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Dynamics of the pelagic food web in St. Georges Bay, southern Gulf of St. Lawrence

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ABSTRACT: Phytoplankton standing stock and production increased between June and October in St. Georges Bay, Nova Scotia, Canada. Inorganic nitrogen is believed to be the limiting nutrient in the Bay and it is deduced that *in situ* regeneration must have satisfied most of the summer demand by primary producers. The proportion of organic matter sedimented, relative to that produced by phytoplankton during this time, depended upon the degree of water stratification. Sedimentation of organic carbon and nitrogen amounted to between 9 and 14 % of that assimilated by phytoplankton during maximum stratification in August, implying that ≈ 90 % of the organic matter produced was recycled above the thermocline. Although copepod biomass decreased, production increased in late June and remained high throughout the summer because of rapid development at high summer temperatures. The production of mackerel and lobster larvae, estimated from studies in other years, was greatest from late July to mid-August. Thus, maximum consumption of the products of phytoplankton production in the water column above the thermocline and minimum transfer of particulate organic matter to the benthos coincided with maximum growth and production rates of copepods and their predators. Calculations of potential food consumption by larval and adult fish, estimated from biomass, showed that standing stocks of planktonic prey organisms could not support the biomass of fish present. The predictable occurrence of warmer waters with rapid production of prey organisms and the restricted exchange with offshore waters makes St. Georges Bay a successful nursery ground for pelagic spawners.

INTRODUCTION

The Marine Ecology Laboratory, Bedford Institute of Oceanography, has undertaken field investigations since the early 1970's to measure the production and survival of larvae of commercially important species. The ultimate aim of this work is to understand the interaction of physical, chemical and biological factors in determining the dynamics of larval growth and survival within the planktonic food web. St. Georges Bay, Nova Scotia, was chosen as the principal study site because it is a small, semi-enclosed body of water with spawning populations of several commercially important species. Initial studies concentrated on the distribution of planktonic fish eggs, fish and lobster larvae and zooplankton biomass (Ware, 1977; Harding et al., 1979; Lambert, 1980; Harding et al., 1982; Lambert et al., 1982; Lambert, 1984; Ware and Lambert, 1984), the physical oceanography (Petrie and Drinkwater, 1978a, b) and some of their possible interrelations (Harding et al., 1983). The average residence time of water in the Bay is approximately 1 mo gyre (Petrie and Drinkwater, 1978a). This indicates that the time scales over which truly planktonic organisms would be expected to remain in the Bay and their generation lengths are similar. In 1977 detailed observations were made on the plankton community to understand the primary and secondary trophic levels in the Bay. Temperature, salinity, phytoplankton production, dissolved nutrient concentrations, sedimentation rates, and zooplankton biomass were measured during the ice-free period between April and November in St. Georges Bay. A complete record of our observations is available in a technical report (Marine Ecology Laboratory, 1980). In this paper, we consider interrelations between the physical environment and primary and secondary production processes, after which we discuss the possible interactions with the larval fish and lobster production in the Bay.

METHODS

Study area. St. Georges Bay 45°45'N, 61°45'W) is a shallow embayment, ≈ 900 km^2 in area with a mean depth of ≈ 24 m and a maximum depth of 40 m at its

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mouth. It is open on the north to Northumberland Strait and the Gulf of St. Lawrence and enclosed on 3 sides by the coasts of mainland Nova Scotia, the Canso Causeway, and Cape Breton Island. Measurements were taken on a weekly to biweekly basis between April 28 to November 14, 1977, along a transect 3 km south of Ballantynes Cove (Fig. 1). Detailed studies of the seasonal cycles of phytoplankton production and particulate sedimentation were carried out at an inner (Station 1, 22 m depth) and outermost (Station 2, 33 m depth) location along the transect. Zooplankton were sampled biweekly from April 26 to November 15, 1977, at a central station (Fig. 1) where the water was expected to have a longer residence time within the Bay.

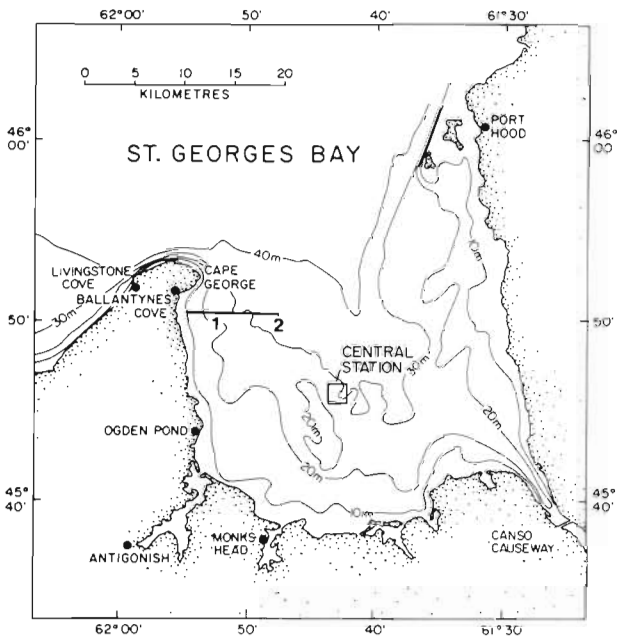

Fig. 1. St. Georges Bay. Bathymetry and sampling locations. Temperature, salinity, dissolved nutrients, phytoplankton production and sedimentation were measured at Stations 1 and 2; plankton biomass, at the central station

Physical oceanography. Temperature and salinity were determined at standard depths along the Ballantynes Cove transect using Nansen bottles with reversing thermometers. Surface measurements were taken from a bucket sample. A Secchi disc (0.5 m diameter) was used to record light penetration.

Phytoplankton. Suspended matter for pigment analysis was collected on a 0.45 µm Millipore filter from 500 ml seawater and placed in a vial with 15 ml of 85 % acetone containing a few drops of $MgCO_3$ solution. Samples were mixed on a Vortex mixer and stored at 5 °C for 18 h before chlorophyll *a* and pheopigments were measured on a Turner fluorometer (Prouse and Hargrave, 1977). The C^{14} method outlined by Strickland and Parsons (1972) was used with *in situ* incubations to measure phytoplankton primary productivity at both stations. Seawater collected at each depth was sieved through 570 µm mesh to remove large predators, placed into two light and one dark glass-stoppered 125 ml bottle with ≈ 5 µC of $C^{14}-Na_2CO_3$. Incubation at standard depths (0, 2.5, 5, 10, 15, 20, 30 m) commenced at approximately 0900 to 1000 h local time and ended 4 to 5 h later. Contents of each bottle were filtered immediately through 0.45 µm Millipore filters, followed by 5 to 10 ml of filtered sea water to remove any remaining inorganic C^{14}, and stored in glassine envelopes. Within 48 h each filter was placed into 10 ml of dioxane based fluor and counted by liquid scintillation spectrometry. Incident radiation was recorded daily with a pyroheliometer located at Ballantynes Cove (Fig. 1) during field experiments.

Dissolved nutrients. Seawater filtrates from pigment determinations were poured into 5 acid-rinsed 100-ml plastic bottles which were frozen for subsequent nutrient analysis. Nitrite, nitrate, phosphate and silicate were analyzed by standard colorimetric methods (Strickland and Parsons, 1972). Ammonia was determined by the phenol-hypochlorite method of Solorzano (1969).

Organic carbon and nitrogen. Suspended particulate carbon and nitrogen were collected by filtering 0.5 to 1 l seawater through pre-combusted 0.8 µm silver filters (Selas Flotronics) and stored in disposable plastic Petri dishes until analysis. Filters were fumed for 30 min over concentrated HCl, dried, then analyzed for organic carbon and nitrogen on a Perkin-Elmer 240 Elemental CHN analyzer.

Surface sediment samples, $\approx$ the upper 5 cm, were taken by dragging a weighted aluminum cylinder (40 x 10 cm) along the bottom. Sediment was mixed, subsampled and stored at 5 °C in a whirl-pack bag. Sediment was dried at 60 °C, then ground with a motar and pestle, and stored until analysis. Samples of 500 to 800 mg dry weight were placed in preweighed vials and weighed before adding 3 ml of 1 N HCl for 1 h. Vials were then placed in a desiccator in an oven (50 °C) and evaporated under vacuum overnight. These samples were reweighed to determine sediment dry weight after acidification. Subsamples from this carbonate-free material were weighed into ashed platinum boats for combustion and elemental analysis.

Zooplankton. All zooplankton collections were made after sunset to reduce the variability in catch that can arise from daily vertical migration. Four conical plankton nets (Table 1), equipped with TSK flow meters, were used to sample plankters of 25 µm up to greater than 2.0 mm in size. In 1977, a 1m diameter 460 µm Nytex net was towed obliquely throughout the water

Table 1. Specifications of plankton nets used in St. Georges Bay

Silk No.	Pore size	Mouth diameter (m)	Length of net** Cylindrical section (m)	Conical section (m)	Surface area Mouth opening S_m (m^2)	Pore openings S_p (m^2)	S_p/S_m (pm)
# 2	460 ± 24*	1	1	2	0.78	2.85	3.7
# 6	224 ± 6	0.75	0.75	1.5	0.44	1.41	3.2
#20	57 ± 3	1	1	2	0.78	1.82	2.3
	20 ± 1	0.5	0.5	1	0.20	0.43	2.2

* Mean ± standard deviation
** All nets have a frontal cylindrical section the same diameter as the mouth opening, followed by a conical section terminating at a canvas cod-end of 10 cm diameter

column (≈ 34 m in depth) at ≈ 3 knots for 15 to 30 min. A 3/4m diameter 224 μm, a 1 m diameter 57 μm, and a 1/2m diameter 20 μm Nytex net were each towed horizontally between 5 to 10 m depth at 1 to 2 knots for 5 to 30 min depending on plankton abundance. In 1979, the 1m diameter 460 μm net and the 3/4m diameter 224 μm net were towed obliquely throughout the water colum at 2 to 3 knots for 15 min. Oblique tows were lowered and raised in a stepped fashion to ensure that all depths were equally sampled. The 1 m diameter 57 μm net and the ½m diameter 20 μm net were repeatedly hauled vertically from the bottom to the surface until ≈ 10 g of material was accumulated.

The contents of each net were graded on deck with a vibrating sieve apparatus (Haver and Boecker, Fabr. Nr. 3596) modified with controllable water jets directed at the bottom of each sample screen. Consistent and rapid sizing of organisms was achieved with this technique. The 509 to 1028, 1028–2035, and > 2035 μm size fractions were obtained from the 460 μm net, the 250 to 509 μm size from the 224 μm net, the 66 to 125 and 125 to 250 μm sizes from the 57 μm net, and the 25 to 66 and a replicate 66 to 125 μm size from the 20 μm net. Plankton samples were placed in preweighed vials or jars and stored on ice until they could be frozen (−20 °C) at the laboratory. Plankton samples were thawed at room temperature and examined for abundant species. Foreign objects such as paint chips and terrestrial objects were removed. Whole samples were weighed fresh, then oven-dried (60 °C) and reweighed.

Sedimentation. Sediment traps described by Prouse and Hargrave (1977) were located 1, 4, 8 m and 1, 3, 8 and 13 m above the bottom at Stations 1 and 2, respectively, and were exposed for ≈ 7 d intervals between May 16 and November 15, 1977. Sedimented material was analyzed for organic carbon and nitrogen, plant pigments and dry matter as previously described. Fecal pellets were also counted from 100 μl subsamples of sedimented material placed in a settling chamber under an inverted microscope. Numbers were related to sample dry weight by filtering each sample through a preweighed Nucleopore filter. Dry weight per pellet, pellet volume and number were similarly derived.

RESULTS

Vertical stratification

During spring and summer the water column in St. Georges Bay is stratified. In 1977 surface waters at Station 2 warmed from less than 4 °C in late April to over 20 °C in August (Fig. 2). Near-bottom water temperatures taken at 30 m, rose from < 0 °C in late April to a maximum of 7 °C in mid-July, declined to 5 °C in

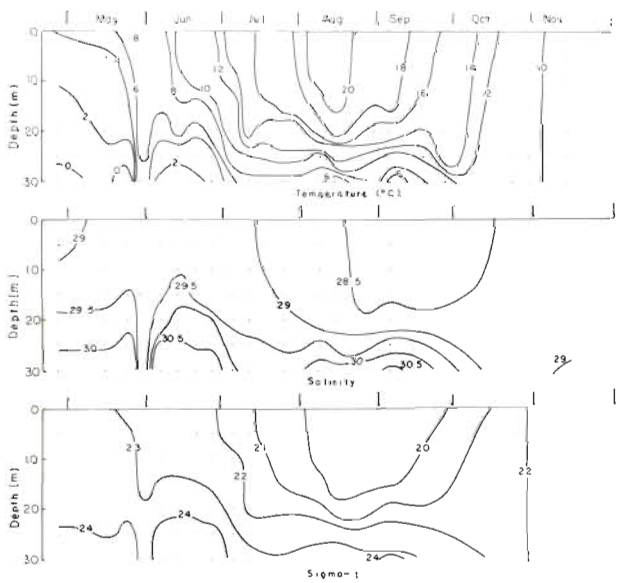

Fig. 2. Seasonal profiles of water temperature and salinity in St. Georges Bay (Station 2) during 1977

mid-August before increasing to a maximum of > 10 °C in October when the water column became isothermal. Salinity measurements (Fig. 2) showed 29 to 29.5 water (Practical Salinity Units 1978) was present in the upper layer until mid-July after which salinity decreased to minimum values of < 28.5 in September.

Observations taken along the Ballantynes Cove transect in 1977 indicate no difference in temperature at surface or 10 m depths between inshore and offshore stations, throughout the sampling period (paired 't'-test, $p > 0.05$). If nearshore upwelling occurs in the Bay, it is sporadic and of short duration.

The mixed-layer depth at Station 2, defined by the location of the maximum change in the temperature gradient above the thermocline, deepened at a rate of ≈ 0.14 m d^{-1} after its formation in early June. This is slower than previous estimates of 0.20 m d^{-1} for a Station 3 km off Cape George in 1974 and 0.19 m d^{-1} at Station 2 in 1976 (Petrie and Drinkwater, 1977; Drinkwater and Taylor, 1979) but it is similar to values calculated for these same years (0.17m d^{-1}, 1974; 0.16m d^{-1}, 1976) by Lambert et al. (1982) based on data from a grid of stations throughout the Bay. Seasonal isopleths of salinity and density at Station 2 show this general increase in mixed-layer depth from mid-June to October (Fig. 2). A time series of temperature taken in 1979 (K. Drinkwater, unpubl.) showed that intermittent wind events can cause short-term changes in the depth of the mixed-layer mainly through advection rather than mixing. The nearly homogeneous water column observed in late May 1977 (Fig. 2) was probably related to the strong NW winds during the previous four days. The seasonal trend, however, is for a thermally homogeneous surface layer to thicken gradually from ≈ 10 m in June to > 30 m by late October.

The depth of the euphotic zone, which is roughly double the Secchi disc reading (Parsons et al., 1977), was inversely related to the mixed-layer depth during our study. Secchi disc visibility decreased at both Stations 1 and 2 from maximum values (10 to 22 m) in May and June to minimum values (4 to 9 m) in October (Fig. 3). During May and June, the euphotic zone depth exceeded that of the homogeneous upper layer. From July onwards, however, mixed-layer depth exceeded the photic depth and the phytoplankton population would have been exposed to less of the available light than earlier in the summer.

Phytoplankton production

Chlorophyll *a* concentrations, integrated over the entire water column, increased irregularly from late June to maximum concentrations in September–October (Fig. 4). High values were also observed in early June and late April. Chlorophyll *a* m^{-2} was consistently higher at our offshore location (paired 't'-test, $p < 0.01$) which was due entirely to its greater depth. Carbon assimilation by phytoplankton increased gradually throughout the summer with maximum rates in August through September. Phytoplankton production per unit volume was highest in the upper 10 m, while the highest chlorophyll *a* concentrations were below this. On average, 86 % of the total phytoplankton production in the water column at Station 2 occurred in the upper 15 m. The percentage was lowest in May (70 %) and highest in October (92 %) which is expected from the seasonal shallowing of the photic-layer depth. Primary production, integrated throughout the water column, was greater offshore ($p < 0.02$) both before and after the summer period of strong stratification. Phytoplankton specific production, photosynthesis per unit chlorophyll, varied thoughout the study from 0.5 to 22 mg C (mg chlorophyll *a*)$^{-1}$ h^{-1} with no clear pattern except for a decrease after August at both stations. Highest values occurred during June and July when chlorophyll concentrations were reduced to minimum levels.

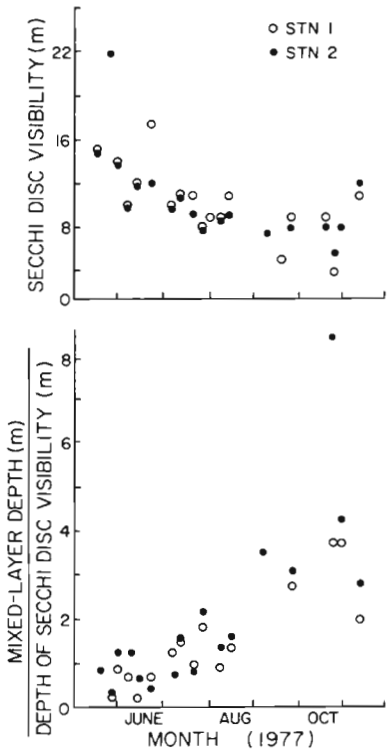

Fig. 3. Secchi disc visibility and ratio of mixed-layer depth to Secchi depth during 1977 at 2 stations in St. Georges Bay

Nutrients

High nutrient concentrations were always present below the thermocline with maximum values occurring in the upper mixed layer during the fall when the water column became homogeneous. Dissolved nitrate, nitrite and phosphate concentrations were relatively uniform and low in the upper mixed layer from May to October, with a pronounced nutricline present in the deeper waters (>20 m, Station 2; Table 2). Both nitrate and nitrite increased significantly in October following the extension of the mixed layer to the bottom. Maximum ammonia concentrations in excess of 5mg–at m^{-3} occurred during summer in the euphotic zone (Table 2). Concentrations this high are not normally observed in unpolluted surface waters. Silicate concentrations generally increased throughout the period of observation both above and below the thermocline. Concentrations of dissolved nutrients nearshore were not significantly different from those at the offshore station either during the period of stratification or when the water column was homogeneous.

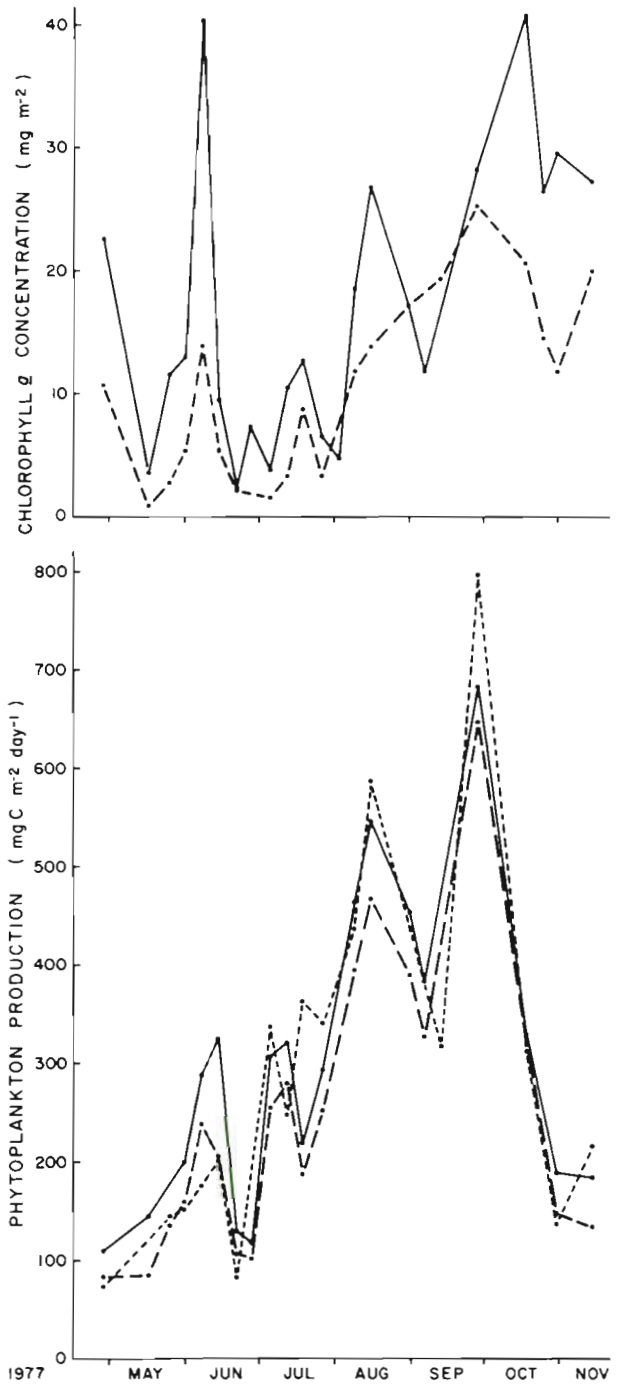

Fig. 4. Suspended chlorophyll *a* and phytoplankton production at Stations 1 (fine dash lines) and 2 (solid lines) in St. Georges Bay in 1977. Integral values were calculated to 15 m at Station 1 and to 30 m at Station 2. The integral for production to 15 m at Station 2 (dash and dot line) is illustrated for comparison

Zooplankton biomass and production

Zooplankton collections from our central station (Fig. 1) are assumed to be representative of the Bay. This premise is based on earlier work where weekly to biweekly sampling was done during the summers of 1974 and 1975 with a grid of stations located throughout the Bay (Lambert et al., 1982). Zooplankton taken with oblique hauls of an Issacs-Kid mid-water trawl (405 µm) was separated into 1050, 860, 602, and 405 µm size fractions. Stations in the center of the Bay had the greatest abundance (g wet wt) of zooplankton averaged over the year and exhibited the least variability (S. D./$\bar{x}$). However, changes in the total zooplankton biomass collected at central stations (16/9 in 1974 and 15/7 in 1975; Lambert et al., 1982) were not different from the mean biomass throughout the Bay ($r=0.77$, $p=0.001$), with best correlations obtained between the smallest size fractions ($r = 0.8$ for both and 405 µm).

Plankton biomass was fractionized into logarithmic size classes. During 1977, the biomass of plankton, in the size range of 25 µm to 4 mm was greatest in April (167 mg dry weight m^{-3}) and declined to less than 60 mg m^{-3} in August and September (Fig. 5). Fluctuations in biomass occurred throughout the sampling period, with increased biomass in different size fractions occurring on different dates (Fig. 6). The low biomass values observed in August and September are reflected in all size fractions except the algae and protozoans (25 to 66 µm). The decline in plankton biomass in the copepod size fractions, starting in mid-July, coincides with a faunal change from a cold water, *Calanus – Temora – Pseudocalanus* community to a *Centropages – Tortanus – Acartia* community (Fig. 7).

This technique of sorting plankton into logarithmic size classes combines a diverse flora and/or fauna in

Table 2. Concentrations of nutrients (mg-at m^{-2}) above and below 20 m depth at Station 2 in St. Georges Bay, 1977

Date	$NO_2 + NO_3$		NH_4		SiO_3		PO_4	
	0–20	20–30	0–20	20–30	0–20	20–30	0–20	20–30
25/5	5.30	11.35	15.13	9.75	16.63	25.07	7.58	5.02
7/6	4.15	5.35	21.75	13.10	27.95	36.35	5.63	5.40
14/6	7.38	9.62	8.38	17.17	19.05	42.75	3.43	5.30
21/6	7.05	5.98	13.50	9.85	29.68	46.30	6.90	5.48
18/7	9.99	7.45	57.45	31.35	29.73	36.95	7.10	5.05
26/7	5.49	12.85	76.56	36.20	38.43	80.70	5.09	7.79
15/8	7.31	15.20	68.26	55.85	47.96	118.20	6.21	7.60
28/9	3.00	10.95	5.76	15.60	40.69	78.45	6.38	5.80
25/10	15.13	15.25	18.73	9.75	105.43	62.10	10.85	5.03
31/10	20.25	10.70	15.63	9.05	107.45	51.70	10.45	4.85
14/11	29.90	10.98	26.80	33.10	96.15	51.78	9.60	3.00

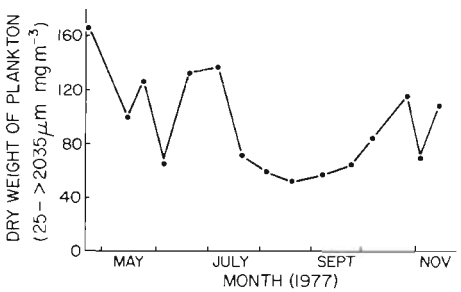

Fig. 5. Zooplankton (25 μm to 4 mm size range) biomass on a m^{-3} basis at the central station in St. Georges Bay

each size fraction which necessarily obscures the population dynamics of individual species. It does, however, enable us to trace roughly specific cohorts by size as they grow within the planktonic community. We assume that similar-sized organisms are predominantly of the same general feeding type. In fact, greater than 90 % of the biomass in the 4 size-classes between 66 and 1028 μm were copepods with one species dominating at any particular time of the year (Fig. 7). The development of copepods from egg to adult can be traced from the temporal changes in biomass of the 4 size fractions (Fig. 6). If lines are drawn between peaks of adult copepod abundance (509 to 1028 μm fraction) and the nearest preceding peak in copepod egg and nauplii, the intermediate peaks in early copepodids (125 to 250 μm) and late copepodids (250 to 509 μm) tend to fall in between. This is encouraging when one considers that sampling dates were 2 wk apart. From this, we can identify 3 major size cohorts which occurred between April and November. The first generation appears to have been initiated in the spring before our sampling began. The second aligns with the early June chlorophyll *a* peak of *Dinophysis* sp., and the third generation corresponds to a late September *Dinophysis* sp. 'bloom'. The first and second generation lines occurred when *Temora longicornis* dominated the community (Fig. 7). Paffenhöfer and Harris (1976) and Harris and Paffenhöfer (1976) report generation times of ≈28 days for *T. longicornis* and *Pseudocalanus minutus* at 12.5 °C, similar to the value extrapolated from the slope of generation line 2 when temperatures were approximately 10 to 14 °C (Fig. 6). Generation line 1 is less steep which one would expect from copepod development at lower temperatures. The third or fall generation of zooplankton occurred after the *Centropages – Tortanus – Acartia* successional community appeared (Fig. 7). *Centropages hamatus* and *Acartia clausa* in Loch Striven, Scotland, have generation times of 21 to 25 d and 28 d, respectively, at ≈13.5 °C (McLaren, 1978) which corresponds with the slope for the development of the fall generation when temperatures were 12 to 16 °C (Fig. 6). All of the calculated generation times are less than the average flushing time ot the Bay, estimated as 30 d by Petrie and Drinkwater (1978 a).

Production estimates of the copepods were calculated from species-specific, temperature-dependent development of naupliar and copepodid stages, separately, (from McLaren, 1978) together with our biomass estimates (Fig. 6). We assumed, as did McLaren, that food was not limiting during the summer because both phytoplankton production and standing crop tended to increase in the Bay from June to the end of September and middle of October, respectively, whereas the herbivore biomass remained relatively constant over the same time period (Fig. 4, 5, and 6). Resultant copepod production rates were continually high from late June through mid-October with a maximum value in early July (Fig. 8).

Sedimentation

Sediment traps suspended 1 m above the bottom collected more particulate material than those located closer to the sea surface (Table 3). These results can be

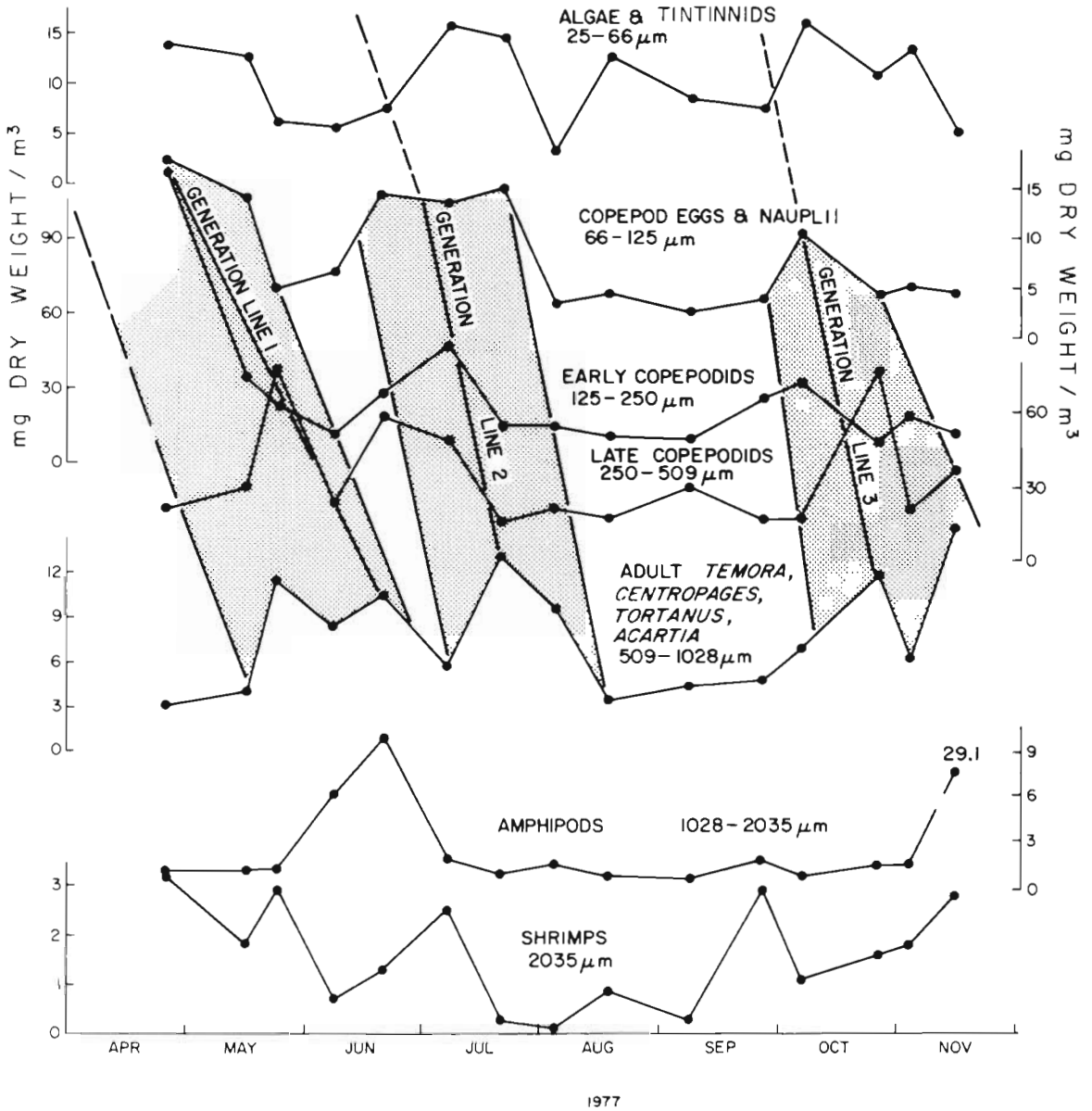

Fig. 6. Biomass of various size fractions of plankton collected at the central station in St. Georges Bay during 1977

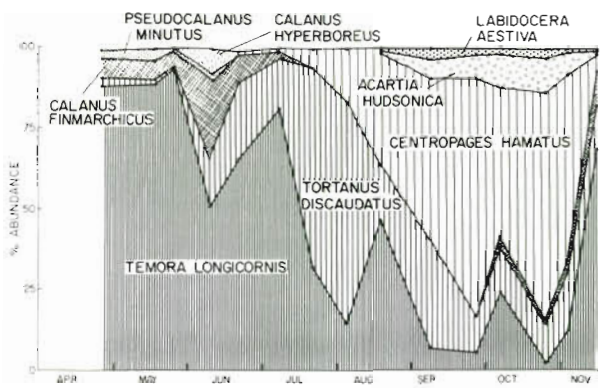

Fig. 7. Major species of zooplankton present at the central station in St. Georges Bay during 1977

explained by the deepest traps sampling a near-bottom nephaloid layer formed by resuspension of bottom sediments. The similarity in sedimentation rates at 8 and 13 m above bottom implies that on average resuspended material does not reach 8 m above bottom. The difference between sedimentation rates at 8 and 1 m above the bottom can be used to calculate the amount of material resuspended. Resuspension was least at both stations between June and early September during maximum stratification and highest in May, mid-September and late October when the water column was nearly homogeneous.

Sedimentation rates, measured as particulate dry matter, organic carbon or nitrogen, were not different

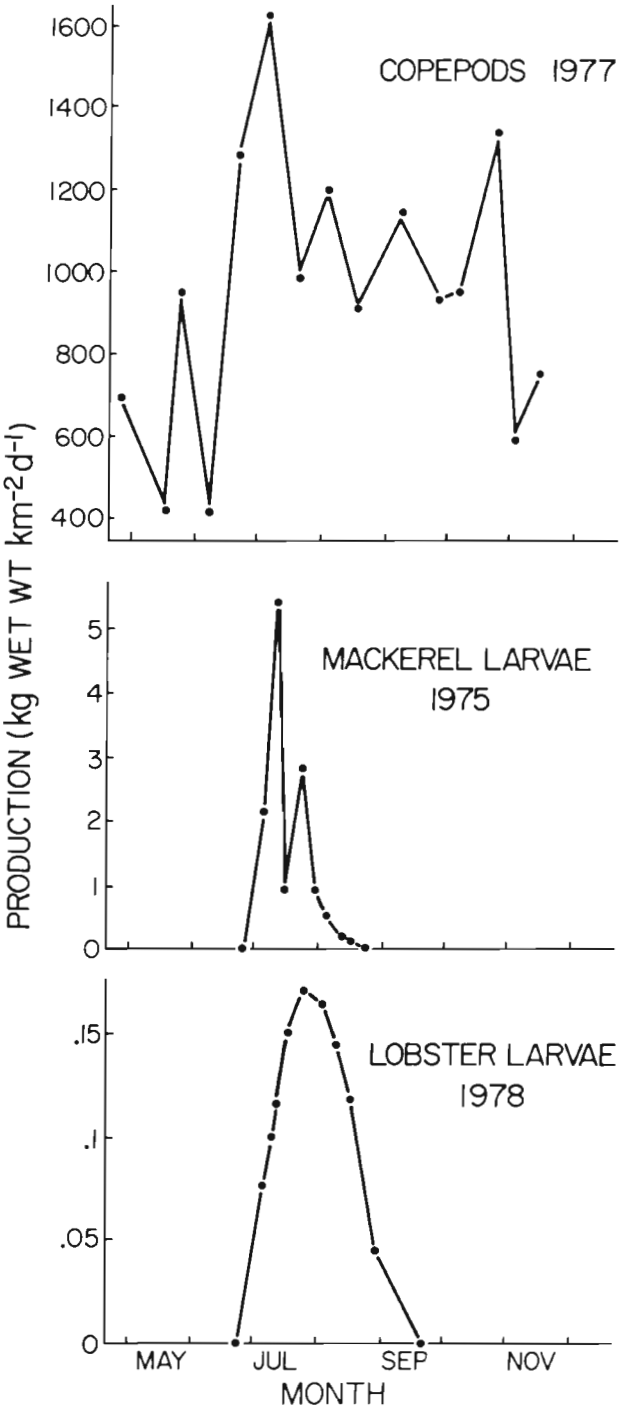

Fig. 8. Production of copepods (125 to 509 µm) larval lobster (cumulative of Stages I–IV) and larval mackerel (cumulative for 3 to 10 mm size classes) in St. Georges Bay during the years indicated

between inshore and offshore locations during spring, summer or fall periods (paired 't'-test, $p > 0.1$). Also, the organic carbon and nitrogen content and plant pigments of surface sediments at the two locations were similar throughout the study ($p > 0.1$). None of our observations, either biological or physical, support the idea that phytoplankton production was enhanced at inshore regions of the Bay.

Seasonal changes in sedimentation are best compared 8 m above the bottom (14 m at Station 1, 25 m at Station 2) where resuspension effects are generally small. At both stations, dry matter, organic carbon and nitrogen deposition were high in late May, low during mid-summer and high in mid-September and late October to November (Table 4; Fig. 9). Mid-summer sedimentation rates were almost equivalent at both stations.

Resuspended debris, phytoplankton, fecal pellets and algal detritus produced by grazing all settle in sediment traps. Sedimentation of particulate organic matter exceeded phytoplankton production in May (Table 4) due to high sedimentation rates during the last week of that month (Fig. 9). These we attribute to resuspension of bottom material which coincided with the water column becoming homogeneous following four days of strong NW winds. Nitrogen assimilated by phytoplankton was calculated from carbon fixation values by assuming a C:N assimilation ratio of 7. Sedimentation of carbon and nitrogen can then be expressed as a percentage of that assimilated by phytoplankton. Nine to 43 % of both the carbon and nitrogen fixed by phytoplankton between June and October settled out of the water column (Table 4). In August, when the mixed layer reached 15 to 20 m depth and the surface temperature was maximum (>20 °C), sedimentation of organic carbon and nitrogen was equivalent to only 10 and 15 % of that produced by phytoplankton. Respiration and mineralization processes within the upper mixed layer must have recycled the remaining 85 to 90 % of carbon and nitrogen assimilated during late summer. Recycling of organic matter in the mixed layer was greatest (12 to 13 g C m^{-2}) in August at both stations. Maximum daily rates of phytoplankton production in the upper mixed layer also occurred in August, although maximum monthly production occurred in September at both stations (Table 4).

Dry weight of fecal pellets in deposited material provides a conservative estimate of the proportion of settled material derived from zooplankton grazing because discrete pellets are not produced by all herbivores or even by the same species at different seasons. Furthermore, an unknown number of pellets are fragmented and decomposed, or consumed in the water column before deposition in traps. Fecal pellets never accounted for more than 5 % of the dry weight deposited. The abundance of pellets in settled material changed seasonally with highest rates of deposition in June through to early July and in October (Fig. 10). Unfortunately we failed to obtain measurements from

Table 3. Sedimentation rates of particulate material in St. Georges Bay between May 16 and November 15, 1977 at various depths

Material	Station 1			Station 2			
Depth: (m)	14	18	21	20	25	30	32
Dry weight g m^{-2} d^{-1}	6.26* ± 8.56 (23)	8.78 ± 11.34 (23)	20.19 ± 33.97 (23)	4.46 ± 5.69 (15)	4.28 ± 4.85 (21)	7.70 ± 8.11 (17)	19.1 ± 26.2 (18)
Carbon mg C m^{-2} d^{-1}	135.0 ± 138.3 (20)	194.0 ± 195.0 (20)	391.2 ± 498.1 (20)		99.6 ± 89.9 (18)	164.7 ± 14.0 (15)	294.6 ± 36.8 (18)
Nitrogen mg N m^{-2} d^{-1}	19.0 ± 20.3 (20)	26.8 ± 28.0 (20)	53.4 ± 75.2 (20)		13.1 ± 12.1 (18)	21.1 ± 18.2 (16)	41.6 ± 51.5 (17)
Chlorophyll *a* µg m^{-2} d^{-1}	548.8 ± 892.3 (23)	427.8 ± 671.2 (23)	989.3 ± 1492.5 (23)		394.2 ± 570.5 (21)	640.1 ± 697.2 (17)	1111.5 ± 1660.9 (18)
Pheopigments µg m^{-2} d^{-1}	802.8 ± 1010.2 (23)	1086.9 ± 1271.2 (23)	2027.4 ± 2426.0 (22)		612.2 ± 786.0 (21)	1100.0 ± 963.3 (17)	1582.0 ± 1641.0 (18)

* Mean, SD and number of observations

mid-August to mid-September (Fig. 10). This seasonal pattern was the inverse of sedimentation of total dry matter or organic carbon and nitrogen (Fig. 9) with deposition low from mid-June to July and in October. However, relative rates of pellet deposition, expressed as a percentage of total dry weight deposited, demonstrate the same pattern although the October peak is now of the same magnitude as in June.

Throughout the study, chlorophyll *a* deposited in sediment traps and in superficial bottom sediments showed intermittent pulses of enrichment (Fig. 11). The timing of these peaks generally coincided with periodic increases in the amount of suspended chlorophyll *a* and phytoplankton production (Fig. 4). There was also a general trend of increasing concentrations of chlorophyll *a* in settled material from June

Table 4. Monthly total phytoplankton production (PP), sedimentation of organic carbon (SC) and nitrogen (SN), ratio (by weight) of organic carbon and nitrogen in sedimented material, ratio of phytoplankton production and mixed-layer depth (from Fig. 2), sedimentation expressed as a percentage of phytoplankton production (SC/PP, SN/PP), and organic carbon respired in the water column (CR = PP – SC) at 2 Stations in St. Georges Bay, during 1977. Sedimentation rates were measured with traps moored at 18 m at Station 1 and at 25 m at Station 2. Phytoplankton production was integrated over the upper 15 m at both Stations

Month	PP g C m^{-2}	SC g C m^{-2}	SN g N m^{-2}	SC/SN	PP/Z_m	$SC \cdot 100$ PP	$SN \cdot 100$ PP	CR g C m^{-2}
				STATION 1				
May	3.7	5.0	0.7	7.1	0.17	135	140	–
Jun	4.8	1.1	0.2	5.5	0.48	23	29	3.7
Jul	9.9	1.1	0.2	5.5	0.66	11	14	8.8
Aug	14.9	1.9	0.3	6.3	0.75	13	14	13.0
Sep	15.1	6.5	0.9	7.2	0.69	43	41	11.6
Oct	12.5	3.8	0.5	7.6	0.57	30	24	8.7
Total	60.5	19.4	2.8					45.8
				STATION 2				
May	3.2	3.8	0.5	7.3	0.11	119	100	–
Jun	5.1	1.5	0.2	7.1	0.51	29	29	3.6
Jul	7.4	1.6	0.2	7.0	0.49	22	18	5.8
Aug	12.7	1.1	0.2	5.8	0.64	9	11	11.6
Sep	14.0	3.9	0.6	7.1	0.56	28	30	10.1
Oct	11.1	3.8	0.5	7.8	0.37	34	31	7.3
Total	53.5	15.7	2.2					38.4

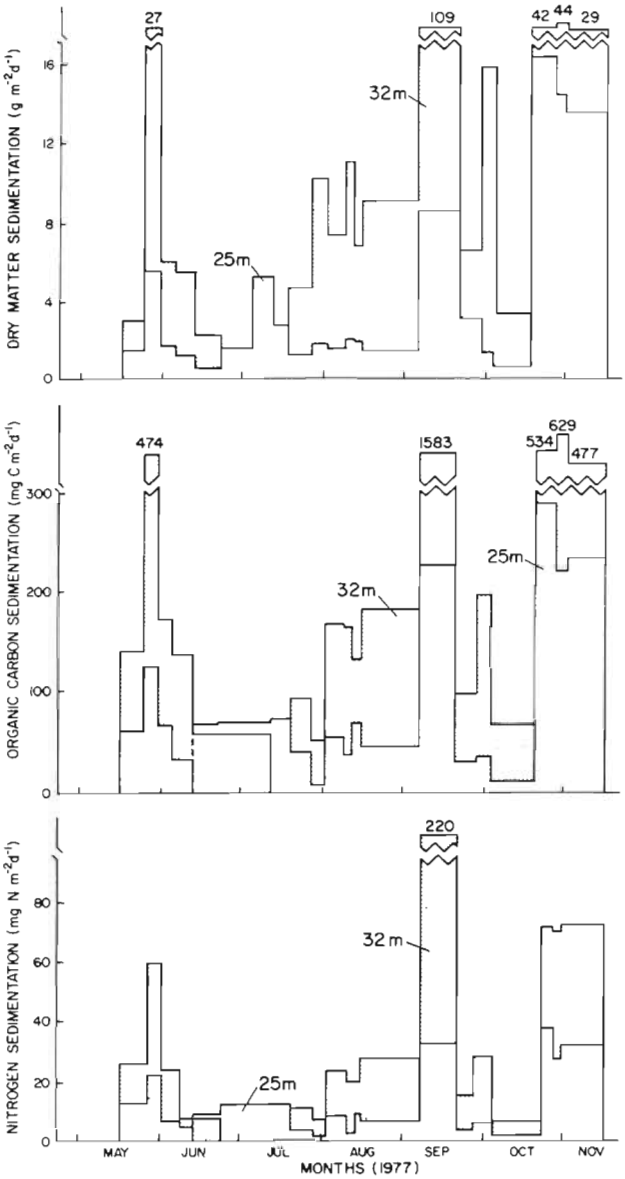

Fig. 9. Seasonal changes in sedimentation of dry matter, organic carbon and nitrogen at 25 and 32 m, Station 2 in St. Georges Bay during 1977

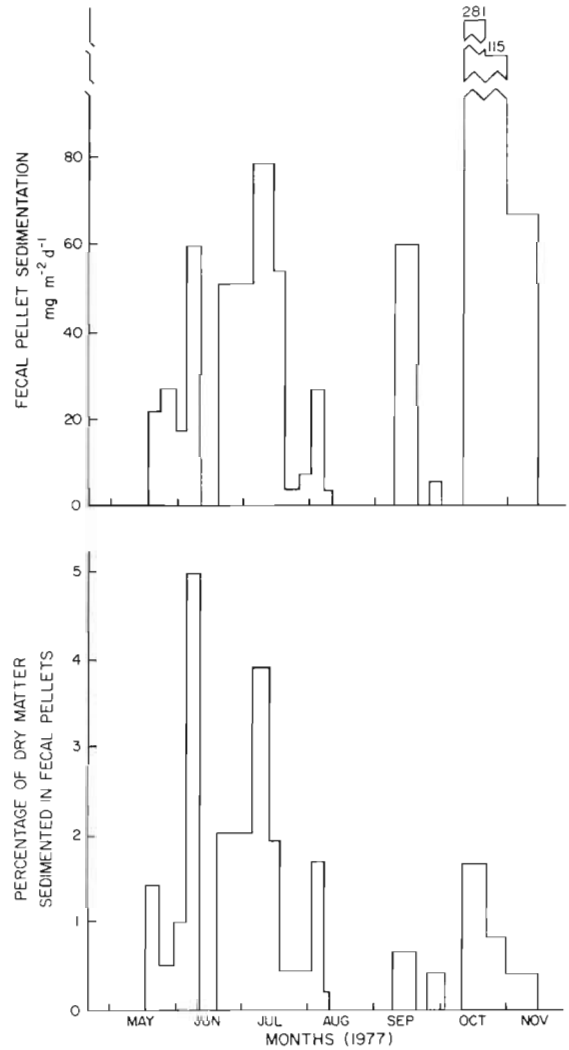

Fig. 10. Seasonal changes in fecal pellet dry weight and percent of total dry matter deposited in sediment traps collected at 25 m, Station 2, in St. Georges Bay. (Zero values denote missing observations)

to October which paralleled increases in suspended concentrations at both stations. Thus, products of high phytoplankton growth reached the bottom rapidly, but concentrations of chlorophyll did not accumulate in the sediments.

DISCUSSION

Phytoplankton and nutrients

The progressive increase in phytoplankton production observed from late spring to fall in St. Georges Bay is typical of temperate coastal embayments and has been observed in several other eastern Canadian regions including the Bras d'Or Lakes in Cape Breton Island (Geen, 1965), the Northumberland Strait in the Gulf of St. Lawrence (Citerella, 1980) and St. Margaret's Bay on the Atlantic coast of Nova Scotia (Platt, 1971). A spring bloom is also typical of temperate coastal embayments. Unstable ice conditions prevented us from directly observing such a bloom in St. Georges Bay in 1977, however, the high deposition rates measured from sediment traps and the uniformly low nutrient concentrations observed in late April indicate that the spring bloom had occurred before intensive sampling began. Suspended chlorophyll, dissolved nutrients and particulate organic carbon data collected through leads in the ice in 1978 (Hargrave and Prouse, 1981) indicated major blooms occurred in the

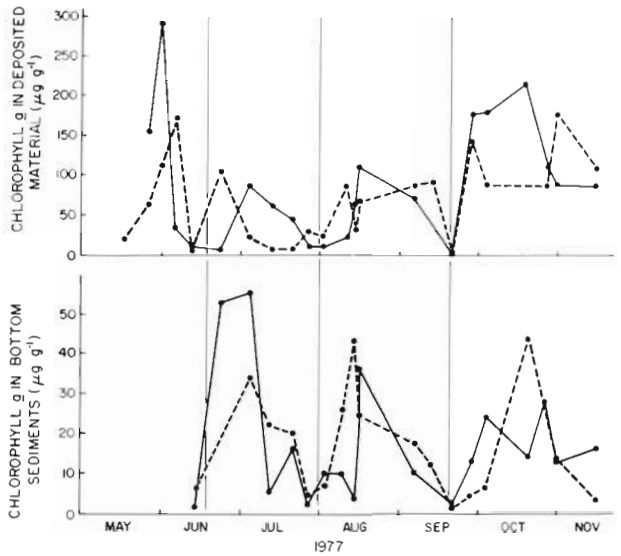

Fig. 11. Chlorophyll *a* concentrations (μg g^{-1} dry weight) in particulate matter deposited in sediment traps (upper panel) located 8 m above the bottom at Station 1 (14 m depth, dashed line) and Station 2 (25 m depth, solid line) and in surface bottom sediments at the same locations (lower panel). Thin vertical lines denote dates of both low relative chlorophyll *a* deposition in the water column and accumulation on the bottom

Bay as early as late winter (Jan to Feb) and also in April. Conversion of the observed decreases in inorganic nitrogen concentrations in the upper 20 m to phytoplankton carbon equivalents (using C:N =7) yields production values of 140 mg C $m^{-2}d^{-1}$ during February and 371 mg C $m^{-2}d^{-1}$ in April.

Phytoplankton production rates in St. Georges Bay between April and October were similar to those observed in the Bras d'Or Lakes but lower than that measured in embayments along the Atlantic coast of Nova Scotia (Table 5). Similarly St. Georges Bay production rates were half the values for shelf regions such as the Grand Banks and New York Bight and close to an order of magnitude lower than certain southern embayments such as Narragansett Bay (Table 5).

The relatively low levels of primary production observed in the Bay during late April and May are believed to be due to the decreased availablitity of nutrients following the spring bloom, as is the case in most coastal waters (Ryther and Dunstan, 1971). Nitrogen appears to be the limiting nutrient for phytoplankton growth in the Bay because N/SiO_3 and N/PO_4 ratios of both shallow and deeper waters are less than normal compositional ratios of these elements in marine phytoplankton. In other words both silicate and phosphate were in excess of growth requirements for phytoplankton when compared to nitrogen. Also, extrapolation of N to SiO_3 and N to PO_4 regression lines results in positive SiO_3 and PO_4 intercepts, implying that these nutrients would be present when the nitrogen was exhausted.

Table 5. Monthly mean integrated primary production (mg C m^{-2} d^{-1}) for May to October in several temperate coastal regions

	May	Jun	Jul	Aug	Sep	Oct	Mean
St. Georges Bay[1]	153	223	290	490	517	403	346
Other Canadian embayments							
Bras d'Or Lakes[2]	123	390	313	427	247	450	325
Bedford Basin[3]	340	1120	693	727	767	507	692
St. Margaret's Bay[4]	433	393	257	580	833	703	533
Other nearshore areas							
Narragansett Bay[5]	2000	4867	3717	3333	1100	600	2599
Off Hudson River[6]	2050	2700	1700	1800	1700	800	1787
North Carolina Estuaries[7]	260	325	480	370	300	–	347
Great Belt off Denmark[8]	161	253	339	290	273	142	243
Shelf regions							
Grand Banks[9]	1710	606	280	238	299	–	629
New York Bight[10]	1133	1150	650	817	617	600	827

[1] Integrated values from 0 to 30 m at Station 2
[2] Geen (1965)
[3] Taguchi and Platt (1977)
[4] Platt (1971)
[5] Durbin and Durbin (1981); mean of 3 stations obtained from their Fig. 5
[6] Malone et al. (1983); Apex data obtained from their Fig. 13
[7] Thayer (1971); from his Fig. 7
[8] Steeman-Nielsen (1958); from his Fig. 2
[9] Hollibaugh and Booth (1981)
[10] Malone et al. (1983); mean of the 3 regions (≤40 m, 41 to 80 m, and 81–1000 m) taken from their Fig. 13

The nitrogen needed to maintain the observed primary production in the Bay during summer cannot be met by our measured surface-layer concentrations. Based on an estimated C:N assimilation ratio of 7 (molar basis), the average concentration of inorganic nitrogen in the upper mixed layer (0 to 15 m) for the period May to August could have only sustained the mean production rate of ≈300 mg C $m^{-2}d^{-1}$ for a period of 5 d. Thus a continuing source of nitrogen must have been made available to the phytoplankton through two principal sources; mixing of nutrient-rich deep waters into the euphotic zone and/or biologically mediated regenerative processes within the euphotic zone. A further possibility is through horizontal exchanges of surface waters in the Bay with those outside. Substantial nutrient supply from this source, however, is unlikely because nutrient levels outside the Bay would be low as a result of high biological consumption in spring.

Estimates of nitrogen flux into the surface waters through vertical mixing can be made by assuming turbulent diffusion, i.e.

$$\frac{\Delta N_s}{\Delta t} = K_z \frac{\Delta N}{(\Delta z)^2} \quad (1)$$

where ΔN_s = increase in total inorganic nitrogen in the surface layer over the time Δt; ΔN = difference in nitrogen between the surface and bottom layers; Δz = average depth between layers (15 m). To determine the vertical diffusion coefficient, K_z, we assume that the increase in temperature in the bottom layer arises through similar diffusive processes, i.e.

$$\frac{\Delta T_b}{\Delta t} = K_z \frac{\Delta T}{(\Delta z)^2} \quad (2)$$

where ΔT_b = change in the depth–averaged bottom layer (15 to 30 m) temperatures; ΔT = temperature difference between the layers. Between June 7 and August 15, 1977, the bottom layer temperatures at Station 2 rose by 10.5 C° with an average ΔT of 4.8 C°. From Eq. (2), this gives a K_z of 0.8 x $10^{-4}m^2s^{-1}$ which is of comparable magnitude to other stratified coastal regions ($10^{-4}m^{-2}s^{-1}$; Garrett, 1979). The average ΔN during the same period was 1 mg–at m^{-3} which from (1) gives a rate of increase of nitrogen in the surface layer of 3 x 10^{-2} mg–at m^{-3} d^{-1} or 0.45 mg–at $m^{-2}d^{-1}$. Assuming again a C:N assimilation ratio of 7, this estimated nitrogen flux yields a production rate of ≈19 mg C m^{-2} d^{-1} which accounts for only 7 % of the observed mean production rate of 280 mg C m^{-2} d^{-1}. Vertical diffusion of nutrients therefore cannot contribute a significant portion of the nitrogen required for primary production in the surface layers. This is more evident when one considers that all the measured nitrogen below the upper mixed layer ($\bar{x}$ = 50 mg–at N m^{-2}) could sustain measured summer primary production levels for only 7d.

In situ nitrogen regeneration must have satisfied most of the nitrogen demand for primary production. Metabolic excretion of nitrogen, principally in the form of NH_4^+, by macrozooplankton has been shown to be an important source of these regenerated nutrients (e. g. Harrison, 1980). Although organism–specific excretion rates vary widely and depend on factors such as body weight, nutritional status, temperature and species (Corner and Davies, 1971), we used mean zooplankton biomass values for April to October (≈100 mg dry wt m^{-3}) and an assumed average specific excretion rate of 1 µg–at N (mg dry wt) $^{-1}$ d^{-1} to estimate their contribution to the phytoplankton nitrogen demand during that period. The resulting daily excretion rates were ≈3 mg–at m^{-2} over a water column of 30 m. Assuming half this amount was available to the mixed layer phytoplankton populations (upper 15 m), ≈63 mg C m^{-2} d^{-1} or about 23 % of the observed primary production could be supported by this nitrogen source. This value is consistent with other observations in coastal marine waters (Harrison, 1980) and suggests that most of the regenerated nutrients are derived from microplankton and bacteria (Harrison, 1978, 1980; Glibert, 1982; Paasche and Kristiansen, 1982; Harrison et al., 1983).

Herbivores

Our observations suggest that herbivore abundance and thus grazing pressure is closely associated with the fluctuating nature of the phytoplankton stocks. There are several clear temporal patterns in the abundance of the four zooplankton size fractions which represent the development of copepod from egg to adult (Fig. 6). Major cohorts originate at the April, June and late–September chlorophyll peaks and develop through to adults over periods appropriate for the species and environmental conditions.

Secondary production of copepod–sized organisms increased from 0.5 to 1.1 g C m^{-2} mo $^{-1}$ between May and July, then was sustained at 0.9–1.0 g C m^{-2} mo^{-1} through to October, which amounted to ≈ 13 % and ≈ 7 % of phytoplankton production, respectively (Table 6). These percentages are similar to annual calculations for the same size fractions in the North Sea (7 %; Steele, 1974), Narragansett Bay (7 %; Kremer and Nixon, 1978), Scotian Shelf (8 %; Mills and Fournier, 1979), Scotian Slope (5 %; Mills and Fournier, 1979), Texas shelf in the Gulf of Mexico (3 %; Flint and Rabalais, 1981) yet lower than four of the six years studied in surface waters of the North Pacific (9 to 35 %; McAlister, 1972). We have not estimated the production of smaller herbivores, such as tintinnids,

Table 6. Comparison of phytoplankton, zooplankton and larval mackerel and lobster production over 6 mo in St. Georges Bay

Month	Phytoplankton*	Zooplankton** (125–1028 μm)	Mackerel** larvae	Lobster** larvae
	g C m^{-2}		mg C m^{-2}	μg C m^{-2}
May	3.5	0.5 (15)***		
Jun	5.0	0.6 (12)	0.4	0.4
Jul	8.7	1.1 (13)	15.6	235.7
Aug	13.8	0.9 (7)	0.8	249.0
Sep	14.6	0.9 (6)	–	13.3
Oct	11.8	1.0 (8)	–	–

* Average monthly values from Stations 1 and 2 (Table 4)
** Derived from monthly integrals of dry weight production. Dry weight converted to carbon by equation of Wiebe et al. (1975)
*** Numbers in parentheses are percentages of phytoplankton production

bivalve larvae, etc. in the < 66 μm sizes which would have elevated our estimates of production closer to expected gross ecological efficiencies of ≥ 20 % (Parsons et al., 1977). This point is illustrated by the work of Capriulo and Carpenter (1983) who recently estimated that the annual food consumption of tintinnids and copepods in Long Island Sound was of the same order of magnitude.

The increase in zooplankton production between May and July in St. Georges Bay coincided with an increase in primary production but thereafter zooplankton production remained relatively constant while phytoplankton production continued to increase. The high level of phytoplankton production in summer coincides with a notable absence of zooplankton biomass in the copepod size-range. Predation is highest on zooplankton at this time of year because large numbers of planktivorous fish such as mackerel, herring, gaspereau and smelts are summer residents in the southern Gulf. Furthermore, larval fishes and scyphomedusae, known planktivores, are a major component of the pelagic ecosystem. Dagg and Turner (1982) found that copepod grazing rate, expressed as a percentage of primary production, decreased from 30 % on Georges Bank (Gulf of Maine) in April to 10 % in July. They also suggested that this reduction in grazing pressure was due to the seasonal larval fish predation on the zooplankton population.

Phytoplankton populations in St. Georges Bay, therefore, are partially controlled by zooplankton grazing during spring and fall but with a sufficient developmental lag on the part of their predators to enable chlorophyll and production peaks to occur. Between July and September, predators appear to contain herbivore populations such that phytoplankton production increases, resulting in the 'fall bloom'.

Sedimentation

The carbon fixed by phytoplankton is not all consumed or assimilated by zooplankton as various amounts are generally observed to settle directly to the bottom (Smetacek et al., 1978; Smetacek, 1980a; Bodungen et al., 1981; Honjo, 1982). In St. Georges Bay spring pulses of undegraded chlorophyll *a*, for example, were observed to sink to the bottom following high phytoplankton densities (Fig. 4 and 11). This mass sinking of phytoplankton populations has been attributed, indirectly, to the slow reproductive response of herbivorous zooplankton at certain times of the year, which allows the phytoplankton population to exceed the carrying capacity of their environment (Gieskes and Kraay, 1977; Smetacek et al., 1978; Wassman, 1983). Nutrient limited diatom populations are known to have high sinking rates and this is particularly so under spring conditions of silicate depletion (Lännergren, 1979; Bienfang, 1981; Bienfang et al., 1982). However, the organic carbon content of bottom sediments in St. Georges Bay never exceeded 2 % of dry weight and declined sharply between pulses of primary production (Marine Ecology Laboratory, 1980). This demonstrates the speed of utilization processes other than that of herbivorous zooplankton in the Bay.

Our observations in St. Georges Bay suggest that the remnants of the spring bloom had settled out of the water column by late April. Dissolved nutrient concentrations and phytoplankton production remained low in May when the water column was weakly stratified. The carbon collected in our sediment traps during May was more than enough to account for that fixed by phytoplankton (Table 4), but this value is likely an overestimate of sedimentation flux due to wind-driven resuspension of bottom sediments. Once

strong thermal stratification was established in June, primary production increased and considerably less carbon and nitrogen fixed by phytoplankton sedimented out (Table 4). Under summer stratified conditions, sedimentary fluxes should be approximately equivalent to the portion of primary production supported by vertical mixing of nutrient-rich deep water, i. e. 'new' production (Dugdale and Goering, 1967; Eppley and Peterson, 1979; Harrison et al., 1983). However, our estimates of 'new' production for vertical NO_3^- diffusion were low, 7 % of the total production from June to August, compared with sedimentary fluxes of ≈16 % during the same period (Tables 3 and 4). As previously discussed, rapid recycling of organic matter with bound nutrients must occur in the upper mixed layer during summer to explain the sustained primary and secondary production observed, when dissolved nitrate, nitrite and phosphate concentrations were uniformly low. The consumptive, decomposition and mineralization processes in the Bay are accelerated by the progressive warming and deepening of the upper mixed layer. This observed seasonal pattern of sedimentation, characterized by: (1) the sinking of a vernal diatom bloom, (2) a summer and fall period of low sedimentation, and (3) a winter period of water column homogeneity dominated by resuspension of mainly inorganic bottom materials, is similar to many temperate shallow-water embayments studied to date (Webster et al., 1975; Smetacek, 1980 a; Peinert et al., 1982; Wassman, 1983).

Fecal pellets are considered to be the main form in which organic matter produced in the euphotic zone is transported to the benthos (Turner and Ferrante, 1979; Sasaki and Nishizawa, 1981; Urrère and Knauer, 1981). Storms resuspend bottom material in St. Georges Bay, making the proportion of fecal pellets to the total settled material in traps minor. This phenomenon has also been observed in Kiel Bight (Smetacek, 1980a), St. Margaret's Bay (Webster et al., 1975), and Bedford Basin (Hargrave, 1980). Detritus, originating largely from phytoplankton, contributed the most to settled organic material in St. Georges Bay during the stratified period, however, very little of this was in the form of recognizable fecal pellets. Both Honjo and Roman (1978) and Paffenhöfer and Knowles (1979) showed experimentally that the surface membranes of copepod fecal pellets were at least partially degraded by microbes within 2 d at 20 to 25 °C. This rapid bacterial breakdown of the pellet form, together with the well known habit of coprophagy in copepods (Paffenhöfer and Knowles, 1979) and also buoyancy of pellets (Krause, 1981) could help to explain the scarcity of fecal pellets collected by our bottom-water sediment traps.

Hofman et al. (1981) modelled fecal pellet production and concluded that only 0.2 % of average daily primary production reaches the bottom (≈35 m) on the shelf off southeast USA and that 63 % of this flux is derived from fecal pellets of advanced copepodids and only 4 % from the more abundant naupliar pellets. Smetacek (1980b) also found that copepod fecal pellets comprised less than 10 % of the suspended organic carbon in Kiel Bight between April and September when the zooplankton biomass was highest. Even in the warm surface waters of the deep ocean greater than 90 % of the organic matter produced in the euphotic zone is recycled in the upper 400 meters (Bishop et al., 1978).

Fish and lobster larvae

The southern Gulf of St. Lawrence accounts for 25 % of the Canadian commercial fish landings on the east coast, although it contains only 15 % of the continental shelf area (Dickie and Trites, 1983). The nearshore waters of the southern Gulf of St. Lawrence serve as an important nursery ground for pelagic larvae of at least 20 species of fish and decapods. Most of these species are resident year-round but others undergo extensive migrations to the southern Gulf each year to spawn and feed. The pelagic fish biomass is almost entirely migratory and is dominated by commercially important stocks of Atlantic mackerel *Scomber scombrus* (Sette, 1950, McKay, 1979) and herring *Clupea harengus* (Winters and Hodder, 1975; Winters, 1976). Approximately 65 to 71 % of the Northwest Atlantic mackerel population spawns in the southern Gulf of St. Lawrence, of which St. Georges Bay is a part (Anderson and Paciorkowski, 1980). Many benthic invertebrates, including the abundant American lobster *Hommarus americanus* and rock crab *Cancer irroratus*, also release planktonic or pelagic larval stages in the Bay.

Our zooplankton sampling done at the central station in 1977 was not extensive enough, nor was it intended to assess the abundance or production of all larval fish and decapods. Multiple-scale, horizontal patchiness in larval distribution (Ware, 1977; Harding et. al., 1982) made simultaneous sampling of larvae and the other variables reported here prohibitive with available resources. However, larval abundance estimates are presently available for the mackerel and lobster. We have calculated the production of mackerel and lobster from studies done in 1975 and 1978, respectively, when abundance was determined seasonally at 12 to 15 stations located randomly throughout the Bay, as described by Ware (1977) and Harding et al. (1982). We believe that we can legitimately compare production between years because the environmental rate of heating which appears to cue

ecological succession (Lambert, 1980; Lambert et. al., 1982) was similar in all 3 yr.

Production was calculated using abundance estimates, size-specific weight conversions, temperature-derived stage durations and fitted exponential survivorship curves as described in Harding et al. (1982). Production of larval lobster and the 3 to 10 mm sizes of mackerel is highest in July through to early August with mackerel production peaking in the first half of July and lobster in late July and early August (Fig. 8). Production by larval mackerel and lobster was 4 to 5 orders of magnitude less than values for their prey, zooplankton, in the 125 to 1028 µm size range (Table 6), but production by these 2 species represents only a small fraction of the total larval production in the Bay. A predictable succession of discrete spawning peaks occurs every year in the Bay. Cod and plaice spawn in May, four-beard rockling and yellow-tail flounder in late June and cunner and white hake in July. Species such as cunner *Tautogolabrus adspersus* with no commercial value make up appproximately 50 % of the larval fish biomass in the Bay and must utilize a considerable amount of the secondary production. We therefore, use mackerel and lobster only as general indicators of larval fish and decapod production cycles in the Bay.

This proliferation of larval fish during the summer, a major proportion of which are due to the influx of large numbers of spawning pelagic fish, must put considerable demands on zooplankton production because the parents as well as their offspring are planktivorous. From a qualitative point of view this seems to be true, as the zooplankton biomass declines abruptly during July when larval fish and decapods abound (Fig. 5 and 6). What is more important, however, is that zooplankton production increased in late June and was sustained at a relatively high level from July through to October in 1977, when observations in similar years show that larval lobster and mackerel growth rates were maximum.

We are able to construct a quantitative estimate of larval fish demands on the zooplankton population by combining our zooplankton biomass values with larval consumption rates recorded in the literature. Zooplankton biomass in St. Georges Bay in the size range suitable for larval fish feeding, 125 to 1028 µm ESD (equivalent spherical diameter, *sensu* Sheldon et al., 1972), had an average value of ≈ 500 mg fresh wt m^{-3} between late June and late October (Fig. 12). We were unable to sample adequately all sizes of larval fish in the Bay within the 1.0 to 10.0 mm ESD range. (Actual fish lengths would be 3 to 4 times greater than the ESD values, depending on their shape.) However, if we assume a flat biomass spectrum (Sheldon et al., 1977), which is supported by our seasonally-averaged phytoplankton and zooplankton data for the Bay, there would be ≈500 mg fresh weight m^{-3} in the 1.0 to 10.0 mm ESD size range.

Larval fish are capable of ingesting more than 100 % of their body weight per day at unusually high food concentrations in the laboratory (Houde and Schekter, 1981); but even at lower prey concentrations, equivalent to the highest values found in nature (Hunter, 1980), many larvae were capable of consuming 30 to 40 % of their weight daily. Highest rations are found in fast growing fish like mackerel. Hunter and Kimbrell (1980) reported that Pacific mackerel in the 3 to 5 mm length range consumed 87 % of their body weight daily. Using their gross growth efficiency of 33 %, mackerel in St. Georges Bay consumed daily rations decreasing from 130 to 81 % body weight as they grew from 3 to 10 mm length. At the other extreme slow growing larvae such as herring also consume decreasing proportions relative to their body weight as they grow but the amounts are far less than mackerel. Gamble et al. (1981) reported a daily food consumption rate of 16 % of body weight for 9 to 17 mm herring larvae held in plastic enclosures. Houde and Schekter (1981), using data of Werner and Blaxter (1981), calculated that four to eight week herring had weight specific rations of 10 % for 13 mm larvae and 5 % for 17 mm larvae.

Thus food consumption by larval fish is highly variable, depending on the species and size as well as on

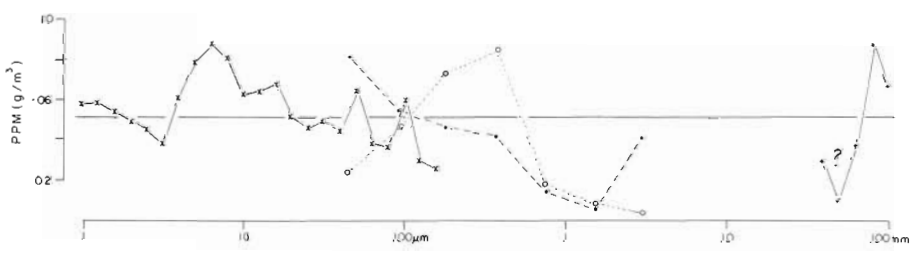

Fig. 12. Average pelagic biomass spectrum of St. Georges Bay; x: average of 75 Coulter counts during June and July, 1977 (courtesy R. W. Sheldon); ○: average of 15 size fractionizations of net-plankton between April and November, 1977; ●: average of 16 size fractionizations of net-plankton between April and October, 1979; +: average of stock assessments for mackerel, herring, gaspereau, caplin and smelt in NAFO district 4T, 1977–1979 (see text)

environmental factors such as prey density and temperature (Hunter, 1980). Nevertheless, an average value of 20 % of body weight for the daily ration of larvae in the size range 1 to 10 mm ESD should not be far wrong for the present purposes. At this rate fish larvae in St. Georges Bay would consume ≈100 mg fresh wt m^{-3} d^{-1}. The zooplankton production in St. Georges Bay in the size range suitable for larval fish feeding, 125 to 1028 µm ESD, varied between 38 and 68 mg fresh wt m^{-3} d^{-1} with an average value of 48 mg m^{-3} d^{-1} between late June and October (Fig. 8). The sustained drop in zooplankton biomass in July-August (Fig. 5), therefore, is probably due to larval fish consumption. However, we must have overestimated fish consumption because consumption is double the rate of prey production. This could have occurred by failing to take into account the piscivorous nature of fast growing fish larvae such as mackerel and hake. Furthermore, once schooling behaviour starts, species such as mackerel leave the open waters for the shallow margins of the Bay where they are presumably obtaining their nourishment from the benthic community. Alternatively, our assumption of a totally flat spectrum in the larval fish region may be incorrect over the time scale in question because the biomass of our largest size fractions from net collections was low during July and August (Fig. 6 and 12).

Juvenile and adult pelagic fish in the 10 to 100 ESD size range are also known to feed on zooplankton in the 500 to 1000 µm ESD size range but they are opportunistic feeders on a much wider range of prey sizes (Sherman and Honey, 1971; De Silva, 1973; McKay, 1979; Grave, 1981). The effect of large fish feeding on plankton and nekton biomass in St. Georges Bay can also be estimated from fish biomass assessments and an assumed daily feeding rate. Juvenile fish biomass between 10 and 65 mm ESD is not available because of inadequate sampling techniques. However, reasonably accurate biomass estimates can be made for the remainder of the 10–100 mm ESD range (Fig. 12). A number of species make up the total pelagic biomass in the 65 to 100 mm ESD, but the summer migrants, mackerel and herring, and to a lesser extent gaspereau, dominate the catch. Assessments of these 3 stocks (Maguire, 1981; Cleary, 1982; and Crawford pers. comm., respectively) were from catch statistics in NAFO district 4 T for 1977–1979. The average biomass estimated this way is equivalent to 150 mg fresh weight m^{-3}, hence approximately 500 mg fresh weight m^{-3} for the entire size range, 10 to 100 mm ESD. This estimate supports our earlier assumption of a seasonally average flat biomass spectrum based on zooplankton biomass. If these planktivorous fish required from 1 to 5 % of their body weight each day (Blaxter and Holliday, 1963; Vesin et al., 1981) they would consume from 5 to 25 mg fresh weight m^{-3} d^{-1}. Our calculations indicate that the secondary production of zooplankton in the 125 to 1028 µm ESD size range could not alone support the fish population and their larvae. The food web must be considerably more complex than our simplifications would indicate with piscivorous and benthic feeding making up the missing food for pelagic fish and their larvae.

CONCLUDING REMARKS

Our studies of the biological dynamics in St. Georges Bay suggest a rapid, close coupling between the supply of particulate organic matter produced, that consumed by either herbivores or carnivores, and nutrient regeneration over the entire water column. Physical processes redistribute nutrient concentrations annually, from top to bottom, during the unstratified period between October and May. The rapid summer heating and stratification of the shallow waters of the Bay increase the metabolic rates of all organisms and thus contribute to the observed rapid recycling of material produced above the thermocline. Daily migration of many planktonic, pelagic and benthopelagic organismus contribute to the recycling of nutrients in the upper mixed layer. Vertical migrations at all time scales make any distinction between pelagic and benthic ecosystems vague in this shallow environment since many benthic invertebrates and demersal fish also have planktonic or pelagic life-stages which feed and grow in the rich, upper mixed layer. The high summer growth rates of larval fish and decapods in St. Georges Bay are dependent on the rapid cycling of all components of the ecosystem and are directly dependent on the rapid turnover of small zooplankters which are optimal food for fast growing larvae.

St. Georges Bay must have characteristics which make it advantageous for spawning even though pelagic fish have to expend large amounts of energy in annual migrations. Many benthic invertebrates also release planktonic or pelagic larval stages in the Bay. The lobster population supports one of the more productive and stable commercial fisheries in the Maritimes (Harding et al., 1983). In the following we consider the possible benefits from depositing young in St. Georges Bay, which ultimately must be expressed in survival value for the species. Several interdependent factors appear to be of importance; the summer surface temperature, prey size, prey production and predation within the Bay.

St. Georges Bay is distinguished by high (>20 °C) and relatively stable summer temperatures in the upper mixed layer (Ware, 1977; Petrie and Drinkwater, 1978a). Although spring and autumn water tempera-

tures are not too different from those on the Scotian Shelf, the rate of warming in the Bay during June is very rapid, and the surface temperatures by mid-summer are about 2 to 6 C° higher than on the Scotian shelf (Drinkwater and Taylor, 1982). The temperature difference between nearshore Scotian shelf water and that in the Bay is even greater, about 6 to 7 C° (Drinkwater and Taylor, 1982). The temperatures in St. Georges Bay by mid-summer are 2 to 4 C° higher than in coastal embayments on the Atlantic coast of Nova Scotia (Sharaf El Din et al., 1970).

Temperature is known to influence the feeding and growth rates of larval fishes. De Silva and Balbontin (1974) found that herring larvae fed to satiation consumed ≈10 and ≈3 % of their body weight d^{-1} at 14.5 and 6.5 °C, respectively. A doubling of ambient temperature in this case more than doubles food consumption and the potential for increased growth is obvious. Cultured Pacific mackerel *Scomber japonicus* grew at a rate of 0.58 mm d^{-1} at 16.8 °C, and 0.92 mm d^{-1} at 22.1 °C (Hunter and Krimbell, 1981) which is almost a doubling of growth rate over a 5 °C rise in temperature.

Fast growth is one way pelagic larvae can improve their chances of survival during the most vulnerable stage of their life history (Ricker and Foerster, 1948; Shepherd and Cushing, 1981). Larger size means increased mobility to avoid both starvation due to patchy food distribution and predation by piscivores. In St. Georges Bay a rapid growth rate, or a brief larval existence, is the strategy evolved by the dominant summer spawners, such as mackerel, hake and lobster. Summer spawners release eggs or larvae over a relatively short period of time which corresponds with peak surface temperatures and maximum prey production. As a result lobster larvae in St. Georges Bay increase their weight by ≈ 6x within a month before assuming a benthic existence. Similarly mackerel attain metamorphosis (15 mm SL) at about 21 d and after 3 mo have gained 10^5x their initial weight or 75 % of their first year's growth. The predictable spring warming rate and relatively stable warm summer temperatures of the southern Gulf are important for both the precise timing of spawning and fast growth of developing larvae.

Available prey size and type are very important factors for the survival of newly hatched larvae in nature (Hunter, 1980; Checkley, 1982; Eggers, 1982). Year-class strength of fish stocks is believed to be determined early in their life history when mortality is high and variable (May, 1974; Shepherd and Cushing, 1981). Stage I larval lobster production in the southern Gulf has been successfully correlated with lobster landings allowing for a 4 yr developmental lag (Harding et al., 1982).

The diet of larval lobster and mackerel in nature is comprised of organisms in the 210 to 610 µm range. Both lobster and mackerel prey upon cladocerans and small copepods which are the main components of the summer plankton (Harding et al., 1982; B. Cote, pers. comm.). In both cases the size of prey increases as the larvae grow. Late stage lobster preferentially consume crab zoea and megalops larvae and mackerel (10 to 15 mm) become, to a large degree, piscivorous, consuming their siblings as well as larvae of other species.

The mean size of zooplankton in St. Georges Bay decreases during spring to late-summer, as the water temperature increases (Ware, 1977; Lambert, 1980). This decline in plankton size coincides with a major successional change from a cold-water *Calanus-Temora-Pseudocalanus* community to a *Centropages-Tortanus-Acartia* community (Fig. 7). Ware (1977) found that mackerel eggs released in the Bay decrease in size over the spawning period, from June to August, and pointed out that this corresponds to a decrease in the prey size available for newly hatched larvae. Lambert and Ware (in prep.) now document that there is a recurrent succession of pelagic spawning by fish in the Bay, the size of the eggs depend on the species as well as the time of spawning. Nearshore spawning of many fish and decapods in the southern Gulf is seen, not surprisingly, to be an adaptation to match the size of hatched larvae with the optimal size of prey organisms (Ware, 1977).

This leaves the question of why St. Georges Bay is a more successful environment for pelagic spawners with fast growing larvae, such as mackerel and lobster, compared to bays on the outer coast of Nova Scotia (Harding et al., 1983). St. Georges Bay is representative of a much larger area in the southern Gulf of St. Lawrence, extending from Northumberland Strait around the coast to Cape Breton Island (Drinkwater et al., 1983; G. Harding, unpubl.). Primary production in St. Georges Bay, measured over the larval season, is consistently lower than that found in other coastal embayments in Nova Scotia (Table 5). The size-spectrum of prey organisms available as food for fish or lobster larvae is similar in St. Georges Bay and St. Margaret's Bay with biomass concentrated in the 125 to 1000 µm ESD size range. One feature radically separates the 2 regions and this can be called environmental predictability. St. Georges Bay has a relatively regular pattern of summer warming in the upper mixed layer which varies little between years (Ware, 1977; Lambert et al., 1982) and an average residence time for the water of approximately one month (Petrie and Drinkwater, 1978a). St. Margaret's Bay and other coastal bays along the outer coast of Nova Scotia have a more erratic thermal regime determined by oceanographic and atmospheric events (Sharaf El Din et al., 1970; Heath, 1973). The average turnover time for the

surface layer in St. Margaret's Bay is approximately 1 wk. The entire bay can flush in a matter of days with strong southwest winds, which are prevalent during the summer (Sharaf El Din et al., 1970). These atmospheric events are thought to be detrimental to pelagic larvae for two reasons. First, a large proportion of the larvae would be carried out onto the Scotian Shelf and presumably starve because an entirely different zooplankton prey assemblage exists, in both species and size composition. Secondly, both larval fish and lobster swept from the bays and those remaining within the bays would be subjected to cooler waters which would result in longer development times and therefore greater mortality as they are very vulnerable to visual predators in the bright surface waters. Thus, the predictable occurrence of warmer waters with rapid production of prey organisms makes St. Georges Bay a more successful nursery ground for pelagic spawners.

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