Population structure and growth of polydorid polychaetes that infest cultured abalone *Haliotis midae*

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Polydorid polychaetes can infest cultured abalone thereby reducing productivity. In order to effectively control these pests, their reproductive biology must be understood. The population dynamics and reproduction of polydorids infesting abalone *Haliotis midae* from two farms in South Africa is described using a length-based, age-structured model. Shells were infested mainly by introduced *Boccardia proboscidea*. *Polydora hoplura* and *Dipolydora capensis* were also present but in numbers too few to identify factors influencing infestation. At both farms, *B. proboscidea* lived for a minimum of 12 months. Growth rate, size at maturity, maximum size, infestation intensity, recruitment, percentage of the population brooding and mortality appear to be affected by abalone feeding regime and water temperature, and these factors need to be considered in controlling infestation. Brooders and recruits were present throughout the year, but increased significantly during mid- to late winter/early spring when water temperature and day length increased. Treatment measures should therefore be implemented throughout the year but with increased effort when water temperature increases.

Introduction

The infestation of commercially important molluscs by polydorid polychaetes has been well documented (e.g. Martin and Britayev 1998). The economic importance of polydorids infesting cultured abalone (*Haliotis* spp.) has become apparent, with infestation records following the rapid expansion of the abalone industry worldwide. Infestations have now been reported from Chile (Radashevsky and Olivares 2005, Vargas *et al.* 2005), Australia (Lleonart *et al.* 2003a, 2003b) and South Africa (Simon *et al.* 2006). In South Africa, the cultured abalone *Haliotis midae* is infested by *Polydora hoplura*, *Dipolydora capensis* and *Boccardia proboscidea* (Simon *et al.* 2006, CAS unpublished data). *P. hoplura* is a well-known pest of cultured shellfish (Nel *et al.* 1996, Handley and Bergquist 1997, Martin and Britayev 1998, Lleonart *et al.* 2003b), whereas *B. proboscidea* has only been reported as a pest since 2000 (Bailey-Brock 2000, Lleonart 2001, Read 2004, Simon *et al.* 2006).

High infestations by polydorid worms have been associated with increased mortality and reduced condition in abalone (Kojima and Imajima 1982, Lleonart *et al.* 2003b, Simon *et al.* 2006). Several treatment methods have therefore been investigated to control infestation. These include hot water, freshwater and chemical treatments, dislodging worms with high pressure water sprays and air-drying (Skeel 1979, Bailey-Brock and Ringwood 1982, Nel *et al.* 1996, Lleonart *et al.* 2003a). Lleonart *et al.* (2003a) have cautioned that air-drying be used prudently to avoid potential suppression of abalone growth that may be associated with prolonged exposure. To improve the effectiveness of any treatment method, it is therefore necessary to administer it when the worms are most vulnerable, i.e., immediately after recruitment and before they have bored too deeply into the shell (cf. Nel *et al.* 1996). Knowledge of the population dynamics and reproductive biology, particularly the timing of recruitment, is, however, required.

Polydorid worms display several characteristics that would predispose them to becoming pests. They display both r-selected (high fecundity, fast maturation rates, a semi-continuous supply of larvae and rapid population growth) and k-selected (encapsulation of eggs which are brooded within the maternal burrow) traits (Simon *et al.* 2005). In addition, polydorid worms draw on both traits by producing larvae that are either planktonic (which promotes dispersal) or benthic (which promotes local recruitment, see Blake and Arnofsky 1999 for review). Recruitment is generally aseasonal with periods of increased production (Gudmundsson 1985, Zajac 1991, Nel *et al.* 1996, Handley and Bergquist 1997, Duchêne 2000, Bolam 2004).

Abalone are cultured in high densities in onshore systems that have reduced water movement and an abundance of particulate matter, which originates from degraded abalone food and abalone faeces, compared with wild habitats (Chalmers 2002, Simon *et al.* 2005). The aim of the present study was therefore to gain a better understanding of the

population structure, growth, mortality rate and reproductive biology of the polydorid species infesting cultured abalone in South Africa by investigating populations at two geographically separated commercial abalone farms. These farms differ primarily with respect to annual water temperature and abalone diet. This information should contribute to the implementation of more effective treatment or control methods, as well as to understanding of the life-history strategies of pest species and the factors that contribute to their ability to flourish on abalone farms.

Material and Methods

Sample sites and experimental animals

Between 13 and 15 spionid-infested abalone shells (between 50mm and 80mm in length) were supplied monthly by abalone farms in Saldanha Bay on the South African west coast (33°00.59'S, 17°56.13'E) and Hermanus on the south coast (34°25.30'S, 19°13.30'E) from February 2005 to February 2006, except for May and November from Saldanha Bay and February 2005 and 2006 from Hermanus. Shells from abalone suffering from high polydorid infestation were sampled by a veterinary researcher affiliated to the Abalone Farmers' Association of South Africa (AFASA) and production managers at the two farms. These animals were chosen as they are usually quarantined from healthy animals (A Mouton, AFASA, pers. comm.) and would therefore be the focus of most intense treatment procedures. Both farms employ shore-based systems in which the abalone are held in baskets suspended in raceways. At the farm in Saldanha Bay, the abalone were kept at stocking densities of 20% of the available surface area and fed kelp whereas at Hermanus the abalone were kept at stocking densities of 18–20% and fed a mixed diet of kelp and the commercial pelleted diet Abfeed™. Water supply to the raceways is pumped in from the sea and is exchanged every few hours.

Sample preparation and identification

The worms in the shells were preserved in 4% seawater formalin and transferred after a maximum of four days to 70% ethanol. Worms were removed by softening the shells in 5% nitric acid in 70% ethanol for 24–48h. Worms were identified by the morphology of the spines on the fifth chaetiger, the spines and hooks on the posterior chaetigers, gill distribution and pygidium shape. Once the worms had been removed and identified, they were photographed and measured using the programme AnalySIS® (Soft Imaging System 2001). Where possible, the length and the width of the fifth chaetiger were measured. These data were used to statistically estimate the lengths of worms where only the widths could be measured (e.g. broken or regenerating worms or those that had curled in a way that made it difficult to measure the lengths). The presence of broods was also noted. For each species and farm, the length of the smallest worm with a brood was taken to be the minimum size at maturity. Therefore, all worms greater or equal to this length were considered adults, whereas all those smaller were considered to be juveniles. Throughout this paper, the intensity of infestation refers to the number of individuals of a particular species per shell (after Margolis et al. 1982).

Annual temperatures

The mean monthly temperature of the water in the abalone raceways was provided by the respective farms. At Hermanus, water temperature was measured using a hand-held thermometer placed 200mm below the surface of the water, at 07:35 every day. At Saldanha Bay, temperature is measured using a Hobo H8 data-logger, every 15min.

Statistical analyses

For B. proboscidea, the data for intensity, number of adults, number of juveniles and number of brooders were square-root (x + 1) transformed, the data for % brooders were arcsine transformed whereas the lengths of brooders were logarithm transformed. The transformed data were homogeneous only for intensity and number of adults and length of brooders using Levene's test, but according to (Underwood 1997) the experimental design was sufficiently robust for a parametric two-way ANOVA. The two-way ANOVA was used to test for the effect of farm and month on the variables. When significant differences were noted, a Newman-Keuls post hoc test was employed. To perform the two-way ANOVA, only months that were sampled at both farms were used. The Kruskal-Wallis test was used to measure the effect of month on intensity, number of adults, juveniles and brooders, and percentage brooders in P. hoplura and D. capensis. To determine whether there was a relationship between the density of B. proboscidea adults and the percentage of the adults brooding, correlation analyses were conducted. Throughout the manuscript, statistics are presented as the mean ± standard error (SE).

Population dynamics

To determine the growth patterns and general population dynamics of B. proboscidea, a length-based age-structured model (modified from the MULTIFAN approach by Fournier et al. 1990, 1991, 1998) were applied to Hermanus and Saldanha Bay datasets. The model assumes that the length frequency samples contained sufficient information to allow for the statistical estimation of the growth parameters, the annual mortality rate and relative recruitment for maximum number of identifiable cohorts.

Notation
Model notation is summarised as follows:
s is an index for each sample,
N_s is the total number of samples,
s_s is the number of individuals in sample s,
a is an index for each identifiable cohort,
N_a is the total number of identifiable cohorts,
l is an index for each length frequency class,
N_l is the total number of length frequency classes,
n_{sl} is the observed number of animals in sample s having a length lying within length class l,

$\hat{n}_{sl}$ is the predicted number of animals in sample s having a length lying within length class l,

$\hat{n}_{sa}$ is the predicted number of animals in sample s within cohort a,

q_{sl} is the observed relative proportion of animals in sample s having a length lying within length class l, such that $q_{sl} = n_{sl}/s_s$,

$\hat{q}_{sl}$ is the predicted relative proportion of animals in sample s having a length lying within length class l,

$\overline{l}_a$ is the predicted mean length of an animal in cohort a,

$\hat{\lambda}$ is the predicted standard deviation of animals in a cohort,

$\hat{l}_{min}$ is the predicted mean length of the youngest cohort,

$\hat{l}_{max}$ is the predicted mean length of the oldest cohort,

$\hat{l}_{\infty}$ is the predicted theoretical asymptotic length,

$\hat{K}$ is the predicted curvature parameter (known as Brody's growth coefficient), describing the rate at which $\overline{l}_a$ approaches $\hat{l}_{\infty}$,

$\hat{p}_{sa}$ is the predicted relative strength of animals in cohort a from sample s across all ages, such that $\sum\limits_{a=1}^{max} \hat{p}_{sa} = 1$,

$\hat{Z}$ is the predicted instantaneous rate of total mortality, and

max is the maximum number of cohorts considered in the analysis.

Numbers at length

Within each normalised length frequency sample, it was assumed that the relative proportion observed at length l for any particular sample s, q_{sl}, was comprised of the sum of all identifiable cohorts. If each cohort a has a mean length $\overline{l}_a$, variance λ^2 and is normally distributed, then the predicted proportion at length l for sample s can be estimated as $\hat{q}_{sl} = \sum\limits_{a=1}^{max} \hat{p}_{sa}\theta(\overline{l}_a,(\hat{\lambda})^2)$ where $\theta(\overline{l}_a,(\hat{\lambda})^2)$ is a normal distribution function.

Numbers at age

The population dynamics component of the model assumes that it was possible to model cohort size recursively based on the exponential decay model as $\hat{n}_{s+1,a+1} = \hat{n}_{sa}\exp(-\hat{Z})$, where n_{sa} is the number of animals alive in cohort a and sample s. The relative number of animals in cohort a from sample s is calculated as $\hat{p}_{sa} = \dfrac{\hat{n}_{sa}}{\sum\limits_{a=1}^{max}\hat{n}_{sa}}$.

Growth

Animals were assumed to grow according to the von Bertalanffy growth model such that $\overline{l}_a = \hat{l}_{\infty}(1 - e^{-\hat{K}a})$. The growth model was reparameterised to improve numerical stability to the form $\overline{l}_a = \hat{l}_{min} + (\hat{l}_{max} - \hat{l}_{min})\left(\dfrac{1 - e^{-\hat{K}(a-1)}}{1 - e^{-\hat{K}(max-1)}}\right)$

where $\hat{l}_{\infty} = \dfrac{\hat{l}_{max} - \hat{l}_{min}\hat{K}^{max-1}}{1 - \hat{K}^{max-1}}$

If $\hat{K}$ is extremely small (say $\hat{K} < 0.001$), then growth is effectively linear between $\hat{l}_{min}$ and $\hat{l}_{max}$.

The age at first maturity (a_m) was calculated from a back transformation of the von Bertalanffy growth model as $a_m = -\hat{K}^{-1}\log_e(1 - b_{50}/\hat{l}_{\infty})$.

Likelihood function

A two-component likelihood function, of the form LL = $LL_{growth} \times LL_{abundance}$, was constructed to allow for the statistical estimation of the model parameters. The first component, a normal likelihood function, was constructed noting that $\hat{q}_{sl}$, while being binomially distributed, can be approximated by a normal distribution. The maximum likelihood parameter estimates are obtained by maximising the likelihood of the form

$$LL_{growth} = \prod_{s=1}^{N_s}\prod_{l=1}^{N_l}\frac{1}{\hat{\sigma}_{sl}\sqrt{2\pi}}\exp\left[\frac{-(q_{sl} - \hat{q}_{sl})^2}{2\hat{\sigma}_{sl}^2}\right]$$

where $\hat{\sigma}_{sl}^2 = \dfrac{\hat{q}_{sl}(1 - \hat{q}_{sl})}{s_s}$ is the standard deviation of $\hat{q}_{sl}$ and s_s is the sample size of sample s. To prevent divide-by-zero errors, a small constant was added to the variance component such that $\hat{\sigma}_{sl}^2 = \dfrac{\hat{q}_{sl}(1 - \hat{q}_{sl}) + 0.1/N_l}{s_s}$ where N_l is the number of length frequency intervals in sample s.

The second component included the relative abundance of each sample to allow for the estimation of $\hat{Z}$ as

$$LL_{abundance} = \prod_{s=1}^{N_s}\left[\ln\left(\sum_{l=1}^{N_l}n_{sl}\right) - \left(\sum_{l=1}^{N_l}\hat{n}_{sl}\right)\right]^2$$

Parameter estimates and variability

A maximum of 12 cohorts were considered in the analyses, because it assumed that animals could live for at most one year of age (Gibson 1997) and it provides sufficient monthly resolution.

The model parameters $(\hat{l}_{min},\hat{l}_{max},\hat{K},\hat{\lambda})$ are therefore the four growth parameters, the age-independent rate of total mortality $\hat{Z}$, $(N_a - 2)$ number of animals from all cohorts in the first sample $(\hat{n}_{12},\hat{n}_{11},...,\hat{n}_{1max})$, and the number of recruits from $(N_s - 2)$ samples $(\hat{n}_{21},\hat{n}_{31},...,\hat{n}_{s1})$.

The number of animals in the first sample and last cohort is calculated as $\hat{n}_{1max} = \left(\prod\limits_{a=1}^{max-1}\hat{n}_{1a}\right)^{-1}$ (see Fournier et al. 1991 for further details). This was necessary because the first sample is considered a reference sample with relative abundance of all other samples scaled to the abundance in the first sample.

In the case of the Saldanha Bay data, the May and November 2005 data were missing. The youngest cohort strengths were still estimated but these months were omitted from the likelihood function. As with Model 1, only 12 cohorts were considered in the analyses.

Analyses were conducted using AD Model Builder (Otter Research Ltd 2000) with parameter estimates obtained through non-linear minimisation of the negative logarithm of each respective likelihood function. Estimates of parameter variability are calculated from the inverse Hessian matrix. This approach assumes that the parameter values are asymptotically normally distributed and involves replacing the log-likelihood surface at the maximum likelihood solution by the quadratic form of the Hessian. Derived parameter $(\hat{l}_{\infty},$ survival = $\exp(-\hat{Z}))$, and age-at-50% brooding $a_{50})$ standard errors were estimated using the delta method.

Results

Species composition

The shells at both farms were infested by *B. proboscidea*, *P. hoplura* and *D. capensis.*

B. proboscidea
There was a significant relationship between the length of *B. proboscidea* and the width of its fifth chaetiger at both farms. Therefore, the length of the worm could be predicted from its width by the equations:

Hermanus: $\log_{10}$ length = 0.94 + 1.39$\log_{10}$ width (r^2 = 0.86, r = 0.92, p < 0.0001)
Saldanha Bay: $\log_{10}$ length = 0.91 + 1.34$\log_{10}$ width (r^2 = 0.85, r = 0.92, p < 0.0001)

The lengths estimated from these equations were included in the general analyses. All parameters were characterised by very high variability. Farm and month had a significant effect on the intensity of infestation and there was a significant interaction between factors (Table 1, Figure 1a). At both farms there was a trend for an increase in intensity peaking in late winter, early spring. At Hermanus, intensity in August (88.53 ± 10.23 [mean ± SE], worms per shell) was significantly higher than in March, April, June, December and January when the mean number of worms per shell ranged from 10.36 to 55.93 (Figure 1a). Intensity in April (10.36 ± 3.36) was significantly lower than all the other months at Hermanus. This was an anomalous month because seven of the 14 shells examined had no *B. proboscidea*. At Saldanha Bay, the increase in intensity was not as great as at Hermanus, and intensity in September (44.47 ± 7.31 worms per shell) was significantly higher than in April (15.47 ± 2.57 worms per shell). In August, intensity was significantly higher at Hermanus than at Saldanha Bay.

The smallest brooding worms were 6.84mm and 5mm at Hermanus and Saldanha Bay respectively. Month, but not farm, had a significant effect on the number of adults infesting the shells, and there was a significant interaction between these factors (Table 1, Figure 1b). At Saldanha Bay, month did not have a significant effect on the number of adults present per shell, with means ranging between 13.1 and 26.27. At Hermanus, the number of adults increased significantly during winter, with numbers in August (36.11 ± 4.14 adults per shell) and October (33.53 ± 7.6 adults per

shell) being significantly higher than in March, April, June and January, when the means ranged between 1.71 and 19.86. Again, April was significantly lower than all the other months (1.71 ± 0.9 adults per shell). Even though farm was not identified as having a significant effect on the number of adults, the means for April belonged to
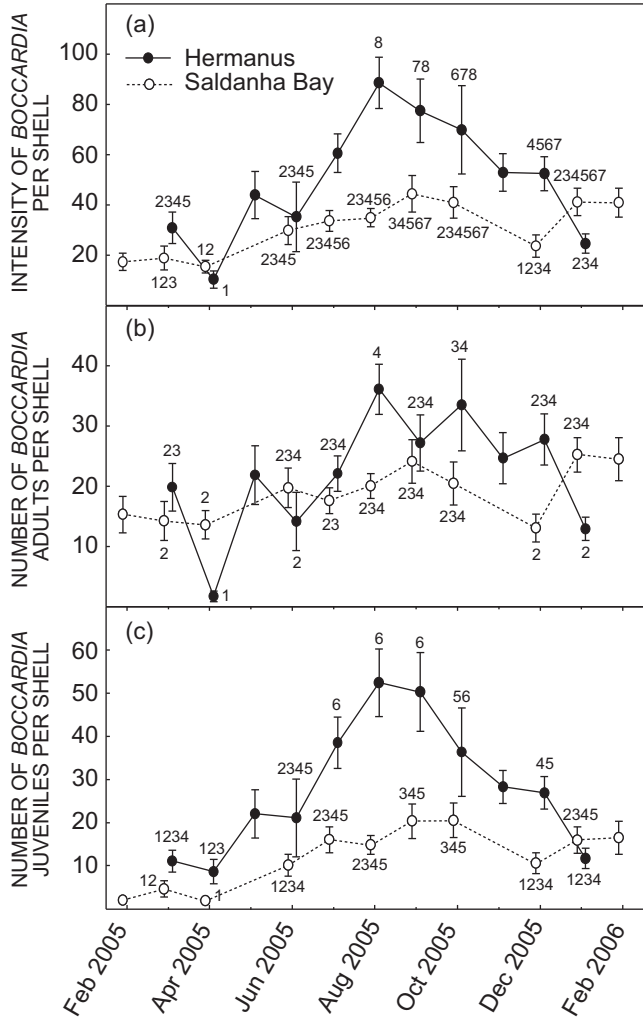

Figure 1: Seasonal fluctuations in the mean intensity of infestation by (a) all *B. proboscidea*, (b) *B. proboscidea* adults and (c) *B. proboscidea* juveniles of abalone at farms in Hermanus and Saldanha Bay. The error bars denote ±SE and the numbers denote homogeneous groups

Table 1: ANOVA results describing the effects of farm and month on different reproductive and population dynamics parameters of *B. proboscidea* at farms in Hermanus and Saldanha Bay

Parameter	Farm	Month	Farm × month
Intensity of infestation	$F_{(1, 246)}$ = 17.3, p < 0.0001	$F_{(8, 246)}$ = 13, p < 0.0001	$F_{(8, 246)}$ = 4.2, p < 0.0001
Mean number of adults per shell	$F_{(1, 246)}$ = 0.3, p = 0.58	$F_{(8, 246)}$ = 9.3, p < 0.0001	$F_{(8, 246)}$ = 6.2, p < 0.0001
Mean number of juveniles per shell	$F_{(1, 246)}$ = 47.7, p < 0.0001	$F_{(8, 246)}$ = 14.9, p < 0.0001	$F_{(8, 246)}$ = 2.8, p < 0.01
Mean number of brooders per shell	$F_{(1, 246)}$ = 23.8, p < 0.0001	$F_{(8, 246)}$ = 13.8, p < 0.0001	$F_{(8, 246)}$ = 4.8, p < 0.0001
Mean percentage of brooders per shell	$F_{(1, 245)}$ = 28.1, p < 0.001	$F_{(8, 245)}$ = 3.6, p < 0.0001	$F_{(8, 245)}$ = 3.3, p < 0.01
Mean size of brooders per shell	$F_{(1, 640)}$ = 4.5, p < 0.05	$F_{(8, 640)}$ = 9.4, p < 0.0001	$F_{(8, 640)}$ = 2.1, p < 0.05

different homogeneous groups (Figure 1b), as determined by the Newman-Keuls test.

Juveniles were present throughout the year at both farms (Figure 1c). Month and farm had a significant effect on the number of juveniles present and there was a significant interaction between the two factors (Table 1, Figure 1c). Numbers increased towards late winter–early spring, with a more significant increase at Hermanus. At that farm, there were significantly more juveniles present from July to September (when the mean number of juveniles per shell ranged between 38.47 and 52.4) than for the rest of the study, except for October. At Saldanha Bay, there were significantly more juveniles during September and October (with means of 20.33 and 20.53 respectively) than March and April (with means of 4.6 and 1.87 respectively). From July to September, there were significantly more juveniles on the shells at Hermanus than at Saldanha Bay.
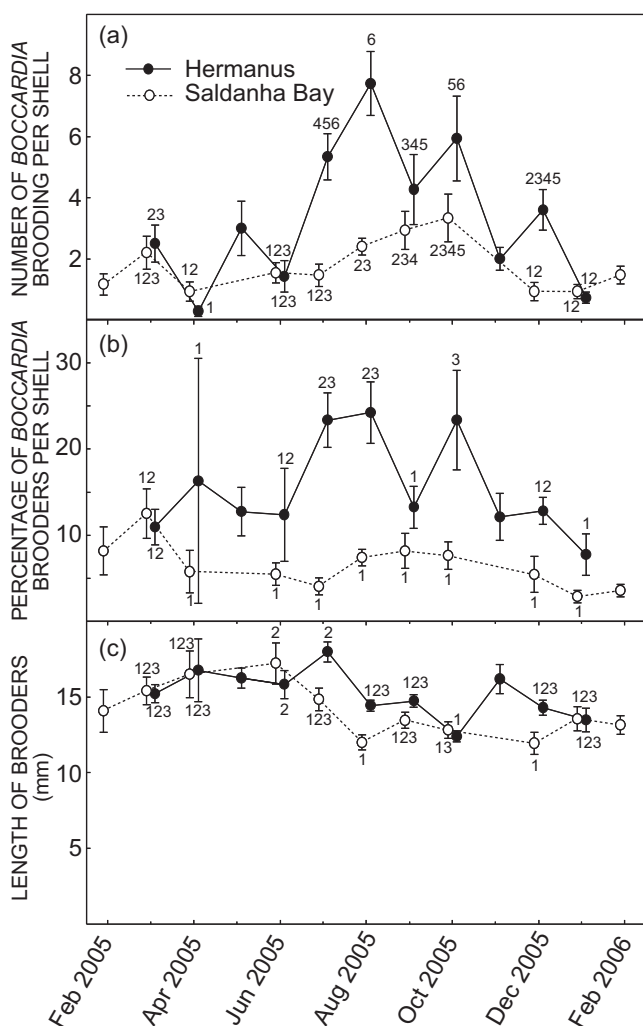

Figure 2: Seasonal fluctuations in the reproductive activity of *B. proboscidea* that infest abalone shells at farms in Hermanus and Saldanha Bay: (a) the mean number of brooding *B. proboscidea*, (b) the mean percentage brooding *B. proboscidea* and (c) the mean length of brooders per shell. The error bars denote ±SE and the numbers denote homogeneous groups

Farm and month had a significant effect on the number of brooders present, and there was a significant interaction between these factors (Table 1, Figure 2a). Brooders were present throughout the study period, but increased during winter. At Hermanus, there was a significant increase in the number of brooders after June, peaking in August (7.73 ± 1.04 brooders per shell). The number of brooders stayed relatively high until October. The change in the number of brooders during the year was much lower at Saldanha Bay, with means ranging between 0.93 and 3.33 brooders per shell. The highest number of brooders was present during October. During July and August, there were significantly more brooders at Hermanus than at Saldanha Bay. To determine whether the proportion of adults brooding offspring differed with time and at the different farms, the effect of these factors was tested on the percentage of the brooders present each month. Both had a significant effect on the percentage brooders present, with a significant interaction between them (Table 1, Figure 2b). Month did not have a significant effect on the percentage brooders present at Saldanha Bay, where brooders made up between 2.87% and 12.52% of the adults. By contrast, brooding adults made up between 7.73% and 24.23% of the adults at Hermanus, with a significantly higher percentage of adults brooding during July, August and October than in the rest of the study.

Farm and month had a significant effect on the mean size (and presumably age) of the brooders, and there was a significant interaction between these factors (Table 1, Figure 2c). At both farms, there was a trend for an increase in the mean length of brooders from the beginning of the study period to June and July for Saldanha Bay and Hermanus respectively, after which the mean length of the brooders decreased. At Hermanus, the brooders were significantly longer in July (17.98 ± 0.66mm) than in October (12.39 ± 0.38mm). At Saldanha Bay, the brooders were significantly longer in June (17.21 ± 1.36mm) than in August and December (12 ± 0.5mm and 11.9 ± 0.72mm respectively). There was a high degree of overlap in length between the two farms, but the length of the brooders at Hermanus during July was significantly longer than that of brooders at Saldanha Bay during August and December.

There was no relationship between the number of adult *B. proboscidea* per shell and the percentage brooders per shell at either farm (Hermanus: $r^2 = 0.0053$, $r = 0.072$, $p = 0.85$; Saldanha Bay: $r^2 = 0.014$, $r = -0.119$, $p = 0.134$).

Growth and population dynamics

The estimated parameters (Table 2) and model fits to the data (Figure 3) showed that the length-based, age-structured model could realistically estimate growth and cohort strength in *B. proboscidea*.

The parameters were well-estimated owing to the large sample sizes in the analyses, with coefficients of variation below 3%. The mean length of the youngest cohort, mean length of the oldest cohort and asymptotic length were estimated as 1.35mm and 2.14mm, 18.26mm and 20.81mm, and 42.71mm and 29.14mm for the Saldanha Bay and Hermanus populations respectively. The curvature parameter ranged between 0.05mm month^{-1} and 0.11mm month^{-1}, suggesting that growth rate decreases slightly with age.

Table 2: Parameter estimates and coefficients of variation for growth (l_{min}, l_{max}, l_∞, K, λ) , total mortality (Z), survival (exp (–Z)) and age at first maturity (a_m) from the length-based age-structured model applied to two populations of *B. proboscidea* from Saldanha Bay and Hermanus

Parameter	Saldanha Bay		Hermanus	
	Estimate	CV (%)	Estimate	CV (%)
l_{min} (mm)	1.35	0.10	2.14	0.10
l_{max} (mm)	18.26	0.04	20.81	0.06
K (mm month^{-1})	0.05	0.60	0.11	0.36
λ (mm)	0.69	0.15	1.09	0.14
l_∞ (mm)	42.71	0.47	29.14	0.20
Z (month^{-1})	0.11	2.91	0.35	1.55
Survival (month^{-1})	0.90	0.31	0.71	0.54
a_m (months)	2.61	0.11	2.50	0.15
Parameters estimated	30		28	

Mortality was higher in the Hermanus population with a monthly survival rate of 0.71 month^{-1} compared to 0.90 month^{-1}.

From the growth parameters, the minimum age-at-maturity was estimated at 2.61 months and 2.50 months for the Saldanha Bay and Hermanus populations respectively.

D. capensis *and* P. hoplura

These species were present at Hermanus throughout the study but were less abundant than *B. proboscidea*. At Saldanha Bay, only one *D. capensis* was found during the entire study, whereas eight *P. hoplura* were found during March, June, September and February 2006. In September, two of the four worms found were brooding capsules. Therefore, only the populations at Hermanus were analysed and will be discussed.

P. hoplura was absent during April, and when present, the mean intensity ranged between 0.07 and 2.53 worms per shell (Figure 4a). Month had a significant effect on the intensity of infestation by this worm (Table 3), with intensity in July being higher than in April. The intensity of infestation by *D. capensis* was usually higher, with means ranging between 1 and 4.67 worms per month. Month did not have a significant effect on the intensity of infestation by *D. capensis* at an adjusted alpha value of 0.00045 (Table 3).

Most of the worms under study were adults. Month had no significant effect on the number of *D. capensis* adults (Table 3, Figure 4b), with means ranging between 1 and 4.6 adults per shell. Whereas month had a significant effect on the number of *P. hoplura* adults present per month (Table 3), *post hoc* tests did not identify heterogeneous groups; possibly because the mean number present per month was low, ranging between 0.07 and 1.15 worms per shell. Month did not have a significant effect on juvenile number (Table 3, Figure 4c) or brooding (Table 3, Figure 4d) by either species. Low numbers of brooding *D. capensis* occurred during most of the year, absent only in January, whereas low numbers of brooding *P. hoplura* were found from July to November.

Annual temperature

The patterns of seasonal temperature fluctuation at the two farms differed (Figure 5). At Hermanus, temperatures fluctuated between 13.2°C and 15.3°C from January to May, after which it dropped steadily to 14°C during August and September. After September, the mean monthly temperature rose rapidly to 16.3°C in December. At Saldanha Bay, there was a clearer seasonal trend with mean monthly temperature decreasing from 17.4°C in January to about 13.5°C in July and August, after which it increased again. From January to April, temperatures were higher at Saldanha Bay, but for most of the study temperatures at Hermanus were 1°–2°C higher.

Discussion

In the current study, abalone at both farms were infested mainly by *B. proboscidea*, with few individuals of *P. hoplura* and *D. capensis* present, supporting a previous study conducted at the same farms (Simon *et al.* 2006).

B. proboscidea

The populations of this species showed several similarities to each other and other polydorid species inhabiting temperate environments. At both farms, worms have a lifespan of approximately 12 months, which is common in polydorids (Gibson 1997, Williams 2001); populations showed polymodal distributions with 10–12 size/age classes present in most months, recruitment occurred throughout the year, and despite constant recruitment, the bulk of the population appears to be comprised of individuals that settle during late winter/early spring and die in mid- to late winter the following year (Dorsett 1961, Zajac 1991, Sardá and Martin 1993, Nel *et al.* 1996, Duchêne 2000, García-Arberas and Rallo 2004).

B. proboscidea is poecilogenous, producing planktotrophic and/or adelphophagic larvae in different locations (see review by Blake and Arnofsky 1999). In the current study, it produced both types of larvae at both farms (CAS unpublished data). The worms matured about 2.5 months after settlement, 2–4 weeks sooner than laboratory-reared *B. proboscidea* (Gibson 1997). Growth at both farms was slightly curvilinear (Table 2), with growth at Saldanha Bay being slower than at Hermanus. This is reflected in the noticeable differences in the minimum size at maturity and the mean length of the oldest cohort. Possible reasons for these differences will be discussed later.
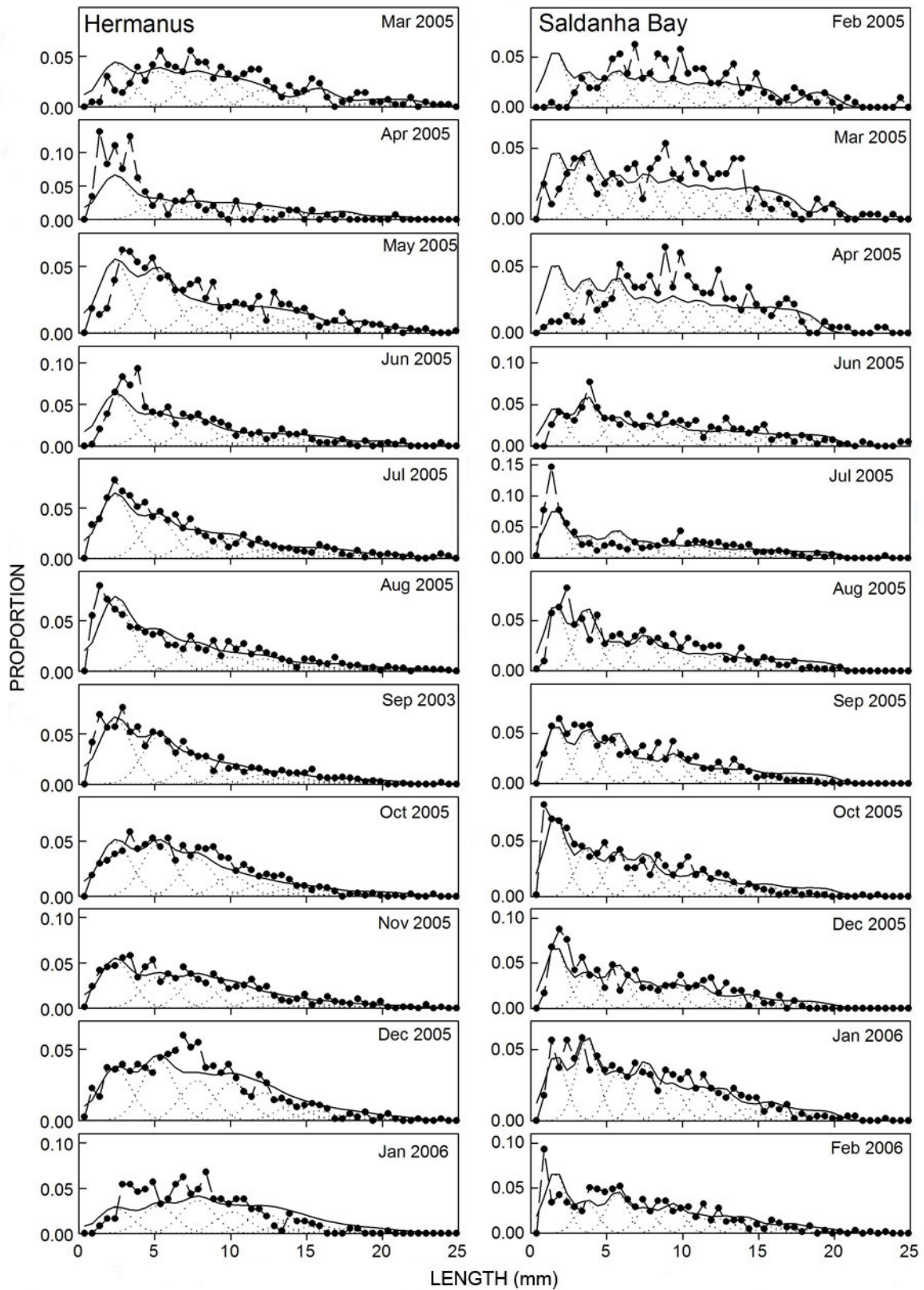
Figure 3: Observed and model predicted population structure of *B. proboscidea* infesting abalone at two abalone farms. The dashed lines with dots are the observed length frequencies, the solid lines the predicted length frequencies, and the dotted lines the model-predicted cohorts
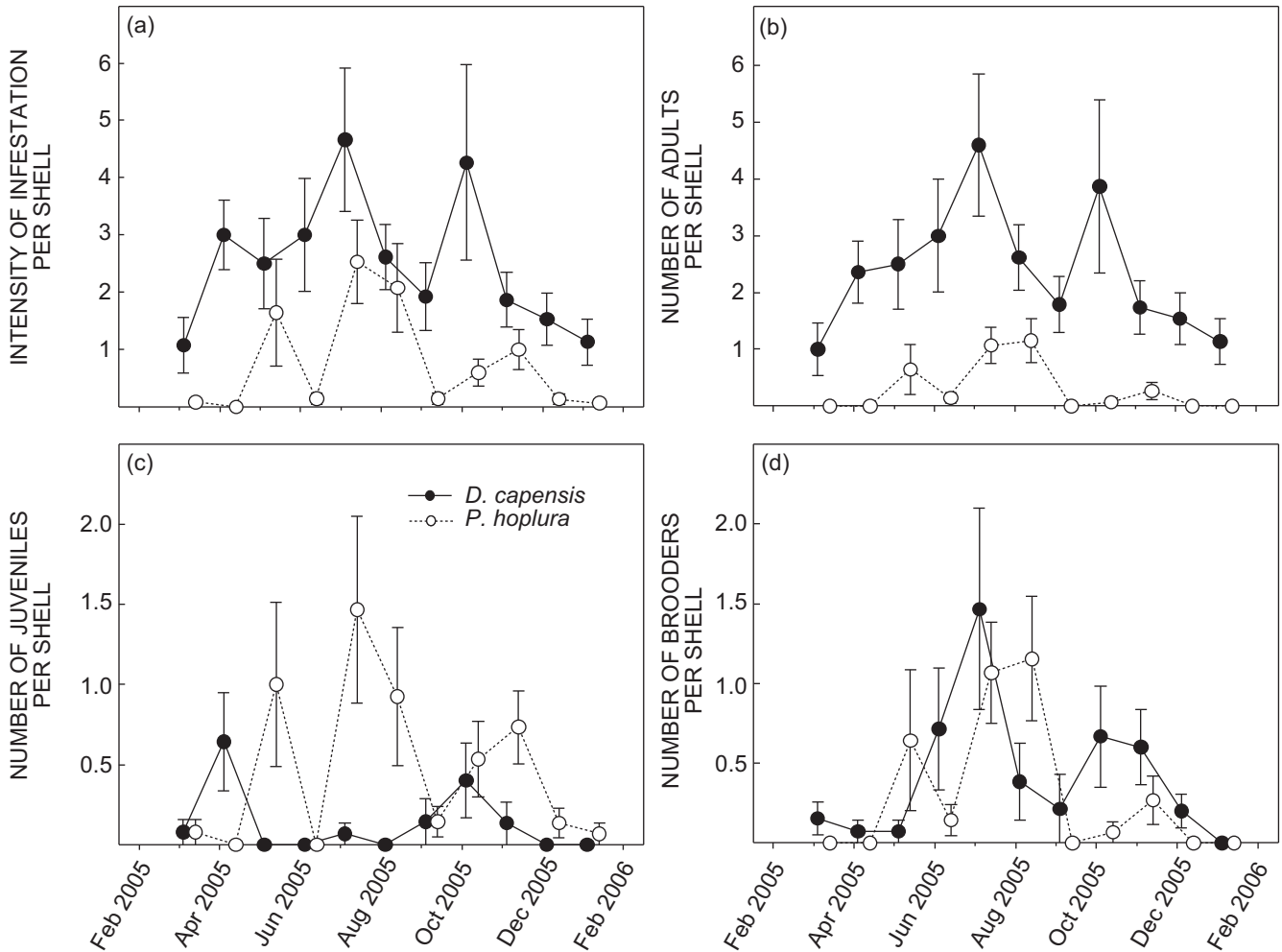
Figure 4: Seasonal fluctuations in (a) the mean intensity of infestation, (b) number of adults, (c) number of juveniles and (d) infesting abalone at farms in Hermanus and Saldanha Bay. The error bars denote ±SE

Table 3: Kruskal-Wallis results describing the effect of month on different reproductive and population dynamics parameters of *P. hoplura* and *D. capensis* at a farm in Hermanus

Parameter	*P. hoplura*	*D. capensis*
Mean intensity of infestation per shell	H(10, 162) = 42.7, p < 0.00045	H(10, 160) = 20, p < 0.05
Mean number of adults per shell	H(10, 159) = 55.5, p < 0.00001	H(10, 162) = 17, p = 0.08
Mean number of juveniles per shell	H(10, 159) = 29.9, p < 0.001	H(10, 160) = 25.1, p < 0.001
Mean number of brooders per shell	H(10, 162) = 35.3, p < 0.0001	H(10, 162) = 19.7, p < 0.05

Population density showed a seasonal peak that was a direct result of increased recruitment (Levin and Huggett 1990, Zajac 1991, Sardá and Martin 1993, García-Arberas and Rallo 2004). This peak in density was followed by a sharp decline after September, which was caused primarily by post-settlement mortality of recruits, similar to that reported for *Polydora ligni* (Zajac 1991). Fluctuations in density and recruitment were not as great at Saldanha Bay. At that farm, the number of adults remained constant throughout the year, with an increase in recruits during September and October. Although the population density and recruitment was signifi-cantly higher at Hermanus than at Saldanha Bay during the late winter, densities at the two farms were remarkably similar for most of the year. The winter increase in density and recruitment would be a consequence of the high proportion of the population brooding at Hermanus, but the higher mortality observed here would probably negate the effect of increased recruitment. Although it was not measured, differences in recruitment may also be a consequence of differences in fecundity related to the size and age of the brooders (cf. Levin and Creed 1986, Zajac 1991). At Saldanha Bay, the increase in the number of juveniles coincided with the decrease in the mean size (and presumably age) of the brooders, suggesting that these juveniles were the first offspring of recently matured
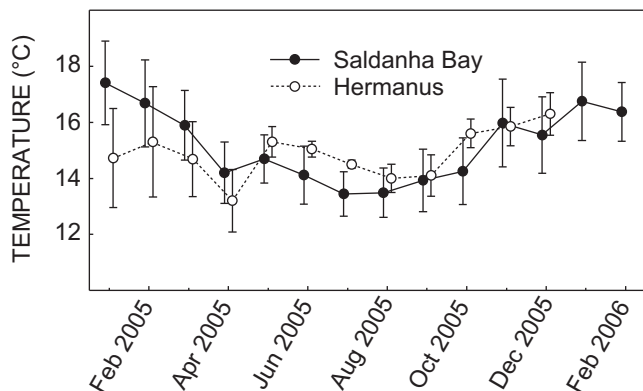
Figure 5: The mean monthly temperatures recorded in the raceways at the farms in Hermanus and Saldanha Bay from January 2005 to December 2005. Error bars denote ±SD

adults. By contrast, the increase in the number of juveniles at Hermanus occurred before the drop in the mean size of the brooders, suggesting that there the late winter recruits were the last offspring of the older worms. It can therefore be hypothesised that, as with *Streblospio benedicti* and *Polydora ligni*, high fecundity in *B. proboscidea* is related to increased body size (Levin 1986, Zajac 1991). The drop in the intensity of infestation observed at Hermanus during April may be related either to the drop in temperature, which was presumably an upwelling event, or a harmful algal bloom that comprised primarily of the dinoflagellates *Dinophysis acuminata* and *D. fortii* that occurred during that month (L Jansen, HIK Abalone Farm, pers. comm.).

Recruitment from a local source can usually be inferred from a close coupling of increased reproductive activity and increased recruitment (e.g. Levin 1984, Zajac 1991, Sardá and Martín 1993, Bolam 2004). At Hermanus and Saldanha Bay, the timing of the increase in the number of brooders roughly coincides with the period of increased recruitment, suggesting that larvae are recruited from a local source. The lack of a lag period (which occurs when larvae have a planktonic phase) could be related to the larval developmental mode of this species. On farms, the adelphophagic larvae will presumably settle on, or close to, their parental hosts, whereas the planktotrophic larvae will be released into the sea where they will develop (Lleonart 2001). Therefore, there is a potential for constant recruitment on the farm, where aldelphophagic larvae produced on-farm will be supplemented by the planktotrophic larvae re-entering the farm. The production of larvae that are maintained within the parental population would retain individuals that are adapted to local conditions (Strathmann 1990), which could result in the increased reproductive success of these pest organisms on farms (Simon *et al.* 2005). The low dispersal of the larvae and consequent increase in densities would have a positive impact on fertilisation success by polydorids like *B. proboscidea*, where males produce spermatophores that are placed close to the tubes of females (Blake and Arnofsky 1999). There is therefore the potential for an exponential increase in density and reproductive success of this worm on farms.

The presence of juvenile worms throughout the year, with periods of increased recruitment, is common in polydorid species in temperate regions. However, the exact timing of increased recruitment depends on the species and location and is usually associated with enhanced reproductive activity induced by annual rises in sea temperature and day length (e.g. Dorsett 1961, Levin 1984, Gudmundsson 1985, Levin and Creed 1986, Chu and Levin 1989, Levin and Huggett 1990, Zajac 1991, Sardá and Martín 1993, Williams 2001, Bolam 2004, García-Arberas and Rallo 2004). However, conspecifics from locations close to each other may demonstrate peak recruitment in different months when conditions differ (e.g. Gudmundsson 1985, Handley and Bergquist 1997, Bolam 2004). In the present study, recruitment of *B. proboscidea* increased from late winter to early spring when both temperature and day length increased (see also Simon *et al.* 2004). Although sea temperature started to increase a month later at Hermanus than at Saldanha Bay, the increase in recruitment started a month earlier at Hermanus, presumably as a result of the higher temperatures experienced there through most of winter.

B. proboscidea at Hermanus were larger, matured at a younger age, and had a higher growth rate, more brooders in the population and more recruits. Such differences are affected by, among others, temperature and food availability and quality (e.g. Levin and Creed 1986, Qian and Chia 1991, Simon *et al.* 2002, Simon *et al.* 2004). For example, Levin and Creed (1986) found that mimicking the winter–spring increase in temperature increased the fecundity of *Streblospio benedicti* and the proportion of the population brooding. Furthermore, high mean annual temperatures have been associated with increased abundance whereas high fluctuations in annual temperature were associated with low abundance in *Streblospio* spp. (Sardá and Martin 1993). Therefore, the increased proportions of brooding individuals observed at Hermanus from late winter to late spring/early summer, relative to that observed at Saldanha Bay, may be a consequence of both higher mean temperatures during winter as well as a lower fluctuation in mean annual temperature at Hermanus.

On abalone farms, polydorids would be exposed to high concentrations of degraded abalone food and abalone faeces (Chalmers 2002) as potential food. It is unlikely that food availability would have limited reproductive output and density at either farm, and the high concentration of potential food available within the abalone raceways would probably also counteract any effect that intraspecific density might have on reproductive output and the proportion of the population that was breeding (cf. Simon *et al.* 2005). However, it can be hypothesised that at Hermanus the increased nutrient quality of the particulate matter arising from the protein- and energy-rich pelleted feed (Chalmers 2002) that are fed to the abalone at this farm would promote increased body size (cf. Qian and Chia 1991), an increase in the population breeding (Levin and Creed 1986, Simon *et al.* 2005) and possibly growth rate.

D. capensis *and* P. hoplura

The presence of these species on the farms was inconsistent, intensity of infestation was considerably lower than that of

B. proboscidea and populations comprised mainly adults. Brooding by *D. capensis* was observed during most months, and by *P. hoplura* only from late winter to late spring. The total number of *P. hoplura* was too low to establish whether this species has a more restricted reproductive season than the other two species. It is therefore probable that the presence of these species on the farms investigated is incidental.

Implications for aquaculture

The current study highlights several factors that could have implications for the control of pest polydorids on abalone and other mollusc farms both locally and internationally because *B. proboscidea* and *P. hoplura* infest cultured shellfish also in Australia and New Zealand (Handley and Bergquist 1997, Lleonart 2001, Lleonart *et al.* 2003b). The annual patterns of recruitment by *B. proboscidea* suggest that farmers would need to implement treatment measures against polydorid infestation throughout the year, but with increased frequency during periods of increased water temperature. In addition, farm-specific conditions such as water temperature, the energy content of particulate organic matter in the abalone raceways and the location of the farm may influence the intensity of infestation and the levels of reproductive activity. These factors may also influence which species become problematic. For example, *P. hoplura* is the main problematic species on an abalone farm in the Eastern Cape Province where water temperature is consistently higher than the farms sampled in the current study (Simon *et al.* 2006). Finally, preliminary evidence suggests that differences in larval developmental mode and the subsequent time spent in the water column before settling may lead to differences in the relative abundance of problematic species (cf. Levin 1984) — *D. capensis* produces planktotrophic larvae (CAS unpublished data) whereas *P. hoplura* produces adelphophagic planktic larvae (Wilson 1928), both of which will spend some time in the water column before settling. By contrast, *B. proboscidea* produces planktotrophic and adelphophagic larvae, with the latter spending limited time in the water column (Gibson 1997).

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