The life history responses of the abalone pest, *Terebrasabella heterouncinata*, under natural and aquaculture conditions

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Abstract

The sabellid, *Terebrasabella heterouncinata*, is a small (<5 mm) intratubular brooder that lives in burrows within the host's shell matrix. It is a semi-continuous breeder and despite producing small numbers of large eggs, infestation by this animal has reached epidemic proportions on local abalone farms. The present study compared the morphometrics and reproductive characteristics of worms from farmed and wild abalone, in the Walker Bay area of the south Western Cape Province of South Africa, to gain insights into why this animal has become so successful under aquaculture conditions. The farms designated farm A and farm B each had one "on-farm" site, and two wild sites, while farm C had two on-farm sites and two wild sites. The wild sites were natural abalone habitats located within 2.5 km of the farms. Our results conclusively showed that environmental conditions prevalent on the farms enhanced the reproductive success of these worms relative to that observed in its natural environment. At farms B and C, worms occurred in significantly higher densities at the on-farm sites than in the corresponding wild samples, but at farm A, density was equally low at the three sites. At all three farms, a greater proportion of the population was reproductively active in the on-farm samples than in the wild samples. Worms on farmed abalone had a higher instantaneous fecundity, brooded more clutches simultaneously and were larger than their conspecifics from the wild. There was a positive correlation between adult size and brood size and the number of clutches brooded simultaneously. Within the three on-farm sites there was a negative correlation between egg volume and brood size, indicating a trade-off between these traits. However, such a trade-off was not apparent between sites, with brood size being higher at the on-farm sites than at the wild sites, irrespective of egg size. This suggests that the stable nutrient-enriched environment on the farm led to an increase in fecundity without compromising the size (and implicitly the quality) of the eggs. Worm density did not have a significant effect on body size or any other reproductive traits at most sites, and the density of *T. heterouncinata* was unaffected by the density of other shell-infesting polychaetes. The results suggest that the farm environment has selected for larger, more fecund worms that breed rapidly with high recruitment success as a consequence of abundant nutrients, high host density, habitat stability and a possible lack of predation and interspecific competition.

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Introduction

The sabellid, *Terebrasabella heterouncinata*, is endemic to South Africa and infests the shells of various gastropods, including the commercially important abalone, *Haliotis midae* (Ruck and Cook *1998*). It is *K*-selected, producing few large eggs that are brooded in the parental burrow until their emergence as crawling, directly developing lecithotrophic larvae (Culver et al. *1997*; Fitzhugh and Rouse *1999*). It reaches sexual maturity at 3–4 months (Ruck and Cook *1998*; Finley et al. *2001*; Simon et al. *2002*), after which it reproduces repeatedly, often brooding offspring of different ages simultaneously (Culver et al. *1997*).

The intensification of abalone farming has allowed this sabellid to settle in an environment different from that in the wild. On abalone farms, abalone are cultured at high population densities (Cook *1998*) in systems with reduced water movement in comparison to wild habitats. The farm environment provides the filter-feeding sabellids with an abundance of nutrient-rich, particulate organic matter originating from the faeces of the intensively fed abalone and degraded abalone food (Chalmers *2002*). It has also been shown that the use of pelleted abalone feed, as opposed to kelp (*Eklonia maxima*), results in abalone faeces with comparatively higher levels of protein and energy (Chalmers *2002*), promoting a higher rate of sabellid reproduction. *Terebrasabella heterouncinata* first became established as a pest on cultured abalone a decade ago (Ruck and Cook *1998*), and several generations of worms have matured under farm conditions which have probably imposed certain selection pressures on these worms (cf. McKillup and Butler *1979*; Prevedelli and Zunarelli Vandini *1998*; Prevedelli and Simonini *2001*). The abalone farms, which support substantial abalone and *T. heterouncinata* populations, therefore provided an opportunity to investigate the degree to which the life history characteristics of this sabellid polychaete have changed in response to an altered environment.

Many successful invasive and pest species mature rapidly, have a high fecundity and thrive in disturbed environments (Mozley 1960, in Grassle and Grassle *1974*; Bright *1999*) and display life history traits similar to those of opportunistic or *r*-selected species (Grassle and Grassle *1974*; Levin *1986*; Zajac *1986*; Qian and Chia *1991*; Qian *1994*). In the marine environment, this has been demonstrated in the invasive mussels *Mytilus galloprovincialis* (Hockey and van Erkom Schurink *1992*) and *Dreissena polymorpha* (Zorpette *1996*; Berkman et al. *1998*) and the sabellid polychaete, *Sabella spallanzanii* (Currie et al. *2000*). These species are characterised by a high fecundity and rapid population growth, both of which are factors that contribute to their ability to successfully compete with local species for resources. Similarly, many problematic shell-infesting polychaetes belonging to the polydorid complex, such as *Polydora websteri*, *P. ciliata* and *Boccardia proboscidea*, exhibit *r*-selected characteristics. These species produce up to 550, 4,000 and 190,000 relatively small eggs per spawn, respectively, and the larvae are planktonic (Blake and Arnofsky *1999*; Lleonart *2001*). These traits have contributed to them becoming pests under aquaculture conditions (Lleonart *2001*). By contrast, *T. heterouncinata* only broods up to ten relatively large eggs that develop into crawling larvae (Culver et al. *1997*; Fitzhugh and Rouse *1999*; Simon et al. *2002*; Gray *2004*). Despite these apparent reproductive limitations, the infestation of abalone by this worm has also become problematic under culture conditions.

While the degree of expression of life history responses of opportunistic, shell-infesting polydorid and invasive polychaete species is well documented (Levin *1986*; Zajac *1986*; Qian and Chia *1991*; Qian *1994*; Blake and Arnofsky *1999*; Currie et al. *2000*), the quantification of the reproductive success of pest polychaetes under natural and altered environmental conditions has received scant attention. No studies have compared the growth and reproduction of *T. heterouncinata* from farmed and wild abalone, although Gray (*2004*) demonstrated a degree of variability in reproductive and morphometric characteristics of this worm sampled from four abalone farms in the Western Cape Province of South Africa. Gray (*2004*) also showed that the number of eggs brooded by worms on different farms ranged between 1 and 10. This is in stark contrast to some shell-boring polydorid polychaetes that show up to 100-fold differences in fecundity under different conditions (Blake and Arnofsky *1999*). The degree to which *T. heterouncinata* can increase its fecundity is probably limited by its small size due to limited coelomic space for storing developing eggs (Hermans *1979*; Olive *1985*), as well as limited storage space within the burrow. The high levels of infestation observed on cultured abalone (Oakes and Fields *1996*; Culver et al. *1997*; Ruck and Cook *1998*; Gray *2004*) can probably be attributed to the short generation time, abundant resources, high larval survival owing to parental care and high recruitment success on abalone farms where the hosts live in close proximity to one another.

This study was therefore designed to compare the reproductive output of sabellids from abalone cultured on three farms with that of worms from wild abalone at varying distances from each of these farms. This was done in an attempt to understand the reproductive characteristics that determine the population growth of *T. heterouncinata* on cultured abalone.

Materials and methods

Sample sites

Sabellid-infested abalone with shell lengths ranging from 70 to 90 mm were collected between 26 September and 2 October 2003 from and in the vicinity of three abalone farms in the Walker Bay area of South Africa (Fig. 1). The identities of the farms have been withheld for the sake of propriety, and are referred to as farms A, B and C, respectively. Farms A and B are situated close to Gansbaai, while farm C is situated close to Hermanus. Abalone were collected on the farms, from the farms' effluent flow, and from the wild in the vicinity of each farm. The following codes will be used throughout the document to distinguish the different farms and their respective sampling sites: farm A-F and farm B-F: abalone were sampled on-farm from the production raceways; farm A-E and farm B-E: at the point where the farm effluent entered the sea at the exit of the outflow pipe; farm A-W: at the wild site 2 km east of farm A; farm B-W: the wild site 1.5 km south of farm B; farm C-F1: on-farm, from the production raceways; farm C-F2:

the farm effluent channel; farm C-W1: in the shallow sub-tidal zone, 60 m from the outflow of farm C; farm C-W2: at a wild site 2.5 km west of farm C (Fig. 1).

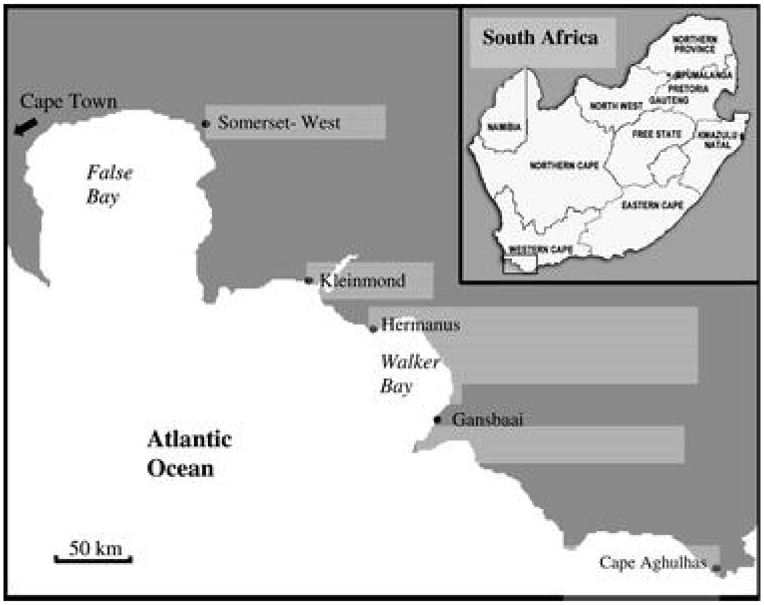

Fig. 1 Walker Bay in the Western Cape Province, South Africa. Farms A and B are situated in the vicinity of Gansbaai, and their associated wild sites were 2 km east and 1.5 km south of the two farms, respectively. Farm C is situated in the vicinity of Hermanus with its associated wild sites situated 60 m and 2.5 km to its west

The three farms employed land-based culture systems, rearing abalone in baskets that were suspended in raceways. The baskets contained vertical plastic plates which served as the attachment surface for the abalone. The dimensions and construction of raceways differed between farms (Table 1). Abalone were fed either freshly harvested kelp (*Eklonia maxima*), a major component of their natural diet, or the artificial pelleted feed, Abfeed, with the frequency of feeding dependent on the food type and farm management practise (Table 1). Abfeed was placed on feeder plates that were positioned horizontally across the top of the vertical plates. At night the abalone emerged to feed on the horizontal plates. Kelp was placed in the baskets between the vertical plastic plates. In these tanks the abalone had continuous access to food. Many management procedures differed between farms. Important differences were the stocking densities of abalone, sorting intervals to maintain a constant stocking density and size variation, tank cleaning routine, and flow rate of water through the tanks. In addition, the average water temperature of the raceway differed between farms (Table 1). The three farms each produced an effluent flow of approximately 1,000 m^3/h. The collection sites at the farm effluent outfalls and the nearby wild sites were typical juvenile abalone habitat (1–3 m depth), with a kelp (*E. maxima*) canopy, abundant sea urchins on the rocky substrate, and the cryptic juvenile abalone found under urchins and in rock crevices. At farm C's effluent outfall the exposed, high relief rocky habitat supporting a dense *Pyura* covering did not appear suitable for juvenile abalone, and only a few large abalone were observed when a collection was attempted. Therefore, abalone were sampled from within the concrete effluent channel on the farm itself.

Table 1 A summary of the environmental conditions and management procedures employed by farms A, B and C

	Farm A	Farm B	Farm C
Abalone diet	Kelp	Abfeed	Kelp and abfeed
Feeding regime	Every 3rd day	Every 2nd day	Daily
Size sorting	Every 6 months	Every 4 months	Every 5 months
Stocking density (% surface area)	30%	20–35%	18–20%
Flow rate (exchange of water/h)	1.5	2.2	3.3
Average temperature (May 2003–October 2003)	Raceway: 16.4 °C	Raceway: 16.1 °C	Raceway: 15.4 °C
	Sea: 14.9 °C	Sea: 14.9 °C	Sea: 15.5 °C
Tank cleaning routine	Information withheld	Weekly	Abfeed: weekly
			Kelp: fortnightly
Tank volume and construction	7.3 m^3	4 m^3	3.5 m^3
	Fibre reinforced concrete	Concrete	Concrete

Removal of worms and measurements

Ten live abalone were sampled from each of the ten sites. The abalone were shucked and worms were preserved in the shells in 4% seawater formalin and transferred to 70% ethanol after 1 week. Blocks of shell measuring approximately 1 cm^2 were cut from the region 1.5–2.0 cm from the growing edge and immediately to the right of the respiratory pores, with the anterior part of the shell facing forwards. The blocks of shell were dissolved in 5% nitric acid in 70% ethanol for 12–24 h. These softened shells were stored in 70% ethanol until the worms were removed. The total number of worms and number of worms brooding was determined for each block. From each block ten brooding worms were sampled for the following measurements:

1. Length of adult worms (mm), excluding the feeding crown, and pre-emergent larvae, i.e., larvae with eye spots, measured with a graduated eyepiece at 2.5 or 5 times magnification.
2. Egg volume (mm^3) calculated according to the equation $V=(^4/_3)\pi A^2B$, where A is the short and B the long axis of the egg (Qian and Chia *1991*).
3. The number of offspring in each burrow (i.e., instantaneous fecundity).

4. The number of clutches per burrow. A clutch signifies all offspring at a similar developmental stage. The clutches are defined as (1) developing oocytes visible within the body cavity, (2) eggs without any signs of segmentation, (3) larvae with visible segmentation but without eye spots, and (4) pre-emergent larvae with eye spots. Thus, up to four clutches could be observed in one burrow.

If there were less than ten brooding worms in a block, non-brooding worms were measured, to make the total up to 10. The number of polydorid polychaetes in each square was also determined.

Data analysis

To avoid pseudoreplication data from worms found on each abalone shell were averaged. Thus, there were up to ten values for each site and comparisons between sites were done using ranks as described below. For each shell, the average length was calculated for gravid and non-gravid adults, and pre-emergent larvae. Egg volume was averaged for each shell. Average instantaneous fecundity was calculated using only the values from tubes containing brooding worms. All values for the number of clutches per brood were used for the analyses (see below). Due to the differences in conditions between farms (Table 1) only data from each farm and its associated sites were compared with each other. The effect of the sampling site on the number of sabellids mm^{-2}, percent sabellids brooding, egg volume, length of pre-emergent larvae and instantaneous fecundity was tested by using the Kruskal-Wallis ANOVA by ranks. This test was chosen due to the small sample sizes. If significant differences between sites were indicated at an error level of 5%, multiple comparisons of average ranks were done according to a method proposed by Siegel and Castellan (*1988*). The effect on adult length of the independent variables "site" and "reproductive state" (i.e., if the adult was gravid or not) was tested using a two-way ANOVA including a test for interactions between these two effects, followed by Tukey's (HSD) test for unequal sample sizes. The effect of sampling site on the number of clutches per brood was analysed using contingency analysis (Zar *1999*). Spearman rank correlations were calculated between different variables related to the worm's morphometrics and reproduction. The minimum size at maturity was calculated as the average length of the 25% shortest mature worms per site.

Results

Density of worms

At farm A there was no significant difference between the sampling sites with respect to the number of worms per mm^2 of shell (H=0.4, P=0.82, Table 2) with values averaging between 0.73 and 0.78 worms mm^{-2}. By contrast at farm B the number of worms per mm^2 shell was 3–5 times higher in abalone sampled on-farm (H=15.74, P=0.004, Table 2) in comparison to the two associated sub-tidal sites. At farm C the lowest number of worms (0.12 worms mm^{-2}) was recorded for the wild site (farm C-W2), 2.5 km to the east, while the abalone sampled from the farm production raceways (farm C-F1), the on-farm effluent channel (farm C-F2), and 60 m from the effluent outfall (farm C-W1) had similar but much higher densities ranging from 0.71 (farm C-W1) to 1.17 (farm C-F2) worms mm^{-2} (H=23.85, P<0.00001, Table 2).

Table 2 Expression of various reproductive traits of *Terebrasabella heterouncinata* on farm A, farm B and farm C, and wild sites at different distances from the farms. All values are average ±SD, followed by the number of values. *Identical letters* denote no significant difference between averages

Reproductive trait	Average±SD			
	Farm A-W	Farm A-E	Farm A-F	
Density (worms mm^{-2})	0.78±0.72, 10^{a}	0.74±0.56, 10^{a}	0.73±0.23, 10^{a}	
% Brooding	13.28±12.34, 10^{a}	26.57±25.69, 10^{b}	80.9±5.39, 10^{c}	
Adult size (mm)	1.36±0.28, 16^{a}	1.74±0.4, 15^{b}	2.41±0.3, 20^{c}	
Number of offspring per adult	1.95±0.72, 8^{a}	2.11±0.44, 7^{a}	8.76±2.31, 10^{b}	
Egg volume (mm^{3})	0.024±0.006, 8^{a}	0.033±0.003, 7^{b,c}	0.027±0.002, 10^{a,c}	
Larvae length (mm)	0.42±0.03, 5^{a}	0.46±0.01, 5^{a}	0.49±0.02, 10^{b}	
Minimum size at maturity (mm)	1.2	1.58	1.67	
	Farm B-W	Farm B-E	Farm B-F	
Density (worms.mm^{-2})	0.3±0.3, 10^{a}	0.42±0.48, 10^{a}	1.48±0.43, 10^{b}	
% Brooding	21.88±29. 9, 10^{a}	12.24±15.2, 10^{a}	62.14±7.97, 10^{b}	
Adult size (mm)	1.35±0.26, 15^{a}	1.37±0.31, 11^{a}	2.25±0.21, 20^{b}	
Number of offspring per adult	1.31±0.41, 8^{a}	2.0±1.2, 5^{a}	4.92±0.92, 10^{b}	
Egg volume (mm^{3})	0.021±0.006, 5^{a}	0.029±0.003, 4^{a}	0.034±0.003, 9^{b}	
Larvae length (mm)	0.48±0.03, 3^{a}	0.44±0.04, 2^{a}	0.56±0.04, 9^{b}	
Minimum size at maturity (mm)	0.95	1.2	1.91	
	Farm C-W1	Farm C-W2	Farm C-F1	Farm C-F2
Density (worms mm^{-2})	0.71±0.75, 10^{b}	0.12±0.11, 10^{a}	0.8±0.4, 10^{b}	1.17±0.67, 10^{b}
% Brooding	15.59±24.39, 10^{a}	19.1±24.32, 10^{a}	67.19±14.66, 10^{b}	58.6±14.85, 10^{a,b}
Adult size (mm): gravid adults	1.61±0.32, 6^{a}	1.74±0.24, 5^{a}	2.29±0.33, 10^{b}	2.55±0.32, 10^{b}

Reproductive trait	Average±SD			
Adult size (mm): non-gravid adults	1.33±0.35, 9^{c}	1.35±0.37, 10^{c}	2.08±0.34, 10^{d}	2.39±0.23, 10^{d}
Number of offspring per adult	1.8±1.2, 6^{a}	2.33±1.1, 3^{a}	5.26±1.28, 10^{b}	5.48±1.23, 10^{b}
Egg volume (mm^3)	0.026±0.005, 5^{a}	0.028±0.003, 3^{a}	0.031±0.003, 10^{a}	0.032±0.003, 10^{a}
Larvae length (mm)	0.47, 1	0.47±0.05, 2^{a}	0.47±0.04, 10^{a}	0.55±0.03, 10^{b}
Minimum size at maturity (mm)	1.52	1.24	1.67	2.1

Percentage of reproductively active worms

For each farm, the percentage of brooding worms was significantly higher for the samples from the production raceways in comparison to the corresponding effluent outfall and wild sites (farm A: H=19.76, P<0.0001; farm B: H=15.74, P<0.0003; farm C: H=19.6, P<0.0002, Table 2). At farm A-F the average percentage of reproductively active worms was approximately 81%, which was about six times more than at farm A-W and farm A-E. Similarly, about 62% of the worms from the farm B-F samples were brooding, and this was 3–4 times more than at farm B-W and farm B-E. Between 67 and 59% of the adult sabellids were brooding in the farm C-F1 and farm C-F2 samples, respectively, while the respective values for the two wild sites (farm C-W1 and farm C-W2) ranged between 16 and 19%, thus suggesting a positive effect of the farm environment on sabellid reproduction.

Body size and minimum size at maturity

There was a significant difference in adult length between all sampling sites at farm A, but reproductive state did not affect length and there were no interactions between the main effects (site effect: F=45.2, P<0.0001; reproductive state effect: F=4, P=0.051, interaction term: F=1.5, P=0.23). Sabellid adult length was greatest on the farm, followed by the effluent, and wild site (Table 2). Similarly, adult length was significantly greater at farm B-F than at farm B-W and farm B-E, and was not affected by reproductive state (site effect: F=61.2, P<0.0001; reproductive state effect: F=1.1, P=0.31; interaction term: F=0.57, P=0.57, Table 2). Thus, the values for adult length of both gravid and non-gravid worms from farm A and farm B were averaged for further analyses. Both site and reproductive state had a significant effect on adult size at farm C (site effect: F=35.5, P<0.0001; reproductive state effect: F=9.8, P<0.003; interaction term: F=0.33, P=0.8). The worms at both farm C-F1 and farm C-F2 were longer than those at the two wild sites (farm C-W1 and farm C-W2) and gravid worms were significantly longer than non-gravid worms (Table 2). At all farms, the minimum size at maturity was greater in sabellids from farmed abalone than the respective wild sites (Table 2). There was a weak negative correlation between the number of worms mm^{-2} and adult length at the farm A-W site (Table 4).

Size of offspring

Site affected the size of the offspring at farm A and farm B in different ways (Table 2). At farm A the average sabellid egg size from animals sampled on farmed abalone was not significantly different from that at the wild sites, but sabellid eggs from the effluent site were significantly larger than eggs from the wild site ($H=9$, $P<0.011$, Table 2). Sabellid larvae on farmed abalone were larger than those from the marine sites ($H=12.74$, $P<0.002$, Table 2). At farm B eggs and larvae on the farm were larger than those from the marine sites ($H=11.18$, $P<0.004$; $H=7.58$, $P<0.02$, for the egg volume and larvae length, respectively). Site had no effect on the volume of eggs from farm C, while the length of the larvae from farm C-F2 was significantly larger than at the other sites ($H=7.3$, $P=0.06$; $H=14.14$, $P<0.001$, for egg volume and larvae length, respectively). At farm C-W1 only one pre-emergent larva was measured, and this site was therefore excluded from the analysis.

Fecundity, number of clutches per burrow and investment per brood

For all farms instantaneous fecundity and the number of clutches per worm were significantly higher at the on-farm sites than at any of the corresponding wild sites (farm A: $H=17.41$, $P<0.002$; $\chi_2=70.7$, $P<0.001$; farm B: $H=16.83$, $P<0.0002$, $\chi_2=87.69$, $P<0.001$ and farm C: $H=16.21$, $P<0.001$; $\chi_2=28.17$, $P<0.001$, for instantaneous fecundity and the number of clutches, respectively). There was a large variation in brood size. The fecundity of worms at the six wild sites ranged from four to eight offspring per brood. The largest brood of 21 eggs and larvae was recorded at farm A-F. The maximum brood size on the farm at farm C-F1 was 15, and 11 at farm B-F. Up to 64% and 59% of the worms from the on-farm sites at farm A and farm B, respectively, brooded three or four clutches while up to 15% and 2.5% of the worms brooded that many clutches at the wild and effluent sites (Table 3). At farm C the differences between the worms from the on-farm and wild sites were not as great; between 17% and 43% of the worms at the wild sites brooded more than two clutches, while 31% to 43% of the worms from the on-farm sites brooded that many clutches. Only 4% of the worms from the wild sites and up to 12% of the worms from the on-farm sites brooded four clutches.

Table 3 The frequency of brooding of different numbers of clutches brooded simultaneously by *T. heterouncinata* (with percentages in *parentheses*) on farm A, farm B and farm C and marine sites at different distances from the farm

No. clutches	Brooding frequency (%)			
	Farm A-W	Farm A-E	Farm A-F	
1	29 (60%)	18 (38%)	8 (9%)	
2	12 (25%)	24 (50%)	25 (27%)	
3	7 (15%)	5 (10%)	42 (45%)	
4	0	1 (2%)	18 (19%)	
	Farm B-W	Farm B-E	Farm B-F	
1	30 (75%)	13 (50%)	7 (7%)	
2	9 (22.5%)	13 (50%)	33 (33%)	
3	1 (2.5%)	0	48 (48%)	
4	0	0	11 (11%)	
	Farm C-W1	Farm C-W2	Farm C-F1	Farm C-F2
1	13 (45%)	5 (22%)	15 (17%)	14 (15%)
2	11 (38%)	8 (35%)	47 (52%)	32 (33%)
3	5 (17%)	9 (39%)	18 (20%)	38 (39%)
4	0	1 (4%)	10 (11%)	12 (13%)

There were significant positive correlations between adult size and instantaneous fecundity as well as number of clutches at most sites (Table 4). At farm C there was no correlation between the length of non-gravid adults and instantaneous fecundity at both wild sites, and there was no correlation between non-gravid adult length and clutch number at farm C-W1. Similarly, no correlation existed between these factors at the farm B-W and farm B-E sites. At all three on-farm sites there was a negative correlation between egg volume and brood size, while this relationship showed a positive correlation at farm B-W (Table 4). Egg volume and the length of pre-emergent larvae were not significantly correlated with each other except at the farm C on-farm site, where the correlation was positive (Table 4). Density and brood size were positively correlated at farm C-W1, farm A-E and farm B-E. The same was found for density and number of clutches at farm A-E. There were negative correlations between density and the number of clutches at farm C-W2 and between density and brood size at farm A-F.

Table 4 Correlations between various life history parameters of *T. heterouncinata* at farm A, farm B and farm C and marine sites at different distances from the farms. The statistics listed are the coefficients of determination (*r*), *P* and *n*. NS=not significant at $P \leq 0.05$. At farms A and B the lengths of gravid and non-gravid worms were not significantly different from each other, and the pooled data were used in the relevant analyses. At farm C the lengths of gravid and non-gravid worms were different, and the relevant analyses were conducted separately for the two groups

Parameter	Statistics			
	Farm A-W	Farm A-E	Farm A-F	
Adult length vs egg volume	NS	NS	–0.26, <0.001, 87	
Adult length vs brood size	0.64, <0.001, 48	0.49, 0.001, 48	0.8, <0.001, 93	
Adult length vs number of clutches	0.48, 0.001, 48	0.51, 0.001, 48	0.52, <0.001, 93	
Log egg volume vs brood size	NS	NS	–0.47, <0.001, 87	
Density vs adult size	–0.35, 0.014, 48	NS	NS	
Density vs brood size	NS	0.31, 0.03, 47	–0.21, 0.048, 93	
Density vs number of clutches	NS	0.34, 0.018, 48	NS	
	Farm B-W	Farm B-E	Farm B-F	
Adult length vs egg volume	NS	NS	NS	
Adult length vs brood size	NS	NS	0.56, <0.001, 99	
Adult length vs number of clutches	NS	NS	0.37, <0.001, 99	
Egg volume vs brood size	0.19, 0.03, 19	NS	–0.21, 0.045, 87	
Density vs adult size	NS	NS	NS	
Density vs brood size	NS	NS	0.57, 0.002, 25	
Density vs number of clutches	NS	NS	NS	
	Farm C-W1	Farm C-W2	Farm C-F1	Farm C-F2
Non-gravid adult length vs egg volume	NS	–0.53, 0.01, 23	NS	NS
Gravid adult length vs egg volume	NS	NS	NS	NS

Parameter	Statistics			
Non-gravid adult length vs brood size	NS	NS	0.73, <0.001, 63	0.71, <0.001, 64
Gravid adult length vs brood size	NS	NS	NS	NS
Non-gravid adult length vs brood size	NS	NS	NS	NS
Gravid adult length vs brood size	0.85, <0.002, 10	0.69, 0.013, 12	0.53, 0.002, 33	0.63, <0.001, 33
Non-gravid adult length vs clutch number	NS	0.52, 0.03, 17	0.52, <0.001, 63	0.61, <0.001, 64
Gravid adult length vs clutch number	0.91, 0.001, 10	0.67, 0.016, 12	0.38, 0.029, 33	0.42, 0.032, 33
Egg volume vs brood size	NS	NS	NS	–0.29, 0.01, 73
Egg volume vs larvae length	NS	NS	NS	0.43, 0.04, 32
Density vs non-gravid adult length	NS	NS	NS	NS
Density vs gravid adult length	NS	NS	NS	NS
Density vs brood size	0.47, 0.025, 21	NS	NS	NS
Density vs number of clutches	NS	–0.4, 0.03, 29	NS	NS

Density of polydorid spp.

The density of *Polydora* spp. at the three farms ranged between 0.007 and 0.09 worms mm^{-2}. There was no significant correlation between the density of polydorid spp. and *T. heterouncinata* at any of the farms.

Discussion

Environmental factors and reproduction

This study showed that the environmental conditions on the abalone farms studied enhanced the sabellid's reproductive success relative to that observed in the adjacent natural environment. On all three farms, a relatively greater percentage of sabellids were brooding offspring and adult worms were larger, had a higher instantaneous fecundity, and brooded more clutches simultaneously than those sampled from the corresponding wild sites. At two of the three farms, the density of worms that had successfully settled on the abalone shells was higher than at the respective wild sites. These findings, together with suggestions from other studies on the biology of this sabellid species (Kuris and Culver *1999*; Chalmers *2002*; Gray *2004*), suggest that the farm environment, with its high availability of food in the form of suspended organic material, stable habitat and high density of potential hosts, favours the reproduction and population growth of this species, enabling it to become a pest under aquaculture conditions.

The combined effects of the farm environment resulted in an increased average sabellid adult size as the worms from farms were 1.4–1.7 times larger than their wild conspecifics. These differences in adult size may be related to the increase in nutrients available on the abalone farms. Analogous differences in body size related to diet have also been observed in *Capitella* sp., where individuals fed *Ulva* were 1.6 times smaller than those fed squid egg capsules (Qian and Chia *1991*). The effect of reproductive state on adult size was not consistent across sites. At farms A and B the reproductive state, i.e., gravid and not gravid, respectively, did not have a significant effect on the length of the adults while at all farm C sites, gravid worms were significantly larger than non-gravid individuals (cf. Simon et al. *2002*). However, at all farm sites the average minimum size of reproductively active worms was generally larger than at the corresponding wild sites. This concomitant increase in the minimum size at sexual maturity with an increase in adult size was also demonstrated in laboratory-reared *T. heterouncinata* (Simon et al. *2002*), *Capitella* sp. I (Bridges et al. *1994*) and *Littorina rudis* (Hart and Begon *1982*). In laboratory-reared *T. heterouncinata* (Simon et al. *2002*) and *Capitella* sp. I (Bridges et al. *1994*), the treatments that resulted in the greatest growth rate and adult size were associated with decreased age-at-maturity. This response is consistent with predictions made by Stearns and Koella (*1986*) for animals with different growth rates. Although the age-at-maturity of *T. heterouncinata* in the present study is not known, it is clear that worms on farms reach maturity at a size greater than the size at which they were observed to become reproductive in the wild. As worms on farms are exposed to increased nutrients, they may be growing more rapidly, and reaching maturity at the same or earlier age, than their wild conspecifics (cf. Stearns and Koella *1986*; Bridges et al. *1994*; Simon et al. *2002*).

In *T. heterouncinata* reproductive success may also be determined by instantaneous fecundity and the time interval between clutches. In this study the worms at the four on-farm sites were between 2.9 and 4.5 times more fecund than their wild conspecifics. This increase in fecundity was probably related to nutrient enrichment or a combination of nutrient enrichment and the stability of the environment, as has been demonstrated in the polychaetes *Capitella* sp. I (Bridges et al. *1994*), *Dinophilus gyrociliatus* (Prevedelli and Simonini *2001*), *Polydora ligni* (Zajac *1986*), *Ophryotrocha labronica* (Prevedelli and Zunarelli Vandini *1998*) and *Capitella* sp. (Qian and Chia *1991*). The number of different age classes of larvae and embryos (i.e., the number of clutches) brooded simultaneously can be used as an indication of the rate at which eggs are being produced (Rouse *1992*). As *T. heterouncinata* living on farmed abalone tended to brood more clutches than their wild conspecifics, they probably produced eggs more rapidly.

Investment in reproduction and trade-off between offspring number and size

Investment in offspring is also determined by the size of the eggs or larvae. Worms from the on-farm sites did not always produce larger eggs and larvae than their wild conspecifics, suggesting that under altered conditions the worms do not adjust the investment per offspring. Furthermore, there was a weak positive correlation between egg volume and larvae length only at one of the on-farm sites at farm C. Thus, the prediction that larger eggs lead to the development of larger larvae (McClintock and Pearse *1986*) does not always hold true.

In order to better understand the investment of energy into offspring correlations between the size of adults and the size and number of offspring were estimated. Findings were not consistent for all farms and sites. At most sites egg size was independent of adult size, i.e., these variables did not correlate. There was, however, a significant negative correlation between adult length and egg volume on farm A. This was coupled with a negative correlation between brood size and egg volume, a positive correlation between adult size and brood size and a very high fecundity. This suggested that on average, larger adults produced more eggs while investing less energy into each egg as brood size increased.

At most sites, there was a positive correlation between adult size and fecundity, and adult size and number of clutches, respectively. Adult size and fecundity have been found to be positively correlated in the polychaetes *Polydora ligni* (Zajac *1986*), *Capitella* sp. (Qian and Chia *1992*; Qian *1994*), *Nereis arenaceodentata* (Moore and Dillon *1993*), *Capitella* sp. I (Bridges et al. *1994*) and *Streblospio benedicti* (Levin *1986*) and the winkle, *Littorina rudis* (Hart and Begon *1982*). This may be related to an increase in space available for the storage of developing oocytes within the body cavity (Hermans *1979*; Olive *1985*; van Dover et al. *1999*). By contrast, there was no relationship between body size and number of spawns in *Capitella* sp. with planktotrophic development (Qian and Chia *1992*) and there was a negative correlation between body size and number of egg capsules in *Nassarius pauperatus* (McKillup and Butler *1979*). The positive relationship found in this study between body size and the number of clutches may have been due to an increase in food availability on the abalone farms that simultaneously allowed sabellids to grow larger and produce eggs more rapidly.

A trade-off exists between the number of offspring produced and the amount of energy invested per offspring. If the amount of energy devoted to reproduction is to remain constant, an increase in fecundity will occur at the expense of the energy devoted to each offspring, but if energy devoted to reproduction is proportional to food availability, both fecundity and egg quality may change (Stearns *1976*; Qian *1994*). At all farms, the fecundity of worms on farmed abalone was greater than that of worms on wild abalone, irrespective of the mean size of the eggs at these sites. This was probably due to (1) the observed greater body size of the “farm” worms, and (2) a probable increase in nutrient availability in the abalone production systems providing the worms with relatively more energy to invest in reproductive output. At all four on-farm sites there was a negative correlation between instantaneous fecundity and egg volume. Similarly, egg volume has been negatively correlated with fecundity in *Capitella* sp. (Qian and Chia *1992*; Qian *1994*), and the molluscs *Littorina rudis* (Hart and Begon *1982*) and, in part, in *Nassarius pauperarus* (McKillup and Butler *1979*). This suggests that in some circumstances, reproductive output is limited either by available space in the body cavity, or by available energy, and that reproductive output is optimised by producing fewer, smaller eggs. The lack of a correlation between these variables in worms from the wild sites suggests that egg number may have been too low to compromise egg volume.

Reproduction and settlement success

At farms B and C, sabellid density, i.e., the number of sabellids per mm^2 of shell, was significantly greater on farmed abalone than on abalone from the related wild sites, and is presumably a consequence of the greater reproductive output or settlement success of the worms at these sites. By contrast, the densities of worms on abalone shells at the three farm A sites were very similar, despite the observed reproductive output of the worms on the farmed abalone being significantly greater than that of worms on the wild abalone. This suggests a relatively low survival rate of worms at this site.

The relationship between sabellid density and their reproductive traits was not consistent across farms, with few significant correlations existing between sabellid density and adult size, brood size and the number of clutches, respectively. Where significant correlations existed, the coefficients of determination were low, and all but one significant correlation was found at the wild sites. Thus only a small percentage of the variation in reproductive traits could be explained by the variation in density. Linke-Gamenick et al. (*1999*) suggested that the negative impact of high density on most reproductive parameters may be related to food limitations. While this may partly explain findings related to the wild sites, food limitation is unlikely to have occurred at the on-farm sites (Chalmers *2002*). Overall, the potentially negative effect of sabellid density on their reproductive success was low, thus intraspecific competition may not have played an important role. This is in contrast to many other sessile marine invertebrates where high settlement densities can lead to intraspecific competition which may affect the survival, growth and reproductive success of individuals within the population (Wilson *1983*; Levin *1986*; Zajac *1986*; Linke-Gamenick et al. *1999*; Hills and Thomason *2003*). Densities of worms on farmed abalone were up to six times higher than in their wild conspecifics, and it is suggested that, under conditions of unlimited food and increased host availability, intraspecific competition was negligible in this species within the range of densities observed.

Interspecific competition may also influence the density and reproductive rate of competing organisms. For example, densities of the competing spionids, *Pygospio elegans* and *Pseudopolydora kempi* were inversely proportional to each other when they occurred at the same site (Wilson *1983*). In addition, an increase in the density of *P. kempi* was also associated with a reduction in reproduction by *P. elegans* (Wilson *1983*). The abalone shells used in the present study were infested by both *T. heterouncinata* and several shell-boring polydorid polychaete species. The polydorids are much larger (between 10 and 15 mm in length, personal observation) than *T. heterouncinata* and could potentially compete with them for space. The density of polydorids was, however, comparatively low, ranging from 1 to 14 worms per block of shell, and there was no correlation between the density of the polydorids and the sabellids.

Changes in the expression of life history traits of the sabellid

Many studies have demonstrated the phenotypic plasticity of the expression of life history traits by polychaetes exposed to different environmental conditions (e.g., Levin *1986*; Zajac *1986*; Grémare et al. *1988*; Qian and Chia *1991*, *1992*; Bridges et al. *1994*; Qian *1994*; Prevedelli and Zunarelli Vandini *1998*; Prevedelli and Simonini *2001*; Simon et al. *2002*). In these studies, the responses to the environmental conditions were usually immediate, and were therefore probably not the result of a change in the genotype of the animal. Thus, the differences in the degree of expression of life history traits in *T. heterouncinata* from different environments might be phenotypic only. However, since its discovery on farmed abalone in 1994 (Ruck and Cook *1998*), *T. heterouncinata* has been present on South African farms for more than 40 generations and it is therefore reasonable to hypothesise that natural selection may have resulted in a possible genetic basis to the observed changes in the expression of life history traits (cf. McKillup and Butler *1979*). Anecdotal evidence suggests that the maximum number of eggs per brood recorded for worms from the on-farm sites has increased in recent years, as a previous study by Gray (*2004*) in 2001 recorded a maximum of 7 and 6 eggs per brood at farm A and C, respectively, while in the present study, 13 and 9 eggs per brood were observed at these farms, respectively. These results suggest that the success of *T. heterouncinata* on the abalone farms may be related to the selection for large worms that produce more offspring more rapidly. This may be a result of abundant food resources, a possible lack of predation, low intra- and interspecific competition, and the increased availability of hosts.

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