

Carbon budget for a coastal inlet in relation to intensive cultivation of suspension-feeding bivalve molluscs

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ABSTRACT: Killary Harbour, a fjordic inlet on the west coast of Ireland, is the site of intensive suspended cultivation of mussels. Data on biomass and production of the macrobenthic infauna and zooplankton in the system are combined with literature data on primary production and wild and cultured mussel production in Killary Harbour to produce a balanced carbon budget. Total particulate carbon input to the system is 1907 tonnes C yr⁻¹. Carbon production by phytoplankton is partitioned between zooplankton, cultured mussels, wild mussels, phytoplankton respiration and the detritus pool. The detritus pool also receives inputs from river carbon, macroalgae, zooplankton faeces, mussel faeces and phytoplankton. There is a carbon deficit which is probably accounted for by DOC input in freshwater, or import of marine POC, which were not measured. The data are used to estimate the maximum potential yield of cultured mussels from the system. This is in the order of 2000 to 3000 tonnes live weight per year. At this level of production, changes in the ecosystem are predicted. These are expected to arise from competition between mussels and zooplankton for food resources, increased sedimentation in localized areas, and disruption of the nitrogen cycle. However, nitrogen should not limit mussel production. Mussel culture, unlike fish culture in sea cages, re-routes the flow of energy and materials in coastal marine ecosystems but does not cause eutrophication by nutrient input. This is discussed in relation to red tides.

INTRODUCTION

Killary Harbour is one of the principal sites in Ireland for intensive suspended cultivation of the mussel *Mytilus edulis*, as well as being the chief area for seeding ropes (Rodhouse et al. 1984a). The mariculture industry is expanding and this raises the question of carrying capacity and potential yield of cultured, suspension-feeding bivalve molluscs in coastal marine sites. The Shellfish Research Laboratory has addressed this question by carrying out an investigation of carbon and nutrient flow in wild and cultured mussel populations, in relation to carbon and nutrient flow in the Killary Harbour system (Rodhouse et al. 1984b, 1985, McMahon & Patching 1984).

Potential bivalve yield in coastal water, if dependent

on *in situ* primary production of phytoplankton, averages about 0.15 tonnes ha⁻¹ yr⁻¹ dry meat weight (= approximately 4% live weight). However, intensive cultivation in small areas has produced 5 to 500 tonnes ha⁻¹ yr⁻¹ (Ryther 1969). These high values result from the concentration into a small area, such as an estuary or fjord, of organic matter produced over a large area. Bivalve production depends upon the food level in the water and the rate at which it is carried to the animals by tidal currents. Raft culture may be more effective in bringing food to the animals, by about 3 orders of magnitude, but since high productivity of bivalves depends upon the level of food produced over a large area, production measured on, for example, a small experimental raft or rafts cannot be extrapolated for the entire area of a mariculture site such as Killary Harbour.

In this paper we present data on the carbon budget for the Killary Harbour system which will be used to estimate the carrying capacity of the inlet for intensive cultivation of mussels.

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MATERIALS AND METHODS

Killary Harbour is a fjordic inlet on the west coast of Ireland. Leenane, the only village on the inlet, is positioned at 53° 57' N, 9° 42' W. The inlet is approximately 11 km in length with an average breadth of about 700 m and an average depth of about 14 m. The deepest part is 45 m immediately inside Inishbarna, an island on the entrance sill. For the purpose of this study the inlet was divided into 5 sectors, A to E, which are shown in Fig. 1. The dimensions of each sector are given in Table 1. The total catchment area of Killary Harbour is some 250 km²; 2 rivers, the Erriff and Bundorragha, drain mountainous bogland.

Primary production and allochthonous carbon sources. Measurement and estimation of phytoplankton production and respiration, riverine discharge of particulate organic carbon (POC) plus 'active' dissolved organic carbon (DOC), and sedimentation and flushing of organic carbon within the Killary Harbour system were described by McMahon & Patching (1984).

Macroalgae cover a small area in Killary Harbour because of rapidly shelving rocky shores or the presence of unstable sand and gravel. Assuming that a 10 m wide strip along 23 km of coastline is covered by

macroalgae (Lambe, cited in Keegan & Mercer 1986), an area of 23×10^4 m² is available for seaweed production. Production rate by macroalgae *Laminaria* spp. is reported to be between 100 and 400 g C m⁻² yr⁻¹ (Raymont 1980).

Benthic microalgal production was estimated to be 7 g C m⁻² yr⁻¹. This is the value given by Raine & Patching (1980) for Roskeeda Bay, further south on the Irish coast, where similar conditions exist of relatively deep water (10 to 20 m) and fine, easily disturbed sediment.

Zooplankton. Sampling methods and the seasonal cycle of abundance of zooplankton in Killary Harbour are given by Ryan et al. (1986).

For copepods, standing crop biomass was estimated for *Acartia clausii* copepodites and adults from length-weight equations given by Durbin & Durbin (1978) and Robertson (1968); for *Oithona nana* and *O. similis* from the equation given by Evans (1977); for all other copepods – mostly *Paracalanus*, *Pseudocalanus*, *Centropages*, *Temora* spp. and copepodites – from the equation given by Robertson (1968) and for copepod nauplii from the equation given by Durbin & Durbin (1978). Estimates of dry weight were converted to carbon assuming carbon content to be 0.5 (Omori 1969). Production was estimated using daily production: biomass (P:B) ratios given by Greze et al. (1968), Greze (1978) and Uye (1982). Where more than one estimate of production could be made from different published P:B ratios, mean values were calculated and are reported here.

Standing crop biomass of *Evadne nordmani* was estimated assuming a mean individual weight of 2 µg C (P. Burkill pers. comm.). To estimate production a P:B ratio for another cladoceran, *Penilia avirostris* (Greze 1978), was applied. For the appendicularian *Oikopleura dioica* linear measurements were converted to biomass using the equation given by Paffenhöfer

Table 1. Surface area and mean depth of Killary Harbour, Ireland

Sector	Surface area (m ²)	Mean depth (m)
A	1.34×10^6	4.04
B	1.41×10^6	11.29
C	2.17×10^6	14.81
D	1.43×10^6	18.95
E	9.55×10^5	23.87
Total	7.29×10^6	–
Mean	–	14.15

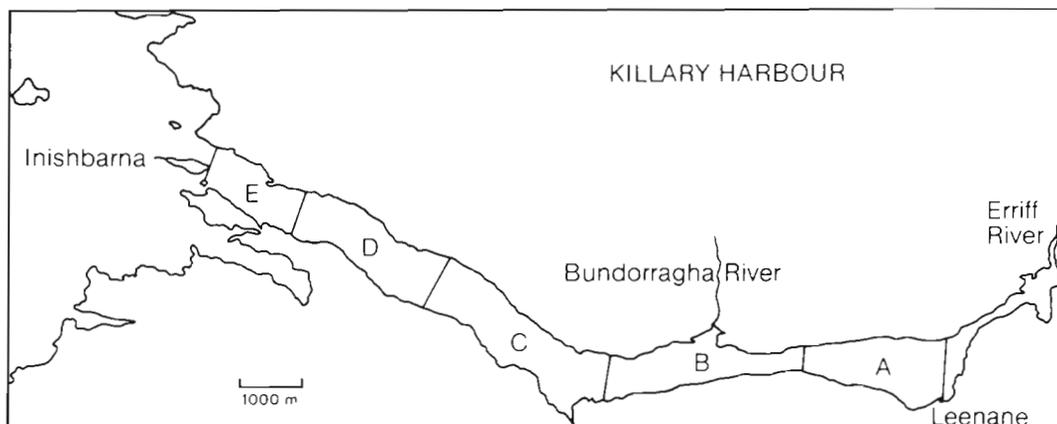


Fig. 1. Killary Harbour, west coast of Ireland, showing sectors

(1976) and converted to carbon assuming a carbon content of 0.4 (Curl 1972). Production of *O. dioica* was estimated from the P:B ratio given by Zaika (1972).

For gelatinous zooplankton the biomass of the ctenophore *Pleurobrachia pileus* was calculated from equations given by Hirota (1974). This incurred an error as the specimens were preserved in formalin and would have shrunk by up to 22% (Yip 1982). Carbon content was assumed to be 0.2 (Curl 1962) and production was calculated from the P:B ratio given for another ctenophore, *Mnemiopsis* sp. (Reeve & Baker 1975). Daily production of medusae was approximated assuming that equal wet volumes of *P. pileus* and medusae have equal production rates.

Production of meroplanktonic bivalve and polychaete larvae was estimated on the assumption that together they accounted for the same fraction (0.13) of holozooplankton herbivore production, as in an Arctic fjord (McLaren 1969). Production of meroplanktonic cirripede larvae was estimated by assuming a mean individual weight of 2.5 μg C for nauplii, 11 μg C for cyprids (Burkill pers. comm.) and a daily P:B ratio of 0.1.

Benthos. Samples were taken between 7 August and 9 September 1980 with a diver-operated suction sampler (Barnett & Hardy 1967). The sample was delivered into a bag with a 1 mm mesh suspended over the side of the support vessel. Details of samples taken in each sector are given in Table 2. Samples were returned to

Table 2. Details of macrobenthos samples taken in each sector

Sector	Date (1980)	Quadrat area (m ²)	n	Depth below chart datum (m)
A	19 Aug	0.25	5	1.4
B	18 Sep	0.25	5	4.7
C	11 Sep	0.25	5	6.5
D	12 Aug	0.25	5	12.2
E	7 Aug	0.25	4	12.5

the laboratory, sorted on a 1 mm mesh and preserved in 5% buffered formalin. They were later split according to taxonomic group and identified to species level.

Annelids, which tended to break up during sorting, and phoronids from each sample were pooled according to species and dried in tared aluminium foil dishes at 90°C for 24 h, weighed, combusted in a muffle furnace at 500°C and re-weighed after cooling in a desiccator. Biomass, as ash-free dry weight (AFDW) of taxonomic groups from which large numbers of individuals were collected, was determined from regression equations relating AFDW (g) to some linear dimension (LD) in mm, which were derived from subsamples. LD was usually length, or disc diameter in the

case of ophiuroids. Where small numbers of a species were present, or the size range was small, biomass of each individual was determined. AFDW determinations for molluscs included the organic component of the shell.

Mussels. Measurement of the production rates and carbon flow in wild and cultivated mussel populations in Killary Harbour was described by Rodhouse et al. (1985).

RESULTS

Primary production and allochthonous carbon sources

Flux of organic carbon in Killary Harbour, given by McMahon & Patching (1984), is summarized in Table 3. They calculated a net export of 459 tonnes C yr⁻¹ from Killary Harbour into the open sea. This is based on the calculated exchange of water at the mouth and the measured concentration of POC at 0, 5, 10 and 20 m in Sector E. Roden et al. (1987) show that a subsurface particulate maximum was frequently recorded at 5 or 10 m throughout the inlet in 1980/1981. Booth (cited in Keegan & Mercer 1986) also recorded a sonic scattering layer in May 1974 at approximately 5 m. This particulate maximum coincided with the depth of the halocline. Calculations of carbon export will be greatly affected by the assumed depth of the upper, outward-flowing layer of water. McMahon & Patching (1984) take this layer to include both the 0 and 5 m sampling points, thus often including the subsurface particulate maximum in the outward-flowing layer. The upper, outward-flowing layer is separated from the deeper inward-moving layer by a halocline (Booth *op. cit.*). An examination of the available salinity data (Hensey 1983) shows that on most sampling dates this halocline was < 5 m deep at Sector E. We therefore think that McMahon & Patching overestimated carbon export from the system. It should be noted that these authors calculated that 75% of carbon export occurs between October and March, the period when phytoplankton growth is minimal.

Table 3. Annual flux of carbon in Killary Harbour from McMahon & Patching (1985)

Source/sink	Tonnes carbon yr ⁻¹
Phytoplankton production	+ 1306
Plankton respiration	+ 1531
River-borne POC	+ 538
River-borne 'active' DOC	+ 610
Sedimentation	- 463
Flushing	- 459

Roden et al. (1987) suggest that phytoplankton is carried into Killary Harbour during the growing season, and Booth (cited in Keegan & Mercer 1986) points out that particles in the lower inward-flowing layer would be retained. The large subsurface chlorophyll maxima revealed by Roden et al. (1987) may be caused by this mechanism. Therefore, there is little reason to believe that there is a net export of phytoplankton from the system; indeed there is some evidence to indicate that it is imported from coastal water.

Detritus derived from land runoff is probably exported. McMahon & Patching (1984) show that large inputs of POC in freshwater runoff are associated with heavy rainfall; these conditions also favour a well-developed seaward-moving brackish layer (Roden et al. 1987).

Total annual macrophyte production is estimated to be 92 tonnes C yr⁻¹ which is less than 10% of phytoplankton production. Applying the data of Johnstone et al. (1979) to this figure would result in approximately 50 tonnes C yr⁻¹ being made available to other trophic levels. Total annual benthic microalgae production is estimated to be 51 tonnes C yr⁻¹.

Zooplankton

Biomass of holozooplankton and gelatinous zooplankton on each sampling date are given in Table 4. Estimated monthly production and total annual pro-

duction for each species or group is given in Table 5. Total annual production of copepods, *Evadne nordmanni*, and *Oikopleura dioica* is estimated to 60.3 tonnes C yr⁻¹. Of this, 76.5% was contributed by copepods, of which calanoid copepods dominated with 64.3% of total holozooplankton production. The most prominent species responsible for calanoid copepod production were *Pseudocalanus elongatus*, *Centropages hamatus*, *Temora longicornis*, *Acartia clausii*, and to a lesser extent *Paracalanus parvus* and *Isias clavipes*. Cyclopoid copepods, although often very abundant, contributed only 12.3% of total holozooplankton production. *Evadne nordmanni* and *Oikopleura dioica* together contributed 23.5% of total holozooplankton production.

There were 2 peaks of gelatinous zooplankton production. The spring peak was dominated by medusae, mostly *Phialella quadrata*, but *Pleurobrachia pileus* was also relatively important. The autumn peak, which was lower than the spring peak was dominated by *P. pileus*. Of the estimated total annual production, 16.3% was contributed by medusae, mainly *Phialella quadrata*, and 37.5% was contributed by *P. pileus*. Estimated gelatinous zooplankton production was 27.0% of holozooplankton production.

Production by meroplankton was estimated to be 11.8 tonnes C yr⁻¹ so that the combined annual herbivorous holozooplankton and meroplankton production estimate is 72.1 tonnes C yr⁻¹.

Table 4. Biomass of holozooplankton (copepods, *Evadne nordmanni* and *Oikopleura dioica*) and gelatinous zooplankton (medusae and *Pleurobrachia pileus*) in Killary Harbour

Date (1981/82)	Holozooplankton			Gelatinous zooplankton		
	Killary tonnes C	mg C m ⁻³	mg C m ⁻²	Killary tonnes C	mg C m ⁻³	mg C m ⁻²
11 Feb	0.11	1.06	15.40	0.0001	0.001	0.02
24 Feb	0.22	2.12	20.80	0.0002	0.002	0.03
10 Mar	0.20	1.93	28.40	0.0005	0.005	0.07
26 Mar	0.36	3.48	60.56	0.0001	0.001	0.01
9 Apr	1.30	12.58	182.79	0.02	0.23	3.28
23 Apr	2.65	25.64	372.55	0.63	6.10	36.32
6 May	7.62	70.25	1020.73	2.43	23.55	333.37
21 May	2.89	27.96	406.25	1.12	10.89	154.11
4 Jun	3.96	38.32	556.79	2.45	23.67	335.10
17 Jun	0.73	7.06	102.58	1.22	11.84	167.64
8 Jul	5.07	49.06	712.84	0.07	0.67	9.45
22 Jul	0.95	9.19	133.53	0.05	0.45	0.63
5 Aug	0.52	5.03	73.08	0.004	0.04	0.52
19 Aug	1.09	10.54	163.15	0.03	0.31	4.42
23 Sep	1.19	11.51	157.24	1.07	10.41	147.29
7 Oct	0.31	3.00	43.59	0.12	1.21	11.11
22 Oct	0.82	7.93	115.22	0.51	4.94	63.94
5 Nov	1.02	9.87	143.41	0.01	0.07	0.99
19 & 24 Nov	0.57	5.51	80.06	0.10	0.95	13.46
2 Dec	0.43	4.16	60.44	0.10	0.98	13.94
6 Jan	0.28	2.71	39.38	0.001	0.01	0.13

Table 5. Monthly production of zooplankton (tonnes C) in Killary Harbour

Month	<i>Acartia clausii</i>	<i>Oithona similis</i>	<i>Oithona nana</i>	Total copepods (mean)	<i>Evadne nordmanni</i>	<i>Oikopleura dioica</i>	Total holozooplankton	Medusae	<i>Pleurobrachia pileus</i>	Total gelatinous zooplankton
Feb	0.007	0.0029	0.126	0.340	0.001	0.013	0.355	0.0004	0.0001	0.0005
Mar	0.083	0.124	0.054	0.688	0.018	0.070	0.776	0.0007	0.0004	0.001
Apr	0.344	0.387	0.215	4.862	1.568	1.278	7.708	1.006	0.007	1.013
May	1.729	0.378	0.077	15.391	2.247	0.012	17.65	5.116	0.736	5.853
Jun	1.660	0.063	0.048	5.429	0.205	0.613	6.247	4.021	1.497	5.518
Jul	2.826	0.694	0.791	7.824	3.575	1.362	12.761	0.005	0.192	0.197
Aug	0.235	0.057	1.297	2.451	1.186	0.174	3.811	0.001	0.071	0.072
Sep	2.671	0.104	1.109	4.299	0.037	1.189	5.525	0.006	1.956	1.962
Oct	0.051	0.029	1.070	1.372		0.088	1.46	0.003	1.101	1.105
Nov	0.433	0.053	0.616	1.956		0.412	2.368	0.002	0.202	0.204
Dec	0.202	0.034	0.409	1.210		0.059	1.269	0.0006	0.346	0.347
Jan	0.039	0.061	0.208	0.532		0.001	0.533	0.0005	0.003	0.003
Total	10.28	2.01	6.02	46.35	8.84	5.27	60.46	10.16	6.11	16.27

Benthos

Regression equations relating biomass to LD in those species for which the regressions were calculated are given in Table 6. In all cases there was significant correlation ($p < 0.05$) between biomass and LD.

Calculated values for biomass (\pm SE) for each species at each of the 5 Killary Harbour sectors are given in Table 7. Each species is designated a trophic role: deposit feeder, suspension feeder, deposit/suspension feeder, or predator according to its mode of feeding. The biomass, per m^2 and per sector, of each phylum, according to its trophic role, is given in Table 8. Values for biomass in terms of carbon were estimated assuming that carbon content is 0.5. This is the approximate carbon content for the ash-free dry soft tissue of *Mytilus edulis* (Rodhouse 1984a, Rodhouse et al. 1984b). The biomass of single large specimens was not included in the calculations for Table 8 because we consider that this would lead to an overestimate of total benthic biomass. The total standing crop biomass of

Table 6. Values for intercepts (A) and slopes (b) in regression equations relating biomass (g AFDW) of macrobenthos species to linear dimension (LD mm): $\log_{10} \text{AFDW} = A + b \log_{10} \text{LD}$

Phylum	Species	A	b	r	df
Mollusca	<i>Abra nitida</i>	-5.54	3.23	0.942	14
	<i>Myrtea spinifera</i>	-6.16	3.83	0.972	12
	<i>Turritella communis</i>	-7.02	3.84	0.948	18
Echino-dermata	<i>Amphiura chiaje</i>	-4.15	2.76	0.920	20
Sipuncu- lida	<i>Golfingia elongata</i>	-4.96	2.07	0.933	12
	<i>Golfingia procerca</i>	-6.83	2.96	0.940	11

macrobenthic infauna in Killary Harbour is calculated to be 44.2 tonnes AFDW or approximately 22.1 tonnes of organic carbon. Standing crop biomass increases towards the mouth of the inlet and this is associated with a general increase in the numbers of species present (Table 9).

The community in Sector A is impoverished and dominated by the mollusc *Abra nitida* whilst in Sectors B, C, D and E there is a richer boreal *Amphiura chiaje* community characteristic of deeper water elsewhere (Thorson 1957, Buchanan 1963). Estimates of annual production per unit area and for each sector, in terms of carbon, are given in Table 10. These estimates are made assuming an annual P:B ratio of 2.5 for Sector A and 0.4 for Sectors B, C, D and E. These ratios were taken from Sanders (1956) for a *Nephtys/Yoldia* community in Long Island Sound, USA, which is considered an iso-community of the *Abra* community of Thorson (1958), and from Buchanan & Warwick (1974) for a *Briopsis/Amphiura* community off the east coast of Northumberland, UK. These ratios reflect the general observation that for *Amphiura* and *Venus* communities the P:B ratio is low and in *Abra* communities it is high (Warwick et al. 1978).

Mussels

Total annual production values and carbon flow for wild and cultivated mussels in Killary Harbour from Rodhouse et al. (1985) are given in Table 11. The data for cultured mussels are based on a total of 1239 m^2 of production rafts, which was the extent of mussel culture in 1982 when data collection for this research was ended. The data for cultivated mussels is actually for a 14 mo period, September to November 1 yr later, but it includes only one production season.

Carbon budget

A carbon flow diagram for the Killary Harbour system is shown in Fig. 2. Symbols are taken from Odum (1972). Particulate carbon input to the system is estimated to be: phytoplankton, 1306 tonnes C yr⁻¹; macroalgae, 50 tonnes C yr⁻¹; benthic microalgae, 51 tonnes C yr⁻¹; river carbon, 500 tonnes C yr⁻¹; making a total of 1907 tonnes C yr⁻¹.

This carbon is consumed by zooplankton, wild mussels, cultured mussels, benthos, bacteria and mi-

crozooplankton. Production of herbivorous zooplankton is 72 tonnes C yr⁻¹; assuming a 20% transfer efficiency (Parsons et al. 1977, Walsh 1981, Walsh et al. 1981) 380 tonnes C yr⁻¹ are required for zooplankton food. In 1981 there were 1239 m² of mussel rafts and, assuming a consumption of 0.06 tonnes C m⁻² yr⁻¹, 68 tonnes C yr⁻¹ would be consumed. Wild mussels are estimated to consume less than 10 tonnes C yr⁻¹. Phytoplankton respiration consumes a proportion of the available carbon, 10 to 40% of total carbon production (Burris 1980). In making the present calculations a

Table 7. Biomass (AFDW: mg m⁻² ± SE) of each benthic species in each sector

Species	Trophic role	Sector				
		A	B	C	D	E
Mollusca						
<i>Nucula turgida</i>	Deposit		3.2	12.6 ± 4.0	37.3 ± 18.4	18.5
<i>Abra nitida</i>	Deposit	199.2 ± 30.2				
<i>Thyasira flexuosa</i>	Deposit/ Suspension					53.3 ± 39.7
<i>Myrtea spinifera</i>	Deposit/ Suspension		21.3 ± 14.7	38.4 ± 15.2	36.0 ± 15.1	112.3 ± 51.5
<i>Dosinia exoleta</i>	Suspension			162.6 ± 69.9	46.9 ± 34.9	39.8 ± 27.2
<i>Venus ovata</i>	Suspension			3.6		8.0
<i>Mya truncata</i> *	Suspension					185.2
<i>Ensis siliqua</i> *	Suspension					5706.4
<i>Turritella communis</i>	Suspension		28.2 ± 25.3	387.0 ± 168.9	5799.6 ± 2969.3	2670.8 ± 672.2
Annelida						
<i>Melinna palmata</i>	Deposit	17.3 ± 1.8	173.2 ± 66.5	674.4 ± 99.3	11.3 ± 8.4	497.2 ± 73.4
<i>Amphicteus gunneri</i>	Deposit		27.0	19.6 ± 8.4	131.5 ± 43.2	
<i>Notomastus latericeus</i>	Deposit	51.2	573.2 ± 163.3	130.9 ± 74.6	70.3	188.8 ± 64.4
<i>Owenia fusiformis</i>	Suspension			23.7 ± 14.5	5.2	946.2 ± 640.8
<i>Nephtys hystrix</i>	Predator	105.6 ± 56.5	770.8 ± 166.4	176.8 ± 51.7	188.0 ± 92.8	448.0 ± 123.8
<i>Nephtys hombergi</i>	Predator	149.6 ± 20.6				
<i>Marphysa belli</i>	Predator		330.0			
<i>Hyalinoecia bilineata</i>	Predator			1175.2 ± 608.2		
<i>Stenelais boa</i>	Predator			91.6	58.4 ± 39.7	269.2 ± 66.2
Phoronida						
<i>Phoronis muelleri</i>	Suspension	3.5 ± 2.2	9.8 ± 5.8	378.0 ± 100.2	7.8 ± 6.3	497.2 ± 36.8
Echinodermata						
<i>Amphiura chiajei</i>	Deposit		148.0 ± 98.1	202.4	2428.8 ± 343.3	2154.8 ± 282.2
<i>Cuccumaria elongata</i>	Deposit					568.3 ± 331.2
<i>Thyone fusus</i> *	Deposit			4388.5 ± 2912.8		
Crustacea						
<i>Upogebia deltaura</i> *	Suspension					1167.6
<i>Hyppolyte</i> sp.	Deposit			78.9 ± 32.5		
Cnidaria						
<i>Edwardsia callimorpha</i>	Predator			2083.6 ± 441.8		511.8 ± 208.5
Sipunculida						
<i>Golfingia elongata</i>	Deposit			932.4 ± 310.2	13.6	256.5 ± 219.5
<i>Golfingia procera</i>	Deposit			204.8 ± 103.2	4.0	46.0
<i>Golfingia vulgaris</i>	Deposit			511.0 ± 421.7	18.0	3641.2
<i>Phascolion strombi</i>	Deposit					3.6 ± 1.4
Rhyncocoela						
<i>Nemertinea</i> sp.	Predator					39.0 ± 22.6

* Single, or 2 only, large specimens

Table 8. Biomass (AFDW and estimated carbon) of major benthic taxa in each sector (biomass of single, or 2 only, large specimens shown in Table 7 omitted in calculating biomass in this table)

Sector	Taxon	Trophic role	AFDW (mg m ⁻²)	AFDW (g) for sector	Carbon (mg m ⁻²)	Carbon (g) for sector
A	Mollusca	Deposit	199.2	2.7 × 10 ⁵	99.6	1.4 × 10 ⁵
	Annelida	Deposit	68.5	9.2 × 10 ⁴	34.3	4.6 × 10 ⁴
		Predator	255.2	3.4 × 10 ⁵	127.6	1.7 × 10 ⁵
	Phoronida	Suspension	3.5	4.7 × 10 ³	1.8	2.4 × 10 ³
B	Mollusca	Deposit	3.2	4.5 × 10 ³	1.6	2.3 × 10 ³
		Dep/sus	21.3	3.0 × 10 ⁴	10.7	1.5 × 10 ⁴
		Suspension	28.2	4.0 × 10 ⁴	14.1	2.0 × 10 ⁴
	Annelida	Deposit	773.2	1.09 × 10 ⁶	386.6	5.5 × 10 ⁵
		Predator	1100.8	1.5 × 10 ⁶	550.4	8.0 × 10 ⁵
	Phoronida	Suspension	9.8	1.4 × 10 ⁴	4.9	7.0 × 10 ³
Echinodermata	Deposit	148.0	2.1 × 10 ⁵	74.0	1.1 × 10 ⁵	
C	Mollusca	Deposit	12.6	2.7 × 10 ⁴	6.3	1.4 × 10 ⁴
		Dep/sus	38.4	8.3 × 10 ⁴	19.2	4.2 × 10 ⁴
		Suspension	553.2	1.2 × 10 ⁶	276.6	6.0 × 10 ⁵
	Annelida	Deposit	824.9	1.8 × 10 ⁶	412.5	9.0 × 10 ⁵
		Suspension	23.7	5.1 × 10 ⁴	11.9	2.6 × 10 ⁴
		Predator	1443.6	3.1 × 10 ⁶	721.4	1.6 × 10 ⁶
	Phoronida	Suspension	378.0	8.2 × 10 ⁵	169.0	4.1 × 10 ⁵
	Echinodermata	Deposit	202.4	4.4 × 10 ⁵	101.2	2.2 × 10 ⁵
	Crustacea	Deposit	78.9	1.7 × 10 ⁵	39.5	9.0 × 10 ⁴
	Cnidaria	Predator	2083.6	4.5 × 10 ⁶	1041.8	2.3 × 10 ⁶
	Sipunculida	Deposit	1648.2	3.6 × 10 ⁶	824.1	1.8 × 10 ⁶
	D	Mollusca	Deposit	37.3	5.3 × 10 ⁴	18.7
Dep/sus			36.0	5.2 × 10 ⁴	18.0	2.6 × 10 ⁴
Suspension			5846.5	8.4 × 10 ⁶	2923.3	4.2 × 10 ⁶
Annelida		Deposit	213.1	3.0 × 10 ⁵	106.6	1.5 × 10 ⁵
		Suspension	5.2	7.4 × 10 ⁴	2.6	3.7 × 10 ⁴
		Predator	246.4	3.5 × 10 ⁵	123.2	1.8 × 10 ⁵
Phoronida		Suspension	7.8	1.1 × 10 ⁴	3.9	6.0 × 10 ³
Echinodermata		Deposit	2428.8	3.5 × 10 ⁶	1214.4	1.8 × 10 ⁶
Sipunculida		Deposit	35.6	5.1 × 10 ⁴	17.8	2.6 × 10 ⁴
E	Mollusca	Deposit	18.5	1.8 × 10 ⁴	9.2	9.0 × 10 ³
		Dep/sus	165.6	1.6 × 10 ⁵	82.8	8.0 × 10 ⁴
		Suspension	2718.6	2.6 × 10 ⁶	1359.3	1.3 × 10 ⁶
	Annelida	Deposit	686.0	6.6 × 10 ⁵	343.0	3.3 × 10 ⁵
		Suspension	946.2	9.0 × 10 ⁵	473.1	4.5 × 10 ⁵
		Predator	717.2	6.8 × 10 ⁵	353.6	3.4 × 10 ⁵
	Phoronida	Suspension	497.2	4.7 × 10 ⁵	248.6	2.4 × 10 ⁵
	Echinodermata	Deposit	2723.1	2.6 × 10 ⁶	1361.6	1.3 × 10 ⁶
	Cnidaria	Predator	511.8	4.9 × 10 ⁵	255.9	2.5 × 10 ⁵
	Sipunculida	Deposit	3947.3	3.8 × 10 ⁶	1973.7	1.9 × 10 ⁶
	Rhynchocele	Predator	39.0	3.7 × 10 ⁴	19.5	1.9 × 10 ⁴

Table 9. Numbers of benthic species and biomass in each sector

Sector	No. of species	Biomass (g AFDW m ⁻²)
A	6	0.53
B	10	2.08
C	20	7.28
D	15	8.86
E	23	12.96

value of 15% was used which reflects the reported values found in many phytoplankton populations. The remaining carbon produced by the phytoplankton is consumed either directly by the microzooplankton, sediments as detritus or is flushed out at the mouth of the harbour. We conclude that carbon production by the phytoplankton is partitioned thus: zooplankton, 380 tonnes C yr⁻¹; cultured mussels, 68 tonnes C yr⁻¹; wild mussels, 10 tonnes C yr⁻¹; phytoplankton respira-

Table 10. Biomass and estimated production of macrobenthic infauna in Killary Harbour

Sector	Biomass (g C m ⁻²)	Biomass in sector (tonnes C)	P:B	Estimated production (g C m ⁻² yr ⁻¹)	Estimated production in sector (tonnes C)
A	0.26	0.36	2.5	0.65	0.90
B	1.04	1.50	0.4	0.42	0.60
C	3.64	8.00	0.4	1.46	3.20
D	4.43	6.45	0.4	1.77	2.58
E	6.48	6.22	0.4	2.59	2.48
Total		22.53			9.76

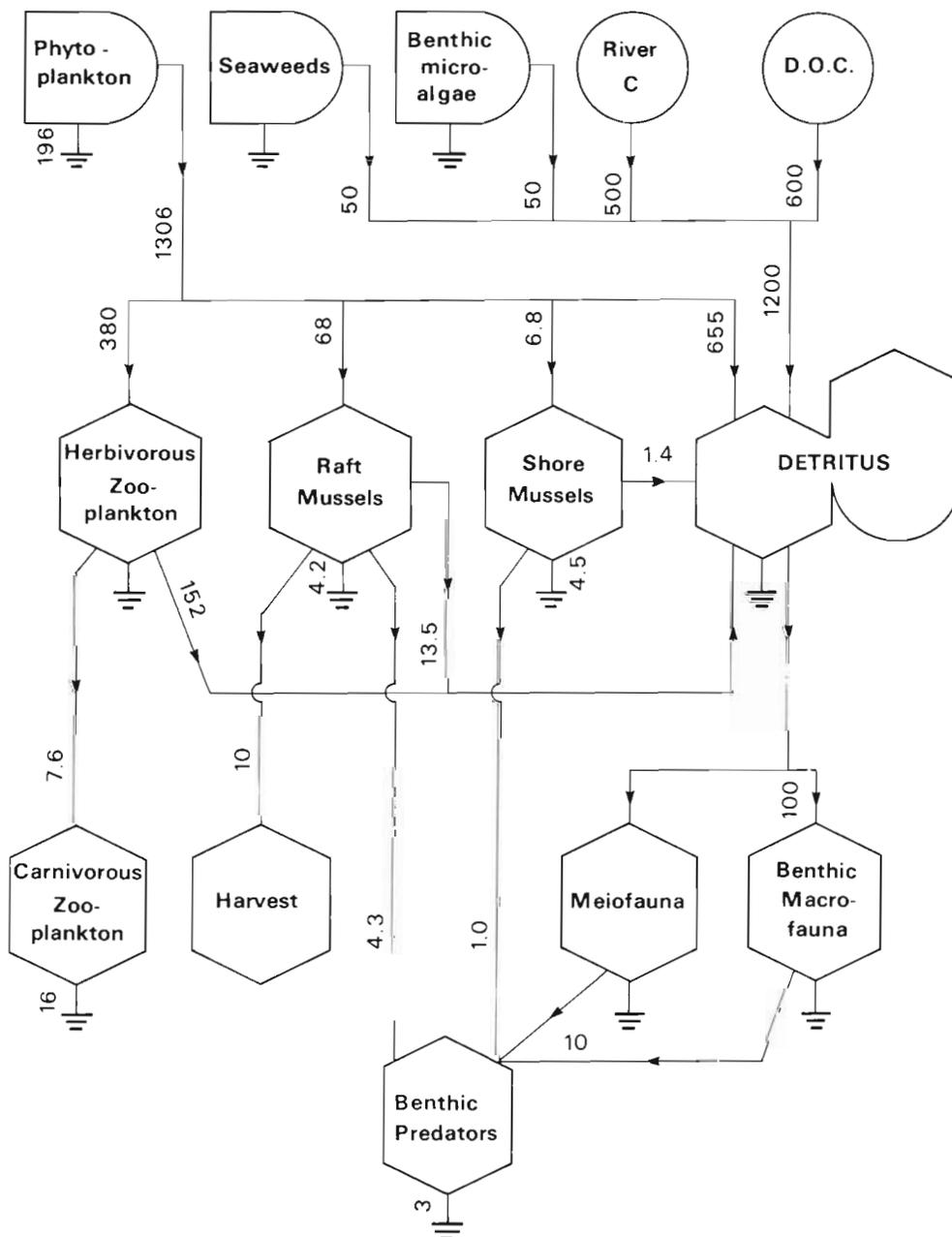


Fig. 2. Carbon flow diagram for Killary Harbour. Numbers are tonnes C yr⁻¹

Table 11. Total annual production and carbon flow (tonnes C yr⁻¹) for wild and cultured mussels in Killary Harbour

	Consumption	Production (including shell)	Gametes	Production + gametes	Respiration	Elimination	Faeces
Wild	6.9	–	–	1.0	4.5	–	1.4
Cultured	68.4	10.8	2.0	12.8	42.4	5.3	13.8

tion, 196 tonnes C yr⁻¹; detritus, 652 tonnes C yr⁻¹; making a total of 1306 tonnes C yr⁻¹.

The large fraction which is not consumed but goes to the detritus pool reflects the finding of other workers who estimate that up to 60% of primary production is not directly consumed (Rosenberg et al. 1977, Walsh 1981).

The remaining carbon sources, river input, macroalgae and benthic microalgae, are not considered here to contribute significantly to mussel or zooplankton production but supply benthic fauna and microzooplankton. The detritus pool receives the following known inputs: river carbon, 500 tonnes C yr⁻¹; macroalgae, 50 tonnes C yr⁻¹; zooplankton faeces, 152 tonnes C yr⁻¹; mussel faeces, 14 tonnes C yr⁻¹; phytoplankton, 652 tonnes C yr⁻¹; making a total of 1368 tonnes C yr⁻¹.

The fate of the detritus pool is complicated because it is derived from 2 very different major sources: phytoplankton which is easily metabolised, produced mainly in the growing season and probably not exported, and detrital carbon, carried into Killary Harbour by runoff. It is present throughout the year but is most prominent during periods of high rainfall. When the upper layer is well developed it is probably exported beyond the inlet. However, Keary (cited in Keegan & Mercer 1986) has shown that the bottom sediments in the inner part of the inlet between Sectors A and C contain up to 9% organic carbon, mainly in the form of humified plant remains. This shows that sedimentation of allochthonous carbon occurs within the Harbour and that this material is not easily metabolised.

The detrital pool can therefore be divided into 2 parts: an easily metabolised fraction which is consumed by the zooplankton and benthos and a refractory part which is incorporated into the sediments or exported. McMahon & Patching (1984) show that a total of 1531 tonnes C yr⁻¹ are metabolised; of this, phytoplankton respiration accounts for 196 tonnes C yr⁻¹. The remaining 1306 tonnes C yr⁻¹ are due to microzooplankton and bacterial respiration. Assuming no net export of carbon, 62 tonnes C yr⁻¹ are then available for sedimentation from the detrital pool.

McMahon & Patching (1984) postulate a supply of metabolically available dissolved organic carbon from land runoff. In addition, the import of phytoplankton in

summer may augment the available detrital carbon pool (Roden et al. 1987). Neither of these sources are easily measured but together with the measured carbon sources, the detrital pool is large enough to support the estimated consumption.

The benthic community was not studied as intensively as the plankton so estimates of carbon requirements are probably less accurate. However, the figure for macrobenthos production, 10 tonnes C yr⁻¹, is probably reasonable and would require an input of 100 tonnes C yr⁻¹, assuming a transfer efficiency of 10%. Meiobenthos have not been estimated.

DISCUSSION

In order to obtain the carbon budget presented here a number of estimations and approximations have been necessary. The use of P:B ratios in calculating production by zooplankton and benthos is open to legitimate criticism because in doing this we infer that conditions at our study site are similar to those in different habitats, in different geographical areas. Also, with the time and manpower available we were not able to sample every sub-component of the system with the same intensity. Sampling was carried out to a degree considered appropriate to the importance of each sub-system, thus the benthos was only sampled at one time of year, late summer, when this community may well be at near maximum biomass. However in view of the relative importance of the benthos in the overall budget we do not consider that this would lead to serious error. In spite of such weaknesses we feel sufficiently confident in our data to attempt to predict the potential carrying capacity of the Killary Harbour system for intensive bivalve culture and to make some general predictions about the effects of this industry.

If total mussel yield (Y) depends on the amount of available food and the conversion efficiency of the mussels then:

$$Y = y \cdot F / f \quad (1)$$

where y = yield per unit area (tonnes C m⁻² yr⁻¹); f = food consumed per unit area (tonnes C m⁻² yr⁻¹); and F = total food available (tonnes C yr⁻¹).

Rodhouse et al. (1985) have shown that for 1 m² of

mussel raft, 0.56 tonnes C yr⁻¹ are consumed and 0.008 tonnes C yr⁻¹ (mussels) can be harvested. We assume in the following calculations that the carbon content of live mussels is 2.95%. Tenore & Gonzalez (1976) and Hanson et al. (1986) have shown that cultured mussels in the Ria de Arosa, Northern Spain, compete with zooplankton for the available food supply. In Killary Harbour, if cultured mussels were to consume all the carbon now consumed by zooplankton as well as that now consumed by cultured mussels (360 + 68 tonnes C yr⁻¹) annual yield would be 2073 tonnes live weight.

Rodhouse et al. (1985) have also shown that during flood and ebb tide approximately 50% of particulates are cleared from suspension by mussel rafts. This was in close agreement with Cabañas et al. (1976) who give a value of 60% removal. If F in Eqn (1) equals 650 tonnes C yr⁻¹, half the total phytoplankton production, then annual yield would be 3162 tonnes live weight.

If the suggestion is correct that phytoplankton accumulate within the inlet from outside (Roden et al. 1987), then this process might supply additional food to the mussels cultured on ropes. However, it is difficult to quantify this process without a clearer understanding of the physical processes which govern it.

These calculations assume that the cultured mussels consume only phytoplankton. Widdows et al. (1979) suggested that detrital carbon and bacteria contribute to mussel nutrition and so it is possible that the above calculations underestimate potential yield. However, there is evidence that the hydrological structure of Killary Harbour is such that the major food resource available to mussels in suspended culture is phytoplankton (Rodhouse et al. 1984a, Roden et al. 1987) and so we conclude that the maximum annual yield of mussels is approximated by these calculations. Once annual yield exceeds about 3000 tonnes over half the primary productivity of the inlet will have been diverted to mussel culture. Beyond this, severe modifications of the environment and decreasing yields per unit area may be expected.

Large-scale mussel culture in coastal marine sites will inevitably cause environmental change. In calculating potential yield it has been assumed here that as yield increases, zooplankton will decrease. Such a substitution of the major grazing community can be expected to alter several aspects of the Killary Harbour system.

At present zooplankton grazing occurs throughout the system and associated processes, such as excretion of ammonia and deposition of faecal pellets, are widespread. By replacing dispersed zooplankton grazing by mussel grazing, concentrated in small areas, these processes will be concentrated resulting in areas of heavy sedimentation interspersed with areas of low sedimentation. This might be expected to alter the

composition and distribution of the benthic fauna (Tenore et al. 1982, Rosenberg & Loo 1983, Kaspar et al. 1985). Dahlback & Gunnarsson (1981) report that sedimentation is increased 3-fold under mussel culture rafts compared to control sites in Sweden. The benthic community is dominated there by large white mats of the sulphate-reducing bacteria *Beggiatoa*. This does not occur in Killary Harbour probably because of differences in the depth of water and tidal current flow (Rodhouse et al. 1985).

Here, potential mussel yield was calculated as carbon but Roden et al. (1987) have shown that primary production was sometimes limited in summer by nitrogen, consequently any effects of mussel culture on the nitrogen budget may be considerable. Because nitrogen is limiting, its removal as mussel tissue must be compensated by additional nitrogen if primary production is not to decline. The substitution of zooplankton grazing by mussel grazing may also alter the rates of nitrogen cycling and loss to the sediments.

Roden et al. (1987) have indicated that nitrate is continually supplied to Killary Harbour from both river runoff and from the sea. The estimated size of nitrate input is 278 tonnes N yr⁻¹ which exceeds the expected maximum quantity harvested, 26 tonnes N yr⁻¹ (= 3200 tonnes live weight) by an order of magnitude. Therefore nitrogen removal should not limit mussel production in Killary Harbour.

Mussel culture may also alter the rate of nitrogen cycling. If the rate were increased an increase in primary production might be expected and the possibility of local blooms of red tide organisms exists. While red tides have caused problems for mussel cultures elsewhere it is not established that these blooms are a result of cultivation. Paralytic and diarrhetic shellfish poisoning have been recorded from mussel growing areas including the Netherlands, Galicia (northwest Spain), and Bantry Bay (southwest Ireland) (Kat 1985, Fraga & Sanchez 1985, Dunne pers. comm.). All these areas have a high natural phytoplankton production which is often a characteristic of red tide prone regions (Holligan 1985). This high productivity is also an advantage in mussel production. While mussel rafts reroute the flow of energy and materials they do not add extra nutrients to the ecosystem, unlike caged fish fed on prepared food. Any increase in algal production due to mussel cultivation will involve processes very different from eutrophication caused by an allochthonous nutrient supply.

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