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Seasonal 'fall out' of sessile macro-fauna from submarine cliffs: quantification, causes and implications

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Submarine cliffs are typically crowded with sessile organisms, most of which are ultimately exported downwards. Here we report a 24 month study of benthic fauna dropping from such cliffs at sites of differing cliff angle and flow rates at Lough Hyne Marine Nature Reserve, Co. Cork, Ireland. The magnitude of 'fall out' material collected in capture nets was highly seasonal and composed of sessile and mobile elements. Sponges, ascidians, cnidarians, polychaetes, bryozoans and barnacles dominated the sessile forms. The remainder (mobile fauna) were scavengers and predators such as asteroid echinoderms, gastropod molluscs and malacostracan crustaceans. These were probably migrants targeting fallen sessile organisms. 'Fall out' material (including mobile forms) increased between May and August in both years. This increase in 'fall out' material was correlated with wrasse abundance at the cliffs (with a one month lag period). The activities of the wrasse on the cliffs (feeding, nest building and territory defence) were considered responsible for the majority of 'fall out' material, with natural mortality and the activity of other large mobile organisms (e.g. crustaceans) also being implicated. Current flow rate and cliff profile were important in amount of 'fall out' material collected. In low current situations export of fallen material was vertical, while both horizontal and vertical export was associated with moderate to high current environments. Higher 'fall out' was associated with overhanging than vertical cliff surfaces. The 'fall out' of marine organisms in low current situations is likely to provide an important source of nutrition in close proximity to the cliff, in an otherwise impoverished soft sediment habitat. However, in high current areas material will be exported some distance from the source, with final settlement again occurring in soft sediment habitats (as current speed decreases).

INTRODUCTION

Submarine cliffs are a coastal habitat common at the panglobal level with the possible exception of the soft sediment dominated arctic basins (Dayton, 1990). Both mobile and sessile components comprise the assemblages and communities inhabiting this hard, steep and stable type of substratum. Many ecological aspects of sessile fauna have been documented *in situ* such as recruitment (Sutherland & Karlson, 1977), competition and community development (Dayton, 1971; Osman, 1977), predator–prey relationships (Paine, 1974) and growth rates (Fowler & Laffoley, 1993). Whilst predation may lead to a degree of *in situ* recycling or export of organism generated carbon, the immediate or surrounds of the base of any cliff seems likely to be the ultimate fate of most biomass (except in high current situations). Although commencement (new settlement and recruitment) and succession of cliff communities have received a high degree of scientific attention over the decades, the end process is comparatively unknown.

Sessile organisms inhabiting submarine cliffs will either concrete onto the substratum (bioconstruction) or become detached from their hard substratum and may then be deposited at the base of the cliff. Most form the latter category, though the timing of the process post mortem is likely to differ between groups. The composition of this 'fall out' material should depend on a number of factors, most obviously the community composition of the cliff under consideration. Causation of marine organism 'fall out' can include natural mortality (Gosselin & Qian, 1996, 1997), activity of predators and other mobile organisms (Turner & Warman, 1991), adverse environmental conditions (Wulff, 1995), morphological unsuitability (Bell & Barnes, 2000a) or damage from anthropogenic activity such as SCUBA diving or fishing (Hawkins et al., 1999; Rouphael & Inglis, 2001). Cliffs are generally prevalent in high energy conditions so although initially material is likely to end up at the base of such cliffs, much biomass will be quickly translocated along an energy gradient. As with saltmarshes and kelp forests (Weigert, 1979; but see Nixon, 1980), cliffs may thus be important as energy exporters albeit at different scales. The material falling from submarine cliffs has the potential to be an important source of nutrition for scavenging, deposit- and possibly even suspension-feeding animals in the adjacent, recipient low energy areas, which might otherwise only receive planktonic fall out. However, the supply of material is likely to be sporadic or seasonal. For many species the fall from a fixed position on hard substratum may not necessarily cause immediate death of the species involved. For example, many sponges can survive for a considerable amount of time after they become detached from a hard substratum (Barthel, 1989; Bell & Barnes, 2001a). Species that can reproduce by fragmentation (Winston, 1983; Wulff, 1995) may even use breakage and subsequent translocation as a method of dispersal and colonization of new habitats.

Submarine cliffs are particularly prevalent around the south-western Irish coast. At one site in particular, Lough Hyne, the cliff fauna experiences a wide range of environmental conditions (Kitching, 1987; Picton, 1991). Cliffs at this semi-enclosed basin are exposed to a wide spectrum of energy from high velocity current regimes to very slight tidal flow regimes. The sheltered nature (all year round) of Lough Hyne, along with the strict diving regulations (O'Donnell, 1991) allows the opportunity to examine the seasonal natural 'fall out' of the dominant space occupiers on submarine cliffs. At Lough Hyne three major groups of sessile fauna dominate the submarine cliffs; ascidians (Picton, 1991), anthozoans (Bell & Turner, 2000; Bell, 2001a) and sponges (Bell & Barnes, 2000a). Many other taxa are, however, present including bryozoans, phoronans, polychaetes, hydroids, barnacles and molluscs which are minor space occupiers, except on boulders (Lilly et al., 1953).

We aimed to answer the following questions: (1) how much overall 'fall out' of sessile organisms is there from submarine cliffs? And how dependant is this 'fall out' on the cliff aspect (i.e. predominantly vertical, overhanging or inclined surfaces) and time (season)? (2) Does current velocity influence sessile organism 'fall out'? (3) Of the major space occupants (sponges, ascidians and anthozoans) which of the factors i.e. season, exhibited morphology (for sponges only) and environmental conditions most influence the probability of 'fall out'? (4) Does the nutritional potential of fallen material (organic content) vary seasonally? (5) As fish (particularly wrasse) are known to feed on sublittoral cliff and reef fauna (Turner & Warman, 1991; Deady & Fives, 1995; Shepherd & Clarkson, 2001), can their seasonal arrival to the cliffs at Lough Hyne be correlated with higher 'fall out' of sessile organisms?

MATERIALS AND METHODS

Study site

Lough Hyne is a small (0.5 km^2) semi-enclosed marine body on the south-west coast of Ireland (51°29′N 09°18′W). Despite its small size, a large range of habitats and hydrographic conditions are encompassed, some (e.g. water flow rate and residence time) along distinct gradients. A narrow constriction (25 m wide) known as the Rapids connects the main body of the lough to the open Atlantic Ocean (Figure 1). A raised sill within the Rapids results in an unusual tidal regime whereby water flows into the lough for approximately four hours and out for eight hours (Bassindale et al., 1957). Water currents within Lough Hyne are essentially unidirectional and are only measurable during inflow of water (Bell & Barnes, 2001b). As inflowing water moves into Lough Hyne it is deflected at Whirlpool Cliff and is circulated in an anti-clockwise gyre in the south basin (Figure 1). However, as water moves from east to west across Lough Hyne the current speed decreases rapidly from up to 200 cm s^{-1} at Whirlpool Cliff to 35 cm s^{-1} at Glannafeen and is reduced to <5 cm s^{-1} at Labhra Cliff (Bell & Barnes, in press a). The location of the five study submarine cliffs are shown in Figure 1, along with a control site in the north basin (NB). Whirlpool Cliff is composed of a series of cliffs and loose rock habitats and experiences fast flowing

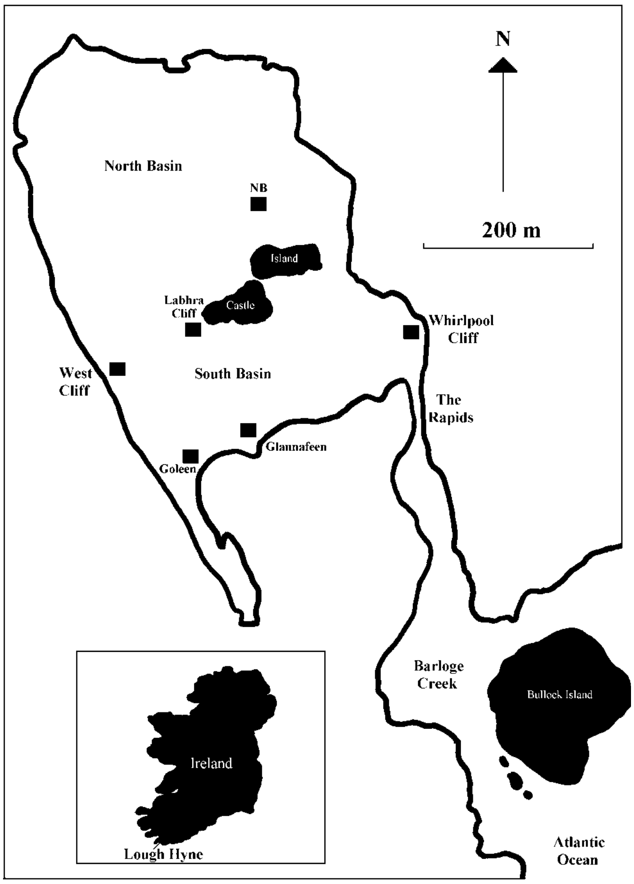

Figure 1. Lough Hyne Marine Nature Reserve, Co. Cork, Ireland. Locations where capture nets were deployed are indicated by shaded boxes.

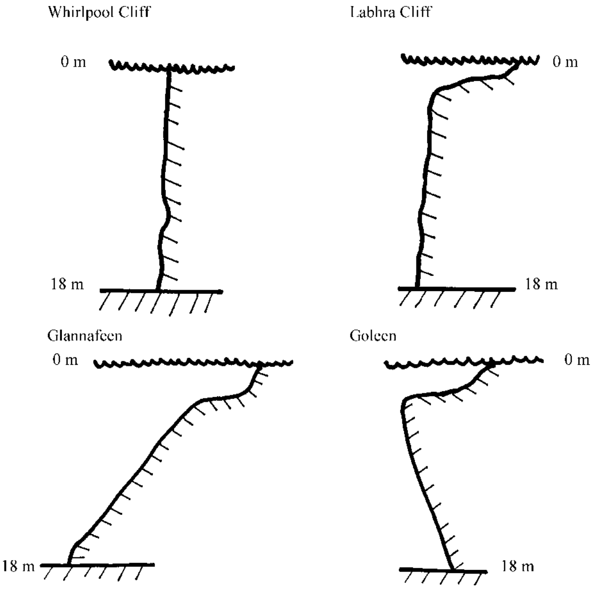

Figure 2. A diagrammatic representation of the cliff profiles immediately above areas where capture nets were placed at four sites at Lough Hyne.

Table 1. *The species found in 1 m² nets placed at the base of sublittoral cliffs at Lough Hyne (replaced monthly) over a two year period.*

Molluscs
Alvaria sp.
Anomia ephippium L.
Bittium reticulatum (da Costa)
Callista chione (L.)
Cerastoderma edule (L.)
Circomphalus casina (L.)
Diodora graeca (L.)
Emarginula fissura (L.)
Helcion pellucidum (L.)
Hiatella artica (L.)
Hinia reticulata (L.)
Hydrobia ulvae (Pennant)
Janthina janthina (L.)
Littorina littorea (L.)
Littorina mariae Sacchi & Rastelli
Littorina sp.
Macoma balthica (L.)
Mangelia brachystoma (Philippi)
Mangelia powisiana (Dautzenberg)
Modiolarca tumida (Hanley)
Monia patelliformis (L.)
Mya sp.
Mytilus edulis L.
Nucula sp.
Patella vulgata L.
Pecten maximus (L.)
Trivia monacha (da Costa)
Turritella communis Risso.
Velutina velutina (Müller)

Annelida
Pomotoceros sp.

Crustacea
Balanus balanus (L.)
Balanus crenatus Bruguière
Carcinus maenas (L.)
Cancer pagurus L.
Hommarus gammarus (L.)
Hyas araneus (L.)
Inachus sp.
Liocarcinus puber (L.)
Maja squinado (Herst)
Semibalanus balanoides (L)

Bryozoa
Cheilostomata

Sponges	**Morphology**
Axinella damicornis (Esper)	Flabellate
Axinella dissimilis (Bowerbank)	Arborescent
Dysidea fragilis (Montagu)	Massive
Dysidea pallescens Schmidt	Massive
Esperiopsis fucorum (Esper)	Massive/repent
Eurypon major Sarà & Siribelli	Encrusting
Haliclona sp. 1	Massive
Haliclona simulans (Johnston)	Repent
Haliclona fistulosa (Bowerbank)	Repent
Haliclona urceolus (Rathke & Vahl)	Tubular
Halichondria bowerbanki Burton	Repent
Hymeniacidon perlevis (Montagu)	Massive
Raspailia hispida (Montagu)	Arborescent
Raspailia ramosa (Montagu)	Arborescent
Scypha ciliatum (Fabricius)	Tubular
Stelligera stuposa (Ellis & Solander)	Arborescent
Stelligera rigida (Montagu)	Flabellate
Suberites carnosus (Johnston)	Pedunculate
Suberites ficus (L.)	Massive
Tethya citrina Sarà & Melone	Massive globulose

Echinoderms
Asterias rubens L.
Echinus esculentus L.
Luidea ciliaris (Philippi)
Marthasterias glacialis (L.)
Ophiothrix fragilis Thomson

Cnidarians
Alcyonium coralloides (Pallas)
Anthopleura ballii (Cocks)
Caryophyllia smithii (Stokes & Broderip)
Corynactis viridis Allman
Epizooanthus couchi (Johnston)

Platyhelminthes
Lineus longissimus (Gunnerus)
Prostheceraeus vittatus (Montagu)

Ascidians
Ascidia mentuala Müller
Ascidiella aspera (Müller)
Ascidiella scabra (Müller)

water conditions (up to 200 cm s^{-1}). Glannafeen is a single gently sloping cliff experiencing much slower current speeds (up to 60 cm s^{-1}). Both Glannafeen and Whirlpool Cliff extend to approximately 18 m depth. The remaining sites under investigation at Goleen and Labhra Cliff both experience very slight current flow (<5 cm s^{-1}) and extend to 21 and >30 m depth respectively (although investigations were carried out at 18 m).

Protocol

Capture nets were constructed of closely woven greenhouse netting which had the edges folded over and sewn down with plastic string to make a flange. A plastic coated cable was then threaded through this flange to act as a drawstring. Each net was constructed such that it had an area of 1 m^2. Three replicate nets were deployed at the base of each of the submarine cliffs. At Glannafeen, Goleen and Labhra Cliff the substratum at the base of cliffs was soft sediment and nets were randomly (in horizontal distance along the base of the cliff) pegged into this sediment. At Whirlpool Cliff boulders were placed at the corners of the nets, as there was no soft sediment into which to peg them (gravel substratum). Wooden struts were placed under the edges of the nets to prevent material from sliding off the nets.

The approximate profiles of cliff areas above the net deployment areas at each cliff are shown in Figure 2. At Whirlpool Cliff nets were deployed with predominantly vertical surfaces above the net deployment area. At Glannafeen nets were deployed below an essentially inclined cliff profile (Figure 2). At Goleen nets were deployed below an overhanging cliff and at Labhra Cliff the three nets were deployed below a large vertical cliff. All nets were deployed at approximately 18 m. A SCUBA diving exclusion zone was placed around all submarine cliffs. This ensured that material collected on the nets was from natural sources (with the exception of limited scientific activity on the same cliffs but in areas away from the nets).

The nets at each site were serially replaced at monthly intervals. This was achieved by removing the pegs and wooden struts and collecting in the corners of the nets. The drawstring was then pulled to form a bag. This prevented material which had fallen on the net from being lost. A knot was tied in the end of the newly created bag. After the three nets were removed clean nets were randomly re-pegged into the sediment and the wooden struts replaced. The first nets were first deployed in February 1999 and replaced monthly until February 2001. Once nets were recovered to the surface, each net was washed in salt water to remove sediment and then in fresh water to remove salt. The nets were then opened and the mobile mega-fauna was recorded and removed from the nets. The sponges and ascidians were separated from the bulk of the material and all material was bagged and removed to the laboratory. The total number and volume (using displacement of water in measuring cylinders) of all specimens was recorded for each sponge and ascidian species. All of the specimens of each species were placed in pre-weighed vials and the wet weight recorded. Samples were then dried for 24 h at 60°C and re-weighed, then combusted for 6 h in a muffle furnace for 6 h at 450°C to remove all organic material from the sample. Samples were then re-weighed for a final time. The same process was repeated for all the remaining material, which was termed 'other material'.

To facilitate inter-site comparisons all volumes and dry weights were calculated per m^2 of cliff face (as cliff did not extend to the surface at all sites), which allowed easier comparison between sites. Monthly counts of the number of wrasse were recorded along 50 m transects at Whirlpool Cliff (18 m) and Labhra Cliff (18 m) only.

RESULTS

Composition of 'fall out' communities

Sessile macro-fauna found in the nets constituted sponges, ascidians, anthozoans, polychaetes, bryozoans and barnacles. Other, mobile, species were present including a large number of molluscs, particularly gastropods, asteroid echinoderms and decapod crustaceans. This larger macro-fauna was removed from the nets, counted and returned (study site is a marine reserve). Twenty-two species of sponge were found in the nets. All but two of these species exhibited essentially 3-D morphologies including arborescent, flabellate, tubular and massive forms (see Bell & Barnes, 2000a). In contrast just three species of ascidian were found (*Ascidiella aspera*, *Ascidiella scabra* and *Ascidia mentuala*) of which the former comprised >95% of individuals. Species found are listed in Table 1. No material was collected in the control nets positioned on open sediment in the North Basin.

Seasonal variability in the 'fall out' of sessile organisms

Seasonal variability in biomass (volume and dry weight) was apparent in both overall (Figure 3) and categorized material at all cliff sites. For ease of interpretation, fauna was classed into sponges (Figure 4A), ascidians (Figure 4B), remaining sessile organisms (Figure 4C) and mobile organisms (Figure 4D). Volume and dry weight of all the material combined began to increase in May 1999 (from 3–7 $cm^3\ m^{-2}\ month^{-1}$ and 1–3 $g\ m^{-2}\ month^{-}$), reaching a peak in August 1999 (to 50–60 $cm^3\ m^{-2}\ month^{-1}$ and 6–20 $g\ m^{-2}\ month^{-1}$). The volumes and dry weights of each component then decreased back to their original levels by October 1999, and remained low until the following May (2000), when similar increases in the overall dry weight and volume were seen as in the previous year. The peak volume of overall material in August 2000 was only 10–20% of that in August 1999, while similar peaks in dry weight were observed in both 1999 and 2000 (Figure 3). Sponges (Figure 4A), other sessile organisms (Figure 4C) and mobile organisms (Figure 4D) showed similar peak volumes and dry weights (to all material collected) in

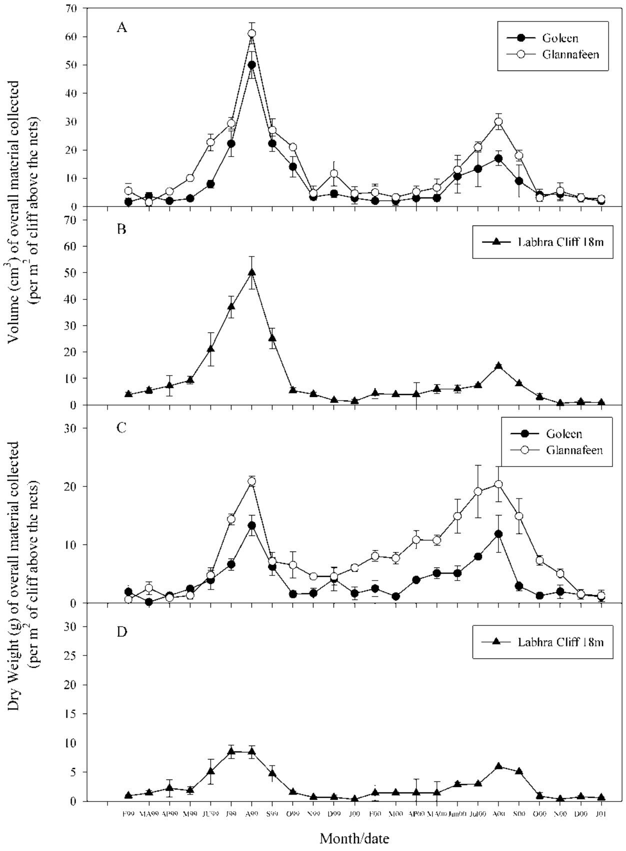

Figure 3. The overall (mobile and sessile organisms) dry weight (g) and volume (cm^3) of material collected in capture nets placed at the base of four submarine cliffs at Lough Hyne over a 24 month period.

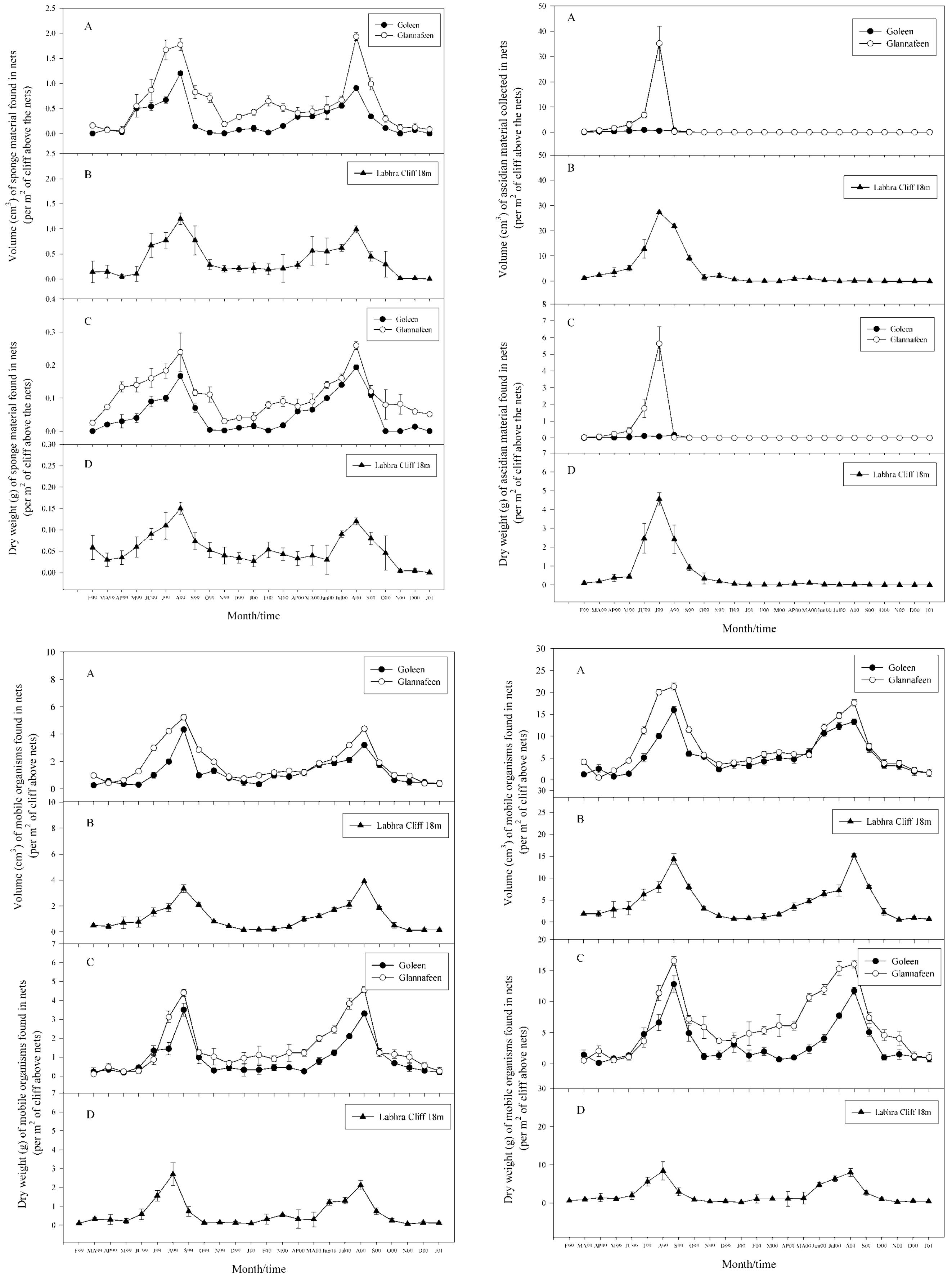

Figure 4. The dry weight (g) and volume (cm^3) of (A) sponges; (B) ascidians; (C) remaining sessile organisms and (D) mobile organisms collected in capture nets placed at the base of four cliffs at Lough Hyne over a 24 month period.

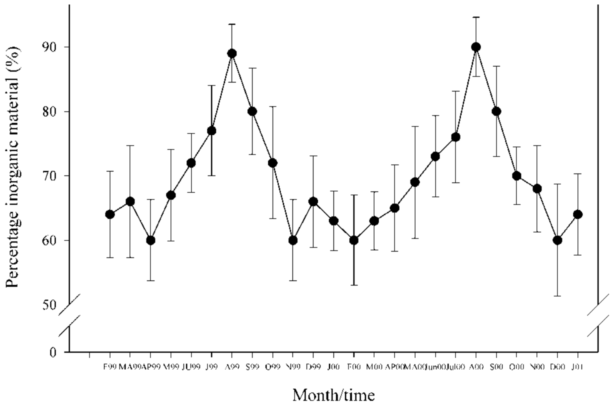

Figure 5. The overall organic content (%) of all material collected in nets combined from all four submarine cliff sites at Lough Hyne over a 24 month period.

both 1999 and 2000, while ascidian biomass (Figure 4B) was massively reduced (to <5%) and absent at most sites in 2000 compared to 1999. After the initial peak in ascidian volume and dry weight in August 1999, ascidians were rarely found in nets.

The importance of cliff profile and current flow rate on 'fall out'

At Whirlpool Cliff, where current flow rates were the highest (>200 cm s^{-1}) no organisms were found on nets placed at the base of the cliff. At Glannafeen a significantly higher (paired *t*-test, $t > 3.44$, $P < 0.05$, df=23) volume of overall material (on average) was found in nets compared to all other sites (Figure 3). However, no significant difference (paired *t*-test, $t = 0.8$, $P = 0.43$, df=23) was seen between the overall material found in nets at Labhra Cliff or Goleen. On average at any given month a higher dry weight of overall material was found at Glannafeen, Goleen and Labhra Cliff respectively. It was not possible to compare the inclined cliff site at Glannafeen directly with the vertical and overhanging cliff sites at Labhra Cliff and Goleen respectively as the latter sites experience similar environmental conditions (low flow, high sedimentation) while Glannafeen experiences moderate current flow which may have confounding effects. However, a significantly (paired *t*-test, $t = 5.57$, $P < 0.001$, df=23) greater dry weight (not volume) of overall material was found in nets beneath the overhanging cliff at Goleen.

A significantly higher (paired *t*-test, $t > 3.13$, $P < 0.001$, df=23) amount of sponge in terms of both volume and dry weight were found at Glannafeen than at Goleen and Labhra Cliff (on average for any given time interval). Goleen and Labhra Cliff showed no significant differences (paired *t*-test, $t < 0.45$, $P > 0.05$, df=23) between sponge volume and dry weight over the study period. Ascidian dry weight and volume was also significantly higher at Glannafeen than all other sites (paired *t*-test, $t = 2.45$, $P < 0.05$, df=23), while Labhra Cliff had significantly higher (paired *t*-test, $t > 2.23$, $P < 0.05$) volumes and dry weights than Goleen, where ascidians were virtually absent from nets. Therefore, a significantly (paired *t*-test, $t > 5.56$, $P < 0.01$, df=23) higher ascidian volume and dry weight was found under the vertical cliff at Labhra Cliff compared to the overhanging cliff at Goleen.

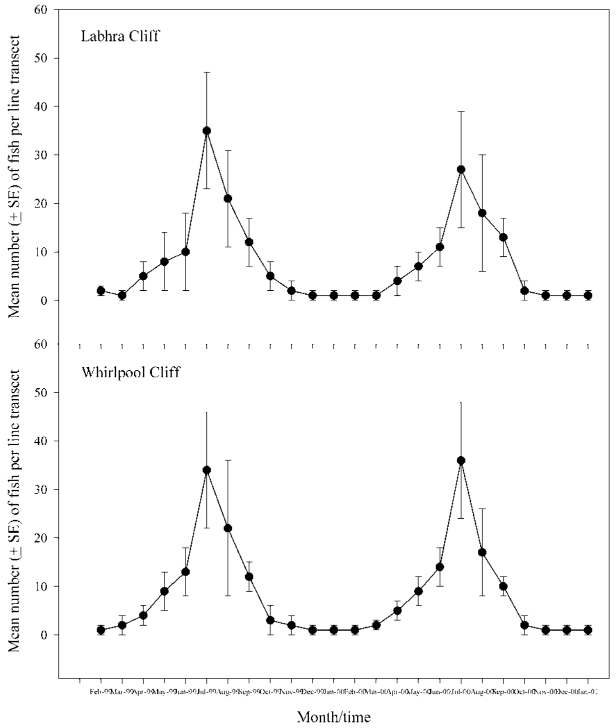

Figure 6. Estimates of wrasse abundance (mean number observed from swimming three 50 m transects between 12–15 m) at two sublittoral cliff sites over a 24 month period at Lough Hyne.

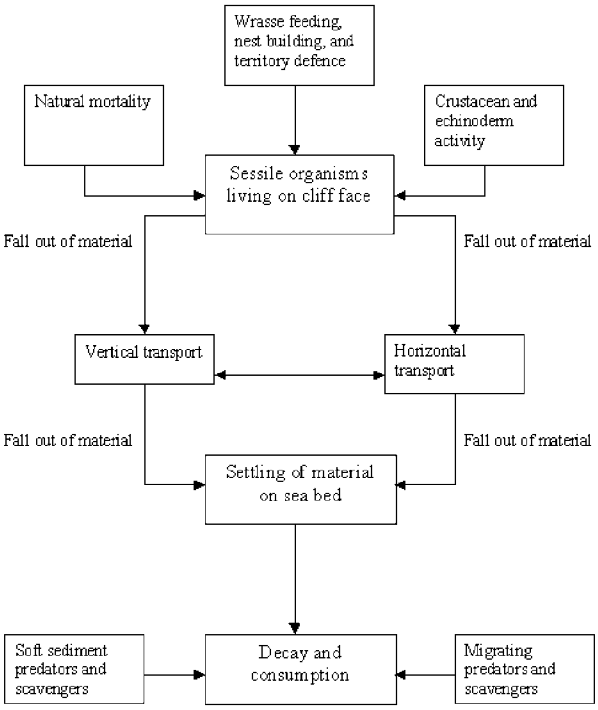

Figure 7. A summary of the processes and pathways effecting the 'fall out' of material from submarine cliffs at Lough Hyne.

The volume and dry weight of the remaining sessile organisms (Figure 4C) and mobile organisms (Figure 4D) was again significantly higher (paired *t*-test, $t > 3.81$, $P < 0.001$, df=23) at Glannafeen than all other sites. Beneath the overhanging cliff at Goleen the volume and dry weight of the remaining sessile organisms and mobile organisms were (on average) significantly higher (paired *t*-test, $t > 4.23$, $P < 0.001$, df=23) than the vertical cliffs at Labhra Cliff.

Does the nutritional potential of fallen material (organic content) vary seasonally?

The mean organic content of all the material collected from all sites (Figure 5) varied considerably over the study period. Higher inorganic content was found between May and October in both 1999 and 2000. The highest mean (±SE) inorganic content was recorded in August 1999 and 2000 (89–90±5%).

The seasonal occurrence of fish at Whirlpool Cliff and Labhra Cliff

Estimated fish counts (wrasse) made at Labhra Cliff and Whirlpool Cliff (Figure 6) showed seasonal variation in fish numbers. The species (Labridae) counted included *Labrus bergylta* Ascanius, *Labrus mixtus* L., *Crenilabrus melops* (L.), *Centrolabrus exoletus* (L.) and *Ctenolabrus rupestris* (L.) which were all common at Whirlpool Cliff and Labhra Cliff. Counts were made of this particular group (Labridae) because they were the principal group seen foraging, feeding, collecting and nest building on the cliffs. Wrasse numbers varied seasonally (Figure 6) over the two year period. Low numbers of wrasse were observed between February 1999 until April 1999, when numbers began to increase (from 1 to 5 fish). This increase continued with the peak fish abundance being recorded in July 1999. Their abundance then decreased (to only three fish observed) by November 1999 and remained at this level until the following April 2000, when numbers began to increase again. The same peak (28–40 individuals) in wrasse abundance was recorded in 2000 as in 1999. No significant difference was observed between fish numbers recorded from Whirlpool Cliff and Labhra Cliff (paired *t*-test, $t = -1.17$, $P = 0.25$, df=23).

DISCUSSION

In the absence of horizontal export or import processes the fauna found at the base of any sublittoral cliff is ultimately controlled by the community composition of the cliff under consideration. For Lough Hyne, these communities are well described (see Kitching, 1987; Picton, 1991; Bell & Barnes, 2000a,b,c; Bell & Turner, 2000; Bell, 2001a,b) and in low current environments have been considered stable over time (Picton, 1991). However, this study has shown that a large amount of material constantly falls from these submarine cliffs providing a potential food source for a number of scavengers and predators (Figure 7).

The seasonal export of material from the submarine cliffs at Lough Hyne can be correlated with the arrival of wrasse species, with a lag period, whereby the peak 'fall out' occurred one month after the peak wrasse abundance (which would be expected). During diving operations throughout the study period wrasse were seen constantly interacting with the cliff faces at all of the study sites, which is consistent with previous observations on submarine cliffs at Lough Hyne (Turner & Warman, 1991; Spring, 1999). Virtually all activities observed (including feeding, nest building and defence of territory) resulted in damage to other organisms living on the cliff face often causing associated material to fall. Although wrasse appear to be a principal agent in the 'fall out' of marine fauna from submarine cliffs, the movement of crustaceans (especially *Hommarus gammarus* and *Maja squinado*) across the cliff was also observed to cause damage, especially to large branching sponges and solitary ascidians. Sponges have low nutrition value due to their high inorganic content (Mercurio et al., 2000), and as such are more likely to be damaged inadvertently by the activities of wrasse rather than from direct consumption. Although ascidians are also of relatively low nutritional value the dominant species found within Lough Hyne (*Ascidiella aspera*) harbours symbiotic bivalves (*Modiolarca tumida*) which settle inside the ascidians and grow within pockets of the test (Hayward & Ryland, 1995). Many of the ascidians that were found in the nets had their internal parts removed along with the symbiotic bivalves. Wrasse were often observed feeding directly on the ascidians, perhaps trying to remove the more nutritional, thin shelled bivalves rather than feeding on the ascidians themselves. However, the bivalves may have also been removed after falling from the cliff by scavenging crustacea or echinoderms. Ascidians were only abundant in nets between May to August 1999 (with the exception of Goleen), after this their abundance decreased rapidly and did not increase again during the following year (2000). The large fall out of ascidians in 1999, represented >95% of the entire solitary ascidian population (J. Bell, personal observation). In 2000, the space occupied by these solitary ascidians was replaced with colonial ascidian species (predominantly *Diplosoma spongiform*). There appears to be an alternation between solitary and colonial types, although the period of this cycle probably exceeds that of the present study. The colonial ascidians were not found in any of the nets probably due to their essentially encrusting nature (as with sponges).

The sponges falling from the cliffs within Lough Hyne were composed essentially of species exhibiting 3-D morphologies. This may be surprising considering the large number of encrusting sponges species (over 30) inhabiting cliffs in Lough Hyne (Bell & Barnes, 2000d). However, sponges exhibiting morphologies that project from the substratum are likely to have a greater probability of being knocked from their fixed position than low profile forms (whether by biological or physical means). Natural mortality was not directly observed for any sessile species recovered from the nets. However, for some arborescent sponge species entire specimens including bases were recovered from the nets. Specimens were usually large such that they may have fallen when they had reached a size too great to be supported by their basal attachment discs.

Sources of mobile organisms found in nets may include members of the infaunal soft sediment community or organisms falling from the cliff either independently from the sessile organisms or while attached to or feeding on them. Also some of the large species, such as echinoderms (e.g. *Marthasterias glacialis*), may migrate from the cliff on to the sediment (Nickell & Sayer, 1998; Kelly, 2001) or in the case of crustaceans from nearby boulder fields (e.g.

Hommarus gammarus). Many of the mobile gastropods found (including *Hinia reticulata*, *Turritella communis*, *Bittium reticulata*) are common to soft sediment habitats (Hayward & Ryland, 1995) and are therefore considered to have migrated onto the nets from the surrounding sediment rather than to have fallen from the cliff. Other species, however, such as *Trivia monacha*, are more commonly associated with hard substratum environments (Hayward & Ryland, 1995) suggesting they may have either migrated from the cliff or have fallen from the cliff, perhaps while feeding on sessile organisms. The large amount of scavenging and predatory organisms found in the nets does create a problem with a study such as this. Much of the material that has fallen onto the nets must have been consumed over the one month period, therefore the true amount of fallen material is likely to be much higher than that measured.

Current flow was shown to have important influences on the 'fall out' of marine organisms. At Whirlpool Cliff, where current flow rates are very high ($>200\,\text{cm}\,\text{s}^{-1}$) compared to the other sites sampled (Bell & Barnes, in press b), no material was found in nets at any time interval. However, damage to marine organisms is considered to be high because of the fast flow rate (Bell & Barnes, 2000a), as is the number of wrasse during summer months, therefore material is certainly removed from cliff faces. Although the absence of material in the control nets in the North Basin demonstrated the lack of horizontal transport in low current areas ($<5\,\text{cm}\,\text{s}^{<1}$), in faster current situations ($>200\,\text{cm}\,\text{s}^{-1}$) such as at Whirlpool Cliff horizontal transport processes are likely to be occurring. The question remains as to the situation at Glannafeen where current flow rate is moderate (up to $60\,\text{cm}\,\text{s}^{-1}$). The highest amounts of material were found in nets at Glannafeen, which is most likely a result of the increased current flow rate rather than cliff profile (see below), which may cause more organisms (especially sponges and ascidians) to be removed from the cliff face. Current flow rate decreases with depth at this site, such that flow rate is reduced from 60 to $20\,\text{cm}\,\text{s}^{-1}$ at 18 m (the base of the cliff). It is possible that although organisms falling from the cliffs are initially transported horizontally (as well as vertically), below a certain depth/current threshold (which has not be determined) transport is essentially in a vertical direction. It is difficult to ascertain the importance of cliff profile in either enhancing or preventing material 'fall out' at Glannafeen as there was no other site with a similar cliff profile experiencing low flow rates (rather than moderate flow rates). However, comparisons can be drawn between vertical and overhanging cliff at Labhra Cliff and Goleen as both these sites experience very similar low flow rates and have similar overall community compositions (Picton, 1991). However, communities inhabiting vertical, overhanging and inclined surfaces have been shown to exhibit marked differences especially with respect to sponge (Bell & Barnes, 2000) and cnidarian (Bell, 2001a) communities. Higher material 'fall out' rates were associated with the overhanging cliff at Goleen than Labhra Cliff. Physical pressures on organisms living on vertical and overhanging cliff surfaces differ including reduced sedimentation leading to increased competition (Maughan & Barnes, 2000) in sediment free overhanging cliff surfaces. Also for 3-D animals such as sponges and solitary ascidians forces acting on basal components (leverage) will be greater on overhanging surfaces than those on vertical or inclined surfaces (Bell, 2001b). Ascidians were rarely found in nets beneath the cliff at Goleen. This is because they are rare on overhanging cliff sites, the reason for such is unclear. The ranking in order of importance to cliff profile, current flow rate and season in the fall out of material from submarine cliffs is very difficult to ascertain. It is likely that certain combinations of these factors may enhance 'fall out'. For example, more material is likely to fall from an overhanging cliff in a high current area during the summer, than an inclined cliff in a low current area during the winter.

It is interesting that the proportion of the overall weight of material devoted to inorganic material actually decreased during summer months, when overall marine productivity is usually at its highest (Gomez, 2001; Light & Beardall, 2001). This paradoxical situation is the result of an increased number of scavenging gastropods feeding on the material fallen, which have a high inorganic component (from shell) but are much reduced in numbers during winter months.

The SCUBA exclusion zone set up around diving sites was important in preventing additional factors contributing to the 'fall out' of marine organisms. Diving activity is well known to cause damage to tropical reefs (Hawkins et al., 1999; Rouphael & Inglis, 2001). However, damage to temperate reefs has received far less attention. Recreational diving can damage temperate reefs from careless fin action, anchor damage, or from exhaust SCUBA bubbles (Spring, 1999). Cliffs in vulnerable areas such as Lough Hyne, Skomer Island (UK) or Lundy Island (UK) may be under threat from SCUBA activity. In the case of Lough Hyne, divers in the past have been considered mostly responsible for causing material to fall from the submarine cliffs. It is unclear if SCUBA activity had been allowed in the areas investigated, how much more material would be found in the nets. It seems likely that this would be proportional to the amount of diving activity allowed. The controlling of diving activities may be extremely important in sensitive areas such as Lough Hyne (which is already controlled) because changes in the amount of material falling from cliffs may have indirect consequences for other communities. Future studies should compare 'fall out' material from dived and un-dived areas to assess the impact of this activity on submarine communities. Also if predictions of global warming are correct, rises in sea temperature (Grainger, 1992; Mason, 1995; Southward et al., 1995; Yonetani & Gordon, 2001) may effect the timing of fish (such as wrasse) movements into shallow water. If fish move into shallower water and begin to damage and feed on the cliffs at an earlier stage in the year, damage to cliff communities may be more extensive. This will, in the short term, lead to an increase in material falling from the cliff (as would increased SCUBA diving), but over the longer term cliff communities are likely to be overgrazed/damaged resulting in lower productivity and smaller amounts of 'fall out' material.

The vertical export of material is certainly important to the soft sediment communities in the vicinity of the cliff. The processes controlling such export appear to be biological in nature in low current environments, while both physical and biological factors are likely to contribute to the 'fall out' of material in high current situations. This contribution to the benthos is likely to provide an important source of food material in an otherwise impoverished environment.

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