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Pteropods, eddies, carbon flux, and climate variability in the Alaska Gyre

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Abstract

Pteropod abundances in net tows and sediment traps are used to evaluate the link between episodic pteropod carbon flux in the North Pacific Ocean and Haida eddies and climate variability. Large deposition events of *Clio pyramidata* (a subtropical species of pteropod) at 3800 m sediment traps at Ocean Station Papa (OSP, 50°N, 145°W; 1983–2000) lag large El Niño events, represented by the Northern Oscillation Index (NOI), in the North Pacific by 1–2 years during observations from 1983 to 2000. Strong ENSO events may inject *C. pyramidata* source populations into the subarctic from southern regions because of greater northward transport of water along the continental margin and in some cases, because of a northward shifting of the subarctic boundary in deeper waters. Subsequently, conditions in the North Pacific following large negative NOI events may allow *C. pyramidata* to build and sustain high populations in the Alaska Gyre. Several very negative NOI years coincided with strong eddy intensity. Eddies are capable of concentrating high densities of pteropods (*C. pyramidata* and *Limacina helicina*) and so may further intensify climate-driven pteropod-based carbon inputs in the North Pacific. Pteropods contribute organic (tissue) and inorganic ($CaCO_3$ = aragonite) carbon to the deep ocean, yet they are not usually included in mass flux sediment trap studies because it is difficult to distinguish “swimmers” (live at the time of capture) from “sinkers” (dead at the time of capture). At $2.5\,\mathrm{g\,m^{-2}\,yr^{-1}}$, $CaCO_3$ flux due to *C. pyramidata* at OSP is comparable to existing pelagic estimates for all open-ocean calcifiers including coccolithophorids, foraminfera, and all pteropods. Particulate inorganic carbon (PIC) from *C. pyramidata* in OSP sediment traps is ~17% of values measured in other studies that do not include pteropods in their totals. Average yearly flux of organic particulates at OSP due to *C. pyramidata* is $1.6\,\mathrm{g\,m^{-2}\,yr^{-1}}$ and is about 49% more than the annual particulate organic carbon (POC) flux estimated by Wong et al. (1999) for OSP.

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1. Introduction

Inputs of carbon to the Alaska Gyre are episodically enhanced via sinking of large numbers of pteropods. In this paper we quantify pteropod carbon flux in the Alaska Gyre using sediment traps at Ocean Station Papa (OSP) near the southern margin of the Alaska Gyre at 50°N, 145°W. We also investigate possible mechanisms for pteropod aggregation and distribution throughout the North Pacific. Climate variability due to El Niño Southern Oscillation (ENSO) events and the Pacific Decadal Oscillation in the North Pacific may affect particulate carbon vertical flux in the Alaska Gyre by increasing densities of pteropods, in particular the density of a large subtropical species, *Clio pyramidata*. Two likely mechanisms of pteropod aggregation and retention in the North Pacific are concentration in anticyclonic Haida and Sitka eddies that form along the west coast of North America and increased northward transport of subtropical waters during years influenced by El Niño. Concentration of pteropods in eddies is probably enhanced in major ENSO years, and thus these two mechanisms are almost certainly linked.

Concern about global warming and the effects of increasing atmospheric CO_2 on the environment motivate scientific interest in the long-term fate of anthropogenic CO_2 in the oceans. Dissolved CO_2 concentrations affect the quantity of CO_2 that can be absorbed from the atmosphere by surface waters. Biological processes that regulate concentrations of dissolved CO_2 include production and oxidation of organic matter and the precipitation–dissolution of $CaCO_3$. $CaCO_3$ production and export is an important mechanism by which carbon is transported from the ocean's surface to its abyss and likely affects regulation of marine CO_2 levels (Francois et al., 2002; Inglesias-Roderiguez et al., 2002). Particulate inorganic carbon export from the surface mixed layer is called the "carbonate pump". Its role with respect to air–sea pCO_2 gradients is unclear and often ignored (Wong and Crawford, 2002). Pteropods are one source of carbonate (aragonite) that has largely been omitted from oceanic carbon flux estimates (Inglesias-Roderiguez et al. (2002); but see: Berger (1978), Berner and Honjo (1981), Betzer et al. (1984) for examples where they have been considered). This omission leads to an underestimate of the amount of $CaCO_3$ produced in shallow water sediments and dissolved in deep water. Data from sediment traps show that aragonite may contribute from 12% to $>50\%$ of total $CaCO_3$ flux in some areas (Lalli and Gilmer, 1989).

Large anticyclonic Sitka and Haida eddies form in late winter along the eastern margin of the subarctic Pacific and then propagate westward into the Alaska Gyre (Crawford and Whitney, 1999; Crawford et al., 2002). Physical and chemical characteristics of Haida eddies are given in Crawford (2002) and Whitney and Robert (2002). In general, Haida eddies are about 100–200 km in diameter, 300–400 m thick and can persist for several years, traveling as far as 1000 km from their origin and carrying nutrients from the nearshore into the North Pacific (Whitney et al., 2005). Haida eddy seaward penetration into the Alaska Gyre can extend westward of 140°W (Crawford et al., 2000). Following very large El Niño events in the North Pacific, eddy number, size, and southward penetration are greater than average (Crawford, 2002; Crawford et al., 2002). Sitka eddies (Tabata, 1982) form along the Alaskan Panhandle north of 55°N and differ from Haida eddies in their water mass characteristics (Crawford, 2002). They generally reside in the northern extreme of the Gulf and sometimes enter the Alaskan Stream. Some biology of Sitka eddies has been studied (Batten and Crawford, 2005).

Zooplankton communities in Haida eddies are a mixture of shelf- and slope-origin species from the nearshore formation region (Mackas and Galbraith, 2002; Batten and Crawford, 2005) and subarctic oceanic species that colonize the eddy from the sides and below, after the eddy leaves the nearshore region (Mackas et al., 2005). Densities of most nearshore-origin species decrease with eddy age (Mackas and Galbraith, 2002), while offshore-origin species approach ambient Alaska Gyre concentrations. Two marked exceptions to this pattern, however, are the pteropods *Limacina helicina* and *C. pyramidata*. Both species are often more abundant within Haida eddies than in any source/sink region. By September 2001, *C. pyramidata* was the dominant contributor to zooplankton biomass in eddies formed in 2000 and 2001 and its abundance within the eddies was 3- to 10-fold greater than in reference waters (Mackas and Galbraith, 2002). A similar pteropod enhancement is found in cold-core rings of the Gulf Stream, where *Limacina inflata*, is enhanced 300 times above background numbers in the Sargasso Sea (The Ring Group, 1981; Wormuth 1981).

L. helicina and *C. pyramidata* are planktonic snails. More precisely, they are holoplanktonic, shelled opisthobranch gastropods (Order Thecosomata), a group collectively known as "pteropods" (shells shown in Fig. 1). *L. helicina* is a cosmopolitan species with adult shell diameters up to 5.5 mm in the northeast Pacific (M. Galbraith, unpublished data in the Canadian Department of Fisheries and Ocean's Zooplankton Database). It is abundant in the subarctic Pacific Ocean north of 45°N and less common in the Transition Zone, from where it can be transported south by the California Current (McGowan, 1971; Bé and Gilmer, 1977). *C. pyramidata* is also a wide-ranging species and has a wide spectrum of morphological variation (Bé and Gilmer, 1977). Adult shell lengths range from 3.5 to 13 mm (van der Spoel, 1973). Its distribution ranges from ~63°N to 40°S in the Atlantic and 50°N to 45°S in the Indo-Pacific Ocean; it is most abundant in the central waters of the North Pacific and rare in the eastern tropical Pacific (Bé and Gilmer, 1977). *C. pyramidata* in the Alaska Gyre are probably derived from more southerly source regions by one of two routes: either cumulative northward leakage across the oceanic Subarctic Front, or by a more localized poleward advection along the North American boundary. Lalli and Gilmer (1989) report that most pteropods are found in the upper 200 m and migrate to the surface at night. Other authors report deeper diurnal migration to 1000 m (e.g., Wormuth, 1981). Both *L. helicina* and *C. pyramidata* alternate active swimming (usually upwards), with periods of slow sinking and/or neutral buoyancy (neutral buoyancy has been observed for up to 6 min; Gilmer and Harbison, 1986). For both species, the slow sinking/neutrally buoyant periods are concomitant with extrusion of a mucus feeding web three to five times their body size (Gilmer and Harbison, 1986).

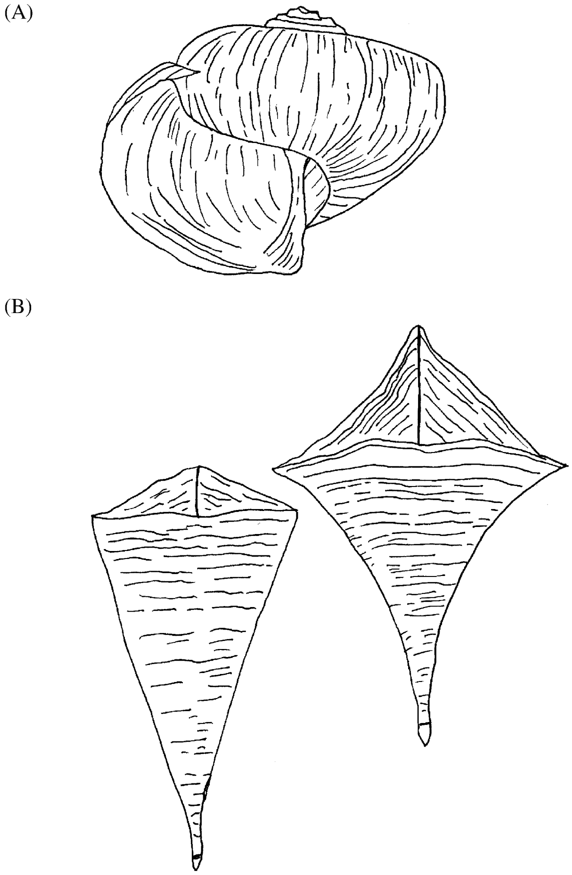


Fig. 1. Shells of (A) *Limacina helicina* forma A; (B) *Clio pyramidata*, two shell forms. The form on the left is *C. pyramidata* forma *pyramidata* and the one on the right is *C. pyramidata* forma *lanceolata*. Most of the *C. pyramidata* found in OSP sediment traps are forma *lanceolata*. Modified from van der Spoel (1972). Scale bar for (A) is 5.5 mm and for (B) is 18 mm.

The El Niño Southern Oscillation (ENSO) cycle is associated with changes in particle flux of carbon and nitrogen in the North Pacific (Wong et al., 1998). In the Alaska Gyre, large ENSO events are correlated with an increased flux of organic and inorganic carbon to OSP sediment traps (Wong and Crawford, 2002).

We examine pteropod abundances in net tows in Haida eddies and at OSP as well as pteropod abundances in a moored sediment trap time-series from OSP. We compare these abundances to measures of eddy intensity and to an index of ENSO variability to evaluate links among episodic carbon flux in the North Pacific (via pteropods), eddies, and climate variability.

2. Methods

2.1. Eddy and Station Papa plankton tows

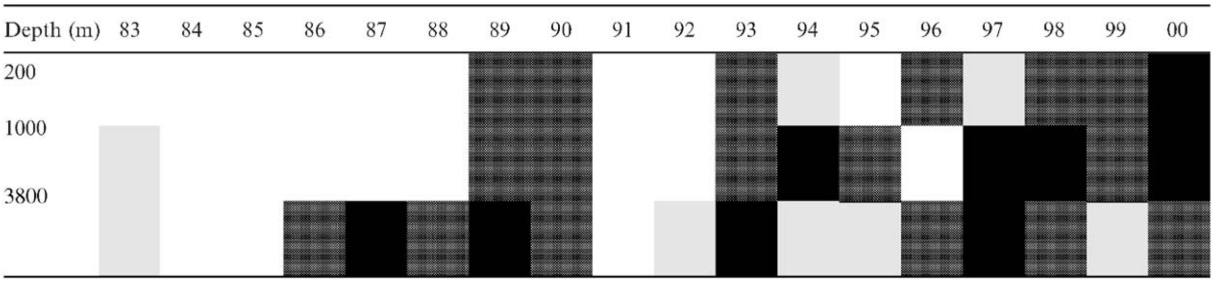
Pteropod abundance (individuals m^{-2}) were measured with day and night vertically hauled plankton tow samples from multi-disciplinary surveys conducted by the Institute of Ocean Sciences and the University of British Columbia in eddy, oceanic, and nearshore waters of the northeast Pacific (Mackas and Galbraith, 2002). Mesh size for these surveys was 0.236 mm. Oceanic abundances of *L. helicina* and *C. pyramidata* were also estimated from plankton tows at OSP in 1996–1997 as part of the Canadian Joint Global Ocean Flux Study of this area (JGOFS; Goldblatt et al., 1999) and 1998–2001 summer surveys by the Hokkaido University vessel *Oshoro Maru*. Mesh size for JGOFS tows was 0.220 mm and for the *Oshoro Maru*, 0.236 mm. Offshore and eddy plankton tows were to 150 m and nearshore tows were to 250 m or bottom depth minus 10 m if the bottom was shallower than 250 m. Data may under-represent true densities as the typical pteropod escape response may bias net collections (Lalli and Gilmer, 1989).

2.2. Sediment trap time-series

The pteropod sedimentation time-series at OSP is from multiple deployments of moored sequencing sediment traps from 1983 to 2000 at 200, 1000, and 3800 m (Table 1). The bottom depth at OSP is ~4300 m. PARFLUX Mark 5 traps (1.1 m^2; 6–12 samples per sequence) were used from 1983 to 1989 and Mark 6 and 7 traps (0.5 m^2; 13–21 samples per sequence) from 1989 to 2000 (Wong et al., 1999). Deployment durations varied from 6 to 12 months, with an average of ~15 days per sampling interval. Details of sample processing are in Wong et al. (1999).

Mesozooplankton larger than 1 mm (including pteropods) were removed from trap samples prior to geochemical analyses, and were counted and/or weighed. All counts are standardized to 1.0 m^{-2} trap mouth area. The multi-year time-series of trap catches is most complete for the 3800 m depth (Table 1). For pteropods, the deepest trap is also probably the most conservative estimate of "sinking" flux. Behavior of pteropods like *Limacina* can bias the results of shallow water sediment trap collections: when pteropods are even gently disturbed, they often swim downward in an escape response (for distances of 20 cm or more; Gilmer and Harbison, 1986). Therefore it is difficult to distinguish "swimmers" (animals caught in traps

Table 1
Ocean Station Papa sediment trap time-series



Depth (m)	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	00
200							▦	▦			▦	░		▦	░	▦	▦	■
1000	░						▦	▦			▦	■	▦		■	■	▦	■
3800	░			▦	■	▦	■	▦		░	■	░	░	▦	■	▦	░	▦

Numbers in the top row are year of deployment. White indicates no coverage for the year. Gray cells represents >25% coverage for the year. Trellis cells represents >50% coverage for the year. Black cells represent ~100% coverage for the year when alive) from "sinkers" (dead or moribund pteropods sinking to the ocean floor). *L. helicina* is rarely found below 300 m (Bé and Gilmer, 1977), and maximum range for *C. pyramidata* is between 350 and 1000 m (van der Spoel, 1973; Wormuth, 1981). Honjo et al. (1982) report that zooplankton swimmers do not affect the results from deep-water traps and water column density of many mesopelagic pteropods substantially decreases below 300 m (McGowan, 1960). Thus, zooplankton trapped at 200 and 1000 m could largely be due to horizontal flux, but the 3800 m trap contents can be assumed to be conservative minimum estimates of true sinking flux of pteropod-derived carbon and used in analyses. We expect that sinking flux is, however, to some degree proportional to abundance in the overlying water column. We therefore extrapolate abundances from 200- and 1000-m traps to 3800 m to fill gaps in the 3800-m record, based on log–log regressions between 200 and 1000 m trap abundances and 3800 m abundances ($p < 0.01$ for both depths, Spearman's ρ; $r^2 = 0.06$ for 200–3800 m; $r^2 = 0.25$ for 1000–3800 m). Abundance (A) extrapolations from 200 m to 3800 m are as follows:

$$A(3800\,\mathrm{m})\text{ per sampling interval} = (E * \mathrm{Abundance}_{200}) - 0.1,$$

where

$$E = \text{antilog of the average of }\log\frac{A(3800\,m + 0.1)}{\mathrm{A}(200\,\mathrm{m}) + 1}$$

and

$$\mathrm{Abundance}_{200} = [A(200\,m) + 1].$$

Abundance extrapolations from 1000 to 3800 m are the same as from 200 m except that 1000-m data are transformed by log $(x + 0.1)$. Monthly abundances are based on cross-year averages of total abundance for each month in all years with data. Some years have missing trap intervals and so coverage is not complete for the year. Annual means for these years are estimated with data from that year (including extrapolations for missing data from the 3800 m record) and with extrapolations for the missing fraction of the year's total. Extrapolations for the missing fraction of a year assume each month represents an average ratio of the year's total.

2.3. Pteropod zoogeographic population origins

Identification of the source regions for pteropod populations found in Haida eddies, Alaska Gyre, and continental margin net tows and OSP sediment traps is based on morphological and chemical comparisons. *L. helicina* has two varieties in the North Pacific and Bering Sea that are distinguished by differing shell height-diameter ratios (McGowan, 1963). One *L. helicina* variety (A) is a coastal form and one (B) is an oceanic morph.

For pteropods, the oldest portion of the shell (the protoconch, the point of the conical shell; see Fig. 1) is laid down within days of hatching (Lalli and Gilmer, 1989). As such, the trace element and isotopic composition of *C. pyramidata* shells should reflect its environmental history. Spatial variability in environmental, trace elemental, and isotopic characteristics of different water masses is often reflected in the geochemistry of biogenic hard parts of marine organisms. Geochemical signatures in fish otoliths have been used for stock discrimination, reconstruction of migration and environmental histories (reviewed by Campana, 1999) and, more recently, to make inferences about larval retention (Swearer et al., 1999) and natal homing (Thorrold et al., 2001) in marine fish populations. The concentration of naturally occurring trace elements in biogenic carbonates also has been used to determine origins of planktonic marine invertebrate organisms (DiBacco and Chadwick, 2001; Zacherl et al., 2003).

In a pilot study, we analyzed *C. pyramidata* shells collected from four distinct regions of the northeast Pacific Ocean: Haida eddies, OSP, the West Coast of Vancouver Island, and southern California Current. Collection sites were selected to maximize the likelihood of finding differences in elemental signatures for each source region and because cataloged samples from these sites were readily available from existing zooplankton collections housed at the Institute of Ocean Sciences and the Scripps Institution of Oceanography. Analytical results were examined for site-specific differences in the trace elemental composition of biogenic protoconch shells. The protoconch, deposited within days of hatching, was targeted to maximize the likelihood that elemental signatures reflected hatching sites.

Laser ablation (New Wave 213 nm Nd:YAG) inductively coupled plasma mass spectrometry (LA-ICPMS) was employed because this analytical approach has proved effective in targeting specific regions of bivalve shells (C. DiBacco, unpub. data) as well as fish otoliths (Thorrold and Shuttleworth, 2000). Setup of the instrument is similar to that described by Günther and Heinrich (1999) and recently applied to otoliths by Thorrold et al. (2001). Quantification of elemental ratios presented follows the approach outlined in Rosenthal et al. (1999). Elements quantified in this study included Ca, Cu, Mg, Mn, Pb, and Sr.

2.4. *Measures of Haida eddy and El Niño intensity*

Large eddies are in approximate geostrophic equilibrium, and eddy centers are associated with high (anticyclonic) or low (cyclonic) sea-surface elevation. Haida eddy intensity in the Northeast Pacific from 1993 to 2000 has been estimated from satellite altimetry data as the deep-ocean area within the region of 40°–60°N, 120°–150°W with mesoscale sea-surface positive height anomalies greater than a threshold value (Colorado Center for Astrodynamics Research; Crawford, 2002). Threshold values of positive sea-surface area anomalies used by Crawford et al. (2002) are 10 and 15 cm. Northeast Pacific El Niño intensity is represented by the Northern Oscillation Index (NOI) available on NOAA's Pacific Fisheries Environmental Laboratory Live Access Server (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix.html). The NOI is an index of climate variability based on the difference in sea-level pressure anomalies at the North Pacific High (35°N, 130°W) in the northeast Pacific and at Darwin, Australia (Schwing et al., 2002). The NOI is highly correlated with the Southern Oscillation Index (SOI) and other El Niño indicators, but appears to provide a more direct indication of climate events that affect the North Pacific. El Niño winters (1982–1983, 1986–1987, 1991–1993, and 1997–1998) have strong negative anomalies in the NOI (Fig. 2), however, the NOI time-series also shows a strong negative anomaly in 1995, which was a weak El Niño year with very large Haida and Sitka eddies, likely due to high coastal sea levels (Crawford, pers. comm.).

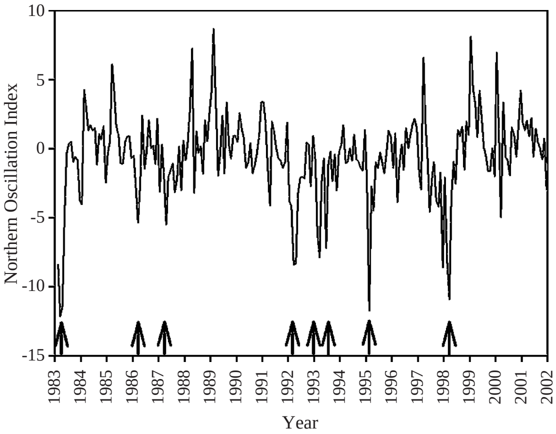


Fig. 2. Northern Oscillation Index (NOI) from January 1983 to January 2002. Data are from the National Oceanic and Atmospheric Administration Pacific Fisheries Environmental Laboratory Live Access Server (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/NOIx/noix.html). Negative values correspond to El Niño years and positive values to La Niña years in the North Pacific. Arrows indicate negative anomalies that correspond to "warm" years in the North Pacific.

2.5. *Data analysis*

All plankton tow data are expressed as vertically integrated abundances m^{-2}. Time-series of sediment trap pteropod abundances are individuals m^{-2} sampling interval^{-1}. The average sampling interval is about 15 days (range = 12–17 days). Statistical correlations are tested in the statistical analysis package, SPSS 9.0. To estimate vertical carbon flux due to pteropods at OSP, *C. pyramidata* of different sizes were weighed and ashed for average inorganic and organic carbon values per individual. These averages are applied to the abundance flux rate from the 3800-m trap depth.

3. Results

3.1. Pteropods in Alaska Gyre and Haida eddy plankton tows

Table 2 summarizes pteropod abundances in the surface 150 m at OSP, the Alaska Gyre, and two Haida eddies (Haida-2000 and Haida-2001) in 2 successive years (map of Haida eddies and Alaska Gyre reference stations in Mackas et al., 2005). *L. helicina* has similar average abundances in OSP plankton tows in March, May and August 1996, and June 1997. *C. pyramidata* is present in OSP plankton tows in March, May, and August 1996, but not present in June 1997. Alaska Gyre background densities for *L. helicina* are maximum in the spring (sampled in June and September).

Eddy abundance for *L. helicina* peaks in June in both eddies. Pteropod densities in eddies are sometimes greater than background numbers, but the trend is not consistent. *C. pyramidata* eddy abundance peaks in the fall; it is abundant in both Haida-2000 and Haida-2001 in September of 2001, and is 4–8 times less abundant at other Alaska Gyre sampling locations.

3.2. Limacina and Clio population origins

In June of 2000, *L. helicina* shell morphologies in Haida-2000 indicate that almost all specimens are juvenile (too small to determine origin) or coastal in origin (Fig. 3). By September 2000, oceanic specimens are more abundant than coastal specimens and juveniles are still the most abundant group. In June of its second year, Haida-2000 contains more than 50% oceanic *L. helicina* and no more than 30% coastal *L. helicina*. Table 2 shows that numbers of *L. helicina* in the Alaska Gyre are higher than in Haida-2000 in Year 2. Data from the first year of Haida-2001 follow the same progression with eddy age (Fig. 3). In September of 2001, *L. helicina* in Haida-2001 have lower abundances than the surrounding waters (Table 2).

However, *Limacina* specimens from OSP sediment traps (1998–1999 and 2001–2002) are all oceanic morphs. *Limacina* specimens from the Alaska Gyre net tows are 100% oceanic morphs.

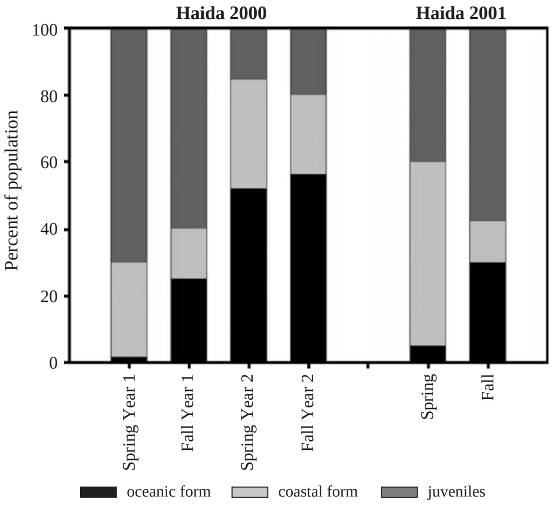


Fig. 3. Percent of the average number of juvenile, coastal, and oceanic forms of *Limacina helicina* m^{-3} in 150 m of water in Haida-2000 and Haida-2001. *L. helicina* forms are distinguished morphologically by shell height-diameter ratios.

Table 2
Abundance of *Limacina helicina* and *Clio pyramidata* in the top 150 m

	Year 1 Haida-2000 June/ September	Alaska Gyre June/ September	Year 2 Haida-2000 June/ September	Haida-2001 June/ September	Alaska Gyre June/ September	OSP 1996/1997
Limacina helicina	13950/4500	4500/7.5	2550/345	6150/45	3000/1950	2443/1133
Clio pyramidata	absent/1.5	360/15	45/975	75/480	105/120	432/0

Numbers are individuals m^{-2}. Eddy and Alaska Gyre data are from Mackas and Galbraith (2002). Ocean Station Papa data are from R. Goldblatt (1999) and are average abundances for five samples (March, May, and August) in 1996 and two samples (June) 1997. Year 1 is the first year of eddy sampling, 2000. Year 2 is the second year of eddy sampling, 2001.

Results from laser ablation analysis of *C. pyramidata* shells proved inconclusive for determining the origins of individual pteropods, and so we do not present these results. Analytical protocols performed as expected, however, elemental signatures were not distinctive enough to accurately classify pteropods with respect to the four reference collection sites; perhaps pteropods originating from the sites in question simply do not differ in their elemental composition. However, this seems unlikely given that the targeted sites are characterized by highly variable parameters such as temperature, salinity and proximity to shore, all known to influence the elemental composition of biogenic carbonates. Conversely, the pteropods may not have originated at the reference sites where they were collected. All pteropods retrieved from the zooplankton collections and employed in this study were adults. Pteropods deposit most of their shells within weeks of hatching, so it was not possible to determine the age of adults by comparing relative sizes. Additionally, we did not have recently hatched individuals to analyze. The life span of *C. pyramidata* is in excess of a year, and thus the potential for physical transport and mixing may be extensive.

Future studies should target newly hatched pteropods, prior to the formation of the adult shell, with well-developed protoconchs to constrain sites of origin and to characterize site-specific, elemental signatures in pteropods. Better proxies for predicting pteropod age may help target younger individuals that have experienced less transport from sites of origin and enhance identifying elemental signatures. Rearing marine invertebrates under controlled laboratory conditions is one approach to determine predictive relationships between environmental factors (e.g., temperature) and the elemental composition of biogenic carbonates. Unfortunately, *C. pyramidata* has not yet been reared successfully in the lab.

3.3. Pteropods in OSP sediment traps

Both *Limacina* and *Clio* are present in low numbers (1–100 m^{-2}) in most OSP sediment trap samples. Occasionally, pteropods are the main catch. Part of the OSP time-series variability is an annual cycle with maximum abundances occurring in the fall between August and December (Fig. 4). Another component of the time-series variability is a 10- to 50-fold inter-annual modulation of the annual cycle (Fig. 5). The largest observed peaks in pteropod abundance in the sediment traps are in 1987, 1994, and 1998, following El Niño winters. Strong negative anomalies in the NOI in 1987–1988, 1991–1993, and 1997–1998 (Fig. 2) graphically correspond to large numbers of pteropods in sediment traps about a year later

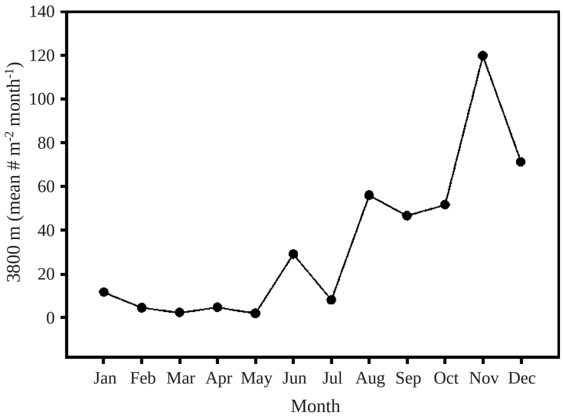


Fig. 4. Mean number of pteropods (*Limacina helicina* and *Clio pyramidata*) at 3800 m (m^{-2} month^{-1}) in OSP sediment traps.

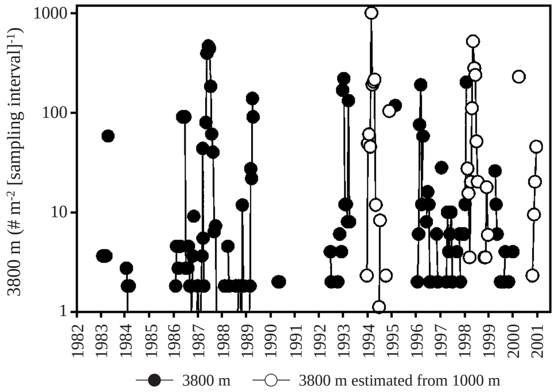


Fig. 5. Number of pteropods (*Limacina helicina* and *Clio pyramidata*) at 3800 m (m^{-2} sampling interval^{-1}) in OSP sediment traps. Black circles are abundances in 3800 m record. Open circles are abundances at 3800 m based on extrapolation from 1000 m record. Lines connecting circles indicate continuous trap data.

(Fig. 5). White (1994) found ENSO signals along the continental margin take 9–18 months to propagate from the equator to the Gulf of Alaska. Thus, Fig. 6 graphs log *C. pyramidata* abundance in OSP sediment traps (y-axis) against the average of the NOI for the previous 2 years. Trap abundances of pteropods are high in "warm" years (1987 and 1994–1998) and low in "cool" years (1986, 1990, 1992, 1999–2000) when there appears to be a relaxation of the factors increasing pteropod abundance in the region. *L. helicina* numbers are also generally higher in years with negative NOI anomalies, but differences in *L. helicina* abundances in OSP sediment traps in negative and positive NOI years are much less than for *C. pyramidata*.

There is no significant correlation between log abundance in traps and the 6 month NOI average for the previous winter ($p<0.164$; Pearson correlation). The Pacific Decadal Oscillation, a measure of regime shifts in the North Pacific characterized by anomaly patterns in sea-surface temperature and other upper ocean measures (e.g., Mantua et al., 1997) is almost significantly correlated with pteropod sediment trap log abundance ($p<0.063$; Pearson correlation). Peaks in Haida and Sitka eddy intensity (Fig. 7) follow warm El Niño winters and/or strong negative NOI years along the BC coast, but there is no significant correlation between eddy intensity and sediment trap abundance of pteropods at OSP ($p<0.266$ for 10-cm anomaly; $p<0.500$ for 15-cm anomaly; Spearman's ρ).

The species ranking in 3800-m traps differed among years (Fig. 6; *Clio* dominates in 1986, 1987, 1994, and 1998; *Limacina* dominates in 1983, 1989, and 1993). *Limacina* and *Clio* are both in very low numbers in 1984, 1988, 1990, 1992, and1997. In 1995–1996 and 2000, numbers of pteropods in sediment traps are high ($\geqslant 100$), but we do not have information on which species make up the total. In 1999, we also do not know which pteropod species dominates the sediment traps, but abundance is low. *Clio* is a much larger animal than *Limacina* and therefore even in years where *Clio* abundance is lower than that of *Limacina*, in terms of biomass (and ultimately, carbon export), it often equals or surpasses biomass inputs from the smaller species.

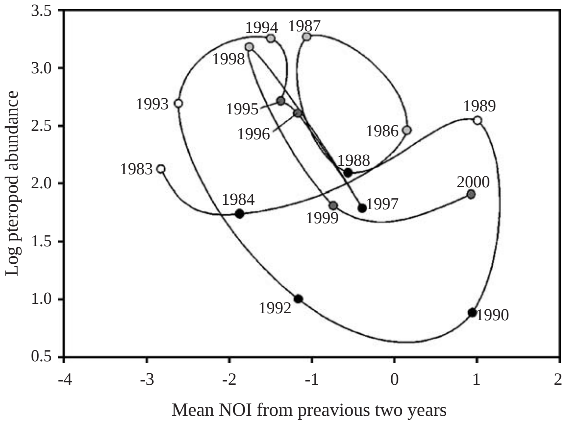


Fig. 6. Log abundance of pteropods in OSP sediment traps (y-axis) versus average of the NOI from the two years previous to years of pteropod catch (x-axis). Black dots indicate years when abundances of *Limacina helicina* and *Clio pyramidata* are both low. Light gray dots indicate that *C. pyramidata* is the dominant organism and *L. helicina* is low in abundance. White dots indicate years of high *L. helicina* abundance and low *C. pyramidata* abundance. Dark gray dots indicate years with no information on which species is more abundant. Strong negative anomalies in the NOI are coincident with "warm" years in the North Pacific and high volume of *C. pyramidata* in OSP sediment traps. The opposite is true for strong positive anomalies in the NOI during "cool" years in the North Pacific.

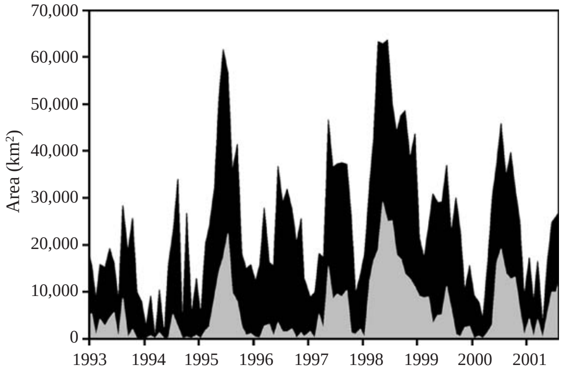


Fig. 7. Eddy intensity in the Gulf of Alaska. Eddy intensity is represented as area with positive, mesoscale sea-surface elevation anomalies from 40° to 60 °N, 120° to 150 °E based on combined TOPEX/Poseidon and ERS-1 and ERS-2 satellite altimetry observations (Crawford, 2002). Black line is area with positive sea-surface anomaly of 10 cm or more. Gray line is area with positive sea-surface anomaly of 15 cm or more. Tick marks denote the start of each year.

Table 3
Downward carbon flux at 3800 m at OSP for *Clio pyramidata* ($g\,m^{-2}\,yr^{-1}$)

Year std. deviations (%)	Dry weight (63.2)	Ash weight (24.6)	Ash-free dry weight (18.6)	PIC (24.6)
1983	1.1	0.8	0.5	0.1
1984	0.4	0.3	0.2	0
1986	2.3	1.7	1.1	0.2
1987	14.5	10.9	6.8	1.3
1988	1.0	0.7	0.5	0.1
1989	2.7	2.1	1.3	0.3
1990	0.1	0	0	0
1992	0.1	0.1	0	0
1993	3.8	2.9	1.8	0.4
1994	14.1	10.6	6.6	1.3
1995	4.0	3.1	1.9	0.4
1996	3.2	2.4	1.5	0.3
1997	0.5	0.4	0.2	0
1998	11.8	8.9	5.6	1.1
1999	0.5	0.4	0.2	0.1
2000	0.6	0.5	0.3	0.1
Average	3.4	2.5	1.6	0.3
Monthly average	0.3	0.2	0.1	0

Plus/minus percent standard deviations are in parentheses. Dry weight = all organics and inorganics. Ash weight = inorganics, primarily $CaCO_3$. Ash-free dry weight = all organics. Particulate inorganic carbon (PIC) is estimated from ash weight (assuming ash weight = $CaCO_3$). Zeroes represent values less than 0.1.

Table 3 gives estimated annual vertical carbon flux due to *C. pyramidata* in the 3800 m sediment trap time-series at OSP. Years of large total *Clio* carbon deposition (1987, 1994, and 1998) have 2–4 times greater flux than the average for the time-series. Seasonal deposition rate of total carbon is maximal from August to December: 1.4 to 3.5 times the monthly average. The ratio of average *Clio* organic to inorganic carbon at 3800 m is 0.62. *L. helicina* contributes little in numbers or biomass to the episodic large pteropod inputs to OSP sediment traps, and carbon flux is not estimated for this species.

3.4. Haida eddies and the NOI

One possible mechanism of pteropod intensification and transport into the Alaska Gyre is via Haida and/or Sitka eddies. Haida eddy number, size, and movement are affected by ENSO events (Crawford, 2002; Crawford et al., 2002). The NOI from 1993 to 2001 is significantly correlated with eddy area represented by a positive sea surface height anomaly of 10 ($p<0.05$; Spearman's ρ) and 15 cm ($p<0.05$; Spearman's ρ) (Figs. 2 and 7). Eddy-mediated pteropod enrichment in the Alaska Gyre thus may be enhanced in years with a strong negative NOI.

4. Discussion

4.1. Pteropods and carbon flux in the Alaska Gyre

There are two principal issues in terms of pteropods and marine CO_2 concentrations in the Alaska Gyre: carbon transport to the deep ocean and the effect of pteropod shell production and dissolution on pCO_2 in the upper ocean. Settling particulates of organic carbon can sequester atmospheric CO_2 on century to millennial time-scales (Francois et al., 2002). Sinking pteropods take organic (tissue) and inorganic ($CaCO_3$) carbon directly from the surface layers and move it to the deep sea. In addition, Francois et al. (2002) found $CaCO_3$ to be important in transferring particulate organic carbon to the deep sea, possibly as a result of its high density and ballasting capacity. Pteropods precipitate $CaCO_3$ during shell formation. This process causes CO_2 to be produced in surface waters ($Ca^{2+}+2HCO_3^- \rightarrow CaCO_3+CO_2+H_2O$) which increases CO_2 vapor pressure and decreases the surface water's capacity to absorb atmospheric carbon (Chierici et al., 2005). Precipitation occurs in surface waters, but dissolution of pteropod shells occurs at depth. When pteropods sink out of surface waters at OSP, all their $CaCO_3$ is dissolved before shells are buried in sediment because the bottom depth is 4300 m but the North Pacific aragonite compensation depth is only ~500 m (Lalli and Gilmer, 1989). $CaCO_3$ dissolution takes CO_2 from solution in the deeper layers and increases the alkalinity, which enhances the deep ocean's capacity to store atmospheric CO_2 (Inglesias-Roderiguez et al., 2002). The effects of $CaCO_3$ formation and dissolution are temporally and vertically segregated. In the short-term, high downward flux of $CaCO_3$ in the Alaska Gyre could reduce the benefit of photosynthesis in drawing CO_2 from the atmosphere in surface waters. Given the complete dissolution of the shells at depth, however, the net effect over longer time scales may be zero.

At $2.5\,g\,m^{-2}\,yr^{-1}$, $CaCO_3$ flux due to *C. pyramidata* at OSP is comparable to pelagic estimates for all open ocean calcifiers including coccolithophorids, foraminifera, and all pteropods (Milliman and Droxler, 1996). Particulate inorganic carbon (PIC) from *C. pyramidata* in OSP sediment traps is an ~17% more than the annual PIC flux estimates in Wong et al. (1999; Table 3), but, like most mass flux sediment trap studies, Wong et al. (1999) did not include "swimmers" such as *Clio* in their flux estimates, although they do mention that aragonite flux events could be another significant mechanism in transferring biogenic elements to the deep ocean. Average yearly flux of organic particulates due to *C. pyramidata* in OSP sediment traps is $1.6\,g\,m^{-2}\,yr^{-1}$. Approximately 36% of that is POC (Lalli and Gilmer, 1989) and thus POC from *C. pyramidata* in OSP sediment traps is an addition of about 49% of the annual particulate organic carbon (POC) flux estimated by Wong et al. (1999) for OSP. Wong and Crawford (2002) estimate mean yearly flux of PIC in 3800-m OSP sediment traps in El Niño and La Niña years. They exclude pteropods larger than 1 mm (i.e. almost all *C. pyramidata*) in their study; yet our annual mean PIC from *C. pyramidata* in 3800 m OSP sediment traps is ~13% of their total for years fully or partially influenced by El Niño and ~8% for years influenced by La Niña. Zooplankton swimmers like pteropods are often excluded from flux estimates, but PIC and POC deposited under the Alaska Gyre due to at least one species of pteropod, *C. pyramidata*, may be substantial and should be included in future flux studies.

4.2. Pteropods, eddies, and climate variability in the Alaska Gyre

4.2.1. Links between pteropods, eddies, and climate variability

Wong and Crawford (2002) report increased flux of inorganic carbon (coccolithophores and foraminiferans) in the North Pacific during years influenced by El Niño between 1982 and 1990. They exclude large pteropods like *C. pyramidata* from their analyses, but our analysis shows a similar link between big negative NOI years and increased carbon flux in the Alaska Gyre due to this species. Large deposition events of *C. pyramidata* in OSP sediment traps observed from 1983 to 2000 lag strongly negative NOI years in the North Pacific by 1–2 years. These large negative NOI years are coincident with (but not limited to) the large El Niño events in the Gulf of Alaska during this time. High total inorganic carbon flux from pteropods, coccolithophores, and foraminiferans in negative NOI years may be due to the same forcing, although the specific mechanisms of how the flux originates may be different. Large negative NOI events may inject *C. pyramidata* source populations into the subarctic from more southern regions both because northward transport of Davidson Current water is greater during ENSO years (Whitney and Freeland, 1999) and/or because the Subarctic Front boundary is shifted northward (Fulton and LeBrasseur, 1985).

Subsequently, conditions in the North Pacific following these events, such as increases in sea-surface and sub-surface temperatures (e.g. Freeland, 2002), may allow *C. pyramidata* to build and sustain high populations in the Alaska Gyre. Eddies are capable of concentrating high densities of pteropods and so may further intensify an ENSO or NOI effect on pteropod-based carbon inputs in the North Pacific. Strong NOI years are correlated to strong eddy intensity (W. Crawford, pers. comm.).

We propose the following scenario for a climate-driven pteropod-mediated increase in carbon flux in the Alaska Gyre: (1) very negative NOI conditions enhance northward transport of *C. pyramidata* from southern waters to eddies and subarctic waters. (2) Some change in the conditions in the subarctic after large negative NOI events allow increased densities of *C. pyramidata* in eddies and in surrounding waters. (3) The more intense Aleutian Low during strong El Niño years brings stronger winds from the south and causes warmer, wetter winters that lead to larger, more frequent eddies in the Gulf of Alaska (Crawford, 2002; Crawford et al., 2002). (4) Eddies support a large pteropod biomass (*L. helicina* and *C. pyramidata*) that is transported into the Alaska Gyre. *L. helicina* and *C. pyramidata* densities are enriched in eddies up to 600 (*L. helicina*) and 4–8 (*C. pyramidata*) times Alaska Gyre background densities (Mackas and Galbraith, 2002).

Large pteropod deposition at OSP follows strong negative NOI winters and heightened eddy intensity, but there is no significant correlation. The lack of significance may be due to the short time-series available: 1983–2000 for sediment traps and only 1993–2001 for eddy intensity as well as to the general tendency of eddies to avoid OSP. A longer time-series is probably necessary to resolve inter-annual cycles. In addition, pteropod enrichment may not always be exactly 1 year following a strongly negative NOI, but effects may be spread over 2–3 years due to the stochastic nature of eddy movement to OSP and multi-year persistence of individual eddies.

Although eddies can be pteropod-rich and may be supplying pteropods to the Gulf of Alaska, we find no significant correlation between eddy intensity and pteropod flux in the Alaska Gyre in OSP sediment traps. There is no altimeter or water property evidence of an eddy at OSP during 1998–1999 when large numbers of pteropods were deposited (Colorado Center for Astrodynamics Research; Whitney, pers. obs.). Finally, there is no Haida eddy trajectory that fits the timescale necessary for arrival at OSP in 1998–1999 (Whitney and Robert, 2002).

4.2.2. Pteropods, eddies, and turbulence

Why do pteropods attain and maintain high abundance in Haida eddies? Pteropod behavior coupled with physical properties of eddies may explain this phenomenon. Most zooplankton taxa that are more abundant in Haida eddy samples than in oceanic and coastal comparison samples have vertical abundance maxima located below the surface mixed layer (Mackas and Galbraith, 2002; Mackas et al., 2005). Sub-surface distribution in an eddy can be a horizontal retention mechanism because animals living below the Ekman layer are much less exposed to rapid horizontal displacement during strong wind events. At the surface of an eddy, flushing and exchange with surrounding waters can be surprisingly rapid. For example, Mackas et al. (2005) estimate that sustained 20–25 $\mathrm{m\,s^{-1}}$ winds result in daily removal rates of 20–50+ % of the surface mixed layer from a 150 km diameter eddy. Wind-driven exchange of deeper water is much weaker. Yelland and Crawford (2005) note that surface (15 m) drifters are seldom trapped by eddies, but that some drifters with drogues at 125 m are trapped for many cycles in eddies.

The same strong air-to-sea transfer of energy that produces rapid Ekman transport also produces strong mechanical stirring of the mixed layer, with intensity of this stirring declining with increasing distance from the air–sea interface. There is increasing interest in the extent to which small scale turbulence affects plankton distribution and ecology (e.g., Yamazaki et al., 2002). Both *Clio* and *Limacina* are diel migrants, but our field observations indicate that they abstain from, or greatly restrict their, nocturnal upward migration when winds and turbulence are strong (Mackas and Galbraith, 2002). We suggest that they do so because strong turbulence disrupts their ability to feed. Thecosomatous pteropods feed by deploying and suspending themselves beneath large, external, and rather fragile mucous feeding webs (Gilmer and Harbison, 1986) that might be disrupted by strong turbulence.

Whether pteropod feeding webs are likely to be disrupted by turbulence and at what scale of turbulence this could occur can be answered by estimating the size of small scale turbulent eddies. It is well known that increasing intensity of turbulence both increases the intensity of small-scale velocity shear and vorticity, and shrinks the spatial scale ("eddy size") at which this shear is most intense. The ecological consequences of this can be examined and quantified using well-established theoretical and empirical relationships (e.g., MacKenzie and Leggett, 1993; Yamazaki et al., 2002) between surface wind speed, depth below the air sea interface, turbulent energy dissipation rate ε, the fluid viscosity v, and the size of the smallest turbulent eddies. The scale at which turbulent shear fluctuations become strongly damped by viscosity is indexed by the so-called Kolmogorov length scale $\eta = (v^3/\varepsilon)^{0.25}$. The turbulent shear spectrum peaks at a "wavelength" of about 60η. Dimensions of the pteropod feeding webs (~1–5 cm, Gilmer and Harbison, 1986) are similar to the turbulent eddies produced by strong wind-generated turbulence. For example, at a wind speed of $15\,\mathrm{m\,s^{-1}}$, the mixed layer dissipation rate ε is about 10^{-5} to $10^{-6}\,\mathrm{W\,kg^{-1}}$ (MacKenzie and Leggett, 1993) which is in turn associated with $60\eta \approx 3$–6 cm and a "turnover" time scale of about 10 s for a small embedded particle (such as a pteropod plus its feeding web). The few observations of pteropod feeding webs (Gilmer and Harbison, 1986; Gilmer, 1990; Harbison and Gilmer, 1992) were made by divers under relatively calm conditions. We therefore lack field observations of whether or not a vigorously stirred pteropod will feed. However, from the above calculations we think it likely that strong wind mixing would prevent useful deployment of the feeding webs, and that a turbulence-perturbed pteropod would have good reason to sink or swim downward into calmer water.

4.3. Pteropod zoogeography

Adult *L. helicina* and *C. pyramidata* are retained in eddies, but are multiple generations propagating in situ? Both species produce buoyant egg masses that remain at the surface. If Mackas et al. (2005) are correct that wind-driven shear displaces eddy surface layers, then pteropod eggs are likely removed from eddies and from close spatial association with their parents. Pteropods in eddies therefore may enter an eddy as adults or juveniles and subsequently be retained. The increasing proportion of oceanic *L. helicina* in eddies over time supports this idea. The coastal-origin eddy populations are gradually diluted by immigration of subarctic populations from outside the eddy. McGowan (1960) noted that *L. inflata* is often in greatest abundance at the periphery of its range in areas of horizontal mixing. He suggested that the species is responding to a trophic enrichment of its environment. Adult and/or juvenile pteropods in the Alaska Gyre may be enhanced in El Niño years and be drawn into eddies because of eddy physical processes and thereafter sustained by higher productivity. Phytoplankton and nutrients are enriched in Haida eddies (Peterson et al., 2005).

C. pyramidata was abundant at OSP in the 1990s and large ENSO events may supply these populations to the Alaska Gyre, but we do not know from where these pteropods are entering the North Pacific. *C. pyramidata* may "leak" into the subarctic from the Transition Zone, or they may arrive via the incursion of southern coastal water. In the subarctic Pacific, an abrupt change in salinity marks the Subarctic Front, a boundary between the Alaska Gyre and the Transition Zone (Freeland et al., 1997). In El Niño years a northward-shifting of the zoogeographic subarctic boundary occurs (Fulton and LeBrasseur, 1985) and this was observed in 1998 (M. Galbraith, pers. obs.). In 1998, *C. pyramidata* was abundant along 145°W as far north as 53°30′N. In 2000, when *C. pyramidata* was again abundant in the North Pacific, it was abundant along 145°W from only 49°N southwards. The observed changes in *C. pyramidata* presence and abundance in the subarctic may support the idea that the Transition zone is the source of some of the

C. pyramidata populations in the Alaska Gyre during El Niño years.

Minimum pteropod abundances at OSP are in late winter-early spring. Seasonal die-off, as determined from sedimentation of both *L. helicina* and *C. pyramidata* at Station Papa, is greatest during the fall (Fig. 4) although *L. helicina* may also spawn out and then die in the spring (Fig. 4, small peak?). In Haida-2000 and -2001, *L. helicina* is most abundant in the spring and *C. pyramidata* is most abundant in the fall. Cummings and Seapy (2003) note that in the California Current *L. helicina* reaches highest density in the summer while *C. pyramidata* has no seasonal abundance pattern. *C. pyramidata* has an annual life cycle and breeds continuously, but breeding peaks in spring with a secondary peak in autumn (van der Spoel, 1973). In the Central Arctic Ocean, *L. helicina* lives one and a half to two years and spawns primarily May–July (Lalli and Gilmer, 1989). Life span and spawning times may differ in other localities and in warmer, temperate waters, the life cycle is shorter and spawning is linked to spring (and autumn if they occur) phytoplankton blooms (C. Lalli, pers. comm.).

The OSP time-series and eddy data set suggest some kind of interspecific interaction between *L. helicina* and *C. pyramidata*. At OSP, there are years of dominance in abundance by one species and times when both species coexist in low numbers. When one species is very abundant, the other species is always at low densities. Although the inverse relationship with respect to both species' abundance is not significant (exact contingency test, $p = 0.3$) because of the infrequency of low abundance years for both species, the maximum segregation is found between species in years with high abundance. When *L. helicina* is dominant at OSP or in the eddies, conditions may be unfavorable for *C. pyramidata* persistence in subarctic waters. When water conditions change and densities of *C. pyramidata* pass a threshold, this larger species may out-compete the smaller one for some resource(s). In September 2001, when both eddies carried large numbers of *Clio*, *Limacina* densities in the eddies were low compared to both the Alaska Gyre and eddies sampled in 2000 and June of 2001.

New information on the distribution of *C. pyramidata* is presented in this paper. According to the OSP time-series, *C. pyramidata* is more common, seasonally and inter-annually, in the subarctic Pacific than previously described (Bé and Gilmer, 1977). Existing zoogeographical information about *C. pyramidata* may have been biased by inadequate sampling or by net avoidance (Bé and Gilmer, 1977; Cummings and Seapy, 2003). An alternate, and we think more likely explanation for the relatively high densities of *C. pyramidata* found in the Alaska Gyre in the 1990s, is that the North Pacific may have experienced a change in oceanographic conditions that allowed the sustained presence of a typically subtropical species like *C. pyramidata*. Whitney and Freeland (1999) report a trend towards warmer and less-saline surface waters and a reduced macronutrient supply during winter mixing in the 1990s compared to the 1970s. Changes in the mixed layer and nutrient supply could affect the phytoplankton community (Whitney et al., 1998) and animals that may graze this phytoplankton such as pteropods. Mackas et al. (2001) found a shift to more "southerly" zooplankton (copepods and chaetognaths) off British Columbia from 1994 to 1998 and a shift back to more "northerly" fauna in 1999. The first shift involved an order-of-magnitude decline in several species endemic to the British Columbia continental shelf and a similar increase in species endemic to the California Current waters to the south. Change in the continental margin zooplankton community was correlated to an anomalously strong poleward flow of the California Current.

Average temperature records at OSP show a slight, but steady increase in temperature since 1956 in the top 500 m (Freeland et al., 1997; Robert et al., 2002). Temperature and salinity data from 1998 to 1999, when there were large numbers of pteropods in OSP sediment traps, indicate a warmer and saltier upper ocean (top 400 m) than is typical for the subarctic (Freeland et al., 1997; Whitney and Freeland, 1999). The presence and abundance of *C. pyramidata* in plankton tows in the North Pacific increased during the 1990s (M. Galbraith, pers. obs.). Other species of zooplankton have been used to determine oceanic water masses (e.g., Parnell, 2001; Beaugrand et al., 2002), and high densities of *C. pyramidata* may also indicate a warm water mass in the subarctic.

A question remains as to whether massive *C. pyramidata* inputs to sediment traps at 3800 m actually represent vertical flux. Examination of these traps in 1998 indicated the presence of whole, fresh-looking organisms (F. Whitney, pers. obs.). From what is known about the ecology of this species, it seems untenable that specimens in 3800 m traps in 1998 were "swimmers". On the other hand, if specimens were "sinkers", as we assume in this paper, a high flux to 3800 m (Fig. 5) implies that large numbers of animals were present over a very large area around OSP: a "patch" of radius equal to or greater than the drift rate times peak pteropod deposition duration. Roughly calculated, this minimum patch size would be on the order of 300 km^2. In June and September 1998, high abundances of *C. pyramidata* (1796 m^{-2} in the top 150 m) were found in vertical net tows at Station 20 (49°30′N, 138°40′W), ~458 km east of OSP. By September 1998, *C. pyramidata* were starting to appear in net tows in the water column over OSP. The timing of *C. pyramidata* arrival at Line-P Station 20 and OSP is consistent with the idea of large patches of *C. pyramidata* moving into the Alaska Gyre in warm years.

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