steele 1978, Levin 1992) have documented the existence of spatial

heterogeneity in natural systems at a variety of spatial scales (i.e. <1m, 1-10 m, 1km etc). In particular, the occurrence of microscale heterogeneity (<10cm) (Pinel-Alloul et al. 1988, Davis et al. 1992, Tiselius 1992), make it probable that localized predator-prey interactions might help to reconcile the model predictions and field dynamics.

Fourth, in order to investigate the effects of differences in mobility and behaviour on population dynamics of real systems it is necessary to compare species that can be studied both at the individual level and population level (i.e. over many generations). The time-scale for behavioural interactions and population-level phenomena of zooplankton make experiments feasible on individual behaviour as well as population dynamics (e.g. Slobodkin 1954, Goulden et al. 1982, Jakobsen and Johnsen 1987, Neary et al 1993).

Finally, the species selected should differ in mobility and/or behaviour but have qualitatively similar life history strategies, numerical responses and functional responses in order to isolate the effects of behaviour on population dynamics. Freshwater cladocerans, and in particular *Daphnia*, are a closely related group of species with similar life history strategies (Lynch 1980, 1992). This similarity, when accompanied by differences in mobility or behaviour, makes these species an appropriate group on which to investigate the effects of behaviour and mobility on population dynamics.

While there has been a tremendous effort studying the biology of *Daphnia*, there are surprisingly few studies on *Daphnia*'s foraging behaviour (see chapter 2), and in particular little is known about *Daphnia*'s ability to respond to small-scale spatial variation in prey density. In

addition, the behavioural attributes of other herbivorous zooplankton, which can often be dominant members of the plankton community (e.g. *Ceriodaphnia*), have not been well described. This information is crucial for describing predator-prey interactions in spatially-structured systems and is the main focus of my experimental work.

In this thesis, I examine both the foraging behaviour and population dynamics of two cladoceran zooplankton, *Ceriodaphnia dubia Richard* and *Daphnia pulex Leydig*, that differ substantially in body-size. In general, differences in body size should lead to differences in mobility, according to general allometric relationships across taxa (e.g from viruses to whales) (Peters 1983). But in comparing closely related taxa, it is important to understand how behavioural responses to light, food and temperature might modify expected differences in mobility. Studies have shown that these species are morphologically similar, utilize the same prey, have similar modes of reproduction, and can coexist (Lynch 1978, Smith and Cooper 1982, Pace et al. 1983, Romanovsky and Feniova 1985). These similarities should allow me to isolate the effects of differences in mobility, and foraging behaviours affecting mobility, on population-level phenomena.

In chapter 2, I examine whether these species differ in their mobility and foraging behaviour when presented with both spatially-homogeneous and heterogeneous food distributions. Under controlled laboratory conditions, I test whether *D. pulex* and *C. dubia* can aggregate in local regions of high food concentration, and investigate possible mechanisms used by individuals to locate and linger in these areas. In the literature, aggregation is used in a variety of ways. Sometimes it denotes swarming

of individuals caused by their mutual attraction (i.e. active aggregation). Throughout this thesis, however, the term aggregation is used only as a description of the spatial distribution of individuals and I test how this spatial distribution changes with variation in the spatial distribution of their food resource. Population-level predictions are then made using this behavioural information, and these predictions are tested using laboratory populations of *C. dubia* and *D. Pulex* (chapter 3). Populations were raised in undisturbed laboratory environments, and their spatial distributions and population dynamics were studied over many generations. Although the chapters are closely linked, they are presented as two scientific papers, each providing a concise literature review of pertinent topics and a detailed statement of the problem being investigated.

CHAPTER 2 FOOD-DEPENDENT AGGREGATION AND MOBILITY OF *CERIODAPHNIA DUBIA* AND *DAPHNIA PULEX*

INTRODUCTION

Herbivorous zooplankton populations are often spatially aggregated in natural systems. The vertical distribution of zooplankton is well documented, along with observations on diurnal variability (e.g. Hutchinson 1967, Leibold 1980, Dodson 1990). Horizontal spatial distributions are less studied (Omari and Hamner 1982), however recent work indicates considerable aggregation does exist in the horizontal plane (Malone and McQueen 1983, Tessier 1983, Threlkeld 1983, Urabe 1989).

These patterns of spatial aggregation can be caused by the interaction of a variety of extrinsic and intrinsic mechanisms. Locally high densities of herbivorous zooplankton could be created by the operation of physical forces, such as advection through wind and current action (Langford and Jermolajev 1966, Malone and McQueen 1983, Haury et al. 1992). Behavioural mechanisms, such as reproductive swarms (Colebrook 1960, Brandl and Fernando 1971), have been thought to cause spatial heterogeneity in population distributions. More recently, factors such as predation and competition have also been implicated (Urabe 1990). Finally, spatial variation in demographic rates may cause a patchy population distribution. For example, local rates of reproduction that exceed rates of diffusion of individuals away from a given region could cause aggregation (Okubo 1978).

These mechanisms can operate on different time-scales and may not be mutually exclusive. In marine systems, physical forces have been thought to dominate the formation of patchy population distributions. However recent studies have shown that even in these high-energy systems, microscale spatial distributions, which most likely result from individual interactions, can persist. For example, Davis et al. (1992) found microscale patchiness (<10cm), patchiness at scales of 1 - 5 m, and large scale trends in abundance (10-200m) concurrently in the distribution of oceanic zooplankton under calm conditions.

While there has been a large amount of work describing spatial patterns, few studies have focused on mechanisms that create spatial heterogeneity, and in particular, the study of behavioural mechanisms in zooplankton has been neglected. This area of research is of interest since it has been suggested that differences in individual mobility and behaviour may create differences in predator-prey distributions and consequently, differences in their population stability (de Roos et al. 1991, McCauley et al. 1993, Wilson et al. 1993).

The major purpose of this chapter is to examine whether cladoceran zooplankton possess behavioral mechanisms that lead to an aggregated distribution of individuals in response to spatial variability in food concentration under controlled laboratory conditions. Conclusions about the similarities or differences in behaviour between species can then be used to make predictions regarding population aggregation and dynamics (see chapter 3).

Few studies of freshwater zooplankton behaviour have been completed, and even fewer studies have related the behaviour of these

organisms to population-level phenomena (i.e. aggregation or population dynamics). Differences in the mobility of cladocera may be related to organism size. Dodson and Ramcharan (1991) showed that the swimming speed of *Daphnia pulex* increased with body length. But consistent differences among species have not yet been found (Riessen et al 1988, Young and Taylor 1990).

Comparisons among studies are also complicated by the axis and number of dimensions in which swimming speed is measured. There appears to be no consistent trend to account for variation among species in the horizontal component of swimming speed. Riessen et al. (1988) found that *Ceriodaphnia dubia*, a very small cladoceran (0.75 mm), actually moved more quickly (3.92 mm/s) than individuals of the larger species *D.pulex* (size = 0.9 mm, speed = 1.23 mm/s and size = 1.8 mm, speed = 3.56 mm/s). Ramcharan and Sprules (1989) observed a much lower swimming speed (1.3 mm/s) for similarly sized *D.pulex* (1.5 mm). Young and Taylor (1990) estimated that one of the smallest cladocerans, *Bosmina longirostris*, which averages a length of 0.3 mm, had a swimming speed of 1.27 mm/s. Comparisons from these experiments must be interpreted with caution since they were performed under a variety of food, light and temperature conditions that may effect mobility.

There are very few studies on the behavioural response of individual cladocerans to varying levels of food, and existing results are often equivocal. For example, Young and Getty (1987) showed that *D.magna* reduces its vertical component of swimming and decreases the rate of turning in response to increasing food level. Porter et al. (1982), however, found no change in swimming speed of *D.magna* that had been moved

from a particle-free culture into an algal suspension. Thus, it is unclear whether cladocerans vary swimming speed or turning behaviour in response to changes in food level.

Similar uncertainty exists concerning the ability of cladocerans to respond to spatially heterogeneous food-distributions. Porter et al. (1982) found no evidence of aggregation of *D.magna* individuals to regions of high food concentration. Jakobsen and Johnsen (1987) did report that *D.pulex* aggregated in regions of high food when placed in an overall condition of relatively low food (0.15 mg C/L) but found no response at high food levels (0.31 - 2.4 mg C/L), which were atypical of natural conditions. However, it is unclear from the experiment that spatial differences in food distribution actually existed in the apparatus used by Jakobsen and Johnsen (1987), which casts doubt on their conclusion.

Neary et al. (1993) attempted to correct the limitations of experiments performed by Jakobsen and Johnsen (1987) by using an apparatus in which a spatial distribution of food could be created over a distance of 0.5 m, and food levels along this gradient monitored directly. Unlike Jakobsen and Johnsen (1987), Neary et al. (1993) found that *D.pulex* actually avoids extremely high food levels. When overall food levels approximated levels in natural environments (0.2 mg C/L), individuals could locate the high-food end of a gradient.

Given the lack of consensus in the literature and the paucity of data on cladoceran species other than *Daphnia*, it seems clear that a systematic comparison among species under similar conditions has yet to be completed. Further, meaningful comparisons of behavioural responses among species must be made under conditions which control light and

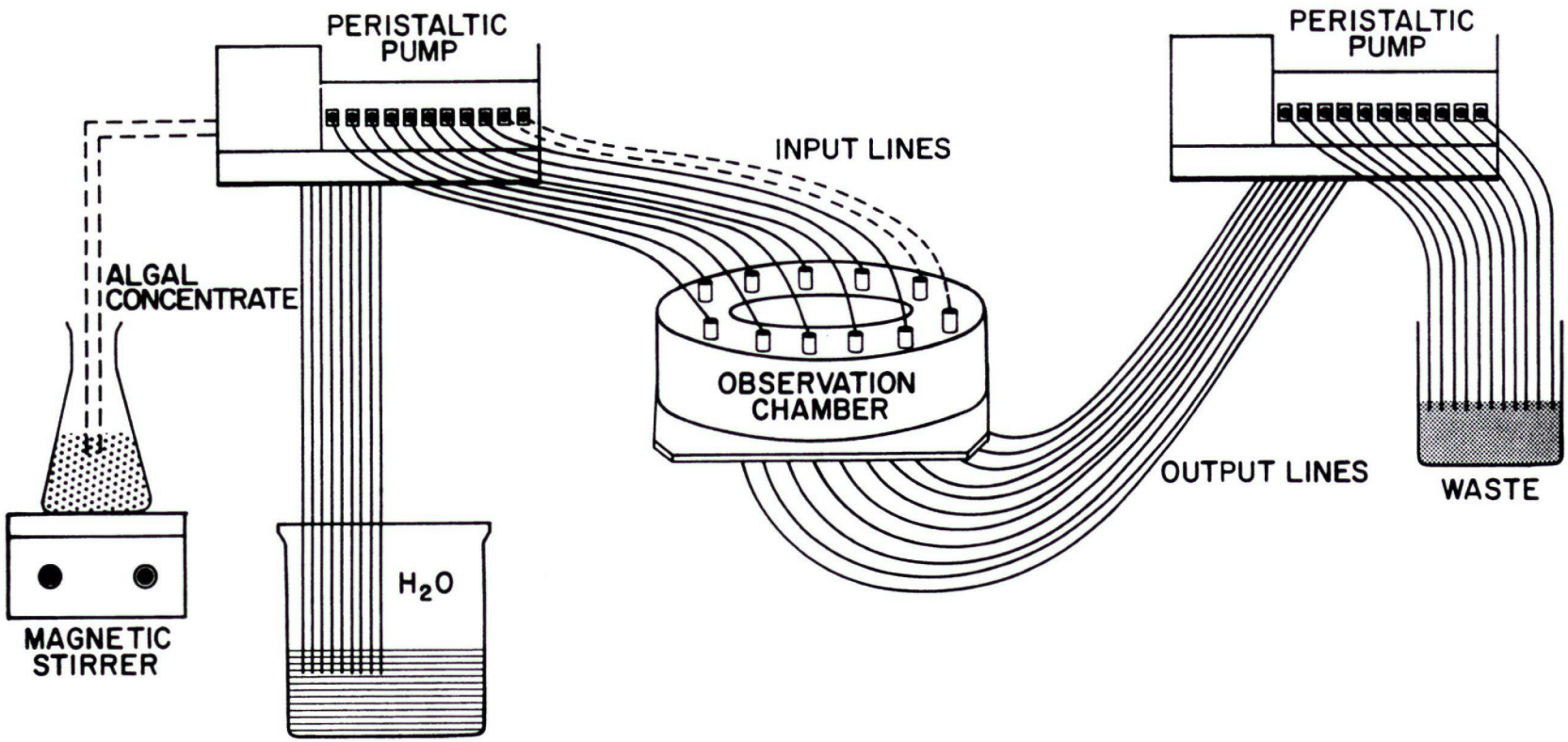
temperature (Buchanan et al. 1982). Since individual behavioural responses to food are important in determining the actual mobility of species, the concentration and distribution of food available during behaviour studies must also be controlled and varied. Finally, to maintain known food concentrations it is necessary to use some sort of flow-through system so that local areas cannot be depleted by the grazing of cladocerans.

Using a flow-through system (Figure 2.1), I examined the mobility and behaviour of individuals of the species *C.dubia* and *D.pulex* under the same temperature and light conditions, using a range of food concentrations that bracket natural food levels. This system can create continuous spatial distributions of food concentrations without the existence of edges or repelling boundaries in the horizontal path of individuals that might influence their mobility. Observations were made on both single organisms and groups of individuals in order to determine the overall behavioural response to food conditions as well as to isolate mechanisms that governed responses. Only behaviour in the horizontal plane was investigated since it was not possible to create and sustain vertical gradients in food concentration without the confounding influence of gravity.

The experiments were designed to answer four major questions:

1. Do *C.dubia* and *D.pulex* differ in their mobility and/or behavioural responses?
2. Do the cladocerans respond to the presence/absence of food or to differences in food concentration, under spatially homogeneous conditions, with a change in mobility or behaviour?

Figure 2.1 Schematic diagram of the circular observation chamber and peristaltic pump system used in the behaviour experiments.


PERISTALTIC PUMP
INPUT LINES
PERISTALTIC PUMP
ALGAL CONCENTRATE
OBSERVATION CHAMBER
OUTPUT LINES
WASTE
H_2O
MAGNETIC STIRRER

3. When presented with heterogeneous food distributions, are *C.dubia* and *D.pulex* capable of locating and exploiting regions of high food concentration?
4. Do the cladocerans respond to a heterogeneous food distribution with a change in mobility or behaviour?

Because *C.dubia* and *D.pulex* have similar morphology, feeding mechanisms, life history, and inhabit similar environments, it seemed unlikely that there would be any large differences between the species in behavioural responses to the presence of food. Based on previous studies of the effects of body size within a species, it did seem reasonable to predict that, under identical environmental conditions, the smaller but morphologically similar *C.dubia* would move less quickly than the larger species of cladocera even though Riessen at al. (1988) have found evidence to the contrary.

Observations were made under various concentrations of homogeneous food to determine if there was any change in swimming speed or behaviour with different food levels, and to determine if any such responses varied between species. It was predicted that individuals should increase their mobility with higher food levels and decrease their rate of turning in order to maximize their feeding efficiency by avoiding previously grazed regions (Young and Getty 1987).

Thirdly, in the absence of spatial heterogeneity of risk and mortality, individuals should move towards regions of high food in a heterogeneous food distribution to maximize energy intake. Both fecundity and survival are positively related to variation in food concentration in cladocera over food levels typical of the field (McCauley et al. 1990a). Consequently, it

was predicted that individuals should aggregate in high-food regions of the observation chamber.

Finally, in order to linger in relatively high food regions, it was predicted that the cladocerans should respond behaviourally to the presence of a patchy food-distribution by increasing their rate of turning and/or decreasing their swimming speed in the high food region.

METHODS AND MATERIALS

EXPERIMENTAL DESIGN

The mobility and behaviour of individuals of both species was observed in a circular Plexiglass chamber (50 cm circumference x 5.5 cm height x 1.5 cm width) (Figure 2.1). Eleven input and output ports were connected to two peristaltic pumps with Tygon tubing (0.8 mm diameter). Inputs were fed from reservoirs containing either aerated synthetic pond-water, made with mineral additions to distilled water, or a suspension of algal cells in this water. Flow rates through the chamber were maintained at rates (approximately 350 mL/hr) that are significantly greater than individual clearance rates (Porter et al. 1982) to prevent individuals from depleting food in local areas.

Chlamydomonas reinhardtii was used as a food source. Cells were raised in an axenic medium, centrifuged, and resuspended in synthetic pond-water to a desired concentration before use. Concentrations of algal cells were determined by cell counts of the concentrate (32 fields at 100X magnification), which was then diluted appropriately.

Two main groups of experiments, which manipulated the spatial distribution of the food source (homogeneous and heterogeneous distributions), were completed using both single individuals and groups of individuals. Under conditions of a homogeneous distribution of food, at least five separate individuals and five groups of 10 individuals of both species were observed at food concentrations of 0, 1000, 4000 and 8000 cells/mL. Under conditions of a heterogeneous food distribution, at least five individuals and five groups of 10 individuals of both species were observed at 1000, 4000, and 8000 cells/mL (Table 2.1). This range of food concentrations was selected to reflect natural food levels (McCauley and Murdoch 1987, McCauley and Murdoch 1990, McCauley et al. 1990a).

The heterogeneous food distributions will be referred to as food gradients throughout the remainder of the chapter even though they are more accurately described as a bell-shaped, continuous spatial distribution.

A number of minor experiments were also completed in order to gain insight into the mechanisms by which individuals locate food. In the gradient experiments, individuals were placed in the chamber at 2 different insertion points (180° and 0° from the high end of the food distribution). As well, preliminary experiments in the absence of food were completed, with and without flow to determine if the individuals responded to water flow with a change in behaviour. These experiments were performed with 5 individuals of each species. More than 200 separate behaviour experiments were performed including experiments to test the attributes of the system (e.g. flow rates).

Table 2.1 Number of replicate individual experiments (Ind) and group experiments (Grp) for each food distribution (homogeneous or heterogeneous), food level (0, 1000, 4000, or 8000 cells/mL), and species (*C.dubia* or *D.pulex*).

Distribution		Homogeneous				Heterogeneous		
Level		0	1000	4000	8000	1000	4000	8000
IND	*C.dubia*	5	5	5	5	5	5	5
	D.pulex	5	5	5	5	5	5	5
GRP	*C.dubia*	5	5	5	5	13	8	12
	D.pulex	5	5	5	5	5	6	6

To establish homogeneous food conditions, the system was allowed to run with all lines feeding from an algal suspension. Food gradients with a high-food concentration of 1000, 4000 or 8000 cells/mL were created by allowing the system to run for 3 hours prior to the introduction of any individuals. Two adjacent lines fed from an algal suspension of 5000, 10000, or 40000 cells/mL and the remaining lines fed from algae-free synthetic pond-water. At the end of a behaviour trial, the concentration of algal cells in the viewing chamber was measured by sampling (at the approximate midpoint in height of the viewing chamber), using syringes inserted through 5 of the input ports. Counts of algal cells for each port were then completed on 200 fields or 200 cells, whichever came first, at 400X magnification using an inverted microscope.

Individuals of *Ceriodaphnia dubia* and *Daphnia pulex* were measured using a dissecting scope and then allowed to clear their guts in food-free water for 1 hour and 3 hours, respectively. These periods were selected based on gut passage rates (Peters 1984). Only parthenogenic females from an equilibrium population were used. Individuals were placed in the viewing chamber, in both the gradient and homogeneous food distribution treatments, at a predetermined position 180° distant from the highest food concentration. Once placed in the chamber, individuals were allowed to acclimatize for 10 minutes, and then the X-Y position of the individual was then noted every 30 seconds for a 15 minute period. Groups of 10 individuals were also allowed to acclimatize for 10 minutes, and then the positions of individuals were noted every 10 minutes for a 60 minute period. An individual would only be used in a single trial, and experiments

measured species behavioural responses in isolation (i.e. mixtures of *C.dubia* and *D.pulex* were not studied).

For all individual experiments, total path length, absolute displacement, degree of turning, and frequency of occurrence in different regions of the viewing chamber were determined and used to compare the responses of the two species. Total path length measured mobility. It was calculated by plotting the position of individuals every 30 s for the 15 min observation period and summing the linear distance between the points. Absolute displacement was restricted to the horizontal plane, and it was calculated by vector addition of clockwise and counter clockwise movement in the circular observation chamber. This measure gave an indication of the actual mobility of the species in terms of area covered.

Degree of turning was also used to compare the behaviour of the species. The turning index was calculated by dividing the absolute displacement by the total path length (Batschelet 1981, Buskey 1984). A turning index of 1 describes a straight path while progressively lower values indicate increasingly tortuous routes. Finally, the frequency of occurrence of individuals in 11 regions of the observation chamber, corresponding to the locations of input and output ports, were used to determine if individuals located and lingered in areas of high food. In the group experiments, since the location of particular individuals could not be determined, only frequency of occurrence was recorded.

DATA ANALYSIS

ANOVA was used to compare the turning index, path length, and displacement of individuals in different treatments. Species, food distribution, and food level were the treatment variables.

To analyze the frequency distribution of individuals in the observation chamber, circular statistics were used (Batschelet 1981). This branch of statistics is used to analyze circular variables such as preferred directions in animal orientation, navigation and biological rhythms (Batschelet 1981). Directions are measured by angles ranging from 0° to 360° with the zero direction selected arbitrarily by the investigator.

Batschelet (1981) suggests both the mean angle and the median angle as measures of location for circular spatial distributions. The mean angle is the most frequently used measure of location and is also the easiest measure to calculate. Consequently, this is the measure of location that was used for this study. It is calculated by estimating the mean angle (ϕ) by: ϕ =arc tan y/x, where $y = 1/n(\Sigma\, n_i \cos\phi_i)$, $x = 1/n(\Sigma\, n_i \sin\phi_i)$, ϕ_i is the observed angle, n is the total number of observations, and n_i is the number of observations at ϕ_i. Dispersion associated with the mean angle was estimated by the angular deviation (s) calculated by: $s = [2(1-r)]^{0.5}$, where $r = (y^2 + x^2)^{0.5}$. Small values of s indicate a large degree of orientation about the mean angle (Batschelet 1981).

ANOVA comparisons were performed for the angular dispersion (s) to determine if the species differed in their degree of orientation, and to determine if the degree of orientation was affected by food distribution or food levels.

An index of location was calculated by the cosine of the difference between an expected direction of orientation (in this case the angular location of the maximum algal concentration) and the observed direction of orientation (the mean angular location of the individuals). (There was some variablity associated with the strength of the algal gradient which

did not affect the ability of individuals to locate regions of high food. (see Appendix 1)). This modification of Batschelet's (1981) v index ($v = r \cos(\phi - \Theta_o)$, where Θ_o is the expected angular direction) was used in order to determine if an oriented behaviour of the individuals centered on regions of high food concentration. Excluding r in the equation avoids confounding the degree of orientation of individuals with the location of individuals relative to the high food location.

If the location of individuals is random, relative to the high food regions, a mean value of zero would be expected for the index. The observed values of the index for the different treatments were tested against a random expectation of zero using t-tests. These tests assessed if there was a difference in the ability of the species to locate the high end of a food gradient, if different food levels influenced this behaviour, and if individuals had a preferred location in the absence of a food gradient.

RESULTS

INDIVIDUAL DATA ON MOBILITY AND SWIMMING BEHAVIOUR

Preliminary experiments

In the absence of food, flow-rate had no demonstrable effect on any behavioural component for *C.dubia* or *D.pulex* (Table 2.2).

Mobility and swimming behaviour of *C.dubia* and *D.pulex* compared

Mobility differed significantly between the two species in the presence of either homogeneous or heterogeneous food distributions (Table 2.3). *D.pulex* swam significantly faster than *C.dubia* (Fig. 2.2a & 2.2b), and *D.pulex* had a significantly higher horizontal displacement (Fig.

Table 2.2 Test statistics for the analysis of the effect of flow/noflow conditions on the path length (path), horizontal displacement (displace), turning index (turn), and dispersion (s) of individual *C.dubia* and *D.pulex*.

	C.dubia	*D.pulex*
path	$F_{1,9}=0.97$	$F_{1,9}=0.00$
displace	$F_{1,9}=1.93$	$F_{1,9}=0.19$
turn	$F_{1,9}=1.12$	$F_{1,9}=0.04$
s	$F_{1,9}=0.19$	$F_{1,9}=2.72$

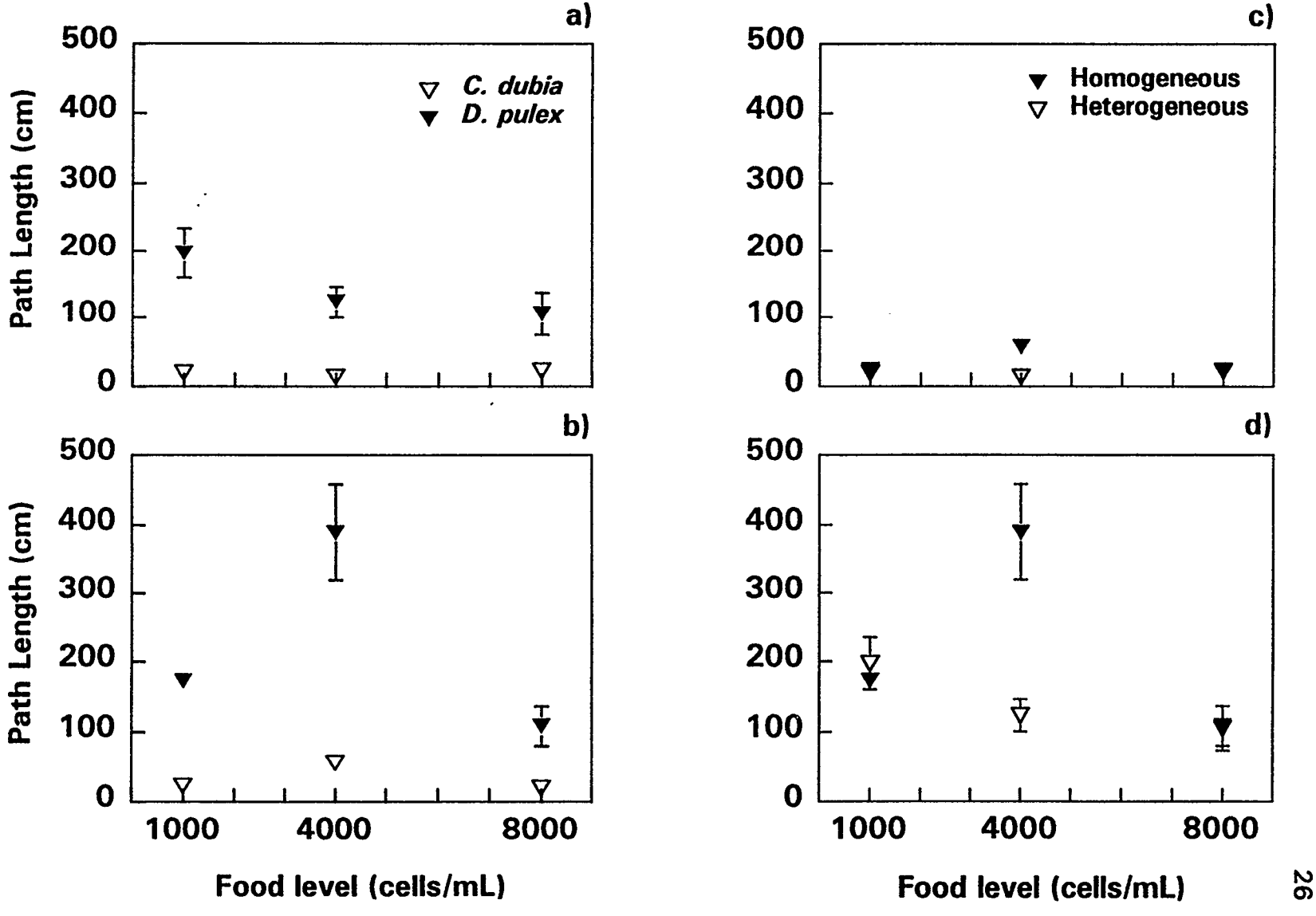
*P<0.05, **P<0.01, ***P<0.001

Table 2.3 Test statistics from the analysis of the effects of species (*C.dubia* or *D.pulex*) and homogeneous or gradient food distribution (distribution) on path length (path), absolute horizontal displacement (displace), the turning index (turn) in the individual experiments.

Effect	Species	Distribution	Species*Dist
path	$F_{1,59}=49.22^{***}$	$F_{1,59}=4.62^{*}$	$F_{1,59}=2.24$
displace	$F_{1,59}=12.31^{***}$	$F_{1,59}=1.94$	$F_{1,59}=1.64$
turn	$F_{1,59}=2.41$	$F_{1,59}=1.23$	$F_{1,59}=0.00$

*P<0.05, **P<0.01, ***P<0.001

Figure 2.2 Path length (cm) of individual *C.dubia* and *D.pulex* at food concentrations of 1000, 4000, and 8000 cells/mL showing comparisons between species when food was distributed a) in a gradient and b) homogeneously and showing comparisons between the two food distributions for c) *C.dubia* and d) *D.pulex*. Error bars in this and all subsequent graphs represent standard errors about the mean.


a)
b)
c)
d)
Path Length (cm)
500
400
300
200
100
0
C. dubia
D. pulex
Homogeneous
Heterogeneous
1000
4000
8000
Food level (cells/mL)

2.3a & 2.3b) (error bars in all figures are standard errors). While there were dramatic differences in mobility between species, their turning behaviour was not significantly different (Fig. 2.4a & 2.4b) (Table 2.3).

Mobility and swimming behaviour of *C.dubia*

Food level and the spatial distribution of food (i.e. homogeneous or heterogeneous) had little effect on the mobility and swimming behaviour of *C.dubia* (Table 2.4). Absolute displacement and the degree of turning were not affected by food distribution or food level (Fig 2.3c & 2.4c). The path length was affected by the interaction between food level and food distribution (Table 2.4).

A closer examination of the individual data revealed that the experiments conducted at 4000 cells/mL (homogeneous food), which were completed much earlier than any of the other treatments, contained significantly larger individuals than any other experiments (Table 2.5). Unfortunately, an analysis which removed the effects of size through the use of a covariate could not be completed because the relationship was highly non-linear. Removing this particular treatment from the analysis modified the results. With the 4000 cells/mL treatment removed, the interaction term between food level and food distribution for the analysis on path length was insignificant (Table 2.6). Only path length was affected by the presence/ absence of food (Table 2.7) and a comparison of the means indicated that path decreased in the presence of food.

Mobility and swimming behaviour of *D.pulex*

D.pulex showed similar responses to changes in spatial distribution and level of food (Table 2.8). The degree of turning of individuals was not affected by the interaction of the main effects (Fig. 2.4d). However, path

Figure 2.3 Absolute displacement (cm) of individual *C.dubia* and *D.pulex* at food concentrations of 1000, 4000, and 8000 cells/mL showing comparisons between species when food was distributed a) in a gradient and b) homogeneously and showing comparisons between the two food distributions for c) *C.dubia* and d) *D.pulex*.

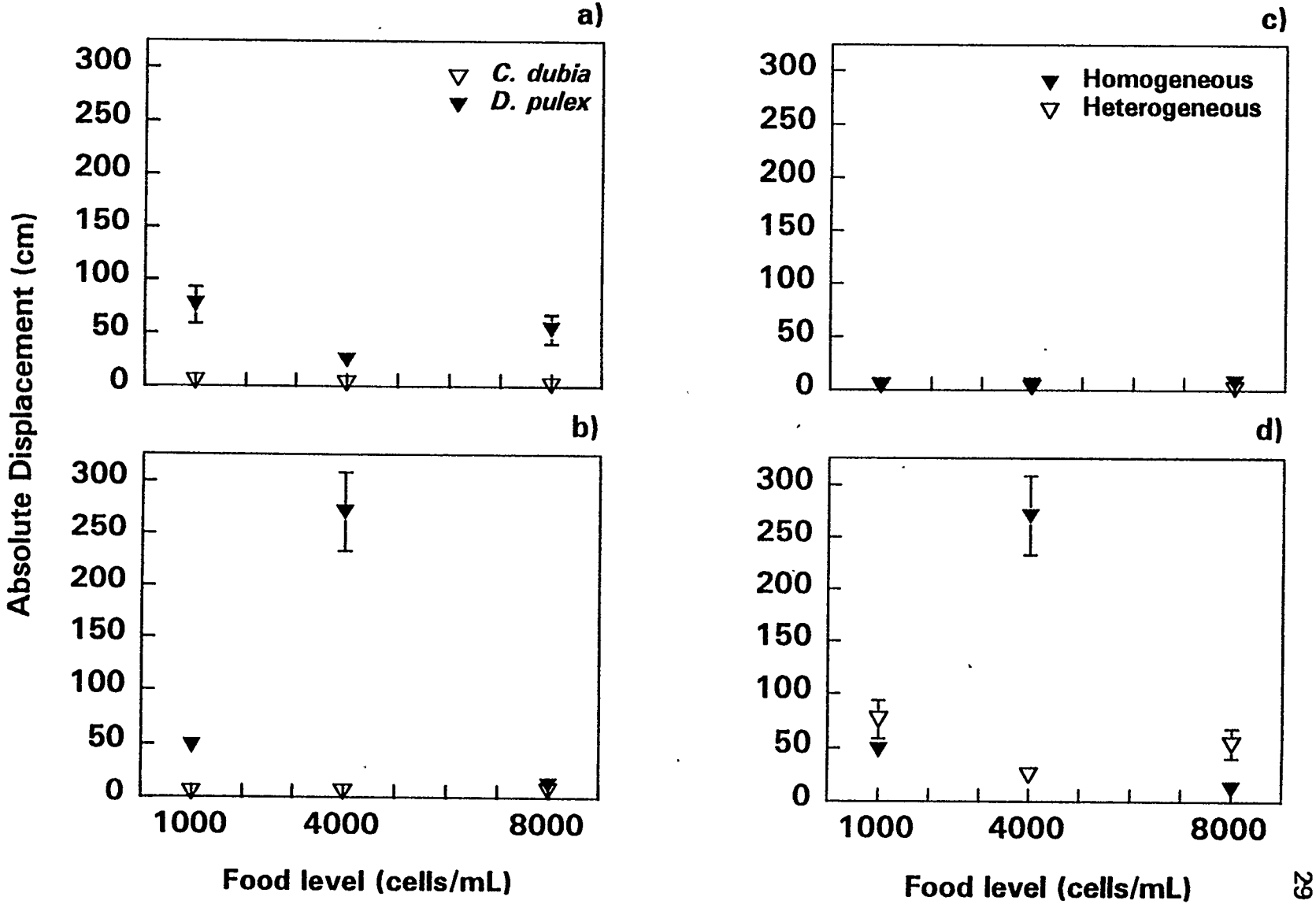
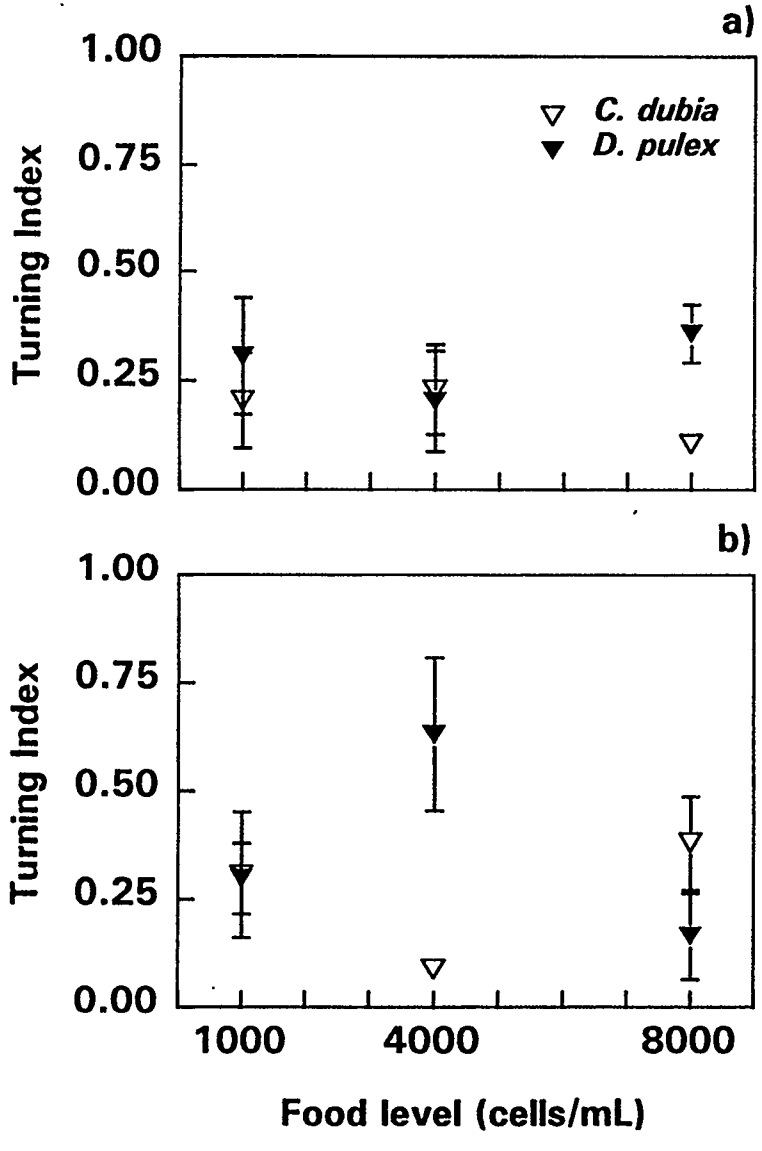

a)
b)
c)
d)
C. dubia
D. pulex
Homogeneous
Heterogeneous
Absolute Displacement (cm)
300
250
200
150
100
50
0
1000
4000
8000
Food level (cells/mL)
Food level (cells/mL)

Figure 2.4 Turning index of individual *C.dubia* and *D.pulex* at food concentrations of 1000, 4000, and 8000 cells/mL showing comparisons between species when food was distributed a) in a gradient and b) homogeneously and showing comparisons between the two food distributions for c) *C.dubia* and d) *D.pulex*.


a)
b)
1.00
0.75
0.50
0.25
0.00
Turning Index
C. dubia
D. pulex
1000
4000
8000
Food level (cells/mL)

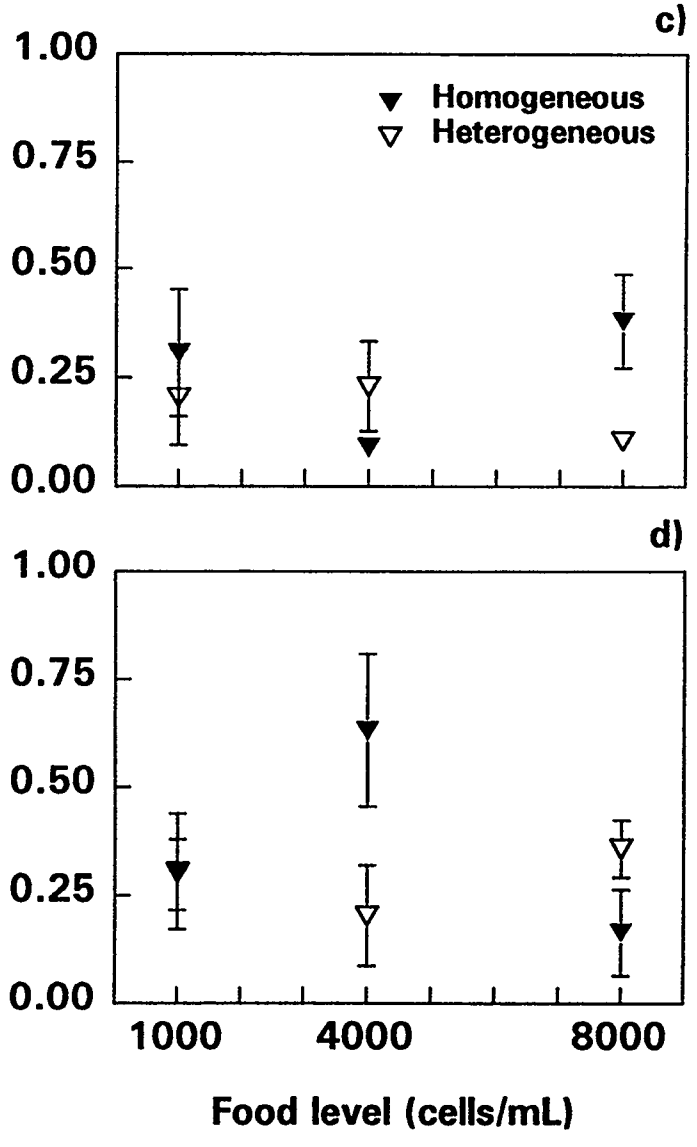

c)
d)
1.00
0.75
0.50
0.25
0.00
Homogeneous
Heterogeneous
1000
4000
8000
Food level (cells/mL)

Table 2.4 Test statistics from the analysis of the effects of homogeneous or gradient food distribution (distribution) and food level (1000, 4000 and 8000 cells/mL) on path length (path), absolute horizontal displacement (displace), and the turning index (turn) of individual *C.dubia*.

Effects	Distribution	Food level	Dist*Food
path	$F_{1,29}=9.87^{**}$	$F_{2,29}=3.99^{*}$	$F_{2,29}=9.51^{***}$
displace	$F_{1,29}=3.27$	$F_{2,29}=0.02$	$F_{2,29}=1.52$
turn	$F_{1,29}=0.97$	$F_{2,29}=0.57$	$F_{2,29}=2.27$

*P<0.05, **P<0.01, ***P<0.001

Table 2.5 Mean body lengths (mm) of *C.dubia* and *D.pulex* used in individual experiments in each food distribution and food level.

Distribution	Homogeneous				Heterogeneous		
Level	0	1000	4000	8000	1000	4000	8000
C.dubia	0.77	0.74	0.79	0.76	0.78	0.75	0.77
D.pulex	2.21	2.02	2.54	1.81	2.10	1.76	1.85

Table 2.6 Test statistics from the analysis of the effects of homogeneous or gradient food distribution (distribution) and food level (1000, 4000 and 8000 cells/mL) on path length (path), absolute horizontal displacement (displace), and the turning index (turn) of individual *C.dubia* with the 4000 cells/mL (homogeneous distribution) treatment removed.

Effects	Distribution	Food level	Dist*Food
path	$F_{1,24}=0.00$	$F_{2,24}=0.56$	$F_{1,24}=0.33$
displace	$F_{1,24}=2.13$	$F_{2,24}=0.01$	$F_{1,24}=2.65$
turn	$F_{1,24}=3.09$	$F_{2,24}=0.17$	$F_{1,24}=0.65$

*P<0.05, **P<0.01, ***P<0.001

Table 2.7 Test statistics from the analysis of the effect of the presence/absence of food on the path length (path), horizontal displacement (displace), and turning index (turn) of individual *C.dubia* and *D.pulex* with the 4000 cells/mL (homogeneous distribution) treatment removed.

Effects	*C.dubia*	*D.pulex*
path	$F_{1,14}=4.55$*	$F_{1,14}=6.39$*
displace	$F_{1,14}=1.03$	$F_{1,14}=1.33$
turn	$F_{1,14}=0.71$	$F_{1,14}=0.00$

*P<0.05, **P<0.01, ***P<0.001

Table 2.8 Test statistics from the analysis of the effects of homogeneous or gradient food distribution (distribution) and food level (1000, 4000 and 8000 cells/mL) on path length (path), absolute horizontal displacement (displace), and the turning index (turn) of individual *D.pulex*.

Effects	Distribution	Food level	Dist*Food
path	$F_{1,29}=6.94$*	$F_{2,29}=7.75$**	$F_{2,29}=8.94$***
displace	$F_{1,29}=3.08$	$F_{2,29}=4.25$*	$F_{2,29}=7.88$**
turn	$F_{1,29}=0.52$	$F_{2,29}=0.78$	$F_{2,29}=3.03$

*P<0.05, **P<0.01, ***P<0.001

length and absolute displacement were significantly influenced by the interaction between food level and distribution (Fig. 2.2d & Fig 2.3d).

When the suspect treatment (4000 cells/mL, homogeneous distribution) was removed from the analysis, there was no effect of food distribution or food level on displacement (Table 2.9). However, path length seemed to decrease with food level (Fig. 2.2d & Table 2.9).

In addition, the presence/absence of food had no significant effect on absolute displacement and the degree of turning (Table 2.7). Path length decreased in the presence of food.

GROUP DATA ON ORIENTATION BEHAVIOUR

Orientation behaviour of *C.dubia* and *D.pulex* compared

There was a significant species effect and an interaction effect between species and food distribution (Table 2.10) on the angular standard deviation (s), which measures spatial dispersion or degree of orientation of individuals. *C.dubia* had a much greater degree of orientation than *D.pulex* based on a Tukey's comparison of means (Fig. 2.5a & 2.5b) when food was homogeneously or heterogeneously distributed. The interaction term shows that this difference was more pronounced under homogeneous conditions.

In the presence of heterogeneous food distributions, *D.pulex* was significantly better than *C.dubia* at locating regions with relatively high food concentrations as measured by the index of location (the cosine the difference between the angular location of the maximum algae concentration and the mean angular location of the individuals) (Fig. 2.6a). The t-tests for the index of location indicated that generally the mean

Table 2.9 Test statistics from the analysis of the effects of homogeneous or gradient food distribution (distribution) and food level (1000, 4000 and 8000 cells/mL) on path length (path), absolute horizontal displacement (displace), and the turning index (turn) of individual *D.pulex* with the 4000 cells/mL (homogeneous distribution) treatment removed.

Effects	Distribution	Food level	Dist*Food
path	$F_{1,24}=0.15$	$F_{2,24}=4.32$*	$F_{1,24}=0.25$
displace	$F_{1,24}=2.08$	$F_{2,24}=1.64$	$F_{1,24}=0.08$
turn	$F_{1,24}=0.72$	$F_{2,24}=0.45$	$F_{1,24}=0.62$

*P<0.05, **P<0.01, ***P<0.001

Table 2.10 Test statistics from the analysis of the effects of species (*C.dubia* or *D.pulex*) and homogeneous or gradient food distribution (distribution) on the degree of orientation (s) for the group experiments (GRP) and individual experiments (IND).

	Species	Distribution	Species*Dist
GRP	$F_{1,72}=129.47$***	$F_{1,72}=3.13$	$F_{1,72}=28.25$***
IND	$F_{1,59}=89.98$***	$F_{1,59}=1.97$	$F_{1,59}=0.03$

*P<0.05, **P<0.01, ***P<0.001

Figure 2.5 The degree of orientation (s) of groups of *C.dubia* and *D.pulex* at food concentrations of 1000, 4000, and 8000 cells/mL showing comparisons between species when food was distributed a) in a gradient and b) homogeneously and showing comparisons between the two food distributions for c) *C.dubia* and d) *D.pulex*.

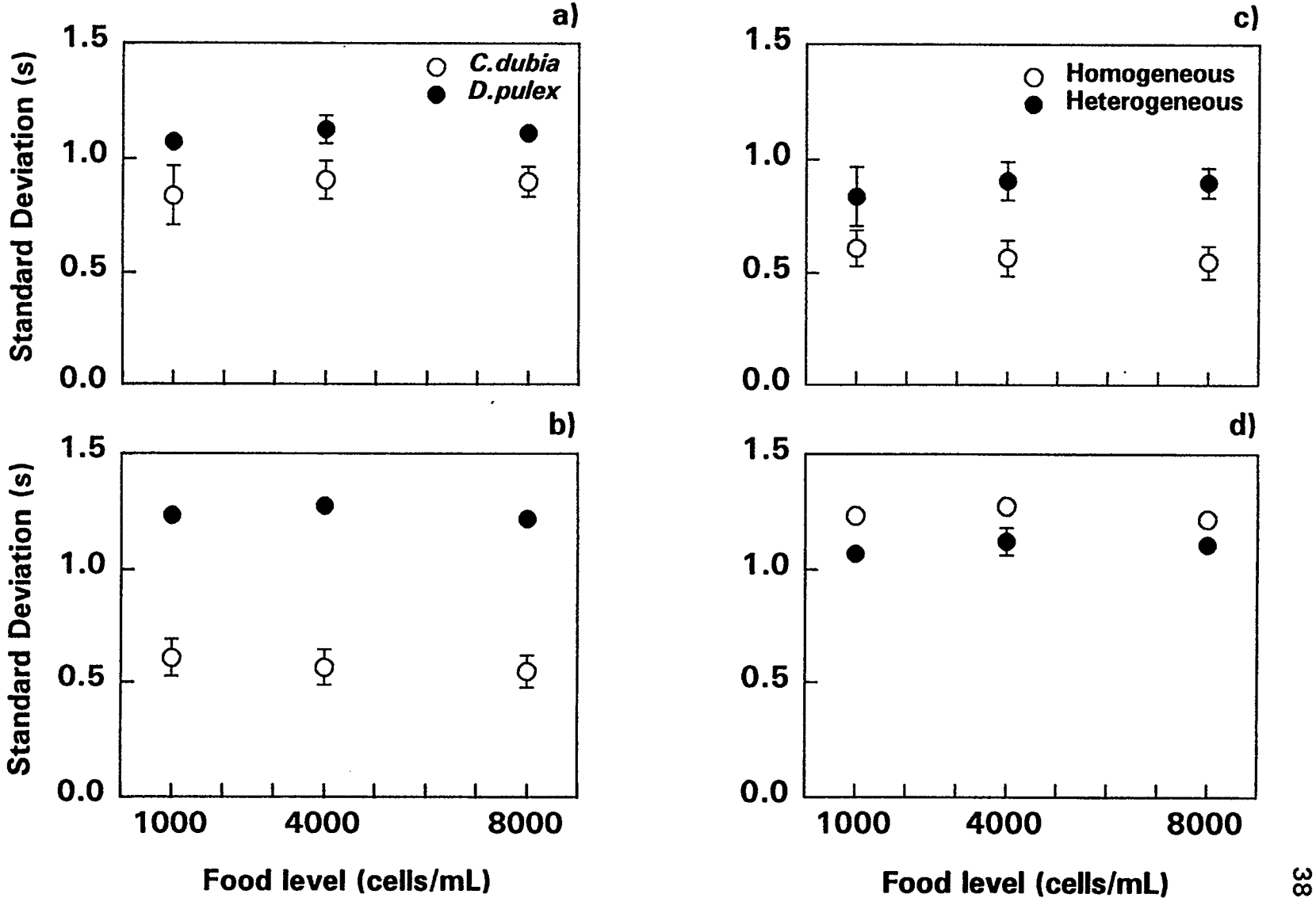
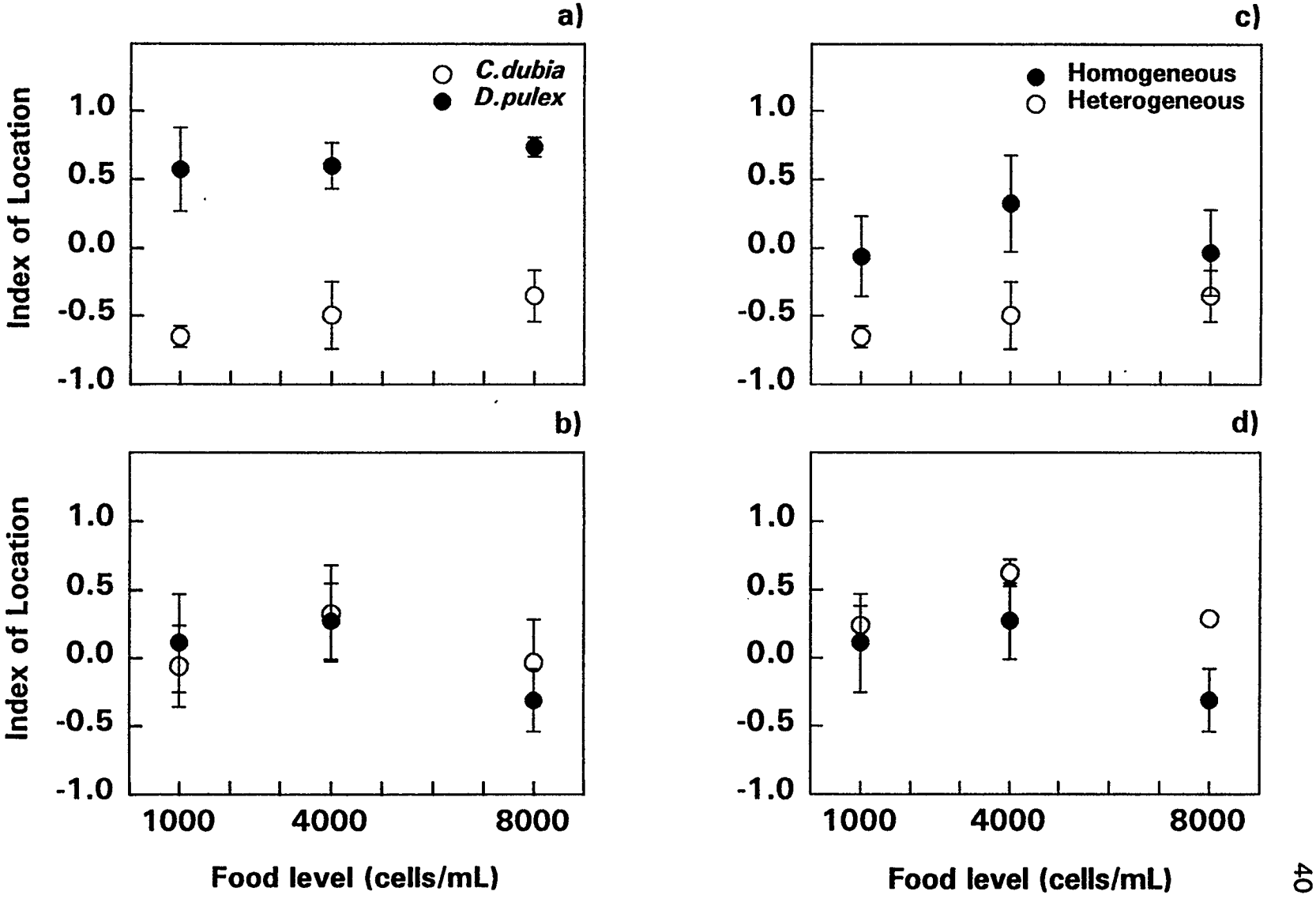

a)
b)
c)
d)
Standard Deviation (s)
1.5
1.0
0.5
0.0
C.dubia
D.pulex
Homogeneous
Heterogeneous
1000
4000
8000
Food level (cells/mL)

Figure 2.6 The index of location for groups of *C.dubia* and *D.pulex* at food concentrations of 1000, 4000, and 8000 cells/mL showing comparisons between species when food was distributed a) in a gradient and b) homogeneously and showing comparisons between the two food distributions for c) *C.dubia* and d) *D.pulex*.


a)
b)
c)
d)
C.dubia
D.pulex
Homogeneous
Heterogeneous
Index of Location
1.0
0.5
0.0
-0.5
-1.0
1000
4000
8000
Food level (cells/mL)

position of *C.dubia* and *D.pulex* were not random in the presence of a food gradient (Table 2.11) and these responses will be discussed in more detail in the next two sections.

Orientation behaviour for *C.dubia*

C.dubia individuals tended to be more oriented about a single point in the homogeneous food treatments (as measured by s) (Table 2.12 & Fig. 2.5c). The dispersion (s) of *C.dubia* was not affected by food level and there was no significant interaction between food level and food distribution (Table 2.12). The presence/absence of food also did not influence the degree of orientation (Table 2.13).

T-tests comparing the index of location to the random expectation of zero indicated that the mean location of individuals was non-random in the gradient experiments and random in the homogeneous treatments (Table 2.11). However, the negative values of the indices obtained for *C.dubia* indicate that individuals did not only fail to locate the high end of a gradient, but they actually oriented on a position >90° distant from the high food location (Fig 2.6c).

The index of location was also not affected by food level. The mean location of individuals was non-random and >90° distant from the high food location in all gradient runs regardless of food level. Similarly, in the homogeneous experiments there was no effect of food level. (Table 2.11).

Orientation behaviour of *D.pulex*

In contrast, *D.pulex* tended to be more oriented about a single point in the gradient treatments (as measured by s) (Fig. 2.5d & Table 2.12). Food level did not affect the spread of individuals in the group experiments, nor did the presence/absence of food (Table 2.13).

Table 2.11 Test statistics for the comparison of the index of location with the random expectation of zero for groups of *C.dubia* and *D.pulex* when food was distributed heterogeneously (GRAD) and homogeneously (HOMO) at food levels of 1000, 4000 and 8000 cells/mL.

Dist	Food	*C.dubia*	*D.pulex*
GRAD	1000	$T_7 = -7.45^*$	$T_5 = 1.86$
	4000	$T_{11} = -4.69^*$	$T_5 = 6.36^*$
	8000	$T_4 = -2.95^*$	$T_4 = 8.09^*$
HOMO	1000	$T_4 = -0.28$	$T_4 = 0.06$
	4000	$T_4 = 1.10$	$T_4 = 4.46^*$
	8000	$T_4 = -0.13$	$T_4 = -1.11$

*P<0.05

Table 2.12 Test statistics from the analysis of the effects of homogeneous or gradient food distribution (distribution) and food level (1000, 4000, or 8000 cells/mL) on the degree of orientation (s) of groups of *C.dubia* and *D.pulex*.

Species	distribution	food level	dist*food
C.dubia	$F_{1,38} = 11.14^{**}$	$F_{2,38} = 0.93$	$F_{2,38} = 2.02$
D.pulex	$F_{1,33} = 20.37^{***}$	$F_{2,33} = 0.81$	$F_{2,33} = 0.28$

*P<0.05, **P<0.01, ***P<0.001

Table 2.13 Test statistics from the analysis of the effect of the presence/absence of food on the degree of orientation (s) of groups (GRP) and individual (IND) *C.dubia* and *D.pulex*.

Experiments	*C.dubia*	*D.pulex*
GRP	$F_{1,19}=0.00$	$F_{1,19}=0.37$
IND	$F_{1,14}=5.46$*	$F_{1,14}=1.04$

*P<0.05, **P<0.01, ***P<0.001

The greater degree of orientation in the gradient treatments corresponded with a tendency for the point of orientation to be closer to the high-food end in the gradient runs (grad = 0.640 approx 50°; homo = 0.023 approx 88°) (Fig. 2.6d). In the homogeneous experiments, the location of individuals was not significantly different from random except at 4000 cells/mL. The location of individuals in the gradient experiments was affected by food level. The location of individuals was non-random at 4000 and 8000 cells/mL but random at the lowest food level of 1000 cells/mL (Table 2.11).

INDIVIDUAL DATA ON ORIENTATION BEHAVIOUR

Orientation behaviour of *D.pulex* and *C.dubia* compared

Due to the difficulty in noting an individual's position every 30 s, the individual experiments were limited to 15 minutes.

As found in the group experiments, there was a significant difference in the degree of orientation (s) (Table 2.10) and the locations of the two species (Table 2.14). *C.dubia* had a much greater degree of orientation (s) than *D.pulex* (Fig. 2.7a & 2.7b). However, *D.pulex* had an ability to locate the high food regions in the gradient experiments that *C.dubia* did not possess (Fig. 2.8a & 2.8b).

Orientation behaviour of *C.dubia*

Analysis on the degree of orientation (s) with the suspect treatment removed, indicated that the degree of orientation in the individual experiments was not affected by food distribution or food level (Table 2.15 & Fig. 2.7c). However, the dispersion of individuals was affected by the presence/absence of food (Table 2.13). A comparison of means

Table 2.14 Test statistics for the comparison of the index of location with the random expectation of zero for individual *C.dubia* and *D.pulex* when food was distributed heterogeneously (GRAD) and homogeneously (HOMO) at food levels of 1000, 4000 and 8000 cells/mL.

Dist	Food	*C.dubia*	*D.pulex*
GRAD	1000	$T_4 = -4.59^*$	$T_5 = -0.12$
	4000	$T_{11} = -3.43^*$	$T_5 = 2.96^*$
	8000	$T_4 = -1.16$	$T_4 = 5.58^*$
HOMO	1000	$T_4 = -8.67^*$	$T_4 = 0.86$
	4000	$T_4 = -4.33^*$	$T_4 = 1.47$
	8000	$T_4 = -0.567$	$T_4 = 0.03$

*P<0.05

Table 2.15 Test statistics from the analysis of the effects of homogeneous or gradient food distribution (distribution) and food level (1000 or 8000 cells/mL) on the degree of orientation (s) of individual *C.dubia* and *D.pulex*.

Species	distribution	food level	dist*food
C.dubia	$F_{1,24} = 0.05$	$F_{2,24} = 0.80$	$F_{1,24} = 0.02$
D.pulex	$F_{1,24} = 0.04$	$F_{2,24} = 1.41$	$F_{1,24} = 0.09$

*P<0.05, **P<0.01, ***P<0.001

Figure 2.7 The degree of orientation (s) of individual *C.dubia* and *D.pulex* at food concentrations of 1000, 4000, and 8000 cells/mL showing comparisons between species when food was distributed a) in a gradient and b) homogeneously and showing comparisons between the two food distributions for c) *C.dubia* and d) *D.pulex*.

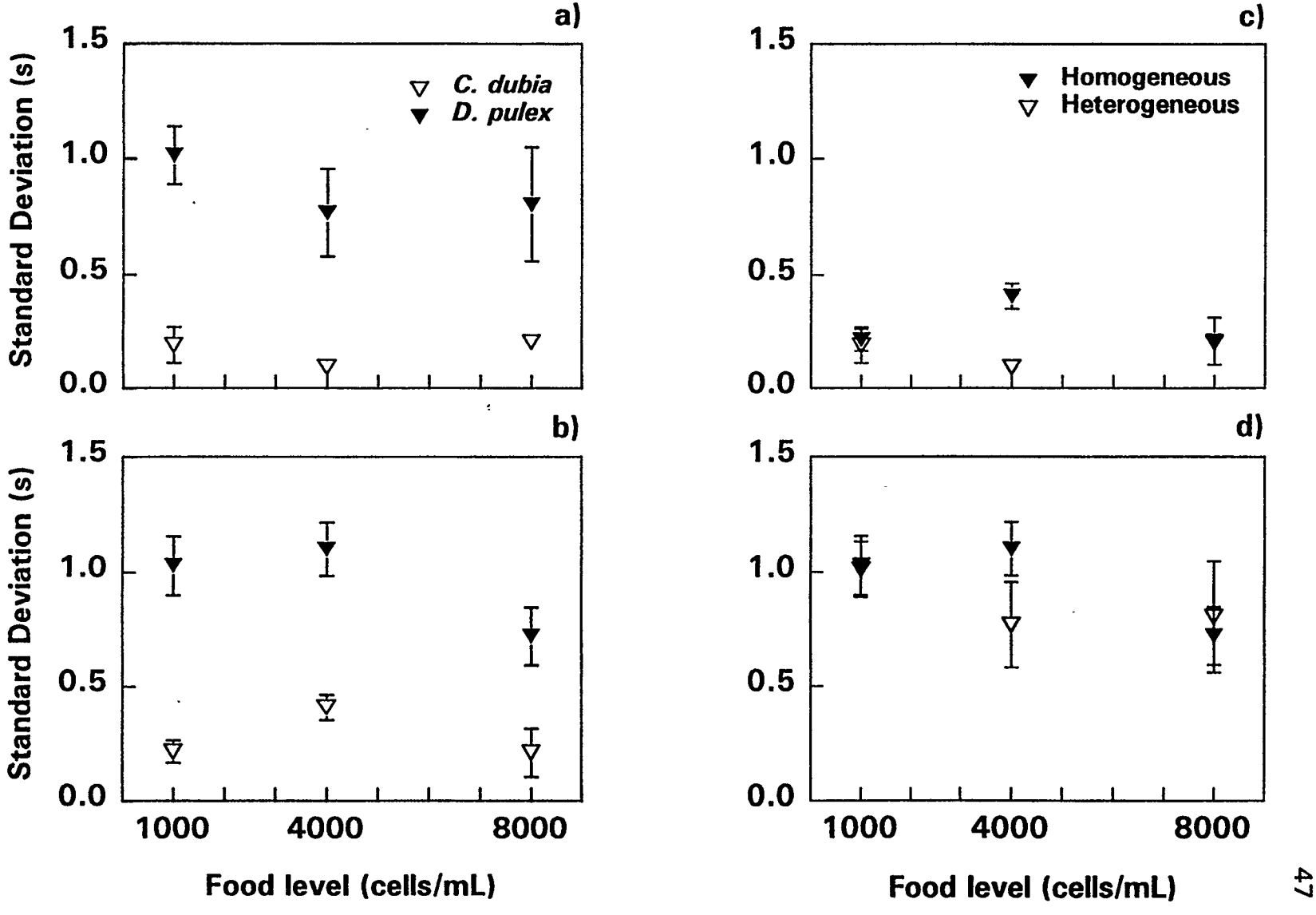
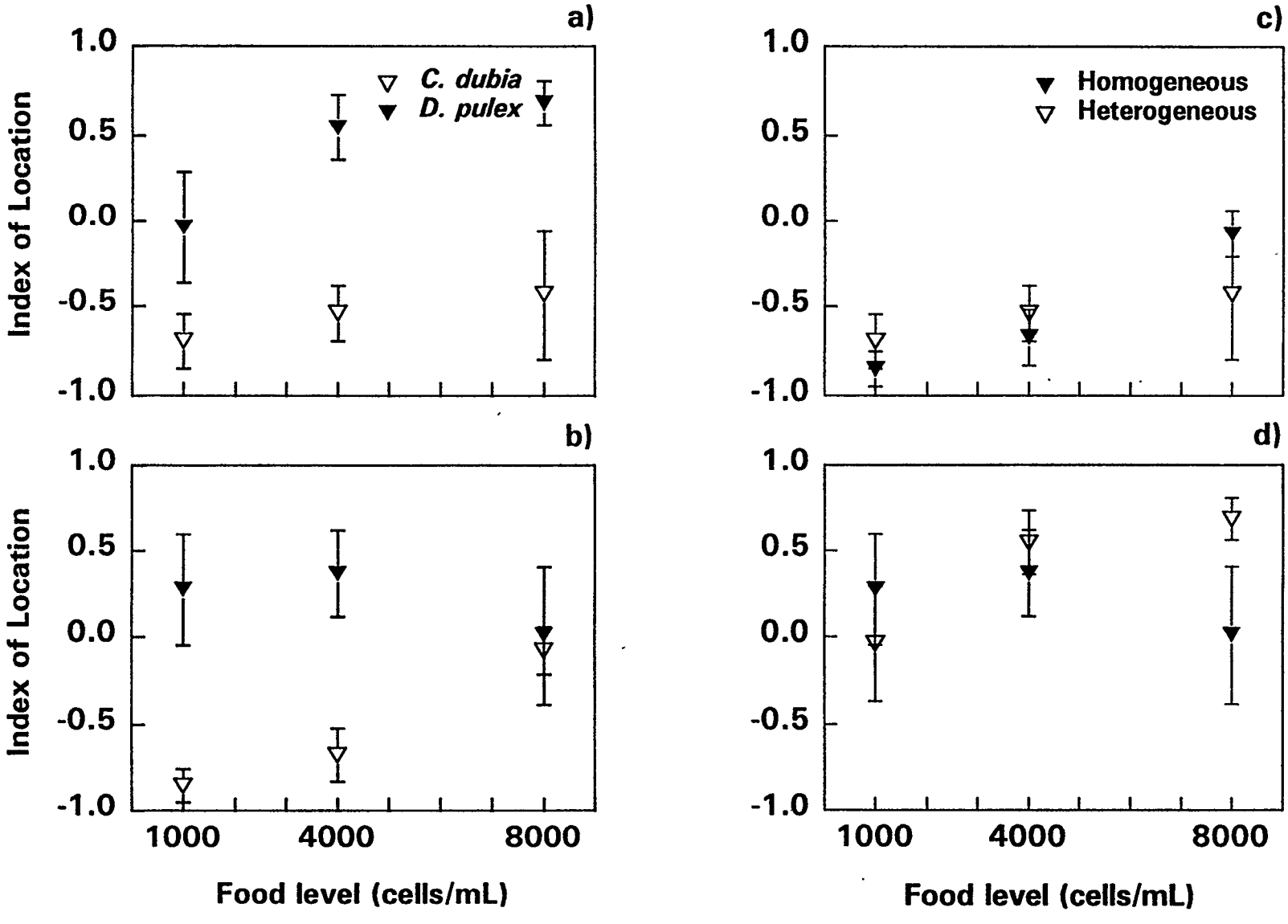

a)
b)
c)
d)
Standard Deviation (s)
1.5
1.0
0.5
0.0
C. dubia
D. pulex
Homogeneous
Heterogeneous
1000
4000
8000
Food level (cells/mL)

Figure 2.8 The index of location for individual *C.dubia* and *D.pulex* at food concentrations of 1000, 4000, and 8000 cells/mL showing comparisons between species when food was distributed a) in a gradient and b) homogeneously and showing comparisons between the two food distributions for c) *C.dubia* and d) *D.pulex*.


a)
b)
c)
d)
1.0
0.5
0.0
-0.5
-1.0
Index of Location
C. dubia
D. pulex
Homogeneous
Heterogeneous
1000
4000
8000
Food level (cells/mL)

showed that individuals were less oriented on the mean location in the absence of food.

A comparison of the index of location with the random expectation showed that the individuals were non-randomly distributed at 1000 and 4000 cells/mL in both the gradient and homogeneous treatments (Table 2.14). The negative values of the indices indicate that this location was >90° from the high food locations (Fig. 2.8c). At 8000 cells/mL in both treatments the location of individuals could not be distinguished from a random orientation (Table 2.14).

Orientation behaviour of *D.pulex*

Analysis for *D.pulex* showed that food distribution and food level did not effect the degree of orientation (s) (Fig. 2.7d) in the individual experiments (Table 2.15). As well, there was no effect of the presence/absence of food on the degree of orientation (Table 2.13).

The comparison of the index of location with the random expectation showed that individuals were randomly situated in the observation chamber in the homogeneous experiments, while in the gradient experiments it was found that the location of individuals was non-random (Table 2.14) and tended to be in the high food regions at the two highest food levels (Fig 2.8d). As in the group experiments, the location of individuals at 1000 cells/mL was not significantly different from the random expectation (Table 2.14).

DISCUSSION

The experiments show that *D.pulex* and *C.dubia* differ significantly in their behavioural response to heterogeneous food distributions. *D.pulex* can locate and forage in regions of high food concentration, whereas *C.dubia* cannot locate these high food regions during the experimental period. Both *D.pulex* and *C.dubia* aggregate in space, but aggregation by *D.pulex* is dependent on food distribution whereas aggregation by *C.dubia* is independent of the food distribution. The striking difference in foraging behaviour between these two species raises several important questions. First, how do these behavioural differences arise? Can differences in the ability to locate high-food regions be explained by differences in swimming behaviour? Second, how does *D.pulex* receive cues that it is in a high food location and modify its behaviour to linger in these regions? Finally, what are the population level consequences of the behavioural differences between *C.dubia* and *D.pulex*?

SWIMMING BEHAVIOUR OF *D.PULEX* AND *C.DUBIA* CONTRASTED

The simplest explanation for the differences between *C.dubia* and *D.pulex* in their ability to locate locally high food concentrations is differences in swimming behaviour. The individual experiments showed large differences in the mobility of *D.pulex* and *C.dubia*. *D.pulex* swims much faster than *C.dubia* and consequently moves through and samples a larger proportion of its environment. This difference in mobility was found for all experiments and food levels.

Before further discussing this difference in mobility, it is important to note that these differences were not produced by the flow properties of the apparatus. *C.dubia* and *D.pulex* did not change their swimming speed or turning rate in response to the flow of liquid through the chamber. Neary et al. (1993) also found that *D.pulex* did not appear to change its behaviour in a flow-through system. In addition, *C.dubia* did not avoid high food levels. When placed in the observation chamber at the high food concentration location, individuals remained near that position (Fig 2.9a). Thus, *C.dubia* displayed relatively stationary behaviour. In contrast to *C.dubia*, *D.pulex* did not remain in the vicinity of the input position (Fig 2.9b), and individuals of this species could locate and linger in high food locations regardless of the insertion point.

While the differences between species in swimming speed are large, individuals of *C.dubia* and *D.pulex* do not differ in their turning rates over the time scales investigated in these experiments (observations every 30 s). *C.dubia* did not aggregate in the insertion location by turning more frequently than *D.pulex*. The swimming behaviour of the two species (as described by turning rate) may be identical, and only the differences in body size may cause the observed differences in the mobility (i.e. mobility scales with body size). In fact, for *C.dubia* there is a significant positive regression between path length (cm) and individual size ($P=0.0001$) (Fig. 2.10).

An alternative hypothesis to explain this difference in mobility is that *C.dubia* and *D.pulex* differ in behaviour on a shorter time-scale (i.e. less than 30 s). Unfortunately, there have been no previous studies which have compared the swimming behaviour of different cladoceran species at

Figure 2.9 The index of location for groups of a) *C.dubia* and b) *D.pulex* at food concentrations of 1000, 4000, and 8000 cells/mL when individuals were placed in the observation chamber close to the region of high food concentration (near) or 180° distant from the high food concentration (far).

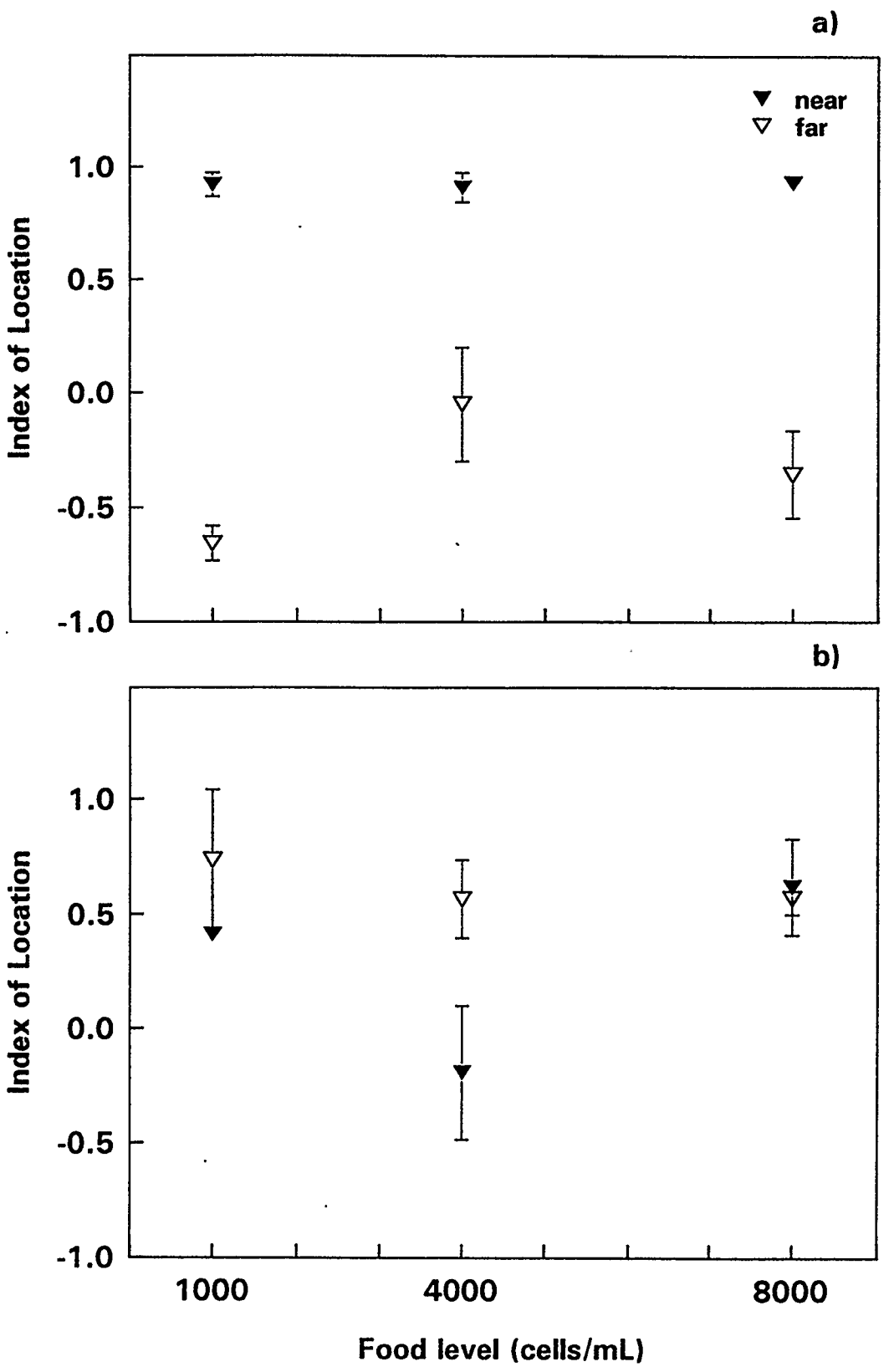
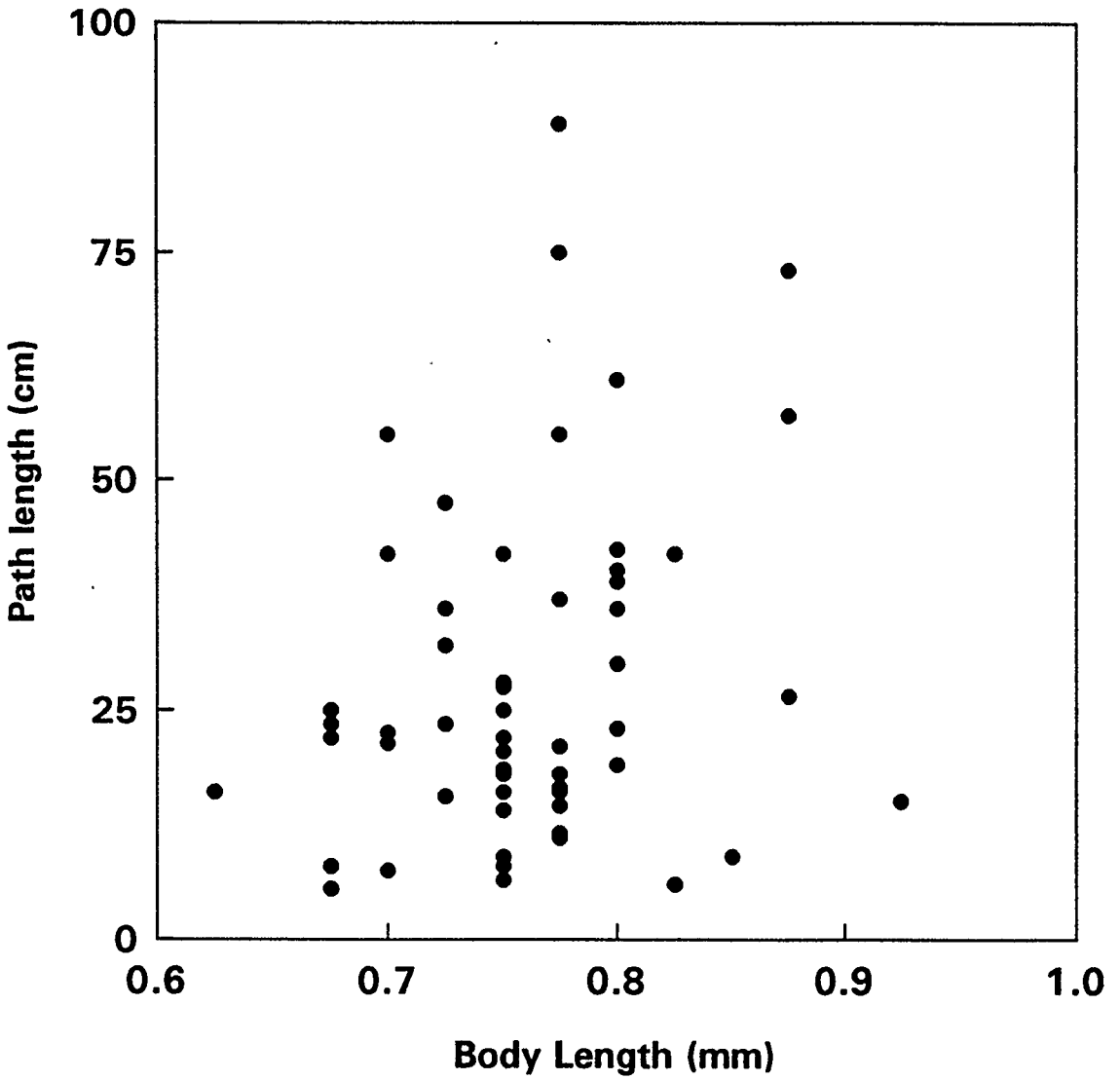

a)
near
far
1.0
0.5
0.0
-0.5
-1.0
Index of Location
b)
1.0
0.5
0.0
-0.5
-1.0
Index of Location
1000
4000
8000
Food level (cells/mL)

Figure 2.10 Path length (cm) versus body length (mm) of *C.dubia*.


100
75
50
25
0
Path length (cm)
0.6
0.7
0.8
0.9
1.0
Body Length (mm)

this time scale. A more extensive sampling of organisms of different size is needed to determine whether this variation in mobility is actually related to organism size for both species in a systematic way.

Since *C.dubia* and *D.pulex* only differ in swimming speed, it could be predicted that given sufficient time, possibly much longer than the 60 min group experiment period, *C.dubia* individuals might also be able to encounter and modify their behaviour to linger in the high food concentrations. However, it could also be argued that individuals smaller than a particular body size may only move significant distances by passive dispersion because their low Reynold's number makes self-propulsion, except on very small scales, energetically costly (Zaret and Kerfoot 1980, Vogel 1981, Brendelberger et al. 1986). (Unfortunately, there are no values for the Reynold's numbers of the two species in the literature). Once individuals pass this threshold body size, self-propulsion over longer distances may become an increasingly profitable behaviour choice because the cost of movement could be more than balanced by the ability to choose more favourable foraging locations. Therefore, although individual's swimming speed may increase with size, some very small species, such as *C.dubia*, may never reach the required threshold body length, and consequently may never be able to locate high food concentrations except by chance encounters.

The difference in mobility between *D.pulex* and *C.dubia*, although based on an among species comparison, is in general agreement with Dodson and Ramcharan (1991) who found an increase in swimming speed with an increase in body size of *D.pulex*. Average swimming speeds (approximately 2.03 mm/s, calculated by dividing the total path length by

the 15 minute experimental period) of the *Daphnia* are within the range reported by other investigators. However, the swimming speed reported by Riessen et al. (1988) for *C.dubia* of 3.96 mm/s is not comparable to the range of average speeds found in this experiment (0.28 - 0.54 mm/s), although maximum values of 3.75 mm/s were observed.

MECHANISMS USED BY *D.PULEX* TO EXPLOIT HIGH-FOOD LOCATIONS

The group experiments on *D.pulex* support and extend the study by Neary et al. (1993) which found that individuals were capable of locating regions of high food concentration. Neary et al. (1993) used a linear experimental chamber and may have limited the mobility of *D.pulex* in the horizontal direction because of edge effects. The results of the present study show that *D.pulex* can orient to regions of high food in a spatially continuous system. It is important to note that the spatially continuous design not only assesses the ability of individuals to locate locally high-food regions but also the ability to remain in that region.

Previous studies (Jakobsen and Johnsen 1987, Neary et al. 1993) have only considered oriented behaviour over longer time scales and it was not possible in these studies to distinguish how individuals choose foraging locations. The results of the group experiments, when coupled with the results describing the orientation in the individual experiments, provide evidence as to the nature of the mechanism used by *Daphnia* to locate and linger in high food regions. Key observations are: 1) individuals could not locate high food regions at the lowest food concentration (i.e. ability to locate locally high-food regions depends on food concentration, 2) individuals found the location of the high-food regions within 15

minutes in the individual experiments, and 3) *D.pulex* tended to decrease its path length at high food levels. It seems likely that individuals remain in high food regions merely by slowing down rather than increasing their turning rate.

Since Neary et al. (1993) have eliminated the possibility that *D.pulex* respond to the taste of algae rather than the concentration of algal cells, these two observations suggest that individuals are using filtering rate and/or ingestion rates as cues to locate high-food regions rather than longer-term processes such as assimilation rates or gut-fullness. Before discussing this hypothesis more fully, it is important to note that mobility in cladocera is determined by the beat frequency of the second antennae and is separate from the beat frequency of the filtering appendages. Individuals can change their swimming speed without modifying their filtering rate.

Filtering rate and ingestion rate are related to food concentration in cladocera (Rigler 1961, Lampert 1977, Porter et al. 1982), and therefore, animals may use changes in the beat frequency of their filtering apparatus or changes in ingestion rate as cues to alter their swimming speed in order to remain in regions of high food concentration. There may be a continuous modification of speed with changes in filtering and/or ingestion rates, or individuals could suddenly change their behaviour when these rates cross a threshold level determined by food concentration. Although these two hypotheses cannot be distinguished by this study, the fact that *D.pulex* individuals are suddenly able to locate high food regions at overall food concentrations >1000 cells/mL suggests that the behaviour

modification is cued by threshold food levels (similar non-linearities in response were observed by Neary et al. 1993).

If we consider the threshold hypothesis, it seems likely that, at high overall food levels, there were regions in the observation chamber which had food concentrations that substantially affected filtering and/or ingestion rates and consequently cued a reduction in swimming speed which acted to prolong the individual's stay in these locations (Smith and Baylor 1953, Diggle 1962). In contrast, at very low overall food levels (e.g. 1000 cells/mL), individuals did not encounter any regions in observation chamber where there was any significant difference in filtering and/or ingestion rates despite the heterogeneous food distribution.

If *D.pulex* can use filtering and/or ingestion rates as cues to reduce swimming speed in high-food locations, are there implications from this hypothesis regarding the ability of *C.dubia* to exploit high-food regions? While it is known that both *C.dubia* and *D.pulex* have type II functional responses (O'Brien 1974, DeMott 1982, Porter et al. 1982), it is not known whether *C.dubia* is more efficient at foraging in low food conditions than *D.pulex*. If it is found that the half-saturation constant of *C.dubia* is lower than that of *D.pulex* (i.e. *C.dubia* are more efficient foragers at low food levels), it can be predicted that *C.dubia* would also be able to locate and linger in high-food regions of similar concentration provided their encounter rates with these regions were increased through increased energy allocation to mobility or faster rates of passive dispersal. However, if the half-saturation constant of *C.dubia* is greater than that of *D.pulex* (i.e. *C.dubia* are less efficient foragers at low food concentrations), individuals would most likely not be able to locate the

high-food regions used in this study even if their encounter rates with these regions were increased. The food concentration in the patches, as well as their encounter rate with these regions, would have to increase before they could demonstrate an ability to locate high-food regions similar to *D.pulex*.

There is some evidence in the individual experiments that *C.dubia* responded to high food levels. While the location of individuals was non-random and related to the position of insertion at 1000 and 4000 cells/mL in both the homogeneous and gradient treatments, the location of individuals was random at 8000 cells/mL. Clearly, there is some change in the behaviour of individuals which affects their location at this food level that was not quantified by the chosen measures of swimming behaviour. This change in behaviour leads me to speculate the *C.dubia* are capable of responding to differences in food levels, but that they require a higher food concentration than *D.pulex* to elicit this response. However, it should be mentioned that food levels of 8000 cells/mL represent rather high concentrations of food which are not typical of equilibrium levels in the field.

In summary, it seems likely that because of the allometric scaling of mobility, the amount of time required for an average sized *C.dubia* to locate the high end of a food gradient may be incredibly long. As well, if the half-saturation constant of *C.dubia* is greater than that of *D.pulex* (i.e. *C.dubia* are less efficient foragers at low food levels), and the behaviour modification required to remain in high food regions is cued by threshold food levels related to the functional response, the average-sized *C.dubia*

may not be able to respond to the high-food regions at the same low concentration as *D.pulex*.

POPULATION-LEVEL CONSEQUENCES OF DIFFERENCES IN THE MOBILITY AND BEHAVIOUR OF *C.DUBIA* AND *D.PULEX*

The large differences in the mobility of these species and their abilities to locate regions of high food concentration have important implications for their respective population distributions and dynamics. The individual-based modelling system of McCauley, de Roos and Wilson (1991, 1993, 1993) claims that, if all other factors are equal, differences in the mobility of the individuals will result in different population-level consequences. This model predicts that slower species such as *C.dubia* will be more heterogeneously distributed and consequently have a more stable population dynamic than more quickly moving species such as *D.pulex*.

However, the ability of *D.pulex* to aggregate in regions of high food concentration may alter predictions based on mobility alone. In addition, the mobility of *D.pulex* was reduced by the presence of food and food level. But, given the large differences in the mobility of *C.dubia* and *D.pulex* at all food levels, it seems likely that the predictions about the relative stability of the two species will not change.

The aggregative behaviour of *D.pulex* and the relative immobility of *C.dubia* found in these experiments also have important implications for the spatial distribution of these organisms in the field. Organisms displayed a preference for different regions of the 50 cm chamber. In fact, regions of preference in the gradient experiments tended to be as small as

10 cm arcs of the circular chamber for *D.pulex* and 4.5 cm for *C.dubia*. The scale of spatial heterogeneity found in populations of these species is potentially much smaller than generally thought.

A third population level consequence that can be extrapolated from these experiments concerns the competitive ability of the two species. Clearly, the greater mobility of *D.pulex* and its ability to locate regions of high food concentration would give this species a decided competitive edge over *C.dubia*. On the basis of these experiments, one would predict that *D.pulex* would outcompete *C.dubia* in most environments.

CHAPTER 3 SPATIAL HETEROGENEITY AND DYNAMICS OF *CERIODAPHNIA DUBIA* AND *DAPHNIA PULEX* POPULATIONS

INTRODUCTION

Behavioural aggregation by predators can theoretically have dramatic effects on the stability of predator-prey dynamics. In metapopulation models, which consider populations that are subdivided into a number of subpopulations inhabiting patches, aggregation by predators can be stabilizing or destabilizing depending on the strength (Ives 1992) and form of aggregation (Chesson and Murdoch 1986, Godfrey and Pacala 1992), as well as environmental differences among patches (Murdoch and Stewart-Oaten 1989, Murdoch et al. 1992a).

The development of metapopulation models has been stimulated primarily by the study of insect parasitoid systems, in which hosts are distributed in distinct patches that are typically imposed by habitat structure (i.e. hosts living on trees in an orchard). It has been shown recently, however, that external subdivision of the environment into patches is not necessary for stability, and that limited mobility of predator and prey can lead to stability in spatially homogeneous systems (i.e. systems without externally imposed patches) (de Roos et al. 1991, McCauley et al. 1993, Wilson et al. 1993). Limited mobility of individuals can create spatial heterogeneity in local prey or predator densities, and the size of these "patches" is related to predator-prey mobility and life-history characteristics (e.g. local recruitment of offspring or broadcast spawning etc.). Stability ensues in these models lacking externally imposed patches,

because the "patches" that develop via local interactions in space and time, yield asynchronous fluctuations in population dynamics.

The models of spatial dynamics of populations predict that, in the absence of an externally imposed patch structure, slower moving species will be more spatially heterogeneous than faster moving species for a given environment size. The greater spatial heterogeneity of the slow species leads to greater stability of population dynamics. Secondly, since the number of "patches" that can be accommodated is limited by the environment size, the models predict that "patchiness" of the population distribution and consequently, population stability should increase with an increase in environment size.

In the previous chapter, it was shown that two herbivorous cladoceran species, *Daphnia pulex* and *Ceriodaphnia dubia*, differ dramatically in their mobility and aggregative behaviour. The purpose of this chapter is to investigate the population dynamics of these species in order to assess whether these dramatic differences have effects on their respective population dynamics under identical environmental conditions.

The population dynamics of *Daphnia* are well studied in both the laboratory (e.g. Slobodkin 1954, Goulden and Hornig 1980, Goulden et al. 1982) and field (McCauley and Murdoch 1987, McCauley et al. 1988, McCauley and Murdoch 1990), and models exist that link populations dynamics to individual biology under spatially homogeneous conditions (McCauley et al. 1988, Nisbet et al. 1989, McCauley et al. 1990b). Unfortunately, there have been no controlled studies of the dynamics of *Ceriodaphnia* populations, and information on its biology (e.g. quantitative

descriptions of their functional response and food-dependent mortality) necessary to parameterize models is lacking.

Thus, in the absence of a model for the spatial dynamics of these populations that takes into account the potential formation of microscale patches (<10 cm), general predictions concerning the effects of limited mobility and behavioural aggregation were tested.

Mobility experiments showed that *C.dubia* individuals move much slower than *D.pulex* individuals. *C.dubia* individuals also have a greater tendency to aggregate regardless of prey density, whereas *D.pulex* have a lesser tendency to aggregate but do so in response to spatial variation in prey density. Thus, it was predicted that: 1) *C.dubia* populations will likely be more spatially heterogeneous, and 2) consequently, more stable (i.e. the populations will be less variable over time) than the *D.pulex* populations. As environment size increases, more ephemeral patches can be accommodated, and therefore, 3) spatial heterogeneity should increase with system size for both species. Finally, an increase in system size, if accompanied by an increase in spatial heterogeneity, 4) should also lead to an increase in population stability for both species.

To test these predictions, experiments were performed to compare the populations dynamics of the 2 cladocerans among environments of different size. Both population density and the spatial distribution of individuals were monitored over time for the two species. Video sampling was used as a non-invasive sampling technique so that the spatial distribution of individuals in the aquaria would not be disturbed.

To test whether population fluctuations were internally generated by the predator-prey interaction between herbivores and plants, versus

externally driven fluctuations caused by environmental variability (e.g. light, temperature, nutrient pulses), the synchrony in the population dynamics was evaluated as suggested by McCauley (1993). If the fluctuations in population dynamics are driven by a periodic environmental factor, then the replicate tanks would be expected to display coincidental dynamics since the fluctuations in abundance are being driven by environmental variation common to all replicate populations (McCauley 1993).

MEASURES OF SPATIAL DISTRIBUTION

Measuring the spatial heterogeneity in populations requires a cautious interpretation of the indices used to describe "patchiness". In this section I will briefly review the indices used to describe spatial heterogeneity and discuss their merits before describing the experimental methods in detail.

Methods for sampling and describing the spatial distribution of animal populations can be classified into two categories: (1) area sampling and (2) nearest-neighbour sampling (Patil and Stiteler 1974). The spatial distribution of animal populations is probably most amiable to analysis using methods which use area sampling (in which the population is sampled with quadrats). For the particular zooplankton populations under consideration, the use of distance methods (which sample a population using the distance to the nearest neighbour of an individual) is possible. However, distance measures to nearest neighbours in a 3-dimensional environment are rather difficult to obtain.

Area methods can further be divided into ratio and regression methods. Indices such as Green's (1966), Morisita's (1962) and the variance-to-mean ratio (Elliot 1977) are calculated by some derivative of the ratio of the variance of the mean density estimate to the mean density (Elliot 1977). For the Poisson distribution $\mu = \sigma^2$, therefore, departures of the value of the ratio from unity will indicate a departure from a random distribution, modelled by the Poisson distribution (Goodall and West 1979). Regression methods such as Taylor's power law (1961) and Iwao's patchiness regression method (1968) use the coefficients of the regression of either the variance or an index of spatial variance on mean density as an index of spatial heterogeneity. Regression methods are designed to reflect possible changing relationships (as density increases or decreases) between density and spatial heterogeneity.

An objective comparison of these two methods has not yet been completed. There is considerable controversy in the literature regarding the properties and suitability of the various indices. Accordingly, the two most highly recommended indices of each type were used.

Morisita's index

Morisita's index is the most highly recommended area-based index and seems to have the properties desirable for this particular study. Morisita's index is based on an index originally proposed by Simpson (1949) and is free from the assumptions of any underlying probability distribution. The index measures how many more times likely it is that two randomly selected individuals will be from the same quadrat, than it would be if the individuals in the population were distributed at random (Hurlbert

1990). The index is calculated by: $I_\delta = n[(\Sigma x^2 - \Sigma x)/((\Sigma x)^2 - \Sigma x)]$, where n is the number of samples taken and Σx is the total number of individuals.

The index ranges in value from $1-[(n-1)/(\Sigma x-1)]$ for a uniform distribution, to 1 for a random distribution, and from 1 to n for aggregated distributions (Elliot 1977, Krebs 1989).

Many authors agree that the index is relatively free from the effects of density (Pielou 1969, Elliot 1977, Downing 1979, Ludwig and Reynolds 1988, Krebs 1989, Hurlbert 1990).

Krebs (1989) notes that I_δ has the desirable statistical property of having a known sampling distribution. However, the only estimates of standard error of the index that have been found in the literature have been generated by jack-knife methods (Reed 1983), and the derivation of the moments of I_δ for the special cases where the values follow the negative binomial or Poisson distributions (Hutcheson and Lyons 1989).

Overall, this index has been highly recommended by a number of authors (Patil and Stiteler 1974, Elliot 1977, Myers 1978, Krebs 1989), and this index seems to be an appropriate one to quantify the degree of aggregation in these experiments.

Taylor's power law

Taylor (1961) suggested that the tendency towards the exponential rate of increase in σ^2 with μ might reflect the tendency of animals to aggregate. Taylor's regression method uses the relationship between log σ^2 and log μ, to determine the exponent b in the expression: $\sigma^2 = a\mu^b$, where a is a sampling factor and b indicates the degree of aggregation (Downing 1979). This regression method is based on the model originally proposed by Bliss (1941); however, Taylor showed that it applies to a

wide variety of organisms (Taylor 1961). The model does not assume any underlying distribution and merely requires a stable relationship between the mean density and the variance.

For a uniform distribution b varies from 0 to <1, a random distribution is indicated by $a=b=1$ and for an aggregated distribution b varies from >1 to infinity (Elliot 1977). Elliot (1977) concluded that b of Taylor's power law is independent of the number of samples (n), the mean density (μ), the total number of individuals counted (Σx), and the quadrat size.

This index of aggregation can be used to compare aggregation among studies (Taylor 1961), since it incorporates the density dependence of aggregation (Taylor et al. 1978). Comparisons between sampled populations can be made by using a comparison of the slopes and intercepts of the log/log regression lines.

There are no strong objections to this index and its independence from mean density make it a particularly appropriate measure to compare aggregation of similar species with differing population densities.

METHODS AND MATERIALS

EXPERIMENTAL DESIGN

Laboratory populations of *D.pulex* and *C.dubia* were set up in aquaria and maintained under constant conditions of 20°C and a 16hr:8hr light:dark regime. *Chlamydomonas reinhardtii* was the prey component of the system. Aquaria were filled with filtered, autoclaved pond water and

inoculated with 1000 cells/ml *C.reinhardtii*. Three volumes of tanks were chosen: 21, 39 and 87L. After allowing 2 days for the algae to establish, all tanks were inoculated with *C.dubia* or *D.pulex* (approximately 0.23 individuals/L) for a number of days until the populations persisted. Previous studies (McCauley and Murdoch 1990, McCauley 1993) have shown that these types of populations equilibrate in approximately one month, so sampling was initiated one month after the populations were established. The same procedure was used for tanks which became extinct.

Tanks were filmed twice a week for a period of 100 days using a digital video camera (Panasonic WVD5000) fitted with a macro lens attachment. The experimental period of 100 days was selected to capture the dynamics of 5 to 6 generations of the species. A 3 second spot of footage was recorded for 12 sampling locations in the tank. Sampling locations were distributed in a weighted, randomized, stratified array across the front of each tank. Three depth levels (proportional to the height of the tank) formed the strata and within these strata either 5(top), 3(middle) or 4(bottom) locations were sampled. Each video shot contained a volume of approximately 340 ml. The focus of the shot was standardized at the middle of the tank and the depth of field was sufficient to identify all individuals across the tank. The number of individuals in each video shot was censused after filming. The video technique was able to distinguish between male and female individuals.

Water lost to evaporation was replaced weekly with oxygenated, filtered, autoclaved pond-water, using narrow gauge tubing and a proportional number of lines to produce a flow rate of approximately 300

mL/hr per 20 L volume. Once monthly the algal growth was removed from the front face of the tanks to increase visibility by gently scraping the glass surface using a razor blade. Attempts were made to control for as many extraneous variables as possible and aside from these maintenance considerations the tanks were undisturbed environments. Consequently, measures of other variables such as pH could not be made.

MEASURES OF SPATIAL DISTRIBUTION

Morisita's index and the b coefficient of Taylor's power law were used to test the hypothesis that differences in mobility of individuals and volume of the environment generate differences in the spatial heterogeneity of the two zooplankton populations.

Comparisons of the values of Morisita's index among the different populations of the two species were made using an ANOVA, with species and volume as treatment variables. This analysis was used to determine if differences in aggregation existed between species and/or aquaria of different volumes.

The coefficients of Taylor's power law were calculated for each species and volume treatment combination using linear regression techniques. The slopes of the relationships for both species and the different volume treatments within species were compared with an ANCOVA.

MEASURES OF STABILITY

Population stability was assessed in two different ways. First, the persistence of the populations was compared by noting the number of zooplankton populations which went extinct. Secondly, the degree of

fluctuations in population density was estimated using two techniques. Before analysis, the long-term seasonal trends were removed from the log transformed data using least-squares polynomial regression (Legendre and Legendre 1983). The residuals from this regression were used to estimate the degree of fluctuations. First, the standard deviation of the residuals for the two species and three tank volumes were compared. And secondly, using non-linear regression, the harmonic model:

residual(time) = amplitude*cos[(2pi/period)*(time + phase shift)

was fitted to the residuals to determine the best estimates for the amplitude and period at which each of the series were cycling (McCauley and Murdoch 1990). The significance of the cycle was assessed by determining if the amplitude was significantly different from zero. The harmonic regression analysis is a crude technique to assess whether there is a dominant periodicity displayed by the population.

Time-series analysis (cross-correlation) was used to compare statistically whether the fluctuations in populations between the tanks were coincidental and therefore possibly due to an external environmental factor.

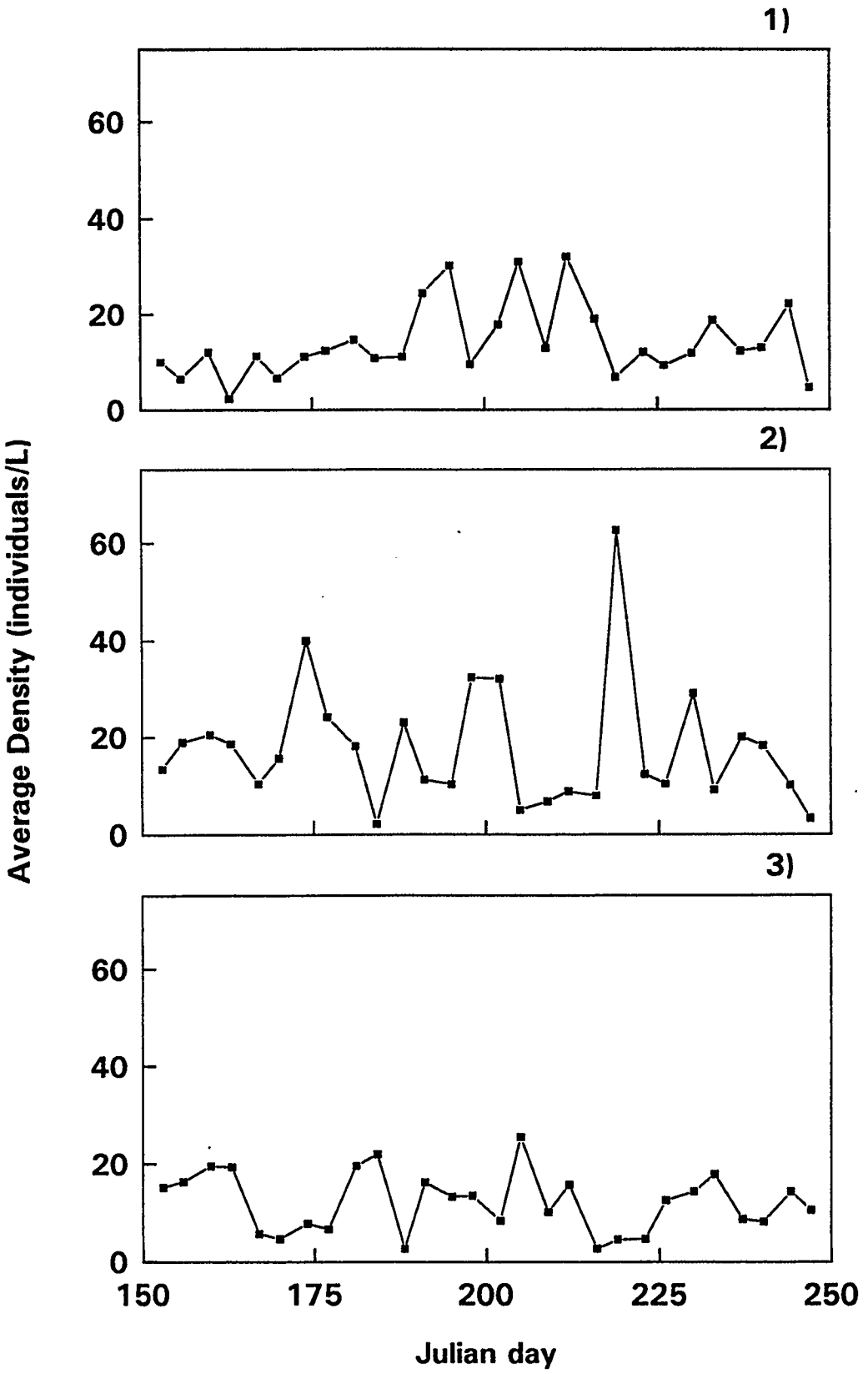
RESULTS

TEMPORAL DYNAMICS

Temporal dynamics of *C.dubia* populations

The density of *C.dubia* individuals fluctuated widely in all tank volumes and replicates (Figs 3.1-3.3). One population (21L Tank 1) did not persist despite attempts at re-inoculation, while another tank came close to extinction but recovered without reinoculation (21L Tank 2).

Figure 3.1 Population density (individuals/L) of *C.dubia* populations in three replicate (1,2,3) large volume (87L) aquaria.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Average Density (individuals/L)
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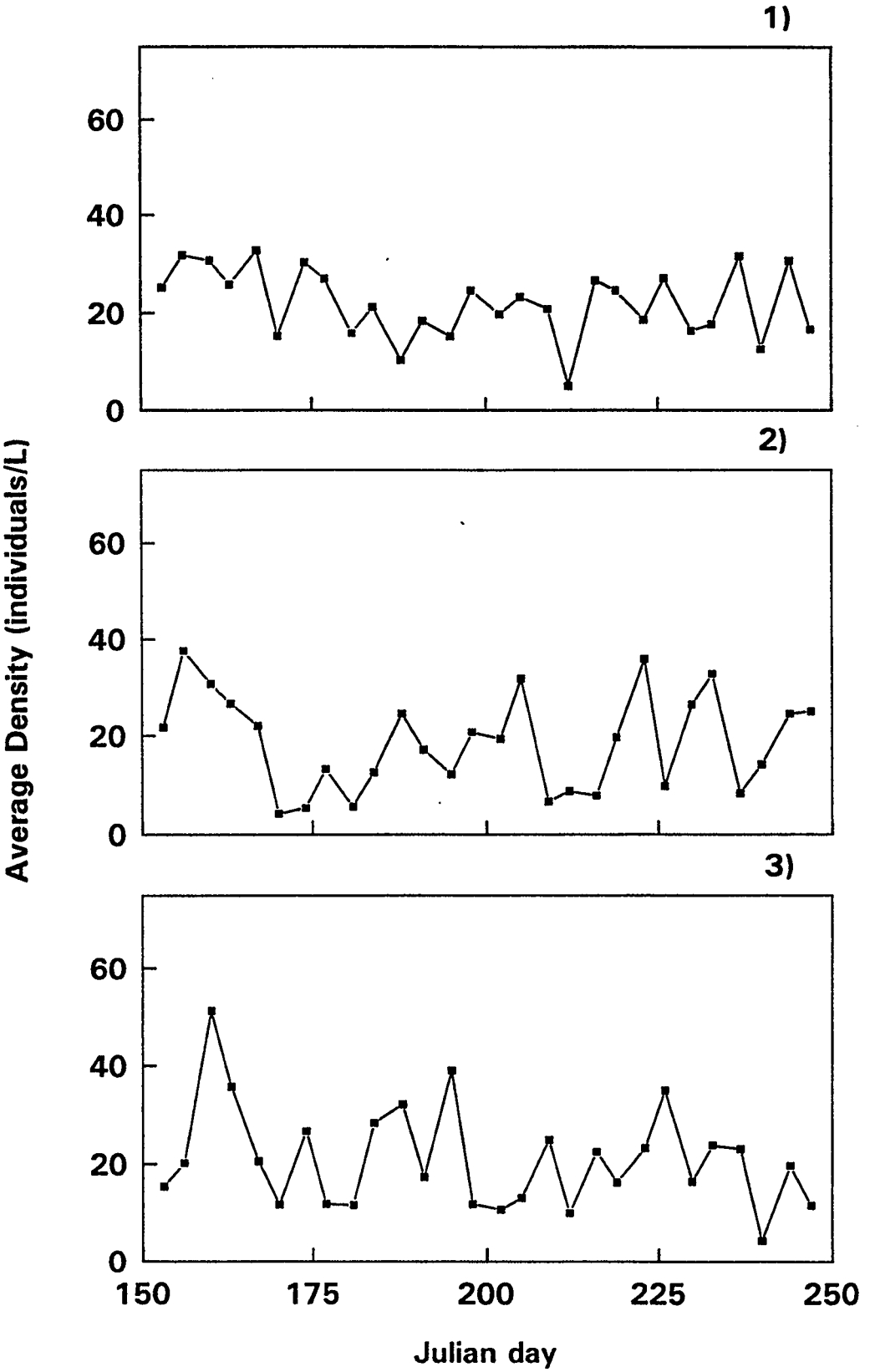
Julian day

Figure 3.2 Population density (individuals/L) of *C.dubia* populations in three replicate (1,2,3) medium volume (39L) aquaria.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Average Density (individuals/L)
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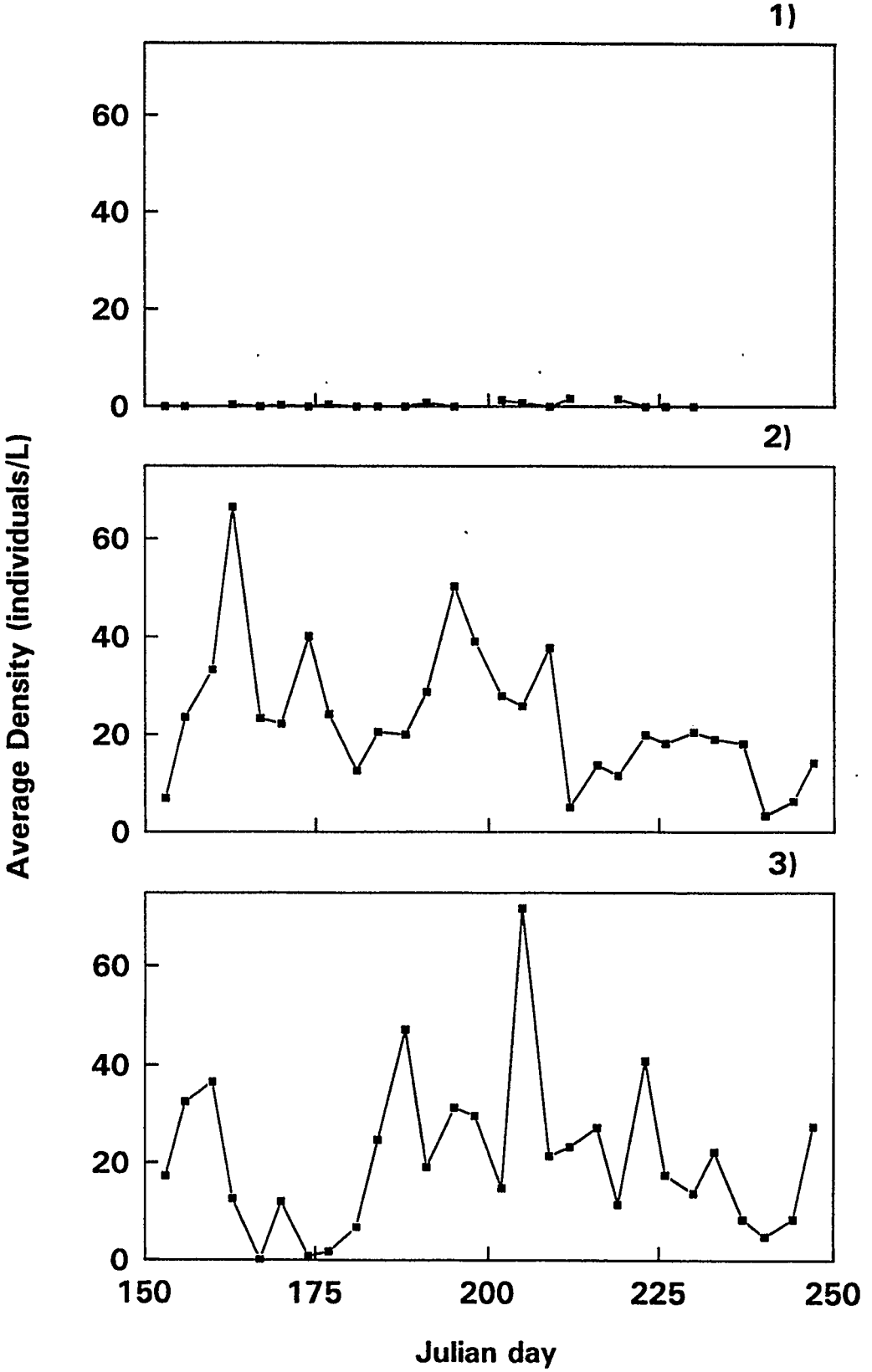
Figure 3.3 Population density (individuals/L) of *C.dubia* populations in three replicate (1,2,3) small volume (21L) aquaria.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Average Density (individuals/L)
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Overall, there did not appear to be any difference in the average density (calculated over the whole experimental period) of individuals among tanks (Tables 3.1-3.3). (Examples of standard errors of the density estimates for particular sampling days are in Appendix 2).

Figures 3.4-3.6 show the dynamics of the populations in the 3 sampling depths for each tank. Individuals tended to be concentrated in the top layer of the aquaria (Tables 3.1-3.3), and this pattern will be described quantitatively in the results section on spatial heterogeneity.

Temporal dynamics of *D.pulex* populations

Among the *D.pulex* populations which persisted, there did not appear to be any large differences in average densities (Tables 3.4-3.6) or the range of fluctuation (Figs. 3.7-3.9). Two 21L populations (Tanks 1 & 2), and one 39L population (Tank 3) went extinct. *D.pulex* had lower population densities than *C.dubia*.

Unlike *C.dubia*, the *D.pulex* populations were not concentrated at one particular depth level (Figs 3.10-3.12), and the densities at the different depths did not fluctuate in phase.

Cross-correlation analysis between different tanks showed that there were no significant correlations between tanks of the same volume containing the same species at a zero time lag (Table 3.7 & 3.8). Populations of *D.pulex* and *C.dubia* in different aquaria were not fluctuating in synchrony (i.e. dynamics in different aquaria were statistically independent).

SPATIAL HETEROGENEITY

The ANOVAs for Morisita's index indicated that there was a significant difference in the degree of aggregation of the *C.dubia* and

Table 3.1 Average densities (individuals/L) and range of *C.dubia* populations in large volume tanks (87L) calculated for the entire aquaria (overall), the top sampling depth (top), the middle sampling depth (middle), and the bottom sampling depth (bottom).

	Tank 1	Tank 2	Tank 3
overall	41.82 (7.11-94.36)	51.78 (6.13-184.07)	35.94 (8.09-75.00)
top	85.99 (11.18-218.24)	106.83 (7.06-423.53)	69.45 (12.34-169.41)
middle	11.13 (0.00-31.37)	12.08 (0.98-31.37)	13.45 (1.96-66.67)
bottom	10.92 (0.00-40.44)	12.61 (0.74-53.92)	10.81 (0.00-66.18)

Table 3.2 Average densities (individuals/L) and range of *C.dubia* populations in medium volume tanks (39L) calculated for the entire aquaria (overall), the top sampling depth (top), the middle sampling depth (middle), and the bottom sampling depth (bottom).

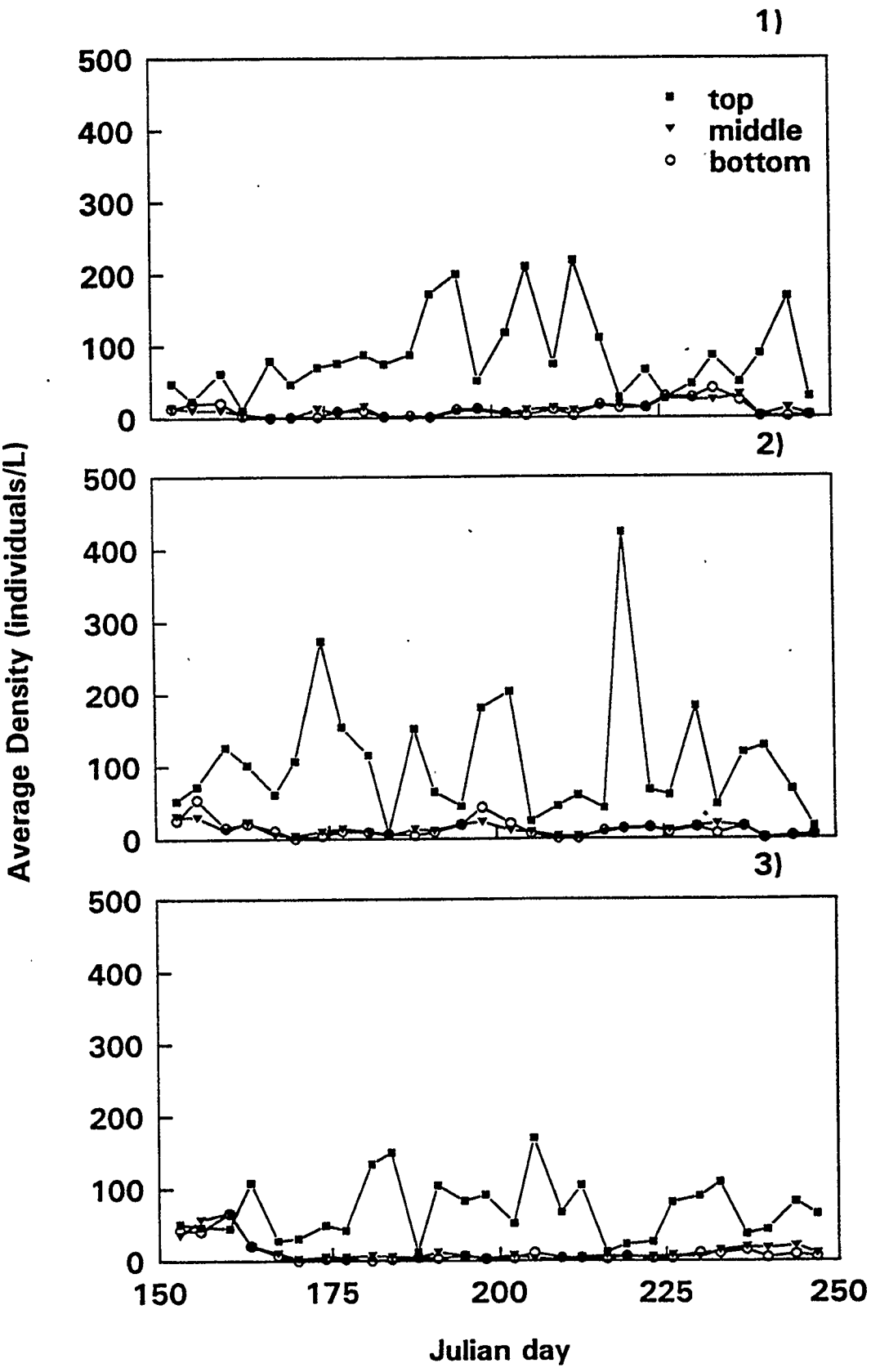
	Tank 1	Tank 2	Tank 3
overall	64.96 (14.71-96.57)	55.19 (12.25-110.70)	62.10 (12.99-150.74)
top	132.09 (33.53-212.94)	110.55 (21.18-221.76)	131.45 (27.65-607.65)
middle	19.82 (0.00-65.67)	18.94 (0.00-93.14)	16.00 (0.00-61.76)
bottom	14.08 (0.00-72.79)	13.98 (0.00-108.82)	9.70 (0.00-2.94)

Table 3.3 Average densities (individuals/L) and range of *C.dubia* populations in small volume tanks (21L) calculated for the entire aquaria (overall), the top sampling depth (top), the middle sampling depth (middle), and the bottom sampling depth (bottom).

	Tank 1*	Tank 2	Tank 3
overall	2.79 (0.98-4.90)	68.44 (9.56-195.72)	61.69 (0.49-211.27)
top	4.63 (1.18-8.82)	145.80 (22.94-456.62)	126.91 (1.18-487.06)
middle	2.57 (0.00-7.84)	15.97 (0.00-55.88)	17.45 (0.00-62.75)
bottom	0.64 (0.00-2.94)	12.89 (0.00-52.21)	12.87 (0.00-67.65)

*Populations which went extinct

Figure 3.4 Population density (individuals/L) of *C.dubia* populations in three replicate (1,2,3) large volume (87L) aquaria in the top, middle, and bottom sampling depths.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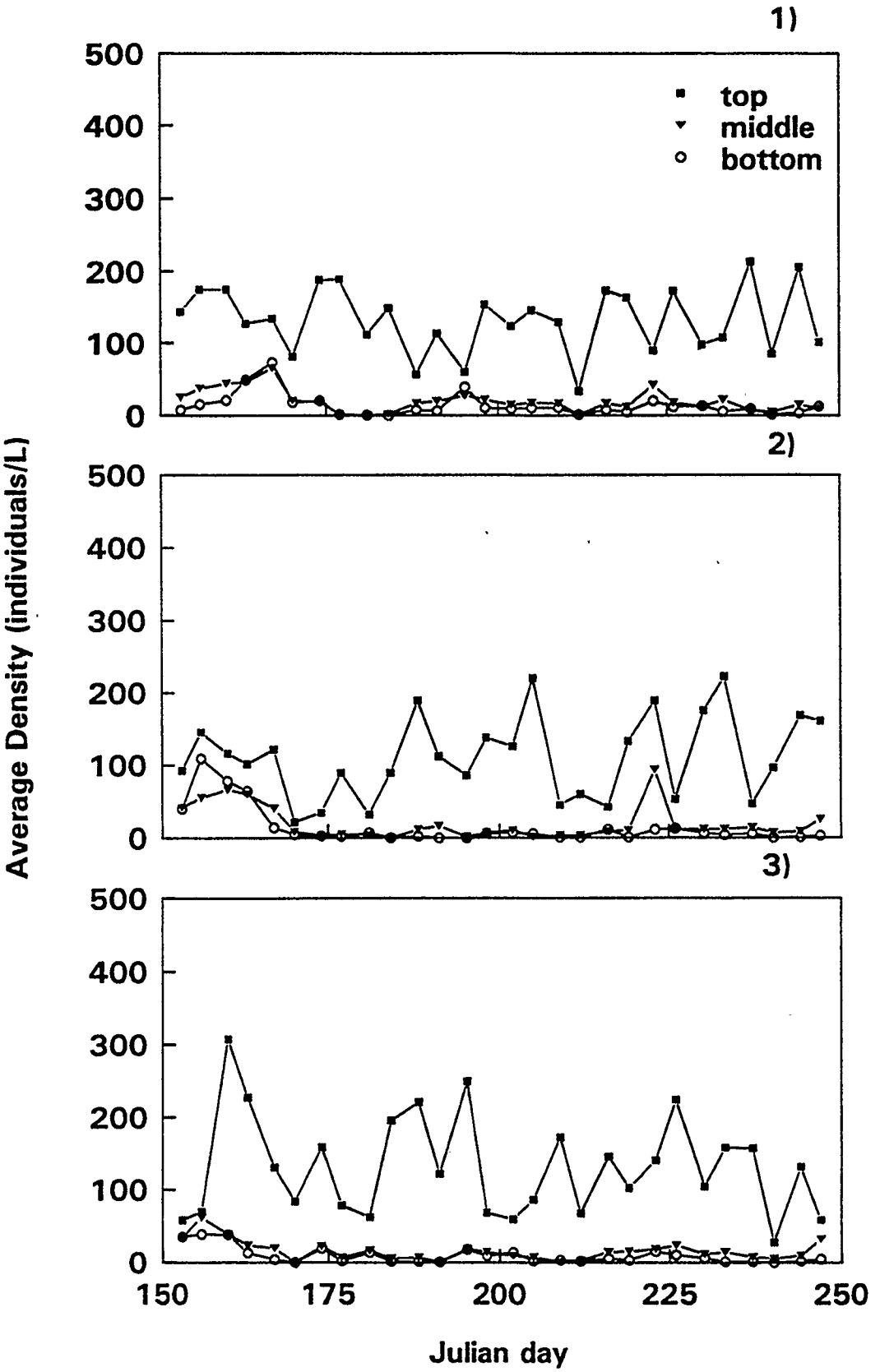
Average Density (individuals/L)
Julian day

Figure 3.5 Population density (individuals/L) of *C.dubia* populations in three replicate (1,2,3) medium volume (39L) aquaria in the top, middle, and bottom sampling depths.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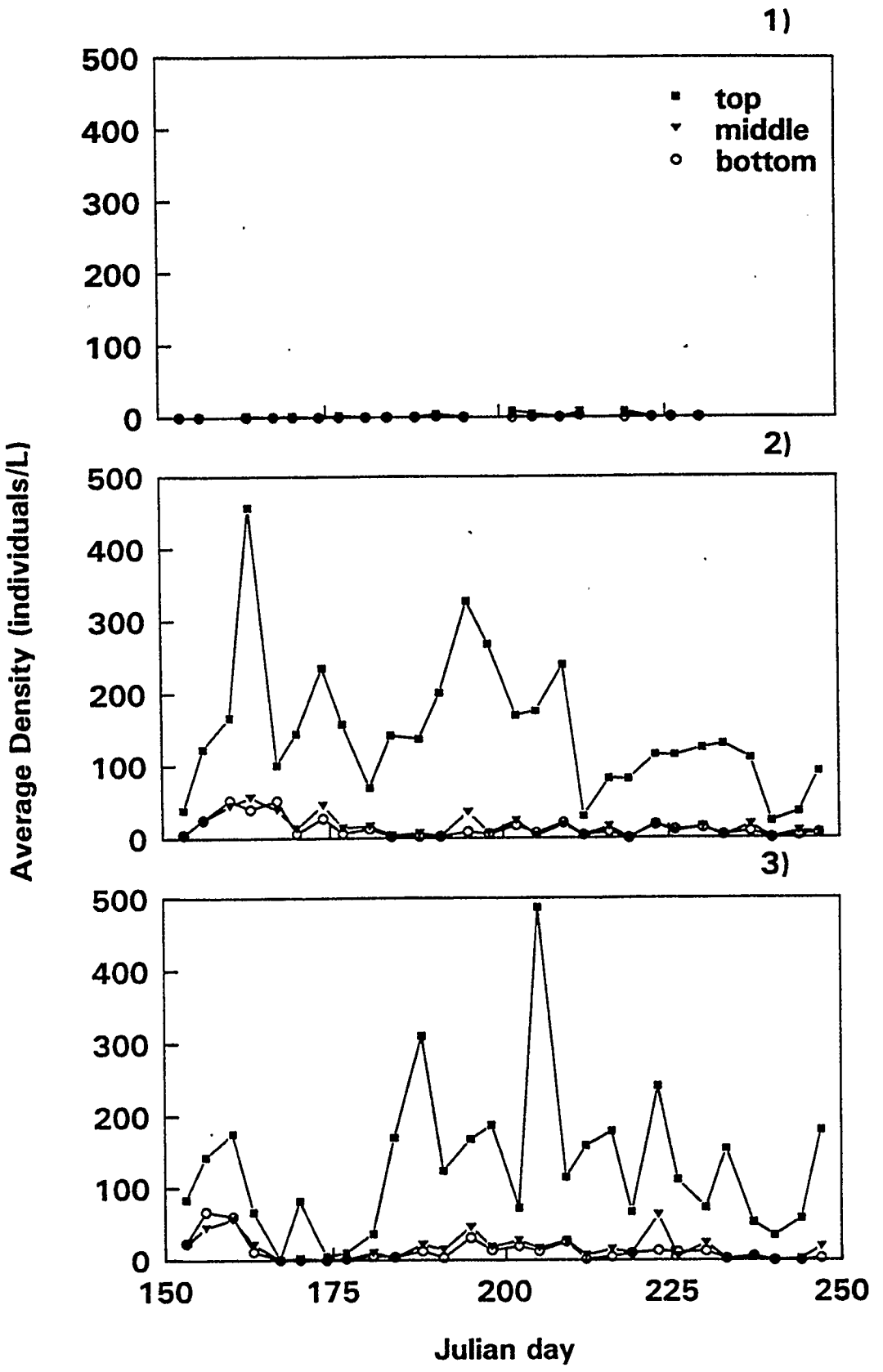
Average Density (individuals/L)
Julian day

Figure 3.6 Population density (individuals/L) of *C.dubia* populations in three replicate (1,2,3) small volume (21L) aquaria in the top, middle, and bottom sampling depths.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Average Density (individuals/L)
Julian day

Table 3.4 Average densities and range of *D.pulex* populations in large volume tanks (87L) calculated for the entire aquaria (overall), the top sampling depth (top), the middle sampling depth (middle), and the bottom sampling depth (bottom).

	Tank 1	Tank 2	Tank 3
overall	19.38 (8.09-52.45)	39.49 (9.31-104.41)	26.61 (7.23-72.30)
top	14.94 (1.76-68.24)	40.19 (5.29-137.65)	21.47 (1.76-73.53)
middle	17.19 (3.92-49.02)	27.80 (3.92-80.39)	22.41 (4.90-85.29)
bottom	26.51 (7.84-107.35)	47.58 (8.82-96.32)	36.28 (5.88-191.91)

Table 3.5 Average densities and range of *D.pulex* populations in medium volume tanks (39L) calculated for the entire aquaria (overall), the top sampling depth (top), the middle sampling depth (middle), and the bottom sampling depth (bottom).

	Tank 1	Tank 2	Tank 3*
overall	24.05 (7.49-40.69)	10.90 (2.45-23.77)	3.93 (0.25-11.27)
top	24.18 (4.823-55.29)	9.59 (0.59-37.65)	2.82 (0.00-10.00)
middle	16.00 (2.94-47.06)	8.68 (0.98-23.53)	4.13 (0.00-12.75)
bottom	30.09 (4.90-76.47)	14.09 (0.74-39.71)	5.19 (0.00-21.32)

*Populations which went extinct

Table 3.6 Average densities and range of *D.pulex* populations in small volume tanks (21L) calculated for the entire aquaria (overall), the top sampling depth (top), the middle sampling depth (middle), and the bottom sampling depth (bottom).

	Tank 1*	Tank 2*	Tank 3
overall	1.75 (0.25-5.15)	8.44 (0.98-27.54)	21.89 (4.66-67.65)
top	1.76 (0.00-5.88)	10.12 (0.59-40.00)	19.49 (2.35-62.35)
middle	2.10 (0.00-8.82)	7.76 (0.00-29.41)	15.61 (1.96-81.37)
bottom	1.47 (0.00-5.15)	6.73 (0.00-21.57)	29.97 (5.15-95.59)

* Populations which went extinct

Figure 3.7 Population density (individuals/L) of *D.pulex* populations in three replicate (1,2,3) large volume (87L) aquaria.

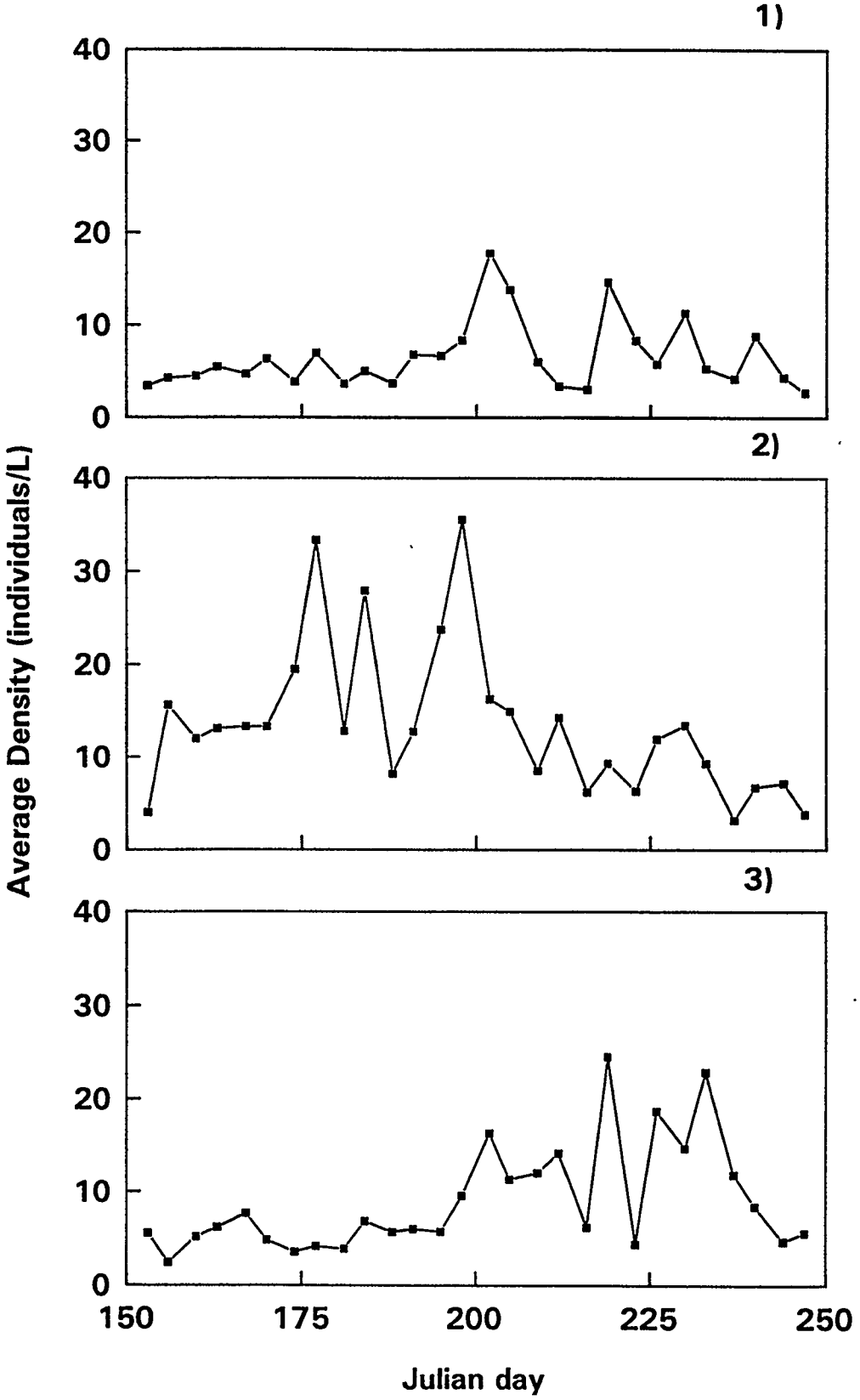
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Figure 3.8 Population density (individuals/L) of *D.pulex* populations in three replicate (1,2,3) medium volume (39L) aquaria.

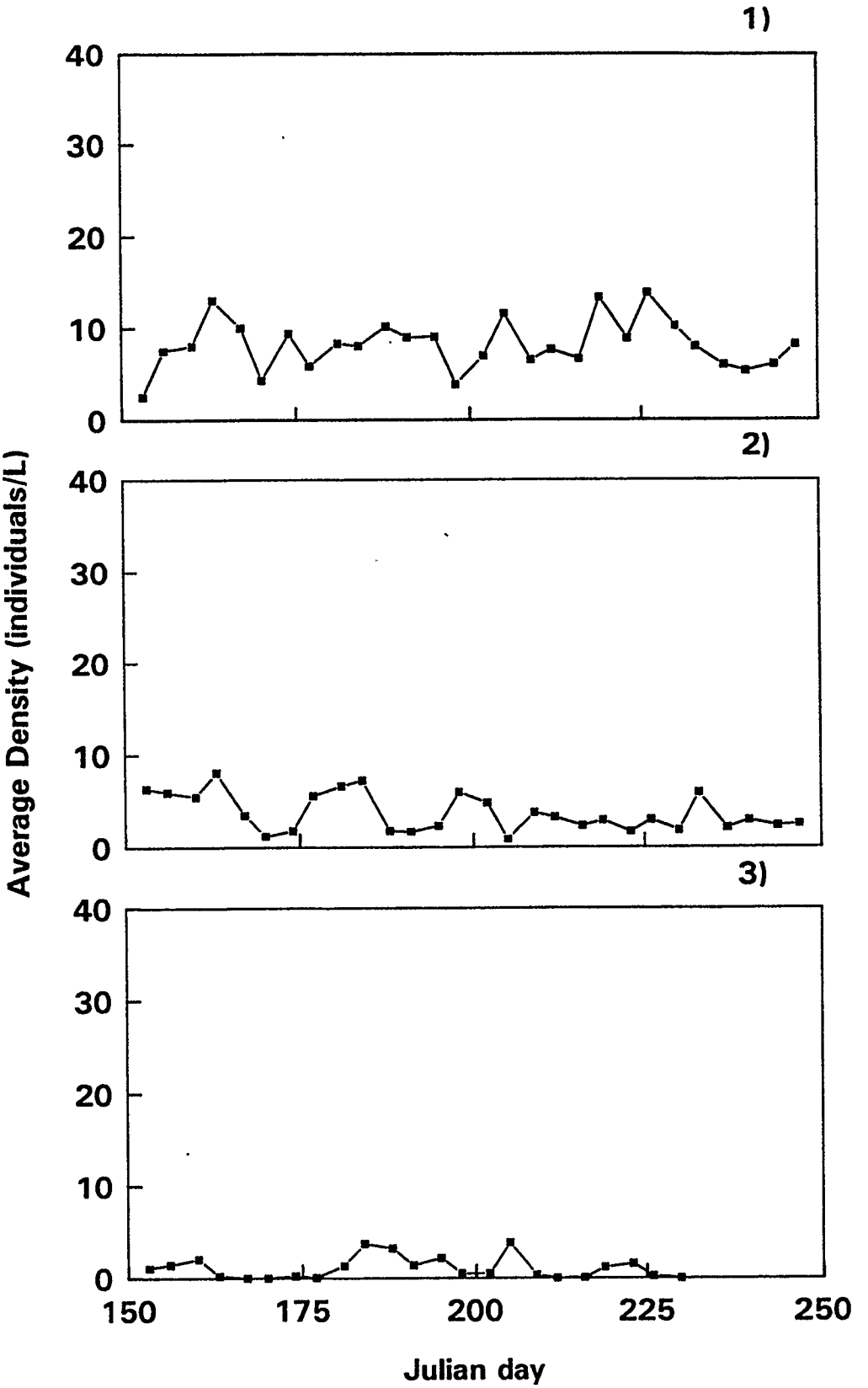
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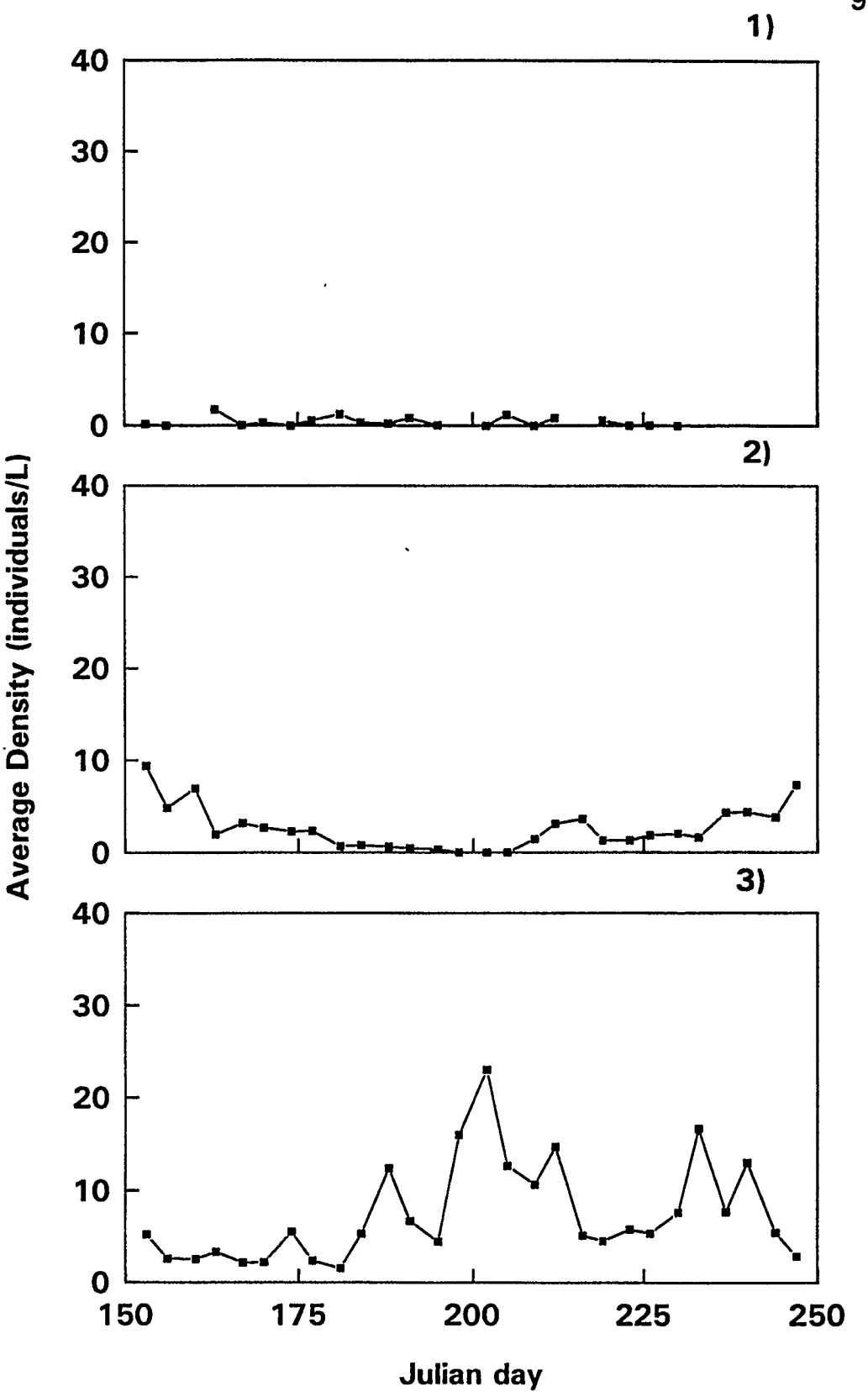
Figure 3.9 Population density (individuals/L) of *D.pulex* populations in three replicate (1,2,3) small volume (21L) aquaria.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Average Density (individuals/L)
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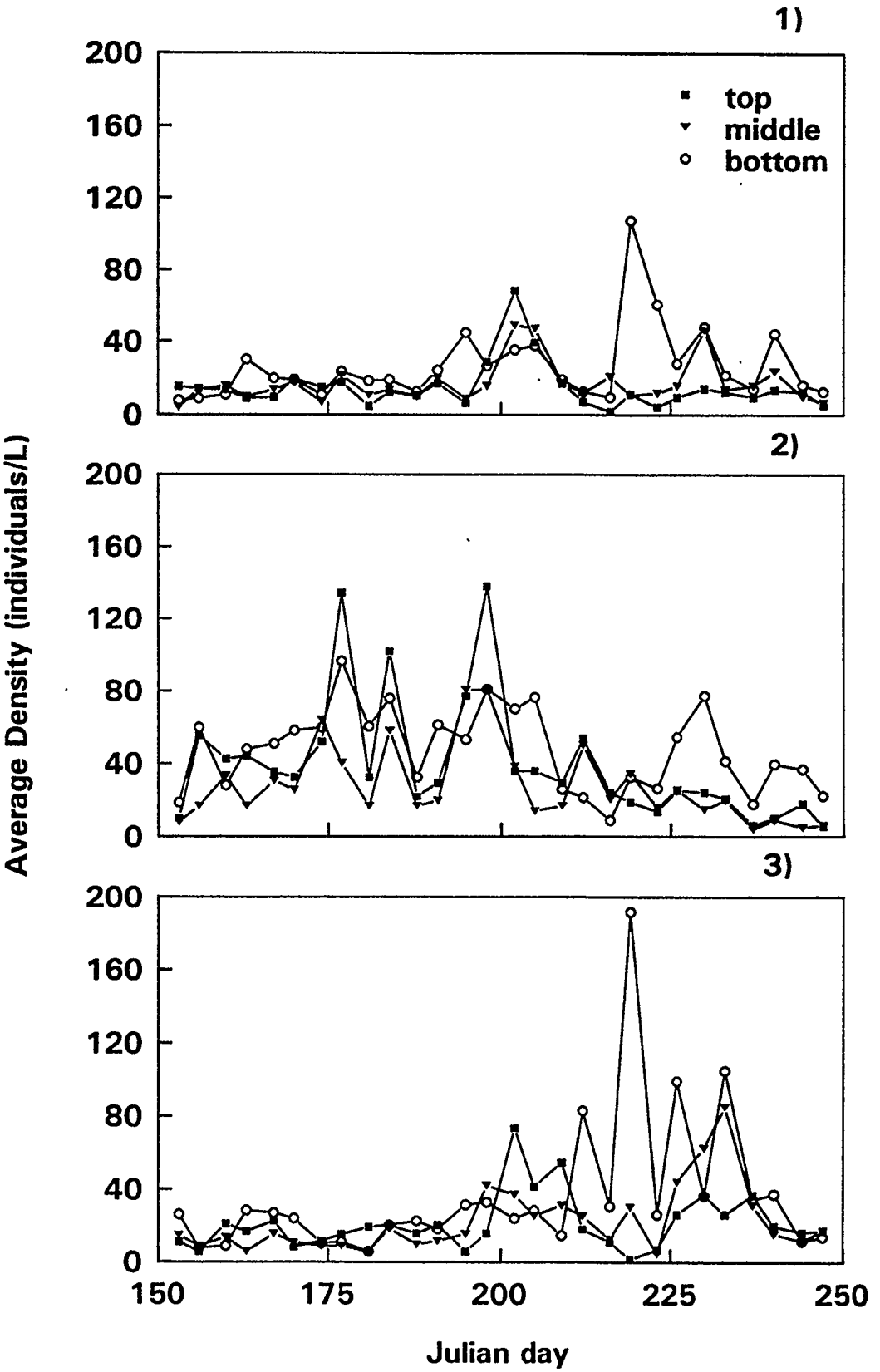
Figure 3.10 Population density (individuals/L) of *D.pulex* populations in three replicate (1,2,3) large volume (87L) aquaria in the top, middle and bottom sampling depths.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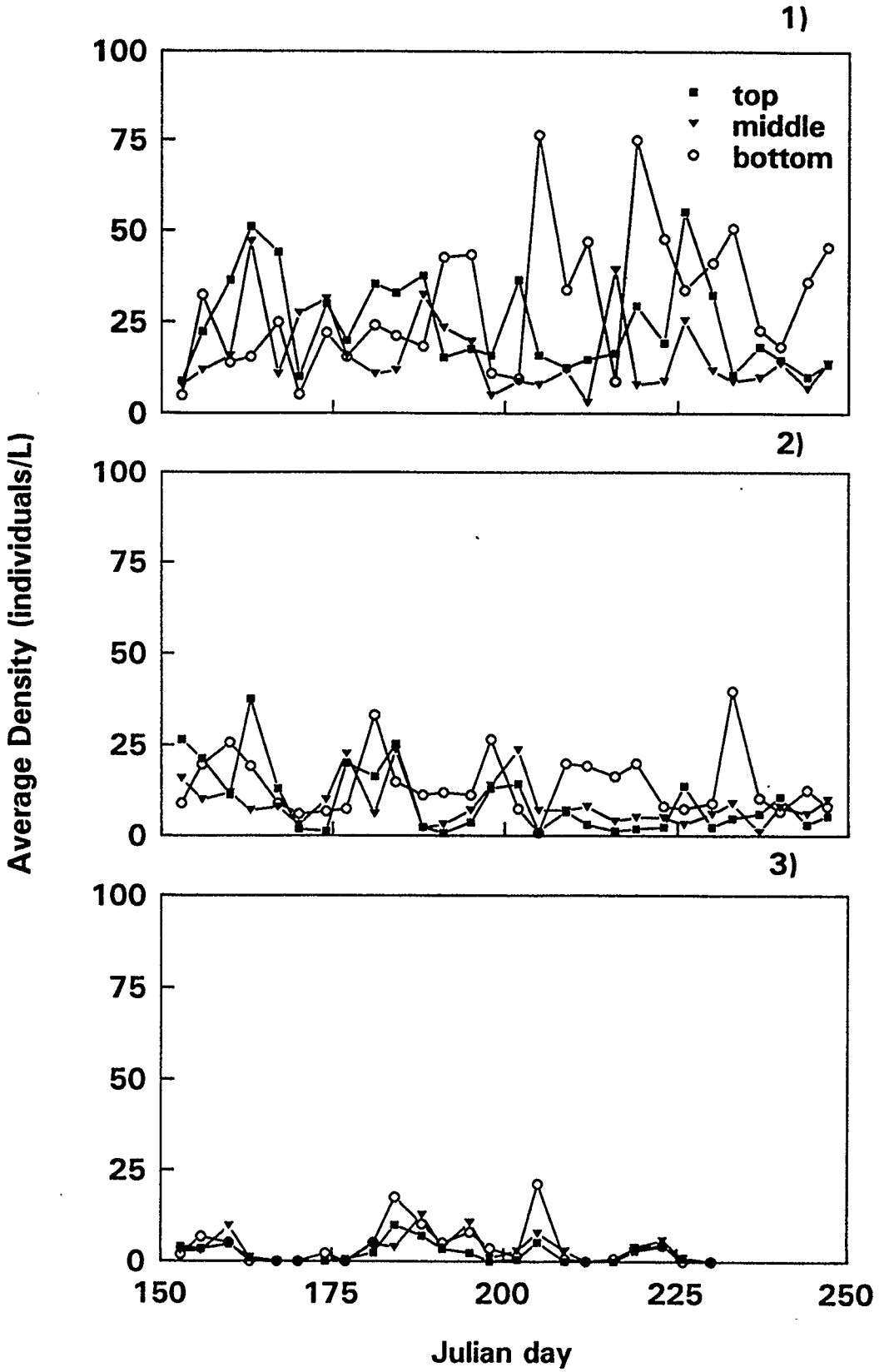
Average Density (individuals/L)
Julian day

Figure 3.11 Population density (individuals/L) of *D.pulex* populations in three replicate (1,2,3) medium volume (37L) aquaria in the top, middle and bottom sampling depths.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Average Density (individuals/L)
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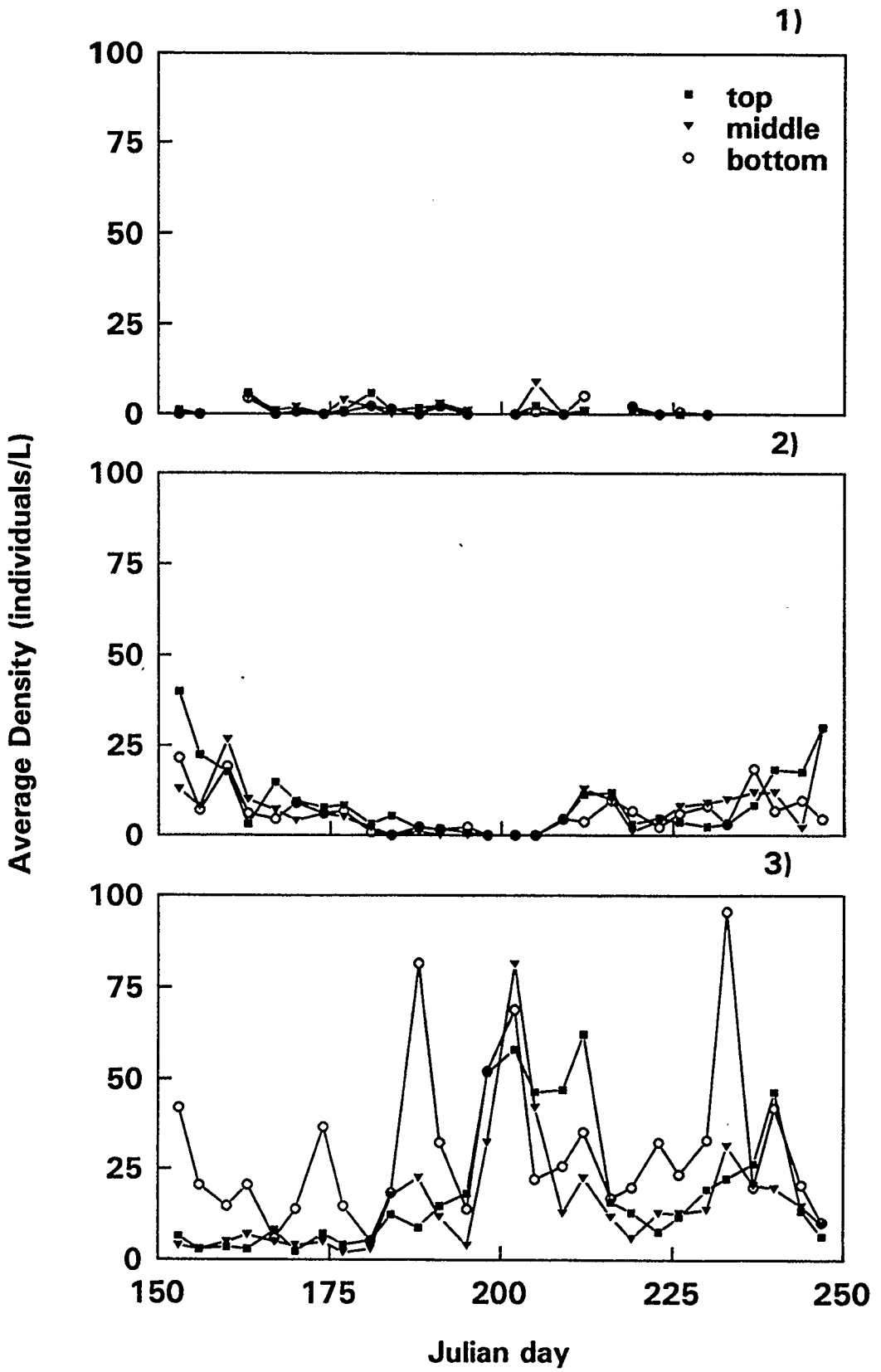
Julian day

Figure 3.12 Population density (individuals/L) of *D.pulex* populations in three replicate (1,2,3) small volume (21L) aquaria in the top, middle, and bottom sampling depths.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Average Density (individuals/L)
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Julian day

Table 3.7 Cross-correlation coefficients at zero time lag of the residual log densities for aquaria of the same volume containing *D.pulex* populations.

Volume	Tanks 1-2	Tanks 1-3	Tanks 2-3
Large (87L)	0.29	0.35	-0.01
Medium (39L)	-0.21	0.15	-0.20
Small (21L)	0.01	0.03	0.06

*P<0.05

Table 3.8 Cross-correlation coefficients at zero time lag of the residual log densities for aquaria of the same volume containing *C.dubia* populations.

Volume	Tanks 1-2	Tanks 1-3	Tanks 2-3
Large (87L)	-0.21	0.27	-0.30
Medium (39L)	0.16	0.37	0.12
Small (21L)	0.02	-0.15	0.14

*P<0.05

D.pulex populations. *C.dubia* populations were more aggregated than the *D.pulex* populations (*C.dubia* $I_\delta = 3.354$, *D.pulex* $I_\delta = 1.654$) and the degree of aggregation did not vary significantly with aquaria volume (Table 3.9).

During the course of the experiments, it became apparent that *C.dubia* populations were concentrated in the top 7 - 11 cm of the aquaria. When only this sampling depth was considered, the degree of aggregation still differed significantly between species, although the values of Morisita's index indicated there was less aggregation within the single sampling depth (*C.dubia* $I_\delta = 1.84$, *D.pulex* $I_\delta = 1.28$) (Table 3.10).

Finally, it is important to note that the mean values of Morisita's index indicate that both *D.pulex* and *C.dubia* populations had aggregated distributions (i.e. $I_\delta > 1$) and that populations in the top and bottom layers were always aggregated (Table 3.11 & 3.12).

Regression analysis of the variance and mean density relationships (i.e. Taylor's power law) for the two species yielded significant relationships and showed that these relationships differed between species (Table 3.13). Comparisons of the slopes of these regression lines revealed that the *C.dubia* populations increased in variance ($b = 1.93$) at a greater rate than *D.pulex* as density increased ($b = 1.55$) ($T_{457} = -5.46$ $P = 0.0008$). An analysis based on the population data from the top depth only gave similar results (Table 3.14)($T_{457} = -5.20$).

When the analysis was completed for each species separately, the degree of aggregation was significantly affected by tank volume for both *C.dubia* and *D.pulex* (Table 3.15). A comparison of the slopes showed that, for both species, the degree of aggregation was greater in the large

Table 3.9 Test statistics from the analysis of the effects of species (*C.dubia* or *D.pulex*) and aquaria volume (21, 39 or 87L) on Morisita's index of aggregation.

Effects	Test statistics
species	$F_{1,452} = 151.92^{***}$
volume	$F_{1,452} = 1.08$
species*volume	$F_{1,452} = 1.31$

*P<0.05,**P<0.01,***P<0.001

Table 3.10 Test statistics from the analysis of the effects of species (*C.dubia* or *D.pulex*) and aquaria volume (21, 29, or 87L) on Morisita's index calculated for only the top sampling depth.

Effects	Test statistics
species	$F_{1,445} = 58.17^{***}$
volume	$F_{1,445} = 2.24$
species*volume	$F_{1,445} = 1.43$

*P<0.05,**P<0.01,***P<0.001

Table 3.11 Average values of Morisita's index calculated for the whole aquaria (overall) and for the top (top), middle (middle) and bottom (bottom) sampling depths for *C.dubia* populations where 'L', 'M' and 'S' indicate large volume aquaria (87L), medium volume aquaria (39L), and small volume aquaria (21L).

Tank	Overall	Top	Middle	Bottom
L1	3.11	1.73	1.00	1.18
L2	4.39	2.44	1.12	1.24
L3	3.17	1.81	1.15	1.19
M1	2.96	1.60	1.16	1.06
M2	3.52	1.80	1.14	1.33
M3	3.56	1.82	1.31	1.48
S1*	3.23	2.69	1.57	2.00
S2	2.93	1.51	0.99	1.35
S3**	3.31	1.74	1.06	1.13

*Populations which went extinct

**Populations which reached very low densities

Table 3.12 Average values of Morisita's index calculated for the whole aquaria (overall) and for the top (top), middle (middle) and bottom (bottom) sampling depths for *D.pulex* populations where 'L', 'M' and 'S' indicate large volume aquaria (87L), medium volume aquaria (39L), and small volume aquaria (21L).

Tank	Overall	Top	Middle	Bottom
L1	1.67	1.29	1.27	1.36
L2	1.50	1.53	1.10	1.21
L3	1.53	1.12	1.22	1.28
M1	1.92	1.35	1.17	1.56
M2	2.17	1.49	1.62	1.65
M3*	1.12	1.04	1.25	1.36
S1*	1.50	1.20	0.60	1.77
S2*	1.59	1.20	1.16	1.35
S3	1.58	1.18	1.25	1.28

*Populations which went extinct

Table 3.13 Test statistics from the analysis of the effects of species (*C.dubia* or *D.pulex*) and log population density on log variance.

Effects	Test statistics
species	$F_{1,457}=0.00$
log density	$F_{1,457}=2423.00^{***}$
log density*species	$F_{1,457}=29.80^{***}$

*P<0.05,**P<0.01,***P<0.001

Table 3.14 Test statistics for the analysis of the effects of species (*C.dubia* or *D.pulex*) and log density on log variance of the top sampling depth.

Effects	Test statistics
species	$F_{1,449}=1.26$
log density	$F_{1,449}=1810.29^{***}$
log density*species	$F_{1,449}=27.01^{***}$

*P<0.05,**P<0.01,***P<0.001

Table 3.15 Test statistics from the analysis of the effects of volume (21, 39, or 87L) and log population density on the log variance of *C.dubia* and *D.pulex* populations.

Effects	*C.dubia*	*D.pulex*
density	$F_{1,231} = 1235.48^{***}$	$F_{1,225} = 1452.63^{***}$
volume	$F_{2,231} = 9.10^{***}$	$F_{2,225} = 8.75^{***}$
density*volume	$F_{2,231} = 9.62^{***}$	$F_{2,225} = 8.61^{***}$

*P<0.05,**P<0.01,***P<0.001

volume aquaria than in the small and medium volume tanks (Table 3.16). When only the top depth layer in the aquaria was considered similar results were obtained (Table 3.17 & 3.18).

STABILITY

Stability, as measured by persistence, may have been greater for *C.dubia* than *D.pulex*. Only one *C.dubia* population (21L tank) crashed, while 3 *D.pulex* (2 21L and 1 39L tank) populations went extinct.

A comparison of the standard deviation of the residuals of the detrended log densities (Table 3.19), and the amplitudes of the harmonic regression (Table 3.20) of populations which did not become extinct shows that *C.dubia* experienced much larger fluctuations in density than *D.pulex*.

As described above, the use of space in the aquaria by *C.dubia* and *D.pulex* was quite different. *C.dubia* was normally found in only the top sampling depth (7-11 cm) while *D.pulex* inhabited the whole tank (Figs 3.4-3.6 & 3.10-3.12). Correlation analysis showed that the proportion of the population for the two species in the top and bottom depths were always negatively correlated (Figs 3.13 & 3.14) (Table 3.21). A negative correlation was not necessarily expected since there were three sampling depths.

For *D.pulex*, time-series analysis showed that the population densities of the three depths were not necessarily correlated at a zero time lag. The top and middle sampling depths were more frequently correlated with each other than with the bottom depth. (Table 3.22).

Table 3.16 Test statistics from the comparison of the slopes of the regression of log variance on log density between small (21L), medium (39L) and large (87L) aquaria for *C.dubia* and *D.pulex* populations.

Effects	*C.dubia*	*D.pulex*
small vs medium	$T_{231} = -0.76$	$T_{225} = 1.73$
small vs large	$T_{231} = 4.10^{***}$	$T_{225} = 4.13^{***}$
medium vs large	$T_{231} = 3.58^{***}$	$T_{225} = 2.88^{**}$

*P<0.05,**P<0.01,***P<0.001

Table 3.17 Test statistics from the analysis of the effects of volume (21, 39, or 87L) and log population density on the log variance of the top sampling depth for *C.dubia* and *D.pulex* populations.

Effects	*C.dubia*	*D.pulex*
density	$F_{1,231} = 757.86^{***}$	$F_{1,217} = 695.39^{***}$
volume	$F_{2,231} = 5.70^{**}$	$F_{2,217} = 3.58^{*}$
density*volume	$F_{2,231} = 8.11^{***}$	$F_{2,217} = 3.84^{*}$

*P<0.05,**P<0.01,***P<0.001

Table 3.18 Test statistics from the comparison of the slopes of the regression of log variance on log density (of the top sampling depth) between small (21L), medium (39L) and large (87L) aquaria for *C.dubia* and *D.pulex* populations.

Effects	*C.dubia*	*D.pulex*
small vs medium	$T_{231} = 0.58$	$T_{217} = 1.16$
small vs large	$T_{231} = 4.02^{***}$	$T_{217} = 2.77^{**}$
medium vs large	$T_{231} = 2.25^{*}$	$T_{217} = 1.81$

*P<0.05,**P<0.01,***P<0.001

Table 3.19 Standard deviation of the residuals of the detrended log densities for each aquaria where 'L' indicates large volume tanks (87L), 'M' indicates medium volume tanks (39L) and 'S' indicates small volume tanks (21L).

Tank	*C.dubia*	Tank	*D.pulex*
L1	0.21	L1	0.19
L2	0.32	L2	0.19
L3	0.27	L3	0.22
M1	0.18	M1	0.16
M2	0.28	M2	0.26
M3	0.22	M3*	0.52
S1*	0.11	S1*	0.45
S2	0.17	S2*	0.23
S3**	0.56	S3	0.25

*Populations that went extinct

**Populations which reached very low levels

Table 3.20 Amplitudes (95% confidence intervals) of the harmonic regression on the detrended log densities of populations in each aquaria where 'L' indicates large volume tanks (87L), 'M' indicates medium volume tanks (39L) and 'S' indicates small volume tanks (21L).

Tank	*C.dubia*	Tank	*D.pulex*
L1	0.11(0.00 - 0.22)	L1	0.13(0.03 - 0.22)
L2	0.23(0.07 - 0.39)	L2	0.12(0.03 - 0.22)
L3	0.21(0.09 - 0.34)	L3	0.12(0.01 - 0.24)
M1	0.11(0.02 - 0.21)	M1	0.12(0.04 - 0.20)
M2	0.20(0.07 - 0.34)	M2	0.18(0.06 - 0.31)
M3	0.17(0.07 - 0.28)	M3*	0.46(0.11 - 0.81)
S1*	0.09(-0.06- 0.24)	S1*	0.28(-0.04- 0.60)
S2	0.23(0.11 - 0.35)	S2*	0.20(0.10 - 0.31)
S3**	0.33(0.05 - 0.61)	S3	0.19(0.07 - 0.30)

*Populations that went extinct

**Populations which reached very low levels

Figure 3.13 Proportion of the total population in the bottom sampling depth versus the proportion of the total population in the top sampling depth of *D.pulex* populations in three replicate large volume (87L) aquaria (a,b,c), medium volume (39L) aquaria (d,e,f) and small volume (21L) aquaria (g,h,i).

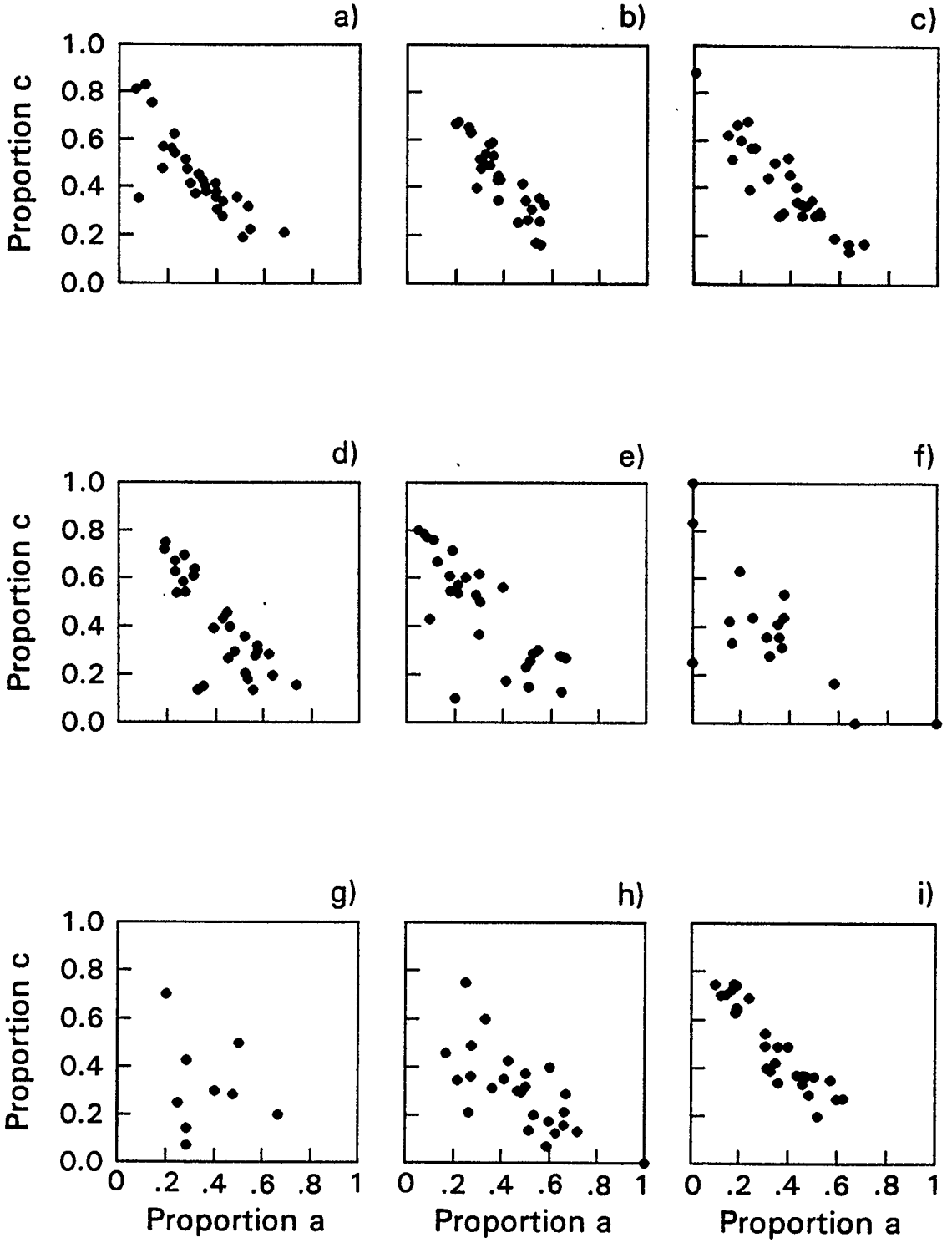

a)
b)
c)
d)
e)
f)
g)
h)
i)
Proportion c
1.0
0.8
0.6
0.4
0.2
0.0
0
.2
.4
.6
.8
1
Proportion a

Figure 3.14 Proportion of the total population in the bottom sampling depth versus the proportion of the total population in the top sampling depth of *C.dubia* populations in three replicate large volume (87L) aquaria (a,b,c), medium volume (39L) aquaria (d,e,f) and small volume (21L) aquaria (g,h,i).

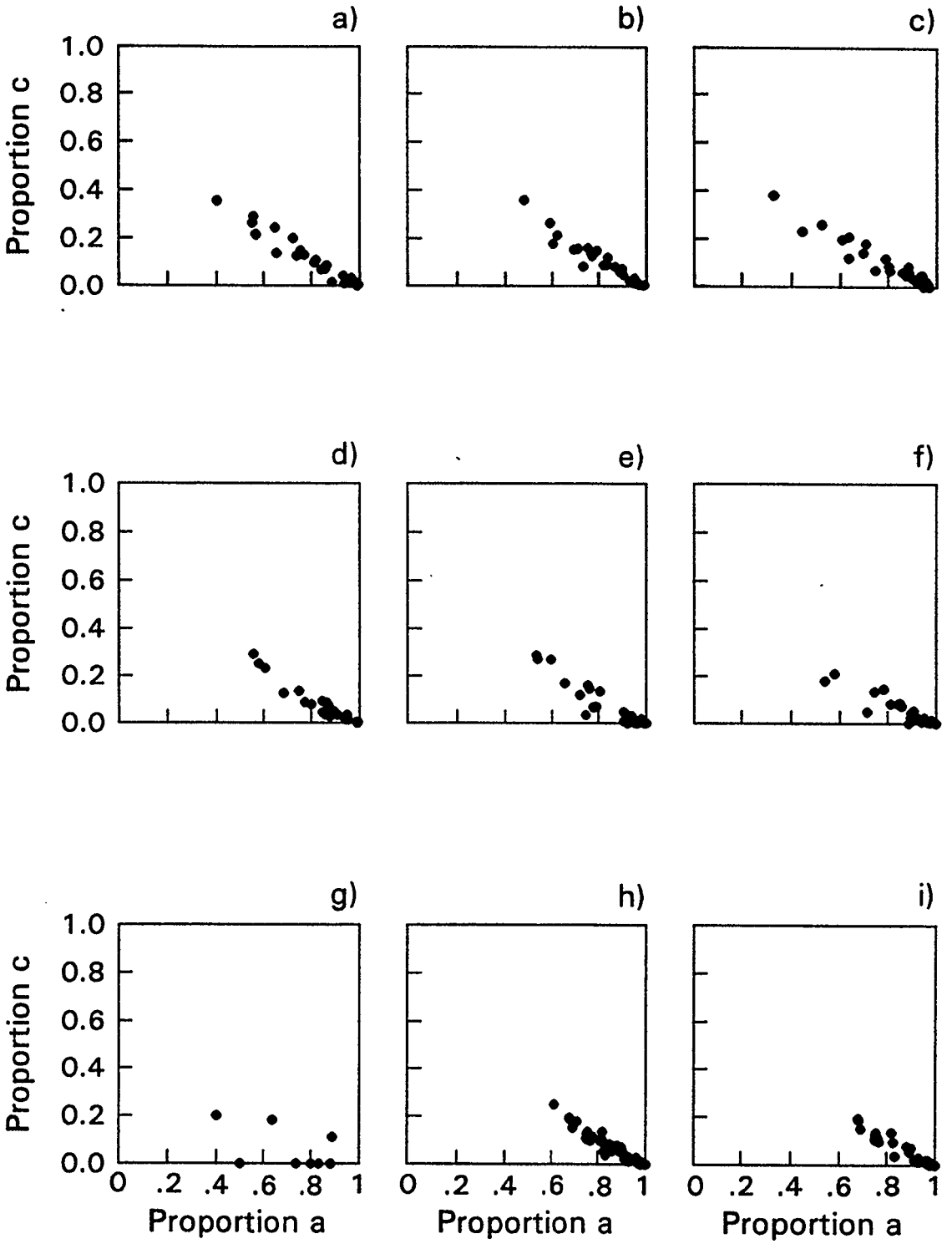

a)
b)
c)
d)
e)
f)
g)
h)
i)
Proportion c
1.0
0.8
0.6
0.4
0.2
0.0
0
.2
.4
.6
.8
1
Proportion a

Table 3.21 Spearman's correlation coefficients of the proportion of the population in the top and bottom sampling depths where 'L' indicates large volume aquaria (87L), 'M' indicates medium volume aquaria (39L) and, 'S' indicates small volume aquaria (21L).

Tank	*C.dubia*	Tank	*D.pulex*
L1	-0.96***	L1	-0.85***
L2	-0.96***	L2	-0.85***
L3	-0.96***	L3	-0.87***
M1	-0.90***	M1	-0.76***
M2	-0.87***	M2	-0.76***
M3	-0.85***	M3+	-0.65**
S1+	-0.35	S1+	-0.18
S2	-0.94***	S2+	-0.71***
S3++	-0.96***	S3	-0.94***

*P<0.05 **P<0.01 ***P<0.001

+Populations which went extinct

++Populations which reached very low levels

Table 3.22 Cross-correlation coefficients at zero time lag of the residual log density of the top (A), middle (B) and bottom (C) sampling depths for each tank containing *D.pulex* where 'L' indicates large volume aquaria (87L), 'M' indicates medium volume aquaria (39L) and 'S' indicates small volume aquaria (21L).

Tank	Depths A-B	Depths A-C	Depths B-C
L1	0.50*	0.23	0.21
L2	0.66*	0.49*	0.22
L3	0.36	-0.26	0.51*
M1	0.34	0.21	-0.18
M2	0.51*	0.30	0.06
M3+	0.53*	0.56*	0.42
S1+	0.38	0.46	-0.43
S2+	0.29	0.33	0.25
S3	0.57*	0.40*	0.62*

*$P<0.05$

+Populations that went extinct

For *C.dubia*, the middle and bottom sampling depths were almost always correlated with each other and the top sampling depth was uncorrelated with either (Table 3.23). However, this result was obtained because there were normally no individuals in the two bottom layers.

There was an effect of volume of the tank on population stability. All populations that did not persist were either from small (21L) or medium sized tanks (39L). For *D.pulex*, population fluctuations were smaller in the large (87L) aquaria (Tables 3.19 and 3.20). Further, the relationships between density fluctuations of the top and bottom depths tended to be more tenuous in the large sized tanks (Fig 3.13).

There did not appear to any consistent trend in the stability of the populations in the three different tank volumes for *C.dubia* (Tables 3.19 and 3.20).

The population stability of the *D.pulex* populations seemed to be affected by the degree of alternation of the population between the top and bottom depths. When the largest proportion of the population tended to switch back and forth between the two depth level rapidly (Julian days 153 -212) (Fig 3.15-3.17), the population dynamics as a whole experienced smaller fluctuations (Figs 3.7-3.9) than when the largest proportion of the population was found in a single depth (Julian days 212-247).

Table 3.23 Cross-correlation coefficients at zero time lag of the residual log density of the top (A), middle (B) and bottom (C) sampling depths for each tank containing *C.dubia* where 'L' indicates large volume aquaria (87L), 'M' indicates medium volume aquaria (39L) and 'S' indicates small volume aquaria (21L). Coefficients for tank S1 could not be calculated because of the number of missing values.

Tank	Depths A-B	Depths A-C	Depths B-C
L1	-0.17	-0.29	0.54*
L2	0.24	0.14	0.84*
L3	0.01	0.12	0.36
M1	0.23	0.12	0.71*
M2	0.33	0.18	0.54*
M3	0.12	0.00	0.65*
S1+	----	----	----
S2	0.31	0.29	0.84*
S3++	0.31	0.15	0.75*

*$P<0.05$

+Populations that went extinct

++Populations which reached very low levels

Figure 3.15 Proportion of the total population in the top (open symbols) and bottom (filled symbols) sampling depths over time of *D.pulex* populations in three replicate (1,2,3) large volume (87L) aquaria.

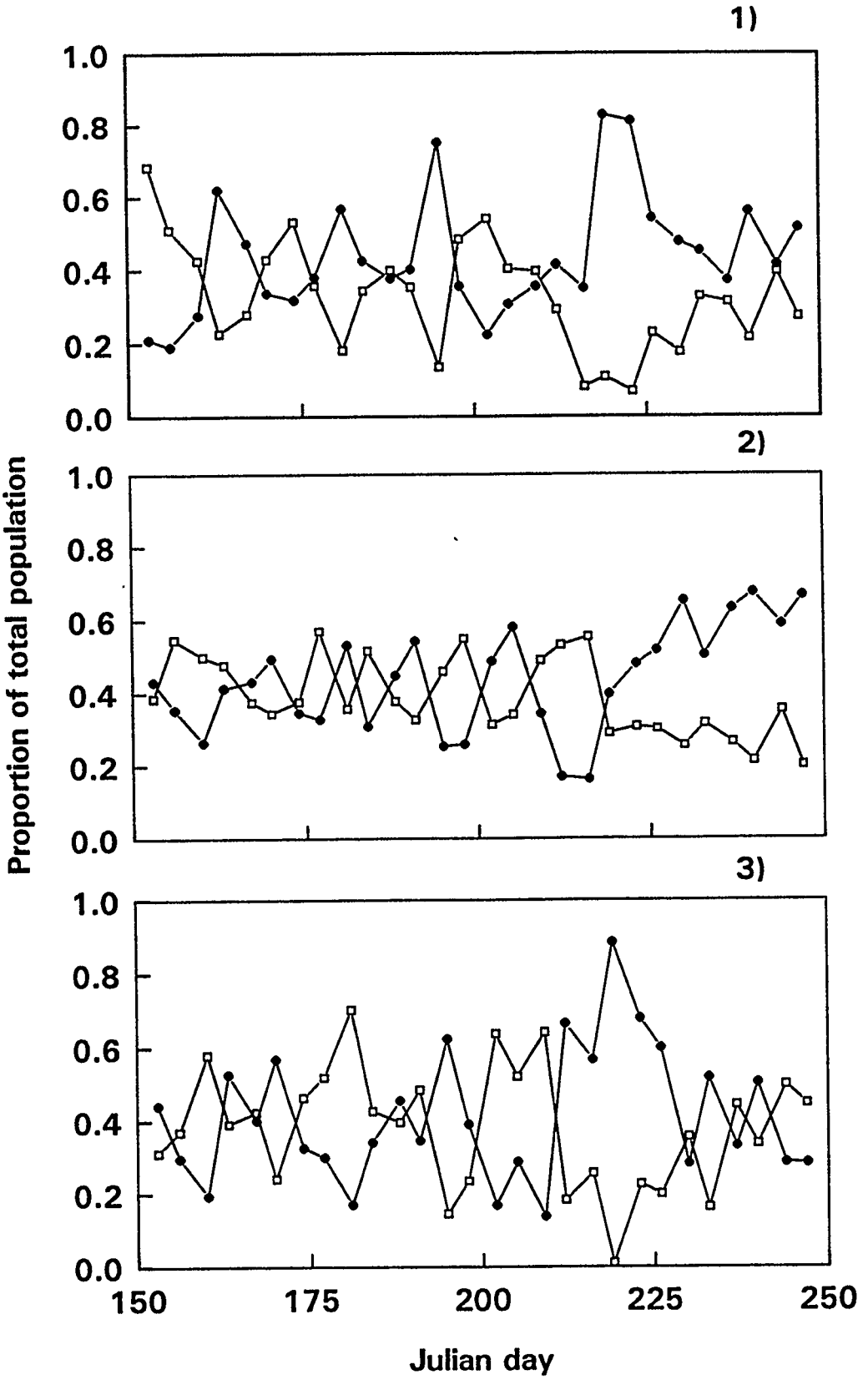

1)
2)
3)
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of total population
150
175
200
225
250
Julian day

Figure 3.16 Proportion of the total population in the top (open symbols) and bottom (filled symbols) sampling depths over time of *D.pulex* populations in three replicate (1,2,3) medium volume (39L) aquaria.

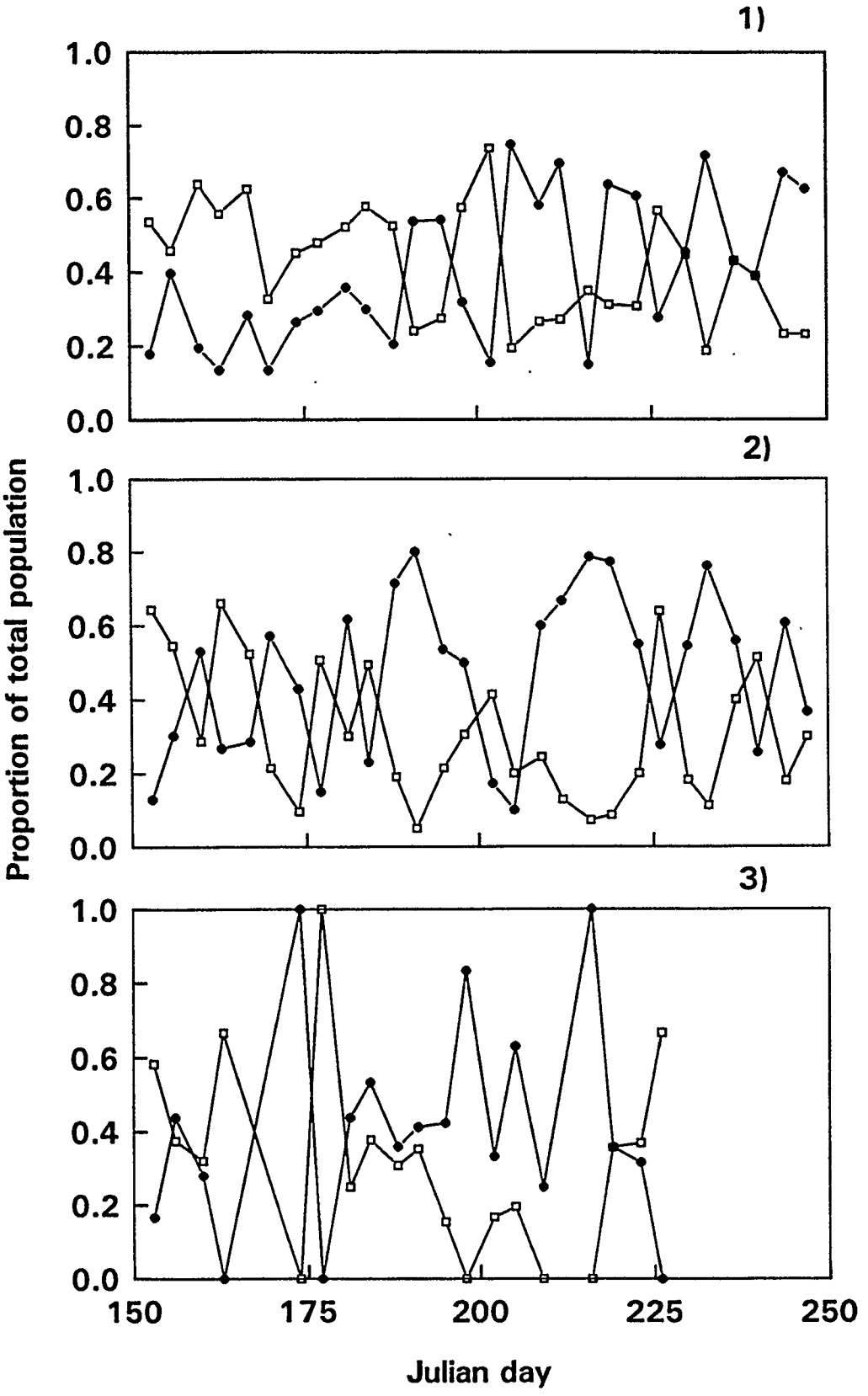
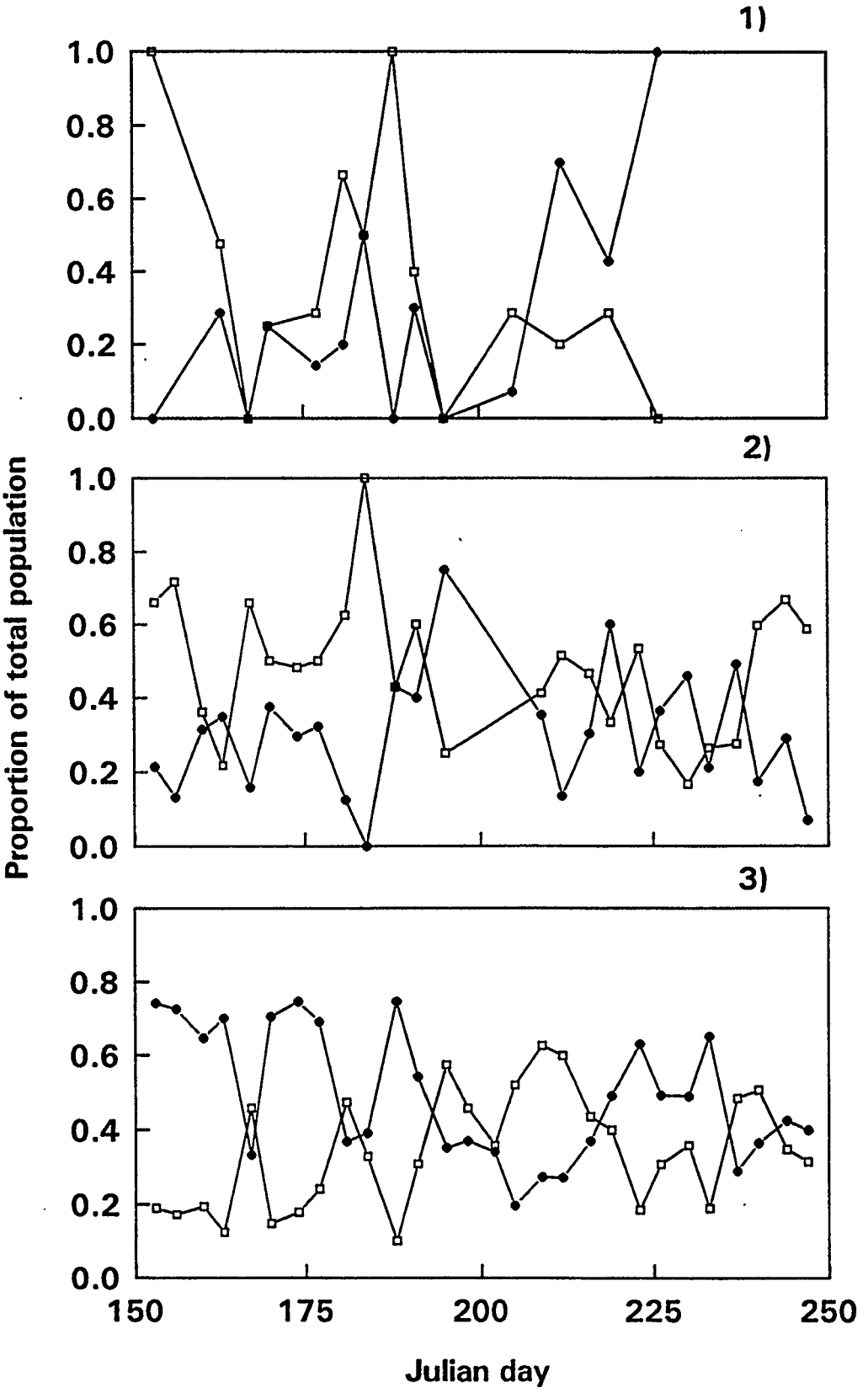

1)
2)
3)
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of total population
150
175
200
225
250
Julian day

Figure 3.17 Proportion of the total population in the top (open symbols) and bottom (filled symbols) sampling depths over time of *D.pulex* populations in three replicate (1,2,3) small volume (21L) aquaria.


1)
2)
3)
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of total population
150
175
200
225
250
Julian day

DISCUSSION

The experiments clearly show that there are marked differences in both the spatial heterogeneity and population dynamics of *C.dubia* and *D.pulex*.

DIFFERENCES IN THE SPATIAL HETEROGENEITY OF *C.DUBIA* AND *D.PULEX*

The most striking difference is the large degree of spatial heterogeneity in *C.dubia* populations as compared to *D.pulex* populations. Both indices of heterogeneity show that the *C.dubia* populations are highly aggregated and concentrated in the top layer of aquaria.

The high degree of aggregation of *C.dubia* compared to *D.pulex* supports general predictions, based on differences in mobility, derived from spatial models (de Roos et al. 1991, McCauley et al. 1993, Wilson et al. 1993). Predators with limited mobility (i.e. *C.dubia*) form more aggregated distributions compared to more mobile species (i.e. *D.pulex*). In addition, this finding is in agreement with Pinel-Alloul et al. (1988) who found that species with smaller body size tended to have a more aggregated distribution. The combination of the findings from the behavioural experiments and these population-level experiments indicates that the decreased mobility in organisms of smaller size can in fact create differences in population distribution.

Secondly, although the prey component of the system could not be monitored directly, the spatial heterogeneity found in these small aquaria supports the hypothesis that local interactions between a predator and

prey can create patchiness at the microscale (<10cm) level. Microscale patchiness has been found in many field studies (Pinel-Alloul et al. 1988, Davis et al. 1992, Tiselius 1992), but it is clear that the spatial heterogeneity found in this study was not the result of physical factors since the systems were not subject to any physical forces such as wind and current action. In addition, the spatial heterogeneity in the aquaria was not produced by temporary phenomena such as mating swarms (Colebrook 1960, Brandl and Fernando 1971), since patchiness was observed throughout the whole of the experimental period.

DIFFERENCES IN THE POPULATION STABILITY OF *C.DUBIA* AND *D.PULEX*

The large differences in the spatial heterogeneity of the two species leads to the prediction that *C.dubia* populations, which had the highest degree of aggregation, should be more stable than the *D.pulex* populations. Observations concerning the persistence of populations may support this prediction, whereas results on the dynamics reject it. Before further discussing the relative stability of the *C.dubia* and *D.pulex* populations, it is important to note that cross-correlation analysis indicated that it is unlikely that the population fluctuations seen in both populations are the result of any external factor.

Populations of the highly mobile species (*D.pulex*) were more likely to go extinct in smaller volume systems than *C.dubia*. But, contrary to predictions from theory, the dynamics of *C.dubia* populations were generally less stable (i.e. experienced larger fluctuations in density) than

populations of *D.pulex* despite the fact that *C.dubia* populations were more spatially aggregated as required by theory.

However, stability in these models requires not only the development of spatial heterogeneity, but also that the patches must be ephemeral or asynchronous. This requirement was not realized for the *C.dubia* populations. It seems likely that the patchiness exhibited by *C.dubia* was not ephemeral since there was no exchange of individuals between the different depth levels (Figs 3.4-3.6). This immobility is in agreement with the findings from the behavioural experiments which indicated that *C.dubia* was relatively stationary when compared to *D.pulex*.

In contrast, population dynamics of *D.pulex* at different depths were generally uncorrelated and this lack of correlation between patches could create a statistical stabilization of the population as a whole. In addition, if there was actual movement of individuals from area of low food to areas of high food concentration, this would tend to damp the fluctuations in population dynamics by allowing different areas to recover algal cell concentration.

In fact, when the time series for the *D.pulex* populations in the large volume tanks is visually inspected (Figs 3.7-3.9), it seems apparent that there is a difference in the stability of the populations as a whole when different rates of exchange between the top and bottom depth layers occur (Figs 3.15-3.17). When the largest proportion of the population switches back and forth between the top and bottom layers of the tank very quickly, the population dynamics of the whole tank seem relatively stable. When the largest portion of the population tends to remain in a

single depth layer, we find that the population dynamics seem to be more unstable.

It seems likely that the mobility of *D.pulex* between the different tank depths may account for the differences in stability between the two species. If *C.dubia* populations formed one or two fixed patches along the aquaria edges, this would generate a large value for indices of aggregation, but would probably not have a large stabilizing effect. One or two patches would not be enough to create a statistical stabilization of the population dynamics of the whole aquaria. Secondly, a fixed patch structure would also not allow for the recovery of the algal prey populations in these local areas.

EFFECTS OF ENVIRONMENT SIZE

The effect of environment size on the degree of aggregation in the populations yielded equivocal results. Morisita's index indicated that there were no differences in the degree of "patchiness" between aquaria of different volumes containing the same species, while coefficients from Taylor's power law suggested that the spatial heterogeneity of large volume aquaria was higher than that of small and medium tanks for both species.

The results regarding the effects of tank volume on the population stability of the two species must be interpreted with caution. Although there seemed to be a general trend for the population fluctuations of *D.pulex* to be reduced with an increase in volume, this effect was not significant. However, it is interesting to note that the only populations which became extinct were in small and medium volume aquaria, while

the large tanks, which Taylor's power law indicated had the largest degree of "patchiness", persisted.

A trend towards a reduction in the population fluctuations with an increase in aquaria volume was not found for *C.dubia* populations, and this lends credence to the hypothesis that "patchiness" in these populations had a fixed character and thus could not promote stability. The increase in the stability of *D.pulex* populations with an increase in aquaria volume seems to be due to the movement of the population between the different sampling depths. The inverse relationship between the proportion of the population in the top and bottom depths is strongest in the large volume tanks (Fig 3.13a,b,and c), and these are the populations which are most stable. The *C.dubia* populations did not develop substantial populations in the bottom sampling depths in any of the aquaria and there does not seem to be any decrease in population fluctuation with an increase in aquaria size.

IMPLICATIONS FOR FUTURE RESEARCH

Possibly the most striking feature of these experiments are the large differences in the spatial heterogeneity of *C.dubia* and *D.pulex*. These species are very similar and one might expect that the population dynamics could be described using very similar models. However, the large differences in behaviour lead to large differences in the spatial heterogeneity and possibly also the population dynamics. Consequently, the predictions about population stability based only on physiological processes may be inadequate.

Obviously these experiments are preliminary in nature. A more complete examination of the effects of limited mobility and behavioural aggregation on population stability will require the formulation of theoretical models, based on the biology of the selected organisms, which predict their relative population stability in the absence and presence of limited mobility. Predictions based on these types of models need to tested by comparing the dynamics of stirred and undisturbed systems as well as by comparing the dynamics of a large variety of system sizes.

CHAPTER 4 CONCLUSIONS

This study provides evidence that individual behaviour and mobility can have profound effects on population distributions and stability of freshwater zooplankton under controlled laboratory conditions.

Specifically, it was found that two very similar species, *C.dubia* and *D.pulex*, have very different mobilities and patterns of aggregation (chapter 2) in response to spatially-heterogeneous food distributions. *C.dubia* is less mobile than *D.pulex*. Both species have a tendency to aggregate, however, the aggregation behaviour of *D.pulex* is related to the spatial distribution of prey, while the aggregation of *C.dubia* individuals is not.

The experiments indicated that filtering and/or ingestion rates were likely cues that alerted *D.pulex* individuals they had entered high-food regions. Changes in these rates, as opposed to longer-term processes such as assimilation rate, possibly triggered a reduction in swimming speed which allowed individuals to remain in these profitable foraging areas. It was speculated that differences in mobility and filtering and/or ingestion rates caused by allometry accounted for the inability of *C.dubia* to locate and linger in high-food locations. Future experiments that examine how aggregative behaviour varies with body-size or stage (i.e. juveniles versus adults) are indicated.

As predicted by models of spatial dynamics (de Roos et al. 1991, McCauley et al. 1993, Wilson et al. 1993), these species also differed in their population distribution (chapter 3). *C.dubia* populations were highly aggregated, however, their low mobility created a "patchiness" that was

fixed in space rather than ephemeral. *D.pulex* populations were less aggregated, but showed an ephemeral "patchiness." The degree of aggregation increased with environment size for both species.

As expected, the ephemeral "patchiness" of the *D.pulex* populations contributed to the stability of the population dynamics. Stability in these populations increased with environment size. However, environment size did not contribute to the stability of *C.dubia* populations because of the fixed nature of their spatial heterogeneity, and in the largest volume tested, *C.dubia* populations were less stable than *D.pulex* populations. A logical next step would be to examine dynamics of populations in mesocosm experiments or using in situ enclosures in the field in which mixing rates can be manipulated.

It is apparent that models of population dynamics must take into account individual mobility and behaviours which affect mobility. Ignorance of these factors can lead to striking incongruities between the predicted population-level effects and the actual consequences of individual-level responses.

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APPENDIX 1 Representative maximum and minimum algal concentrations (cells/mL) for each target food level for experiments with individual (IND) and groups (GRP) of *C.dubia* and *D.pulex*. The ratio between the maximum and minimum concentrations was used as a covariate in the analysis of the measures of behaviour but did not explain a significant amount of the variation.

	SPECIES	TARGET	MAX	MIN
IND	*C.dubia*	1000	1275.0	396.9
			1180.9	523.5
		4000	5294.4	469.5
			2675.0	949.2
		8000	17129.6	2937.5
			24456.5	4517.3
	D.pulex	1000	1180.9	523.5
			1592.8	100.8
		4000	5294.4	469.6
			3650.6	700.9
		8000	17129.6	2937.5
			24456.5	4517.3
GRP	*C.dubia*	1000	1512.5	93.8
			1140.6	151.6
		4000	3218.8	687.5
			2675.0	949.2
		8000	10937.5	687.5
			9103.1	656.3
	D.pulex	1000	1593.8	778.1
			1750.0	315.6
		4000	3843.8	234.4
			4203.0	300.0
		8000	10996.9	675.0
			9537.5	1134.4

APPENDIX 2 Values of the means and standard errors (in brackets) of the populations densities (individuals/mL) (calculated for the three different sampling depths and over the whole tank) of *C.dubia* and *D.pulex* populations in 87, 39 or 21 L aquaria on selected sampling dates.

				JULIAN DAY		
SPECIES	VOLUME	TANK	DEPTH	174	198	223
C.dubia	87 L	1	top	70.0 (27.2)	51.2 (24.4)	65.9 (21.1)
			middle	12.7 (4.2)	10.8 (1.0)	13.7 (2.0)
			bottom	1.5 (0.8)	12.5 (2.8)	14.0 (2.5)
			overall	32.8 (14.3)	28.2 (11.2)	35.5 (11.3)
	39 L	1	top	187.6 (80.0)	153.5 (34.8)	90.0 (17.7)
			middle	18.6 (0.98)	21.6 (9.9)	42.2 (7.8)
			bottom	20.6 (4.0)	10.3 (10.3)	20.6 (2.4)
			overall	89.7 (15.0)	72.8 (24.8)	54.9 (11.7)
	21 L	3	top	5.9 (2.1)	187.6 (65.0)	241.2 (69.4)
			middle	0.0 (0.0)	18.6 (3.9)	62.7 (16.7)
			bottom	0.0 (0.0)	14.0 (4.0)	13.2 (1.5)
			overall	2.5 (1.2)	87.5 (34.0)	120.6 (41.5)

				JULIAN DAY		
SPECIES	VOLUME	TANK	DEPTH	174	198	223
D.pulex	87 L	1	top	14.7 (1.61)	28.8 (3.9)	4.1 (2.2)
			middle	6.9 (2.6)	15.7 (4.3)	11.8 (10.3)
			bottom	11.0 (4.2)	26.5 (7.9)	60.3 (43.9)
			overall	11.5 (1.8)	24.8 (3.4)	24.8 (15.5)
D.pulex	39 L	1	top	30.0 (8.3)	15.9 (9.4)	19.4 (3.6)
			middle	31.4 (8.0)	4.9 (1.0)	8.8 (2.9)
			bottom	22.1 (11.1)	11.0 (7.3)	47.8 (25.3)
			overall	27.7 (5.1)	11.5 (4.5)	26.2 (9.1)
	21 L	3	top	7.1 (2.4)	51.8 (3.9)	7.6 (1.5)
			middle	4.9 (3.5)	32.4 (6.1)	12.7 (4.3)
			bottom	36.8 (14.3)	52.2 (5.1)	32.4 (16.1)
			overall	16.4 (6.2)	47.1 (3.6)	17.2 (6.0)