ELSEVIER

Deep-Sea Research II 52 (2005) 909–932

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Macronutrient dynamics in an anticyclonic mesoscale eddy in the Gulf of Alaska

Tawnya D. Peterson[a,*], Frank A. Whitney[b], Paul J. Harrison[c]

[a]*Department of Earth and Ocean Sciences, University of British Columbia, 6270 University Blvd., Vancouver, BC, Canada V6T 1Z4*
[b]*Institute of Ocean Sciences, Fisheries and Oceans Canada, Sidney, BC, Canada V8L 4B2*
[c]*AMCE Program, Hong Kong University of Science and Technology, Clear Water Bay, Kowloon, Hong Kong*

Accepted 7 February 2005
Available online 2 April 2005

Abstract

Each winter, long-lived anticyclonic eddies are spawned off the southern tip of the Queen Charlotte Islands off the British Columbia coast. An anticyclonic eddy that formed in winter 2000 (Haida-2000) was sampled six times over 20 months as it traveled from the coast into High Nitrate-Low Chlorophyll waters of the Subarctic northeast Pacific. Repeated shipboard observations coupled with satellite radar altimetry and ocean colour suggest that Haida-2000 underwent a phytoplankton bloom early in life while still in coastal waters. This bloom caused a near depletion in eddy surface nutrients (nitrate, phosphate, silicic acid). While nitrate concentrations were restored to initial levels during winter 2001, the silicic acid inventory within Haida-2000 remained lower than initial observations. Below the euphotic zone, deep nutrient concentrations were altered by eddy decay, interactions with bathymetric features, and by the coalescence of a second, younger eddy that restored coastal characteristics within the core of Haida-2000. Estimates of new production (3–3.5 mmol $NO_3^- \, m^{-2} \, d^{-1}$) derived from seasonal changes in nitrate inventories fell between values previously reported for coastal and mid-gyre environments for both years studied. In contrast, removal of silicic acid was twice as high (7.0 mmol $Si(OH)_4 \, m^{-2} \, d^{-1}$) as nitrate during the first year, but less than half as high in Year 2 (1.3 mmol $Si(OH)_4 \, m^{-2} \, d^{-1}$). Changes in the timing of nutrient drawdown accompanied the shift from high to low $Si(OH)_4{:}NO_3^-$ drawdown ratios, with the maximum changing from spring to autumn, similar to long-term observations at Ocean Station P (50°N, 145°W). Relative to the local environment, the eddy evolved from a nutrient-rich to a nutrient-poor body of water, indicating that the path of these anticyclonic eddies determines their role in nutrient supply and distribution in the Gulf of Alaska.

1. Introduction

The eastern Gulf of Alaska can be broadly divided into coastal and High Nitrate-Low Chlorophyll (HNLC) waters that are separated by the

*Corresponding author. Fax: +1 604 822 6091.
E-mail address: tpeterson@eos.ubc.ca (T.D. Peterson).

0967-0645/$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2005.02.004

Alaska Current, the northward-flowing arm of the Subarctic Current (Fig. 1; Whitney and Freeland, 1999; Wong et al., 2002a). Sources of nutrients to the region include coastal upwelling in summer, outflow from major rivers such as the Fraser and Columbia, and deep mixing in winter. Recently, mesoscale eddies spawned from the coast have been shown to carry nutrients (Whitney and Robert, 2002) and Fe (Johnson et al., 2005) into the Gulf of Alaska and therefore represent another important contribution to total nutrient supply. In other areas, such as the Gulf Stream and Kuroshio current systems, mesoscale eddies have been shown to be important in closing annual nutrient budgets and in estimating annual primary productivity (e.g., McGillicuddy and Robinson, 1997; McGillicuddy et al., 1998; Siegel et al., 1999).

Mesoscale eddy activity has long been noted in the Gulf of Alaska, beginning with observations of temperature and salinity anomalies in hydrographic data (Tully et al., 1960; Tabata, 1982) and model outputs that predicted the formation of eddies off the coasts of British Columbia and Alaska (Melsom et al., 1999). More recently, data derived from satellite remote sensors have revealed the presence of many mesoscale features, including eddies. Sea-surface height (SSH) anomalies (from TOPEX-POSEIDON/ERS-2 radar altimeter; Meyers and Basu, 1999; Crawford, 2002), surface temperature anomalies (Advanced Very High Resolution Radiometer; Gower and Tabata, 1993; Gower, 1998), and high-chlorophyll patches (Sea-Viewing-Wide-Field-of-View sensor; Crawford et al., 2005) all correspond to the position of mesoscale eddies in the Gulf of Alaska. Most eddies spawned along the eastern/northeastern perimeter of the Alaska Gyre are long-lived and anticyclonic (Tabata, 1982; Crawford et al., 2000).

Recently, shipboard observations combined with satellite SSH imagery led to the discovery of an eddy spawning site at the southern tip of the Queen Charlotte Islands, British Columbia (Crawford and Whitney, 1999). These eddies, named "Haida" after the islands inhabited by First Nation peoples ("Haida Gwaii", or Queen Charlotte Islands), transport large volumes of warm fresh water from Queen Charlotte Sound into the Gulf of Alaska (Crawford and Whitney, 1999;

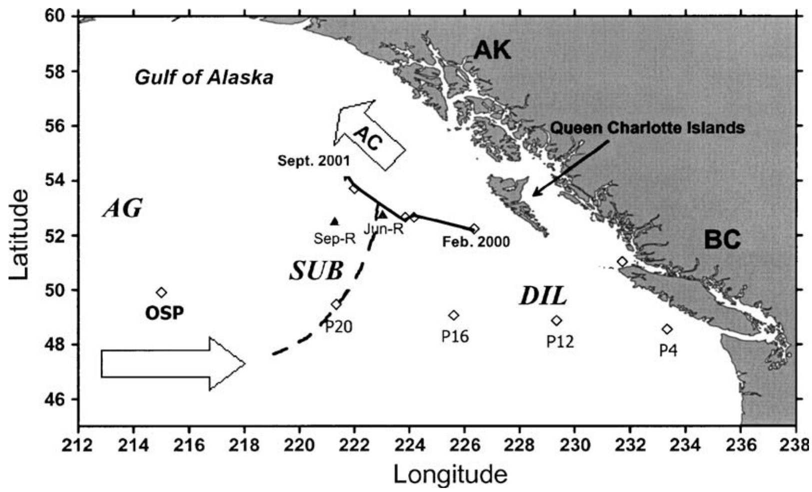

Fig. 1. Regional map showing the location of the centre of Haida-2000 as it traveled northwestward into the Gulf of Alaska. The eddy trajectory followed the line from February 2000 to September 2001 with each symbol representing the position of the centre at the time of sampling. Reference stations in 2000 were located ca. 30–50 km from the southern edge of Haida-2000 (not shown), while in 2001 reference stations were located further away; these are denoted as Jun-R and Sept-R for June and September sampling periods. For reference, time series Line P stations (P4 to OSP) are included. Arrows indicate direction of major currents; AC—Alaska Current, SAC—Subarctic Current. Current/nutrient domains (Favorite et al., 1976; Wong et al., 2002a) are designated AG—Alaska Gyre domain, SUB—Subarctic Current domain, DIL—Dilute domain.

Whitney and Robert, 2002). Haida eddies are defined as those anticyclonic vortices generated south of 54.5°N along the coast of the Queen Charlotte Islands (Crawford, 2002), and they are named by the year in which they are spawned (e.g., Haida-2000, formed in February 2000). Haida eddies generally have a diameter of 150–300 km and a core depth of 500–600 m at the centre where salinity does not exceed 33.9 (Crawford, 2002; Whitney and Robert, 2002). These eddies persist for one to several years (Crawford and Whitney, 1999).

Eddies spawned from eastern boundary currents are important because they carry water westward (Nof, 1981) against the prevailing currents and persist for long periods of time compared to those spawned from western boundary currents such as the Gulf Stream (Joyce et al., 1984). Eastern boundary current eddies thus serve to transport coastal waters offshore into oceanic regions (Whitney and Robert, 2002) that are generally either oligotrophic or lacking in trace metals (HNLC) (Longhurst, 1998). The paths of Haida eddies can be modified by climatology so that they either track due west, northwest or southwest (Whitney and Robert, 2002). Thus, these anticyclonic eddies can travel either into HNLC waters to the west or northwest or into seasonally nutrient-depleted waters to the southwest. Whitney and Robert (2002) were the first to document the impacts of mesoscale eddies in an HNLC region. They noted that eddies that travel into these waters appear nutrient poor relative to surroundings, presumably due to high phytoplankton growth and drawdown of nutrients compared to iron-limited (Martin and Fitzwater, 1988; Boyd et al., 1996), macronutrient replete (Anderson et al., 1969; Whitney and Freeland, 1999) HNLC waters.

In contrast to the HNLC regions, waters just off the continental margin can become nitrate depleted in summer, limiting phytoplankton growth (Whitney et al., 1998). If Haida eddies travel southward into these regions where nitrate becomes exhausted, they appear nutrient rich compared to their surroundings due to their high coastal nutrient reservoirs (Whitney and Robert, 2002). Since eddies transport both macronutrients (Whitney and Robert, 2002) and Fe (Johnson et al., 2005) into the Alaska Gyre, they are important in making annual estimates of primary productivity and nutrient supply in the region no matter what path they take. It is thus necessary to understand their evolution once they leave the coast in order to assess how they might impact the waters through which they travel.

The coastal nature of eddies and their tendency to transport waters great distances from the continent extends "coastal-type" transition zone waters further offshore. The presence of high-chlorophyll waters extends much farther into the open ocean than can be accounted for by the location of the narrow continental shelf along the west coast of British Columbia and Alaska (Okkonen et al., 2003). It has been suggested that this phenomenon arises due to the entrainment of coastal waters by the anticyclonic rotary motion of eddies, pushing these high-chlorophyll waters offshore as oceanic waters are drawn toward shore (Crawford et al., 2005). Thus, the delivery of nutrients and effects of stirring and entrainment by eddies could be a particularly important influence on primary productivity in the transition region between the coast and the open Alaska Gyre.

Since Haida Eddy formation appears to be influenced by climatic events such as El Niño (Mysak, 1985; Melsom et al., 1999), understanding the impact that they have on ecosystem productivity is important in strengthening our ability to make predictions about the large-scale response of biological communities within the Gulf of Alaska to changes in climate. In particular, the nature of nutrient supply within Haida eddies and its influences on primary production have not yet been explored. In other oceanic regions eddies have been shown to supply nutrients via transport from deep waters along isopycnals (Lee and Williams, 2000) and through secondary circulation patterns induced by rotary motions and ageostrophic currents (Simpson, 1984; Martin and Richards, 2001), and to enhance productivity by creating physical fronts (Franks, 1992, 1997).

One way of assessing the relationship between nutrient supply and its biological consequences is to examine rates of new production by primary producers. "New" production describes phytoplankton growth that is fuelled from an external, or non-recycled, source of nutrients (Dugdale and Goering, 1967). Nitrate is the major currency used to describe this growth, and the main source of new nitrate is from upwelling (e.g., Platt et al., 1989), although other sources such as nitrogen fixation can be important as well, particularly in tropical environments (Karl et al., 1997). Under steady-state conditions, the nitrate used by phytoplankton and exported below the pycnocline is replaced predominantly by nitrate from below, so that nitrate loss approximates the export of particulate material (i.e., export production). The vertical downward flux of particulate material drives the "biological pump" and mediates the flux of CO_2 from the atmosphere to the surface ocean.

This paper examines the changes in nutrient concentrations in surface waters and in the eddy core of one Haida Eddy (Haida-2000) as it evolved over 20 months on a journey from the coast to HNLC waters of the Gulf of Alaska. The study of nutrient dynamics within such a quasi-closed system allows us to examine changes in the eddy core that result from aging processes such as frictional decay and dilution. Evolution of core waters can influence local mesopelagic nutrient distributions by supplying nutrients along isopycnals (Lee and Williams, 2000) or through frictionally induced changes in meridional flow (e.g., Fukumori, 1992). Surface nutrient dynamics track biological production and likely reflect changes in iron availability as eddies age and trace metals are stripped out of the euphotic zone.

2. Materials and methods

2.1. Sampling

Haida-2000 was spawned in late January/early February 2000, and surveyed six times between February 2000 and October 2001 on the C.C.G.S. *John P. Tully* (Table 1). For each cruise, the location of Haida-2000 was first determined using TOPEX/POSEIDON-ERS-2 satellite altimetry and then sampled along a transect bisecting the eddy on each cruise in order to identify the specific location of the centre and edges. In spring and summer of 2000 and 2001, more detailed chemical and biological sampling was conducted at three stations, one at the eddy centre, one at the edge, and one at a reference station outside the eddy. The reference sites were located in waters just outside the eddy, ca. 30–50 km from the eddy edge at the time of sampling in June and September 2000, while in June and September 2001 reference sites were located further away (180 km to the southeast in June 2001, and 160 km to the south in September 2001; Fig. 1).

Conductivity, temperature, and depth (CTD) were profiled during each cruise at 10 stations across the eddy with data collected to 1000–3000 m, employing a Seabird 911plus CTD mounted on a 24-bottle rosette frame. Sigma-θ values were based on CTD data. Fewer stations (4 in 2000, 2 in 2001) were sampled in February due to time constraints. Duplicate nutrient analyses (nitrate + nitrite, silicic acid, phosphate) were performed for 10–15% of depths sampled, with a mean standard deviation for all cruises of $\pm 0.13\,\mu M$ for nitrate, $\pm 0.76\,\mu M$ for silicic acid, and $\pm 0.012\,\mu M$ for phosphate. Sampling depths extended from 0 to 1000–3000 m, with more fine-scaled sampling at shallow depths. Nutrient samples were collected into 15 ml plastic test tubes filled from Niskin bottles mounted on the rosette. Samples were stored at 4 °C until analysis was possible onboard (usually within 12 h) or at −20 °C for samples collected in September 2001 and processed ashore. Samples were run on a Technicon II AutoAnalyzer® following procedures in Barwell-Clarke and Whitney (1996). Eddy core nutrient concentrations were integrated from 75 m to the depth of the 27.0 isopycnal by the trapezoidal integration method.

2.2. Statistics

Due to the small number of observations and coarse sampling scheme, statistical analyses were not useful for all comparisons. When appropriate, a Student's *t*-test was used to compare integrated nutrient concentrations between the eddy and surrounding waters over time. Statistical tests were performed using *JmpIn*© 4.0 software.

Table 1
Cruise dates, locations, mixed layer depths (MLD), Sea-Surface Height (SSH) anomalies, and eddy dimensions (km) for Haida-2000 sampling

Cruise	Station	Date	Latitude (°N)	Longitude (°W)	MLD (m)	SSH (cm)	Dimensions (km) N–S × E–W	Isopycnal depression (m)
Feb 2000	Out	14/02/00	52.33	131.99	52	12	144 × 211	100
	Centre	15/02/00	52.34	134.67	110			
	Edge	16/02/00	52.33	133.67	68			
June 2000	Out	18/06/00	51.74	135.84	24	20	167 × 311	150–200
	Centre	20/06/00	52.75	135.83	29			
	Edge	21/06/00	52.25	135.83	28			
Sept 2000	Out	26/09/00	51.75	136.17	32	12	200 × 266	100
	Centre	27/09/00	52.75	136.16	31			
	Edge	27/09/00	52.24	136.17	28			
Feb 2001	Out	16/02/01	53.80	139.50	81	10	100 × 178	200
	Centre	17/02/01	53.80	138.00	81			2001
June 2001	Out	07/06/01	52.75	137.00	24	5	100 × 167	100
	Centre	09/06/01	54.42	138.17	19			
	Edge	11/06/01	54.92	138.16	20			2001
Sept 2001	Out	27/09/01	52.50	138.75	32	10	222 × 189	200
	Centre	23/09/01	54.50	138.33	33			
	Edge	27/09/01	54.00	138.75	23			

Out refers to reference stations chosen outside but in the vicinity of Haida-2000, centre refers to the eddy centre as identified by satellite altimetry and hydrographic data, and the edge is defined as waters in the region of most steeply sloping isopycnals and swiftest currents. SSH data from TOPEX/POSEIDON-ERS-2 satellite radar altimetry processed by Colorado Center for Astrodynamical Research (CCAR) (http://www-ccar.colorado.edu/~realtime/gsfc_global-real-time_ssh/; R. Leben). Dimensions are in latitudinal (N–S) and longitudal (E–W) directions in km and are derived from the SSH plots. Depth of depression of deep isopycnals (m) represents the depth to which the 26.8 and 27.0 isopycnals are depressed relative to surrounding waters.

2.3. Definitions

The eddy centre refers to the site of highest sea-surface/dynamic-height anomaly and the location where the 27.0 isopycnal was deepest. The edge was chosen as the region with the strongest slope of isopycnals at depths of 200–500 m and the swiftest currents according to Acoustic Doppler Profiler Current measurements (Yelland and Crawford, 2005).

The eddy core is defined as those waters contained in the volume between the eddy surface and the maximum depth at which coastal waters are found. This includes waters of salinity less than 34.0 and extends to the depth where spread between the 26.8 and 27.0 isopycnals is observed (see Fig. 2). The top of the core water was defined as the depth at which there is less than a 0.1 sigma-θ difference between centre and outside (ca. 75 m).

The bottom of the mixed layer is defined as the depth at which there is an increase in sigma-θ of 0.125 units compared with the surface density (Levitus, 1982). Nutrient concentrations within the mixed layer were calculated by averaging the discrete concentrations at depths between 0 m and the bottom of the mixed layer.

3. Results

3.1. Eddy evolution and structure

3.1.1. Chronology

Haida-2000 was characterized by a depression of isopycnals and nutrient isopleths throughout

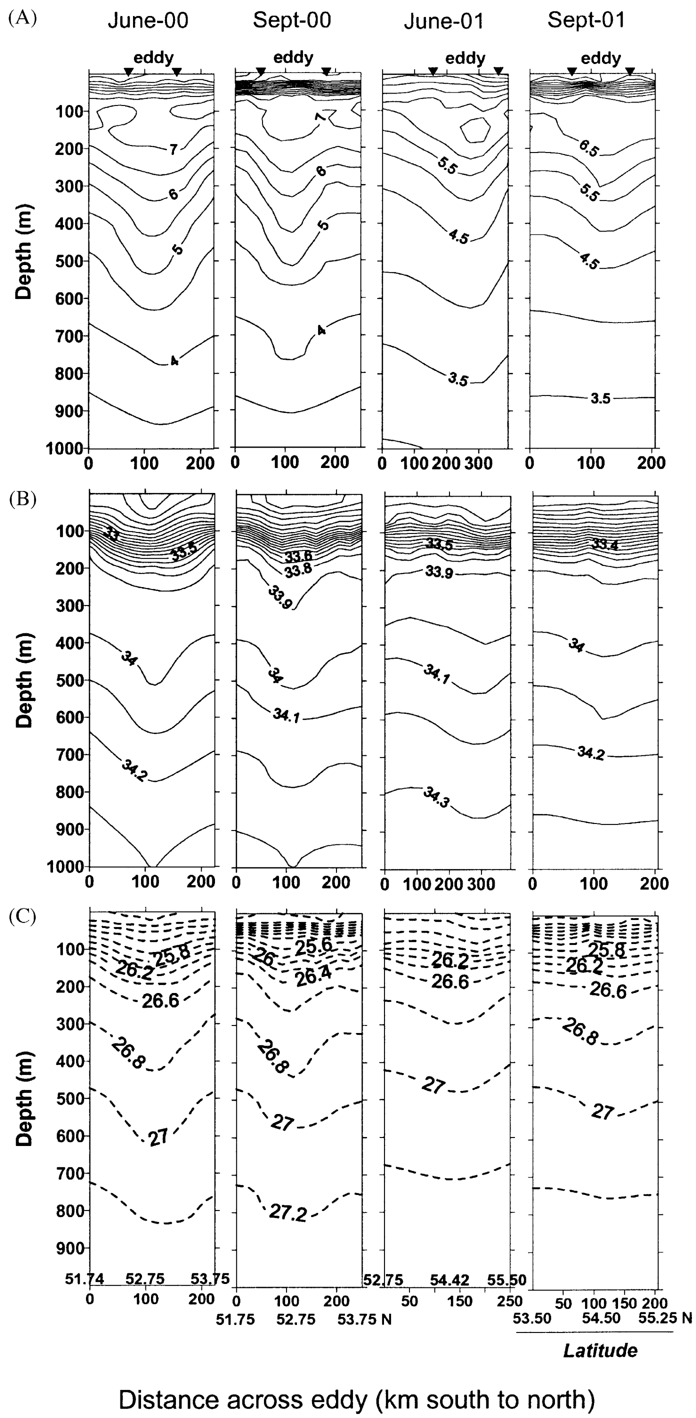

Fig. 2. Contours of temperature (A), salinity (B), and sigma-θ (c) across Haida-2000. Distance is given in km from south to north and in degrees of latitude except for September 2001, where the plot is a composite of two half-transects with distance given as south to centre and centre to southwest. The contouring intervals are 0.5 °C for temperature, 0.1 units for salinity, and 0.2 units for sigma-θ. Arrows along the tops of the panels indicate the location of eddy edges delimiting the extent of Haida-2000 (marked "eddy").

the sampling period (Figs. 2 and 3). The Haida-2000 eddy was detected as a SSH anomaly of roughly 12 cm by radar satellite altimetry in February 2000. The shape was slightly oblong, with surface dimensions of approximately 144 km (N–S) by 211 km (E–W; Table 1). The core extended to 600 m deep with isopycnals distorted to a depth of at least 1000–2000 m.

The trajectory followed by Haida-2000 is shown in Fig. 1. After breaking away from the coast in February 2000, Haida-2000 moved 90 km westward, stalling over Bowie Seamount (53.5°N, 135.6°W) from May to September, and drifted only 40 km westward over the summer. The interaction with the shallow seamount (pinnacle ~35 m below sea surface) distorted the shape of the eddy in the northern region (see eddy dimensions in Table 1). After breaking away from the seamount, Haida-2000 tracked north westward approximately 325 km from September 2000 to September 2001. By our final survey in September 2001, Haida-2000 had drifted 750 km away from the coast and was sitting in HNLC waters. As Haida-2000 traveled westward away from the coast, it moved first into seasonally nitrate-depleted waters designated as the Dilute Domain (DIL), and then into HNLC waters of the Subarctic Current domain (SUB; see Wong et al., 2002a; Fig. 1).

By June 2001, isopleths of temperature, salinity, and nitrate had shoaled in comparison with observations from Year 1 (June and September 2000), likely reflecting eddy decay (see Section 3.1.3). Between June and September 2001 a second eddy merged with Haida-2000, injecting fresh, warm water into the eddy core. This coalescence was evident in increased satellite SSH (Fig. 4), by an influx of heat and fresh water (Fig. 2; Crawford, 2005), and by a depression of isopycnals and nutrient isopleths between sampling dates in June and September 2001 (Fig. 3). Since the merging of the two eddies was likely a slow process taking weeks to months, the shoaling and distortion of deep isopycnals (27.0, 27.2) and nutrient isopleths also may have resulted from the coalescence; however, it is impossible to isolate the effects of eddy coalescence from frictional decay during the June sampling period.

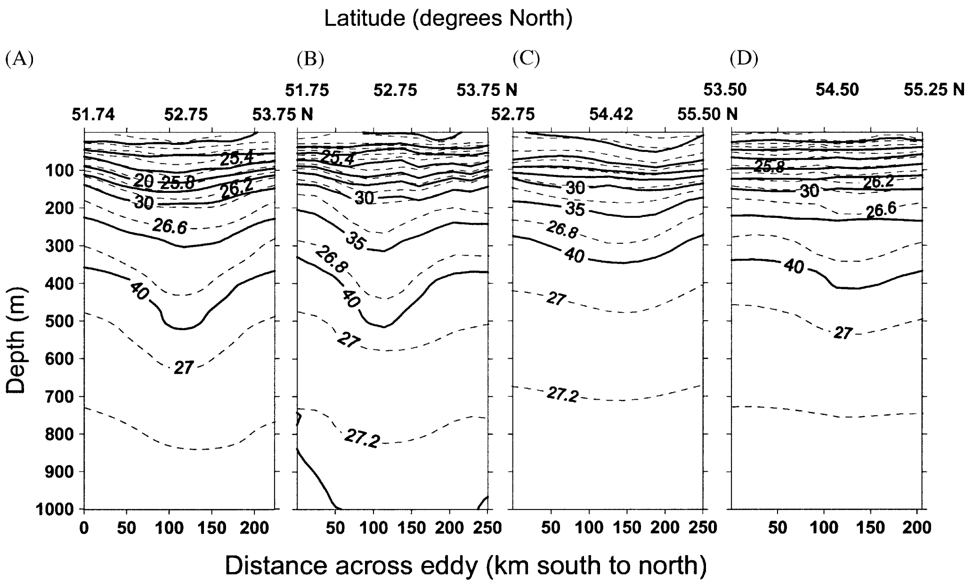

Fig. 3. Solid contours show nitrate (μM) across the Haida-2000 eddy (panels a–d) with dashed contours representing sigma-θ. Four panels represent, from left to right, cruises in June 2000 (A), September 2000 (B), June 2001 (C), and September 2001 (D). The contouring interval is 5 μM for nitrate, 0.2 units for sigma-θ. Contour constructed for September represents a composite of two half-transects from outside to centre (south to centre and centre to southwest) rather than one full transect in a north to south direction.

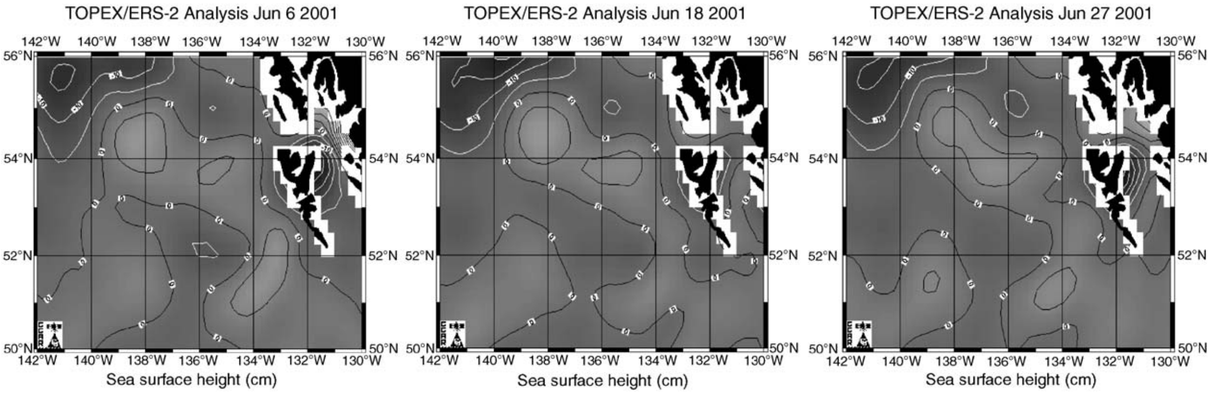

Fig. 4. Three consecutive sea-surface height anomaly plots from TOPEX/POSEIDON-ERS-2 radar altimetry showing the merging of a second, younger eddy with Haida-2000.

3.1.2. *Temperature–salinity characteristics of eddy waters*

Haida-2000 was both warmer and fresher than surrounding waters (Figs. 2A and B). As the eddy aged, the temperature anomaly in surface waters weakened (Fig. 2A), but the isopycnal tilting and salt deficit remained. Contours of salinity show that the surface waters of the eddy remained isolated from surroundings in both June and September 2000, but that in 2001 these waters exchanged freely with surroundings (Fig. 2B). Compared to the reference sites, temperature–salinity relationships within Haida-2000 changed less over the 20-month time period (not shown), illustrating that the eddy core volume remained relatively isolated from surroundings for depths below the mixed layer.

3.1.3. *Eddy decay*

The decay of Haida-2000 was slow between February 2000 and February 2001, as inferred by only slight changes in the depth of isopycnal depression (Fig. 2) and small decreases in SSH anomaly (Table 1). From February 2001 to June 2001, however, the depth of the deepest isopycnal defining the eddy core (27.0) shoaled by approximately 100 m (ca. 0.89 m d^{-1}; Table 1) and decay was assumed to be more rapid, although, as noted above, eddy coalescence also could have contributed to this occurrence. At the same time, the SSH anomaly was smallest in June 2001 (Table 1). Between June and September 2001 an increase of 100 m in the depth of the depression of the 27.0 isopycnal (to ca. 600 m) was observed, following completion of the merging of the second eddy (Fig. 2). Likewise, following the merging event the height anomaly increased from 5 cm to 10 cm (Table 1). The changes in sea-level anomaly should be interpreted with some caution since they are calculated relative to surroundings; along Line P (Fig. 1) isopycnals and sea-level tilt upward from inshore toward the centre of the Alaska Gyre (see Whitney and Freeland, 1999). This could cause an apparent decrease in SSH that was larger than the actual change if the eddy was sitting on a flat surface.

3.2. *Surface processes: evolution of mixed layer nutrient concentrations*

3.2.1. *Year 1*

When Haida-2000 eddy broke away from the coast, the mixed layer depth (MLD) at the centre was 50 m greater than in surrounding waters (Table 1). Table 2 shows nitrate and silicic acid concentrations (μM) at the surface (0–2 m), at the approximate depth of the mixed layer (75 m for winter, 50 m for spring and summer), at 75 m (depth of the top of the eddy core), at 300 m (within the eddy core) and at the bottom of the eddy (600 m in Year 1, 500 m in Year 2).

Depth-averaged mixed layer concentrations of nitrate and silicic acid were 14.8 and 24.8 μM, respectively, at the eddy centre compared to 10.3 and

Table 2
Nitrate and silicic acid concentrations at selected depths for centre, edges, and outside reference stations for all observation sets (μM)

Date	Depth	Centre			North (east) edge			South (west) edge			Reference			OSP	P4
		NO_3^-	$Si(OH)_4$	Chl	NO_3^-	$Si(OH)_4$	Chl	NO_3^-	$Si(OH)_4$	Chl	NO_3^-	$Si(OH)_4$	Chl	Chl	Chl
Feb-00	0	14.6	24.7	0.28	10.7	18.9	0.56	13.9	25.4	0.39	9.0	16.5	0.68		
	75	14.9	25.1		15.2	23.7		14.3	24.4		14.0	21.6			
	150	23.4	35.3		20.4	30.4		21.9	34.1		30.2	45.3			
	300	34.5	56.5		35.2	62.0		34.1	55.3		35.0	59.7			
	600	43.0	95.3		43.5	101.5		42.7	94.0		42.1	92.4			
June-00	0	4.2	3.0	0.38	4.5	5.5	n.d.	4.45	6.9	0.28	4.19	12.6			
	50	7.7	13.1		8.9	13.7		7.68	13.1		10.6	16.8			
	75	10.5	15.9		12.3	17.7		10.53	15.9		17.8	27.1			
	300	35.1	58.4		35.4	59.0		36.0	62.1		38.1	68.5			
	600	43.3	99.7		43.3	96.2		43.32	99.7		44.4	107.8			
Sept-00	0	b.d.	6.0	0.47	b.d.	3.4	0.55	0.6	5.1	0.41	0.6	7.4		0.53	0.66
	30	4.1	9.8		0.1	3.5		1.1	5.4		0.9	7.6			
	50	12.1	17.7		8.5	12.3		7.4	12.1		8.2	12.9			
	75	14.5	21.1		12.3	16.3		10.7	15.0		15.2	20.0			
	300	34.0	55.4		36.3	60.9		36.5	62.9		39.4	71.6			
	500	38.7	71.8		41.8	85.8		42.0	90.1		43.9	98.1			
Feb-01	0	13.9	16.4	0.29	13.9	16.3	0.35	12.5.	16.8	0.30	15.6	23.0		0.32	0.51
	75	15.4	17.7		n.d	n.d.		n.d.	n.d.		15.6	23.1			
	100	25.0	32.3		n.d	n.d.		n.d.	n.d.		27.3	43.5			
	300	37.0	58.6		n.d.	n.d.		n.d.	n.d.		43.4	90.6			
	600	43.7	97.9		n.d	n.d.		n.d.	n.d.		44.9	121.8			
June-01	0	8.8	15.1	0.52	8.4	13.9	0.39	10.6	16.8	0.43	10.1	16.2		0.45	
	50	11.2	17.3		9.7	15.4		12.2	17.7		11.3	17.0			
	75	13.2	19.0		11.3	16.5		13.9	19.6		12.4	17.9			
	300	38.1	69.9		38.6	70.4		40.6	79.1		40.6	79.0			
	600	44.0	108.0		44.3	107.6		44.2	113.6		44.4	115.4			
Sept-01	0	3.4	12.1	0.55	3.6	10.9	0.57	3.4	10.9	0.52	9.0	13.1		0.31	
	50	12.1	17.3		14.4	18.6		11.8	15.9		14.1	20.2			
	75	16.3	21.9		18.0	23.6		14.8	19.4		16.6	25.8			
	300	36.3	60.8		39.7	75.0		38.2	68.9		42.0	85.3			
	600	43.1	95.5		44.3	106.5		43.6	101.6		43.8	110.1			

Values for northern and southern edges are given for all cruises except February 2000 where edges were located to the east and west of the eddy centre; n.d.—no data available, b.d.—below detection. Analytical precision was $\pm 0.13\,\mu M$ for nitrate and $\pm 0.76\,\mu M$ for silicic acid. Based on duplicate chlorophyll *a* determinations in June 2000 and September 2001, the precision was $\pm 0.02\,\mu g\,l^{-1}$.

18.0 μM in outside waters (Table 2). While surface nutrient concentrations (0 m; both nitrate and silicic acid) were lower in outside waters compared to the eddy centre and edges, values near the bottom of the mixed layer (75 m) differed only marginally between sites in February 2000 for nitrate (Table 2). Silicic acid concentrations were highest at the bottom of the mixed layer at the eddy centre and edges in February 2000 (Table 2; 25.1, 23.7, and 24.4 μm at the centre and east/north and west/south edges, respectively), while the outside reference site had a silicic acid concentration that was slightly lower than at the centre (21.6 μm). After the first spring, mixed layer nutrient concentrations inside the eddy were at all times lower than initial values (Table 2). The greatest losses in mixed layer nutrients occurred between the two initial observations (February and June; Table 3). Drawdown of nitrate was

Table 3
Change in average nutrient concentrations (μM month^{-1}) within the mixed layer over time at eddy centre between sampling dates

Nutrient	Feb–June 2000	June–Sept 2000	Sept–Feb 2001	Feb–June 2001	June–Sept 2001
NO_3^-	−2.6	−0.9	3.3	−1.2	−1.5
$Si(OH)_4$	−5.4	0.9	2.5	−0.2	−1.0
$Si(OH)_4$:NO_3^- ratio	2.1	1	0.8	0.2	0.7

Signs associated with numbers indicate loss (negative) or gain (positive) and the $Si(OH)_4$:NO_3^- ratios of loss or gain for the different time periods are shown.

2.6 μmol month^{-1}, while removal of silicic acid was twice as high as nitrate (5.4 μmol month^{-1}). By June 2000, the mixed layer silicic acid concentration was only 3.0 μM within the eddy compared to 12.6 μM outside (Fig. 5). While silicic acid concentrations were four times lower inside the eddy compared to surroundings in June 2000, nitrate levels were similar (4.2 and 4.3 μM, inside and outside the eddy, respectively). Whereas within the eddy the decrease in silicic acid was twice as large as the loss of nitrate, the drawdown ratio of silicic acid to nitrate was 0.9 in outside waters (not shown; note that Reference stations were in different but proximate locations for the two cruises). The removal rates of silicic acid and nitrate were only 25% and 60% (1.4 μmol month^{-1} $Si(OH)_4$, 1.5 μmol month^{-1} NO_3^-) as high, respectively, in surrounding waters compared to eddy waters (not shown).

Over the first summer, the average surface $Si(OH)_4$ concentration at the eddy centre within the mixed layer doubled from 3.0 to 6.0 μM, while the nitrate concentration decreased from 4.3 μM to below detection (removal of 0.9 μM month^{-1} NO_3^-). Although the lowest nitrate concentrations were found inside the eddy, surrounding surface waters in the DIL domain also held low nitrate (less than 1 μM; Fig. 3). Silicic acid was lowest at the eddy edges, with depressed $Si(OH)_4$ isopleths apparent to a depth of ca. 200 m at the edge (Fig. 6) and 600 m at the centre (not shown).

3.2.2. Year 2

Winter ventilation (September 2000—February 2001) injected nutrients into the mixed layer and nitrate values were returned to the initial average concentration. The average nitrate concentration was slightly lower than in surroundings (compare 14.3 μM at the eddy centre with 15.6 μM outside; Fig. 5). However, eddy waters were not replenished in silicic acid by winter mixing, and mixed layer concentrations at the centre were lower than in surrounding waters in the SUB domain in February 2001. The mixed layer silicic acid concentration at the eddy centre in February 2001 was 16.7 μM compared to the initial value of 24.8 μM (Fig. 5). Surrounding waters held 22.9 μM $Si(OH)_4$ in February 2001.

The rate of nitrate loss between February and June 2001 within the eddy mixed layer was 50% as high as the previous year (1.2 μM month^{-1} NO_3^- lost between February and June 2001; Table 3). Silicic acid drawdown was only 4% that of the first spring (0.2 μM month^{-1} $Si(OH)_4$ lost between February and June 2001). By September 2001 there was little difference between mixed layer silicic acid concentrations inside or outside the eddy (11.8 μM $Si(OH)_4$ within the eddy, 12.9 μM $Si(OH)_4$ outside), although nitrate was 3.5 μM inside the eddy compared to 9.0 μM in surrounding waters (Fig. 5).

3.3. Nutrient drawdown and new production

We used the difference between February and June nitrate concentrations to estimate seasonal (spring) drawdown, when nitrate utilization is typically the highest (Wheeler, 1993; Varela and Harrison, 1999). Annual new production was taken as the drawdown occurring between February and September/October. We report daily drawdown rates for comparison with other studies, with the caveat that the bulk of nitrate utilization occurs between April and June (Wheeler, 1993; Whitney and Freeland, 1999).

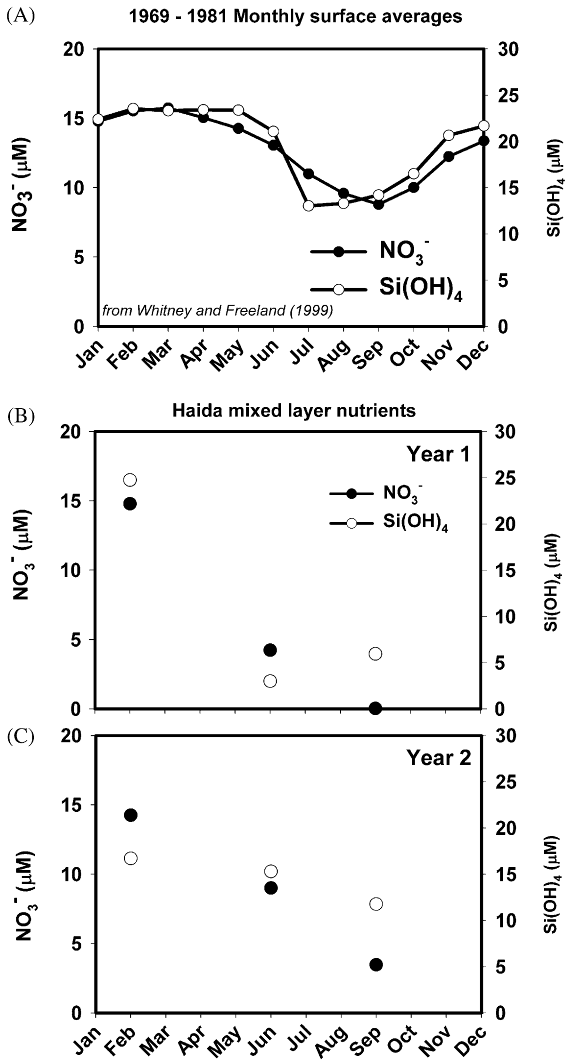

Fig. 5. Monthly averages of nitrate and silicic acid concentrations at Ocean Station P (50°N, 145′W) from 1969 to 1981 (adapted from Whitney and Freeland, 1999) (A). Average mixed layer nutrient concentrations in Haida-2000 during Year 1 (B; February 2000–September 2000) and Year 2 (C; February 2001–September 2001) were computed from ambient concentrations from the surface to the bottom of the mixed layer. Eddy formation occurred in February 2000 (= 0 months) and the study ended in September 2001 (= 20 months).

From losses of nitrate in the upper 50 m of the water column (see Table 4 for integrated nitrate and silicic acid inventories for 0–50 m), estimates of new production were derived for Haida-2000 (Table 5). Losses within the upper 50 m were calculated for time periods between February and June or February and September (Table 5). The former represents spring drawdown while the latter estimates yearly drawdown, assuming that the maximum NO_3^- concentration occurred in February and the minimum in September. Between February and June 2000 (ca. 120 d), 374.5 mmol m^{-2} of nitrate were removed from the mixed layer at the eddy core, equivalent to approximately 3.0 mmol m^{-2} d^{-1}. Between February and September, 417.7 mmol m^{-2} of nitrate were removed from the mixed layer, resulting in a removal rate of 3.5 mmol m^{-2} d^{-1}.

In the second year of eddy evolution, nitrate drawdown was 193.4 mmol m^{-2} from February to June, half as high as the previous year (removal rate of 1.6 mmol m^{-2} d^{-1}). The annual nitrate removal (February–September 2001) was 417.1 mmol m^{-2}, not different from the nitrate loss that occurred in the mixed layer between February and September 2000 in the first year of eddy life (ca. 3.5 mmol m^{-2} d^{-1}). Thus, the only difference in nitrate losses between young eddy and older eddy waters was a difference in the timing of nitrate drawdown.

If we examine the losses of silicic acid in order to estimate diatom production, there were large differences between Year 1 and Year 2 (see Table 4 for silicic acid inventories from 0–50 m; see Table 5 for removal rates). There was a spring bloom of diatoms (7.0 mmol $Si(OH)_4$ m^{-2} d^{-1} removed) in the spring of 2000 that was followed by little to no silicic acid drawdown over the summer months. In fact, silicic acid was gained within the mixed layer, with mixed layer $Si(OH)_4$ (0–50 m) almost tripling. The annual drawdown was 4.5 mmol $Si(OH)_4$ m^{-2} d^{-1} in the first year. Although growth was much slower in Year 2 (1.3 mmol m^{-2} d^{-1} removed from February to September), it continued throughout the summer. The annual drawdown of silicic acid in Year 2 was ca. 30% of that in Year 1, but the spring drawdown in Year 2 represented only 0.05 mmol m^{-2} d^{-1}, or 4%, of the annual drawdown.

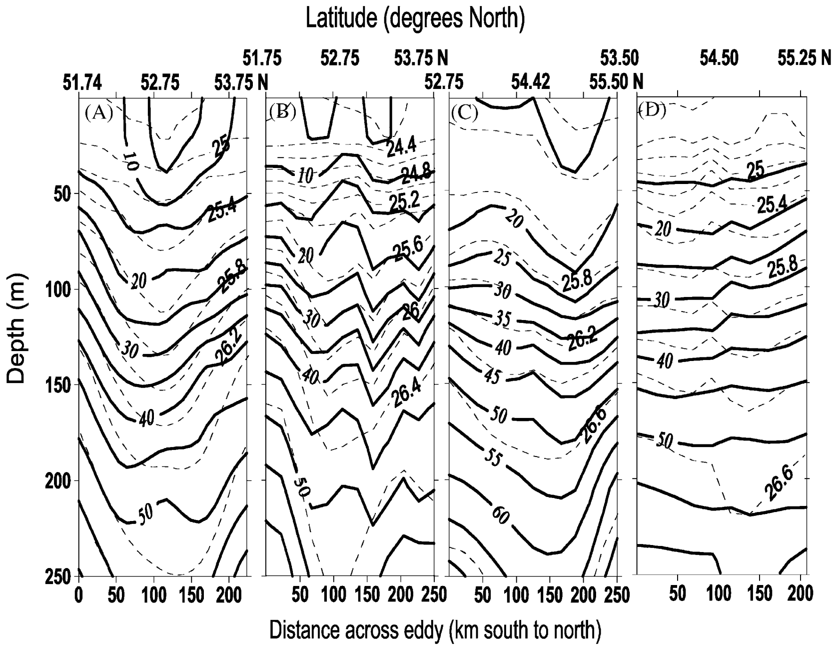

Fig. 6. Solid contours show silicic acid (μM) across the Haida-2000 eddy (panels A–D), with dashed contours representing sigma-θ. Four panels represent, from left to right, cruises in June 2000 (A), September 2000 (B), June 2001 (C), and September 2001 (D). The contouring interval is 5 μM for silicic acid, 0.2 units for sigma-θ. Contour constructed for September represents a composite of two half-transects from outside to centre (south to centre and centre to southwest) rather than one full transect in a north to south direction. Minimum value at the surface in June 2000 was 3.0 μM.

Table 4
Nutrient inventories (mmol m^{-2}) integrated over 0–50 m in February, June, and September of 2000 and 2001 at the centre of Haida-2000

Nutrient	Date					
	2000			2001		
	Feb	Jun	Sept	Feb	Jun	Sept
NO_3^-	600.5	226.0	182.8	672.5	479.1	255.4
$Si(OH)_4$	1003.4	161.7	462.4	791.0	785.0	632.5

3.4. Deep-water processes: evolution of eddy core waters

3.4.1. Nutrients within the eddy core

Contours of nitrate (Fig. 3) and silicic acid (not shown) exhibited depressed isopleths to depths that corresponded approximately with the base of the eddy core (ca. 600 m), demonstrating the presence of anomalous coastal-type water. Phosphate distributions followed those of nitrate (Table 6; contours not shown), and so are not discussed further.

Nutrient concentrations within the eddy core changed little over the study period (see Table 2 for concentrations at selected depths). Nutrient-salinity relationships also remained similar throughout the 20-month period (Fig. 7) and lay between typical oceanic values (e.g., at Ocean Station P) and coastal ones (e.g., P4) for both nitrate and silicic acid. Differences between eddy waters and coastal/oceanic waters were greater for silicic acid than for nitrate, with eddy nitrate–salinity relationship being similar to oceanic waters for salinities less than ca. 33.5 (Fig. 7). Silicic acid per unit salinity remained lower within the core of Haida-2000 compared to oceanic HNLC waters throughout the study.

The shoaling of deep isopycnals over time resulted in (1) smaller integrated nutrient

Table 5
Estimates of annual and spring new production (NP) and $Si(OH)_4$ drawdown ($mmol\,m^{-2}\,d^{-1}$) at the eddy centre from 0 to 50 m in 2000 and 2001

Month	Spring NP ($mmol\,N\,m^{-2}\,d^{-1}$)	Annual NP ($mmol\,N\,m^{-2}\,d^{-1}$)	Spring $Si(OH)_4$ ($mmol\,m^{-2}\,d^{-1}$)	Annual $Si(OH)_4$ ($mmol\,m^{-2}\,d^{-1}$)
Year 1	3.0	3.5	7.0	4.5
Year 2	1.6	3.5	0.05	1.3

Annual NP was calculated assuming maximum nutrient inventories in February and minima in September, while spring new production captures nitrate-based growth between February and June.

Table 6
Integrated concentrations of nitrate, phosphate and silicic acid ($mol\,m^{-2}$) and $Si(OH)_4$:NO_3^- ratio at the eddy core and at outside reference stations

Date	NO_3^-		HPO_4^{2-}		$Si(OH)_4$		Si:N:P		Si:N	
	In	Out	In	Out	In	Out	In	Out	In	Out
Feb 2000	17.8 (20.1–21.36)	18.4	1.30 (1.47–1.56)	1.32	32.4 (36.6–38.9)	34.7	25:14:1	26:14:1	1.82	1.88
June 2000	21.2	19.5	1.38	1.41	38.6	37.8	28:15:1	27:14:1	1.82	1.94
Sept 2000	17.5	15.7	1.28	1.13	30.6	29.0	24:14:1	26:14:1	1.75	1.85
Feb 2001	19.2	12.8	1.40	0.92	33.4	25.6	24:14:1	24:14:1	1.74	2.0
June 2001	15.1	11.7	1.08	0.84	28.0	21.6	26:14:1	26:14:1	1.85	1.85
Sept 2001	18.9	11.7	1.37	0.85	34.5	22.5	25:14:1	26:14:1	1.83	1.92

Integration depth corresponds to the eddy core, from the depth of flat isopycnals at the top (ca. 75 m) to the 27.0 σ_θ isopycnal at the bottom. In February 2000 the true centre was not sampled; the numbers represent a station closer to the edge. Numbers in brackets represent the estimated nutrient concentrations at the eddy centre in February 2000 calculated from the enrichment factor (centre value/edge value) from June and September 2000. Analytical precision was $\pm0.065\,mol\,m^{-2}$ for nitrate and $\pm0.38\,mol\,m^{-2}$ for silicic acid.

inventories (Table 6) and (2) higher nutrient concentrations for a given depth (Fig. 8). The eddy held significantly more nitrate ($p = 0.04$) and silicic acid ($p = 0.04$) between 75 m and the 27.0 isopycnal compared to surroundings when all time points were considered. June 2001 saw the most dramatic shoaling of deep isopleths, which resulted in smaller depth-integrated inventories of nitrate and silicic acid between 75 m and the 27.0 isopycnal. Although the concentrations per volume were lower than surroundings when the eddy sat in HNLC waters (see Table 2), the volume of water contained between the mixed layer and the 27.0 isopycnal was greater within Haida-2000 compared to surroundings; in nearby non-eddy waters the 27.0 isopycnal sat at a depth of 300 m, while at the eddy centre it was depressed to 500–600 m. Thus, despite the fact that the concentrations of macronutrients were lower within Haida-2000, the total integrated inventory was still higher than in surroundings (Table 6), and offshore nutrient transport was substantial.

In June 2001, when isopycnals and nutrient isopleths within the eddy shoaled, nutrient profiles exhibited higher concentrations at depths below ca. 300 m compared to the other sampling periods (Fig. 8). The trend was more apparent in the silicic acid profiles than for nitrate where concentrations in June 2001 were only slightly higher. The shoaling of deep isopycnals injected nutrients into the eddy core, enriching these waters, particularly in silicic acid. Nutrient increases within the eddy core occurred at a $Si(OH)_4$:NO_3^- ratio of ca. 2.1.

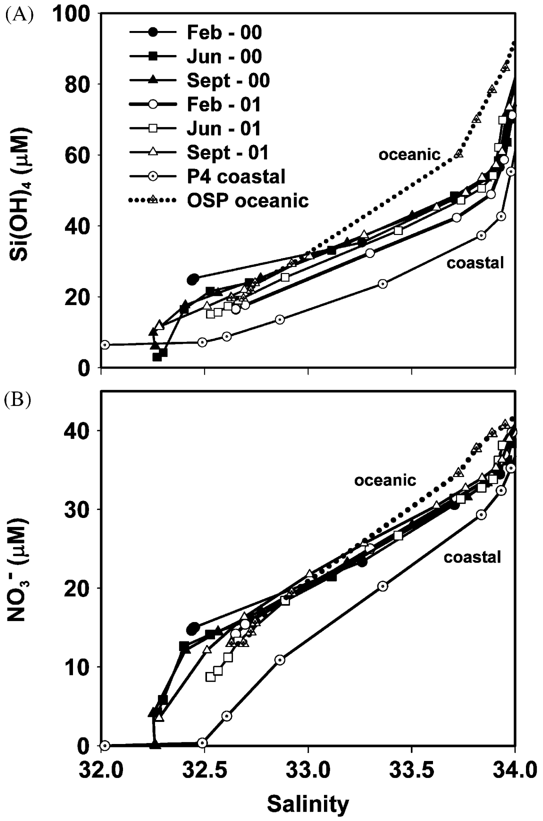

Fig. 7. Silicic acid (A) and nitrate (B) versus salinity at the eddy centre for February, June, and September 2000 and 2001 at the eddy centre. A coastal upwelling station (P4) and an oceanic station (OSP) are included for reference.

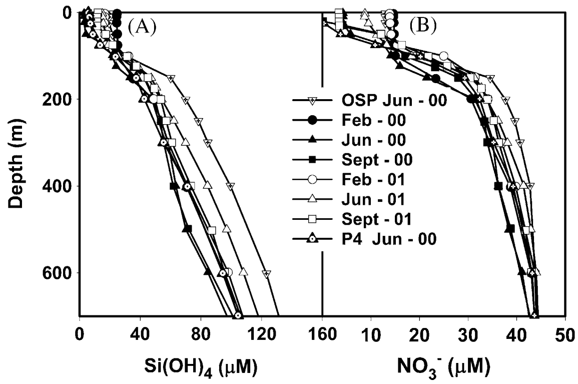

Fig. 8. Silicic acid (A) and nitrate (B) profiles for six cruises conducted from February 2000 to September 2001 at the centre of Haida-2000. The surface concentrations of $Si(OH)_4$ increase with age or distance from the point of origin, becoming more similar to surrounding High Nitrate-Low Chlorophyll waters. A coastal upwelling station (P4; see Fig. 1) and a station located in High Nitrate-Low Chlorophyll waters (OSP) are included for reference.

3.4.2. Influence of eddy deformation and merging on nutrient distributions

The shape of Haida-2000 was altered as it encountered physical obstacles and interacted with other eddies. When the centre sat directly over Bowie Seamount in June and September 2000, the northern edge was distorted and the eddy shape was more oblong compared to other sampling times. The changes in eddy shape are reflected in asymmetric rather than Gaussian contours of sigma-θ and nutrient distributions (Figs. 2 and 3). Nutrient isopleths generally followed isopycnals (Fig. 3). Once the eddy broke away from the seamount, it regained a more circular shape (e.g., in February and June 2001), which was stretched in a north–south direction during the coalescence of a second younger eddy between June and September 2001 (Table 1).

4. Discussion

4.1. Biological drawdown of eddy nutrients

In February 2000, a mesoscale eddy (Haida-2000) detached from the British Columbia coast and began traveling westward, first moving through waters designated as the Dilute Domain (DIL) and then into HNLC waters of the Subarctic Current System (SUB, Fig. 1; Favorite et al., 1976; Whitney and Freeland, 1999; Wong et al., 2002a). This eddy was followed for nearly 2 years as it drifted westward. For a description of the history and physical features of Haida-2000, see Miller et al. (2005), Crawford (2005), and Yelland and Crawford (2005). In the first year, surface waters within Haida-2000 held low nitrate concentrations, similar to waters in the DIL Domain. Silicic acid, however, was much lower within the eddy compared to surroundings. By the second year, surface waters of Haida-2000 were similar to those of the HNLC domain characterized by high nitrate and silicic acid concentrations.

The very low levels of nitrate, phosphate, and silicic acid in the mixed layer within the Haida-2000 eddy followed an April spring bloom observed by SeaWiFS satellite imagery (Crawford et al., 2005), indicating that nutrient losses were due to biological consumption. The satellite pictures showed that chlorophyll within the Haida-2000 eddy was ca. 5–10 $\mu g\,l^{-1}$, or approximately 10 times higher than surrounding levels. Silicic acid drawdown between February and June 2000 exceeded nitrate drawdown at a ratio of approximately 2:1, implying that diatoms were responsible for the high chlorophyll production. It was during the initial spring period that Haida-2000 acted as a important sink for carbon dioxide, exhibiting a significantly higher drawdown of CO_2 compared to surroundings (Chierici et al., 2005). This role diminished over eddy evolution.

New production refers to primary production fueled by "new" nutrients from deep upwelled water, in nitrogen currency (Dugdale and Goering, 1967). The disappearance of nitrate from surface waters on a seasonal or annual basis approximates new production. New production differs from export production (the removal of particulate carbon produced by phytoplankton from the upper ocean), because remineralization processes can lead to the recycling of particulate material that may have accumulated in the mixed layer, preventing particle export. We do not address the question of export production in this manuscript (see Chierici et al., 2005) but focus on the utilization of nutrients within the Haida-2000 eddy.

Neglecting the inputs of nitrate from nitrogen fixation or nitrification, annual and spring new production rates were estimated from the difference in nitrate inventory between 0 and 50 m from February to September, and February to June, respectively. The 0–50 m layer represents the average depth of the euphotic zone in the Subarctic North Pacific (Longhurst et al., 1995; Boyd and Harrison, 1999; Harrison et al., 1999) and allows a comparison of our estimates with the larger collection of observations from the Subarctic Pacific (e.g., Wheeler, 1993; Wong et al., 2002a; Childers and Whitledge, 2005). Estimates for new production in the Gulf of Alaska come from studies at Ocean Station P (Wheeler, 1993; Varela and Harrison, 1999), from ship-of-opportunity cruises in the Alaska Gyre (Wong et al., 2002a), and from the US JGOFS Seward Line time series (Childers and Whitledge, 2005). We hoped to minimize the complicating effects of advection (see Wheeler, 1993) by focusing our efforts on an isolated parcel of water held within an eddy. Although there was some exchange with outside waters, the surface waters remained relatively isolated from surroundings, at least within the first year (see Yelland and Crawford, 2005; Chierici et al., 2005).

Annual new production estimates derived from differences in maximum (winter) and minimum (summer) mixed layer integrated nutrient content suggested that new production was similar in the first year of eddy life compared to Year 2 (Table 5). Spring new production (February–June) was twice as high in Year 1 compared to Year 2, reflecting a difference in the timing of nitrate drawdown rather than a difference in the magnitude of nutrient utilization. As the eddy aged, not only did the drawdown ratios of $Si(OH)_4$:NO_3^- decrease, but the timing of maximum nutrient drawdown shifted from spring to summer (Table 3; Fig. 5). At OSP the maximum drawdown rates of silicic acid occur in May–June, while nitrate concentrations reach a minimum in July (Whitney and Freeland, 1999, Fig. 5A). The shift in timing of the nitrate minimum from Year 1 to Year 2 (from June to September) may have reflected the evolution of eddy waters toward HNLC conditions characterized by maximum drawdown rates that occur in late summer.

It is possible that the gain in silicic acid observed over the spring–summer period in 2000 could have been achieved by lateral advection induced by Ekman transport or the onset of winter mixing. However, the salinity differences between June and September at the eddy centre were very small (detail not shown) except at a depth of 50 m, which is below the summer seasonal pycnocline (ca. 30 m). It is thus more likely that the silicic acid came from below, and represented either the onset of winter mixing or a faster rate of eddy diffusion due to weaker stratification at the eddy centre. However, estimates of the buoyancy frequency across the mixed layer were similar at the centre and outside stations (Brünt–Väisälä frequency, N^2, as were estimates of potential energy required to homogenize the mixed layer [see calculations in Nelson et al., 1989]; data not shown), suggesting that any differences between stratification in eddy versus outside waters above 50 m were small. Regardless, the gain in silicic acid without apparent increase in nitrate has the consequence that the latter was probably also supplied but was not detected due to biological removal. Given that the 50-m integrated silicic acid inventory increased over the first summer by approximately 3-fold, we may have underestimated nitrate-based new production rates for this time period. Based on silicic acid supply, nitrate uptake could have been as high as 10 mmol N m^{-2} d^{-1}. Corresponding chlorophyll *a* concentrations were higher in September than in June, particularly at the eddy edges (Table 2; also see Crawford et al., 2005).

An extensive survey of surface nutrient dynamics in the Subarctic Pacific by Wong et al. (2002a) on ships-of-opportunity from 1995 to 2000 included regions that corresponded to the location of the Haida-2000 eddy. They estimated annual new production rates of 0.98 mmol N m^{-2} d^{-1} for the DIL domain, 1.0 mmol N m^{-2} d^{-1} for the SUB domain, and 1.5 mmol m^{-2} d^{-1} for the AG, which includes OSP. The latter included the year 2000, which exhibited one of the highest rates of new production measured in the region (2.5 mmol N m^{-2} d^{-1}) during a period when an old eddy may have transported iron to this region (Whitney et al., 2005); without this value the average dropped to 1.3 mmol N m^{-2} d^{-1}. Our estimates for annual new production NP_a of 3.5 mmol m^{-2} d^{-1} (both years) were thus higher than the regional averages, even considering the anomalously high removal rate noted in 2000 for the Alaska Gyre. The Haida Eddy estimates were at the low end of the range of values presented by Childers and Whitledge (2.1–17.0 mmol m^{-2} d^{-1}; 2005) for northern coastal waters in the Gulf of Alaska, were slightly higher than values estimated from an ^{15}N-tracer study reported by Varela and Harrison (1999) for OSP (pooled seasonal average of 2.6 mmol m^{-2} d^{-1}), and fell within the range of spring-summer pooled average values reported by Wheeler for an earlier ^{15}N-tracer study at OSP (2.3–4.3 mmol m^{-2} d^{-1}; 1993).

The most remarkable difference in nutrient utilization and inventories within Haida-2000 was the large drawdown of silicic acid in spring of Year 1 and near absent drawdown at all time points thereafter. Unfortunately, our sampling program began too late in 2000 to catch the bloom and make in situ measurements, but the $Si(OH)_4$ disappearance suggests that diatoms were an important component of the phytoplankton assemblage (also see Batten and Crawford, 2005). Since diatoms play an important role in vertical carbon flux in the Gulf of Alaska (Wong et al., 2002a), it is important to note the influences on their distributions.

Diatom growth is limited in the Subarctic northeast Pacific by the lack of iron (Martin and Fitzwater, 1988; Boyd et al., 1996; Maldonado et al., 1999). While macronutrient concentrations were slightly higher in waters outside of the eddy, Fe (Johnson et al., 2005) and other trace metals (Zn, M.C. Lohan pers. comm.; Cd, Al, Ga, Mn, S.M. Crispo and K.J. Orians pers. comm.) were enriched within eddy waters. It is likely that the presence of higher concentrations of these trace elements enhanced primary productivity within anticyclonic eddies and promoted growth of diatoms in particular.

Wong et al. (2002b) noted that the low $Si(OH)_4$ supply to the eastern Subarctic Pacific may be responsible, in combination with low Fe concentrations, for the HNLC character of the Alaska Gyre. Diatoms in the DIL, SUB, and AG regions have high silicic acid requirements compared to nitrate (Wong et al., 2002b). Wong et al. (2002b) estimated a $Si(OH)_4$:NO_3^- requirement of 2.7:1 based on species assemblage data combined with bulk nutrient removal rates throughout the eastern Subarctic Pacific. This may reflect the higher $Si(OH)_4$:NO_3^- uptake ratios that result from Fe limitation of diatom growth (Hutchins and Bruland, 1998; Takeda, 1998), but probably reflects the slower remineralization rate of biogenic silica compared to nitrogen. Our estimate of $Si(OH)_4$:NO_3^- drawdown for the period encompassing the spring bloom was 2.3, which is close to Wong et al. (2002b) estimate for diatom requirements in the NE Pacific. As Haida-2000 aged and evolved, its winter mixed layer $Si(OH)_4$:NO_3^- concentration ratios decreased from 1.7 to 1.2 mol: mol, below the requirements of diatoms for silicic acid compared to nitrate estimated by Wong et al. (2002b). Large diatoms were rare in eddy waters at all sampling points following the April bloom (Peterson, 2005), resulting in the lower $Si(OH)_4$ drawdown rates observed within eddy waters after Year 1. This likely reflected the loss of Fe that occurred as Haida-2000 aged (Johnson et al., 2005).

The spring $Si(OH)_4$:NO_3^- drawdown ratio of 2.1 observed in this study (Table 3) was similar to that reported by Whitney and Robert (2002) for the larger Haida-1998 eddy that tracked into more southerly waters (2–3). At all points after the first spring period, nutrient ratios were less than or equal to 1. The greater-than 2:1 drawdown ratio may reflect differences in recycling processes between nitrate and silicic acid that include the preferential remineralization of nitrate at shallower depths than silicic acid (see Whitney et al., 2005), the low-nitrate environment of the DIL domain that would drive $Si(OH)_4$: NO_3^- uptake rates in excess of 1:1 (Whitney and Freeland, 1999), or a high silicic acid requirement by diatoms in the DIL domain (Wong et al., 2002b). The spring drawdown of nutrients in this study was accompanied by high chlorophyll *a* biomass, suggesting either the first or second explanation.

4.2. *Physical processes influencing nutrient distributions*

Coastal waters off British Columbia are characterized by high nutrients and phytoplankton biomass nearshore with decreasing concentrations of each moving across the continental shelf break (Mackas and Yelland, 1999). The extension of the poleward California Undercurrent delivers water northward at depths between 150–300 m (Freeland et al., 1984; Huyer et al., 1991). These waters, characterized by low nutrients and phytoplankton, flow northward, resulting in the relatively "dilute" nature of the region between the Alaska Current and coastal waters off Vancouver Island (Mackas and Yelland, 1999). An increasing gradient in macronutrients from the vicinity of the Alaska Current toward HNLC waters (Whitney and Freeland, 1999) occurs concomitantly with a decrease in iron concentrations (Nishioka et al., 2001). As noted above, in HNLC waters the availability of Fe is important in regulating phytoplankton production and community structure (Harrison et al., 1999; Harrison, 2002).

Haida eddies are formed in Dilute Domain coastal waters characterized by macronutrient concentrations that are lower than in the HNLC Domain (Whitney and Robert, 2002; Whitney et al., 1998), but which have a higher trace metal content (Nishioka et al., 2001). Haida-2000 was more important in delivering trace metals such as iron rather than macronutrients, as was the case for Haida-1998 which traveled into DIL domain waters (see Whitney and Robert, 2002). This illustrates the very different roles, in terms of nutrient transport, that Haida eddies can play depending on which path they follow. At the time of formation, the silicic acid and nitrate contents within Haida-2000 were higher per unit salinity compared to coastal waters but were lower with respect to HNLC stations (e.g., P26 or OSP; Fig. 7). As the eddy drifted further offshore, it appeared increasingly poor in nutrients relative to surroundings, reflecting the coast-to-offshore nutrient gradient.

Following the initial sampling period in February 2000, integrated nutrient inventories (between 25.0 and 27.0 isopycnals) were higher at the eddy centre compared to outside waters (Table 6). This reflects, in part, an artefact of our method of integration, since eddy decay led to a shoaling of the eddy bottom which decreased the depth over which nutrients were integrated. However, it is a functional definition since the integrations were performed according to isopycnal depth and thus reflect total inventory along density planes. It is possible that frictional decay and shoaling of the eddy bottom led to lateral outflow and spreading close to the surface. In such a case our estimates of nutrient loss might have simply reflected the bias introduced by the differences in integration depth, despite the fact that total nutrient content within the eddy volume might not have changed.

4.2.1. Eddy decay and secondary circulation

Haida-2000 underwent slow decay from September 2000, when it broke away from Bowie Seamount, to June 2001. During this period, isopycnal rebound within Haida-2000 occurred at a rate of approximately $0.9\,\mathrm{m\,d^{-1}}$, similar to reports by Cheney and Richardson (1976) and Olson et al. (1985; $1\mathrm{md^{-1}}$) for Gulf Stream cold-core and warm-core rings, respectively. Deep nutrient concentrations at specific depths within the eddy increased over time. The shoaling of isopycnals due to frictional decay and eddy spin down were likely responsible for the increase in nutrient concentrations within the core of Haida-2000, similar to observations by Olson et al. (1985) for warm-core rings of the Gulf Stream. The nutrient gains occurred at a $Si(OH)_4$:NO_3^- ratio greater than 2, suggesting that deep waters high in nutrients were being entrained into the eddy core. Changes in nutrient content over time within the eddy were not of similar magnitude or sign as reference sites, indicating that the changes observed in nutrient content within Haida-2000 did not merely reflect the increasing distance from the coast, but rather reflected the influences of different physical processes such as eddy coalescence, frictional decay, or biological processes such as phytoplankton growth and zooplankton grazing.

Models of the decay of a Gulf Stream warm-core ring showed that changes in available potential energy (APE) created by frictional decay can lead to modifications in azimuthal velocity that produce horizontal currents directed inward near the surface and in deeper waters, with an outward flow at mid-depths and an upward flow at the centre (e.g., Flierl and Mied, 1985; Franks et al., 1986; Fukumori, 1992). These frictionally induced modifications of the density and nutrient fields led to slow upwelling at the centre of Gulf Stream warm-core ring 82-B, which facilitated wind-induced mixing in the surface layer and led to an increase in nutrient availability at the ring centre (Nelson et al., 1989). Reminiscent of those responses to frictional decay, contours of sigma-θ and nutrients domed at the centre of Haida-2000 between 75–100 m depths, particularly in September 2000 and 2001. The density structure could have exhibited the effect of frictionally induced slow upwelling at the centre of the eddy; alternatively, it could have represented the onset of winter ventilation at the eddy centre in September, the interleaving of surrounding waters at the eddy boundaries (Simpson, 1984), or ageostrophic circulation patterns within the eddy (Martin and Richards, 2001). Although there are many differences between Gulf Stream warm core rings and Haida eddies, it is possible that some of the changes in structure of the nutrient and density fields observed during the decay of Haida-2000 were due to similar processes of decay-enhanced upwelling at the eddy centre.

The effects of frictional decay and the enhanced nutrient availability on phytoplankton growth have been modeled for Gulf Stream warm-core rings (Franks et al., 1986), and it was found that a chlorophyll maximum developed as a ring decayed. The shift in chlorophyll maximum from edge to centre between September 2000 and June 2001 may reflect a response to decay processes, although our sparse data points allow for speculation only. The high chlorophyll *a* band observed in Crawford et al. (2005) lay along the 25.4 isopycnal at the eddy centre and edges; this isopycnal outcropped in the surface waters outside the eddy, approximately 81 km from the eddy centre. Simpson (1984) noted that the water masses in frontal zones around eddies tend to be highly diffusive in nature and that in some systems, e.g., in eddies of the California Current System (CCS) and the East Australia Current (EAC; Scott, 1981), high-density waters can be entrained into the eddy along isopycnal surfaces and directed toward the centre. The band of high chlorophyll *a* may have resulted from an enrichment of phytoplankton growth in surface waters at the frontal boundary.

Martin and Richards (2001) note that ageostrophic circulation within eddies can induce large vertical velocities that could enrich surface waters with nutrient from below. Yelland and Crawford (2005) discuss several factors that contribute to the creation of ageostrophic currents within Haida eddies, including interaction with seamounts, inertial currents, and deep barotropic currents. It is likely that ageostrophic effects contributed to nutrient vertical and horizontal fluxes within Haida eddies, but we have yet to quantify these effects.

4.2.2. Overwash and surface dilution

Mackas et al. (2005) note the importance of rapid Ekman transport events where waters within a shallow mixed layer are laterally advected by strong wind shear. Tranter et al. (1982) discussed this phenomenon in eddies of the EAC and used the term "overwash" to describe the replacement of the upper layer of a ring or eddy by surrounding waters (also see Evans et al., 1985). Overwash appears to be an important process in rings during their interaction with their parent current (Evans et al., 1985), while in anticyclonic eddies that do not possess streamers (e.g., Haida Eddies, CCS and EAC eddies) lateral advection of outside surface waters is likely a more important process. Despite the occurrence of lateral advection in Haida Eddies, salinity and mixed layer nutrient concentrations above the eddy were different than in surrounding waters during the first year of the study, suggesting that waters at the eddy centre can remain isolated from surroundings for several months at a time (also see Yelland and Crawford, 2005). Periods of isolation appear to be long enough to promote differences in nutrient draw-down between eddy and non-eddy waters.

4.2.3. Eddy deformation and merging

In addition to nutrients supplied by frictionally induced changes in flow and entrainment, interactions with bathymetric features such as seamounts and vortex–vortex interactions (e.g., coalescence events) also modified nutrient distributions. Vortex–vortex interactions are well documented in mesoscale eddies. For example, in the Gulf Stream warm-core rings become absorbed by the strong Gulf Stream current (Evans et al., 1985), and in the Gulf of Mexico cyclonic vortices spin off anticyclonic eddies as they migrate westward (Forristall et al., 1992). Rapid changes in eddy structure induced by external influences can lead to major changes in APE, potential vorticity, and biological community composition in warm core rings of the Gulf Stream (Joyce et al., 1984). In the case of Haida Eddies, the interaction with seamounts did not cause a break-up of the eddy, but it may have influenced the current structure and nutrient distributions. Either the interaction with Bowie Seamount or other effects of secondary circulation within the eddy (e.g. upwelling along the edges) led to the distortion of isopycnals and corresponding nutrient distributions (Fig. 3); these influences are particularly evident in September 2000 where nutrient isopleths and isopycnals show deviations from Gaussian symmetry near the northern edge (Fig. 3B).

The coalescence of a younger eddy led to a renewal of coastal nutrient characteristics within Haida-2000. This included a depression of deep isopycnals, a 0.1 unit decrease in core salinity, stretching of the eddy shape, a temperature increase of 0.7 °C, and a decrease in deep nutrient content. Iron concentrations were two times higher in September compared to June 2001 in the upper waters of Haida-2000 (75–200 m), indicating that iron was also delivered by the merging event (Johnson et al., 2005). Such events appear to be important in restoring coastal characteristics and extending the range of coastal type waters further from the continental margin.

4.2.4. Nutrient supply

Compared to HNLC regions, the surface and core waters of Haida eddies possessed low nitrate and silicic acid concentrations, but Haida-2000 contained more iron in the core relative to outside (Johnson et al., 2005). Nutrient supply to intermediate depths could come from deep nutrients transported along isopycnals as they flatten at ca. 150–300 m. Insufficient resolution in sampling at the eddy edges precluded determinations of detailed along-isopycnal nutrient gradients that would confirm supply from deep to intermediate waters. The nutrient-salinity relationships did not change significantly, suggesting that this mechanism was not important in nutrient supply, at least with respect to the eddy core. However, if deep, iron-rich water was carried along isopycnals near the eddy bottom, it could thus be transferred to shallower depths at the eddy boundaries. Such "leakage" could be an important source of trace metals (including Fe) to the intermediate ocean (100–200 m) where they would be transported through winter ventilation to the euphotic zone.

The vertical diffusive flux of nutrients at the eddy centre was estimated by

$$\Delta D = \frac{\partial(\mathrm{NO_3^-}\ \text{or}\ \mathrm{Si(OH)_4})}{\partial z} K_v, \qquad (1)$$

where ∂nutrient/∂z is the difference in nutrient concentration over the depth spanning the mixed layer in $\mathrm{mmol\,m^{-3}}$, and K_v is the diffusivity coefficient (Denman and Gargett, 1983). Using Dillon and Caldwell's (1980; DC80) eddy diffusivity coefficient (K_v, $8.6 \times 10^{-6}\,\mathrm{m^2\,s^{-1}}$) as an approximation, diffusive supply was of the same magnitude in eddy waters and surrounding waters as those estimated at Station P ($+0.3\,\mathrm{mmol\,m^{-2}\,d^{-1}}$; Wong et al., 2002c, Table 7). We note that K_v values are likely to be different between eddy waters (higher than DC80) and surroundings (similar to DC80), but K_v estimates were not made during eddy cruises, so the DC80 coefficients were used. These values are thus conservative estimates for eddy waters. Although vertical density gradients were generally smaller both across the mixed layer and between 75 and 100 m at the eddy centre (Table 7), this could not account for increases in mixed layer nutrient concentration. Between June and September (ca. 100 d) silicic acid concentration doubled; vertical mixing contributed only between 0.1% and 0.3% of mixed layer nutrient concentration over this time period.

Other sources of nutrients to the mixed layer include lateral advection, remineralization of biogenic material within the mixed layer, and increased mixing with the onset of winter ventilation. Chierici et al. (2005) note that horizontal nutrient gradients were likely very small (maximum $0.03\,\mu\mathrm{mol\,kg^{-1}\,km^{-1}}$) and could not account for the observed changes in the carbon system. Likewise, biogenic silica concentrations within the mixed layer in June and September were much too small to double the nutrient concentration, even assuming 100% dissolution (Peterson, 2005). Adding the contributions from vertical flux, horizontal flux, and remineralization gives approximately a 5% contribution to nutrient content within the mixed layer between June and September 2000. Thus, 95% of the nutrient content within the mixed layer in September must have been supplied from a greater flux from below. We estimate that approximately 20% of the surface waters would need to be replaced by waters from below the mixed layer in order to account for the doubling of silicic acid concentration over this time period. Therefore, the most likely source of nutrient re-supply was by mixed layer deepening in

Table 7
Estimates of vertical nutrient flux ($\mathrm{mmol\,m^{-2}\,d^{-1}}$) and density gradients ($\Delta\sigma - \theta\,\mathrm{m}^{-1}$) across the mixed layer within Haida-2000 (centre) and at nearby reference sites (out) for all cruises

Cruise	Depth	$\Delta\sigma - \theta\,\mathrm{m}^{-1}$		$\mathrm{NO_3^-}$ flux ($\mathrm{mmol\,m^{-2}\,d^{-1}}$)		$\mathrm{Si(OH)_4}$ flux ($\mathrm{mmol\,m^{-2}\,d^{-1}}$)		Si:$\mathrm{NO_3^-}$ flux	
		Out	In	Out	In	Out	In	Out	In
June 2000	ML	0.017	0.015	0.19	0.21	0.13	0.37	0.7	1.8
	50–75 m	0.014	0.0045						
Sept. 2000	ML	0.056	0.032	0.25	0.29	0.19	0.29	0.8	1.0
	75–100 m	0.018	0.0080						
Feb. 2001	ML	0.021	0.014	0.37	0.29	0.64	0.44	1.7	1.5
	100–150 m	0.018	0.014						
June 2001	ML	0.0042	0.0045	0.03	0.06	0.03	0.05	1.0	0.8
	75–100 m	0.020	0.0087						
Sept. 2001	ML	0.048	0.045	0.19	0.33	0.28	0.22	1.5	0.7
	75–100 m	0.011	0.0081						

See text for calculations.

September. Although this represents the main mechanism of nutrient supply to the euphotic zone, the enhanced nutrient fluxes into the mixed layer at the eddy centre during the first year could have promoted increased phytoplankton growth when the mixed layer was shallow and nutrients were nearly depleted (also see Chierici et al., 2005).

While the fluxes into the mixed layer were not much greater than in outside waters, the supply to the 75–100 m region (top of the eddy) would be incorporated into this layer during winter ventilation and deep mixing. Higher nutrient fluxes into upper eddy waters in Year 2 represent the only way to account for higher productivity in Haida-2000 compared to surroundings since winter MLDs were similar inside the eddy and outside. In particular, Fe supplied to the euphotic zone during deep winter mixing could enhance phytoplankton productivity. The iron concentrations that would be injected into the permanent pycnocline from depths ca. 50–150 m were two times higher within Haida-2000 than in surrounding waters (Johnson et al., 2005) and at least an order of magnitude higher than HNLC waters at Ocean Station P (W.K. Johnson and N.E. Sutherland, pers. comm.). In winter 2001, the concentration of Fe was 20 times higher at 100 m inside the eddy compared to outside (Johnson et al., 2005). Thus, enrichment of upper waters within the eddy due to frictional decay and the induction of local upwelling (e.g., Fukumori, 1992; Nelson et al., 1989) could be important in enhancing winter nutrient (including Fe) supply.

5. Summary

The Haida-2000 eddy showed higher nutrient-drawdown rates compared to HNLC waters throughout its lifetime, with the most dramatic removal occurring in a single spring bloom early in eddy evolution. Seasonal patterns of phytoplankton growth, as inferred from nutrient drawdown rates, changed over the course of eddy evolution; the timing of maximum nutrient drawdown shifting from spring to summer between Year 1 and Year 2, becoming more similar to oceanic seasonal patterns observed in the Alaska Gyre (e.g., Ocean Station P).

The drawdown of silicic acid was ca. 10 times higher in the first spring compared to the second, indicating a shift from a diatom-dominated to a non-diatom dominated phytoplankton species assemblage over eddy evolution. In contrast to silicic acid, nitrate drawdown rates remained similar for both years studied. Annual and seasonal new production estimates derived from changes in surface nitrate were higher within Haida-2000 compared to long-term averages determined for the Subarctic northeast Pacific.

Haida Eddies can be viewed as models for the transformation of coastal systems into oceanic ones as iron and silicic acid become limiting, providing insight into controls on HNLC ecosystem dynamics (see Whitney et al., 2005). Haida eddies act as coastal eddies while in a coastal environment (e.g., Simpson, 1984), but as oceanic eddies in an oceanic environment in terms of structure, nutrient distribution and photosynthetic biomass (Krom et al., 1992, 1993). These eddies appear nutrient impoverished when in HNLC waters, but nutrient-rich in DIL domain waters. Because of their longevity and long distance travel, Haida Eddies are important in re-distributing nutrients in the eastern Gulf of Alaska and contribute to enhanced productivity (e.g., Crawford et al., 2005) in regions far removed from their coastal origin.

Acknowledgements

We acknowledge the captain and crew of the C.C.G.S. vessel *John P. Tully* for expert assistance in the field. W. Richardson and J. Barwell-Clarke kindly analyzed nutrient samples. M. Robert, D. Mackas and L. Miller kept sampling efforts running smoothly, and H. Maclean, D. Anderson, D. Yelland and S. Toews were of great assistance in sampling at sea. Thanks to E. Bornhold for helping to initiate this study. R. Leben of the Colorado Center for Astrodynamics Research developed and maintains the web site used to display near-real-time-satellite elevation contours. The comments from three anonymous reviewers greatly improved the manuscript. Funding from a Department of Fisheries and Oceans Strategic Grant (FAW, PJH) supported this work and fellowships from NSERC, DFO, and UBC awarded to TDP are gratefully acknowledged.

References

Anderson, G.C., Parsons, T.R., Stephens, K., 1969. Nitrate distribution in the Subarctic Northeast Pacific Ocean. Deep-Sea Research 16, 329–334.

Barwell-Clarke, J., Whitney, F., 1996. Nutrient methods and analysis. Canadian Technical Report of Hydrography and Ocean Sciences 182 (vi), 1–43.

Batten, S.D., Crawford, W.R., 2005. The influence of coastal origin eddies on oceanic plankton distributions in the eastern Gulf of Alaska. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2005.02.009].

Boyd, P.W., Harrison, P.J., 1999. Phytoplankton dynamics in the NE subarctic Pacific. Deep-Sea Research II 46, 2405–2432.

Boyd, P.W., Muggi, D.L., Varela, D.E., Goldblatt, R.H., Chretien, R., Orians, K.J., Harrison, P.J., 1996. In vitro iron enrichment experiments in the NE subarctic Pacific. Marine Ecology Progress Series 136, 179–193.

Cheney, R.E., Richardson, P.L., 1976. Observed decay of a cyclonic Gulf-Stream ring. Deep-Sea Research 23 (2), 143–155.

Chierici, M., Miller, L.A., Whitney, F.A., Johnson, W.K., Wong, C.S., 2005. Biogeochemical evolution of the carbon dioxide system in the waters of long-lived mesoscale eddies in the Northeast Pacific Ocean. Deep-Sea Research II, this issue.

Childers, A.R., Whitledge, T.E., 2005. Seasonal and interannual variability in the distribution of nutrients and chlorophyll *a* across the Alaska shelf: 1998–2000. Deep-Sea Research II, in press.

Crawford, W.R., 2002. Physical characteristics of Haida eddies. Journal of Oceanography 58, 703–713.

Crawford, W.R., 2005. Heat and fresh water transport by mesoscale eddies into the Gulf of Alaska. Deep-Sea Research II, this issue.

Crawford, W.R., Whitney, F.A., 1999. Mesoscale eddy aswirl with data in the Gulf of Alaska. Eos, Transactions, American Geophysical Union 80 (33), 365, 370.

Crawford, W.R., Cherniawsky, J.Y., Foreman, M.G.G., 2000. Multi-year meanders and eddies in the Alaskan Stream as observed by TOPEX/Poseidon altimeter. Geophysical Research Letters 27 (7), 1025–1028.

Crawford, W.R., Brickley, P.J., Peterson, T.D., Thomas, A.C., 2005. Impact of Haida Eddies on chlorophyll distribution in the eastern Gulf of Alaska. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2005.02.011].

Denman, K.L., Gargett, A.E., 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. Limnology and Oceanography 28 (5), 801–815.

Dillon, T.M., Caldwell, D.R., 1980. The Batchelor spectrum and dissipation in the upper ocean. Journal of Geophysical Research—Oceans and Atmospheres 85 (NC4), 1910–1916.

Dugdale, R.C., Goering, J.J., 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnology and Oceanography 12, 196–206.

Evans, R.H., Baker, K.S., Brown, O.B., Smith, R.C., 1985. Chronology of Warm-Core Ring 82-B. Journal of Geophysical Research-Oceans 90 (NC5), 8803–8811.

Freeland, H.J., Crawford, W.R., Thomson, R.E., 1984. Currents Along the Pacific Coast of Canada. Atmosphere-Ocean, 22 (2), 151–172.

Favorite, F., Dodimead, A.J., Nasu, K., 1976. Oceanography of the subarctic Pacific region, 1960–71. International North Pacific Fisheries Commission Bulletin 33, 187pp.

Flierl, G.R., Mied, R.P., 1985. Frictionally induced circulations and spin down of a warm-core ring. Journal of Geophysical Research 90 (C5), 8917–8927.

Forristall, G.Z., Schaudt, K.J., Cooper, C.K., 1992. Evolution and kinematics of a Loop Current eddy in the Gulf of Mexico during 1985. Journal of Geophysical Research 97 (C2), 2173–2184.

Franks, P.J.S., 1992. Sink or swim: accumulation of biomass at fronts. Marine Ecology Progress Series 82, 1–12.

Franks, P.J.S., 1997. New models for the exploration of biological processes at fronts. ICES Journal of Marine Science 54, 161–167.

Franks, P.J.S., Wroblewski, J.S., Flierl, G.R., 1986. Prediction of phytoplankton growth in response to the frictional decay of a warm-core ring. Journal of Geophysical Research 91 (C6), 7310–7603.

Fukumori, I., 1992. Meridional circulation and mixing associated with the decay of warm-core ring 82B. Deep-Sea Research 39 (Suppl. 1), S45–S65.

Gower, J.F.R., 1998. Use of SeaWIFS and AVHRR for detecting plankton blooms. Journal of the Advanced Marine Science and Technology Society 4 (2), 165–174.

Gower, J.F.R., Tabata, S., 1993. Measurement of eddy motion in the north-east Pacific using the Geosat Altimeter. In: Jones, I.S.F., Sugimori, Y., Stewart, R.W. (Eds.), Satellite Remote Sensing of the Oceanic Environment. Seibutsu Kenkyusha, Tokyo, pp. 375–382.

Hutchins, D.A., Bruland, K.W., 1998. Iron-limited diatom growth and Si:N uptake ratios in a coastal upwelling regime. Nature 393, 561–564.

Huyer, A., Kosro, P.M., Fleischbein, J., Ramp, S.R., Stanton, T., Washburn, L., Chavez, F.P., Cowles, T.J., Pierce, S.D., Smith, R.L., 1991. Currents and Water Masses of the Coastal Transition Zone Off Northern California, June to August 1988. Journal of Geophysical Research-Oceans 96 (C8), 14809–14831.

Harrison, P.J., 2002. Station Papa time series: insights into ecosystem dynamics. Journal of Oceanography 58, 259–264.

Harrison, P.J., Boyd, P.W., Varela, D.E., Takeda, S., Shiomoto, A., Odate, T., 1999. Comparison of factors controlling phytoplankton productivity in the NE and NW subarctic Pacific gyres. Progress in Oceanography 43, 205–234.

Johnson, W.K., Miller, L.A., Sutherland, N.E., Wong, C.S., 2005. Iron transport by mesoscale Haida Eddies in the Gulf of Alaska. Deep-Sea Research II, this issue.

Joyce, T.M., Backus, R., Baker, K., Blackwelder, P., Brown, O., Cowles, T., Evans, R., Fryxell, G., Mountain, D., Olson, D., Schlitz, R., Schmitt, R., Smith, P., Smith, R., Wiebe, P., 1984. Rapid evolution of a Gulf Stream warm-core ring. Nature 308, 837–840.

Karl, D.M., Letelier, R.M., Tupas, L., Dore, J., Christian, J., Hebel, D., 1997. The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. Nature 388, 533–538.

Krom, M.D., Brenner, S., Kress, N., Neori, A., Gordon, L.I., 1992. Nutrient dynamics and new production in a warm-core eddy from the Eastern Mediterranean Sea. Deep-Sea Research I 39 (3-4A), 467–480.

Krom, M.D., Brenner, S., Kress, N., Neori, A., Gordon, L.I., 1993. Nutrient distributions during an annual cycle across a warm-core eddy from the E. Mediterranean Sea. Deep-Sea Research I 40 (4), 805–825.

Lee, M-M., Williams, R.G., 2000. The role of eddies in the isopycnal transfer of nutrients and their impact on biological production. Journal of Marine Research 58, 895–917.

Levitus, S., 1982. Climatological Atlas of the World Ocean. NOAA Professional Paper 13, US Government Printing Office, Washington, DC 173pp.

Longhurst, A.R., 1998. Ecological Geography of the Sea. Academic Press, San Diego, pp. 1–398.

Longhurst, A., Sathyendranath, S., Platt, T., Caverhill, C., 1995. An estimate of global primary production in the ocean from satellite radiometer data. Journal of Plankton Research 17 (6), 1245–1271.

Mackas, D.L., Tsurumi, M., Galbraith, M.D., Yelland, D.R., 2005. Zooplankton Distribution and Dynamics in a North Pacific Eddy of Coastal Origin: II. Mechanisms of eddy colonization by and retention of offshore species. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2005.02.008].

Mackas, D.L., Yelland, D.R., 1999. Horizontal flux of nutrients and plankton across and along the British Columbia continental margin. Deep-Sea Research II 46 (11–12), 2941–2967.

Maldonado, M.T., Boyd, P.W., Harrison, P.J., Price, N.M., 1999. Co-limitation of phytoplankton growth by light and Fe during winter in the NE subarctic Pacific Ocean. Deep-Sea Research II 46 (11–12), 2475–2485.

Martin, J.H., Fitzwater, S.E., 1988. Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. Nature 331, 341–343.

Martin, A.P., Richards, K.J., 2001. Mechanisms for vertical nutrient transport within a North Atlantic mesoscale eddy. Deep-Sea Research II 48, 757–773.

McGillicuddy, D.J., Robinson, A.R., 1997. Eddy-induced nutrient supply and new production in the Sargasso Sea. Deep-Sea Research I 44 (8), 1427–1450.

McGillicuddy, D.J., Robinson, A.R., Siegel, D.A., Jannasch, H.W., Johnson, R., Dickey, T.D., McNeil, J., Michaels, A.F., Knap, A.H., 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. Nature 394, 263–266.

Melsom, A., Meyers, S.D., Hurlburt, H.E., Metzger, J.E., O'Brien, J.J., 1999. ENSO effects on Gulf of Alaska eddies. Earth Interactions 3 (http://EarthInteractions.org).

Meyers, S.D., Basu, S., 1999. Eddies in the eastern Gulf of Alaska from TOPEX/POSEIDON altimetry. Journal of Geophysical Research 104 (C6), 13333–13343.

Miller, L.A., Robert, M., Crawford, W.R., 2005. Preface: the large, westward-propagating Haida Eddies of the Pacific eastern boundary. Deep-Sea Research II, in press.

Mysak, L.A., 1985. On the interannual variability of eddies in the northeast Pacific Ocean. In: Wooster, W.S., Fluharty, D.L. (Eds.), El Niño North: Niño Effects in the Eastern Subarctic Pacific Ocean. Washington Sea Grant Program, Seattle, pp. 97–106.

Nelson, D.M., McCarthy, J.J., Joyce, T.M., Ducklow, H.W., 1989. Enhanced near-surface nutrient availability and new production resulting from the frictional decay of a Gulf Stream warm-core ring. Deep-Sea Research 36 (5), 705–714.

Nishioka, J., Takeda, S., Wong, C.S., Johnson, W.K., 2001. Size-fractionated iron concentrations in the northeast Pacific Ocean: distribution of soluble and small colloidal iron. Marine Chemistry 74 (2–3), 157–179.

Nof, D., 1981. On the β-induced movement of isolated baroclinic eddies. Journal of Physical Oceanography 11, 1662–1672.

Okkonen, S.R., Weingartner, T.J., Danielson, S.L., Musgrave, D.L., Schmidt, G.M., 2003. Satellite and hydrographic observations of eddy-induced shelf-slope exchange in the northwestern Gulf of Alaska. Journal of Geophysical Research 108 (C2), 3033.

Olson, D.B., Schmitt, R.W., Kennelly, M., Joyce, T.M., 1985. A two-layer diagnostic model of the long-term physical evolution of warm-core ring 82B. Journal of Geophysical Research 90 (C5), 8813–8822.

Peterson, T.D., 2005. Studies on the biological oceanography of Haida eddies. Ph.D. Thesis, University of British Columbia, Vancouver, B.C.

Platt, T., Harrison, W.G., Lewis, M.R., Li, W.K.W., Sathyendranath, S., Smith, R.E., Vezina, A.F., 1989. Biological production of the oceans—the case for a consensus. Marine Ecology—Progress Series 52 (1), 77–88.

Scott, B.D., 1981. Hydrological structure and phytoplankton distribution in the region of a warm-core eddy in the Tasman Sea. Australian Journal of Marine and Freshwater Research 32, 479–492.

Siegel, D.A., McGillicuddy, D.J., Fields, E.A., 1999. Mesoscale eddies, satellite altimetry, and new production in the Sargasso Sea. Journal of Geophysical Research 104 (C6), 13359–13379.

Simpson, J.J., 1984. An offshore eddy in the California Current system Part III: chemical structure. Progress in Oceanography 13, 71–93.

Takeda, S., 1998. Influence of iron availability on nutrient consumption ratio of diatoms in oceanic waters. Nature 393, 774–777.
Tabata, S., 1982. The Anticyclonic, Baroclinic Eddy off Sitka, Alaska, in the Northeast Pacific Ocean. Journal of Physical Oceanography 12, 1260–1282.
Tranter, D.J., Leech, G.S., Vaudrey, D.J., 1982. Biological significance of surface flooding in warm-core ocean eddies. Nature 297, 572–574.
Tully, J.P., Dodimead, A.J., Tabata, S., 1960. An anomalous increase of temperature in the ocean off the Pacific coast of Canada through 1957 and 1958. Journal of the Fisheries Research Board of Canada 17 (1), 61–80.
Varela, D.E., Harrison, P.J., 1999. Seasonal variability in nitrogenous nutrition of phytoplankton assemblages in the northeastern subarctic Pacific Ocean. Deep-Sea Research II 46 (11–12), 2505–2538.
Wheeler, P.A., 1993. New production in the subarctic Pacific Ocean: net changes in nitrate concentrations, rates of nitrate assimilation and accumulation of particulate nitrogen. Progress in Oceanography 32, 137–161.
Whitney, F.A., Freeland, H.J., 1999. Variability in upper-ocean water properties in the NE Pacific Ocean. Deep-Sea Research II 46 (11–12), 2351–2370.
Whitney, F., Robert, M., 2002. Structure of Haida eddies and their transport of nutrient from coastal margins into the NE Pacific Ocean. Journal of Oceanography 58, 715–723.
Whitney, F.A., Wong, C.S., Boyd, P.W., 1998. Interannual variability in nitrate supply to surface waters of the Northeast Pacific Ocean. Marine Ecology Progress Series 170, 15–23.
Whitney, F.A., Crawford, D.W., Yoshimura, T., 2005. The uptake and export of silicon and nitrogen in HNLC waters of the NE Pacific. Deep-Sea Research II, this issue.
Wong, C.S., Waser, N.A.D., Nojiri, Y., Johnson, W.K., Whitney, F.A., Page, J.S.C., Zeng, J., 2002a. Seasonal and interannual variability in the distribution of surface nutrients and dissolved inorganic carbon in the Northern North Pacific: influence of El Niño. Journal of Oceanography 58, 227–243.
Wong, C.S., Waser, N.A.D., Nojiri, Y., Whitney, F.A., Page, J.S., Zeng, J., 2002b. Seasonal cycles of nutrients and dissolved inorganic carbon at high and mid latitudes in the North Pacific Ocean during the *Skaugran* cruises: determination of new production and nutrient uptake ratios. Deep-Sea Research II 49 (24–25), 5317–5338.
Wong, C.S., Waser, N.A.D., Whitney, F.A., Johnson, W.K., Page, J.S., 2002c. Time-series study of the biogeochemistry of the North East subarctic Pacific: reconciliation of the Corg/N remineralization and uptake ratios with the Redfield ratios. Deep-Sea Research II 49 (24–25), 5717–5738.
Yelland, D.R., Crawford, W.R., 2005. Currents in Haida eddies. Deep-Sea Research II, this issue.