

Differences between epilithic and epizoic hydroid assemblages from commercial scallop grounds in the Bay of Fundy, northwest Atlantic

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ABSTRACT: Hydroid assemblages from the shells of 104 live scallops *Placopecten magellanicus* and 136 cobbles were sampled from 39 sites on heavily dredged commercial scallop grounds in the Bay of Fundy, northwest Atlantic. The scallop shells were considered pseudo-controls, representing undisturbed 'island habitats' naturally interspersed amongst the cobbles. Cobbles were expected to represent disturbed habitat. Samples yielded 51 taxa from 24 genera across substrata. The number of taxa was significantly lower on cobbles. Multidimensional scaling plots and statistical analyses on presence-absence data discriminated 2 divergent assemblages consistent with substratum. Cobble assemblages were characterized by *Campanularia volubilis*, *Clytia hemisphaerica* and *Clytia* sp., while those on the live scallop shells were characterized by the small auto-epizoite *Calycella syringa* and its hosts *Sertularia cupressina* and *Obelia dichotoma*. Species discriminating between the substrata are considered substrate generalists. Fishing effort was introduced as a factor in an analysis of similarity and accounted for a significant proportion of the variance within and between substrata, with larger R^2 values associated with the cobble assemblages, as expected. Runner-like forms with small, unbranched colonies and medusa life stages were more frequently found on cobbles than on live scallop shells. Assemblage and life history divergence associated with fishing effort, widespread substrate generalism amongst the principle taxa, and observations from other studies suggest that these observed differences could be related to chronic disturbance of cobbles caused by fishing.

KEY WORDS: Hydroids · Scallop dredging · Epizoic · Epilithic · Disturbance · Life histories · Bay of Fundy

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INTRODUCTION

Fishing gear that contacts the sea floor has the potential to damage or remove fragile, emergent epifauna, and over time may shift benthic communities from a high diversity and low abundance state to one of low diversity and high abundance (Veale et al. 2000). With repeated disturbance, taxon composition changes from assemblages dominated by large rigid colonies to those with more flexible runner-like ('guerilla' growth type strategists sensu Lovett Doust 1981) or encrusting growth forms (Gili et al. 1987, Collie et al. 2000, Hutchings 1990, Pitcher et al. 2000, Bradshaw et al. 2001, 2002). The vulnerability of

sponges and other colonial epifauna, e.g. many cnidarians, hydroids, bryozoans and tunicates, to fishing disturbance is a particularly important issue to address (Hutchings 1990, Kaiser et al. 1999, Collie et al. 2000) as these animals provide biogenic habitat for juvenile and demersal fish and shellfish (Bradstock & Gordon 1983, Auster et al. 1996, Kaiser et al. 1998, Stevens 2003, Stoner & Titgen 2003).

Benthic hydrozoans ('hydroids') are frequently encountered in the Bay of Fundy (Fuller et al. 1998, Magee et al. 1999, 2000) and have historically clogged dredge nets (Caddy 1970). Hydroids colonize a variety of substrata in this region, e.g. sea scallop and mussel shells, rocky substrata, macroalgae and wharves

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(Fraser 1944, Caddy 1970, Logan 1988, Fuller et al. 1998, Magee et al. 1999, 2000; Fig. 1). They exhibit broad life-history diversity, ranging from large, slow-growing, arborescent forms to those with fast growth and small stolonial colonies. Approximately half of the species produce free medusae, while the rest liberate less motile planulae (Cornelius 1981). These characteristics make hydroids good model organisms to study the impacts of fishing on the life history and ecology of colonial epifauna.

The objective of this study was to examine hydroid assemblage structure in a region exposed to long-term chronic bottom fishing. The study was conducted in the Bay of Fundy (northwest Atlantic) on heavily fished scallop grounds near Digby, Nova Scotia (Fig. 2) where sea scallops *Placopecten magellanicus* (Gmelin, 1791) have been commercially fished with dredges for about a century. Due to the absence of permanently closed areas in the Bay of Fundy, we chose to explore the use of living substrata as pseudo-controls for fishing disturbance, as these scallops represent naturally replicated 'island habitats' (Schoener 1974) that can be examined over different spatial and temporal scales (Ward & Thorpe 1991, Berkman 1994).

Older surviving bivalves (Fig. 1) may provide relatively unharmed epifaunal refuges from dredging, and are naturally interspersed with other substrata, which facilitates attributing assemblage divergence to fishing impacts rather than spatial habitat differences. Scallops that are not captured are unlikely to have much contact with bottom gear. Small scallops (<100 mm

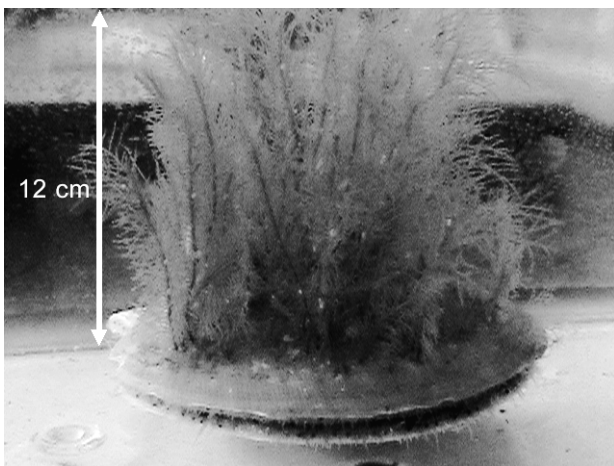


Fig. 1. Dense hydroid growth observed on a live sea scallop *Placopecten magellanicus* from commercial scallop grounds in the Bay of Fundy

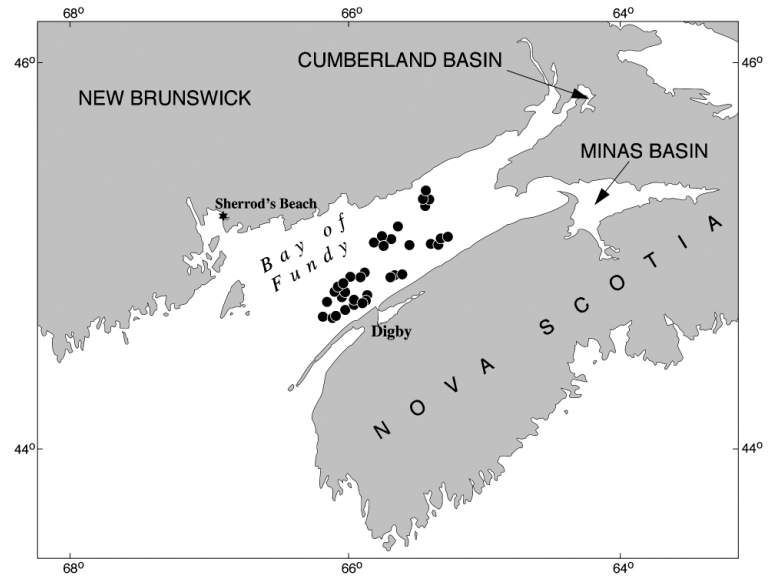


Fig. 2. Dredge survey sites of hydroids from the Bay of Fundy in June 2000. Each dot represents 1 tow sample (of 39). Location of field experiment at Sherrod's Beach indicated by asterisk

shell height) are active swimmers and may avoid the gear or be pushed away by its pressure wave. Larger individuals are able to recess in softer substrates, avoiding capture, while those caught and returned (due to size restrictions) or damaged *in situ* can be distinguished by shock marks on the shell (Caddy 1968, 1973). Cobbles may experience abrasion, impact, displacement, burying, or processing on board vessels before being discarded (Caddy 1973, Robinson et al. 2001). Thus, of the 2 substrates, the surviving older scallops (epizoic substrata) are expected to experience less disturbance due to fishing than cobbles (epilithic substrata).

The use of live scallops as pseudo-controls may introduce potentially confounding effects of microhabitat differences (e.g. the presence of bacterial films or mineralogy) which may influence hydroid settlement and assemblage succession (Nishihira 1973, Orlov 1996a,b, Bavestrello et al. 2000a). *In situ* colonization experiments were undertaken to determine the degree to which microhabitat differences influence epifaunal taxon composition in this region.

Taxonomic difficulties associated with hydroid identification have led to organisms being grouped into coarse taxonomic units when reporting in benthic surveys (e.g. Kenchington et al. 2001). This masks natural biogeographic variation between species (Warwick 1988, Smith & Simpson 1993) and could facilitate demonstrating impacts of bottom fishing (e.g. Coggan et al. 2001). Recording taxonomic data to coarser levels can result in a loss of information, particularly when

data transformations are used in community analyses (Olsgard et al. 1997, Chapman 1998). Thus, as a second objective, we used our data set to evaluate the practical utility of using coarser taxonomic information versus species-level information.

MATERIALS AND METHODS

Field methods for surveying hydroid assemblages.

Sampling was performed on board the CCGC 'J. L. Hart' in June 2000 during an annual inshore Bay of Fundy scallop survey with the Canadian Department of Fisheries and Oceans. Tow locations were pre-determined following a stratified random design used for the scallop assessments (cf. Smith & Lundy 2002). Stations were located using a global positioning system. In total, 39 tows were made (Fig. 2) with a swath of 4 m width and approximately 800 m length (ca. 8 min duration), and individual tows were maintained on approximately the same bottom-type (M. Lundy, Department of Fisheries and Oceans, Dartmouth, pers. comm.). Four-gang dredges, with 2 of the buckets lined with 38 mm polypropylene stretch mesh netting to sample smaller scallops, were used in the tows to sample the scallops and cobbles.

In total, 240 substrata (104 legal-size live scallops i.e. ≥ 95 mm shell height, and 136 cobbles, approximately 71 cm² upper surface area) were collected between 38 and 108 m water depth (Fig. 2). The naturally interspersed distribution of live scallops and cobbles permitted both substrata to be collected from each tow in most cases. Between 2 and 5 of each substrate type were randomly sampled from the scallop dredges. Only cobbles with approximately the same upper surface area as that of the minimum legal size of scallops were collected and careful attention was made to collect only scallops in pristine condition e.g. those with unchipped shells or growth anomalies, the presence of which could reflect past damage by gear. Each substrate collected had to be colonized by at least one hydroid colony, a condition that was easily met as most hard substrata collected in these tows were colonized by hydroids.

Cobbles and scallops were placed in open plastic bags and kept in an open tank with a steady supply of seawater while on board, then frozen at -72°C upon return to the laboratory. The presence or absence of all hydroids was determined to the lowest possible taxonomic level using a Nikon SMZ 1500 dissecting microscope. Only hydroids with intact hydranths and/or stems were included in the analyses.

Statistical analyses of hydroid assemblages. Assuming that many hydroid taxa in the collections would be very small, uncommon, and difficult to physically separate from their substrata, taxon biomass estimates were considered to be too inaccurate for assemblage analyses. Thus, all analyses were performed simply on presence and absence data.

The number of taxa was estimated as the number of distinct taxa per substratum. The mean number of taxa (μ_s) was compared between substrata with an unpaired 2-tailed *t*-test assuming equal or unequal variances as determined by Levene's test ($p < 0.05$).

Differences in taxon composition were analysed using PRIMER v5 (Clarke & Gorley 2001). A similarity matrix of pairwise Sørensen indices was constructed from presence and absence data using the SIMILARITY procedure. Multidimensional scaling (MDS) and analysis of similarity percentages (ANOSIM) procedures were performed on the similarity matrix to determine whether the assemblages could be discriminated based on the 2 substrate types. Characteristic taxa of each assemblage and those that best discriminated between substrate types (i.e. those that explained up to 90% of the dissimilarity between assemblages) were identified using the similarity percentages (SIMPER) procedure.

Taxa were assigned *a priori* into categories of several 'biological attributes' (cf. Bremner et al. 2003): growth-type strategy (e.g. phalanx form = closely compacted colony, guerilla form = hydroid polyps or stems connected but spread further apart from each other), maximum colony height (base to furthest tip of colony), typical degree of branching (e.g. no branching = simple polyp or stem, branches once = primary branches appear on the main stem, branches twice = secondary branching appears from the primary branches, etc.) and the mode of sexual reproduction (Table 1), based on published reports and our present observations. The null hypothesis that hydroids on cobbles would possess the same frequencies of life-history traits in each category as those on scallops was tested using *G*-tests for goodness-of-fit for each life-history category

Table 1. Life history traits of colonial hydroids in relation to commitment to long-term colony survival (modified from Jackson 1979 to reflect biology of hydroids)

Increasing commitment to colony survival ↓	Growth type strategy	Maximum colony height (mm)	Degree of branching (branching order in parentheses)	Sexual reprod. mode
	Guerilla	<2	No branching (0)	Medusa
Mixed	2–50	Branches once (1°)	Sessile medusoid	
Phalanx	>50	Branches twice (2°) Branches 3 or more times ($\geq 3^{\circ}$)	Planula	

(Sokal & Rohlf 1995). Only taxa that discriminated up to 90 % of the SIMPER dissimilarity between substrata were included in these analyses.

MDS and ANOSIM analyses were repeated for data resolved to genera and families. The abilities of these data to discriminate between epizoic and epilithic assemblages were assessed by correlating similarity matrices in a pairwise manner (i.e. species-level with genus-level matrices, and species-level with family-level matrices) to estimate Spearman's rank coefficients using the RELATE procedure in PRIMER.

Fisheries data from the Department of Fisheries and Oceans, Canada (Marine Science Virtual Data Centre 2003; <http://mfdvdc.bio.dfo.ca>) were compiled to relate differences in hydroid assemblages to recent scallop fishing effort in the study area. Logged effort data for the previous 3.5 yr were aggregated into latitude and longitude (to the nearest 1/1000 min) in the data centre. These data were used to categorize each of the 39 study sites into 3 groups as evenly as possible: 0–75 h (14 sites), 75–150 h (13 sites), >150 h (12 sites) of scallop dredging. Separate ANOSIM analyses were done: (1) between substrata and (2) within substrata to examine whether taxon composition changed with increasing fishing effort.

Field manipulations of hydroid assemblages. Short-term hydroid colonization experiments were undertaken from July to October 2002 over the natural hydroid settlement period. Ten live scallops and 10 small cobbles devoid of epifauna were collected between 50 and 80 m depth near Digby in June 2002, scraped clean with a bristle brush, and kept in running seawater upon return to the laboratory.

Square plastic tabs with punched circular holes were epoxied onto the hinged ear of each live scallop. Each scallop was individually tethered by 30 cm-long string run through the tag, and tied to a building brick. Each brick and transplanted cobble substrate was marked with red acrylic paint to identify the upper surface in case cobbles became overturned. The substrata were transported to the experimental site at Sherrod's Beach (Fig. 2), a sheltered cove located in Passamaquoddy Bay, southwestern New Brunswick in July 2002. Substrata were deployed at 2 m depth below mean low water by snorkelling parallel to a straight stretch of beach at low tide. Substrata were haphazardly interspersed by drawing them from mesh dive bags and placing them at approximately 1 m intervals. Substrata were checked approximately every 3 wk for substrate turnover until October 2002 (cobbles were never observed on lower unmarked surfaces), at which point they were retrieved and placed in individual Ziploc™ bags and transported to the laboratory for taxonomic sorting. The effects of substrate type on taxon composition in

the absence of dredge disturbances were analysed using the SIMILARITY, MDS and ANOSIM procedures as described above.

RESULTS

Hydroid assemblage analyses

In total, 51 taxa from 24 genera were observed. Several specimens were degraded or not sexually mature, thus preventing their assignments to species level. In general, campanulariids, notably *Campanularia volubilis*, and the sertulariid *Sertularia cupressina* were the most frequently (>50 %) encountered hydroids from the scallop fishing grounds in the study region (Table 2)

The number of hydroid taxa per substratum ranged from 1 to 10 on live scallops and from 1 to 9 on cobbles. The mean number of taxa was significantly lower on cobble substrata ($\mu_s = 3.750$) than on live scallops ($\mu_s = 4.356$) according to the *t*-test ($t = 2.670$, $df = 192$, 2-sided $p = 0.006$). However, from an ecological point of view, this significance may not be meaningful, as each substratum had on average close to 4 taxa and the high number of replicates of each substrate type increased the chance of making a Type I error in this test.

The MDS ordination produced 2 somewhat divergent hydroid assemblages consistent with the epizoic (scallop) and epilithic (cobble) substrata (Fig. 3). Despite moderate convergence of shared taxa between the 2 assemblages (stress = 0.2), divergence was statistically significant at all taxonomic levels (ANOSIM global $R \geq 0.280$, $p < 0.05$). However, the correlation between species and coarser data similarity matrices declined from species to family levels, and a decline in discriminating ability with higher-level taxonomic information was evident (Fig. 3, Table 3).

Similarity within epizoic assemblages was explained primarily by the presence of 9 taxa, particularly *Calycella syringa*, *Obelia dichotoma* and *Sertularia cupressina* (Table 4). Similarity within epilithic communities was largely due to 8 taxa, especially the campanulariids *Campanularia volubilis*, *Clytia hemisphaerica* and *Clytia* sp. (the latter taxon possibly being the same species as *C. hemisphaerica* but several specimens of *Clytia* sp. could not be firmly identified to species (Table 4).

Average dissimilarity between epizoic and epilithic assemblages ($\delta = 87.33$) was mostly explained by 25 of the 51 taxa (Table 5). *Calycella syringa* was the principal discriminating species between the 2 communities, most commonly found on *Obelia dichotoma* and *Sertularia cupressina* (*a posteriori* Sørensen indices for association with *C. syringa* = 46.5 and 43.3, respectively).

The life-history traits of these 25 hydroid taxa (Table 5) are also significantly different between epizoic and

Table 2. List of all 51 hydroid taxa combined and ordered by their frequencies from 240 collections of cobbles and live scallops *Placopecten magellanicus* from the Bay of Fundy in June 2000

Species	Family	Overall frequency	Rank
<i>Campanularia volubilis</i> (Linnaeus, 1758)	Campanulariidae	0.987	1
<i>Clytia hemisphaerica</i> (Linnaeus, 1767)	Campanulariidae	0.699	2
<i>Clytia</i> sp.	Campanulariidae	0.697	3
<i>Obelia dichotoma</i> (Linnaeus, 1758)	Campanulariidae	0.665	4
<i>Calycella syringa</i> (Linnaeus, 1767)	Campanuliniidae	0.617	5
<i>Obelia geniculata</i> (Linnaeus, 1758)	Campanulariidae	0.604	6
<i>Sertularia cupressina</i> Linnaeus, 1758	Sertulariidae	0.586	7
<i>Rhizocaulus verticillatus</i> (Linnaeus, 1758)	Campanulariidae	0.482	8
Bougainvilliid (erect)	Bougainvillidae	0.435	9
<i>Bougainvillia</i> sp. (stolonial)	Bougainvillidae	0.400	10
<i>Obelia longissima</i> (Pallas, 1766)	Campanulariidae	0.365	11
<i>Halecium undulatum</i> Billard, 1922	Haleciidae	0.312	12
<i>Gonothyrea loveni</i> (Allman, 1859)	Campanulariidae	0.222	13
<i>Halecium sessile</i> Norman, 1867	Haleciidae	0.218	14
<i>Symplectoscyphus tricuspoidatus</i> (Alder, 1856)	Sertulariidae	0.217	15
<i>Abietinaria abietina</i> (Linnaeus, 1758)	Sertulariidae	0.190	16
<i>Sertularella polyzonias</i> (Linnaeus, 1758)	Sertulariidae	0.176	17
<i>Sertularia tenera</i> G.O. Sars, 1874	Sertulariidae	0.159	18
<i>Hydrallmania falcata</i> (Linnaeus, 1758)	Sertulariidae	0.149	19
<i>Diphasia fallax</i> (Johnston, 1847)	Sertulariidae	0.121	20
<i>Lafoea dumosa</i> (Fleming, 1820)	Lafoeidae	0.116	21
<i>Sertularia</i> sp.	Sertulariidae	0.104	22
<i>Diphasia margareta</i> (Hassall, 1841)	Sertulariidae	0.097	23
<i>Eudendrium ramosum</i> (Linnaeus, 1758)	Eudendriidae	0.095	24
<i>Filellum serpens</i> (Hassall, 1848)	Lafoeidae	0.086	25
<i>Bougainvillia superciliaris</i> (L. Agassiz, 1849)	Bougainvillidae	0.078	26
<i>Ectopleura crocea</i> (L. Agassiz, 1862)	Tubulariidae	0.076	27
<i>Eudendrium capillare</i> Alder, 1856	Eudendriidae	0.073	28
<i>Obelia</i> sp.	Campanulariidae	0.072	29
<i>Sertularia latiuscula</i> Stimpson, 1853	Sertulariidae	0.055	30
<i>Abietinaria filicula</i> (Ellis and Solander, 1786)	Sertulariidae	0.054	31
<i>Sertularia fabricii</i> Levinsen, 1893	Sertulariidae	0.045	32
<i>Diphasia</i> sp.	Sertulariidae	0.042	33
<i>Grammaria borealis</i> (Levinsen, 1893)	Lafoeidae	0.034	34
<i>Halecium</i> sp.	Haleciidae	0.034	34
<i>Sertularia similis</i> Clark, 1877	Sertulariidae	0.031	36
<i>Halecium muricatum</i> (Ellis and Solander, 1786)	Haleciidae	0.027	37
<i>Lafoea fruticosa</i> M. Sars, 1851	Lafoeidae	0.027	37
<i>Grammaria abietina</i> (M. Sars, 1850)	Lafoeidae	0.024	39
Campanulariid	Campanulariidae	0.021	40
<i>Halecium corrugatum</i> Nutting, 1899	Haleciidae	0.021	40
<i>Thuiaria</i> sp.	Sertulariidae	0.021	40
<i>Bougainvillia</i> sp. (erect)	Bougainvillidae	0.014	43
<i>Keratosum maximum</i> (Levinsen, 1893)	Incertae Sedis	0.014	43
<i>Nemertesia americana</i> (Nutting, 1900)	Plumulariidae	0.014	43
<i>Sarsia tubulosa</i> (M. Sars, 1835)	Corynidae	0.014	43
<i>Cuspidella</i> sp.	Campanuliniidae	0.010	47
<i>Diphasia rosacea</i> (Linnaeus, 1758)	Sertulariidae	0.010	47
<i>Eudendrium</i> sp.	Eudendriidae	0.010	47
<i>Halecium labrosum</i> Alder, 1859	Haleciidae	0.010	47
<i>Thuiaria articulata</i> (Pallas, 1766)	Sertulariidae	0.010	47

epilithic assemblages across all life-history categories (Table 6). Taxa on cobbles were characterized by low-lying runner-like growth forms and mixed growth forms. These taxa tended to be smaller with less branching, and possessed medusa life stages (Table 6). Hydroid taxa on scallops were more typically erect tree-shaped phalanx growth forms, with larger and more heavily branched colonies and planula larvae life stages (Table 6).

There was evidence of increasing divergence between the taxon composition of epilithic and epizoic hydroid assemblages when sites were categorized into levels of recent fishing effort. Sites with the highest fishing effort showed the greatest hydroid assemblage divergence between cobbles and scallops (Table 7) but sites with lower fishing effort also showed significant divergence between substrate types.

Field colonization experiments

Nineteen of the original 20 substrata were retrieved: 1 scallop had broken free of the tag and could not be re-located. Nine hydroid taxa were found on the transplanted substrata after 3 mo. Hydroids that colonized these substrata were dominated by tubulariids, bougainvilliids and campanulariids with rapid stolonal growth and short life-spans. Differences in taxon composition between epizotic and epilithic assemblages were not statistically significant (Global R = -0.099 ,

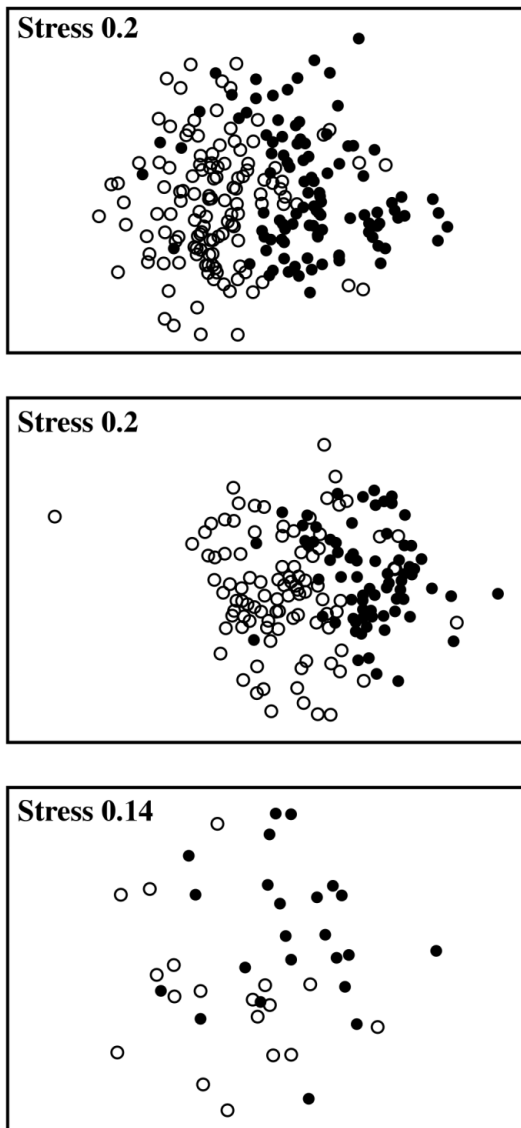


Fig. 3. Non-metric multidimensional (MDS) ordination of hydroid assemblages from scallop *Placopecten magellanicus* (●) and cobble (○) substrata using species- (top plot), genus- (middle plot) and family-level (bottom plot) data. Note that the apparent reduction in the number of samples in genus- and family-level analyses actually reflects overlapping of shared genera or families by taxa in MDS plots

$p = 0.948$) and 2 assemblages could not be distinguished with MDS (Fig. 4). All substrata were colonized by *Obelia longissima*, and both *Gonothyraea loveni* and *Opercularella lacerata* were approximately as frequent on live scallops as they were on cobbles (Table 8).

DISCUSSION

The lack of unfished reference areas necessitates finding alternative methods for examining biological impacts of bottom fishing e.g. using historical datasets (Frid et al. 1999, 2000, Rumohr & Kujawski 2000, Bradshaw et al. 2002) or establishing comparison sites near shipwrecks that impede bottom fishing (Ball et al. 2000). The use of live scallops as 'pseudo-controls' or 'island-habitats' is a novel way to include controls in studies that examine bottom-fishing impacts on certain types of organisms in areas with no closed or relatively unfished areas. This method may not apply to epifauna with lifespans or biomass greater than the scallop. For example, mollusc shells are not suitable as long-term substrata for scleractinian corals because mollusc hosts cannot grow fast enough to support continual growth of the corals that eventually topple the coral and its mollusc host (Yamamoto et al. 1998). Furthermore, commensalisms between hydroids and bivalves are highly reciprocal relationships. Juvenile bivalves use hydroids for spat attachment and protection from predators (Pulfrich 1996). Later, hydroids offer the host bivalve camouflage, defense from predators, parasites and injuries (Vance 1978, Piraino et al. 1994, Cerrano et al. 2000). Bivalve hosts, in turn, may provide hydroids with space for settlement and adult colonies receive water currents, nutrition, spatial refuges from predators and space to grow (Boero 1981, Kubota 1983, Piraino et al. 1994, Cerrano et al. 2000). Thus, hydroids may preferentially settle on scallop hosts rather than on inert substrata such as cobbles. Each of these alternate approaches using pseudo-controls brings with it assumptions that the substrata in question are equal and therefore valid for comparison.

Table 3. Contrasting abilities of the level of taxonomic resolution to detect differences in hydroid communities in the Bay of Fundy, using analysis of similarities (ANOSIM) and similarity of percentages (SIMPER) analyses. Correlations between pairs of taxonomic units are represented by Spearman's ρ . * $\alpha = 0.05$

Taxonomic level	ANOSIM Global R	Average SIMPER δ	Spearman's ρ Species Genus	
Species	0.34*	87.3	–	–
Genus	0.35*	73.9	0.64*	–
Family	0.28*	47.2	0.32*	0.43*

Table 4. Characteristic hydroid taxa of assemblages on live scallop *Placopecten magellanicus* shells and cobbles in the Bay of Fundy and contributions to mean similarity. Mean similarity within assemblages on live scallops = 24.2, mean similarity within communities on cobbles = 25.3

	Freq- uency	Contri- bution (%)	Cumula- tive contri- bution (%)
On live scallops (n = 104)			
<i>Calycella syringa</i>	0.59	28.2	28.2
<i>Obelia dichotoma</i>	0.42	20.4	48.6
<i>Sertularia cupressina</i>	0.36	11.7	60.3
<i>Rhizocaulus verticillatus</i>	0.33	9.1	69.4
<i>Obelia geniculata</i>	0.30	7.8	77.2
<i>Obelia longissima</i>	0.21	4.3	81.5
<i>Campanularia volubilis</i>	0.23	3.8	85.3
<i>Halecium sessile</i>	0.19	2.8	88.1
<i>Clytia</i> sp.	0.16	2.2	90.3
On cobbles (n = 136)			
<i>Campanularia volubilis</i>	0.55	30.2	30.2
<i>Clytia hemisphaerica</i>	0.43	18.9	49.1
<i>Clytia</i> sp.	0.39	16.3	65.4
Bougainvilliid (erect)	0.32	9.9	75.3
<i>Obelia geniculata</i>	0.23	4.9	80.3
<i>Bougainvillia</i> sp. (stolonial)	0.21	4.0	84.3
<i>Halecium undulatum</i>	0.20	3.9	88.1
<i>Obelia dichotoma</i>	0.16	2.9	91.0

The most striking difference between the substrata is in their respective surficial properties, which suggests that the substrata are not equal and therefore invalid for comparison. Scallop shells are composed of calcium carbonate with a detailed surface microstructure. In contrast, the cobbles in our study area were products of glacial till and vary in composition from sandstone through to granite, with a wide range in porosity and microstructure. However, despite well-documented obligate associations, the majority of hydroids are substrate generalists (Boero 1984, Calder 1991, Gili & Hughes 1995), including most of the taxa that discriminated between substrata in the present study; e.g. *Sertularia cupressina* (Schmidt & Warner 1991) and *Obelia dichotoma* (Cornelius 1995). *O. dichotoma* exhibits a wide tolerance of substrate host-type and has been found attached to both inert and living substrata, both sessile and mobile, including shark fins, turtles, sea horses and crustaceans (Cornelius 1995). Therefore it is unlikely that its predominance on scallop substrata reflects an affinity for scallop hosts over cobbles. Substrate generalism is further supported by our experimental evidence, which demonstrated a high similarity of hydroid assemblages (Table 8, Fig. 4)

Table 5. Hydroid taxa that can best discriminate between assemblages on cobbles versus live scallops *Placopecten magellanicus* in the Bay of Fundy (mean dissimilarity between assemblages on scallops and cobbles = 87.3). Life-history categories of hydroids determined *a priori* to differ between assemblages on the 2 substrata. Life-history traits were determined from the literature and observations made during the present study (for descriptions of each life-history category see Table 1). *: life-history trait was attributed based on specimens collected from the present study

Discriminating species	Frequency on live shells (n = 104)	Frequency on cobbles (n = 136)	Contribution dissimilarity (%)	Cumulative contribution (%)	Growth form	Maximum colony height (mm)	Typical branch order	Dispersive stage
<i>Calycella syringa</i>	0.59	0.01	7.9	7.9	Guerilla	<2	0	Planula
<i>Campanularia volubilis</i>	0.23	0.55	7.9	15.8	Guerilla	<2	0	Planula
<i>Obelia dichotoma</i>	0.42	0.16	7.2	23.0	Guerilla	>50	≥3°	Medusa
<i>Clytia hemisphaerica</i>	0.12	0.43	6.6	29.6	Guerilla	<2	0*	Medusa
<i>Clytia</i> sp.	0.16	0.39	6.4	36.0	Guerilla	<2*	0*	Medusa
<i>Sertularia cupressina</i>	0.36	0.14	5.9	41.9	Phalanx	>50	≥3°	Planula
<i>Obelia geniculata</i>	0.30	0.23	5.7	47.6	Guerilla	2–50	0	Medusa
<i>Rhizocaulus verticillatus</i>	0.33	0.11	5.2	52.8	Phalanx	>50	1°	Planula
Bougainvilliid (erect)	0.00	0.32	4.6	57.4	Phalanx	2–50*	≥3°	?
<i>Obelia longissima</i>	0.21	0.10	3.9	61.3	Guerilla	>50	≥3°	Medusa
<i>Bougainvillia</i> sp. (stolonial)	0.10	0.21	3.8	65.1	Guerilla	<2*	0*	Medusa
<i>Halecium undulatum</i>	0.01	0.20	3.0	68.1	Phalanx	2–50	≥3°	Planula
<i>Halecium sessile</i>	0.19	0.03	2.8	70.8	Phalanx	>50	≥3°	Planula
<i>Gonothyrea loveni</i>	0.03	0.14	2.3	73.1	Phalanx	2–50	≥3°	Sessile medusoid
<i>Symplectoscyphus tricuspoidatus</i>	0.15	0.06	2.3	75.4	Phalanx	>50	2°	Planula
<i>Sertularella polyzonias</i>	0.13	0.03	2.0	77.4	Phalanx	>50	≥3°	Planula
<i>Abietinaria abietina</i>	0.00	0.14	2.0	79.3	Phalanx	>50	2°	Planula
<i>Sertularia tenera</i>	0.14	0.01	1.8	81.1	Phalanx	2–50	0	Planula
<i>Hydrallmania falcata</i>	0.12	0.01	1.8	82.9	Phalanx	>50	≥3°	Planula
<i>Sertularia</i> sp.	0.10	0.00	1.7	84.5	Phalanx	2–50*	0*	Planula
<i>Diphasia fallax</i>	0.09	0.02	1.3	85.9	Phalanx	>50	2°	Planula
<i>Ectopleura crocea</i>	0.06	0.01	1.1	87.0	Phalanx	>50	0*	Medusa
<i>Lafoea dumosa</i>	0.03	0.07	1.1	88.1	Mixed	>50	≥3°	Planula
<i>Eudendrium ramosum</i>	0.00	0.07	1.1	89.1	Phalanx	>50	≥3°	Planula
<i>Eudendrium capillare</i>	0.08	0.00	1.0	90.1	Phalanx	2–50	≥3°	Planula

Table 6. Mean frequencies and statistical differences in life-history categories in epizoic versus epilithic hydroid assemblages. Sum of frequencies in a category do not equal unity because only traits from the 25 discriminating hydroid taxa were used. Expected frequencies were calculated by multiplying cobble sample size by the mean frequency of a trait on scallop *Placopecten magellanicus*. * $\alpha = 0.05$; G: test for goodness-of-fit

Life history category	Frequency on scallop shells	Frequency on cobbles	G
Growth strategy			*12.35 > $\chi^2_{0.5, 2}$ = 5.99
Guerilla	0.52	0.58	
Mixed	<0.01	0.02	
Phalanx	0.39	0.35	
Colony size			*69.08 > $\chi^2_{0.5, 2}$ = 5.99
<2 mm	0.25	0.45	
2–50 mm	0.12	0.24	
>50 mm	0.51	0.25	
Colony branching			*37.30 > $\chi^2_{0.5, 3}$ = 7.82
No branches	0.32	0.40	
1° branching	0.07	0.03	
2° branching	0.08	0.17	
≥3° branching	0.42	0.34	
Dispersive stage			*23.19 > $\chi^2_{0.5, 2}$ = 5.99
Medusa	0.30	0.40	
Sessile medusoid	0.02	0.04	
Planula	0.57	0.50	

between transplanted substrata in a shallow-water location for a relatively short period. However, the relatively uniform surficial properties of scallop shells, compared to the more variable surfaces of the cobbles, may account for the greater variance (spread across samples) seen in the latter in the species-level MDS ordination (Fig. 3).

Table 7. Summary of ANOSIM analyses (global R) to detect statistical differences between assemblages on cobble and live scallop *Placopecten magellanicus* shell substrata across different levels of fishing effort combined from January 1997 to June 2000. Divergence in hydroid taxon composition between areas with 0–75 and >150 h were analysed separately on cobbles and scallops. * $\alpha = 0.05$

Factor	Category	ANOSIM Global R
Grouped by fishing effort (h)		
Substrate (cobbles, shells)	0–75 (h)	0.31*
	75–150 (h)	0.39*
	>150 (h)	0.36*
Grouped by substratum		
Fishing effort (3 levels)	Cobbles	0.12*
	Scallop shells	0.03*
Grouped by substratum		
Fishing effort (0–75 and >150 h)	Cobbles	0.20*
	Scallop shells	0.05*

Hydroid larvae and stolons often colonize nearby hosts (Kubota 1983, Piraino et al. 1994, Bavestrello et al. 2000b, Cerrano et al. 2000); host distribution affects hydroid populations (Rayyan et al. 2002) and may have influenced the assemblage composition reported in the present study. However, the large area sampled and interspersed distribution of live scallops and cobble substrata exploited in our sampling strategy should have reduced variance associated with small-scale patch dynamics. Sampling cobbles and live scallop shells from the same general location would generally have spread the effect of host distribution between tows, rather than between substrata within tows.

While the hydroid assemblages on the 2 substrate types from the survey data were significantly different, with a high level of dissimilarity (87%), the ANOSIM with substratum as the factor explained only 11% of the variance in the data ($R = 0.339$). In order to examine the effect of fishing disturbance on the hydroid assemblages, cumulative fishing effort was used as an indicator. We consider this measure imprecise as effort is not randomly distributed and it may introduce elements of spatial variation by grouping neighbouring tows together (hence, the relatively low explanatory power of this factor). Nevertheless, it was the best independent measure of fishing disturbance available to us. When effort data were used to categorize the data into 3 bins, the 2 substrata continued to show significantly different communities. However, in agreement with expectation, the substratum factor explained less variation in the lowest effort bin (approx. 9%) than in the 2 bins with higher fishing effort (approx. 15 and 13% respectively). When fishing effort was used as a factor, it explained a higher percentage of variance between cobble assemblages (approx. 2%, increasing to 4% if only the highest and lowest levels of effort are

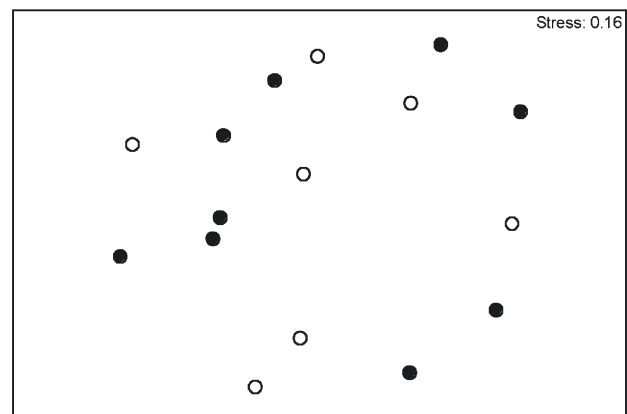


Fig. 4. Non-metric multidimensional (MDS) ordination of hydroid assemblages that colonized transplanted scallop *Placopecten magellanicus* shells (●) and cobble (○) substrata at Sherrod's Beach

Table 8. Frequencies of hydroid taxa that colonized transplanted substrata (2 m depth) over 3 mo at Sherrod's Beach

Taxon	Frequency on live scallops (n = 9)	Frequency on cobbles (n = 10)
<i>Bougainvillia</i> sp. (erect)	0.3	0.5
<i>Ectopleura crocea</i> (L. Agassiz, 1862)	0.3	0.3
<i>Ectopleura larynx</i> (Ellis and Solander, 1786)	0.0	0.1
<i>Obelia</i> sp.	0.1	0.1
<i>Obelia longissima</i> (Pallas, 1766)	1.0	1.0
<i>Gonothyrea loveni</i> (Allman, 1859)	0.6	0.6
<i>Opercularella lacerata</i> (Johnston, 1847)	0.3	0.4
<i>Clytia hemisphaerica</i> (Linnaeus, 1767)	0.1	0.0
<i>Halecium</i> sp. (stolonial)	0.2	0.1

used in the analysis) compared with scallop assemblages (0.0009%, increasing to 0.002%). This result is also consistent with our hypothesis that surviving scallops would be less disturbed by fishing than the cobbles. We conclude that fishing disturbance is an important agent influencing hydroid assemblages.

All levels of taxonomic resolution can be used to discriminate between the 2 significantly distinct assemblages associated with the epilithic and epizoic substrata, but the greatest average dissimilarity between assemblages was produced using species-level information (Table 3).

Epilithic hydroids were predominantly characterized by the campanulariids *Campanularia volubilis*, *Clytia hemisphaerica* and *Clytia* sp., as well as an erect bougainvilliid species. Colonies were usually patchily distributed over cobble surfaces, but the stolonial growth strategies of the campanulariids produced rather diffusely organized colonies within patches. Hydroid assemblages on scallop shells were characterized by the presence of *Calycella syringa*, a minute stolonial annual species usually found on other hydroids (an 'auto-epizoite' *sensu* Millard 1973). This species also characterized less fished areas in the Gulf of Maine, south of the Bay of Fundy (Pugh 1999). In the present study, *C. syringa* was almost exclusively found on the large arborescent hydroids *Sertularia cupressina* and *Obelia dichotoma*, both of which also characterized scallop shell assemblages.

Calycella syringa was also the species that best discriminated between the assemblages on the substrata. The relatively lower frequency of erect arborescent hydroids on cobbles probably explains the virtual absence of *C. syringa* from these substrata except in rare instances when it occurred on dead sertulariid stems still attached to rock surfaces. The large arborescent species *Obelia dichotoma* also discriminated between assemblages, being more frequent on scallop shells. *O. dichotoma* has a relatively longer lifespan than other campanulariids that characterized

the epilithic assemblages. Many of the same taxa in the Gulf of Maine south of the Bay of Fundy responded in similar ways to bottom fishing e.g. reduced *C. syringa* and *Symplectoscyphus tri-cuspidatus* and increased *Clytia* spp. (Pugh 1999).

Further insight into hydroid assemblage divergence was gained by contrasting the life-history strategies of taxa on cobbles versus live scallop shells. Both substrata were colonized by taxa with runner-like growth strategies as well as upright phalanx forms; however, the former were significantly

more common on the cobbles while the latter were less so. The most striking contrast in substrate type was the high frequency of large-sized colonies in epizoic assemblages (51%) compared with epilithic assemblages, where colonies less than 2 mm predominated (45%) (Table 6). Similarity between assemblages on scallop shells was largely explained by taxa with a wide range of life histories. This diversity in life-history traits suggests that the shells of live scallops are sufficiently undisturbed so as to support large slow-growing erect hydroids and yet have enough resources (e.g. unoccupied space, food availability) to allow the colonization of more opportunistic taxa. In contrast, physically variable marine habitats tend to be dominated by opportunistic hydroids characterized by rapid recruitment, early resource exploitation and good recovery abilities following perturbations (Calder 1991). For example, opportunistic hydroids dominated commercially trawled fishing grounds on the Catalan shelf in northeast Spain (Gili et al. 1987). Similarly, in the present study, small stolonial unbranched campanulariids with medusa stages distinguished cobble assemblages from those on scallops in the present study.

'Attribute syndromes' are positive associations between life-history traits that characterize organisms found in certain habitats (Dupré & Diekman 2001). A particular trait in the syndrome may truly have evolutionarily adaptive value, but it may also be correlated to another trait that is adaptive, or it may simply be constrained by phylogeny. For example, allometric constraints imposed by colony architecture affect investment into other life-history aspects e.g. colony dimensions, shape and parental investment in young (Jackson 1979, Lasker & Sánchez 2002). The production of medusae versus sessile medusoids versus planulae may have little consequence for substrate colonization (Boero 1984, Bavestrello 1985), as the potential for wide dispersal is often not realized. Instead, the distribution of reproductive strategies on certain substrata probably reflects the correlation of this trait to other life-history

traits, such as colony size and growth type strategy (Cornelius 1990, 1991). Phylogeny may also constrain the distribution of life-history traits. For example, it is thought that most sertulariids produce planula larvae (but see e.g. Migotto 1998 and Gravier-Bonnet & Lebon 2002) while *Obelia* spp. release free medusae. Thus, the high frequency of medusa life stages in epilithic hydroids could simply reflect the evolution of medusa stages in particular taxa e.g. *Clytia* spp., *Obelia* spp., which possess other traits, e.g. colony size and growth form, relevant to colony survival on disturbed versus more stable substrata. Attribute syndromes are overall still useful as they point to traits associated with habitat disturbance, and could be used to assign 'indicator' status to certain taxa.

Taxa with relatively good recovery capacities mature early, have high fecundity and wide dispersal, and are predicted to eventually dominate epifaunal assemblages in heavily fished areas (Pitcher et al. 2000). Post-fished assemblage structure therefore depends on life-history traits of resident taxa and the timing of life-history events that determine recovery potential (Van Dolah et al. 1987, Hutchings 1990, Jones 1992, Auster et al. 1996, Christie et al. 1998, Bergman & Van Santbrink 2000, McConnaughey et al. 2000, Bradshaw et al. 2001, Jennings et al. 2001, Kenchington et al. 2001, Bradshaw et al. 2002, Gordon et al. 2002). The epizoic community, occupying relatively undisturbed island habitats interspersed amongst disturbed substrata, may act as refugia and 'seed banks' for species vulnerable to disturbance. While the spatial extent of these communities is limited compared to that of the assemblages colonizing disturbed epilithic substrata, the presence of epizoic assemblages may influence the rate at which disturbed epifaunal communities proceed toward a low diversity and high abundance state.

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