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The behavioural ecology of epibenthic scavenging invertebrates in the Clyde Sea area : field sampling using baited traps.

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Abstract : Routine monthly sampling was carried out at two regular stations (13 m and 113 m) in the Clyde Sea area, using five small-mesh and five large-mesh baited creels on every occasion. A third station (86 m) was sampled on two occasions with baited funnel traps. A consistently higher species diversity of scavenging invertebrates was found at 113 m than at 13 m. No obvious seasonal changes in species richness occurred. Four dominant species were common to both stations : *Asterias rubens, Buccinum undatum, Ophiura albida,* and *Pagurus bernhardus.* Crustacea dominated the list of species at the deep station, headed by *P. bernhardus.* Total monthly catch of two species *(Pandalina brevirostris* and *Ophiocomina nigra)* showed a significant correlation with a notional "Spring Factor" devised to test the theory that variations in current speed over the spring/neap tidal cycle might explain variations in catch. The month catch of the other major species showed no relationship with "Spring Factor". Large numbers of the necrophagous isopod *Natatolana borealis* and amphipod *Scopelocheirus hopei* were the only species collected at the third station.

No end-creel effect was apparent at either routine station. As expected, large-mesh creels consistently selected larger size animals. From the literature on feeding of these species it is deduced that few of these species are obligate scavengers ; rather, most are omnivores which scavenge opportunistically.

Mean bottom current speeds at both stations differed significantly at spring and neap tides, though maxima and minima were of the same order for the two tidal periods. Currents in excess of 0.1 m s^{-1} were present for more than 50 % of the time at both stations, and currents in excess of 0.3 m s^{-1} were encountered rarely.

Résumé : L'échantillonnage mensuel de routine a été effectué sur deux stations régulières (13 m et 113 m) dans la Mer du Clyde, utilisant à chaque fois cinq paniers à petites mailles avec appât, et cinq paniers à larges mailles avec appât. Une troisième station (86 m) a été échantillonnée à deux reprises avec des pièges en forme d'entonnoir garnis d'appâts. Une plus grande variété d'espèces de charognards invertébrés a été régulièrement trouvée à 113 m qu'à 13 m. Il ne s'est produit aucun changement saisonnier manifeste dans la richesse des espèces. Quatre espèces dominantes sont communes aux deux stations : *Asterias rubens, Buccinum undatum, Ophiura albida* et *Pagurus bernhardus.* Les crustacés dominaient la liste d'espèces à la station profonde, les *P. bernhardus* venant en tête de liste. La prise mensuelle globale de deux espèces *(Pandalina brevirostris* et *Ophiocomina nigra)* a montré une corrélation significative avec un "facteur de vive-eau" conceptuel, mis au point pour tester la théorie selon laquelle des changements dans la vitesse du courant pendant la marée de vive-eau/marée de morte-eau expliqueraient les variations dans les prises. La prise mensuelle des principales autres espèces n'a montré aucun rapport avec le "Facteur de vive-eau". Un grand nombre d'isopodes nécrophages *Natatolana borealis* et l'amphipode *Scopelocheirus hopei* ont été les seules espèces recueillies à la troisième station.

Aucun effet de fin de panier n'était apparent/visible à aucune des stations de routine. Comme prévu, les paniers à larges mailles prélevaient régulièrement des animaux de plus grande taille. A partir de la documentation sur la nourriture de ces espèces, on peut conclure que peu de ces espèces sont des charognards obligatoirement ; la plupart sont plutôt des omnivores qui se transforment en nécrophages de façon opportune.

Les vitesses moyennes de courant de fond aux deux stations changent considérablement entre la marée de vive-eau et la marée de morte-eau, quoique les maxima et minima soient du même ordre pour les deux périodes de marées. Les courants excédentaires de 0.1 m s^{-1} ont été présents pendant plus de 50 % du temps aux deux stations, et les courants excédentaires de 0.3 m s^{-1} ont été rarement rencontrés.

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INTRODUCTION

The attraction of many invertebrates to carrion has long been known (Jeffreys, 1867 ; Sars, 1899 ; Isaacs, 1969). The use of baited net-walled traps or creels to catch commercially important scavengers is now standard (Forbes & Hanley, 1853 ; Holdsworth, 1874 in Edwards, 1979). Trapping in baited, solid-walled containers is an established method of sampling smaller natant species from deep-sea habitats for research (Paul, 1973 ; Shulenberger & Barnard, 1976 ; Ingram & Hessler, 1983). For instance, Antarctic scavenging amphipods have been collected in this way (Walker, 1907 ; Stockton, 1982).

Field sampling was initiated using creels and traps at several stations in the Clyde Sea area to determine, a) the range of scavenging species in the Clyde, b) the possible differences in species over grounds at different depths and with differing substrata and, c) the variation over time in the composition of these scavengers.

Bottom currents have been shown to be a significant environmental factor influencing the ecology of epibenthic organisms (Kirby-Smith, 1972 ; Vogel, 1981 ; Jumars & Gallagher, 1982 ; Lampitt & Burnham, 1983 ; Lampitt *et al.*, 1983). Thus Anger *et al.*, (1977) observed strong bottom currents actually lifting the scavenging starfish *Asterias rubens* (see Tables II and III for taxonomic authorities) off the bottom [as also did Warner (1971) with the brittlestar *Ophiothrix fragilis* and Lewis & Nichols (1979) with the sea urchin *Echinus esculentus*], while Busdosh *et al.* (1982) suggested that the activity of Arctic scavenging amphipods was related to the cycle of tidal currents. Gorzula (1976) observed the brittlestar *Ophiocomina nigra* aggregating in dense clumps in response to strong tidal currents in the Clyde. Clearly, the bottom current velocity will affect both the maximum rate of movement of epibenthic animals as well as the diffusion rate of carrion odours (Sainte-Marie, 1986).

Few detailed studies have been published on the hydrography of the Clyde Sea area. Those studies which do exist have been concerned mainly with mass water circulation (Barnes & Goodley, 1961 ; Dooley, 1970), or water movement in the upper reaches of the estuary (Collar, 1974). Few data have been published on bottom current velocities. In order to determine the range of bottom current velocities (especially the maximum value) at the stations sampled, a short programme of field monitoring was undertaken encompassing both neap and spring tide periods [note : current metering facilities were not available at the time of the initial field trapping programme].

MATERIALS AND METHODS

TRAPPING

Routine monthly sampling was carried out at two stations, one in shallow water (the Clach, 13 m) in Millport Bay, Great Cumbrae Island (lat. 55° 44.81' N ; long. 4° 56.25' W) and one in deep water to the west of the lighthouse on Little Cumbrae Island (the Elbow, 113 m, lat. 55° 43.35' N ; long. 4°58.99' W). The level bottom at the Elbow consisted of soft muddy sand, compared with the level harder sand at the inshore (Clach) station. Sampling consisted of laying a single fleet of five large-followed by five small-mesh (stretched diagonals 20 mm and 7 mm respectively) creels along the depth contour at each station. Creels were standard west coast scampi creels (550 x 440 x 330 mm with eye diameter 80 mm in the large and 42 mm in the small-mesh creels). The creels were laid 3 m apart in each fleet, with both stations being sampled on the same day. Creels were normally baited with salted cod (*Gadus morhua* L.) but, when unavailable, salted saithe (*Pollachius virens* L.) and very occasionally fresh spotted dogfish (*Scyliorhinus canicula* L.) were used. Although salted fish may be a less attractive bait than fresh fish (Thomas, 1952), its use was the only way to achieve a degree of guaranteeable bait availability. Creels were normally set around 14 : 00 h, left overnight and retrieved either during the morning or afternoon of the following day. Bennett (1974) found that catch-per-unit-effort of lobsters decreased after one day's creel immersion. Certainly, long soak times of creels are counter-productive (Robertson, 1989) and only encourage predators like octopods (Morgan, 1974) and fish to feed on trapped scavengers. Upon retrieval the contents of the creels were rough-sorted into large containers on deck, and the species composition of each creel was noted, wherever possible, on deck. Further enumeration, measuring (see Table I), sexing and identification of species was carried out at the laboratory. The catch data of carideans were not attributed to species on deck, but species were identified at the laboratory during later analyses. Sampling was begun in January 1983 and continued on a monthly basis until February 1984.

A third, more distant, sampling station (Skipness, 86 m, lat. 55° 44.77' N ; long. 5° 18.14' W) was investigated on two occasions, 3 November 1982 and 23 January 1984. Work consisted of laying a string of 12 funnel traps [modelled after those used by Ingram & Hessler (1983)] (see Nickell, 1989, for description) onto longlines which were being used at

TABLE I

Morphological criteria for size measurements.

Asteroidea - distance from centre of disc to tip of longest arm (mm)
Ophiuroidea - disc diameter (mm)
Gastropoda - shell length (mm)
Amphipoda - cord of peraeon length (mm) for *Scopelocheirus hopei* (body curled post-fixation)
Isopoda - body length (mm)
Caridea - carapace length from posterior margin of eye socket to dorsal posterior margin of carapace (mm)
Nephropsidae - length from posterior margin of eye socket to tip of telson (mm)
Galatheidae - length from tip of rostrum to tip of telson (mm)
Paguridae - length from tip of rostrum to dorsal posterior margin of hard porion of carapace (mm)
Brachyura - carapace width (mm)

the same time to catch spotted dogfish. The traps were baited with frozen cod muscle and left for 3 h during the afternoon. Upon retrieval, the traps were emptied into separate baths of running seawater ; the animals being kept alive until they could be either fixed and preserved at the laboratory or retained for use in behavioural experiments. Similar funnel traps (*n* =10) were also deployed at the other two stations on every sample trip, but nothing was ever caught in them.

Lunar cycles of light intensity have been shown to influence creel catches of the western rock lobster *Panulirus cygnus* (Morgan, 1974). Lunar periodicity in catch could also emanate from animals' responses to variations in tidal current speeds. In order to examine the possible effect of positioning of the sampling date within the fortnightly tidal cycle, a notional "Spring Factor" was created by multiplying the tidal range of the sample day (from Admiralty Tide Tables) by the number of days from neap tide, so that a sample day at neap tide with a tidal range of 2 m would have a "Spring Factor" of 1 x 2 = 2 ; similarly a sample day at spring tide (7) with a tidal range of 3.5 m would yield a "Spring Factor" of 24.5. The possibility that catch-per-unit-effort of the most important species might be related to "Spring Factor" at each station was investigated by ranking month catch with the "Spring Factor" for the same month for each species.

The possibility of an "end creel" effect (where the end creel in a string fishes in ways different from the rest, or from creels in the middle of the array) was examined for small- and large-mesh creels separately at both stations. Data for end creels, however, were only identified for 10 months during the sampling programme.

CURRENTS

Near-bottom currents were investigated at both the Elbow and Clach stations. The Elbow station was monitored at neap tide during 21-22 May, and spring tide, 26-27 May 1987 using a self-recording Valeport BFM 208 current meter, reading every 10 min. It was deployed *ca* 1 m off the bottom, weighted with 40 kg ballast and suspended from a subsurface buoy to eliminate ship motion. Data were offloaded and analysed on a BBC Master microcomputer. The Clach station was monitored only during spring tide, 22 February 1985, using a direct reading Plessey MO 27 current meter, also suspended *ca* 1 m off the bottom. Repeated attempts to monitor the Clach station for a whole tidal cycle and at neap tide had to be abandoned due to heavy weather. The minimum current speed detectable by both of these propeller type current meters is in the range of 0.02-0.03 m s^{-1}.

RESULTS

TRAPPING

Tables II and III reveal a consistently higher species diversity at the deeper (Elbow) station compared with the shallower (Clach) station, and also show that no obvious changes in species richness occurred seasonally.

TABLE II

List of scavengers trapped at the Elbow station.

	Total	Rank	Numbers caught per month													
Species	numbers	order	J	F	M	A	M	J	J	A	S	O	N	D	J	F
Echinodermata																
Asterias rubens L.	64	8	7	1	4	1	3	7	9	12	2	8	-	2	4	4
Ophiocomina nigra (Abildgaard)	54	9	1	27	10	-	1	1	-	3	3	-	-	-	-	8
Ophiothrix fragilis (Abildgaard)	5	19	-	-	-	1	1	-	-	-	1	2	-	-	-	-
Ophiura albida Forbes	95	6	-	-	-	3	-	-	8	29	11	-	26	-	-	18
O. ophiura L.	1	28.5	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Mollusca																
Buccinum undatum L.	443	3	-	29	19	65	26	59	38	21	61	33	40	14	14	24
Colus gracilis (da Costa)	102	4	2	4	4	10	11	9	11	6	6	5	8	4	6	16
Neptunea antiqua (L.)	79	7	2	3	2	2	5	12	3	4	9	11	10	2	5	9
Crustacea																
Epimeria cornigera (Fabricius)	2	23.5	-	-	1	-	-	-	-	1	-	-	-	-	-	-
Natatolana borealis (Bruce)	13	15	-	-	-	2	-	8	-	1	-	-	-	-	2	-
Caridion gordoni (Bate)	1	28.5	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Spirontocaris lilljeborgi Danielssen	44	11	4	1	1	-	3	-	14	4	-	4	3	1	7	2
Hippolyte varians Leach	1	28.5	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Pandalina brevirostris (Rathke)	97	5	5	14	7	24	5	18	10	2	1	4	-	1	5	1
Pandalus montagui Leach	481	2	59	3	3	13	8	4	5	4	29	57	116	82	88	10
P. propinquus G.O. Sars	23	12	-	2	-	1	1	2	2	-	-	5	2	5	3	-
Crangon allmani Kinahan	3	22	-	1	-	1	-	-	-	-	-	-	-	-	1	-
Pontophilus spinosus (Leach)	6	18	-	-	-	-	-	-	-	-	-	6	-	-	-	-
Nephrops norvegicus (L.)	1	28.5	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Munida rugosa (Fabricius)	2	23.5	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Galathea strigosa (L.)	1	28.5	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Pagurus bernhardus (L.)	1790	1	68	192	116	130	17	68	55	48	194	207	452	105	92	46
P. prideauxi (Leach)	4	20.5	-	-	-	1	-	-	-	-	-	-	1	1	1	-
P. pubescens (Krøyer)	12	16	-	-	-	-	-	1	7	-	1	-	-	-	1	2
Anapagurus laevis (Bell)	4	20.5	-	-	-	-	-	-	-	-	-	-	-	3	-	1
Hyas coarctatus Leach	49	10	3	1	2	4	2	-	4	3	20	4	-	1	2	3
Inachus dorsettensis (Pennant)	7	17	-	-	-	-	-	-	1	1	-	3	2	-	-	-
I. leptocheirus Leach	21	13	-	-	1	-	-	-	-	-	3	-	16	1	-	-
I. phalangium (Fabricius)	1	28.5	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Macropodia tenuirostris (Leach)	1	28.5	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Liocarcinus depurator (L.)	19	14	-	2	-	2	1	1	1	-	1	4	-	5	2	-
Cancer pagurus L.	1	28.5	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Total number of species	32		10	13	12	16	15	13	14	14	14	15	13	14	17	13

TABLE III

List of scavengers trapped at the Clach station.

Species	Total numbers	Rank order	Numbers caught per month													
			J	F	M	A	M	J	J	A	S	O	N	D	J	F
Echinodermata																
Asterias rubens L	326	1	7	15	3	12	8	17	60	37	28	42	40	14	24	19
Marthasterias glacialis (L.)	10	11	2	-	-	-	-	-	1	1	1	2	2	-	1	-
Ophiocomina nigra (Abildgaard)	232	2	114	36	5	-	76	1	-	-	-	-	-	-	-	-
Ophiura albida Forbes	56	7	-	-	-	-	-	9	27	18	2	-	-	-	-	-
Mollusca																
Buccinum undatum L.	118	4	2	10	3	3	-	16	6	6	6	43	2	13	6	2
Crustacea																
Eualus gaimardii (H. Milne-Edwards)	1	17.5	-	-	-	-	-	-	-	-	-	1	-	-	-	-
Hippolyte varians Leach	5	12	-	-	-	-	-	-	-	-	-	5	-	-	-	-
Dichelopandalus bonnieri (Caullery)	1	17.5	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Pandalina brevirostris (Rathke)	2	14	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Pandalus montagui Leach	2	14	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Galathea intermedia Lilljeborg	2	14	-	-	-	-	-	-	-	-	-	1	1	-	-	-
Pagurus bernhardus (L.)	85	5	8	11	4	-	1	1	10	3	7	2	18	6	11	3
Ebalia tuberosa (Pennant)	1	17.5	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Hyas araneus (L.)	140	3	2	34	15	25	3	34	-	-	-	-	-	9	5	13
Macropodia tenuirostris (Leach)	1	17.5	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Carcinus maenas (L.)	24	10	-	1	1	-	-	-	-	-	1	2	-	9	1	9
Liocarcinus depurator (L.)	82	6	1	3	-	3	1	1	5	9	41	4	11	-	1	2
L. puber (L.)	45	9	-	-	-	-	-	-	-	-	3	12	9	20	1	-
Cancer pagurus L.	50	8	5	4	3	18	2	-	-	-	1	2	8	6	-	1
Total number of species	19		12	9	7	5	6	7	6	6	9	11	8	7	8	7

Only eight species were present at either station in large numbers throughout the year (see Tables II and III). Of the eight dominant species, four were common to both stations : *Asterias rubens*, *Buccinum undatum*, *Ophiura albida* and *Pagurus bernhardus*. Of these, *A. rubens* was significantly more abundant (χ^2 test on deviation from unity = 184.12, $P < 0.001$) at the shallow station whilst the other three species were significantly more abundant at the deep station (*B. undatum* : $\chi^2 = 190.46$, $P < 0.001$; *O. albida* : $\chi^2 = 10.39$, $P < 0.01$; *P. bernhardus* : $\chi^2 = 1553.39$, $P < 0.001$). The numbers, sex ratios and mean sizes of trapped species in which males and females were distinguished are presented for both stations in Table IV.

Taking the data for the deeper Elbow station first, the list of species trapped is shown in Table II. Thirty two scavenging species from three Phyla were collected during the sampling period. Crustacea dominated with 24 species. Numerically, the hermit crab *P. bernhardus* dominated with a total catch of 1790 individuals. It was present year-round, with the

TABLE IV

The numbers, sex ratio, size range and mean size of animals caught in baited creels at the Elbow and Clach stations. χ^2 tests for deviation of sex ratio from unity, P = level of significance. Trans. = transforming male *Pandalus montagui*, Juv. = juveniles. Note : echinoderms not included as sexes were not separated.

	Numbers						Size range ♂ (mm)	Mean size ♂ (mm)	Size range ♀ (mm)	Mean size ♀ (mm)
Species	♂	♀	Trans.	Juv.	χ^2	P				
Elbow										
Pagurus bernhardus	1045	740		5	52.12	$P < 0.01$	2.6 - 22.0	10.2	3.1 - 19.3	9.7
Pandalus montagui	339	131	10	1	92.05	$P < 0.01$	6.7 - 16.8	11.2	5.44 - 21.4	14.2
Buccinum undatum	226	217			0.18	$P > 0.05$	45.0 - 101.0	76.7	35.6 - 98.7	75.7
Colus gracilis	50	52			0.04	$P > 0.05$	53.0 - 74.0	66.3	50.0 - 72.0	65.9
Pandalina brevirostris	67	30			14.11	$P < 0.01$	4.2 - 7.1	6.1	5.1 - 8.2	6.6
Neptunea antiqua	53	26			9.23	$P < 0.01$	49.0 - 111.0	83.4	40.0 - 129.0	85.6
Clach										
Hyas araneus	62	78			1.83	$P > 0.05$	30.0 - 65.0	54.0	27.8 - 59.0	48.2
Buccinum undatum	64	54			0.85	$P > 0.05$	77.0 - 123.6	102.9	29.0 - 120.0	100.6
Pagurus bernhardus	50	34		1	3.05	$P > 0.05$	3.5 - 19.8	16.3	5.0 - 17.4	12.5
Liocarcinus depurator	60	22			17.61	$P < 0.01$	20.0 - 50.1	42.3	36.1 - 49.8	41.7
Cancer pagurus	31	19			2.88	$P > 0.05$	67.4 - 132.0	100.8	84.0 - 114.1	97.4

monthly catch varying from 17 (May) to 411 (November). Summer catches (May to August) were significantly less than those of winter (September to December) (Mann-Whitney U-test, $U = 0$, $P < 0.05$). Males significantly outnumbered females (Table IV).

All of the trapped species over the 14 months sampling period were ranked in descending order (separately for each station) and their individual month catches compared with the "Spring Factor" for each month using Spearman's rank correlation. Of the eight numerically dominant species, *Pagurus bernhardus* nearly always ranked first (the most dominant) regardless of "Spring Factor". It dropped only once to a rank of two, at a time coinciding with the first of its biannual breeding periods in the Clyde (Elmhirst, 1922), though causality should not be assumed. The correlation between the "Spring Factor" and month catch for *P. bernhardus* was not statistically significant ($P > 0.05$).

The next most numerous scavenger (rank order two), the pink shrimp *Pandalus montagui*, had a male-dominant sex ratio which was significantly different from unity (Table IV). Monthly catches varied from four (July to August) to 116 (November). The summer catch (May to August) was significantly less than the winter (September to December) (Mann/Whitney $U = 0$, $P < 0.05$). Bimodal size distributions for male *P. montagui* were noted in January and December 1983 as well as January 1984 ; the modes were centred around 11 and 15 mm for all three months. For other months with male samples of $n \geq 10$ the median size varied litle (8.0 to 11.1 mm). Female *P. montagui*, which were less abundant for all months, displayed bimodal distributions in all months where $n \geq 10$ (October 1983 - January 1984) ; shifts in peak size were from 10 mm (October) to 13 mm (January 1984).

The mean size of male *Buccinum undatum* showed a decrease from March to May 1983, and an increase from August to December. Female size distribution showed no discernible trends. Sex ratio overall was not significantly different from unity (Table IV). Monthly catch data showed little seasonal change, though some short term periodicity was discernible. Following its short breeding season the month rank of *B. undatum* increased from 11 to 2 in February 1983 and from 3 to 2 in February 1984.

At no time did the number of males or females of the spindle whelk *Colus gracilis* reach 10 in any month. Overall, the sex ratio was not significantly different from unity (Table IV). No seasonal variation was apparent in the catch data. Month rank and catch varied with time in a similar way to the variation in "Spring Factor", but neither proved to be significantly correlated ($P > 0.05$). The size distribution of *Pandalina brevirostris* did not vary greatly in months when it was present in large numbers ($n \geq 10$). Sex ratio was male-dominated (Table IV). There was significant seasonal variation between the spring (January to April) catch and the winter catch (September to December) (Mann-Whitney $U = 0$, $P < 0.05$). Month catch and "Spring Factor" (Fig. 1) followed each other closely and a significant correlation (Spearman's Rank Correlation Coefficient $r_S = 0.589$, $P < 0.05$) emerged between them. The brittlestar *0. albida* was third in rank with 95 individuals overall (mean 5.8 mm, range 2.8-8.3 mm). It only appeared in six months and in large numbers ($n \geq 10$) only in four.

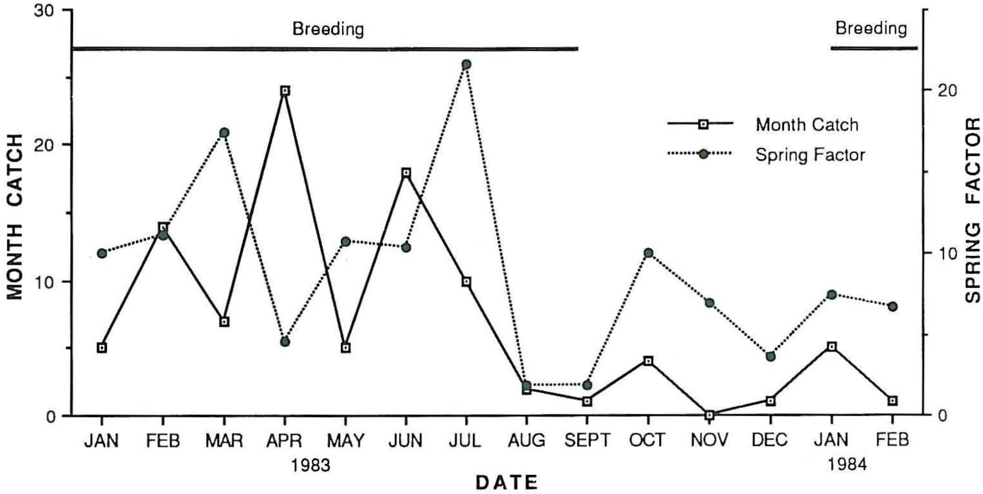

Fig. 1 : Seasonal variation in Spring Factor and month catch of *Pandalina brevirostris* at the Elbow station, January 1983 - February 1984.

The sex ratio of *Neptunea antiqua* was significantly male-dominated (Table IV). Although *N. antiqua* was present in every month, the number of males or females never exceeded nine in any one month. The least abundant of the top eight scavengers (rank order eight) was the common starfish *A. rubens*, with 64 individuals (mean 86.1 mm, range 27.0-159.7 mm). It was present in all months except November but only in August did numbers exceed 10. There were no clear seasonal trends in catch data.

Turing now to the shallower Clach station, only 19 scavenging species were recorded, the list again being dominated by Crustacea (14 species) (Table III). The numerically dominant animal, however, was the common starfish *A. rubens* with 326 individuals trapped. It was present in every month, with a mean size of 54.5 mm and size range was 10.8-157 mm. Median size gradually increased from 50.0 mm in January to 57.0 mm in June, fluctuating thereafter. Though only present in five months, the next (second) in rank was the brittlestar *Ophiocomina nigra* with 232 individuals (mean 13.3 mm, range 2.8-20.0 mm). Month catch and "Spring Factor" were significantly correlated ($r_S = 0.635$, $P < 0.05$) (Fig. 2). It only occurred in numbers greater than 10 in three out of the five months ; in these the mean size showed no trends. There was no consistent seasonal trend in the catch data.

The next most abundant scavenger at the Clach station was the spider crab *Hyas araneus* with 140 individuals (Table IV). This species was caught more commonly during winter months. The female-dominated sex ratio was not statistically significant (Table IV). Numbers of males only rose above 10 in February and June, while females were present in large numbers in February, March, April and June, when their median size declined from 50.5 to 46.9 mm.

The whelk *B. undatum* was fourth in rank with 118 individuals. This species was captured in every month but May, with catch showing no appreciable seasonal trends. Males out-

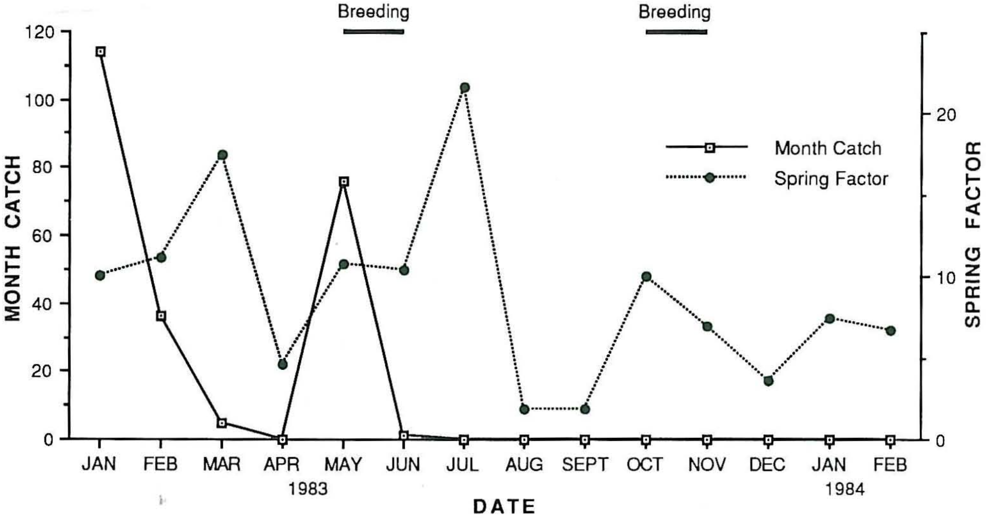

Fig. 2 : Seasonal variation in Spring Factor and month catch of *Ophiocomina nigra* at the Clach station, January 1983 - February 1984.

numbered females, but not significantly so (Table IV). Males were present in large numbers only in June and October, while females exceeded 10 only in October.

Next in abundance was the hermit crab *Pagurus bernhardus* with 85 individuals overall. The sex ratio was not significantly different from unity (Table IV). Males were present in numbers greater than 10 only in November, while females were never captured in large numbers. No discernible seasonal trends were apparent in the catch data. The swimming crab *Liocarcinus depurator* was sixth in rank with 82 individuals. The male-dominated sex ratio was statistically significant (Table IV). Numbers of both sexes were low throughout the year ; the males and females only rising above 10 in September. The catch data indicated that *L. depurator* may have been more attracted to bait during the warmer autumn months, though no significant difference in catch was detected statistically.

Seventh in rank was the brittlestar *O. albida* with 56 individuals captured in only four months. Mean size was 5.9 mm and ranged from 2.7 to 8.2 mm. It was only present in large numbers in July and August. The least abundant of the top eight scavengers at the Clach station (rank order 8) was the edible crab *Cancer pagurus* with 50 individuals. The sex ratio was not statistically different from unity (Table IV). Male *C. pagurus* only occurred in large numbers in April, while females were never present in numbers greater than 10. No seasonal trends in catch were apparent.

The third station (Skipness), sampled twice with funnel traps yielded only two species, the lysianassid amphipod *Scopelocheirus hopei* Costa and the cirolanid isopod *Natatolana* (= *Cirolana*) *borealis* Bruce, both in abundance. On the first date 683 individuals of *N. borealis* were captured, 220 males (mean 21.1 mm, range 8.0-32.1 mm), 129 females (mean 16.2 mm, range 10.1-27.7 mm) and 334 juveniles (mean 9.4 mm, range 5.7-12.7 mm). The male-dominated sex ratio differed significantly from unity ($\chi^2 = 23.73$, $P <$

0.01). The bimodal male size distribution was centred around peaks at 12 and 22 mm, while the females were similarly distributed around 12 and 23 mm. The catch of *N. borealis* on 23 January 1984 yielded a total of 442 individuals, 185 males (mean 17.7 mm, range 6.1-30.5 mm), 134 females (mean 13.8 mm, range 9.8-26.5 mm) and 123 juveniles. The sex ratio was again significantly male-dominated, differing statistically from unity ($\chi^2 = 8.15$, $P < 0.01$). The males were distributed bimodally about 13 and 25 mm.

Only one sample (3 November 1982) of 58 *S. hopei* was measured and sexed. It was dominated by immature animals. Females significantly outnumbered males ($\chi^2 = 4.45$, $P < 0.05$) and nearly half the females were ovigerous. Those ovigerous females carried 2 to 12 eggs.

The catch data for creels at different positions in the creel string were examined. Data for the middle and end creels in the string were compared over the 10 month period when such records were kept. At the Elbow station the numbers of the top eight scavengers caught in the large-mesh end creels were not significantly different from those caught in the middle creels (Mann-Whitney *U*-test, $U = 76.0$, $P > 0.05$), nor was the catch of these same species in the small-mesh end creels significantly different from that in the middle ones ($U = 132.5$, $P > 0.05$). The data for the shallow Clach station yielded similar results ; there was no effect of creel position on catch in either the large-mesh ($U = 59.0$, $P > 0.05$) or small-mesh creels ($U = 31.0$, $P > 0.05$).

At the Elbow station large-mesh creels caught significantly more *B. undatum* ($\chi^2 = 40.62$, $P < 0.001$) and *N. antiqua* ($\chi^2 = 8.24$, $P < 0.01$), but significantly fewer Caridea ($\chi^2 = 610.40$, $P < 0.001$) and *O. albida* ($\chi^2 = 97.00$, $P < 0.001$) than small-mesh creels. At the Clach station large-mesh creels captured significantly more *H. araneus* ($\chi^2 = 126.45$, $P < 0.001$), *B. undatum* ($\chi^2 = 104.31$, $P < 0.001$), *P. bernhardus* ($\chi^2 = 16.12$, $P < 0.001$) and *C. pagurus* ($\chi^2 = 50.00$, $P < 0.001$) than small-mesh creels. Small-mesh creels, however, caught significantly more *A. rubens* ($\chi^2 = 7.86$, $P < 0.01$), *Ophiocomina nigra* ($\chi^2 = 36.17$, $P < 0.001$), *L. depurator* ($\chi^2 = 40.91$, $P < 0.001$) and *Ophiura albida* ($\chi^2 = 57.00$, $P < 0.001$) than the large-mesh creels.

Table V compares the size-distributions of the top eight scavenging species between the large- and small-mesh creels at the Elbow and Clach stations. It is clear from inspection of these data that (as expected) the large-mesh creels consistently selected larger animals at both stations. Descriptively, the following points emerge. At the Elbow, the size range of both male and female *P. bernhardus* is greater in the large-mesh creels, as is the mean size for both sexes. While no male *P. montagui* were caught in the large-mesh creels, the mean size of the females was greater in the large- than the small-mesh creels, though the female size range was greater in the small-mesh creels. Both the size range and mean size for male and female *B. undatum* were greater in the large-mesh creels. The size ranges of male and female *C. gracilis* were greater in the small-mesh creels while the mean size of the males was greater in the large-mesh, the mean size of the females being greater in the small-mesh creels. No individuals of the small species *P. brevirostris* or *O. albida* were caught in the large-mesh creels. Both the size ranges and mean sizes of both sexes of *N. antiqua* were

TABLE V

Size-distribution comparisons (in mm) between the eight commonest species captured in large- and small-mesh creels at the Elbow and Clach stations, January 1983 - February 1984. Note : echinoderms not sexed.

	Large mesh				Small mesh			
	Size range		Mean size		Size range		Mean size	
Species	♂	♀	♂	♀	♂	♀	♂	♀
Elbow								
Asterias rubens	27.0-186.7		90.5		40.1-141.0		81.8	
Neptunea antiqua	49.0-111.0	40.0-129.0	84.2	85.8	51.5-93.7	76.0-93.0	81.6	85.0
Ophiura albida	-		-		2.8-8.3		5.9	
Pandalina brevirostris	-	-	-	-	4.2-7.1	5.1-10.4	6.1	10.7
Colus gracilis	56.0-74.0	50.0-71.0	66.6	64.5	53.0-72.0	59.0-72.0	66.1	67.2
Buccinum undatum	46.0-101.0	35.6-98.7	80.0	78.3	45.0-87.0	51.0-89.7	71.2	70.3
Pandalus montagui	-	16.3-19.8	-	18.4	6.7-16.8	5.4-21.4	11.2	14.1
Pagurus bernhardus	4.6-17.8	4.1-19.3	12.1	11.0	2.6-15.0	3.1-14.7	8.0	8.6
Clach								
Cancer pagurus	67.4-132.0	84.0-114.1	99.4	97.4	-	-	-	-
Ophiura albida	-		-		2.7-8.2		5.9	
Liocarcinus depurator	41.1-49.8	36.7-44.9	44.5	41.5	20.0-50.1	36.1-49.8	41.9	41.8
Pagurus bernhardus	5.1-19.8	6.2-17.4	15.4	14.6	3.5-11.3	5.0-8.4	7.8	6.6
Buccinum undatum	77.0-123.6	73.8-120.0	102.8	103.2	-	29.0-101.9	-	$n< 10$
Hyas araneus	36.5-65.0	27.8-59.0	54.7	48.3	30.0-32.2	34.0-49.7	$n<10$	$n<10$
Ophiocomina nigra	10.3-20.0		14.9		2.8-19.0		12.6	
Asterias rubens	24.9-100.0		58.9		10.8-157.0		51.3	

greater in the large-mesh creels, and *A. rubens* showed a similar trend with both size range and mean size being greater in the large-mesh creels.

At the shallow Clach station, as was the case at the deeper Elbow station, the large-mesh creels generally selected animals of a larger mean size. The size ranges of both sexes of *P. bernhardus* and *H. araneus* were greater in the large-mesh creels, but were variable in the other species ; male and female *L. depurator* had a greater size range in the small-mesh, as did male *B. undatum*. Both *A. rubens* and *Ophiocomina nigra* had larger size ranges in the small-mesh samples. The large edible crab *C. pagurus* was never recorded in the small-mesh creels, while the small brittlestar *Ophiura albida* was again only present in the small-mesh ones. Mean sizes of female *B. undatum* and both sexes of *H. araneus* (all from the small-mesh creels) were not computed due to the low numbers of animals caught.

BOTTOM CURRENTS

At the Elbow station, maximum bottom current velocities at different tidal states were very similar (0.31 m s^{-1} at neap, 0.30 m s^{-1} at spring tide). The mean velocities over neap and spring tides, however, were significantly different (Student's t-test, $P < 0.001$) ; 0.14 and 0.18 m s^{-1} respectively. Minimum current velocities (0.02 m s^{-1}) were recorded at high and low tide slack water, while the velocity apparently never dropped to zero (note : recording such low speeds would, however, be compromised by the sensitivity of the meter).

The maximum, minimum and mean values for bottom current velocities at the Clach during spring tide were of the same order as those observed at the Elbow for both neap and spring tides (maximum = 0.31 m s^{-1}, mean = 0.11 m s^{-1}). Current speed at the Clach also apparently never dropped to zero (minimum = 0.02 m s^{-1}), although minima were not as close to expected times of high and low tide as at the Elbow.

From Table VI it can be seen that mean current speed at the Elbow was 24 % stronger at spring than at neap tide. Also, mean current speeds at the Elbow were 36 % stronger at spring tide than at the Clach. The duration of moderately strong currents (≥ 0.2 m s^{-1}) was considerably longer at spring than at neap tides at the Elbow (or spring tide at the Clach). Currents in excess of 0.1 m s^{-1} were experienced for more than 50 % of the time at both stations. Currents hardly ever exceeded 0.3 m s^{-1} at any time at either station.

TABLE VI

Percentage of time that current speeds equalled or exceeded stated values at the two study stations on different tides, together with values for mean velocity (m s^{-1}) (± standard deviation).

Current speed (m s^{-1})	Elbow (neap tide)	Elbow (spring tide)	Clach (spring tide)
≥ 0.05	95.6 %	96.0 %	93.9 %
≥ 0.10	72.7 %	80.8 %	53.3 %
≥ 0.15	37.6 %	70.6 %	19.8 %
≥ 0.20	11.7 %	42.6 %	10.7 %
≥ 0.25	3.7 %	11.5 %	4.1 %
≥ 0.30	0.7 %	1.2 %	0.5 %
Mean velocity (m s^{-1})	0.14 ± 0.06	0.18 ± 0.07	0.11 ± 0.06
Number of logged data points	142	142	48
Spring Factor	2.5	16.8	12.4

DISCUSSION

That no octopods or predatory fish were collected, encourages the view that creel soak time was appropriate to sampling scavengers and that insignificant loss of catch to predators occurred in the creels (see Morgan, 1974).

While certain species (*Pagurus bernhardus, Pandalus montagui and Pandalina brevirostris*) showed seasonal variation in catch data, the general lack of seasonal differences in the trap catch for the remainder of the species suggests that scavenger population density on the ground and/or vulnerability to the gear was not seasonally variable (cf. Morgan, 1979). Unfortunately, contemporary sea-bed temperature data for the creel stations are not available. However, Dr. R. Powell (pers. comm.) has found (1987) that temperatures above the sea-bed in the Main Channel between the Cumbrae Islands and the Isle of Bute varied between 4.5 (Feb.) and 12.5 °C (Oct.). Sea surface temperatures at Millport vary typically between 6.9 (Feb.) and 13.4 °C (Aug.) (20 yr average : data in Moore, 1980), ie. as would be expected, deeper waters are colder. It is interesting that the warmest time of year at the bottom of the Main Channel is appreciably later than that experienced at the surface, doubtless representing the time lag involved in heat transfer from surface to deeper water. The possible late summer/autumn enhanced catches of *Ophiura albida* at both stations may thus be associated with increased activity at the time of maximum sea-bed temperatures. Catches of *Asterias rubens* were possibly also enhanced during the summer at the shallower Clach station, though this species showed no such trend in deeper water. Conversely, catches of *Pagurus bernhardus* were significantly reduced at the deeper (Elbow) station during the warmest time of the year. In spite of this limited seasonal variability in catch diversity and catch-per-unit-effort of individual species, it is clear that variability in catch exists. A likely contributor to this variation (beyond mere chance effects) was felt to be the current regime prevailing during the time that the creels were in place, ie. according to the spring/neap tidal cycle. However, significant correlation emerged between monthly catch and the notional "Spring Factor" only for *Pandalina brevirostris* and *Ophiocomina nigra*.

In spite of this result, we feel that it remains a strong possibility that the relative prominence of different species might be sensitive to variations in current speed, eg. as evidenced by differential locomotory capabilities. Ideally, of course, a bottom current meter should have been placed *in situ* throughout the sample period at both stations to yield reliable information on actual currents experienced. In the absence of such ideal facilities, the "Spring Factor" was formulated. Several hypotheses could be invoked in explanation of the surprising failure of the "Spring Factor" to explain catch variation ; a) that in reality bottom currents were no stronger at spring tide than at any other time ; b) that these scavenging species do not respond to currents over the spring/neap tide range here experienced ; or c) that the "Spring Factor" itself was too crude a construct to mimic the local variation of bottom currents experienced over a spring/neap cycle. Bottom currents clearly are stronger at spring tide than at neap tide as a general rule. Additionally, it has been shown that another local scavenging species, the burrower *Nephrops norvegicus* (Newland *et al.*, 1988), does show decreased activity (and thus reduced catches) at spring tides. Cyclical variations of activity associated with tides have also been shown for natant epibenthic scavengers elsewhere (Lampitt *et al.*, 1983), and have been associated with lunar rhythms of light intensity for rock lobsters (Morgan, 1974).

Had only one of the 16 possible correlations between month catch and "Spring Factor" been significant at the 5 % level, this might have been regarded as merely a chance occurrence (1 in 16 is 6.25 %). However, month catch and "Spring Factor" were significantly associated for two species and so cannot be so easily dismissed.

Given these considerations, in spite of the general lack of correlation between catch data with "Spring Factor", it seemed injudicious to reject entirely the notion of current speed being ecologically important to the suite of species under study. More likely would seem to be alternative c) above ; that the formulation of the "Spring Factor" itself was at fault and too imprecise for the purposes intended.

The trap data from the deeper Elbow station demonstrated the overwhelming dominance of Crustacea as scavengers, compared with Mollusca and Echinodermata. All of the important scavenging crustaceans at the Elbow were decapods, and decapods made up the majority of the species trapped at the Clach. Opportunistic scavenging is the general mode of feeding in the Decapoda (Barnes, 1980 ; Nickell, 1989).

At the Elbow, the most abundant scavenging species trapped, the hermit crab *Pagurus bernhardus*, consistently scored highly on the monthly rank, reflecting both its abundance and the importance of scavenging in its feeding strategy (Jackson, 1913 ; Orton, 1927 ; Brightwell, 1951 ; cf. Gerlach *et al.*, 1976 ; Erri Babu, 1988). *Pagurus bernhardus* has been reported as feeding upon a wide variety of prey items, ranging from live brittlestars (armtips) (Gorzula, 1976), Foraminifera, diatoms (Orton, 1927), lamellibranchs, echinoderms (Hunt, 1925), dead fish (Jackson, 1913) and soft corals (*Alcyonium digitatum*), to scyphozoans (*Cyanea capillata*) stranded on the seabed (Moore, 1983). Scavenging is therefore only a part of this species' wide feeding repertoire. It ranked only fifth, however, at the Clach, probably reflecting differences in bottom sediment grade. Erikson *et al.* (1975) reported that it preferred hard substrata to soft, but present data suggest the reverse propensity.

At the shallower Clach station, Echinodermata dominated numerically. There, *A. rubens* was the most abundant scavenger. *Asterias rubens* was significantly more numerous at the Clach than the Elbow. This difference in abundance between the deep-and shallow-water station can again probably be attributed to differences in substratum, since *A. rubens* prefers hard bottoms (Erikson *et al.*, 1975) to the softer ground offshore.

Although in certain areas where creel-fishing is practiced, an end-creel effect (when a creel at the end of a string fishes more effectively than those in the middle, sometimes even without the presence of bait) has been noticed (Jaeger, 1972), no such effect was observed at either of the Clyde stations, probably due to the circularity of current direction vectors experienced over the 24 h creel immersion period. Such end-creel effects may well be related to local hydrographic conditions, with the dispersal of bait odours across the creel string being governed by local bottom topography, for example. End-creel effects may then be unique to the area being fished and may depend on creel string orientation with respect to prevailing current flow.

That the large-mesh creels captured significantly more *B. undatum* and *N. antiqua* at the Elbow, and significantly more *H. araneus, B. undatum, P. bernhardus* and *C. pagurus* at the Clach may be due to the smaller eye of the small-mesh creels excluding such large species. Not surprisingly this smaller creel eye proved no obstacle to entry by the smaller gastropod *Colus gracilis*. The fact that animals bigger than the creel eye in the dimension measured (see Table I) occurred consistently in creels at both stations (Table V), serves merely to establish that their orientation at access was other than perpendicular to the dimension measured, ie. crabs progress crabwise. It seems likely that large-mesh creels would attract as many of the smaller species (such as carideans, *Ophiura albida, Ophiocomina nigra*) as the small-mesh creels in which such species were significantly retained, but that during the act of creel hauling these smaller species get washed out of the large-mesh creels. That the small swimming crab *L. depurator* would find it much easier to escape through the eye of a large-mesh creel but would find escape through the eye of a small-mesh creel much more difficult, might explain the preponderance of this species in small-mesh creels at the Clach.

At the Skipness station, the only scavengers encountered were *Natatolana borealis* and *Scopelocheirus hopei*. Lysianassid amphipods such as *S. hopei* are commonly necrophagous (Dahl, 1979), and the isopod *N. borealis* has long been known to feed voraciously on carrion, prompting Sars (1899) to call it (as *Cirolana borealis*) "...one of the most effective scavengers of the sea...". Although only a few samples were taken presently, the number of isopods taken in each was large ($n > 400$). Out of these, only one female *N. borealis* was found in breeding dress (with fully formed oostegites), suggesting that the females of this species (at least) may not feed during breeding, as is the case for the related American species *Cirolana harfordi* (Johnson, 1976). By contrast, the feeding of *S. hopei* did not appear to be inhibited by reproductive activity, since nearly half the females captured in the baited traps were ovigerous.

The data available from both stations during spring and neap tides suggest that bottom currents in the area of the Cumbrae Islands differ significantly between spring and neap tides, although maximum and mean velocities remain of the same order within sites. So, although current meter data are not available for a full neap/spring tidal cycle at either station, it is reasonable to assume that the maximum bottom current velocity in this area does not greatly exceed 0.30 m s^{-1}, while the mean is in the region of 0.10-0.20 m s^{-1} (depending on station). Additional unpublished data (moored meters, run 25 h continuously) from Strathclyde University working four stations around the neighbouring Little Cumbrae Island in 1969 reinforce this conclusion. They recorded a maximum velocity of 0.35 m s^{-1} and a mean of 0.08 m s^{-1}. This is also in broad agreement with the mean of 0.10 m s^{-1} observed in the Outer Firth by Edwards *et al.* (1986).

Some justification for the use of the "Spring Factor" approach can be seen from these data on current speeds, since at the Elbow station a lower mean current velocity (0.14 m s^{-1}) was associated with a low "Spring Factor" (2.5) at neap tide, and a higher current velocity (0.18 m s^{-1}) with a correspondingly high "Spring Factor" (16.8) at spring tide. Similarly, at spring tide the lower mean current velocity (0.11 m s^{-1}) at the Clach was associated with a lower "Spring Factor" (12.4) than at the Elbow. Clearly, though, with so little data of this type available it is impossible to prove whether a linear relationship exists between mean current velocity and "Spring Factor".

Overall then, while a reasonable body of data is available on the gross hydrography of the Inner Firth (Edwards *et al.*, 1986 notwithstanding), a local picture of bottom currents emerges which will undoubtedly be complicated in detail by a combination of irregular bottom topography, the proximity to an amphidromic point west of the Isle of Bute (within 10 km of the sampled stations), and the general pattern of bottom water in-and outflow through the main channel to the west of the Cumbrae Islands. It should be noted, however, that the purpose of the present bottom current investigations was not to conduct a detailed hydrographic survey of the area, merely to ascertain realistic gross environmental current speeds in order to run laboratory experiments on important scavenging species under conditions which approximated to those in the field (Nickell, 1989). Additionally, inferences made above (eg. variable scavenger behaviour) based on the assumption that current velocities locally are stronger at spring tides than at neaps are seen to have been based on a valid premise.

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