

Sea urchin fecal production and accumulation in a rocky subtidal ecosystem

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ABSTRACT: We used a spatial model of destructive grazing of kelp beds by dense aggregations (fronts) of sea urchins *Strongylocentrotus droebachiensis*, together with measures of sea urchin absorption efficiency and fecal degradation rate, to predict rates of fecal production and accumulation during the transition from a kelp bed to a barrens state in a rocky subtidal ecosystem of Nova Scotia, Canada. The rate of fecal production as dry mass reached $9.17 \text{ g m}^{-2} \text{ d}^{-1}$ at 10 yr after the formation of a grazing front, with associated rates of carbon and nitrogen production of $2.12 \text{ g C m}^{-2} \text{ d}^{-1}$ and $0.21 \text{ g N m}^{-2} \text{ d}^{-1}$. Fecal production rate exceeded the rates of physical, chemical, and microbial degradation, such that up to 193.6 g of feces, 70.2 g of C, and 4.0 g of N accumulated per linear m of front after 10 yr. The extent of sea urchin grazing fronts along the Atlantic coast of Nova Scotia was estimated at 280 km in 2000, which translates to a total fecal production rate of 6423 kg of feces d^{-1} and an accumulation of 54 200 kg of feces after 10 yr of front formation, based on our model. This temporally variable flux of organic matter likely has a profound effect on adjacent deeper-water macrobenthic communities utilizing the feces as a food source.

KEY WORDS: Fecal production · Organic matter flux · Degradation · Kelp bed · Sea urchin · *Strongylocentrotus droebachiensis*

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INTRODUCTION

Kelp beds or forests form extensive biogenic habitats in temperate coastal regions and are among the most productive ecosystems in the ocean (Mann 2000). While kelp beds are relatively resilient to disturbance, they are periodically decimated by thermal fluctuations, storms, and herbivore outbreaks (Dayton et al. 1998, Steneck et al. 2002). Large-scale destructive grazing of kelp beds by sea urchins can cause a shift to an alternative community state—coralline-dominated barrens (Lawrence 1975, Uthicke et al. 2009).

In the Northwest Atlantic, the sea urchin *Strongylocentrotus droebachiensis* plays a pivotal role in determining community structure in the rocky subtidal zone (Scheibling & Hatcher 2007). At high densities (up to 500 ind. m^{-2}), sea urchins form grazing aggregations (fronts) along the lower margins of kelp

beds, driving the transition to barrens (Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007). These grazing fronts, which can extend from 100s of meters to kilometres alongshore (Miller & Nolan 2000), consume large quantities of kelp (up to $1 \text{ kg (m front)}^{-1} \text{ d}^{-1}$; Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007). Estimates of sea urchin absorption efficiency suggest that 30 to 50% of this material is defecated as globular, mucus-covered fecal pellets that are 1 to 3 mm in diameter (Miller & Mann 1973, Larson et al. 1980, Sauchyn & Scheibling 2009a). These fecal pellets are transported by waves and currents and deposited in sedimentary habitats in deeper waters (Sauchyn & Scheibling 2009a). Thus, defecation by sea urchins may represent a significant path of detrital export from the kelp bed ecosystem.

Feces are an important source of organic matter for the microbial community, stimulating the growth of attached and free-living bacteria and protozoa

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(Povero et al. 2003, Thor et al. 2003). In turn, microbes increase the nutritional value of the feces by contributing to the labile organic matter fraction (González & Biddanda 1990, Fabiano et al. 1994) through remineralization of dissolved organic matter (Urban-Rich 1999, Povero et al. 2003) and uptake of dissolved inorganic nutrients from the water column (Wotton & Malmqvist 2001, Povero et al. 2003). Microbial degradation of sea urchin feces leads to an increase in the available energy content and a decrease in the fecal C:N ratio (Sauchyn & Scheibling 2009b), suggesting that the degraded feces are an important food source for suspension and deposit feeding invertebrates in the rocky subtidal zone and in adjacent sedimentary habitats in deeper water (Newell 1965, Frankenberg & Smith 1967, Lopez & Levinton 1987). While fecal production and biodeposition have been well studied in suspension feeding invertebrates such as bivalves (Haven & Morales-Alamo 1966, Kautsky & Evans 1987, Fabiano et al. 1994, Norling & Kautsky 2007, 2008), the role of sea urchins and other benthic grazers in these processes remains poorly understood (Mamelona & Pelletier 2005, Sauchyn & Scheibling 2009a,b).

In this paper, we combined a spatial population dynamics model of destructive grazing of kelp by *Strongylocentrotus droebachiensis* (Lauzon-Guay et al. 2009) with estimates of absorption efficiency and fecal degradation rate to predict fecal production by sea urchins during the transition from kelp bed to urchin barrens states. This modelling exercise allowed us to further explore the ecological consequences of state shifts in a rocky subtidal ecosystem of Nova Scotia, in terms of material and energy flow via grazing and detrital pathways.

MATERIALS AND METHODS

Model description

We used the model developed by Lauzon-Guay et al. (2009) to calculate the amount of kelp *Saccharina longicruris* consumed by a grazing front of sea urchins *Strongylocentrotus droebachiensis* after urchin mass mortality. The model tracks sea urchin density and kelp biomass over a 1-dimensional domain extending from the surviving sea urchin population (at >20 m depth) to the shore. The only site-specific parameter is bathymetry, which determines the off-shore distance between the surviving urchin population and the remaining kelp bed (<8 m depth, in wave exposed habitats). The sea urchin population

was modelled using a size-structured integro-difference equation (Neubert & Caswell 2000), with size-specific survival and growth, and habitat-specific (barrens, front, kelp bed) growth and recruitment. The initial biomass of algae between the kelp bed and the deeper, surviving population of sea urchins after mass mortality was assumed to be 50 g m^{-2} , and re-establishment of the kelp bed was modelled using Ricker's model of growth (Turchin 2003) with an added term for grazing, and assuming large dispersal distances for kelp (Gaylord et al. 2004). The model assumes that sea urchins move in random directions in the absence of kelp and remain stationary when kelp is present. The model also assumes that sea urchins can only forage on erect macroalgae when feeding in groups, and above a threshold ratio of urchin to kelp biomass (0.5). Initial conditions and parameter estimates were obtained from the literature and detailed descriptions of the model structure and parameter estimates are provided by Lauzon-Guay et al. (2008, 2009). Previous work has described the reformation and subsequent advance of a sea urchin feeding front following a mass mortality, in terms of both the density of urchins within the front and the rate of advance of the front over time (Lauzon-Guay et al. 2009).

In the present study, we describe changes over time in the amount of kelp consumed by an urchin front and the resultant fecal material made available in the system after physical, chemical, and microbial degradation. We used simulation results corresponding to the reformation of a feeding front and its expected propagation over a period of 10 yr at a site (Splitnose Point) near Halifax, Nova Scotia following the last mortality event which occurred there in September 1999 (Lauzon-Guay & Scheibling 2007, Lauzon-Guay et al. 2009). While the sea urchin grazing model is spatially explicit and sea urchins move within the system, we did not account for resuspension or horizontal advection of fecal material once it has been deposited by sea urchins. Therefore, fecal material was assumed to remain where it was produced by sea urchins within the front. Although this does not allow us to determine where the feces will accumulate, it enables prediction of the flux of fecal pellets that can be incorporated into energy budgets.

Fecal production

The mass of feces produced ($W_f(x)$) at time t (days) at position x (in m) was calculated by multiplying the dry weight of kelp eaten ($k_t(x)$) by the absorption effi-

ciency (as dry weight) of sea urchins feeding on kelp (α_k , 64.8% \pm 3.0 SE; Sauchyn & Scheibling 2009a):

$$W_t(x) = (1 - \alpha_k)k_t(x) \quad (1)$$

The dry weight of kelp eaten was obtained by multiplying the total mass of kelp consumed by sea urchins (obtained from the model output) by a wet to dry weight conversion factor of 0.159 (\pm 0.011 SE) for *Saccharina longicuris* (Sauchyn & Scheibling 2009a).

Fecal degradation

Degradation of feces through time was modelled by Sauchyn & Scheibling (2009b) using an exponential decay function:

$$F_d = 0.682e^{-0.411d} + 0.317 \quad (2)$$

where F_d is the proportion of feces (as dry weight) remaining d days after they were produced. Similarly, the proportions of organic carbon and nitrogen remaining as feces were modelled as:

$$C_d = 0.090e^{-0.601d} + 0.142 \quad (3)$$

and

$$N_d = 0.015e^{-0.935.166d} + 0.008 \quad (4)$$

where C_d and N_d are respectively the proportions of the initial dry weight of feces that remain as organic carbon and nitrogen, d days after the feces were produced. Eqs. (3) & (4) evaluated at $d = 0$ represent the production of organic carbon and nitrogen, respectively. We did not differentiate between carbon and nitrogen originating from the feces from those originating from attached bacteria. Therefore, our estimates represent the total organic carbon and nitrogen present in the feces and likely underestimate the actual degradation rates. Measurements used to estimate fecal production and degradation rates were obtained from field experiments conducted at Splitnose Point and from laboratory experiments with sea urchins and kelp collected from this site (Sauchyn & Scheibling 2009a,b). Feces used to determine *in situ* degradation rates were maintained in containers covered with 63 μ m mesh for 19 d. This mesh size allowed exchange of bacteria and most Protozoa with the surrounding sea water, but excluded larger metazoans. Therefore, losses of fecal mass, organic carbon, and nitrogen were due to microbial degradation and physical and chemical processes. Field experiments indicate that depth (from 6 to 16 m) and temperature (from 4 to 18°C across depth and time) have no significant effects on degradation of sea urchin feces

(Sauchyn & Scheibling 2009b); therefore, the same equations were used to estimate fecal degradation at all positions x .

Feces available

The total mass of fecal material ($TF_t(x)$) at some position x at time t is the sum of the remaining feces produced per linear m of urchin front over the previous 19 d, calculated as:

$$TF_t(x) = \sum_{d=0}^{19} F_d W_{t-d}(x) \quad (5)$$

Similarly, the total mass of organic carbon ($TC_t(x)$) and nitrogen ($TN_t(x)$) in fecal material at position x at time t , produced per linear m of urchin front over the previous 19 d, are respectively:

$$TC_t(x) = \sum_{d=0}^{19} C_d W_{t-d}(x) \quad (6)$$

and

$$TN_t(x) = \sum_{d=0}^{19} N_d W_{t-d}(x) \quad (7)$$

The 19 d interval was based on the duration of the *in situ* degradation experiment. After 19 d, 70% of the total mass of fecal material had been lost (Sauchyn & Scheibling 2009b). While our model was run over 10 yr, we did not track feces and nutrients over the entire span of our simulation. At any one location, feces were tracked for 19 d, after which they were assumed to have been fully degraded.

Elasticity analysis

We conducted an elasticity analysis on the total production of feces over 10 yr. We calculated the proportional change in biomass of feces produced by a 1 m wide section of the front in response to a 10% increase in several parameters of the model (for urchins: movement, growth survival, recruitment, grazing; for kelp: carrying capacity, growth).

RESULTS

At the start of our simulation, kelp started to grow down to the upper limit of the surviving sea urchin population (20 m depth), where a grazing front formed and advanced to 5 m depth within 10 yr (Fig. 1). Over this period, fecal production (dry weight) increased from 0.95 to 22.94 g (m front)⁻¹ d⁻¹ as kelp consumption increased due to an increase

in urchin density from 13.1 to 129.4 ind. m^{-2} within the grazing front (Fig. 2a). The production of organic carbon and nitrogen increased concomitantly from 0.22 to 5.32 $g\ C\ (m\ front)^{-1}\ d^{-1}$ and from 0.02 to 0.52 $g\ N\ (m\ front)^{-1}\ d^{-1}$ (Fig. 2b). For a 2.5 m wide front

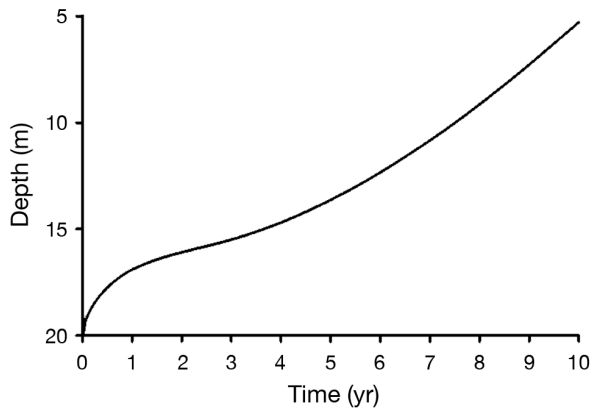


Fig. 1. *Strongylocentrotus droebachiensis*. Predicted depth of sea urchin front over time at Splitnose Point, Nova Scotia, over a 10 yr period following mass mortality of sea urchins

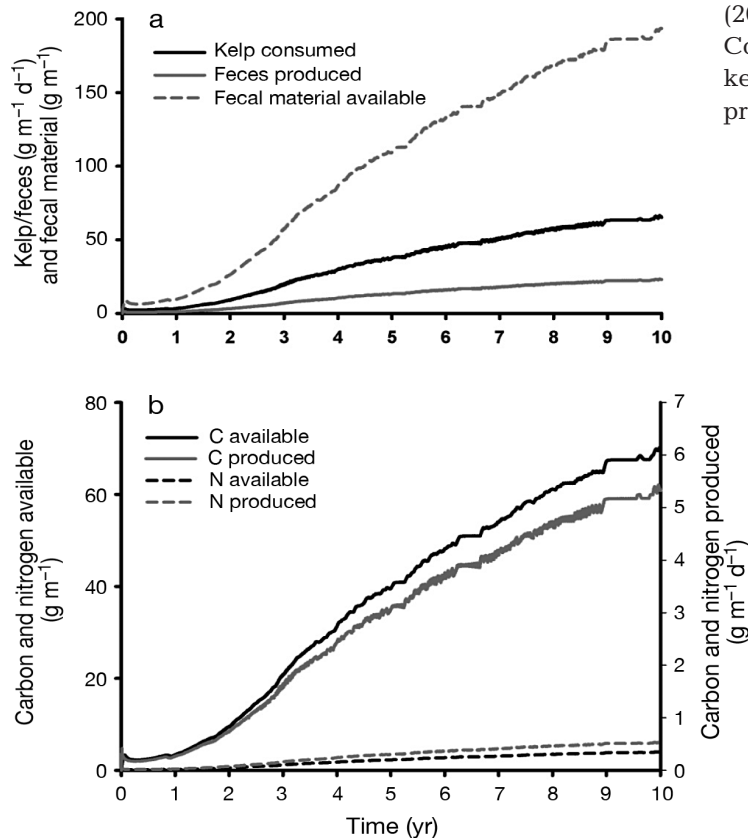


Fig. 2. *Strongylocentrotus droebachiensis*. (a) Kelp consumed, fecal material produced, and fecal material available per linear m of sea urchin front over time. (b) Organic carbon and nitrogen in the fecal material produced and available per linear m of front over time

(Lauzon-Guay & Scheibling 2007) with 129 urchins m^{-2} , our model predicted a fecal production rate of 9.17 $g\ m^{-2}\ d^{-1}$ and associated carbon and nitrogen production rates of 2.12 $g\ C\ m^{-2}\ d^{-1}$ and 0.21 $g\ N\ m^{-2}\ d^{-1}$, at 10 yr.

The rate of fecal production exceeded that of physical, chemical, and microbial degradation, such that the mass of feces produced per linear m of front accumulated behind the advancing front, up to 193.55 g dry weight over a 19 d period at 10 yr after front formation (Figs. 2a & 3). The concomitant accumulation of organic carbon and nitrogen in the feces over 19 d was 70.22 $g\ C$ and 4.01 $g\ N$ at 10 yr (Figs. 2b & 3). We did not include dispersal of feces in our model. Therefore, the patterns of accumulation of fecal mass, organic carbon, and nitrogen in our model followed that of kelp consumption and fecal production, and were maximal at the interface of the kelp bed and urchin barrens (Fig. 3).

Total fecal production rate over the 10 yr following a mass mortality of urchins, was most sensitive to an increase in parameters affecting the sea urchin population (Fig. 4). Specifically, fecal production was most sensitive to an increase in urchin survival (20.6%), movement (10.3%) and growth (7.1%). Conversely, increases in parameters pertaining to kelp dynamics had relatively small effects on the production of feces (<5%).

DISCUSSION

Feces production

In the rocky subtidal zone of Nova Scotia, marked changes in the production and export of particulate matter as sea urchin feces occur on a decadal time scale, following major transitions in ecosystem state (Scheibling et al. 1999, Lauzon-Guay et al. 2009). As grazing fronts advance and sea urchins transform kelp beds into coralline-dominated urchin barrens, vast amounts of feces are produced (Sauchyn & Scheibling 2009a). During this transition, the rates of destructive grazing and fecal production increase over time due to an increase in sea urchin density at the front (Lauzon-Guay et al. 2009). According to our model, fecal production per linear m of front increases to 9.17 $g\ m^{-2}\ d^{-1}$ after 10 yr, with carbon and nitrogen production rates of 2.12 $g\ C\ m^{-2}\ d^{-1}$ and 0.21 $g\ N\ m^{-2}\ d^{-1}$. These fecal production rates are higher than those estimated by Mamelona & Pelletier (2005) for a front of *Strongylocentrotus droebachiensis* feeding on the kelp *Alaria*

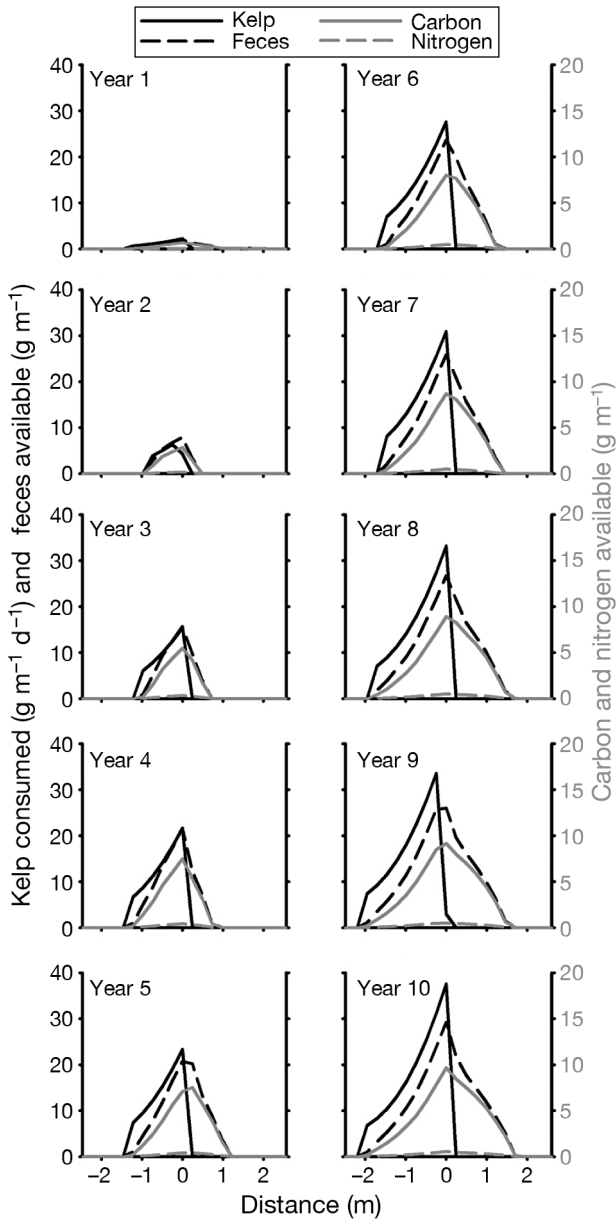


Fig. 3. *Strongylocentrotus droebachiensis*. Kelp consumed, and fecal mass, organic carbon, and nitrogen available at the sea urchin grazing front at 1 to 10 yr after sea urchin mass mortality and front formation. Distance on the x-axis is relative to the position of the kelp bed/barrens interface. 0: leading edge of the urchin front, negative values: within kelp bed, and positive values: within barrens

esculenta ($5.6 \text{ g m}^{-2} \text{ d}^{-1}$), based on laboratory measurements of feeding and defecation rates (Table 1). Feces were collected up to 3 d after defecation in their study, during which time there was significant degradation and loss of fecal material (Sauchyn & Scheibling 2009b), which could partly explain the lower fecal production rates they obtained. The density of sea urchins at a front is predicted to be most sensitive to

changes in survival, growth and movement rate of individuals (Lauzon-Guay et al. 2009). Accordingly, our sensitivity analysis indicates that prediction of fecal production was also most sensitive to variation in these parameters.

As the sea urchin front advances, it ultimately reaches an upper depth limit (which varies both spatially and seasonally) where wave action inhibits destructive grazing (Chapman & Johnson 1990). At this point, fecal production dramatically decreases and remains low while the system is in the barrens state. Barrens can persist indefinitely, as urchin populations may be sustained by drift algae from intertidal and shallow subtidal habitats, and by microalgal and microbial films, and coralline crusts (Johnson & Mann 1982). The re-establishment of the alternative, kelp-bed state occurs following the sporadic introduction of a pathogenic amoeba that causes widespread mass mortality of sea urchins (Scheibling 1986, Scheibling & Lauzon-Guay 2010). Survival and growth of the amoeba is temperature dependent (Jellett & Scheibling 1988) and sea urchins have a thermal refuge below $\sim 20 \text{ m}$, where temperature remains below an infection threshold (10°C) for paramoebiasis (Brady & Scheibling 2005). The release from grazing pressure in the shallow subtidal zone enables rapid colonization and re-growth of luxuriant kelp beds within 2 to 3 yr (Scheibling 1986, Johnson & Mann 1988). Sea urchin populations in shallow water eventually recover through recruitment and immigration from deeper, colder waters. The time required for reformation of the front depends on the linear distance between the surviving sea urchin population and the kelp bed,

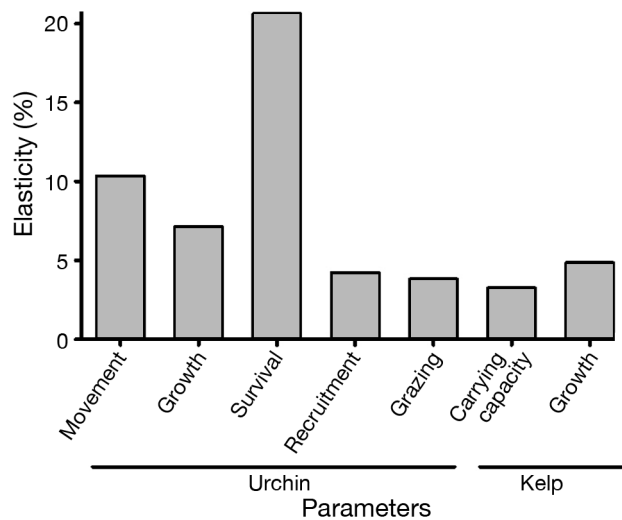


Fig. 4. Elasticity of fecal material production over 10 yr to a 10% increase in model parameters

Table 1. Total fecal, carbon, and nitrogen production rates ($\text{g dwt m}^{-2} \text{d}^{-1}$) of several species of suspension feeding bivalves, gastropod molluscs, planktivorous reef fish, and blackfly larvae in comparison to the sea urchin *Strongylocentrotus droebachiensis*

Species	Site	Density (ind. m^{-2})	Production ($\text{g m}^{-2} \text{d}^{-1}$)			Source
			Total	Carbon	Nitrogen	
Suspension feeding bivalves						
<i>Adamussium colbecki</i> (Antarctic scallop)	Terra Nova Bay, Ross Sea, Antarctica	50–60	0.68	0.06	0.01	Chiantore et al. (1998)
<i>Crassostrea virginica</i> (American oyster)	York River, Virginia, USA		62	14	0.77	Haven & Morales-Alamo (1966)
<i>Chlamys farreri</i> (Zhinkong scallop)	Sishili Bay, China	120	9.05	0.47	0.06	Zhou et al. (2006)
<i>Mytilus chilensis</i> (Chilean blue mussel)	Quele River Estuary, Chile	250–300	234	14.04	0.94	Jaramillo et al. (1992)
<i>Choromytilus chorus</i> (giant mussel)	Quele River Estuary, Chile	250–300	271	17.34	0.81	Jaramillo et al. (1992)
<i>Mytilus edulis</i> (blue mussel)	Magdalen Islands, Canada	764	16.8			Callier et al. (2009)
<i>Crassostrea gigas</i> (Pacific oyster)	Ofunato Estuary, Japan	1100	270	8.1–32.4	1.08–4.05	Hayakawa et al. (2001)
<i>Dreissena polymorpha</i> (zebra mussel)	Western Lake Erie, Canada	1180–1835	26			Klerks et al. (1996)
Gastropod molluscs						
<i>Tegula funebris</i> (black turban snail)	Mukkaw Bay, Washington, USA	412–800	1.18 – 2.78			Paine (1971)
<i>Bithynia graeca</i> (freshwater snail)	Lake Kerkini, Greece	12 172	0.55			Eleutheriadis & Lazari- dou-Dimitriadou (1996)
Planktivorous reef fish						
<i>Chromis chromis</i> (damselfish)	Rocky reef, Bay of Calvi, France	1	0.006– 0.015	0.0005– 0.002	0.00005– 0.0002	Pinnegar & Polunin (2006 ^a)
<i>Chromis punctinnis</i> (blacksmiths)	Rocky reef, California, USA	6.4	63	8		Bray et al. (1981)
Blackfly larvae						
<i>Metacnephia lyra</i> , <i>Simulium</i> spp.	Vindel River, northern Sweden	93 000	(192	7.5		Malmqvist et al. (2001)
<i>Simulium</i> spp.	Stream in northern Sweden	600 000	966	37.95		Wotton et al. (1998)
Sea urchin						
<i>S. droebachiensis</i> (green sea urchin)	St. Lawrence River, Canada	150	5.6			Mamelona & Pelletier (2005)
<i>S. droebachiensis</i> (green sea urchin)	Nova Scotia, Canada	129	9.17	2.12	0.21	This study

^aRange from fall to spring

which is determined largely by the bathymetry of a given site (Lauzon-Guay et al. 2009).

Like many other temperate marine systems, the flux of particulate organic matter along the coast of Nova Scotia also varies seasonally due to changes in urchin grazing rate and absorption efficiency. The grazing rate of *Strongylocentrotus droebachiensis* is highest in mid-summer, then decreases in late summer and remains low through fall and winter (Meidel & Scheibling 1998, Scheibling et al. 1999). The absorption efficiency of sea urchins also varies by up to 30% seasonally and is highest in the fall (Miller & Mann 1973, Larson et al. 1980). Seasonal changes in grazing rate and absorption efficiency are likely linked to the reproductive cycle of *S. droebachiensis* (Larson et al. 1980, Meidel & Scheibling 1998). Our model did not account for seasonal variation; we used a yearly-averaged grazing rate and an absorption efficiency calculated for fall. Therefore, our estimates of fecal production are likely to be conservative on

an annual basis. These estimates for sea urchins are in the lower range of fecal production rates reported for suspension feeding bivalves, gastropod molluscs, planktivorous reef fish, and blackfly larvae (Table 1).

Feces quality and degradation

The rate and process of degradation of sea urchin feces also determines their availability as a food source for microbial and metazoan communities. In a previous study at Splitnose Point, we observed an exponential loss of fecal mass after defecation (Eq. 2; Sauchyn & Scheibling 2009b), which we attributed to the dissolution of organic matter (DOM) and microbial hydrolysis of particulate organic matter (Urban-Rich 1999, Thor et al. 2003). The release of DOM may stimulate microbial activity (Povero et al. 2003, Thor et al. 2003) and provide nutrients for kelp production (Bert-

ness 1984, Kautsky & Evans 1987). After egestion, feces produced by urchins grazing the kelp *Saccharina longicruris* have a relatively high C:N ratio (30.7; Sauchyn & Scheibling 2009a), suggesting that they are not easily degraded and are a poor food source for detritivores (Parsons et al. 1984). However, as bacteria use up the labile organic nitrogen within the fecal pellets, they actively take up dissolved inorganic nitrogen from the surrounding seawater (Povero et al. 2003), contributing to the nitrogen content of the feces and decreasing the C:N ratio to 15.9 within 2.5 wk of egestion (Sauchyn & Scheibling 2009b). In addition to increasing the nitrogen content, microbial activity also results in a relative increase in organic carbon, lipid, and available energy content of the feces during the second week after egestion (Sauchyn & Scheibling 2009b). The aged feces, with a relatively low C:N ratio and high available energy content, accumulate within the system, where they are likely an important food source for suspension and deposit feeding invertebrates (Newell 1965, Frankenberg & Smith 1967, Lopez & Levinton 1987).

The production rate and chemical composition of urchin feces can vary with diet (Mamelona & Pelletier 2005, Sauchyn & Scheibling 2009a). This model is based on consumption of *Saccharina longicruris*, which along with *Laminaria digitata* is a dominant macroalgal species at Splitnose Point (Lauzon-Guay & Scheibling 2007). These kelps account for the vast majority of food consumed by the urchin front, although turf algae, epiphytic bryozoa and small benthic invertebrates are also ingested (Knip & Scheibling 2007).

The rates of microbial degradation in marine environments vary with seasonal changes in temperature (Pomeroy & Wiebe 2001); however, such variation is unlikely to have a large effect on our model predictions. Sauchyn & Scheibling (2009b) found no effect of depth on fecal degradation rate when temperature varied from 3.9°C at 16 m to 18.2°C at 6 m. In a review of 68 studies, Rivkin et al. (1996) observed only a very weak positive relationship between temperature and microbial activity.

Feces dispersal

Although we did not include dispersal of the fecal pellets in our model, the fate of this material is an important consideration in our overall understanding of the role of fecal production by sea urchins in organic matter flux and energy flow in this system. Based on the significant wave height observed at our study site, it was estimated that recently defecated

fecal pellets (<24 h old) produced by a grazing front can travel as bedload to depths of 28 m in summer and 47 m in winter, and are deposited there (Sauchyn & Scheibling 2009a). However, as fecal pellets degrade, they become less dense and are therefore more readily transported to even deeper, less productive waters (Taghon et al. 1984, Sauchyn & Scheibling 2009a).

CONCLUSION

Biodeposition by aquatic organisms supplies a large proportion of the energy demand of suspension and deposit feeding communities, affecting their abundance, biomass, and species composition (Wotton et al. 1998, Norkko et al. 2001, Pinnegar & Polunin 2006, Norling & Kautsky 2007, 2008). Our mathematical model and previous empirical studies (Sauchyn & Scheibling 2009a,b) indicate that sea urchin feces represent a significant source of organic matter for benthic populations in rocky subtidal zone and adjacent sedimentary habitats. Fishery surveys estimated that sea urchins destructively grazed 280 km of kelp beds along the Atlantic coast of Nova Scotia in the mid to late 1990s (Miller & Nolan 2008). This equals a fecal production rate of 6423 kg feces d⁻¹ based on our estimate of fecal production after 10 yr of front advance.

Recent changes in the rocky subtidal ecosystem of the Northwest Atlantic underscore the importance of elucidating the role of *Strongylocentrotus droeachiensis* in detrital food webs. Oceanographic regime shifts and the changing frequency and intensity of the strongest storms are associated with an increase in the frequency of sea urchin mass mortality events along the coast of Nova Scotia over the last 30 yr (Scheibling & Lauzon-Guay 2010). Storms can also cause extensive defoliation of kelp beds and alter sea urchin grazing activity (Steneck et al. 2002). Invasive species that destroy or displace kelp, such as the epiphytic bryozoan *Membranipora membranacea* and the green alga *Codium fragile*, also affect fecal production by sea urchins. Loss of kelp fronds due to outbreaks of *M. membranacea* may accelerate destructive grazing by increasing the ratio of sea urchin density to kelp biomass (Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007). In addition, changes in the availability and quality of algal food affect the production rate, chemical composition, and dispersal of sea urchin feces (Sauchyn & Scheibling 2009a). Sea urchins grazing on bryozoan-encrusted kelp produce a slightly greater amount of

higher quality feces that are deposited at shallower depths, while those grazing on *C. fragile* produce a smaller amount of higher quality feces that are deposited at greater depths, compared to sea urchins that consume non-encrusted kelp (Sauchyn & Scheibling 2009a). The sea urchin dive fishery, which typically targets feeding fronts, can also impact grazing and fecal production rates, especially in areas where sea urchin stocks have seen rapid declines.

In benthic marine ecosystems, variation in the flux of particulate organic matter accounts for a large proportion of the variation in macrobenthic biomass (Grebmeier et al. 1988, Johnson et al. 2007) as suspension and deposit feeders rapidly respond to inputs of this energy source (Whitlatch 1980, Rudnick et al. 1985). Therefore, large-scale changes in the rocky subtidal ecosystem that are associated with natural and anthropogenic stressors and disturbances, are likely to have profound effects on the structure and functioning of adjacent communities that utilize sea urchin feces as a food resource (Pearson & Rosenberg 1987). This connectivity in the flux of organic matter and energy between different benthic assemblages across a depth gradient remains largely unexplored.

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