



Influence of mesoscale eddies on ichthyoplankton assemblages in the Gulf of Alaska

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ABSTRACT

Mesoscale eddies (100–200 km in diameter) propagating along the shelf-break in the Gulf of Alaska are ubiquitous and have been shown to influence the ecosystem, but their influence on ichthyoplankton species composition and diversity has not been described. Evidence for larval fish entrainment in these eddies was examined using data from a cruise in 2005 that sampled three eastern Gulf of Alaska mesoscale eddies, and sampling that compared shelf to slope ichthyoplankton assemblages in the northern Gulf of Alaska (2002–2004). Hierarchical cluster analysis of oceanographic data showed that stations grouped according to location within an eddy. Species hierarchical cluster analysis revealed a latitudinal turnover in species composition, and an abundant species group. Species richness was correlated with distance from eddy center ($P = 0.00025$), and assemblages within eddies were significantly different ($P < 0.05$) from those in surrounding basin and shelf waters. These results suggest that mesoscale eddies propagating along the continental shelf-break influence larval fish assemblages over the shelf and slope, which has implications for the timing and extent of larval fish distribution in the Gulf of Alaska.

Key words: assemblage, cross-shelf water exchange, eddy, Gulf of Alaska, ichthyoplankton abundance, species diversity, transport

INTRODUCTION

Drift trajectories of eggs and larvae can influence fish growth, survival, and recruitment. Both local and large scale oceanographic conditions can impact dispersal of young fish, either propelling them towards areas that support high growth and survival, or diverting them away from suitable habitat. For many fish species that spawn along the Gulf of Alaska (GOA) continental slope, eggs and larvae benefit from slope to continental shelf transport, where larvae encounter favorable feeding and growth conditions prior to the onset of winter (Bailey *et al.*, 2008). For some shelf-spawning species, retention over the continental shelf is critical (Lanksbury *et al.*, 2007). Export of shelf-spawned larvae to the continental slope would likely result in poor feeding conditions, lower growth, and potentially higher mortality. Despite the importance of retention and advection to larval fish survival, our understanding of how ichthyoplankton are influenced by variation in shelf-slope circulation is limited.

One mechanism that results in significant shelf-slope water exchange is the intermittent presence of mesoscale eddies propagating along the shelf edge (Rogachev *et al.*, 2007; Ladd *et al.*, 2009), potentially influencing shelf circulation for periods ranging from months to years (Janout *et al.*, 2009). Previous studies have shown that eddies strongly influence nutrient concentrations, notably iron and dissolved inorganics (Johnson *et al.*, 2005; Ladd *et al.*, 2007), as well as chlorophyll concentrations and zooplankton densities (Mackas and Galbraith, 2002; Crawford *et al.*, 2005, 2007). Few studies have examined the influence of eddies on ichthyoplankton (Bailey *et al.*, 1997), but it seems likely that mesoscale eddies over the continental shelf break could similarly influence GOA larval fish assemblages.

Cyclonic and anticyclonic mesoscale eddies are ubiquitous around the world, including the GOA and

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Bering Sea. Anticyclonic eddies are postulated to have a significant role in water movement between the GOA slope and shelf (Crawford, 2002). In contrast, cyclonic eddies in the GOA are less persistent and have little influence on cross-shelf water exchange. Large-scale circulation in the GOA is counterclockwise, with the broad Alaska Current flowing northwest along the coasts of British Columbia and Alaska, becoming the narrower but stronger Alaska Stream flowing southwest along the Aleutian Island chain. Eddies result from instabilities in these flows, through either differences in water density (Crawford, 2002; Di Lorenzo *et al.*, 2005) or interactions with the ocean bottom (Swaters and Mysak, 1985; Melsom *et al.*, 1999; Murray *et al.*, 2001). During eddy formation, a parcel of shelf water may be sequestered and trapped in the eddy core (Ladd *et al.*, 2007). These features are 100–200 km in diameter and can depress isopycnal surfaces at depths in excess of 2500 m. As an eddy matures, there is little exchange between eddy-core water and that accumulated around the rim (Yelland and Crawford, 2005). Eddies forming farther north in the GOA tend to follow the shelf break, continually influencing cross-shelf exchange as shelf water is wrapped around eddy edges and pulled into the basin (Okkonen *et al.*, 2003; Ladd *et al.*, 2007). As an eddy moves away from the slope, exchange with shelf water diminishes.

There are three types of anticyclonic mesoscale eddies in the GOA, named for the region in which they form (Fig. 1a). Haida eddies form through an agglomeration of smaller eddies caused by advection of warm, fresh water masses flowing south out of Hecate Strait (Crawford *et al.*, 2002; Di Lorenzo *et al.*, 2005). Sitka eddies result from baroclinic instabilities in northward flowing currents and interaction with bathymetry along the continental slope near Baranof Island (Swaters and Mysak, 1985; Melsom *et al.*, 1999; Murray *et al.*, 2001). Yakutat eddies form farther north (near Yakutat, AK) where the continental shelf is wider, presumably by the same mechanisms as Sitka eddies (Ladd *et al.*, 2009). El Niño-Southern Oscillation events have been shown to influence GOA eddy formation through destabilization of the Alaskan Current (Melsom *et al.*, 1999), with the largest measured Haida eddy observed in 1998 with a diameter between 120 and 200 km (Crawford *et al.*, 2002; Whitney and Robert, 2002).

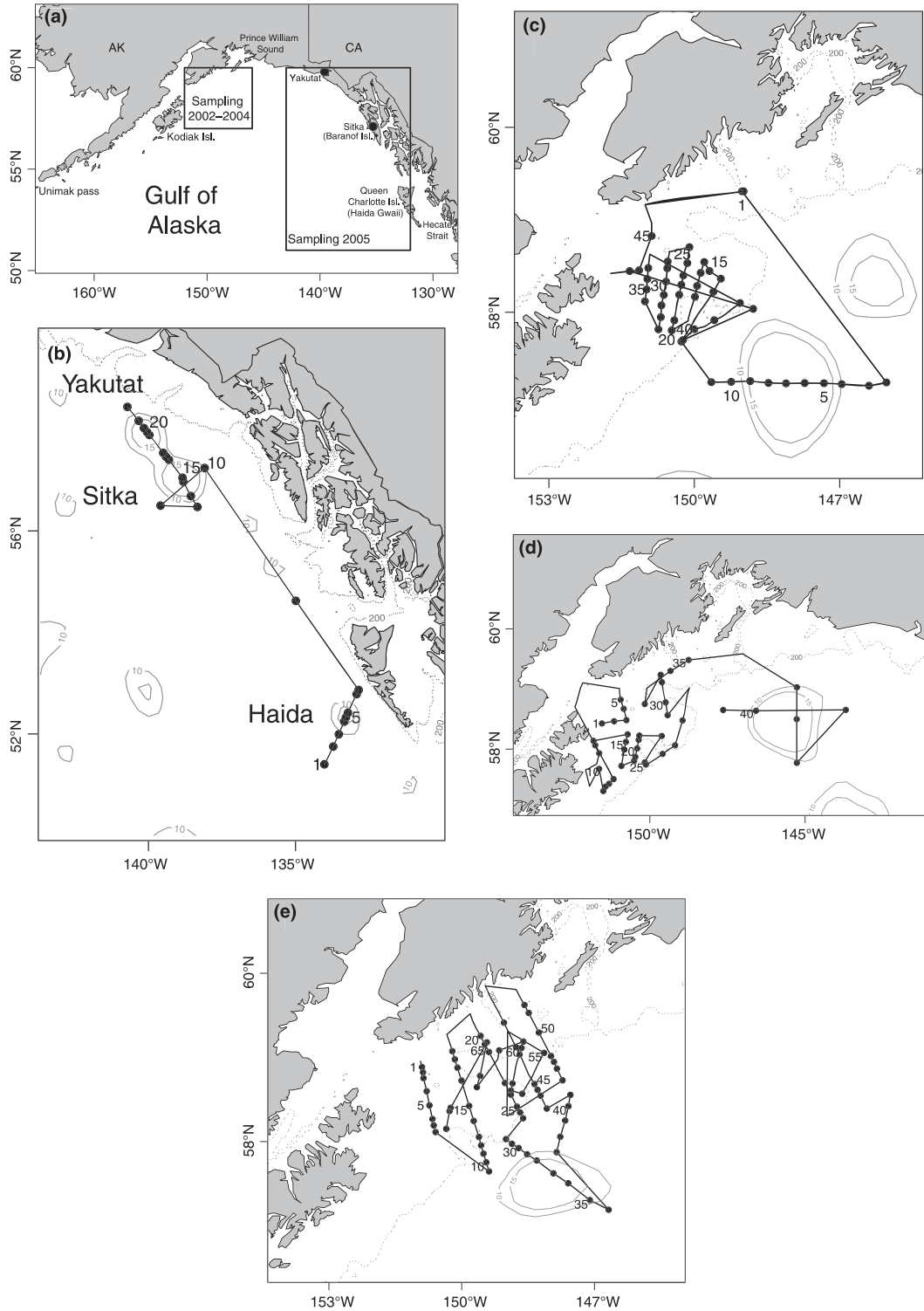
Haida, Sitka, and Yakutat eddies propagate westward, moving at nominal speeds of 0.5–2 km day⁻¹ (Crawford, 2002; Mackas and Galbraith, 2002; Crawford *et al.*, 2007). Despite slow propagation, these eddies may travel thousands of kilometers. It is

not uncommon for eddies originating in the eastern GOA to be found as far northwest as Kodiak Island, or as far west as Ocean Station P (Okkonen *et al.*, 2003; Ladd *et al.*, 2005a; Ladd, 2007). The longest recorded duration of an eddy is over 5 years (Janout *et al.*, 2009). Water mass properties measured in eddy-core water near Kodiak Island are similar to shelf water mass properties in the eastern Gulf (Ladd *et al.*, 2005a), which supports hypothesized eddy formation near the eastern GOA shelf.

Primary production associated with eddies is typically high compared to the high nitrogen-low chlorophyll waters of the GOA basin. Satellite images from SeaWiFS (sea-viewing wide field-of-view sensor) of surface chlorophyll pigmentation show that anticyclonic eddies transfer primary production from the shelf to the basin (Batten and Crawford, 2005; Crawford *et al.*, 2007). Nearshore zooplankton species have been found to be positively correlated with eddy centers (e.g., *Pseudocalanus mimus*), while oceanic species are accumulated around the rim during off-shelf propagation (Mackas and Galbraith, 2002). Eddy studies in other parts of the world have found similar results. Coastal zooplankton species are associated with coastal-formed eddies in the Bay of Biscay (Fernández *et al.*, 2004). Off Western Australia, both cyclonic and anticyclonic eddies have been found to enhance zooplankton concentrations in comparison with surrounding Indian Ocean water (Strzelecki *et al.*, 2007). Eddies are a common feature of the Kuroshio Current System (Li *et al.*, 1998; Jia and Qinyu, 2004), and primary production was enhanced within a cyclonic eddy in the Luzon Strait of the South China Sea compared to outside oceanic waters (Chen *et al.*, 2007). The Agulhas Current System generates high energy eddies (Lutjeharms and Gordon, 1987; Duncombe Rae, 1991). Primary production in Agulhas eddies is increased around eddy edges but not at eddy centers, due to light limitation and convection instability of the water column (Dower and Lucas, 1993). We will use the term 'entrainment' to indicate the accumulation of ichthyoplankton (fish eggs and larvae) in an eddy through water movement. This includes both the initial sequestering of shelf water into the eddy during formation, and the later wrapping of shelf water around the rim of an eddy. When referring to egg and larval fish 'concentration', we mean number of individuals per unit area (per 10 m²) integrated over the water column.

To investigate relationships between ichthyoplankton and mesoscale eddies propagating along the shelf break in the GOA, we examined eddy influence

Figure 1. (a) Cruise locations within the Gulf of Alaska (GOA). The GOA is bordered by Alaska (AK) and British Columbia, Canada (CA). (b) Cruise track in 2005 showing station numbers, with an initial transect across the southern Haida eddy followed by a short east–west transect across the middle Sitka eddy, finishing with a long northward transect bisecting Sitka and then Yakutat eddies. Cruise track sampling showing station numbers east of Kodiak Island (c) in 2004, (d) in 2003, and (e) in 2002. Shelf break indicated by the 200 m depth contour (dashed line), and sea-level height anomaly showing eddy location (solid lines).



on species composition and population concentration of larval assemblages through the initial sequestering of coastal water over the slope during eddy formation, and enhanced offshore flow associated with an eddy propagating along the shelf-break. We conducted this analysis in two parts: exploration of ichthyoplankton assemblage patterns within young eddies in the eastern GOA, and comparison of ichthyoplankton assemblages inside of older eddies to assemblages in surrounding water (basin and shelf) in the western GOA. The objective of the first analysis was to investigate eddy entrainment of semi-passive fish eggs and larvae during and directly after eddy formation. The second analysis assessed strength of eddy effect about 1 year after formation through differences in ichthyoplankton assemblage patterns within and outside of an eddy.

METHODS

Study area

Initial analyses investigating whether ichthyoplankton were concentrated at eddy centers, examined three eddies (Haida, Sitka, and Yakutat) close to formation in the eastern GOA (Fig. 1b) during a cruise in April and May 2005 (FOCI 1TT05, R/V *Thomas G. Thompson*). Further investigations of eddy effects on ichthyoplankton species composition and life history stages was based on data collected in the western GOA during 2002–2004 on and near the continental shelf east of Kodiak Island (Fig. 1c–e). These data provided more samples from the shelf than the 2005 data, but at lower resolution within eddies. In the 2002–2004 data, eddies were sampled approximately 1 year after formation (Table 1). We did not assume

direct links in larval fish assemblages between the 2002–2004 data with those of 2005, but examined these data sets separately and then used both data sets to generalize about the effects of mesoscale eddies on ichthyoplankton assemblages. Lifetime trajectories of the 2002–2004 eddies are described in Ladd (2007).

Oceanographic data

Oceanographic data from the 2005 cruise were collected using a SeaBird 911 plus Conductivity, Temperature, and Depth sensor (CTD) and Niskin bottle water samplers (Table 1). Variables included bottom depth (m), temperature ($^{\circ}\text{C}$), salinity, and concentrations of chlorophyll ($\mu\text{g L}^{-1}$), oxygen (mL L^{-1}), PO_4 , SiO_4 , and NO_3 (all in $\mu\text{mol L}^{-1}$). Water density (σ_t , in kg m^{-3}) was estimated using temperature, salinity, and pressure data. A complete description of the oceanographic data can be found in Ladd *et al.* (2009). To focus analysis on the section of the water column inhabited by the majority of larval fish species spawned on the shelf (Brodeur and Rugen, 1994) and over the continental slope (Bailey *et al.*, 2008), only oceanographic data from the upper 100 m were used in comparisons with ichthyoplankton data. Locations of eddy center were estimated using trajectories from satellite-tracked drifters drogued at 40 m and deployed within the three eddies (Appendices S1–S3). Sea-level height anomalies (SLA, cm) over the study area were obtained using the Archiving, Validation and Interpretation of Satellite Oceanographic data (AVISO) estimates from a merged data set of Topex/Poseidon, Jason-1 + ERS, and Envisat. Positive SLA corresponds to anticyclonic eddies, indicating approximate eddy position and diameter. Distance

Table 1. Biological and physical sampling during the 2005 and 2002–2004 cruises. Physical oceanographic data have been interpreted by Ladd *et al.* (2005a, 2007, 2009). The 2004 eddy formed in the northern GOA that same year, and did not originate near Sitka or Yakutat.

| Cruise | Time period | No. of stations sampled | | | | Eddies sampled | Physical oceanographic data |
|--------|----------------|-------------------------|-------------|-------|-------|----------------------------------|-----------------------------------------------------------------------------------------------------------------------------|
| | | Within- eddy | Slope/ocean | Shelf | Total | | |
| 1TT05 | April/May 2005 | 18 | 2 | 3 | 23 | Haida, Sitka, Yakutat (all 2005) | Bottom depth, temperature, salinity, density, chlorophyll, oxygen, PO_4 , SiO_4 , and NO_3 , SLA |
| 2HX04 | July 2004 | 5 | 6 | 35 | 46 | N GOA 2004 | Bottom depth, temperature, salinity, chlorophyll, SLA |
| 2KM03 | April/May 2003 | 2 | 4 | 35 | 41 | Yakutat 2003 | Bottom depth, temperature, salinity, chlorophyll, SLA |
| 2EW02 | May/June 2002 | 5 | 11 | 52 | 68 | Sitka 2001 | Bottom depth, temperature, salinity, chlorophyll, SLA |

to eddy center from sampling locations was calculated based on our estimate of eddy center from drifter trajectories, and was only calculated for the eddy within which the samples were taken.

Oceanographic variables measured during cruises in 2002–2004 (Table 1) included: bottom depth (m), temperature (°C), and salinity. These last two variables were averaged above 100 m. Location of an eddy was determined by SLA data in excess of 12 cm and drifter trajectories tracing curved eddy current vectors. Different habitats (shelf, basin, within eddy) were determined using bottom depth and SLA data. Stations shallower than 500 m were grouped in ‘Shelf’, and those deeper in ‘Off-shelf’. The latter group was further divided based on SLA, with stations having values of SLA > 10 cm in a group labeled ‘Eddy’ and the remainder in a ‘Basin’ group.

Ichthyoplankton assemblage sampling

Egg and larval fish concentration data from all cruises were collected using oblique, paired bongo tows from a depth of 300 m or 10 m off bottom if shallower, sampled during day and night (Appendices S4–S7). Catches from one bongo net (153 μm mesh, 20 cm diameter) were used for zooplankton sampling, while the other (333 μm mesh, 60 cm diameter) was sampled for ichthyoplankton and other zooplankton. Catches were immediately fixed in 5% buffered formalin, and sent to the Plankton Sorting and Identification Center in Szczecin, Poland, for taxonomic identification and measurement. Concentrations of fish eggs and larvae were reported in numbers per sea surface area (10 m²), using a standard haul factor which integrates the volume and depth of water sampled by each haul. Some larvae were not identifiable beyond the genus or family level (e.g., *Sebastes* spp. or Myctophidae) and were left as a species complex in the dataset.

Data analysis: 2005

Rare species (occurring in <5% of the samples) were removed from the data set, and the remaining species concentration matrix was transformed (fourth-root, $x^{1/4}$) to reduce relative influence of abundant and less common species (McCune and Grace, 2002). Diversity at each station (i.e., alpha diversity) was examined using species richness, or the number of different species found in a haul. Ichthyoplankton assemblage patterns within and between eddies were analyzed using hierarchical cluster analysis (Lance and Williams, 1967), which is not constrained by assumed knowledge of underlying gradients in the data. This method groups species that were commonly found in

samples. Measures of dissimilarity and the clustering method used are usually contentious points in hierarchical cluster analysis. McCune and Grace (2002) suggest that the Bray–Curtis dissimilarity index be used for community data, which accounts for relative abundances of species and changes in species composition between all station pairs. Flexible beta ($\beta = -0.25$) clustering is the recommended compatible method with Bray–Curtis dissimilarity to reduce chaining in the resulting dendrogram. The species matrix was not standardized prior to calculating the Bray–Curtis dissimilarity index as this method intrinsically includes standardization (Anderson, 2006). The minimum number of clusters was determined by analyzing dendrograms and scree plots. The rules we followed for determining minimum number of clusters from a dendrogram are to pick a value along the vertical axis that leaves the highest amount of information in the data (i.e., the lowest point on the vertical axis), and does not cut any ‘chains’ in the dendrogram. A chain is a sequence of divisions that separate only one unit from the group at a time. Final grouping was checked using separation of groups from a non-metric multidimensional scaling ordination (NMDS: Kruskal, 1964). NMDS is a preferable choice for ordinating ecological data because of its flexibility with unknown gradients, as the strength of this method depends on appropriate use of matrix standardizations or transformations and preserves rank dissimilarity between pairs of stations (Clarke, 1993). Stress is a measure of model fit to the data in ordination. Values below 12 suggest little chance for false inferences of station grouping (McCune and Grace, 2002).

Oceanographic variables associated with young eddies sampled during 2005 were analyzed using hierarchical cluster analysis, in which stations with similar water properties were objectively grouped. The oceanographic variable matrix was standardized to reduce disparities resulting from comparing data with different units. We followed suggestions by McCune and Grace (2002), who recommend that environmental dissimilarity be measured using Euclidean distance and clustered using Ward’s method. The minimum number of clusters was determined using the same approach taken for the biological data. Validity of grouping was assessed using separation of groups in NMDS ordination space.

We used a heatmap analysis (Wilkinson, 1994) to compare patterns in the species concentration dendrogram to the physical oceanographic dendrogram. A heatmap analysis is a graphical representation of the species concentration matrix, color-coded for the relative concentration of each species at each station,

and is solely used for pattern recognition. The species concentration matrix is organized by column using one dendrogram placed along the top, and by row according to a second dendrogram placed along the side. Population concentration patterns in clusters were visually assessed.

Observed patterns in species richness (from the diversity analysis) and species concentration (from the heatmap analysis) were further investigated using generalized linear models, with distance from eddy center as a predictor. Error structure was determined using the Shapiro–Wilk test, Kolmogorov–Smirnov test, Q–Q plots, and frequency histograms of both the response (ichthyoplankton concentration data) and the residuals of the regressions.

Data analysis: 2002–2004

To investigate the effect of an older eddy on ichthyoplankton development stages, the following analysis was applied to each age class (eggs, larvae). The species concentration matrix was fourth-root transformed for the reason listed above. To characterize communities in each group (shelf, basin, eddy), assemblage patterns within each group were indexed by concentration and occurrence using an indicator species analysis (Duf re and Legendre, 1997). This metric is based on the presence/absence and concentration of a species within a group. The significance of an indicator value for a species within a group was estimated using the same randomization test procedure suggested by Duf re and Legendre (1997). Our method differed in that significance of every species within a group was tested, as opposed to only the species with the maximum indicator value for a group.

We further examined separation between shelf, basin, and eddy communities based on the Bray–Curtis measure of dissimilarity. Separation between groups was estimated using two randomization tests under a null hypothesis of random station assortment: analysis of similarity (ANOSIM; Clarke, 1993), and multiple response permutation procedure (MRPP; Biondini *et al.*, 1988). The *R* statistic (ANOSIM) and *A* statistic (MRPP) are measurements of agreement between groups, with values ranging between -1 and 1 , where values closer to 1 indicate higher dissimilarity between groups. These methods are similar to a multivariate analysis of variance (MANOVA) but do not include distributional assumptions about the data. We have not encountered any formal comparison of ANOSIM and MRPP, and thus investigated whether both metrics produced consistent results.

Within-group separation between points (dispersion) can be interpreted as a measure of species spatial

turnover (Anderson *et al.*, 2006). Dispersion of points between groups was tested using a Permutation Multivariate Dispersion procedure (PERMDISP; Anderson, 2006; Anderson *et al.*, 2006). Significant differences in species spatial turnover, a measure of change in assemblage composition, would suggest that fish assemblages within eddies, basin, and over the shelf are distinct. This is a recently proposed method for estimating community beta diversity (Anderson, 2006; Anderson *et al.*, 2006).

In an initial analysis, an abundant species group was identified in a hierarchical cluster analysis of the Bray–Curtis dissimilarity matrix. Off-shelf measurements of abundant species group concentration were regressed against distance from the eddy center to more closely examine within eddy dynamics. Species richness was also regressed against this distance. Error structure was identified using the same suite of methods used for the 2005 analysis.

RESULTS

Oceanographic structure of young eddies: 2005 data

Hierarchical clustering of the oceanographic matrix in 2005 revealed station groupings consistent with our understanding of eddy water dynamics (Fig. 2). Stations clustered into interpretable groups when ordered in geographical space (Fig. 2a), fitting into three categories: outside of eddies, at eddy edges, and in eddy centers. In the dendrogram (Fig. 2b) center stations of Haida and Sitka eddies were more similar to each other than to any of the other stations. The next most closely related group was a Sitka/Yakutat intermediate water group, and then the Yakutat center group. Stress of the ordination was low (2.915), and center station groups were distinct in NMDS space (Fig. 2c).

Assemblage patterns within young eddies: 2005 data

Species occurring within eddies were primarily deep-water and slope-spawning species, though some shelf-spawning species were also observed (Appendix S4). The number of different species at a given station varied between 5 and 12 (Fig. 3a). The maximum species richness occurred at the center of the Haida eddy. This concentration of species at the eddy center was comparable to the other observed peak in species richness at a basin station (Station 9).

When examining broad-scale patterns in species occurrence, two interpretable groups were identified: (i) the presence of a southern fish species group (*Tarletonbeania crenularis*, *Protomyctophum crockeri*,

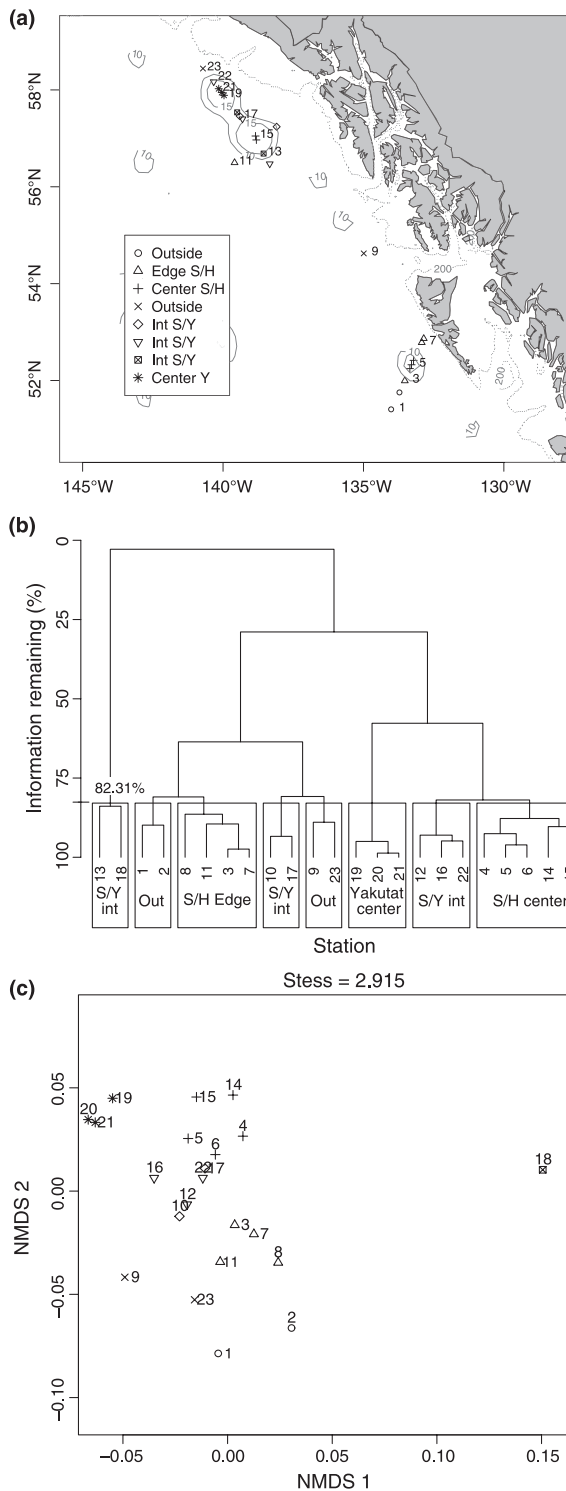
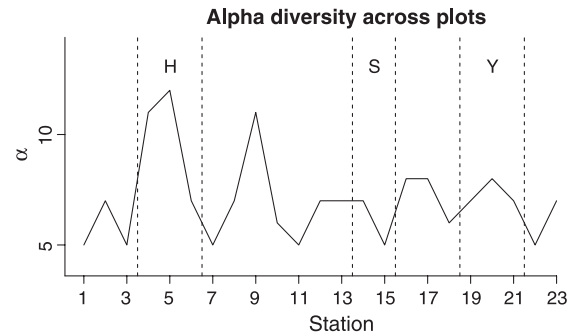


Figure 2. Clustering analysis on the upper 100-m oceanographic matrix. (a) Station grouping in geographical space from the clustering analysis on the upper 100-m oceanographic matrix. Approximate eddy locations are traced by sea-level anomaly contours (solid lines) in excess of 10 cm, and the shelf break is indicated by the 200-m bathymetry contour (dashed lines). (b) Dendrogram from cluster analysis on the upper 100-m oceanographic matrix, geographic interpretation appears below each group (S, Sitka; H, Haida; Y, Yakutat; Int, intermediate water.). Station grouping left 82.31% of the information in the data set. (c) Separation between stations in ordination space based on oceanographic properties, measured using non-metric multidimensional scaling. Stress was 2.915, a measure of model fit to the data.

Figure 3. Measure of species richness in each haul for the cruise in 2005. Eddy stations are surrounded by dashed lines (H, Haida; S, Sitka; Y, Yakutat.).

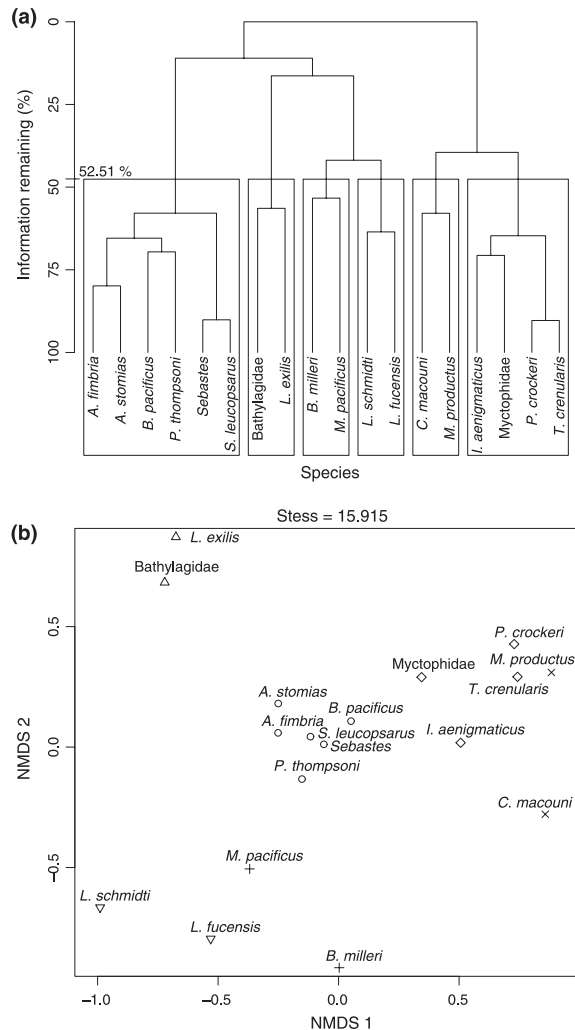


mias, and *Anoplopoma fimbria*) making up more than 70% of the total catch. Groups were delineated in the hierarchical cluster analysis of the species concentration matrix (Fig. 4a), and species groups were distinct from one another in NMDS space (stress = 15.915, Fig. 4b). While this stress was >12, suggesting some possibility of false inferences, the distinct separation in ordination space between these two groups suggested that this is a correct inference. Comparison of the oceanographic dendrogram to the species concentration dendrogram using a heatmap analysis (Fig. 5) suggested higher concentrations of the abundant species in the center eddy groups.

The relationship between station location within an eddy and species abundance was investigated using regression analysis. Concentration of the abundant species group appeared to increase closer to the eddy centers, but the relationship was not significant (Fig. 6; *F*-test, $R^2 = 0.074$, $P = 0.118$). Species richness was negatively correlated with distance from eddy center (Fig. 7; Pearson's goodness of fit, $P = 0.001$, $R^2 = 0.41$). This result suggested a higher concentration of fish

and *Icosteus aenigmaticus*) concentrated primarily in the Haida eddy, and (ii) an abundant species group (*Stenobranchius leucopsarus*, *Sebastes* spp., *Bathylagus pacificus*, *Protomyctophum thompsoni*, *Atheresthes sto-*

Figure 4. Clustering analysis on the species concentration matrix. (a) Dendrogram of cluster analysis on the species concentration matrix, showing associations of similarly occurring species. Final grouping left 52.51% of the information remaining in the data. (b) Separation between species in ordination space, measured using Non-metric multidimensional scaling. Stress was 15.915, a measure of model fit to the data.



species within eddy centers, although the significance of this relationship was primarily driven by Haida eddy samples.

Assemblage patterns within and outside of older eddies: 2002–2004 data

Ichthyoplankton assemblages were different within eddies compared to those in adjacent basin water and over the continental shelf (Table 2). Shelf spawners (deep-sea sole, *Embassichthys bathybius*) were occasionally found as eggs within the eddy group. In

2002, rex sole (*Glyptocephalus zachirus*) were a characteristic shelf species as eggs, but as larvae, were indicative of the eddy group. Arrowtooth flounder (*Atheresthes stomias*) were consistent larval constituents of the eddy group across all years. It is also interesting to note that ragfish (*Icosteus aenigmaticus*) were present in the 2004 eddy samples, which is a primarily southern spawning species identified in the 2005 eddy analysis.

Tests for between-group differences using ANOSIM and MRPP showed significant differences between the three groups (Table 3), suggesting that species assemblages were different between the shelf, basin, and eddy. This result corresponds to conclusions from the 2005 data analysis that fish assemblages were different within eddies compared to surrounding basin and continental shelf waters. MRPP and ANOSIM agreed on significant differences between groups for three of five comparisons.

Species spatial turnover rates were different between groups (Table 4), estimated using between-group homogeneity in dispersion (PERMDISP). In 2002, fish egg measurements were evenly dispersed in all three groups, which suggested equal species turnover rates. Within-eddy distances for larvae were much less dispersed and significantly different compared to the basin and shelf measurements ($P = 0.019$ and 0.001). This pattern suggests lower rates of larval species turnover within the eddy, or that a larval species assemblage was more homogeneous within the eddy compared to the shelf. In 2003, fish egg species turnover rates were greater within the eddy, but were not significantly different from the shelf or basin ($P > 0.05$). Larvae had a higher species turnover rate on the shelf (indicating more spatial variability in assemblage composition) compared to that in the basin or in an eddy. In 2004, there were no significant differences in species spatial turnover rates between the shelf, basin, and eddy measurements ($P > 0.05$).

The abundant species groups were rarely correlated with distance from eddy center (Table 5). In 2002, fish eggs were negatively correlated with distance suggesting lower concentrations along the eddy rim ($P = 0.008$, $R^2 = 0.39$). Species richness estimates were also rarely correlated with distance from eddy center (Table 6). This relationship was negative in 2002 (similar to 2005), suggesting a greater diversity of species eggs at eddy center ($P = 0.001$, $R^2 = 0.53$). In 2003, fish eggs were more diverse along the edge of the eddy, or in other words, positively correlated with distance from eddy center ($P = 0.005$, $R^2 = 0.86$).

Figure 5. Heatmap comparing upper 100-m oceanographic dendrogram to the species clustering dendrogram. Shading corresponds to relative fish concentration. Oceanographic dendrogram is on top, and geographical group interpretation is listed at the bottom (S, Sitka; H, Haida; Y, Yakutat; Int, intermediate water; Cen, center; Out, outside of eddy.). Left is the species dendrogram, with individual species to the right. Dashed white lines separate clusters. Full species names are listed in the Appendices.

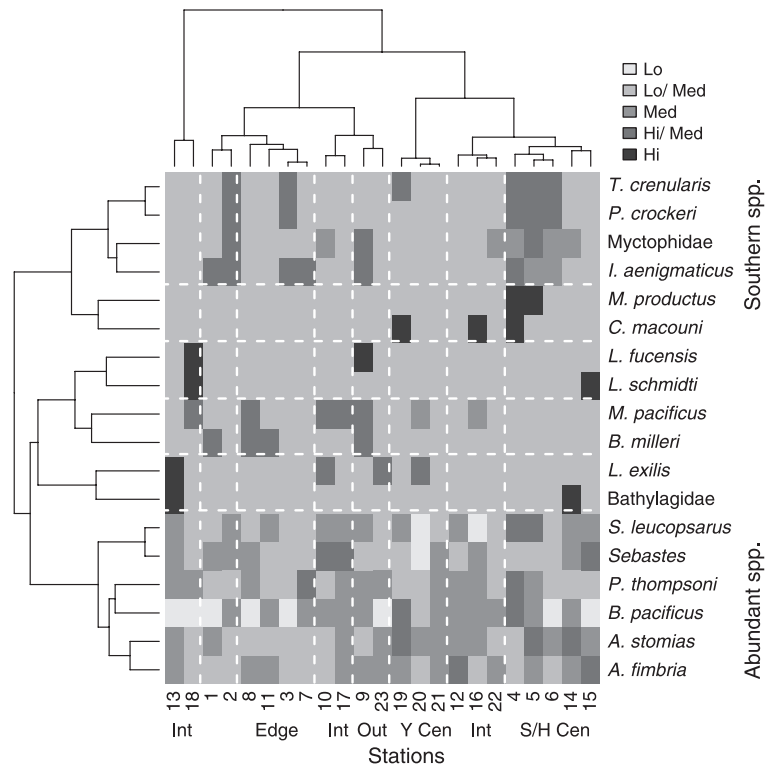


Figure 6. Regression of abundant species concentration on distance from eddy center using simple linear regression (normal error structure). Station data are plotted, and coded for sampling time (white center = between sunrise and sunset, gray = crepuscular, black = night) and for sampling location (Haida = circles, Sitka = squares, Yakutat = triangles).

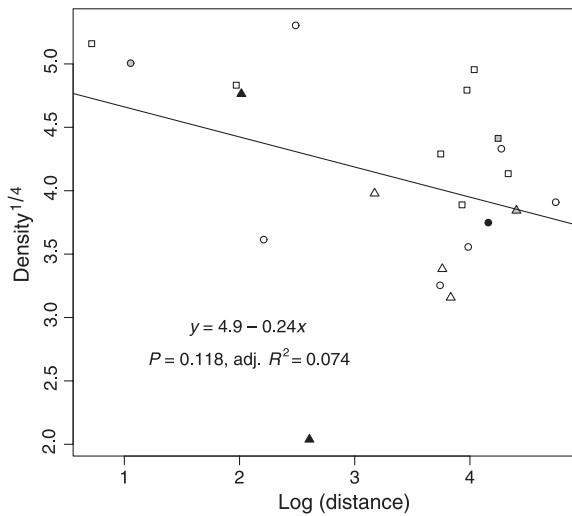
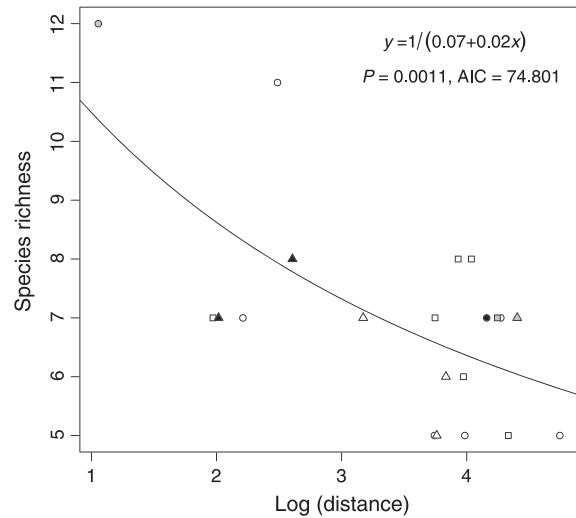


Figure 7. Regression of species richness on distance from eddy center, using a generalized linear model (gamma error structure). Station data are plotted, and coded for sampling time (white center = between sunrise and sunset, gray = crepuscular, black = night) and for sampling location (Haida = circles, Sitka = squares, Yakutat = triangles).



DISCUSSION

Oceanographic samples above 100 m from stations in 2005 clustered in interpretable groups that matched

our understanding of mesoscale eddy dynamics. The three eddies sampled in 2005 were in different phases of formation. In 2005, the Haida eddy was determined to have already been fully mature, the Sitka eddy had

Table 2. Significant species (permuted $P \leq 0.1$) from indicator species analysis of the 2002–2004 data sets. Species were analyzed in egg and larval stages. An empty box appears where no species were significant.

| Year | Stage | Shelf | Basin | Eddy |
|------|--------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------|
| 2004 | Eggs | – | <i>Leuroglossus schmidti</i> (0.01) | <i>Icosteus aenigmaticus</i> (0.096) |
| | Larvae | <i>Mallotus villosus</i> (<0.001), <i>Bathymaster</i> (0.030), <i>Ronquilus jordani</i> (0.059) | <i>Microstomus pacificus</i> (0.001), <i>L. schmidti</i> (0.007), <i>Protomyctophum thompsoni</i> (0.022), <i>Stenobranchius leucopsarus</i> (0.026), <i>Bathylagus pacificus</i> (0.079) | – |
| 2003 | Eggs | <i>Hippoglossoides elassodon</i> (<0.001) | <i>L. schmidti</i> (0.034) | – |
| | Larvae | <i>Ammodytes hexapterus</i> (<0.001), <i>Theragra chalcogramma</i> (0.094) | <i>B. pacificus</i> (0.021), <i>Sebastes</i> (0.028), <i>M. pacificus</i> (0.029), <i>S. leucopsarus</i> (0.077) | <i>L. schmidti</i> (0.049), <i>Atheresthes stomias</i> (0.093) |
| 2002 | Eggs | <i>Glyptocephalus zachirus</i> (0.074) | Macouridae (<0.001) | <i>M. pacificus</i> (0.012), <i>L. schmidti</i> (0.025), <i>Embassichthys bathybius</i> (0.051) |
| | Larvae | <i>Bathymaster</i> (<0.001), <i>BathYGONUS alascanus</i> (0.001), <i>H. elassodon</i> (0.002), <i>T. chalcogramma</i> (0.003), <i>Icelus</i> (0.043), <i>A. hexapterus</i> (0.052), <i>Icelinus</i> (0.099) | <i>Anoplopoma fimbria</i> (0.018), <i>S. leucopsarus</i> (0.028), <i>P. thompsoni</i> (0.03) | <i>B. pacificus</i> (0.001), <i>A. stomias</i> (0.037), <i>M. pacificus</i> (0.076), <i>G. zachirus</i> (0.081) |

Table 3. Comparison for each year testing whether ichthyoplankton differ in regional species composition and concentration, separated by life history stage (eggs and larvae). *R* (ANOSIM) and *A* (MRPP) statistic values indicate strength of difference, with values closer to one indicating complete difference, along with permuted *P*-values. Regions compared were eddy, basin, and shelf. Egg samples in 2004 were limited, occurring at one eddy station and two basin stations, and were omitted in the analysis.

| Year | Stage | ANOSIM | | MRPP | |
|------|--------|----------|----------|----------|----------|
| | | <i>R</i> | <i>P</i> | <i>A</i> | <i>P</i> |
| 2004 | Eggs | N/A | – | N/A | – |
| | Larvae | 0.284 | 0.001 | 0.080 | <0.001 |
| 2003 | Eggs | 0.480 | 0.004 | 0.083 | 0.005 |
| | Larvae | 0.189 | 0.053 | 0.100 | <0.001 |
| 2002 | Eggs | 0.383 | <0.001 | 0.151 | <0.001 |
| | Larvae | –0.009 | 0.526 | 0.058 | <0.001 |

newly formed, and Yakutat was determined to be the youngest of the three (Ladd *et al.*, 2009). In the hierarchical clustering of oceanographic variables, the center stations of the two older eddies (Haida and Sitka) were more closely related to each other than the Yakutat center group. Given that outside-of-eddy stations clustered, the separation of the Yakutat center from the Haida/Sitka center group may be attributed

Table 4. Species spatial turnover rates between groups (E, eddy; B, basin; S, shelf) using dispersion (PERMDISP), separated by life history stage (eggs and larvae). When mean distance between station and central tendency (centroid) differed between groups, the relative relationship between groups is noted using inequality signs to indicate direction along with *P*-values for paired comparisons (Tukey's HSD). There were no significant differences in 2004. Species turnover can be measured over space or time (Anderson *et al.*, 2006; Blackburn and Gaston, 1996; Harrison *et al.*, 1992; Koleff *et al.*, 2003).

| Year | Stage | Comparison of groups | | |
|------|--------|----------------------|-----------|----------|
| | | E to B | S to B | S to E |
| 2004 | Eggs | – | – | – |
| | Larvae | – | – | – |
| 2003 | Eggs | – | – | – |
| | Larvae | – | >(<0.001) | >(0.002) |
| 2002 | Eggs | – | – | – |
| | Larvae | <(0.019) | – | <(0.001) |

to the different ages of the three eddies rather than latitudinal gradients in oceanographic properties.

From hierarchical cluster analysis of the species concentration matrix, we identified a group of primarily southern-occurring species and an abundant species group. The southern species group was identified through qualitative examination of species

Table 5. General linear regression of abundant species groups on distance from eddy center separated by eggs and larvae. Constituents of abundant species for each life history stage identified using hierarchical cluster analysis are listed, along with error structure, *P*-value, correlation structure (Neg. = negative, Pos. = positive), and adjusted R^2 to account for number of predictors in the model. Egg samples in 2004 were not sufficient to support analysis (N/A).

| Year | Stage | Abundant species group | | | | Species | Species richness | | | |
|------|--------|------------------------|-----------------|------------|-------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------|-----------------|------------|-------|
| | | Family | <i>P</i> -value | Adj. R^2 | Corr. | | Family | <i>P</i> -value | Adj. R^2 | Corr. |
| 2004 | Eggs | N/A | | | | | N/A | | | |
| | Larvae | Normal | 0.287 | 0.03 | Neg. | Bathymaster, <i>Sebastes</i> spp., <i>Stenobranchius leucopsarus</i> | Normal | 0.177 | 0.1 | Neg. |
| 2003 | Eggs | Normal | 0.052 | 0.57 | Pos. | Pleuronectidae, <i>Theragra chalcogramma</i> | Normal | 0.005 | 0.86 | Pos. |
| | Larvae | Normal | 0.84 | -0.24 | Neg. | <i>Atheresthes stomias</i> , <i>Sebastes</i> spp., <i>S. leucopsarus</i> , <i>Ammodytes</i> <i>hexapterus</i> , <i>Bathyagonus</i> <i>alascanus</i> , <i>T. chalcogramma</i> | Normal | 0.101 | 0.41 | Pos. |
| 2002 | Eggs | Normal | 0.008 | 0.39 | Neg. | <i>Leuroglossus schmidti</i> , Macouridae | Normal | 0.001 | 0.53 | Neg. |
| | Larvae | Gamma | 0.009 | 0.43 | Neg. | <i>Sebastes</i> spp., <i>A. stomias</i> , <i>S. leucopsarus</i> , <i>Bathylagus</i> <i>pacificus</i> , <i>L. schmidti</i> | Gamma | 0.698 | 0.01 | Neg. |

Table 6. General linear regression of species richness on distance from eddy center separated by eggs and larvae. Values listed include error structure, *P*-value, correlation structure (Neg. = negative, Pos. = positive), and adjusted R^2 to account for number of predictors in the model. Egg samples in 2004 were not sufficient to support analysis (N/A).

| Year | Stage | Family | <i>P</i> -value | Adj. R^2 | Corr. |
|------|--------|--------|-----------------|------------|-------|
| 2004 | Eggs | N/A | – | – | – |
| | Larvae | Normal | 0.177 | 0.1 | Neg. |
| 2003 | Eggs | Normal | 0.005 | 0.86 | Pos. |
| | Larvae | Normal | 0.101 | 0.41 | Pos. |
| 2002 | Eggs | Normal | 0.001 | 0.53 | Neg. |
| | Larvae | Gamma | 0.698 | 0.01 | Neg. |

composition and we found that the southern species only occurred within the Haida eddy. Larval distribution maps (Matarese *et al.*, 2003) of the species group sampled in the Haida eddy revealed that three species (*Tarletonbeania crenularis*, *Protomyctophum crockeri*, and *Icosteus aenigmaticus*) primarily occur along the central west coast of North America (Baja California to southern British Columbia). The Haida eddy was also the southernmost of the three eddies sampled, with core water originating from warmer, fresher water flowing south out of Hecate Strait (Crawford *et al.*, 2002; Di Lorenzo *et al.*, 2005; Ladd *et al.*, 2009), which is at a lower latitude than the formation regions for either the Sitka or Yakutat eddies. It is thus not surprising to find these southern-occurring species in the southern-most eddy sampled

in 2005. The pattern observed for the southern species group suggests that species composition over the continental shelf is important to eddy species assemblages when an eddy is forming. This is similar to the pattern observed in Gulf Stream eddies, where assemblages of fish, zooplankton, and phytoplankton within eddy cores depend on seed populations present during formation (Wiebe *et al.*, 1976; Ring Group, 1981; Olson, 1991).

Species assemblage pattern analysis within eddies suggested higher species richness within centers of a newly formed eddy. We noted in the regression analysis that the species richness relationship was primarily driven by Haida eddy-core samples (Fig. 7). Eddy-core water consists of coastal water sequestered during formation (Ladd *et al.*, 2007). Given that Haida was the southern-most eddy sampled in 2005, but also contained many of the same oceanic species as found in the Sitka and Yakutat eddies, the species richness results reinforce that assemblage structure is likely correlated with the geographic region when a GOA eddy is formed.

Qualitative heatmap analysis of the abundant species group in the 2005 eddies suggested a higher ichthyoplankton concentration within eddy centers, but this result was not significant. This could be due to the young age of the Sitka and Yakutat eddies. It would be interesting to trace how fish assemblages within an eddy center change during formation and over the lifespan of a GOA eddy, as has been documented for zooplankton species assemblages in Gulf Stream eddies (Wiebe *et al.*, 1976; Olson, 1991). Unfortunately the two data sets

used in this study were not correlated in space and disconnected in time by at least 1 year. These data cannot be used to draw conclusions regarding evolution of fish assemblages within eddies over time.

Eddies sampled in 2002–2004 contained different ichthyoplankton assemblages than surrounding slope and basin waters. An eddy travelling in a straight line, at a high propagation speed of 2 km day^{-1} , would take about 14 months to get from Sitka to east of Kodiak Island. The 2002–2004 pattern suggests that older eddies continue to carry anomalies in species abundance and composition in the deeper ocean of the GOA. Eddy species assemblages change during the months after an eddy has matured and begun to propagate away from its formation region (Olson, 1991). Fish species composition within eddies sampled in 2002–2004 and nearby shelf larval fish assemblages were not similar. After formation, water movement around eddies can consist of shelf water that is either entrained around the rim, or deflected from the boundary current into the GOA basin as a streamer (Janout *et al.*, 2009; Ladd *et al.*, 2009). Strong wind events can blow surface water out of an eddy core (Mackas *et al.*, 2005), but the deeper portion of core water can remain distinct for many months (Ladd *et al.*, 2007). It is not surprising that, despite low numbers of inner eddy samples from 2002 to 2004, eddy water had a different larval fish assemblage than that of the nearby shelf. Within-eddy samples for these data (2002–2004) were very sparse, and these results should be treated as exploratory. Propagation time likely has a strong effect on fish species assemblages within eddies, as fish sequestered during formation will fluctuate due to feeding conditions, predator abundances, developmental changes, and wind-driven advection of surface water. Fish species with benthic juvenile and adult stages will likely encounter higher mortality if they are unable to escape an eddy situated over the slope and basin (Gaughan, 2007).

The presence of rex sole (*G. zachirus*) eggs, a slope-spawning species, over the shelf in 2002 was an interesting observation. Rex sole are known to spawn in deep water over the slope, but their eggs and larvae are often collected in surface waters (Abookire and Bailey, 2007; Bailey *et al.*, 2008). Our results suggest that positively buoyant rex sole eggs were either transported towards shore by wind, or were retained in shoreward, near-surface currents associated with the eddy at that time. Both mechanisms are plausible, the first given the low retention index found for zooplankton species inhabiting the mixed layer of eddies (Mackas *et al.*, 2005). The second mechanism is supported by evidence from another system, where on-

shore transport of larval and juvenile bluefish (*Pomatomus saltatrix*) towards estuary nursery habitats is benefitted by streamers associated with warm core-eddies positioned shoreward of the Gulf Stream (Hare and Cowen, 1996).

Ichthyoplankton response in 2002, quantified using species richness and abundant species group concentration to distance from eddy centers, followed a similar pattern to that observed in 2005. Egg species richness was strongly correlated with distance from eddy center in 2002 and 2003, but larval species richness was not correlated with distance from eddy center for the 3 years sampled. Larval fish increase their mobility with growth and development, and are assumed to be less affected by flow patterns associated with eddy activity. Results in 2003 indicated higher species diversity occurred around the rim of an eddy, evidenced by a switch in correlation from negative in 2002 to positive in 2003. This pattern may be explained by a streamer of coastal water that was entrained around the edge of Yakutat 2003 (Ladd *et al.*, 2005b). During the lifetime of an eddy, streamers of coastal water may become wrapped around the edge of an eddy located along the shelf-break, but are usually not incorporated into eddy-core water (Yelland and Crawford, 2005; Janout *et al.*, 2009). The results from 2003 suggest that the streamer of shelf water contained a higher diversity in species of fish egg, which would cause this pattern of higher diversity around the eddy rim.

The presence, intensity, and duration of mesoscale eddies along the continental shelf edge could be beneficial or detrimental to any particular fish species, depending on their life history. Species that spawn over the continental shelf benefit from heightened concentrations of prey, and many demersal and flatfish species also require retention near potential nursery habitat over the shelf. During the early larval pelagic period, if a shelf-break eddy entrains coastal water containing shelf-dependent larvae around the rim, fish could be advected over the slope and potentially encounter lowered prey concentrations and unfavorable juvenile habitat.

Some slope-spawning species (e.g., Pacific halibut *Hippoglossus stenolepis*, arrowtooth flounder *Atheresthes stomias*) were collected from mesoscale eddies sampled in this study. These species rely on connectivity between the slope and the shelf during their late larval stage (Bailey *et al.*, 2008). Females of both species migrate offshore and spawn over the slope. Eggs and larvae remain deep in the water column, and depend on biological and physical factors to transport larvae toward mid-shelf nursery habitats. Mechanisms such as onshore flow up deep-sea valleys and troughs, and

enhanced shoreward transport during El Niño events have been suggested to be important for bringing slope-spawned larvae onto the continental shelf (Bailey *et al.*, 1997; Bailey and Picquelle, 2002). Increased cross-shelf flow due to mesoscale eddies is another feasible mechanism of delivery. Haida, Sitka, and Yakutat eddies have been observed from satellite surface chlorophyll measurements to either entrain coastal water around the rim, or send jets of coastal water into the basin (Crawford *et al.*, 2005; Ladd *et al.*, 2009). High flow rates are associated with the edge of an eddy (azimuthal velocity: 25–50 cm s⁻¹), and pelagic late stage larval fish swimming <10 cm s⁻¹ will not be able to swim against this flow. If transport is along the equator-ward edge of a clockwise spinning (anticyclonic) eddy in the eastern GOA, then net flow will be offshore and larvae may not be able to reach appropriate nursery habitat on the shelf. Along the higher latitude eddy edge, flow will be onshore and could provide on-shelf transport for these larvae to appropriate nursery habitat.

Eddies could also benefit fish species not dependent on retention over the continental shelf, such as the deepwater-spawning northern lampfish (*Stenobrachius leucopsarus*). Eddies could benefit lampfish through increased primary productivity over the slope and basin, which may increase potential prey concentrations. Biological productivity associated with eddies is typically elevated in comparison with surrounding oceanic waters (Peterson *et al.*, 2005; Gaughan, 2007; Bibby *et al.*, 2008), and could affect abundances of mesopelagic fishes (Olson, 1991; Muhling *et al.*, 2007). Higher trophic level taxa that respond to enhanced feeding conditions within eddies through extended stays or changes in feeding trip trajectories include penguins (Cotté *et al.*, 2007), seabirds (Nel *et al.*, 2001; Weinmerskirch *et al.*, 2004; Hyrenbach *et al.*, 2006), sea turtles (Polovina *et al.*, 2004, 2006; Revelles *et al.*, 2007), seals (Ream *et al.*, 2005), and whales (Griffin, 1999).

Examining eddies as potential mechanisms of larval exchange between the shelf and continental slope water has wide applicability to other marine systems. Given documented entrainment of zooplankton species (Mackas and Galbraith, 2002; Strzelecki *et al.*, 2007), ichthyoplankton entrainment is also likely (Wiebe *et al.*, 1976; Wroblewski and Cheney, 1984; Flierl and Wroblewski, 1985), which could affect larval survival and subsequent recruitment (Myers and Drinkwater, 1989; Gaughan, 2007). The results of this study cannot be used to answer the question of whether eddies are significant contributors to variation in fish populations in the GOA. These results do suggest

that eddies have an impact on larval fish assemblages, and that these impacts can change depending on the age of an eddy. Future studies with higher resolution sampling of both within-eddy and outside of eddy ichthyoplankton assemblages, and how these assemblages change over time, would answer how eddy activity impacts ichthyoplankton communities in the GOA. An understanding of the impact of mesoscale eddies on larval abundance would contribute to better estimates of recruitment success, potentially improving management decisions in the Gulf of Alaska.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Trajectory of ARGOS drifter #43698, used to estimate eddy center location in 2004.

Appendix S2. Trajectory of ARGOS drifter #37492, used to estimate eddy center location in 2003.

Appendix S3. Trajectory of ARGOS drifter #36263, used to estimate eddy center location in 2002.

Appendix S4. Raw data from the 2005 cruise (FOCI #1TT05), showing station and total concentration (m^{-2}) for all species sampled.

Appendix S5. Raw data from the 2004 cruise (FOCI #2HX04), showing station and total concentration (m^{-2}) for all species sampled.

Appendix S6. Raw data from the 2003 cruise (FOCI #2KM03), showing station and total concentration (m^{-2}) for all species sampled, with larval catches listed separately than egg catches.

Appendix S7. Raw data from the 2002 cruise (FOCI #2EW02), showing station and total concentration (m^{-2}) for all species sampled, with larval catches listed separately than egg catches.

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