

## Spatial-temporal patterns in intra-annual gray whale foraging: Characterizing interactions between predators and prey in Clayquot Sound, British Columbia, Canada

T. A. NELSON

Spatial Pattern Analysis and Research (SPAR) Laboratory,  
Department of Geography, University of Victoria,  
P. O. Box 3060, Victoria, British Columbia V8W 3R4, Canada  
E-mail: trisalyn@uvic.ca

D. A. DUFFUS

Whale Research Laboratory,  
Department of Geography, University of Victoria,  
P. O. Box 3060, Victoria, British Columbia V8W 3R4, Canada

C. ROBERTSON

Spatial Pattern Analysis and Research (SPAR) Laboratory,  
Department of Geography, University of Victoria,  
P. O. Box 3060, Victoria, British Columbia V8W 3R4, Canada

L. J. FEYRER

Whale Research Laboratory,  
Department of Geography, University of Victoria,  
P. O. Box 3060, Victoria, British Columbia V8W 3R4, Canada

### ABSTRACT

In Clayquot Sound, British Columbia, gray whales (*Eschrichtius robustus*) forage primarily on mysids (Family *Mysidae*) and also on crab larvae (Family *Porcellanidae*) that are constrained to specific habitat, which relate to bathymetric depths. In this paper we characterize the interactions of gray whales and their prey by analyzing fine scale spatial-temporal patterns in foraging gray whale distribution within a season. Kernel density estimators are applied to two seasons (1998 and 2002) of high-resolution data on foraging by gray whales. By partitioning data from each foraging season into several time periods (12 in 1998 and 11 in 2002), using a temporal autocorrelation function, and generating kernel density estimated surfaces for each time period, it is possible to identify discrete areas of increasing and declining foraging effort. Our results indicate that gray whales forage on mysids throughout a season and opportunistically forage on crab larvae. The episodic crab larvae feeding may reduce, but not eliminate, pressure to mysid populations enabling mysids to reassemble swarms and continue to support gray whale foraging in the latter part of the season. Results suggest that when managing marine environments, gray whale populations require multiple and connected habitats for summer foraging.

Key words: spatial pattern analysis, spatial-temporal patterns, whale foraging, change detection, kernel density estimation, predator-prey interactions, gray whale, *Eschrichtius robustus*.

During the summer foraging season, gray whales migrate north to the Bering Sea and south to the Arctic Ocean. However, some individuals remain in the coastal waters of British Columbia, in areas such as Clayquot Sound, to forage on several prey types. The principal prey item in British Columbia is swarming, epi-benthic mysids (Family *Mysidae*) that overwinter and replenish during the spring phytoplankton bloom before the whales return from their winter migration (Dunham and Duffus 2001, 2002). Whales arriving in Clayquot Sound in late May and early June begin feeding on mysid stocks. As foraging effort increases through the summer, the number of mysids, and subsequently the size, density, and number of swarms, decline. A swarm may either disappear for the duration of the season or be dispersed (*i.e.*, local densities reduced) and then reformed (Stelle 2001). As well, new swarms may be generated or remnant swarms restocked by within-season generation of young. Episodically, crab larvae (Family *Porcellanidae*) are also available for gray whale feeding. This is consistent with inter-annual research (1997–2005) that found 53% of foraging effort in Clayquot Sound occurred within 250 m of the 10 m bathymetric contour, which is mysid habitat.<sup>1</sup>

Observations of marine mammal habitat use are tied to the spatial and temporal scales of data collection and analysis (Jaquet 1996, Halpin *et al.* 2006, Redfern *et al.* 2006). Long migrations, and scale-coupling between spatially extensive productivity regimes, for example, have both broad coarse grain components with very fine grain elements nested in them. To date, marine mammal research has often emphasized population demographics, summarizing temporal changes in whale populations within a spatial region (*e.g.*, Gregr *et al.* 2000, Moore *et al.* 2002, Shelden and Laake 2002). These studies characterize temporal variation in regional habitat use. Within a smaller area, however, habitat use will vary both temporally and spatially (Nerini 1984, Oliver and Slattery 1985, Moore *et al.* 2003). When the spatial variability in habitat use is considered, typically, study areas are partitioned and temporal trends for each partitioned area compared (*e.g.*, Jaquet and Gendron 2002), or variations are descriptively summarized for a region (Sumich 1984). Fine-scale research on the spatial variation of habitat use is needed to isolate the mechanisms causing variability.

Fine-scale spatial and temporal variability in whale foraging is, at least in part, a response to variability in prey populations (Oliver and Slattery 1985, Croll *et al.* 1998, Moore *et al.* 2003). Whales can only feed where prey biomass is sufficient (Piatt and Methvan 1992) and they should not leave a productive foraging area unless the prey biomass is depleted and inefficient to access, or a better prey patch becomes available (Dunham and Duffus 2001, Kenney *et al.* 2001, Kerr and Duffus 2005). Within a foraging season, variability in the location and magnitude of foraging effort reflects change in the availability of prey density and biomass, more immediately than changes in environmental conditions. This is particularly true if change is investigated over a fine temporal scale (*i.e.*, days and weeks, rather than months). Many fine-scale processes operating in a marine environment will impact gray whale prey. The response of the whales is a signal of when and where the changes in prey quality or quantity occur.

<sup>1</sup>Unpublished data.

Using the spatial pattern of foraging as a signal for the interaction between gray whales and their prey (Dunham and Duffus 2001, 2002; Nelson<sup>1</sup>), our goal is to characterize how prey–predator interactions vary through space and over time within a foraging season. This study is conducted at fine spatial (1-m resolution within 50-km<sup>2</sup> study area) and temporal scales (2- to 3-d resolution within a 3-mo foraging season). Spatial-temporal change in foraging within a summer season is characterized using change detection *via* kernel density estimation, and spatial data were partitioned into time periods for change detection using the temporal dependence in the foraging data, as detected by a temporal autocorrelation function (ACF). We use kernel density estimation to identify discrete areas where gray whale foraging activity increases or declines with statistical significance. The spatial-temporal distribution of change areas is then explored as a signature for the interaction between gray whales and their prey within a foraging season and is interpreted in the context of known prey habitats.

## METHODS

### *Study Area and Data*

Our study area is approximately 50 km<sup>2</sup> along the southwest coast of Flores Island, Clayquot Sound, British Columbia (Fig. 1). During the summers from 1997 to 2006, whale surveys were conducted during daylight every 4–5 d, weather permitting, to create a representative sample of summer foraging effort. A minimum of four observers viewing a 360° area from a 7-m open skiff logged gray whale foraging locations using handheld GPS. Given the confined spatial extent of our survey and the replication in surveyor observations these data have been found to have few omission or commission errors.

Our study design relies on experience gained during the 15-yr data collection program in this region. Over this time we have employed plankton net tows, underwater video surveys, diver surveys, and twin beam sonar surveys to establish the relationship between gray whales and prey. Field observations and past research (Dunham and Duffus 2001, 2002) indicate a spatial link between whales, mysids, and crab larvae. The presence of foraging whales is indicative of prey and each prey type is confined to a specific bathymetric habitat, with mysids occurring in shallow waters (~10 m) and crab larvae occurring in deeper conditions (>20 m) (see Fig. 1 for prey habitat locations) (Dunham and Duffus 2001, 2002).

Our analysis uses surveys from 1998 and 2002, the 2 yr with the most abundant foraging activity. In 1998, we conducted 59 surveys from 1 June to 5 September and 569 foraging events were identified (Fig. 2). Foraging effort, which can be viewed in the frequency distributions of Figure 2, increased and declined from early July to late August in this year, and there was feeding in a large amount of crab larvae habitat. In 2002 we carried out 42 surveys over the same time frame and sited 453 foraging events (Fig. 2). Foraging effort increased and declined more gradually, from late June to early September, than in 1998 and less foraging occurred in crab habitat.

### *Selection the Intra-Annual Temporal Resolution*

The temporal extent of the data collection was 97 d (1 June to 5 September) and data could be grouped into many temporal periods (*i.e.*, days, weeks, or months), for

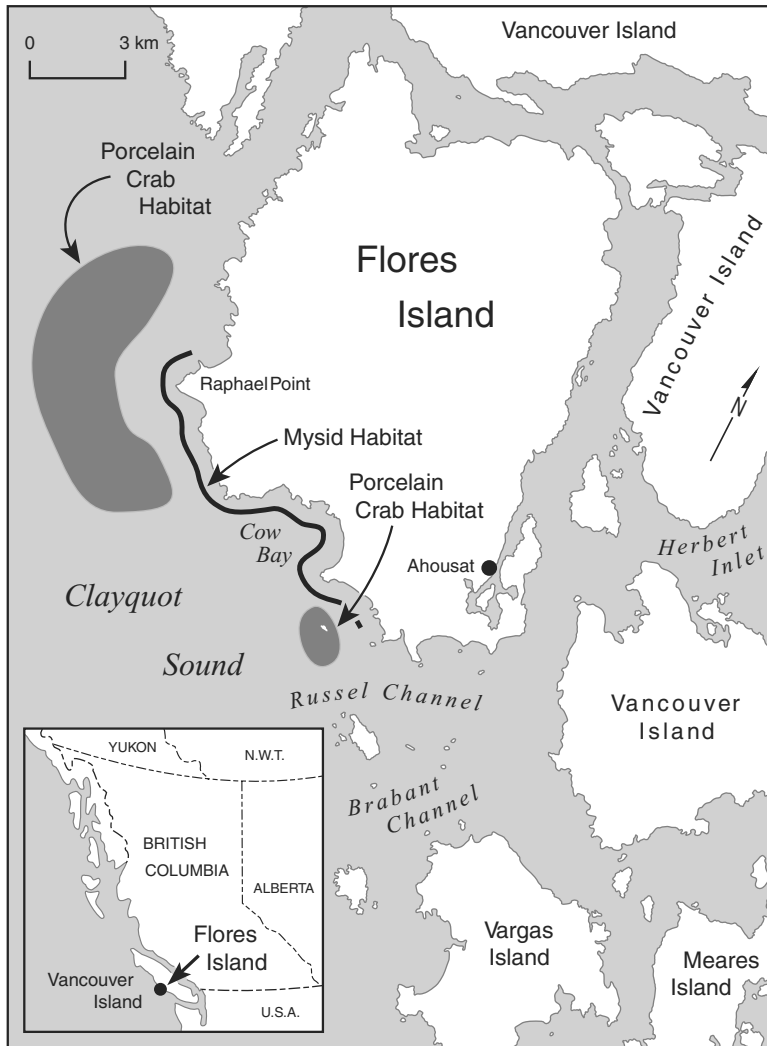


Figure 1. Flores Island, Clayquot Sound, British Columbia, Canada. This map indicates the study area location, as well as, the location of mysid and crab habitats.

change detection. For this analysis, we used ACF analysis to inform an appropriate temporal partition. The ACF analysis determines the temporal partitions necessary to minimize variability within a time period and maximize variability between time periods (for details on ACF methods see Kendall 1984).

For 1998 and 2002 a time series was constructed of whale survey data, which was assumed to be a single realization of an unknown stochastic process. The ACF estimates the degree to which sample observations are correlated for a given temporal lag, which we define by days. The results of the ACF for each time series were plotted as the strength of autocorrelation for different time lags. We define significant

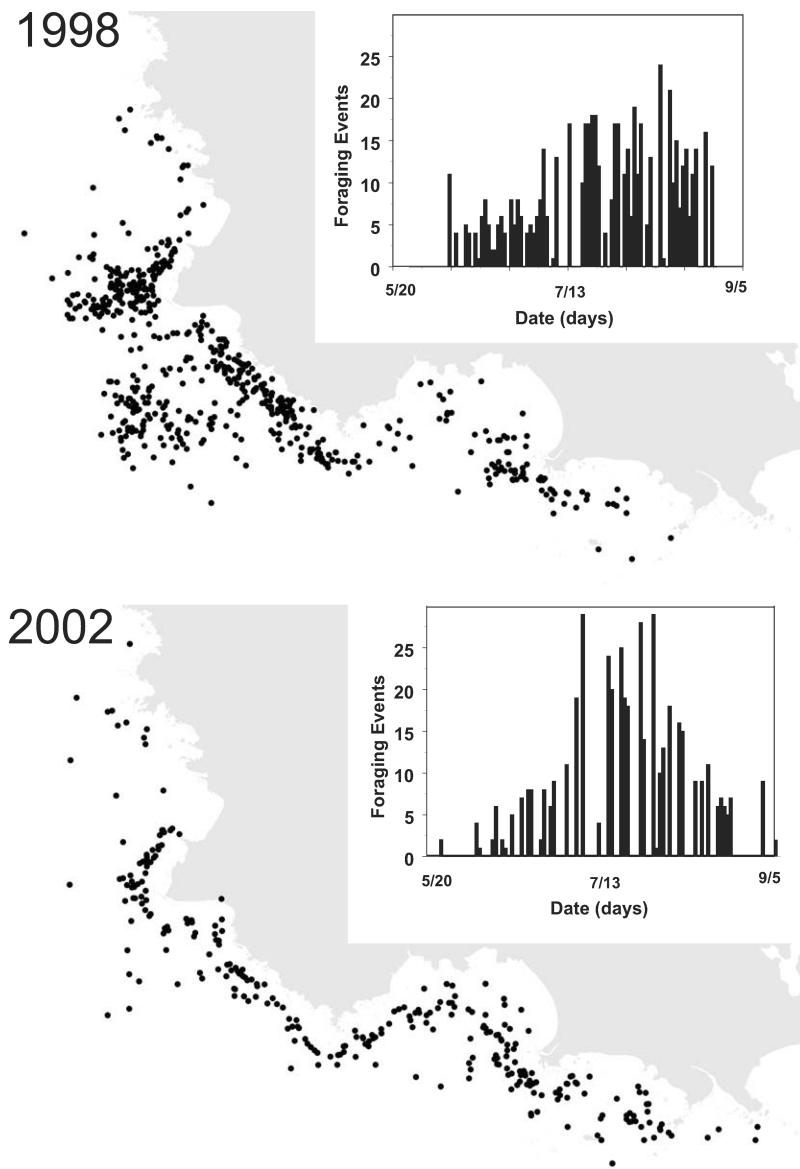


Figure 2. Gray whale surveys in the 1998 and 2002 foraging seasons. Locations of gray whales are shown as points. Frequency distributions show the frequency of foraging events through time within the foraging season.

autocorrelation using the 95% Bartlett's band, equivalent to the convergence of the sample correlation coefficients to a normal distribution (Box and Jenkins 1970). The lag used to temporally partition the data was the smallest significant temporal lag that enabled enough data in each temporal partition to support kernel density estimation (*i.e.*, each time period had approximately 25 whale foraging locations).

### *Detecting Change in Intra-Annual Foraging Activity*

Kernel density estimators are commonly used to characterize the spatial distribution of animals and to identify home ranges (*e.g.*, Worton 1989, 1995; Seaman and Powell 1996; Potvin *et al.* 2003; Righton and Mills 2006; Shi *et al.* 2006). When animal locations are identified as points, kernel density estimation can convert those data into an intensity surface. Kernel density estimators provide a quantitative description of the amount of time animals spend at a particular location (Seaman and Powell 1996). As well, the kernel density estimator's representation of the data improves visualization of abundant data and methods exist for identifying locations of change in multiple kernel density surfaces (Bowman and Azzalini 1997, pp. 112–117; Fotheringham *et al.* 2000, pp. 155–157).

Conceptually, the intensity  $\lambda(z)$  at a particular location ( $z$ ) can be estimated by the kernel estimator

$$\hat{\lambda}(z) = \frac{\text{the number of events in a circle centered on } z}{\text{area of the circle}} \quad [1]$$

A more precise estimate,  $\hat{\lambda}_\tau(z)$  is defined by

$$\hat{\lambda}_\tau(z) = \frac{1}{p_\tau(z)} \left\{ \sum_{i=1}^n \frac{1}{\tau^2} k \left( \frac{(z - z_i)}{\tau} \right) \right\} \quad \hat{\lambda}_\tau(z) = \frac{1}{p_\tau(z)} \left\{ \sum_{i=1}^n \frac{1}{\tau^2} k \left( \frac{(z - z_i)}{\tau} \right) \right\} z \square A \quad [2]$$

where  $z$  and  $A$  is the study area,  $\tau$  is the radius of a circle centered on  $z$ ,  $k(\cdot)$  is the kernel or a probability density function that is symmetric around about the origin,  $z_i$  ( $i = 1, \dots, n$ ), are locations of  $n$  observed events. The term  $p_\tau(z) = \int_A k[(z - u)/\tau] du$  is an edge correction equivalent to the volume under the scaled kernel centered on  $z$  that lies inside of  $A$  (Diggle 1985).

The smoothness of kernel density estimates is controlled by  $\tau$  (Bowman and Azzalini 1997). We determined the value of  $\tau$  using the least-squares cross-validation method, which has been demonstrated to be effective for ecological applications and is commonly used for the delineation of home range (Seaman *et al.* 1999). The least-squares cross-validation method minimizes the estimate of the integrated square error for each density estimate over a range of  $\tau$  (Silverman 1986, pp. 48–51; Worton 1989). For 1998 and 2002 data, we set  $\tau$  to the geometric mean of all time periods in the year. In order to implement kernel density estimated change detection approaches it is best to use a consistent  $\tau$  for all intra-annual time periods in a given year. For 1998 we set  $\tau$  to 344 m; for 2002 we used a  $\tau$  of 574 m.

We detected change in intra-annual foraging whale activity using a method for comparing two kernel density estimated surfaces (Bowman and Azzalini 1997, pp. 112–117; Fotheringham *et al.* 2000, pp. 155–157). This method assumes both surfaces are generated using the same  $\tau$  and uses the square root of the density estimates

$$\text{var} \left\{ \sqrt{\hat{\lambda}_\tau(z)} \right\} \approx \left[ \int (k(z))^2 dz \right]^2 / 4n\tau^2, \quad [3]$$

where  $n$  is the sum of the attribute values, and does not depend on the unknown (true) density,  $\lambda_\tau(z)$  (Bowman and Azzalini, 1997, 29). If  $\hat{\lambda}_\tau(z)$  is the kernel density

estimate for year  $t$ , and  $\hat{\lambda}_{t+1}(z)$  is the kernel density estimate for the following year,  $\sqrt{\hat{\lambda}_{t+1}(z)} - \sqrt{\hat{\lambda}_t(z)}$  will have mean zero if the true surfaces are identical. Thus, for a given location  $i$ , change between two consecutive intra-annual time periods  $t$  and  $t + 1$ ,  $change_{i\Delta t}$ , is

$$change_{i\Delta t} = \frac{\sqrt{\hat{\lambda}_{i,t+1}} - \sqrt{\hat{\lambda}_{i,t}}}{\sqrt{\left[\int (\hat{k}(z))^2 dz\right]^2 / [4\tau^2 (n_{t+1}^{-1} + n_t^{-1})]}} \quad [4]$$

where  $\hat{\lambda}_{i,t}$  is the kernel density estimate at location (pixel)  $i$  in time period  $t$ , and  $\hat{\lambda}_{i,t+1}$  is the kernel density estimate at location (pixel)  $i$  in time period  $t+1$ , and  $\hat{\lambda}_{i,t+1}$  is the kernel density estimate at the same location in the following time period, and  $n_t$  and  $n_{t+1}$  are the number of whales in the respective time periods. If the surfaces are identical in both years, Equation 4 has zero mean and unit variance for all  $i$ . We define significant positive change as occurring at location  $i$  when  $change_{i\Delta t} > 2$  and significant negative change to occur when  $change_{i\Delta t} \leq -2$ . Otherwise, no significant change is assumed to have occurred. Kernel density estimators produce estimates, thus, statistically significant change between density surfaces is also estimated (see Fotheringham *et al.* 2000). To ensure consistency in the quality of estimates, we limited change detection to time periods that included  $\geq 25$  foraging whale points. In 1998 we created kernel density estimated surfaces for nine time periods, from 17 June to 27 August. In 2002 we created kernel density estimated surfaces for seven time periods, from 19 June to 19 August.

#### *Exploring Change in Intra-Annual Foraging Activity*

Using the kernel approach to change detection, we detected change at individual locations, or grid cells, within the study area. Our interest is in discrete areas of change, and we define discrete spatial groupings of similar types of change in foraging activity as change patches. Positive change patches indicate an increase in foraging effort, while negative change patches suggest foraging effort is declining. We mapped change patches and considered how patch number, type (*i.e.*, positive or negative), and size varied through time. Using digitized bathymetric data (scale 1:250,000) from the Canadian Hydrographic Service, we used the average bathymetry of change patches to characterize whether the patch occurred in mysid and crab larvae habitats, as these habitat types are restricted by bathymetric depth (see Fig. 1).

## RESULTS

#### *Intra-Annual Temporal Resolution*

Results of the ACF analysis are shown in Figure 3. Several temporal lags had significance, and significance was not impacted by the start date. In 1998 the strongest positive temporal autocorrelation occurs for a lag of 8 d. The longest temporal lag with significant autocorrelation is 14 d. Temporal partitions created using an 8 d lag are shown in Table 1.

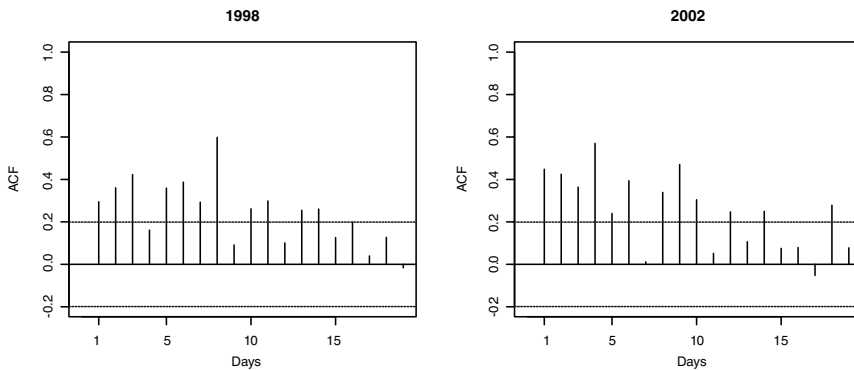


Figure 3. Results of the temporal autocorrelation function (ACF) analysis. ACF values that fall outside the horizontal lines are statistically significant. In 1998 the ACF is strongest for eight days. In 2002 the ACF is strongest for 4 and 9 d, respectively.

In 2002 a lag of 4 d has the strongest positive autocorrelation. The next strongest autocorrelation occurs for a 9-d lag. An 18-d lag is the longest time lag with significant autocorrelation. If 4 d were used to define the temporal resolution for change detection, many time periods would have few points. Partitioning data using a 9-d lag, temporal partitions for analysis ensured that most time periods have a sufficient number of points for effective kernel density estimation.

#### *Exploring Change in Intra-Annual Foraging Activity*

In 1998 significant positive or negative changes were found for the five periods of change (using six time periods), from 11 July to 27 August (Table 1, Fig. 4A). In 2002 significant positive or negative changes were identified for five periods of change

Table 1. Temporal partitions for 1998 data using 8-d lags. Dates that are not shaded or underlined have enough whale observations to enable kernel density estimation, whereas dates shaded gray do not. Underlined dates had significant positive and/or negative change detected.

Temporal ID	Number of whales	Date range
1	15	1–8 June
2	20	9–16 June
3	32	17–24 June
4	40	25 June–2 July
5	48	3–10 July
6	44	11–18 July
7	77	19–26 July
8	95	27 July–3 August
9	60	4–11 August
10	85	12–19 August
11	53	20–27 August
12	0	28 August–5 September



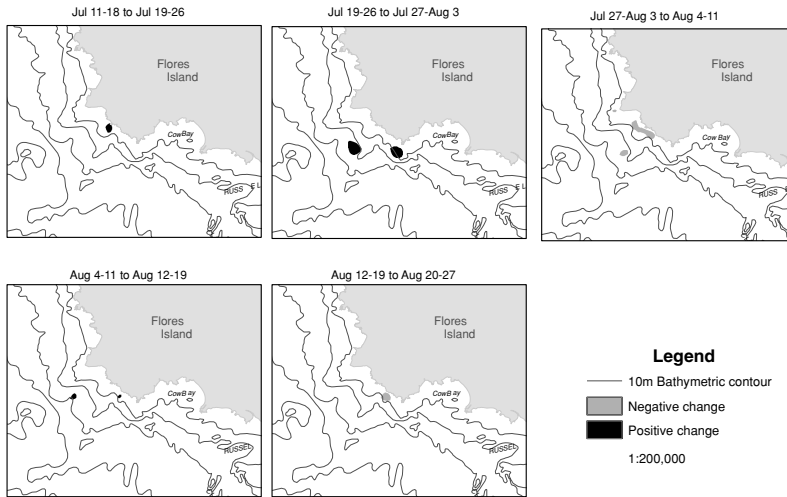
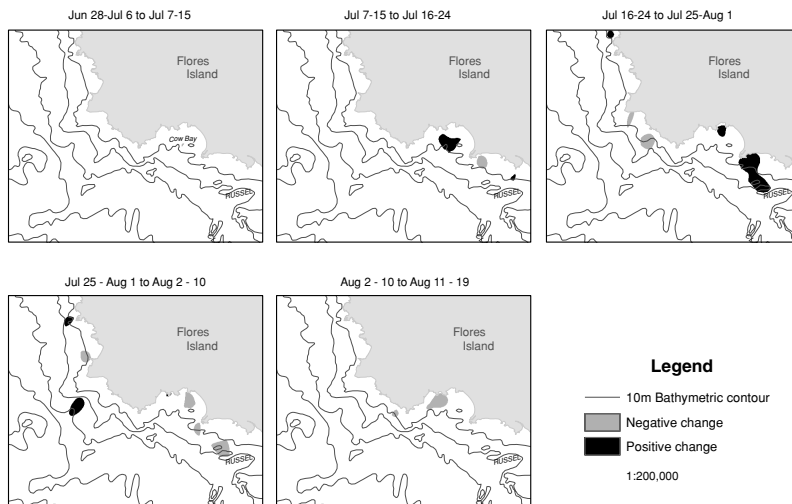
**(A) 1998 Whale Density Change****(B) 2002 Whale Density Change**

Figure 4. (A) Patches, in 1998, of intra-annual change, both positive and negative, in the density of foraging gray whales; (B) 2002 patches of intra-annual change, both positive and negative, in the density of foraging gray whales.

(using six time periods), from 28 June to 19 August (Table 2, Fig. 4B). Significant change occurs later in 1998 than in 2002, but in both cases change occurs once >15 foraging whales are sighted in a single day. This may suggest sighting 15 whales per day is a threshold required for the detection of statistically significant change in foraging effort. In 1998 there are nine change patches, five are positive and four are negative (Fig. 5). The size of change patches varies and the largest patches are

*Table 2.* Temporal partitions for 2002 data using 9-d lags. Dates that are not shaded or underlined have enough whale observations to enable kernel density estimation, whereas dates shaded gray do not. Underlined dates had significant positive and/or negative change detected.

Temporal ID	Number of whales	Date range
1	7	1–9 June
2	21	10–18 June
3	32	19–27 June
4	40	28 June 28–6 July
5	57	7–15 July
6	82	16–24 July
7	97	25 July–1 August
8	58	2–10 August
9	36	11–19 August
10	12	20–28 August
11	11	29 August–5 September

found in the second and third change period. Although the average sizes are the same regardless of whether they are positive ( $0.24 \text{ km}^2$ ) or negative ( $0.24 \text{ km}^2$ ), there are more small negative than positive change patches. In 1998, when change is detected between two time periods, it is either all positive or all negative. In 2002 there is more change overall and 20 change patches are detected, eight are positive and 12 are negative (Fig. 5). The average size of the patches is similar regardless of type ( $0.32 \text{ km}^2$ ), but there are more very small patches associated with negative change. The largest change patches are found in the second and third change periods. In 2002 both positive and negative change patches are detected between the same time periods.

Change patches in 1998 fall into two groupings based on depth (Fig. 5). Patches are observed at depths ranging from  $>4 \text{ m}$  to  $10 \text{ m}$  or at deeper than  $25 \text{ m}$ . The shallow change patches are associated with mysids, while the deeper patches are evidence of crab larvae located in waters south of Raphael Point (Fig. 4A). Change in the foraging effort within mysid habitat occurs in five change periods (from 11 July to 27 August) while change in the foraging effort in crab habitat occurs in only three time periods (from 19 July to 19 August). In the crab larvae habitat there is a patch showing an increase in foraging effort between the period of 19–29 July and the period of 27 July to 3 August. This corresponds with the peak in foraging effort, which also occurs in the 27 July to 3 August time period. All crab larvae habitat change patches occurring later in the season intersect this initial patch. After the initial increase, the foraging effort decreases locally (27 July to 11 August), and then increases over an even smaller area (4 August to 19 August). Once change in the crab larvae habitat ceases, all change associated with mysid habitat indicates declining foraging effort.

Foraging activity in 2002 also occurs in both mysid and crab larvae habitat (Fig. 5). Change in the foraging effort within mysid habitat occurs in five change periods (from 28 June to 19 August) while change in the foraging effort in crab habitat occurs in only two time periods (from 16 July to 10 August). As with 1998, the presence of positive change patches in crab larvae habitat is synchronous with the seasonal peak in foraging effort. Change in foraging effort during the period beginning on 16 July and 1 August, is found to the east of Cow Bay, and is part of a large positive change

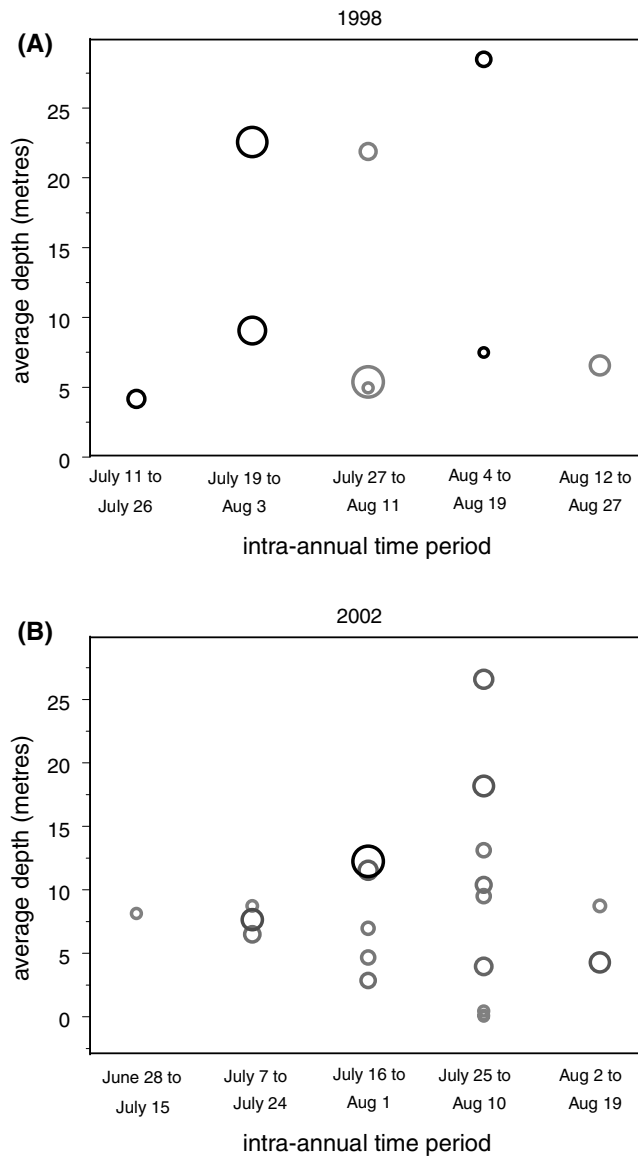


Figure 5. Time periods of intra-annual positive and negative change patches *vs.* average patch depth. Symbol color indicates the type of change (black is positive change and gray is negative change). Symbol size is proportional to the size of the change patch.

patch that extends across both mysid and crab larvae habitat. The portion of this change patch that occurs in crab larvae habitat experiences negative change in the following time period (25 July to 10 August). From 25 July to 10 August, there is also an increase in foraging effort in crab larvae habitat off Raphael Point. Unlike the crab change patches, mysid change patches in each time period do not intersect

when viewed through time. In Cow Bay, however, there are two time periods showing increased foraging effort (7 July to 1 August) followed by two change periods with decreasing foraging effort (25 July to 19 August). Also similar to 1998, once change in the crab larvae habitat ceases, all change associated with mysid habitat indicates declining foraging effort.

## DISCUSSION

The temporal interaction between patches of increasing and declining foraging effort provide evidence for prey–predator interactions. In the 1998 crab larvae habitat, foraging effort increased in the 10 July to 3 August time period, declined in the next time period (27 July–11 August), and increased locally in a third time period (4–19 August). This indicates the whales are feeding heavily on crab larvae for 8 d, in the next 8 d the foraging pressure is reduced. This reduction in foraging pressure allows for spatially localized recovery in crab larvae and enables increased foraging pressure in a smaller area. In 2002 the trend is different, but the increased foraging effort in the mixed prey habitat east of Cow Bay is followed by a significant decline in feeding activity.

In both 1998 and 2002 the final significant change in foraging patterns is declining effort in mysid habitat. The whales continue to forage on the mysids once the crab populations have been diminished. The mysid swarms are the primary source of prey early and late in the foraging season. The periodic availability of crab larvae provides an alternative high-quality energy source for whales, and while some of the whales are feeding on crab larvae, mysid populations can reswarm and support continued foraging later in the season. Inter-annual trends also indicate variability in foraging activity between crab and mysid habitat in this study region, with mysid populations recovering more quickly than crab larvae populations.

Differences in the prey–predator interactions in 1998 and 2002 may be associated with foraging effort in the year prior. The average number of whales per census survey in the 1997 season was 7.28 compared to 10.65 in 1998. The average number of whales per survey in 2001 was 2.24 compared with 12.20 in 2002, and 2001 foraging effort was among the lowest in our 10-yr record. Patches of change in 1998 foraging effort tend to be smaller and have more temporal overlaps than in 2002. This indicates localized fluctuations, in space and time, in prey availability. In 2002 foraging effort changed over larger areas and there is less evidence that prey populations rebounded locally through a season. This may indicate that prey populations in 1998 were diluted by moderate foraging pressure in 1997, whereas low foraging effort in 2001 resulted in higher initial mysid biomass in the 2002 season. The presence of higher biomass at the beginning of the season may also explain the gradual increase in 1998 foraging effort relative to the monotonic increase and decline in observed in 2002. This will be the subject of further research.

On fine scales, the whales exert strong top–down pressure on prey populations. Gray whales are highly mobile and switch prey types quickly, in the matter of a day, over spaces of 1–10 km (Duffus 1996). The net effect of foraging processes, coupled to the overwintering population ecology of the prey, is that gray whale foraging is a variable process that creates a high degree of change within and between seasons. Characterizing fine-scale variation in gray whale summer foraging is of ecological interest because it enables insight on the response of prey to top–down pressure.

At the between season scale, the top-down pressure of foraging whales can cause even greater variability and may disturb prey to the point of permanent community change (Oliver and Slattery 1985). Such change will have significant impact on the active recreational whale-watching industry in this area, and implies that gray whale populations require multiple and connected habitats for summer foraging.

In this paper we characterize the fine-scale spatial and temporal variability in the interaction between gray whales and their prey within a foraging season. Here, we demonstrate a novel GIS approach by using kernel density estimation for detecting and analyzing change in the spatial-temporal pattern of marine phenomenon. These methods can be applied when  $n$  is relatively large (*i.e.*,  $>25$ ) and locations of events (*i.e.*, flora or fauna locations) are recorded as points. Using kernel density estimation for change detection is advantageous, as many ecologists and biologist are familiar with this approach for home-range detection. In future work, we aim to extend this research by developing additional approaches that will assist in detecting change in sparse data.

#### ACKNOWLEDGMENTS

Field data collection represents a large effort over a long time. Field crew leaders A. Bass, J. Dunham, C. Malcolm, C. Tombach, S. Meier, H. Patterson, C. Short, S. Olsen, and C. Pasztor led a number of talented and dedicated research staff members to collect and collate this data. We thank the late Chief E. M. George and the Ahousaht First Nation for their long time support of our research in their traditional territory. Thanks to anonymous reviewers for comments and feedback that helped improve this paper.

#### LITERATURE CITED

- BOWMAN, A., AND A. AZZALINI. 1997. Applied smoothing techniques for data analysis: The kernel approach. Clarendon Press, Oxford, UK.
- BOX, G. P., AND M. JENKINS. 1970. Time series analysis: Forecasting and control. Holden-Day, San Francisco, CA.
- CROLL, D. A., B. R. TERSHEY, R. P. HEWITT, D. A. DEMER, P. C. FIEDLER, S. E. SMITH, E. ARMSTRONG, J. M. POPP, T. KIEKHEFER, V. R. LOPEZ, J. R. URBAN AND D. GENDRON. 1998. An integrated approach to the foraging ecology of marine birds and mammals. *Deep Sea Research II* 45:1353–1371.
- DIGGLE, P. 1985. A kernel method for smoothing point process data. *Applied Statistics* 34:138–147.
- DUFFUS, D. A. 1996. The recreational use of grey whales in southern Clayquot Sound, Canada. *Applied Geography* 16:179–190.
- DUNHAM, J. S., AND D. A. DUFFUS. 2001. Foraging patterns of gray whales in central Clayquot Sound, British Columbia, Canada. *Marine Ecology Progress Series* 223:299–310.
- DUNHAM, J. S., AND D. A. DUFFUS. 2002. Diet of gray whales (*Eschrichtius robustus*) in Clayquot Sound, British Columbia, Canada. *Marine Mammal Science* 18:419–437.
- FOTHERINGHAM, A., C. BRUNSDON AND M. CHARLTON. 2000. Quantitative geography: Perspectives on statial data analysis. Sage Publications, London, UK.
- GREGG, E., N. NICHOL, J. FORD, G. ELLIS AND A. W. TRITES. 2000. Migration and population structure of northeast Pacific whales off the coast of British Columbia: Analysis of commercial whaling records from 1908–1967. *Marine Mammal Science* 16:699–727.

- HALPIN, P. N., A. J. READ, B. D. BEST, K. D. HYRENBACH, E. FUJIOKA, M. S. COYNE, L. B. CROWDER, S. A. FREEMAN, AND C. SPOERRI. 2006. OBIS-SEAMAP: Developing a biogeographic research data commons for the ecological studies of mammals, seabirds, and sea turtles. *Marine Ecology Progress Series* 316:239–246.
- JACQUET, N. 1996. How spatial and temporal scales influence understanding of sperm whale distribution: A review. *Mammal Review* 26:51–65.
- JACQUET, N., AND D. GENDRON. 2002. Distribution and relative abundance of sperm whales in relation to key environmental features, squid landings and the distribution of other cetacean species in the Gulf of California, Mexico. *Marine Biology* 141:591–601.
- KENDALL, M. G. 1984. Time series. Oxford University Press, Oxford, UK.
- KENNEY, R. D., C. A. MAYO AND H. E. WINN. 2001. Migration and foraging strategies at varying spatial scales in western North Atlantic right whales: A review of hypotheses. *Journal of Cetacean Research and Management* 2:251–260.
- KERR, K. A., AND D. A. DUFFUS. 2005. Timing of larval release in the Porcelain crab, *Petrolisthes cinctipes* (Decapoda, Anomura), in Clayquot Sound, British Columbia. *Crustaceana* 78:1041–1051.
- MOORE, S. E., J. M. WAITE, N. A. FRIDAY AND T. HONKALEHTO. 2002. Cetacean distribution and relative abundance on the central-eastern and the southeastern Bering Sea shelf with reference to oceanographic domains. *Progress in Oceanography* 55:249–261.
- MOORE, S. E., J. M. GREBNEIER AND J. R. DAVIES. 2003. Gray whales distribution relative to forage habitat in the northern Bering Sea: Current conditions and retrospective summary. *Canadian Journal of Zoology* 81:734–742.
- NERINI, M. 1984. A review of gray whale feeding ecology. Pages 423–450 in M. L. Jones, S. L. Swartz and S. Leatherwood, eds. The gray whale, *Eschrichtius robustus*. Academic Press, New York, NY.
- OLIVER, J. S., AND P. N. SLATTERY. 1985. Destruction and opportunity on the sea floor: Effects of grey whale feeding. *Ecology* 66:1965–1975.
- PIATT, J. F., AND D. A. METHVEN. 1992. Threshold foraging behavior in baleen whales. *Marine Ecology Progress Series* 84:205–210.
- POTVIN, F., B. BOOTS AND A. DEMPSTERS. 2003. Comparison among three approaches to evaluate winter habitat selection by white-tailed deer on Anticosti Island using occurrences from an aerial survey and forest vegetation maps. *Canadian Journal of Zoology* 81:1662–1670.
- REDFERN, J. V., M. C. FERGUSON, E. A. BECKER, K. D. HYRENBACH, C. GOOD, J. BARLOW, K. KASCHNER, M. F. BAUMGARTNER, K. A. FORNEY, L. T. BALLANCE, P. FAUCHALD, P. HALPIN, T. HAMAZAKI, A. J. PERSHING, S. S. QIAN, A. READ, S. B. REILLY, L. TORRES AND F. WERNER. 2006. Techniques for cetacean-habitat modeling. *Marine Ecology Progress Series* 310:271–295.
- RIGHTON, D., AND C. MILS. 2006. Application of GIS to investigate the use of space in coral reef fish: A comparison of territorial behaviour in two Red Sea butterflyfishes. *International Journal of Geographical Information Science* 20:215–232.
- SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- SEAMAN, D. E., J. J. MILLSAUCH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDK AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- SHELDEN, K. E. W., AND J. L. LAAKE. 2002. Comparison of the offshore distribution of southbound migrating gray whales from aerial survey data collected off Granite Canyon, California, 1979–96. *Journal of Cetacean Research and Management* 4:53–56.
- SHI, H., E. J. LAURENT, J. LEBOUTON, L. RACEVSKIS, K. R. HALL, M. DONOVAN, R. V. DOEPKER, M. B. WALTERS, F. LUPI AND J. LIU. 2006. Local spatial modeling of white-tailed deer distribution. *Ecological Modelling* 190:171–189.
- SILVERMAN, B. 1986. Density estimation for statistics and data analysis. Chapman Hall, New York, NY.

- STELLE, L. L. 2001. Behavioural ecology of gray whales (*Eschrichtius robustus*) feeding on mysids in British Columbia, Canada. Ph.D. thesis, University of California, Los Angeles, CA. 166 pp.
- SUMICH, J. L. 1984. Gray whales along the Oregon Coast in summer, 1977-1980. *The Murrelet* 65:33-40.
- WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.
- WORTON, B. J. 1995. A convex hull-based estimator of home-range size. *Biometrics* 51:1205-1216.

Received: 28 June 2007

Accepted: 9 January 2008