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SPATIAL PATTERNS OF WILD OYSTERS IN THE HAWKESBURY RIVER, NSW, AUSTRALIA

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ABSTRACT The native Sydney rock oyster, *Saccostrea glomerata*, is under increasing threat from QX disease, competition with nonnative *Crassostrea gigas* and coastal development. Knowledge of the distribution and population structure of *S. glomerata* and *C. gigas* is essential if oysters and their ecosystem services are to be successfully managed. We determined spatial patterns of abundance, condition, and size-structure of *S. glomerata* and *C. gigas*, across two key habitats, mangroves, and rocky shores of the Hawkesbury River, a highly modified estuary 50 km north of Sydney. Sampling of five sites per habitat, spanning a 15 km stretch of river, revealed abundant populations of *S. glomerata*, averaging 514 ± 185 m^{-2}, in mangroves and on rocky shores. The native oyster accounted for 99% of all oysters sampled, with *C. gigas* found only at two of the five sites sampled within each habitat. Overall, rocky shores supported over eight times the oyster cover as mangroves. Among rock sites, live oyster cover and condition generally decreased with distance upstream. Although, at present, the Hawkesbury River estuary supports abundant wild oyster populations, ongoing monitoring of oyster populations is required to ensure that appropriate management strategies are established to ensure the persistence of this important component of the ecosystem. Our sampling of two key oyster habitats provides an important baseline against which future studies can assess change.

KEY WORDS: *Crassostrea gigas*, mangrove, oyster, rocky shore, *Saccostrea glomerata*, spatial distribution

INTRODUCTION

Oysters are instrumental in maintaining estuarine health and integrity (e.g., Coen & Luckenbach 2000, Ruesink et al. 2005). Their filter feeding and biodeposition improve water quality, and mediate energy flow, nutrient cycling and flux between the water column and the benthos (Newell 2004). Oysters form structurally and functionally complex habitat that enhances biodiversity and modifies abiotic processes such as deposition and desiccation (Gutiérrez et al. 2003). Oysters and associated fauna form the basis of food webs (e.g., Breitburg & Fulford 2006) and support economically valuable fish species (Breitburg 1999, Peterson et al. 2003).

Knowledge of the status and distribution of wild oyster populations is necessary for effective estuarine management because of their large influence on ecosystem function (Ruesink et al. 2005). Disease, climatic change, and human activities, such as harvesting, aquaculture, industrial pollution, nutrient enrichment, and habitat destruction have greatly changed the composition and abundance of wild oyster populations in benthic systems (Rothschild et al. 1994, Jackson et al. 2001, Kirby 2004). Extraction of *Crassostrea virginica* (Gmelin, 1791) on the east coast of the USA has, for example, severely reduced its population abundance (Rothschild et al. 1994, Jackson et al. 2001, Kirby 2004). Introduction of the Pacific oyster, *Crassostrea gigas* (Thurnberg 1973) for aquaculture resulted in invasion of coastlines in Argentina, Australia, Canada, France, New Zealand, the USA, and many other countries (Ruesink et al. 2005).

Along the east coast of Australia, populations of the native Sydney rock oyster, *Saccostrea glomerata*, already heavily impacted by historical over-harvest (Kirby 2004), are under increasing threat from Queensland unknown (QX) disease, competition with nonnative *C. gigas* and coastal development. QX disease, caused by the protozoan parasite, *Marteilia sydneyi*, invades the gills and digestive glands of *S. glomerata* and can cause death by starvation. During the 1970s, outbreaks of QX disease were mostly confined to southern Queensland (Nell & Hand 2003), but in 1994 the disease killed up to 80% of all *S. glomerata* in the upper reaches of the Georges River, near Sydney (Nell & Perkins 2006). Since then, the parasite has been identified within oyster populations in at least 12 more New South Wales (NSW) estuaries, causing major disease outbreaks in several of these. QX mortality has been particularly high in upstream aquaculture leases, particularly after periods of heavy rain (e.g., Butt et al. 2006).

Invasive *C. gigas* represents a further threat to *S. glomerata* populations. *C. gigas*, probably illegally imported into NSW from Tasmanian farms in the 1980s (Holliday & Nell 1985), is present at low abundance in most NSW estuaries and in all but Port Stephens (where it is so prolific, culture of reproductive individuals is permitted) is regarded as a noxious pest. *C. gigas* can rapidly overgrow and smother *S. glomerata* at low to mid intertidal elevations (Krassoi et al. 2008). Spread and proliferation of the nonnative may be hastened by the recent decision by the NSW Department of Primary Industries to allow the cultivation of sterile triploid *C. gigas* in a number of QX-impacted estuaries. Although culture of triploids reduces the risk of the nonnative invading natural habitats, the process of producing triploids is not perfect. Some estimates suggest that ca. 3% of supposed triploids are reproductively viable (Marine Pollution Research 2005).

Here, we assess the distribution and abundance of wild oyster populations in the highly modified Hawkesbury River, New South Wales, Australia. Formerly the second greatest oyster producing region in NSW, the river's aquaculture-based *S. glomerata* oyster industry recently collapsed because of outbreaks of QX disease that have occurred annually since 2004. Several farmers are now trialing the culture of triploid *C. gigas*, and small populations (accounting for 1% to 8% of total oyster abundances) have previously been detected in the Hawkesbury River (Marine Pollution Research 2005). We determine the along-river distribution, abundance and

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condition of native *S. Glomerata*, and nonnative *C. gigas* in the two major natural habitats occupied by oysters in this estuary, mangroves, and intertidal rocky shore. We test the null hypotheses that: (1) rocky shores and mangroves represent a similar quality of habitat for native *S. glomerata* (as indicated by abundance, % mortality, condition, and population structure); (2) within each of these habitats, sites support similar populations of oysters, irrespective of position along the river; and (3) all sites, irrespective of habitat are equally invaded by *C. gigas*. Our survey provides an important baseline of wild oyster resources currently present in this heavily impacted estuary, against which future change can be assessed and managed.

METHODS

We sampled five rocky shore and five mangrove (mud flats) sites along the Hawkesbury River (33°34′S, 151°18′E), NSW, Australia in June 2006 (Fig. 1). The sites were situated ~11–26 km from the mouth of this drowned river valley and spanned salinities of 25–34 ppt (Hornsby Shire Council, unpublished data 2008). Sites were interspersed among the former locations of *S. glomerata* oyster leases that had been impacted by QX disease, with the most westerly sites (mangrove sites 1–3, rock site 2; Fig. 1) adjacent to those leases that had experienced greatest (>90%) mortality in 2004 (Butt & Raftos 2007).

Rocky shore sites were dominated by Hawkesbury sandstone. Mangrove sites were characterized by *Avicennia marina*, a species, which produces pneumatophores. Sampling was timed to avoid the peak *S. glomerata* spawning season, which can introduce variability in tissue condition (Mason & Nell 1995).

Sampling was done 0.5 to 1.0 m above ISLW, within the tidal range across which the two species commonly coexist (Krassoi 2001). Within each site, we determined the cover of live and dead oysters under 100 points of 20 randomly placed 0.50 × 0.50 m quadrats. Following the box count method of Ford et al. (2006) only empty, articulated ("box") valves were included in counts of dead oysters. Assessment of the abundance of dead, as well as live, oysters enabled us to compare recent oyster mortality between mangroves and rocky shores. Because of morphological similarity between *S. glomerata* and *C. gigas* and conspecific plasticity, destructive sampling was required to discriminate between the species (Thomson 1954). Within six randomly positioned quadrats (0.50 × 0.50 m in the mangrove habitat or 0.25 × 0.25 m in the rock habitat, where oysters were denser), we removed all oysters from the substrate. In the laboratory oysters were separated, washed, and cleaned of fouling organisms. Anterio-posterior shell height was measured using digital callipers (±0.02 mm). Oysters were weighed then shucked and identified following the taxonomic key of Thomson (1954).

Condition indices (CI) were calculated according to the method of Crosby & Gale (1990):

$$\mathrm{CI} = \frac{\text{Dry soft tissue (g)}}{\text{Valve cavity capacity (g)}} \times \frac{100}{1}$$

Valve cavity capacity (g) was determined by subtracting dry valve weight (g) from total weight (g). Quadrat data were pooled to calculate condition indices. To maximize accuracy of cavity capacity calculations, gaping oysters were excluded (Abbe & Albright 2003).

Spatial patterns in oyster cover, % mortality, shell height, and CI were analyzed using mixed model ANOVA with the two factors, habitat (2 levels: rock, mangrove) and site (5 levels, nested in habitat, random). Differences among means were compared using Student Newman Keuls (SNK) tests (Underwood 1997). Data were ln(x + 1) transformed where variances were heterogeneous (Cochran test).

RESULTS

On rocky shores and in mangrove forests of the Hawkesbury River estuary, live *S. glomerata* abundance ranged from 40 to

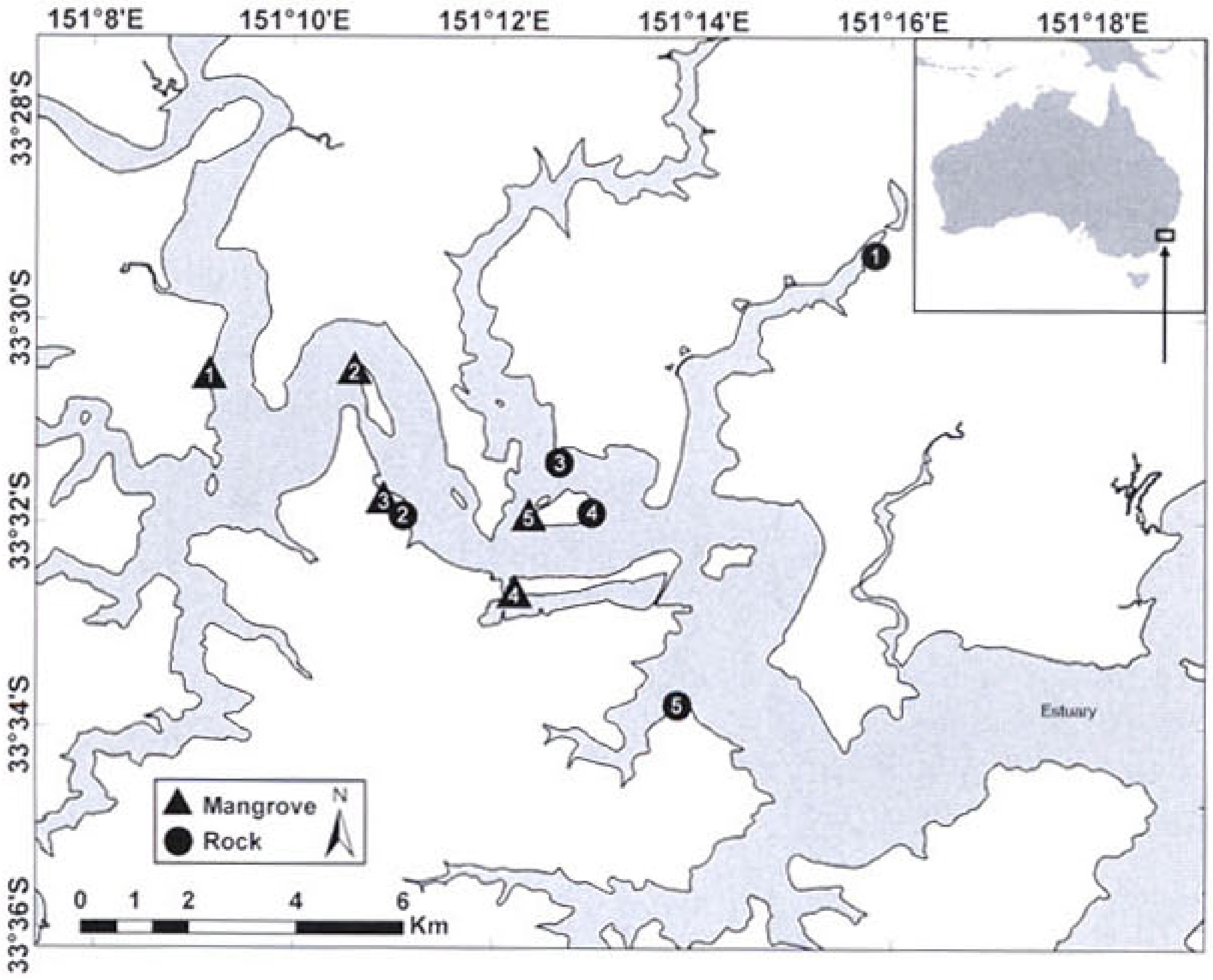

Figure 1. Map of Hawkesbury River, New South Wales, Australia showing sites sampled in rock (●) and mangrove (▲) habitats. Site numbers correspond with numbers on bar graphs (Fig. 2).

1,379 m^{-2} with an average (± SE) of 514 ± 185 m^{-2} (Table 1). The native represented 99% of all oysters sampled and 82% of the articulated oyster shells sampled contained live animals. The remaining oysters were *C. gigas*, which were depauperate (9 ± 7 m^{-2}; Table 1) and found at only two sites in each habitat (rock sites 1 and 3, mangrove sites 4 and 5; Fig. 1.). Of the articulated *C. gigas* shells encountered, 84% contained live animals and most (99%) inhabited rock. The small numbers of identified *C. gigas* did not give adequate sample sizes for analysis of spatial patterns.

Oyster cover varied spatially according to habitat (ANOVA: $F_{1,8} = 45.93$, $P < 0.01$) and position along the river (ANOVA: $F_{8,190} = 18.21$, $P < 0.05$; Fig. 2A). On rock, cover ranged from 5% to 97%, with a mean of 58% to 8%. On mangrove habitat, cover was 0% to 60% (7% ± 2%). Cover among rock sites generally decreased with distance upstream (Fig. 2A).

Live *S. glomerata* on rock significantly outnumbered those in mangroves (ANOVA: $F_{1,8} = 5.66$, $P < 0.05$; Table 1), but there was no difference in proportionate mortality between habitats (ANOVA: $F_{1,8} = 0.02$, $P > 0.05$; Fig. 2B; Table 1). Across the two habitats, box shells accounted for only 28% ± 10% of oyster assemblages. Proportionate mortality displayed a weak trend of increase with distance from the estuary mouth and, among rock sites, was greatest at rock site 1, situated within a creek tributary (64% ± 12%; SNK: $P < 0.05$; Fig. 2B).

S. glomerata on mangrove substrate possessed larger CIs than rock counterparts, but this difference was not significant (ANOVA: $F_{1,6} = 1.46$, $P > 0.05$; Fig. 2C; Table 1). Within rock sites, CI displayed a weak trend of increase in condition with proximity to the ocean whereas, within mangrove sites, the opposite pattern was apparent (Fig. 2C).

The mean shell height of *S. glomerata* was 28.5 ± 8.0 mm on rock substrate and 23.0 ± 1.0 mm on mangrove habitat (Table 1). Across mangrove sites, the length of live *S. glomerata* did not differ (SNK: $P > 0.05$) whereas on rock, oysters inhabiting the creek site, where densities were lowest, were longer than those in each other rock site (SNK: $P < 0.05$). In both habitats *C. gigas* measurements were considerably larger than native counterparts (Table 1).

DISCUSSION

Our sampling of two key habitats, mangroves, and rocky shores, revealed abundant populations of *S. glomerata* along the Hawkesbury River estuary, New South Wales, Australia. Mangroves and rock on average supported 514 ± 185 oysters per m^2, a comparable density to within other New South Wales estuaries that have not experienced the same catastrophic QX mortality of cultured oysters as the Hawkesbury (M.J. Bishop unpubl. data). *S. glomerata* populations contained a wide size range of individuals, indicative of multiple cohorts, and were dominated by adult oysters of sufficient size to be greater than 1 y old (see Hand et al. 1999).

Rock, on average, supported 10 times the *S. glomerata* density as mangroves. This pattern was consistent with the much greater availability of hard substratum for attachment on rocky shores than in mangroves, a predominantly sedimentary environment where oysters are confined to pneumatophores and tree trunks. Between the two habitats, oyster populations contained a similarly low proportion (28 ± 10%) of articulated box shells, and had statistically indistinguishable condition indices. Oysters were, however, generally larger on rock than in mangroves, perhaps reflecting the greater availability of space for growth in the former habitat.

Despite the lack of evidence for widespread and severe mortality of wild *S. glomerata*, there was a slight trend for an increasing proportion of box shells with distance from the estuarine mouth. Along-estuary gradients in salinity and/or hydrodynamics may explain this pattern. Previous laboratory studies have documented maximal survival of *S. glomerata* spat at salinities of 30 ppt, with spat unable to survive prolonged exposure to salinities less than 19 ppt (Dove & O'Connor 2007). Adult *S. glomerata* display optimal growth between 25 and 35 ppt (Holliday 1995). The greater number of boxes at upstream sites is also consistent with the observation of greatest QX mortality of cultured oysters under low salinity conditions (Butt et al. 2006). Yet, at upstream sites, near aquaculture leases that had experienced >90% QX mortality of oysters in 2004 (Butt & Raftos 2007), dead oysters accounted for less than 30% of wild

TABLE 1.

Range (mean ± SE) of univariate measures of *S. glomerata* and *C. gigas* (density, shell height, percent mortality and condition indices).

		Rock Habitat		Mangrove Habitat	
		S. glomerata	*C. gigas*	*S. glomerata*	*C. gigas*
Live	density	40–1,379 m^{-2} (940 ± 251 m^{-2})	0–176 m^{-2} (17 ± 13 m^{-2})	53–134 m^{-2} (88 ± 14 m^{-2})	0–4 m^{-2} (<1 m^{-2})
	l	5–88 mm (28.5 ± 8.0 mm)	41–109 mm	7–63 mm (23.0 ± 1.0 mm)	25–49 mm
	CI	3.3–9.0 (6.4 ± 0.8)	*	4.1–10.5 (7.4 ± 0.5)	10.18–10.24
Dead	density	45–325 m^{-2} (196 ± 58 m^{-2})	0–16 m^{-2} (2 ± 5 m^{-2})	17–58 m^{-2} (36 ± 7 m^{-2})	0 m^{-2}
	l	6–91 mm (35.7 ± 8.0 mm)	43–82 mm	10–59 mm (28.1 ± 1.4 mm)	*
	% m	3%–29% (28 ± 10%)	*	23%–45% (29 ± 4%)	*

l = anterio-posterior shell height, % m = percent mortality, CI = condition indices, * = data not available.

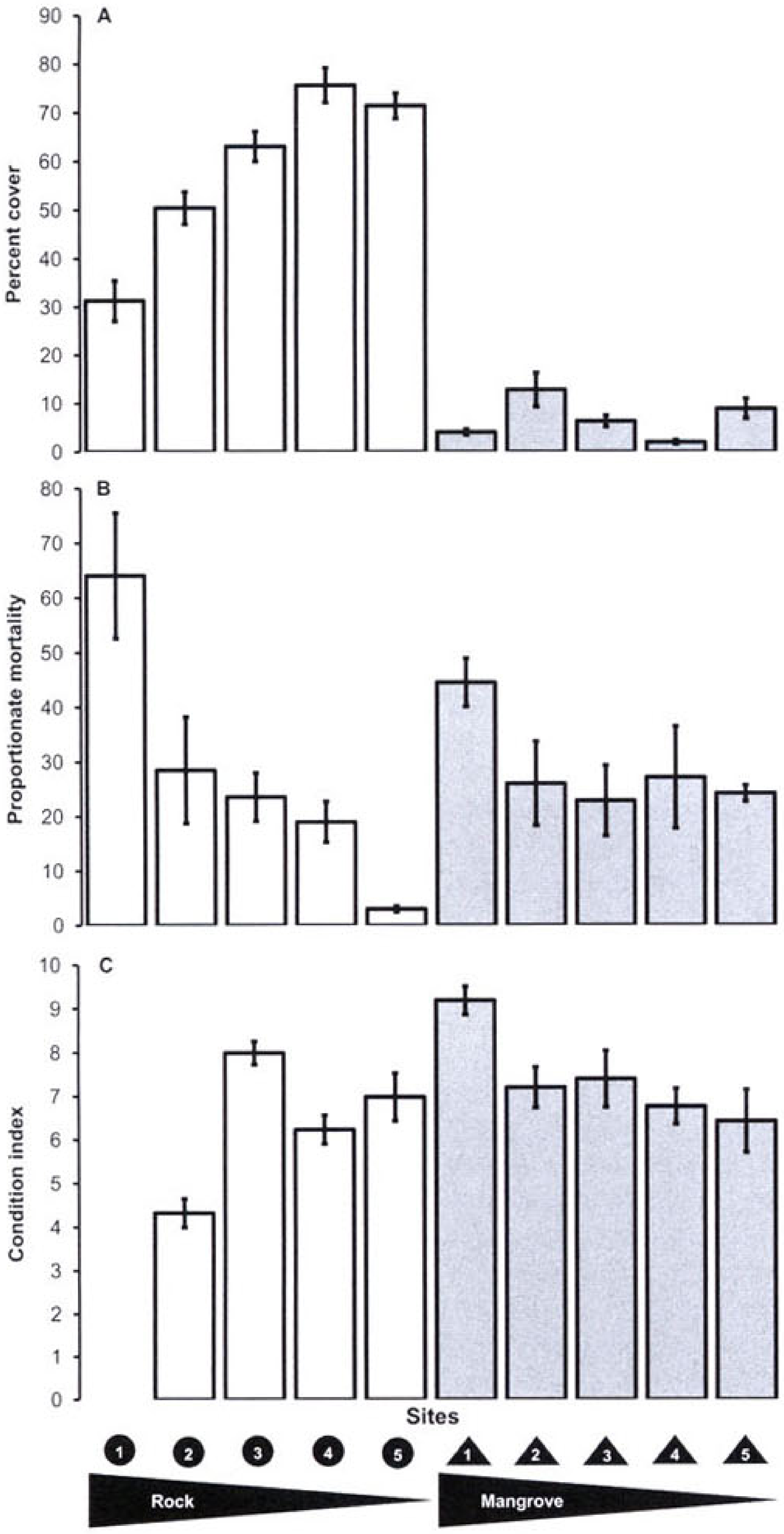

Figure 2. Mean (± SE) (A) percent cover, (B) proportionate mortality and (C) condition indices in rock (white bars) and mangrove (grey bars) habitats. Within each habitat, sites are ordered from left to right according to increasing proximity to the estuary mouth and numbered as per Fig. 1. $n = 5$.

oyster assemblages. Moreover, greatest wild oyster mortality was recorded in a tributary of the Hawkesbury, away from these most affected aquaculture leases suggesting that the mortality gradient was unrelated to QX disease.

Across rocky shore and mangrove habitats, nonnative *C. gigas* constituted less than 1% of wild oyster populations. Although, in each habitat, it was present at two of the five sites sampled, it was like *S. glomerata* more abundant on rocky shores, where it reached densities of up to 176 m^{-2} compared with a maximal density of 4 m^{-2} in mangroves. At the time of sampling, triploid *C. gigas* had only recently been introduced as a strategy for restoring the estuary's QX-affected aquaculture industry. Ongoing monitoring is needed to ensure that the nonnative oyster does not become a pest species within the estuary.

Whereas QX has devastated native *S. glomerata* aquaculture in the Hawkesbury, the persistence of sizable wild oyster populations contrasts the pattern in other NSW estuaries subject to QX outbreaks. In the Georges River, QX disease has devastated wild populations of *S. glomerata* and facilitated *C. gigas* invasion in up to 80% of areas (Nell & Hand 2003). Within the Hawkesbury estuary, the confinement of widespread and pervasive *S. glomerata* mortality to aquaculture may reflect stresses particular to farming (e.g., high stocking densities and reduced flows) that serve to increase susceptibility to the parasite or allow proliferation of the parasite to disease-causing doses. Greater mortality of cultured than wild oyster populations to QX disease may also reflect modern grow-out practices. Historically, cultured stocks were principally derived from wild recruits (Nell 1993, Nell 2001). In recent times the use of hatchery bred spat has increased (e.g., Nell & Perkins 2005) and, in the Hawkesbury River, now exceeds natural spatfalls as the main supply (Stubbs pers. comm. 2008). It is therefore possible that wild stocks in some estuaries, in contrast to cultured oysters reared from imported spat, have naturally selected characteristics predisposing them to QX resistance.

With the potential for burgeoning human populations to further degrade this already modified estuary, ongoing monitoring of oyster populations is required to ensure that appropriate management strategies are established to guarantee the persistence of this important component of the ecosystem. Our sampling of two key oyster habitats provides an important baseline against which future studies can assess change.

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