Aspects of the ecology and population genetics of the bivalve *Corbula gibba*

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ABSTRACT: The bivalve mollusc *Corbula gibba* (Olivi) is often regarded as an invasive weed species that forms monospecific stands in organically enriched hypoxic habitats. However, despite its status as a potential menace, surprisingly little is known about its basic biology, including its dispersal capacity. Measurement of the respiration rate of *C. gibba* revealed a respiratory demand of 3.12 µl O_2 h^{-1} and a respiratory quotient of 0.61, which suggests that *C. gibba* adopts a conservationist rather than exploitative mode of life. Examination of the hypoxic tolerance of *C. gibba* determined that adults could survive for >34 d ($LT_{50} \geq 34$ d) and juveniles for >30 d ($LT_{50} = 14$ d), indicating that this species is well adapted to living in low oxygen habitats. Unusually, adults under hypoxia had a greater survival rate than control adults in normoxic conditions. Investigation of the salinity tolerance of *C. gibba* revealed that it could readily survive for 2 d at 0 to 16 psu, with increasing mortality for up to 10 d. In brackish seawater, survival was indistinguishable from that in normal seawater. Examination of the population genetics of 6 different populations of *C. gibba* separated over various spatial scales, using RAPD PCR methodology, determined that all populations were genetically distinct from each other, including populations separated by as little 5 km, although this may in part be due to the influence of a localised front. This suggests that the larval longevity and dispersal capacity of *C. gibba* is much less than has been previously considered. In light of all the results, it is concluded that instead of being an insidious pest species, *C. gibba* is more likely to be an inferior competitor, present in background numbers in normoxic habitats, and only becomes dominant when a system becomes hypoxic, thereby removing competitors and allowing *C. gibba* to flourish in the habitat to which it is adapted.

KEY WORDS: Dispersal · *Corbula gibba* · Hypoxia · RAPD · Respiration · Salinity · Teleplanic

INTRODUCTION

The bivalve mollusc *Corbula gibba* (Olivi) is generally regarded as an invasive pest species (Crema et al. 1991, Wilson et al. 1998, Currie & Parry 1999, Talman & Keough 2001) colonising organically enriched environments resulting in monospecific stands (Pearson & Rosenberg 1978, Jensen 1990, Theodorou 1994, Giacobbe & Rinelli 2002). Accordingly, the accidental introduction of *C. gibba* into non-indigenous habitats, through ballast water, sea chests etc. (Carlton 1985, Coutts et al. 2003) has led some authors to suggest that *C. gibba* may pose a serious biological threat (Currie & Parry 1999, Talman & Keough 2001).

However, given the alleged menace of *C. gibba*, it is surprising that there are only a few, mainly descriptive, studies in the literature about its biology and ecology. In addition, very little is known about its developmental strategy, i.e. length of larval life, and hence there are no estimates of its dispersal potential and/or the speed with which it can colonise new habitats.

In terms of what is known, *Corbula gibba* is widely distributed from the Norwegian Sea southwards to the west coast of Africa (Tebble 1966). It is commonly found subtidally, in coastal and estuarine silts and muddy gravels. In locations where *C. gibba* is prevalent, it can account for >80% of the total benthic

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biomass, at densities of 1000 to 4500 individuals m^{-2} (Rosenberg 1977, Jensen 1990, Moodley et al. 1998, Giacobbe & Rinelli 2002), and is considered to be one of the most productive bivalve species (Laureta 1986, Jensen 1990). *C. gibba* is both a highly efficient filter feeder, even more so than mussels (Kiørboe & Mohlenberg 1981) and a surface deposit raker (Yonge 1946). Longevity is around 5 yr (Jensen 1990) and sexes are separate (dioecious), with external ferti-lisation leading to the production of larvae (Yonge 1946). The length and mode, i.e. planktotrophic or lecithotrophic, of larval life is unknown, although some authors estimate it as greater than 3 mo (i.e. tele-planic) (Jorgensen 1946, Thorson 1946, Jones 1956, Hrsbrenko 1981), whilst others consider it to be less than 1 mo (i.e. actae/anchiplanic) (Yonge 1946, Muus 1973). Thus, the timing of recruitment and frequency (voltism) of spawning appear to be highly variable. It is worth noting, with the exception of Yonge (1946), that all other authors (Jorgensen 1946, Thorson 1946, Jones 1956, Muus 1973, Hrsbrenko 1981) have inferred the larval longevity of *C. gibba* from the appearance of recruits in the benthos, whereas Yonge (1946) observed that the large yolky eggs of *C. gibba* were more indicative of a short rather than a long larval life (see also Laureta 1986).

Because of its normal habitat, i.e. muddy hyposaline sediments, *Corbula gibba* is considered to be resistant to both hypoxia and low salinity conditions. However, the only observation directly pertaining to the hypoxic tolerance of *C. gibba* is observational in nature, and concluded that adult *C. gibba* could survive hypoxic conditions for 57 d (Christensen 1970). There are no observations in the literature as to the salinity toler-ance of *C. gibba*.

The aims of this study were: (1) to measure the respi-ration rate of *Corbula gibba* to determine its respira-tory quotient, i.e. Kleiber's (1961) constant β, and hence determine (in combination with other data) its functional strategy, i.e. exploitative vs. conservationist (see Holmes et al. 2002 for details); (2) to examine the hypoxic tolerance of *C. gibba*, adults and juveniles, to determine if this offers an advantage to *C. gibba* under hypoxic conditions; (3) to measure the salinity toler-ance of *C. gibba*; (4) using a RAPD PCR methodology, examine the population genetics of several geographi-cally separated *C. gibba* populations to assess both its dispersal potential and larval longevity. For this paper, the terms normoxia and hypoxia are used in accor-dance with Diaz & Rosenberg (1995) and exploitative and conservationist strategies are as defined by Holmes et al. (2002). For Kleiber's (1961) constant, i.e. the gradient β for the regression of log dry flesh weight (i.e. weigth without shell) vs. log respiration, if β falls within the range 0.75 to 1, then the organism is likely

to exhibit a conservationist type strategy, i.e. growth, metabolism and/or fecundity are low in order to sustain maintenance costs. In contrast, if β falls within the range 1.00 to 1.25, then the organism is likely to exhibit an exploitative type strategy, i.e. maturation is maximal in the absence of nutritional limits (see Riis-gard 1988, Holmes et al. 2002 for full details and West et al. 2002 for discussion).

MATERIALS AND METHODS

Physiological observations. *Collection and mainte-nance of specimens:* All experiments were carried out at Kristineberg Marine Research Station, Fiskeback-skil, Sweden, in the autumn of 2000 and 2001. All spec-imens were collected at the top of Abyfjorden, Sweden (58° 28′ N, 11° 30′ E) using an Agassiz trawl, 1 mm mesh size. The average population density was ~1800 ± 200 ind. m^2 covering a broad size range from 2 to 16 mm (shell length of the largest valve, 0 to 5+ yr). Once collected, the animals were stored in seawater and transported (within 3 h of collection) to the marine station, placed into tanks filled with clean sediment, and supplied with fresh running seawater (~10°C). Examination of the state of the gonads in both years over a wide size range revealed that all but a few were fully spent, suggesting that a spawning event had taken place in September.

Respiration quotient: Oxygen consumption was measured individually for 26 randomly selected ani-mals covering a size range of 7 to 12 mm (shell length of the largest valve) at 10°C using oxygen electrodes in closed system, 50 ml (total volume) respirometers (Model No: OXY046A, Rank Brothers). Respiration was only measured within the normoxic range of oxy-gen concentration, i.e. >2 ml O_2 l^{-1}, over a period of 4 h, at 10 min intervals, replicated 3 times for each indi-vidual. At the end of the experiment, the organisms were dried and their dry flesh and whole dry weight recorded.

Hypoxic tolerance: Measurement of the hypoxic tol-erance of adult and juvenile (i.e. <2.0 mm shell width) *Corbula gibba* was in an identical manner to that out-lined by Holmes et al. (2002), with the exception that water controls were taken every 4 d in the first in-stance, and every 8 d in the second instance. Since after ~12 d the control death rate (due to starvation) was indistinguishable from the treatment death rate (due to starvation and hypoxia) in the first series of experi-ments, a second series of experiments were run, whereby a ~10 mg portion (dry weight) of Algarde vacation food block (Algarde Aquatic Products) was added to each container at the start of the experi-ment. The vacation food block consists of freeze dried

algae embedded in plaster-of-paris, which dissolves slowly over time releasing the algae gradually. The vacation food block portions were microwaved, to ensure sterility, and pre-soaked in autoclaved filtered (0.2 μm) seawater (AFS) to eliminate trapped air.

Salinity tolerance: The salinity tolerance of *Corbula gibba* was examinated as follows: (1) a series of 5 dilutions of AFS at 100% (32.70), 75% (24.52), 50% (16.35), 25% (8.17) and 0% (0) psu were made using distilled water. The salinity at the collection site ranged between 30 and 34, depending on the amount of freshwater runoff; (2) 100 bottles of 15 ml nominal capacity were filled with the water for each dilution (salinity), i.e. n = 500 in total; (3) 3 randomly selected adult *C. gibba* were then placed into each pre-filled 15 ml bottle. All bottles were left under a 12 h day/night cycle and maintained at 10°C for the duration of the experiment. Each day, all bottles were visually checked to determine whether the animals were alive or dead. Dead individuals were removed from the

Table 1. Locations of populations, size range and distance from nearest population (pop.)

| Collection site | Lati-tude (N) | Longi-tude (E) | Code | n | Shell width (mm) | | Nearest pop. km (Code) |
					Range	Mean ± SD	
Sweden							
Abyfjorden	58° 28′	11° 30′	Sweden	30	4.1–6.9	4.7 ± 0.4	625 (FF1)
Frisian Front							
Site 1	54° 10′	05° 00′	FF1	30	3.9–7.4	5.2 ± 0.5	20 (FF2)
Site 2	54° 00′	05° 00′	FF2	30	4.2–7.5	4.9 ± 0.6	20 (FF1)
Site 3	53° 50′	04° 30′	FF3	35	4.3–6.7	4.8 ± 0.4	5 (FF5)
Site 4	53° 48′	04° 30′	FF4	30	4.2–7.0	5.3 ± 0.6	5 (FF3)
Site 5	53° 57′	04° 30′	FF5	30	4.2–7.3	5.4 ± 0.6	13 (FF3)

bottles and their deaths recorded. If the relevant bottles contained other bivalves, the water was changed and the bottles returned to the experiment. The experiment was ended after 10 d.

Population genetics. Adult *Corbula gibba* (30 individuals per population) covering a range of sizes were dredged from 5 different sites in the North Sea and 1 site (outgroup) in Sweden in 2001 (Table 1, Fig. 1). Selection of the populations (sites) was based on both the presence of *C. gibba* and their relative position/distance in regard to to other populations, such that the Frisian Front populations FF3, FF4 and FF5 were relatively close to each other (5 to 13 km) but at an intermediate distance (33 km) from the FF1 and FF2 populations (20 km separation) which, in turn, were close (20 km) to each other but far (625 km) from the Swedish outgroup population. Once collected, all specimens were immediately frozen (–80°C) and stored at –20°C for future processing.

Total DNA extractions, RAPD PCR protocol and fragment identification: DNA extraction, the RAPD protocol adopted and fragment identification were identical to those outlined by Holmes et al. (2004), with the exception that the 5 different 10 base-pair (bp) primers were selected along with their individually optimised 2nd step cycle number are given in Table 2. Mixed sample batches (i.e. individuals from several populations) were run together in each PCR reaction.

Fig. 1. Locations of populations sampled (descriptions and site codes in Table 1)

Table 2. Primers selected and number of cycles in second step of amplification procedure. %GC: % guanine/cytosine; Opt. no.: optimal number of second-step cycles; No. polymorph: no. of polymorphic bands

Primer	Sequence (5′-3′)	% GC	Opt. no.	Total bands	No. poly-morph
OPC04	CCGCATCTAC	60	35	23	22
OPG07	GAAVVTGCGG	70	35	26	26
OPM18	CACCATCCCT	60	29	16	14
UBC212	GCTGCGTGAC	70	29	25	24
UBC167	CCAATTCACG	50	35	20	20

Random retrials were performed for each primer to ensure reproducibility between both PCR reaction conditions and gel resolution with a randomly selected series of samples from all populations (n = 26). If the results on a gel appeared to be erroneous, i.e. in comparison to existing samples, then a fresh gel was run and a repeat PCR amplification made for those samples.

RADP data analysis: Initially, a matrix of Euclidean (squared) distances was calculated from the RAPD data (n = 180). The resulting matrix was subjected to principal coordinates analysis (PCO) using MVSP (version 3.13d, Kovach Computing Services), and the resulting factors plotted. A discriminant analysis was performed on the resultant factors, to assess the reliability with which individuals could be ascribed to their respective populations. To test the population structure derived from the PCO analyses, the data was then examined with AMOVA (analysis of molecular variance) using the ARLEQUIN package (Version 2; Schneider et al. 2000). One thousand random permutations of the data matrix were carried out to assess the significance of the variance components and of the pairwise variances for each population.

A neighbour joining (NJ) analysis was then performed on the data from a distance matrix derived using Parsimony, PAUP* (Swofford 2002), and the robustness of the resulting tree tested by bootstrapping the data, by resampling each individual 1000 times. Finally, a series of Mantel tests were performed to examine the correlation, if any, between the geographical distances between the populations and Φ_{ST}, Slatkin's (1985) linearised F_{ST} and the distances derived from the NJ analysis.

RESULTS

Respiration, metabolism and production

Linear regression of the mean amount of oxygen consumed by each bivalve (i.e. n = 26) against whole dry weight and dry flesh weight (DFW) revealed a positive relationship for both variables (Fig. 2). The mean ± standard error (SE) respiration rate of an average sized *Corbula gibba* (0.084 ± 0.003 g DFW) was 3.12 ± 0.05 µl O_2 h^{-1} (0.063 ± 0.001 J h^{-1}). The calculated respiratory quotient (β) (i.e. for the dry flesh weight) was 0.61 ± 0.16, falling within the range 0.75 to 1 (p = 0.03, calculated using *t*-tests).

Hypoxic tolerance

The initial oxygen concentration (mean ± SE) of the seawater at the start of both experiments was ≤1.61 ± 0.23 ml O_2 l^{-1}; that is, the seawater can be regarded as
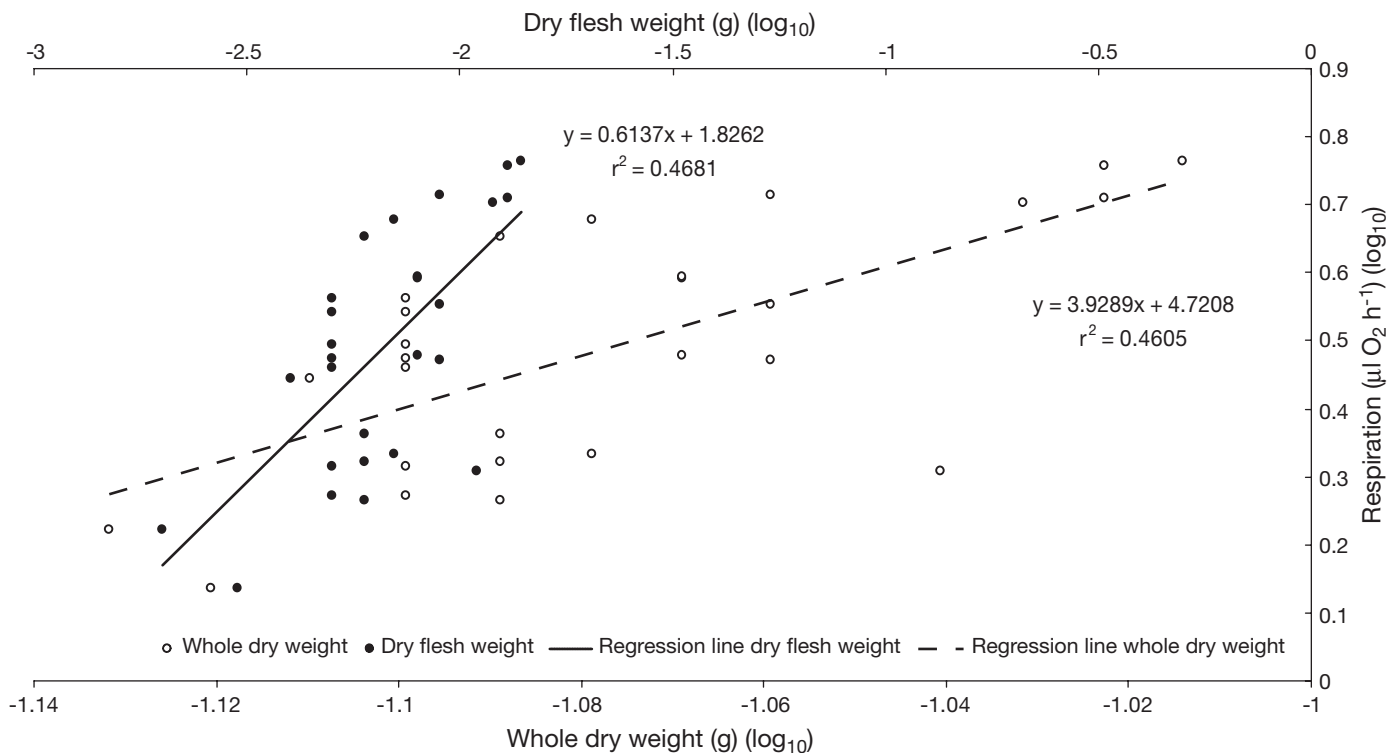

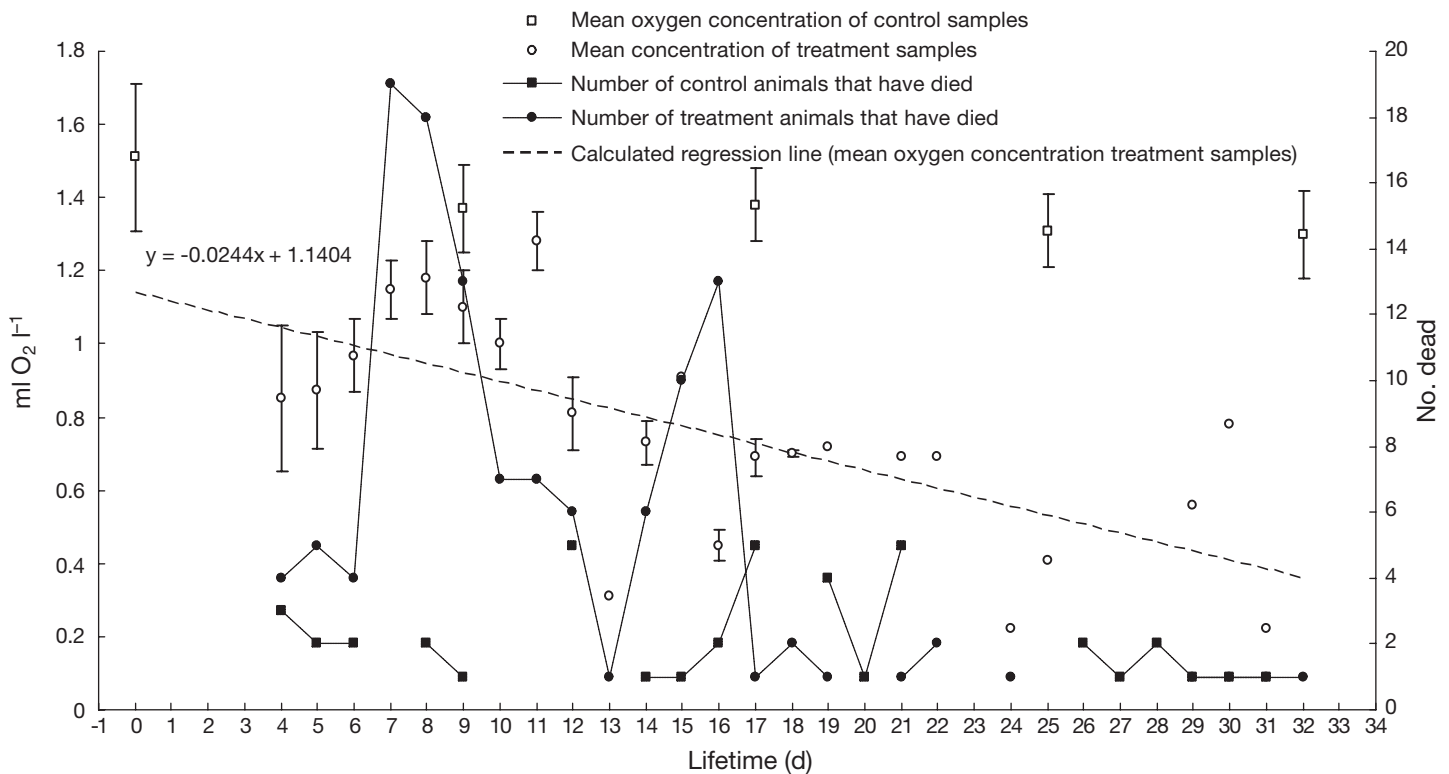Fig. 2. Linear regression of respiration data for *Corbula gibba*

Fig. 3. Mortality of fed *Corbula gibba* juveniles (2nd experiment) under hypoxia

being hypoxic at the start of the experiments (Diaz & Rosenberg 1995). Comparison of the oxygen concentrations of the water controls during the experiments, using a one-way analysis of variance, revealed that the oxygen concentration of the control water did not change over the duration of any experiment (Fig. 3). (In Fig. 3, only data for the second series of experiments are presented, for brevity).

For the first series of experiments, analysis of the survival data for *Corbula gibba* over time, using the Kaplan-Meier procedure with log rank comparison and accounting for censored observations revealed (1) that the survival rate of the adult treatment animals, over the whole experiment, was different to that of the juvenile treatment and adult and juvenile control animals ($p > 0.001$) (Fig. 4); (2) that there was no difference between the survival rate of the juvenile treatment, juvenile control and treatment control animals ($p = 0.284$); (3) that for the adult treatment animals the mean ± SE survival time was 25.40 ± 0.85 d (median = >34 d, $LT_{50} \cong$ >34 d) whilst the mean survival time for the adult control animals was 21.86 ± 0.88 d (median = 22 d, $LT_{50} \cong$ 22 d) (Fig. 4); (4) that for the juvenile treatment animals the mean ± SE survival time was 16.98 ± 0.79 d (median = 14 d, $LT_{50} \cong$ 14 d) whilst the mean survival time for the juvenile control animals was 19.73 ± 1.39 d (median = 19 d, $LT_{50} \cong$ 20 d) (Fig. 4).

An alternative analysis of the adult data, however, using a Cox regression model derived from the weighted residuals, revealed that survival of adult *Corbula gibba* differed between treatment and control conditions during the early part of the experiment ($\chi^2 = 9.85$, $p \leq 0.01$); i.e. (1) until approximately Day 8, there was a difference between survival rates of treatment and control adults, with the treatment adults dying more often than controls (Fig. 4); (2) after Day 8, mortality of the control adults rapidly increased until, by Day 10, it had reached a rate approximately equal to that of the treatment adults, with both rates thereafter remaining proportionately equal.

In effect, mortality of the treatment adults due to hypoxia was distinguishable from mortality due to starvation up to Day 8. Thereafter, mortality from hypoxia was indistinguishable from and equal to that from starvation. For the first series of experiments using juveniles, control survival was indistinguishable from treatment survival for the entire duration of the experiment. This suggests that, for this experiment, starvation was more important than hypoxia in determining the ability of *Corbula gibba* to survive. In both the adult treatment and control samples ~90% of the bivalves had died by the end of the experiment (30 d), and in the juvenile treatment and control samples ~60% had died by the end of the experiment (14 d).
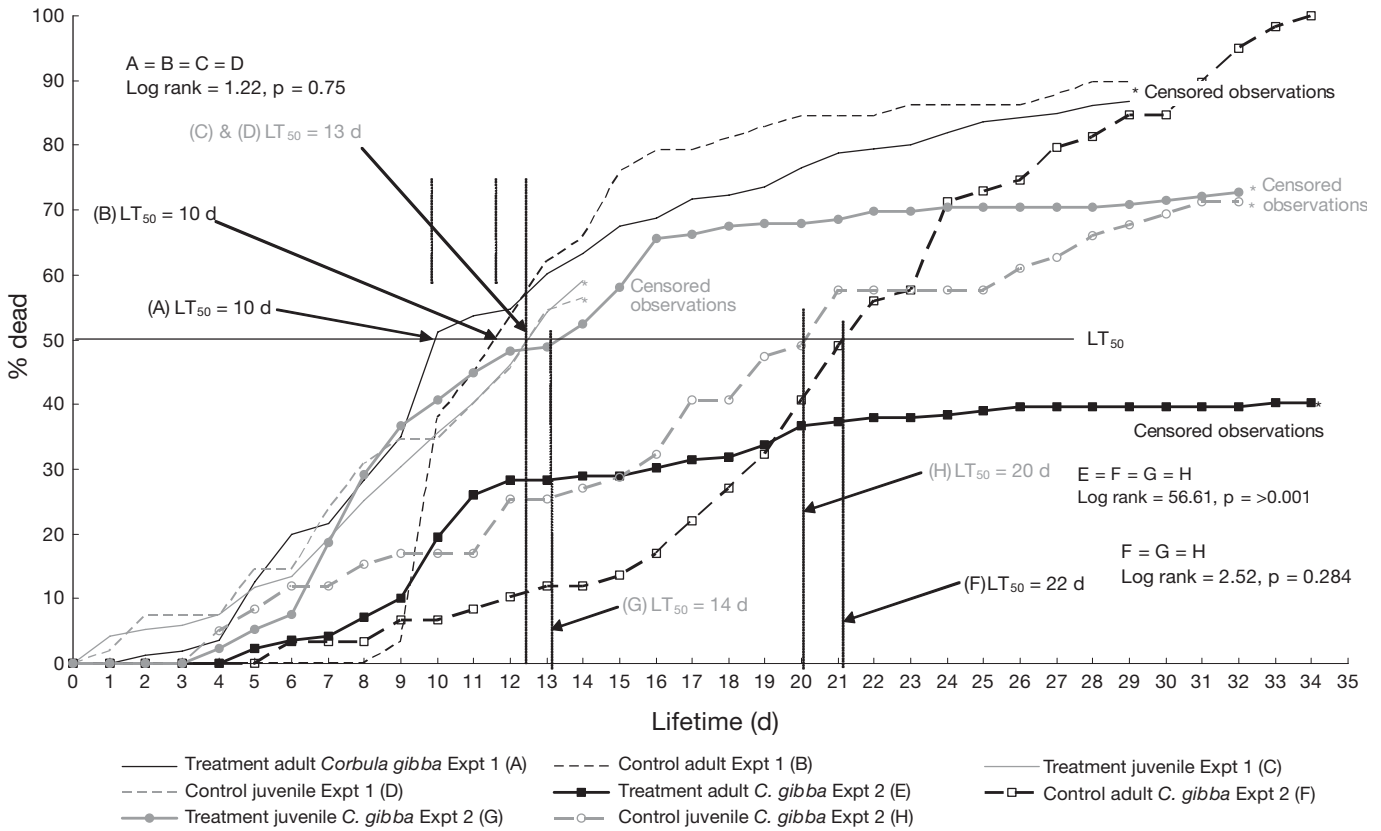
Fig. 4. Cumulative percent mortality during hypoxia experiments

For the second series of experiments, analysis of the survival data of *Corbula gibba* over time, using the Kaplan-Meier procedure with log rank comparison and accounting for censored observations, revealed that (1) the survival rate of the treatment adults over the whole experiment differed from that of the treatment juveniles and adult and juvenile controls (p > 0.001); (2) there was no difference between the survival rate of the treatment juveniles, control juveniles and control adults (p = 0.284); (3) the mean ± SE survival time was 25.40 ± 0.85 d (median = >34 d, LT_{50} ~ >34 d) for treatment adults and 21.86 ± 0.88 d (median = 22 d, LT_{50} ~ 22 d) for control adults; (4) the mean ± SE survival time was 16.98 ± 0.79 d (median = 14 d, LT_{50} ~ 14 d) for treatment juveniles and 19.73 ± 1.39 d (median = 19 d, LT_{50} ~ 20 d) for control juveniles (Fig. 4).

It would appear that under hypoxic conditions, adult *Corbula gibba* can survive better than juvenile *C. gibba* and adult *C. gibba* under normoxic and low quality conditions.

An alternative analysis of the juvenile data, using a Cox regression model, derived from the weighted residuals, revealed that survival of juvenile *Corbula gibba* between treatment and control conditions differed for the duration of the experiment (χ^2 = 11.31, p 0.01), i.e. (1) until approximately Day 6, there was

no difference between survival rates of treatment and control juveniles (Fig. 4); (2) after Day 6, the death of treatment juveniles increased, such that by Day 7 it exceeded that of the controls, with both rates thereafter remaining relatively proportionate to each other until approximately Day 29, when they converged (Fig. 4).

In effect, in the second juvenile experiment, the increase in mortality of juvenile *Corbula gibba* from hypoxia, was evident from Day 6 of the experiment. By Day 29, mortality rates due to hypoxia and starvation (i.e. poor quality conditions) were effectively equal.

Correlation, using Spearman's rho (R_{SC}), of the shell length, height, width and whole body dry weight data to the survival data, failed to produce any statistically significant correlation for any experiment, i.e. death due to hypoxia did not appear (in these experiments) to be related to body size. Correlation analysis, using Spearman's rho of the lifetime of *Corbula gibba* vs. the mean oxygen concentration of the treatment water samples at the time of death for that day, produced a negative correlation for all experiments, i.e. the O_2 concentration in the water containing the treatment animals dropped over time, as they respired, leading to their eventual death (Fig. 3). Correlation of the number of animals dying per day against the mean O_2 concentration of the animals that died on that day (using
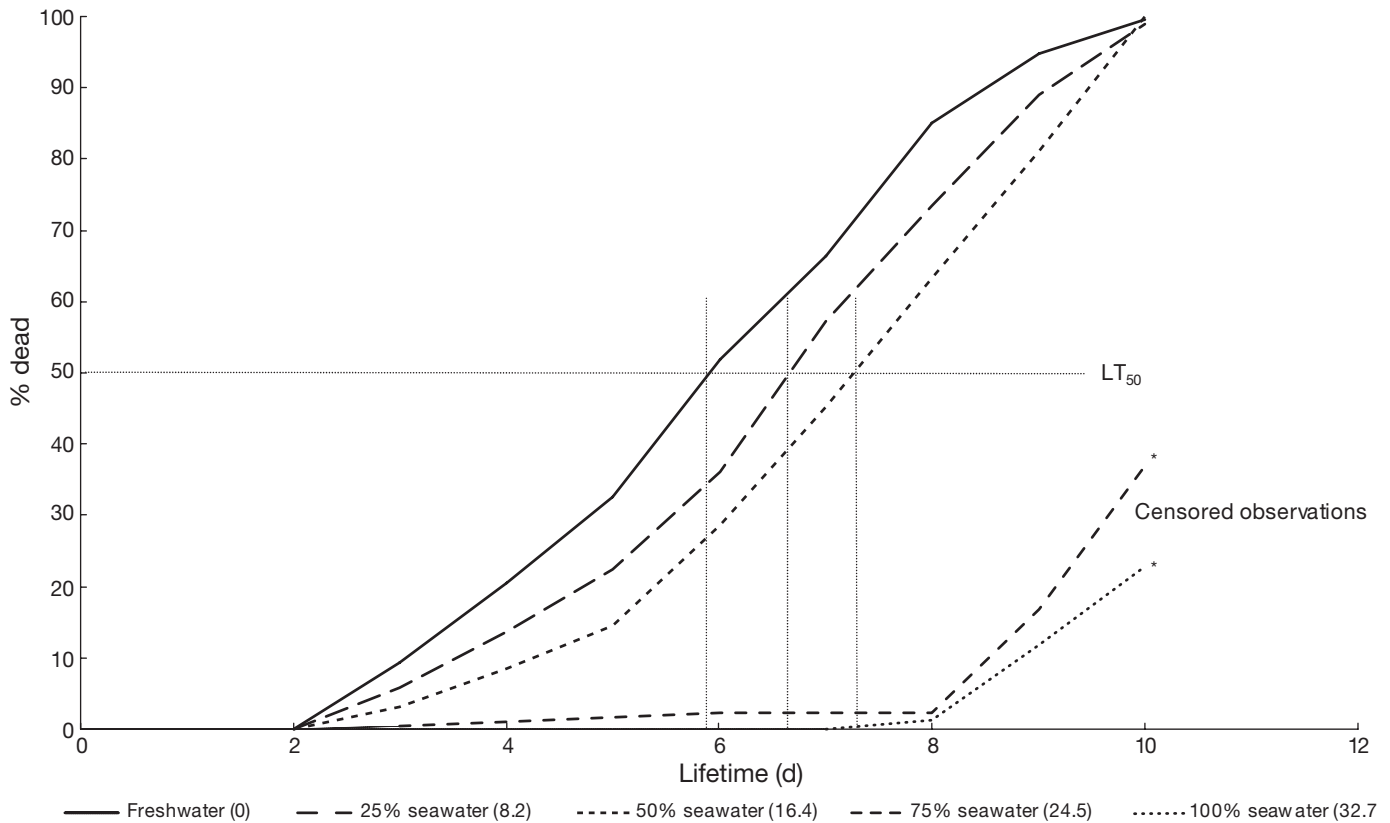
Fig. 5. Cumulative percent mortality of *Corbula gibba* as a function of salinity. Numbers in brackets represent practical salinity units (psu)

Spearman's rho to determine if there was a threshold O_2 concentration lower than that at the start of the experiment that caused death) produced no statistically significant correlation, i.e. the initial O_2 concentration of the water was sufficient to cause death due to hypoxia (Fig. 3).

Salinity tolerance

Analysis of the survival data for *Corbula gibba* over time, using the Kaplan-Meier procedure with log rank comparisons and assuming that each individual is an independent observation, revealed that the survival rates of the animals differed as a function of salinity, ($p \leq 0.001$) (Fig. 5) as follows: (1) the mean ± SE survival time at 0 psu (0% seawater) = 6.46 ± 0.16 d (maximum survival time = 10 d; median = 6 d; LT_{50} = 6 d); (2) for the 8.17 psu (25% seawater) treatment, the mean ± SE survival time was 7.10 ± 0.16 d (maximum survival time of 10 d; median = 7 d; LT_{50} = 7 d); (3) for the 16.35 psu (50% seawater) treatment the mean ± SE survuval time was 7.60 ± 0.14 d (maximum survival time of 10 d; median = 8 d; LT_{50} = 8 d); (4) for the 24.52 psu (75% seawater) treatment, the mean ± SE survival time was 9.77 ± 0.07 d with a maximum sur-

vival time of >10 d (median > 10; LT_{50} > 10 d; (5) for the 32.70 psu (100% seawater) treatment, the mean ± SE survival time was 9.89 ± 0.04 d (maximum survival time of > 10 d; median > 10; LT_{50} > 10). Although there is a statistically significant difference between mean survival in the 100 and 75% seawater treatments, this difference is effectively negligible (Fig. 5).

In summary, in water from 0 to 16.35 psu, *Corbula gibba* can survive for up to 2 d without mortality and up to 10 d with increasing mortality. Survival of *C. gibba* in brackish seawater (i.e. the 75% seawater treatment) is little different from that in normal seawater.

Population genetics (RAPD analysis)

From the 180 individuals of the 6 populations studied, the 5 primers used, amplified a total of 106 different polymorphic fragments (Table 2). A complete data set of the banding patterns for all populations and primers can be obtained at www.sebby.co.uk/data. htm. Analysis of the data using principal coordinates analysis (PCO) extracted 4 factors, accounting for 29, 19, 16 and 9% of the total variance, respectively. A plot of these factors revealed that all populations appeared

to be different from each other. In line with the PCO results, discriminant analysis revealed that individuals could be assigned to their source population on the basis of their banding patterns (molecular phenotype) with 100% accuracy.

Analysis of molecular variance based on the precept (arising from the PCA analysis) that all populations were different from each other, revealed that ~55% of the total variance could be attributed to between-population differences and the remaining ~45% to within-population differences (Table 3). Any attempts at sub-dividing the populations into groups, e.g. combining the Frisian Front populations, resulted in a decrease in the between-population variance and a corresponding increase in the within-population variance. In effect, the majority of the variance between samples arises from between-population rather than the within-population differences. Calculation of the pairwise between-population variances (Φ_{ST}), after correction for multiple comparisons, revealed that the genetic identity (determined by the RAPD banding patterns) of all

Table 3. AMOVA tables for RAPD data. ***Significant at p ≤ 0.001

Source	df	SS	Variance	% variance	Fixation index
Among-groups	5	1698.72	11.02	55.01	0.55*** (Φ_{ST})
Within-populations	174	1568.77	9.02	44.99	
Total	179	3267.48	20.04		

Table 4. Pairwise population variance, Φ_{ST} (F_{ST}) (all significant at p ≤ 0.01). Site codes as in Table 1

	FF1	FF2	FF3	FF4	FF5
FF2	0.57				
FF3	0.47	0.56			
FF4	0.62	0.69	0.48		
FF5	0.54	0.59	0.47	0.54	
Sweden	0.54	0.62	0.49	0.55	0.45

populations differed from each other (Table 4). In addition, both the among-population (Table 3) and between-population (Table 4) Φ_{ST} values were high, indicating a considerable degree of genetic structuring.

Construction of a neighbour joining tree revealed, as did the discriminant analysis, that the individuals from
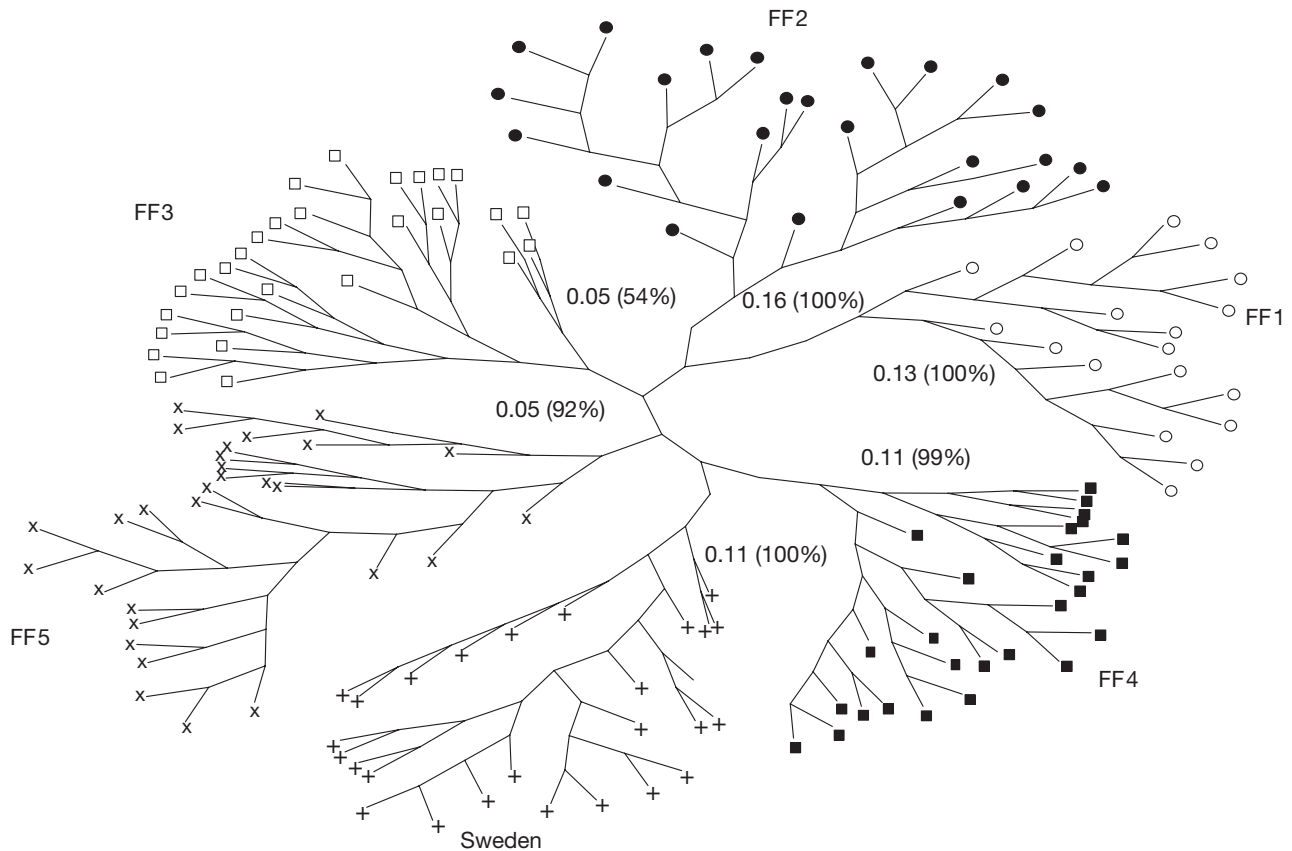

Fig. 6. Unrooted dendrogram calculated from RAPD penotypes using neighbour-joining analysis. Numbers along main branches: branch length (from center); numbers in brackets: bootstrap values (% accuracy calculated from 1000 replicates) for relevant branches. Site codes as in Table 1

Table 5. Comparison of respiratory rates of various bivalve molluscs. na: not applicable

Species	Mean/range respiration (ml O_2 g^{-1} DFW h^{-1})	Respiratory quotient (β)	T (°C)	Habitat	Functional strategy	LT$_{50}$ hypoxia	Hypoxic limit (d)	Salinity tolerance (range)(psu)	Max. tolerance at 0 salinity (d)	Source
Corbula gibba	0.45	0.61	10	Muddy[b]		Adults >34, juveniles 20	Adults >34, juveniles >32	0–34	10	Present study
C. gibba	0.79	0.71	10	Muddy[b]						Laureta (1986)
C. gibba	0.37	0.60	10	Muddy[b]						Pisarovic et al. (2000)
Arctica islandica			11	Muddy[b]	Conservationist	~83	28			Taylor (1974), Theede (1973), Christensen (1970)
Scrobicularia plana	0.14	0.75	10	Muddy[b]	Conservationist	23	na	2–34	<1	Hughes (1970), Theede et al. (1969), Green (1957)
Mya arenaria	0.24	0.73	10	Muddy[b]	Conservationist		~35	4–34	3	Kennedy & Mihursky (1972), Grant & Thorpe (1991), Newell & Hidu (1986)
Nucula nitidosa	0.14	0.92	10	Sandy[a]	Conservationist	2	10, 7, 3	27–34		Holmes et al. (2002), Rachor (1976), Trevallion (1965)
N. nucleus	0.22	1.28	10	Muddy[a]	Exploitative	7	>12			Holmes et al. (2002)
N. tenuis	0.55		10	Muddy[a]	Conservationist		17			Bayne & Thurberg (1988), Moore (1931)
N. sulcata	0.04		10	Muddy[a]	Conservationist	14	21			Taylor et al. (1995)
Mytilus edulis	0.381	1.03, 0.90	12	na	Exploitative as juveniles			0–34		Bayne (1971), Hamburger et al. (1983), Bayne et al. (1976), Widdows (1985)
Cerastoderma edule	0.76	0.52	15	Sandy[b]	Conservationist	~4	na	3–34		Newell & Northcroft (1967), Theede (1973), Rygg (1970)
Venus gallina	Unknown		10	Sandy[b]	Conservationist	4	8,37			De Zwaan et al. 2001, Christensen (1970)
Astarte montagui	Unknown		10	Muddy[b]	Conservationist		36			Christensen (1970)

[a]Tebble (1966), [b]Allen (1954)

all populations could be separated into the respective populations on the basis of their banding patterns (Fig. 6). Bootstrapping, based on resampling each individual, of the derived tree revealed (although with less accuracy than the discriminant analysis) that the assignment of a particular individual to a particular population could be made for the majority of the populations with ≥92% accuracy (100% accuracy for the FF1 and FF2 populations, 99% accuracy for the FF4 population, 92% for the FF5 population and 54% for the FF3 population) (Fig. 6).

Mantel tests performed to examine the correlation, if any, between genetic and geographical distances/differences between the populations using Φ_{ST}, Slatkin's (1985) linearised F_{ST} and the results derived from the neighbour-joining analysis, revealed that there appeared to be no relationship between geographical and genetic distance for any metric used.

DISCUSSION

Measurement of the respiration of *Corbula gibba* revealed that an average sized individual (~9 mg dry flesh weight) had a respiratory demand of ~75.0 µl O_2 24 h^{-1} (1.50 J ind.$^{-1}$ 24 h^{-1}), which is of the same order as that recorded by Laureta (1986) and by Pisarovic et al. (2000) (Table 5). In terms of secondary production, for the population sampled at Abyfjorden this equates to 457 kJ m^{-2} yr^{-1} (see Holmes et al. [2002] for calculation details and Laureta [1986], Jensen [1990] for comparisons). Calculation of the respiratory quotient (Kleiber's constant β) for *C. gibba* produced a value of 0.61, in line with the value calculated by Laureta (1986) using a different methodology (Table 5). Hence in terms of its metabolism, it is concluded that *C. gibba* adopts a conservationist type strategy, i.e. β falls within the range of 0.75 to 1 (see Riisgard 1998, Holmes et al. 2002). It should be noted that because the measurements were made at roughly the same time over 2 yr, there may be seasonal variation in the respiratory quotient of *C. gibba*, which has not been

accounted for (see Heilmayer et al. 2004 for example). Comparison of the respiration rate and quotient obtained for *C. gibba* with those of other conservationist type species revealed little difference (Table 5).

Examination of the hypoxic tolerance of *Corbula gibba* determined that both adults and juveniles could survive for more than 32 d. Even after 34 d, adult *C. gibba* supplied with food had not attained 50% mortality (LT_{50}). Compared to the hypoxic tolerance recorded for other species, *C. gibba* would appear to be one of the most resistant species (Table 5). The only recorded exceptions are data of Theede et al. (1969) for *Arctica islandica* and *Mytilus edulis*; however, their results may differ because of their different and possibly less stringent methodologies. In terms of resistance to starvation/poor quality conditions the first hypoxic experiment revealed that adult *C. gibba* could survive for >30 d without food with an LT_{50} of 12 to 13 d for the adult and juvenile control specimens. In the second hypoxic experiment, juvenile *C. gibba* were less tolerant than the adults with the juveniles surviving for >31 d with a LT_{50} of 14 d.

Surprisingly, the treatment adult *Corbula gibba* had a much greater survival rate than the corresponding controls, with all control individuals having died by the end of the experiment compared to <50% of the treatment individuals. It is likely that under hypoxic conditions *C. gibba* reduces its metabolic rate and hence its maintenance costs, resulting in increased tolerance (McMahon & Wilson 1981). Alternatively, the build up of anaerobic metabolites may provide some form of enhanced resistance (Abele-Oeschger & Oeschger 1995). The greater susceptibility of juveniles to hypoxia, combined with the increased success of adults, may explain both the patchy and fixed size class stands recorded by some authors (see Muus 1973, Hrsbrenko 1981, Jensen 1990, Rueda et al. 2001 for details). It is worth noting, given the supposedly pernicious nature of *C. gibba*, that samples taken by boxcores in Abyfjorden consisted of a wide range of fauna including *Arctica islandica*, *Nucula nitidosa*, *Abra prismatica*, *A. nitida* and *Mysia undata* along with a variety of other organisms, with *A. islandica* making up >50% of the total biomass of the cores (n = 5).

Examination of the salinity tolerance of *Corbula gibba* revealed that individuals could readily survive for 10 d at ~24 psu. Below 24 psu, mortality rapidly increased with decreasing salinity, with a maximal survival time of ~10 d in freshwater (LT_{50} = 6 d). In comparison with the salinity tolerance of other bivalve species (Table 5), *C. gibba* appears to be extremely well adapted to living in hyposaline conditions, reflective of its lotic and lentic cousins. The salinity tolerance of *C. gibba* suggests, as does its hypoxic tolerance, that it is adapted to occupying highly stressful (marginal) habitats. In general, species that successfully occupy highly stressful environments, although dominant within their own ecosystem are inferior competitors occupying what is effectively a suboptimal habitat with reduced or absent competitive pressures. The benefit of reduced competition is weighed against the cost of high maintenance/adaptive costs associated with living in such an environment. For *C. gibba*, this is borne out by the fact that populations are frequently found in unstable, perturbed and/or denuded habitats (Crema et al. 1991, Theodorou 1994, Currie & Parry 1999, Pruvot et al. 2000, Giacobbe & Rinelli 2002 for examples). Its success (Wilson et al. 1998, Currie & Parry 1999, Talman & Keough 2001) in occupying less stressful habitats in locations outside its normal distribution (e.g. in Australia) can be explained by the absence in such locations of its usual competitors. It is worth noting that during a 30+ yr bi-annual survey data (Dekker & Beukema 1993) *C. gibba* was never found in the Western Wadden Sea, although suitable habitats exist there and there is an extant population some 30 km northwards in the North Sea (the FF4 population).

Examination of the population genetics of *Corbula gibba* revealed that populations separated by as little as 5 km were genetically distinct from each other. Similarly, there was no correlation between genetic and geographical distance irrespective of the metric used. Similar levels of genetic differentiation, using the same methodology, have been recorded for the actaeplanic bivalve *Arctica islandica* (Holmes et al. 2003) and the aplanic bivalve *Abra tenuis* (Holmes et al. 2004).

The lack of any genetic similarity between the different populations is surprising, especially over such short spatial scales, if we consider that *Corbula gibba* is teleplanic as suggested by Jorgensen (1946), Thorson (1946), Jones (1956) and Hrsbrenko (1981). Under a panmictic hypothesis (i.e. mode of reproduction/development is correlated with dispersal capacity), our results would suggest that *C. gibba* adopts an anchi/aplanic strategy. However, similar results have been recorded for both actaeplanic and teleplanic species in both population genetic (Burton & Fieldman 1982, Heipel et al. 1998) and other (Moore 1977, Johannesson 1988) studies. For example, Bhaud (1998) showed that there is no relationship between the mode of reproduction/developmental strategy adopted by polychaetes and their dispersal potential, with some direct developers having a more widespread dispersal than closely related teleplanic species. Such species may produce along-lived larval life stage not to ensure dispersal (dispersal can occur alternatively in the juvenile or adult phase, see Highsmith 1985, Olivier et al. 1996 for examples), but rather to reduce conspecific predation and/or to avoid competition with the parental generation etc. (see Pechenik 1999 for discussion). Irrespective of these

considerations, it is probable, given Yonge's (1946) observations and the population genetic data recorded herein, that *C. gibba* adopts an anchi/actaeplanic rather than teleplanic distribution mode. However, in the absence of any direct observations on its reproduction, there is no way to substantiate this proposal.

In terms of the observed genetic structure, it is probable that the populations derive from a few individuals, with considerable inbreeding and self recruitment (the pairwise population Φ_{ST}'s were reasonably high: Table 4). There is some evidence for the Frisian Front populations at least, that the prevailing water currents may constrain and concentrate existing populations/larval dispersal (see Creutzberg 1986). However, without further studies this remains speculation.

In summary, *Corbula gibba* appears to have a considerable hypoxic and salinity tolerance combined with a conservationist metabolic strategy, suggesting that, rather than being an invasive weed, it is in fact an inferior competitor that occupies very specific habitats to which it is adapted, hence its high maintenance costs and low respiratory quotient (β). Correspondingly, the population genetic data demonstrate that, irrespective of its reproduction/developmental strategy, *C. gibba* has a very restricted dispersal capacity contrary to what would be required if it were an invasive species. The only possible negative biological effect of *C. gibba* on other species may derive from its sheer abundance. However, such events are likely to be limited to the duration of the perturbation which has resulted in the change of the local environmental conditions and/or the decline of more competitive species.

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