Manipulation of host behaviour by parasites: ecosystem engineering in the intertidal zone?

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Understanding the influence of parasites on the community ecology of free-living organisms is an emerging theme in ecology. The cockle *Austrovenus stutchburyi* is an abundant mollusc inhabiting the sheltered shores of New Zealand. This species, which lives just a few centimetres under the surface, plays a key role for many benthic invertebrate species, because in these habitats the cockle shell is the only available hard surface where invertebrates can establish. However, the behaviour of this cockle can be altered locally by a parasite, the trematode *Curtuteria australis*. Indeed, heavily infected cockles are unable to bury perfectly and typically lie entirely exposed at the surface of the mud. In this study, we investigated the ecological consequences of this behavioural alteration for two invertebrate species commonly associated with cockles, the anemone *Anthopleura aureoradiata* and the limpet *Notoacmea helmsi*. A field study first demonstrated that in both infected and non-infected populations of cockles, there was a negative relationship between the number of anemones and limpets found on cockles. In the laboratory, we showed that predation of limpets by anemones is possible when they share the same cockle shell. In a heavily infected population of cockles, limpets were significantly more frequent and more abundant on cockles manipulated by *C. australis* than on cockles with a normal behaviour. A colonization test conducted in natural conditions demonstrated that the predominance of limpets on manipulated cockles results from a direct habitat preference. Conversely, anemones were significantly less frequent and less abundant on manipulated cockles than on cockles manipulated by *C. australis*. A desiccation test revealed that, relative to limpets, they had a lower resistance to this physical stress. We discuss our results in relation to current ideas on ecosystem engineering by organisms.

Keywords: *Curtuteria australis*; parasitism; ecosystem engineer; *Austrovenus stutchburyi*; invertebrate; community ecology

1. INTRODUCTION

In recent years, a great deal of attention has been devoted to understanding the relative importance of direct and indirect interactions between species in structuring natural communities (Strauss 1991; Daily *et al*. 1993; Bertness & Callaway 1994; Jones *et al*. 1994, 1997; Menge 1995; Flecker 1996; Bertness & Leonard 1997; Hacker & Gaines 1997; Miller & Travis 1997). Yet, evidence suggests that many species have the potential to change the environment via their own physical structures (autogenic engineer (Jones *et al*. 1994, 1997)), or by transforming living or non-living materials from one physical state to another (allogenic engineer; Jones *et al*. 1994, 1997). Knowing that these changes can markedly influence the diversity of ecosystems, understanding engineering processes and their consequences is one of the current goals of community ecology (Jones *et al*. 1997).

To date, most of the studies illustrating the key role of parasites in structuring animal communities rely on evidence for a differential susceptibility of closely related host species to infection or its consequences (Park 1948;

Barbehenn 1969; Feener 1981; Freeland 1983; Holt & Pickering 1985; Price *et al*. 1986; Boulétreau *et al*. 1991; Minchella & Scott 1991; Thomas *et al*. 1995; Combes 1996; Bonsall & Hassel 1997). Given the diversity of ways in which parasites affect host species, we may, however, expect processes other than a differential susceptibility of hosts to influence the structure of animal communities. Parasite-induced alterations in host phenotype have been frequently reported in a wide range of protozoan and metazoan parasites with complex life cycles (Combes 1991; Poulin 1998). Because alterations in the phenotype of parasitized hosts are sometimes substantial, it is not unrealistic to consider that manipulated hosts can be equivalent to new organisms in the ecosystem, involved in new direct and/or indirect interactions with other species (e.g. Lafferty 1992; Thomas *et al*. 1997*a*, 1998). When a host species constitutes an important component of habitat structure, manipulative parasites altering the characteristics of host populations could have a variety of indirect effects on other species. However, ecological consequences of phenotypic alterations induced by parasites remain largely unexplored.

The cockle *Austrovenus stutchburyi* is an extremely abundant bivalve in sheltered shores of New Zealand

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(Morton & Miller 1973; Thomas & Poulin 1998). This mollusc usually lives between 0 and 2 cm below the surface, and individuals closest to the surface play a crucial role for benthic invertebrate species (Morton & Miller 1973). Indeed, the shell of *A. stutchburyi* constitutes in many shores of New Zealand the only hard surface where benthic invertebrate species can establish. Whereas some of these invertebrates live almost exclusively on cockle shells and form a distinctive community (Morton & Miller 1973), other species can also be found on rocky habitat elsewhere (F. Thomas and R. Poulin, unpublished observations).

Recently, Thomas & Poulin (1998) demonstrated that the burrowing behaviour of *A. stutchburyi* is strongly altered by the trematode *Curtuteria australis*. Indeed, metacercariae of this parasite handicap the host by reducing the growth of its foot. Heavily infected cockles with a stunted foot typically lie entirely exposed at the surface of the mud and experience a higher risk of predation by oystercatchers, the definitive host of the parasite (Thomas & Poulin 1998). This parasite can be locally very common with a prevalence of 100% among cockles and with intensities of infection sometimes greater than one thousand cysts per cockle (Thomas & Poulin 1998).

Given the important ecological differences (light, temperature and desiccation) between living under or above the mud surface, manipulated cockles undoubtedly constitute a new type of habitat for benthic invertebrates. The aim of this study was to analyse the consequences of this behavioural alteration for the organization of the invertebrate community living on cockles. We first investigated in the field and at the laboratory the distribution of, and the nature of, the interactions between two invertebrate species typically found on *A. stutchburyi*, the anemone *Anthopleura aureoradiata* and the small limpet *Notoacmea helmsi*. Then, we observed the pattern of their distributions in a population of cockles heavily infected by *C. australis*, and conducted several experiments to identify the processes by which *C. australis* indirectly structures this invertebrate community.

2. MATERIALS AND METHODS

(a) *Field study*

To analyse the distribution of limpets and anemones on cockles and the nature of their interactions, we first collected at low tide three large samples of cockles (S1, $n = 424$; S2, $n = 546$; and S3, $n = 478$) in three localities (Oyster Bay, 41°18′ S, 174°7′ E; Akaroa Harbour, 43°45′ S, 172°55′ E; Company Bay, 45°50′ S, 170°40′ E, respectively) on the South Island coast of New Zealand during November 1997. To avoid any bias during sampling, all cockles were collected using quadrats (50 cm × 50 cm) thrown at random on the surface of the sediment along a transect parallel to the sea. We collected all the cockles present in three quadrats. In the heavily infected population (S3), we also used the quadrat to collect along the same transect 103 cockles entirely exposed at the surface (i.e. cockles manipulated by *C. australis*; Thomas & Poulin 1998). Given the demonstrated relationship between parasite load and cockle behaviour (Thomas & Poulin 1998), we only determined the mean parasite load of each sampling site by counting the number of *C. australis* metacercariae in 50 cockles chosen randomly in each sample. To describe the characteristics

of the infection by *C. australis* and the colonization by anemones and limpets, we used the terminology (prevalence, abundance and intensity) proposed by Margolis *et al.* (1982).

(b) *Predation experiment*

To examine the possibility that limpets are eaten by anemones when sharing the same cockle, we first determined in the laboratory whether limpets were palatable prey for anemones. For this, one limpet was gently placed on the tentacle circle of 11 anemones. To check whether anemones were able to capture limpets by themselves, we placed 24 cockles with a normal behaviour and harbouring at least one anemone (26 anemones in total) in an aquarium (30 cm × 12 cm) containing 4 cm of natural sediment (mixture of sand and mud) and filled with constantly aerated seawater (18 °C, 38‰). Cockles burrowed rapidly under the sediment and, as in natural conditions, only anemones and sometimes a small part of the cockle shell emerged at the surface of the sediment. We then placed 25 limpets in this aquarium for 96 h, placing them on the surface of the sediment and at a distance of at least 2 cm from the closest anemone. We concluded that predation had occurred when a limpet was found digested (empty shell) close to an anemone.

(c) *Resistance to desiccation*

To compare the resistance to desiccation between anemones and limpets, we collected 56 cockles in the field (Company Bay) harbouring one anemone, and 56 cockles harbouring one limpet. We conducted the experiment in open air during a normal summer day in Dunedin (20 °C). Cockles were placed on the floor with the side harbouring limpets or anemones directly exposed to the sun for 1 h. Then, we placed all the cockles in oxygenated seawater (15 °C, 38‰) and examined the activity of cockles and both limpets and anemones for 12 h; we concluded that death had occurred when no activity was observed during this time.

(d) *Colonization test*

We conducted a colonization test under natural conditions to investigate whether the habitat preference of limpets for manipulated or non-manipulated cockles was a direct phenomenon, or resulted from the interaction with the anemones. For this, we collected in Company Bay 102 cockles manipulated by *C. australis*, and 102 cockles with a normal behaviour during June 1997. The mean shell length of these two groups was not significantly different (*t*-test, $t = 0.2$, d.f. $= 202$, $p = 0.84$). In the laboratory, we removed all the invertebrates present on the shells. Because cockles in the field may be displaced by currents, or may be difficult to find again under the sediment, we attached them to iron stakes using a transparent string (20 cm) with a small piece of brown tissue (1 cm × 0.5 cm) glued onto the shell with 'superglue'. On each of 51 stakes, we attached two cockles manipulated by *C. australis* and two cockles with a normal behaviour. Although the repeatability of the behaviour for the two categories of cockles is very high in the field (Thomas & Poulin 1998), we darkened, for manipulated cockles only, the part of the string closest to the stake over 2 cm with a water resistant pen, allowing us to discriminate at any time the two categories of cockles on each stake. These cockles were returned to Waipuna Bay, a site located in the Otago Harbour of Dunedin opposite Company Bay. Indeed, in this area, limpets are commonly found on cockles, while anemones are scarce (F. Thomas, unpublished observations). Stakes were planted 1 m

Table 1. *Characteristics of the colonization by limpets and anemones on cockles in the three samples*

	number infected (prevalence)	mean abundance ± s.e. (range)	mean intensity ± s.e.
S1 ($n=424$)			
limpets	30 (7.1%)	0.10 ± 0.02 (0–4)	1.47 ± 0.16
anemones	153 (36.1%)	0.53 ± 0.04 (0–5)	1.46 ± 0.07
S2 ($n=546$)			
limpets	78 (14.3%)	0.23 ± 0.03 (0–5)	1.59 ± 0.10
anemones	28 (5.1%)	0.05 ± 0.01 (0–2)	1.04 ± 0.04
S3 ($n=478$)			
limpets	68 (14.2%)	0.17 ± 0.02 (0–3)	1.18 ± 0.06
anemones	289 (60.5%)	1.18 ± 0.06 (0–6)	1.96 ± 0.06

Table 2. *Relationships* (*Spearman rank correlations*) *between abundance and intensity of limpets and anemones and shell length of cockles in the three samples*

	limpets	p	anemones	p
S1				
abundance and shell size	$r_s = 0.26$	< 0.0001	$r_s = 0.42$	< 0.0001
intensity and shell size	$r_s = 0.44$	0.02	$r_s = 0.34$	< 0.0001
S2				
abundance and shell size	$r_s = 0.06$	0.18	$r_s = -0.01$	0.77
intensity and shell size	$r_s = 0.20$	0.08	$r_s = -0.01$	0.95
S3				
abundance and shell size	$r_s = 0.11$	0.02	$r_s = 0.18$	0.0001
intensity and shell size	$r_s = 0.02$	0.84	$r_s = 0.20$	0.0006

apart along a transect running parallel to the low-water mark. We started this experiment in August (winter) and we stopped it three weeks later. We recorded colonization by counting limpets present on the shells of all cockles. In several cases, cockles were found unglued or predated by oystercatchers, so that the final comparison of colonization rates was conducted between 76 cockles manipulated by *C. australis* and 99 cockles with a normal behaviour. There is no reason to believe that this loss of marked cockles could change the results or their interpretation.

All statistical tests were performed following Sokal & Rohlf (1995) and Siegel & Castellan (1988). All tests were two-tailed. Results were considered significant at the 5% level.

3. RESULTS

Dissection revealed that in both S1 and S2, *C. australis* had a lower prevalence and a lower intensity of infection among cockles compared with S3 (prevalence: S1 = 16%, S2 = 6%, S3 = 100%, Fisher's exact test, $p < 0.0001$; mean intensity ± s.e.: S1, 2.1 ± 0.6, $n=8$; S2, 1 ± 0, $n=3$; S3, 144.6 ± 14.9, $n=50$; Kruskal–Wallis ANOVA, $H=25.9$, d.f. = 2, $p < 0.0001$). Whereas in S1 and S2 there were no manipulated cockles at the surface of the mud, they could easily be found in S3, as they were several months earlier in this area (Thomas & Poulin 1998).

Despite broad similarities between the study sites, the mean shell length of cockles was significantly different (mean ± s.e.: S1, 26.3 mm ± 0.3 mm; S2, 22.6 mm ± 0.2 mm; S3, 31.1 mm ± 0.1 mm; ANOVA, $F_{2,1445} = 390.03$, $p < 0.0001$). In the three sampling areas, we observed limpets and anemones colonizing the shell of cockles. Within each quadrat, anemones and limpets were only found on cockle shells. For both limpets and anemones, there were significant variations between sites in prevalence (table 1, Fisher exact test: limpets, $p < 0.0001$; anemones, $p < 0.0001$), abundance (table 1, Kruskal–Wallis ANOVA: limpets, $H=14.3$, d.f. = 2, $p < 0.0008$; anemones, $H=382.3$, d.f. = 2, $p < 0.0001$), and in intensity (table 1, Kruskal–Wallis ANOVA: limpets, $H=11.1$, d.f. = 2, $p < 0.004$; anemones, $H=49.7$, d.f. = 2, $p < 0.0001$). Relationships between abundances and intensities of these invertebrates and the shell lengths of cockles tended to be positive and significant, but this was not a consistent pattern in all samples (table 2).

Among cockles harbouring at least one anemone and/or one limpet, there was for all samples a negative and significant relationship between the number of anemones and the number of limpets found on the cockle shell (Spearman rank order correlation coefficient: S1, $r_s = -0.30$, $n=169$, $p < 0.0001$; S2, $r_s = -0.74$, $n=103$, $p < 0.0001$; S3, $r_s = -0.39$, $n=323$, $p < 0.0001$). This relationship was also significant when observed among the two categories of cockles in S3 (non-manipulated cockles, $r_s = -0.29$, $n=249$, $p < 0.0001$; manipulated cockles, $r_s = -0.51$, $n=74$, $p < 0.0001$).

In the heavily infected population (S3), distributions of limpets and anemones on manipulated cockles were significantly different compared with those observed on non-manipulated cockles. Indeed, among cockles harbouring at least one invertebrate species, limpets were significantly more frequent (figure 1, Fisher exact test, $p < 0.0001$) and more abundant (figure 2, Mann–Whitney U-test, $z = -5.7$, $p < 0.0001$) on manipulated cockles than on cockles with a
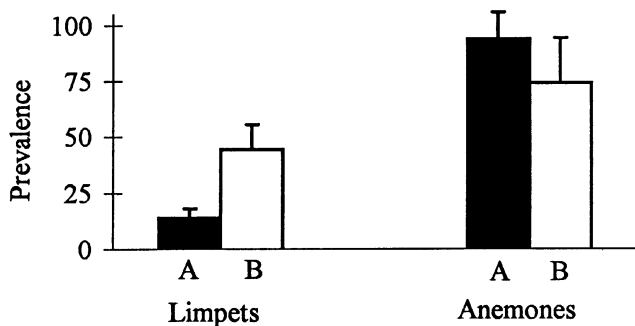
Figure 1. Prevalence (%) of limpets and anemones (*a*) on cockles with a normal behaviour and (*b*) on cockles manipulated by *C. australis* (error bars represent 95% confidence limits).
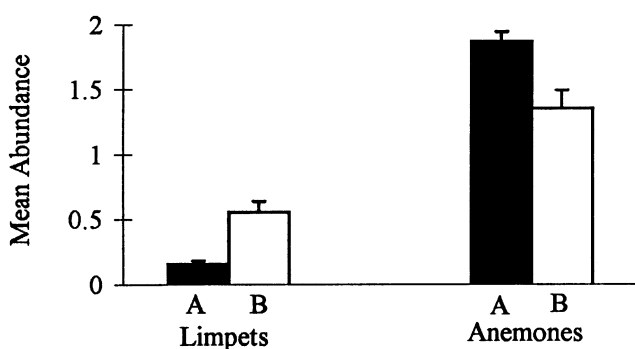

Figure 2. Mean abundance (±s.e.) of limpets and anemones (*a*) on cockles with a normal behaviour and (*b*) on cockles manipulated by *C. australis*.

normal behaviour. Conversely, anemones were significantly less frequent (figure 1, Fisher exact test, $p < 0.0001$) and less abundant (figure 2, Mann–Whitney *U*-test, $\mathcal{Z} = -3.6$, $p < 0.0003$) on manipulated cockles than on cockles with a normal behaviour. Manipulated cockles were also significantly larger than non-manipulated ones (mean ± s.e.: non-manipulated, 30.7 mm ± 0.2 mm; manipulated, 32.4 mm ± 0.3 mm; *t*-test, $t = -4.9$, $p < 0.0001$). However, when controlling for this size difference (residuals of the abundance of each invertebrate species (ln+1 transformed data) as a function of cockle shell length (ln transformed data)), the same patterns of colonization remained significant (comparison of residuals: limpets on non-manipulated cockles, -0.054 ± 0.017; limpets on manipulated cockles, 0.183 ± 0.048; *t*-test, $t = -5.9$, $p < 0.0001$; anemones on non-manipulated cockles, 0.063 ± 0.025; anemones on manipulated cockles, -0.21 ± 0.06; *t*-test, $t = 4.8$, $p < 0.0001$). In the laboratory, limpets gently placed on the surface of anemones were rapidly ingested in all 11 cases. In no more than 6 h, all the limpets were digested, with their shells expelled outside the anemones. After 96 h, 4 out of the 25 limpets initially placed in the aquarium were missing and we found their empty shells near four different anemones.

The desiccation test revealed that none of the 112 cockles exposed to the sun died during the experiment. However, mortality was observed for the other two invertebrate species as 28 anemones (50%) and six limpets (10.7%) out of 56 initially exposed were dead. These rates of mortality are significantly different (Fisher exact test, $p < 0.0001$) and thus indicate a lower resistance of anemones compared to limpets as regards desiccation.

The colonization test demonstrated that even in the absence of anemones, limpets colonize the shells of manipulated cockles significantly more often than those of cockles with a normal behaviour. Indeed, whereas 43 manipulated cockles out of 76 harboured at least one limpet after three weeks, only two cockles with a normal behaviour out of 99 were colonized by limpets (Fisher's exact test, $p < 0.0001$).

4. DISCUSSION

Understanding the factors that govern the organization of intertidal communities has been the topic of numerous studies (Lewis 1960; Dayton 1971; Connell 1972; Menge 1976; Peterson 1979; Menge & Lubchenco 1981; Paine 1984; Menge & Farell 1989; Wilson 1991). Physical gradients, spatial heterogeneity, competition, predation, disturbance and refuge are traditionally recognized as major factors influencing the structure of these communities. Although most of the organisms living in intertidal habitats are hosts for parasites (Laukner 1987; Sousa 1991; Thomas *et al.* 1997*b*), ecologists in general have paid little attention to the possible influence of parasites in structuring intertidal communities.

Our study first gives support to the idea that *A. stutchburyi* is an important component of habitat structure in sheltered shores of New Zealand. Indeed, in our study sites, the shell of *A. stutchburyi* was obviously the main hard surface available for limpets and anemones. In addition to these species, we also observed in other localities cockles harbouring mussels, bryozoans, chitons, spionid worms and barnacles in areas without rocky surfaces (F. Thomas, F. Renaud and T. de Meeûs, unpublished observations). The large density of this cockle and the fact that it burrows only 1–2 cm are likely to be important factors explaining the key role of this mollusc for benthic invertebrate communities. Because the cockle *A. stutchburyi* is a direct provider, through its shell, of living space for numerous species, it can be considered as an autogenic physical engineer (*sensu* Jones *et al.* 1997).

In all our samples, the distribution of limpets and anemones was consistent with a negative relationship between the abundance of these two invertebrates. Several phenomena could explain this relationship, for instance, competition for living space on the cockle shell. In addition, the physical presence of anemones on the shell is likely to directly limit the grazing surface of limpets. Our results also indicated that, at least in experimental conditions, predation of limpets by anemones is possible. This is probably due to the concentration of both anemones and limpets on the part of the shell closest to, or slightly emerging from, the surface of the mud. Further information is necessary to determine precisely the contribution of these different phenomena to the observed pattern.

The most striking pattern of distribution remains, however, the differential colonization rate of limpets and anemones on manipulated and non-manipulated cockles. Indeed, as opposed to anemones, limpets were more frequent and more abundant on cockles manipulated by *C. australis* than on cockles with a normal behaviour. This distribution is not a consequence of interactions between

limpets and anemones, as the colonization test showed that limpets prefer manipulated cockles even when anemones are absent. Several advantages could be obtained by limpets from the colonization of manipulated hosts rather than from hosts with a normal behaviour. First, substrate location is probably easier on manipulated cockles than on cockles partly or completely buried (limpets do not burrow in the mud to find a substrate). Second, when anemones are present in the ecosystem, competition for living space and predation risk by anemones are likely to be reduced because of the lower abundance of anemones on manipulated cockles. The reason why anemones are less abundant on manipulated cockles might be their higher susceptibility to desiccation at low tide compared to limpets. Colonization could be, for instance, random during the recruitment period of anemones, but a differential mortality through time between anemones living on manipulated cockles and those living on non-manipulated cockles would lead to the observed pattern. It is also possible that direct avoidance of manipulated cockles by anemones, rather than a differential mortality, explains the differential colonization observed in nature. This would be a possible illustration of the evolutionary importance of indirect effects in ecosystems (Miller & Travis 1996). However, further experiments are needed to address this last point. Another interesting aspect is that cockles are larger at sites with a higher prevalence of parasites. It could be possible that reduction in foot growth caused by parasites allows an increased allocation of resources to shell growth. Given that there are also positive relationships between shell length and invertebrate abundance and intensity, this effect should be explored in more detail.

In any event, our results suggest that parasites that alter the phenotype of their host can have several indirect effects on the whole community. Using the terminology of Jones *et al*. (1994), the parasite *C. australis* would be an allogenic engineer as it turns living material (i.e. its host) from one physical state (buried) into a second physical state (surface). This act of engineering alters both the availability and the quality of habitats for other species. Although limpets apparently benefit from the new environment created, anemones experience less favourable conditions than on non-manipulated cockles. Further research is needed in order to understand the net effects of *C. australis* on the rich invertebrate community living on *A. stutchburyi*.

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