



Octopus tetricus (Mollusca: Cephalopoda) as an ecosystem engineer

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Summary: The Sydney octopus (*Octopus tetricus*) occurs in unusual numbers on a shell bed of its prey remains that have accumulated as an extended midden where additional octopuses excavate dens. Here, *O. tetricus* are ecosystem engineers, organisms that modulate availability of resources to other species and to their own species by causing physical state changes in materials. A community of invertebrate grazers and scavengers has developed on the shell bed. Fishes are attracted to the shell bed in numbers significantly greater than in nearby habitats. Large predators, including wobbegong sharks, were attracted to and fed on concentrations of fish, inhibiting the activities of the original engineers, the octopuses. Positive feedbacks included the accumulation of shell debris, increasing shelter availability for additional octopuses and aggregating fish. Negative feedbacks included reductions of nearby prey size and availability, aggression among octopuses, and predator limitation to octopus activity that would otherwise maintain the shell bed.

Keywords: Jervis Bay; social; population density; denning; aggregation.

Octopus tetricus (Mollusca: Cephalopoda) como ingeniero de ecosistemas

Resumen: El pulpo Sydney (*Octopus tetricus*) aparece en cantidades inusuales en un fondo de cascajo producido por los restos de sus presas que se han acumulado como un extenso estercolero donde otros pulpos excavan sus guaridas. Aquí, *O. tetricus* se comportan como ingenieros del ecosistema, organismos que modulan la disponibilidad de recursos a otras especies y su propia especie provocando cambios físicos en los materiales. Una comunidad de invertebrados herbívoros y carroñeros se desarrolló en el fondo de cascajo. Los peces son atraídos a dicho fondo en número significativamente mayor que en hábitats cercanos. Grandes depredadores, como los tiburones wobbegong son atraídos y se alimentan a partir de concentraciones de peces inhibiendo las actividades originales de los ingenieros de los pulpos. La reacción positiva a la acumulación de escombros incrementa la disponibilidad de refugio para los otros pulpos y la concentración de peces. Los efectos negativos incluyen la reducción de la disponibilidad y el tamaño de los peces, la agresión entre los pulpos, y la limitación de la actividad de los pulpos para mantener el fondo de cascajo como resultado de la presencia de depredadores.

Palabras clave: Jervis Bay; social; densidad de población; guaridas; agregación.

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INTRODUCTION

Octopuses modify their habitats by excavating dens and by accumulating midden piles of prey remains. Much has been made of this latter behaviour in examining octopus diet (e.g. *Octopus vulgaris*: Mather 1991; *O. tetricus*: Anderson 1997; *Enteroctopus dofleini*: Scheel et al. 2007). Octopuses may also modify their habitats in more subtle ways, by differentially providing habitat to small hermit crabs while

preying on larger ones (Gilchrist 2003) or altering habitat selection decisions made by lobsters (Berger and Butler 2001).

These broader habitat effects have in common that they are trophic interactions: octopuses are active predators that prey on crustaceans, including lobsters and hermit crabs. Their predation alters hermit population density and lobster habitat choice. These trophic choices by octopuses may permeate further through the food web (Lyons 2006). Octopus den associates appear

primarily to be scavengers of prey remains (Hartwick and Thorarinsson 1978). The possible non-trophic effects of octopuses on ecosystems through excavation or shell accumulations in middens have not received much attention.

Major ecological interactions between organisms are traditionally trophic: resource competition, predation, parasitism, and mutualism. Jones et al. (1994) point out an additional important form of interaction through physical state changes of materials that mediate the availability of resources to other species. Organisms that effect such changes are termed ecosystem engineers. Ecological effects of engineering species occur in all ecosystems (Jones et al. 1997) and all species affect the physical environment in some ways (Wilby 2002). The concept identifies an important biological principle, and has also proved valuable in focusing attention on interactions among organisms mediated by the physical rather than trophic environment. In marine ecosystems, important engineers have been equated with those that create more complex habitats (Coleman and Williams 2002). Marine habitat builders include corals, bivalves, sabellid worms, coralline algae and marine plants, whose shells or bodies themselves comprise a complex habitat. Excavators, including worms, clams, crustaceans, sea cucumbers, fishes, sea turtles and dugongs that form burrows, pits or other excavations, also increase the structural complexity of marine habitats (Coleman and Williams 2002).

Octopuses are an interesting group in this regard in that they excavate dens and, by virtue of central-place foraging from those dens and their habit of returning to dens to consume some of their prey items, actively aggregate habitat comprised of the shells of their prey. Ecosystem engineers will have both positive and negative effects on other species (Jones et al. 1997). Positive effects will comprise a form of facilitation (Bruno et al. 2003) although not all facilitation is engineering. Mollusks are considered important ecosystem engineers due to their abundance and the persistence of their shells (Gutiérrez et al. 2003). Octopuses lack shells and are sometimes considered rare, however, and therefore the possible role of octopuses as engineers may have been overlooked.

The biology of *Octopus tetricus* (the common Sydney octopus, also known as the gloomy octopus) was reviewed by Joll (1983) but overall it has received relatively little scientific attention. This species occurs in the waters of eastern Australia and northern New Zealand. *O. tetricus* is a member of an *O. vulgaris* complex (Acosta-Jofré et al. 2012) and may be conspecific with the disjunct Western Australia common Perth octopus (*O. cf. tetricus*), but further taxonomic work is needed.

Reproductive biology and growth in this species (Le Souef 1933, Le Souef and Allan 1937, Joll 1976, 1977, 1978) are typical of large benthic octopus species. Juveniles settle to the benthos at a size of about 0.3 to 1.7 g (Joll 1978) and these octopus may live about one year (Joll 1983). Aggression by males to females during mating occurs, males have been observed having their exposed arm during mating attacked by a fish, and mating thus exposes octopuses to attacks (Huffard and Godfrey-Smith 2010).

A northern New Zealand study by Anderson (1997) in a reef habitat described a summer population maximum declining by the end of that season. Octopus midden remains in this study included about two-thirds soft-sediment bivalves, and Anderson (1997) suggested that this species occupies rocky reef habitat during the summer breeding season but otherwise occurs in soft-sediment habitats (where they are anecdotally reported from scallop dredges) on which den availability may be limiting (Katsanevakis and Verriopoulos 2004).

In this report, we examine the positive and negative feedback effects of octopus middens on octopus habitat itself but also on the aggregation across several trophic levels of other marine fauna at a specific site in Jervis Bay, Australia (Godfrey-Smith and Lawrence 2012). In this context, *Octopus tetricus* act as ecosystem engineers that, by accumulation of bivalve shells in a large midden, alter biogenic materials in ways that influence the availability of resources to a number of other species and thereby transform the ecosystem.

MATERIALS AND METHODS

We studied *Octopus tetricus* at Jervis Bay (approximately 35°S, 150.7°E, Fig. 1), an eastern Australian temperate marine embayment. The study site at 17 m depth has previously been described (Godfrey-Smith and Lawrence 2012) and has formed around an unidentified, partially buried and heavily encrusted artifact about 30 cm in length where it emerges from the sediment that provides a single hard-substrate den (sometimes occupied on two sides) in a soft-sediment habitat dominated by scallops (see Results). Remains of bivalves preyed upon by octopuses have accumulated around the artifact as an extended midden, forming a shell bed.

Jervis Bay has a maximum depth of 30 m, and is roughly 15 km (north to south) by 8 km (east to west), with relatively little freshwater input. The perimeter of the bay includes a variety of marine habitats, including shallow rocky reefs, sandy beaches, and mangroves and salt marshes. The centre of the bay below 10 m depth is predominantly (70%) sediments (CISRO 1994), with occasional biogenic structures (clumps of scallops, algae and polychaete hummocks, Ward and Jacoby 1992). The study site occurs in unconsolidated sediment. The bay is managed primarily as either sanctuary or protected habitat and our study site was located in protected habitat (trawling and scallop dredging not permitted).

Sampling was conducted via SCUBA diving using still photography or video from temporarily placed GoPro cameras mounted about 20 cm above the substrate on small tripods. To avoid disturbing the site, we examined shell bed depth without excavation and only by inserting a 35 cm metal probe as deep as it would go every 20 cm along a 20 m transect across the centre of the shell bed. Although the probe could be fully inserted into soft sediment, it did not penetrate hard materials such as scallop shells. This method thus yielded a minimum depth of soft substrate at each point. Excavation of the site to examine the hard ma-

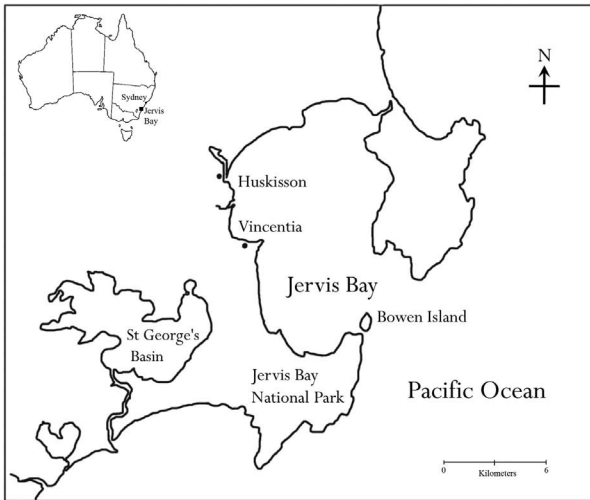


Fig. 1. – The study site is located in the southern portion of Jervis Bay.

materials was not attempted, but surface hard materials were either scallop shells or the artifact forming the centrally-located main den.

We counted octopuses on the shell bed and around adjacent objects and recorded video as described in Godfrey-Smith and Lawrence (2012) on one or more dives during irregular opportunistic site visits in the period July 2010 to October 2013. If more than a single octopus count was obtained, the average of counts across days in a dive series was used as the census for that visit. The location of each octopus was recorded, as well as its size as small (estimated mantle length <10 cm), medium (mantle length 10-15 cm) or large (16-20 cm and presumed to be an adult, based on mating observed by octopuses in this size class).

During October 2012 and August 2013, the abundance of associated animals was assessed from counts within 0.25x0.25 m (hermit crabs) and 0.5x0.5 m quadrats (scallops), and 2x0.5 m line transects (Fortescue). Quadrats and transects were located on the shell bed (within the perimeter), near the shell bed (outside the perimeter but within 3 m of the edge) and far from the shell bed (20 m or further from the edge). Larger pelagic and epipelagic fish were counted from video.

On two sequential days in August 2013, paired time-synchronized cameras were stationed facing away from each other, one located on the outer edge of the shell bed facing inward, and the other 5 m away from the edge of the shell bed facing outward. To compare fish visiting the site (on shell bed) with those in nearby non-bed habitat (off shell bed), all fish visible on the first video frame of each minute on the video clock from each camera were counted and identified to species. This yielded paired samples of fish on and off the shell bed at a given moment in time (within a few seconds).

Fish counts occurring on- and off-bed were compared using the Wilcoxon signed-rank test. Although it was not possible to recognize fish individuals from the video, we nevertheless treated fish counts as independent paired samples. Counts were paired by each on-bed and off-bed sample occurring simultaneously

within a few seconds. Each count was separated by one minute and considered independent due to the high movement rates of the fish. Movement rates were high in two respects: fish swam in and out of the sampling frame in each video; and the distance between the on-bed sample and the off-bed sample was small relative to movement rates and the time between samples. The correlations of counts were compared at different time lags and were essentially zero at one-minute intervals and remained below 0.25 over longer intervals, allowing us to statistically treat counts as independent.

RESULTS

The shell bed was comprised overwhelmingly of scallop valves of several species. Fresh shells collected at occupied dens were *Mimachlamys asperimus* (Doughboy scallop, 100% of N=17 bivalves). Rarely, fresh remains of crabs such as *Nectocarcinus integrifrons* (the sea grass swimmer crab) were also found on the midden. Older eroded shells with pitted or overgrown inner surfaces included primarily *M. asper-*

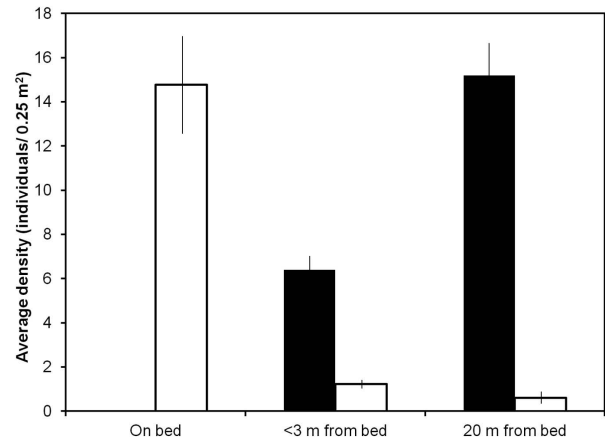


Fig. 2. – The density of live *Mimachlamys asperimus* (doughboy scallop) was lower near and on the shell bed than at a distance of 20 m (dark bars). The density of hermit crabs (species not distinguished during counts) was higher on the shell bed than at a distance of 20 m (open bars). See text and Figure 5 for hermit crab species.

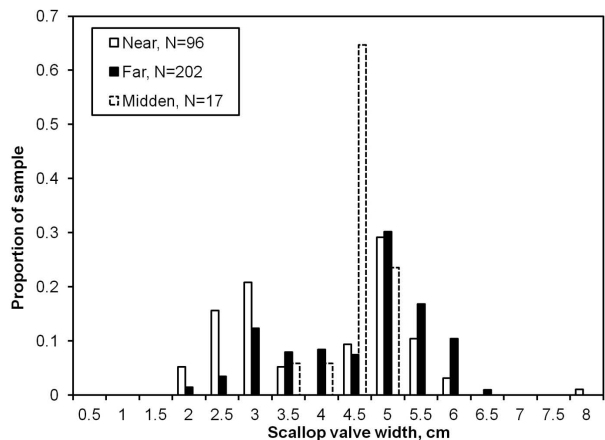


Fig. 3. – The size distribution by scallop valve width of *Mimachlamys asperimus* (doughboy scallop) in an extended midden of *Octopus tetricus*, and at 3 m (near) and >20 m (far) from the midden periphery.

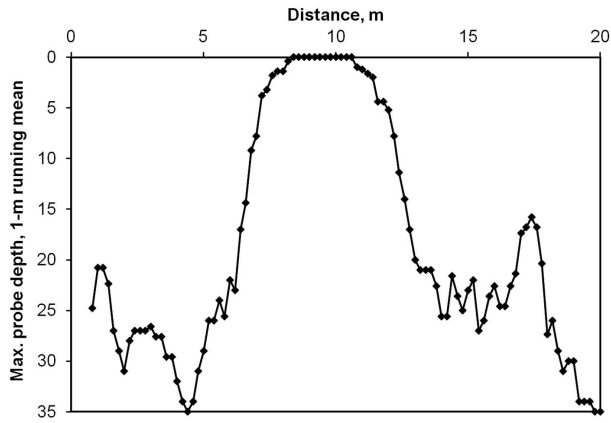


Fig. 4. – The one-metre running average of the depth to which a metal probe could be inserted into the substrate measured at 0.2-m intervals along a 20-m transect crossing the midden shell bed. The central artifact was at metre-mark 9.4, and the visible perimeters of the shell bed were detectable as a greatly increased depth to which the probe could be inserted into soft sediments on either side.

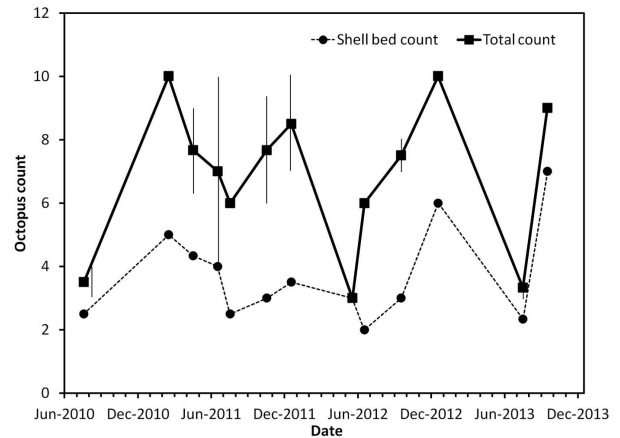


Fig. 5. – The census count of *Octopus tetricus* individuals occupying the shell bed and nearby diver-placed objects (Godfrey-Smith and Lawrence 2012) (solid line with square markers); and the census count for the shell bed only (dashed line with round markers). See Methods for census details.

rimus, but also some commercial scallops, *Pecten fumatus*, which only occurred on the surface in disturbed areas of the bed, such as near octopus excavations or where a large animal, possibly a ray, had excavated a depression. No fresh *P. fumatus* remains were detected.

Live scallops occurred only individually and sparsely on the shell bed and were too scarce to count in the quadrats. Live scallops were over twice as abundant at 20 m (N=13; 0.5x0.5 m quadrats) as at 3 m (Fig. 2; N=15 quadrats; Wilcoxon rank sums test, U=188, p=0.000). Larger scallops (>4.5-5 cm) comprised a



Fig. 6. – Representative examples of fauna of the shell bed, including invertebrates and fishes occupying scallop shells and interstitial spaces. Invertebrates shown (a-c) are snails (a, reticulated dog whelk, *Nassarius particeps*), unidentified gastropod eggs (b, on a scallop shell which the octopus (*Octopus tetricus*) is using as cover in its den), and hermit crabs of several species (c, boxer hermit crab *Paguristes pugil*). Fishes shown (d-f) are Fortescue (d, *Centropogon australis*), banjo ray (e, *Trygonorrhina fasciata* shown covered with hermit crabs that have crawled over it from the shell bed), and southern red scorpionfish (f, *Scorpaena papillosa*), just a few of over 20 fish species recorded on the shell bed. A large ornate wobbegong shark (g-h, *Orectolobus halei*), dominates the background while in the foreground an octopus is visible in its den in the shell bed (g, arrow). A school of Green horse mackerel and mado is visible (g, upper left), on which wobbegongs successfully foraged while on the shell bed (h) as caught on video. The scattered remnants of the fish school are visible in the water column. The dark object in the centre foreground is the artifact used as one den; a GoPro camera on a tripod is visible behind and just to the left of the artifact. Images a, c, d and f and g by DS; b, gastropod eggs by PGS; e, banjo ray with hermits by ML; and h, screen capture from video.

larger portion of the sample at 20 m from the shell bed, whereas the scallop population at 3 m from the shell bed was partially depleted of scallops at this size and relatively enriched in smaller individuals (<3.5 cm, Fig. 3). Far and near scallop size distributions were significantly different (chi-square test with counts binned at one centimetre intervals [2, 3, 4, 5, and >5 cm]: $\chi=23.8$, $df = 4$, $p=0.000$), and the size class above which larger scallops were relatively depleted in the near sample matched the predominant size class of the sample of fresh prey remains collected from the midden.

Flat, unconsolidated substrate (silt and sand) generally >30 cm depth found throughout the area was interrupted by the surface bed of scallop shells (Fig. 4), providing the only epibenthic hard substrate detected in the vicinity (other than associated objects described in Godfrey-Smith and Lawrence 2012).

Although there was no multi-year trend in octopus counts, we recorded higher *Octopus tetricus* counts in the austral summer around November to February (Fig. 5; N=13 site visits). Annual lows occurred in the winter months June to August. Of N=61 *O. tetricus* observations for which size estimates were available, 25 (41%) were of large size, 20 (33%) were medium and 16 (26%) were small. There were no detectable seasonal differences in the size-class distributions within this sample.

Small hermit crab species detected on the site include *Paguristes pugil* (boxer hermit crab, Fig. 6c), *Pagurixus jerviensis*, possibly *Lophopagurus nanus*

(Henderson’s hermit crab, Edgar 2012), and at least one other unidentified species. The density of hermit crabs in 0.25x0.25 m quadrats on the shell bed was approximately ten times higher than that on unconsolidated sediment near the bed or at 20 m distance (Fig. 1. Chi-square test, N=209 hermits total [in 13 quadrats on-bed, 9 near, and 10 far]: $\chi=288$, $df=2$, $p=0.000$). Although these were not counted, small invertebrate predators, grazers and scavengers commonly occurred in the interstitial spaces of the shell bed (e.g. *Hapalochlaena fasciata*, the blue-lined octopus, *Gnathophyllum* sp., a bumblebee shrimp, *Clanculus undatus*, the wavy top shell, and see Fig. 6a-c).

Two counts of the small fish *Centropogon australis* (Fig. 6d) along sequential 2x0.5 m transects yielded counts of 6 and 4 on the shell bed, 3 and 2 at the shell bed edge, and 0 and 0 at 2-4 m from the shell bed. A number of fish species similar in size and habit (Table 1: halfbanded sea perch, southern red scorpionfish (Fig. 6f), bearded rock cod, and dwarf lionfish) occurred on the shell bed but due to their small size and close association with the substrate, these and similar fishes could not be reliably counted from the video frames. As with the Fortescue, these fish species were not noted away from the shell bed. An exception was the butterfly gurnard (Table 1), which was noted near but not on the shell bed.

A total of at least 22 fish species from 17 different families identified from video, on-site still photography or

Table 1. – Species common on the shell bed. Counts are the maximum count in a single sampled video frame (N of 70 frames in which species was present in parenthesis, see Methods). Bold indicates habitats with significantly more individuals on at least one of two video-frame sample periods. None of these species are commonly (C) encountered in nearby off-shell bed habitats except where indicated, although some are occasionally recorded (R).

Family (fishes) Class (invertebrates)	Species name	Common name	Count: ¹ on-bed (N)	Off-bed (N)
Carangidae	<i>Trachurus declivis</i>	Greenback horse mackerel	207 (54)	72 (26)
Kyphosidae	<i>Atypichthys strigatus</i>	Mado	34 (68)	3 (10)
Mullidae	<i>Parupeneus spilurus</i>	Blacksaddle goatfish	26 (26)	6 (4)
Monacanthidae	<i>Nelusetta ayraud</i>	Chinaman leatherjacket	25 (34)	8 (10)
Mullidae	<i>Upeneichthys vlamingii</i>	Bluespotted goatfish	8 (29)	0 (0)
Sparidae	<i>Pagrus auratus</i>	Cockney bream ²	5 (24)	4 (21)
Scorpaenidae	<i>Centropogon australis</i>	Eastern Fortescue	3 (39)	0 (0)
Moridae	<i>Pseudophycis barbata</i>	Southern bastard codling	3 (70)	0 (0)
Serranidae	<i>Hypoplectrodes maccullochi</i>	Halfbanded sea perch	1 (4)	0 (0)
Enoplosidae	<i>Enoplosus armatus</i>	Old Wife	1 (1)	0 (0)
Orectolobidae	<i>Orectolobus halei</i>	Ornate wobbegong	1 (70)	0 (0)
Rhinobatidae	<i>Trygonorrhina fasciata</i>	Banjo ray	1 (9)	0 (0)
Scorpaenidae	<i>Scorpaena papillosa</i>	Southern red scorpionfish	1 (47)	0 (0)
Diodontidae	<i>Diodon nichthemerus</i>	Porcupine fish	0 (0)	1 (2)
Heterodontidae	<i>Heterodontus portusjacksoni</i>	Port Jackson shark	0 (0)	1 (1)
Scorpaenidae	<i>Dendrochirus brachypterus</i>	Dwarf lionfish	C	
Carangidae	<i>Pseudocaranx wrighti</i>	Skipjack travally	C	
Platycephalidae	<i>Platycephalus caeruleopunctatus</i>	Bluespotted flathead	C	
Myliobatidae	<i>Myliobatis australis</i>	Southern eagle ray	C	R
Urolophidae	<i>Urolophus kapalensis</i>	Kapala Stingaree	C	
Monacanthidae	<i>Meuschenia scaber</i>	Velvet leatherjacket	C	
Triglidae	<i>Lepidotrigla vanessa</i>	Butterfly gurnard		C
<u>Cephalopoda</u>	<i>Octopus tetricus</i>	Gloomy octopus	C	
<u>Cephalopoda</u>	<i>Hapalochlaena fasciata</i>	Blue-lined octopus	R	
<u>Cephalopoda</u>	<i>Sepioteuthis australis</i>	Southern calamary	C	
<u>Crustacea</u>	Paguridae: <i>Pagurixus jerviensis</i>	Hermit crabs	C	
<u>Crustacea</u>	Diogenidae: <i>Paguristes pugil</i>	Hermit crabs	C	
<u>Bivalvia</u>	<i>Mimachlamys asperrimus</i>	Doughboy scallop		C
<u>Echinoidea</u>	<i>Goniocidaris tubaria</i>	Stumpy pencil urchin		R

¹ Indicated significant differences were between on-site and off-site counts using simultaneous samples of 35 minutes each on two different days, using only first frame in each minute sampled, Wilcoxon paired signed-ranks tests.

² *Pagrus auratus* (following Edgar 2012) is listed as invalid by the Integrated Taxonomic Information System, which lists *Chrysophrys auratus* as valid.

field notes occurred typically on-bed and rarely off-bed. We identified and counted fish in 35 frames of video in paired cameras on each of two sequential days, for a total sample of 140 frames of video over two 35-min periods. The total count (N=6501 individuals) cannot be considered the number of fish using the vicinity, because most were occupying the shell bed and therefore may have appeared in more than one counted video frame.

Counts of five of the six common species identified from video were significantly higher in on-bed than off-bed counts in paired simultaneous video frames on at least one of two days (Table 1, all $p \leq 0.003$). The exception was the cockney bream, a school of which was counted on-bed in some video frames and off-bed in others. Greenback horse mackerel were also detected in some numbers off-bed, but at less than half the numbers that occurred on-bed.

On almost all visits, numerous Port Jackson sharks (*Heterodontus galeatus*) and banjo rays (*Trygonorrhina fasciata*, Fig. 6e) were found resting on the site, and stingarees (*Urolophus kapalensis*) were commonly encountered on the site or its periphery. However, in August of 2012 and 2013, large ornate wobbegong sharks (*Orectolobus halei*, Fig. 6g-h) occupied the site and its periphery, and the Port Jackson sharks, banjo rays and stingarees were not in attendance. On the dates of paired on-bed/off-bed video sampling in August 2013, the ornate wobbegongs occupied the site and its periphery on every dive on each of three days. These sharks appeared to be attracted to the site by the large numbers of fish present (Fig. 6g), and exhibited foraging behaviours recorded on video, including at least two apparently successful lunges at greenback horse mackerel (Fig. 6h), and close investigation of an octopus cautiously attempting to leave the den during daylight. When the ornate wobbegong approached, the octopus immediately retreated back into its den. A few minutes later, the ornate wobbegong returned to its prior location. No octopus was recorded on video leaving its den during daylight in the presence of wobbegongs, whereas one octopus was detected outside its den on a dive conducted shortly after dark, suggesting that when the sharks occupied the site, octopuses deferred their usual daytime activity until dark. In the absence of wobbegongs, octopuses were often recorded leaving their dens, interacting, excavating and foraging during daylight hours.

Other predators observed from video visiting the site and investigating octopuses included a dolphin (species unknown), the smooth stingray ray (*Dasyatis brevicaudata*) and southern eagle rays (Table 1). Off the site in the absence of den cover, an octopus was attacked and eaten by a school of Chinaman leather-jacket (Table 1).

DISCUSSION

We examined the substrate, nearby prey, and associated fauna at a site where the Sydney octopus (*Octopus tetricus*) occur living in close proximity surrounding a single den that has been occupied continu-

ously since at least 2009. Scallop shells, the remains of octopus prey, interrupt the predominant soft sediment accumulated as a midden and form a shell bed in which additional octopuses excavate dens. In this context, *O. tetricus* act as ecosystem engineers, defined as organisms that modulate availability of resources to other species by causing physical state changes in biotic or abiotic materials (Jones et al. 1994). The accumulation of biotic materials as a shell bed transformed the habitat on which a community of invertebrate grazers and scavengers developed (Fig. 6a-c). Benthic and epibenthic fishes are attracted to the habitat and occurred at the shell bed in numbers significantly greater than in nearby habitats (Table 1). Large predators, including wobbegong sharks were attracted to and fed on concentrations of fish (Fig. 6g-h), inhibiting the activities of the original engineers the octopuses. Positive feedbacks to this process included the accumulation of shell debris that provided shelter for additional octopuses and acted as fish-aggregating habitat. Negative feedbacks included a reduction of scallop size and density in the vicinity of the site, aggression among octopuses, and predator limitation to octopus activity that would otherwise maintain the shell bed.

Octopuses have been reviewed as predators (Mather 1993) and their role in food webs has been considered (e.g. Ambrose 1986, Onthank 2008). Octopuses are often regarded as unselective among their typical prey of bivalves and crustaceans. Although substantial datasets have yet to be published, nonetheless it is clear that octopus preferences also influence diet along with prey availability (Ambrose 1984, Scheel and Anderson 2012). As was apparent in this study, although the predominant content of octopus middens reflected the local abundance of scallops, occasional crabs were also included in midden contents. The middens of the giant Pacific octopus (*Enteroctopus dofleini*) were similarly dominated by bivalve prey in a habitat where bivalves were large and superabundant (Scheel and Anderson 2012), although in that habitat no shell beds were detected where discarded bivalve shells had accumulated.

Godfrey-Smith and Lawrence (2012) raise the question whether the shell bed originated through *Octopus tetricus* activity or was initially formed by another process. We cannot rule out the possibility that an initial load of scallop shells may have been dropped along with the unidentified central object at the site, whose age is unknown, but if so, a large number of shells appear to have accumulated through octopus foraging since that time. These authors observed octopuses bringing scallops to the bed, consuming them, and dumping shells and debris excavated during den maintenance, and they have documented expansion of the shell bed over time. They estimated the remains of octopus prey would accumulate coverage of over 1 m² per year. Further, both Godfrey-Smith and Lawrence (2012) and this report found that shells of varying age (judged by overgrowth and erosion) comprise the bed, from fresh to old and pitted, as would be expected if the bed had been accumulated by octopus foraging. Here, we additionally show that the nearby populations of scallops appear depleted of individuals in the

size range of fresh items found at occupied octopus dens (Figs 2-3). This provides further support for the contention that the octopuses themselves have accumulated the shell bed over time.

The association of octopuses with other organisms has also been the focus of study, and in a sense, this report is a continuation of that work. Like most octopuses, *Enteroctopus dofleini* excavates dens in suitable substrate, and associated with this octopus were scavenging fish, sea stars and crustaceans (Hartwick and Thorarinsson 1978). Active predators, particularly groupers, also associate with tropical foraging octopuses and thereby obtain access to otherwise inaccessible prey (Diamant and Shpigel 1985). However, these examples are affiliated with single objects (a den, an octopus) and individual trophic links (scavenging, foraging). At the site considered here, positive feedback resulted in the creation of new denning habitat for octopuses that also served as shelter for epibenthic invertebrates, to aggregate fish, and to attract additional predators. Thus, the interaction extended across several trophic levels and multiple taxa. The key factor separating individual cases of association with octopuses from ecosystem engineering as described here may be the superabundance of prey in a habitat with limited shelter. In this circumstance, the accumulation of remains of prey consumed at the den and their subsequent use for additional dens for octopuses increased shelter availability locally, greatly concentrating the effects of octopuses on their habitat.

The reason these fishes aggregate on the site are likely diverse. Those in the water column may be attracted to the algal growth, and may utilize the site for shelter, camouflage, and to find prey among the shell bed. Hartwick and Thorarinsson (1978) also reported fish, primarily various sculpins, that cohabitated within the dens of *Enteroctopus dofleini*. The presence of bivalve remains has also been implicated in ecosystem engineering by other authors (Coleman and Williams 2002, Gutiérrez et al. 2003), although in this case discarded bivalve shells (rather than live bivalves) accumulated as a shell bed and functioned to provide hard substrate.

As these animals aggregate, negative feedbacks on both further aggregation and on-site growth begin to occur. The presence of predators may discourage additional accumulations of schooling fish, and it also discouraged octopus daytime activity, limiting foraging time and the deposition of scallop remains to the shell bed. Large excavations within the site itself appear to be the actions of a ray or other flat fish that shuffled and disturbed the bed, perhaps reducing its suitability for further octopus dens. In addition, the octopuses themselves have been observed to engage in interference and aggressive interactions, including going out of their way to excavate their den debris into the den of a neighbouring octopus, and attacking another octopus leading to temporary retreat. It therefore appears that as the local octopus density increases, negative interactions with neighbours may limit further aggregation.

Other similar biogenic aggregations of structures include that of snail shells by foraging *Octopus* (*O.*

vulgaris and *O. briareus*), the presence of which enhances hermit crab populations (Gilchrist 2003), and the deposition of squid egg beds and skate egg case beds. At squid egg beds (Shashar and Hanlon 2013) large numbers of squid lay eggs on the substrate over a period of a few nights or more. The spawned-out squids attract scavengers and predators (e.g. Smale et al. 2001), but the egg masses themselves may also provide temporary habitat for some organisms. The skates (Family Rajidae) spawn in areas where hatched or depredated egg cases accumulate in the sediment, and attract invertebrate predators (Hoff 2009). The extent to which this habitat is important to other species aside from egg predators is unknown. However, small octopuses, for example, have been known to use skate or shark egg cases as dens.

With the possible but relatively unstudied exception of skate egg case concentrations, these examples lack the multi-trophic level effects across diverse taxa demonstrated at the shell bed of *Octopus tetricus* in Jervis Bay. This study demonstrates that modifications to the substrate made by octopuses through the accumulation of remains of their prey may have a large impact on local ecology. The effects range from locally altered sizes and abundances of octopus prey to aggregations of schooling fish and predators above the habitat. Despite producing no shell as do other mollusks that act as ecosystem engineers, by their excavating behaviours and their habit of leaving prey remains surrounding their dens, octopuses may constitute a unique type of marine ecosystem engineer, combining aspects of both habitat builders (or in their case, accumulators) and habitat excavators.

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