Influence of Mussel Aquaculture on Nitrogen Dynamics in a Nutrient Enriched Coastal Embayment

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Running Head: Mussel aquaculture and coastal nitrogen dynamics

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1   **ABSTRACT:** The combined influences of intensive mussel aquaculture and watershed

2   nutrient inputs on nitrogen dynamics in Tracadie Bay (Prince Edward Island, Canada)

3   were examined using a nitrogen budget and an ecosystem model. Budget calculations

4   and inputs and parameters for the model were based on extensive field data. Both

5   approaches showed that mussel aquaculture has a dominant influence on all aspects of the

6   nitrogen cycle and dramatically alters pathways by which nitrogen reaches the

7   phytoplankton and benthos. A large proportion of phytoplankton production is supported

8   by land-derived nitrogen and this anthropogenic input is important for sustaining existing

9   levels of mussel production. The amount of nitrogen removed in the mussel harvest is

10 small compared to agricultural nitrogen inputs and the amounts excreted and

11 biodeposited on the seabed. Mussel biodeposition greatly increases the flux of nitrogen to

12 the benthos, with potentially serious eutrophication impacts. Results from the observation

13 based nitrogen budget and dynamic model were compared and both support the above

14 conclusions. However, the ability of the model to test different scenarios and to provide

15 additional information (e.g. fluxes) over a finer spatial scale led to insights unattainable

16 with a nitrogen budget. For example, food appears to be less available to mussels at the

17 head of the Bay than at the mouth, despite the lower density of grow-out sites in the

18 former location. The number of fundamental ecosystem processes influenced by the

19 mussels and the complexity of their interactions makes it difficult to predict the effects of

20 mussels on many ecosystem properties without resorting to a model.

21

22 **KEY WORDS:** eutrophication, nitrogen cycling, nitrogen budget, ecosystem model,

23 ecophysiology**,** biodeposition, excretion

24 **INTRODUCTION**

25

26   Natural and farmed populations of suspension-feeding bivalve molluscs exert a

27 dominant influence on energy flow and nutrient cycling in many coastal marine

28 ecosystems, particularly in inlets where water residence time is long and bivalve biomass

29 is high (Smaal and Prins 1993; Dame 1996; Dame and Prins 1998; Cranford et al. 2003;

30 Newell 2004; Grant et al. 2005). By creating structurally complex shell habitat and

31 performing a wide array of ecological functions, bivalve populations can substantially

32 modify benthic and pelagic communities at different trophic levels and alter energy flow

33 and nutrient cycling over the scale of entire coastal ecosystems. Potential mechanisms for

34 ecosystem effects include the utilization of particulate food resources by the bivalves, the

35 biodeposition of faeces and pseudofaeces, and the excretion of metabolites. Bivalve

36 aquaculture is expanding rapidly in many countries and a comprehensive understanding

37 of the influence of this industry on coastal ecosystems, as well as interactions with other

38 anthropogenic stressors, is fundamental for developing strategies for the sustainable

39 management of the coastal zone as well as the aquaculture industry.

40

41   Dense bivalve populations and communities are known to influence the nitrogen

42 cycle in coastal ecosystems with the degree of control depending largely on site-specific

43 hydrographic conditions (Dame 1996; Newell 2004). Bivalves exert "bottom-up" nutrient

44 control on the phytoplankton by (1) the excretion of large amounts of nitrogen (primarily

45 ammonia) and (2) by depositing organic matter from ingested phytoplankton and detritus

46 (also includes remnants from ingested auto- and heterotrophic microplankton and

47 zooplankton), which facilitates the benthic recycling of nitrogen. The increased organic

48 loading of sediments from biodeposition may enhance the retention of nutrients, coming

49 from both the sea and land, in coastal systems and stimulate mineralization and nitrogen

50 release rates (Newell 2004; Nizzoli et al. 2006). Nitrogen fluxes from the recycling of

51 biodeposits trapped within suspended bivalve culture ropes and other structures are also

52 ecologically significant and can be higher than benthic fluxes (Mazouni 2004; Richard et

53 al. 2006; Nizzoli et al. 2006). Accelerated nitrogen cycling and coastal nitrogen retention

54 directly attributed to bivalve excretion and biodeposition may significantly accelerate

55 phytoplankton turnover and production (Doering and Oviatt 1986; Doering et al. 1989;

56 Asmus and Asmus 1991; Prins et al. 1995).

57

58   Coastal ecosystems are increasingly stressed by many human activities and the

59 potential effects of aquaculture should not be considered in isolation. Significant

60 ecosystem-level interactions are expected between bivalve aquaculture and

61 eutrophication (Dame 1996; Cloern 2001; Newell 2004). Applications of agricultural

62 fertilizer to farm lands enrich nutrient concentrations in surface and ground water. Upon

63 reaching coastal systems, these nutrients stimulate plant growth and can disrupt the

64 natural balance between the production and metabolism of organic matter. Large

65 populations of bivalve filter-feeders are believed to control coastal ecosystem responses

66 to nutrient loading by ingesting large quantities of microalgae and thereby increasing the

67 estuary's grazing, or "top down", control of excess phytoplankton biomass (Dame 1996;

68 Cloern 2001; Newell 2004). In addition to potentially having the capacity to clear excess

69 phytoplankton from suspension, it has been suggested that bivalve aquaculture may help

70 ameliorate the impacts of nitrogen enrichment in eutrophic coastal waters by removing

71 excess nitrogen in the shellfish harvest (e.g. Rice 2000; 2001). This has led to suggestions

72 that shellfish aquaculture be incorporated in a nutrient trading system as an alternative to

73 nitrogen reduction for improving coastal water quality (Lindahl et al. 2005).

74

75   The number of ecosystem processes potentially influenced by bivalve culture and the

76   complexity of their interactions (e.g. simultaneous top down and bottom up controls on

77   phytoplankton) makes it difficult to predict the effects of the bivalves on many ecosystem

78   properties. Such predictions are further complicated by ecological interactions between

79   bivalve suspension feeders and eutrophication (Cloern, 2001). The present study was

80   conducted to further scientific understanding of the nitrogen dynamics of a coastal

81   aquaculture embayment receiving nutrient inputs from land-use. Two different

82   approaches were applied to analyzing major elements of the nitrogen cycle; an

83   observation based nitrogen budget and a dynamic ecosystem model. Results were

84   compared to provide insights into the individual strengths and limitations of each

85   approach with respect to their possible applications. A related objective was to apply

86   these approaches to test hypotheses and refine theories including; (1) the potentially

87   dominant role of mussel aquaculture in nitrogen dynamics at the coastal ecosystem scale,

88   (2) the influence of mussel culture on coastal nutrient retention, and (3) the capacity of

89   the mussel harvest to ameliorate impacts from nitrogen enrichment.

90

91   The site used in this study is Tracadie Bay (Fig. 1), one of the more extensively

92   leased mussel aquaculture inlets in Prince Edward Island (PEI; Fig. 1). PEI coastal inlets

93   supply 77% of the $30 million total value of the mussel culture industry in Canada (DFO

94   2005). Many PEI embayments, including Tracadie Bay, receive agriculture run-off, and

95   nutrient inputs from fertilizers have resulted in eutrophic conditions (Raymond et al.

96   2002). Tracadie Bay has been the focus of several studies and extensive field sampling

97   programs have been conducted to document the physical oceanography (Dowd et al.

98   2001; 2002) and biogeochemistry of the Bay and adjacent waters (e.g. Bates and Strain

99   2006). The bio-physical control of the distribution of phytoplankton in Tracadie Bay has

100   been examined using a simple tracer model (Dowd 2003), a lower trophic level

101   ecosystem box model (Dowd 2005) and a spatially explicit ecosystem model of seston

102   depletion by the mussel culture (Grant et al. submitted). All three approaches suggest that

103   mussel grazing strongly affects phytoplankton levels in this inlet, and that the spatial

104   pattern is also dictated by water motion and nitrogen run-off. Dowd (2005) developed an

105   ecosystem box model approach and conducted a preliminary examination of how mussels

106   affect nitrogen cycling in the bay. This approach was further refined for the present study

107   and applied to quantitatively describe nitrogen dynamics dictated by the major interacting

108   ecosystem components (nutrients, phytoplankton, mussels, detritus and benthos).

109   Detailed biological and chemical field data for Tracadie Bay, which were not available

110   during initial model development, are compared to model output. Whenever possible,

111   actual field data are used in the budget calculations and to determine parameters and

112   initial and boundary conditions for modelling purposes.

113

114   **MATERIALS AND METHODS**

115

116   **Study Site.** Tracadie Bay (Fig. 1) is a small (16.4 km^2 at mean tide and 13.8 km^2 at

117   low tide), shallow (mean depth 2.5 m; maximum depth 6 m), barrier beach inlet with

118   predominantly diurnal tides having a mean range of 0.6 m. There are currently 6.98 km^2

119   of water column mussel leases in Tracadie Bay (50% and 68% of the low tide area and

120   volume, respectively) containing a standing stock of approximately 4500 tonnes of

121   mussels (see Fig. 4.3 in Cranford et al. 2006). Annual mussel production is

122   approximately 1900 tonnes, or approximately 11% of the value of the PEI mussel

123   industry.

124

125   Information on the Tracadie Bay drainage basin and land-use was supplied by the PEI

126 Department of Environment for calculation of drainage basin and land type areas using

127 GIS (ArcInfo Ver. 9.1). The Tracadie Bay watershed (Fig. 2) totals 146.2 km^2 and land

128 types include forest (46.8% of total area), agriculture (32.7%), wetlands and beach

129 (12.5%), and urban and other (8.0%). The Winter River watershed (Fig. 2) is the largest

130 drainage sub-basin to the Bay (69.7 km^2) and a relatively large fraction (41.4%) is used

131 for agriculture (grain, potato, hay and pasture).

132

133 **Water Chemistry.** Water samples were collected by Niskin bottle from 1 and/or 3 m

134 depth at 12 stations in Tracadie Bay (circles in Fig. 2) approximately once per month in

135 the ice-free seasons (June to November) for two years (2002-2003). Some limited

136 sampling was also conducted through the ice in winter months. Additional nutrient data

137 were available from samples collected in a previous program conducted in 1998-99,

138 which included sampling in the months July through October. Vertical profiles with a

139 portable CTD (SeaBird 25) provided supporting salinity and temperature data. Dissolved

140 inorganic nutrients were determined for all samples, using standard autoanalyzer

141 techniques for nitrate and nitrite (Strain and Clement 1996), and ammonia (Kérouel and

142 Aminot 1997). In this paper we will use 'nitrate' to refer to the total oxidized inorganic

143 nitrogen (nitrate + nitrite), and TIN (total inorganic nitrogen) to refer to nitrate + nitrite +

144 ammonia. Nutrient samples were also collected from eight stations in the Winter River

145 (squares in Fig. 2) approximately weekly from May to November 2003 by hand dipping

146 sample bottles into the surface layer from shore.

147

148   Suspended particulate matter (SPM) in the water samples was collected on 1.7 μm

149   nominal pore size glass fibre filters (25 mm diameter Micro Filtration Systems type GC).

150   SPM was collected in triplicate on prewashed, precombusted (450 °C for 4 h), tared glass

151   fibre filters. SPM levels were determined after rinsing the filters under vacuum with

152   isotonic ammonium formate to remove salt and drying the filters at 60°C and weighing to

153   the nearest 0.01 mg. Particulate organic matter (POM) concentration was determined as

154   total weight loss upon ignition at 520°C for 6 h and the organic fraction (f_{POM}) was

155   calculated as POM/SPM. Samples to characterize the SPM and organic matter were

156   provided from the Niskin water sampling surveys described above and using a moored

157   Water Transfer System (McLane Research Laboratories, Inc., Falmouth MA, USA) that

158   filters water *in situ* at programmed intervals onto glass fibre filters (47 mm diameter

159   Micro Filtration Systems type GC). This system made it possible to collect frequent SPM

160   samples for the evaluation of f_{POM}. Chlorophyll *a* in SPM samples collected on glass fibre

161   filters (same type as above) during the Niskin survey was determined from the *in vitro*

162   fluorescence (Turner Designs fluorometer calibrated against pigment from spinach) of

163   90% acetone extracts of the filtered material.

164

165   **Nitrogen Cycle.** Table 1 lists the important reservoirs, internal fluxes, and external

166   inputs and outputs that are elements of the nitrogen cycle in Tracadie Bay. The letters

167   identifying the reservoirs in Table 1 will be used throughout this paper. Note that the

168   TIN reservoir is distinguished from other reservoirs and fluxes expressed in nitrogen

169   equivalents. Table 1 also shows which components are quantified in the nitrogen budget

170   and modelling approaches.

171

172   Whenever possible, we have used field data for constructing the nitrogen budget and

173   for setting boundary / initial conditions for the models and assessing their performance.

174   For many such purposes, we synthesized the available field data and produced seasonal

175   cycles (monthly) using objective analysis. Objective analysis is sometimes referred to as

176   an 'optimal estimator', because the Gauss-Markov theorem on which it is based claims

177   that "Given the statistics of the field being measured and the noise levels involved, no

178   other [linear] analysis could perform better" (Bretherton et al. 1976).

179

180   To characterize the nitrogen cycle, we require estimates of the nitrogen levels in the

181   phytoplankton (P), dissolved nutrients (TIN) and detritus (D) reservoirs within Tracadie

182   Bay and for the offshore. We have formulated both the nitrogen budget and the models

183   to use a common currency for the different ecosystem reservoirs and fluxes, expressing

184   all quantities in nitrogen equivalents. For many quantities, we use units of tonnes

185   nitrogen or tonnes nitrogen per year (t N or t N y^{-1}). P was determined from the

186   chlorophyll *a* distribution, converted to nitrogen using a carbon:chlorophyll *a* ratio of 50,

187   and a Redfield C:N ratio of 106:16 (molar) in the phytoplankton. The TIN values require

188   no conversion, but require summing the nitrate and ammonia concentrations. The detritus

189   is considered here to be the fraction of organic matter not associated with living

190   phytoplankton cells. Since most of the living cells in the water column are

191   phytoplankton, the amount of nitrogen in detritus (N_D) can be calculated from the

192   difference between nitrogen in the total particulate organic matter (N_{POM}) and the

193   nitrogen in the phytoplankton (N_P):

194   $$N_D = N_{POM} - N_P.$$

195   N in bacteria, either free-living in the water column or associated with detritus, is not

196   considered in these calculations.

197

198   For areas inside Tracadie Bay, we have sufficient data for POM and P to calculate

199   N_D. P is converted to N_P as described above; N_{POM} is calculated using the Redfield C:N

200   ratio and 1.9 as a typical ratio of organic matter:organic carbon. These N_D values were

201   then objectively analyzed in the same way as the other parameters. However, the extra

202   steps in the calculation add to the uncertainty of the resulting seasonal cycle. For the

203   offshore station, sufficient POM data are not available for this calculation. Instead, we

204   have used the observation that N_P+N_D is approximately constant (~6.4 _M N) in data

205   from the Tracadie Bay area to approximate offshore D from the offshore seasonal cycle

206   of P. Although the determination of the nitrogen in both P and D are operational, they

207   are internally consistent because the same filters to collect SPM were used in both

208   measurements.

209   P, TIN and D levels in offshore waters influencing Tracadie Bay are boundary

210   conditions required for both the nitrogen budget and the models. Seasonal cycles for

211   these quantities were predicted by objective analysis for the offshore region using both

212   data from this study at Station W12 (Fig. 2) and data from the BioChem data archive

213   maintained by the Department of Fisheries and Oceans for adjacent areas of the

214   Magdalen Shallows in the Gulf of St. Lawrence. Concentrations were predicted for 5 m

215   depth at W12 for the middle of each month. Julian day is used for the time axis (i.e. data

216   from all years are merged), and the data set is expanded to cover the range 0 to 365 days

217   ±182 days to avoid biasing estimates at each end of the calendar year. Fig. 3 shows one

218   such seasonal cycle predicted for nitrate at Station W12, and the distribution of data

219   points on which it is based (~ 1400 measurements). The corresponding seasonal cycles

220   for ammonia and chlorophyll were also determined (not shown), and these cycles were

221   used to calculate seasonal cycles for P, TIN and D in nitrogen equivalents as described

222   above.

223

224   Objective analysis was also used to estimate seasonal cycles for areas within Tracadie

225   Bay for comparison with model predictions and for calculating mean nitrogen inventories

226   for the nitrogen budget. Estimates have been made for each box used in the model

227   described below. For these analyses, the seasonal cycle was predicted for each point on a

228   200 m grid in Tracadie Bay. Data for each month for each point in each model box were

229   then averaged to produce a seasonal cycle for the model box. For example, Fig. 4 shows

230   the predicted chlorophyll cycle for the boxes of the lower trophic level model.

231

232   The seasonal cycles predicted in this way for both the offshore and the model boxes

233   within Tracadie Bay describe conditions that are averaged over all the available data and

234   do not describe a specific year's annual cycle. The temporal and spatial distributions of

235   these data vary between the different model boxes and the offshore. Some gaps in the

236   sampling exist, such as during the spring due to ice break-up. This limitation is most

237   serious with TIN, for which the few available winter measurements are highly variable

238   (7 – 150 _M) with a mean value (52 _M) that is much higher than observed at other times

239 of year. Although all these estimates are based on data, they are still idealized

240 representations of the annual cycle.

241

242 **Lower Trophic Level Model.** Dowd (2005) developed a lower trophic level

243 ecosystem model for Tracadie Bay, implemented with three spatial boxes (Fig. 5), that

244 predicts the levels of phytoplankton (P), zooplankton, dissolved nutrients (TIN) and

245 detritus (D), as well as their interactions with a simplified benthos (B) that includes terms

246 for particle settling, permanent burial, resuspension and nutrient remineralization. Water

247 exchange coefficients were derived from a heat budget calculation using observed

248 temperature time series. The impacts of mussel aquaculture (M) are evaluated by

249 superimposing the grazing activity of the mussels onto this system. The elements of the

250 nitrogen cycle described by the model are listed in Table 1. As used in this study, the

251 model formulation differs from that of Dowd (2005) in the following ways:

252 • The units have been converted to nitrogen equivalents.

253 • Since tests showed that the zooplankton pelagic state variable (Z) had little impact

254 on the nitrogen dynamics, it has been eliminated. Ecosystem closure is achieved

255 by a quadratic loss term $\lambda_P P^2$ that represents mortality and grazing of

256 phytoplankton. This loss term is put back into the detritus pool, resulting in the

257 following equation for P (which replaces Eq. 1 in Dowd, 2005):

258
$$\frac{dP}{dt} = f\{N; k_n\} \gamma_P P - \lambda_P P^2 - I_m P + K(P_\infty - P)$$

259 The corresponding zooplankton terms have been dropped from the equations for

260 N and D, D has been adjusted for the flux from P, and the equation for B is

261 unchanged.

262   • The convolution integral that governed benthic remineralization has been replaced

263   with a simple temperature and B dependent efflux (rather than being based on the

264   weighted time history of the input flux).

265   • The external N source has been replaced with a seasonally variable freshwater N

266   source term (i.e. river inputs, land runoff); see below for more details. This

267   source is input into Box 2 (Winter Harbour; Fig 5).

268   • Mussel grazing, I_m, is partitioned amongst the boxes to correspond with present

269   conditions. Winter Harbour has no grazing (primarily a mussel spat collection

270   site) and I_m values for the other two boxes have been determined from the

271   nitrogen budget of the cultured mussel population (see below).

272

273   **Annual Nitrogen Budget.** The average annual nitrogen inventories in Tracadie Bay

274 reservoirs were calculated as follows. N_p was calculated using the seasonal cycle of P

275 concentrations estimated from the objective analysis and the water volumes of the bay

276 (same procedure as described above for the boxes used in the lower trophic level model).

277 Nitrogen in the farmed mussel biomass was estimated based on a total harvested biomass

278 of approximately 1900 t wet weight (shell included). This number does not account for

279 mussel mortality, drop-off, or discarding of damaged or undersize mussels during

280 harvest. Estimates based on industry lease reporting place the biomass of mussels in the

281 bay at approximately 4500 t (Cranford et al. 2006). The nitrogen in mussel tissue

282 (excluding shell) was estimated using a typical fraction of wet meat to total weight of

283 40%, a water content of the meat of 85.5% (PJ Cranford unpublished data for Tracadie

284 Bay) and average nitrogen content of 7.79% (Smaal and Vonck 1997).

285

286   The amount of phytoplankton and detritus nitrogen consumed by mussels depends on

287   the rate at which mussels filter water (i.e. their clearance rate) and the nitrogen content of

288   the suspended particulate matter in the water column. Clearance rate depends primarily

289   on the size of the mussels. We used a linear growth model to estimate the average

290   monthly size of Tracadie Bay mussels over a 24 month grow-out period to 0.7 g dry

291   weight at harvest. Meat weight trajectories in Tracadie Bay vary each year (Waite et al.

292   2005) and the linear function represents average conditions. The clearance rate (C) for

293   each mussel was calculated for each month using the allometric equation of Smaal et al.

294   (1997), which is based on similar natural dietary conditions as Tracadie Bay. Monthly

295   ingestion rates were calculated by multiplying C by the estimated number of mussels in

296   the harvest (161×10^6) and the average SPM-N concentration (2.5 mg SPM L^{-1} x 0.04 =

297   0.10 mg N L^{-1}). Nitrogen ingestion was summed over the 24 month period to estimate

298   annual ingestion. Note that summing monthly estimates from one cohort over a two year

299   period is equivalent to the actual situation where two cohorts (Age 1 and Age 2) are

300   present in the Bay each year. To estimate how much of the nitrogen in ingested food is

301   derived from phytoplankton and detritus, we assumed f_{POM} values of 0.8 and 0.2,

302   respectively, for each food resource. Using the mean SPM value of 2.5 mg L^{-1}, and an

303   average annual seston f_{POM} value of 0.30 (SD = 0.14; n = 80; from the 2003 Niskin and *in*

304   *situ* water sampling survey), we estimate that approximately 40% of ingested seston

305   organic matter originates from phytoplankton. A similar proportion may be expected for

306   nitrogen ingestion. At the relatively low SPM concentrations found in Tracadie Bay, the

307   limited production of pseudofaeces does not significantly affect ingestion or

308   biodeposition estimates (Smaal et al. 1997; Cranford and Hill 1999), and is not

309   considered here.

310

311   The amount of nitrogen in the faeces produced by the mussels can be determined

312   from the difference between the nitrogen ingested and the nitrogen absorbed by the

313   mussels. The latter depends on the absorption efficiency (AE) of the ingested food,

314   which is in turn dependent on the concentration of organic matter in the SPM (f_{POM}). We

315   estimated AE based on an empirical relationship between AE and f_{POM};

316     $$AE = 0.85(1 - e^{-5*(f_{POM} - 0.2)}),$$

317   derived from data reported for *M. edulis* by Cranford and Hill (1999) and Figueiras et al.

318   (2002). The average annual f_{POM} value of 0.30 (above) resulted in an AE value of 0.33.

319   Absorption rate was then calculated as the product of AE and nitrogen ingestion rate and

320   faeces production rate was calculated as ingestion rate minus absorption rate.

321

322   The annual excretion of nitrogen by mussels was estimated by two approaches. First,

323   data presented in Hawkins and Bayne (1985) showed that, on average, 34% of absorbed

324   nitrogen (calculated above) is excreted by mussels. Second, the allometric equation from

325   Smaal et al. (1997) was used to estimate the excretion of NH_4-N by different size classes

326   of mussels in the same way as described above for estimating N ingestion. Most of the

327   excreted nitrogen is in the form of dissolved ammonia.

328

329   Freshwater inputs used in the nitrogen budget are based on monthly averaged

330   freshwater flow data for Winter River during 1968 to 2004, obtained from the

331   Environment Canada hydrometric database (www.wsc.ec.gc.ca) for the station near

332   Suffolk (46º19'56" N; 36º3'53"W; 37.5 km^2 drainage area). Average flow rate

333   measurements from this station were adjusted by watershed areas not gauged to estimate

334   the total monthly freshwater outflow from Winter River and the total freshwater run-off

335   from all drainage sub-basins to Tracadie Bay. Data on nutrient concentrations from two

336 sampling stations (surface water at WR1 and from 1 m depth at W1), both located near

337 the mouth of Winter River (Fig. 2), supplemented by estimates of levels during the winter

338 months for similar environments, were used along with the flow data for estimating TIN

339 fluxes in freshwater flowing into Tracadie Bay.

340

341   Exchanges of nitrogen between Tracadie Bay and the offshore were estimated from

342 the tidal volume of the Bay and the concentrations of materials of interest in inflowing

343 and outflowing waters. The seasonal cycles for P, TIN and D were estimated for the

344 northern part of Tracadie Bay (defined as Box 1 of the lower trophic level model; Fig. 5)

345 and for offshore waters to characterize the outflow and inflow, respectively. These data

346 were combined with an estimate of 1.17 tidal volumes per day to yield gross estimates of

347 nitrogen export and import for each parameter. The number of tidal volumes per day was

348 based on assessing flushing times for the bay by fitting a harmonic that describes the

349 three major components of the mixed tide (the O_1 and K_1 diurnal and the M_2 semi-

350 diurnal) to spring and neap tides.

351

352   **RESULTS**

353

354   **Nitrogen Budget**

355

356   Estimates for the average nitrogen inventories in Tracadie Bay and the internal and

357 external annual nitrogen fluxes are shown schematically in Figure 6A.

358

359   **Reservoirs.** We estimated an annual P inventory in Tracadie Bay of 1.2 t of nitrogen.

360 The equivalent inventory of TIN is 13 t N, and for detritus is 3.0 t N. The inventory of

361 nitrogen in mussel tissues in the Bay was estimated at 20 t N, with 9 t N y^{-1} removed

362 annually in the mussel harvest. Our confidence in the former value is relatively low, so

363 the N budget (and the lower trophic level model) only considers the influences of a

364 mussel biomass equal to the 9 t N y^{-1} harvest (Fig. 6A), for which there was reliable data.

365 The mussels harvested each year are estimated to ingest 230 t N y^{-1}, with 92 t N y^{-1}

366 originating directly from phytoplankton consumption. To the extent that this calculation

367 does not include a large, but poorly quantified, standing stock of cultured or wild

368 mussels, this ingestion rate should be interpreted as a lower limit. Applying a known

369 relationship for the absorption of organic matter by *M. edulis* resulted in estimates for

370 absorption and faeces production rates of 76 t N y^{-1} and 154 t N y^{-1}, respectively. Our two

371 estimates for nitrogen excretion provided comparable results, with 26 t N y^{-1} calculated

372 based on the typical proportion of absorbed N that is excreted, and 23 t N y^{-1} derived by

373 applying the allometric equation of Smaal et al. (1997).

374

375 **Freshwater Inputs.** Monthly freshwater flows from Winter River over the period

376 between 1964 and 2004 averaged between 0.5 (August - September) and 3.0 m^3 s^{-1}

377 (April), with an annual mean of 1.2 m^3 s^{-1}. Scaling these flows to the remaining Tracadie

378 Bay watershed gave an average annual freshwater input of 2.6 m^3 s^{-1} (C.V. = 0.21).

379 Combining monthly average N concentrations at the mouth of Winter River with monthly

380 water flows to Tracadie Bay yielded an estimate of 88 t N y^{-1} for the annual freshwater

381 input of TIN. This estimate assumes that the water samples collected from the surface

382 layer had zero salinity (salinity data are not available for these samples). Since TIN

383 concentrations in Winter River are much higher than those in Tracadie Bay or offshore in

384 the Gulf of St. Lawrence, this estimate is a lower limit with respect to the presence of

385 some saltwater in the samples. The sub-surface (1 m depth) samples collected at the

386 adjacent sampling site (W1) had an average salinity of 27.1 psu. The freshwater

387 concentrations corresponding to the W1 samples were estimated using a two-component

388 mixing model, the average salinity (28.9 psu) at 15 m at the offshore station (W12), and

389 the monthly average TIN levels at W12 determined from the objective analysis of

390 offshore data as described above. The corresponding TIN fluxes based on these data are

391 equivalent to an annual flux of 124 t N y^{-1}.

392

393   These two data-based estimates for the TIN flux can be compared to one based on

394 land use. Frink (1991) reviewed export coefficients for nutrients from watersheds to

395 estuaries and derived a model that predicted N coefficients (±SE) for agricultural,

396 forested and urban land types of 7.6±2.2, 2.4±0.5 and 13.4±2.6 kg N ha^{-1} y^{-1},

397 respectively. Combining these numbers with the corresponding land-use areas yields an

398 average flux of 69 t N y^{-1} from the Tracadie Bay watershed with a predicted range from

399 52 to 86 t N y^{-1}. N export from wetland areas was assumed to be minimal since they act

400 as N sinks (i.e. denitrification, sedimentation and plant uptake). Assuming an N

401 coefficient of 8 kg N ha^{-1} y^{-1} for atmospheric deposition (Frink 1991), the beach areas

402 would contribute approximately an additional 8 kg N y^{-1}, giving a total predicted TIN

403 flux of 76 kg N y^{-1}. The three estimates of total TIN inputs to Tracadie Bay are

404 reasonably consistent. For discussion purposes, we use a value of 100 t N y^{-1} in our N

405 budget, which is based on the extensive Winter River measurements (flow and nutrient

406 concentrations) and includes some correction for nutrient dilution in river mouth samples

407 by seawater. TIN input from agriculture is estimated to be 50 t N y^{-1} based on the

408 measured drainage basin land use and the above export coefficient for agriculture land.

409 Particulate nitrogen fluxes from land run-off are probably much less than the TIN fluxes

410 and have been assumed negligible in our budget.

411

412   **Offshore Exchanges.** Combining the seasonal cycles of phytoplankton (P) in

413   outflowing (northern Tracadie Bay) and inflowing (offshore) water with the daily tidal

414   flushing volume yielded a gross export of 122 t N y^{-1} and a gross import at 100 t N y^{-1},

415   which results in a net export of 22 t N y^{-1}. For TIN, gross export was 836 t N y^{-1} and

416   gross import was 183 t N y^{-1}, giving a net export of 654 t N y^{-1}. Tracadie Bay is a net

417   exporter of TIN in all months except January and November. The high winter TIN levels

418   in Tracadie Bay contribute substantially to the large net export. For detritus (D), gross

419   export was estimated to be 275 t N y^{-1} and gross import was 274 t N y^{-1}, for a net export

420   of 1 t N y^{-1}.

421

422   **Lower Trophic Level Model**

423

424   **Model Inputs and Parameters.** The variables, parameters, and inputs to the model

425   are summarized in Table 2. Computation of the maximum light limited phytoplankton

426   growth rate, $\_p$(t), was based on a photosynthesis-irradiance relationship with the

427   maximum photosynthetic rate modulated by temperature. A carbon to chlorophyll *a* ratio

428   of 50 was used to convert the P-I relationship to a growth rate (see Dowd 2005). Daily

429   values for the far field concentrations of P_∞(t), N_∞(t) and D_∞(t), and for nitrogen inputs,

430   N_{in}(t), into Winter Harbour (box 2) were derived using the objective analysis results

431   described above. Values used for the N pool were total inorganic nitrogen (TIN = nitrate

432   + nitrite + ammonia). Detritus inputs, D_{in}(t), due to freshwater inputs and internal sources

433   like the decay of macrophytes are essentially unknown and not considered, however, note

434   that the model is not particularly sensitive to changes in this forcing term (Dowd, 2005).

435   The model was run to produce an annual cycle for the ecosystem state variables. A spin-

436   up period of two years ensured the system (mainly B) was in a statistical steady state.

437   Note that stochastic resuspension implies that the system will not repeat exactly year to

438   year and so annual fluxes may not exactly balance.

439

440   Some of the calculations for the mussel portion of the nitrogen budget are also used to

441   set parameters in the lower trophic level model. The model requires estimates for the

442   total filtration rate of the mussel population and the fractions of ingested nitrogen that are

443   harvested or excreted. Clearance rate of the annually harvested mussel biomass (9 t N y$^-$

444   ^{1}) was determined during the ingestion rate calculation (above). Summing the clearance

445   rate over all size classes yields a total filtration rate of 6.3 x 10^6 m^3 d^{-1}. Although detailed

446   stocking information that would allow calculation of the numbers of mussels in each

447   model box is not available, using the leased areas known to support mussel grow-out (as

448   opposed to leases used for spat collection) as proxies allocates ~ 92 % of the mussels to

449   box 1, ~ 1 % to box 2, and ~ 7 % to box 3. Scaling the total filtration rate to the volume

450   of each box using these mussel densities produces ingestion rate, I_m , values of 0.29 d^{-1}

451   for box 1 and 0.043 d^{-1} for box 3. We have set I_m equal to 0 for box 2 because of the

452   relatively clearance capacity of mussel spat. From the nitrogen budget, the excreted

453   fraction $_m$ = 26/230 = 0.11. Since the mussel portion of the budget is not fully balanced,

454   we have treated the assimilated fraction, $_m$, as a tuneable parameter, and chosen its value

455   so that the assimilated nitrogen matches the annual harvest of 9 Tons N y^{-1}. The resulting

456   value of $_m$ is 0.048. (Note that the assimilation efficiency is not the same as the

457   absorption efficiency, but they are related by AE = $_m$ + $_m$).

458

459   **Model Applications.** The LTLM box model was applied to Tracadie Bay under

460   three specific scenarios:

461   1.   *Cumulative Effect* scenario representing the current state of Tracadie Bay with both

462   the cultured mussel population (M) and land-based TIN inputs at present day levels.

463   2.   *Enrichment Effect s*cenario without cultured mussels, but with land-based N inputs

464   at present levels. This scenario will be used to assess the impact of the cultured

465   mussels on the nitrogen dynamics of the ecosystem.

466   3.   *Baseline* scenario without cultured mussels, and without land-based inputs of N.

467   This scenario tests the effect of the mostly agricultural land-based nitrogen source

468   on nitrogen dynamics.

469

470   The model outputs are presented in Figures 7-10 with each pane in these figures

471   showing the model predictions for the above three scenarios. In addition, the plots for P,

472   N and D (Figs. 7-10) show the observed concentrations (daily interpolations from the

473   objective analysis) in each box and the offshore concentrations. Table 3 lists the amount

474   of nitrogen in each reservoir and the annual fluxes between reservoirs as predicted by the

475   model for each box.

476

477   First, we can compare the model predictions for the present day scenario (cumulative

478   effects of mussels and nutrient enrichment) with the observations for P, N and D in each

479   of the model boxes. Both the P concentration ranges and the general seasonal patterns of

480   the P distributions predicted by the model are consistent with observations. The model

481   predicts spring and fall blooms in all three boxes, with summer values falling to 1-2 _M

482   N l^{-1} (Fig. 7). However, the timing of the blooms predicted by the model are offset from

483   the observations by up to one month: e.g. the predicted spring blooms in box 1 and 3 are

484   about one month later than the observed blooms, while the predicted spring bloom in box

485   2 is approximately one month earlier. In addition, the fall blooms predicted by the model

486   tend to be more intense than those observed. In the model, the highest spring P values

487   occur in box 2 (Winter Harbour) due to the high N levels and lack of mussel grazing

488   pressure, but observations show the highest values are in box 3 (head of Tracadie Bay).

489

490   The general spatial and temporal patterns in TIN (Fig. 8) conform with observations

491   with highest values in spring falling to near zero concentrations in summer, and smaller

492   increases early in fall that decline before the return of high values in the winter. Their

493   spatial pattern is also consistent (highest in box 2, then box 3, then box 1). However, the

494   predicted magnitudes are much smaller than the observations in spring. As previously

495   mentioned, the high TIN observations are based on a small number of samples collected

496   through the ice and gaps in the sampling occur in the spring. We do not have data to

497   indicate exactly when the high wintertime concentrations decrease, and whether or not

498   they contribute to spring productivity. The levels predicted by the model are consistent

499   with a typical temperate seasonal cycle, modified by high inputs into box 2 (especially

500   during the spring freshet).

501

502   The modelled water column detrital pool (Fig. 9) shows a fairly constant mean level

503   near 5 _M N, with episodic fluctuations due to resuspension events, which is similar to

504   both the observations in the individual boxes and to the levels offshore. The model also

505   correctly predicts the shape and magnitude of the increase in D that occurs in box 2 in the

506   spring.

507

508   The benthos in the model may be thought of as an ecologically active pool (or layer)

509   of nitrogen in which processes operate that result in resuspension, remineralization and

510   burial of nitrogen. The model predicts highest values for the cumulative effects scenario,

511   with box 1 (greatest biomass of mussels) containing the vast majority of benthic nitrogen.

512   The scenarios without mussels exhibited similar patterns and magnitude. Although the

513   benthos is an ecologically significant reservoir, there are no measurements suitable for

514   comparison with the model predictions shown in Fig. 10.

515

516   **DISCUSSION**

517

518   **Lower Trophic Level Model Scenarios**

519

520   A comparison of estimated annual average phytoplankton levels in the different

521   model boxes for the Cumulative (mussels) and Enrichment (no mussels) scenarios (Table

522   3) show that mussel culture in Tracadie Bay affects all aspects of the nitrogen cycle to

523   some degree. Mussel grazing reduces phytoplankton levels by 15, 9 and 13% in boxes 1

524   (mouth of Tracadie Bay), 2 (Winter Harbour) and 3 (head of Bay), respectively. Although

525   the majority of mussels are located in box 1, phytoplankton depletion occurs throughout

526   the system owing to water exchange. The relatively large effect near the head of the bay,

527   despite the presence of only 7% of the cultured mussel population, results from poor

528   exchange with the offshore. Conversely, the impacts near the mouth are relatively small,

529   given that this area contains 92% of the cultured mussels, showing the importance of

530   offshore exchange and the supply of phytoplankton from Winter Harbour in regulating

531   phytoplankton levels. The conclusion that P is more reduced at the head of the bay than

532   in the mouth, is consistent with observations of reduced mussel growth near the head of

533   the bay (Waite et al. 2005), as well as theoretical studies considering the competing role

534   of P growth, M grazing, and the differential exchange processes (Dowd 2003).

535

536   Our predictions of reduced annual average P and D concentrations (13 and 14%

537   reductions, respectively) in the scenario with mussels (Table 3; Figs. 7 and 9) are

538   consistent with results from other studies of Tracadie Bay. Grant et al. (submitted) used a

539   more complex ecosystem model to investigate seston depletion and reported considerably

540   more severe effects of mussel culture on the overall P biomass than reported here. Those

541   predictions were validated using results from detailed surveys of the bay-wide

542   chlorophyll-*a* distribution. The density of second year mussels in the Grant et al.

543   (submitted) study (10 individuals m^{-3}) represents total mussel stocking levels and is

544   approximately double the value used in the current model application, which only

545   considers the effects of the harvested stock. The falling trend detected in the weight of

546   mussels harvested from Tracadie Bay during the 1990's, when annual stocking density

547   was steadily increasing (Figs. 4.3 and 4.4 in Cranford et al. 2006), implies a negative

548   feedback on meat yields caused by bivalve-induced food limitation. Over a 5-year period

549   when mussel biomass in the bay increased by more than 40%, the average mass yield of

550   mussel socks declined by 30%. Together, these observations and model results indicate

551   that the mussel production carrying capacity of Tracadie Bay has been exceeded.

552

553   The pathways by which the nitrogen reaches the phytoplankton are dramatically

554   altered in the presence of the farmed mussels. Mussel deposition (M _ B) sends 156 t

555   N y^{-1} to the benthos and the flux of nitrogen out of the sediments (B _ TIN + B _ D) is

556   estimated to increase by 100 t N y^{-1}, enough to supply more than 70% of phytoplankton

557   nitrogen requirements. In the presence of mussels, P _ D, D _ B, and D _ TIN fluxes are

558   smaller in all three boxes (Table 3), presumably because mussel grazing consumes P and

559   D that would otherwise be part of these fluxes. Asmus and Asmus (1991) raised the

560 possibility that mussels promote phytoplankton production by remineralizing detrital

561 material and by increasing rates of phytoplankton recycling during periods when N

562 demand is high and ambient concentrations are low. The model estimates that the mussels

563 ingest approximately twice as much detritus N than phytoplankton N (Fig. 6B; Table 3).

564 The recycling of detrital N through mussel excretion and biodeposition pathways will

565 promote phytoplankton growth during periods of N limitation and intensify bottom-up

566 controls on the phytoplankton. However, similar fluxes of TIN _ P in model runs with

567 and without mussels (Table 3) suggest no effect on annual phytoplankton production.

568

569 The impact of freshwater nitrogen inputs on annual average P levels in the different

570 boxes can be seen from a comparison of the Baseline (no mussels or inputs from land)

571 and Enrichment (no mussels) model runs (Table 3). As expected, freshwater inputs

572 increased TIN and P in all three boxes, with the greatest increases in Winter Harbour

573 (box 2), where the freshwater inputs occur. Removal of freshwater inputs resulted in P

574 reductions in Winter Harbour by as much as 62% during the spring bloom (Fig. 7), and

575 levels are reduced by as much as 50% in the remainder of the bay. Although these large P

576 reductions occur only in the spring (probably because the fall bloom is fuelled by

577 nutrients from offshore), the changes are large enough to have a sizeable impact on total

578 annual phytoplankton growth (TIN _ P), which changes from 125 t N y^{-1} in the nutrient

579 enriched scenario to 72 t N y^{-1} in the Baseline scenario (Table 3). Therefore, a substantial

580 fraction of the P present in Tracadie Bay is fuelled by land-derived nitrogen. P levels

581 outside Winter Harbour remained virtually the same as the current condition (when both

582 freshwater inputs and mussels are removed (compare the Cumulative and Baseline

583 scenarios in Table 3). These comparisons indicate; (1) the effect of freshwater nitrogen

584 on P levels is substantially greater than changes due to mussel grazing, and (2) cultured

585   mussels in Tracadie Bay depend on terrestrial nitrogen inputs to produce much of their

586   food. The latter agrees with ecosystem model predictions of the large effect of watershed

587   nitrogen inputs on oyster production levels in the Thau lagoon (Chapelle et al. 2000).

588

589   Comparisons of box model results for scenarios with and without mussels suggest

590   that the presence of mussels increases retention of nitrogen from freshwater and offshore

591   sources within the bay. The mussels change the TIN export and M _ B and B _ TIN

592   fluxes by 101, 156, and 91 t N y^{-1} (increased by 2.3, 14 and 12 times, respectively).

593   Smaller changes (2.5 – 15%) also occur in the TIN _ P and D _ TIN fluxes when mussels

594   are present. Inspection of import / export terms in Table 3 shows that the TIN export

595   from Tracadie Bay is much larger in the presence of mussels (176 t N y^{-1}) than in their

596   absence (75 t N y^{-1}), but this change is more than offset by the corresponding reduction in

597   P exports (51 t N y^{-1}) and the increase in D imports (78 t N y^{-1}). The combined effect of

598   all these changes is to produce slightly higher pelagic TIN levels and a much larger

599   benthic nitrogen pool when mussels are present than when they are not (Table 3; Figs. 8

600   and 10).

601

602   Dramatic changes in the relative role of the benthos in nitrogen cycling are apparent

603   in the presence of mussels. Mussel biodeposition is 3.5 times greater than the natural

604   sedimentation (D _ B) when mussels are not present (Table 3) and nitrogen burial

605   increases by 72 t N y^{-1}, which is 11.8 times more than if no mussels were present.

606   Resuspension (B _ D) and remineralization (B _ TIN) increase by factors of 2.2 and 11.8,

607   respectively. As expected. the bulk of the benthic flux in the model run with mussels

608   occurs in box 1, where the majority of mussel grow-out takes place. The high B level in

609   this region represents a potential for severe eutrophication effects on benthic

610 communities. In contrast, the Enrichment model run indicated that freshwater inputs

611 have little impact on the nitrogen stored in the benthos (Table 3). It should be noted that

612 the model predictions of the fate of nitrogen after it reaches the benthos are only as good

613 as the model parameters controlling resuspension, remineralization and burial. Although

614 there are no field data to validate these specific estimates, model formulations of the

615 benthic component are based on robust equations of the important geochemical processes

616 involved (Dowd 2005). Model predictions are also parallel the results of a 2003 benthic

617 geochemical survey of Tracadie Bay that showed that hypoxic and anoxic sediment

618 conditions, indicative of extensive organic enrichment, were only found within mussel

619 lease boundaries and that the majority (77%) of sampling sites with free sulphide

620 concentrations exceeding 1500 µM (13 sites) were located within box 1 (Cranford et al.,

621 2006). Benthic macroinvertebrate communities throughout Tracadie Bay are described as

622 having low diversity and a very low number of species (Miron et al. 2005).

623

624   Discrepancies between model predictions and observations (Figs. 7-10) could be due

625 to model errors in the forcing and far field conditions. They might also be due to errors of

626 representativeness in the point observations, e.g. a high productivity zone at the head of

627 Winter Harbour may have been under-sampled and so affect the seasonal cycles

628 constructed by objective analysis. Also critical to this comparison is that the model

629 scenarios are based on the influence of a mussel population equal to the amount harvested

630 each year. Although estimates are not well constrained, the total mussel biomass in the

631 bay appears to be double the annual harvest even without consideration of wild mussel

632 beds and oyster culture. The additional influences on nitrogen dynamics of large

633 populations of other herbivores residing on mussel culture structures would also need to

634 be modelled for a direct comparison between model output and observations to be valid.

635 Finally, it should be noted that the modelling approach does consider potential

636 aquaculture-induced changes to phytoplankton community composition.

637 Picophytoplankton cells, which are not captured by bivalves due to their small size,

638 appear to contribute substantially to phytoplankton biomass in extensively cultured

639 aquaculture embayments (Courties et al. 1994; Prins et al. 1998; Bec et al. 2005),

640 including Tracadie Bay (WKW Li personal communication; Cranford et al. 2006). The

641 philosophy of the parsimonious LTLM model has been to offer simplicity, but not

642 triviality, to quantitative descriptions of aquaculture systems by including only dominant

643 processes (Dowd, 2005). Although some realism is sacrificed for generality, the model

644 applications are based on robust parameterizations and approximations, well defined

645 boundary forcing, and data-driven estimation of mixing coefficients. We feel that the

646 resulting descriptions of observed parameters are therefore sufficient for the systematic

647 testing of hypotheses concerning the effects of nutrient enrichment and mussel culture on

648 nitrogen dynamics (Dowd, 2005).

649

650   **Nitrogen Budget**

651

652 Biomass and fluxes involving mussels in the budget and the model cannot be

653 considered truly independent (calculated from similar underlying information) and will

654 not be compared. However, it is possible to directly compare some budget calculations

655 (Fig. 6A) with summed or averaged model estimates for the whole year for the combined

656 mussel and nutrient enrichment (Cumulative) scenario (Fig. 6B). Nitrogen inventories in

657 the different reservoirs from the budget and the model are similar except for TIN, for

658 which the model estimates are much lower (3.4 compared to 13 t N). A little less P (2.4

659 versus 22 t N y^{-1}) and a lot less TIN (176 versus 654 t N y^{-1}) are exported in the model

660   than in the budget, and a significant amount of D is imported in the model (106 t N y^{-1}),

661   compared to D being in approximate balance in the budget (Fig. 6). The TIN levels and

662   fluxes in the budget may have been biased by the high values obtained for the few

663   available winter measurements. The budget has external nitrogen sources and sinks out

664   of balance by 568 t N y^{-1}. In contrast, sources and sinks are nearly in balance for all three

665   model scenarios (Table 3).

666

667   The nitrogen budget presented here was based on relatively simple concepts applied

668   to some basic characteristics of Tracadie Bay and measurements or estimates of nitrogen

669   levels in a few reservoirs, freshwater inputs, and relatively simple attempts to

670   characterize the marine exchanges and fluxes associated with mussel feeding and

671   excretion. Despite the simplifications, it was possible to derive the following noteworthy

672   inferences on mussel/ecosystem interactions from the budget and associated calculations.

673

674   A comparison of the amount of nitrogen consumed by mussels with the inventories

675   of nitrogen in their food (P and D) and in the mussels themselves, shows that mussels

676   exert a dominant role in the flow of nitrogen through the Tracadie Bay ecosystem (Fig.

677   6A). The mussels ingest approximately 50 times the average standing stock of the total

678   nitrogen found in phytoplankton and detritus, which is equivalent to completely

679   processing the available food supply once a week. The mussels turn over plankton

680   nitrogen at an even higher rate (~5 days). Given that the mussel biomass in Tracadie Bay

681   is roughly double the amount used for this budget, the phytoplankton production

682   timescale would have to be on the order of a few days to support this level of aquaculture.

683   Dowd (2003) estimated a production timescale of 2-5 days for phytoplankton in

684   temperate coastal waters typical of Tracadie Bay during summer. Although primary

685   production data for this bay indicate remarkably high turnover times of 0.2-2.3 days (WG

686   Harrison, personal communication), the intensity of culture, in combination with the

687   other herbivores (including zooplankton, wild mussel reefs, some oyster culture and the

688   extensive fouling community on the mussel lines), is likely consuming available food at a

689   faster rate than can be replenished by internal production. Seston transported into the Bay

690   from offshore supplements the internal production. However, water residence time in

691   Tracadie Bay (3.4 days; Grant at al. 2005) is longer than the two days estimated for

692   mussel clearance of the tidal prism (Dowd, 2003). A high potential for bay-wide food

693   depletion is therefore indicated as was also concluded from the model results.

694

695   The budget cannot test hypotheses on the effects of mussels or freshwater inputs on

696   many important nitrogen reservoirs or internal fluxes, such as the biomass and

697   productivity of phytoplankton, ambient TIN levels and benthic storage of nitrogen.

698   Stated in other terms, the budget is not capable of testing the responses of Tracadie Bay

699   to forcing due to mussels, freshwater inputs or to different scenarios in general. Models

700   must be used to examine such internal processes and to test different scenarios. In

701   addition, the model, unlike the budget, provided spatial information resolved to the

702   geographic scale of the model boxes.

703

704   Although the budget has more limited application for testing hypotheses compared

705   with the model, comparisons of nitrogen fluxes associated with the mussels with other

706   fluxes in the budget (Fig. 6A) provide insights into potential pathways of aquaculture

707   effects and have practical application. For example, a prevalent theory that can be

708   addressed by the budget is that introduced bivalves modulate coastal eutrophication by

709   clarifying the water and removing excess nitrogen in the harvest. The capacity for water

710   clarification has already been confirmed (see above). The ability of the bivalve harvest to

711   remove anthropogenic nitrogen inputs from land-use was examined by comparing

712   freshwater inputs with the exported biomass. Mussel harvesting removes 9 t N y^{-1} from

713   Tracadie Bay, which is equivalent to 9% of the total freshwater nitrogen input and 18%

714   of nitrogen input estimates from agricultural run-off. Given that phytoplankton accounted

715   for 40% of the total ingested nitrogen (Fig. 6A), only 3.6 t N y^{-1} of the mussel harvest

716   could result directly from phytoplankton uptake of agricultural nitrogen, with an

717   additional small amount removed via the P _ D _ M pathway (Fig. 6A). Therefore, only a

718   small fraction of the agricultural nitrogen run-off (<10%) appears to be removed by the

719   intensive mussel culture operations in this bay. Although the harvest does represent the

720   loss of a considerable amount of anthropogenic nitrogen from the coastal zone, intensive

721   bivalve aquaculture in Tracadie Bay does not appear to be an effective tool for coastal

722   managers to control nutrient emissions from land-use.

723

724   Mussel excretion and biodeposition represents significant fluxes in the nitrogen

725   budget (Fig. 6A) and must be considered along with grazing in any assessment of the

726   overall effects of aquaculture, including potential interactions with the effects of nitrogen

727   enrichment. Annual excretion by the harvested biomass returns an amount of nitrogen to

728   the water column equivalent to approximately 50% of the agricultural runoff, while

729   biodeposition was estimated to be three times greater than agricultural inputs (Fig. 6A).

730   Both fluxes from mussels were similar in magnitude to estimates from the lower trophic

731   level model (Fig. 6) and similar conclusion can be drawn on their potential ecologically

732   significance. Excretion by suspended mussels recycles nitrogen directly into nutrient

733   depleted waters. TIN levels in Tracadie Bay in late summer and fall, although low, are

734   dominated by ammonia, and silicate is generally the limiting nutrient for diatom growth

735 and carrying capacity (Bates and Strain 2006). A combination of rapid uptake of TIN by

736 microalgae and the net export of nitrogen to the offshore likely maintains ambient TIN at

737 depleted levels during much of the year (Fig. 3).

738

739   Our estimate of the flux of nitrogen to the sediments due to the harvested mussel

740 biomass (154 t N y^{-1}) is equivalent to 105 mg N m^{-2} d^{-1} if the deposition was uniformly

741 distributed over the ~4 km^2 area of mussel grow-out leases and is approximately 200

742 mg N m^{-2} d^{-1} when scaled up to the total mussel biomass in the bay (approximately twice

743 the harvested biomass). Grant et al. (2005) measured sedimentation rates in Tracadie Bay

744 and observed that rates under mussel lines were approximately double those at reference

745 sites. An average biodeposition flux of 405 mg N m^{-2} d^{-1} was estimated from Grant et al.

746 (2005) by subtracting natural sedimentation at the reference sites from total vertical flux

747 at the mussel sites and assuming a N content of 1.5% of dry faeces weight (Kautsky and

748 Evans 1987). This flux is higher than in our budget, as would be expected considering

749 that the sediment traps were placed close to the mussel lines, while our estimate also

750 includes areas between lines spaced ~5 m apart.

751

752   **Reliability of Budget Estimates.** A discussion of the nitrogen budget must consider

753 the confidence with which the budget estimates are determined. Three independent

754 means (two data-based and one based on nutrient export coefficients) were available for

755 estimating the freshwater inputs of TIN and they agreed to within ± 26%, which makes

756 the freshwater input well known by the standards of these kinds of calculations. The

757 agricultural component of the freshwater input is based on applying published nutrient

758 export coefficients for nitrogen loading and comprehensive databases on land use and

759 river flow. Although nutrient loading will vary with the type of agriculture (Frink 1991),

760 applying the known range of coefficients does not significantly affect our conclusions.

761

762   The nitrogen exchanges due to the mussels are expected to be reasonably constrained

763 by the basic physiology of the mussels. Although these fluxes are based on laboratory

764 measurements of individual mussels that were scaled up to an entire population in a real

765 environment, this is a common practice and the allometric relationships employed for

766 clearance rate provide results comparable with field measurements on mussel cohorts

767 (Cranford and Hill 1999). One test of the mussel component of the budget is to compare

768 the total inputs and outputs of nitrogen to the mussels. The mussels consumed 230 t N y^{-1},

769 and 189 t N y^{-1} of that consumption is accounted for in mussel production, urine and

770 faeces (Fig. 6A). Overall, nitrogen processed through mussels is balanced to within

771 ~ 18%, which is within the bounds expected for this kind of a budget.

772

773   The offshore exchange estimates in the nitrogen budget must be considered first

774 order. Tidal prism calculations usually overestimate tidal transport because the

775 underlying assumptions of complete mixing within the Bay and infinite dilution outside

776 the Bay are approximations only. These calculations only consider exchanges due to the

777 tide and do not include exchanges due to other processes such as wind and storm events.

778 Applying the exchange coefficient for Tracadie Bay and the offshore, derived from a heat

779 budget calculation (K_∞ = 1.3 d^{-1}; Dowd 2005), resulted in net export estimates for P, TIN

780 and D of 28, 850 and 1.6 t N y^{-1}, respectively. These values are somewhat higher than

781 those predicted from the tidal prism (Fig. 6A), but they are within the same range. The

782 budget estimates a large net export of all nitrogen forms from Tracadie Bay of 568 t N y^{-1}

783 (= _ outputs − _ inputs). A large export value was predicted independent of whether the

784 tidal prism or heat budget exchange calculation was used, and is most likely due to the

785 high winter TIN concentrations that heavily influenced the TIN inventory. Despite a

786 potential for bias, the TIN inventory was only 13 t N and the calculations of the nitrogen

787 held in P and D are not subject to this uncertainty. Given these evaluations of confidence

788 in the different budget estimates, conclusions derived from the freshwater inputs and the

789 mussel processing of nitrogen are based on a more solid foundation than those derived

790 from the marine exchanges of nitrogen. The focus of the above discussion was therefore

791 on the former two aspects of Tracadie Bay nitrogen dynamics.

792

793 **CONCLUSIONS**

794

795   The following general conclusions about the cumulative influence of nutrient

796 enrichment and mussel aquaculture in Tracadie Bay were derived from the nitrogen

797 budget and lower trophic level model:

798 • mussels play a dominant role in nitrogen cycling in Tracadie Bay and influence all

799   aspects of the nitrogen cycle,

800 • a substantial fraction of the phytoplankton production in this inlet is fuelled by land-

801   derived nitrogen,

802 • the mussels depend on nitrogen in agricultural discharges to produce phytoplankton

803   biomass, as well as on phytoplankton and detritus (a major part of the food supply)

804   imported from offshore. That is, the internal production of the bay is insufficient to

805   support the harvested biomass of mussels,

806 • mussels are consuming available food at a faster rate than can be replenished by

807   internal and external processes. The budget and box model calculations indicate that

808   the productive capacity of Tracadie Bay for mussel aquaculture has been reached,

809   •   food may be less available to mussels at the head of the Bay than at the mouth,

810   despite the lower density of grow-out sites in the former location,

811   •   the amount of nitrogen removed in the mussel harvest is small (<10 %) compared to

812   the nitrogen in agricultural inputs,

813   •   mussels direct ~ 20 times more nitrogen to the water column and sediments in their

814   urine and biodeposits than is removed in the harvest and these processes increase

815   coastal nitrogen retention and dramatically alter pathways by which nitrogen reaches

816   the phytoplankton,

817   •   mussel biodeposition results in a very large flux of nitrogen to the benthos, with

818   potentially serious eutrophication effects.

819

820   At the modeled level of mussel production, the pelagic ecosystem components are

821 much less sensitive to the effects of mussels than the benthic components, due to the

822 ability of external exchanges and feedbacks within the pelagic system to mitigate much

823 of the effect. However, the rapid depletion of external food supplies by mussels places

824 increased pressure on accelerated benthic remineralization processes and benthic/pelagic

825 fluxes to maintain the phytoplankton reservoir. Bivalve aquaculture utilizes nutrients

826 already present in the system, including those originating from land-use, and therefore

827 does not cause coastal nutrient enrichment. However, it does determine where

828 eutrophication from excess nutrient runoff is expressed by accelerating organic matter

829 transport to the seabed and thereby facilitating the retention of nutrients in the coastal

830 zone. Excessive benthic organic loading from biodeposition can lead to sediment anoxia.

831 Anoxic conditions inhibit nitrification and denitrification (Newell 2004) and

832 dissimilatory nitrate reduction to ammonium (Nizzoli et al. 2006) and would contribute to

833 a greater impact on N dynamics than estimated by the present model.

834

835   The nitrogen budget is a relatively simple representation of the marine exchanges and

836   fluxes associated with mussel aquaculture and terrestrial inputs in Tracadie Bay

837   compared with the dynamic ecosystem model. However, results from both approaches

838   are consistent and the lower trophic level model results do not contradict any important

839   conclusions from the budget. However, the finer resolution of the box model and the

840   ability to test different scenarios and predictions leads to additional conclusions. The

841   number of fundamental ecosystem processes influenced by mussels and the complexity

842   of their interactions makes it difficult to predict the impacts of mussels on many

843   ecosystem properties without resorting to a model. The detailed insight provided by a

844   dynamic model on ecosystem function can provide important information on issues like

845   suitable distributions of leases in an inlet that are beyond the scope of a budget.

846

847   **ACKNOWLEDGEMENTS**

848

857

858   **Figure Legends**

859

860   Fig. 1.   Site maps showing Prince Edward Island, Canada, Tracadie Bay (including

861   Winter Harbour), and the distribution of suspended mussel culture leases.

862   Fig. 2.   Map of the Tracadie Bay watershed showing the locations of the five (A-E) land

863   drainage sub-basins, including the Winter River sub-basin (highlighted region

864   B). Pie charts presented for each sub-basin show the total area and percent land-

865   use by categories as identified in the inset. Water sampling stations in Winter

866   River (squares) and inside and outside (Station W12) Tracadie Bay are shown.

867   Fig. 3.   Seasonal cycle of nitrate in waters offshore from Tracadie Bay. Vertical lines

868   show the errors (± 1 _) associated with each monthly prediction. The histogram

869   shows the monthly distribution of data points available for predicting the

870   seasonal cycle.

871   Fig. 4.   Seasonal chlorophyll cycles predicted for the three boxes of the lower trophic

872   level model (Fig. 4), and the distribution of data used to make these estimates.

873   Fig. 5.   Map of Tracadie Bay showing the three boxes and boundaries used in the lower

874   trophic level model. The intertidal and 2 m depth contours are also shown.

875   Fig. 6.   Nitrogen reservoir inventories and flux pathway in Tracadie Bay calculated

876   from (A) the nitrogen budget and (B) the "cumulative effects" scenario (present

877   conditions) of the lower trophic level model (LTLM). Both approaches are for

878   a mussel population equal to the annual mussel harvest. P = phytoplankton, TIN

879   = inorganic nitrogen, D = detritus, B = benthos, M = mussels. Solid arrows

880   represent internal fluxes and dashed arrows are external inputs/outputs.

881   Inventories in reservoirs are annual averages (t N) and all other quantities are

882   annual fluxes (t N y^{-1}). For external fluxes, positive numbers represent gains to

883   Tracadie Bay and negative numbers are losses.

884   Fig. 7.   Lower trophic level model predictions for phytoplankton concentrations (P),

885   expressed as nitrogen equivalents. The model was run for three scenarios:

886   1) Cumulative = present day levels of mussels and freshwater nitrogen inputs,

887   2) Enrichment = no mussels, but freshwater nutrient input to the Bay, and

888   3) Baseline = no mussels present and no freshwater nitrogen input. The top of

889   the stippled area is the daily interpolated data for the offshore P concentration.

890   The top of the shaded area is the daily interpolated data for the observations in

891   each box.

892   Fig. 8.   Lower trophic level model predictions for nitrogen concentrations (TIN). The

893   model was run for the three scenarios described in Fig. 7. The top of the

894   stippled area is the daily interpolated data for the offshore TIN concentration.

895   The top of the shaded area is the daily interpolated data for the observations in

896   each box.

897   Fig. 9.   Lower trophic level model predictions for detritus concentrations (D), expressed

898   as nitrogen equivalents. The model was run for the three scenarios described in

899   Fig. 7. The top of the stippled area is the daily interpolated data for the offshore

900   D concentration. The top of the shaded area is the daily interpolated data for the

901   observations in each box.

902   Fig. 10.   Lower trophic level model predictions for nitrogen levels in the benthos (B).

903   The model was run for the three scenarios described in Fig. 7.

904

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Table 1. Elements of the nitrogen cycle in Tracadie Bay. Quantities calculated or predicted by each model are indicated by 'y' and those not considered by 'n'. P = phytoplankton, TIN = inorganic nitrogen, D = detritus, B = benthos, and M = mussels.

Symbol	Description	N Budget	Lower Trophic Level Model
Reservoirs			
P	Phytoplankton	y	y
TIN	Inorganic nitrogen	y	y
D	Detritus	y	y
B	Benthos	n	y
M	Cultured mussels	y	Specified
Internal Fluxes			
TIN _ P	Photosynthesis	n	y
P _ D	Mortality	n	y
D _ TIN	Remineralization (water column)	n	y
B _ TIN	Remineralization (benthos)	n	y
D _ B	Sedimentation	n	y
B _ D	Resuspension	n	y
P _ M	Ingestion	y	y
D _ M	Ingestion	y	y
M _ B	Biodeposition	y	y
M _ TIN	Excretion	y	y
External Fluxes			
M Harvest		y	y
River	Winter River discharge	TIN only*	TIN only*
Offshore	Marine exchange	P, TIN and D	P, TIN and D
Burial		n	y
Atmospheric	Denitrification	n	n

*P and D river discharge assumed negligible

Table 2. Definition of quantities in the lower trophic level model. Groupings are according to variable type. For each quantity the following information is given: units, its numerical value (or its source), and a brief definition. Explicit functional dependence on time (t) or temperature (Temp) is indicated. P = phytoplankton, TIN = inorganic nitrogen, D = detritus, B = benthos, and M = mussels. Other symbols are defined in Dowd (2005).

Quantity	Units	Value	Definition
(i) State Variables			
P	mmol N m^{-3}	See text	phytoplankton
N	mmol N m^{-3}	See text	nutrients
D	mmol N m^{-3}	See text	water column detritus
B	mmol N m^{-2}	See text	benthic detritus
(ii) Parameters			
K	d^{-1}	Dowd (2005)	exchange/flushing coefficient
k_n	mmol N m^{-3}	2.5	half-saturation for N uptake by P
_p(t)	0.2 - 1	eq. (8), Dowd (2005)	P growth rate
_p	mmol N m^{-3} d^{-1}	0.05	grazing loss of P
_d(Temp)	d^{-1}	0.02 - 0.1	remineralization rate of D to TIN
_d	d^{-1}	0.05	sinking rate for D
_b(Temp)	d^{-1}	0.01	remineralization rate for B to TIN
r(t)	mmol N m^{-3} d^{-1}	varies	resuspension flux
_	-	0.01	burial fraction
I_m	d^{-1}	see text	ingestion rate of bivalves
_m	-	0.065	assimilated fraction for bivalves
_m	-	0.11	excreted fraction for bivalves
_	m	4	water depth
(iii) External Inputs			
$P_\infty(t)$	mmol N m^{-3}	see Fig	far-field P
$N_\infty(t)$	mmol N m^{-3}	see Fig	far-field TIN
$D_\infty(t)$	mmol N m^{-3}	see Fig	far-field D
$N_{in}(t)$	mmol N m^{-3} d^{-1}	varies	external TIN input
$D_{in}(t)$	mmol N m^{-3} d^{-1}	0	external D input

Table 3. Nitrogen inventories (annual averages, t N) and fluxes (t N y^{-1}) calculated from the lower trophic level model. Model scenarios are defined in the text. 'Exchange' terms for boxes 1-3 are the net exchanges with other boxes or the offshore (positive terms are a net gain to the box). The 'Total' column is the exchange between box 1 and the offshore, and represents the material lost or gained in all of Tracadie Bay by marine exchange. P = phytoplankton, TIN = inorganic nitrogen, D = detritus, B = benthos, and M = mussels.

|	Cumulate Effects (Scenario 1)				Enrichment Effects (Scenario 2)				Baseline (Scenario 3)			
	Box 1	Box 2	Box 3	Total	Box 1	Box 2	Box 3	Total	Box 1	Box 2	Box 3	Total
P	0.55	0.43	0.33	1.31	0.65	0.47	0.38	1.51	0.57	0.33	0.32	1.23
TIN	1.45	1.24	0.71	3.40	1.24	1.15	0.59	2.98	0.97	0.49	0.49	1.96
D	1.08	0.56	0.50	2.14	1.25	0.65	0.59	2.48	1.18	0.53	0.54	2.24
B	8.02	0.11	0.30	8.43	0.36	0.13	0.13	0.62	0.34	0.10	0.12	0.56
TIN _ P	47	48	28	122	48	49	28	125	32	20	20	72
P _ D	18.4	25	13.0	56	26	29	17.3	72	19.4	12.8	12.2	44
D _ TIN	40	20	18.2	78	46	23	21	90	44	19.2	20	82
B _ TIN	92	1.9	4.4	99	4.2	2.3	2.0	8.4	3.9	1.78	1.79	7.5
D _ B	20	10.2	9.1	39	23	11.8	10.8	45	21	9.6	9.8	41
B _ D	13.6	2.0	3.7	19	4.4	2.3	2.1	8.8	4.2	1.88	1.90	8.0
P _ M	58	0	5.1	63	0	0	0	0	0	0	0	0
D _ M	114	0	8	122	0	0	0	0	0	0	0	0
M _ B	145	0	11	156	0	0	0	0	0	0	0	0
M _ TIN	19.0	0	1.4	20.4	0	0	0	0	0	0	0	0
M harvest	8.3	0	0.6	8.9	0	0	0	0	0	0	0	0
TIN River	0	101	0	101	0	101	0	101	0	0	0	0
P Exchange	30.1	-22.9	-9.5	-2.4	-22	-21	-10.3	-53	-13.0	-7.4	-7.5	-28
TIN Exchange	-105	-75.2	3.6	-176	-2.1	-77	4.5	-75	-14.9	-0.80	-1.67	-17.4
D Exchange	101	-2.8	7.4	106	25	-3.2	6.1	28	29	8.5	9.5	47
burial	74	1.53	3.5	79	3.3	1.81	1.60	6.7	3.1	1.43	1.44	6.0
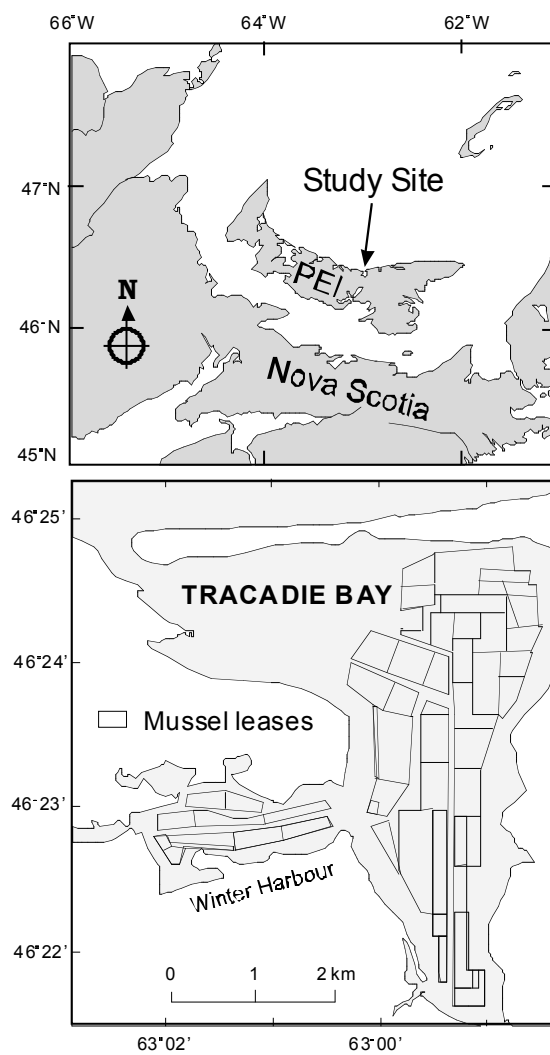
Fig. 1.
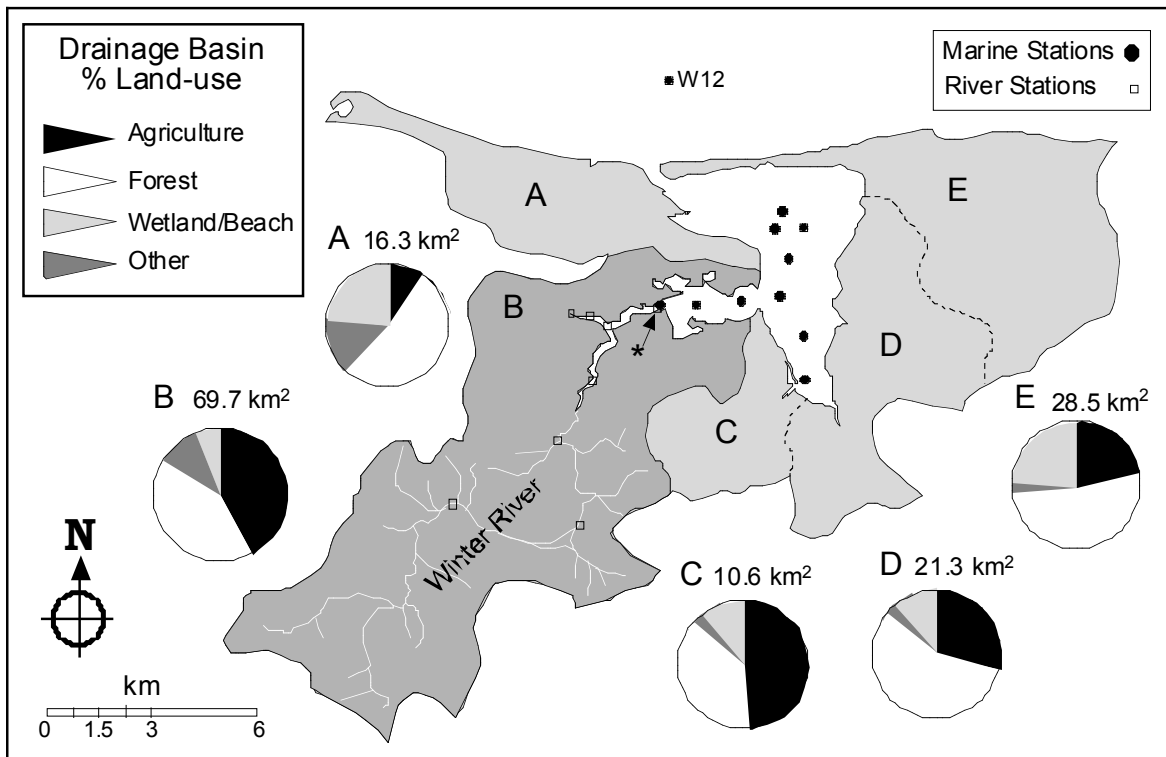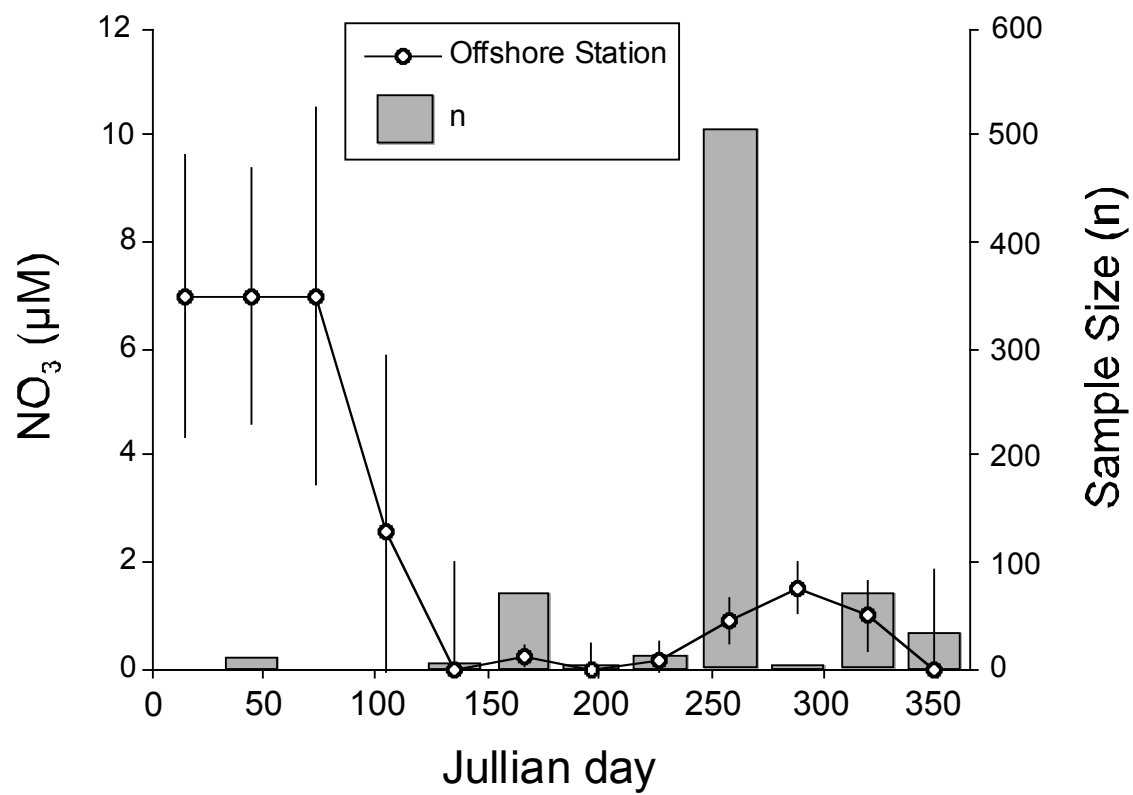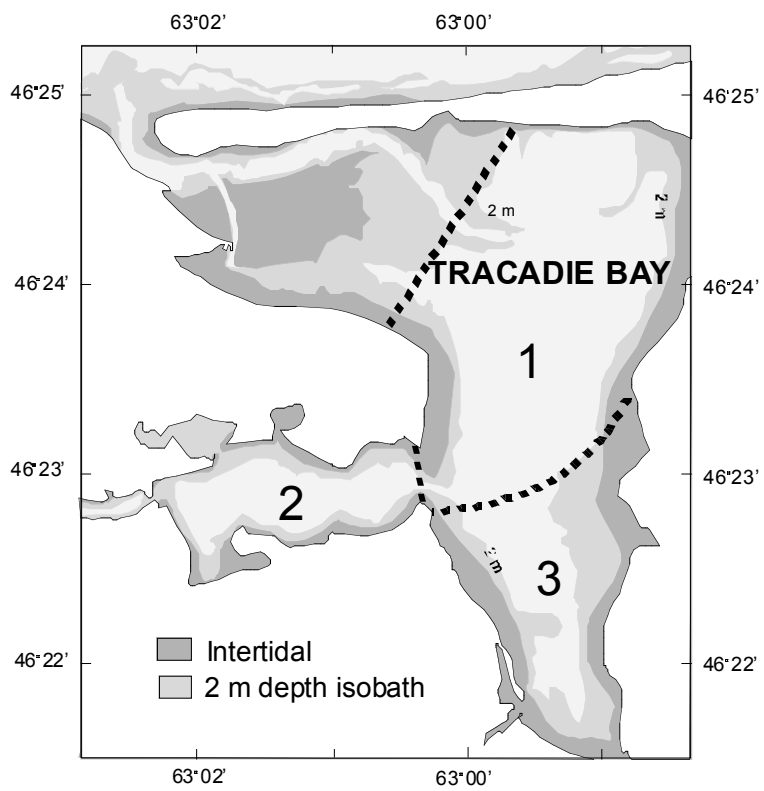
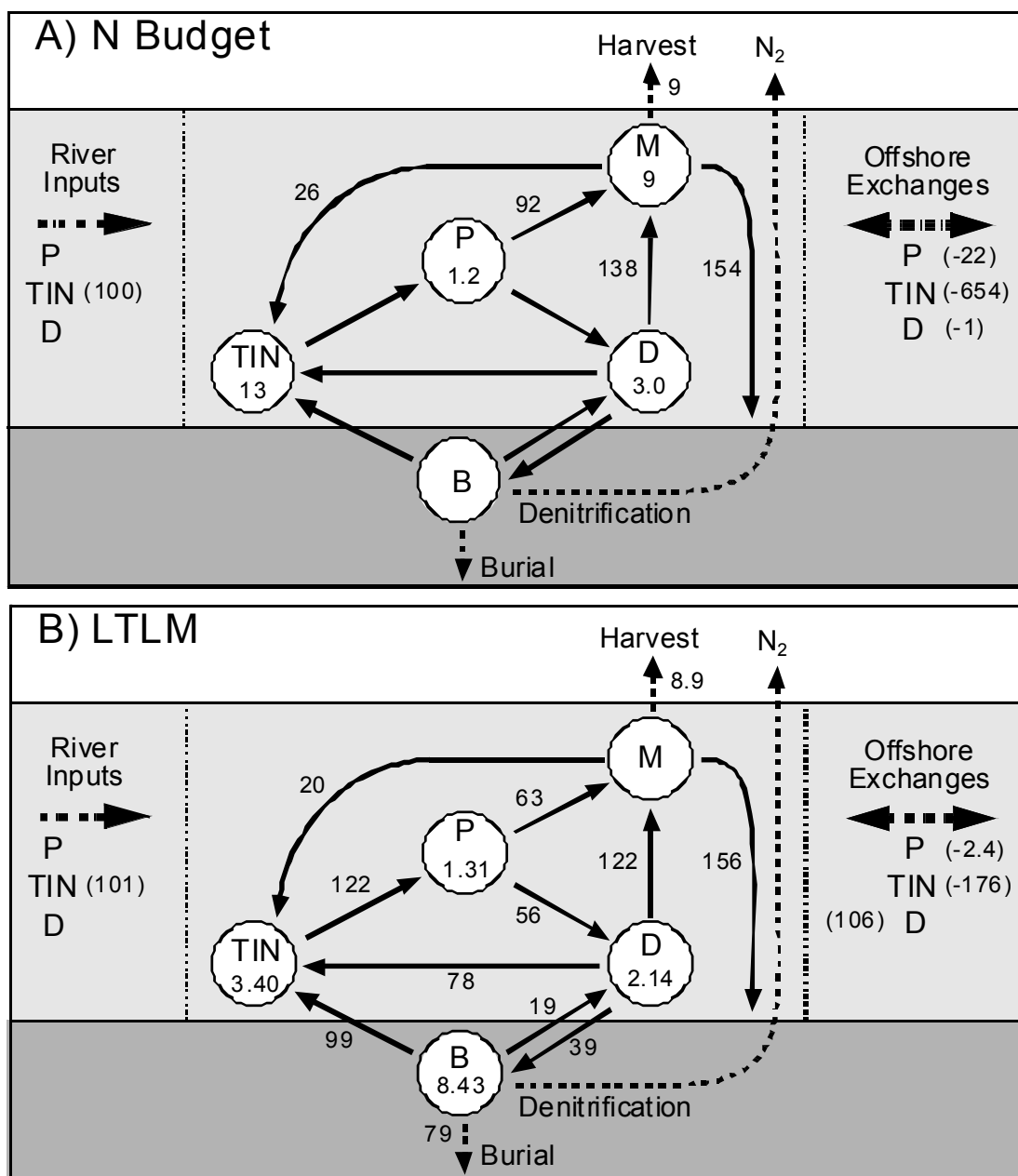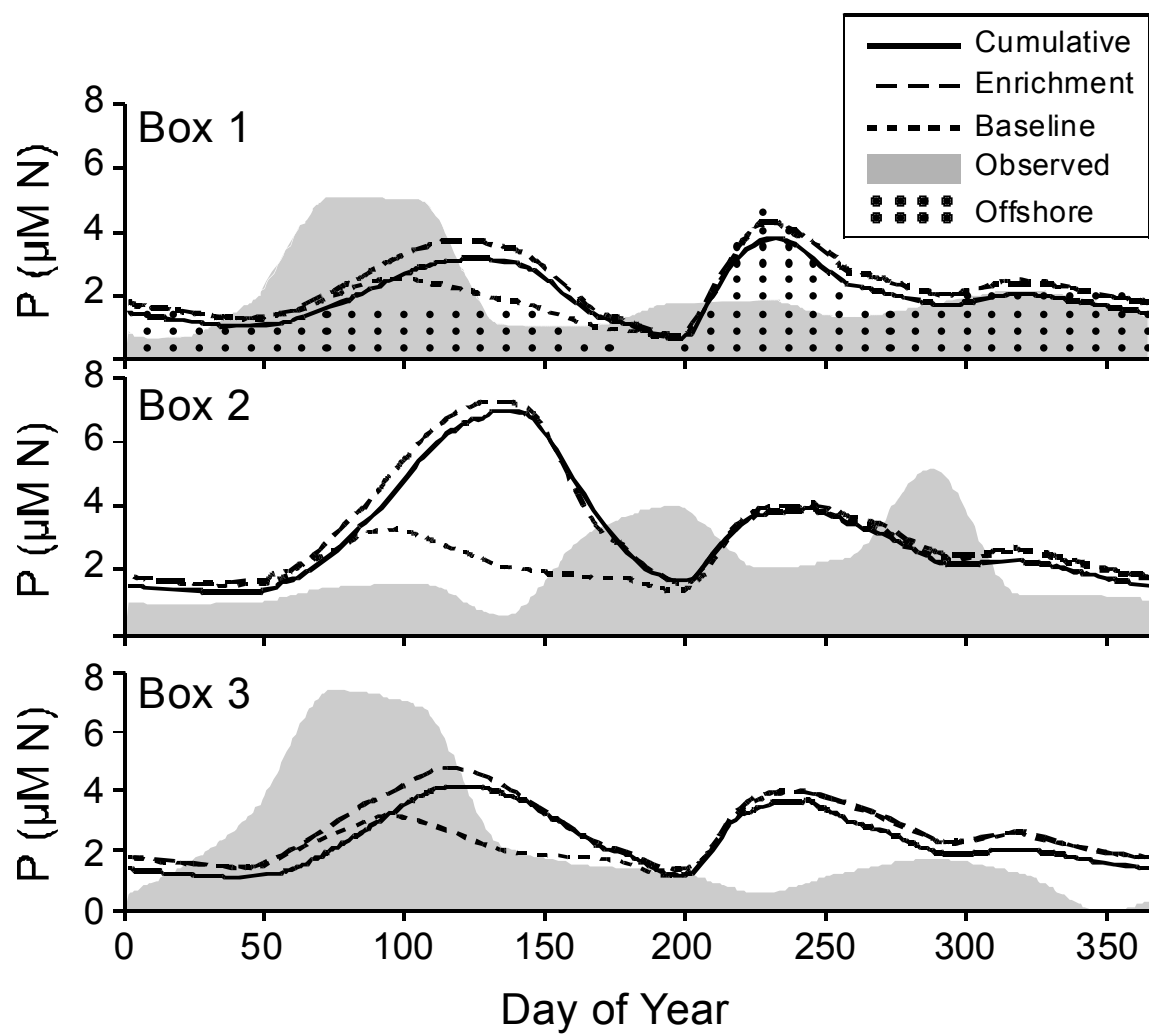* Water sampling stations: WR1 (left square) and W1 (right circle).

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

Fig. 6.

Fig. 7.

Fig. 8.

Fig. 9.

Fig. 10.