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Underwater television observations of *Serpula vermicularis* (L.) reefs and associated mobile fauna in Loch Creran, Scotland

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Abstract

The behaviour of *Serpula vermicularis* reef worms and associated mobile fauna in Loch Creran, on the west coast of Scotland, was recorded for six weeks using underwater television. The reef worms were extended almost continually, generally only retracting when stimulated by the close proximity of a predator. The length of hiding time varied according to the species triggering the reaction. The mean length of time retracted was 21 s. Fauna associated with the reefs included the corkwing wrasse *Crenilabrus melops*, ballan wrasse *Labrus bergylta*, black squat lobster *Galathea squamifera* and velvet swimming crabs *Necora puber*. There were few significant associations between tidal cycle and the presence/activity of associated fauna but a number of fish and crustacean species appeared to be influenced by the diurnal cycle. Gobies were recorded during daylight only with peak observations around midday while wrasse, butterfish *Pholis gunnellus* and cod *Gadus morhua* were crepuscular. The dawn and dusk appearance of juvenile cod in large shoals is suggestive of a nightly migration.

Keywords: *Serpula vermicularis*; serpulid reef; underwater television; diurnal cycles; cod; predation; Scotland

1. Introduction

Serpula vermicularis is a sedentary serpulid polychaete that secretes a calcareous tube. Serpulids are tentaculate suspension-feeders. *Serpula vermicularis* has a sub-littoral distribution around Britain, particularly on the west and southern coasts (Hayward and Ryland, 1990). Generally, *S. vermicularis* occurs as solitary individuals or in small clumps, encrusting hard substrata such as bivalve shells and stones. At a few sites, *S. vermicularis* has also been recorded as forming hard structures up to 2 m high. Larvae settle on or near conspecifics to form monospecific aggregations. After an initial encrusting stage, the worm tubes grow upwards intertwining to form complex bush-like shapes (Bosence, 1979). These structures have been termed "reefs" as they form a discrete hard, biogenic structure which is elevated above the surrounding muddy seabed (Holt et al., 1998). Reef formation is not unusual in serpulids, large fossil reefs and subfossil reefs consisting mainly of serpulids have been recorded (Leeder, 1973; ten Hove, 1979; ten Hove and van den Hurk, 1993; Berra and Jadoul, 1996). About 10% of present-day serpulid species are reported to form environmentally induced aggregations (ten Hove, 1979). All present-day serpulid species which form such reefs also occur singly (ten Hove, 1979). However, reef formation is extremely rare in *S. vermicularis*.

Living *Serpula vermicularis* reefs are described from only one site in the UK, Loch Creran on the west coast of Scotland (Fig. 1; Moore et al., 1998). Living reefs are also found in Ardbear Lough and Killary Harbour on

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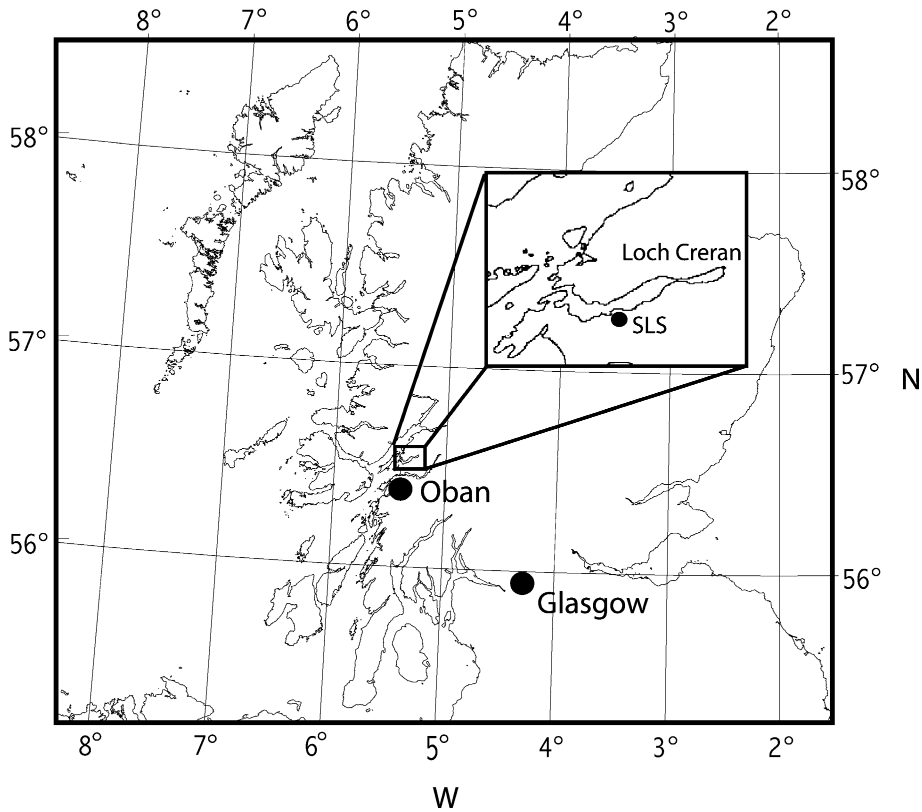

Fig. 1. West coast of Scotland with Loch Creran (inset). SLS indicates the position of the Scottish Sea Life Sanctuary, adjacent to study site.

the west coast of Ireland but Loch Creran contains the most abundant and best developed reefs (Bosence, 1973, 1979; Minchin, 1987). Loch Creran has been designated as a Special Area of Conservation (SAC) under the Habitats Directive (European Council Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Fauna and Flora) for biogenic reefs of *S. vermicularis* and *Modiolus modiolus* (horse mussel). Serpulid reefs are also listed as a priority habitat under the UK Biodiversity Action Plan (UK BAP). Loch Creran is a fjordic sea loch which is 12.8 km long and has a maximum depth of 49 m (Edwards and Sharples, 1986). *Serpula vermicularis* reefs fringe most of the loch down to 14 m depth, with most abundant reef cover occurring between 6 and 10 m in areas where the seabed is predominately muddy sand (Moore et al., 1998).

Animals living in close proximity may incur associated costs and benefits such as increased intraspecific competition, increased reproductive success and reduced predation risk (Wu, 1980; Wethey, 1984; Bertness and Grosholz, 1985; Dalby, 1995; Bertness et al., 1998). *Serpula vermicularis* responds to predation threat by retreating rapidly into its tube which is then sealed by the operculum. The crown also acts as a mechanism for gas exchange (Williams, 1852) so, when retracted, respiration is reduced and the worm cannot feed. Hiding time can therefore be considered as a trade-off between food acquisition and predator avoidance (Dill and Fraser, 1997). Aggregation may infer a benefit by shortening mean hiding times. Hidden individuals may be able to detect when neighbours resume feeding thus receiving a signal that predation risk has been lowered (Mauck and Harkless, 2001).

Despite the potential importance of these serpulid reefs as promoters or attractors of local biodiversity, relatively little is known of their use by mobile fauna. Studies by SCUBA divers have listed a rich associated fauna which includes the ascidian *Diplosoma listerianum*, other serpulids such as *Pomatoceros triqueter*, and the brittlestar *Ophiothrix fragilis* (Bosence, 1979; Minchin, 1987; Connor, 1990). Bosence (1979) records the major mobile predators seen feeding on the serpulid reefs in Ardbear Lough, namely the echinoids *Echinus esculentus* and *Psammechinus miliaris*, the asteroid *Asterias rubens*, and the wrasses *Ctenolabrus rupestris* and *Crenilabrus melops*. Observations by SCUBA divers are necessarily time limited and cannot provide much information on longer cycles of activity and behaviour of larger mobile fauna. In addition, divers may influence the behaviour of these species by inducing hiding and inhibiting feeding behaviour.

In this study, we aimed to build a more comprehensive picture of the behaviour of mobile fauna and the reef worms themselves, using a non-intrusive observation technique—underwater television (UW TV). Our specific objectives were: (1) to investigate branchial crown emergence in relation to diurnal and tidal cycles in situ; (2) to quantify rate of predation on reef worms in situ; and (3) to determine associated mobile fauna and, for abundant species, to elucidate diurnal and/or tidal patterns of their presence at reefs.

2. Methods

The study site (56°31′ N, 05°20′ W) was in the lower basin of Loch Creran, close to the Scottish Sea Life Sanctuary at Barcaldine (Fig. 1). The study reefs were approximately 50 m offshore and at a depth of 10 m. A colour, UW TV camera (Bowtech BPL3C HR A4) was mounted horizontally, parallel to the seabed, on a frame measuring 1 m^3. A 200 m umbilical linked the camera system to the control unit on shore and a time-lapse VHS video recorder (Panasonic AG6720A) with a time-code generator (IMP Electronics V9000A). The camera was deployed by SCUBA divers next to a serpulid reef on 17 July 2003. The reef was filmed continuously over four weeks with ambient light only during the day.

The equipment was then lifted and a black and white UW TV camera (OE1390, Simrad Osprey Ltd.), which was sensitive to infrared wavelengths, was attached to the frame. Two 300 W underwater lights (Osprey OE1132), fitted with infrared filters, were also attached. A timer switched the infrared lights on at 19:00 and off at 06:00, before sunset and after sunrise, respectively. The equipment was redeployed on a second reef at approximately 10 m depth, close to the original reef. Filming was carried out continuously for a further two weeks and all equipment removed from the loch on 28 August 2003.

Filming during the day with ambient light only produced good quality pictures with the colour camera equipment. This camera gave a wide field of view compared to the black and white camera (Fig. 2). The first 10 min of each half hour of colour footage (daytime only) from the first four weeks deployment and the first 10 min of each hour of black and white 24-h footage

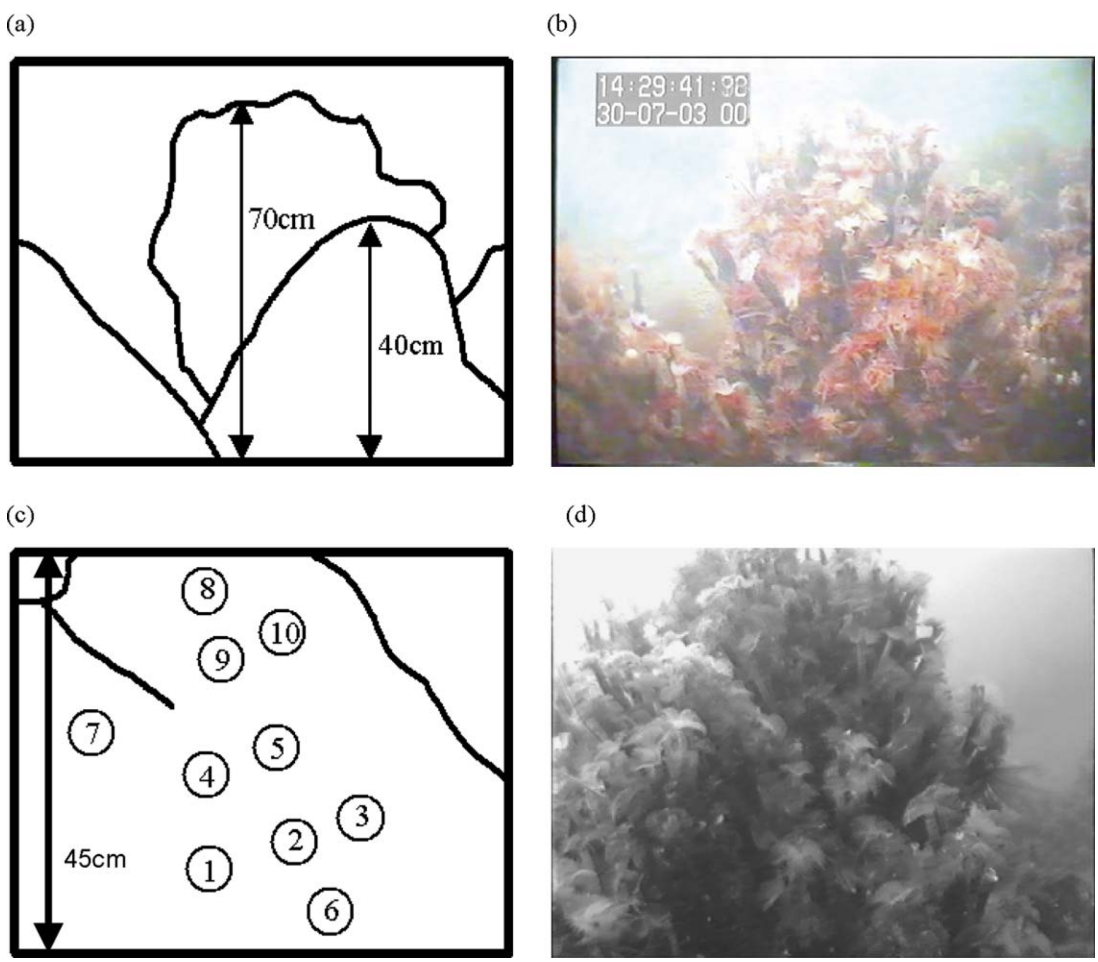

Fig. 2. Schematic view and actual view of *Serpula vermicularis* reefs in Loch Creran at approximately 10 m depth captured by ((a) and (b)) colour underwater television camera and ((c) and (d)) black and white underwater television camera. Approximate sizes of the reefs indicated in schematic views. The positions of the branchial crowns of individual worms examined to determine behaviour over 24 h are shown in (c).

from the last two weeks were analysed. The numbers and type of mobile fauna seen in, on and around the reef were recorded. Where possible, individuals were identified to species level. With gobies and wrasses, it was not always possible to identify individuals to species level so these were simply classified as groups. The activity of species living within the reefs, such as *Pholis gunnellus* and *Galathea squamifera*, were analysed for diurnal and tidal patterns. Similarly, presence at the reefs of more far-ranging species, such as crabs and wrasse, were also evaluated.

Times of sunset, sunrise and high and low tide for each day of deployment were taken from POLTIPS for Windows (Proudman Oceanographic Laboratory) for Barcaldine Pier, Loch Creran. Day length decreased over the six-week observational period by 2 h 50 min. Hourly presence and absence data for 20 species from the colour UW TV (daytime only) and 9 species from the monochrome UW TV (24-h footage) were analysed using sine and cosine interpolation of the tidal and diurnal cycle (Gibson et al., 1996, 1998). The state of the tide was expressed for each observation period as the sine and cosine of the time in hours relative to high water divided by the length of the tidal cycle (12.4 h) $\times 2\pi$. Time of day was similarly expressed as sine and cosine functions of the time in hours divided by 24 h $\times 2\pi$. Logistic models, including these four variables, were fitted to the presence/absence data for each species using PROC CATMOD in SAS (SAS Institute, 2003). Probabilities of test statistics were adjusted for the number of species being compared using the sequential Bonferroni technique (Rice, 1989) to reduce the likelihood of falsely rejecting the null hypothesis (Type I error).

Hiding behaviour of reef worms was examined over a randomly selected period. Hiding behaviour of 10 individuals was observed for 24 h from 09.06 GMT on 17 August 2003. The position of the branchial crowns on the reef is shown in Fig. 2. The length of each hiding event was taken as the time from the onset of hiding to full re-emergence of the crown. Where there was an obvious cue for a hiding event, such as a crab walking across the reef, this was also noted. As well as retracting when under threat, the reef worms showed a very distinctive "turning" behaviour when a worm rotates in its tube. The worm raises slightly out of the tube, rotates up to 180° in one direction then the other, before settling back into its tube. Turning behaviour of 10 worms was examined over the same 24-h period.

3. Results

3.1. Hiding and turning behaviour of *Serpula vermicularis*

The worms were extended almost continuously over the 24-h period. A total of 314 hiding events were observed for all 10 individuals (Fig. 3). Hiding time was very variable ranging between 3 and 1301 s with a mean of 21 s. Total time retracted for each individual over the

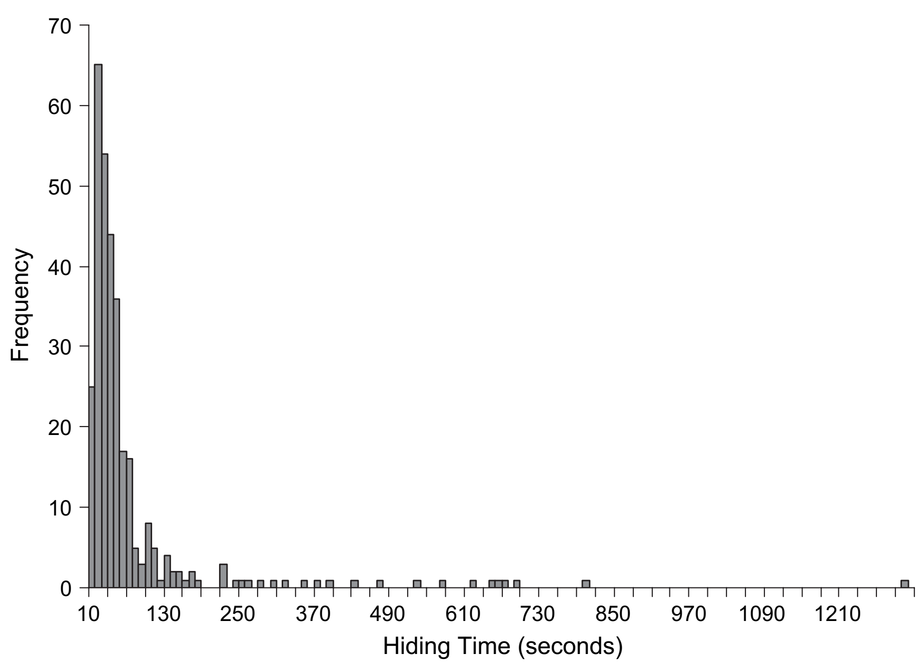

Fig. 3. Frequency histogram of length of hiding by *Serpula vermicularis* in Loch Creran. Pooled observations of 10 individuals from a single reef over 24 h.

24-h period was less than 1 h. There was no tidal or diurnal pattern in hiding.

The majority of hiding events were triggered by close proximity of fishes, mostly wrasses and *Pholis gunnellus*. The average length of time a worm spent retracted was less than a minute when the cause was a wrasse (29 s), cod (33 s) or if there was no discernable cause (23 s) and around 1 min if triggered by *P. gunnellus* (63 s) or a crab (70 s). Generally, the longest hiding events were triggered by gobies (96 s; Fig. 4). A one-way ANOVA of natural-log transformed data indicated that the differences between groups were statistically significant ($P < 0.001$). Post hoc analysis (Fisher's least significant difference test) indicated that hiding events triggered by cod, wrasses and unidentified causes were significantly less than those triggered by gobies, *P. gunnellus* and crabs at $P < 0.05$.

The worms were very sensitive to sudden drops in light levels as was noted using a 30 W white light which was integral with the colour UW TV (switched off during the study). Switching the light on produced no response in the worm colony but when the light was turned off, all worms within the camera view retracted immediately. This was tried at different times of the day and night and the response was always the same. However, turning off the infrared lights did not invoke a response.

The number of turns recorded for individual worms in 24 h varied between individuals with worm 4 being the most active (15 turns) and worm 9 the least (3 turns). The 24-h period was split into 15-min intervals and intervals scored with a 1 if a turning event occurred or a 0 if no turn was made. No more than one turn was made within a 15-min time period by any individual. If the probability of an individual performing a turn in any period is independent of the probability of turning in previous periods, the expected distribution would be exponential (Haccou and Meelis, 1992). A log survivor plot of intervals between turning events was used to detect deviations from exponentiality. The plot is initially horizontal, indicating a time-lag between turns (Fig. 5; Haccou and Meelis, 1992). There is a minimum duration of 45 min between sequential turns. The remainder of the plot (longer than 45 min) is approximately linear thus following an exponential distribution.

Ninety-seven turns were recorded in 970 15-min observation periods giving a probability of 0.1 that a turn occurs in any observation period. A cumulative binomial distribution function was fitted to the data to calculate expected frequency distribution of turns in 15-min periods if turning by different worms was independent. A chi-squared test indicated this was not the case ($P < 0.001$).

3.2. Frequency of predation events

There was little evidence of predation on the reef worms. Only one incident of an attempted predation event by *Necora puber* was observed when the crab 'tested' a number of worm tubes before snipping the top off one. Crabs manipulate potential prey with their chelae before accepting or rejecting them (Elner and Hughes, 1978). It was undetermined whether the crab managed to extract the worm due to its orientation to the camera. Wrasses were seen frequently to make 'darting' movements or lunges at the reefs. It is unlikely these were predation events on the worms themselves. The worms responded rapidly and were fully retracted before the wrasse reached them. The lunges appeared to be aimed further down the outside of the tubes, possibly at epifauna. Twice wrasses were seen extracting, and

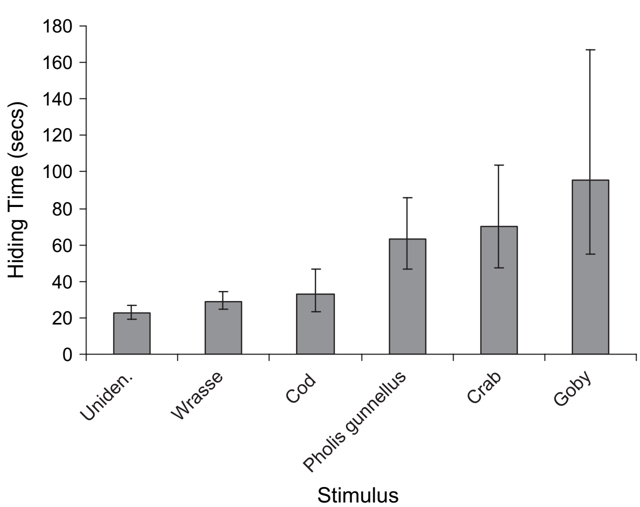

Fig. 4. Mean hiding time (s) observed for *Serpula vermicularis* in Loch Creran when triggered by mobile fauna (uniden. = stimulus undetermined). Pooled observations of 10 individuals from a single reef over 24 h. 95% confidence intervals shown.

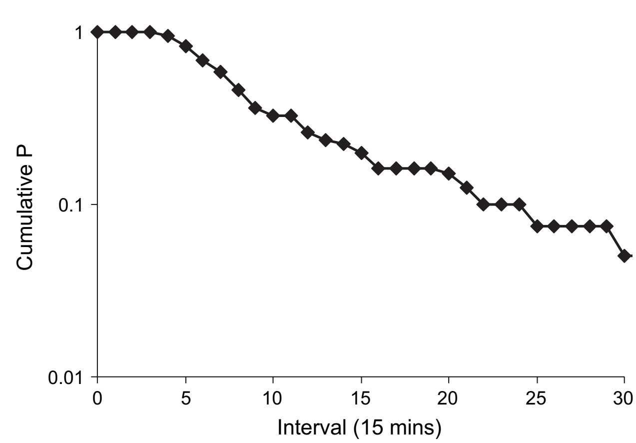

Fig. 5. Log survivorship curve for the turning behaviour of *Serpula vermicularis* in Loch Creran in 15-min intervals. Pooled observations of 10 individuals from a single reef over 24 h.

eventually swallowing, free-living polychaetes from among the worm tubes. Gobies occasionally made high-speed lunges which appeared to be aimed at the serpulid branchial crowns. The worms always re-emerged after such attacks but these may have been sub-lethal cropping events.

3.3. Presence and activity of mobile fauna

A list of all observed mobile fauna, from both cameras combined, is given in Table 1 together with the total number of 10-min time periods in which they were observed. Cod were either seen as individuals or as large shoals; these were recorded separately. Individual cod may have temporarily been separated from a nearby shoal which was outside the camera field of view. The reefs also provided substrata for sessile and sedentary fauna such as *Ophiothrix fragilis*, and ascidians, crinoids and sponges but these were not identified from the videos.

The most commonly observed fish were wrasse, gobies, cod and *Pholis gunnellus*. Wrasse species recorded were *Labrus bergylta*, *Centrolabrus exoletus*, *Ctenolabrus rupestris*, and *Crenilabrus melops* which are frequent species in coastal waters on the west coast of Scotland (Treasurer, 1994). Identification to species depended on orientation to the camera and so was not always possible. Wrasse and cod tended to swim around and through reefs while gobies frequently rested on worm tubes. *Pholis gunnellus* were seen moving within the reefs, winding through the worm tubes, and occasionally swimming between reefs. Of the crustacea, *Galathea squamifera*, *Necora puber* and *Pagurus bernhardus* were the most numerous.

Tidal state had little influence on the presence of mobile fauna at the reefs (Tables 2 and 3). However, significant associations ($P < 0.10$) with the time of day were found in the day-only data set for the presence of cod, wrasse, gobies and the activity of *Pholis gunnellus* within the reefs (Table 2). Cod, wrasse and *P. gunnellus* were more likely to be present at dawn and dusk than around midday or midnight (Fig. 6). These fishes also appeared in greater numbers at dawn and dusk, with cod tending to be in shoals and groups of wrasse swimming rapidly around and through the reefs. Analysis of the 24-h data set further indicated that wrasse and cod were more likely to be present during the day than the night ($P < 0.05$; Table 3). *Pholis gunnellus* were seen no more often by day than by night ($P < 0.05$). They were most active just before and after dawn and dusk, while wrasse and cod were most likely to be seen just after sunrise and before sunset (Fig. 7). Gobies were only observed during daylight (Table 3), in particular around midday (Fig. 6; Table 2).

Table 1
Mobile fauna recorded by underwater television on and around *Serpula vermicularis* reefs at approximately 10 m depth in Loch Creran, Scotland

Species	Common name	Obs
Osteichthyes		
Pomatoschistus sp.	Gobies	224
Gadus morhua	Total cod	148
	Individuals	86
	Shoals	62
Myoxocephalus scorpius	Bull rout	2
Pholis gunnellus	Butterfish	159
	Wrasse	304
Labrus bergylta	Ballan	
Ctenolabrus rupestris	Goldsinny	
Centrolabrus exoletus	Rock cook	
Crenilabrus melops	Corkwing	
Lepadogaster candollei	Connemara clingfish	23
Clupea harengus	Herring shoal	3
Spinachia spinachia	Fifteen spined stickleback	2
Cyclopterus lumpus	Lumpsucker	1
Lipophrys pholis	Shanny	9
Zeugopterus punctatus	Topknot	1
Syngnathus acus	Greater pipefish	1
Chondrichthyes		
Squalus acanthias	Spurdog	1
Crustacea		
Liocarcinus depurator	Harbour crab	22
Galathea squamifera	Black squat lobster	406
Munida rugosa	Long-claw squat lobster	111
Necora puber	Velvet swimming crab	198
Cancer pagurus	Edible crab	6
Pagurus bernhardus	Hermit crab	167
Palaemon serratus	Shrimp	11
Carcinus maenas	Shore crab	2
Macropodia tenuirostris	Spider crab	39
Echinodermata		
Asterias rubens	Common starfish	73
Psammechinus miliaris	Green sea urchin	2
Mollusca		
Archidoris pseudoargus	Sea lemon	7
Cnidaria		
Aurelia aurita	Moon jelly	7
Annelida		
–	Unidentified polychaete	1
Aves		
Phalacrocorax aristotelis	Shag	1

First 10 min of each half hour of daylight from 19 July to 13 August 2003 inclusive and first 10 min of each hour (day and night) from 14 August to 28 August inclusive were analysed. Observations correspond to the number of 10-min periods, of a total of 1146, during which a particular fauna was recorded.

4. Discussion

4.1. Hiding and turning behaviour of *Serpula vermicularis*

Hiding times varied between a few seconds and over 21 min in length. The strength of the stimuli appeared to influence hiding times, with stronger stimuli inducing

Table 2
Summary of effects shown by statistical significance and sign of parameter estimates in maximum likelihood model fitting (SAS: PROC CATMOD) for mobile fauna observed by colour underwater television during daylight only on *Serpula vermicularis* reefs in Loch Creran

Species	Cosday midday vs dusk/dawn	Sinday am vs pm	Costide LW vs HW	Sintide ebb vs flood	*n*
Gobies	++	ns	ns	ns	166
Gadus morhua					
Individual	(−)	ns	ns	ns	53
Total	−−	ns	ns	ns	101
Shoal	(−)	ns	ns	ns	50
Pholis gunnellus	−−	ns	ns	ns	121
Wrasse	(−)	ns	ns	ns	223
Lepadogaster candollei	ns	ns	ns	ns	23
Clupea harengus	ns	ns	ns	ns	3
Lipophrys pholis	ns	ns	ns	ns	8
Liocarcinus depurator	ns	ns	ns	ns	22
Galathea squamifera	ns	(+)	ns	ns	361
Munida rugosa	ns	ns	ns	ns	111
Necora puber	ns	ns	ns	ns	149
Cancer pagurus	ns	ns	ns	ns	6
Pagurus bernhardus	ns	ns	ns	ns	166
Palaemon serratus	ns	ns	ns	ns	3
Carcinus maenas	ns	ns	ns	ns	2
Asterias rubens	ns	ns	ns	ns	53
Archidoris pseudoargus	ns	ns	ns	ns	7
Aurelia aurita	ns	ns	ns	ns	7

Analysis of first 10 min of each 30 min of video footage recorded over four weeks from 17 July 2003. Probabilities were adjusted for the number of species compared (20) using the sequential Bonferroni procedure, ns = $P > 0.10$, (+)/(−) = $0.05 < P < 0.10$, +/− = $0.01 < P < 0.05$, ++/−− = $0.001 < P < 0.01$, +++/−−− = $P < 0.001$. If sign = + then species more likely to be present at midday, am (before midday), at low water or on an ebb tide for cosday, sinday, costide and sintide respectively. If sign = − then fauna more likely to be present at dusk/dawn, pm (after midday), at high water or on a flood tide for cosday, sinday, costide and sintide, respectively.

longer hiding times. Contact with the branchial crown (gobies) produced the longest hiding times although gobies also tended to rest on tube apertures so inhibiting re-emergence of the worm. Movement of crabs and *Pholis gunnellus* over and through the reefs would mechanically agitate tubes as well as producing intense pressure waves in the water. These also induced long hiding times. The shortest hiding events were produced by *Gadus morhua* and wrasse swimming past the reefs. The worms were probably reacting to a drop in light levels, as observed by switching off artificial white light, or light pressure waves in the water.

Table 3
Summary of effects shown by statistical significance and sign of parameter estimates in maximum likelihood model fitting (SAS: PROC CATMOD) for mobile fauna observed by black and white underwater television with infra red lighting on *Serpula vermicularis* reefs in Loch Creran

Species	cosday dusk vs dawn	sinday day vs night	cos2day midday/midnight vs dawn/dusk	sin2day am day/pm night vs pm day am night	costide LW vs HW	sintide ebb vs flood	*n*
Gobies	ns	+	ns	ns	ns	ns	58
Gadus morhua							
Individual	ns	(+)	(−)	ns	ns	ns	33
Total	ns	+	−	ns	ns	ns	44
Pholis gunnellus	ns	ns	−−−	ns	ns	ns	38
Wrasse	ns	+++	−−−	ns	ns	ns	81
Galathea squamifera	ns	ns	ns	ns	ns	ns	45
Necora puber	ns	ns	ns	ns	ns	ns	49
Asteria rubens	ns	ns	ns	ns	ns	ns	20
Macropodia tenuirostris	ns	ns	ns	ns	ns	ns	39

Analysis of first 10 min of each hour of video footage recorded over two weeks from 14 August 2003. Probabilities were adjusted for the number of species compared (9) using the sequential Bonferroni procedure, ns = $P > 0.10$, (+)/(−) = $0.05 < P < 0.10$, +/− = $0.01 < P < 0.05$, ++/−− = $0.001 < P < 0.01$, +++/−−− = $P < 0.001$. n = number of observations. If sign = + then species more likely to be present at dusk, during daylight, at midday and midnight, during the early part of the day and night, at low water or on an ebb tide for cosday, sinday, cos2day, sin2day, costide and sintide, respectively. If sign = − then fauna more likely to be present at dawn, during dark, at dawn/dusk, during the late part of the day and night, at high water or on a flood tide for cosday, sinday, cos2day, sin2day, costide and sintide, respectively.

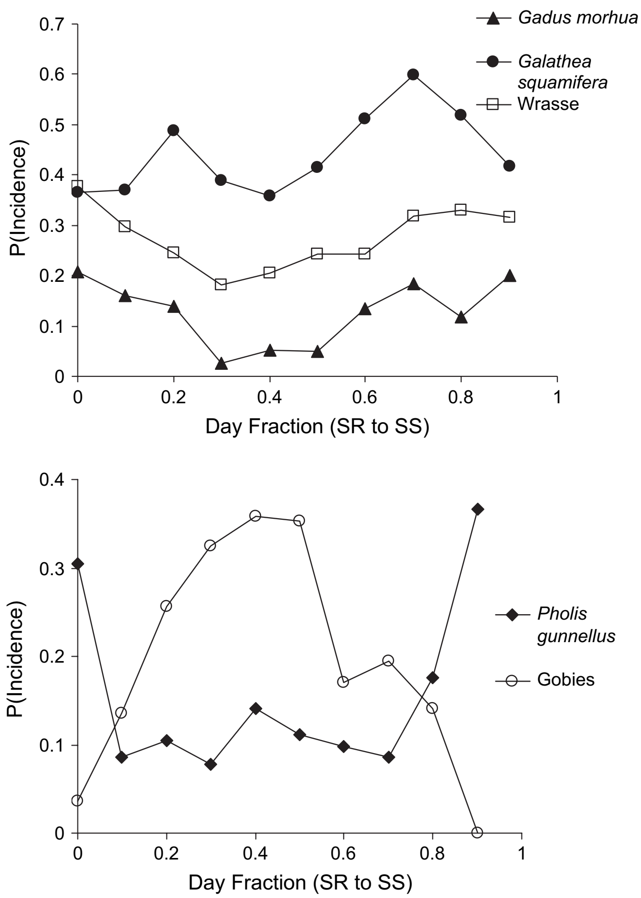

Fig. 6. Probability of observing mobile fauna on and around *Serpula vermicularis* reefs in Loch Creran at fractions of the day between sunrise (SR) and sunset (SS). Results of analysis of the first 10 min of each 30 min of video footage recorded during daylight by a colour underwater television over four weeks from 17 July 2003.

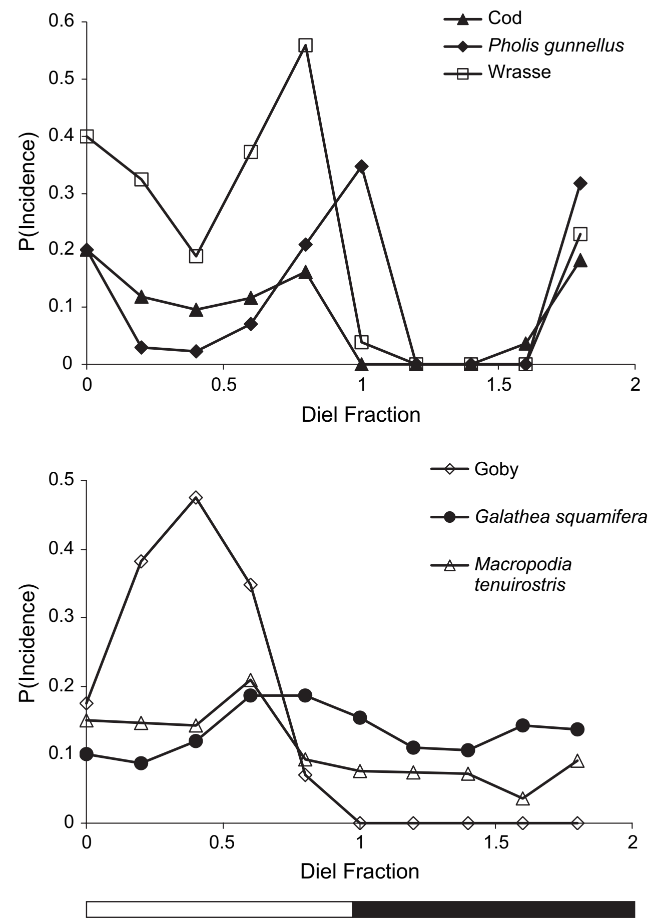

Fig. 7. Probability of observing mobile fauna at *Serpula vermicularis* reefs in Loch Creran at fractions of the diel cycle. 0 refers to sunrise, 1 is sunset and 2 is sunrise the following day, bottom bar indicates day and night period. Results of analysis of the first 10 min of each hour of video footage recorded by a black and white underwater television, with infrared lighting at night, over two weeks from 14 August 2003.

Length of hiding time was highly variable among individuals and type of stimulus. Hiding time can be considered as a trade-off between feeding and risk of predation (Dill and Fraser, 1997). Food availability for sessile suspension feeders can be highly patchy over time (Dill and Fraser, 1997). When food availability is high the cost of continued hiding, in terms of lost feeding opportunity, will be relatively high. The best strategy may be to shorten hiding time and resume feeding. Experiments with non-reef serpulids have shown that when food availability is high, hiding times are reduced (Dill and Fraser, 1997). Additionally, high variability in hiding time may also be an adaptive strategy to avoid predation (Hugie, 2003). If there is a single optimal hiding time for prey then predators could detect the regularity and choose a slightly longer waiting time for a high probability of capturing the prey.

Aggregated living carries some costs such as increased competition for resources. There are also a number of benefits to group living including increased anti-predator vigilance, dilution of predation risk and predator confusion (Krause and Ruxton, 2002). Group membership should reduce hiding time. In the temperate intertidal barnacle, *Semibalanus balanoides*, group-living barnacles were found to emerge from hiding more rapidly than solitary individuals (Mauck and Harkless, 2001). Re-emergence was not simultaneous within a group. If group-living individuals can detect when neighbours resume feeding, than the lowered predation risk will be communicated through the group. The natural variation in re-emergence behaviour will lead to at least one individual in a group resuming feeding relatively quickly. These factors should result in shorten hiding times in reef-building *Serpula vermicularis* than in solitary individuals but further experiments are required.

The position of the branchial crown on the reef itself may confer some feeding advantage if an individual is elevated above its neighbours. Reef-forming *Serpula vermicularis* shows a change in growth form switching from an initial encrusting stage to growing upwards, away from the substrata (Bosence, 1979). There is a lack of suitable hard substrate for larval settlement in Loch

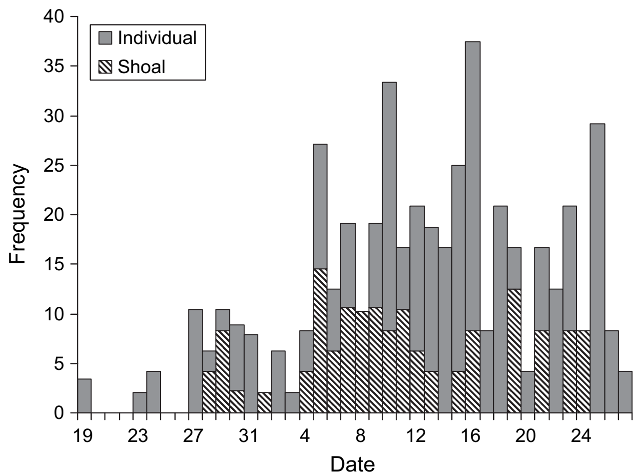

Fig. 8. Probability of observing *Gadus morhua* individuals and shoals at *Serpula vermicularis* reefs in Loch Creran from 19 July 2003 to 27 August 2003. Data from the first four weeks from analysis of the first 10 min of each 30 min of video footage recorded during daylight by a colour underwater television. Data from the last two weeks from the first 10 min of each hour of video footage recorded by a black and white underwater television with infrared lighting at night.

Creran. Morphological modifications in response to high competition for space are seen in other sessile fauna such as the barnacle *Semibalanus balanoides*. At high densities *S. balanoides* forms hummocks, individuals grow long and elongated away from the substrate (Barnes and Powell, 1950; Bertness et al., 1998). Individuals at the high points of the hummocks have greater food acquisition success and faster growth rates than individuals in a trough or solitary individuals (Bertness et al., 1998). Individuals within hummocks are provided with some structural support by their neighbours so reducing skeletal support costs and enabling more resources into somatic growth and reproduction.

A serpulid reef is a complex three-dimensional structure so height on the reef may not be a good indicator of optimal positioning for food acquisition. As reefs develop, the aggregations themselves provide further substrata for larval settlement (Bosence, 1979). Position relative to neighbouring crowns may be a better indicator of optimal positioning. An individual that is overshadowed by other individuals may have a lower rate of particle capture. Positioning of tube apertures in *Serpula vermicularis* reefs shows an even spacing of 10–15 mm to nearest neighbour apertures (Bosence, 1979). Worms are growing to positions where the expanded branchial crowns will not overlap or interfere. High competition for space and suspension feeding sites is likely to be a major factor driving the development of *S. vermicularis* reefs.

The function of turning behaviour, marked by rotation of the branchial crown, remains obscure. This may be related to laying down tube matrix which is secreted by gland cells on the membranous collar behind the branchial crown (Hedley, 1956). A degree of synchronisation of turning amongst groups of worms suggests a response to some external cue. Without a diurnal or tidal pattern in turning this suggests that cues may be associated with a more transient event such as a lowered predation threat or excessive sedimentation prompting some cleaning response.

4.2. Associated fauna and predation frequency

Using UW TV successfully allowed long-term observations of *Serpula vermicularis* reefs and associated fauna. In general, the reefs appear to attract a rich diversity of mobile fauna which use the reefs as a refuge, a feeding ground and/or a habitat. An exceptional sighting was a European shag, *Phalacrocorax aristotelis*, swimming rapidly, probably in pursuit of the numerous fish found around the reefs. This seabird is known to dive to depths up to 40 m (Wanless et al., 1993, 1999) and is a year-round resident on the west coast of Scotland.

The appearance of juvenile cod shoals at dawn and dusk is suggestive of a nightly migration. Juvenile cod are known to use inshore coastal waters as nursery areas and many of the sandy beaches and sea lochs on the west coast of Scotland provide such areas (Burrows et al., 1994; Gibson et al., 1996, 1998). Periodicity in diurnal foraging and activity patterns are among antipredation behaviours and/or optimal foraging behaviours exhibited by shallow water fish and other marine animals (Burrows, 1994; Burrows et al, 1994; Gibson et al., 1996, 1998). Observations with subtidal UW TV (<1 m below low water) during summer on the west coast of Scotland, observed peak numbers of gadoids just before sunrise and just after sunset with more activity at night than during the day (Burrows et al., 1994). The young gadoids were migrating onshore at night. Juvenile cod appear in shallow coastal waters around Scotland in the summer months (Magill and Sayer, 2002). The increase in the frequency of cod after the end of July may reflect this influx (Fig. 8). The drop in cod shoals apparent after 13 August was probably the result of changing the camera system to one with a narrower field of view.

Minchin (1987), using SCUBA equipment, observed predation on *Serpula vermicularis* worms in Ardbear Lough by *Cancer pagurus* and *Carcinus maenas*. Bosence (1979), using SCUBA, also observed adult *C. pagurus* on reefs in Ardbear Lough but saw no predation. He suggested that the crabs may be using the reef solely as a refuge. This appears to be the case in Loch Creran, where both *C. pagurus* and *Necora puber* were frequently observed backing into the reefs and remaining there for long periods. Once the crabs stop moving, the worms re-emerge providing very effective cover for the crab. Bosence (1979) also describes *Ctenolabrus rupestris* and

Crenilabrus melops biting open serpulid tubes and extracting worms. Although these wrasse species were common in Loch Creran, there was little evidence of the fish feeding on *S. vermicularis*.

Sea urchins, *Echinus esculentus* and *Psammechinus miliaris* are considered a major threat to serpulid reef worms (Bosence, 1979). It is unlikely that the sea urchins feed directly on the worms but rather feed indiscriminately on the tube for the sake of its epifauna and flora, destroying the tubes in the process (Bosence, 1979). This may damage the worm itself or leave the worms vulnerable to attack from predators if the tube is damaged. Few sea urchins were viewed in the video footage but urchins may have been inconspicuous, moving inside the reef structure. Loch Creran is known to support a large population of *P. miliaris* (Otero-Villanueva, pers. comm.) and is commonly observed by SCUBA divers in the reefs (pers. obs.).

The complex structure afforded by the *Serpula vermicularis* reefs supports a rich diversity of associated fauna and flora. Habitat diversity promotes species diversity and the complexity of carbonate bioconstructions promotes biological diversity (Cocito, 2004). Fish such as *Ctenolabrus rupestris* were common around the serpulid reefs. Generally, this species is only observed on or near habitats such as rocks and reefs that provide refuges (Sayer et al., 1993). Underwater television has proved a useful tool to assess the diversity and activity of the larger, mobile fauna around the reefs as well as the behaviour of the reef worms themselves.

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