



Long-term coexistence of non-indigenous species in aquaculture facilities

Marc Rius^{a,*}, Kevin G. Heasman^b, Christopher D. McQuaid^c

^a Centre for Invasion Biology, Zoology Department, University of Cape Town, Rondebosch 7701, South Africa

^b Cawthron Institute, Private Bag 2, Nelson, New Zealand

^c Department of Zoology and Entomology, Rhodes University, Grahamstown 6140, South Africa

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ABSTRACT

Non-indigenous species (NIS) are a growing problem globally and, in the sea, aquaculture activities are critical vectors for their introduction. Aquaculture introduces NIS, intentionally or unintentionally, and can provide substratum for the establishment of other NIS. Little is known about the co-occurrence of NIS over long periods and we document the coexistence over decades of a farmed NIS (a mussel) with an accidentally introduced species (an ascidian). Both are widespread and cause serious fouling problems worldwide. We found partial habitat segregation across depth and the position of rafts within the studied farm, which suggests competitive exclusion of the mussel in dark, sheltered areas and physiological exclusion of the ascidian elsewhere. Both species exhibit massive self-recruitment, with negative effects on the industry, but critically the introduction of NIS through aquaculture facilities also has strong detrimental effects on the natural environment.

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1. Introduction

Non-indigenous species (NIS) dramatically alter native species distributions and can have extensive economic impacts (Lodge, 1993; Mack et al., 2000; Simberloff et al., 2005), but the problem is particularly acute in the case of coastal ecosystems (Carlton, 1996) which are subject to high frequencies of inoculation by propagules of NIS through ever increasing shipping activity (Carlton, 1985; Coutts and Dodgshun, 2007; Kaluza et al., 2010; Liu and Tsai, 2011). Even allowing for sampling bias, it is clear that marine NIS are more common in sheltered environments such as harbours and marinas than on the open coast (Bax et al., 2003). These sorts of conditions are also favoured for the establishment of aquaculture facilities, and recent research has identified the aquaculture industry as a major vector for the introduction of NIS (Minchin, 2007), particularly macroalgae (McQuaid and Arenas, 2009). Although the most important environmental impact of aquaculture activities is regarded as the introduction of NIS (McKindsey et al., 2007; Wallentinus and Nyberg, 2007; Rilov and Crooks, 2009), they can have many other negative environmental consequences (Whiteley and Bendell-Young, 2007; Lutz-Collins et al., 2009; McKindsey et al., 2009; Nickell et al., 2009). Ironically, not only do aquaculture facilities act as a conduit for NIS, they also suffer

economically and ecologically from the effects of NIS as fouling organisms (McKindsey et al., 2007; Wallentinus and Nyberg, 2007; Lutz-Collins et al., 2009; Rilov and Crooks, 2009). Despite this, the establishment of invasive species in aquaculture facilities is still poorly understood. For example, although the introduction of aquaculture structures creates novel gradients of physical conditions, little is known about the mechanisms that enable, regulate and promote the distribution of NIS across artificial surfaces of aquaculture structures. Another aspect that remains poorly investigated is the temporal aspect of such colonisations. We know that the abundance of NIS on aquaculture activities can suffer important short-term fluctuations (Ramsay et al., 2008), but the long-term consequences of such introductions remain unknown. This includes questions such as whether the populations are more or less permanent and whether they act as source populations that can inoculate natural communities in the surrounding area.

Fouling organisms have negative consequences for human activities worldwide (e.g. Lesser et al., 1992; Schultz, 2007), largely due to their rapid colonisation and growth rates (Bailey-Brock, 1989; Lutz-Collins et al., 2009), and this is particularly problematic for aquaculture (Tovar et al., 2000; Borja et al., 2009). Both fouling by other organisms (Mook, 1981; Lawrence et al., 2000; Carver et al., 2003; Bourque et al., 2007; Rocha et al., 2009) and self-recruitment of the cultivated species (Lutz et al., 1991; Enright, 1993) can be problems that affect the economic returns from aquaculture operations (Campbell and Kelly, 2002; Rodriguez and Ibarra-Obando, 2008). Because aquaculture facilities often rely on floating structures that provide shading in protected bays where high inputs of organic matter

* Corresponding author. Present address: Department of Evolution and Ecology, University of California, One Shields Avenue, Davis, CA 95616, USA. Fax: +1 530 752 1449.

E-mail addresses: mrius@ucdavis.edu (M. Rius), Kevin.Heasman@cawthron.org.nz (K.G. Heasman), C.McQuaid@ru.ac.za (C.D. McQuaid).

occur (e.g. Pérez-Camacho et al., 1991), they can provide ideal conditions for fouling organisms.

The development of a fouling community depends on the presence of a surface with suitable biofilm (Lappin-Scott and Costerton, 1989), and is affected by a wide range of factors including sedimentation (Airoldi, 2003) and microtopography (Bers and Wahl, 2004; Bers et al., 2010). The intrinsic characteristics of the substratum are also critical and recent research has shown that fouling organisms establish more readily on floating structures than fixed ones (Dafforn et al., 2009). Perhaps two of the most important factors influencing the establishment of epibiotic communities are water flow and light availability, which are particularly strongly altered in aquaculture situations. Hydrodynamic forces reduce sedimentation while supplying oxygen and nutrients, but strong water flow, for example over the hulls of moving vessels, can inhibit fouling (Coutts et al., 2010). Consequently, where nutrient and oxygen supply are not problematic, relatively sheltered conditions favour epibenthic communities (Bax et al., 2002). Light intensity is closely linked to the distribution of benthic organisms in shallow subtidal communities (Miller and Etter, 2008), with many species showing strong phototactic responses during settlement (Wendt and Woolacott, 1999; Rius et al., 2010). The distribution of such organisms is also strongly influenced by biotic interactions such as predation and competition that can affect adults, but can also directly control recruitment (Osman and Whitlatch, 1998; Rius et al., 2009).

One of the most notorious invasive marine species worldwide is the vase tunicate, *Ciona intestinalis* (Linnaeus 1758), a species considered indigenous to the northern Atlantic Ocean (Monniot et al., 2001) that is now a common fouling organism throughout the world (Lambert and Lambert, 1998; McDonald, 2004; Castilla et al., 2005; Iannelli et al., 2007; Lutz-Collins et al., 2009; Rius et al., 2010). Although this species does not appear to compete with other organisms under natural conditions, when it becomes invasive it is a major driver of change in the composition of sessile communities, affecting local species diversity and altering community processes (Blum et al., 2007). Similarly, *C. intestinalis* causes serious fouling problems for shellfish farms in North America (Uribe and Etchepare, 2002; Carver et al., 2003; Lutz-Collins et al., 2009) where, due to its size and its densities when aggregated, it affects the growth and survival of the cultivated blue mussel *Mytilus edulis* by competing for food (Lesser et al., 1992). Although *C. intestinalis* has been identified as a fouling problem in northern hemisphere regions, there are few such reports from the southern hemisphere (McDonald, 2004). *C. intestinalis* was first discovered in South Africa in the mid 20th century (Millar, 1955, 1962), and first detected on shellfish farms there in July 1991 (C.L. Griffiths pers. comm.).

Shellfish farming is an economically important activity worldwide (Carlton, 1992; Boyd and Heasman, 1998; Borja et al., 2009) and in South Africa it is based on two NIS. During the introduction of mussel farming in South Africa in the 1980s and early 1990s attempts were made to grow indigenous mussel species, including *Perna perna* and *Choromytilus meridionalis* (Griffiths et al., 2004). However, these failed and the Mediterranean mussel, *Mytilus galloprovincialis* (Lamarck 1819), became the main species farmed, well ahead of the other cultured bivalve species, the oyster *Crassostrea gigas* (Griffiths et al., 2004). *M. galloprovincialis* is a highly successful fouling species (Lee and Chown, 2007) that has spread around the world (Apte et al., 2000; Branch and Steffani, 2004; Castilla et al., 2005) and is believed to have been accidentally introduced into South Africa in the 1970s (Grant and Cherry, 1985), probably through shipping (Grant et al., 1984). *M. galloprovincialis* has subsequently expanded along more than 2000 km of the South African coastline (Robinson et al., 2005) and now dominates the entire mussel zone of the west coast and shows partial habitat segregation with the indigenous mussel *P. perna* on the south coast

(Bownes and McQuaid, 2006; Rius and McQuaid, 2009). The coast of South Africa is open to powerful wave action (Steffani and Branch, 2003; Zardi et al., 2006), with few sites that are suitable for open water aquaculture. Of these, the only site with mussel farms is the sheltered Saldanha Bay, located on the west coast of the country. This sets the scene for a unique situation in which two introduced, invasive species can be studied; *M. galloprovincialis* is cultivated through aquaculture, while *C. intestinalis* forms a fouling nuisance to this industry.

Our aim was to quantify spatial and temporal patterns to assess the persistence of *C. intestinalis* and self-recruitment of *M. galloprovincialis* as biofoulers. We conducted surveys a few years after the first date of detection of *C. intestinalis* on mussel farms and again almost two decades later. Our sampling design included gradients of conditions across the aquaculture facilities to understand the factors influencing the establishment, distribution and long-term persistence of the studied NIS.

2. Material and methods

This study was conducted in Saldanha Bay (Fig. 1), on the upwelling-dominated west coast of South Africa, where primary production within the bay is regulated by coastal upwelling

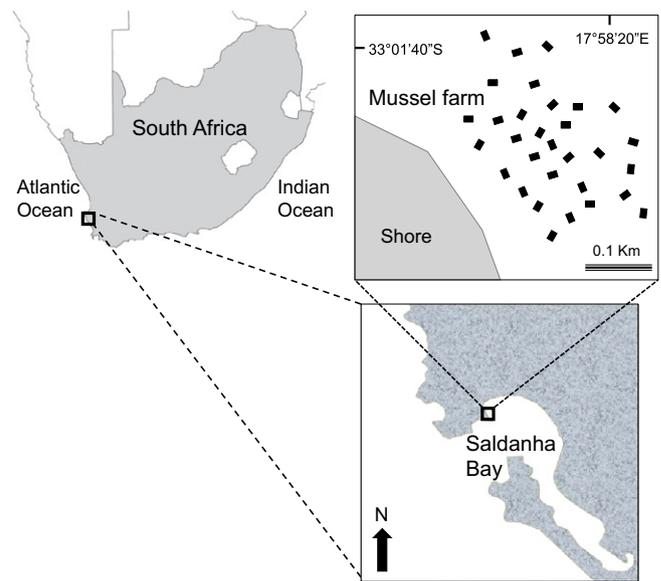


Fig. 1. Map of the studied site showing both the geographic position of Saldanha Bay on the west coast of South Africa and the rafts (black rectangles) within the mussel farm area. The different exposure levels were chosen according to the distance from the shore (see text for details).

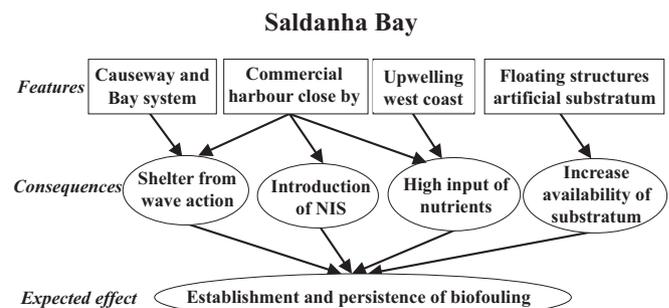


Fig. 2. Diagram summarizing the characteristics of the studied system, as well as the characteristics that are likely to influence the distribution of the fouling species. Arrows indicate positive effects.

(Grant et al., 1998). This bay houses an important commercial harbour accommodating both transoceanic and transcontinental shipping. The studied mussel farm was located in the north part of the bay, which is relatively sheltered from wave action but considered to be a high-energy environment due to storms or strong wave action during early winter (Heasman et al., 1998). Water currents within the bay are primarily influenced by tide, wind and an oscillating bay resonance wave (Boyd and Heasman, 1998). At the farm site, water currents are dominated by wind

forces at the surface and by tidal influences below 2 m depth (Boyd and Heasman, 1998). Thus, several factors combine to establish favourable conditions for biofouling in this situation (Fig. 2), especially for filter-feeder organisms. In order to cover the full range of biotic and abiotic factors experienced by rafts, we identified three regions across the mussel farm – rafts situated on the side closest to the shore (most protected from wave action), rafts facing the bay (most exposed), and rafts situated in the centre of the farm.

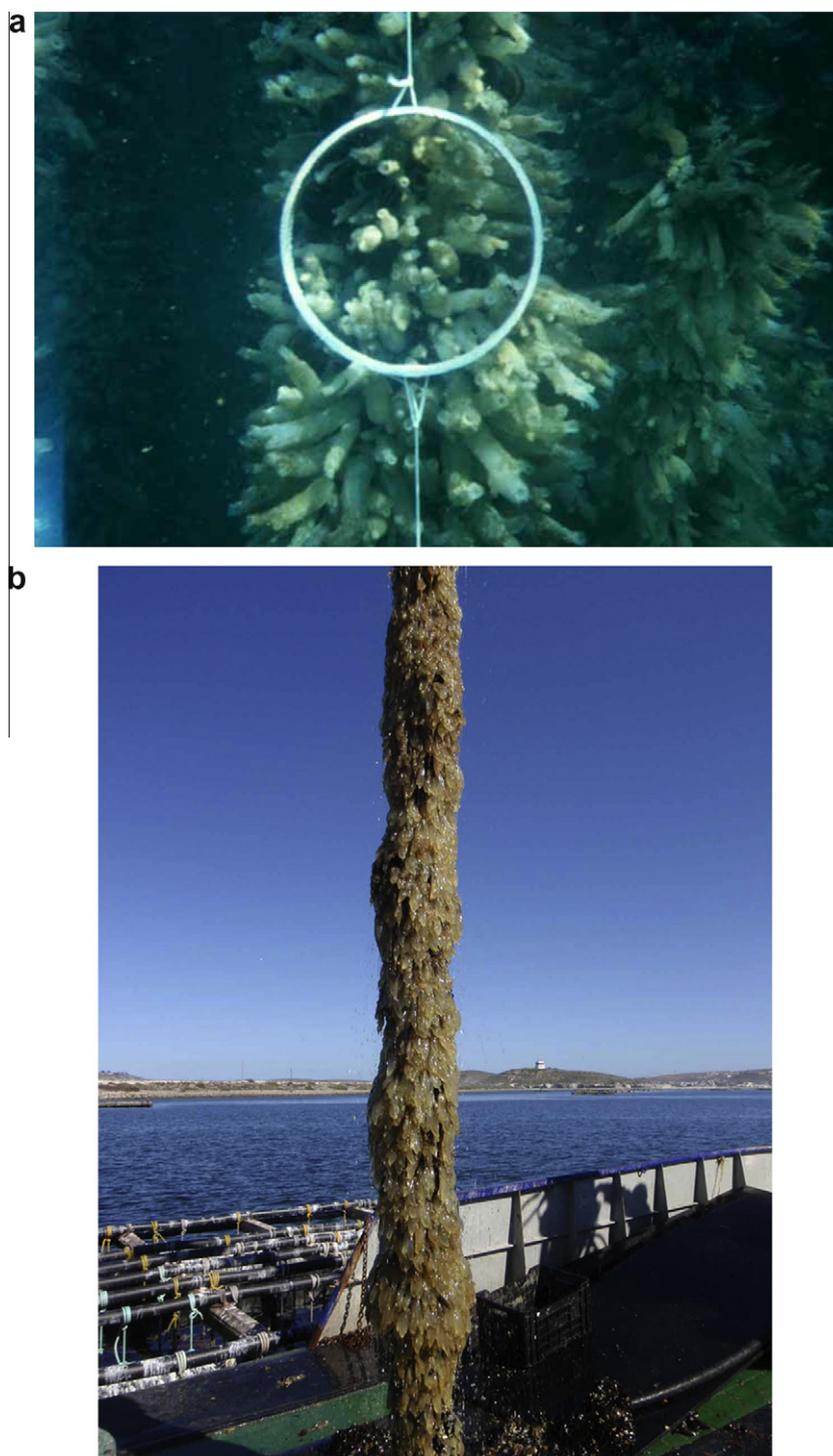


Fig. 3. Photographs of the mussel ropes fouled by 100% cover of *Ciona intestinalis* from the two surveyed years: (a) 1994, underwater photograph; (b) 2010, photograph of a mussel rope when pulled out from the water. The sampling ring is 20 cm in diameter.

Three rafts were randomly chosen, one in each of the three regions within the mussel farm described above, from each of which we sampled six randomly selected ropes. We divided each rope into five sections (0, 1.5, 3, 4.5 and 6 m depth) and sampled these points to obtain abundance estimates for both *C. intestinalis* and mussel spat. Here we differentiate between mussel spat, which are naturally settling mussels, and seed mussels, which are bound onto production ropes for cultivation. For the sampling, we made use of a 20 cm diameter ring, which delimited an area of 314.2 cm² (Fig. 3a). Considering the three-dimensional nature of mussel beds and tunicate aggregates, which normally form multi-layer matrices, we considered, in addition to the animals found on the surface of the ring area, the ones underneath until reaching the actual attachment rope.

We conducted surveys in May 1994 and March 2010. As seed mussels are collected from wild populations within Saldanha Bay (Griffiths et al., 2004) and deployed during December (A. Wood pers. comm.), the sampled rafts contained similar age ropes in both sampled years. The 1994 surveys were done using SCUBA. We lowered a rope with 20 cm rings spaced 1.5 m apart alongside each mussel rope. The numbers of *C. intestinalis* within each ring were assessed in situ. Mussel spat abundance was assessed by stripping mussels within the sampling ring, from the same rafts and ropes where *C. intestinalis* samples were obtained. All individuals >0.5 cm within the sampling circle area were counted. During 2010 the use of SCUBA was not possible due to logistical constraints. The surveys were conducted by removing the ropes from

the water using a motorized crane located on board a boat used for mussel farming activities, which allowed us to obtain destructive samples of both mussel spat and *C. intestinalis* by removing all fouling individuals found within the sampling ring at the different depths. All individuals >0.5 cm were then transported to the laboratory and counted.

We tested the abundance of fouling species using Analysis of Variance (ANOVA) tests with Depth as a fixed orthogonal factor considering each species and sampling year separately. Significant results were followed by Tukey HSD *post hoc* tests. We did all statistical analyses using R 2.11.1 (R Development Core Team 2010).

3. Results

We found that mussel ropes were massively fouled by *C. intestinalis* and wild mussel spat in both sampled years, although *C. intestinalis* fouling was more apparent because they had overgrown the mussels (see Fig. 3b). Although we have no data on variation in abundance either within the sampled or among the intervening years, the results indicate that numbers of *C. intestinalis* were rather lower in 2010 than 1994, while the opposite trend was found for *M. galloprovincialis* (see below).

For *C. intestinalis* we found the same depth trend in both years, with abundance increasing steadily with depth (Fig. 4a). The three rafts sampled in 1994 showed similar abundances of *C. intestinalis* (Fig. 5a), while in 2010 the middle (most protected) raft had

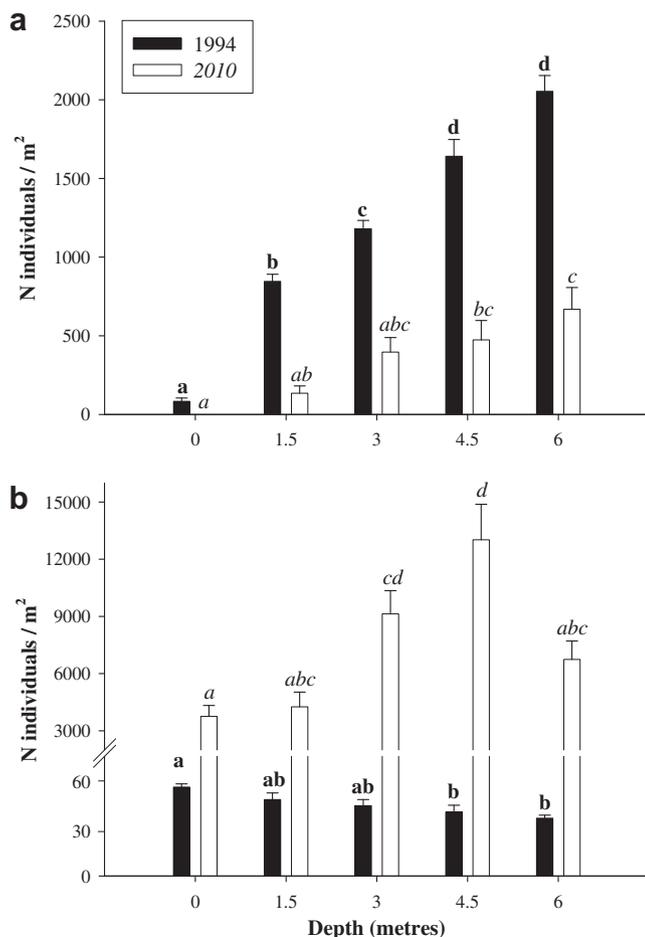


Fig. 4. Mean numbers of individuals across different depths of: (a) *Ciona intestinalis* and (b) wild mussel spat. Letters indicate homogenous groups as determined by Tukey HSD *post hoc* tests. Vertical bars denote standard errors.

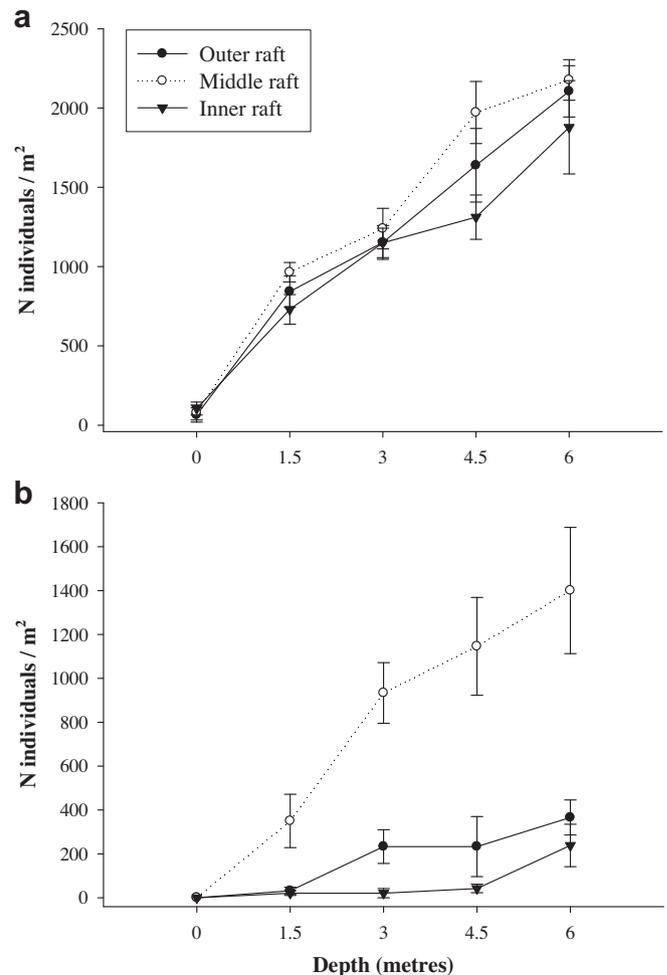


Fig. 5. Mean densities of *Ciona intestinalis* across different depths for the three surveyed rafts in (a) 1994 and (b) 2010. Vertical bars denote standard errors.

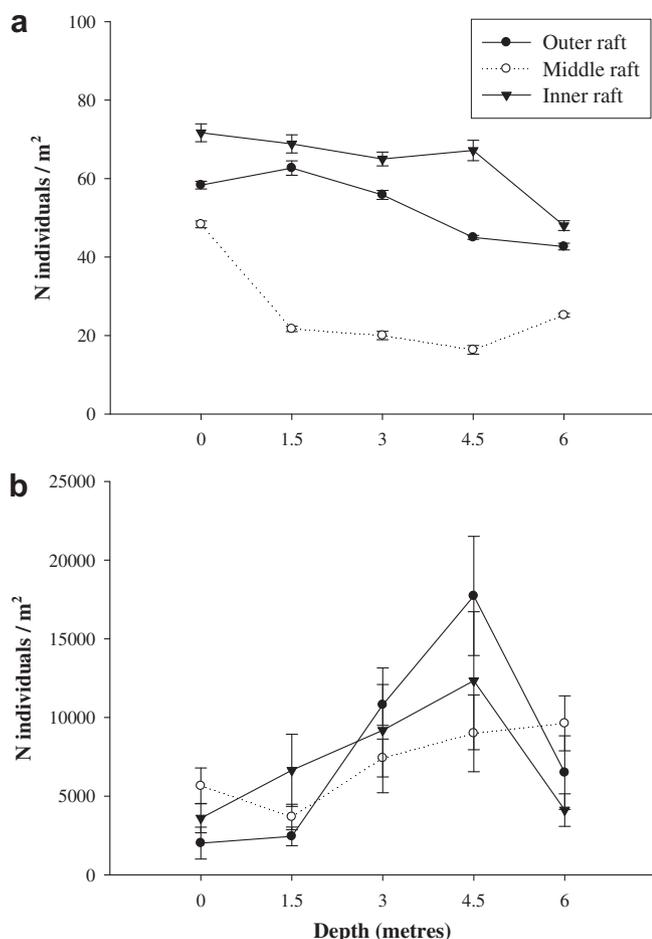


Fig. 6. Mean densities of wild mussel spat across different depths for the three surveyed rafts in (a) 1994 and (b) 2010. Vertical bars denote standard errors.

considerably higher abundances of *C. intestinalis* than the other two rafts (Fig. 5b).

The situation was quite different for mussel spat. We found vast differences when we compared the sampled years (Fig. 4b), with the trend of spat abundance among different depths being quite different between years. In 1994 mussel spat decreased with depth, while in 2010 they increased with depth to 3 and 4.5 m and then decreased at 6 m. The differences among rafts (Fig. 6) were essentially the opposite to the findings for *C. intestinalis* (Fig. 5). In 1994 the middle raft had the lowest abundance of mussel spat (Fig. 6a), while in 2010 there was little difference among rafts (Fig. 6b). Thus the distribution of the two species was basically complementary among rafts.

Regarding depth trends of *C. intestinalis*, we found significant effects of Depth in 1994 (ANOVA, $F_{4,85} = 129.146$, $P < 0.001$), and *post hoc* comparisons showed significant results in almost all comparisons (Tukey test, $P < 0.05$, see Fig. 4a). Regarding the 2010 data, we found significant effects of Depth (ANOVA, $F_{4,85} = 5.950$, $P < 0.001$), and pairwise comparisons showed significant results between deeper and shallower conditions (Tukey test, $P < 0.05$, Fig. 4a). Overall the results indicate a clear preference of *C. intestinalis* for areas that are deeper (i.e. darker) and more protected from wave and current energy, and therefore the mussel ropes in the middle of rafts tended to carry much heavier loads of *C. intestinalis* than those towards the raft perimeter.

For mussel spat we found that the effects of Depth were significant in both 1994 and 2010 (ANOVA, $F_{4,85} = 3.655$, $P < 0.01$; $F_{4,85} = 7.967$, $P < 0.001$; respectively). *Post-hoc* tests in 1994

showed significant differences between deep and shallow regions of the mussel ropes (Tukey test, $P < 0.05$, see Fig. 4b), and in 2010 the significant differences were mostly between the central depths (3 and 4.5 m) and the rest (Tukey test, $P < 0.05$, Fig. 4b).

Other fouling species were found in much lower abundances on the mussel ropes, including considerable numbers of sea cucumbers (*Thyone aurea*) and colonial ascidians (*Botrylloides* sp.), along with fewer ribbed mussel (*Aulacomya ater*), ascidians *Pyura stolonifera*, *Styela plicata* and *Diplosoma listerianum*, goby fishes, sea-stars, tube worms, brittle stars and crabs.

4. Discussion

By becoming invasive, NIS inevitably interact with the indigenous biota, but in areas hosting multiple NIS, they will also interact with one another. Simberloff and Von Holle (1999) and Simberloff (2006) suggested that interspecific facilitation among multiple invasive species could result in accelerating rates of new introductions, leading to invasion meltdown. While there have been no recorded examples of this, there are examples of invasive species facilitating each other's survival (e.g. Grosholz, 2005) and also of invasive species facilitating native species (Rodriguez 2006). Although we did not find any evidence of one NIS facilitating the other, we show that 20-year co-existence of two NIS is clearly possible, largely because the aquaculture facility offers them favourable conditions. The presence of artificial substratum in the form of mussel rafts has offered a niche for the long-term persistence of NIS at huge abundances. Therefore, shellfish farms represent an ideal situation for the establishment and proliferation of nuisance species that can co-exist within aquaculture facilities for decades.

We revealed that the partial habitat segregation found between the studied fouling NIS occurs at two levels: among rafts and within ropes (i.e. depths). On one hand, we found higher abundances of *C. intestinalis* on more protected areas and in deeper sections where less light was available. This correlates well with the distribution of *C. intestinalis* in natural conditions where it generally favours calmer, darker conditions where water shear movement is minimised (Havenhand and Svane, 1991; Howes et al., 2007), as well as the settlement behaviour of its larvae, which prefer shadowed areas (Rius et al., 2010). On the other hand, we found self-recruitment of *M. galloprovincialis*, with variable depth trends, in parts of the mussel farm that were exposed to greater water movement. Because *M. galloprovincialis* is present both on wave exposed and wave sheltered shores along the west coast of South Africa (Steffani and Branch, 2003), we expected similar abundances of mussels both on exposed and sheltered sections of the mussel farm. However, we found partial habitat segregation with *M. galloprovincialis* spat on the rafts at the most wave exposed sections, i.e. periphery of the mussel farm, while *C. intestinalis* primarily colonised centrally placed rafts. This suggests that losses of mussel production due to *C. intestinalis* fouling will be greater on larger rafts and in larger farms that provide greater protection from wave energy. *C. intestinalis* remains highly competitive at chlorophyll-*a* concentrations as low as 1.5–4 µg/l (Petersen et al., 1995) and this might explain why *C. intestinalis* survival rates appear to be greatest in the centre of the farm, where the lowest abundances of fouling by mussel spat was found. This, together with the evidence that *C. intestinalis* generally overgrows cultivated mussels, using them as secondary substratum, suggests that *C. intestinalis* fouling on sheltered parts of the raft results in the exclusion of mussel spat. Thus, these results suggest asymmetric competition, with higher abundances of mussel spat where wave movement and light are stronger, reflecting physical exclusion by *C. intestinalis*, rather than preferential settlement or exclusion by mussels.

The invasive potential of *M. galloprovincialis* in South Africa has proven to be very high (Robinson et al., 2005) and a possible mechanism to explain its success is the high propagule pressure it exerts on the native community (Branch and Steffani, 2004). Both studied NIS occurred at extremely high densities on the mussel farm. *C. intestinalis* had abundances of up to 2700 individuals m^{-2} in both sampled years and extrapolating from ca. 450 mussel ropes on a raft of 22 m \times 11 m (Boyd and Heasman, 1998; Heasman et al., 1998), this indicates an average of between 7 and 8×10^5 individuals on the ropes of a single raft. Regarding wild mussel spat, we found impressive densities of up to 30,000 individuals m^{-2} in 2010 (which extrapolates to an average of $16\text{--}17 \times 10^7$ individuals on the ropes of a single raft). Although the main concern for mussel growers is the effect of *C. intestinalis* on seed mussel mortality (Ramsay et al., 2008), mussel spat fouling represents another concern in Saldanha Bay and elsewhere. The high settlement of wild mussel spat in farmed mussels increases mussel densities dramatically, and in aggregated benthic organisms this can result in slower growth rates and exclusion by space limitation (Hughes and Griffiths, 1988). In addition, the increase in mussel numbers on the ropes through fouling makes their handling more difficult and costly, as the mussel ropes are heavier and sorting of production mussels by size is more difficult.

The enormous differences in wild spat numbers detected between years may reflect monthly rather than interannual variation in settlement rates and spawning period. Pfaff et al. (2011) showed that recruitment of mussels was highly consistent among years with a strongly seasonal variability along 400 km of shoreline on the west coast of South Africa where Saldanha Bay is located. Seasonality in recruitment is presumably based on strong seasonality in spawning. For example, Heasman et al. (1998) observed major spawning events in Saldanha Bay during early summer (October) in 1993 and 1994. Pfaff et al. (2011) also found that mussel recruitment peaked during austral summer, corresponding to seasonal wind events that alter coastal upwelling patterns, with recruitment diminishing after February. The extremely high values we observed in March 2010 are almost certainly reflect the accumulation of recruits over the preceding summer, while the low numbers in May 1994 were likely due to post-settlement mortality following the major recruitment period. Post-settlement is known to be extremely high in marine benthic invertebrates (e.g. Stoner 1990) and, for mussels on the coast of South Africa, has been estimated at around 60–64% within the first week (von der Meden et al., unpubl. data).

In the present study two forms of both inter and intraspecific competition were expected, competition for space and competition for food. Given the densities involved, both seem probable. Firstly, the partial habitat partitioning found between the studied NIS across the mussel farm is likely to reflect interspecific competition for space, as *C. intestinalis* naturally avoids exposed conditions and it is likely to exclude mussel spat competitively from sheltered regions. Secondly, food limitation can occur in Saldanha Bay, especially when densities of organisms growing on ropes are high (Heasman et al., 1998) and/or because the mussel farms themselves affect water flow (Boyd and Heasman, 1998). Despite possible competition for both food and space, other factors such as physiology or settlement behaviour may also be important. For instance, work on the interactions of intertidal populations of *M. galloprovincialis* and the indigenous mussel *P. perna* on the South African coast shows that habitat segregation can result from the complex interplay of multiple effects, including initial settlement, physiological limitation and post-settlement mortality (Bownes and McQuaid, 2006, 2009, 2010), as well as competitive interaction of adults (Rius and McQuaid, 2006, 2009).

Ascidians disperse during a short-lived lecithotrophic larval stage, which is the only motile phase of their life cycle and has ex-

tremely short larval swimming times and limited dispersal capabilities (Olson, 1985; Davis and Butler, 1989; Svane and Young, 1989). Thus, ascidian larvae generally settle close to the parent population (Davis and Butler, 1989; Petersen and Svane, 1995; Manríquez and Castilla, 2007) so that the number of settled larvae is significantly greater around adults or mimics of adults. This is largely due to small scale hydrodynamic effects rather than larval behaviour (Havenhand and Svane, 1991). Laboratory experiments showed that artificially fertilized eggs of *C. intestinalis* take 14–24 h to hatch (depending on water temperature) and settlement occurs preferentially between the first few minutes after hatching up to 36 h later (K.H. and M.R. unpubl. data). Many eggs remain in a mucus strand and they adhere to structures close by, which in our study is likely to be an adjacent mussel rope. Mussels on the other hand have long-lived larvae with settlement occurring weeks after spawning (Seed and Suchanek, 1992), so that larvae are theoretically capable of dispersing over huge distances (Scheltema, 1986). They have limited behavioural control over their dispersal and their realised advection depends heavily on hydrodynamics (Pineda, 1994, 2000). In some situations, this results in dispersal over much smaller distances than expected, particularly where wind-driven currents prevail (McQuaid and Phillips, 2000). There is increasing evidence that bays in general are areas where biological materials, including larvae, tend to accumulate (Gaines and Bertness, 1992; von der Meden et al., 2008). It appears, therefore, that the system studied here, and probably many similar systems, constitute at least semi-closed populations with self-seeding promoting positive feedback between adult populations of the two NIS species and the intensity of biofouling. In addition to the larval stage, ascidians can be passively transported through human-mediated transport (e.g. fouling hulls or sea chests of ships, attached to debris trapped in ballast tanks, etc.), which can facilitate dispersal over thousands of km. As a sheltered bay surrounded by wave exposed shores, Saldanha Bay is an isolated habitat on the west coast of South Africa. However, individuals of *C. intestinalis* living in this bay share the most common mtDNA haplotype found in harbours along the coast of South Africa (M.R. unpubl. data) suggesting that genetic exchange with other *C. intestinalis* populations is probably through shipping.

Mussel rafts in Saldanha Bay are anchored on a sandy bottom and affect the local macrofauna through the accumulation of debris and the development of anoxic conditions below the rafts (Stenton-Dozey et al., 2001). They also offer new habitat for fouling species in the form of both debris and the mussel ropes themselves which must exacerbate the problem of fouling faced by the industry. In this situation it is necessary to ask whether it is economically viable or even possible to control these fouling species. Fouling animals can be removed to maximise growth and reduce growth deformities in shellfish farms (Taylor et al., 1997). Biological control, for example through the introduction of sea urchins (Lodeiros and García, 2004), remains a controversial possibility. Measures to reduce the effects of fouling ascidian species have been implemented in Canada (LeBlanc et al., 2007), Chile (Zapata et al., 2007) and New Zealand (Coutts et al., 2007), but the topic remains contentious because of the cost implications (LeBlanc et al., 2003) and possible pollution issues (e.g. the use of chemicals to control fouling species, see LeBlanc et al., 2007). Mussel growers in Saldanha Bay argue that the presence of fouling organisms including *C. intestinalis* is not a cause for concern. Certainly this industry has coexisted with this invasive ascidian for 20 years, but this could change given a particularly favourable year for *C. intestinalis*, which could cause significant economic loss. This is exactly what happened in 2000 in the Marlborough Sounds in New Zealand when a devastating settlement of *C. intestinalis* occurred (K.H. per. obs.). In such circumstances mussel growers could be forced to find alternative solutions, such as those developed

elsewhere. Fouling organisms are not always perceived as posing an economic threat for aquaculture activities (Rodríguez and Ibarra-Obando, 2008; A. Wood pers. comm.; K. Heasman pers. obs.), but the costs of non-control are not borne by the industry alone so that the necessity or possibility of controlling fouling species, particularly NIS, should form part of a larger debate affecting aquaculture systems around the world. Arguably these costs include the environmental problem of aquaculture systems acting as vectors and sources of propagules of NIS inoculating nearby and possibly even quite distant natural communities. Therefore, beyond the straightforward economic costs to the industry, aquaculture facilities can create problems far beyond their own boundaries.

On the south coast of South Africa, a mussel farm established in Algoa Bay was the direct route of the introduction of *M. galloprovincialis*. This NIS, although already abundant on the west coast of South Africa, was absent from the south coast until it was introduced there for aquaculture purposes in 1988. As it had previously been unrecorded along this coast, the mussel farm acted as single point source from which daughter populations emerged in the vicinity over the next few years (McQuaid and Phillips, 2000). The key role of the mussel farm as a parent source population was clearly demonstrated when the daughter populations, still at very low densities, died out shortly after cultivation of *M. galloprovincialis* was discontinued at that site in 1992. Although early detection and strict eradication is always the preferred option (Field 1999), marine introductions after a period of limited dispersal, can naturally die out as is clear from the example in Algoa Bay. In situations such as Saldanha Bay, where this has clearly not occurred, and NIS become well established, the entire system will continue to act as an incubator for these species. Elevated concentrations of NIS propagules will be present in the waters of the bay, which is likely to promote and maintain the supply of propagules to the outskirts of the bay, as well as re-stocking intra and interregional vectors (e.g. shipping) during their stops in the bay. By providing ideal conditions for *C. intestinalis* and actively culturing *M. galloprovincialis* in close physical proximity to a major harbour, there is the clear possibility that aquaculture activities have contributed significantly to the proliferation of these NIS. Overall, the interaction between NIS, as well as the mechanisms that facilitate biofouling on aquaculture facilities, deserve further monitoring, especially in situations where profitable aquaculture is linked to broader environmental impacts.

Author's contributions

Marc Rius – designed the project, collected the data, analysed the data and led the writing.

Kevin G. Heasman – conceived the ideas, designed the project, collected the data, and contributed to the writing.

Christopher D. McQuaid – conceived the ideas, designed the project and contributed to the writing.

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