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Adaptive classification of marine ecosystems: Identifying biologically meaningful regions in the marine environment

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Abstract

The move to ecosystem-based management of marine fisheries and endangered species would be greatly facilitated by a quantitative method for identifying marine ecosystems that captures temporal dynamics at meso-scale (10s or 100s of kilometers) resolutions. Understanding the dynamics of ecosystem boundaries, which may differ according to the species of interest or the management objectives, is a fundamental challenge of ecosystem-based management. We present an adaptive ecosystem classification that begins to address these challenges. To demonstrate the approach, we quantitatively bounded distinct, biologically meaningful marine regions in the North Pacific Ocean based on physical oceanography. We identified the regions by applying image classification algorithms to a comprehensive description of the ocean's surface, derived from an oceanographic circulation model. Our resulting maps illustrate 15 distinct marine regions. The size and location of these regions related well to previously described water masses in the North Pacific. We investigated seasonal and long-term changes in the pattern of regions and their boundaries by dividing the oceanographic data into four seasons and two 10-year time periods, one on either side of the 1976–1977 North Pacific Ocean climate regime shift. We compared our results for each season across the regime shift and for sequential seasons within regimes using the Kappa Index of Agreement and the index of Average Mutual Information. Seasonal patterns were more similar between regimes than from one season to the next within a regime, while the magnitude of seasonal transitions appeared to differ before and after the regime shift. We assessed the biological relevance of the identified regions using seasonal maps derived from remotely sensed chlorophyll-*a* concentrations ([chl-a]). We used Kruskal–Wallis and Wilcoxon rank sum tests to evaluate the correspondence between the [chl-a] maps and our post-regime shift regions. There was a significant difference in [chl-a] among the regions in all seasons. We found that the number of regions with distinct chlorophyll signatures, and the associations between different regions, varied by season. The overall pattern of association between the regions was suggestive of observed, broad-scale patterns in the seasonal development and distribution of primary production in the North Pacific. This demonstrated that regions with different biological properties can be delineated using only physical variables. The flexibility of our approach will enable researchers to visualize the geographic extents of regions with similar physical conditions, providing insight into ocean dynamics and changes in marine ecosystems. It will also provide resource managers with a powerful tool for broad application in ecosystem-based management and conservation of marine resources.

Keywords: Ecoregion; Biogeography; Ecosystem management; Habitat modeling; Ecosystem models; Habitat classification; North Pacific

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1. Introduction

Studies at the ecosystem level are relevant to both fisheries management and protected areas definition. Fisheries managers are increasingly required to take ecosystem considerations into account when assessing commercially exploited stocks, while conservation efforts are increasingly focused on delineating areas that will protect habitats of species at risk at all life stages. The determination of habitat boundaries (e.g., essential or critical habitat) for both endangered and commercial marine species has been a legal requirement in the United States for decades under both the Endangered Species Act (1973) and the Magnuson-Stevenson Fisheries Conservation and Management Act (1996). In Canada, similar legislation is now in place in the form of the Species at Risk Act (2002). This increasing focus on ecosystem-based management, first advocated at least 70 years ago (Allee, 1934), presents significant challenges, including the mapping of marine ecosystems in space and time.

Ecosystem mapping—the characterization of a physical environment and its associated biota—is complex. Even in terrestrial ecology, commonly described as being decades ahead of marine ecology in terms of ecosystem classification, there is no single, general non-taxonomic classification system for ecological units beyond the species level (Morrison et al., 1998). Instead, terrestrial regions are often delineated based on biological, geographic, and climatic characteristics (e.g., biogeoclimatic zones). This works well as an operational definition of terrestrial ecosystems because the biological component (i.e., flora) is relatively immobile. It is only an operational definition because it does not include the more mobile components of the terrestrial ecosystem (e.g., insects, birds, ungulates). Biogeoclimatic zones thus provide landscape ecologists a bio-physical pattern, a spatial context, in which the more mobile components of the terrestrial ecosystem exist.

There has been limited success in applying the methods of landscape ecology to the oceans. While even a cursory examination reveals physical and biological patterns in the oceans at a range of spatial and temporal scales (e.g., Bakun, 1996; Mann and Lazier, 1996), the patterns are ephemeral and manifest themselves differently across spatial scales. In contrast to the landscape, marine primary production (phytoplankton) is patchy, ephemeral, and quickly consumed by higher trophic levels. The processes responsible for creating the patterns in phytoplankton distribution are largely a function of physical forcing and the associated biological response (Platt and Sathyendranath, 1999). The overall biogeographic patterns (ecosystems) thus represent a combination of environmental structure, species behavior, and population dynamics (MacArthur, 1972).

Variability in physical forcing results in physical patterns with different spatial and temporal scales that provide the environmental structure for the overlying biology. However observations of these biological patterns and their integration into the classification can be complicated by species at various trophic levels, operating at different spatio-temporal scales (Steele, 1989). Given the dynamic nature of the marine environment and the mobility of the species of interest (marine mammals and commercial fishes), methods for delineating ecological marine boundaries must be adaptable to a range of spatial and temporal scales. The delineation and mapping of a dynamic geo-physical context has the potential to be as useful to marine ecology as biogeoclimatic zones are to terrestrial ecology.

In this study, our objective was to apply image classification techniques to the marine environment as a method for classifying this environmental structure. We hypothesized that regions of similarity identified by a classification based solely on physical parameters would have both physical and biological significance, and consequently assessed the resulting maps in terms of both physical and biological relevance. Since we are undertaking the task of mapping ocean regions that are both physically and biologically meaningful, a brief look at previous efforts to classify the marine environment into meaningful regions is warranted.

1.1. Existing classification systems

Marine ecosystems have commonly been defined in one of four ways (Laevastu et al., 1996): the nature of the dominant organisms (e.g., planktonic ecosystems); specific physical features (e.g., reef and benthic ecosystems); geographic locations (e.g., Bering Sea ecosystem); or some combination of these. Classification systems have been developed to describe such boundaries. A shared characteristic of most classification schemes is that they operate on a single spatial and temporal scale. Generally, these scales tend to be large (coarse resolution) and have no temporal variability. Higher resolution (i.e., meso-scale) classifications have been limited to nearshore areas (particularly reefs, coastlines, and estuaries) because of the tendency to associate ecological boundaries with tangible features (e.g., bathymetry) or with political boundaries. Explicitly temporal (i.e., seasonal) classifications are extremely rare.

Marine classifications using some combination of biological and physical features, and geographic location, are by far the most common. The three most frequently cited systems are: Cowardin's (1979) classification of wetlands and deepwater habitats; Sherman's (1986) Large Marine Ecosystems (LMEs); and Longhurst's (1998) biomes and provinces. These can be characterized as bottom-up classifications, where lower trophic biology, physics, and/or chemistry are used to define marine boundaries assumed to be meaningful for an entire multi-trophic ecosystem.

Cowardin's (1979) system is primarily designed for wetlands, with the marine portion limited to substrate characterization. LMEs (Fig. 1a), described as being characterized by unique hydrographic regimes, submarine topography, and trophically-linked populations, have been extensively applied to ecosystem studies and management (Sherman, 1986). While the LME approach has been useful, we could find no quantitative description of how LME boundaries were identified, or how the distinctiveness of each LME might be quantified. Longhurst's (1998) classification of the world's oceans into biomes and provinces (Fig. 1b) does integrate physical oceanography with biogeography. However, Longhurst (1998) cautions that the boundaries illustrated are somewhat arbitrary, intended to represent approximate spatial relationships between the provinces.

Classifications have also been undertaken at local scales, typically applied to shelf waters (e.g., Zacharias et al., 1998, in British Columbia; Bredin et al., 2001, in the Bay of Fundy). These can be termed 'cookie cutter' approaches, because data layers are overlaid, and regions are defined as the intersection of the categories contained in each layer. Boundaries are thus a function of the spatial intersection of the source data and are often driven by spatially invariant bathymetry or benthic categories. When dynamic variables such as temperature or salinity are included, seasonality is typically ignored.

We found a single "top–down" approach that attempted to identify regions based on biologically dominant species and communities occurring there. Ray and Hayden (1993) applied Principal Component Analysis to the habitat ranges of 86 species in the Bering, Chukchi, and Beaufort Seas and mapped six 'provinces' based on the highest loading principal components. They noted that these provinces did not correspond well to the outer, middle, and inner shelf domains that are typically used to characterize the Bering Sea, suggesting that a single ecosystem classification does not suit all applications.

Roff and Taylor (2000) proposed a hierarchical scheme for classifying representative or distinctive marine habitats for marine conservation. Their proposed approach for linking biological and physical attributes, while similar to ours, does not address the dynamic nature of boundaries. From a conservation perspective, the consequences of dynamic ecosystem boundaries are significant (Wilson et al., 2004).

Finally, Platt and Sathyendranath (1999) proposed an operational definition of ocean structure

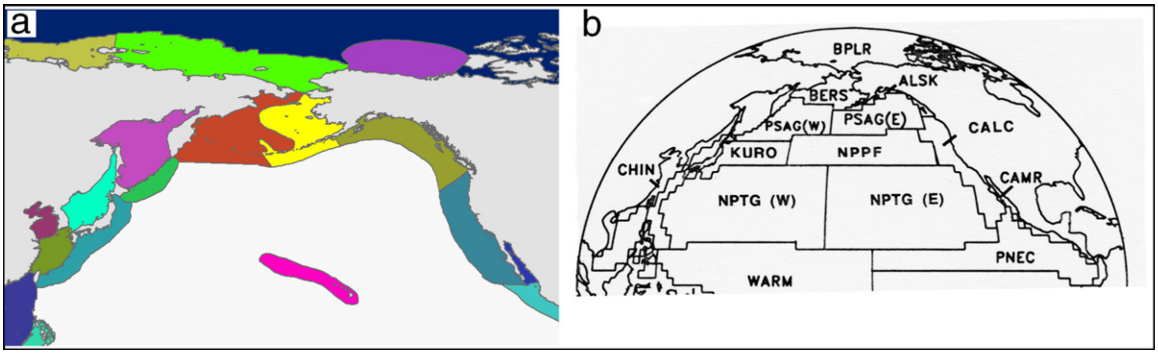

Fig. 1. Ecosystem boundaries according to two well-known marine classification systems applied to the North Pacific by (a) Sherman (1986) and (b) Longhurst (1998).

for identifying production domains using biological rate parameters derived from remotely sensed chlorophyll. Their approach maps dynamic, biogeochemical provinces, lends itself to seasonal analyses, and provides a framework for investigating the underlying physical processes. However, extending this approach to higher trophic levels would require identification of the appropriate rate parameters, and their integration over the appropriate spatial and temporal scales.

While these approaches to classification have helped us understand some aspects of oceanic structure, they do not provide a means of quantifying and mapping the dynamics of ecosystem boundaries. For example, if understanding that a California Current ecosystem exists is important, delineating its seasonal and spatial extents in any given season or year must be equally important.

1.2. Adaptable marine classification

Certainly, there is not one correct way to classify marine ecosystems (Grossman et al., 1999; Steele, 1989). Rather, management objectives (Grossman et al., 1999; Perry and Ommer, 2003), processes (Morrison et al., 1998), or species (deYoung et al., 2004) determine the appropriate methods and scales (in terms of extent and resolution). By definition, the multi-species objectives of ecosystem management require a classification approach that can adapt to multiple temporal and spatial scales. There is some evidence that species distributions at higher trophic levels (e.g., pelagic fish and squid) are spatially linked to specific water masses and that these links persist across time and across contrasting physical conditions (e.g., Garrison et al., 2002; Polovina et al., 2001). This suggests that identifying regions of similar hydrographic properties over appropriate temporal scales may provide useful descriptions of species' habitats.

In this study, we address this issue by illustrating a classification approach that is adaptable in terms of scale and input data sets, and bounds hydrographic structures in the oceanic marine environment. Our approach differs from other marine classification efforts because it allows available physical and biological data to be integrated across any specified spatial or temporal scale supported by the data. While the relevant scales will be somewhat species-specific, resource managers must deal with seasonal and inter-annual temporal dynamics and spatial scales on the order of 10s or 100s of kilometers. Thus, any relevant definition of a marine ecosystem must provide information at these scales.

2. Methods

We applied image classification (a method for identifying classes in remotely sensed images) to a comprehensive physical oceanographic data set describing the surface of the North Pacific to find regions of similarity within the seascape (Fig. 2). We examined the oceanographic and ecological relevance of the identified regions in three ways. First, we qualitatively compared them to documented upper zone, hydrographic features, such as major water masses and surface currents. Second, we compared changes in the patterns of regions to documented changes resulting from the 1976–1977 regime shift (e.g., Anderson and Piatt, 1999; Benson and Trites, 2002). We also calculated the relative similarity of the patterns of regions among and between seasons for two 10-year time periods before and after this regime shift. Finally, we assessed the biological significance of the regions identified in the post-regime shift period by testing for differences in seasonal chlorophyll-*a* concentrations ([chl-a]), derived by remote sensing, among the regions.

2.1. Study area and resolution

We conducted our basin-wide classifications of the temperate North Pacific on a 100 by 100 km grid for all oceanic waters between 30°N and 65°N. We selected this grid size partly because of the resolution of the source data (1° longitude–latitude grid), but also because the coupling of space and time scales suggests that this may be an appropriate resolution for examining meso-scale patterns typically observed in open ocean ecosystems (Mann and Lazier, 1996, p. 258). Since seasonal changes can be relatively pronounced at these latitudes, we chose a temporal resolution of four seasons. To visualize and evaluate changes in the oceanic regions due to decadal scale changes in ocean climate, we produced seasonal results for two 10-year periods (1966–1975 and 1980–1989). We did not evaluate inter-annual changes.

2.2. Data

The nature of our analysis placed several constraints on the suitability of data sets. We required

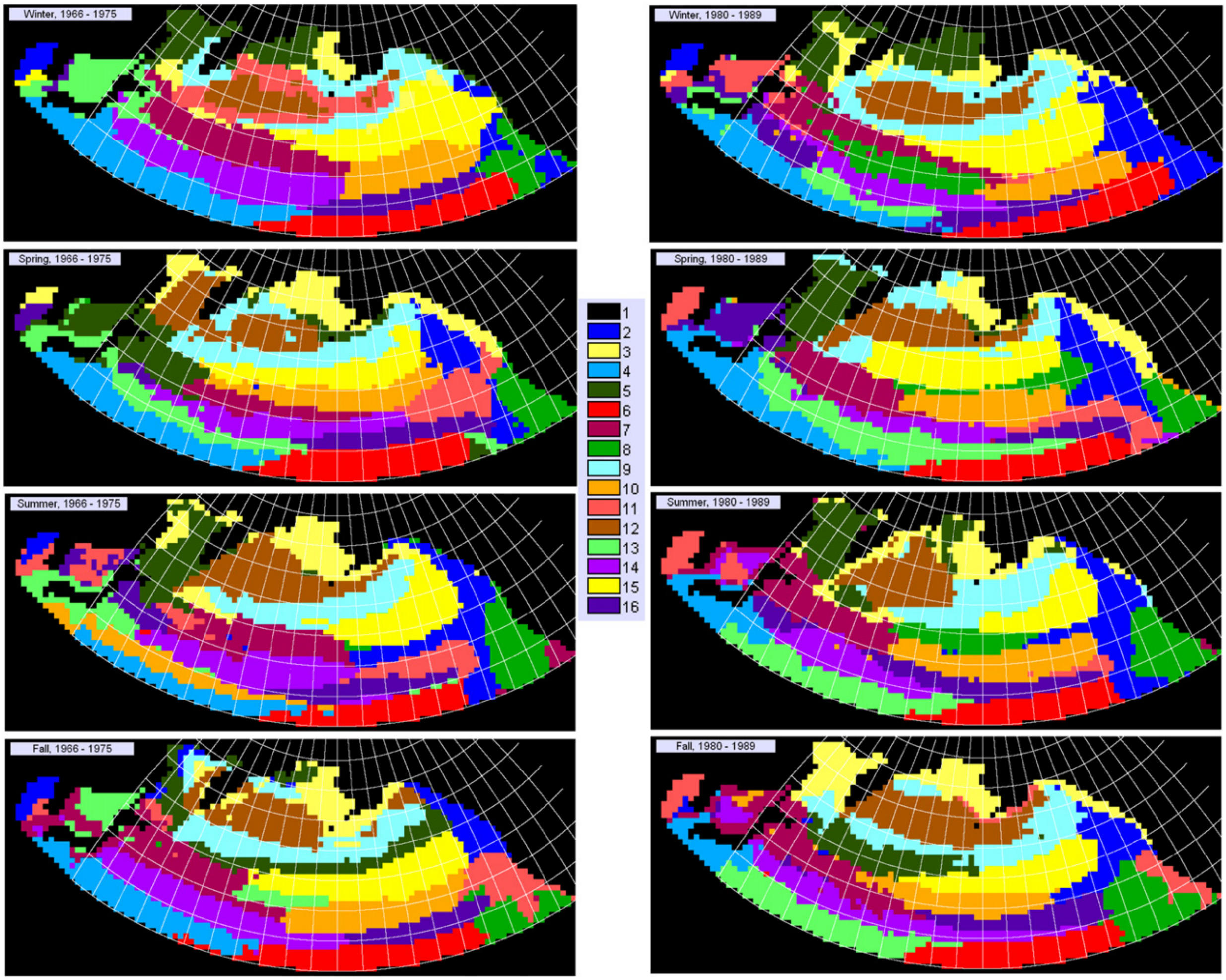

Fig. 2. Results of the image classification applied to five input variables to generate 15 regions per seasonal partition.

spatially comprehensive data and long-term seasonal averages pre-dating contemporary satellite-based sensors. Thus, we relied on the output from a basin-scale General Circulation Model (GCM) from which we derived seasonal averages for a suite of physical oceanographic variables. GCMs are predictive models of the marine environment typically used by oceanographers to characterize oceanic currents and conditions for a range of applications including studies of climate change, oceanographic processes, and primary production. These models are the only source of a comprehensive, four-dimensional (latitude, longitude, depth, time) description of the marine environment, and as such were amenable for our study.

We used five different physical variables output from a ROMS (Regional Ocean Modeling System—see http://marine.rutgers.edu/po/index.php?model=roms) GCM of the North Pacific (Yi Chao, unpublished data, Jet Propulsion Laboratory, California Institute of Technology). We obtained monthly averages for wind stress (dyn cm^{-2}), surface current velocity ($\mathrm{m\,s}^{-1}$), sea surface height (SSH, cm), sea surface salinity (SSS, psu), and sea surface temperature (SST, °C) for two ten-year periods (1966–1975 and 1980–1989) spanning the 1976–1977 regime shift.

We used surface variables for two reasons: First, because surface features (fronts, upwellings, etc.) are the manifestation of larger physical processes, they adequately describe observed oceanic patterns. Second, because [chl-a] is closely associated with the surface layer, surface variables were appropriate to test our hypothesis that such a classification would result in biologically meaningful regions.

We divided the year into four equal three-month seasons starting with January–March. This resulted in a total of 40 coverages (i.e., digital maps), each representing one of five input variables for eight temporal snapshots (four seasons in each of two time periods).

2.3. *Image classification*

We used an unsupervised cluster analysis algorithm provided by the IDRISI software system (Clark Labs, 2003) to statistically organize the oceanographic input variables into distinct marine regions. The approach is analogous to terrestrial classifications of multi-spectral satellite imagery into landscape classes (e.g., agricultural, urban, forest, etc.). The algorithm partitions the study area into a specified number of regions according to the variance structure of the data.

Clustering results are most robust if the input variables are standardized and transformed to a multivariate-normal parameter space. We therefore examined the histograms for each variable and applied a transformation to improve normality when necessary. The values were then standardized by converting each file to byte format (256 classes).

We applied IDRISI's ISOCLUST routine (based on H-means and K-means clustering procedures—Hartigan, 1975) to create clusters representing regions of similarity. We chose the number of clusters to keep by examining histograms of pixels per cluster for significant breaks in the slope. The breaks in slope represent different levels of generalization of the data. Clusters with small numbers of pixels (i.e., where the slope of the histogram flattens) are relatively insignificant. To allow comparisons among seasons and regimes, the resulting partitions (mapped results) required the same number of clusters. We chose to keep 15 clusters based on a visual examination of the eight histograms.

2.4. *Evaluating classification results*

To evaluate the oceanographic relevance of our regions, we compared our results with the upper zone domains identified by Dodimead et al. (1963). Specifically, we projected the results from our summer pre-1976 analysis into geographic (lat–lon) coordinates and overlaid the schematic drawn by Dodimead et al. (1963), which was based on an analysis of summer SST, SSS, and surface current data from 1955–1959. These domains have proven to be robust over time in the sense that they are still referred to by name in oceanographic literature. We also qualitatively compared our results to features commonly mentioned in the oceanographic literature.

We compared seasonal partitions within and between time periods using both the Kappa Index of Agreement (KIA) (Pontius Jr., 2000) and the Average of Mutual Information (AMI) (Finn, 1993). KIA is a measure of the similarity of two images and takes into account the location and quantity of pixels in matching regions. KIA, when used as a measure of model accuracy to compare modeled output to reference data, assumes that the regions compared between images match or represent the same class. In our case, because each partition was the output from an independent classification analysis, there was no inherent relationship between the regions in one partition and the regions in another. We therefore matched regions between images using a cluster separation measure and consistency of location as our guides, and used KIA scores to provide a relative measure of similarity between partitions.

On the other hand, AMI quantifies the amount of information shared between two images. AMI is described as a measure of consistency rather than correctness (Finn, 1993). To quantify shared information, AMI calculates the conditional probabilities that an area in one map is a member of a particular class given the class of that area in the second map (Finn, 1993). Thus, AMI provides a means of quantifying similarity between maps with different themes (Couto, 2003).

We calculated KIA scores, using IDRISI's VALIDATE module (Clark Labs, 2003), for sequential seasonal partitions within time periods and paired seasonal partitions before and after the 1976–1977 regime shift. KIA values range from -1, indicating complete disagreement, to $+1$, meaning perfect agreement. Positive KIA values indicate that two partitions are more similar than chance alone would dictate, and greater similarity scores higher. Negative KIA values indicate that two images are more different than one would expect due to chance. We calculated AMI scores for the same image pairs for which we calculated the KIA. Since AMI scores depend on the application, we calculated the maximum theoretical value for two identical maps of 15 regions and reported both absolute scores and scores as a proportion of the maximum.

To assess the potential biological relevance of the regions identified in our classification analyses, we compared seasonal [chl-a] among our post-1976 regions in the North Pacific. We obtained monthly, remotely sensed [chl-a] climatologies (long-term averages) from September 1997 to March 2006 (SeaWiFS Project, 2006), projected these climatologies onto our study grid, and calculated seasonal averages. While there is evidence for additional regime shifts in 1989 and 1998, these are not thought to have reversed the 1976–1977 shift (Bond et al., 2003). Therefore, the [chl-a] climatologies represent the best available biological data with which to evaluate the relevance of our regions.

We tested the null hypothesis that there were no significant differences in distributions of [chl-a] among the regions within each season using the Kruskal–Wallis *H*-test. We then examined the significant results for each season by testing all pair-wise comparisons for a significant difference using the Wilcoxon rank sum test (also known as the Mann–Whitney test) with a Bonferroni corrected alpha level (Sokal and Rohlf, 1995). Both of these tests are non-parametric, rank-based tests and are consequently robust to non-normality in the distributions. In cases where parametric methods would also be applicable, these non-parametric tests are considered to be 95% as powerful (Zar, 1996). The normal approximation of the Wilcoxon test statistic was used because of the large sample sizes in our study.

3. Results

3.1. Oceanic regions

Overall, the individual oceanic regions (Fig. 2) were reasonably spatially coherent despite the non-spatial nature of the image classification (i.e., the locations of pixels were not considered during the clustering). Visual inspection of the results suggested that some geographic areas of the North Pacific exhibit greater relative variability than others within the time period captured. This was demonstrated by a higher number of smaller, less contiguous clusters. For example, the Sea of Japan appeared quite variable especially in summer and fall when it was divided among three or four different clusters. In contrast, the large coastal shelf in the eastern Bering Sea was always represented by one or two clusters, suggesting greater homogeneity. The Sea of Okhotsk also appeared to be a fairly homogenous region (except in fall pre-1976), while the area east of Japan (the location of the dynamic Kuroshio Current) was dominated by high variability across most seasons in both regimes.

3.2. Correspondence with known features

The patterns of oceanic regions for summer pre-1976 were very similar to the upper zone domains described by Dodimead et al. (1963) (Fig. 3). In fact, several features in the schematic were associated quite clearly with colored regions and their boundaries. The Alaska Gyre corresponded well to the pale blue region (#9), although this region extended further west and also encompassed most of the western subarctic gyre. The subarctic boundary and the northern boundary of the transitional domain both corresponded roughly to boundaries between colored regions and this correspondence persisted across seasons and regimes. However, some of the features in the schematic were not well represented in our map of regions including the Okhotsk Sea gyre and the Bering Sea gyre. Furthermore, while the partition contained several divisions from east to west, the boundary between western and central subarctic domains depicted by Dodimead et al. (1963) intersected the middle of two colored regions. Similarly, the Bering Sea was split into two regions in our analysis, but the boundary between them was offset from the boundary of the Bering Sea coastal domain shown on the schematic. The locations of these boundaries between regions shifted considerably in both latitude and longitude among the seasons and between climate regimes in our results (Fig. 2).

Dodimead et al. (1963) recognized five major domains, based on an analysis of sparse shipboard sampling. The results of our classification were best represented by 15 unique, relatively homogenous regions. It was therefore not surprising that some of the domains identified by Dodimead et al. (1963) were best represented by a combination of regions. For example, the central subarctic domain contained the bright yellow region (#15), part of the Alaska Gyre pale blue region (#9), and part of the burgundy region (#7) (Fig. 3). Similarly, the transitional domain contained portions of several regions, most notably deep blue (#2), green (#8), and peach (#11) (Fig. 3). In contrast, the Alaskan stream domain did not correspond to a unique colored region in any of our results (Fig. 2). Although our results distinguished between the Alaskan stream domain and the Alaska Gyre area,

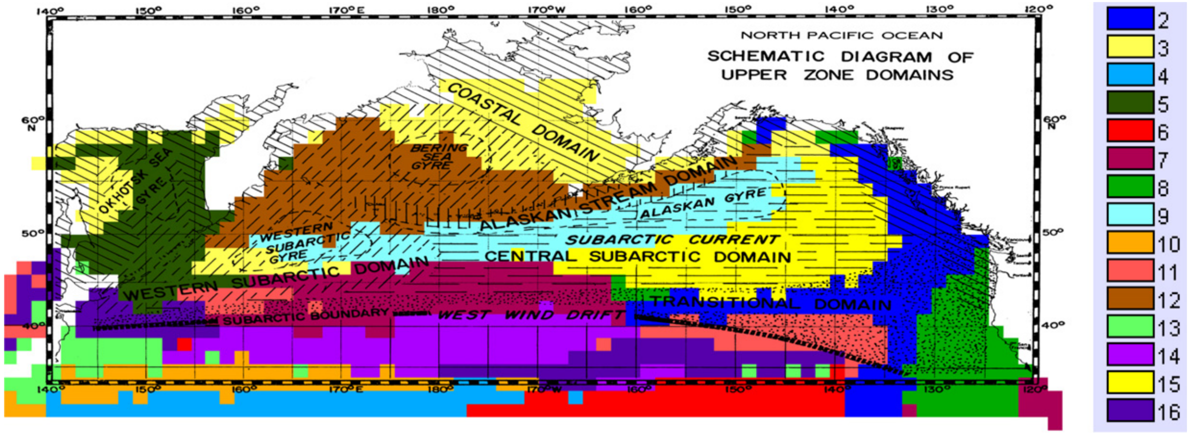

Fig. 3. Upper zone domains of Dodimead et al. (1963) overlaid with regions identified by our classification method for summer pre-1976.

the former was not always distinct from the Bering Sea shelf or the western Bering Sea/western subarctic. In addition, our analyses divided the Dodimead et al. (1963) coastal domain into numerous regions across the study area, except in spring pre-1976 and fall post-1976 (Fig. 2), when the coast was classified as fairly homogenous. Finally, our results suggested that the single western subarctic domain was both heterogeneous within each partition and differed considerably among seasons and regimes.

The transitional domain was, not surprisingly, made up of several regions in all partitions. However its southern extent (the subarctic boundary), which stretches eastward across the Pacific at about 40°N from the Japan coast to about 150°W and then veers south, was evident in all partitions, though its location fluctuated by a few degrees latitude among partitions (Fig. 2).

The location identified as the bifurcation of the subarctic current (including parts of the central subarctic and transitional domains) was an area of high change between seasons and regimes in our results (as indicated by the pattern of multiple regions within most partitions—Fig. 2). The pattern of a northward curve of the northern transition zone boundary was evident in most partitions as a boundary between regions and was quite persistent across partitions, though the precise location fluctuated.

3.3. *Seasonal and regime transitions*

In our search for qualitative descriptions of how oceanic domains change seasonally we found a single description of how a North Pacific upper zone domain or water mass shifted in location by season. Ware and McFarlane (1989) described the average position of the subarctic current as fluctuating seasonally between near 50°N in summer and 45°N in winter. In our post-1976 partitions, the bright yellow cluster (#15—Fig. 2) straddled 45°N in winter, between 175°W and 135°W, and was located progressively further north in spring and summer, when it lay almost completely north of 45°N. This cluster may therefore capture the spatial extents and seasonal movements of the subarctic current.

The Aleutian Low pressure system, which dominates the climatological winter pattern in the North Pacific and stretches from Kamchatka to the Alaska Peninsula, is strongest in the winter and weakens as it shifts to the northwest in the spring (Ware and McFarlane, 1989). Our analysis identified a region (#12, brown—Fig. 2) that corresponded to this description of location and seasonal shift of the Aleutian Low in both the pre- and post-1976 partitions. This correspondence may illustrate an unspecified mechanistic connection between atmosphere and ocean.

Several notable changes related to the 1976–1977 regime shift included a deepening and eastward shift of the Aleutian Low pressure system resulting in a stronger flow in the Alaskan Gyre (Benson and Trites, 2002), a warming of the Northeast Pacific, especially in a broad band along the North American coast, the cooling of the central North Pacific (Hare and Mantua, 2000), and reduced sea ice extents in the Bering Sea (Wyllie-Echeverria and Wooster, 1998). The stronger Aleutian Low may be reflected in the larger, more contiguous brown region (#12—Fig. 2) in winter post-1976 compared to pre-1976, especially in the area of the Alaskan Gyre. Some of the highest variance in the pattern of regions did occur in the areas of greatest SST change: in the area where greatest cooling occurred in winter (between 39°N and 44°N, from 170°E to 175°W—see Fig. 8a in Hare and Mantua, 2000), a 'new' green region (#8—Fig. 2) appeared in our post-1976 winter partition. Similarly, the Northeast Pacific coastal areas, where the greatest warming occurred (see Fig. 8a in Hare and Mantua, 2000), differed greatly between pre- and post-1976, especially the size and location of the dark blue and pale yellow winter regions (#2 and #3—Fig. 2). In addition, the extent and location of regions on the eastern Bering Sea shelf differed between pre-1976 and post-1976 winter partitions, possibly indicative of changes in sea ice cover over time.

3.4. Similarity of oceanic partitions

Visual comparison of the different partitions showed considerable seasonal and inter-regime differences. The KIA and the AMI quantified these differences in terms of the size and location of regions, and the consistency of the patterns of regions, respectively. The KIA scores were lower between seasons in the within-regime comparison ($\mu_{\text{pre-1976}} = 0.40$, $\mu_{\text{post-1976}} = 0.38$) than within a season across regimes ($\mu = 0.49$) (Table 1). Therefore, patterns for consecutive seasons were consistently more different than the patterns for the same seasons between regimes. KIA scores comparing patterns between regimes showed little variation among season (e.g., ranged from 0.47 to 0.50), suggesting that any regime shift effects were manifested equally across the seasonal oceanic patterns.

While our KIA scores could not be tested for statistically significant differences (because we did not compare model results to data), a relative comparison of the scores for consecutive seasons implied that fall and winter were more similar before than after the regime shift. Conversely, summer and fall were more similar after 1976 than before (Table 1).

Overall, the AMI scores (Table 1) were consistent with the KIA results and likewise suggested that any seasonal pattern was a better predictor of the same season post-regime shift than it was of the subsequent season in the same regime. Summer was a better predictor of fall post-1976, than it was pre-1976, corroborating the KIA results.

Table 1
Kappa index of agreement (KIA) and Average of Mutual Information (AMI) scores for comparisons of partitions (classification results) between consecutive seasons within regimes and between regimes for each season

Regime/season	KIA	AMI	Prop. of Max
	Within-regime comparison		
Pre-1976			
Winter–spring	0.32	2.192	0.56
Spring–summer	0.42	2.222	0.57
Summer–fall	0.38	2.062	0.53
Fall–winter	0.47	2.286	0.59
Mean	0.40		
Post-1976			
Winter–spring	0.29	2.102	0.54
Spring–summer	0.41	2.185	0.56
Summer–fall	0.50	2.334	0.60
Fall–winter	0.32	2.277	0.58
Mean	0.38		
	Between-regime comparison		
Winter	0.50	2.461	0.63
Spring	0.50	2.310	0.59
Summer	0.47	2.442	0.63
Fall	0.49	2.410	0.62
Mean	0.49		

Prop. of max. is the proportion of the maximum theoretical value (3.906) achieved by the AMI score.

3.5. Biological relevance

The Kruskal–Wallis test score allowed us to reject the null hypothesis of no difference in [chl-a] between regions in all four post-regime shift partitions. When we applied pair-wise comparisons of regions using the Wilcoxon rank sum test to identify the region(s) with significantly different [chl-a] distributions, we rejected the null hypothesis (that [chl-a] distributions were identical between regions) when p-values were less than 0.000476. This corresponded to a Bonferroni-corrected alpha level of 0.05, for 105 pair-wise comparisons done for each season (Sokal and Rohlf, 1995). Overall, we failed to reject 42 pair-wise comparisons in spring, 14 in summer, only 6 in fall, and 13 in winter (Fig. 4) showing that many regions were significantly different from each other in terms of the distribution of their [chl-a].

Specifically, our spring season (Jan–Mar) showed the least differences between clusters, implying a relatively homogenous [chl-a] distribution throughout the study area at the scale of these regions. Exceptions included regions #3 and #11 with high concentrations, and region #6 with the lowest concentration (Fig. 5).

Summer showed a distinction developing between the regions as [chl-a] began to increase in some regions. Regions #3 and #5 were not statistically different and, when combined, potentially capture the spring bloom in the Bering Sea and the Sea of Okhotsk. Regions #6 and #13 were distinct from all other regions in this season, though both had very low [chl-a]. Their location at the southern extent of our study area (near 30°N) strongly implied their association with the less productive sub-tropical gyre.

Regions were most distinct in the fall, with 4 unique regions, 3 of which (#6, #13, and #14) again showed low chlorophyll concentrations. This was potentially related to the northward movement of the Transition Zone Chlorophyll Front in summer (Polovina et al., 2001). [Chl-a] distributions in clusters #11 and #12 were not dissimilar and combined they formed a region with the second highest chlorophyll concentration. While #11 is located in the vicinity of the California upwelling (and the Yellow Sea) and #12 is in the Bering Sea, the co-occurrence of clusters #11 and #12 along the Alaskan peninsula and the Aleutian Islands suggested that different combinations of physical

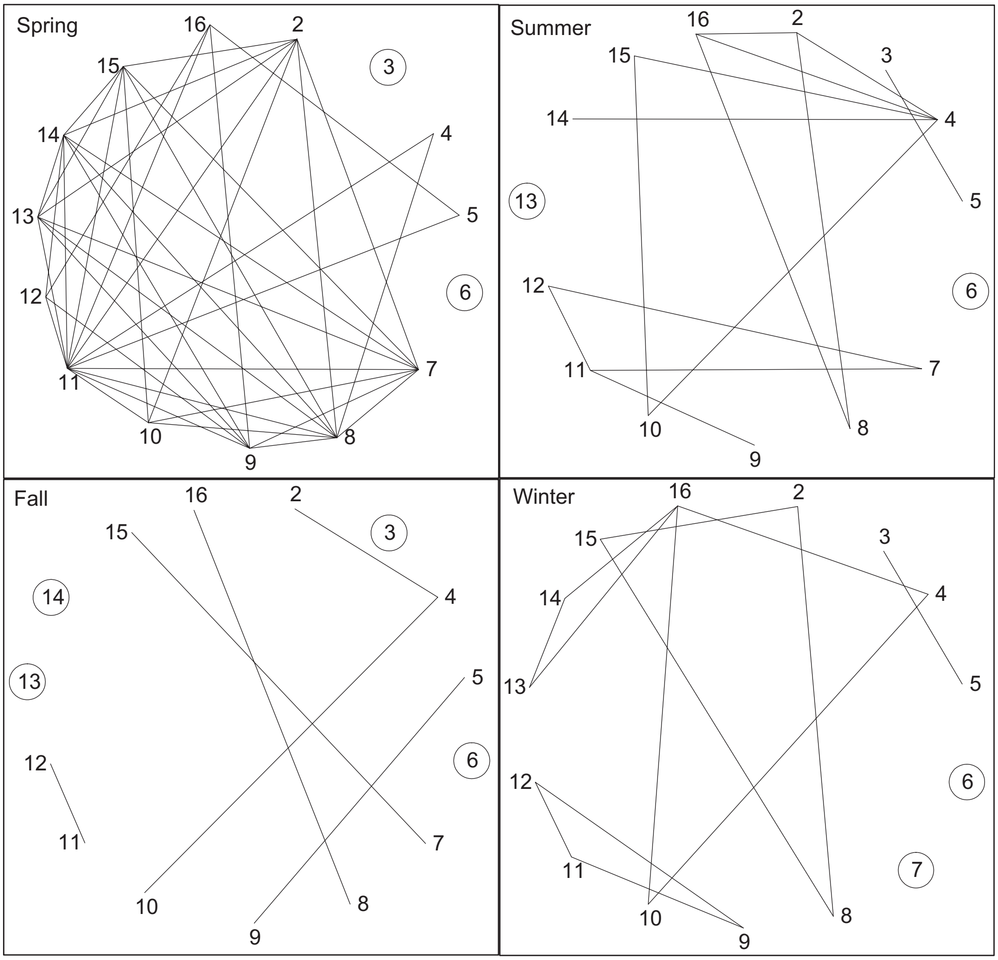

Fig. 4. Plot of results from multiple comparisons tests for each season. Pairs of regions for which the null hypothesis (H_o: the distribution of [chl-a] values within the two regions is identical) could not be rejected are connected with lines. Regions that were significantly different from all others are circled.

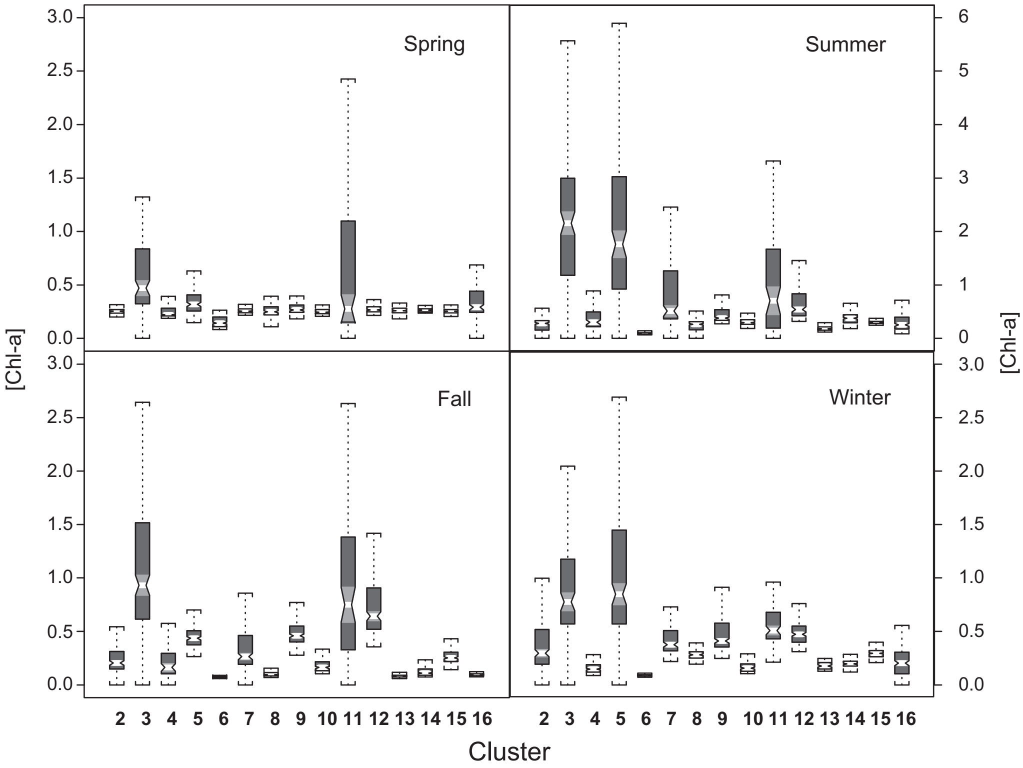

Fig. 5. Bar plots of [chl-a] concentrations for each of the regions identified in our basin-wide classification analyses for each season, post-1976. Note the scale for the summer season is 2x that of the other three seasons.

variables—with possibly different mechanisms—gave rise to similar [chl-a].

In winter, region #2 expanded to include a large portion of the eastern coastal region, and the associated mean chlorophyll concentration doubled from the previous season (Fig. 5). Regions #3 and #5 in the Gulf of Alaska and Bering Sea were again not significantly different from each other and showed the highest chlorophyll concentrations (Fig. 5).

4. Discussion

Our results demonstrate that relatively contiguous oceanic regions can be identified using decadal averages of physical oceanographic variables and a seasonal temporal resolution. Also, these regions can be related, by size and location, to previously well-known water masses (e.g., the Alaskan Gyre, the subarctic current) before and after the 1976–1977 regime shift, and differences between partitions can be related to seasonal variations in these water masses. Given the spatial autocorrelation (i.e., spatial coherence) of the input variables, some homogeneity in the result was to be expected. Nevertheless, the temporal analysis we conducted provides insight into the dynamics of these spatial correlations.

Statistical comparisons using indices of similarity showed that the seasonal patterns of regions were more similar between regimes than from one season to the next within a regime, and indicated differences in seasonal comparisons before and after the regime shift. We also found significant correspondence with the spatial distribution of chlorophyll concentrations, suggesting that the regions identified by our classification analyses have both biological and physical relevance.

4.1. Comparison with other classification systems

While the comparison with large-scale classic domains demonstrates some similarities between the two maps, differences were also apparent between our regions and those of Dodimead et al. (1963) (Fig. 3). This may simply be due to the different number of regions defined in our analysis (15) versus the 11 domains identified by Dodimead et al.

(1963). A higher fidelity with Dodimead et al.'s (1963) regions may therefore have been achieved by reducing the number of regions (clusters retained in the analyses) and/or the number of variables in our study, and perhaps adjusting the temporal bounds of the seasons.

However, our objective was not to duplicate any previous classifications, or to generate a new classification scheme for the North Pacific. Rather we wanted to demonstrate the value of identifying biologically relevant regions for a particular marine environment, by classifying physical variables in a spatial context. Thus, while our adaptive classification approach likely could, through the selection of appropriate variables and scales, produce results similar to Dodimead's domains or Sherman's LME's, that was not our intent. This is also the rationale for not including chlorophyll concentration in the classification scheme, but rather using it as a test of biological relevance.

4.2. *Temporal transitions*

While the seasonality of physical properties has been extensively examined at many locations in the eastern North Pacific, we have found little published literature on seasonal changes of *water masses*. A notable exception is the work done on meso-scale eddies in the eastern North Pacific (e.g., Thomson and Gower, 1998). Our analysis strongly suggests that marine domains (e.g., Alaskan Gyre, subarctic current) are less spatially static across time (seasons and regimes) than is commonly assumed in ecological studies. We believe that seasonal transitions are of crucial biological importance, because essential life processes of many temperate species are tied to seasonality. In our within-regime comparisons of seasonal partitions, a notable difference was increased similarity between summer and fall, and decreased similarity between fall and winter, pre-1976 compared to post-1976 (Table 1). This implies either a change in the magnitude of seasonal transitions or a change in the temporal boundaries of seasons. Bograd et al. (2002) investigated the variable phase and amplitude of seasonal sea level pressure at two locations in the North Pacific and concluded that long term changes in the North Pacific may be associated with changing seasonality. These seasonal transitions therefore warrant more ecological attention.

In addition, the equivalence of the similarity scores in the season to season, between-regime comparisons (Table 1) implies that the influence of the studied regime shift was similar across all seasons. This balanced impact was surprising because many of the indices of regime shifts in the North Pacific are dominated by the intensity of the Aleutian Low (Benson and Trites, 2002); a phenomenon with a very pronounced seasonal cycle, strongest in winter. Our results provide evidence that seasonal atmospheric influences are manifested throughout the year. Our approach may therefore facilitate the 'discovery' and description of seasonal changes and help formulate hypotheses about the processes involved in seasonal transitions.

4.3. *Biological relevance*

Several of the boundaries and regions identified in our study correspond to well-described biogeographic distributions. The southern boundary of the transitional domain, evident in all our partitions, corresponds to a well-documented steep latitudinal gradient of phytoplankton and zooplankton biomass between 38°N and 43°N (McGowan and Williams, 1973). The signature of the Transition Zone Chlorophyll Front's (Polovina et al., 2001) seasonal northward movement in the summer months could be reflected in the increasing chlorophyll concentrations in region #2 (blue–Fig. 3).

The northern boundary of the transitional domain appeared as a boundary in most partitions although the actual location fluctuated (Fig. 3). This region has been subject to zoogeographic classification (e.g., McGowan, 1971; McGowan, 1974) and much fisheries oceanography research (Fulton and LeBrasseur, 1985; Ware and McFarlane, 1989; Zebdi and Collie, 1995). Ware and McFarlane (1989) described the transition zone in terms of three major fisheries production domains, while Fulton and LeBrasseur (1985) documented interannual variation in the amount of northward versus southward flow as well as possible effects on some faunal distributions. Others since have noted that herring recruitment (Zebdi and Collie, 1995) and salmon survival (Mueter et al., 2002) patterns are synchronous within domains but not between domains. Our results can be seen to bolster the conclusions of these studies, while application of our classification approach could help to determine regional boundaries and defining characteristics for studies such as these.

Our statistical analysis demonstrated significant associations between chlorophyll concentrations and the oceanic regions identified. This demonstrates the biological relevance of the patterns identified by our physically based classification. We note that three of the surface variables we used (sea surface temperature, wind stress, and sea surface height) are related to processes linked to plankton production. However, our oceanic regions were based on long-term, seasonal averages of these physical conditions, for a different decade than the seasonally averaged chlorophyll concentrations. Thus, either our results are spurious, or we might expect that a classification using oceanographic data contemporaneous with the [chl-a] data may demonstrate even stronger associations.

Since our classification integrated long-term, average values, we suggest that the linkages responsible for the biological correspondence are related to the persistence and predictability of particular features important to phytoplankton production. These features are driven by physical processes and thus they were 'captured' in our classification results. For example, areas corresponding to higher chlorophyll concentrations probably represent locations where oceanographic conditions regularly provide enrichment, concentration, and/or entrainment features (Bakun, 1996) that allow plankton blooms to occur on a predictable basis. While the processes responsible for plankton production have been studied for decades, few studies, if any, have mapped the spatial extents and seasonal variability in the extents of the underlying processes. This is a critical aspect of ecosystem-based management that can be addressed using an adaptive classification approach.

4.4. Characteristics of adaptive classification

Adaptive classification provides enormous flexibility in terms of variable selection, spatial extent, and resolution. One consequence of this flexibility is that the resulting region boundaries are dependent on the nature (mean, variance, etc.) of physical parameters used and on their spatial and temporal resolution. Thus, the partitioning of a suite of data for any region is a somewhat exploratory exercise. However, the range of options can be narrowed with a clear statement of objectives since the appropriate scale of analysis will be best determined by the questions and species of interest. In fact, the flexibility of the approach is crucial for linking the biology to the physics, because species experience their world at space and time scales relative to their size and life history.

Constrained only by the need to have comprehensive (study-area wide) coverage, the analysis is also adaptable in terms of the nature (variables and resolution) of the oceanographic data used. In our examples we identified self-similar regions based on mean oceanographic conditions, derived from an oceanographic model. However, regions could also be defined on the basis of dynamic oceanography (i.e., high variance), extreme conditions, or any other derived characteristic. We are currently exploring how the inclusion of the temporal variance of parameters and extreme values, in addition to means, affects the partitioning. One testable hypothesis is to investigate whether generalist species are more closely associated with regions based on mean values, and habitat specialists are more closely associated with regions identified using extreme values.

Finally, while an association between classified regions and known species occurrence or habitat provides an indication that the physically defined regions have biological relevance, it is worth considering what the regions actually represent. This issue is most clearly illustrated by a series of images such as those showing seasonal change (Fig. 2). The colored regions generally do not have similar oceanographic characteristics from one period to the next—i.e., they do not represent the same water mass in a different season, and this raises fundamental questions regarding the nature of marine ecosystem boundaries: Are marine ecosystems (relatively) fixed in space, with characteristics that change from season to season? Or do regions/water masses with consistent characteristics move around in response to the physics, moving their associated ecosystems with them? These questions could be explored by comparing the similarity of neighboring regions between seasons. Common marine ecosystem features such as upwelling zones, gyres, fronts, etc., are inherently ephemeral, and although they occur with repeatability from year to year, there may be considerable spatial and temporal variance in their location and composition. The issue of bounding ecosystems in space and time is a complex one and our classification approach, while only scratching the surface, does provide a means to visualize the spatial and temporal changes.

In our study, the regions and boundaries were intimately tied to the issue of scale. The regions changed in both their boundaries and composition, depending on the spatial (i.e., size of the study unit) or temporal (i.e., seasonal and inter-annual) aggregation. Our approach captures boundaries for a snapshot in time, which may be a year, a decade, or longer. However, the boundaries apply only to that particular (in this case temporal) aggregation. We suggest that this dynamic approach to marine ecosystem boundaries may be the most reasonable representation of ecosystems in the dynamic environment that is the ocean.

One aspect of the pattern comparison that remains a challenge is the determination of significant differences. While KIA scores can be evaluated for significant differences (Couto, 2003), the comparison depends on the use of a reference image that represents the 'truth'. Lacking any such a priori definition, new methods will be needed to determine if various regions are significantly different from one another. It may well be that such tests of significance are best related back to the biota for which the regions were defined (i.e., a partition would be significantly 'better' if it was significantly more correlated with the species, or community of interest).

4.5. Variable and scale selection

Although selecting the input variables for exploratory classification analyses such as ours is complicated, there are several guidelines that we tried to follow. Variables should be as widely representative of variation in the domain as possible (Howard, 1991). In our analysis, we were interested in mapping the water masses in the surface domain, so we chose a suite of physical oceanographic variables that we assumed represented the variation in this domain. Variables should also be chosen to reflect the phenomenon of interest. We were interested in coherent and persistent water masses, so we chose long-term seasonal mean values for our parameters. The correspondence of our long-term regions with primary production showed how persistent these ecosystems are over time, despite the relatively ephemeral nature of the biotic component. If one wished to more precisely capture domains of primary productivity, it would be appropriate to aggregate the physical and biological components at a finer temporal resolution. On the other hand, if identifying well-mixed zones were the goal of the analysis, the use of variables such as sea surface height and current velocities might be appropriate. Moreover, some variables are more appropriate than others for particular study areas. For example, bathymetry is appropriate in an on-shelf classification, perhaps to depths of around 400 m, and around sea mounts, but unless the species of interest are primarily demersal or benthic, bathymetry is likely to be less important.

As variables are added, several undesirable features begin to emerge including multicolinearity (resulting in the unintentional weighting of certain features and interactions over others) and the danger of unnecessary model complexity (Howard, 1991). We chose to ignore any possible effects due to multicolinearity or autocorrelation for two reasons. First, despite the common assumptions of stationarity and isotropy (see Haining, 1990), any auto- or cross-correlations are not likely to be consistent across space with extents such as ours. Thus, while the signal that identifies regions of similarity may be enhanced by correlations between variables in some regions, individual variables may drive the variability independently in other regions. Second, there appears to be no analytical reason to exclude regions of high correlation (or autocorrelation) a priori, as these regions may be of interest. The same applies to the putative problem of unintentional weighting. The question of unnecessary complexity requires further research, but could be addressed operationally with an exploratory approach where results based on different combinations of variables are examined and compared.

Selecting the (temporal and spatial) resolution of the study should also be related to the phenomena of interest. While data availability plays a role, there are temporal and spatial aspects to this resolution question. Temporally, an annual average will have a poorer correspondence with a two or three week phenomenon than a monthly or even a seasonal average because the averaging removes the ephemeral peaks of interest. The complication is that the converse—where a monthly resolution will be less able to detect a multi-year trend—is also true, making the selection of temporal resolution of fundamental importance. Spatially, the question is more straightforward, since the analysis is best carried out at the highest resolution possible. The possibility of over-sampling and masking signals of interest due to too much detail is, from our experience, fairly low, and if over-sampling is suspected, a posteriori aggregation of pixels is a straightforward task.

In addition to resolution, spatial extents will also affect analytical results since the size of the study area determines the means, variances, and range of each variable. For example, we initially ran the clustering algorithm on extents that ran from coast to coast across the Pacific and from the equator to 65°N. In that analysis, most of the variability was south of 30°N, resulting in little discrimination in the Gulf of Alaska and Bering Sea. By reducing the extents of our study area, we achieved greater discrimination in the off-shelf, North Pacific, our area of interest. The implication is that study area boundaries should be informed by the objective of the analysis and possibly by exploratory analyses in order to capture the appropriate data structure (data range and variance).

Generally, the identification of region boundaries of importance for specific species would be enhanced by the careful selection of variables, scales and extents. While this may appear to be the ideal approach, it is complicated when considering multiple species in ecosystem studies. Things are further complicated by the trade-off between this increased specificity and the generality of the results. Classifications based on many averaged properties, like the examples we presented here, are likely to yield general regions which, while less likely to be optimal for any single purpose, do prove sufficient for more general applications. A classification based on a few purposefully selected properties, while potentially optimal with respect to those properties, would also be of less general use (Sokal, 1974).

The parameterization of an analysis must therefore consider this trade-off between specificity and generality. The selected variables, extents, and resolution will predispose the relevance of the subsequent regions to those biological processes that are related to the selected variables, at the specified scales. Fortunately, virtually all marine species operate at several spatial scales during their life span. Therefore, regions defined at a particular scale may be biologically meaningful to species at a corresponding life history stage(s).

Finally, there is no reason comprehensive biological variables (e.g., [chl-a]) could not be used as inputs to this kind of classification approach. This would be most appropriate if they were believed to create a context for the species or management objective of interest. Unfortunately, most biological data are patchy and thus not suitable for inclusion as input, but would be valuable correlates to classification results.

4.6. Applications

Our approach provides a means of visualizing the inter-annual and seasonal changes in the patterns of water masses in the oceans. This has implications for a wide range of research activities including competition studies, species–habitat relationships, trophic balance models, ecosystem indicator selection and use, and the design of sampling programs. All these activities make (often implicit) assumptions about the study area, which is typically defined by boundaries of convenience (e.g., political, geographic, or management units) rather than boundaries derived quantitatively, based on physics or ecology. While such boundaries of convenience are sufficient for some applications, we believe that quantitatively derived boundaries will be an improvement in many cases especially where consistency and repeatability are important.

Studies of spatial overlap and competition between species are likely to be essential for the delineation of multi-species marine protected areas. These are often based on analyses of species–habitat relationships and predictions of spatial distribution typically conducted on a spatial grid (e.g., Austin, 2002; Guisan and Zimmerman, 2000; Redfern et al., 2006). However, the analysis of spatially gridded data continues to face a number of methodological hurdles, including the validity of various statistical methods, the selection of study area boundaries, and a lack of spatial validation methods. Gregr (2004) described the problem of sample size and spatial autocorrelation associated with using grid cells as the study unit. This problem would be eliminated by using regions identified in a classification analysis as the study units. This would also have the advantage of making such studies tractable for larger spatial extents at finer resolution—something that is constrained when using gridded data because of the processing requirements of 100s of thousands of grid cells. Using regions defined from high resolution grid cells as study units would effectively trade-off an unmanageable number of grid cells for a much smaller number of relatively homogeneous regions.

Studies of species–habitat relationships using spatial data also typically assume that the processes under study are spatially invariant, meaning that the relationships identified apply equally throughout the study area. Since the boundaries of such studies are commonly based on non-ecological factors, this assumption may be invalid. A preliminary spatial classification of the independent variables to be used in the species–habitat analysis could provide more ecologically defensible study area boundaries, and lend greater validity to the assumption of stationarity.

Species–area relationships developed using more traditional approaches could also be tested using classified marine regions because they are, by definition, regions of similarity. For example, Frank and Shackell (2001) showed a positive relationship between the number of finfish species and the total area of submarine offshore banks, implicitly assuming that all banks provided similar habitat. Quantitative classification could be used to test this assumption and to refine the analysis by exploring the relationships between species and the different regions identified by the classification. The degree of species overlap in the different regions could also provide an indication of habitat use and partitioning, further informing studies of spatial competition.

Finally, trophic balance models are typically applied to regions with vague or arbitrarily defined boundaries and generally lack a spatially explicit component. These models address the flow of biomass into and out of the study area using dispersal or migration values (Christensen et al., 2004). Combined with our approach, these "leakage" parameters could be used as a metric to identify boundaries with the least leakage for the area of interest. For example, in a recent effort to define marine ecosystem boundaries from the perspective of apex predator, Ciannelli et al. (2002) calculated the biomass import required for study areas with three different radii (50, 100, and 150 nm) and found that the 100 nm study area had the lowest biomass import. They concluded that this distance represented an ecosystem boundary but recognized the need to allow for more realistically shaped boundaries. Our classification approach may provide a reasonable mechanism to define such boundaries. Further, by developing a regional trophic balance model for each of the regions within a particular partition, ecosystem models could be extended spatially without resorting to the computational expense of creating a grid for the study area (e.g., as with EcoSpace; Christensen et al., 2004).

Fisheries managers in particular, would benefit from quantitative, repeatable boundary identification for at least two reasons. First, if ecosystem-based indicators are to be comparable across years with different oceanographic conditions, a quantitative method to bound regions of comparison seems essential. Second, fisheries managers in the US have been mandated to define essential fish habitat for commercially harvested species since the Magnuson–Stevens Act was passed in 1996. While this effort has produced tractable classification schemes for coral reefs, shallow bays, and estuaries, it has led to only very general descriptions of habitat in the pelagic marine environment. If fish species could be differentially associated with ecologically significant physical regions—ecoregions—then comprehensive habitat maps could be rapidly developed, tested, and updated over time.

5. Conclusions

Effective ecosystem-based management and the designation of marine protected areas ultimately depend on operational definitions of the geographic area of interest. The approach we demonstrated in this paper represents a method of combining input variables to identify regions of similarity and their boundaries. The method is robust, quantitative, and adaptable in terms of the spatial and temporal scales of interest and the range of input variables that may be used. It applies a minimal set of straightforward assumptions and integrates the inherent dynamic nature of our oceans.

We combined variables describing the physical ocean environment and found that the regions identified did have biological relevance. To our knowledge, this is the first report of biological relevance being quantified in relation to physically derived patterns (traditionally, the biology of interest is included in the analysis). We feel this represents the first step towards a quantitative description of ecosystem boundaries in the marine environment that apply across a range of biota rather than a single species or taxonomic group.

By integrating spatial data on species assemblages into this approach, which would inherently integrate interactions between and within the biological and physical components, we may begin to visualize realistic ecosystem boundaries—as originally envisioned by Tansley (1935). Quantitative classification appears to be rich with possibilities and has the potential to significantly benefit both management and conservation efforts.

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