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Horizontal internal-tide fluxes support elevated phytoplankton productivity over the inner continental shelf

Andrew J. Lucas¹, Peter J. S. Franks¹, and Christopher L. Dupont^{1,2}**Abstract**

The narrow continental shelf of the Southern California Bight (SCB) is characterized by elevated primary productivity relative to the adjacent open ocean. This persistent gradient is maintained by the nitrate fluxes associated with internal waves of tidal frequency (the internal tide). Here we provide the first estimates of the internal-tide-driven horizontal fluxes of nitrate, heat, energy, and salinity, calculated from high-resolution, full water-column data gathered by an autonomous wave-powered profiler and a bottom-mounted current meter. The vertically integrated nitrate, heat, and energy fluxes were onshore over the 3-week period of the field experiment. The inner-shelf area- and time-averaged dissipation rate due to the onshore horizontal energy flux, $2.25 \times 10^{-7} \text{ W kg}^{-1}$, was elevated relative to open ocean values. The magnitude of the vertically integrated horizontal nitrate flux ($136.4 \text{ g N m}^{-1} \text{ d}^{-1}$) was similar to phytoplanktonic nitrate uptake rates over the inner-shelf. This nitrate flux was variable in time, capable of supporting $0\text{--}2800 \text{ mg C m}^{-2} \text{ d}^{-1}$ (mean approx. $774 \text{ mg C m}^{-2} \text{ d}^{-1}$) of “new” primary productivity, depending on the energetics of the internal tide and the cross-shore distribution of nitrate. We postulate that the horizontal, internal-tide-driven nitrate flux is the primary cause of the persistently elevated phytoplankton biomass and productivity over the narrow SCB inner shelf. Furthermore, these results suggest that horizontal fluxes of nutrients driven by internal waves may contribute significantly to primary productivity along the boundaries of aquatic environments.

Keywords: internal waves, mixing, new productivity, nitrate flux, nutrient dynamics, Reynolds fluxes

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Introduction

[1] In nutrient-limited oceanic environments, the rate of nutrient supply to the euphotic zone—typically mediated by physical dynamics—controls the rate of phytoplankton productivity and the character of the phytoplankton community and, at steady-state, sets the proportion of that productivity which can be exported to higher trophic levels and out of

the euphotic zone (“new” productivity, sensu Dugdale and Goering 1967). Quantifying the physical supply of nutrients to the sunlit surface ocean is therefore of fundamental importance in understanding oceanic ecosystem function.

[2] The elevated primary productivity of the coast ocean relative to adjacent offshore waters is due to the operation of physical dynamics that act to inject nutrients into the

euphotic zone (Behrenfeld and Falkowski 1997; Behrenfeld et al. 2006). In areas where continental runoff or wind-forced upwelling is absent, nutrient supply is typically controlled by mixing processes. Although horizontal mixing length scales in the ocean are typically many orders of magnitude larger than vertical mixing length scales (Gregg 1987), vertical nutrient gradients are large and often coincident with the base of the euphotic zone, so it is regularly assumed that the vertical component is the dominant and biologically relevant flux pathway for nutrients. More completely, of course, both horizontal and vertical components must be considered to quantify the total mixing-driven nutrient flux into a control volume of interest.

[3] The internal tide (defined here as internal waves of M_2 frequency) has been shown to contribute to the nitrate budget of the euphotic zone in a number of oceanographic settings (Holligan et al. 1985; Sharples et al. 2001; Leichter et al. 2003). Without exception, nitrate flux in these studies is quantified as a vertical process resulting from mixing driven by energy derived from the internal tide. Although the manner of estimating the available mixing energy differs among studies (microstructure surveys, the convergence of energy flux, and shear and strain measurement, among others), such estimates always rely on the parameterization of small-scale turbulent phenomena working on a vertical gradient in nitrate distribution.

[4] Given the appropriate temporal and vertical resolution, profiles of water-column velocity and the vertical distribution of density, temperature, salinity, and nutrients can be used to directly calculate horizontal fluxes of internal-wave energy (Kunze et al. 2002; Nash et al. 2005; Moum et al. 2007) and scalar quantities (see below), particularly for a phenomenon such as the internal tide, which has a narrow bandwidth and a timescale on the order of hours. This direct flux estimation avoids some of the complications inherent in the parameterization of mixing and the logistical challenges of directly measuring the dissipation of turbulent kinetic energy (Nash et al. 2005). In particular, this approach is useful over the inner portion of the continental shelf, which, in a time-averaged, vertically integrated sense, is entirely dependent on cross-shore exchange with the adjacent outer shelf.

Elevated Phytoplankton Primary Productivity over the Inner Shelf of the Southern California Bight

[5] The continental shelf of the southern portion of the Southern California Bight (SCB) underlies a nitrate-limited ecosystem that is characterized by elevated phytoplankton biomass and total and nitrate-fueled (new) primary productivity relative to waters of the outer continental shelf and farther offshore (Eppeley et al. 1979; Eppeley 1992; Lucas et al. 2011). The inner-shelf phytoplankton community assemblage is dominated by phytoplankton adapted to rapid inputs of nitrate, including diatoms and coastal ecotypes of cyanobacteria (*Synechococcus* spp.) and picoeukaryotes (*Ostreococcus* spp.; Lucas et al. 2011). Horizontal gradients in density, nitrate concentrations, phytoplankton biomass, and phytoplankton productivity are much stronger in the cross-shore direction than in the along-shore direction (Eppeley et al. 1978; Hickey et al. 2003; Lucas et al. 2011).

[6] In the SCB, wind-forced upwelling is generally weak (Winant and Olson 1976; Winant and Dorman 1997; Pringle and Riser 2003), and energetic internal waves dominate water-column density structure and currents during much of the year (Winant 1974; Lerczak 2000; Lerczak et al. 2003). Of the broad range of frequencies present, the internal tide is by far the most energetic and has been implicated in the nutrient budget in the SCB for decades (Cooper 1947; Armstrong and LaFond 1966; Cullen et al. 1983). The SCB internal tide is characterized by predominantly mode-1 cross-shore currents and weaker surface-enhanced alongshore currents, and it appears to propagate onto and across the continental shelf (Lerczak et al. 2003). The up-shelf transport of subthermocline waters brings high nitrate concentrations inshore to depths <5 m (see below; J. McGowan, pers. comm.). This process was described by Winant (1974) as an “internal surge,” in an analogy to surf-zone dynamics. Implicit in this analogy are strongly nonlinear dynamics and elevated rates of mixing, processes that lead to fluxes of momentum, heat, and nutrients over the inner shelf.

Internal Tide Fluxes to the Inner Shelf

[7] We begin by showing analytically that the horizontal component of nitrate flux dominates the nitrate budget

over the inner shelf. We consider a two-dimensional (x, z) wedge-shaped domain with a constant bottom slope ($\alpha = 0.01$). The origin of the domain is at the shoreline, with x and cross-shore velocity u positive onshore, and z and vertical velocity w positive upwards (Fig. 1). The depth D of the wedge is a linear function of offshore distance, $D(x) = \alpha x$. This domain is an idealized form of the SCB inner shelf. We can write the two-dimensional conservation of a scalar quantity such as nitrate within the inner-shelf wedge as

$$\frac{\partial N}{\partial t} + \nabla \cdot (\bar{\mathbf{u}}\bar{N}) = -\nabla \cdot \langle \mathbf{u}'N' \rangle + q_+ - q_-, \quad (1)$$

where N is the concentration of nitrate (or any scalar quantity), $\mathbf{u}$ is a velocity vector, and q_+ and q_- are sources and sinks of nitrate. Velocity and nitrate concentration can be separated into mean (overbar) and perturbation (prime) quantities via Reynolds decomposition ($\mathbf{u} = \bar{\mathbf{u}} - \mathbf{u}'$, $N = \bar{N} - N'$). The product of the mean quantities is the advective flux, whereas the average of the product of the perturbation quantities is the diffusive flux. Bracket averaging ($\langle \rangle$) is performed over

many integral periods of the frequency of interest (e.g., multiple M_2 periods for calculations of internal-tide fluxes).

[8] We assert that velocity and therefore flux is zero at the bottom boundary ($w'N' = 0$ at $z = \alpha x$ and $u'N' = 0$ at $x = 0$) and that there is no flux of scalar quantities through the water surface (i.e., $w'N' = 0$ at $z = 0$), and we assume that nitrification within the domain (q_+) is negligible. We proceed by integrating equation (1) in the vertical and cross-shore directions:

$$\frac{\partial \mathbf{N}}{\partial t} + \mathbf{Q}_- = - \int_E^0 \int_{\alpha x}^0 \left[\frac{\partial}{\partial x} \langle u'N' \rangle + \frac{\partial}{\partial z} \langle w'N' \rangle + \frac{\partial}{\partial x} (\bar{u}\bar{N}) + \frac{\partial}{\partial z} (\bar{w}\bar{N}) \right] dz dx, \quad (2)$$

where bold, uppercase letters indicate rates integrated over the domain, E is the position of the offshore edge of the domain, and we have written the equation in component form. The no-flux boundary conditions require that the vertically integrated vertical fluxes

Fig. 1 (A) Merged MODIS and SeaWiFS 5-day composite image of chlorophyll *a* in Southern California Bight (SCB) for 14 August to 18 August 2006. The southern portion of the SCB region extends south from the Palos Verdes peninsula to the upwelling system south of the United States–Mexico border. Chlorophyll concentrations are elevated in a narrow band over the continental shelf. This image is typical of chlorophyll *a* images in the region during stratified summer months (see Eppley 1992 for similar images) and exemplifies the weak alongshore gradients found in biological and physical properties in the southern SCB. (B and C) ISPX study area. The upper panel (B) shows the locations of the bottom-mounted ADCPs and WW profiler. The lower panel (C) shows the inner-shelf domain as described in the text.

must be zero

$$\left(\int_{\alpha x}^0 \frac{\partial}{\partial z} \langle w'N' \rangle dz = 0, \int_{\alpha x}^0 \frac{\partial}{\partial z} (\bar{w}\bar{N}) dz = 0 \right)$$

and that the horizontally integrated horizontal flux must be equal to the horizontal fluxes through the offshore edge of the domain:

$$\begin{aligned} & - \int_E^0 \left[\frac{\partial}{\partial x} \langle u'N' \rangle + \frac{\partial}{\partial x} (\bar{u}\bar{N}) \right] \partial x \\ & = \langle u'N' \rangle|_{x=E} + (\bar{u}\bar{N})|_{x=E} \end{aligned} \quad (3)$$

Therefore, the change in nitrate concentration over time plus the sinks of nitrate concentration (i.e., phytoplankton uptake) integrated over the inner-shelf wedge is simply equal to the vertically integrated diffusive and advective horizontal fluxes through the outer edge of the domain, where H is the depth of the outer edge of the domain ($x = E$):

$$\frac{\partial N}{\partial t} + Q_- = \int_{-H}^0 \langle u'N' \rangle|_{x=E} \partial z + \int_{-H}^0 (\bar{u}\bar{N})|_{x=E} \partial z \quad (4)$$

[9] Calculation of the internal-tide contribution to the cross-shore diffusive flux into the inner shelf (e.g., in the case of nitrate, $\langle u'N' \rangle_{M_2}$) is the primary focus of this study. A full analysis of the advective fluxes to the inner shelf of the SCB is outside the scope of this article. However, subtidal alongshore and cross-shore transports were weak during the experiment period considered here (Lucas et al. 2011). More broadly, alongshore gradients are generally weak in the southern portion of the SCB given the large-scale spatial coherence of sea surface temperature (Hickey et al. 2003) and alongshore currents (Winant 1983), and cross-shore transport associated with wind-forced upwelling is generally weak or absent during much of the year in the SCB, as discussed above. Therefore, on the timescale of a small number of tidal periods, the internal tide is likely to be the dominant source of inner-shelf variability (Lerczak et al. 2003).

Methods

The Inner Shelf Productivity Experiment

[10] The Inner Shelf Productivity Experiment (ISPX: 1 August 2006 and 24 August 2006 off Mission Beach, CA) comprised three interrelated field and laboratory approaches: a 24-day mooring deployment of bottom-mounted acoustic Doppler current profilers (ADCP) and an autonomous, wave-driven Wirewalker profiler (WW) equipped with a conductivity, temperature, and depth sensor (CTD) and chlorophyll *a* fluorometer; transects across the continental shelf and slope to acquire profiles with a live-wired CTD, fluorometer, and in situ ultraviolet spectrophotometric nitrate sensor (ISUS version 2) and to collect water at the surface and chlorophyll maximum; and laboratory studies, including radioisotope-labeled (^{14}C) primary productivity measurements, stable-isotope (^{15}N) nitrogen uptake experiments, and nutrient, chlorophyll, and phytoplankton community composition measurements. Experimental details of the laboratory studies can be found in Lucas (2009) and Lucas et al. (2011).

WW and ADCP Moorings

[11] The ISPX mooring array was designed to provide detailed cross-shore and vertical resolution of currents and density structure over the inner shelf. The WW wave-powered autonomous profiler, developed at Scripps Institution of Oceanography (SIO) by R. Pinkel, uses the surface wave field to power vertical profiling (Rainville and Pinkel 2001). We deployed a WW at 22 m, in association with a 600-kHz ADCP (Fig. 1B). Horizontal currents at the ADCP were rotated clockwise 7° according to local bathymetry to obtain along-shore (positive $\sim$ northward) and cross-shore (positive onshore) components.

[12] The WW sampled the upper 19.5 m of the water column (relative to the surface). The 3-week WW deployment included two scheduled turnaround periods. There were several unplanned gaps in the data that were short relative to the semidiurnal timescale and so were interpolated using a linear, low-pass interpolation scheme. The scheduled turnarounds took approximately 8 h and remain in the final time series

from the profiler, separating the WW time series data into three periods (periods I, II, III; 6.2 d, 5.4 d, and 6.2 d, respectively).

[13] The WW was suspended from a buoy and always sampled a fixed depth range relative to the surface, one that was required to be less than the depth range at the mooring at the lowest tide during the deployment. The bottom-mounted ADCP sampled in 1-m depth intervals relative to the bottom (height above bottom, m). In order to provide collocated observations, the WW profiles were shifted from a free-surface frame of reference to a height-above-bottom frame of reference by utilizing the ADCP pressure sensor to “de-tide” the WW profiles. Finally, by interpolating from the deepest WW sampling point of each profile to an ADCP-mounted conductivity-temperature sensor, we produced complete depth profiles of temperature, salinity, and density with the same time and depth intervals as the ADCP data.

[14] The estimates of horizontal fluxes due to the internal tide require forming averages over integral tidal ($M_2 = 12.42$ h) periods. Therefore, ADCP and WW data were interpolated onto a 9.936-min grid (75 time steps per M_2 period). This interval was chosen to assure ≥ 1 WW profile per time step. The final resolution of the gridded data was 1 m vertically by 9.936 min in time, determined by the sampling resolution of the ADCP and profile rate of the WW, respectively.

Estimating Nitrate Concentration from Temperature

[15] Nitrate and temperature are closely correlated in the SCB (Eppley 1992; McPhee-Shaw et al. 2007; Todd et al. 2009; Fig. 2). Measureable nitrate is almost never observed in waters $> 14.5^\circ\text{C}$ (Eppley et al. 1979); nitrate increases linearly with decreasing temperature below 14.5°C . We computed a linear fit between nitrate and temperature as determined by the ISUS-CTD package, incorporating data from all stations occupied over the shelf during the experiment ($n = 56$ stations, Fig. 2A). Nitrate was nearly undetectable in bottle samples ($< 0.1 \mu\text{mol L}^{-1}$) at any temperature above 14.5°C and was well below the ISUS detection limit at those

Fig. 2 Nitrate–temperature relationship based on profiles collected during ISPX (A) and 43 years of CalCOFI bottle samples from Line 93 (B). Stars in (A) represent nitrate determined from bottle samples plotted against temperature determined from the CTD at the depth the bottle sample was taken during ISPX. Nitrate concentrations are at or below the detection limit of the ISUS (approx. $1 \mu\text{mol L}^{-1}$) above 14.5°C . Linear fits of nitrate to temperature below 14.5°C account for 95% of variance in both the ISPX and CalCOFI time series. Both the short-term (A) and long-term (B) records demonstrate the utility of temperature as a proxy for nitrate in the SCB.

temperatures, so nitrate was fit as

$$\begin{aligned} T > 14.5^\circ\text{C}, & \quad [\text{NO}_3^-] = 0, \\ T < 14.5^\circ\text{C}, & \quad [\text{NO}_3^-] = aT - b, \end{aligned} \quad (5)$$

where $a = -4.84 \pm 0.04 \mu\text{mol L}^{-1}^\circ\text{C}^{-1}$ and $b = 68.6 \pm 0.5 \mu\text{mol L}^{-1}$ (mean $\pm$ standard error, $n = 6030$,

$r^2 = 0.95$, $p < 0.01$; Fig. 2). The nitrate–temperature fit calculated from 40 years of California Cooperative Fisheries Investigation (CalCOFI) data in the study area (where $a = -5.09 \pm 0.07 \mu\text{mol L}^{-1} \text{ } ^\circ\text{C}^{-1}$ and $b = 72.3 \pm 0.8 \mu\text{mol L}^{-1}$, $n = 3126$, $r^2 = 0.88$, $p < 0.01$; Fig. 2B) is nearly equivalent to the fit calculated above, demonstrating the stability of the nitrate–temperature relationship in the SCB. Given the stability of the relationship, we use the ISPX fit to generate nitrate concentrations from the full-profile WW temperature data. These proxy nitrate concentrations are used in the flux calculations that follow. We address in the discussion section the potential complications of utilizing a nitrate–temperature fit in the flux calculations.

Salinity Processing

[16] Vertical salinity gradients were weak during ISPX, but temperature gradients could exceed $0.5 \text{ } ^\circ\text{C m}^{-1}$, causing significant salinity spiking. We employed a modified version of the method of Ferrari and Rudnick (2000) to reduce salinity spiking by estimating a frequency-dependent phase correction for temperature from the cross-spectrum of conductivity and temperature. Corrected temperature, observed conductivity, and pressure were then used to generate despiked salinity data, which was then passed through a boxcar filter with a 10-s window width. Finally, density was calculated from corrected salinity, corrected temperature, and pressure.

Time Series Analyses

[17] Variance-preserving power spectral density (PSD) estimates were calculated from cross-shore velocities from the 22-m ADCP and isotherm displacements (ξ) from the WW. Velocities and displacement were broken into overlapping 3-day segments and passed through a Hamming window. The final PSD estimates had 12 degrees of freedom.

[18] Time-domain empirical orthogonal function (EOF) analysis was used to examine the vertical structure and temporal behavior of the first mode of variability in the cross-shore current data. Lucas (2009) showed that the first mode of this EOF decomposition was effective at extracting the internal-tide signal from other modes of variability in the velocity time series.

Reynolds Fluxes of Energy, Heat, Salinity, and Nitrate

[19] In order to calculate the internal tide contribution to the energy, heat, nitrate, and salinity budgets over the inner shelf, we separate the instantaneous measurements of density, temperature, salinity, and nitrate into mean and fluctuating components:

$$\begin{aligned}\rho'(z, t) &= \rho(z, t) - \bar{\rho}(z), \\ T'(z, t) &= T(z, t) - \bar{T}(z), \\ S'(z, t) &= S(z, t) - \bar{S}(z), \\ N'(z, t) &= N(z, t) - \bar{N}(z),\end{aligned}\quad (6)$$

[20] The mean vertical profiles represent the water column in the absence of internal waves, which requires that the averages be formed over many internal-wave periods. The contribution of slowly evolving water-column variability acts to define these mean quantities (Nash et al. 2005). In the case of our data, subtidal changes to the water column were apparent throughout the 3-week deployment, and the overbar quantities were therefore calculated as a running mean over 6 M_2 periods, which ensured that the contribution of low-frequency variability to the perturbation quantities was minimized (see Nash et al. 2005 for a discussion of the contribution of mesoscale variability to internal-wave energy-flux calculations).

[21] The linear component of the internal-tide cross-shore energy flux ($J_e = \langle u'p' \rangle_{M_2}$) was calculated following Nash et al. (2005). We assume that the internal tide was hydrostatic, as the average buoyancy frequency during the experiment, $6.8 \times 10^{-3} \text{ s}^{-1}$, was two orders of magnitude higher than the M_2 frequency. Pressure perturbation was therefore estimated by vertically integrating the density perturbation profile:

$$p'(z, t) = p_{\text{surf}}(t) + \int_{-H}^0 \rho'(\hat{z}, t) g d\hat{z}, \quad (7)$$

where the integration is over the dummy variable $\hat{z}$. The surface pressure $p_{\text{surf}}(t)$ was calculated by requiring that the pressure perturbation be baroclinic (i.e., $\langle p'(z, t) \rangle_H = 0$; Kunze et al. 2002; Nash et al. 2005; Moum et al. 2007).

[22] Similarly, the velocity perturbation was calculated as

$$u'(z, t) = u(z, t) - \bar{u}(z) + u_o(t), \quad (8)$$

where $\bar{u}(z)$ was the time-mean vertical profile of velocity, and the time-dependent surface velocity $u_o(t)$ was calculated by requiring that the depth-averaged velocity perturbation be zero (i.e., $\langle u'(z, t) \rangle_H = 0$).

[23] Semidiurnal variability in cross-shore velocity (u'), pressure (p'), temperature (T'), salinity (S'), and nitrate concentration (N') perturbations were extracted using a band-pass filter between frequencies of $1/11 \text{ cycles h}^{-1}$ and $1/14.5 \text{ cycles h}^{-1}$ (Lerczak et al. 2003). Least squares harmonic analysis (e.g., Nash et al. 2005) is not appropriate for extracting the baroclinic tidal variability in the SCB, as previous studies have shown that the phase of the baroclinic tide is not constant (Winant and Bratkovich 1981; Lerczak et al. 2003).

[24] Heat flux (J_q), salinity flux (J_s), and nitrate flux (J_N) were calculated as

$$\begin{aligned} J_q &= \rho_0 C_p \langle u' T' \rangle_{M_2} \quad (\text{W m}^{-2}), \\ J_s &= \rho_0 \langle u' S' \rangle_{M_2} \quad (\text{kg m}^{-2} \text{ s}^{-1}), \\ J_N &= \langle u' N' \rangle_{M_2} \quad (\text{mol m}^{-2} \text{ s}^{-1}), \end{aligned} \quad (9)$$

where C_p is the specific heat capacity of seawater ($3860 \text{ J kg}^{-1} \text{ }^\circ\text{C}^{-1}$), ρ_0 is the mean density over the course of the experiment (1024 kg m^{-3}), and bracket averaging is carried out over integral M_2 periods. In all cases, positive fluxes are onshore, whereas negative fluxes are offshore.

[25] Finally, the horizontal flux estimates were converted to area-averaged quantities over the inner shelf for comparison with laboratory results and previous studies (where the area of domain inshore of the WW-ADCP mooring is $1 \times 10^5 \text{ m}^2$).

Significance Estimates

[26] We used a Monte Carlo approach to calculate probability density functions (pdf) from synthetic data with the same amplitude as the perturbation measurements but with randomized phases. Phase was randomized

within each period by shuffling the observations individually, resulting in observation-by-observation randomization. This has the effect of removing the autocorrelation in the data and removing the phase relationship between the perturbation quantities. The synthetic pdfs, derived from the product of the phase-randomized perturbation quantities (1000 realizations per depth bin), were averaged and then used to create 95% significance intervals around zero. That is, those flux values that fell outside the bounds calculated from the pdfs are significantly different from zero at $p < 0.05$. This approach provides a null hypothesis that represents the magnitude of fluxes that would be

Fig. 3 Variance-preserving power spectral density estimates of near-surface and near-bottom cross-shore velocity (A) and isotherm displacement ξ (B), from periods of 3 days to 10 min at the 22-m ADCP and WW. Inertial (f) and M_2 frequencies are shown as vertical dashed lines. The variability in velocity in all panels is most energetic at the semidiurnal frequency and is narrow-band, permitting effective separation of the internal-tide signal from other frequency bands.

produced exclusively from random covariation between the perturbation quantities.

Results

The Semidiurnal Internal Tide

[27] Semidiurnal variability, centered on the M_2 frequency, dominated the current and isotherm displacements over the course of the experiment (Fig. 3A, B). Semidiurnal-band cross-shore currents exceeded 0.25 m s^{-1} near the surface and bottom during energetic internal tides. Mid-water-column isotherm displacements were $> 15 \text{ m}$ for much of the deployment.

[28] The internal tide was predominantly mode 1 (Fig. 4): EOF analysis of the cross-shore velocity field indicated that 60% of the variance in the time series was in the first mode (Fig. 4C). Variability in the mode-1 temporal amplitude was centered on the M_2 frequency

(Fig. 4A, D). The amplitude of current fluctuations due to the internal tide was variable in time, peaking during period II, with weaker fluctuations during the beginning and end of the experimental period (Fig. 4A).

Cross-Shelf Internal-Tide–Driven Fluxes

[29] The observed water-column properties and perturbation quantities reflect the variability in the strength of the internal tide over the length of the deployment, as well as the changes in water-column structure, salinity, chlorophyll concentration, and nitrate availability (Figs. 5 and 6). The instantaneous fluxes showed that changes in water-column structure and the strength of the internal tide impacted the magnitude of the energy, heat, salinity, and nitrate fluxes and their vertical structure (Fig. 7). Instantaneous fluxes of all quantities were strongest during period II (Fig. 7), corresponding with

Fig. 4 Empirical orthogonal function (EOF) decomposition of the cross-shore velocity at the 22-m ADCP (A). The first vertical mode (B) captures $> 60\%$ of the variance (C) in the unfiltered velocities. (D) The temporal amplitude of the first mode is dominated by variability at the M_2 frequency. This representation demonstrates the mode-1 nature of the internal tide and shows the variability in the strength of the internal tide during the experimental period, peaking around 12 August (during period II).

Fig. 5 (A) Cross-shore velocity (u) from the 22-m ADCP, (B) density (σ_t), (C) temperature (T), (D) salinity, (E) nitrate calculated from temperature according to the fit presented in Fig. 2, and (F) chlorophyll a concentration over the course of the ISPX. Data are binned into 1-m by 9.936-min bins and are referenced to height above bottom (m) as described in the text. The importance of the internal tide is apparent in the semidiurnal variability in all quantities. In addition to the internal-tide-driven variability, there are low-frequency changes to the water column over the 3-week experiment period. Warm, salty, and nitrate-poor waters gave way to cooler, less saline waters with measurable nitrate by the second half of the first period, whereas chlorophyll concentrations increased accordingly.

Fig. 6 Perturbation fields of (A) cross-shore velocity, (B) pressure, (C) heat content, (D) salinity, and (E) nitrate from the 22-m ADCP and WW moorings, band-passed around the semidiurnal frequency ($1/11$ to $1/13.5$ cycles h^{-1}). Cross-shore velocity (u') and pressure (p') perturbations are dominated by the mode-1 vertical structure of the internal tide. The strength of the semidiurnal variability is at a maximum during period II in all of the perturbation quantities.

Fig. 7 The instantaneous fluxes of (A) energy, (B) heat, (C) salinity, and (D) nitrate. These values are shown for heuristic purposes and to demonstrate the nature of the phase relationship between the velocity perturbation and scalar quantities; meaningful estimates of the net fluxes require averaging over integral tidal periods. Mid-water-column semidiurnal variability in temperature, salinity, density, and nitrate concentration leads near-bottom semidiurnal variability in cross-shore velocity by approx. 90° , as shown in previous studies (Lerczak et al. 2003), giving the instantaneous fluxes variability at $2 \times M_2$ periods.

the maximum semidiurnal band currents (Fig. 4), strongest stratification (Fig. 5), and largest isotherm displacements (Fig. 5).

Energy Flux (J_e)

[30] The semidiurnal internal-tide energy flux was onshore over the entire course of the experiment. The

vertically integrated, deployment-mean net energy flux was 2.31 W m^{-1} , implying a time- and area-averaged dissipation rate of $2.25 \times 10^{-7} \text{ W kg}^{-1}$ over the inner shelf (Table 1). The vertical structure of J_e was surface- and bottom-intensified (Fig. 8A–C) during all periods. Vertically integrated, single tidal-period averages of J_e were variable over approximately an order of magni-

Table 1 Cross-shelf internal-tide energy (J_e), heat (J_q), salinity (J_s), and nitrate (J_N) fluxes. Deployment mean was calculated over 38 M_2 periods. Period I: 3–9 August 2006, 12 M_2 periods. Period II: 10–15 August 2006, 10 M_2 periods. Period III: 16–23 August 2006, 12 M_2 periods. All mean values are reported $\pm$ standard error.

	$\int_z J_e dz$ ($W m^{-1}$)	$\epsilon_{IS} \times 10^{-7}$ ($W kg^{-1}$) ^a	$\int_z J_q dz$ ($kW m^{-1}$)	Daily ΔT_{IS} ($^{\circ}C d^{-1}$) ^b	$\int_z J_s dz$ ($kg m^{-2} s^{-1}$)	Daily $\Delta S_{IS} \times 10^{-5}$ (d^{-1}) ^c	$\int_z J_N dz$ ($g N m^{-1} d^{-1}$)	P_{NEW} ($mg C m^{-2} d^{-1}$) deployment ^d
Mean	2.3 ± 0.4	2.3 ± 0.4	124 ± 32.3	0.28 ± 0.07	0.85 ± 0.2	8.7 ± 2.0	136.4 ± 22.6	774.8 ± 128.5
I	1.4 ± 0.3	1.3 ± 0.3	82.2 ± 43.3	0.18 ± 0.09	1.0 ± 0.5	3.7 ± 1.7	92.8 ± 41.0	526.9 ± 232.9
II	4.5 ± 0.8	4.5 ± 0.8	176.8 ± 88.4	0.39 ± 0.2	0.43 ± 0.31	1.3 ± 0.9	209.0 ± 46.1	1186.9 ± 261.8
III	1.1 ± 0.2	1.1 ± 0.2	128.0 ± 36.1	0.27 ± 0.07	1.1 ± 0.2	3.9 ± 0.7	107.5 ± 24.0	610.5 ± 136.4
Single M_2 estimates	7.6	7.43	504	1.11	3.8	11.5	495.6	2814.4
Maximum	0.1	0.11	–226	–0.49	–0.69	2.0	–25.8	0
Minimum								

^a Dissipation is calculated as the onshore energy flux (J_e) divided by the domain area ($A = 1 \times 10^5 m^2$) and reference density ($\rho_0 = 1024 kg m^{-3}$): $\epsilon_{IS} = J_e A^{-1} \rho_0^{-1}$, where the subscript (IS) refers in all cases to averages calculated over the inner-shelf domain.

^b Domain-averaged temperature change per day was calculated as the vertically integrated heat flux (J_q) divided by the domain area (A), specific heat capacity of seawater (C_p), and a reference density (ρ_0): $\Delta T_{IS} = [J_q A^{-1} C_p^{-1} \rho_0^{-1}] \times 86,400 s(d^{-1})$.

^c The daily ΔS_{IS} is calculated in the same manner as ΔT_{IS} . Salinity is reported as a unitless quantity. Nitrate fluxes are reported per day to facilitate comparison to bottle incubations and previously reported values.

^d A domain-averaged potential “new” primary productivity (P_{NEW}) is calculated as the product of the domain-averaged nitrate flux, the Redfield ratio ($C:N = 106:16$ by atom), and the ratio of the molecular weights of C and N, which we vertically integrated in the middle of the domain to facilitate comparison to CalCOFI estimates of primary productivity ($P_{NEW} = \kappa \int_{-0}^0 A^{-1} \int_z J_N dz dz$ ($mg C m^{-2} d^{-1}$), where κ is the product of the Redfield ratio and the molecular weight ratio of carbon to nitrogen).

tude, peaking between 11 August and 12 August with a value $> 7.5 W m^{-1}$ (Fig. 9). Although the time series is too short to assess the relationship between spring/neap variability in the barotropic tide and the strength of internal tidal energy flux, the maximum energy flux occurred roughly two tidal periods after the spring tide.

Cross-Shelf Heat Flux (J_q)

[31] The vertically integrated, time-mean cross-shelf heat flux was $124 kW m^{-1}$ (an inner-shelf area-averaged heat flux of $12.4 W m^{-3}$), implying a net onshore heat flux equivalent to an inner-shelf area-averaged increase in temperature of $0.28 ^{\circ}C$ per day (Table 1). The vertical structure of J_q was onshore at the surface and offshore at depth, and varied in both magnitude and the depth of the zero heat flux crossing among the three periods (Fig. 8D–F). The J_q zero-crossing depth was approximately the mean depth of the thermocline during each period. This heat flux signature is consistent with the expected pattern given mixing inshore of the mooring: the surface waters were slightly cooled due to mixing inshore relative to offshore, resulting in a net onshore heat flux in the surface. Below the thermocline, the waters were slightly warmed, leading to an offshore heat flux there.

Cross-Shelf Salinity Flux (J_s)

[32] The vertically integrated time-mean cross-shore salinity flux was $0.84 kg m^{-2} s^{-1}$ (Table 1). The vertical structure of J_s was consistent among deployments and was weakly onshore throughout the water column (Fig. 8G–I). The time-integrated salinity change averaged over the inner shelf that would result from the cross-shore salinity flux was 0.12 over the course of the ~ 20 -day experiment, whereas the daily rate of change was $0.0087 d^{-1}$ (Table 1).

Cross-Shelf Nitrate Flux (J_N)

[33] The vertically integrated time-mean cross-shelf nitrate flux was onshore over the course of the experiment ($136.4 g N m^{-1} d^{-1}$; Table 1). The onshore flux nitrate was strongest at near-bottom, reversed sign (indicating an offshore flux) at approximately the average depth of pycnocline, and was zero at the surface in all

Fig. 8 The vertical distribution of time-mean semidiurnal fluxes of energy, heat, salinity, and nitrate (blue line) for each period. The shaded areas are the bounds of 95% confidence intervals calculated from Monte Carlo simulations using randomized phases as described in the text. Estimates that fall outside the shaded areas are different from zero at $p < 0.05$. Energy, heat, and nitrate fluxes have mid-water-column minima. (A–C) Energy flux is onshore throughout the water column. (D–F) Heat flux is onshore at the surface and offshore at depth. (G–I) Salinity fluxes were weakly onshore throughout the water column. (J–L) Nitrate flux is dominated by the onshore flux of nitrate at depth and suggests offshore nitrate flux above the mean position of the nitracline.

three periods (Fig. 8J–L). The depth of the maximum onshore J_N shoaled between the periods, similar to the shoaling zero crossing of J_q . In all periods, the maximum onshore J_N was below the pycnocline and below the depth of the chlorophyll maximum (Fig. 5).

[34] Single tidal-period (M_2) averages of J_N were variable in time, ranging over two orders of magnitude (0 to approx. $500 \text{ g N m}^{-2} \text{ d}^{-1}$), and were coherent with the internal-tide energy flux and heat flux (Fig. 8). Given that nitrate is not building up over the shelf (Fig. 2), the time-averaged cross-shelf nitrate flux is capable of supporting a vertically integrated time-mean value of $774 \text{ mg C m}^{-2} \text{ d}^{-1}$ of new productivity over the inner shelf, using the Redfield ratio to convert between nitrogen and carbon (Table 1). Single tidal-period averages of J_N , when converted to new productivity, ranged from 0 to $2814.4 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Table 1, Fig. 9).

Discussion

Nitrate and the Internal Tide

[35] During ISPX, primary productivity and nitrate uptake increased from offshore to onshore across the shelf and peaked in the shallow waters of the inner shelf (Lucas 2009; Lucas et al. 2011). Laboratory determination of nitrate uptake rates agreed remarkably well with the horizontal internal-tide nitrate-flux calculations. The mean nitrate uptake rate over the inner shelf was $16.7 \pm 3.9 \text{ mg N m}^{-3} \text{ d}^{-1}$ ($n = 16$, including both surface and chlorophyll a maximum samples), whereas the domain- and deployment-average horizontal nitrate flux rate was $13.7 \pm 2.3 \text{ mg N m}^{-3} \text{ d}^{-1}$ ($n = 34 \text{ } M_2$ periods). Qualitatively, changes in ni-

Fig. 9 Single M₂ tidal-period averages of the vertically integrated fluxes of (A) energy (J_e), (B) heat (J_h), (C) salinity (J_s), and (D) nitrate (J_n) (left axes); and (A) area-averaged dissipation (ϵ), (B) heat flux, (D) effective vertical flux of nitrate, and potential new production calculated across the inner shelf as described in the text (right axes). Shaded areas represent the 95% confidence interval as described in Fig. 8. Vertically integrated fluxes of all quantities are maximal at the middle of first period, at the end of the second period, and at the end of the third period. Internal-tide fluxes of heat and nitrate were variable by two orders of magnitude over the 3-week deployment period.

nitrate uptake rates for the three sampling days were consistent with the variability in horizontal internal-tide nitrate flux ($14.8 \pm 2.3 \text{ mg N m}^{-3}$ on 11 August, $15.1 \pm 6.0 \text{ mg N m}^{-3}$ on 14 August, and $22.1 \pm 7.9 \text{ mg N m}^{-3}$ on 17 August; compare to Table 1, Fig. 9). Estimating new productivity at the nearest

CalCOFI station (Table 2) by applying the f-ratio determined during ISPX (approx. 0.5) to the CalCOFI total productivity, we found that potential inner-shelf new productivity (Table 1) is, by roughly a factor of 2, larger than that at the CalCOFI station offshore. The strong agreement with nitrate uptake rates over the inner shelf

Table 2 Vertically integrated primary productivity^a (PP ± standard error [SE]) values from CalCOFI line 93.3 station 26.7 (63 m depth), 1984–2008, for the stratified summer and early fall months.

Month	Mean PP ± SE (mg C m ⁻² d ⁻¹)	Maximum PP (mg C m ⁻² d ⁻¹)	Number of obs.
July	889 ± 36.6	1751	11
August	712 ± 257.5	1629	5
September	612 ± 151.2	997	4
October	838 ± 275.1	2120	6

^a The PP values here represent estimates offshore of the ISPX inner-shelf mooring array and are therefore expected to be somewhat smaller than estimates made over the inner shelf, given the observed onshore increase in PP (this study, Eppley 1992).

and with historical primary productivity rates provides evidence that the horizontal nitrate flux driven by the internal tide supports the elevated primary productivity over the inner shelf of the SCB, and it indicates that variability in the inner-shelf phytoplankton community will be correlated with physical modulation of the internal-tide–forced nitrate flux. Internal-wave–mediated horizontal nutrient flux may be important in other boundary regions where advective nutrient supply is weak or during times when the typically dominant advective forcing is temporarily quiescent.

[36] The result that the net heat flux and nitrate flux were both onshore was surprising when considering that nitrate and temperature are negatively correlated (Fig. 2). This relationship can be viewed as a biogeochemical feedback loop on a small spatial and temporal scale. Heat flux is dominated by the surface layer, whereas nitrate concentration is due to the biological uptake of nitrate—are near zero at the surface (Fig. 8). Correspondingly, surface cross-shore nitrate flux is near zero, and the nitrate flux in the lower layer controls the horizontal nitrate flux budget. The elevated phytoplankton concentrations and nitrate uptake rates at and above the nitracline provide the sink for this cross-shelf nitrate flux, preventing nitrate concentrations from increasing over the inner shelf and, in the process, decoupling the direction of the heat and nitrate fluxes. This elevated phytoplankton nitrate demand, which maintains the horizontal and vertical gradients across which the internal tide is working, balances the continued onshore transport of nitrate by the internal tide, thus providing

for the maintenance of elevated rates of phytoplankton production over the inner shelf.

Vertical Redistribution of Nitrate within the Inner Shelf

[37] We have shown analytically that the cross-shore nitrate flux controls the nitrate budget over the inner shelf in a spatially integrated sense. However, the elevated surface primary productivity and phytoplankton biomass in the surface waters (Lucas et al. 2011) imply vertical redistribution of nitrate within the inner-shelf domain. Our attempts to directly calculate the vertical nitrate-flux divergence across the nitracline due to the internal tide ($\partial/\partial z \langle w'N' \rangle_{M_2}$) using vertical velocity measured by the ADCP were inconclusive due to the poor resolution of the ADCP vertical currents and the generally weak vertical velocities ($<0.01 \text{ m s}^{-1}$). Another approach is to estimate vertical nitrate fluxes based on the convergence of the onshore internal-tide energy flux. The linear energy flux estimates provided here were similar to those calculated for the inner shelf of Oregon during periods of relaxation from upwelling ($2\text{--}9 \text{ W m}^{-1}$, Torgerson and Hickey 1979; Moum et al. 2007) and with estimates of internal-tide energy flux over the New England Shelf (approx. 100 W m^{-1} , MacKinnon and Gregg 2003a). The inner-shelf–averaged values of dissipation were similar to those obtained in other internal-wave–forced continental shelf settings (approx. $10^{-7} \text{ W kg}^{-1}$, Largier 1994; MacKinnon and Gregg 2003b; Sharples et al. 2007). As a calculation example, we estimated the vertical component of mixing (K_z) according to the Osborn-Cox parameterization (Osborn 1980), $K_z = \Gamma(\epsilon/N^2)$, where the constant mixing efficiency Γ was taken to be 0.2, ϵ was calculated as the area-averaged dissipation rate during period II, and N^2 was the mean buoyancy frequency during period II. This results in $K_z = 9.5 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$. The mean nitrate gradient ($\partial N/\partial z$) at the WW mooring during period II was 0.34 mol m^{-4} , leading to approximately $40 \text{ mg N m}^{-2} \text{ d}^{-1}$ vertical nitrate-flux rate, or approximately 40% of the vertically averaged horizontal nitrate flux for period II, scaled by the vertical-to-horizontal length scales of the domain ($\alpha = 0.01$; Table 1).

[38] Given the shallow depths of the inner shelf and the large amplitude of the internal tide, it is likely that the total internal-tide energy flux contains a signifi-

cant nonlinear component, which is not included in the energy flux calculated above. For example, Moum et al. (2007) showed that the nonlinear advection of wave energy is approximately twice the pressure-work term ($\langle u'p' \rangle$) for nonhydrostatic, nonlinear waves impinging on the Oregon continental shelf (see Scotti et al. 2006 for similar estimates from Massachusetts Bay). The lower-frequency internal tide may have a smaller nonlinear component than the waves of elevation discussed there. Nevertheless, our estimates of energy flux (and subsequently of area-averaged dissipation rates) only consider the linear component of the flux and are likely to be smaller than the total internal-tide energy flux to the inner shelf.

[39] Regardless of the exact value of the onshore energy flux, mixing must be enhanced over the inner shelf, and this mixing accounts for the elevated nitrate-uptake rates and biomass in the surface waters of the inner shelf. The source of this mixing is a subject of current study. High-frequency internal waves associated with the internal tide propagate across the continental shelf, losing energy and causing mixing (Lucas 2009). Bottom boundary-layer processes also appear to be important—overturns in density occur during the up-shelf transport of cold water forced by the internal tide.

Internal-Tide–Forced Fluxes in the Context of Low-Frequency Variability

[40] Although we were unable to find comparable estimates in the peer-reviewed literature, the magnitude of the vertically integrated cross-shelf heat flux, $O(100 \text{ kW m}^{-1})$, appears to be physically realistic. For example, the vertically and time-averaged onshore heat flux was approximately 5 kW m^{-2} in approximately 20 m depth. Given the aspect ratio of the inner shelf ($\alpha = 0.01$), an equivalent heat flux through the surface is approximately 50 W m^{-2} , smaller than the average surface heat flux due to insolation observed at the SIO pier over the length of the deployment (approx. $250 \pm 78 \text{ W m}^{-2}$), estimated as a simple average including nighttime data (data not shown).

[41] In the absence of the large-scale forcing that maintains the persistent cross-shore tilt of the pycnocline (see Lucas et al. 2011 for a discussion of other scales of variability in the SCB), the onshore heat flux

would lead to warming inshore and eventually dissipate the cross-shore temperature gradient. Using a nonhydrostatic numerical model of the SCB internal tide (which disregarded surface heat flux), J. Lerczak (unpubl.) showed that the nonlinear evolution of the internal tide tends to “pile up” warm water over the shelf, depressing the pycnocline and causing a residual subtidal alongshore flow. Whereas our estimates of onshore heat flux corroborate the model results, the larger-scale forcings—vertical shear in alongshore currents, coastally trapped waves, pan-Pacific variability such as El Niño Southern Oscillation (Lucas et al. 2011)—are of sufficient magnitude to overwhelm the onshore heat flux driven by the internal tide, given the persistent cross-shore temperature gradients in the study area (Eppley et al. 1979; Eppley 1992; Lucas et al. 2011).

[42] Salinity fluxes were weak and lacked a well-defined vertical structure, but as an independent, conservative variable, salinity fluxes provided assurance that the flux-calculation methodology was not providing spurious results. The low-frequency change in the salinity field was dominated by a shift toward the end of period I, when the mean salinity changed by 0.2 in the course of 2 days. This change was at least an order of magnitude larger than the internal-tide–driven salinity flux, and therefore it appears that the shelf salinity budget is also typically controlled by large-scale dynamics.

Boundary Conditions

[43] We utilized no-flux boundary conditions to justify our assertion that the inner-shelf nitrate budget is controlled by cross-shelf exchange [equation (4)]. In the case of nitrate, we expect the surface no-flux boundary conditions to be true to the first order. Recent studies have demonstrated that the sediment of the inner shelf can be either a net sink or a net source of nitrate, depending on the organic load and the character of the sediments (Santoro et al. 2006). In addition, there are a number of locally important benthic macroalga species and dense forests of the giant kelp *Macrocystis pyrifera*—which have been shown to utilize internal-wave–delivered nitrate (Fram et al. 2008)—to the south of the study area. Future consideration of the nitrate budget of the inner shelf should include estimation of the local (non-phytoplanktonic) sinks of nitrate, in

addition to the capacity for (de-)nitrification in the water column and in the sediment.

The Nitrate–Temperature Relationship

[44] Estimating nitrate concentrations based on temperature is an imperfect method. On timescales that are short relative to the capability of phytoplankton to take up nutrients, the temperature–nitrate relationship is unstable, and nitrate concentrations will be higher than the canonical value on an isotherm in a region of flux convergence. On timescales similar to those of phytoplankton uptake [$O(\text{hours})$], a light-saturated but nutrient-limited phytoplankton assemblage will consume available nitrate at a rate proportional to both the phytoplankton concentration and the phytoplanktonic capacity to upregulate nitrate uptake. This leads to a negative bias relative to the canonical nitrate–temperature relationship.

[45] We expect that, given the multitude of observations that verify the long-term stability of the nitrate–temperature relationship in the SCB, temperature provides an excellent proxy for nitrate when calculating the flux over the entire duration of the experiment. Single M_2 tidal averages, however, would likely include error due to deviations from the average nitrate–temperature relationship. However, our estimates of the nitrate flux are conservative: a fractional sink inshore (in the direction of the flux) relative to that offshore would make the true tidal-averaged flux higher than estimates based on a strictly conservative nitrate–temperature relationship.

Significance to Aquatic Environments

[46] We have used a novel application of Reynolds flux calculations to estimate the cross-shelf fluxes of energy, heat, salinity, and nitrate due to the semidiurnal internal tide. Our estimates of the nitrate flux compared well with our observations of nitrate uptake rates over the inner shelf and with estimates of new productivity based on 20 years of CalCOFI data acquired at a nearby station. The internal-tide–induced fluxes varied by factor of 5 or more over the course of the 3-week experiment, and there were periods when the nitrate flux to the inner shelf appeared to relax the nitrate limitation of

primary productivity, which in turn led to increasing phytoplankton concentrations (Fig. 5; Lucas et al. 2011). We expect that the horizontal flux of nitrate due to the internal tide is the primary driver of the cross-shelf gradients in phytoplankton biomass, surface chlorophyll concentrations, new productivity, and total productivity in the SCB.

[47] Horizontal nutrient flux pathways are well studied in advective phenomena, such as wind-forced upwelling. This study demonstrates that the horizontal component of mixing-driven nutrient flux is sufficient to account for a productive inshore ecosystem. It is not surprising that there is a significant horizontal mixing-driven nutrient flux in an anisotropic system such as the coastal ocean, where cross-shore gradients in the distribution of nutrients and the intensity of mixing are to be expected. These results emphasize that a comprehensive nutrient budget must explicitly consider horizontal mixing fluxes and that an a priori assumption that vertical mixing-driven fluxes control new phytoplankton productivity in internal-wave–dominated systems is not justified, particularly in coastal regions.

[48] In areas with wide continental shelves, such as the east coast of the Americas, or areas where wind-forced upwelling or continental runoff are important, the horizontal internal-wave nitrate delivery mechanism is likely of secondary importance in general but may be the primary nitrate flux mechanism on occasion, when other forcing is absent. In other continental shelf seas and limnological settings where velocity, density, and nitrate variability are dominated by the internal wave field—most commonly in narrow and steep boundary areas—we expect that this mechanism would be of first-order importance.

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