

Ecosystem Indicators of Water Quality Part I. Plankton Biomass, Primary Production and Nutrient Demand

W. Glen Harrison (✉) · Tim Perry · William K. W. Li

Biological Oceanography Section, Ocean Sciences Division, Fisheries and Oceans
Canada, Bedford Institute of Oceanography, P.O. Box 1006,
Dartmouth, Nova Scotia, B2Y 4A2, Canada
HarrisonG@mar.dfo-mpo.gc.ca, PerryT@mar.dfo-mpo-gc.ca, LiB@mar.dfo-mpo.gc.ca

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Abstract Seasonal measurements of plankton (phytoplankton and bacteria) biomass and abundance, primary production, and nutrient demand were conducted in the coastal waters of southwestern New Brunswick (SWNB) in 2000–2002 to investigate the far-field effects of finfish (salmon) aquaculture on the pelagic ecosystem. Plankton biomass and production varied seasonally with peak concentrations and activity in summer–fall and lows in winter. Nutrient demand followed a similar pattern with nitrogen (nitrate and ammonium) turnover times ranging from greater than a week in winter to less than a few days in summer. Ammonium concentrations were elevated at the aquaculture sites relative to control sites, however, effects on other nutrients, phytoplankton biomass, bacterial abundance, and primary production were not discernible despite the significant flux of nutrients into the system from finfish farming. Several lines of evidence point to the conclusion that primary production in SWNB is under light rather than nutrient control and that phytoplankton there have limited capacity to process additional nutrients produced as aquaculture in the region expands. The ratio of bacterial abundance to phytoplankton biomass (B/P ratio) is proposed as an easily measured water-quality indicator for assess-

ing the trophic balance (autotrophy vs. heterotrophy) of the pelagic ecosystem in coastal waters.

Keywords Aquaculture · Phytoplankton · Bacteria · Primary production · Nitrate · Ammonium · Nutrient demand · Light-limitation · Water quality

1 Introduction

Finfish aquaculture is a fast growing industry worldwide. In southwestern New Brunswick (SWNB), Canada, the farming of Atlantic salmon has grown dramatically in the last 30 years with the number of active farms doubling and the harvest increasing fourfold over the last 10 years [1]. The growth of this industry has been accompanied by mounting concern about its environmental impacts on coastal ecosystems. There exists now an extensive literature and several comprehensive reviews on the documented and potential environmental effects of aquaculture in the coastal zone (e.g. [2]).

In reviewing existing knowledge and research needs on environmental effects of finfish aquaculture, Hargrave [3] noted that surprisingly little is known about far-field effects (ecosystem-scale), particularly on the pelagic ecosystem, when compared with knowledge of near-field effects (within or adjacent to fish farms), especially on the benthos. Aquaculture impacts on the water-column are mainly concerned with farm effluents/wastes, i.e. inorganic and organic nutrient enrichment and their effects on plankton growth dynamics and community structure, i.e. eutrophication (e.g. [4]). Eutrophication is the consequence of nutrient enrichment [5, 6] and manifests itself in the pelagic zone as increases in plankton (phytoplankton and bacteria) biomass and production (including increased frequency and intensity of benign and Harmful Algal Blooms, HABs [7]) and changes in community structure and trophic state [8]. Among the latter are concerns about the effects of aquaculture on the balance between autotrophic and heterotrophic biomass/production that determine the pelagic oxygen balance of coastal ecosystems [9]. A fundamental question, therefore, is, “Can ecosystems maintain their natural state under the influence of aquaculture activity and for how long?”. More specifically for the pelagic zone, “What is the capacity of plankton to process the effluents of aquaculture?”

This question was at the core of a recently completed multidisciplinary project, Environmental Studies for Sustainable Aquaculture (ESSA), aimed at

1. Evaluating current far-field environmental effects of salmon aquaculture on three contrasting Canadian coastal ecosystems;
2. Constructing models to predict future ecosystem changes and;
3. Developing standard methodologies for effective management of the Canadian finfish aquaculture industry for sustainability [10, 11].

This and the accompanying chapter [9] report on results of the research carried out during the ESSA project to evaluate the effects of salmon aquaculture activity on the pelagic component of the SWNB coastal ecosystem. Properties of the pelagic ecosystem addressed in this paper include water-column transparency, inorganic nutrient concentrations (specifically nitrogen), particulate organic matter, microbial biomass (phytoplankton) or abundance (bacteria), and phytoplankton production (inorganic carbon and nitrogen utilisation rates). Emphasis is placed on nitrogen because of its established role in the regulation of coastal primary production [6, 12, 13]. The chapter that follows [9] looks at dissolved organic matter, microbial respiration and the production/respiration (P : R) balance. Both papers offer simple indices that may be useful in assessing the capacity of pelagic ecosystem in SWNB to process aquaculture wastes now and under future projections.

2

Methods

2.1

Sampling

The SWNB study area, which includes Passamaquoddy Bay and adjacent waters at the western mouth of the Bay of Fundy (Fig. 1), is a shallow (< 100 m at the mouth) semi-enclosed system with irregular bathymetry and coastline inundated with numerous islands and channels that lead to a strong and highly complex and structured tidal circulation that dominates the flow fields in the region [14, 15]. Fresh water input from the St. Croix River in the west and seawater exchange through the Western and Letete Passages in the south and east set up a cyclonic circulation in Passamaquoddy Bay; the residence time of bay waters is on the order of 15 days [14, 16]. The ESSA aquaculture sites were concentrated principally in the shallow (< 30 m) northeastern, Letang/Letete region where water exchange occurs predominantly through the Letete Passage and open Bay of Fundy and residence times are on the order of 9 days [16].

Observations were conducted from fall 2000 to spring 2002. Three process study sites were chosen in close proximity to fish farms (i.e. within a few 100 meters), two in Lime Kiln Bay and one in Bliss Harbour (Fig. 1). Samples were collected for nutrients, biomass (particulate organic matter, chlorophyll a) and phytoplankton productivity over four seasons: fall, 19–21 September, 2000; summer, 24–26 July, 2001; winter, 4–6 December, 2001; and spring, 15–17 May, 2002. The inner and outer Lime Kiln Bay sites were only about 0.5 km apart and the Bliss Harbour site about 3 km from them. An

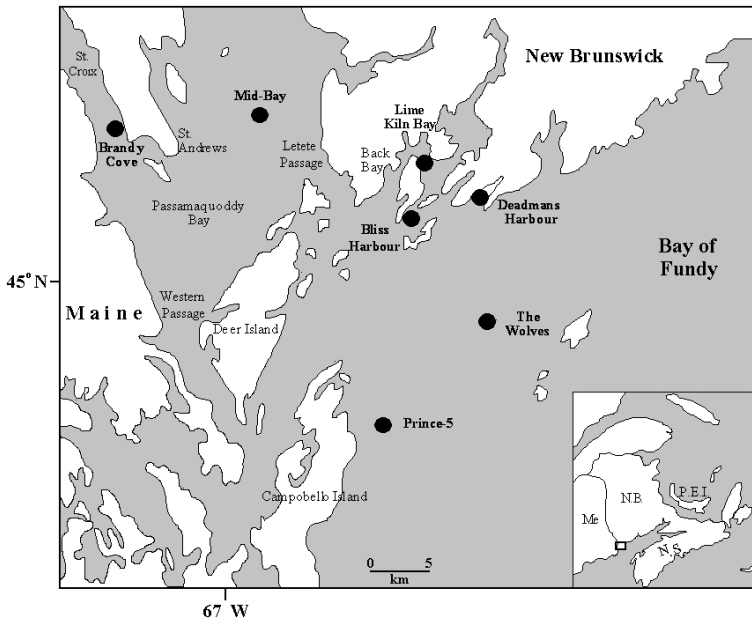


Fig. 1 Locations of aquaculture (Bliss Harbour, Deadman's Harbour, Lime Kiln Bay) and control (Brandy Cove, Mid-Passamaquoddy Bay, Prince-5, The Wolves) sampling sites in southwestern New Brunswick (SWNB)

offshore control site (~ 10 km to the southeast of the aquaculture sites) at The Wolves was also selected for study but due to logistical constraints and weather, it was only sampled in fall. In addition to the seasonal process studies, additional samples for chlorophyll a, water transparency and nutrient concentrations were taken approximately bi-weekly at the Lime Kiln and The Wolves sites in 2000 (chlorophyll measurements started mid-2000) and continued throughout 2001. During the later portion of this time-series (May–Nov, 2001), samples were also collected for bacterial abundance at these two sites, and two additional aquaculture sites (Brandy Cove, Deadman's Harbour) and a control site, mid-Passamaquoddy Bay, far removed from fish farms [17]. Due to unforeseeable problems (weather, logistics constraints), comparative measurements of some properties at aquaculture and control sites were made only during the fall period. Relevant data (chlorophyll a, water transparency, nutrients) collected at another offshore (control) site during 2001, Prince-5, located ~ 15 km south of the aquaculture sites and southwest of The Wolves but not part of the ESSA program, were also used in this study. The Prince-5 data are collected as part of Canada's eastern Atlantic Zone Monitoring Program, AZMP [18, 19].

2.2

Analytical

Water samples for nutrients, biomass and productivity measurements were collected with Niskin bottles at up to 7 “light depths” (approx. 90, 50, 25, 15, 10, 5, 1% surface light) determined from a Secchi disc. Nutrient samples were frozen (polyethylene bottles) and later analysed in the laboratory for nitrate, nitrite, ammonium, phosphate, silicate using standard automated methods [20]. Chlorophyll a was measured fluorometrically [21] and for particulate organic carbon (POC) and nitrogen (PON) by high temperature combustion [22]. Bacteria were fixed in paraformaldehyde (1%) and stored at -80°C . In the laboratory, bacteria were stained with the DNA-binding fluorochrome SYBR Green-1 and detected by green fluorescence in flow cytometric analysis [23]. Productivity measurements were made using stable isotopes (^{13}C -bicarbonate, ^{15}N -nitrate, ^{15}N -ammonium) at tracer concentrations, i.e. 0.2 mol m^{-3} for ^{13}C , and 0.1 mmol m^{-3} for ^{15}N . Water samples collected for productivity measurements were transported to a nearby shore facility, dispensed into 500 ml polycarbonate bottles, inoculated with the isotope tracers and incubated for $\sim 3\text{ h}$ under natural light conditions in attenuated incubator boxes. At the end of incubation, the particulate material was collected on pre-combusted (475°C , 12 h) glass-fibre filters and stored for later mass spectrometric analysis (Europa Scientific) in the laboratory. Nutrient utilisation rates were calculated using standard equations [24]. No corrections were made for “isotope dilution” (due to biological production of ammonium in particular) during the incubation.

Non-parametric statistics (Wilcoxon-Mann-Whitney Rank Sum test) were employed where appropriate to assess differences in properties among aquaculture sites and between them and control sites.

3

Results

3.1

Phytoplankton Biomass, Bacterial Abundance and Primary Production

The seasonal cycle of phytoplankton biomass (chlorophyll a) in waters close to fish farms (Lime Kiln Bay) and at the control site (The Wolves), revealed from the time-series measurements in 2000 and 2001, were remarkably similar in temporal pattern and magnitude (2a). Surface chlorophyll a concentrations varied from a low of $< 1\text{ mg m}^{-3}$ in winter (January–February) to a high of $\sim 10\text{ mg m}^{-3}$ during the pronounced spring (May) and late summer/fall (August–October) blooms. A similar seasonal cycle in chlorophyll a concen-

tration was seen at the Prince-5 station in 2001 although the spring maximum was not as pronounced. Overall, surface chlorophyll concentrations at the aquaculture site were not statistically different from concentrations at the control sites. Other oceanographic properties observed during the time-series studies (surface temperature and salinity) were also similar between the aquaculture and control sites, however, marked difference were seen in water transparency (2b). Secchi depths at The Wolves varied from 4–8 m (summer to winter) but were only 2–5 m in Lime Kiln Bay. Secchi depths did not show much seasonal variability at Prince-5, remaining in the range of 7 ± 1 m and similar in magnitude to Secchi depths at The Wolves. Differences in Secchi depths between the aquaculture site and control sites were statistically significant.

Due in part to their close proximity to each other, particulate biomass (chlorophyll a, POC and PON concentrations) and compositional ratios (C : N) measured during the process studies showed similar patterns among the three aquaculture sites, both within and among seasons (Tables 1 and 2). Particulates were highest in fall and lowest in winter. The spring peak in chlorophyll a seen in 2001 in the time-series observations (2a) was not seen during the process studies in May, 2002 where concentrations were

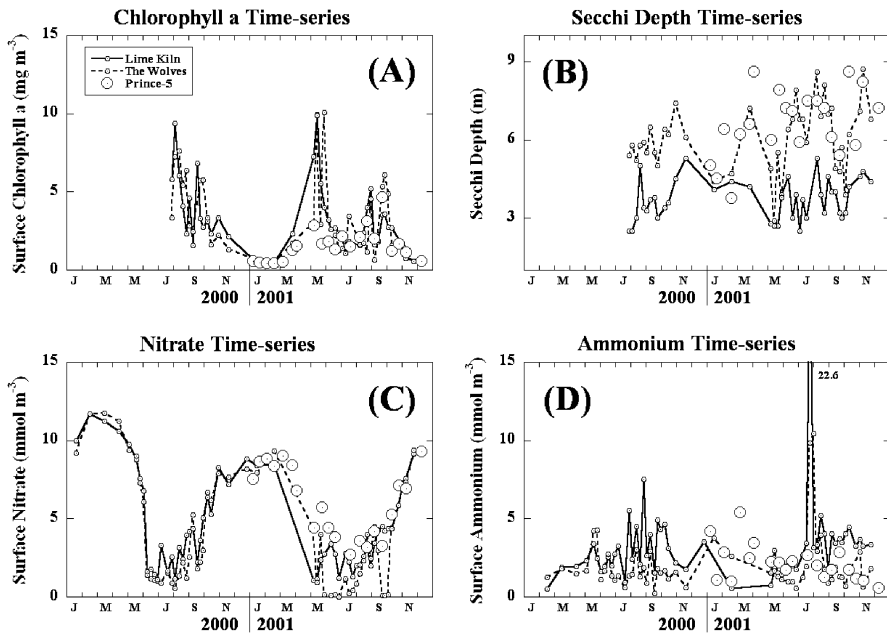


Fig. 2 Seasonal variability in surface chlorophyll a concentrations (a), Secchi depths (b), surface nitrate concentrations (c), and surface ammonium concentrations at the Lime Kiln Bay aquaculture site and The Wolves and Prince-5 control sites in 2000 and 2001

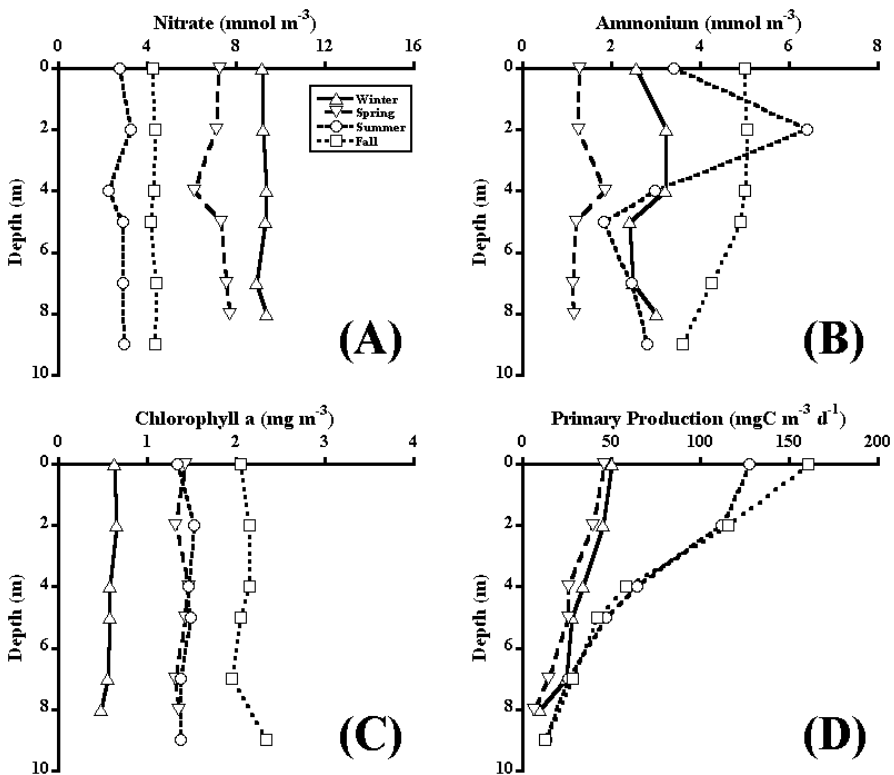


Fig. 3 Seasonal variability and vertical structure of nitrate (a) and ammonium (b) concentrations, chlorophyll a (c) and primary production (d) at the (Inner) Lime Kiln Bay aquaculture site

$< 1.5 \text{ mg m}^{-3}$. Compositional ratios (C:N) varied little among stations or seasons and were higher (8–10) than the so-called “Redfield Ratio” [25] of 7. Analysis of variance revealed that season was the most important factor accounting for the variability of particulates while site was of minor significance. Chlorophyll a, POC, PON concentrations and compositional ratios at The Wolves were statistically indistinguishable from concentrations and ratios at Lime Kiln Bay or Bliss Harbour in fall, the only season in which the complete suite of variables were measured at both aquaculture and control sites. The shallow waters of SWNB are “macro-tidal” (mean tidal range $> 2 \text{ m}$) with strong tidal mixing which explains the uniform vertical distribution of particulates (chlorophyll a, POC, PON) seen at the aquaculture sites in all seasons (3c). Likewise, chlorophyll a concentrations are generally uniform with depth for most of the year at the deeper Prince-5 control site where tidal mixing is also important [19]. At The Wolves, in contrast, stratification of the upper water-column was evident in fall; highest chlorophyll a, POC and PON concentrations were observed in near-surface ($< 10 \text{ m}$) waters (4c).

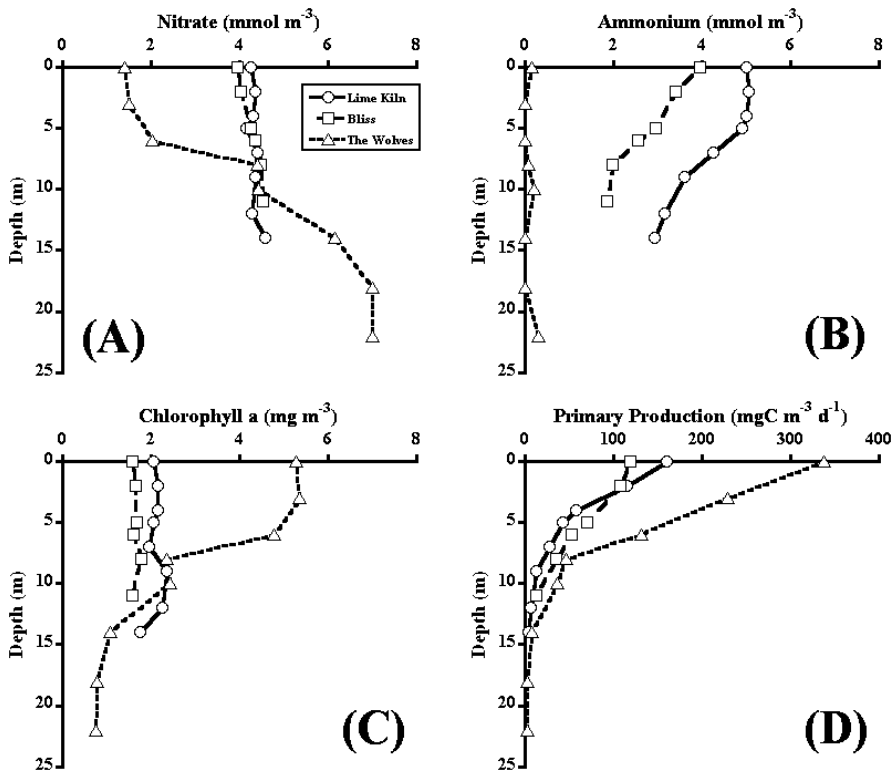


Fig. 4 Vertical structure of nitrate (a) and ammonium (b) concentrations, chlorophyll a (c) and primary production (d) at the aquaculture (Lime Kiln Bay and Bliss Harbour) and control (The Wolves) sites in fall (19–21 September), 2000

From May to November 2001, there was a general coherence in the seasonal development of bacteria in SWNB, which ranged from 0.4 to 2 million cells mL^{-1} . Throughout the entire sampled region, cell abundance was low in spring, increased from the summer solstice to the fall equinox, and then decreased with the approach of winter (5f). In surface waters, the difference in bacterial abundance between Lime Kiln Bay (5d) and The Wolves (5e) was not statistically significant. However, these two sites together with Deadman's Harbour (5c) were, on average, less abundant in bacteria (but not statistically different) than the two innermost sites of Brandy Cove (5a) and Mid Passamaquoddy Bay (5b).

Primary production rates were also similar among the three aquaculture sites. Highest rates were observed in summer ($60\text{--}100 \text{ mg C m}^{-3} \text{d}^{-1}$) and lowest rates in winter ($10\text{--}30 \text{ mg C m}^{-3} \text{d}^{-1}$) (Tables 1 and 2; 3d). Rates were somewhat higher in Bliss Harbour than in Lime Kiln Bay but the difference was not statistically significant. During the fall sampling, primary production rates were significantly higher at the control site (The Wolves) than at

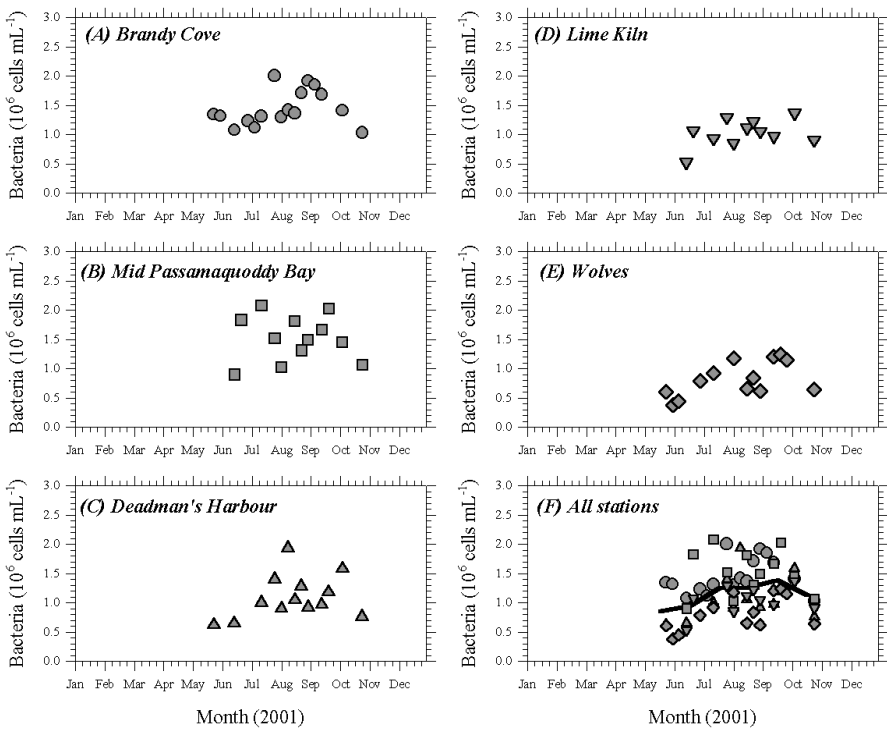


Fig. 5 Bacterial abundance (cells mL^{-1}) in the surface waters (1 m) at 5 locations in SWNB from May to November, 2001. The *solid trend line* in panel (f) is the monthly average for all stations combined

the aquaculture sites, whether calculated on a column-average or areal basis, (4d), however, when normalised to chlorophyll biomass (P : B, Table 1), the differences were not significant. Stratification and higher water transparency likely resulted in a more favourable light environment for phytoplankton at the control site and contributed to the higher absolute production there.

Vertical profiles of primary production and light penetration measurements, i.e. from Secchi depths, showed that euphotic depths ($\sim 3 \times$ Secchi depth) or compensation depths, D_c (depth of zero primary production) were on the order of 10 m or less at the aquaculture sites and 20 m at the control site (Tables 1, 2; (3d), (4d)). In all cases, euphotic depths were shallower than estimated (from vertical temperature profiles) mixing depths: 10–17 m at the aquaculture sites, 43 m at the control site.

3.2

Nutrient Concentrations, Demand and Turnover

Surface nutrient concentrations from time-series measurements in 2000–2001 at the Lime Kiln aquaculture site and The Wolves and Prince-5 control sites were similar in magnitude and seasonality as seen for chlorophyll concentrations. Nitrate concentrations were high in winter (8–12 mmol m⁻³) and decreased to minimum values in summer (2c). Summertime nitrate concentrations were highest at Prince-5 (~ 4 mmol m⁻³) and lowest at The Wolves (< 1 mmol m⁻³). Concentrations at The Wolves were significantly lower than at Prince-5 and Lime Kiln whereas concentrations at the latter two sites were statistically indistinguishable. Similar magnitudes and patterns were seen during the more detailed seasonal process studies (Tables 1 and 2). Concentrations were relatively uniform with depth at the aquaculture sites due to strong tidal mixing (3a) but increased with depth in the stratified waters of The Wolves in fall (4a). Nitrite, phosphate and silicate concentrations (not shown) followed the seasonal pattern of nitrate. Surface ammonium concentrations from the time-series measurements, in contrast to nitrate, were lowest in winter (< 1 mmol m⁻³) and highest in summer/fall (> 4 mmol m⁻³ and on occasion > 20 mmol m⁻³) (2d). In winter, ammonium represented ~ 25% of the total inorganic-N but almost 50% in summer. Overall, ammonium concentrations were significantly higher at the aquaculture site than at the two control sites. This was also evident from the process studies where ammonium concentrations at The Wolves in fall were < 0.1 mmol m⁻³ compared with > 2 mmol m⁻³ at the two aquaculture sites (Table 1). Note, however, that these concentrations at The Wolves were considerably lower than observed in fall during the time-series study (2d). In contrast to the vertical distribution of nitrate, ammonium concentrations were not uniform with depth at the aquaculture sites but were somewhat higher in near surface waters, particularly in summer and fall ((3b), (4b)). Concentrations at The Wolves, however, were uniform (and low) despite the highly stratified water column apparent at that site. Analysis of nutrient ratios showed that the aquaculture sites were enriched in ammonium in summer and fall (relative to nitrate) compared with ratios at the control sites. Nitrate: ammonium ratios at the aquaculture sites in fall, for example, averaged 1.2 compared with a ratios 12–66 at control sites. N : P and N : Si ratios at the aquaculture sites, however, were statistically indistinguishable from ratios at the control sites. N : P ratios at all sites in fall (i.e. 6–8) were significantly lower than requirements for phytoplankton growth, i.e. 16, the Redfield Ratio [25].

Regional and seasonal variations in nitrogen utilisation rates at the aquaculture sites were similar to concentration variations, i.e. nitrate utilisation was highest in spring and winter (40–120 μmol m⁻³h⁻¹) when nitrate concentrations were highest and ammonium utilisation was highest in summer and fall (40–100 μmol m⁻³h⁻¹) when concentrations peaked (Tables 1 and 2). Pat-

Table 1 Water-column properties (euphotic depth average) at the SWNB aquaculture and control sites

	Spring		Summer		Fall		Winter	
	Lime Kiln	Bliss	Lime Kiln	Bliss	Lime Kiln	Bliss	The Wolves	Bliss
Euphotic depth (m)	9	11	8	11	9	11	22	10
Mixing depth (m)	10	12	10	12	10	12	43	10
Nutrients								
NH ₄ (mmol m ⁻³)	1.38	0.91	3.44	2.36	4.14	2.73	0.07	2.88
NO ₃ (mmol m ⁻³)	7.13	8.0	2.89	2.73	4.36	4.27	4.55	9.25
Biomass								
CHL (mg m ⁻³)	1.38	1.36	1.44	1.45	2.14	1.64	2.59	0.59
PON (mmol m ⁻³)	2.5	2.1	3.0	2.6	3.4	3.4	3.3	1.9
POC (mmol m ⁻³)	22.6	20.9	24.0	22.7	25.8	29.1	27.7	17.5
C : N (molar)	9.0	10.0	8.0	8.7	7.6	8.6	8.5	9.4
Productivity								
NH ₄ Util (μmol m ⁻³ h ⁻¹)	13	13	74	51	38	40	8.1	17
NO ₃ Util (μmol m ⁻³ h ⁻¹)	53	118	55	72	2.1	4.5	32	53
Prim prod (mgC m ⁻³ d ⁻¹)	28	38	65	89	46	65	80	34
f-ratio	0.81	0.90	0.43	0.58	0.05	0.10	0.80	0.76
P : B (mg C mg CHL ⁻¹ h ⁻¹)	1.7	2.3	3.7	5.1	1.8	3.3	2.6	4.9
NH ₄ turnover (d)	4.6	2.9	2.0	1.9	4.6	2.9	0.35	7.3
NO ₃ turnover (d)	5.6	2.8	2.2	1.6	88	39	5.8	7.2

$$f\text{-ratio} = [\text{NO}_3\text{Util}/(\text{NO}_3\text{Util} + \text{NH}_4\text{Util})]$$

terns and magnitudes were similar among the aquaculture sites; an analysis of variance showed that season was the most significant factor contributing to variability. Nitrate utilisation exceeded ammonium utilisation much of the year, i.e. nitrate fuelled 80–90% of the primary production in spring and winter, 40–50% in summer and < 10% in fall (see f-ratios, Tables 1 and 2). Nitrate-based production at The Wolves control site in fall was on the same order as winter/spring values at the aquaculture sites, i.e. f-ratio \sim 0.8, and significantly higher than nitrate-based production at the aquaculture sites in fall (f-ratio: 0.05–0.10). The anomalously low ammonium concentrations measured at The Wolves in fall, however, may have accounted for the low ammonium utilisation and high f-ratios observed. Short-term carbon (primary production): nitrogen (nitrate plus ammonium uptake) utilisation ratios (molar) at the aquaculture sites were well below Redfield ratios in winter (C : N Util: 2–3), but increased through spring and summer (C : N Util: 3–5) to ratios above Redfield in fall (C : N Util: 8–10); highest ratios (C : N Util: 13) were observed at the offshore control site where surface inorganic nitrogen concentrations were lowest.

Table 2 Comparison of water-column properties (euphotic depth average) between inner and outer Lime Kiln Bay, SWNB

	Spring		Summer		Winter	
	Inner	Outer	Inner	Outer	Inner	Outer
Euphotic depth (m)	9	11	8	10	10	12
Mixing depth (m)	10	17	10	17	10	17
Nutrients						
NH ₄ (mmol m ⁻³)	1.38	1.64	3.44	5.43	2.88	2.07
NO ₃ (mmol m ⁻³)	7.13	7.50	2.89	2.29	9.25	9.21
Biomass						
CHL (mg m ⁻³)	1.38	1.64	1.44	1.86	0.59	0.57
PON (mmol m ⁻³)	2.5	2.4	3.0	3.8	1.9	1.3
POC (mmol m ⁻³)	22.6	33.3	24.0	29.4	17.5	12.2
C : N (molar)	9.0	14.1	8.0	7.7	9.4	9.3
Productivity						
NH ₄ Util (μmol m ⁻³ h ⁻¹)	13	12	74	101	17	9
NO ₃ Util (μmol m ⁻³ h ⁻¹)	53	39	55	56	53	36
Prim prod (mg C m ⁻³ d ⁻¹)	28	26	65	104	34	10
f-ratio	0.81	0.77	0.43	0.36	0.76	0.80
P : B (mg C mg CHL ⁻¹ h ⁻¹)	1.7	1.3	3.8	4.7	4.8	1.4
NH ₄ turnover (d)	4.6	5.7	2.0	2.2	7.3	9.7
NO ₃ turnover (d)	5.6	8.0	2.2	1.7	7.2	10.8

$$\text{f-ratio} = [\text{NO}_3\text{Util}/(\text{NO}_3\text{Util} + \text{NH}_4\text{Util})]$$

Table 3 Comparison of mean inorganic nutrient concentrations and nutrient ratios in Bliss Harbour, SWNB: 1990–2002. DIN(dissolved inorganic nitrogen) = $\text{NO}_3 + \text{NH}_4$

	SiO_3 (mmol m^{-3})	PO_4 (mmol m^{-3})	NO_3 (mmol m^{-3})	NH_4 (mmol m^{-3})	DIN : SiO_3 (molar)	DIN : PO_4 (molar)	$\text{NO}_3 : \text{NH}_4$ (molar)	Ref
1990								[33]
Spring	10.6	0.7	9.0	1.3	1.0	14.4	6.8	
Summer	1.4	0.6	1.8	3.0	3.4	8.4	0.6	
Fall	3.9	1.0	3.6	5.3	2.3	9.0	0.7	
Winter	10.1	1.0	9.4	1.1	1.0	10.6	8.9	
1999								[34]
Spring	-	-	-	-	-	-	-	
Summer	-	-	-	-	-	-	-	
Fall	1.8	0.6	1.0	2.5	1.9	5.8	0.4	
Winter	-	-	-	-	-	-	-	
2000–2002								[Present study]
Spring	8.5	0.8	8.0	0.9	1.1	11.5	8.8	
Summer	4.0	0.6	2.7	2.4	1.3	8.0	1.2	
Fall	5.3	0.9	4.3	2.7	1.3	7.7	1.6	
Winter	9.6	1.0	9.6	1.5	1.2	11.1	6.6	

Nitrate and ammonium turnover (concentration/utilisation rate) was comparable at the aquaculture sites for most seasons, i.e. turnover times were on the order of a week in spring and winter and ~ 2 days in summer. During the fall, ammonium turnover times were still relatively short (3–5 days) but nitrate turnover was 40–90 days, due to the low utilisation rates then, and only $\sim 10\%$ of the summer rates. An explanation for the anomalously low nitrate utilisation rates observed in fall at both Lime Kiln Bay and Bliss Harbour is unclear. In contrast, nitrate and ammonium turnover times at The Wolves in fall were short; < 1 day for ammonium and less than a week for nitrate.

4

Discussion

One of the principal environment concerns surrounding the aquaculture industry is eutrophication: increased (above natural levels) biomass and/or production of autotrophs (phytoplankton and macrophytes) and microheterotrophs (bacteria in the sediments or water-column) from the addition of inorganic and organic nutrients to the ecosystem from the industry's wastes. In addition to increased biomass and metabolism, alterations in community structure and disruption of the natural balance between autotrophic and heterotrophic processes are also known consequences [2, 26]. The ability to quantify environment impacts of aquaculture is considerably more difficult when dealing with far-field, ecosystem-level effects compared with near-field, localised effects [3], due in large part to the often dominant influence of other anthropogenic sources of nutrients (domestic sewage, industry, agriculture) in coastal waters [27, 28]. Understanding far-field effects of finfish aquaculture on the pelagic ecosystem is a great challenge as evidenced by the lack of published information on the subject [3]. Detailed mass-balance calculations of fish farm wastes in SWNB [16, 29] have shown that nitrogen fluxes from farms, for example, dominate anthropogenic nitrogen inputs to the region and can exceed natural nitrogen fluxes by as much as threefold in some locations. The question is: how are these excess nutrients affecting the pelagic (and benthic) ecosystems of SWNB?

4.1

Phytoplankton Biomass, Bacterial Abundance and Particulate Organic Matter

Similarities in the seasonal cycles of phytoplankton (chlorophyll a concentration) in SWNB at sites close to salmon pens and sites far removed lead one to the conclusion there are no discernible effects of the aquaculture activity on this ecosystem property. Differences in the vertical distribution of phytoplankton between the aquaculture sites and The Wolves control site were

observed in fall but can be explained by local hydrography. The upper water-column at The Wolves is highly stratified in summer and fall but well-mixed at the aquaculture sites year-round due to strong tidal forcing. A more appropriate comparison, i.e. between the well-mixed aquaculture sites and the well-mixed Prince-5 control site, showed that the magnitudes and seasonal cycles of phytoplankton biomass were similar. In a like manner, the concentrations and elemental composition (C : N ratio) of particulate organic matter were similar at the aquaculture and control sites. Although these properties were measured at both sites only in fall, the impacts of aquaculture wastes on the pelagic ecosystem may be most significant then [16, 30]. In an earlier study of finfish aquaculture effects on water chemistry and plankton in SWNB, Wildish et al. [31] came to similar conclusions about phytoplankton biomass, i.e. no measurable differences were observed in chlorophyll a concentrations in the proximity of and away from fish farms. Evidence in the literature of significant effects of finfish aquaculture wastes on phytoplankton biomass and associated particulates from other regions is lacking [3, 26].

Seasonal measurements of bacterial abundance showed no clear differences between the aquaculture and control sites either. Bacterial abundances relative to phytoplankton biomass (B/P ratios) were slightly higher at the Lime Kiln Bay aquaculture site compared with The Wolves control site but well within the range of ratios seen in offshore shelf and oceanic waters far from the influence of aquaculture and other human activities. We found one study in the literature that has investigated near- and far-field effects of finfish aquaculture on bacteria, in Gokasho Bay, Japan (34.3N 136.6E) in late summer [32]. This is a shallow system (15–30 m) but with much higher temperatures ($> 25^{\circ}\text{C}$ compared with late summer maximum temperatures in SWNB of $< 15^{\circ}\text{C}$), nutrients and plankton biomass than seen in SWNB. They observed sharp spatial gradients in nutrients, chlorophyll a and bacterial abundance and production rates with highest levels closest to the fish farms and lowest levels at the mouth of the Bay, some 4 km away. Bacterial biomass and production rates were an order of magnitude higher at the farms compared with the mouth of the Bay. Chlorophyll a and nutrients were higher at the farms by a factor of five and dissolved organic matter by a factor of two. Unfortunately, the data were not presented in a way that B/P ratios could be calculated and compared with those observed in SWNB.

4.2

Primary Production and Nutrient Demand

Similar to the results for phytoplankton biomass, primary production rates varied seasonally at the aquaculture sites but differences among the sites were insignificant overall. Comparative data at The Wolves control site were collected only during fall and productivity (normalised to biomass, P : B) there was not significantly different from P : B ratios at the aquaculture sites;

again, impacts of aquaculture activities on ecosystem properties in the water-column may be most significant during the summer-fall seasons [16, 30]. At the aquaculture sites, nitrate was the dominate nitrogen source fuelling primary production in winter and spring at all sites and ammonium was relatively more important in summer and fall. Nitrate, however, was the principal source for production at the offshore control site in fall but the anomalously low ammonium concentrations observed then may have contributed. We are not aware of any published studies of the effects of aquaculture on nutrient utilisation by phytoplankton, however, our observations are similar to those seen in other coastal waters where aquaculture is not an issue. L'Helguen et al. [33], for example, investigated the seasonal cycles of nitrate and ammonium in permanently well-mixed coastal waters in the western English Channel off the coast of France and found magnitudes and patterns of nitrate and ammonium utilisation remarkably similar to what we observed in SWNB. Our estimates of nitrate and ammonium turnover times were similar among the experiment sites, ranging from the order of a week in winter and spring to 2 days in summer. The anomalously long nitrate turnover times at the aquaculture sites in fall (40–80 days) are difficult to explain but resulted from very low measured utilisation rates. At the offshore control site, extremely low ammonium concentrations in fall resulted in very short turnover times, < 1 day. From the time-series study, it would appear that much higher ammonium concentrations are typical at that site in fall and thus turnover times may generally be longer.

Because the sources of nutrients in SWNB vary [16, 29], it is difficult to attribute observed levels to aquaculture activity specifically. Analysis of absolute nutrient levels and nutrient ratios, however, suggests that the aquaculture sites were enriched in recycled nitrogen and ammonium (relative to nitrate) compared with the control sites. Wildish et al. [31] carried out an earlier (1989–1990) seasonal study of the influence of salmon aquaculture activity on phytoplankton biomass and nutrients in SWNB. Similar to our results, they found no evidence of elevated concentrations of nitrate and silicate in the proximity of fish farms compared with open water control sites. However, ammonium concentrations, and phosphate to a lesser extent, were high near the farms. A more recent fall survey in SWNB almost 10 years later, 1999, [34] showed, again, elevated ammonium concentrations and low N : Si and N : P ratios at the aquaculture sites but nutrient concentrations and ratios were not substantially different from those seen in 1989–1990 (Table 3). Gowen and Bradbury [26] observed elevated ammonium concentrations in the vicinity of finfish farms in Scottish coastal waters but no apparent effects on phytoplankton biomass. Over the long term, changes in nutrient concentration ratios in coastal waters as a result of nitrogen enrichment from a variety of sources, including aquaculture, have been implicated in dramatic alterations in phytoplankton community composition, and increases in the frequency and intensity of phytoplankton blooms, including harmful algal

blooms (HABs) world-wide (e.g. [7]). In other cases, the alterations are more subtle and can only be discerned from a long record of measurements made over many years. For example, in Bedford Basin, it appears that annual average ratios of N : Si and P : Si are higher now than they were 30 years ago. Concomitantly, there has been an increase in the abundance of smaller phytoplankters (pico- and nanoplankton), which do not generally use silicate as a macro-nutrient [35]. Potentially, this change in the size structure of the primary producers may have an influence on ecosystem dynamics. Phytoplankton community structure in SWNB observed over the past decade, including the incidence of HABs, has not changed appreciably with the growth of the aquaculture industry [36, 37]. Absence of evidence at present of significant effects of aquaculture activity in SWNB on nutrients or phytoplankton may not continue indefinitely into the future, however. Salmon rearing and fish processing are the dominant anthropogenic sources of nutrients and oxygen demand in this region [16, 29] and continued expansion will translate to increasing nutrient loads and stress on the oxygen balance of the system (see also [9, 30]). How much longer the pelagic ecosystem of SWNB can absorb these inputs without negative consequences is a critical unknown.

4.3

Light vs. Nutrient Limitation of Primary Production

Observations made during this study strongly suggest that primary production rates at both the aquaculture and control sites were not under the control of nutrient supply. Seasonal variability in nutrient concentrations indicated that at no time were nutrients completely depleted in surface waters, even at the control sites. Moreover, during summer–fall when winter nutrient stores (e.g. nitrate) are reduced due to biological utilisation, internally recycled nutrients (e.g. ammonium) reached their maximum levels at the aquaculture sites and control sites. Both nitrate and ammonium turnover times exceeded the normal doubling time of coastal phytoplankton (~ 1 doubling d^{-1}), even in summer/fall when concentrations were lowest, suggesting further that nutrient supply was not limiting in this region. Nutrient concentration ratios indicated that phosphorus and silicate were sufficient for or in excess of metabolic requirements even during summer. Taken together, these observations provide convincing evidence that factors other than nutrients are controlling primary production (and setting an upper limit on nutrient demand) in SWNB.

Primary production profiles and measurements of water transparency during this study showed that euphotic depths were exceeded at all stations by mixing depths, a strong indicator of light-limitation. In offshore coastal and oceanic waters, the attenuation of light is largely due to the presence of phytoplankton and phyto-detritus [38]. However, this is not the case for strongly mixed, shallow inshore waters, including at least one of the con-

trol sites in this study, where other dissolved and particulate constituents dominate the optical attenuation of water. At Prince-5, for example, extinction coefficients (K_d) calculated from phytoplankton biomass [39] were significantly less ($0.06\text{--}0.25\text{ m}^{-1}$) than those determined from Secchi depths ($0.17\text{--}0.38\text{ m}^{-1}$) which is a measure of total light extinction. The indication is that in these waters, phytoplankton account for half or less of the light attenuation. In a similar way, phytoplankton contributed $< 25\%$ to light attenuation at the aquaculture sites compared with the Wolves control site (2b).

In shallow macro-tidal coastal waters such as SWNB, turbidity is an important factor limiting primary production and evaluating the response of phytoplankton in these environments to nutrient over-enrichment from human activities such as aquaculture is not straight forward [8, 40]. In an attempt to address this problem, Cloern [41] developed a simple index of the relative sensitivity of natural phytoplankton populations to light and nutrients based on knowledge of the resource (i.e. submarine light conditions and nutrient concentrations) and physiological properties of the phytoplankton (i.e. growth response to light and nutrients). Cloern determined light sensitivity from estimates of the mean euphotic zone light field (from incident light and extinction coefficient) scaled by the half-saturation growth constant for coastal phytoplankton grown under light-limited conditions. Similarly, nutrient sensitivity was determined from the local euphotic zone nutrient concentration scaled by the half-saturation growth constant for coastal phytoplankton grown under nutrient-limited conditions. The ratio of these sensitivity estimates (R) is then the basis for evaluating light versus nutrient limitation, i.e. $R = 1$ is the partition between light and nutrient limitation where $R > 1$ is the light-limited domain ($R > 10$ represents strong light limitation) and $R < 1$ is the nutrient limited domain ($R < 0.1$ represents strong nutrient limitation).

We applied this procedure in a similar way to our data from SWNB using incident light, extinction coefficients (calculated from Secchi depths) and observed inorganic nitrogen concentrations. A single growth half-saturation constant for light (derived from photosynthesis versus light curves in local waters, i.e. 50 W m^{-2} or $\sim 235\text{ }\mu\text{E m}^{-2}\text{s}^{-1}$) was applied to all data. Similarly, a single half-saturation constant for nutrient limited growth (1.5 mmol m^{-3}), typical for coastal phytoplankton [41] was used. Physiological response to both light and nutrients can change with resource conditions (i.e. half-saturation constants are not truly constant), however, Cloern's sensitivity analysis suggests that this limitation index is robust, i.e. fairly insensitive to changes in the growth constants. It is evident from this analysis that phytoplankton at both the aquaculture and control sites in SWNB are strongly light-limited, even in summer when incident light is at its maximum (Fig. 6). Severity of light-limitation is highest in winter when incident light is at its minimum and day-length shortest. Interestingly, light-limitation was more acute at the Prince-5 control site than at the aquaculture sites despite the

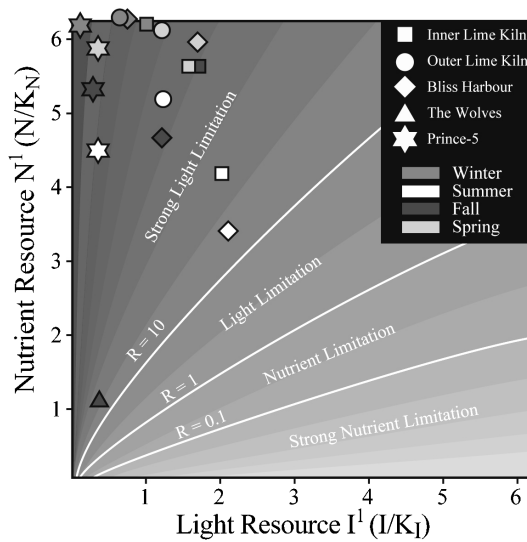


Fig. 6 Index (ratio, R) of the relative strength of light and nutrient limitation on phytoplankton growth from [41]: seasonal data from SWNB aquaculture and control sites superimposed

fact that turbidity was greater inshore, by at least a factor of two. Because mixing depths are much greater (~ 90 m) at Prince-5 compared with the aquaculture sites (10–20 m), however, the “average” light levels that Prince-5 phytoplankton would be exposed to were far less than average levels at the shallow aquaculture sites, resulting in stronger light-limitation at the former site.

Because aquaculture activity has not measurably affected the pelagic primary producers in SWNB, one might conclude that their capacity to process nutrients has not been exceeded. However, an important implication of the results described here is that the phytoplankton in SWNB may, in fact, have little excess capacity for increasing growth and production in response to increased nutrient loading. It is apparent that light has basically set the upper limit on pelagic primary production in this system. Moreover, light-limitation will likely follow a course of greater severity as suspended particulates and turbidity increase with increasing aquaculture activity. In general, therefore, it might not be unreasonable to suggest that the autotrophic component of the pelagic ecosystem in SWNB is probably at or close to its capacity and that any further response to aquaculture activity (and nutrient loading) may only be manifest in the micro-heterotrophs. The same may not be true for the macro-flora, however, where there is some evidence that nutrient enrichment from fish farms in SWNB may have influenced the growth of inter-tidal green macroalgal mats (*Enteromorpha* and *Ulva* species) [42, 43].

4.4

Bacteria

In offshore coastal and oceanic waters which do not receive significant allochthonous input of organic matter, the maximum realised abundance of bacteria depends on an interplay between bottom-up control by phytoplankton and top-down control by bacterivores and viruses. A global macroecology of the bacteria-phytoplankton relationship in oceanic regions [44] indicates a well-defined domain within which almost all of 13 974 paired observations have been recorded (7a). In this context, the SWNB measurements occur close to the median trend (7b), with Lime Kiln bacteria just slightly more abundant than The Wolves bacteria when scaled to phytoplankton biomass. This is in contrast to two other marine inlets: Bedford Basin, Nova Scotia (44°41'N, 63°38'W), heavily impacted by municipal and industrial wastes (7c), and Tracadie Bay, Prince Edward Island (46°24'N, 63°00'W), a site of intense shellfish (mussel) aquaculture activity (7d). In these latter cases, bacteria occur at abundances (scaled to phytoplankton abundance) far exceeding the maximum levels realised in natural coastal and oceanic regions remote from anthropogenic influence. More important, however, is the observation that at present, bacterial abundance at aquaculture sites in SWNB does not appear to be significantly higher in most cases than levels seen at sites far removed from salmon farms. Bacterial abundance in SWNB, similar to phytoplankton biomass, shows little effect from aquaculture activity. Moreover, bacterial abundance relative to phytoplankton biomass, i.e. B/P ratios, in these waters are statistically indistinguishable from ratios observed in offshore and oceanic waters far-removed from anthropogenic inputs. In contrast to the expected response of phytoplankton to increasing aquaculture activity, the micro-heterotrophs are not constrained by light and would be expected to respond positively to increased nutrient loading (inorganic and organic; particulate and dissolved) relatively unchecked. Low short-term C : N utilisation ratios compared with particulate elemental ratios observed in this study during most seasons (below Redfield ratios) suggest that bacteria may be competing with phytoplankton for inorganic nitrogen [45] and that micro-heterotrophs are already playing a significant role in the nitrogen dynamics in SWNB. With the production side of oxygen balance in the water-column effectively in check through light-limitation, increasing bacteria abundance and metabolism will tip the balance in the water-column to excess respiration and subsequent oxygen depletion [9]. Not only does this have implications for the ecosystem but for the aquaculture industry as well [30]. The shift from a balanced towards a heterotroph-dominated system, although not evident yet in SWNB, is nonetheless a distinct possibility and has already been observed in coastal waters close by impacted heavily by municipal and industrial wastes (Bedford Basin, Nova Scotia) and waters supporting extensive shellfish aquaculture (Tracadie Bay, Prince Edward Island). It would be interesting to know

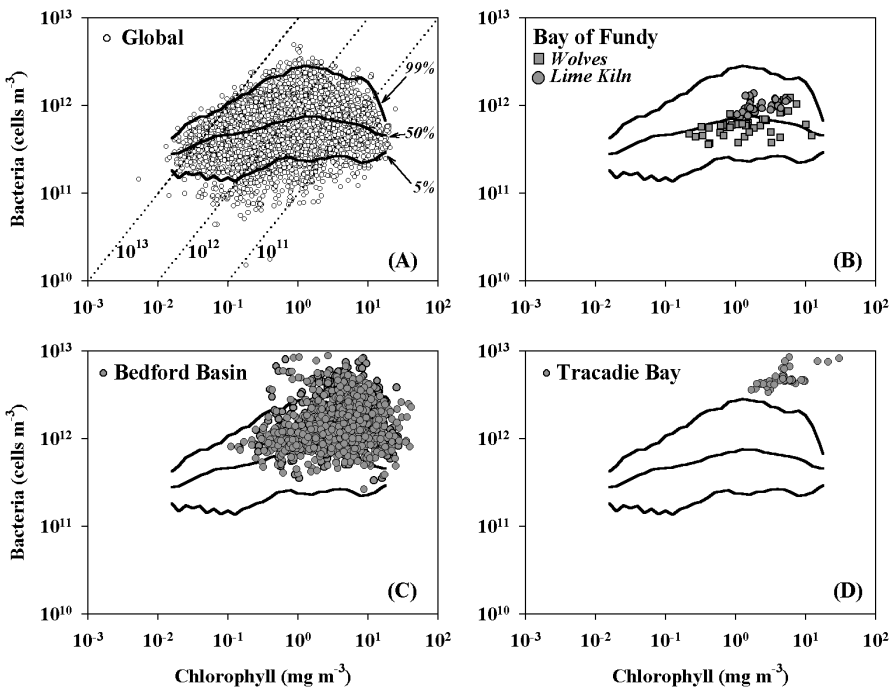


Fig. 7 Macroecological analysis of the relationship between bacterial abundance (Cells m^{-3}) and chlorophyll concentration ($mg\ m^{-3}$). (a) A global dataset of 13 974 paired measurements in coastal offshore and oceanic waters [44]. Quantile lines are constructed from bacterial distributions within successive binned chlorophyll intervals of 0.1 logarithmic unit (99 percentile = *upper*; 50 percentile = *middle*; 5 percentile = *lower*). *Straight dashed lines* indicate bacteria to chlorophyll ratios of 10^{13} , 10^{12} and 10^{11} cells mg^{-1} . (b) SWNB – finfish aquaculture and control sites. (c) Bedford Basin, Nova Scotia – major metropolitan/industrial area. (d) Tracadie Bay, Prince Edward Island – major shellfish aquaculture site

to what extent the different B/P ratios seen in SWNB and Tracadie Bay are due to differences in nutrient loading or more a consequence of the fact that phytoplankton are the major food source for shellfish (mussel in the case of Tracadie) as opposed to finfish culture [46] and the industry may be a major phytoplankton loss term in that ecosystem.

4.5

Water-Quality Indicators

Several properties of the water-column and plankton were evaluated as indicators of far-field effects of finfish aquaculture on the pelagic ecosystem of SWNB. Relatively complicated measures of plankton production provide information on nutrient demand and turnover and data useful for determin-

ing oxygen budgets. However, more simple measures such as water transparency, residual nutrient concentrations in summer, phytoplankton biomass (chlorophyll a) and bacterial abundance also provide useful information for detecting and evaluating anthropogenic disturbances in the region. In the present study, bacteria were enumerated using a flow cytometer but more conventional microscopic methods would work as well [23]. The B/P ratio, for example, may be a sensitive and robust indicator of trophic status, i.e. balance between autotrophs and heterotrophs, with implications for the health of both the local ecosystem and the aquaculture industry.

5

Summary and Conclusions

Standard measurements of pelagic primary producers and microheterotrophs at aquaculture and control sites in SWNB provided no clear evidence that increased nutrient inputs associated with the local finfish aquaculture industry [16, 29] resulted in elevated phytoplankton biomass, primary production or bacterial abundance, however, this is not totally unexpected due to the complex nature of coastal pelagic ecosystems [2–4, 26]. Evaluating the influence of aquaculture specifically on the pelagic ecosystem in SWNB will require a longer time-series of observational data (i.e. monitoring on the time scale of industry development), robust mass-balance calculations [16, 29] and sophisticated bio-physical models. [30] with the capability of predicting system response to aquaculture inputs against a large and highly variable suite of inputs and exchanges from natural and other anthropogenic sources [3].

Several lines of evidence point to strong light-limitation of phytoplankton growth and suggest that the pelagic autotrophs in SWNB have little capacity to process the increased nutrient loads that will accompany further growth in the aquaculture industry in the region. Although there is no evidence at present of a serious imbalance in the autotrophic and heterotrophic components of the water-column in SWNB, the constraints imposed on phytoplankton by light do not affect bacteria and pelagic microheterotrophs which may continue to increase in abundance and metabolism as aquaculture grows. The result will likely be negative consequences for the system's oxygen balance and water quality affecting both the ecosystem and the industry. Simple measures such as chlorophyll a concentration and bacterial abundance (and derived B/P ratios) may prove to be useful indicators of pelagic trophic status and water quality in coastal system stressed by human activities. More complex indices of productivity and nutrient demand will be useful for mass-balance calculations and modelling and provide insight into the physiological mechanisms by which the pelagic ecosystem responds to anthropogenic stresses.

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