

Organic matter production of American lobsters (*Homarus americanus*) during impoundment in Maine, United States

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Abstract Lobster impoundments are dammed coastal embayments utilised to hold American lobsters (*Homarus americanus*) before shipping to market. The impacts of lobster impoundments on the environment have not been previously studied. Here, the digestive functioning of American lobsters was examined to assess the quantity and quality (TVS, total volatile solids) of lobster faeces produced under the temperatures and feeding regimens these animals were subjected to during the impoundment period. Overall it was determined that quantity and quality of faeces did not differ among the experimental temperatures (5, 10, and 15°C), and that animals fed every 1–2 days produced greater quantity and quality of faeces than those fed every 3–18 days, or those animals fed less than every 18 days. As a first estimate of organic matter production in active lobster impoundments, it was calculated that a typical lobster impoundment produced 0.79 ± 0.35 (average ± 1 SD) g TVS $m^{-2} day^{-1}$ during the impoundment period, equivalent to $3.11 \pm 0.60\%$ of the total weight of lobsters stocked into the impoundment. This level of organic matter production is below the level produced by other aquaculture operations, and that at which benthic impacts might be expected.

Keywords benthic impact; faecal production; *Homarus americanus*; lobster impoundment; Maine; organic matter; total volatile solids

INTRODUCTION

Impoundments are an important component of the American lobster (*Homarus americanus*, H. Milne Edwards 1837) fishery. They are cordoned-off coastal areas, ranging from the simple damming of a tidal embayment, to a three-sided corral, with the fourth side being the shoreline. In all instances, there is a gate within the dam that can be opened or closed. When the gate is closed, water is prevented from draining completely from the impoundment. The water generally is dammed to a depth of 1.5 m, thus only around the period of high tide will there be water exchange over the top of the dam. When lobsters are not stocked in the impoundment, the gate is opened, and the impoundment can be drained completely, thereby exposing virtually the entire impoundment bottom.

The highest landings in the American lobster fishery occur in September–November. During this time, excess animals are stored in the impoundments. These animals then are released slowly into the market during a time (February–March; winter in the Northern Hemisphere) when fishing is unsafe and landings are generally lower. Impounding lobsters, and the subsequent slow release of impounded animals to the market, avoids a market glut in the autumn, thereby helping to stabilise market prices.

In Maine, United States, there are a total of 56 active impoundments that can hold up to 2257 t of lobster (H. Hodkins, Maine Lobster Pound Association pers. comm.). In addition to Maine's present impoundments, there is much interest in developing new impoundments. Within the last half-decade, there have been over a dozen new applications for impoundment licenses (J. Sowles, Maine Department of Environmental Protection pers. comm.). These new impoundments will be developed in prime coastal habitat, and thus it is critical to ensure that these impoundments do not significantly degrade the habitat. One method to accomplish this is to determine the holding or environmental assimilative capacity of impoundments. Thus for new impoundments, biologically feasible loadings

can be determined *a priori* as part of the effort to ensure that the industry proceeds in an environmentally sustainable manner (Rosenthal 1994; Olsen 1996; Pillay 1996), and to prevent lobster health problems that come with crowding.

To date, lobster impoundments have not had the advantage of biological monitoring to the same degree as other sectors of the aquaculture industry. Although several studies have considered environmental effects on lobster growth and health (Jansen & Groman 1993; Speare et al. 1996; Bayer et al. 1998), no studies have looked at the reverse issue of lobster impacts on the environment, especially of impoundments. This lack of information for lobster impoundments is exemplified by the fact that regulatory agencies within the Gulf of Maine do not currently have a formal environmental component associated with impoundment licensing and applications. In the past decade, the scientific and practical knowledge of how other aquaculture sectors impact the environment has increased substantially (Pillay 1992; Ervik et al. 1997). One main tenet from this environmental work is that if the industry develops in a suitable area and at a reasonable level of effort, the impacts to the environment are negligible or even non-existent (O'Connor et al. 1991; Olsen 1996; Tlusty et al. 1999).

The issue of environmental impacts in lobster impoundments is timely for three reasons. First, there is heightened public awareness of aquaculture impacts on the environment (Positive Aquaculture Awareness, 2004, "Issues in Aquaculture Farmed Salmon, PCBs, Activists, and the Media" www.farmfreshsalmon.org/images/PDFS/rptupdate.pdf, accessed 20 January 2004). Some of the initial public concern was justified, but lately the public has done a poor job of discerning perception from fact. In addition, concern about environmental impacts is often used as a proxy argument for other issues such as visual impacts and the "not-in-my-backyard" attitude. Regardless, the heightened awareness of potential impacts to the environment makes it necessary that all new aquaculture ventures promptly and effectively address this issue. Second, effluent production standards have been considered for lobster impoundments (USEPA 2002). Although the standards were not implemented, they likely will be reconsidered, and possibly acted upon in the future. If regulations are developed for impoundments without appropriate scientific backing, any policies put forth would be based on untested principles. Finally, there is current concern that lobster health in impoundments is compromised, as

shell disease is often noticed within impoundments (Bayer et al 1978; Prince et al. 1995). Improper diets can lead to increased incidence of disease which can be further exacerbated if impoundments are overstocked, leading to environmental degradation. Understanding the relationship between stocking and organic matter production will assist in the analysis of disease states within these areas.

Although in use for over a century, little work has been done on the ecology of these areas—particularly regarding how the impoundment process may alter ecosystem function. One particularly interesting area concerns how the lobster's biology, specifically digestive functioning at winter temperatures, interacts with ecosystem function. Impoundments are point sources for the concentration of organic matter (USEPA 2002). The lobsters are fed during the impoundment period, and likewise excrete metabolic wastes, thus increasing the input of organic matter to the ecosystem at these points. It is unknown how completely the lobsters process the food inputs, and thus what contribution lobster impoundments have on the net organic matter loading to the ecosystem. A majority of the previous research on dietary processing of lobsters was concerned with food digestibility and time for food to pass through the lobster's gastrointestinal tract (Conklin 1995). However, in examining environmental impacts, metabolic wastes need to be considered in a slightly different light. The important features determining how metabolic wastes may impact the environment include the long-term quantity and quality of the produced wastes. Thus, the quantity and quality of faeces produced, and how these values change at different environmental temperatures and different feeding regimens, was addressed. This information was then used to estimate how much organic matter was deposited in a lobster impoundment during the period lobsters were held within. This estimate was intended to be an upper limit value, which will create a starting point to better address environmental impacts of lobster impoundments.

METHODS

To assess the faecal organic matter production by American lobsters, animals were held at the New England Aquarium, Boston, MA, United States, and fed a diet with a known content of total volatile solids (TVS). Their faeces were collected daily, and these samples were analysed for faecal output ($\text{g faeces}_{\text{dry weight}} / \text{g lobster}_{\text{wet weight}} (\text{WW})$) and its TVS content. Lobsters were held individually in a recirculating

sea-water system (10% daily exchange) in 8-litre plastic containers within a larger 200-litre fibreglass tank. Each individual container had six mesh panels in the top 5 cm. Water was recirculated through each plastic tub at a rate of 4 litres/h. Each lobster was scheduled to be tested under three feeding regimes (a single food presentation, once every 4 days, and every day) at three temperatures (5, 10, and 15°C, Table 1). However, because of the length of time needed to conduct these experiments, two groups of lobsters were used. The first group was acclimated to a set temperature of 10°C for 10 days, during which time the animals were not fed. On the 11th day, the tank was thoroughly cleaned, and animals were then fed a single meal. Each animal was fed shrimp (*Panaeus monodon*) at 3% of their body weight ($\text{food}_{\text{WW}}/\text{lobster}_{\text{WW}}$). Faeces were collected daily by siphoning the particulate waste off the bottom. Midway through this trial, one lobster died. It was not replaced, and the initial data from this animal were not used in any of the analyses. After 17 days, the feeding regimen was then increased to once every 4 days (intermittent feed) for four feeding cycles. On days that the animals were fed, faeces were collected before the feeding event. At this point, the temperature of the incoming water was lowered to 5°C. These animals were then re-acclimated to the lower temperature for 8 days. During this period, they remained on the intermittent feeding schedule. Faecal samples were then collected for four intermittent feeding cycles. A second group of five lobsters was acquired, and acclimated at 15°C for 15 days, during which time they were not fed (Table 1). On the 16th day, their containers were thoroughly cleaned and the animals fed a single meal. Faecal

collection started, and continued daily for the remainder of the experiment. After 8 days, the animals were then fed intermittently for four feeding cycles. Finally, this group of animals was fed daily for 8 days.

The faecal samples were processed immediately for storage. A majority of the water was removed, and the samples were then placed into 2.5 ml microcentrifuge tubes and stored at -80°C until they were analysed. Each sample was analysed for %DM and %TVS (Thlusty et al. 2000b). Samples were rinsed to remove salt, weighed, then dried for 24 h from which dry matter was calculated. Next, the samples were ashed in a muffle furnace at 500°C for 8 h, cooled, and re-weighed. TVS was determined as the % loss of mass on ignition ($\text{LOI}_{500\text{C}}$).

Data analyses

All data were checked for normality and equal variance. Those failing these tests were analysed utilising ranked data (Sigma-Stat 2.03). Because not all lobsters were tested at each temperature × feed-interval combination (Table 1), analysing the complete data set was difficult because the repeated-measures ANOVA was unbalanced. Relevant subsets of the data were analysed by grouping similar feeding regimen trials across temperatures, or different feeding regimens within temperature. The resultant analyses were two-way repeated-measure ANOVAs. One factor was always the number of days, which was the sequential count in the single and daily feeding regimens. In the intermittent trial, “days” was the 4 days after feeding, with values being averaged over the four replicated feeding events. The repeated measure occurred on one or

Table 1 Summary of experimental designs, and the temporal sequence in which they occurred. Two groups of American lobsters (*Homarus americanus*) were used. The first experienced 10 and 5°C, the second only 15°C. Animals were held for a acclimation (Acc.) period in which they were not fed, or fed once every for days (Acc.*). The feeding trials consisted of animals being fed a single time (Sing.), once every 4 days (Int.), or every day (Daily). Days refers to the sequential count of days for each experimental group of animals. For the five comparisons listed, the groups being statistically compared are identified by similar letters.

Animals	1-4	→→	→→	→→	→→	6-10	→→	→→	→→
Temp. (°C)	10	→→	→→	5	→→	15	→→	→→	→→
Feed trial	Acc.	Sing.	Int.	Acc.*	Int.	Acc.	Sing.	Int.	Daily
Days	1-10	11-29	30-46	47-54	55-70	1-15	16-24	24-40	41-48
Comparison									
1							a	a	a
2		b	b						
3			c		c				
4			d					d	
5		e					e		

both factors depending on whether the analysis compared the same animals at different temperatures (5 versus 10°C) or different animals at different temperatures (10 versus 15°C). Treatment comparisons were made with Tukey's test. Power was calculated with $\alpha = 0.05$.

Modelling cumulative organic matter production

The model of the cumulative production of organic matter within impoundments was accomplished by assessing production of TVS throughout the impoundment period. This required knowing the daily amount biomass of lobsters in the impoundments, the feeding schedule, and the quantity and quality (TVS content) of faeces produced specific to the feeding regimen. Data on the rate of stock addition, feeding, and stock removal for each lobster impoundment was gathered by relying on the impoundment owners to share their information. Information was supplied by three owners for four impoundments. Two of the impoundment owners supplied data for 3 years, and one for only a single year. Similarly, two owners supplied all three pieces of information (addition, feeding, and removal) whereas one owner only supplied stock addition and feeding data.

The stock addition and removal data were used to create a time series of cumulative weight of animals in the impoundment. The feeding schedule was analysed to determine the feeding regimen (days between feedings). This cumulative weight of lobsters was then multiplied by both the average weight of faeces produced and TVS content of the faeces produced (determined in the previously-described laboratory experiments) specific for the feeding regimen, to arrive at the estimation of the organic matter produced per day per impoundment. Since complete stocking data were lacking for all impoundments, the cumulative production of TVS was first calculated through the feeding period for all impoundments. The feeding period was defined as 17 days post-terminal feeding, as this was the longest observation period investigated in the laboratory study, and the point at which the model utilised a lower value for TVS production. The cumulative production of TVS throughout the entire impoundment period was then determined for the four impoundments in which there were complete data. The percentage difference between the cumulative TVS production through the feeding period and the entire impoundment period was calculated. This value was used to interpret cumulative TVS production throughout the entire impoundment

period for the impoundments in which the removal data were lacking.

The total net weight of TVS produced was of little use by itself, as it varied with the total number of lobsters in the impoundment, as well as with the total area of the impoundment. Thus, this value was altered to become a valuable metric for assessing impacts of lobster impoundments on the environment, and for managers to estimate organic matter loading from lobster impoundments. To assess impact of impoundment on the environment involves shifting this number to a rate of production of TVS per area per unit time. Thus the weight of TVS produced was converted into $\text{g TVS m}^{-2} \text{ day}^{-1}$. For managers, it is best to be able to predict TVS loading from lobster impoundments by being able to estimate TVS production with different stocking levels. Thus the total weight of TVS produced was also converted to the %TVS production, $\% \text{TVS}(\text{kg}_{\text{DW}})/\text{lobster}(\text{kg}_{\text{WW}})$, for the entire impoundment period.

RESULTS

Feeding regimen

Data from animals tested under different feeding regimens were analysed to examine how food delivery affected excretory processing. At 15°C, animals were tested under all three feeding regimens (comparison 1, Table 1). Here, a statistically significant feeding regimen \times day (4 days) interaction was observed for the faecal output (two-way repeated measures ANOVA on ranked data, $F_{6,24} = 4.936$, $P < 0.002$, power = 0.920). In general, animals fed daily produced a greater amount of faeces. An analysis of simple effects demonstrated that the amount of faeces (g_{DW}) per lobster (g_{WW}) per day did not change over 4 days for animals fed a single time or daily (for all pair-wise comparisons, Tukey's test, $q < 3.17$, $P > 0.13$). However, for animals fed intermittently, more faeces were produced on day 1 than any other day (for all comparisons to day 1, Tukey's test, $q > 4.13$, $P < 0.03$, Fig. 1).

Unlike the faecal output, there was no significant day \times feed regimen interaction for TVS content of the faeces (two-way repeated measures ANOVA on ranked data, $F_{6,24} = 1.694$, $P > 0.15$, power = 0.220). Animals fed daily produced faeces with a greater TVS than the other two regimens (two-way repeated measures ANOVA on ranked data, $F_{2,8} = 8.424$, $P < 0.01$, power = 0.819, for all comparisons, Tukey's test, $q > 4.69$, $P < 0.03$). There was no statistically significant difference between the faecal output of

Fig. 1 Faecal output (10^{-5} g faeces_{dry weight (DW) / g lobster_{wet weight (WW)}) and total volatile solid content of the faeces (% loss on ignition at 500°C) for five lobsters (*Homarus americanus*) fed a single time, intermittently every 4 days, or daily at 15°C. Daily values are for the first 4 days in the single and daily trial, and averaged over the first four feeding cycles for animals fed intermittently. Data were non-normal and analysed as ranked data. Unranked values are presented here (± 1 SE) since the ranking did not significantly alter the interpretation of the analyses.}

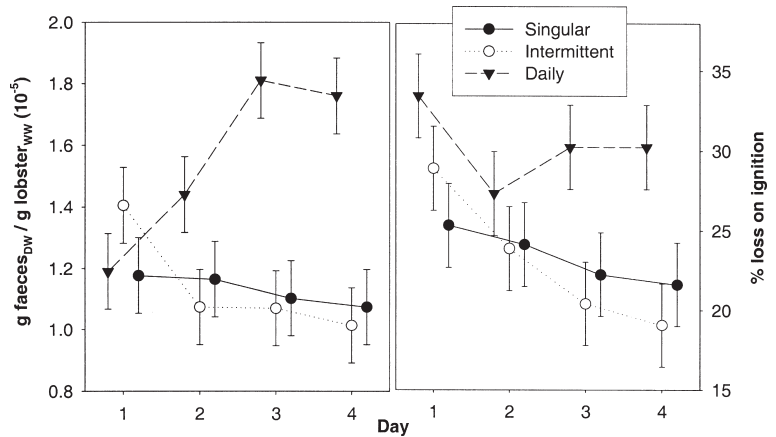
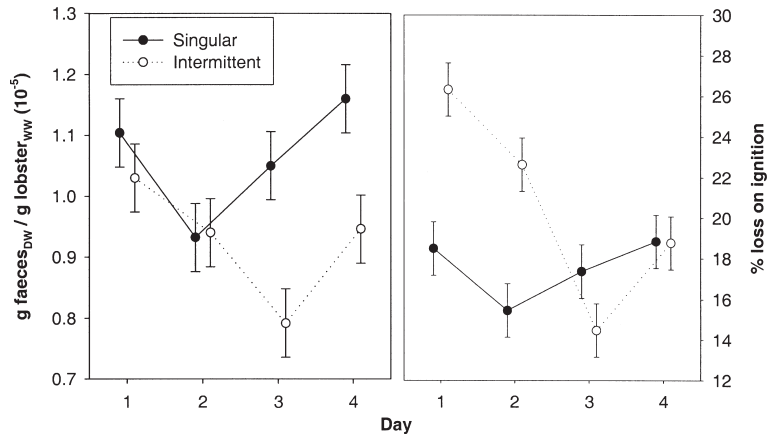


Fig. 2 Faecal output (10^{-5} g faeces_{DW} / g lobster_{WW}) and total volatile solid content of the faeces (% loss on ignition at 500°C) for four lobsters (*Homarus americanus*) fed a single time, intermittently every 4 days, or daily at 10°C. Daily values are for the first 4 days in the single trial, and averaged over the first four feeding cycles for animals fed intermittently. Data were non-normal and analysed as ranked data. Unranked values are presented here (± 1 SE) since the ranking did not significantly alter the interpretation of the analyses.



animals fed a single time compared with those fed intermittently (Tukey’s test, $q = 0.625$, $P > 0.89$, Fig. 1). The number of days post-feeding did not influence TVS content of the faeces (two-way repeated measures ANOVA on ranked data, $F_{3,12} = 1.449$, $P > 0.27$, power = 0.113).

For animals tested under multiple feeding regimes at 10°C (comparison 2, Table 1), the results generally were similar to those presented above, with a few minor differences. An analysis of the rate of faecal production exhibited no significant treatment interaction term (two-way repeated measures ANOVA on ranked data, $F_{3,9} = 3.285$, $P > 0.07$, power = 0.396), and thus main effects were examined. The feeding regimen treatment was the only statistically significant factor (two-way repeated-measures ANOVA on ranked data, feed regimen $F_{1,3} = 31.708$,

$P < 0.01$, power = 0.946, day $F_{3,9} = 2.014$, $P > 0.15$, power = 0.191). However, in this instance, animals produced more faeces per day when fed a single time compared with when they were fed intermittently (Fig. 2). The TVS content of the faeces did exhibit a significant day × feed regimen interaction term (two-way repeated measures ANOVA on ranked data, $F_{3,9} = 6.271$, $P < 0.02$, power = 0.772). An analysis of simple effects shows that there was no significant difference in the TVS content of faeces between days for animals fed a single time (for all comparisons, Tukey’s test, $q < 2.38$, $P > 0.25$). The same animals fed intermittently exhibited a general decrease in the TVS content in their faeces over the 4 days (Fig. 2). Day 1 was not significantly different from day 2 (Tukey’s test, $q = 1.59$, $P > 0.65$), day 2 was not significantly different from day 4 (Tukey’s

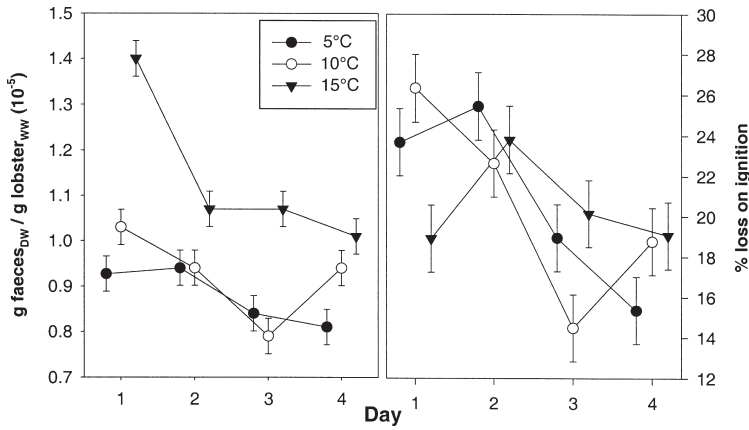


Fig. 3 Faecal output (left graph) and total volatile solid content (right graph) for each of 4 days after lobsters (*Homarus americanus*) were fed intermittently (every 4 days). Values were averaged (± 1 SE) over four feeding cycles—same four lobsters were tested at 5 and 10°C while five different lobsters were tested at 15°C. (DW, dry weight; WW, wet weight.)

Table 2 Analyses of the effect of temperature on faecal output (g faeces_{dry weight (DW)}/g lobster_{wet weight (WW)}) and total volatile solids (TVS) measured as the % loss on ignition at 500°C. Analyses are two-way repeated measures ANOVA with one or both factors repeated. Non-normal data were ranked, and indicated as such. Values for each day after feeding were averaged from four feeding cycles, and the first 4 days, except for when the lobsters were fed singly in which it was calculated over 6 days. Power was calculated with $\alpha = 0.05$.

Source of variation	d.f.	g faeces _{DW} /g lobster _{WW}				TVS			
		MSE	F	P	Power	MSE	F	P	Power
Four lobsters held at two temperatures (5 and 10°C), fed intermittently (faecal output and TVS ranked)									
Lobster	3	306.25				338.531			
Temp.	1	112.5	0.965	0.398	0.05	0.781	0.0259	0.882	0.05
Temp. × lobster	3	116.583				30.198			
Day	3	177.917	3.13	0.08	0.37	941.865	19.712	<0.001	1.00
Day × lobster	9	56.833				47.781			
Temp. × day	3	27.417	1.124	0.39	0.06	103.865	2.88	0.095	0.33
Residual	9	24.389				36.059			
Total	31	88.000				161.249			
Four lobsters held at 10°C and five lobsters held at 15°C, fed intermittently (TVS ranked)									
Temp.	1	4.05E-09	4.269	0.078	0.34	70.313	0.366	0.564	0.05
Lobster (temp.)	7	9.48E-10				192.027			
Day	3	1.43E-09	7.465	0.001	0.94	528.205	14.083	<0.001	1.00
Temp. × day	3	4.24E-10	2.209	0.117	0.27	53.872	1.436	0.26	0.12
Residual	21	1.92E-10				37.508			
Total	35	5.91E-10				111.000			
Four lobsters held at 10°C and five lobsters held at 15°C, fed a single time (faecal output ranked)									
Temp.	1	182.522	0.307	0.597	0.05	222.749	5.308	0.055	0.43
Lobster (temp.)	7	590.899				41.924			
Day	5	226.108	1.429	0.24	0.14	10.703	0.479	0.789	0.05
Temp. × day	5	265.72	1.68	0.167	0.21	24.599	1.102	0.378	0.07
Residual	34	158.202				22.331			
Total	52	229.647				28.116			

test, $q = 2.74$, $P > 0.25$), and day 4 was not significantly different from day 3 (Tukey's test, $q = 3.36$, $P > 0.610$). TVS exhibited a slightly different trend in that intermittent feeding exhibited

significantly greater TVS values for the first 2 days than the third and fourth days, whereas animals fed singularly exhibited little day-to-day variation (Fig. 2).

Temperature

Temperatures between 5 and 15°C had virtually no impact on the quantity or quality of faeces produced by lobsters fed a single time or intermittently. In this experiment, three valid comparisons regarding temperature could be made: (1) the same animals fed intermittently at 5 and 10°C for 4 days; (2) different animals fed intermittently at 10 and 15°C for 4 days; and (3) different animals fed once at 10 and 15°C for 6 days (comparisons 3–5, Table 1). In each of these comparisons, the temperature factor and the temperature × day factor were not statistically significantly different (Table 2, Fig. 3). Of the three comparisons, the most valid pertaining to temperature was the first, as it compared faecal production in the same animals at two temperatures (Table 2). The lack of a significant temperature effect in this comparison, coupled with a lack of significant temperature effect of the other two comparisons lends further credence for failure to reject the null hypothesis of no relationship between temperature and the quality or quantity of faeces produced by lobsters (Fig. 3).

The significant day-after-feeding-treatment effect for lobsters fed intermittently (Table 2) further supports the results discussed previously that lobsters produce more faeces with a greater TVS content the first 2 days after feeding than if more time has elapsed since feeding (Fig. 3).

Duration of faeces production

The animals that experienced a single feeding regimen at 10°C had their faeces evaluated for 17 days post-feeding, whereas those animals tested at 15°C had their faeces collected for 8 days. In both trials, lobsters continually produced faeces for the first 6 days post-feeding. For the animals at 10°C, one animal did not produce faeces on the seventh and 17th days, and two did not produce faeces on the eighth day. At 15°C, one animal missed faecal production on the seventh day, and one on the eighth day. Excluding these days of no faecal production, there was no observed change in amount of faeces produced over the 17 days (one-way repeated measures ANOVA, $F_{11,33} = 1.37, P > 0.24$), or the TVS content of the faeces (%LOI_{500C}, one-way repeated measures ANOVA, $F_{11,33} = 1.36, P > 0.25$). The longest interval for which any of the feeding trials were carried out was 17 days. Although the data were collected as 24-h periods post-feed, the missed days of faecal production represented a period of between 24 and 48 h, as opposed to a stringent 48-h period.

It is likely that faecal production becomes more sporadic the longer after the animal was fed. The few days that lobsters did not produce faeces during the 17 days of monitoring was just the beginning of this pattern of reduced faecal output. Further evidence for long-term faecal production comes from lobster wholesalers. William Atwood Lobster Co, Spruce Head Island, ME, United States, held 680 t of newly caught lobsters for 3 months in an indoor flow-through system in 2003. In this production scenario, the lobsters produced c. 0.49 t of wet faecal waste. Assuming that lobster faeces were 7.3% DM (data from the previously-discussed laboratory experiments), this equates to 5.84×10^{-7} g faeces_{DW}/g lobster_{WW} day⁻¹. This faecal production value was significantly lower than the c. 1.0×10^{-5} g faeces_{DW}/g lobster_{WW} day⁻¹ faecal production by lobsters during the feeding experiments (Fig. 2 and 3). It was likely that there was a degree of soluble loss of constituent faecal components, as well as loss of finer particles (Thlusty et al. 2000b). However, even with this loss of fine particles, these data suggested that there was a significantly lower faecal production by unfed lobsters over a 3-month period than that observed within the first 2 weeks. Thus any long-term estimate of faecal production by unfed lobsters will need to account for this decreased output.

Modelling cumulative organic matter production within lobster impoundments

The results presented above regarding the amount and organic matter content of lobster faeces, measured as TVS, can be used to estimate total organic matter production per impoundment over the course of the impoundment season. To simplify this modelling exercise, the experimental results for faecal production and TVS content of American lobster faeces needed to be pared to parsimonious trends. From the data presented above, it was first assumed that faecal production did not vary with temperature when winter-time temperatures (<10°C) were considered. Second, the quantity and quality of faeces produced did not vary with size of the meal fed as a % of the lobster's weight. In the experiments on faecal production described above, a meal of 3% g food/g body was utilised. Although this was the amount that was often fed to lobsters at the beginning of the impoundment season, by the end of the season, when temperatures were colder, food was being delivered at a rate of <1% g food/g body day⁻¹ (Fig. 4). This ration was completely consumed, as American lobster will consume up to 50% (wet weight basis) of their body mass daily (Donahue et

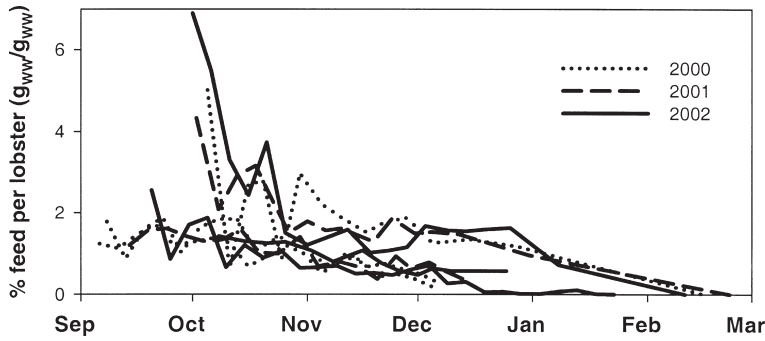


Fig. 4 Amount of food fed (% on a wet weight (WW) basis) to lobsters (*Homarus americanus*) in 10 impoundments during three seasons. Decrease in the amount of food delivered to the lobsters corresponded to a decrease in water temperature.

Table 3 Physiological conditions of faecal output used to model the cumulative production of organic matter by American lobsters (*Homarus americanus*) held in impoundments. Values were ascertained from the previous feeding trial studies. (DW, dry weight; WW, wet weight.)

Days between feedings	g faeces _{DW} /g lobster _{WW}	% volatile solids (LOI _{500C})
<3	1.10E-05	25
3–17	8.70E-06	20
>18	5.87E-07	15

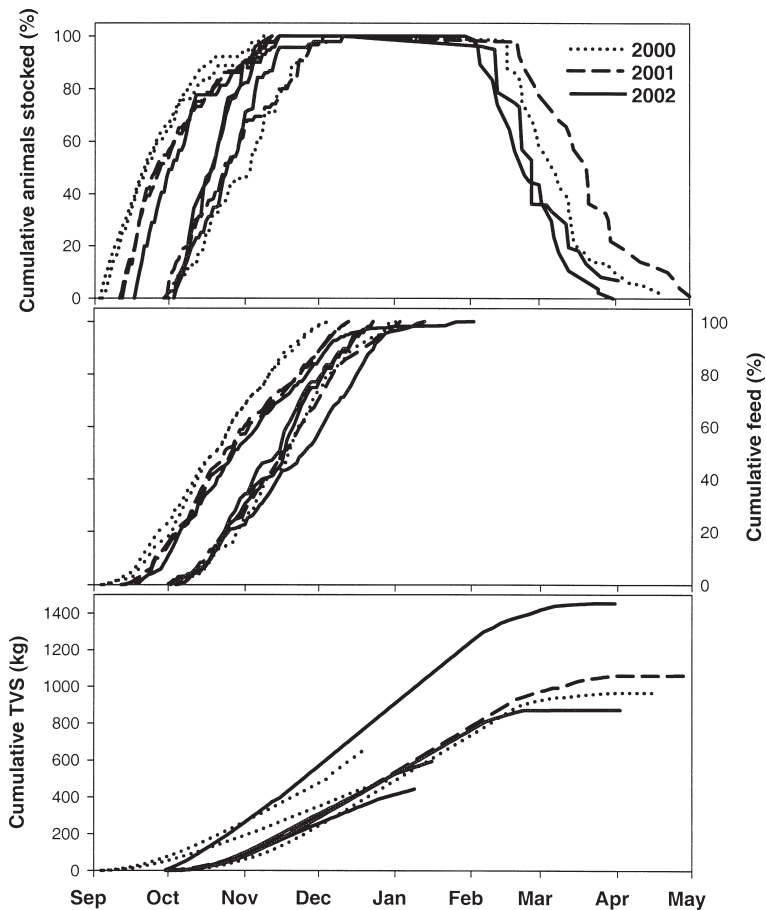
al. 1997). Ration size would influence digestion via a change in the gut retention time, where larger and more frequent meals would decrease the amount of time the food was processed in the gut (Stephens & Krebs 1986; Hilton et al. 2000). In other animals, the time food is retained in the gut is negatively related to digestive efficiency (Johnston & Mathias 1996; Hilton et al. 2000). However, given the relatively low ratio of food fed in these experiments, it is questionable as to whether faecal quality would change significantly with a decrease in feeding ration. The third and final control rule was that animals fed every day or every other day produced more faeces with higher TVS than those animals fed intermittently, and animals fed every 3–18 days produced more than those animals fed once every 18 days or more (Fig. 3).

The control rules as they were used in this modelling exercise are listed in Table 3. Using these values to calculate TVS production, it was observed that TVS production varied between impoundments and years (Fig. 5). In general, the stocking of animals into the impoundment began between the first week of September and the first week of October. The impoundments were fully stocked over the next 40–75 days, and were completely stocked with an average of 3.79 ± 1.29 (± 1 SD) kg lobster_{WW} m⁻².

Animals were fed daily or every other day during the stocking period, and as the temperatures became colder and the animals “bed” down, feeding became intermittent. A majority of owners fed for 80 to 120 days following the first day of stocking, although one owner fed for 155 days (Fig. 5). Animals were removed beginning in January or February, and the impoundments were generally clear of animals by April, c. 190–210 days after the animals were first added to the impoundment (Fig. 5).

The variability in animal density, feeding protocol, rates of stocking and removal influenced the total amount of TVS produced. Through the feeding period, an average of 661.70 ± 289.89 (± 1 SD, $n = 10$) kg TVS were produced per impoundment. This represented $77.9 \pm 15.3\%$ (± 1 SD, $n = 4$) of the TVS produced during the entire impoundment period. Adjusting the impoundments lacking the lobster removal data to account for TVS production through the entire impoundment cycle, the average cumulative TVS produced per impoundment was 849.4 ± 367.0 kg_{DW}. This corresponded to a production rate of 0.79 ± 0.35 (average ± 1 SD) g TVS m⁻² day⁻¹ for the 10 impoundments examined here, equivalent to $3.11 \pm 0.60\%$ TVS_{DW}/lobster_{WW} of the total weight of lobsters stocked into the impoundment.

Fig. 5 Stocking (top), feeding (middle), and the modelled cumulative organic matter production (total volatile solids (TVS) measured as loss on ignition at 500°C, bottom) for 10 lobster (*Homarus americanus*) impoundments over three seasons.



DISCUSSION

The impoundment of American lobsters is best thought of as an aquaculture operation. Animals are held, fed, and occasionally medicated, for periods up to 6 months. Thus, the estimates of organic matter production within these impoundments (based on both production per unit area and per unit lobster produced) need to be compared to other types of aquaculture operations. Salmon aquaculture operations will be used as the main comparator, as it is also carried out in coastal waters of North America. The general observation has been that carbon flux rates to the benthos in excess of 1 g carbon m⁻² day⁻¹ exceed mineralisation capabilities thus causing anoxic sediments (Oviatt et al. 1987; Hargrave 1994). Above this rate, the oxidation-reduction potential of the sediment eventually becomes negative causing anoxia, subsequently leading to decreased infaunal diversity and hydrogen sulfide

production (Brown et al. 1987; Findlay et al. 1995; Black et al. 1996; Brooks 2001). Total organic carbon is c. 63% of the TVS (Brooks 2001), thus the corresponding TVS loading that will not lead to increased deposition of sedimentary organic matter was 1.58 g TVS m⁻² day⁻¹. Data from reference areas and those areas removed from anthropogenic input supported this value as they tended to have TVS deposition rates below 2.0 g TVS m⁻² day⁻¹ (Morrisey et al. 2000; Brooks 2001). Salmon farms had organic matter levels up to 18–24 g TVS m⁻² day⁻¹ observed immediately beneath the farm (Brooks 2001). The upper limit for the 95% confidence interval for TVS production in lobster impoundments examined in this study was 0.99 g TVS m⁻² day⁻¹, which was below the value of 1.58 g TVS m⁻² day⁻¹ that was assumed to be within the ability of the environment to assimilate, thereby giving minimal impact. This analysis considers only

lobster-derived effluents, and not natural deposition. Lobster impoundments are active in the winter, a time when the natural productivity of ecosystems is low. It was unlikely that natural organic matter deposition in the impoundment areas during the winter would be equivalent to the amount being produced by the lobsters. A pulse of organic matter deposition was observed between April and September, the period when lobster impoundments are not being used, thereby corresponding to natural productivity associated with the North American summer (Tlusty 2003). Therefore, lobster impoundments were unlikely to reach the mark of $1.58 \text{ g TVS m}^{-2} \text{ day}^{-1}$, and thus indicating that the solid waste production of lobster impoundments was low enough not to lead to an increase in deposition of organic matter to the benthos.

The estimate of organic matter production within lobster impoundments in Maine created through this procedure were an upper limit estimation. Because of the food that was utilised, and the temperatures at which the animals were held, organic matter production is likely to be greater than it would be under an actual impoundment scenario. The shrimp being fed to the experimental animals was likely to be more digestible than that in an actual working impoundment (most commonly herring or salted cod). Second, the laboratory animals were restricted in movement compared with animals in an impoundment. Finally, the lowest water temperature examined here was still greater than the 0°C commonly observed in the impoundments during winter. Furthermore, this estimated amount is the starting point before any subsequent environmental processing (soluble, transport, and consumption losses, Tlusty et al. 2000b). That being said, it was important to note the relatively low level of organic matter production observed by the lobsters under the simulated impoundment conditions. To understand how lobster impoundments compare to other aquaculture operations, this estimated upper limit value can be compared to real values for salmon and shellfish operations.

Because of the point source loading of aquaculture effluents, sediment organic matter tends to be greater adjacent to an aquaculture site than it is at a distance (Brooks 2001 and references within). The distribution of sedimentary organic matter is patchy, and although TVS content below salmon farms can range upwards of 65% (Samuelsen et al. 1988; Cornel & Whoriskey 1992; Tlusty et al. 2000b), it typically averages <20% (Hargrave et al. 1997). The Scottish Environmental Protection Agency uses 27%

as the limit below which no remediative action is required (Heinig 2001). In shellfish aquaculture operations, rates of sediment deposition are comparable to that of salmon farms, although differences between faeces and pseudo-faeces can impact the quality of organic matter being deposited. Impacts ranged from negligible (Grant et al. 1999) to TVS values of between 20% and 25% (Dahlbäck & Gunnarsson 1981; Mattsson & Lindén 1983). In light of these values for TVS production, the lobster impoundment produced significantly less TVS than any other aquaculture operation, and the rate of TVS accumulation equalled that of the background areas referenced above. The TVS in surficial sediment samples from Maine lobster impoundments, measured as the %LOI₅₀₀, averaged <5% (Tlusty 2003), and was often lower, especially within the lobster impoundments. These data further support the conclusions from modelling of solid effluent production that lobster impoundments produce relatively low levels of organic matter, which is being biologically processed instead of accumulating on the benthos.

The low levels of TVS being created and deposited in lobster impoundments compared to the greater levels around salmonid farms can assist in elucidating the factors important for minimising environmental impacts of marine aquaculture operations. The difference between these two types of aquaculture operations include differences in the digestion and feeding regimens of crustaceans compared to finfish, the length of fallowing periods utilised, stocking densities, and physical disruption of the benthos. The first factor leading to the relatively lower rate of TVS deposition was the lower rate of lobsters' faecal production compared with that of other aquacultured organisms. In addition to the different food types (although artificial diets fed to both are created similarly), the digestive system of lobsters is more complex than that of finfish. Lobsters have both a mid-gut and hind-gut caecum, which increases digestive and absorptive capabilities (Factor 1995). Salmonids have a more linear digestive system without additional ceecal capacity. These physiological differences resulted in lobster faecal TVS ranging from 15% to 25% depending on time since last feeding. In salmon, TVS content of faeces varied between 50% and 80%, although values as great as 90% in the winter were observed (Tlusty et al. 1998, 2000b). In addition to physiological differences, much of the cause behind the lower lobster faecal production in lobsters was the fact that they were fed

for c. 50% of their time in holding. Lobsters were not fed for months at a time, particularly after the temperatures reached their winter minima. Salmon were fed throughout the winter, although at a much reduced rate (Thlusty et al. 1998). These differences in digestion and feeding regimens ultimately resulted in different levels of organic matter production throughout the production cycle. During the impoundment period, TVS production was 3% of the total stocked lobster biomass. In comparison, estimates for total faecal production of salmonids through the production cycle averaged 16% (Bergheim & Åsgård 1996).

Second, lobster impoundments were not utilised continually throughout the year. They were empty, or fallowed, for up to 6 months per year. Fallowing was beneficial in that natural ecosystem functions were allowed to bioprocess any accumulated organic matter. Organic matter was assimilated through consumption, translocation, and diffusion (Thlusty et al. 2000b). Displaced organisms recolonised the disrupted areas during the fallow period, and their activity assisted to reoxygenate the benthos. This activity functioned to return the aquaculture area to a pre-disruption state. Although a low level of organic matter was deposited, the relatively lengthy fallow period further assisted in minimising the environmental impact of lobster impoundments. The benefits of fallowing within aquaculture operations are just now becoming more fully appreciated, and lobster impoundments serve as a positive example of their benefits.

Third, stocking density of lobsters was lower than that for salmonids, a function of the finish operations occurring in a volume of water as opposed to the planar stocking of lobsters. Salmon are stocked at a density of c. 18 kg m⁻³. A salmon cage 50 m in circumference and 5 m deep, is stocked with 17 904 kg of fish. In terms of an areal impact, this would translate to a stocking density of 90 kg m⁻². Also, the bottom of a salmon cage is further removed from the benthos, and although this may lead to greater dispersal of organic solid waste over the area of the substrate (Findlay et al. 1995), often wastes are functionally dispersed immediately below the cages (Thlusty et al. 2000a). The dispersal of wastes on their path to the benthos would have to be significant to reduce the effluent production of salmon aquaculture sites to a level equal that of lobster impoundments.

Finally, lobsters are active on the benthos. Until winter temperatures reach their minima, the lobsters are moving around feeding. Their relatively thin

walking legs will penetrate the soft surficial sediments. This serves to aerate and mix the upper few centimetres of the sediment, redistributing the pore water and ultimately maintaining a positive oxidation-reduction potential in the surficial sediment. This is similar to the idea of harrowing, which is often used to decrease the benthic impacts of aquaculture operations (Boyd 2003).

The research reported here was the first attempt to predict TVS production by impounded American lobsters. For this modelling effort, three control variables were incorporated into the model. The quantity and quality of faecal production did not vary with: (1) temperature <10°C; or (2) the feeding rate as a % of the body weight of lobsters; but (3) did vary with the feeding regimen. Specifically that more faeces of higher quality were produced when animals were fed daily or every other day compared to intermittently or not at all. The evidence for the first assumption was presented as the analysis of the feeding experiments conducted as part of this research programme. Physiologically, American lobsters respond differently to temperatures above in contrast to below 10°C. Maturity and egg development will remain in stasis or at a greatly reduced rate below 8°C, whereas above this temperature, animal growth and development proceeds rapidly (Cooper & Uzman 1971; Aiken & Waddy 1989). It is likely that manifestation of temperature-mediated developmental differences have their basis in enzymatic and digestive functioning.

The second assumption that quantity and quality of faecal production did not vary with feeding rate as a % of the body weight of lobsters is less assured. Although the rate of 3% food/body weight was within the range of feeding rates used within the impoundments examined here, for a majority of the time, animals were fed <2% of their body weight daily (Fig. 4). In general, when animals were fed at a lower rate, gut retention time tended to increase, increasing nutrient absorption and thus leading to a decrease in TVS production (Stephens & Krebs 1986; Hilton 2000). Any decrease in faecal quantity or quality with the decreased rate of feeding likely will lead to subsequent decreases in the TVS production of the impounded animals. More work will be needed to assess the concomitant decrease in TVS production with a decrease in feeding rate. If TVS production is positively associated to feeding rate, then the estimations for TVS production can be considered an overestimation, as lower feeding rates would lead to lower levels of TVS production. Finally the third assumption, that more faeces of

higher quality were produced when animals were fed daily or every other day compared to intermittently or not at all, was also supported by the analysis of the feeding experiments conducted as part of this research programme. This observation coalesces with foraging theory (Stephens & Krebs 1986).

In addition to these control rules, there was also the implicit assumption that all food was consumed by the lobsters. The model developed here to estimate lobster impoundment TVS production assumed that all TVS is derived from faeces. If all food was not consumed by the lobsters, then the TVS content of the unconsumed feed would have to be accounted for in the estimation of TVS production. Functionally, uneaten feed would increase the amount of TVS reaching the benthos, and would increase the subsequent measure of sedimentary TVS. Food is placed in lobster impoundments directly on the bottom, and hence uneaten food would also increase the spatial variation of TVS throughout the impoundment.

The main tenet of sustainable aquaculture progress is that careful development of a suitable area at a reasonable effort can lead to an industry that has low to no impact on the environment (O'Connor et al. 1991; Olsen 1996; Tlusty et al. 1998). The best way to foresee potential impacts is to model the system to determine appropriate loading levels (Hargrave et al. 1994). It is critical to complete this work as early in the development of the industry as possible. When this work is put off the industry can outpace itself, which can result in a wide variety of environmental problems and subsequent public outcry. Proactive environmental work has the ability to quell any concerns citizen groups may have about negative environmental impacts (Tlusty unpubl. data). This work demonstrating low levels of organic matter loading in lobster impoundments and subsequent minimal impact on the naturally-occurring fauna was a necessary but long overdue component to assure the continued sustainable development of both aquaculture operations and the lobster fishing industry.

Recently, the United States Environmental Protection Agency listed lobster impoundments as aquaculture facilities that do not need active monitoring (USEPA 2002). The modelling presented here along with environmental assessments of impacts (Tlusty 2003) support the EPA ruling. However, lobster impoundment owners along with all aquaculture operators need to be cognizant of the effects and subsequent impacts that aquaculture can have on the environment. Lobster impoundments

produce less organic loading to marine benthos than do respective salmon or shellfish aquaculture operations. This lower organic matter production and minimal resultant observable environmental impacts are because of the sparse feeding of impounded lobsters, a more efficient digestive process, the low organic matter production in the faeces, and the long fallow times each year. These results stress the importance of proper feed management, stocking, and fallowing in all aquaculture operations to continue to progress toward environmentally benign operations. Given the importance of lobster impoundment to the lobster fishing industry, coupled with the minor environmental impacts, it behoves regulatory agencies not to overburden the impoundment owners with unnecessary monitoring activities.

ACKNOWLEDGMENTS

This work could not have been completed without the immense assistance of R. Bell and L. Rohrbaugh who conducted the organic matter analyses, organised data, and assisted in the field sampling. D. Cowan, S. Ellis, and J. Sowles provided valuable critique on the formation of this project, and V. Pepper, M. R. Anderson, and L. L. Wolf greatly influenced Michael Tlusty's philosophical approaches to aquaculture monitoring, modelling, and integrative biology. J. Petersdorf provided data on long-term faecal production. L. Kaufman provided access to laboratory facilities for some of the messier analyses. D. Fiore helped maintain lobsters in the laboratory. S. Ellis and D. O'Grady provided further assistance in the field. We also thank J. Burke, D. Cowan, C. Howard, K. Smalley, R. Watkins, T. Watkins, and G. Worthley for allowing access to their properties. Comments from V. Pepper and two anonymous reviewers greatly improved a draft version of this manuscript. This work was supported by MIT Sea Grant No. 5710001239 to M. Tlusty.

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