Species-specific effects of marine reserves: mortality and growth differ within and among heavily exploited and rarely exploited limpets

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ABSTRACT: The effects of marine reserves on the growth and mortality rates of 2 commonly exploited (*Helcion concolor* and *Scutellastra longicosta*) and 2 rarely exploited (*Cellana capensis* and *Scutellastra granularis*) limpets were investigated at 2 reserve and 2 non-reserve sites in South Africa. Two hypotheses were tested: (1) growth of commonly exploited species would be reduced in reserves due to higher densities and stronger intraspecific competition, with no effect for rarely exploited species; (2) commonly exploited species would show higher mortality rates outside than inside reserves, with no effect for rarely exploited species. Both the exploited *H. concolor* and *C. capensis* (sometimes mistaken for *H. concolor* by harvesters) exhibited faster growth at non-reserve sites where their densities were generally lower. No effect of reserve status was detected for the growth rates of *S. granularis* (rarely exploited) or *S. longicosta* (commonly exploited). *S. longicosta* showed no reserve effect on growth because it is territorial, and density has no effect on territory size. Reserve effects were only observed for the survival probability of *S. longicosta*, the most commonly exploited species, and the probability of capture (but not survival) of the 2 rarely exploited species. The results indicate that the effects of reserves on growth and mortality are species-specific and are difficult to generalize even within the categories of commonly and rarely exploited limpets.

KEY WORDS: *Helcion concolor* · *Cellana capensis* · *Scutellastra longicosta* · *Scutellastra granularis* · Growth rate · Mortality rate

INTRODUCTION

No-take marine reserves are often promoted as an ecosystem-level management tool for exploited species (Pillans et al. 2005). Such reserves prohibit harvesting and potentially offer a way to conserve marine biodiversity whilst at the same time sustaining fisheries (Roberts & Hawkins 1999, Halpern 2003, Lubchenco et al. 2003). Reserves may restore and protect marine resources within their boundaries, particularly the reproductive component, and act as sources of larvae that could eventually settle outside of the reserve (Rakitin & Kramer 1996, Pelc et al. 2009). Although models suggest that this is achievable, the proportional increase in recruitment outside reserves can be difficult to detect in the field (Pelc et al. 2010, Cole et al. 2011) and there is debate about whether marine reserves can benefit fisheries, as well as acting as a conservation tool (Stobutzki 2001, Gaylord et al. 2005, Sale et al. 2005).

Because reserve status will presumably affect mortality rates of target species, this will have implications for their densities and consequently intraspecific competition and growth within reserves.

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Although a degree of illegal poaching has been documented for reserves in our study area, they experience far lower levels of exploitation than unprotected sites, where the number of harvesters interviewed during a separate study ranged between approximately 29 and 48 d^{-1} (M. D. V. Nakin & C. D. McQuaid unpubl. data). Intraspecific competition at increased densities (e.g. within reserves) has been shown to greatly affect the growth and mortality of limpet species (Underwood 1978, Creese & Underwood 1982, Espinosa et al. 2006). In the present study, we tested whether the effects of reserve status override the background factors that affect growth and mortality rates in 4 species of limpets that are exploited to different degrees, including one species that is territorial. Artisanal level exploitation of intertidal species has a long and well-documented history in the Transkei region of South Africa (Hockey & Bosman 1986, Hockey et al. 1988, Dye et al. 1994, Lasiak & Field 1995, Lasiak 1998, 2006), with the primary target organism being the mussel *Perna perna* (Lasiak & Dye 1989). The different exploitation intensities of limpet species in this area can also have knock-on effects for levels of grazing and overall community structure (Jenkins et al. 2005, Coleman et al. 2006). We compared growth and mortality rates of 4 limpet species: *Scutellastra longicosta* (a territorial species that defends gardens of algae against other limpets) and *Helcion concolor* are commonly harvested, while *Cellana capensis* and *S. granularis* are rarely targeted, but are occasionally taken in error, or (rarely) because preferred species are not available. The commonly exploited species show significant differences in densities between reserve and non-reserve sites as does *C. capensis* in some months (M. D. V. Nakin & C. D. McQuaid unpubl. data).

Ignoring human exploitation, mortality is driven by biotic (e.g. food, predators) and/or abiotic (e.g. heat stress, desiccation) conditions that differ markedly spatially (i.e. both among and within sites). The assumption is that the reduction in mortality from harvesting is great enough to be discernible in reserve areas, despite intrinsic differences in background mortality rates. Apart from differences in physical conditions, background drivers of mortality in limpets include predation by a range of animals such as oystercatchers (Bosman et al. 1989, Coleman et al. 1999, Kohler et al. 2009), crabs (Cannicci et al. 2002, Silva et al. 2004) and fish (Lechanteur & Prochazka 2001), and it is possible that human activities may displace some bird predators from exploited shores into less disturbed reserve areas. Similarly, limpet growth rates are influenced by a wide range of factors, including abiotic conditions linked to seasonality and where the animals live (Branch 1981, Creese & Underwood 1982, Underwood 1984), biotic factors such as competition for food (Branch 1976, Jenkins & Hartnoll 2001) and the presence of predators (Akester & Martel 2000), as well as intrinsic factors such as genetic differentiation (Denny & Blanchette 2000, Trussell 2002).

We tested 3 *a priori* hypotheses on growth, based on the assumption that intraspecific competition for food is important. These were that (1) growth rates of rarely exploited species will be the same inside and outside reserves, (2) growth rates of commonly exploited territorial species will be the same inside and outside reserves, and (3) growth rates of exploited non-territorial species will be higher outside reserves than inside reserves due to relaxed intraspecific competition. The second hypothesis was based on the fact that territorial species avoid exploitation competition through interference competition so that species density will have no direct effect on food availability and growth unless it is so great that territories are reduced in size. We also tested 2 hypotheses related to mortality: (1) commonly exploited species will show higher mortality rates outside reserves than inside reserves due to the combined effects of natural and human predation, and (2) rarely exploited species will show no differences in mortality rates inside and outside the reserves.

MATERIALS AND METHODS

Individual tagging

Growth and mortality were estimated from a capture-recapture experiment conducted over a period of 15 mo. At the start of the experiment, approximately 50 individuals of each species were marked in 2 areas within each of 2 reserve (Dwesa and Cwebe) and 2 non-reserve (Nqabara and Xhora) sites (Fig. 1) using non-toxic paint (colour coded to give individual numbers) and numbered bee tags (Opalithplattchen) embedded in a rapidly setting epoxy glue (Lohse 1993, Jenkins & Hartnoll 2001). Each limpet was double-tagged with 2 bee tags that were covered with clear epoxy to minimise abrasion. Limpets were chosen at random from each population. The size spectrum reflected the population structure from the smallest size that could be effectively tagged upwards.

Subsequent length measurements were made *in situ*, without removing the limpets from the substra-
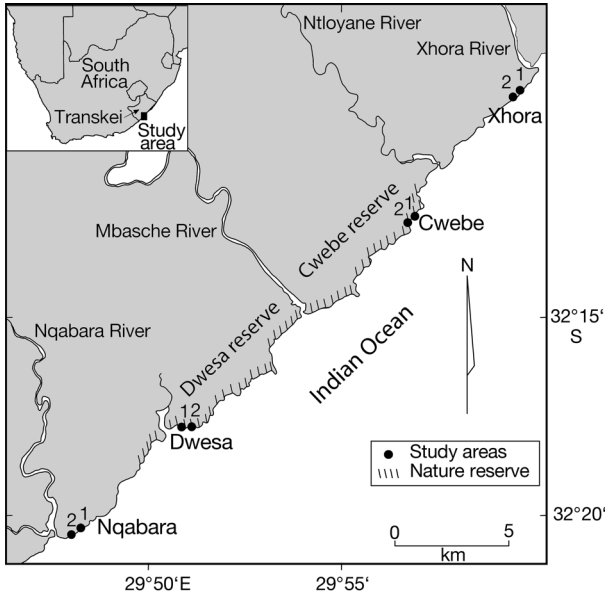
Fig. 1. Location of the 4 study sites (with 2 study areas at each site) on the Transkei coast of South Africa

tum to avoid manipulation stress or mortality. Measurements were taken with a pair of dividers at approximately monthly intervals from February 2003 to June 2004. This method allows rapid *in situ* measurement of a large number of limpets during a low-tide period (Tablado et al. 1994, Clarke et al. 2004). Measurements were later read to the nearest mm, a precision confirmed by direct measurements of limpets with Vernier calipers. Some tags were shed after several months and recovery rates varied among species. Limpets that lost only one tag remained individually identifiable.

Estimation of growth

Annual growth rates were calculated from all recaptured individuals. Growth was estimated from mean monthly growth increments by fitting a modified Von Bertalanffy growth equation (VBGE). In this modelling approach it is assumed that (1) tagged limpets are uniquely and correctly recorded at release and recapture, (2) the lengths of limpets are measured without bias at release and recapture, and (3) a wide range of limpet sizes are represented among the recaptures.

Growth in length, L, as a function of time t was modelled as $L_t = L_\infty (1-e^{-kt})$ where L_∞ is the theoretical asymptotic length and k the rate at which L_t approaches L_∞.

The VBGE is derived from the differential equation

$$\frac{\mathrm{d}L}{\mathrm{d}t} = k(L_\infty - \bar{L}) \qquad (1)$$

where the growth rate $\frac{\mathrm{d}L}{\mathrm{d}t}$ is the change in length corresponding to the period between measurements, and $\bar{L}$ is the mean length between time periods. Maximum likelihood estimates of L_∞ and k for all species S and populations P were estimated simultaneously by non-linear minimisation, a negated, natural logarithm-transformed normal likelihood (LL) of the form:

$$\mathrm{LL} = \sum_{s=1}^{S} \sum_{j=1}^{P} \frac{n_{SP}}{2} \ln \left(\sum_{i=1}^{n_{SP}} \sum_{s=1}^{S} \sum_{j=1}^{P} (O_{isj} - E_{isj})^2 \Big/ \sum_{s=1}^{S} \sum_{j=1}^{P} n_{SP} \right) \quad (2)$$

where O_{isj} and E_{isj} denote the observed and model expected $\frac{\mathrm{d}L}{\mathrm{d}t}$ of individual i of species s in population j, respectively, and n_{SP} is the total number of individuals of species s in population j. All analyses were conducted using AD Model Builder (Otter Research Ltd 2004). Asymptotic estimates of parameter variability were obtained from the inverse Hessian matrix.

The Gallucci-Quinn index (Gallucci & Quinn 1979), $\omega = L_\infty k$, was used to compare growth curves among species and between reserve and non-reserve locations. This index is considered appropriate to compare growth curves as it compares maximal growth rate (ω) when $L \to 0$ (Charnov 2010).

The null hypotheses that L_∞, k and ω were equal across all populations of each species, and the null hypotheses that L_∞, k and ω were equal for reserves and non-reserves were tested using a likelihood ratio test (Hearn & Polacheck 2002). The likelihood ratio test is the ratio of the likelihoods of the reduced and fully parameterized models. The full (saturated) model has all estimated parameters and the reduced model has a subset of the parameters from the full model such that $\Lambda = 2(\mathrm{LL}_{reduced} - \mathrm{LL}_{full})$. This ratio ($\Lambda$) is asymptotically chi-square distributed with the degrees of freedom (ν) being equal to the difference in parameters between the 2 models.

Estimation of mortality rate

At the end of the capture-recapture experiment, a capture history of each animal was constructed. For each sampling occasion, each limpet was given a '1' if it was captured and a '0' otherwise. For instance, in a 3-sample experiment, a limpet with a capture history of '101' denotes that it was captured, tagged and

released at the first sampling occasion, not observed on the second sampling occasion, but recaptured and released on the third sampling occasion.

The Cormack-Jolly-Seber (CJS) model (Pollock et al. 1990) was chosen to estimate the probability of capture and the probability of survival for each sampling occasion for each limpet individual. In the CJS model only apparent survival probability (ϕ) can be estimated such that $1 - \phi$ reflects that a limpet either died or permanently left the population through emigration.

The model assumes that (1) all animals present at time i have the same probability of being captured, (2) all animals present immediately following sample time i have the same probability of surviving to sample time $i + 1$, (3) no tags are lost and all tags are correctly identified, (4) sampling occurs instantaneously and animals are released immediately, (5) emigration from the sample area is permanent, such that emigration is indistinguishable from death, and (6) the survival and capture of an animal is independent of the survival and capture of all other animals.

Maximum likelihood estimates of the probability that a limpet is captured at sampling occasion j, p_j, and the probability that a limpet alive at sampling occasion j survives to sampling occasion $j+1$, ϕ_j, were obtained by minimising the negated multinomial log-likelihood of the form:

$$LL = -\ln\left(\prod_{i=1}^{n_\omega} \chi(l_i) \prod_{j=f_i}^{l_i-1} \phi_j \prod_{j=f_i+1}^{l_i} p_j^{\omega_{ij}} (1-p_j)^{1-\omega_{ij}} \right) \quad (3)$$

where f_i is the first time limpet i was observed, l_i is the last time limpet i was observed, n_ω is all capture histories, ω_{ij} is an indicator variable given a '1' if limpet i was captured at sampling occasion j and a '0' if the limpet was not captured, and χ_j is the probability that a limpet is not observed after time j, given that it was alive at time j such that:

$$\chi_j = \begin{cases} (1-\phi_j)+\phi_j(1-p_{j+1})\chi_{j+1} & \text{if } j < T \\ 1 & \text{if } j = T \end{cases} \quad (4)$$

where T is the total number of sampling occasions.

Four modelling scenarios were compared for each of the 4 species and 4 study sites. These scenarios were based on the different combinations of temporally independent, denoted as ($\cdot$), or temporally dependent, denoted as (t), capture (p) and survival (ϕ) probabilities. The scenarios are therefore summarized as $p(\cdot)\phi(\cdot)$, $p(\cdot)\phi(t)$, $p(t)\phi(\cdot)$ and $p(t)\phi(t)$, respectively. Parameter redundancy was investigated for each model using the Hessian method advocated by Gimenez et al. (2004).

To assist with parameter comparison between species and sites, the temporally independent model is presented for all species. Likelihood ratio tests were conducted to test the null hypotheses that capture probabilities were equal for all populations within each species. The most parsimonious model was identified as the model with the lowest value of Akaike's information criterion (AIC) (Pollock et al. 1990) where AIC = 2(LL + parameters).

RESULTS

Growth

Commonly exploited species

Helcion concolor. An asymptotic length of ~42 mm was attained in their third year at the 2 non-reserve sites, while at the reserve sites growth either became constant (Cwebe) or gradually decreased (Dwesa) after the second year (Fig. 2). The highest and lowest maximum sizes were 43 mm at Xhora and 29 mm at Cwebe (Table 1, Fig. 2). Maximum asymptotic length was smaller in the reserve than the non-reserves sites (Table 2). Maximum growth rate, ω, was generally higher in non-reserve sites, the exception being Cwebe (48.89 mm yr^{-1}) that had an intermediate growth rate between that of Nqabara (35.89 mm yr^{-1}) and Xhora (107.85 mm yr^{-1}). Growth rate can be ranked as: Xhora > Cwebe > Nqabara > Dwesa.

Scutellastra longicosta. Parameter variability was high and resulted in no clear trends being noted for any of the parameters estimated either between reserve and non-reserve sites or within populations (Table 1). The largest sizes were attained at Nqabara, which was significantly different (p < 0.05) from all other sites that were considered to form a statistically homogenous (p > 0.05) group. Growth rates, ranked Dwesa > Xhora > Cwebe > Nqabara, were not found to be statistically different between reserve and non-reserve sites (Table 2).

Rarely exploited species

Cellana capensis. In non-reserve sites, growth rate was found to be statistically different from (p < 0.05), and approximately double, that estimated for the reserve sites (Table 1). The pooled data showed a statistically significant ~50% increase in growth rate (Table 2). Growth rate can be ranked as Nqabara > Xhora > Dwesa > Cwebe. Asymptotic
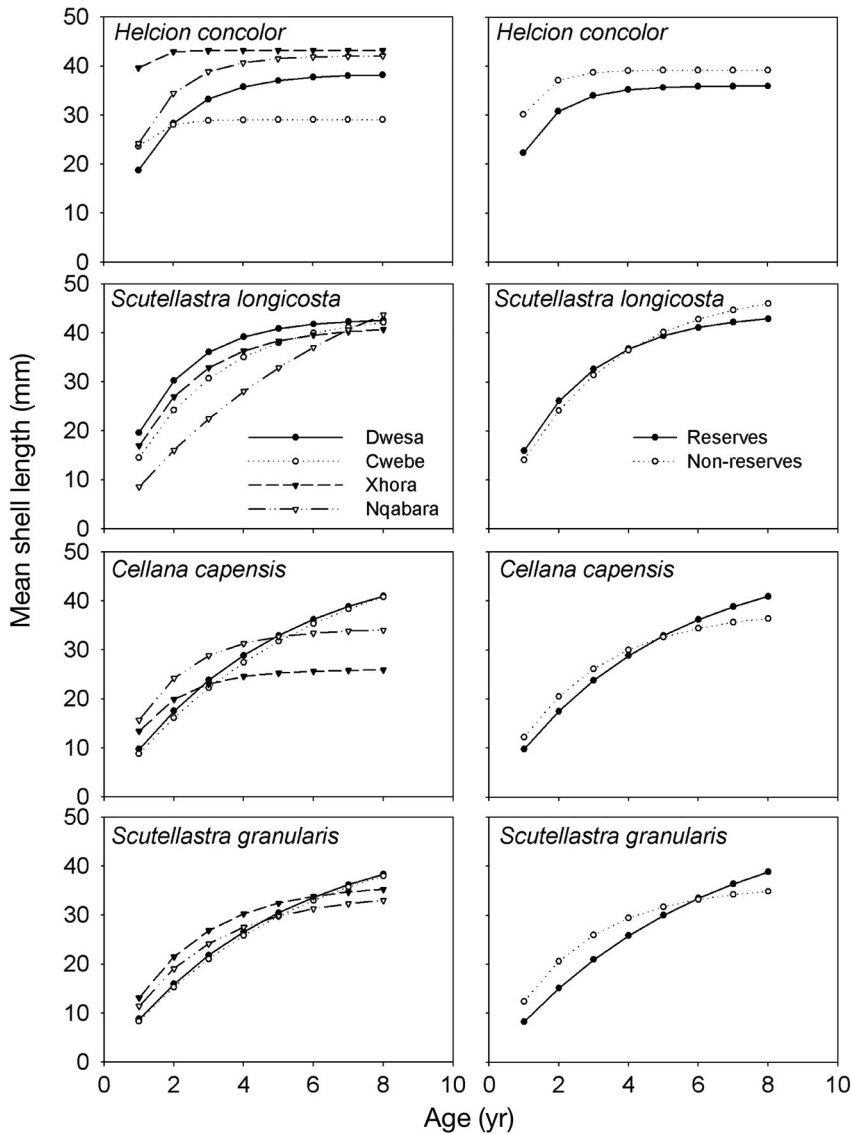
Fig. 2. Model-predicted Von Bertalanffy growth curves of each limpet species obtained from tagging among the 4 sites and within reserve (Dwesa and Cwebe) and non-reserve (Nqabara and Xhora) sites

length was significantly (p < 0.05) greater in reserves (54 mm) than in non-reserves (38 mm), whereas the growth coefficient, k, was lower in reserves (0.18 yr^{-1}) than in non-reserves (0.39 yr^{-1}) (Fig. 2). Thus, this species grew more slowly and reached larger sizes in reserves.

Scutellastra granularis. The trends in all growth parameters were similar to those of *Cellana capensis*, with asymptotic length being larger, but the growth coefficient and maximum growth rate being lower, in reserves compared to non-reserves (Tables 1 & 2, p < 0.05 in all cases). Maximum growth rate for *S. granularis* declined in the order: Xhora > Nqabara > Dwesa

> Cwebe. Asymptotic length, as with *C. capensis*, was reached earlier at the 2 non-reserve sites, Nqabara and Xhora, than at the reserve sites Dwesa and Cwebe, due to the high growth coefficients.

Mortality

Commonly exploited species

Helcion concolor. The model $p(\cdot)\phi(\cdot)$ that assumes constant capture and survival probabilities, was the most parsimonious at Cwebe and Nqabara, while the model $p(\cdot)\phi(t)$, assuming constant capture probability and time dependent survival, was the most parsimonious for Dwesa. No model could be fitted to the Xhora population due to a lack of recaptures (Table 3).

Scutellastra longicosta. At 3 of the 4 sites investigated, the time dependent capture and survival model $p(t)\phi(t)$ was the most parsimonious (Table 3). The model $p(\cdot)\phi(t)$ was the most parsimonious for the Xhora population. There were no significant (p > 0.05) effects of sites or reserve status on capture probability, but survival probability was significantly (p < 0.05) greater at Cwebe and Nqabara than at Dwesa and Xhora (Table 4, Fig. 3).

Rarely exploited species

Cellana capensis. $p(\cdot)\phi(t)$ was the most parsimonious model for all sites (Table 3, Fig. 3). There was no significant effect of site on survival probability (p > 0.05), but capture probabilities differed between Nqabara and both Dwesa and Xhora (Table 4). The lowest capture probabilities were 0.88 ± 0.17 mo^{-1} at Nqabara and 0.93 ± 0.12 mo^{-1} at the other sites.

While reserve sites formed a homogenous group (92 to 93 %, p > 0.05), the group also included Xhora (63 %). Capture probability at Nqabara was slightly, but significantly, lower at 88 %. Reserve status did not affect survival probability (p > 0.05), which was

estimated to range between 0.82 and 0.86 yr^{-1} (Table 4).

Scutellastra granularis. The $p(\cdot)\phi(t)$ model was the most parsimonious for Dwesa, Cwebe and Nqabara, while the time-dependent capture and survival model, $p(t)\phi(t)$, was the most parsimonious for Xhora (Table 3, Fig. 3). Capture probability was ranked Cwebe (1.00 ± 0.01 mo^{-1}) > Dwesa (0.96 ± 0.12 mo^{-1}) = Nqabara (0.96 ± 0.14 mo^{-1}) > Xhora (0.93 ± 0.27 mo^{-1}) and was significantly greater (p < 0.05)

Table 1. Von Bertalanffy growth parameter estimates (mean ± SE) based on tagging of 4 limpet species sampled at 4 sites (status: R = reserve, N = non-reserve). Differences in model parameters, grouped by species, were determined using a likelihood ratio test. Superscripts denote homogenous groups (p > 0.05). The Gallucci-Quinn index is the maximal growth rate $\omega = L_\infty k$ where L_∞ is the theoretical asymptotic length and k is the rate at which L_t (length as a function of time) approaches L_∞

Species Population	Reserve status	L_∞	k	ω	R^2	n
Commonly exploited species						
Helcion concolor						
Dwesa	R	38.39[b] ± 2.47	0.67[d] ± 0.11	25.69[c] ± 3.49	0.82	8
Cwebe	R	29.05[c] ± 1.89	1.68[b] ± 0.24	48.89[b] ± 4.87	0.92	5
Nqabara	N	42.10[a] ± 3.07	0.85[c] ± 0.19	35.89[bc] ± 6.80	0.63	12
Xhora	N	43.19[a] ± 1.38	2.50[ac] ± 0.21	107.85[a] ± 9.10	0.97	4
Scutellastra longicosta						
Dwesa	R	42.89[b] ± 2.77	0.61[a] ± 0.11	26.25[a] ± 3.59	0.55	25
Cwebe	R	43.85[b] ± 5.32	0.40[c] ± 0.11	17.61[a] ± 3.04	0.25	41
Nqabara	N	63.67[a] ± 14.55	0.15[d] ± 0.06	9.24[b] ± 2.09	0.14	33
Xhora	N	41.26[b] ± 12.67	0.53[bc] ± 0.31	21.89[ab] ± 6.54	0.08	32
Rarely exploited species						
Cellana capensis						
Dwesa	R	49.64[b] ± 8.03	0.22[cd] ± 0.07	10.81[a] ± 1.58	0.09	105
Cwebe	R	53.50[a] ± 3.57	0.18[d] ± 0.17	9.61[a] ± 2.66	0.01	95
Nqabara	N	34.30[c] ± 2.51	0.61[b] ± 0.11	20.99[b] ± 2.51	0.28	100
Xhora	N	25.98[d] ± 3.66	0.73[a] ± 0.24	18.90[b] ± 3.80	0.08	76
Scutellastra granularis						
Dwesa	R	47.69[a] ± 4.71	0.20[cd] ± 0.11	9.71[a] ± 2.28	0.05	73
Cwebe	R	48.72[a] ± 20.4	0.19[d] ± 0.12	9.20[a] ± 2.18	0.06	40
Nqabara	N	34.34[c] ± 4.63	0.41[b] ± 0.11	13.94[ab] ± 2.14	0.24	41
Xhora	N	36.26[b] ± 4.91	0.45[a] ± 0.11	16.33[b] ± 1.98	0.27	45

Table 2. Von Bertalanffy growth parameter estimates (mean ± SE) based on tagging of 4 limpet species sampled within reserve and non-reserve sites. Differences in model parameters by species were determined using a likelihood ratio test. Superscripts denote homogenous groups (p > 0.05). The Gallucci-Quinn index is the maximal growth rate $\omega = L_\infty k$ where L_∞ is the theoretical asymptotic length and k is the rate at which L_t (length as a function of time) approaches L_∞

Species Population	L_∞	k	ω	R^2	n
Commonly exploited species					
Helcion concolor					
Reserves	35.94[a] ± 2.30	0.96[a] ± 0.14	34.82[a] ± 3.51	0.8	13
Non-reserves	39.18[a] ± 2.69	1.48[a] ± 0.27	57.51[b] ± 8.97	0.64	16
Scutellastra longicosta					
Reserves	44.11[a] ± 4.05	0.45[a] ± 0.11	19.76[a] ± 2.34	0.32	66
Non-reserves	49.35[a] ± 13,61	0.34[a] ± 0.19	16.61[a] ± 2.25	0.21	65
Rarely exploited species					
Cellana capensis					
Reserves	54.06[a] ± 5.80	0.18[a] ± 0.12	9.81[b] ± 0.98	0.07	200
Non-reserves	38.18[b] ± 3.09	0.39[b] ± 0.18	14.72[a] ± 1.72	0.08	176
Scutellastra granularis					
Reserve	50.01[a] ± 12.50	0.19[a] ± 0.07	9.27[b] ±1.48	0.05	113
Non-reserve	36.07[a] ± 3.66	0.42[b] ± 0.08	15.27[a] ± 1.49	0.24	86

Table 3. Summary of Akaike's information criterion (AIC) statistics with the number of estimated parameters in parentheses, for 4 different mark-recapture models applied to 4 limpet species at 4 localities. The most parsimonious model for each model-species-location combination is underlined, while substantially similar models (Anderson 2007) with an AIC with a difference ≤3 from the most parsimonious model are italicised. p: probability of capture; ϕ: probability of survival. (t) and ($\cdot$): temporally dependent and independent probability parameters, respectively. NP: not possible to estimate parameters as there were no recaptures

Species Population	Model			
	$p(\cdot)\phi(\cdot)$	$p(\cdot)\phi(t)$	$p(t)\phi(\cdot)$	$p(t)\phi(t)$
Helcion concolor				
Dwesa	*78.48* (2)	*76.35* (4)	80.49 (3)	*76.49* (5)
Cwebe	*57.26* (2)	58.89 (5)	59.95 (4)	62.45 (7)
Nqabara	*133.74* (2)	140.16 (10)	139.76 (9)	144.85 (17)
Xhora	NP	NP	NP	NP
Scutellastra longicosta				
Dwesa	250.2 (2)	*243.66* (6)	254.21 (5)	*241.51* (9)
Cwebe	551 (2)	*534.07* (12)	547.1 (11)	*533.48* (21)
Nqabara	389.38 (2)	*350.49* (10)	380.53 (9)	*349.1* (17)
Xhora	316.89 (2)	*303.54* (8)	320.2 (7)	309.72 (13)
Cellana capensis				
Dwesa	815.36 (2)	*782.18* (12)	811.78 (11)	*783.7* (21)
Cwebe	783.7 (2)	*764.04* (13)	791.79 (12)	772.83 (23)
Nqabara	745.7 (2)	*738.2* (14)	753.94 (13)	745.91 (25)
Xhora	754.19 (2)	*706.5* (13)	744.4 (12)	*707.9* (23)
Scutellastra granularis				
Dwesa	524.11 (2)	*490.69* (14)	535.79 (13)	499.72 (25)
Cwebe	316.61 (2)	*301.91* (14)	337.84 (13)	323.82 (25)
Nqabara	430.8 (2)	*358.93* (11)	427.99 (10)	366.61 (19)
Xhora	423.09 (2)	*348.27* (11)	418.01 (10)	*348.20* (19)

Table 4. Temporally independent monthly estimates of capture $p(\cdot)$ and survival $\phi(\cdot)$ probabilities (mean ± SE) obtained from the Cormack-Jolly-Seber (CJS) model for both commonly and rarely exploited species at each site. NP: not possible to estimate parameters as there were no recaptures. Superscripts denote homogenous groups ($p > 0.05$). R: reserve site, N: non-reserve site

Species Population	Reserve status	$p(\cdot)$	$\phi(\cdot)$
Commonly exploited species			
Helcion concolor			
Dwesa	R	0.53[a] ± 0.18	0.43[a] ± 0.1
Cwebe	R	0.27[c] ± 0.15	0.52[a] ± 0.15
Nqabara	N	0.44[b] ± 0.11	0.51[a] ± 0.07
Xhora	N	NP	NP
Scutellastra longicosta			
Dwesa	R	0.67[a] ± 0.65	0.60[b] ± 0.42
Cwebe	R	0.71[a] ± 0.38	0.69[a] ± 0.27
Nqabara	N	0.74[a] ± 0.44	0.67[a] ± 0.32
Xhora	N	0.75[a] ± 0.57	0.56[b] ± 0.38
Rarely exploited species			
Cellana capensis			
Dwesa	R	0.93[a] ± 0.12	0.83[a] ± 0.15
Cwebe	R	0.92[a] ± 0.13	0.86[a] ± 0.14
Nqabara	N	0.88[b] ± 0.17	0.85[a] ± 0.15
Xhora	N	0.93[a] ± 0.12	0.82[a] ± 0.15
Scutellastra granularis			
Dwesa	R	0.96[b] ± 0.12	0.80[a] ± 0.19
Cwebe	R	1.00[a] ± 0.00	0.78[a] ± 0.24
Nqabara	N	0.96[b] ± 0.14	0.76[a] ± 0.23
Xhora	N	0.93[c] ± 0.27	0.79[a] ± 0.23

in reserves (96 to 100%) than non-reserves (93 to 96%) (Table 4, Fig. 3). There was no significant effect of site or reserve status on survival probability (Table 4).

DISCUSSION

Our hypotheses were largely supported, particularly for the exploited species, but there were some anomalous results and this was particularly the case for the rarely exploited species. Of the 3 growth rate hypotheses tested, 2 were supported and the third was partly supported. The first hypothesis that growth rates of rarely exploited species will be the same inside and outside reserves was supported for *Scutellastra granularis* but not for *Cellana capensis*. The unexpected existence of a reserve effect on the growth rate of *C. capensis* may possibly reflect its confusion with *Helcion concolor* and the fact that density of this species shows a reserve effect (density is greater within reserves) in some months (authors'

unpubl. data). Secondly, the hypothesis that growth rates of the commonly exploited territorial *S. longicosta* would be similar inside and outside reserves was supported. Lastly, the hypothesis that growth rates of exploited non-territorial species (*H. concolor*) would be higher outside than inside the reserves was supported.

With respect to mortality, the hypothesis that commonly exploited species would show higher mortality rates outside reserves was supported only for *Scutellastra longicosta* and not for *Helcion concolor*. Secondly, the hypothesis that rarely exploited species (*Cellana capensis* and *S. granularis*) would show no differences in mortality rates inside and outside the reserves was supported.

Growth

The results revealed an expected general decrease in growth rate with an increase in the mean shell length for all species at all sites. This is probably an

effect of age (Branch 1974) related to senescence or a shift in energy allocation from growth to reproduction in older limpets (Takada 1995, Alfaro & Carpenter 1999). Apart from ontogenetic effects, shell thickness can be important. Thick-shelled limpets generally grow less in length than similarly shaped thin-shelled species (Trussell & Nicklin 2002), and in our case *Helcion concolor*, with the thinnest shell of the 4 species, showed the fastest growth rates.

The observed differences in growth rates among our sites are presumably attributable to differences in food supply (Hindell & Quinn 2000). Food availability is related to emersion duration of a given intertidal level (Cusson & Bourget 2005) and many intertidal grazers show ontogenetic changes in zonation as they age and their tolerance of abiotic stresses alters (Paine 1966, Branch 1971, McQuaid 1981, 1982). Our study species do not show such age-dependent migration and occur at similar shore heights at all sites so that differences in growth rates will be mainly due to differences among sites in food availability. Our hypothesis of faster growth for *Hel-*
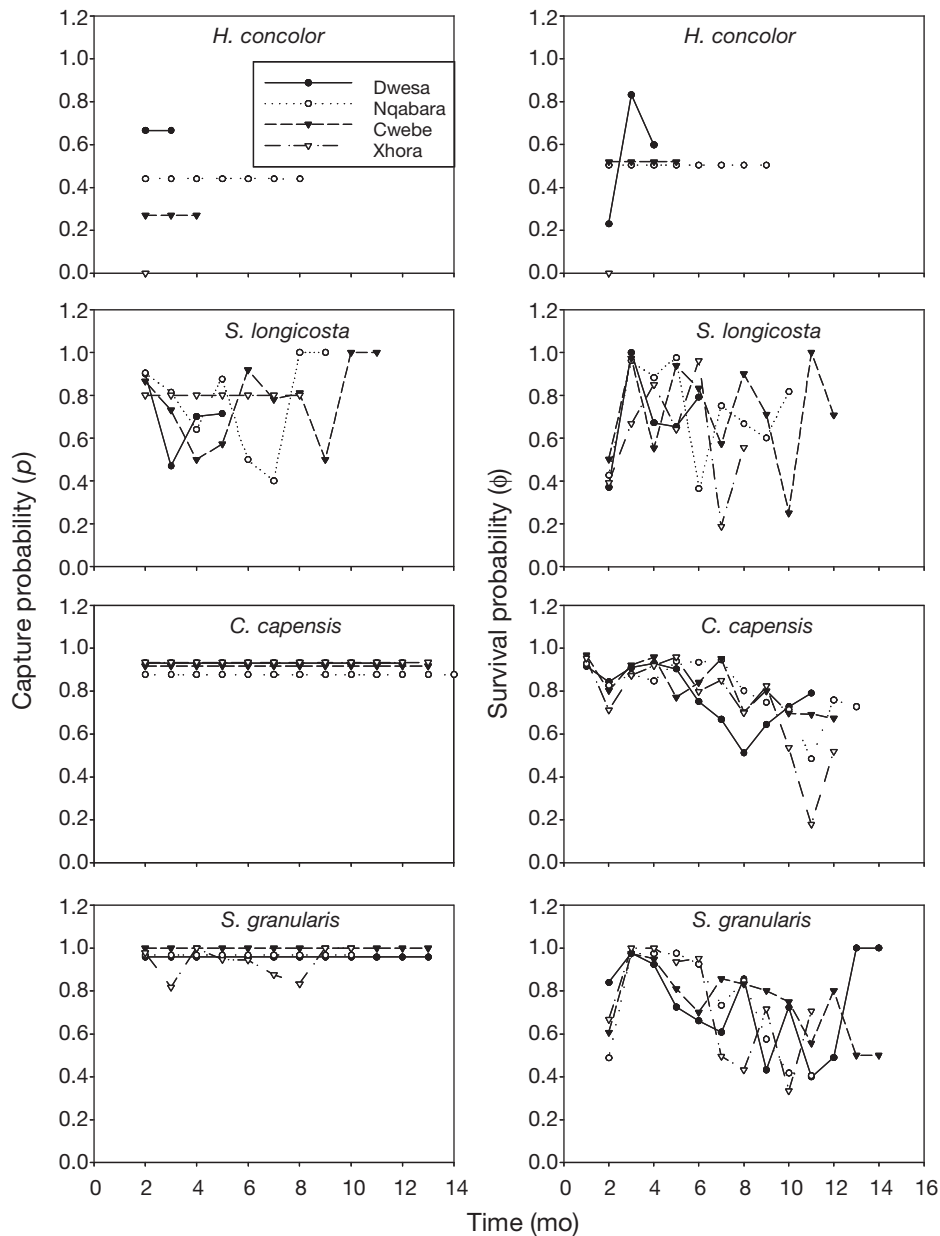

Fig. 3. Estimated monthly capture and survival probabilities of each limpet species among sites throughout the sampling period

cion concolor outside reserves (which was supported) was based on the assumption that food availability is driven largely by competition (Creese & Underwood 1982, Underwood 1984, Dunmore & Schiel 2003). Growth rates of intertidal gastropods increase when densities are experimentally reduced due to intra-specific competition, including intra- size-class competition (Underwood 1976, Marshall & Keough 1994). Densities of limpets varied and for this species they were higher in almost all months, though not always significantly so, at reserve (range 4 to 8 m^{-2}) than at non-reserve sites (range 4 to 6 m^{-2}, M. D. V. Nakin & C. D. McQuaid unpubl.).

Branch (1974) noted that non-territorial species such as *Scutellastra granularis, Cellana capensis, Helcion concolor* and other patellid limpets over-exploit their food supplies and have faster growth rates, higher mortality and decreased longevity relative to territorial species such as *S. longicosta*, an observation supported by our findings. Our hypothesis that *S. longicosta* would show no effect of reserve on growth rate was supported. This species feeds on, and actively defends, patches or 'gardens' of the encrusting brown alga *Ralfsia verrucosa* (Branch 1974, McQuaid & Froneman 1993). These gardens vary with the size of the limpet and are not affected by density under natural conditions so that we had no reason to assume that either territory size or productivity for a given limpet size would be affected by reserve status. Growth was, however, particularly slow at the non-reserve site Nqabara, with no differences among the other 3 sites. There is more sand at Nqabara than any other site (M. D. V. Nakin pers. obs.), which can reduce grazing and survival in limpets (Airoldi & Hawkins 2007).

As expected, there was no significant reserve effect on the growth rate of the least exploited species *Scutellastra granularis*, but its maximum size was greater in non-reserves. This may be due to the interaction of *S. granularis* with barnacles, which appeared to be more abundant in the reserve sites (authors' pers. obs.). Barnacles can filter out settling algal spores and render benthic food inaccessible because their irregular shape interferes with grazing, so that limpet size can be negatively related to barnacle cover (Lewis & Bowman 1975, Branch 1981). The most anomalous result was faster growth for *Cellana capensis* outside reserves. Interviews with harvesters indicate that this species is occasionally confused with *Helcion concolor* and in many months its densities were significantly higher at reserve sites (range 13 to 23 m^{-2}) than at non-reserve sites (range 8 to 23 m^{-2}, M. D. V. Nakin & C. D. McQuaid unpubl.).

Mortality

There was a strong reserve effect on the survival probability of the most commonly exploited species *Scutellastra longicosta*. The documented result was expected because *S. longicosta* is the preferred species by harvesters. There were, however, unexpected reserve affects on the capture probability of the rarely exploited species, both having higher probabilities within reserves. For *Cellana capensis*, this may again be related to the fact that it is occasionally harvested in error or in the absence of the preferred species (Lasiak 1993), but we have no explanation for *S. granularis*.

Likewise, the lack of a significant reserve effect on survival of *Helcion concolor* was unexpected. *H. concolor* had the lowest recapture probability of all species investigated and the absence of any recaptures from Xhora suggests very high mortality from human predation.

The observed inconsistent reserve effects in capture and survival probabilities of these limpets may be due to spatial heterogeneity. As limpets age, specific size classes may become more or less likely to be captured relative to the rest of the population. In many limpet populations, different size classes occupy different habitats and have different tenacities (Branch & Marsh 1978). For example, small limpets are concentrated in crevices, which act as refuges from waves while adult limpets are more often found on flat/less irregular rocks. Heterogeneity in capture probabilities can lead to bias in estimates of survival (Nichols 1992, Clobert 1995) and growth (Trites 1993) but is unlikely in the present study, as we took care to minimise this type of bias. Nevertheless, variation in the number of crevices among sites may have affected survival probabilities.

It is also important to note that the CJS model cannot separate between mortality and emigration and only estimates apparent mortality. The variability of the estimated capture and survival probabilities were higher in commonly exploited than in rarely exploited species, indicating a lower degree of precision in the former. The capture and survival probabilities differed not only between commonly and rarely exploited species but also within these classes. The overall results indicated consistent reserve effects on the capture probabilities of the rarely exploited species, with inconsistent reserve effects for the survival probabilities of the commonly exploited species (i.e. *Scutellastra longicosta* showed significant results and *Helcion concolor* non-significant results).

Overall, while there were some species-specific effects of reserves, there were no clear overall effects as these were overwhelmed by inter-site and species-specific differences. Our results have important management implications as they suggest that reserve efficacy is strongly species dependent.

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