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## The composition of strand-line dead-shell accumulations on the Isle of Cumbrae, Scotland

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### ABSTRACT

Data are presented on the composition of identifiable molluscan shell debris from the surface of supralittoral strand-line accumulations from three topographically distinct coastal sites and aspects on the Isle of Cumbrae, Scotland sampled in summer and winter. Interpretation of these death assemblages, termed taphocoenoses, is given with reference to the biology and distribution of the same species living on- and off-shore and prevailing physical conditions at each site. Understanding such relationships allows the reconstruction of fossil deposits of dead shells, termed thanatocoenoses. The significance of dead-shell accumulations as carbon sinks has relevance to current modelling of climate change.

### INTRODUCTION

“An assemblage of dead shells commonly represents the accumulation of material over a period of time and is likely to be a mixture of many successive populations” (Brenchley & Harper, 1998). Such death assemblages (DAs), also termed taphocoenoses, are defined as “a set of taxonomically identifiable, dead or discarded organic remains present in the surficial mixed layer of a landscape or seafloor” (Kidwell, 2013; “surficial” means “surface” in this context). These remains represent a time-averaged assemblage, the composition of which varies with time according to episodic supply mechanisms and weathering events on a variety of time-scales: modern and geological. Carroll *et al.* (2003) stated that environmental factors and local fluctuations in populations in shell-producing organisms are more likely to be the principal determinants of time-averaging in marine benthic assemblages. Molluscan data tend to predominate such studies due to their calcareous (aragonitic) body covering which resists attrition and dissolution. Seasonal impacts, especially winter storms, will affect the supply of material (modern and, in some cases, reworked fossil material) thrown-up onto beaches and will also affect subsequent particle comminution and mixing of shells depending on the characteristics of the surrounding site, *viz.* aspect, exposure to wave action, the supply of stones, proximity of hard surfaces etc. Such processes have obvious, and well recognised, import for environmental (physical as well as biological) interpretation of fossil assemblages, termed thanatocoenoses.

DAs have considerable environmental significance in

Scotland. Ritchie & Mather (1984) reported that over 50 Scottish beaches are composed almost entirely of shelly carbonate sand (see Farrow *et al.* (1978) and Wilson (1979) for offshore data). Some Scottish shell accumulations are, of course, man-made. The enormous back-shore shell middens on Oronsay (Inner Hebrides, Scotland) are the result of centuries of human shellfish exploitation of limpets, periwinkles, whelks, oysters, cockles, scallops and razorshells since Mesolithic times (Mellers, 1981, 1987; Pollard, 1994), collected for food and bait (Allan, 2017). Modern-day commercial exploitation of shellfish species still results in the disposal of “waste” shell material (Morris *et al.*, 2019). As reported in 2017, every year more than seven million tonnes of mollusc shells were discarded by the U.K. seafood industry; the majority ending-up in landfill or dumped at sea (Anon., 2017), sometimes as cultch for oysters (see Lown & Cameron, 2020). Industrial plants may process mollusc or crustacean shells from which all flesh has been removed (not an easy process) when intended for the production of aggregates for a variety of commercial uses: such as in gardens, construction, maintenance, repair of footpaths, draining the land and ornamental purposes (Archer, 2010). “Shell hash” of mussel shells falling to the seabed both from mussel farms in Scotland (generating anoxic sea-bed patches; see Wilding & Nickell, 2013), and from fouled coastal fish-farming cages (Sanchez-Jerez *et al.*, 2019) also affect benthic ecosystems. Humans are still generating taphocoenoses.

Apart from my earlier DA observations on the dogwhelk (*Nucella lapillus*) (Moore, 1985), no recent work seemingly exists on the topic on the Isle of Cumbrae, North Ayrshire, Scotland (though Boyd (1982) comes geographically closest), since Robertson (1877) noted that the fauna of raised beaches was identical with that living in neighbouring seas. Having been aware, over years of casual observation, of the considerable differences that exist between the appearance of strand-line shell accumulations on different beaches on this small island and of the often different appearance of strand-line material in summer and winter at Ballochmartin Bay, I decided to investigate further. Such a study may not be as esoteric as it might seem, since it has been estimated recently that 1,738 million tonnes (MtC) of inorganic carbon is stored as non-living shell material in Scotland (Burrows *et al.*, 2014) and

carbon sequestration is of prime environmental concern at present.

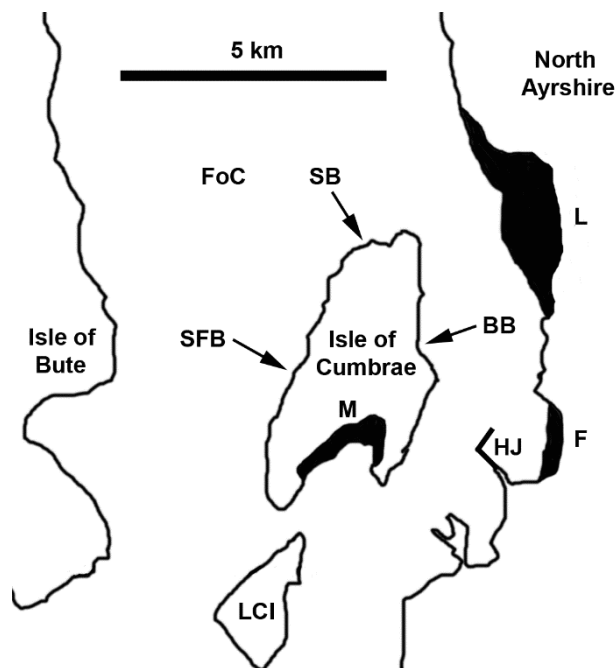
## METHODS

A haphazard (not statistically randomised) sample of surficial strand-line dead-shell accumulations from each of three high-shore sites on the Isle of Cumbræ (Table 1; Figs. 1-4, 6) was shovelled into plastic tubs and returned to base where they were riddled through a 1.0 cm mesh sieve. The surficial sample depth was *ca.* 3 cm and each sample produced, after sieving, *ca.* one litre of retained material. Retained material was identified to species wherever possible and counted. Most bivalve shells were disarticulated (at the very least). Such

disarticulated valves were counted whenever the hinge line was present. The dry weight (to nearest gram) of each taxonomic category, including broken fragments that could be attributable to species, was recorded wherever possible. Molluscs were identified variously with reference to Tebble (1966), Hayward & Ryland (1990), Oliver *et al.* (2016) and Wigham & Graham (2017). Local habitat information regarding molluscs can be found in Quayle (1952), Clark & Milne (1955) and Allen (1962). All material examined was eventually returned to the site of origin, respecting conservation ideals (Ballochmartin Bay, for instance, is a Site of Special Scientific Interest (SSSI)).

Site	Grid Ref.	Dates sampled	Characteristics
Ballochmartin Bay	NS181571	15/06/2020 07/02/2021	Very sheltered embayment, facing due East (90°), with <i>ca.</i> 2.5 km wave fetch; shallow sloping sandy littoral with stable boulders.
South of Fintray Bay	NS155565	16/06/2020 07/02/2021	Steeply shelving, stepped, coarse sand pocket beach, with stones and solid rock in midshore, nearly West facing (256°), between rock ledges, with <i>ca.</i> 5.5 km non-deflected wave fetch ( <i>ca.</i> 18.5 km deflected from SW).
Stinking Bay	NS171590	16/06/2020 07/02/2021	East corner of small coarse-sand beach, North-west facing (290°) with <i>ca.</i> 7.5 km wave fetch, a sediment trap with stones and boulders midshore, adjacent to rocky platforms.

**Table 1.** Sampling site characteristics on the Isle of Cumbræ, Scotland.



**Fig. 1.** Map showing the sites mentioned on Isle of Cumbræ, North Ayrshire, Scotland and surrounding locations. BB, Ballochmartin Bay; F, Fairlie; FoC, Firth of Clyde; HJ, Hunterston jetty; L, Largs; LCI, Little Cumbræ Island; M, Millport.



**Fig. 2.** The appearance of the strand-line at Ballochmartin Bay, Isle of Cumbrae, 16th June 2020. (Photo: P.G. Moore)



**Fig. 3.** The appearance of the strand-line south of Fintray Bay, Isle of Cumbrae, 18th June 2020. (Photo: P.G. Moore)



**Fig. 4.** The appearance of the strand-line at Stinking Bay, Isle of Cumbrae, 19th June 2020. (Photo: P.G. Moore)



**Fig. 5.** Fragment of razorshell (*Ensis* sp.) shell (left) with inner surface fouled by *Spirobranchus triqueter*, and a right valve of *Dosinia exoleta* (right) fouled with *Balanus crenatus*. Both shells from South Fintray Bay, Isle of Cumbrae, 27th June 2020. (Photo: P.G. Moore)



**Fig. 6.** The high-shore, storm-created berm feature at Ballochmartin Bay, Isle of Cumbrae, 7th February 2021. The pole is 95 cm tall. (Photo: P.G. Moore)

## RESULTS

Table 1 shows the physical characteristics of the three sites investigated and Figs. 2-4 and 6 their appearance. Prevailing winds are south-westerlies (215°). Table 2 shows the composition of the surficial dead shells recovered from the strand-lines at the three sites

investigated both during summer (June 2020) and winter (February 2021) seasons. Clear differences are apparent between the relative contributions of different species to the shell accumulations at the three sites investigated in summer. The Ballochmartin Bay material was dominated by common cockle (*Cerastoderma edule*), common mussel (*Mytilus edulis*) and common periwinkle (*Littorina littorea*) shells, reflective of the shallow expanse of sandy sediments in the shallow bay, interrupted by permanent boulders in the mid- to low-shore. The site at Stinking Bay was dominated by shells (*L. littorea*), also associated with the sheltered aspect of that site and its extensive rocky platform shore. The South Fintray Bay site was dominated by larger, heavier shells: a mixture of limpets (*Patella vulgata*) and offshore bivalves: rayed artemis (*Dosinia exoleta*) with plentiful broken razorshell (*Ensis* spp.) valves, indicative of the energetic sea conditions impinging on this site.

Recovered shells were mostly damaged. Bivalves were almost universally disarticulated and often greatly fragmented. The most fragile and vulnerable-to-damage bivalves were *M. edulis* shells. The summer strand-line shell sand at Ballochmartin Bay was substantially composed of comminuted *M. edulis* shell debris together with undamaged disarticulated *C. edule* valves. Brittle *Ensis* spp. shells were also substantially fragmented (notably at the South Fintray Bay site). Valve fragments (both outsides and insides) of sublittoral species from offshore (like *Ensis* spp., *D. exoleta* and blunt gaper (*Mya truncata*) were often fouled by calcareous epifauna: barnacles (*Balanus crenatus*) and serpulid tubeworms (*Spirobranchus* sp.) (Fig. 5), indicating that they had lain exposed on the seabed for some time before being thrown onto the beach during storms). The most intact valves of bivalve species were of robust and more-rounded shaped species like *C. edule*, pullet carpet shell (*Venerupis pullastra*), branded venus (*Clausinella fasciata*), trough shells *Spisula* spp. and *D. exoleta*.

Regarding gastropods, the damage to limpet shells (*Patella vulgata*) depended on size. The largest shells were typically undamaged. The tall, thick shells of the largest specimens betokened an origin high on the rocky shore (Wigham & Graham, 2017), and so these would not have been carried far from their point of origin. Smaller limpets, with thinner, flatter shells emanating from lower down the shore, where growth conditions were more amenable, often had missing apices, giving the appearance of halos. *L. littorea* shells had spires missing and broken lips, some were "rotten" with worm holes made by the polychaete *Polydora ciliata*. Some of the larger gastropod shells (red whelk (*Neptunea antiqua*), *B. undatum*, pelican's foot (*Aporrhais pespelecani*)) were often reduced to the columella with only a section of the body whorl remaining. Most intact were the more robust, globular shells of flat periwinkles (*Littorina obtusata* and *L. fabalis*). Top shells (*Gibbula* spp.) too, being of a squat body form, were more often reasonably intact except often the periostracum was abraded away to expose the underlying shiny nacreous was the comparative rarity of dog whelk (*N. lapillus*)

<b>BALLOCHMARTIN BAY</b>		<b>(Summer)</b>		<b>(Winter)</b>	
<b><u>Littoral species</u></b>	Number	Dry weight (g)	Number	Dry weight (g)	
<i>Patella vulgata</i>	13 (7)	17 (5)	4 (2)	6 (2)	
<i>Littorina littorea</i>	30 (16)	28 (9)	75 (42)	77 (24)	
<i>L. saxatilis</i>	1 (0.5)	<1	-	-	
<i>L. obtusata</i>	18 (10)	8 (3)	34 (19)	19 (6)	
<i>L. fabalis</i>	4 (2)	1 (0.3)	2 (1)	2 (1)	
<i>Gibbula cineraria</i>	7 (4)	5 (2)	5 (3)	3 (1)	
<i>G. umbilicalis</i>	1 (0.5)	1 (0.3)	-	-	
<i>Nucella lapillus</i>	2 (1)	2 (1)	5 (3)	9 (3)	
<i>Buccinum undatum</i> (i)	1 (0.5)	<1	-	-	
<i>Mytilus edulis</i> (fr)	-	65 (21)	-	34(11)	
<i>Cerastoderma edule</i> (v)	92 (49)	162 (52)	44 (24)	129 (41)	
<i>Venerupis pullastra</i> (v)	4 (2)	3 (1)	1 (0.6)	6 (2)	
<b><u>Sublittoral species</u></b>					
<i>Aporrhais pespelecani</i>	1 (0.5)	<1	-	-	
<i>Buccinum undatum</i>	-	-	1 (0.6)	20 (6)	
<i>Neptunea antiqua</i>	1 (0.5)	8 (3)	-	-	
<i>Ensis</i> sp. (fr)	-	8 (3)	-	4 (1)	
<i>Clausinella fasciata</i> (v)	3 (2)	1 (0.3)	-	-	
<i>Macoma balthica</i> (v)	1 (0.5)	<1	-	-	
<i>Spisula solida</i> (v)	8 (4)	5 (2)	9 (5)	8 (3)	
<i>S. subtruncata</i> (v)	1 (0.5)	<1	-	-	
<b><u>Total</u></b>	188 (100)	314 (100)	180 (100)	317 (100)	
<b>SOUTH FINTRAY BAY</b>		<b>(Summer)</b>		<b>(Winter)</b>	
<b><u>Littoral species</u></b>					
<i>Patella vulgata</i>	106 (40)	336 (40)	46 (50)	158 (40)	
<i>Littorina littorea</i>	86 (32)	81 (10)	24 (26)	35 (9)	
<i>L. saxatilis</i>	1 (0.3)	<1	3 (3)	1 (0.3)	
<i>L. fabalis</i>	2 (0.6)	<1	1 (1)	<1	
<i>Gibbula cineraria</i>	17 (6)	8 (1)	7 (8)	9 (2)	
<i>Nucella lapillus</i>	18 (7)	33 (4)	4 (4)	6 (2)	
<i>Cerastoderma edule</i> (v)	1 (0.3)	6 (0.7)	-	-	
<i>Venerupis pullastra</i> (v)	6 (2)	28 (3)	-	-	
<b><u>Sublittoral species</u></b>					
<i>Buccinum undatum</i> (fr)	5 (2)	35 (4)	1(1)	26 (7)	
<i>Neptunea antiqua</i>	3 (1)	21 (2)	-	-	
<i>Ensis</i> sp. (fr)	-	158 (19)	-	109 (27)	
<i>Mya truncata</i> (v)	1 (0.3)	11 (1)	-	-	
<i>Dosinia exoleta</i> (v)	14 (5)	122 (14)	6 (7)	53 (13)	
<i>Cerastoderma edule</i> (v)	1 (0.3)	6 (0.7)	-	-	
<b><u>Total</u></b>	267 (100)	845 (100)	92 (100)	398 (100)	
<b>STINKING BAY</b>		<b>(Summer)</b>		<b>(Winter)</b>	
<b><u>Littoral species</u></b>					
<i>Patella vulgata</i>	15 (5)	17 (9)	16 (40)	12 (39)	
<i>Tectura virginea</i>	1 (0.4)	<1	-	-	
<i>Littorina littorea</i>	170 (60)	87 (45)	8 (20)	7 (23)	
<i>L. obtusata</i>	32 (11)	13 (7)	3 (8)	1 (3)	
<i>L. saxatilis</i>	5 (2)	<1	-	-	
<i>L. fabalis</i>	21 (7)	9 (5)	2(5)	<1	
<i>Gibbula cineraria</i>	12 (4)	5 (3)	-	-	
<i>G. umbilicalis</i>	1 (0.4)	<1	4(10)	2(6)	
<i>Nucella lapillus</i>	15 (5)	5 (3)	4(10)	3(10)	
<i>Mytilus edulis</i> (fr)	2 (1)	2 (1)	3(8)	3(10)	
<i>Cerastoderma edule</i> (v)	1 (0.4)	13 (7)	-	-	
<i>Venerupis pullastra</i> (v)	1 (0.4)	14 (7)	-	-	
<b><u>Sublittoral species</u></b>					
<i>Ensis</i> sp. (fr)	4 (1)	6 (3)	-	2(6)	
<i>Dosinia exoleta</i> (v)	1 (0.4)	19 (10)	-	-	
<i>Clausinella fasciata</i> (v)	4 (1)	3 (2)	-	-	
<b><u>Total</u></b>	285 (100)	193 (100)	40(100)	31(100)	

**Table 2.** Species composition (% of sample in parentheses, rounded up) of surficial strand-line dead-shell accumulations at three sites on Isle of Cumbrae, Scotland in summer and winter (fr = fragments; i = immature; v = valves).

layer. What was immediately noticeable, considering their abundance on the rocky shores locally, however, shells and the absence of crustacean remains. It should be noted, however, that disarticulated barnacle plates were not retained on the sieve mesh used. Smaller gastropods like rough periwinkle (*Littorina saxatilis*), although abundant on mid- to high-shore rocks locally, were not retained in any numbers by the sieve mesh used either. All these materials will, of course on the first sampling, have accumulated over a considerable period of time.

Samples were re-taken in February 2021 after a lengthy period of strong easterly gales during the first week of February, during which time gusts to 60 knots were recorded locally. The huge *Valaris* DS4 drill ship, berthed at Hunterston jetty opposite the island, snapped its moorings on the evening of 2nd February and was only fifteen minutes from being wrecked on Cumbrae before its anchors thankfully held (Corral, 2021). The appearance of the upper shore at the Ballochmartin Bay site was considerably changed by these storms with a tall vertical berm (height variously 0.5 to >1 m) of shell-sand thrown-up among the supralittoral vegetation (Fig. 6) together with considerable kelp and wrack material (*Laminaria* spp. and *Fucus* spp.) cast-up around the high-tide mark. *M. edulis* shells especially, being relatively fragile, were markedly comminuted, the most intact shell valves being of the most robust species (*L. littorea*, *B. undatum*, *C. edule*). There was no increase in sublittoral species apparent, apart from a single large adult *B. undatum* shell.

At South Fintray Bay, the winter collection was again dominated by robust shells (*P. vulgata*, *L. littorea*, *Ensis* spp. fragments, *D. exoleta*), with a high proportion of the larger bivalve shell valves (*D. exoleta*, *Ensis* spp.) heavily fouled on their concave surfaces with serpulid tubeworms (*Spirobranchus* sp.). In both the summer and winter collections from this site a large proportion of broken fragments of robust bivalve shells (not censused) was present. *M. edulis*, however, was not in evidence, either as fragments or intact valves. The winter collection at Stinking Bay was dominated by gastropod shells (notably *L. littorea*), although a substantial proportion of this species' shells was too small to be retained by the sieve, as compared with the summer sample. The shells of *P. vulgata* were notably smaller than those from the South Fintray Bay site.

## DISCUSSION

On an island, differing site topography, aspect and degrees of fetch-dependent wave action will impact onshore given different offshore bathymetric conditions, ground characteristics and hence faunal composition. Frey & Dörjes (1988) contrasted the effects of fair- and foul-weather on shell accumulations on a Georgia, U.S.A beach and highlighted the role of longshore (parallel to the shore) transport (see Lamont (1945) regarding beach material in the Clyde Sea Area). Longshore transport of shells will be of lesser importance on small local pocket beaches, with strand-line accumulations of entrapped dead shells reflective of

adjacent living assemblages.

The predominant winds in the northern hemisphere are those from the south-west and the north-east (Lamont, 1945). Smith (1986) stated that “the Prestwick [Ayrshire] wind rose [see his Fig. 2] displays only moderate bias towards wind directions between west (260°–280°) and south (170°–190°) for it is clear that easterlies are also well able to reach the coast here,” and that “westerlies are funnelled up the Clyde estuary” and “most of the gales are from the west”. In his Table 1, Smith (1986) reported that the average annual maximum gust speed for Millport, Isle of Cumbrae was 68.9 knots. Of the three Cumbrae sites investigated, therefore, that most prone to rough seas from the south-west quadrant would be the South Fintray Bay site. That more-or-less west-facing site, adjacent to the deep water of the Main channel between the islands of Bute and Cumbrae, accounts for the prevalence of deeper-dwelling offshore species in the strand-line accumulations there, given wave refraction effects (*cf.* Moore, 1985, Table 2). The fact that easterly gales, although less frequent, can still on occasion generate high seas at Ballochmartin Bay resulted in the comminution of fragile *M. edulis* shells there, and have had other reported ecological effects (Moore, 2005). The more robust shell valves of *C. edule* (see Wilson, 1967; Farrow, 1974) fared better at Ballochmartin Bay long-term, so the superficial appearance of the strand-line death assemblage of molluscan shells there, unsurprisingly, varied according to prevailing weather events.

Although only occasional live native oysters (*Ostrea edulis*) are today to be found on Ballochmartin Bay, in the nineteenth century the bay supported a thriving population (Moore, 2020). Oyster shells are very robust, as witness their prevalence in prehistoric shell middens (see Introduction) and in archaeological sites from Roman to Mediaeval times (Winder, 1993). It is surprising therefore that no oyster-shell remains were discovered in the strand-line shell accumulations at Ballochmartin Bay. Since this could be due to only surficial samples being taken, a limited excavation (to double spade depth) was made in the supralittoral vegetation abutting the strand-line to check for buried oyster shells: none was discovered. There are biological agencies, like rabbit burrowing activity at the site (Moore, 2004), that can redistribute material but wind-blown sand and wave action during winter storms will have the biggest impact. It is often the case that easterly storms in winter lift beach sand, gravel and drift seaweed onto the adjacent coastal road at this site, so a century of deep burial could have obliterated the historical contribution of oyster shells.

Shells of sublittoral fringe populations of *Ensis* spp. may arrive onshore as a result of predation at lowest tides by herring gulls (*Larus argentatus*) (Moore, 2020). Mortality of offshore infaunal bivalve molluscs has also been recorded caused by harmful phytoplankton blooms (red tides) caused by dinoflagellates (Griffith *et al.*, 2019). I recall seeing an extensive stranding of *Ensis* spp. shells, along with burrowing heart urchins

(*Echinocardium cordatum*), washed-up along the beach at Fintray Bay many years ago (date unrecorded); another biological agency generating shell debris. Red-tide impacts can be widely detrimental to marine life; Jones *et al.* (1982) reported a red-tide killing pond-reared salmon in local sea lochs.

Moore (1985) compared the shell shape of fossil *N. lapillus* from the raised beach near Shell Hole, Cumbrae (OS Grid ref. NS15085416), a site to the south of the present South Fintray Bay site, with data on the adjacent modern strand-line molluscan death assemblage (his Table 2). Some 16.6% of the modern death assemblage from Shell Hole (sampled in 1983), a more exposed site, were *N. lapillus*. The general paucity of dogwhelk shells in the samples from all three sites here reported, chimes more with the fossil findings (2.6% of Moore (1985) and comments by Robertson (1888), the latter noting that “post-Tertiary beds of the Clyde ... contain very few examples of this shell” (but note Robertson, 1877) and could relate to that species' habit of aggregating in rock clefts and crevices, especially during winter (Feare, 1971) and, by such means, being able to avoid or resist removal by damaging wave action (note also Burrows & Hughes, 1989).

Some of the shell fragments of both bivalves (*M. edulis*) and gastropods (*L. littorea*) had holes drilled into them by *N. lapillus*, betokening dogwhelk predation as the proximate reason for their mortality. Limpets fall prey to crabs, fishes and starfish at high tide and to birds like oystercatchers (*Haematopus ostralegus*) at low tide. Pettitt (1975) has comprehensively reviewed the predators of *Littorina* spp. and his findings have a wider relevance for other rocky-shore gastropods and will not be rehearsed here. Those damaged *L. littorea* shells with missing spires or broken lips probably resulted from predation by the shore crab *Carcinus maenas* (Hughes & Elner, 1979) and Warner (1997) has examined the role played by the shell-burrowing polychaete *Polydora ciliata* or the boring sponge *Cliona celata* in weakening the shells of *L. littorea*. Thus biological agencies probably supply the empty coiled gastropod shells and may be secondarily re-distributed by hermit crabs (Frey & Dörjes, 1988). Regarding limpets, the hydrodynamics of the limpet body shape render them well-adapted to survive physical wave pounding (Denny, 2000). Once loose on a rocky shore, however, small empty limpet shells will be prone to waves smashing them against rocks, the shock to the apex resulting in breakage and the halo-shape "skirt" being the result. It is unlikely that wave stress alone would dislodge limpets. Even such small clinging amphipod crustaceans as *Apothysa prevosti* (as *H. nilssoni*) were not dislodged from channelled wrack (*Pelvetia canaliculata*) tufts by an onshore Force 9 westerly gale impinging on a high-shore site near to the South Fintray site (Moore, 1977).

The impact of seasonality (summer *vs.* winter) on strand-line deposits of dead shells thus depended on site aspect and the impact of particular storms. The longevity of different species' shells in the deposit will depend on

their relative robustness, something that can be enhanced by calcareous epifauna (e.g. serpulid tubeworms on *D. exoleta* valves) or degraded by shell-boring organisms. Strandings of shells of sublittoral species reveal the impact of past storm events. Strand-line shell accumulations are thus episodic, time-averaged records of past energetic (particularly extreme) sea conditions whose history will stretch back decades and millennia. Storm surges in the Firth of Clyde are not unusual. Between 1985 and 2014, the Millport tide gauge recorded 92 surge events that exceeded 1 m (Sabatino *et al.*, 2016). Hickey (2001) has reported in detail on one such storm's impact across Scotland. Both in the U.K. (Long & Wilson, 2007) and elsewhere (Kitamura, 2018), tsunami effects represent an extreme case in point. Taphocoenoses, then, are incipient thanatocoenoses. The relative abundance of littoral/sublittoral species in modern death assemblages finds explanation in environmental correlation and facilitates habitat and climate reconstruction of thanatocoenoses (*cf.* Norton, 1967, 1970; Boyd, 1982; Peacock, 1989, 1993; Tyler & Kowalewski, 2017).

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