

## Determining carrying capacity from foraminiferal time-series

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**ABSTRACT** – The carrying capacity  $K$  is the equilibrium population density of a species that an area can support while adequately meeting the needs of every individual. Although widely used in ecology, it has yet to be applied rigorously to living foraminifera.  $K$  is readily determined from time-series of population densities. Given that  $N_{t+1} = N_t + RN_t$ , in which  $N_t$  is the population densities at time  $t$ ,  $N_{t+1}$  is the density at a subsequent time  $t+1$  and  $R$  is the per capita rate of change in population density, then linear regression gives  $R_t = R_m - sN_t$ , in which  $R_t$  is the per capita rate of increase at time  $t$ , the constant  $R_m$  is the maximum possible individual rate of increase, and the negative slope  $s$  represents the strength of intraspecific interactions. Setting  $R_t = 0$ , so that  $N_t = K$  and  $R_m - sK = 0$ , gives  $K = R_m/s$ , which is applicable in aseasonal environments. There are two carrying capacities in seasonal environments, depending on whether the season is favourable ( $K_{\max}$ ) or unfavourable ( $K_{\min}$ ). Values of  $K_{\max}$  and  $K_{\min}$  are estimated for *Nonion depressulus* in the Exe estuary, UK (25 monthly samples), *Quinqueloculina* spp. in the Indian River Lagoon, USA (60 monthly samples) and *Haynesina germanica* in Cowpen Marsh, UK (25 fortnightly samples). The most precise estimate was for *H. germanica*, but it was unclear if this was due to the high rate of sampling or the large number of replicates used to erect this time-series. *J. Micropalaeontol.* 31(2): 111–119, July 2012.

**KEYWORDS:** *Nonion depressulus*, *Quinqueloculina*, *Haynesina germanica*, *Exe estuary*, *Indian River Lagoon*, *Cowpen Marsh*, population dynamic, seasonality, carrying capacity

### INTRODUCTION

Early work by Bandy *et al.* (1965) showed that foraminifera can play a major role in assessing the environmental impact of human activities on the marine environment. They have subsequently been widely applied in assessing the impact of sewage outfalls, oil rigs, developments along shorelines and abrupt catastrophes (Alve, 1995; Nigam, 2005; Nigam *et al.*, 2006). The environmental effect of any development is determined through monitoring of the live foraminiferal community before and after the development is implemented (Wilson, 2000; Scott *et al.*, 2001), which can determine whether a development has forced a regime shift in which there has been an abrupt, anthropogenically induced change in the ecosystem from one self-stabilizing state to another that is not readily reversible (Genkai-Kato, 2007).

Foraminiferal micropalaeontologists have acquired a considerable number of time-series (e.g. Boltovskoy & Lena, 1969; Buzas *et al.*, 1977, 2002; Murray, 1983; Basson & Murray, 1995; Wilson, 2000; Wilson & Ramsook, 2007), with samples taken regularly at fortnightly or monthly intervals. These can be used as training sets in the development of new environmental applications of foraminiferal time-series. One such technique is detecting changes in the environment's carrying capacity  $K$  for species. As originally defined by Errington (1934),  $K$  is the equilibrium population of a species that an area can support while adequately meeting the needs of all individuals (see also Kashiwai, 1995).  $K$  is thus shaped by the 'interdependent relationships between finite resources and the consumers of those resources' (Monte-Luna *et al.*, 2004, p. 488). Foraminiferal workers have so far mostly evaluated  $K$  qualitatively (e.g. Hohenegger, 2004). Quantitative knowledge of  $K$  is useful, however, for assessing the sustainability of the economic development of a region (Wang, 2010), especially as anthropogenically induced regime shifts are known to

force changes in an area's carrying capacities (Peterman, 1977; Berryman, 1999).

A change in the carrying capacity of an impacted area indicates that its economic development is having a negative impact on the ecosystem. There is thus a need for a simple method for determining  $K$  from foraminiferal time-series. This paper presents such a method but notes that many time-series currently available are inadequate for determining  $K$  precisely.

### ALGEBRAIC BACKGROUND TO CALCULATING CARRYING CAPACITY $K$ FROM A TIME-SERIES

#### Aseasonal environments

A population is a group of conspecific individuals that exist together in time and space (Levin *et al.*, 2009). Population dynamics examines temporal changes in such a group (Berryman, 1999; Turchin, 2003). Lee & Muller (1973) found that foraminiferal species have extremely high intrinsic rates of increase that allow them to exploit the rapid changes in the microbial community structure that take place throughout favourable months. Murray (1967) concluded that the annual production of benthonic foraminifera is a product of four main factors: the initial size of the standing crop, the proportion of individuals that reproduce, the frequency of reproduction and the number of surviving new individuals resulting from each reproductive phase. He proposed a method for assessing production from time-series. Nigam *et al.* (2009) noted that pollutants affect the per capita rate of reproduction. The method outlined in this section is suited for estimating  $K$  in an aseasonal environment, where  $K$  does not vary throughout the year.

Murray (1983) introduced a model for foraminiferal population dynamics in which the change in the number of members of a foraminiferal population over time ( $\Delta N$ ) was equal to the number

of inputs (births  $B$ , immigrants  $I$ ) less the number of outputs (deaths  $D$ , emigrants  $E$ ), such that

$$\Delta N = B - D + I - E. \quad (1)$$

It follows that a given population of  $N_t$  at time  $t$  (the standing crop of Murray, 1967) will at a later time  $t+1$  have changed to a population  $N_{t+1}$  as follows:

$$N_{t+1} = N_t + B - D + I - E. \quad (2)$$

Thus,  $\Delta N = N_{t+1} - N_t$  and may be positive (population growth), zero (population stable) or negative (population decline), depending on the balance of inputs and outputs.

For  $\Delta N$  to be meaningful, an independent variable is needed against which to measure changes in the number of individuals forming the population. Measuring  $N_t$  per spatial unit (area, volume) is more informative than is a census of an unconstrained population and is termed the population density. The expression  $\Delta N = N_{t+1} - N_t$  per spatial unit measures the change in population density between time  $t$  and  $t+1$ . For the remainder of this paper,  $N_t$  and  $N_{t+1}$  signify population densities.

Whether the density of a studied population increases, is static or decreases between times  $t$  and  $t+1$  depends on the actions of the individual specimens, as it is individuals that live, die, procreate and migrate (Berryman & Kindlmann, 2008). Where the population density is low relative to the resources (food, mates, predator-free space) available and individuals do not have to compete intraspecifically to satisfy their needs, the population density will increase over time because (a) most offspring will survive to reproduce, (b) the need to emigrate in search of resources will be low and (c) there will be an influx of immigrants. These factors collectively raise inputs and lower outputs to the population. When the population density exceeds the resources available and individuals must compete intraspecifically to satisfy their needs, the population density will decrease over time as demand for resources outstrips supply and (a) the birth rate decreases, (b) the weaker specimens die and (c) some members of the population emigrate.

As Berryman & Kindlmann (2008, p. 35) noted, it is more meaningful to express changes in population density in terms of the individual organism rather than the entire population. The per capita rate of change in population density  $R$  is given by

$$R = \Delta N / N_t = (N_{t+1} - N_t) / N_t, \quad (3)$$

algebraic manipulation of which gives

$$N_{t+1} = N_t + RN_t, \quad (4)$$

in which the population density at time  $t+1$  is determined by the density at the previous time  $t$  and the individual rate of population density increase  $R$ . The value of  $R$  in equations (3) and (4) may be positive (in which case the population density increases), zero (density remains stable) or negative (density decreases). Equation (4) is a positive feedback loop; the number at time  $t+1$  can be fed back into the right-hand side of (4) to predict the population

density at time  $t+2$  and so on. If  $R$  is positive and remains constant, then the population density will increase exponentially. This is likely only when a population is faced with an abundance of resources such that supply exceeds demand (as, say, in the first stages of the succession following the arrival of a foraminiferal species in an area – cf. Alve, 1999). If  $R$  is constant but negative, such that the supply of resources (which will be finite in the short term) is outstripped by demand, then equation (4) will lead the species into local eradication. Only when  $R = 0$  will the population density remain unchanged.

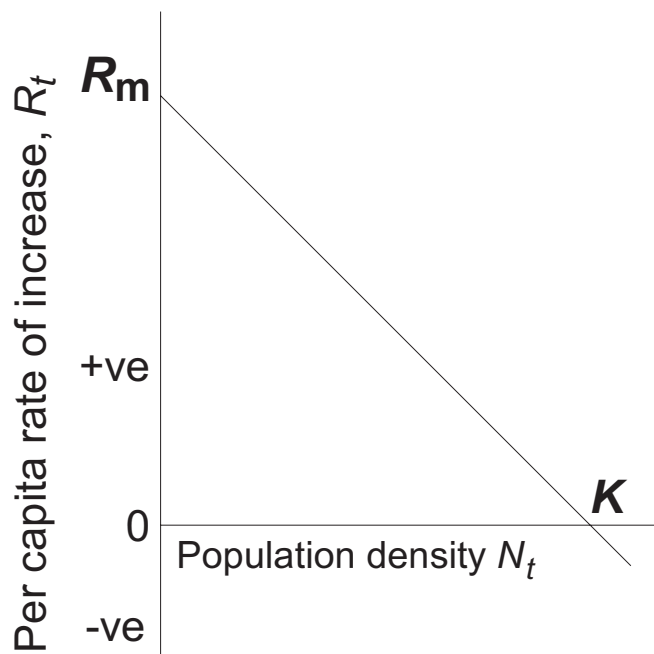
For a species to survive indefinitely at a site, the positive feedback loop in equation (4) must be countered by at least one stability-inducing, negative feedback loop through changes in the rates of births, deaths or migration (Malthus, 1798). This is incorporated into equation (4) because  $R$ , the individual rate of increase, is dependent on the population density at time  $t$  (Berryman & Kindlmann, 2008). At a time when population density is low relative to resources,  $(B + I)$  will be high and  $(D + E)$  low such that the individual rate of increase  $R$  approaches a maximum limit  $R_m$ . As the population density increases,  $(B + I)$  will decrease and  $(D + E)$  increase and  $R$  will decrease proportionally. Assuming that  $R$  is linearly related to population density (Berryman & Kindlmann, 2008), it follows that

$$R_t = R_m - sN_t, \quad (5)$$

in which  $R_t$  is the per capita rate of increase at time  $t$ , the constant  $R_m$  is the maximum possible individual rate of increase,  $N_t$  is the population density at time  $t$  and the negative slope  $s$  represents the strength of intraspecific interactions. The value of  $s$  is a function of the proportion of the available resources used by the individual and is, therefore, larger for macrofauna than for meiofauna, such as foraminifera. Graphing the simple linear regression (5) for  $R_t$  against  $N_t$  indicates not only  $R_m$ , which occurs when the population density approaches zero (i.e. at the intercept on the y-axis), but also a population density  $K$  (the carrying capacity) at which  $R_t = 0$  (Fig. 1). The population density  $K$  represents the density at which the needs of all the members of the population density are precisely met. Thus, the carrying capacity acts as an attractor towards which the population density is drawn (Morin, 1999). The goodness of fit in equation (5) is given by the coefficient of determination  $r^2$ , in which  $0 < r^2 < 1$ . This coefficient indicates the strength of the linear association and the percentage of the data close to the line of best fit. If, for example,  $r^2 = 0.75$ , then 75% of the total variation in  $R$  is explained by the linear relationship between  $N_t$  and  $R_t$ . The remaining 25% of the variation in  $R$  is unexplained. Analysis of variance (ANOVA) determines whether the variables  $R_t$  and  $N_t$  are sufficient to explain the values of  $R_m$  and  $s$  obtained. In populations with cyclical fluctuations in population density, higher values of  $r^2$  and significant results from ANOVA are obtained by graphing  $R_t = R_m - sN_t$  at the lag of the feedback mechanism, whether it is  $N_{t+2}$ ,  $N_{t+3}$ , etc. (Berryman et al., 1987).

Setting  $R_t = 0$  in equation (5), such that  $N_t = K$  and  $R_m - sK = 0$ , it follows that

$$K = R_m / s. \quad (6)$$



**Fig. 1.** Graph showing the determination of the maximum per capita rate of population density increase ( $R_m$ ) and carrying capacity  $K$  from the linear regression of  $R_t = R_m - sN_t$  where  $R_t$  measured the per capita rate or reproduction at time  $t$  and the slope  $s$  measures the strength of interaction between individuals. The per capita rate of reproduction  $R_t$  may be positive, zero or negative.

Thus,  $K$  can be readily determined after conducting the linear regression in equation (5) and substituting  $R_m$  and  $s$  into equation (6).

### Seasonal environments

Aseasonal environments are likely to be rare. For example, Tedesco & Thunell (2003) and Wilson (2010) detected seasonality among planktonic and nearshore benthonic foraminiferal faunas, respectively, in the tropical Caribbean area, even though temperatures there vary little throughout the year. Gooday (2002) noted that benthonic ecosystems at abyssal depths, where temperatures are virtually constant, are sustained by organic matter (phytodetritus) that settles seasonally from the euphotic zone. Small, opportunistic species, such as *Alabaminella weddellensis* (Earland, 1936) and *Epistominella exigua* (Brady, 1884), exploit this phyto-detrital rain and thus fluctuate seasonally. This section examines means of determining  $K$  in a seasonally variable (phenological) environment.

Population dynamics in a phenological environment constitute chaotic systems in which it is not possible to predict precisely the population density for any month in successive years (Conrad, 1986). Fretwell (1972, fig. 12) has shown, however, that  $K$  varies phenologically, being high ( $K_{\max}$ ) at that time of year when the resource supply in the environment is favourable and low ( $K_{\min}$ ) when it is not (see also Holt, 2008). Hence,  $K_{\max}$  and  $K_{\min}$  act as attractors comparable in form to the Lorenz chaotic attractor (cf. Lü & Chen, 2002, fig. 1; Turchin & Taylor, 1992, fig. 10), with the interaction of  $N_t$ ,  $R_t$  and environmental favourability cycling between  $K_{\max}$  and  $K_{\min}$  over time. To calculate  $K_{\max}$  and  $K_{\min}$ , a seasonally variable time-series must, therefore, be split into two

subsets of data: those occasions (weeks, months) that contribute towards  $K_{\min}$  and those that contribute to  $K_{\max}$ . It is inadvisable to partition the time-series using samples with more or less than the mean population density as the mean is influenced by outliers (Schwerdtfeger, 1941) that greatly reduce the number of sample points contributing to  $K_{\max}$ . The time-series is instead partitioned here using the median population density. Also, given that the population  $N_{t+1}$  shows density dependence on the population density  $N_t$ , it is not possible simply to splice together (albeit in order of time) all population density readings either above or below the median and analyse these as a single time-series using equations (5) and (6). This yields linear regression curves with very low values of  $r^2$  because  $R_t = R_m - sN_t$  is not applicable across the splices. Instead, the longest continuous sets of readings above and below the median must be analysed separately to give estimates of  $K_{\max}$  and  $K_{\min}$ , respectively. This method is demonstrated here using time-series from Murray (1983), Buzas *et al.* (2002) and Horton & Murray (2006).

### MATERIALS AND METHODS

Three time-series are analysed here, each for a different reason. Murray (1983) presented the time-series for monthly population densities for live *Nonion depressulus* (Walker & Jacob, 1798) in the Exe estuary, England, from which he developed equations (1) and (2), and this is reanalysed here for comparison. The monthly study of *Quinqueloculina* spp. in the Indian River Lagoon, Florida by Buzas *et al.* (2002) is included because of the length of the time-series (60 months). In contrast, Horton & Murray (2006) sampled foraminiferal populations in Cowpen Marsh, England, at fortnightly rather than monthly intervals.

Murray (1983) collected two replicate samples with a total volume of 90 ml each month from a tidal pool. Samples were taken from January 1979–July 1981 and the number  $N_t$  of live *N. depressulus* per month was recorded (Murray, 1983, table 2). The median population density was calculated for this time-series and used to extract shorter time-series for which the monthly population density  $N_t$  was greater or lower than the median. For the longest of these shorter time-series the monthly values of per capita  $R_t = (N_{t+1} - N_t) / N_t$  were calculated and linearly regressed against  $N_t$  to give  $R_t = R_m - sN_t$ , and the carrying capacity  $K_{\min}$  and  $K_{\max}$  derived from  $K = R_m / s$ .

Several measures not determined by Berryman & Kindlmann (2008) were calculated. The goodness of fit ( $r^2$ ) of the linear regression was determined, as were the 95% confidence limits for  $R_m$  and  $s$ . ANOVA was computed to determine whether the explanatory variables  $R_t$  and  $N_t$  were sufficient to explain the values of  $R_m$  and  $s$  and accepted as significant where  $p \leq 0.05$ . Substituting the upper and lower confidence limits on  $R_m$  and  $s$  into equation (6) gives possible ranges for  $K_{\min}$  and  $K_{\max}$ .

Buzas *et al.* (2002) collected monthly sediment samples of 80 ml containing *Quinqueloculina* spp. (four replicates of 20 ml each) from Station 3 in the Indian River Lagoon, Florida, to give a five-year time-series that Wilson & Dawe (2006) showed to be seasonal. Carrying capacity strictly counts individuals of a population of a single species, but Buzas *et al.* (2002) combined the *Quinqueloculina* spp. in the Indian River samples into a single test subject. It is possible that closely related species have developed more or less different ecologies so as to avoid direct competition for limited resources (Rockwood, 2006). The time-series of

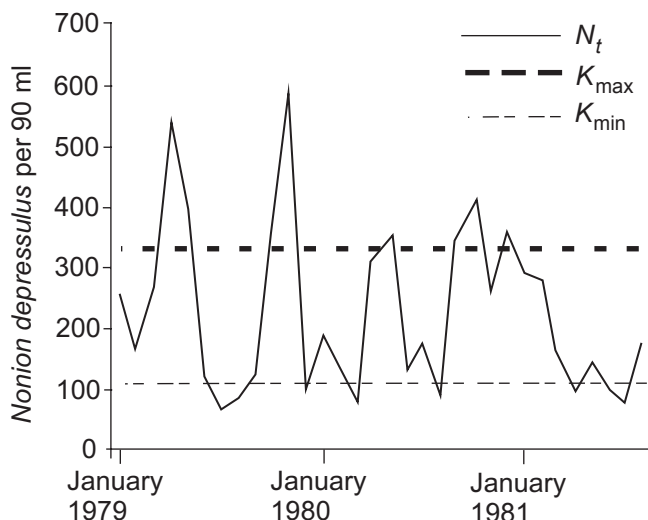


Fig. 2. Time-series of population densities  $N_t$  of *Nonion depressulus* in the Exe estuary, UK. Estimated values of minimum ( $K_{\min}$ ) and maximum ( $K_{\max}$ ) carrying capacities are superimposed across the entire time-series.

Buzas *et al.* (2002) is nevertheless used to demonstrate the technique of calculating  $K$ , in this case for a genus.

Horton & Murray (2006) collected 10 ml samples every two weeks from 31 sites at Cowpen Marsh between 1 May 1995 and 3 May 1996. Replicates were not taken and Stations 28–31 (lowest relative to mean sea-level) were not sampled on each occasion. Horton & Edwards (2006) divided the marsh into upper, middle and lower marsh environments using the relative abundance of *Haynesina germanica* (Ehrenberg, 1840), *Miliammina fusca* (Brady, 1870) and *Jadammina macrescens* (Brady, 1870). Population densities for live *H. germanica* in Stations 15–27 (foraminiferal Zone II of Horton & Edwards, 2006) were grouped as a metapopulation, the population dynamics and carrying capacity of which were analysed.

## RESULTS

### *Nonion depressulus* in the Exe Estuary

The monthly population density of *N. depressulus* in the Exe estuary (the standing crop of Murray, 1983) ranged from 67 to 584 specimens per 90 ml (median 170; Fig. 2). Of 31 monthly readings of population density, fifteen were greater than and fifteen less than 170 foraminifera per 90 ml, while July 1980 had a population density of 170 foraminifera per 90 ml. The longest continual time-series of population densities <170 foraminifera/90 ml comprised five samples only (Table 1). Linear regression of  $R_{t+1}$  against  $N_t$  returned  $R_t = 0.920 - 0.008N_t$  ( $r^2 = 0.493$ ). This equates to a  $K_{\min}$  of 115 *N. depressulus* per 90 ml. However, ANOVA indicated that there was no significant linear relationship  $R_t$  and  $N_t$  ( $F_{(1,2)} = 1.943$ ,  $p = 0.298$ ). Substituting the 95% confidence limits for  $R_m$  and  $s$  into equation (6) gives a range for  $K_{\min}$  of -72 to 251 *N. depressulus* per 90 ml (Table 2a). Negative carrying capacities being an ecological impossibility,  $K_{\min}$  is taken as ranging from 0–251 *N. depressulus* per 90 ml (this rule is applied to subsequent records of negative values for  $K$ ).

The longest continual time-series for *N. depressulus* exceeding the median population density consisted of six samples for which

Table 1. Time-subseries for *Nonion depressulus* population densities ( $N_t$ ) in the Exe Estuary, UK: (a) subseries of continuous population densities lower than the median; (b) subseries of continuous population densities greater than the median.

Date	$N_t$	$R_t$
(a) $N_t < \text{median}$		
March 1981	164	-0.35976
April 1981	105	0.31429
May 1981	138	-0.17391
June 1981	114	-0.28070
July 1981	82	n/a
(b) $N_t > \text{median}$		
September 1980	341	0.20235
October 1980	410	-0.36098
November 1980	262	0.35115
December 1980	354	-0.17514
January 1981	292	-0.04110
February 1981	280	n/a

n/a, not applicable.

linear regression of  $R_{t+1}$  against  $N_t$  returned  $R_t = 1.336 - 0.004N_t$  ( $r^2 = 0.659$ ), which indicates  $K_{\max}$  of 334 *N. depressulus* per 90 ml. However, ANOVA indicated that there was no significant linear relationship  $R_t$  and  $N_t$  ( $F_{(1,3)} = 5.744$ ,  $p = 0.096$ ) while the 95% confidence limits for  $R_m$  and  $s$  indicate that  $K_{\max}$  lies somewhere between 0 and 2368 *N. depressulus* per 90 ml.

### *Quinqueloculina* spp. in the Indian River Lagoon

The monthly population densities of *Quinqueloculina* at Station 3 in the Indian River Lagoon ranged between 91 and 3517 specimens per 80 ml of sediment (median 653; Fig. 3). Of the 60 monthly samples, the 30 with a lower than median population density contained only four short continual time-subseries, each of four months (Table 3). The linear regressions from these suggested values of  $K_{\min}$  of 262–10 487 *Quinqueloculina* per 80 ml. However, ANOVA showed a significant linear relationship between  $R_t$  and  $N_t$  for only for one of these subseries (January–April 1996;  $F_{(1,1)} = 263.2$ ,  $p = 0.039$ ). Substituting the 95% confidence limits for  $R_m$  and  $s$  for all four subseries in equation (6) suggested  $K_{\min}$  to range from 0–10 487 specimens per 80 ml (Table 2b).

The longest subseries for *Quinqueloculina* spp. with population densities greater than the median consisted of seven samples (May–November 1996) for which  $R_t = 1.015 - 0.001N_t$  ( $r^2 = 0.46$ ), which equates to a  $K_{\max}$  of 2011 *Quinqueloculina* per 160 ml. However, ANOVA did not indicate a significant linear relationship between  $R_t$  and  $N_t$  ( $F_{(1,4)} = 3.40$ ;  $p = 0.139$ ). Substituting the 95% confidence limits for  $R_m$  and  $s$  into equation (6) indicates that  $K_{\max}$  probably lies between 0 and 9457 *Quinqueloculina* per 80 ml.

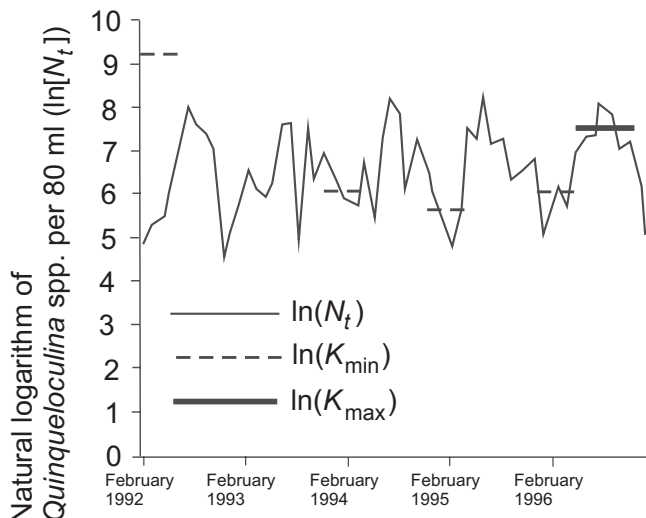
### *Haynesina germanica* in Cowpen Marsh

#### Foraminiferal Zone II

Of the 25 samples in this time-series, the longest subseries with lower than the median population density of 528 specimens per 130 ml of sediment contained five samples only

**Table 2.** Intercept  $R_m$  and slope  $s$  from linear regression  $R_t = R_m - sN_t$  and estimated minimum ( $K_{min}$ ) and maximum ( $K_{max}$ ) carrying capacities for time-subseries for selected foraminifera in seasonal environments: (a) *Nonion depressulus* in Exe Estuary; (b) *Quinqueloculina* spp. in Indian River lagoon, Florida, USA ( $K_{min}$  1–4 = four subseries of four samples each); (c) *Haynesina germanica* in lower Cowpen Marsh, UK, with  $K_{max}$  calculated at lags of  $N_{t+1}$  and  $N_{t+3}$ .

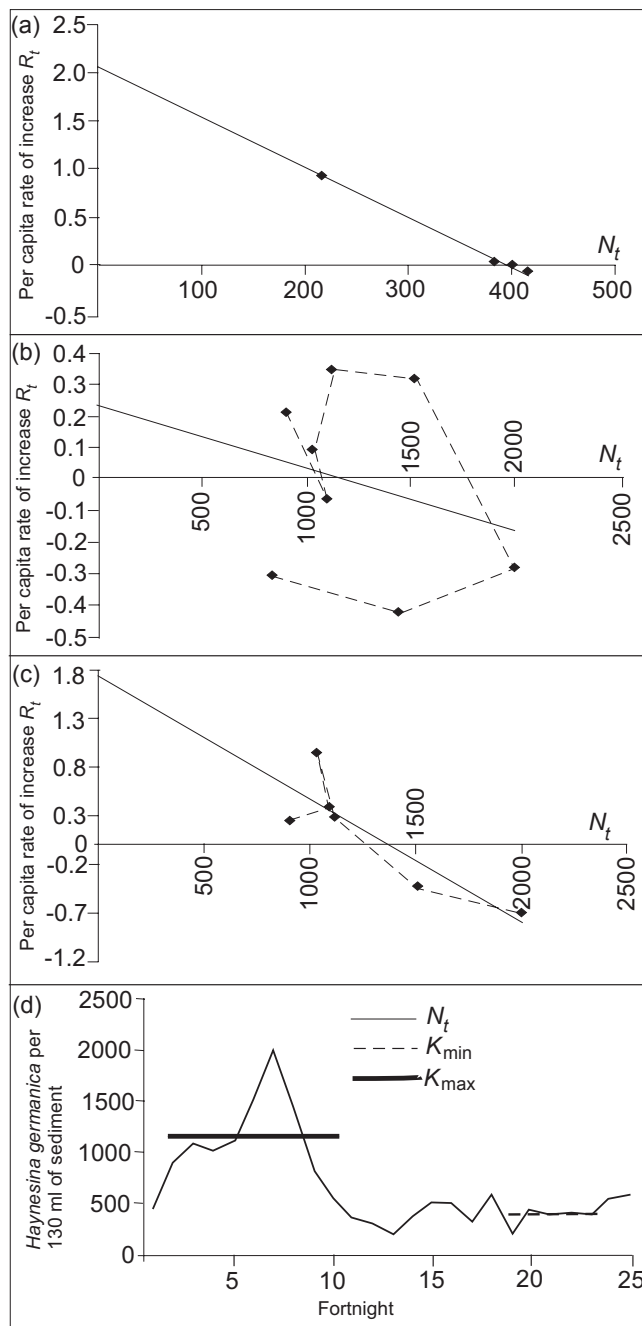
Time-series	Carrying capacity	Measure	Value	Lower bound (95%)	Upper bound (95%)	
(a) Murray (1983), <i>Nonion depressulus</i> in the Exe Estuary	$K_{min}$	$R_m$	0.921	-2.356	4.198	
		$s$	-0.008	-0.033	0.017	
	$K_{max}$	$K_{min}$	115	-72	251	
		$R_m$	1.336	-0.465	3.137	
		$s$	-0.004	-0.009	0.001	
		$K_{max}$	331	-49	2368	
(b) Buzas <i>et al.</i> (2002), <i>Quinqueloculina</i> in the Indian River Lagoon	$K_{min}$ 1	$R_m$	0.48	-7.064	8.025	
		$s$	0.00005	-0.038	0.038	
	$K_{min}$ 2	$K_{min}$ 1	10487	-184	210	
		$R_m$	0.509	-15.056	16.074	
	$K_{min}$ 3	$s$	0.0012	-0.033	0.030	
		$K_{min}$ 2	436	-462	531	
	$K_{min}$ 4	$R_m$	1.348	-11.852	14.549	
		$s$	-0.005	-0.053	0.043	
	$K_{max}$	$K_{min}$ 3	262	-222	338	
		$R_m$	2.153	0.677	3.629	
	(c) Horton & Murray (2006), <i>Haynesina germanica</i> in Cowpen Marsh	$K_{min}$	$s$	-0.005	-0.009	-0.001
			$K_{min}$ 4	412	73	3202
		$K_{max}$	$R_m$	1.015	-0.379	2.409
			$s$	-0.001	-0.001	0.000
		$K_{max}$ at $N_{t+1}$	$K_{max}$	2012	-300	9457
			$R_m$	2.017	1.78	2.252
		$K_{max}$ at $N_{t+3}$	$s$	-0.0051	-0.00572	-0.00442
			$K_{min}$	398	312	510
$K_{max}$ at $N_{t+3}$		$R_m$	0.231	-0.738	1.201	
		$s$	-0.0002	-0.00095	0.00055	
$K_{max}$ at $N_{t+3}$		$K_{max}$	1180	-781	2170	
		$R_m$	1.735	0.358	3.112	
$K_{max}$ at $N_{t+3}$		$s$	-0.0013	-0.0023	-0.00023	
		$K_{max}$	1368	155	13 317	



**Fig. 3.** Time-series of population densities  $N_t$  of *Quinqueloculina* spp. in the Indian River Lagoon, Florida, USA. The four estimated values of minimum ( $K_{min}$ ) and the one of maximum ( $K_{max}$ ) carrying capacities are superimposed only in the vicinity of the samples used to determine them. Population densities have been plotted as natural logarithms due to the wide range of values.

(18 February–4 April 1996; Table 4). Linear regression of  $R_t$  against  $N_t$  gave  $R_t = 2.017 - 0.005N_t$  ( $r^2 = 0.998$ ), indicative of a  $K_{min}$  of 398 *H. germanica* per 130 ml (Fig. 4a). ANOVA indicated a significant linear relationship between  $R_t$  and  $N_t$  ( $F_{(1,2)} = 1130.8, p = 0.001$ ), while substituting the 95% confidence limits for  $R_m$  and  $s$  into equation (6) indicates that  $K_{min}$  probably lies between 312 and 510 *H. germanica* per 130 ml (Table 2c).

The longest subseries with a greater than median density consisted of nine samples (14 May–9 September 1995) for which linear regression of  $R_t$  against  $N_t$  at a lag of  $t+1$  gave  $R_t = 0.231 - 0.00019N_t$  ( $r^2 = 0.064$ ). The graph of  $R_t$  against  $N_t$  at a lag of  $t+1$  is indicative of cyclical population dynamics (Fig. 4b). Linear regression of  $R_t$  against  $N_t$  at a lag of  $t+3$  gave a much better fit ( $R_t = 1.735 - 0.0013N_t, r^2 = 0.743, K = 1348$  *H. germanica* per 130 ml; Fig. 4c) for which ANOVA indicated a significant linear relationship between  $R_t$  and  $N_t$  ( $F_{(1,4)} = 11.59, p = 0.027$ ) and for which substituting the 95% confidence limits for  $R_m$  and  $s$  into equation (6) indicates that  $K_{max}$  lay somewhere between 156 and 13 317 *H. germanica* per 130 ml. It is inferred from this that negative feedback between May and September acted on the population with a delay of six weeks (Fig. 4d).



**Fig. 4.** Determining the maximum and minimum carrying capacities for *Haynesina germanica* in the lower Cowpen Marsh, UK. (a) Linear regression of  $R_t = R_m - sN_t$  for a subseries of four samples with a lower than median population density  $N_t$ . (b) Linear regression of  $R_t = R_m - sN_t$  for a subseries of eight samples with a greater than median population density  $N_t$  at a lag of  $t+1$ , showing evidence of cyclical population dynamics. (c) As (b), but plotted at a lag of  $t+3$ . (d) Time-series of population densities  $N_t$  of *H. germanica* in Lower Cowpen Marsh, UK. The estimated values of minimum ( $K_{\min}$ ) and maximum ( $K_{\max}$ ) carrying capacities are superimposed only in the vicinity of the samples used to determine them.

## DISCUSSION

McLeod (1997) used the concept of carrying capacity  $K$  to estimate potential, short-term yields of red kangaroos that could be

**Table 3.** Time-subseries for *Quinqueloculina* spp. population densities ( $N_t$ ) in the Indian River Lagoon, Florida, USA: (a–d) subseries of continuous population densities lower than the median; (e) subseries of continuous population densities greater than the median.

Date	$N_t$	$R_t$
<b>(a) <math>N_t &lt; \text{median}</math> (1)</b>		
February 1992	126	0.56349
March 1992	197	0.25888
April 1992	248	0.59274
May 1992	395	n/a
<b>(b) <math>N_t &lt; \text{median}</math> (2)</b>		
December 1993	494	0.13765
January 1994	562	-0.25623
February 1994	418	-0.07656
March 1994	386	n/a
<b>(c) <math>N_t &lt; \text{median}</math> (3)</b>		
December 1994	385	-0.35065
January 1995	250	-0.51200
February 1995	122	1.01639
March 1995	246	n/a
<b>(d) <math>N_t &lt; \text{median}</math> (4)</b>		
January 1996	176	1.22159
February 1996	391	0.16113
March 1996	454	-0.25991
April 1996	336	n/a
<b>(e) <math>N_t &gt; \text{median}</math></b>		
May 1996	985	0.64873
June 1996	1624	-0.07081
July 1996	1509	0.83830
August 1996	2774	-0.17628
September 1996	2285	-0.47921
October 1996	1190	0.09916
November 1996	1308	n/a

n/a, not applicable.

harvested from semi-arid shrub-land in SE Australia. Goss-Custard *et al.* (2002) used it to argue that, because migratory birds frequently starve or emigrate well before  $K$  is reached, it is unsafe to propose that a change in site management would not affect birds. Gregr *et al.* (2008) used it to estimate the target population for sea otter recovery around British Columbia. Thus,  $K$  has been widely used by ecologists working with large, multicellular organisms. Foraminifera differ from kangaroos, migratory birds and sea otters not only in size but also in being polyvoltine (they reproduce several times each year; Murray, 1983) and in having short life spans that make them ideal for environmental monitoring (Murray, 2000; 2006; Schafer, 2000; Barbieri *et al.*, 2006). Although polyvoltine (Ernst *et al.*, 2006) and univoltine (Piatt *et al.*, 1990) taxa both are impacted rapidly by environmental catastrophes, populations of univoltine organisms require much time to recover (Monson *et al.*, 2000) whereas polyvoltine foraminifera recover relatively quickly (Schafer, 1982; Ellison & Peck, 1983). This rapid recovery gives foraminifera an advantage over univoltine organisms as a tool for assessing environmental impacts. Accurate knowledge of carrying capacity  $K$  is required,

**Table 4.** Time-subseries for *Haynesina germanica* population densities ( $N_t$ ) in lower Cowpen Marsh, UK: (a) subseries of continuous population densities lower than the median; (b) subseries of continuous population densities greater than the median,  $R_t$  calculated using  $N_t$  and  $N_{t+1}$ ; (c) subseries of continuous population densities greater than the median,  $R_t$  calculated using  $N_t$  and  $N_{t+3}$ .

Date	$N_t$	$R_t$
<b>(a) <math>N_t &lt; \text{median}</math></b>		
18 February 1996	216	0.925926
5 March 1996	416	-0.07692
19 March 1996	384	0.041667
4 April 1996	400	0
17 April 1996	400	n/a
<b>(b) <math>N_t &gt; \text{median} (t+1)</math></b>		
14 May 1995	904	0.212389
1 June 1995	1096	-0.06204
12 June 1995	1028	0.093385
28 June 1995	1124	0.346975
12 July 1995	1514	0.321004
27 July 1995	2000	-0.28
10 August 1995	1440	-0.42222
26 August 1995	832	-0.30769
9 September 1995	576	n/a
<b>(c) <math>N_t &gt; \text{median} (t+3)</math></b>		
14 May 1995	904	0.243363
1 June 1995	1096	0.381387
12 June 1995	1028	0.945525
28 June 1995	1124	0.281139
12 July 1995	1514	-0.45046
27 July 1995	2000	-0.712
10 August 1995	1440	n/a
26 August 1995	832	n/a
9 September 1995	576	n/a

n/a, not applicable.

however, if foraminifera are to be used to their full potential in environmental monitoring and disaster mitigation.

Interpretation of population density time-series from foraminifera in the wild may, however, be made problematic by biotic interactions. For example, Buzas *et al.* (1977) suggested that, in some tropical environments at least, changes in species densities are regulated biotically. Biotic interactions, such as interspecific competition and cropping of foraminifera by predators (Buzas, 1978; Buzas & Severin, 1982), can greatly affect densities and in some cases overwhelm environmental influences. Nevertheless, ecologists continue to calculate carrying capacity  $K$  from time-series.

This paper examined three foraminiferal time-series (Murray, 1983; Buzas *et al.*, 2002, Station 3; Horton & Murray, 2006) from environments known to be seasonal. Whereas samples were taken monthly by Murray (1983) and Buzas *et al.* (2002), the latter comprising one of the longest foraminiferal time-series published, Horton & Murray (2006) collected samples fortnightly. All three time-series showed what Price (1999) called a boom-and-bust pattern, which is typical of species having members with life spans shorter than the duration of phenological environmental fluctuations. Such species are typically small organisms that produce many offspring, rely on the probability that only a few of their

offspring will survive to reproduce and do little to enhance their offspring's chance of survival.

No matter what their length, the three foraminiferal time-series contained only short subseries with population densities greater or lower than the median. Linear regression of  $R_t$  against  $N_t$  for these short subseries for *N. depressulus* and *Quinqueloculina* spp. did not estimate  $K_{\min}$  and  $K_{\max}$  reliably or distinguish between them, there being much overlap of the 95% confidence intervals for  $R_m$  and  $s$ . One estimate of  $K_{\min}$  for *N. depressulus* exceeded that for  $K_{\max}$ . Murray (1991, p. 39) discussed the carrying capacity of *N. depressulus* but assumed that the maximum standing crops were the carrying capacities (410–584 per 90 cm<sup>2</sup>). Thus, the observed densities of *N. depressulus* are much smaller than the calculated  $K_{\max}$  (2368 individuals). This probably arose from the time-subseries containing so few samples that the signal was temporally aliased (cf. Hayek & Buzas, 2010) and so failed to sample all fluctuations in  $N_t$  adequately (cf. Weedon, 2005). The subseries for *H. germanica*, in comparison, showed significant linear relationships between  $R_t$  and  $N_t$  and high values of  $r^2$ , despite containing about the same number of samples as the subseries for *N. depressulus* and *Quinqueloculina* spp. There was nevertheless some overlap between the potential values of  $K_{\min}$  and  $K_{\max}$  for *H. germanica*.

If  $K_{\min}$  and  $K_{\max}$  for foraminiferal population densities are to be used in environmental monitoring, then some means must be found to increase the values of  $r^2$  and narrow the confidence intervals for  $R_m$  and  $s$ . Wilson & Dawe (2006) grouped the data for *Quinqueloculina* spp. for Stations 1–3 (12 replicate samples of 20 ml each) of Buzas *et al.* (2002) to produce a metapopulation that they analysed for seasonality. Carrying capacities for subseries for this metapopulation (analyses of which are not presented here) had lower values of  $r^2$  and wider confidence intervals for  $R_m$  and  $s$  than did the subseries from Station 3 alone. This indicates that increasing the number of replicate samples over a wide geographical area in an attempt to overcome patchiness does not improve the estimates of  $R_m$ ,  $s$ ,  $K_{\min}$  and  $K_{\max}$ . Instead, it seems from analysis of *H. germanica* that replicate samples must be collected at more frequent (fortnightly, weekly) intervals. It is noted, however, that many replicate (i.e. foraminiferal Zone II) samples were used to develop the *H. germanica* time-series, so further work is required to ascertain if more frequent sampling or the taking of a greater number of geographically closely spaced replicates is needed for the reliable estimation of carrying capacity.

Calculating  $K$  using the method described yields information regarding two other factors: the maximum per capita rate of reproduction  $R_m$  and the strength of interaction between individuals in the population  $s$ . Monitoring  $R_m$  and  $K$  over time will indicate changes in the favourability of the environment for the species in question (Berryman & Kindlmann, 2008, fig. 3.8), whether phonologically induced or longer term due to anthropogenic effects.

## CONCLUSIONS

The concept of the carrying capacity  $K$  of a population is central to the study of population dynamics and has an advantage over the concept of sustainability in that it can be quantified (Sayre, 2008). Carrying capacities for many organisms are known to be adversely affected by anthropogenic impacts and there is no reason why foraminifera should react differently. In seasonal

environments,  $K$  for many species varies phenologically. This paper shows that foraminiferal carrying capacities vary likewise and that minimum and maximum carrying capacities ( $K_{\min}$  and  $K_{\max}$ , respectively) can be readily calculated from time-series of foraminiferal population densities. However, the precision with which they can be calculated depends on the quality of the time series. Further work is required to see if the quality is improved by collecting a large number of replicates or frequent (weekly, fortnightly) samples of relatively few replicates. Armed with this knowledge, foraminiferal workers will be able to contribute significantly to environmental impact assessments. They will, in particular, be able to detect recovery (or lack thereof) from adverse environmental impacts much more quickly than those working with longer-lived organisms.

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#### REFERENCES

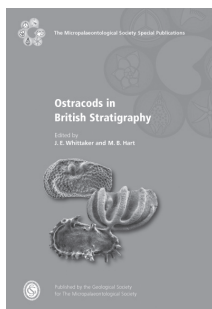
- Alve, E. 1995. Benthic foraminiferal responses to estuarine pollution: A review. *Journal of Foraminiferal Research*, **25**: 190–203.
- Alve, E. 1999. Colonization of new habitats by benthic foraminifera: a review. *Earth-Science Reviews*, **46**: 167–185.
- Bandy, O.L., Ingle, J.C. & Resig, J.M. 1965. Foraminiferal trends, Hyperion Outfall, California. *Limnology and Oceanography*, **10**: 314–332.
- Barbieri, R., Hohenegger, J. & Pugliese, N. 2006. Foraminifera and environmental micropaleontology. *Marine Micropaleontology*, **61**: 1–3.
- Basson, P.W. & Murray, J.W. 1995. Temporal variations in four species of intertidal foraminifera, Bahrain, Arabian Gulf. *Micropaleontology*, **41**: 69–76.
- Berryman, A.A. 1999. *Principles of Population Dynamics and their Application*. Stanley Thornes Publishers, Cheltenham, UK, 243pp.
- Berryman, A.A. & Kindlmann, P. 2008. *Population Systems: A General Introduction*. Springer-Verlag, New York, 222pp.
- Berryman, A.A., Stenseth, N.C. & Isaev, A.S. 1987. Natural regulation of herbivorous forest insect populations. *Oecologia*, **71**: 174–184.
- Boltovskoy, E. & Lena, H. 1969. Seasonal occurrences, standing crop and production in benthic foraminifera of Puerto Deseado. *Contributions from the Cushman Foundation for Foraminiferal Research*, **20**: 87–95.
- Buzas, M.A. 1978. Foraminifera as prey for benthic deposit feeders: results of predator exclusion experiments. *Journal of Marine Research*, **36**: 617–625.
- Buzas, M.A. & Severin, K.P. 1982. Distribution and systematics of foraminifera in the Indian River, Florida. *Smithsonian Contributions to the Marine Sciences*, **16**: 1–73.
- Buzas, M.A., Smith, R.K. & Beem, K.A. 1977. Ecology and systematics of foraminifera in two *Thalassia* habitats, Jamaica, West Indies. *Smithsonian Contributions to Paleobiology*, **31**: 1–139.
- Buzas, M.A., Hayek, L.-A.C., Reed, S.A. & Jett, J.A. 2002. Foraminiferal densities over five years in the Indian River lagoon, Florida: A model of pulsating patches. *Journal of Foraminiferal Research*, **32**: 68–92.
- Conrad, M. 1986. What is the use of chaos? In Holden, R.V. (Ed.), *Chaos*. Princeton University Press, Princeton, New Jersey, 3–14.
- Ellison, R.L. & Peck, G.E. 1983. Foraminiferal recolonization on the continental shelf. *Journal of Foraminiferal Research*, **13**: 231–241.
- Ernst, S.R., Morvan, J., Geslin, E., Le Bihan, A. & Jorissen, F.J. 2006. Benthic foraminiferal response to experimentally induced Erika oil pollution. *Marine Micropaleontology*, **61**: 76–93.
- Errington, P.L. 1934. Vulnerability of bob-white populations to predation. *Ecology*, **15**: 110–127.
- Fretwell, S.D. 1972. *Populations in a Seasonal Environment*. Princeton University Press, Princeton, New Jersey, 217pp.
- Genkai-Kato, M. 2007. Regime shifts: catastrophic responses of ecosystems to human impacts. *Ecological Research*, **22**: 214–219.
- Gooday, A.J. 2002. Biological responses to seasonally varying fluxes of organic matter to the ocean floor: A review. *Journal of Oceanography*, **58**: 305–322.
- Goss-Custard, J.D., Stillman, R.A., West, A.D., Caldow, R.W.G. & McGrorty, S. 2002. Carrying capacity in overwintering migratory birds. *Biological Conservation*, **105**: 27–41.
- Gregg, E.J., Nichol, L.M., Watson, J.C., Ford, J.K.B. & Ellis, G.M. 2008. Estimating carrying capacity for sea otters in British Columbia. *Journal of Wildlife Management*, **72**: 382–388.
- Hayek, L.-A.C. & Buzas, M.A. 2010. *Surveying Natural Populations: Quantitative Tools for Assessing Biodiversity*. Columbia University Press, New York, 590pp.
- Hohenegger, J. 2004. Depth coenoclines and environmental considerations of western Pacific larger foraminifera. *Journal of Foraminiferal Research*, **34**: 9–33.
- Holt, R.D. 2008. Habitats and seasons. *Israel Journal of Ecology and Evolution*, **54**: 279–285.
- Horton, B.P. & Edwards, J.C. 2006. Quantifying Holocene sea-level change using intertidal foraminifera: Lessons from the British Isles. *Cushman Foundation for Foraminiferal Research, Special Publication*, **40**: 1–97.
- Horton, B.P. & Murray, J.W. 2006. Patterns in cumulative increase in live and dead species from foraminiferal time-series of Cowpen Marsh, Tees Estuary, UK: implications for sea-level studies. *Marine Micropaleontology*, **58**: 287–315.
- Kashiwai, M. 1995. History of carrying capacity concept as an index of ecosystem productivity (review). *Bulletin of the Hokkaido National Fisheries Research Institute*, **59**: 81–101.
- Lee, J.J. & Muller, W.A. 1973. Trophic dynamics and niches of salt marsh foraminifera. *American Zoologist*, **13**: 215–223.
- Levin, S.A., Carpenter, S.R., Godfray, H.C. J. et al. 2009. *The Princeton Guide to Ecology*. Princeton University Press Princeton, New Jersey, 848pp.
- Lü, J. & Chen, G. 2002. A new chaotic attractor coined. *International Journal of Bifurcation and Chaos*, **12**: 659–661.
- Malthus, T.R. 1798. *An essay on the principle of population, as it affects the future improvement of society with remarks on the speculations of Mr. Godwin, M. Condorcet, and other writers*. J. Johnson in St. Paul's Church-Yard, London, UK, 125pp.
- McLeod, S.R. 1997. Is the concept of carrying capacity useful in variable environments? *Oikos*, **79**: 529–542.
- Monson, D.H., Doak, D.F., Ballachey, B.E., Johnson, A. & Bodkin, J.L. 2000. Long-term impacts of the Exxon Valdez oil spill on sea otters, assessed through age-dependent mortality patterns. *Proceedings of the National Academy of Science, USA*, **97**: 6562–6567.
- Monte-Luna, P.d., Brook, B.W., Zetina-Rejón, M.J. & Cruz-Escalona, V.H. 2004. The carrying capacity of ecosystems. *Global Ecology and Biogeography*, **13**: 485–495.
- Morin, P.J. 1999. *Community Ecology*. Blackwell Science, Malden, Massachusetts, 432pp.



- Murray, J.W. 1967. Production in benthic foraminiferids. *Journal of Natural History*, **1**: 61–68.
- Murray, J.W. 1983. Population dynamics of benthic foraminifera; results from the Exe Estuary, England. *Journal of Foraminiferal Research*, **13**: 1–12.
- Murray, J.W. 1991. *Ecology and Palaeoecology of Benthic Foraminifera*. Longman, Harlow, UK, 397pp.
- Murray, J.W. 2000. When does environmental variability become environmental change? The proxy record of benthic foraminifera. In Martin, R.E. (Ed.), *Environmental Micropaleontology: Topics in Geobiology*. Kluwer Academic/Plenum Publishers, New York, 7–37.
- Murray, J.W. 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press, Cambridge, UK, 438pp.
- Nigam, R. 2005. Addressing environmental issues through foraminifera – case studies from the Arabian Sea. *Journal of the Palaeontological Society of India*, **50**: 25–36.
- Nigam, R., Saraswat, R. & Panchang, R. 2006. Application of foraminifera in ecotoxicology: Retrospect, prospect and prospect. *Environment International*, **32**: 273–283.
- Nigam, R., Linshy, V.N., Kurtarkar, S.R. & Saraswat, R. 2009. Effects of sudden stress due to heavy metal mercury on benthic foraminifer *Rosalina leei*: Laboratory culture experiment. *Marine Pollution Bulletin*, **59**: 362–368.
- Peterman, R.M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. *Journal of the Fisheries Research Board of Canada*, **24**: 1130–1142.
- Piatt, J.F., Lensink, C.J., Butler, W., Kendziorek, M. & Nysewander, D.R. 1990. Immediate impact of the 'Exxon Valdez' oil spill on marine birds. *The Auk*, **107**: 387–397.
- Price, D. 1999. Carrying capacity reconsidered. *Population and Environment*, **21**: 5–26.
- Rockwood, L.L. 2006. *Introduction to Population Ecology*. Blackwell Publishing, Oxford, UK, 352pp.
- Sayre, N.F. 2008. The genesis, history, and limits of carrying capacity. *Annals of the Association of American Geographers*, **98**: 120–134.
- Schafer, C.T. 1982. Foraminiferal colonization of an offshore dump site in Chaleur Bay, New Brunswick, Canada. *Journal of Foraminiferal Research*, **12**: 317–326.
- Schafer, C.T. 2000. Monitoring nearshore marine environments using benthic foraminifera: Some protocols and pitfalls. *Micropaleontology*, **46**: 161–169.
- Schwerdtfeger, F. 1941. Über die Ursachen des Massenwechsels der Insekten. *Zeitschrift für Angewandte Entomologie*, **28**: 254–303.
- Scott, D.B., Medioli, F.S. & Schafer, C.T. 2001. *Monitoring of Coastal environments using Foraminifera and Thecamoebian indicators*. Cambridge University Press, Cambridge, UK, 192pp.
- Tedesco, K.A. & Thunell, R.C. 2003. Seasonal and interannual variations in planktonic foraminiferal flux and assemblage composition in the Cariaco Basin, Venezuela. *Journal of Foraminiferal Research*, **33**: 192–210.
- Turchin, P. 2003. *Complex Population Dynamics: A Theoretical/Empirical Synthesis*. Princeton University Press, Princeton, New Jersey, 466pp.
- Turchin, P. & Taylor, A.D. 1992. Complex dynamics in ecological time series. *Ecology*, **73**: 289–305.
- Wang, X. 2010. Research review of the ecological carrying capacity. *Journal of Sustainable Development*, **3**: 263–265.
- Weedon, G.G. 2005. *Time-Series Analysis and Cyclostratigraphy: Examining Stratigraphic Records of Environmental Cycles*. Cambridge University Press, Cambridge, UK, 276pp.
- Wilson, B. 2000. Benthonic foraminifera as a tool in environmental quality control: Two Caribbean examples. In Transactions of the GSTT 2000 SPE Conference and Exhibition, Geological Society of Trinidad and Tobago, Port of Spain, Trinidad (CD-ROM).
- Wilson, B. 2010. Effect of hurricanes on guilds of nearshore epiphytal foraminifera, Nevis, West Indies. *Journal of Foraminiferal Research*, **40**: 327–343.
- Wilson, B. & Dawe, R.A. 2006. Detecting seasonality using time series analysis: Comparing foraminiferal population dynamics with rainfall data. *Journal of Foraminiferal Research*, **36**: 108–115.
- Wilson, B. & Ramsook, A. 2007. Population densities and diversities of epiphytal foraminifera on nearshore substrates, Nevis, West Indies. *Journal of Foraminiferal Research*, **37**: 213–222.



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